Non-hierarchical competition and priority effects 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 collected empirical data and developed a dynamic model of a grassland community with two native and three exotic species. 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 (80% of outcomes), while a complex mixture of non-hierarchical competition and coexistence between native and exotic species occurred in a substantial minority (20%) of posterior estimates. 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

the timescale of experiments. Theoretical coexistence models based on species differences offer a powerful alternative for predicting competitive outcomes (Burdon and Chilvers, 1974; Tilman, 1980; Holt et al., 1994). However, linking models to real ecological communities is challenging because realistic parameter estimates are rarely available for species interacting within a single ecological context. Moreover, existing theoretical approaches often make simplifying assumptions–such as reducing analyses to pairs of interacting species rather than considering the full dynamics of the assemblage–that may affect the inferred outcomes. As a result, considerable uncertainty remains about the relative importance of various proposed diversity-maintenance mechanisms, and the outcome of competition can be difficult to predict.

Among several theoretical frameworks for species interactions that have been proposed, modern coexistence theory clarifies the mechanisms through which species differences affect the outcome of competition via their effects on niche differences and fitness differences (Chesson, 2000). Niche differences are the differences between species in resource use, natural enemies, habitat requirements, or other factors that force per-capita impacts of competition within species to exceed those between species (Chesson, 2000). These niche differences cause population growth to be negatively frequency-dependent because species achieve their highest per-capita growth rates when they are rare and interact with mostly heterospecific competitors, while per-capita growth declines as species become common and interact with many conspecific competitors. By contrast, in this framework, fitness differences are those differences between species that determine per-capita growth rates independent of relative abundance, often including differences in fecundity, resource acquisition, or survival. Coexistence occurs when niche differences, which generate negative frequency-dependent population growth or 'stabilization', are strong enough to overcome fitness differences between species (Chesson, 2000). Alternatively, priority effects can occur when population growth is positively frequency-dependent, allowing any species that is initially more common to exclude others but preventing species from invading when rare in the presence of competitors (Mordecai, 2011; Fukami et al., 2016). While assessing competitive outcomes in pairs of species with known parameter values is straightforward in this framework, predicting multispecies outcomes remains a challenge (Saavedra et al., 2017).

Modern coexistence theory has motivated a suite of studies that empirically measure the strength of niche differences and fitness differences, and ultimately the outcome of competition, in natural plant or algal communities. Many of these studies have found a strong influence of stabilizing niche differences on species coexistence (Turnbull et al., 2005; Adler et al., 2006; Levine and HilleRisLambers, 2009; Adler et al., 2010; Narwani et al., 2013; Godoy et al., 2014; Kraft et al., 2015; Godoy et al., 2017). However, almost all empirical applications of modern coexistence theory use pairwise growth rates when rare to assess community-wide outcomes (*e.g.,* Adler et al., 2007; Levine and HilleRisLambers, 2009;

Adler et al., 2010; HilleRisLambers et al., 2012; Mordecai, 2013; Godoy et al., 2014; Kraft et al., 2015; Mordecai et al., 2015). A growing body of theory shows that outcomes of competition may depart from pairwise predictions when all species are analyzed simultaneously (*e.g.,* Case, 1995; Allesina and Levine, 2011; Saavedra et al., 2017; Mayfield and Stouffer, 2017). Deviations from pairwise predictions may originate from non-hierarchical interactions, in which competitive impacts are intransitive, or higher-order interactions, in which the per-capita impact of one species on another is mediated by interactions with a third species. In complex communities it is theoretically possible to observe priority effects within groups of species with high niche overlap and fitness similarity, which occur alongside deterministic coexistence or competitive exclusion between groups of species with larger niche differences and fitness differences. Despite these theoretical developments, there are few empirical examples of communities in which multispecies outcomes depart from two-species predictions (but see Mayfield and Stouffer, 2017; Godoy et al., 2017). It is unknown whether departures between pairwise and multispecies predictions are a common biological phenomenon or a quirk of mathematical models. Moreover, it is not clear how ecological contexts – such as the coevolutionary history of the competing species and the level of disturbance – may influence the likelihood of complex multispecies dynamics as compared to negative frequency-dependent stabilization (Ocampo-Ariza et al., 2018).

We hypothesized that complex multispecies dynamics would be likely to emerge in recently invaded systems, in which competing species have not had long coevolutionary histories and hence may not have had sufficient time to evolve into distinct niches (MacDougall et al., 2009). Such systems may be far from equilibrium, and hence may represent an opportunity to study complex multispecies dynamics in the absence of strong stabilizing mechanisms driven by niche differentiation. Moreover, predicting competitive outcomes in recently invaded systems is a pressing concern for conservation, and understanding the processes that have the largest impact on the persistence of native species could help preserve endemic biodiversity. In this study, we investigated competitive outcomes in California grasslands, one of the most ecologically important and widespread ecosystems in the Western U.S. As part of the California floristic province, this ecosystem is a key reservoir of biodiversity and endemic species (Myers et al., 2000). Simultaneously, California grasslands are heavily invaded and human-impacted since the 19th century (Mack, 1989), and exotic annual grasses have driven native perennial bunchgrasses and annual forbs to very low density throughout much of their extent. In the long term, it is not clear whether the exotic annual grasses will competitively exclude native perennial grasses, whether native grasses will stably persist (at reduced densities), or whether priority effects will determine whether native or exotic grasses dominate at a local scale.

Here, we combine field experiments with mathematical models to predict the outcome of competi-

tion in a community of five co-occurring native and exotic grasses in a Northern California grassland ecosystem. We develop and empirically parameterize population dynamics models for the species in this complex California grassland community. The models incorporate a suite of demographic rates experimentally measured for three different exotic annual grasses and two native perennial grasses at a single Northern California grassland site and include the impact of fungal pathogens on those demographic rates, which may affect competitive outcomes by altering fitness differences or by inducing negative frequency dependence of growth rates (Mordecai, 2011, 2013). We estimate parameters of the model statistically from field observations of seed output, germination, establishment, seed infection, and adult survival for each of five competing species of exotic annual and native perennial grasses. Using the parameterized model, we study the multispecies outcome of competition, with and without pathogens. Specifically, we ask: (1) How strong are intra- and interspecific competition between native and exotic grass species? (2) What is the predicted outcome of competition? (3) Do complex outcomes, including priority effects and/or intransitive competition, emerge from the dynamics of the full multispecies assemblage? (4) How strongly do foliar and seed pathogen impacts on demographic rates influence the outcome of competition? (5) Which demographic rates most strongly influence the outcome of competition?

Methods

Empirical data collection and parameter estimation

Study system

We chose five focal species that are highly abundant and widespread in California grasslands across coastal-to-inland, northern-to-southern, and open grassland-to-oak savanna environments: the exotic annual grasses *Avena barbata*, *Bromus diandrus*, and *Bromus hordeaceus*, and the native perennial bunchgrasses *Stipa pulchra* and *Elymus glaucus*. For each species, we measured a full complement of demographic rates that determine population growth: seed germination, seedling establishment, the impact of competition on per-capita seed production, and over-summer survival (for both seedling and adult perennial bunchgrasses). All experimental work was conducted in Jasper Ridge Biological Preserve, located in San Mateo County, California (3724'N, 12213'30"W; 66 - 207 m). This 485-hectare biological preserve is managed by Stanford University and has a Mediterranean climate with cool, wet winters and warm, dry summers (mean annual precipitation = 622.5 mm) (Ackerly et al., 2002). All demographic rates (with the exception of those pertaining to perennial seedling to adult transition; see below) were measured in

the 2015-2016 winter to spring growing season (hereafter, the 2016 growing season); with a total of 601 mm precipitation distributed over 20 precipitation events, this was an average rainfall year.

Competition experiment & transect sampling

Seed output is an important component of plant fitness, and is strongly impacted by competitor density for many plants (Mordecai, 2013; Mordecai et al., 2015). Therefore, we gathered data on seed output as a function of competitor density for the five focal species. We varied the density of each plant species in monoculture and in mixed-species plots and measure per-capita impact on seed production for each competitor species (Mordecai, 2013; Levine and HilleRisLambers, 2009). The 1-m^2 competition plots were randomly assigned to five competitor density treatments ranging from 10% - 100% of each species' estimated natural density in monoculture, for each of the seven background 'species-groups' (*A. barbata, B. diandrus, B. hordeaceus, E. glaucus* seedlings, *E. glaucus* adults, *S. pulchra* seedlings, and *S. pulchra* adults). We used weed matting, weeding, and seed addition to manipulate competitor densities. At the end of the 2016 growing season we measured seed output from up to three focal plants per species per plot (as available). See Supplementary Materials for a complete description of the competition experiment.

We also measured the impacts of competition on seed production in transects that naturally varied in plant composition. 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. Three of the transects were dominated by *S. pulchra* at the perennial end, and the other three were dominated by *E. glaucus*. For each focal plant in the transects we estimated seed output, in both the 2015 and 2016 growing seasons.

To assess pathogen damage and its relationship with seed production and competitor density, we estimated leaf area damaged by fungal infection on a subset of leaves sampled from each focal plant in both the transects and experimental plots. We used these data to quantify the impact of foliar fungal infection on seed output, as well as the impact of plant species local relative abundance on pathogen damage. We note that this approach could underestimate the impact of fungal infection if resistance is generally costly, and most surveyed plants are actively fighting infections.

Our attempt to manipulate competitor densities in the experimental plots was only partially successful because of recruitment from the seed bank. As a result, we combined all plants into a single data set of seed outputs and observed competitor densities (rather than using the target densities for the experimental plots). Our final dataset included 439 *A. barbata*, 399 *B. hordeaceus*, 319 *B. diandrus*, 387 *S. pulchra*, and 234 *E. glaucus* individuals (see Supplementary Materials for further details).

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

petition (α), and foliar infection (β) from our competition experiment data (see dynamic model section and Table 1 for parameter definitions), and performed simulation-based validation of our estimation procedure. Full details of this estimation procedure and its validation are provided in the Supplementary Materials, along with a more detailed description of the experimental design. Out of concern that combining across experimental and observational data could induce artifacts, we repeated the parameter inference procedures on subsets of the data that included either only the experimental plots or only the transects. Although there are subtle differences between the predictions made from each dataset, we found that parameter values were of similar magnitude and generally had overlapping posterior distributions, and that estimates of pairwise invasion produced very similar results across datasets (see Fig. S7 and Supplementary Materials).

Germination data

We planted marked seeds of each focal species to track germination and seedling establishment. We established 30 plots and planted 25 individuals of each of the five focal species into each plot on November 19, 2015. During the germination and establishment period in January - February, their status was recorded weekly for four weeks as missing (M), alive (A), or alive with $> 50\%$ of leaf area with pathogen damage (P) each week. We used a Markov model to estimate the probability of establishing, surviving, and becoming heavily infected for each species. Specifically, we constructed a 3 x 3 matrix of all possible state transitions between M, A, and P, and used the weekly observation data to calculate weekly transition probabilities by plant species. Starting with the observed distribution of states in week 1, we used the matrix to project forward four weeks to estimate the overall probability of germinating (being alive at some time step) and establishing (being alive at the final time step). We repeated this calculation both with pathogens present (as observed in the data) and with pathogens removed (*i.e.*, as if all individuals experienced the establishment rates of uninfected individuals), in order to understand the impact of pathogens on seedling establishment. Inferred germination (g_j) and establishment (ϕ_j^U and ϕ_j^I for uninfected and infected individuals, respectively) parameters for each species j are plotted in Fig. S1.

Seed survival and infection data

Seeds that remain dormant in the seed bank during the first year after they are produced may still contribute to population growth when they eventually germinate. To assess survival of non-germinating seeds between years, we buried 30 mesh seed bags that each contained five sewn compartments (one per focal species): each compartment contained 100 seeds of a single focal plant species. The bags were

buried 2-5 inches deep from November 19, 2015 to July 11, 2016. Upon recovery, we retrieved all intact seeds and scored them for "Black Fingers of Death" (BFOD) pathogen damage (Beckstead et al., 2010; Mordecai, 2013), which is likely caused by one of the numerous *Pyrenophora* spp. that are common in these sites (Spear and Mordecai, 2018). We tested all intact, non-germinated seeds for viability using established methods (Mordecai, 2012): we first attempted to germinate the seeds in plastic boxes on wetted germination paper at ambient laboratory temperature for three weeks (following a one-week cold treatment at 15°C), then used gibberellic acid to stimulate germination in the remaining non-germinated seeds, and finally cut a subset of non-germinated seed embryos to assess whether they appeared viable. Since all of the cut embryos were clearly non-viable, we did not proceed with tetrazolium staining as in previous work (Mordecai, 2012). Estimates of seed infection with BFOD for each species are plotted in Fig. S2. We parameterize the fraction of seeds that succumbed to BFOD infection as γ_j for species j.

Adult survival data

Perennial transition from seedling to adult

We modeled perennial seedling over-summer survival and maturation into adulthood as a function of competitor density and per-capita competitive effects. We used data and fitted parameters from previously published work (Mordecai et al., 2015). Briefly, we modeled perennial seedling over-summer survival and transition into adulthood as a Beta-Binomially distributed process where for each observation k, the number of surviving seedlings maturing into adulthood was:

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

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 survival and maturation to adulthood probability in the absence of competition, α_j are the per-capita competitive effects of individuals of species j, and D_{kj} are the number of individuals of species j in observation k. In the Beta-Binomial distribution d is a parameter that affects the mean and variance, and n_k is the number of trials in observation k. The equation for Y_k is parameterized so that its mean is equal to μ_k. In fitting this model, we lacked the data to separately estimate α_j for each individual species in our sample, so we estimate a distinct α_j for each of the following competitor groups: perennial adults, perennial seedlings, and exotic annuals.

Population dynamic model

Model structure

We developed a dynamic model that captures the effects of competition and fungal infection on growth rates for each grass species in our system, including both exotic (annual) and native (perennial) species. The model is structurally similar to models developed in previous work (Mordecai, 2013; Mordecai et al., 2015), with some modifications as described below. To model the effects of competition on the long-term growth of each species, we suppose that each plant of species j has a seed output of λ_j in the absence of competition, and that competition reduces seed output by a factor of $\frac{1}{1+\sum_l \alpha_{jl} D_l(t)}$, where $D_l(t)$ is the density of competitor species l per m^2 at time t. Similarly, infection reduces seed output by a factor of $\frac{1}{1+A_j\beta_j}$, such that

$$S_j(t) = \lambda_j f_j(t), \tag{2}$$

where $S_j(t)$ is seed output after accounting for foliar infection and competition, $f_j(t) = \frac{1}{1+\left(\sum_l \alpha_{jl} D_l(t)\right)+A_j\beta_j}$ and A_j is the mean leaf area that was infected on individuals of species j (note that we will later use n_j to denote the total number of seeds produced by species j, whereas S_j is the number of seeds produced by one individual of species j). We do not explicitly model transmission of fungal pathogens in this system, since we do not have information about transmission between individuals. Instead, when we include infection in the model, we assume that each individual is infected at the mean level of observed foliar fungal infection per unit area for species j. Hence, the seed output for all individuals of species j in a given patch is the same, because all share the same density of competitors and the same level of infection.

For each species j, we suppose that a fraction g_j of the seeds germinate, and among these a fraction γ_j are infected with a fungal seed pathogen (BFOD). Seeds that germinate and are not infected may then establish, or may be eliminated before they ever produce seeds. We supposed that the probability of establishment might depend on the presence or absence of foliar fungal infection, and as described in the Germination Data section, we separately estimated the probability of establishment for infected and uninfected seedlings. Therefore, for each species j we let the proportion of seedlings that establish be ϕ_j^I for infected individuals and ϕ_j^U for uninfected individuals. The proportion of seedlings that are infected during the transition is given by P_j^I.

Perennial seedlings are presumed to be weak competitors and are not included in the competition model and produce no seeds in the first year of life (Mordecai et al., 2015), but are subject to competition

in their survival over their first summer. Perennial seedlings survive at rate $\nu_j(t)$, given by

$$\nu_j(t) = \frac{\nu_j^0}{1 + \alpha_s D_s(t) + \alpha_a D_a(t) + \alpha_n D_n(t)}, \tag{3}$$

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

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

$$n_j^a(t+1) = n_j^a(t)\left(g_j\left(1-\gamma_j\right)\left(\phi_j^U(1-P_j^I) + \phi_j^I P_j^I\right)\lambda_j f_j(t) + (1-\gamma_j)(1-g_j)\right), \tag{4}$$

$$n_j^p(t+1) = a_j(t)\lambda_j f_j(t) + n_j^p(t)(1-\gamma_j)(1-g_j), \tag{5}$$

$$a_j(t+1) = a_j(t)\xi_j + n_j^p(t) g_j\left(1-\gamma_j\right)\left(\phi_j^U(1-P_j^I) + \phi_j^I P_j^I\right)\nu_j(t). \tag{6}$$

To simulate under this model, we require estimates of each of the relevant parameters. The germination, adult survival, seed infection, and seedling transition parameters were estimated as described in the previous sections. The competition (α), seed output (λ), and foliar infection burden (β) were estimated using custom MCMC software, as described in the supplemental methods. For convenience, we include a table of all parameters and variables relevant to the population dynamic model (Tab. 1).

Separating infectious processes from competition

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

Inferring the outcome of competition

We used the parameterized models to investigate the outcome of competition using both pairwise and multispecies approaches, to assess any differences in the outcome across approaches and to understand potentially complex outcomes more mechanistically. First, we used the posterior parameter estimates and the population dynamic model to compute growth rate when rare (GRWR) for each pair of species. If a pair of species each have GRWR> 1 (i.e., log(GRWR)> 0, where log is the natural logarithm), then stable coexistence is predicted because the rarer species is expected to increase in prevalence, preventing either species from being excluded (Turelli 1978; but see Case 1995). Pairwise competition calculations were performed in the presence of fungal infection (*i.e.*, including all model parameters pertinent to foliar or seed fungal infection).

To calculate GRWR for each species pair, we sampled the relevant demographic rate parameters from the posterior distributions of parameter estimates and simulated one species forward to its stable monoculture density, and then computed the growth rate of an invader of another species. For perennials, we computed GRWR as the dominant eigenvalue of the 2-x-2 matrix describing the rate of transition between seed and adult stages, which allows for accurate growth rate calculations that account for their stage-structured life history (Mordecai, 2013). For exotic annuals, we calculated GRWR by simulating the addition of a single individual to the monoculture species and calculating the growth rate in the second generation after this introduction by taking the ratio of the number of plants in generation 2 to generation 1. We also calculated percent difference in GRWR (pdGRWR) as $100\left(1-\frac{A}{B}\right)$, where B is the GRWR in an empty plot, and A is the GRWR under invasion conditions.

Second, we investigated competitive outcomes for the full species assemblage using simulations. Because outcomes could be initial condition-dependent, we initialized our simulations at a range of natural densities (*i.e.*, the observed transect densities). We censused the population 600 years later (Mordecai, 2013). For species that were not present in a sampled transect, we introduced a pseudo-count of one individual such that each species is initially present in each simulation. We consider species with population sizes exceeding one individual at the end of the simulation to have "persisted", while species with less than one individual are "excluded."

Lastly, we performed invasion experiments to better understand the dynamics underlying some of the coexistence outcomes that were predicted under our model. In these experiments, we compared the ability of *E. glaucus* to invade established *S. pulchra* plots with and without the presence of an exotic annual competitor. We considered only the subset of posterior parameter estimates in which *S. pulchra* was predicted to coexist with *B. diandrus*, excluding all replicates in which single species dominance was predicted. We simulated 100 years of *S. pulchra* growth in the absence of competitors to allow

it to establish. Subsequently, at time $t = 100$, we either invaded *B. diandrus* or allowed *S. pulchra* to continue in the absence of competitors for another 100 years, and finally we introduced a single *E. glaucus* individual at time $t = 200$. We summarized these experiments by calculating the proportion of posterior samples in which *S. pulchra* is able to prevent *E. glaucus* from invading. We sampled one set of parameters randomly from among the posterior estimates to display this invasion experiment, but note that we vary the timing of the invasions for the purpose of visualization (Fig. 4).

Parameter sensitivity analysis

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.

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, we would expect each species to 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, each species competes with itself at its stable monoculture density, and as expected, 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 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 (see "Seed survival and infection data" section).

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 the two 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. By contrast, if the outcomes are not strongly dependent on the initial densities, uncertainty is likely the main cause of the broad posterior distribution of outcomes (Fig. 2). 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 (Fig. 2).

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.

When the native perennials competed in the absence of exotic annuals, their dynamics are nearly-neutral, as indicated by the near identity of both intraspecific and interspecific competition strength (Fig. 1A). Although neutral dynamics cannot result in long-term stable coexistence (because even infinitesimal fitness differences or drift results in the eventual extinction of one of the competitors without a stabilizing mechanism), 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 evidence for relatively 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 these expectations. 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 invasion 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. The result is 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).

Native GRWR is sensitive to over-summer survival

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. 5). *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.

Discussion

The long-term outcome of competition is difficult to observe directly in nature, making empirically parameterized mathematical models 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. The model suggests that competition in multispecies assemblages can lead to complex outcomes that mix deterministic competitive exclusion or coexistence across groups of species 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 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).

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*, effectively augmenting the priority effect exerted by *S. pulchra* on its native perennial competitor through non-hierarchical competition. Hence, invasion by an exotic species with moderate niche overlap may increase resilience to invasion by native competitors with high niche overlap. Since the two native species are predicted to compete nearly-neutrally in the model, almost all predicted outcomes precluded their long-term stable coexistence, meaning that *S. pulchra* may indirectly benefit from invasion by *B. diandrus* via its negative

effect on *E. glaucus* (Fig. 4).

Studies applying modern coexistence theory have often documented substantial niche differences between species pairs, while variation in the magnitude of fitness difference determines the potential for coexistence or competitive exclusion. However, these studies typically explore communities in which species have long coevolutionary histories and belong to similar functional guilds (*e.g.*, native annual forbs) (Levine and HilleRisLambers 2009; Adler et al. 2010; Godoy et al. 2014; Kraft et al. 2015; Narwani et al. 2013; but see Godoy and Levine 2014). In such systems, we might expect that co-occurrence over long timescales has led species to minimize their fitness differences, maximize their niche differences, or both, leading to long-term stable coexistence. In invaded systems, exotic species must have fitness advantages, niche differences, or both with respect to the native species in order to have successfully invaded (MacDougall et al., 2009). Our study found support for large fitness advantages of invading species, and modest niche overlap that was potentially small enough to promote coexistence (20% posterior probability). This is consistent with the possibility that recently invaded systems may have substantially different short-term dynamics than most systems that have been studied to date, and that competitive exclusion and priority effects may be common long-term outcomes in such communities. Despite the *a priori* expectation of strong stabilization within coevolved communities based on previous work, our study did not predict substantial niche differences between the two native species or the two exotic *Bromus* species with an overlapping European home range. Our study suggests a role for nearly-neutral dynamics in determining competition outcomes in some pairs of species with long coevolutionary histories.

Among the mechanisms that may maintain diversity in complex communities, intransitive competition has received a great deal of interest, with studies arguing that intransitive competition could promote coexistence (Laird and Schamp, 2006; Allesina and Levine, 2011; Soliveres et al., 2015; Matías et al., 2018; Stouffer et al., 2018). However, a recent study combining empirical parameter estimates and population dynamic models found that intransitive competition was uncommon and not likely to promote coexistence among a set of 18 competing annual grass species (Godoy et al., 2017). In our study, we found evidence for non-hierarchical competition, and simulations suggested that non-hierarchical competition was unlikely to lead to coexistence of more than two species. However, this does not imply that non-hierarchical competition has no role in diversity maintenance in this system or others. Priority effects (similar to those reported here) could lead to a spatial patchwork of competitors, with disturbance and stochastic recolonization explaining the distribution of competing species.

Previous empirical work on the outcome of competition in invaded California grasslands has suggested a wide range of possible outcomes and coexistence mechanisms, including (1) the requirement for previous disturbance to explain the invasion of exotics in perennial-dominated plots (Stromberg and Griffin, 1996;

Seabloom et al., 2003; Corbin and D'Antonio, 2004), (2) competitive dominance of exotic annuals over *S. pulchra* (Dyer and Rice, 1997), and (3) spatial variation in outcomes determined by seed dispersal (DiVittorio et al., 2007) and habitat (Everard et al., 2009). A limitation of most previous work considering more than two competing species is that the empirical results were not linked to a dynamic model, making it difficult to project dynamics over long timescales. Our parameterized model is inconsistent with (1) because it predicts that exotic species can invade undisturbed perennial plots, and consistent with (2) because a portion of predicted outcomes led to unconditional exotic dominance (albeit with the winning species determined by a priority effect), as predicted in a previous two-species model (Mordecai et al., 2015).

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

In addition to the outcome of competition, identifying explanatory mechanisms is paramount for understanding the assembly of ecological communities and their potential to respond to species invasions. Pathogens are widely hypothesized to promote species diversity by specializing on common host species, 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 culturable 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 (*i.e.*, in plots where a focal species was more abundant), 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 (*e.g.*, invaded systems). 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.

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Figures

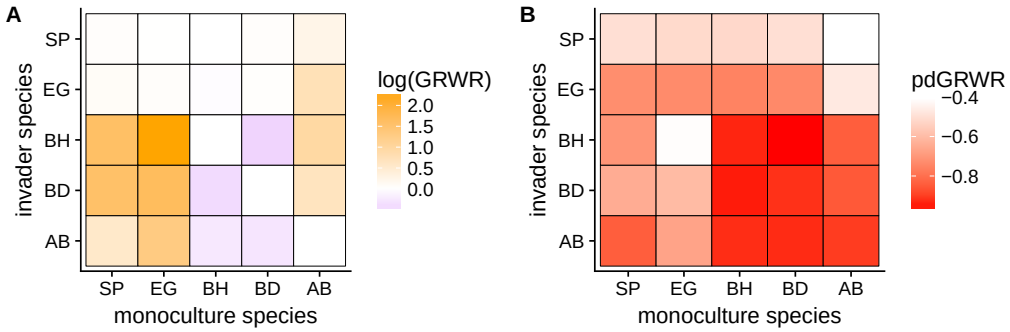

Figure 1: Inferred pairwise competition strength for each species in our dataset when an invader competes with a resident species at its monoculture density. A: log of growth rate when rare (GRWR) – log(GRWR)> 0 is the invasion criterion. B: shows the proportional difference in each species growth rate in the presence of the resident species as compared to its growth rate in the absence of competition. (Abbreviations: perennial native species (*S. pulchra* (SP), *E. glaucus* (EG)), annual exotic species (*A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD))).

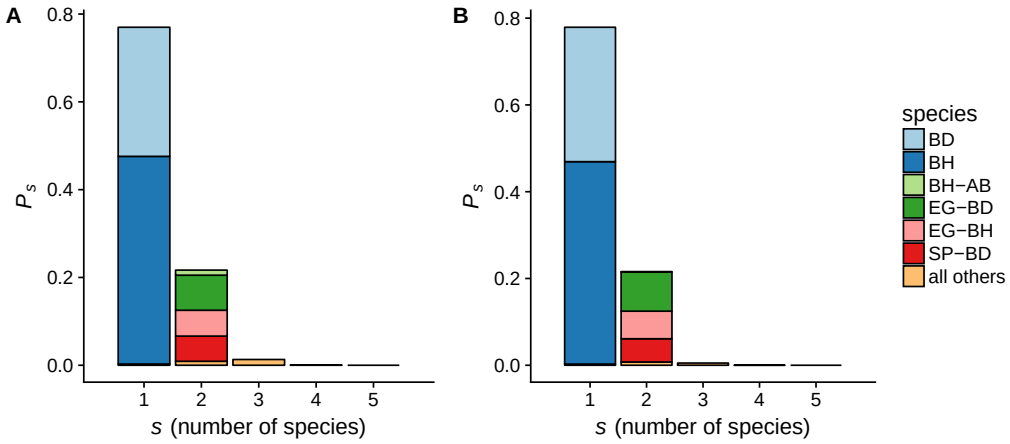

Figure 2: Predicted equilibrium species composition from the population dynamic model, marginalized across posterior parameter estimates. Each replicate represents a single sample from the posterior distribution of the model parameters, and initial competitor densities from a randomly sampled transect 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))).

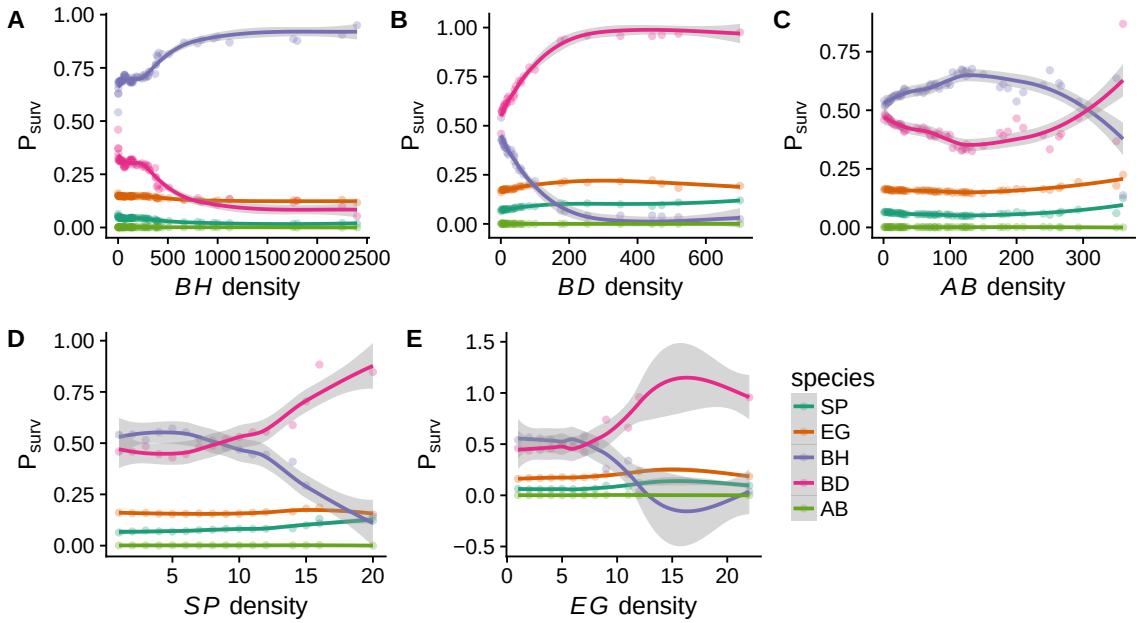

Figure 3: Effect of initial conditions on the outcome of competition. Estimated probability of persistence (P_{surv}) of each species (colored points and lines) as a function of initial density of each species in the simulation (x-axis). Points represent the proportion of simulations resulting in persistence that were initialized at the corresponding density, while the lines 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.

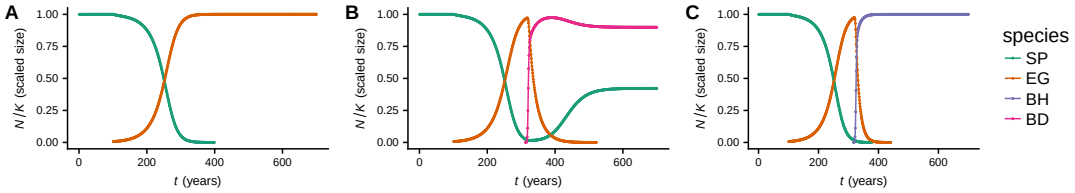

Figure 4: Effect of exotic annuals on invasion dynamics. A-C correspond to a single set of parameter estimates sampled from the posterior distribution. A: *EG* invades at $t = 100$, and is able to establish and eventually replace *SP* . B: *EG* invades at $t = 100$, and is able to establish and gradually 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*. (Abbreviations: perennial native species (*S. pulchra* (SP), *E. glaucus* (EG)), annual exotic speices (*B. hordeaceus* (BH), and *B. diandrus* (BD))).

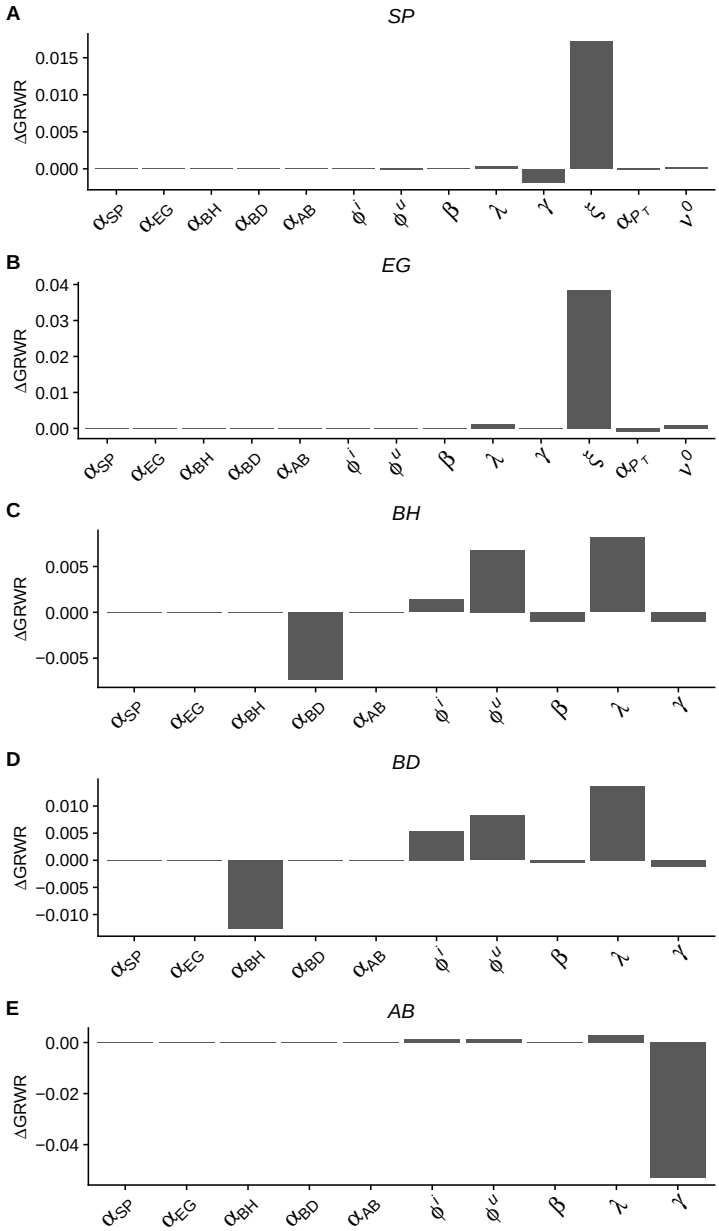

Figure 5: Sensitivity analysis results. For each species, we plot the proportional difference in GRWR when the corresponding parameter is increased by 5%. α_{SP} denotes the impact of *S. pulchra* on the focal species, α_{EG} represents the impact of *E. glaucus* on the focal species, etc. Parameters 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))).

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*. On the week of November 9, 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 on December 9, 2015. All transplants were watered to settle the soil. We then added approximately 10 seeds of each non-background species on January 12-13, 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 on January 15, 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. 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. 9), we allow S to follow a negative binomial distribution.

$$P(S|r,p) = \frac{\Gamma[S+r]}{\Gamma[S+1]\Gamma[r]}(1-p)^r p^S, \tag{7}$$

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

$$f_{ij} = \frac{1}{1 + (\sum_l \alpha_{jl} D_l) + A_{ij}\beta_j} \tag{8}$$

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 of species j. We constrain the $\vec{\alpha}$ and β values to be non-negative, which captures our strong prior expectation that interactions between species and infection should have a deleterious effect on fitness.

This competition model was previously studied in other systems (Mayfield and Stouffer, 2017). We incorporate the competition model into seed output S by allowing the mean of the negative binomial distribution to follow eqn. 8, while preserving the shape of the negative binomial. To do so, we allow the r parameter of the negative binomial to be given by

$$r = r_0 f_{ij}, \tag{9}$$

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

$$P(S|r_0, p, \vec{\alpha}_j, \beta_j) = \frac{\Gamma[S + r_0 f(\vec{\alpha}_j, \beta_j)]}{\Gamma[S+1]\Gamma[r_0 f(\vec{\alpha}_j, \beta_j)]}(1-p)^{r_0 f(\vec{\alpha}_j, \beta_j)} p^S. \tag{10}$$

Estimating competition and foliar infection parameters

We wrote custom MCMC software in Python to perform parameter estimation under our model of competition and infection within a growing season. We suppose that the data correspond to a vector of observed seed outputs, competitor densities, and leaf-area infected for each plant, and we seek to infer each of the α and β parameters with this method. Our software implements a standard Metropolis-Hastings algorithm. We compute the likelihood function with eqn. 10, and apply an uninformative Γ-shaped prior on $\vec{\alpha}$ and β such that these parameters are constrained to be non-negative. We thinned the observed MCMC traces such that we do not observe strong autocorrelations. We performed 20 independent MCMC runs for each focal species, and found nearly identical parameter estimates across independent runs. Our software is freely available by request and will be posted on the web at a future date.

To assess the performance of our MCMC-based inferences, we performed simulations of seed output under our model and assessed our ability to recapture the parameters that were used to generate the simulated data. For each simulation, we selected a focal plant species j and randomly selected competition parameters ($\vec{\alpha}_j$) and infection parameters (β_j) from uniform priors. We then selected the p and r_0 parameters such that the observed mean seed output would exactly match the expected seed output in the simulations. For each plant of species j in our dataset, we then simulated a new seed output based on the true density of competitors for this plant and the randomly sampled competition and infection parameters. We then ran our MCMC pipeline on the simulated data, and compared the mean of the posterior distribution of inferred parameter estimates to the true parameter estimates. We find that our method is approximately unbiased and reasonably accurate. A subset of the results of this experiment are plotted in Fig. S5.

Having obtained estimates for the full suite of parameters of our model, we sought to compare predicted seed densities from our model to field observations. For each focal species, we obtained field estimates of the seed density when grown in monoculture and compared them to simulation-based predictions under our demographic model. For each species j, we selected a random estimate for the competition parameters α_{jj} and infection parameters β as well as estimates of the other relevant parameters by sampling from the inferred posterior distribution of each parameter and then used a forward simulation under our population dynamic model to obtain an estimate of the final monoculture density. We then compared this set of predicted monoculture densities to the median estimates obtained from our field observations. While monoculture density estimates from our model are noisy, they are concordant with and of similar magnitude to the field estimates (Fig. S6).

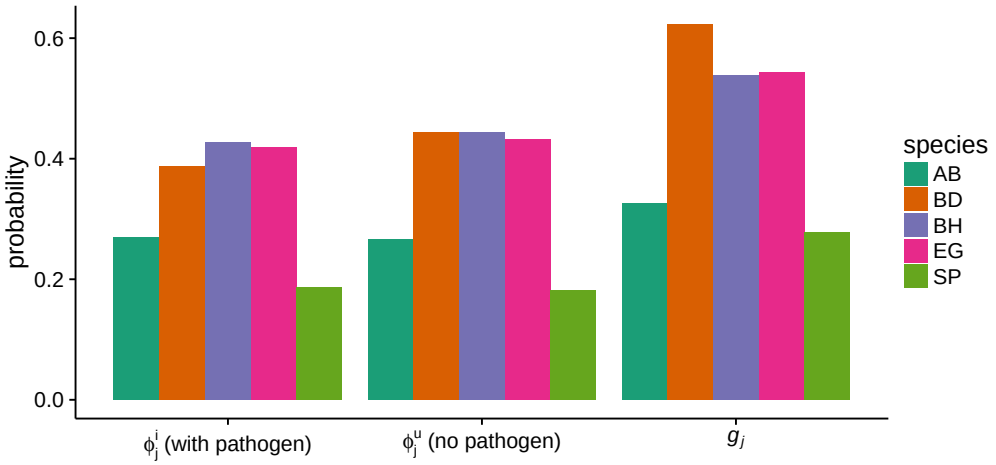

Figure 6: Estimated germination (g_j) and establishment (ϕ_j) probabilities for each species j. Establishment probability was estimated in the presence and absence of foliar fungal pathogens.

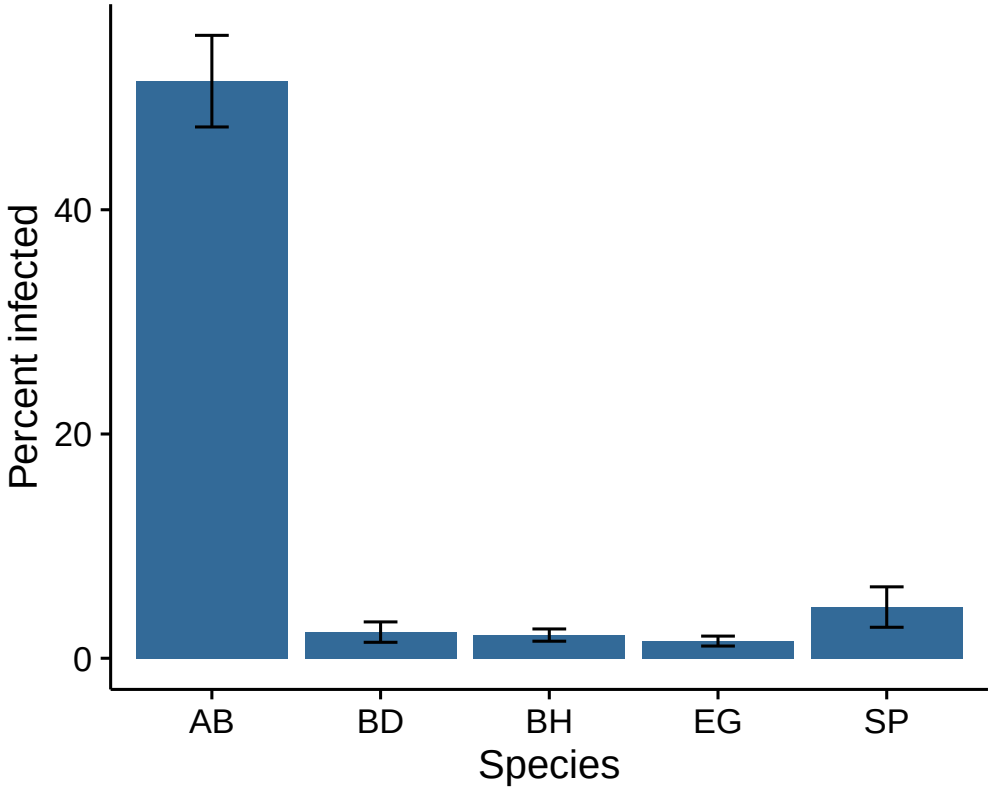

Figure 7: The proportion of seeds that were infected by the Black Fingers of Death pathogen in a seed bag experiment, by species. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).

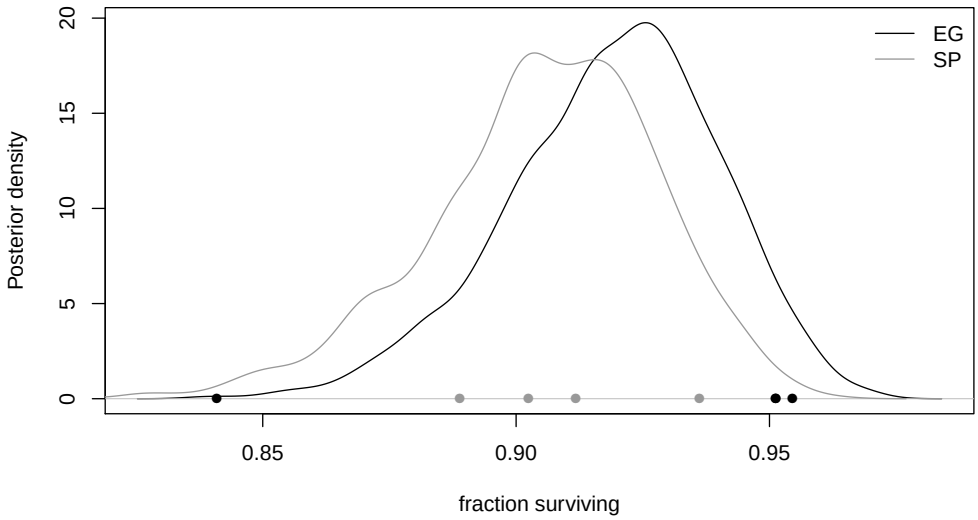

Figure 8: Estimates of the probability of adult perennial over-summer survival rate (which we term ξ_j in our model). The observed fraction of plants surviving across four sampling sites are plotted as points along the x-axis, while the curves represent the posterior density. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG)).

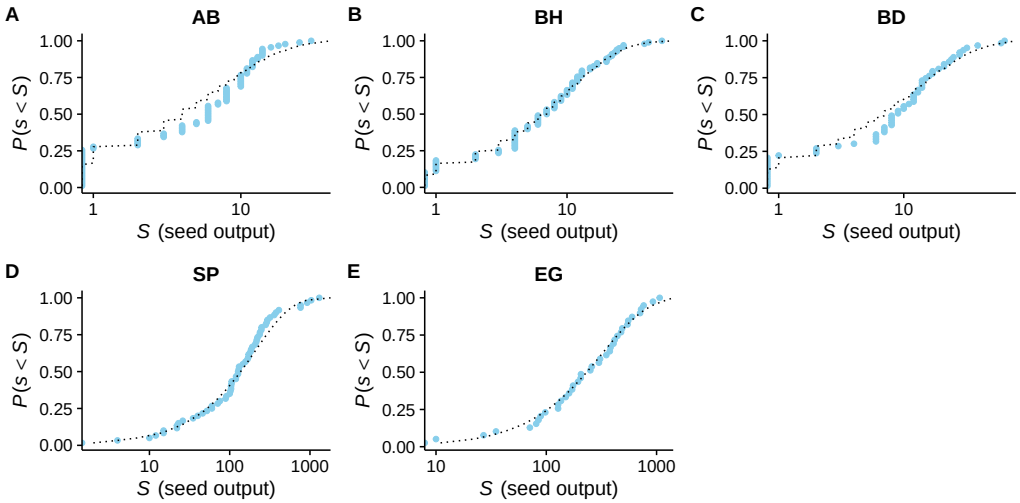

Figure 9: The cumulative distribution of observed seed counts ($P(s > S)$) is plotted as a function of seed count S. Each point represents the fraction of plants that have a seed count less than S. The dashed blue lines show the cumulative distribution of the best fitting negative binomial distribution, obtained my maximum likelihood. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).

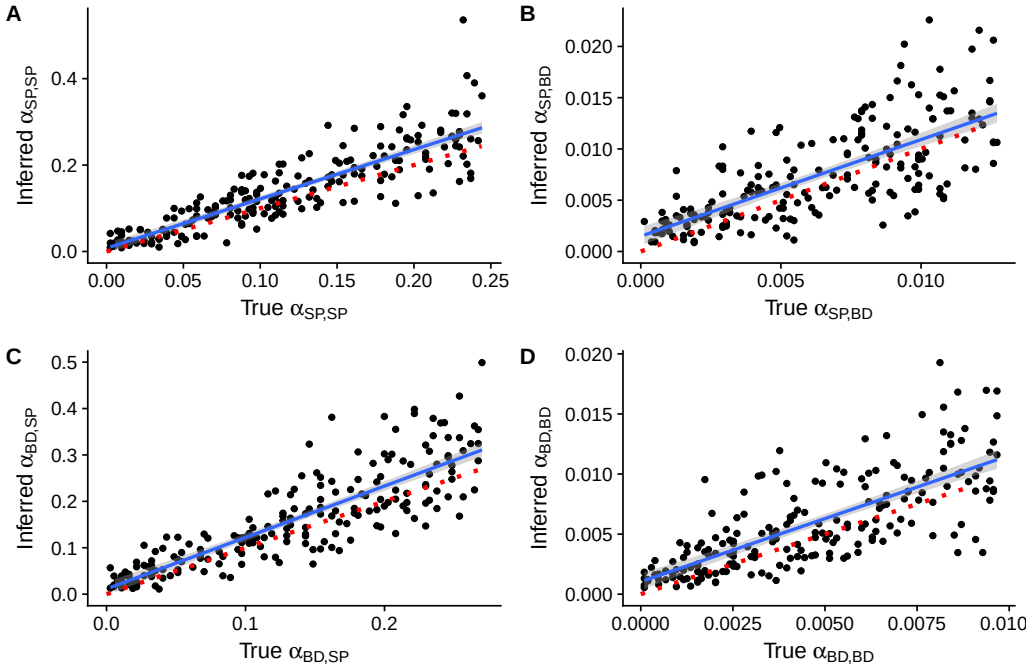

Figure 10: True and inferred parameter values as determined by our MCMC method, as obtained from simulation. The inferred values represent the mean of the inferred posterior distribution. The lines and envelopes (in gray) were fit with the method `"lm"` in the function `geom_smooth` in `ggplot2`, while 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)).

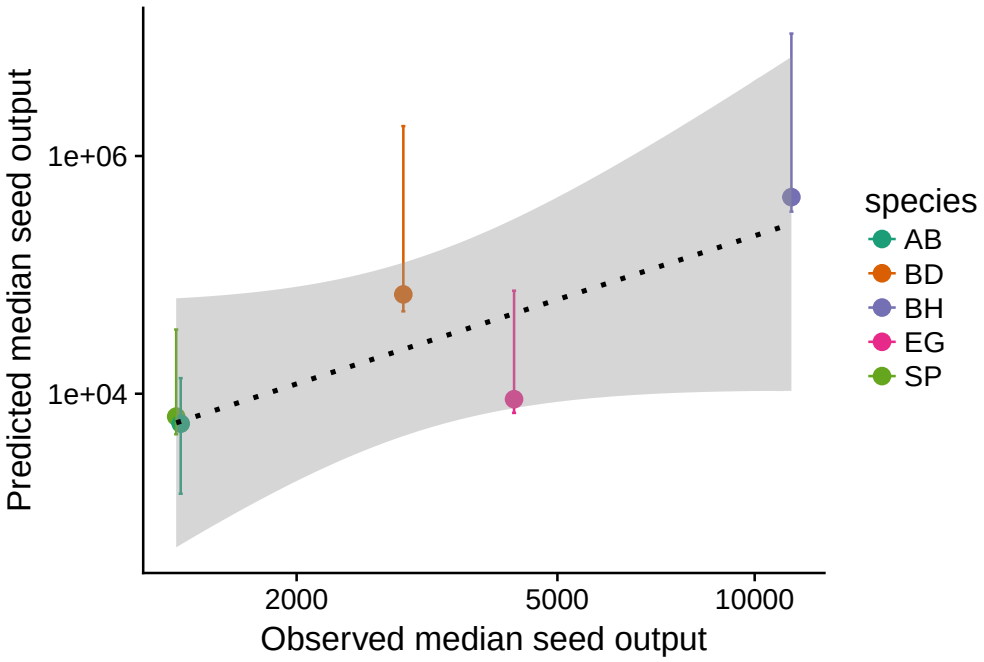

Figure 11: Observed median monoculture seed output densities plotted against those predicted by our population dynamic model. Error bars represent the inner 95% of parameter estimates from our model. The line and envelope (in gray) were fit with the method `"lm"` in the function `geom_smooth` in `ggplot2`. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).

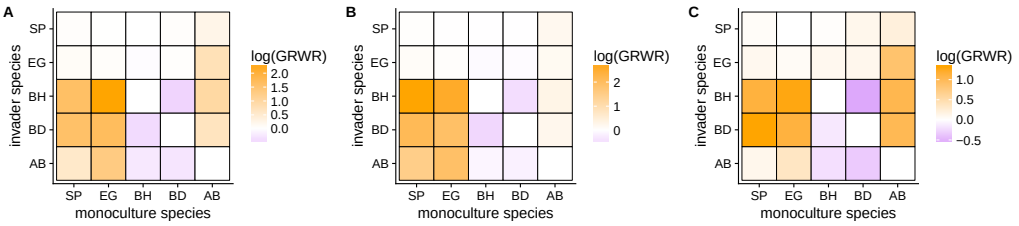

Figure 12: Comparison of pairwise invasion analyses using A: all data (competition plots and transects), B: only the data from the competition experiment, or C: only data from the transects. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).