Priority effects and non-hierarchical competition shape species composition in a complex grassland community

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Abstract

Niche and fitness differences control the outcome of competition, but determining their relative importance in invaded communities – which may be far from equilibrium – remains a pressing concern. Moreover, it is unclear whether classic approaches for studying competition, which were developed predominantly for pairs of interacting species, will fully capture dynamics in complex species assemblages. We parameterized a population dynamic model using competition experiments of two native and three exotic species from a grassland community. We found evidence for minimal fitness differences or niche differences between the native species, leading to slow replacement dynamics and priority effects, but large fitness advantages allowed exotics to unconditionally invade natives. Priority effects driven by strong interspecific competition between exotic species drove single-species dominance by one of two exotic species in 80% of model outcomes, while a complex mixture of non-hierarchical competition and coexistence between native and exotic species occurred in the remaining 20%. Fungal infection, a commonly hypothesized coexistence mechanism, had weak fitness effects, and is unlikely to substantially affect coexistence. In contrast to previous work on pairwise outcomes in largely native-dominated communities, our work supports a role for nearly-neutral dynamics and priority effects as drivers of species composition in invaded communities.

Introduction

Understanding the long-term outcome of competition in diverse species assemblages is a major goal of ecology, but measuring outcomes empirically is often infeasible when dynamics proceed slowly relative to

34 the timescale of experiments. Theoretical coexistence models based on species differences offer a powerful

35 alternative for predicting competitive outcomes (Burdon and Chilvers, 1974; Tilman, 1980; Holt et al.,

36 1994). However, linking models to real ecological communities is challenging because realistic param-

37 eter estimates are rarely available for species interacting within a single ecological context. Moreover,

38 existing theoretical approaches often make simplifying assumptions–such as reducing analyses to pairs of

39 interacting species rather than considering the full dynamics of the assemblage–that may affect the in-

40 ferred outcomes. As a result, considerable uncertainty remains about the relative importance of different

41 proposed diversity-maintenance mechanisms, and the outcome of competition can be difficult to predict.

42 Among several existing theoretical frameworks for species interactions, modern coexistence theory

43 clarifies the mechanisms through which species differences affect the outcome of competition via their

44 effects on niche differences and fitness differences (Chesson, 2000). Niche differences are the differences

45 between species in resource use, natural enemies, habitat requirements, or other factors that force per-

46 capita impacts of competition within species to exceed those between species (Chesson, 2000). These

47 niche differences cause population growth to be negatively frequency-dependent because species achieve

48 their highest per-capita growth rates when they are rare and interact with mostly heterospecific com-

49 petitors, while per-capita growth declines as species become common and interact with many conspecific

50 competitors. By contrast, in this framework, fitness differences are those differences between species

51 that determine per-capita growth rates independent of relative abundance, often including differences in

52 fecundity, resource acquisition, or survival. Coexistence occurs when niche differences, which generate

53 negative frequency-dependent population growth or 'stabilization', are strong enough to overcome fitness

54 differences between species (Chesson, 2000). Alternatively, priority effects can occur when population

55 growth is positively frequency-dependent, allowing any species that is initially more common to exclude

56 others but preventing species from invading when rare in the presence of competitors (Mordecai, 2011;

57 Fukami et al., 2016). While assessing competitive outcomes in pairs of species with known parameter val-

58 ues is straightforward in this framework, predicting multispecies outcomes remains a challenge (Saavedra

59 et al., 2017; Barabás et al., 2018).

60 Modern coexistence theory has motivated a suite of studies that empirically measure the strength of

61 niche differences and fitness differences, and ultimately the outcome of competition, in natural plant or

62 algal communities. Many of these studies have emphasized the influence of stabilizing niche differences

63 on species coexistence (Turnbull et al., 2005; Adler et al., 2006; Levine and HilleRisLambers, 2009; Adler

64 et al., 2010; Narwani et al., 2013; Godoy et al., 2014; Kraft et al., 2015; Godoy et al., 2017). However,

65 almost all empirical applications of modern coexistence theory use pairwise growth rates when rare

66 to assess community-wide outcomes (*e.g.,* Adler et al., 2007; Levine and HilleRisLambers, 2009; Adler

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67 et al., 2010; HilleRisLambers et al., 2012; Mordecai, 2013; Godoy et al., 2014; Kraft et al., 2015; Mordecai

68 et al., 2015). A growing body of theory shows that outcomes of competition may depart from pairwise

69 predictions when all species are analyzed simultaneously (*e.g.,* Case, 1995; Allesina and Levine, 2011;

70 Saavedra et al., 2017; Mayfield and Stouffer, 2017), and that even two-species models can depart from

71 the predictions of invasion analyses in some settings (Barabás et al., 2018). Deviations from pairwise

72 predictions may originate from indirect effects on competitor density, non-hierarchical interactions, in

73 which competitive impacts are intransitive, or higher-order interactions, in which the per-capita impact

74 of one species on another is mediated by interactions with a third species. In complex communities it

75 is theoretically possible to observe priority effects within groups of species with high niche overlap and

76 fitness similarity, which occur alongside deterministic coexistence or competitive exclusion between groups

77 of species with larger niche differences and fitness differences. Despite these theoretical developments,

78 there are few empirical examples of communities in which multispecies outcomes depart from two-species

79 predictions (but see Mayfield and Stouffer, 2017; Godoy et al., 2017), although alternative stable states

80 have been empirically documented outside the coexistence literature (Staver et al., 2011; Carpenter

81 et al., 2011; Fukami et al., 2005). It is unknown whether departures between pairwise and multispecies

82 predictions are a common biological phenomenon or a quirk of mathematical models. Moreover, it is not

83 clear how ecological contexts – such as the coevolutionary history of the competing species and the level

84 of disturbance – may influence the likelihood of complex multispecies dynamics as compared to negative

85 frequency-dependent stabilization (Ocampo-Ariza et al., 2018).

86 We hypothesized that complex multispecies dynamics would be likely to emerge in recently invaded

87 systems, in which competing species have not had long coevolutionary histories and hence may not have

88 had sufficient time to evolve into distinct niches (MacDougall et al., 2009). Such systems may be far from

89 equilibrium, and may represent an opportunity to study complex multispecies dynamics in the absence of

90 strong stabilizing mechanisms driven by niche differentiation. Moreover, predicting competitive outcomes

91 in recently invaded systems is a pressing concern for conservation, and understanding the processes that

92 have the largest impact on the persistence of native species could help preserve endemic biodiversity. In

93 this study, we investigated competitive outcomes in California grasslands, one of the most ecologically

94 important and widespread ecosystems in the Western U.S. and a key reservoir of endemic biodiversity

95 (Myers et al., 2000). Simultaneously, California grasslands are heavily invaded and human-impacted since

96 the 19th century (Mack, 1989); exotic annual grasses now dominate while native perennial bunchgrasses

97 and annual forbs have declined to very low density throughout much of their extent. In the long term, it

98 is not clear whether the exotic annual grasses will competitively exclude native perennial grasses, whether

99 native grasses will stably persist (at reduced densities), or whether priority effects will determine whether

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100   native or exotic grasses dominate at a local scale.

101   Here, we combine field experiments with mathematical models to predict the outcome of competition

102   in a community of five co-occurring native and exotic grasses in a grassland ecosystem. We develop

103   and empirically parameterize population dynamics models for the species in this complex community.

104   The models incorporate a suite of demographic rates experimentally measured for three different exotic

105   annual grasses and two native perennial grasses at a single Northern California grassland site and include

106   the impact of fungal pathogens on those demographic rates, which may affect competitive outcomes

107   by altering fitness differences or by inducing negative frequency dependence of growth rates (Mordecai,

108   2011, 2013). We estimate parameters of the model statistically from field observations of seed output,

109   germination, establishment, seed infection, and adult survival for each of five competing species of exotic

110   annual and native perennial grasses. Using the parameterized model, we study the multispecies outcome of

111   competition, with and without pathogens. Specifically, we ask: (1) How strong are intra- and interspecific

112   competition between native and exotic grass species? (2) What is the predicted outcome of competition?

113   (3) Do complex outcomes, including priority effects and/or intransitive competition, emerge from the

114   dynamics of the full multispecies assemblage? (4) How strongly do foliar and seed pathogen impacts on

115   demographic rates influence the outcome of competition?

Methods

Empirical data collection and parameter estimation

Study system

119   We chose five focal species that are highly abundant and widespread in California grasslands: exotic an-

120   nual grasses *Avena barbata*, *Bromus diandrus*, and *Bromus hordeaceus*, and native perennial bunchgrasses

121   *Stipa pulchra* and *Elymus glaucus*. For each species, we measured a full complement of demographic rates

122   that determine population growth: seed germination, seedling establishment, the impact of competition

123   on per-capita seed production, and over-summer survival (for both seedling and adult perennial bunch-

124   grasses). We also assessed seed infection and survival with a common fungal pathogen that causes a

125   disease called "black fingers of death," which can kill native and exotic grass seeds (Beckstead et al.,

126   2010). All experimental work was conducted in Jasper Ridge Biological Preserve, located in San Mateo

127   County, California (37°24'N, 122°13'30"W; 66 - 207 m). This 485-hectare biological preserve is managed

128   by Stanford University and has a Mediterranean climate with cool, wet winters and warm, dry summers

129 (mean annual precipitation = 622.5 mm) (Ackerly et al., 2002). All demographic rates (except the peren-

130 nial seedling to adult transition probability; see below) were measured in winter 2015 to spring 2016

131 (the 2016 growing season), an average rainfall year with 601 mm total precipitation distributed over 20

132 precipitation events.

Competition experiment & transect sampling

134 Seed output is an important component of plant reproduction, and is strongly impacted by competitor

135 density for many plants (Mordecai, 2013; Mordecai et al., 2015). We measured seed output as a function of

136 competitor density by varying the density of each plant species in monoculture and in mixed-species plots

137 and measuring per-capita impact on seed production for each competitor species (Mordecai, 2013; Levine

138 and HilleRisLambers, 2009). The 1-m^2 competition plots were randomly assigned to five competitor

139 density treatments ranging from 10% - 100% of each species' estimated natural density in monoculture,

140 for each of the seven background 'species-groups' (*A. barbata*, *B. diandrus*, *B. hordeaceus*, *E. glaucus*

141 seedlings, *E. glaucus* adults, *S. pulchra* seedlings, and *S. pulchra* adults). We also cleared 4-m^2 plots

142 of competitors to measure seed output on individuals of each species at low competitor density (though

143 natural recruitment from the seed bank meant that these plots were not completely clear of competition).

144 We used weed matting, weeding, and seed addition to manipulate competitor densities. At the end of

145 the 2016 growing season we measured seed output from up to three focal plants per species per plot (as

146 available). See Supplementary Materials for a complete description of the competition experiment.

147 We also measured the impacts of competition on seed production in six transects that naturally

148 varied in plant composition. Each transect varied in grass composition from native perennial-dominated

149 at one end to exotic annual-dominated at the other, with five 1-m^2 plots spanning each transect spaced

150 approximately 5-10m apart. For each focal plant in the transects we estimated seed output, in both the

151 2015 and 2016 growing seasons (see Supplementary Materials).

152 To assess pathogen damage and its relationship with seed production and competitor density, we

153 visually estimated leaf area damaged by fungal infection on a subset of leaves on each focal plant in both

154 the transects and experimental plots. We used these data to quantify the impact of foliar fungal infection

155 on seed output, as well as the impact of plant species local relative abundance on pathogen damage.

156 We note that this approach could underestimate the impact of fungal infection if resistance is generally

157 costly, and most surveyed plants were actively fighting infections.

158 Our attempt to manipulate competitor densities in the experimental plots was only partially successful

159 because of recruitment from the seed bank. As a result, we combined all focal plants into a single data

160 set of seed outputs and observed competitor densities (rather than using the target densities for the

5

161 experimental plots). Our final dataset included 439 *A. barbata*, 399 *B. hordeaceus*, 319 *B. diandrus*, 387

162 *S. pulchra*, and 234 *E. glaucus* individuals (see Supplementary Materials for further details).

163   We used Markov Chain Monte Carlo (MCMC) to infer parameters relevant to seed output (λ), com-

164 petition (α), and foliar infection (β) from our competition experiment data (see dynamic model section

165 and Table 1 for parameter definitions), and performed simulation-based validation of our estimation pro-

166 cedure. Full details of this estimation procedure and its validation are provided in the Supplementary

167 Materials, along with a more detailed description of the experimental design. We repeated the parameter

168 inference procedures on subsets of the data that included either only the experimental plots or only the

169 transects, and found that parameter values were of similar magnitude and with overlapping posterior

170 distributions (see Fig. S7 and Supplementary Materials).

Germination data

172 We planted marked seeds of each focal species to track germination and seedling establishment in 30 plots

173 of 25 individuals of each species in November 2015. We recorded their status weekly for four weeks in

174 January - February as missing (M), alive (A), or alive with $> 50\%$ of leaf area with pathogen damage (P).

175 We used a Markov model to estimate the probability of establishing, surviving, and becoming heavily

176 infected for each species by calculating weekly transition probabilities between these three states by plant

177 species, then using the matrix to project forward four weeks to estimate the overall probability of germi-

178 nating and establishing. We repeated this calculation both with pathogens present and with pathogens

179 removed (*i.e.*, as if all individuals experienced the establishment rates of uninfected individuals), in order

180 to understand the impact of pathogens on seedling establishment (Fig. S1 shows inferred germination g_j

181 and establishment ϕ_j^U and ϕ_j^I for uninfected and infected individuals, respectivelyfor each species j) .

Seed survival and infection data

183 Seeds that remain dormant in the seed bank may contribute to population growth when they germinate

184 in future years. To assess survival of non-germinating seeds between years, we buried 30 mesh seed bags

185 contained five sewn compartments of 100 seeds of each focal plant species 2-5 inches deep from November

186 2015 - July 2016. We retrieved all intact seeds and scored them for "Black Fingers of Death" (BFOD)

187 pathogen damage (Beckstead et al., 2010; Mordecai, 2013), which is likely caused by one of the numerous

188 *Pyrenophora* spp. that are common in these sites (Spear and Mordecai, 2018). We tested all intact,

189 non-germinated seeds for viability using germinatino, gibberellic acid, and cut tests as in previous work

190 (Mordecai, 2012). We parameterize the fraction of seeds killed from BFOD infection as γ_j for species j

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191 (Fig. S2)

Adult survival data

193 To assess the survival of *S. pulchra* and *E. glaucus*, we marked 200 adult perennial bunchgrasses with flags

194 in June 2015 at four sites for each species, and revisited prior to senescence in June 2016. We recovered

195 167 *S. pulchra* and 170 *E. glaucus* flags on the second visit and recorded them alive or dead based

196 on observnig green tissue and/or new fruiting stalks. We fit binomially distributed models of survival

197 probability for each species using beta-distributed priors with parameters $\alpha = 1$, $\beta = 1$ (Fig. S3).

Perennial transition from seedling to adult

199 We modeled perennial seedling over-summer survival as a function of competitor density and per-capita

200 competitive effects using data and fitted parameters from previously published work (Mordecai et al.,

201 2015). Briefly, we modeled perennial seedling over-summer survival as a Beta-Binomially distributed

202 process where for each observation k, the number of surviving seedlings maturing into adulthood was:

$$Y_k \sim \texttt{BetaBinomial}(d, \frac{d(1-\mu_k)}{\mu_k}, n_k), \tag{1}$$

203 where $\mu_k = \frac{\nu}{1+\sum_k \alpha_j D_{kj}}$ is the expected value, over all competitor species j. Here, ν is the per-capita

204 survival probability in the absence of competition, α_j are the per-capita competitive effects of individuals

205 of species j, and D_{kj} are the number of individuals of species j in observation k. In the Beta-Binomial

206 distribution d affects the mean and variance, and n_k is the number of trials in observation k. The equation

207 for Y_k is parameterized so that its mean is equal to μ_k. Since we lacked the data to separately estimate

208 α_j for each individual species in our sample, we estimated an α_j for perennial adults, perennial seedlings,

209 and exotic annuals, respectively.

Population dynamic model

Model structure

212 We developed a dynamic model that captures the effects of competition and fungal infection on growth

213 rates for each grass species in our system, which is structurally similar to models developed in previous

214 work (Mordecai, 2013; Mordecai et al., 2015). All parameters and variables in the population dynamic

215 model are listed in Table 1. To model the effects of competition on the population growth of each species,

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216 we suppose that each plant of species j has a seed output of λ_j in the absence of competition, and that
217 competition and infection reduce seed output by

$$f_j(t) = \frac{1}{1 + (\sum_l \alpha_{jl} D_l(t)) + A_j \beta_j}, \tag{2}$$

218 where $D_l(t)$ is the density of competitor species l per m^2 at time t and A_j is the mean leaf area that was
219 infected on individuals of species j. The expected seed output of a single individual $S_j(t)$ is then

$$S_j(t) = \lambda_j f_j(t). \tag{3}$$

220 In the absence of transmisison information we do not explicitly model transmission of fungal pathogens,
221 but simply assume that each individual is infected at the mean level of observed foliar fungal infection
222 for species j.

223   For each species j, we suppose that a fraction g_j of the seeds germinate, and among these a fraction
224 γ_j are infected with a fungal seed pathogen (BFOD). Seeds that germinate and are not infected may
225 then establish, or may be eliminated before they ever produce seeds. We supposed that the probability
226 of establishment depends on foliar fungal infection status, and separately estimated the probability of
227 establishment for infected (ϕ_j^I) and uninfected (ϕ_j^U) seedlings for each species j. The proportion of
228 seedlings that are infected during the transition is given by P_j^I.

229   Perennial seedlings are presumed to be weak competitors and are not included in the competition
230 model and produce no seeds in the first year of life (Mordecai et al., 2015), but are subject to competition
231 in their survival over their first summer. Perennial seedlings survive at rate $\nu_j(t)$, given by

$$\nu_j(t) = \frac{\nu_j^0}{1 + \alpha_s D_s(t) + \alpha_a D_a(t) + \alpha_n D_n(t)}, \tag{4}$$

232 where D is the density of competitors, the subscripts s, a, and n represent perennial seedlings, perennial
233 adults, and annuals, respectively, and ν_j^0 is the survival rate in the absence of competition. For this
234 aspect of the model, we group all annual and perennial plants together instead of computing each species
235 competitive effect separately because we lacked the data necessary to infer the parameters for each
236 species individually. Perennial seedlings that survive the summer then become adults in the following
237 year. Perennial adults are also subject to over-summer mortality at rate $(1\text{-}\xi_j)$, modeled as competition-
238 independent because deaths of adult bunchgrasses are relatively rare (Fig. S3).

239   We model germination rate G_j after accounting for infection and establishment (see "Seed survival
240 and infection data" section) with

$$G_j = g_j \left(1 - \gamma_j\right) \left(\phi_j^U (1 - P_j^I) + \phi_j^I P_j^I\right). \tag{5}$$

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241 Additionally, we suppose that the proportion of seeds remaining in the seed bank after germination and
242 infection B_j is given by

$$B_j = (1 - \gamma_j)(1 - g_j). \tag{6}$$

243 At each time step, for each species j we track the number of seeds $n_j^a(t)$ for exotic annuals, or the
244 number of seeds $n_j^p(t)$ and adults $a_j(t)$ for perennials. Combining across seed production, competition,
245 foliar fungal infection, fungal seed infection, germination, establishment, and over-summer survival, the
246 full population growth equations are

247
$$n_j^a(t + 1) = n_j^a(t) \left(G_j \lambda_j f_j(t) + B_j \right), \tag{7}$$

248
$$n_j^p(t + 1) = a_j(t)\lambda_j f_j(t) + n_j^p(t)B_j, \tag{8}$$

$$a_j(t + 1) = a_j(t)\xi_j + n_j^p(t)G_j\nu_j(t). \tag{9}$$

249 The germination, adult survival, seed infection, and seedling transition parameters were estimated as
250 described in the previous sections. The competition (α), seed output (λ), and foliar infection burden (β)
251 were estimated using custom MCMC software, as described in the supplemental methods. Simulations of
252 each species in monoculture shows a strong positive correlation with observed monoculture densities in
253 the field (Fig. S6), suggesting that our model parameterization with independently measured demographic
254 rates accurately describes the system.

255 Separating infectious processes from competition

256 Initially we considered three broad classes of models that 1) did not include the impacts of infection,
257 2) included only foliar infection, and 3) included both foliar infection and BFOD pathogen. Since foliar
258 infection had a negligible impact on dynamics and competitive outcomes, we compare models that include
259 only foliar fungal infection to models that include both foliar infection and BFOD. The foliar infection
260 model includes both the parameters relevant to infection of perennial seedlings during their transition to
261 adults and infection of leaves of adult perennials and exotic annuals.

262 Inferring the outcome of competition

263 We used the parameterized models to investigate the outcome of competition using both pairwise and
264 multispecies approaches, to assess any differences in the outcome across approaches and to understand
265 potentially complex outcomes more mechanistically. First, we used the posterior parameter estimates
266 and the population dynamic model to compute growth rate when rare (GRWR) for each pair of species.

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267 If a pair of species each have GRWR> 1 (i.e., log(GRWR)> 0, where log is the natural logarithm), then

268 stable coexistence is predicted because the rarer species is expected to increase in prevalence, preventing

269 either species from being excluded (Turelli 1978; but see Case 1995). Pairwise competition calculations

270 were performed in the presence of fungal infection (*i.e.*, including all model parameters pertinent to foliar

271 or seed fungal infection).

272 To calculate GRWR for each species pair, we sampled the relevant demographic rate parameters from

273 their posterior distributions and simulated one species forward to its stable monoculture density, then

274 computed the growth rate of an invader of another species. For perennials, we computed GRWR as the

275 dominant eigenvalue of the 2x2 matrix describing the rate of transition between seed and adult stages,

276 which accounts for their stage-structured life history (Mordecai, 2013). For exotic annuals, we calculated

277 GRWR by simulating the addition of a single individual to the monoculture species and calculating the

278 growth rate in the second generation. We also calculated percent difference in GRWR (pdGRWR) as

279 $100\left(1 - \frac{A}{B}\right)$, where B is the GRWR in an empty plot, and A is the GRWR under invasion conditions.

280 Second, we investigated competitive outcomes for the full species assemblage using simulations. Be-

281 cause outcomes could be initial condition-dependent, we initialized our simulations at a range of observed

282 densities from the transects. We simulated 600 years and report results of species mixtures at this time

283 point (Mordecai, 2013). For species that were not present in a sampled transect, we introduced a pseudo-

284 count of one individual so that each species is initially present in each simulation. We consider species

285 with population sizes exceeding one individual at the end of the simulation to have "persisted", while

286 species with less than one individual are "excluded."

287 Lastly, we performed invasion experiments to better understand the dynamics underlying some of

288 the coexistence outcomes that were predicted under our model. In these experiments, we compared the

289 ability of *E. glaucus* to invade established *S. pulchra* plots with and without the presence of an exotic

290 annual competitor. We considered only the subset of posterior parameter estimates in which *S. pulchra*

291 was predicted to coexist with *B. diandrus*, excluding all replicates in which single species dominance

292 was predicted. We simulated 100 years of *S. pulchra* growth in the absence of competitors to allow

293 it to establish. Subsequently, at time $t = 100$, we either invaded *B. diandrus* or allowed *S. pulchra*

294 to continue in the absence of competitors for another 100 years, and finally we introduced a single *E.*

295 *glaucus* individual at time $t = 200$. We summarized these experiments by calculating the proportion of

296 posterior samples in which *S. pulchra* is able to prevent *E. glaucus* from invading after 600 simulated

297 years post-invasion. We sampled one set of parameters randomly from among the posterior estimates to

298 display this invasion experiment, but note that we vary the timing of the invasions for the purpose of

299 visualization (Fig. 4).

10

Results

Evidence for strong interspecies competition

We calculated the pairwise log(GRWR), where zero is the threshold for invasion, of each species invading a monoculture of each other species to assess the pairwise outcomes of competition (Fig. 1A). We also calculated the proportional decrease in GRWR relative to the growth rate in the absence of competition to assess the overall impact of competition on population growth (pdGRWR, Fig. 1B). The values plotted in Fig. 1 represent the mean over 250 independent samples of the parameters from their posterior distribution. If there were strong niche differences between all pairs of species, each species would strongly constrain its own growth rate but to have a relatively weak competitive impact on other species. By contrast, we observed high niche overlap in this system, in which interspecific competition constrains invasion growth rates as much or more than intraspecific competition (Fig. 1A). Along the diagonal, where each species competes with itself at its stable monoculture density, the log(GRWR) was always very near zero (Fig. 1A). When the native perennial species (*E. glaucus* and *S. pulchra*) were the invaders, they were constrained to log growth rates close to zero by all competitors except *A. barbata*, which is unable to constrain either species. By contrast, neither perennial species reduced the log(GRWR) of any of the annual species to below zero. *B. hordeaceus* and *B. diandrus* tightly constrained each others' growth rates, but were not strongly constrained by the perennial competitors. *A. barbata* was a poor competitor in this community, and only constrained itself while being tightly constrained by both of its annual competitors.

These results are not driven solely by some species having low overall (competition-independent) growth rates, because competition reduced GRWR for nearly all species pairs (Fig. 1B). The strongest impacts of competition were of *B. diandrus* and *B. hordeaceus* on each other, resulting in growth rates reduced by $95 - 96.4\%$ relative to the absence of competition. *E. glaucus* and *S. pulchra* were also subject to competition with each other, reducing *S. pulchra*'s growth rate $49.3 - 51\%$ and *E. glaucus*'s growth rate by $72.7 - 73.6\%$ relative to growth rates in absence of competition. The impacts of *B. diandrus* and *B. hordeaceus* on the perennials were of similar magnitude to the observed perennial-perennial impacts.

Predicted community composition is exotic annual-dominated

We next sought to investigate competitive outcomes when all five species compete simultaneously. Although it would be possible to perform a multispecies invasion analysis, such analyses can provide misleading results because GRWR exceeding 1 does not necessarily imply stable persistence when more than

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two species are included (Case, 1995; Dormann and Roxburgh, 2005; Saavedra et al., 2017). Instead, we examined the outcomes of competition by directly assessing the final simulated community composition across a range of empirically observed densities as initial conditions. For this analysis (Fig. 2A) we included the impact of foliar fungal infection on demographic rates, but not the pathogen BFOD.

Based on our two-species competition observations (Fig. 1), we expected that either *B. hordeaceus* or *B. diandrus* would persist in most simulations because they have large growth rates even when invading a monoculture of native perennial competitors. Since this species pair displayed large interspecific competition coefficients, we also expected that they would rarely coexist. The pairwise invasion analysis also suggests that *A. barbata* should rarely persist given its low growth rate in the presence of its competitors, and that the native perennials *S. pulchra* and *E. glaucus* would sometimes persist, given that their mean replacement rates were typically near one (Fig. 1A). Consistent with these expectations, either *B. hordeaceus* or *B. diandrus* persisted in 99.7% of simulation replicates (Fig. 2A), while the two species almost never coexisted with each other (0.32% of replicates). *A. barbata* was nearly always excluded. Native perennials persisted in 22.0% of replicates, usually by coexisting with either *B. hordeaceus* or *B. diandrus*, but rarely coexisting with each other (0.39% of replicates).

The wide range of possible outcomes could reflect either uncertainty in the parameter estimates or dependence on the initial conditions of our simulations. To differentiate between these possibilities, we investigated persistence as a function of initial competitor densities (Fig. 3). If each species' success is strongly dependent on initial conditions, this suggests that priority effects play a much larger role in determining community composition than uncertainty in parameter estimates, and vice versa. We observed that the perennial species' persistence in multispecies competition was weakly dependent on initial community composition: the probability of *S. pulchra* persistence increased modestly with its initial density. By contrast, the annual species *B. hordeaceus* and *B. diandrus* showed striking priority effects driven by strong interspecific competition across the densities of all competitors except *A. barbata*, which had only modest effects on any species.

Non-hierarchical competition between natives and exotics

Notably, the two native perennial species were not equally likely to coexist with each of the dominant exotic annuals: *S. pulchra* was much more likely to coexist with *B. diandrus* than *B. hordeaceus*. To better understand the dynamics driving these outcomes, we compared invasion simulations that included only the native perennials to simulations in which an exotic annual invader preceded the native perennial invader.

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When the native perennials competed in the absence of exotic annuals, their dynamics are nearly-neutral, as indicated by the near equality intraspecific and interspecific competition strength (Fig. 1A). Although neutral dynamics cannot result in long-term stable coexistence, they are expected to result in relatively slow loss of one of the species (Adler et al., 2007). Nearly-neutral dynamics could result in priority effects if interspecific competition is slightly stronger than intraspecific competition. Consistent with these expectations, we observed slow replacement dynamics and priority effects when the native perennial species competed directly (Fig. 4A). When *S. pulchra* was introduced first, 36.4% of simulation replicates resulted in dominance by *S. pulchra*, whereas 99.9% of replicates in which *E. glaucus* was introduced first resulted in dominance by *E. glaucus*. The two perennial species coexisted in only 0.1% of replicates.

We next tested how the invasion of exotic annuals might alter competition outcomes between the two perennial species. When *B. diandrus* invaded simulated monocultures of *S. pulchra*, the priority effect preventing *E. glaucus* from invading was substantially stronger. Among replicates in which *S. pulchra* and *B. diandrus* coexisted, *E. glaucus* was able to invade in only 4.5% (as compared to 52.9% of these same parameter sets when *B. diandrus* was not included in the simulation). Hence, when coexistence was predicted between *S. pulchra* and *B. diandrus*, the presence of the exotic annual *B. diandrus* increased the likelihood of persistence for *S. pulchra* at the expense of *E. glaucus* (Fig. 4). These results suggest a strong impact of non-hierarchical competition on outcomes in this system, in which no single species can dominate and coexistence is only possible given specific arrival orders. These dynamics result in deterministic competitive exclusion or coexistence mediated by priority effects that make the final composition dependent on stochastic arrival order.

Seed infection hampers a weak competitor, *A. barbata*

While the simulation and invasion results suggest that exotic annuals will dominate perennials and either competitively exclude them or reduce their population sizes, pathogens could reduce this effect if exotic annuals incur a higher fitness cost than perennials from infection. We repeated the simulation experiments in the previous section with the impact of fungal infection by BFOD included (Fig. 2B). BFOD decreased the overall success of *A. barbata*, which was already the weakest annual competitor. *A. barbata* persisted in 1.98% of replicates that excluded BFOD, but almost never persisted in its presence (0.12% of replicates). Species other than *A. barbata* were only minimally affected by BFOD, consistent with low rates of infection that we observed empirically (Fig. S2).

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Discussion

The long-term outcome of competition is difficult to observe directly in nature, so empirically parameterized mathematical models are critical for predicting when competitive exclusion, coexistence, or priority effects are most likely. To date, most studies have focused on pairwise outcomes in multispecies communities, emphasizing the relative strength of niche differences versus fitness differences (Levine and HilleRisLambers, 2009; Adler et al., 2010; Narwani et al., 2013; Godoy and Levine, 2014; Godoy et al., 2014; Kraft et al., 2015). By contrast, we found a large degree of niche overlap in an empirically parameterized model of an invaded California grassland (Fig. 1A). The model suggests that competition in multispecies assemblages can lead to complex outcomes that mix deterministic competitive exclusion or coexistence with stochastic priority effects that determine the identity of persisting species. Although a previous model predicted exotic annual dominance over native perennials, with a small probability of native coexistence with exotics, it did not predict priority effects among pairs of exotic or native species because it relied solely on a pairwise approach and composite parameter estimates from a range of species (Mordecai et al., 2015). Our work supports the results from a growing body of theoretical studies suggesting that competitive outcomes in complex communities can depart from predictions from pairwise species comparisons (Case, 1995; Allesina and Levine, 2011; Saavedra et al., 2017; Mayfield and Stouffer, 2017), and provides evidence that slowly occurring, nearly-neutral dynamics may play an important role in competitive outcomes (Adler et al., 2007). The results suggest that methods for assessing the outcome of competition in multispecies assemblages that move beyond invasion analyses are an important avenue for theoretical and empirical development (Saavedra et al., 2017; Barabás et al., 2018).

We found that the population growth model parameterized with field estimates of demographic rates accurately predicted species densities in monoculture (Fig. S6), suggesting that it can realistically capture equilibrium outcomes. In this five-species assemblage we found species pairs with high niche overlap—exotic annuals *B. diandrus* and *B. hordeaceus*; and native perennials *E. glaucus* and *S. pulchra*—and non-hierarchical competition such that no single species was dominant over all others (Fig. 1). This results in a complex posterior distribution of competitive outcomes that includes competitive exclusion of all other species by either *B. diandrus* or *B. hordeaceus*, or coexistence of one of these exotic annuals with one native perennial, either *E. glaucus* or *S. pulchra* (Fig. 2). The outcome of competition between the two congeneric exotic annuals was driven by strong interspecific competition, resulting in priority effects (Fig. 3). Among the subset of outcomes in which coexistence was predicted between *S. pulchra* and *B. diandrus*, the presence of *B. diandrus* usually prevented the subsequent invasion of *E. glaucus*, augmenting the priority effect exerted by *S. pulchra* on its native perennial competitor through non-

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423 hierarchical competition. Hence, invasion by an exotic species with moderate niche overlap may increase

424 resilience to invasion by native competitors with high niche overlap. Since the two native species are

425 predicted to compete nearly-neutrally in the model, almost all predicted outcomes precluded their long-

426 term stable coexistence, meaning that *S. pulchra* may indirectly benefit from invasion by *B. diandrus* via

427 its negative effect on *E. glaucus* (Fig. 4).

428 Studies applying modern coexistence theory have often documented substantial niche differences be-

429 tween species pairs, while variation in the magnitude of fitness difference determines the potential for

430 coexistence or competitive exclusion. However, these studies typically explore communities in which

431 species have long coevolutionary histories and belong to similar functional guilds (*e.g.*, native annual

432 forbs) (Levine and HilleRisLambers 2009; Adler et al. 2010; Godoy et al. 2014; Kraft et al. 2015; Narwani

433 et al. 2013; but see Godoy and Levine 2014). In such systems, we might expect that co-occurrence over

434 long timescales has led species to minimize their fitness differences, maximize their niche differences,

435 or both, leading to long-term stable coexistence. In invaded systems, exotic species must have fitness

436 advantages, niche differences, or both with respect to the native species in order to have successfully

437 invaded (MacDougall et al., 2009). Our study found support for large fitness advantages of invading

438 species and modest niche overlap that was potentially small enough to promote coexistence (20% poste-

439 rior probability). This is consistent with the possibility that competitive exclusion and priority effects

440 may be common long-term outcomes in invaded communities. Despite the *a priori* expectation of strong

441 stabilization within coevolved communities, our study did not identify substantial niche differences be-

442 tween the two native species or the two exotic *Bromus* species with an overlapping European home range.

443 Instead, the results suggest that nearly-neutral dynamics determine competitive outcomes in some pairs

444 of species with long coevolutionary histories.

445 Among the mechanisms that may maintain diversity in complex communities, intransitive competition

446 has received a great deal of interest (Laird and Schamp, 2006; Allesina and Levine, 2011; Soliveres et al.,

447 2015; Matías et al., 2018; Stouffer et al., 2018). However, a recent study using empirically parameterized

448 population dynamic models found that intransitive competition was uncommon and not likely to promote

449 coexistence among a set of 18 competing annual grass species (Godoy et al., 2017). In our study, although

450 we found evidence for non-hierarchical competition, simulations suggested that it was unlikely to promote

451 coexistence of more than two species. However, this does not imply that non-hierarchical competition

452 has no role in diversity maintenance. Priority effects, like those reported here, could lead to a spatial

453 patchwork of competitors, with disturbance and stochastic recolonization determining the distribution of

454 competing species.

455 Previous empirical work on the outcome of competition in invaded California grasslands has suggested

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456 a wide range of possible outcomes and coexistence mechanisms, including (1) the requirement for previous
457 disturbance to explain the invasion of exotics in perennial-dominated plots (Stromberg and Griffin, 1996;
458 Seabloom et al., 2003; Corbin and D'Antonio, 2004), (2) competitive dominance of exotic annuals over
459 *S. pulchra* (Dyer and Rice, 1997), and (3) spatial variation in outcomes determined by seed dispersal
460 (DiVittorio et al., 2007) and habitat (Everard et al., 2009). A limitation of most previous work considering
461 more than two competing species is that the empirical results were not linked to a dynamic model, making
462 it difficult to project dynamics over long timescales. Our parameterized model is inconsistent with (1)
463 because it predicts that exotic species can invade undisturbed perennial plots, and consistent with (2)
464 because a portion of predicted outcomes led to unconditional exotic dominance, as predicted in a previous
465 two-species model (Mordecai et al., 2015).

466 While our study did not attempt to assess environmental and spatial variation in competitive out-
467 comes (*i.e.*, prediction (3) above), coexistence mechanisms occurring over broad temporal and spatial
468 scales may be an important contributor to observed species distributions. The five focal species in our
469 system have co-occurred at the study site and other California grassland sites for over a hundred years, im-
470 plying that co-occurrence may be driven by non-equilibrium dynamics that play out over long timescales,
471 or that stabilizing processes occur over larger spatial or temporal scales. Although soil moisture and nu-
472 trient availability vary spatially at both neighborhood and regional scales across California grasslands and
473 precipitation varies several-fold between years, demographic studies of species interactions are regularly
474 conducted at small spatial and temporal scales, as in the present study (Seabloom et al., 2003; Corbin and
475 D'Antonio, 2004; DiVittorio et al., 2007). Environmental variation combined with the long lifespans of
476 perennial bunchgrasses and the high seed production of annual grasses could provide ample opportunity
477 for environmental fluctuations to promote coexistence over space or time (Warner and Chesson, 1985;
478 Cáceres, 1997; Chesson, 2000; Chesson et al., 2005; Li and Chesson, 2018; Usinowicz et al., 2017). An
479 alternative to larger-scale stabilizing processes is that priority effects occur at small spatial scales, while
480 the turnover and random colonization of sites allows patches of different species composition to persist
481 in a matrix of mutually non-invasible patches (Vannette and Fukami, 2014). Our results are consistent
482 with this priority effect mechanism, and do not preclude the possibility of coexistence mechanisms occur-
483 ring over larger scales. A major challenge for future work in systems with large and variable geographic
484 ranges is to incorporate multi-scale spatial and temporal variation that may contribute to patterns of
485 co-occurrence.

486 In addition to the outcome of competition, identifying explanatory mechanisms is paramount for
487 understanding the assembly of ecological communities and their potential to respond to species invasions.
488 Pathogens are widely hypothesized to promote species diversity by specializing on common host species,

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causing a demographic disadvantage to common species and an advantage to rare species (Mordecai, 2011, 2013; Bagchi et al., 2014; Petermann et al., 2008; Gilbert et al., 1994; Augspurger and Kelly, 1984; Augspurger, 1983). As with strong niche differences more generally, this Janzen-Connell effect has been demonstrated mostly in native-dominated plant communities (Augspurger, 1983, 1984; Augspurger and Kelly, 1984; Gilbert et al., 1994; Petermann et al., 2008; Bagchi et al., 2014). By contrast, pathogen impacts in this invaded grassland community differ in two important ways. First, the foliar fungal pathogens in this community typically infect multiple grass hosts, including native and exotic species (Spear and Mordecai, 2018). Second, the demographic impacts were mostly minimal, except the negative impact exerted by the Black Fingers of Death pathogen on *A. barbata* (Fig. 2B). Another study in this system found no evidence that pathogen load or impacts increased on locally common species, suggesting that coexistence is not substantially affected by fungal infection (Spear and Mordecai, 2018). However, because the two native perennial species compete almost neutrally in our model, even modest pathogen impacts could have a substantial effect; because their fitness differences are small, our study may have been underpowered to investigate this specific outcome.

Though the outcome of competition in invaded systems is often poorly understood, our work shows that stabilizing niche differences, and particularly the role of pathogens in that stabilization, are not ubiquitous at local scales in nature, especially in systems with short coevolutionary histories between species. Assessing the strength of stabilization and the outcome of competition is important not only for fundamental ecological understanding but also for maintaining resilient ecosystems as they respond to global change. Future work in other systems that are potentially far from equilibrium, such as invaded ecosystems, is necessary to test the generality of our results, and to predict the long-term outcome of competition in nature.

Acknowledgments

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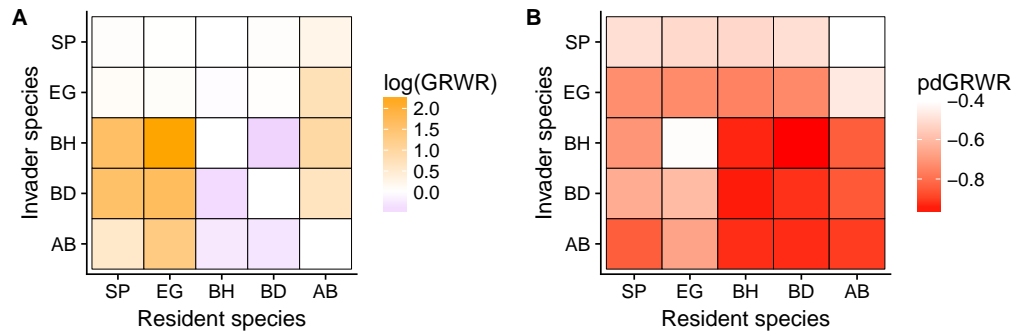
Figures

Figure 1: Strength of pairwise competition inferred from the growth rates of invaders introduced at low density to established monocultures of residents. A: log of growth rate when rare (GRWR) – log(GRWR)> 0 is the invasion criterion. Larger positive values (darker yellow/orange) represent high niche overlap, while darker purple represents less overlap. B: shows the proportional difference in each species growth rate in the presence of the resident species as compared to its growth rate in the absence of competition. p. (Abbreviations: perennial native species (*S. pulchra* (SP), *E. glaucus* (EG)), annual exotic species (*A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD))).
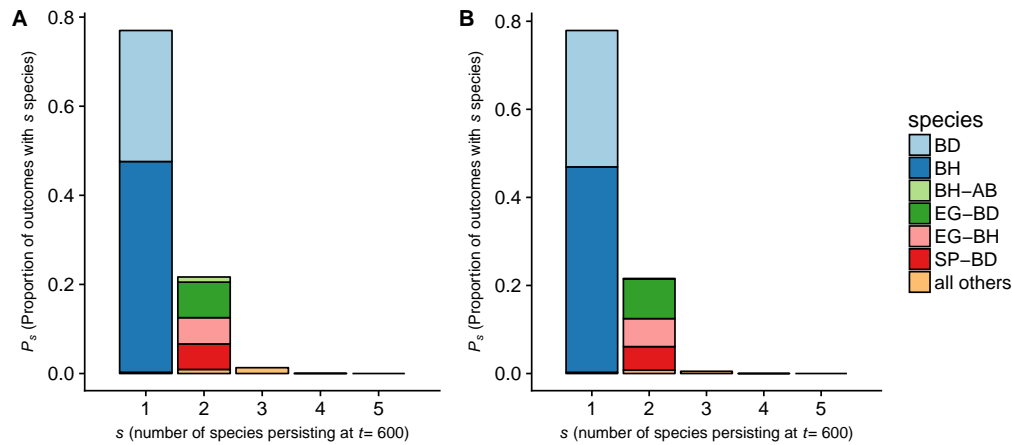
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Figure 2: The proportion of outcomes in which a given species or species combination persisted after 600 generations in the population dynamic model. Each replicate represents a single sample from the posterior distribution of the model parameters, and initial competitor densities from a randomly sampled transect from among the set of transects that we measured. The x-axis corresponds to the number of species (s) that persisted over 600 simulated years, while the y-axis corresponds to the proportion of replicates (P_s) that resulted in this outcome. Each bar is subdivided into the specific set of species that were observed to have log(GRWR)> 0 for a particular parameter set and transect sample. All compositions that occurred in under 1% of replicates are grouped into a single color. A: results from a model that includes foliar fungal infection but not BFOD; B: results from the model that includes both foliar fungal infection and BFOD. (Abbreviations: perennial native species (*S. pulchra* (SP), *E. glaucus* (EG)), annual exotic species (*A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD))).
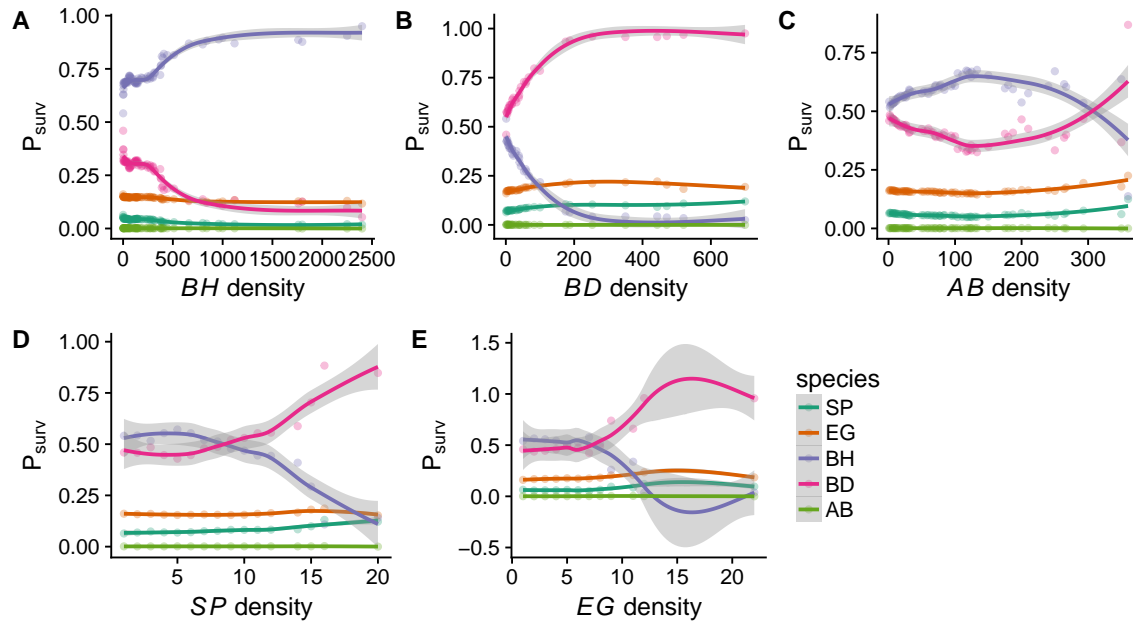
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Figure 3: Effect of initial conditions on the outcome of competition. Estimated probability of persistence (P_{surv}) of each species (colored points and lines) as a function of initial density of each species in the simulation (x-axis). Points represent the proportion of simulations resulting in persistence that were initialized at the corresponding density, while loess curves (and gray uncertainty envelopes) were fit with the function `geom_smooth` in `ggplot`. (Abbreviations: perennial native species (*S. pulchra* (SP), *E. glaucus* (EG)), annual exotic species (*A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD))). Priority effects occur when the probability of persistence depends strongly on initial density.
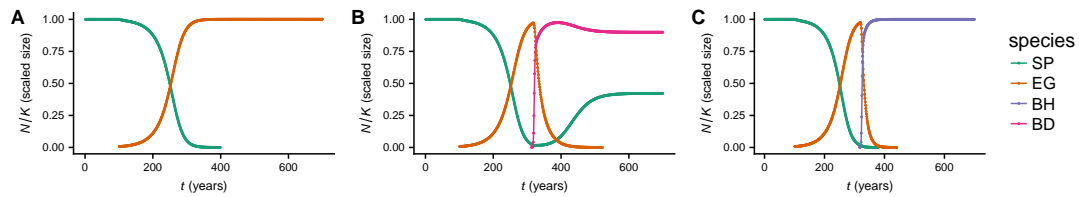
Figure 4: Effect of exotic annuals on invasion dynamics. A-C correspond to a single set of parameter estimates sampled from the posterior distribution. A: EG invades at $t = 100$, and is able to establish and eventually replace SP . B: EG invades at $t = 100$, and is able to establish and gradually replace SP. BD invades at $t = 220$, and coexists with SP, reversing the invasion of EG and preventing EG and BH from invading in the future. C: EG invades at $t = 100$, and is able to establish and gradually replace SP. BH invades at $t = 220$, and out-competes both perennials. BD cannot invade due to the priority effect between BD and BH. Units on the y-axis correspond to population sizes relative to monoculture density (Abbreviations: perennial native species ($S.$ $pulchra$ (SP), $E.$ $glaucus$ (EG)), annual exotic speices ($B.$ $hordeaceus$ (BH), and $B.$ $diandrus$ (BD))).

Parameters & variables	Description
α_{jl}	per-capita competition impact of species l on species j
β_j	impact of foliar fungal infection per unit area infected
A_j	mean leaf area infected
λ_j	mean seed output in the absence of infection and competition
$f_j(t)$	compound impact of competition and infection on seed output
S_j	seed output after accounting for competition and infection
g_j	germination fraction
γ_j	seed survival rate in presence of BFOD pathogen
ν_j	seedling survival rate
ϕ_j^I	establishment probability for infected seedlings
ϕ_j^U	establishment probability for un-infected seedlings
D_l	density of competitor species l per m^2
ν_j^0	seedling transition rate in the absence of competition
$\nu_j(t)$	seedling transition rate after accounting for competition
α_s	impact of seedlings on seedling-adult transition
α_a	impact of perennials on seedling-adult transition
α_n	impact of exotic annuals on seedling-adult transition
D_s	density of seedlings per m^2
D_a	density of exotic annuals per m^2
D_n	density of perennials per m^2
P_j^I	proportion of seedlings infected during seedling-adult transition
ξ_j	rate of perennial adult over-summer survival
$n_j^a(t)$	number of annual seeds at time t
$n_j^p(t)$	number of perennial seeds at time t
$a_j(t)$	number of perennial adults at time t

Table 1: Descriptions of parameters and variables that are relevant to our population dynamic model. Where not otherwise specified, j subscript refers to species j.

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Supplemental methods & figures

Competition experiment

To measure the impact of intra- and interspecific competition on seed production, we set up an experiment to vary the density of each plant species in monoculture and measured its per-capita impact on seed production for each competitor species (Mordecai, 2013; Levine and HilleRisLambers, 2009). We attempted to limit the seed bank by preventing seed set the year prior to the experiment. In the spring of 2015 before seed set, we laid down weed matting across a 35m x 35m area near the Sun Field Station in Jasper Ridge Biological Preserve. We cut holes in the matting to allow existing adult perennial plants (mostly *S. pulchra*) to survive. In fall 2015 before the first major rains, we removed the weed matting and established 210 1-m^2 competition plots and 30 4-m^2 competition-free plots. All plots had a 1-m untreated buffer area from all other plots on all sides.

We manipulated background competitor species density and fungal abundance in a factorial design. The competition plots were randomly assigned to treatments across five densities, seven background "species-groups" (*Avena barbata, Bromus diandrus, Bromus hordeaceus, Elymus glaucus* seedlings, *E, glaucus* adults, *Stipa pulchra* seedlings, and *S. pulchra* adults), and three fungal manipulations (fungicide, water controls, or fungal inoculation with liquid inoculum). Because the fungal inoculum was not successful in increasing fungal infection and fungicide only modestly reduced fungal load, we pooled all three treatments into a single dataset, and we do not describe fungal growth, inoculation, and fungicide methods here. In total there were two replicate plots of each background species x density x fungal treatment. We additionally established competition-free plots that aimed to have a single individual of each of the seven focal species-groups growing in the absence of competition with all other plants removed from the 2m x 2m plot area.

In the competition plots we sought to create a gradient of densities with each species-group as the 'background' species that comprised the dominant competitor environment, plus each remaining species-group present in low density to gauge the impact of the competitor environment on per-capita seed production for each species. Background competitor densities aimed for 10%, 20%, 40%, 80%, and 100% of the density of each plant species in monoculture, where monoculture densities were estimated by counting plants m^{-2} in the surrounding area. Monoculture densities were estimated at 10 adults m^{-2} for each of the two perennial species, 1,715 seeds m^{-2} for *A. barbata*, 3,209 seeds m^{-2} for *B. diandrus*, 12,544 seeds m^{-2} for *B. hordeaceus*, 4,585 seeds m^{-2} for *E. glaucus*, and 1,466 seeds m^{-2} for *S. pulchra*. In November, 2015, we added seeds and transplanted adult *S. pulchra* plants to achieve the desired density treatment in each plot, removing excess bunchgrasses from plots as needed. We transplanted adult *E. glaucus* plants from an area 1 km away into the plots in December, 2015. All transplants were watered to settle the soil. We then added approximately 10 seeds of each non-background species in January, 2016, marked with plastic cutlery stuck into the ground, and one adult of each perennial species, marked with a small plastic ring, to each plot to ensure that all focal species were represented in each plot. These would become the focal individuals on which we would assess seed production. In the competition-free plots we seeded approximately 10 seeds/species into separate locations within the 2m x 2m plots, each marked by plastic cutlery, plus one individual adult of each perennial species, marked by plastic rings. Finally, we reseeded 18 of the 240 plots with 75-100% of their original treatment seed weight in January, 2016 following low germination.

In addition to applying weed matting to prevent seed set the prior year, we weeded the plots extensively to remove target and non-target species and to thin plots to the desired density. However, despite these efforts a substantial density of non-target plants naturally recruited into the plots. As a result, although the experiment manipulated competitor density, it did not achieve the predetermined plant density targets. For this reason, we censused plant density and species at peak flowering in the spring, and used these actual competitor density estimates as inputs into all competition models.

We attempted to harvest seeds from all marked focal individuals in all plots in May-June 2016 when they matured but before they dehisced and dispersed. Because the seeds of *A. barbata* and *S. pulchra* dehisced very quickly at maturity and the timing varied within an individual, we harvested and counted the glumes of those individuals and estimated the number of seeds per glume to get an overall estimate of seed production (two seeds per glume for *A. barbata* and one seed per glume for *S. pulchra*).

Transect plots

We also measured the impacts of competition on seed production in plots that naturally varied in plant composition, to understand the strength of competition in established plant communities. In the 2015 growing season, we set up six transects in the area surrounding the Sun Field Station at Jasper Ridge Biological Preserve. Each transect varied in grass composition from native perennial-dominated at one end to exotic annual-dominated at the other, with five 1-m^{-2} plots spanning each transect spaced approximately 5-10m apart. Individual plots were placed based on desired plant community compositions, thus plots were unevenly spaced (3 to 18m apart). Transects ranged from 20m to 50m in length. Three of the transects were dominated by *S. pulchra* at the perennial end, and the other three were dominated by *E. glaucus*. We surveyed plant density and community composition in the 2015 growing season. In 2016 we returned to these transects and used only the first, third, and fifth plot in each transect, representing perennial-dominated, intermediate, and annual-dominated plots, respectively. We paired each plot with two additional 1-m^2 plots next to each original plot that were visually similar in composition, for a total of three sets of triplet plots per transect. In each triplet of plots, one received fungicide, one received a water control, and one received fungal inoculum. Again, the fungal inoculation was not successful at increasing pathogen infection, and fungicide only modestly decreased pathogen load, so we combined data from all treatments. We seeded approximately 20 seeds of each focal species, and transplanted an adult *S. pulchra* and/or an adult *E. glaucus* plant into each plot that lacked these species (seeding and transplanting were done on the same days as the competition plots described above). We censused the density of each plant species during peak flowering (when grasses are easiest to identify), then harvested all seeds from up to three individuals of each focal species present in each plot. We used data on the number of seeds per individual and competitor density to parameterize competition models, as described below.

Competition & infection model

We use a simple model of competition between individuals on a patch, in which seed output S is affected by the density of competing individuals and infection burden. Since we observe that S has an over-dispersed distribution that is well described by a negative binomial (Fig. S4), we allow S to follow a negative binomial distribution.

$$P(S|r,p) = \frac{\Gamma[S+r]}{\Gamma[S+1]\Gamma[r]}(1-p)^r p^S, \tag{10}$$

where Γ is the gamma function, and p and r are parameters that govern the mean and variance of the negative binomial distribution. We suppose that the expected fitness f of individual i in species j is a function of the number of individuals competing in the patch, and the amount of infected leaf tissue of each individual such that

$$f_{ij} = \frac{1}{1 + (\sum_l \alpha_{jl} D_l) + A_{ij}\beta_j} \tag{11}$$

where D_l is the density of individuals of species l, and α_{jl} captures the strength of the impact of individuals of species l on j ($\vec{\alpha}_j$ is the vector of α_{jl} values). A_{ij} is the area of infected leaf tissue of individual i, and β_j is the impact of foliar fungal infection per unit leaf area infected on fitness for individuals

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749 of species j. We constrain the $\vec{\alpha}$ and β values to be non-negative, which captures our strong prior
750 expectation that interactions between species and infection should have a deleterious effect on fitness.
751 This competition model was previously studied in other systems (Mayfield and Stouffer, 2017). We
752 incorporate the competition model into seed output S by allowing the mean of the negative binomial
753 distribution to follow eqn. 11, while preserving the shape of the negative binomial. To do so, we allow
754 the r parameter of the negative binomial to be given by

$$r = r_0 f_{ij}, \tag{12}$$

755 where r_0 is the r parameter in the absence of competition and infection. This model formulation constrains
756 the mean seed output to be decreased proportional to the plant's competitive fitness f_{ij} given its local
757 competitors and its infection burden. Hence, the full likelihood of the observed seed output S given
758 competitor density is

$$P(S|r_0, p, \vec{\alpha}_j, \beta_j) = \frac{\Gamma[S + r_0 f(\vec{\alpha}_j, \beta_j)]}{\Gamma[S+1]\Gamma[r_0 f(\vec{\alpha}_j, \beta_j)]}(1-p)^{r_0 f(\vec{\alpha}_j, \beta_j)} p^S. \tag{13}$$

Estimating competition and foliar infection parameters

760 We wrote custom MCMC software in Python to perform parameter estimation under our model of
761 competition and infection within a growing season. We suppose that the data correspond to a vector of
762 observed seed outputs, competitor densities, and leaf-area infected for each plant, and we seek to infer each
763 of the α and β parameters with this method. Our software implements a standard Metropolis-Hastings
764 algorithm. We compute the likelihood function with eqn. 13, and apply an uninformative Γ-shaped prior
765 on $\vec{\alpha}$ and β such that these parameters are constrained to be non-negative. We thinned the observed
766 MCMC traces such that we do not observe strong autocorrelations. We performed 20 independent MCMC
767 runs for each focal species, and found nearly identical parameter estimates across independent runs. Our
768 software is freely available by request and will be posted on the web at a future date.
769   To assess the performance of our MCMC-based inferences, we performed simulations of seed output
770 under our model and assessed our ability to recapture the parameters that were used to generate the
771 simulated data. For each simulation, we selected a focal plant species j and randomly selected competition
772 parameters $(\vec{\alpha}_j)$ and infection parameters (β_j) from uniform priors. We then selected the p and r_0
773 parameters such that the observed mean seed output would exactly match the expected seed output in
774 the simulations. For each plant of species j in our dataset, we then simulated a new seed output based
775 on the true density of competitors for this plant and the randomly sampled competition and infection
776 parameters. We then ran our MCMC pipeline on the simulated data, and compared the mean of the
777 posterior distribution of inferred parameter estimates to the true parameter estimates. We find that our
778 method is approximately unbiased and reasonably accurate. A subset of the results of this experiment
779 are plotted in Fig. S5.
780   Having obtained estimates for the full suite of parameters of our model, we sought to compare
781 predicted seed densities from our model to field observations. For each focal species, we obtained field
782 estimates of the seed density when grown in monoculture and compared them to simulation-based predic-
783 tions under our demographic model. For each species j, we selected a random estimate for the competition
784 parameters α_{jj} and infection parameters β as well as estimates of the other relevant parameters by sam-
785 pling from the inferred posterior distribution of each parameter and then used a forward simulation under
786 our population dynamic model to obtain an estimate of the final monoculture density. We then compared
787 this set of predicted monoculture densities to the median estimates obtained from our field observations.
788 While monoculture density estimates from our model are noisy, they are concordant with and of similar
789 magnitude to the field estimates (Fig. S6).

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Sensitivity analyses

To better understand which demographic parameters are most important for determining the outcome of competition (*i.e.*, GRWR) for each species, we independently increased each parameter by 5% for each posterior estimate. For simplicity, for each species, we limited this experiment to the set of parameters that directly impact its growth (*i.e.*, its own demographic rates: for each species j, only parameters subscripted with j). To further reduce the number of parameters, we simultaneously increased all parameters pertaining to the impact of competition on perennial transition from seedling to adult (*i.e.*, α_a, α_n, and α_s), which we then denote as a composite parameter α_{P_T}. We included both BFOD infection and fungal foliar infection for this analysis, although the impact of foliar infection was negligible. We compared the predicted GRWR for each species with and without the 5% increase and computed the change in GRWR as ΔGRWR. We report the median ΔGRWR over all posterior samples.

The population growth of both perennial species was most sensitive to the over-summer survival of adult individuals (ξ), and essentially insensitive to all other parameters (Fig. S8). *A. barbata* was highly sensitive to γ (*i.e.*, the proportion of seeds escaping infection by BFOD), which is unsurprising given the large impact of BFOD on *A. barbata* in the previous analyses and the large burden of infection on *A. barbata* seeds (Fig. S2). *B. diandrus* and *B. hordeaceus* were modestly positively impacted by increasing the probability of establishment for both infected and uninfected seedlings (ϕ^i and ϕ^u), and per-capita seed production, λ, but negatively impacted by increases in γ and interspecific competition with each other.
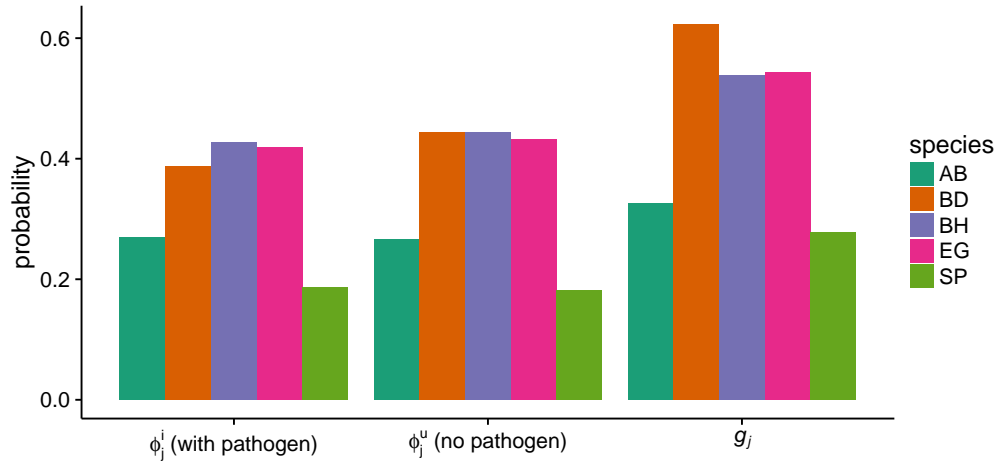
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Figure S1: Estimated germination (g_j) and establishment (ϕ_j) probabilities for each species j. Establishment probability was estimated in the presence and absence of foliar fungal pathogens.
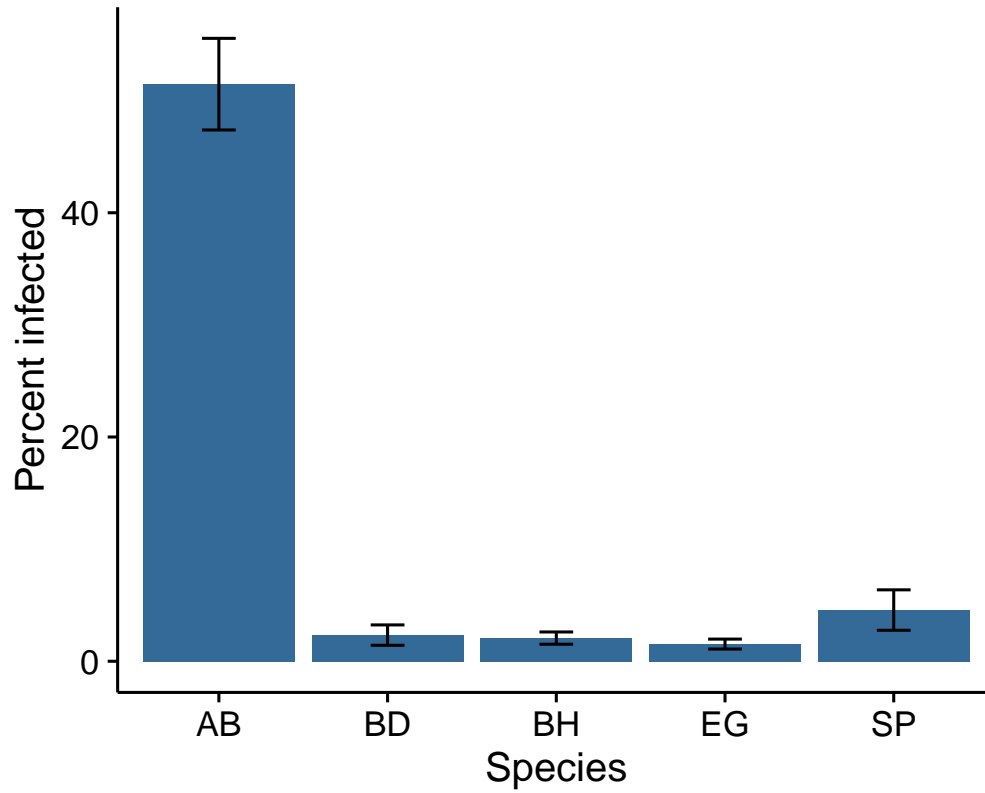
Figure S2: The proportion of seeds that were infected by the Black Fingers of Death pathogen in a seed bag experiment, by species. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).
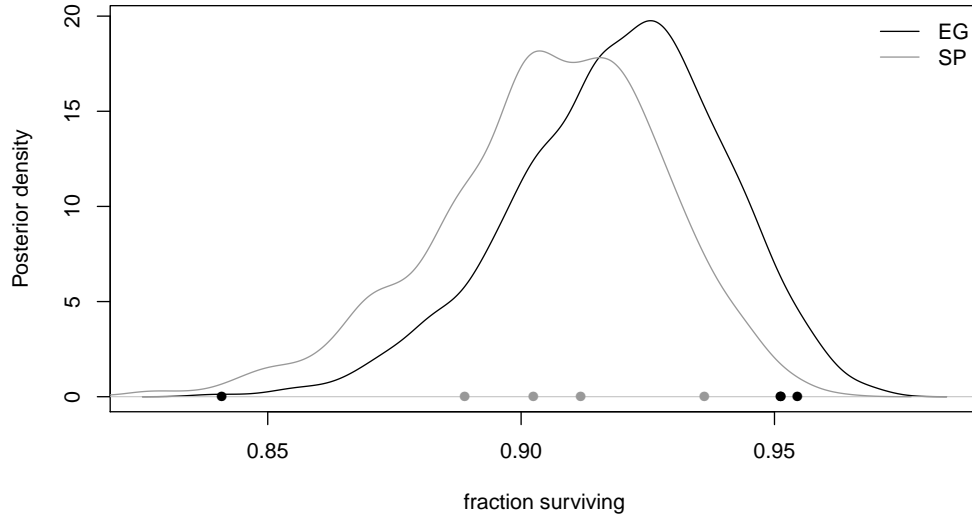
Figure S3: Estimates of the probability of adult perennial over-summer survival rate (which we term ξ_j in our model). The observed fraction of plants surviving across four sampling sites are plotted as points along the x-axis, while the curves represent the posterior density. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG)).
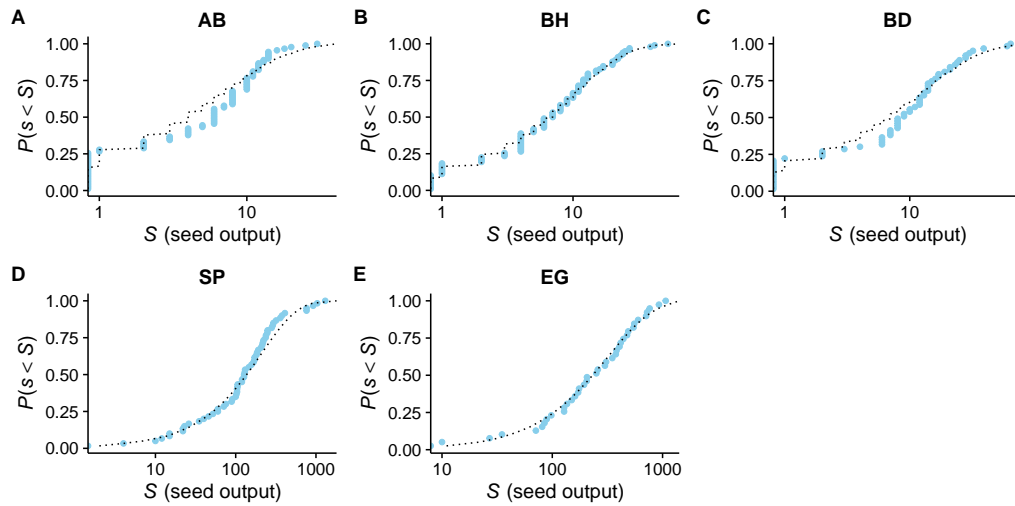
Figure S4: The cumulative distribution of observed seed counts ($P(s > S)$) is plotted as a function of seed count S. Each point represents the fraction of plants that have a seed count less than S. The dashed blue lines show the cumulative distribution of the best fitting negative binomial distribution, obtained my maximum likelihood. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).
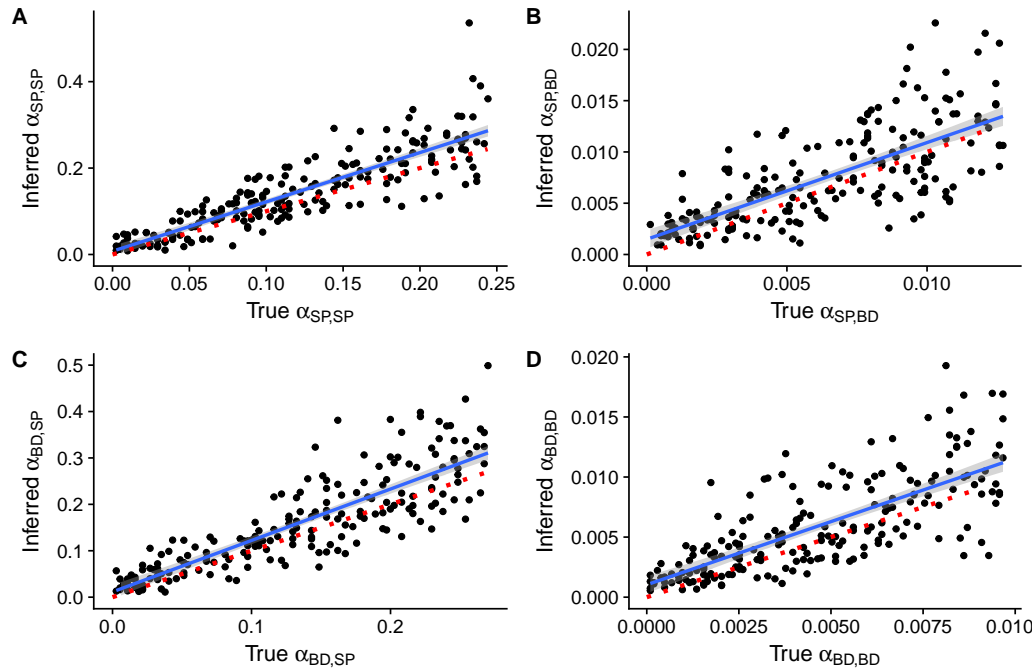
Figure S5: True and inferred parameter values as determined by our MCMC method, as obtained from simulation. The inferred values represent the mean of the inferred posterior distribution. The lines and envelopes (in gray) were fit using a simple linear model of the form $y\ mx + b$ with the method `"lm"` in the function `geom_smooth` in `ggplot2`, while the red dashed lines show the diagonal (*i.e.*, the expectation if inference were perfect). $\alpha_{BD,SP}$ is the impact of *S. pulchra* on *B. diandrus*. (Abbreviations: *S. pulchra* (SP) and *B. diandrus* (BD)).
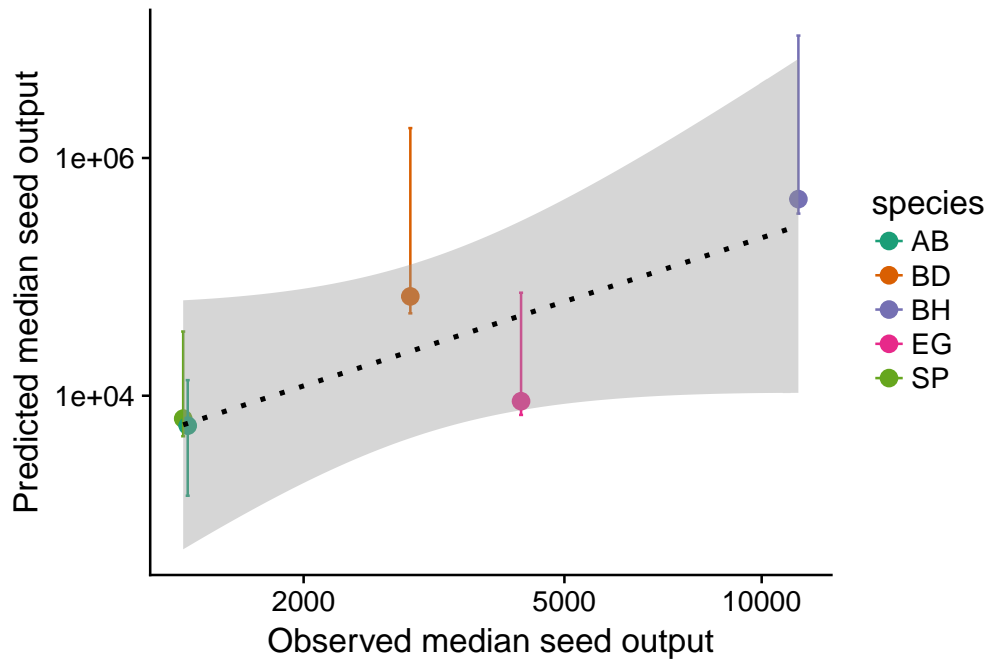
Figure S6: Observed median monoculture seed output densities plotted against those predicted by our population dynamic model. Error bars represent the inner 95% of parameter estimates from our model. The line and envelope (in gray) were fit using a simple linear model of the form $y\ mx{+}b$ with the method `"lm"` in the function `geom_smooth` in `ggplot2`. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).
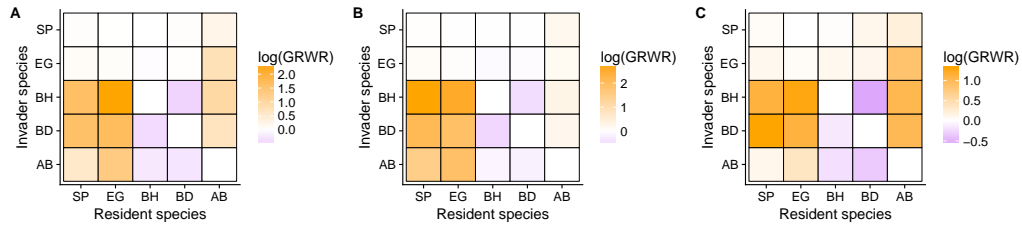
Figure S7: Comparison of pairwise invasion analyses using A: all data (competition plots and transects), B: only the data from the competition experiment, or C: only data from the transects. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).
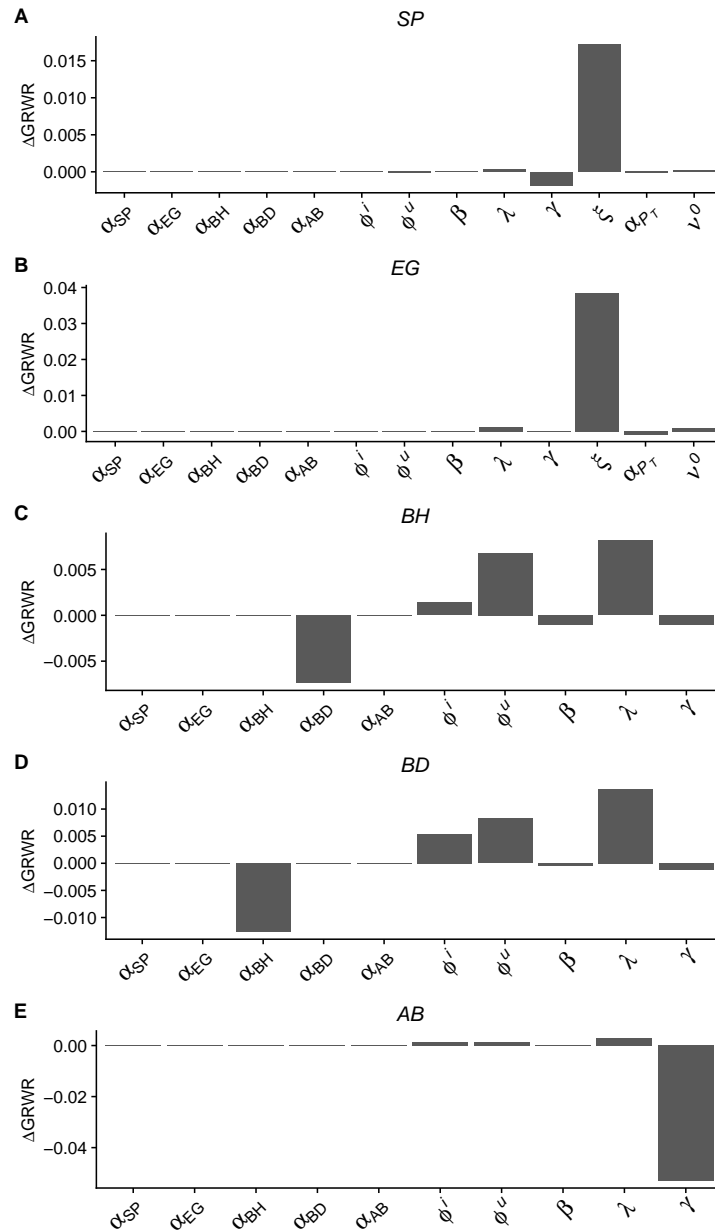
Figure S8: Sensitivity analysis results. For each species, we plot the proportional difference in GRWR when the corresponding parameter is increased by 5%. α_{SP} denotes the impact of *S. pulchra* on the focal species, α_{EG} represents the impact of *E. glaucus* on the focal species, etc. Parameters are defined in Table 1. (Abbreviations: perennial native species (*S. pulchra* (SP), *E. glaucus* (EG)), annual exotic species (*A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD))).