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. Blah, blah, blah…

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

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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 (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).

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:

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

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

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

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. The single resource R is replenished with daily pulse,

r_τ, randomly drawn from a log normal distribution: $r_\tau = \text{LogNormal}(R_\mu, R_\sigma)$. 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. We assume resource density does not change 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 μ_R and standard deviation σ_R. Our formulation assumes that at the end of each season all accumulated living biomass $[N(T^-)]$ is converted to dormant biomass.

Table 1: Definition of model parameters.

Parameter	Definition
m_D	dormant state mortality rate
r	live state maximum resource uptake rate
K	live state half-saturation constant for resource uptake rate
m_N	live state mortality rate
a	resource turnover rate
S	resource supply rate
g	dormant-to-live biomass transition fraction

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 g 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 g 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 g, the inferior competitor (species with lower r) can persist.

Following Adler and Drake (2008), we generated sequences of (un)correlated dormant-to-live state transition rates (g) for each species by drawing from multivariate normal distributions with mean 0 and a variance-covariance matrix (Σ_g) of

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

where σ_E^2 is the variance and ρ is the correlation between between the two species' transition rates. For environmental variability, here induced as variability in g, to promote coexistence via the storage effect, ρ must be less than 1. 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. So we can compare this model to the storage effect model, we still allow the germination rate g to vary, but both species are perfectly correlate – that is, $\rho = 1$.

Results

Discussion

References

Adler, P. B., and J. M. Drake. 2008. Environmental variation, stochastic extinction, and competitive coexistence. The American Naturalist 172:186–195.

Adler, P. B., J. HilleRislambers, and J. M. Levine. 2007. A niche for neutrality.

Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. Ecology 92:1157–1165.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31:343–366.

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.

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.

Pachepsky, E., R. M. Nisbet, and W. W. Murdoch. 2008. Between discrete and continuous: Consumer-resource dynamics with synchronized reproduction. Ecology 89:280–288.

Tilman, D. 1982. Resource competition and community structure. Pages 1–296.

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.