

# How coexistence mechanisms mediate temporal stability

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## Introduction

It is now clear that species richness tends to increase the temporal stability of biomass production in competitive plant communities. It is even becoming clear that a few core mechanisms related to compensatory dynamics among species through temporal or functional complementarity can explain the positive relationship between diversity and stability. What remains unclear is how the coexistence mechanism that maintains species richness influences the strength of compensatory dynamics. Theoretical studies based on Lotka-Volterra models have given us insight into the mechanisms that promote stability in communities where species coexist by fluctuation-independent mechanisms. A remaining challenge is to explore the importance of proposed mechanisms behind diversity-stability relationships in communities where species coexistence is maintained by temporal variability. Specifically, we seek to understand the mechanisms that promote temporal stability in communities where species coexistence is achieved because of temporal variability.

To that end, we will analyze a general consumer-resource model under different fluctuation-dependent 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  $N$  (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,  $\tau$ , as seasons. Seasonal (within-year) dynamics are modeled as three differential equations:

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

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

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

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 Hill function,  $f_i(R) = r_i R^{\alpha_i} / (\beta_i^{\alpha_i} + R^{\alpha_i})$ . Resource depletion is equal to the sum of each species' consumption,  $\sum_{i=1,2} f_i(R)N_i$ . 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 season, Eqs. 1-3 are solved given the initial conditions:

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

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

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

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

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

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

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

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

51 where  $D(T^-)$ ,  $N(T^-)$ , and  $R(T^-)$  are the densities of each state at the end of the year and  $g$   
 52 is a time-fluctuating activation rate that regulates how much dormant biomass is converted  
 53 to growing-season live biomass each year.  $R(T^+)$  is a randomly generated resource pulse  
 54 from a log-normal distribution with mean  $\mu_R$  and standard deviation  $\sigma_R$ . Our formulation  
 55 assumes that at the end of each season all accumulated living biomass  $[N(T^-)]$  is converted  
 56 to dormant biomass.

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## 58 Implementing the storage effect

59 To make this a “storage-effect” model, we need to satisfy three conditions: (1) the organisms  
 60 must have a mechanism for persistence under unfavorable conditions, (2) species must respond  
 61 differently to environmental conditions, and (3) the effects of competition on a species must  
 62 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 (??), 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 ( $\Sigma_g$ ) of

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

where  $\sigma_E^2$  is the variance and  $\rho$  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,  $\rho$  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,  $\rho = 1$ .

## 84 Results

### 85 Storage effect model

## 86 **References**

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