

# Fluctuation-dependent coexistence mechanisms generate positive and negative relationships between species richness and ecosystem stability

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## Abstract

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

**Keywords:** coexistence, storage effect, relative nonlinearity, diversity-stability hypothesis, pulsed differential equation, consumer-resource dynamics, synchrony

## Introduction

The alarming rate of local species loss across the globe prompted three decades of theoretical and experimental work to understand the consequences of diversity loss (???). One important consequence is that ecosystems may become more variable through time because species richness tends to confer ecosystem stability (Loreau and de Mazancourt 2013). The prediction that the diversity-stability relationship is positive (richness begets stability)

Hints of the idea that diverse ecosystems are more stable through time than species-poor ecosystems go back as far as Darwin (Darwin 1859), who, in passing, mentions the ‘division of labor’ that arises from niche differentiation among species (Turnbull et al. 2013).

Species-specific responses to non-constant environmental conditions can stabilize species coexistence (Chesson 2000) and ecosystem function (Loreau 2010). This means that

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fluctuation-dependent mechanisms of species coexistence are the very same mechanisms that link biodiversity and ecosystem function. Yet, the theory that has developed over the past 20 years to explain the, generally, positive relationship between species richness and stability of ecosystem function has implicitly assumed species coexistence (Loreau 2010), or, when explicitly considered, coexistence is maintained by fluctuation-independent mechanisms (Turnbull et al. 2013). Despite rapid theoretical developments in the fields of species coexistence and biodiversity-ecosystem function, a gulf remains between the two lines of inquiry (Carroll et al. 2011, Turnbull et al. 2013). This is especially surprising since stable coexistence, however maintained, is a prerequisite for biodiversity to confer stability of ecosystem function in the long term.

Among the dizzying array of mechanisms that can maintain diversity, Chesson (2000) formalized two broad classes: fluctuation-independent and fluctuation-dependent mechanisms. Both classes of mechanisms rely on niche differences being greater than relative fitness differences for all species pairs in a community (Chesson 2000, Adler et al. 2007). In a fluctuation-independent case, species coexistence can be maintained by resource partitioning so long as each species is limited by a different resource (Tilman 1982). Much of the theoretical literature aimed at deciphering the mechanisms behind the diversity-stability relationship implicitly assumes fluctuation-independent coexistence. For example, Lotka-Volterra models have been widely used and include coexistence by keeping competition coefficients less than one (e.g., Loreau and de Mazancourt 2013). Our focus, on the other hand, is on the interaction between species coexistence and ecosystem stability in communities where coexistence is dependent on environmental fluctuations.

There are two ways that species coexist in temporally fluctuating environments. First, there is the storage effect, where species coexistence is stable if the following three conditions are met: (i) have unique responses to environmental conditions, (ii) have some way to persist in unfavorable years, and (iii) the effects of competition must be greater in ‘good’ years relative to ‘bad’ years (Chesson 2000). Second, there is relative nonlinearity, where species have unique, nonlinear responses to a shared resource that fluctuates through time (Chesson 2000).

Both the storage effect and relative nonlinearity require that species have unique responses to environmental conditions. Not only do such species-specific responses stabilize coexistence, they can also stabilize ecosystem function by creating compensatory dynamics. All else being equal, ecosystem stability is highest when species responses to the environment are perfectly uncorrelated. Under the storage effect, uncorrelated species responses to the environment also results in the most stable conditions for coexistence. It stands to reason, then, that the strength of the storage effect should predict the degree to which species asynchrony stabilizes ecosystem function. However, the exact relationship between storage effect strength and ecosystem stability could take many, unknown, forms.

Unlike the potential interaction between the storage effect and ecosystem stability, how relative nonlinearity might interact with ecosystem stability is less clear.

## Model and Analysis

To discover how fluctuation-dependent coexistence mechanisms affect the diversity-stability relationship, we developed a semi-discrete, mechanistic consumer-resource model that allows coexistence of two species 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

**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 ( $\gamma$ ) 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)

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

$$R(\tau_k^+) = R^+, \quad (5)$$

$R^+$  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  $\gamma$  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  $\gamma$  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  $\gamma$ , the inferior competitor can persist. We created competitive hierarchies in the storage effect version of the model by altering species' biomass conversion efficiencies ( $\epsilon$ )

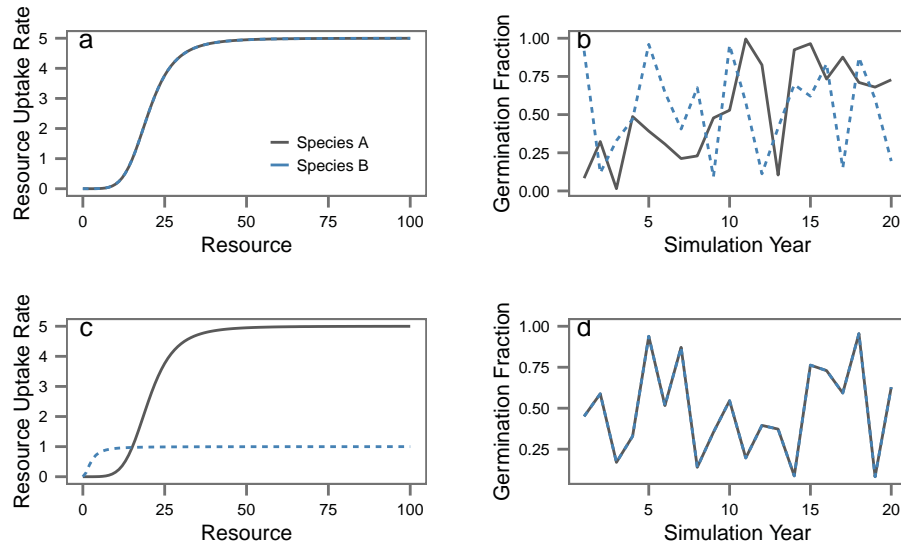
We generated sequences of (un)correlated dormant-to-live state transition rates ( $\gamma$ ) for each species by drawing from multivariate normal distributions with mean 0 and a variance-covariance matrix ( $\Sigma(\gamma)$ ) of

$$\Sigma(\gamma) = \begin{bmatrix} \sigma_E^2 & \rho\sigma_E^2 \\ \rho\sigma_E^2 & \sigma_E^2 \end{bmatrix} \quad (6)$$

where  $\sigma_E^2$  is the variance of the environmental cue and  $\rho$  is the correlation between the two species' transition rates.  $\rho$  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 ( $\gamma$ ) 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.

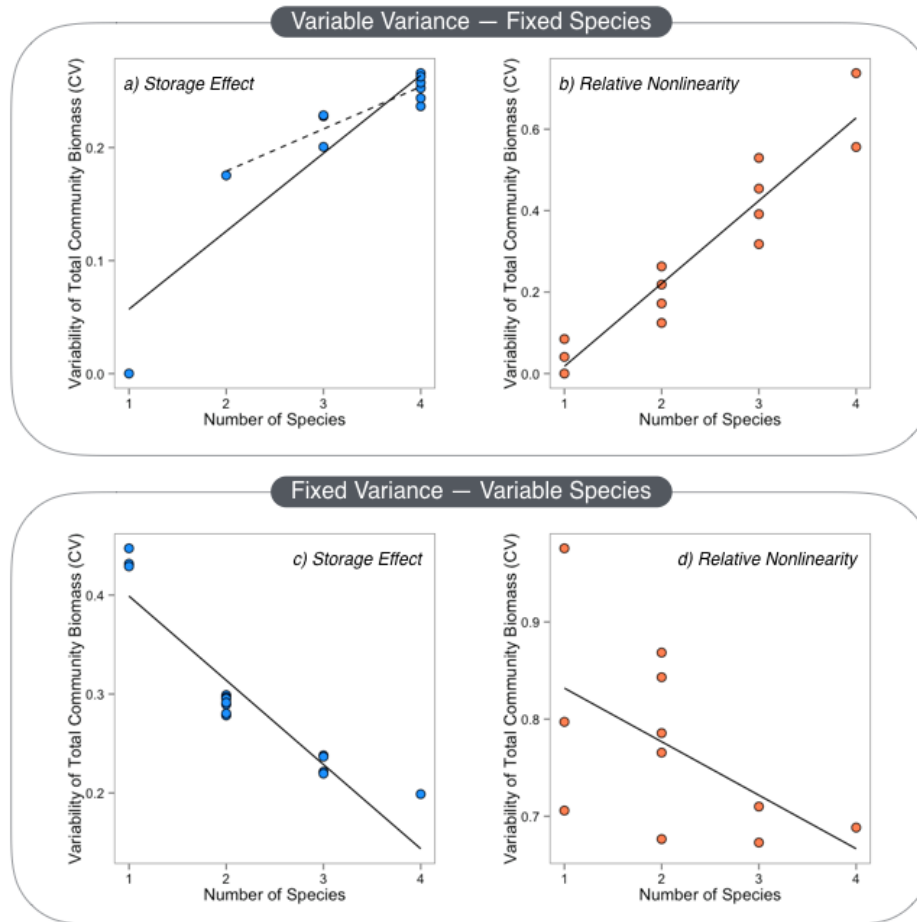
This required simulating communities with all species initially present across a gradient of annual resource variability (for relative nonlinearity) or environmental cue variability (for the storage effect). Second, we chose parameter values that allowed coexistence of all four species, and performed 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).

## Results and Discussion

The direction of the diversity-variability relationship can be positive and negative (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 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).



**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.

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