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Unraveling the Processes of Plant Community Assembly In an Era of Global Change: Insights From a Dryland Ecosystem

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Tesa R. Madsen-Hepp

December 2024

Dissertation Committee:
- Dr. Marko Spasojevic, Chairperson
- Dr. Janet Franklin
- Dr. Loralee Larios
- Dr. Kurt Anderson

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2024

The Dissertation of Tesa R. Madsen-Hepp is approved:

Committee Chairperson

University of California, Riverside

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The text of Chapter 1 of this dissertation is a reprint of the material as it appears in “Plant functional traits predict heterogeneous distributional shifts in response to climate change”, Functional Ecology, 2023.

DEDICATION

This dissertation is dedicated to my precious daughter, Flora, and all children comprising the incoming generation. May our increased understanding of nature inspire a more beautiful future for humanity where we recognize our interdependence with each other and with the more-than-human multispecies entanglements that we call collectively “biodiversity”.

ABSTRACT OF THE DISSERTATION

Unraveling the Processes of Plant Community Assembly In an Era of Global Change: Insights From a Dryland Ecosystem

by

Tesa R. Madsen-Hepp

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, December 2024
Dr. Marko Spasojevic, Chairperson

Global climate change is driving the rapid redistribution of plant species, and, in dryland ecosystems in particular, we lack an understanding of how species have and will continue to respond to novel abiotic conditions. This gap exists largely because, while the performance of plant species is influenced by abiotic conditions, interactions with co-occurring species at the community level are also key determinants of their persistence and success. Thus, to predict the novel plant assemblages of the future, we require a more mechanistic understanding of how plant species respond to variation in both abiotic and biotic conditions simultaneously. In this dissertation, I investigate how plant functional traits of populations can explain interspecific responses to long-term climate change (Chapter 1), how biotic interactions at the level of the community interact with abiotic drivers to structure the functional composition of plant assemblages (Chapter 2), and how the plant functional diversity of the surrounding neighborhood influences the interaction outcome of a focal species across drought conditions (Chapter 3). To address these questions, I utilized fine-scale observational plant community data from a steep elevational gradient in the desert mountains of southern California and a greenhouse experiment manipulating community trait diversity across contrasting abiotic conditions. In Chapter 1, I documented substantial range shifts among perennial species across a large aridity gradient and showed that functional traits related to resource use and biotic interactions are predictive of range dynamics spanning the last forty years. In Chapter 2, I discovered that both competition and facilitation are ubiquitous in plant communities and that their relative prevalence varies with abiotic conditions to structure the functional trait composition of plant communities. In Chapter 3, I show that both the community functional composition of neighboring species, the trait values of a focal species, and the distance between the two are all important determinants of the net interaction outcome of a focal species when growing in diverse assemblages. Overall, my dissertation highlights that plant functional traits sampled at the appropriate scale can lend predictability to species' distributions and community-level interspecific interactions and that patterns of functional trait composition can be explained by accounting for diverse interactions and how they change across environmental gradients.

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Introduction

Anthropogenic climate change is causing shifts in the distributions of plants around the world. As species try to cope with rapidly changing conditions, a general upward shift to higher elevations and latitudes has been observed in many instances (Chen et al., 2011; Kelly & Goulden, 2008; Lenoir et al., 2008). However, there is substantial variability in species' responses—in the rate, magnitude, and even direction from that expected due to global warming trends -- with some species even moving downslope to warmer climates (Crimmins et al., 2011; Lenoir & Svenning, 2015; Rapacciuolo et al., 2014). To forecast long-term dynamics for terrestrial ecosystems, it is critical to better understand the mechanisms governing plant species' range redistributions. In general, climate influences species' geographical ranges by restricting which plant species can persist under a given set of climatic conditions. This can broadly be predicted based on the functional traits (morphological and physiological characteristics) of plant species which allow them to establish and persist in a given environment (Violle et al., 2014). Climate change is expected to reorganize vegetation patterns by imposing novel limitations on these traits, which will have cascading impacts on the functioning of ecosystems (Madani et al., 2018).

Furthermore, while temperature and precipitation are widely understood to be important drivers of plants' distribution and performance (e.g., Humboldt & Bonpland,1805; Adler et al. 2014), recent pioneering studies have shown that interactions among plant species are critical to determining patterns of plant diversity under novel climatic conditions (Alexander et al., 2015; Catford et al., 2020). However, since these critical species interactions are context-dependent, it is unclear how their outcomes might be altered along with shifts in climate, what their relative importance will be compared to direct abiotic changes, and what the consequences of both will be for future biodiversity patterns. Therefore, there is an urgent need to understand how community-level plant-plant interactions influence patterns of functional diversity, and how their variation across abiotic gradients might contribute to turnover in community taxonomic and functional composition. To more realistically predict how vegetation patterns will respond to ongoing climatic variation, we need to shift our focus to the level of the community—the nexus of species interactions—and refine our understanding of how both biotic and abiotic factors interactively structure the diversity of plant communities (Cazelles et al., 2016; Hillerislambers et al., 2012; Lavergne et al., 2010).

While climate change is rapidly altering ecosystems worldwide, our understanding of the impact on dryland ecosystems is notably sparse compared to more mesic ecosystems, which is concerning given that dryland ecosystems constitute >40% of the global terrestrial landmass—the largest of any single biome—and are a dominant driver of global biogeochemical cycling (Ahlström et al., 2015). This knowledge gap is additionally concerning given that dryland ecosystems are already experiencing extensive drought-induced plant mortality of stress-tolerant species, due to anthropogenic-driven elevated temperatures and increased chronic and extreme drought (Williams et al., 2020), which is leading to widespread ecosystem-type conversion (Batllori et al., 2020; Berdugo et al., 2020; Breshears et al., 2005). Indeed, while drylands have been perceived as resilient to heat and drought, a growing body of literature shows the high sensitivity of dryland ecosystems to climate change (Burrell et al., 2020; Schlaepfer et al., 2017; Shriver et al., 2022). This could partially be due to the unique mechanisms of plant community organization among dryland plant species, such as facilitation-mediated recruitment that breaks down with the mortality of dominant stress-tolerant species (Shriver et al., 2022). Given that the ecological mechanisms that uniquely govern dryland ecosystem functioning—such as drying-wetting cycles, photodegradation, and plant-plant facilitation—will likely govern other ecosystems under globally warmer conditions (Berdugo et al., 2020; Grünzweig et al., 2022), it is critical that we increase our mechanistic understanding of how plant species in dryland ecosystems respond to abiotic and biotic changes that will accompany a rise in global average temperatures.

A recent conceptual synthesis in community ecology recognizes that, like alleles in a population, the functional diversity of species in a regional species pool provides the template for niche selection (changes in presence or abundance of species owing to deterministic fitness differences), which, in combination with ecological drift (random fluctuations in species' relative abundances with respect to their identities), dispersal (movement of individuals from one place to another), and ongoing speciation (divergence of former discrete entities into multiple new discrete entities), produce the patterns of biodiversity in nature (Spasojevic et al., 2018; Vellend, 2010). This synthesis has led to a revised model of the theory of community assembly which considers species' functional traits, rather than taxonomic identity, as determinants of their differential success in contrasting environments (Fukami et al., 2005; Keddy, 1992; McGill et al., 2006). Within this framework, abiotic niche selection on species' traits comprises the primary filter, which restricts membership in a community, followed by biotic niche selection comprising the next successive filter operating at the scale of local assemblages, which then determines species' relative abundances. However, trait-based approaches to community assembly have yet to appropriately account for three key issues incommunity assembly theory: 1) species within communities interact in a variety of ways, not exclusively via resource competition, 2) the outcome of interactions is contingent on the entire neighborhood, not just on pairwise relationships; and 3) the strength, outcome, and importance of interactions are mediated by abiotic conditions.

First, while community assembly theory has often focused on competitive interactions, positive interactions also occur among plants and can play a central role in mediating patterns of plant community diversity (Brooker et al., 2008; Kikvidze et al., 2015). Plant-plant facilitation can occur through direct mechanisms, such as through the amelioration of environmental stressors such as heat or drought, or indirectly, by providing defense against herbivory or suppressing competitors (Mcintire & Fajardo, 2014). While facilitative interactions have previously been assumed to occur only under conditions of severe environmental stress, recent work suggests a more ubiquitous nature of facilitative interactions in plant communities (Bimler et al., 2024; Wright et al., 2015). Importantly, recent work has shown that facilitative interactions, by modifying abiotic conditions that attenuate the larger abiotic filter, may increase taxonomic, functional, and phylogenetic community diversity (Chacón-Labella et al., 2016; Madrigal-González et al., 2020; Schöb et al., 2012).

Second, while modern coexistence theory (Chesson, 2000) has provided a robust demographic framework to study long-term species interactions, and led to refined models of community assembly theory (Hillerislambers et al., 2012), it often is limited in practice by a focus on pairwise interactions, ignoring the complex indirect and higher-order interactions that often emerge in real-world communities (Levine et al., 2017). For instance, stronger environmental filtering with drought may intensify competitive interactions among species pairs, whereas indirect interactions could increase coexistence opportunities in multispecies assemblages (Aschehoug & Callaway, 2015; Levine et al., 2017). Indeed, emerging work analyzing multispecies coexistence shows that results from pairwise interactions are not always applicable in diverse communities (Zepeda & Martorell, 2021; Granjel & Allan, 2023). Thus, accurately predicting the impact of climatic changes on plant communities depends critically on our understanding of species interactions within diverse communities (Gilman et al., 2010) rather than just between species pairs.

Third, the strength and outcome of species' interactions can vary according to environmental conditions (Chamberlain et al., 2014; Wainwright et al., 2019), which challenges classic ideas of separate and sequential abiotic and biotic filters in community assembly. For instance, a large body of work suggests that interactions among co-occurring plant species have shown to shift from competitive (negative) to facilitative (positive) with increasing environmental stress (stress gradient hypothesis SGH) (Bertness & Callaway, 1994; Callaway et al., 2002). Similarly, changes in the strength of competition across abiotic gradients have been attributed to shifting competitive mechanisms, where productive environments are characterized by stronger hierarchical competition and more harsh environments are characterized by “flatter” competitive hierarchies or non-hierarchical competition (Maestre et al., 2009; Soliveres & Allan, 2018). Thus, abiotic and biotic processes may operate as interactive, rather than separate and sequential, filters structuring trait diversity (Kraft et al., 2015; Thakur & Wright, 2017).

In this dissertation, I address how contemporary climate change is reorganizing the distribution of plant species and additionally address the above shortcomings of community assembly theory to increase our understanding of ecological assembly in an era of rapid global change. For my first chapter, I resurveyed a long-term vegetation dataset spanning over forty years to investigate how species have responded to climate change by analyzing changes in their distribution and abundance across a large elevation gradient. For my second chapter, I used the same survey data to create spatial association networks to disentangle how diverse interspecific interactions vary across a large abiotic gradient to influence community functional structure. For my third chapter, I conducted an experiment manipulating the functional diversity of communities to understand how the functional diversity of a community influences the outcome of net interactions for a focal species. These combined results reveal the overall importance of plant functional traits in determining species’ responses to both abiotic and biotic conditions, and how consideration of diverse interactions at the community level can lend more realistic insight into community reorganization mechanisms.

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Chapter 1

Plant functional traits predict heterogeneous distributional shifts in response to climate change

Abstract

Climate change is causing the rapid redistribution of vegetation as plant species move to track their climatic optima. Despite a global trend of upward movement in latitude and elevation, there is extensive heterogeneity among species and locations, with few emerging generalizations. Greater generalization may be achieved from considering multidimensional changes in species' distributions as well as incorporating ecologically relevant functional traits into studies of range shifts. To better understand how recent changes in climate are influencing the elevational distribution of plant species and how species' functional traits mediate distributional changes, we resampled a 2,438 meter elevation transect spanning a distance of 16 kilometers which encompasses desert scrub, pinyon-juniper woodland, chaparral, and coniferous forest plant communities. Over the last 42 years, total perennial cover and species' average cover increased at lower elevations and decreased at higher elevations while average elevational leading-edge increased 116 m and elevational rear edge decreased 84 m. Notably, these changes were mediated by species' functional traits, where species exhibiting more conservative traits (lower SLA, greater $\delta^{13}C$, larger seed mass) and taller height shifted upward in their leading-edge range limit, average elevation, and trailing edge range limit, while declining in abundance at the median and trailing edge of their range. Species possessing more acquisitive traits (higher SLA, lower $\delta^{13}C$, smaller seed mass) and shorter height shifted downward and increased in abundance at their trailing edge, with increases in their total range size. Our results provide clear evidence that heterogeneous range dynamics under recent climate change can be generalized by considering ecologically relevant plant functional traits, and how they respond to localized climate exposure. Further, by documenting changes across a steep elevational gradient comprising a large aridity gradient, we show divergent patterns for plants occupying contrasting positions along the global spectrum of plant form and function, which provides critical insight into how trait-mediated changes under increasing aridity will impact ecosystem functioning.

Keywords: biodiversity change, range shifts, functional diversity, aridification, climate change, drylands, Boyd Deep Canyon

Introduction

Global climate change is causing rapid modifications to terrestrial biodiversity (Díaz et al., 2019). Among plants, there is a global trend of upward movement in latitude and elevation as species track their optimum conditions under accelerated warming (Kelly & Goulden, 2008; Lenoir et al., 2008; Rumpf et al., 2018). However, numerous recent long-term studies have also found either lagged responses of species failing to track their shifting climatic optima (Alexander et al., 2018; Zhu et al., 2012) or unexpected directional changes such as downward elevational and latitudinal shifts (Crimmins et al., 2011; Lenoir et al., 2010; Rumpf et al., 2019). These distributional changes will scale up to influence ecosystem productivity, nutrient cycling, carbon storage, and land-atmosphere feedbacks (Anderegg et al., 2019a; Madani et al., 2018; Pecl et al., 2017), however, three major limitations have hindered generalizations. First, most existing studies have only assessed changes to one dimension of species' geographic ranges—typically leading-edge or average elevation (Lenoir & Svenning, 2015). Second, there has been a failure to incorporate ecologically relevant functional differences among species undergoing distributional shifts. Lastly, the majority of long-term studies of plant redistributions have been conducted within temperate alpine and boreal ecosystems, which has limited our understanding of more xeric ecosystems, which as a biome collectively comprise the largest proportion of terrestrial surface (Cherlet et al., 2018).

Despite decades of research, most studies have primarily assessed distributional changes over time at the leading range edge (high elevation or latitudes) (Chen et al., 2011; Pauli et al., 2012) or at the center of the range (Crimmins et al., 2011; Kelly & Goulden, 2008; Lenoir et al., 2008). However, a recent metanalysis showed that trailing edge range margins have comparable rates of movement (Rumpf et al., 2019). Critically, understanding the response of plant species to changing climate requires examination of change in not only species' range limits, but also changes in abundance across species' entire distributions (Ehrlén & Morris, 2015; Lenoir & Svenning, 2015). Lags in dispersal, establishment, and extinction are expected to be widespread among species shifting along elevation gradients, and the magnitude of these lags – captured by range-wide population abundance changes – will likely vary among populations throughout individual species' ranges (Alexander et al., 2018; Peterson et al., 2019). For instance, different life stages and/or locally adapted populations can show divergent demographic responses to the same climate drivers (Hargreaves & Eckert, 2019; Valladares et al., 2014), and the importance of different demographic rates to population growth can vary across a species' range (Oldfather et al., 2021).

Ultimately, while multiple factors will influence the rate and direction of range redistributions, a species' ability to respond to changing climate will depend on the extent that its functional traits enable persistence under novel climate regimes or enable movement to favorable climatic conditions (Angert et al., 2011; Damschen et al., 2012; Dawson et al., 2011; MacLean & Beissinger, 2017). Plant functional traits reflect species' morpho-physiological strategies to optimize fitness under a given suite of environmental conditions (Lavorel & Garnier, 2002; Violle et al., 2014) and have strong theoretical support for predicting range dynamics under contemporary climate change (Estrada et al., 2016; Funk et al., 2016). However, functional approaches for predicting range dynamics have historically focused on dispersal traits (Estrada et al., 2016; Zhu et al., 2012) or categorical plant functional types (Lenoir et al., 2008; Rumpf et al., 2018), while largely ignoring that establishment potential and competitive ability in new habitats as well as survival in existing habitats will be dependent on traits relating to resource acquisition and utilization (Griffin-Nolan et al., 2018; Liancourt et al., 2020; MacLean & Beissinger, 2017), which are often orthogonal to dispersal traits (Laughlin, 2014; Westoby et al., 2002). Furthermore, traits within species are often coordinated (i.e., the plant economics spectrum), with global patterns of plant resource-use and acquisition strategies represented by a continuum from ‘fast’, resource-acquisitive strategies that optimize carbon gain by constructing cheap tissues with shorter lifespan, taking advantage of brief periods of resource availability, while resource conservative strategies invest more in longer-lived tissues with greater construction costs for enhanced survival in more stressful conditions (Reich, 2014). While resource-use traits conferring tolerance to drought and heat stress (e.g., high water use efficiency (WUE), lower specific leaf area (SLA)) are typically adaptive under the warmer and drier conditions expected with climate change, these conservative strategies become maladaptive under increasing aridity given their susceptibility to hydraulic failure (Bennett et al., 2015; Berdugo et al., 2022; Carvajal et al., 2019).

Finally, while fine-scaled longitudinal data documenting species’ range and abundance dynamics has been collected from a variety of ecosystems, most of these studies are confined to temperate alpine and boreal ecosystems. Mountainous regions exhibit high heterogeneity of abiotic factors over short distances, and subsequently host high elevational variation in plant communities (Körner, 2007). Such high rates of turnover along compressed climatic gradients in mountainous systems serve as a natural laboratory for assessing long-term responses to climate change (Sundqvist et al., 2013), especially given that transition zones between habitat types will likely facilitate novel species’ interactions and subsequent unexpected and/or accelerated range dynamics (Beckage et al., 2008; Solarik et al., 2020). Here, we resampled the Deep Canyon Transect, a long-term dataset spanning a steep elevational gradient in Southern California, to understand how recent climate change is influencing the distributions of plants and to ask what role species' functional traits play in mediating their responses. In 2019, we resampled 20 400-m long vegetation sub-transects by identifying all perennial plant species that intercepted each sub-transect at every centimeter (80,000 data points) and compared our findings to surveys in 1977 (Zabriskie, 1979) and 2008 (Kelly & Goulden, 2008). We calculated changes in range edges and abundances across species' entire elevational distributions for all species that were recorded in the original survey. We additionally measured key morphological traits of abundant species and related them to individual species' response to four decades of climate change. Specifically, our goals were to determine the direction and extent of range redistributions of diverse species across multiple ecological zones—including patterns of abundance throughout each species' range—and to assess whether long-term responses are mediated by interspecific functional traits. Given the higher evaporative demand from anomalously dry and warm conditions in our study region throughout the late 20th and early 21st centuries (Overpeck & Udall, 2020; Williams et al., 2020), we predicted that species exhibiting a conservative strategy would show more pronounced upward shifts with decreases in cover at the lower part of their range, while more acquisitive species would show increasing cover and range expansions at their trailing edge margins.

Materials and Methods

Study site. The Deep Canyon Transect, part of the Boyd Deep Canyon Desert Research Center, is a steep elevational gradient gaining 2,438 meters over a distance of 16 kilometers (Fig. 1). The gradient encompasses nine distinctly described plant communities represented by over 600 species documented in the original survey of 1976-1977 (Zabriskie, 1979). In 2008, Kelly and Goulden (Kelly & Goulden, 2008) documented extensive range shifts in the ten most widely distributed species attributed to recent climate change (although fire history has subsequently been argued as a significant factor, (see Schwilk & Keeley, 2012)).

Climate data. To determine if climatic variables in the area have changed significantly, we used local weather station data from stations within 75 km of the study site, representing the elevation range within the transect, and containing nearly continuous records since 1947. For these stations, we analyzed changes in the following climatic variables: mean annual temperature, mean annual maximum and minimum temperatures, mean annual precipitation, interannual precipitation variability using the coefficient of variation of monthly precipitation, number of days with maximum temperature less than 0°C, number of days with maximum temperature exceeding 32.2° C, and number of days receiving 2.54 mm in each month. We also analyzed site-specific weather station data from the Boyd Deep Canyon Desert Research Center, which is the only climate dataset available from the study site which includes years preceding the first survey in 1977. Further, to compare how climatic variables across the elevation gradient have changed in direction and rate, we analyzed changes in 800-m resolution gridded climate data (PRISM; PRISM Climate Group 2014) using the location of transects at the lowest, highest, and middle elevations. PRISM data are interpolated from nearby climate station data that are physiographically similar by calculating a local climate-elevation regression that also uses six other topographic predictors; they accurately characterize topoclimate in mountainous areas of the western US (Daly et al., 2008). For these data, we evaluated trends in annual minimum, maximum, and mean temperature, along with annual precipitation and vapor pressure deficit (VPD). Climatic changes across survey intervals were compared between each survey period using t-tests.

Vegetation surveys. To understand how vegetation has responded to ongoing climatic changes, we resurveyed the plant communities following the same protocol used in the original surveys by Zabriskie (Zabriskie, 1979) also followed by Kelly and Goulden (Kelly & Goulden, 2008). The original survey consisted of 22 linear transects along the elevation gradient, equally spaced at 122-meter intervals beginning at 24 meters elevation and following 400 m isocontours. Due to urban development in the Coachella Valley, the lowermost transect was lost forever beneath an irrigated golf course subdivision, and therefore we only resurveyed 21 of the original transects. We surveyed all transects at peak biomass across the elevational gradient, from March 2019 at the lowest elevation, to August 2019 at the highest elevation. At each 400-m transect, we identified all perennial plant species, and abundance was estimated as the amount of foliage intercepted by the tape to the nearest centimeter. Permits were obtained for sampling on the Boyd Deep Canyon reserve and no permits were needed at other locations.

Functional trait data. Since the raw transect data were not available for the 1977 survey, we retained the 36 species with published abundance values (Zabriskie, 1979) for subsequent analyses assessing long-term elevational trends. The 36 species were chosen by the original author to be published given their widespread distribution and dominance across the ecological communities spanning the gradient. From ten individuals of each of these 36 species, we collected functional trait data but only collected leaf trait data on the 31 non-CAM species following standard protocols (Pérez-Harguindeguy et al., 2013; Table S2). For species spanning multiple habitat types we collected 10 individuals from each habitat type to account for intraspecific trait vacation along the gradient. We focused on ten commonly measured traits that reflect well-documented tradeoffs in plant ecological strategies and are all known to affect the ability of plants to establish, persist and reproduce in variable environments (Westoby et al., 2002) including plant height, SLA, leaf dry matter content (LDMC), leaf area (LA), leaf water content (LWC), seed mass, chlorophyll content, foliar $\delta^{13}C$, leaf nitrogen content, and foliar $\delta^{15}N$. Plant height is related directly to growth rates and resource availability, and along with SLA has been shown to reflect biotic interactions in dryland communities (Gross et al., 2013). Additionally, plant height influences the extent of decoupling between free air temperature and leaf or canopy temperature (Frenne et al., 2021; Körner, 2007). SLA, chlorophyll content, and LDMC are traits related to a plant's ability to acquire and use nutrients, while LA and LWC are related to light availability and water use (Pérez-Harguindeguy et al., 2013). Seed mass influences a plant's dispersal potential and establishment success (Moles & Westoby, 2004). Intrinsic water use efficiency (WUEi), measured as $\delta^{13}C$, reflects the relative efficiency of carbon gain through photosynthesis, in regard to water transpired (Farquhar et al., 1989), and can capture site water availability (Livingston & Spittlehouse, 1996). Leaf nitrogen content is associated with higher photosynthetic capacity (Evans, 1989) and foliar δ^{15}N can shed light on short-term dynamics of the N cycle (Craine et al., 2015).

Upon collecting leaves in the field, we placed them in water picks to hydrate for 24 hours before processing. We measured leaf area (cm^2) by scanning fresh leaves with a flat-bed digital scanner and then calculated leaf area using ImageJ (Schneider et al., 2012). After scanning, fresh leaf mass (g) was determined using a digital balance, and subsequently dried at 60°C for at least 72 hours prior to determining dry mass (g). Leaf dry matter content was calculated as dry mass divided by fresh mass. Chlorophyll content was measured using a digital chlorophyll meter (Konica Minolta) and averaged across three measurements per leaf. We measured plant height as the distance from the ground to the highest photosynthetically active tissue. We used seed mass data retrieved from the TRY database (Kattge, 2020). Leaf δ^{13}C and δ^{15}N were measured at the University of Wyoming Stable Isotope Facility (http://www.uwyo.edu/sif/) where samples were ground with a steel ball mil and analyzed for δ^{13}C and δ^{15}N on a Carlo Erba 1110 Elemental Analyzer coupled to a Thermo Delta V IRMS. Isotope ratios were calculated as

$$\delta[^{13}\mathrm{C}, {}^{15}\mathrm{N}]samples = (\frac{R_{sample}}{R_{standard}} - 1)\ x\ 1000$$

where R_{sample} and R_{standard} are the δ^{13}C/^{12}C or δ^{15}N/^{14}N molar abundance ratios of samples, with 36-UWSIF-Glutamic 1 and 39-UWSIF-Glutamic 2 used as reference samples.

Data analysis. We tested for temporal changes in community-level attributes of total perennial plant cover, species richness (alpha diversity), and Shannon diversity by building linear mixed effect models with fixed effects of elevation, year, their interaction, and habitat. We used transect ID as a random effect to account for the non-independence of our observational units (transects). We expressed coefficients of determination as both marginal and conditional R2, where the former is the variation explained by fixed effects, and the latter the variation explained by both fixed and random effects. Models were conducted using the ‘lme4’ package (Bates et al., n.d.), and tests of significance were assessed with the package ‘lmerTest’ (Kuznetsova et al., 2017) using Satterthwaite’s method.

We assessed changes in individual species’ elevational distributions over time based on changes in leading edge range limits, rear edge range limits and average elevation for each species (Fig. 3A). Leading edge and rear edge limits were defined as the highest and lowest transects of occurrence across the elevation gradient. We also calculated the average abundance-weighted elevation for each species per survey year because range shift detection can potentially be misleading for species’ upper and lower boundaries compared to changes in mean elevation (Shoo et al., 2006). To capture the complex changes in abundance across each species’ entire range, we calculated probability density functions for each species spanning the entire gradient separately for each survey year using the *density* function with Gaussian kernel smoothing and weighing by species’ cover values at each elevation (Rumpf et al., 2018). We used density estimation rather than comparing changes in abundance at each transect over time due to substantial range limit and abundance fluctuations between both survey intervals. Abundance was therefore defined as the integral of density functions. We then used the sum of modified density functions to calculate absolute changes in abundance across survey years, as well as changes in elevation optima defined as the peak of the density distribution and changes in maximum density to account for abundance changes at optimum range positions. Since abundance changes of individual species can differ substantially among range positions (leading versus rear edge), we assessed abundance changes at the 25% and 75% quantiles of density functions between original and most recent surveys. To account for changes at the median of species' distributions, we additionally evaluated the 50% quantiles. Additionally, we tested whether species' range limits, including average and optimum elevation, were contingent upon their original elevation for each survey interval. Changes in individual species' range dynamics were assessed using linear mixed effect models with survey year as a fixed effect and species as a random effect. To assess differences among survey intervals, we used paired t-tests for all the above range attributes.

To understand how functional traits might be related to observed range dynamics, we performed linear regressions using changes in range attributes as response and each individual trait as a predictor. Individual traits were tested for normality using Shapiro-Wilk normality tests, and traits not conforming to normality were log-transformed. In addition to individual traits, we conducted a principal components analysis (PCA) after scaling trait variables, retaining the first two principal components, and obtained scores on these two components for each species to use as predictors. Composite trait predictors from our PCA were only available for 26 species due to missing traits. Individual trait regressions were performed using trait data for 36 species, with some species missing traits either due to their physiology (cactus species were not collected for leaf traits) or due to missing data.

Results

Climatic changes. Nearby weather station data showed pronounced changes since 1947, with general increases in nearly all temperature variables (Table S1). Gridded climate data from the lowest, middle, and highest elevation transects showed substantial warming trends, with annual minimum temperature increasing by 2.77°C at the lowest, 3.84°C at the middle, and 2.3°C at the highest elevation between the years preceding the first and most recent surveys (Fig. 2; Table S2). Notably, there were heterogeneous changes among different elevations, where rate and magnitude of warming was generally highest at the middle elevation, while the lowest elevation exhibited increases in precipitation (54 mm) and decreases in VPD (-2.17 kPa) and maximum temperature (-2.17°C) between the first and second surveys (between the third and fourth quarters of the 20th century). Long-term climate data dating to 1961 from the Boyd Deep Canyon center station (Table S1), showed a trend toward increased interannual precipitation variability (measured as the coefficient of variation, F=2.84, p=0.091), and no overall significant changes in mean annual or seasonal (winter and summer) precipitation (MAP: F=0.02, p=0.884; winter precipitation: F=0.01, p=0.93; summer: F=0.44, p=0.506). However, there was a significant increase in average minimum temperature (0.98°C; F=10.5, p=0.001) and average maximum temperature (3.61°C; F=108.8, p<0.001) over the same time period (see SI for details).

Range dynamics. We found evidence for both species range edge shifts and population abundance changes, and that these changes were predicted by interspecific differences in functional traits. First, we found substantial changes in leading edge distributions, with an average elevation increase of 116.1 meters from 1977 to 2019 (1977 mean: 1612 ± 34.6 (SE) m; 2019 mean: 1728.1 ± 34.6 (SE) m, t=3.44, p=0.001, Fig. 3B) and substantial changes in rear edge range limits with an average downward shift of 84.9 meters (1977 mean: 1389.4 ± 28.12 (SE) m; 2019 mean: 1304.49 ± 28.12 (SE) m, t=3.01, p=0.004, Fig. 3C). Species with higher $\delta^{13}C$, indicating higher intrinsic WUE, showed greater upward shifts (F=5.08, p=0.034, Fig. 4A; Table 1) and species exhibiting higher SLA (F=11.55, p=0.002) and shorter species (F=6.66, p=0.016) shifted downward in their lower edge elevation range (Table 1). Moreover, principal component axis 1 (PC1 accounting for 37.8% of total trait variation and associated with seed mass (0.49), SLA (-0.40), $\delta^{13}C$ (0.38), and height (0.37) (Fig. 4B)) showed a positive relationship with lower elevation margin changes (F=8.25, p=0.008), where species with lower PC1 scores showed downward shifts (Fig. 4D; Table 1). In addition, total elevational range size increased across sampling years (t=4.28, p<0.0001), owing to a large increase in average range size from 1977-2008 (1977 mean: 222.62 ± 50.9 (SE) m; 2008 mean: 485.46 ± 50.9 (SE) m, t=5.15, p<0.0001) where shorter statured species increased their range span while taller species exhibited range contractions (F=6.95, p=0.01; Table 1). However, like maximum elevation limits, there was a reversal where average range size contracted from 2008-2019 by an average of 61.8 m (2008 mean: 485.46 ± 25.4 (SE) m; 2019 mean: 423.65 ±

25.4 (SE) m, t=-2.43, p=0.020). Range contractions during the most recent survey interval were positively associated with LDMC, where lower LDMC species showed greater range contractions (F=4.94, p=0.034) (Table 1). Changes in overall range size was correlated with rear edge elevation changes (F=23.3, p<0.001), where species that shifted downward in their rear edge showed the greatest increases in range size while species shifting upward showed range contractions.

In addition to distributional changes, we found that interspecific differences in functional traits predicted patterns of population abundance change. There was an upward shift in species' optimum elevation as defined by the peak of density distributions (1977 mean: 1491.8 ± 69.8 (SE) m; 2019 mean: 1547 ± 64.1 (SE) m, t=-2.8, p=0.006) (Fig. 3D) where species possessing lower chlorophyll content shifted their optima downward, and vice versa (F=4.91, p=0.035; Table 1). Due to divergent responses among species correlated with directional changes in range margins, average abundance-weighted elevation showed no overall change from 1977 to 2019 (1977 mean: 1504.49 ± 17.8 (SE) m; 2019 mean: 1521.04 ± 17.8 (SE) m, t=1.05, p=0.297). However, the divergent responses were captured by differences in functional traits, where species showing an upward shift in abundance-weighted elevation had lower SLA (F=7.55, p=0.010) and higher $\delta^{13}C$ (F=7.25, p=0.012) (Table 1) and had higher PC1 scores (F=8.39, p=0.008; Fig. 4C). While average leading-edge abundance (75% quantiles of density functions) among species showed no change overall (F=-0.83, p=0.411; Fig. S3), average abundance at median elevation (50% quantiles of density distributions) decreased (t = -2.98, p = 0.038), and trailing-edge abundance (25% quantiles of density functions) decreased (t=-2.22, p=0.029; Fig. S4). Importantly, species with higher LDMC (F=4.3, p=0.046), lower SLA (F=6.09, p=0.019), higher seed mass (F=6.86, p=0.014), higher $\delta^{13}C$ (F=7.2, p=0.011), and taller stature (F=4.12, p=0.052) tended to decrease in median elevation abundance across the survey period (Table 1). Consequently, PC1 was the strongest predictor of median elevation abundance change, where species scoring higher declined the most (F=9.46 p=0.005). However, PC1 was a weaker predictor of abundance changes in rear edge abundance, where species scoring lower (smaller seed mass, shorter stature, and lower LDMC) showed increases (F=4.22, p=0.051) and no other trait being predictive. Lastly, species showing declines in abundance at the leading edge were associated with higher $\delta^{13}C$ (F=5.07, p=0.029), larger seeds (F=13.5, p=0.004), and greater LDMC (F=7.04, p=0.018; Table 1).

Finally, changes in leading and rear edge abundance were positively related (F=4.51, p=0.041), where species increasing at one range margin tended to increase at the other, and likewise, species that declined at one margin declined in the other. Species that increased their overall range size likewise showed significant increases in their proportional abundance (F=6.43, p=0.016). Similarly, species shifting upward at their leading-edge range margins showed a decreasing trend in abundance at their median (F=4.82, p=0.035) and rear edge (F=3.07, p=0.089). Species occupying a lower historic average elevation showed more pronounced upward shifts in their leading edge, and vice versa, from 1977-2008 (F=4.215, p=0.047). Similarly, historic leading-edge elevation was predictive of leading-edge range shifts, where species with historically lower elevation margins showed more pronounced upward leading-edge shifts (F=9.81, p=0.003). A similar pattern was found for optimum elevation, where species with historically lower elevation optima showed greater upward shifts in their optimum elevation (F=7.64, p=0.009). However, while these range redistributions were correlated with historic elevation, only one trait—chlorophyll content—showed systematic variation with historic range attributes, where species occupying lower elevations tended to have higher chlorophyll content and vice versa (Table S6). Species that were historically more abundant showed stronger decreases in total abundance, and vice versa, from 1977-2008 (F=8.47, p=0.006). Changes in total perennial plant cover remained relatively stable across the survey period, but habitat-specific changes reflected changes in species abundance patterns, where cover increased at the lowest elevation transects and decreased at the highest elevations (Fig. S1; Table S3).

Discussion

While recent work has identified plant functional traits associated with growth and survival under climate warming and drying within species' current distributions (Kühn et al., 2021; Soudzilovskaia et al., 2013), few studies have consistently predicted distributional responses of species across ecosystems. Here, we find strong support for the ability of plant functional traits associated with resource use and acquisition to predict plant distributional responses to long-term climate change (Fig. 4), especially when considering the multidimensional nature of species' distributions. Concordant with global average rates across other biomes (i.e., 5-30 m/decade (Kelly & Goulden, 2008; Lenoir et al., 2008), we found a 29 m/decade average upslope shifts for species' leading edge and that taller species exhibiting more conservative traits (lower SLA, greater $\delta^{13}C$, larger seed mass) shifted upward in their leading-edge range limit as well as their average elevation, and trailing edge range limit. However, we also find substantial downward shifts where shorter species with more acquisitive traits (higher SLA, lower $\delta^{13}C$, smaller seed mass) shifted downward, increased in abundance at their trailing edge, and increased their total range size, adding to accumulating long-term studies showing downward shifts in elevation or latitude (Abella et al., 2019; Fei et al., 2017; Kopp & Cleland, 2014). Critically, our results suggest that these divergent responses among species in distributional shifts can be understood by examining the variation in coordinated functional traits among species.

Dryland ecosystems are experiencing anthropogenic-driven elevated temperatures and increased chronic and extreme drought (Williams et al., 2020) which has and will continue to decrease soil moisture (Bradford et al., 2020), disproportionately impacting species reliant on deeper soil water (Schlaepfer et al., 2017). Our results are consistent with recent work showing that this is already happening in southern California (Goulden & Bales, 2019), as taller species with more conservative traits which typically rely on deeper water sources show upward shifts and decline at their lower and median elevations. Specifically, our results show that across the entire survey period (1977-2019) species possessing traits scoring higher on PC1 (taller height, lower SLA, greater $\delta^{13}C$, and larger seed mass) shifted upward in their leading-edge range limit, average elevation, and rear edge range limit, while declining in trailing edge abundance and range median abundance. If extreme drought is an important driver of the observed range redistributions, these results are contrary to what would be expected for seed mass and $\delta^{13}C$, since seed mass plays a critical role in enhancing seedling survival under drought stress (Moles & Westoby, 2004), and higher $\delta^{13}C$ values are associated with greater intrinsic water use efficiency (Farquhar et al., 1989). However, taller plants have wider water-conducting conduits, which make taller species more susceptible to embolisms, and therefore increase their vulnerability to drought (Olson et al., 2018). Thus, the observed declines in rear edge and center abundance are potentially due to drought-induced embolism, while the same species have increased in abundance at their leading edge owing to their larger seed mass and higher iWUE conferring increased survival of juveniles.

Interestingly, we found that species in this system are highly responsive to recent climatic changes, which adds to the growing body of literature showing high sensitivity of dryland ecosystems to climate change (Burrell et al., 2020; Schlaepfer et al., 2017; Shriver et al., 2022). Both local weather station data and gridded climate data showed long-term patterns consistent with warming temperatures, where substantial increases in winter minimum temperatures showed the most dramatic increases, which were more pronounced at lower and mid elevations These results support recent work highlighting elevational differences in warming rates (Pepin et al., 2015), and our findings of elevational differences in climate helps explain some of the heterogeneity of range redistributions. For instance, the downward shift in lower elevation range margins occurred following a period of cooler and wetter conditions at the lowest elevation, while the upward shifts in leading edge margins occurred over the same interval, where the middle and highest elevations showed pronounced increases in temperature and VPD. Additionally, we found a downward shift in leading edge margins between the second and most recent survey, which was characterized by anomalously warm regional drought which caused extensive mortality (Dong et al., 2019; Goulden & Bales, 2019), and which likely caused mortality in newly establishing juveniles of species that had previously shown upward leading-edge shifts. Furthermore, we found that lower-elevation species tended to exhibit more substantial upward range shifts, consistent with recent long-term trends from other mountainous ecosystems (Mamantov et al., 2021; Rumpf et al., 2018). While prevailing explanations include trait covariation with elevation and higher-elevation species having a broader thermal tolerance being adapted to greater diurnal and seasonal temperature fluctuations, only one trait—chlorophyll content—varied with elevation, and wasn’t predictive of any range attribute changes, while our elevation gradient shows an opposite pattern of lower elevations experiencing greater temperature fluctuations than higher elevations. Thus, in contrast to more temperate mountain ecosystems (Pepin et al., 2015), our findings of elevation-dependent range shifts likely reflect that our dryland system is experiencing more rapid warming at lower elevations, consistent with recent work highlighting the potential for differences in climate exposure to drive geographic variation in species’ responses (Kling et al., 2020; Oldfather et al., 2019). Despite this heterogeneity in climate change exposure, species showed responses consistent with increasing aridification, where more variable precipitation and hotter drought periods across southern California have promoted the replacement of stress-tolerant species with more resource-acquisitive species that possess drought-avoidant traits (Berdugo et al., 2020).

While recent work examining trait-mediated fitness responses to climate change have found that lower SLA and higher iWUE tend to show positive responses to increasing temperatures (Kühn et al., 2021), our long-term results provide contrasting evidence. Intriguingly, while species inhabiting resource-poor environments tend to exhibit more conservative traits than species in resource rich environments (Reich, 2014), recent studies suggest that there is a reversal in the plant economics spectrum under more arid conditions (Carvajal et al., 2019). Specifically, resource acquisitive strategies may allow plants to exploit more sporadic and seasonal precipitation, while conservative traits require greater energy expenditure (Mooney & Dunn, 1970). This reversal might also be partially explained by recent work on leaf thermoregulation which has shown that plant species strategize along a spectrum of leaf thermal stability and photosynthetic thermal stability, with more acquisitive species having larger thermal photosynthesis range (Michaletz et al., 2016). Furthermore, plants on the leaf economic spectrum exhibit contrasting extent of decoupling of leaf temperature from ambient air temperature during carbon assimilation, where species with shorter stature and lower WUEi (lower $\delta^{13}C$) show greater temperature decoupling, allowing them to have cooler leaves while inhabiting low-elevation arid sites (Liancourt et al., 2020). Ultimately, since most long-term vegetation monitoring has occurred in temperate ecosystems, our results likely reflect the differences in trait selection between arid and temperate biomes. However, our results have important implications more generally, as species with drought-adapted, conservative traits are experiencing extensive mortality worldwide at their driest range margins in response to climate stress exceeding their physiological limits (Anderegg et al., 2019b), and such drought-induced mortality is leading to widespread ecosystem-type conversion (Batllori et al., 2020).

Finally, recent work has questioned the reliability of “snapshot resampling” when inferring climate change impacts, owing largely to the potential for interannual variation to obscure long-term trends (McCain et al., 2016; Stuble et al., 2021). Interannual fluctuations in population abundance, as well as a high frequency of local extinctions and recolonization events could both lead to inaccurate detection through over- or underestimation of range dynamics through time (McCain et al., 2016). However, several aspects of our study make our results robust. First, the plants in our long-term study are all dryland perennial species, which have notoriously slow population dynamics - the median longevity of several of our species is greater than a century (Cody, 2000). Second, while species’ range edges are often characterized by high population variability (Sexton et al., 2009), we assessed multiple dimensions of species’ distribution dynamics, which all showed consistent patterns based on the synchronous species’ responses strongly correlating with their functional traits. Importantly, long-term vegetation data collected at high spatial resolution and spanning decades provides a unique opportunity for understanding biodiversity response to rapidly changing climatic conditions (Magurran et al., 2010) and can overcome many of the issues associated with “snapshot resampling”.

In conclusion, our results suggest that idiosyncrasies in range shifts can be understood by pursuing a more comprehensive focus on multiple dimensions of species' ranges and by considering functional traits associated with resource use. We found a clear pattern of species' distributional responses to contemporary climate change being mediated by their functional traits, where species possessing more conservative resource-use traits shifted upwards and declined in abundance, while species with more resource-acquisitive traits shifted downward and increased in abundance. Ultimately, the high incidence of range-shifting species within our study has the potential to result in novel biotic interactions, including both the gain in antagonistic interactions (novel competitors, pathogens, and herbivores) as well as the loss of mutualists (soil microbes and pollinators), which could either facilitate or hinder species' distributional changes (Alexander et al., 2015; Hagedorn et al., 2019; Keeler et al., 2021). Moreover, as dryland ecosystems have a disproportionate role in the global carbon budget (Ahlström et al., 2015), the replacement toward more acquisitive leaf traits in response to climate change should alter nutrient cycling and carbon sequestration (Buzzard et al., 2019). The increasing prevalence of acquisitive leaf traits in dryland ecosystems may, furthermore, be associated with the beginning of an "ecosystem breakdown" threshold of aridification, where the mortality of resource conservative species occurs as they are no longer able to cope with increasingly scarce water and nutrient availability (Berdugo et al., 2020). Indeed, NDVI patterns across southern California's Sonoran desert region show declining vegetation cover (particularly in the more xeric areas) suggesting that the region may already be crossing this threshold (Hantson et al., 2021). Given the paucity of long-term vegetation data from dryland ecosystems, and that more than 20% of the Earth's terrestrial surface is expected to cross at least one threshold of aridification by 2100 (Berdugo et al., 2020), our results provide critical insight into the distributions of dryland plant species under rapidly changing conditions and how trait-mediated changes might impact future ecosystem functioning.

Figures and Tables

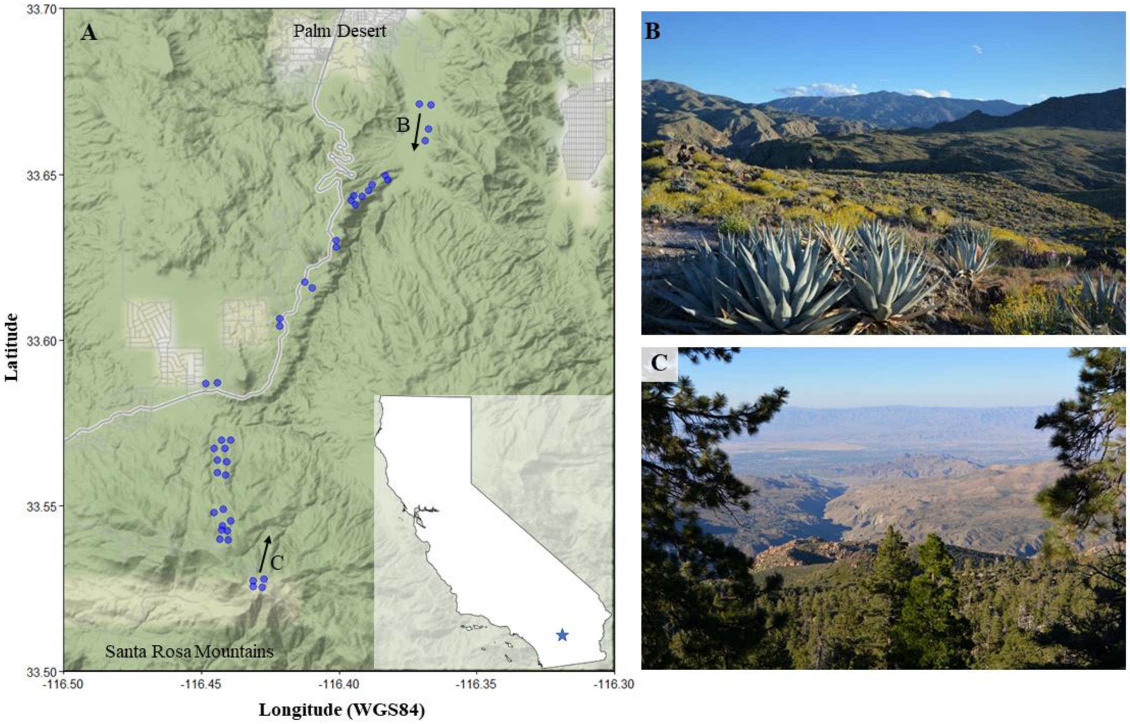

Figure 1.1. Study location of elevation gradient in southern California. A) elevational distribution of sub-transects where each paired dots represent east and west boundaries of a 400 m sub-transect. Start depicts general location of the deep canyon transect. B) View from sub-transect 1 looking to sub-transect 20, marked with a “B” and an arrow depicting direction of view in A. C) View from sub-transect 20 looking to sub-transect 1, marked with a “C” and an arrow depicting direction of view in A.

Table 1.1 Plant functional traits describing long-term changes in distributional range attributes across multiple survey periods between 1977 and 2019.

Range attribute	**Trait**	**Change 1977-2008**			**Change 2008- 2019**			**Change 1977-2019**		
		Coefficient	**R2**	**p-value**	**Coefficient**	**R2**	**p-value**	**Coefficient**	**R2**	**p-value**
Average elevation	Chlorophyll content	34.08	0.164	0.014						
	Leaf area	27.11	0.133	0.025						
	Specific leaf area	-0.88	0.118	0.033				-1.14	0.179	0.01
	13C							102.73	0.168	0.012
	PC1							31.13	0.228	0.008
Optimum elevation	Chlorophyll content							62.9	0.115	0.025
Leading edge range limit	13C	27	0.147	0.018				187.94	0.16	0.013
Rear edge range limit	Chlorophyll content	48.4	0.108	0.04	-37.69	0.106	0.042			
	Specific leaf area	-1.94	0.233	0.004				-1.83	0.308	0.001
	Height	70.52	0.29	0.001				45.5	0.162	0.016
	seed mass	31.44	0.172	0.012						
	13C	167.86	0.196	0.007						
	PC1							39.08	0.26	0.008
Total range size	LDMC				589.7	0.116	0.034			
	Height	-90.41	0.17	0.014						
Leading edge	LDMC	-1.13	0.178	0.018						

abundance (75% quantile)							
	13C	-0.03	0.15	0.029			
	seed mass	-0.05	0.27	0.004			
Rear edge abundance (25% quanitle)	PC1				-0.07	0.114	0.051
Median abundance (50% quantile)	LDMC	-1.27	0.144	0.02	-1.19	0.1	0.046
	seed mass	-0.05	0.113	0.037	-0.06	0.163	0.014
	SLA				0	0.145	0.02
	13C	-0.04	0.126	0.026	-0.04	0.167	0.012
	PC1				-0.1	0.253	0.005
Optimum abundance (peak of density distribution)	Leaf area	-0.11	0.297	0.001			
Absolute abundance (sum of density distribution)	13C				0.21	0.12	0.03
Proportional change in abundance	13C	0.09	0.105	0.039	0.09	0.142	0.019

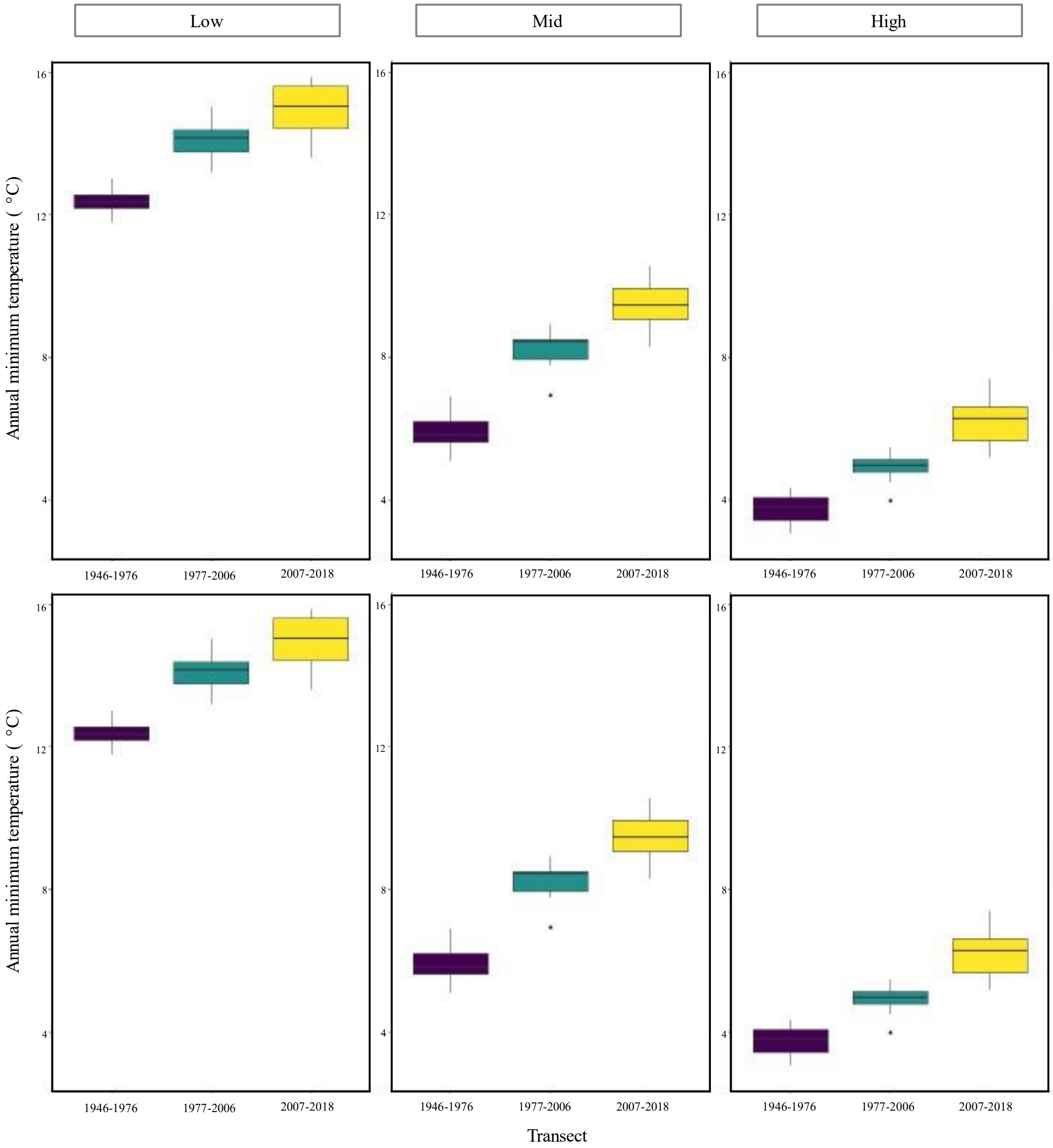

Figure 1.2 Annual minimum temperature and annual maximum vapor pressure deficit (VPD) in the years preceding each survey (Survey 1 in 1977: 1946-1976; Survey 2 in 2007/8: 1977-2006; Survey 3 in 2019: 2007-2018) from the lowermost (low), middle (mid), and highest (high) elevation transects across the sampled gradient.

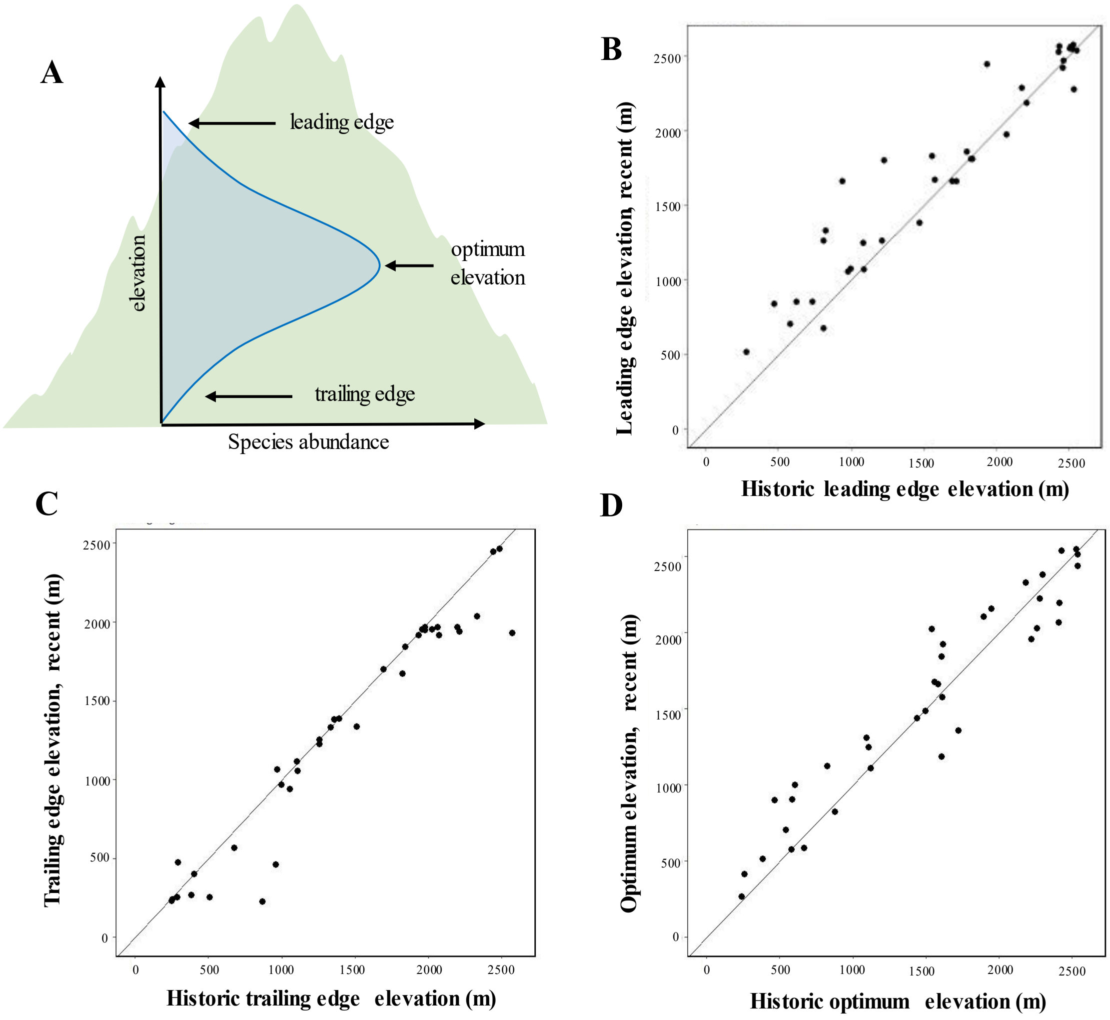

Figure 1.3 (A) Schematic describing elevational range attributes. (B)changes over time in species' leading edge, (C) trailing edge, and (D) optimum elevational distributions. N = 37 species. Each data point represents a single species. Diagonal (1:1) line represents no elevational change. Points above the line indicate X and points below the line indicate Y.

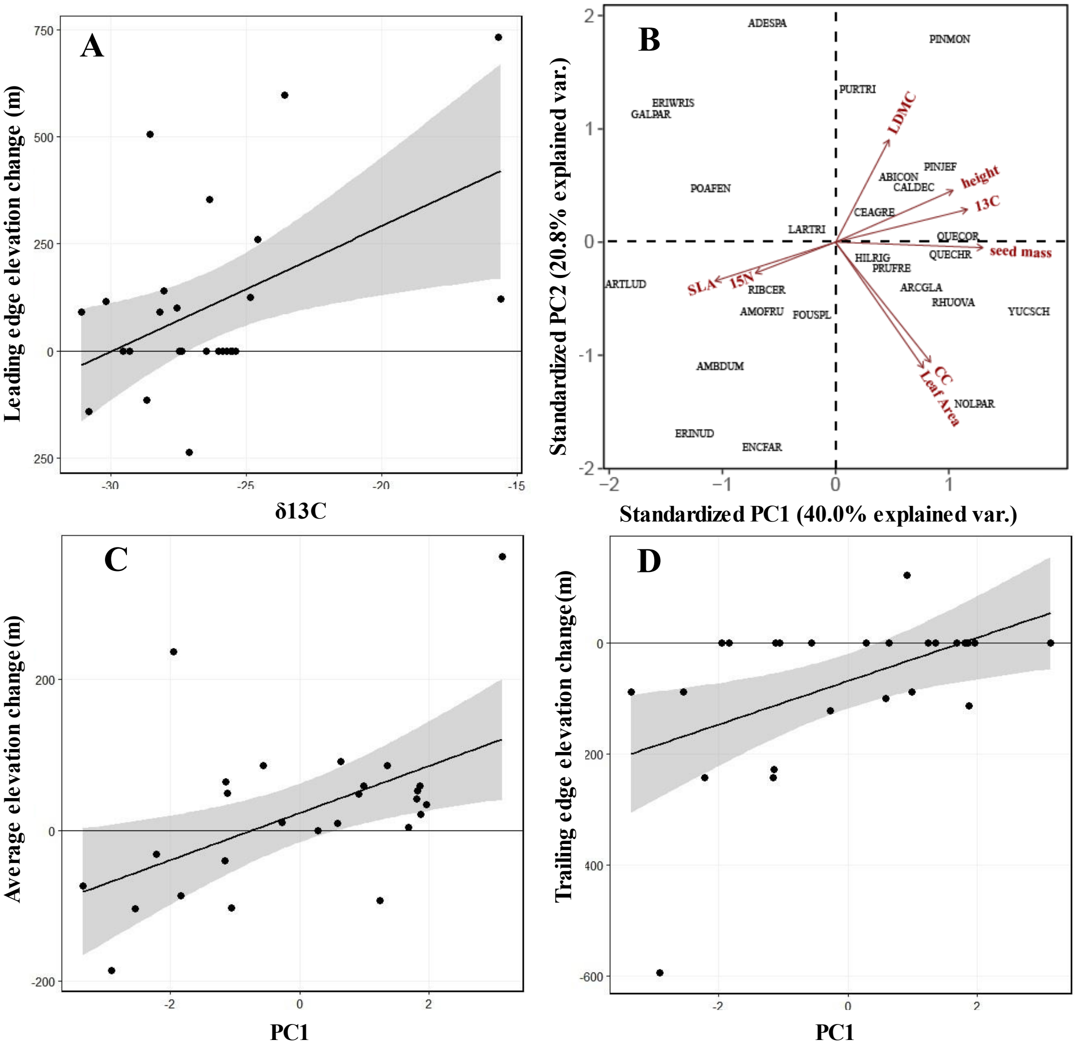
A
Leading edge elevation change (m)
750
500
250
0
250
-30
-25
-20
-15
δ13C
B
Standardized PC2 (20.8% explained var.)
Standardized PC1 (40.0% explained var.)
2
1
0
-1
-2
−2
−1
0
1
ADESPA
PINMON
PURTRI
ERIWRIS
GALPAR
LDMC
PINJEF
ABICON
CALDEC
height
POAFEN
13C
CEAGRE
LARTRI
QUECOR
seed mass
QUECHR
HILRIG
PRUFRE
ARTLUD
SLA
15N
RIBCER
ARCGLA
RHUOVA
AMOFRU
FOUSPL
YUCSCH
AMBDUM
CC
Leaf Area
NOLPAR
ERINUD
ENCFAR
C
Average elevation change (m)
200
0
-200
-2
0
2
PC1
D
Trailing edge elevation change (m)
0
200
400
-600
-2
0
2
PC1

Figure 1.4 Functional traits predict range dynamics in response to 42 years of climatic change. A single trait, 13C, explained changes in leading edge elevational changes (A), while multidimensional traits associated with PC axis 1 (B) explained changes in average (abundance-weighted) elevation (C) and trailing edge range limits (D). Lines and their shades represent significant linear regression models (Table 1) with shading depicting 95% confidence intervals. Species' codes: *Abies concolor* = ABICON, *Adenostoma sparsifolium* = ADESPA, *Ambrosia Dumosa* = AMBDUM, *Amorpha fruticosa* = AMOFRU, *Arctostaphylos glauca* = ARCGLA, *Arctostaphylos patula* = ARCPAT, *Arctostaphylos pringlei* = ARCPRI, *Artemisia ludoviciana* = ARTLUD, *Bernardia incana* = BERINC, *Calocedrus decurrens* = CALDEC, *Ceanothus greggii* = CEAGRE, *Encelia farinosa* = ENCFAR, *Eriogonum nudum* var. *pauciflorum* = ERINUD, *Eriogonum wrightii* var. *subscaposum* = ERIWRIS, *Fouquieria splendens* = FOUSPL, *Galium parishii* = GALPAR, *Hilaria rigida* = HILRIG, *Larrea tridentata* = LARTRI, *Lupinus formosus* = LUPFOR, *Nolina parryi* = NOLPAR, *Pinus jeffreyi* = PINJEF, *Pinus monophyla* = PINMON, *Poa fendleriana* = POAFEN, *Prunus fremontii* = PRUFRE, *Psorothamnus schottii* = PSOSCH, *Purshia tridentata* = PURTRI, *Quercus chrysolepis* = QUECHR, *Quercus cornelius-mulleri* = QUECOR, *Rhus ovata* = RHUOVA, *Ribes cereum* = RIBCER, *Symphoricarpos rotundifolius* var. *parishii* = SYMPAR, *Yucca schidigera* = YUCSCH.

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Chapter 2

Plant interaction networks structure the functional composition of plant communities across a steep environmental gradient

Abstract

The structure of plant communities has long been conceptualized as arising from primarily abiotic and secondarily biotic filters acting upon the traits of colonizing species. However, despite the increasing recognition of the dual importance of biotic and abiotic drivers of community composition, it is still unclear how both competitive and facilitative interactions vary with abiotic conditions, and how biotic interactions influence community trait patterns relative to abiotic factors. Here, I investigated the direct and indirect influence of plant-plant interactions and abiotic heterogeneity across a steep environmental gradient by analyzing species co-occurrences as plant interaction networks. I found that positive spatial associations (facilitative interactions between species) were common across the entire gradient and played a relatively minor role in explaining trait patterns. In contrast, while negative spatial associations (competitive interactions) were less common than expected by chance, they played a large role in promoting species richness and functional diversity. Further, I found that network metrics capturing emergent properties of the community—such as the ratio of positive to negative interactions and the average number of interactions per species—were the strongest biotic drivers of trait patterns. Taken together my results suggest that biotic interactions must be

examined at the level of the entire community if our goal is to elucidate the processes structuring the trait composition of communities.

Introduction

The functional trait composition of plant communities has demonstrably important consequences for ecosystem-level processes (e.g. Anderegg et al., 2018; Wu et al., 2016), yet it remains unclear how multiple processes interact to drive functional trait patterns. Classic models of plant community assembly suggest that the composition of a local community is a result of sequential abiotic and biotic filters acting on species' traits in the regional species pool (Hillerislambers et al., 2012; Keddy, 1992; Mittelbach & Schemske, 2015). Under this model, once species can disperse to a local site, they must first be able to survive and grow under the local abiotic conditions. This abiotic filter is thought to impose selection on the traits of species in the community such that those possessing trait values close to an environmentally determined optimum will have the highest fitness causing abundance-weighted mean trait values to vary across abiotic gradients (Cornwell & Ackerly, 2009; Kandlikar et al., 2022; Kraft et al., 2008; Laughlin et al., 2012). Plant species adapted to abiotic conditions must then be able to survive and grow in the presence of biotic interactions, which are classically predicted to cause trait dispersion within assemblages, under the assumption that species with similar traits compete more intensely (Chesson, 2000; MacArthur & Levins, 1967; Weiher & Keddy, 1995). However, advances in trait-based community assembly theory have questioned these classic predictions and suggested that multiple processes can produce similar trait patterns (Mayfield & Levine, 2010; Spasojevic & Suding, 2012). For instance, in addition to abiotic filtering, trait-based competitive hierarchies can lead to trait clustering (Carmona et al., 2019; Holden & Cahill, 2024; Kraft et al., 2014; Weigelt et al., 2007; Yin et al., 2021) and facilitation between functionally dissimilar species and can increase community functional diversity (Schöb et al., 2012). While a large body of research has focused on inferring processes from patterns (e.g. Ramachandran et al., 2023), few of these frameworks consider how the outcome and importance of plant-plant interactions are contingent on abiotic conditions (Germain et al., 2018; Van Dyke et al., 2022), and, therefore, abiotic filters may indirectly filter functional traits by altering species interactions.

Indeed, a growing body of work suggests that biotic interactions depend on abiotic context (Bertness & Callaway, 1994; Callaway et al., 2002), which challenges the community assembly model of separate and sequential abiotic and biotic filters. However, most studies to date addressing context-dependent interactions have primarily focused on a single type of interaction (competition or facilitation) involving only a small subset of species in a given community. For example, robust tests of the stress gradient hypothesis—which predicts that facilitative interactions replace competitive interactions under high abiotic stress (Bertness & Callaway, 1994; Callaway et al., 2002)—have tended to solely examine facilitative interactions (Soliveres & Maestre, 2014) or diverse outcomes among single pairs of species (He et al., 2013). Given this narrow focus, we lack an understanding of how diverse interactions at the level of the entire community vary across environmental gradients. Similarly, previous work addressing the impact of competition and facilitation on functional trait patterns have narrowly focused on either competitive or facilitative interactions among a subset of species in the community to infer their effect on community-level trait composition (e.g. Chacón-Labella et al., 2016; Schöb et al., 2017; Vega-Álvarez et al., 2019). Given that facilitation and competition occur simultaneously in many communities (Callaway and Walker 1997; Callaway et al. 2002) it is likely that the functional structure of communities can only be understood by accounting for both types of interactions among all species in a community, and how their frequency and balance change across abiotic gradients.

One promising approach to account for emergent interaction patterns within and across plant communities is the application of network theory. By accounting for all pairwise interactions among locally occurring species, network metrics can describe emergent patterns of species interactions, such as the the relative dominance of facilitation vs competition (link ratio; Alados et al., 2017) and the average number of interactions per species (link density), which have shown to improve predictions of biodiversity patterns (Losapio et al., 2019; Saiz, Gómez-Gardeñes, et al., 2018). For example, a recent global study found that community network metrics contributed significantly to explaining richness and evenness patterns across dryland plant communities worldwide (Saiz et al., 2018). While the impact of plant interaction networks on community composition has recently been incorporated in community assembly studies (Alados et al., 2017; Losapio et al., 2018, 2021; Saiz et al., 2018), no study to date has assessed how plant-plant interaction networks contribute to the functional structure of communities across large environmental gradients where both biotic and abiotic filters likely determine the composition and structure of plant communities interactively.

Here, I sought to disentangle abiotic and biotic drivers of functional trait patterns by examining how plant interaction networks vary across a steep environmental gradient. Since abiotic conditions often mediate biotic interactions, I tested for the influence of both direct and indirect effects of abiotic drivers on trait composition, in addition to the direct effects of biotic interaction networks (Figure 1). I predicted not only that facilitation would be more common under more stressful conditions (Bertness & Callaway, 1994; Callaway et al., 2002) and competition would be more common under more benign conditions (Grime 1977), but that the overall ratio of the two interaction types and other metrics (such as how connected species are through positive and negative interactions) would be more informative in explaining functional trait patterns than simply the number of positive or negative interactions. While mixed results have been found for the influence of facilitation on functional traits, I predicted that a higher proportion of facilitative interactions would generally have a positive effect on trait diversity and that this might be mediated by an increase in species richness, while competitive interactions would have the opposite effect on trait diversity. Finally, I predicted that abiotic variables would be more important drivers of community-level mean traits, while interaction networks would be more important drivers of functional diversity.

Methods

Study site. Our study was conducted at the Deep Canyon Transect, a large elevation gradient in Southern California spanning an elevation gain of 2,438 m, from 202 m to 2563 m, over a distance of 16 kilometers (33°40'15.6"N 116°22'00.3"W to 33°31'32.1"N 116°25'51.9"W). The study site was primarily located within the Boyd Deep Canyon Desert Research Center, encompassing nine distinctly described plant communities represented by over 600 species documented in historical vegetation surveys in 1976-1977 (Zabriskie 1979) which were resurveyed in this study. The lowest elevations lie within the Colorado desert region, which is the westernmost extent of the greater Sonoran desert (Belnap et al., 2016) where average annual temperatures range from a low of 17.9 °C to a high of 29.6 °C. Precipitation is highly biseasonal, where extreme precipitation events can be common during the summer monsoon season, in which most water is lost to surface runoff or evaporation, whereas winter precipitation from frontal winter storms results in deeper water percolation (Belnap et al., 2016). The Colorado desert subsection is characterized by having the lowest summer precipitation and high potential evapotranspiration, making it the hottest and driest desert region in North America (Belnap et al., 2016; Walter, 1971). The substrate of much of the Colorado desert is fine-grained alluvium as a result of runoff from the Transverse ranges and the Colorado River (Belnap et al., 2016). While there is extensive overlap among plant species of the adjacent Mojave and Arizona Sonoran deserts, the Colorado desert harbors extensive unique plant diversity which includes many genera of South American lineages (Thorne et al. 1986). The most common vegetation type throughout the Colorado desert is creosote bush scrub, dominated by *Larrea tridentata* (Zygophyllaceae) and *Ambrosia dumosa* (Asteraceae), with a cactus scrub community dominating xeric slopes including *Fouquieria splendens* (Fouquieriaceae), *Encelia farinosa* (Asteraceae), *Agave deserti* (Agavaceae), and numerous cacti species (Schoenherr and Burk 2007 in Barbour et al. 2007). Slightly higher elevations receiving more moisture and having lower temperatures transition into pinyon-juniper woodland with *Pinus monophyla* (Pinaceae) and *Juniperus californica* (Cupressaceae). The higher elevations of our study site lie within the Santa Rosa Mountains where the mid elevation slopes consist of chaparral communities, with dominant species such as *Adenostoma sparsifolium* (Rosaceae) and *Ceanothus greggii* (Ramnaceae) and the highest elevations are dominated by *Abies concolor* (Pinaceae), *Quercus chrysolepis* (Fagaceae), and *Pinus jeffreyi* (Pinaceae).

Community vegetation surveys. In 2019, I re-surveyed 22 linear transects across the elevation gradient spaced at roughly 122-meter intervals. Transects were 400 m in length following isocontours at each elevation. All transects were surveyed at peak biomass from March to August. For each transect, I identified all annual and perennial plant species intercepting the transect to the nearest centimeter, recording the specific location on the transect of each occurrence. Thus, our data on species composition was spatially explicit and able to account for the exact amount of overlap among co-occurring species to the nearest centimeter. Due to the large amount of data contained in each transect (40,000 cm), I subdivided the first and last 100 m segments to create interaction networks, and I refer to these 100 m segments as transects (for a total of 42 transects).

Abiotic factors. Abiotic filtering can drive community assembly at multiple scales, and therefore, I accounted for both macro- and micro-environmental variables within each community. In particular, a recent global analysis reveals that climate and soil fertility jointly explain global patterns in the two main axes of plant functional trait variation (Joswig et al., 2022), and therefore, I focused on these two categories of abiotic variables. Climatological data were derived from long-term PRISM (Daly et al., 2008) dataset at 800-m resolution and included average precipitation, average mean temperature, average maximum temperature, average minimum temperature, and average maximum vapor pressure deficit. I additionally calculated precipitation seasonality as the coefficient of variation (CV) of annual precipitation. Soil samples were collected from four locations (every 100 meters) across each of 21 elevations in 2019 and analyzed for organic matter, phosphorous, potassium, magnesium, calcium, sodium, pH, and cation exchange capacity (CEC) at A & L Western Agricultural Laboratories (Modesto California). For each transect, I averaged the soil variables from both ends of the (100-m) linear transect. To reduce collinearity among soil variables, I conducted a principal components analysis (PCA) and retained the first two PC axes which explained 37% and 19% total variation respectively. PC axis 1 was negatively associated with pH, CEC, and calcium and positively associated with hydrogen, sodium, and potassium (Figure S1). PC axis 2 captured a positive association with organic matter content and magnesium. In addition to climate and soil variables, topographic heterogeneity can also contribute to functional diversity and the outcome of biotic interactions (Vernham et al., 2023). Thus, I extracted topographic variables from a digital elevation model from the NASA Shuttle Radar Topographic Mission (SRTM) at 90-meter resolution. Variables included aspect, slope, Topographic Ruggedness Index (TRI), Topographic Position Index (TPI), and roughness (Amatulli et al., 2018). TRI is the mean of the absolute differences between the value of the cell and its 8 surrounding cells, while TPI is the difference between the value of a cell and the mean value of its 8 surrounding cells, and roughness is the difference between the maximum and the minimum value of a cell and its 8 surrounding cells. Topographic data were downloaded and extracted using the R packages "terra", "raster", and "sf". To reduce collinearity in our abiotic variables, I calculated correlations among environmental variables and removed highly correlated (Pearson r>0.7) variables (Figure S2). For correlated variables, I chose to retain those known to be important drivers of plant community organization in dryland ecosystems. For our final analyses, I used the following uncorrelated variables: average maximum temperature, precipitation seasonality, soil PC2, and topographic roughness.

Functional traits measurements. Functional trait measurements for species comprising over 80% (Pakeman & Quested, Helen, 2007) of cover across the gradient (92 species) were collected in 2019 (collected as part of Chapter 1 – see above), and included traits related to resource acquisition and known to influence biotic interactions in dryland ecosystems. For ten individuals from each of the most abundant annual and perennial species from each distinct habitat, I measured the following traits according to standardized protocols (Pérez-Harguindeguy et al., 2013): vegetative height (cm), leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), and chlorophyll content. Plant height is related directly to growth rates and resource availability, and along with SLA has been shown to reflect biotic interactions in dryland communities (Gross et al., 2013). SLA, leaf area, LDMC, and chlorophyll content are related to the tradeoff between the acquisition and conservation of resources as captured by the leaf economic spectrum (Wright et al. 2004). In dryland ecosystems, co-occurring species often exhibit either drought-tolerant strategies characterized by low SLA, high LDMC, longer-lived tissues, and lower rates of photosynthesis, or drought-avoidant strategies characterized by the opposite trait syndromes and accelerated phenology which allows for the rapid acquisition of resources during short windows of favorable conditions (Carvajal et al., 2019; Poorter et al., 2009; Reich, 2014).

Functional trait indices. I calculated community functional trait diversity for each 100 m transect using three indices shown to capture different dimensions of community functional diversity of each transect: functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve) (Mouchet et al., 2010). Functional richness (FRic) captures the total functional trait space occupied in a community without regard for differences in abundance and captures the most extreme trait values comprising a community. Functional evenness (FEve) refers to the uniformity of species abundances in functional trait space, where a high FEve reflects all trait values having a similar abundance in a community (Mouchet et al., 2010). Functional dispersion (FDis) is the mean distance from the centroid of each community in multidimensional trait species weighted by species abundance. I calculated FEve and FDis for individual traits, in addition to the multivariate indices, since different traits can show contrasting relationships to abiotic gradients and biotic interactions (Spasojevic & Suding, 2012). Trait indices were calculated using the *dbFD* function in the FD R-package (Laliberté & Legendre, 2010).

Interaction networks. Spatial associations among plants have been successfully used as a proxy for species interactions when measured at a fine resolution (Soliveres & Maestre, 2014; Tirado & Pugnaire, 2005). While this approach has been criticized, interactions derived from abundance data, rather than presence-absence, and collected at ecologically relevant scales, can provide more reliable proxies for plant interactions (Blanchet et al., 2020). Since plants are sessile organisms, species that aggregate in space more frequently than would be expected by random chance are assumed to benefit from their co-distribution, and therefore may represent the existence of a positive interaction (Pugnaire et al., 2004; Tirado & Pugnaire, 2005). Likewise, if species tend to not spatially co-occur, it can be assumed that there is a negative interaction that prevents co-occurrence. Particularly in dryland ecosystems, species interactions have shown to govern the spatial patterning of plant communities, and thus have been inferred from spatial data to successfully address questions in community ecology (Saiz, Gómez-Gardeñes, et al., 2018). Thus, I constructed association networks for each transect using the above described spatially explicit dataset, where nodes are plant species and links are the spatial associations between species.

For each of twenty-one transects, two paired association networks spanning the first and last 100 meters were constructed by calculating the total centimeter overlap of each pair of species. Since one transect did not have any species occurring in the first 100 meters, I ended up creating 41 networks. Spatial associations between species were determined using the method developed by Saiz and Alados (2012) by comparing the number of times species i and j co-occurred at the same place (c_{ij}) to the expected number of co-occurrences based on species abundances ($e_{ij} = n_i/T \times n_j/T \times T$, probability of i appearing at a single point multiplied by the probability of j appearing at a single point multiplied by the total number of points). Since I collected spatially explicit data (every exact centimeter accounted for), overlap between each species pair represents the total number of centimeters that included both species, and species abundances were the total number of centimeters that each species occupied across each transect. To determine whether each pairwise association was significant, I compared each c_{ij} to a Poisson distribution with e_{ij} as parameter, where c_{ij} was considered significant if it fell outside of the 95% confidence interval of e_{ij}. If c_{ij} was significantly higher than e_{ij}, a positive association between plant species was assumed, and set to +1, while if significantly lower, the association was assumed to be negative and set to -1. The absence of a significant association was set to 0.

Network metric calculations. The plant-plant association matrix using the above signs were used to calculate the total number of links in the network (L); the ratio of positive to negative links ($Ratio = (L^{+} - L^{-})/(\mathrm{L}^{+} + \mathrm{L}^{-})$), where positive $Ratio$ values indicate the greater frequency of positive associations and negative values indicate the greater frequency of negative associations (Saiz et al. 2017); link density, which is the average number of links per node, and describes how prevalent significant interactions are in the community; link weight heterogeneity, which is the kurtosis of the link weight distribution and indicates the variety of spatial patterns found in the community; node link heterogeneity, which is the kurtosis of species with links in the community, where lower values indicate that the links of each species tend to be more heterogeneous; and isolation, which represents the percentage of species with no links in the community (Pelliza et al., 2021). Prior to analyses, I tested for collinearity among all network metrics and did not remove any variables for initial analyses due to low correlation (Figure S3). To test the significance of network metrics, I constructed null models for each network which randomized the spatial cover of each species' occurrence while keeping the length of occurrence constant—thus, changing the connectivity of the networks for the indices used which incorporate the number, sign, and structure of positive and negative interactions. For each real network, I generated 999 randomized networks and then compared the real values of network metrics to the 95% confidence intervals of the simulated networks.

Statistical analyses

Since abiotic and biotic drivers of community structure can often covary across abiotic gradients, I sought to disentangle the direct and indirect influences of the environment and network variables on trait composition using structural equation modeling (SEMs).

SEMs are causal models that allow for the modeling of direct and indirect relationships among variables by estimating a global variance-covariance matrix (Grace 2006, 2008). Since our relatively small sample size constrained the number of pathways in our models (10 data points per observed variable; Bentler & Chou, 1987). I first identified the strongest variables predicting each trait metric using a model selection procedure and retained the predictor variables that were included in the best-fitting linear models, defined by having ΔAICc values less than two (Burnham and Anderson 2004). For these models, I first used a linear mixed effect model structure with transect as a random variable to account for potential spatial autocorrelation from the paired design of the networks. I compared models with and without transect as a random effect since in nearly all models the variance explained was close to zero and resulted in convergence issues and a poorer model fit (higher AIC). Therefore, I fit models as linear regressions without the random effect structure. I fitted both linear and quadratic terms for abiotic factors to account for potential nonlinear relationships. Based on our metamodel predicting functional composition (Figure 1), I then constructed an initial SEM for each functional diversity metric (FDis, FEve, Fric) that included all predictor variables appearing in the top models using the above procedure. Additionally, since patterns of multivariate trait metrics can be obscured due to individual traits showing opposing patterns across environmental gradients (Spasojevic & Suding, 2012), I also constructed SEMs for each trait CWM and FDis. I used a stepwise elimination process to remove pathways with the lowest coefficients and retained non-significant variables that improved the overall model fit for each focal trait metric and retained the strongest network indices for each trait to test for indirect abiotic effects. Model fit was assessed using the chi-square (χ^2) statistic, the root mean squared error of approximation (RMSEA), and the comparative fit index (CFI). χ^2 values with a P value >0.05 suggest that observed and expected covariance matrices are not different and therefore adequately describe the data. RMSEA values less than 0.1 and CFI scores greater than 0.9 are considered good-fitting models. All statistical analyses were conducted using R version 4.3.2. Linear models were fitted and selected using the lme4 (Bates et al. 2014) and MuMIN packages (Barton 2020). SEMs were constructed using the lavaan package (Rosseel, 2012).

Results

Elevational patterns of functional diversity and network metrics. Overall, FDis, Fric, and species richness all exhibited a unimodal distribution with peaks at the lower to mid elevations coinciding with desert scrub and pinyon-juniper woodland habitats (Figure 2a, 2b, 2d), while FEve showed no elevational trend (Figure 2c). Negative links and link density showed unimodal patterns across the gradient with similar peaks at lower to mid elevations, with link density having a broader peak extending into the chaparral habitat (Figure 3b and 3d). Positive links were generally higher across the lower to mid-elevations, with a slight increase at the highest elevations. The ratio of positive to negative links exhibited a U-shaped distribution with higher ratio at lower and higher elevations, indicating that there were more positive links relative to negative links at these elevations. Results from our null models showed that nearly all transects exhibited significantly more positive associations than expected by chance, and significantly less negative associations (Table 1). Similarly, nearly all networks had a significantly higher ratio than the null model, indicating that positive-to-negative associations were nearly always higher than expected by chance. Most networks across the elevation gradient were less dense and more isolated than expected by chance, indicating that individual species had fewer total positive and negative associations and that a greater number of species had no significant associations, respectively. Finally, node link heterogeneity was higher than expected by chance at the lower elevations, suggesting that individual species tended to have more uniform interaction types (primarily positive, negative, or neutral).

Direct and indirect drivers of functional diversity. The best-fit SEMs for all multivariate and individual traits had a good fit (in all cases: $\chi 2$ P > .05; GFI > 0.9, and RMSEA less than 0.1), and relatively high R^2 values for all traits except for FEve (Table 2). Multivariate FDis was more strongly driven by direct biotic variables (ratio and negative links), with negative links being the strongest direct driver (Figure 4). Maximum temperature was a strong indirect driver of FDis via its positive effect on network ratio, promoting more positive relative to negative interactions. Precipitation seasonality was the strongest direct abiotic driver of both FDis and FRic and was overall the strongest driver of FRic. In contrast to FDis, FRic was primarily determined by abiotic variables rather than biotic variables, with maximum temperature, soil PC2, and precipitation seasonality all promoting FRic (Figure 4). Link density was the strongest biotic driver of FRic, though it had a minimal overall contribution. Topographic roughness was the strongest direct driver of FEve (Figure S4), though all direct pathways had low explanatory power. Ratio, negative links, and node link heterogeneity were all direct positive drivers of FEve, with abiotic variables otherwise having indirect effects (Fig. S4).

All CWM traits, with the exception of leaf area, were more strongly determined by abiotic variables compared to biotic interactions, with average maximum temperature being the strongest direct driver (Figure S5-S9). Maximum temperature had a strong positive effect on SLA (Figure S5) and CC (S8) and a strong negative effect on height (Figure S9) and LDMC (Figure S7). Link density was the strongest direct driver of CWM LA (Figure S6) and was indirectly promoted by temperature and precipitation seasonality having a positive effect on link density. Similarly, CWM height, CWM SLA, and CWM CC all were also driven by indirect effects of abiotic variables mediated by network ratio or network density. Network ratio was the strongest biotic driver of CWM SLA, CWM CC, and CWM height, while link density and node link heterogeneity were the strongest network drivers of CWM LA and CWM LDMC, respectively. FDis SLA, FDis LA, and FDis LDMC were all more strongly driven by biotic interactions relative to abiotic variables. FDis SLA was most strongly associated with ratio, followed by link density and negative links (Figure S10). Maximum temperature was a relatively strong indirect driver of FDis SLA via its positive effect on network ratio. Precipitation seasonality had direct and indirect effects on FDis LA (Figure S11) and FDis LDMC (Figure S12), through its positive impact on link density and negative links, respectively. Likewise, precipitation seasonality had positive direct and indirect effects on FDis CC (Figure S13).

Maximum temperature was the strongest direct and indirect driver of FDis height (Figure S14), with negative direct effects and positive indirect effects via network ratio.

Discussion

The recognition of the complexity of variation in abiotic and biotic processes along abiotic environmental gradients has highlighted a critical need for understanding how both biotic and abiotic filters interactively determine the composition and structure of plant communities (Bimler et al., 2018; Borges et al., 2019; Thakur & Wright, 2017). The spatial structure of vegetation—captured by plant-plant association networks—has shown to be a significant predictor of species diversity, especially in dryland ecosystems (Alados et al., 2017; Saiz et al., 2018), and I show here that plant association networks also play an important role in structuring the functional composition of communities across a steep environmental gradient. Overall, I found that both abiotic conditions and biotic interactions were important drivers of community trait composition, with their relative importance differing for each dimension of trait composition. I also found that the direct influence of biotic interactions was mediated by environmental drivers, and therefore provide additional evidence that abiotic and biotic drivers must be considered jointly for their direct and indirect effects. Furthermore, our results highlight the importance of spatial association networks in structuring community trait composition, as I found that, in addition to the total number of positive and negative interactions in each community, network metrics accounting for the structure of those interactions—such as the ratio of the two—were important predictors of different aspects of functional trait composition.

An extensive body of literature has sought to understand how competition and facilitation among plant species change across environmental gradients, however, very few studies have examined interactions among all species occurring in a community, which has limited our understanding of how diverse interactions contribute to community composition. I found general support for the stress gradient hypothesis, where positive interactions prevailed under more abiotically stressful conditions at lower elevations, and competitive interactions were more frequent at higher elevations (Figure 3; Bertness & Callaway, 1994; Callaway et al., 2002). This result is surprising given that there has been inconsistent support for SGH predictions (Maestre et al., 2009), especially for longer gradients that encompass extensive species turnover (Soliveres & Maestre, 2014) where species replacement is likely to obscure the overall effects of stress due to corresponding turnover in niche optima (Liancourt et al., 2005). However, while total facilitative interactions were generally higher in communities at lower elevations, positive interactions occurred in all communities and were more prevalent than expected by chance in most communities, as shown by our null models (Table 1). Indeed, recent work has highlighted that facilitative interactions are likely ubiquitous in many communities (Bimler et al., 2018, 2024), even in more spatially continuous vegetation (Liancourt & Dolezal, 2020). While plant facilitation is generally expected to increase functional diversity at the community level (Butterfield & Briggs, 2011; Chacón-Labella et al., 2016; Schob et al., 2017; Schöb et al., 2012), I found that it played a relatively minor role overall, primarily increasing the presence of species with extreme trait values—shown by the positive indirect effect of positive interactions on functional richness (Figure 4). Therefore, our results support the idea that rare or subordinate species are primarily impacted by facilitation (Bruno et al. 2003). However, I also found that facilitative interactions weakly promoted the functional dispersion (FDis) of LDMC (Figure S12). Since LDMC is related to the ability of a leaf to store and exchange heat with the environment (Michaletz et al., 2015, 2016), this finding likely reflects the role of facilitation in creating favorable microclimates which maintain species in the community with otherwise less adapted traits.

Importantly, since our approach accounted for both positive and negative interactions in each community across a large environmental gradient, I was able to show that competitive interactions played a strong role in promoting taxonomic and functional diversity. Specifically, competitive interactions were the strongest direct driver of multivariate FDis (Figure 4), promoting FDis of nearly every trait measured, and indirectly influencing trait composition through direct effects on network ratio and link density. Thus, our results support classic predictions of the positive role of competition in driving trait differences among co-occurring species (Chesson, 2000; MacArthur & Levins, 1967; Weiher & Keddy, 1995) and are consistent with other work showing that spatial segregation as a proxy for competition increases trait dispersion in dryland communities (Gross et al., 2013). This is important since most tests of the SGH, including those conducted at the community level, have focused solely on facilitation and how it changes across relatively short gradients (Soliveres & Maestre, 2014), which has likely resulted in an overlooking of the frequency of competition in abiotically harsh ecosystems. Indeed, the importance and even existence of competitive interactions in arid regions have long been a subject of debate (Fowler, 2008; Goldberg & Novoplansky, 2009; J.P. Grime, 1973), though experimental approaches have confirmed that competition is common in drylands (Fowler, 2008; Maestre et al., 2009; Woods et al., 2019), and observational approaches have found a positive role for competitive interactions in promoting functional diversity (Gross et al., 2013; Saiz, Le Bagousse-Pinguet, et al., 2018).

However, it's also possible that the positive relationship between spatial segregation as a proxy of competitive interactions and functional diversity may be the product of niche differentiation in response to variation in the timing of precipitation since I found that precipitation seasonality was strongly correlated with functional dispersion and competitive interactions (Figure S15) and promoted the density of both types of interactions. Indeed, plant species in drylands often exhibit temporal and spatial niche partitioning for water resources, where coexisting species access water from different depths and/or at different times (Aschehoug et al., 2016; Guo et al., 2018; Ward et al., 2013), which contribute, through a variety of mechanisms, to their coexistence (Chesson et al., 2004). Across the southwestern US, there is a bimodal pattern of seasonal precipitation where pulse-driven convective precipitation events favor shallow-rooted species with acquisitive traits, and deeper percolation with frontal winter storms favors deeply-rooted species with more conservative traits (Guo et al., 2018; Schwinning & Ehleringer, 2001). Ultimately, the extent of competition between species exhibiting divergent strategies for water uptake will depend on whether uptake during precipitation pulses is correlated with survival during interpulse periods (Goldberg & Novoplansky, 2009) and requires experimentation to disentangle. Given that I used non-random patterns of spatial segregation as a proxy for competition, it is likely that a combination of long-term competition among similar species (Fowler, 2008; King & Woodell, 1973) and differential resource utilization over time and space (e.g., storage effects) both have contributed to promoting diversity in our pulse-driven study system (Chesson et al., 2004).

While I found that biotic interactions, as captured by network metrics, were generally stronger predictors of functional diversity, I also found that abiotic factors were generally stronger drivers of CWM trait values. For instance, maximum temperature was the strongest direct driver of most CWM values, where higher temperatures at lower elevations were associated with shorter height, higher SLA, higher chlorophyll content, and lower LDMC (Figure S9, S5, S8, S7). These results are consistent with classic predictions and a large body of empirical evidence, which supports the idea of community trait convergence toward optimum values across abiotic conditions (Cornwell & Ackerly, 2009; Grime, 2006). In arid and semiarid ecosystems, stress-tolerant species investing in longer-lived, thicker leaves with lower rates of photosynthesis are generally favored, though, increasing levels of aridity tend to favor the presence of stress-avoidant and drought-deciduous strategies, leading to more acquisitive strategies with thinner leaves investing in more chlorophyll for increased rates of photosynthesis (Carvajal et al., 2019; Niinemets, 2001; Poorter et al., 2009). Taller species are also disfavored under conditions of increasing aridity, due to the increased risk of cavitation (McDowell et al., 2008), which explains our negative temperature-CWM height relationship. While competitive interactions were the strongest biotic driver of multivariate functional dispersion (Figure 4)—through the strong positive effects of negative links on FDis CC and FDis LDMC—the functional dispersion of all other traits was most strongly driven by either link density or network ratio, indicating that the average number of competitive and facilitative interactions per species as well as the ratio of facilitative to competitive interactions, respectively, promoted functional diversity across our study site. Thus, the biotic interaction metrics most consistently explaining trait diversity were emergent properties of the interaction networks rather than simply the number of positive and negative interactions, which were only evident by analyzing plant communities as interaction networks. While network theory has advanced our understanding of the role of trophic interactions in community assembly (Ponisio et al., 2019), the application of network approaches in plant community assembly has been generally under-utilized (Losapio et al., 2019), though recent work has shown that plant-plant interaction networks can predict plant community diversity (Alados et al., 2017; Saiz, Gómez-Gardeñes, et al., 2018). Since accumulating work is showing that both facilitation and competition often occur simultaneously in plant communities (Bimler et al., 2024), our results offer additional support to the idea that the balance of the two plays a key role in structuring communities (Losapio et al., 2021).

While our results generally supported decades of theoretical expectations underlying community assembly theory, I recognize that our approach has important limitations, which could have obscured the influence of other unmeasured factors. First, while spatial associations have been shown experimentally to reflect the outcome of biotic interactions (Tirado & Pugnaire, 2005), it is also possible that spatial aggregation and segregation patterns could be due to microhabitat variables not being measured since habitat heterogeneity at small spatial scales can also promote trait diversity in plant communities (Stark et al., 2017). Second, recent work on multispecies coexistence shows that interaction asymmetry is key for understanding long-term coexistence (Allen-Perkins et al., 2023) and is something I could not account for using an observational approach. Third, plant functional traits are known to be important drivers of plant-plant interactions, where others have often used traits to infer interactions in communities (Chalmandrier et al., 2021). Indeed, while there is extensive support for the environmental dependence of plant interactions, the strength and direction of species' interactions have also shown to be dependent on the traits of interacting species (Butterfield & Briggs, 2011; Ochoa-Hueso et al., 2018), and thus, causality could be opposite. Future experimental work should attempt to disentangle the causal relationships among traits and plant-plant interactions.

In conclusion, I showed that accounting for biotic interactions at a fine scale across a large abiotic gradient can reveal the signature of biotic and abiotic processes. However, importantly, I showed that both biotic and abiotic drivers simultaneously contribute to structuring community trait patterns through both direct and indirect mechanisms. Therefore, I echo others' call to abandon the conceptualization of separate and sequential filters driving community assembly, and instead continue to disentangle how these filters interact (Bimler et al., 2024; Borges et al., 2019; Cadotte & Tucker, 2017; Germain et al., 2018; Loughnan & Gilbert, 2017; Thakur & Wright, 2017). While I found broad support for the stress-gradient hypothesis, I found that both positive and negative spatial associations—capturing facilitative and competitive interactions, respectively—occurred in all communities, and their ratio along with the average number of interactions per species were the most common biotic predictors of functional trait composition. Therefore, the relationship between biotic and abiotic filters is likely to be only understood by accounting for diverse interactions among all species in a community and the overall structure of those interactions. I suggest that interaction networks will continue to be an illuminating tool in understanding the drivers of plant community organization.

Tables and figures

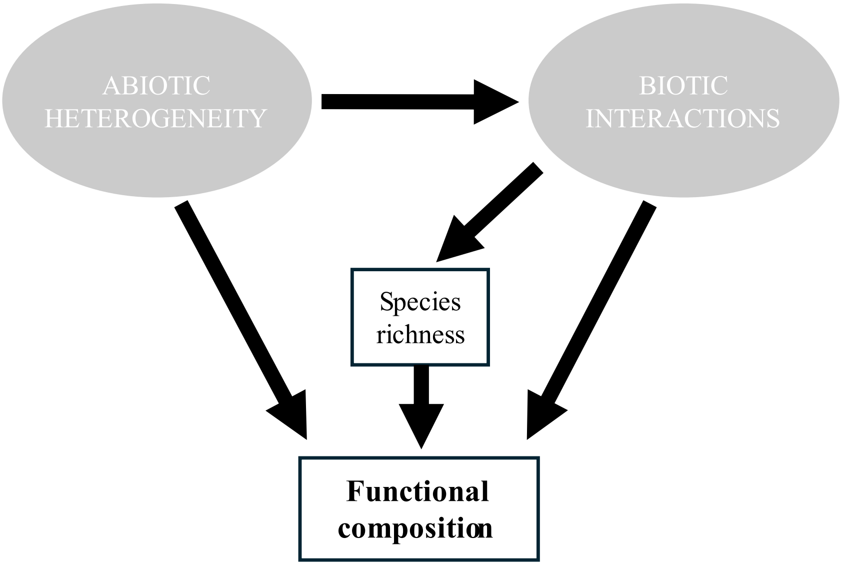


Figure 2.1 Hypothesized causal relationships used as the meta-model for all structural equation models (SEMs). In addition to the direct effects of abiotic and biotic variables known to structure functional trait composition of communities, I also tested for potential indirect effects of abiotic variables mediated by interaction network metrics, as well as indirect effects of biotic interactions mediated by species richness.

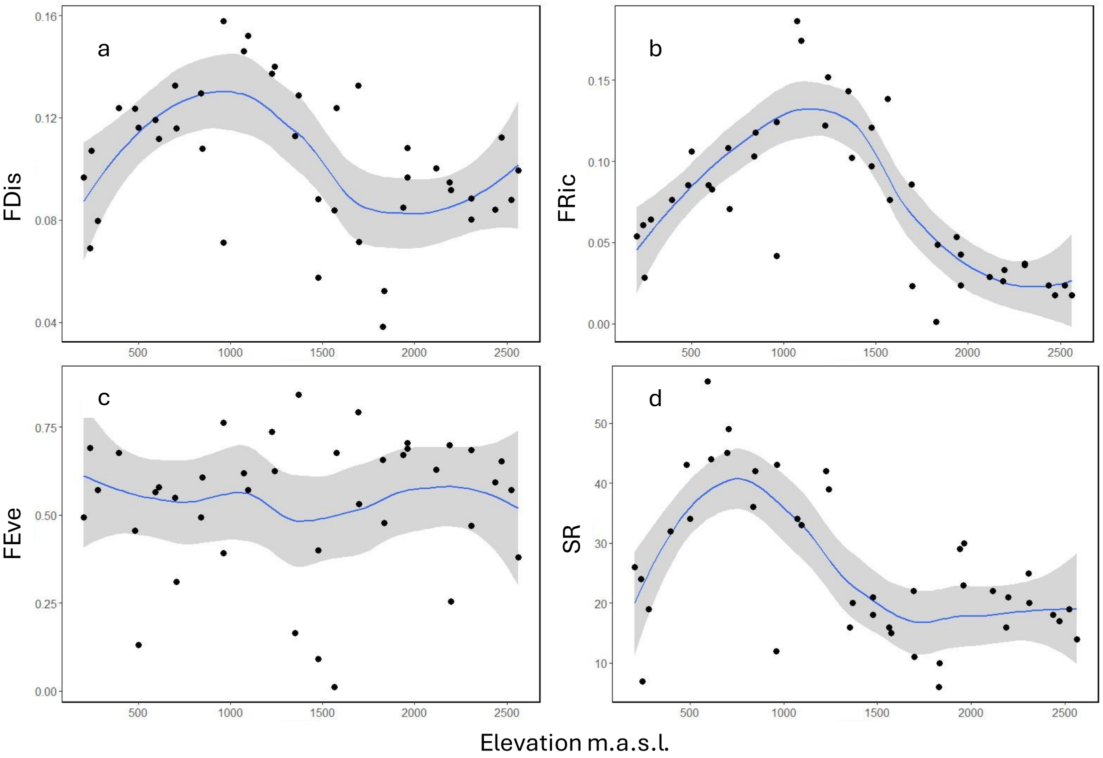


Figure 2.2 Patterns of functional trait diversity and species richness across the study elevation gradient (m.a.s.l. = meters above sea level). While functional dispersion (a), functional richness (b), and species richness (d) showed similar unimodal relationships across elevation, functional evenness (c) exhibited no clear relationship with elevation.

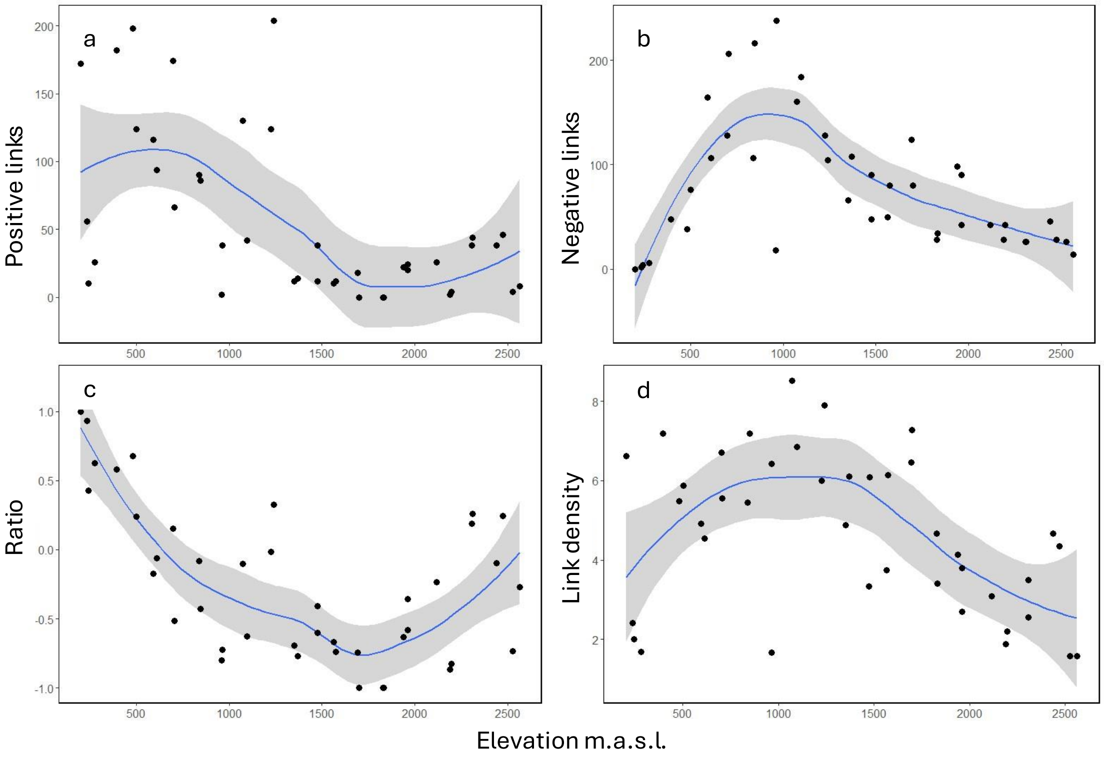


Figure 2.3 Network metrics most strongly associated with functional traits exhibited diverse patterns across the elevation gradient (m.a.s.l. = meters above sea level). Positive links (a) were generally higher at lower elevations, while negative links (b) were higher in the mid to high-elevation communities, declining with elevation. Therefore, the ratio of the two (c) was highest at lower elevations with an increase again in the highest-elevation communities. Link density (d)—the average number of interactions (links) per species—showed a unimodal relationship with elevation, peaking across the lower-middle elevations.

Table 2.1 Species richness and network indices for all transects across the elevation gradient and their associated significance as determined by null models. Positive and negative links are proxies of facilitation and competition, respectively. Ratio is the relative frequency of facilitative compared to competitive interactions. Density is the average number of interactions per species. Isolation represents the percentage of species with no links in the community, and node link heterogeneity, is the kurtosis of species with links in the community, where lower values indicate that the links of each species tend to be more heterogeneous. The significance of each metric is indicated by * for greater than 95% CI or *(-) for lower than 95% CI.

transect	**interval**	**species richness**	**Positive links**	**Negative links**	**ratio**	**density**	**isolation**	**Node link heterogeneity**
1	100	24	56*	2*(-)	0.93*	2.4	0.33	4.94
1	400	26	172*	0*(-)	1.00*	6.6*	0.23	1.78*
2	100	7	10*	4*(-)	0.42*	2.0*(-)	0.14*	1.75
2	400	19	26*	6*(-)	0.62*	1.6*(-)	0.36	3.73*
3	400	32	182*	48*(-)	0.58*	7.18*(-)	0.09*	6.01*
4	100	34	124*	76*(-)	0.24*	5.88*(-)	0.17	2.62*
4	400	43	198*	38*(-)	0.67*	5.48*(-)	0.16*(-)	5.77*
5	100	44	94*	106*(-)	-0.06*	4.54*(-)	0.34*	2.40*
5	400	57	116*	164*	-0.17*	4.91*	0.31	2.28
6	100	45	174*	128*(-)	0.15*	6.71*(-)	0.20*	4.52*
6	400	49	66*	206*(-)	-0.51*	5.55*	0.22*	2.97
7	100	36	90*	106*(-)	-0.08*	5.44*(-)	0.13*	2.99*
7	400	42	86*	216*(-)	-0.43*	7.19*(-)	0.26*	3.30*
8	400	12	2*	18*(-)	-0.80*	1.66*(-)	0.33*	3.10*
8	100	43	38*	238*	-0.72*	6.41*	0.00*	14.14*
9	100	33	42*	184*(-)	-0.62*	6.84*(-)	0.18*(-)	1.69*
9	400	34	130*	160*(-)	-0.10*	8.52*(-)	0.14*	1.82*
10	100	42	124*	128*(-)	-0.01*	6.00*(-)	0.23*	2.00*(-)
10	400	39	204*	104*(-)	0.32*	7.89*(-)	0.12*(-)	2.93*
11	100	16	12*	66*(-)	-0.69*	4.87*(-)	0.18*	1.32*(-)
11	400	20	14*	108*(-)	-0.77*	6.10*(-)	0.10	1.59*(-)

12	100	21	38*	90*(-)	-0.40*	6.09*(-)	0.09	2.90*
12	400	18	12*	48*(-)	-0.60*	3.33*(-)	0.22	2.04
13	100	16	10*	50*(-)	-0.66*	3.75*(-)	0.37*	1.51
13	400	15	12*	80*(-)	-0.73*	6.13*(-)	0.06	2.07
14	100	22	18*	124*(-)	-0.74*	6.45*(-)	0.00	1.88
14	400	11	0	80*(-)	-1.00	7.27*(-)	0.09*	6.01*(-)
15	100	6	0	28	-1.00	4.66	0.00	1.50
15	400	10	0	34*(-)	-1.00	3.40*(-)	0.30*	1.43*(-)
16	100	29	22*	98*(-)	-0.63*	4.13*(-)	0.24*	3.89*
16	400	30	24*	90*(-)	-0.57*	3.80*(-)	0.23*	2.20
17	100	23	20*	42*(-)	-0.35*	2.69*(-)	0.39*	2.41
17	400	22	26*	42*(-)	-0.23*	3.09*(-)	0.27*	3.04*
18	100	16	2*	28*(-)	-0.86*	1.87*(-)	0.43*	2.28
18	400	21	4*	42*(-)	-0.82*	2.19*(-)	0.42*	2.99
19	100	25	38*	26*(-)	0.18*	2.56*(-)	0.36*	4.07
19	400	20	44*	26*(-)	0.25*	3.50*(-)	0.30*	1.43*(-)
20	100	18	38*	46*(-)	-0.09*	4.66*(-)	0.11*	1.80
20	400	17	46*	28*(-)	0.24*	4.35*(-)	0.11	2.43
21	100	19	4*	26*(-)	-0.73*	1.57*(-)	0.57*	2.55
21	400	14	8*	14*(-)	-0.27*	1.57*(-)	0.42*	3.23*

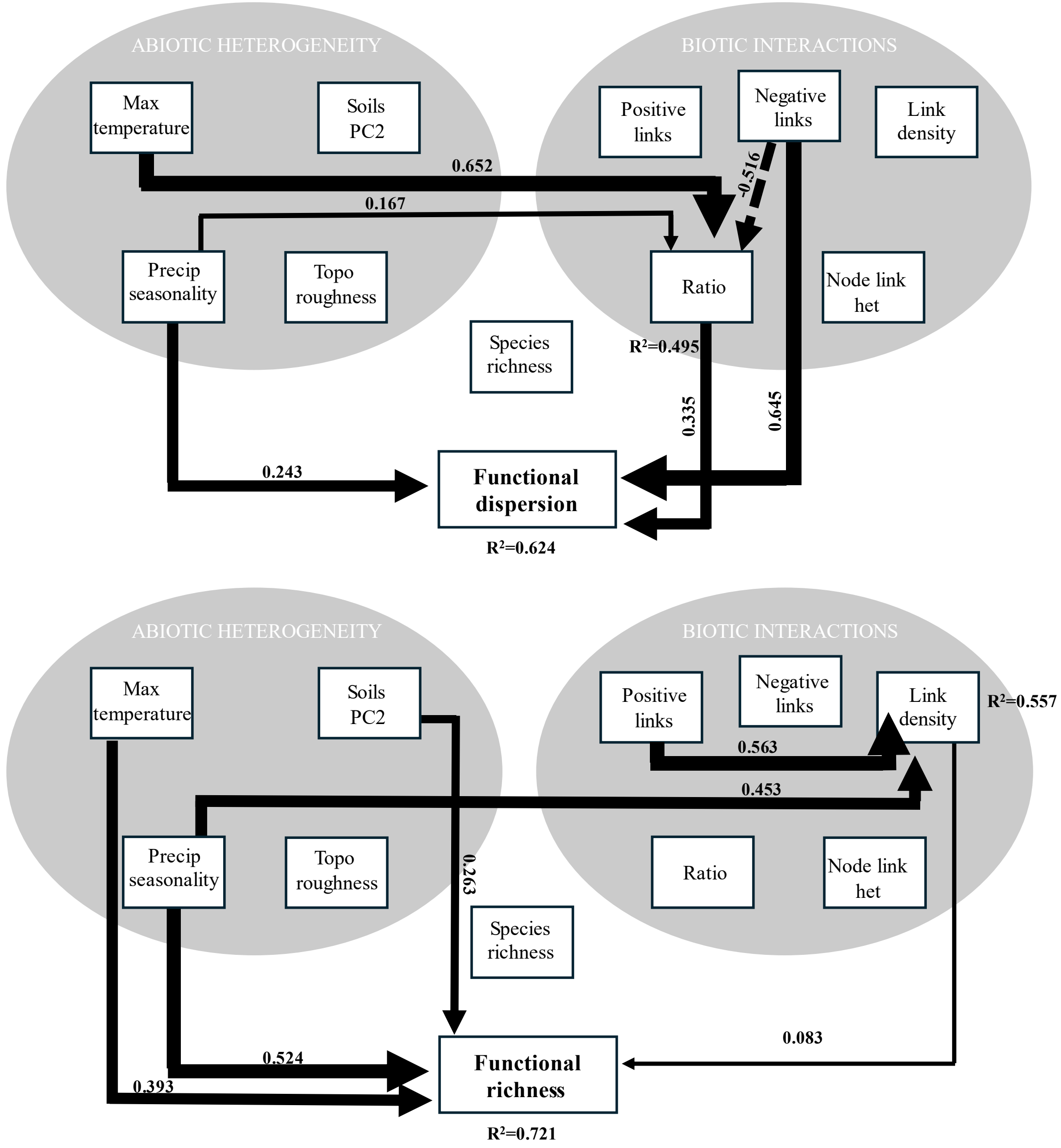


Figure 2.4 Structural equation models (SEMs) describing functional richness and multivariate functional dispersion through direct and indirect effects of abiotic and biotic variables. Overall, functional dispersion was more strongly influenced by biotic variables than abiotic ones, where negative (competitive) interactions and ratio (positive/negative interactions) were the strongest direct drivers, and maximum temperature was a strong indirect driver. Functional richness was primarily influenced by maximum temperature and precipitation seasonality. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships.

Table 2.2 Model fit metrics for all structural equation models describing functional trait composition. Models with $\chi 2$ P-values greater than 0.05, GFI scores greater than 0.9, and RMSEA less than 0.1 were interpreted as providing a good fit for the data. Abbreviations: FDIS=functional dispersion, FEVE=functional evenness, FRIC=functional richness, CWM=community weighted mean, SLA=specific leaf area, LA=leaf area, CC=chlorophyll content, LDMC=leaf dry matter content

TRAIT	X2	X2 P-VALUE	GFI	RMSEA	AIC	TRAIT R2
FDIS	0.332	0.564	0.997	0.000	178.5	0.624
FEVE	1.965	0.580	0.964	0.000	221.6	0.066
FRIC	2.520	0.472	0.992	0.000	165.4	0.816
CWM SLA	0.117	0.732	0.999	0.000	170.9	0.658
CWM LA	0.123	0.725	0.997	0.000	210.5	0.331
CWM CC	0.358	0.949	0.998	0.000	161.7	0.772
CWM LDMC	0.536	0.911	0.994	0.000	196.6	0.634
CWM HEIGHT	1.500	0.472	0.996	0.000	155.5	0.660
FDIS SLA	0.002	0.962	1.000	0.000	200.8	0.358
FDIS LA	0.001	0.982	1.000	0.000	196.4	0.445
FDIS CC	0.105	0.746	0.999	0.000	153.6	0.803
FDIS LDMC	0.976	0.807	0.979	0.000	216.0	0.339
FDIS HEIGHT	0.463	0.496	0.999	0.000	173.1	0.696

Supplementary figures

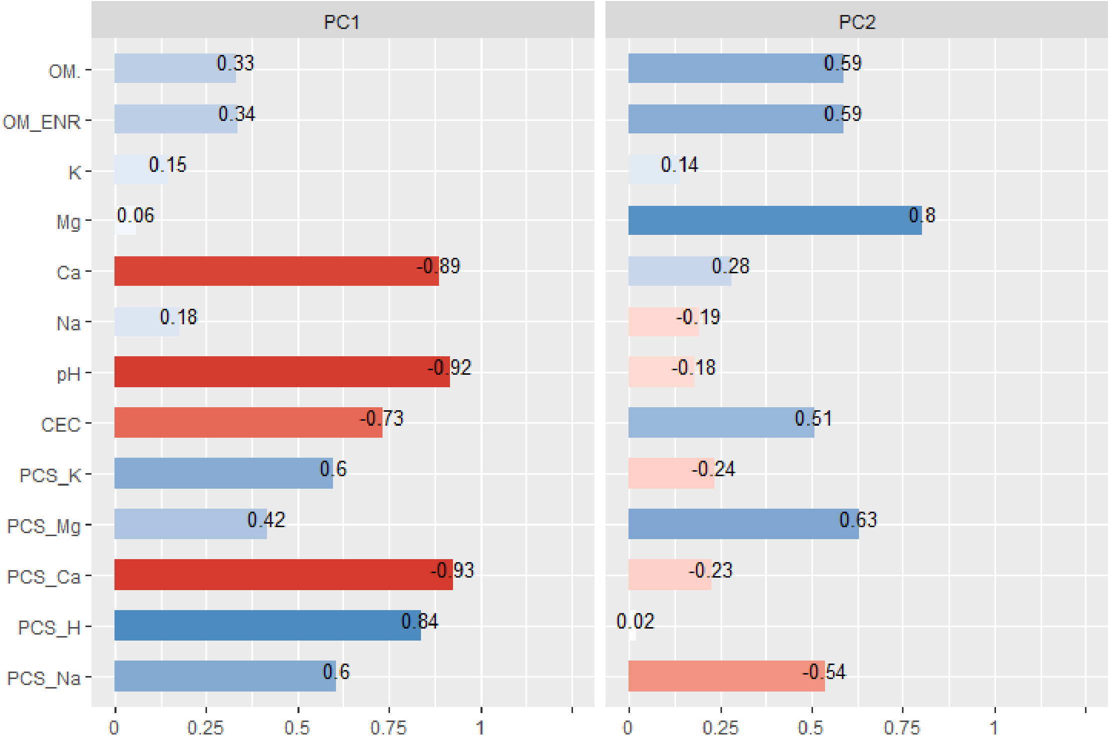
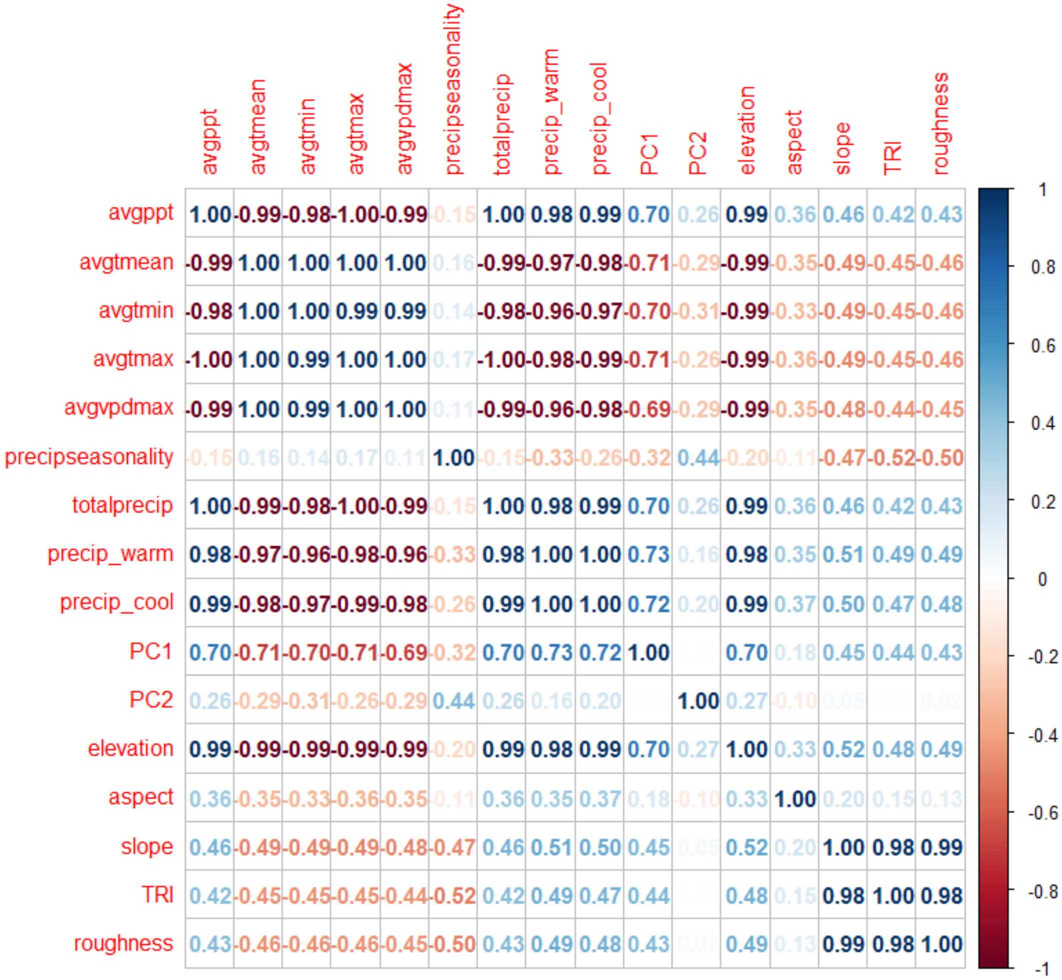
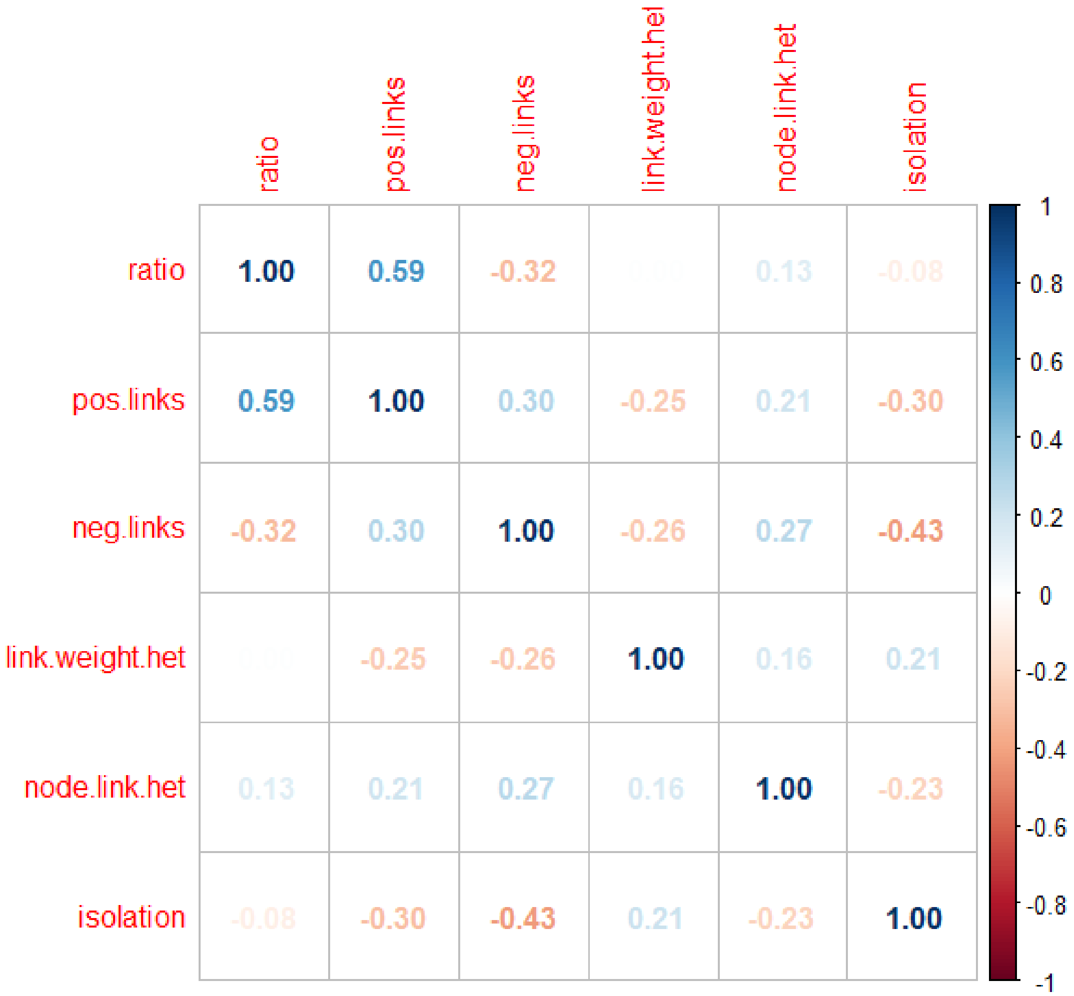


Figure 2.S1 Loadings from principal component analysis of soil variables. Abbreviations: OM=organic matter, OM_ENR=organic matter estimated nitrogen release, K=potassium, Mg=magnesium, Ca=calcium, Na=sodium, CEC=cation exchange capacity, PCS=percent cation saturation.



	avgppt	avgtmean	avgtmin	avgtmax	avgvpdmax	precipseasonality	totalprecip	precip_warm	precip_cool	PC1	PC2	elevation	aspect	slope	TRI	roughness
avgppt	1.00	-0.99	-0.98	-1.00	-0.99	-0.15	1.00	0.98	0.99	0.70	0.26	0.99	0.36	0.46	0.42	0.43
avgtmean	-0.99	1.00	1.00	1.00	1.00	0.16	-0.99	-0.97	-0.98	-0.71	-0.29	-0.99	-0.35	-0.49	-0.45	-0.46
avgtmin	-0.98	1.00	1.00	0.99	0.99	0.14	-0.98	-0.96	-0.97	-0.70	-0.31	-0.99	-0.33	-0.49	-0.45	-0.46
avgtmax	-1.00	1.00	0.99	1.00	1.00	0.17	-1.00	-0.98	-0.99	-0.71	-0.26	-0.99	-0.36	-0.49	-0.45	-0.46
avgvpdmax	-0.99	1.00	0.99	1.00	1.00	0.11	-0.99	-0.96	-0.98	-0.69	-0.29	-0.99	-0.35	-0.48	-0.44	-0.45
precipseasonality	-0.15	0.16	0.14	0.17	0.11	1.00	-0.15	-0.33	-0.26	-0.32	0.44	-0.20	-0.11	-0.47	-0.52	-0.50
totalprecip	1.00	-0.99	-0.98	-1.00	-0.99	-0.15	1.00	0.98	0.99	0.70	0.26	0.99	0.36	0.46	0.42	0.43
precip_warm	0.98	-0.97	-0.96	-0.98	-0.96	-0.33	0.98	1.00	1.00	0.73	0.16	0.98	0.35	0.51	0.49	0.49
precip_cool	0.99	-0.98	-0.97	-0.99	-0.98	-0.26	0.99	1.00	1.00	0.72	0.20	0.99	0.37	0.50	0.47	0.48
PC1	0.70	-0.71	-0.70	-0.71	-0.69	-0.32	0.70	0.73	0.72	1.00	0.00	0.70	0.18	0.45	0.44	0.43
PC2	0.26	-0.29	-0.31	-0.26	-0.29	0.44	0.26	0.16	0.20	0.00	1.00	0.27	-0.10	0.05	0.00	0.02
elevation	0.99	-0.99	-0.99	-0.99	-0.99	-0.20	0.99	0.98	0.99	0.70	0.27	1.00	0.33	0.52	0.48	0.49
aspect	0.36	-0.35	-0.33	-0.36	-0.35	-0.11	0.36	0.35	0.37	0.18	-0.10	0.33	1.00	0.20	0.15	0.13
slope	0.46	-0.49	-0.49	-0.49	-0.48	-0.47	0.46	0.51	0.50	0.45	0.05	0.52	0.20	1.00	0.98	0.99
TRI	0.42	-0.45	-0.45	-0.45	-0.44	-0.52	0.42	0.49	0.47	0.44	0.00	0.48	0.15	0.98	1.00	0.98
roughness	0.43	-0.46	-0.46	-0.46	-0.45	-0.50	0.43	0.49	0.48	0.43	0.02	0.49	0.13	0.99	0.98	1.00

Figure 2.S2 Correlation matrix among all abiotic variables using Pearson correlation coefficients. Positive correlations are indicated by blue colors, while negative correlations are indicated by red colors. PC1 and PC2 are the first two PCA axes of soil variables. Abbreviations: avgppt=average precipitation, avgtmean, average mean temperature, avgtmin=average minimum temperature, avgtmax=average maximum temperature, avgvpdmax=average maximum vapor pressure deficit, precipseasonality=precipitation seasonality, totalprecip= total annual precipitation, precip_warm=warm season precipitation, precip_cool=cool season precipitation, TRI=Topographic Ruggedness Index



	ratio	pos.links	neg.links	link.weight.het	node.link.het	isolation
ratio	1.00	0.59	-0.32	0.00	0.13	-0.08
pos.links	0.59	1.00	0.30	-0.25	0.21	-0.30
neg.links	-0.32	0.30	1.00	-0.26	0.27	-0.43
link.weight.het	0.00	-0.25	-0.26	1.00	0.16	0.21
node.link.het	0.13	0.21	0.27	0.16	1.00	-0.23
isolation	-0.08	-0.30	-0.43	0.21	-0.23	1.00

Figure 2.S3 Correlation matrix among all network variables using Pearson correlation coefficients. Positive correlations are indicated by blue colors and negative relationships are indicated by red colors.

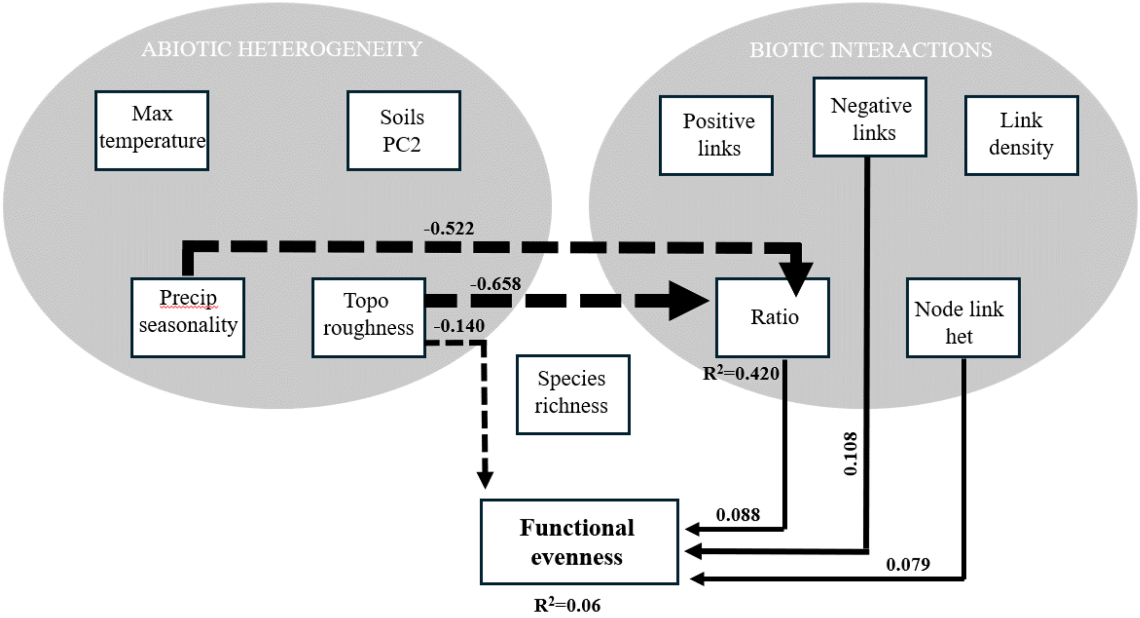


Figure 2.S4 Structural equation model (SEM) describing functional evenness through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

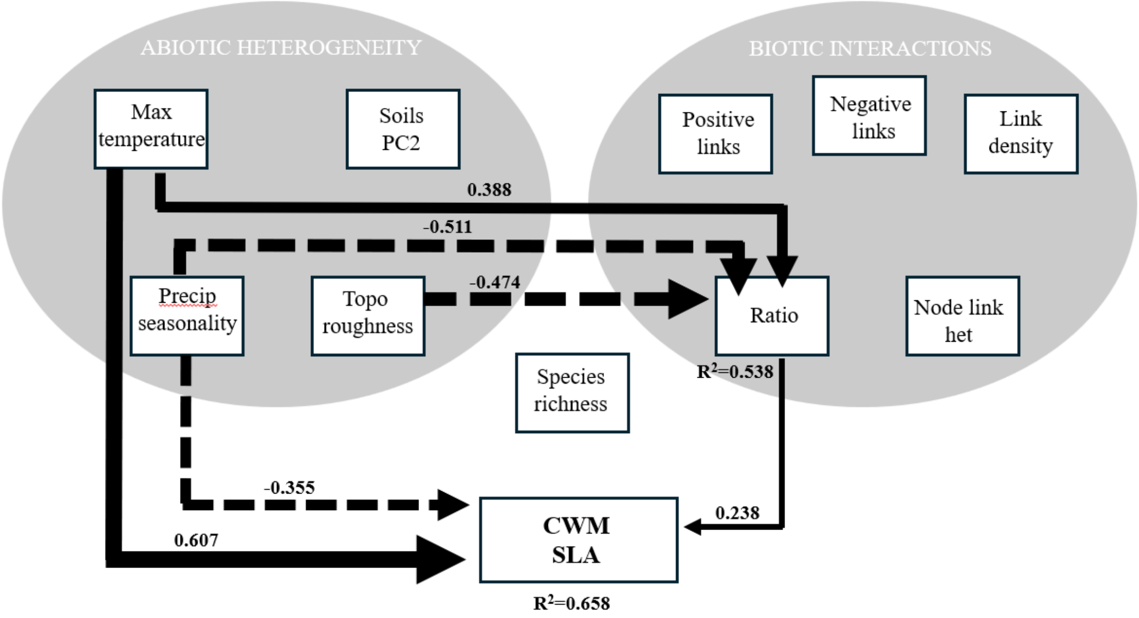


Figure 2.S5 Structural equation model (SEM) describing CWM SLA through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

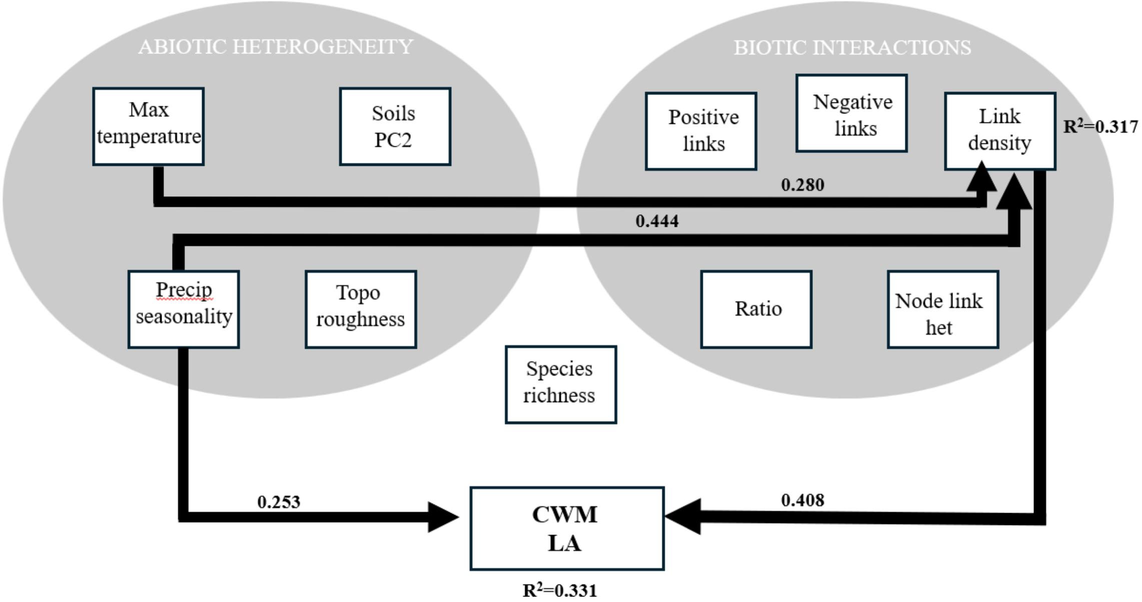


Figure 2.S6 Structural equation model (SEM) describing CWM leaf area through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships.

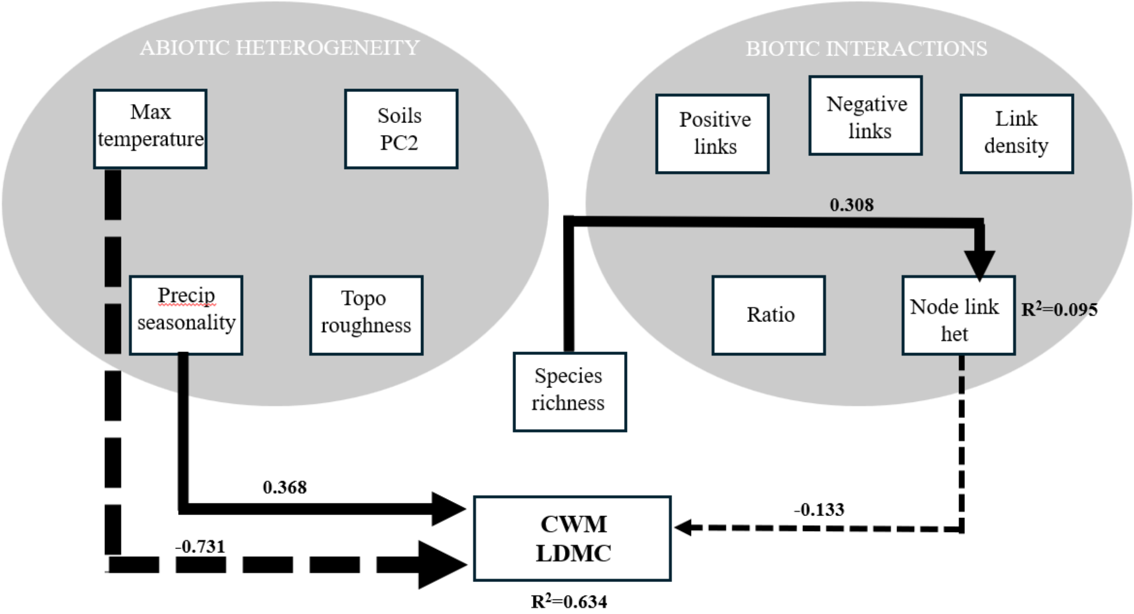


Figure 2.S7 Structural equation model (SEM) describing CWM LDMC through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

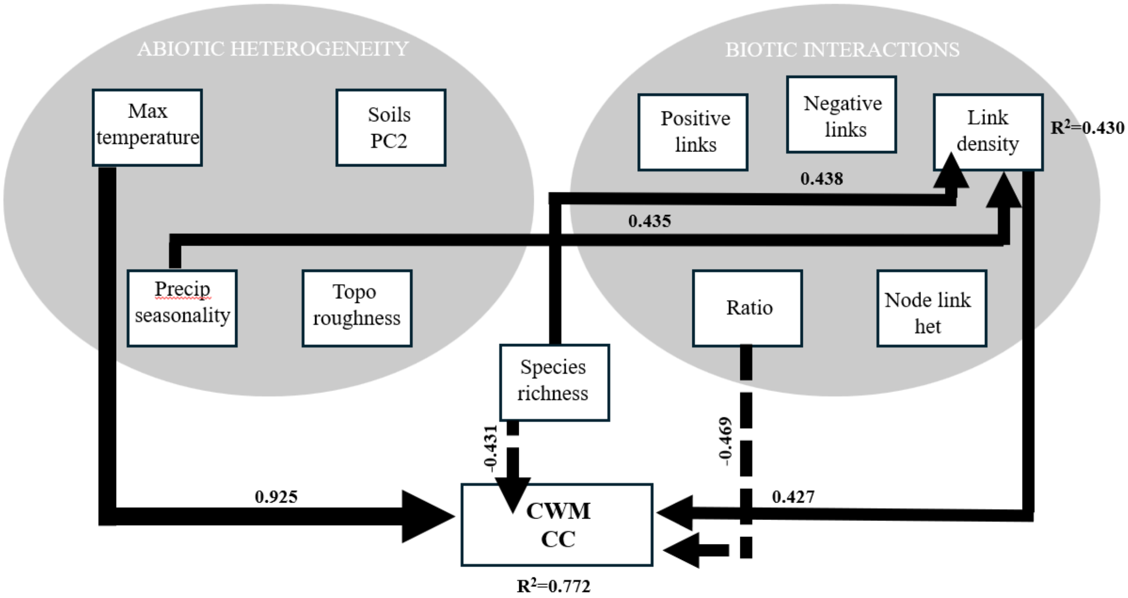


Figure 2.S8 Structural equation model (SEM) describing CWM chlorophyll content through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

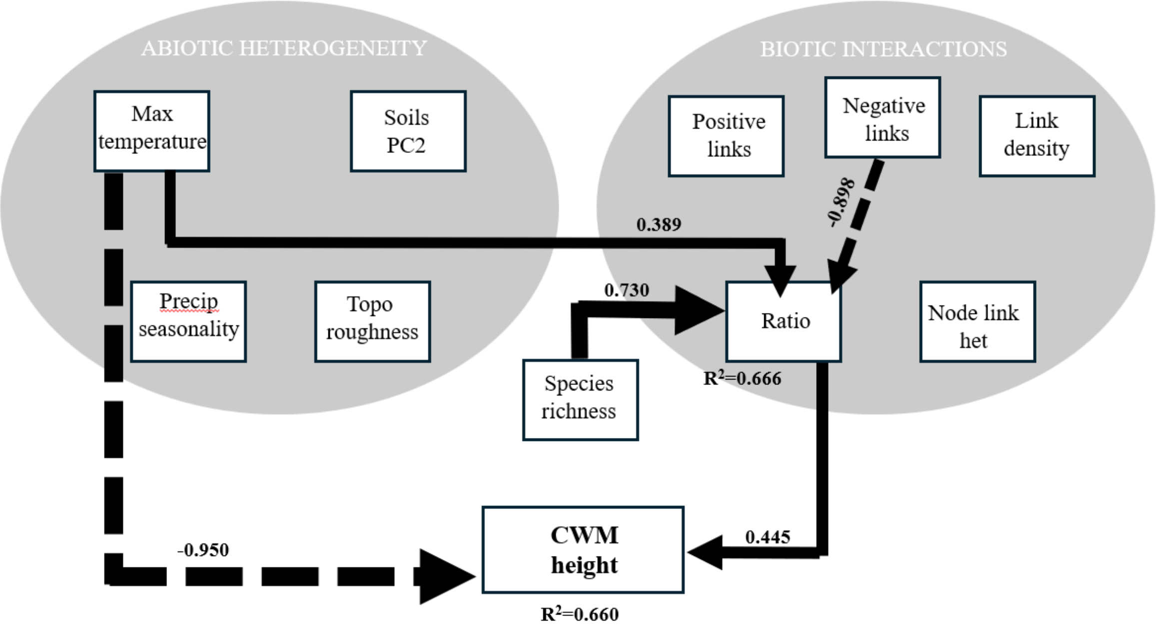


Figure 2.S9 Structural equation model (SEM) describing CWM height through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

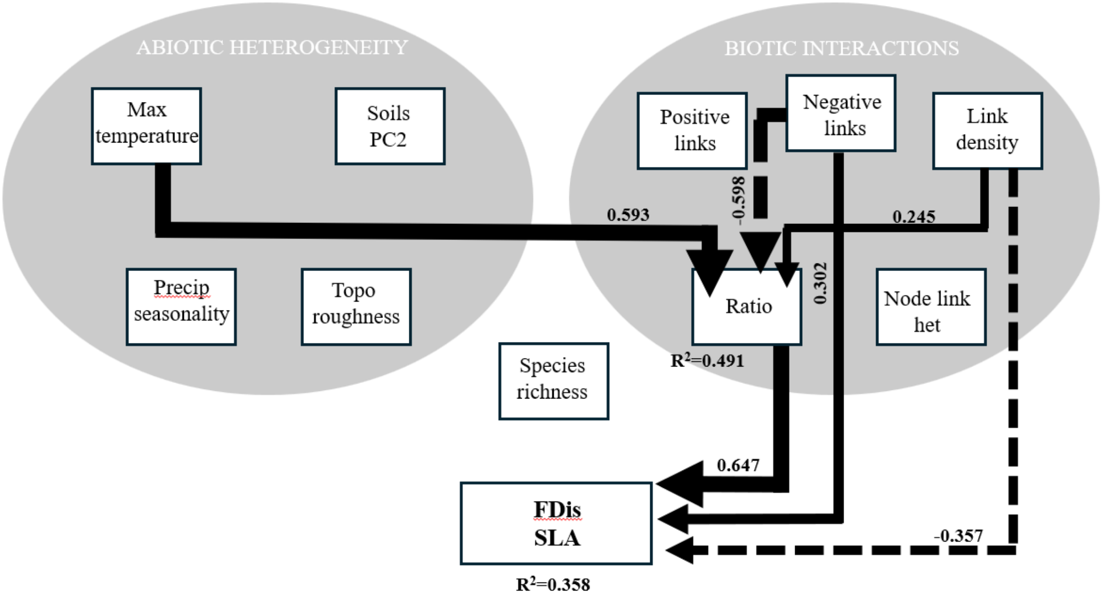


Figure 2.S10 Structural equation model (SEM) describing functional dispersion of SLA through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

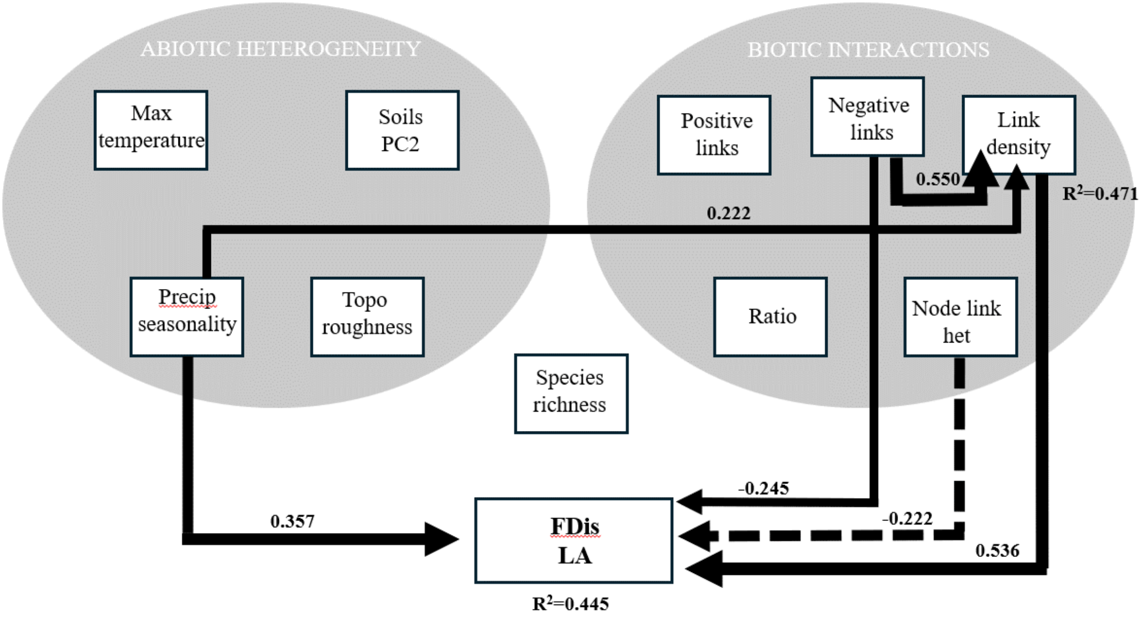


Figure 2.S11 Structural equation model (SEM) describing functional dispersion of leaf area through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

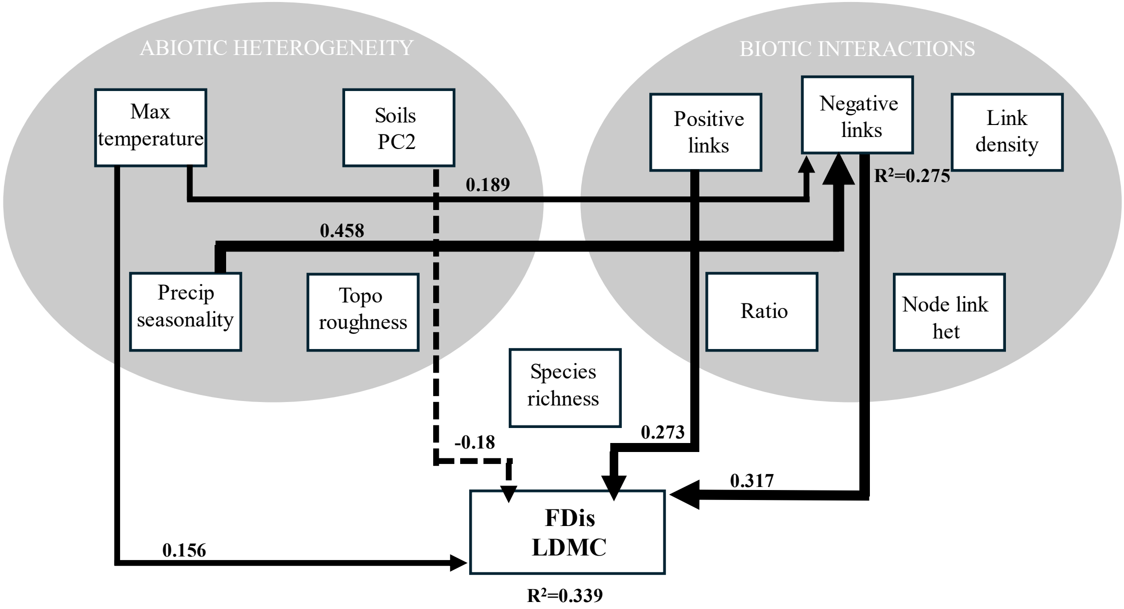


Figure 2.S12 Structural equation model (SEM) describing functional dispersion of leaf dry matter content (LDMC) through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships.

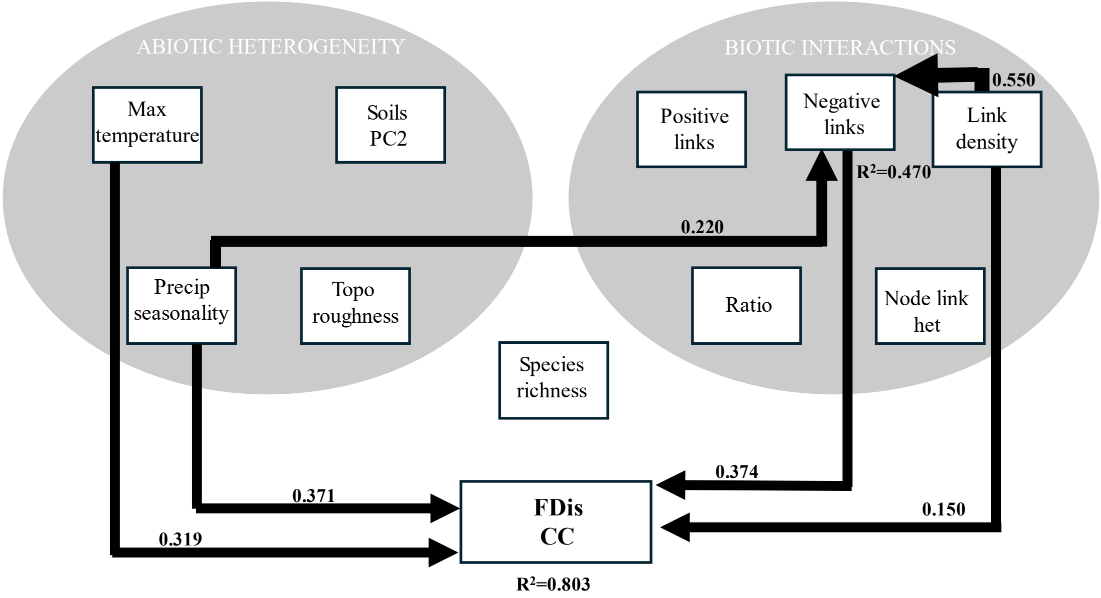


Figure 2.S13 Structural equation model (SEM) describing functional dispersion of chlorophyll content through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships.

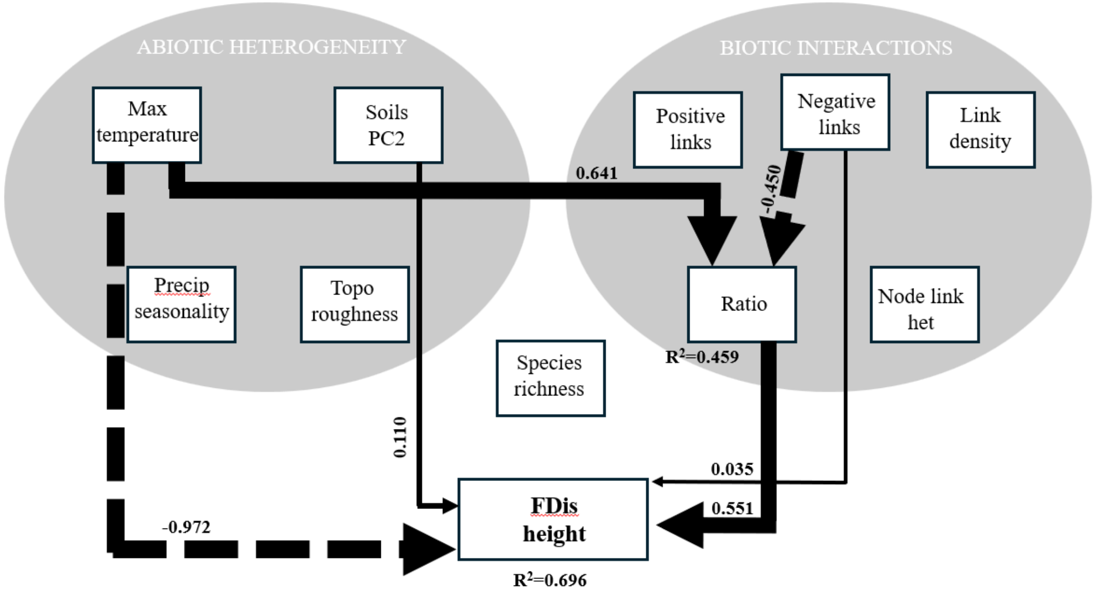


Figure 2.S14 Structural equation model (SEM) describing functional dispersion of height through direct and indirect effects of abiotic and biotic variables. Arrows represent the inferred direction of causality, while the thickness of lines represents the strength of causal relationships. Solid lines represent positive effects, while dashed lines represent negative effects.

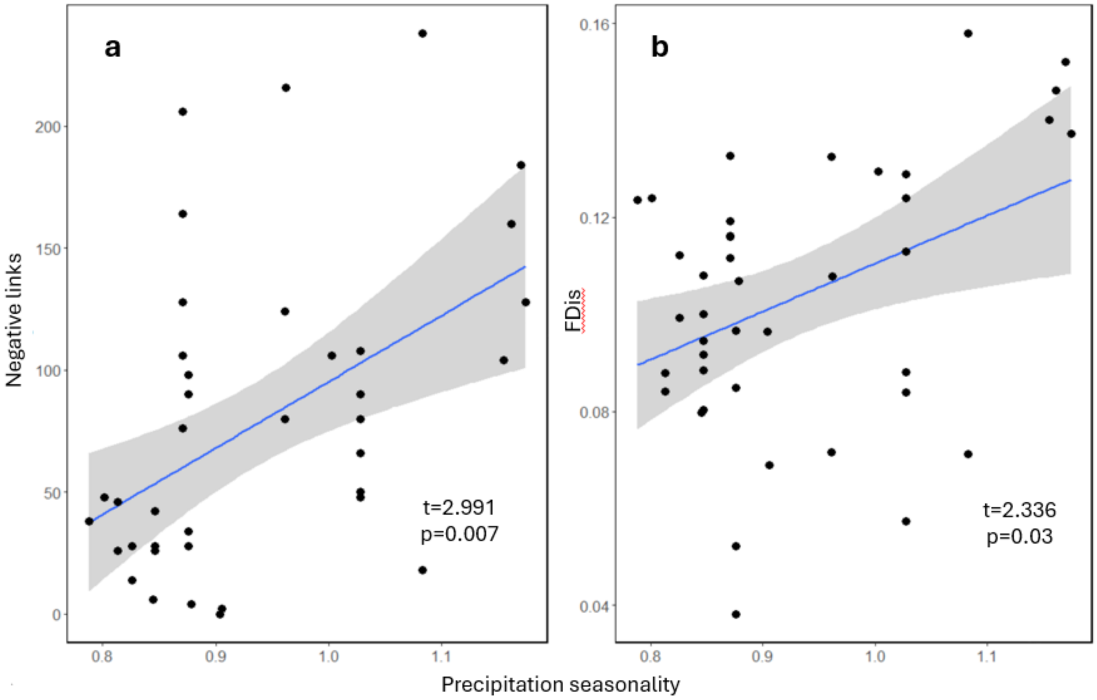


Figure 2.S15 Precipitation seasonality positively influenced negative links (a) and functional dispersion (b). Statistics are the results of linear mixed effect models, where t-tests were calculated using Satterthwaite's method.

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Chapter 3

Trait-based mechanisms of plant interactions depend on the interplay between community traits, abiotic conditions, and traits of focal species

Abstract

The degree of phenotypic differentiation among interacting species has long been recognized as an important determinant of their coexistence. Yet, we lack an understanding of how trait differentiation at the community level influences the net effects of neighbors, and to what extent phenotypic plasticity versus average trait differences are more important. Here, I established a mesocosm experiment manipulating the functional composition of desert annual plant communities under contrasting water regimes to assess how community functional traits interact with altered abiotic conditions and determine the interaction outcome of two focal species with divergent trait strategies. I tested whether the surrounding community's trait composition, the focal individuals' trait expression, or the distance between the two are more important in determining the outcome of interactions under contrasting abiotic conditions. As part of this experiment, I also tested whether the average trait differences among interacting species or accounting for intraspecific trait variation better predicted interaction outcomes. I used model comparison to identify the strongest predictors of the interaction intensity (log response ratio) for each of the focal species. I found that the trait composition of the surrounding community, the trait values expressed by focal species in response to diverse neighbors, and the distance between focal and neighborhood traits were all important predictors of

interaction outcomes. Moreover, I found evidence of both trait hierarchies and niche partitioning, where hierarchical competition was better captured by ITV, and niche partitioning was better captured by average trait values. Finally, I found that the trait composition of the community and the ITV of focal species were equally important determinants of interactions. Overall, these results support the idea that both the mean and variance of functional traits in a given community can predict the outcome of species interactions between a resident community and a focal species and that functional traits can generalize the effects of community composition on the coexistence and performance of a given species.

Introduction.

Trait differences and similarities among co-occurring, interacting species have long been recognized as important for understanding patterns of species coexistence (Chesson, 2000; Levine & HilleRisLambers, 2009; Weiher et al., 1998). In some cases, differences among interacting species stabilize their coexistence (Chesson, 2000), where segregation in resource acquisition strategies minimizes competition for shared resources (limiting similarity principle; MacArthur & Levins, 1967). In other cases, similarities among species can promote the coexistence of species with similar traits if a given phenotype is more competitive and trait-based competitive hierarchies are formed (Herben & Goldberg, 2014; Mayfield & Levine, 2010). Despite advances in coexistence theory incorporating trait differences (Adler et al., 2013; Kraft et al., 2015; Van Dyke et al., 2022), the relative importance of limiting similarity versus hierarchical competition in determining species interactions is still unresolved and likely depends on environmental conditions (Carmona et al., 2019; Perez-Ramos et al., 2019). Furthermore, experimental approaches focused on understanding the net effects of neighbors suggest that the outcome of interactions in more realistic multispecies assemblages is contingent on the trait distance from that of the surrounding community (Holden & Cahill, 2024), rather than just pairwise trait distances. Additionally, in some cases, a focal species' mean trait values were more important than their trait distance from the community in explaining species' performance in diverse communities (Galland et al., 2019; Roscher, Gubsch, et al., 2018). Ultimately, the outcome of biotic interactions within multi-species assemblages is likely mediated through multiple pathways, including a combination of community functional traits, the traits of the focal species, and the distance between the two.

Since both limiting similarity and trait hierarchies are mediated by trait dissimilarity between co-occurring species, the functional trait composition of neighboring species could predict the trait-based mechanisms governing the outcome of net interactions (Galland et al., 2019; Roscher, Buchmann, et al., 2018). For instance, if traits reflect stabilizing niche differences among species, assemblages with greater functional diversity (FD) could reduce the performance and survival of focal species if more complementary resource use results in niche saturation—consistent with widely observed negative diversity-invasibility relationships (Byun et al., 2013; Levine et al., 2004; Li et al., 2022). However, another body of literature has found that resource partitioning might benefit species growing in more diverse assemblages (Barry et al., 2019; Loreau & Hector, 2001). Alternatively, if a given trait primarily reflects differences in fitness leading to competitive hierarchies, then the community average trait value (CWM) could be a stronger predictor of interaction outcome. For instance, shifts in the mean trait values of plant communities often reflect changes in environmentally determined optimum trait values (Kandlikar et al., 2022), which could favor a given phenotype over others and lead to competitive exclusion of species differing from the community mean.

While community FD and CWM can simultaneously be important determinants of interactions acting on different traits (Galland et al., 2019), it is less clear whether the influence of community trait composition on interactions is contingent on a focal species traits or whether effects might be more generalizable. For instance, community functional composition could also affect the outcome of interactions regardless of a focal species' traits if higher FD communities promote abiotic facilitation (Wright et al., 2021) or ameliorate strong intraspecific competition (Mahaut et al., 2020). However, since multiple traits likely determine niche differences, while fitness differences often depend on single traits (Kraft et al., 2015), it is likely that more than one mechanism operates simultaneously to structure the outcome of interactions (Hillerislambers et al., 2012; Mayfield & Levine, 2010).

Critically, the outcome of net interactions can be influenced by the context-dependent trait expression of co-occurring species, which might better predict interactions compared to average species trait differences. While plant functional traits vary more among different species than within species, intraspecific trait variation accounts for a substantial portion of total community trait variability (25-30%) and can strongly influence the outcome of species interactions and community assembly (Albert et al., 2011; Siefert et al., 2015). Indeed, biotic interactions and abiotic conditions can influence an individual's trait expression (Waterton et al., 2023), which can then affect that individual's trait-based response to biotic interactions (Bennett et al., 2016; Burns & Strauss, 2012). For instance, several studies have shown that species' trait values vary across gradients of community diversity (Bennett et al., 2016; Gubsch et al., 2011; Le Bagousse-Pinguet et al., 2015; Lipowsky et al., 2015), which could alter the estimates of limiting similarity and hierarchical competition by changing the distance among a focal species and its competitors. Similarly, the trait plasticity of the interacting community also likely influences the trait expression of a focal individual and the subsequent outcome of biotic interactions. However, given how time-consuming it is to measure the traits of all individuals in an experiment, this has rarely been investigated at the scale of the entire community. Thus, it is largely unknown to what extent species interactions in communities are regulated by average trait values or trait values expressed under varying biotic and abiotic conditions.

Here, I sought to disentangle the role of community trait composition in regulating the trait-based mechanisms of species interactions. I designed a mesocosm experiment manipulating community trait diversity across two contrasting drought conditions to understand how traits mediate the outcome of net neighbor effects on two focal species. I ask: 1) How does the functional composition of a community influence species interactions under contrasting abiotic conditions; 2) What are the mechanisms underlying interaction outcomes (trait hierarchies vs limiting similarity); and 3) how do they change under biotic and abiotic conditions? I answer these questions using both a species mean trait approach, as well as incorporating ITV to better understand the predictive power of each.

Methods. *Study species*. To address the above questions, I designed a mesocosm experiment manipulating the functional diversity of communities of annual plant species from the Sonoran Desert under experimental drought and ambient conditions. I selected species of annual plants ranging in functional trait values (Table 1) since their lifetime fitness in response to abiotic and biotic conditions can be estimated from biomass accumulation in a single growing season. Seeds for the experiment were sourced from the California Botanic Garden, and accessions were chosen based on germination rates and availability, resulting in the following species for the experiment: *Eriophyllum wallacei* (Asteraceae), *Phacelia distans* (Boraginaceae), *Calyptridium monandrum* (Montiaceae), *Cryptantha micrantha* (Boraginaceae), *Perityle emoryi* (Asteraceae), *Chaenactis fremontii* (Asteraceae), *Malacothrix glabrata* (Asteraceae), and *Plantago ovata* (Plantaginaceae). To understand how the outcome of interactions differed among species with divergent resource-use strategies, I chose *Phacelia distans* and *Eriophyllum wallacei*, as focal phytometer species (referred to by genus hereafter) as these two species differed the most from each other in multivariate trait space among all species in the experiment that had sufficient germination to replicate among communities (Fig. S1).

Experimental design. The experiment was conducted at the University of California Riverside greenhouse under semi-controlled conditions. Seeds were sown and germinated in peat pellets (January 23-27, 2023) at 18 degrees Celsius, misted daily. Approximately three weeks later due to variation in germination timing (February 21-22, 2023), seedlings were transplanted into experimental communities in 5-gallon/12” pots with soil that consisted of approximately 55% sand and 42% peat moss. Pots with competition included one focal species in the center with five individuals of other species placed equally around the focal species at a distance of 4 cm (Figure 1) - a distance that has previously been established as capturing the effect of biotic interactions in desert annual plants (Pantastico-Caldas & Venable, 1993). I established a gradient of community functional diversity calculated from the FDis of species’ average specific leaf area (SLA), since SLA has shown to play a strong role in competitive outcomes among annual plants (Kraft et al., 2015). Within each watering treatment, ten different communities comprising a gradient of functional diversity were established and were replicated twice for each focal species (n=20), resulting in 40 total communities. To disentangle the effect of the abiotic treatment without interactions, I grew ten individuals of each focal species alone in both watering regimes (n=20). Due to mortality, the total number of each focal species grown alone was 14 for *Eriophyllum* and 19 for *Phacelia*. I also grew each focal species in monoculture to understand the response of each to intraspecific competition. Due to the limited germination of each focal species, I grew two monoculture replicates of *Eriophyllum* in each drought treatment (four total), and three replicates of *Phacelia* in each drought treatment (six total).

Three weeks after communities were established, when each plant had at least two true leaves, two watering treatments were established. A high-water treatment received approximately 3 mL of water daily, while low-water treatments received approximately 3 mL of water twice a week. Pots were rearranged on greenhouse benches twice per week to account for variation in local environment across benches. The experiment was harvested when species began flowering (May 18-20, 2023), after growing for three months in the respective biotic and abiotic treatments. Each individual plant in the experiment was carefully removed from the pot and excess soil from the roots was rinsed off. Total plant biomass (above and belowground) for each individual was then dried at 60°C for 4 days and weighed to ±0.001g.

Trait measurements. To understand the role of functional trait expression at the community level on the outcome of interactions under contrasting abiotic conditions, I measured traits known to mediate the fitness of annual plant species in response to both biotic and abiotic conditions. Furthermore, since our goal was to disentangle the relative importance of both interspecific and intraspecific traits for community-level interactions, I measured relatively easy-to-collect functional traits on all individuals in the experiment (n=340 individuals). Maximum vegetative height is a key trait involved in regulating access to light and competitive interactions, while specific leaf area (SLA), leaf dry matter content (LDMC), and chlorophyll content (CC) are all important traits reflecting resource utilization and overall position across the global leaf economic spectrum (Díaz et al., 2015; Poorter et al., 2009; Reich, 2014; Westoby et al., 2002).

Vegetative height was measured before harvesting the experiment, and all other traits were measured after harvesting according to established protocols (Pérez-Harguindeguy et al., 2013). I measured plant height as the distance from the soil to the highest photosynthetically active tissue. Three leaves per individual, once fully hydrated, were used to measure leaf traits in the lab. For leaf area (cm2), I scanned fresh leaves using a flat-bed digital scanner and then calculated leaf area using ImageJ (Schneider et al., 2012). Fresh leaf mass was then determined with a digital balance and then dried at 60°C for 72 hours before determining leaf dry mass (g). Leaf dry matter content (LDMC) was determined by dividing dry leaf mass by fresh mass, and specific leaf area (SLA) was calculated as leaf area divided by leaf dry weight. Chlorophyll content was measured with a digital chlorophyll meter (Konica Minolta) by averaging across three measurements per leaf. Due to the loss of a small amount of individual trait data, I imputed missing trait measurements (27 trait measurements out of 1,700 total) using a random forest imputation algorithm implemented in the funspace R package (Carmona et al., 2024).

Estimating interaction outcome. I estimated the outcome of interactions for each focal individual in the presence of all communities in each watering treatment by calculating the log response ratio (LRR) with the biomass of target individuals grown alone relative to the biomass produced when grown in interaction with other individuals. Negative values reflect competition where individuals experience reduced biomass production relative to when grown alone, while positive values reflect facilitation where individuals achieve greater biomass production than when grown alone. Log response ratios are widely used to evaluate the outcome of competition among plants due to their approximately normal distribution and low potential for bias (Hedges et al., 1999).

Community trait indices. Since individual mortality altered the FD values in the experimental design, I first calculated both functional diversity and community-weighted mean (CWM) trait values using species' average trait values. I calculated functional diversity as functional dispersion (FDis), which is the average distance of each species to the community-weighted centroid (Laliberté & Legendre, 2010). FDis was calculated for each individual trait and using all traits simultaneously in a multivariate metric. I further calculated the community-weighted mean (CWM) of each trait as the mean trait value of each community as weighted by each species' abundance. To assess the importance of intraspecific trait variability, I additionally calculated the above trait metrics using the trait values of individuals measured in each community.

In addition to evaluating the outcome of species interactions in response to different community functional metrics, I investigated the trait-based mechanisms underlying them by measuring three values shown to influence the outcome of plant interactions. First, the absolute value of the trait distance of trait values between focal individuals and their surrounding community ($|T_{focal} - T_{comm}|$; DIST), which assumes that the absolute distance between species' traits determines the outcome of interactions, where, under the limiting similarity hypothesis, a focal individual or species performs better with increasing trait distance from the surrounding community—regardless of the direction. Second, the directional dissimilarity between focal individuals and their surrounding community, where the closer a focal individual's trait value is to an "optimum", the better their performance ($T_{focal} - T_{comm}$; HIER). Third, the change in the trait values of focal individuals between their average when grown alone and when grown in the presence of other individuals in a community ($T_{focal\text{-}AVG} - T_{focal\text{-}ITV}$). For calculating DIST and HIER, I used the CWM and FDis of each community as the community trait values.

For all the above trait metrics and dissimilarity indices, I calculated each value twice using both the average (AVG) traits for both the community and focal species, and the community-specific values accounting for intraspecific trait variability (ITV), which reflect the influence of community interactions under particular abiotic conditions. For dissimilarity indices using ITV values, ITV traits were used for both focal species and the surrounding community, and likewise for AVG dissimilarity indices.

Statistical analyses. First, to understand how the background communities shifted their trait indices across abiotic and biotic conditions, I tested how the background community trait indices changed across our drought treatment and between AVG and ITV calculations using paired t-tests. Similarly, I used t-tests to determine how the response ratios and trait values differed between monoculture and mixture plots for each focal species. I then tested the effects of community traits, focal species traits, distance between focal and community traits, and focal species' ITV on focal species' interaction outcome by fitting linear mixed effect models using the LRR as the response variable with trait metrics, focal species, and watering regime as fixed effects and including watering regime as an interaction. I included species richness as a random factor to account for differences in richness due to mortality within experimental communities (richness varied between 4 and 5 background species). Linear mixed models were fitted using the R package lmerTest (Kuznetsova et al., 2017). Since our watering treatment often did not result in differences in biomass (see below), I fitted the above models both with and without the water interaction and chose the simpler model by comparing AIC values. I then used multi-model inference to identify the best fitting models, based on minimizing the AICc, for species' interaction response by fitting two separate global models. First, to assess whether interaction outcome is contingent upon average traits of interacting species or on ITV trait values, I built one global model of significant average species trait predictors and one using significant trait predictors reflecting ITV in response to biotic and abiotic conditions. Second, I included in each of these respective global models all significant predictor variables capturing trait distance from the community—both dissimilarity and hierarchical—to disentangle which mechanism might be important for interaction outcome as well as to compare the overall relative importance of trait distance from the community compared to community trait metrics alone. For both global models, trait predictors were included with a water interaction if the interaction was significant in individual models. For model selection, I used the *dredge* function in the MuMIn package (Barton, 2024) with trait predictors as fixed effects and species richness as a random effect. Since correlation among predictor variables can bias variable importance estimates, I first tested for collinearity among variables in global models. If predictor variables showed high correlation (R > 0.5), I retained the variable which better predicted the response variable by comparing AIC values. I then performed a model-averaging procedure (Barton, 2024) on the top subset of models from these two global models based on their ranked AICc (deltaAICc <5) to determine the standardized coefficients for the best overall set of trait predictors. All trait predictors were log-transformed when necessary and standardized prior to analyses. Finally, since phytometer/target species frequently exhibited divergent responses, I performed the same model selection procedure separately for each phytometer.

Results

Background community. Community $FDis_{ITV}$ for multivariate and individual traits showed no significant differences among water treatments (Table S1, but several CWM_{ITV} values significantly differed where leaf area (t=-2.79, p=0.012), height (t=-2.12, p=0.04), and chlorophyll content (t=-2.46, p=0.02) were reduced while $LDMC_{ITV}$ increased under drought conditions (t=2.21, p=0.04). Community functional dispersion differed significantly when calculated with average versus ITV traits (Table S2). Most individual trait FDis were significantly lower when calculated using ITV values rather than AVG trait values (height: t=-6.39, p=<0.000; SLA: t=-6.12, p=<0.000; LDMC: t=-5.19, p=<0.000; leaf area: t=3.23, p=0.002; chlorophyll: t=-5.19, p=<0.000), while multivariate FDis and leaf area FDis were higher (FDis: t=3.34, p=0.002; LA FDis: t=3.23, p=0.002). CWM SLA was similarly lower when calculated with ITV traits rather than averages (t=-7.74, p=<0.000), while other CWM traits showed no significant differences (Table S2).

Drought effect on focal species. Overall, our drought treatment did not affect focal species' LRR while growing in the presence of diverse communities (t=-0.58, p=0.564). The trait values of focal species also showed no response to the drought treatment when growing in diverse communities (Table S1). However, the trait values expressed by focal species growing alone differed among drought and ambient treatments for several traits, with lower SLA (t=-6.64, p=<0.000) and chlorophyll content (t=-7.76, p=<0.000), and higher LDMC (t=9.08, p=<0.000) and height (t=21.48, p=<0.000), in drought compared to ambient conditions.

Community effects on focal species. Across both species, response ratios did not differ between mixture and monoculture pots, but this was due to divergent responses among focal species to interspecific versus intraspecific competition. *Eriophyllum* experienced lower LRR in mixture than monoculture (t=-2.75, p=0.04), while *Phacelia* experienced a higher LRR in mixture and lower LRR in monoculture (t=3.53, p=0.01; Figure S2). This pattern was further supported by *Eriophyllum* having higher total biomass in drought monoculture than monoculture under ambient conditions (F=46.62, p=0.02)—suggesting stronger facilitative effects under drought stress. *Phacelia* showed no difference in biomass between drought and ambient treatments when growing in monoculture (F=1.085, p=0.35).

Community trait composition of the surrounding community played a strong role in the outcome of interactions for both of our focal species, as shown by the results of our model averaging procedure (Table 2, Figure 2). Specifically, functional dispersion of the surrounding community had a consistent positive effect on the interaction outcome, where higher multivariate FDis communities facilitated both focal species under drought and ambient conditions, while lower FDis increased the intensity of competition (Figure 2A). Similarly, FDis LDMC had a facilitative effect on both focal species, but only under drought conditions, exhibiting a significant interaction with the different water regimes (Figure 2D). In addition to functional diversity, the weighted average SLA of communities also played a strong role in interaction outcome, where both focal species were negatively affected by increasing CWM SLA of the surrounding community (Figure 2C). Interestingly, the strongest community trait predictors as shown in our overall model coefficients were average trait values rather than ITV. In addition to the trait composition of the surrounding community, the height expressed by the focal species was strongly predictive of the interaction outcome (Figure 2B), where both species showed more positive interaction outcomes with increasing height, regardless of the surrounding community.

While overall predictors of interaction outcome for both focal species were related primarily to the functional composition of the community, focal species' independent interaction outcomes were contingent on a combination of community trait composition, focal species' trait expression, and trait distance between focal species and the surrounding community (Figure 3). The standardized coefficients for the global model of *Eriophyllum* showed that this species' success in a given community is contingent on abiotic-mediated trait expression, where a higher or lower leaf area was advantageous in ambient and drought conditions, respectively (Table 2; Figure 3C). Similarly, the distance between this species' SLA and that of the surrounding community showed a positive relationship in ambient conditions and negative relationship in drought conditions (Fig 3D). While the later predictive variable was determined by average trait values, the former was reflective of ITV trait values, and thus the importance of both for this species. The strongest trait predictor mediating the success of *Phacelia* in diverse communities was FDis_{AVG}, followed by $\text{height}_{\text{DIST-ITV}}$ (Table 2; Figure 3A-3B) where this species showed increasingly positive interaction outcomes by having an increasing distance of height from the rest of the community and in more functionally diverse assemblages.

Discussion

Since equalizing mechanisms of coexistence have been recognized (Chesson, 2000) and incorporated into empirical work (Herben & Goldberg, 2014), trait hierarchies have been found to operate as a mechanism of competition in many different communities. In contrast, support for limiting similarity is often weak or absent (Kunstler et al., 2012). In this study, I found support for both hierarchical competition and limiting similarity, but overall, limiting similarity played a larger role in determining the interaction outcomes for both species, since trait hierarchies were only important for a single trait for one of the focal species. The more competitive focal species, *Phacelia*, benefitted from having a greater leaf area relative to the surrounding community, while the presence of trait hierarchies was not an important determinant of net interaction effects for *Eriophyllum*. In contrast, limiting similarity was more important for both species, where *Phacelia* showed a positive response ratio with increasing distance from the surrounding community in height and LDMC, and *Eriophyllum* showed a positive response ratio with increasing SLA distance from the surrounding community. Thus, the importance of competitive mechanism was trait-dependent, as has been shown in other studies (Herben & Goldberg, 2014). Since hierarchical competition has been shown to depend on abiotic conditions, being more important in more productive, high-nutrient conditions (Carmona et al., 2019; Goldberg et al., 2017), our results showing a greater overall importance for limiting similarity might be related to the more arid study system than others have investigated.

While the trait distance between focal species and the surrounding community played a role in determining net interactions in our study, the trait composition of the surrounding communities also had important general effects regardless of focal species' traits. In our model averaging approach combining both focal species, significant predictors were primarily community trait indices, which also had the highest coefficients, rather than metrics capturing the trait distance between focal species and the surrounding community (Table 2). I found that both of our focal species were facilitated to some extent by the functional diversity of the surrounding community, as multivariate $FDis_{AVG}$ was the strongest predictor of interaction outcome in our overall model. This result is consistent with wide-scale support for biodiversity-ecosystem functioning relationships and recent developments suggesting that species producing higher biomass in mixture could result from multiple facilitative mechanisms, including abiotic and indirect biotic facilitation (Barry et al., 2019; Wright et al., 2017, 2021). For both of our focal species, interaction outcomes were also negatively related to CWM SLA and showed a strong positive relationship with FDis LDMC under drought conditions, where lower FDis LDMC suppressed focal species' growth. In contrast, we also found patterns that indicate plants were experiencing some level of competition. Regardless of watering conditions, focal plant performance slightly decreased as the community exhibited a more resource-acquisitive strategy of higher SLA suggesting a transition from neutral to weak competitive interactions. We also observed that the diversity of LDMC was linked to decreased growth but only in drought conditions. LDMC is strongly linked to leaf-level drought tolerance and competitive superiority under more arid conditions (Mount et al., 2024), and, since most of our species had relatively low LDMC (Table 1), the lower FDis of this trait likely reflected strong competitive effects of drought-resistant species. However, while more conservative traits were competitively superior under drought conditions, higher SLA communities negatively affected focal species under both abiotic conditions. While apparently contradictory results, the strong competitive effect is likely due to the high biomass produced by the dominant species *Phacelia.* Overall, these results support previous work demonstrating that both the mean and variance of functional traits in a given community can predict the outcome of species interactions between a resident community and a focal species (Borges et al., 2019; Li et al., 2022), and that there may be generalizable effects of community composition on the coexistence and performance of a given species. Finally, our results are consistent with others that have found niche differences to be captured by multiple traits, while fitness differences leading to trait hierarchies are captured by single traits (Kraft et al., 2015).

An accumulating body of research is highlighting the importance of intraspecific trait variability in response to both abiotic and biotic factors (Hess et al., 2022; Laughlin & Messier, 2015; Turcotte & Levine, 2016), and yet, it's still unresolved to what extent plant species' average trait values versus ITV values are more useful predictors of their fitness under contrasting biotic and abiotic conditions. Furthermore, while ITV has shown to promote coexistence among species pairs (Hess et al., 2022), it is unknown to what extent the ITV of the surrounding community might influence the fitness of a focal species. I found that species' average trait values of the surrounding community better captured the outcome of net interactions when analyzing both focal species combined—thus, better capturing general effects—while ITV trait values of the focal species and surrounding community were stronger predictors for each species' individual success (Table 2). For example, the importance of trait distance from the surrounding community (limiting similarity and trait hierarchies) was only detected when accounting for ITV of both the focal species and surrounding community. This is likely because assemblages exhibited patterns of trait convergence toward optimum values across contrasting abiotic conditions, where communities shifted their CWM values and reduced FDis compared to when calculating with average trait values, which influenced the trait distance from the focal species. However, I also found that, for some traits, the focal species' trait values when considering ITV were important for net interaction outcome regardless of their distance from the rest of the co-occurring species. For instance, both focal species showed positive outcomes with increasing focal plant height, which is indicative of hierarchical competition for light, since plant height is a key indicator of light utilization strategy and competitive ability (Díaz et al., 2015; Kunstler et al., 2016). While all measured community traits had lower FDis when using ITV traits (indicating convergence toward optimum values), I found that only a few traits—height, leaf area, and SLA—were important in conferring fitness differences, which is consistent with other work showing the hierarchical importance of these traits (Carmona et al., 2019; Kraft et al., 2014). Our overall results highlight that, while there are general relationships between the effect traits (sensu Goldberg 1990) of a community considering species' average trait differences, incorporating the context-dependent trait values of a focal species (response trait) and its surrounding community (effect traits) can give more accurate insight into the interaction mechanisms maintaining coexistence in multispecies assemblages.

While I found generalizable effects of community trait composition on net interaction effects that extended to both of our focal species, our results were also likely driven to some extent by differences between focal species in their overall response to intraspecific and interspecific competition. Similar to other studies using dryland plant species (Mount et al., 2024), the species with more conservative traits, *Phacelia*, was a stronger competitor (taller, consistently produced more biomass, etc.), and exhibited stronger intraspecific competition. Thus, the stronger facilitative effects experienced by this species in more diverse communities was likely due to alleviation of strong intraspecific competition. Our other, less competitive focal species, *Eriophyllum*, possessed more acquisitive traits that made it more sensitive to drought stress, and therefore, its response to the surrounding community was more contingent on abiotic conditions, with drought stress more strongly alleviated by intraspecific versus interspecific facilitation. Thus, consistent with other recent work, our study further suggests that biomass gains in mixture are dependent to some extent on species-specific density-dependence, with an inverse relationship between intra- and interspecific competition (Mahaut et al., 2020; Turnbull et al., 2013). While our monoculture replications were few, due to low seed germination in our study, species-specific density-dependence as a mechanism driving the outcome of multispecies interactions is an area worthy of further investigation, especially given that, while many species experience stronger self-limitation than limitation by competitors (Adler et al., 2018), intraspecific facilitation can occur, particularly in abiotically stressful habitats (Fajardo & McIntire, 2011; Sarneel et al., 2022).

A surprising result from observational and experimental approaches to understanding global change effects on plant communities has been that individual plant species experiencing novel abiotic conditions are frequently more affected by interactions with their neighbors than abiotic regime change (Alexander et al., 2015; Catford et al., 2020; Meineri et al., 2020). Our experiment provides additional support for the primary importance of neighborhood interactions, as I found that our focal species generally responded more to co-occurring species than drought when growing in communities compared to when grown alone. While our results could indicate that there were minimal differences between drought treatments, I did find that species responded to drought with changes in their trait values when growing alone. Since ours is the first study that I am aware of to account for ITV among all individuals, our results suggest that the trait composition of communities is a stronger driver of individual fitness than changes in abiotic conditions, and lends further support to the idea that the processes underlying biodiversity maintenance may depend on species interactions at the community level (Allesina & Levine, 2011; Isbell et al., 2009; Levine et al., 2017).

In conclusion, I found that the ITV of a focal species and the functional trait composition of its surrounding community largely determine the performance of a focal species while growing in the presence of diverse neighbors. While I found that both trait hierarchies and limiting similarity mediated the outcome of interactions, I also found that, when considering both focal species, the trait composition of the surrounding community and intraspecific trait variation of the focal species were more important. Therefore, there may be general properties of plant communities that mediate community-level interactions, while distance-based mechanisms are more species-specific. Furthermore, I found that average species' trait values when considering the trait composition of the community were overall stronger drivers of interaction outcome, which suggests that, in many cases, using average species' trait values may be sufficient for predicting competitive and facilitative interactions in a community. While more experimental work is needed to disentangle whether trait distance among interacting species versus the trait composition of the surrounding community is a more important driver of interactions in multispecies assemblages, this study highlights the importance of community-level interactions for coexistence.

Figures and Tables

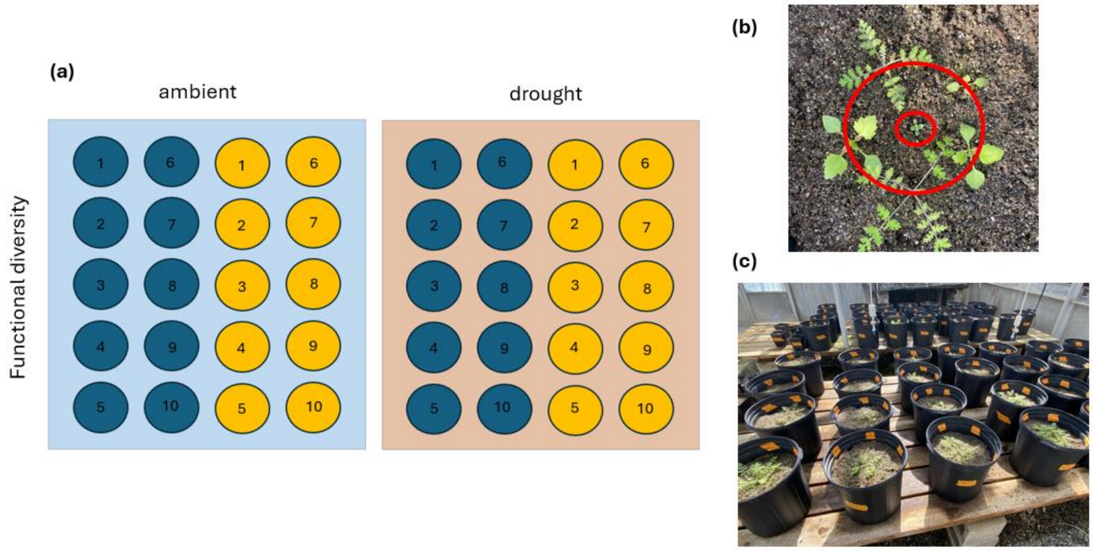

Figure 3.1 Mesocosm experimental design and setup. (a) Communities were planted in a gradient of functional diversity (#1-10), which were replicated for each focal species (blue vs orange) and under two watering regimes. (b) Focal species were planted in the center of each pot with five neighboring species planted four inches from the focal species. (c) Pots arranged on greenhouse benches.

Table 3.1 Species used in the experiment and their average trait values across both watering regimes. Species abbreviations: ERIWAL=*Eriophyllum wallacei (Asteraceae)*, PHADIS=*Phacelia distans (Boraginaceae)*, CALMON=*Calyptridium monandrum (Montiaceae)*, CRYMIC=*Cryptantha micrantha (Boraginaceae)*, PEREMO=*Perityle emoryi (Asteraceae)*, CHAFRE=*Chaenactis fremontii (Asteraceae)*, MALGLA=*Malacothrix glabrata (Asteraceae)*, PLAOVA=*Plantago ovata (Plantaginaceae)*. Trait abbreviations: LDMC=leaf dry matter content, SLA=specific leaf area

Species	**Chlorophyll content**	**LDMC (mg g–1)**	**SLA (m2 kg–1)**	**height (cm)**	**leaf area (mm2)**
calmon	42.11	0.10	121.19	26.25	1.25
chafre	23.36	0.18	171.08	75.00	6.47
crymic	6.04	0.23	408.48	31.60	0.66
eriwal	32.73	0.16	492.34	22.06	0.89
malgla	11.57	0.15	131.16	91.50	5.80
peremo	19.59	0.16	232.88	69.91	5.32
phadis	22.86	0.19	385.18	80.71	5.84
plaova	18.15	0.18	71.84	24.00	0.90

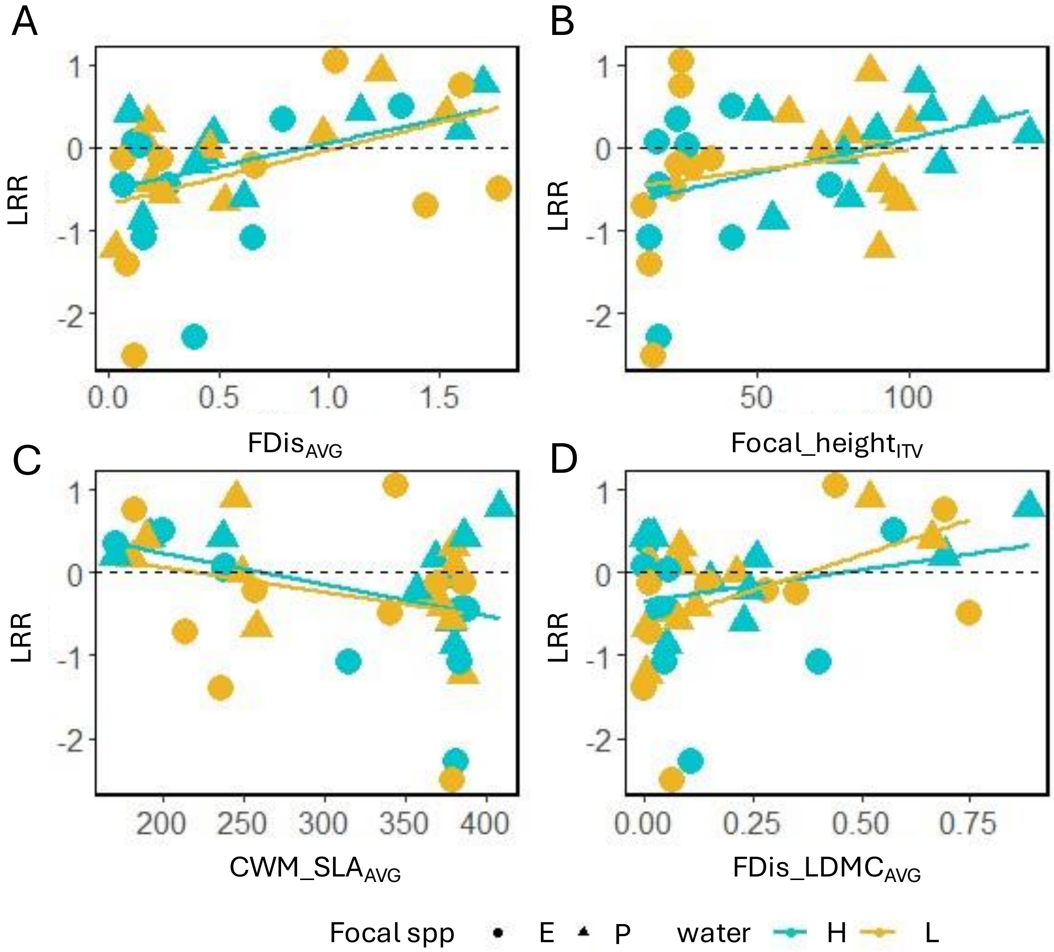

Figure 3.2 Strongest trait predictors of log response ratio (LRR) for the global model using both focal species combined across drought (L, yellow) and ambient (H, blue) conditions. Functional dispersion (FDis) using average species' trait values (A) and the height of focal species when accounting for plasticity (B) had positive effects on LRR, while the community-weighted mean (CWM) of SLA using species' average traits had a negative effect (C). Functional dispersion (FDis) of LDMC using species' average trait values positively influenced LRR under drought conditions and had a weak negative influence under ambient conditions.

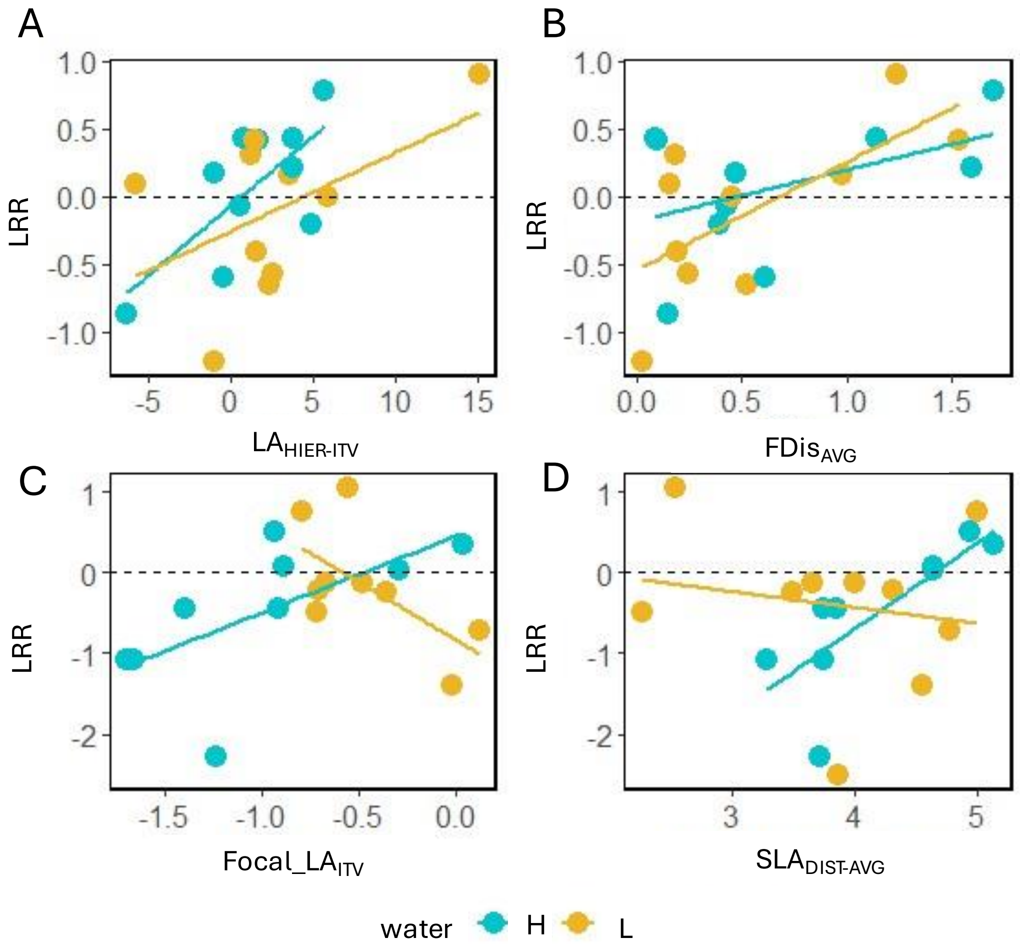

Figure 3.3 Strongest variable predictors of interaction outcome for *Phacelia* (top row) and *Eriophyllum* (bottom row) across drought and ambient conditions. The strongest predictor of interaction outcome for the more drought-tolerant and competitive focal species (*Phacelia*) was community functional diversity using multivariate traits, possibly owing to the amelioration of strong intraspecific competition. The strongest predictors for the more drought-sensitive focal species (*Eriophyllum*) was SLA dissimilarity and ITV of leaf area—both of which were dependent on the abiotic treatment.

Table 3.2 Model-averaged standardized coefficients for the global model combining both focal species (overall) and for each focal species independently. For trait indices reflecting the distance from focal species to the community, either DIST or HIER is given to reflect absolute distance or hierarchical trait distance, respectively. Similarly, for all trait indices, either AVG or ITV is shown to indicate whether indices used average or context-dependent trait values. Abbreviations: FDIS=functional dispersion, CWM=community weighted mean, SLA=specific leaf area, LDMC=leaf dry matter content, LA=leaf area

	Estimate	Standard Error	Adj Standard Error	z-value	p-value
overall					
Intercept	-0.21	0.12	0.12	1.71	0.10
FDis$_{\text{AVG}}$	0.66	0.24	0.25	2.61	0.00
focal_height$_{\text{ITV}}$	0.61	0.21	0.22	2.73	0.00
CWM_SLA$_{\text{AVG}}$	-0.62	0.28	0.28	2.12	0.03
FDis_LDMC$_{\text{AVG}}$	0.47	0.20	0.32	2.19	0.02
Phacelia					
Intercept	-0.02	0.11	0.12	0.14	0.89
FDis$_{\text{AVG}}$	0.54	0.23	0.25	2.13	0.03
height$_{\text{DIST-ITV}}$	0.47	0.22	0.24	1.94	0.05
LA$_{\text{HIER-ITV}}$	0.49	0.26	0.27	1.78	0.08
CWM.LA$_{\text{ITV}}$	-0.47	0.27	0.29	1.65	0.10
LDMC$_{\text{DIST-ITV}}$	0.36	0.29	0.31	1.15	0.25
Eriophyllum					
Intercept	-0.28	0.25	0.27	1.07	0.29
CWM_LA$_{\text{AVG}}$	-0.61	0.39	0.43	1.42	0.16
CWM_SLA$_{\text{AVG}}$	-0.66	0.45	0.49	1.35	0.18
focal_LA$_{\text{ITV}}$	0.17	0.52	0.56	0.30	0.77
focal_LA$_{\text{ITV}}$ * water	-2.54	0.88	0.98	2.59	0.01
SLA$_{\text{DIST-AVG}}$	0.35	0.64	0.67	0.52	0.60
SLA$_{\text{DIST-AVG}}$ * water	-2.09	0.68	0.76	2.75	0.01

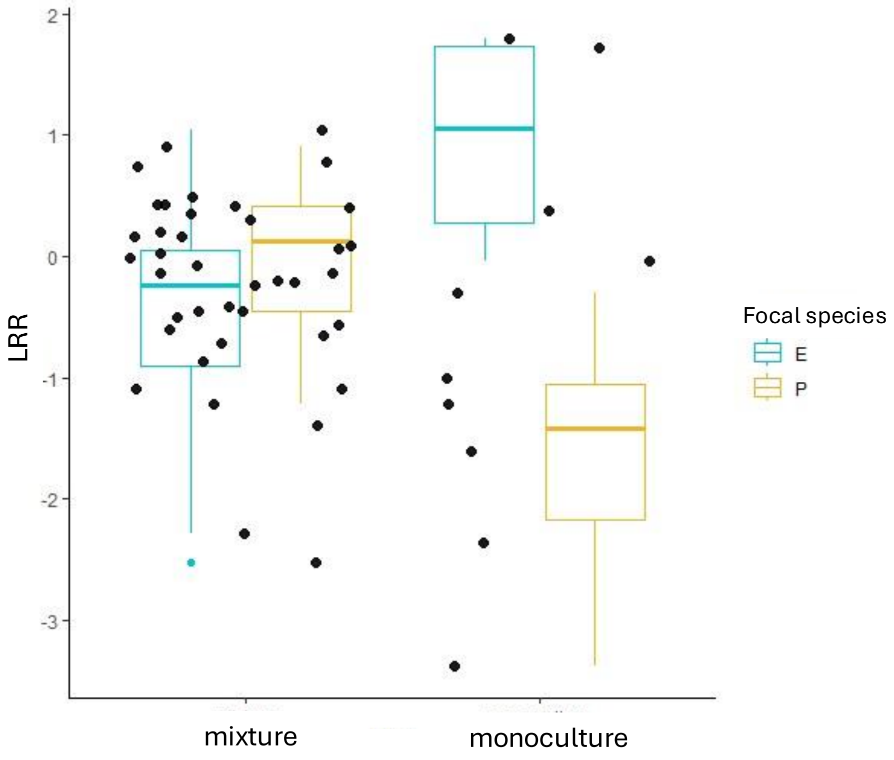

Figure 3.S1 Response of focal species to interspecific versus intraspecific competition across both drought and ambient conditions. *Phacelia* (yellow) had a higher LRR in mixture than monoculture, while *Eriophyllum* (blue) had a higher LRR in monoculture than in mixture. Significance determined using paired t-tests.

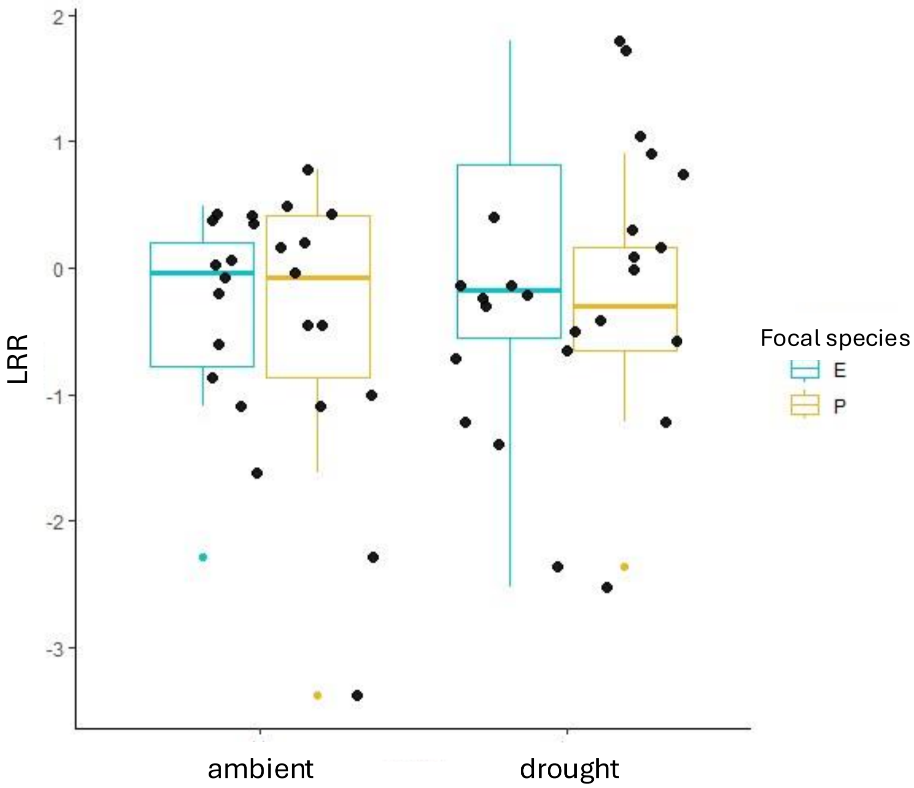

Figure 3.S2 Differences in response to interspecific competition (mixture) across drought treatments. Both *Eriophyllum* (red) and *Phacelia* (blue) showed no difference in interaction response across drought versus ambient conditions. Significance determined using paired t-tests.

Table 3.S1 Differences in trait values when accounting for ITV for all individuals across drought conditions for community traits, focal species' traits in mixture, and focal species' traits grown alone. Values were compared using paired t-tests. Abbreviations: FDIS=functional dispersion, CWM=community weighted mean, SLA=specific leaf area, LDMC=leaf dry matter content, CC=chlorophyll content, LA=leaf area

	TRAIT	DF	T-VALUE	P-VALUE	AMBIENT MEAN	DROUGHT MEAN
COMMUNITY						
	FDis	19	-1.39	0.18	0.94	0.78
	FDis_LA	19	-1.79	0.08	0.60	0.39
	FDis_SLA	19	0.94	0.36	0.04	0.06
	FDis_CC	19	-0.50	0.63	0.04	0.04
	FDis_LDMC	19	1.53	0.14	0.00	0.01
	FDis_height	19	-0.37	0.72	0.05	0.04
	CWM_LA	19	-2.79	0.01	7.11	4.77
	CWM_SLA	19	-1.65	0.11	181.90	153.50
	CWM_CC	19	-2.46	0.02	23.93	21.11
	CWM_LDMC	19	2.21	0.04	0.16	0.18
	CWM_height	19	-2.12	0.04	80.27	68.23
FOCAL SPECIES IN MIXTURE						
	focal_LA	19	0.12	0.91	3.58	3.86
	focal_SLA	19	-0.28	0.78	267.70	267.70
	focal_CC	19	-0.09	0.93	26.96	26.80
	focal_LDMC	19	1.89	0.07	0.15	0.17
	focal_height	19	-1.41	0.17	61.85	54.60
FOCAL SPECIES ALONE						
	focal_LA	19	-0.67	0.17	3.90	3.65
	focal_SLA	19	-6.64	<0.00	271.60	243.10
	focal_CC	19	-7.76	<0.00	33.88	27.63
	focal_LDMC	19	9.07	<0.00	0.13	0.16
	focal_height	19	21.47	<0.00	67.81	107.97

Table 3.S2 Differences in community trait indices when calculated using species' average versus ITV traits for each individual. Values were compared using paired t-tests. Abbreviations: FDIS=functional dispersion, CWM=community weighted mean, SLA=specific leaf area, LDMC=leaf dry matter content, CC=chlorophyll content, LA=leaf area

TRAIT	DF	T-VALUE	P-VALUE	AVG MEAN	ITV MEAN
FDIS	39	3.34	0.00	0.62	0.86
FDIS_HEIGHT	39	-6.39	<0.000	0.28	0.04
FDIS_SLA	39	-6.12	<0.000	0.24	0.05
FDIS_LDMC	39	-5.19	<0.000	0.21	0.00
FDIS_CC	39	-5.19	<0.000	0.25	0.03
FDIS_LA	39	3.23	0.00	0.29	0.49
CWM_HEIGHT	39	0.75	0.46	72.27	74.25
CWM_SLA	39	-7.74	<0.000	309.40	167.71
CWM_LDMC	39	-0.21	0.84	0.17	0.17
CWM_CC	39	0.76	0.45	22.00	22.52
CWM_LA	39	1.62	0.11	5.11	5.94

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