

1 **Title**

2 Character displacement in the presence of multiple trait differences: Evolution of the storage
3 effect in germination and growth
4

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20 **Abstract**

21 Ecological character displacement is a prominent hypothesis for the maintenance of ecological
22 differences between species that are critical to stable coexistence. Models of character
23 displacement often ascribe interspecific competitive interactions to a single character, but
24 multiple characters contribute to competition, and their effects on selection can be nonadditive.
25 Focusing on one character, we ask if other characters that affect competition alter evolutionary
26 outcomes for the focal character. We address this question using the variable environment seed
27 bank model for two species with two traits. The focal trait is the temporal pattern of germination,
28 which is evolutionary labile. The other trait is the temporal pattern of plant growth, which is
29 assumed fixed. We ask whether evolutionary divergence of germination patterns between species
30 depends on species differences in plant growth. Patterns of growth can affect selection on
31 germination patterns in two ways. First, cues present at germination can provide information
32 about future growth. Second, germination and growth jointly determine the biomass of plants,
33 which determines demand for resources. Germination and growth contribute to the selection
34 gradient in distinct components, one density-independent and the other density-dependent.
35 Importantly, the relative strengths of the components are key. When the density-dependent
36 component is stronger, displacement in germination patterns between species is larger. Stronger
37 cues at germination strengthen the density-independent component by increasing the benefits of
38 germinating in years of favorable growth. But cues also affect the density-dependent component
39 by boosting a species' biomass, and hence its competitive effect, in good years. Consequently,
40 cues weaken character displacement when growth patterns are similar for two competitors, but
41 favor displacement when growth patterns are species-specific. Understanding how these
42 selection components change between contexts can help understand the origin and maintenance
43 of species differences in germination patterns in temporally fluctuating environments.
44

45 **Keywords:** Divergent evolution, predictive germination, competition, coexistence, adaptive
46 dynamics, variable environment

47 **1. Introduction**

48 Ecological differences between species are the foundation for the coexistence of competitors
49 (Chesson 2000). How these differences arise is of great interest to understanding the
50 maintenance of species diversity in nature. One hypothesis is divergent selection between species
51 inhabiting different environments (Schluter 2000b, ch. 4). An alternative is ecological character
52 displacement (hereafter simply “character displacement”), in which between-species competitive
53 interactions favor the evolution of ecological differences (Brown and Wilson 1956, Slatkin 1980,
54 Abrams 1986). Between-species competitive interactions can be a powerful diversifying agent
55 because they have the potential to enhance pre-existing differences, thereby strengthening
56 coexistence mechanisms beyond the minimum necessary to allow two or more species to live
57 together in the same habitat (Pfennig and Pfennig 2009). Moreover, character displacement
58 potentially contributes to the process of ecological speciation (Doebeli and Dieckmann 2000,
59 Pfennig and Pfennig 2010). Therefore, it may play a role in both the origin and maintenance of
60 species diversity.

61
62 Despite the long history of character displacement as a concept (Brown and Wilson 1956, Dayan
63 and Simberloff 2005, Stuart and Losos 2013), theory has not dealt with the many biological
64 realities of competition, due in large part to a focus on Lotka-Volterra models (Dayan and
65 Simberloff 2005). In these models, interspecific competition increases with niche overlap, which
66 is assumed to be high when species are similar in character, often described as body size (Slatkin
67 1980). MacArthur (1970, 1972) provided justification for this approach by showing that
68 competition between two species for a suite of resources can, under certain assumptions, be
69 studied using Lotka-Volterra models. Lotka-Volterra style models have been enormously
70 influential (Dayan and Simberloff 2005), but they may be limited in their current use because
71 they do not account for the fact that competition often results from the combined action of
72 multiple traits (Kraft et al. 2015, Kunstler et al. 2016). Yet, empirical studies of character
73 displacement do consider multiple characters (e.g., see Stuart et al. 2014, Kooyers et al. 2017)
74 sometimes reducing the dimensionality of multidimensional trait data using ordination methods
75 (Grant and Grant 2006). Regardless, biologists recognize the importance of multiple traits in
76 sculpting competitive interactions. This raises the question, does character displacement proceed
77 differently when multiple traits jointly affect competition?

78
79 Although it is simpler to study one trait at a time, a multi-trait perspective is often necessary,
80 since traits may often interactively influence evolutionary outcomes. Traits can be in
81 physiological conflict, where some combinations are physiologically impossible under finite
82 resources. For example, increasing survival and reproduction are both advantageous, but
83 resource allocation under finite resources means that both cannot be maximized together
84 (Williams 1966, Morrissey et al. 2012). Traits can also be in genetic conflict, as in the case of
85 antagonistic pleiotropy (Keith and Mitchell-Olds 2019) or linkage disequilibrium. Furthermore,
86 ecological context can put traits in selective conflict, leading to evolutionary responses that do
87 not represent selection on each trait alone (Lande and Arnold 1983). Selective conflicts
88 originating with the ecology of competition between species are our focus.

89
90 Annual plants in arid environments provide an example where two traits jointly affect
91 competition. These traits are yearly patterns of germination and growth, both of which are
92 strongly affected by the physical environment (Venable and Kimball 2013) and have key roles in

93 species coexistence mechanisms (Angert et al. 2009). Annual plant demography in arid
94 environments is notably variable, with germination, seedling survival, and reproduction changing
95 each year in response to between-year variation in abiotic conditions (Went 1949). Germination
96 and growth influence competition because they each affect the standing biomass—and thus
97 demand for resources—in the community in any year. All else equal, years favorable to seed
98 germination increase plant density and competition for resources. Likewise, years of more
99 vigorous plant growth increase demand for resources per unit plant density. Empirical (Angert et
100 al. 2009, Holt and Chesson 2014) and theoretical work (Chesson et al. 2005) suggest that
101 species-specific germination and growth responses contribute to stable coexistence in these
102 communities via the temporal storage effect, which is a form of temporal niche partitioning
103 (Chesson et al. 2013).

104
105 We do not yet know the origin of species-specific differences in germination and plant growth,
106 but character displacement may be involved. Abrams et al. (2013) showed that the storage effect
107 may evolve in an analogous way to character displacement for resources using a stochastic
108 model with two environment types and two species of perennial organisms. They found that a
109 requirement for the evolution of species-specific differences is that phenotypes trade off in
110 performance in alternative environments. Similar outcomes hold for models with deterministic
111 seasonal variation (Kremer and Klausmeier 2017, Miller and Klausmeier 2017) and deterministic
112 within-year variation (Mathias and Chesson 2013). However, in annual plants, species-specific
113 responses exist for two demographic responses, germination and plant growth (Angert et al.
114 2009), which prior theory does not account for. Furthermore, there is reason to expect these
115 differences may be in conflict.

116
117 Previous theory and experiments predict that germination timing should align with times when
118 plants grow best (Donohue 2002), which is sometimes referred to as predictive germination
119 (Snyder and Adler 2011, Gremer et al. 2016). The timing of germination has enormous
120 consequences for plant fitness (Gremer et al. 2020) in no small part because germination timing
121 sets the environmental conditions a plant experiences as it grows (Donohue et al. 2005). Plant
122 growth strategies that are poorly matched with germination timing are likely to be disfavored by
123 selection (Donohue et al. 2010), resulting in a positive correlation between plant yield and the
124 germination fraction between years (Cohen 1967). Importantly, predictive germination may only
125 evolve when there is a cue at the time of germination that provides information about future
126 growing conditions (Cohen 1967).

127
128 In some circumstances, selection for predictive germination may be at odds with character
129 displacement. Divergent character displacement favors differences between species. Selection on
130 germination patterns favors predictive germination in models without competition. When species
131 have similar plant growth strategies, selection favoring predictive germination increases species
132 similarity in germination (Donohue et al. 2010, Huang et al. 2016). Hence, selection on
133 predictive germination suggests that character displacement may only be possible for species that
134 are already different when they come into contact. This prediction suggests an interesting
135 conflict with the theory of character displacement. Commonly, character displacement is thought
136 to be strongest for similar species because they are most likely to compete for resources
137 (Schluter 2000a, Pfennig and Pfennig 2010), although convergent character displacement is also
138 possible (Abrams 1986, Fox and Vasseur 2008). Here, we investigate this selective conflict

139 using models, asking about the role of two traits, and how the initial similarity of one trait affects
140 selection for character displacement in another.

141
142 Our investigation of the effects of one trait on character displacement in another uses a model of
143 annual plant dynamics in a yearly fluctuating environment. We characterize germination and
144 plant growth as functions of the environment, which fluctuates over time. Traits, which are
145 represented in the model as parameters of these functions, determine the temporal pattern of
146 variation in germination and plant growth, given the underlying environmental variation. These
147 traits are best considered as each species' germination and growth niches. Of most interest is
148 how the germination niches are related between species, which can be measured by the
149 correlations between their temporal germination patterns. To maintain tractability of our
150 analysis, we allow the temporal patterns of germination for both species to coevolve in our
151 model, and we fix differences between species in their temporal patterns of growth. The
152 overriding question is whether the coevolutionary trajectories of species in one trait (temporal
153 patterns of germination) are influenced by the presence and difference between species in
154 another trait (temporal patterns of plant growth). We also evaluate the ecological effects of
155 coevolution by measuring changes in the strength of the storage effect and species average
156 fitness differences (Chesson 2018).

157 158 **2. Model**

159 *2.1 Ecological Dynamics*

160 Ecological dynamics follow a two-species seed bank model in a fluctuating environment. We
161 describe population density of each species j ($j = 1, 2$), $N_j(t)$, as the density of seeds present in the
162 soil just prior to the start of the growing season for year t . For annual plants, the entire population
163 is present as seeds at this time, and so $N_j(t)$ then measures the entire population of species j . A
164 seed in year t can follow one of two fates during the growing season. It may germinate with
165 probability $G_j(t)$ or remain dormant with probability $1 - G_j(t)$. Germination (and dormancy) are
166 functions of t , indicating their dependence on environmental conditions that fluctuate from year
167 to year. A fraction s of the seed that remains dormant survives to the following growing season.
168 A seed that germinates becomes a plant that grows, sets seed, and then dies. We assume that a
169 plant of species j grows to reach biomass $V_j(t)$ in the absence of competition. The quantity, $V_j(t)$,
170 is called "vigor" in the terminology of Chesson et al. (2005). Like germination, vigor varies in
171 response to fluctuating environmental conditions and so is time-dependent, defining the temporal
172 pattern (year to year pattern) of plant growth for the species.

173
174 Plants of species j growing alone without competition would produce y_j seeds per-unit biomass.
175 However, competition reduces seed yield per-unit biomass to $y_j/C'(t)$, where $C'(t)$ is the intensity
176 of competition. Hence, a plant's realized seed yield is $y_j V_j(t)/C'(t)$ and the total seed yield for a
177 species in year t is $[y_j/C'(t)]V_j(t)G_j(t)N_j(t)$. The density of seeds the following growing season is
178 thus

$$179 \quad N_j(t+1) = \lambda_j(t)N_j(t), \quad (1)$$

180 where

$$181 \quad \lambda_j(t) = s(1 - G_j(t)) + y_j V_j(t)G_j(t) / C'(t). \quad (2)$$

182 This quantity $\lambda_j(t)$ is the fitness of a seed of species j and equation (2) represents it as a weighted
183 average of seed survival and yield, the weights being $1 - G_j(t)$ and $G_j(t)$.

184

185 We assume that larger individuals demand more resources and so have larger competitive effect.
 186 To incorporate this assumption, the total competitive effect (accounting for both species) in year
 187 t is proportional to the total biomass density of growing plants across both species, i.e.,
 188 $N_1(t)G_1(t)V_1(t) + N_2(t)G_2(t)V_2(t)$. We write the competitive effect in year t as

$$189 \quad C'(t) = 1 + \alpha(G_1(t)V_1(t)N_1(t) + G_2(t)V_2(t)N_2(t)), \quad (3)$$

190 where α is the competition coefficient per-unit biomass. $C'(t) = 1$ for zero plant density
 191 (individual yield in this case is $y_j V_j(t)$), and C' increases with the biomass of plants, irrespective
 192 of species identity. It is important to highlight here that per unit competitive effects are the same
 193 for both species, which means that species do not coexist in the absence of temporal variation in
 194 this model. Species coexist only when the environment fluctuates and responses to the
 195 environment are species-specific.

196 197 *2.2 Germination and Vigor Distributions*

198 Germination and vigor responses, being variable over time, are best modeled as stochastic
 199 processes defined by statistical distributions. For simplicity, we assume values of the process
 200 fluctuate independently from year to year and have the same probability distribution for each of
 201 the two species. The processes are not necessarily independent between species, however,
 202 allowing the temporal patterns of fluctuation to differ between species to an extent that depends
 203 on the between-species correlation (i.e., their cross-correlation over years). Because the
 204 distributions are the same, the means, variances, and higher moments are the same for both
 205 species. Although differences between distributions would contribute to differences between
 206 species in germination responses, the key issue here is differences in their patterns of variation
 207 over time, which is defined adequately by the between-species correlation to a first order of
 208 approximation. Vigor distributions are assumed to be fixed traits of species, meaning they do not
 209 evolve. All distributions are identical and independently distributed over time (i.i.d.), reflecting
 210 the common assumption that the environment is stationary with no temporal autocorrelation.
 211 However, temporal patterns of germination evolve over time, leading to changes in the between-
 212 species correlation. Nonetheless, we assume that the underlying environmental factors are i.i.d.
 213 (as discussed below), meaning germination distributions are stationary at any given trait value.

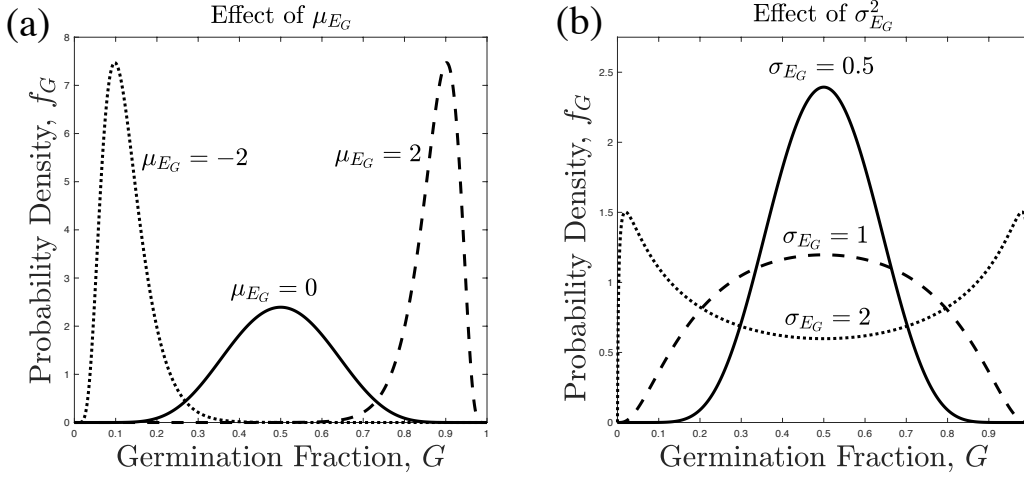
214
 215 We model germination as Johnson S_B distributions (Johnson 1994, pg. 34), which are
 216 transformations of normally distributed variables to a specified range. The germination fraction
 217 of species j can be written as

$$218 \quad G_j(t) = \frac{e^{E_{G_j}(t)}}{1 + e^{E_{G_j}(t)}}, \quad (4)$$

219 where $E_{G_j}(t)$ is a normally distributed variable with mean μ_{E_G} and variance $\sigma_{E_G}^2$, and $0 < G_j < 1$
 220 (see SI S1, “The Johnson S_B distribution” for details). In the parlance of coexistence theory, E_G is
 221 an environmental response. Larger values of E_G correspond to larger germination fractions.
 222 Because G is a nonlinear transformation of E_G , μ_{E_G} is not the mean of G but instead determines
 223 the median G , which is $\exp(\mu_{E_G}) / [1 + \exp(\mu_{E_G})]$ (Fig 1a). Similarly, $\sigma_{E_G}^2$ is not the variance of
 224 G , as normally defined, but is the variance on the log-odds scale. The distribution of G is
 225 unimodal for small $\sigma_{E_G}^2$ and bimodal for large $\sigma_{E_G}^2$ (Fig 1b).

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Figure 1. Density functions for the Johnson S_B germination distributions. (a) Unimodal distributions showing effect of μ_{E_G} with small $\sigma_{E_G}^2 = 0.5$ and (b), the effect of σ_{E_G} with fixed $\mu_{E_G} = 0$.

We model plant size distributions as lognormal, which means vigor is normal on the log scale. Vigor for species j can thus be written as

$$V_j(t) = \exp(E_{V_j}(t)), \quad (5)$$

where $E_{V_j}(t)$ is a normally distributed variable with mean $\mu_{E_{V_j}}$ and variance $\sigma_{E_{V_j}}^2$. As with G , $\mu_{E_{V_j}}$ is not the mean of V , but rather determines the median V , which is $\exp(\mu_{E_{V_j}})$. Likewise, $\sigma_{E_{V_j}}^2$ is the variance of V on the log scale.

2.3 Correlations Between Species and Between Traits Within Species

Character displacement reflects the fitness benefits of niche differentiation, which in a fluctuating environment occurs via differential responses of species to shared environmental factors. Traditionally, these differential responses are referred to in storage effect theory as species-specific environmental responses (Chesson et al. 2013). For questions of selection, we need a model of environmental responses where evolutionary change can either bring about or erode species-specific differences.

We model each environmental response as a linear combination of two environmental factors, with species having potentially different sensitivities to these factors. The equation for a species' germination response is

$$E_{G_j}(t) = \mu_{E_G} + \sigma_{E_G} (e_{j1}X_1(t) + e_{j2}X_2(t)), \quad (6)$$

where e_{jk} is species j 's germination sensitivity to environmental factor X_k , which is standard normal. We assume that X_1 and X_2 are independent of one another and independent and identically distributed (i.i.d.) over time. Here, μ_{E_G} is the mean of E_G . We constrain the environmental sensitivities such that $e_{j1}^2 + e_{j2}^2 = 1$, meaning that σ_{E_G} is the standard deviation of E_G (setting $\sigma_{E_G} = 0$ gives a model of constant germination each year). Vigor responses are modeled similarly. The equation for a species' vigor response is

257
$$E_{V_j}(t) = \mu_{E_V} + \sigma_{E_V} (v_{j1}Z_1(t) + v_{j2}Z_2(t)), \quad (7)$$

258 where v_{jk} is species j 's vigor sensitivity to environmental factor Z_k , which is also standard
 259 normal. Here, we also assume Z_1 is independent of Z_2 and i.i.d. over time. We place the same
 260 constraint on vigor sensitivities ($v_{j1}^2 + v_{j2}^2 = 1$), meaning that μ_{E_V} and σ_{E_V} are the mean and
 261 standard deviation of E_V (setting $\sigma_{E_V} = 0$ gives a model of constant plant growth each year).

262
 263 The specifics of the model are summarized in Table 1, but a biological interpretation is as
 264 follows. Environmental factors (e.g., temperature and the timing of rainfall) vary year-to-year
 265 and with each species responding to these with some sensitivity determined by the traits of the
 266 species. The traits are not explicitly defined but we interpret them to be traits associated with
 267 common plant growth strategies, such as leaf traits (Westoby and Wright 2006), and seed
 268 germination strategies, such as seed size, seed coat thickness and biochemical responses to
 269 environmental cues (Baskin and Baskin 2014, chs. 4, 5, and 6). Different trait values yield
 270 different sensitivities to the environment and therefore different patterns of germination and
 271 vigor over time (i.e., species-specific environmental responses). Natural selection acts on
 272 phenotypic variation in the germination sensitivities, and so germination patterns evolve—as
 273 well as correlations between species—while vigor sensitivities are fixed properties of the species
 274 and so do not evolve.

275
 276 The constraint on environmental sensitivities fundamentally represents a tradeoff between
 277 phenotypes in performance across different year types. Increasing sensitivity to any one
 278 environmental variable comes with reduced sensitivity to the other. This means that we can
 279 reduce each species' two-dimensional sensitivities to a single dimensional quantity representing
 280 the angle of the sensitivities in polar coordinates. The angle is $\theta_{Gj} = \arctan(e_{j1}/e_{j2})$ ($-\pi/2 \leq \theta_G \leq$
 281 $\pi/2$) for germination (Fig 2a) and $\theta_{Vj} = \arctan(v_{j1}/v_{j2})$ ($-\pi/2 \leq \theta_V \leq \pi/2$) for vigor.

282
 283 The angular representation has the advantage of being a single value to represent the temporal
 284 niche of each species. As such, we will refer to θ_{Gj} as the *germination strategy* of species j and
 285 θ_{Vj} as the *vigor strategy* of species j . The reasoning is that species with different values of θ_G
 286 respond differently to the same environmental state whereas two species with similar values of
 287 θ_G respond similarly to the same environmental state (Fig 2). As a more concrete interpretation, one
 288 could consider the values of θ_G as representing points along a continuum of species' germination
 289 preference for temperature, which previous studies have shown differ among species in desert
 290 annual communities (Adondakis and Venable 2004, Facelli et al. 2005, Venable 2007, Chesson
 291 et al. 2013).

292
 293 Using the polar coordinate representation of germination sensitivities, the between-species
 294 correlation in germination fractions over time can be written as

295
$$\text{Corr}(E_{G_1}(t), E_{G_2}(t)) = \cos(\theta_{G_1} - \theta_{G_2}) \quad (8)$$

296 (derivation in SI section S2). Eqn (8) is a decreasing function of the difference in the angles $\theta_{G_1} -$
 297 θ_{G_2} (Fig 2b), implying that species with larger differences in germination strategies are less
 298 similar in their germination patterns over time. Since the cosine function is symmetric about 0,
 299 only the magnitude of $\theta_{G_1} - \theta_{G_2}$ —and not the sign—determines the correlation. Germination
 300 patterns are identical when $\theta_{G_1} = \theta_{G_2}$, (see Fig 2c), independent when $|\theta_{G_1} - \theta_{G_2}| = \pi/2$, (Fig 2d),
 301 and exactly opposite when $|\theta_{G_1} - \theta_{G_2}| = \pi$ (Fig 2e). Importantly, the strength of the storage effect

302 increases with $|\theta_{G1} - \theta_{G2}|$. Just like germination, vigor responses have between-species
 303 correlation

304
$$\text{Corr}(E_{V_1}(t), E_{V_2}(t)) = \cos(\theta_{V_1} - \theta_{V_2}), \quad (9)$$

305 which has the same behavior as Eqn (8).

306

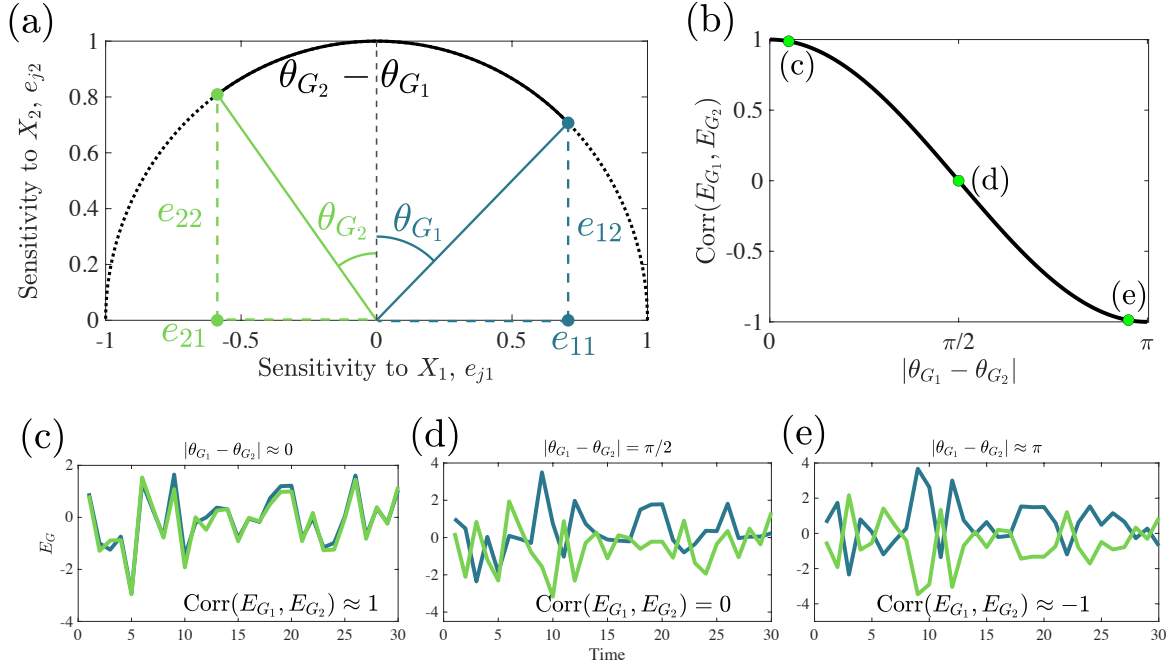
307 Table 1. Notation and description of model components.

Variables/ Parameter	Description	Formula/Parameter Range
$G_j(t)$	Germination fraction of species j in year t	$G_j(t) = e^{E_{G_j}(t)} / (1 + e^{E_{G_j}(t)})$
$V_j(t)$	Plant biomass in the absence of competition of species j in year t (vigor)	$V_j(t) = e^{E_{V_j}(t)}$
$E_{G_j}(t)$	Species j 's germination response in year t (log-odds $G_j(t)$)	$E_{G_j}(t) = \mu_{E_G} + \sigma_{E_G} (e_{j1}X_1(t) + e_{j2}X_2(t))$
$E_{V_j}(t)$	Species j 's vigor response in year t ($\ln V_j(t)$)	$E_{V_j}(t) = \mu_{E_V} + \sigma_{E_V} (v_{j1}Z_1(t) + v_{j2}Z_2(t))$
μ_{E_G}, μ_{E_V}	Mean environmental responses of germination and vigor, respectively.	$-\infty < \mu_{E_G} < \infty, -\infty < \mu_{E_V} < \infty,$
$\sigma_{E_G}, \sigma_{E_V}$	Standard deviation of the environmental response of germination and vigor.	$\sigma_{E_G} \geq 0, \sigma_{E_V} \geq 0$
e_{jl}, v_{jl}	Sensitivity of species j 's germination, e (vigor, v) response to environmental factor l .	$-1 \leq e_{j1}, v_{j1} \leq 1, 0 \leq e_{j2}, v_{j2} \leq 1,$ $e_{j1}^2 + e_{j2}^2 = 1$ and $v_{j1}^2 + v_{j2}^2 = 1$
$X_l(t), Z_l(t)$	Environmental factors affecting germination (X) and plant size (Z)	$X_l \sim N(0,1)$ $Z_l \sim N(0,1)$ for all and t .
ρ	Correlation between environments affecting germination and vigor	$\rho = \text{Corr}(X_1, Z_1) = \text{Corr}(X_2, Z_2); 0 \leq \rho < 1$
$\theta_{G_j}, \theta_{V_j}$	Germination and vigor strategies, respectively, of species j	$\theta_{G_j} = \arctan(e_{j1} / e_{j2}), -\frac{\pi}{2} \leq \theta_{G_j} \leq \frac{\pi}{2}$ $\theta_{V_j} = \arctan(v_{j1} / v_{j2}), -\frac{\pi}{2} \leq \theta_{V_j} \leq \frac{\pi}{2}$
y_j	Seed yield per unit biomass of a plant of species j	$y_j > 0$
β_j^\dagger	Equilibrium fraction of seed lost from the seed bank	$\beta_j = 1 - s(1 - G_j^*)$
γ_j	Buffered population growth	$\beta_j(1 - \beta_j)$

308 [†]Details in SI S4.

309

310



311
 312 Figure 2. Relationship between environmental sensitivities, species traits, and patterns of
 313 environmental responses. (a) A plot of the environmental sensitivities on each axis for two species,
 314 species 1 in blue and species 2 in green. The black dotted line illustrates the constraint $e_{j1}^2 + e_{j2}^2 = 1$.
 315 θ_{G_j} is the angle of the point (e_{j1}, e_{j2}) relative to the vertical dashed line. The differences between θ 's of
 316 the two species give a measure of the difference between species along the trade-off. (b) The
 317 correlation between two species' germination responses declines with differences in θ 's. Examples
 318 of a time-series of germination responses for (c) small trait differences, (d) intermediate trait
 319 differences, and (e) near maximum trait differences.

320
 321 This model, while appearing complicated, has the benefit that predictive germination evolves as
 322 germination strategies (θ_G) evolve with fixed vigor strategies (θ_V). Predictive germination occurs
 323 because the conditions at the time of germination contain information about future growing
 324 conditions. We describe this information content by $\rho = \text{Corr}(X_l, Z_l)$ ($l = 1, 2$) [note $\text{Corr}(X_k, Z_l) =$
 325 0 for $k \neq l$], the correlation between environmental factors acting during germination and growth
 326 (details in SI section S3). In short, ρ is the strength of an environmental cue. Predictive
 327 germination is proportional to ρ , which can be seen because the correlation between germination
 328 and vigor responses can be written as

329
$$\text{Corr}(E_{G_j}(t), E_{V_j}(t)) = \rho \cos(\theta_{G_j} - \theta_{V_j}) \quad (10)$$

330 (derivation in SI section S2). From Eqn (10), it follows that predictive germination is maximized
 331 when the germination and vigor strategies are aligned, i.e., $\theta_G = \theta_V$. Predictive germination in this
 332 case is $\text{Corr}(E_G, E_V) = \rho$. Thus, selection favoring predictive germination reduces $|\theta_{G_j} - \theta_{V_j}|$. If $\rho =$
 333 0 , there is no cue about future growing conditions, and $\text{Corr}(E_G, E_V) = 0$ regardless of the values
 334 of θ_G and θ_V .

335
 336 The model of environmental responses, which are linear combinations of independent standard
 337 normal variables, is sufficient to model all possible correlations between germination and vigor

338 for two species (for a technical explanation, see SI section S3). In particular, this model ensures
 339 that all correlations in the model are self-consistent and have a simple form related to evolving
 340 traits of species. The model is sufficiently general to account for other environmental
 341 possibilities. For example, it is likely that more than two environmental variables (possibly
 342 correlated) determine germination for real organisms. However, the two environmental factors
 343 X_1 and X_2 can be considered as a dimensional reduction of a more complex environment that
 344 retains the information distinguishing the biology of two species. Alternatively, most of the
 345 variation in germination between species could be dominated by a single environmental variable,
 346 such as temperature at the time of rainfall. Our construction also accounts for this possibility.
 347 Details on these possibilities are discussed in SI section S3.

348

349 3. Analysis

350 Our interest is in how patterns of plant vigor, characterized by θ_V , influence selection on patterns
 351 of germination, characterized θ_G . We understand this relationship by way of the selection
 352 gradient for species j with respect to θ_{Gj} . The selection gradient is a valid predictor of
 353 evolutionary change given sufficiently small phenotypic variation (Abrams 2001) and predicts of
 354 evolutionary change in the absence of any non-selective constraints such as pleiotropy. Here,
 355 germination and vigor interact in their effect on selection when the selection gradient depends on
 356 θ_{Vj} . The role of interspecific competition can also influence selection, depending on the
 357 competitors' values of θ_G and θ_V .

358

359 When investigating the contribution of interspecific competition on selection, an accounting for
 360 intraspecific competition is necessary. We do this by comparing selection acting on a species
 361 growing alone (allopatry) and selection acting on species growing with interspecific competitors
 362 (sympatry). Evolutionary outcomes in allopatry reflect intraspecific, but not interspecific
 363 competition. Evolutionary outcomes in sympatry reflect the joint selective effects of intraspecific
 364 and interspecific competition. Provided that the environmental conditions are identical in
 365 sympatry and allopatry, differences in evolutionary outcomes represent the selective effects of
 366 interspecific competition (Goldberg and Lande 2006).

367

368 In a fluctuating environment, selection responds to the long-term growth rate, which integrates
 369 the effects of selection over changing environmental conditions. Assuming stationarity of the
 370 environment, the long-term growth rate is $\bar{r} = E[\ln \lambda(t)]$, the average of $r(t)$ (log-fitness in a year)
 371 over the distribution of environmental states. It predicts long-term growth of a population or
 372 lineage (Metz and Geritz 2016) and gives an adaptive topography for populations in quantitative
 373 genetics models (Lande 2007). We further assume that evolutionary trait responses to selection
 374 follow the assumptions of adaptive dynamics (Metz and Geritz 2016). Adaptive dynamics
 375 assumes haploid genetics and rare mutations of small effect, meaning the selection gradient is
 376 evaluated for a mutant phenotype θ'_{Gj} (present at effectively zero density) invading a population
 377 with resident phenotype θ_{Gj} , where the invader phenotype differs marginally from the resident.

378 To calculate the selection gradient, we need the long-term growth rate of the mutant phenotype
 379 \bar{r}'_j in the presence of the resident, which is

$$380 \quad \bar{r}'_j = E \left[\ln \left\{ s \left(1 - G'_j(t) \right) + \frac{y_j G'_j(t) V_j(t)}{1 + \alpha (G_1(t) V_1(t) N_1(t) + G_2(t) V_2(t) N_2(t))} \right\} \right]. \quad (11)$$

381 In expression (11), G_j' is the invader phenotype germination distribution with corresponding trait
 382 value θ'_{G_j} . Given the mutant has negligible density, it is absent from the competition term.

383
 384 In allopatry, only intraspecific competition occurs (i.e., $N_j > 0$ and $N_k = 0$ for $k \neq j$). In sympatry,
 385 both intraspecific and interspecific competition influence mutant fitness (i.e., $N_1 > 0$ and $N_2 > 0$).
 386 Mutant phenotypes increase in abundance when $\bar{r}_j' > 0$ and go extinct when $\bar{r}_j' < 0$.

387
 388 The derivative of expression (11) with respect to the invading phenotype, $d\bar{r}_j'/d\theta'_{G_j}$, once
 389 evaluated at a resident value for both species, gives the local selection gradient at the phenotype
 390 θ_{G_j} . Solutions to the selection gradient for θ_{G_j} represent candidate evolutionarily stable states
 391 (ESSs). Stability of each candidate ESS is determined by the curvature of the \bar{r}_j' near the ESS.
 392 Concave curvatures indicate that the ESS cannot be invaded by nearby strategies and so is
 393 locally stable. Convex curvature indicates locally unstable ESSs (see Metz and Geritz 2016 and
 394 references therein for background). Coevolutionary dynamics follow from single species
 395 selection applied to both species. Phenotypes at stable points for both species represent possible
 396 evolutionarily stable coalitions (ESC) (Dieckmann and Law 1996). Finally, note here that in our
 397 analyses and simulations, we never observed evidence for evolutionary branching, which is a
 398 prominent feature of adaptive dynamics models.

399 400 4. Results

401 4.1. Components of Selection

402 An approximate expression for the selection gradient uncovers two main components of
 403 selection, a density-independent (d.i.) component and a density-dependent (d.d.) component.
 404 These two components are helpful to distinguish because they represent two fundamentally
 405 different ways that germination and vigor together influence fitness. Moreover, they have
 406 different effects on species coexistence. Under the assumption of small environmental
 407 fluctuations, the selection gradient can be written as

$$408 \quad \frac{d\bar{r}_j'}{d\theta'_{G_j}} \approx \gamma_j \left[\underbrace{\frac{d}{d\theta'_{G_j}} \text{Cov}(E'_{G_j}, E_{V_j})}_{\text{independent of density}} - \underbrace{\frac{d}{d\theta'_{G_j}} \text{Cov}(E'_{G_j}, C)}_{\text{dependent on density}} \right], \quad (12)$$

409 where γ_j is a constant related to seed dormancy, called buffered population growth in the
 410 parlance of storage effect theory, and $C = \ln C'$ measures competition on the log-scale (derivation
 411 in SI S4). The constant γ_j is a scaling factor and so only the two terms in brackets determine the
 412 direction of selection.

413
 414 The first term of (12) is density-independent and measures the effect of the correlation between
 415 germination and vigor responses on selection. When present alone, it favors increased
 416 correlations between germination and vigor, i.e., predictive germination (see SI S5, “The single
 417 species case”). The d.i. component is proportional to ρ , the strength of the cue, which can be seen
 418 by noting that the d.i. component can be rewritten as

$$419 \quad \frac{d}{d\theta'_{G_j}} \text{Cov}(E'_{G_j}, E_{V_j}) = -\rho \sin(\theta'_{G_j} - \theta_{V_j}). \quad (13)$$

420 Eqn (13) is zero when $\rho = 0$, i.e., when there is no cue, which shows that selection acting on
421 predictive germination is conditional on a cue (Cohen 1967). When $\rho > 0$, Eqn (13) is positive
422 for $\theta'_{G_j} < \theta_{V_j}$, zero for $\theta'_{G_j} = \theta_{V_j}$, and negative for $\theta'_{G_j} > \theta_{V_j}$. Hence, the d.i. component, when
423 acting alone, favors $\theta'_{G_j} = \theta_{V_j}$, the maximum alignment of germination and vigor strategies and
424 the value of θ_G that maximizes correlations between germination and vigor. This result agrees
425 with Cohen's (1967) model that assumed no density-dependence. However, the d.i. component
426 here does not act alone and must be combined with the d.d. component for an overall prediction.

427
428 The d.d. component involves the effect of CovEC, the interaction between germination responses
429 (E_G) and competition (C). CovEC measures the association between the germination pattern of a
430 species and its contribution to competition. The distribution of C differs based on whether a
431 species is found in allopatry or in sympatry and so makes different predictions in these two
432 cases. The d.d. component vanishes in allopatry, leaving only the d.i. component as the sole
433 contributor to selection (SI S5, "The single species case"). Even though the d.d. component is
434 absent in allopatry, this does not mean there is no density-dependence; it is that density-
435 dependence is not appreciably different for resident and mutant phenotypes of the same species
436 under the assumption of small effect mutations. The evolutionary endpoint in allopatry is then
437 $\theta_{G_j} = \theta_{V_j}$, the value of θ_{G_j} that maximizes correlations between G and V . In sympatry, the d.d.
438 component is dominated by the effects of interspecific competition. It favors smaller values of
439 CovEC (SI S5, "Uncorrelated germination and vigor"), which occur when germination responses
440 are species-specific (Chesson 1994). Thus, this component favors large differences between
441 species in their values of θ_G (i.e., large $|\theta_{G1} - \theta_{G2}|$) in sympatry. Such differentiation in
442 environmental responses represents character displacement in a temporally fluctuating
443 environment.

444
445 Although d.d. and d.i. components of selection are written as additive in Eqn (12), they interact
446 in their effect on selection in sympatry. Their interaction stems from the fact that competition in
447 the d.d. component is influenced by correlations between G and V . Positive correlations between
448 germination and vigor enhance variation in competition across years (Kortessis and Chesson
449 2019), providing a pathway for predictive germination to influencing character displacement.

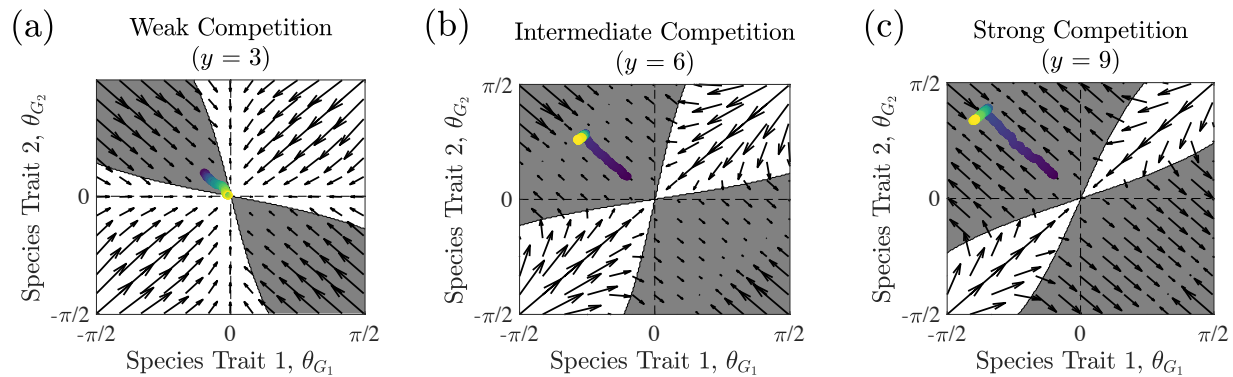
450
451 To understand how the d.i. and d.d. components jointly affect trait evolution in sympatry, we
452 plotted selection on both species as vectors in phenotype space (see Fig 3). Vectors point in the
453 expected direction of coevolution with the magnitude of the vector representing the relative
454 strength of selection. We find these by first simulating the dynamics of a model (1)-(2) initiated
455 with both species present. We then use the resulting distribution of population densities to
456 calculate the long-term growth rates of resident and mutant phenotypes, \bar{r}_j and \bar{r}'_j , respectively.
457 We then approximate the selection gradient as $(\bar{r}'_j - \bar{r}_j)/(\theta'_{G_j} - \theta_{G_j})$ for each species assuming
458 $\theta'_{G_j} - \theta_{G_j}$ is small (see SI section S6 "Calculating selection gradients from simulations"). Doing
459 this for a broad range of trait values yields a selective map depicting coevolutionary trait
460 trajectories. But not all trait trajectories may be realized because coexistence does not occur for
461 all trait combinations. Those for which the species stably coexist are given by gray areas,
462 whereas regions of phenotype space where exclusion occurs are given in white (see Fig 3). We
463 say species coexist if they satisfy the conditions of mutual invasibility, which is sufficient for our
464 model (Schreiber et al. 2011, Chesson 2018, simulation details in SI section S6 "Calculating

465 invader growth rates from simulations"). Trajectories that pass through white regions reflect
 466 exclusion of one species upon adaptive evolution (Fig 3). Further evolutionary change then
 467 follows single-species evolutionary dynamics.

468
 469 *4.2 Patterns of displacement for species with identical vigor responses ($\theta_{V_1} = \theta_{V_2}$)*

470 We first consider the special case of identical vigor responses for the species ($\theta_{V_1} = \theta_{V_2}$),
 471 meaning plant size is variable from year to year, but the two species have synchronous size
 472 fluctuations. Selection on predictive germination (the d.i. component) favors the same value of
 473 θ_G for both species. Hence, the evolutionary equilibrium in allopatry corresponds to identical
 474 germination strategies, i.e., $\theta_{G_1} - \theta_{G_2} = 0$, meaning that germination is variable across years, but
 475 the value of G fluctuates synchronously for the two species, and with the assumptions here,
 476 means $G_1(t) = G_2(t)$ for all t . By contrast, the d.d. component favors species-specific germination
 477 responses (i.e., nonzero $|\theta_{G_1} - \theta_{G_2}|$). The two components thus act in direct opposition. The net
 478 outcome of selection that results from these conflicting components in sympatry depends on their
 479 relative strengths.

480



481
 482 Figure 3. Effect of the strength of competition on coevolutionary selection. Each panel shows the
 483 coevolutionary selection portrait for different values of seed yield, y , with arrows indicating the
 484 direction and strength of selection. Competition increases with seed yield, y (see justification in SI
 485 S7). For all panels, gray indicates stable coexistence of competitors with those trait values whereas
 486 white indicates exclusion one species. The selection maps are symmetric across the axis given by
 487 the line $\theta_{G_2} = -\theta_{G_1}$ because species are identical in all other model parameters. The dashed lines
 488 cross at the allopatric equilibrium ($\theta_{G_1} = 0, \theta_{G_2} = 0$). Colors show the progression of trait evolution
 489 in adaptive dynamics simulations from initial trait values (purple) to final values (yellow).
 490 Parameters: $s = 0.9, \alpha = 1, \sigma_{E_G}^2 = \sigma_{E_V}^2 = 0.5, \mu_{E_G} = \mu_{E_V} = 0$, and $\rho = 1$.

491 We find that the evolutionary equilibrium in sympatry can range from no evolutionary change to
 492 complete differentiation. The dominant factor determining the evolutionarily stable state in
 493 sympatry is the total strength of competition (Fig 3), which can be independently varied by the
 494 seed yield parameter when it is the same across species ($y_1 = y_2 = y$) rather than the competition
 495 coefficient, α . A complete justification is given in SI S7, but in short, total seed density increases
 496 with y , meaning that the total combined contribution of intra- and inter-specific competition also
 497 increases with y , whereas seed density declines with increasing α , keeping total competitive
 498 effect, C' , constant. A different value of α is in fact equivalent to a change of units in measuring
 499 population density, and changes nothing in material terms.

500 For small y , the selection vector space has a single, globally attractive equilibrium where
501 germination responses are identical across species, $\theta_{G1} = \theta_{G2}$, (Fig 3a). This sympatric
502 equilibrium is equivalent to the allopatric equilibrium (the intersection of the dashed lines in Fig
503 3), indicating no character displacement. Two locally stable evolutionary equilibria of
504 intermediate trait divergence—separated by an unstable ridge—emerge for intermediate values
505 of y (Fig 3b). (The two equilibria are identical in terms of the magnitude of trait difference and
506 so are redundant, being identical once exchanging the labels of the species.) Selection in
507 sympatry is sufficient in this case for θ_G to diverge, meaning the evolution of species-specific
508 responses when there was none in allopatry. Further increasing y separates the sympatric
509 equilibria from the allopatric equilibrium (Fig 3c), indicating stronger divergent character
510 displacement and less correlated germination responses. Figure 4a summarizes these outcomes
511 by showing that sympatric trait divergence ($|\theta_{G1} - \theta_{G2}|$) increases with y . Note that, as a
512 consequence of trait divergence in sympatry, predictive germination, which is maximized for
513 both species in allopatry, declines in sympatry for both species.

514

515 The variance in vigor, $\sigma_{E_V}^2$, and the strength of the cue, ρ , both weaken selection for divergence
516 (Fig 4a,c). Both ρ and $\sigma_{E_V}^2$ increase the strength of the d.i. component of selection over the d.d.
517 component because both increase the benefits of predictive germination on long-term growth
518 (see SI S5, “Large vigor variation relative to germination variation with equal vigor”).

519

520 In the more realistic scenario of competitive inequalities between species, the relative strengths
521 of d.i. and d.d. components in sympatry differ between species. Competitive inequalities vary
522 with the relative values of y between species, where the species with larger y is dominant. With
523 competitive asymmetry, the selection vector space again has two convergent stable points, but
524 these points are no longer symmetric across species (Fig 5a). For each stable point, the dominant
525 has near maximum predictive germination (i.e., θ_{G_j} near θ_V) and the subordinate has negative
526 correlations between E_G and E_V (i.e., θ_{G_j} distant from θ_V) (Fig 5a).

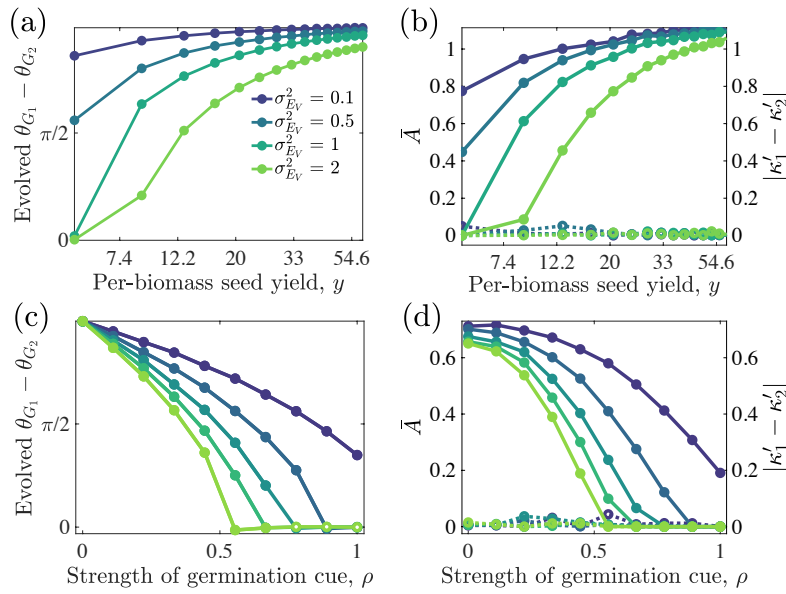
527

528 Character displacement here reduces predictive germination for both species, but the reduction is
529 slight for the dominant and severe for the subordinate competitor. In fact, predictive germination
530 for the subordinate in sympatry is $\text{Corr}(E_G, E_V) \approx -1$ —its minimum possible value—indicating
531 that the years with the highest germination fraction correspond to years when plants are the
532 smallest.

533

534 Asymmetrical evolution of species in sympatry can be understood from differences in the
535 strength of interspecific competition experienced by each species. The dominant species, having
536 higher y , grows to higher density than the subordinate. Thus, intraspecific competition governs
537 selection on the dominant species, favoring high predictive germination. Contrast this with the
538 subordinate species which, having lower y , is at lower density than the dominant. Interspecific
539 competition drives selection on the subordinate, which favors divergence from the dominant,
540 even at the cost of lower predictive germination.

541



542
 543 Figure 4. Species divergence and stability of coexistence as a function of the strength of competition
 544 and the strength of the cue present at germination. (a) Divergence as a function of per biomass seed
 545 yield, y (note log scale), which scales the strength of competition (see justification in SI S7). (b)
 546 Associated total stabilizing mechanisms, \bar{A} , (solid lines) and species average fitness differences, $|\kappa_1'$
 547 $-\kappa_2'|$ (dotted lines). (c) Divergence as a function of ρ , the strength of the cue present at the time of
 548 germination. (d) Associated stabilizing mechanisms \bar{A} (solid lines) and fitness differences $|\kappa_1' - \kappa_2'|$
 549 (dotted lines). For all panels, species have the same vigor responses, and so $\theta_{G_1} - \theta_{G_2} = 0$ in allopatric
 550 evolutionary equilibrium. Parameters: $s = 0.9$, $\alpha = 1$, $\sigma_{E_G}^2 = 1$, and $\mu_{E_G} = \mu_{E_V} = 0$. $\rho = 1$ in (a) and (b). y
 551 $= 4$ in (c) and (d).

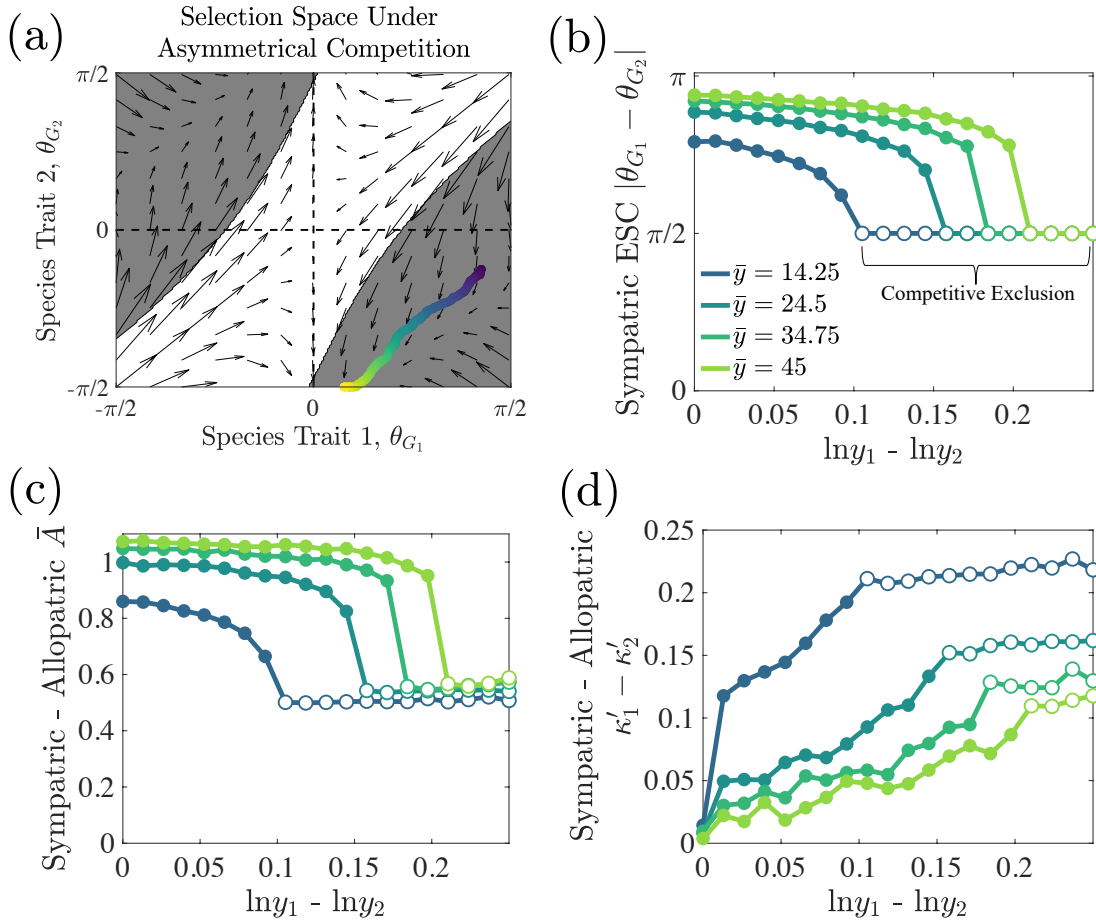
552
 553 *4.3 Patterns of divergence for species with different vigor responses ($\theta_{V_1} \neq \theta_{V_2}$)*

554 When vigor responses differ (i.e., vigor responses are species-specific), selection on each species
 555 in allopatry alone result in ecological differences in germination because the d.i. component
 556 favors $\theta_{G_i} = \theta_{V_i}$ for each species. This means that species that come into contact both in sympatry
 557 do so with species-specific vigor *and* germination. We ask whether species differences in
 558 germination are enhanced by evolution in sympatry.

559
 560 Interestingly, species-specific vigor can allow for the evolution of species-specific germination
 561 when it would not for species with identical vigor responses. To illustrate this result, consider the
 562 previous example of strong d.i. selection (small y and $\rho = 1$) for species with identical vigor
 563 responses, ($\theta_{V_1} = \theta_{V_2}$). This example was considered in Fig 3a and there was no character
 564 displacement. Now consider the same scenario, except that vigor traits differ by a small amount,
 565 $\theta_{V_1} - \theta_{V_2} = \pi/4$. The selection portrait under these conditions (Fig 6a) shows sizeable divergent
 566 displacement occurs. All that is changed is that we have made vigor responses less than perfectly
 567 correlated ($\text{Corr}(E_{V_1}, E_{V_2}) \approx 0.7$). The allopatric equilibrium is given by the intersection of the
 568 dashed lines in Fig 6a. If differences in vigor strategies had no effect, we expect the allopatric
 569 equilibrium to be the sympatric coevolutionary equilibrium. But the selection vectors point

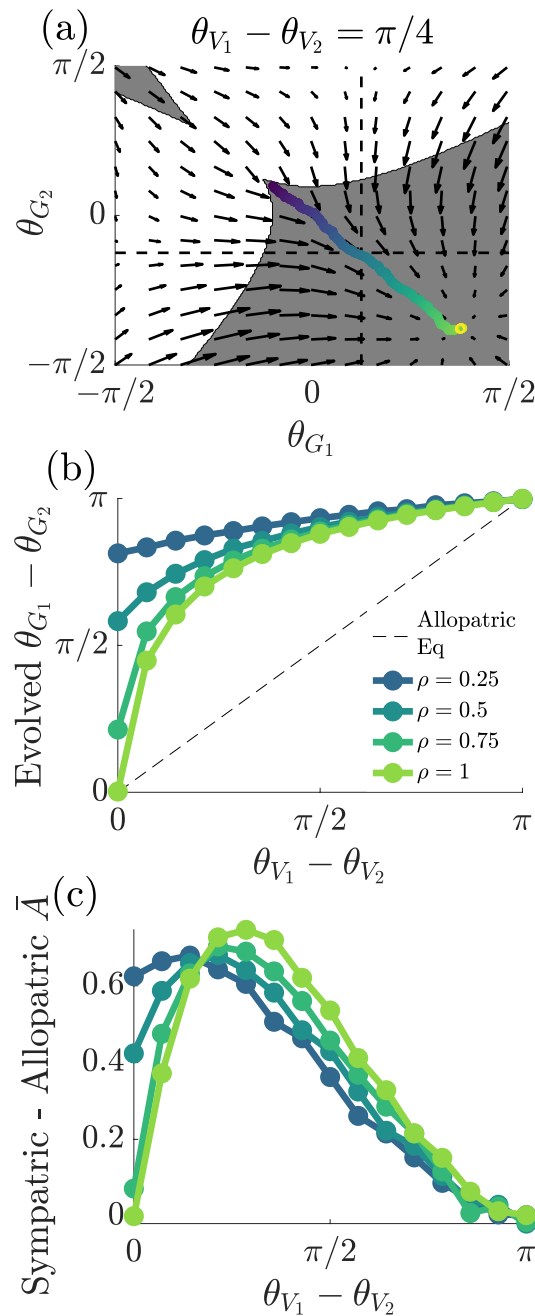
570 toward a globally stable coevolutionary equilibrium away from the allopatric equilibrium. This
 571 example demonstrates that interspecific competition, which is insufficient to cause character
 572 displacement when species have identical vigor traits, is sufficient to cause character
 573 displacement when vigor traits differ.

574
 575



576
 577 Figure 5. Evolution of unequal competitors favors asymmetric evolution between species and the
 578 evolution of enhanced fitness differences and weakened stabilizing mechanisms. (a) Coevolutionary
 579 phase space as in figure 3 but with species 1 competitively superior to species 2 ($y_1 = 7.1$ and $y_2 =$
 580 6.9). The evolutionary endpoint is near the maximum and minimum predictive germination for the
 581 dominant and subordinate, respectively. (b) Evolved germination trait differences in sympatry as a
 582 function of competitive inequalities. (c) Increase in \bar{A} in sympatry compared to allopatry. (d)
 583 Increase in species average fitness inequality, $\kappa'_1 - \kappa'_2$, in sympatry compared to allopatry. The
 584 overall strength of competition increases from blue to light green in (b), (c), and (d). Parameters: s
 585 $= 0.9$, $\alpha = 1$, $\sigma_{E_g}^2 = \sigma_{E_v}^2 = 1$, $\mu_{E_g} = \mu_{E_v} = 0$, and $\rho = 1$.

586
 587



589

590 Figure 6. Evolutionary and ecological consequences of selection when species differ in vigor
 591 patterns. (a) Selection portrait as in Fig 3 but where species differ in their vigor
 592 patterns. The dashed lines indicate the values of θ_V for the two species. (b) Evolutionarily stable germination trait
 593 differences in sympatry as a function of fixed between-species differences of vigor traits, $|\theta_{V_1} - \theta_{V_2}|$.

594 The dashed line is the difference in germination traits at evolutionary equilibrium assuming both
 595 species evolve in allopatry. (c) The increase in total stabilizing mechanism strength, \bar{A} , in sympatry
 596 at evolutionary equilibrium compared to allopatric equilibrium. $\rho = 1$ in (a). In all panels, $y_1 = y_2 = 4$,

597 $\mu_{E_G} = \mu_{E_V} = 0$, $\sigma_{E_G} = \sigma_{E_V} = 1$, and $s = 0.9$.

598 Provided a cue is present, differences in vigor strategies (i.e., differences in $\theta_{V1} - \theta_{V2}$) facilitate
 599 character displacement in germination strategies. This is illustrated in Fig 6b, where the
 600 sympatric evolutionary equilibrium $\theta_{G1} - \theta_{G2}$ is plotted as a function of $\theta_{V1} - \theta_{V2}$. Divergent
 601 displacement occurs when the equilibrium $\theta_{G1} - \theta_{G2}$ in sympatry is larger than the allopatric
 602 equilibrium (dashed line; fig 6b). Across the entire range of $\theta_{V1} - \theta_{V2}$ (i.e., species differences in
 603 vigor response), equilibrium $\theta_{G1} - \theta_{G2}$ values in sympatry exceed the allopatric equilibrium. In
 604 other words, germination responses are less correlated than vigor responses. Differences in vigor
 605 strategies ($\theta_{V1} - \theta_{V2}$) have larger effects when there are stronger environmental cues during
 606 germination about future vigor conditions, ρ . Small increases in $\theta_{V1} - \theta_{V2}$ above zero result in the
 607 most rapid rise in the magnitude of displacement in θ_G when ρ is near 1. These results suggest
 608 that the evolution of species differences in germination can be facilitated by the existence of
 609 species-specific differences in vigor.

610

611 *4.4 Strength of coexistence under selection*

612 As species evolve, competitive relationships between species change. But not all ecological
 613 differences influence competition and coexistence equally. On one hand, ecological differences
 614 may reduce niche overlap between species, thereby revealing coexistence opportunities. On the
 615 other hand, they may make one species more or less dominant to others, regardless of any niche
 616 differentiation. Each aspect of ecological differences arising from adaptation can be quantified
 617 by measuring \bar{A} , total community average stabilizing mechanisms, and $|\kappa_i' - \kappa_j'|$, adjusted species
 618 average fitness inequality (Chesson 2018). Adjusted species average fitness inequalities reflect
 619 ecological differences that do not stabilize competition; \bar{A} measures the amount to which
 620 ecological differences between species do.

621

622 Community average stabilization and adjusted species average fitness inequality differ subtly
 623 from the species-specific versions often used in previous theory (Chesson 2000). Community
 624 average measures account for asymmetries between species that often obscure the true nature of
 625 stabilizing mechanisms. Furthermore, they provide a better definition of equalizing mechanisms
 626 (Chesson 2018). The quantity \bar{A} is defined as the simple average across species of the sum total
 627 stabilizing mechanisms that boost invader recovery rates. Therefore, \bar{A} measures how much
 628 stabilizing mechanisms benefit all species in the community (Chesson 2003, 2018). The quantity
 629 \bar{A} must be above zero for coexistence to be possible (Chesson 2018).

630

631 Coexistence, however, depends not on the absolute size of \bar{A} , but instead on the size of \bar{A} relative
 632 to $|\kappa_i' - \kappa_j'|$, with more unequal competitors able to coexist with larger \bar{A} . To see why, note first
 633 that species stably coexist when both can recover from low density, i.e., each species has positive
 634 long-term growth rates when at zero density (Schreiber et al. 2011, Chesson 2018). The invader
 635 recovery rate \bar{r}_i/β_i can be written as

636

$$\frac{\bar{r}_i}{\beta_i} = \kappa_i' - \kappa_j' + \bar{A}, \quad (14)$$

637 where subscript i ($i \neq j$) indicates *species* i as invader, and β_i is the equilibrium fraction of seed
 638 lost from the seed bank per year, which puts the long-term growth rate on a generation timescale
 639 (see SI S6 for derivation). Species thus coexist when Eqn (14) is positive for both species. The
 640 condition for coexistence is straightforward: species coexist stably when $\bar{A} > |\kappa_i' - \kappa_j'|$ (Chesson

2018). We use this partitioning scheme to ask how adaptation to competitors contributes to changes in \bar{A} and $|\kappa_i' - \kappa_j'|$. It is often (implicitly) assumed that character displacement increases \bar{A} . We evaluate this conception of character displacement in relation to changes in $|\kappa_i' - \kappa_j'|$. In our model, multiple mechanisms comprise \bar{A} and $|\kappa_i' - \kappa_j'|$. Their expressions are in Table 2. Table 3 gives some context for how mechanisms change in the cases we consider.

Table 2. Coexistence mechanisms contributing to the recovery rate of species, \bar{r}_i/β_i . $C^{\{-i\}}$ is competition with the invader species i absent. Note that $\gamma_i > 0$ for viable species with $s > 0$. A_i is total stabilizing mechanisms for species i as invader. When $y_1 = y_2$, $\beta_1 = \beta_2 = \beta$. Derivation and details in SI section S6.

Component of Invader Growth Rate	General Formula	Formula Assuming Equal Seed Yield ($y_1 = y_2 = y$)
Species Average Fitness Difference, $ \kappa_i - \kappa_j $	$\ln \frac{y_i}{y_j} + \frac{(\beta_j - \beta_i)}{2} \left[\frac{(1-s)}{\beta_i \beta_j} \sigma_{E_G}^2 + \sigma_{E_V}^2 \right] + \frac{\gamma_i}{\beta_i} \text{Cov}(E_{G_i}, E_{V_i}) - \frac{\gamma_j}{\beta_j} \text{Cov}(E_{G_j}, E_{V_j})$	$(1-\beta) \left[\text{Cov}(E_{G_i}, E_{V_i}) - \text{Cov}(E_{G_j}, E_{V_j}) \right]$
Relative Nonlinearity, ΔJ_i	$\frac{1}{2}(\beta_i - \beta_j) \text{Var}(C^{\{-i\}})$	$\Delta J_i = 0$
Germination Storage Effect, ΔI_{Gi}	$\frac{\gamma_j}{\beta_j} \text{Cov}(E_{G_j}, C^{\{-i\}}) - \frac{\gamma_i}{\beta_i} \text{Cov}(E_{G_i}, C^{\{-i\}})$	$(1-\beta) \text{Cov}(E_{G_j} - E_{G_i}, C^{\{-i\}})$
Vigor Storage Effect, ΔI_{Vi}	$\frac{\gamma_j}{\beta_j} \text{Cov}(E_{V_j}, C^{\{-i\}}) - \frac{\gamma_i}{\beta_i} \text{Cov}(E_{V_i}, C^{\{-i\}})$	$(1-\beta) \text{Cov}(E_{V_j} - E_{V_i}, C^{\{-i\}})$
Total Stabilizing Mechanisms, A_i	$\Delta J_i + \Delta I_{Gi} + \Delta I_{Vi}$	$\Delta I_{Gi} + \Delta I_{Vi}$

4.5 Ecological consequences of selection with identical vigor responses ($\theta_{V_1} - \theta_{V_2} = 0$)

As expected, character displacement increases stabilizing mechanisms in sympatry compared to allopatry. When species are equivalent except for their evolving germination traits, the storage effect from germination is the only stabilizing mechanism (SI section S6), and its strength increases as germination responses are less correlated (i.e., with larger $|\theta_{G_1} - \theta_{G_2}|$; Fig 2b). Since the allopatric equilibrium equates to ecological equivalence of the two species, $\bar{A} = 0$ and $\kappa_1' = \kappa_2'$ in allopatry. Character displacement in sympatry raises stabilizing mechanisms, \bar{A} , above zero (Fig 4b,d, solid lines) with negligible effect on species average fitness inequalities, $\kappa_1' - \kappa_2'$ (Fig 4b,d, dashed lines). Factors that favor more divergent displacement (i.e., larger $|\theta_{G_1} - \theta_{G_2}|$), also lead to the largest shift in stabilizing mechanisms, \bar{A} , upon evolution in sympatry (Fig 4).

Adaptive coevolution with competitive inequalities increases stabilizing mechanisms, but at the same time reinforces fitness inequalities, potentially leading to collapse of coexistence. As

665 discussed in section 4.1, selection in sympatry favors species-specific germination (i.e., increases
 666 $|\theta_{G1} - \theta_{G2}|$), even for unequal competitors (Fig 5a,b). The evolution of species-specific
 667 germination in sympatry increases stabilizing mechanisms, \bar{A} (Fig 5c). However, $|\kappa_1' - \kappa_2'|$ also
 668 increases in sympatry (Fig 5d) because species evolve asymmetrical predictive germination.
 669 Differential strengths of d.i. and d.d. selection across species erodes predictive germination much
 670 more for the subordinate than the dominant species. Competitive inequalities magnify because
 671 predictive germination is a dominant component of species average fitness inequalities (Tables 2
 672 and 3). For large inequalities, the increase in \bar{A} arising from character displacement in
 673 germination is insufficient to overcome the increase in $|\kappa_1' - \kappa_2'|$, leading to exclusion in
 674 sympatry (open circles; Fig 5d).

675
 676 *4.6 Ecological consequences of selection with different vigor responses ($\theta_{V1} \neq \theta_{V2}$)*

677 In allopatry, species coexistence is stabilized by two factors: species-specific vigor responses
 678 ($\theta_{V1} \neq \theta_{V2}$), which create a storage effect from vigor (ΔI_V), and species-specific germination
 679 responses ($\theta_{G1} \neq \theta_{G2}$). Remember that evolutionary equilibria in allopatry correspond to
 680 equivalent species-specificity of germination and vigor (i.e., $\theta_{G1} - \theta_{G2} = \theta_{V1} - \theta_{V2}$; dashed line
 681 Fig 6b) and that evolution in sympatry makes germination patterns diverge. The remaining
 682 question is what role this selection for greater divergence of germination has on the strength of
 683 coexistence. The answer is straightforward. Character displacement in sympatry further stabilizes
 684 competitive interactions through increases in \bar{A} as compared to allopatry (Fig 6c).

685
 686 Table 3. Ecological factors affecting coexistence mechanisms for special cases for each species.

Component of Invader Growth Rate	Special Cases		
	Identical Vigor Responses $\theta_{V1} = \theta_{V2} = \theta_V$ ($E_{V1} = E_{V2} = E_V$)	Equal Seed Yield $y_1 = y_2 = y$ ($\gamma_1 = \gamma_2 = \gamma; \beta_1 = \beta_2 = \beta$)	$\theta_{V1} = \theta_{V2} = \theta_V$ and $y_1 = y_2 = y$
Species Average Fitness Inequality, $ \kappa_i - \kappa_j $	Determined by relative predictive germination and $\ln(y_1/y_2)$	Determined by relative predictive germination	
Relative Nonlinearity, ΔJ_i	Negative for dominant; Positive for subordinate	Zero	
Storage Effect from Germination, ΔI_{Gi}	Positive for both species when $\theta_{G1} \neq \theta_{G2}$		
Storage Effect from Vigor, ΔI_{Vi}	Negative for dominant; Positive for subordinate	Positive for both species when $\theta_{V1} \neq \theta_{V2}$	Zero
Total Stabilizing Mechanisms, A_i	$\Delta J_i + \Delta I_{Gi} + \Delta I_{Vi}$	$\Delta I_{Gi} + \Delta I_{Vi}$	ΔI_{Gi}

687
 688 One might assume that greater magnitude of displacement leads to larger stabilization of
 689 coexistence as measured by \bar{A} (Chesson 2018). The largest value of \bar{A} occurs under the largest
 690 values of the cue, ρ (light green line; Fig 6c). Yet, the magnitude of displacement is smallest for
 691 large ρ (Fig 6b). Stated differently, species with more correlated germination in an environment
 692 with strong cues are more stabilized than species with less correlated germination in an

693 environment with weak cues. How are we to understand this apparent discrepancy between
694 stabilizing effects and trait differentiation? The coexistence mechanisms operating here are both
695 storage effects (Table 3, “Equal Seed Yield”), which have two components: buffered population
696 growth and the comparison of resident and invader CovEC (ΔCovEC) (Table 2, “Equal Seed
697 Yield”). Buffered population growth does not change with θ_G or θ_V and so plays no role. Instead,
698 we find that ΔCovEC is larger under strong germination cues (i.e., larger ρ) even when
699 germination responses are more correlated (i.e., smaller $|\theta_{G1} - \theta_{G2}|$). We suspect that stronger cues
700 intensify intraspecific competition for residents because G and V tend to be large for residents in
701 favorable years (SI S7). Invaders species avoid such intense demand because of species-specific
702 germination responses (i.e., $|\theta_{G1} - \theta_{G2}| > 0$).

703

704 **5. Discussion**

705 Multiple traits often act together to influence competitive interactions between species, which
706 raises the possibility that selection responds to the joint action of multiple traits. We set out to
707 answer the question of whether a fixed, unevolving trait affecting competition between species
708 alters the process of character displacement on another trait affecting competition. We answered
709 this question with a model of two annual plant species that coexist in a temporally fluctuating
710 environment via the storage effect. The fixed trait is a species’ temporal pattern of plant growth,
711 which we call θ_V , and the evolving trait is a species’ temporal pattern of germination, which we
712 call θ_G . Character displacement occurs when θ_G differs between species (i.e., germination is
713 species-specific) more in sympatry than in allopatry. Importantly, germination and plant growth
714 can be correlated within species provided two things occur: a cue is present at the time of
715 germination about future growing conditions, which we model with ρ ($0 \leq \rho \leq 1$), and the
716 temporal pattern of germination aligns with the temporal pattern of plant growth.

717

718 We found that accounting for plant growth patterns in our model influences selection on
719 germination patterns, depending on two factors: (1) the information content of the cue, ρ , about
720 future growing conditions, and (2) the between-species correlation in plant growth. Character
721 displacement occurs readily when there is no cue, or it is weak (small ρ , Fig 4c). When the cue is
722 strong, character displacement occurs for species with uncorrelated plant growth patterns (Fig 6,
723 large $|\theta_{V1} - \theta_{V2}|$), but not for species with highly correlated growth patterns (Fig 6, small $|\theta_{V1} -$
724 $\theta_{V2}|$). For species with highly correlated growth responses in the presence of a strong cue,
725 character displacement may only occur for productive species (Fig 3,4a), i.e., when competition
726 is intense (SI S7).

727

728 In all cases, character displacement is larger in magnitude when the strength of competition is
729 large compared to benefits of predictive germination. We understand this fact by writing the
730 selection gradient as a sum of two components, one density-independent (d.i.) and the other
731 density-dependent (d.d.) (Eqn 12). The d.i. component favors increased predictive germination
732 within species, which favors the alignment of temporal patterns of germination and plant growth.
733 The d.i. component has analogues in other systems when selection optimizes the integrated
734 phenotype of an organism—rather than an individual trait (Murren 2012, Armbruster et al.
735 2014). The d.d. component favors species differences in germination patterns over time (i.e.,
736 favors reduced between-species correlations in germination) and represents the action of
737 character displacement. Any factor that increases the strength of density-dependence increases
738 the strength of the d.d. component and the magnitude of displacement, which in our model

739 occurs because of more intense competition (Fig 3,4a). Tension between the strengths of the d.i.
740 and d.d. components determine the overall magnitude of character displacement, with larger d.d.
741 relative to d.i. components resulting in larger displacement in sympatry. The strength of the cue,
742 ρ , and plant growth patterns, θ_V , each influence the d.i. and d.d. components, and therefore can
743 influence the overall magnitude of displacement in germination patterns, θ_G .

744

745 Stronger cues inhibit character displacement for species with highly correlated growth responses
746 because the best years for one species to germinate (i.e., those best for growth) are also the best
747 years for its competitor to germinate. When species have highly correlated growth responses,
748 differentiating from a competitor comes at the cost of less predictive germination. In effect, the
749 d.i. and d.d. components are in direct opposition. Benefits to predictive germination are large
750 when cues are informative (Cohen 1967), meaning there is little benefit to a species in
751 differentiating from a competitor in that case. Given strong cues, differentiation is only
752 beneficial when competition is intense (i.e., γ is large; Fig 3c,4a). Intense competition might
753 explain why some empirical studies find that observed correlations between germination and
754 plant size are suboptimal (see e.g., Gremer et al. 2016, Gremer et al. 2020), although other
755 factors, such as recent climate that differs from historical patterns, should not be discounted.

756

757 Even though strong cues inhibit character displacement for species with correlated plant growth,
758 character displacement can occur in the presence of strong cues if species' growth responses are
759 uncorrelated (Fig 6b). Hence, the evolutionary outcome of germination patterns is sensitive to
760 the values of plant growth patterns for each species. Why? Positive correlations between
761 germination and plant growth increase total demand for resources in favorable years because
762 many seeds germinate, *and* each plant grows large. With strong competition in favorable years,
763 interspecific competition has greater fitness effects, elevating the role of the d.d. component and
764 favoring character displacement. Other studies have documented the importance of species-
765 specific germination and plant growth. Angert et al. (2009) partitioned the independent and
766 combined effects of variation in both on species coexistence: germination variation alone
767 contributed 50%, variation in plant growth alone contributed 25%, and the remaining 25% is due
768 to the covariance between germination and plant growth. Snyder and Adler (2011) also found
769 predictive germination to be critical in a model of evolution; germination variance is maintained
770 by selection when germination is predictive of plant yield but evolves to zero without predictive
771 germination. Given that species-specific growth responses are well-documented in some annual
772 communities (Angert et al. 2007, Angert et al. 2009), character displacement appears to be a
773 viable hypothesis to explain some of the species-specific germination responses characteristic of
774 these systems (Pake and Venable 1996, Adondakis and Venable 2004, Chesson et al. 2013, Holt
775 and Chesson 2016, Li and Chesson 2018).

776

777 Our finding that character displacement is larger in magnitude for species with species-specific
778 plant growth (Fig 6b) conflicts with a dominant hypothesis from the theory of character
779 displacement. One prevailing hypothesis is that similar species are more likely to undergo
780 character displacement, under the assumption that similar species are more likely to share
781 resources and experience strong interspecific competition (Brown and Wilson 1956, Grant 1972,
782 Schluter 2000a, Dayan and Simberloff 2005, Pfennig and Pfennig 2010). We find that the
783 benefits of differentiation are greater when species differ in a non-evolving trait, in opposition to
784 the traditional prediction. In our model, very similar species (defined by their temporal

785 correlation in plant growth) may share similar selection pressures acting along other dimensions
786 (here predictive germination) that conflict with and overwhelm character displacement.
787 Dissimilar species may not have such selective conflicts. The two predictions can be reconciled
788 under a unifying feature—the strength of density-dependent feedback loops. Stronger density-
789 dependent feedback loops make character displacement more likely and larger in magnitude,
790 regardless of the number of traits involved in density-dependence.

791

792 We also studied the consequences of character displacement on the stability of coexistence
793 between species in sympatry, as measured by total stabilizing mechanisms and species average
794 fitness differences (Eqn 14). In all cases, stabilizing mechanisms increase with the magnitude of
795 displacement (Figs 4,5,6), as hypothesized previously (Germain et al. 2018) and seen in other
796 models (Pastore et al. 2021). However, we find that the cue can have an important role. A strong
797 cue during germination may limit displacement, but it also enhances the strength of stabilizing
798 mechanisms for a given magnitude of divergence (contrast Fig. 6b and 6c). Stronger feedback
799 loops that facilitate displacement in the presence of a strong cue also enhance the benefits of
800 species-specific germination.

801

802 Previous studies also predict that character displacement reduces differences in species average
803 fitness (Germain et al. 2018, Pastore et al. 2021). We find this to be the case for equal
804 competitors (Figs 4b,c) but not for unequal competitors, for which character displacement
805 enhances fitness inequalities (Fig 5d). Fitness inequalities are enhanced upon adaptive evolution
806 because the major determinant of fitness differs for competitive dominants and subordinates.
807 Dominants experience mostly intraspecific competition whereas competitive subordinates
808 experience mostly interspecific competition. Density-dependent feedback loops favoring
809 displacement are concentrated on the subordinate, which diverges from its competitor. But
810 divergence from competitors comes at the cost of less predictive germination (Fig 5a), which
811 may explain the observation that germination is less predictive in nature than expected from
812 models (Gremer et al. 2016). Such asymmetric evolution may be typical; some of the best
813 examples of character displacement are asymmetric (Grant and Grant 2006, Stuart et al. 2014).

814

815 Our results shows that species-specific responses—which are required for the storage effect—are
816 evolutionarily stable under multiple trait differences. Species-specific responses are generally
817 found to be favored in previous models (Abrams et al. 2013, Mathias and Chesson 2013, Kremer
818 and Klausmeier 2017, Miller and Klausmeier 2017), although our model is the first to consider a
819 full between-year stochastic analysis. We also show that multiple storage effects from variation
820 in multiple demographic rates (Table 2) are jointly favored. Other studies have found that
821 selection may act against components of the storage effect, e.g., germination variance (Snyder
822 and Adler 2011), but such an analysis assumes no tradeoffs between performance in different
823 year types (Abrams et al. 2013). Our model includes such tradeoffs by fixing the total sensitivity
824 of all phenotypes, which is the temporal analogue to keeping the area under species' utilization
825 curves fixed in MacArthur-style models (Abrams et al. 2013). Tradeoffs, and their particular
826 form, determine if character displacement results (Abrams et al. 2013) and, more generally,
827 whether selection favors specialists or generalists (Mazancourt and Dieckmann 2004). The
828 tradeoff we use has the analytical convenience that the variance is constant for all phenotypes.
829 Other tradeoff shapes will come with changes to the variance, and those phenotypes with lower
830 variances will generally benefit (Snyder and Adler 2011). In order to understand other tradeoff

831 shapes, both the effects of variance and niche differentiation need to be considered to make an
832 overall prediction of evolution.

833
834 Selection on species-specific differences is just one component of the storage effect and is
835 conditional on the presence of other components. One critical component is buffered population
836 growth. In annual plants, buffered population growth is ensured by a persistent seed bank, and is
837 present in the selection gradient (Eqn (12)) as the quantity γ . Without a persistent seed bank, $\gamma =$
838 0, and the selection gradient vanishes. Hence, all our results are conditional on the presence of a
839 between-year seed bank, meaning that the evolution of species-specific differences requires that
840 species are buffered. We previously identified that buffered population growth is likely to evolve
841 in response to strong competition (Kortessis and Chesson 2019), but that study included only one
842 species and therefore had no role for species-specific environmental responses. It remains an
843 open question how buffered population growth and species-specific differences jointly evolve.
844 An answer will be necessary before understanding the eco-evolutionary stability of coexistence
845 mechanisms in fluctuating environments.

847 **6. Conclusion**

848 Ecologists and evolutionary biologists recognize that traits do not act independently to shape the
849 fitness of an organism. The combined action of multiple traits on competition can have disparate
850 selective effects, both density-independent and density-dependent. Instead of evaluating
851 evolutionary change of multiple traits in isolation, a multi-trait perspective may often be
852 necessary, especially when two traits influence the strength of competition in a nonadditive way.
853 In such cases, trait combinations may yield unexpected outcomes, such as favoring character
854 displacement between dissimilar species.

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861 **Data Statement**

862 Code used to generate the figures and run both the ecological and evolutionary dynamics of the
863 model are available at <https://github.com/kortessis/Character-Displacement-Storage-Effect>.

865 **Conflicts of Interest**

866 The authors declare no conflicts of interest.

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