Supporting Appendix

Results from an Alternative Model

The results we present in the main text come from a statistical model that predicts state-to-state transitions of each cell as a function of underlying, and unobserved, survival and colonization processes. To test whether our conclusions are robust to model choice, we developed a phenomenological statistical model that estimates cell transitions without making any assumptions about the underlying processes. Here, we (*i*) describe this model, a hierarchical version of a multinomial regression; (*ii*) use this model to test the three conditions of the storage effect and to quantify the strength of the storage effect; and (*iii*) compare the results of the multinomial model with the survival/colonization model described in the main text.

Model Description. One way to model cell transitions from one year to another is with a transition matrix containing all possible state-to-state transitions. For our three grass species and bare ground, this would be a 4×4 matrix in which row 1, column 1 gives the probability that a cell occupied by species 1 remains in state 1; row 2, column 1 is the probability that a cell occupied by species 1 makes a transition to species 2; and so on. Each of the columns sums to 1. Because of the fine spatial scale of our data, these transitions are not constant across the entire quadrat, or grid; instead, the entries in our 4×4 transition matrix are conditional on the abundances of each species in the cell's local neighborhood. This model differs from our survival/colonization model in that it makes no assumptions about how row and column transitions are related. In other words, the transition from state 1 to state 2 in this model is unrelated to the transition from state 3 to state 2 or from state 1 to state 3. In contrast, in our survival/colonization model, transitions from states 1 and 3 to state 2 are linked because both require species 2 to colonize; similarly, transitions from state 1 to states 2 or 3 are linked because both require species 1 to die.

Multinomial logit regression is a standard technique for estimating a categorical response conditional on covariates. Because we have $k = 4$ possible states, the system of equations is:

$$P(y = \text{spp1}) = \frac{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t})}{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{2,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{3,j,t}\mathbf{x}_{c,t})}$$

$$P(y = \text{spp2}) = \frac{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t})}{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{2,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{3,j,t}\mathbf{x}_{c,t})}$$

$$P(y = \text{spp3}) = \frac{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t})}{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{2,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{3,j,t}\mathbf{x}_{c,t})}$$

$$P(y = \text{bare}) = \frac{1}{\exp(\boldsymbol{\beta}_{1,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{2,j,t}\mathbf{x}_{c,t}) + \exp(\boldsymbol{\beta}_{3,j,t}\mathbf{x}_{c,t})}$$

Each $\boldsymbol{\beta}$ is a vector of regression coefficients for each of the three species, and the vector of covariates, $\mathbf{x}$, gives the abundances of each species in the neighborhood of the focal cell, c, at time t. Note that we do not distinguish between cells belonging to the same plant as the focal cell and cells occupied by other neighboring conspecific plants (as we do in the survival/colonization model), because including these terms prevents Markov Chain Monte Carlo (MCMC) convergence. The $\boldsymbol{\beta}$s are unique for each year in the dataset, as indicated by the subscript t. In addition, we expect that the influence of each species in the neighborhood will depend on the state of the cell at time t, so we specify a different set of $\boldsymbol{\beta}$s for each possible previous state, j.

The hierarchical nature of the model is important for two reasons. First, in order to estimate the strength of the storage effect, we needed to estimate the value of all $\boldsymbol{\beta}$s in a constant, average environment. We could simply average all year-specific $\boldsymbol{\beta}$s, but this weights all years equally. The hierarchical approach allows us to treat the $\boldsymbol{\beta}$s as random effects and estimate their underlying mean values, taking into account different degrees of uncertainty in the different year-specific parameters (due, for example, to annual variability in the abundance of a particular species). Second, the hierarchical approach allows us to "borrow strength." If a particular transition is not observed often in a

particular year, but when it is observed the outcome is unusual, the maximum-likelihood approach might estimate an extreme value for the parameter. The hierarchical approach will use information about the mean response for that transition to dampen such extreme values. We fit the model by using Bayesian computational methods for practical reasons (WinBUGS software) and to ensure a fitting procedure consistent with the original survival/colonization model. We used the same prior distributions for year-specific and mean parameters and the same diagnostics to check for convergence of the MCMC chains (*Supporting Methods*).

Model Comparison. Although the multinomial regression model contained more parameters than the survival/colonization model, the deviance explained was no lower at convergence, and the deviance information criterion (DIC) was slightly higher. This difference in DIC may indicate that the survival/colonization model better represents biological processes, but it also reflects the inclusion of terms in the survival/colonization model that distinguish between neighboring self and nonself conspecific cells. Regardless of the outcome of this model comparison, we were interested in whether the multinomial model would arrive at the same conclusion as the survival/colonization model when used to test the storage effect.

Results and Discussion.

Conditions 2 and 3 of the storage effect. We used the same simulations described in *Materials and Methods* to test for conditions 2 and 3 of the storage effect, simply substituting the multinomial regression model for the survival/colonization model to calculate the expected abundances for each grid. Results were qualitatively consistent with those from the survival/colonization model, providing evidence of species-specific responses to interannual variation (compare Fig. 2 *D–F* with Fig. A1 *D–F*) and of more severe competition in more favorable years (compare Fig. 2 *G–I* with Fig. A1 *G–I*). However, there are some differences between the two sets of results. The range in yearly intrinsic growth rates projected by the multinomial model is greater than the range predicted by the survival/colonization model. The multinomial model also produced a

much greater range in the effects of competition on growth, and it predicts many positive values (facilitation), especially for *Schizachyrium scoparium*, presumably because in the multinomial model we could not separate within- and between-plant conspecific effects as we did in the survival model. The wider ranges in predicted growth rates and competitive effects projected by the multinomial model may indicate that over-parameterization in this model generated some extreme values.
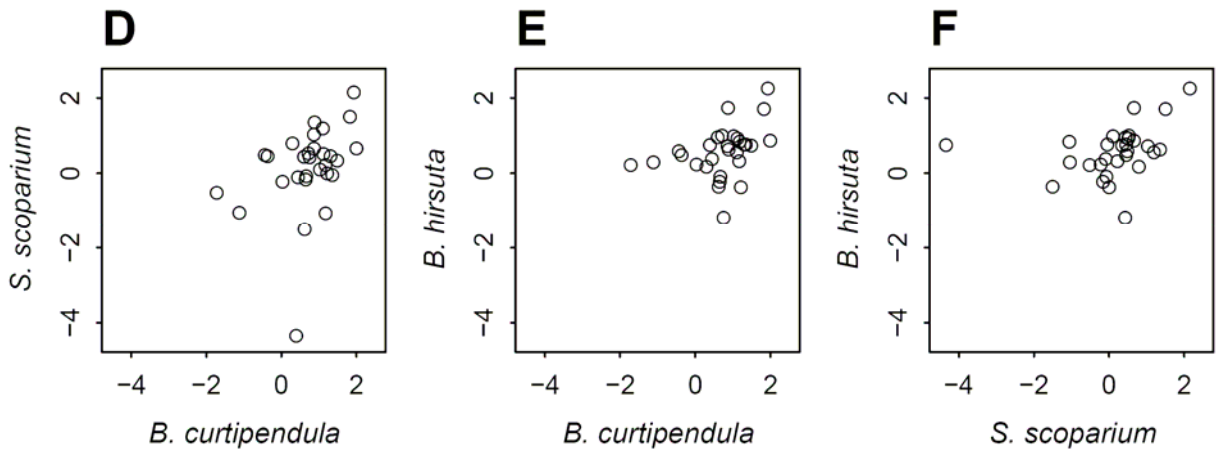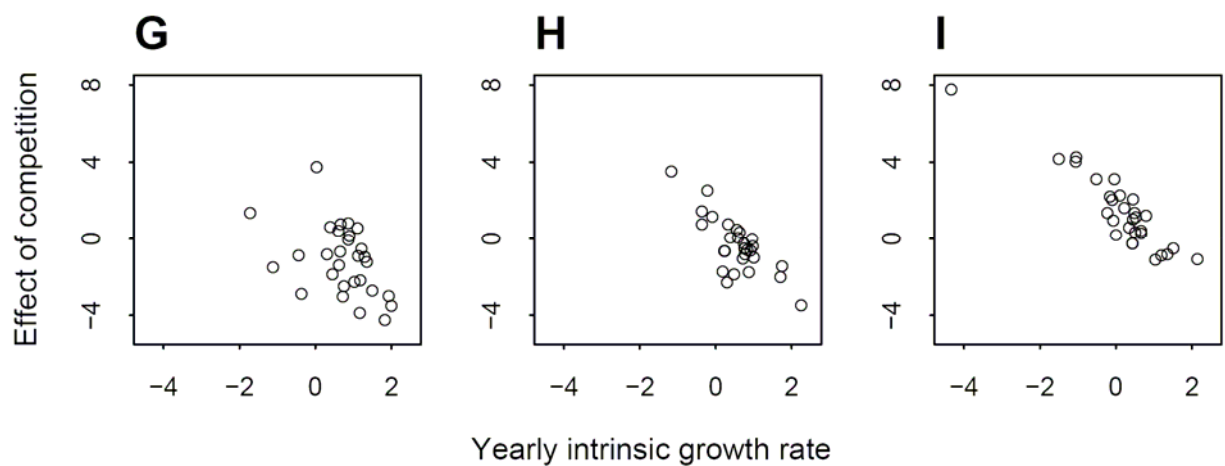
Fig. A1. Evidence for conditions 2 (*D–F*) and 3 (*G–I*) of the storage effect, based on projections of the multinomial regression model.

Strength of the storage effect. In *Materials and Methods*, we describe the two stages of simulation used to quantify the strength of the storage effect. First, we determine equilibrium abundances for all possible pairs of the three species in a constant environment (by using the across-year mean parameters) and in variable environments (by randomly choosing year-specific parameters at each time step). Second, we introduce the focal species at low density into grids initialized with its two competitors at their equilibrium abundances and then project growth over 1 year for a constant or variable environment.

When we repeated the first stage of simulation (pairwise equilibriums) using the multinomial model, we found that in each case one species quickly filled the entire grid. This result is biologically unrealistic because basal cover reached 100%, much higher than the observed maximum basal cover. When we introduce the focal species at low density into such fully occupied grids, the growth rates of these species are always extremely negative. Because the multinomial regression model produces unreasonable equilibrium densities, we chose to invade a community in which each pair of resident species is fixed at an empirically realistic 20% cover.

By using these fixed resident species abundances, we found that the average low-density growth rates for all three species were higher in variable than in constant environments, consistent with the results of the survival/colonization model (Fig. A2). The purely phenomenological approach thus supports the qualitative conclusions of the more mechanistic model. In contrast to our survival/colonization model, population growth rates when these species were rare were positive for all three species in the constant environment. However, direct comparison of the growth rates is complicated by our fixed definition of the resident community equilibrium for the analysis of the multinomial model.
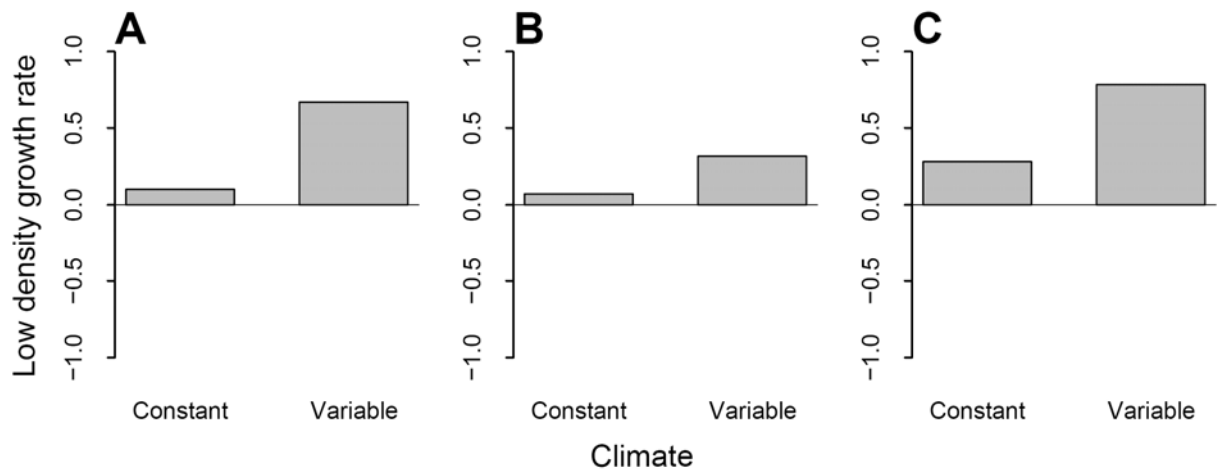
Fig. A2. The multinomial regression model predicts that all three species would have higher average low-density growth rates in a variable than a constant environment.