How fluctuation-dependent species coexistence affects the diversity-stability relationship

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Abstract

For biodiversity to increase the temporal stability of ecosystem function in the long-term, coexistence must be stable. Species-specific respones to environmental variation through time is key to understanding fluctuation-dependent coexistence mechanisms and how asynchrony in species dynamics can arise to stabilize ecosystem function. Despite the shared dependence on environmental fluctuations, theory on species coexistence and the relationship between species richness and ecosystem stability have developed independently. To formally link the two bodies of theory, we use consumer-resource models where coexistence between two species utilizing a single resource is maintained by two fluctuation-dependent mechanisms: the storage effect and relative nonlinearity. We examine how the strength of species coexistence relates to the temporal stability of aggregate ecosystem function and how the effect of environmental variability on stability is mediated by the mechanism of coexistence. Blah, blah, blah...

INTRODUCTION

MacArthur (1955), Elton (1958), and even Darwin (Turnbull et al. 2013) recognized that species can compensate for each other and stabilize functioning in ecosystems subject to temporal variation in environmental conditions. This idea underlies the "insurance hypothesis" (Yachi and Loreau 1999), which suggests stability increases with diversity because species respond dissimilarly to environmental conditions – species A has highest growth rates under conditions X whereas species B has highest growth rates under conditions Y. More species confer temporal stability by broadening the range of conditions under which the community maintains function (Loreau 2010). Diverse models all predict a positive relationship between species richness and ecosystem stability (Lehman and Tilman 2000, Ives and Hughes 2002, Loreau and de Mazancourt 2013), and experimental tests tend to support such a prediction (Tilman et al. 2006, Hector et al. 2010). However, empirical support for a positive diversity-stability relationship is not unequivocal (Jiang and Pu 2009). Furthermore, theory on the relationship between biodiversity and ecosystem stability often ignores the processes that determine species coexistence in variable environments (Loreau 2010, but see Chesson et al. 2001).

Theoretical (Chesson 2000, Chesson et al. 2004) and empirical (Cáceres 1997, Descamps-Julien and Gonzalez 2005, Adler et al. 2006, Angert et al. 2009) work has identified temporally fluctuating environmental conditions as an important ingredient for stable species coexistence. Such "fluctuation-dependent" coexistence (Chesson 2000) requires that species have unique environmental responses and that environmental conditions vary enough for each coexisting species to experience good and bad conditions. Thus, there is reason to expect environmental variability to promote species richness when coexistence is maintained by a fluctuation-dependent mechanism (Adler and Drake 2008). Of course, increasing environmental variability may also decrease ecosystem stability through time by increasing the fluctuations of individual species, regardless of species richness.

The countervailing effects of environmental variability present an interesting paradox: increasing variability should decrease ecosystem stability, but may also increase richness, which

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may offset the decrease in stability. Such a paradox complicates predictions about how ecosystems will respond as environmental conditions exceed historical ranges of variability because we do not know the net effect of environmental variability on ecosystem stability when species coexistence is fluctuation-dependent. The unknown net effect of environment variability may be reflected in the mixed results from empirical studies on the diversity-stability relationship. Observational tests of the diversity-stability relationship, which require sampling across natural diversity gradients, have yielded positive (Hautier et al. 2014), neutral (Valone and Hoffman 2003, Cusson et al. 2015), and negative (Sasaki and Lauenroth 2011) relationships. In a meta-analysis of diversity-stability relationships, Jiang and Pu (2009) found no significant evidence for an effect of species richness on ecosystem stability from observational studies in terrestrial ecosystems. Thus, there appears to be a gap between the consistency of theoretical studies and the equivocation of empirical studies.

We argue this gap exists because the two bodies of theory that have developed to explain species coexistence on the one hand, and diversity-stability relationships on the other, have diverged. One reason these two disciplines have diverged is because they have focused on slightly different questions. Biodiversity-ecosystem stability studies typically ask how ecosystem variability responds to different levels of species richness at a given level of environmental variability (reviewed in Kinzig et al. 2001, Loreau 2010), whereas coexistence studies ask how the long term stability of species coexistence responds to different levels of environmental variability (Chesson and Warner 1981).

To reconcile these two bodies of theory, we require a synthetic theory that fully accounts for the linkages among environmental variability, species coexistence, and ecosystem stability. Here, we extend theory on the relationship between species richness and ecosystem stability to cases in which species coexistence explicitly depends on environmental fluctuations and species-specific responses to environmental conditions. We focus on the storage effect and relative nonlinearity using a general consumer-resource model. First, we use model simulations to investigate the diversity-stability relationship across a gradient of environmental variability. Counter to common expectations, we find that a negative diversity-stability relationship should be expected when sampling occurs over

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natural diversity gradients and species coexistence is fluctuation-dependent. Importantly, and in line with previous theory (Ives and Hughes 2002, Loreau 2010, Mazancourt et al. 2013), at a given level of environmental variability, increasing species richness stabilizes ecosystem function, even when coexistence is fluctuation-dependent. Second, we explore the net effect of increasing environmental variability on ecosystem stability by isolating the gain in stability due to increased richness and the loss in stability due to increased amplitude of species fluctuations. We find that increasing environmental variability does not always lead to a decrease in ecosystem stability because stabilization via species' additions can potentially offset destabilization via increased species fluctuations. However, whether or not increasing environmental variability results in species gains depends on the traits of resident species and the traits of the species in the regional pool.

MATERIALS AND METHODS

Consumer-resource model

To discover how fluctuation-dependent coexistence mechanisms affect the diversity-stability relationship, we developed a semi-discrete consumer-resource model that allows many species to coexist on one resource by either the storage effect or relative nonlinearity. In our model, the consumer can be in one of two-states: a dormant state D and a live state N. The dormant state could represent, for example, the seedbank of an annual plant. Transitions between N and D occur at discrete intervals τ with continuous-time consumer-resource dynamics between discrete transitions. Thus, our model is formulated as "pulsed differential equations" (Pachepsky et al. 2008, Mailleret and Lemesle 2009, Mordecai et al. 2016). For clarity we refer to τ as years and the growing time between years as seasons with daily (t) time steps.

During a growing season, consumer-resource dynamics are modeled as two differential equations:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \epsilon_i f_i(R), \quad t \neq \tau_k \tag{1}$$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = -\sum_{i=1,2} f_i(R) N_i, \quad t \neq \tau_k \tag{2}$$

where the discrete transitions between N and D occur between seasons at times τ_k, $k = 1, 2, 3, \ldots, K$. The subscript i denotes species, N is the living biomass state, and ϵ_i is each species' resource-to-biomass conversion efficiency. The growth rate of living biomass is a resource-dependent Hill function, $f_i(R) = r_i R^{a_i}/(b_i^{a_i} + R^{a_i})$, where r is a species' intrinsic growth rate and a and b define the curvature of the function. Resource depletion is equal to the sum of each species' consumption.

Along with resource uptake, consumer population growth depends on the production of dormant biomass (D), the activation of dormant biomass to live biomass ($D \to N$), and the survival of living biomass from one year to the next. The biomass of each species' states at the start of a growing season are equal to

$$D_i(\tau_k^+) = (1 - \gamma_{i,\tau_k})[\alpha_i N_i(\tau_k) + D_i(\tau_k)](1 - \eta_i) \tag{3}$$

$$N_i(\tau_k^+) = (1 - \alpha_i) N_i(\tau_k) + \gamma_{i,t}[\alpha_i N_i(\tau_k) + D_i(\tau_k)](1 - \eta_i), \tag{4}$$

where $D(\tau_k)$, $N(\tau_k)$, and $R(\tau_k)$ are the abundances of each state at the end of growing season k and τ_k^+ denotes the beginning of growing season $k = 1$. The activation of dormant biomass to live biomass is controlled by γ, which is year (k) and species (i) specific. Dormant biomass is equal to a constant fraction (α) of live biomass at the end of the previous season ($N_i(\tau_k)$), plus survival ($1 - \eta_i$) of dormant biomass ($D_i(\tau_k)$) at the end of the previous year and dormant biomass remaining after live biomass activation ($D_i(\tau_k)(1 - \gamma_{i,\tau_k})$). Live biomass is equal to newly activated dormant biomass ($\gamma_{i,t}[D_i(\tau_k)$), minus some fraction of live biomass that is converted to dormant

Table 1 Default values of model parameters and their descriptions. Parameters that vary depending on the mode and strength of species coexistence or depending on species copmetive hierarchies are labeled as "variable" in parantheses. The dormant-to-live biomass transition fraction (γ) is a function of other parameters, so has no default value.

Parameter	Description	Value
r	maximum per capita growth rate	1 (variable)
a	Hill function rate parameter	2 (variable)
b	Hill function curvature parameter	2.5 (variable)
ϵ	resource-to-biomass conversion efficiency	0.5
α	allocation fraction of live biomass to dormant biomass	0.5 (variable)
γ	dormant-to-live biomass transition fraction	–
ρ	correlation of species' response to the environment	0 (variable)
σ_E	variance of the environmental cue	2 (variable)
η	dormant biomass mortality rate	0.1
$\mu(R^+)$	mean annual resource pulse	20 (non-log scale)
$\sigma(R^+)$	standard deviation of annual resource pulse	0 (variable)

130 biomass $((1 - \alpha_i)N_i(\tau_k))$ We assume the resource pool is not replenished within a growing season.

131 Resource replenishment occurs between growing seasons, and the resource pool (R) at the start

132 of the growing season k+1 is $R(\tau_k^+) = R^+$, where R^+ is a random resource pulse drawn from a

133 log-normal distribution with mean $\mu(R^+)$ and standard deviation $\sigma(R^+)$. Model parameters and

134 notation are described in table 1.

Implementing the Storage Effect   To make this a storage effect model, we need to satisfy

136 three conditions: (1) the organisms must have a mechanism for persistence under unfavorable

137 conditions, (2) species must respond differently to environmental conditions, and (3) the effects

138 of competition on a species must be more strongly negative in good years relative to unfavorable

139 years. Our model meets condition 1 because we include a dormant stage with very low death rates.

140 We satisfy condition 2 with our model whenever γ is not perfectly correlated between species.

141 Lastly, our model meets condition 3 because condition 2 partitions intraspecific and interspecific

142 competition into different years. Thus, during a high γ year for one species, resource uptake is also

143 inherently high for that species, which increases intraspecific competition relative to interspecific

144 competition. So, given adequate variability in γ, the inferior competitor can persist. We created

145 competitive hierarchies in the storage effect version of the model by altering species' biomass

146 conversion efficiencies (ϵ)

We generated sequences of (un)correlated dormant-to-live state transition rates (γ) for each species by drawing from multivariate normal distributions with mean 0 and a variance-covariance matrix ($\Sigma(\gamma)$) of

$$\Sigma(\gamma) = \begin{bmatrix} \sigma_E^2 & \rho\sigma_E^2 \\ \rho\sigma_E^2 & \sigma_E^2 \end{bmatrix} \tag{5}$$

where σ_E^2 is the variance of the environmental cue and ρ is the correlation between between the two species' transition rates. ρ must be less than 1 for stable coexistence. The inferior competitor has the strongest potential to persist when $\rho = -1$ (perfectly uncorrelated transition rates).

Implementing Relative Nonlinearity When considering consumer-resource dynamics, species coexistence by relative nonlinearity requires that each species has different nonlinear responses to resource availability, and resource availability must fluctuate through time. In a constant resource environment, the species with the lowest $R*$ will always exclude the other species. To create competitive hierarchies among species we altered species resource uptake curves (Fig. SX). We still allow the germination rate (γ) to vary, but both species are perfectly correlated – that is, $\rho = 1$ (Fig. 1).

Model simulations

We simulated the model with four species under two scenarios for each coexistence mechanism. First, we allowed the variance of the environment to determine how many species can coexist, akin to a community assembly experiment with a species pool of four species. This required simulating communities with all species initially present across a gradient of annual resource variability (for relative nonlinearity) or environmental cue variability (for the storage effect). Second, we chose parameter values that allowed coexistence of all four species and performed species removals. We
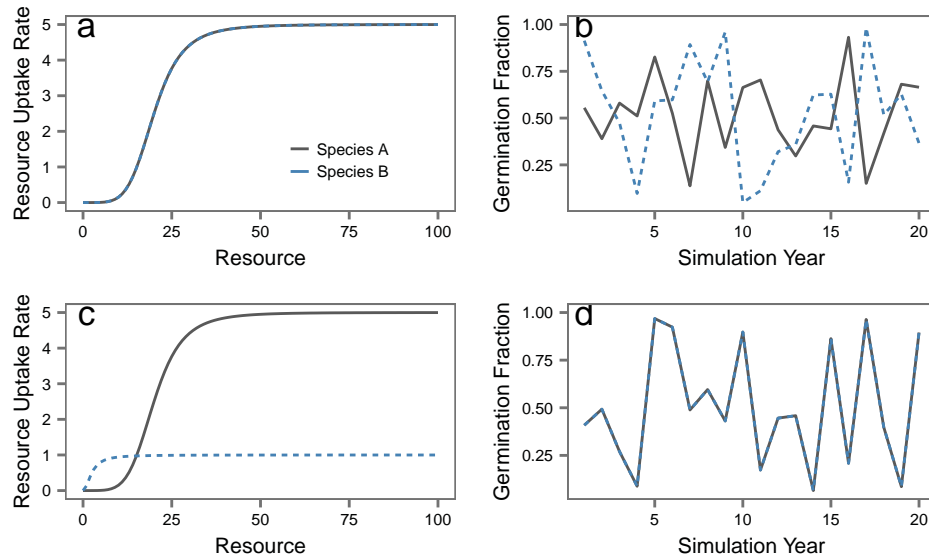
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Figure 1 Resource uptake functions and example time series of (un)correlated germination fractions for the storage effect (*a,b*) and relative nonlinearity (*c,d*) formulations of the consumer-resource model. The resource uptake functions for both species are equivalent for the storage effect, but their germination fractions are uncorrelated in time. The opposite is true for relative nonlinearity: the two species have unique resource uptake functions, but their germination fractions are perfectly correlated in time.

ran simulations for 10,000 seasons with 20 day growing seasons. We averaged biomass over the growing season. After discarding an initial 1,000 seasons to reduce transient effects on our results, we calculated the coffecient of variation of summed species biomass through time. For simulations where environmental variability determined species coexistence, we calculated species richness as the number of species whose average biomass was greater than 1 over the course of the simulation. Within-season dynamics were solved given initial conditions using the package `deSolve` (Soetaert et al. 2010) in `R` (Team 2013). All model code has been deposited on Dryad (*link*) and is available on GitHub at http://github.com/atredennick/Coexistence-Stability.

RESULTS AND DISCUSSION

The diversity-stability relationship

The direction of the diversity-variability relationship can be positive and negative when species coexistence is maintained by fluctuation-dependent mechanisms (Fig. 2). Ecosystem variability
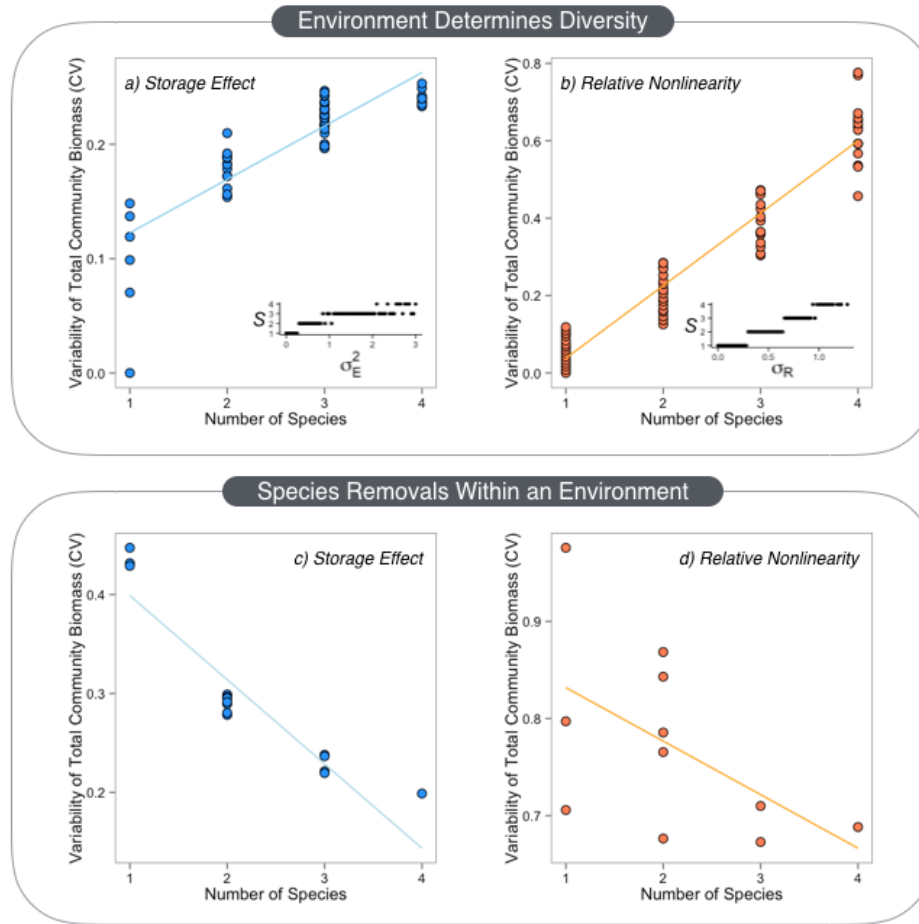
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Figure 2 Variability of total community as function of species richness when coexistence is maintained by the storage effect (a,c) or relative nonlinearity (b,d). Top panels show results from simulations where environmental or resource variance determine the number species that coexist in a community. Bottom panels show results from simulations where environmental or resource variance is fixed at a level that allows coexistence of all four species, but speces are removed to manipulate diversity. In the most general sense, the top panels represent regional diversity-stability relationships across natural diversity gradients, whereas the bottom panels represent local diversity-stability relationships.

179 is positively correlated with species richness when species richness is measured across a gradient

180 of envrionmental variability, which maintains diversity and promotes ecosystem variability (Fig.

181 2a,b). If environmental conditions are sufficient to maintain coexistence, removing species increases

182 ecosystem variability (Fig. 2c,d). Thus, our results both confirm and contrast with theoretical and

183 experimental findings that diversity begets stability.

184   When we held environmental variability constant and removed species, we produced the

185 typical negative diversity-variability relationship (Fig. 2c,d), consistent with theoretical expecations

186 from models with species coexistence maintained by fluctuation-dependent mechanisms. Likewise,

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our results from the species removal simulations are consistent with results from biodiversity-ecosystem functioning experiments showing a negative relationship between species richness and ecosystem variability. This is encouraging because species almost certainly coexist by some combination of fluctuation-independent (e.g., resource partitioning) and fluctuation-dependent mechanisms. By extending theory to communities where species richness is explicitly maintained by temporal variability, we have gained confidence that experimental findings are generalizable to many communities. In other words, in local settings where environmental variability is relatively homogenous, reductions in the number of species will reduce the stability of ecosystem functioning, regardless of how coexistence is maintained.

When we allowed a gradient of environmental variability to determine species coexistence, we discoverd a positive relationship between species richness and ecosystem variability (Fig. 2a,b). While surprising when viewed through the lens of previous theory and experimental findings, such a relationship is a direct consequence of how diversity can be maintained in fluctuating environments. The storage effect and relative nonlinearity both require envrionmental fluctuations to allow niche differentiation between species pairs (Chesson 2000). Therefore, species coexistence gains strength, for both mechanisms, as the envrionment becomes more variable (Fig. SX).

Our results may explain why deviations from the negative diversity-variability relationship often come from observational studies. Observational studies must rely on natural diversity gradients, and if species richness depends environmental variability, it is entirely possible to observed positive diversity-variability relationships. For example, Sasaki and Lauenroth (2011) found a negative relationship between species richness and the temporal stability of plant abundance (a positive diversity-variability relationship) in a semi-arid grassland. Their data came from a six sites that were 6 km apart. Thus, it is possible that each site experienced slightly different levels of environmental variability that influenced species coexistence. Indeed, fluctuation-dependent coexistence mechanisms may be common in arid and semi-arid environments [Chesson et al. (2004); Angert et al. (2009)[.

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The impact of increasing environmental variability on ecosystem variability

The magnitude of environmental variability directly influences the variability of aggregate ecosystem properties, such as net primary production, when species' population growth and community dynamics track environmental conditions. It is clear that, at a given level of environmental variabilty, species richness begets ecosystem stability (Tilman et al. 2006, Hector et al. 2010, Loreau and de Mazancourt 2013), and our work adds support for the traditional diversity-stability relationship in cases where coexistence is fluctuation-dependent. However, we also find that increasing environmental variability has the potential to decrease ecosystem variability by allowing for more species to coexist (Fig. 3).
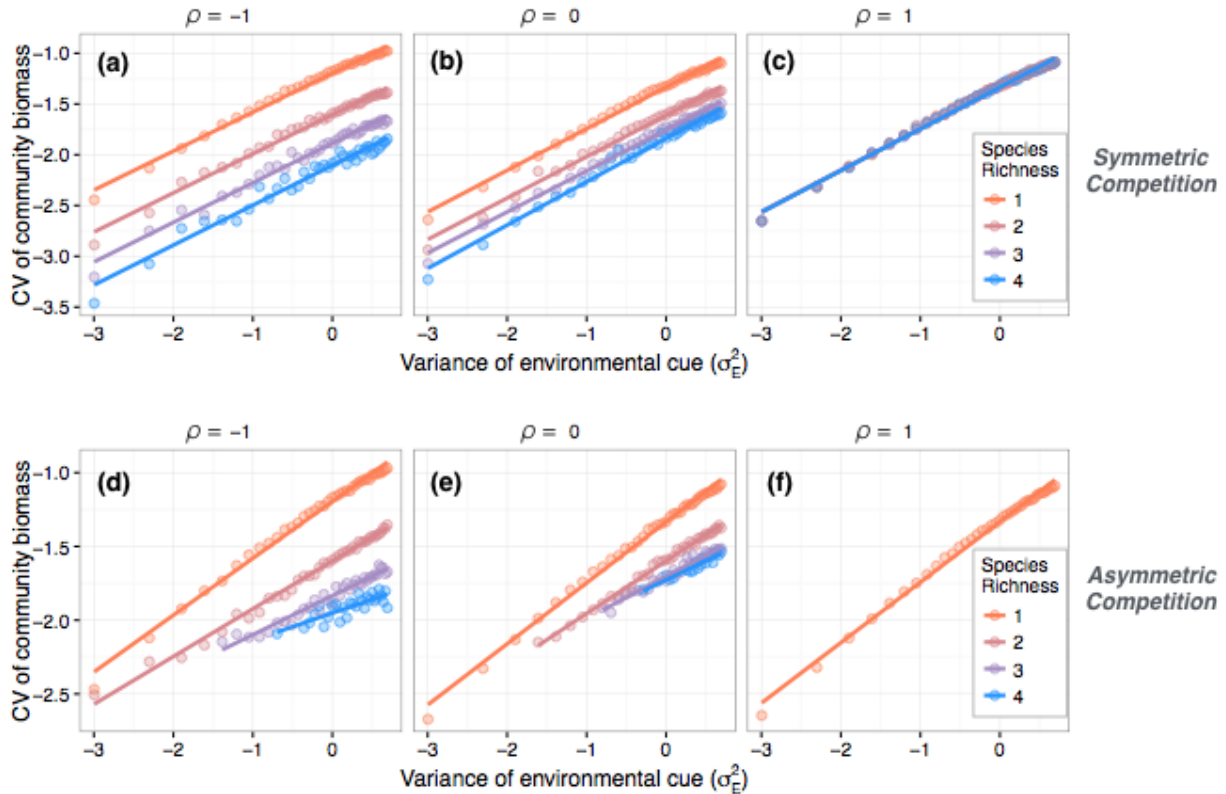
Figure 3 The effect of environmental variability on ecosystem variability with associated effects of species richness when species coexist via the storage effect. Panels (a-c) show simulation results where species have symmetrical competitive effects, whereas panels (d-f) show results when competition is assymetric (that is, in the absence of environmental fluctuations, all species but the superior competitor would be competitively excluded). We show results for different levels of correlations of species' environmental responses, ρ. At a given level of environmental variability, it is always better to have more species, as also shown in Fig. 2. Likewise, increasing environmental variance can, in some cases, actually decrease ecosystem variability if the increase is enough to allow species from the regional pool to enter the community. In essence, increasing environmental variance allows ecosystems to jump from one line to another as species are added. Note that the *x* and *y* axes are on the log scale for visual clarity.

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