

1 The diversity-stability relationship is shaped by the mechanism of  
2 coexistence

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## Abstract

Theory relating species richness to ecosystem stability typically ignores the potential for environmental variability to promote species coexistence. Failure to account for fluctuation-dependent coexistence mechanisms may explain observed deviations from the expected positive diversity-stability relationship, and limits our ability to predict the consequences of future increases in environmental variability. We use a consumer-resource model to explore how coexistence via the temporal storage effect and relative nonlinearity affects ecosystem stability. We show that a negative, rather than positive, diversity-stability relationship is possible when ecosystem function is sampled across a natural gradient in environmental variability and diversity. We also show how fluctuation-dependent coexistence can buffer ecosystem functioning against increasing environmental variability by promoting species richness and portfolio effects. Our work provides a general explanation for variation in observed diversity-stability relationships and highlights the importance of conserving regional species pools to help buffer ecosystems against predicted increases in environmental variability.

## INTRODUCTION

MacArthur (1955), Elton (1958), and even Darwin (Turnbull et al. 2013) recognized the potential for compensatory dynamics among species to stabilize ecosystem functioning in fluctuating environments. This idea underlies the “insurance hypothesis” (Yachi and Loreau 1999), which suggests stability increases with diversity because species respond dissimilarly to environmental conditions, broadening the range of conditions under which the community maintains function (Loreau 2010). A variety of theoretical 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, the ability of biodiversity-ecosystem functioning (BEF) experiments to accurately represent real-world dynamics is debated (Wardle 2016, Eisenhauer et al. 2016). Much of the debate centers around the fact BEF experimental protocols do not allow species gains to offset species losses. Theoretical work on diversity-stability relationships typically suffers from the same limitation: it recognizes the role of environmental variability in driving population fluctuations which destabilize ecosystems, but ignores the potential for environmental variability to promote species richness and thereby help stabilize ecosystems (Loreau 2010, but see Chesson et al. 2001).

Fluctuating environmental conditions are an important ingredient for stable species coexistence, both in theoretical models (Chesson 2000a, Chesson et al. 2004) and in natural communities (Cáceres 1997, Descamps-Julien and Gonzalez 2005, Adler et al. 2006, Angert et al. 2009). Such “fluctuation-dependent” coexistence requires that species have unique environmental responses and that environmental conditions vary so that each species in a community experiences favorable and unfavorable conditions, which prevents competitive exclusion (Chesson 2000a). When coexistence is maintained by a fluctuation-dependent mechanism, an increase in environmental variability might lead to an increase in species richness

and, consequently, an increase in ecosystem stability. However, increasing environmental variability may also decrease ecosystem stability by increasing the fluctuations of individual species, regardless of species richness. These countervailing effects of environmental variability present an interesting paradox: increasing variability should decrease ecosystem stability, but the potential for an increase in richness might offset the decrease in stability. Such a paradox complicates predictions about how ecosystems will respond to predicted departures from the historical ranges of environmental variability.

The opposing effects of environmental variability on stability might explain 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 based on observational studies in terrestrial ecosystems, Jiang and Pu (2009) found no significant evidence for an effect of species richness on ecosystem stability. The idiosyncratic results of these empirical studies contrast with the consistent conclusions from theoretical work which ignores feedbacks between variability and richness.

The gap between theoretical expectations and empirical results of richness-stability relationships reflects the divergence of theory developed to explain species coexistence and theory developed to explain diversity and stability. One reason these two disciplines have diverged is because they have focused on different questions. Diversity-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 species richness responds to different levels of environmental variability (Chesson and Warner 1981).

To reconcile these two perspectives, 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 temporal storage effect and relative nonlinearity using a general consumer-resource model. We use the model to investigate three questions:

1. Does the diversity-stability relationship remain positive when species coexistence is fluctuation-dependent?
2. When species coexistence is fluctuation-dependent, how does increasing environmental variability impact ecosystem stability?
3. Do our answers to the previous two questions depend on the specific fluctuation-dependent coexistence mechanism (i.e., storage effect vs. relative nonlinearity)?

## MATERIALS AND METHODS

### Consumer-resource model

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  $\tau$  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  $\tau$  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  $\tau_k$ ,  $k = 1, 2, 3, \dots, K$ . The subscript  $i$  denotes species,  $N$  is the living biomass state, and  $\epsilon_i$  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  $\tau_k^+$  denotes the beginning of growing season  $k = 1$ . The activation of dormant biomass to live biomass is controlled by  $\gamma$ , which is year ( $k$ ) and species ( $i$ ) specific. Dormant biomass is equal to a constant fraction ( $\alpha$ ) 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 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** For the storage effect to operate, we need species-specific responses to environmental variability, density-dependent covariance between environmental conditions and competition ( $EC$  covariance), and subadditive population growth (Chesson 1994, 2000b). Regardless of the mechanism, long-term coexistence is possible when all species can increase when rare. In the storage effect, rare species increase by escaping the effects of  $EC$  covariance. This happens because common species will experience greater than average competition ( $C$ ) in good environment ( $E$ ) years because common species cannot avoid intraspecific competition. Rare species do not have this problem and can increase rapidly in a good  $E$  year.  $EC$  covariance is included in our model because dormant-to-live transition rates ( $\gamma$ ) are species-specific and vary through time. In a high  $\gamma$  year for a common species, resource uptake will be above average, while in a high  $\gamma$  year for a rare species, resource uptake will be below average.

Subadditive population growth buffers populations against large population decreases in unfavorable years. It is included in our model through a dormant stage with very low death rates, which limits large population declines. In combination, subadditive population growth limits population declines in bad  $E$  years, and  $EC$  covariance ensures species can increase rapidly when rare but suffer when common.

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

$$\Sigma(\gamma) = \begin{bmatrix} \sigma_E^2 & \rho_{1,2}\sigma_E^2 & \rho_{1,3}\sigma_E^2 & \rho_{1,4}\sigma_E^2 \\ \rho_{2,1}\sigma_E^2 & \sigma_E^2 & \rho_{2,3}\sigma_E^2 & \rho_{2,4}\sigma_E^2 \\ \rho_{3,1}\sigma_E^2 & \rho_{3,2}\sigma_E^2 & \sigma_E^2 & \rho_{3,4}\sigma_E^2 \\ \rho_{4,1}\sigma_E^2 & \rho_{4,2}\sigma_E^2 & \rho_{4,3}\sigma_E^2 & \sigma_E^2 \end{bmatrix} \quad (5)$$

where  $\sigma_E^2$  is the variance of the environmental cue and  $\rho_{i,j}$  is the correlation between the species  $i$ 's and species  $j$ 's transition rates.  $\rho$  must be less than 1 for stable coexistence, and in all simulations we placed that constraint that  $\rho_{i,j} = \rho_{j,i}$  for each species pair. The inferior competitor has the strongest potential to persist when  $\rho = -1$  (perfectly uncorrelated transition rates). We used the R function `mvrnorm` to generate sequences of (un)correlated variates  $E$  that we converted to germination rates in the 0-1 range:  $\gamma = e^E/1 + e^E$ . Note that  $\Sigma(\gamma)$  must be positive definite. So, after defining  $\Sigma(\gamma)$  with all  $\rho_{i,j}$ s and  $\sigma_E^2$ , we used the `nearPD` function from the `Matrix` package in R to coerce the variance-covariance matrix to be positive definite.

**Implementing Relative Nonlinearity** In the absence of environmental fluctuations, the outcome of competition between two species limited by the same resource is determined by the shape of their resource uptake curves. That is, at constant resource supply, whichever species has the lowest resource requirement at equilibrium ( $R^*$ ) will exclude all other species (Tilman 1982). Resource fluctuations create opportunities for species coexistence because the resource level is then not fixed at the  $R^*$  of the superior competitor. If the resource uptake curves of each species are relatively nonlinear, then some species will be able to take advantage of resource levels that other species cannot (Chesson 1994).

For example, in Fig. 1C we show two species' resource uptake curves that are relatively nonlinear. Species B has the lowest  $R^*$  and would competitively exclude species A in the absence of environmental fluctuations. But, fluctuating resource supplies can benefit species



A because it can take advantage of relatively high resource levels due its higher saturation point. Stable coexistence is only possible, however, if each species creates a disadvantage for itself when abundant. This occurs in our model because when a resource conservative species (e.g., species B in Fig. 1C) is abundant, resource levels will remain high for a longer period of time because its draw down of resources starates. Likewise, when a resource acquisitive species (e.g., species A in Fig. 1C) is abundant, it quickly draws down resources to levels that favor resource conservative species. Such reciprocity ensures species can increase when rare and stablizes coexistence (Armstrong and McGehee 1980, Chesson 2000a, Chesson et al. 2004).

## **Numerical simulations**

To explore 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. To do this, we simulated 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 then performed species removals, akin to a biodiversity-ecosystem function experiment. 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 species pool sizes and environmental cue or resource variability. For each size of species pool (1, 2, 3, or 4 species), we simulated the model at 15 evenly-spaced levels of environmental cue (range = 0.1,2) for the storage effect and 25 evenly-spaced levels of resource variability (range =

0.1,1.4) for relative nonlinearity. We also explored the influence of asymmetries in species' competitive abilities and correlations in species' environmental responses within the storage effect model.

Under relative nonlinearity, species' resource response curves (Fig. S1-1) 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 500 seasons to reduce transient effects on our results, we calculated the coefficient of variation ( $CV$ ) of summed species biomass through time, which represents ecosystem variability, 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). R code for our model function is in the Supporting Information Appendix S1. All model code has been deposited on Figshare ([link](#)) and is available on GitHub at <http://github.com/atredennick/Coexistence-Stability>.

## RESULTS

When we allowed the variance of the environment to determine which of four initial species coexist, we found a positive relationship between richness and variability (Fig. 2A,C). This was true for the storage effect, where coexistence is maintained by fluctuating transition rates ( $\gamma$ ), and for relative nonlinearity, where coexistence is maintained by annual resource

pulses. The relationship is driven by the fact that, under both coexistence mechanisms, the strength of species coexistence increased with environmental variability (Fig. S1-2). Therefore, more variable conditions promoted species richness, creating a positive relationship between diversity and variability.

When we performed species removals but held environmental variability at given levels, we found the typical negative diversity-variability relationship (Fig. 2B,D). The relationship was very constrained for the storage effect because all species have similar temporal variances. Therefore, regardless of species identity, having more species will always stabilize ecosystem functioning through portfolio effects. On the contrary, the relationship was weaker for relative nonlinearity (Fig. 2D) because each species has unique temporal variance depending on its resource uptake curve. Depending on the specific combination of species, two-species communities were sometimes less variable than three-species communities.

To understand how much species additions can stabilize ecosystem functioning, we simulated our model over a range of environmental variance and species pool sizes. Realized species richness increased with environmental variability and, in some cases, increasing variability completely offset the effect of increasing environmental variability on stability. More species rich communities were less variable on average and increased in ecosystem  $CV$  at a slower rate than communities with fewer species (e.g., lower slopes in log-log space; Fig. S1-3).

The dampening effect of fluctuation-dependent coexistence on increasing environmental variability depends on the specific traits (parameter values) of the species in the regional pool. Asymmetric competition makes it more difficult for new species to enter the local community (Fig. 3; compare top and bottom panels). Relatively high competition also increases the rate at which ecosystem  $CV$  increases with environmental variance (Fig. S1-3) because the abundance of inferior competitors is reduced and therefore does not influence ecosystem  $CV$  as much as when competition is symmetric. The correlation of species' environmental

responses also mediates the relationship between environmental variance, species richness, and ecosystem  $CV$ : lower correlations make it easier for new species to enter the community and unique environmental responses are always stabilizing (Fig. 3).

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, species additions buffer the ecosystem 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. S1-1). 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).

## DISCUSSION

Theory developed for biodiversity-ecosystem function experiments emphasizes that increases in species richness should reduce ecosystem variability. Consistent with theoretical expectations from models in which species coexistence is maintained by fluctuation-independent mechanisms, we produced the typical negative diversity-variability relationship (Fig. 2B,D) from a model with fluctation-dependent species coexistence (also see Chesson et al. 2001). 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,C). 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 2000a). Therefore, species coexistence gains strength, for both mechanisms, as the environment becomes more variable (Fig. S1-2), but the increase in environmental variability also increases ecosystem variability.

Our results may explain why deviations from the negative diversity-variability relationship often come from observational studies (Jiang and Pu 2009). Observational studies must rely on natural diversity gradients, and if species richness depends on environmental variability, it is entirely possible to observe 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 six sites that were 6 km apart. While Sasaki and Lauenroth explained their results in terms of dominant species' effects, it is also possible that each site experienced slightly different levels of environmental variability that influenced species coexistence. DeClerck et al. (2006) also found a positive diversity-variability when sampling conifer richness and the variability of productivity across a large spatial gradient in the Sierra Nevada.

While our modeling results show that fluctuation-dependent coexistence can create positive diversity-variability relationships, whether such trends are detected will depend on the particular traits of the species in the community and the relative influence of fluctuation-dependent and fluctuation-independent coexistence mechanisms, which are not mutually exclusive. Thus, our results may also help explain observational studies where no relationship between diversity and variability is detected. For example, Cusson et al. (2015) found no relationship between species richness and variability of abundances in several marine macro-benthic ecosystems. Many of their focal ecosystems were from highly variable intertidal environments. If coexistence was at least in part determined by environmental fluctuations, then the confounding effect of variability and species richness could compensate any direct effect of species richness on variability. Previous theoretical work showed how environmental variation can mask the effect of species diversity on ecosystem productivity when sampling across sites (Loreau 1998). Our mechanistic model extends that conclusion to ecosystem stability.

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 by increasing the fluctuations of individual species' abundances.

When coexistence is fluctuation-dependent, however, the outcome is less certain. By simulating communities with different species pool sizes across a gradient of environmental variability, we showed that species gains due to increasing environmental variability can buffer the direct effect of environmental variability on ecosystem variability (Figs. 3 and 4). These 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 promoting increased species richness. Whether our theoretical predictions hold in real communities is unknown and requires empirical tests. Doing so would require manipulating environmental variability in 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 (Fig. 5A,B). 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 (Fig. 5C,D). 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 (Fig. 5).

## ACKNOWLEDGMENTS

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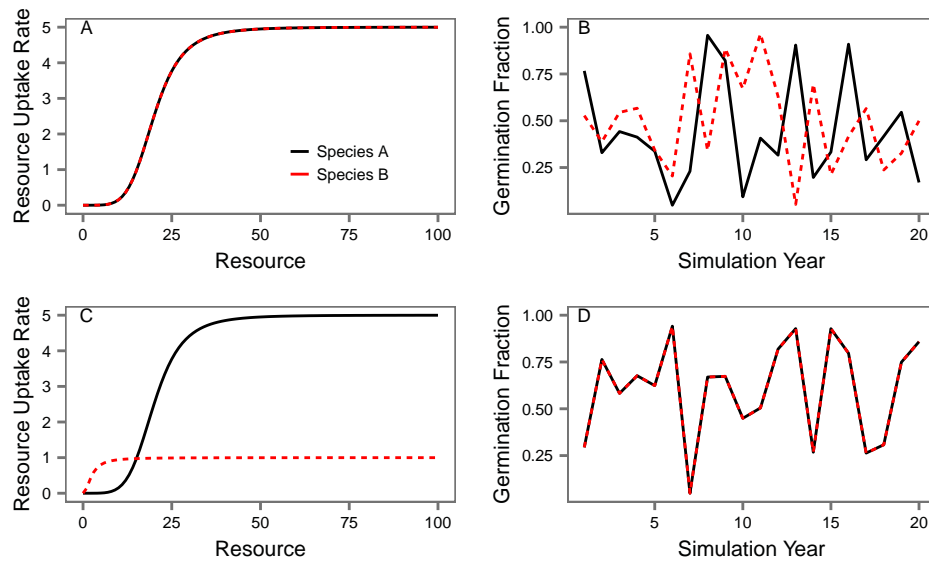


# TABLE

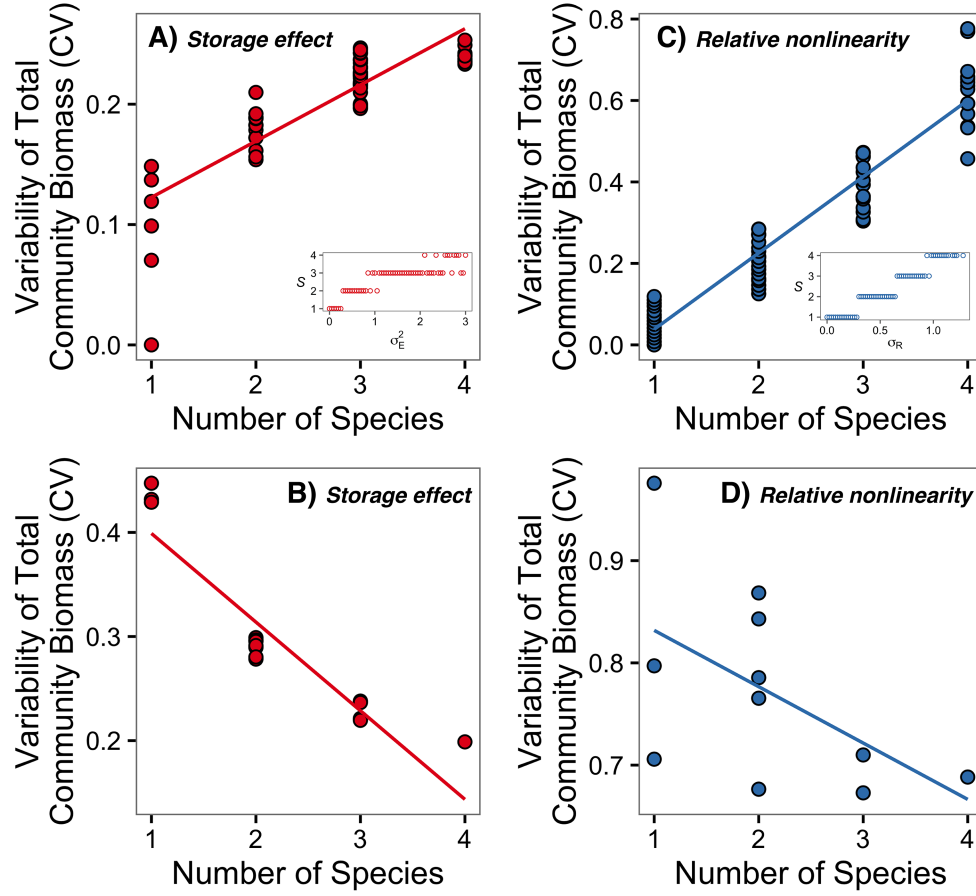
**Table 1** Default values of model parameters and their descriptions. Parameters that vary depending on the mode and strength of species coexistence or depending on species competitive hierarchies are labeled as "variable" in parentheses. The dormant-to-live biomass transition fraction ( $\gamma$ ) 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)
$\epsilon$	resource-to-biomass conversion efficiency	0.5
$\alpha$	allocation fraction of live biomass to dormant biomass	0.5 (variable)
$\gamma$	dormant-to-live biomass transition fraction	–
$\rho$	correlation of species' response to the environment	0 (variable)
$\sigma_E$	variance of the environmental cue	2 (variable)
$\eta$	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)

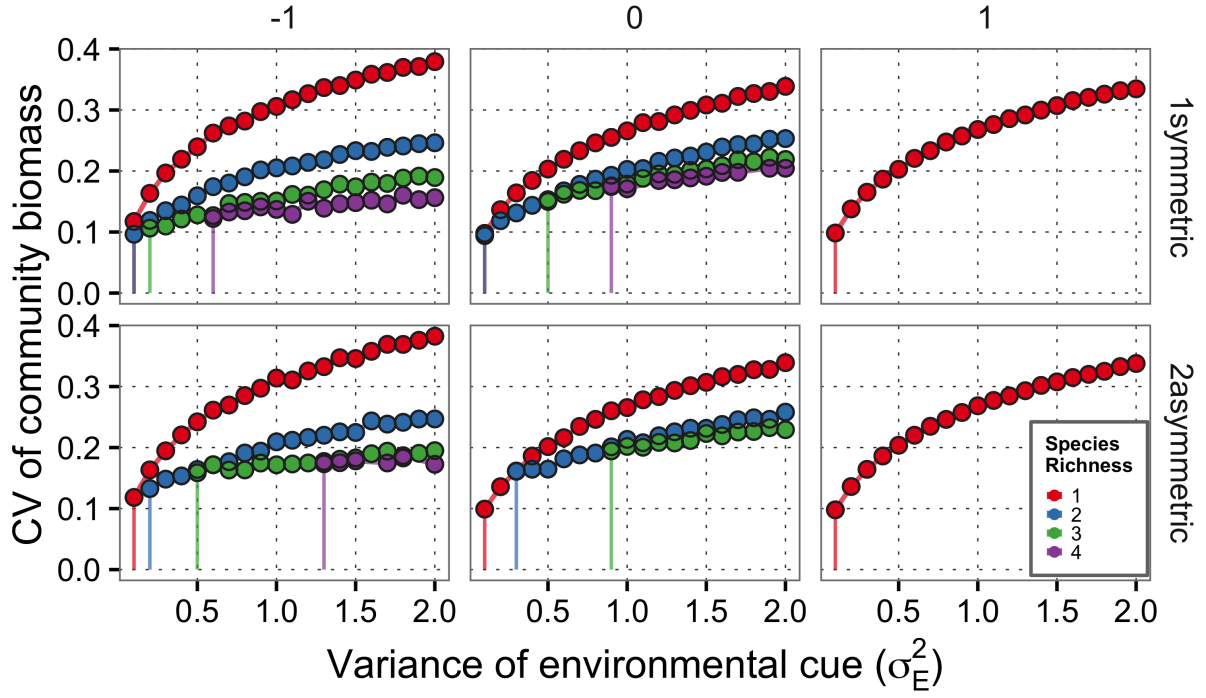
## FIGURES



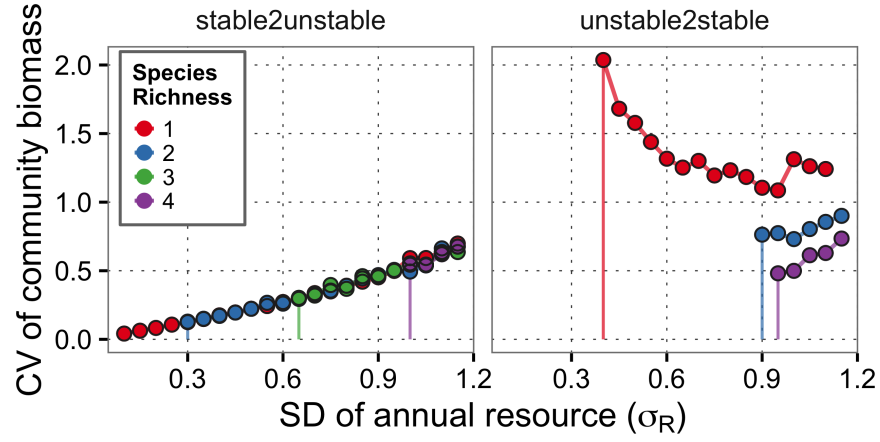
**Figure 1** Resource uptake functions and example time series of (un)correlated germination fractions for the storage effect (A,B) and relative nonlinearity (C,D) formulations of the consumer-resource model. The resource uptake functions for both species are equivalent for the storage effect, but their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



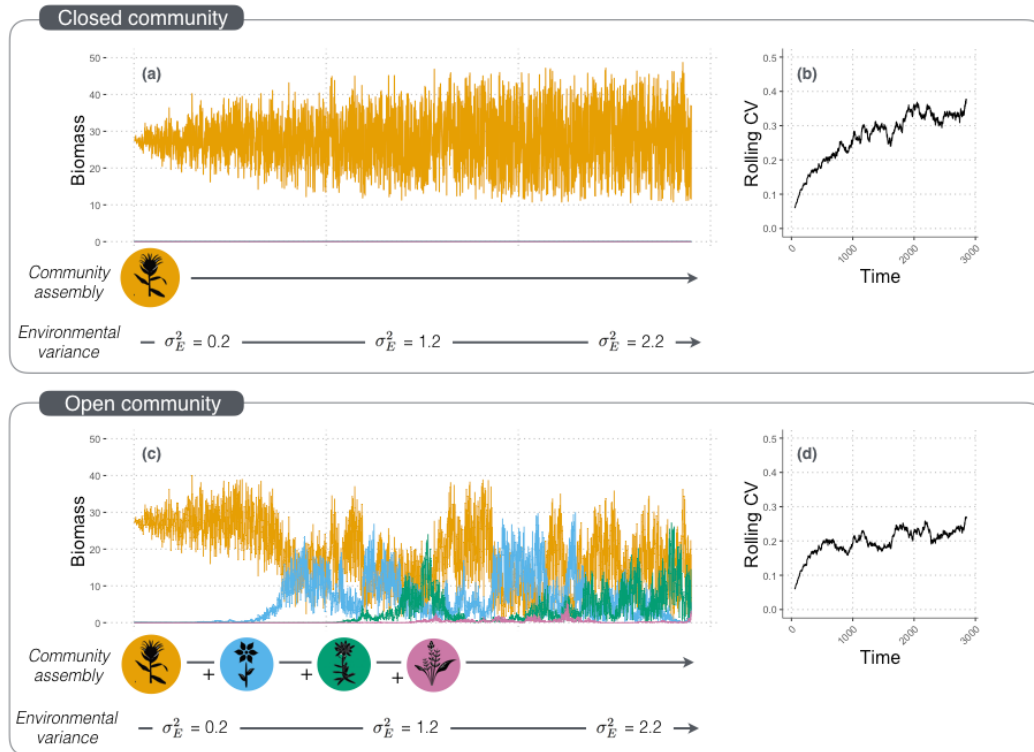
**Figure 2** Variability of total community as function of species richness when coexistence is maintained by the storage effect (A,B) or relative nonlinearity (C,D). Top panels show results from simulations where environmental or resource variance determine the number species that coexist in a community. 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. The top panels represent regional diversity-stability relationships across natural diversity gradients, whereas the bottom panels represent local diversity-stability relationships.



**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 slightly asymmetrical competitive effects, whereas panels (D-F) show results when competition is more asymmetric. We show results for different levels of correlations of species' environmental responses,  $\rho$ . Colored vertical lines show the level of environmental variability at which each level of species richness first occurs.



**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 (though, the fourth species was unable to coexist under these parameter values). In this case increasing environmental variability allows for greater realized species richness and can temper the effect of environmental variability.



**Figure 5** Example of how species additions under increasing environmental variability can buffer ecosystem stability when species coexistence is fluctuation-dependent via the storage effect. Environmental variability ( $\sigma_E^2$ ) increases linearly with time. (A) Time series of species' biomasses (colored lines) in a closed community where colonization of new species is not possible and (B) its associated coefficient of variation (Rolling CV; calculated over 100-yr moving window) through time. (C) Time series of species' biomasses in an open community where colonization by new species from the regional pool of four species becomes possible as environmental variation increases. The trajectory of total biomass CV in the open community (D) asymptotes at lower variability than in the closed community (B) due to the buffering effect of species richness.

## REFERENCES

- 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.
- Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the United States of America* 106:11641–11645.
- Armstrong, R. A., and R. McGehee. 1980. Competitive Exclusion. *The American Naturalist* 115:151–170.
- Brown, J. H., and A. Kodric-Brown. 1997. Turnover Rates in Insular Biogeography : Effect of Immigration on Extinction. *Ecology* 58:445–449.
- 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.
- Chesson, P. 2000a. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Chesson, P. 2000b. General theory of competitive coexistence in spatially-varying environments. *Theoretical population biology* 58:211–37.
- Chesson, P. L. 1994. Multispecies Competition in Variable Environments. *Theoretical Population Biology* 45:227.
- Chesson, P. L., and R. R. Warner. 1981. Environmental Variability Promotes Coexistence in Lottery Competitive Systems. *The American Naturalist* 117:923–943.
- Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253.
- Chesson, P., S. W. Pacala, and C. Neuhauser. 2001. Environmental Niches and Ecosystem Functioning. Pages 213–245 *in* A. P. Kinzig, S. W. Pacala, and D. Tilman, editors. *The functional consequences of biodiversity: Empirical progress and theoretical extensions*. Princeton University Press, Princeton.
- Cusson, M., T. P. Crowe, R. Araújo, F. Arenas, R. Aspden, F. Bulleri, D. Davoult, K. Dyson, S. Fraschetti, K. Herkül, C. Hubas, S. Jenkins, J. Kotta, P. Kraufvelin, A. Migné, M. Molis, O. Mulholland, L. M.-L. Noël, D. M. Paterson, J. Saunders, P. J. Somerfield, I. Sousa-Pinto, N. Spilmont, A. Terlizzi, and L. Benedetti-Cecchi. 2015. Relationships between biodiversity and the stability of marine ecosystems: Comparisons at a European scale using meta-analysis. *Journal of Sea Research* 98:5–14.
- DeClerck, F. A. J., M. G. Barbour, and J. O. Sawyer. 2006. Species richness and stand stability in conifer forests of the Sierra Nevada. *Ecology* 87:2787–2799.
- Descamps-Julien, B., and A. Gonzalez. 2005. Stable coexistence in a fluctuating environment: An experimental demonstration. *Ecology* 86:2815–2824.

- Eisenhauer, N., A. D. Barnes, S. Cesarz, D. Craven, O. Ferlian, F. Gottschall, J. Hines, A. Sendek, J. Siebert, M. P. Thakur, and M. Türke. 2016. Biodiversity-ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. *Journal of Vegetation Science* 27:1061–1070.
- Elton, C. 1958. *The Ecology of Invasions by Animals and Plants*. Pages 1689–1699. University of Chicago Press, Chicago.
- Hautier, Y., E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, H. Hillebrand, E. M. Lind, A. S. MacDougall, C. J. Stevens, J. D. Bakker, Y. M. Buckley, C. Chu, S. L. Collins, P. Daleo, E. I. Damschen, K. F. Davies, P. a Fay, J. Firn, D. S. Gruner, V. L. Jin, J. a Klein, J. M. H. Knops, K. J. La Pierre, W. Li, R. L. McCulley, B. a Melbourne, J. L. Moore, L. R. O’Halloran, S. M. Prober, A. C. Risch, M. Sankaran, M. Schuetz, and A. Hector. 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508:521–5.
- Hector, A., Y. Hautier, P. Saner, L. Wacker, R. Bagchi, J. Joshi, M. Scherer-Lorenzen, E. M. Spehn, E. Bazeley-White, M. Weilenmann, M. C. Caldeira, P. G. Dimitrakopoulos, J. a. Finn, K. Huss-Danell, A. Jumpponen, and M. Loreau. 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91:2213–2220.
- Ives, A. R., and J. B. Hughes. 2002. General relationships between species diversity and stability in competitive systems. *The American naturalist* 159:388–395.
- Jiang, L., and Z. Pu. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist* 174:651–659.
- Kinzig, A. P., S. W. Pacala, and D. Tilman (Eds.). 2001. *The functional consequences of biodiversity: Empirical progress and theoretical extensions*. Pages i–365. Princeton University Press, Princeton.
- Lehman, C. L., and D. Tilman. 2000. Biodiversity, Stability, and Productivity in Competitive Communities. *The American Naturalist* 156:534–552.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: A framework for multi-scale community ecology.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of the National Academy of Sciences of the United States of America* 95:5632–5636.
- Loreau, M. 2010. *From Polutations to Ecosystems: Theoretical Fondations for a New Ecological Synthesis*.
- Loreau, M., and C. de Mazancourt. 2013. Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters* 16:106–115.
- MacArthur, R. 1955. Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology* 36:533–536.
- Mailleret, L., and V. Lemesle. 2009. A note on semi-discrete modelling in the life sciences.



- Philosophical transactions. Series A, Mathematical, physical, and engineering sciences 367:4779–4799.
- Mordecai, E. A., K. Gross, and C. E. Mitchell. 2016. Within-Host Niche Differences and Fitness Trade-offs Promote Coexistence of Plant Viruses. *The American Naturalist* 187:E13–E26.
- Pachepsky, E., R. M. Nisbet, and W. W. Murdoch. 2008. Between discrete and continuous: Consumer-resource dynamics with synchronized reproduction. *Ecology* 89:280–288.
- Sasaki, T., and W. K. Lauenroth. 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia* 166:761–768.
- Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. Package deSolve : Solving Initial Value Differential Equations in R. *Journal Of Statistical Software* 33:1–25.
- Team, R. 2013. R Development Core Team. R: A Language and Environment for Statistical Computing.
- Tilman, D. 1982. Resource competition and community structure. Pages 1–296.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- Turnbull, L. A., J. M. Levine, M. Loreau, and A. Hector. 2013. Coexistence, niches and biodiversity effects on ecosystem functioning. *Ecology Letters* 16:116–127.
- Valone, T. J., and C. D. Hoffman. 2003. A mechanistic examination of diversity-stability relationships in annual plant communities. *Oikos* 103:519–527.
- Wang, S., and M. Loreau. 2014. Ecosystem stability in space:  $\alpha$ ,  $\beta$  and  $\gamma$  variability. *Ecology Letters* 17:891–901.
- Wardle, D. A. 2016. Do experiments exploring plant diversity-ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? *Journal of Vegetation Science* 27:646–653.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* 96:1463–1468.