Exotic species dominate due to niche overlap in a complex grassland community

Lawrence H. Uricchio[1†], S. Caroline Daws[1],
Erin R. Spear[1], Erin A. Mordecai[1†]

[1]Department of Biology, Stanford University, Stanford, CA
[†]To whom correspondence should be addressed: emordeca@stanford.edu, uricchio@stanford.edu

Keywords: competition, invasion, coexistence, communities, disease ecology

Abstract

Niche differentiation can maintain biological diversity, but assessing whether it is sufficient to stabilize invaded communities – which may be far from equilibrium – remains a pressing concern. We collected experimental data and developed a dynamic model to predict competitive outcomes in a complex grassland community including both native and exotic species. We found evidence for strong competition exerted on exotic grasses, but weaker competitive impacts on California natives. Nonetheless, our model predicts that at least one exotic species will persist with high probability, while native species persist in only half of predicted outcomes. Coexistence of multiple native and exotic species is unlikely in our model. We found that fungal infection has a weak impact in this system and is unlikely to substantially affect coexistence. The results suggest that despite strong competitive impacts on exotic species, exotics are likely to out-compete some or all California native grass species in the absence of other stabilizing mechanisms. However, conservation efforts focused on the preservation of native adult bunchgrasses could substantially increase the likelihood of native species' persistence.

Introduction

Understanding the long-term impact of exotic species invasion on native communities is a major goal of ecology, and an important research need for conservation. One of the most fundamental but unknown aspects of invader impacts is whether invasive species competitively exclude native species, suppress them to low density, or drive priority effects in which the long-term outcome depends on whether native or exotic species are initially more abundant. Although the effects of invaders on native communities have

often been described empirically (Levine et al., 2003), it is surprisingly difficult to predict their long-term impact because population dynamics can operate slowly, and because invasions often occur in concert with other disturbances. Understanding whether native species can stably coexist with invasive species under current environmental conditions is critical for designing restoration strategies, and for maintaining extant populations of native species.

Because stable coexistence is difficult to infer directly in the field, theory is instrumental for determining the long-term outcome of competition and the mechanisms that maintain species diversity. Species differences have long been thought to contribute to both coexistence and competitive exclusion (Burdon and Chilvers, 1974; Tilman, 1980; Holt et al., 1994). Modern coexistence theory (Chesson, 2000) clarifies the ways in which species differences affect the outcome of competition via their effects on niche differences and fitness differences. In this framework, 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 (density-independent) 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. Alternatively, priority effects can occur when population growth is positively frequency-dependent, allowing any species that is initially more common to exclude others but allowing no species to invade when rare in the presence of competitors.

The development of modern coexistence theory over the past 20 years 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, these studies have largely focused on co-occurring native species, but have not often examined invaded systems that may be far from equilibrium. One study that measured the strength of niche differences and fitness differences in pairs of native and exotic competitors found that competitive exclusion occurred between most species pairs, that plants with later phenology had fitness advantages that far exceeded niche differences, and that exotic species tended to

have fitness advantages over native species (Godoy and Levine, 2014). Nonetheless, coexistence between some pairs of native and exotic competitors has also been observed (Freckleton et al., 2000). While strong niche differences that stabilize coexistence are expected to be widespread in native-dominated systems with long coevolutionary histories or between species with dramatically different resource usage (Fargione et al., 2003), the strength of niche differences in invaded communities is less clear. Exotic species must have either large niche differences with or large fitness advantages over native species in order to establish in novel regions, but only fitness advantages allow exotic species to become dominant over natives (MacDougall et al., 2009).

Of many ecological mechanisms that might contribute to niche and fitness differences, pathogens may be particularly important because they adapt to available hosts and because they often affect demographic rates that limit population growth (Gilbert, 2002; Mordecai, 2011). As a result, the influence of pathogens on the outcome of competition between host species has been a major focus of research on community dynamics. Pathogens may drive both the negative frequency-dependent population growth that is required for niche differences and cause apparent competition between host species that modifies fitness differences (Mordecai, 2011). Host-specialized pathogens may regulate species abundances so that they differentially suppress common species and thereby benefit rare species (*i.e.*, the Janzen-Connell effect) (Augspurger, 1983, 1984; Augspurger and Kelly, 1984; Gilbert et al., 1994; Bagchi et al., 2014). By contrast, invasive species may escape limitation by host-specific pathogens while native species suffer greater pathogen regulation, promoting invasive species dominance (Mitchell and Power, 2003). However, in some communities invasive species share pathogens with native species, particularly if exotic species are closely related to abundant native species (Beckstead et al., 2010; Mordecai, 2013*b*; Parker et al., 2015). The accumulation of pathogens as exotic species become established and spread within new ecosystems may help to limit invasive species' impact on native plant communities (Nijjer et al., 2007; Flory and Clay, 2013). Alternatively, if exotic species are more tolerant of (*i.e.*, less demographically limited by) shared pathogens, they may serve as reservoir hosts that drive pathogen spillover onto native species, suppressing native species and benefiting exotics (Mordecai, 2013*a*). In sum, shared pathogens can promote coexistence, competitive exclusion, or priority effects between native and exotic host species (Mordecai, 2011, 2013*a*). Given this range of potential impacts, how pathogens mediate the outcome of competition between native and exotic species in nature remains highly uncertain.

In this study, we combine field experiments with mathematical models to understand the outcome of competition and the role of foliar and seed pathogens in shaping that outcome in a community of co-occurring native and exotic grasses in a Northern California grassland ecosystem. California grasslands are one of the most ecologically important and widespread ecosystems in the Western U.S., and as part

of the California floristic province they are a key reservoir of biodiversity and endemic species (Myers et al., 2000). At the same time, they are heavily invaded and human-impacted (Mack, 1989), and exotic annual grasses have largely replaced communities of California native perennial bunchgrasses and annual forbs throughout most of the extent of this ecosystem. However, native perennial bunchgrasses like *Stipa pulchra* (formerly *Nassella pulchra*) and *Elymus glaucus* remain relatively common in some grassland sites, particularly less-disturbed and wetter sites (more coastal versus inland and northern versus southern) (Corbin and D'Antonio, 2010). As a result, 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. This outcome may depend on how local environmental conditions influence plant demographic rates.

Previous work inferred the outcome of competition between native perennial and exotic annual grasses in California grasslands using population growth models parameterized with empirical data from published and unpublished studies (Mordecai et al., 2015). This work found that exotic annuals were most likely to competitively exclude native perennials, although stable coexistence occurred in a substantial subset of the posterior distribution. Survival of adult perennial bunchgrasses was the most important demographic rate controlling this outcome. However, the previous study has several limitations. First, only one native and one exotic species were included, leaving open the possibility that more complex species assemblages would have more complex dynamics. Second, the study did not explicitly include the role of pathogen infection on plant demographic rates, which has the potential to either promote coexistence or drive competitive exclusion. Third, because a full suite of demographic information was not available for a single species, the parameter estimates combined data from multiple native perennial grasses and multiple exotic annual grasses into a single suite of perennial and annual grass demographic rates. Finally, the data came from studies conducted across a range of sites spanning six degrees of latitude and by various authors.

Here, we develop and empirically parameterize a model of competition and infection in a complex California grassland community. It incorporates 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 includes the impact of fungal pathogens on those demographic rates. 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 outcome of competition, with and without pathogens. Specifically, we ask: (1) How strong is intra- and interspecific competition between native

and exotic grass species? (2) What is the predicted outcome of competition? (3) How strongly do foliar and seed pathogen impacts on demographic rates influence the outcome of competition? (4) 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 common throughout 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 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 can be used as a proxy for plant fitness, and is strongly impacted by competitor density for many plants (Mordecai, 2013*b*; Mordecai et al., 2015). Therefore, we gathered data on seed output as a function of competitor density for the five focal species. We set up an experiment to vary the density of each plant species in monoculture and measure its per-capita impact on seed production for each competitor species (Mordecai, 2013*b*; 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). 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.

Although we used weed matting, weeding, and seed addition to manipulate competitor densities, the competition experiment density manipulation was only partially successful in achieving the target species densities 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* individuals, 399 *B. hordeaceus* individuals, 319 *B. diandrus* individuals, 387 *S. pulchra* individuals, and 234 *E. glaucus* individuals (see Supplementary Materials for further details).

We used MCMC to infer parameters relevant to seed output (λ), competition (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.

Germination data

We planted marked seeds of each focal species to track germination and seedling establishment. We established 30 plots, each with 25 marked individuals of each of the five focal species. Individuals were marked with toothpicks and planted 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*b*), which is likely caused by one of the numerous *Pyrenophora* spp. that are common in these sites (Spear and Mordecai, 2017). 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 in a cold room 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 succombed to BFOD infection as γ_j for species j.

Adult survival data

To assess the survival of *S. pulchra* and *E. glaucus*, 200 adult perennial bunchgrasses were marked with flags on June 16, 2015 at four sites for each species, and revisited prior to senescence on June 6, 2016.

For each species, adults were marked at four sites, with 50 individuals per site. We recovered 167 *S. pulchra* and 170 *E. glaucus* flags on the second visit, and for each flagged plant recorded whether it was alive or dead based on the presence of green tissue and/or new fruiting stalks. We fit binomially distributed models of survival probability for each species using beta-distributed priors with parameters $\alpha = 1$, $\beta = 1$. The posterior distribution of adult survival estimates is plotted in Fig. S3.

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*b*; 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 $e^{-\sum_l \alpha_{jl} D_l(t)}$, 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 $e^{-A_j\beta_j}$, 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, $f_j(t) = e^{-\left(\sum_l \alpha_{jl} D_l(t)\right) - A_j\beta_j}$ 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 then may 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 (Table 1).

Separating infectious processes from competition

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 very weak impact on dynamics and competitive outcomes, we do not report results from models that excluded all fungal infection parameters. Instead, 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 our posterior parameter estimates and the population dynamic model to compute growth rate when rare (GRWR) for each pair of species as an indicator of the outcome of competition. If a pair of species each have GRWR>1 (i.e., log(GRWR)>0), then stable coexistence is predicted because the rarer species is expected to increase in prevalence, preventing either species from being excluded (Turelli, 1978). Pairwise competition calculations were performed in the presence of fungal infection (*i.e.*, including all model parameters pertinent to foliar or seed fungal infection).

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*b*). 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 investigated competition outcomes for the full species assemblage. 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 generations later (Mordecai, 2013*b*). 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 observe which species have population sizes exceeding one individual at the end of the simulation, and we consider these species to have "persisted", while species with less than one individual are "excluded".

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 computed the log(GRWR), where zero is the threshold for invasion, of the invading species in the context of this monoculture (Fig. 1A), as well as the proportional decrease in GRWR relative to the growth rate in the absence of competition (pdGRWR, Fig. 1B). The values plotted in Fig. 1 represent

the mean obtained over 250 independent samples of the parameters from the posterior distribution of our parameter estimates. If there were strong niche differences between all pairs of species, we would expect to observe that each species strongly constrains its own growth rate, but has a comparatively weak competitive impact on other species. In contrast, we observe a great deal of niche overlap in this system (Fig. 1A). Along the diagonal, each species competes with itself at its stable monoculture density, and as expected, the log(GRWR) is always very near zero (Fig. 1A). When the native perennial species (*E. glaucus* and *S. pulchra*) invade, they are constrained to log growth rates that are close to zero by all competitors except *A. barbata*, which is unable to constrain either species. In contrast, both perennial species are unable to reduce log(GRWR) of the annual species *B. diandrus* and *B. hordeaceus* to below zero, and *A. barbata* is also able to invade *E. glaucus* dominated plots. *B. hordeaceus* and *B. diandrus* tightly constrain each others' growth rates, but are not strongly constrained by the perennial competitors. *A. barbata* is a poor competitor in this community, and only constrains 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 reduces GRWR for nearly all species pairs (Fig. 1B). The strongest impacts of competition are on *B. diandrus* and *B. hordeaceus* when they invade tracts dominated by either *B. hordeaceus* or *B. diandrus*, respectively, resulting in growth rates reduced by $89.4 - 91.6\%$ relative to the absence of competition. *E. glaucus* and *S. pulchra* are also subject to competition with each other, reducing *S. pulchra*'s growth rate $48.4 - 50.2\%$ and *E. glaucus*'s growth rate by $72.5 - 73.0\%$ 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 competition outcomes when all five species compete simultaneously. Although it would be possible to perform a multi-species invasion analysis, such analyses can provide misleading results because GRWR>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 community composition using simulations under the population dynamic model. For this set of experiments (Fig. 2A) we included the impact of foliar fungal infection on demographic rates, but not the pathogen BFOD (see next section).

Based on our two-species competition observations (Fig. 1), we expected that either *B. hordeaceus* or *B. diandrus* would persist in most replicates, because they have large growth rates even when invad-

ing 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, we observe that either *B. hordeaceus* or *B. diandrus* persisted in 94% of simulation replicates (Fig. 2A), while the two species almost never coexist (0.43% of replicates). *A. barbata* is nearly always excluded. Native perennials persisted in 50.3% of replicates, usually by coexisting with either *B. hordeaceus* or *B. diandrus*. *S. pulchra* and *E. glaucus* rarely coexist (0.8% of replicates).

We sought to further understand these outcomes by investigating persistence as a function of initial competitor densities. If each species' success is strongly dependent on initial conditions, this suggests that priority effects play a role in determining community composition. We computed the proportion of replicates that resulted in each species' persistence as a function of initial competitor density (Fig. 3). We observe that the perennial species' success is only weakly dependent on initial community composition, with the exception of the density of *S. pulchra*. As *S. pulchra* density increases, *S. pulchra* persistence increases in likelihood while *E. glaucus* persistence decreases in likelihood. In contrast, the annual species *B. hordeaceus* and *B. diandrus* show striking priority effects across the densities of all competitors except *A. barbata*, which had only modest effects on any species.

Seed infection may weakly hamper native perennial persistence

While the simulation and invasion results suggest that exotic annuals will dominate perennials and either completely 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, this time including the impact of fungal infection by BFOD (Fig. 2B). BFOD strongly decreases the overall success of *A. barbata*, which is already the weakest annual competitor. *A. barbata* persists in 3.6% of replicates that exclude BFOD, but almost never persists in its presence (0.7% of replicates). Native perennial species are weakly hampered by the further suppression of *A. barbata* by BFOD, with 49.4% of replicates resulting in the persistence of at least one perennial (as compared to 50.3% of replicates without BFOD), indicating that the removal of *A. barbata* as a competitor is more beneficial to the other exotic species than it is to native perennials. However, we stress that species other than *A. barbata* were only minimally affected by BFOD, consistent with low rates of BFOD infection that we observed empirically (Fig. S2).

Native perennial GRWR is most sensitive to adult over-summer survival

Both perennial species are most sensitive to the over-summer survival of adult individuals (ξ), and essentially insensitive to all other parameters. *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, while being slightly deleteriously impacted by an increase in γ.

Discussion

Despite intensive interest in managing and restoring California grasslands and their native perennial grasses, we poorly understand the long-term outcome of competition between California native and exotic grasses. The heavily invaded California grassland study system exhibited strong niche overlap and large fitness differences that prevented most species from stably coexisting, in contrast to other well-studied native-dominated communities (Levine and HilleRisLambers, 2009; Adler et al., 2010; Godoy et al., 2014; Kraft et al., 2015). We showed that single-species dominance by an exotic annual (most often *B. diandrus* or *B. hordeaceus*) is the most likely outcome of competition. Multiple species coexist in less than half of posterior estimates, usually involving one of the *Bromus* species and one native perennial species.

Previous empirical work in California grasslands has made mixed predictions about the outcome of competition between native and exotic grasses. Long-term surveys have suggested that priority effects might occur, because areas subjected to cultivation and cleared of native perennial grasses remained dominated by exotic annuals 30-100 years later, while native perennial grasses persisted only in previously uncultivated areas, particularly with clay soils and steeper slopes (Stromberg and Griffin, 1996). Two experimental competition studies between California native and exotic grasses showed that native perennial grasses were strong competitors with exotic annuals once established, although their competitive impacts were limited prior to adult bunchgrass establishment (Seabloom et al., 2003; Corbin and D'Antonio, 2004). These studies suggest that annual grass dominance must have required disturbance that removed native perennial bunchgrasses, without which exotic annual grasses could not have competitively displaced native perennials. By contrast, another experiment found strong effects of competition with exotic annuals on *S. pulchra* growth and mortality (Dyer and Rice, 1997), suggesting strong niche

overlap and exotic annual competitive dominance. When adult bunchgrasses are removed, seed dispersal may be an important limitation on re-establishment of native perennial species (Seabloom et al., 2003), which were strongly limited by abundant exotic annual grass seeds in a field survey of 58 California grassland species (DiVittorio et al., 2007). An empirically parameterized model of competition between California native and exotic grasses for nitrogen, mediated by water availability, predicted that the outcome of competition varies from exotic annual dominance in drier areas to native perennial coexistence with exotic annuals in wetter areas (Everard et al., 2009). Finally, a previous modeling study–which used a similar modeling approach as the present study but studied a simple community of two species and combined data assembled from multiple grass species, studies, and geographic locations into a single set of parameters–also found that exotic annual grass dominance was the most likely outcome of competition, while coexistence with native perennial grasses occurred for a substantial minority of the posterior distribution (Mordecai et al., 2015).

Taken together, these studies suggest that the outcome of competition could range from annual dominance to stable coexistence of native perennial and exotic annual species, with the outcome partly determined by priority effects (though few explicitly evaluated the long-term outcome of competition). The strength of interspecific competition may depend on environmental conditions, including water and nitrogen availability, soil type, slope, and disturbance history. Our results indicate strong niche overlap and interspecific competition between native and exotic species, leading to priority effects, single-species dominance by *B. diandrus* or *B. hordeaceus*, or multi-species coexistence (Fig. 2 and Fig. 4). Even within a single site and year and at a relatively small spatial scale, uncertainty in demographic rates is large enough preclude a single definitive outcome of competition (Fig. 2). Impacts of environmental variation on demographic rates could further affect the outcome of competition and increase spatial and temporal variation in this outcome. In other words, native perennials may co-occur with exotic annuals in California grasslands at a landscape scale because of patchworks of local-scale priority effects, stable single-species dominance, and local coexistence across multiple environmental gradients. Indeed, our results suggested strong priority effects between exotic annuals and modest priority effects between perennials (Fig. 4).

In our focal system, coexistence of more than two species was rarely predicted, yet the five focal species have co-occurred at the study site and other California grassland sites for over a hundred years. Therefore, co-occurrence of multiple exotic annuals and native perennials must occur either due to (1) non-equilibrium dynamics that play out over long time scales or (2) 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, *e.g.*, 1-m^2 plots and single growing seasons as in the present study (Adler et al., 2006; Levine and HilleRisLambers, 2009; Adler et al., 2010; Godoy and Levine, 2014; Godoy et al., 2014). 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). An alternative to larger-scale stabilizing processes is that priority effects occur at small spatial scales, allowing one plant species to establish and repel invasion, 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).

In addition to the outcome of competition, identifying the mechanisms that promote this outcome 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. 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 major ways. First, the culturable fungal pathogen community is mostly host-generalist (Spear and Mordecai, 2017). Second, the demographic impacts are mostly minimal, except the negative impact exerted by the Black Fingers of Death pathogen on *A. barbata* (Fig. 2B). This disproportionate effect on *A. barbata* may have in part resulted from inadvertently harvesting and using some immature seeds in the buried seed experiment. Those immature seeds may have been prone to slow germination, and by extension, BFOD infection (Beckstead et al., 2010). In another study in this system, we found no evidence that pathogen load or impacts increased on locally common species (*i.e.*, in plots where a focal species was more abundant) (Spear and Mordecai, 2017). Together, the results suggest that both native and exotic focal grasses are well defended against the endemic pathogen community, and capable of limiting both pathogen burden (mean percent leaf area damaged) and demographic impacts.

Understanding the impact of competition, pathogen infection, and other demographic rates on the outcome of competition yields several insights into conservation efforts in California grasslands. In agreement with earlier work (Mordecai et al., 2015), the population growth rate of native perennial plants was most sensitive to the rate of survival of adult bunchgrasses, and essentially insensitive to other parameters of our model. This suggests that conservation efforts should be pitched towards preserving or introducing adults and not necessarily removing competitors – indeed, our results suggest that adult perennials in

this system are no more sensitive to competition by exotic annuals than other perennials (Fig. 1). In contrast, exotic annuals (especially *A. barbata*) were most sensitive to the Black Fingers Of Death fungal seed pathogen or establishment and seed production. Although our study does not suggest that BFOD substantially helps drive coexistence in this system, our field work was performed in an average rainfall year. Variation in rainfall (or other climate variables) could substantially alter the success of BFOD in infecting annual seeds, so it is plausible that BFOD infection could be a weakly stabilizing force given temporal variability, with annuals performing better in years when BFOD is less successful.

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, may not be as common in invaded systems as they are thought to be in systems with long coevolutionary histories between species. Understanding the strength of stabilization and the outcome of competition is important for management efforts and for responding to global change, where disturbance, further species invasions, and climate change threaten to disrupt ecosystems that may already be away from equilibrium. Future work in heavily invaded systems is necessary to test the generality of our results, and to determine strategies for preserving biodiversity.

Acknowledgments

We acknowledge generous support and assistance from Teri Barry, Nona Chiariello, Phillippe Cohen, Joe Sertich, Reuben Brandt, Johannah Farner, Steve Gomez, Bill Gomez, Stuart Koretz, Cary Tronson, Divya Ramani, Ryan Tabibi, Esther Liu, Sandya Kalavacherla, Vidya Raghvendra, Jason Zhou, Virginia Parra, Claudia Amadeo-Luyt, Gaurika Duvar, the Jasper Ridge Kennedy endowment fund, the Stanford University Vice Provost for Undergraduate Education summer research fellowship for undergraduates, and the Stanford University Raising Interest in Science and Engineering (RISE) summer internship program. We thank members of the Fukami, Peay, and Mordecai labs for helpful comments on the project. LHU was supported by the NIH IRACDA fellowship (NIGMS grant K12GM088033). EAM was supported by a grant from the National Science Foundation (DEB-1518681).

References

Ackerly, D., C. Knight, S. Weiss, K. Barton, and K. Starmer. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130:449–457.

Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. Proceedings of the National Academy of Sciences 103:12793–12798.

Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology letters 13:1019–1029.

Augspurger, C. K. 1983. Seed dispersal of the tropical tree, platypodium elegans, and the escape of its seedlings from fungal pathogens. The Journal of Ecology pages 759–771.

———. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712.

Augspurger, C. K., and C. K. Kelly. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61:211–217.

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506:85.

Beckstead, J., S. E. Meyer, B. M. Connolly, M. B. Huck, and L. E. Street. 2010. Cheatgrass facilitates spillover of a seed bank pathogen onto native grass species. Journal of Ecology 98:168–177.

Burdon, J., and G. Chilvers. 1974. Fungal and insect parasites contributing to niche differentiation in mixed species stands of eucalypt saplings. Australian Journal of Botany 22:103–114.

Cáceres, C. E. 1997. Temporal variation, dormancy, and coexistence: a field test of the storage effect. Proceedings of the National Academy of Sciences 94:9171–9175.

Case, T. J. 1995. Surprising behavior from a familiar model and implications for competition theory. The American Naturalist 146:961–966.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics 31:343–366.

Chesson, P., M. J. Donahue, B. A. Melbourne, and A. L. Sears. 2005. Scale transition theory for understanding mechanisms in metacommunities. Metacommunities: spatial dynamics and ecological communities pages 279–306.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283.

———. 2010. Not novel, just better: competition between native and non-native plants in california grasslands that share species traits. Plant Ecology 209:71–81.

DiVittorio, C. T., J. D. Corbin, and C. M. D'Antonio. 2007. Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. Ecological Applications 17:311–316.

Dormann, C. F., and S. H. Roxburgh. 2005. Experimental evidence rejects pairwise modelling approach to coexistence in plant communities. Proceedings of the Royal Society of London B: Biological Sciences 272:1279–1285.

Dyer, A., and K. Rice. 1997. Intraspecific and diffuse competition: the response of nassella pulchra in a california grassland. Ecological Applications 7:484–492.

Everard, K., E. W. Seabloom, W. S. Harpole, and C. de Mazancourt. 2009. Plant water use affects competition for nitrogen: why drought favors invasive species in california. The American Naturalist 175:85–97.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences 100:8916–8920.

Flory, S. L., and K. Clay. 2013. Pathogen accumulation and long-term dynamics of plant invasions. Journal of Ecology 101:607–613.

Freckleton, R., A. Watkinson, P. Dowling, and A. Leys. 2000. Determinants of the abundance of invasive annual weeds: community structure and non–equilibrium dynamics. Proceedings of the Royal Society of London B: Biological Sciences 267:1153–1161.

Gilbert, G., R. Foster, and S. Hubbell. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. Oecologia 98:100–108.

Gilbert, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. Annual Review of Phytopathology 40:13–43.

Godoy, O., and J. M. Levine. 2014. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology 95:726–736.

Godoy, O., N. J. Kraft, and J. M. Levine. 2014. Phylogenetic relatedness and the determinants of competitive outcomes. Ecology Letters 17:836–844.

Godoy, O., D. B. Stouffer, N. J. Kraft, and J. M. Levine. 2017. Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. Ecology 98:1193–1200.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. The American Naturalist 144:741–771.

Kraft, N. J., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences 112:797–802.

Levine, J. M., and J. HilleRisLambers. 2009. The importance of niches for the maintenance of species diversity. Nature 461:254.

Levine, J. M., M. Vila, C. M. Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London B: Biological Sciences 270:775–781.

MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. Plant invasions and the niche. Journal of Ecology 97:609–615.

Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Biological invasions: a global perspective .

Mayfield, M. M., and D. B. Stouffer. 2017. Higher-order interactions capture unexplained complexity in diverse communities. Nature Ecology & Evolution 1:0062.

Mitchell, C. E., and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421:625.

Mordecai, E. A. 2011. Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. Ecological Monographs 81:429–441.

———. 2012. Soil moisture and fungi affect seed survival in california grassland annual plants. Plos One 7:e39083.

———. 2013*a*. Consequences of pathogen spillover for cheatgrass-invaded grasslands: coexistence, competitive exclusion, or priority effects. The American Naturalist 181:737–747.

———. 2013*b*. Despite spillover, a shared pathogen promotes native plant persistence in a cheatgrass-invaded grassland. Ecology 94:2744–2753.

Mordecai, E. A., N. A. Molinari, K. A. Stahlheber, K. Gross, and C. D'Antonio. 2015. Controls over native perennial grass exclusion and persistence in california grasslands invaded by annuals. Ecology 96:2643–2652.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Narwani, A., M. A. Alexandrou, T. H. Oakley, I. T. Carroll, and B. J. Cardinale. 2013. Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. Ecology Letters 16:1373–1381.

Nijjer, S., W. E. Rogers, and E. Siemann. 2007. Negative plant–soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. Proceedings of the Royal Society of London B: Biological Sciences 274:2621–2627.

Parker, I. M., M. Saunders, M. Bontrager, A. P. Weitz, R. Hendricks, R. Magarey, K. Suiter, and G. S. Gilbert. 2015. Phylogenetic structure and host abundance drive disease pressure in communities. Nature 520:542–544.

Petermann, J. S., A. J. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen-connell effects are widespread and strong enough to maintain diversity in grasslands. Ecology 89:2399–2406.

Saavedra, S., R. P. Rohr, J. Bascompte, O. Godoy, N. J. Kraft, and J. M. Levine. 2017. A structural approach for understanding multispecies coexistence. Ecological Monographs .

Seabloom, E. W., W. S. Harpole, O. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native california grassland species. Proceedings of the National Academy of Sciences 100:13384–13389.

Spear, E. R., and E. A. Mordecai. 2017. Foliar pathogens of california grasses are multi-host and spatially widespread: implications for grassland diversity. under review .

Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal california grasslands in relation to cultivation, gophers, and grazing. Ecological Applications 6:1189–1211.

Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. The American Naturalist 116:362–393.

Turelli, M. 1978. Does environmental variability limit niche overlap? Proceedings of the National Academy of Sciences 75:5085–5089.

Turnbull, L. A., L. Manley, and M. Rees. 2005. Niches, rather than neutrality, structure a grassland pioneer guild. Proceedings of the Royal Society of London B: Biological Sciences 272:1357–1364.

Vannette, R. L., and T. Fukami. 2014. Historical contingency in species interactions: towards niche-based predictions. Ecology Letters 17:115–124.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. The American Naturalist 125:769–787.

Figures

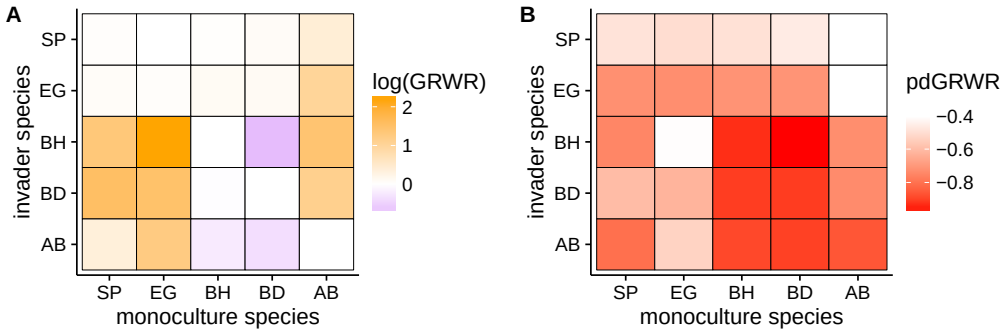

Figure 1: Inferred pairwise competition strength for each species in our dataset when an invader competes with a resident species at its monoculture density. Panel A shows the log of growth rate when rare (GRWR), while B shows the proportional difference in each species growth rate in the presence of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

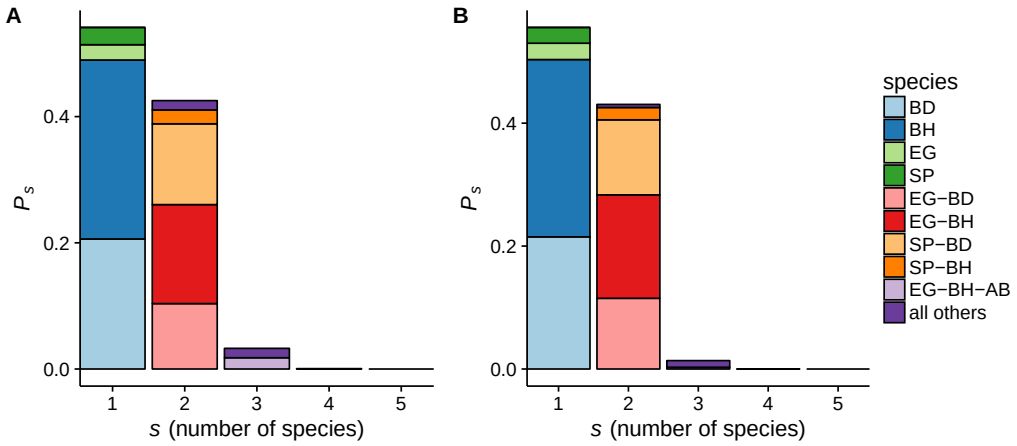

Figure 2: Predicted equilibrium species composition from our population dynamic model, marginalized across posterior parameter estimates. Each replicate represents a single sample from the posterior distribution of the model parameters, and initial competitor densities from a randomly sampled transect 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 then subdivided into the specific set of species that were observed to have GRWR>1 for a particular parameter set and transect sample. All compositions that occurred in under 1% of replicates are grouped into a single color. The height of the bar represents the proportion of replicates that have the corresponding value of s on the x-axis, while the stacked colors correspond to specific community compositions, given in the legend. Panel A displays results corresponding to a model that includes foliar fungal infection but not BFOD, while B includes both foliar fungal infection and BFOD. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).

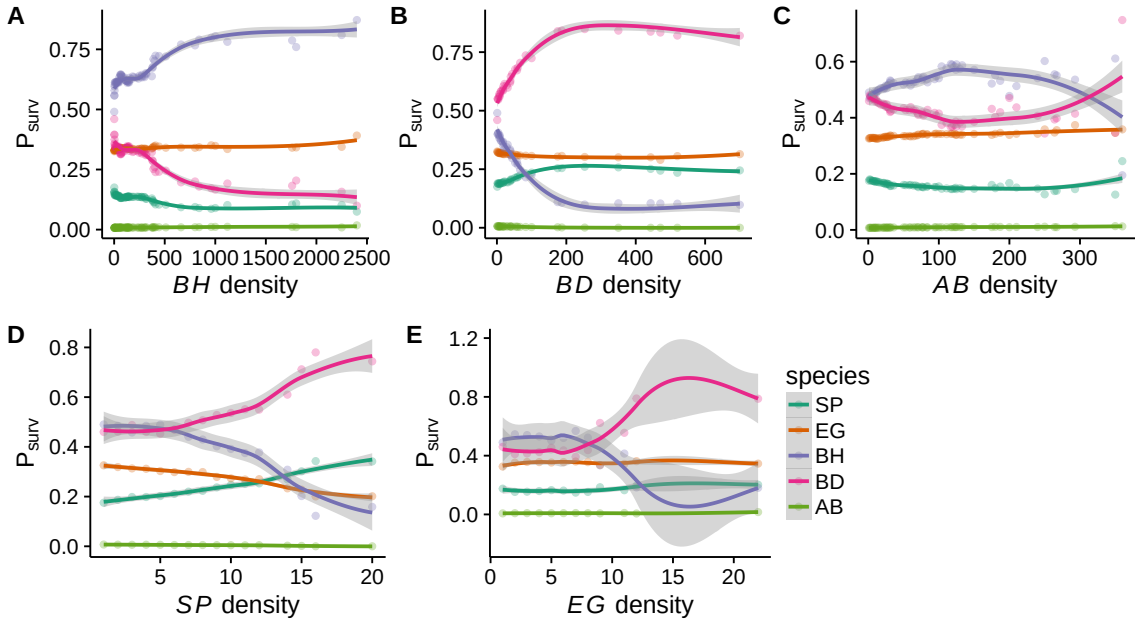

Figure 3: Effect of initial conditions on the outcome of competition. Estimated probability of persistence (P_{surv}) of each species (colored points and lines) as a function of initial density of each species in the simulation (x-axis). Points represent the proportion of simulations resulting in persistence that were initialized at the corresponding density, while the lines were fit with the function geom_smooth in ggplot. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)). Priority effects occur when the probability of persistence depends strongly on initial density.

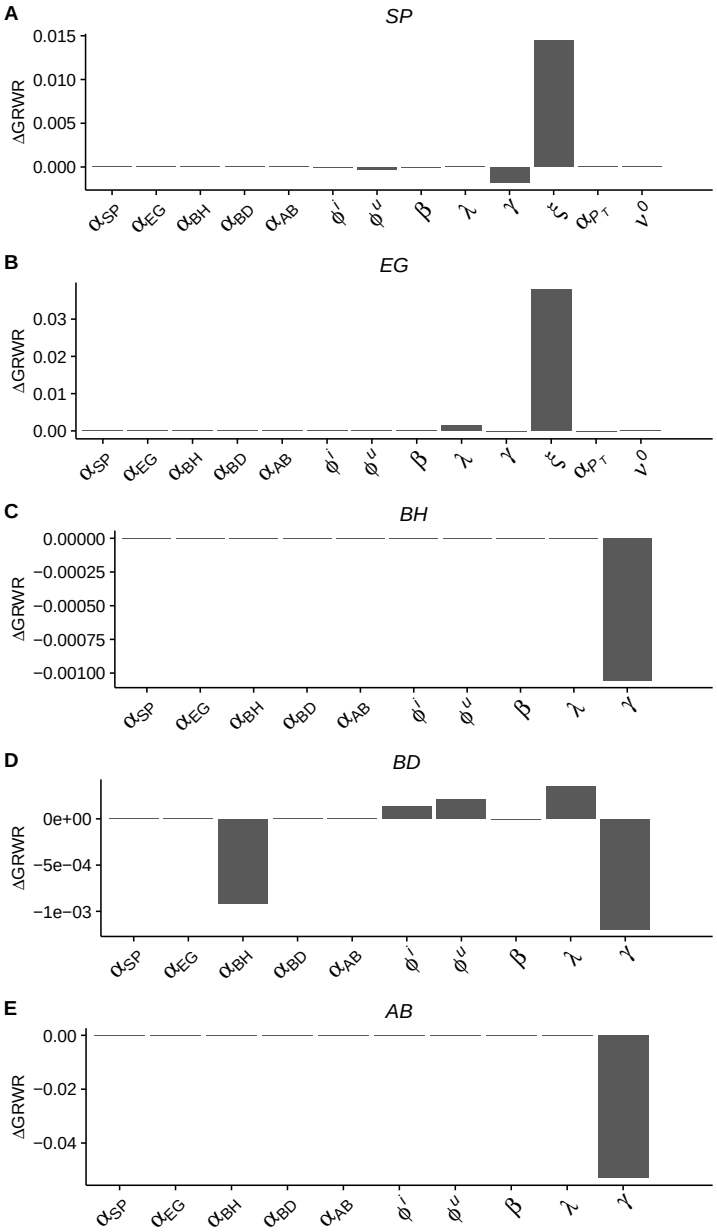

Figure 4: Sensitivity analysis results. For each species, we plot the proportional difference in GRWR when the corresponding parameter is increased by 5%. α_{SP} denotes the impact of *S. pulchra* on the focal species, α_{EG} represents the impact of *E. glaucus* on the focal species, etc. Parameters are defined in Table 1. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *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.

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 measure its per-capita impact on seed production for each competitor species (Mordecai, 2013*b*; 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, E. glaucus* seedlings, *Elymus glaucus* adults, *Stipa pulchra* seedlings, and *Stipa 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 overdispersed distribution that is well described by a negative binomial (Fig. S4), we allow S to follow a negative binomial distribution.

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

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

$$f_{ij} = e^{-\left(\left(\sum_l \alpha_{jl} D_l\right) + A_{ij}\beta_j\right)} \tag{8}$$

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).

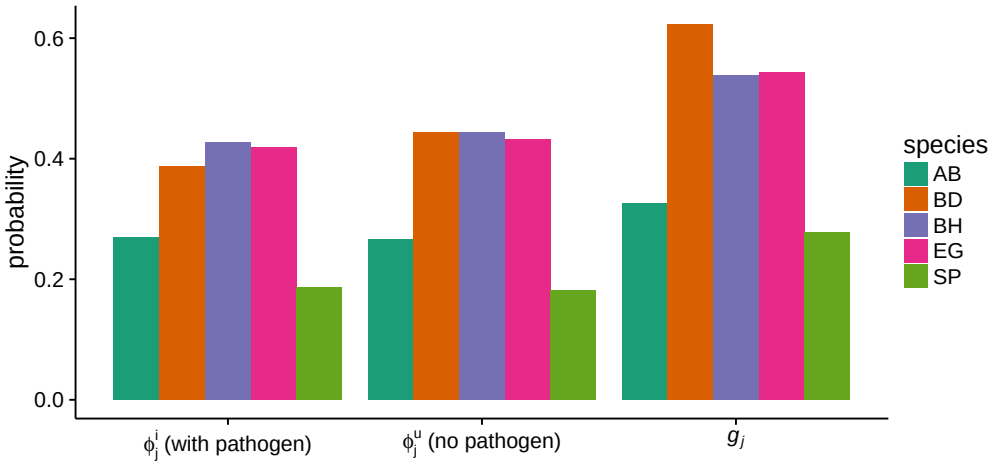

Figure S1: Estimated germination (g_j) and establishment (ϕ_j) probabilities for each species j. Establishment probability was estimated in the presence and absence of foliar fungal pathogens.

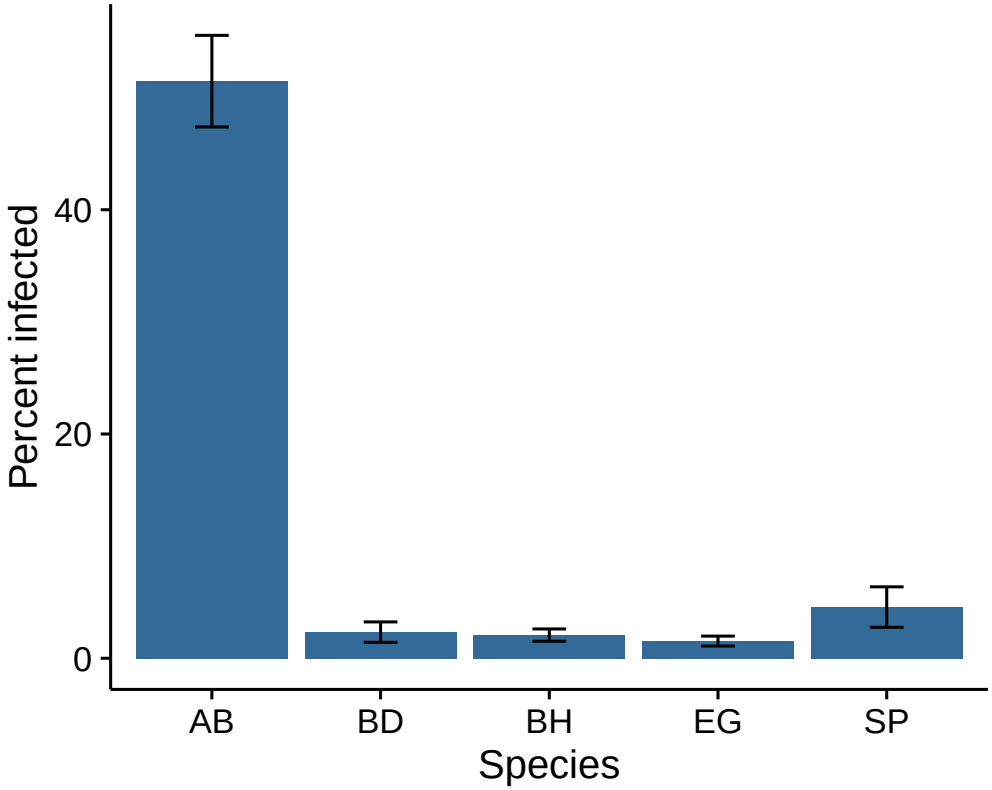

Figure S2: The proportion of seeds that were infected by the Black Fingers of Death pathogen in a seed bag experiment, by species. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).

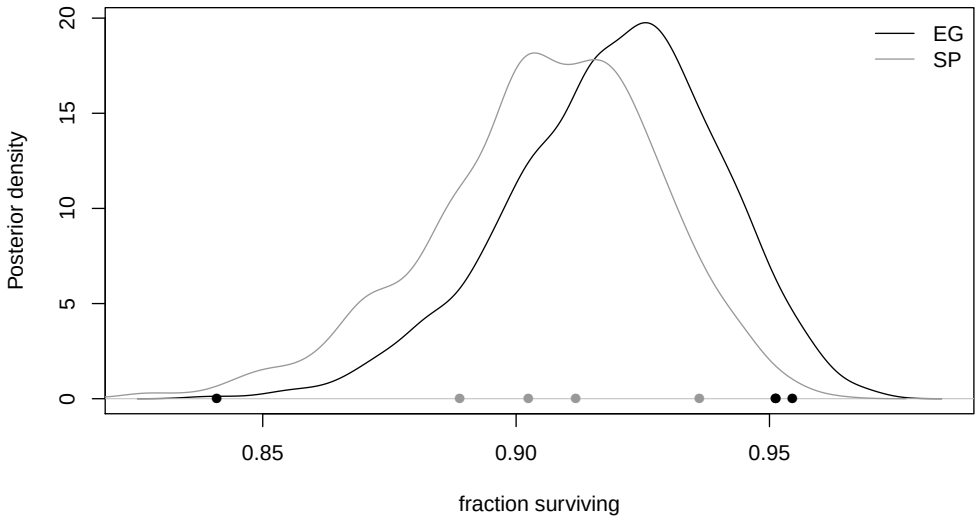

Figure S3: Estimates of the probability of adult perennial over-summer survival rate (which we term ξ_j in our model). The observed fraction of plants surviving across four sampling sites are plotted as points along the x-axis, while the curves represent the posterior density. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG)).

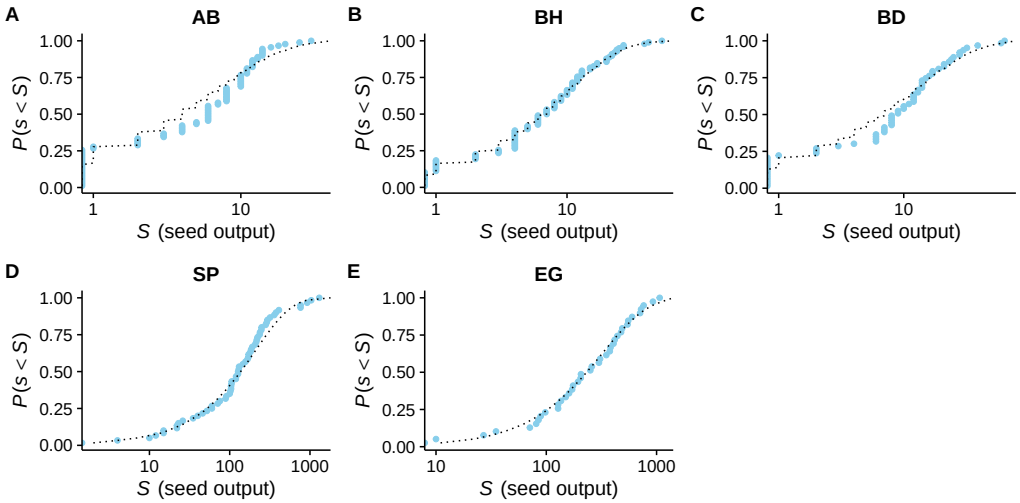

Figure S4: The cumulative distribution of observed seed counts ($P(s > S)$) is plotted as a function of seed count S. Each point represents the fraction of plants that have a seed count less than S. The dashed blue lines show the cumulative distribution of the best fitting negative binomial distribution, obtained my maximum likelihood. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).

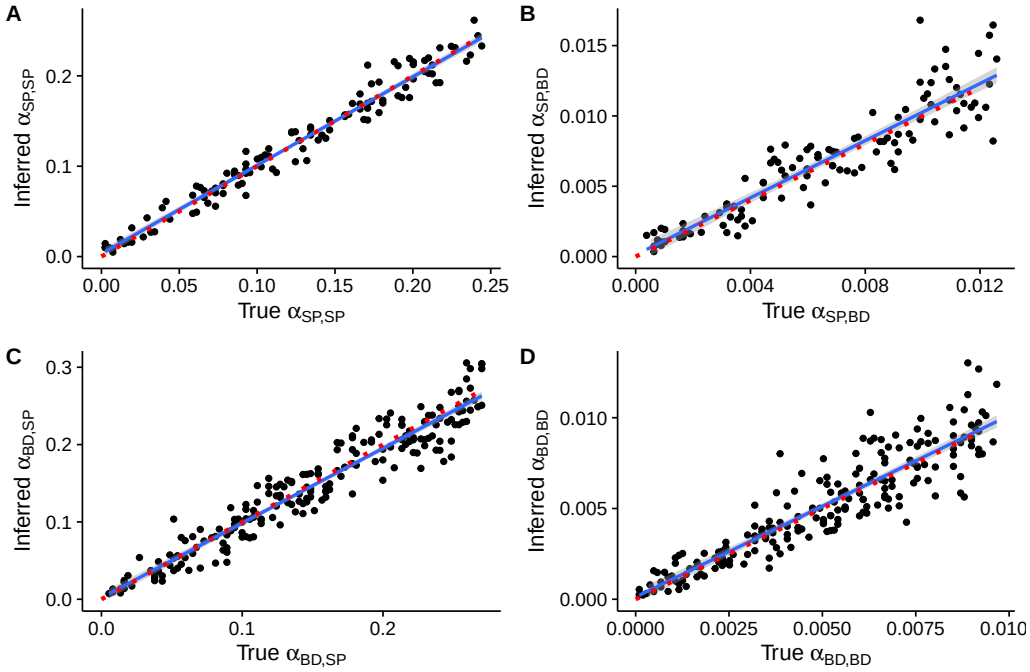

Figure S5: True and inferred parameter values as determined by our MCMC method, as obtained from simulation. The inferred values represent the mean of the inferred posterior distribution. The lines and envelopes (in gray) were fit with the method `"lm"` in the function `geom_smooth` in `ggplot2`, while 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)).

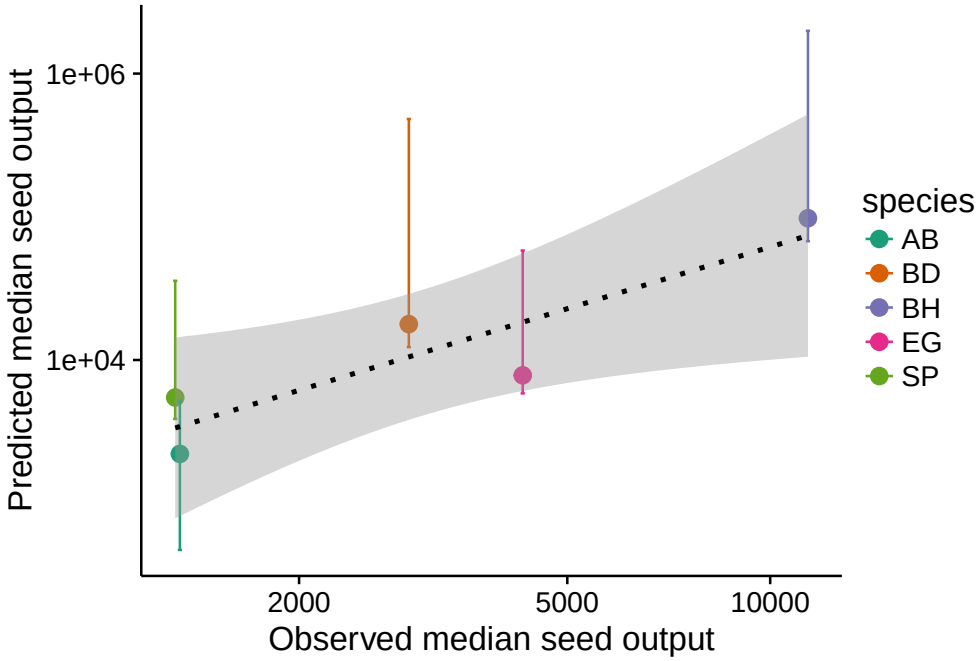

Figure S6: Observed median monoculture seed output densities plotted against those predicted by our population dynamic model. Error bars represent the inner 95% of parameter estimates from our model. The line and envelope (in gray) were fit with the method `"lm"` in the function `geom_smooth` in `ggplot2`. (Abbreviations: *S. pulchra* (SP), *E. glaucus* (EG), *A. barbata* (AB), *B. hordeaceus* (BH), and *B. diandrus* (BD)).