The Effects of Drought and Biotic Interactions on Community Stability and Coexistence

by

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DISSERTATION ABSTRACT

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Title: The Effects of Drought and Biotic Interactions on Community Stability and Coexistence

The frequency and severity of droughts are increasing in grasslands globally, alongside changes to the biotic community such as the introduction and spread of invasive species and changes in grazing regimes. Grasslands cover over 30% of the terrestrial land surface and support high biodiversity as well as other key ecosystem services including forage production, carbon storage, and pollination. They remain one of the most threatened and least protected biomes, due to ongoing land use conversion and degradation and are increasingly vulnerable to a changing climate. The goal of my dissertation is to explore how the interplay between drought and biotic interactions – both within plant communities and through top-down pressure – shapes species coexistence and ecological stability in grasslands and rangelands. Here, I examine the effects of drought at three scales: on pairwise interactions between species, on individual species responses within communities across a large-scale precipitation gradient, and finally on community stability through time. I explore this in three systems, each with different interacting biotic factors. In Chapter II, I tested how pairwise interactions between a native legume and introduced grass species vary over neighbor density and rainfall gradients and the consequences for their coexistence in California grasslands, which are characterized by highly variable rainfall and an abundance of introduced species. In Chapter III, I test whether species spatial and temporal abundance distributions can predict direct and lagged drought responses in six North American grasslands across a large-scale precipitation gradient. Finally, in Chapter IV, I explore how these concepts scale up to the community level by testing how drought interacts with herbivory to influence ecological stability through time in a semi-arid Kenyan savanna, where diverse wild herbivores persist alongside livestock. Throughout this work, I collaborated with scientists from multiple disciplines and employed a variety of methods, including field and greenhouse experimentation, population modeling, and data synthesis. Understanding the impacts of altered precipitation regimes on species and community level responses will help manage grasslands in the future with

more frequent and extreme droughts. This dissertation includes previously published and unpublished coauthored material.

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DEDICATION

To Diana.

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CHAPTER I

INTRODUCTION

The frequency and severity of droughts are increasing in grasslands worldwide due to anthropogenic climate change (Chiang et al., 2021; Dai, 2013; Naumann et al., 2018), with widespread consequences at the level of individual species, communities, and ecosystems (Smith et al., 2024; Wainwright et al., 2019). The effects of drought can occur both directly on species' physiology and demographic rates, and through indirect responses mediated by species interactions (Adler et al., 2012; Suttle et al., 2007; Wainwright et al., 2019). Additionally, alterations to different trophic levels within ecosystems can further shape responses to drought (Riginos et al., 2018), thereby further complicating our ability to understand the effect of drought in grassland systems. Understanding how direct and indirect effects impact community composition and maintenance of diversity as well as ecosystem level properties will be key to managing grasslands in a changing world (Gilman et al., 2010). The goal of my dissertation is to explore how the interplay between drought and biotic interactions, both within and across trophic levels, shapes species coexistence and ecological stability in grasslands and rangelands.

Grasslands are one of the most threatened and least protected biomes, due to ongoing land use conversion, degradation and climate change (Hodgson et al., 2005; Scholtz & Twidwell, 2022). They cover over one third of the terrestrial land surface and support key ecosystem services like high biodiversity, forage production, carbon storage, and pollination (Bengtsson et al., 2019; Herrero et al., 2013). Grasslands are precipitation limited systems, characterized by high precipitation variability and frequent precipitation deficits (Knapp & Smith, 2001). At the ecosystem level, drought reduces productivity in grasslands (Smith et al., 2024), but has more idiosyncratic effects on individual species and the strength and direction of interactions between

species (Wainwright et al., 2019).While grasslands are drought adapted and generally resist or recover well from drought at the ecosystem level (Bazzichetto et al., 2024), changes to component species and interactions can be persistent (Gutbrodt et al., 2011; Knapp et al., 2020; Riginos et al., 2018). A challenge of studying drought impacts on grassland plant communities is developing an integrative understanding of the net effect of various levels of responses, and separating direct effects from effects mediated through changes in interactions or community dynamics.

We can use ecological theory to understand how changes to species vital rates and interactions influence community and ecosystem dynamics in response to drought. Modern coexistence theory (MCT) provides a framework to quantify how the environment and species differences either stabilize coexistence or promote a competitive hierarchy among species which therefore informs how biodiversity is maintained in communities. (Chesson, 2000). Stabilizing factors, termed niche differences, reflect the diverse ways that species use their environment (Levine & HilleRisLambers, 2009; Tilman, 1982). For example, two species with little overlap in resource use will have large niche differences and will therefore be limited more by individuals of their own species than other species, and thus if their population declines, they are no longer limited by intraspecific interactions and the population growth rate increases (Adler et al., 2007). Coexistence among species occurs when niche differences are larger than any inherent competitive differences between species, termed fitness inequalities (Chesson, 2000; Spaak et al., 2021).

While MCT can determine how individual species responses determine mutual persistence or exclusion, ecological stability characterizes how community dynamics shape the ecosystem level. Ecological stability is defined as constancy in an aggregate property, like primary production, and can be linked to internal community dynamics that stabilize production through time or promote variability (Hallett et al., 2014; Loreau et al., 2021; Valencia et al., 2020). Stability

in plant communities is driven by external factors such as precipitation and herbivory as well as internal species dynamics like synchrony or dominant species' population stability that together interact and change over time (Grman et al., 2010; Hallett et al., 2014; Liang et al., 2021). By altering the presence and abundance of species in the community, external drivers can shift how dynamic a system is in several ways. First, a diverse community of species allows for a greater diversity of responses to changes in the environment, as not all species experience population declines at the same time or of the same magnitude, buffering aggregate community properties (Loreau et al., 2021; Yachi & Loreau, 1999). Additionally, having a greater number of species also means the mean of aggregate properties is more likely to be stable as declines in some species are balanced by smoother declines or increases in other species (Loreau et al., 2021; Schindler et al., 2015). Finally, dominant species can drive overall community stability as a result of their abundance in the community (Yang et al., 2017).

To explore these domains, I used a combination of experimentation, modeling, and data synthesis. In Chapter II "*Rainfall, density, and mutualistic rhizobia tip the balance between persistence or competitive exclusion of a native legume with an invasive grass*" I tested how the balance of species interactions – from facilitative to competitive – shifts with density under drought compared to well-watered conditions using a native nitrogen (N) fixing legume and an invasive grass. Facilitation is often predicted to increase in stressful environments (Bertness & Callaway, 1994; He et al., 2013), but in systems with multiple limiting resources, facilitation may be strongest when it acts on the primary limiting resource, which may appear to be a higher resource condition. To test the context-dependent nature of species interactions and implications for coexistence of the native legume and invasive grass, I performed a greenhouse experiment manipulating rainfall, neighbor density, and the soil microbial community and parameterized

population models to estimate density dependent interactions (Buche et al., 2025) and assess coexistence use the mutual invasion criterion and niche and fitness differences (Chesson, 2000; Spaak et al., 2021). This chapter was co-authored with my undergraduate mentees, Julia Albertson, Aidan Foster-Green, Thomas Brugnara, and Tetianna L. Smith-Drysdale, my lab mate Lisa Buche, and Lauren M. Hallett.

In Chapter III "*Drought reorders plant communities through expansion of spatially sparse and temporally intermittent species*," I scaled up to assess general patterns of species' drought responses based on abundance patterns and the environment. Rare species are typically assumed to be more susceptible to perturbations, but extreme drought may also reduce more common species that are well-adapted to modal environmental conditions (Gherardi & Sala, 2015). Resolving these contrasting effects is key to predicting species re-ordering in response to extreme drought. We explored how species' drought responses varied by their spatial and temporal abundances at six sites across a gradient of mean annual precipitation. This chapter was co-authored with Beatriz A. Aguirre, Y. Anny Chung, Lukas Bell-Dereske, Lauren M. Hallett, David L. Hoover, Lau Gherardi, Joan Dudney, Megan Wilcots, Jennifer Rudgers, Melinda D. Smith, Forest Isbell, Tad Fukami, Hanan Farah, and Cristina Portales-Reyes as part of the Ecosystem Transitions working group hosted by the National Center for Ecological Analysis and Synthesis.

Finally, I explore how these concepts scale up to the community level in Chapter IV "*Herbivory and drought reduce the temporal stability of herbaceous cover by increasing synchrony in a semi-arid savanna*," by testing how drought interacts with herbivory to influence ecological stability. Ecological stability in plant communities is shaped by bottom-up processes like environmental resource fluctuations and top-down controls such as herbivory, each of which

have demonstrated direct effects on stability but may also act indirectly by altering plant community dynamics (Hallett et al., 2014; Liang et al., 2021). These indirect effects, called biotic stability mechanisms, have been studied across environmental gradients, but few studies have assessed the importance of top-down controls on biotic stability mechanisms in conjunction with bottom-up processes. Here we use a long-term herbivore exclusion experiment in central Kenya to explore the joint effects of drought and herbivory (bottom-up and top-down limitation, respectively) on three biotic stability mechanisms: (1) species asynchrony, in which a decline in one species is compensated for by a rise in another (Loreau & De Mazancourt, 2008), (2) stable dominant species driving overall stability, and (3) the portfolio effect, in which a community property is distributed among multiple species (Loreau et al., 2021). We calculated the temporal stability of herbaceous cover and biotic stability mechanisms over a 22-year time series and with a moving window to examine changes through time. This chapter was co-authored with lab mates Madelon F. Case and Chhaya M. Werner, as well as collaborators from the Kenya Long Term Exclosure Experiment, Lauren M. Porensky, Kari E. Veblen, Harry B. M. Wells, Duncan M. Kimuyu, Ryan E. Langendorf, Truman P. Young, and Lauren M. Hallett.

Chapter V summarizes the results of these studies.

CHAPTER II

RAINFALL, DENSITY, AND MUTUALISTIC RHIZOBIA TIP THE BALANCE BETWEEN PERSISTENCE OR COMPETITIVE EXCLUSION OF A NATIVE LEGUME WITH AN INVASIVE GRASS

Contributions

CW, JA, and LMH conceived the research idea; CW, JA, and LMH designed the research. CW, JA, AFG, TB, TSD performed the experiment and collected samples. CW analyzed data with input from LB, AFG; CW wrote the manuscript with contributions from all authors.

Introduction

Positive interactions between species within the same trophic level are common in nature and can support both biodiversity and non-native species in plant communities (Cavieres, 2021; Cavieres et al., 2014; Ortiz & Wolf, 2024; Valiente-Banuet et al., 2006). Facilitation occurs when an individual alleviates resource stress or provides other benefits for its neighbors such as microclimate modifications, attracting shared pollinators, or providing physical protection (Bergamo et al., 2018; Cabal et al., 2024; Carroll & MacDougall, 2024). While facilitators provide a benefit to neighboring species, the interactions they receive in turn are often competitive, thereby incurring a cost on facilitators and posing a dilemma about how these interactions can persist through time (Cabal et al., 2024; Schöb, Prieto, et al., 2014). Studies of facilitation have highlighted that interactions can shift from facilitative to competitive depending on the environmental context (Bertness & Callaway, 1994; Holmgren et al., 1997; Ortiz & Wolf, 2024; R. Zhang & Tielbörger, 2020), but typically focus on the interspecific facilitative interaction as an independent phenomenon from reciprocal interactions. This leaves us unable to

predict long term community dynamics or characterize how facilitators persist with their beneficiaries (Bronstein, 2009; Hart, 2023; Schöb, Prieto, et al., 2014). We need a generalized understanding of the factors that stabilize facilitative interactions as well as measurements of reciprocal interactions to effectively predict coexistence between facilitator and beneficiary species.

The net outcome of an interaction between plant species arises from competition for shared resources and any simultaneously occurring positive effects – the relative strength of which may change across environmental gradients (Gross, 2008; Holmgren et al., 1997). Under a classic stress-gradient hypothesis, facilitation is expected to increase in stressful environments, where facilitative species ameliorate the stress (Bertness & Callaway, 1994; He et al., 2013), and competition is expected to intensify with available resources (Louthan et al., 2015; Z. Zhang et al., 2022). In systems with multiple limiting resources, however, facilitation may instead be strongest when it acts upon the *primary* limiting resource (Güsewell, 2004; Harpole & Tilman, 2007).

This may, in fact, appear to be a higher resource condition. For example, in a dual water-N limited system, such as many grasslands (Fay et al., 2025), species interactions may be competitive and centered on the lower resource water acquisition under low rainfall conditions. In high rainfall conditions, when ample water is available, species interactions may shift to center on N availability. Under these conditions, facilitators that alter soil nutrients, such as legumes, may be particularly impactful. Legumes commonly facilitate neighboring plants by enriching soil N due to their symbiosis with N-fixing rhizobia (Ortiz & Wolf, 2024). Under high rainfall, all species in the system may benefit from N-fixation from legume species (Arfin Khan et al., 2014), shifting the balance of interactions from competitive to facilitative. Similarly,

density may regulate shifts in these interactions (Buche et al., 2025; Hart & Marshall, 2013; R. Zhang & Tielbörger, 2020). For example, at low densities legumes may provide a boost in nitrogen without causing strong competition for water (**Figure 2.1B**), whereas at high legume densities increased competition for water may override any benefit from N-fixation (**Figure 2.1C**).

Many facilitative relationships, such as the legume-grass scenario above, are asymmetrical, which can result in antagonistic facilitation interactions. Antagonistic facilitation occurs when the beneficiary exerts a negative effect on the facilitator, such that the facilitative effect of the facilitator on the beneficiary feeds back to compound the competitive effect it experiences (Schöb, Prieto, et al., 2014). In the example above, while both the legume and neighboring species are expected to benefit from N-fixation, the legume in turn may receive stronger competitive interactions from its neighbors (**Figure 2.1D**) (Schöb, Michalet, et al., 2014). The long-term persistence of antagonistic facilitative interactions are difficult to reconcile, as increasing the success of a competitor may lead to exclusion of the facilitator (Cabal et al., 2024; Schöb, Prieto, et al., 2014). Indeed, in successional communities, early N-fixing facilitators often persist in a transient state where they are eventually excluded after later successional species gain traction (Bytnerowicz & Menge, 2021), while in other communities, the facilitator may evolve to avoid providing a benefit for neighbors (Bronstein, 2009). Alternatively, context dependent interactions – both over environmental or density gradients – as well as feedbacks of facilitation on beneficiary intraspecific interactions may limit the imbalance in interactions (Hart & Marshall, 2013; Raath-Krüger et al., 2021; Schöb, Callaway, et al., 2014). Assessing facilitation in context with other direct effects of the environment on vital rates and indirect effects on reciprocal and intraspecific interactions is therefore essential (Hart, 2023).

Linking species interactions to community outcomes is necessary to predict species coexistence with their neighbors. Modern coexistence theory (MCT) provides a framework to quantify how species interactions and the environment contribute to stabilizing coexistence or promoting a competitive hierarchy between species (Chesson, 2000). Stabilizing niche differences describe species' use of their environment (Tilman, 1982), where greater differences between species cause species to limit their own populations more than they limit others (Adler et al., 2007; Chesson, 2000). This generates negative frequency dependence, where species at low frequency in a community have a higher growth rate, allowing them to bounce back from rarity (Chesson, 2000). Coexistence depends on stabilizing niche differences outweighing the inherent competitive differences between species, termed fitness inequalities (Spaak & De Laender, 2020). Multiple nutrient limitation may create more opportunities for niche differentiation via trade-offs between species in their resource acquisition and requirements (Harpole & Tilman, 2007) and would therefore increase niche differentiation if both water and N are supplied at once, but may intensify competition if one is in lower supply.

We explored how the balance of species interactions – from facilitative to competitive – changes with rainfall, the legume-rhizobia mutualism, and density-dependent interactions and the consequences for species coexistence in California grasslands, using a native legume, *Acmispon americanus*, and an invasive grass, *Bromus hordeaceus*. We manipulated the total and relative densities of the legume and grass species under three rainfall conditions, and with or without soil symbionts in a greenhouse experiment, to test two questions: 1) How does facilitation change with shifting limiting resources, and how is this moderated by the environment and species density? Additionally, we asked 2) Can species in an antagonistic facilitative relationship coexist and what leads to their ability or failure to persist together? We hypothesized that neighbor

density and water would drive changes in the effect of the legume on the grass, where facilitation would peak at low to intermediate densities and greater water availability would increase the potential for facilitation if *B. hordeaceus* was co-limited by water and nitrogen. We also expected that removing soil symbionts would cause the interaction to shift from facilitative to competitive. Finally, we hypothesized that the shift in interaction sign from facilitative to competitive would allow the legume to limit the grass at high densities and stabilize their coexistence. Overall, understanding whether and how invasive species are facilitated by native counterparts is key to predicting their population dynamics and determining management strategies, particularly in California grasslands, which are heavily invaded by introduced grasses, that have reduced native species abundance and diversity (LaForgia et al., 2020).

Methods

Study System

California grasslands experience a mediterranean climate with cool, wet winters and hot, dry summers. Rainfall amount varies substantially from year to year, driving species composition and vegetation dynamics (Hallett et al., 2019). We selected two annual species to test our questions: *Acmispon americanus,* a native legume, and *Bromus hordeaceus*, an invasive grass, both of which are common across California grasslands as well as our reference site, Sierra Foothills Research and Extension Center (SFREC) in Northern California (39∘15’ 04.2 N, 121∘ 18’ 39.0 W).

Greenhouse Experiment

We conducted a greenhouse experiment to test how facilitation changes with shifting limiting resources, and the consequences for persistence of an antagonistic facilitative relationship. We grew focal individuals of each species in varying neighbor densities (10 levels for *A. americanus* backgrounds; 4 levels for *B. hordeaceus backgrounds*) and water levels (3 levels: low, intermediate, high). We included more densities of *A. americanus* as we were particularly interested in the influence of neighbor density on interspecific facilitative interactions. To test the role of soil symbionts we crossed a soil microbiome treatment (live soil vs. sterilized soil) with the existing density and water treatments only in *A. americanus* backgrounds (**Figure S2.1**).

We collected soil from our field site (top 30cm) before fall rains began. We sieved (2mm), homogenized, and autoclaved field soil (99-minute cycle at 123 ºC with 1-minute dry time, 2x 24 hours apart) (King et al., 2024) before mixing it with autoclaved sand (Sakrete Multi-purpose) in a 60:40 ratio. We used 10.8cm^2 pots (depth = 12.4cm) and in live soil pots, we replaced 40g of sterilized field soil with live field soil in a thin layer ~5cm below the soil surface. We planted 10 background densities of *A. americanus* and 4 background densities of *B. hordeaceus*, with 4-5 replicates per density (Inouye, 2001). For *A. americanus* backgrounds, we sowed 0, 5, 9, 18, 27, 37, 55, 73, 92, and 128 seeds per pot to achieve target densities of 0, 3, 6, 12, 18, 24, 36, 48, 60, 84 individuals per pot (germination rate = 0.655). For *B. hordeaceus* backgrounds we sowed 0, 12, 25, and 62 seeds/pot to achieve 0, 12, 24, and 60 plants/pot (germination rate = 0.967). We purchased seeds from Hedgerow Farms (2023). In sterilized soil pots, *A. americanus* seeds were surface sterilized with 75% ethanol for 1 minute, then rinsed in distilled water to avoid transfer of microbes from seeds (Magnoli & Lau, 2020).

We sowed 8 focal individual seeds per pot. Focal *A. Americanus* seeds were scarified with sandpaper to improve germination. Due to poor germination, we replanted 39 of 330 pots sixteen days into the experiment after removing any existing individuals. We thinned pots to 4 focal individuals by 2 weeks post-planting date and 2 focal individuals by 4 weeks post-planting date in most pots. In select densities (0, 12, 24, 48) we thinned pots to 4 focal individuals and sampled one of these at 28 days post-emergence and a second at 56 days post-emergence. The three water levels were set using a percentage of the field capacity of the 60:40 soil:sand mixture: high = 100%, intermediate = 75%, and low = 60% and were hand watered 3-4 times per week to maintain these levels. Sterilized and live pots were organized into separate trays and placed 15-25 cm apart and hand watered to avoid contamination of sterilized treatments through water droplets. We initially watered all pots to full water capacity to mimic fall rains and ensure germination and gradually reduced intermediate and low water treatments.

Data Collection

We measured the leaf C:N ratio, %N, and delta 13C on pre-flowering adult *B. hordeaceus* individuals at two months post-emergence in target densities 0, 12, 24, 48 and oven dried them at 60ºC for 48h. Leaf samples were processed at the University of Utah Stable Isotope Ratio Facility for Environmental Research lab for carbon and nitrogen isotope analysis using an isotope ratio mass spectrometer coupled to an elemental analyzer. When *B. hordeaceus* set seed, we collected the aboveground biomass of all focal and background individuals in a pot. Due to later phenology, we harvested *A. americanus* at peak biomass, before seed set. We oven dried all biomass samples at 60ºC for 48h and weighed them to nearest 0.001 g. We washed roots with tap water over a 2mm sieve to remove soil particles from *A. americanus* background densities 6, 18, 60 and counted root nodules on density 18 pots to check for contamination (**Figure S2.2**). As

there were only a few contaminated individuals and other sterilized pots contained 0 nodules, we quantified nodule presence/absence for densities 6 and 60. Contaminated individuals were removed from analyses. We used allometric relationships to estimate seed output for each species from aboveground biomass (**Table S2.1**).

Analyses

All analyses were conducted in R version 4.4.3 (R Core Team, 2025). We calculated species interactions in two ways: 1) from an additive intensity index (Díaz-Sierra et al., 2017) and 2) by parameterizing population models.

Additive intensity index

The additive intensity index (AII) is calculated as:

$$Additive\ intensity\ index = 2 * \frac{\Delta P}{P_{-N} + |\Delta P|} \quad \textbf{Equation 2.1}$$

where ΔP is the change in per-capita seed production of focal individuals with neighbor presence, $\Delta P = P_{+N} - P_{-N}$ (Díaz-Sierra et al., 2017). We calculated an AII value for *B. hordeaceus* focal individuals in each density in all water levels. We calculated P_{-N} as the average per-capita seed output of focal individuals in control (no neighbor) pots within a water level x soil treatment, as replicates were randomly dispersed not paired, and compared this to the per-capita seed output in each other replicate of each density within the water level.

Estimating intrinsic growth rates and interaction coefficients

We fit Bayesian models of annual plant fecundity separately for *B. hordeaceus* and *A. americanus* in each of the three water treatments to estimate the posterior distributions of the intrinsic growth rate in the absence of neighbors (λ_i) and intra- and inter-specific interaction

coefficients (α) using the Ricker model (Ricker, 1954). This model describes the expected per-capita seed production (*F*) of species *i* at the end of the growing season.

$$F_{i,t} = \lambda_i e^{\alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} \qquad \textbf{Equation 2.2}$$

Where N_i and N_j are the population sizes of species *i* and *j*, respectively, at the beginning of the growing season, *g* is the germination rate, α_{ii} is the per-capita effect of species *i* on itself, and α_{ij} is the per-capita effect of an individual of species *j* on species *i*.

We modeled the effects of the soil microbial community and density-dependent interactions separately, to balance the number of model parameters required with the number of observations, as the soil sterilization treatment was not factorially crossed with focal species and included only *B. hordeaceus* focal individuals in *A. americanus* backgrounds in sterilized soil, not the reciprocal interaction (**Figure S2.1**).

<u>*Soil microbial community models*</u>: we modeled sterilized soil parameters relative to live soil parameters, by including a deviation parameter for λ_i, α_{ii}, and α_{ij},

$$F_{i,t} = (\lambda_i + \lambda_{i\_dev}) e^{(\alpha_{ii} + \alpha_{ii\_dev}) g_i N_{i,t} + (\alpha_{ij} + \alpha_{ij\_dev}) g_j N_{j,t}} \qquad \textbf{Equation 2.3}$$

In live soil conditions, all _dev parameters were set to 0 and in sterilized soil, all _dev parameters were included. We then calculated parameters in sterilized soil by adding posterior distributions of each parameter and its deviation together, taking care to match model runs together.

<u>*Density dependent interaction models*</u>: To model density-dependent interactions we separately fit Bayesian models of fecundity for both species as before, but included data from live soil only,

removed deviation parameters, and modeled *inter*specific interactions as scaled sigmoidal functions of density (Buche et al., 2025).

$$\alpha_{ij} = \alpha_{0,ij} + \frac{C*(1- e^{\alpha_{slope,ij}\left(N_j - N_0\right)})}{1+ e^{\alpha_{slope,ij}(N_j - N_0)}} \text{ , } \textbf{Equation 2.4}$$

Here $\alpha_{slope,ij}$ is the density-dependent effect of j on i, N_0 is the optimal density of the neighboring species j, and $\alpha_{0,ij}$ is the constant density independent effect of j on i, which defines the effect when the density of neighboring species j is optimal, $N_j = N_0$. c is a constant that stretches the function vertically and is bounded by –1 and 0. We modeled all *intra*specific interactions as static coefficients to reduce the number of estimated parameters in the model and because individuals had relatively lower variation in seed production across density than interspecific interactions (**Figure S2.3**).

For all models, we modeled per-capita seed production (*F*) as a negative binomial distribution using the package rstan (Stan Development Team, 2024), running each model with 4 MCMC chains for 8000 iterations and thinning by two iterations to remove autocorrelation. See **Tables S2.2** and **S2.3** for prior distributions. We assessed model convergence by Rhat values < 1.001 and checked trace plots visually for chain mixing.

Linear models of additive intensity index and leaf nutrients

To experimentally test how water and neighbor treatments alter water and nitrogen limitation, we measured *B. hordeaceus* leaf $\delta^{13}C$ and leaf percent N across the *A. americanus* density gradient and the three water levels. Leaf $\delta^{13}C$ is leaf carbon isotope ratio of ^{13}C to ^{12}C. Larger values indicate greater water use efficiency, and are expected to occur when a plant is experiencing water stress (Ehleringer & Cooper, 1988).

To link $\delta^{13}C$ and leaf percent N to estimated species interaction effects, we used separate linear models to evaluate the response of interaction values (measured by AII) to leaf $\delta^{13}C$ and leaf percent N along with main effects of water treatment and the number of background individuals. In the model for $\delta^{13}C$, we included an interaction between the water level and $\delta^{13}C$ values, to reflect that $\delta^{13}C$ will likely vary with different water levels.

Assessing coexistence

We assessed coexistence between our species with two methods: the mutual invasion criterion (Chesson, 2000) and niche and fitness differences (Spaak et al., 2021; Spaak & De Laender, 2020). Under the mutual invasion criterion, stable coexistence occurs if each focal species can increase from rarity when the other is at an equilibrium abundance, while niche and fitness differences detect coexistence when niche differences > fitness differences (Spaak et al., 2021). We selected these niche and fitness difference metrics as they accommodate facilitative interactions. We used an established discrete time annual plant model (Levine & HilleRisLambers, 2009):

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)s_i + g_i F_{i,t}, \textbf{ Equation 2.5}$$

where s_i is the proportion of seeds that survive in the seedbank, to analytically solved for the equilibrium population abundance, N_i^*, of each species, $N_i^* = \frac{1}{\alpha_{ii} g_i} \log\left(\frac{1-(1-g_i)s_i}{\lambda_i g_i}\right)$, and calculate the invasion growth rate, r_i. We introduced one individual of the other species into a community of the other at equilibrium abundance and calculated its growth rate at the next time step, $r_i = \ln\left(\frac{N_{i,t+1}}{N_{i,t}}\right)$. To propagate uncertainty from posterior distributions, we calculated the invasion

growth rate with 400 random draws from the 80% high density interval of the posterior distribution of each parameter.

Niche (*ND*) and fitness differences (*FD*) were calculated as:

$$ND = \frac{r_i - \eta_i}{\mu_i - \eta_i} \quad \textbf{Equation 2.6}$$

$$FD = \frac{-\eta_i}{\mu_i - \eta_i} \quad \textbf{Equation 2.7}$$

Where r_i is the invasion growth rate, η_i is the no-niche growth rate, and μ_i is the intrinsic growth rate (Spaak et al., 2021; Spaak & De Laender, 2020). We calculated each metric with the same 400 random draws from the 80% high density interval of the posterior distributions of each parameter to estimate uncertainty.

Results

Interactions and nutrient co-limitation

The effect of *A. americanus* on *B. hordeaceus* changed with water availability and plant density, but not the soil microbial community, as measured by the additive intensity index. In general, interactions became more competitive as water availability declined, both across water treatments (**Figure 2.2A,B, Table 2.1, Table S2.4;** $F_{2,258} = 22.858$, $p < 0.001$) and within water levels (**Figure 2.2C, Table 2.2**). *A. americanus* facilitated *B. hordeaceus* at low densities and had a competitive effect at intermediate and high densities that saturated around 24 individuals (**Figure 2.2A, Table 2.1** $F_{1,258} = 177.44$, $p < 0.001$). The observed facilitation at low densities was present mainly in high water levels, although error bars overlapped zero at densities 3 and 6 in the low water treatment.

Interactions became more competitive as water stress increased (**Figure 2.2C, Table S2.5;** $F_{1,59} = 8.922$, p =0.004) and less competitive as leaf %N increased (**Figure 2.2D, Table 2.3, Table S2.6;** $F_{1,59} = 8.922$, p =0.004). This was dependent on water level: intermediate and low water levels had a negative relationship between water stress ($\delta^{13}C$) and interaction strength, while in high water, interaction strength did not vary with water stress, likely as water was not limiting. Interactions in high water responded to leaf %N, while low water interactions did not have as strong of a relationship with high leaf %N (**Figure 2.2D**).

Benefits of the legume-rhizobia mutualism varied with water level

The legume rhizobia mutualism had a positive effect on both *A. americanus* and *B. hordeaceus*, but the strength of the effect depended on water level. *A. americanus* seed output increased in live soil relative to sterilized soil under high and intermediate water conditions, especially in low *intra*specific densities with fewer than 10-20 individuals (**Figure S2.4A, Tables S2.7, S2.8;** $F_{1,222} = 13.567$, p-value <0.001), leading to an overall increase in intrinsic growth rate (**Figure 2.3A**). The increase in growth rate was greatest in high relative to low water. The positive effect of the mutualism on *B. hordeaceus* was mediated through the interspecific effect of *A. americanus*, which changed from competitive in low water levels to facilitative in high water (**Figure 2.3D**). *B. hordeaceus* seed output increased in sterilized soil relative to live soil (**Figure S2.4B, Tables S2.7, S2.8;** $F_{1,259} = 18.474$, p-value <0.001), but the intrinsic growth rate did not change between live and sterilized soil (**Figure 2.3B**). Water level also changed the effect of *B. hordeaceus* on *A. americanus*, with stronger competition when water was limiting (**Figure 2.3C**). Finally, *A. americanus* experienced stronger competition from *intra*specific neighbors in live soil than sterilized soil (**Figure 2.3E**), and *B. hordeaceus* intraspecific competition relaxed with water availability (**Figure 2.3F**).

Rainfall determined coexistence outcomes between the invasive grass, *B. hordeaceus*, and legume, *A. americanus*. *B. hordeaceus* increased from rarity in the presence of *A. americanus* at an equilibrium density in all rainfall conditions (**Figure 2.4B**), while *A. americanus* could only increase from rarity in the high water treatment and was competitively excluded under intermediate and low water treatments (**Figure 2.4A**). *A. americanus* coexistence was also contingent on its rhizobial symbionts, as even high water was not enough for a positive invasion growth rate in sterilized soil. Consistent with the facilitative interaction from *A. americanus*, the invasion of growth rate of *B. hordeaceus* was greater in live soil than sterilized soil and in high water invasion growth rate was greater than intrinsic growth rate.

Density dependent facilitation

Modeled interaction coefficients indicated that *A. americanus* facilitated *B. hordeaceus* at low densities in all rainfall conditions, with the strongest facilitation in high water, and as density increased, the interaction coefficient reached an asymptote near zero for all water levels (**Figure 2.5A**). Legume density also changed *B. hordeaceus* leaf $\delta^{13}C$ and leaf percent N. *B. hordeaceus* experienced greater water stress as density increased in low and intermediate water treatments (**Figure S2.5A**) and had lower leaf %N with greater neighbor density (**Figure S2.5B**).

Population models estimated more facilitation than the additive intensity index (**Figure 2.2A, B; Figure 2.3D; Figure 2.5A**), for several possible reasons. First, AII was calculated relative to an average control as replicates were not paired and does not reflect the range of seed outputs from control individuals. Second, modeled interactions also estimated intraspecific effects of other *B. hordeaceus* focal individuals (2-4 individuals per pot) alongside the

interspecific effect of *A. americanus*. Further, the modeled data included per-capita seed output of *B. hordeaceus* at higher intraspecific densities that were not included in the AII calculations.

Density dependent facilitation alters frequency dependence at relevant neighbor densities

B. hordeaceus experienced negative frequency dependence in all rainfall conditions, indicating that it limits itself more than it is limited by *A. americanus* (**Figure 2.5 C-E**). Density-dependent interactions shaped frequency dependence: at high *intra*specific frequencies (i.e., low frequency of legume), *B. hordeaceus* growth rate increased faster than at lower *intra*specific frequencies (high legume frequency). This effect changed with the total community density as well, where the steeper increase in growth rate at high frequencies persisted until lower frequencies of *B. hordeaceus* in lower total density communities.

A. americanus experienced positive frequency dependence in low and intermediate water levels, indicating that it was regulated more by the grass than by itself, and only became self-limiting in high water levels (**Figure 2.5C-E**). At low total community densities, *A. americanus* growth rate did not strongly depend on frequency, and overall *A. americanus* experienced stronger density dependence than frequency dependence. This led to increased fitness inequalities with total community density.

Fitness differences led to exclusion of the legume under low water availability

Water level changed coexistence outcomes primarily by shifting the balance of fitness differences between species, allowing *A. americanus* to persist in high water, and had smaller effects on niche differentiation (**Figure 2.6**). Note that species with lower fitness difference values are predicted to be competitively superior in the absence of niche differences, and when niche differences are greater than one (i.e. facilitation) fitness differences matter less for

persistence of that species (Spaak et al., 2021). *B. hordeaceus* is therefore expected to become more competitively superior to *A. americanus* in intermediate and low water treatments, while *A. americanus* would be competitively superior at high water levels if they occupied the same niche.

Niche differences also reveal high level community processes such as frequency dependence or positive interactions in a community. *B. hordeaceus* had niche differences > 1, indicating that it was facilitated by the legume in all water conditions, as expected from the density-dependent interactions. *A. americanus* mean niche differences were below 0, indicating that it experienced positive frequency dependence and was more limited by *B. hordeaceus* than itself. The distribution overlapped zero in high and intermediate water levels, indicating that in some instances *A. americanus* may be able to limit itself.

Discussion

We investigated how rainfall, neighbor density, and the soil microbial community shaped the interactions between a native legume and an invasive grass species in California, and the outcomes for coexistence of both species. Water stress generally led to a stronger competitive effect of the legume on the grass, while greater leaf percent N was associated with relaxed competition or facilitation, likely reflecting the benefits of N-fixing neighbors (Ortiz & Wolf, 2024). Importantly, when water was amply available, the effect of the legume on the grass did not vary with water stress but became less competitive with increasing leaf percent N, indicating that the interaction responded most strongly to the primary limiting factor (Carroll & MacDougall, 2024), as well as variation in N-fixation with water availability (Arfin Khan et al., 2014; Dovrat & Sheffer, 2019). In turn, facilitative interactions were dependent on the presence

and activity of rhizobial symbionts. Overall, as interactions are shaped by multiple factors concurrently, it is necessary to understand the interplay and relative importance of drivers to predict net outcomes (Carroll & MacDougall, 2024; Gross, 2008; Holmgren et al., 1997).

It is well appreciated that interactions are modified by environmental factors (Bimler et al., 2018; Holmgren et al., 1997; Ortiz & Wolf, 2024), however, exploring density itself as a mediator of interactions is a relatively new direction (Buche et al., 2025; Molofsky et al., 1999; R. Zhang & Tielbörger, 2020). Processes that shape species interactions often shift in importance with density, including competition for limiting resources like water, herbivore protection, the soil microbial community, or N-fixation (Carroll & MacDougall, 2024; Cavalieri et al., 2020). We found that density increased the amount of water stress and decreased leaf percent N in grass leaves while also reducing the benefits the legume experienced from N-fixation. Consequently, facilitation of the grass by the legume was strongest at low legume densities and declined to weakly competitive or neutral with increased density. Density and competitor induced changes to the rhizosphere microbial community may have also shaped the interaction. A study of a different legume species, *Trifolium pratense*, showed increased genes associated with N-fixation under competition from heterospecific neighbors, despite declines in *Rhizobium* abundance, and the opposite pattern with conspecific neighbors (Cavalieri et al., 2020). While changes to microbial communities are likely difficult to generalize between species, the uptick in N-fixation potential with heterospecific competitors and reduction with conspecific neighbors, could explain the increase in facilitation at low legume densities and decline in benefit from N-fixation with increasing conspecific density.

While there is evidence that interactions become less competitive or even facilitative under a stressful low-resource environment (He et al., 2013), our findings diverged from the

stress gradient hypothesis in two ways. First, our measured facilitative interactions were strongest with ample water availability, likely as the mechanism of facilitation, N-fixation, did not ameliorate stress from the main limiting factor and was regulated by water availability (Walsh, 1995). Second, we found that the strength of competition – particularly *inter*specific – increased with water stress, indicating that competition for limiting resources became the overriding factor shaping the interaction in low water environments (Holmgren & Scheffer, 2010). It is possible that water was especially limiting in the greenhouse setting, given the small pot size. However, competition weakened or turned facilitative even from the intermediate to the high water treatment, indicating that this pattern is not solely due to the experimental setting. Our findings therefore caution that considering both the mechanism of facilitation and the primary limiting resource is necessary to predict when an interaction between species may shift in strength or direction along a stress gradient.

Placing facilitative interactions in context with density independent effects, such as intrinsic growth rate, along with density-dependent effects, i.e. intraspecific and reciprocal interactions, is key to determining population outcomes (García-Cervigón et al., 2013; Hart & Marshall, 2013; Raath-Krüger et al., 2021). The legume-rhizobia mutualism increased the legume's intrinsic growth rate but also led to facilitation of a superior competitor at high water availability. At the same time, the legume also benefited from relaxed *inter*specific competition as water availability increased, allowing the legume to coexist with the grass with ample water, contingent on presence of symbionts. Reciprocal interactions from the grass became more competitive as water availability declined, leading to the competitive exclusion of the legume in low and intermediate water treatments. Altogether, exclusion of the legume was driven by a combination of lack of niche differentiation due to strong regulation of the grass, plus large

fitness inequalities with lower water availability, similar to other studies of coexistence outcomes with drought (Matías et al., 2018; Muehleisen et al., 2025; Wainwright et al., 2019).

Tests of coexistence use equilibrium densities of species to ensure that coexistence is robust (Chesson, 2000; Spaak & De Laender, 2020), but species are rarely at their equilibrium densities. California grasslands are often considered non-equilibrium systems (Muehleisen et al., 2025) and are commonly used for livestock grazing, which can reduce plant density. Therefore, understanding shifts in growth rates with neighbor density, in addition to environmental context, is important for understanding the persistence of species. The invasive grass experienced stabilization both at rarity from reduced intraspecific competition (Adler et al., 2007), and when it was common, from density-dependent facilitation. For instance, if the grass was at a high frequency and declined slightly, the facilitation by the low frequency legume – which peaks at low abundances of the legume – would increase the grass' growth rate more than the small release from *intra*specific competition, thereby stabilizing the grass even at a relatively high frequency. This stabilizing effect was stronger in lower density communities than at high densities closer to equilibrium. Examples of facilitation increasing niche differences often invoke allowing a species to persist in a wider range of conditions (Bulleri et al., 2016), we show that a facilitator can stabilize a species' population even if that species does not depend on the facilitator for persistence. In contrast, the legume growth rate was influenced more by total community density rather than frequency of either species, indicating that grazing or similar density reducing mechanisms disturbance could support legume persistence (Aoyama et al., 2022; Hernández et al., 2021). The legume experienced apparent positive frequency dependence in low and intermediate water levels due to strong regulation by the grass and only became self-regulating with enough water, indicating that water availability increased niche differentiation.

Our tests of coexistence at multiple rainfall levels and with different biotic drivers indicate that coexistence is sensitive to the environment, which in turn shapes biotic feedbacks. The legume is strongly regulated by the grass, especially when water is limiting, indicating that the antagonistic facilitative relationship is likely unstable. A key future direction will be exploring whether variability through time stabilizes coexistence of these species (Chesson, 2000). California grasslands experience highly variable rainfall through time that promotes coexistence between a common non-native grass and non-native forb (Hallett et al., 2019), but is not enough to mitigate fitness differences between a broader pool of species (Muehleisen et al., 2025). Here it will depend on whether the benefit to the legume's growth rate as well as relaxed interspecific competition from the grass under high water outweighs the regulation by invasive grass during lower water conditions. Altogether, a future of increasing drought frequency and severity (Chiang et al., 2021), will lead to greater risk of competitive exclusion of the native legume and indicates that interventions such as grazing that maintain lower community densities may be particularly beneficial to the legume (Hernández et al., 2021).

Figures

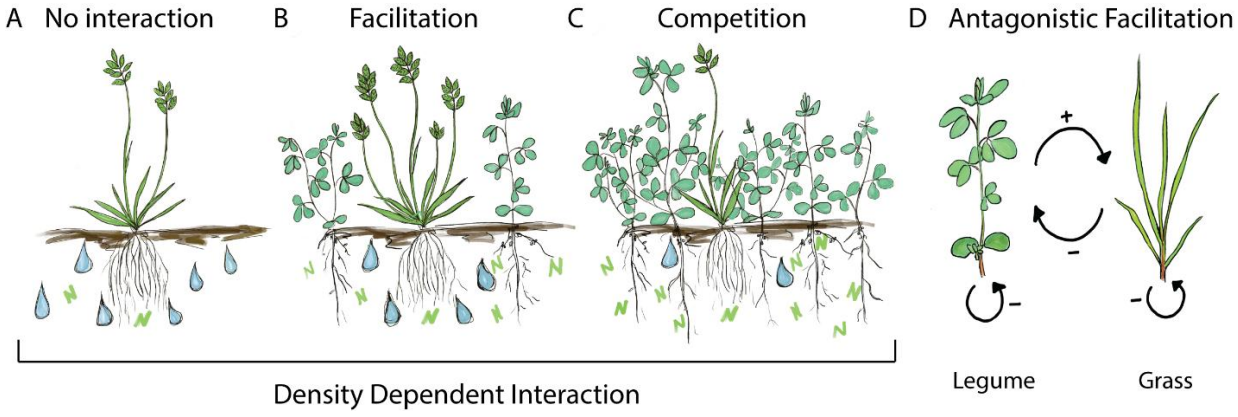

Figure 2.1. Conceptual figure of density dependent interactions (A-C) and antagonistic facilitation (D) between a legume and a grass. In panel A, a grass grows alone with ample water,

but limiting N. A legume neighbor at low density may enrich soil N without causing strong competition for water, leading to facilitation. However, a high density of legume neighbors will cause more competition for water that outweighs the benefits of the additional soil N.

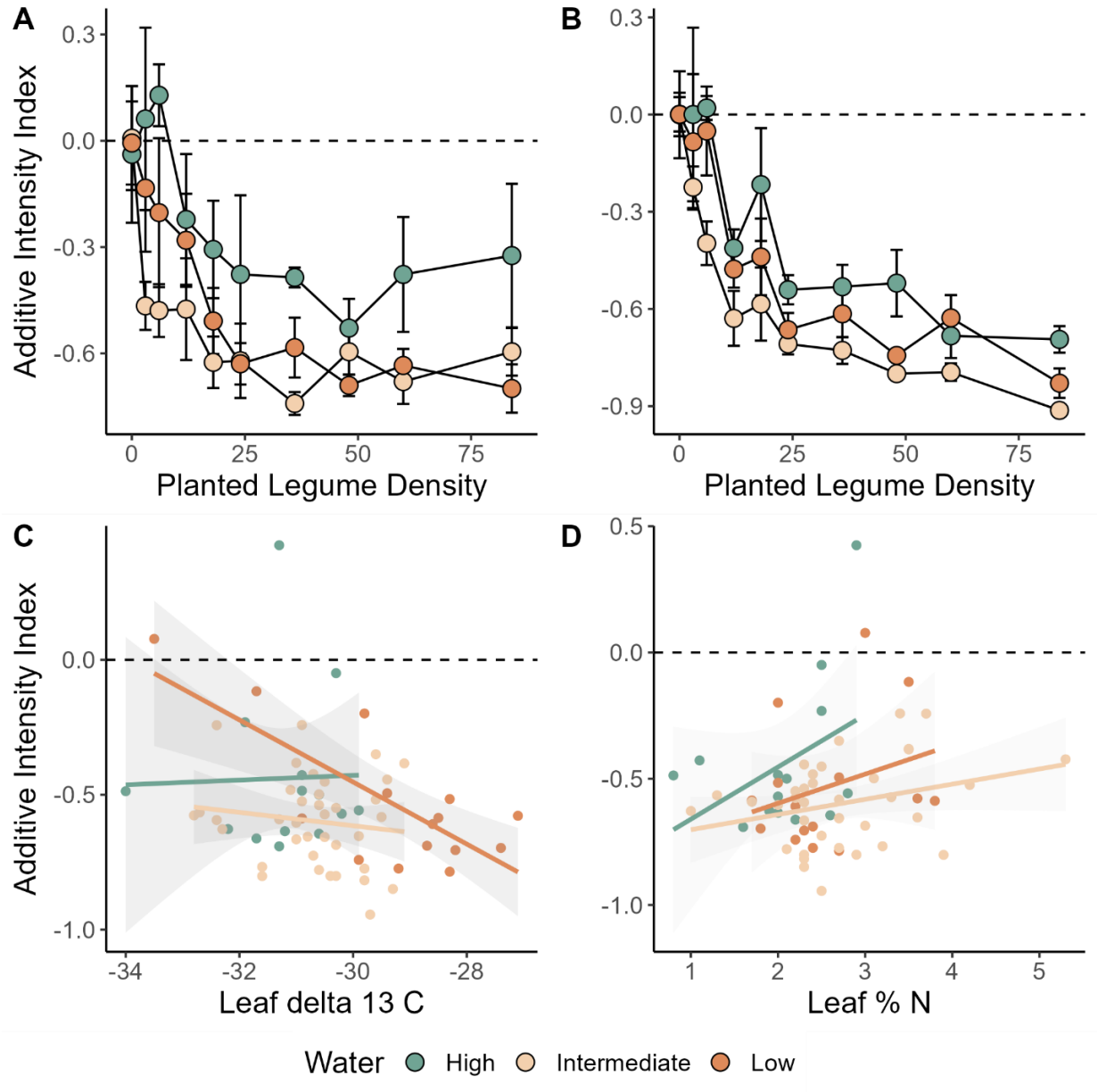

Figure 2.2. The effect of legume *A. americanus* on invasive grass *B. hordeaceus* seed output, measured using the additive intensity index as a function of neighbor density in live soil (A) and sterilized soil (B), and as a function of leaf δ13C (C) and leaf % N (D). The additive intensity index measures the change in per-capita seed production of focal individuals with neighbor presence standardized by the sum of seed production with no neighbors plus the change with neighbors. Leaf δ13C is a proxy of water stress, where less negative values indicate a leaf is experiencing greater stress.

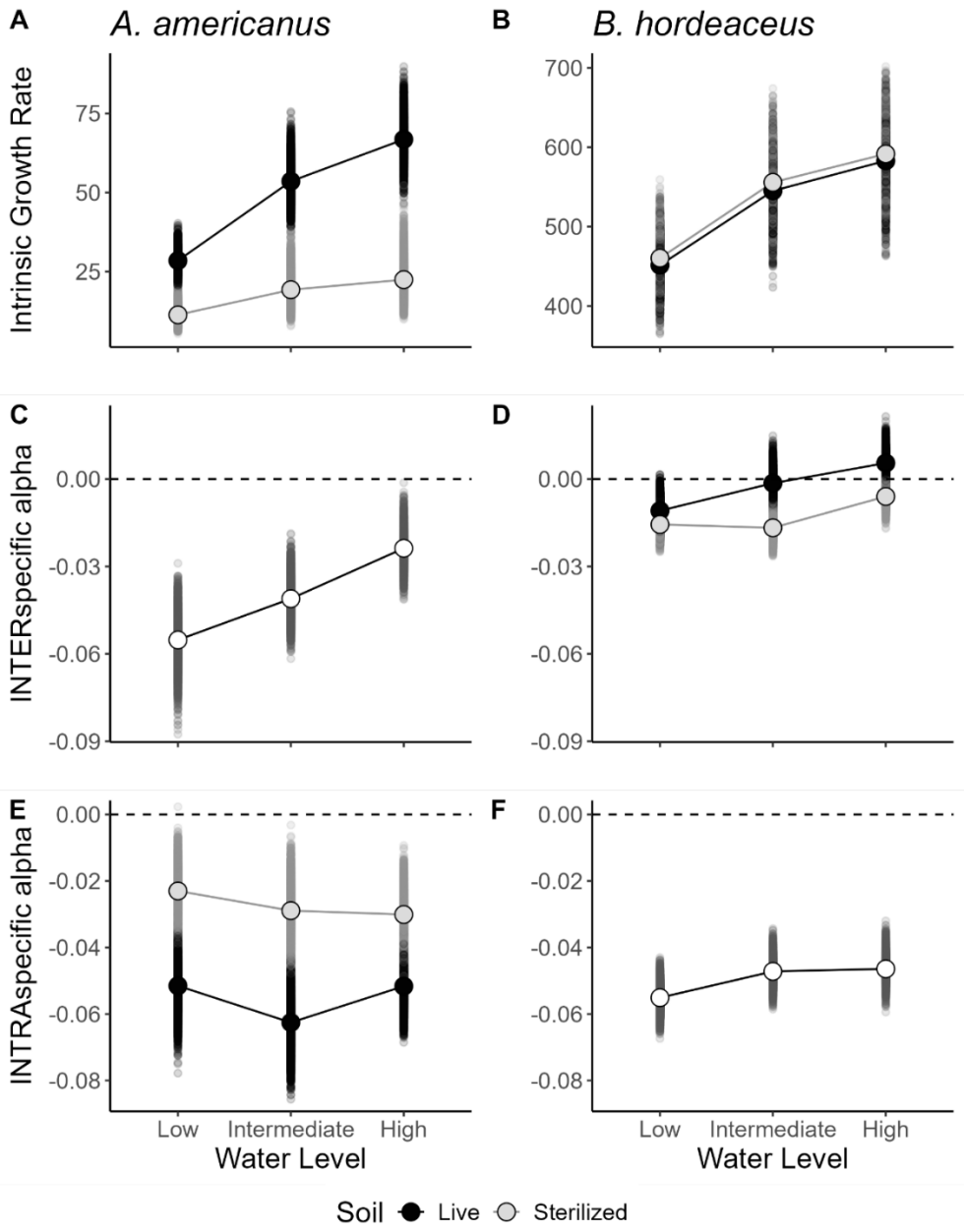

Figure 2.3. Posterior distributions of *A. americanus* (left column) and *B. hordeaceus* (right column) intrinsic growth rate (A, B) *inter*specific interaction coefficient (C, D) and *intra*specific interaction coefficient (E, F) across the three water levels. Large points show the mean of the posterior distribution, and smaller points show the 80% high density interval of the posterior distribution. Positive values in C-F indicate facilitative interactions and negative values indicate competition. Colors denote the soil microbial treatment, where black = live soil and gray = sterilized soil. Points in panels C and F are not colored as the parameters could not be estimated separately for live and sterilized soil due to experimental design (**Figure S2.1**).

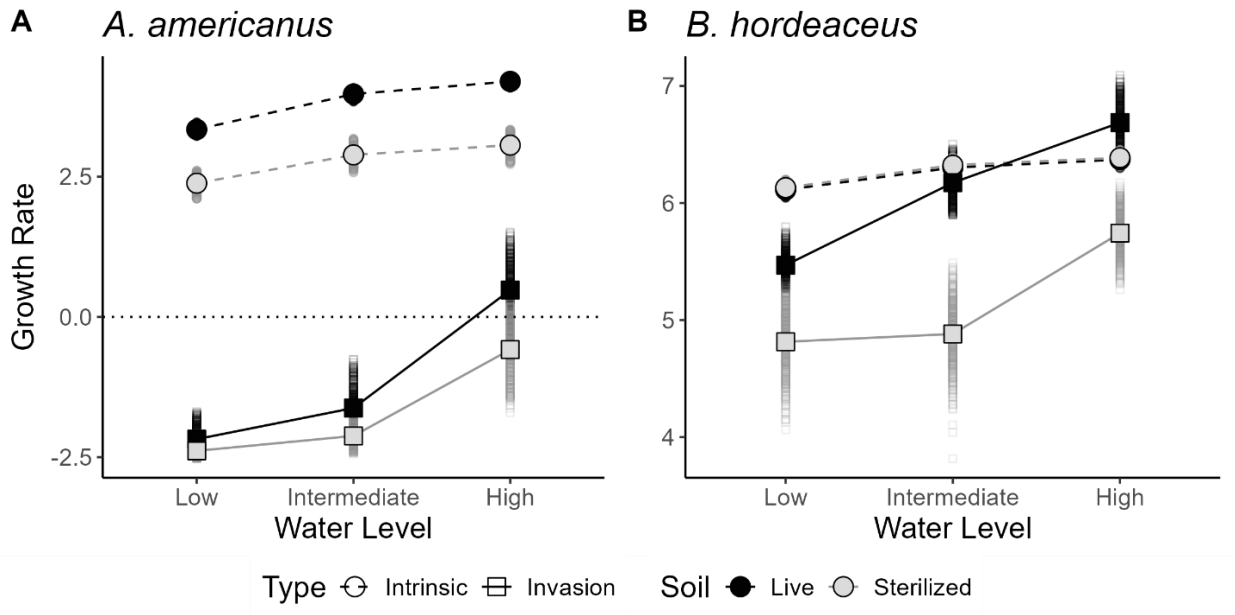

Figure 2.4. The intrinsic (λ_i) and invasion growth rates (r_i) of *A. americanus* (A) and *B. hordeaceus* (B) in live and sterilized soil. Large points show the mean of the posterior distribution, and smaller points show the 80% high density interval of the posterior distribution. Point shape indicates the type of growth rate, where intrinsic growth rate (circle) is the per-capita growth rate in the absence of interactions, and the invasion growth rate (square) is the per-capita growth rate in an equilibrium density of a neighboring species. Invasion growth rate > 0 indicates a species can persist with the neighboring species, while invasion growth rate < 0 indicates a species will be competitively excluded. Growth rates are on a log scale. Colors denote the soil microbial treatment, where black = live soil and gray = sterilized soil.

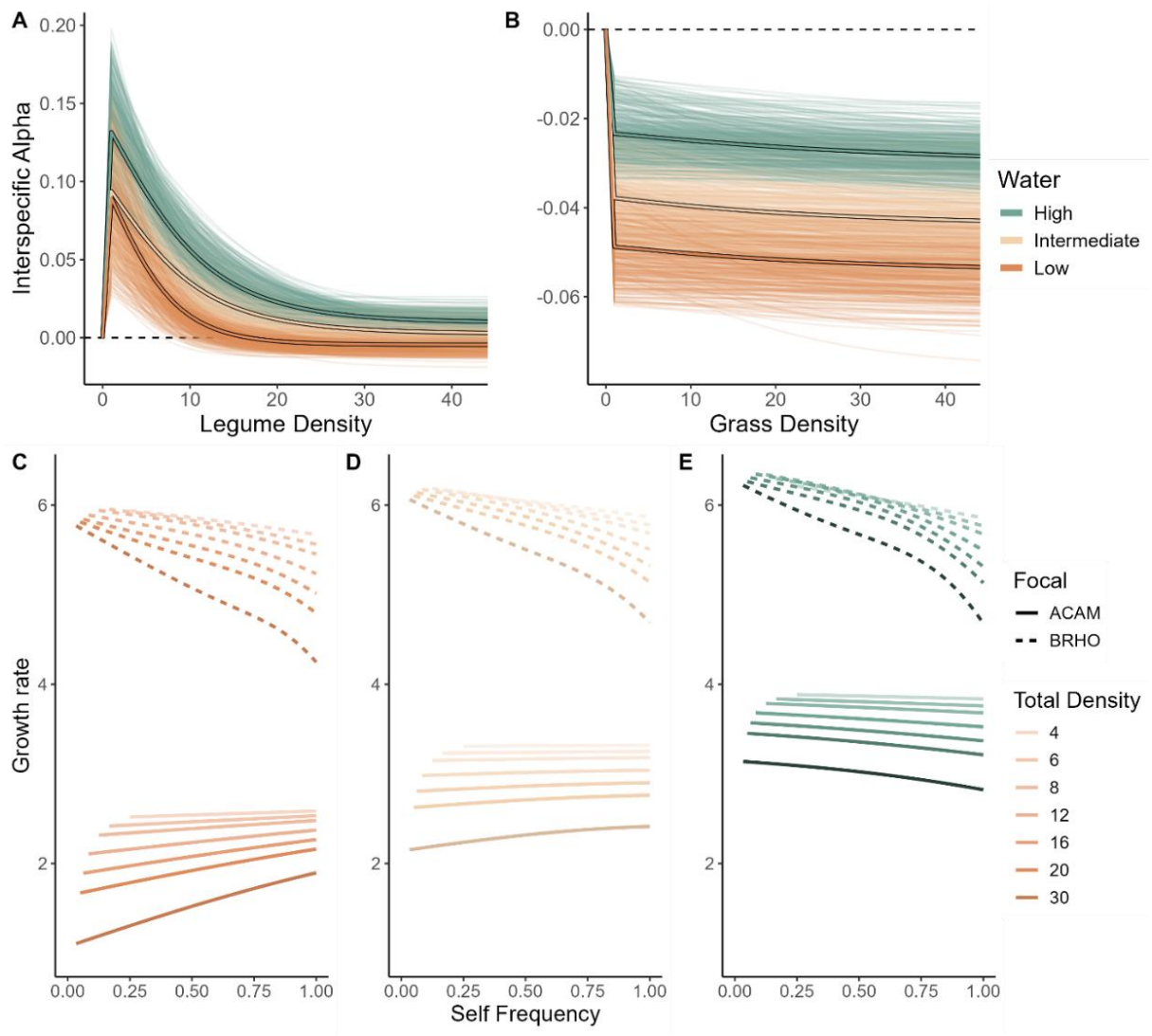

Figure 2.5. Density dependent interactions (A, B) and frequency dependent growth rates (C-E). The density-dependent facilitative effect of *A. americanus* on *B. hordeaceus* (A) and the reciprocal effect of *B. hordeaceus* on *A. americanus* (B) all as functions of neighbor density. In (A) and (B), lines show the mean of 400 random draws from the 80% high density interval of each posterior distribution and semi-transparent background lines show each random draw. Positive values in (A) and (B indicate facilitative interaction*s* and negative values indicate competition. The frequency dependent growth rate of *B. hordeaceus* (dashed lines) and *A. americanus* (solid lines) across water levels and at select densities (C-E), chosen to reflect a range of realistic field densities. Growth rates were calculated with the mean of the 80% high density interval of posterior distributions for each parameter.

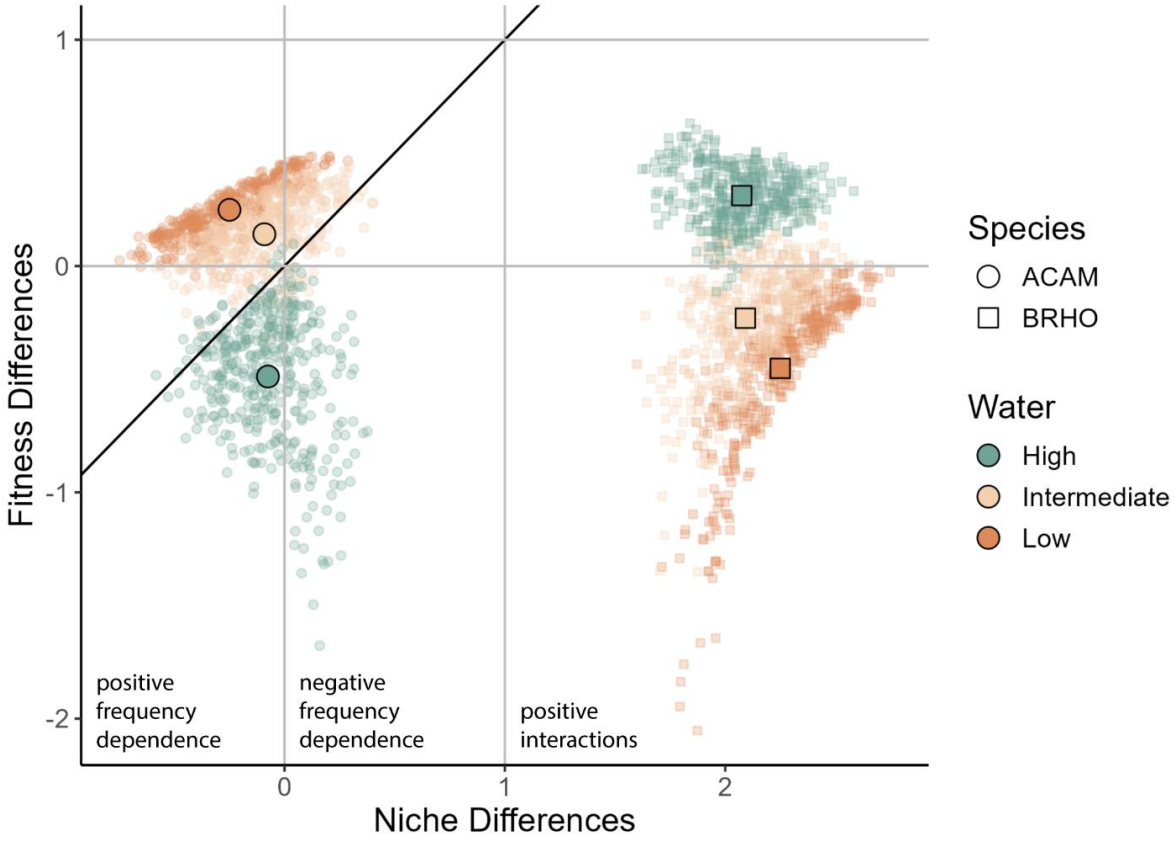

Figure 2.6. The niche and fitness differences of *A. americanus* (ACAM, circles) and *B. hordeaceus* (BRHO, squares) in each water treatment. The black line indicates persistence, where Niche differences > Fitness differences. Niche and fitness differences were calculated with **Equations 2.5** and **2.6**, respectively *(Spaak et al., 2021)*. Large points show mean values, and small points show niche and fitness differences calculated with 400 draws from the 80% high density interval of posterior distributions.

Tables

Table 2.1. ANOVA table from the linear model predicting the interspecific interaction of *A. americanus* on *B. hordeaceus*, calculated with the additive interaction intensity, from the number of background individuals, water level, and the soil microbial treatment.

Coefficient	**Sum Sq**	**Df**	**F value**	**Pr(>F)**	
Number background indiv	11.724	1	177.44	<0.001	***
Water Level (Lo, Int, Hi)	3.021	2	22.858	<0.001	***
Soil (Live vs. Sterilized)	0.024	1	0.356	0.551	
Residuals	17.046	258			

Table 2.2. ANOVA table from the linear model predicting the additive interaction intensity from *B. hordeaceus* leaf $\delta^{13}C$, the number of background individuals, water level, and the interaction between leaf $\delta^{13}C$ and water level.

Coefficient	Sum Sq	Df	F value	Pr(>F)	
Intercept	0.4	1	11.499	0.001	**
$\delta^{13}C$	0.31	1	8.922	0.004	**
Water level (Lo, Int, Hi)	0.185	2	2.656	0.079	.
Number background Indiv	0.544	1	15.658	<0.001	***
$\delta^{13}C$: Water level	0.199	2	2.86	0.065	.
Residuals	2.051	59			

Table 2.3. ANOVA table from the linear model predicting the additive interaction intensity from *B. hordeaceus* leaf percent N, the number of background individuals, and water level.

Coefficient	Sum Sq	Df	F value	Pr(>F)	
%N	0.177	1	4.876	0.031	*
Water level	0.514	2	7.076	0.002	**
Number background Indiv	0.65	1	17.918	0	***
Residuals	2.214	61	NA	NA	

Table 2.4. ANOVA table from linear models predicting 1) *A. americanus* per-capita seed output from the number of *intra*specific neighbors, the soil microbial treatment, water level, and the interactions between all factors and 2) *B. hordeaceus* per-capita seed output from the additive effects of the number of *inter*specific neighbors, the soil microbial treatment and water level.

Species	Coefficient	Sum Sq	Df	F value	Pr(>F)	
A. americanus	Intercept	4.513	1	32.415	<0.001	***
	Num Indiv	0.986	1	7.078	0.008	**
	Soil Treatment	0.201	1	1.446	0.23	
	Water Level	0.752	1	5.403	0.021	*
	Num Indiv: Soil Treatment	0.001	1	0.004	0.947	
	Num Indiv: Water Level	0.06	1	0.433	0.511	
	Soil Treatment: Water Level	1.889	1	13.567	<0.001	***
	Num Indiv: Soil Treatment: Water Level	0.27	1	1.937	0.165	
	Residuals	30.909	222			
B. hordeaceus	Intercept	291.891	1	3001.041	<0.001	***
	Num Indiv	23.486	1	241.466	<0.001	***
	Soil Treatment	1.797	1	18.474	<0.001	***
	Water Level	20.348	1	209.205	<0.001	***
	Residuals	25.191	259			

Bridge

My work has identified that a lack of niche differentiation as well as large fitness inequalities between two species would lead to exclusion of the facilitator/weaker competitor (depending on conditions) under drought. In my next chapter, I scale responses of two species up to the community level, which experiences a wide range of direct and indirect interactions between species. While the data needed to quantify niche differences and fitness inequalities would be prohibitive across the six grasslands I studied, I consider how a signature of niche differentiation – negative frequency dependence – may be at play in six communities across a gradient of mean annual precipitation. This is an effort to understand whether we can predict species drought responses by their local abundances and whether these responses align with niche differences or if rarer species are limited more by competitive interactions, like the legume in this chapter.

CHAPTER III

DROUGHT REORDERS PLANT COMMUNITIES THROUGH EXPANSION OF SPATIALLY SPARSE AND TEMPORALLY INTERMITTENT SPECIES

Contributions

CW led analyses with input from BA, LBD, YAC, MW, JD, and CPR; CW and LH contributed to writing, and MS provided data. The manuscript was developed through conversations with the entire author list and all authors contributed to manuscript edits.

Introduction

The frequency and severity of droughts are increasing in grasslands globally with climate change (Cook et al., 2015; Dai, 2013), yet predictions of how drought will alter grassland plant communities are complicated by the varied and at times opposing ways that drought affects species performances. For example, drought often has a negative direct effect on species' physiology, but can also have a beneficial indirect effect by reducing interspecific competition (Cavin et al., 2013; Levine et al., 2010). These phenomena can occur both during the drought and afterward, in which slow physiological recovery or delayed propagule availability can lead to persistent negative responses post-drought (Dudney et al., 2017; Farrer et al., 2010; Sala et al., 2012), while species that can respond quickly to post-drought rainfall might benefit from lessened interspecific competition or soil legacies (Schärer et al., 2023). Species abundance distributions may yield insights into which species will exhibit net negative or net positive drought responses. Rare species, for example, are typically assumed to be more sensitive to extreme events than dominant species and may be slow to recover post-perturbation (Arnoldi et

al., 2018; Duwyn & MacDougall, 2015; Pimm et al., 1988). On the other hand, common species are likely best adapted to modal environmental conditions (Gherardi & Sala, 2015) and their high biomass and frequency in the community may become a disadvantage when environmental conditions don't match their environmental optimums and resources become limited under drought (Diez et al., 2021). Reconciling these contrasting perspectives on how and when rare or common species respond to drought may provide a general framework for anticipating drought effects on grassland plant community structure.

Within a local community, species abundance versus rarity can be thought of along two axes: space and time (Gillett et al., 2011; Rabinowitz, 1981; Wilfahrt et al., 2021). Species abundance distributions are most frequently calculated across space, such that we would term spatially rare species as "sparse" and spatially abundant ones as "common" (Hanski, 1982). However, species abundance versus rarity can also be conceptualized over time, such that temporally rare species can be considered "intermittent" and temporally abundant species "persistent" (Chen et al., 2016; Wilfahrt et al., 2021). Spatial and temporal abundances are often but not always positively correlated (Magurran & Henderson, 2003) and may reflect different life histories. Species that differ in spatial and temporal rarity may diverge in response and recovery to severe drought, and resolving these differences may provide greater insight into how different suites of species respond to drought.

Spatially common species are often temporally persistent and tend to be well adapted to modal environmental conditions as they have a strong linkage between the environment, their performance, and their traits (Castillioni & Isbell, 2023; Ge et al., 2019; Gherardi & Sala, 2015; Umaña et al., 2017). During drought, they may decline due to reduced environmental suitability or stronger negative frequency dependence (Diez et al., 2021; Gherardi & Sala, 2015), although

species with drought escape or tolerance mechanisms, such as a dormant bud bank, may persist through drought and recover quickly afterwards (Hoover et al., 2014). In contrast, spatial and temporal abundances are less tightly linked in species that are rare in some way. As a whole, small populations can be more vulnerable to decline due to demographic stochasticity, and risks from environmental fluctuations and extreme events (Duwyn & MacDougall, 2015; Pimm et al., 1988). Resource specialists may be persistent but sparse, especially if they are limited by strong interspecific competition or occupy a narrow, stable niche (Hallett et al., 2018; McKane et al., 2002; Yenni et al., 2017), potentially allowing them to respond to competitive release during drought (Prugh et al., 2018). Temporally intermittent species have a weaker link between their traits and the environment or unique temporal niches (Ge et al., 2019; Gherardi & Sala, 2015; Umaña et al., 2017), both of which may cause them to be spatially sparse as well. Finally, temporally intermittent species, that can "store" during unfavorable periods (such as in the seed bank) and capitalize on resource pulses through time or space, may become spatially common following drought (Angert et al., 2009).

The interaction between species rarity and the abiotic environment at a site, particularly mean annual precipitation, may further influence species drought responses. At the community level, sensitivity to drought in grasslands is expected to vary inversely with the mean annual precipitation at a site (Huxman et al., 2004; Knapp et al., 2015; Mount et al., 2024). At the population level, species in low resource environments are expected to be limited by abiotic conditions, while mesic environments are limited by competitive interactions (Louthan et al., 2015). As such, all species in arid sites may be more vulnerable to extreme drought, whereas in mesic sites drought may release the competition experienced on less common species. The average conditions at a site can also shape the overall community structure - for example, the

degree of dominance in the community (Silva et al., 2010) as well as the species pool (Keddy, 1992). Higher dominance in a community should lead to greater competitive release if dominant species decline during drought (McCain et al., 2010). Finally, filtering of the species pool may cause certain traits or types of rarity to be more prevalent in some environments, for example intermittent seed-banking annuals in the desert or C_3 species in colder environments (Ehleringer et al., 1997) .

To test species' direct and lagged drought responses in relation to their abundance, we analyzed species cover data from the Extreme Drought in Grasslands Experiment. Severe drought was experimentally imposed for 4-7 years at six sites across a gradient of mean annual precipitation. We monitored communities for 4 years post-drought, allowing us to examine species recovery, which is an understudied component of grassland responses to extreme disturbances (Isbell et al., 2015; Vilonen et al., 2022). We characterized the responses of 299 plant species to address the following questions: 1) Does a species' spatial and temporal rarity predict its response during and after an extreme drought? And 2) How do responses vary across sites along a gradient of mean annual precipitation? We hypothesized that rare species would respond more positively during drought than common species, and that the type of rarity (spatial or temporal) would determine the strength of the response. Specifically, we expected that spatially rare species would experience competitive release during drought and temporally rare species would respond most positively after drought during windows of reduced competition and increased precipitation. We expected rare species responses to be particularly positive at mesic and intermediate sites due to competitive release from common species, and less positive at arid sites where species may be at the edge of their abiotic tolerances. Overall, linking species

abundance and probable drought response trajectories will help predict species re-ordering in response to a severe drought.

Methods

Study System

We used species-level percent cover data from six sites of the Extreme Drought in Grasslands Experiment (EDGE) across the US: Konza Prairie (KNZ), Hays Agricultural Research Center (HYS), High Plains Grasslands Research Center (CHY), Short Grass Steppe (SGS), Sevilleta Black Grama (SBK), and Sevilleta Blue Grama (SBL). Sites span a west - east precipitation gradient and a north-south mean annual temperature gradient (**Figure 3.1A, B**; **Table 3.1**) (Griffin-Nolan et al., 2018). Each site had twenty plots (6x6m at KNZ, HYS, CHY, SGS and 3x4m at SBL, SBK) arranged into ten blocks of two plots each. Within each block, one plot received ambient rainfall (n=10), and the other was droughted (n=10) during the growing season (April – mid September) using rainfall exclusion shelters that block 66% of rainfall. Drought treatments lasted from 2014 - 2017 at KNZ, HYS, CHY, and SGS and 2013 – 2019 at SBK and SBL, after which shelters were removed and post-drought monitoring continued for 4 years, until 2021 and 2023, respectively. We assessed species composition during the spring and fall of each year using aerial percent cover within four $1m^2$ subplots per plot. At SBK and SBL, we sampled four $1m^2$ subplots from 2012 – 2018 and only two $1m^2$ subplots per plot from 2019 onward.

Data cleaning

All analyses were conducted in R version 4.4.2 (R Core Team, 2025). We excluded 187 subplot level observations with unknown species identification from a total of 73046

observations. The unknown observations ranged from 1-8% cover, with 87% of the values below 4%. When species identification was not consistent within a site, we consulted site experts to determine whether to lump, split, or remove taxa. We selected the maximum cover of each species within each subplot, in each year (spring or fall) and then filled all missing subplot values for each species with 0 to account for species abundance across space and time.

Calculating spatial and temporal rarity

We quantified each species' spatial rarity (S_R) as $S_R = 1 - percent\_rank(\overline{C_C})$ (**Equation 3.1**), where $\overline{C_C}$ is species' mean cover across all years in all control subplots at a site, using the percent_rank() function in the dplyr package (Wickham et al., 2023). Spatial rarity ranges between 0-1, where values approaching 1 indicate rare species and a values near 0 indicate species with high cover that appear in many plots. We measured temporal rarity (T_R) for all species in control plots by scoring presence in any plot as a 1 and absence as 0 to calculate $T_R = 1 - \frac{\#\ years\ present}{total\ years}$ (**Equation 3.2**). Temporal rarity also ranges from 0-1 where values close to 1 indicate species that are present very few years and 0 indicates species that are present every year. We tested the correlation between spatial and temporal rarity with Pearson's correlation coefficient and found they were correlated, but the correlation varied between sites (**Figure S3.1**; **Table S3.1**). Thus, we retained both metrics in our analyses.

Species abundance typologies

We categorized species into abundance typologies using both spatial and temporal rarity to explore drought responses associated with different rarity types. We considered a species *spatially sparse* if $S_R \geq 0.25$ and *spatially common* if $S_R < 0.25$. Similarly, species were defined as *temporally intermittent* if $T_R \geq 0.5$ and *temporally persistent* if $T_R < 0.5$. Species therefore fall

into four categories: common and persistent species that were not rare on either axis, species that were rare either spatially or temporally but not both (sparse but persistent species, or common but intermittent species), and finally sparse and intermittent species that were rare both spatially and temporally.

Calculating drought and post-drought responses

To assess species' responses to drought and post-drought periods, we calculated a response ratio (Armas et al., 2004): $Response\ Ratio = \frac{C_D - C_C}{C_D + C_C}$ (**Equation 3.3**), where C_D and C_C are the mean cover values of a species in the drought or control treatment, respectively, across all subplots and across all years of the specified drought or post-drought period. This metric ranges from -1 to 1 and is positive when a species' cover in drought plots is greater than controls and negative when a species' cover is lower in drought plots than controls.

We calculated a response ratio for each species at each site over the first four years of the drought period and separately over the four-year post-drought period. As sites differed in drought length (4-years at KNZ, HYS, CHY, SGS; 7-years at SBL and SBK), we also calculated a response ratio over the full 7-year drought period for species at SBL and SBK to confirm that this does not change the outcome (**Figure S3.2**). To assess whether species' differences from control plots declined over the post-drought period, we divided the post-drought period into the first 2 years and the final 2 years and calculated response ratios for each.

Statistical analyses

To test for an overall effect of rarity on a species response during and after drought, we used a linear mixed effects model with rarity as a predictor of response ratio and a random effect of site using the LmerTest package (Kuznetsova et al., 2017). We modeled spatial and temporal rarity

in separate models for both the drought and post-drought periods. We then tested the significance of effects using Type II analysis of variance with the Anova() function in the Car package (Fox & Weisberg, 2019). To explore whether the effects of rarity varied at each site, we ran linear models for each site separately, using separate models for each rarity type and for the drought vs. post-drought periods.

Site level predictors

We obtained long term mean annual precipitation (MAP) and mean annual temperature (MAT) data for each site from Griffin-Nolan et al. (2018). To measure site-level dominance by a single species, we calculated the Berger-Parker dominance of every plot in every year at a site and took the average of these values. We used these predictors in separate linear models testing whether each predictor was related to the slope of the rarity-response ratio relationship at each site. To characterize site level differences in species' growth forms, we calculated the proportion annual vs perennial species for all species at a site and within each abundance typology. For grasses, we also compared the proportion of C_3 vs. C_4 species.

Results

Rarity predicts species' responses during and post-drought

Across all sites there was a general pattern in which rare species, whether calculated spatially or temporally, increased in cover during drought while common species declined (**Figure 3.2A, B, Table 3.2**). This was reflected by higher positive drought response ratios for rarer species and a positive relationship between rarity and change in abundance under drought (**Table S3.2**). Common species declined by approximately 20-30% during drought relative to controls, although the effect varied by site (average intercept among sites: S_R = -0.303, T_R = -0.218). The

combined reduction in common species and increase in rare species aligns with our hypothesis that competitive release allows rare species to increase during drought. Although this was a general trend, individual species varied considerably in their responses, and different life histories had broadly different patterns. Specifically, annual species often increased in cover during and after drought regardless of their abundance, while perennial species drove the overall abundance-based pattern of a decline in common species and increase in rarer species (**Figure S3.3; Table S3.3**).

Post-drought, both spatially and temporally rare species tended to maintain their increased cover in drought plots relative to controls, whereas common species generally continued to respond negatively (**Figure 3.2C, D; Table S3.2**). This sustained increase in rare species post-drought indicates lagged effects post-drought. Common species still had lower cover compared to control levels (intercepts: S_R = -0.23, T_R = -0.13), but intercept values were closer to zero than during drought, indicating some recovery (**Table S3.2**). We did not find a difference between the initial and final two years of the post-drought period (**Figure S3.4**, **Table S3.4**), thus the average across the four years is representative of the lack of recovery.

Lag effects depended on a species' abundance typology.

Spatially and temporally calculated species abundances were positively correlated (**Figure S3.1, Table S3.1**) which may have contributed to the parallel patterns between spatial and temporal rarity and drought response. Spatially common and temporally persistent species were the most likely to have directionally similar direct and lagged responses to drought (whether positive or negative; **Figure 3.3A**). Spatially sparse and temporally persistent species often shared direct and lagged responses to drought, but some that responded negatively during drought returned to, or overshot control abundances (**Figure 3.3B**). In contrast, spatially sparse

and temporally intermittent species, had a wide range of positive and negative responses but no correlation between direct and lagged effects (**Figure 3.3D**). Finally, there were few spatially common, temporally intermittent species, but these species responded positively both during and after drought (with the exception of one species that declined during drought and recovered after) (**Figure 3.3C**).

Site characteristics

Sites spanned a west-east precipitation gradient (**Figure 3.1A**) and north-south temperature gradient (**Figure 3.1B**). Along with the abiotic variation among sites, the biotic communities varied in the average level of dominance (**Figure 3.1C**), the proportion of annual vs. perennial species (**Figure 3.1D, Figure S3.5**) and the proportion of common C_3 vs. C_4 grasses (**Figure 3.1E**). Sites were grouped into mesic, intermediate, and arid categories based on their precipitation level. At mesic sites (KNZ, HYS), nearly all common, persistent species were perennial and most common grasses were C_4. Intermediate sites (CHY, SGS) had a high proportion of common C_3 grasses, but differed in the proportion of common, persistent annual species. Arid sites had relatively high dominance relative to other sites, a high proportion of common, persistent annual species, and all common grasses were C_4.

Responses to rarity differ by site

The effects of spatial and temporal rarity on species' drought responses varied by site (**Figure S3.6**) but did not align with the gradient of MAP as expected (S_R p = 0.706, T_R p = 0.979; **Figure 3.4A, D)**. Rather, the two mesic and two arid sites (KNZ, HYS, SBL, and SBK) had positive slopes that matched the overall trend, while the intermediate precipitation sites, (CHY, SGS) had no relationship between rarity and drought response (**Figure S3.6, Tables S3.5,**

S3.6). Mean annual temperature predicted the slope between rarity and drought response (S_R p = 0.016, T_R p = 0.021; **Figure 3.4B, E; Table S3.7**), likely because the two non-responsive sites were the coldest, while the four responsive sites had similar temperatures (**Figure 3.1B**; **Table 3.1**). Finally, site-level dominance marginally significantly predicted the slope of temporal rarity (S_R p = 0.215, T_R p = 0.086; **Figure 3.4C, F; Table S3.7**), indicating that having a highly dominant species might lead to greater competitive release with drought. Common species responded negatively during drought at three sites (KNZ, HYS, SBK), and showed some recovery at SBK (**Figure S3.6**; **Tables S3.5, S3.6**).

Discussion

Ecological communities are characteristically uneven, with several abundant species and many more low abundance species (Diaz et al., 2021; Fisher et al., 1943). Where a species falls along this continuum may help explain their drought responses, as both frequency dependent responses and traits or adaptations of rare and common species may shape responses (Kleinhesselink & Adler, 2015). We found a general pattern in which rare species - both spatially and temporally - benefited from both the immediate and lagged effects of drought, while common species declined, consistent with species' responses to natural (Prugh et al., 2018) and experimental droughts (Mariotte et al., 2013). The decline in common species cover during drought may result from direct negative effects of a less suitable environment (Gherardi & Sala, 2015) as well as an increase in negative frequency dependence, which can become stronger in drought due to greater competition with conspecifics (Diez et al., 2021). Typically, however, rare species are expected to experience stronger negative frequency dependence (i.e. niche differences) than common species (Comita et al., 2010; Yenni et al., 2012), and therefore should

be less sensitive to changes in other species' abundances (Adler et al., 2012). Our finding that many rare species increased alongside the reduction of common species implies that much of their response was indirect and that heterospecific competition was more limiting to many species than conspecific competition (Kleinhesselink & Adler, 2015).

Species responses were often correlated during and after drought, but this was driven in large part by common, persistent species. Common, persistent species had strongly correlated responses during and after drought with rare exceptions, indicating that strong inertia of these species (Wilfahrt et al., 2023) or lagged effects of drought maintained their altered abundances (Goebel et al., 2011; Gutbrodt et al., 2011; Müller & Bahn, 2022). Rare species - especially those that were both sparse and intermittent - reflected a much wider range of responses during and after drought. Sparse, *persistent* species' responses during and after drought were less correlated than common species, where if they responded positively during drought, they maintained the boost after drought, while some initial negative responders could increase post-drought. In contrast, sparse, *intermittent* species' direct and lagged responses were not correlated. As a group, rare species tend to be more functionally diverse in their traits, life history (i.e. annual and perennial), and photosynthetic strategies (i.e. C_3 and C_4), allowing for a wider breadth of drought tolerance and recovery strategies (Griffin-Nolan et al., 2019; Matos et al., 2021).

We expected that the relationship between rarity and drought response would depend on modal rainfall conditions, where rare species at mesic and intermediate sites experience greater competitive release, while species at arid sites tend to respond negatively regardless of rarity, because they are limited more by abiotic conditions (Louthan et al., 2015). Instead, rare species responses were more associated with endogenous factors such as species growth form and dominant species' responses (Ónodi et al., 2025). For example, annual species are often well

suited to persisting through drought as early maturation allows them to escape drought (Volaire, 2018) and across sites, annual species on average increased during drought regardless of their rarity. At cool, intermediate precipitation sites, many common species were early season C3 annuals and did not have a strong negative response, despite having demonstrated negative responses to water deficits (Ehleringer et al., 1997; Griffin-Nolan et al., 2023), indicating that they avoided the experimentally imposed summer drought (Griffin-Nolan et al., 2019; Knapp et al., 2020). Rarer species therefore did not experience a large release from competition at these sites and had varied positive and negative responses. At mesic and arid sites, common species – particularly perennial grasses – had large relative declines, leaving space for increases in forbs and shrubs, especially sparser species. Dominant grass species' at these sites have different suites of functional traits and drought strategies, but similar productivity responses to soil moisture (Griffin-Nolan et al., 2023). Given that large scale geographic precipitation and productivity data cannot predict species level drought responses, our work has important implications for understanding and predicting how common and rare species within a community respond during and after drought.

Changes to species relative abundances that occurred during the multi-year drought lasted for four years after the drought, indicating persistent shifts in community composition. While it is well documented that plant productivity generally declines during drought (Aguirre et al., 2021; Smith et al., 2024), we show that individual plant species responses can differ from this overall declining trend. We find that sparse and intermittent species increased in cover during drought which may have helped offset productivity declines from the loss of common, persistent species cover in this experiment (Yu et al., 2025). Sparse and intermittent species had a wider range of drought responses and showed more plasticity in their ability to adapt and recover from

drought. On the other hand, the majority of common, persistent species did not recover as readily post-drought. Our work highlights that rare (sparse and intermittent) species are as important as common, persistent species within a community since rare species make significant contributions to community productivity during and after drought. Without parsing the relative productivity contributions of rare and common species during and after drought, the important role of rare species in maintaining ecosystem functioning would be missed. Our work highlights that rare species can buffer against environmental stressors that result from climate change (Mouillot et al., 2013), and can contribute to the productivity and functional diversity of a community.

Figures

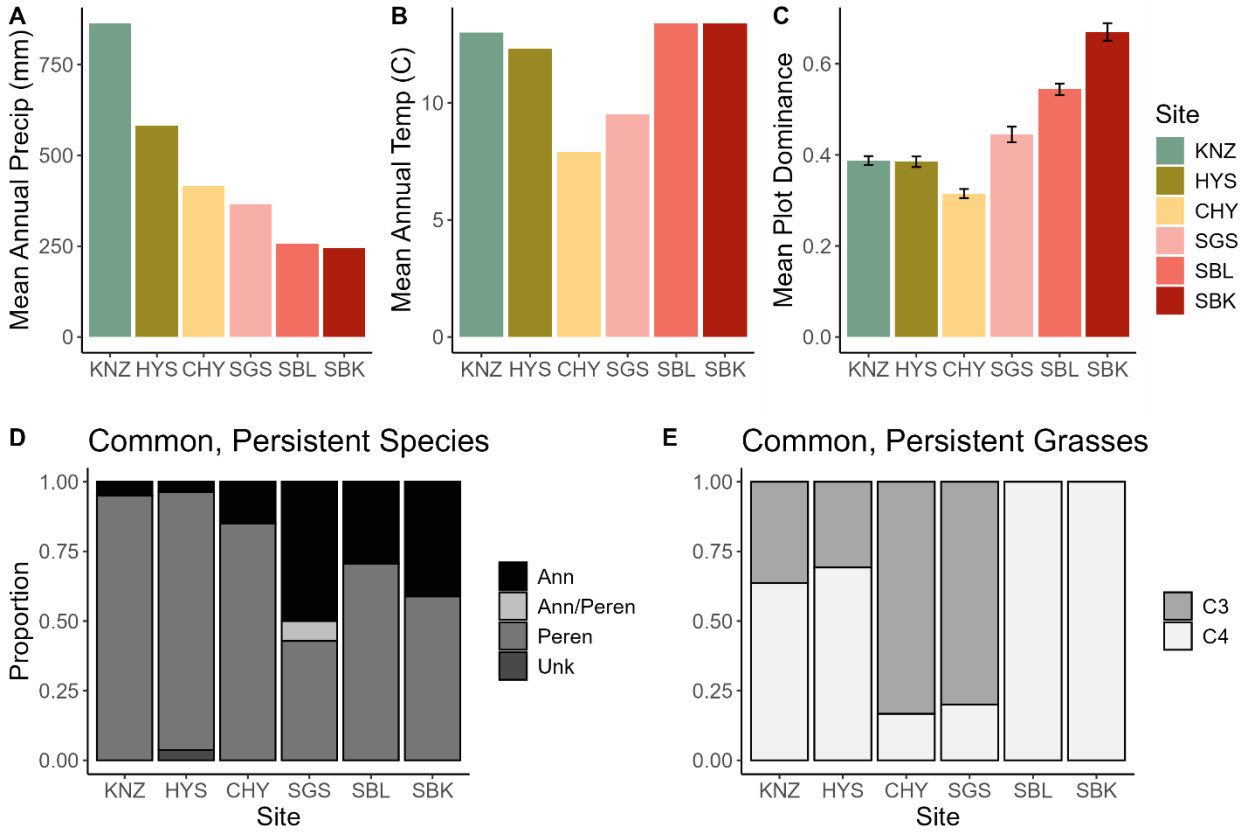

Figure 3.1. Abiotic and biotic characteristics of the six Extreme Drought in Grasslands Experiment sites. The mean annual precipitation in mm (A), mean annual temperature in ºC (B), and mean plot Berger-Parker dominance (C) at each site. The proportion of common, persistent

species in each life history category by site (D) and the proportion of common, persistent grasses with C_3 or C_4 photosynthetic pathways (E). Ann = Annual, Peren = Perennial, and Unk = Unknown.

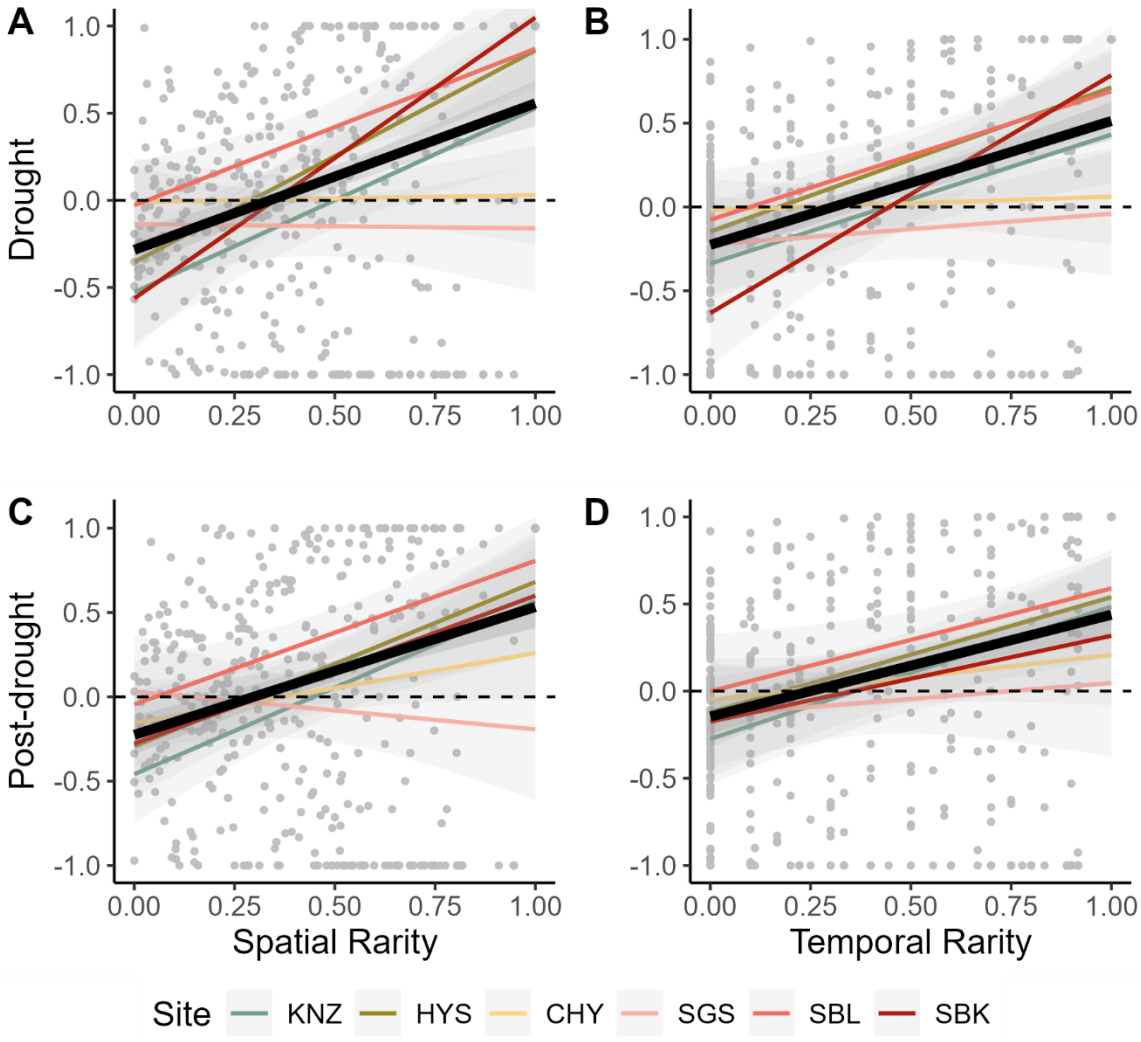

Figure 3.2. The effect of spatial (A, C) and temporal (B, D) rarity on a species' response ratio values during drought (A, B) and post-drought (C, D). Each point shows one species. Black lines indicate the overall response, while colored lines indicate site responses. Positive values of the response ratio indicate a species' cover is greater in drought plots than controls and negative values are when a species' cover is lower in drought plots than controls (**Equation 3.3**). Spatial or temporal rarity values near 1 indicate a species is rare and values near 0 indicate a common species. Linear model results can be found in **Table 2**.

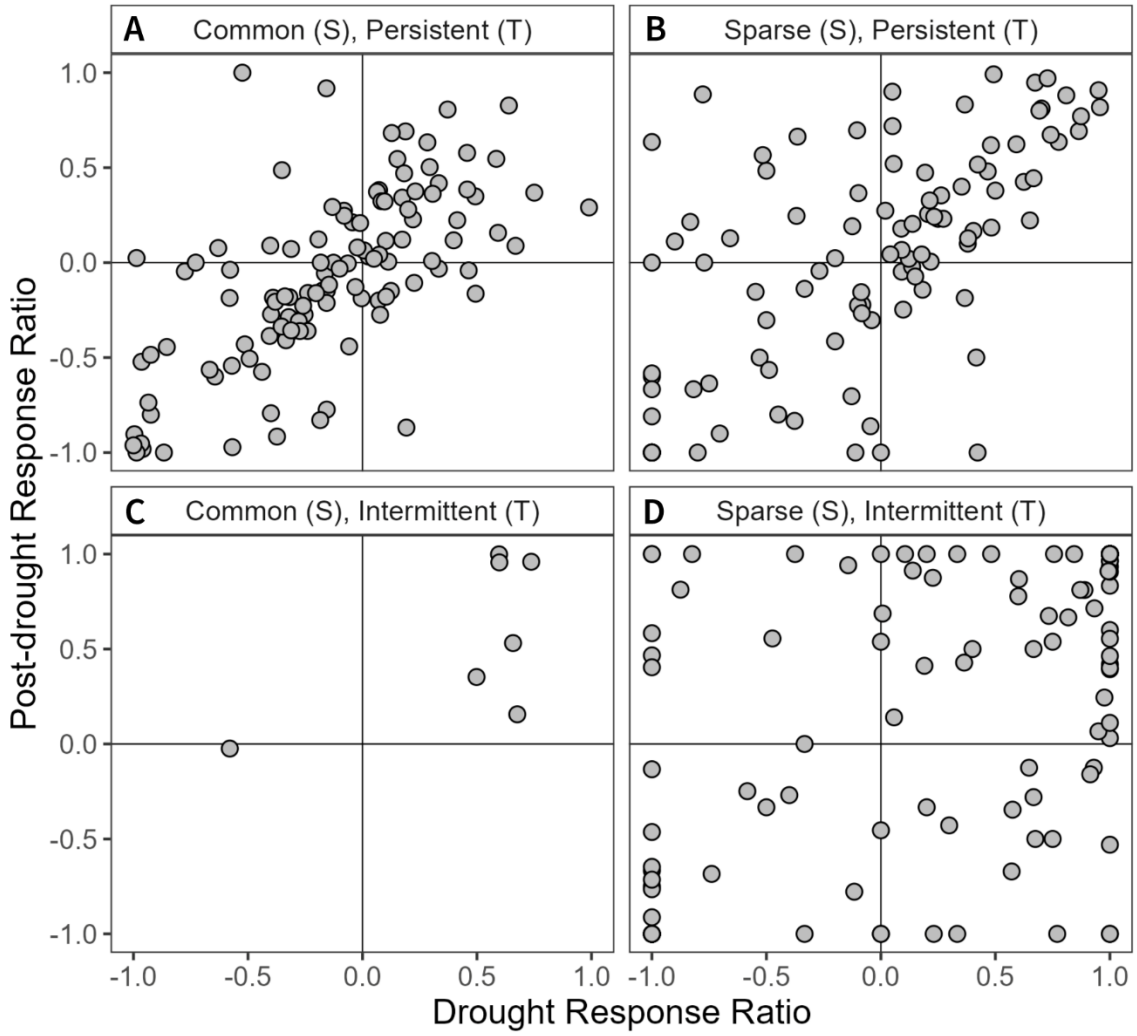

Figure 3.3. The drought response ratio plotted against the post-drought response ratio for each species, separated into panels by their spatial and temporal rarity. Species are defined as being spatially sparse if they have a spatial rarity value (1 – percent rank) greater than 0.25 and spatially common otherwise. Species are defined as temporally intermittent if they have a temporal rarity value greater than 0.5 and temporally persistent otherwise.

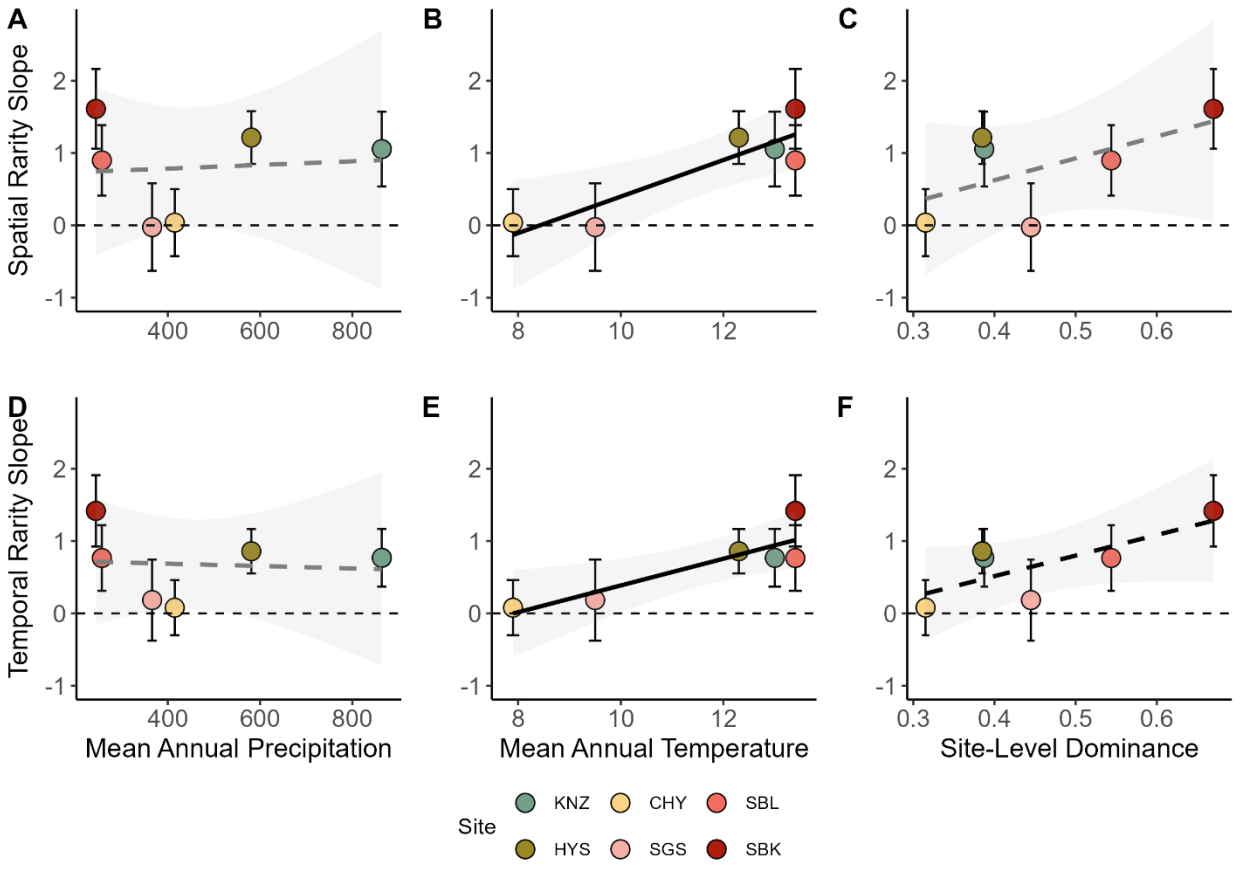

Figure 3.4. Slopes from linear models testing the effect of spatial rarity (top row) and temporal rarity (bottom row) on the response ratio during drought as a function of site predictors: mean annual precipitation (mm) (A, D), mean annual temperature (ºC) (B, E), and the average Berger-Parker dominance at a site (C, F). Line type and color indicate significance: Solid black lines = significant, dashed black lines = marginally significant, and gray dashed lines = non-significant. Error bars on points show the 95% confidence interval and point color indicates site.

Tables

Table 3.1. Characteristics of the six grassland sites from the Extreme Drought in Grasslands Experiment used in this study.

Site Code	Grassland type	MAP (mm)	MAT (C)	Site dominance	Dominant species
KNZ	Tallgrass	864	13	0.39	*Andropogon gerardii, Sorghastrum nutans*
HYS	Mixed-Grass	581	12.3	0.38	*Bouteloua curtipendula, Schizachyrium scoparium, Sporobolus asper*

Table 3.1. (continued)

Site Code	Grassland type	MAP (mm)	MAT (C)	Site dominance	Dominant species
CHY	Mixed-Grass	415	7.9	0.31	*Bouteloua gracilis, Carex Eleocharis*
SGS	Shortgrass	366	9.5	0.42	*Bouteloua gracilis, Elymus elymoides*
SBL	Shortgrass	257	13.4	0.54	*Bouteloua eriopoda, Bouteloua gracilis*
SBK	Desert	244	13.4	0.67	*Bouteloua eriopoda, Kallstroemia parviflora*

Mean annual precipitation (MAP) and mean annual temperature (MAT) were obtained from Griffin-Nolan et al. (2018).

Table 3.2. Type II ANOVA table for linear mixed effects models testing rarity as a predictor of response ratio with a random effect of site.

	Coefficient	F	Df	Df.res	Pr(>F)	
Drought	Spatial	70.79	1	386	<0.001	***
	Temporal	72.05	1	389	<0.001	***
Post-Drought	Spatial	56.05	1	404	<0.001	***
	Temporal	44.64	1	362	<0.001	***

Bridge

In Chapter III, I highlight how an extreme drought led to different species' responses depending on a species' spatial and temporal abundance. Diverse species responses to the environment are the foundation of asynchronous dynamics among species in a community, which drive overall community stability (Valencia et al., 2020). The asynchronous increase in rare species may have buffered total cover to declines in common species in this experiment (Yu et al., 2025). In Chapter IV, I test how asynchronous responses among species, as well as two other community dynamics shape stability over multiple droughts and in tandem with herbivores.

CHAPTER IV.

HERBIVORY AND DROUGHT REDUCE THE TEMPORAL STABILITY OF HERBACEOUS COVER BY INCREASING SYNCHRONY IN A SEMI-ARID SAVANNA

From Ebel, C. R., Case, M. F., Werner, C. M., Porensky, L. M., Veblen, K. E., Wells, H. B. M., Kimuyu, D. M., Langendorf, R. E., Young, T. P., Hallett, L. M. 2022. Herbivory and Drought Reduce the Temporal Stability of Herbaceous Cover by Increasing Synchrony in a Semi-arid Savanna. *Frontiers in Ecology and Evolution*.

Contributions

CE led analysis and writing. MC, CW, and LH assisted in analytical methods. TY, KV, DK, and LP designed, implemented, and maintained the KLEE plots. All authors contributed to the article, interpretation of results, manuscript envisioning, editing, and approved the submitted version.

Introduction

Ecological stability–the tendency of aggregate community properties such as primary productivity to be stable through time–is a key metric for understanding ecosystem dynamics and predicting responses to a changing environment. Stability can be shaped by bottom-up processes, for instance when ecosystem properties like primary productivity and total vegetative cover directly track environmental resource fluctuations (Craine et al., 2012; La Pierre et al., 2011; Power, 1992). At the same time, stability can be structured by top-down processes, such as when episodic herbivory temporally shifts plant investment in productivity, or when the effect of

herbivory shifts seasonally (Hairston et al., 1960; Porensky et al., 2013; Van Langevelde et al., 2003). However, top-down processes remain understudied relative to environmental variability. Finally, stability can be influenced by dynamics among species within the community. Biotic stabilizing mechanisms occur when species dynamics result in a community that is more stable than predicted by external variability. The presence of such dynamics complicates assessment of the impacts of bottom-up and top-down drivers; beyond their direct impacts on the stability of ecosystem properties, we must also consider indirect effects via influences on species composition and community dynamics.

Multiple biotic stability mechanisms can contribute additively or differentially toward the stability of aggregate community properties (Lehman & Tilman, 2000). These include: (a) asynchronous dynamics, also known as compensatory dynamics, where declines in one species are compensated for by a rise in another, (b) stable dominant species, where aggregate stability depends on a few dominant species with high population stability, or (c) species richness driving portfolio effects, in which the community property is distributed among multiple species in a diverse community (especially when asynchronous). A growing body of work has highlighted that biotic stability mechanisms depend on the environmental context, with most studies exploring this in relation to bottom-up resource dynamics (Grman et al., 2010; Hallett et al., 2014; Hautier et al., 2020; Xu et al., 2014). Biotic stability mechanisms can shift along environmental gradients (Hallett et al., 2014), and resource variability can also cause shifts in mechanisms over time in the same system. For example, drought can both reduce biomass (Alon & Sternberg, 2019; Aroca, 2012; Craine et al., 2012; Grant et al., 2014) and increase variability if production tracks rainfall fluctuations (La Pierre et al., 2011). Both a decline in the mean and

increase in the (relative) variance can decrease the stability of primary productivity and alter the strength of underlying biotic mechanisms (Muraina et al., 2021).

Top-down effects on community stability are also likely mediated by biotic stability mechanisms, but few studies have delineated these mechanistic relationships (Campana et al., 2022; Fu et al., 2021; Liang et al., 2021; Qin et al., 2019). It is well-known, however, that top-down pressure can directly alter both community stability and structure (Beck et al., 2015; Ganjurjav et al., 2019; Riginos et al., 2018; Sankaran et al., 2004). Changes in top-down effects, such as herbivore loss or a reduction of historic herbivory levels, can cause slow, directional compositional change (Porensky et al., 2016, 2017; Riginos et al., 2018), potentially shifting the importance of different biotic mechanisms. For instance, herbivores may reduce asynchronous dynamics by opening space that allows other species to increase synchronously (Porensky et al., 2013), or by limiting temporary pulses of dominant species (Mortensen et al., 2018) that could have produced asynchronous dynamics. Additionally, herbivores may preferentially consume abundant species, thereby freeing resources and space for new species (Borer et al., 2014; Hillebrand et al., 2007; Koerner et al., 2018; Mortensen et al., 2018; Porensky et al., 2013); these effects would reduce dominant species population stability while simultaneously strengthening diversity-associated portfolio effects. Herbivore abundance and the functional composition of herbivore communities also likely influence biotic stability mechanisms, as variation in herbivore pressure and identity each determine the extent of herbivore impacts on plant community composition (Augustine & McNaughton, 1998; Fynn & O'Connor, 2000; Riginos et al., 2018; Veblen et al., 2016).

Most plant communities are simultaneously subject to both bottom-up and top-down control, and we must consider how ecological stability and biotic stability mechanisms respond

to such drivers in tandem. While drought and herbivory may both limit plant production and enhance the variability of production through time (Aroca, 2012; Craine et al., 2012; Gill, 2007; Muthoni et al., 2014), they do so in different ways, and thus their effects on biotic stability mechanisms may sometimes be aligned and sometimes different. Drought occurs episodically in semi-arid grasslands and savannas and affects all species simultaneously, while herbivory continually operates, but may have greater effects on certain plant species than others due to selective herbivory and the diets of different herbivore guilds (Augustine & McNaughton, 1998). We expect both types of disturbance to increase synchrony: fluctuations in year- to year rainfall can drive synchronous dynamics (Tredennick et al., 2017), while herbivory may enhance synchrony by freeing space or resources for less abundant species to increase simultaneously (Porensky et al., 2013). We also expect that drought and herbivory will both negatively affect the population stability of dominant species, as competitive dominant species can be especially drought-sensitive (Kardol et al., 2010), and as herbivores preferentially consume all of the dominant species in this system (Odadi et al., 2013). While we expect drought and herbivory will produce similar effects on synchrony and population stability, we expect that their effects on species diversity and the portfolio effect will be opposing. Specifically, selective herbivory of the dominant species may provide opportunities for subordinate species to thrive and thus increase richness (Bråthen et al., 2021; Koerner et al., 2018; Porensky et al., 2013). On the other hand, we expect the reduction in water availability with drought will reduce species richness (Adler & Levine, 2007; Harrison et al., 2018). As a result, the combination of drivers may jointly sum to produce a greater effect on stability than either alone when they have similar effects on a biotic mechanism, or they may buffer impacts of the other if their effects on a particular mechanism differ.

Here, to investigate how drought and herbivory affect stability and its underlying mechanisms, we leverage the Kenya Long-Term Exclosure Experiment (KLEE), which has measured plant responses to six levels of herbivory from experimental combinations of domestic and wild large mammalian herbivores across 22 years, including multiple drought events. Because drought is a temporal phenomenon, we calculated stability and biotic mechanisms over a moving window and assessed stability at different temporal scales. We first hypothesized that (H1) drought and herbivory would both reduce the stability of herbaceous cover (Figure 1). Second, we hypothesized that (H2) the importance of different biotic stability mechanisms would depend on drought and herbivore pressure (Figure 1). Specifically, we expected that (2a) Asynchronous dynamics would decrease with drought and herbivore pressure, (2b) drought and herbivory would reduce the population stability of the palatable, dominant species, and (2c) species richness and the portfolio effect would decrease with drought but increase with the intensity of herbivory. Finally, we hypothesized that (H3) the effects of drought and herbivory on stability would be mediated by these biotic mechanisms (Figure 1). Consistent with the broader literature on biotic stability mechanisms, we hypothesized that (3a) stability would increase with increasing asynchronous dynamics (Valencia et al., 2020), (3b) stability would increase with dominant species population stability (Sasaki & Lauenroth, 2011; Yang et al., 2017), and (3c) stability would increase with species richness and the portfolio effect (Thibaut & Connolly, 2013).

Methods

Site and Experiment Description

We analyzed the temporal stability of herbaceous cover in the Kenya Long-term Exclosure Experiment (KLEE), located on the Mpala Ranch and Conservancy (0◦17' N, 36◦52' E; 1,800 m asl) in Laikipia, Kenya. During our study period (1999–2020), rainfall at the site averaged 605 ± 39 mm/year (mean ± SE; range 351–1,009 mm/year). The study site is a semi-arid savanna ecosystem underlain with nutrient-rich vertisols (black cotton soils) with >50% clay content and >30% sand content (Young et al., 1997) and dominated by the tree *Acacia drepanolobium* (syn. *Vachellia drepanolobium*) and five grass species: *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Brachiaria lachnantha* (Hochst.) Stapf. (Porensky et al., 2013). Mpala supports a diverse variety of native herbivores and is managed for both livestock production and wildlife conservation (Young et al., 1997).

The KLEE plots were established in 1995 and use semipermeable barriers to create six replicated herbivore exclosure treatments arranged in three blocks (North, Central, and South), each with six 200 × 200 m plots, for a total of 18 plots with 3 treatment replicates. Treatments are composed of combinations of three herbivore groups: wild mesoherbivores (15–1,000 kg, e.g., zebras, gazelles), wild megaherbivores (giraffes and elephants), and cattle. Treatment combinations and abbreviations are as follows: O = all large herbivores (>15 kg) excluded, W = wild mesoherbivores present, C = cattle present, WC = cattle and wild mesoherbivores present, MW = megaherbivores and wild mesoherbivores present, MWC = all herbivores present. Cattle are grazed in C, WC, and MWC plots in groups of 100–120 for 2 h on each of two to three consecutive days, typically three to four times per year. At the moderate cattle stocking rates

applied to our experimental plots, plant community composition corresponds more to herbivory intensity than herbivore identity (Charles et al., 2017; Riginos et al., 2018; Veblen et al., 2016), although this is not the case at high cattle stocking rates (Wells et al., 2022). Across treatments, herbivore pressure increases from lowest to highest in the order of O, W, MW, C, WC, MWC, based on estimates of herbivore densities and body mass per unit area (from Veblen et al., 2016): all wild mesoherbivores = 730 kg/km2, all megaherbivores = 880 kg/km2, and cattle = 4,740 kg/km2 (Augustine, 2010; Georgiadis et al., 2007; Veblen et al., 2016). While the cattle stocking rate is moderate relative to pastoral areas, which are increasingly devoid of wildlife, it is high relative to wildlife densities, which is common. See Young et al. (1997) and Veblen et al. (2016) for more site and experimental details.

Sampling

Aerial herbaceous vegetation cover data was collected annually in June following the March–May primary rainy season in the central hectare of each of the 18 KLEE plots. Each central hectare is divided into a 10 × 10 grid of 100 sampling stations spaced 10 m apart, and at sampling stations aerial plant cover and composition were assessed by counting the number of pins hit by each species over a 10-point pin frame, with vertical pins separated by 5 cm. Only the first hit per pin was recorded for each species (i.e., a maximum of 10 hits per pin frame per species) to assess aerial cover. All 100 grid points were sampled from 1999 to 2005. From 2006 to 2020, every fifth grid point was sampled for the five dominant grasses and alternate grid points (i.e., 50) were sampled for less common species.

Data Analysis

All analyses were carried out in R version 4.1.2 (R Core Team, 2021). We used herbaceous cover data from 1999 to 2020 in our analyses. For years 1999 and 2003 where data from surveys following the March-May primary rainy season were missing, we used data from September 1999 and February 2003 surveys as the species composition remained similar between 1999–2000 and 2002–2004 (Riginos et al., 2018). We accounted for subsampling of dominant species, by expressing all values as the number of first hits per 500 pins (10 pins x 50 sampling locations). The raw first hits for the dominant species were multiplied by 2.5 (50/20 sampling locations) for post-2006 data, while first hits of all other species were left as row values. Pre-2006 data were subsampled to account for the change in sampling effort. We removed rare species (<5% cover) and bare ground pin hits (i.e., when no plants were hit by a pin) (see Veblen et al., 2016; Riginos et al., 2018 for more details). Total cover was calculated as the sum of all individual pin hits in a plot, excluding bare ground and rare species, and could sum to >100% cover.

Calculating Stability and Biotic Mechanisms Over the Full Timeseries

We used herbaceous cover data to calculate the temporal stability of the aggregate community (S_c) as $S_c = \frac{\mu}{\sigma}$ (the inverse of the coefficient of variation), where $\boldsymbol{\mu}$ is the temporal mean of total cover, divided by the standard deviation, $\boldsymbol{\sigma}$ (codyn package; (Hallett et al., 2016)). To characterize the three biotic stability mechanisms, we used the following metrics: (1) the variance ratio as a measure of *asynchronous dynamics*, (2) the mean population stability of five dominant species as a measure of *dominant species population stability*, and (3) species richness as a measure of the *portfolio effect*.

Asynchronous dynamics: We used the classic variance ratio (VR) to measure asynchronous dynamics, which compares the variance of the aggregate community (C) to the variance expected with independent species population fluctuations (P_i) (Peterson, 1975; Schluter, 1984).

$$VR = \frac{var\ (C)}{\sum_{i=1}^{n} var\ (P_i)}$$

where

$$var(C) = \left[\sum_{i=1}^{n} var(P_i)\right] + 2\left[\sum_{i=1}^{n}\sum_{j=1}^{n} cov(P_i P_j)\right]$$

A variance ratio >1 indicates synchronous dynamics, and <1 indicates asynchronous (or compensatory) dynamics (Schluter, 1984). We calculated the variance ratio for all species in the community and additionally for the five most abundant species, hereafter the dominant species. Dominant species (*B. lachnantha*, *P. stramineum*, *L. nutans*, *T. triandra*, and *P. mezianum*) were identified from Porensky et al. (2013) as the species composing 85% of herbaceous cover. To investigate the effects of timescale on asynchrony, we used the timescale specific variance ratio which decomposes the classic variance ratio into timescales of distinct contributions (Zhao et al., 2020).

Dominant species population stability: We calculated population temporal stability (Sp) as $S_p = \frac{\mu}{\sigma}$, where μ is the temporal mean of a species' cover divided by the standard deviation, σ, for each of the five dominant species individually. We then used the average of all five dominant species' population stability values in analyses.

Portfolio Effect: We calculated species richness as the number of unique species present at all sample points in the 1-hectare sampling area. To verify that species richness enhanced the

portfolio effect in this system, we used Taylor's power law, $\sigma^2 = c\mu^z$, where σ^2 is the variance in species abundance, μ is the mean species abundance, and c and z are constants (Taylor, 1961). The portfolio effect is enhanced by species richness when the variances in species abundances increase more steeply than their mean abundances, or when z > 1 (Doak et al., 1998a; Tilman, 1999). At our site, z = 1.95, so we used species richness as a measure of the portfolio effect in analyses. The fit was slightly sublinear for this model (Supplementary Figure S1), suggesting that dominant species are more stable than expected from a classic Taylor's power law and underscoring the potential importance of dominant stability for overall stability.

Moving Window Calculations

While we expected that aggregating across the full time series would provide the most complete picture for comparisons among herbivore treatments, analyzing the influence of drought required a time-varying approach and careful attention to the choice of time scale. To explore whether stability and the stabilizing effect of different biotic mechanisms varied over time in relation to drought events, we calculated stability, biotic mechanisms, and a drought score over a moving window. Moving window analyses entail taking a subset (window) of the data of a particular number of years and calculating a given metric over this window. The starting point of the window is then shifted one time point until the whole data set has been covered. To assess sensitivity to the choice of time scale, we repeated our analyses with different sized windows (ranging from 5 to 21 years) to assess variation in stability and biotic mechanisms over the temporal scale of calculation (**Supplementary Figure S4.2**). We compared the relationship between stability and biotic mechanisms at 5-, 10-, and 15-year window sizes because these correspond to approximately a quarter, half, and three-quarters of our time series, similar to the approach in (Bueno de Mesquita et al., 2021). The window sizes included enough

years in the window to calculate all metrics, had enough windows to examine trends over the 22-year time series, and allowed us to visualize shorter term fluctuations in stability and mechanisms vs. longer term trends. The responses of stability and its underlying mechanisms to herbivore treatments were consistent across timescales, indicating that the patterns we see are robust to timescale (**Supplementary Figure S4.2**). Further, relationships between stability and synchrony, population stability, and richness were similar over the different timescales (**Supplementary Figure S4.3**). Thus, we chose to retain only the 10-year window size for further analyses as this balanced capturing variability through time with reducing the noise from the shorter time windows. We also include results from the full time series for comparisons of herbivore treatments alone, but any analyses involving drought (examining the effects of drought alone, or in combination with herbivore treatments in a multiple regression or structural equation modeling approach) use 10-year moving-window metrics because drought effects had to be examined in a time-varying way.

Calculating Drought and the Drought Score

We calculated rainfall on an annual basis using the total rainfall over 12 months starting in July of the previous year through June of the sampling year (e.g., July 2005–June 2006 for the sampling that took place in June 2006). The timeframe was adjusted for years 1999 and 2003 to cover the 12 months before each respective (non-June) sampling period. The total rainfall varied from 211 to 1,082 mm in these defined periods and drought was classified as a rainfall value in the first quartile (≤494 mm rain). We identified droughts as those preceding the 2000 (350 mm), 2006 (373 mm), 2008 (458 mm), 2009 (484 mm), 2014 (490 mm), and 2017 (211 mm) sampling periods (**Figure 4.2A**). These drought years align with droughts identified by season in Riginos

et al. (2018) and match periods where there was compositional change in the plant community (Riginos et al., 2018).

Our timeseries contained multiple drought events occurring at variable intervals, making it difficult to parse the effects of individual droughts on stability. As such, we chose to define a metric of drought impact for any given period of years. Our metric addresses three considerations: (1) the number of droughts in the period of time, assuming that a greater number of droughts would have a greater impact on the time window, (2) how severe each drought was relative to others, assuming that more severe droughts produce greater impacts, and finally (3) that droughts have lagged effects on the ecosystem (Dudney et al., 2017; Ye et al., 2020).

(1) Calculating the number of droughts: In each time window we assigned years with drought as 1 and all others as 0. Therefore, the number of droughts, N_d, in a window of n years can be written as:

$$N_d = \sum_{i=1}^{n} \begin{cases} 1, if\ drought \\ 0, if\ otherwise \end{cases}$$

(2) Defining drought severity: To approximate the severity of each drought in a window, we calculated the percentile of precipitation values in the first quartile (Q1). In order to bound the severity metric between 0 and 1 and make it inversely proportional to the precipitation amount, we defined drought severity as:

$$S = 1 - \frac{p - 1}{d}$$

where p is the precipitation percentile, and d is the number of divisions in the first quartile (here 25 as we chose to use percentiles). Finally,

(3) accounting for lagged effects: We considered lagged effects (L) only in the year after a drought and set the magnitude as half that of a drought year. We scored years by whether there was a drought in the previous year and if so, multiplied severity (S) by 1⁄2 assuming that the effect will not be as large as the year in which the drought occurred, such that:

$$L = \sum_{i=1}^{n} \begin{cases} \frac{1}{2}, if\ after\ drought \\ 0, if\ otherwise \end{cases}$$

Drought score (Ds) is comprised of these three functions (divided by n years to normalize the function):

$$D_S = \frac{\sum_{i=1}^{n} \begin{cases} 1\text{x}\left(1 - \frac{p-1}{d}\right), if\ drought \\ \frac{1}{2}\text{x}\left(1 - \frac{p-1}{d}\right), if\ after\ drought \\ 0, if\ otherwise \end{cases}}{n}$$

When calculated over each 10-year window used in the main moving window analyses, the drought score ranged from 0.076 (less severe drought) to 0.216 (more severe drought).

Linear Mixed Effects Models

We analyzed whether overall stability and component biotic mechanisms were affected by drought and herbivore treatment, using linear mixed effects models due to repeated sampling of plots through time (lme4 package; (Bates et al., 2015)). We used metrics calculated over the full time series to separately model (1) stability, (2) the classic variance ratio, (3) dominant species average population stability, and (4) species richness as functions of three herbivore groups: cattle, mesoherbivores, and megaherbivores, with block as a random effect. Similarly, we analyzed whether stability and component biotic mechanisms were related to the drought score

and herbivore treatment, using data from the 10-year moving window calculations in sets of linear mixed effects models. We separately modeled (1) stability, (2) the classic variance ratio, (3) dominant species average population stability, and (4) species richness as functions of drought score and the three herbivore groups: cattle, mesoherbivores, and megaherbivores, with block and plot as separate random effects. To select models with the best predictors, we compared the Akaike Information Criterion with correction for small sample sizes (AIC_c) values between models with all factorial combinations of predictors and a null model. We evaluated whether our data fit the assumptions of this analysis by plotting the residuals vs. fitted values and checking the normality of residuals using a q-q plot.

To investigate which biotic mechanisms were the strongest drivers of temporal stability, we used a set of linear mixed effects models analyzing stability as a function of the classic variance ratio, dominant species average population stability, and species richness, with block as a random effect and no interactions between predictors. Before including predictors, we compared the correlation between all pairs of the three variables using Pearson's correlation test. No significant correlations were found (Pearson r values from −0.21 to 0.25), so we retained all three mechanisms as predictors. We selected the best set of predictor variables by comparing AIC_c values of models with all possible subset combinations of predictors.

Structural Equation Modeling

We examined our a priori hypothesized causal pathways between drought, herbivory, biotic mechanisms, and stability (**Figure 4.1**) using a piecewise structural equation model (SEM) (package piecewiseSEM,(Lefcheck, 2016)). We investigated Pearson's correlation coefficients (**Supplementary Figure S4.4**) and checked for multicollinearity using variance inflation factors (VIFs). There was minimal concern over multicollinearity as the greatest VIF in all three

structural equation models was 1.79 (**Supplementary Table S4.1**) and generally, VIFs >5 indicate multicollinearity (James et al., 2013).

We modeled each of the three herbivore groups (mesoherbivores, megaherbivores, and cattle) in separate structural equation models so that herbivory could be coded numerically as a binary presence (1) or absence (0) of a particular herbivore group, as models with a categorical variable of more than two levels prohibit simple interpretation. With the piecewiseSEM package, we combined a series of multiple regressions predicting stability and the three biotic stability mechanisms, each fitted using lme4 with block as a random effect. For the regression model predicting stability, we removed the random effect of block as it did not explain any extra variance and caused singularity issues. All variables used in models were calculated over the 10-year moving window. The overall model fit was determined by testing the significance of pathways that were not included, where a well-supported model has a high Goodness-of-Fit p-value. Among our unincluded pathways, we identified significant relationships (test of directed separation, $p < 0.05$) between population stability and the variance ratio in the Cattle and Megaherbivore SEMs. Although this was identified as a missing pathway in two of our models, we did not change our structural equation models to include them as there was not a strong a priori hypothesized reason for doing so and it is likely a result of a small but significant correlation between the variance ratio and population stability, $r = -0.159$ (**Supplementary Figure S4.4**). Model coefficients can still be interpreted.

Standardized coefficients were calculated for each pathway using scale standardized coefficients (b), where the unstandardized coefficient (β) was scaled by the ratio of the standard deviation of x over the standard deviation of y, $b = \beta * (\frac{sd_x}{sd_y})$. For the herbivory, the coefficients represent the change in y as x changes from state "0"– particular herbivore group not present, to

the other state "1"–herbivore group present. We calculated indirect effects, by multiplying the standardized coefficients of significant paths along an effect. Marginal and conditional R^2 values represent the variance explained by fixed effects alone and the variance explained by both fixed and random effects (Nakagawa et al., 2017).

Results

Total cover fluctuated through time after an initial recovery from pre-treatment levels (**Figure 4.2B**). Treatment differences in total cover remained mostly consistent through time, and treatments followed the same fluctuations, with sharp drops in total cover during droughts, even in plots with few (W) or no (O) large herbivores (non-excluded herbivores included rodents, hares, and small <15kg ungulates). Species richness also varied through time (**Figure 4.2C**). It was not consistently ordered by herbivore pressure, although when richness sharply increased after dry periods, treatments that included wildlife had the greatest plant species richness (**Figure 4.2C**).

Bottom-Up and Top-Down Control of Stability

Consistent with H1, the temporal stability of total herbaceous cover declined with both drought and increasing herbivore pressure (**Figure 4.3**). Stability was negatively associated with greater drought score values (periods with more frequent or severe droughts) when calculated over the 10year moving window ($\beta = -7.28$, **Figure 4.3A**, **Table 4.1**). The mean total cover (**Supplementary Figure S4.5A**) and variance (**Supplementary Figure S4.5B**) also declined with drought. Declines in stability (10-year) were associated most strongly with the presence of cattle ($\beta = -1.62$) and mesoherbivores ($\beta = -0.91$) judged by inclusion in the top model (**Supplementary Tables S4.2, S4.3**). The other highly ranked models (within 2 Δ AIC_c of the

lowest AIC_c model) included megaherbivores, indicating some support for the hypothesis that all herbivore groups impact stability (**Supplementary Tables S4.2, S4.3**). Stability over the full time series also declined with herbivory (**Figure 4.3B, Table 4.1**) and had three models (37.5% of all models) within 2 Δ AIC_c. The preferred model (simplest model within 2 Δ AIC_c of the lowest AICc model) included only cattle ($\beta = -0.92$), but other top ranked models included mesoherbivores and megaherbivores also (**Supplementary Tables S4.2, S4.3**). The mean total cover (**Supplementary Figure S4.6A**) and variance (**Supplementary Figure S4.6B**) also declined with herbivore pressure, with the highest values in the herbivore exclusion treatment to lowest in the mesoherbivores + cattle treatment. Although treatments with greater herbivory did not vary as much in terms of absolute magnitude over time (had lower variance in herbaceous cover), this was outweighed by reductions in mean cover that led to lower relative stability overall.

Bottom-Up and Top-Down Control of Biotic Stability Mechanisms

Asynchronous dynamics (i.e., patterns of synchrony) were altered by both top-down and bottom-up drivers. Periods with a higher drought score (indicating more frequent or severe droughts) were generally associated with greater synchrony (variance ratio > 1; $\beta = 3.48$), supporting H2a that drought would increase synchrony **(Figure 4.4A, Table 4.2, Supplementary Table S4.4**). On average, the variance ratio of the full community increased from weak asynchronous dynamics in the herbivore exclusion treatment to synchronous dynamics in the higher herbivory treatments, also consistent with H2a that herbivory would increase synchrony (**Figure 4.4B**). Specifically, cattle ($\beta = 0.61$) and megaherbivores ($\beta = 0.52$) had a positive relationship with synchrony when calculated over the full time series (**Table 4.3**), while cattle ($\beta = 0.61$) and mesoherbivores ($\beta = 0.46$) had a positive relationship with synchrony

over the 10year moving windows (**Table 4.2**). The variance ratios of just the five dominant species showed similar responses to herbivore treatment (**Figure 4.4B**) but were on average less synchronous than the full community and four of six treatments (O, W, MW, and C) showed asynchronous dynamics (variance ratio < 1, **Figure 4.4B**).

Synchronous and compensatory dynamics varied by timescale in all herbivore treatments. At short timescales (< 4 years), synchrony dominated in all treatments (O = 1.66 to WC & MWC = 3.19, **Supplementary Figure S4.7**). Long timescales (> 4 years) ubiquitously had lower variance ratios than short timescales, where there were weak compensatory dynamics in the lowest grazing treatments (O = 0.854, W = 0.763), and all other herbivore treatments showed synchronous dynamics (**Supplementary Figure S4.7**). The timescale specific variance ratio followed the same pattern as the classic variance ratio, where increased herbivory was associated with increased synchronous dynamics.

The mean population stability of dominant species did not vary significantly between herbivore treatments when averaged across the time series (**Figure 4.4D, Table 4.3, Supplementary Table S4.5**). However, over a 10-year window, cattle negatively affected stability ($\beta = -0.47$), providing mixed support for H2b and suggesting that the influence of herbivory on population stability may depend on the timescale of calculation (**Figure 4.4C, Table 4.2, Supplementary Table S4.4**). The preferred model (simplest model within 2 AIC_c of the lowest AICc model) included only cattle, but other highly ranked models included mesoherbivores and the drought score, indicating some support for the hypothesis that these factors also impact dominant species stability (**Supplementary Tables S4.3, S4.4**).

Species richness was significantly negatively associated with drought score ($\beta = -6.73$; **Figure 4.4E, Table 4.2, Supplementary Table S4.4**) and positively associated with

mesoherbivores (β = 1.32; Table 3, **Supplementary Table S4.5**), generally supporting H2c that richness would decline with drought and increase with herbivore intensity, but with different responses to specific herbivore treatments than were predicted. Species richness did not vary linearly along the gradient of herbivore pressure but did vary more predictably with herbivore diversity. Treatments with the lowest herbivore species richness (O and C) also had the lowest plant species richness (O = 19.2 and C = 19.3), while the most diverse herbivore treatment had the greatest plant species richness (MWC = 21.0; **Figure 4.4F**).

Biotic Stability Mechanisms as Predictors of Overall Stability

As hypothesized in H3a and H3b, temporal stability was negatively associated with synchrony (β = −1.11; **Figure 4.5A**) and positively associated with the mean population stability of dominant species (β = 0.92; **Figure 4.5B**). Synchrony and population stability together predicted temporal stability better than either mechanism on its own (**Table 4.4**). In contrast with H3c, richness did not predict stability (**Figure 4.5C**); instead, the variance ratio and dominant species population stability together were the best predictors (Table 4, Supplementary Table S6).

Timescale

To assess the sensitivity of our findings to the choice of timescale, we evaluated metrics of stability and biotic mechanisms across timescales ranging from 5-year moving windows to the full 22-year time series (**Supplementary Figure S4.2**), and examined all bivariate relationships for 5-year, 10-year, and 15-year windows (**Supplementary Figures S4.3, S4.8, S4.9**). The responses of stability and biotic mechanisms to herbivore treatments were consistent across timescales (**Supplementary Figure S4.2**). Stability, synchrony, and population stability values declined as they were calculated over larger window sizes, but the relative ordering of these

response variables with respect to herbivore treatment was consistent regardless of window size (**Supplementary Figure S4.2**). The relationship between drought and stability was negative across all three window sizes (**Supplementary Figure S4.8**). The 15-year moving window had the weakest relationship likely because the window was large enough to average over trends (**Supplementary Figure S4.8C**). The total herbivore exclusion treatment was decoupled from this trend in the 5-year window analysis; at high drought score values it also had high stability **(Supplementary Figure S4.8A**), which may be due to one instance where it exhibited high resistance to drought (**Figure 4.2B**−2017). The relationship between synchrony (variance ratio) and the drought score were positive at all timescales, although the slope flattened slightly as the timescale increased (**Supplementary Figures S4.9A–C**). There was no relationship between drought and population stability at any timescale (**Supplementary Figures S4.9D–F**), and richness had a negative relationship with drought at all timescales (**Supplementary Figures S4.9G–I**). The relationships between stability and biotic mechanisms remained the same at all timescales (**Supplementary Figure S4.3**).

Relative Importance of All Drivers

To quantify the relative importance of top-down and bottomup drivers as well as their indirect effects, we generated a piecewise structural equation model for each herbivore group: mesoherbivores (**Figure 4.6A, Supplementary Table S4.7**), megaherbivores (**Figure 4.6B, Supplementary Table S4.8**), and cattle (**Figure 4.6C, Supplementary Table S4.9**). These models explained 82 to 84% of the variation in community stability. They confirmed the direct negative effects of drought (standardized coefficient range: −0.134 to −0.116) and herbivory (standardized coefficient range: −0.165 to −0.002). However, the magnitude of direct effects of synchrony (standardized coefficient range: −0.593 to −0.523) and population stability

(standardized coefficient range: 0.498 to 0.575), were always greater than the magnitude of direct drought and herbivory effects. The direct effect of species richness on stability remained nonsignificant except for a small positive effect on stability in the megaherbivore model (standardized coefficient = 0.075). Given the strong direct effects of the plant community on stability, the indirect effects of drought and herbivory as mediated through the plant community were important in determining stability. The indirect effects of drought (standardized coefficient range: −0.148 to −0.130) were similar in magnitude to its direct effects and always mediated through synchrony (**Table 4.5**). In the megaherbivore model, the indirect effects of drought were also mediated through richness. Cattle and mesoherbivore herbivory produced large indirect effects (standardized coefficients: −0.502 and −0.380) relative to their direct effects, mediated through both synchrony and population stability (**Table 4.5**). Megaherbivore herbivory on the other hand, had direct and indirect effects (standardized coefficients: −0.087 and 0.129) that were similar in magnitude and mediated through synchrony and species richness (**Table 4.5**).

Discussion

Unraveling the determinants of ecological stability is a core theoretical and empirical pursuit in ecology with important implications for land management and conservation in a changing world. Here, we explored the effects of herbivory and episodic drought on stability directly and as mediated through biotic stability mechanisms, using a 22-year time series of herbaceous cover data from an herbivore exclusion experiment in a semi-arid savanna. We analyzed stability and biotic mechanisms over a moving window, allowing us to incorporate the effects of periodic drought into temporal stability analyses and understand the top-down and bottom-up drivers of stability through time. Drought and herbivory both directly decreased the

temporal stability of herbaceous cover (**Figure 4.3**) but varied in their effects on mediating biotic mechanisms. Both drought and herbivory increased synchrony (a destabilizing dynamic) while herbivory, but not drought, reduced the population stability of dominant species (**Figure 4.4**). Although both drivers affected species richness, and in contrasting ways (**Figures 4.4E,F**), richness was not significantly associated with overall stability (**Figure 4.5**). Overall, the direct effects of drought and herbivory on stability were smaller in magnitude than their indirect effects mediated through biotic stability mechanisms (**Figure 4.6**).

Grasslands and savannas are disturbance-dependent systems that are frequently described by non-equilibrium dynamics (Bond, 2008; Fuhlendorf & Engle, 2001; Higgins et al., 2000; Riginos et al., 2018) and our findings highlight the dynamic nature of this savanna rangeland system. Here we found that the direct effects of both bottom-up and top-down drivers structured stability. Specifically, drought and herbivory reduced the temporal stability of total herbaceous cover in an additive fashion, supporting H1 (**Figure 4.3**). The relationship between herbivory and stability was particularly strong, and treatments appeared to pair into groups of O and W, MW and C, WC, and MWC (**Figure 4.3B**). Overall, the reductions in stability were largely driven by a reduction in the mean cover (**Supplementary Figures S4.5A, S4.6A**). Although both drivers also reduced the variance in absolute terms (**Supplementary Figures S4.5B, S4.6B**), the relative variance increased because we defined stability as the mean total cover divided by the standard deviation. Drought reduces the total amount of biomass as water stress limits production(Aroca, 2012; Craine et al., 2012; Grant et al., 2014), and also introduces greater variability to the system when production tracks rainfall fluctuations through time (La Pierre et al., 2011). At the same time, temporal variation in herbivore behavior and population dynamics may either buffer or enhance variability in vegetative cover (Abraham et al., 2019; Augustine &

McNaughton, 1998; Fynn & O'Connor, 2000; Staver et al., 2019). Herbivores limit mean total cover by removing plant tissue (Gill, 2007; Muthoni et al., 2014), and may either suppress production by reducing photosynthetic potential and removing nutrients (Sitters et al., 2020) or stimulate productivity when plants compensate for herbivore damage by increasing growth rates (Agrawal, 2000; Knapp et al., 2012; Strauss & Agrawal, 1999). While there is evidence that herbivores increase productivity in this system (Charles et al., 2017), the effect of this on stability was outweighed by tissue removal. Herbivore identity and stocking rate also mattered: cattle and mesoherbivores were the only groups that significantly reduced stability, and cattle had a stronger effect likely because they were stocked at higher biomass densities (4,740 vs. 730 kg/km2). This is consistent with previous findings that total herbivore pressure is a stronger predictor of productivity and shifts in community composition than herbivore identity, but individual herbivore types are more likely to drive variation in productivity across space and time and changes in individual species (Charles et al., 2017; Veblen et al., 2016; Wells et al., 2022).

Although asynchronous dynamics are commonly observed in terrestrial systems(Zhao et al., 2020) but see (Houlahan et al., 2007) and are often a key stabilizing mechanism (Valencia et al., 2020), we observed instead varying levels of synchronous dynamics (defined as variance ratio >1) which appeared to drive the dynamic nature of vegetative cover in this system (**Figures 4.4A,B**). In other words, under no conditions did species asynchrony stabilize herbaceous cover per se, but there was variation in the degree to which synchrony was a destabilizing dynamic, associated with drought and herbivory. Both drought and herbivory indirectly reduced stability by increasing synchrony (**Figures 4.4A,B**): synchronous dynamics increased during time periods with more frequent or severe droughts and in communities experiencing more herbivory,

supporting H2a. Further, these indirect effects were similar to or greater in magnitude than the direct effect of either driver (**Figure 4.6, Table 4.5**). The finding with respect to drought does contrast with other findings across precipitation gradients (a spatial comparison rather than a temporal one), which find that asynchronous (compensatory) dynamics are strongest in places with high precipitation variability–implying that precipitation fluctuations can decrease synchrony rather than increasing it as we found here (Hallett et al., 2014). Dominant species were on average less synchronous than the full community (**Figure 4.4B**), indicating that subordinate species also substantially contribute to community synchrony. This effect is likely attributed to a reduction in palatable dominant species under higher herbivory, which creates space for subordinate species to fluctuate synchronously in response to rainfall variability (Porensky et al., 2013).

Counter to the effects of synchrony, dominant species population stability promoted community stability, especially at low levels of herbivory (**Figures 4.5B, 4.6**). Herbivores commonly influence community structure by preferentially consuming dominant species (Borer et al., 2014; Hillebrand et al., 2007; Koerner et al., 2018; Mortensen et al., 2018; Porensky et al., 2013). We found that the population stability of dominant species declined with increased herbivory, particularly when cattle or mesoherbivores were present. In this system, herbivores consume all of the dominant species, particularly *B. lachnantha* and *T. triandra* (Odadi et al., 2013), likely contributing to the reduction in average population stability. In particular, *B. lachnantha* showed large increases when released from herbivore pressure (Veblen et al., 2016). Contrary to expectations, the population stability of dominant species as a whole did not respond to drought. However, total herbaceous cover and stability did decline during drought periods even as the stability of dominant species did not, implying that drought-related reductions in

stability result more from the response of the community as a whole than from the sensitivity of dominant species. Overall, the stability of total herbaceous cover correlated well with the population stability of dominant species, consistent with previous findings (Grman et al., 2010; Liang et al., 2021).

Although the portfolio effect is often noted as important in determining stability, where more diverse communities have more stable ecosystem properties overall (Hautier et al., 2015; Isbell et al., 2015; Loreau et al., 2021; Yachi & Loreau, 1999), we did not find evidence for this here (**Figures 4.4E,F**), contrary to H3c that species richness would be positively correlated with temporal stability. Indeed, an increasing number of studies find that asynchrony and dominant species stability have a greater influence on stability than richness (Hallett et al., 2014; Muraina et al., 2021; Valencia et al., 2020). The portfolio effect predicts that aggregate ecosystem properties will vary less in diverse communities due to some form of compensatory dynamics and thus, species richness should reduce synchrony (Loreau et al., 2021; Valencia et al., 2020). We included this relationship in our structural equation models but when this pathway was significant (only in the model including cattle herbivory) richness increased synchrony and thus had a small negative indirect effect on stability (**Figure 4.6C**). This phenomenon is likely explained by richness fluctuations in response to the combination of bottom-up and top-down drivers. Species richness declined with drought, a signal that was weakly detected over a 10-year moving window (**Figure 4.4E**) but apparent in the time series (**Figure 4.2C**), and increased transiently when rain followed after drought (**Figure 4.2C**), especially where herbivory opened space for rarer species (Porensky et al., 2013). These transient increases in richness (of rarer species) may contribute to some of the observed synchrony patterns, especially as dominant species were on average less synchronous than the full community (**Figure 4.4B**).

Drivers of stability fluctuate through time, which may produce timescale dependent effects on stability (Clark et al., 2021; Ross et al., 2021; Zelnik et al., 2018). To address the potential effects of timescale on our analyses, we considered stability and its underlying mechanisms at three timescales of 5-, 10-, and 15-year moving windows. In particular, synchronous dynamics are timescale dependent phenomena and our results show that synchrony dominated at shorter timescales (**Supplementary Figures S4.2B, S4.7**), consistent with evidence in grasslands that synchrony is stronger at short timescales, while asynchronous dynamics often dominate at longer timescales (Shoemaker et al., 2022; Zhao et al., 2020). Despite this, stability declined when calculated over longer timescales, likely reflecting the intuitive outcome that including more years in the calculation leads to a higher chance of including more variation. Even the effects of drought, an inherently temporal phenomenon, did not change substantially with timescale (**Supplementary Figure S4.8**). The relationship between stability and synchrony remained unchanged by timescale (**Supplementary Figures S4.3A–C**). We similarly found no difference in the relationships between population stability or richness and stability at different timescales (**Supplementary Figures S4.3D–I**), showing that although temporal variation in precipitation amounts as well as herbivore abundance, types, or intensity could alter the importance of biotic stability mechanisms depending on the timescale of observation, they did not here. Therefore, while synchrony was timescale dependent and the timescale of calculation influenced the magnitude of stability values, timescale did alter the effects of herbivore treatments or drought events on stability and biotic mechanisms.

Delving into the role of both bottom-up and top-down processes in structuring stability is critical to understanding the full picture, but the majority of theoretical and empirical work on this topic has focused on variation across bottom-up gradients only (Grman et al., 2010; Hallett

et al., 2014; Hautier et al., 2020; Xu et al., 2015). In examining an herbaceous community subject to strong bottom-up (drought) and top-down (herbivory) limitation, we found that these stressors affect biotic mechanisms of stability in sometimes similar and sometimes contrasting ways. Drought and herbivory both reduced the stability of total herbaceous cover by increasing species synchrony, suggesting a commonality of mechanism. In both cases, the more stressed a community was, whether by water limitation or herbivore consumption, the less capacity there was for species to differ asynchronously in their responses to variability. On the other hand, drought and herbivory differed in how they affected two other potential mediators of stability: herbivory reduced dominant species population stability while drought had little effect, and herbivory increased average species richness while drought decreased it. In an applied context, this means considering that the stability of plant biomass for livestock or other consumers is a function not only of how much production the abiotic environment can support, but also how grazing feeds back to influence stability both directly and indirectly.

Climate change is expected to lead to more extreme and variable precipitation patterns (Allan & Soden, 2008; Funk et al., 2021; Intergovernmental Panel on Climate Change (IPCC), 2023; Trenberth et al., 2014), and at the same time, in savanna ecosystems such as the one studied here, large herbivores are being lost from some areas (Ripple et al., 2015) and restored (Seddon et al., 2014; Stalmans et al., 2019) or replaced by increased livestock in others (Du Toit & Cumming, 1999). Understanding how bottom-up and top-down drivers alter stability and stabilizing community dynamics will provide more ability to predict and adapt to these changing landscapes. In particular, in a future of increasing drought, we may expect to see an increase in synchronous dynamics in plant communities and a decrease in temporal stability as observed here, but these effects will in turn be mediated by changes in herbivore communities and their

direct and indirect impacts on plant community dynamics. Livestock replacement of wildlife is generally at higher stocking densities than the wild herbivores lost, particularly in semi-arid parts of the African continent (Hempson et al., 2017). An increase in total herbivore pressure will likely amplify the effects of drought, although wild meso- and megaherbivores are likely to have smaller effects on stability than cattle. In considering the applications of ecological stability, it is important to note that there are many facets of stability. We measured the invariability of herbaceous cover here, which reflects aggregate patterns over time and can incorporate but not directly measure other facets of stability such as resistance to perturbations or the rate of recovery to initial conditions, i.e., resilience (Donohue et al., 2016). How "stability" itself aligns with management goals will depend on the values applied to a particular system; the constancy of total herbaceous cover, for example, may be a desirable quality for forage availability and erosion control (Fynn & O'Connor, 2000), while temporal variability and heterogeneity support other key ecosystem functions and dimensions of biodiversity (Bråthen et al., 2021; Fuhlendorf & Engle, 2001; Porensky et al., 2013). Overall, our ability to understand the sources of variation and stability in dynamic systems will be essential to predicting future patterns of stability and navigating a changing world.

Figures

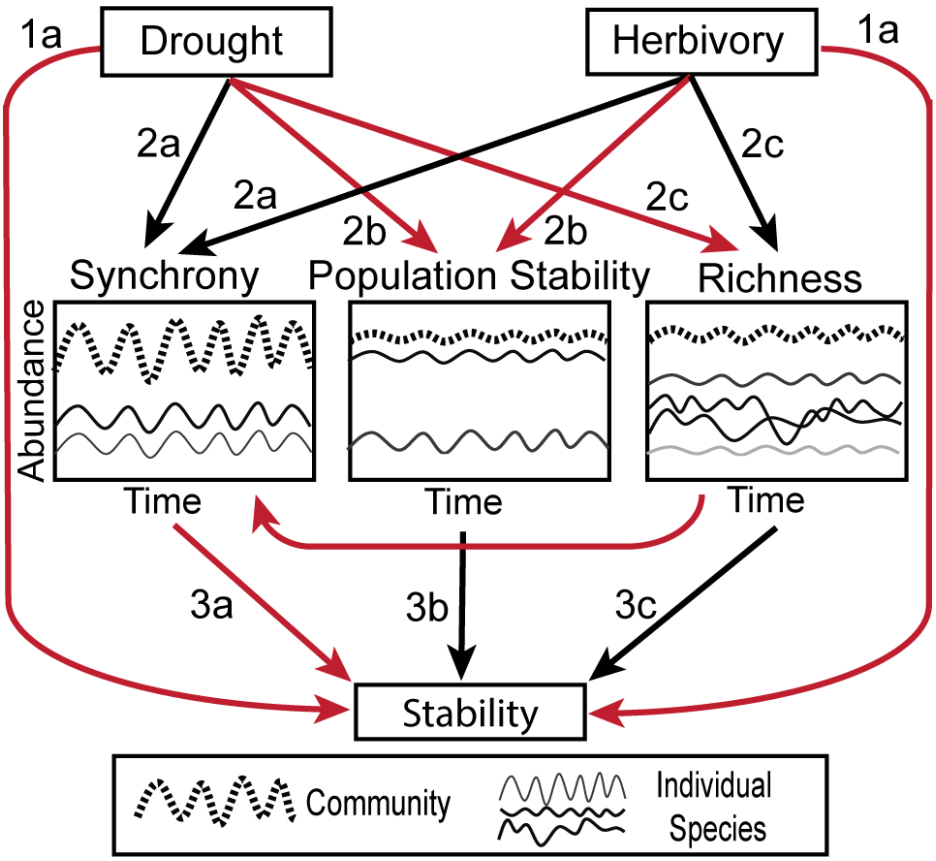

Figure 4.1. Conceptual figure illustrating the hypothesized relationships between herbivory, drought, biotic stability mechanisms and temporal stability. Black arrows indicate positive relationships, while red arrows indicate negative. Compare to Figure 6. The biotic mechanisms are illustrated as follows: Synchrony—two individual species' abundances (thin solid lines) fluctuate in unison, causing the full community (thick dashed line) to be more variable. Population Stability–one of the two individual species is dominant compared to the other (thin solid lines) and the population stability of the dominant species heavily influences the stability of the overall community (thick dashed line). Richness—when a community is composed of many species (thin solid lines), they average out to make the full community (thick dashed line) more stable than the individual components.

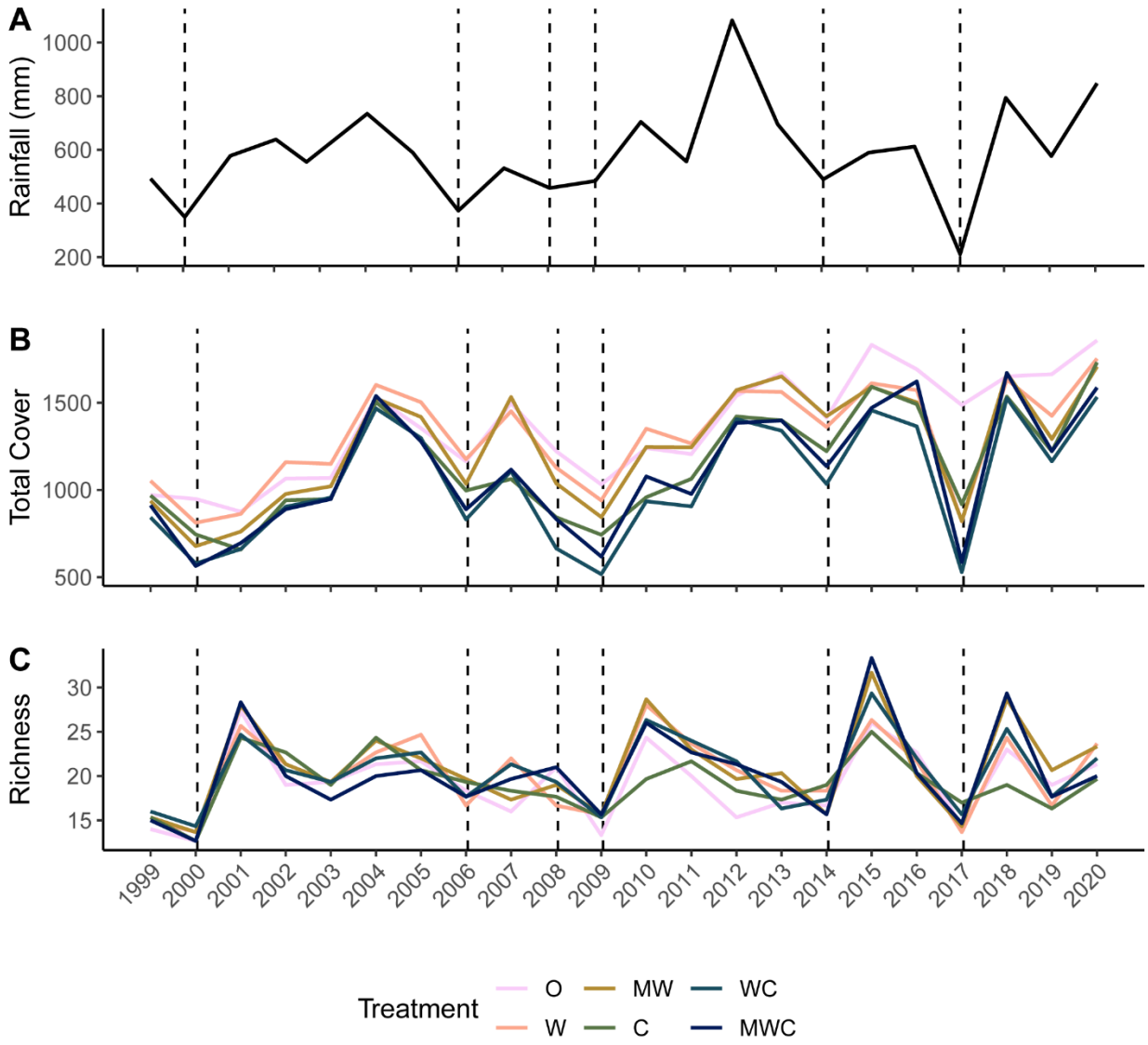

Figure 4.2. Precipitation (mm) calculated over the 12-months before the annual June sampling period (A), mean total cover (B) and species richness (C) at each sampling point (annually in June) from 1999-2020 colored by herbivore treatment. Herbivore treatments (ordered by total herbivore biomass) are: O, No herbivores; W, Wild mesoherbivores; MW, Wild megaherbivores and wild mesoherbivores; C, Cattle; WC, Wild mesoherbivores and cattle; MWC, Wild megaherbivores, wild mesoherbivores, and cattle. Dashed lines indicate low rainfall (<the 25th percentile, defined here as a drought) in the 12 months preceding the sampling point.

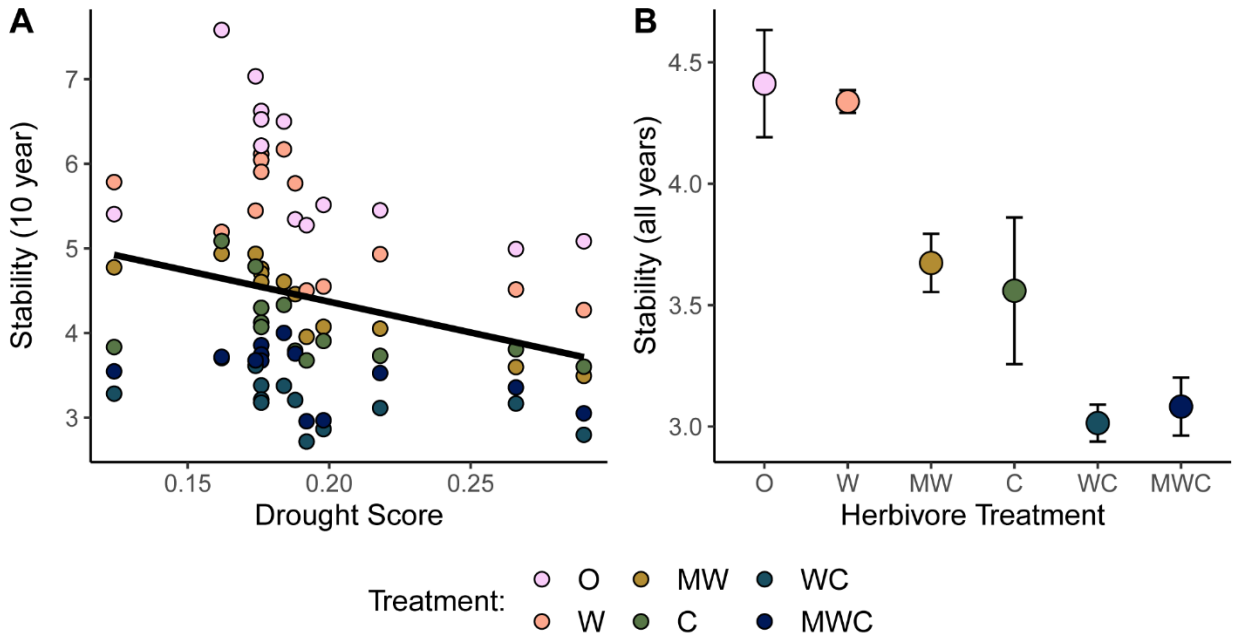

Figure 4.3. Temporal stability (μ/σ) of herbaceous cover as a function of the drought score (A) and herbivore treatment (B). Stability is calculated over a 10-year moving window in (A) in order to compare to the corresponding drought score of each time window. Higher drought score values indicate more severe drought. The black regression line in (A) is plotted as the predictor was included in the top model. In (B) stability is calculated over the full time series and points are colored by herbivore treatment. Herbivory patterns are consistent on a 10-year scale (Supplementary Figure S2A). Figures are based on raw data, but statistical models include random effects to account for spatial and temporal autocorrelation. See Table 1 for model details. Herbivore treatments (ordered by total herbivore biomass) are: O, No herbivores; W, Wild mesoherbivores; MW, Wild megaherbivores and wild mesoherbivores; C, Cattle; WC, Wild mesoherbivores and cattle; MWC, Wild megaherbivores, wild mesoherbivores, and cattle.

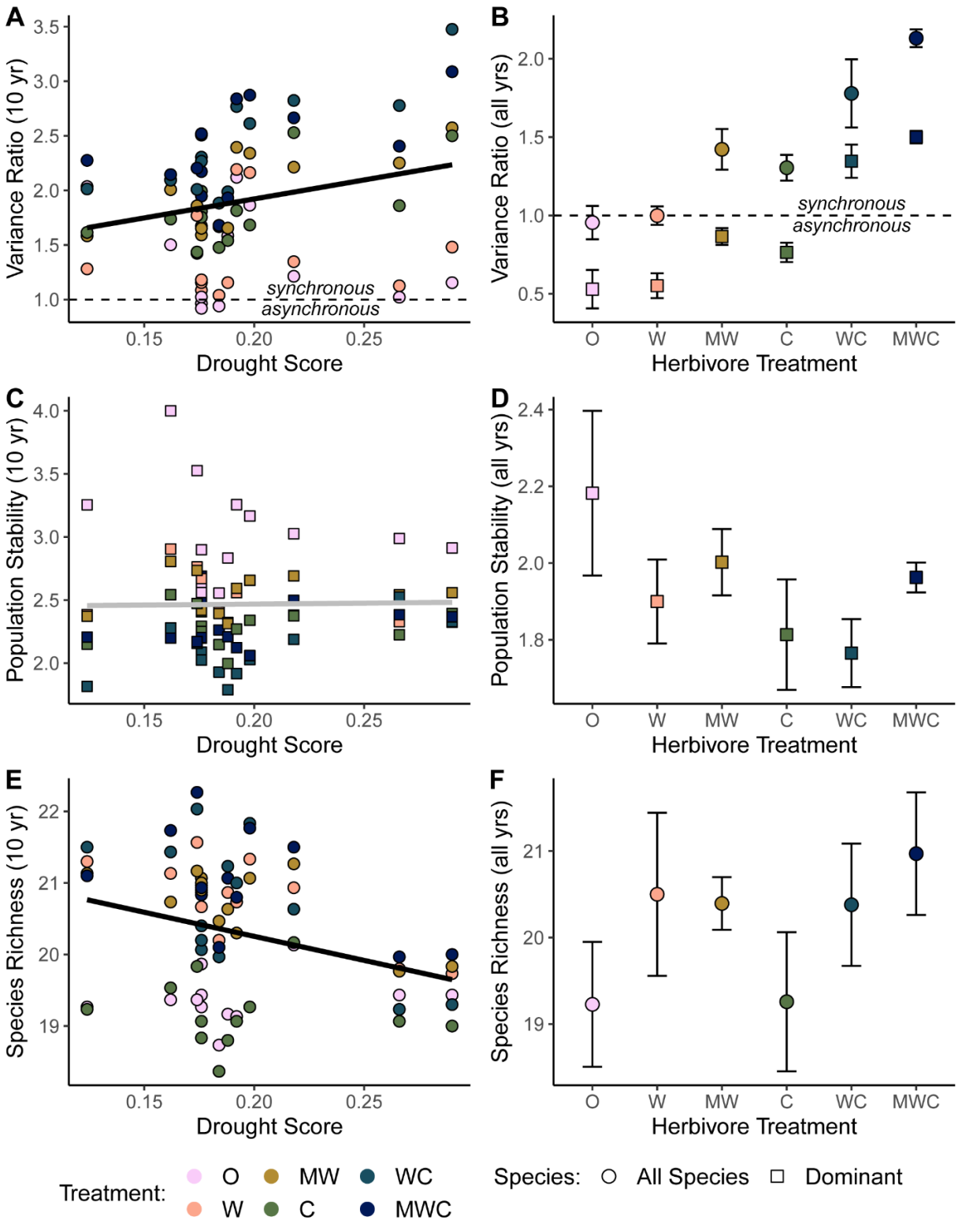

Figure 4.4. The relationship between the variance ratio (A), dominant species population stability (C), species richness (E) and drought, all calculated over a 10-year moving window in

order to compare to the corresponding drought score of each time window. The effects of herbivore treatment on the variance ratio (B), dominant species population stability (D), and species richness (F) calculated as an average over the full timeseries. A variance ratio less than one indicates asynchronous dynamics, and greater than one indicates synchronous dynamics. Shape indicates whether the biotic mechanism is calculated using all species in the community (circles) or only the five dominant species (squares). Bars are one standard error. Black regression lines in (A,E) are plotted when the predictor was included in the top model and the gray regression line in (C) indicates that this predictor did not have an effect. Figures are based on raw data, but statistical models include random effects to account for spatial and temporal autocorrelation. See Tables 2, 3 for model details. Herbivore treatments (ordered by total herbivore biomass) are: O, No herbivores; W, Wild mesoherbivores; MW, Wild megaherbivores and wild mesoherbivores; C, Cattle; WC, Wild mesoherbivores and cattle; MWC, Wild megaherbivores, wild mesoherbivores, and cattle.

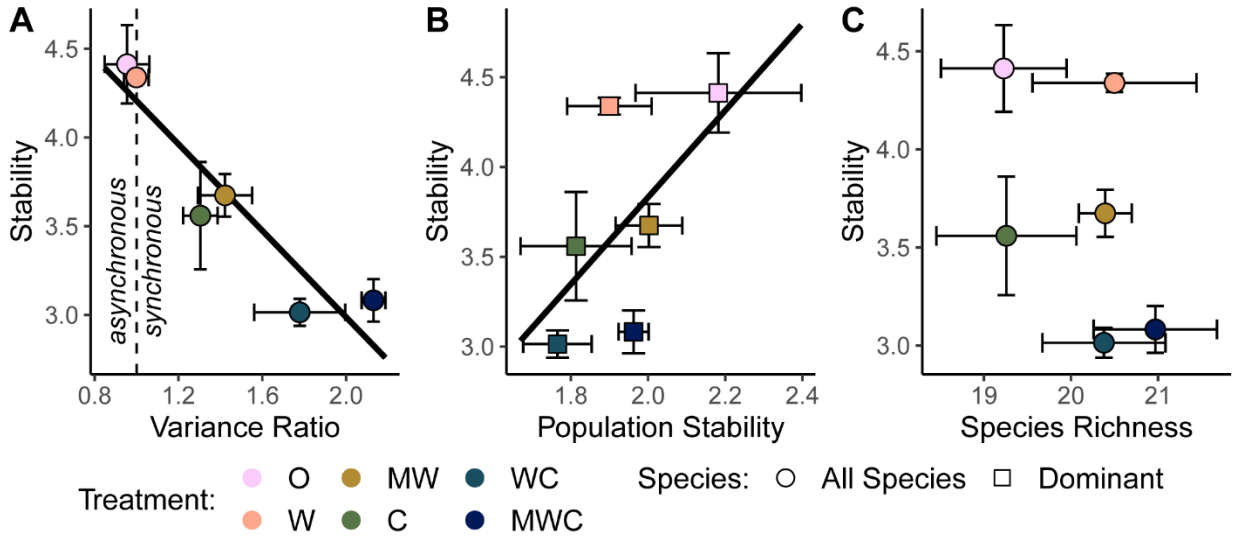

Figure 4.5. The relationship between stability and the variance ratio (A), dominant species population stability (B), and species richness (C), all calculated over the full timeseries. A variance ratio less than one indicates asynchronous dynamics, and greater than one indicates synchronous dynamics. Black regression lines in (A) and (B) are plotted when the predictor was included in the top model. Figures are based on raw data, but statistical models include random effects to account for spatial and temporal autocorrelation. See Table 4 and Supplementary Table S6 for statistical model details. Herbivore treatments (ordered by total herbivore biomass) are: O, No herbivores; W, Wild mesoherbivores; MW, Wild megaherbivores and wild mesoherbivores; C, Cattle; WC, Wild mesoherbivores and cattle; MWC, Wild megaherbivores, wild mesoherbivores, and cattle.

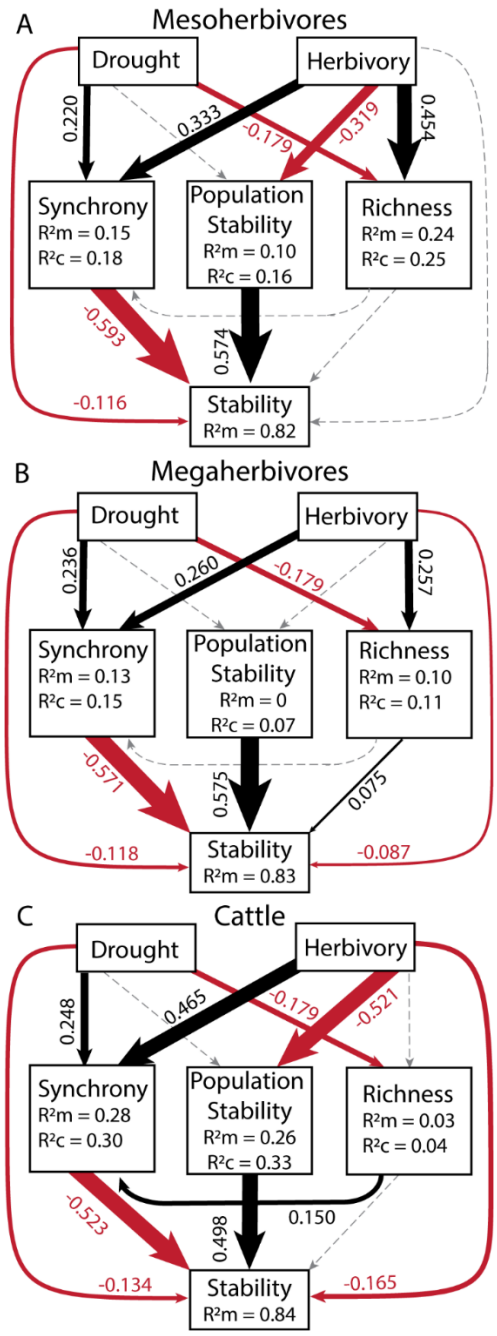

Figure 4.6. Structural equation models for each herbivore group: mesoherbivores (A), megaherbivores (B), and cattle (C) to determine the relative strength of direct vs. indirect effects of drought and herbivory. All variables in the model were calculated over a 10-year moving window in order to compare to the corresponding drought score of each time window. Goodness of Fit values were: for mesoherbivores C = 4.00, p = 0.406, df = 4 (A), for megaherbivores C = 8.86, p = 0.065, df = 4 (B), and for cattle C = 13.79, p = 0.008, df = 4 (C). Values next to arrows (direct effects) are scale standardized estimates of coefficients and arrow width is scaled to their magnitude. Black arrows denote positive effects, red arrows show negative effects, and gray, dashed arrows show non-significant effects. Model coefficients and outputs can be found in

Supplementary Tables S7–S9. The R2m of each response variable provides the variance explained by fixed effect(s) alone and Rc2 is the variance explained by both the fixed and random effects (Block = random). No Rc2 value is present for stability as we removed random effects from the model because they did not explain any variance and caused singularity issues. See Table 5 for indirect effects.

Tables

Table 4.1. Model outputs from linear mixed effects models predicting stability and selected for the lowest AIC_c value.

Model	Variable	Coeff	Std. Error	t
Stability (10 year) ~ drought score + cattle + mesoherbivores	Main Effects			
	Intercept	7.25	0.31	23.20
	Drought Score	−7.28	0.89	−8.16
	Cattle	−1.62	0.25	−6.56
	Mesoherbivores	−0.91	0.26	−3.49
Stability ~ cattle	Main effects			
	Intercept	4.14	0.16	26.24
	Cattle	−0.92	0.18	−5.23

The first model includes only herbivore groups as predictors of stability over the full time series, with block as a random effect. The second model includes drought score and herbivore groups as additive predictors of stability calculated over a moving window of 10 years, with block and plot as random effects. Both models had several models within 2 Δ AIC_c. We report the most parsimonious here, other equivalent models can be found in **Supplementary Table S4.8**. See **Supplementary Table S4.1** for model selection and 1 AIC_c values. Models correspond to **Figures 4.3A,B**, respectively.

Table 4.2. Model outputs from linear mixed effects models with herbivore treatment and drought score as predictors of biotic stability mechanisms, with block and plot as random effects.

Model	Variable	Coeff.	Std. Error	t
Variance ratio (10 year) ~ drought score + cattle + mesoherbivores	*Main effects*			
	Intercept	0.62	0.20	3.12
	Drought score	3.48	0.73	4.79
Variance ratio (10 year) ~ drought score + cattle + mesoherbivores	Cattle	0.61	0.14	4.38
	Mesoherbivores	0.46	0.15	3.11
Population stability (10 year) ~ cattle	*Main effects*			
	Intercept	2.70	0.10	27.80
	Cattle	-0.47	0.13	-3.65
Richness (10 year) ~ drought score + mesoherbivores	*Main effects*			
	Intercept	20.60	0.55	37.62
	Drought score	-6.73	1.24	-5.41
	Mesoherbivores	1.51	0.60	2.50

The population stability model had three models within 2 Δ AIC_c. We report the most parsimonious here, other equivalent models can be found in **Supplementary Table S4.8**. See **Supplementary Table S4.3** for model selection and Δ AIC_c values. Models correspond to **Figures 4.4B,D,F**, respectively.

Table 4.3. Model outputs from linear mixed effects models with herbivore treatment as a predictor of biotic stability mechanisms, with block as a random effect.

Model	Variable	Coeff.	Std. Error	t
Variance ratio ~ cattle + megaherbivores	*Main effects*			
	Intercept	0.95	0.10	9.67
	Cattle	0.61	0.11	5.57
	Megaherbivores	0.52	0.12	4.43
Population stability ~ 1	*Main effects*			
	Intercept	1.94	0.08	25.45
Richness ~ mesoherbivores	*Main effects*			
	Intercept	19.24	0.45	42.57
	Mesoherbivores	1.32	0.55	2.38

The model of species richness is a linear model with no random effects as incorporating random effects did not explain additional variance and caused singularity issues with the model. See **Supplementary Table S4.2** for model selection and Δ AIC_c values. Models correspond to **Figures 4.4A,C,E,** respectively.

Table 4.4. Model outputs from linear mixed effects models predicting stability as a function of biotic mechanisms.

Model	Variable	Coefficient	Std. Error	t
Stability ~ variance ratio + population stability	*Main effects*			
	Intercept	3.49	0.47	7.39
	Variance ratio	-1.11	0.11	-10.22
	Population stability	0.92	0.22	4.21

The model shown had the lowest delta AICc value. See **Supplementary Tables S4.4, S4.5** for model selection and Δ AIC_c values. Model corresponds to **Figure 4.5**.

Table 4.5. Direct, indirect, and net effects of drought and herbivory on stability.

Driver	Direct effect	IE: synchrony	IE: richness	IE: population stability	IE: richness - synchrony	Total IE	Net Effect
Drought	**-0.116**	-0.130	NA	NA	NA	**-0.130**	-0.246
Mesoherbivores	--	-0.197	NA	-0.183	NA	**-0.380**	-0.380
Drought	**-0.118**	-0.135	-0.013	NA	NA	**-0.148**	-0.266
Megaherbivores	**-0.087**	-0.148	0.019	NA	NA	**-0.129**	-0.216
Drought	**-0.134**	-0.130	NA	NA	0.014	**-0.116**	-0.250
Cattle	**-0.165**	-0.243	NA	-0.259	NA	**-0.502**	-0.667

Effect sizes are standardized effects from structural equation models, see **Figure 6** for pathway diagram. Indirect effect sizes were calculated as the product of standardized effect sizes along a

pathway. Herbivory is modeled as the presence or absence of a particular herbivore group and there is a separate structural equation model for each herbivore group. Indirect effect is abbreviated as IE. IE: synchrony means an indirect path of a driver (drought or herbivory) on stability mediated through synchrony. When a relationship was not significant in the SEM, we did not calculate an indirect effect size for the pathways that included that relationship.

CHAPTER V.

CONCLUSIONS

Forecasting species and community responses to drought is challenging due to the direct and indirect effects of drought as well as varied species ecologies. Ecological communities are complex, and therefore it is necessary to study responses at multiple levels to understand the relationships between levels. Over the course of my dissertation, I tested how demographic rates and species interactions between a native legume and invasive grass change across density and rainfall gradients (Chapter II), how species local abundance distributions predict drought responses within communities (Chapter III), and how periodic droughts interact with herbivory to shape ecological stability through community dynamics (Chapter IV). Characterizing drought responses across scales is essential due to ongoing climate change and altered precipitation regimes causing harsher and more frequent droughts across the globe.

In Chapter II, I tested whether a native legume and invasive grass species can persist together, despite the legume benefiting its competitor. Overall, facilitation of the grass by the legume was strongest under high water availability and a low density of legumes. Under these conditions, the legume also benefited enough from its symbiotic partners and a relaxation in interspecific competition to coexist with the grass. However, reciprocal interactions from the grass became more competitive as water availability declined, leading to the competitive exclusion of the legume in low and intermediate water treatments. In a non-equilibrium system like California grasslands that experiences high rainfall variability through time, characterizing the role of environmental variability in stabilizing or destabilizing coexistence is a key next step (Hallett et al., 2019; Muehleisen et al., 2025).

Further, in real systems, species interact – both directly and indirectly via shifting abundances – with a diversity of other species (Saavedra et al., 2017). There is evidence that legumes benefit neighbor biomass, but reduce community diversity (Ortiz & Wolf, 2024), which my findings suggest may stem from the legume benefitting competitive species in a community at the expense of others. Scaling up to understand how facilitation by a legume changes interactions and coexistence within a diverse community of species in response to perturbations will be key to a more realistic and comprehensive understanding of the role of facilitation in biodiversity maintenance.

In Chapter III, I tested whether species' responses to an extreme drought could be predicted by their local spatial and temporal abundances. In general, both spatially sparse and temporally intermittent species responded positively during and after drought, while common and persistent species declined. Across the six experimental sites, responses did not align with the large-scale precipitation gradient but rather were dependent on characteristics of common species such as life history, photosynthetic pathway, and degree of dominance. By quantifying how common species in a system respond, we may gain an idea of how the rest of the community will respond. Additionally, positive responses of rare species persisted for four years after drought, indicating that this extreme drought resulted in lasting shifts to community composition. This work highlights the important role of rare species in maintaining productivity under extreme disturbance (Yu et al., 2025) as well as the importance of assessing species recovery to periodic environmental disturbances (Vilonen et al., 2022). My work highlights that groups of species may fluctuate asynchronously from each other with drought, based on their local abundances. A key next question would be whether asynchronous dynamics in a

community arise at the level of individual species or are maintained by groups of species with similar responses.

In Chapter VI, I tested how top-down grazing and bottom-up resource fluctuations change ecological stability directly and indirectly through community dynamics like synchrony. Disentangling the mechanisms of ecological stability is a core theoretical and empirical pursuit in ecology with important implications for land management and conservation in a changing world. Additionally, this work is one of the first to explore bottom-up and top-down drivers of stability in tandem, and to use a sliding window analysis to identify periodic drought effects on stability. I found that both drought and herbivory directly reduced the temporal stability of herbaceous cover, mediated through synchrony and the stability of dominant species. Overall, the direct effects of drought and herbivory on stability were smaller in magnitude than their indirect effects mediated through biotic stability mechanisms.

While my work provides novel insights into how drought alters species, communities, and ecosystem, it also provides insights into areas of future research. For example, as species interactions are dependent on multiple processes at the same time, it is essential to understand how multiple drivers shape interactions and whether there are general patterns in which drivers shape the net outcome. Further, relating coexistence mechanisms, including species interactions, to the community dynamics they generate – such as asynchrony or species level stability – and directly relating this to ecosystem level stability will enhance our understanding of the drivers of ecological stability as well as the ecosystem level outcomes of species coexistence (Godoy et al., 2020). Finally, as droughts are increasing in frequency (Chiang et al., 2021), testing how species interactions and community dynamics change with repeated stressors will provide insight into whether communities can buffer repeated disturbance or are changing directionally.

In conclusion, my dissertation results highlight that drought alters individual species demographic rates and abundances, species interactions, community dynamics, and ecosystem stability. These changes are interrelated; shifts in individual demographic rates and interactions change abundances and lead to overall changes in community dynamics and ultimately the stability of the system. While direct effects are important, my work highlights that the magnitude of indirect effects in communities is often larger than the direct effects of drivers themselves (Suttle et al., 2007). Indirect effects may buffer or exacerbate the effects of drought and therefore better understanding of indirect effects will lead to better ability to manage and restore grasslands in a changing world.

APPENDIX A

SUPPLEMENTAL MATERIALS FOR CHAPTER II

Supplementary Figures

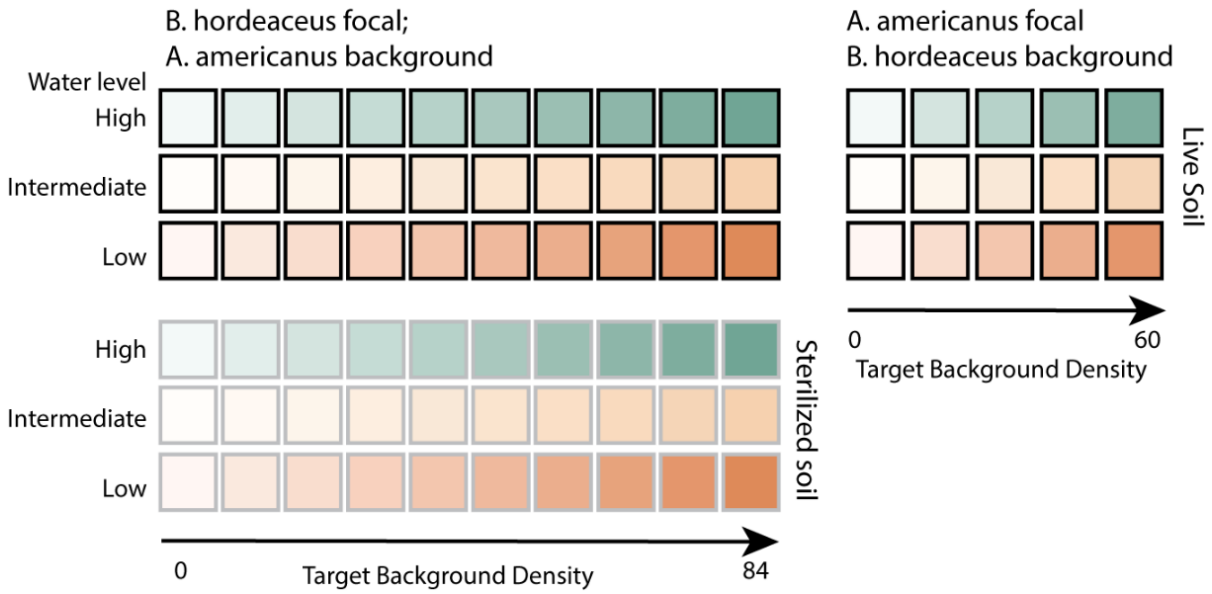

Figure S2.1. Greenhouse experimental set up. Each focal x water x soil treatment combination was replicated at least 4 times. An additional replicate was included for select densities 0, 12, 24, 48 to accommodate student projects.

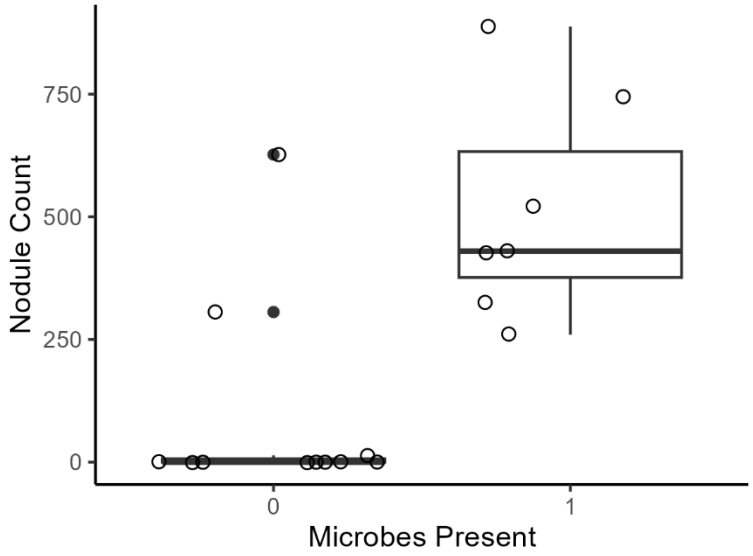

Figure S2.2. Nodule counts on bulk roots from density 18 pots.

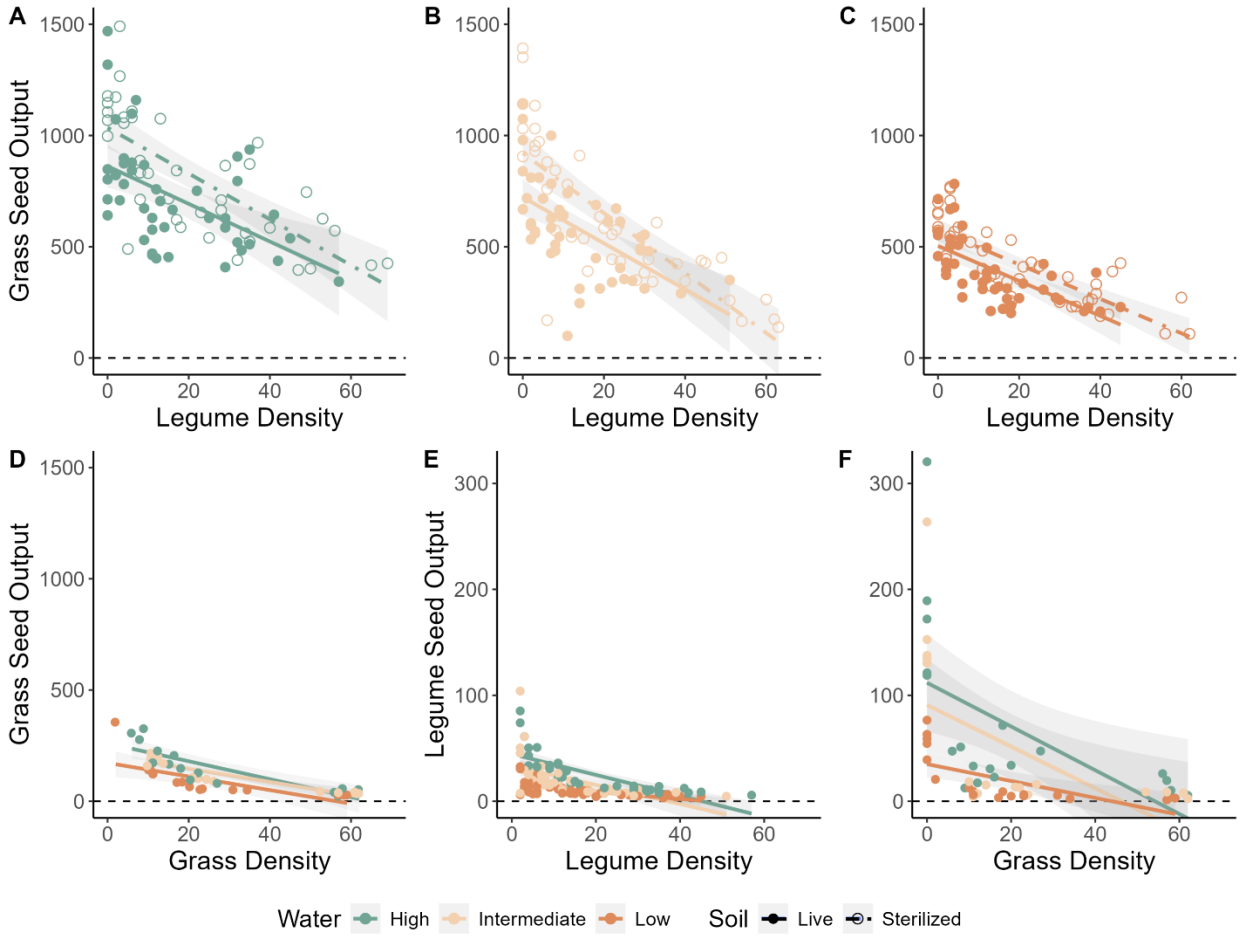

Figure S2.3. Per-capita seed production of grass individuals (A-D) and legume individuals (E, F) as a function of neighbor density. Note that the y-axis scale changes between grass and legume plots. Color indicates water level and both line type and point fill indicate soil treatment, where solid lines are live soil and dashed lines are sterilized soil.

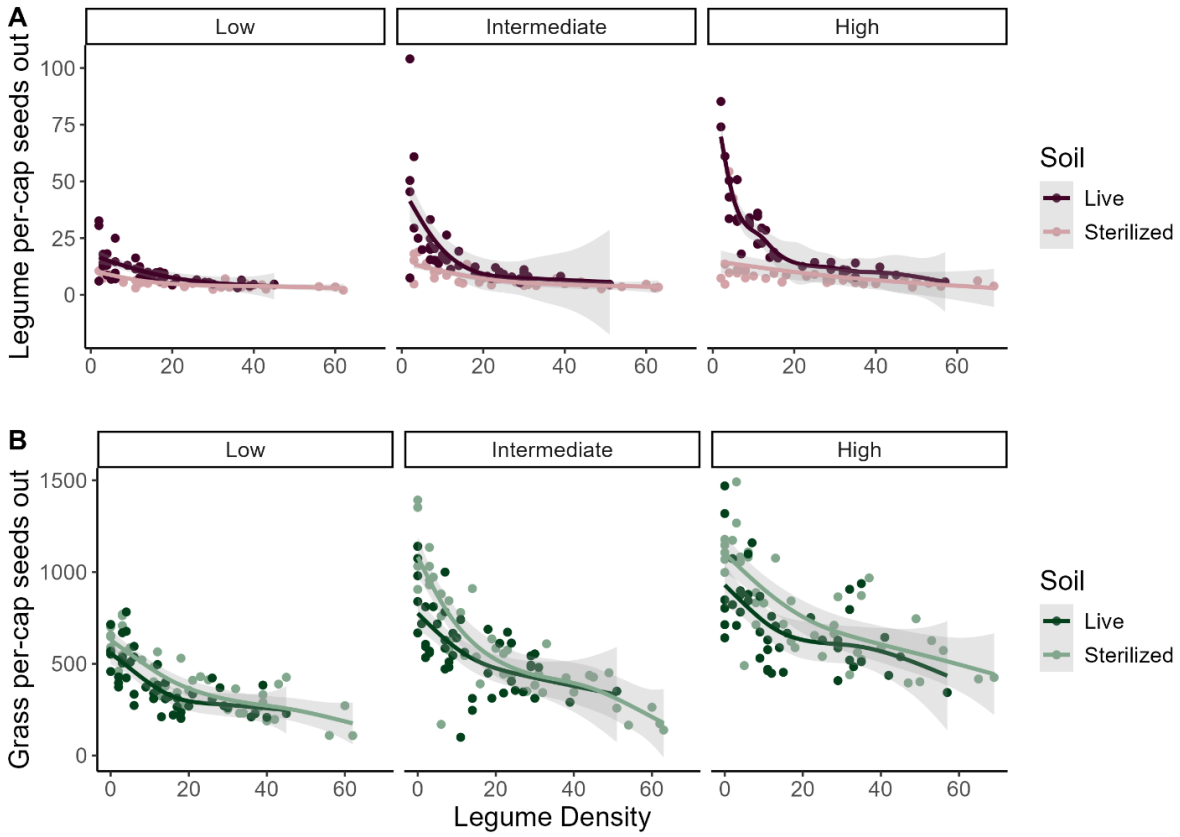

Figure S2.4. Per-capita seed output of *A. americanus* (A) and *B. hordeaceus* (B) over a density gradient of *A. americanus* in live and sterilized soil. Panels show water level.

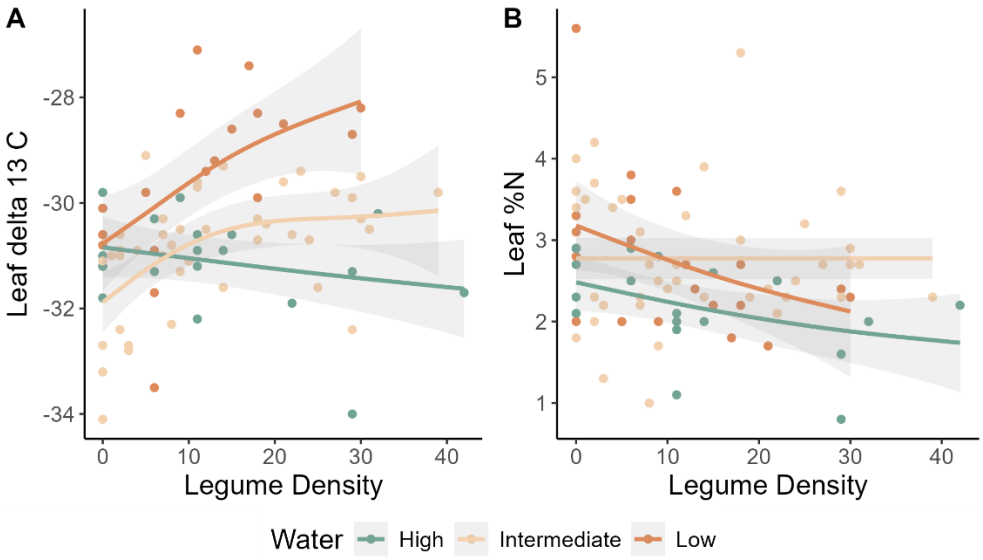

Figure S2.5. *B. hordeaceus* leaf $\delta^{13}C$ (A) and percent N (B) across a density of neighboring *A. americanus.*

Supplementary Tables.

Table S2.1. Allometric relationships between total biomass and seed output for *B. hordeaceus* and *A. americanus* calculated from samples in a field experiment.

Species	Relationship	Slope (p-value)	Viable seeds per flower
B. hordeaceus	Total biomass to seed number	388.25 (<0.001)	NA
A. americanus	Total biomass to flower number	34.93 (<0.001)	1.67

Table S2.2. Prior distributions used for static models.

Parameter	Definition	Species	Distribution	Mean	SD	Source
λ	Intrinsic growth rate in absence of competition	BRHO	Normal	200	50	Watkins et al. unpublished data
		ACAM	Normal	62	30	
λ deviation	Change in λ from live to sterilized soil	BRHO	Normal	0	12	
		ACAM	Normal	0	12	
α_{ii}	Intraspecific interaction coefficient	BRHO	Normal	-0.057	0.25	Watkins et al. unpublished data
		ACAM	Normal	0.185	0.25	
α_{ii} deviation	Change in α_{ii} from live to sterilized soil	BRHO	Normal	0	0.05	
		ACAM	Normal	0	0.25	
α_{ij}	Interspecific interaction coefficient	BRHO	Normal	0.099	0.25	Watkins et al. unpublished data
		ACAM	Normal	-0.024	0.25	
α_{ij} deviation	Change in α_{ij} from live to sterilized soil	BRHO	Normal	0	0.25	
		ACAM	Normal	0	0.05	
Disp	$1/\text{disp}^2$ = dispersion of negative binomial distribution	BRHO	Cauchy	Location: 0	Scale: 1	
		ACAM	Cauchy	0	1	

Note, standard deviations of alpha_ii and alpha_ij were increased to avoid having too specific of priors. In deviation parameters, we constrained the potential variance of the effect of *B.*

hordeaceus on itself and on *A. americanus* as we did not have good data to estimate this in sterilized soil.

Table S2.3. *Prior distributions used for sigmoidal models.*

Parameter	Definition	Species	Distribution	Mean	SD	Source
λ	Intrinsic growth rate in absence of interactions	BRHO	Normal	200	50	Watkins et al. unpublished data
		ACAM	Normal	62	30	
α_{ii}	Intraspecific interaction coefficient	BRHO	Normal	-0.057	0.25	Watkins et al. unpublished data
		ACAM	Normal	0.185	0.25	
$\alpha_{slope,ij}$	The density-dependent effect of j on i	BRHO	Normal	-0.2	0.2	Buche et al. 2025
		ACAM	Normal	0	0.1	
$\alpha_{0,ij}$	The density independent effect of j on i	BRHO	Normal	0.099	0.25	Watkins et al. unpublished data
		ACAM	Normal	-0.024	0.25	
c	A constant that stretches the function vertically	BRHO	Normal	0	0.1	Buche et al. 2025
		ACAM	Normal	0	0.1	
N_0	The optimal density of neighboring species j	BRHO	Exponential	0.9	--	
		ACAM	Exponential	2	--	
disp	1/disp^2 = dispersion of negative binomial distribution	BRHO	Cauchy	Location: 0	Scale: 1	
		ACAM	Cauchy	0	1	

Table S2.4. Linear model coefficients for response of the additive intensity index to the number of *A. americanus* background individuals, water level, and the soil microbial treatment.

Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-0.058	0.035	-1.629	0.105
Num Indiv	-0.013	0.001	-13.321	0
Water Level, Intermediate	-0.263	0.039	-6.717	0

Table S2.4. (continued).

Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
Water Level, Low	-0.161	0.039	-4.132	0
Soil Treatment, Sterilized	0.019	0.032	0.597	0.551

Table S2.5. Linear model coefficients from the linear model predicting the additive interaction intensity from *B. hordeaceus* leaf δ13C, the number of background individuals, water level, and the interaction between leaf δ13C and water level.

Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-3.036	0.895	-3.391	0.001
$\delta^{13}C$	-0.09	0.03	-2.987	0.004
Water Level, Intermediate	3.018	1.324	2.28	0.026
Water Level, High	1.796	1.848	0.971	0.335
Num Indiv	-0.01	0.003	-3.957	0
$\delta^{13}C$: Water Level, Intermediate	0.104	0.044	2.377	0.021
$\delta^{13}C$: Water Level, High	0.059	0.06	0.979	0.331

Table S2.6. Linear model coefficients from the linear model predicting the additive interaction intensity from *B. hordeaceus* leaf percent N, the number of background individuals, and water level.

Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-0.573	0.107	-5.379	<0.001
% N	0.072	0.033	2.208	0.031
Water Level, Intermediate	-0.076	0.059	-1.303	0.197
Water Level, High	0.163	0.073	2.239	0.029
Num Indiv	-0.01	0.002	-4.233	<0.001

Table S2.7. ANOVA table from linear models predicting 1) *A. americanus* per-capita seed output in from the number of *intra*specific neighbors, the soil microbial treatment, water level, and the interactions between all factors and 2) *B. hordeaceus* per-capita seed output from the additive effects of the number of *inter*specific neighbors, water level, and the soil microbial treatment.

Species	Coefficient	Sum Sq	Df	F value	Pr(>F)	
A. americanus	**Intercept**	4.513	1	32.415	<0.001	***
	Num Indiv	0.986	1	7.078	0.008	**
	Soil Treatment	0.201	1	1.446	0.23	
	Water Level	0.752	1	5.403	0.021	*
	Num Indiv: Soil Treatment	0.001	1	0.004	0.947	
	Num Indiv: Water Level	0.06	1	0.433	0.511	
	Soil Treatment: Water Level	1.889	1	13.567	<0.001	***
	Num Indiv: Soil Treatment: Water Level	0.27	1	1.937	0.165	
	Residuals	30.909	222			
B. hordeaceus	**Intercept**	291.891	1	3001.041	<0.001	***

Table S2.7. (continued)

Species	Coefficient	Sum Sq	Df	F value	Pr(>F)	
B. hordeaceus	**Num Indiv**	23.486	1	241.466	<0.001	***
	Soil Treatment	1.797	1	18.474	<0.001	***
	Water Level	20.348	1	209.205	<0.001	***
	Residuals	25.191	259			

Table S2.8. Linear model coefficients from the model predicting A. americanus per-capita seed output in from the number of intraspecific neighbors, the soil microbial treatment, water level, and the interactions between all factors.

Species	Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
A. americanus	Intercept	1.679	0.295	5.693	<0.001
	Num Indiv	-0.026	0.01	-2.661	0.008
	Soil Treatment	-0.485	0.403	-1.203	0.23
	Water Level	0.855	0.368	2.324	0.021
	Num Indiv: Soil Treatment	0.001	0.016	0.067	0.947
	Num Indiv: Water Level	0.008	0.012	0.658	0.511
	Soil Treatment: Water Level	1.86	0.505	3.683	<0.001
	Num Indiv: Soil Treatment: Water Level	-0.028	0.02	-1.392	0.165
B. hordeaceus	Intercept	5.355	0.098	54.782	<0.001
	Num Indiv	-0.019	0.001	-15.539	<0.001
	Soil Treatment	-0.169	0.039	-4.298	<0.001
	Water Level	1.699	0.117	14.464	<0.001

APPENDIX B

SUPPLEMENTAL MATERIALS FOR CHAPTER III

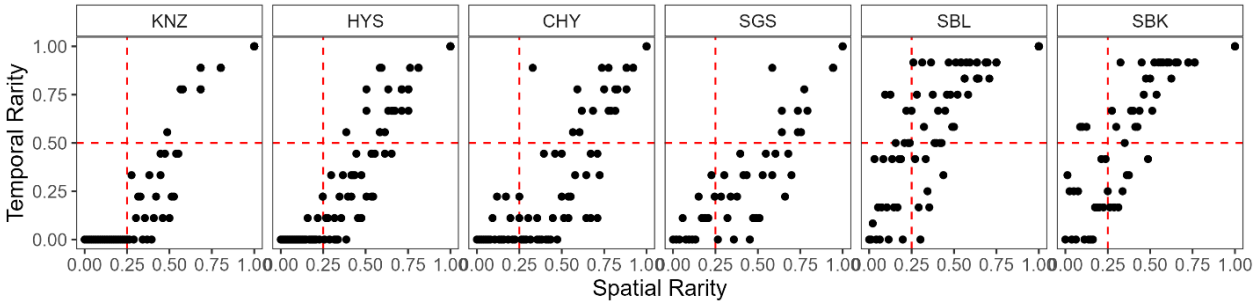

Figure S3.1. Points show each species' spatial and temporal rarity at each of the sites in the experiment. Red dashed lines show the cutoffs for rarity categories.

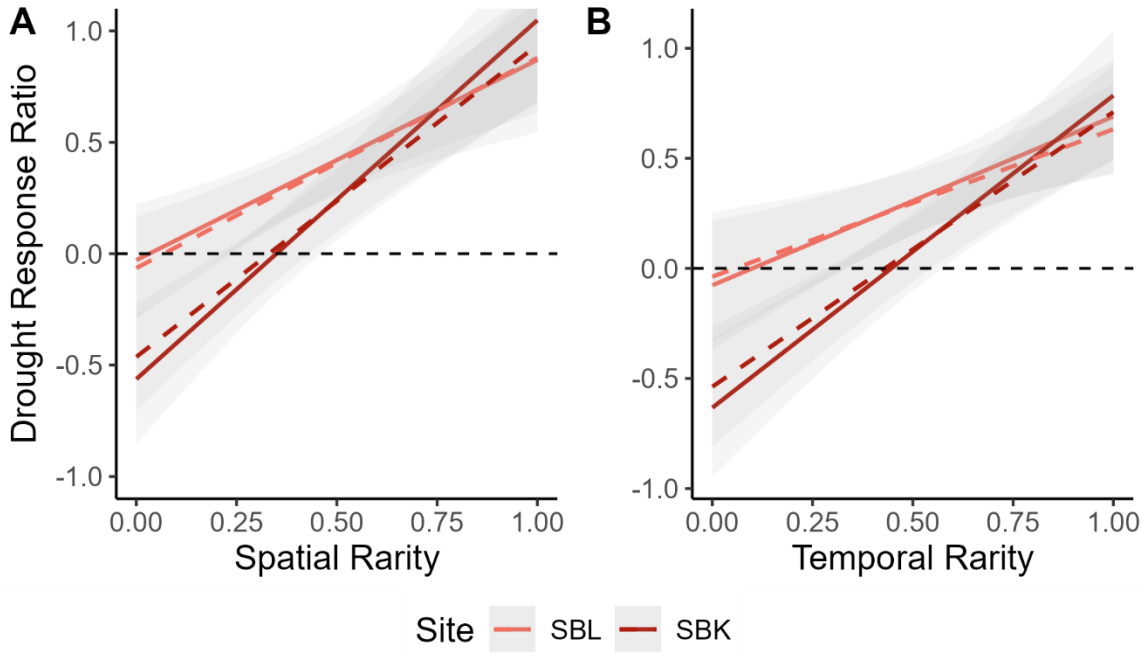

Figure S3.2. The effect of spatial (A) and temporal (B) rarity on a species' response ratio values calculated over 4 years (solid lines) or 7 years (dashed lines) of drought.

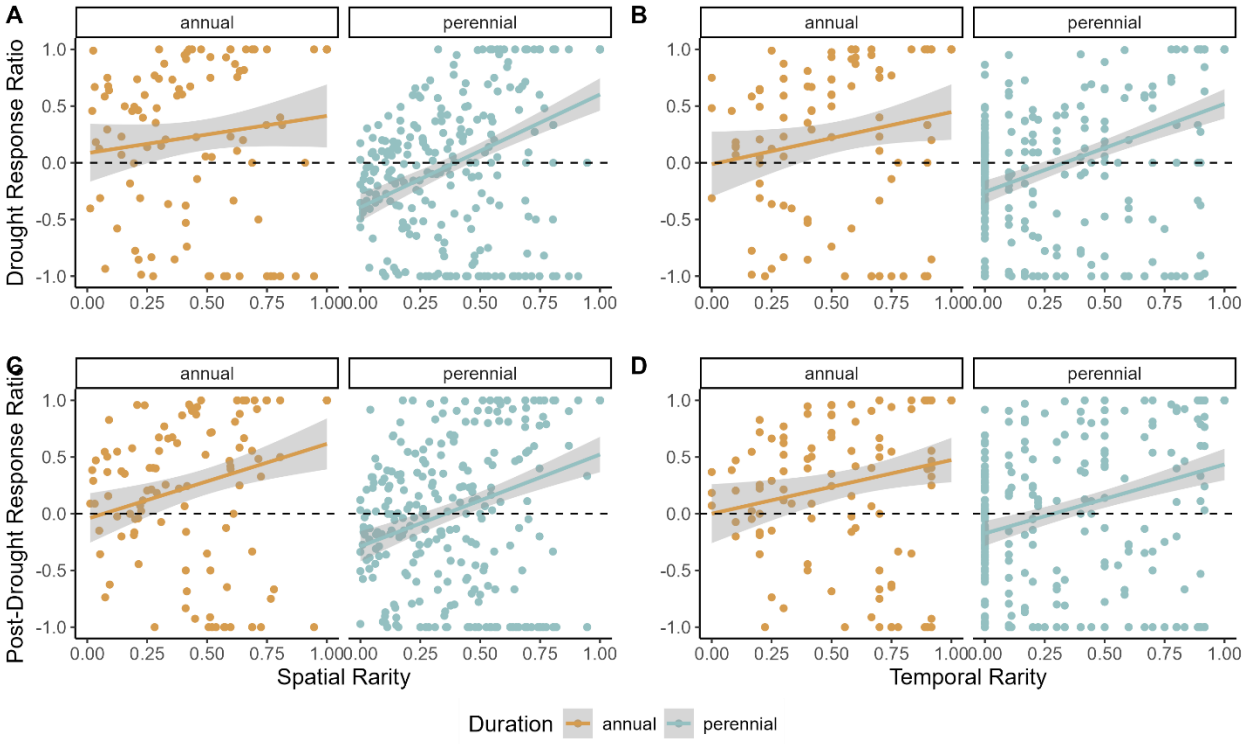

Figure S3.3. Response ratio vs. rarity relationships split by whether species are annual vs. perennial.

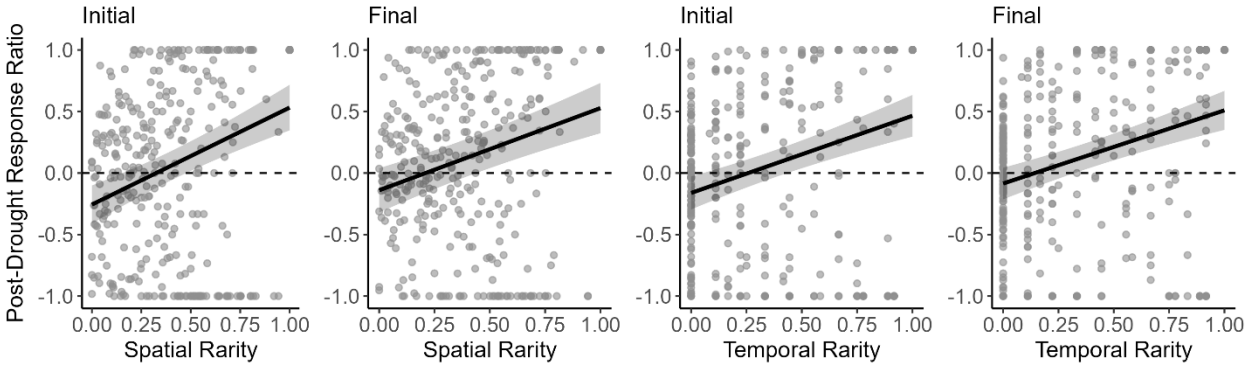

Figure S3.4. The effect of spatial and temporal rarity on a species response during the initial two years and final two years of the four-year post-drought period. The plotted lines are linear mixed effects models with site as a random effect. Each point shows one species. Positive values of the response ratio indicate a species' cover is greater in drought plots than controls and negative values are when a species' cover is lower in drought plots than controls (**Equation 3.3**). Spatial or temporal rarity values near 1 indicate a species is rare and values near 0 indicate a common species.

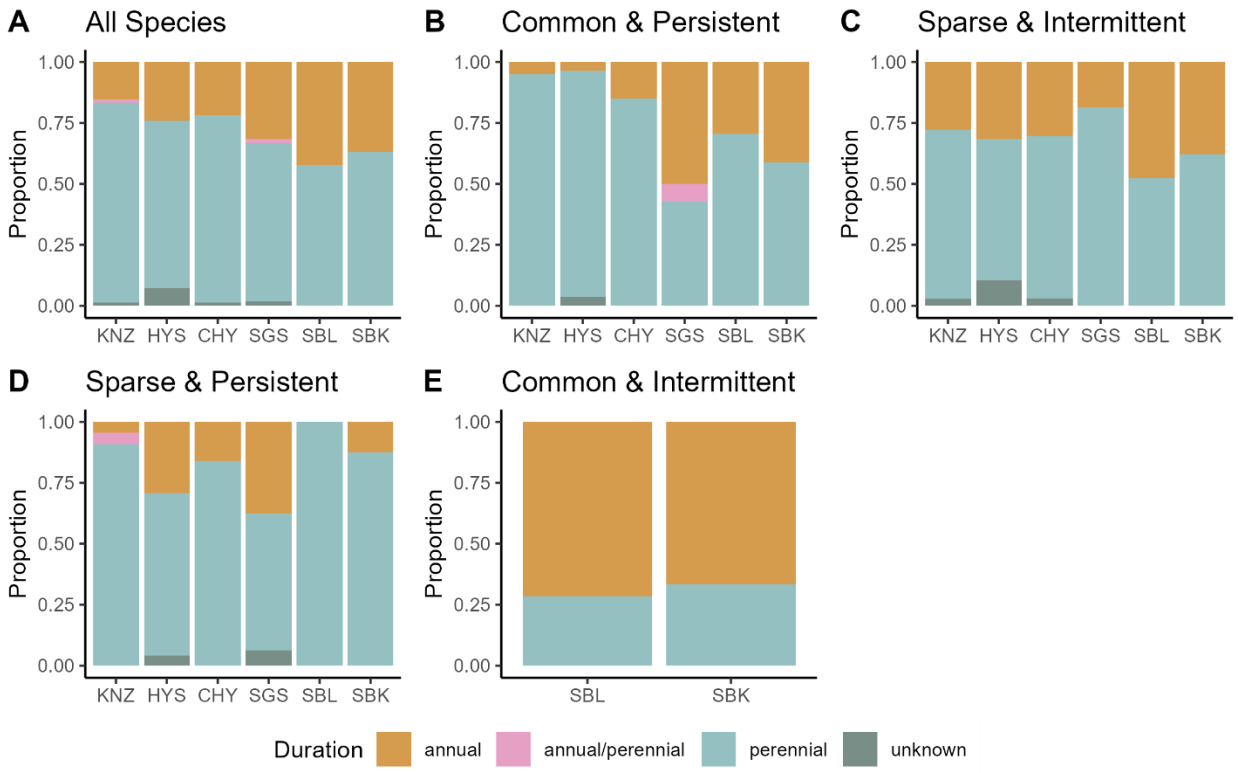

Figure S3.5. Proportions of species life history categories for all species (A), spatially common and temporally persistent species (B), spatially sparse and temporally intermittent species (C), spatially sparse and temporally persistent species (D), and spatially common and temporally intermittent species (E). Spatially common species have a value of < 0.25 of spatial rarity (1 – percent rank) and all others are considered spatially sparse. Temporally persistent species have a value of < 0.50 of temporal rarity (1 – proportion of years present), while all others are considered temporally intermittent species.

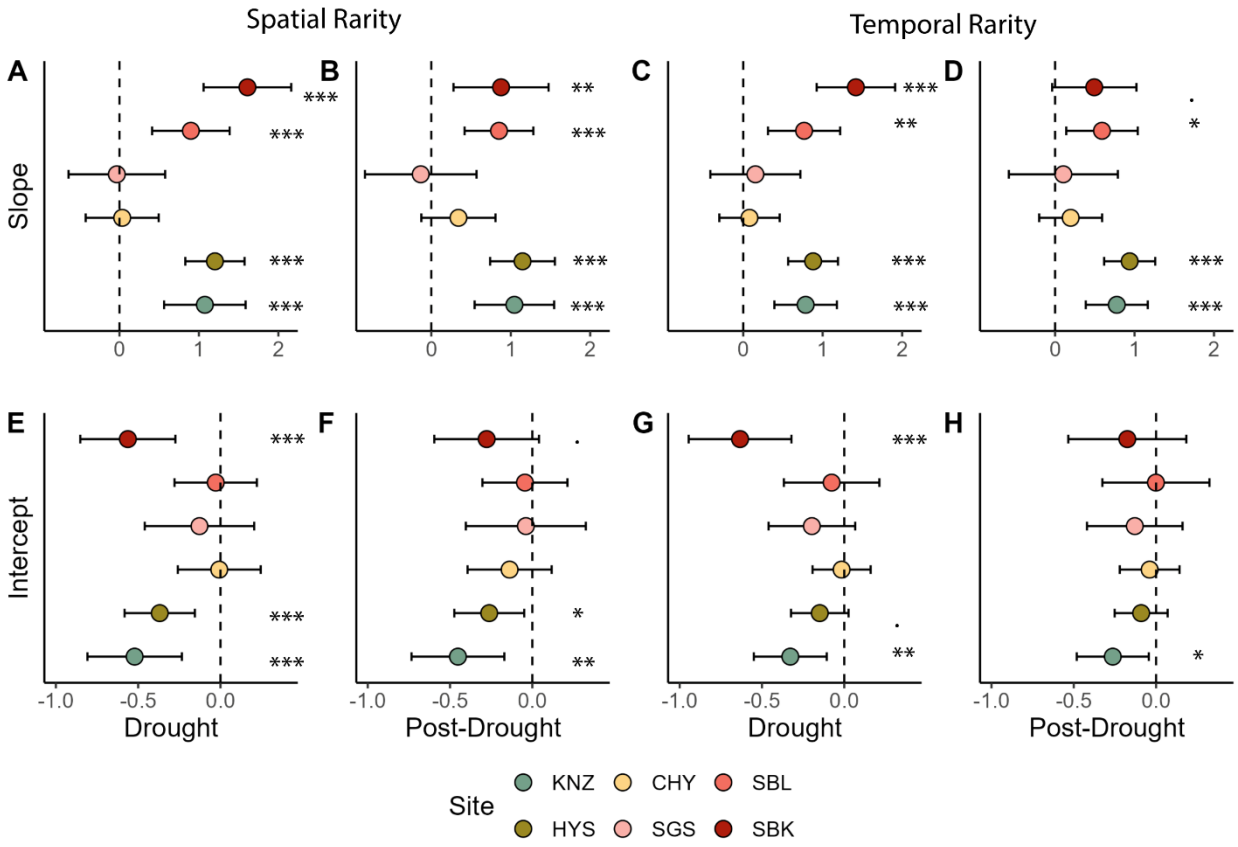

Figure S3.6. Coefficients from linear models testing the effect of rarity on response ratio individually at each site. Panels show both slope estimates (top row) and intercept estimates (bottom row) for spatial rarity models during drought (A, E) and post-drought (B, F) and temporal rarity models during drought (C, G) and post-drought (D, H). Error bars show the 95% confidence intervals of coefficients. Points are colored by site. *** < 0.001, ** <0.01, * <0.05, . <0.1. Further model details can be found in **Table S2** and **Table S3**.

Table S3.1. Correlation of spatial and temporal rarity by site

Site	Correlation
KNZ	0.949163
HYS	0.9515216
CHY	0.8644545
SGS	0.9007801
SBL	0.8288133
SBK	0.8622506

Table S3.2. Fixed effects coefficients for the linear mixed effects models exploring the overall effect of rarity on species' response ratio, with a random effect to account for differences in sites.

		Coeff	Estimate	Std. Error	Df	t value	Pr(>|t|)	
Drought	Spatial	Intercept	-0.30	0.09	9.15	-3.41	0.008	**
		Rarity	0.86	0.10	385.89	8.42	<0.001	***
	Temporal	Intercept	-0.22	0.06	10.08	-3.40	0.007	**
		Rarity	0.73	0.09	389.09	8.55	<0.001	***
Post-Drought	Spatial	Intercept	-0.23	0.08	11.47	-2.87	0.015	*
		Rarity	0.77	0.10	403.91	7.49	<0.001	***
	Temporal	Intercept	-0.13	0.07	11.43	-2.08	0.061	.
		Rarity	0.60	0.09	363.45	6.82	<0.001	***

Table S3.3. ANOVA table from linear mixed effects model of rarity and duration (annual vs. perennial) as predictors of the drought response ratio with site as a random effect.

		Coefficient	F	Df	Df.res	Pr(>F)	
Drought	Spatial	Intercept	0.410	1	40.271	0.526	
		Rarity	2.148	1	379.499	0.144	
		Duration	14.843	1	380.870	0.00012	**
		Rarity:Duration	9.915	1	379.443	0.0018	**
Post-Drought		Intercept	0.009	1	57.294	0.927	
		Rarity	10.096	1	394.754	0.0016	**
		Duration	5.135	1	395.908	0.024	*
		Rarity:Duration	0.911	1	394.753	0.340	

Table S3.4. Model coefficients from linear mixed effects models testing the effect of rarity and post-drought period (initial 2 years vs. final 2 years) on species' response ratios, with a random effect to account for differences in sites.

Rarity	Coeff	F	Df	Df.res	Pr(>F)	
Spatial	Rarity	71.409	1	704.128	<0.001	***
	PD period	2.137	1	704.471	0.144	
Temporal	Rarity	68.955	1	682.083	<0.001	***
	PD period	1.946	1	705.101	0.163	

Table S3.5. Model coefficients from site-level linear models exploring the effect of temporal rarity on species' response ratio.

	Site	Coeff	Estimate	Std Error	Statistic	p-value	
Drought	KNZ	Intercept	-0.328	0.111	-2.955	0.004	**
		Temporal rarity	0.786	0.197	3.986	<0.001	***
	HYS	Intercept	-0.149	0.088	-1.689	0.095	.
		Temporal rarity	0.880	0.158	5.570	<0.001	***
	CHY	Intercept	-0.016	0.088	-0.180	0.858	
		Temporal rarity	0.079	0.190	0.416	0.678	
	SGS	Intercept	-0.197	0.131	-1.503	0.139	
		Temporal rarity	0.154	0.282	0.545	0.588	
	SBL	Intercept	-0.077	0.145	-0.528	0.560	
		Temporal rarity	0.767	0.227	3.378	0.001	**
	SBK	Intercept	-0.633	0.156	-4.066	<0.001	***
		Temporal rarity	1.418	0.246	5.766	<0.001	***
Post-Drought	KNZ	Intercept	-0.263	0.110	-2.405	0.019	*
		Temporal rarity	0.776	0.195	3.980	<0.001	***
	HYS	Intercept	-0.091	0.081	-1.124	0.264	
		Temporal rarity	0.939	0.162	5.808	<0.001	***
	CHY	Intercept	-0.039	0.0911	-0.432	0.667	
		Temporal rarity	0.196	0.198	0.989	0.326	
	SGS	Intercept	-0.129	0.144	-0.900	0.373	
		Temporal rarity	0.104	0.340	0.305	0.762	
	SBL	Intercept	-0.001	0.163	-0.006	0.995	
		Temporal rarity	0.590	0.226	2.611	0.011	*
	SBK	Intercept	-0.175	0.179	-0.976	0.333	
		Temporal rarity	0.493	0.265	1.857	0.068	.

Table S3.6. Model coefficients from site-level linear models exploring the effect of temporal rarity on species' response ratio.

	Site	Coeff	Estimate	Std Error	Statistic	p-value	
Drought	KNZ	Intercept	-0.522	0.144	-3.632	<0.001	***
		Spatial rarity	1.075	0.257	4.180	<0.001	***
	HYS	Intercept	-0.369	0.107	-3.434	<0.001	***
		Spatial rarity	1.202	0.188	6.395	<0.001	***
	CHY	Intercept	-0.007	0.126	-0.058	0.954	
		Spatial rarity	0.035	0.230	0.150	0.881	
	SGS	Intercept	-0.128	0.165	-0.773	0.444	
		Spatial rarity	-0.033	0.302	-0.109	0.913	
	SBL	Intercept	-0.029	0.125	-0.230	0.819	
		Spatial rarity	0.899	0.244	3.687	<0.001	***
	SBK	Intercept	-0.563	0.144	-3.912	<0.001	***
		Spatial rarity	1.611	0.275	5.863	<0.001	***
Post-Drought	KNZ	Intercept	-0.452	0.141	-3.206	0.002	**
		Spatial rarity	1.045	0.250	4.179	<0.001	***
	HYS	Intercept	-0.262	0.107	-2.454	0.016	*
		Spatial rarity	1.148	0.205	5.606	<0.001	***
	CHY	Intercept	-0.138	0.128	-1.079	0.284	
		Spatial rarity	0.341	0.234	1.460	0.149	
	SGS	Intercept	-0.039	0.181	-0.218	0.829	
		Spatial rarity	-0.133	0.348	-0.384	0.703	
	SBL	Intercept	-0.045	0.130	-0.348	0.729	
		Spatial rarity	0.852	0.217	3.918	<0.001	***
	SBK	Intercept	-0.278	0.159	-1.743	0.086	.
		Spatial rarity	0.877	0.299	2.934	0.005	**

Table S3.7. Coefficients from linear models testing the effect of rarity on the response ratio during drought as a function of a site-level dominance index, site mean annual precipitation (mm), and site mean annual temperature (C).

Rarity	Predictor	Coefficient	Estimate	Std. Error	t value	Pr(>|t|)	
Spatial	Precipitation	Intercept	0.798	0.295	2.702	0.054	.
		Slope	0.135	0.323	0.418	0.698	
	Temperature	Intercept	0.798	0.134	5.958	0.004	**
		Slope	0.592	0.147	4.036	0.016	*
	Dominance	Intercept	-0.654	0.909	-0.719	0.512	
		Slope	3.209	1.943	1.652	0.174	
Temporal	Precipitation	Intercept	0.681	0.227	2.994	0.040	*
		Slope	0.019	0.249	0.076	0.943	
	Temperature	Intercept	0.681	0.108	6.313	0.003	**
		Slope	0.439	0.118	3.716	0.021	*
	Dominance	Intercept5	-0.638	0.571	-1.117	0.327	
		Slope	2.913	1.220	2.389	0.075	.

Table S3.8. Coefficients from linear models testing the effect of rarity on the response ratio post-drought as a function of a site-level dominance index, site mean annual precipitation (mm), and site mean annual temperature (C).

Rarity	Predictor	Coefficient	Estimate	Std. Error	t value	Pr(>|t|)	
Spatial	Precipitation	Intercept	0.688	0.195	3.534	0.024	*
		Slope	0.239	0.213	1.122	0.325	
	Temperature	Intercept	0.688	0.138	4.977	0.008	**
		Slope	0.384	0.152	2.536	0.064	.
	Dominance	Intercept	0.281	0.847	0.332	0.756	
		Slope	0.899	1.810	0.497	0.645	
Temporal	Precipitation	Intercept	0.516	0.110	4.678	0.009	**
		Slope	0.216	0.121	1.783	0.149	
	Temperature	Intercept4	0.516	0.099	5.227	0.006	**
		Slope	0.241	0.108	2.228	0.090	.
	Dominance	Intercept5	0.439	0.577	0.761	0.489	
		Slope	0.172	1.232	0.139	0.896	

APPENDIX C.

SUPPLEMENTAL MATERIALS FOR CHAPTER III

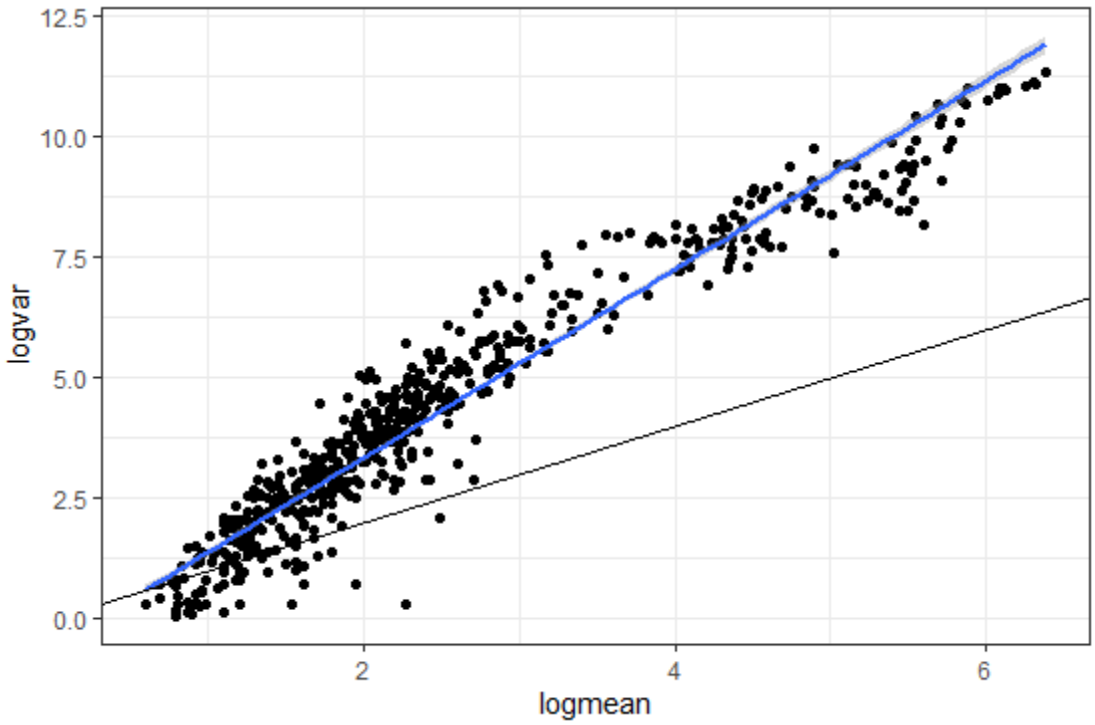

Figure S4.1. The log mean cover vs. the log variance of each species in each plot. The blue line is the linear relationship between the mean total cover and the variance of total cover, while the black line has slope z = 1. The portfolio effect is enhanced by species richness when the variances in species abundances increase more steeply than their mean abundances, or when $1 < z < 2$ *(Doak et al., 1998b)*. The slope of the blue line is, z = 1.95, indicating that species richness can be used as a metric of the portfolio effect in our system because the variance of total cover increases more steeply than the mean of total cover.

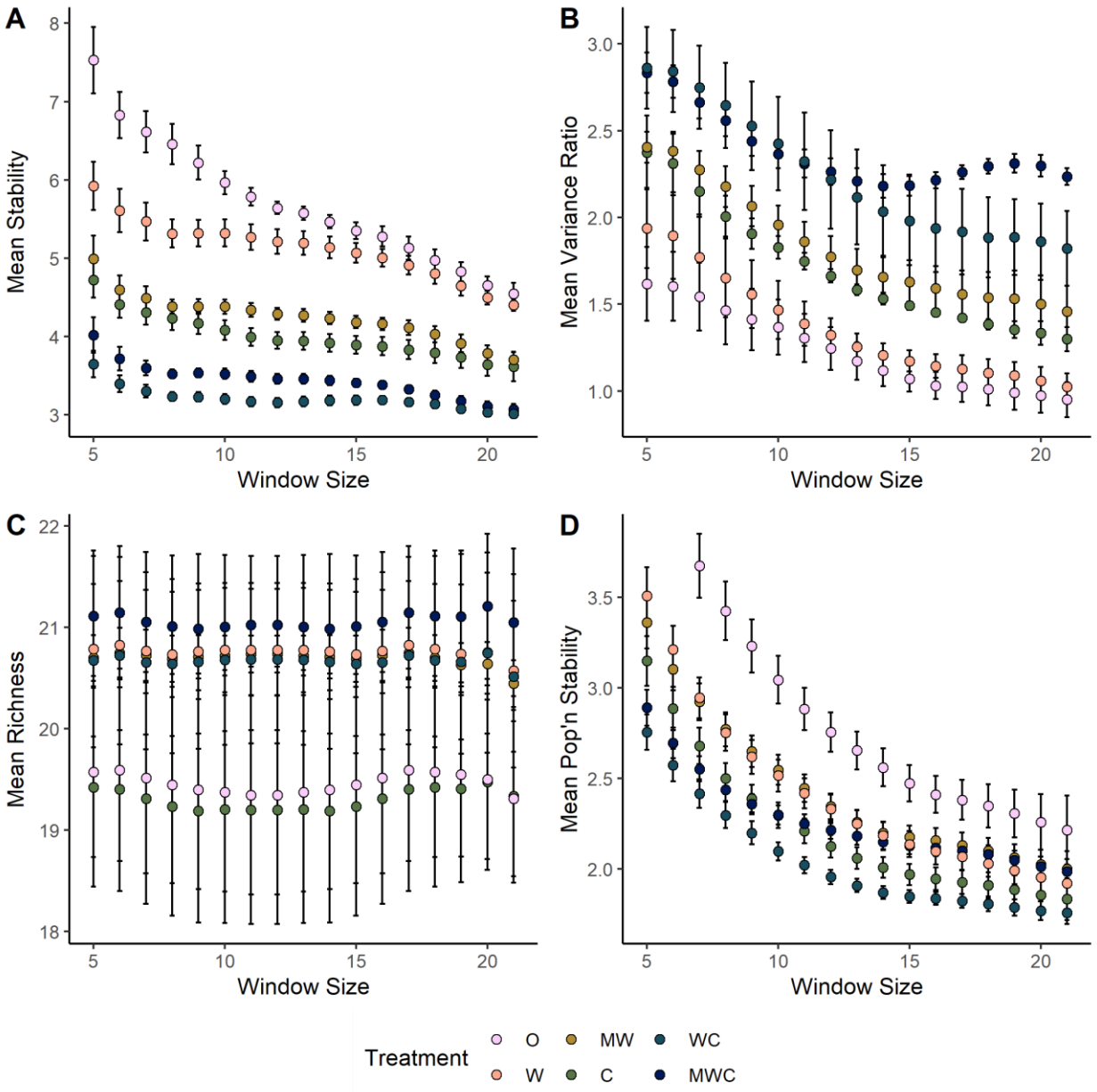

Figure S4.2. The mean temporal stability (A), variance ratio (B), species richness (C), and population stability (D) for each window size ranging from 5-21 years. We calculated these metrics over a subset (window) of the data set. The starting point of this window was shifted one time point until the whole time series was covered. This calculation was then done for each window size ranging from 5-21 years and the mean was calculated for each window size. Bars are one standard error. Herbivore treatments (ordered by total herbivore biomass) are: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C = Cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

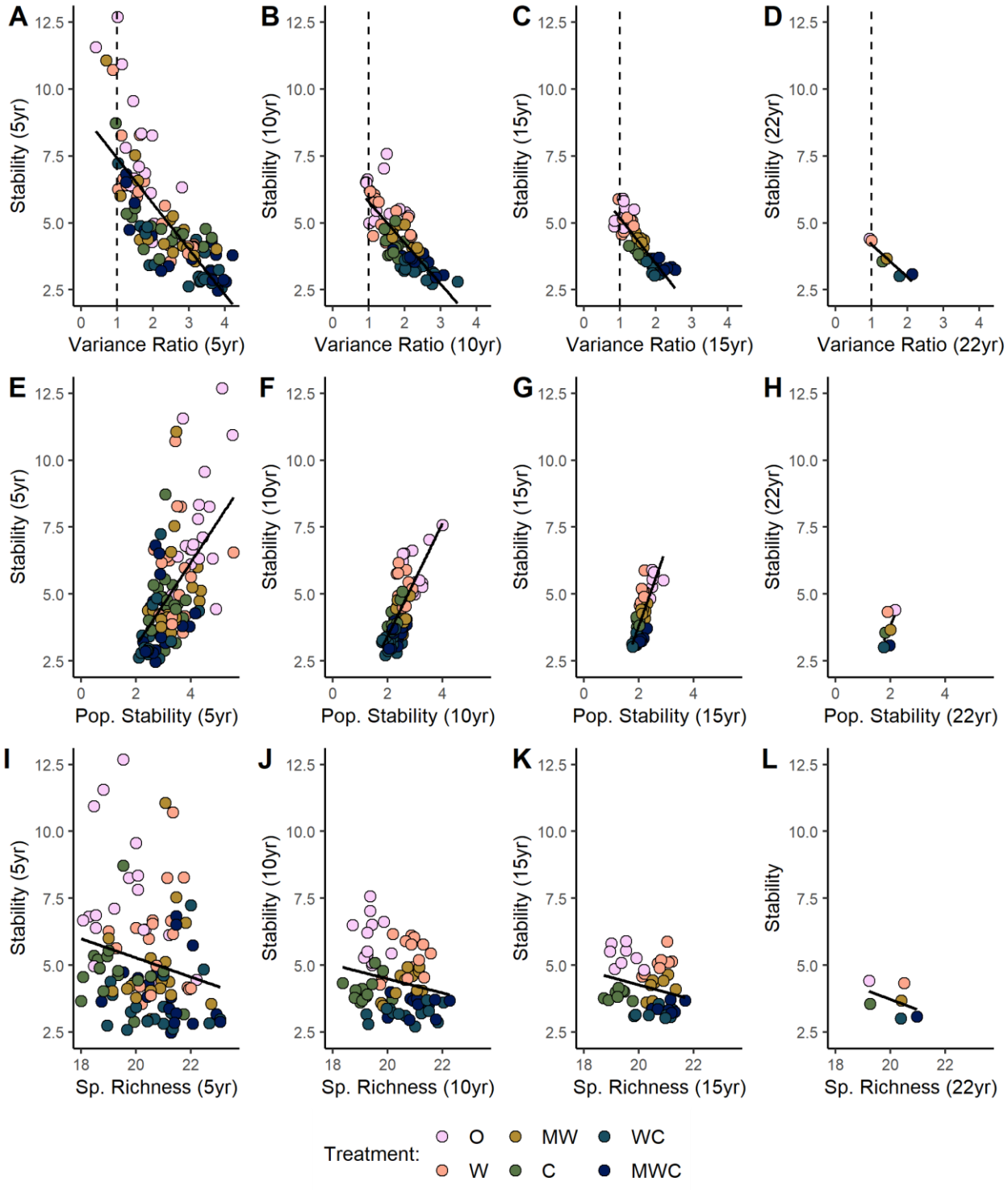

Figure S4.3. The relationship between the mean temporal stability and biotic stability mechanisms (synchrony A – D, population stability E – H, and species richness I – L) at four timescales: 5 years (column 1), 10 years (column 2), 15 years (column 3), and the full time series of 22 years (column 4). Timescales of 5-, 10-, and 15- years are over a moving window. A variance ratio less than one indicates asynchronous dynamics, and greater than one indicates

synchronous dynamics. Points are colored by herbivore treatment. Herbivore treatments (ordered by total herbivore biomass) are: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C = Cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

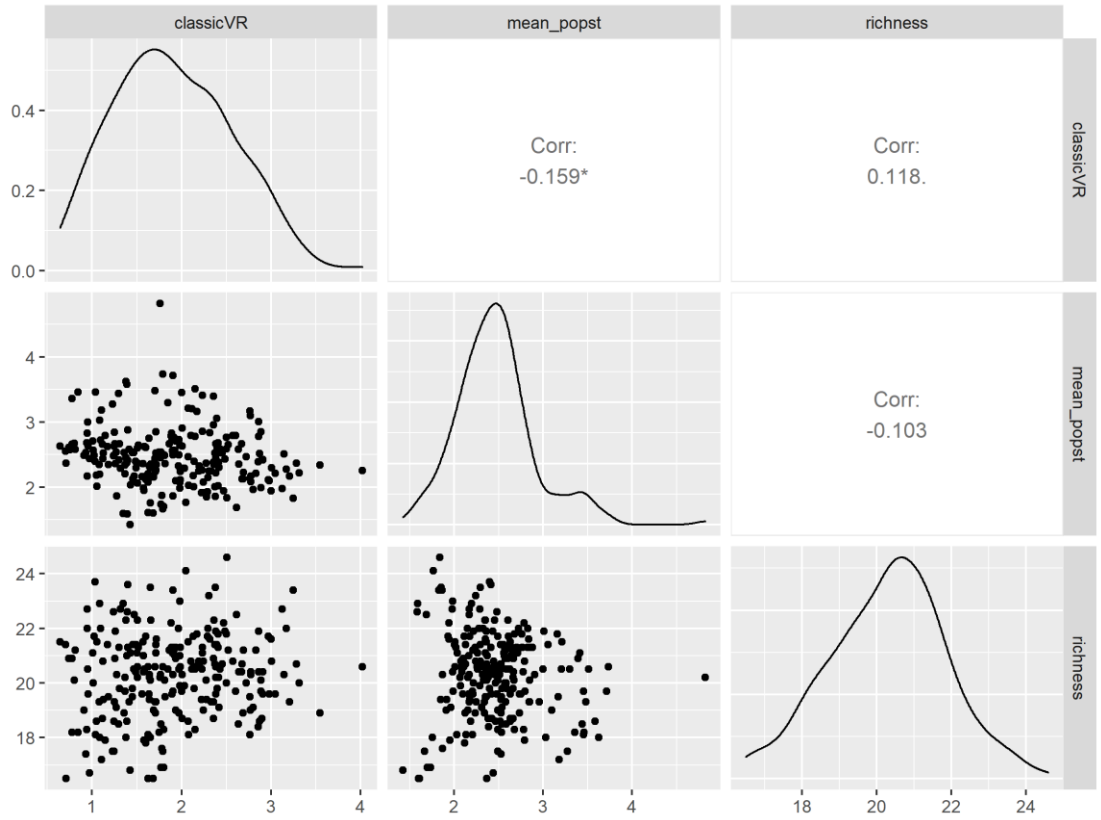

Figure S4.4. Correlation matrix of the variance ratio (classicVR), the dominant species population stability (mean_popst), and species richness (richness) all calculated over 10-year moving windows.

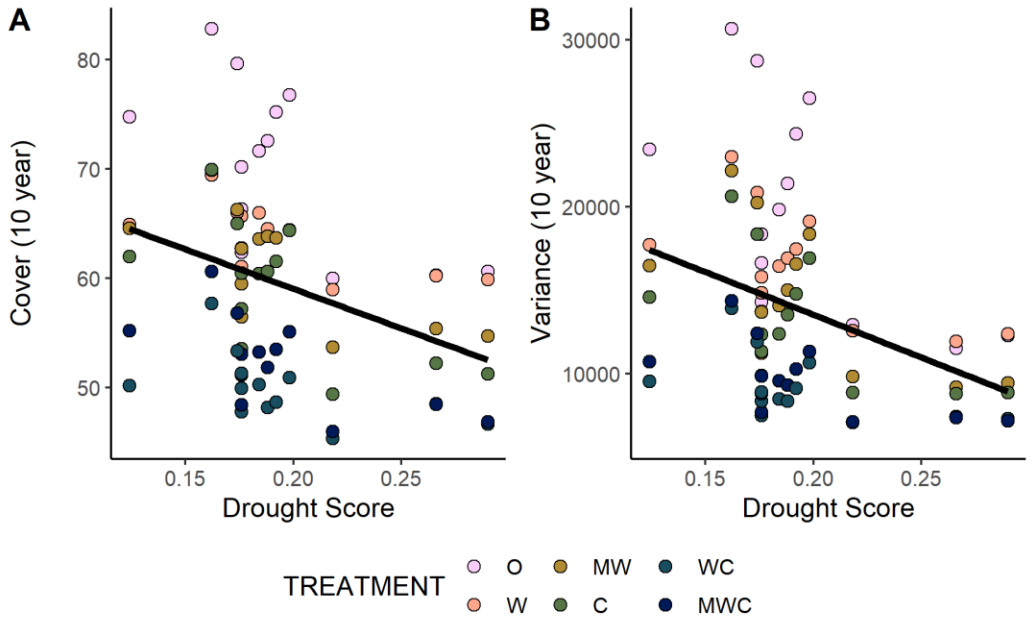

Figure S4.5. The total herbaceous cover (A), and the variance of herbaceous cover (B) as a function of the drought score. Points are colored by herbivore treatment, arranged in order of herbivore pressure measured in kg herbivores/km^2 (Veblen et al. 2016). Treatment abbreviations are as follows: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C = cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

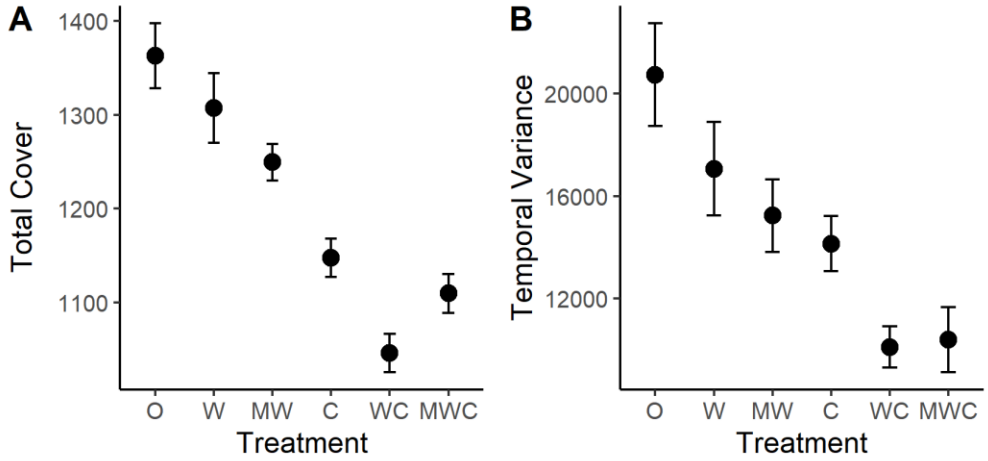

Figure S4.6. The total herbaceous cover (A), and the variance of herbaceous cover (B) for each herbivore treatment. Herbivore treatments are arranged in order of herbivore pressure, measured in kg herbivores/km2 (Veblen et al. 2016). Bars are one standard error. Treatment abbreviations are as follows: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C = cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

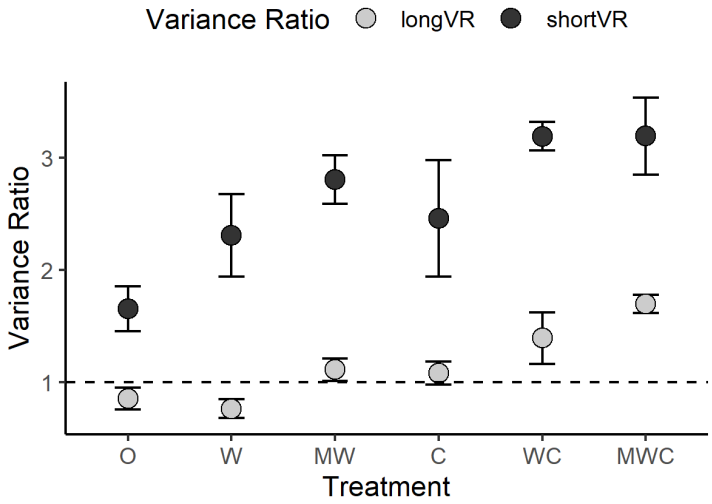

Figure S4.7. The timescale-specific variance ratio divided into the short variance ratio (less than 4 years) and long variance ratio (greater than 4 years) for each herbivore treatment. A variance ratio less than one indicates asynchronous dynamics, and greater than one indicates synchronous dynamics. Bars are one standard error. Herbivore treatments (ordered by total herbivore biomass) are: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C = Cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

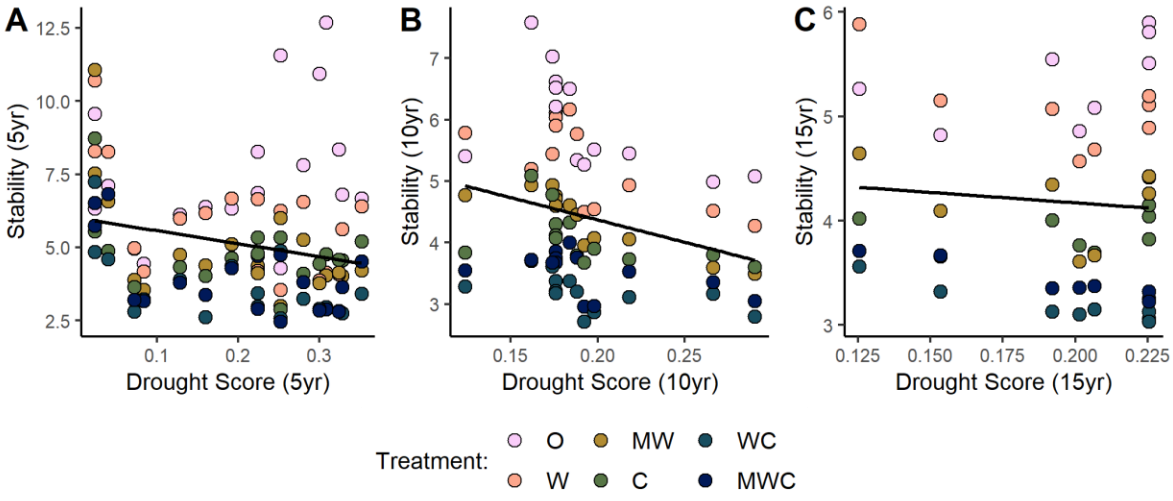

Figure S4.8. The relationship between temporal stability (μ/σ) of herbaceous cover and the drought score calculated at three timescales: 5-year moving window (A), 10-year moving window (B), and 15-year moving window (C). Higher drought score values indicate more severe drought. The black regression lines are plotted to show the trend, but do not correspond to a model. Herbivore treatments (ordered by total herbivore biomass) are: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C = Cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

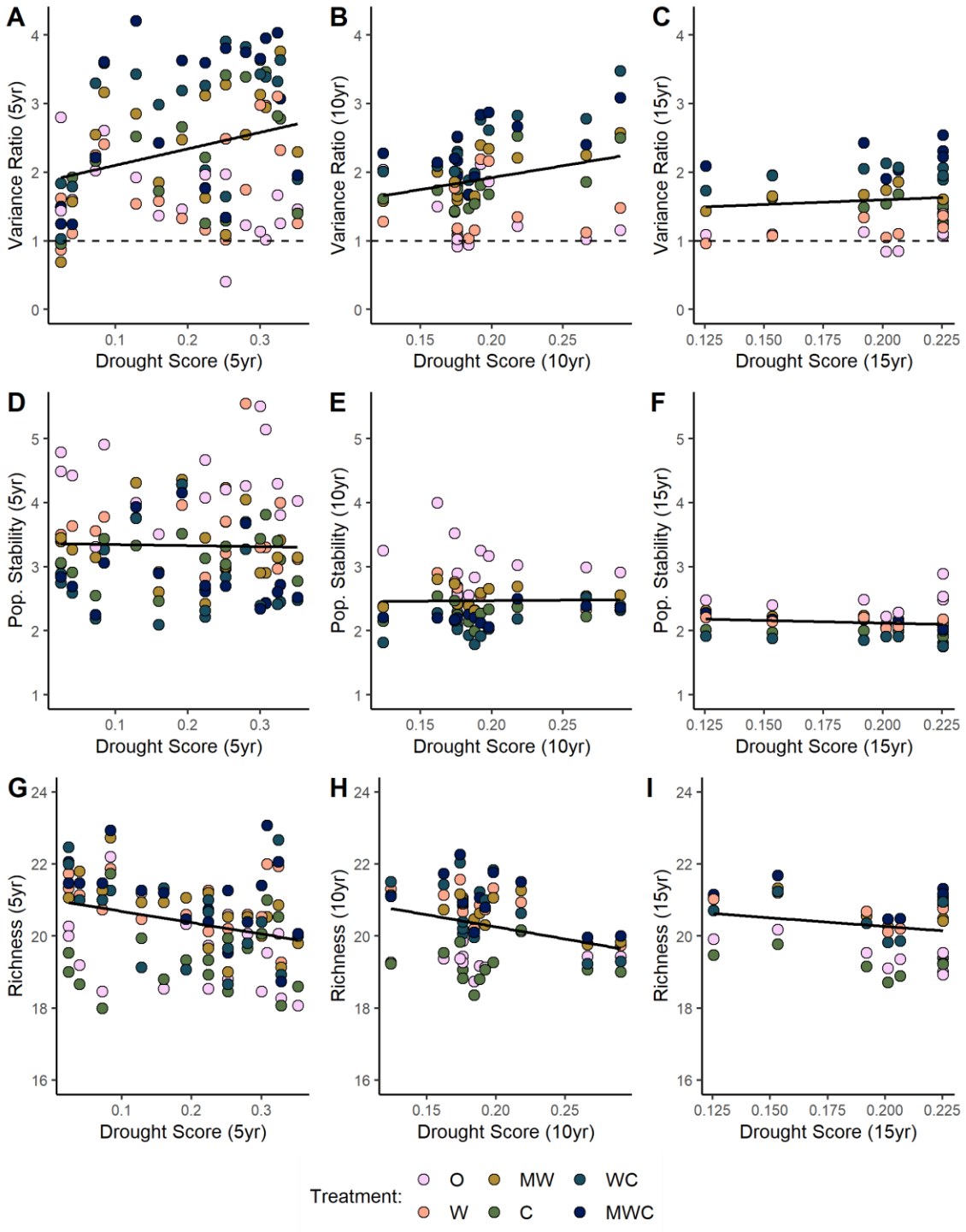

Figure S4.9. The relationship between the drought score and underlying biotic mechanisms: synchrony (A – C), dominant species population stability (D – F), and species richness (G – I) at three different timescales (5-years, 10-years, and 15-years). Higher drought score values indicate more severe drought. Herbivore treatments (ordered by total herbivore biomass) are: O = No herbivores, W = Wild mesoherbivores, MW = Wild megaherbivores and wild mesoherbivores, C

= Cattle, WC = Wild mesoherbivores and cattle, MWC = Wild megaherbivores, wild mesoherbivores, and cattle.

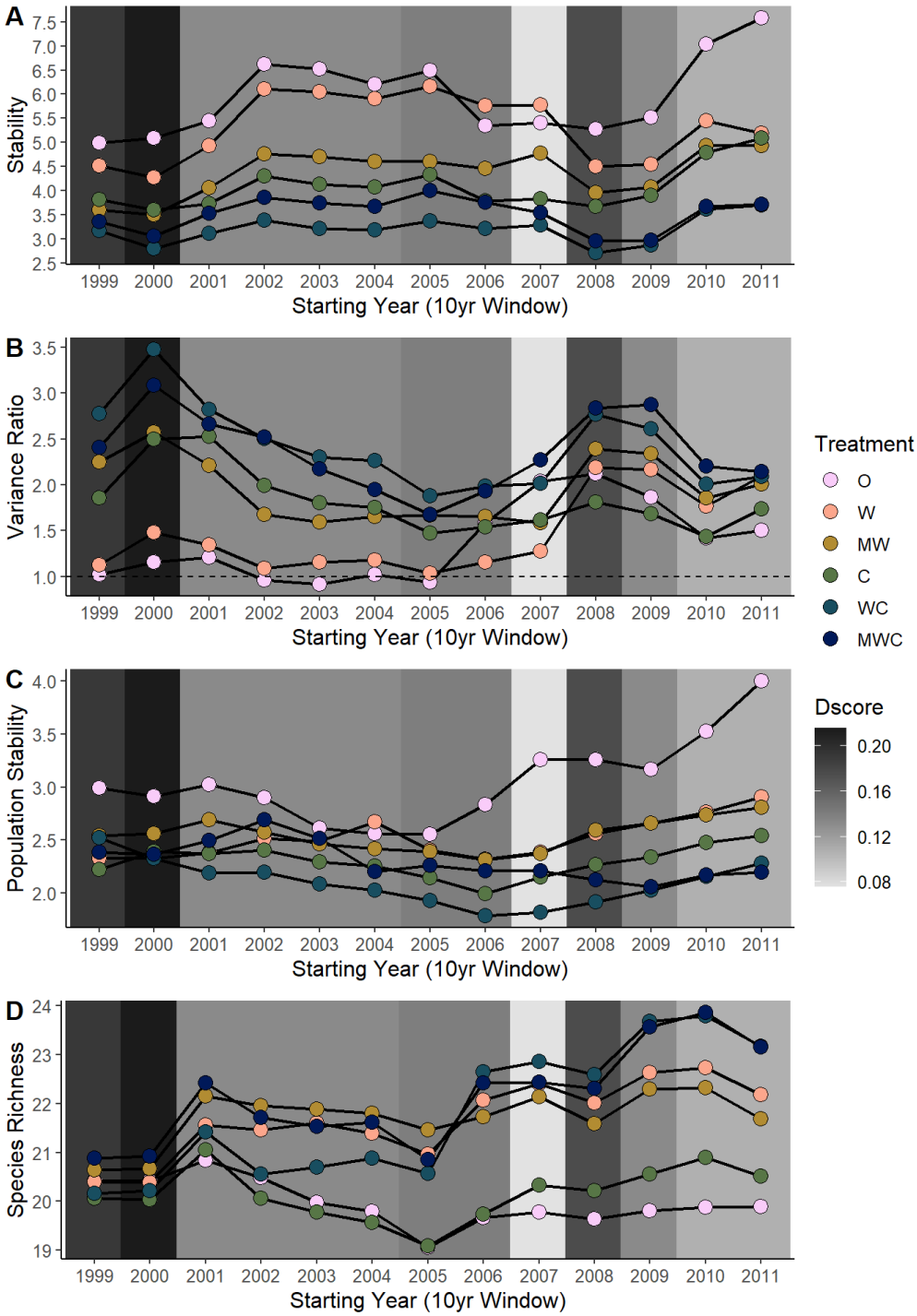

Figure S4.10. Stability (A), the classic variance ratio (B), the mean population stability of the dominant species (C), and the mean species richness (D) are calculated over a 10-year subset (window) of the data set. The starting point of this window is shifted one time point until the

whole data set has been covered. Point color indicates the herbivore treatment while background color indicates the drought score of a window, which is a function of the number and severity of droughts in a window. A variance ratio less than one indicates compensatory dynamics, and greater than one indicates synchronous dynamics.

Table S4.1. Variance inflation factors of predictors in the following three piecewise SEM models: mesoherbivores, megaherbivores, cattle.

	Model	Drought	Herbivory	Synchrony	Population stability	Richness
Mesoherbivores	Stability ~ drought + mesoherbivores + variance ratio + population stability + richness	1.10	1.51	1.19	1.12	1.32
	Variance ratio ~ drought + mesoherbivores + richness	1.04	1.27			1.32
	Population stability ~ drought + mesoherbivores	1	1			
	Richness ~ drought + mesoherbivores	1	1			
Megaherbivores	Stability ~ drought + megaherbivores + variance ratio + population stability + richness	1.10	1.15	1.18	1.03	1.13
	Variance ratio ~ drought + megaherbivores + richness	1.04	1.07			1.11
	Population stability ~ drought + megaherbivores	1	1			
	Richness ~ drought + megaherbivores	1	1			
Cattle	Stability ~ drought + cattle + variance ratio + population stability + richness	1.12	1.79	1.44	1.42	1.09
	Variance ratio ~ drought + cattle + richness	1.03	1			1.03
	Population stability ~ drought + cattle	1	1			
	Richness ~ drought + cattle	1	1			

Table S4.2. AICc and Δ AIC_c values from linear mixed effects models of stability calculated over the full time series and over a 10-year moving window as a function of herbivory (first model) and drought and herbivory (second model).

Model/Predictor variables	**AIC_c**	**Δ AIC_c**
Stability ~ cattle + mesoherbivores	29.2	0.00
Stability ~ cattle + megaherbivores	29.4	0.23
Stability ~ cattle	**31.0**	**1.86**
Stability ~ cattle + mesoherbivores + megaherbivores	32.2	3.05
Stability ~ 1	42.3	13.11
Stability (10yr) ~ drought score + cattle + mesoherbivores	455.6	0.00
Stability (10yr) ~ drought score + cattle + mesoherbivores + megaherbivores	457.3	1.66

Table S4.2. (continued).

Model/Predictor variables	AIC_c	ΔAIC_c
Stability (10yr) ~ drought score + cattle + megaherbivores	460.1	4.43
Stability (10yr) ~ drought score + cattle	461.9	6.30
Stability (10yr) ~ drought score + mesoherbivores	473.7	18.05
Stability (10yr) ~ 1	532.9	77.31

The top five models and the null model are shown. For models of stability over the full time series, the null model was one of the top five. Bolded models are presented in the main text.

Table S4.3. Model outputs from top ranked models that are not included in main text.

Model	Variable	Coeff.	Std. Error	t
Stability ~ cattle + mesoherbivores	*Main effects*			
	Intercept	4.45	0.18	25.05
	Cattle	-0.92	0.14	-6.66
	Mesoherbivores	-0.46	0.15	-3.12
Stability ~ cattle + megaherbivores	Main effects			
	Intercept	4.29	0.16	27.45
	Cattle	-0.92	0.14	-6.60
	Megaherbivores	-0.45	0.15	-3.05
Stability (10yr) ~ drought score + cattle + mesoherbivores + megaherbivores	*Main effects*			
	Intercept	7.25	0.31	23.22
	Drought score	-7.28	0.89	-8.16
	Cattle	-1.62	0.25	-6.57
	Mesoherbivores	-0.76	0.30	-2.52
	Megaherbivores	-0.31	0.30	-1.02
Population stability (10yr) ~ cattle + mesoherbivores	*Main effects*			
	Intercept	2.91	0.12	24.60
	Cattle	-0.47	0.11	-4.38
	Mesoherbivores	-0.31	0.11	-2.68
Population stability (10yr) ~ drought score + cattle + mesoherbivores	*Main effects*			
	Intercept	2.88	0.15	19.36
	Drought score	0.15	0.47	0.33
	Cattle	-0.47	0.11	-4.38
	Mesoherbivores	-0.31	0.11	-2.68
Richness (10yr) ~ drought score + mesoherbivores + megaherbivores	*Main effects*			
	Intercept	20.60	0.56	36.69
	Drought score	-6.73	1.24	-5.41
	Mesoherbivores	1.44	0.72	2.01
	Megaherbivores	0.13	0.72	0.19
Richness (10yr) ~ drought score + cattle + mesoherbivores	*Main effects*			
	Intercept	20.59	0.63	32.50
	Drought score	-6.73	1.24	-5.41
	Cattle	0.01	0.59	0.01
	Mesoherbivores	1.51	0.62	2.42

Table S4.4. AICc and Δ AIC_c values from linear mixed effects models of 1) the variance ratio, 2) dominant species population stability, and 3) species richness calculated over a 10-year moving window as functions of drought and herbivory.

Model/Predictor variables	AIC_c	Δ AIC_c
Variance ratio (10yr) ~ drought score + cattle + mesoherbivores	**348.8**	**0.00**
Variance ratio (10yr) ~ drought score + cattle + mesoherbivores + megaherbivores	351.0	2.22
Variance ratio (10yr) ~ drought score + cattle + megaherbivores	351.2	2.41
Variance ratio (10yr) ~ drought score + cattle	352.6	3.78
Variance ratio (10yr) ~ drought score + mesoherbivores	357.7	8.90
Variance ratio (10yr) ~ 1	379.5	30.75
Population stability (10yr) ~ cattle + mesoherbivores	148.7	0.00
Population stability (10yr) ~ cattle	**150.2**	**1.53**
Population stability (10yr) ~ drought score + cattle + mesoherbivores	150.4	1.72
Population stability (10yr) ~ drought score + cattle	151.9	3.22
Population stability (10yr) ~ cattle + mesoherbivores + megaherbivores	152.3	3.56
Population stability (10yr) ~	156.0	7.28
Richness (10yr) ~ drought score + mesoherbivores	**622.1**	**0.00**
Richness (10yr) ~ drought score + mesoherbivores + megaherbivores	623.0	0.95
Richness (10yr) ~ drought score + cattle + mesoherbivores	623.5	1.39
Richness (10yr) ~ drought score + cattle + mesoherbivores + megaherbivores	624.4	2.29
Richness (10yr) ~ drought score + megaherbivores	625.8	3.77
Richness (10yr) ~	654.1	32.06

The top five models and the null model are shown. Bolded models are presented in the main text.

Table S4.5. AICc and Δ AIC_c values from linear mixed effects models of biotic stability mechanisms as functions of herbivore treatment with block as a random effect.

Model/Predictor variables	AIC_c	Δ AIC_c
Variance ratio ~ cattle + megaherbivores	**20.8**	**0.00**
Variance ratio ~ cattle + mesoherbivores + megaherbivores	23.5	2.74
Variance ratio ~ cattle + mesoherbivores	24.7	3.92
Variance ratio ~ cattle	27.3	6.56
Variance ratio ~ megaherbivores	31.6	10.83
Variance ratio ~ 1	32.7	11.96
Population stability ~ 1	**8.3**	**0**
Population stability ~ cattle	11.1	2.74
Population stability ~ mesoherbivores	13.6	5.27
Population stability ~ megaherbivores	13.9	5.58
Population stability ~ cattle + mesoherbivores	16.9	8.62
Richness ~ mesoherbivores	**64.0**	**0.00**
Richness ~ 1	66.4	2.42
Richness ~ mesoherbivores + megaherbivores	66.8	2.81
Richness ~ megaherbivores	67.1	3.05
Richness ~ cattle + mesoherbivores	67.3	3.26

The top five models and the null model are shown. Bolded models are presented in the main text.

Table S4.6. AICc and Δ AIC_c values from linear mixed effects models of stability as a function of biotic mechanisms and block as a random effect.

Model/Predictor variables	**AIC_c**	**Δ AIC_c**
Stability ~ variance ratio + population stability	**14.2**	**0**
Stability ~ variance ratio + population stability + species richness	18.4	4.26
Stability ~ variance ratio	21.5	7.31
Stability ~ variance ratio + species richness	28.4	14.26
Stability ~ population stability	40.8	26.64
Stability ~ 1	42.3	28.12

The top five models and the null model are shown. Bolded models are presented in the main text.

Table S4.7. Model outputs from the Mesoherbivore structural equation model.

Response	**Predictor**	**Est.**	**Std Err**	**DF**	**Crit Val**	**P-val**	**Std. Est.**
Stability	Drought	-3.39	0.85	228	-3.99	0.0001	-0.116
Stability	Mesoherbivores	-0.01	0.09	228	-0.07	0.945	-0.002
Stability	Synchrony	-1.10	0.06	228	-19.58	0	-0.593
Stability	Population Stability	1.54	0.08	228	19.54	0	0.574
Stability	Richness	0.04	0.02	228	1.77	0.0777	0.056
Variance Ratio	Drought	3.46	0.96	228	12.86	0.0004	0.220
Variance Ratio	Mesoherbivores	0.46	0.09	228	24.13	0	0.333
Variance Ratio	Richness	-0.003	0.03	229	0.01	0.9181	-0.007
Population Stability	Drought	0.15	0.66	229	0.05	0.8194	0.014
Population Stability	Mesoherbivores	-0.31	0.06	229	27.56	0	-0.319
Richness	Drought	-6.73	2.15	229	9.81	0.002	-0.179
Richness	Mesoherbivores	1.51	0.19	229	63.25	0	0.454

All variables in the model were calculated over a 10-year moving window. Goodness of Fit values were: C = 4.00, p = 0.406, df = 4.

Table S4.8. Model outputs from the Megaherbivore structural equation model.

Response	**Predictor**	**Est.**	**Std Err**	**DF**	**Crit Val**	**P-val**	**Std. Est.**
Stability	Drought	-3.44	0.83	228	-4.12	0.0001	-0.118
Stability	Megaherbivores	-0.22	0.08	228	-2.98	0.0032	-0.087
Stability	Synchrony	-1.06	0.05	228	-19.30	0	-0.571
Stability	Population Stability	1.54	0.07	228	20.75	0	0.575
Stability	Richness	0.06	0.02	228	2.59	0.0102	0.075
Variance Ratio	Drought	3.71	0.97	228	14.45	0.0002	0.236
Variance Ratio	Megaherbivores	0.36	0.09	228	17.03	0.0001	0.260
Variance Ratio	Richness	0.03	0.03	229	1.59	0.2079	0.082

Table S4.8. (continued).

Response	Predictor	Est.	Std Err	DF	Crit Val	P-val	Std. Est.
Population Stability	Drought	0.15	0.70	229	0.05	0.8288	-0.014
Population Stability	Megaherbivores	-0.07	0.06	229	1.14	0.2872	-0.069
Richness	Drought	-6.73	2.34	229	8.26	0.0044	-0.179
Richness	Megaherbivores	0.85	0.21	229	17.09	0.0001	0.257

All variables in the model were calculated over a 10-year moving window. Goodness of Fit values were: C = 8.86, p = 0.065, df = 4.

Table S4.9. Model outputs from the Cattle structural equation model.

Response	Predictor	Est.	Std Err	DF	Crit Val	P-val	Std. Est.
Stability	Drought	-3.92	0.82	228	-4.78	0	-0.134
Stability	Cattle herbivory	-0.40	0.09	228	-4.66	0	-0.165
Stability	Synchrony	-0.97	0.06	228	-16.46	0	-0.523
Stability	Population Stability	1.34	0.08	228	15.77	0	0.498
Stability	Richness	0.03	0.02	228	1.31	0.1912	0.036
Variance Ratio	Drought	3.90	0.88	228	19.55	0	0.248
Variance Ratio	Cattle herbivory	0.61	0.07	228	71.12	0	0.465
Variance Ratio	Richness	0.06	0.02	229	7.04	0.0085	0.150
Population Stability	Drought	0.15	0.59	229	0.07	0.7985	0.014
Population Stability	Cattle herbivory	-0.47	0.05	229	91.98	0	-0.521
Richness	Drought	-6.73	2.43	229	7.69	0.006	-0.179
Richness	Cattle herbivory	0.01	0.20	229	0.0012	0.9730	0.002

All variables in the model were calculated over a 10-year moving window. Goodness of Fit values were: C = 13.79, p = 0.008, df = 4.

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