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When the neighborhood matters: contextual selection on seedling traits in native and non-native California grasses

Joseph Waterton[1,3], [ID], Susan J. Mazer[2], [ID], Elsa E. Cleland[1], [ID]

[1]Ecology, Behavior and Evolution Section, University of California San Diego, La Jolla, CA, United States
[2]Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, United States
[3]Present address: Department of Biology, Indiana University, 1001 E. 3rd St., Bloomington, IN 47405, United States

Corresponding author: Ecology, Behavior and Evolution Section, University of California San Diego, 9500 Gilman Dr., La Jolla, CA 92093, United States.
Email: jwaterto@iu.edu

Abstract

Plants interact extensively with their neighbors, but the evolutionary consequences of variation in neighbor identity are not well understood. Seedling traits are likely to experience selection that depends on the identity of neighbors because they influence competitive outcomes. To explore this, we evaluated selection on seed mass and emergence time in two California grasses, the native perennial *Stipa pulchra*, and the non-native annual *Bromus diandrus*, in the field with six other native and non-native neighbor grasses in single- and mixed-species treatments. We also quantified characteristics of each neighbor treatment to further investigate factors influencing their effects on fitness and phenotypic selection. Selection favored larger seeds in both focal species and this was largely independent of neighbor identity. Selection generally favored earlier emergence in both focal species, but neighbor identity influenced the strength and direction of selection on emergence time in *S. pulchra*, but not *B. diandrus*. Greater light interception, higher soil moisture, and greater productivity of neighbors were associated with more intense selection for earlier emergence and larger seeds. Our findings suggest that changes in plant community composition can alter patterns of selection in seedling traits, and that these effects can be associated with measurable characteristics of the community.

Keywords: community composition, natural selection, competition, emergence time, seed mass, priority effect, California grasslands

Introduction

Neighboring plants interact extensively through processes such as resource competition, allelopathy, and facilitation. Plant–plant interactions play a central role in structuring plant communities (Bashirzadeh et al., 2022; Soliveres & Maestre, 2014), but the resulting evolutionary consequences for populations have historically received little attention (Thorpe et al., 2011). There is growing evidence that variation in the surrounding plant community influences the strength and direction of natural selection exerted on key fitness-related traits (e.g., Beans & Roach, 2015; Lau, 2008; Parachnowitsch et al., 2014), and that it shapes the evolutionary trajectories of plant populations (e.g., Callaway et al., 2005; Fletcher et al., 2016; Kleynhans et al., 2016; Lankau, 2012; Leger, 2008; Meilhac et al., 2020; van Moorsel et al., 2018b, 2019, 2021). However, we currently have a limited understanding of the mechanisms by which community composition determines the strength or direction of selection. As drivers of global change, such as climate change and species introductions, alter the composition of plant communities worldwide (Kuebbing et al., 2013; van Kleunen et al., 2015), understanding how plant community composition shapes selection will facilitate predictions of the total evolutionary responses of plant populations to global change.

In seasonal environments, seedling traits such as emergence time and seed mass strongly influence fitness from early life stages through to adulthood (reviewed in Larios et al., 2018; Verdú & Traveset, 2005). Emerging earlier than competitors provides longer windows for growth and reproduction before favorable conditions deteriorate, as well the potential to pre-empt resources and suppress the growth of individuals that emerge later (i.e., priority effects; Vannette & Fukami, 2014). Accordingly, meta-analysis shows that earlier seedling emergence tends to enhance fitness (Verdú & Traveset, 2005). Similarly, the greater energy reserves present in larger seeds can lead to more rapid seedling growth and greater final size, and these benefits can be enhanced in stressful conditions such as drought (Gross & Smith, 1991; Larios et al., 2014; Mojonnier, 1998; Stanton, 1984; Wulff, 1986). These competitive benefits are not without cost; for example, earlier emergence can result in increased susceptibility to early-season abiotic stress such as late frost (Skálová et al., 2011) and the production of larger seeds is traded off with producing fewer seeds (Leishman, 2001; Smith & Fretwell, 1974). In competition, differences in early size can be magnified over the course of growth due to asymmetry of competition (particularly light; Weiner, 1990). As a result, the effects of seed mass and emergence time on fitness are likely to be sensitive to the phenotypes of competitors. Seed mass itself can influence emergence time (Simons & Johnston, 2000; Susko & Lovett-Doust, 2000; Waterton et al., 2020; Wulff, 1986), and so the selective effects of neighbors on seed mass and emergence

time are likely to be mediated by correlations between them (i.e., indirect selection).

The identity of neighboring plants is likely to shape patterns of selection on seedling traits. Neighboring plants can influence the availability of light, soil nutrients, and soil moisture availability (Seabloom et al., 2003; Williams et al., 2021), and variation in each of these resources can influence the strength and/or direction of phenotypic selection on plant traits (McGoey & Stinchcombe, 2009; Navarro et al., 2022; Waterton et al., 2022). Neighbors that cause different seedling phenotypes to experience differing availabilities of limiting resources may alter the strength of selection. For example, communities that intercept more light may result in relatively less light available for later vs. earlier emerging individuals and thus increasingly favor earlier emergence. Selection among members of a focal species may also be stronger in communities that more severely reduce that species' mean population fitness; this is because—all else being equal—the variance in relative fitness within a population (i.e., the opportunity for selection) increases when mean fitness decreases in absolute terms (i.e., all individuals produce 10 fewer seeds; Benkman, 2013; Fugère & Hendry, 2018; Rundle & Vamosi, 1996).

The selective effects exerted by neighbors may be predictable based on factors such as (a) origin status (i.e., native vs. non-native) and (b) species diversity. Non-native species often differ from their native counterparts with respect to their traits and impacts on competitors. Compared to their native counterparts, non-natives often emerge earlier (Pérez-Fernández et al., 2000; Deering & Young, 2006; Abraham et al., 2009, reviewed in Gioria & Pyšek, 2016), differ from natives with respect to the uptake of resources such as light and soil moisture (te Beest et al., 2014; Morris et al., 2002; Seabloom et al., 2003), and reduce mean fitness to a greater extent (Vilà et al., 2011), potentially causing consistent differences in selection exerted by native versus non-native dominated communities. Consistent with this, several studies have documented that non-native species alter the strength or direction of selection in co-occurring species (Leger et al., 2017), or lead to evolved differences in the traits or performance in co-occurring species (Callaway et al., 2005; Fletcher et al., 2016; Leger, 2008). Trait differences between natives and non-natives might also influence the selective responses of each to variation in the surrounding biotic community; for example, non-native species that emerge rapidly (i.e., the phenotypic distribution is shifted earlier) may experience selection on seedling traits that is less sensitive to neighbor identity as even relatively late emerging individuals emerge earlier than the surrounding community. More taxonomically diverse communities can be characterized by more complete resource uptake via sampling and/or complementarity effects (Aarssen, 1997; Anten & Hirose, 1999; Guderle et al., 2017; Tilman et al., 1997; Wacker et al., 2009), which might lead to stronger selection exerted by communities with high versus low species diversity. Supporting this, a long-term biodiversity experiment found that plant populations from mixed-species communities evolved greater niche differentiation compared to populations from monocultures (van Moorsel et al., 2018a; Zuppinger-Dingley et al., 2014).

We carried out a field experiment to test the hypothesis that neighboring community composition influences phenotypic selection on seedling traits, and that patterns of selection are determined by characteristics of the neighboring community. Field experiments are a powerful tool for evaluating how variation in surrounding community composition influences patterns of selection because, unlike observational studies across natural gradients, they mitigate the effects of other confounding factors that might influence both community composition patterns of phenotypic selection (Wade & Kalisz, 1990). We grew two widespread California grasses, the long-lived perennial native *Stipa pulchra* (Hitchc.) Barkworth and non-native annual *Bromus diandrus* (Roth), in each of nine "neighbor treatments" that varied in the identity, origin status, and number of species. We measured the mass of caryopses (hereafter "seeds"), emergence time and fitness in focal individuals and quantified aspects of the neighboring community in each treatment to further investigate factors influencing mean fitness and patterns of selection. Specifically, we predicted that (a) selection on seedling traits would vary with neighbor identity, such that (b) selection would be stronger under one or more of the following conditions: when neighbors uptake more limiting resources, reduce mean fitness to a greater extent, are non-native, or are more taxonomically diverse.

Methods

Overview

We evaluated phenotypic selection on emergence time and seed mass in *B. diandrus* and *S. pulchra* growing in one of nine neighbor treatments (Table 1). These comprised eight "neighbor-present" treatments including six single species treatments (three natives and three non-natives, taxonomically balanced at the genus level) and two mixed-species treatments (all three native or all three non-natives), and a "neighbor-absent" treatment. The seeding rate of each neighbor species in mixed treatments was one third of that in single species treatments, such that the intended total density of emerging seedlings remained the same across both treatment types (i.e., a "replacement series"; Jolliffe, 2000). We quantified five neighbor metrics in each treatment: emergence time, peak seedling density, light interception, soil water availability, and total aboveground biomass. We evaluate only linear selection to limit model complexity and because more complex fitness functions are less amenable to formally testing for associations with neighbor metrics.

We carried out the experiment at the University of California San Diego Biological Field Station (32.89° N, 117.23° W; Supplementary Text S1). The climate is Mediterranean, with most precipitation typically falling between November and May, during which the majority of seedling emergence and subsequent growth occurs. The experiment lasted two growing seasons in 2017 (Season 1) and 2018 (Season 2), with the non-native annual *B. diandrus* grown in Season 1 only and the native perennial *S. pulchra* grown over Seasons 1 and 2. For *B. diandrus*, we evaluated fecundity in Season 1 via the probability of reproducing and total seed weight in reproducing individuals. For *S. pulchra*, we evaluated two fitness measures: (a) fecundity across Seasons 1 and 2 via the probability of reproducing and total seed weight in reproducing individuals and (b) aboveground vegetative biomass at the end of Season 2 via the probability of surviving and aboveground vegetative biomass in surviving individuals. We evaluate both fitness measures in *S. pulchra* for three reasons: first, because this species can reproduce clonally (Dyer & Rice, 1997; Hull & Muller, 1977); second, because surviving plants that do not produce seeds within two seasons still have the potential

Table 1. Focal species and neighbor treatments in the field m²experiment.

Name	Origin	Diversity	Life history strategy	Code	Seeding rate (m²)
Focal species					
Bromus diandrus	Non-native	–	Annual	–	–
Stipa pulchra	Native	–	Perennial	–	–
Neighbor treatments					
Neighbor-absent	–	–	–	ABS	–
Bromus carinatus	Native	Single	Perennial	BRCA	1,353
Festuca microstachys	Native	Single	Annual	FEMI	1,527
Hordeum brachyantherum	Native	Single	Perennial	HOBR	2,557
Native mixture	Native	Mixed	Mixed	NATMIX	1,812
Bromus hordeaceus	Non-native	Single	Annual	BRHO	1,196
Festuca myuros	Non-native	Single	Annual	FEMY	1,389
Hordeum murinum	Non-native	Single	Annual	HOMU	1,125
Non-native mixture	Non-native	Mixed	Mixed	NONMIX	1,236

Note. Neighbor treatments comprised eight "neighbor-present" treatments, including six single species treatments and two mixed species treatments, and a "neighbor-absent" treatment. The native and non-native mixture treatments contained all three natives and non-natives, respectively, each at a third of the seeding rate in single species treatments.

for future sexual reproduction, and; third, because vegetative biomass is strong predictor of fecundity in perennial grasses (Cheplick, 2021). Biomass of *S. pulchra* at the end of Season 2 was strongly positively correlated with total fecundity (i.e., the sum of fecundity in Seasons 1 and 2; $r = .87$, $t_{(688)} = 45.3$, $p < .001$; Supplementary Figure S1). We also evaluated neighbor effects on emergence probability and emergence time because previous work shows that emergence is sensitive to neighboring seeds and seedlings (Dyer et al., 2000; Tielbörger & Prasse, 2009).

Study system and seed material

Bromus diandrus (ripgut brome) is an annual grass native to Eurasia that has become naturalized in California since European settlement (Jackson, 1985). This species is particularly dominant in disturbed areas, such as abandoned agricultural fields (Stromberg & Griffin, 1996). *Bromus diandrus* is largely self-fertilizing (selfing rate > .99; Kon & Blacklow, 1990). *Stipa pulchra* (purple needlegrass) is a long-lived perennial bunchgrass native to California that is found in woodland, chaparral, and grassland from Baja California to northern California (Baldwin et al., 2012). The potential post-germination lifespan of *S. pulchra* under field conditions is conservatively estimated at 100 years (Hamilton et al., 2002). *Stipa pulchra* also has high rates of self-fertilization (reported selfing rate ≈ 1; Larson et al., 2001) and can also reproduce clonally (Dyer & Rice, 1997; Hull & Muller, 1977). *Bromus diandrus* and *S. pulchra* often co-occur throughout California (Waterton et al., 2020).

For both focal species, we used field collected seeds from naturally occurring populations exhibiting high seedling emergence percentages in a previous study (*S. pulchra*: Sedgwick Reserve; *B. diandrus*: Elliott Chaparral Reserve; see Supplementary Text S1 for details). For each focal species, we used a total of 84 seeds in each of the nine neighbor treatments, with seven seeds from each of 12 maternal lines (*N* = 756 in each focal species). For each maternal line, we selected seeds that outwardly appeared viable (e.g., filled and undamaged) and randomly assigned them to neighbor

treatments. We obtained neighbor seeds through a commercial supplier (S&S Seeds, Carpinteria, CA, USA), with the exception of *Hordeum murinum* seeds which we collected in bulk from the site of the field experiment in February 2015.

Field experiment
Establishing plots and planting seeds

Prior to Season 1, we established nine 0.9 × 1.05 m plots in a fully randomized block design replicated seven times, with each neighbor treatment represented once per block (Figure 1). In January 2017, we watered and tilled plots to deplete the seed bank. For each focal species, we planted one seed from each of 12 maternal lines into two rows of six in each plot half, leaving a 30 cm wide strip in the middle of each plot separating each focal species (Figure 1). We sowed neighbor seeds evenly across plots on the soil surface at a intended density of 900 seedlings m⁻², with seed numbers adjusted for emergence percentages observed in greenhouse trials. We planted focal seeds by gently pressing them into the soil at a depth of 1 cm with radicles pointing downwards. To identify emerging focal individuals, we planted focal seeds in a 1.9 cm diameter, 0.5 cm height PVC ring that was covered while we sowed neighbor seeds. We planted all seeds into dry soil between 14 and 15 February. We watered plots on 16 February, with days to emergence calculated from this date.

Prior to Season 2, we re-established the neighbor component of *S. pulchra* plot halves (.45 × 1.05 m), as we harvested neighbor plants after Season 1 (see Neighbor metrics). Dry winter conditions delayed the onset of the growing season until after a large rain event on January 9, 2018. Because we harvested neighbor aboveground biomass at the end of Season 1, we resowed plots with neighbor seeds on January 18, 2018. We adjusted seed densities from the first season to achieve the original intended density of 900 seedlings m⁻². In both growing seasons, supplemental water was provided both to initiate germination and to prevent mass mortality due to drought, and non-neighbor weeds were carefully removed (full details are provided in Supplementary Text S1).
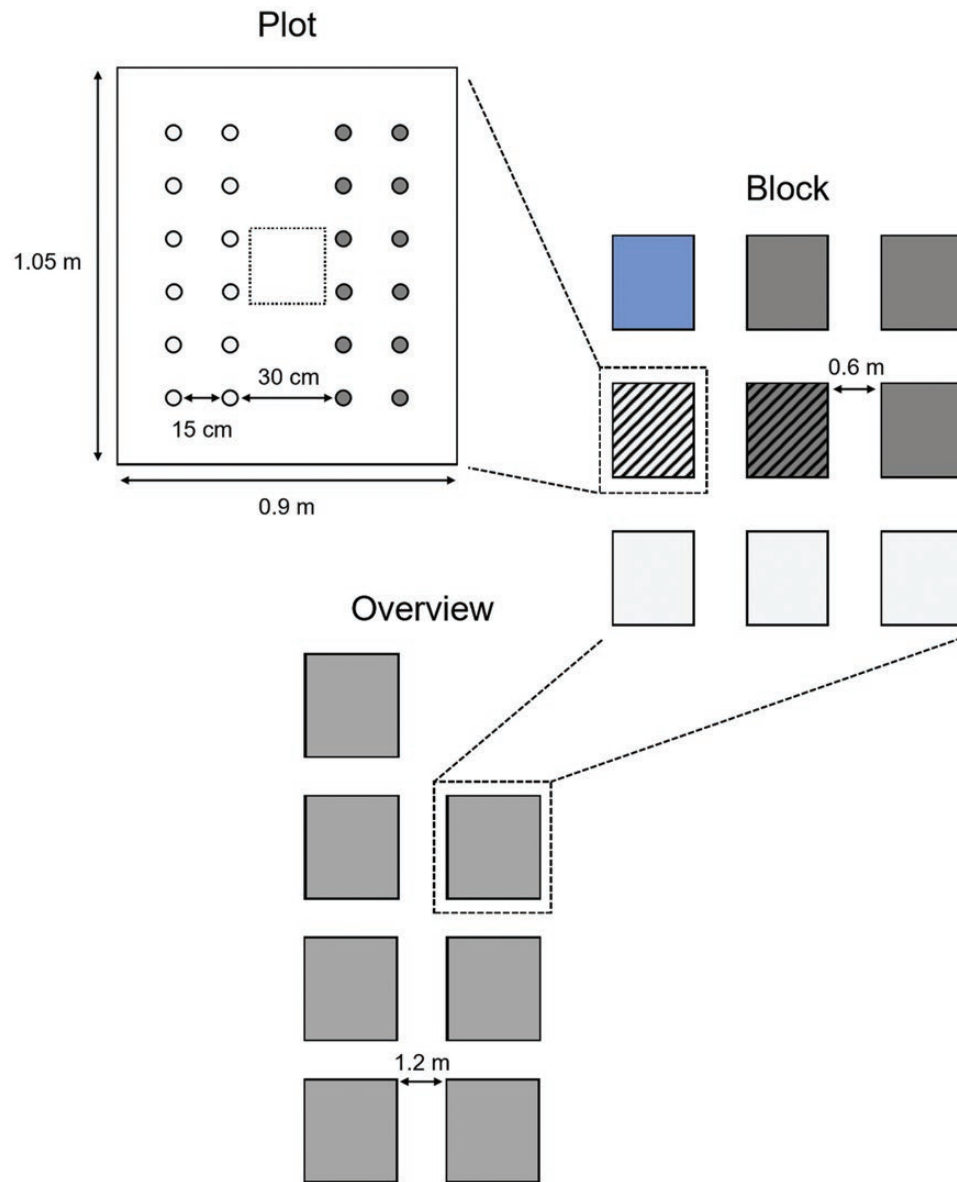
Figure 1. Layout of the field experiment with an example block layout. Dark gray and light gray squares represent native and non-native neighbor plots, respectively; striped and nonstriped squares represent mixed species and single species plots, respectively; blue represents neighbor-absent plots. Light gray and dark gray circles represent *B. diandrus* and *S. pulchra* individuals, respectively.

Traits and fitness of focal individuals

To quantify initial seed mass, we weighed each focal seed, including lemmas and awns, to the nearest .01 mg prior to planting. In Season 1 only, we monitored daily the emergence (i.e., visible radicle) of focal individuals until we had observed no emergence for three consecutive days. We were unable to monitor any emergence on February 27, 11 days after initial watering, due to a rainstorm; therefore, any plants that emerged on this day were recorded as having emerged on February 28. In Seasons 1 and 2, we harvested seeds of focal plants whenever seeds had matured but were still attached to culms; seeds were collected in coin envelopes and maintained at room temperature before weighing total seed production for each individual to the nearest 0.01 mg. At the end of Season 2 on May 17, 2018, we harvested *S. pulchra* aboveground biomass and dried it at 40 °C for 3 days before weighing to the nearest .01 g.

Quantifying neighbor metrics

We quantified five neighbor metrics in each plot in Season 1: (a) emergence time, (b) peak seedling density, (c) light interception, (d) soil water availability, and (e) total aboveground biomass. Full details of data collection for neighbor metrics are given in Supplementary Text S1. Briefly, we monitored emergence of neighbors in a 20 × 20 cm quadrat in the center of each plot daily between February 20 and March 14, 2017. For each plot, we calculated the number of days to reach 50% of total neighbor emergence and the peak density of emerging neighbor seedlings (i.e., prior to the onset of mortality). To characterize light interception, we measured photosynthetically active radiation (PAR) at ground level and above the canopy within an hour of the solar zenith on May 18, 2017 in cloudless weather and calculated the percentage of light intercepted by the canopy. To quantify soil water availability, we measured volumetric water content (VWC) from 0 to

15 cm depth over four consecutive days following a rain event on May 8 and calculated mean VWC across the 4 days. To quantify total aboveground biomass, we carefully clipped all neighbor aboveground biomass to soil level 31 July–2 August. We dried biomass at 40 °C for 3 days before weighing to the nearest 0.01 g.

Statistical analyses

We conducted all statistical analyses using R version 4.2.2 (R Core Team, 2022), analyzing each focal species separately. We tested the significance of fixed effects in all models with Type II Wald chi-square tests using the Anova function in the package car (Fox & Weisberg, 2019). To assess the suitability of error distributions and data transformations, we used the simulate Residuals function in the package DHARMa (Hartig, 2022).

Neighbor metrics

We tested whether neighbor metrics (emergence time, peak seedling density, PAR interception, soil VWC, total aboveground biomass), were influenced by each of the following fixed effects: neighbor treatment, neighbor origin, and neighbor diversity using separate PERMANOVAs fit using the adonis2 function in the package vegan (Oksanen et al., 2022). We excluded the neighbor-absent treatment from these analyses because it did not have associated data for emergence time, peak seedling density, and total aboveground biomass. In the case that a full PERMANOVA model was statistically significant, we fit separate univariate models for each neighbor metric. Full details of multivariate PERMANOVAs and univariate models are provided in Supplementary Text S1.

Emergence of focal individuals

To test whether and how each focal individual's seed mass, neighbor treatment, neighbor origin, and neighbor diversity influence the probability of emergence, we fit binomial generalized linear mixed models (GLMMs) with a logit link using the glmmTMB function in the package glmmTMB (Brooks et al., 2017). We tested how each factor influenced mean emergence time with linear mixed models (LMMs) using the lmer function in the package lme4 (Bates et al., 2015). Full details of emergence analyses are provided in Supplementary Text S1.

Analysis of fitness

Fitness (fecundity in *B. diandrus*; fecundity and biomass in *S. pulchra*) was zero-inflated and overdispersed; therefore, we analyzed mean fitness and phenotypic selection using hurdle negative binomial GLMMs (cf. MacTavish & Anderson, 2022; Wadgymar et al., 2015; Waterton & Cleland, 2021). These models proceed in two parts: first, a "zero model" comprising a binomial regression with logit link function modeling if plants reproduced or survived until biomass was harvested (*S. pulchra* only); second, a "non-zero model" comprising a negative binomial regression with log link function modeling the fecundity of seed-producing individuals or the biomass of survivors. We rounded fecundity and biomass to the nearest 1 mg and 1 g, respectively, because negative binomial models require integer values for response variables.

Mean fitness

To test the effect of neighbor treatment on mean fitness, we fit a hurdle GLMM (glmmTMB package; Brooks et al., 2017)

in which fitness was predicted by neighbor treatment, with block and plot as random intercepts. In the case of significant neighbor treatment effects in zero or nonzero model parts, we carried out two post hoc tests using the emmeans function in the package emmeans (Lenth et al., 2022): first, we tested the effect of neighbor presence vs. absence by comparing the neighbor-absent treatment to the average of the eight neighbor-present treatment levels; second, we tested the effect of neighbor identity with pairwise comparisons among the eight neighbor-present treatment levels.

To investigate whether and how neighbor characteristics influence mean fitness, we examined the Pearson correlations between mean absolute fitness (including individuals with zero and nonzero fitness values) and each neighbor metric. Additionally, to test the effects of neighbor origin (native vs. non-native) and diversity (single vs. mixed species) on mean fitness, we fit separate hurdle GLMMs (glmmTMB package; Brooks et al., 2017) in which fitness was predicted by neighbor origin/diversity, with neighbor treatment, block, and plot as random intercepts.

Phenotypic selection

We tested the effect of neighbor identity on patterns of direct selection on seed mass and emergence time. Direct selection acting on a trait is that which acts after accounting for selection acting on other correlated traits (i.e., indirect selection). For phenotypic selection analyses, we standardized trait values to a mean of 0 and a *SD* of 1 across all neighbor treatments to maintain the same relative order of trait values for analyses of neighbor treatment, neighbor origin, and neighbor diversity; we note that standardizing within neighbor treatments gave similar results. To test whether direct selection differed between neighbor treatments, we fit hurdle GLMMs (glmmTMB package; Brooks et al., 2017) in which fitness was predicted by seedling traits (seed mass and emergence time), neighbor treatment, and the trait × neighbor treatment interactions, with random intercepts for block and plot. When trait × treatment interactions were significant, indicating context-specific selection, we carried out two post hoc tests using the emtrends function in the package emmeans (Lenth et al., 2022): first, we tested the effect of neighbor presence vs. absence on selection by comparing the coefficient in the neighbor-absent treatment to the average coefficient of all other treatment levels; second, we tested the effect of neighbor identity on selection with pairwise comparisons among the coefficients of the eight neighbor-present treatments.

To investigate whether and how neighbor metrics and mean fitness are associated with selection on seedling traits, we examined the Pearson correlations between standardized selection gradients (β) and each neighbor metric and mean fitness. We estimated standardized selection gradients in each neighbor treatment from LMMs (lme4 package; Bates et al., 2015) of within-treatment level relative fitness (i.e., individual fitness divided by mean fitness) predicted by traits, neighbor treatments, and the trait × neighbor treatment interactions with random intercepts for block and plot. We relativized fitness within treatment levels as is appropriate for traits, such as emergence time, that are subject to strong soft selection (De Lisle & Svensson, 2017; Weis et al., 2015). To test the effects of neighbor origin (native vs. non-native) and diversity (single vs. mixed species) on selection, we fit separate hurdle GLMMs (glmmTMB package; Brooks et al., 2017) in which fitness was predicted by traits, neighbor origin/diversity, and

trait × neighbor origin/diversity interactions, with random intercepts for neighbor treatment, block, and plot. We estimated the mean value of selection gradients across each level of neighbor origin and diversity with LMMs (lme4 package; Bates et al., 2015) of within-origin/diversity level relative fitness predicted by the relevant traits with random intercepts for neighbor treatment, block, and plot.

To test whether direct selection exerted by neighbors was consistent between *B. diandrus* and *S. pulchra*, we examined the Pearson correlations between standardized selection gradients for each trait in the two focal species across the eight neighbor-present treatments. Below, we focus on the results for *S. pulchra* selection gradients based on fecundity as these are most comparable to *B. diandrus* selection gradients. For a given trait, a significant, positive correlation between selection gradients in each species indicates that neighbor environments exerted consistent direct selection in each focal species. We note that estimates of selection in each species are not fully independent as individuals of both species were present in the same plots. That is, latent, unmeasured attributes of each plot may contribute to correlations between the selection gradients estimated for each focal species.

Results

Neighbor metrics

Neighbor metrics differed significantly among neighbor treatments (pseudo-$F_{(7)}$ = 6.26, p = .001). This overall effect was driven by significant differences among neighbor treatments in emergence time ($\chi^2_{(7)}$ = 55.4, p < .001; Figure 2A), peak seedling density ($\chi^2_{(7)}$ = 42.4, p < .001; Figure 2B), light interception ($\chi^2_{(7)}$ = 69.2, p < .001; Figure 2C), soil moisture availability ($\chi^2_{(7)}$ = 18.2, p = .011, note that all pairwise comparisons were nonsignificant; Figure 2D), and total aboveground biomass ($\chi^2_{(7)}$ = 126.1, p < .001; Figure 2E). However, neighbor metrics did not differ significantly between native and non-native communities (pseudo-$F_{(1)}$ = 0.98, p = .48) nor between single- and mixed-species communities (pseudo-$F_{(1)}$ = 0.18, p = .96).

Emergence of focal individuals

Bromus diandrus
In *B. diandrus*, 80.6% of seeds emerged across 24 days with a mean emergence time of 7.8 days (SD = 2.85, n = 609). Heavier seeds were more likely to emerge ($\chi^2_{(1)}$ = 8.35, p = .004; Supplementary Figure S2A) and emerged earlier ($\chi^2_{(1)}$ = 29.9, p < .001; Supplementary Figure S3A) than relatively light seeds. Emergence probability, but not emergence time, was influenced by neighbor treatment, with lower emergence probability in the presence of the non-native *Bromus hordeaceus* compared to non-native *H. murinum*, but neighbor origin and diversity had no effect on emergence time or probability (Supplementary Tables S1, S2; Supplementary Figures S4A and S5A).

Stipa pulchra
In *S. pulchra*, 91.3% of seeds emerged across 20 days with a mean emergence time of 10.5 days (SD = 2.86, n = 690). Heavier *S. pulchra* seeds were more likely to emerge ($\chi^2_{(1)}$ = 10.9, p < .001; Supplementary Figure S2B) and emerged earlier ($\chi^2_{(1)}$ = 43.2, p < .001; Supplementary Figure S3B). Neighbor, neighbor origin, and neighbor diversity had no effect on either emergence time or emergence probability

(Supplementary Tables S1 and S2; Supplementary Figures S4B and S5B).

Mean fitness

Bromus diandrus
Neighbor treatment had a marginally nonsignificant effect on the probability of reproduction in *B. diandrus* (Table 2; Figure 3A) and significantly influenced the mean fecundity of seed-producing individuals (Table 2; Figure 3B). The latter effect was driven not by the presence vs. absence of neighbors, but by differences among neighbor-present treatments (Figure 3B). Mean fecundity was negatively correlated with neighbor aboveground biomass but was not correlated with any other neighbor metric (Table 3). Neighbor origin did not affect the probability of reproduction, but non-natives reduced the fecundity of seed-producing individuals of *B. diandrus* by a marginally nonsignificant 18% (Table 2; Supplementary Figures S6A and B). More diverse communities reduced the probability of reproduction by 8%, but neighbor diversity did not influence the mean fecundity of seed-producing individuals (Table 2; Supplementary Figures S7A and B).

Stipa pulchra
Neighbor treatment significantly affected the probability of reproduction in *S. pulchra* (Table 2; Figure 3C). This was driven by a lower probability of reproduction in the presence vs. absence of neighbors and by differences among neighbor-present treatments (Figure 3C). Neighbor treatment also affected the mean fecundity of seed-producing *S. pulchra* individuals, driven by lower mean fecundity in the presence vs. absence of neighbors and by differences among neighbor-present treatments (Table 2; Figure 3D). Neighbor treatment did not significantly influence survival probability (Table 2; Figure 3E) but significantly influenced biomass among survivors (Table 2; Figure 3F). This latter effect was driven by lower biomass in the presence vs. absence of neighbors and by differences among neighbor-present treatments. Mean fecundity was weakly, and mean biomass significantly, negatively correlated with total neighbor aboveground biomass (Table 3). However, mean fitness via either fitness measure was not correlated with any other neighbor metric (Table 3). Compared to native neighbors, non-natives lowered fecundity via reproduction probability and biomass via nonzero biomass (Table 2; Supplementary Figures S6C–F). More diverse neighbors lowered reproduction and survival probability, but neighbor diversity had no effect on nonzero fecundity or biomass (Table 2; Supplementary Figures S7C–F).

Phenotypic selection

Standardized selection gradients (β) for *S. pulchra* and *B. diandrus* in each neighbor treatment, neighbor origin, and neighbor diversity groups are provided in Supplementary Table S3.

Bromus diandrus
Direct selection favored heavier sown seeds via nonzero fecundity consistently across neighbor treatments (Table 4; Figure 4B). Later emerging plants were more likely to reproduce, but of those that reproduced, earlier emerging plants had higher fecundity. Selection on emergence time via both fitness components did not differ significantly among neighbor treatments (Table 4; Figure 5A and B). Standardized seed
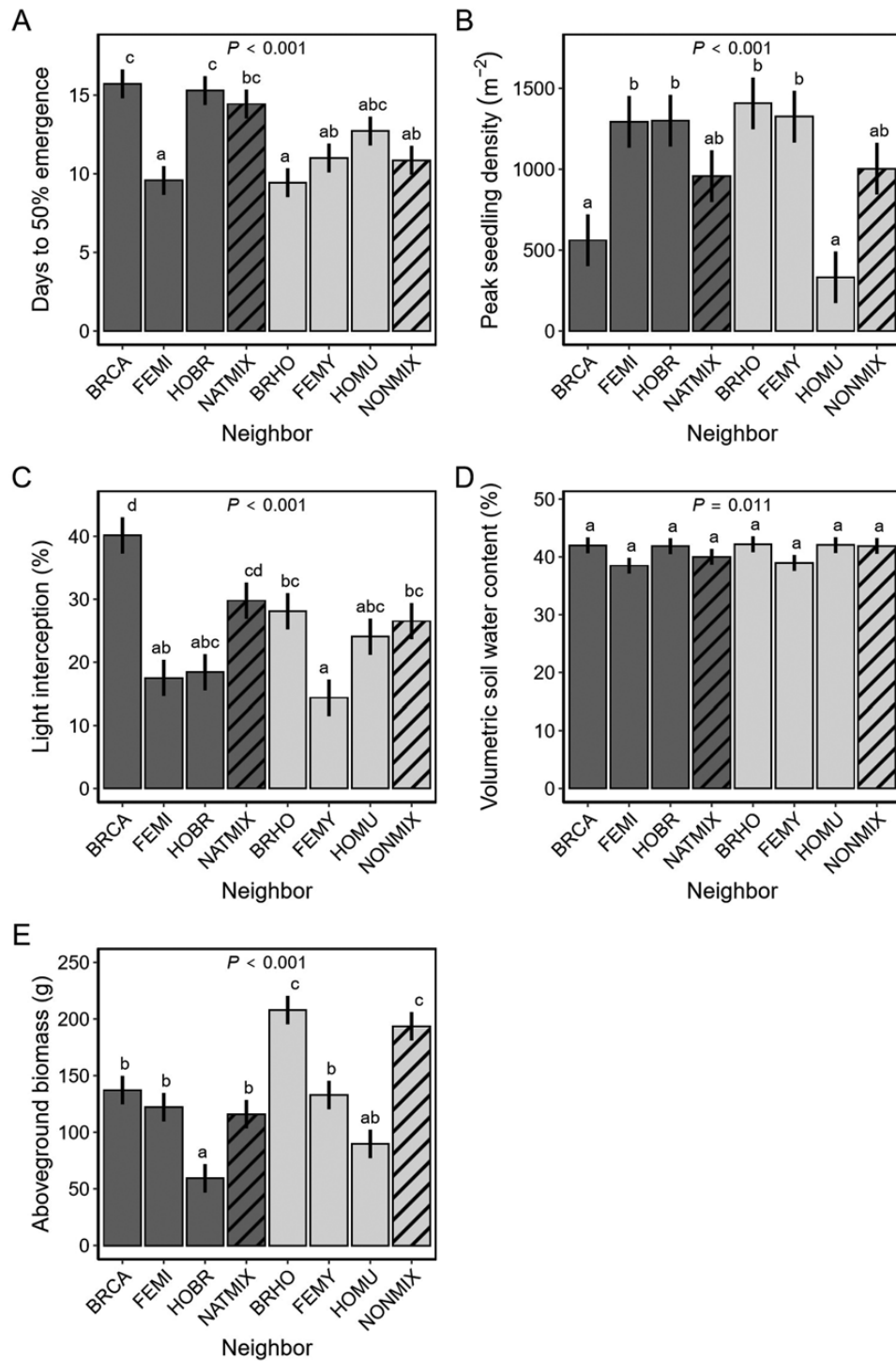
Figure 2. Estimated marginal means of neighbor metrics ± *SE* in neighbor-present treatments. *p*-Values are from linear mixed models (LMMs) testing the effects of neighbor treatment on each neighbor metric. Post hoc pairwise comparisons among the eight treatments are shown (letters indicate significant differences). Dark gray and light gray bars represent native and non-native neighbor treatments, respectively; striped and nonstriped bars represent mixed species and single species treatments, respectively. Neighbor treatment codes: BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

mass selection gradients were significantly positively correlated with total neighbor biomass, indicating that heavier sown seeds were increasingly favored when surrounded by neighboring communities with greater aboveground biomass (Table 5). However, no other neighbor metrics or mean

fitness were associated with selection on either trait (Table 5). Neither neighbor origin nor neighbor diversity affected the strength or direction of selection on either trait via the probability of reproduction or the fecundity of seed-producing individuals (Table 4; Supplementary Figures S8–S11).

Table 2. Significance of fixed effects in hurdle generalized linear mixed models (GLMMs) testing effects of neighbor treatment, neighbor origin, and neighbor diversity on mean fitness.

Fitness component	Model/fixed effect	Zero model			Nonzero model		
		χ^2	df	p	χ^2	df	p
B. diandrus							
Fecundity	Neighbor	13.86	8	.085	17.9	8	**.022**
	Origin	0.93	1	.33	3.11	1	.078
	Diversity	6.35	1	**.012**	0.10	1	.75
S. pulchra							
Fecundity	Neighbor	40.1	8	**<.001**	61.2	8	**<.001**
	Origin	8.20	1	**.004**	2.69	1	.10
	Diversity	9.32	1	**.002**	0.36	1	.55
Biomass	Neighbor	12.5	8	.13	83.8	8	**<.001**
	Origin	2.75	1	.097	4.33	1	**.037**
	Diversity	4.06	1	**.044**	2.22	1	.14

Note. Zero models are binomial regressions with a logit link function modeling if plants reproduced or survived until biomass was harvested (*S. pulchra* only). Nonzero models are negative binomial regressions with a log link function modeling the fecundity of seed-producing individuals or the biomass of survivors (*S. pulchra* only). *p*-Values < .05 are highlighted in bold. See Figure 3, Supplementary Figures S6–S7 to view the direction and magnitude of each fixed effect level on mean fitness.

Stipa pulchra

Plants from lighter seeds were more likely to reproduce, but of those that reproduced and survived, plants from heavier seeds had higher fecundity and vegetative biomass; this selection did not differ among neighbor treatments (Table 4; Figure 4C and D). Plants that emerged later were more likely to reproduce and survive (Table 4; Figure 5C and D), and this selection did not differ among neighbor treatments. Among surviving plants, selection via biomass generally favored earlier emergence, but differed significantly among some neighbor-present treatments resulting from selection for later emergence in the presence of the non-native *Festuca myuros* that differed significantly from selection for earlier emergence in non-native *B. hordeaceus* (Table 4; Figure 5F). Standardized selection gradients for emergence time via fecundity and biomass were significantly negatively correlated with soil water availability; selection for earlier emergence was stronger in communities with higher soil moisture (Table 5). Selection gradients for emergence time via both fitness measures were also weakly negatively correlated with light interception, indicating a trend of stronger selection for earlier emergence when neighbors intercepted more light (Table 5). Selection on neither trait was associated with mean fitness (Table 5). Neither neighbor origin nor neighbor diversity influenced selection on either seedling trait via fecundity or biomass (Table 4; Supplementary Figures S8–S11).

Consistency of selection exerted by neighbors

Direct selection on seed mass exerted by neighbors was not consistent in the two focal species, as indicated by a nonsignificant correlation among standardized seed mass selection gradients for *B. diandrus* and *S. pulchra* via fecundity (*r* = .44, *p* = .27, Figure 6A). However, this result was strongly influenced by the *Hordeum brachyantherum* treatment, which when excluded resulted in a significant positive correlation among seed mass selection gradients (*r* = .79, *p* = .036). Direct selection on emergence time exerted by neighboring communities was consistent, as indicated by a significant positive correlation among standardized emergence time selection gradients for *B. diandrus* and *S. pulchra* (*r* = .80, *p* = .018; Figure 6B). Correlations between *B. diandrus* selection gradients and *S. pulchra* selection gradients via biomass were qualitatively similar, being nonsignificant for seed mass (*r* = .41, *p* = .32, Supplementary Figure S12A) and marginally significantly positive for emergence time (*r* = .71, *p* = .051; Supplementary Figure S12B).

Discussion

Plant–plant interactions are important for shaping plant community structure (Bashirzadeh et al., 2022; Soliveres & Maestre, 2014), but less is known about how they drive evolutionary change in constituent populations (Thorpe et al., 2011). We hypothesized that the identity of neighboring plants influences natural selection on seedling traits by determining environmental conditions, and that patterns of selection are predictable based on the characteristics of the neighboring community. We found mixed support for Prediction 1 that the strength or pattern of selection would vary with neighbor identity: neighbor identity influenced patterns of selection on seedling traits in the native perennial *S. pulchra* but not the non-native annual *B. diandrus*. We found mixed support for Prediction 2 that selection would be stronger when neighbors uptake more resources, reduce mean fitness to a greater extent, are non-native, or are more species-rich: selection on seedling traits was most strongly associated with measures of neighbor resource uptake and productivity, but not neighbor effects on mean fitness or other characteristics such as origin or diversity. Here, we discuss these key results, their implications in the context of global change, and outline future directions for understanding the evolutionary effects of neighboring plants.

Prediction 1: neighbors shaped selection in *S. pulchra*, but not *B. diandrus*

In *S. pulchra*, surviving plants that emerged earlier tended to have higher biomass but this selection differed between neighbors, notably with selection for later emergence observed in
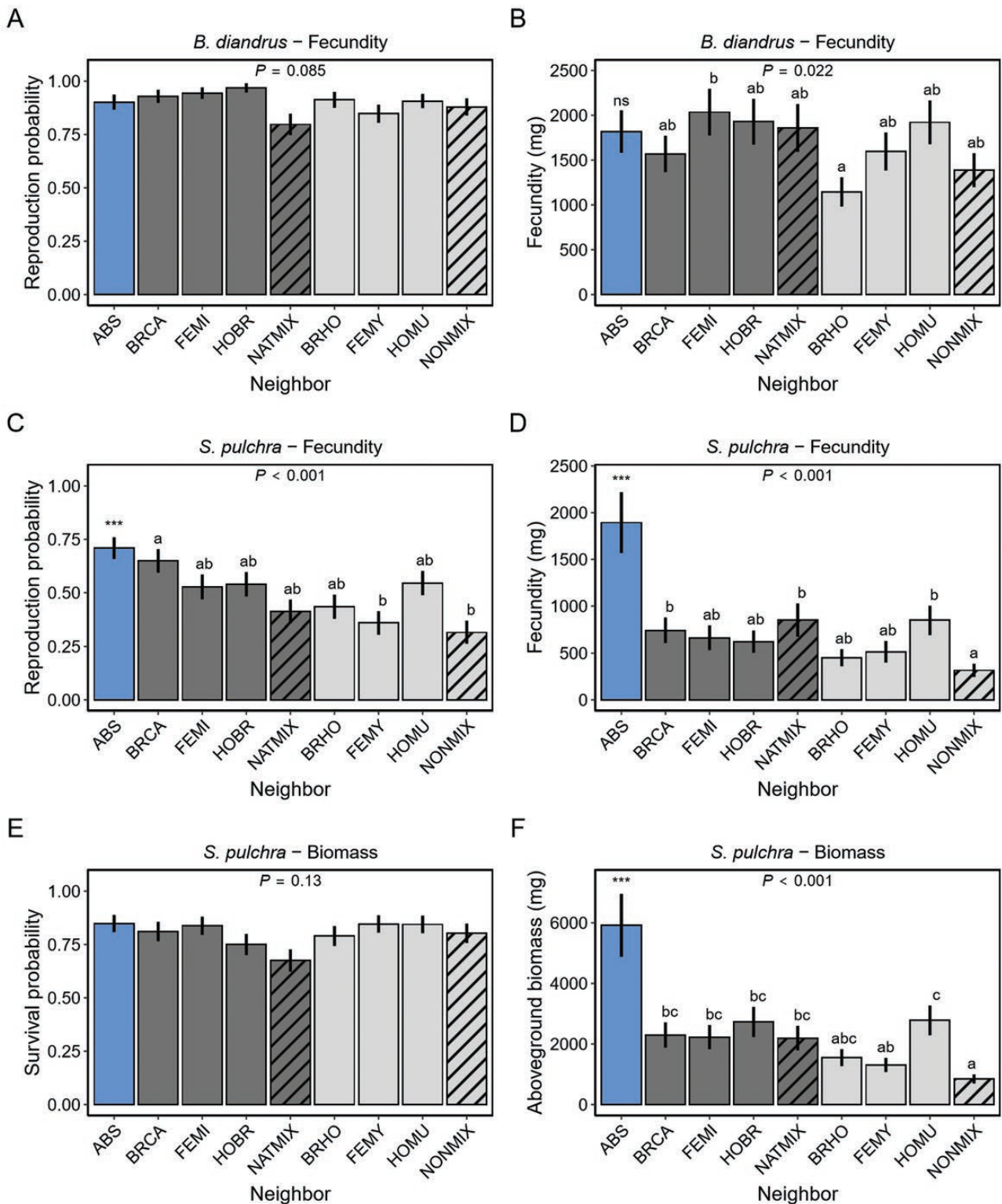
Figure 3. Estimated marginal mean fitness ± *SE* in neighbor treatments in (A, B) *B. diandrus* and (C–F) *S. pulchra*. *p*-Values are from hurdle generalized linear mixed models (GLMMs) testing the effects of neighbor treatment on fitness components. Two types of post hoc tests are shown: (a) neighbor presence vs. absence (indicated above neighbor-absent treatment; significance: †*p* < .1, **p* < .05, ***p* < .01, ****p* < .001); (b) pairwise comparisons among the eight neighbor-present treatments (letters indicate significant differences). Dark gray and light gray bars represent native and non-native neighbor treatments, respectively; striped and nonstriped bars represent mixed species and single species treatments, respectively; blue represents the neighbor-absent treatment. Neighbor treatment codes: ABS = Neighbor-absent; BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

Table 3. Correlations between mean fitness and neighbor metrics.

Fitness component	Neighbor metric				
	Emergence time	Peak seedling density	Light interception	Soil water availability	Total aboveground biomass
B. diandrus					
Fecundity	0.30	–0.17	–0.41	–0.27	–0.86**
S. pulchra					
Fecundity	0.52	–0.52	0.26	–0.079	–0.65[†]
Biomass	0.46	–0.37	–0.042	0.007	–0.81*

Note. Correlations are based on neighbor-present treatments only. Significance: [†]$p< .1$, *$p < .05$, **$p < .01$, ***$p < .001$.

the presence of non-native *F. myuros*. This variable selection among neighbor treatments is consistent with previous work showing that selection for earlier emergence in velvetleaf (*Abutilon theophrasti*) was more intense in a community of weed species vs. corn crops (Weinig, 2000). However, our results differ in that neighbors altered not just the strength but also the direction of selection on emergence time. This suggests that community composition could contribute to temporal or spatial variation in optimum emergence time (cf. Kalisz, 1986), and could be cryptic driver of geographic clines in emergence timing (e.g., Gutterman & Edine, 1988; Torres-Martínez et al., 2017; Waterton et al., 2020).

In contrast, selection on seedling traits in the non-native annual *B. diandrus* did not differ significantly among neighbor treatments. This suggests that selection on seedling traits in this species acts more independently of the competitive neighborhood, and instead may be influenced more by other abiotic and biotic environmental factors. This is consistent with the results for mean fitness: neighbor treatment did not affect the probability of reproduction and mean fecundity did not differ between neighbor-present vs. neighbor-absent treatments. One potential reason for this lower sensitivity of selection to neighbor identity in *B. diandrus* versus *S. pulchra* could be because the former emerged more rapidly (i.e., the phenotypic distribution is shifted earlier), such that most individuals, regardless of phenotype, start growing before the different neighboring communities begin to exert any variable effects. We also note that all neighbor species were grasses (representing three genera), and although this reflects the dominant biomass in grassland communities, it likely represents a fraction of the potential phylogenetic and functional diversity present in many natural communities, potentially leading to less variable selection in our experiment than in natural communities.

Prediction 2: patterns of selection were most strongly associated with measures of neighbor resource uptake and productivity

Stronger selection for earlier emergence in *S. pulchra* in neighbor communities with higher soil moisture availability was counter to Prediction 2, which states that selection will be stronger where neighbors take up more resources (or, e.g., where water is more limiting). However, our measurements of soil moisture were between 0 and 15 cm, and *S. pulchra* is deep-rooted (up to 1 m) with the greatest amount of roots found at 15–30 cm depth (Hull & Muller, 1977). Thus, neighbors that reduced soil moisture the most may have done so at soil depths that have a lesser impact on *S. pulchra* growth.

The weak trend of stronger selection for earlier emergence when neighbors intercepted more light was consistent with Prediction 2; however, we expect that this pattern will only hold for neighbor communities in which earlier emergence provides greater light acquisition and not in those where even the earliest emerging plants are shaded. Supporting this, Weinig (2000) found that earlier emergence enhanced velvetleaf fitness in the presence of neighbors for which it allowed greater light capture (short-statured weeds), but not in the presence of taller-statured neighbors where light was limited regardless of emergence time (corn crops). In *B. diandrus*, selection for heavier seeds was stronger neighbor communities with higher aboveground productivity, consistent with Prediction 2. Compared to *S. pulchra*, *B. diandrus* is characterized by a more light-acquisitive growth strategy (e.g., allocating more biomass to shoots vs. roots; Holmes & Rice, 1996), which may explain why the benefits of heavier seeds were more pronounced for *B. diandrus* in environments characterized by stronger aboveground competition.

Mean fitness was not associated with the strength of selection in either focal species, contradicting the theoretical prediction that selection will be stronger in environments that reduce mean fitness to a greater extent (Benkman, 2013; Fugère & Hendry, 2018; Rundle & Vamosi, 1996). However, our result is consistent with several studies showing that lower mean fitness in plant populations does not increase the opportunity for selection (Case & Ashman, 2007; Sletvold et al., 2017; Waterton et al., 2022). Our results suggest that neighbor characteristics other than effects on mean fitness, such as functional traits or measures of resource uptake, will be more informative for predicting their selective effects. We also note that lifetime fitness estimates are not as reliable in perennial *S. pulchra* as in annual *B. diandrus* due to its potential longevity (>100 years; Hamilton et al., 2002) and the relatively short duration of this study (2 years).

Implications for evolutionary adaptation to global change

Adaptive evolution in seedling traits is considered to be an important component of in situ responses to global change that will promote long-term species persistence (Cochrane et al., 2015; Walck et al., 2011). Most studies that aim to predict how plant populations will adaptively evolve and persist under drivers of global change such as climate change and nitrogen enrichment have focused on the direct selective effects (Anderson et al., 2012; Dickman et al., 2019; Etterson & Shaw, 2001; Franks et al., 2007; Petipas et al., 2020), but rarely consider the potential for plant–plant interactions to

Table 4. Significance of fixed effects in hurdle generalized linear mixed models (GLMMs) testing effects of neighbor treatment, neighbor origin, and neighbor diversity on phenotypic selection.

Fitness component	Model	Fixed effect	Zero model			Nonzero model		
			χ^2	df	p	χ^2	df	p
B. diandrus								
Fecundity	Neighbor	Neighbor	11.3	8	.19	25.6	8	**.001**
		Seed mass	0.018	1	.89	6.54	1	**.011**
		Emergence time	4.65	1	**.031**	8.31	1	**.004**
		Neighbor × seed	6.55	8	.59	5.07	8	.75
		Neighbor × emergence	11.2	8	.19	4.85	8	.77
	Origin	Origin	0.70	1	.40	2.85	1	.091
		Seed mass	0.24	1	.62	7.10	1	**.008**
		Emergence time	6.24	1	**.012**	7.99	1	**.005**
		Origin × seed	1.61	1	.20	0.0002	1	.99
		Origin × emergence	3.23	1	.072	1.85	1	.17
	Diversity	Diversity	5.66	1	**.017**	0.11	1	.75
		Seed mass	0.18	1	.67	7.27	1	**.007**
		Emergence time	5.98	1	**.015**	7.83	1	**.005**
		Diversity × seed	0.90	1	.34	0.28	1	.60
		Diversity × emergence	0.058	1	.81	0.12	1	.73
S. pulchra								
Fecundity	Neighbor	Neighbor	35.9	8	**<.001**	64.5	8	**<.001**
		Seed mass	4.85	1	**.028**	4.00	1	**.046**
		Emergence time	6.25	1	**.012**	0.009	1	.92
		Neighbor × seed	12.7	8	.12	6.44	8	.60
		Neighbor × emergence	11.7	8	.16	4.31	8	.83
	Origin	Origin	7.10	1	**.008**	2.63	1	.11
		Seed mass	6.53	1	**.011**	1.44	1	.23
		Emergence time	8.51	1	**.004**	0.0005	1	.98
		Origin × seed	1.45	1	.23	0.16	1	.69
		Origin × emergence	1.24	1	.27	0.60	1	.44
	Diversity	Diversity	7.20	1	**.007**	0.38	1	.54
		Seed mass	6.35	1	**.012**	1.55	1	.21
		Emergence time	8.88	1	**.003**	0.009	1	.92
		Diversity × seed	0.25	1	.62	0.63	1	.43
		Diversity × emergence	0.002	1	.96	0.92	1	.34
Biomass	Neighbor	Neighbor	9.08	8	.34	100.8	8	**<.001**
		Seed mass	0.075	1	.78	8.88	1	**.003**
		Emergence time	16.4	1	**<.001**	17.7	1	**<.001**
		Neighbor × seed	7.59	8	.47	7.04	8	.53
		Neighbor × emergence	10.5	8	.23	18.4	8	**.018**
	Origin	Origin	3.74	1	.053	3.60	1	.058
		Seed mass	0.088	1	.77	7.51	1	**.006**
		Emergence time	23.2	1	**<.001**	11.7	1	**<.001**
		Origin × seed	0.35	1	.55	0.11	1	.74
		Origin × emergence	0.80	1	.37	0.002	1	.97
	Diversity	Diversity	2.22	1	.14	2.18	1	.14
		Seed mass	0.052	1	.82	7.05	1	**.008**
		Emergence time	23.1	1	**<.001**	12.4	1	**<.001**
		Diversity × seed	2.46	1	.12	0.33	1	.57
		Diversity × emergence	0.63	1	.43	1.11	1	.29

Note. Zero models are binomial regressions with a logit link function modeling if plants reproduced or survived until biomass was harvested (*S. pulchra* only). Nonzero models are negative binomial regressions with a log link function modeling the fecundity of seed-producing individuals or the biomass of survivors (*S. pulchra* only). *p*-Values < .05 are highlighted in bold. See Figures 4 and 5, Supplementary Figures S8–S11 to view the direction and magnitude of each fixed effect level on selection coefficients from hurdle GLMMs.
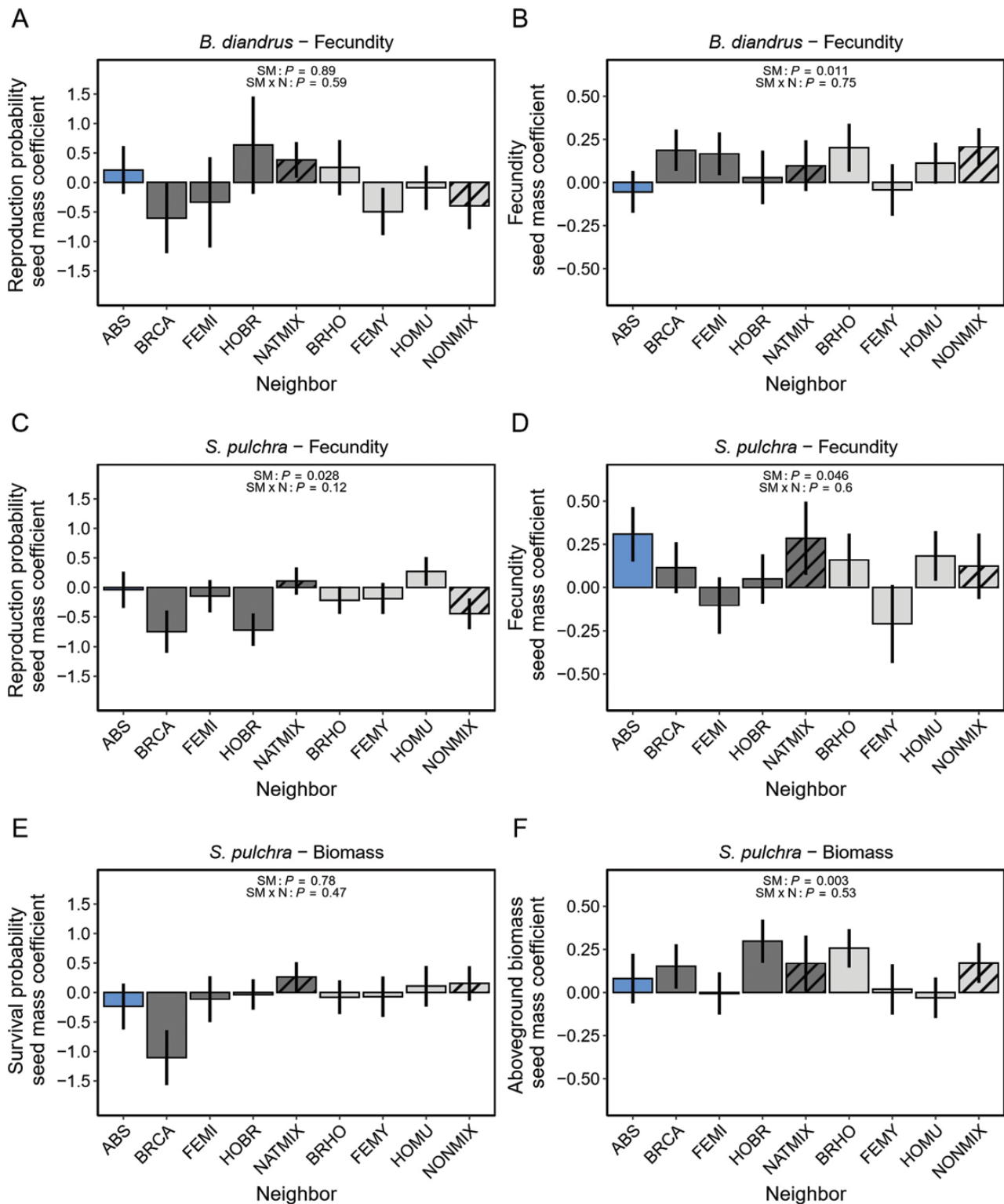
Figure 4. Seed mass selection coefficients ± *SE* from hurdle GLMMs in neighbor treatments in (A, B) *B. diandrus* and (C–F) *S. pulchra*. *p*-Values are for the seed mass (SM) and seed mass × neighbor treatment interaction (SM × N) terms in hurdle GLMMs testing the effects of seedling traits (seed mass and emergence time), neighbor treatment, and the trait × neighbor treatment interactions. Dark gray and light gray bars represent native and non-native neighbor treatments, respectively; striped and nonstriped bars represent mixed species and single species treatments, respectively; blue represents the neighbor-absent treatment. Neighbor treatment codes: ABS = Neighbor-absent; BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

mediate adaptive evolutionary responses. The results presented here indicate that such changes in the taxonomic composition of a species' neighbors resulting from global change

can affect the strength and even direction of phenotypic selection on seedling traits, although the potential for such effects will be greater in some species (e.g., *S. pulchra*) than others
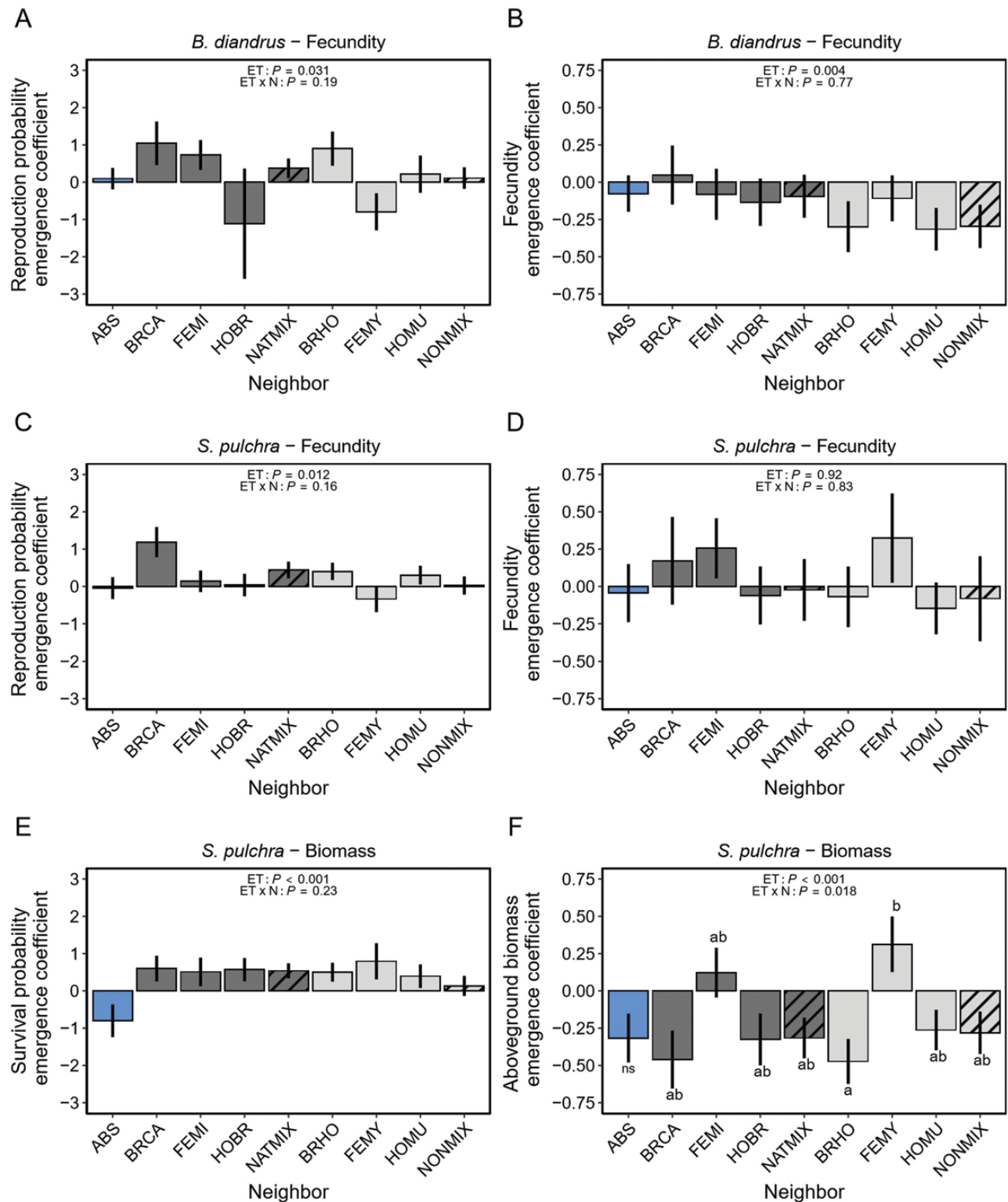
Figure 5. Emergence time selection coefficients ± *SE* from hurdle GLMMs in neighbor treatments in (A, B) *B. diandrus* and (C–F) *S. pulchra*. *p*-Values are for the emergence time (ET) and emergence time × neighbor treatment interaction (ET × N) terms in hurdle GLMMs testing the effects of seedling traits (seed mass and emergence time), neighbor treatment, and the trait × neighbor treatment interactions. Two types of post hoc tests are shown: (a) neighbor presence vs. absence (indicated above neighbor-absent treatment; significance: †*p* < .1, *p < .05, **p < .01, ***p < .001); (b) pairwise comparisons among the eight neighbor-present treatments (letters indicate significant differences). Dark gray and light gray bars represent native and non-native neighbor treatments, respectively; striped and nonstriped bars represent mixed species and single species treatments, respectively; blue represents the neighbor-absent treatment. Neighbor treatment codes: ABS = Neighbor-absent; BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

Table 5. Correlations between selection gradients for fitness-related traits (seed mass and emergence time) and neighbor metrics and mean fitness.

Fitness component	Trait	Neighbor metric					Mean fitness
		Emergence time	Peak seedling density	Light interception	Soil water availability	Total aboveground biomass	
B. diandrus							
Fecundity	Seed mass	−.45	−.056	.35	.23	.75*	−.41
	Emergence time	.21	.26	−.16	−.56	−.13	.11
S. pulchra							
Fecundity	Seed mass	.19	.15	.35	.40	.12	.08
	Emergence time	−.047	.38	−.70†	−.74*	−.40	−.069
Biomass	Seed mass	.15	.34	.33	.29	.23	−.045
	Emergence time	−.30	.28	−.61	−.84**	−.20	−.045

Note. Correlations are based on neighbor-present treatments only. Significance: †$p < .1$, *$p < .05$, **$p < .01$, ***$p < .001$.
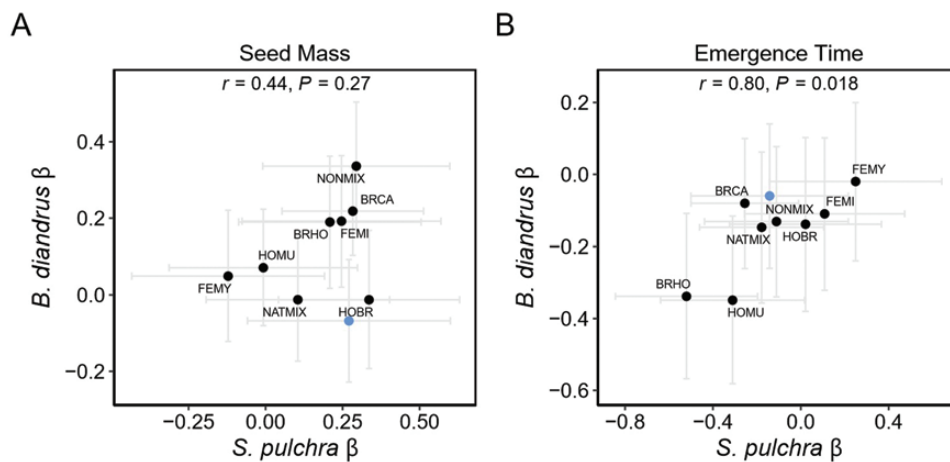

Figure 6. Association between selection gradients (β ± *SE*) in *S. pulchra* (based on fecundity) and *B. diandrus* in neighbor-present treatments for (A) seed mass and (B) emergence time. Selection gradients in the neighbor-absent treatment are shown for reference (blue points). Neighbor treatment codes: BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

(e.g., *B. diandrus*) and will depend on how neighbor identity changes (e.g., differences in light or soil moisture). Such changes in the intensity of selection could potentially promote or impede adaptation to drivers of global change depending on whether they are concordant with or antagonistic to long-term shifts in directly imposed selection.

Towards predicting neighbor-mediated evolution

Our results suggest that neighbor traits can be used to predict their evolutionary effects, but our study is limited in this regard. First, selection is likely to be determined by neighbor characteristics that we did not quantify, including belowground traits such as rooting depth or allelopathy (cf. Lankau, 2012). Second, selection on seedling traits may be driven by interactions between different neighbor characteristics, such as light interception and emergence time (cf. Weinig, 2000). With only eight neighbor-present treatments, we are unable to test for such interactions. Third, as has been found in previous studies, selection on seedling traits via fitness components expressed at different times was discordant (Akiyama &Ågren, 2014; Gómez, 2004; Kelly, 1992; Stratton, 1992); however, because we

quantified each neighbor metric at a single time point we are unable to examine how neighbors influence selection acting at different life stages. Finally, with only two focal species, we have limited capacity to investigate the extent to which neighbors exert consistent selection in different focal species, and how this might relate to life history, phenological or morphological traits intrinsic to focal species. Characterizing the mechanisms underlying neighbor-mediated selection will therefore require larger experiments with more focal and neighbor species, which will be logistically challenging given the large sample sizes that generally are required to detect natural selection in the field (Hersch & Phillips, 2004).

Conclusions

Our results demonstrate that neighboring plants can shape selection on seedling traits, suggesting that shifts in plant community composition due to various drivers of global change or other local environmental disruptions may lead to cascading changes in selection. However, these responses will likely differ considerably among species, with the direction and strength of selection in some species being less sensitive

to neighbors than in others. Furthermore, we show that patterns of selection on seedling traits are associated with neighbor characteristics such as resource uptake, suggesting that a trait-based approach has considerable potential to increase our understanding of the evolutionary consequences of plant–plant interactions.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data, metadata, and the R script for reproducing data analyses and figures can be accessed on the Dryad Data Repository https://doi.org/10.5061/dryad.jdfn2z3g9.

Author contributions

J.W. and E.E.C. conceived the ideas and designed the methodology, J.W. collected and analyzed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Acknowledgments

References

Aarssen, L. W. (1997). High productivity in grassland ecosystems: Effected by species diversity or productive species? *Oikos*, 80(1), 183–184. https://doi.org/10.2307/3546531

Abraham, J. K., Corbin, J. D., & D'Antonio, C. M. (2009). California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology*, 201, 445–456.

Akiyama, R., & Ågren, J. (2014). Conflicting selection on the timing of germination in a natural population of *Arabidopsis thaliana*. *Journal of Evolutionary Biology*, 27(1), 193–199. https://doi.org/10.1111/jeb.12293

Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R.I., & Mitchell-Olds, T. (2012). Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 279(1743), 3843–3852. https://doi.org/10.1098/rspb.2012.1051

Anten, N. P. R., & Hirose, T. (1999). Interspecific differences in above-ground growth patterns result in spatial and temporal partitioning of light among species in a tall-grass meadow. *Journal of Ecology*, 87(4), 583–597. https://doi.org/10.1046/j.1365-2745.1999.00365.x

Baldwin, B. G., Goldman, D. H., Keil, D. J., Patterson, R., Rosatti, T. J., & Wilken, D. H. (Eds.). (2012). *The Jepson manual: Vascular plants of California* (2nd ed.). University of California Press.

Bashirzadeh, M., Soliveres, S., Farzam, M., Ejtehadi, H., & Bahn, V. (2022). Plant–plant interactions determine taxonomic, functional

and phylogenetic diversity in severe ecosystems. *Global Ecology and Biogeography*, 31, 649–662.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.

Beans, C. M., & Roach, D. A. (2015). An invasive plant alters phenotypic selection on the vegetative growth of a native congener. *American Journal of Botany*, 102(2), 217–224. https://doi.org/10.3732/ajb.1400355

te Beest, M., Esler, K. J., & Richardson, D. M. (2014). Linking functional traits to impacts of invasive plant species: A case study. *Plant Ecology*, 216(2), 293–305. https://doi.org/10.1007/s11258-014-0437-5

Benkman, C. W. (2013). Biotic interaction strength and the intensity of selection. *Ecology Letters*, 16(8), 1054–1060. https://doi.org/10.1111/ele.12138

Brooks, M. E., Kristensen, K., Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378.

Callaway, R. M., Ridenour, W. M., Laboski, T., Weir, T., & Vivanco, J. M. (2005). Natural selection for resistance to the allelopathic effects of invasive plants. *Journal of Ecology*, 93(3), 576–583. https://doi.org/10.1111/j.1365-2745.2005.00994.x

Case, A. L., & Ashman, T. L. (2007). An experimental test of the effects of resources and sex ratio on maternal fitness and phenotypic selection in gynodioecious *Fragaria virginiana*. *Evolution*, 61(8), 1900–1911. https://doi.org/10.1111/j.1558-5646.2007.00148.x

Cheplick, G. P. (2021). Fitness components and the determinants of fecundity in populations of a native perennial grass (*Tridens flavus*). *Plant Species Biology*, 36(2), 322–337. https://doi.org/10.1111/1442-1984.12318

Cochrane, A., Yates, C. J., Hoyle, G. L., & Nicotra, A. B. (2015). Will among-population variation in seed traits improve the chance of species persistence under climate change? *Global Ecology and Biogeography*, 24, 12–24.

De Lisle, S. P., & Svensson, E. I. (2017). On the standardization of fitness and traits in comparative studies of phenotypic selection. *Evolution*, 71(10), 2313–2326. https://doi.org/10.1111/evo.13325

Deering, R. H., & Young, T. P. (2006). Germination speeds of exotic annual and native perennial grasses in California and the potential benefits of seed priming for grassland restoration. *Grasslands*, 16, 14–16.

Dickman, E. E., Pennington, L. K., Franks, S. J., & Sexton, J. P. (2019). Evidence for adaptive responses to historic drought across a native plant species range. *Evolutionary Applications*, 12(8), 1569–1582. https://doi.org/10.1111/eva.12803

Dyer, A. R., Fenech, A., & Rice, K. J. (2000). Accelerated emergence in interspecific competitive neighbourhoods. *Ecology Letters*, 3, 523–529.

Dyer, A. R., & Rice, K. J. (1997). Evidence of spatial genetic structure in a California bunchgrass population. *Oecologia*, 112(3), 333–339. https://doi.org/10.1007/s004420050317

Etterson, J. R., & Shaw, R. G. (2001). Constraint to adaptive evolution in response to global warming. *Science*, 294(5540), 151–154. https://doi.org/10.1126/science.1063656

Fletcher, R. A., Callaway, R. M., & Atwater, D. Z. (2016). An exotic invasive plant selects for increased competitive tolerance, but not competitive suppression, in a native grass. *Oecologia*, 181(2), 499–505. https://doi.org/10.1007/s00442-016-3584-7

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Franks, S. J., Sim, S., & Weis, A. E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences USA*, 104, 1278–1282.

Fugère, V., & Hendry, A. P. (2018). Human influences on the strength of phenotypic selection. *Proceedings of the National Academy of Science of the United States of America*, 115, 10070–10075.

Gioria, M., & Pyšek, P. (2016). Early bird catches the worm: Germination as a critical step in plant invasion. *Biological Invasions*, 19(4), 1055–1080. https://doi.org/10.1007/s10530-016-1349-1

Gómez, J. (2004). Bigger is not always better: Conflicting selective pressures on seed size in Quercus ilex. *Evolution*, 58, 71–80.

Gross, K. L., & Smith, A. D. (1991). Seed mass and emergence time effects on performance of *Panicum dichotomitlorum* Michx. across environments. *Oecologia*, 87(2), 270–278. https://doi.org/10.1007/BF00325266

Guderle, M., Bachmann, D., Milcu, A., Gockele, A., Bechmann, M., Fischer, C., Roscher, C., Landais, D., Ravel, O., Devidal, S., Roy, J., Gessler, A., Buchmann, N., Weigelt, A., Hildebrandt, A., & Field, K. (2017). Dynamic niche partitioning in root water uptake facilitates efficient water use in more diverse grassland plant communities. *Functional Ecology*, 32, 214–227.

Gutterman, Y., & Edine, L. (1988). Variations in seed germination of *Helianthemum vesicarium* and *H. ventosum* seeds from populations of two different altitudes in the Negev highlands, Israel. *Journal of Arid Environments*, 15(3), 261–267. https://doi.org/10.1016/s0140-1963(18)31063-2

Hamilton, J. G., Griffin, J. R., & Stromberg, M. R. (2002). Long-term population dynamics of native *Nassella* (Poaceae) bunchgrasses in central California. *Madroño*, 49, 274–284.

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level/ mixed) regression models [R package version 0.4.6].

Hersch, E. I., & Phillips, P. C. (2004). Power and potential bias in field studies of natural selection. *Evolution*, 58(3), 479–485.

Holmes, T. H., & Rice, K. J. (1996). Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Annals of Botany*, 78, 233–243.

Hull, J. C., & Muller, C. H. (1977). The potential for dominance by Stipa Pulchra in a California grassland. *The American Midland Naturalist*, 97(1), 147–175. https://doi.org/10.2307/2424692

Jackson, L. E. (1985). Ecological origins of California's Mediterranean grasses. *Journal of Biogeography*, 12(4), 349–361.

Jolliffe, P. A. (2000). The replacement series. *Journal of Ecology*, 88(3), 371–385. https://doi.org/10.1046/j.1365-2745.2000.00470.x

Kalisz, S. (1986). Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution*, 40(3), 479–491. https://doi.org/10.1111/j.1558-5646.1986.tb00501.x

Kelly, C. A. (1992). Spatial and temporal variation in selection on correlated life-history traits and plant size in *Chamaecrista fasciculata*. *Evolution*, 46(6), 1658–1673. https://doi.org/10.1111/j.1558-5646.1992.tb01160.x

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cardenas, D., Cardenas-Toro, J., Castano, N., Chacon, E., Chatelain, C., Ebel, A. L., … Figueiredo, E. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525, 100–103.

Kleynhans, E. J., Otto, S. P., Reich, P. B., & Vellend, M. (2016). Adaptation to elevated CO2 in different biodiversity contexts. *Nature Communications*, 7, 12358. https://doi.org/10.1038/ncomms12358

Kon, K. F., & Blacklow, W. M. (1990). Polymorphism, outcrossing and polyploidy in *Bromus diandrus* and *B. rigidus*. *Australian Journal of Botany*, 38, 609–618.

Kuebbing, S. E., Nuñez, M. A., & Simberloff, D. (2013). Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species. *Biological Conservation*, 160, 121–129. https://doi.org/10.1016/j.biocon.2013.01.009

Lankau, R. A. (2012). Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 11240–11245.

Larios, L., Búrquez, A., Becerra, J. X., & Venable, D. L. (2014). Natural selection on seed size through the life cycle of a desert annual plant. *Ecology*, 95, 3213–3220.

Larios, E., Venable, D. L., & Brody, A. (2018). Selection for seed size: The unexpected effects of water availability and density. *Functional Ecology*, 32, 2216–2224.

Larson, S. R., Cartier, E., McCracken, C. L., & Dyer, D. (2001). Mode of reproduction and amplified fragment length polymorphism variation in purple needlegrass (*Nassella pulchra*): Utilization of natural germplasm sources. *Molecular Ecology*, 10(5), 1165–1177. https://doi.org/10.1046/j.1365-294x.2001.01267.x

Lau, J. A. (2008). Beyond the ecological: Biological invasions alter natural selection on a native plant species. *Ecology*, 89(4), 1023–1031. https://doi.org/10.1890/06-1999.1

Leger, E. A. (2008). The adaptive value of remnant native plants in invaded communities: An example from the Great Basin. *Ecological Applications*, 18(5), 1226–1235. https://doi.org/10.1890/07-1598.1

Leger, E. A., Goergen, E. M., & Flory, L. (2017). Invasive *Bromus tectorum* alters natural selection in arid systems. *Journal of Ecology*, 105, 1509–1520.

Leishman, M. R. (2001). Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos*, 93(2), 294–302. https://doi.org/10.1034/j.1600-0706.2001.930212.x

Lenth, R. V., Buerkner, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2022). emmeans: Estimated marginal means, aka least-squares means [R package version 1.8.2].

MacTavish, R., & Anderson, J. T. (2022). Water and nutrient availability exert selection on reproductive phenology. *American Journal of Botany*, 109(11), 1702–1716.

McGoey, B. V., & Stinchcombe, J. R. (2009). Interspecific competition alters natural selection on shade avoidance phenotypes in *Impatiens capensis*. *New Phytologist*, 183(3), 880–891. https://doi.org/10.1111/j.1469-8137.2009.02934.x

Meilhac, J., Deschamps, L., Maire, V., Flajoulot, S., & Litrico, I. (2020). Both selection and plasticity drive niche differentiation in experimental grasslands. *Nature Plants*, 6(1), 28–33. https://doi.org/10.1038/s41477-019-0569-7

Mojonnier, L. (1998). Natural selection on two seed-size traits in the common morning glory *Ipomoea purpurea* (Convolvulaceae): Patterns and evolutionary consequences. *The American Naturalist*, 152(2), 188–203. https://doi.org/10.1086/286161

van Moorsel, S. J., Hahl, T., Wagg, C., De Deyn, G. B., Flynn, D. F. B., Zuppinger-Dingley, D., & Schmid, B. (2018a). Community evolution increases plant productivity at low diversity. *Ecology Letters*, 21(1), 128–137. https://doi.org/10.1111/ele.12879

van Moorsel, S. J., Schmid, M. W., Hahl, T., Zuppinger-Dingley, D., & Schmid, B. (2018b). Selection in response to community diversity alters plant performance and functional traits. *Perspectives in Plant Ecology, Evolution and Systematics*, 33, 51–61. https://doi.org/10.1016/j.ppees.2018.05.002

van Moorsel, S. J., Schmid, M. W., Wagemaker, N., Gurp, T. van, Schmid, B., & Vergeer, P. (2019). Evidence for rapid evolution in a grassland biodiversity experiment. *Molecular Ecology*, 28, 4097–4117.

van Moorsel, S. J., Hahl, T., Petchey, O. L., Ebeling, A., Eisenhauer, N., Schmid, B., & Wagg, C. (2021). Co-occurrence history increases ecosystem stability and resilience in experimental plant communities. *Ecology*, 102(1), e03205. https://doi.org/10.1002/ecy.3205

Morris, L. M., Walck, J. L., & Hidayati, S. N. (2002). Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera ligustrina* (Oleaceae): Implications for the invasion and persistence of a nonnative shrub. *International Journal of Plant Sciences*, 163, 1001–1010.

Navarro, J., Powers, J. M., Paul, A., & Campbell, D. R. (2022). Phenotypic plasticity and selection on leaf traits in response to snowmelt timing and summer precipitation. *New Phytologist,* 234, 1477–1490.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Evangelista, H. (2022). vegan: Community ecology package [R package version 2.6-4].

Parachnowitsch, A. L., Cook-Patton, S. C., & McArt, S. H. (2014). Neighbours matter: Natural selection on plant size depends on the identity and diversity of the surrounding community. *Evolutionary Ecology*, 28(6), 1139–1153. https://doi.org/10.1007/s10682-014-9727-6

Pérez-Fernández, M. A., Lamont, B. B., Marwick, A. L., & Lamont, W. G. (2000). Germination of seven exotic weeds and seven native species in south-western Australia under steady and fluctuating water supply. *Acta Oecologica*, 21(6), 323–336. https://doi.org/10.1016/s1146-609x(00)01084-5

Petipas, R. H., Bowsher, A. W., Bekkering, C. S., Jack, C. N., McLachlan, E. E., White, R. A., Younginger, B. S., Tiemann, L. K., Evans, S. E., & Friesen, M. L. (2020). Interactive effects of microbes and nitrogen on *Panicum virgatum* root functional traits and patterns of phenotypic selection. *International Journal of Plant Sciences*, 181(1), 20–32. https://doi.org/10.1086/706198

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rundle, H. D., & Vamosi, S. M. (1996). Selection may be strongest when resources are scarce: A comment on Wilson. *Evolutionary Ecology*, 10(5), 559–563. https://doi.org/10.1007/bf01237885

Seabloom, E. W., Harpole, W. S., Reichman, O. J., & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences USA*, 100, 13384–13389.

Simons, A. M., & Johnston, M. O. (2000). Variation in seed traits of *Lobelia inflata* (Campanulaceae): Sources and fitness consequences. *American Journal of Botany*, 87(1), 124–132.

Skálová, H., Moravcová, L., & Pyšek, P. (2011). Germination dynamics and seedling frost resistance of invasive and native *Impatiens* species reflect local climatic conditions. *Perspectives in Plant Ecology, Evolution and Systematics*, 13(3), 173–180. https://doi.org/10.1016/j.ppees.2011.03.005

Sletvold, N., Tye, M., Ågren, J., & Campbell, D. (2017). Resource- and pollinator-mediated selection on floral traits. *Functional Ecology*, 31, 135–141.

Smith, C. C., & Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *The American Naturalist*, 108(962), 499–506. https://doi.org/10.1086/282929

Soliveres, S., & Maestre, F. T. (2014). Plant-plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology Evolution and Systematics*, 16(4), 154–163. https://doi.org/10.1016/j.ppees.2014.04.001

Stanton, M. (1984). Seed variation in wild radish: Effect of seed size on components of seedling and adult fitness. *Ecology*, 65, 1105–1112.

Stratton, D. A. (1992). Life-cycle components of selection in *Erigeron annuus*: I. Phenotypic selection. *Evolution*, 46(1), 92–106. https://doi.org/10.1111/j.1558-5646.1992.tb01987.x

Stromberg, M. R., & Griffin, J. R. (1996). Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications*, 6(4), 1189–1211. https://doi.org/10.2307/2269601

Susko, D. J., & Lovett-Doust, L. (2000). Patterns of seed mass variation and their effects on seedling traits in *Alliaria petiolata* (Brassicaceae). *American Journal of Botany*, 87(1), 56–66.

Thorpe, A. S., Aschehoug, E. T., Atwater, D. Z., & Callaway, R. M. (2011). Interactions among plants and evolution. *Journal of Ecology*, 99(3), 729–740. https://doi.org/10.1111/j.1365-2745.2011.01802.x

Tielbörger, K., & Prasse, R. (2009). Do seeds sense each other? Testing for density-dependent germination in desert perennial plants. *Oikos*, 118(5), 792–800. https://doi.org/10.1111/j.1600-0706.2008.17175.x

Tilman, D., Lehman, C., & Thompson, K. T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Science of the United States of America*, 94, 1857–1861.

Torres-Martínez, L., Weldy, P., Levy, M., & Emery, N. C. (2017). Spatiotemporal heterogeneity in precipitation patterns explain population-level germination strategies in an edaphic specialist. *Annals of Botany*, 119(2), 253–265. https://doi.org/10.1093/aob/mcw161

Vannette, R. L., & Fukami, T. (2014). Historical contingency in species interactions: Towards niche-based predictions. *Ecology Letters*, 17(1), 115–124. https://doi.org/10.1111/ele.12204

Verdú, M., & Traveset, A. (2005). Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis. *Ecology*, 86(6), 1385–1394. https://doi.org/10.1890/04-1647

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14(7), 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Wacker, L., Baudois, O., Eichenberger-Glinz, S., & Schmid, B. (2009). Effects of plant species richness on stand structure and productivity. *Journal of Plant Ecology*, 2(2), 95–106. https://doi.org/10.1093/jpe/rtp010

Wade, M. J., & Kalisz, S. (1990). The causes of natural selection. *Evolution*, 44(8), 1947–1955. https://doi.org/10.1111/j.1558-5646.1990.tb04301.x

Wadgymar, S. M., Cumming, M. N., & Weis, A. E. (2015). The success of assisted colonization and assisted gene flow depends on phenology. *Global Change Biology*, 21(10), 3786–3799. https://doi.org/10.1111/gcb.12988

Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, 17(6), 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x

Waterton, J., & Cleland, E. E. (2021). Vertebrate herbivory weakens directional selection for earlier emergence in competition. *Evolution Letters*, 5(3), 265–276.

Waterton, J., Hammond, M., & Lau, J. A. (2022). Evolutionary effects of nitrogen are not easily predicted from ecological responses. *American Journal of Botany*, 109(11), 1741–1756. https://doi.org/10.1002/ajb2.16095

Waterton, J., Mazer, S. J., Meyer, J. R., & Cleland, E. E. (2020). Trade-off drives Pareto optimality of within- and among-year emergence timing in response to increasing aridity. *Evolutionary Applications*, 14(3), 658–673.

Weiner, J. (1990). Asymmetric competition in plant populations. *Trends in Ecology & Evolution*, 5(11), 360–364. https://doi.org/10.1016/0169-5347(90)90095-U

Weinig, C. (2000). Differing selection in alternative competitive environments: Shade-avoidance responses and germination timing. *Evolution*, 54(1), 124–136. https://doi.org/10.1111/j.0014-3820.2000.tb00013.x

Weis, A. E., Turner, K. M., Petro, B., Austen, E. J., & Wadgymar, S. M. (2015). Hard and soft selection on phenology through seasonal shifts in the general and social environments: A study on plant emergence time. *Evolution*, 69(6), 1361–1374. https://doi.org/10.1111/evo.12677

Williams, L. J., Butler, E. E., Cavender-Bares, J., Stefanski, A., Rice, K. E., Messier, C., Paquette, A., & Reich, P. B. (2021). Enhanced light interception and light use efficiency explain overyielding in young tree communities. *Ecology Letters*, 24(5), 996–1006. https://doi.org/10.1111/ele.13717

Wulff, R. D. (1986). Seed size variation in *Desmodium paniculatum*: II. Effects on seedling growth and physiological performance. *Journal of Ecology*, 74(1), 99–114. https://doi.org/10.2307/2260351

Zuppinger-Dingley, D., Schmid, B., Petermann, J. S., Yadav, V., De Deyn, G. B., & Flynn, D. F. (2014). Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*, 515(7525), 108–111. https://doi.org/10.1038/nature13869