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

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1 **ABSTRACT**

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

18

19 **KEYWORDS:** Community composition, natural selection, competition, emergence time,  
20 seed mass, priority effect, California grasslands, *Stipa pulchra*, *Bromus diandrus*

## 21 INTRODUCTION

22 Neighboring plants interact extensively through processes such as resource  
23 competition, allelopathy, and facilitation. Plant-plant interactions play a central role in  
24 structuring plant communities (Soliveres and Maestre 2014, Bashirzadeh et al. 2022), but the  
25 resulting evolutionary consequences for populations have historically received little attention  
26 (Thorpe et al. 2011). There is growing evidence that variation in the surrounding plant  
27 community influences the strength and direction of natural selection exerted on key fitness-  
28 related traits (e.g., Lau 2008, Parachnowitsch et al. 2014, Beans and Roach 2015), and that it  
29 shapes the evolutionary trajectories of plant populations (e.g. Callaway et al. 2005, Leger  
30 2008, Lankau 2012, Fletcher et al. 2016, Kleynhans et al. 2016, van Moorsel et al. 2018b, van  
31 Moorsel et al. 2019, Meilhac et al. 2020, van Moorsel et al. 2021). However, we currently  
32 have a limited understanding of the mechanisms by which community composition  
33 determines the strength or direction of selection. As drivers of global change, such as climate  
34 change and species introductions, alter the composition of plant communities worldwide  
35 (Kuebbing et al. 2013, van Kleunen et al. 2015), understanding how plant community  
36 composition shapes selection will facilitate predictions of the total evolutionary responses of  
37 plant populations to global change.

38 In seasonal environments, seedling traits such as emergence time and seed mass  
39 strongly influence fitness from early life stages through to adulthood (reviewed in Verdú and  
40 Traveset 2005, Larios et al. 2018). Emerging earlier than competitors provides longer  
41 windows for growth and reproduction before favorable conditions deteriorate, as well the  
42 potential to pre-empt resources and suppress the growth of individuals that emerge later (i.e.,  
43 priority effects; Vannette and Fukami 2014). Accordingly, meta-analysis shows that earlier  
44 seedling emergence tends to enhance fitness (Verdú and Traveset 2005). Similarly, the  
45 greater energy reserves present in larger seeds can lead to more rapid seedling growth and

46 greater final size, and these benefits can be enhanced in stressful conditions such as drought  
47 (Stanton 1984, Wulff 1986, Gross and Smith 1991, Mojonier 1998, Larios et al. 2014).  
48 These competitive benefits are not without cost; for example, earlier emergence can result in  
49 increased susceptibility to early-season abiotic stress such as late frost (Skálová et al. 2011)  
50 and the production of larger seeds is traded off with producing fewer seeds (Smith and  
51 Fretwell 1974, Leishman 2001). In competition, differences in early size can be magnified  
52 over the course of growth due to asymmetry of competition (particularly light; Weiner 1990).  
53 As a result, the effects of seed mass and emergence time on fitness are likely to be sensitive  
54 to the phenotypes of competitors. Seed mass itself can influence emergence time (Wulff  
55 1986, Simons and Johnston 2000, Susko and Lovett-Doust 2000, Waterton et al. 2020), and  
56 so the selective effects of neighbors on seed mass and emergence time are likely to be  
57 mediated by correlations between them (i.e., indirect selection).

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

70 absolute terms (i.e., all individuals produce 10 fewer seeds; Rundle and Vamosi 1996,  
71 Benkman 2013, Fugère and Hendry 2018).

72         The selective effects exerted by neighbors may be predictable based on factors such  
73 as: (1) origin status (i.e., native vs. non-native), and (2) species diversity. Non-native species  
74 often differ from their native counterparts with respect to their traits and impacts on  
75 competitors. Compared to their native counterparts, non-natives often emerge earlier (Pérez-  
76 Fernández et al. 2000, Deering and Young 2006, Abraham et al. 2009, reviewed in Gioria and  
77 Pyšek 2016), differ from natives with respect to the uptake of resources such as light and soil  
78 moisture (Morris et al. 2002, Seabloom et al. 2003, te Beest et al. 2014), and reduce mean  
79 fitness to a greater extent (Vilà et al. 2011), potentially causing consistent differences in  
80 selection exerted by native vs. non-native dominated communities. Consistent with this,  
81 several studies have documented that non-native species alter the strength or direction of  
82 selection in co-occurring species (Leger et al. 2017), or lead to evolved differences in the  
83 traits or performance in co-occurring species (Callaway et al. 2005, Leger 2008, Fletcher et  
84 al. 2016). Trait differences between natives and non-natives might also influence the selective  
85 responses of each to variation in the surrounding biotic community; for example, non-native  
86 species that emerge rapidly (i.e., the phenotypic distribution is shifted earlier) may experience  
87 selection on seedling traits that is less sensitive to neighbor identity as even relatively late  
88 emerging individuals emerge earlier than the surrounding community. More taxonomically  
89 diverse communities can be characterized by more complete resource uptake via sampling  
90 and/or complementarity effects (Aarssen 1997, Tilman et al. 1997, Anten and Hirose 1999,  
91 Wacker et al. 2009, Guderle et al. 2017), which might lead to stronger selection exerted by  
92 communities with high vs. low species diversity. Supporting this, a long-term biodiversity  
93 experiment found that plant populations from mixed-species communities evolved greater

94 niche differentiation compared to populations from monocultures (Zupping-Dingley et al.  
95 2014, van Moorsel et al. 2018a).

96 We carried out a field experiment to test the hypothesis that neighboring community  
97 composition influences phenotypic selection on seedling traits, and that patterns of selection  
98 are determined by characteristics of the neighboring community. Field experiments are a  
99 powerful tool for evaluating how variation in surrounding community composition influences  
100 patterns of selection because, unlike observational studies across natural gradients, they  
101 mitigate the effects of other confounding factors that might influence both community  
102 composition patterns of phenotypic selection (Wade and Kalisz 1990). We grew two  
103 widespread California grasses, the long-lived perennial native *Stipa pulchra* (Hitchc.)  
104 Barkworth and non-native annual *Bromus diandrus* (Roth), in each of nine “neighbor  
105 treatments” that varied in the identity, origin status, and number of species. We measured the  
106 mass of caryopses (hereafter “seeds”), emergence time and fitness in focal individuals and  
107 quantified aspects of the neighboring community in each treatment to further investigate  
108 factors influencing mean fitness and patterns of selection. Specifically, we predicted that (1)  
109 selection on seedling traits would vary with neighbor identity, such that (2) selection would  
110 be stronger under one or more of the following conditions: when neighbors uptake more  
111 limiting resources, reduce mean fitness to a greater extent, are non-native, or are more  
112 taxonomically diverse.

## 113 **METHODS**

### 114 **Overview**

115 We evaluated phenotypic selection on emergence time and seed mass in *B. diandrus*  
116 and *S. pulchra* growing in one of nine neighbor treatments (Table 1). These comprised eight  
117 “neighbor-present” treatments including six single species treatments (three natives and three

118 non-natives, taxonomically balanced at the genus level) and two mixed species treatments (all  
119 three native or all three non-natives), and a “neighbor-absent” treatment. The seeding rate of  
120 each neighbor species in mixed treatments was one third of that in single species treatments,  
121 such that the intended total density of emerging seedlings remained the same across both  
122 treatment types (i.e., a “replacement series”; Jolliffe 2000). We quantified five neighbor  
123 metrics in each treatment: emergence time, peak seedling density, light interception, soil  
124 water availability, and total aboveground biomass. We evaluate only linear selection to limit  
125 model complexity and because more complex fitness functions are less amenable to formally  
126 testing for associations with neighbor metrics.

127         We carried out the experiment at the University of California San Diego Biological  
128 Field Station (32.89° N, 117.23° W; Supplementary Text S1). The climate is Mediterranean,  
129 with most precipitation typically falling between November and May, during which the  
130 majority of seedling emergence and subsequent growth occurs. The experiment lasted two  
131 growing seasons in 2017 (Season 1) and 2018 (Season 2), with the non-native annual *B.*  
132 *diandrus* grown in Season 1 only and the native perennial *S. pulchra* grown over Seasons 1  
133 and 2. For *B. diandrus*, we evaluated fecundity in Season 1 via the probability of reproducing  
134 and total seed weight in reproducing individuals. For *S. pulchra*, we evaluated two fitness  
135 measures: 1) fecundity across Seasons 1 and 2 via the probability of reproducing and total  
136 seed weight in reproducing individuals, and 2) aboveground vegetative biomass at the end of  
137 Season 2 via the probability of surviving and aboveground vegetative biomass in surviving  
138 individuals. We evaluate both fitness measures in *S. pulchra* for three reasons: first, because  
139 this species can reproduce clonally (Hull and Muller 1977, Dyer and Rice 1997); second,  
140 because surviving plants that do not produce seeds within two seasons still have the potential  
141 for future sexual reproduction, and; third, because vegetative biomass is strong predictor of  
142 fecundity in perennial grasses (Cheplick 2021). Biomass of *S. pulchra* at the end of Season 2



143 was strongly positively correlated with total fecundity (i.e., the sum of fecundity in Seasons 1  
144 and 2;  $r = 0.87$ ,  $t_{(688)} = 45.3$ ,  $P < 0.001$ ; Fig. S1). We also evaluated neighbor effects on  
145 emergence probability and emergence time because previous work shows that emergence is  
146 sensitive to neighboring seeds and seedlings (Dyer et al. 2000, Tielbörger and Prasse 2009).

#### 147 Study system and seed material

148 *Bromus diandrus* (ripgut brome) is an annual grass native to Eurasia that has become  
149 naturalized in California since European settlement (Jackson 1985). This species is  
150 particularly dominant in disturbed areas, such as abandoned agricultural fields (Stromberg  
151 and Griffin 1996). *B. diandrus* is largely self-fertilizing (selfing rate  $> 0.99$ ; Kon and  
152 Blacklow 1990). *Stipa pulchra* (purple needlegrass) is a long-lived perennial bunchgrass  
153 native to California that is found in woodland, chaparral, and grassland from Baja California  
154 to northern California (Baldwin et al. 2012). The potential post-germination lifespan of *S.*  
155 *pulchra* under field conditions is conservatively estimated at 100 years (Hamilton et al.  
156 2002). *S. pulchra* also has high rates of self-fertilization (reported selfing rate  $\approx 1$ ; Larson et  
157 al. 2001) and can also reproduce clonally (Hull and Muller 1977, Dyer and Rice 1997). *B.*  
158 *diandrus* and *S. pulchra* often co-occur throughout California (Waterton et al. 2020).

159 For both focal species, we used field collected seeds from naturally occurring  
160 populations exhibiting high seedling emergence percentages in a previous study (*S. pulchra*:  
161 Sedgwick Reserve; *B. diandrus*: Elliott Chaparral Reserve; see Supplementary Text S1 for  
162 details). For each focal species, we used a total of 84 seeds in each of the nine neighbor  
163 treatments, with seven seeds from each of 12 maternal lines ( $N = 756$  in each focal species).  
164 For each maternal line, we selected seeds that outwardly appeared viable (e.g., filled and  
165 undamaged) and randomly assigned them to neighbor treatments. We obtained neighbor  
166 seeds through a commercial supplier (S&S Seeds, Carpinteria, CA USA), with the exception

167 of *H. murinum* seeds which we collected in bulk from the site of the field experiment in  
168 February 2015.

## 169 **Field experiment**

### 170 ***Establishing plots and planting seeds***

171 Prior to Season 1, we established nine  $0.9 \times 1.05$  m plots in a fully randomized block  
172 design replicated seven times, with each neighbor treatment represented once per block (Fig.  
173 1). In January 2017, we watered and tilled plots to deplete the seed bank. For each focal  
174 species, we planted one seed from each of 12 maternal lines into two rows of six in each plot  
175 half, leaving a 30 cm wide strip in the middle of each plot separating each focal species (Fig.  
176 1). We sowed neighbor seeds evenly across plots on the soil surface at a intended density of  
177 900 seedlings  $\text{m}^{-2}$ , with seed numbers adjusted for emergence percentages observed in  
178 greenhouse trials. We planted focal seeds by gently pressing them into the soil at a depth of 1  
179 cm with radicles pointing downwards. To identify emerging focal individuals, we planted  
180 focal seeds in a 1.9 cm diameter, 0.5 cm height PVC ring that was covered while we sowed  
181 neighbor seeds. We planted all seeds into dry soil between 14 – 15 February. We watered  
182 plots on 16 February, with days to emergence calculated from this date.

183 Prior to Season 2, we re-established the neighbor component of *S. pulchra* plot halves  
184 ( $0.45 \times 1.05$  m), as we harvested neighbor plants after Season 1 (see *Neighbor metrics*). Dry  
185 winter conditions delayed the onset of the growing season until after a large rain event on 9  
186 January 2018. Because we harvested neighbor aboveground biomass at the end of Season 1,  
187 we re-sowed plots with neighbor seeds on 18 January 2018. We adjusted seed densities from  
188 the first season to achieve the original intended density of 900 seedlings  $\text{m}^{-2}$ . In both growing  
189 seasons, supplemental water was provided both to initiate germination and to prevent mass

190 mortality due to drought, and non-neighbor weeds were carefully removed (full details are  
191 provided in Supplementary Text S1).

### 192 ***Traits and fitness of focal individuals***

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

### 204 ***Quantifying neighbor metrics***

205 We quantified five neighbor metrics in each plot in Season 1: (1) emergence time, (2)  
206 peak seedling density, (3) light interception, (4) soil water availability, and (5) total  
207 aboveground biomass. Full details of data collection for neighbor metrics are given in  
208 Supplementary Text S1. Briefly, we monitored emergence of neighbors in a 20 × 20 cm  
209 quadrat in the center of each plot daily between 20 February – 14 March 2017. For each plot,  
210 we calculated the number of days to reach 50% of total neighbor emergence and the peak  
211 density of emerging neighbor seedlings (i.e., prior to the onset of mortality). To characterize  
212 light interception, we measured photosynthetically active radiation (PAR) at ground level and  
213 above the canopy within an hour of the solar zenith on 18 May 2017 in cloudless weather and

214 calculated the percentage of light intercepted by the canopy. To quantify soil water  
215 availability, we measured volumetric water content (VWC) from 0 – 15 cm depth over four  
216 consecutive days following a rain event on 8 May and calculated mean VWC across the four  
217 days. To quantify total aboveground biomass, we carefully clipped all neighbor aboveground  
218 biomass to soil level 31 July – 2 August. We dried biomass at 40 °C for three days before  
219 weighing to the nearest 0.01 g.

### 220 **Statistical analyses**

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

### 226 ***Neighbor metrics***

227 We tested whether neighbor metrics (emergence time, peak seedling density, PAR  
228 interception, soil VWC, total aboveground biomass), were influenced by each of the  
229 following fixed effects: neighbor treatment, neighbor origin, and neighbor diversity using  
230 separate PERMANOVAs fit using the adonis2 function in the package vegan (Oksanen et al.  
231 2022). We excluded the neighbor-absent treatment from these analyses because it did not  
232 have associated data for emergence time, peak seedling density, and total aboveground  
233 biomass. In the case that a full PERMANOVA model was statistically significant, we fit  
234 separate univariate models for each neighbor metric. Full details of multivariate  
235 PERMANOVAs and univariate models are provided in Supplementary Text S1.

### 236 ***Emergence of focal individuals***

237 To test whether and how each focal individual's seed mass, neighbor treatment,  
238 neighbor origin, and neighbor diversity influence the probability of emergence, we fit  
239 binomial generalized linear mixed models (GLMMs) with a logit link using the glmmTMB  
240 function in the package glmmTMB (Brooks et al. 2017). We tested how each factor  
241 influenced mean emergence time (log-transformed to improve the normality of residuals)  
242 with linear mixed models (LMMs) using the lmer function in the package lme4 (Bates et al.  
243 2015). Full details of emergence analyses are provided in Supplementary Text S1.

#### 244 *Analysis of fitness*

245 Fitness (fecundity in *B. diandrus*; fecundity and biomass in *S. pulchra*) was zero-  
246 inflated and over-dispersed; therefore, we analyzed mean fitness and phenotypic selection  
247 using hurdle negative binomial GLMMs (cf. Wadgymar et al. 2015, Waterton and Cleland  
248 2021, MacTavish and Anderson 2022). These models proceed in two parts: first, a “zero  
249 model” comprising a binomial regression with logit link function modeling if plants  
250 reproduced or survived until biomass was harvested (*S. pulchra* only); second, a “non-zero  
251 model” comprising a negative binomial regression with log link function modeling the  
252 fecundity of seed-producing individuals or the biomass of survivors. We rounded fecundity  
253 and biomass to the nearest 1 mg and 1 g, respectively, because negative binomial models  
254 require integer values for response variables.

#### 255 *Mean fitness*

256 To test the effect of neighbor treatment on mean fitness, we fit a hurdle GLMM  
257 (glmmTMB package; Brooks et al. 2017) in which fitness was predicted by neighbor  
258 treatment, with block and plot as random intercepts. In the case of significant neighbor  
259 treatment effects in zero or non-zero model parts, we carried out two post hoc tests using the  
260 emmeans function in the package emmeans (Lenth et al. 2022): first, we tested the effect of

261 neighbor presence vs. absence by comparing the neighbor-absent treatment to the average of  
262 the eight neighbor-present treatment levels; second, we tested the effect of neighbor identity  
263 with pairwise comparisons among the eight neighbor-present treatment levels.

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

#### 271 *Phenotypic selection*

272 We tested the effect of neighbor identity on patterns of direct selection on seed mass  
273 and emergence time. Direct selection acting on a trait is that which acts after accounting for  
274 selection acting on other correlated traits (i.e., indirect selection). For phenotypic selection  
275 analyses, we standardized trait values to a mean of 0 and a standard deviation of 1 across all  
276 neighbor treatments to maintain the same relative order of trait values for analyses of  
277 neighbor treatment, neighbor origin, and neighbor diversity; we note that standardizing  
278 within neighbor treatments gave similar results. To test whether direct selection differed  
279 between neighbor treatments, we fit hurdle GLMMs (glmmTMB package; Brooks et al.  
280 2017) in which fitness was predicted by seedling traits (seed mass and emergence time),  
281 neighbor treatment, and the trait  $\times$  neighbor treatment interactions, with random intercepts for  
282 block and plot. When trait  $\times$  treatment interactions were significant, indicating context-  
283 specific selection, we carried out two post hoc tests using the emtrends function in the  
284 package emmeans (Lenth et al. 2022): first, we tested the effect of neighbor presence vs.

285 absence on selection by comparing the coefficient in the neighbor-absent treatment to the  
286 average coefficient of all other treatment levels; second, we tested the effect of neighbor  
287 identity on selection with pairwise comparisons among the coefficients of the eight neighbor-  
288 present treatments.

289 To investigate whether and how neighbor metrics and mean fitness are associated  
290 with selection on seedling traits, we examined the Pearson correlations between standardized  
291 selection gradients ( $\beta$ ) and each neighbor metric and mean fitness. We estimated standardized  
292 selection gradients in each neighbor treatment from LMMs (lme4 package; Bates et al. 2015)  
293 of within-treatment level relative fitness (i.e., individual fitness divided by mean fitness)  
294 predicted by traits, neighbor treatments, and the trait  $\times$  neighbor treatment interactions with  
295 random intercepts for block and plot. We relativized fitness within treatment levels as is  
296 appropriate for traits, such as emergence time, that are subject to strong soft selection (Weis  
297 et al. 2015, De Lisle and Svensson 2017). To test the effects of neighbor origin (native vs.  
298 non-native) and diversity (single vs. mixed species) on selection, we fit separate hurdle  
299 GLMMs (glmmTMB package; Brooks et al. 2017) in which fitness was predicted by traits,  
300 neighbor origin/diversity, and trait  $\times$  neighbor origin/diversity interactions, with random  
301 intercepts for neighbor treatment, block, and plot. We estimated the mean value of selection  
302 gradients across each level of neighbor origin and diversity with LMMs (lme4 package; Bates  
303 et al. 2015) of within-origin/diversity level relative fitness predicted by the relevant traits  
304 with random intercepts for neighbor treatment, block, and plot.

305 To test whether direct selection exerted by neighbors was consistent between *B.*  
306 *diandrus* and *S. pulchra*, we examined the Pearson correlations between standardized  
307 selection gradients for each trait in the two focal species across the eight neighbor-present  
308 treatments. Below, we focus on the results for *S. pulchra* selection gradients based on  
309 fecundity as these are most comparable to *B. diandrus* selection gradients. For a given trait, a

310 significant, positive correlation between selection gradients in each species indicates that  
311 neighbor environments exerted consistent direct selection in each focal species. We note that  
312 estimates of selection in each species are not fully independent as individuals of both species  
313 were present in the same plots. That is, latent, unmeasured attributes of each plot may  
314 contribute to correlations between the selection gradients estimated for each focal species.

## 315 **RESULTS**

### 316 *Neighbor metrics*

317 Neighbor metrics differed significantly among neighbor treatments (pseudo- $F_{(7)} =$   
318 6.26,  $P = 0.001$ ). This overall effect was driven by significant differences among neighbor  
319 treatments in emergence time ( $\chi^2_{(7)} = 55.4$ ,  $P < 0.001$ ; Fig. 2A), peak seedling density ( $\chi^2_{(7)} =$   
320 42.4,  $P < 0.001$ ; Fig. 2B), light interception ( $\chi^2_{(7)} = 69.2$ ,  $P < 0.001$ ; Fig. 2C), soil moisture  
321 availability ( $\chi^2_{(7)} = 18.2$ ,  $P = 0.011$ , note that all pairwise comparisons were nonsignificant;  
322 Fig. 2D), and total aboveground biomass ( $\chi^2_{(7)} = 126.1$ ,  $P < 0.001$ ; Fig. 2E). However,  
323 neighbor metrics did not differ significantly between native and non-native communities  
324 (pseudo- $F_{(1)} = 0.98$ ,  $P = 0.48$ ) nor between single- and mixed species communities (pseudo-  
325  $F_{(1)} = 0.18$ ,  $P \approx 0.96$ ).

### 326 *Emergence of focal individuals*

#### 327 *Bromus diandrus*

328 In *B. diandrus*, 80.6% of seeds emerged across 24 days with a mean emergence time  
329 of 7.8 days (SD = 2.85,  $n = 609$ ). Heavier seeds were more likely to emerge ( $\chi^2_{(1)} = 8.35$ ,  $P =$   
330 0.004; Fig. S2A) and emerged earlier ( $\chi^2_{(1)} = 29.9$ ,  $P < 0.001$ ; Fig. S3A) than relatively light  
331 seeds. Emergence probability, but not emergence time, was influenced by neighbor treatment,  
332 with lower emergence probability in the presence of the non-native *Bromus hordeaceus*



333 compared to non-native *Hordeum murinum*, but neighbor origin and diversity had no effect  
334 on emergence time or percent (Tables S1, S2; Figs. S4A, S5A).

335 *Stipa pulchra*

336 In *S. pulchra*, 91.3% of seeds emerged across 20 days with a mean emergence time of  
337 10.5 days (SD = 2.86,  $n = 690$ ). Heavier *S. pulchra* seeds were more likely to emerge ( $\chi^2_{(1)} =$   
338 10.9,  $P = 0.001$ ; Fig. S2B) and emerged earlier ( $\chi^2_{(1)} = 43.2$ ,  $P < 0.001$ ; Fig. S3B). Neighbor,  
339 neighbor origin, and neighbor diversity had no effect on either emergence time or emergence  
340 probability (Tables S1, S2; Figs. S4B, S5B).

341 **Mean fitness**

342 *Bromus diandrus*

343 Neighbor treatment had a marginally nonsignificant effect on the probability of  
344 reproduction in *B. diandrus* (Table 2; Fig. 3A) and significantly influenced the mean  
345 fecundity of seed-producing individuals (Table 2; Fig. 3B). The latter effect was driven not  
346 by the presence vs. absence of neighbors, but by differences among neighbor-present  
347 treatments (Fig. 3B). Mean fecundity was negatively correlated with neighbor aboveground  
348 biomass but was not correlated with any other neighbor metric (Table 3). Neighbor origin did  
349 not affect the probability of reproduction, but non-natives reduced the fecundity of seed-  
350 producing individuals of *B. diandrus* by a marginally nonsignificant 18% (Table 2; Figs.  
351 S6A, B). More diverse communities reduced the probability of reproduction by 8%, but  
352 neighbor diversity did not influence the mean fecundity of seed-producing individuals (Table  
353 2; Fig. S7A, B).

354 *Stipa pulchra*

355 Neighbor treatment significantly affected the probability of reproduction in *S. pulchra*  
356 (Table 2; Fig. 3C). This was driven by a lower probability of reproduction in the presence vs.  
357 absence of neighbors and by differences among neighbor-present treatments (Fig. 3C).  
358 Neighbor treatment also affected the mean fecundity of seed-producing *S. pulchra*  
359 individuals, driven by lower mean fecundity in the presence vs. absence of neighbors and by  
360 differences among neighbor-present treatments (Table 2; Fig. 3D). Neighbor treatment did  
361 not significantly influence survival probability (Table 2; Fig. 3E) but significantly influenced  
362 biomass among survivors (Table 2; Fig. 3F). This latter effect was driven by lower biomass  
363 in the presence vs. absence of neighbors and by differences among neighbor-present  
364 treatments. Mean fecundity was weakly, and mean biomass significantly, negatively  
365 correlated with total neighbor aboveground biomass (Table 3). However, mean fitness via  
366 either fitness measure was not correlated with any other neighbor metric (Table 3). Compared  
367 to native neighbors, non-natives lowered fecundity via reproduction probability and biomass  
368 via non-zero biomass (Table 2; Figs. S6C-F). More diverse neighbors lowered reproduction  
369 and survival probability, but neighbor diversity had no effect on non-zero fecundity or  
370 biomass (Table 2; Figs. S7C-F).

### 371 **Phenotypic selection**

372 Standardized selection gradients ( $\beta$ ) for *S. pulchra* and *B. diandrus* in each neighbor  
373 treatment, neighbor origin and neighbor diversity groups are provided in Table S3.

#### 374 *Bromus diandrus*

375 Direct selection favored heavier sown seeds via non-zero fecundity consistently  
376 across neighbor treatments (Table 4; Fig. 4B). Later emerging plants were more likely to  
377 reproduce, but of those that reproduced, earlier emerging plants had higher fecundity.  
378 Selection on emergence time via both fitness components did not differ significantly among

379 neighbor treatments (Table 4; Fig. 5A, B). Standardized seed mass selection gradients were  
380 significantly positively correlated with total neighbor biomass, indicating that heavier sown  
381 seeds were increasingly favored when surrounded by neighboring communities with greater  
382 aboveground biomass (Table 5). However, no other neighbor metrics or mean fitness were  
383 associated with selection on either trait (Table 5). Neither neighbor origin nor neighbor  
384 diversity affected the strength or direction of selection on either trait via the probability of  
385 reproduction or the fecundity of seed-producing individuals (Table 4; Fig. S8-S11).

### 386 *Stipa pulchra*

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

### 403 *Consistency of selection exerted by neighbors*

404           Direct selection on seed mass exerted by neighbors was not consistent in the two focal  
405 species, as indicated by a nonsignificant correlation among standardized seed mass selection  
406 gradients for *B. diandrus* and *S. pulchra* via fecundity ( $r = 0.44$ ,  $P = 0.27$ , Fig. 6A). However,  
407 this result was strongly influenced by the *Hordeum brachyantherum* treatment, which when  
408 excluded resulted in a significant positive correlation among seed mass selection gradients ( $r$   
409  $= 0.79$ ,  $P = 0.036$ ). Direct selection on emergence time exerted by neighboring communities  
410 was consistent, as indicated by a significant positive correlation among standardized  
411 emergence time selection gradients for *B. diandrus* and *S. pulchra* ( $r = 0.80$ ,  $P = 0.018$ ; Fig.  
412 6B). Correlations between *B. diandrus* selection gradients and *S. pulchra* selection gradients  
413 via biomass were qualitatively similar, being nonsignificant for seed mass ( $r = 0.41$ ,  $P = 0.32$ ,  
414 Fig. S12A) and marginally significantly positive for emergence time ( $r = 0.71$ ,  $P = 0.051$ ;  
415 Fig. S12B).

### 416 **DISCUSSION**

417           Plant-plant interactions are important for shaping plant community structure  
418 (Soliveres and Maestre 2014, Bashirzadeh et al. 2022), but less is known about how they  
419 drive evolutionary change in constituent populations (Thorpe et al. 2011). We hypothesized  
420 that the identity of neighboring plants influences natural selection on seedling traits by  
421 determining environmental conditions, and that patterns of selection are predictable based on  
422 the characteristics of the neighboring community. We found mixed support for Prediction 1  
423 that the strength or pattern of selection would vary with neighbor identity: neighbor identity  
424 influenced patterns of selection on seedling traits in the native perennial *S. pulchra* but not  
425 the non-native annual *B. diandrus*. We found mixed support for Prediction 2 that selection  
426 would be stronger when neighbors uptake more resources, reduce mean fitness to a greater

427 extent, are non-native, or are more species-rich: selection on seedling traits was most strongly  
428 associated with measures of neighbor resource uptake and productivity, but not neighbor  
429 effects on mean fitness or other characteristics such as origin or diversity. Here, we discuss  
430 these key results, their implications in the context of global change, and outline future  
431 directions for understanding the evolutionary effects of neighboring plants.

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

433         In *S. pulchra*, surviving plants that emerged earlier tended to have higher biomass but  
434 this selection differed between neighbors, notably with selection for later emergence  
435 observed in the presence of non-native *F. myuros*. This variable selection among neighbor  
436 treatments is consistent with previous work showing that selection for earlier emergence in  
437 velvetleaf (*Abutilon theophrasti*) was more intense in a community of weed species vs. corn  
438 crops (Weinig 2000). However, our results differ in that neighbors altered not just the  
439 strength but also the direction of selection on emergence time. This suggests that community  
440 composition could contribute to temporal or spatial variation in optimum emergence time (cf.  
441 Kalisz 1986), and could be cryptic driver of geographic clines in emergence timing (e.g.,  
442 Gutterman and Edine 1988, Torres-Martínez et al. 2017, Waterton et al. 2020).

443         In contrast, selection on seedling traits in the non-native annual *B. diandrus* did not differ  
444 significantly among neighbor treatments. This suggests that selection on seedling traits in this  
445 species acts more independently of the competitive neighborhood, and instead may be  
446 influenced more by other abiotic and biotic environmental factors. This is consistent with the  
447 results for mean fitness: neighbor treatment did not affect the probability of reproduction and  
448 mean fecundity did not differ between neighbor-present vs. neighbor-absent treatments. One  
449 potential reason for this lower sensitivity of selection to neighbor identity in *B. diandrus* vs.  
450 *S. pulchra* could be because the former emerged more rapidly (i.e., the phenotypic

451 distribution is shifted earlier), such that most individuals, regardless of phenotype, start  
452 growing before the different neighboring communities begin to exert any variable effects. We  
453 also note that all neighbor species were grasses (representing three genera), and although this  
454 reflects the dominant biomass in grassland communities, it likely represents a fraction of the  
455 potential phylogenetic and functional diversity present in many natural communities,  
456 potentially leading to less variable selection in our experiment than in natural communities.

457 ***Prediction 2: Patterns of selection were most strongly associated with measures of***  
458 ***neighbor resource uptake and productivity***

459 Stronger selection for earlier emergence in *S. pulchra* in neighbor communities with  
460 higher soil moisture availability was counter to Prediction 2, which states that selection will  
461 be stronger where neighbors take up more resources (or, for example, where water is more  
462 limiting). However, our measurements of soil moisture were between 0 – 15cm, and *S.*  
463 *pulchra* is deep-rooted (up to 1 m) with the greatest amount of roots found at 15 – 30 cm  
464 depth (Hull and Muller 1977). Thus, neighbors that reduced soil moisture the most may have  
465 done so at soil depths that have a lesser impact on *S. pulchra* growth. The weak trend of  
466 stronger selection for earlier emergence when neighbors intercepted more light was  
467 consistent with Prediction 2; however, we expect that this pattern will only hold for neighbor  
468 communities in which earlier emergence provides greater light acquisition and not in those  
469 where even the earliest emerging plants are shaded. Supporting this, Weinig (2000) found  
470 that earlier emergence enhanced velvetleaf fitness in the presence of neighbors for which it  
471 allowed greater light capture (short-statured weeds), but not in the presence of taller-statured  
472 neighbors where light was limited regardless of emergence time (corn crops). In *B. diandrus*,  
473 selection for heavier seeds was stronger neighbor communities with higher aboveground  
474 productivity, consistent with Prediction 2. Compared to *S. pulchra*, *B. diandrus* is  
475 characterized by a more light-acquisitive growth strategy (e.g., allocating more biomass to

476 shoots vs. roots; Holmes and Rice 1996), which may explain why the benefits of heavier  
477 seeds were more pronounced for *B. diandrus* in environments characterized by stronger  
478 aboveground competition.

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

#### 490 ***Implications for evolutionary adaptation to global change***

491 Adaptive evolution in seedling traits is considered to be an important component of *in*  
492 *situ* responses to global change that will promote long-term species persistence (Walck et al.  
493 2011, Cochrane et al. 2015). Most studies that aim to predict how plant populations will  
494 adaptively evolve and persist under drivers of global change such as climate change and  
495 nitrogen enrichment have focused on the direct selective effects (Etterson and Shaw 2001,  
496 Franks et al. 2007, Anderson et al. 2012, Dickman et al. 2019, Petipas et al. 2020), but rarely  
497 consider the potential for plant-plant interactions to mediate adaptive evolutionary responses.  
498 The results presented here indicate that such changes in the taxonomic composition of a  
499 species' neighbors resulting from global change can affect the strength and even direction of

500 phenotypic selection on seedling traits, although the potential for such effects will be greater  
501 in some species (e.g., *S. pulchra*) than others (e.g., *B. diandrus*) and will depend on how  
502 neighbor identity changes (e.g., differences in light or soil moisture). Such changes in the  
503 intensity of selection could potentially promote or impede adaptation to drivers of global  
504 change depending on whether they are concordant with or antagonistic to long-term shifts in  
505 directly imposed selection.

### 506 ***Towards predicting neighbor-mediated evolution***

507         Our results suggest that neighbor traits can be used to predict their evolutionary  
508 effects, but our study is limited in this regard. First, selection is likely to be determined by  
509 neighbor characteristics that we did not quantify, including belowground traits such as  
510 rooting depth or allelopathy (cf. Lankau 2012). Second, selection on seedling traits may be  
511 driven by interactions between different neighbor characteristics, such as light interception  
512 and emergence time (cf. Weinig 2000). With only eight neighbor-present treatments, we are  
513 unable to test for such interactions. Third, as has been found in previous studies,  
514 selection on seedling traits via fitness components expressed at different times was discordant  
515 (Kelly 1992, Stratton 1992, Gómez 2004, Akiyama and Ågren 2014); however, because we  
516 quantified each neighbor metric at a single time point we are unable to examine how  
517 neighbors influence selection acting at different life stages. Finally, with only two focal  
518 species, we have limited capacity to investigate the extent to which neighbors exert consistent  
519 selection in different focal species, and how this might relate to life history, phenological or  
520 morphological traits intrinsic to focal species. Characterizing the mechanisms underlying  
521 neighbor-mediated selection will therefore require larger experiments with more focal and  
522 neighbor species, which will be logistically challenging given the large sample sizes that  
523 generally are required to detect natural selection in the field (Hersch and Phillips 2004).



## 524 *Conclusions*

525 Our results demonstrate that neighboring plants can shape selection on seedling traits,  
526 suggesting that shifts in plant community composition due to various drivers of global change  
527 or other local environmental disruptions may lead to cascading changes in selection.  
528 However, these responses will likely differ considerably among species, with the direction  
529 and strength of selection in some species being less sensitive to neighbors than in others.  
530 Furthermore, we show that patterns of selection on seedling traits are associated with  
531 neighbor characteristics such as resource uptake, suggesting that a trait-based approach has  
532 considerable potential to increase our understanding of the evolutionary consequences of  
533 plant-plant interactions.

## 534 **DATA AVAILABILITY**

535 Data, metadata, and the R script for reproducing data analyses and figures can be  
536 accessed on the Dryad Data Repository <https://doi.org/10.5061/dryad.4tmpg4fgp>.

## 537 **SUPPLEMENTARY MATERIAL**

538 **Supplementary Text S1.** Supplemental methods.

539 **Table S1.** Significance of fixed effects in generalized linear mixed models (GLMMs) testing  
540 effects of neighbor treatment, neighbor origin, and neighbor diversity on emergence percent.

541 **Table S2.** Significance of fixed effects in linear mixed models (LMMs) testing effects of  
542 neighbor treatment, neighbor origin, and neighbor diversity on emergence time.

543 **Table S3.** Standardized selection gradients in neighbor treatments and across levels of  
544 neighbor origin and neighbor diversity.

545 **Figure S1.** Association between *S. pulchra* aboveground biomass and total fecundity.

546 **Figure S2.** Effect of seed mass on emergence probability in *B. diandrus* and *S. pulchra*.

547 **Figure S3.** Effect of seed mass on emergence time in *B. diandrus* and *S. pulchra*.

548 **Figure S4.** Estimated marginal mean emergence probability in neighbor treatments in *B.*  
549 *diandrus* and *S. pulchra*.

550 **Figure S5.** Estimated marginal mean emergence time in neighbor treatments in *B. diandrus*  
551 and *S. pulchra*.

552 **Figure S6.** Estimated marginal mean fitness in neighbor origin status in *B. diandrus* and *S.*  
553 *pulchra*.

554 **Figure S7.** Estimated marginal mean fitness in neighbor diversity level in *B. diandrus* and *S.*  
555 *pulchra*.

556 **Figure S8.** Seed mass selection coefficients from hurdle GLMMs in neighbor origin status in  
557 *B. diandrus* and *S. pulchra*.

558 **Figure S9.** Emergence time selection coefficients from hurdle GLMMs in neighbor origin  
559 status in *B. diandrus* and *S. pulchra*.

560 **Figure S10.** Seed mass selection coefficients from hurdle GLMMs in neighbor diversity level  
561 in *B. diandrus* and *S. pulchra*.

562 **Figure S11.** Emergence time selection coefficients from hurdle GLMMs in neighbor  
563 diversity level in *B. diandrus* and *S. pulchra*.

564 **Figure S12.** Association between selection gradients in *S. pulchra* (based on biomass) and *B.*  
565 *diandrus* in neighbor-present treatments for seed mass and emergence time.

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- 807



## 808 TABLES

809 Table 1. Focal species and neighbor treatments in the field experiment.

Name	Origin	Diversity	Life history strategy	Code	Seeding rate (m <sup>-2</sup> )
<b><i>Focal species</i></b>					
<i>Bromus diandrus</i>	Non-native	--	Annual	--	--
<i>Stipa pulchra</i>	Native	--	Perennial	--	--
<b><i>Neighbor treatments</i></b>					
<i>Neighbor-absent</i>	--	--	--	ABS	--
<i>Bromus carinatus</i>	Native	Single	Perennial	BRCA	1353
<i>Festuca microstachys</i>	Native	Single	Annual	FEMI	1527
<i>Hordeum brachyantherum</i>	Native	Single	Perennial	HOBR	2557
<i>Native mixture</i>	Native	Mixed	Mixed	NATMIX	1812
<i>Bromus hordeaceus</i>	Non-native	Single	Annual	BRHO	1196
<i>Festuca myuros</i>	Non-native	Single	Annual	FEMY	1389
<i>Hordeum murinum</i>	Non-native	Single	Annual	HOMU	1125
<i>Non-native mixture</i>	Non-native	Mixed	Mixed	NONMIX	1236

810 Notes: Neighbor treatments comprised eight “neighbor-present” treatments, including six  
811 single species treatments and two mixed species treatments, and a “neighbor-absent”  
812 treatment. The native and non-native mixture treatments contained all three natives and non-  
813 natives, respectively, each at a third of the seeding rate in single species treatments.

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

Fitness component	Model/fixed effect	Zero model			Non-zero model		
		$\chi^2$	df	<i>P</i>	$\chi^2$	df	<i>P</i>
<i>B. diandrus</i>							
Fecundity	Neighbor	3.86	8	0.085	17.9	8	<b>0.022</b>
	Origin	0.93	1	0.33	3.11	1	0.078
	Diversity	6.35	1	<b>0.012</b>	0.10	1	0.75
<i>S. pulchra</i>							
Fecundity	Neighbor	40.1	8	<b>&lt; 0.001</b>	61.2	8	<b>&lt; 0.001</b>
	Origin	8.20	1	<b>0.004</b>	2.69	1	0.10
	Diversity	9.32	1	<b>0.002</b>	0.36	1	0.55
Biomass	Neighbor	12.5	8	0.13	83.8	8	<b>&lt; 0.001</b>
	Origin	2.75	1	0.097	4.33	1	<b>0.037</b>
	Diversity	4.06	1	<b>0.044</b>	2.22	1	0.14

817 Notes: Zero models are binomial regressions with a logit link function modeling if plants  
818 reproduced or survived until biomass was harvested (*S. pulchra* only). Non-zero models are  
819 negative binomial regressions with a log link function modeling the fecundity of seed-  
820 producing individuals or the biomass of survivors (*S. pulchra* only). *P*-values < 0.05 are  
821 highlighted in bold. See Figs. 3, S6-7 to view the direction and magnitude of each fixed effect  
822 level on mean fitness.

823 **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
<i>B. diandrus</i>					
Fecundity	0.30	-0.17	-0.41	-0.27	-0.86*
<i>S. pulchra</i>					
Fecundity	0.52	-0.52	0.26	-0.079	-0.65†
Biomass	0.46	-0.37	-0.042	0.007	-0.81*

824 Notes: Correlations are based on neighbor-present treatments only. Significance: † $P < 0.1$ , \* $P$

825  $< 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

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

Fitness component	Model	Fixed effect	Zero model			Non-zero model		
			$\chi^2$	df	<i>P</i>	$\chi^2$	df	<i>P</i>
<i>B. diandrus</i>								
Fecundity	Neighbor	Neighbor	11.3	8	0.19	25.6	8	<b>0.001</b>
		Seed mass	0.018	1	0.89	6.54	1	<b>0.011</b>
		Emergence time	4.65	1	<b>0.031</b>	8.31	1	<b>0.004</b>
		Neighbor x seed	6.55	8	0.59	5.07	8	0.75
	Origin	Neighbor x emergence	11.2	8	0.19	4.85	8	0.77
		Origin	0.70	1	0.40	2.85	1	0.091
		Seed mass	0.24	1	0.62	7.10	1	<b>0.008</b>
		Emergence time	6.24	1	<b>0.012</b>	7.99	1	<b>0.005</b>
	Diversity	Origin x seed	1.61	1	0.20	0.0002	1	0.99
		Origin x emergence	3.23	1	0.072	1.85	1	0.17
		Diversity	5.66	1	<b>0.017</b>	0.11	1	0.75
		Seed mass	0.18	1	0.67	7.27	1	<b>0.007</b>
		Emergence time	5.98	1	<b>0.015</b>	7.83	1	<b>0.005</b>
		Diversity x seed	0.90	1	0.34	0.28	1	0.60
		Diversity x emergence	0.058	1	0.81	0.12	1	0.73
<i>S. pulchra</i>								
Fecundity	Neighbor	Neighbor	35.9	8	<b>&lt; 0.001</b>	64.5	8	<b>&lt; 0.001</b>
		Seed mass	4.85	1	<b>0.028</b>	4.00	1	<b>0.046</b>
		Emergence time	6.25	1	<b>0.012</b>	0.009	1	0.92
		Neighbor x seed	12.7	8	0.12	6.44	8	0.60
		Neighbor x emergence	11.7	8	0.16	4.31	8	0.83
	Origin	Origin	7.10	1	<b>0.008</b>	2.63	1	0.11
		Seed mass	6.53	1	<b>0.011</b>	1.44	1	0.23
		Emergence time	8.51	1	<b>0.004</b>	0.0005	1	0.98
		Origin x seed	1.45	1	0.23	0.16	1	0.69
	Diversity	Origin x emergence	1.24	1	0.27	0.60	1	0.44
		Diversity	7.20	1	<b>0.007</b>	0.38	1	0.54
		Seed mass	6.35	1	<b>0.012</b>	1.55	1	0.21
		Emergence time	8.88	1	<b>0.003</b>	0.009	1	0.92
		Diversity x seed	0.25	1	0.62	0.63	1	0.43
			Diversity x emergence	0.002	1	0.96	0.92	1
Biomass	Neighbor	Neighbor	9.08	8	0.34	100.8	8	<b>&lt; 0.001</b>
		Seed mass	0.075	1	0.78	8.88	1	<b>0.003</b>
		Emergence time	16.4	1	<b>&lt; 0.001</b>	17.7	1	<b>&lt; 0.001</b>
		Neighbor x seed	7.59	8	0.47	7.04	8	0.53
	Origin	Neighbor x emergence	10.5	8	0.23	18.4	8	<b>0.018</b>
		Origin	3.74	1	0.053	3.60	1	0.058
		Seed mass	0.088	1	0.77	7.51	1	<b>0.006</b>
		Emergence time	23.2	1	<b>&lt; 0.001</b>	11.7	1	<b>&lt; 0.001</b>
		Origin x seed	0.35	1	0.55	0.11	1	0.74
	Diversity	Origin x emergence	0.80	1	0.37	0.002	1	0.97
		Diversity	2.22	1	0.14	2.18	1	0.14
		Seed mass	0.052	1	0.82	7.05	1	<b>0.008</b>
		Emergence time	23.1	1	<b>&lt; 0.001</b>	12.4	1	<b>&lt; 0.001</b>
		Diversity x seed	2.46	1	0.12	0.33	1	0.57
		Diversity x emergence	0.63	1	0.43	1.11	1	0.29

829 Notes: Zero models are binomial regressions with a logit link function modeling if plants  
830 reproduced or survived until biomass was harvested (*S. pulchra* only). Non-zero models are  
831 negative binomial regressions with a log link function modeling the fecundity of seed-

832 producing individuals or the biomass of survivors (*S. pulchra* only). *P*-values < 0.05 are  
833 highlighted in bold. See Figs. 4-5, S8-11 to view the direction and magnitude of each fixed  
834 effect level on selection coefficients from hurdle GLMMs.

835 **Table 5. Correlations between selection gradients for fitness-related traits (seed mass**  
 836 **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	
<i>B. diandrus</i>							
Fecundity	Seed mass	-0.45	-0.056	0.35	0.23	0.75*	-0.41
	Emergence time	0.21	0.26	-0.16	-0.56	-0.13	0.11
<i>S. pulchra</i>							
Fecundity	Seed mass	0.19	0.15	0.35	0.40	0.12	0.08
	Emergence time	-0.047	0.38	-0.70†	-0.74*	-0.40	-0.069
Biomass	Seed mass	0.15	0.34	0.33	0.29	0.23	-0.045
	Emergence time	-0.30	0.28	-0.61	-0.84**	-0.20	-0.045

837 Notes: Correlations are based on neighbor-present treatments only. Significance: † $P < 0.1$ , \* $P$   
 838  $< 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

839 **FIGURE LEGENDS**

840 **Figure 1. Layout of the field experiment with an example block layout.** Dark grey and  
841 light grey squares represent native and non-native neighbor plots, respectively; striped and  
842 non-striped squares represent mixed species and single species plots, respectively; blue  
843 represents neighbor-absent plots. Light grey and dark grey circles represent *B. diandrus* and  
844 *S. pulchra* individuals, respectively.

845

846 **Figure 2. Estimated marginal means of neighbor metrics  $\pm$  SE in neighbor-present**  
847 **treatments.** *P*-values are from linear mixed models (LMMs) testing the effects of neighbor  
848 treatment on each neighbor metric. Post hoc pairwise comparisons among the eight  
849 treatments are shown (letters indicate significant differences). Dark grey and light grey bars  
850 represent native and non-native neighbor treatments, respectively; striped and non-striped  
851 bars represent mixed species and single species treatments, respectively. Neighbor treatment  
852 codes: BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum*  
853 *brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca*  
854 *myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

855

856 **Figure 3. Estimated marginal mean fitness  $\pm$  SE in neighbor treatments in (A, B) *B.***  
857 ***diandrus* and (C – F) *S. pulchra*.** *P*-values are from hurdle generalized linear mixed models  
858 (GLMMs) testing the effects of neighbor treatment on fitness components. Two types of post  
859 hoc tests are shown: 1) neighbor presence vs. absence (indicated above neighbor absent  
860 treatment; significance: †*P* < 0.1, \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001); 2) pairwise  
861 comparisons among the eight neighbor-present treatments (letters indicate significant  
862 differences). Dark grey and light grey bars represent native and non-native neighbor

863 treatments, respectively; striped and non-striped bars represent mixed species and single  
864 species treatments, respectively; blue represents the neighbor-absent treatment. Neighbor  
865 treatment codes: ABS = Neighbor-absent; BRCA = *Bromus carinatus*; FEMI = *Festuca*  
866 *microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO =  
867 *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX =  
868 Non-native mixture.

869

870 **Figure 4. Seed mass selection coefficients  $\pm$  SE from hurdle GLMMs in neighbor**  
871 **treatments in (A, B) *B. diandrus* and (C – F) *S. pulchra*. *P*-values are for the seed mass**  
872 **(SM) and seed mass  $\times$  neighbor treatment interaction (SM  $\times$  N) terms in hurdle GLMMs**  
873 **testing the effects of seedling traits (seed mass and emergence time), neighbor treatment, and**  
874 **the trait  $\times$  neighbor treatment interactions. Dark grey and light grey bars represent native and**  
875 **non-native neighbor treatments, respectively; striped and non-striped bars represent mixed**  
876 **species and single species treatments, respectively; blue represents the neighbor-absent**  
877 **treatment. Neighbor treatment codes: ABS = Neighbor-absent; BRCA = *Bromus carinatus*;**  
878 **FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NAMIX = Native**  
879 **mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum***  
880 ***murinum*; NONMIX = Non-native mixture.**

881

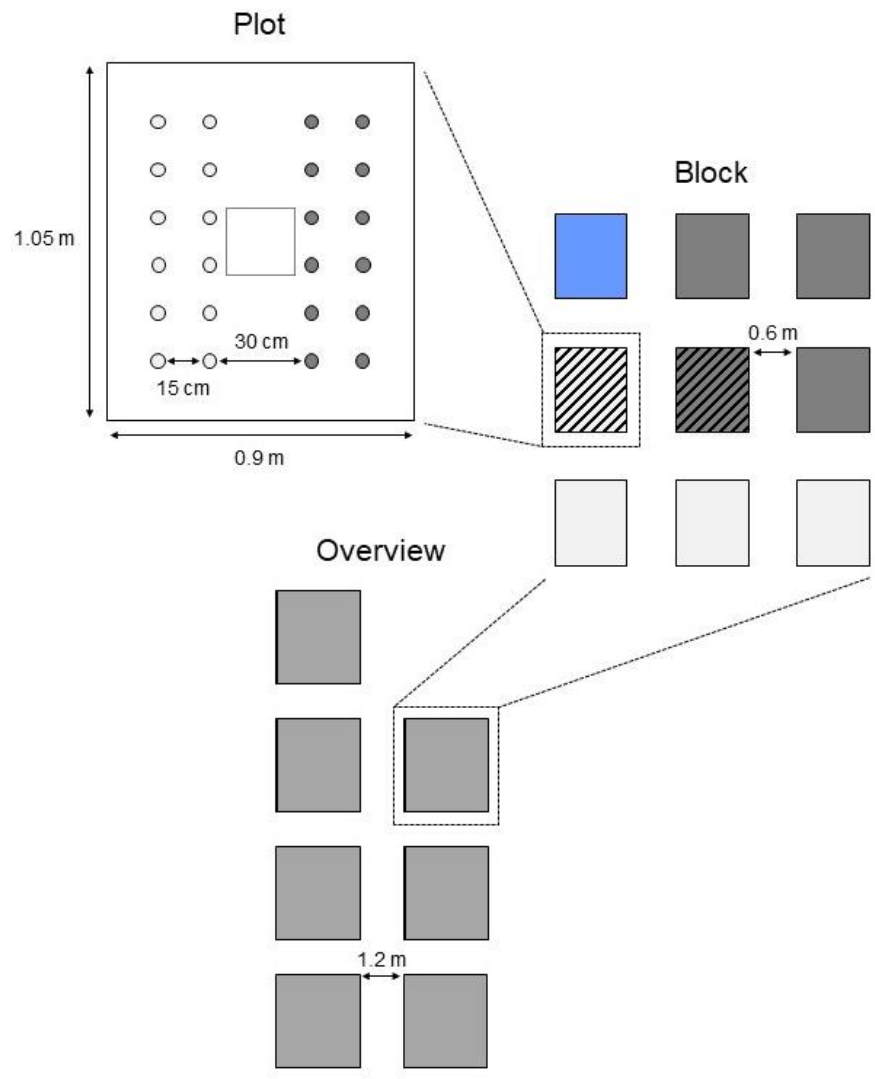
882 **Figure 5. Emergence time selection coefficients  $\pm$  SE from hurdle GLMMs in neighbor**  
883 **treatments in (A, B) *B. diandrus* and (C – F) *S. pulchra*. *P*-values are for the emergence**  
884 **time (ET) and emergence time  $\times$  neighbor treatment interaction (ET  $\times$  N) terms in hurdle**  
885 **GLMMs testing the effects of seedling traits (seed mass and emergence time), neighbor**  
886 **treatment, and the trait  $\times$  neighbor treatment interactions. Two types of post hoc tests are**

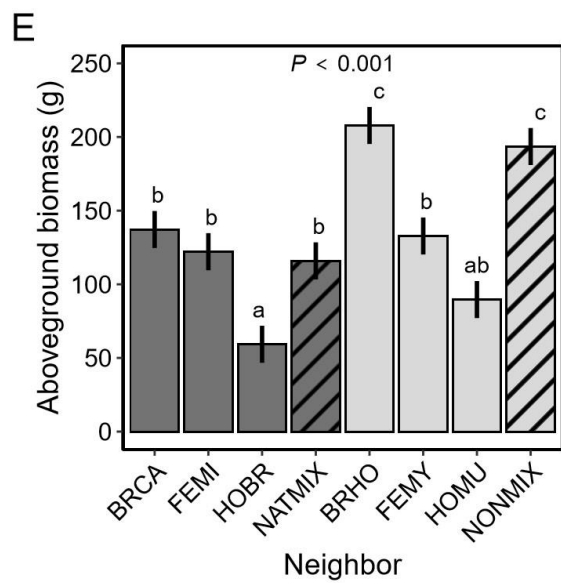
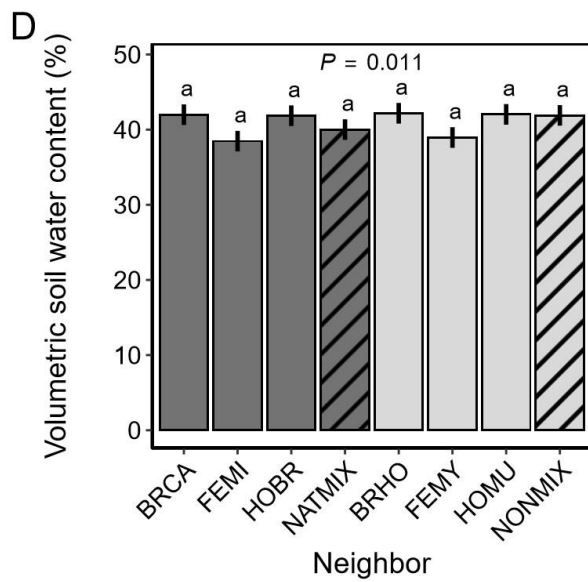
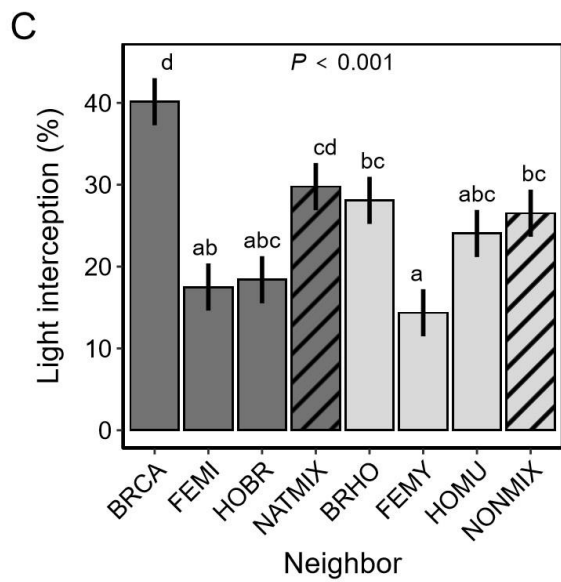
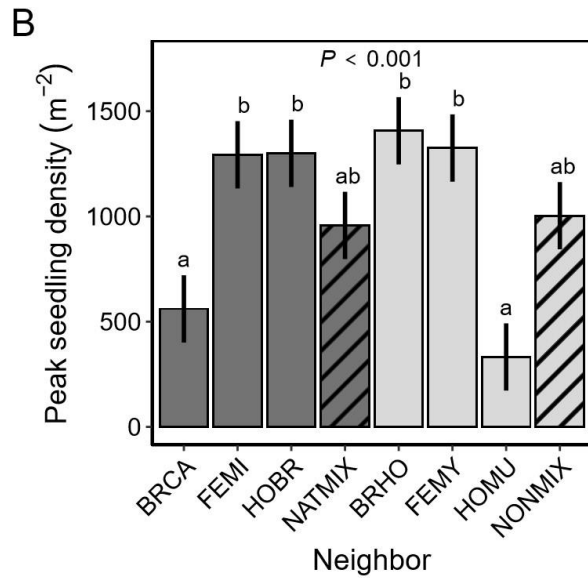
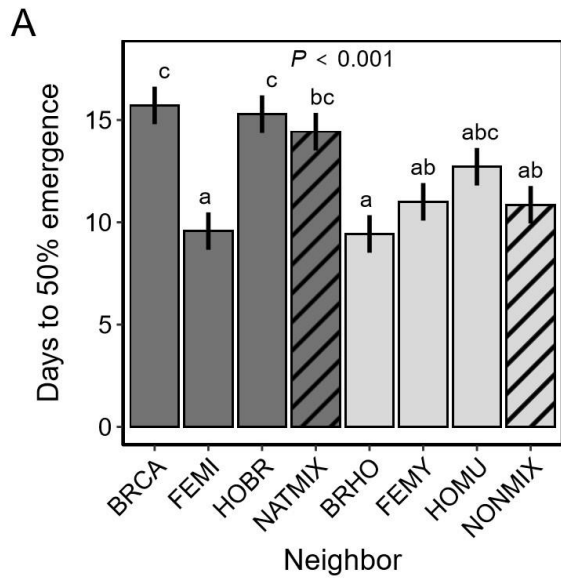


887 shown: 1) neighbor presence vs. absence (indicated above neighbor absent treatment;  
888 significance: † $P < 0.1$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ); 2) pairwise comparisons  
889 among the eight neighbor-present treatments (letters indicate significant differences). Dark  
890 grey and light grey bars represent native and non-native neighbor treatments, respectively;  
891 striped and non-striped bars represent mixed species and single species treatments,  
892 respectively; blue represents the neighbor-absent treatment. Neighbor treatment codes: ABS  
893 = Neighbor-absent; BRCA = *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR =  
894 *Hordeum brachyantherum*; NAMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY  
895 = *Festuca myuros*; HOMU = *Hordeum murinum*; NONMIX = Non-native mixture.

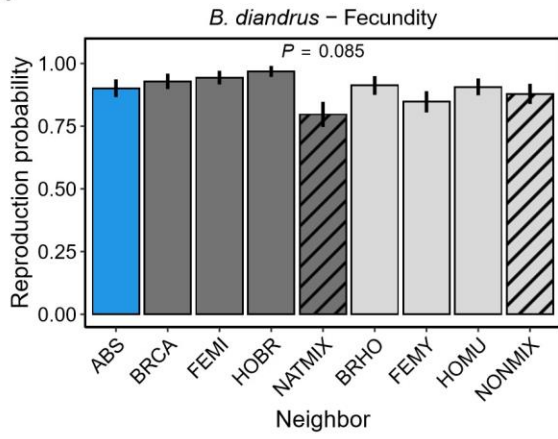
896

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

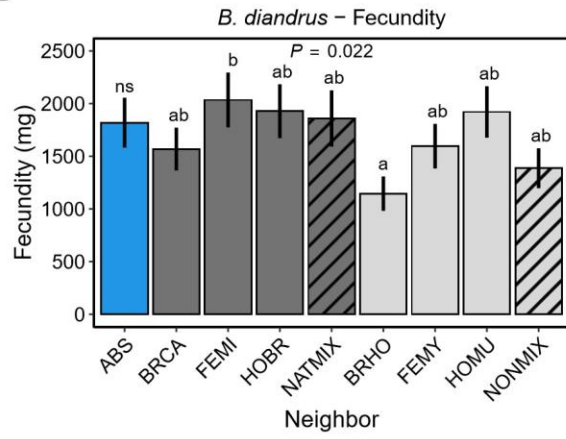




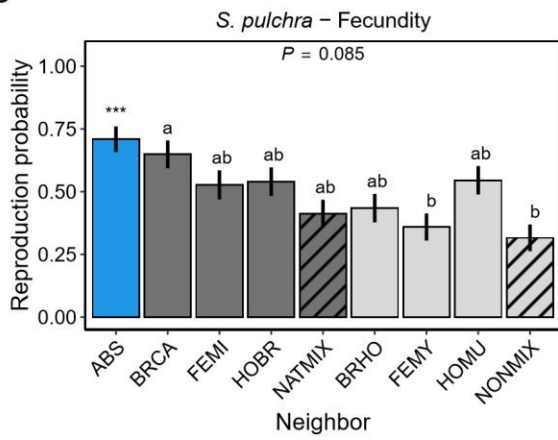
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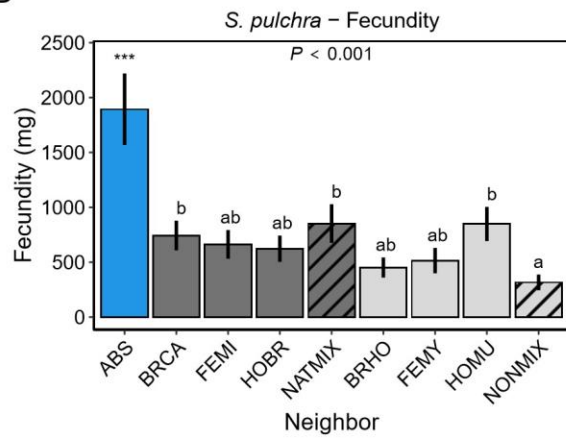
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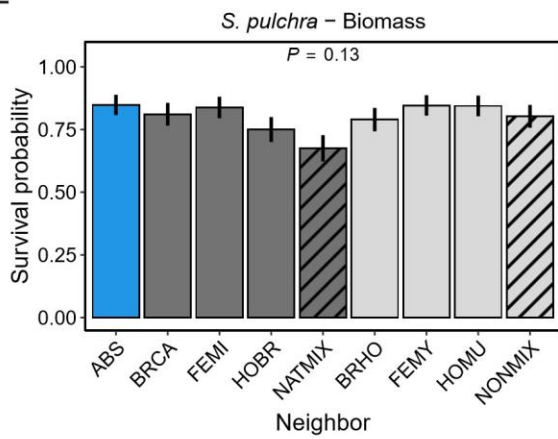
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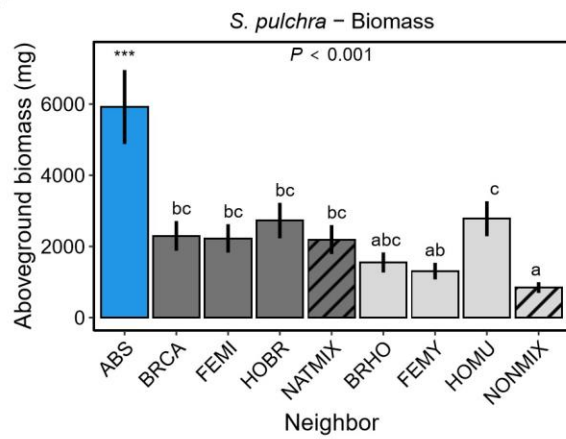
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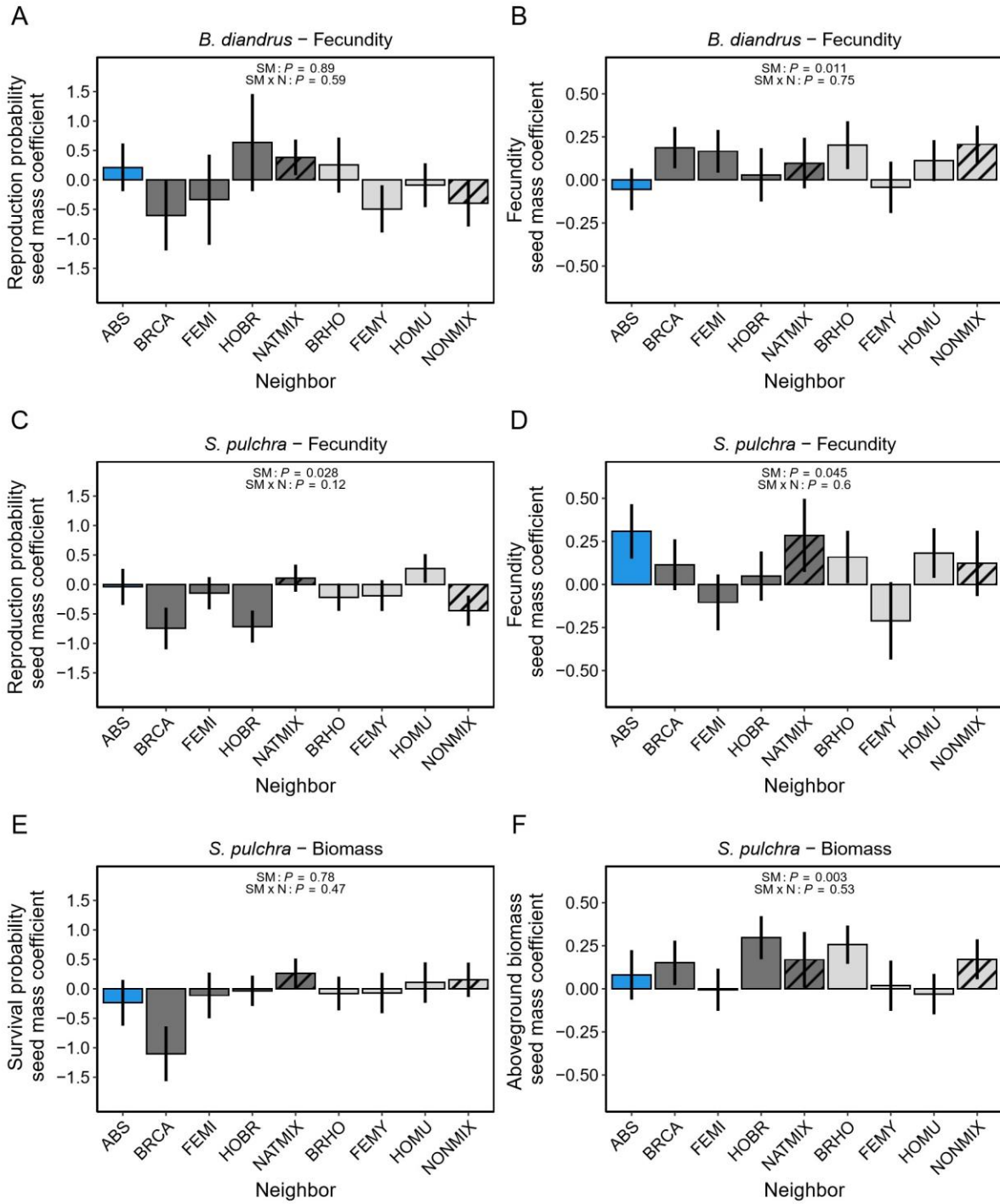


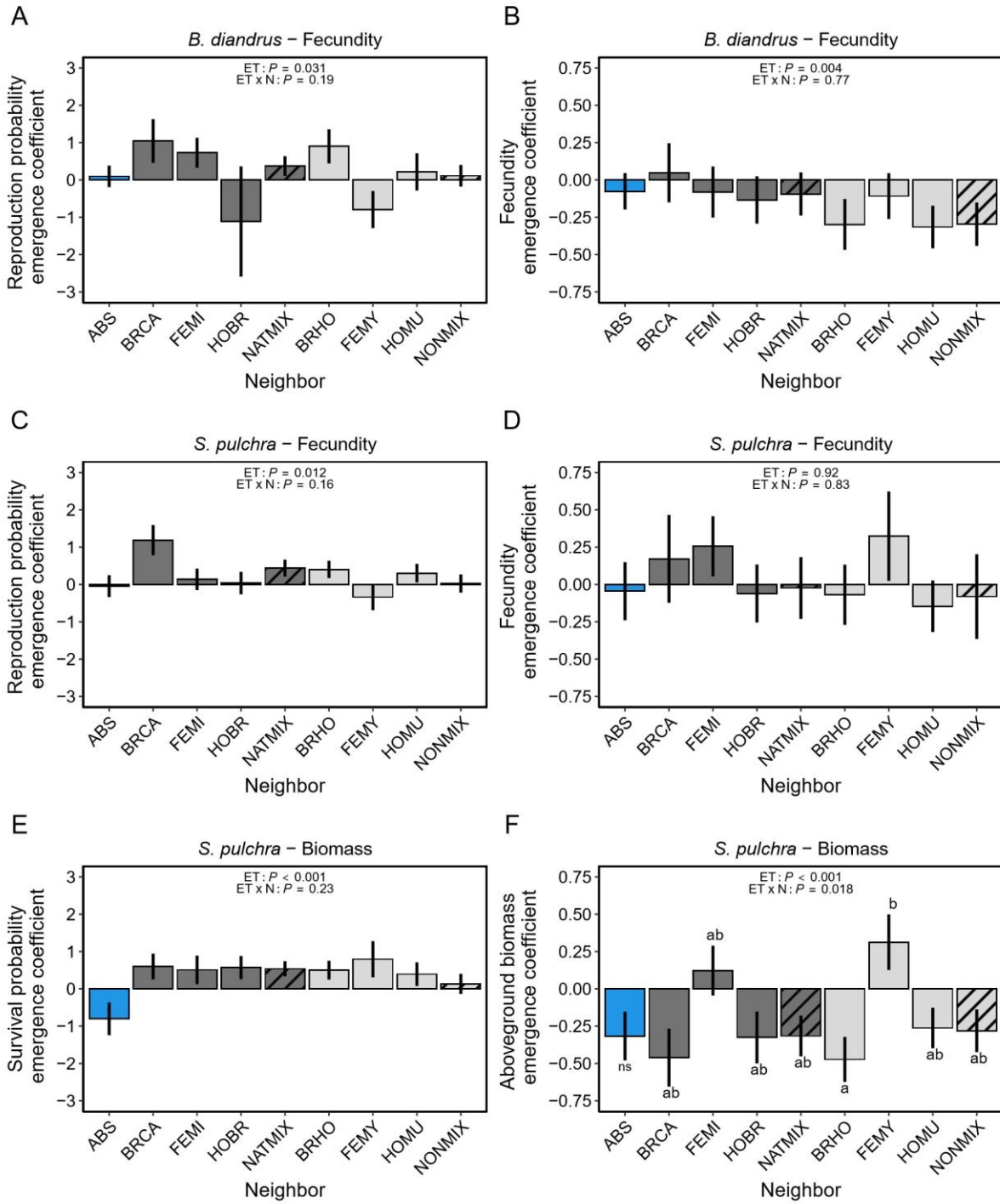
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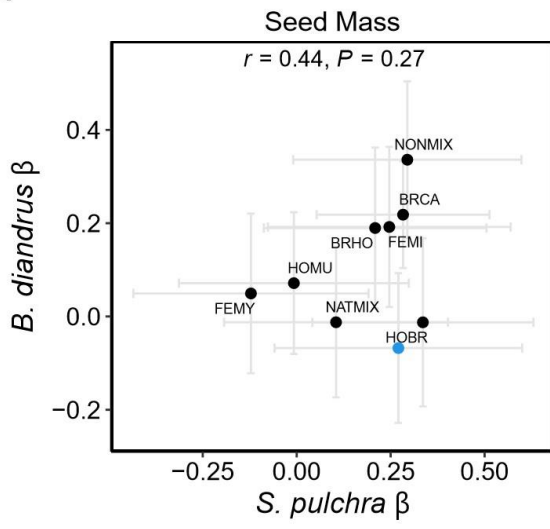
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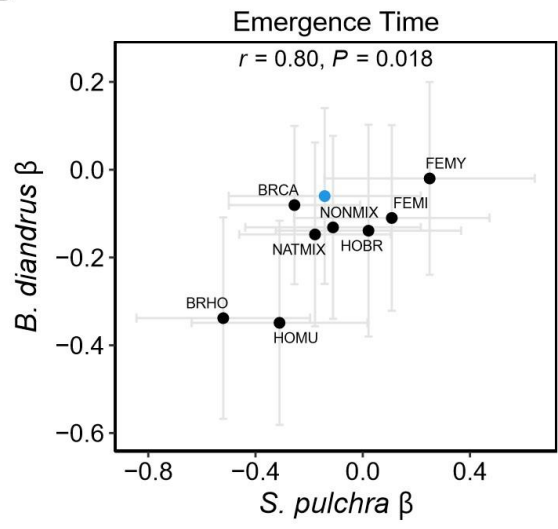




A



B



910

1     **When the neighborhood matters: contextual selection on seedling traits in native and**  
2                                    **non-native California grasses**  
3                                    **SUPPORTING INFORMATION**

4     **Contents**

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31    **Figure S12.** Association between selection gradients in *S. pulchra* (based on biomass) and *B.*  
32    *diandrus* in neighbor-present treatments for seed mass and emergence time. ....19



33 **Supporting Text S1. Supplemental methods.**

34 **Site information**

35 The experimental site is flat, regularly tilled, and is classified as having sandy clay  
36 loam soil. The climate is Mediterranean, with most precipitation typically falling between  
37 November and May, during which the majority of seedling emergence and subsequent  
38 growth occurs. Where not weeded, the site is typically dominated by exotic annual species  
39 including *Hordeum murinum* (Poaceae), *Erodium cicutarium* (Geraniaceae), and *Malva*  
40 *parviflora* (Malvaceae).

41

42 **Seed collection**

43 We collected seeds of both species in April 2015. We collected *Stipa pulchra* seeds in  
44 Sedgwick Reserve from a naturally occurring population on the Byrne observatory mesa  
45 (34.692° N 120.043° W) and *Bromus diandrus* seeds in Elliott Chaparral Reserve from a  
46 naturally occurring population several hundred yards west of the Nutrient Network site  
47 (32.889° N, 117.091° W). *S. pulchra* can reproduce clonally, with distances of 30 cm  
48 between clones having been reported (Hull and Muller 1977). Therefore, we collected from  
49 maternal plants spaced at least 5m apart to avoid collecting from closely related plants or  
50 clones. We stored all seeds in a refrigerator at 4° C until use.

51

52 **Neighbor metrics**

53 We monitored the emergence of neighbor seeds in a 20 × 20 cm quadrat in the center  
54 of each plot daily between 20 February – 14 March 2017 (Season 1) by which point no new  
55 germinating seedlings were recorded for 3 days in all but [two plots]. In the mixed species  
56 treatments, we recorded the total number of emerged individuals for the three constituent  
57 species combined. We calculated the number of days to emergence from 16 February, the  
58 date on which we first watered plots. For each plot, we calculated the number of days to  
59 reach 50% of total neighbor emergence, and the peak density of emerging neighbor seedlings  
60 per square meter (i.e., prior to the onset of mortality). We were unable to monitor any  
61 emergence on 27 February due to a rainstorm; therefore, some individuals that we recorded  
62 as having emerged on 28 February may have emerged a day earlier.

63 To characterize soil water availability, we measured volumetric water content (VWC)  
64 from 0-15 cm depth using a FieldScout 150 soil moisture probe (Spectrum Technologies Inc.,  
65 Aurora, IL USA) at five points in each plot (each corner and the center) over four consecutive  
66 days following a rain event on 8 May 2017 (Season 1). We calculated mean soil VWC for  
67 each plot using all measurements from across the four days. To characterize light interception  
68 in each plot, on the afternoon of 18 May 2017 (Season 1), when the sky was clear, we  
69 recorded photosynthetic active radiation (PAR) above the canopy and at ground level along  
70 both diagonals of each plot using an AccuPAR LP-80 PAR Ceptometer (Decagon Devices  
71 Inc., Pullman, WA USA) We calculated the percentage of PAR intercepted in each plot by  
72 subtracting the mean of the two ground-level measurements from the mean of the two above-  
73 canopy measurements and dividing this by the above-canopy mean.

74 At the end of Season 1, we harvested all neighbor aboveground biomass in plots  
75 around surviving *S. pulchra* plants from 31 July - 2 August 2017. We dried neighbor biomass  
76 for each plot at 40 °C for three days before weighing. We did not repeat any measurements of  
77 community context in remaining plot halves during Season 2.

78

79 **Watering and weeding**

80 At the start of each season of the experiment (16 February 2017 in Season 1, 18  
81 January 2018 in Season 2), we gently applied 3 l of water across each plot (~ 3 mm, which  
82 represents half the weekly rainfall at the site [prism.oregonstate.edu/]) to settle sown seeds  
83 into the soil and to initiate germination. In Season 2, because of low neighbor germination  
84 after the first rain event, we gently applied 3 l of water daily across each plot from 29 January  
85 2018 until the next rain event on 21 February 2018. In Seasons 1 and 2, we watered plots to  
86 avoid the risk of mass mortality due to prolonged drought. Except for weeks in which there  
87 was forecasted rain event, we supplied 3 l of water evenly across each plot twice a week, two  
88 days apart, until 13 May 2017 in Season 1 and until 20 April 2018 in Season 2.

89 Throughout the experiment, we carefully pulled all weeds from neighbor-absent  
90 treatment plots and all non-grass weeds from plots of all other treatments. We only removed  
91 non-grass weeds from neighbor-present treatments because these could be confidently  
92 distinguished from sown neighbors.

93

94 **Statistical analyses**

95 *Neighbor metrics*

96 We tested whether neighbor metrics, (emergence time, peak seedling density, light  
97 interception, soil water availability, total aboveground biomass), were influenced by each of  
98 the following fixed effects: neighbor treatment, origin, and diversity using PERMANOVAs  
99 fit using the `adonis2` function in the package `vegan` (Oksanen et al. 2022). We excluded the  
100 neighbor-absent treatment from these analyses because it did not have associated data for  
101 emergence time, peak seedling density, and total aboveground biomass. To test the effect of  
102 neighbor treatment, we used the Euclidean distance metric on plot-level values of neighbor  
103 metrics, standardized to a mean of 0 and standard deviation of 1, and performing 999  
104 permutations and including block as a blocking factor. In the case that PERMANOVA for  
105 neighbor treatments were statistically significant, we fit separate univariate linear mixed  
106 models (LMMs) with random intercepts for block for each neighbor metric using the package  
107 `lme4` (Bates et al. 2015). To test the effects of neighbor origin and neighbor diversity, we  
108 used the Euclidean distance metric on mean neighbor treatment values across all blocks of  
109 each metric (to avoid pseudo-replication from non-independence of plot-level values within  
110 each neighbor treatment), standardized to a mean of 0 and standard deviation of 1, and  
111 performing 999 permutations. In the case that PERMANOVA for neighbor origin or neighbor  
112 diversity were statistically significant, we fit separate univariate linear models with the `lm`  
113 function for each neighbor metric.

114 *Emergence of focal individuals*

115 To test whether and how each focal individual's seed mass, neighbor treatment,  
116 neighbor origin, and neighbor diversity influenced the probability of emergence, we fit  
117 binomial generalized linear mixed models (GLMMs) with a logit link using the `glmmTMB`  
118 function in the package `glmmTMB` (Brooks et al. 2017). To test whether and how each factor  
119 influenced mean emergence time, we fit LMMs using the `lmer` function in the package `lme4`  
120 (Bates et al. 2015). In these models, emergence probability/time was predicted by neighbor  
121 treatment, seed mass, and their interaction, with block and plot as random intercepts. In the  
122 case of significant neighbor treatment effects, we carried out two post hoc tests using the  
123 `emmeans` function in the package `emmeans` (Lenth et al. 2022): first, we tested the effect of  
124 neighbor presence vs. absence by comparing the neighbor-absent treatment to the average of  
125 neighbor-present treatments; second, we tested the effect of neighbor identity with pairwise

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126 comparisons among the eight neighbor-present treatment levels. To test the effects of  
127 neighbor origin and diversity on emergence probability and emergence time, we fit separate  
128 GLMMs (glmmTMB package; Brooks et al. 2017) and LMMs (lme4 package; Bates et al.  
129 2015) in which emergence probability/time was predicted by either neighbor origin/diversity,  
130 seed mass, and their interaction, with neighbor treatment, block, and plot as random  
131 intercepts.

132

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150

151 **Table S1. Significance of fixed effects in generalized linear mixed models (GLMMs)**  
 152 **testing effects of neighbor treatment, neighbor origin, and neighbor diversity on**  
 153 **emergence percent.**

Model	Fixed effect	Zero model		
		$\chi^2$	df	<i>P</i>
<i>B. diandrus</i>				
Neighbor	Neighbor	18.5	8	<b>0.018</b>
	Seed mass	8.35	1	<b>0.004</b>
	Neighbor × seed mass	7.21	8	0.51
Origin	Origin	0.037	1	0.85
	Seed mass	8.19	1	<b>0.004</b>
	Origin × seed mass	0.004	1	0.95
Diversity	Diversity	0.43	1	0.51
	Seed mass	8.12	1	<b>0.004</b>
	Diversity × seed mass	0.13	1	0.72
<i>S. pulchra</i>				
Neighbor	Neighbor	3.54	8	0.90
	Seed mass	10.9	1	<b>0.001</b>
	Neighbor × seed mass	10.7	8	0.22
Origin	Origin	0.19	1	0.66
	Seed mass	14.8	1	<b>&lt; 0.001</b>
	Origin × seed mass	0.027	1	0.87
Diversity	Diversity	0.66	1	0.42
	Seed mass	14.2	1	<b>&lt; 0.001</b>
	Diversity × seed mass	3.55	1	0.059

154 Notes: *P*-values < 0.05 are highlighted in bold.

155 **Table S2. Significance of fixed effects in linear mixed models (LMMs) testing effects of**  
 156 **neighbor treatment, neighbor origin, and neighbor diversity on emergence time.**

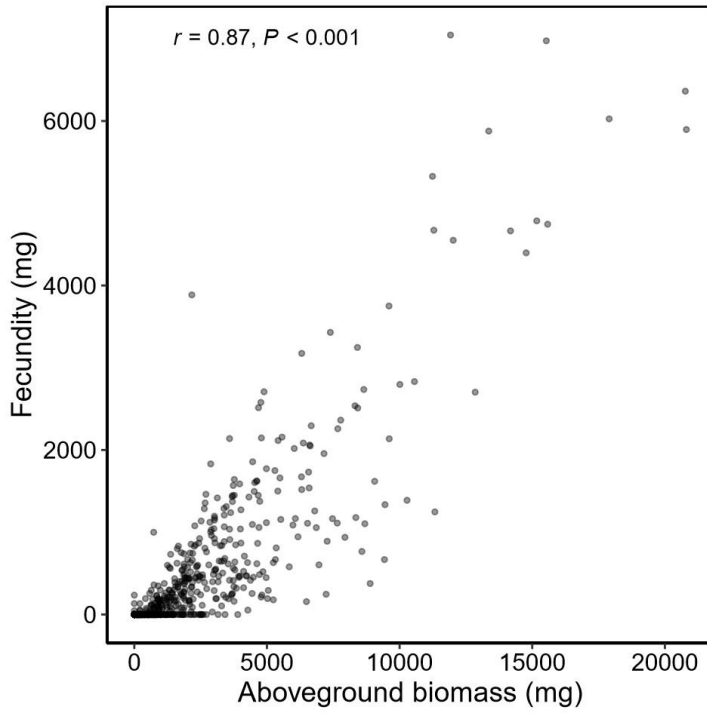
Model	Fixed effect	Zero model		
		$\chi^2$	df	<i>P</i>
<i>B. diandrus</i>				
Neighbor	Neighbor	12.5	8	0.13
	Seed mass	29.9	1	< <b>0.001</b>
	Neighbor × seed mass	11.3	8	0.18
Origin	Origin	2.59	1	0.11
	Seed mass	32.3	1	< <b>0.001</b>
	Origin × seed mass	0.82	1	0.36
Diversity	Diversity	0.085	1	0.77
	Seed mass	31.6	1	< <b>0.001</b>
	Diversity × seed mass	3.18	1	0.074
<i>S. pulchra</i>				
Neighbor	Neighbor	7.20	8	0.52
	Seed mass	43.2	1	< <b>0.001</b>
	Neighbor × seed mass	12.6	8	0.13
Origin	Origin	1.54	1	0.21
	Seed mass	35.6	1	< <b>0.001</b>
	Origin × seed mass	0.33	1	0.56
Diversity	Diversity	1.28	1	0.26
	Seed mass	35.5	1	< <b>0.001</b>
	Diversity × seed mass	2.99	1	0.084

157 Notes: Emergence time was log-transformed. *P*-values < 0.05 are highlighted in bold.

158 **Table S3. Standardized selection gradients (with SE) in neighbor treatments and across**  
 159 **levels of neighbor origin and neighbor diversity.**

Fitness component	Trait	Neighbor										Origin		Diversity	
		ABS	BRCA	FEMI	HOBH	NATMIX	BRHO	FEMY	HOMU	NONMIX	Native	Non-native	Single	Mixed	
<i>B. thlandrus</i>															
Fecundity	Seed mass	-0.068 (0.16)	0.22 (0.11)	0.19 (0.17)	-0.013 (0.18)	-0.012 (0.16)	0.19 (0.17)	0.049 (0.17)	0.071 (0.15)	0.34 (0.17)	0.092 (0.084)	0.14 (0.058)	0.10 (0.094)	0.14 (0.081)	
	Emergence time	-0.060 (0.20)	-0.081 (0.18)	-0.11 (0.21)	-0.14 (0.24)	-0.15 (0.21)	-0.34 (0.23)	-0.020 (0.22)	-0.35 (0.23)	-0.13 (0.21)	-0.13 (0.088)	-0.19 (0.063)	-0.16 (0.091)	-0.16 (0.073)	
<i>S. pinckra</i>															
Fecundity	Seed mass	0.27 (0.33)	0.28 (0.23)	0.25 (0.32)	0.34 (0.29)	0.10 (0.30)	0.21 (0.30)	-0.12 (0.31)	-0.007 (0.31)	0.29 (0.30)	0.23 (0.15)	0.042 (0.10)	0.17 (0.18)	0.13 (0.15)	
	Emergence time	-0.14 (0.36)	-0.25 (0.25)	0.11 (0.36)	0.022 (0.35)	-0.18 (0.28)	-0.52 (0.32)	0.25 (0.39)	-0.31 (0.33)	-0.11 (0.33)	-0.12 (0.16)	-0.31 (0.12)	-0.19 (0.17)	-0.23 (0.13)	
Biomass	Seed mass	0.15 (0.21)	0.28 (0.15)	0.15 (0.21)	0.24 (0.19)	-0.004 (0.19)	0.21 (0.19)	-0.007 (0.20)	-0.11 (0.20)	0.14 (0.20)	0.16 (0.096)	0.011 (0.067)	0.11 (0.11)	0.023 (0.096)	
	Emergence time	-0.19 (0.23)	-0.29 (0.16)	0.099 (0.23)	-0.26 (0.22)	-0.28 (0.18)	-0.49 (0.21)	0.027 (0.25)	-0.31 (0.21)	-0.17 (0.21)	-0.20 (0.10)	-0.30 (0.080)	-0.25 (0.11)	-0.31 (0.085)	

184

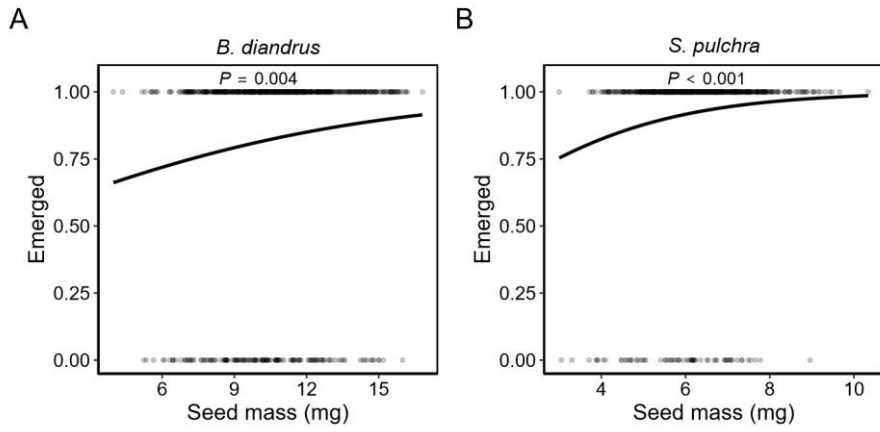


185

186 **Figure S1. Association between *S. pulchra* aboveground biomass and total fecundity.**

187 Biomass was harvested at the end of Season 2; total fecundity is the sum of fecundity in

188 Seasons 1 and 2.  $n = 690$ , the total number of seeds that germinated.



189

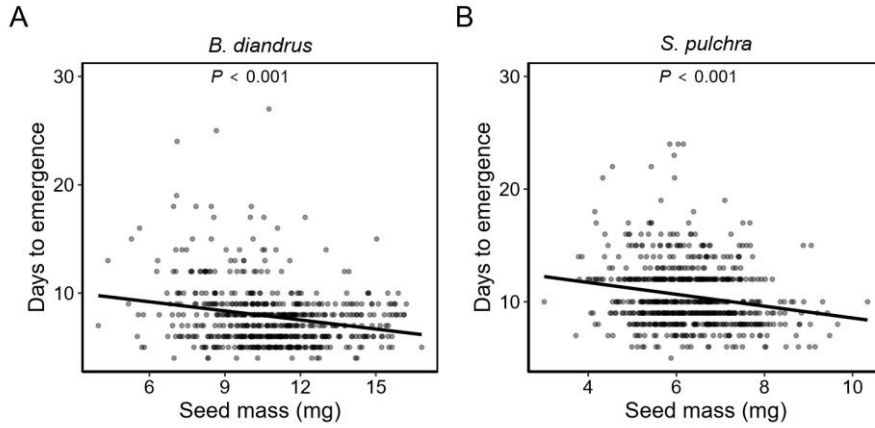
190 **Figure S2. Effect of seed mass on emergence probability in (A) *B. diandrus* and (B) *S.***

191 ***pulchra*. P-values are for the seed mass term from generalized linear mixed models**

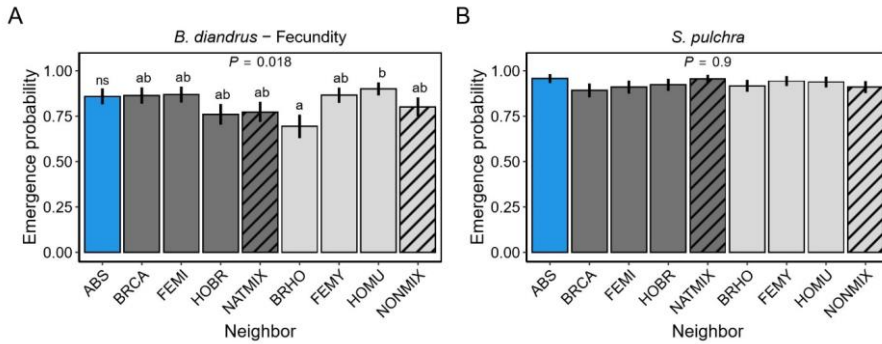
192 **(GLMMs) testing the effects of neighbor treatment, seed mass, and neighbor treatment × seed**

193 **mass interaction on emergence.**

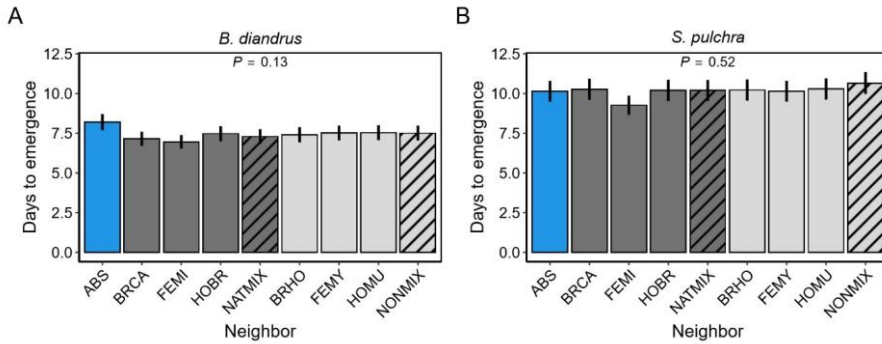




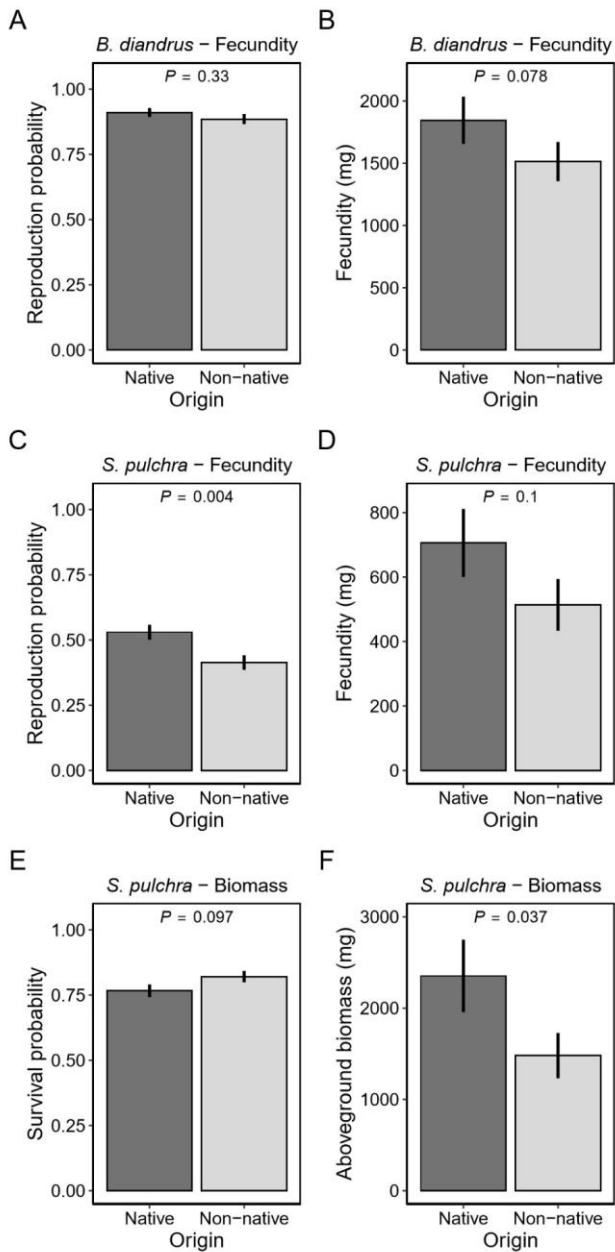
194  
 195 **Figure S3. Effect of seed mass on emergence time in (A) *B. diandrus* and (B) *S. pulchra*.**  
 196 *P*-values are for the seed mass term from linear mixed models (LMMs) testing the effects of  
 197 neighbor treatment, seed mass, and neighbor treatment × seed mass interaction on emergence.  
 198 We were unable to monitor any emergence 11 days after initial watering due to a rainstorm;  
 199 therefore, any plants emerging on this day were recorded as having emerged 12 days after  
 200 watering.



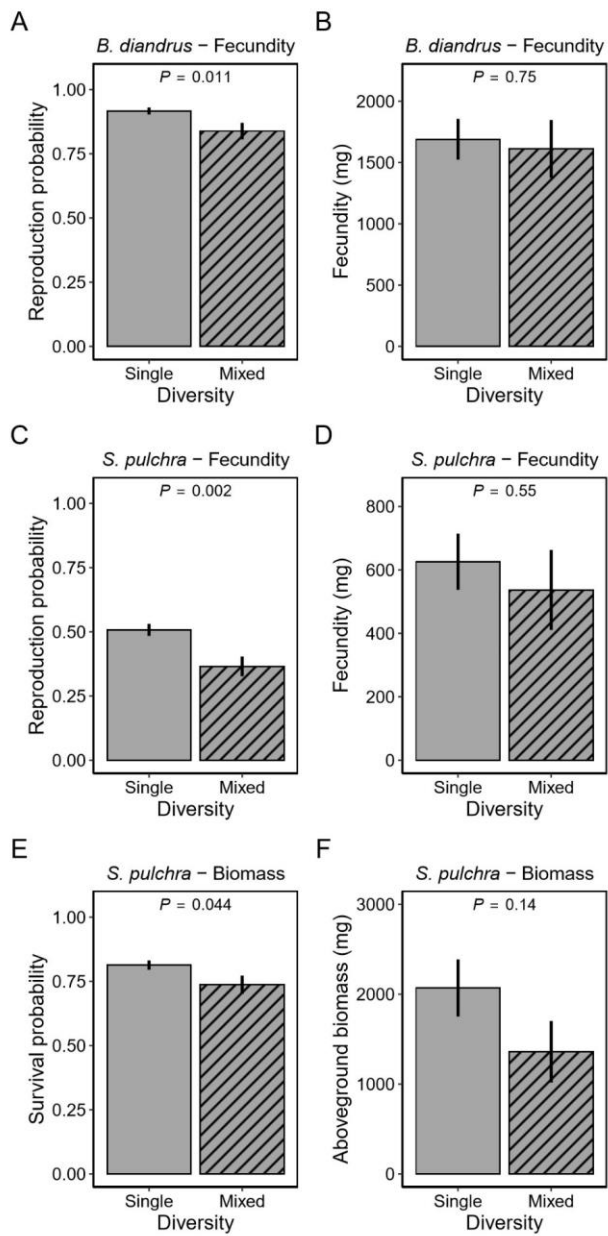
201  
 202 **Figure S4. Estimated marginal mean emergence probability  $\pm$  SE in neighbor**  
 203 **treatments in (A) *B. diandrus* and (B) *S. pulchra*.** *P*-values are for the neighbor treatment  
 204 term from generalized linear mixed models (GLMMs) testing the effects of neighbor  
 205 treatment, seed mass, and neighbor treatment  $\times$  seed mass interaction on emergence  
 206 probability. Two types of post hoc tests are shown: 1) neighbor presence vs. absence  
 207 (indicated above neighbor absent treatment; significance: †*P* < 0.1, \**P* < 0.05, \*\**P* < 0.01,  
 208 \*\*\**P* < 0.001); 2) pairwise comparisons among the eight neighbor-present treatments (letters  
 209 indicate significant differences). Dark grey and light grey bars represent native and non-  
 210 native neighbor treatments, respectively; striped and non-striped bars represent mixed species  
 211 and single species treatments, respectively; blue represents the neighbor-absent treatment.  
 212 Neighbor treatment codes: ABS = Neighbor-absent; BRCA = *Bromus carinatus*; FEMI =  
 213 *Festuca microstachys*; HOBR = *Hordeum brachyantherum*; NATMIX = Native mixture;  
 214 BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*;  
 215 NONMIX = Non-native mixture.



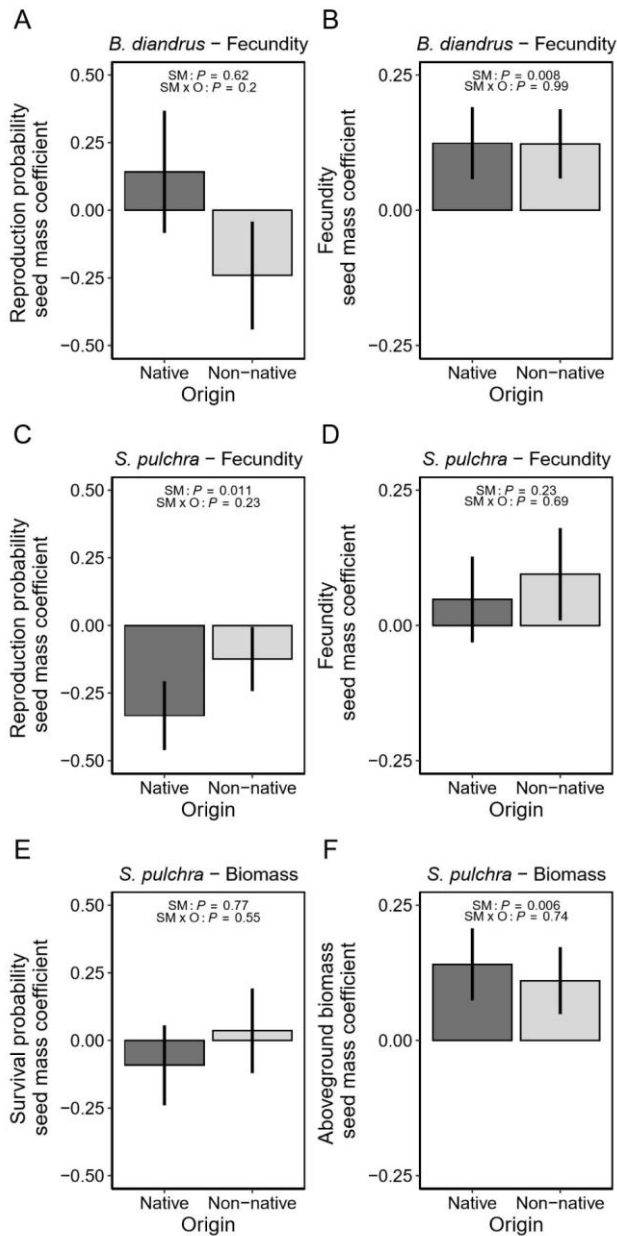
216  
 217 **Figure S5. Estimated marginal mean emergence time  $\pm$  SE in neighbor treatments in**  
 218 **(A) *B. diandrus* and (B) *S. pulchra*.** *P*-values are for the neighbor treatment term from linear  
 219 mixed models (LMMs) testing the effects of neighbor treatment, seed mass, and neighbor  
 220 treatment  $\times$  seed mass interaction on emergence time. Dark grey and light grey bars represent  
 221 native and non-native neighbor treatments, respectively; striped and non-striped bars  
 222 represent mixed species and single species treatments, respectively; blue represents the  
 223 neighbor-absent treatment. Neighbor treatment codes: ABS = Neighbor-absent; BRCA =  
 224 *Bromus carinatus*; FEMI = *Festuca microstachys*; HOBR = *Hordeum brachyantherum*;  
 225 NATMIX = Native mixture; BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU  
 226 = *Hordeum murinum*; NONMIX = Non-native mixture.



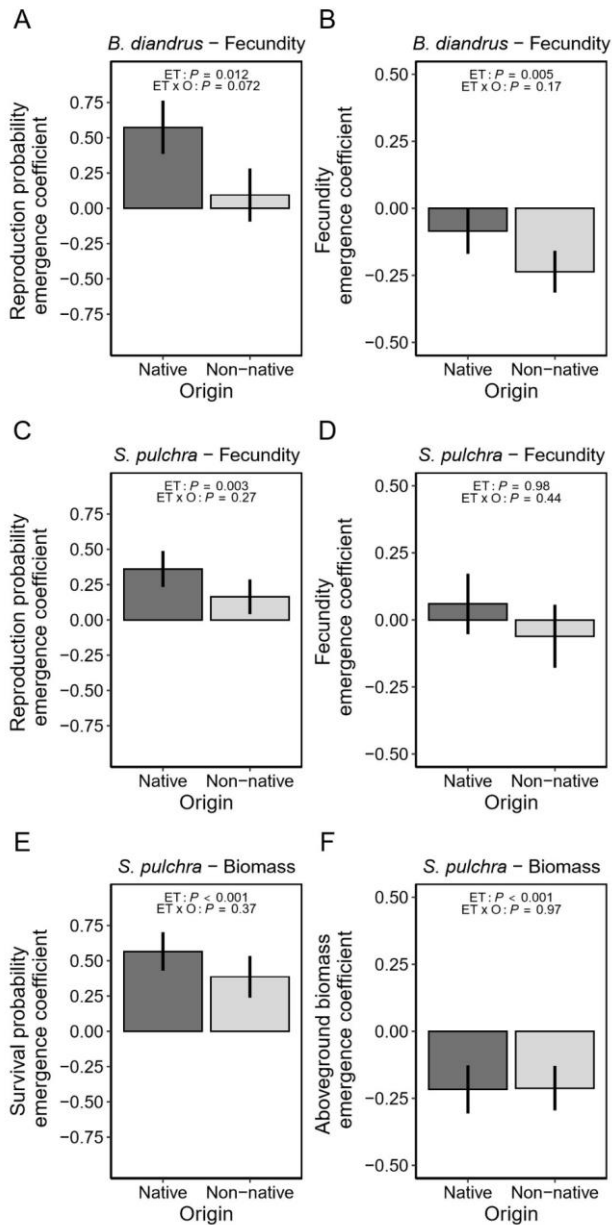
227  
 228 **Figure S6. Estimated marginal mean fitness  $\pm$  SE in neighbor origin status in (A, B) *B.***  
 229 ***diandrus* and (C – F) *S. pulchra*. P-values are from hurdle generalized linear mixed models**  
 230 **(GLMMs) testing the effects of neighbor origin on fitness components.**



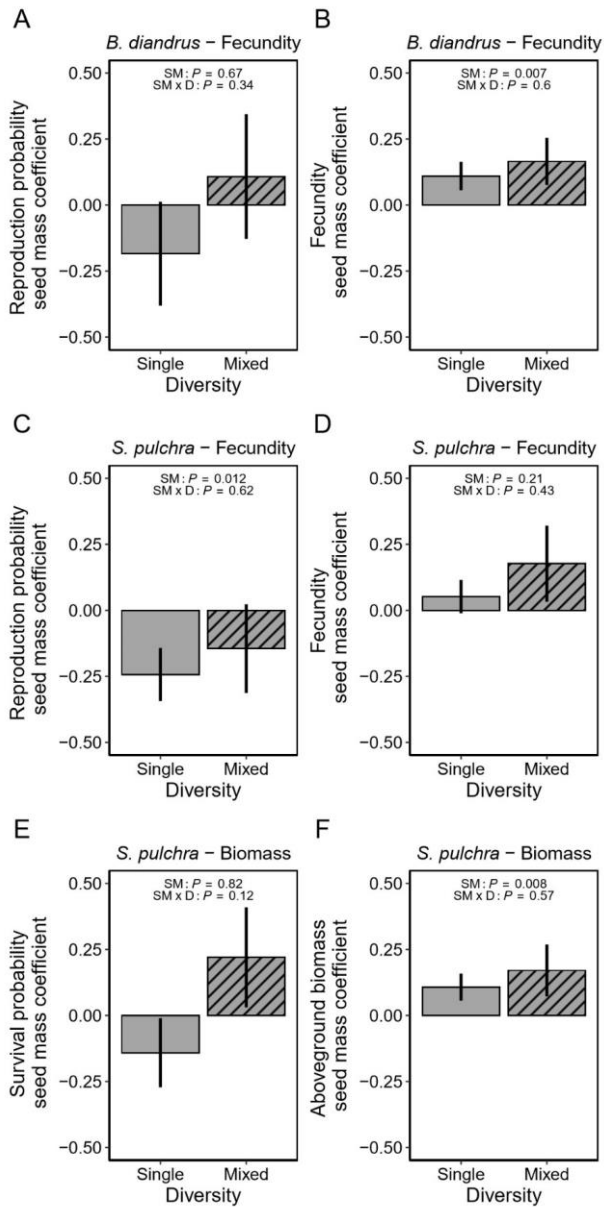
231  
 232 **Figure S7. Estimated marginal mean fitness  $\pm$  SE in neighbor diversity level in (A, B) *B.***  
 233 ***diandrus* and (C – F) *S. pulchra*. P-values are from hurdle generalized linear mixed models**  
 234 **(GLMMs) testing the effects of neighbor diversity on fitness components.**



235  
 236 **Figure S8. Seed mass selection coefficients  $\pm$  SE from hurdle GLMMs in neighbor origin**  
 237 **status in (A, B) *B. diandrus* and (C – F) *S. pulchra*.  $P$ -values are for the seed mass (SM)**  
 238 **and seed mass  $\times$  neighbor origin interaction (SM  $\times$  O) terms in hurdle GLMMs testing the**  
 239 **effects of seedling traits (seed mass and emergence time), neighbor origin, and the trait  $\times$**   
 240 **neighbor origin interactions.**

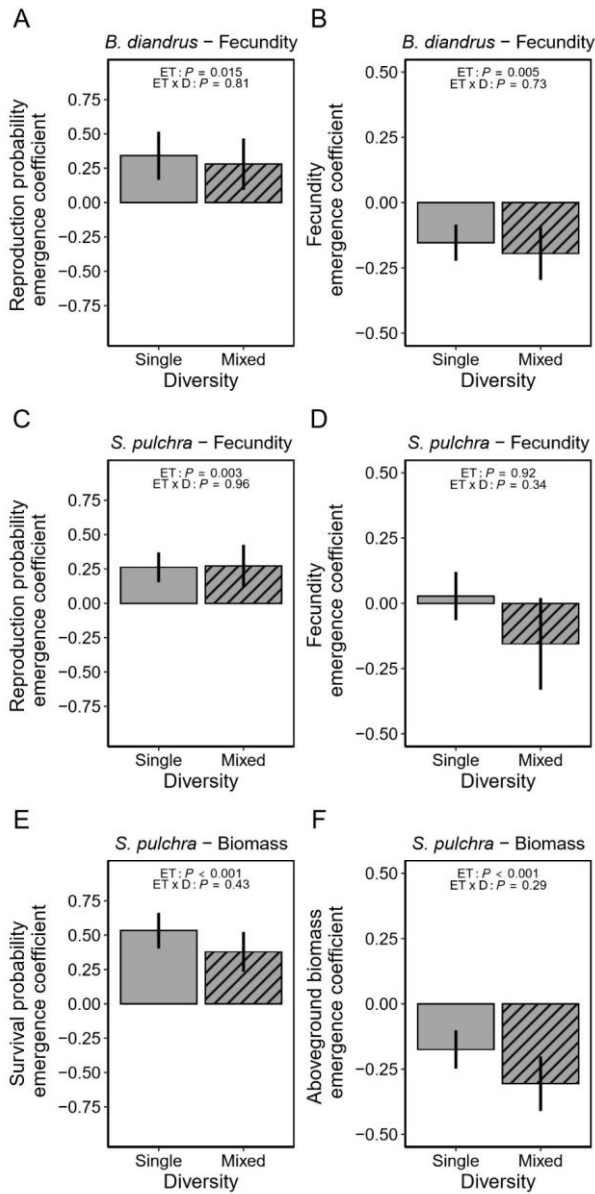


241  
 242 **Figure S9. Emergence time selection coefficients  $\pm$  SE from hurdle GLMMs in neighbor**  
 243 **origin status in (A, B) *B. diandrus* and (C – F) *S. pulchra*. P-values are for the emergence**  
 244 **time (ET) and emergence time  $\times$  neighbor origin interaction (ET  $\times$  O) terms in hurdle**  
 245 **GLMMs testing the effects of seedling traits (seed mass and emergence time), neighbor**  
 246 **origin, and the trait  $\times$  neighbor origin interactions.**

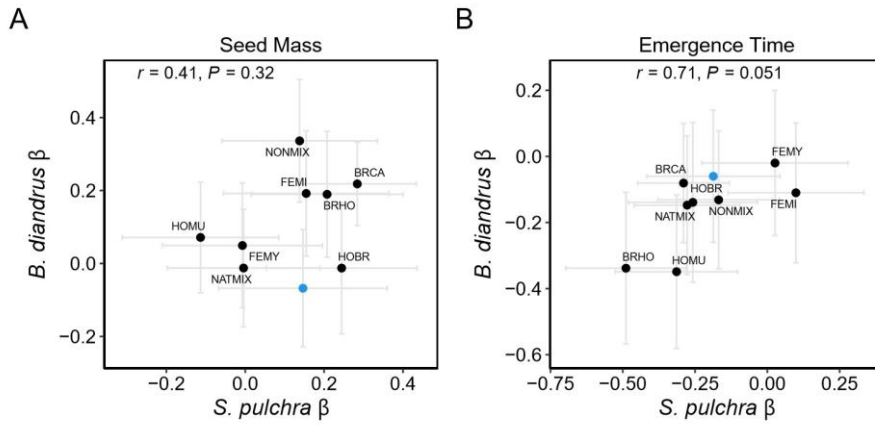


247  
 248 **Figure S10. Seed mass selection coefficients  $\pm$  SE from hurdle GLMMs in neighbor**  
 249 **diversity level in (A, B) *B. diandrus* and (C – F) *S. pulchra*. P-values are for the seed mass**  
 250 **(SM) and seed mass  $\times$  neighbor diversity interaction (SM  $\times$  D) terms in hurdle GLMMs**  
 251 **testing the effects of seedling traits (seed mass and emergence time), neighbor diversity, and**  
 252 **the trait  $\times$  neighbor diversity interactions.**





253  
 254 **Figure S11. Emergence time selection coefficients  $\pm$  from hurdle GLMMs in neighbor**  
 255 **diversity level in (A, B) *B. diandrus* and (C – F) *S. pulchra*. P-values are for the emergence**  
 256 **time (ET) and emergence time  $\times$  neighbor diversity interaction (ET  $\times$  D) terms in hurdle**  
 257 **GLMMs testing the effects of seedling traits (seed mass and emergence time), neighbor**  
 258 **diversity, and the trait  $\times$  neighbor diversity interactions.**



259

260 **Figure S12. Association between selection gradients ( $\beta \pm SE$ ) in *S. pulchra* (based on**  
 261 **biomass) and *B. diandrus* in neighbor-present treatments for (A) seed mass and (B)**  
 262 **emergence time.** Selection gradients in the neighbor-absent treatment are shown for  
 263 reference (blue points). Neighbor treatment codes: BRCA = *Bromus carinatus*; FEMI =  
 264 *Festuca microstachys*; HOB = *Hordeum brachyantherum*; NATMIX = Native mixture;  
 265 BRHO = *Bromus hordeaceus*; FEMY = *Festuca myuros*; HOMU = *Hordeum murinum*;  
 266 NONMIX = Non-native mixture.