Contrasting effects of competition on plant fitness and distributions along environmental gradients

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Abstract

Species distributions depend on the interplay between demographic performance and biotic interactions along environmental gradients, such that competition can decouple species' realized distributions from intrinsic responses to environmental heterogeneity. However, logistical challenges often necessitate simplifying assumptions about competition across environments, limiting our ability to explain or predict species distributions. Here, we experimentally quantify the consequences of spatially variable competition for the demography and distributions of eight annual plant species across an edaphically heterogeneous grassland. Competition had contrasting effects on demographic responses to the environment depending on the species and environmental gradient. Specifically, competition dampened species' intrinsic responses to a soil texture gradient, but had relatively little effect on responses to a nutrient (Ca:Mg) gradient. We find congruence between demography and occurrence, as well as absences from suitable sites consistent with competitive exclusion and dispersal limitation. Our work highlights the complex relationship between demography, competition, and spatial distributions in real-world landscapes.

Keywords: California, competition, demography, invasion, neighbor removal, population growth rate, serpentine grassland, species distributions, spatial heterogeneity, stress gradient

Introduction

Understanding how the abiotic environment and biotic interactions jointly shape species distributions is a long-standing challenge in ecology and biogeography (Dobzhansky 1950; Louthan *et al.* 2015; MacArthur 1972). This is an especially pressing issue in the face of environmental change driving shifts in the abundance and distributions of species within and across ecological communities (e.g., Bowler *et al.* 2017; Chen *et al.* 2011; Feeley *et al.* 2020; Kelly & Goulden 2008; Parmesan & Yohe 2003; Rosenblad *et al.* 2023). Critically, biotic interactions are a major source of uncertainty in explaining or predicting species distributions (Alexander *et al.* 2016; Davis *et al.* 1998; Gilman *et al.* 2010; HilleRisLambers *et al.* 2013). Among the numerous interactions that can influence distributions (Wisz *et al.* 2013), competition has often been invoked for its potential to exclude species from otherwise suitable habitats (e.g., Bertness & Ellison 1987; Bullock *et al.* 2000; Connell 1961). However, dissecting the role of competition in shaping species distributions requires a detailed understanding of how demography and resulting population dynamics vary along environmental gradients, which can be difficult to achieve empirically due to logistical constraints.

The demographic performance of species along environmental gradients is the foundation for species distributions, including range shifts in response to environmental change (Ehrlén & Morris 2015; Holt 2009; Pulliam 2000; Schurr *et al.* 2012). Generally, a species is expected to persist in environments where it has a positive population growth rate (i.e., fitness) when rare (Grainger *et al.* 2019; Hutchinson 1978). While one might assume that species distributions should reflect variation in intrinsic fitness (i.e., fitness in the absence of biotic interactions) across environments, various processes (e.g., biotic interactions, dispersal limitation, source-sink dynamics, demographic stochasticity) can complicate the relationship between fitness and distribution (Pulliam 2000). In particular, competition impacts the fitness of species in ecological communities (Chesson 2000b; MacArthur & Levins 1967), potentially creating mismatches between intrinsic fitness and realized distributions (Davis *et al.* 1998). The role of competitive population dynamics in shaping species distributions has received much theoretical (e.g., Godsoe *et al.* 2017; Svenning *et al.* 2014; Usinowicz & Levine 2018) and empirical (e.g., Armitage & Jones 2020; Usinowicz & Levine 2021) attention in recent years. Nevertheless, our understanding of the complex interplay between performance, competition, and distribution along real-world environmental gradients lags behind theoretical developments (but see e.g., Anderegg & HilleRisLambers 2019; Craig *et al.* 2023; Schultz *et al.* 2022; Stanton-Geddes *et al.* 2012).

The consequences of competition for species distributions can be understood in terms of how competitors alter species' demographic responses to the environment and drive competitive exclusion. In theory, competitive exclusion can occur in the absence of altered demographic responses to environmental gradients (or vice versa) (Figure 1), making it important to quantify these interrelated phenomena together. First, competition can prevent species from establishing or persisting in certain environments by reducing fitness to below self-replacement levels. Such competitive exclusion can occur if the magnitude of competitive effects is sufficiently large relative to intrinsic fitness (Figure 1 a). Second, competitors can alter the response of fitness to environmental gradients if competitive effects vary across environments (Figure 1 b–c) due to variation in any combination of the strength of per capita interactions, the density of competitors,

or the identity of competitors (Louthan *et al.* 2015). For example, in a classic study, Connell (1961) demonstrated that a competitor species more strongly limited the performance and occurrence of the barnacle *Chthamalus stellatus* in lower zones of the rocky intertidal. More recent work has demonstrated that competition can mediate species' responses to environmental change (e.g., Esch *et al.* 2018; Liancourt *et al.* 2013) and that environmental context can alter outcomes of competition (e.g., Germain *et al.* 2018; Van Dyke *et al.* 2022; Wainwright *et al.* 2019). Whereas competitive exclusion may directly limit species distributions over relatively short time spans, the consequences of altered demographic responses to the environment may manifest quantitatively over longer time spans (e.g., by limiting population growth and slowing range expansion in response to environmental change, Ettinger & HilleRisLambers 2013; Svenning *et al.* 2014) and are more difficult to identify amid the various processes that can contribute to realized distributions.

The prediction that competition is most intense in fertile or productive environments where species have high intrinsic fitness is foundational for the study of plant strategies (e.g., CSR model, Grime 1977) and species coexistence (Chesson 2000a) in spatially variable environments. This idea is also found in the stress-gradient hypothesis, which posits that competition increases in frequency or strength and dominates over facilitation in more benign abiotic environments (Bertness & Callaway 1994; Maestre *et al.* 2009). Such co-variation between intrinsic fitness and competition can emerge, for example, if species share functional traits or evolutionary histories that promote similar responses to the environment (Adler *et al.* 2013; Mayfield & Levine 2010), but is underappreciated in the context of species distributions. Perhaps counterintuitively, if the fitness benefits of favorable environments are sufficiently large relative to the detrimental effects of competition, a species might be more likely to occur toward these highly competitive environments (i.e., dampened response; Figure 1 b). Conversely, if competitive effects overwhelm fitness benefits, the species might be excluded toward these intrinsically favorable environments (i.e., reversed response; Figure 1 c). Finally, if competitive effects offset gains in intrinsic fitness, the species' realized fitness and distribution might be effectively decoupled from the environment. Taken together, competition can produce a spectrum of mismatches between intrinsic fitness and realized distributions. This complexity illustrates how the practical assumption that realized distributions reflect intrinsic responses to the environment can produce misleading conclusions about the demographic underpinnings of species distributions in the face of interspecific competition (Davis *et al.* 1998; Pearson & Dawson 2003). Yet, revealing how spatial variation in competition shapes species' performance and distributions remains difficult, in part due to practical challenges associated with quantifying fitness along real-world environmental gradients.

Here, we conducted a spatially distributed demographic experiment to evaluate the consequences of competition for plant demography and distributions in an edaphically variable California annual grassland. We experimentally quantified how the demography and lifetime fitness of eight annual plant species respond to variation in the abiotic environment, either in the presence or absence of natural competitors. Specifically, we asked: (1) What are species' intrinsic demographic responses to the abiotic environment? (2) How does competition modify these intrinsic responses? (3) Is competition expected to exclude species from intrinsically suitable environments? Finally, combining these demographic results with community surveys, we asked: (4) How do species' realized distributions at the landscape scale reflect demographic responses to

the environment and competition? Our work builds up from the first principles of demography and population dynamics to highlight the complexity in how spatially variable competition shapes species distributions.

Materials and methods

Study system

We conducted our study at the University of California Natural Reserve System Sedgwick Reserve in Santa Barbara County, California, USA. This region experiences a Mediterranean climate with hot, dry summers and cool, wet winters. We focused on a ~4-ha area of the reserve characterized by serpentine-derived hummocks interspersed among a grassland matrix (Figure 2, Figure S1). The hummocks host many native annual forbs, whereas the matrix is dominated by invasive annual grasses (e.g., *Avena* spp., *Bromus* spp.) (Gram *et al.* 2004). The edaphic heterogeneity of this landscape, coupled with the dominance of experimentally tractable annual plants, makes this system well-suited for addressing our research questions.

Demographic experiment

We conducted a spatially distributed demographic experiment to quantify the demographic responses of annual plant species to spatial variation in the environment and competition. We initiated the experiment in November 2019 by planting seeds of eight native annual plant species (Table 1) at seven experimental sites distributed across the study area (Figure 2). These sites represent a subset of sites previously selected to capture environmental variation across this area (Kandlikar *et al.* 2022). Each site was comprised of 20 0.5 m $\times$ 0.5 m plots, evenly divided among two neighborhood treatments in which the resident community was either removed or left intact prior to planting. Each plot was divided into eight subplots, each of which was seeded at its center with 24 to 40 seeds of one of the eight focal species. Seeds were collected and aggregated from across the study area in 2016–2018.

In January–February 2020, we recorded germination rate (g) in each subplot by counting the number of germinants found in the seeded locations, then thinned these germinants down to a single focal individual. We marked focal individuals with toothpicks and tracked them for the duration of the growing season. Due to below-average rainfall in January–February (County of Santa Barbara 2024), we added ~0.6 in of water to all plots following germination, equivalent to a typical storm at this time of year. In April–July 2020, as focal individuals started to show signs of senescence, we estimated the lifetime fecundity (F) of each individual. See Appendix S1 for detailed methods for estimating fecundity. In total, we recorded germination rate in 1,078 subplots and estimated fecundity for 708 focal individuals. We maintained the neighborhood removal treatment by weeding out any background germinants throughout the experiment.

Community surveys

To characterize the realized distributions of our focal species across the study landscape, we revisited all uncleared experimental plots in April–May 2021 and surveyed the occurrence of each focal species. We also conducted these surveys at 61 sites distributed across the study area (Figure 2). We selected the locations of these survey sites by overlaying on the study area a 7×9 grid of 25 m $\times$ 25 m cells and randomly generating a point within each grid cell using QGIS (QGIS Development Team 2020). Each survey site was comprised of a single 0.5 m $\times$ 0.5 m plot, equivalent to one experimental plot.

Soil sampling

Concurrent with community surveys, we collected soil samples to characterize the soil environment at all study sites. We collected soil from ~5–10 cm below the soil surface at three locations within each site. We aggregated soil samples for each site and submitted them to A&L Western Laboratories in Modesto, California, USA for chemical and physical analysis. We similarly collected soil samples following a rainfall event and estimated soil moisture as gravimetric water content. See Table S1 for descriptions of all soil variables used in this study.

Statistical analyses

To describe the soil environment at our study sites, we performed a principal component analysis (PCA) of the 20 soil variables in Table S1 (Figure 2, Figure S2, Figure S3). We retained the first four axes, corresponding to 77% of cumulative variance explained (PC1 = 32.6%, PC2 = 18.2%, PC3 = 16.9%, PC4 = 9.3%), for all subsequent analyses. This allowed us to reduce the dimensionality of our analyses while including much of the observed environmental variation.

To quantify the consequences of competition for demography and fitness, we modeled the demographic responses of our focal species to the soil environment and experimental treatment (neighbors present vs. absent) using Bayesian generalized linear mixed models. We fit models with germination rate or fecundity as the response, species, treatment, and soil PC1–PC4 as predictors, and site as a group-level (random) intercept. We allowed three-way species $\times$ treatment $\times$ soil interactions. For germination rate, we used a beta-binomial likelihood with a logit link function for the mean parameter (μ) and allowed the precision parameter (ϕ) to differ by species. For fecundity, we used a zero-inflated negative binomial likelihood with a log link function for the mean parameter (μ) and allowed the shape parameter (ϕ) to differ by species. We selected these likelihood functions to accommodate overdispersion in the germination and fecundity data. For the fecundity model, we introduced a zero-inflation component in light of excess zeros in the fecundity data. See Table S2 for details regarding the specification of the zero-inflation component.

In addition to modeling individual demographic rates, we quantified the response of fitness to the soil environment and neighborhood treatment. We computed fitness for each focal individual as

the finite rate of increase (r) in the functional form of a model of seed banking annual plants (Chesson 1990; MacDonald & Watkinson 1981):

$$\frac{N_{t+1}}{N_t} = (1-g)s + gF \tag{1}$$

$$r = \ln\left(\frac{N_{t+1}}{N_t}\right) \tag{2}$$

where N_t is the number of seeds in year t and s is the annual rate of seed survival in the seed bank. We used species-specific estimates of s from previous work in this study area (Godoy *et al.* 2014, 2017; Levine & HilleRisLambers 2009), assuming s to be constant across sites. We observed bimodalities in experimentally estimated fitness values, likely due to the excess zeros in the fecundity data. Therefore, rather than modeling fitness directly, we implemented a joint model of the germination and fecundity models described above. We used predictions from this joint model to compute fitness as needed. We note that our fitness estimates do not necessarily correspond to low-density growth rates (Grainger *et al.* 2019) because our focal species were sometimes present in the resident community, but these estimates still provide valuable information about population-level performance (McGraw & Caswell 1996; but see Pande *et al.* 2020). We used `emmeans` (Lenth 2024) to compute the estimated marginal effects of the soil environment and neighborhood treatment on performance. See Appendix S3 for a detailed description of these analyses.

Finally, we quantified how our focal species' realized distributions reflect demographic responses to the environment and competition. We modeled occurrence using Bayesian generalized linear models with species and soil PC1–PC4 as predictors, allowing two-way species $\times$ soil interactions. We used a beta-binomial likelihood with a logit link function for the mean parameter (μ) and allowed the precision parameter (ϕ) to differ by species. We then evaluated whether the estimated relationship between occurrence and each environmental axis was consistent with the estimated response of fitness to that axis. We also evaluated whether observed occurrence (present vs. absent) aligned with predicted fitness ($r > 0$ vs. $r < 0$) at each study site. See Appendix S4 for additional details of these analyses.

We conducted analyses using R version 4.3.3 (R Core Team 2024) and implemented Bayesian statistical models using `brms` (Bürkner 2017). We used prior predictive simulations (Gabry *et al.* 2019; Wesner & Pomeranz 2021) to select weakly informative priors that were meant to keep parameters within plausible ranges based on prior work in our study system (e.g., Godoy *et al.* 2014; Kandlikar *et al.* 2022; Kraft *et al.* 2015b). We inspected diagnostic quantities ($\hat{R}$, N_{eff}/N) and trace plots to confirm model convergence and used graphical posterior predictive checks to assess model fit (Gabry *et al.* 2019). We present results with over 95% posterior support unless explicitly noted otherwise. See Appendix S2 for details of our statistical modeling approach. See Appendix S5 for additional details of each model used in our analyses.

Results

Soil environment

The first two soil PCA axes together explained 50.8% of variation in the soil environment across study sites (Figure 2). Soil PC1 was characterized by a gradient in soil texture, with clay content loading positively and sand content loading negatively along the axis. Cation exchange capacity (CEC), cation content, and soil moisture positively co-varied with clay content along soil PC1. As such, this axis also represents a nutrient availability gradient. Soil PC2 was characterized by a gradient in cation composition, with Mg saturation loading positively and Ca saturation loading negatively along the axis. All sites exhibited an excess of Mg relative to Ca (Ca:Mg < 1) characteristic of serpentine soils (Brady *et al.* 2005; Fernandez-Going *et al.* 2012). Soil PC3 and PC4 appeared to reflect variation in pH and organic matter content, respectively (Figure S2). Below, we focus on results for soil PC1 and PC2, which together represent variation in the canonical physical and chemical properties of serpentine soils (Gram *et al.* 2004; Walker 1954).

Demographic responses to environment and competition

We found widespread effects of the soil environment on the intrinsic demographic performance of our focal species. In the absence of neighbors, germination rate increased with soil PC1 or PC2 for most (6 of 8) species (Figure S3.1, Figure S3.2, Table S3.1). Responses of fecundity to the soil environment were less clear (Figure S3.3, Figure S3.4, Table S3.4), but several (4 of 8) species were likely to exhibit increased fecundity with soil PC1 ($\Pr(\beta_0 > 0) > 0.9$; see Table S3 for a summary of mathematical symbols used in this study). Combining these demographic rates, fitness increased with soil PC1 or PC2 for all but one species (FEMI) (Figure 3, Figure 4, Table S3.7). Overall, our focal species tended to exhibit higher intrinsic performance toward more fine-textured soils with higher Mg saturation.

Neighbors had contrasting effects on demographic performance along different environmental axes. For all but one species (LACA), neighbors did not clearly alter the response of germination rate to soil PC1 (Figure S3.1, Table S3.3). In contrast, neighbors decreased the effect of soil PC1 on fecundity for 4 of 8 species (Figure S3.3, Table S3.6). For some of these species (e.g., ACWR, HECO), the response of fecundity to soil PC1 was reversed from trending positive in the absence of neighbors ($\Pr(\beta_0 > 0) > 0.94$; Table S3.4) to trending negative in the presence of neighbors ($\Pr(\beta < 0) > 0.94$; Table S3.5). Generally, neighbors did not clearly alter the intrinsic responses of germination rate (all species; Figure S3.2, Table S3.3) and fecundity (7 of 8 species; Figure S3.4, Table S3.6) to soil PC2.

In terms of fitness, neighbors dampened responses to soil PC1 for all but one of the six species with positive intrinsic responses to this axis (SACO) (Table S3.7, Table S3.9). Consequently, these species were predicted to exhibit relatively little variation in realized fitness along soil PC1 (Figure 3, Table S3.8). For FEMI, whose intrinsic response to soil PC1 was only weakly positive, competition resulted in decreased fitness with soil PC1. Fitness increased with soil PC2 for several (4 of 8) species in the presence of neighbors (Table S3.8), similar to intrinsic responses (Figure 4, Table S3.9), although neighbors dampened responses to this axis for two species

(FEMI, HECO). Overall, competition largely diminished responses of fitness to a soil texture gradient (PC1) while having relatively minimal effect on responses of fitness to a soil nutrient (Ca:Mg) gradient (PC2).

Despite widespread effects of neighbors on performance, we found mixed evidence for competitive exclusion from intrinsically suitable environments, at least within the range of conditions captured by our experimental sites. In the absence of neighbors, most species were predicted to achieve positive fitness along much of soil PC1 and PC2 (Figure S3.5). Failure to persist in the absence of neighbors (i.e., environmental filtering *sensu* Kraft *et al.* 2015a) was predicted for ACWR, LACA, and SACO toward sandy soils (low PC1) with high Ca saturation (low PC2) and for CHGL toward fine-textured soils (high PC1) with high Ca saturation (low PC2). Although competition was prevalent (Figure S3.7), especially toward fine-textured soils, only some species were expected to experience competitive exclusion based on their predicted demographic responses to soil PC1 and PC2 (Figure S3.8). LACA and SACO had high probabilities of competitive exclusion from fine-textured soils (high PC1) with high Ca saturation (low PC2) characteristic of the grassland matrix. Conversely, CHGL had high probability of competitive exclusion from soils with intermediate texture (PC1) and moderately high Mg saturation (PC2). Competition is thus expected to shape these species' realized distributions via exclusion from intrinsically suitable environments (but note that the predicted probability of competitive exclusion reached above 95% only for LACA).

Demographic underpinnings of species distributions

Using occurrence surveys in 128 plots at 67 sites distributed across the study landscape, we identified complex relationships between species' realized distributions and demographic responses to the environment and competition. For at least two species (ACWR, LACA), the probability of occurrence increased over the range of soil PC2 captured by experimental sites (Figure S4.4, Table S4.3), consistent with positive intrinsic fitness responses to this axis (Table S3.7). However, some species (e.g., FEMI, HECO, PLER) exhibited an increased probability of occurrence with soil PC2 without an associated increase in fitness (Table S3.8). Despite widespread positive intrinsic fitness responses to soil PC1 (Table S3.7), only HECO demonstrated an increased probability of occurrence over the range of soil PC1 captured by experimental sites (Figure S4.2, Table S4.3). For other species, the probability of occurrence tended to peak around intermediate values of soil PC1 and decreased toward either end of this axis where intrinsic fitness was low (low PC1; Figure 3) or competitive effects were strong (high PC1; Figure S3.9). This discrepancy between intrinsic fitness and realized occurrence is consistent with dampened fitness responses to soil PC1 in the presence of neighbors (Table S3.9). Additionally, reduced probability of occurrence in fine-textured soils (high PC1) is consistent with predicted competitive exclusion for LACA (and to lesser extents for CHGL and SACO) (Figure S3.8).

Comparing observed occurrence to predicted fitness, we found that most species were frequently absent from sites where they were expected to persist (i.e., $r > 0$, absent) (Figure 5). Occurrence in other sites was largely congruent with predicted fitness and sink populations (i.e., $r < 0$, present) were rare. Notably, for LACA and SACO, fitness in the presence of neighbors was a better predictor of observed absences than intrinsic fitness, consistent with predicted competitive

exclusion (Figure S3.8). In all, both competitive exclusion and altered demographic responses to the environment in the presence of competitors are reflected in species' realized distributions, but occurrence patterns could not be fully explained by these demographic processes alone.

Discussion

Building up an understanding of how the demographic consequences of competition translate to species distributions along real-world environmental gradients is a pressing challenge in an era of environmental change (HilleRisLambers *et al.* 2013). In this study, we experimentally quantified the demographic responses of annual plant species to spatial variation in the soil environment and competition in order to evaluate the demographic underpinnings of species distributions in a California grassland. We found that competition can decouple occurrence from intrinsic fitness, not only by driving competitive exclusion from intrinsically suitable environments, but also by altering species' fitness responses to environmental gradients. Notably, competition had contrasting effects on fitness and occurrence along different environmental gradients. Our findings illustrate the importance of accounting for variation in competition across environments in the study of species distributions and challenge the practical but simplifying assumption that realized distributions approximate species' intrinsic responses to environmental gradients.

Variable effects of competition on performance and distributions

Competition presents a challenge for our empirical understanding of species distributions by exerting variable effects on species' performance and distributions along environmental gradients (Figure 1). Most often, competition is described as shaping species distributions by excluding species from intrinsically suitable environments (e.g., Bertness & Ellison 1987; Bullock *et al.* 2000; Connell 1961). In our demographic experiment, three out of eight focal species were likely to experience such competitive exclusion (Figure S3.8). This was reflected in the realized occurrence patterns of at least two of these species (LACA, SACO), with observed absences from sites being more accurately predicted by fitness in the presence of neighbors than by intrinsic fitness unmodified by neighbors (Figure 5). However, for other species, evidence for competitive exclusion based on predicted demographic responses to spatial variation in the environment and competition was limited despite the existence of widespread and sometimes strong competitive effects (Figure S3.9, Figure S3.10). These results illustrate that proxies of the strength of competition (e.g., population density) must be used with caution in predicting species distributions (e.g., with correlative species distribution models), as the same competitive environment can result in either persistence or exclusion depending on species' sensitivities to competition relative to intrinsic fitness.

A more subtle way that competition can influence species distributions is by altering the relationship between fitness and the environment. In our experiment, competitors largely masked species' intrinsic fitness responses to a soil texture gradient (PC1; Figure 3). For all but one species (HECO), realized occurrence patterns failed to clearly track intrinsic fitness along this environmental axis (Figure S4.2). In contrast, competitors had relatively little effect on species'

fitness responses to a Ca:Mg gradient (PC2; Figure 4). Realized occurrence patterns for at least two species (ACWR, LACA) aligned with intrinsic fitness responses to this environmental axis even in the presence of neighbors (Figure S4.4). Expanding on previous findings that competition can alter species' demographic responses to the environment (e.g., Esch *et al.* 2018; Liancourt *et al.* 2013), our results suggest that such altered responses can quantitatively impact species distributions alongside the direct effects of competitive exclusion. Over the long term, reduced population growth due to competition might increase chances of stochastic local extinction (Lande 1993) or limit responses to environmental change (Ettinger & HilleRisLambers 2013; Svenning *et al.* 2014).

Our results also have important implications for whether the demographic underpinnings of species distributions can be inferred from realized distributions. If competition alters the relationship between fitness and the environment, species' realized distributions are unlikely to mirror intrinsic responses to the environment (Davis *et al.* 1998; Pearson & Dawson 2003). Importantly, we show that competition-driven mismatches between intrinsic fitness and realized distributions can vary for different species and environmental gradients. Therefore, careful consideration of how species experience competition along particular environmental gradients is needed when attempting to understand species distributions.

Understanding variation in competition across environments

The dampened responses of fitness to soil PC1 in the presence of neighbors (Figure 3) appeared to be driven by co-variation between intrinsic fitness and competition along this environmental axis, such that competitive effects were stronger where intrinsic fitness was higher (Figure 1 b–c). We also found support for facilitation toward sandy soils (low PC1) for some (3 of 8) species (Figure S3.7). These patterns, consistent with Grime's (1977) CSR model and the stress-gradient hypothesis (Bertness & Callaway 1994; Maestre *et al.* 2009), underscore the importance of understanding variation in competition along environmental gradients. While evaluating the mechanisms underlying variation in competition was beyond the scope of this study, there was substantial turnover in species cover across our experimental sites (Figure S4), pointing to species identity or density as important determinants of competitive effects in this system. In particular, sites with fine-textured soils (high PC1) where competitive effects were strong (Figure S3.9) tended to have high cover of invasive grasses such as *Avena fatua*, *Bromus diandrus*, and *Bromus hordeaceus* (Figure S4). These invasive species have been shown to suppress native plants in California serpentine grasslands through a variety of mechanisms, including resource competition, habitat modification, and recruitment limitation (e.g., Chen *et al.* 2018; Hamilton *et al.* 1999; LaForgia 2021; Seabloom *et al.* 2003a, b). Additionally, recent work in our study system demonstrated that small changes in environmental conditions can have large effects on per capita competitive interactions (Van Dyke *et al.* 2022). Thus, quantifying how different sources of variation in competition contribute to species distributions is an important next step (see also Louthan *et al.* 2015).

Future directions

Past review studies have noted that there is limited empirical evidence that competition shapes the distributions or co-occurrence of plant species at broad spatial scales (Götzenberger *et al.* 2012; Wisz *et al.* 2013). Our results show that competition can leave discernible imprints on plant species' occurrence patterns at the spatial scale of local populations. However, occurrence could not be fully explained by demographic responses to the soil environment and competition alone. Notably, our finding that species were frequently absent from suitable sites (Figure 5) is consistent with widespread dispersal limitation. This result aligns with previous findings that the (re-)establishment of native plants in California grasslands is severely seed-limited (Germain *et al.* 2017; Seabloom *et al.* 2003a, b). Surprisingly, we also found that occurrence of HECO was better predicted by intrinsic fitness than by fitness in the presence of neighbors (Figure 5). This result might reflect the possibility of more complex (e.g., unimodal) relationships between performance and environment that are not represented by our statistical models, at least for some species (e.g., HECO in Figure 4). Incorporating the additional complexity of non-monotonic demographic responses to the environment, alongside metacommunity processes (Gilbert & O'Connor 2013; Godsoe *et al.* 2017), is an important next step toward better understanding species distributions at the landscape scale.

Our study captured only a single generation of population dynamics in a system with substantial interannual variation in rainfall (Levine & Rees 2004). While our demographic experiment was conducted in a water year with about average total rainfall (2019–2020 = 21.57 in + 0.6 in added manually, mean = 21.44 in, County of Santa Barbara 2024), some of the observed mismatches between species' performance and occurrence may arise in part from complexities in how competitive population dynamics play out over longer time scales (Chesson 1994). In particular, rainfall-driven variation in the competitive environment (e.g., Hallett *et al.* 2019; Hobbs *et al.* 2007; Pitt & Heady 1978) could mean that positive fitness in one year may not ensure persistence in subsequent years. It is notable that we were able to detect imprints of competition on occurrence in this study, but further work is needed to understand how spatiotemporal variation in competition shapes species distributions.

Conclusions

The complex and variable interplay between performance, competition, and distribution (Figure 1) presents a challenge for explaining or predicting species distributions, but can be understood by studying how competitors modify the demographic performance of species along environmental gradients. Here, we provided evidence that competition contributes to plant species' distributions in an edaphically variable landscape, not only by driving competitive exclusion, but also by altering species' intrinsic fitness responses to the environment. Importantly, the effect of competition on performance and distributions varied by species and environmental gradient. Our findings emphasize the importance of disentangling species' demographic responses to variation in the abiotic environment and biotic interactions, especially with environmental change threatening to upend current environments and communities. Demographically informed studies of species distributions that account for variation in

competition along environmental gradients, especially across broader spatial extents, will provide valuable insights into the determinants species' current and future distributions.

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Statement of authorship

KTH and NJBK conceptualized the study and developed the methdology. KTH led investigation, data curation, and formal analysis with input from NJBK. KTH led writing of the original draft of the manuscript with substantial input from NJBK. KTH and NJBK contributed to review and editing of the manuscript.

Data accessibility statement

Data generated for this study and code for analyses will be archived on Zenodo prior to publication.

Tables

Table 1: Plant species used in this study.

Code	Species	Family
ACWR	*Acmispon wrangelianus*	Fabaceae
CHGL	*Chaenactis glabriuscula*	Asteraceae
FEMI	*Festuca microstachys*	Poaceae
HECO	*Hemizonia congesta*	Asteraceae
LACA	*Lasthenia californica*	Asteraceae
PLER	*Plantago erecta*	Plantaginaceae
SACO	*Salvia columbariae*	Lamiaceae
URLI	*Uropappus lindleyi*	Asteraceae

Figures

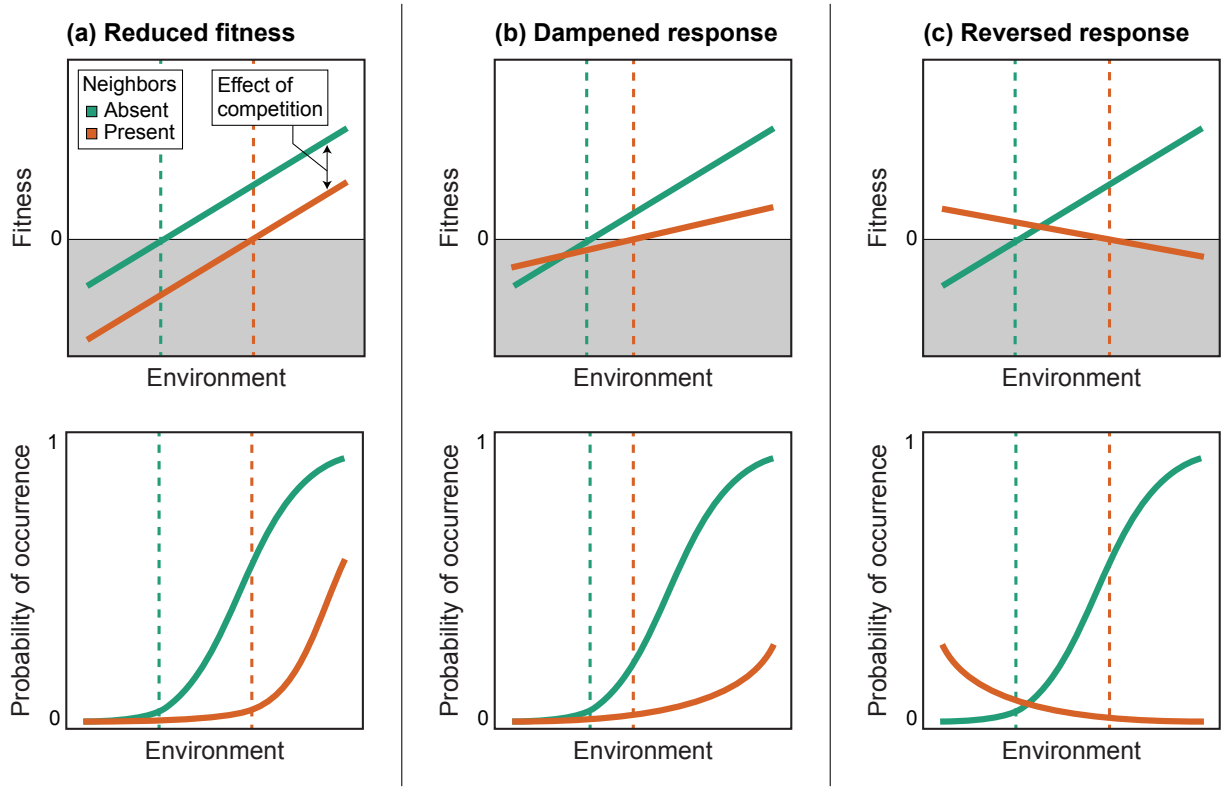

Figure 1: Different ways that competition can affect a species' fitness and distribution (represented here as the probability of occurrence) along an environmental gradient. (a) Competition uniformly reduces fitness, causing competitive exclusion in some environments. (b–c) The effect of competition co-varies with intrinsic fitness, altering the realized response of fitness to the environment. (b) Competition dampens the response of fitness to the environment, allowing occurrence toward favorable environments at reduced probability. (c) Competition reverses the response of fitness to the environment, driving exclusion toward intrinsically favorable environments. Note that positive effects of neighbors (i.e., facilitation) are allowed here, but are not necessary for these scenarios to play out within a given range of environmental conditions. Also note that these scenarios are not comprehensive and more complex (e.g., unimodal) relationships are plausible. Vertical dashed lines denote the environmental conditions where fitness = 0, with occurrence expected where fitness > 0.

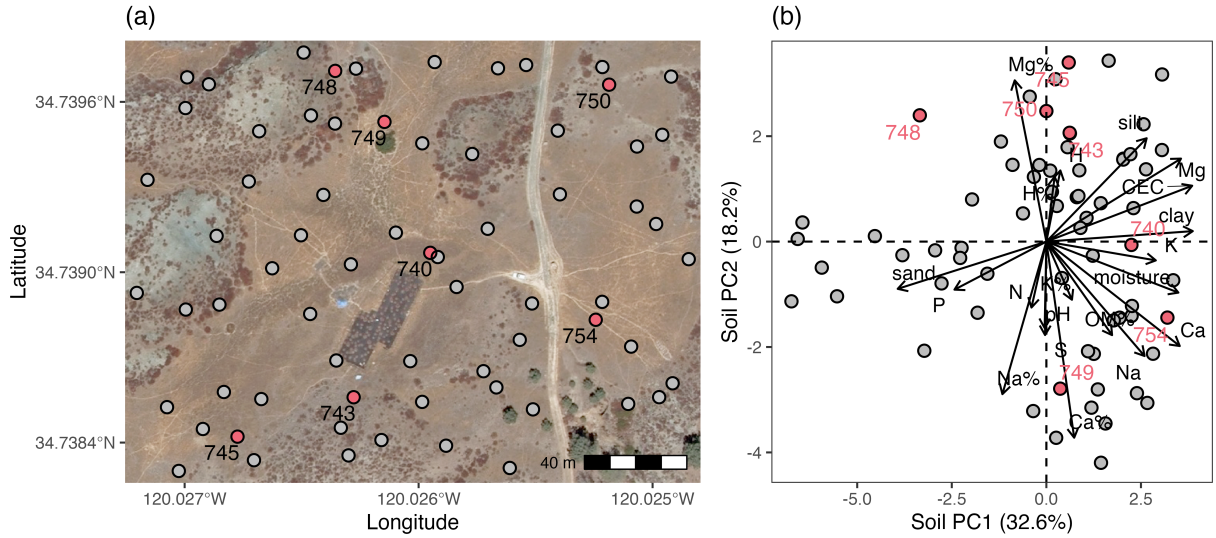

Figure 2: Locations and soil environments of study sites. Red and gray points correspond to experimental sites and survey sites, respectively. Experimental sites are labeled with their site IDs. (a) Map of study sites. High resolution orthoimagery courtesy of the U.S. Geological Survey. (b) Principal component analysis of soil variables at study sites. Arrows represent the correlations of individual soil variables with PC1 and PC2. The percentage of variance explained by each axis is shown in parentheses.

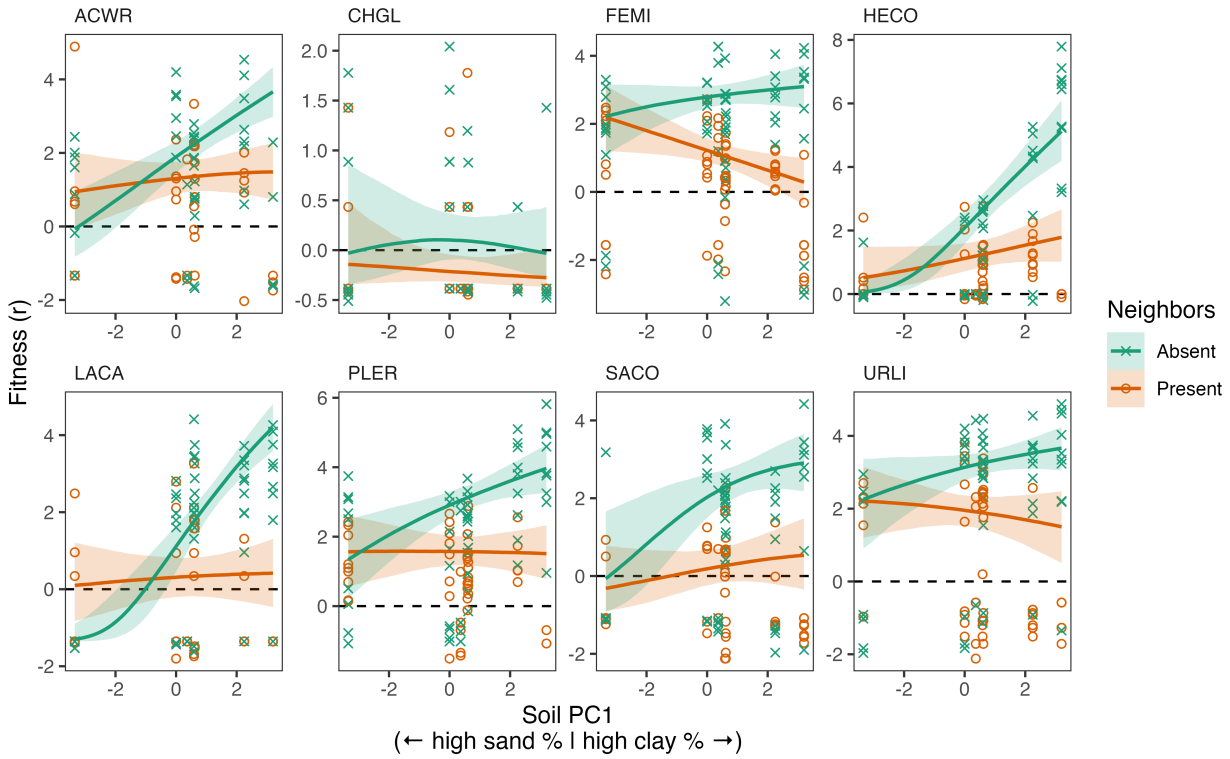

Figure 3: Predicted fitness (r) for each species conditional on neighborhood treatment and soil PC1. All other predictors are fixed at their average values. Solid lines represent posterior medians; shaded areas represent 95% quantile credible intervals.

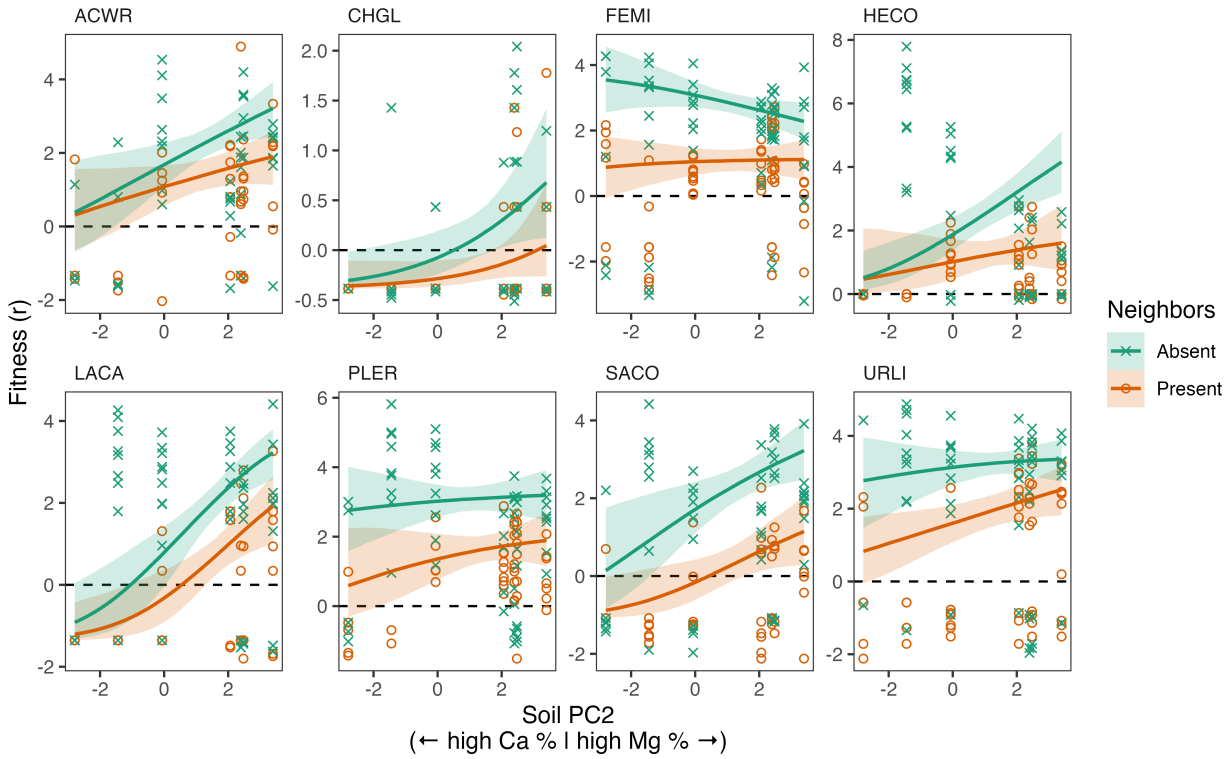

Figure 4: Predicted fitness (r) for each species conditional on neighborhood treatment and soil PC2. All other predictors are fixed at their average values. Solid lines represent posterior medians; shaded areas represent 95% quantile credible intervals.

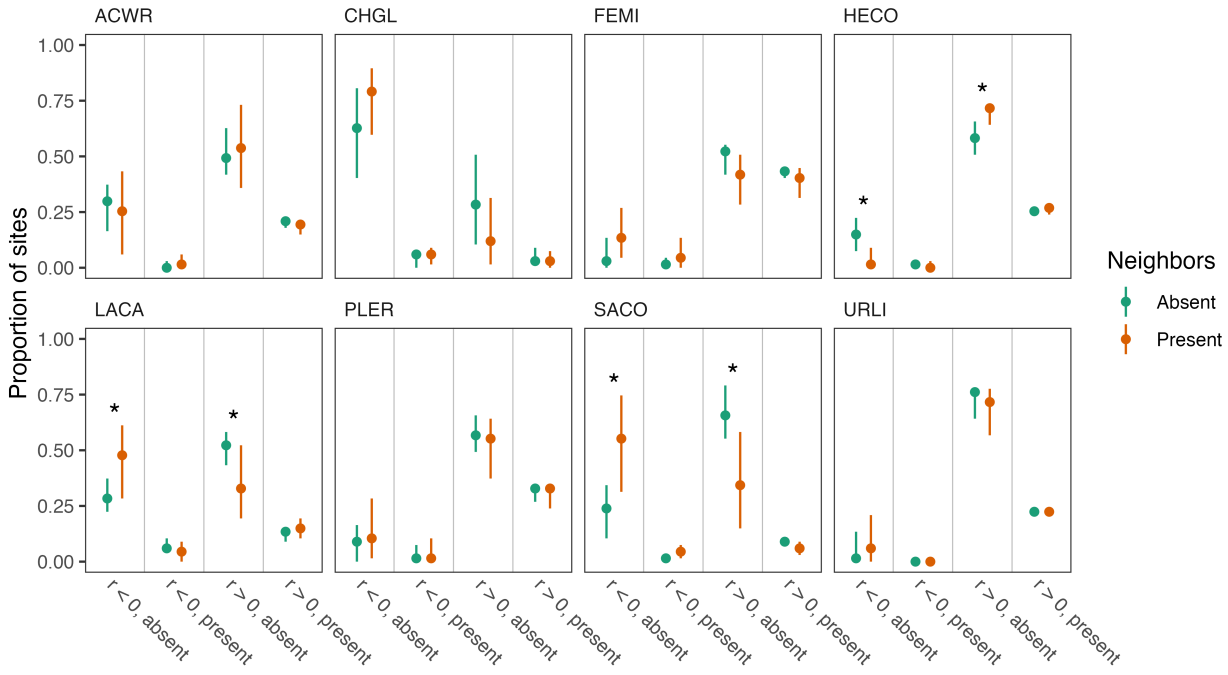

Figure 5: Frequency distributions of study sites with respect to predicted fitness ($r > 0$ vs. $r < 0$) and observed occurrence (present vs. absent) for each species. Fitness was predicted with neighbors either absent or present. Asterisks are used to highlight differences with over 95% posterior support (note that these annotations are not results of statistical significance tests). Points represent posterior medians; lines represent 95% quantile credible intervals.

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