Evolutionary Processes Shaping Plant Population Responses to Climate Change and Species Interactions

by

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DISSERTATION ABSTRACT

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Title: Evolutionary Processes Shaping Plant Population Responses to Climate Change and Species Interactions

How evolutionary history and functional traits structure competitive interactions among co-occurring species, and how populations respond to novel environments through plasticity and evolutionary processes, are both current and unresolved questions in ecology and evolution. In this dissertation, I address these questions across three empirical chapters using both a model system, scarlet monkeyflower (*Mimulus cardinalis*), and annual plant communities from the Pacific Northwest. In my second chapter, I ask whether phylogenetic relatedness and functional trait dissimilarity predict the strength and outcome of pairwise competitive interactions among co-occurring annual forbs. I use a greenhouse competition experiment and modern coexistence theory to estimate pairwise competition coefficients and niche differences and fitness inequalities to evaluate two longstanding hypotheses about the role of evolutionary history in structuring competitive communities. I found that phylogenetic distance did not predict trait differences among species, or niche and fitness differences. Despite this, functional traits differences did predict competitive outcomes: focal species with greater leaf area than their competitors had higher relative demographic performance and greater competitive resistance, and dissimilarity in root mass fraction simultaneously amplified fitness inequalities and weakly reduced niche differences. In my third chapter, I examine how phenotypic plasticity varies across the range of scarlet monkeyflower and whether it evolved following an extreme drought. Using a resurrection common garden approach, I compare ancestors and descendants collected before and after a

severe drought from populations spanning the species' latitudinal range, asking whether plasticity tracks climate variability, evolves in response to an extreme drought event, and has fitness consequences. I found that plasticity in the date of first flower was greatest in central and trailing-edge populations experiencing greater interannual variability in precipitation. Additionally, while plasticity in first flower date evolved in three populations, the adaptive value of those traits depended on the trait. First-flower-date plasticity was adaptive in one trailing-edge population, while specific leaf area and leaf dry matter content were maladaptive in one central population. In my fourth chapter, I test how multiple co-occurring prairie annuals from climatically distinct populations respond to drought stress through genetic differentiation and phenotypic plasticity. I subjected populations to a water manipulation experiment to ask whether co-occurring species exhibit parallel or divergent responses to drought. I found diverse strategies across species to tolerate drought conditions, including substantial phenotypic plasticity in all traits. However, populations rarely showed consistent patterns across species (e.g. warmer/drier populations were not consistently earlier to flower). There was consistent positive directional selection for earlier flowering time across species and populations, but selection on other traits and trait plasticity was rare. These chapters highlight how trait variation determines ecological and evolutionary outcomes, and their implications for how plant communities will persist under global change. This dissertation includes previously unpublished, coauthored material.

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TABLE OF CONTENTS

I. INTRODUCTION 10
Contributions 14
Introduction 14
Methods 17
Study Species & Phylogeny Construction 17
Greenhouse Competition Experiment 18
Traits Measurements 19
Statistical Analyses 20
Results 25
Discussion 26
Functional traits predict competitive interactions independently of evolutionary history 27
Phylogenetic distance does not predict trait similarity or competitive structure 28
Limitations and future directions 30
Implications for restoration practice 31
Figures 32
Bridge 35
III. THE EVOLUTION OF PLASTICITY IN DROUGHT-RELATED TRAITS IN CENTRAL AND EDGE POPULATIONS OF MIMULUS CARDINALIS 36
Contributions 36
Introduction 36
Methods 41
Study System 41
Experimental Design 42
Data Collection 44
Quantifying phenotypic plasticity 45
Statistical Analyses 46
Results 50
Population variation in phenological plasticity tracks climate variability 50
Plasticity in phenology, but not leaf traits, evolved between ancestors to descendants following drought 51
Plasticity is largely neutral, and sometimes maladaptive, in relation to fitness 52
Discussion 53
Support for the climate variability hypothesis is trait-specific 53
Divergent evolution of plasticity may have contrasting consequences for range persistence 56
Spatial environmental gradients may not reliably select for adaptive plasticity 58
Conclusion 60
Figures 61
Bridge 64

IV. ASSESSING POPULATION DIFFERENTATION IN PLASTIC RESPONSES TO DROUGHT AMONG CO-OCCURING ANNUALS 64
Contributions 64
Introduction 64
Methods 69
Study System 69
Soil Collection 71
Experimental Design and Treatments 71
Data Collection 72
Statistical Analyses 73
Results 76
Site differences 76
Species show evidence of genetic differentiation among populations in trait means 77
Few consistent patterns in trait expression are shared across populations and species 77
Substantial phenotypic plasticity in response to drought across traits 78
Populations differ in the magnitude of plastic responses across traits 78
Earlier flowering leads to greater fitness, but leaf trait-fitness relationships are inconsistent 79
Plasticity has adaptive, maladaptive, and neutral fitness consequences across populations 79
Discussion 80
Drought responses reflect multiple strategies and are largely idiosyncratic across populations 80
Adaptive plasticity is rare and fitness consequences are highly context-dependent 83
Implications for changing climate 85
Conclusion 86
Figures 87
V. CONCLUSION 91
REFERENCES CITED 94

LIST OF FIGURES

Figure 1. Conceptual framework linking evolutionary history (phylogenetic relatedness), functional traits, and coexistence outcomes..... 32

Figure 2. Competition coefficients (α) as a function of trait distance for each trait. 33

Figure 3. Competitive response ratio and demographic ratio as a function of trait distance for each trait. 34

Figure 4. Niche differences and fitness inequalities as a function of trait distance for each trait. 35

Figure 5. Map of *Mimulus cardinalis* focal populations, winter precipitation, and historical vs. contemporary coefficient of variation in winter precipitation. 61

Figure 6. Plasticity in first flower date, specific leaf area, and leaf dry matter content of ancestors and descendants. 62

Figure 7. Relative fitness (averaged over northern, central, and southern gardens)as a function of plasticity in first flower date, specific leaf area, and leaf dry matter content. 63

Figure 8. Locations of five focal source populations, mean precipitation and temperature, and their seasonality. 87

Figure 9. Reaction norms for all species, populations, treatments, and traits..... 88

Figure 10. Relative fitness as a function of population and treatment for each species and trait. 89

Figure 11. Estimated effect of trait plasticity on relative fitness (averaged across treatments), for each species and population. 90

I. INTRODUCTION

Ecological communities are shaped by processes operating on multiple timescales, from deep evolutionary history that shapes trait distributions among species and influences whether species can coexist (Cavender-Bares et al., 2009; Kraft et al., 2014; McPeek, 2025), to contemporary environmental pressures that determine whether populations can persist in rapidly shifting environments (Franks et al., 2007; Wooliver et al., 2020). Functional traits serve as a bridge between these timescales, because they are simultaneously rooted in evolutionary history, and are responsive to ecological interactions and environmental conditions. Traits such as flowering time, leaf area, and root length are heritable, relatively easy to measure, and directly tied to fitness, making them a product of past selection, and a target of ongoing selection (Reich et al., 2014; Violle et al., 2007). Because traits are shaped by evolutionary history, and themselves shape how organisms interact with the environment and each other, variation in traits has multiple consequences for plant species. Understanding where trait variation comes from, how it is maintained, and what their consequences are for individuals, populations, and communities is a central challenge in ecology, particularly as environments shift at unprecedented rates.

Ecologists have hypothesized that species' phylogenetic relatedness may influence their interactions and the composition of ecological communities (Cavender-Bares et al., 2009; Webb et al., 2002). Closely related species are generally expected to compete more strongly with each other because similar traits lead to overlap in resource use, which should decrease their ability to co-occur in communities (Cahill et al., 2008; Darwin, 1859; Lemos-Costa et al., 2024). From this perspective, evolutionary relatedness is a useful predictor of competitive dynamics, where more closely related species compete more intensely. However, closely related species may also be similarly adapted to their environment, leading to more equivalent fitness and increasing the

likelihood of coexistence (Mayfield & Levine 2010; Rohr et al., 2025). These countervailing hypotheses both depend on the assumption that traits relevant to competition are phylogenetically conserved, but the effects of traits and phylogenetic relatedness on competitive dynamics have rarely been considered simultaneously (Godoy et al., 2014; Narwani et al., 2013). Disentangling their relative importance requires directly measuring the traits that mediate competition and linking them to competitive outcomes.

Evolutionary history and trait variation among species not only shapes competitive interactions, but also whether population can persist as environments change. Over contemporary timescales, populations can respond to environmental change through two key mechanisms: genetic change (Benning et al., 2023; Jump & Peñuelas, 2005) and phenotypic plasticity, the ability of a single genotype to express different trait values across environments ((Bradshaw, 1965; Münzbergová et al., 2017; Zettlemoyer & Peterson, 2021). The Climate Variability Hypothesis provides an important framework for predicting how plasticity should vary across space: genotypes from more environmentally variable locations are expected to evolve greater plasticity, because they experience a wider range of conditions (Ghalambor, 2006; Janzen, 1967). When adaptive, plasticity may buffer populations against environmental variability, climate change, and extreme events (Ghalambor et al., 2007; Nicotra et al., 2010; Sultan & Bazzaz, 1993). Given this, it is critical to understand how much plasticity populations possess, and whether it is adaptive. Despite vulnerability of range-edge populations, how plasticity and its evolution vary across species ranges remains poorly understood, leaving a gap in our ability to predict which populations can track rapidly shifting environments.

An additional challenge is that how communities will respond to climate change cannot be addressed at the population level or the community level alone, both are necessary. How multiple co-occurring species will respond collectively to environmental change and whether co-

occurring species exhibit divergent plastic responses or converge on similar strategies in response to environmental pressures, remains poorly understood (Cleland et al., 2006; Hamman et al. 2018; Liancourt et al., 2015). These gaps pose major challenges for predicting how plant communities will shift under climate change, as climate responses are likely to vary widely among species (Liancourt et al., 2015). Additionally, these questions are not only theoretically important but have direct implications for conservation and restoration. Our limited understanding of how multiple co-occurring species may respond to environmental change may constrain the development of effective restoration strategies for fostering resilient communities. As climate change becomes more intense, restoration practitioners face the challenge of conserving and restoring communities that are resilient to novel conditions (both competitive dynamics and plastic response across species; Barton et al., 2026; Espeland et al., 2018; Fiedler et al., 2018). Trait-based approaches may offer a path towards a more mechanistic understanding, if we know how traits vary across species and populations, and also, how trait differences influence interactions within communities (Aoyama et al., 2022; Laughlin et al. 2016).

In this dissertation I addresses these challenges. In Chapter 2, I ask whether evolutionary history and functional trait differences predict the strength and outcome of competitive interactions among co-occurring annual plants to better understand the effects of traits, potentially mediated by phylogeny, on species interactions and coexistence. Using a greenhouse competition experiment with a set of herbaceous forbs found in prairies in the Pacific Northwest, we estimated pairwise competition coefficients and derived niche differences and fitness inequalities from annual plant population models. This chapter was co-authored with Dr. Jeremy Collings, Narda Trivino Silva, and Dr. Jeffrey Diez.

In Chapters 3 and 4, I shift to more contemporary timescales, asking how populations respond to drought stress through genetic differentiation and phenotypic plasticity. In chapter 3, using scarlet monkeyflower (*Mimulus cardinalis),* I combined a resurrection approach with common gardens to test whether central and edge populations differ in plasticity in drought-associated traits, whether there were evolutionary shifts in plasticity following an extreme drought, and whether plasticity was adaptive. I measured plasticity in first flower date, specific leaf area, and leaf dry matter content across two leading-edge, two range-center, and two trailing-edge populations, comparing pre-drought ancestors and post-drought descendants grown in three gardens spanning the latitudinal range. This chapter was co-authored with Dr. Lucas J. Albano, Xitlaly Gomez-Vega, Katelin Kutella, Mariam Moazed, Marissa Strebler, Dachuan Wang, Dr. Christopher D. Muir, Dr. Lluvia Flores-Renteria, Dr. Jason P. Sexton, Dr. Seema Nayan Sheth, and Dr. Jeffrey Diez.

While Chapter 3 examines plasticity within a single species across its range, Chapter 4 scales up to ask whether co-occurring species within a community exhibit similar or contrasting plastic responses to drought. I investigated population differentiation and plastic responses to drought stress in five co-occurring prairie annuals native to the Pacific Northwest, and the relationship between plasticity and species' fitness. We grew populations from three environmentally distinct regions in a greenhouse common garden experiment with manipulated soil moisture to assess phenological and morphological plasticity and drought tolerance. This chapter was co-authored with Katelin Kutella, Dr. Seema Nayan Sheth, and Dr. Jeffrey Diez.

II. EFFECTS OF PHYLOGENETIC RELATEDNESS AND TRAITS ON COMPETITIVE INTERACTIONS AMONG PACIFIC NORTHWEST ANNUAL PLANTS

Contributions

Emily Cook, Narda Trivano-Silva, and Dr. Jeffrey Diez designed the research idea and performed the experiment; Emily Cook analyzed the data with input from Dr. Jeffrey Diez and Dr. Jeremy Collings; Emily Cook wrote the manuscript with contributions from all authors.

Introduction

Understanding what determines the outcome of competition among co-occurring species' is a central challenge in ecology. Ecologists have long recognized that both evolutionary history and functional traits influence how species interact, but predicting the outcome of those interactions remains difficult. One long-standing hypothesis, dating back to Darwin (Darwin, 1859), suggests that more closely related species compete more strongly because shared evolutionary history produces shared traits, leading to greater overlap in resource use (the competition-relatedness hypothesis). An alternative view emphasizes that species may reduce competition by partitioning the environment into distinct niches, with functional traits determining how individuals acquire resources and interact with competitors (Chase & Leibold, 2009). Both perspectives share the implicit assumption that species differences in functional traits and/or evolutionary history shape the strength and outcome of competitive interactions. However, the relationship between traits, evolutionary history, and competition is not straightforward, and understanding it requires distinguishing among different ways that species differences can influence competitive dynamics.

Modern coexistence theory (MCT) provides a useful way to think about how species differences may impact species interactions and community-level outcomes in coexistence. Specifically, coexistence among species depends on the relative strength of niche differences, which stabilize competitive dynamics by limiting species' own population growth more than that of competitors, and fitness differences, which reflect asymmetries in competitive ability and/or baseline demographic performance that can lead to exclusion (Chesson, 2000). Critically, species differences, whether in traits or evolutionary history, can contribute to both niche and fitness differences (Mayfield & Levine, 2010). A single trait difference can simultaneously generate niche differences that promote stable coexistence and fitness differences that favor one competitor. For example, differences in phenology have been found to increase stabilizing niche differences, while also allowing creating fitness asymmetries, where later phenology species produced more seed, giving them a fitness advantage (Godoy & Levine, 2014). This means that identifying differences among species is not sufficient on its own; we must also determine how those differences map onto niche and fitness differences to understand how they structure competitive interactions. Closely related species may compete more intensely because shared evolutionary history generates trait similarity and niche overlap, but if that same history also produces similar competitive abilities and demographic performance, fitness differences may be minimal and coexistence likely. Conversely, distantly related species may differ substantially in competitive abilities and demographic performance, generating fitness differences that promote exclusion despite niche partitioning. Whether phylogenetic distance or trait dissimilarity predicts the strength and outcome of competition thus depends on which component of competitive dynamics they influence (Figure 1).

A further complication is that phylogeny and traits are often assumed to covary, but this assumption is rarely tested in the context of competitive interactions. Phylogenetic signal (the

tendency for related species to resemble one another phenotypically) is well documented for some traits (Ávila-Lovera et al., 2023; Blomberg et al., 2003; Burns & Strauss, 2012) and has motivated the use of phylogenetic relatedness as a proxy for functional similarity when trait data are unavailable (Webb et al., 2002; Cavender-Bares et al., 2004). This is not an unreasonable proxy if phylogenetic distance tracks functional similarity, but it remains uncertain whether the traits that are phylogenetically conserved are the same traits that determine species interactions and coexistence outcomes. Consequently, phylogeny will only predict the structure of competition if it captures the traits that influence niche and fitness differences (Godoy et al., 2014). On the one hand, if niche differences increase with phylogenetic relatedness, competitors that are more closely related species will compete more strongly, limiting the likelihood of their coexistence. Alternatively, if fitness differences increase with phylogenetic relatedness, then more closely related species will be more likely to coexist. Even if phylogenetic signal exists in some traits, it may not exist in the traits that matter for species competitive interactions. Consistent with this, recent studies applying MCT to questions of phylogenetic relatedness have produced mixed results, with some finding no relationship between niche differences and phylogenetic differences (Godoy, et al., 2014), and others finding that niche differences explained coexistence outcomes better than fitness differences, but that relatedness itself does not predict those outcomes (Narwani et al., 2013). These results highlight the difficulty of interpreting phylogenetic patterns without explicit links to traits and mechanisms that structure competition, and motivate empirical tests that examine traits, phylogeny, and competitive dynamics jointly.

Here we address this gap using a community of co-occurring annual forbs native to Pacific Northwest prairies. We fit pairwise competition models to empirical data from 14 annual forb species, quantified competitive coefficients for 20 species pairs, and derived niche and

fitness differences using MCT. We then asked whether evolutionary history and functional traits predict the competitive interactions in this community. Specifically, we addressed three questions: (1) Is phylogenetic relatedness associated with functional trait similarity among species? (2) Does the direction of trait differences between competitors predict the strength of competitive suppression experienced by a focal species? (3) Does trait dissimilarity between species pairs predict the structure of pairwise competitive interactions, including niche and fitness differences, and if so, in a direction that promotes or inhibits coexistence? Greater trait dissimilarity could increase niche differences and stabilize competition, or alternatively amplify fitness differences and promote exclusion, depending on the trait axes involved. Together, these questions allow us to evaluate whether and how evolutionary history and functional traits shape competitive dynamics in a diverse plant community.

Methods

Study Species & Phylogeny Construction

We conducted our competition experiment at the University of Oregon greenhouses in Eugene, Oregon. We selected 14 herbaceous annual species that commonly co-occur in prairie habitats in the Pacific Northwest (Supplemental Table 1). We selected species from 5 different families in order to have a range of phylogenetic relatedness among the study species.

We used the R package V.Phylomaker (Jin & Qian, 2019) using scenario 3 to estimate time since divergence and create a phylogenetic tree for all of our species. V.phylomaker places species onto a larger backbone phylogeny (GBOTB.extended megatree), built from published DNA sequence data, fossil records, molecular data from GenBank and phylogenetic data from the Open Tree of Life (Smith & Brown, 2018) to infer evolutionary distances into a phylogeny.

For species not directly represented in the backbone, V.Phylomaker infers placement based on genus- and family-level relationships. Branch lengths are estimated from the backbone rather than derived from species-specific DNA sequences, meaning they are approximate divergence times rather than exact molecular distances. In scenario 3 (default), when species are absent from the backbone phylogeny, they are bound to their genus or family branch. All scenarios have been shown to produce similar results (Jin & Qian, 2019; Qian & Jin, 2016). This approach is well-suited for comparative analyses focused on broad evolutionary patterns across genera and families, though it may not fully resolve relationships among congeneric species, or provide precise branch length estimates.

Greenhouse Competition Experiment

All species were sown into pots (2.7 x 8" Deepot™ Cells & Trays; Stuewe & Sons, Inc.) in October 2021 using seed produced by a local native plant nursery (Friends of Buford Park and Mt. Pisgah Native Plant Nursery, Oregon), which sources seed from local Willamette Valley populations. Each species was planted as a focal in two treatments: alone (0 competitors) and with 2-5 individuals of either the same species (intraspecific competition) or different species (interspecific competition). Each focal x competitor species combination was replicated three times, with realized competitor density varying among replicates due to germination, so that focal individuals collectively spanned a gradient of competition. Because not all species established successfully, we estimated competition coefficients for 20 pairwise combinations among the species retained for analysis. Pots were placed on tables under supplemental LED lighting to 12-hour days (8am-8pm) and were watered daily. Temperatures were set to a min/max of 4°C/18°C. Pot location was randomized on trays with 13 pots to a tray, and trays were rotated throughout the experiment (13 pots per tray x 19 trays = 244 total pots).

As the measure of each focal plant's performance, we collected fitness data in May 2022 after the majority of flowering had taken place, and before plants began to senesce. We calculated fitness for each focal individual as the total number of seeds produced. This fitness value was modeled as a function of the number and identity of competitors in the pot to determine the strength of intra- and inter-specific competition (as described below).

Traits Measurements

We measured several key functional traits known for their importance in plant competition, resource acquisition and survival on a subset of 5 individuals per species, following Perez, 2013: total plant height, specific leaf area (SLA), leaf dry matter content (LDMC), leaf area (LA), carbon nitrogen ratio (CN), δ13C (a proxy for water-use efficiency, WUE, (less negative = more efficient)), root-mass fraction (RMF), and total biomass. We estimated SLA as leaf area / dry mass, and leaf dry matter content as leaf dry mass / leaf fresh mass. SLA and LDMC are common traits in the "leaf economics spectrum" (LES) and represent tradeoffs between "conservative" and "acquisitive" carbon gain, leaf maintenance and growth (Wright et al., 2004). Greater SLA and lower LDMC are generally associated with thin, large leaves that are quick to grow. Greater CN generally signifies greater nitrogen use efficiency and has frequently been shown to be important for energy investment (Luong et al., 2021; Nobel, 1991), and growth rate traits such as plant height or size (Ågren, 2004; Peng et al., 2023). High WUE is often associated with the "slow" strategy leaves (thick, dense, and long-lived) while low WUE is associated with leaves that prioritize rapid carbon gain over water conservation (Reich, 2014). We harvested plants and separated plant shoots from roots. Roots were removed from soil, cleaned, and placed in 80% ethanol and fresh biomass was placed in moist paper towels in plastic bags. Both were stored in a refrigerator at 3°C for short-term processing. We measured

height as the length from the base of the stem to directly below the terminal inflorescence. We weighed whole plants including reproductive material on a VWR-603B2T balance, collected 3-5 fresh leaves, weighed, and scanned the leaves on a Lipson Expression 12000XL scanner to calculate total leaf area in Adobe Photoshop (version 24.7.0). Fresh leaves, aboveground biomass and roots were dried separately in coin envelopes in an oven at 35°C for 3 days and weighed again for dry weight. Root-mass fraction was calculated as the proportion of roots in dry biomass. We estimated WUE using stable isotope analysis. We sealed ~2 mg of ground plant material in tin capsules (Costech) and samples were analyzed at the UC Davis stable Isotope Facility (Davis, California, USA). We report water-use efficiency as the carbon isotope ratio relative to the V-PDB standard (RPDB), where less negative values indicate greater water use efficiency. See Supplemental Table 1 for all species trait means.

Statistical Analyses

All models described below were fitted using the brms package (Version 2.220; Burker 2017, 2018) in R (Version 4.4.2) (R. Core Team, 2021). Each model was run with 4 chains of 4,000 iterations, with the first 2,000 discarded as warmup, yielding 8,000 post-warmup draws. To improve sampling, we set adapt_delta = 0.98 and max_treedepth = 17. Convergence was assessed by inspecting trace plots, $\hat{R}$ values (convergence criterion $\hat{R} < 1.01$) (Gelman & Rubin, 1992), and adequate characterization of posterior distributions was assessed by bulk and tail effective sample sizes (ESS). Posterior predictive checks were used to evaluate model fit by comparing the distribution of observed seed counts to posterior predictions.

Annual plant competition models

We estimated pairwise competition coefficients (α) and intrinsic fecundity in the absence of competition (λ) for each focal species by fitting Ricker form annual plant models to observed seed production data. In these models, focal seed output declined exponentially with neighborhood density:

$$\text{seeds} \sim \text{NegBin}(\mu, \varphi)$$
$$\log(\mu) = \lambda - \alpha \times N$$

where exp(λ) is intrinsic fecundity in the absence of competition, α is the per-neighbor competitive effect, and N is observed neighbor density. Seed counts were modeled with a negative binomial error distribution to accommodate overdispersion. Models were fit separately for each focal x competitor species combination in a Bayesian framework using brms. See Supplemental Figure 3 and 4 for estimates of λ and Supplemental Figure 4 for estimates of α for all species pairs.

One species, (*Plectritis*) was grown only in monoculture and lacked interspecific competition data; it was excluded from all pairwise analyses. For all remaining focal species, which had two or more competitor species, we fit hierarchical models with partial pooling of competitor-specific α estimates via random effects on log-α. *Madia*, *Collomia*, and *Plagiobothrys nothofulvus* lacked plants grown without competition. These species were excluded as focal species from coexistence analyses (below) but were retained as competitor species in competition models for other focal species.

We specified priors for λ individually for each focal species as Normal(log(max observed seed count), 0.7). To constrain $\alpha > 0$, we estimated it on the log scale with a Normal(−1, 1) prior for log-α, centering competition coefficients around $\exp(-1) \approx 0.37$, indicating a modest competitive effect. We specified an Exponential(2) prior on the standard deviation of the random effects distribution for log-α across competitors. The negative binomial shape parameter had a Gamma(2, 0.1) prior.

Coexistence metrics

From the posterior distributions of α and λ, we derived pairwise coexistence metrics for all species pairs following Godoy & Levine (2014). For each species pair, we used intraspecific competition coefficients (α_{ii}, α_{jj}) and interspecific coefficients (α_{ij}, α_{ji}), along with intrinsic growth rates in the absence of competition (λ_i, λ_j), to calculate the following metrics: Niche difference (ND) is a stabilizing mechanism that can permit coexistence if sufficiently greater than fitness inequalities and quantifies the degree to which intraspecific competition exceeds interspecific competition: $ND = 1 - \sqrt{((\alpha_{ij} \times \alpha_{ji}) / (\alpha_{ii} \times \alpha_{jj}))}$. The competitive response ratio (CR) captures each species' sensitivity to competition relative to its competitor: $CR_i = \sqrt{(\alpha_{ji} \times \alpha_{jj}) / (\alpha_{ii} \times \alpha_{ij})}$. The demographic ratio (DR) captures intrinsic fitness differences: $DR_i = \lambda_i / \lambda_j$. Fitness differences (FD), which drives competitive exclusion, is the product of the competitive response and demographic ratios: $FD_i = CR_i \times DR_i$, and fitness inequalities (FI) for a pair of species is the maximum of the two FD (or the FD when i is the competitively superior species). We computed CR, DR for both species in each pair (i and j). We estimated FI and ND to calculate expected coexistence outcomes (coexistence, competitive exclusion, and priority effects for each species pair. Stable coexistence requires that niche differences exceed fitness inequalities ($1 - ND < FI < 1/(1 - ND)$); when fitness inequalities exceed niche differences, the more fit species excludes the

other, and when neither species can invade when rare, priority effects determine the outcome such that whichever species establishes first excludes the other. Because greenhouse pot experiments cannot include all of the likely sources of variation that can impact coexistence in nature, and species pairs are often predicted to not coexist in such experiments, we focus on the structure of competitive interactions rather than coexistence outcomes per se (see Supplemental Figure 5 for probability of coexistence for all species pairs).

Trait differences as predictors of competitive suppression

Because traits can be strongly correlated, we estimated pairwise correlations among trait means using the GGally package (Supplemental Figure 1) and estimated covariation among traits using principal components analysis for all traits (Supplemental Table 3, Supplemental Figure 2). We found correlations among height, CN, LA and LDMC as well as SLA and WUE, so we chose three traits for downstream analyses (LA, which represents plant size, WUE which represents resource or water acquisition and RMF which represents above and belowground allocation).

To ask whether the direction of trait differences predicts competitive suppression experienced by a focal species, we fit three separate Bayesian models regressing pairwise α, CR, and DR onto directional trait differences (species i minus species j) in LA, WUE, and RMF. These models used lognormal error distributions, appropriate for competition coefficients, demographic ratios, and competitive response ratios which are strictly positive and included random intercepts for both focal species (i) and competitor species (j) to account for non-independence of pairwise observations. Directional rather than absolute differences were used here to ask whether being larger, more water-use efficient, or more root-allocated than a

competitor predicts a species' fecundity or sensitivity to competition. Trait distances were standardized to a mean of 0 and standard deviation of 1 prior to analysis.

Trait dissimilarity, phylogeny, and coexistence

We evaluated the relationships between phylogenetic distance and functional trait dissimilarity. Trait distances (LA, WUE, RMF) were computed as absolute pairwise differences and standardized to a mean of 0 and standard deviation of 1 prior to analysis. Each trait was modeled separately as a function of phylogenetic distance. We also assessed whether trait distances influenced ND and FI. Median ND and FI were each modeled as a function of all three trait distances simultaneously. ND was assumed to follow a Gaussian distribution, and FI was modeled with a lognormal family given its right-skewed distribution bounded by 1. Fixed effects of α, DR, CR, ND, and FI are reported in Supplemental Table 2. Fixed effects of phylogenetic distance and trait distance are reported in Supplemental Table 4. Finally, we assessed whether phylogenetic distance directly influenced ND and FI. Median ND (Gaussian distribution) and FI (lognormal) was modeled as a function of pairwise phylogenetic distance (fixed effects in Supplemental Table 5).

Because some traits were correlated, we conducted a parallel PCA-based analysis in which trait distances along the first three principal components replaced individual trait distances in all models. To evaluate the relationships among phylogenetic distance and functional trait dissimilarity, and the structure of pairwise competitive interactions, we fit a Bayesian structural equation model (SEM) using brms. PC distances were computed as absolute pairwise differences and standardized to a mean of zero and standard deviation of one prior to analysis. The SEM included paths from pairwise phylogenetic distance to each PC distance, and from each PC distance to ND and FI. This structure allowed us to simultaneously estimate phylogeny-to-trait

and trait-to-coexistence pathways while accounting for indirect effects. Results were broadly consistent with the direct-trait approach; we report PCA loadings (Supplemental Table 3), α -PC models (Supplemental Figure 6), and the corresponding SEM (Supplemental Figure 7) and favor the direct-trait approach here for its mechanistic interpretability.

Results

Phylogenetic history was not related to traits or competitive interactions (niche and fitness differences). While we found significant species-level variation in measured traits (Supplemental Table 1), we found no effect of phylogenetic distance on any trait distance (water-use efficiency (WUE), root mass fraction (RMF), and leaf area (LA) distance) (Supplemental Figure 8) or on niche or fitness differences (Supplemental Table 5).

Trait asymmetries influenced the strength of competitive suppression experienced. Focal species that had larger LA and allocated more to belowground biomass than aboveground biomass (RMF) relative to their competitor, experienced weaker inter-specific competition (Figure 2). WUE distance had no effect on competition coefficients (Figure 2).

Trait asymmetries also influenced both the competitive advantage via the competitive response ratio (CR) and overall fitness via the demographic ratio (DR). Focals with larger LA than their competitors gained a competitive advantage both through greater intrinsic fitness (DR) (Figure 3D) and lower competition (CR) (Figure 3A). Similarly, species with greater RMF (i.e. higher allocation to belowground biomass relative to above ground biomass) than their competitors experienced less competition (CR) (Figure 3B). However, greater RMF was associated with reduced intrinsic fitness relative to competitors (DR) (Figure 3E). Species with greater WUE had significantly reduced effects of competition (CR, Figure 3C), but WUE had no significant effect on DR (Figure 3F).

Overall, trait dissimilarities had few effects on niche differences (ND) and fitness inequalities (FI) (Figure 4). LA and WUE had marginal positive effects on ND (PD > 83%) (Figure 4A, C), while RMF had a marginal negative effect on ND (PD > 82%) (Figure 4B). Greater dissimilarity in root mass fraction amplified FI (Figure 4E), while LA had a marginal positive effect on FI (PD > 89%) (Figure 4D) and WUE had little effect (Figure 4F). Across all species pairs, the most probable outcome was competitive exclusion: niche differences were insufficient to overcome fitness inequalities in 18 out of 20 of the pairwise combination (Supplemental Figure 5).

Discussion

A central goal of community ecology is to understand how species differences shape the competitive interactions that determine community composition. Two longstanding and competing hypotheses predict opposite effects of phylogenetic relatedness on species coexistence: closely related species may either compete more strongly due to shared traits and overlapping resource use, and therefore be less likely to coexist, or their shared evolutionary history may confer similar environmental tolerances that make them more likely to coexist. Both hypotheses implicitly assume that phylogenetic distance is related to functional similarity, and that functional similarity, in turn, structures competitive dynamics. We found no relationship between phylogenetic distance and functional trait dissimilarity, and no direct relationship between phylogenetic distance and either niche differences or fitness inequalities. Nevertheless, functional traits did predict competitive outcomes: focal species with greater leaf area than their competitors had higher relative demographic performance and greater competitive resistance, and dissimilarity in root mass fraction simultaneously amplified fitness inequalities and weakly

reduced niche differences. These results suggest that functional trait differences, rather than shared evolutionary history, are primary determinants of competitive interactions in this system.

Functional traits predict competitive interactions independently of evolutionary history

Our results support the broader view that functional traits are meaningful predictors of competitive dynamics, even in a community where those traits show no phylogenetic signal. Focal species with greater leaf area than their competitors experienced less competitive suppression (α), had higher intrinsic fitness relative to competitors (demographic ratio), and were more competitively resistant (competitive response ratio). Dissimilarity between species in leaf area was also marginally positively associated with fitness inequalities and with niche differences. Overall, this pattern suggests that larger, more acquisitive plants are better able to capture above-ground resources, such as light, and that this capability may lead to reduced sensitivity to competition and greater reproductive output. These results align with prior work showing that asymmetries in leaf area increased fitness inequalities among co-occurring annuals (Kraft et al., 2015).

The effects of root mass fraction (RMF) on competitive interactions were more nuanced. Species with proportionally greater root allocation than their competitors experienced less interspecific competitive suppression, suggesting that greater below-ground investment confers some degree of competitive resistance, possibly by improving access to soil resources such as water or nutrients. A previous study found that rooting depth, among other traits (later phenology, larger height and leaf area), predicted greater average fitness relative to competitors among annual plants (Kraft et al., 2015); however, here greater RMF was also associated with lower intrinsic fitness relative to competitors (demographic ratio), reflecting a potential

allocation tradeoff, where investment in below-ground structures may come at the cost of reproductive output.

Water-use efficiency (WUE), by contrast, had little relationship with niche differences, fitness inequalities, or pairwise competition coefficients, though species with greater WUE than their competitors did experience reduced overall sensitivity to competition (competitive response ratio, CR). This may reflect the growing conditions of our greenhouse experiment, where water was supplied daily and no drought stress was imposed. WUE has been shown to predict competitive dynamics and long-term population performance in water-limited systems. For example, Gremer et al. (2013) found that a high-WUE species showed greater competitive resistance under low-water conditions in Sonoran Desert winter annuals. It is possible that WUE would emerge as a more important predictor of competitive interactions in field conditions, where water availability is scarcer. Future studies could extend our findings by pairing competition experiments with field-based or water-limited treatments, to better detect competitive effects of traits that are primarily relevant under environmental stress.

Phylogenetic distance does not predict trait similarity or competitive structure

Despite these study species spanning five families and a broad range of phylogenetic distances, we found no relationships between evolutionary relatedness and dissimilarity in leaf area, water-use efficiency, or root mass fraction. Phylogenetic distance also did not predict niche differences or fitness inequalities between species pairs. Because phylogenetic distance did not structure variation in functional traits that influenced competitive interactions, it also did not predict the competitive outcomes in this community. Thus, neither the competition-relatedness hypothesis (more closely related species compete more strongly due to trait overlap) nor the environmental filtering hypothesis (closely related species co-occur due to shared environmental

adaptations) received support. This outcome is broadly consistent with prior empirical work that found no relationship between phylogenetic distance and niche differences in a California annual plant community (Godoy et al., 2014), and in an algal community (Narwani et al., 2013). Numerous other studies have been unsuccessful in linking traits to phylogeny (reviewed in Cadotte et al., 2017), although some studies have found evidence for a phylogenetic signal in specific traits (Blomberg et al., 2003; Luong et al., 2021; Luzuriaga et al., 2025). It is also possible that other unmeasured traits, such as seed mass or phenology, show stronger phylogenetic signal and contribute to competitive dynamics in ways we were not able to capture. Phenological differences, in particular, have been shown to influence both niche and fitness differences among co-occurring annuals (Godoy & Levine 2014).

The relationship between phylogenetic distance, functional traits, and competition may depend on taxonomic scale, so the appropriate taxonomic scale for testing competition-relatedness hypotheses remains an open question (Cadotte et al. 2017), In this study, phylogenetic distances among our study species showed a roughly bimodal distribution, with pairs either closely related (within-family) or distantly related (across families), and few intermediates. We explored the distribution of relatedness among a larger pool of species within this community (136 herbaceous perennials and forbs native to the PNW), and among those species, the pattern was mostly unimodal (most species are more distantly related, with few closely and intermediately related). The distribution of relatedness in our results reflects our deliberate selection of species from multiple families to span a broad range of relatedness, but it limits our ability to characterize competitive dynamics across the full continuum of phylogenetic distance. We explored whether our conclusions held when analyzed separately within each phylogenetic distance group (either closely or distantly related) and found consistent results. Future studies might better explain these relationships by studying communities that have more

even distributions of phylogenetic relationships, or sampling densely within clades to better characterize how evolutionary divergence within families shapes competitive dynamics.

Limitations and future directions

Our study used species mean trait values to characterize functional differences between competitors, but theory suggests that both intraspecific trait variation and phenotypic plasticity can independently influence coexistence outcomes (Turcotte & Levine, 2016). Species may differ substantially in trait variance or in their capacity for plastic responses to competition, and these differences could contribute to niche and fitness differences in ways that means alone cannot capture. For example, previous empirical research has shown plasticity in response to watering regime influenced both niche and fitness differences among annual plants (Pérez-Ramos et al., 2019). Future work in this system might pair competition experiments with trait measurements made under varied environmental conditions to assess whether intraspecific variation and plasticity modify the competitive dynamics we observed here.

A broader challenge in our interpretations of this study is that the relationships among evolutionary history, functional traits, and competitive outcomes are not strictly one-directional. In natural communities, these relationships are dynamic and multi-directional: competition can drive rapid trait evolution (Colom & Baucom, 2020), and the resulting trait changes can in turn alter competitive dynamics and community composition (Hairston Jr et al., 2005; Schoener, 2011). If competition was a historical driver in trait divergence among co-occurring species, we would still expect correlations between phylogenetic distance, trait dissimilarity, and competitive outcomes. Whether the trait patterns we observed reflect the direct effects of evolutionary history, adaptive divergence in response to competition, or some combination of these processes is a question that cannot be resolved from a single competition experiment. Approaches that

include populations at different stages of competitive history would be valuable for untangling these processes.

Implications for restoration practice

Phylogenetic relatedness has been proposed as a practical guide for selecting species combinations in restoration, with the expectation that more distantly related species will compete less intensely and be more likely to coexist (Mazel et al., 2017; Verdú et al., 2011). The study species here were chosen in part because they are widely used in restoration seed mixes across Pacific Northwest prairies. Our results suggest that using phylogenetic dispersion of seed mixes may be oversimplistic in this system: because phylogenetic distance did not predict the traits structuring competitive interactions, and did not predict niche or fitness differences, selecting species on the basis of phylogenetic distance is unlikely to optimize for competitive compatibility or coexistence outcomes. While restoration practitioners may choose to enhance phylogenetic diversity for other restoration goals, prioritizing trait combinations that minimize fitness inequalities or promote niche differences may be more important than phylogenetic diversity for helping shape coexistence outcomes. More broadly, translating coexistence theory into restoration practice remains an active challenge (Hallet et al., 2023); while modern coexistence theory provides a powerful framework for understanding species persistence, restoration outcomes depend on a broader suite of mechanisms, including environmental fluctuations, facilitation, or indirect interactions that are difficult to capture in pairwise greenhouse experiments.

Figures

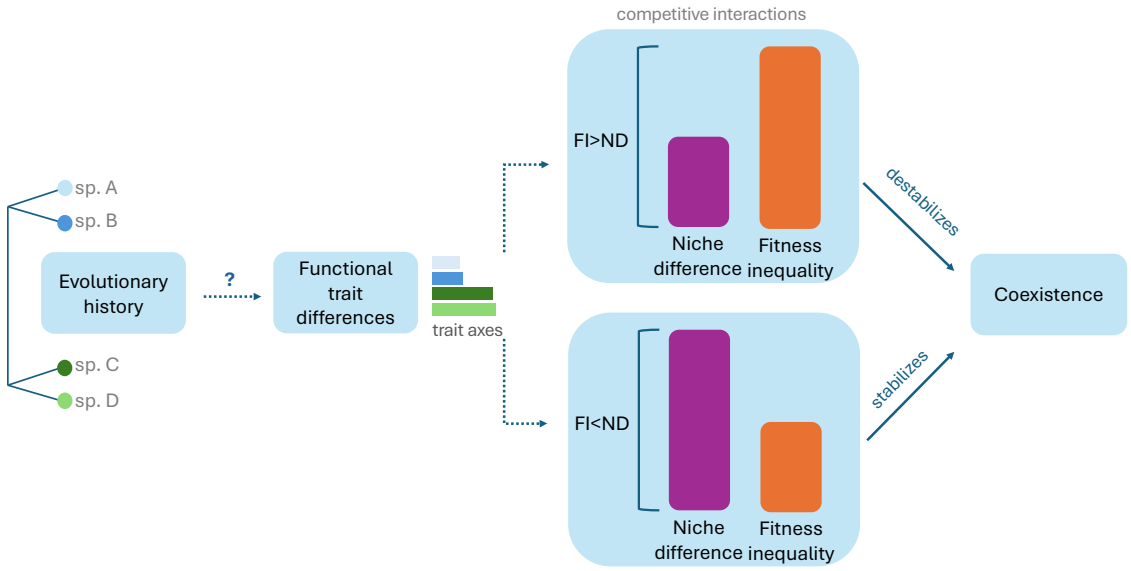


Figure 1. Conceptual framework linking evolutionary history (phylogenetic relatedness), functional traits, and coexistence outcomes.
Phylogenetic distance between species pairs may predict functional trait differences, though this relationship depends on the degree of phylogenetic signal in traits (more closely related species may have more similar traits). Functional traits are hypothesized to influence niche differences (ND) and fitness inequalities (FI) through their effects on competitive interactions (α), though the direction and magnitude may vary. Trait distances could lead to increased or decreased ND, FI, or neither. ND stabilizes coexistence by reducing competitive overlap between species, while FI destabilizes coexistence by leading to asymmetrical competitive ability and fitness. Whether species pairs coexist or one excludes the other depends on the relative magnitude of FI and ND: coexistence is predicted when ND is sufficient to overcome FI, and exclusion when FI exceeds the stabilizing effect of ND (Chesson 2000; Godoy & Levine 2014).

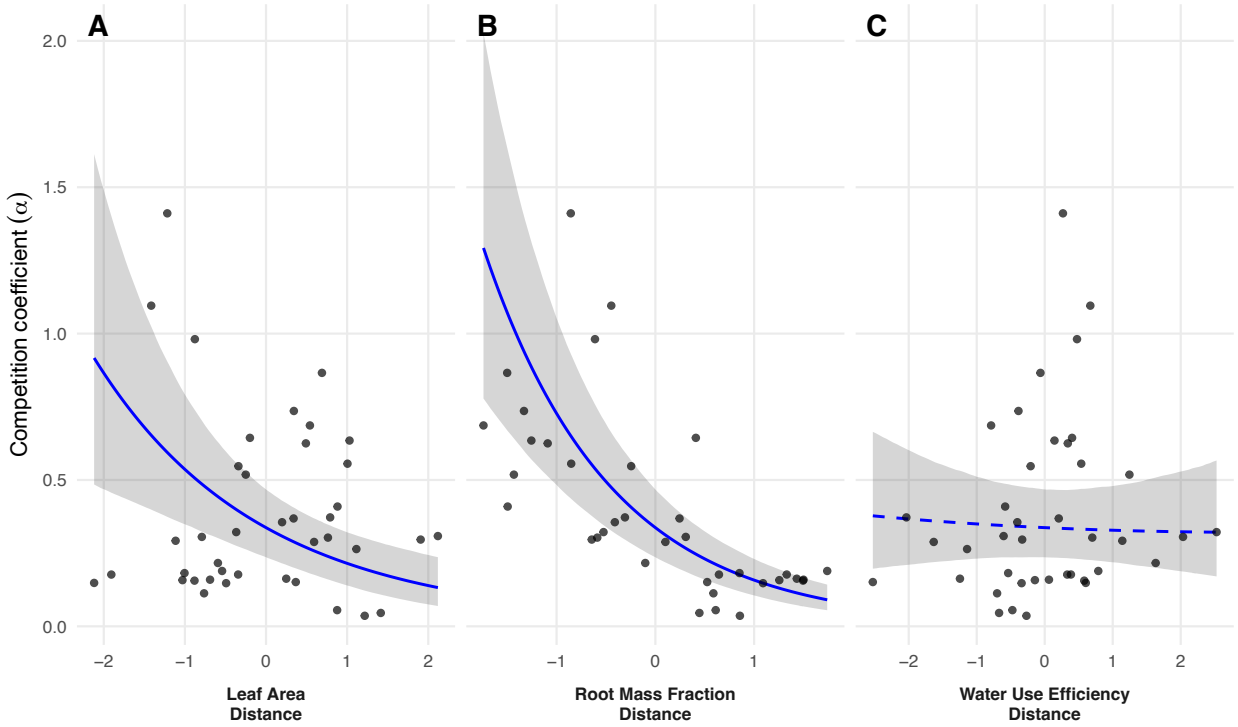


Figure 2. Competition coefficients (α) as a function of pairwise trait distance for each trait. Traits shown are: **A)** leaf area, **B)** root mass fraction, and **C)** water use efficiency. Points represent species-pairs as focal - competitor (α_{ij}, and α_{ji}). Predicted relationships are shown with solid lines, whereas dashed lines represent slopes that are not significantly different from zero. Grey shading represents 50% credible intervals. For each pair, we calculated trait distance as i - j for α_{ij}, and j – i for α_{ji}. Thus, positive trait distances reflect the focal species having higher trait values than competitor. Trait distances were standardized to mean zero and standard deviation of one. We modeled competition coefficients (α) using Bayesian regression with lognormal likelihood as a function of LA, RMF, and WUE (no interactions) with random effects of $species_i$ and $species_j$. See Supplemental Table 2 for all effect sizes, 95% credible intervals, and probability of difference (PD).

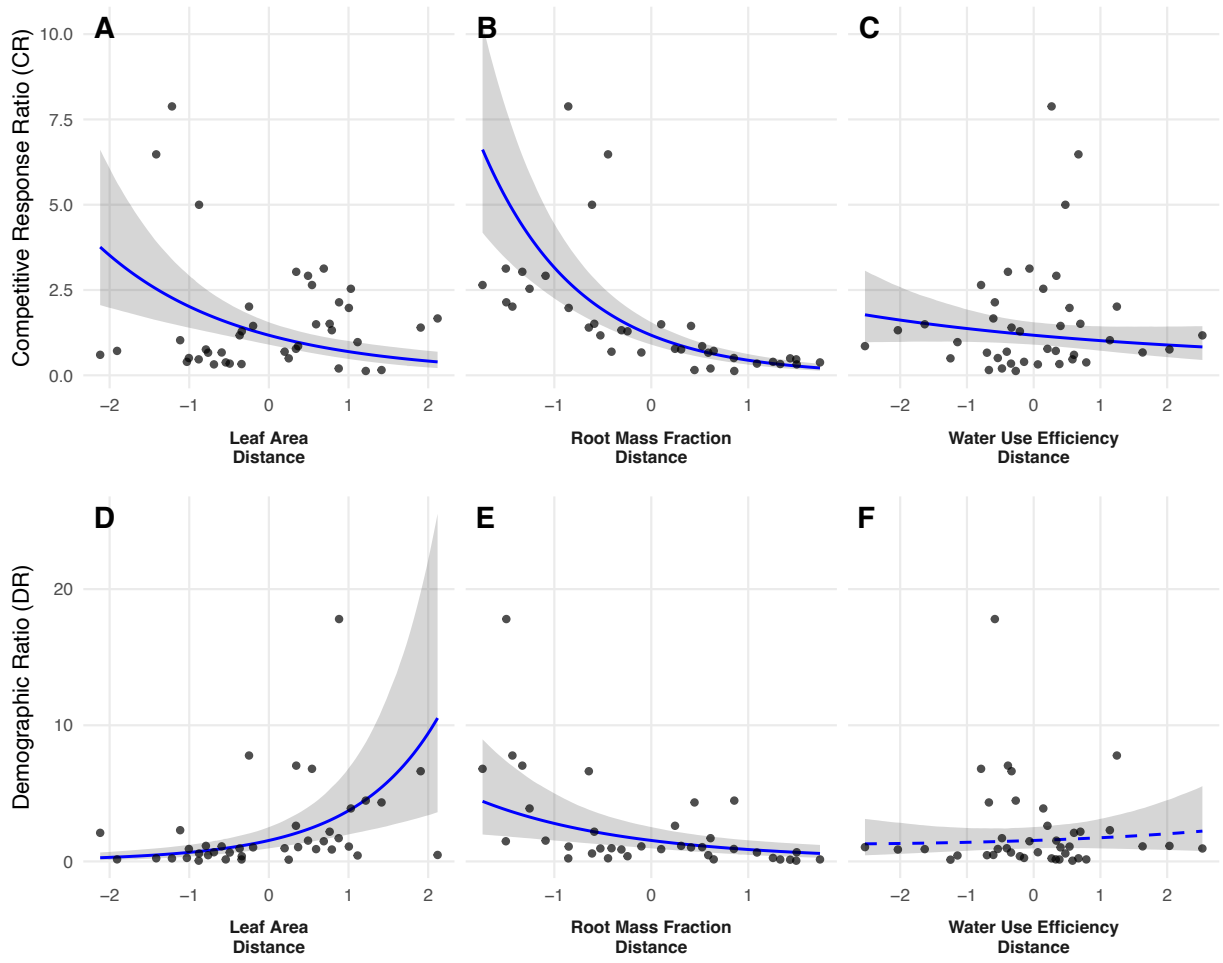


Figure 3. Competitive response ratio and demographic ratio as a function of trait distance for each trait.
Traits shown are: **A, D)** leaf area, **B, E)** root mass fraction, and **C, F)** water use efficiency. Points represent species pairs. Predicted relationships are shown with solid lines, whereas dashed lines represent slopes that are not significantly different from zero. Grey shading represents 50% credible intervals. For each pair, we calculated trait distance as i - j for demographic ratio $(DR)_i$ and competitive response ratio $(CR)_i$, and j – i for DR_j and CR_j. Positive trait distance reflects focal species scoring higher than competitor. Trait distances were standardized to mean of zero and standard deviation of one. We modeled the DR and CR with Bayesian regression with lognormal likelihood as a function of LA, RMF, and WUE (no interactions) with random effects of $species_i$ and $species_j$. Larger DR values represent focal species having greater fitness than its competitor, while smaller CR values represents focals that are more resistant to competition than their competitors (large CR values represent focals less resistant to competition). See Supplemental Table 2 for all effect sizes, 95% credible intervals, and probability of difference (PD).

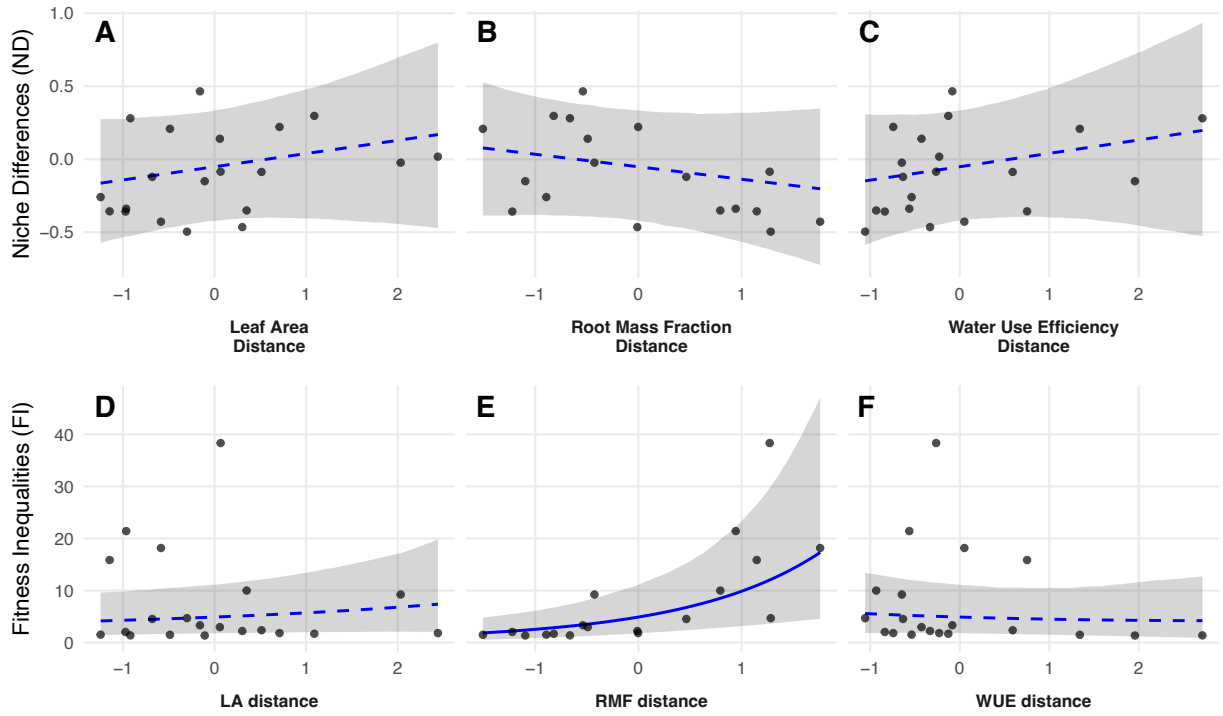


Figure 4. Niche differences and fitness inequalities as a function of trait distance for each trait. Traits shown are: **A, D)** leaf area, **B, E)** root mass fraction, and **C, F)** water use efficiency. Points represent species pairs. Predicted relationships are shown with solid lines, whereas dashed lines represent slopes that are not significantly different from zero. Grey shading represents 50% credible intervals. For each pair, we calculated trait distance as the absolute value of i - j. Positive trait distance reflects focal species scoring higher than competitor. Trait distances were standardized to mean of zero and standard deviation of one. We modeled niche differences and fitness inequalities with Bayesian regression as a function of LA, RMF, and WUE (no interactions). See Supplemental Table 2 for all effect sizes, 95% credible intervals, and probability of difference (PD).

Bridge

This chapter examined how evolutionary relatedness and trait dissimilarity influenced competitive interactions in a group of herbaceous annual plants. We found that phylogenetic distance had no relationship with measured traits, suggesting evolutionary relatedness is a poor proxy for similarity of functional traits in this community. Nevertheless, trait dissimilarity predicted competitive interactions: focal species with greater leaf area than their competitors had both greater fitness and competitive resistance, while greater dissimilarity in root mass fraction amplified fitness inequalities and reduced niche differences. These results suggest that functional

traits contribute to competitive outcomes independently of evolutionary history, and that the same trait can simultaneously promote and/or hinder coexistence via niche and fitness differences. Evolutionary history and trait variation among species not only shapes competitive interactions, but also population persistence across a changing environment. My third chapter explores how phenotypic plasticity and its evolution vary across a species' range in response to a historic drought.

III. THE EVOLUTION OF PLASTICITY IN DROUGHT-RELATED TRAITS IN CENTRAL AND EDGE POPULATIONS OF MIMULUS CARDINALIS

Contributions

Emily Cook, Dr. Seema Nayan Sheth, and Dr. Jeffrey Diez conceived the research idea; Emily Cook, Dr. Seema Nayan Sheth, Dr. Jeffrey Diez, Dr. Lucas J. Albano, Xitlaly Gomez-Vega, Katelin Kutella, Mariam Moazed, Marissa Strebler, Dachuan Wang, Dr. Christopher D. Muir, Dr. Lluvia Flores-Renteria, Dr. Jason P. Sexton performed the experiment; Emily Cook analyzed the data with input from Dr. Seema Nayan Sheth, Dr. Jeffrey Diez; Emily Cook wrote the manuscript with contributions from all authors.

Introduction

Climate change is expected to have far-reaching consequences for biodiversity and extinction risk worldwide (Anderson & Song, 2020; Blanco-Sánchez et al., 2023). Shifts in temperature and precipitation regimes are already driving geographic range changes, with many species expanding at their leading edges; i.e., shifting poleward in latitude and upward in elevation (Parmesan, C., Yohe, G., 2003). In contrast, trailing-edge populations, typically found at lower latitudes and elevations, may be experiencing demographic decline or even local extinction as conditions become less favorable (Sheth & Angert, 2016). Range-edge populations

are of particular interest because the demographic and evolutionary consequences of environmental change often vary across species' geographic distributions, making them important for understanding range dynamics and persistence under climate change (Hampe & Petit, 2005; Sexton et al., 2009). The persistence of range-edge populations may depend on the interplay between rapid evolutionary responses (Benning et al., 2023; Gienapp et al., 2008; Jump & Peñuelas, 2005) and phenotypic plasticity, the ability of a single genotype to express multiple phenotypes in different environments (Bradshaw, 1965; Münzbergová et al., 2017; Zettlemoyer & Peterson, 2021). Although evolutionary change at range edges has received considerable attention (Angert et al., 2020; Colautti et al., 2010; Macel et al., 2017), the roles of phenotypic plasticity, and particularly the evolution of plasticity itself, remain less well understood at range margins (Anstett et al., 2021).

Theoretical and empirical work has shown that phenotypic plasticity has the potential to buffer populations from environmental change and to shape evolutionary trajectories (Ghalambor et al., 2007; Nicotra et al., 2010; Sultan & Bazzaz, 1993). Plasticity can be adaptive (increasing fitness), maladaptive (decreasing fitness), or neutral with respect to fitness (Scheiner, 1993). Theory suggests that selection may therefore favor increased, reduced, or unchanged plasticity depending on environmental context, and associated costs (DeWitt et al., 1998; Ghalambor et al., 2007). Even when plasticity is adaptive, selection may favor an intermediate magnitude of plasticity, as plastic responses can incur fitness costs, such as the energetic cost of producing and maintaining plasticity (DeWitt et al., 1998; Scheiner, 2013), a prediction supported by empirical work (Anderson et al., 2021). Plastic responses may also influence the rate of evolutionary change. Theoretical models suggest that by allowing phenotypes to adjust to novel environments, plasticity can weaken selection and slow evolutionary responses when the plastic response is highly favored in the new environment (Ghalambor et al., 2007; Price et al., 2003). Alternatively,

plasticity can “buy time” for adaptive evolution to take place (Baldwin effect; Baldwin, 1896; Lambert et al., 2025) and reduce the likelihood of extinction in new environments (Ghalambor et al., 2007). Thus, plasticity is both a mechanism of persistence and a driver of evolutionary dynamics, especially in rapidly changing climates.

Given the potential importance of plasticity for population persistence, understanding how plasticity varies across species’ ranges is critical for predicting plant responses to climate change (Cicchino et al., 2024; Lázaro-Nogal et al., 2015; Li et al., 2016; Molina-Montenegro & Naya, 2012). Theory has suggested that plasticity should vary spatially across species’ ranges, reflecting environmental heterogeneity (Chevin & Hoffmann, 2017; Levins, 1963; Scheiner, 1993). The Climate Variability Hypothesis (CVH) (Janzen, 1967) posits that populations experiencing greater climatic fluctuations should evolve broader environmental tolerances and greater plasticity than populations experiencing more stable conditions (Ghalambor, 2006). Although this hypothesis traditionally focuses on temperature seasonality, it could apply to other aspects of climatic variation such as inter-annual variation in precipitation. When environments are consistently variable, selection may favor increased plasticity if plastic responses are adaptive in those conditions, on the other hand, if range environments are consistently harsh or stressful, than edge environments may also favor loss of plasticity (canalization) if plastic responses are maladaptive (Zettlemoyer & Peterson, 2021), where the costs of maintaining plasticity in a stressful environment outweighs the benefit. For example, arid edge populations of wild emmer wheat (*Triticum dicoccoides)* showed lower plasticity than core populations in response to water stress, consistent with the idea that consistently stressful environments may favor fixed rather than plastic responses (Volis et al., 2015). These contrasting expectations, plasticity favored under variable conditions versus constrained under harsh ones, highlight that range edges may harbor either enhanced or reduced plasticity, depending on their environmental

and selective history. In addition to environmental conditions, the demographic and evolutionary processes may also constrain plasticity. For example, empirical work has shown that range-edge populations can be small, isolated, and genetically depauperate (Ellstrand & Elam, 1993; Jump et al., 2003; Pironon et al., 2015), which can limit the genetic variation needed for plasticity to evolve.

Phenotypic plasticity can evolve via natural selection when heritable variation in plastic responses is present, and both spatial and temporal environmental variation can drive this evolution by imposing selection on reaction norms, modeled by theory (Chevin & Lande, 2010; Lande, 2009; Scheiner, 1993). Although the CVH is typically applied to spatial gradients, it is also relevant in the context of temporal variability in the environment (Wooliver et al., 2020). Theory predicts that novel shifts in the environment (e.g., prolonged drought, shifts in precipitation variability) may select for increased plasticity when environmental fluctuations are consistently variable (e.g. temporally autocorrelated), such that past conditions reliably predict future ones, and individuals can adaptively track environmental cues (Botero et al., 2015; Lande, 2009; Vinton et al., 2022). Empirical support for this has been shown in experimental evolution in microalga, where plasticity evolved to lower levels under less predictable environmental fluctuations (Leng et al., 2023). Moreover, the potential for plasticity to evolve depends not only on current selective pressures but also on how contemporary environments differ from those experienced historically (Snell-Rood & Ehlman, 2021). Yet relatively few studies have examined how recent climatic events act as agents of contemporary evolution of plasticity at range edges. Taken together, theory predicts that phenotypic plasticity may vary across species' ranges and may also evolve through time in response to fluctuating environments, but the direction and magnitude of these changes at range edges are uncertain. Addressing this gap requires integrating spatial and temporal data to understand how plasticity influences persistence and evolutionary

potential in the face of climate change (Chevin et al., 2010; King & Hadfield, 2019; Preston et al., 2022).

We focus on scarlet monkeyflower, *Mimulus cardinalis, syn. Erythranthe cardinalis* (Fraga, 2018), a riparian perennial herb distributed across a broad latitudinal gradient in western North America. Populations span substantial climatic variation, with southern, trailing-edge populations experiencing greater historical inter-annual variability in precipitation than northern, leading-edge populations (Muir & Angert, 2017). Populations experienced a severe drought between 2012 and 2015, which increased contemporary inter-annual variability in precipitation, particularly in central and trailing-edge populations (Figure 5). The populations used in the current study were previously evaluated for evolutionary responses of trait means (specifically, flowering phenology, specific leaf area (SLA), leaf dry matter content (LDMC)) to this drought (Sheth et al., 2026). In that study, individuals in the northern garden flowered earliest, whereas individuals in the southern garden exhibited the greatest SLA and least LDMC (Sheth et al., 2026). LDMC was under weak stabilizing selection in the southern garden, SLA was under weak negative directional selection in the southern garden, and first flower date experienced strong selection for earlier flowering time across all gardens. Finally, evolutionary responses between ancestors and descendants were limited, with some population exceptions (Sheth et al., 2026). These results provide a baseline for examining the importance of phenotypic plasticity and selection on plasticity in the present study.

Here, we evaluate how phenotypic plasticity varies across the species' range, whether plasticity has evolved in response to this extreme drought, and whether plasticity is adaptive. Using a resurrection approach, we compared ancestors and descendants collected before and after the drought from two leading-edge, two central, and two trailing-edge populations. We transplanted individuals into three common gardens spanning the species' range, and we

measured key drought-related traits and fitness. We address the following research questions: (Q1) Does the magnitude of phenotypic plasticity differ among populations from regions that differ in climatic variability? (Q2) Did the magnitude of plasticity evolve following an extreme drought? (Q3) Is phenotypic plasticity associated with higher fitness, and if so, does this relationship differ among source populations from across the range?

We hypothesized that (H1) phenotypic plasticity varies across the range of *Mimulus cardinalis*, with populations from historically more climatically variable regions exhibiting greater plasticity; specifically, trailing-edge populations (greatest historical inter-annual precipitation variability) are predicted to be the most plastic, central populations intermediate, and leading-edge populations (lowest variability) the least plastic. (H2) The magnitude of plasticity will evolve to be greater in descendant populations following the historic drought if genotypes having greater plasticity are selected for. Alternatively, the drought could favor reduced plasticity if drought conditions consistently favor a canalized response, or if plastic responses are costly. (H3) Central and trailing-edge populations experiencing greater contemporary climatic variability will exhibit adaptive plasticity (plastic phenotypes associated with higher fitness), whereas leading-edge populations will not. This study provides novel insight into the magnitude, evolution, and adaptive value of phenotypic plasticity at range edges, identifying when and where plasticity may facilitate population persistence under environmental change.

Methods

Study System

Here, we use *Mimulus (Erythranthe) cardinalis* (Phrymaceae) to address the hypotheses described above. *M. cardinalis* is a perennial, hummingbird-pollinated forb, which grows in

riparian habitats across a strong environmental gradient varying in temperature and increasing in inter-annual variation in precipitation from central Oregon to northern Baja California, Mexico (Figure 1) (Muir & Angert, 2017; Anstett et al., 2021). We focus on three traits of known importance for coping with drought: date of first flower, specific leaf area (SLA), and leaf dry matter content (LDMC). These traits fall into two strategies that plants use to survive under drought conditions: drought escape, where plants reduce their exposure to drought through rapid development and reproduction, and drought avoidance, where plants limit growth and water loss to maintain fitness under drought conditions (Kooyers, 2015; Ludlow, 1989). Plastic responses could be expressed through shifts toward either accelerated reproduction (escape) or more conservative leaf morphology (avoidance), depending on environmental conditions.

Experimental Design

We used data from a study across 3 field common gardens with a resurrection approach (methods detailed in Sheth et al., 2026) (Figure 5). We compared ancestors and descendants collected before and after a historic drought between 2012 and 2015 from two northern leading-edge (N1, N2), two central (C1, C2), and two southern trailing-edge (S1, S2) populations. Seeds were collected from each population from ~ 50-200 individuals before the drought, in 2010 (ancestors), and after the drought, in 2017 (descendants) (Sheth et al., 2026). All seeds were grown in a greenhouse at North Carolina State for a "refresher generation" to control for maternal and seed storage effects (Franks et al., 2007) and then were crossed within each population and cohort to generate seeds of known pedigree. We followed a nested, paternal half-sibling design in order to estimate quantitative genetic parameters for other studies in the ancestral cohort (Supplemental Table 1) (Sheth et al., 2026).

Seedlings from each cohort (pre-drought ancestors and post-drought descendants) and each population were propagated in trays in greenhouses, and then transplanted in 2023 when seedlings were approximately 6 weeks old, into 3 common gardens in the western United States: close to the northern edge of the species range at the Friends of Buford Park and Mt. Pisgah Native Plant Nursery in Eugene, OR, the latitudinal center in Sierra National Forest's Batterson Work Center in Oakhurst, CA, and near the southern range limit at San Diego State University's Santa Margarita Ecological Reserve in Temecula, CA (Sheth et al., 2026). Plants were arranged in a complete randomized block design so that each sire from each population was represented and positioned randomly in each of the 10 blocks in each garden (n = ~14,293 plants in total). Plants were irrigated with drip tape (Aqua-Traxx; Toro, El Cajon, CA, USA) along each row in each garden 5-7 days per week to promote seedling establishment, and we reduced the irrigation gradually as the growing season advanced, and discontinued irrigating at the start of winter precipitation (Sheth et al., 2026).

The climate conditions during the 2023 field season did not exhibit drought conditions, the southern and central common gardens experienced unusually wet conditions, while the northern garden experienced unusually dry conditions (Figure 5C; DeFlorio et al., 2024). Despite this, the gardens did experience meaningful climatic differences during the study period even if this variation did not replicate the magnitude or structure of historical drought regimes. Mean spatial precipitation variability across gardens from May to August 2023 (CV = 0.71) provides a coarse comparison with long-term interannual climate variability. This suggests that plants experienced warmer and drier conditions in the southern garden compared to the northern garden.

Data Collection

As described in Sheth et al., (2026), we measured three traits of known importance for coping with drought throughout the growing season in 2023. Before the majority of plants had begun to flower, fully expanded, healthy leaves from the uppermost node of the main stem on each plant were collected and scanned to measure leaf area (in cm^2) using FIJI version 2.14.0 (Schindelin et al., 2012), then weighed in grams using an analytical balance (Model SPX123 Scout Balance, Ohaus, Parsippany, NJ) to estimate fresh mass. We dried leaves at 76° C for approximately 48 hours and weighed again to estimate dry mass. With these measurements, we estimated specific leaf area (SLA, cm^2/g) as leaf area / leaf dry mass and leaf dry matter content (LDMC, g/g) as leaf dry mass / leaf fresh mass. Plants in the central garden were transplanted later than the other gardens due to high snowfall, and subsequent delays in accessing and developing the site, and consequently were delayed in their phenology in 2023. This led to central garden plants being smaller at the time of leaf trait collection in the other gardens, and it was a relatively wet growing season in this region, so we did not collect leaf traits in the central garden. We surveyed the gardens twice per week and recorded the date that the first flower on each plant opened. At the end of the 2023 growing season, we estimated plant fitness by counting the number of stems with reproductive structures (buds, flowers, fruits, and pedicels) and approximating the total number of reproductive structures on each plant by counting the number of reproductive structures on up to three stems (see Sheth et al., 2026), rather than total seeds per individual, due to the difficulty of counting seeds per fruit in *M. cardinalis*, which can produce thousands of seeds per fruit. As *M. cardinalis* is a perennial, this represents an estimate of first-year fitness only. To verify that counts of reproductive structures were a reliable fitness proxy, we validated them against more direct measures of fitness (total successful fruits and dry

biomass) on a subset of 100 plants per garden. We found significant positive correlations in all three gardens, confirming that reproductive structures are a strong predictor of plant fitness in this study (Sheth et al., 2026). To account for different seedling transplant dates among gardens, we standardized date of first flower within each garden by subtracting the earliest observed flowering date from each garden from all individuals within that garden. Date of first flower represents the number of days after the earliest flower in that garden, with the minimum value set to zero.

Quantifying phenotypic plasticity

To calculate trait plasticity for each family, we used a version of the Relative Distance Plasticity Index (Valladares et al., 2006). We restricted analyses to full-sibling families represented by at least two replicates in each garden (Supplemental Table 1). We calculated all pairwise differences in trait values across the three common gardens within each family from each population and cohort. RDPI is typically defined as the pairwise difference in trait values divided by the sum of the two trait values (Valladarez et al., 2006). However, with this formulation, families with identical absolute trait shifts can appear to have different RDPI values solely because they differ in baseline trait magnitude. Because mean trait values varied substantially among populations, cohorts, and gardens, we divided each pairwise trait difference by a single global mean of the trait, calculated across all populations, cohorts, and gardens. This version of the RDPI yields an index of plasticity that is not biased by mean trait differences among groups. For each family, we then averaged these pairwise values to obtain a plasticity index. Because some genotypes may exhibit shifts opposite to the overall direction of trait change across gardens, potentially indicating maladaptive plasticity, we retained the sign of each pairwise difference (following Anderson et al., 2021). This yields positive values for responses

consistent with the overall trend and negative values when genotypes shift in the opposite direction.

For leaf morphological traits, we were unable to collect measurements from the central garden; thus, leaf-trait plasticity indices reflect pairwise comparisons between only the northern and southern gardens. To maintain comparability, we also estimated first flower date plasticity using northern and southern gardens only in the supplement, as inclusion of the central garden produces slightly different values (Supplemental Table 2). Plasticity estimates were generally higher for all populations and cohorts when calculated using only the northern and southern gardens; however, this pattern was not consistent across all populations, as S1 showed reduced plasticity when the central garden was excluded.

Statistical Analyses

All models described below were fit as Bayesian models in R (Version 4.4.2; R Core Team 2025) using the 'brms' package (Version 2.22.0; Burkner, 2017). We ran each model with four chains, 2000 warm-up iterations and 2000 sampling iterations. We assessed model convergence using the Gelman–Rubin statistic (R), where values close to 1.0 indicate convergence across chains (Gelman & Rubin, 1992). We visually inspected trace plots of the four independent chains to check for adequate mixing.

Spatial variation in trait plasticity

We used linear models for each trait to compare trait plasticity among populations and cohorts, with fixed effects of population, cohort and a population × cohort interaction. To assess the effect of population on trait plasticity while accounting for cohort differences, we computed marginal posterior predictions from our model by averaging over cohorts. For each draw from

the posterior distributions, we then calculated pairwise differences among all populations and the posterior probability that each population difference differed from zero (posterior probability of difference, PD) as either the probability of being greater than zero or the probability of being less than zero, whichever probability was greater. For plasticity analyses (Q1), we used the default priors in 'brms': improper flat priors for all fixed effects, a Student-t(3, 0.3, 2.5) prior for the intercept, and a Student-t(3, 0, 2.5) prior for the residual standard deviation.

To assess whether plasticity estimates differed from zero, we extracted posterior predictions for each population × year combination and summarized the posterior predictive distribution by computing the mean and 95% credible interval. We calculated the probability that plasticity was different from zero (PD), where a PD approaching 1.0 indicates that nearly all posterior draws fall on one side of zero, providing strong evidence for non-zero plasticity. Estimates of plasticity are reported in Supplemental Table 2 (first flower date plasticity), Supplemental Table 3 (SLA plasticity), and Supplemental Table 4 (LDMC plasticity).

Evolution of trait plasticity

To assess the overall effect of cohort (2010 vs. 2017) on each trait's plasticity while accounting for population differences, we computed marginal posterior predictions from the same model we used from Q1 by averaging over populations. We estimated the cohort effect as the difference in marginal predictions between cohorts and examined the posterior distribution of these differences. To identify which populations specifically showed evidence for evolved plasticity between ancestors and descendants, we computed population-specific cohort effects by calculating marginal posterior predictions for each population × cohort combination. Pairwise differences between cohorts within each population were then estimated and visualized using posterior distributions. We used the posterior distribution of each pairwise comparison to

calculate the probability that cohorts were different (posterior probability of difference, PD). This approach allowed us to detect population-level changes in plasticity between cohorts even in cases where the overall cohort effect was not significant, providing a clear assessment of population × cohort interactions.

Adaptive value of trait plasticity

We evaluated whether plasticity in date of first flower, SLA, and LDMC was adaptive, where the most plastic full-sibling families had the greatest average fitness across environments (Van Kleunen & Fischer, 2005). We quantified selection on plasticity using the family-level plasticity indices described above (Q1). For each trait, fitness was modeled as a function of plasticity while accounting for population and cohort. Because plasticity may incur costs to fitness leading to an intermediate optimum, we compared linear models to alternative models that included a quadratic plasticity term, and its interaction with population, to assess the possibility of stabilizing selection. Model support was evaluated using the expected log predictive density (ELPD) via loo_compare in the 'LOO' package (Vehtari et al., 2017). The best-supported model for each trait was identified as the model with the smallest ELPD difference relative to its standard error. Because models including quadratic terms were not better supported than linear models (Supplemental Table 5), we used a consistent linear model structure for all traits. The final model took the form:

Fitness ~ population * cohort + plasticity + population : plasticity

This model tests (1) whether plasticity is associated with fitness on average (directional selection), and (2) whether the strength or direction of selection on plasticity differs among

populations. To estimate selection acting across all gardens, we calculated mean fitness for each family across gardens. Fitness was relativized by dividing each family's mean fitness by the mean of all families' fitness. Because we calculated plasticity in the date of first flower with all three gardens, we assessed fitness averaged across all three gardens (Supplemental Table 7) and using only the northern and southern gardens (Supplemental Table 6). Plasticity values were standardized (mean = 0, SD = 1) before analysis. Populations were treated as independent, rather than being averaged within regions, because although populations within regions share broad climatic context (i.e. leading-, central, and trailing-edge), they represent distinct local environmental histories. We evaluated whether our results were sensitive to aggregating populations into regions and re-ran our analyses with region as a predictor while including population as a random effect. These analyses yielded similar results to our population-level models and given that our main goal is to highlight variation among populations, we retained the population-level results.

For selection analyses, we used weakly informative priors to improve convergence and reflect the scale of standardized predictors and relativized fitness. Specifically, the model intercept was assigned a Normal (1, 1) prior reflecting mean relativized fitness near one, all fixed-effect coefficients (including main effects and interactions) were assigned Normal (0, 2) priors, and the residual standard deviation was assigned an Exponential (1) prior. Posterior distributions of plasticity slopes were extracted using emtrends from the 'emmeans' package (Lenth, 2018). We summarized uncertainty, quantified the posterior probability that each slope differed from zero, and visualized both the slope distributions and the predicted relationship between plasticity and fitness. All parameter estimates and credible intervals (CIs) were summarized using the median and 95% quantile intervals of the posterior distribution.

Results

Population variation in phenological plasticity tracks climate variability

All traits exhibited substantial plasticity; however, the pattern and magnitude of plasticity differed among traits, populations, and cohorts (Figure 6).

First flower date plasticity: There was significant plasticity in the timing of first flower date in all populations. Specifically, across all genotypes, the mean plasticity value (0.34) corresponds to an average shift in date of first flower of ~8 days across gardens (Figure 6A). Consistent with our hypothesis that populations experiencing greater inter-annual variability in precipitation would exhibit greater plasticity, we observed clear regional differences. On average, leading-edge populations, which have experienced lower inter-annual variation in precipitation, (Figure 5C) were significantly less plastic than both central and trailing-edge populations experiencing higher variability in precipitation (Figure 6A, Supplemental Figure 3). One central population (C1) was more plastic than both trailing-edge populations. Within regions, populations also differed in magnitudes of plasticity: While not significant, N2 tended to be less plastic than N1 (Probability of difference (PD) = 0.90, Supplemental Figure 3), and C1 was significantly more plastic than C2.

When excluding central garden plants from estimates of first flower date plasticity, central populations, which have experienced intermediate historic inter-annual variation in precipitation (Figure 6C), were the most plastic, followed by southern trailing-edge populations, and northern leading-edge populations showing the lowest plasticity (Supplemental Figure 1). One central population (C1) was more plastic than all populations except S2, while C2 was greater than N1 and S1, but not S2. One leading-edge population (N2) was less plastic than both trailing-edge populations (S1 and S2), but N1 and S2 were not significantly different. Within

regions, populations sometimes differed in magnitudes of plasticity: S2 had greater plasticity than S1 (Supplemental Figure 1).

Leaf trait plasticity: There were significant differences in plasticity among populations in both leaf traits. However, in contrast to our hypothesis, population-level differences in plasticity did not follow our prediction that there would be greater plasticity in the central and trailing-edge populations that experienced greater inter-annual variation in precipitation. Specifically, in SLA plasticity (Figure 6B), one trailing-edge population (S2) exhibited the greatest plasticity overall. The two leading-edge populations (N1, N2) showed intermediate plasticity, being higher than both central populations (C1, C2) and one trailing-edge population (S1), but lower than S2 (Supplemental Figure 5). The central populations and S1 had the lowest plasticity, with no meaningful differences among them. In LDMC plasticity (Figure 6C), both leading and central populations were less plastic than one trailing-edge population (S2), while N2 was greater than C2. Additionally, S1 was less plastic than S2 (Supplemental Figure 7).

Plasticity in phenology, but not leaf traits, evolved between ancestors to descendants following drought

Patterns of evolutionary change in plasticity between pre-drought ancestors and post-drought descendants varied among traits and populations. When including the central garden in analyses, there was not a strong overall effect of cohort on first flower date plasticity (PD = 0.90), but we found evidence of a population x cohort interaction: evolution of increased plasticity in one center (C1) and one trailing-edge population (S1) from ancestors to descendants, and evolution of decreased plasticity in one leading-edge (N2) population (Figure 6A; Supplemental Figure 4). In contrast, there was no overall effect of cohort in SLA (PD = 0.77) or

LDMC (PD = 0.55) plasticity and no change within individual populations in plasticity between cohorts (Figure 6B, 6C; Supplemental Figure 6, 8).

When excluding the central garden in analysis, we found evidence of an overall effect of cohort on first flower date plasticity (PD = 0.99), and a population x cohort interaction: one leading-edge population (N2) showed reduced plasticity in 2017 descendants compared to 2010 ancestors, whereas both central populations and one trailing-edge population exhibited increased plasticity from ancestors to descendants (Supplemental Figure 2).

Plasticity is largely neutral, and sometimes maladaptive, in relation to fitness

Relationships between plasticity and fitness were limited across traits and populations. When including central garden in average fitness, we found positive directional selection on first flower date plasticity in one trailing-edge population (S2) (Figure 7A, Supplemental Figure 10; Supplemental Table 7). We found negative selection on SLA plasticity in one center population (C1) and weak negative selection on one trailing-edge population (S2) (Figure 7B, Supplemental Figure 12), and weak negative selection on LDMC plasticity in one center population (C1) (Supplemental Figure 14).

When excluding central garden in average fitness, we found evidence for negative directional selection on first flower date plasticity in one trailing-edge population (S1) (Supplemental Table 6, Supplemental Figure 9, 15A), where increased plasticity was associated with lower fitness. We also detected negative directional selection on SLA plasticity (Supplemental Table 6; Supplemental Figure 11, 15B) and LDMC plasticity (Supplemental Table 6; Supplemental Figure 13, 15C) in a central population (C1).

Discussion

Despite the potential importance of plasticity for population persistence, studies exploring plasticity at range margins remain rare, even though range edge populations are often considered to be most vulnerable to novel conditions. Here, testing how plasticity varies across *M. cardinalis'* range and following an extreme drought event, we found significant phenotypic plasticity in all measured traits and populations. However, plasticity in first flower date was the only measured trait that was consistent with predictions from the Climate Variability Hypothesis (CVH), with greater plasticity in first flower date in trailing-edge populations that experience greater inter-annual variation in precipitation. Moreover, plasticity did not consistently increase after an extreme drought, and we found an overall lack of adaptive plasticity in most cases. These results highlight the potential for plasticity at range margins to buffer against future demographic declines as a result of climate change but also suggest that both spatial climatic gradients and extreme climatic events, alongside other factors such as costs of plasticity or limits to genetic variation, may contribute to trait and population specific limits on the evolution and adaptive value of plasticity.

Support for the climate variability hypothesis is trait-specific

Spatial variation in phenotypic plasticity is expected when populations experience different degrees of climatic variability, as predicted by the Climate Variability Hypothesis (CVH) (Janzen, 1967; Ghalambor et al., 2006). In our system, trailing-edge populations have experienced greater historical variability in inter-annual precipitation than central and leading-edge populations (Figure 5), providing an opportunity to evaluate whether variation in plasticity across the species' range is consistent with CVH predictions. The plasticity of first flower date in trailing-edge and central populations were more plastic than leading-edge populations (Figure

6A), consistent with the prediction that greater inter-annual precipitation variability favors the evolution of increased plasticity in phenology.

This result aligns with previous studies showing that plants originating from environments with higher precipitation variability exhibit greater plasticity in phenology (Pratt & Mooney, 2013; Scheepens et al., 2018) and a meta-analysis that found that, although most studies did not detect significant differences between leading and trailing edges, when differences occurred, trailing-edges more frequently exhibited greater phenological plasticity (Zettlemoyer & Peterson, 2021). Explicit tests of the CVH for phenological traits remain rare, as CVH studies have more commonly focused on leaf morphology, physiology and growth-related traits (Gianoli & González-Teuber, 2005; Lázaro-Nogal et al., 2015; Molina-Montenegro & Naya, 2012).

Results from our study contrast with Anstett et al., (2021), who found greater plasticity in first flower date in central and leading-edge *M. cardinalis* populations when drought was imposed in a greenhouse environment. This difference could reflect contrasting environmental contexts of the two studies: Anstett et al. quantified plasticity using a controlled water-availability treatment, whereas our common garden experiment exposed plants to a suite of climatic conditions, including variation in photoperiod, temperature, soil properties, and moisture across a wide climatic gradient. Plasticity in our field study likely reflects responses to several climatic cues rather than water limitation alone, since we did not impose an experimental drought treatment. Because *M. cardinalis* is a riparian species that requires irrigation for survival in a common garden, our results necessarily reflect responses to broader climate gradients than drought. However, the gardens did experience meaningful climatic differences during the study period even if this variation did not precisely replicate the magnitude or structure of historical drought regimes. There was significant precipitation variability among gardens from May to August in 2023 (CV = 0.71), which exceeded the interannual precipitation variability typically

experienced by any given population over 30 years (CV = 0.33 - 0.56). This suggests that the climate gradients plants experienced across gardens were meaningful, even if spatial variation did not precisely replicate historic drought regimes.

When excluding the central garden in our plasticity estimates, spatial variation of flowering time plasticity was slightly altered. The plasticity of first flower date was greater in one trailing-edge (S2) and both central populations compared to leading-edge populations (Supplemental Figure 1), consistent with CVH predictions. However, the other leading-edge population (N1) was not significantly different than one trailing-edge population (S2) and the two trailing-edge populations were significantly different from one another, suggesting that plasticity does not always increase uniformly with historic climatic variability across the range.

We did not detect a significant geographic pattern of plasticity in leaf traits. Plasticity in specific leaf area (SLA; Figure 6B) and leaf dry matter content (LDMC; Figure 6C) varied idiosyncratically among populations, with neither leading, central, nor trailing-edge populations consistently exhibiting the greatest plasticity, despite a pronounced gradient in inter-annual precipitation variability. This contrasts with previous studies that found positive associations between inter-annual precipitation variability and plasticity in drought-related leaf morphological traits (Gianoli & González-Teuber, 2005; Lazaro-Nogal et al., 2015), though this relationship is not universal (Welles & Funk, 2021).

Together these results suggest that patterns of plasticity across species ranges may depend on the specific pathways of drought adaptation. In *M. cardinalis*, plasticity in flowering phenology may be an important target of selection under increasing drought severity and variability (discussed below). Even though we only found evidence for the CVH in first flower date plasticity, this nonetheless suggests that greater environmental variability may sometimes select for greater plasticity. Identifying more key traits, and under what ecological or climatic

contexts variability favors plasticity, represents an important direction for future research and could improve predictions of when plasticity evolves in response to long-term environmental heterogeneity at range edges.

Divergent evolution of plasticity may have contrasting consequences for range persistence

Evolutionary responses have important potential consequences for population persistence and range dynamics. At the trailing-edge and range center, where populations may face the greatest climatic stress and variability (Cohen et al., 2025; Fredstone, 2021; Gaston, 2003; Hoffmann & Parsons, 1997).The evolution of increased plasticity can broaden the range of conditions a population can tolerate, potentially facilitating their persistence under novel conditions (Chevin et al., 2013; Scheiner, 1993). Support for the hypothesis that populations would evolve increased plasticity between the ancestor and descendant cohorts following drought depended on the population and trait. We found that plasticity in first flower date evolved between ancestors and descendants in three of six populations, but the direction and magnitude of change varied. Specifically, first flower date plasticity increased in one trailing-edge population (S1) and one central population (C1), while one leading-edge population (N2) evolved a loss of plasticity (Figure 6A).

These results partially support our hypothesis and could be explained by the fact that both S1 and C1 experienced greater inter-annual variability in precipitation during the drought period than their typical winter climate (Figure 5C), consistent with CVH predictions. Increased plasticity in first flower date in a central and a trailing-edge population could buffer populations across variable years, aiding their persistence in this Mediterranean-climate system characterized by precipitation whiplash (defined by increasingly extreme swings between drought and wet years) (Swain et al., 2018) and could buffer under future precipitation whiplash, which is not

only stronger in Southern California, but is projected to intensify across nearly all of California (Swain et al., 2018). Increased plasticity in trailing-edge populations may help buffer populations under these conditions, potentially contributing to survival and buying time for evolutionary rescue (Chevin et al., 2010, 2013), if the fitness advantage of plasticity outweighs the fitness reductions imposed by more severe drought. However, the absence of increased plasticity in the remaining center and trailing-edge populations, despite similarly high precipitation variability (CV), and the loss of plasticity in N2, indicate that the evolution of plasticity is not solely determined by the magnitude in climatic variability experienced.

In contrast, the observed evolution of decreased plasticity in first flower date from ancestors to descendants in one leading-edge population (N2; Figure 6A) may reflect a canalizing effect (loss of plasticity) of the drought period in this trait. N2 has a history of relatively stable precipitation (low inter-annual variability), suggesting it may not have been subject to strong selection for plasticity in flowering time. The sustained drought may have acted as a consistent pressure favoring earlier flowering phenotypes over plastic responses, reducing plasticity between ancestors and descendants. Consistent with this interpretation, Anstett et al. (2021) found a loss of plasticity in SLA in a trailing-edge population of *M. cardinalis,* illustrating that climate variability does not always select for greater plasticity. Other studies have also found reduced transcriptional plasticity (Preston et al., 2022) and narrower thermal performance breadth (Wooliver et al., 2020) in descendant populations of *M. cardinalis* after this great drought. At the same time, reduced plasticity or a lack of evolution in plasticity in other populations, could reflect costs associated with maintaining plastic responses. At the leading-edge, reduced plasticity could limit the ability of populations to cope with increasingly variable conditions, potentially constraining their northward expansion. Alternatively, if environments at the leading-edge are relatively stable, reduced plasticity may represent an adaptive response

(Matesanz et al., 2010) if reduced genetic diversity and weaker or less predictable droughts lead to fixed trait expression, rather than plastic phenotypes. In either case, reduced plasticity could increase population vulnerability to future extreme events, increasing the risk for local decline. We found no evidence of evolution of plasticity in leaf traits (SLA, LDMC) in any population, suggesting that flowering time may be more responsive to selection imposed by drought than leaf morphological traits. Given that the inclusion of the central garden altered our results of flowering time plasticity, it is possible that leaf trait results would similarly differ with a complete dataset, and future analyses including the central garden data would help in drawing more definitive conclusions.

To further dissect the variation in evolutionary responses in plasticity among populations, future studies could assess which populations, leading-edge, trailing-edge, or central, harbor the most standing genetic variation in plasticity, and thus the greatest potential for adaptive evolution under future climatic change.

Spatial environmental gradients may not reliably select for adaptive plasticity

While plasticity produced substantial trait variation across environments, overall, there was very little evidence for adaptive plasticity across populations and traits. The detection of adaptive or maladaptive plasticity depended on whether the central garden was included or not, which further solidifies the overall pattern of negligible selection on plasticity. In one trailing-edge population (S2), plasticity in first flower date was under positive directional selection, with greater plasticity associated with greater reproductive success (Figure 7A). SLA and LDMC plasticity were also maladaptive in a central population (C1) (Figure 7B, Figure 7C, respectively) suggesting that plastic shifts in these traits translate into lower fitness. Previous studies have found that SLA plasticity was nonadaptive in response to drought conditions in *Lobelia*

cardinalis (Caruso et al., 2006), but adaptive in response to earlier snowmelt in *Ipomopsis aggregata* (Navarro et al., 2022). While plasticity is often thought to be adaptive because it allows individuals to shift their traits in an optimal direction, empirical evidence of adaptive plasticity remains scarce ((Arnold et al., 2019; Gianoli & González-Teuber, 2005) but see Anderson et al., 2021; Baythavong & Stanton, 2010; Boyd et al., 2022; Lázaro-Nogal et al., 2015; Love & Ferris, 2025), particularly at range margins.

Several factors may explain the generally weak or sometimes maladaptive effects of plasticity. Adaptive plasticity requires the environmental cues to reliably predict the selective conditions; when cues are unreliable, plastic responses may be mismatched to the environment, driving selection of reduced plasticity (Bonamour et al., 2019; Snell-Rood & Ehlman, 2021). In addition, the magnitude and direction of selection can be variable over time (Wadgymar et al., 2017), particularly in systems where drought intensity and temperature fluctuates substantially. Thus, even if plasticity appears adaptive at one point in time, its long-term adaptive value may differ. During data-collection in 2023, the southern and central common gardens experienced unusually wet conditions, while the northern garden experienced unusually dry conditions (Figure 5C; DeFlorio et al., 2024). Thus, our experiment captures plastic responses over a spatial environmental gradient, rather than temporal variation within a single site, and these approaches may expose plants to different environmental cues. Across gardens, factors such as temperature, precipitation, and photoperiod, for example, may covary, whereas temporal variation within a single site would primarily reflect interannual climatic variation under a constant photoperiod. These differences could influence the magnitude and adaptive value of plasticity.

Finally, our estimates are based on a single growing season and a proxy for fitness (reproductive structures rather than the number of seeds produced due to the challenges of counting seeds per fruit in *M. cardinalis* which can produce thousands of seeds per fruit), which

may not capture lifetime fitness in this perennial species. We were unable to assess inter-annual variation in selection because mortality reduced sample sizes substantially after the first year in the southern common garden (Sheth et al., unpublished data). Future studies assessing the temporal variation in the strength of selection on plasticity across years may help evaluate the long-term adaptive value of plastic traits.

Conclusion

This study provides a unique empirical test of the role of phenotypic plasticity in shaping population responses to environmental variability at species' range edges. We demonstrate that plasticity in drought-related traits can vary geographically, evolve over contemporary time scales, and cause fitness consequences, though these effects are trait and context specific. Together, these findings suggest that plasticity is unlikely to provide a universal buffer against environmental heterogeneity across species ranges, but instead, may contribute to persistence in some populations and environmental contexts. Our results also suggest that the evolution of plasticity does not consistently track climate variability, and that adaptive plasticity is relatively rare, even across a strong environmental gradient, and after an extreme drought event. Thus, plasticity may only buffer some range-edge populations from negative effects of climate change. Future work is needed to better understand when and where plasticity contributes to adaptation at range margins. In particular, estimating genetic variation in plasticity across populations, and estimating lifetime fitness over multiple years will help understand the conditions under which plasticity evolves, and is favored by selection. Understanding these patterns is critical for predicting species' persistence, range dynamics, and adaptive capacity in the face of ongoing climate change.

Figures

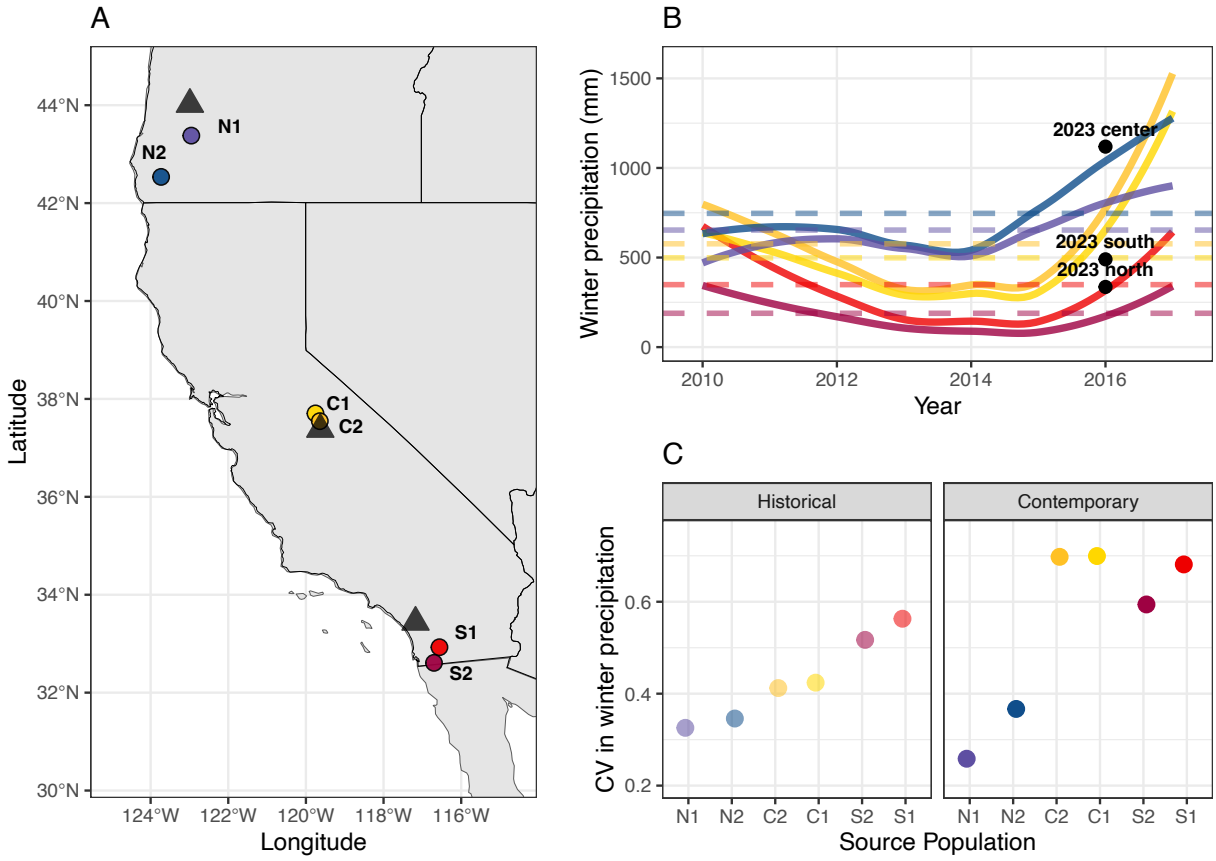


Figure 5. Map of *Mimulus cardinalis* focal populations, winter precipitation, and historical vs. contemporary coefficient of variation in winter precipitation.
A) Map of *Mimulus cardinalis* focal populations (filled and colored circles), and locations of common gardens (black triangles). We compared ancestors and descendants collected before and after a historic drought between 2012 and 2015 from two northern leading-edge (N1, N2), two central (C1, C2), and two southern trailing-edge (S1, S2) populations. **B)** Winter precipitation, where solid lines represent mean winter precipitation for each focal population from 2010 to 2017, dashed lines represent 30-year averages from 1981 to 2010, and values for each common garden in 2023 are shown as points. **C)** Historical (1981 – 2010) vs. contemporary (2011-2017) coefficient of variation (CV) in winter precipitation ranked for each population from lowest to highest historical CV. Mean spatial precipitation variability across gardens in 2023 (CV = 0.71) is provided for comparison with long-term interannual climate variability. Climate data for all focal populations was sourced from ClimateNA (ver. 7.30), and data from each common garden was sourced from the web version of ClimateNA (ver. 7.60; Wang et al. 2016).

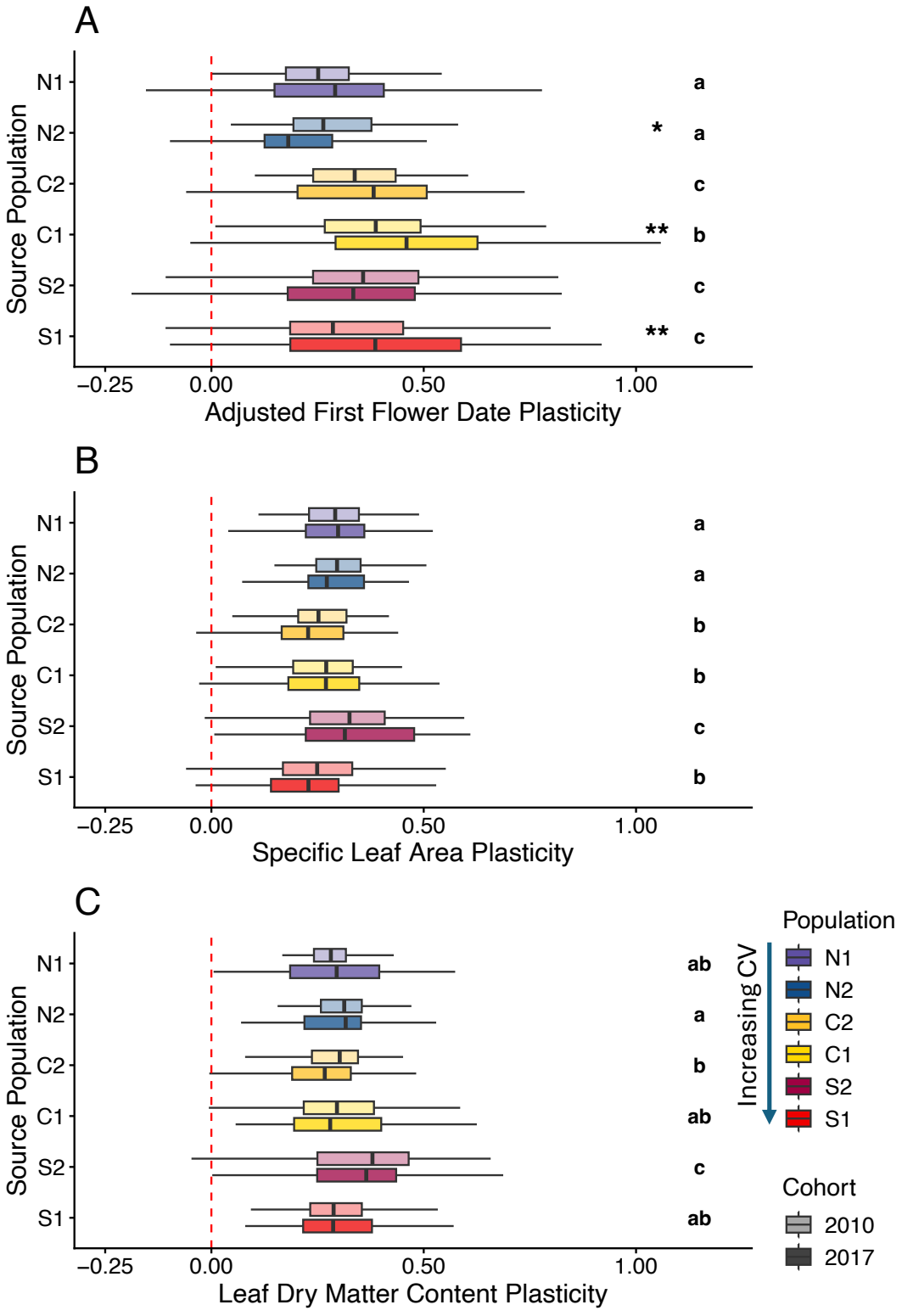


Figure 6. Plasticity in first flower date, specific leaf area, and leaf dry matter content of ancestors and descendants.

A) adjusted first flower date (first flower date – first flower date minimum), **B)** specific leaf area (SLA), and **C)** leaf dry matter content (LDMC) of ancestors (lighter hues) and descendants (darker hues), ranked in order from low winter precipitation CV (N1) to high winter precipitation CV (S1). For first flower date plasticity, plasticity was estimated with northern, central, and southern gardens. Boxplots show medians and interquartile ranges of the raw data; whiskers extend to 1.5× the interquartile range. Asterisks indicate support for differences between cohorts within populations *(PD ≥ 0.95*, ≥ 0.99**, ≥ 0.999***)*, where PD represents the posterior probability that cohort means differ, and letters denote differences across populations, independent of cohort, where groups sharing a letter are not statistically different from each other. On average values will go in positive direction but allows for negative values when genotypes shift trait value in opposite direction. Given a mean adjusted first flower date of ~24 days, a plasticity value of 0.25 corresponds to ~6 days, and 0.5 corresponds to ~12 days of shift in first flower date.

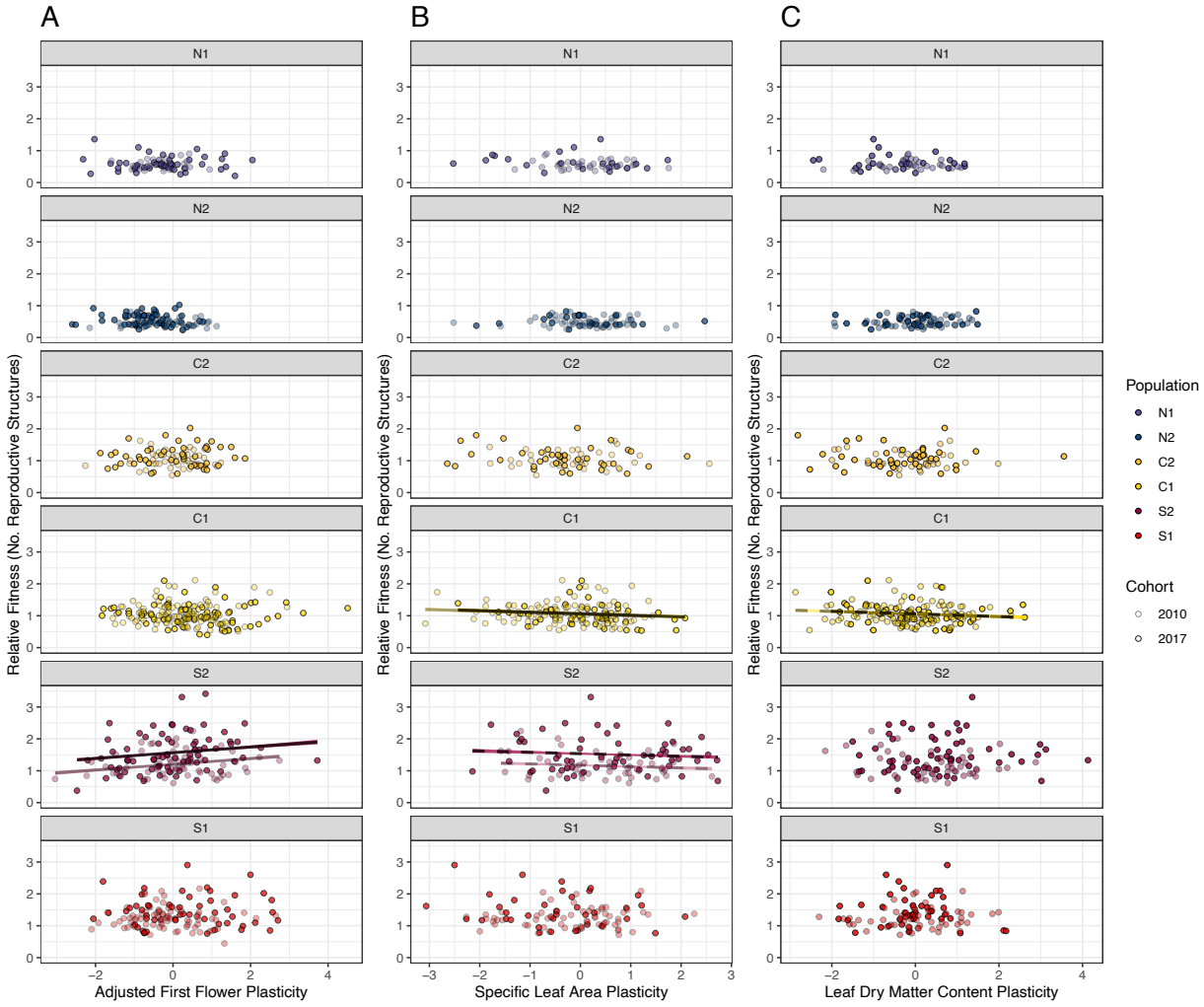


Figure 7. Relative fitness (averaged over northern, central, and southern gardens)as a function of plasticity in first flower date, specific leaf area, and leaf dry matter content.

A) first flower date, **B)** SLA, and **C)** LDMC. Points show full-sibling family averages, colored by population, and transparency indicates cohort (Dark hues = 2010, light hues = 2017). Predicted relationships (solid lines) are shown for slopes that were significantly different from zero, dashed lines represent marginal slopes (PD = 90%) with uncertainty visualized as 50% credible intervals. We estimated slope distributions for the effect of plasticity on fitness while accounting for differences in population and cohort in brms. Posterior distributions of plasticity slopes were extracted using emtrends from emmeans, and uncertainty was visualized with tidybayes.

Bridge

My work has shown that plasticity is shaped by both spatial and temporal environmental variation, highlighting the need to examine trait- and population-level responses to understand selection on plasticity at across species' ranges. In my next chapter, I move from exploring a single species' response novel environments to the response of multiple co-occurring species, as an effort to better understand community level responses to changing environments.

IV. ASSESSING POPULATION DIFFERENTATION IN PLASTIC RESPONSES TO DROUGHT AMONG CO-OCCURING ANNUALS

Contributions

Emily Cook and Dr. Jeffrey Diez designed the study; Emily Cook conducted the experiment and collected the data with the help of Katelin Kutella; Emily Cook performed all statistical analyses with the help of Dr. Seema Nayan Sheth and Dr. Jeffrey Diez; Emily Cook wrote the manuscript with contributions from all authors.

Introduction

Climate change is rapidly altering environmental conditions, posing major challenges for plant species globally. To survive under these novel conditions, species may persist through migration, adaptation via evolutionary change, and phenotypic plasticity (the capacity of individual genotypes to adjust their phenotype in response to environmental conditions),

processes that can occur together and interact to shape species range shifts (Usui, T., Lerner, D., Eckert, I., 2023; Valladares et al., 2014). While considerable research has shown species range shifts (Davis & Shaw, 2001; Parmesan, C., Yohe, G., 2003) and rapid evolution as responses to novel climates (Anderson et al., 2021; Anstett et al., 2021; Benning et al., 2023; Franks, 2011), phenotypic plasticity may provide an immediate response by enabling adjustments in phenology, morphology, physiology, and reproduction (Matesanz et al., 2010), potentially buffering populations until genetic adaptation can occur (Jump & Penuelas et al., 2005; Nicotra et al., 2010). However, we lack a clear understanding of the relative contributions of phenotypic plasticity and spatial genetic variation among populations in shaping responses to climate change, and how these processes jointly influence persistence under climate change.

One of the most pervasive consequences of climate change is the increasing frequency and severity of drought, with climate models predicting substantial increases in drought frequency across many regions globally (Cook et al., 2014; Dai, 2011), including the Pacific Northwest of North America, where summers are projected to become hotter and drier for longer periods (Mote & Salathé, 2010). Water availability can act as a major ecological filter, strongly influencing plant traits important for reproduction and survival (Cornwell & Ackerly, 2009; Gao et al., 2015; Ogle & Reynolds, 2004), and species distributions (Engelbrecht et al., 2007). Understanding how plants respond to increasing drought stress is therefore critical for predicting how plant species will persist under a changing climate.

To cope with drought conditions, plants have various strategies often presented through corresponding suites of functional traits: drought escape, where plants reduce their exposure to drought through rapid development and early reproduction, and drought avoidance, where plants limit growth and water loss to maintain fitness under drought conditions (Ludlow 1989; Kooyers 2015). Escape strategies are frequently associated with traits that facilitate rapid resource

acquisition and fast life history strategies, such as high specific leaf area, reflecting relatively thin 'cheap' leaves, and earlier flowering time to escape the greatest impacts of drought conditions. In contrast, drought avoidance strategies are frequently expressed as more conservative trait strategies, including lower specific leaf area which results in denser, more long-lasting leaves, higher water-use efficiency, or reduced aboveground biomass to maintain growth and reproduction during intense drought periods.

Trait variation observed across individuals and populations can arise from both genetic differences reflecting local adaptation, and plastic responses of individual genotypes to their immediate environment. Both sources of variation can be shaped by differential selection regimes across a species' range due to climate gradients, leading to differentiation in both trait means and plastic responses. For example, populations from arid regions have frequently been found to flower earlier compared to populations from wetter climates (Franks, 2011; Galliart et al., 2020). At the same time, populations may differ in the magnitude or direction of plastic responses to environmental change. Plasticity itself can evolve and may be greater in populations that have historically experienced more variable or heterogeneous environments (Nicotra et al., 2010; van Kleunen et al., 2005). When populations respond differently to the environment the result is genotype-by-environment interactions (GxE), where the expression of traits in response to the environment varies among populations or genotypes. Because climate change may not affect all populations equally across a species' range, populations may face very different levels of future drought stress. Thus, studying the interplay between genetically-based trait differences and plastic responses across multiple populations is essential to predict species-wide responses under future environmental change.

Phenotypic plasticity and genetic differentiation in traits are only consequential insofar as they translate into differences in fitness. Drought can act as a strong selective agent, favoring

trait combinations that enhance survival and reproduction under water limitation (Engelbrecht et al., 2007; Franks, 2011; Knapp et al., 2015; Kooyers, 2015). As a result, populations from historically drier climates may exhibit trait values that confer higher performance under drought conditions. These genetically based differences in trait means among populations may influence baseline performance, independent of plastic responses. However, while past selection has shaped trait differences among populations, whether those differences confer a performance advantage under novel drought conditions remains an open question.

The fitness consequences of plasticity are not straightforward: the literature is strikingly mixed on whether plastic responses are adaptive or maladaptive (Cooper et al., 2019; Ehrlén et al., 2023). Adaptive plasticity occurs when plastic responses enhance fitness, whereas maladaptive plasticity occurs when plasticity reduces fitness, and can arise when plastic responses are in the opposite direction from those favored by selection. For example, Dudley (1996a, 1996b) found selection for increased WUE in *Cakile* grown in dry conditions. However, plants growing in the dry conditions actually expressed lower WUE than those grown in moist conditions, a plastic shift directly counter to the direction of selection. Thus, whether plasticity is adaptive or not has consequences for persistence under increasingly frequent droughts. Fully assessing population persistence requires evaluating not only whether populations differ in trait means and plasticity, but whether those differences translate into fitness advantages under drought, and whether the fitness consequences of plasticity vary predictably with population climate history.

While many studies have highlighted the importance of both genetic and plastic responses, the majority of this work has been conducted in single-species studies and in model organisms ((Cooper et al., 2019; Franks, 2011; Muir & Angert, 2017; Stinchcombe et al., 2004) but see Blanco-Sánchez et al., 2023; Tiwari et al., 2026; Zhang et al., 2025). These studies have

been instrumental in demonstrating that plastic responses to climate can be substantial, adaptive, and can vary across populations and environmental gradients. However, they represent a narrow portion of biodiversity and offer limited insight into how multiple co-occurring species within a community may differ in their capacity to respond to climate change. Whether co-occurring species exhibit divergent plastic responses or converge on similar strategies in response to environmental pressures, remains poorly understood. These gaps pose major challenges for predicting how plant communities will shift under climate change, as climate responses are likely to vary widely among species (Liancourt et al., 2015).

Here we explore population differentiation and plastic responses to drought stress in five co-occurring prairie annuals sampled from three populations spanning climatic gradients in the Pacific Northwest of North America. This system regularly experiences seasonal drought and is likely to experience greater heat and drought intensity due to climate change in the future (Abatzoglou et al., 2014; Bumbaco & Mote, 2010; Heeter et al., 2023; Jung & Chang, 2012; Zhang et al., 2025), making it an ideal system to test drought responses. By integrating population-level differentiation in trait means, trait plasticity, and their fitness consequences, we evaluate the relative roles of genetic differentiation and plasticity in mediating drought performance. We hypothesize that (H1a) Populations within each species will show evidence of genetic differentiation in trait means, reflecting their historical climate (e.g., warmer/drier populations will differ from cooler/wetter populations). (H1b) Across species, populations from similar climate backgrounds will exhibit parallel trait patterns (e.g., drier populations will flower earlier or have lower SLA than wetter populations). (H2a) Populations will exhibit phenotypic plasticity in response to water availability. (H2b) The magnitude of plasticity will differ among populations (P x E). (H3a) Trait means will be associated with fitness differences within treatments, and these relationships may vary by population climate history. (H3b) Trait plasticity

will provide a fitness advantage across treatments (plasticity is adaptive), but the fitness consequences may differ among populations with different climate histories.

Methods

Study System

We test these questions using a five winter annual herbaceous forbs from Pacific Northwest prairie habitats: *Clarkia purpurea, Collinsia grandiflora, Gilia capitata, Microsteris gracilis, Plectritis congesta.* These species represent diverse phylogenetic, phenological, and morphological diversity that co-occur across a broad array of environmental differences from seasonally wet to upland prairies and rocky bluffs. All species are primarily outcrossing but possess the ability to self (*Clarkia purpurea* (Raven, 1979); *Collinsia grandiflora* (Ganders & Krause, 1986); *Gilia capitata* (Grant & Grant, 1965); *Plectritis congesta* (Layton & Ganders, 1984)) with the consequence of reduced seed set in most cases, with the exception of *Microsteris gracilis*, which is primarily self-compatible (Grant & Grant, 1965).

These annuals are well suited for studying trait plasticity and evolutionary responses to environmental variation because lifetime fitness can be measured in a single generation, which allows us to quantify selection with lifetime fitness. Several of these species have been used in precipitation exclusion and competitive interaction experiments (Callie et al., 2025; Collings et al., 2024; Reed et al., 2019) but to our knowledge have not previously been used to explore phenotypic plasticity/genetic responses to drought. Finally, PNW prairies are a highly threatened ecosystem (Dunwiddie & Bakker, 2011; Klausmeyer & Shaw, 2009) and annual species historically contributed disproportionately to prairie biodiversity (Dunwiddie et al., 2014). As a result, these species are of high conservation value and are commonly included in restoration

seed mixes in the Willamette Valley, suggesting an important functional role in a restoration context.

For seed collection, we selected natural populations which experience dissimilar environmental conditions across a 320-km latitudinal gradient in the Pacific Northwest (PNW) (Figure 8). We focused on one northern site in central-western Washington, two low elevations (~150 m.a.s.l.) sites in the Willamette Valley and one high elevation (~750 m) site in the Cascade Mountain Range foothills of Oregon, USA. The northernmost site is a ~10-year-old restored upland prairie situated in the Puget Trough eco-region at Deschutes Preserve and is a low-elevation site with mesic summer soil moisture and cool mean annual temperatures (Reed et al., 2019). The low-elevation Willamette Valley sites are seasonally wet prairies with deep soils and intermediate soil moisture and temperature. Because not all species were present at one site within the Willamette Valley, we chose two prairies approximately 5 km apart located near Eugene, Oregon. The high elevation site is an exposed ridgeline at the Horse Rock Ridge Research Natural Area near Marcola, Oregon, and managed by the Bureau of Land Management with dry, shallow soils and steep, south-facing slopes (Jones et al., 2023). These sites characterize diverse ecological extremes within a comparable latitudinal range, across which all five study species are known to occur in PNW prairies. In Summer 2023, we collected seeds from 30-40 maternal plants from each site of each species, keeping each parent plant separate (representing maternal families). Seeds were stored at ambient temperatures for approximately one month to ensure full maturation was reached, then refrigerated for an additional month prior to the experiment. Because we used field-collected seeds for the experiment, we gathered a family level average seed weight (10 seeds per maternal family) for each population and species to help account for maternal effects.

Soil Collection

At the time of seed collection, we took soil samples from each site to estimate carbon, nitrogen, organic matter, and soil texture. We used a soil core to procure ~ 100 grams of soil and refrigerated at 3° C until processing. We sieved soil with 2 mm mesh sieve and further analyses were performed at Oregon State University Soil Health Lab.

Experimental Design and Treatments

In November of 2023, we conducted an experiment in the greenhouses at the University of Oregon, in Eugene, Oregon. For each population of each species, we planted three seeds from each maternal plant into ~ 60 replicate pots (2.7 x 8" Deepot™ Cells & Trays; Stuewe & Sons, Inc.) using 1 part sand and 2 parts soil (supernatural mix; Lane Forest Products) and thinned to one plant per pot after plants had germinated. Extra seeds were seeded into trays to ensure transplants were available for pots whose seeds did not germinate or died in the first 10 days. Plants from each population and species were randomized onto trays with ~12 individuals per tray. We then rotated trays within and across tables once per week to minimize block effects within the greenhouse. Temperature was set to between 4/15 °C, plus 8 hours of supplemental greenhouse lighting (0800 to 1600).

Pots were split into two watering treatments: drought (n=388) and mesic (n=403), with each maternal family replicated once within each treatment. For the first four weeks, all plants were watered daily to saturation. In the fifth week, we continued watering plants in the mesic treatment to saturation daily, while plants in the drought treatment were watered to mimic a severe drought, then maintained at the minimum amount necessary for plants to survive and reproduce (~ once per week). In the drought treatment, plants showed signs of water stress (wilting of leaves, browning and folding at leaf margins) from the onset of imposing drought

treatments. The *Microsteris gracilis* population from the Fern Ridge site had delayed germination, so we delayed the onset of drought for this species by 3 weeks and followed the same drought protocol. To ensure that treatments were different, we used 12 TOMST TMS-4 loggers (TOMST measuring system) to track soil moisture in pots for the entire experiment. Most plants senesced by July 2024.

Data Collection

We assessed the response to drought in a suite of traits important for drought adaptation: date of first flower, date of last flower, flowering duration (difference between date of first and last flower), specific leaf area (SLA), leaf dry matter content (LDMC), and water use efficiency (13C isotope analysis) (WUE). We measured traits according to standardized protocols (Pérez-Harguindeguy et al., 2016). We recorded germination daily, and flowering phenology twice weekly. After plants reached peak reproductive maturity, we measured leaf traits (SLA, LDMC, and WUE) and counted the total number of flowers for all individuals as a proxy for lifetime fitness. We scanned one fresh, intact leaf per plant at 300 dpi using an Epson Expression Scanner (12000 XL) and used Adobe Photoshop (version 24.7.0) to estimate leaf area. We weighed leaves fresh and after drying to calculate SLA (area of leaf/dry mass) and LDMC (dry mass/fresh mass). For a subset of individuals (n ~17 per species and population) we estimated WUE using stable isotope analysis. We sealed ~2 mg of ground leaf tissue in tin capsules (Costech) and analyzed samples at the UC Davis stable Isotope Facility (Davis, California, USA). We report water-use efficiency as the carbon isotope ratio relative to the V-PDB standard (R_{PDB}), where less negative values indicate greater water use efficiency.

Statistical Analyses

All models below were fit as Bayesian models in R (Version 4.4.2; R Core Team 2025) using the 'brms' package (Version 2.220; Burkner 2017). We ran each model with four chains, 2000 warm-up iterations and 2000 sampling iterations. We assessed model convergence using the Gelman-Rubin statistic (R), where values close to 1.0 indicate convergence across chains (Gelman & Rubin, 1992), and visually inspected trace plots of the four independent chains to check for adequate mixing.

To assess whether populations within each species show evidence of genetic differentiation in trait means (H1a), whether populations exhibit plasticity in response to water availability (H2a), and whether populations vary in their plastic responses (H2b) we fit linear models separately for each species with population, treatment and their interaction as fixed effects. We generated posterior predictions for all population-treatment combinations and summarized these predictions using posterior medians and 95% credible intervals (2.5% and 97.5% quantiles) (Supplemental Table 2). To estimate marginal effects, we averaged posterior predictions across treatment levels to obtain population effects to represent the average difference across environmental conditions, across populations to obtain treatment effects, and calculated differences in treatment responses among populations to quantify population x treatment interactions. For each posterior draw, we then calculated pairwise differences among all populations (for population effect), between treatments (for treatment effect), and among population-specific treatment responses (interaction effects). We quantified support for each contrast using the posterior probability of difference (PD), calculated as the larger of the probabilities that the contrast was greater than or less than zero (Supplemental Table 3).

To explore whether populations followed similar patterns across species (H1b), we fit Bayesian linear mixed-effect models for each trait with population, treatment, and their interaction, with species included as a random effect. We made pairwise population contrasts using the hypothesis() function in 'brms'.

To further assess P x E (H1c) we quantified trait plasticity within families (offspring from each single parent plant) in each population and species using a modified version of the relative distance plasticity index (RDPI) (Valladares et al., 2006). We restricted analyses to families with at least one replicate in each treatment. As in RDPI, for each population and species, we calculated all pairwise differences in trait values between wet and dry treatments within each maternal family. Unlike the original RDPI formulation, which scales differences by the sum of the trait values for each pair, we standardized each pairwise difference across populations by dividing by a single global mean trait value for each species. This modification avoids differences in plasticity estimates driven solely by baseline trait magnitude among populations or species. To capture differences in the magnitude of plasticity, we calculated plasticity as the average of all pairwise differences in traits within a maternal family divided by the global species mean of the trait value. To capture differences in the direction of plasticity, we calculated separate RDPIs which retained the sign of each pairwise difference (as in Anderson et al., 2021) to distinguish genotypes whose trait responses opposed the overall direction of plasticity, which may indicate maladaptive plasticity. For both absolute value and non-absolute value RDPIs, we tested whether populations differed in plasticity by fitting Bayesian linear models. For each species and trait, plasticity was modeled as a function of population. Posterior predictions were then used to calculate pairwise differences among all populations for each draw, and support for each contrast was quantified using the posterior probability of difference (PD), calculated as either the larger of the probabilities that the contrast was greater than or less than zero.

To assess whether any of the measured traits were under selection within each treatment (H3a) we standardized traits to a mean of zero and a standard deviation of one and relativized fitness of each genotype by the average genotype within each species and treatment. This allowed for comparison of fitness-trait relationships across species and traits. We compared six candidate models that differed in whether they included linear or quadratic trait effects (to test for nonlinear selection on traits), and whether selection varied among populations, treatments or both. Models included: (1) population specific linear effects, (2) population specific quadratic effects, (3) treatment specific linear effects, (4) treatment specific quadratic effects, (5) linear effects with both population and treatment interactions, and (6) quadratic effects of both population and treatment interactions. We used leave-one-out cross-validation (LOO package, function loo(); Vehtari et al. 2017) based on the expected log pointwise predictive density (ELPD) relative to its standard error of ELPD. The final model included population and treatment main effects, main effect of each trait, and a three-way interaction between population, treatment and trait (linear terms only; quadratic models were not preferred by LOO for any trait or species; Supplemental Table 4). Posterior distributions of trait slopes were extracted using emtrends from emmeans. We calculated the probability that each slope differed from zero and called this the probability of difference (PD). We repeated final models including maternal family seed mass as a covariate; this did not improve predictive performance nor qualitatively change estimates of selection gradients and so were not included in the final models.

To test for selection on plasticity (H3b) we standardized plasticity in each trait to a mean of zero and standard deviation of 1, and relativized fitness averaged across treatments by each species mean. We fit Bayesian linear models with fitness as a function of population, plasticity and the interaction between population and plasticity. For comparison, we also fit quadratic models including a squared plasticity term and its interaction with population to test for potential

nonlinear selection. Model comparison was performed using leave-one-out cross-validation (LOO) to select the best-supported model. For all traits and species, linear models were either preferred or indistinguishable from quadratic models by LOO (Supplemental Table 5), so all reported results are from linear models. Posterior slopes of plasticity on fitness were extracted using emtrends() from the emmeans package and summarized with tidybayes. For each slope we calculated PD.

We assessed whether traits or trait's plasticity were correlated, by generating a correlation matrix using the 'ggpairs' function from the 'GGally' package (Supplemental Figure 3). Because SLA and LDMC, and date of first flower and flowering duration are highly correlated, we chose to exclude LDMC and flowering duration for the final selection analyses.

Results

Site differences

Site conditions for all populations differed in mean annual precipitation and temperature (Figure 8). HR and SS were the wettest and coldest sites, whereas FR and HD were the driest and warmest. Sites also differed in intra-annual variability: FR and HD experienced greater seasonal variability in precipitation than HR and SS, while HR exhibited the highest intra-annual temperature variability, followed by HD, FR, and SS (Figure 8). Soil texture and nutrient composition varied substantially among the four sites (Supplemental Table 1). HR and SS had sand-dominated soils (56% and 74% sand, respectively) with relatively low clay content (10–11%). In contrast, HD and FR had markedly higher clay proportions (52% and 29%, respectively) and lower sand content (22–30%). Organic matter (OM), carbon (C), and nitrogen (N) followed similar patterns: the two sandier sites (HR and SS) had the highest OM (18.6% and

15.9%), C (9.29% and 7.93%), and N (0.71% and 0.64%), whereas the clay-rich valley sites (HD and FR) had substantially lower concentrations (OM 5.2–6.9%; C 2.58–3.44%; N 0.24–0.29%). These results indicate pronounced edaphic differences among populations, with valley sites characterized by finer-textured, low-nutrient soils and HR and SS sites characterized by coarse, nutrient-rich soils (Supplemental Table 1).

Species show evidence of genetic differentiation among populations in trait means

All species showed signs of genetic differentiation among populations (significant population effects) in at least one trait, and the majority of species showed signs of genetic differentiation among populations in multiple or all traits. One species, *Gilia*, showed weak signs of genetic differentiation overall among populations (only had significant population effect in WUE) (Figure 9). There was also a range in the magnitude of difference populations exhibited across species: In some species, population differences were quite small, while in others, differences were relatively large (Figure 9). For example, *Collinsia* from the SS population flowered 52-70 days earlier than the populations from HD and HR, and maintained flowering substantially longer, lasting 41 and 55 days longer than HD and HR, respectively. *Plectritis* from the HD population had SLA ~23% times larger than the other populations. *Microsteris* from the FR population had LDMC ~21% larger than other populations.

Few consistent patterns in trait expression are shared across populations and species

We asked whether certain populations exhibited consistent patterns across species for each trait. Across species, plants from the HR population (our highest elevation, coldest and wettest site) tended to flower latest, HD/FR tended to flower intermediately, and SS (northernmost site) population tended to flower earliest (Figure 9). In two species (*Microsteris*

and *Plectritis*) the HR population tended to have longer flowering duration, but in *Collinsia* and *Clarkia* those populations had the shortest flowering duration. Across species, flowering duration tended to be longest in SS in comparison to the other populations (HR, HD and FR tended to have shorter flowering duration). In *Collinsia* and *Plectritis,* SLA of the HD populations tended to be greater than HR and SS. In *Gilia* and *Microsteris,* LDMC from the SS and HR populations tended to be smaller than FR. For *Collinsia, Clarkia*, and *Plectritis,* WUE was generally highest in the HD population, for *Collinsia* and *Microsteris* WUE was intermediate in the SS population, and WUE was lowest for most species in the HR population.

Substantial phenotypic plasticity in response to drought across traits

All species exhibited plasticity in response to drought in at least one trait (Figure 9, Supplemental Figure 1, 2). On average, the date of first flower shifted earlier with drought in two species (*Plectritis* and *Microsteris*). Flowering duration was shorter with drought in three species (*Collinsia*, *Microsteris* and *Plectritis*), but there was one case in *Gilia* where the population from HR flowered longer with drought. SLA increased in drought for *Gilia* and *Plectritis*. LDMC tended to decrease with drought in *Clarkia, Gilia, Plectritis*, and *Microsteris*. All species and populations increased WUE in drought conditions. *Plectritis* was the only species which had a significant treatment effect on every trait, while *Collinsia* had significant treatment effects on two traits, and *Clarkia* only had one significant treatment effect (Figure 9).

Populations differ in the magnitude of plastic responses across traits

All species showed population differentiation in plastic responses in at least one trait (significant population × treatment interactions; Figure 9), and population also significantly

affected the plasticity metric (Supplemental Figure 2, 3). *Collinsia*, *Gilia*, and *Microsteris* each had at least three traits with significant P × E (Figure 9).

Earlier flowering leads to greater fitness, but leaf trait-fitness relationships are inconsistent

We found significant differences in fitness across species and populations (Supplemental Figure 4). In *Collinsia* and *Microsteris*, populations from SS outperformed populations from HD, FR and HR regardless of treatment, while in *Clarkia*, HD was greater than HR, in *Gilia*, FR was greater than SS, and in *Plectritis*, HD was greater than HR and SS (Supplemental Figure 4). Plants that flowered earlier had greater fitness in most species, populations, and treatments (Figure 10). Relationships between fitness and the remaining traits were rare and idiosyncratic (Figure 10). We found selection for lower SLA in the *Microsteris* populations from the SS and HR sites in the wet treatment and in the *Plectritis* population from the HD site in the dry treatment (Figure 10). In *Collinsia*, fitness was greatest for individuals with greater water use efficiency in the dry treatment (from HR), but fitness was greatest for individuals with less water use efficiency in the wet treatment (from HD; PD = 0.94). The opposite pattern was observed in the *Gilia* population from FR, where fitness was highest for individuals with less water use efficiency in the drought, and greatest water use efficiency in the wet treatment (PD = 0.95). In the *Microsteris* population from SS, fitness was also greatest in low water use efficiency individuals in the wet treatment (Figure 10).

Plasticity has adaptive, maladaptive, and neutral fitness consequences across populations

There were several cases of both adaptive and maladaptive plasticity (Figure 11). Greater plasticity in the date of first flower resulted in greater fitness in *Gilia* from the SS population and *Clarkia* from the HD population (PD = 0.94) but came at a cost to fitness in *Plectritis* from the

HD population. Greater plasticity in WUE resulted in greater fitness in *Collinsia* from the HD population but came at a cost to fitness in *Gilia* from the FR population (Figure 11).

Discussion

This greenhouse common garden experiment, using five annual species collected from three environmentally distinct populations, showed that populations often differed in both baseline trait values and plastic responses to water availability. We detected selection for earlier flowering time in most populations of each species; however, trait means and plasticity rarely influenced fitness. Together, these results suggest that while genetic differentiation and plasticity are pervasive across co-occurring prairie species, the fitness consequences of trait variation may be trait- and context-dependent, underscoring the complexity of predicting community-level responses to climate change.

Drought responses reflect multiple strategies and are largely idiosyncratic across populations

We hypothesized that populations of each species would show genetic differentiation in trait means, potentially reflecting historical climate across co-occurring species; for example, we expected that across species, plants from populations originating from drier or warmer source environments to flower earlier, have lower SLA, and higher WUE. We found clear evidence of population-level genetic differentiation in trait means for at least one trait across species, though the direction and magnitude varied considerably across species and populations. For example, in most species we saw clear genetic differentiation among populations in flowering time and water use efficiency (Figure 9). However, consistent population-level patterns across species were limited, and did not always reflect aridity or temperature of origin. For example, across species,

the HR population (highest elevation, coldest and wettest site) tended to flower latest, and the SS population (northernmost) tended to flower earliest, a pattern that could be more consistent with growing season length or temperature than aridity alone. For leaf traits, patterns were less consistent: in some species, SLA tended to be greater in the HD population, while WUE was generally highest in HD and lowest in HR populations, which partially aligns with historical aridity patterns but was not universal. Other studies exploring populations across aridity gradients have found that drier populations tend to display traits that often lead to faster development enabling individuals to avoid harsh drought conditions, such as earlier flowering, higher WUE, and thinner leaves (Kigel et al., 2011; Metz et al., 2020; Tiwari et al., 2026; Welles & Funk, 2021), but not always (Hänel & Tielbörger, 2015). Together, these results suggest that while some population-level signals are detectable across species, they are widely trait-specific and do not reflect a single underlying climate axis, suggesting that in these species, there are not broad generalizations about how co-occurring populations will respond concordantly to future drought.

Drought responses are typically categorized into two strategies: drought escape, where plants reduce exposure to drought through rapid development and early reproduction (generally more acquisitive), and drought avoidance, where plants limit growth and water loss to maintain fitness under drought conditions (more conservative) (Ludlow 1989; Kooyers 2015). Studies have shown that annual plants show marked variation in plant responses and often differ from acquisitive/conservative expectations (Tiwari et al., 2026; Franks et al., 2007). Our drought treatment induced shifts in traits associated with both strategies, including earlier flowering time and changes in WUE. Nearly all genotypes shifted toward greater WUE under drought, indicating a broadly shared avoidance response, yet other trait responses varied considerably across individuals, populations, and species, not sorting cleanly into one strategy or the other. In

particular, *Plectritis* flowered earlier with shorter flowering duration, higher SLA and lower LDMC, all consistent with drought escape, yet simultaneously increased WUE, consistent with drought avoidance. Together this suggests that species may use escape and avoidance-related traits simultaneously and highlights the value of measuring multiple traits simultaneously rather than relying on single traits as proxies for drought strategy.

In all species, we detected significant population level variation in plasticity (P x E) for at least one, but oftentimes several traits, indicating that populations differed in their plastic responses to drought. In several cases, populations exhibited similar magnitudes of plasticity but shifted in opposite directions; for example, in *Gilia* and *Microsteris*, some populations flowered earlier under drought, while others flowered later (Figure 9, Supplemental Figure 1). In other cases, populations differed in the magnitude of their plastic responses, with some populations showing stronger responses to drought than others. However, these differences in plasticity did not correspond to any generalizable pattern across species, and we found no support that populations experiencing greater historical climate variability exhibited greater plasticity (Supplemental Figure 3), as predicted by the Climate Variability Hypothesis (CVH; Janzen 1967). This is consistent with studies that also failed to find positive relationships between climate variability and plasticity (Franks et al., 2011; Welles & Funk 2021), while other studies have found support for this relationship (Gianoli & González-Teuber, 2005; Lázaro-Nogal et al., 2015; Molina-Montenegro & Naya, 2012). This suggests that the conditions under which historic climate variability predicts plasticity remains an open and important question. Overall, population-level differences in plasticity were common, but idiosyncratic, reinforcing that trait responses to drought are nuanced, and highly population- and trait-specific.

Adaptive plasticity is rare and fitness consequences are highly context-dependent

We tested whether trait means and/or plasticity were associated with fitness differences and asked whether those relationships varied by population climate history. We found cases of linear selection in several traits. For example, we found selection for earlier flowering time in most species and populations (Figure 10), consistent with previous findings across a wide range of plant species (Kenney et al., 2014; Munguía-Rosas et al., 2011). Earlier flowering was strongly correlated with longer flowering duration (Supplemental Figure 3), highlighting the advantage of a longer reproductive period and potential to escape strong drought conditions (Franks et al., 2007).

However, selection rarely followed patterns predicted by historical climate, and differences between warmer/drier versus cooler/wetter populations were generally inconsistent. In one case within *Plectritis*, in the dry treatment, the HD population experienced stronger selection than the SS population (Figure 10), but otherwise slopes were largely similar across populations within species. This result may partly reflect a limitation of the common garden design: Natural environments impose multiple interacting stressors (e.g. temperature, humidity, canopy cover, competitors), and thus responses to selection observed here may not fully represent those expressed under field conditions. More broadly, this reflects that the selective environment is a complex suite of conditions, and population climate history may not be a good predictor of selection here.

Selection is known to vary substantially across environments and over time (Anderson et al., 2021; Sherrard & Maherali, 2006; Siepielski et al., 2009; Weinig et al., 2003) and we see this reflected in our results, with diverse patterns of selection between treatments. For example, water use efficiency can buffer plants during drought by reducing water-loss, but it can come at a cost

of reduced carbon gain under well-watered conditions (Dudley, 1996a; Heschel et al., 2004). This tradeoff could explain why the direction of selection on WUE flipped between treatments, and species (*Gilia* and *Collinsia*). In the dry treatment, higher WUE was favored in the cool/wet HR population of *Collinsia*, whereas in the wet treatment was penalized in HD (warm/dry population) (Figure 10). *Gilia* showed the opposite pattern, with the dry treatment favoring lower WUE, and the wet treatment penalizing higher WUE in the warm/dry FR population. Selection on SLA also varied: smaller SLA was favored in cooler/wetter *Microsteris* populations in the wet treatment, and also in warm/dry HD population of *Plectritis* under dry treatment. These results suggest diverse fitness consequences, strongly dependent on the environmental context.

Overall, cases of adaptive plasticity were rare, which is consistent with broader reviews that plasticity is common, but adaptive plasticity is not (Murren et al., 2015; Palacio-López et al., 2015). However, we found diverse fitness consequences between selection and plasticity in several cases, which revealed potential tradeoffs among traits. We found one case where in *Gilia*, adaptive plasticity in date of first flower appeared to be coupled with maladaptive plasticity in WUE (Figure 11): plants shifted flowering time in an adaptive direction under drought, but WUE shifted away from the selective optimum, and selection also favored reduced plasticity in WUE in the same population. This indicates that certain genotypes may not be simultaneously plastic in all traits in ways that maximize fitness under drought. Trait correlations could constrain adaptive plasticity across multiple traits, potentially explaining why some populations cannot optimize both flowering time and WUE in response to drought. While flowering time and WUE are frequently correlated as trait means, the direction of that relationship has been found to vary across species and environments (Franks, 2011; Kenney et al., 2014; Pearse et al., 2020), and how plasticity in these two traits covaries has received less attention, making this an interesting

direction for future work. Together, these results suggest that while some trait plasticity can be adaptive, it is highly population- and trait- specific.

Several factors may have constrained our ability to detect strong selection on trait means and plasticity. First, as noted above, our experiment in the greenhouse likely differs from field selection, and common garden or reciprocal transplant experiments coupled with treatments across the natural climate gradient of these species would strengthen inference about adaptive plasticity in nature (see Tiwari et al., 2026; Urbas & Zobel, 2000). Additionally, because species differed in their drought sensitivity, the same drought treatment likely imposed more drought stress on some species than others, potentially limiting our ability to detect selection in less affected species. Despite this, our detection of cases where plasticity was adaptive suggest that at least some populations harbor the potential for both trait means and plastic responses to influence reproductive success.

Implications for changing climate

The population-level variation in plasticity observed across species in our study suggests meaningful potential for adaptive responses to future climate change. The presence of differential plastic responses among populations indicates that these species harbor some variation in how individuals respond to drought. This variation could buffer species if populations with greater plastic responses are 'pre-adapted' to future climates that are more variable or extreme than previously experienced (Matesanz & Ramírez-Valiente, 2019), and/or buy time for evolutionary rescue (Chevin et al., 2013).

Because we used field-collected seeds without performing controlled crosses, or generating replicated genotypes, our study could not fully partition phenotypic variance into genetic, maternal or environmental components within populations. Having multiple replicates

per maternal family would have allowed for finer partitioning of within versus among family variance and stronger inference about the genetic basis of plastic responses. Although seed mass differences among families were minimal (Supplemental Figure 5), we cannot fully rule out maternal effects. Our models did not perform better when including maternal family seed mass as a covariate, suggesting that maternal effects are unlikely to strongly influence our results. Despite these limitations, the variation in plastic responses we observed among populations suggests that plasticity could evolve in the future. How the evolution of plasticity influences genetic adaptation remains poorly understood (specifically, whether plasticity slows evolutionary responses, or alternatively buys time for adaptive evolution to occur) despite its potential importance for population persistence under climate change (Matesanz & Valladares, 2014; Nicotra et al., 2010). Future work should test whether sufficient additive genetic variation in plasticity exists within populations for selection to favor increased plastic responses under future climate scenarios.

Conclusion

Understanding how the patterns of genetic variation among populations influences trait expression and plasticity across environmental gradients is critical for conservation and seed sourcing for restoration (Newton et al., 1999; Valladares & Gianoli, 2007), as well as for understanding the evolutionary potential of species to persist in the context of climate change (Espeland et al., 2018). While studies have shown that phenotypic plasticity can be beneficial in buffering the effects of environmental change, whether plasticity is a trait that should be prioritized in restoration remains an open question (Aoyama et al., 2023; Espeland et al., 2018; Thomas & Prunier, 2024; Valladares & Gianoli, 2007). Our study revealed substantial genetic and population by environment interactions in most traits and species; however relationships

with fitness were highly context specific, which has important implications for population persistence and restoration success. Our results indicate that maximizing plasticity is unlikely to be advantageous for all species or traits in this system. At the same time, the diversity of responses we observed among species and populations suggests that plant communities possess multiple strategies for coping with increasingly stressful conditions predicted under future climate change scenarios. We need more studies exploring how traits and plasticity influence plant fitness to inform restoration strategies (Funk et al., 2024). Critically, identifying when plasticity is adaptive, and for which species and traits, could inform whether sourcing seeds from more plastic populations would improve restoration outcomes in changing environments. Our study emphasizes that considering multiple species and traits is important for evaluating drought responses within plant communities across environmental gradients.

Figures

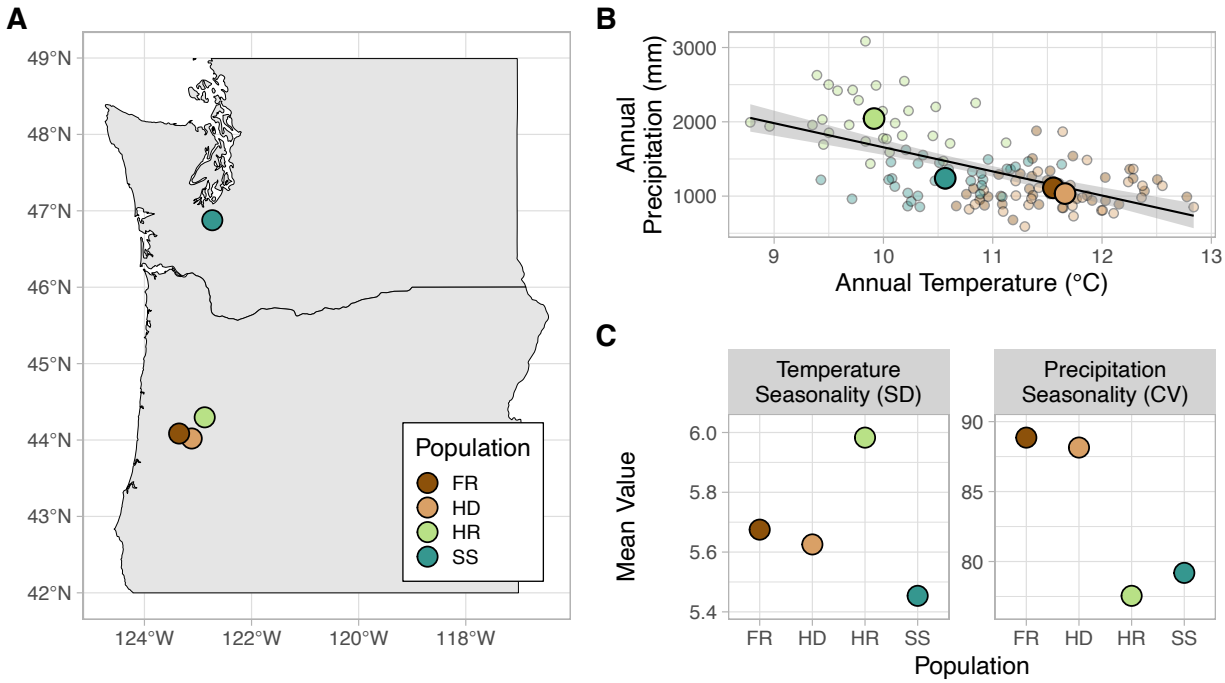


Figure 8. Locations of five focal source populations, mean precipitation and temperature, and their seasonality.

A) Locations of source populations of collected seeds of five focal species across Oregon and Washington. **B)** Mean 30-year (1993-2023) temperature (MAT), precipitation (total accumulation; MAP). **C)** Temperature seasonality (SD), and precipitation seasonality (CV) by seed collection site (PRISM climate data).

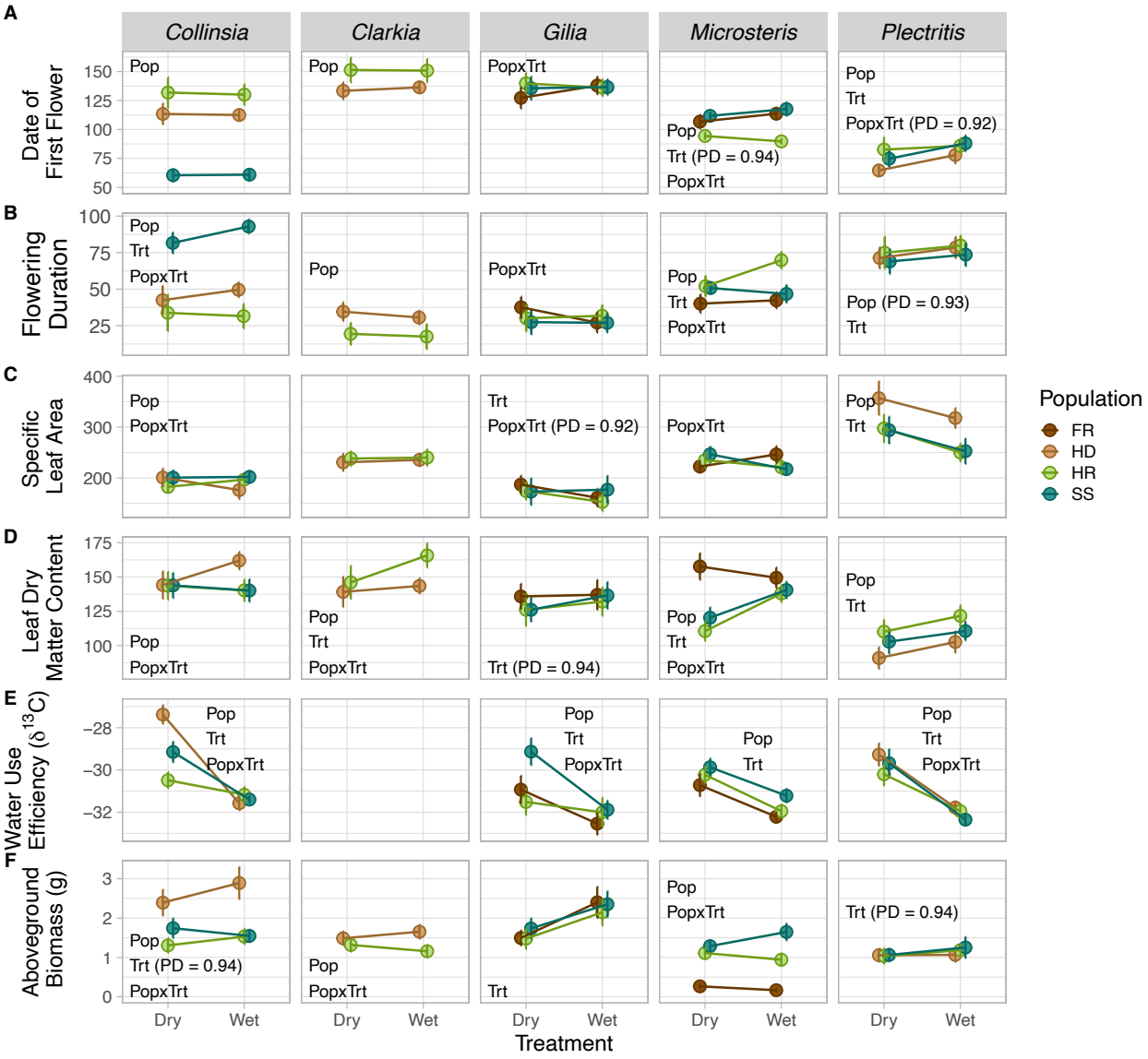


Figure 9. Reaction norms for all species, populations, treatments, and traits.
Traits shown are: **A)** Date of first flower, **B)** flowering duration, **C)** specific leaf area, **D)** leaf dry matter content, **E)** water use efficiency, and **F)** above ground biomass. Points represent means of raw data and error bars represent 95% confidence intervals. For each species we fit Bayesian linear models in brms to test whether populations differed in trait means independent of treatment, we calculated marginal posterior predictions within each population by averaging predicted values across treatments within each posterior draw. Pairwise contrasts among populations were then computed for each draw (e.g. HD – HR, HD - SS, HR – SS). For each contrast, we estimated the posterior probability that the difference was different from zero. This was repeated for treatment. Pop denotes that at least one population significantly differs in trait

values, Trt denotes significant effect of watering treatment, Pop x Trt denotes significant interaction between population and treatment (at least one pairwise population difference is significantly different). We were unable to estimate water use efficiency in *Clarkia* due to its faster senescence of leaves than other species.

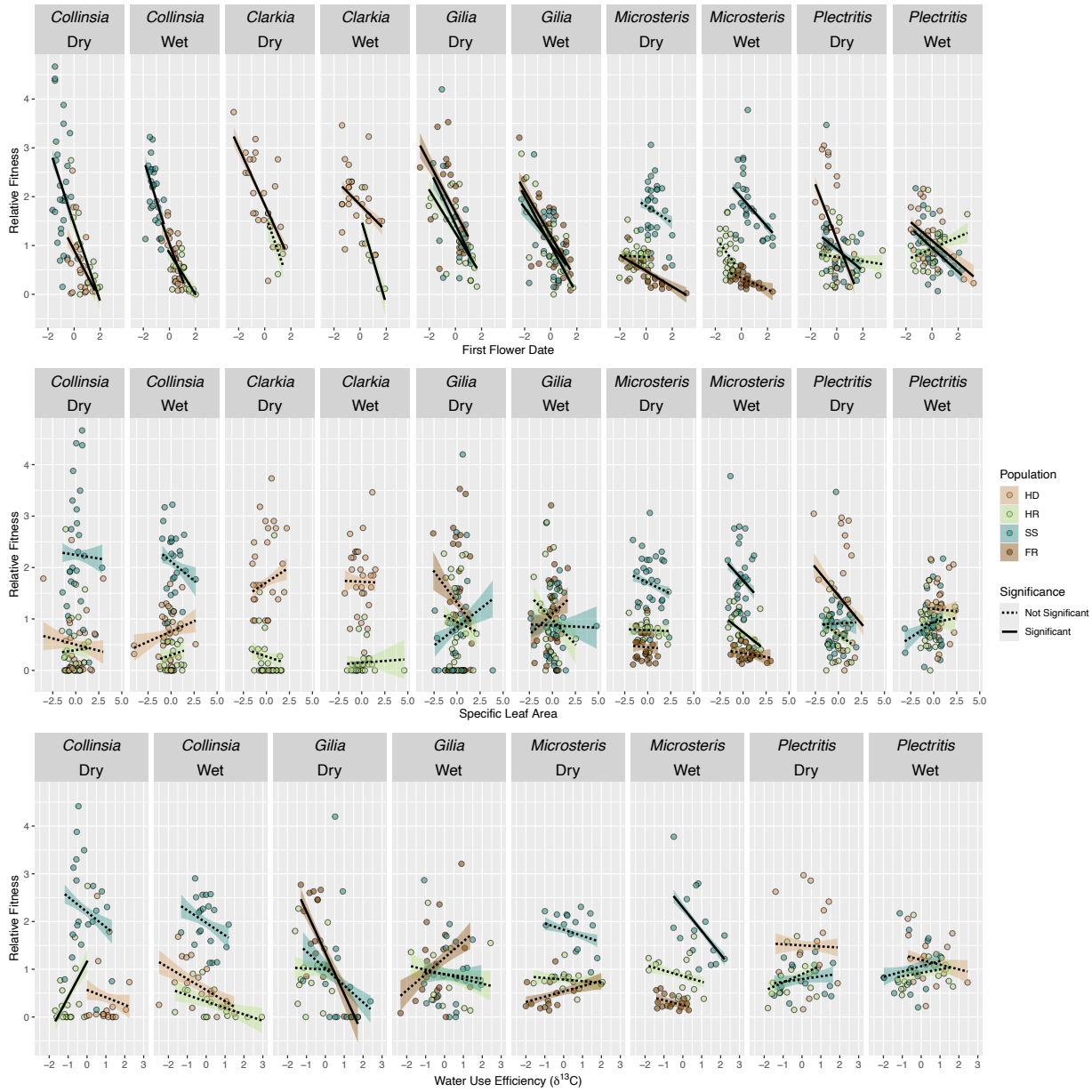


Figure 10. Relative fitness as a function of population and treatment for each species and trait. Traits shown from top to bottom are: Date of first flower, specific leaf area, and water use efficiency. Traits were standardized to a mean of 0 and standard deviation of 1. Fitness was relativized within each treatment. Predicted relationships are shown as solid lines for slopes that were significantly different from zero and dashed lines where they did not. Shading represents 50% credible intervals. Negative standardized WUE values represent low water use efficiency, positive values represent high water use efficiency. We did not collect water use efficiency for

Clarkia. Models with quadratic terms were not preferred by model selection, all relationships shown are linear.

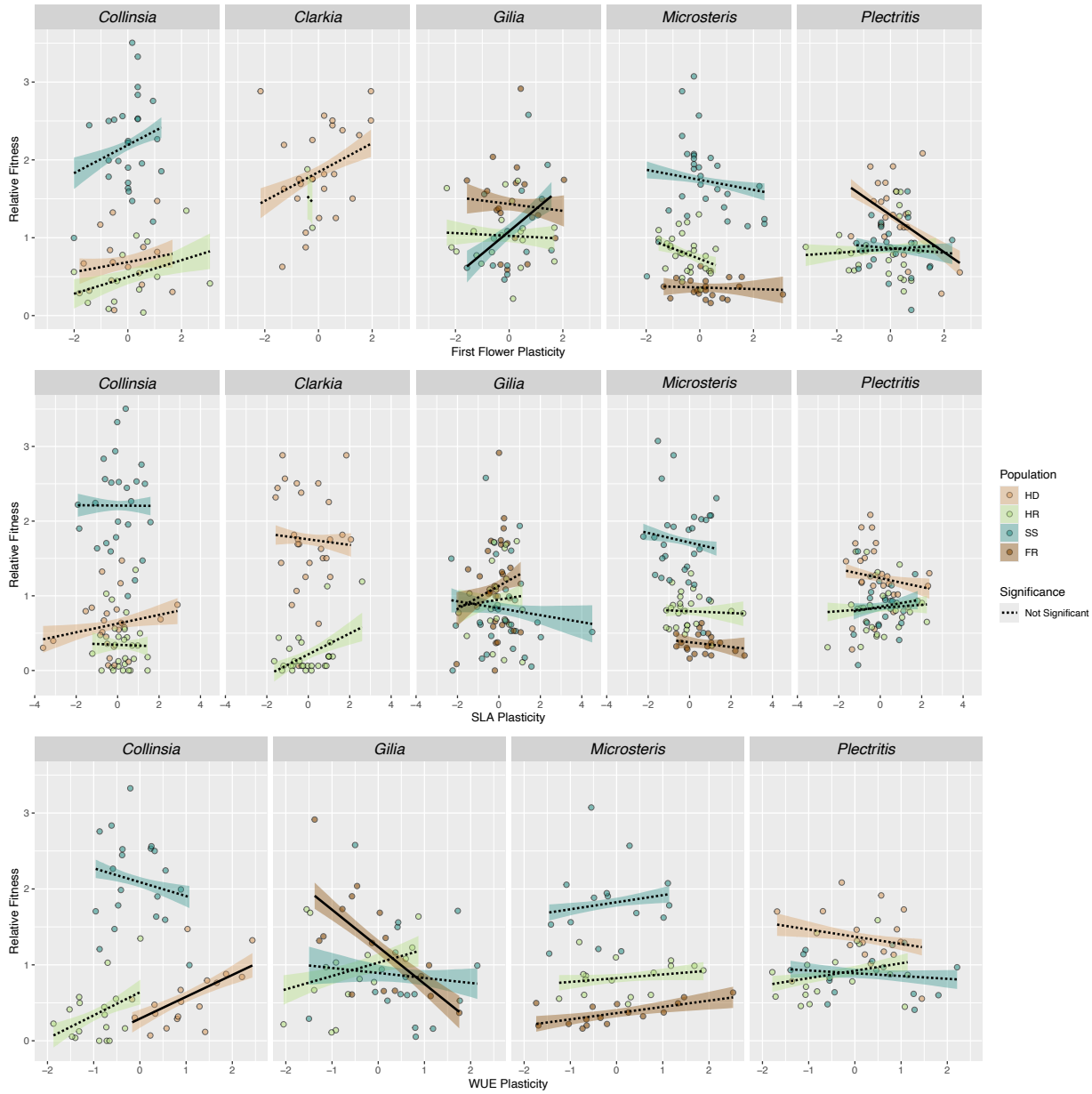


Figure 11. Estimated effect of trait plasticity on relative fitness (averaged across treatments), for each species and population.
Traits shown from top to bottom are: Date of first flower plasticity, specific leaf area plasticity, and water use efficiency plasticity. Plasticity metrics were standardized to a mean of 0 and standard deviation of 1. Significance of slopes was assessed at the 95% credible interval. Shading represents 50% credible intervals. Predicted relationships are shown as solid lines for slopes that were significantly different from zero and dashed lines where they did not. We did not collect water use efficiency for *Clarkia*. Models with quadratic terms were not preferred by model selection, all relationships shown are linear.

V. CONCLUSION

Understanding how species and populations persist in different environmental contexts (whether it be in the face of competition or novel droughts) requires integration across multiple scales, from the evolutionary history and function traits that structure species interactions, to the plastic and genetic responses that allow populations to track shifting environments. My dissertation has addressed these challenges across three chapters, asking how trait variation shapes competitive outcomes in co-occurring species, how plasticity evolves in response to extreme climates in a single species, and how multiple co-occurring species differ in their capacity to respond to drought. Together, these chapters highlight that trait variation is a strong driver of ecological and evolutionary dynamics, yet its expression is highly context-dependent, and varies across species, populations, traits, and environments. Across multiple chapters, I found that simple proxies (phylogenetic distance as a proxy for functional similarity, or climate variability as a predictor of plasticity) often failed to capture complex biological responses, highlighting the need for future work in mechanistic, trait-based approaches.

In my second chapter, I explore how phylogenetic distance and trait dissimilarity relate to the competitive interactions that determine species coexistence (niche differences and fitness inequalities). Few empirical studies to date have explored both phylogeny and traits simultaneously within a modern coexistence theory framework (Godoy et al., 2014; Narwani et al., 2013). Contrary to expectations, I found little phylogenetic signal in measured traits within our study species, suggesting that phylogeny is not a reliable proxy for functional trait dissimilarity, or downstream coexistence outcomes. Instead, traits such as leaf area and root mass fraction were the strongest predictors of competitive suppression and fitness inequalities, pointing to the importance of measuring multiple traits rather than inferring differences from

phylogeny. Future studies can expand this work to include more species, perhaps with a greater range of phylogenetic relatedness, and other traits relevant for competition, such as phenology.

In my third chapter, I explore population-level variation in plasticity, and its evolution in response to an extreme drought. Using a novel resurrection common garden approach, I compared ancestors and descendants transplanted across three experimental plots spanning the species' range. I demonstrated that phenotypic plasticity can sometimes track climate variability, evolve after an extreme drought period, and have important fitness consequences. The evolution of plasticity was population- and trait-specific, with trailing-edge and central populations showing the greatest evolutionary responses. Plasticity is thought to be widely adaptive, yet relatively few studies have been able to detect its relationship with fitness (Cooper et al., 2019; Ehrlén et al., 2023). Future studies that pair experimental treatments with reciprocal transplants, may have a greater ability to detect selection pressures similar to what has historically shaped the evolution of plasticity across this species' range.

Finally, in my fourth chapter, I tested how multiple, co-occurring species from multiple populations differentially respond to drought. Few studies have incorporated multiple species simultaneously (Garbowski et al., 2025; Hamman et al., 2018; Liancourt et al., 2015), and even fewer have explored multiple populations, leaving our understanding of how communities-level responses to climate change relatively unexplored. I found substantial plasticity in response to drought across species and populations, as well as population differentiation in trait means and plasticity. Despite this, I found few population-level patterns across species, suggesting that species and populations will respond in unique ways, depending on the trait and environmental context. Additionally, selection on trait means and plasticity was rare, and among the responses to selection, I found patterns which suggest that genotypes may not be able to be plastic in all traits that maximize fitness.

Each of my chapters has explored mechanisms that allow species to persist in their environments, and together they reveal responses that are highly variable and context-dependent responses. These results suggest both a challenge and a source of encouragement. The challenge is that generalizing across species and environments is difficult; the encouragement is that the diversity of strategies I observed highlights the potential resilience of plant communities in the face of competition, drought, and future climate change. These findings carry important implications for restoration and conservation managers working to build climate-resilient plant communities and they suggest that community-level responses to drought may not be easily predicted by single-species studies alone. Seed sourcing and species selection may not rely on broad generalizations (e.g. whether phylogenetic relatedness, climate of origin, or single-species performance experiments), as reliable guides to community-level outcomes. Restoration of climate-resilient plant communities may require species- and population-level data on drought responses, where functional traits such as leaf area, root allocation, and their plasticity in responses are evaluated across focal species and populations. This may be particularly relevant for sourcing genotypes that are able to perform well under current and novel drought regimes. Trailing-edge populations may have climate-adapted genetic variation, and should be prioritized in these studies, as possible populations to include in seed mixes or conservation sites. Because species and population responses responded idiosyncratically to drought in my fourth chapter, there is a challenge in restoration ecology to be able to predict successful restoration outcomes for diverse plant communities. Integrating competitive dynamics, plasticity, and evolutionary responses into unified research will be essential for predicting future plant responses to global change, and for translating that knowledge into restoration in practice.

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