

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

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Abstract

Theory relating species richness to ecosystem stability typically ignores interactions between environmental variability and species coexistence, or fluctuation-dependent coexistence. This may explain why we lack general explanations for observed deviations from the predicted positive diversity-stability relationship, and it limits our ability to predict the consequences of increasing environmental variability. Here we use a consumer-resource model to explore how fluctuation-dependent coexistence via the storage effect and relative nonlinearity affects ecosystem stability. First, we find that a negative, rather than positive, diversity-stability relationship is possible when ecosystem function is sampled across a natural diversity gradient. Second, we find that fluctuation-dependent coexistence can buffer ecosystem functioning against increasing environmental variability because species richness increases with environmental variability, which helps to stabilize ecosystem function via the portfolio effect. Our work provides a general explanation for non-positive diversity-stability relationships, and highlights the importance of conserving regional species pools so that species can be added to fluctuation-dependent communities as environmental variability increases.

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

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

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:

$$\frac{dN_i}{dt} = N_i \epsilon_i f_i(R), \quad t \neq \tau_k \quad (1)$$

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

where the discrete transitions between N and D occur between seasons at times τ_k , $k = 1, 2, 3, \dots, K$. 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 ($D \rightarrow N$), 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

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

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

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 competitive 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)

biomass $((1 - \alpha_i)N_i(\tau_k))$ We assume the resource pool is not replenished within a growing season. Resource replenishment occurs between growing seasons, and the resource pool (R) at the start of the growing season $k+1$ is $R(\tau_k^+) = R^+$, where R^+ is a random resource pulse drawn from a log-normal distribution with mean $\mu(R^+)$ and standard deviation $\sigma(R^+)$. Model parameters and notation are described in Table 1.

Implementing the Storage Effect To make this a storage effect model, we need to satisfy three conditions: (1) the organisms must have a mechanism for persistence under unfavorable conditions, (2) species must respond differently to environmental conditions, and (3) the effects of competition on a species must be more strongly negative in good years relative to unfavorable years. Our model meets condition 1 because we include a dormant stage with very low death rates. We satisfy condition 2 with our model whenever γ is not perfectly correlated between species. Lastly, our model meets condition 3 because condition 2 partitions intraspecific and interspecific competition into different years. Thus, during a high γ year for one species, resource uptake is also inherently high for that species, which increases intraspecific competition relative to interspecific competition. So, given adequate variability in γ , the inferior competitor can persist. We created competitive hierarchies in the storage effect version of the model by altering species' biomass 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

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

where σ_E^2 is the variance of the environmental cue and ρ is the correlation 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).

Numerical simulations

To understand how fluctuation-dependent coexistence can affect the diversity-stability relationship, 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

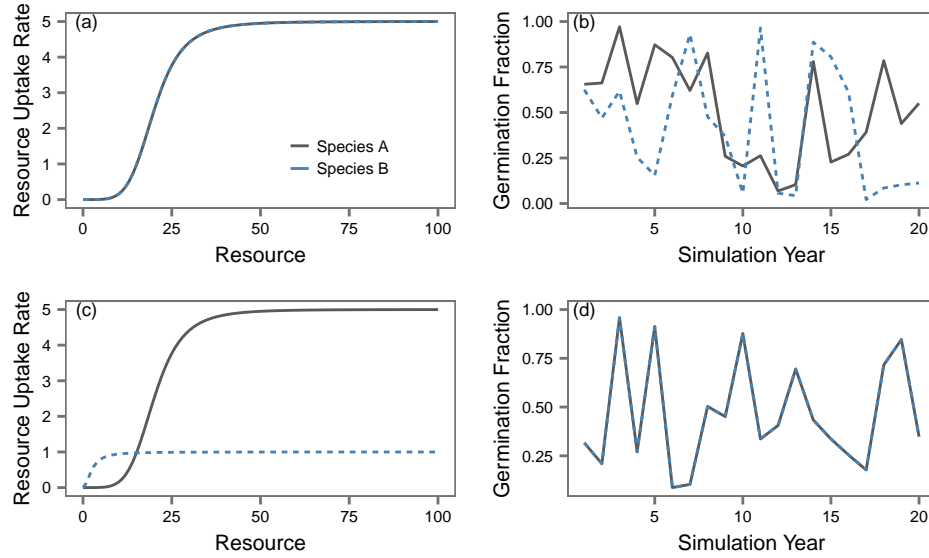


Figure 1 Resource uptake functions and example time series of (un)correlated germination fractions for the storage effect (*a,b*) and relative nonlinearity (*c,d*) formulations of the consumer-resource model. The resource uptake functions for both species are equivalent for the storage effect, but their 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.

parameter values that allowed coexistence of all four species and performed species removals. The two simulation experiments correspond to (i) sampling ecosystem function across a natural gradient of species richness and (ii) sampling ecosystem function across diversity treatments within a site.

To understand how increasing environmental variability will impact ecosystem stability when coexistence is fluctuation-dependent, we simulated the model over a range of environmental cue variability and species pool sizes. Thus, for each size of species pool (1, 2, 3, or 4 species), we simulated the model at 41 evenly-spaced levels of environmental cue (range = 0,2) or resource variability (range = 0,1.5). We also explored the influence of species asymmetries in competitive ability and species' correlations of environmental responses in the storage effect model. Under the storage effect, if all species are perfectly symmetrical, that is, there is no superior competitor, then coexistence is fluctuation-independent. We use one such parameterization of our model to contrast the response of ecosystem stability in fluctuation-dependent and fluctuation-independent communities to environmental variation. Likewise, under relative nonlinearity, species' resource response curves (Fig. SX) reflect traits that determine the intrinsic stability of each species. Therefore, we ran two

sets of simulations for relative nonlinearity: one where the species pools increased from stable to unstable species and vice versa. For example, if species A is the most stable species and species D is the least stable we ran simulations where the species pool increased from one to four species as A then B then C then D. We then ran simulations with that order reversed.

All simulations were run for 5,000 seasons with 20-day growing seasons. We averaged biomass over the growing season, and those yearly values were used to calculate total community biomass in each year. After discarding an initial 1,000 seasons to reduce transient effects on our results, we calculated the coefficient of variation of summed species biomass through time. Therefore, in our results we refer to ecosystem variability, which is the inverse of ecosystem stability. We calculated species richness as the number of species whose average biomass was greater than 1 over the course of the simulation. Parameter values for specific results are given in figure captions. 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-variability 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 is positively correlated with species richness when species richness is measured across a gradient of environmental variability, which maintains diversity and promotes ecosystem variability (Fig. 2a,b). If environmental conditions are sufficient to maintain coexistence, removing species increases ecosystem variability (Fig. 2c,d). Thus, our results both confirm and contrast with theoretical and experimental findings that diversity begets stability.

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

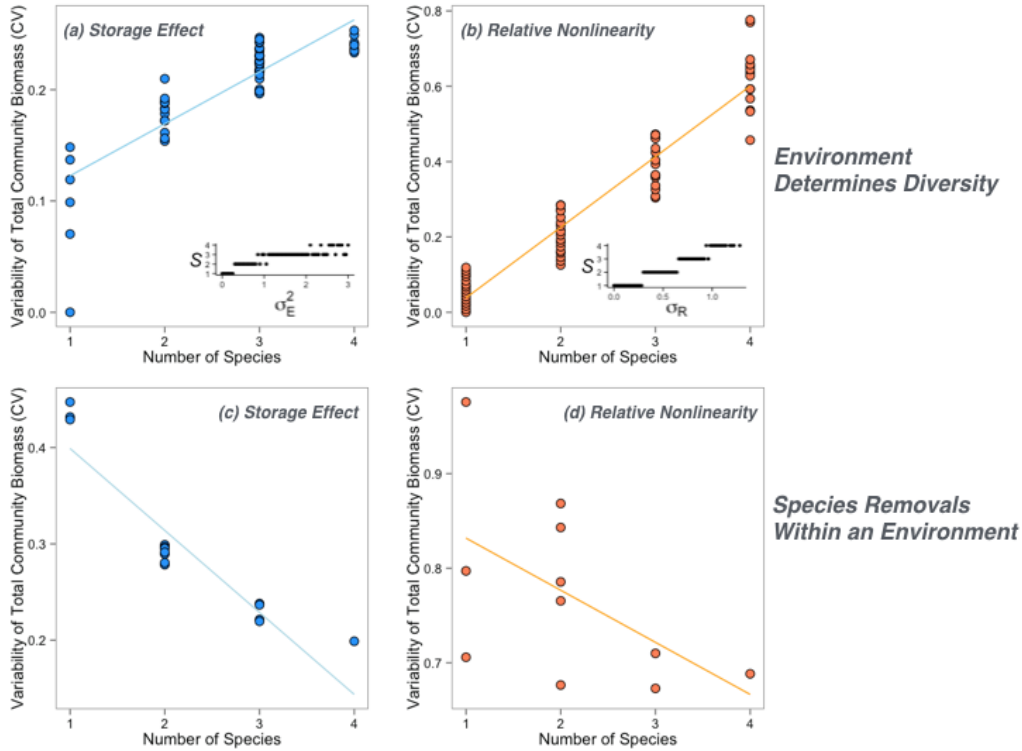


Figure 2 Variability of total community as function of species richness when coexistence is maintained by the storage effect (a,c) or relative nonlinearity (b,d). Top panels show results from simulations where environmental or resource variance determine the number species that coexist in a community. Bottom panels show results from simulations where environmental or resource variance is fixed at a level that allows coexistence of all four species, but species 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.

typical negative diversity-variability relationship (Fig. 2c,d), consistent with theoretical expectations from models with species coexistence maintained by fluctuation-dependent mechanisms. Likewise, 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 discovered 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 environmental fluctuations to allow niche differentiation between species pairs (Chesson 2000). Therefore, species coexistence gains strength, for both mechanisms, as the environment 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. Fluctuation-dependent coexistence mechanisms may be most common in arid and semi-arid environments (Chesson et al. 2004, Angert et al. 2009), making them particularly well-suited for future efforts aimed at empirically testing our theoretical results.

The impact of increasing environmental variability on ecosystem variability

Whether coexistence is fluctuation-independent or fluctuation-dependent becomes especially important when we consider how ecosystem stability responds to increasing environmental variability. In the fluctuation-independent case, species richness is essentially fixed because the species' inequalities that determine coexistence (niche and fitness differences) are not linked to environmental variability. Therefore, increasing environmental variability will always increase ecosystem variability. We can examine one example of this situation with the storage effect version of our model

where all species are equivalent. We find that the rate at which ecosystem variability increases with environmental variability is constant regardless of species richness, but that, as expected, more species rich communities are more stable on average (Fig. 3a-c). The difference in ecosystem variability among communities of different diversity depends on the strength of the correlations of their environmental responses (Fig. 3a-c).

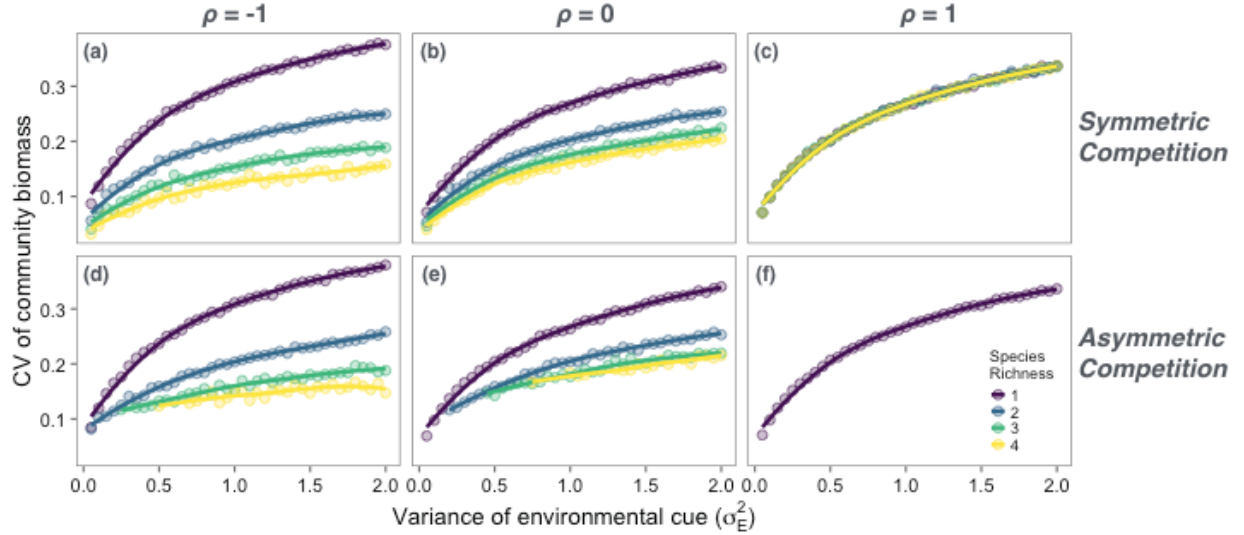


Figure 3 The effect of environmental variability on ecosystem variability with associated effects of species richness when species coexist via the storage effect. Panels (a-c) show simulation results where species have symmetrical competitive effects, whereas panels (d-f) show results when competition is asymmetric (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.

When species coexistence is fluctuation-dependent via the storage effect, increasing environmental variability has much more interesting effects on ecosystem variability. In Fig. 3d-f we show storage effect simulation results where environmental variability determines species coexistence from a regional species pool of four species. We also show results from nested subsets of the four species pool (e.g., only two species in the pool instead of four) to show the trajectory of ecosystem variability if new species are not present to join the local community. In accordance with coexistence theory, we find that species richness increases with environmental variability and, in some cases, increasing variability can actually completely temper the effect of increasing

environmental variability. For example, consider the single species local community at $\sigma_E^2 = 0.14$ in Fig. 3d. If a global change causes environmental variability to increase to $\sigma_E^2 = 0.6$, then there is a chance for four species to coexist, rather than one, and the *CV* of total community biomass remains almost constant. Thus, depending on the specific traits (parameter values) of the species in the regional pool, increasing environmental variability need not cause increases in environmental variability. There is potential for ecosystem variability to actually decrease, but this case may be rare because it would require a very large increase in environmental variability.

In communities where species coexist via relative nonlinearity, whether or not the direct impact of environmental variability on ecosystem variability is tempered by species additions depends on the species traits of immigrating species. When additional species, which immigrate from the regional pool, are less intrinsically stable than the resident species, ecosystem variability increases at a constant rate even as species are added (Fig. 4a). On the contrary, if more stable species are added, there is potential for species additions to buffer ecosystems from increasing environmental variability (Fig. 4b). The stability of individual species in our relative nonlinearity model is determined by their respective resource response curves (Fig. SX). Trait differences among species affects the degree to which species additions can buffer ecosystems under the storage effect (Fig. 3d-f). Under relative nonlinearity, we find that the buffering effect of species additions depends on species traits, and the order in which species enter the local community. Indeed, if all species in the regional pool are less stable than the resident species, then no stabilization occurs as species are added (Fig. 4a).

Our simulation results lead to two conclusions. First, when predicting the impacts of increasing environmental variability on ecosystem stability, the mechanism of coexistence in the community matters. Fluctuation-dependent coexistence can buffer ecosystems from increasing environmental variability by allowing for species additions. As shown in previous work (Loreau and de Mazancourt 2013), the stabilizing effect of species additions depends on the correlations of their environmental responses (Fig. 3e-f). Whether our theoretical predictions hold in real communities is unknown and requires empirical tests. Doing so would require manipulating environmental variability in

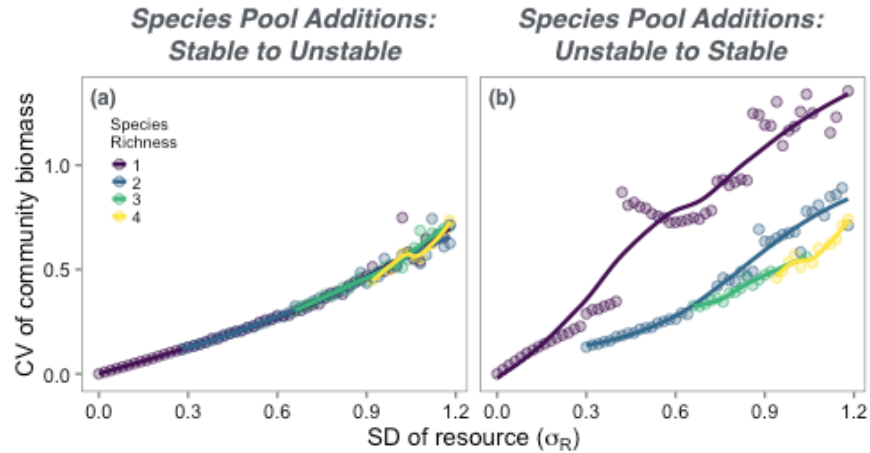


Figure 4 The effect of environmental variability on ecosystem variability with associated effects of species richness when species coexist via relative nonlinearity. (a) The species pool increases from 1-4 four species, with the fourth species being most unstable. Increasing environmental variability (the SD of annual resource availability) allows for greater species richness, but species additions do not modulate the effect of environmental variability on ecosystem variability. (b) The species pool increases from 1-4 four species, with the fourth species being most stable. In this case increasing environmental variability allows for greater realized species richness and can temper the effect of environmental variability.

communities where coexistence is known to be fluctuation-dependent, at least in part. Such data do exist (Angert et al. 2009), and a coupled modeling-experimental approach could determine if our predictions hold true in real communities.

Second, whether local fluctuation-dependent communities can receive the benefit of additional species depends on a diverse regional species pool. If the regional pool is not greater in size than the local species pool, than ecosystem stability will decline with environmental variability in a similar manner as in fluctuation-independent communities because species richness will be fixed. Metacommunity theory has made clear the importance of rescue effects to avoid species extinctions (Brown and Kodric-Brown 1997, Leibold et al. 2004). Here, instead of local immigration by a resident species working to rescue a species from extinction, immigration to the local community by a new species rescues ecosystem processes from becoming less stable. Thus, our results reinforce the importance of both local and regional biodiversity conservation. Just as declines in local species richness can destabilize ecosystem functioning (Tilman et al. 2006, Hector et al. 2010, Hautier et al. 2014), species losses at larger spatial scales can also weaken stability. Wang and Loreau (2014) show that regional ecosystem stability depends on regional biodiversity through its effects on beta

diversity and, in turn, the asynchrony of functioning in local communities. Our results show that, when coexistence is fluctuation-dependent, regional biodiversity declines could also affect local ecosystem functioning by limiting local species additions that could be possible under scenarios of increasing environmental variability.

Species coexistence in real ecological communities probably emerges from some combination of fluctuation-independent and fluctuation-dependent mechanisms (Chesson 2000, Clark et al. 2010). Likewise, environmental conditions in real ecosystems are unlikely to change only in their variability without an associated change in the mean (Avolio et al. 2015). Therefore, environmental change has the potential to alter the niche and fitness differences among species in multiple ways, some of which were not present in our current analysis. Mean changes in environmental conditions could reorder competitive hierarchies (CITATION) and/or alter the availability of niches (Harpole et al. 2016). Associated changes in ecosystem stability will depend upon the magnitude of environmental change, each species response to the particular environmental driver, and biotic interactions (Hallett et al. 2014). Thus, it is becoming clear that understanding how ecosystem stability will respond to global change will require a traits-based approach.

CONCLUSIONS

How does fluctuation-dependent coexistence affect the diversity-stability relationship? At a given level of environmental variability, the typical negative diversity-stability relationship holds because having more species always stabilizes ecosystem functioning. However, counter other theoretical studies, we found that a positive diversity-stability relationship could be encountered if sampling occurs across a natural diversity gradient and species coexistence is dependent on environmental fluctuations. We also found that fluctuation-dependent species coexistence may help ecosystems buffer increasing environmental variability because environmental variability promotes species richness, which, in turn, promotes stability. Where fluctuation-dependent species coexistence prevails, our findings suggest that conserving regional species pools and conduits of dispersal

between local communities is especially important as environmental variability increases.

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