

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

Andrew T. Tredennick^{1,*}, Peter B. Adler¹, and Frederick R. Adler²

¹*Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322;* ²*Departments of Biology and Mathematics, University of Utah, Salt Lake City, Utah*

Abstract

For biodiversity to increase the temporal stability of ecosystem function in the long-term, coexistence must be stable. Species-specific responses 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...

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*Corresponding author; email: atredenn@gmail.com

21 Introduction

22 Environmental variability is a ubiquitous feature of ecosystems. On the one hand, envi-
23 ronmental fluctuations are disruptive, creating year-to-year variability that decreases the
24 stability of ecosystem functions like annual productivity (Isbell et al. 2015). On the other
25 hand, environmental fluctuations are stabilizing, providing opportunities for species to coexist
26 (Chesson 2000). While seemingly unrelated, the countervailing effects of environmental
27 variability become inexorably linked when we consider the relationship between biodiversity
28 and ecosystem stability. The emerging consensus is that species rich ecosystems are more
29 stable than species poor ecosystems, implying a positive relationship between biodiversity
30 and stability (Loreau and de Mazancourt 2013). For the benefits of biodiversity to be realized
31 in the long term, species coexistence, which maintains biodiversity, must be stable (Turnbull
32 et al. 2013). Yet, contemporary coexistence theory is largely absent from theoretical studies
33 aimed toward understanding the diversity-stability relationship (reviewed in Loreau 2010).

34 A compelling reason to revisit how species coexist in the context of the diversity-stability
35 relationship is their shared dependence on species-specific responses to environmental condi-
36 tions, and environmental variability more generally. Modern coexistence theory can be divided
37 into two broad classes: fluctuation-dependent mechanisms and fluctuation-independent mech-
38 anisms (Chesson 2000). Classic work on resource partitioning (Tilman 1982) describes
39 fluctuation-independent species coexistence, where stable coexistence depends on limiting
40 resource requirements, not fluctuations in population abundances or environmental condi-
41 tions. In contrast, fluctuation-dependent coexistence mechanisms require the environment
42 to fluctuate over time for species to coexist. Indeed, the two most well-known fluctuation-
43 dependent coexistence mechanisms, the storage effect and relative nonlinearity, depend on
44 species-specific responses to environmental conditions, among other things, for species to
45 stably coexist (Box 1). Thus, two forces can strengthen species coexistence: 1) the uniqueness
46 of their environmental responses and 2) the variability of environmental conditions. In other

words, there is reason to expect environmental variability to promote species richness when coexistence is maintained by a fluctuation-dependent mechanism (Adler and Drake 2008). Why, then, does nearly all theoretical work on the diversity-stability relationship predict a positive relationship? In short, because such work has ignored fluctuation-dependent coexistence (Loreau 2010).

Theory on the diversity-stability relationship has mainly employed modeling approaches that separate species interactions and species' responses to the environment (Loreau 2010, Loreau and de Mazancourt 2013). For example, population dynamical approaches that follow Lotka-Volterra dynamics typically include deterministic species interactions, which in turn determine species coexistence, and an additive, stochastic environmental component (e.g., Ives et al. 1999, Lehman and Tilman 2000, Loreau and de Mazancourt 2013). In such models, species coexistence is pre-determined by the pairwise interaction coefficients and environmental variability does not impact whether species coexist or not. Therefore, so long as species' environmental responses are not perfectly correlated, increasing the number of species at a given level of environmental variability generally increases ecosystem stability (Ives and Hughes 2002, Loreau and de Mazancourt 2013). Because there is no interaction between species coexistence and environmental variability, only the correlation of species' environmental responses determines ecosystem stability. Despite the lack of fluctuation-dependent coexistence in theory on the diversity-stability relationship, several large experiments have confirmed theoretical predictions (Tilman et al. 2006, Hector et al. 2010). But, the balance of evidence from all empirical tests is less consistent (Jiang and Pu 2009).

Empirical tests of the theoretical prediction that species richness increases ecosystem stability have relied on both experimental and observational approaches. Experimental tests involve manipulating the number of species present in a plot by randomly drawing a specific number of species from a pre-defined species pool (Hector et al. 1999, Tilman et al. 2001). Results from such experimental tests, which have focused on plant species richness and the temporal stability of aboveground biomass production, have been surprisingly consistent:

temporal stability is greater in communities with more species (Tilman et al. 2006, Hector et al. 2010). Observational tests of the diversity-stability relationship, which require sampling across natural diversity gradients, have been less consistent. Positive, neutral, and negative diversity-stability relationships have all been reported from observational studies. Indeed, 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. Thus, 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. Counter to common expectations, we find that negative diversity-stability relationships 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. By revisiting species coexistence, our results help to reconcile why observed diversity-stability relationships are both positive and negative.

Model and Analysis

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 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

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 (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) |

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).

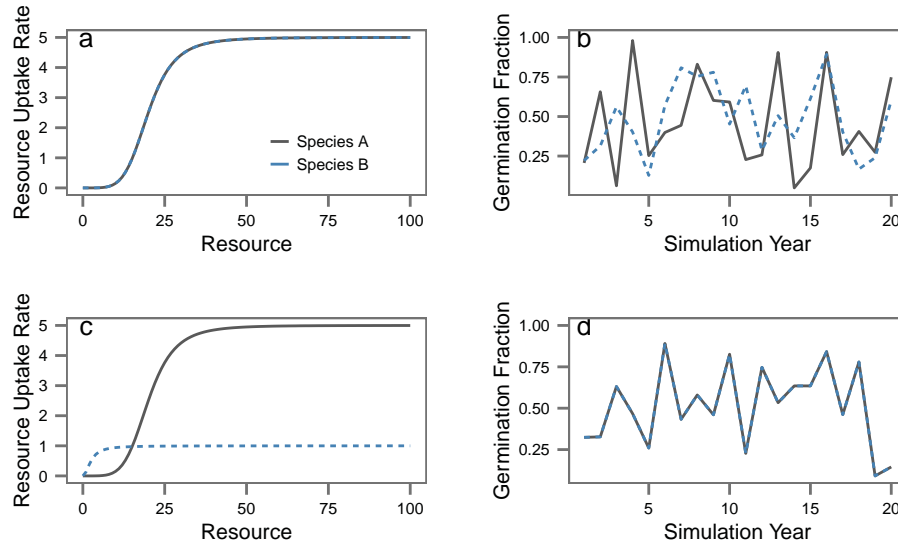


Figure 1: Resource uptake functions and example time series of (un)correlated germination fractions for the storage effect (*a,b*) and relative nonlinearity (*c,d*) formulations of the consumer-resource model. The resource uptake functions for both species are equivalent for the storage effect, but their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

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 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 coefficient 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 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 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

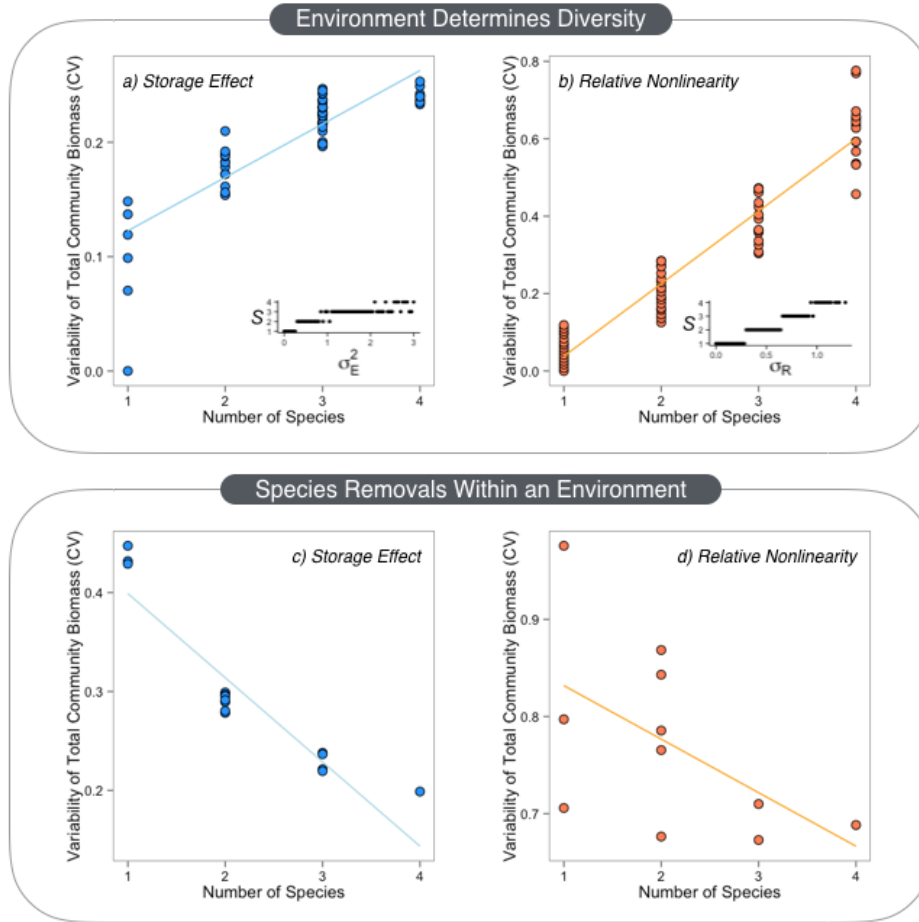


Figure 2: Variability of total community as function of species richness when coexistence is maintained by the storage effect (a,c) or relative nonlinearity (b,d). Top panels show results from simulations where environmental or resource variance determine the number species that coexist in a community.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

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. Indeed, fluctuation-dependent coexistence mechanisms are particularly common in arid and semi-arid environments (CITATIONS).

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