Appendix from L. H. Uricchio et al., “Priority Effects and Nonhierarchical Competition Shape Species Composition in a Complex Grassland Community” (Am. Nat., vol. 193, no. 2, p. 213)

**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 (Levine and HilleRisLambers 2009; Mordecai 2013). 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 35 × 35-m area near the Sun Field Station in Jasper Ridge Biological Preserve. We cut holes in the matting to allow existing adult perennial plants (mostly *Stipa pulchra*) to survive. In fall 2015, before the first major rains, we removed the weed matting and established 210 1-m² competition plots and 30 4-m² 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 (respective seedlings of *Avena barbata*, *Bromus diandrus*, *Bromus hordeaceus*, and *Elymus glaucus*; *E. glaucus* adults; *S. 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 data set, and we do not describe fungal growth, inoculation, and fungicide methods here. In total, there were two replicate plots of each background species × density × 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 2 × 2-m 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 per square meter in the surrounding area. Monoculture densities were estimated at 10 adults m⁻² for each of the two perennial species, 1,715 seeds m⁻² for *A. barbata*, 3,209 seeds m⁻² for *B. diandrus*, 12,544 seeds m⁻² for *B. hordeaceus*, 4,585 seeds m⁻² for *E. glaucus*, and 1,466 seeds m⁻² for *S. pulchra*. In November 2015, we added seeds and transplanted adult *S. pulchra* plants to achieve the desired density treatment in each plot, removing excess bunchgrasses from plots as needed. We transplanted adult *E. glaucus* plants from an area 1 km away into the plots in December 2015. All transplants were watered to settle the soil. We then added to each plot approximately 10 seeds of each nonbackground species in January 2016, marked with plastic cutlery stuck into the ground, and one adult of each perennial species, marked with a small plastic ring, to ensure that all focal species were represented in each plot. These would become the focal individuals on which we would assess seed production.

In addition to applying weed matting to prevent seed set the prior year, we weeded the plots extensively to remove nontarget species and to thin plots to the desired density. However, despite these efforts, a substantial density of nontarget 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 \textit{A. barbata} and one seed per glume for \textit{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 5–10 m apart. Individual plots were placed based on desired plant community compositions; thus plots were unevenly spaced (3–18 m apart). Transects ranged from 20 to 50 m in length. Three of the transects were dominated by \textit{S. pulchra} at the perennial end, and the other three were dominated by \textit{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 plots 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 \textit{S. pulchra} and/or an adult \textit{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) and 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 and 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. A4), we allow $S$ to follow a negative binomial distribution:

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

where $\Gamma$ 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 $j$ 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

\[
f_j = \frac{1}{1 + \left(\sum_i \alpha_i D_i\right) + A_j \beta_j},
\]

where $D_i$ is the density of individuals of species $i$, and $\alpha_j$ captures the strength of the impact of individuals of species $i$ on $j$ ($\alpha_j$ is the vector of $\alpha_j$ values). Here $A_j$ is the area of infected leaf tissue of individual $i$, and $\beta_j$ is the impact of foliar fungal infection per unit leaf area infected on fitness for individuals of species $j$. We constrain the $\alpha$ and $\beta$ values to be nonnegative, 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 equation (A2), while preserving the shape of the negative binomial. To do so, we allow the $r$ parameter of the negative binomial to be given by

\[
r = r_0 f_j,
\]

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 $f_j$ given its local competitors and its infection burden.
Hence, the full likelihood of the observed seed output $S$ given competitor density is

$$P(S|r_0, p, \alpha_j, \beta_j) = \frac{\Gamma[S + r_0 f(\alpha_j, \beta_j)]}{\Gamma[S + 1] \Gamma[r_0 f(\alpha_j, \beta_j)]} (1 - p)^{r_0 f(\alpha_j, \beta_j)}.$$  \hspace{1cm} (A4)

**Estimating Competition and Foliar Infection Parameters**

We wrote custom Markov chain Monte Carlo (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 $\alpha$ and $\beta$ parameters with this method. Our software implements a standard Metropolis-Hastings algorithm. We compute the likelihood function with equation (A4) and apply an uninformative $\Gamma$-shaped prior on $\alpha_j$ and $\beta_j$ such that these parameters are constrained to be nonnegative. 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 ($\alpha_j$) and infection parameters ($\beta_j$) 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 data set, 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 figure A5.

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 $\alpha_j$ and infection parameters $\beta_j$ 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. A6).

**Sensitivity Analyses**

To better understand which demographic parameters are most important for determining the outcome of competition (i.e., GRWR) for each species, we independently increased each parameter by 5% for each posterior estimate. For simplicity, for each species, we limited this experiment to the set of parameters that directly impact its growth (i.e., its own demographic rates: for each species $j$, only parameters subscripted with $j$). To further reduce the number of parameters, we simultaneously increased all parameters pertaining to the impact of competition on perennial transition from seedling to adult (i.e., $\alpha_j$, $\alpha_a$, $\alpha_e$, and $\alpha_s$), which we then denote as a composite parameter $\alpha_{Pj}$. We included both black fingers of death (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 $\Delta$GRWR. We report the median $\Delta$GRWR over all posterior samples.

The population growth of both perennial species was most sensitive to the over-summer survival of adult individuals ($\xi$) and essentially insensitive to all other parameters (fig. A8). *Avena barbata* was highly sensitive to $\gamma$ (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. A2). *Bromus diandrus* and *B. hordeaceus* were modestly positively impacted by increasing the probability of establishment for both infected and uninfected seedlings ($\phi'$ and $\phi''$) and per capita seed production, $\lambda$, but negatively impacted by increases in $\gamma$ and interspecific competition with each other.
Figure A1: Estimated germination ($g_j$) and establishment ($\phi_j$) probabilities for each species $j$. Establishment probability was estimated in the presence and absence of foliar fungal pathogens. AB = *Avena barbata*, BD = *Bromus diandrus*, BH = *Bromus hordeaceus*, EG = *Elymus glaucus*, SP = *Stipa pulchra*.

Figure A2: Proportion of seeds, by species, infected by the black fingers of death pathogen in a seed bag experiment. AB = *Avena barbata*, BD = *Bromus diandrus*, BH = *Bromus hordeaceus*, EG = *Elymus glaucus*, SP = *Stipa pulchra*. 
Figure A3: Estimates of the probability of adult perennial over-summer survival rate (which we term \( \xi \) 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. \( EG = Elymus glaucus \), \( SP = Stipa pulchra \).

Figure A4: Cumulative distribution of observed seed counts (\( P(s < S) \)) plotted as a function of seed count \( S \). Each point represents the fraction of plants that have a seed count less than \( S \). The dotted blue lines show the cumulative distribution of the best-fitting negative binomial distribution, obtained by maximum likelihood. \( AB = Avena barbata \), \( BH = Bromus hordeaceus \), \( BD = Bromus diandrus \), \( SP = Stipa pulchra \), \( EG = Elymus glaucus \).
Figure A5: True and inferred parameter values as determined by our Markov chain Monte Carlo method, as obtained from simulation. The inferred values represent the mean of the inferred posterior distribution. The lines and envelopes (in gray) were fit using a simple linear model of the form $y = mx + b$ with the lm method in the function geom_smooth in ggplot2, while the red dotted lines show the diagonal (i.e., the expectation if inference were perfect). The value $\alpha_{BD,SP}$ is the impact of *Stipa pulchra* (SP) on *Bromus diandrus* (BD).

Figure A6: Observed median monoculture seed output densities plotted against those predicted by our population-dynamic model. Error bars represent the inner 95% of parameter estimates from our model. The line and envelope (in gray) were fit using a simple linear model of the form $y = mx + b$ with the lm method in the function geom_smooth in ggplot2. AB = *Avena barbata*, BD = *Bromus diandrus*, BH = *Bromus hordeaceus*, EG = *Elymus glaucus*, SP = *Stipa pulchra*. 

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Figure A7: Comparison of pairwise invasion analyses using all data (competition plots and transects; A), only the data from the competition experiment (B), or only data from the transects (C). SP = *Stipa pulchra*, EG = *Elymus glaucus*, BH = *Bromus hordeaceus*, BD = *Bromus diandrus*, AB = *Avena barbata*. Appendix from L. H. Uricchio et al., Priority Effects and Nonhierarchical Competition Shape Species Composition in a Complex Grassland Community
Figure A8: Sensitivity analysis results. For each species, we plot the proportional difference in growth rate when rare (GRWR) when the corresponding parameter is increased by 5%. The impact of Stipa pulchra on the focal species is denoted by $\alpha_{SP}$, $\alpha_{EG}$ represents the impact of Elymus glaucus on the focal species, and so on. Parameters are defined in table 1. Perennial native species: S. pulchra (SP), E. glaucus (EG); annual exotic species: Bromus hordeaceus (BH), Bromus diandrus (BD), Avena barbata (AB).