Title

The effects of temporal variation in precipitation on plant coexistence in an annual grassland community

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Van Dyke, Mary N.

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Los Angeles

The effects of temporal variation in precipitation on plant coexistence

in an annual grassland community

A dissertation submitted in partial satisfaction

of the requirements for the degree

Doctor of Philosophy in Biology

by

Mary Nancy Van Dyke

2023

ABSTRACT OF THE DISSERTATION

The effects of temporal variation in precipitation on plant coexistence in an

annual grassland community

by

Mary Nancy Van Dyke

Doctor of Philosophy in Biology

University of California, Los Angeles

Professor Nathan Kraft, Chair

This dissertation aims to contribute to our understanding of plant coexistence and explore how global change could disrupt these dynamics thus altering the composition of future communities. I have attempted to answer these broad ecological questions by studying the coexistence mechanisms operating in an annual grassland in coastal southern California that experiences high interannual variability in climate, particularly in precipitation. I have explored multiple mechanisms of coexistence operating in the community and the physiological bases of the interacting plant species to make my results more broadly applicable. Each chapter also discusses how the results can inform our predictions about how plant communities will continue to respond to global change.

Chapter one explores how interactions between neighboring species are altered by changes in rainfall. Precipitation patterns have long been known to shape plant distributions but how changes in these patterns effect species interactions and thus community composition is less understood. As precipitation patterns across the globe are altered by global change, understanding how interactions like competition between plants is impacted will help us anticipate potential community composition changes. We studied how changes in precipitation altered competitive dynamics by studying the direct effects of changes on individual species, as well as, by the changing strength of competitive interactions between species. We grew six annual species under two rainfall conditions with varying densities and identities of competitors. We parameterized a population growth model that allowed us to determine stabilizing niche differences and fitness differences between species pairs which determine their ability to coexist. We found that reduced precipitation had little direct impact on species grown alone, but it qualitatively shifted predicted competitive outcomes for 10 of 15 species pairs. We also found that species that were more similar in their functional traits were less likely to experience changes in their competitive outcomes than species that were less similar.

In chapter 2, we investigated the mechanism that might be driving the changes in species competitive interactions that we found with changes in precipitation. We hypothesized that species flowering phenology (timing) might contribute to species ability to coexist by separating resource intensive periods for species over the growing season. These critical temporal dynamics could be disturbed if changes in precipitation affect the flowering phenology of some species and not others. We found that changes in rainfall shift some species flowering phenology, but sensitivity differed among neighboring species. Four of seven species we studied started and/or

peaked flowering earlier in response to reduced water availability. The idiosyncratic responses among neighboring species has the potential to disrupt temporal coexistence mechanisms because it alters the flowering overlap between species pairs. We found the species pairs whose competitive interactions changed in the experiment described in chapter one had larger differences in their phenological responses to reduced rainfall than pairs whose competitive outcomes did not change. This shows that species pairs whose flowering time overlap changed more, were more likely to experience a change in their competitive interaction. Therefore, current temporal spacing between peak flowering times likely contributes to coexistence in the community and if changes in rainfall disrupt this, species may lose their ability to coexist, altering the composition of the community.

Chapter 3 explores coexistence at a broader timescale and investigates how multiple mechanisms of coexistence operate simultaneously. Southern coastal California experiences high interannual variation in rainfall. Modern coexistence theory suggests that coexistence mechanisms, such as the temporal storage effect, may be important in communities experiencing fluctuating abiotic conditions. To examine the effects of temporal variation in abiotic conditions on coexistence, we studied an annual grassland community that experiences high interannual variation in precipitation. We found that species demographic rates from the last 15 years, including germination rate and low-density fecundity, are rarely strongly positively correlated with other species in the community, indicating that species differ in which years they perform best, and therefore likely specialize on distinct abiotic conditions. Variation in response to interannual differences in rainfall concentrates intraspecific interactions relative to interspecific interactions and favors coexistence. Additionally, we found that species differences in functional

traits, especially rooting depth, water use efficiency, and leaf nitrogen were well correlated with differences in species demographic responses, such that species with similar traits did best in the same years. Taken together this deepens our understanding of coexistence in the community and provides greater context for how plant communities may respond to future increases in climatic variability.

The dissertation of Mary Nancy Van Dyke is approved.

Morgan Tingley

Lawren Sack

Elsa Cleland

Nathan Kraft, Committee Chair

University of California, Los Angeles

2023

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Acknowledgements

There are many people, places and plants that helped me achieve this dissertation. Completing this PhD has been a long and difficult journey with times when I doubted whether it would happen, and I am very grateful to all my friends, family, and mentors who helped me along the way. First, I want to thank my advisor Dr. Nathan Kraft who has been an amazing mentor and fostered a wonderful lab at UCLA which I was lucky to be a part of. He always asked thought provoking questions and provided just the right amount of support to help me take my small ideas and transform them into large field experiments. He encouraged me to persevere when I planted a drought experiment prior to the rainiest season of my six years living in Southern California. He showed me that Home Depot is not simply a home improvement store, but actually a field biologist's greatest resource. Nathan has taught me to think critically, challenge assumptions and pursue questions that excite me, and I am incredibly grateful to have him as a mentor and collaborator.

I want to thank my committee, Dr. Elsa Cleland, Dr. Morgan Tingley, and Dr. Lawren Sack for their support and helpful feedback on my research. I also want to thank Dr. Jonathan Levine who led pioneering coexistence research at Sedgwick and has been a pivotal mentor during my graduate school career. Jonathan is a co-author on chapter 1 and was very involved in the ideas and analyses of chapter 3. In addition to research mentors, I also benefitted from teaching with excellent professors in the Ecology and Evolutionary Biology department at UCLA. Dr. Leryn Gorlitsky, Dr. Alison Lipman, and Nathan, all helped me grow considerably as

an educator by exposing me to research backed pedagogy and including me in course development.

At UCLA, Nathan has created a lab where we have stimulating scientific discussions and feel safe sharing the earliest stages of our work to give each other helpful feedback. We have fun and productive lab meetings helping each other develop our research ideas and supporting each other's diverse interests. I want to thank all my lab mates through the years for listening to many semi-prepared presentations, driving with me to Sedgwick to count miniscule germinates or build rainout shelters, reading many first drafts, helping me debug my R code, and being great friends. These include Gaurav Kandlikar, Marcel Vaz, Kenji Hayashi, Andy Kleinhesselink, Samantha Catella, Hannah Carroll, Lauren Glevanik, Jordan Yanowitz, Haley Oyler, Suzanne Ou, Claire Fortunel, Aubrie James, and Ian McFadden. There were also many undergraduates who I had the pleasure of working with and helped me considerably setting up and getting data from the experiments that led to chapters 1 and 2. They include Heather Lindsay, Megan Clark, Ian Morris, Leontyne Henderson, Leah Andino, Lidoor Levy, Abita Venkatesh, and Anmol Dhaliwal. The data for chapter 3 was collected by both members of the Kraft lab and Dr. Jonathan Levine's lab beginning in 2007. Additionally, all the field work needed for my research never would have been possible without the helpful staff at Sedgwick reserve including Kate McCurdy, Avery Hardy, and Lyza Johnsen.

I want to thank my cohort from UCLA especially Ioana Anghel, Marvin Browne, and Chris Kyriazis who have been there to cheer me on during the highs and commiserate during the lows. Building a good community of friends in LA was essential to my success and happiness

during graduate school. I want to thank my partner Simon Montague for being an amazing field assistant and a huge support in the periods when I doubted myself. I also want to thank my family; Franny, Ted, Hugo, Chris, Shruti, Astri, Sherry, Jim, Hannah, and Oliver for your love and support and some working visits to my field site during torrential rain as well as extreme heat. I especially want to thank my brothers for taking me hiking from an early age and introducing me to BBC's best Sir David Attenborough who was the first to make me want to be an ecologist.

My love of ecology as a science and desire to pursue a PhD flourished at Carleton College where I had amazing professors and peers. Particularly courses taught by professors Dan Hernandez, Mark McKone and Annie Bosacker were formative in building my interest in ecology and evolution. Hannah Specht was the teaching assistant for the undergraduate field ecology course that I took and was instrumental in inspiring me to go to graduate school and reading through all my application materials. Additionally, Carleton's extensive arboretum is where I fell in love with grasslands and learned the power of restoration.

Lastly, I want to acknowledge the Chumash peoples as the traditional caretakers of the land where all of the field research conducted during my PhD took place. The Chumash territory, which expanded roughly from Morro Bay to Malibu, inland to Kern county and some of the channel islands, has been inhabited by humans for at least 13,000 years and at the time of European arrival, there were over 150 Chumash villages and towns. Today's Sedgwick Reserve, where I set up my experiments and gathered data, is located between two of the historically largest Chumash towns in the Santa Ynez valley; Soxtonokmu' to the northwest and Kalawashaq'

to the south. The area between was likely used for hunting and gathering and as a trade route between towns. Salvia columbariae, one of my study species, was a very important resource whose seeds were gathered and cultivated due to their high nutritional value by native people all over Southern California which likely effects where its populations are found today. Some names for it include, ilépesh (Barbareño Chumash), 'itepesh (Ventureño Chumash), paanihac (Serrano), pasal (Cahuilla), and pashal (Luiseño). The Spanish began to settle the territory in ~1770 and forced the Chumash people to relocate to their Christian missions where many died of European diseases and the rest were subjected to forced labor and a suppression of their culture. The land where Sedgwick reserve lies then became part of various ranches for livestock grazing until it was acquired by the UC Reserve system in 1997 for teaching and research purposes. The plant community that we find on Sedgwick today was considerably shaped by its history which in turn shaped the questions I asked and the research that makes up this dissertation.

Curriculum Vitae
Mary Nancy Van Dyke

Education

2020   Ph.D. Candidate, Ecology and Evolutionary Biology, University of California, Los Angeles. Advisor: Dr. Nathan Kraft

2013   B.A. Biology, Carleton College, Northfield, MN

Publications

1) Van Dyke, M.N., Levine, J.M., & Kraft, N.J.B. *Nature*. Small rainfall changes drive substantial changes in plant coexistence. (2022)

Professional and Research Experience

2016-2017 *Research Technician* in Dr. Nathan Kraft's Plant Community Ecology Lab, UCLA

2016 *Desert Tortoise Research Assistant*, USGS, Americorps, Barstow, CA

2015 *Planning Specialist,* Division of Parks and Trails, Minnesota Department of Natural Resources, Americorps, Saint Paul, MN

2014 *Restoration Technician and Youth Outdoors Field Crew Member*, Conservation Corps of Minnesota and Iowa, Saint Paul, MN

2012 *Restoration Management Assistant*, Carleton College, Northfield, MN

2012 *Research Assistant* in Dr. Daniel Hernandez Biology Lab, Carleton College

2011 *Research Assistant* in Dr. Bereket Haileab Geology Lab, Carleton College

Teaching Experience

2017-2023 *Teaching Assistant*: Plant Ecology 161, Restoration Ecology 136, Tropical Ecology 151, Plants and People 187, California Ecosystems 154, Ecology and Evolutionary Biology Dept. UCLA

2013 *Intern Instructor*, Spruce Knob Mountain Institute, Circleville, WV

2011 *Teaching Assistant,* Introduction to Geology, Geology Dept. Carleton College, MN

Research Presentations

2022 Van Dyke M.N., Levine, J., Kraft N.J.B., California annual plant community demographic responses to long term variation in climate - implications for coexistence and global change, contributed poster at the California Native Plant Society meeting, San Jose, CA

2022 Van Dyke M.N., Levine, J., Kraft N.J.B., California annual plant community demographic responses to long term variation in climate - implications for coexistence and global change, contributed talk at the Ecological Society of America (ESA) meeting, Montreal, QC

2021 Van Dyke, M.N., Kraft N.J.B., How changes in phenology affect coexistence in an annual grassland, contributed talk at ESA meeting, virtual

2019 Van Dyke, M.N., Kleinhesselink A., Kraft N. J.B., Small changes in rainfall drive large shifts in competition and species coexistence in an annual grassland community. Contributed talk at ESA meeting, August 2020, virtual

2019 Van Dyke, M.N., Kleinhesselink A., Kandlikar G., Kraft N.J.B., Changes in precipitation alter species coexistence, contributed talk at Sedgwick Reserve's Research Symposium, Santa Ynez, CA

2017 Van Dyke, M.N., Kandlikar G., Kraft N. J.B., Do competitors drive intraspecific trait shifts? An experimental test with serpentine annuals," late breaking poster at ESA, Portland, OR

2011 Van Dyke, M.N., English. E, Haileab B., Geochemical analysis of surface water quality in Rice County, MN, contributed poster at Geological Society of America meeting, Minneapolis, MN

Honors and Funding

2022 California Native Plant Society Santa Monica Mountains and Los Angeles chapter Conference Scholarship

2021 Vavra Research Fellowship and travel grant, UCLA EEB Dept.

2020 Research grant, UCLA EEB Dept.

2019 Vavra Research Fellowship and travel grant, UCLA EEB Dept.

2018 La Kretz Center at Sedgwick Reserve Funding Award, UC Reserve System

2018 Vavra Research Fellowship and travel grant, UCLA EEB Dept.

2018 California Native Plant Society Conference Student Funding Award

2015 The Society of Outdoor Recreation Professionals' New Professional Conference Scholarship

Service

2016-2020 *Volunteer docent for the UCLA Mildred E. Mathias Botanical Garden*

2018-2023 *Undergraduate Research Mentor*

2018 *First year graduate student trip leader*

Introduction to the thesis

Ecologists have long sought to understand the biotic and abiotic processes that shape natural communities. We wonder why we find certain species and characteristics in certain places. We ask, how and why organisms interact with each other and their abiotic surroundings. And now more and more we ask, how are human's actions altering the land and the organisms we find there. The answers to these questions are ongoing and complex. My dissertation tries to contribute to these answers by investigating the coexistence dynamics shaping an annual grassland community specifically the influence of temporal coexistence mechanisms. Additionally, I explore how these dynamics inform the potential consequences that changes in climate will have on plant species interactions in diverse communities.

The Mediterranean climate and heterogenous bedrock of coastal southern California hosts a diverse and unique plant community. The historically cold, wet winters and hot, dry summers lends itself well to an annual life cycle for plants where germination occurs sometime in the late fall/early winter as the rainy season begins and senescence occurs throughout the spring as rainfall wanes. While much of the grasslands in southern California are highly invaded by non-native annuals, the areas with serpentine bedrock have avoided invasion due to the harsh soil conditions and thus there are still patches of high diversity maintained. The short life cycles, high biodiversity and substantial spatial and temporal variability has made the annual grassland community a model system for studying plant coexistence. I have built on this foundational research by empirically testing coexistence theory using manipulative experiments and population growth models. I have worked to understand what coexistence mechanisms maintain diversity in the annual grassland system and how plant functional traits can be used to explain

the mechanisms and interaction dynamics we find there. All of my research has also considered the underlying consequences of climate change and attempts to use this model system and plant functional traits to make the findings more broadly informative.

To anticipate the consequences of climate change on plant communities and prevent biodiversity loss we want to know how species distributions and the composition of communities will change in response to changes in climate. To do this, we need to understand how abiotic changes directly affect individual species but also how those changes affect interactions between species in a community. Species ranges are set by a species ability to withstand the abiotic conditions in an area as well as their ability to tolerate their competitors and we do not have a clear understanding of how competitive interactions may be altered by climate change. My first chapter tries to address this issue by exploring how competitive interactions between neighboring plants in a semi-arid annual grassland are affected by changes in rainfall. We grew annual plants with differing densities and identities of competitors under two rainfall treatments to parameterize a population growth model that allowed us to predict the long-term coexistence outcomes between pairs of species. We quantified the extent to which adding intra and interspecific competitors reduced an individual's seed production to calculate stabilizing niche differences and fitness differences between pairs which determine coexistence. Using six annual plant species from the community we assessed how reduced rainfall impacted species when grown without competitors and how it affected the long-term coexistence outcomes between pairs. We found that four of the six species showed little to no direct effect of reduced precipitation on seed production, yet 10 of the possible 15 pairs experienced changes in their competitive outcome predictions. We find that competitive interactions can change with different

abiotic conditions even when a species individually shows no response. This highlights the need to incorporate species competitive interactions when working to predict how species may move in response to climate change. We also found that species pairs who were more functionally similar were less likely to have their coexistence outcome altered by changes in rainfall indicating that competitive interactions in functionally diverse communities may be more impacted than in less functionally diverse communities.

Changes in species phenology (the timing of life history events) is a clear outcome of climate change that is occurring all over the globe. The actual demographic consequences this has on plant populations, however, is difficult to determine. Changes in phenology may not affect reproductive output for an individual plant, but it is possible that it could affect interactions with neighboring plants that may ultimately have demographic effects. We hypothesized that this could be a potential mechanism for the results we found in chapter 1. Species in the annual grassland community usually flower between February and June. Separation in flowering phenology can promote coexistence if it reduces heterospecific pollen transfer and separates species' resource intensive life stages over the season. Therefore, we recorded flowering periods for seven annual plant species from the grassland community under an ambient and a reduced precipitation regime. We found idiosyncratic responses amongst species with four of the seven species flowering earlier in the reduced rain treatment and three of the species experiencing no difference. The idiosyncratic responses changed the amount of time species pairs overlapped in their flowering time. We also found that the more different two species flowering phenology response was, the more likely that their competitive outcome prediction changed with reduced rainfall in the experiment described in chapter 1. This shows that changes in rainfall, in addition

to temperature can cause changes in flowering phenology and that idiosyncratic responses amongst neighboring species may explain changes in competitive interactions due to disrupting existing temporal coexistence mechanisms.

Within season temporal separation of flowering is likely an important mechanism for coexistence in the annual grassland community, but high interannual variation in climate may also be an important temporal coexistence mechanism. Southern California experiences the highest interannual variation in precipitation of anywhere in the US (Dettinger et al. 2011). Over the last one hundred years, the semi-arid annual grassland where my research takes place has had yearly rainfall range from 16.3cm total rainfall over the growing season in the driest year on record (2007) to 119.1cm total rainfall during the wettest year (1998). With climate change, such extremes are only expected to increase here and generally around the globe (Begum et al. 2022). Understanding how large fluctuations in abiotic conditions affects coexistence in communities can help us understand how current biodiversity is maintained and how future communities may be altered if fluctuations increase. Modern coexistence theory suggests that fluctuations in the abiotic environment can promote coexistence through mechanisms such as the storage effect. If coexisting species perform best at different levels of the fluctuating resource and can survive the periods when they are not favored, this promotes coexistence. Figure 1 shows the same spot at our field site photographed at the same time during the season but on two years with very different levels of rainfall. The densities and identities of species are clearly different in the two photographs. We explored the role high interannual variation in rainfall has on coexistence in the community by analyzing demographic data of sixteen species over the last 15 years. We found that few species pairs were strongly positively correlated in their yearly germination rates or seed

production without competitors, indicating that species specialize and do best during different years. We also found that species with more similar functional traits, particularly, rooting depth, water use efficiency and leaf nitrogen content had stronger positive year to year correlations in germination rates than species who had less similar traits. The results from chapters 1 and 3 coupled with the fact that all of these species maintain long lived seedbanks shows that interannual variation in precipitation helps maintain coexistence in the community by favoring different species different years through changes in their germination rates, low-density fecundity, and competitive interactions.
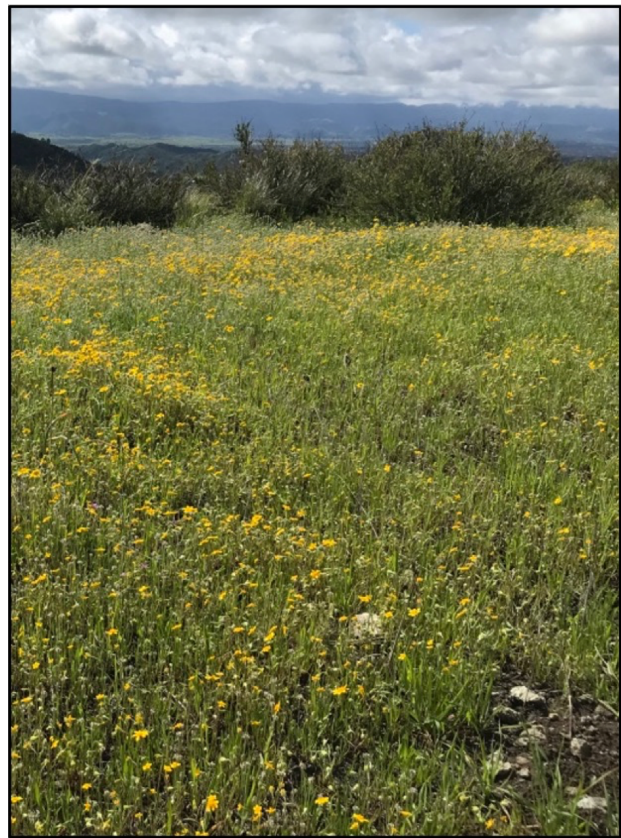
March 16, 2016:	March 21, 2019:
37.5 cm rainfall	61.3 cm rainfall

Figure 1: The same spot photographed three years apart in mid-march after receiving very different levels of rainfall. Observations like these inspired me to investigate the role of high interannual variation in rainfall on coexistence in the community.

Plants make up the backbone of any terrestrial community and it is clear that a more diverse plant community supports more diversity of other life forms as well. As our world faces the possibility of massive biodiversity loss, understanding the mechanisms that maintain diverse plant communities is more important than ever. The complexity of communities and the interconnectedness of the species that compose them, however, make it very difficult to find general rules that dictate composition and species population trajectories. My dissertation tries to break these broad questions down in chapters 1 and 2 by studying species interactions and changes in water availability at the neighborhood scale. In chapter 3, I try to unite the neighborhood scale studies and explore the multiple mechanisms that contribute to coexistence in this community long-term.

Chapter 1

Small rainfall changes drive substantial changes in plant coexistence

This chapter was originally published as Van Dyke, M. N., J. M. Levine, and N. J. B. Kraft. 2022. Small rainfall changes drive substantial changes in plant coexistence. Nature 611:507–511.

MVD and NJBK conceived and led the project. MVD, JML, and NJBK developed the methods. MVD carried out the field experiment and collected the data. Data analyzed and visualized by MVD. Initial manuscript written by MVD and NJBK with substantial contributions from JML.

Abstract:

Though precipitation patterns have long been known to shape plant distributions (Schimper 1903), the impact of changing climate on species interactions and therefore community composition is far less understood (HilleRisLambers et al. 2013, Alexander et al. 2015). Using an annual grassland community, we explored how changes in precipitation alter competitive dynamics via direct effects on individual species, as well as by the changing strength of competitive interactions between species. We grew plants under ambient and reduced precipitation in the field to parameterize a competition model (Chesson 2000) with which we quantified the stabilizing niche differences and fitness differences that determine species coexistence in each rainfall regime. Here we show that reduced precipitation had little direct impact on species grown alone, but it qualitatively shifted predicted competitive outcomes for 10 of 15 species pairs. Additionally, species pairs that were more functionally similar were less likely to experience altered outcomes, indicating that functionally diverse communities may be most threatened by changing interactions. Our results highlight how important it is to account for changes to species interactions when predicting species and community response to global change.

Main Text:

Ecologists and biogeographers have understood for centuries that plants respond to climate (Schimper 1903) and this forms the foundation for our understanding of plant responses to global change. However, we know much less about how changing species interactions may help or hinder the capacity of species to persist given the shifting location of their preferred climate (Loarie S. R. et al. 2010, Alexander et al. 2015). For a species to persist in a community impacted by global change, it must not only survive the direct physiological effects of climate change but also the effects of altered densities, interaction strengths and identities of neighbors (Alexander et al. 2015, HilleRisLambers et al. 2013). Though it has long been clear that the abiotic context influences interactions between species (Callaway et al. 2002, Dybzinski and Tilman 2007, Hautier et al. 2009, HilleRisLambers et al. 2013), predicting how these changes will impact population growth and community composition in a robust manner has proven challenging. Overcoming this challenge requires an understanding of how each individual species will respond directly to climate, how species interactions will be altered, as well as a theoretically justified framework for predicting the longer term outcome of the altered species interactions (Chesson 2000, Levine and HilleRisLambers 2009, Kraft et al. 2015).

Pioneering studies on rainfall effects on competitive outcomes have used climate manipulations such as rainout shelters or natural precipitation gradients to quantify precipitation-driven changes in biomass and species composition over time; results in some cases were likely driven by altered species interactions (Knapp et al. 2002, Sandel et al. 2010, Esch et al. 2018, Alon and Sternberg 2019). However, the response variables typically measured in these studies,

such as biomass change, offer limited insight into how changing species interactions will shape long-term competitive outcomes. Modern coexistence theory (Chesson 2000, 2018, Barabás et al. 2018, Ellner et al. 2019), offers a useful mathematical approach for doing just that.

In modern coexistence theory, competitive outcomes between pairs of species are determined by the relative strength of stabilizing niche differences that promote coexistence and fitness differences that drive competitive exclusion (Chesson 2000, Adler et al. 2007). Stabilizing niche differences reduce interspecific competition and increase each species' ability to recover from low density, a hallmark of stable coexistence. Fitness differences are frequency-independent advantages that favor one species over another regardless of their relative abundance in the community. For a pair of species to coexist, stabilizing niche differences must exceed fitness differences, giving both species the ability to recover from low density (Chesson 2000, Adler et al. 2007). While it may be tempting to regard niche and fitness differences as fixed properties of a pair of species, these differences depend on the abiotic conditions under which species compete (Germain et al. 2018), and thus may change as the climate changes. Quantifying how they do so will therefore give insights into future competitive outcomes and community composition.

Separate from their ability to predict competitive outcomes, stabilizing niche differences and fitness differences lie at the heart of numerous hypotheses for how altered precipitation will influence competitive dynamics. For example, fitness differences between competitors are invoked when altered precipitation differentially harms the dominant competitor to the benefit of subordinates, increasing species diversity (Knapp et al. 2002). Alternatively, stabilizing niche

differences are invoked when reduced precipitation is thought to increase competitive exclusion by compressing the growing season and reducing the phenological differences between species (Fargione and Tilman 2005, Pau et al. 2011). However, these hypotheses about why competitive interactions change with climate are almost never quantitatively evaluated. Thus, measuring the effect of precipitation change on niche and fitness differences can offer fundamental insights into why changes in environmental conditions impact long-term coexistence and species diversity in a plant community.

Novel approaches to quantifying stabilizing niche differences and fitness differences in field settings (Levine and HilleRisLambers 2009, Godoy et al. 2014, Kraft et al. 2015) under different climate treatments offer the opportunity to understand how environmental change affects plant performance, competitive interactions and the long-term consequences of those interactions. Although these approaches are nearly impossible to execute in any diverse community with long-lived species, annual plant communities lend themselves to just this kind of work. Lifetime fitness is attained in just one year, many plants can be feasibly grown in a field plot, and the simple life cycles are reasonably described by the mathematical models necessary for quantifying stabilizing niche and fitness differences and predicting competitive outcomes (Levine and HilleRisLambers 2009, Godoy et al. 2014, Kraft et al. 2015). While annual plants have less complex demography than perennials, they are nonetheless part of the same continuous global spectrum of plant function (Díaz et al. 2016) that is widely used to extrapolate findings from one system or set of species to another (Kunstler et al. 2016).

In order to assess the impact of precipitation change on species coexistence, we grew six California annual grassland plant species in pairwise competition in the field under ambient and 20% reduced rainfall and quantified their competitive dynamics. The six species were selected from our previous work (Levine and HilleRisLambers 2009, Kraft et al. 2015) to span the breadth of ecological strategies found in the annual plant community at the site. Climate forecasts for the region over the next century predict increases in inter-annual variability and modestly less rainfall (Diffenbaugh et al. 2015, Swain et al. 2018), a change mimicked by a rainfall exclusion treatment in our experimental design. We used results from the field experiment to parameterize a plant competition model that describes the dynamics of annual plant populations as a function of species' intrinsic demographic rates and the effects of pairwise competition (Chesson 1990). We used fitted germination rates, plant fecundity in the absence of competition, and pairwise competition strengths, all under the two rainfall treatments (see Methods) for six interacting species to quantify their stabilizing niche and fitness differences (Godoy et al. 2014). These metrics allowed us to predict the long-term outcome of competition for each pair of species under different rainfall treatments (Fig. 1.1).
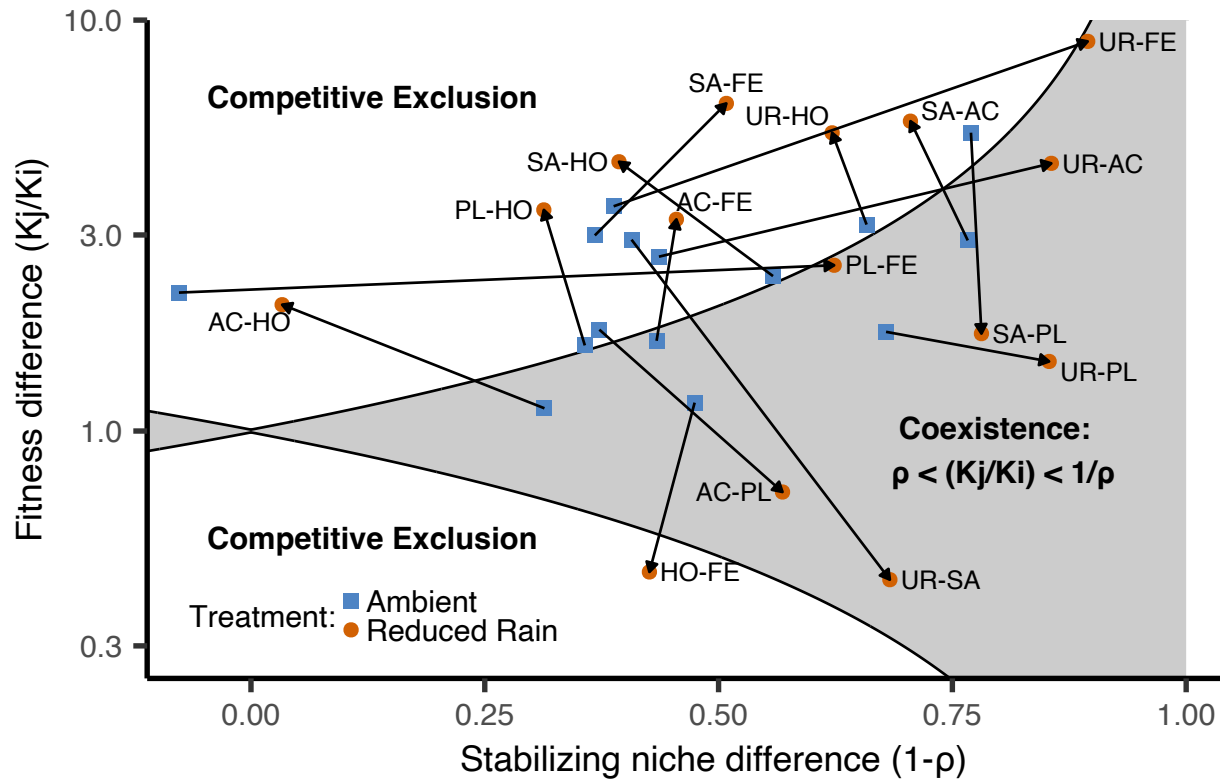
Figure 1.1: Effects of water treatment on competing pairs' stabilizing niche and fitness differences: Species pairs' stabilizing niche and fitness differences under the ambient (blue square) and reduced rain (red circle) treatments predict coexistence. Pairs coexist when $\rho < K_j/K_i < 1/\rho$ indicated by the grey shaded region. When this inequality is not met, as indicated by the unshaded region, one species will exclude the other. See Table S1.1 for species labels.

Our results revealed qualitative effects of rainfall change on the predicted coexistence of 10 of 15 species pairs in our study (Fig. 1.1), changes that were driven by rainfall exclusion effects on stabilizing niche and fitness differences (Table S1.2). For these 10 species pairs, coexistence was predicted in one rainfall treatment but not in the other. Specifically, four pairs were predicted to coexist under an ambient regime, but not the reduced rainfall treatment. Six other pairs were predicted to coexist under reduced rainfall but not the ambient treatment (Fig. 1.1, Table S1.2, Fig. S1.1). Four pairs were not predicted to coexist in either treatment, and one pair was predicted to coexist in both.

Notably, while reducing rainfall had substantial effects on predicted competitive outcomes, it had smaller effects on each species when grown alone (Fig. 1.2, Table S1.1). Four of the six species showed no difference in fecundity in the two treatments, while only two species, *Festuca microstachys* and *Uropappus lindleyi* experienced lower fecundity (by an average of 62% and 71%, respectively) in the reduced rainfall treatment. The fact that four species were insensitive to reduced rainfall was surprising as decreasing water availability often decreases growth and fecundity (Aronson et al. 1992, Alon and Sternberg 2019). However, these species are adapted to a Mediterranean climate with frequent dry years. For these four species, reduced rainfall may not limit fecundity without neighbors also competing for that same water and further reducing soil water to a truly limiting level. Additionally, the year in which we conducted our study was a relatively wet one, meaning that our 20% reduction treatment and ambient treatment fell within this community's typical rainfall range (*Santa Barbara County Public Works Water Resources Hydrology: Historical Rainfall Data: Daily and Monthly Rainfall* 2019). Taken together, these results highlight how even modest changes in rainfall (20% less) that have minimal effects on most species' fecundity in the absence of competitors (Fig. 1.2) can nonetheless drive substantial changes in competitive outcomes (Fig. 1.1).
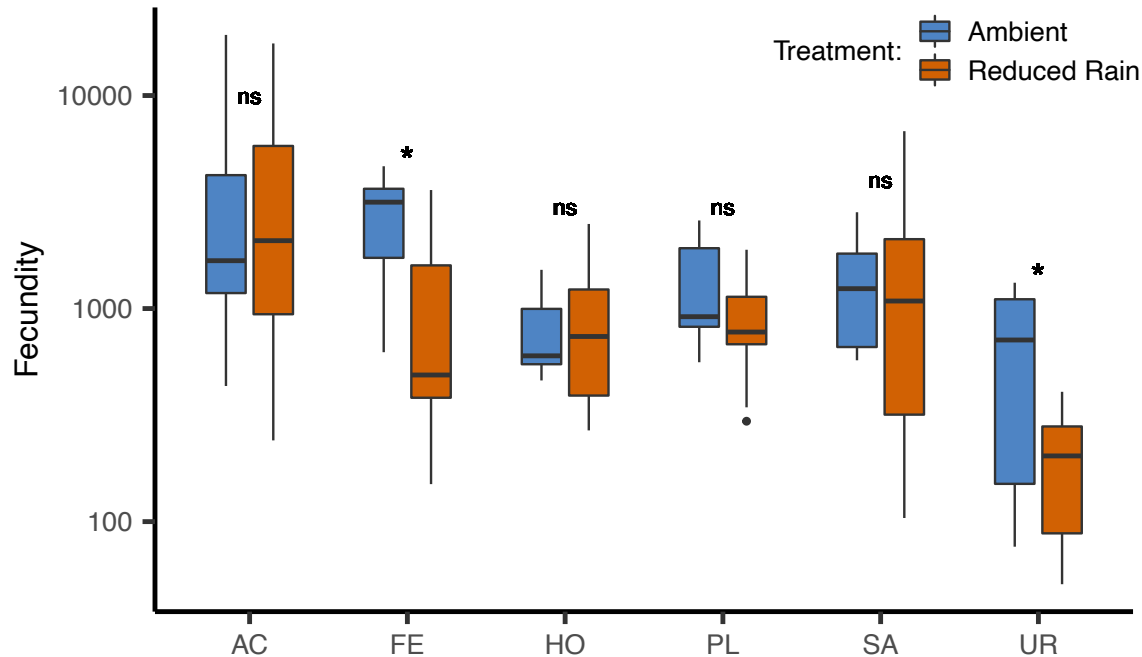
Figure 1.2: Effects of water treatment on species' fecundity when grown without competitors: Seeds produced per germinant (fecundity, note log scale) from plants grown without competitors under the ambient and reduced rain treatments. See table ED1 for species codes and number of replicates (n). Differences were assessed using a generalized linear mixed effects model: fecundity~ species x treatment + plot, (* indicates $p < 0.001$, ns = not significant).

To evaluate the degree to which precipitation effects on coexistence resulted from changing competitive interactions versus changing demographic potential (driven by fecundity in the absence of neighbors), we quantified how rainfall-driven changes to each of these quantities altered species' invasion growth rates. A species' invasion growth rate is the rate at which it can invade a system in which their competitor is at its "resident" equilibrium state. Invasion growth rates therefore determine competitive outcomes (see Methods) and depend on both the resident's per capita suppression of its own growth relative to that of the invader (a ratio of competition coefficients), and the demographic potential of the invader relative to its competitor (capturing species' direct responses to the environment, equation 5). We found that reduced rainfall altered

the relative strength of the competition coefficients more strongly than the differences in

demographic potential (Fig. 1.3).
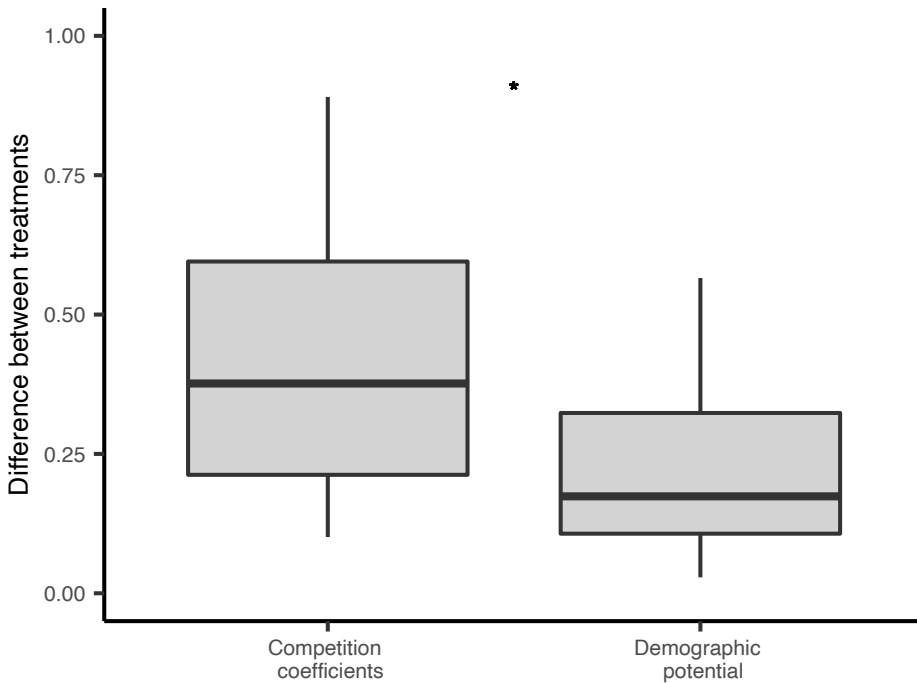
Figure 1.3: Effect of water treatment on components of species' invasion growth rates: Changing

precipitation differentially altered two quantities that shape species' invasion growth rate across

all species pairs. These are (1) competition coefficients, defined as a log ratio of the resident

species' intra and interspecific competition effects and (2) demographic potential, defined as a

log ratio of the demographic potential of the invader relative to resident species. See methods for

full details and theoretical justification for this analysis (* indicates $p = 0.044$).

In sum, the changes in predicted competitive outcomes between species in the rainfall

manipulation were most strongly driven by changes in species interactions (Fig.1.1, S1.1). As

there was variation across species pairs in how the rainfall manipulation affected their

coexistence, we sought to better understand the potential mechanisms underlying this diversity of

competitive changes. Specifically, we tested whether the variation across species pairs in the effect of rainfall manipulation on competitive outcomes was correlated with functional or ecological strategy differences between species. We quantified strategy differences using functional trait measurements of our focal species, which capture variation in species' life history strategies and can explain variation in species interactions (Kraft et al. 2015). To quantify aggregate functional trait differences between species, we conducted a principal component analysis (PCA) of 11 previously measured functional traits of 23 species from the community (Fig. S1.2) (Kraft et al. 2015, Kandlikar et al. 2022) and extracted the scores of our six focal species along the first principal components axis, which explained 22.7% of the trait variation among species. The traits measured included key leaf, stem and root functional traits that are widely sampled globally to capture a diversity of plant strategies (Díaz et al. 2016) and competitive outcomes (Kunstler et al. 2016), as well as less widely sampled traits related to competition for water in our system, such as rooting depth, phenology and integrated water use efficiency (via carbon stable isotopes) (Table S1.3). This suite of traits has also been shown to relate to niche and fitness differences (Kraft et al. 2015) in our system.

We found that the greater the functional dissimilarity between species, the more their fitness differences changed with altered rainfall (Mantel R^2 = 0.54, p = 0.028, Figs. 1.4a and S1.2). Underlying this finding was a weak relationship between trait dissimilarity and fitness differences in the ambient rainfall treatment and a much stronger relationship when rainfall was reduced (Fig. 1.4c). Consistent with previous work in this system showing that fitness differences but not niche differences between species are correlated with their functional trait differences (Kraft et al. 2015), we did not find any relationship between trait dissimilarity and

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stabilizing niche differences either within or between treatments (Fig. 1.4b & 1.4d). Taken

together, these results suggest that there is a functional basis to how rainfall affects fitness

differences and therefore competitive outcomes, an area worthy of further investigation. This

aligns with our understanding of trait variation, as species with similar functional traits often

respond to the environment in similar ways (Sandel et al. 2010, Kandlikar et al. 2022) and thus

their interactions should be less likely to change. It also suggests that communities with high

functional diversity, and therefore a greater proportion of pairwise interactions between

functionally distinct species, may be most at risk for climate-driven changes in interaction

outcomes in the future.
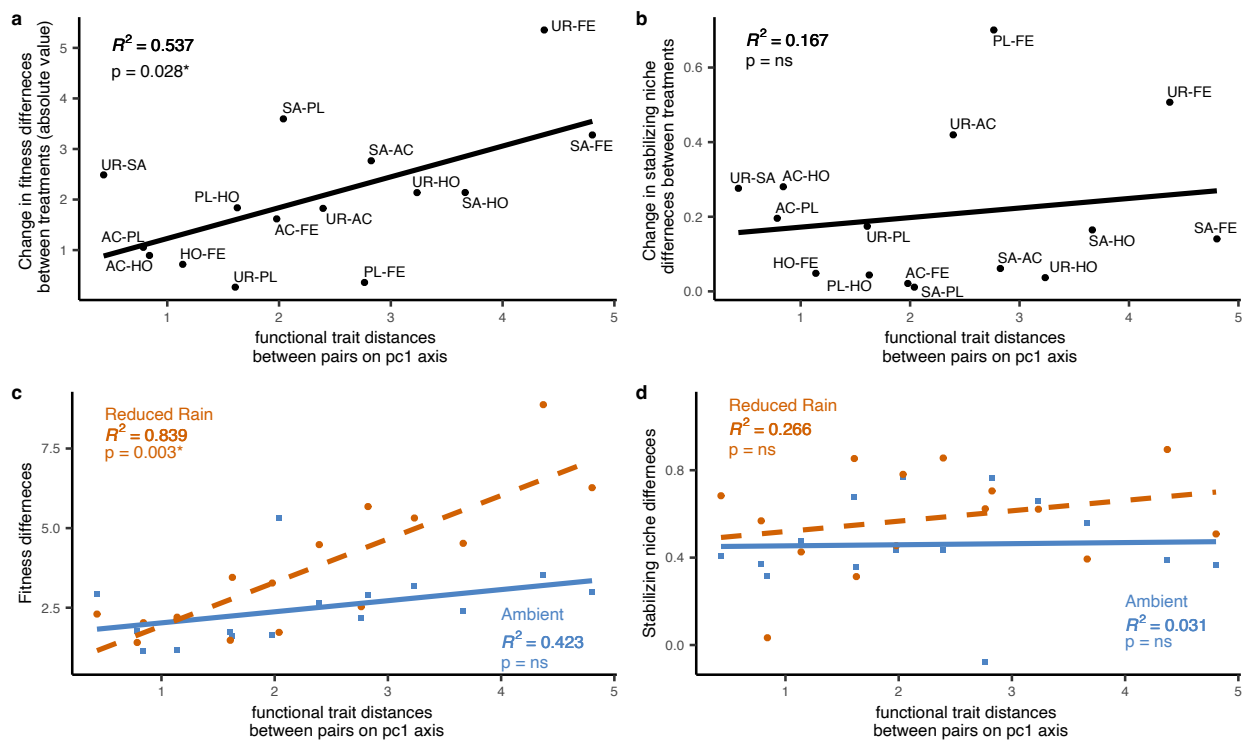
Figure 1.4: Effect of differences in functional traits on pairwise competition outcomes within

and between water treatments: **a**) Change in fitness differences with rainfall treatment plotted

against the functional trait distance between species along PCA axis 1. **b**) Change in stabilizing

niche differences with rainfall treatment plotted against the functional trait distance between species along PCA axis 1. **c**) Fitness difference between species plotted against their functional trait distance along PCA axis 1, for each of the two rainfall treatments. **d**) Stabilizing niche difference between species plotted against their functional trait distance along PCA axis 1, for each of the two rainfall treatments (* indicates significant p-value from mantel test).

A great diversity of processes are known to contribute to species coexistence in communities (Chesson 2000, Cleland et al. 2013, Usinowicz et al. 2017, Germain et al. 2018, Kandlikar et al. 2019), including a number potential mechanisms of coexistence which our study was not able to quantify. For example, broader scale spatial and temporal heterogeneity likely impact coexistence in this community, and this explains the fact that not all pairs are predicted to coexist in the ambient rainfall treatment. Although these and other factors contribute to coexistence at larger landscape scales and are worthy of future study, understanding the long-term predicted competition outcomes at a neighborhood scale under different rainfall conditions as we have done here provides an important template on which we can overlay other coexistence mechanisms in conjunction with future abiotic changes.

Finally, although community ecology has frequently assumed that species' pairwise interactions can be combined to predict whole community outcomes, higher order interactions challenge this assumption. Unfortunately, it is often logistically daunting to properly quantify these interactions empirically (Kleinhesselink et al. 2022), let alone do so in different rainfall environments. Nonetheless, as a step towards a multispecies perspective on our results, we applied a previously developed structural approach (Saavedra et al. 2017) to our pairwise

interaction results in order to assess how the rainfall treatment affected the potential for coexistence in systems with three or more of the study species. This analysis quantifies structural analogues of niche and fitness differences which can be used to assess the potential for any number of species to coexist. Consistent with past work in our system (Saavedra et al. 2017), we found that the fraction of possible pairs coexisting (11 of 15 in at least one treatment, Fig. 1.1, Tables S1.2, S1.4) was greater than the fraction of coexisting triplets (4 of 20, Table S1.5), which was greater than the fraction of quadruplets, quintuplets and sextuplets (always 0, Table S1.6). Importantly, however, just as 10 of 11 pairs predicted to coexist only coexisted in one rainfall treatment (Fig. 1.1, Tables S1.2, S1.4), 4 of 4 triplets predicted to coexist only coexisted in one of the two rainfall treatments (Table S1.5). This suggests that the pairwise results we report above extend to systems with more than two species, though more work on the multispecies implications of our findings are warranted.

Our results demonstrate the importance of accounting for species interactions when predicting the impacts of global change. Our rainout experiment generated a modest 20% reduction in precipitation with insignificant effects on the fecundity of four of our six species when grown without competitors (Fig. 1.2, Table S1.1). These responses are small enough to be inconsequential in any global change forecast built on species' direct responses to changes in climate. However, this small rainfall change strongly impacted species competitive interactions, so much so that the predicted coexistence outcome changed for 10 of 15 species pairs (Fig. 1.1). Of these pairs, we found that species with more similar functional traits showed smaller shifts in their competitive imbalance. Thus, our results show that studies that rely solely on species' direct climate responses to predict future communities or species distributions may miss critical

changes in the effect of competitive interactions. Our results suggest that scenarios in which global change alters resource availability (such as water) may have fundamentally different consequences for species interactions and community structure than cases where temperature alone is altered. If this is true, consumer-resource models (Farrior et al. 2013, Levine et al. 2022) may be particularly powerful for exploring the community consequences of such changes. While the logistical challenge of assessing changes in species interactions is not trivial, especially when considering longer lived organisms, our results show just how important such changes can be for predicting the consequences of global change.

Methods:

Field experiment

      The experiment was conducted at the University of California, Santa Barbara's Sedgwick Reserve in Santa Barbara County, USA (34° 40′ N, 120° 00′ W), 730m above sea level. Precipitation determines the growing season in this Mediterranean climate, which is characterized by cool, wet winters and hot, dry summers. The landscape is heterogeneous with patches of serpentine soil that support diverse native flora, in part because they are resistant to invasion by European annual grasses which dominate much of the grasslands in this region (Harrison et al. 2006). Most of the annual species in this grassland community germinate after early season rainfall in December and January and senesce sometime between February and June. From surveys of the area, we have recorded and identified 55 species of annual forbs or grasses (Kandlikar et al. 2022). We chose six species for the experiment that differ in core functional traits (Pérez-Harguindeguy et al. 2013, Kraft et al. 2015, Kandlikar et al. 2022) as well as their phenology across the growing season, and were known to germinate and grow reliably in previous studies (Table S1.1). We collected seed for the experiment in spring and summer 2018 from the reserve. In fall 2018, we planted a pairwise competition experiment with two different precipitation regimes.

      Experimental competition plots (each 60 x 75cm) were cleared of vegetation and any visible seeds and then sown with seed from our six focal species in late October 2018 before the onset of winter rains. The plots were located within a fenced area which excludes deer and

gophers. Each plot was randomly assigned to receive seeds of one of six focal species in the background at one of 5 sowing densities ranging from 0 to 12 grams of seed per m^2 with 4 replicate plots per density per background species. As the 0 gm^{-2} plots are identical in composition across background species, for efficiency we only sowed a total of 10, 0 gm^{-2} plots, resulting in 106 plots (10 plots with 0 gm^{-2}, 96 plots with 2-12 gm^{-2}). Natural density of this grassland community corresponds to roughly 8 gm^{-2} in a typical year, so our treatments range from no competitors to ~150% of typical density (Levine and HilleRisLambers 2009). The central region of each plot was divided into 12 15x15cm sub-plots, with a 7.5 cm buffer around the edges. The center point of each sub-plot was sown with 25 viable seeds from one of our six focal species, with each focal species sown into two sub-plots per plot. Germination in the sub-plots allowed us to measure the average germination rate of each focal species, and following germination, the focal plant species in each sub plot was thinned to a single focal individual, located no closer than 15 cm to a focal individual in neighboring subplots to minimize competitive interactions among focal plants. If one of the six species emerged at an undesignated spot in the plot but was at least 10 cm away from another focal and the edge, we included it in the data collection. This design then results in each of the 6 focal species competing against intra- and all interspecific competitors at 5 different densities. Seed viability was quantified prior to sowing using methods from previous experiments with these species (Kraft et al. 2015). Our 106 plots were evenly divided between ambient and reduced rain treatments and randomly assigned to a rainout shelter. Fourteen large rainout shelters (1 m tall) were built around groups of adjacent plots. The shelters consisted of wooden frames that could be covered with plastic sheeting that channeled water into gutter systems that transported the rain away from the experimental plots. The sheeting was only deployed during rain events to minimize unwanted

treatment effects in between storms. In order to further reduce artifacts between treatments, we opted to exclude rain for all plots in the experiment regardless of treatment and then return the appropriate amount of water based on rainfall during the storm to the ambient plots using collected rainwater. We deployed plastic sheeting over our rainout shelter frames during 15 of the 18 rain events that occurred between February 15 and June 1st, immediately returning collected rainwater to the ambient plots using backpack sprayers at the end of the storm at a watering rate equal to the rainfall total of the storm.

Both rainfall regimes received identical ambient rain until mid-February, which allowed plants to germinate and establish under similar conditions, thereby focusing the effects of our reduced rain treatment on the post-germination growth and reproduction phase. In January 2019, we recorded germination rates and thinned each of the focal seedlings that resulted from the original 25 seeds to a single individual. Any recruits from the seed bank were weeded out throughout the season unless the recruit was designated a focal because of its identity and position within the plot (or if the recruit was the background competitor species). We then recorded lifetime fecundity for each focal individual and censused the number of competitors in a 10 cm radius around each focal plant. We tracked germination, fecundity and number of neighbors for over 1600 plants in our plots.

Ultimately, the reduced rain treatment received 12.75 centimeters less rain than the ambient plots corresponding to a 20% reduction in total rain over the lifetime of the plants. Soil gravimetric water content (gwc; (wet weight - dry weight)/dry weight) was measured three times during the experiment from our 8 g/m^2 plots on March 27, April 21, and May 17, 2019 (Table

S1.7). Soil samples were taken from 3 different plots in each treatment in March and from 8

different plots in each treatment in April and May. Soil was weighed and then dried in a 60°C

oven for three days and weighed again. According to t-tests, the reduced rain plots experienced

significantly lower gwc than the ambient plots on all three dates (Table S1.7) with the reduced

rainfall plots measuring a gwc that was 68%, 71%, 78% of the ambient plots, respectively. The

site received above average rainfall in the 2018-2019 growing season (*Santa Barbara County*

Public Works Water Resources Hydrology: Historical Rainfall Data: Daily and Monthly Rainfall

2019), resulting in the reduced rain treatment receiving 2.25cm of rainfall below the average and

the ambient treatment receiving 10.5cm above the average.

Model parameterization

To quantify the niche and fitness differences critical to understanding coexistence

between species pairs, we parameterized an annual plant demographic model that describes the

dynamics of annual plant populations with a seed bank, and includes species-level variation in

germination rates, seed survival in the seed bank, fecundity and pairwise competition coefficients

(equation 1). The population dynamic model allowed us to calculate stabilizing niche and fitness

differences from the fitted parameters using a previously developed approach (Levine and

HilleRisLambers 2009, Kraft et al. 2015). Briefly, the per capita growth rate of species *i* in year *t*

(left side of equation 1) is modeled as a function of its germination rate (g_i), seed survival rate

(s_i), and per germinant fecundity (F_i):

$$\frac{N_{i,\,t+1}}{N_{i,t}} = (1 - g_i)s_i + g_iF_i \qquad [1]$$

The model tracks the growth of $N_{i,t}$, the density of species i in the fall of year t before germination, as the sum of two terms. The first is the growth contributed by seeds that do not germinate that year, a function of the seed germination and survival rate. Previous work at this site measured seed survival for each species by testing their viability before and after burying bags of seed in the ground for a year, and we assumed these rates were unchanged from previous years. The germination rates were determined from averaging each species germination rate across plots from the 25 viable seeds sowed for each focal. The second term, $g_i F_i$ describes the growth contributed by seeds that do germinate. The term F_i refers to the per germinant fecundity or the amount of seeds added to the fall seed bank by each germinated individual of species i. F_i can be expressed as a function that describes how fecundity decreases with increasing density of intra- and interspecific competitors (Chesson 1990, 2000, Kraft et al. 2015).

$$F_i = \frac{\lambda_i}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} \qquad [2]$$

The numerator (λ_i) denotes the fecundity of a germinated individual of species i when it is growing in the absence of any competition. The inter- and intra-specific competition parameters (α_{ii} and α_{ij}) represent species i's competitive effect on itself and species j's competitive effect on species i, respectively. The $g_j N_{j,t}$ term represents the density of germinated competitors of species j.

We used the collected data to fit the parameters in equation (2) in R using the non-linear least squares method (nlstools package in R version 4.2.0). We allowed lambda (low density seed

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production, λ_i) and alphas (competition interaction coefficients for each pair, $\alpha_{ii}, \alpha_{ij}, \alpha_{jj}, \alpha_{ji}$) to vary as a function of rainfall treatment, competitor density, and competitor identity, and used the non-linear least squares test to estimate each parameter. We bootstrapped the data and re-estimated the parameters 1000 times to estimate error for the parameters. Given previous work at the site showing strong competition between species, we constrained all parameters to be positive, which eliminates the possibility of facilitation (i.e. via a negative interaction coefficient estimate). Of the 72,000 alphas estimated from the bootstrapped data, less than 0.02% of them were equal to the constrained value of 0.001.

Stabilizing niche differences between two species are calculated as $1-\rho$, where ρ measures niche overlap(Chesson 1990, 2000, Kraft et al. 2015), described as:

$$\rho = \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}}\frac{\alpha_{ji}}{\alpha_{ii}}} \qquad [3]$$

Niche overlap therefore captures the extent to which a species limits conspecific individuals (represented by the intraspecific interaction coefficients in the denominator of equation 3) more than it limits heterospecific individuals (captured by the interspecific interactions in the numerator of equation 3), and relates to species' ability to increase when rare. If a species limits conspecific individuals more than heterospecifics, niche overlap is low, and invasion growth rates are more positive (Godoy et al. 2014, Kraft et al. 2015).

Similarly, fitness differences between two species can be described by a ratio (κ_j/κ_i), which is calculated by the following equation (Kraft et al. 2015).

$$\frac{\kappa_j}{\kappa_i} = \left(\frac{\eta_j - 1}{\eta_i - 1}\right)\sqrt{\frac{\alpha_{ij}}{\alpha_{jj}}\frac{\alpha_{ii}}{\alpha_{ji}}} \qquad [4]$$

where

$$\eta_i = \frac{\lambda_i g_i}{1 - (1 - g_i)(s_i)} \qquad [5]$$

The fitness ratio compares species inherent competitive abilities and is the product of two terms; the 'demographic ratio' $\left(\frac{\eta_j - 1}{\eta_i - 1}\right)$ and the 'competitive response ratio' $\sqrt{\frac{\alpha_{ij}}{\alpha_{jj}}\frac{\alpha_{ii}}{\alpha_{ji}}}$.(Kraft et al. 2015) Therefore, high competitive fitness can come either from a species producing a large total number of seeds when not experiencing competition (i.e. favorable demographic ratio), or by being relatively insensitive to the total effects of competitors (i.e.- favorable competitive response ratio) (Kraft et al. 2015).

Long term coexistence is predicted when stabilizing niche differences (ρ) and fitness differences $\left(\frac{\kappa_j}{\kappa_i}\right)$ satisfy the following inequality (equation 6).

$$\rho < \frac{\kappa_j}{\kappa_i} < 1/\rho \qquad [6]$$

To assess the direct effect of rainfall on individual species, we compared the low-density plot fecundities of each species under each precipitation treatment (Fig. 1.2). We then compared the estimated competitive interaction parameters ($\alpha_{ii}, \alpha_{ij}, \alpha_{jj}, \alpha_{ji}$) for each pair of species under each precipitation treatment. Note that the germination rate did not differ by treatments because

the rainfall exclusion was started after the germination inducing rain event, and the seed bank

survival was taken from previous work at the site. Lastly, we used equations 3, 4, and 5 to

calculate stabilizing niche and fitness differences and thus predicted long-term competitive

outcomes between pairs under each treatment. To estimate error we calculated stabilizing niche

and fitness differences 1000 times from each of the 1000 bootstrapped parameter estimates (Fig.

S1.1).

Invasion growth rate analysis

We decomposed the invasion growth rates of species pairs in order to determine the

extent to which changes in species' interaction strengths versus changes in fecundity drove the

widespread changes to species coexistence (Fig. 1.1) with rainfall manipulation. For a species

pair to coexist, each species must be able to invade an equilibrium population of the other from

low density. In our annual plant model, species i can invade species j when (Godoy and Levine

2014):

$$\frac{\alpha_{jj}}{\alpha_{ij}} > \frac{(\eta_j - 1)}{(\eta_i - 1)} \qquad [7]$$

where α_{ij} describes the competitive effect of species j on species i, and η_i captures the seeds

produced per seed lost from the seed bank for species i, which is a function of seed production in

the absence of competitors (λ), germination rate (g), and seed survival in the seed bank (s)

(Equation 5). This inequality can be rearranged into the following expressions:

$$\frac{(\eta_i - 1)}{(\eta_j - 1)} * \frac{\alpha_{jj}}{\alpha_{ij}} > 1 \qquad [8]$$

$$log10\left(\frac{\eta_i - 1}{\eta_j - 1}\right) + log10\left(\frac{\alpha_{jj}}{\alpha_{ij}}\right) > 0 \qquad [9]$$

where the capacity for species *i* to invade species *j* depends both on the relative demographic

potential of the competitors (ratio of the η's reflecting species' direct responses to the

environment) and the degree to which the resident species harms itself relative the invader (ratio

of the α's reflecting inter- and intraspecific competition). We investigated which of these two

elements changed more with the rainfall exclusion treatment by calculating the absolute value of

the differences in each term between treatments. We then performed a paired t-test on the

magnitudes (absolute value) of the two differences and found that across species pairs, the

competition coefficients term (α ratios) changed significantly more than the demographic

potential (η ratios) (Fig. 3, p = 0.044). This indicates that the changes in species coexistence that

we observed in our experiment were driven more by shifts in species interactions than by

changes in species direct responses to the environment.

Functional trait analysis

Eleven functional traits including leaf nitrogen content, phenology, leaf dry matter

content (LDMC), leaf area, specific leaf area (SLA), maximum height, seed mass, rooting depth,

specific root length (SRL), integrated water use efficiency (WUE, estimated with leaf tissue

$\delta^{13}C$), and canopy shape index were measured for 23 species, including our six focal species, at

the site in a previous year (Pérez-Harguindeguy et al. 2013, Kraft et al. 2015, Kandlikar et al.

2022)(see Table S1.3 for units and descriptions). In selecting traits, we sought to include both

traits that are widely sampled (such as SLA, seed size and maximum height measures), as well as traits that can be harder to sample but we expect matter more for competitive interactions among annuals, including rooting depth, phenology, and measures of canopy architecture. In terms of competition for water, we have sampled rooting depth, fine root structure (via specific root length) and integrated water use efficiency (via carbon stable isotopes). We created a principal component analysis with the measured traits of 23 annual plant species from the site (Fig. S1.2) to determine the extent to which species differed in their functional traits. We used differences between species on the PC1 axis (which explained 22.68% of the variability) as an overall measure of trait dissimilarity between the six species. The study species broadly span the functional trait spectrum of the annual plant community with considerable variation in traits, including for example a 40-fold difference in leaf area and a sixfold difference in seed size. Given the pairwise nature of our data, following previous work at the site (Kraft et al. 2015) we used mantel tests to test if either stabilizing niche or fitness differences between species pairs were correlated with trait dissimilarity, both within and between treatments.

Multi-species-structural analysis

Following recent methodological developments (Saavedra et al. 2017), we used a structural approach to derive metrics analogous to niche (Ω) and fitness differences (θ) that determine the range of demographic rates sufficient for multispecies coexistence given their intrinsic growth rates and their pairwise interaction coefficients scaled by germination. This allowed us to include the indirect interaction effects on competitive outcomes that can occur when more than two species are competing. It also allowed us to see how these structural

analogues of niche and fitness differences changed with rainfall for all possible pairs, triplets, quadruplets, quintuplets, and one sextuplet (Tables S1.4 – S1.6). When analyzing the species pairs, consistent with our main analysis (Table S1.2), we find that the same 10 of 15 pairs (67%) had altered coexistence outcomes in the rainfall manipulation treatment (Table S1.2 and S1.4). Extending the structural approach to all species triplets showed that 4 of 20 (20%) of the triplets experienced altered coexistence outcomes with rainfall manipulation (Table S1.5), which extends the overall pairwise results into a multispecies context. When we explored coexistence of species quadruplets, quintuplets, and the sextuplet of all species, we noted changes in the parameters between rainfall treatments (e.g. Ω and θ, Table S1.6), though the method did not predict stable coexistence of any of the larger species groupings in either treatment.

Acknowledgements:

All data and code for this analysis are available on Zenodo: https://doi.org/10.5281/zenodo.7083314

Data were recorded in Microsoft Excel (v.16.63.1) and analyzed in R (v.4.2.0). Figures and tables were created in R (v.4.2.0)
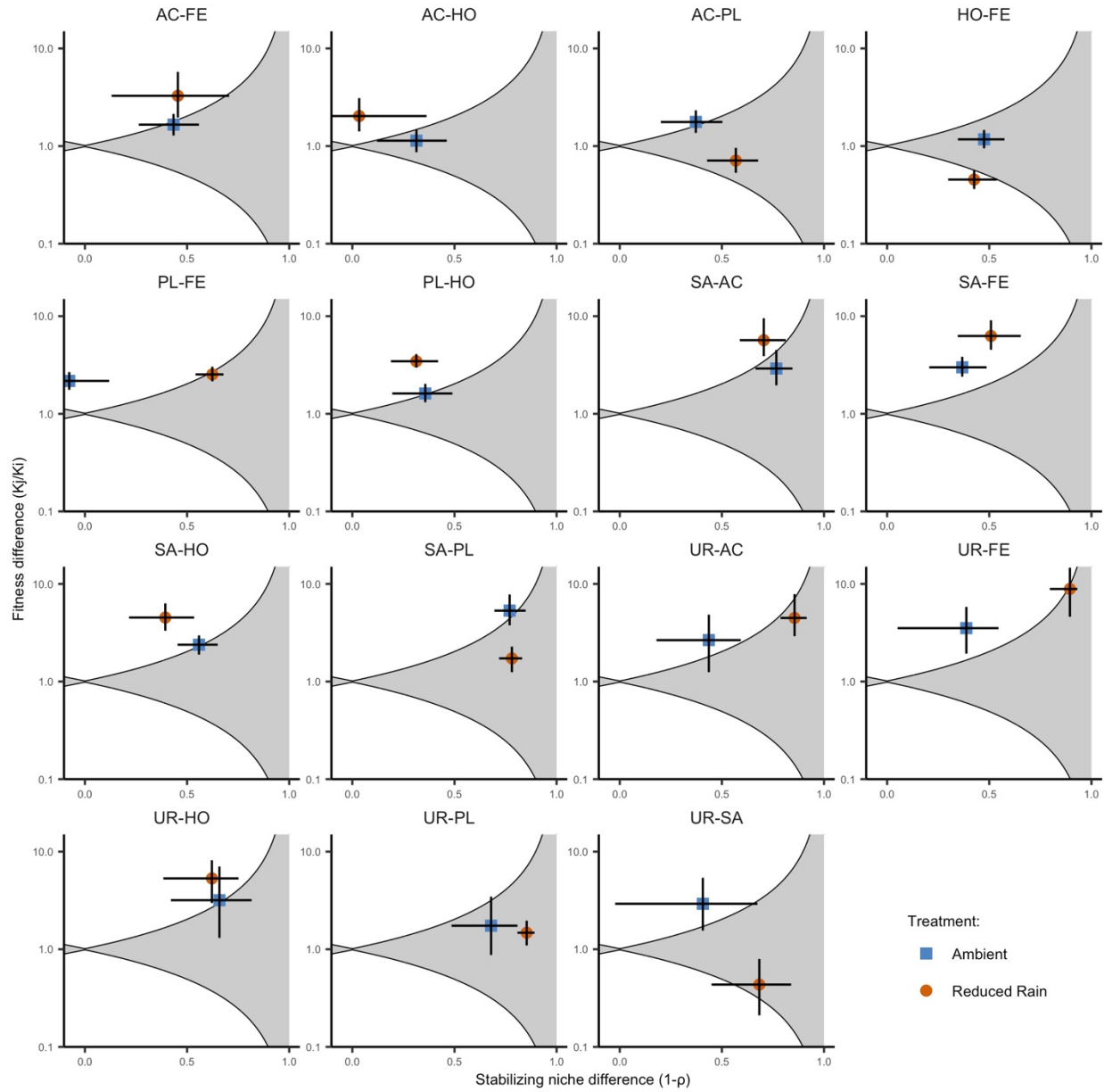
Figure S1.1: Effects of water treatment on each competing pairs' stabilizing niche and fitness differences: Each species pair shown separately with confidence intervals (+/- 1 SD) for stabilizing niche and fitness differences obtained from bootstrapping. Inside the grey shaded region indicates coexistence, outside indicates competitive exclusion.
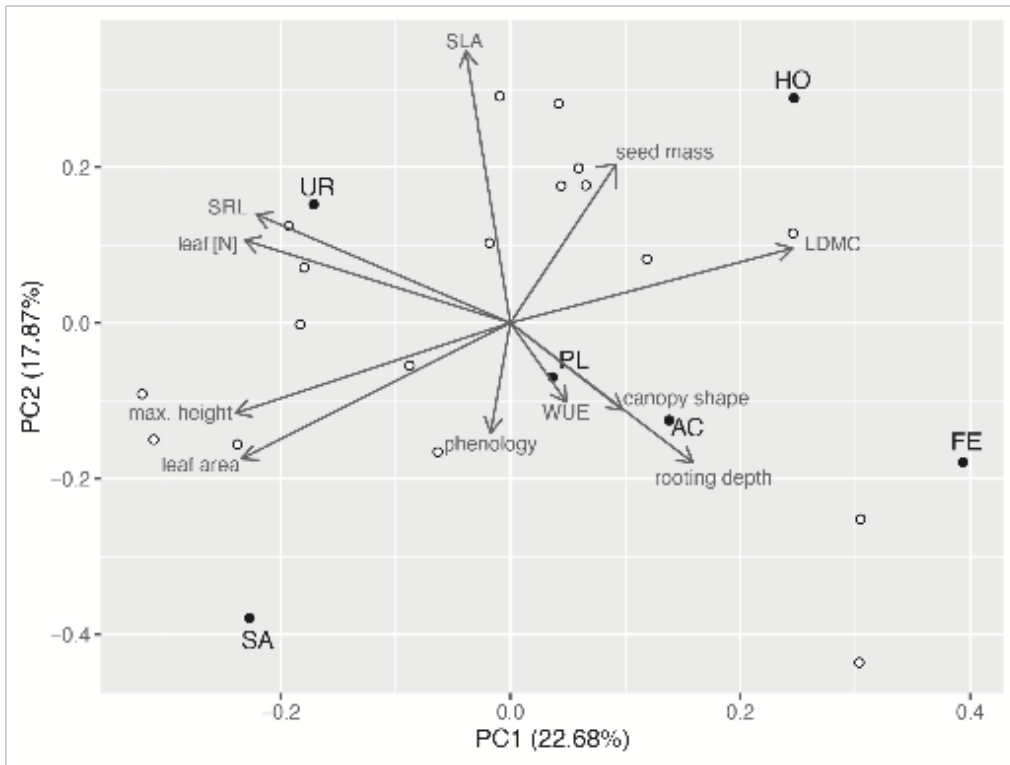
Figure S1.2: Principal component analysis of functional traits from the focal plant community: Principal component analysis with 23 species and eleven functional traits from previous work at the site[10,29]. The six species from this study are filled in circles and labeled following Table S1.1. The open circles represent other species in the community. See Table S1.3 for trait descriptions.

Table S1.1: Each species' mean per capita seed production without competitors in the two treatments from the $0g/m^2$ background plots ± standard error. P-values obtained from generalized linear mixed effects model: fecundity ~ species*treatment + plot.

| Family | Species | Code | Ambient Rainfall | | | Reduced Rain | | | |
			Mean Fecundity	Standard error	n	Mean Fecundity	Standard error	n	p-value
Fabaceae	*Acmispon wrangelianus*	AC	4,925.6	2,944.3	6	4,395.6	1,247.3	16	0.3597
Poaceae	*Festuca microstachys*	FE	2,793.0	507.9	8	1,069.1	284.8	14	0.0006*
Poaceae	*Hordeum murinum*	HO	810.9	145.8	7	944.7	198.9	12	0.6869
Plantaginaceae	*Plantago erecta*	PL	1,332.0	272.4	8	873.9	90.0	21	0.067
Lamiaceae	*Salvia columbariae*	SA	1,390.9	340.9	7	1,828.0	614.1	12	0.4452
Asteraceae	*Uropappus lindleyi*	UR	661.2	201.0	7	194.2	34.5	11	<0.0001*

Table S1.2: Stabilizing niche and fitness difference calculations for each species pair under two rainfall treatments. Stabilizing niche differences are calculated as $1-\rho$ and fitness differences as κ_j/κ_i. Species pairs are predicted to coexist long term when $\rho < \kappa_j/\kappa_i < 1/\rho$. Species pairs with similar predictions of coexistence in the two treatments are grouped together.

	Species Pair	Ambient Rainfall			Reduced Rain		
		Stabilizing niche difference	Fitness difference	Predicted Outcome	Stabilizing niche difference	Fitness difference	Predicted Outcome
Coexist in ambient but not reduced rainfall	AC-FE	0.434	1.658	coexist	0.455	3.275	FE wins
	AC-HO	0.314	1.136	coexist	0.033	2.030	HO wins
	HO-FE	0.474	1.172	coexist	0.426	0.454	HO wins
	SA-AC	0.766	2.910	coexist	0.705	5.677	AC wins
Coexist in reduced rainfall but not ambient	AC-PL	0.373	1.765	PL wins	0.568	0.711	coexist
	PL-FE	−0.077	2.172	FE wins	0.624	2.532	coexist
	SA-PL	0.770	5.322	PL wins	0.781	1.726	coexist
	UR-AC	0.436	2.656	AC wins	0.856	4.482	coexist
	UR-FE	0.388	3.523	FE wins	0.895	8.877	coexist
	UR-SA	0.407	2.922	SA wins	0.683	0.435	coexist
Coexist in both	UR-PL	0.679	1.743	coexist	0.853	1.477	coexist
Coexist in neither	PL-HO	0.357	1.616	HO wins	0.313	3.453	HO wins
	SA-FE	0.368	2.993	FE wins	0.508	6.270	FE wins
	SA-HO	0.558	2.383	HO wins	0.394	4.522	HO wins
	UR-HO	0.658	3.180	HO wins	0.621	5.317	HO wins

Table S1.3: The eleven functional traits used to create the PCA in ED figure 1.2 with their units and descriptions.

	Trait	Units	Description
Leaf	Leaf area	cm²	One-sided area of an individual leaf.
	Specific leaf area (SLA)	cm²/g	Area of fresh leaf divided by oven-dry mass.
	Leaf nitrogen concentration	mg/g	Total amount of N per unit of dry leaf mass.
	Leaf dry matter content (LDMC)	mg/g	Oven-dry mass (mg) of leaf, divided by its water saturated fresh mass (g).
Root	Rooting depth	cm	Maximum soil depth from which resources can be acquired.
	Specific root length (SRL)	m/g	The ratio of root length to dry mass of fine roots - a ratio of acquisition to investment.
Whole plant	Maximum height	cm	Maximum stature a typical mature individual of a species attains in a given habitat.
	Canopy shape index	dimensionless	A measure of investment in vertical vs. lateral growth.
	Phenology (peak fruiting)	day of year	Day of peak fruiting for a species.
	Carbon isotope composition	$\delta_{13}C$	A measure of intrinsic water use efficiency (WUE).
Seed	Seed mass	g	Oven-dry mass of an average seed of a species.

Table S1.4: Ω, a structural analog of stabilizing niche differences and θ, a structural analog of fitness differences[36] for each species pair and their predicted competition outcome using the structural method under the two rainfall treatments.

		Ambient Rainfall			Reduced Rain		
	Species	Ω	θ	Predicted Coexistence?	Ω	θ	Predicted Coexistence?
Coexist in ambient but not reduced rainfall	AC-FE	0.305	13.08	yes	0.209	24.09	no
	AC-HO	0.205	2.87	yes	0.016	17.34	no
	HO-FE	0.260	5.50	yes	0.246	17.53	no
	SA-AC	0.607	19.44	yes	0.494	35.70	no
Coexist in reduced rainfall but not ambient	AC-PL	0.216	12.55	no	0.463	5.96	yes
	PL-FE	0.046	17.01	no	0.376	15.83	yes
	SA-PL	0.455	24.82	no	0.715	17.62	yes
	UR-AC	0.187	11.91	no	0.758	32.18	yes
	UR-FE	0.082	6.70	no	0.861	38.57	yes
	UR-SA	0.214	15.82	no	0.167	3.33	yes
Coexist in both	UR-PL	0.323	11.34	yes	0.490	17.60	yes
Coexist in neither	PL-HO	0.243	12.38	no	0.104	23.85	no
	SA-FE	0.271	25.01	no	0.255	42.10	no
	SA-HO	0.379	18.84	no	0.197	37.43	no
	UR-HO	0.439	20.67	no	0.531	31.15	no

Table S1.5: Ω, a structural analog of stabilizing niche differences and θ, a structural analog of fitness differences[36] for each species triplet and their predicted competition outcome using the structural method under the two rainfall treatments.

	Species	Ambient Rainfall			Reduced Rain		
		Ω	θ	Predicted Coexistence?	Ω	θ	Predicted Coexistence?
Coexist in ambient but not reduced rainfall	AC-HO-PL	0.050	8.81	yes	0.000	15.87	no
Coexist in reduced rainfall but not ambient	AC-PL-UR	0.036	11.22	no	0.185	16.79	yes
	FE-PL-UR	0.007	12.67	no	0.154	24.10	yes
	PL-SA-UR	0.091	19.46	no	0.101	28.90	yes
Coexist in neither	AC-FE-HO	0.035	13.06	no	0.028	23.64	no
	AC-FE-PL	0.013	17.38	no	0.071	18.05	no
	AC-FE-SA	0.066	21.12	no	0.065	36.45	no
	AC-FE-UR	0.016	11.56	no	0.141	31.03	no
	AC-HO-SA	0.071	16.12	no	0.010	30.28	no
	AC-HO-UR	0.028	10.63	no	0.004	20.54	no
	AC-PL-SA	0.092	20.18	no	0.210	23.78	no
	AC-SA-UR	0.063	16.69	no	0.069	43.23	no
	FE-HO-PL	0.008	16.88	no	0.024	23.57	no
	FE-HO-SA	0.047	21.89	no	0.045	38.91	no
	FE-HO-UR	0.017	5.73	no	0.141	23.21	no
	FE-PL-SA	0.000	22.57	no	0.114	29.39	no
	FE-SA-UR	0.025	19.09	no	0.035	47.75	no
	HO-PL-SA	0.081	20.96	no	0.030	23.74	no
	HO-PL-UR	0.053	14.88	no	0.033	22.59	no
	HO-SA-UR	0.065	21.00	no	0.028	41.44	no

Table S1.6: Ω, a structural analog of stabilizing niche differences and θ, a structural analog of fitness differences[36] for each species quadruplet, quintuplet and sextuplet, and their predicted competition outcome using the structural method under the two rainfall treatments.

	Species	Ambient Rainfall			Reduced Rain		
		Ω	θ	Predicted Coexistence?	Ω	θ	Predicted Coexistence?
Quadruplets	AC-FE-HO-PL	0.0016	16.96	no	0.0040	20.40	no
	AC-FE-HO-SA	0.0055	19.57	no	0.0078	32.61	no
	AC-FE-HO-UR	0.0018	11.37	no	0.0135	24.16	no
	AC-FE-PL-SA	0.0042	20.20	no	0.0220	27.65	no
	AC-FE-PL-UR	0.0004	14.52	no	0.0251	21.90	no
	AC-FE-SA-UR	0.0053	17.81	no	0.0084	43.18	no
	AC-HO-PL-SA	0.0170	16.36	no	0.0003	22.59	no
	AC-HO-PL-UR	0.0065	10.71	no	0.0003	17.34	no
	AC-HO-SA-UR	0.0058	15.91	no	0.0017	37.20	no
	AC-PL-SA-UR	0.0118	16.90	no	0.0256	32.22	no
	FE-HO-PL-SA	0.0002	21.31	no	0.0073	29.13	no
	FE-HO-PL-UR	0.0008	13.61	no	0.0075	24.77	no
	FE-HO-SA-UR	0.0038	18.11	no	0.0055	44.08	no
	FE-PL-SA-UR	0.0012	18.39	no	0.0142	36.46	no
	HO-PL-SA-UR	0.0123	19.56	no	0.0042	29.53	no
Quintuplets	AC-FE-HO-PL-SA	0.0003	19.35	no	0.0011	26.21	no
	AC-FE-HO-PL-UR	0.0000	14.64	no	0.0017	21.29	no
	AC-FE-HO-SA-UR	0.0002	17.13	no	0.0008	38.16	no
	AC-FE-PL-SA-UR	0.0001	17.53	no	0.0023	34.01	no
	AC-HO-PL-SA-UR	0.0012	15.49	no	0.0001	28.80	no
	FE-HO-PL-SA-UR	0.0003	18.26	no	0.0011	34.14	no
Sextuplet	AC-FE-HO-PL-SA-UR	0.0000	17.26	no	0.0002	31.09	no

Table S1.7: Gravimetric water content (GWC) measured at three different times during the experiment. P-values determined by t-tests for samples on each date.

Date	Ambient Rainfall Mean GWC	Reduced Rain Mean GWC	p-value
March 27, 2019	0.283	0.195	0.00050
April 21, 2019	0.182	0.129	0.00004
May 17, 2019	0.182	0.143	0.01700

Chapter 2

The impact of altered rainfall on flowering phenology in an

annual grassland and its implications for coexistence

Mary N. Van Dyke[1*], Nathan J.B. Kraft[1]

[1.] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los

Angeles, CA, USA

Abstract:

Shifts in the timing of life history events, or phenology, have been recorded across many taxa and biomes in response to global change. These phenological changes are likely to have cascading effects on biotic interactions and community structure, but untangling the realized demographic consequences of these shifts is challenging. Focusing on an annual grassland plant community, we examined how experimental changes in precipitation affect flowering phenology in a community context and explore the implications of these shifts for competitive interactions and species coexistence. We found that changes in rainfall shift some species flowering phenology, but sensitivity differed among neighboring species. Four of seven species we studied started and/or peaked flowering earlier in response to reduced water availability. The idiosyncratic shifts in flowering phenology we observed have the potential to alter existing temporal dynamics that may be maintaining coexistence, such as temporal separation of resource use amongst neighbors. We show how rainfall induced phenology changes may have impacted competition outcomes between species pairs due to differences in their response to reduced water availability. More research on the effects of phenology changes on coexistence and the community level repercussions they cause due to changes in competitive interactions is essential for mitigating the impacts of climate change.

Introduction:

The phenology, or timing of life history events such as bird migration, insect emergence, and plant flowering are shifting across the globe because they are sensitive to changes in climate (Parmesan and Yohe 2003, Rosenzweig et al. 2008). Changes in phenology can have far-reaching effects on communities if interacting species respond to climate changes in different ways (e.g. Cleland et al. 2007, Burkle et al. 2013, Ovaskainen et al. 2013, Rafferty et al. 2013, Thackeray et al. 2016, Kharouba et al. 2018), as paleoecology suggests is often the case (Williams et al. 2004, Nogués-Bravo et al. 2018). For example, plants that shift their flowering phenology may have different temporal overlap with their pollinators or predators than previously, which can either reduce or enhance their population growth (e.g. Visser and Holleman 2001, Post and Forchhammer 2007, Burkle et al. 2013, Johansson et al. 2015). Less clear is how within-trophic level interactions such as competition are affected by phenology changes, due in part to the difficulty in quantifying the realized demographic effects caused by phenology changes. In addition, in long term observational studies where phenology changes have been detected, it can often be difficult to identify the factors driving demographic change because of covariance between climate and other factors over time (reviewed in Miller-Rushing et al. 2010). Pioneering studies on flowering phenology have primarily focused on changing temperatures and snowmelt (Forrest et al. 2010, Aldridge et al. 2011, Diez et al. 2012, Ellwood et al. 2013, CaraDonna et al. 2014), but changes in precipitation also have the potential to shift phenologies especially in regions with strong seasonal rainfall or where changes in rainfall are leading to more stressful conditions (Peñuelas et al. 2004, Gordo and Sanz 2010, Matthews and Mazer 2016, Takeno 2016, Shaw et al. 2022, Castillioni et al. 2022). Changes in temperature and precipitation can

also combine to reduce soil moisture, another mechanism shown to alter reproductive phenology (Flores et al. 2023). Progress in this area will require identifying the many potential causes of phenology changes and evaluating how those changes affect demography and community dynamics. Here, we experimentally isolated the effect of rainfall on flowering phenology and examined the possible consequences it could have on communities due to changes in competitive interactions in an annual grassland.

Flowering phenology influences community assembly through species interactions (Rathcke and Lacey 1985, Sargent and Ackerly 2008, E-Vojtkó et al. 2020, Albor et al. 2020), therefore, climate induced changes to phenology are likely to influence future community composition. However, general predictions about the impact can be challenging to make because overlap in flowering time can have context-dependent effects on neighboring plant species. Overlap can lead to competition for pollinators and a greater chance of heterospecific pollen transfer (and therefore reduced fitness), but co-flowering can also benefit species in some cases, such as by increasing per capita pollinator visitation rates (Ims 1990, Elzinga et al. 2007, Mitchell et al. 2009, Liao et al. 2011, James 2023). Flowering phenology can also influence resource acquisition timing leading to indirect competitive interactions between neighboring plants (Gulmon et al. 1983, Nord and Lynch 2009, Kleinhesselink et al. 2022). While overlapping flowering is ubiquitous in communities, so too is the spread of peak flowering times across the growing season, a likely product of temporal niche partitioning (Veresoglou and Fitter 1984, Rathcke and Lacey 1985, Rocha et al. 2005, Wilsey et al. 2011, Craine et al. 2012, Wolkovich and Cleland 2014).

Modern coexistence theory asserts that fluctuations in resources and climate over time can be an important driver of coexistence in communities (Brown 1989, Chesson 2000, Adler et al. 2006). Therefore, exploring how phenology responds to climatic variation and its effect on plant coexistence will help us better understand the consequences climate change might have on interacting plants and communities. We utilized an annual grassland community in Southern California where a Mediterranean climate of cold, wet winters and hot dry summers constrain the short growing season. Climate, in particular rainfall, is extremely variable in this system and is predicted to become even more volatile, including a higher percentage of extreme dry seasons and wet seasons expected in the future (Diffenbaugh et al. 2015, Swain et al. 2018). This increased volatility could have significant impacts on plant dynamics if changes in water alter temporal dynamics between neighboring plants. Several studies have shown that germination phenology is affected by the timing of early season rains and that earlier germinates often end up with a competitive advantage against neighbors (Chu and Adler 2015, Usinowicz et al. 2017, Hallett et al. 2019, Perez-Ramos et al. 2019, Blackford et al. 2020). Flowering phenology has also been linked to coexistence outcomes in herbaceous plant communities (Godoy and Levine 2014, Kraft et al. 2015, Alexander and Levine 2019, Johnson et al. 2022, James et al. 2023), indicating that shifts in flowering phenology have the potential to alter coexistence. However, it is more difficult to experimentally manipulate than germination so its role in coexistence outcomes is less understood.

The annual plant species at our study site generally flower at the height of their vegetative growth and die soon after, leading to pulses of resource acquisition activity that shape the competitive dynamics (Gulmon et al. 1983, Mooney et al. 1986, Kleinhesselink et al. 2022,

Levine et al. 2022). Most annuals in this climate germinate with the onset of the rainy season and senesce sometime in the following months as precipitation wanes. The timing of rainfall events also influences Nitrogen and other resource availability in the soil and flowering phenology can influence species' ability to take advantages of those pulses of available nutrients (James et al. 2006, Mauritz et al. 2014). The relative timing of species flowering within the growing season is often correlated with functional traits that determine species life history strategies (Molau 1993, Kraft et al. 2015, Wang et al. 2020). For example, species that flower earlier in the season may invest in faster growth while those that flower later, may invest in more drought resistant traits such as deeper roots. The spread in peak flowering phenology among neighboring species therefore results in different resource acquisition needs and abilities during their lifespans, which may in turn contribute to the maintenance of biodiversity through temporal separation in resource use.

Our study aims to explore how variation in yearly rainfall affects flowering phenology among neighboring species and discern the potential implications that species specific sensitivity to rainfall changes could have on community composition in future climates. We focus on the effects of decreased rainfall during the growing season and hypothesize that species will flower earlier in years with less rain because water limitation will force them to senesce earlier. The phenological sensitivity to rainfall changes or the amount of time they shift may not be the same for all species, however, which could have cascading effects on community dynamics. While any climate change study of this sort could have many potential outcomes, we attempted to bracket the range of possible outcomes with four characteristic scenarios of how communities may respond phenologically and their potential to affect competing species interactions (Figure 2.1).

First, all species could flower earlier, shifting by similar amounts which would shift the entire growing season earlier but not alter the relative timing between competing species, and thus may not disrupt temporal coexistence mechanisms. Second, there could be a correlation between species' historical average phenology and their sensitivity to change, such that later flowering species could be more phenologically sensitive than earlier flowering ones, as later flowering species are required to live longer into the drier season and will therefore experience more drought time than earlier flowering species (Figure S2.1). This would constrict the growing season and cause later season species to overlap more in their flowering time than previously. Third, species may also have idiosyncratic phenological sensitivities with no clear pattern resulting in increases in overlap between some species and decreases in overlap between others. These three scenarios all assume species' flowering phenology shifts uniformly across their duration (the shape of the phenopase curve does not change), however, studies have shown this is not always the case (ex. CaraDonna et al. 2014, Jiang et al. 2016). Scenario 4 shows the possibility that some species shift their flowering start or duration without shifting their peak or vice versa. Scenarios 2, 3, and 4, or some combination of them, could alter competitive interactions between neighboring plants as flowering overlap between species changes and disrupts historical temporal patterns (Figure 2.1). Specifically, we asked, Q1) Do neighboring species' flowering phenologies change with changes in growing season rainfall? Q2) If they change, are they changing by the same magnitude and direction? We discuss the consequences of these questions on the potential impact on species competition and coexistence.
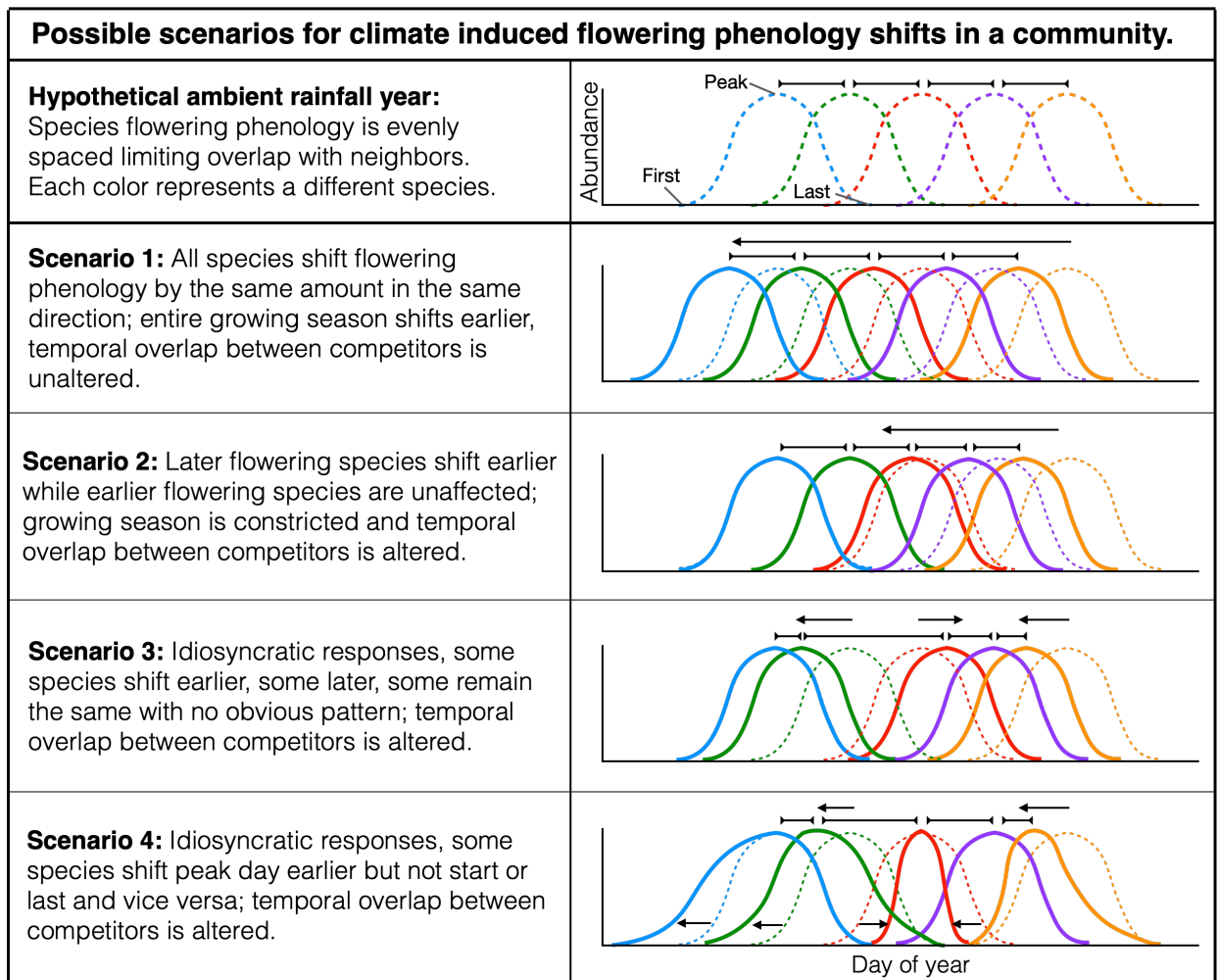
Figure 2.1: Conceptual figure showing possible deviations in flowering phenology from an average year to a year with less water in a hypothetical community of five species where each color represents a species' flowering phenophase curve.

Methods:

Field Experiment and Data Collection

The experiment took place at the University of California, Santa Barbara's Sedgwick Reserve in Santa Barbara County, USA (34° 40′ N, 120° 00′ W, 730m above sea level). Twenty 0.75m*0.75m plots were established in October 2019 in a fenced area designed to exclude deer and gophers, the two primary mammalian herbivores in the system. The plots were paired into ten blocks. Each plot was sown with the same seed mixture of 17 annual plant species with an aim of producing 100 germinants per species. Seed viability was determined for each species prior to planting using established methods which informed the number of seeds of each species added to the mixture (Kraft et al. 2015). Due to the inherent year to year variation in rainfall in our system, only 7 species germinated and survived at high enough densities for the purposes of our analyses and are the focus of the results here. The latest flowering species, *Navarretia atractyloides,* had far fewer individuals in the plots than the other six species, though this is consistent with our observations that later phenology species tend to achieve larger sizes and occur at lower densities.

Cameras (Meidase Trail Camera SL122) were mounted above each plot to take daily photos of the plots. Rain reduction shelters designed to divert 50% of incoming rain (Yahdjian and Sala 2002) were placed over five of the blocks and therefore half of the plots on February 8, 2020. This timing allowed all plants to germinate and establish with the same ambient rainfall conditions, resulting in the rainfall exclusion treatment impacting just the growth and reproduction phase of the plants' life cycle. Ultimately the ambient plots received 398mm of rain

and the sheltered plots received 283mm from October 2019 to August 2020 when our monitoring ended (cumulative rain at the peak flowering day for each species is shown in table 2.2, and figure S2.1).

The plots were visited in person and surveyed for flowers every two weeks throughout the spring of 2020 as COVID restrictions on research allowed. Number of individuals and number of flowers for each species in each plot were counted at each visit. Due to COVID restrictions on access to the site in Spring 2020, photos were then used to interpolate between in person visits of the seven most abundant and most visible species (see Table 2.1). We used daily pictures to identify flowering windows (first day of flowering to last). We then counted the number of flowers in the photos over that time period avoiding images that were obscured by condensation, rain, wind, or camera movement. This resulted in counts of open flowers approximately every 1 to 5 days for each species during their flowering period. Due to challenges in image resolution, in some species we recorded composite flowers, clusters, or spikelets as a single flower, even though they are anatomically made up of multiple small flowers (see Table 2.1 for details). While this would compromise comparisons of total flower production across species, it should not impact our goal of assessing peak phenology for each species under the two treatments.

Table 2.1: Study species with their family and abbreviation codes for figure labels, as well as details about how flowering phenology was recorded.

Family	Species	Label	Flowering phenololgy methods details:
Plantaginaceae	*Plantago erecta*	PLER	Flower cluster recorded as 1 flower when flower structure had developed and was more than 50% green.
Asteraceae	*Lasthenia californica*	LACA	Composite flowers recorded as 1 flower.
Asteraceae	*Uropappus lindleyi*	URLI	Composite flowers recorded as 1 flower.
Fabaceae	*Acmispon wrangelianus*	ACWR	Individual flowers recorded.
Poaceae	*Festuca microstachys*	FEMI	Spikelets recorded as one flower when they were more than 50% green.
Poaceae	*Hordeum murinum*	HOMU	Spikelets recorded as one flower when they were more than 50% green.
Polemoniaceae	*Navarretia atractyloides*	NAAT	Flower cluster recorded as 1 flower.

Statistical Analyses

In order to assess phenological responses to changes in rainfall, we fit flowering phenophase curves for each species using statistical methods from Edwards and Crone (2021). Specifically, we fit Gaussian curves to each species' flowering period using generalized linear mixed models with a negative binomial distribution (Flower abundance ~ Treatment + Day of year:Treatment + Day of year^2:Treatment + 1|block/plot, using the glmmTMB package in R). This allowed us to model each species' flowering phenology and identify key phenological metrics from the parameters of the fitted Gaussian curve. These metrics include peak flowering day (μ of the Gaussian curve, equivalent to the 0.5 quantile), as well as the shape of the flowering curve (the standard deviation of the curve). Because first flowering dates are often difficult to measure and detect (Miller-Rushing et al. 2010), Edwards and Crone defined the first flowering date as the 0.1 quantile of the Gaussian. Flowering duration was measured as the number of days between the 0.1 and 0.9 quantiles (Edwards and Crone 2021). Following their method, we used parametric bootstrapping to estimate 95% confidence intervals around each of

the phenological metric parameters (Table 2.2), as well as the difference in metrics between treatments (Figure 2.2C).

In addition to our single species measures described above, we also calculated species pairwise phenological overlap to see how it was influenced by our rainout treatment. Following previous studies (Fox 2003, Miller-Rushing et al. 2010, Rivest et al. 2021), we calculated the area which two standardized curves overlap by summing the minimum number of flowers open of two overlapping species (ex: a and b) at each time t (0.1 day increments) from the first day of flowering to the last. We standardized the curves by dividing the number of flowers open at each time increment (a_i) by the total number of flowers summed across all increments ($\sum a$). This standardizes the total area under each species curve to one (figure S2.2), so we find an overlap value between 0 (indicating no overlap) and 1 (indicating complete overlap). We did this for each possible pair of species and assessed how they differed between treatments (Figure 2.3). We used the same bootstrapping technique to estimate 1000 potential overlap calculations for each pair and took the mean and 95% confidence intervals to compare them between treatments (Figure 2.3).

$$\text{Overlap}_{ab} = \sum_{i=1}^{n} \min\left(a_i / \sum a, b_i / \sum b\right) \qquad [1]$$

Results:

The fitted phenophase curves show that most of the species shift their flowering time earlier in the reduced rain plots, as hypothesized, though the degree of shift varied across species. On average first day of flowering shifted 4.5 days earlier in the reduced rain treatment (ranging from 1 to 7.8 days) and species peak flowering day shifted 3.3 days earlier (ranging from 0.2 to 7.2 days). Specifically, *Lasthenia californica, Uropappus lindleyi* (native forbs), and *Hordeum murinum* (non-native grass) started flowering earlier in the reduced rain plots having non-overlapping 95% confidence intervals for their first day metric between treatments (Figure 2.2a, 2.2b, Table 2.2). Although if we take the difference in first flowering date between treatments for each bootstrap, only *Plantago erecta* (native forb) has a 95% confidence interval which does not cross zero (Figure 2.2c). *P. erecta, U. lindleyi* and *H. murinum* also had non-overlapping 95% confidence intervals for peak flowering day in both treatments (Figure 2.2a, 2b, Table 2.2) and differences with 95% confidence intervals that do not cross zero (Figure 2.2c). Only *Festuca microstachys* (native grass) did not show any evidence of shifting flowering time with treatment. The other two species, *Acmispon wrangelianus* and *Navarretia atractyloides* (native forbs) trended earlier but their 95% confidence intervals for first day and peak day shifts overlapped (Figure 2.2, Table 2.2). Many species appeared to flower slightly longer in the reduced rain plots but none of the durations had non-overlapping 95% confidence intervals (Figure 2.2, Table 2.2).
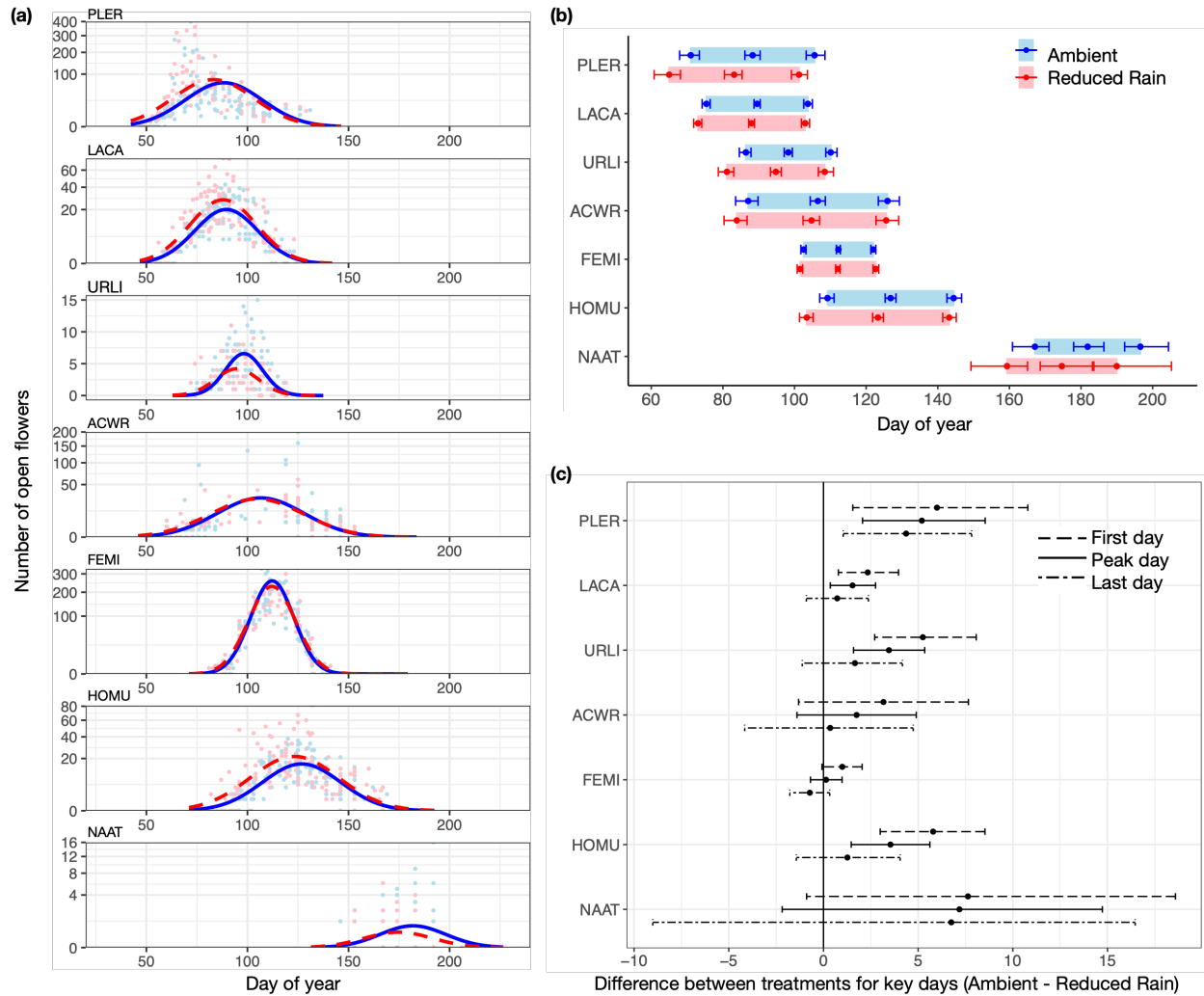
Figure 2.2: (a) Individual species phenophase curves for each treatment with recorded flower counts. Standardized versions of the phenophase curves are shown in figure S2.2. (b) Flowering duration with points derived from the Gaussian phenophase curves that correspond to average first flowering date, peak flowering date, and last flowering date for each species in each treatment. (c) Average difference in days between the two treatments for first, peak and last flowering day. All error bars represent 95% confidence intervals from parametric bootstrapping. See table 2.1 for species codes.

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Table 2.2: Phenological metrics calculated from fitted Gaussian curves for each species in each treatment and the cumulative amount of rain that had fallen since October 2019 at the time of each species' peak flowering day. 95% confidence intervals for each metric are in parentheses. Stars indicate confidence intervals do not overlap between treatments. See Table 2.1 for species codes. (a) shows results from the ambient plots, (b) shows results from the reduced rain plots.

(a)

Species		Ambient Rain				
	First		Peak		Duration		Rainfall at peak
PLER	71.0	(67.9-73.4)	88.3*	(86.1-90.4)	34.6	(31.7-38.4)	307.3
LACA	75.4*	(74.2-76.4)	89.6	(88.7-90.4)	28.3	(26.9-30)	307.3
URLI	86.4*	(84.6-87.9)	98.3*	(97.1-99.4)	23.7	(21.8-26.3)	373.1
FEMI	102.5	(101.8-103.2)	112.2	(111.7-112.8)	19.4	(18.6-20.4)	395.7
ACWR	87.0	(83.5-89.8)	106.5	(104.4-108.6)	38.9	(35.3-43.8)	395.2
HOMU	109.2*	(107-111)	126.8*	(125.3-128.3)	35.2	(32.8-38.3)	395.7
NAAT	167.1	(160.9-171)	181.8	(177.9-186.4)	29.4	(24.6-39.3)	398.3

Units: First and Peak refer to the day of year. Duration is number of days. Rainfall is in mm, cumulative total since October, 2019.
* Metric has non-overlapping 95% confidence intervals between treatments

(b)

Species	First		Peak		Duration		Rainfall at peak
PLER	65.0	(60.8-68.2)	83.1*	(80.4-85.4)	36.3	(33.2-40.5)	236.9
LACA	73.0*	(71.8-74.1)	88.0	(87.2-88.8)	29.9	(28.5-31.6)	237.5
URLI	81.1*	(78.7-83)	94.8*	(93.3-96.3)	27.3	(24.8-30.9)	237.5
FEMI	101.5	(100.7-102.3)	112.1	(111.5-112.7)	21.1	(20.3-22.2)	281.7
ACWR	83.9	(80.3-86.7)	104.7	(102.4-107)	41.7	(38-46.7)	281.4
HOMU	103.4*	(101.4-105.2)	123.3*	(121.8-124.8)	39.8	(37.6-42.3)	281.7
NAAT	159.3	(149.3-165.1)	174.6	(168.6-183.2)	30.7	(24.1-49.4)	283.0

Units: First and Peak refer to the day of year. Duration is number of days. Rainfall is in mm, cumulative total since October, 2019.
* Metric has non-overlapping 95% confidence intervals between treatments

Flowering phenology overlap between species pairs was also affected by the treatment. Fourteen of the 21 species pairs had an average greater overlap in the reduced rain plots than in the ambient rain plots although only four of these had overlap differences with 95% confidence intervals that did not overlap zero (Figure 2.3a). The largest change in a species pairs' overlap was found between the two grass species, *F. microstachys* and *H. murinum* which overlapped 11% more in the reduced rain plots than the ambient plots (Figure 2.3b).
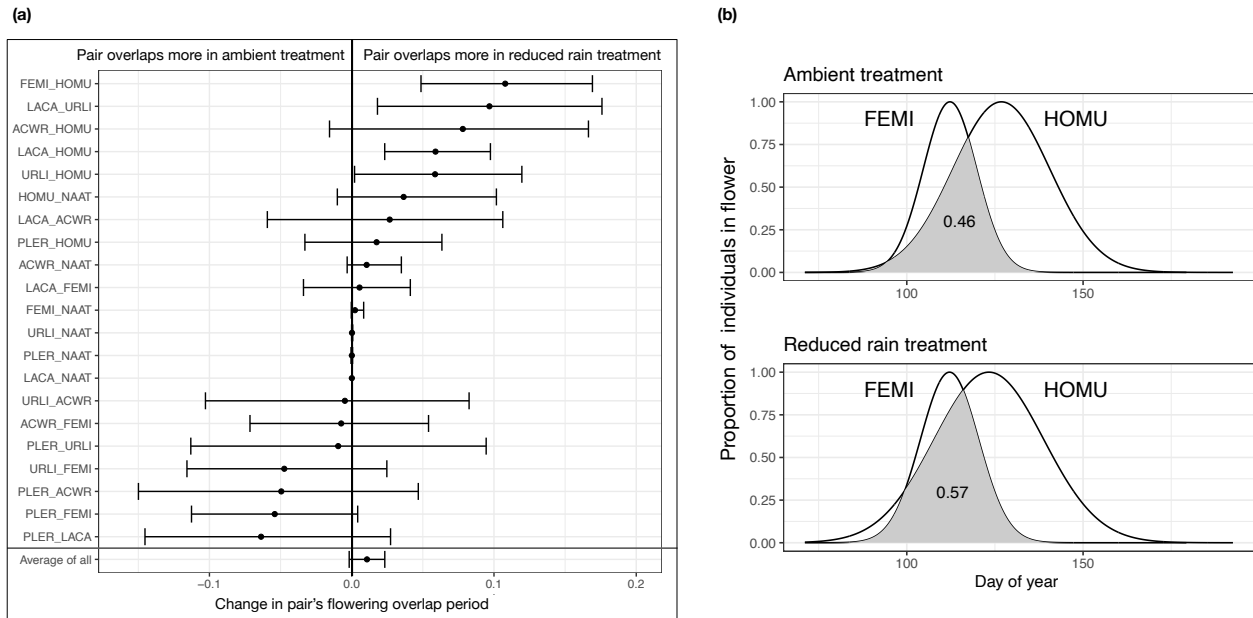
Figure 2.3: (a) Difference in phenological overlap between treatments for each possible pair of species. Positive points right of the center line, indicate the pair's overlap increased in the reduced rain treatment. Negative points indicate the pair overlapped less with the reduced rain treatment. Error bars represent 95% confidence intervals around the mean difference generated from parametric bootstrapping. (b) Example showing overlapping standardized phenophase curves of the two grasses *F. microstachys* and *H. murinum* in each treatment.

We found no evidence that species which historically flowered later in the season were more sensitive to rainfall changes and altered their phenology more than species which historically flower earlier in the season (scenario 2, figure 2.1). Correlation tests between ambient flowering time and the number of days species shifted in both their first and peak flowering days were not significant (figure S2.3).

Lastly, we examined the number of flowers produced by each species in each treatment. Using classic Student t-tests, we found that the flower counts between treatments were no different for all 7 species (figure S2.4) meaning treatment did not influence species flower production total.

Discussion:

Climate change has substantial potential to disrupt ecological processes and alter the composition of natural communities. While the consequences of global change have already begun to influence the natural world, it can be difficult to quantify the aggregate outcomes of all the changes occurring on species demography and community dynamics. Here, we show that changes in rainfall alone can alter flowering phenology in species-specific ways that have the potential to affect competitive interactions. The differences in phenological response to rainfall changes are a potential threat to temporal coexistence dynamics that may be essential for maintaining diversity in plant communities.

Our results find that four of the seven species in our experiment (*P. erecta*, *L. californica*, *U. lindleyi* and *H. murinum*) flowered earlier in the reduced rain treatment with two others trending earlier (*A. wrangelianus*, *N. attractyloides*). Only *F. microstachys* seemed unresponsive to the treatment. There was some variation in the shape of the phenophase responses (Figure 2.1, scenario 4). Figure 2.2c shows the differences between first, peak, and last day metrics for each

species, and while no individual species shifted one of these days significantly more than the other, the last day didn't change for three of the species whose first and peak days did. Flowering duration was relatively unchanged but trended shorter in the ambient treatment (Table 2.2). The shifts may seem minor, but the result that species exhibit different levels of phenological sensitivity to rainfall alone could have consequential effects on community dynamics. Our experimentally imposed rainfall treatment was relatively mild, especially for the earlier flowering species as the total difference in rain between treatments increased with time (Figure S2.1). Rainfall data from the past 60 years at our field site show that the difference between our treatments is only about 13% of the actual range in yearly rainfall at this site (220mm to 1131mm), with both our treatments below average (541mm). A year with much more or much less rainfall could amplify the differences between species responses altering their overlap even more (See supplemental materials and figure S2.5 for demonstration of this).

We did not find evidence that later flowering species shifted their phenology more in response to rainfall changes as we originally hypothesized but instead found no obvious pattern (Figure S2.3). Our results most closely match scenarios 3 and 4 from figure 2.1. Because species do not respond to changes in rainfall in the same way, flowering overlap between species pairs will be altered, changing the competitive environment. Species that overlap more in time in the reduced rain scenario could be driven to no longer coexist and temporal niche space could be created that allow another species to expand or invade (Wolkovich and Cleland 2011). For 14 of the 21 species pairs, average flowering time overlap increased in the reduced rain treatment, consistent with these scenarios (Figure 2.3).

Given that species phenology responds to rainfall changes in species-specific ways, the next step is to explore the consequences of this for coexistence. In our system, we know competitive interactions are affected by changes in water availability, but the exact mechanism of these changes is unknown (Van Dyke et al. 2022). In a previous experiment, we parameterized a population growth model that predicted whether pairs of species could coexist long-term under a similar reduced rain and ambient rain treatment (Van Dyke et al. 2022). Given our results here, we suspect changes in flowering phenology may play a role in the changes in competitive outcomes that we found. To explore this, we analyzed the 5 species that were used in common in both experiments, and found that the more different two species' phenological responses to rainfall changes are from each other, the more likely their competitive interaction changed between rainfall treatments (t-test with the ten species pairs, Figure S2.6). We used the difference in the average number of days peak flowering shifted and the average number of days first flowering shifted, as measures of the difference in phenological response. For example, *F. microstachys* and *H. murinum* differed in their phenological response, with *F. microstachys'* peak flowering time shifting earlier by an average of 0.1 days in response to reduced rainfall and *H. murinum*'s peak flowering time shifting earlier by an average of 3.5 days (Table 2.2, Figure 2.2). We found that the more different these average shifts are between species, the more likely their competitive outcomes changed between treatments (Figure S2.6). *F. microstachys* and *H. murinum* were predicted to coexist in the ambient treatment but *H. murinum* is predicted to outcompete *F. microstachys* in the reduced rain treatment, where our results show their flowering time would overlap more. For 6 of the 7 pairs whose coexistence outcome changed in our previous experiment, the pair is predicted to coexist in the treatment where their flowering time

overlaps less.

Our results show that changes in water availability alone can affect flowering phenology in this Mediterranean annual grassland community. Reduced rainfall does not affect all species the same way, however, which impacts the extent to which neighboring species overlap in their timing of resource use and flowering periods. Therefore, the ability of neighboring species to continue to coexist long-term and the current composition of communities may be threatened as the climate continues to change. It is well documented that flowering phenology is changing all over the world but the effects on competitive dynamics between neighboring species and the resulting demographic impacts on communities are not well-understood and is an exciting and critical avenue for future research.

Supplementary Materials:

Phenological sensitivity:

We estimated the phenological sensitivity of each species to changes in rainfall by taking the average change in peak flowering time between treatments divided by the difference in rainfall at peak flowering time.

(μ ambient – μ reduced rain) / (total rainfall at μ ambient – total rainfall at μ reduced rain)

We obtained rainfall data from our field site for the past 60 years and determined the average cumulative rainfall per growing season (September to September) is 541mm. The driest year on record was 2006/2007 where 220mm of rain fell and the wettest year was 1982/1983 where 1,131mm of rain fell. The ambient plots in our experiment received 398mm of rain and the reduced rain plots received 283mm. Our treatment, therefore, covered just a small portion of the possible range of rainfall at this site and both treatments were below average. Using the sensitivity estimations, we projected phenophase curves for each species in a hypothetical dry year, average year, and wet year in addition to our two treatments (Supplemental figure 5). It is clear that overlap between species is very different in the three hypothetical years because differences in species sensitivity to the changes in rainfall results in greater overlap changes when rainfall levels are more extreme.
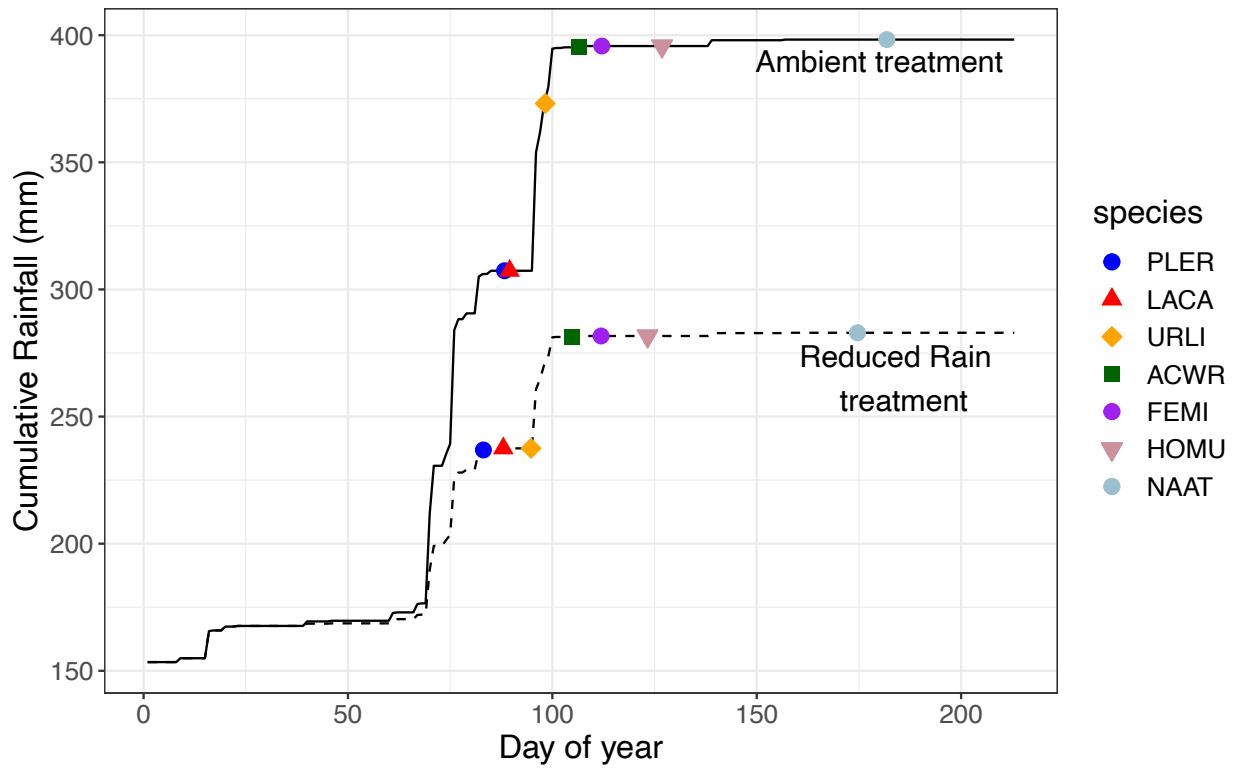
Supplemental Figures:

Figure S2.1: Cumulative amount of rain fallen in the ambient and reduced rain plots. Dots show peak flowering day for each species in each treatment. Note that total difference in rainfall received between treatments increases for later phenology species.
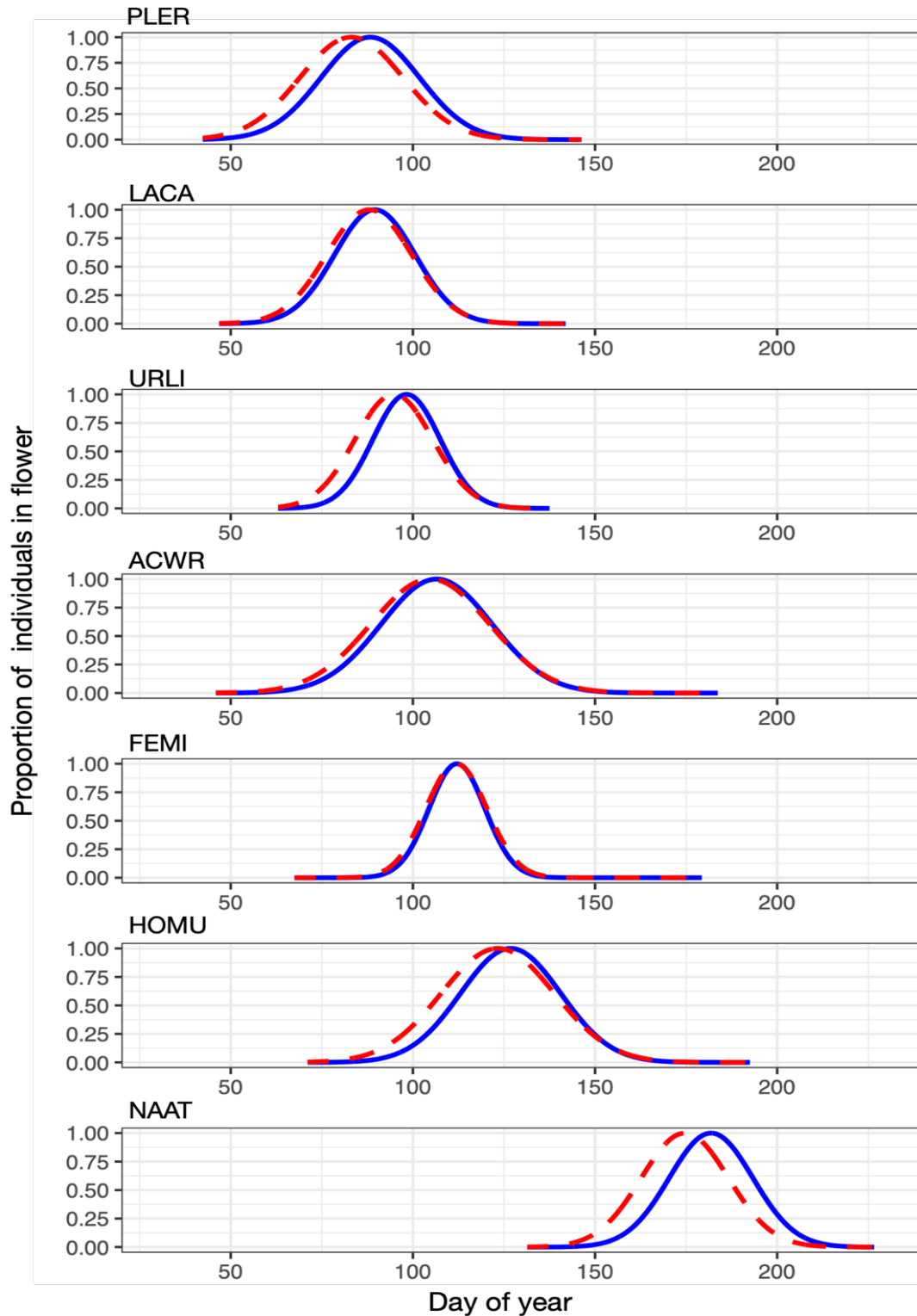
Figure S2.2: Standardized phenophase curves for each species under each treatment. Blue lines show curves from ambient plots, red dashed lines show curves from reduced rain plots. Standardizing in this way was a first step in assessing flowering period overlap between species pairs.
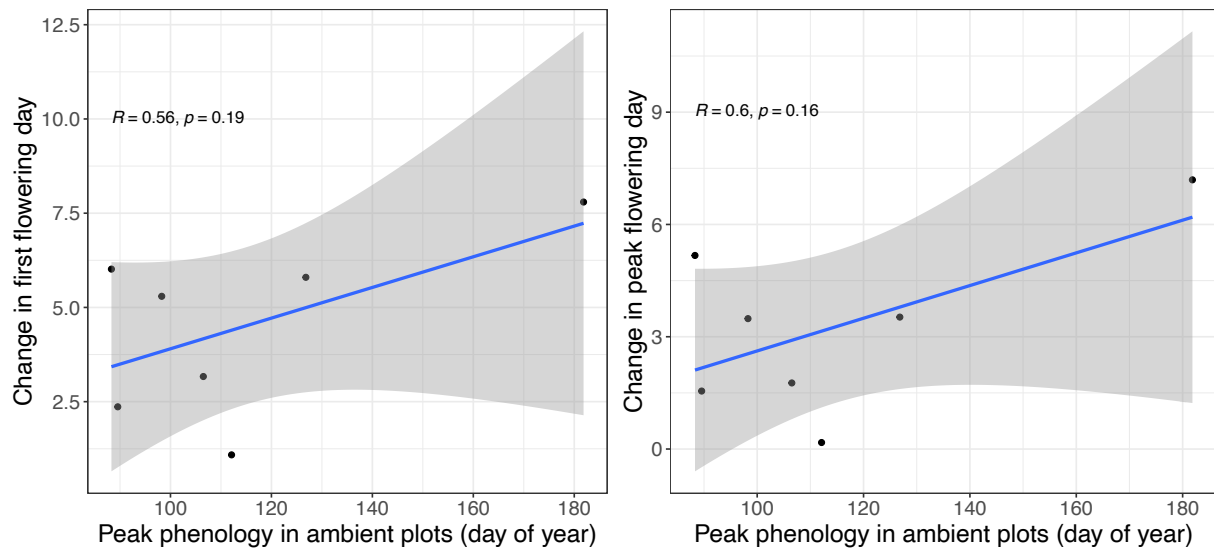
Figure S2.3: Examining relationship between average peak flowering day and the average number of days species shifted their first and peak flowering day. Neither are significant meaning later flowering species are not more likely to shift their flowering phenology as hypothesized in scenario 2 in figure 1.
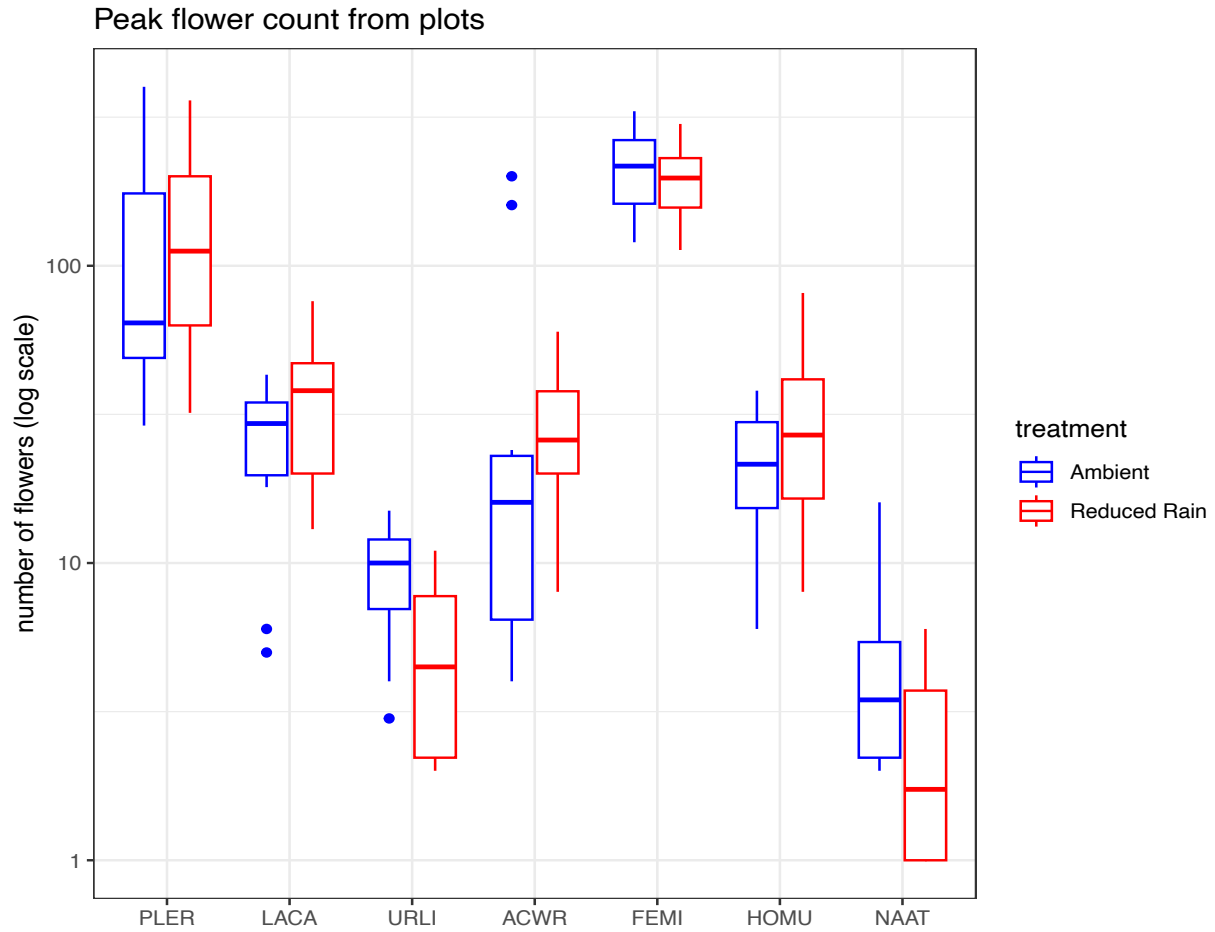
Figure S2.4: Peak flower counts from each species in each treatment of ten plots. Students t-test of 10 peak counts from each treatment show no significant difference for any of the species.
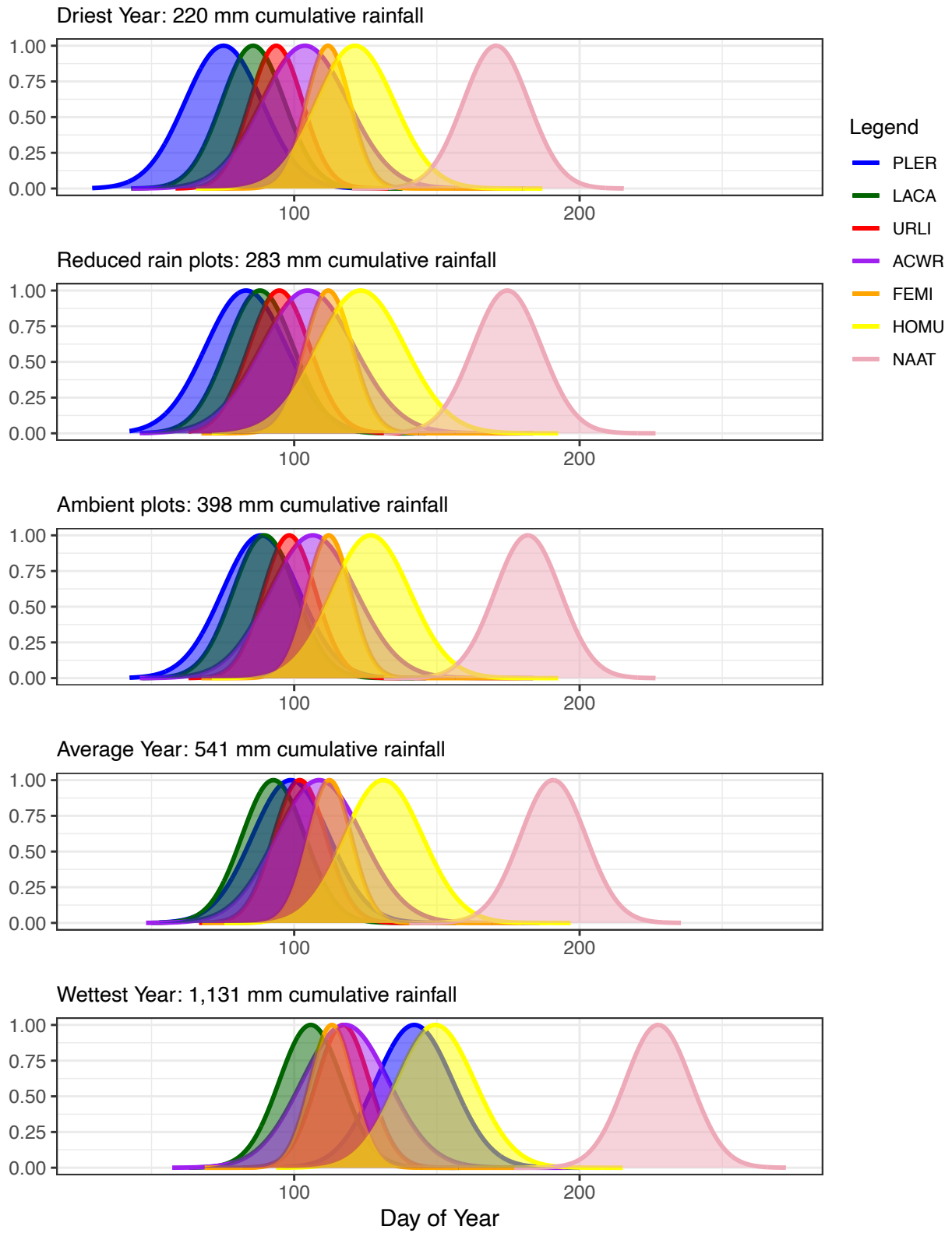
Figure S2.5: Projected phenophase curves using estimated sensitivities for each species for three hypothetical years with different rainfall as well as for our two treatments.
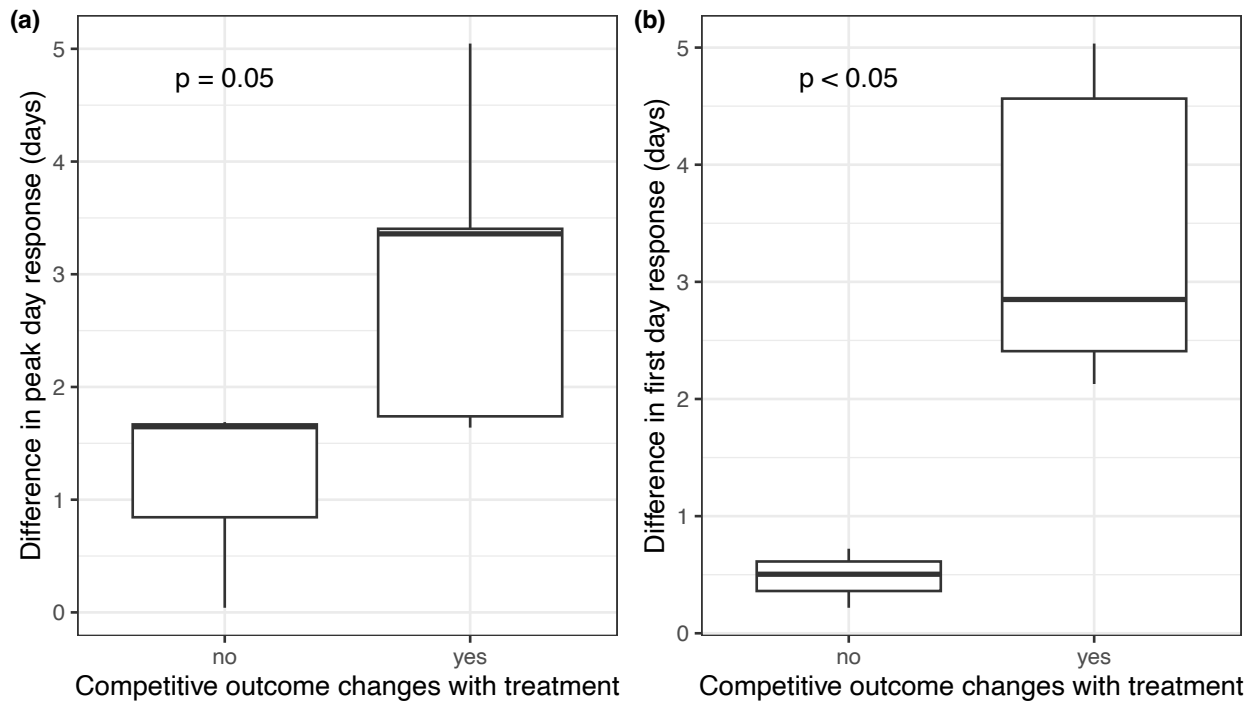
Figure S2.6: Boxplot with the difference between a species pair's response to treatment in terms of their shift in peak and first flowering day vs. whether that pair's competitive interaction changed with treatment (Student's t-test).

Chapter 3

California annual plant species with more similar functional traits have stronger correlations in demographic responses to long-term variation in climate: implications for coexistence and global change

Mary N. Van Dyke[1*], Nathan J.B. Kraft[1]

[1.] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, USA

Abstract: The processes that shape diversity have long been of interest in ecology, but progress on this question has become more critical as biodiversity is threatened by climate change. One future consequence is that precipitation is generally expected to become more irregular with higher incidences of extremes which may have profound effects on plant coexistence. Modern coexistence theory suggests that coexistence mechanisms, such as the temporal storage effect, may be important in communities experiencing fluctuating abiotic conditions, and therefore understanding these phenomena can help predict how communities will respond to future variability. To examine the effects of temporal variation in abiotic conditions on coexistence, we studied an annual grassland community that experiences high interannual variation in precipitation. We found that species demographic rates from the last 15 years, including germination rate and low-density fecundity, are rarely strongly positively correlated with other species in the community, indicating that species differ in which years they perform best, and therefore likely specialize on distinct abiotic conditions. Variation in response to interannual differences in rainfall concentrates intraspecific interactions relative to interspecific interactions and favors coexistence. Additionally, we found that species differences in functional traits, especially rooting depth, water use efficiency, and leaf nitrogen were well correlated with differences in species demographic responses, such that species with similar traits did best in the same years. Taken together this deepens our understanding of coexistence in the community and provides greater context for how the community may respond to future increases in climatic variability.

Key Words: Coexistence, temporal storage effect, plant functional traits, annual grassland, climate change, variable precipitation

Introduction:

The question of coexistence and how diversity is maintained has long interested ecologists (Hutchinson 1957, Chesson 2000, Levine et al. 2017). As the global climate rapidly changes and we face record losses in biodiversity (Costello et al. 2022), understanding coexistence within communities is more important than ever (Blois et al. 2013, Alexander et al. 2015, Copeland et al. 2016, Harrison et al. 2017). While there has been considerable development of coexistence theory over the history of community ecology (Hutchinson 1961, Macarthur and Levins 1967, MacArthur 1970, Chesson 2000, Amarasekare 2003, Barabás et al. 2018, Ellner et al. 2019, etc.), empirical assessments of species coexistence in natural systems are less common, (e.g. Siepielski and McPeek 2010, but see Angert et al. 2009, Levine and HilleRisLambers 2009, Kraft et al. 2015, Hallett et al. 2019, Wainwright et al. 2019). Pioneering empirical studies have explored the role of temporal fluctuations on coexistence (Angert et al. 2009, Cleland et al. 2013, Usinowicz et al. 2017, Hallett et al. 2019), but few studies have considered the simultaneous impact of multiple coexistence mechanisms at once (but see, Amarasekare 2007, Kuang and Chesson 2010). A major consequence of climate change is that many places on the planet are experiencing a more variable climate with dramatic changes year to year (Begum et al. 2022). Because climate change is altering temporal variability in conditions, it is more critical that we understand how this relates to coexistence in communities in terms of maintaining diversity and operating alongside other coexistence mechanisms that may be important for community stability.

Modern coexistence theory posits that temporal heterogeneity can promote coexistence through the storage effect (Chesson 2000). The storage effect operates if species are favored at

different periods of time and can persist during the times that are not as favorable. This concentrates intra-specific competitive interactions in time, so the most favored species is also experiencing the most competition from conspecifics which promotes coexistence. To know the strength of the storage effect, one needs to know species responses to temporal fluctuations in the environmental factor from a resident and an invader state (Chesson 2000, Adler et al. 2013, Ellner et al. 2016). Obtaining this kind of data from enough species in the community to actually test for the storage effect is a difficult task, however, temporal coexistence mechanisms have been well studied in the Sonoran desert annual community which experiences high levels of precipitation variation. In multiple studies, researchers found that rainfall timing and strength affected germination, survival, and fecundity rates differently for species in the community (Pake and Venable 1995, Angert et al. 2009). Different species are favored during different years and species responses to the inter-annual environmental variability, as well as altered identities and densities of competitors, year to year maintains coexistence. The authors conclude that this is mainly due to a tradeoff between relative growth rate and water use efficiency. Because of inter-annual variability in rainfall, different strategies along this trade-off are favored certain years leading to a range of successful phenotypes and long-term coexistence. While this important work in the Sonoran system shows evidence of the storage effect, we do not know how temporal coexistence mechanisms may act in concert with other coexistence mechanisms to maintain diversity in the semi-arid annual grassland we study.

We hypothesize that similar temporal coexistence dynamics may be occurring in the semi-arid annual grassland system because it experiences similar precipitation variability and consists of plants with similar life history traits. In contrast to the Sonoran system, a previous

study in the same annual grassland calculated stabilizing niche and fitness differences at the neighborhood scale for most of the species pairs included in our study and found that very few of them were predicted to coexist (Kraft et al. 2015). Yet we know they are found on the same landscape, which suggests that there are multiple mechanisms of coexistence operating. This contradictory result therefore makes the annual grassland a compelling community to study how multiple coexistence mechanisms may be operating at once.

To explore the role temporal variation may have in the community, we tested for a critical prerequisite of the storage effect by measuring species demographic performance through time to know whether species differ in their performance across years, which typically arises when species respond to environmental conditions in different ways (figure 3.1a). To explore the functional basis of these responses, we measured key plant functional traits and tested if species with similar functional traits share similar demographic responses to interannual variation in conditions (figure 3.1b). Plant functional traits are easy to measure characteristics of plants that influence growth, survival, or reproduction (McGill et al. 2006, Westoby and Wright 2006). They have the potential to offer mechanistic links between environmental phenomena and ecological processes such as community assembly or coexistence (Cornwell and Ackerly 2009, Adler et al. 2013, Kraft et al. 2015, Kunstler et al. 2016, Kandlikar et al. 2022)
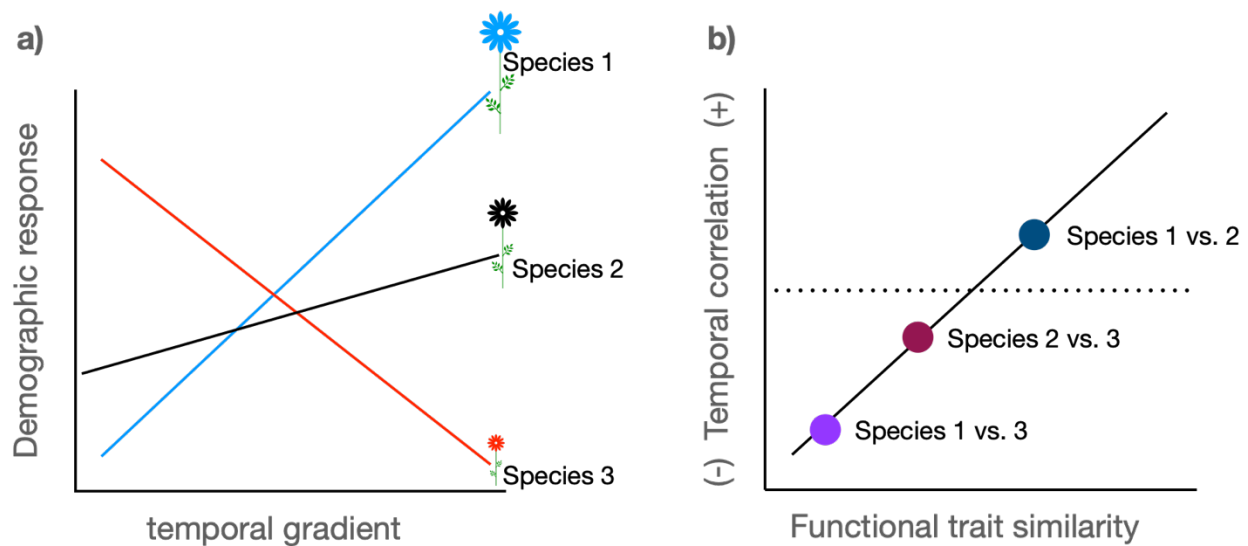
Figure 3.1: Conceptual figure of analyses showing three species (red, blue, black) that respond to temporal variation in an environmental condition differently and a hypothetical functional trait that may explain variation in their response. a) Species' demographic response to an environmental factor that changes with time. b) Each species pair's temporal correlation in demographic response and functional trait similarity. If the trait is explanatory, temporal correlation should increase as trait similarity increases.

We tested for temporal coexistence dynamics in the community by examining two key demographic responses to the environment of several species over many years. We measured germination rate in January of each year and total seed production at senescence from manipulated plots that had no competitors. Since annual plants only live one year, the total seed production was a measure of lifetime fecundity. These two demographic rates (from now on referred to as germination rate and low-density fecundity) are good measures of species direct responses to the environment, uninfluenced by competition. With data collection starting in

2007, we have 16 species with at least 4 years of data and some species with up to 15 years of data (Table 3.1, Figure S3.1). From these measurements we were able to estimate temporal correlation in annual demographic rates for 89 pairs of species. We also measured nine plant functional traits (Table 3.2) for 14 of the species and computed trait similarity indices for all possible species pairs. We chose functional traits that we hypothesized could inform species water use strategies and therefore might explain year to year variation caused by fluctuating precipitation. Specifically, we asked:

Q1. Are all species annual demographic performance rates perfectly positively correlated or is there evidence that species specialize in the community?

Q2. How do plant functional traits predict species responses to temporal heterogeneity in climate?

Table 3.1: Species that are included in the experiment and the number of years we have recorded data from them.

Family	Species	Code	Years of data
Fabaceae	*Acmispon wrangelianus*	ACWR	15
Asteraceae	*Centaurea melitensis*	CEME	4
Asteraceae	*Chaenactis glabriuscula*	CHGL	9
Polygonaceae	*Chorizanthe palmeri**	CHPA	6
Onagraceae	*Clarkia purpurea*	CLPU	4
Euphorbiaceae	*Euphorbia peplus*	EUPE	4
Poaceae	*Festuca microstachys*	FEMI	12
Asteraceae	*Hemizonia congesta spp. Luzulifolia*	HECO	5
Asteraceae	*Lasthenia californica*	LACA	12
Fabaceae	*Medicago polymorpha*	MEPO	4
Asteraceae	*Micropus californicus*	MICA	8
Polemoniaceae	*Navarretia atractyloides*	NAAT	10
Plantaginaceae	*Plantago erecta*	PLER	15
Lamiaceae	*Salvia columbariae*	SACO	15
Fabaceae	*Trifolium willdenovii**	TRWI	6
Asteraceae	*Uropappus lindleyi*	URLI	9

* No functional trait data

Table 3.2: Descriptions of all plant functional traits that were measured and their units.

Trait	Units	Description
Leaf size	cm²	One-sided area of an individual leaf.
Specific leaf area (SLA)	cm^2/g	Area of fresh leaf divided by oven-dry mass.
Leaf nitrogen concentration	mg/g	Total amount of N per unit of dry leaf mass.
Seed mass	g	Oven-dry mass of an average seed of a species.
Rooting depth	cm	Maximum soil depth from which resources can be acquired.
Specific root length (SRL)	m/g	The ratio of root length to dry mass of fine roots - a ratio of acquisition to investment.
Maximum height	cm	Maximum stature a typical mature individual of a species attains in a given habitat.
Phenology (peak fruiting)	day of year	Day of year when more than half of the individuals in a population are bearing fruit.
Carbon isotope composition	$\delta_{13}C$	A measure of intrinsic water use efficiency (WUE).

Methods:

Fieldwork:

The fieldwork for this project took place at the University of California, Santa Barbara's Sedgwick Reserve in Santa Barbara County, USA (34° 40′ N, 120° 00′ W, 730m above sea level). The region experiences a Mediterranean climate with hot, dry summers and warm, wet winters. Germination rate and seed production without competitors was collected for some or all of the species for the past 15 years (2007-2022).

The plants for obtaining the demographic rates grew in plots in the same area of the reserve each year. This area lies between several serpentine rock outcrops and is mainly dominated by invasive European annuals, but all species included in the experiment can be found there. Generally, seeds were collected the spring before they were planted and were exclusively from the reserve. Plots were cleared of plant matter and the top layer of soil to remove any seeds naturally in the seed bank. Germination rate was obtained by recording the number of seeds

sown in each marked designated spot and then counting the number of germinates that emerged in December/January. After establishing, all but one of the germinates was cleared. As those individuals grew the plots were continually cleared of any recruits from the soil to ensure no competition within a ten-centimeter radius of the focal plant. Once individuals had fruited, number of seeds or number of fruits were counted to obtain total lifetime seed production or low-density fecundity. The number of individuals that were averaged each year to obtain those key demographic performance measures of germination rate and low-density fecundity was not consistent, but included a minimum of at least ten germination counts and ten full grown individuals.

Functional traits:

We measured nine key leaf, stem, root, and seed functional traits for each species (see Table 3.2). All functional traits were obtained in years 2011, 2016 and 2019 using standard methods (Pérez-Harguindeguy et al. 2013, Kraft et al. 2015).

Analyses:

All analyses were performed in R version 4.2.0. We compiled data from the 15 years and calculated an average low-density fecundity and an average germination rate for each species each year we had data. We then calculated correlation coefficients (pearson's r) for the two scaled demographic rates for each species pair that had at least three years of overlapping data (89 pairs out of the possible 120 from 16 different species, figure 3.3). We calculated p-values for the correlation coefficients and used the 'Benjamini Hochberg' (BH) method to adjust p-values to account for multiple comparisons (Benjamini and Hochberg 1995).

To answer Q2 concerning whether plant functional traits can explain correlations in species pair's demographic rates, we calculated similarity indices for each species pair for each of the nine plant functional traits of interest. We did this by taking the absolute value of the difference between the two species in each pair and dividing by the maximum difference of that trait between any of the pairs. We then subtracted this from 1 to calculate similarity which therefore ranged from 0 (the least similar pair) to 1 (the most similar pair). We also created a principal component analysis (pca) with all the functional traits and calculated species similarity on the two primary axes (figure 3.4, figure S3.3).

Similarity calculation:

Trait measurement species 1 – trait measurement species 2 = trait difference (d)

Normalized d = d/max(d)

similarity = 1- (normalized d)

We then examined whether pair's trait similarities were correlated with their demographic rate correlations using a weighted correlation calculation (function wtd.cor() in weights package). We weighted demographic correlations by the inverse of the standard deviation of the correlation coefficients between species pairs. Therefore, pairs who had more precise correlation coefficients in their demographic rates counted more toward the correlation coefficient with trait similarity than pairs with more variable demographic correlation coefficients. Lastly, we used the BH method to adjust p-values for multiple comparisons (Benjamini and Hochberg 1995).

Results:

We found substantial variation in species demographic rates across years (figure 3.2), indicating that there was no single year that was best or worst for all species. Of the 89 species pairs that we could calculate correlations for, 8 were significantly positively correlated (p<0.05) in their low-density fecundity measures and 1 was significantly positively correlated in their germination rates (figure 3.3). Both histograms of the species pair's correlation rates are skewed right with more positive correlations, but include strong negative, positive and weak correlations showing a wide range of responses each year (figure 3.3). Taken together these results show that our study system contains species that differ in their demographic responses to interannual variation in conditions.

(a)
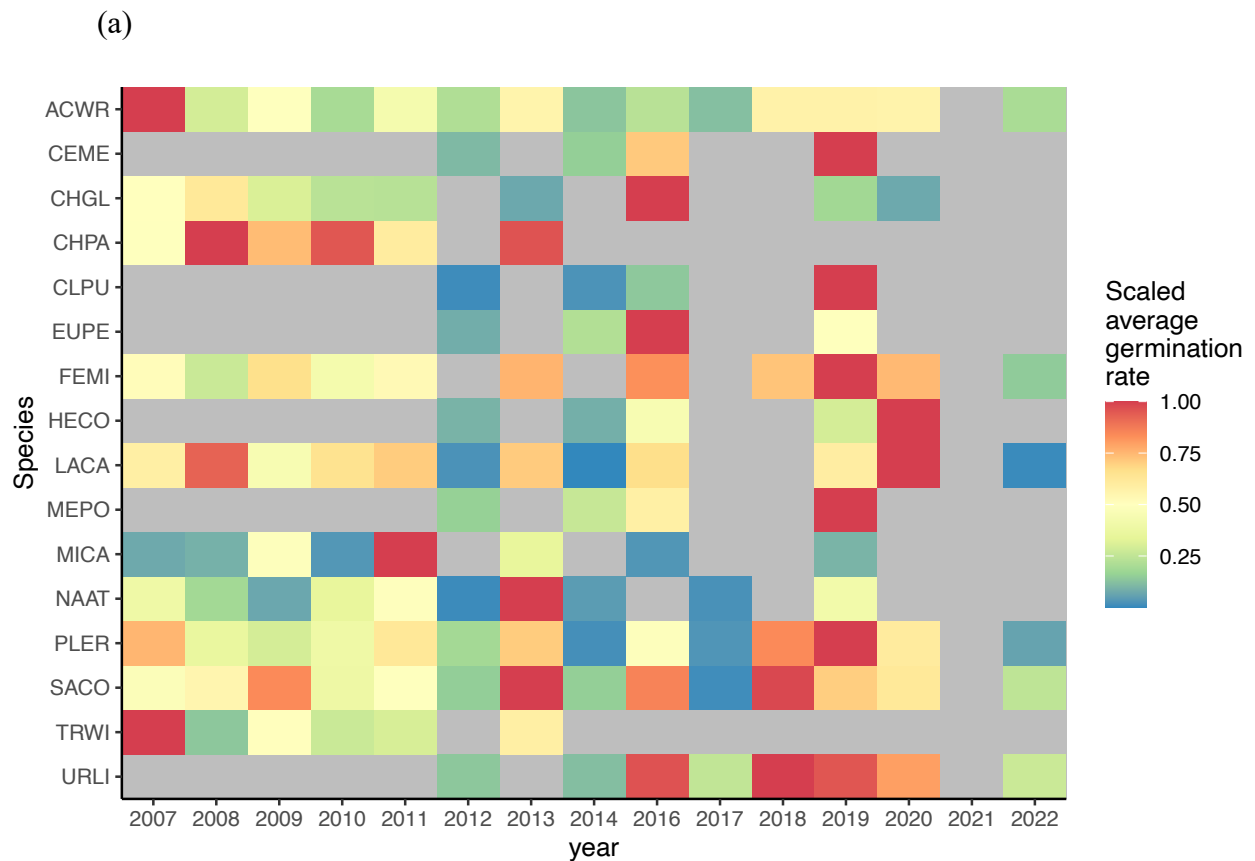
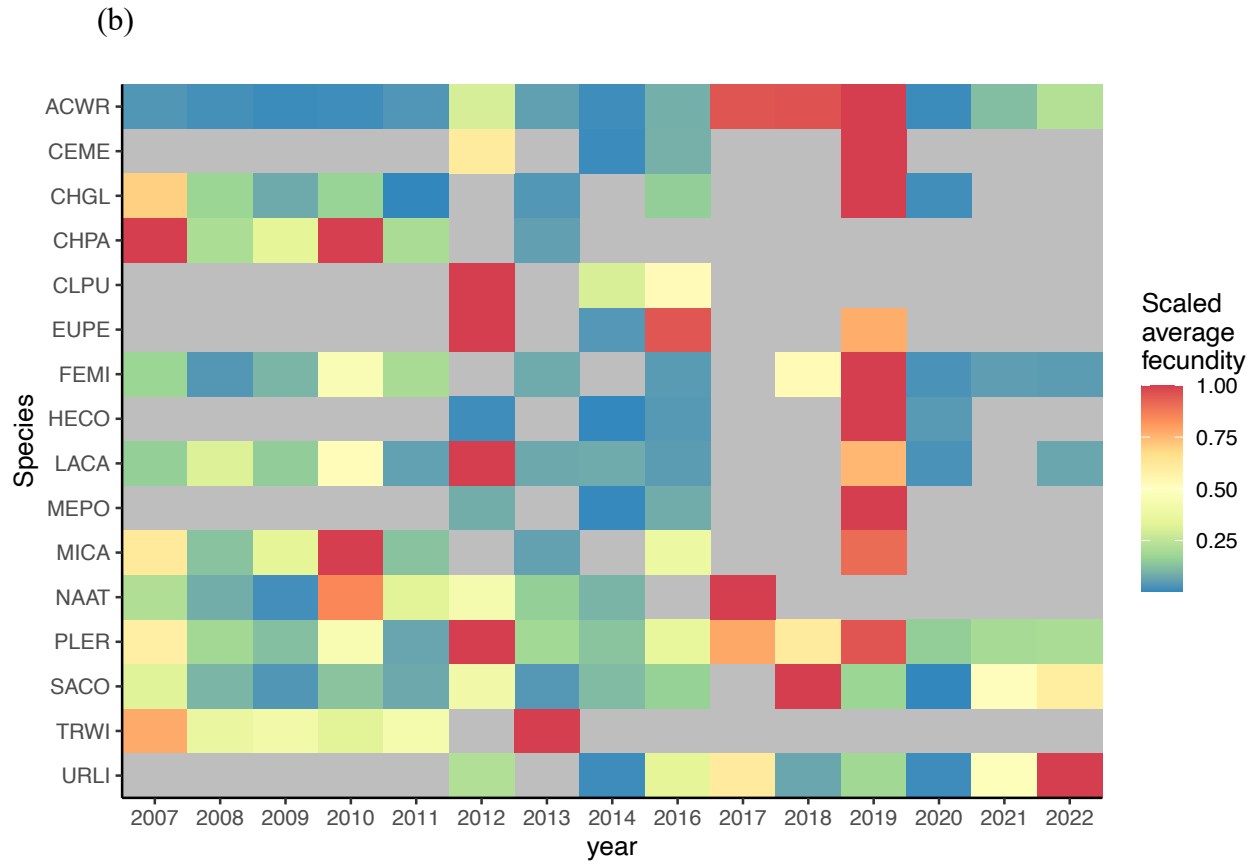Figure 3.2: Scaled average (a) germination rate and (b) low density fecundity over 15 years. In order to visually remove the effect of species differences in average fecundity and germination overall, we rescaled these rates to range from 0-1 by dividing them by each species highest observed rate in the dataset, such that 1 corresponds to their most successful year and zero to their least successful year.
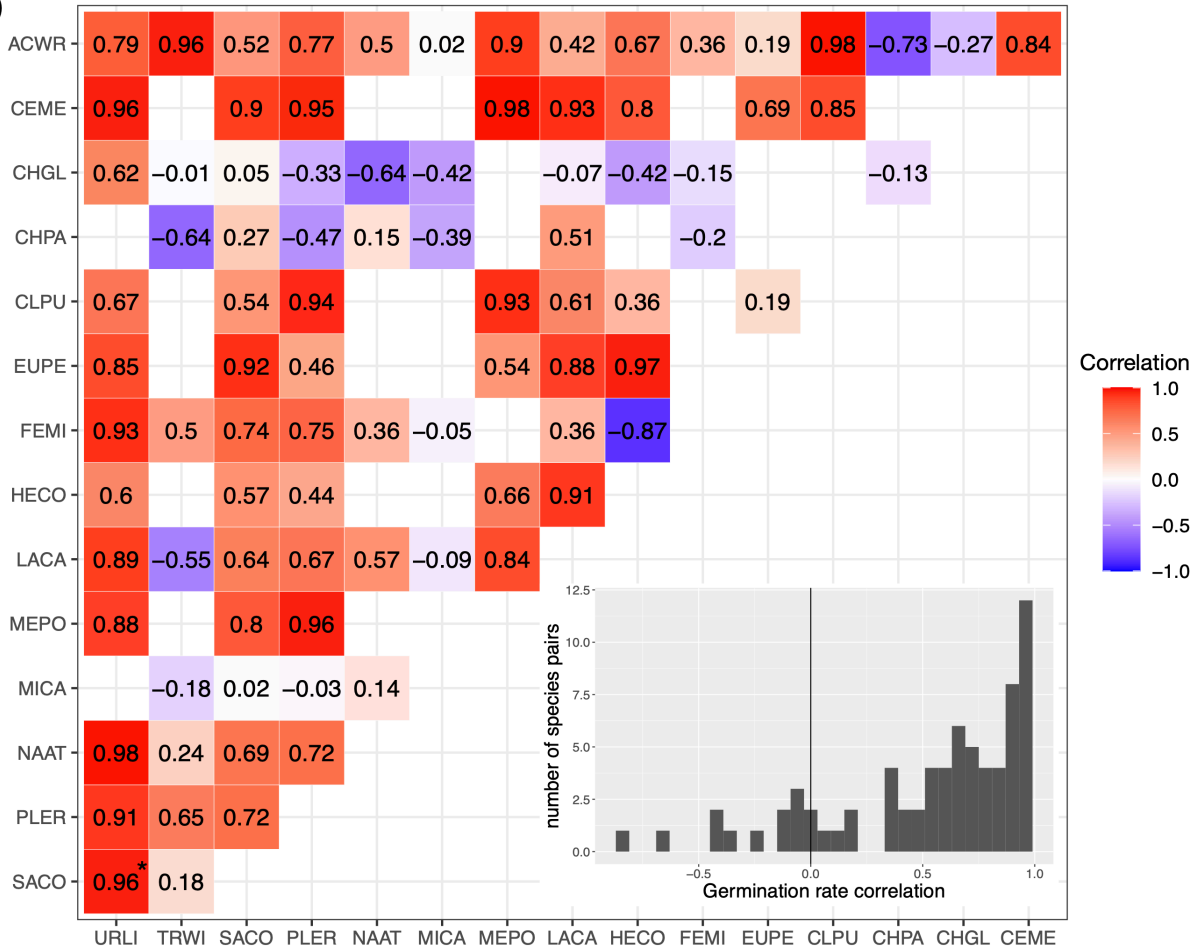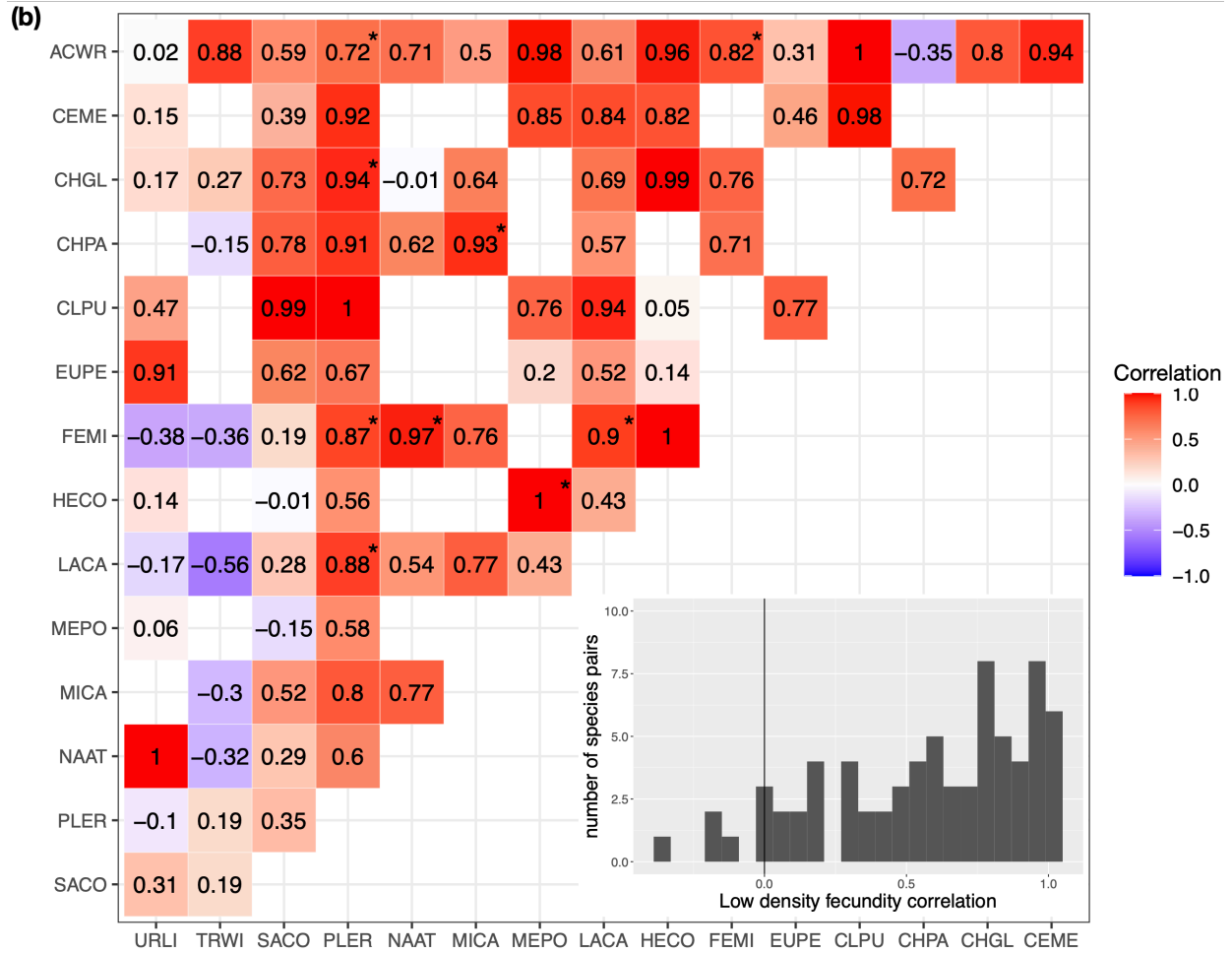
Figure 3.3: Correlation grids for species pairs and histograms of species pairs correlations in (a) germination rate and (b) low-density fecundity. * indicates significant correlation coefficient at the p< 0.05 level.

Several functional traits were significantly correlated with similarity in species germination rates. Pairs that were more similar in their yearly germination rates were more similar in rooting depth, water use efficiency (δ_{13}C), leaf N, and on the primary pca axis (table 3.3, figure 3.4, figure S3.3). Also pairs that were more similar in their germination rates were less

similar in their maximum height and on the secondary pca axis. Trait similarity was never a good predictor of species similarity in low density fecundity (table 3.3, figure 3.4, figure S3.3).

Table 3.3: Correlation coefficients and adjusted p-values for species pairs' functional trait similarity and demographic response correlations. Bolded traits indicate correlation with similarity in species germination rates.

Functional trait	Low-density fecundity correlation		Germination correlation	
	r	p-value	r	p-value
pc1 axis	−0.226	0.205	**0.462**	**<0.001**
pc2 axis	0.084	0.679	**−0.256**	**0.061**
seed mass	0.015	0.966	−0.106	0.518
leaf size	−0.005	0.966	−0.065	0.643
specific leaf area	−0.139	0.674	−0.079	0.623
maximum height	−0.236	0.205	**−0.251**	**0.061**
specific root length	−0.103	0.679	0.191	0.170
rooting depth	0.082	0.679	**0.576**	**<0.001**
leaf N	−0.122	0.674	**0.272**	**0.057**
water use efficiency	−0.038	0.920	**0.282**	**0.057**
fruiting phenology	−0.271	0.205	−0.052	0.664
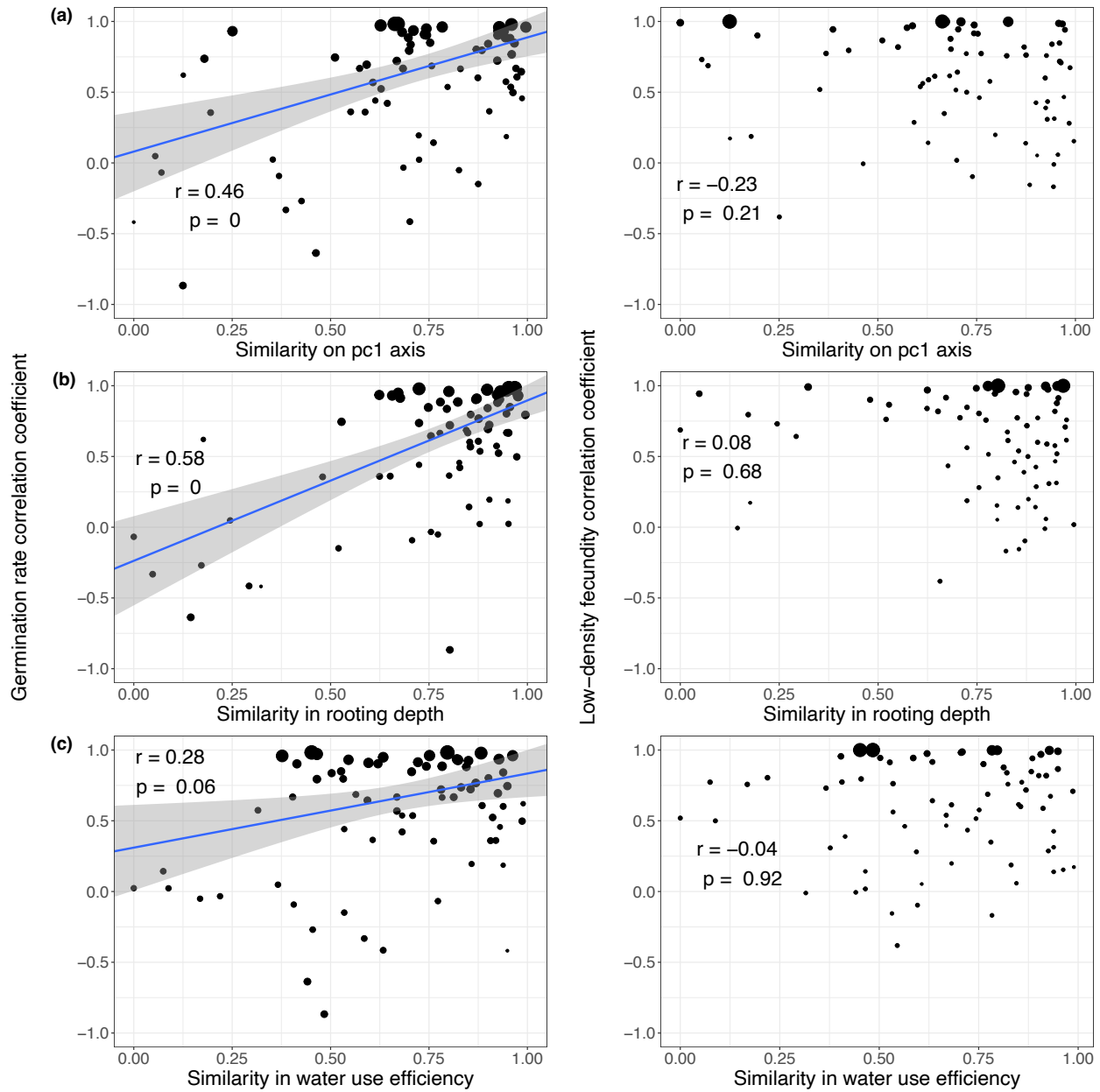
Figure 3.4: Correlation plots for species pairs similarity in demographic rates and similarity in functional traits. Each data point represents one species pair. Correlations are weighted by the inverse standard deviation of their demographic correlation coefficient which is represented by the size of the data point. The grey represents the confidence interval around the weighted regression line. Species that are more similar (a) on the primary pca axis, (b) in rooting depth, and (c) in water use efficiency are more likely to be similar in their yearly germination rates.

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Discussion:

Our results show that although demographic rates for most species pairs were positively correlated across years, there was considerable variation in the strength of the correlations, which indicates that species differ in their responses to interannual variation. This is an important prerequisite for temporal environmental variability to contribute to species coexistence. If species specialize, then different years will favor different species meaning there is no such thing as a good year for all species. Therefore, interannual variation may be important for promoting biodiversity and maintaining coexistence within the community by favoring different species at different times.

Species germination rates were more variable across species over time than low-density fecundity, indicating that differences in germination cues may be more impactful on community composition year to year than low-density fecundity rates. Since plants must germinate to survive and reproduce, germination is the first step towards a demographically successful year. Plants should break dormancy in years where they will also have high survival and seed production. If this is true then good germination years would also lead to a higher density of conspecifics which concentrates intra-specific competitive interactions, another prerequisite of the temporal storage effect (Chesson 2000, Angert et al. 2009).

Functional trait differences were a better predictor of species shared germination responses than their low-density fecundity responses to interannual variation. Four of the nine functional traits we examined seemed to be connected to variation in species year-to-year

germination rates while none of the traits showed any correlation with variation in low-density fecundity. Of the four traits, three of them were positively correlated with germination correlations including water use efficiency, rooting depth, and leaf N (table 3.3, figure 3.4, figure S3.3). The more similar species were in these three functional traits the more similar their annual germination rates were. This implies that plants with similar adult functional traits have similar germination cues. The only trait that was significantly negatively correlated with germination rate was maximum height.

Southern California, where the semi-arid annual grassland field site is located, experiences the greatest interannual variation in rainfall in the U.S. (Dettinger et al. 2011). Several of the functional traits whose similarity between pairs was significantly correlated with species pairs germination correlation coefficients are important indicators for species water use strategies. For example, high water use efficiency, deep rooting depth, higher specific root length, smaller leaves and low leaf N are all beneficial for lower water environments (Westoby et al. 2002, Wright et al. 2004, Kandlikar et al. 2022). Species with these traits may be favored in low-rain years and vice versa. This implies that species with different germination cues have different water strategies as adults. Since we identified several traits pertaining to water use, we tested whether germination rates or low-density fecundity for each species was correlated with various rainfall measures. We examined total rain over the growing season (October through September), total fall rain (defined as rainfall from October through January), total December rain, and total January rain. While there were significant effect sizes with some species seeming to benefit from higher rain years and others not, we found very few significant correlations between the rainfall measures and the demographic rates (tables S3.1 and S3.2). It is possible we

are not examining the correct rainfall factors or it could be that other climatic variables such as temperature are key as well (Levine et al. 2008, 2011, Angert et al. 2009).

It is difficult to study multiple potential coexistence mechanisms at once even though this is what is likely happening in all diverse communities. The annual grassland has served as a model system where ecologists have been able to study coexistence at many scales. At a neighborhood scale we measured stabilizing niche differences and fitness differences and found that not many of the species we find on the landscape are predicted to coexist (Kraft et al. 2015). The neighborhood scale is only examining one growing season and one spatial environment, however. When we look at larger spatial scales (Kandlikar et al. 2022) and now temporal scales, it is clear that several coexistence mechanisms are operating in the community and that some functional traits can help explain which processes might be the most critical.

Acknowledgements

Supplementary Materials:

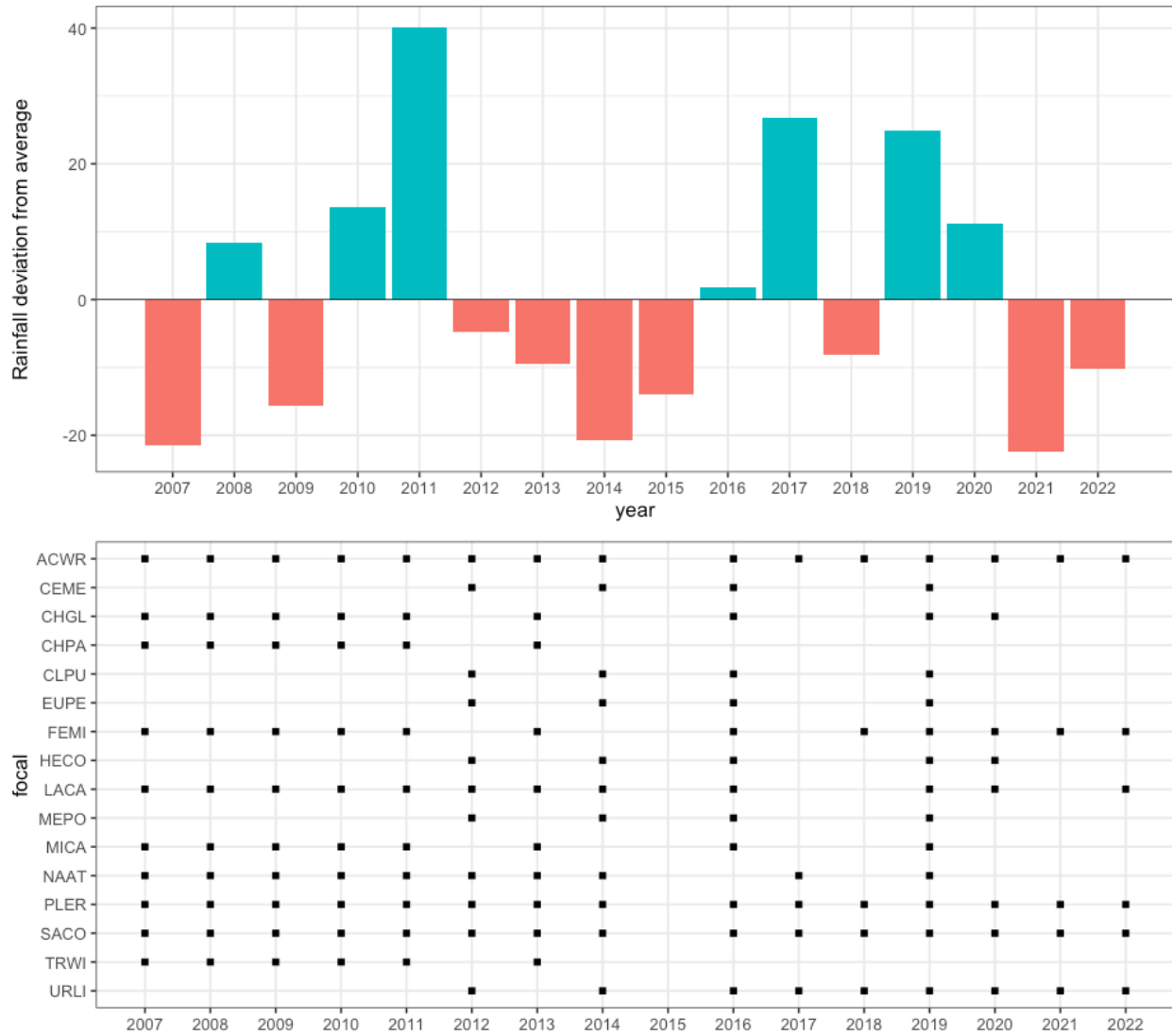Figure S3.1: (a) Rainfall deviation from average from 2007-2022. (b) Whether or not demographic data was collected that year for each species from 2007-2022. A black square indicates data was collected.
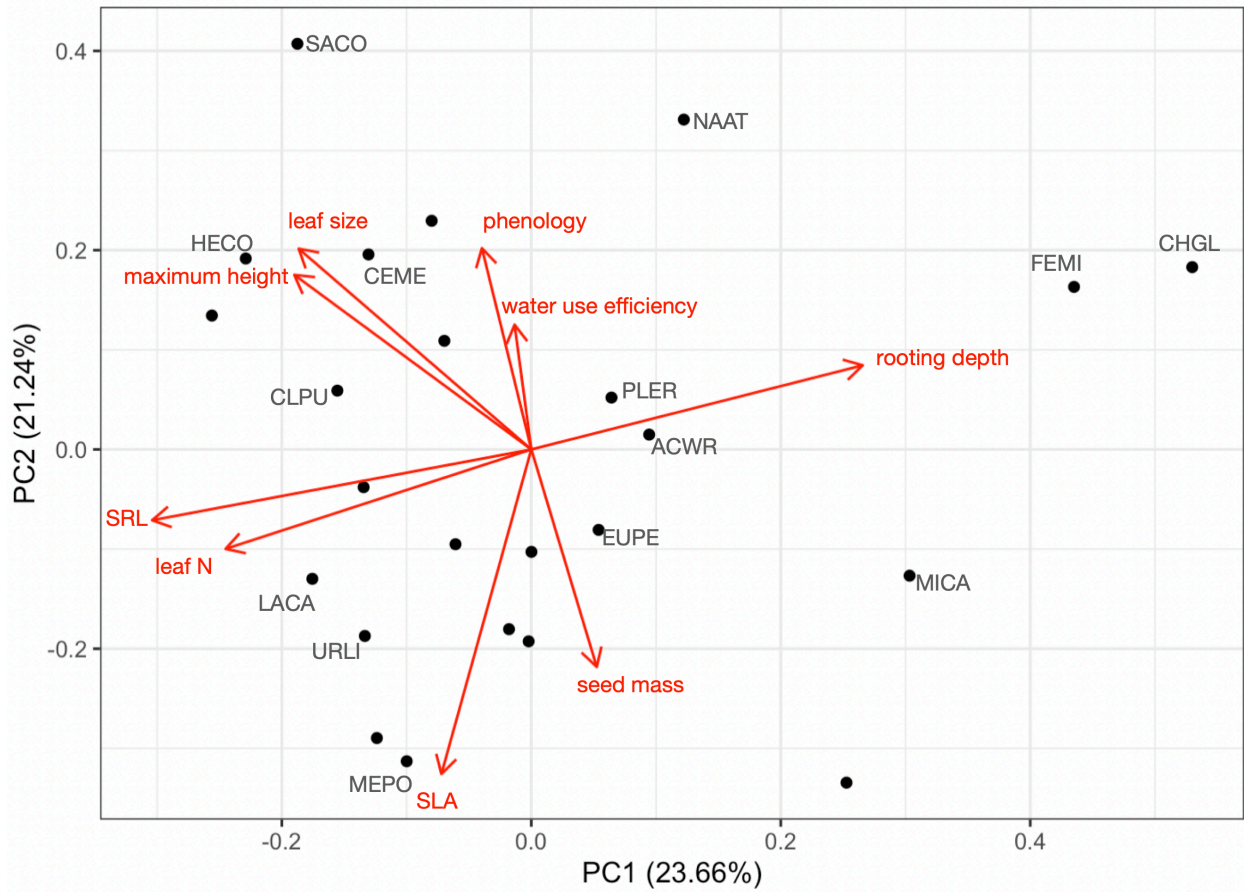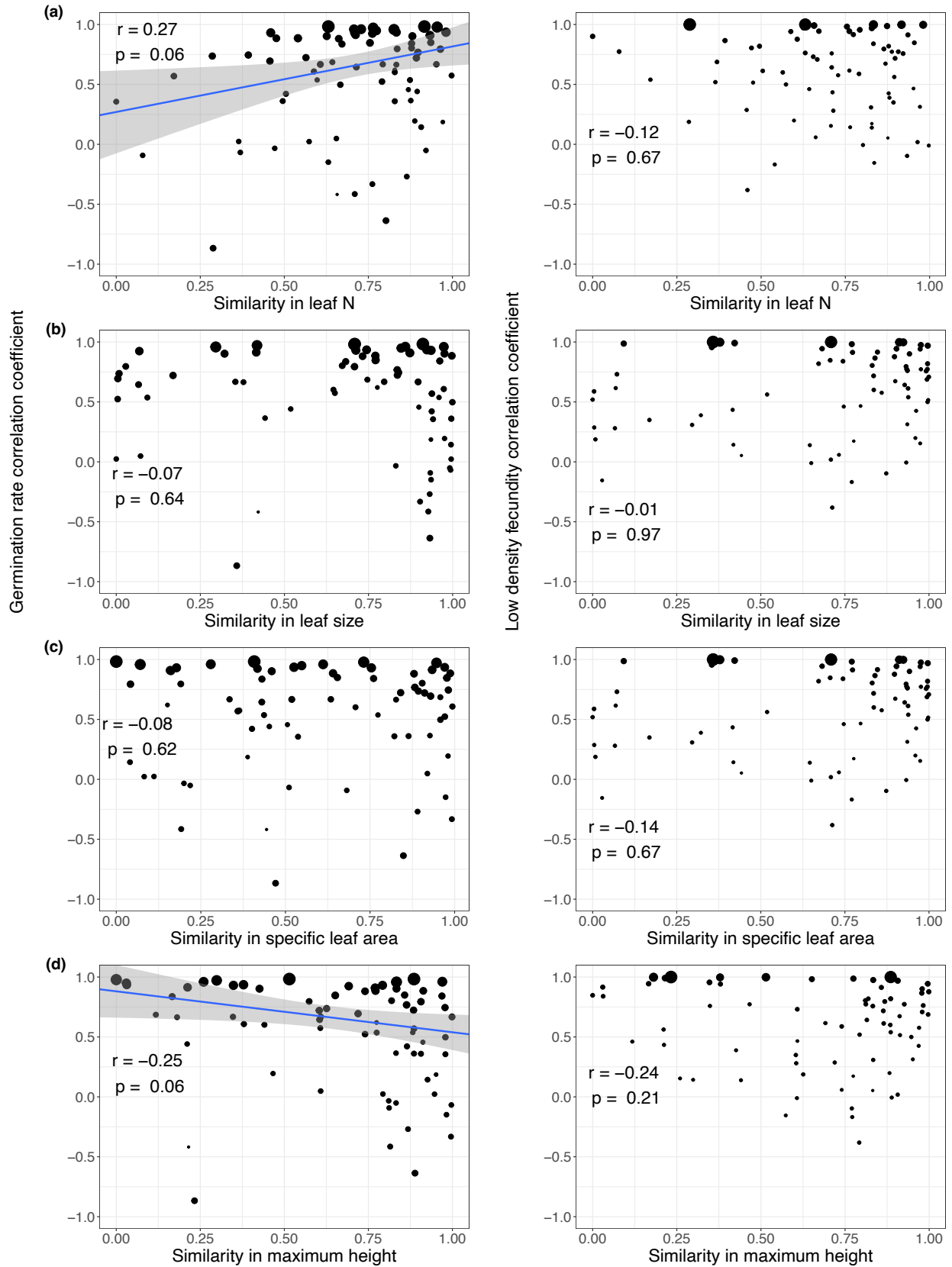
Figure S3.2: Principal component analysis for the 9 functional traits using 23 species from the community. Species used in this experiment are labeled with codes that can be found in table 3.1.
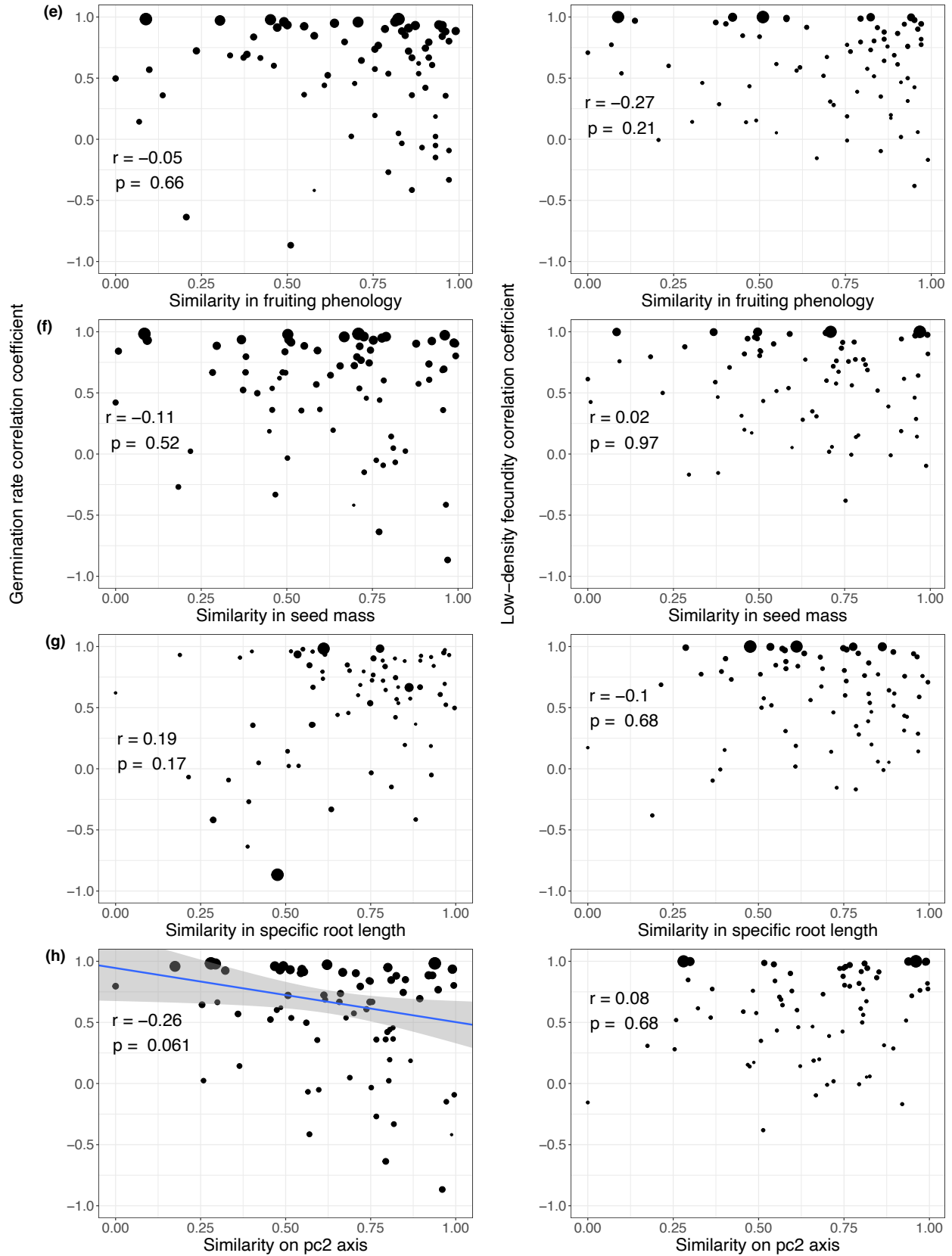
Figure S3.3: Correlation plots for species pairs similarity in demographic rates and similarity in all functional traits not shown in the main text. Functional traits include, (a) Leaf N, (b) Leaf size, (c) Specific leaf area, (d) maximum height, (e) fruiting phenology, (f) seed mass, (g) specific root length, (h) similarity on secondary PCA axis. Correlations are weighted by the inverse standard deviation of the pair's demographic correlation coefficients which is represented by the size of the data points.

Table S3.1: Correlation coefficients and their corresponding p-values of total growing season rainfall vs. yearly germination rates and low-density fecundity.

| Species | Total rainfall | | | |
	germination correlation	p-value	low-density fecundity correaltion	p-value
CHGL	−0.220	0.569	−0.022	0.955
CHPA	0.075	0.888	−0.227	0.665
LACA	0.508	0.092	0.191	0.552
ACWR	−0.218	0.455	0.321	0.244
MICA	0.402	0.323	0.101	0.813
NAAT	0.076	0.835	0.587	0.097
PLER	0.183	0.531	0.196	0.484
SACO	−0.134	0.647	−0.355	0.213
TRWI	−0.719	0.108	−0.530	0.280
FEMI	0.151	0.657	0.401	0.196
URLI	0.323	0.435	−0.013	0.973
CEME	0.885	0.115	0.814	0.186
CLPU	0.900	0.100	0.525	0.648
EUPE	0.373	0.627	0.572	0.428
HECO	0.477	0.416	0.759	0.137
MEPO	0.891	0.109	0.902	0.098

Table S3.2: Correlation coefficients and their corresponding p-values for each species germination rates vs. total fall rainfall (October to January), December rain, and January rain.

Species	Fall rainfall		December rainfall		January rainfall	
	germination correlation	p-value	germination correlation	p-value	germination correlation	p-value
CHGL	−0.169	0.665	−0.412	0.271	0.383	0.308
CHPA	0.352	0.494	−0.087	0.870	0.776	0.070
LACA	0.463	0.129	0.234	0.464	0.491	0.105
ACWR	−0.309	0.282	−0.020	0.947	−0.291	0.312
MICA	0.462	0.249	0.843	0.009	−0.560	0.149
NAAT	0.259	0.469	0.511	0.131	−0.063	0.863
PLER	−0.021	0.943	0.103	0.738	0.040	0.893
SACO	−0.161	0.582	0.073	0.814	−0.007	0.982
TRWI	−0.804	0.054	−0.432	0.392	−0.667	0.148
FEMI	−0.299	0.373	−0.375	0.286	−0.002	0.995
URLI	−0.046	0.913	−0.002	0.996	0.281	0.500
CEME	0.862	0.138	0.939	0.061	0.916	0.084
CLPU	0.822	0.178	0.614	0.386	0.715	0.285
EUPE	0.431	0.569	0.894	0.106	0.682	0.318
HECO	0.362	0.550	0.979	0.004	−0.136	0.828
MEPO	0.839	0.161	0.856	0.144	0.844	0.156

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