

How fluctuation-dependent species coexistence affects ecosystem stability

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Environmental variability

All organisms exist in variable environments, and this provides **challenges** and **opportunities**.

- **Challenges:** organisms have to survive, makes the ecosystem more variable (less predictable)
- **Opportunities:** can “divvy up” niche space, allowing species to coexist

Paradox: environmental variability can maintain biodiversity, and higher biodiversity is predicted to increase ecosystem stability. But, if environmental variability promotes species coexistence, shouldn't more species rich communities also have higher ecosystem variability?

All theory that predicts a positive relationship between species richness and ecosystem stability either:

1. Ensures coexistence via **fluctuation-independent** mechanisms (e.g., resource partitioning)
2. Selects parameters that ensure species coexistence, even if coexistence depends, in part, on temporal fluctuations.

The model

- Two (or more) plant species coexisting on a single resource that replenishes once at the beginning of the growing season.
- Plants exist in two states: dormant (e.g., seedbank for annuals) and live.
- Transitions between the two states occur between growing seasons and depend on plant responses to an environmental cue temperature.
- Two sources of environmental variation: the resource and the environmental cue.

The model: growing season dynamics

Within a growing season, live plant state dynamics are modeled with classic **consumer** (N)-**resource** (R) dynamics

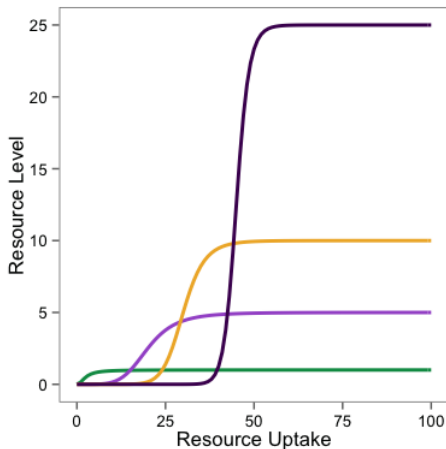
$$\frac{dN_i}{dt} = N_i \epsilon_i f_i(R), \quad t \neq \tau_k \quad (1)$$

$$\frac{dR}{dt} = - \sum_{i=1,2} f_i(R) N_i, \quad t \neq \tau_k \quad (2)$$

- ϵ = biomass conversion efficiency
- $f_i(R)$ = resource-dependent resource uptake function

The model: resource uptake function

$$f_i(R) = r_i R^{a_i} / (b_i^{a_i} + R^{a_i}) \quad (3)$$



The model: between growing season dynamics

Biomasses of each species' state (**N**, **D**) at the start of the growing season (τ_k^+) equal to...

$$D_i(\tau_k^+) = \alpha_i N_i(\tau_k) + D_i(\tau_k)(1 - \gamma_{i,\tau_k}) + D_i(\tau_k)(1 - \eta_i) \quad (4)$$

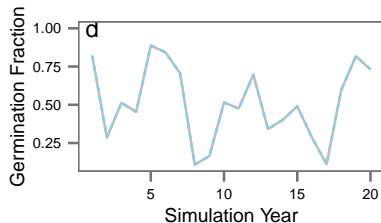
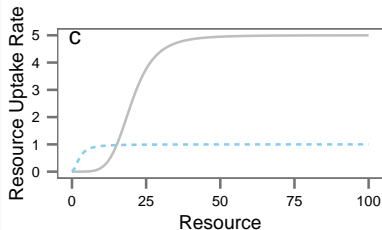
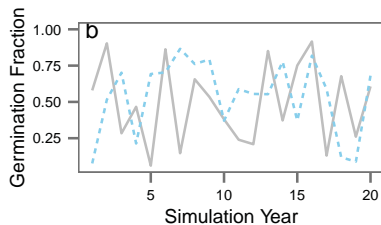
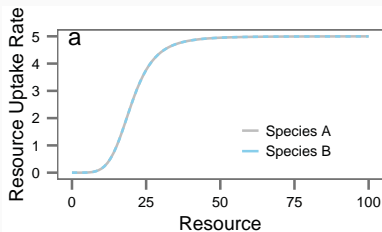
$$N_i(\tau_k^+) = \beta_i(1 - \alpha_i)N_i(\tau_k) + \gamma_{i,t}[D_i(\tau_k) + \alpha_i N_i(\tau_k)](1 - \eta_i) \quad (5)$$

Dormant state population growth - Some biomass comes in to storage from the live state, some gets activated to the live state, some biomass survives to stay in the dormant state.

Live state population growth - Some biomass survives (β) from τ_k and is stored (α) in the dormant state, some biomass gets activated from the dormant state.

Coexistence mechanisms

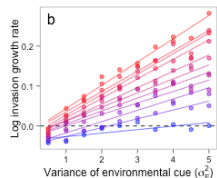
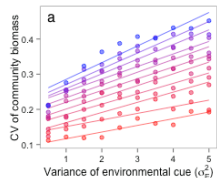
1. Storage effect (a,b)
2. Relative nonlinearity (c,d)



1. How do the storage effect and relative nonlinearity affect ecosystem stability in a 2-species community at various levels of resource and environmental variance?
2. How do the storage effect and relative nonlinearity affect the diversity-stability relationship?

Question 1: Results

Storage Effect

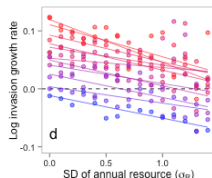
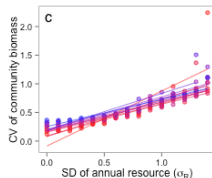


Correlation of species' environmental response (ρ)

— -1 — -0.8 — -0.6 — -0.4 — -0.2 — 0

— 0.2 — 0.4 — 0.6 — 0.8 — 1

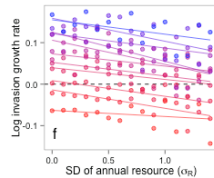
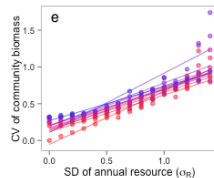
Relative Nonlinearity



Correlation of species' environmental response (ρ)

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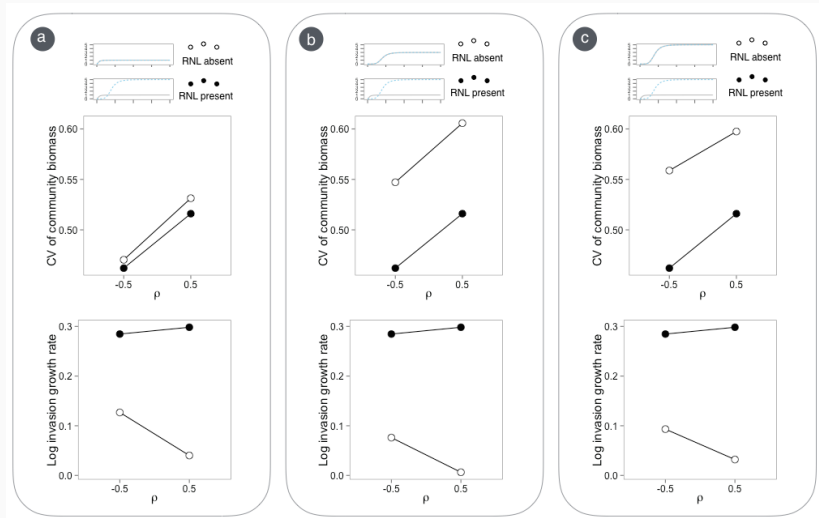


Variance of environmental cue (σ_E^2)

— 0 — 0.5 — 1 — 1.5 — 2 — 2.5

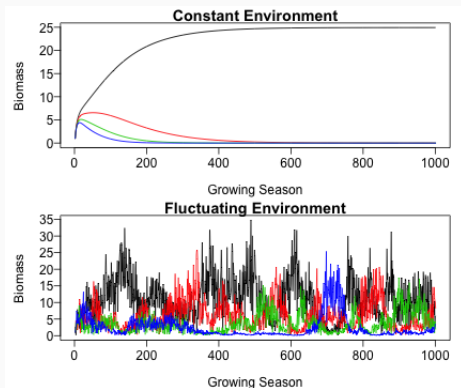
— 3 — 3.5 — 4 — 4.5 — 5

Question 1: Results

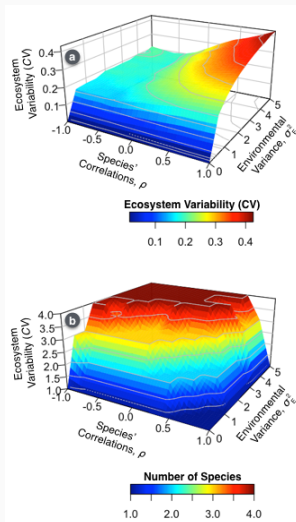


Question 2: Methods

1. Create four unique species
2. Start with all of them in the community
3. See which ones survive

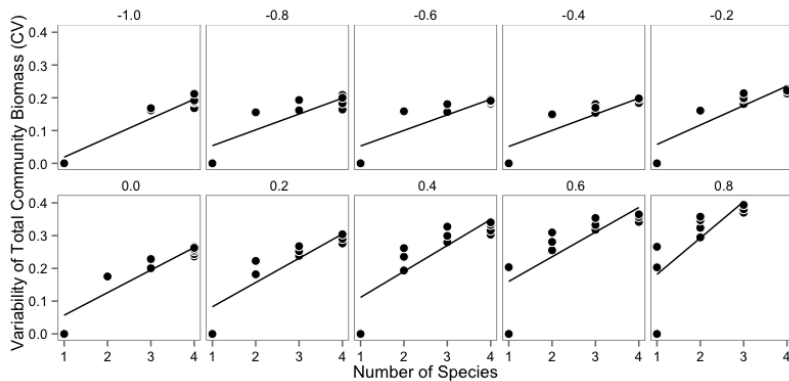


Question 2: Results: Storage Effect



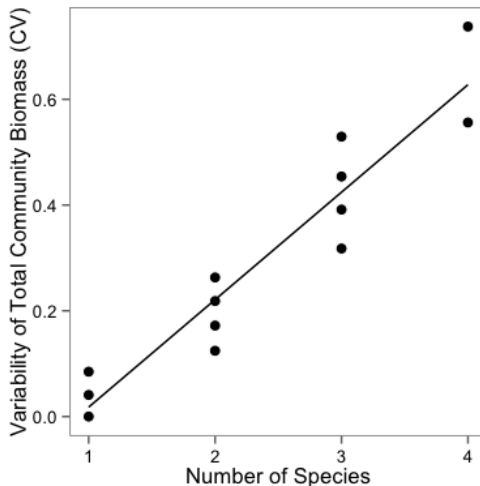
Question 2: Results: Storage Effect

The diversity-variability relationship is positive across a natural diversity gradient!



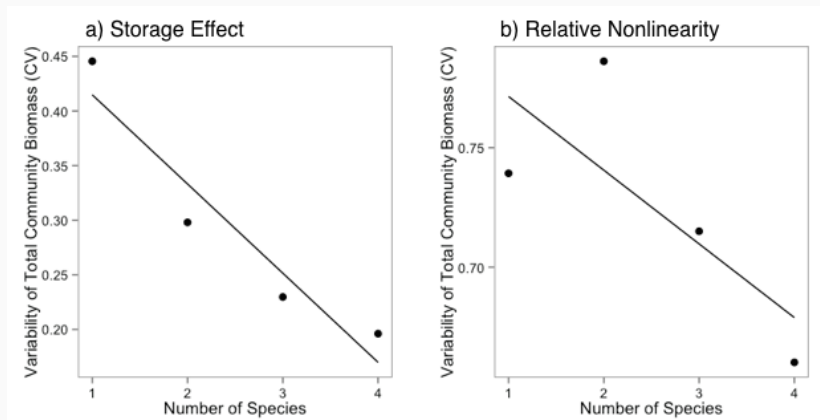
Question 2: Results: Relative Nonlinearity

The diversity-variability relationship is positive across a natural diversity gradient!



Question 2: Results: “Within-sites”

Within a level of environmental variance, more species is always better, as predicted by other theories and found in BEF experiments (whew!).



- Deviations from expected negative diversity-stability relationship probably due to fluctuation-dependent coexistence mechanisms.
- Given that plant coexistence is probably maintained by some mixture of fluctuation-independent and fluctuation-dependent mechanisms, we should not be surprised to find all sorts of patterns between diversity and stability in natural systems with natural diversity gradients.
- However, at a give level of environmental variability, more species is always better.