How Fluctuation-Dependent Coexistence Mechanisms Affect the Temporal Stability of Ecosystem Function

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Abstract

For biodiversity to increase the temporal stability of ecosystem function in the long-term, coexistence must be stable. Species-specific respones to environmental variation through time is key to understanding fluctuation-dependent coexistence mechanisms and how asynchrony in species dynamics can arise to stabilize ecosystem function. Despite the shared dependence on environmental fluctuations, theory on species coexistence and the relationship between species richness and ecosystem stability have developed independently. To formally link the two bodies of theory, we use consumer-resource models where coexistence between two species utilizing a single resource is maintained by two fluctuation-dependent mechanisms: the storage effect and relative nonlinearity. We examine how the strength of species coexistence relates to the temporal stability of aggregate ecosystem function and how the effect of environmental variability on stability is mediated by the mechanism of coexistence. When species coexisted via the storage effect, the strength of coexistence, as measured by invasion growth rates, was 'blank' associated with ecosystem variability (rank correlation =). On the other hand, ecosystem variability and the strength of coexistence were 'blank' associated under relative nonlinearity (rank correlation =) because the ability of an inferior competitor to persist increases with resource variability. Total community biomass was always less

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variable when species coexisted via the storage effect rather than relative nonlinearity. Our analysis confirms the intuitive idea that stable coexistence and stable ecosystems go hand-in-hand, but only for the storage effect. However, coexistence by relative nonlinearity is likely to be less common in nature, meaning our results from storage effect simulations may be most relevant to field studies.

Introduction

Species-specific responses to non-constant environmental conditions can stabilize species coexistence (Chesson 2000) and ecosystem function (Loreau 2010). This means that 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 coexistece, however maintained, is a preqrequisite 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

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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.

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Model and Analysis

A General Consumer-Resource Model

We start with a general consumer-resource model where the consumer can be in one of two-states: a dormant state D and a live state N (Fig. 1). Transitions between N and D occur at discrete intervals T, so our model is formulated as "pulsed differential equations" (Pachepsky et al. 2008, Mailleret and Lemesle 2009). For clarity we refer to T as years and the growing time between years as seasons with daily (τ) time steps. Seasonal (within-year) dynamics are modeled as three differential equations:

$$\frac{\mathrm{d}D_i}{\mathrm{d}\tau} = N_i a_i - (m_{D,i} D_i) \tag{1}$$

$$\frac{\mathrm{d}N_i}{\mathrm{d}\tau} = N_i[f_i(R) - m_{N,i} - a_i] \tag{2}$$

$$\frac{\mathrm{d}R}{\mathrm{d}\tau} = -\sum_{i=1,2} f_i(R)N_i \tag{3}$$

where i denotes species, D is the dormant (long-lived) biomass state, N is the living biomass (fast-growing, shorter-lived) state, a is fraction of life biomass allocated to seed production, and m is the biomass loss rate. The growth rate of living biomass is a resource-dependent Hill function, $f_i(R) = b_i R^{\alpha_i}/(\beta_i^{\alpha_i} + R^{\alpha_i})$, where b is a species' intrinsic growth rate and α and β define the curvature of the function. Resource depletion is equal to the sum of each species' consumption, $\sum_{i=1,2} f_i(R)N_i$.

At the beginning of each season we start with initial conditions defined as V_t, W_t, and Z_t for the dormant state, the live state, and the resource, respectively. So for each season, eqs. 1-3 are solved given the initial conditions:

$$D_i(0) = V_{i,t} \tag{4}$$

$$N_i(0) = W_{i,t} \tag{5}$$

$$R(0) = Z_t \tag{6}$$

The consumers transition between N and D instantaneously between years. So, at the yearly transition:

$$V_{i,t+1} = [N_i(T^-) + D_i(T^-)](1 - g_t) \tag{7}$$

$$W_{i,t+1} = [N_i(T^-) + D_i(T^-)]g_t \tag{8}$$

$$Z_{t+1} = R(T^-) + R(T^+) \tag{9}$$

where $D(T^-)$, $N(T^-)$, and $R(T^-)$ are the densities of each state at the end of the year and g is a time-fluctuating activation rate that regulates how much dormant biomass is converted to growing-season live biomass each year. $R(T^+)$ is a randomly generated resource pulse from a log-normal distribution with mean R_μ and variance R_{σ^2} (same mean and variance used to generate daily pulses). Our formulation assumes that at the end of each season all accumulated living biomass $[N(T^-)]$ is converted to dormant biomass. Parameter notations and definitions are 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

Table 1: Definition of model states and parameters. 'Constant' parameters do not fluctuate during a simulation, while 'variable' parameters do fluctuate through time in a given simulation.

Parameter	Definition
N	live biomass
D	dormant biomass
R	resource supply
m_D	dormant state mortality rate (constant)
b	live state maximum resource uptake rate (constant)
m_N	live state mortality rate (constant)
a	allocation fraction of live biomass to seed bank (constant)
g	dormant-to-live biomass transition fraction (variable)
ρ	correlation of species' responses transition cue (constant)
σ_E^2	variance of transition cue (constant)
R_μ	mean resource pulse, on log scale (constant)
R_{σ^2}	variance of daily resource supply, on log scale (variable)

104 differently to environmental conditions, and (3) the effects of competition on a species must

105 be more strongly negative in good years relative to unfavorable years. Our model meets

106 condition 1 because we include a dormant stage with very low death rates. We satisfy

107 condition 2 with our model whenever g is not perfectly correlated between species. Lastly,

108 our model meets condition 3 because condition 2 partitions intraspecific and interspecific

109 competition into different years. Thus, during a high g year for one species, resource uptake

110 is also inherently high for that species, which increases intraspecific competition relative to

111 interspecific competition. So, given adequate variability in g, the inferior competitor (species

112 with lower r) can persist.

113   Following Adler and Drake (2008), we generated sequences of (un)correlated dormant-

114 to-live state transition rates (g) for each species by drawing from multivariate normal

115 distributions with mean 0 and a variance-covariance matrix (Σ_g) of

$$\Sigma_g = \begin{bmatrix} \sigma_E^2 & \rho\sigma_E^2 \\ \rho\sigma_E^2 & \sigma_E^2 \end{bmatrix} \tag{10}$$

116 where σ_E^2 is the variance and ρ is the correlation between between the two species' transition

117 rates. For environmental variability, here induced as variability in g, to promote coexistence

118 via the storage effect, ρ must be less than 1. The inferior competitor has the strongest

119 potential to persist when $\rho = -1$ (perfectly uncorrelated transition rates).

Implementing Relative Nonlinearity

121 When considering consumer-resource dynamics, species coexistence by relative nonlinearity

122 requires that each species has different nonlinear responses to resource availability, and

123 resource availability must fluctuate through time. In a constant resource environment, the

124 species with the lowest R* will always exclude the other species. To compare this model to

125 the storage effect model we still allow the germination rate g to vary, but both species are

126 perfectly correlated – that is, $\rho = 1$ (fig. 1).

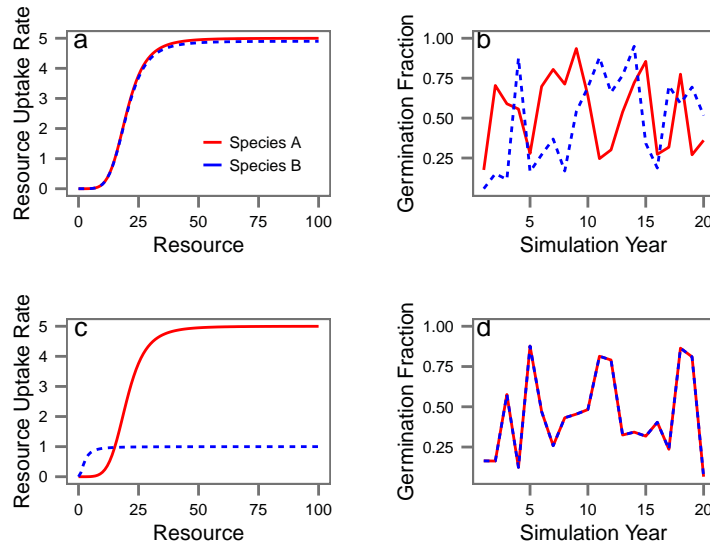

Figure 1: Resource uptake functions and example time series of (un)correlated germination fractions for the storage effect (a,b) and relative nonlinearity (c,d) formulations of the consumer-resource model. The resource uptake functions for both species are equivalent for the storage effect, but their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

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Model Simulations

For each coexistence mechanism (storage effect, relative nonlinearity), we ran model simulations at different levels of resource variance (R_{σ^2}), environmental cue variance (σ_E), and correlation of species responses to the environmental cue (ρ). We ran simulations for 100 'seasons' with 60 day growing seasons. We averaged biomass over the growing season. After discarding an initial 100 seasons to reduce transient effects on our results, we calculated the stability of summed species biomass through time and species synchrony through time. For storage effect simulations, species were equivalent in their ability to capture and assimilate the resource (R) but had different, depending on ρ, germination rates. For relative nonlinearity simulations, species had equivalent germination rates ($\rho = 1$) but different resource acquisition functions (fig. 1). We explored a limited set of parameter space where the storage effect and relative nonlinearity were operating simultaneously. Within-season dynamics were solved given initial conditions using the package 'deSolve' (Soetaert et al. 2010) in R (Team 2013).
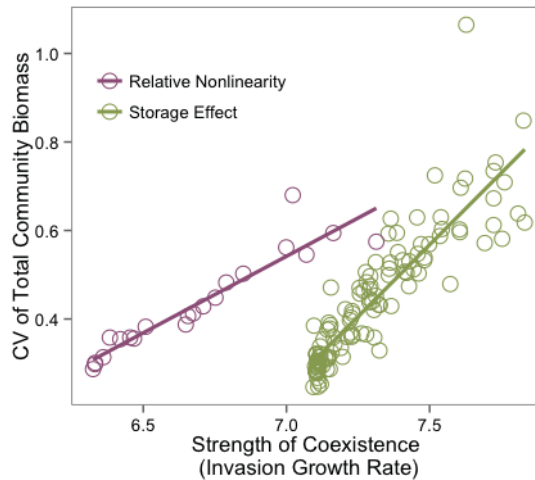
Results

Figure 2: Relationship between the strength of coexistence (invasion growth rate of inferior competitor) and ecosystem variability.
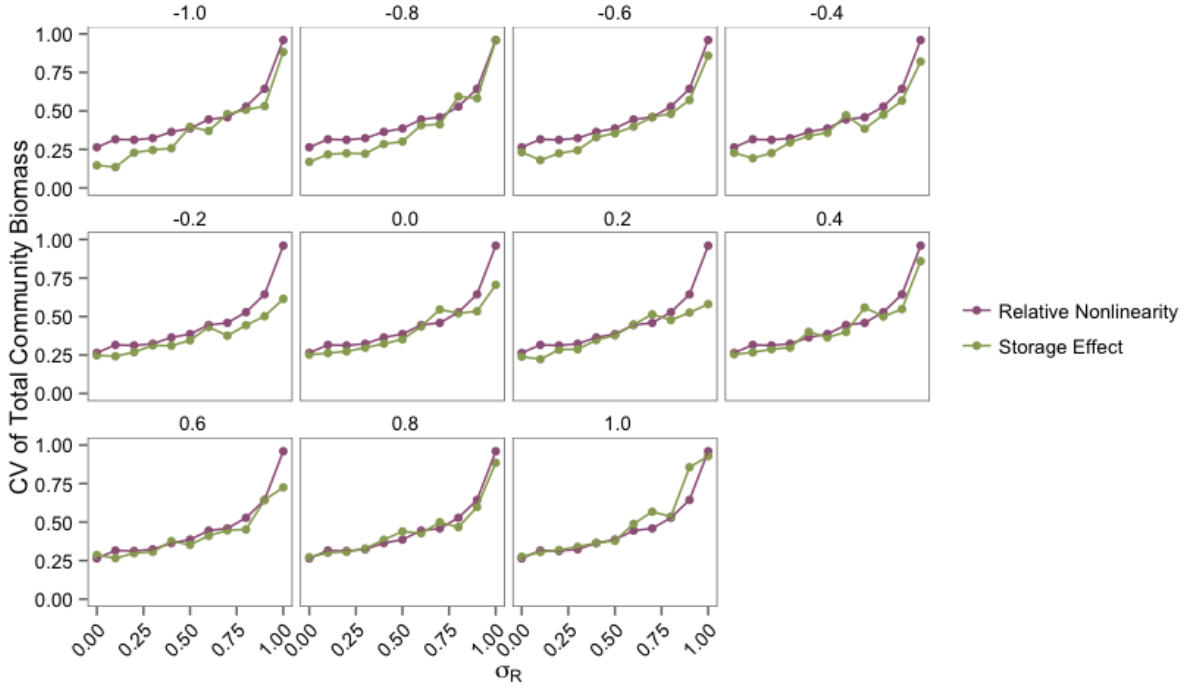
Figure 3: Relationship between resource variability (σ_R) and the coefficient of variation of total community biomass for both coexistence mechanisms. Each panel shows results from different levels of environmental cue correlations (ρ) for the storage effect; $\rho = 1$ across all panels for relative nonlinearity results. On average, the storage effect leads to less variable biomass production through time.

Discussion

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