How coexistence mechanisms mediate temporal stability

Andrew T. Tredennick[1], Peter B. Adler[1], and Frederick Adler[2]

[1]*Department of Wildland Resources and the Ecology Center, Utah State University*
[2]*Departments of Biology and Mathematics, University of Utah*

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1 Introduction

Theoretical work aimed toward identifying the mechanisms by which species richness promotes temporal stability has treated species coexistence as a foregone conclusion. In so doing, that large body of work implicitly assumes that the interaction between environmental variability and the mechanism(s) by which species coexist is trivial. However, under the same conditions of environmental variability, population dynamics will respond differently depending on the coexistence context. In turn, this leads to different dynamics at the community and ecosystem levels depending on how species interact. So, it stands to reason that identifying the key mechanisms that promote ecosystem stability requires a solid understanding of how species coexistence mediates temporal stability in fluctuating environments.

To that end, we will analyze a general consumer-resource model under different coexistence assmptions. Our starting point is a model of two plant consumers and one resource (e.g., soil moisture or nitrogen). We will focus on three cases of species coexistence:

1. Relative nonlinearty

2. Temporal storage effect

3. A combination of both mechanisms

Each scenario requires different model assumptions and structure, so we will describe each in turn. Although the structure may change slightly to incorporate different coexistence mechanisms, the strength of our approach lies in the similarities among the models since we work under a unified consumer-resource framework.
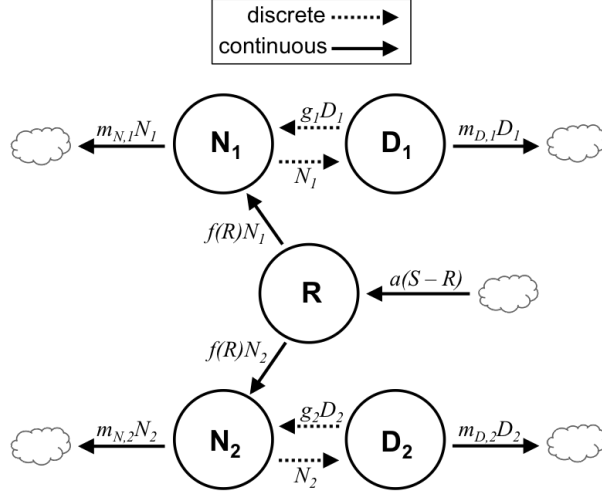
Figure 1: Schematic of our semi-discrete consumer-resource model. See text for parameter definitions.

1.1 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 (Figure 1). Transitions between N and D occur at discrete intervals T, so our model is formulated as "pulsed differential equations". For clarity we refer to T as years and the growing time between years, τ, as seasons. Seasonal (within-year) dynamics are modeled as three differential equations:

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

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

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

where i denotes species, D is the dormant (long-lived) biomass state, N is the living biomass (fast-growing, shorter-lived) state, and ms are biomass loss rates. The growth rate of living biomass is a resource-dependent function, $f(R) = r_i R/(K_i + R)$, where r is the maximum growth rate and K is the resource level at which growth is one-half r. For the resource dynamics, whose state is denoted by R, we use a linear resource renewal equation where a scales resource turnover rate and S is the resource equilibrium when consumers are absent, and an offtake of the resource equal to the sum of each species' consumption, $\sum_{i=1,2} f(R)N_i$. Note that since transitions between N and D are pulsed, only biomass loss occurs throughout the season for D.

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

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

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:

$$V_{i,t+1} = [N_i(T^-) + D_i(T^-)](1 - g_t) \tag{7}$$
$$W_{i,t+1} = [N_i(T^-) + D_i(T^-)]g_t \tag{8}$$
$$Z_{t+1} = R(T^-) \tag{9}$$

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. Our formulation assumes that at the end of each season all accumulated living biomass $[N(T^-)]$ is converted to dormant biomass.

1.1.1 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 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
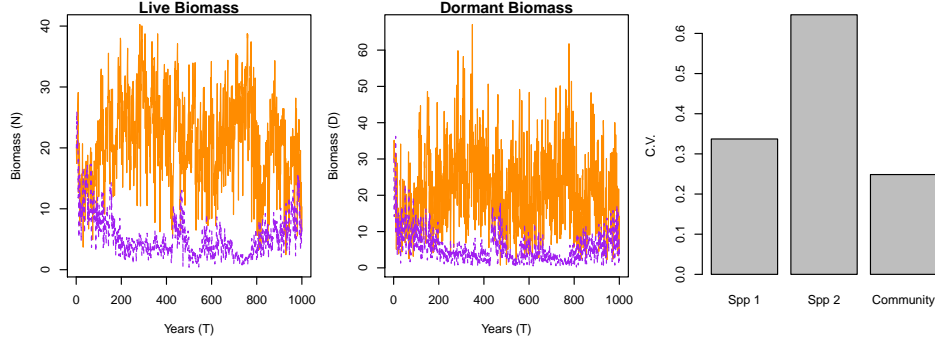
Figure 2: Example time-series from our pulsed consumer-resource model where g is perfectly uncorrelated (storage effect operating), $r_1 = 2.2$, and $r_2 = 2$. Species 1 is orange, species 2 is purple. The far right panel shows the population, by species, and community-level coefficient of variation.

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 of

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

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).

1.2   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, $\rho = 1$.
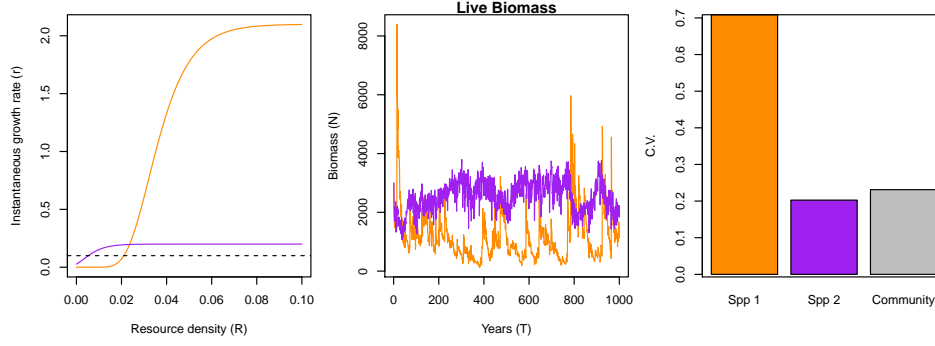
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Figure 3: Example time-series from our pulsed consumer-resource model where $g_{1,2} = 1$, but species have different nonlinear uptake rate responses to resource supply (A). Species 2 has the lowest R* but its resource response saturates at a lower level than species 2. Species 1 is orange, species 2 is purple. The far right panel shows the population, by species, and community-level coefficient of variation.

2 Results

2.1 Storage effect model

Some preliminary results from running simulations of the storage effect version of the model at different levels of environmental cue variability (σ_E) and resource supply variability (σ_S). I ran 20 simulations at each combination of σ_E and σ_S shown in Figure 4 (the points are the means across the 20 simulations, each run for 2,000 time-steps, with the initial 1,000 time-steps discarded before calculating anything). There is a weak trend of community CV to saturate at high levels of resource supply variability (Figure 4, top panel).

One of the things we are interested in is how well the community buffers itself against resource variability. Really I should calculate some kind of asynchrony metric, but for now I just looked at the ratio of the resource CV to the community CV (Figure 4, bottom panel). Kind of difficult to interpret, but it is interesting that at high levels of variability in the environmental cue that drives the storage effect, the ratio decreases with resource supply variability. The opposite occurs at lower levels of variability in the environmental cue.

NOTE: I should probably also put a check in the code somewhere to make sure we don't have extinctions...
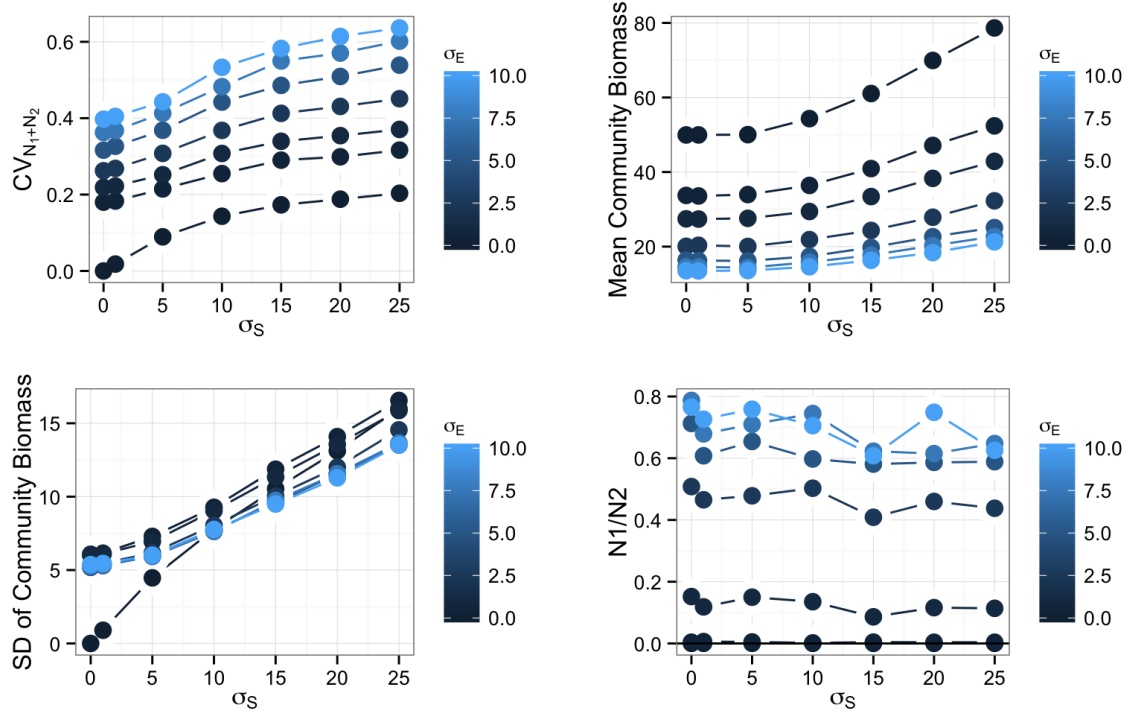
Figure 4: Preliminary results from model simulations under storage effect conditions.