

How coexistence mechanisms mediate temporal stability

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Introduction

Species richness tends to confer temporal stability of biomass production in competitive plant communities via compensatory dynamics among species. Two classes of mechanisms can produce compensatory dynamics: (1) temporal complementarity among species and (2) functional complementarity among species. Temporal complementarity results in asynchronous population fluctuations that, when aggregated over all populations in a community, dampens variability at the community or ecosystem level. Such asynchrony in population dynamics through time is driven by either species-specific responses to variable environmental conditions or differences in the rate at which species respond to disturbance.

In contrast to temporal complementarity, functional complementarity increases community stability by reducing the strength of interspecific competition. Once thought to be stabilizing at the community level, recent work suggests interspecific competition is actually destabilizing. This is because functional complementarity and competition are negatively correlated, and functional complementarity among species (i.e., non-temporal niche differences) generally results in the productivity of species in mixture being greater than expected from monocul-

tures. So called overyielding increases mean productivity more than its variance, leading to greater temporal stability.

This implies a strong role for the mode and stability of species coexistence. Yet, theoretical work aimed toward identifying the mechanisms by which species richness promotes temporal stability has treated species coexistence as a foregone conclusion. Most studies either assume coexistence a priori or ensure coexistence by non-temporal forms of niche differentiation. 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.

To that end, we will analyze a general consumer-resource model under different coexistence assumptions. 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 nonlinearity
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.

Model description 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 (Figure~??). Transitions between N and

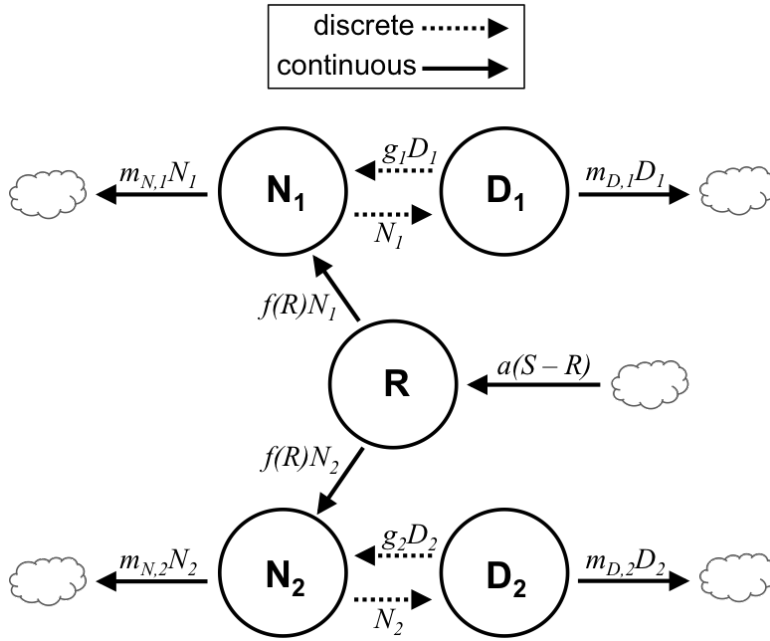


Figure 1: Diagram of our semi-discrete consumer-resource model. Solid lines show continuous dynamics while dashed lines show the discrete transitions.

46 D occur at discrete intervals T , so our model is formulated as “pulsed differential equations”
 47 (Pachepsky et al. 2008, Mailleret and Lemesle 2009). For clarity we refer to T as years and
 48 the growing time between years, τ , as seasons. Seasonal (within-year) dynamics are modeled
 49 as three differential equations:

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

$$\frac{dN_i}{d\tau} = f_i(R)N_i - m_{N,i}N_i \quad (2)$$

$$\frac{dR}{d\tau} = a(S - R) - \sum_{i=1,2} f_i(R)N_i \quad (3)$$

50 where i denotes species, D is the dormant (long-lived) biomass state, N is the living biomass
 51 (fast-growing, shorter-lived) state, and ms are biomass loss rates. The growth rate of living
 52 biomass is a resource-dependent function, $f_i(R) = r_i e^{-\alpha_i e^{-\beta_i R}}$. For the resource dynamics,
 53 whose state is denoted by R , we use a linear resource renewal equation where a scales resource
 54 turnover rate and S is the resource equilibrium when consumers are absent, and an offtake of
 55 the resource equal to the sum of each species’ consumption, $\sum_{i=1,2} f_i(R)N_i$. Note that since
 56 transitions between N and D are pulsed, only biomass loss occurs throughout the season for
 57 D .

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

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

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

$$R(0) = Z_t \quad (6)$$

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

61 The consumers transition between N and D instantaneously between years. We assume
62 resource density does not change between years. So, at the yearly transition:

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

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

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

63 where $D(T^-)$, $N(T^-)$, and $R(T^-)$ are the densities of each state at the end of the year and g
64 is a time-fluctuating activation rate that regulates how much dormant biomass is converted
65 to growing-season live biomass each year. Our formulation assumes that at the end of each
66 season all accumulated living biomass $[N(T^-)]$ is converted to dormant biomass.

67

68 Implementing the storage effect

69 To make this a “storage-effect” model, we need to satisfy three conditions: (1) the organisms
70 must have a mechanism for persistence under unfavorable conditions, (2) species must respond
71 differently to environmental conditions, and (3) the effects of competition on a species must
72 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 of

$$\begin{bmatrix} \sigma_E^2 & \rho\sigma_E^2 \\ \rho\sigma_E^2 & \sigma_E^2 \end{bmatrix} \quad (10)$$

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

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~?? (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~??, 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~??, 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.

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