

Effects of species interactions and environmental drivers on the stability of freshwater communities

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Algebra!

Geometry!

Calculus!

Statistics!

History!

Ecology!

Intrigue!

Suspense!



Predation

Competition

Facilitation



Anne Paine



Adam
Hinterthuer

Ecological Monographs, 73(2), 2003, pp. 301–330
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ESTIMATING COMMUNITY STABILITY AND ECOLOGICAL INTERACTIONS FROM TIME-SERIES DATA

A. R. IVES,^{1,4,5} B. DENNIS,^{2,4} K. L. COTTINGHAM,^{3,4} AND S. R. CARPENTER^{1,4}

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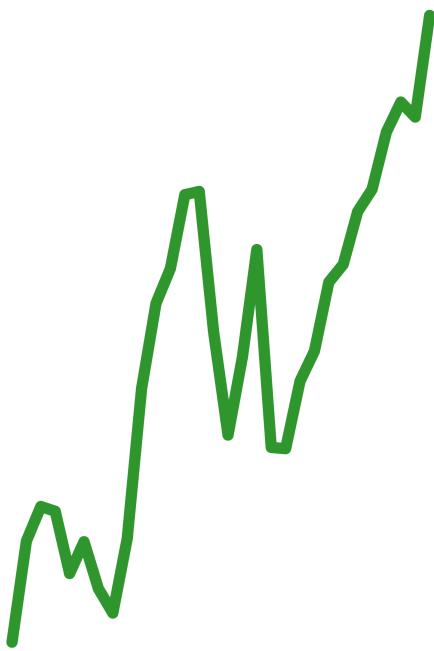
²*Department of Fish and Wildlife Resources and Division of Statistics, University of Idaho,
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³*Department of Biology, Dartmouth College, Hanover, New Hampshire 03755 USA*

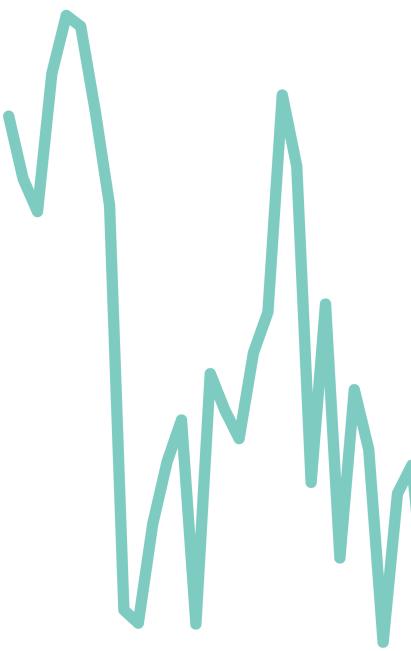
⁴*National Center for Ecological Analysis and Synthesis, University of California,
Santa Barbara, California 93101-5504 USA*

We can use time series of abundance...

Producer



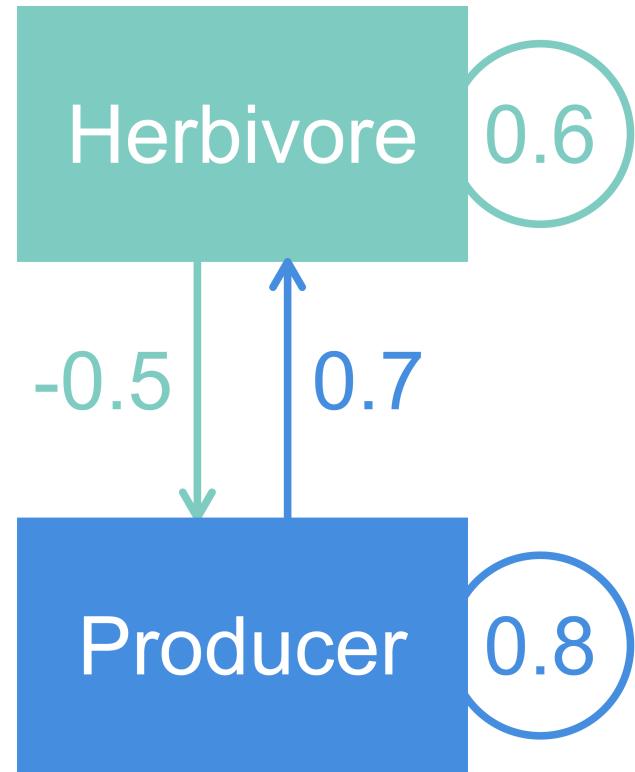
Herbivore



Predator

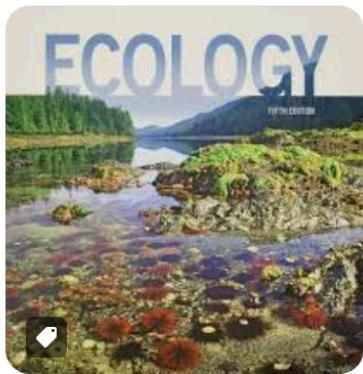


to get intra- & interspecific interaction strengths

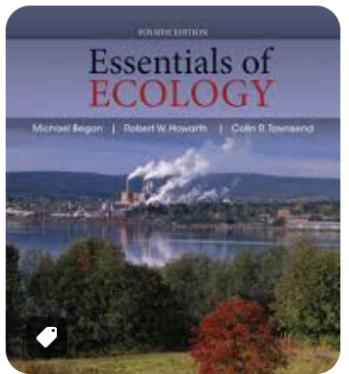


How does one do this?!

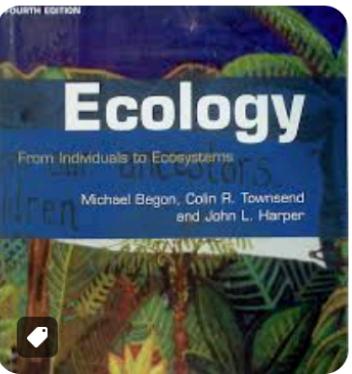
Let's begin with a model for population size



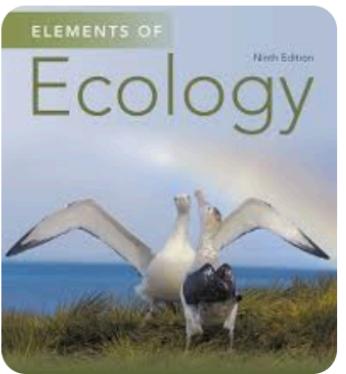
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Bowman, William D., Ha...



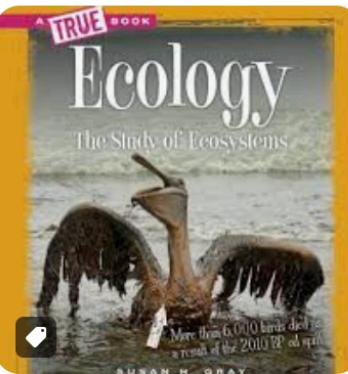
Wiley
Essentials of Ecology [...]



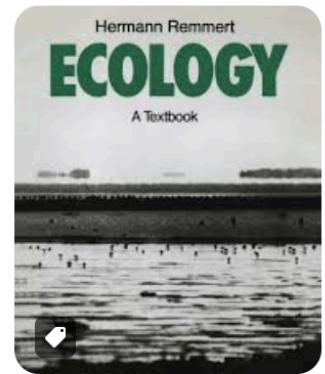
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Ecology: From Individua...



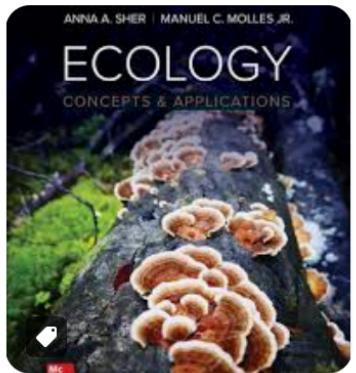
Pearson
Elements of Ecology



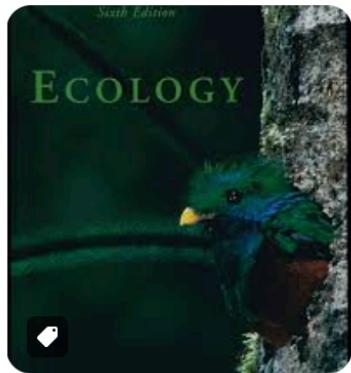
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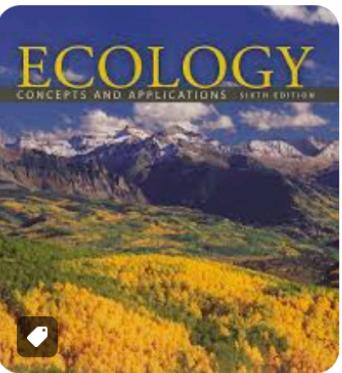
SpringerLink
Ecology: A Textbook...



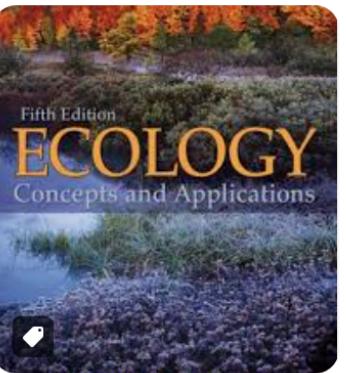
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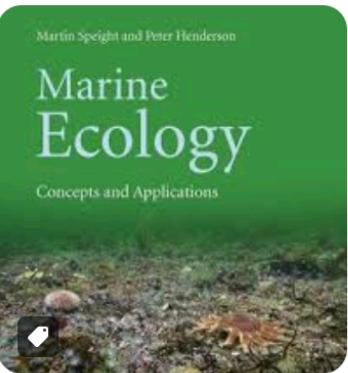
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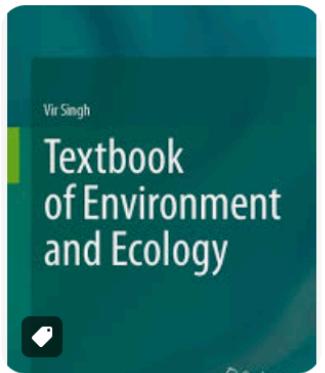
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Assumptions



The size of a population can change over time

Those changes are density dependent



Discrete-time Gompertz model

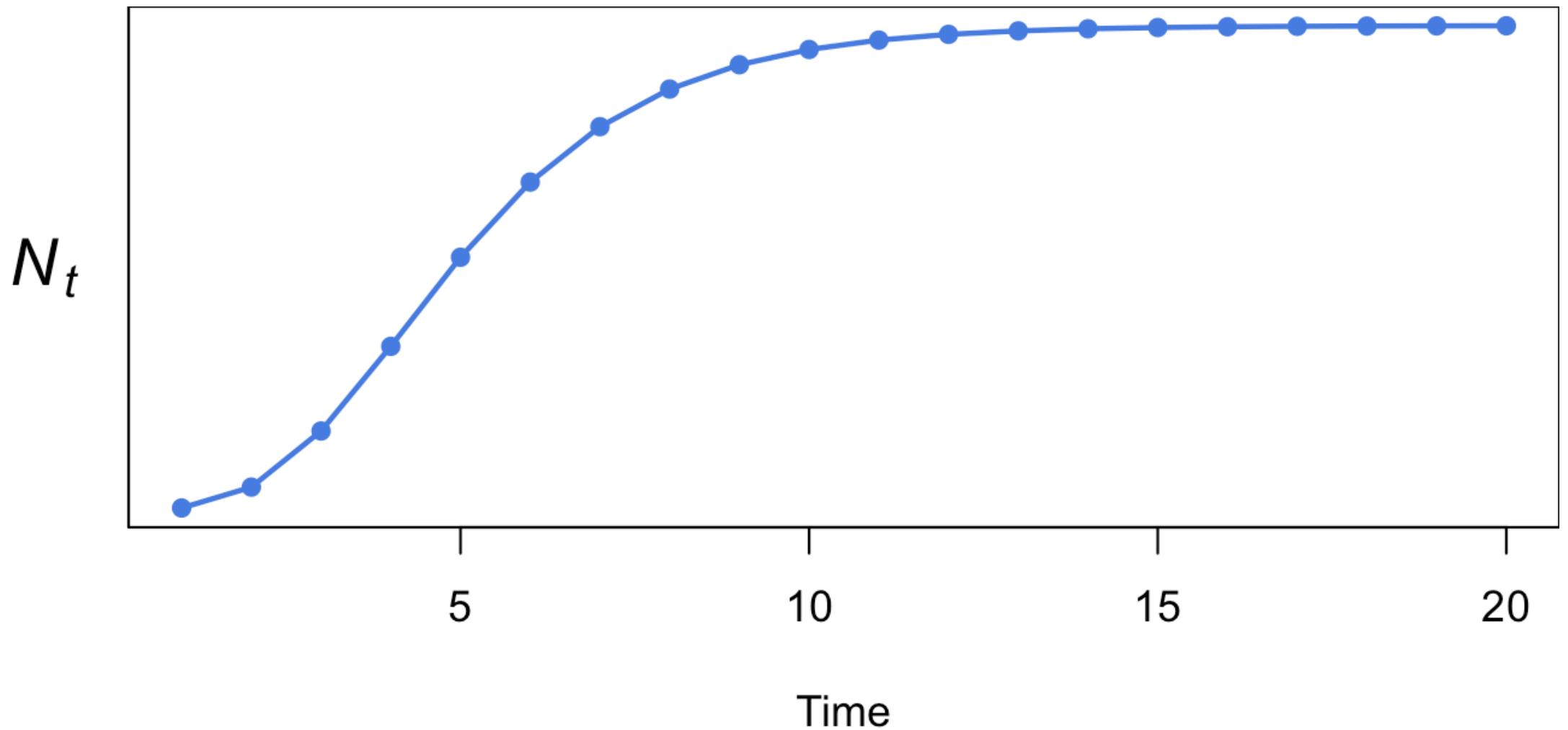
$$N_t = N_{t-1} \exp(r_{\max} + (b - 1) \log(N_{t-1}))$$



In other words

A population grows smoothly toward its carry capacity

Example of Gompertz population growth





DeepAI.org

Assumptions



The size of a population changes over time

Some changes are density dependent

Some changes owe to an unpredictable environment



Discrete-time Gompertz model

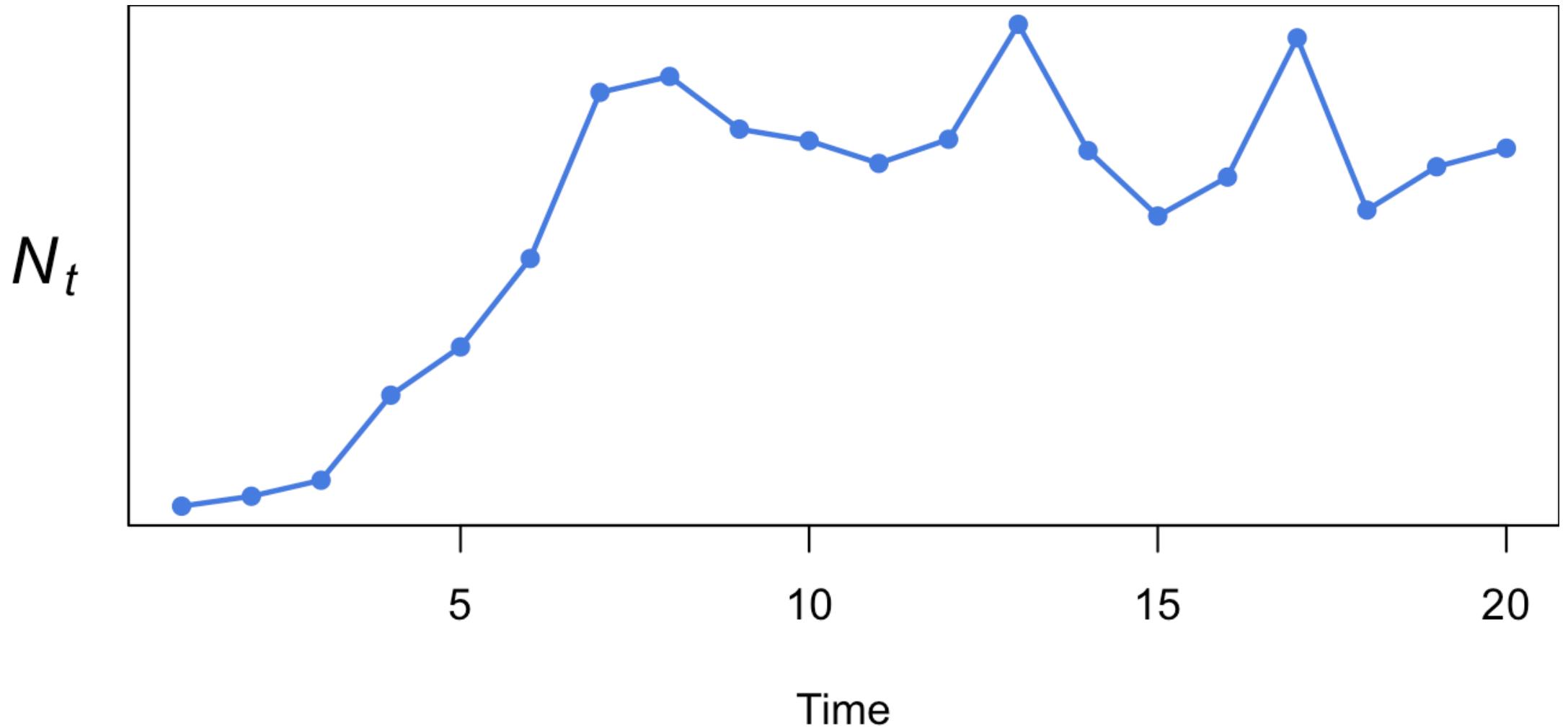
$$N_t = N_{t-1} \exp \left(r_{\max} + (b - 1) \log(N_{t-1}) \right) \underbrace{\exp(w_t)}_{environment}$$



In other words

A population bumps up & down toward its long-term mean

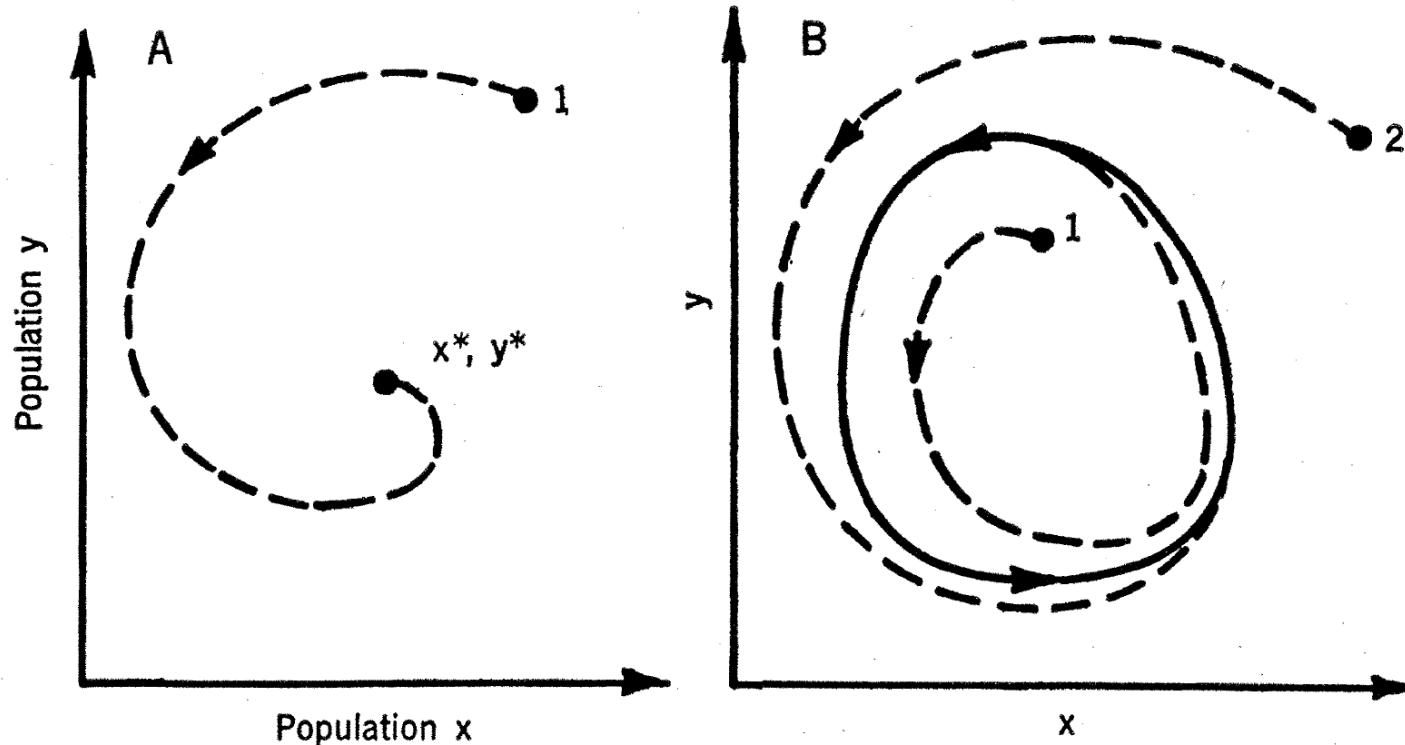
Example of stochastic Gompertz dynamics



Quantifying population stability

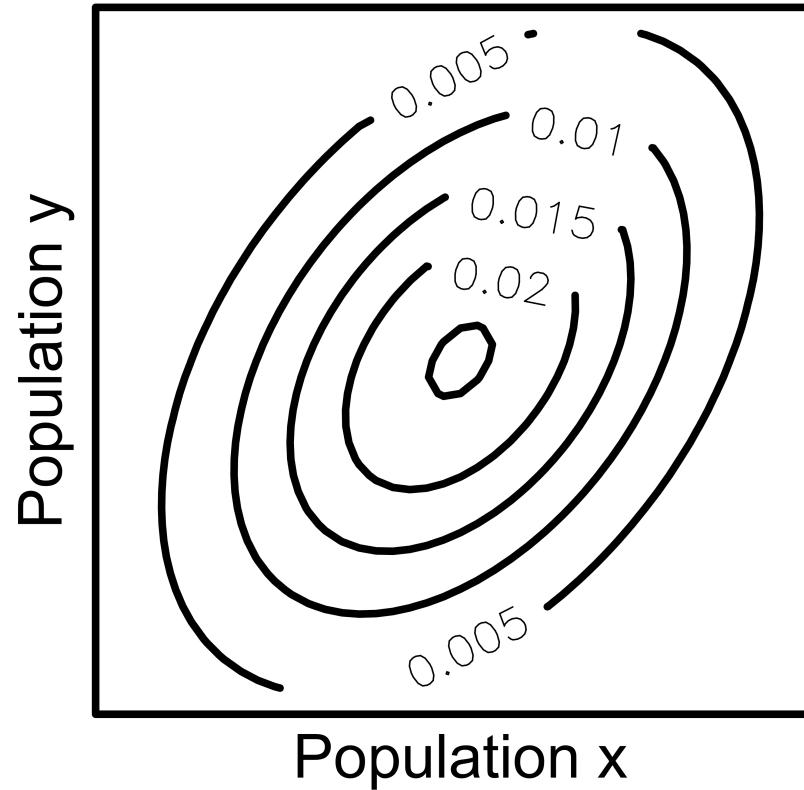
Population equilibria

In deterministic models, equilibria are a point or stable limit cycle



Population equilibria

In stochastic models, the "equilibrium" isn't – it's a *stationary distribution*



Another look at our Gompertz model

$$N_t = N_{t-1} \exp(r_{\max} + (b - 1) \log(N_{t-1})) \exp(w_t)$$

Another look at our Gompertz model

$$N_t = N_{t-1} \exp(r_{\max} + (b - 1) \log(N_{t-1})) \exp(w_t)$$

Complex. Nonlinear. Meh.

A log-transformed Gompertz model

$$x_t = r_{max} + bx_{t-1} + w_t$$

Simple. Linear. Clean.

A log-transformed Gompertz model

$$x_t = r_{max} + bx_{t-1} + w_t$$

if we assume that

$$0 < b < 1; \quad w_t \sim N(0, q)$$

then this process is *stationary*

A log-transformed Gompertz model

$$x_t = r_{max} + bx_{t-1} + w_t$$

and we can show that

$$\text{Var}(x_t) = \frac{\text{Var}(w_t)}{1 - b^2}$$

Assumptions



The size of a population changes over time

Some changes are density dependent

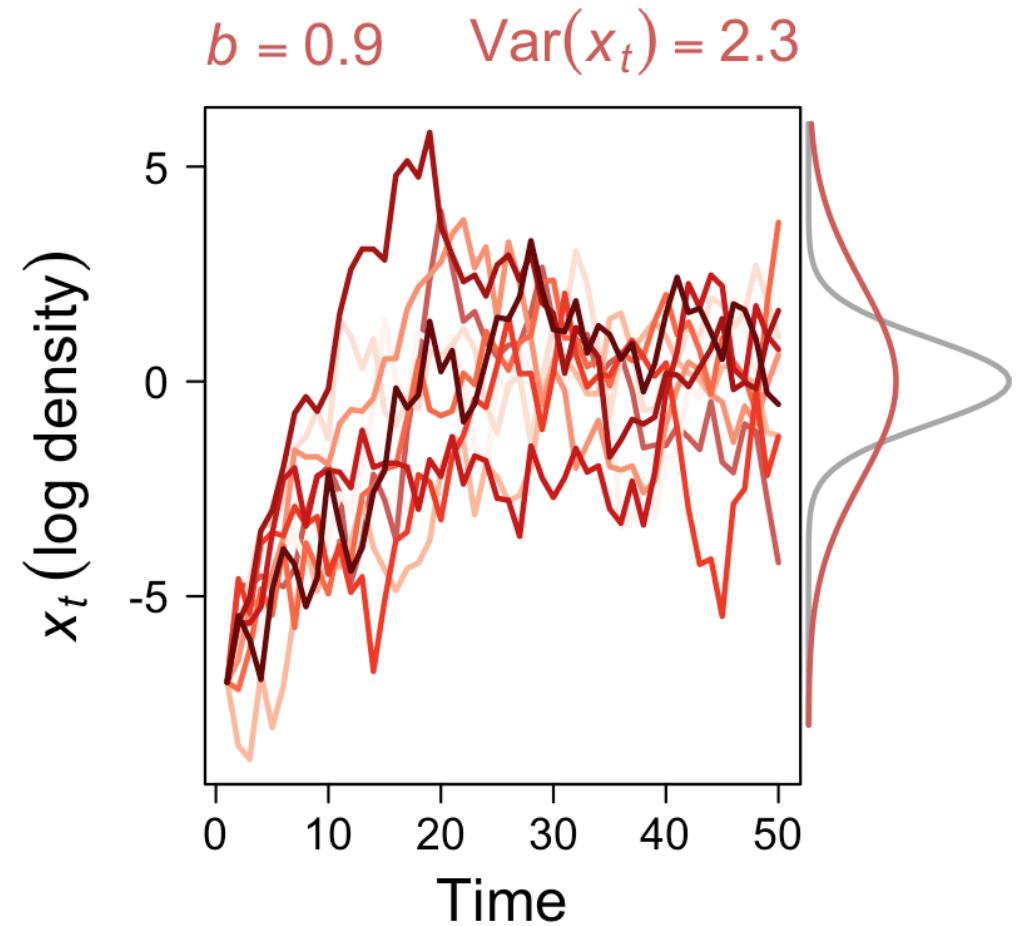
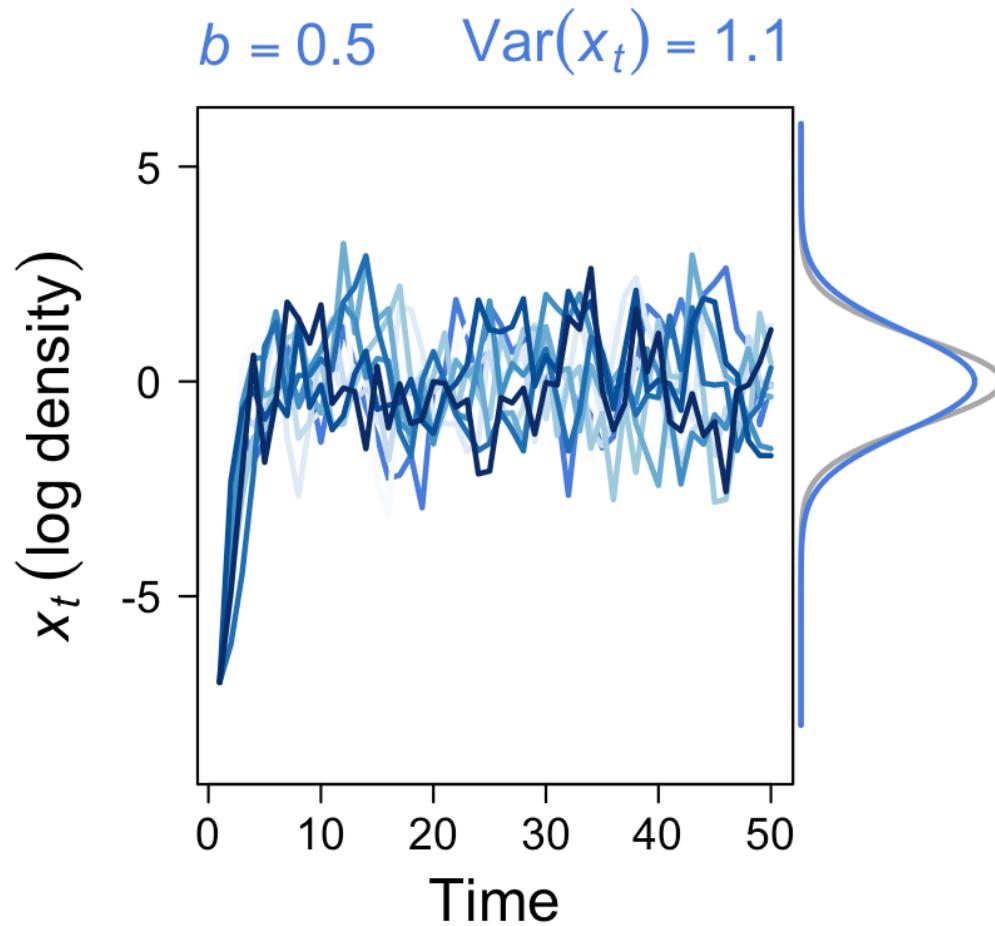
Some changes owe to an unpredictable environment

Stability is inversely related to variance

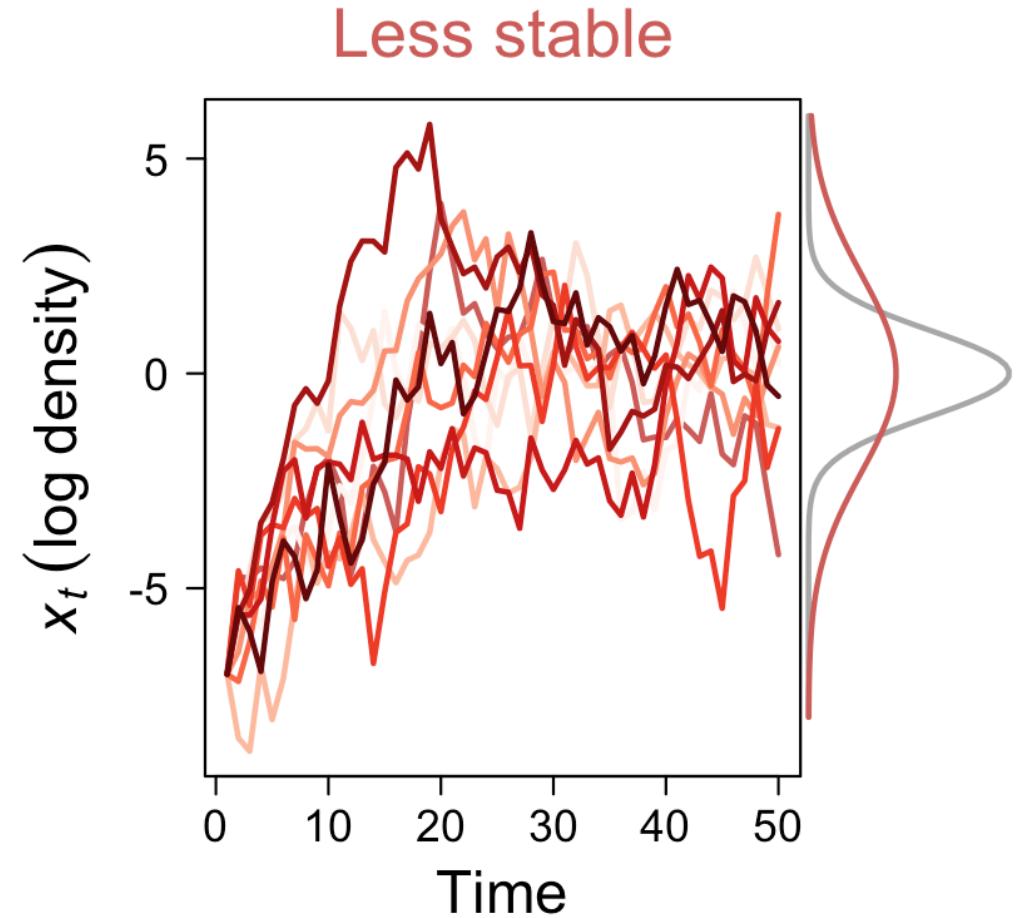
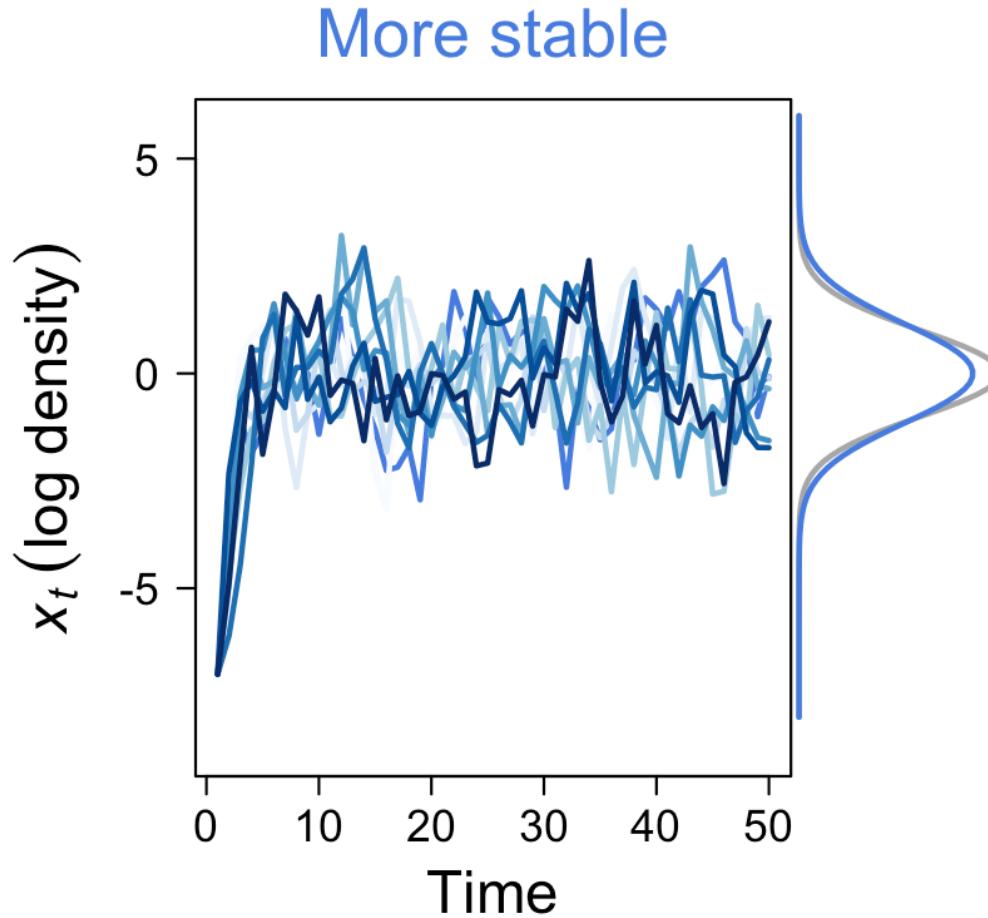
$$stability = \frac{1}{\text{Var}(popn)} = \frac{DD}{\text{Var}(env)}$$

implying a population is more stable when
the strength of density-dependence increases
and the environment is less variable

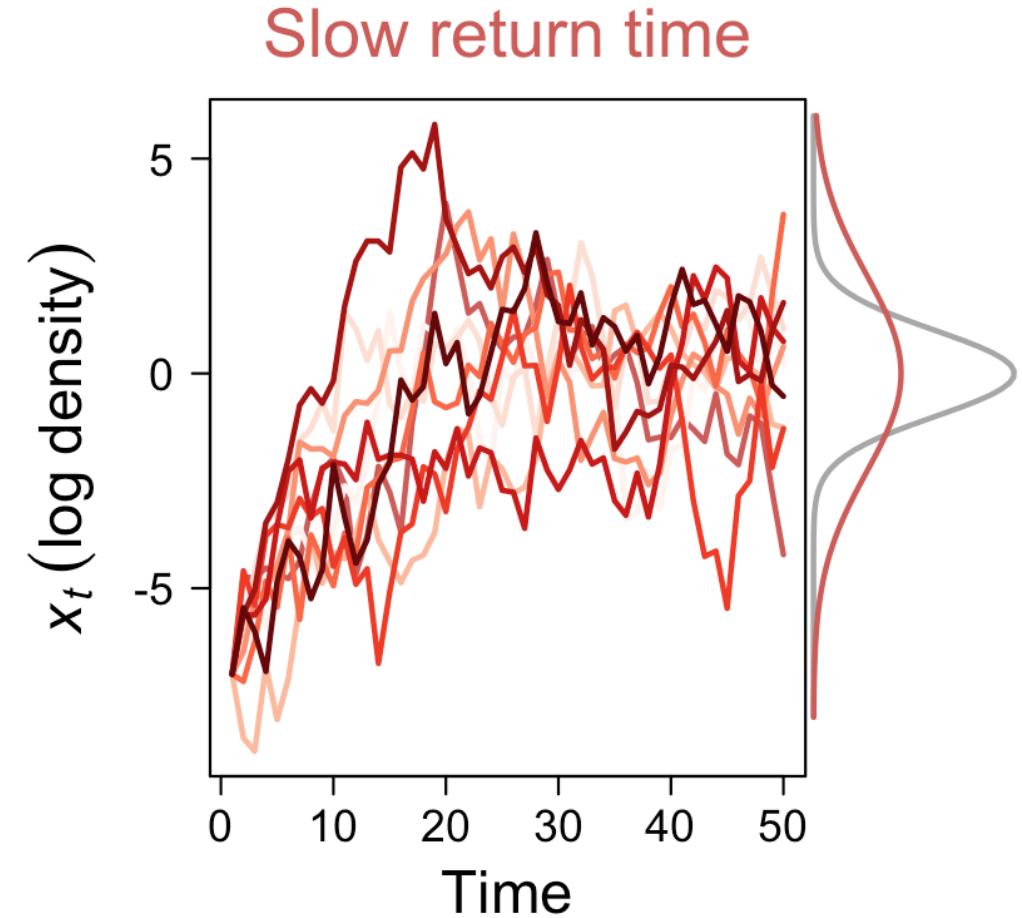
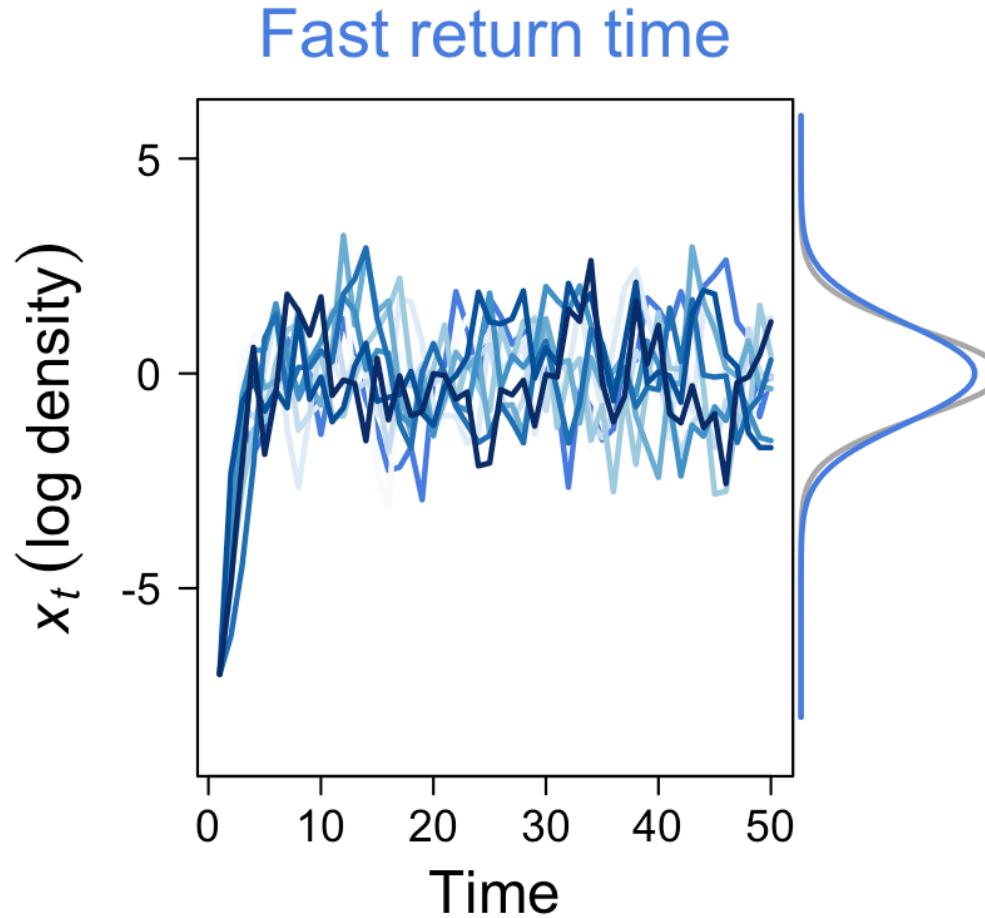
Populations within the same environment



Populations within the same environment



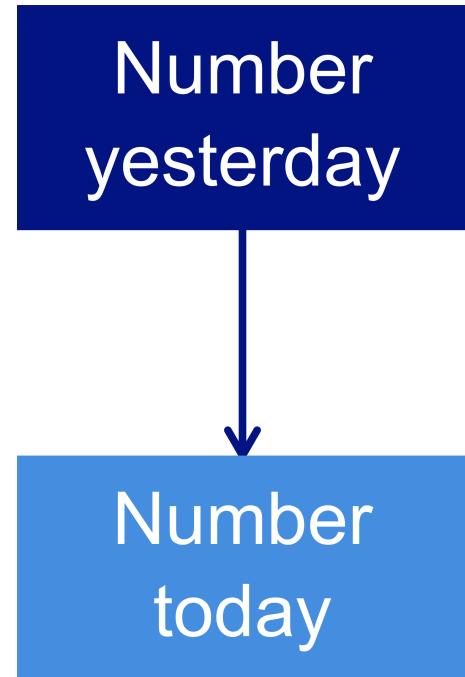
Populations within the same environment



Changes in a community over time

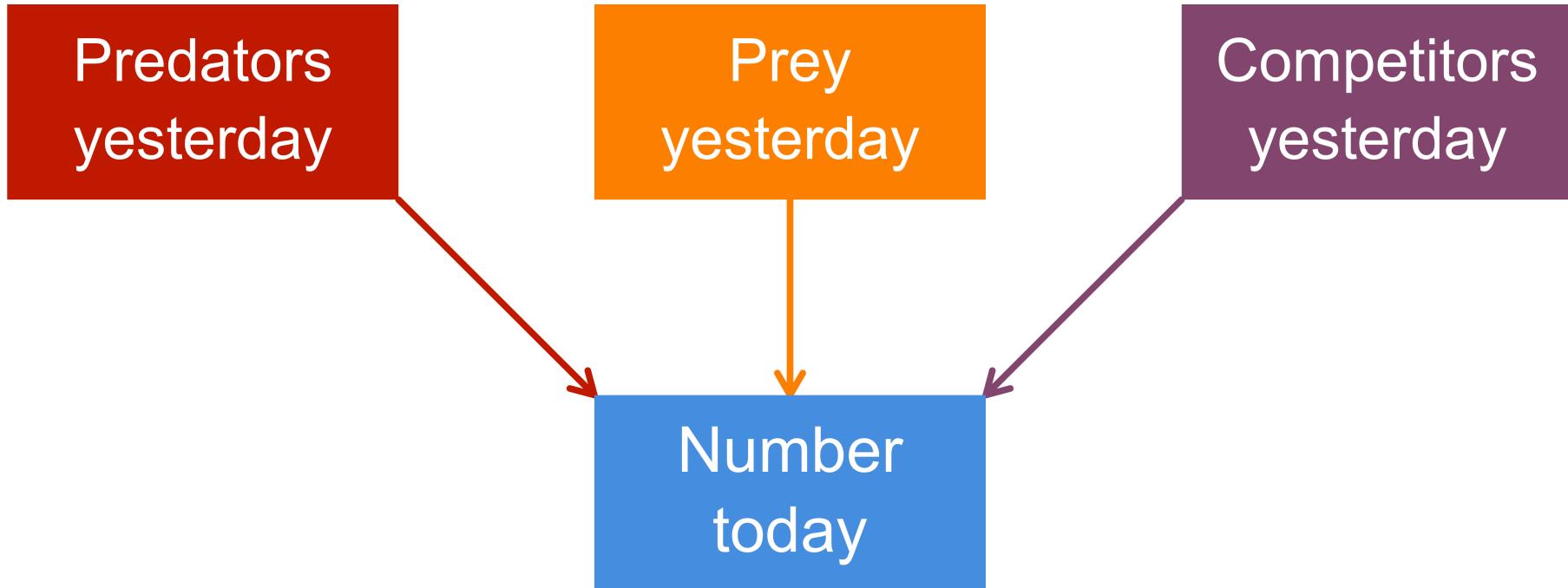
Drivers of community dynamics

Number today is a function of the number yesterday...



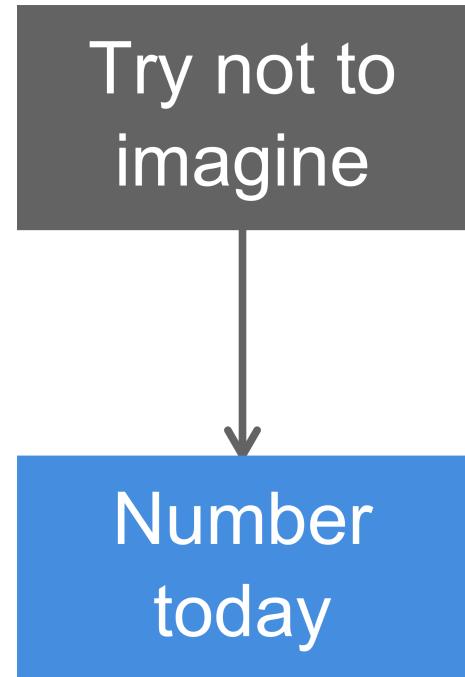
Drivers of community dynamics

and the number of predators, prey & competitors...



Drivers of community dynamics

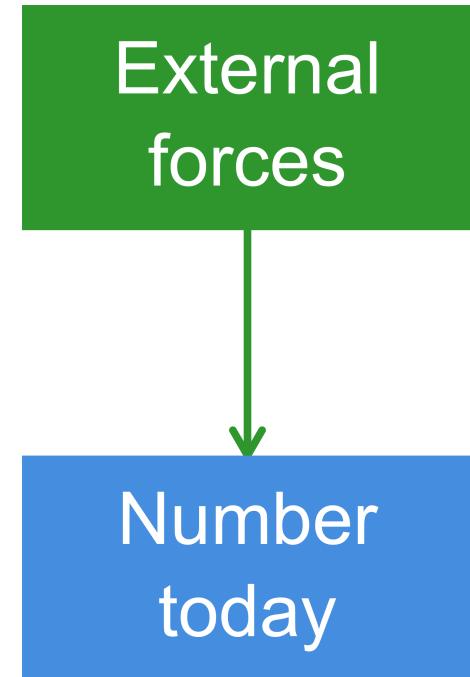
and parasites*, diseases, etc...



*C Wood, pers comm

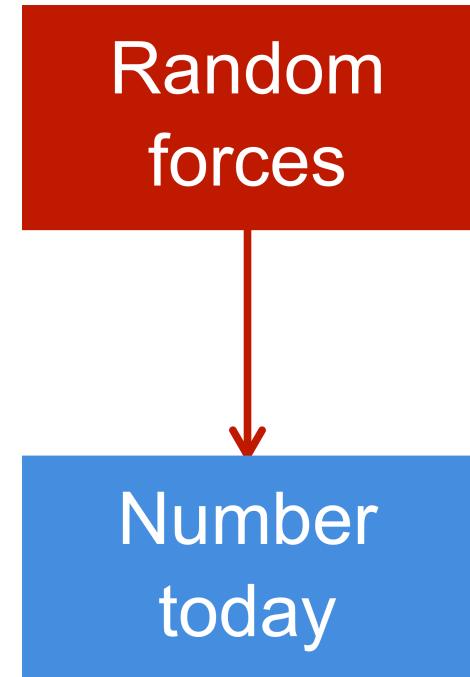
Drivers of community dynamics

and *known* external forces...



Drivers of community dynamics

and *unknown* random forces



Model for community dynamics

$$x_{i,t} = r_{max,i} + \underbrace{\sum_{j=1}^N b_{i,j} x_{j,t}}_{\text{species interactions}} + \underbrace{\sum_{k=1}^P c_{i,k} z_{k,t-h}}_{\text{external drivers}} + \underbrace{w_t}_{\text{random stuff}}$$

(in log space)

What proportion of the total variance in a community comes from species interactions?

Model for community dynamics

$$\mathbf{x}_t = \mathbf{r} + \mathbf{B}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{z}_{t-h} + \mathbf{w}_t$$

$$\mathbf{w}_t \sim \text{MVN}(\mathbf{0}, \mathbf{Q})$$

(in log space with matrix notation)

First we need to estimate these matrices

Existing R packages

{**dlm**}, {**vars**}, {**MARSS**}

Code-your-own languages

JAGS, Stan, TMB

E. E. Holmes, M. D. Scheuerell, and E. J. Ward

Analysis of multivariate time
series using the MARSS package

version 3.11.7

May 19, 2023

NOAA Fisheries and USGS WA Cooperative Fish and
Wildlife Research Unit
Seattle, WA, USA

How are we going to calculate the proportions?

Recall for a single population

$$\text{Var}(popn) = \frac{\text{Var}(env)}{1 - b^2}$$

Recall for a single population

$$\text{Var}(popn) = \frac{\text{Var}(env)}{1 - b^2}$$

(via algebra) the proportion owing to density dependence is

$$\frac{\text{Var}(popn) - \text{Var}(env)}{\text{Var}(popn)} = b^2$$

Model for community dynamics

$$\mathbf{x}_t = \mathbf{r} + \mathbf{B}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{z}_{t-h} + \mathbf{w}_t$$

$$\mathbf{w}_t \sim \text{MVN}(0, \mathbf{Q})$$

What is the stationary (co)variance?

Stationary variance for a community

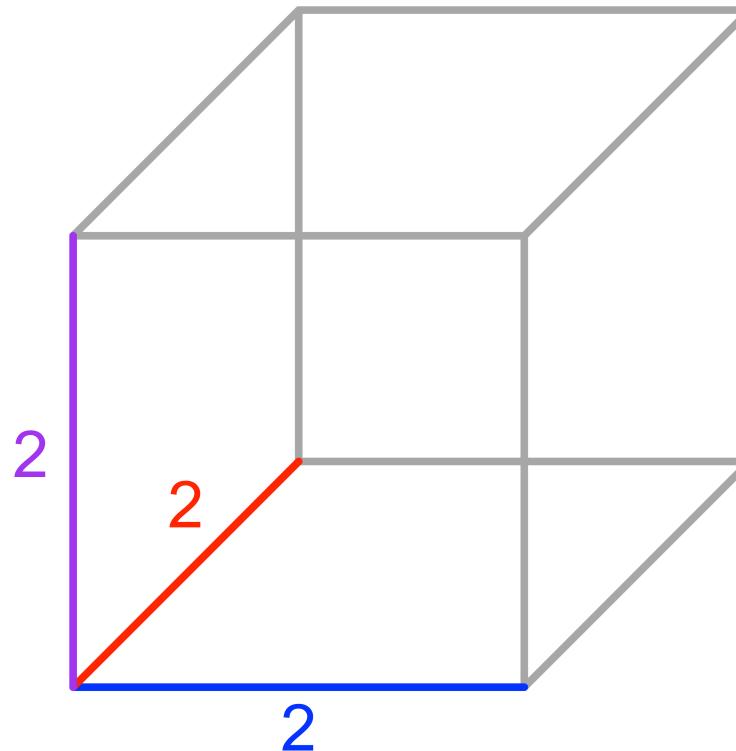
$$\text{Var}(\mathbf{x}_t) = \mathbf{B}\text{Var}(\mathbf{x}_t)\mathbf{B}^\top + \mathbf{C}\text{Var}(\mathbf{z}_{t-h})\mathbf{C}^\top + \mathbf{Q}$$

This isn't going to be easy

We need some help

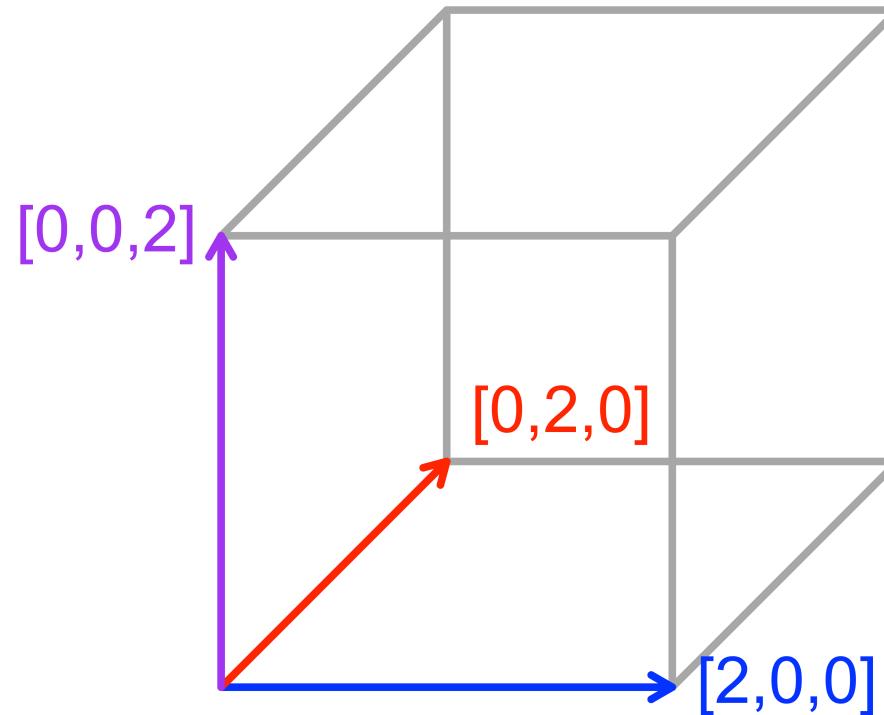
Do you ever reflect on how awesome geometry is?

"Wow—A cube whose sides are all 2 units has a volume of 8 cubic units."



And then did you ever think?

"You know, we can define this cube with 3 vectors for the cube's vertices."



Oh. My. God. 😱

If we combine the 3 vectors into a matrix, the *determinant* gives the volume!

$$\det \begin{bmatrix} 2 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 2 \end{bmatrix} = 8$$

Matrix determinants!

*Helping
mathematicians
since 1812*



For a whole community

Proportion attributable to species interactions

$$\frac{\det[\text{Var}(\textit{comm}) - \text{Var}(\textit{env})]}{\det[\text{Var}(\textit{comm})]} = \det(\mathbf{B})^2$$

What proportion of the total variance in a community comes from species interactions?

A previous meta-analysis found

| moths in the United Kingdom (11-54%)

A previous meta-analysis found

moths in the United Kingdom (11-54%)

nearshore fishes & inverts in the UK (2-15%)

A previous meta-analysis found

moths in the United Kingdom (11-54%)

nearshore fishes & inverts in the UK (2-15%)

birds in New Hampshire (1-17%)

A previous meta-analysis found

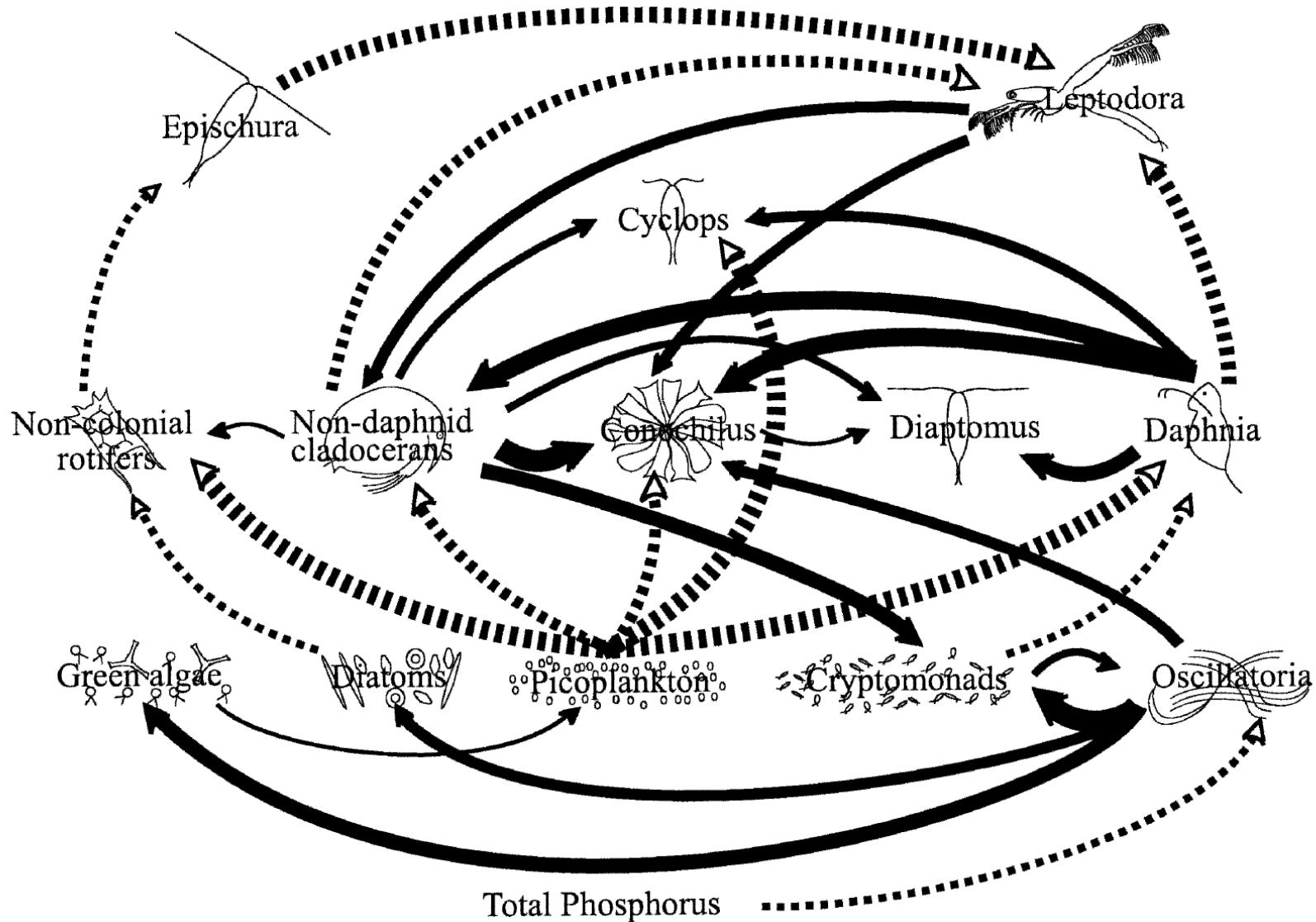
moths in the United Kingdom (11-54%)

nearshore fishes & inverts in the UK (2-15%)

birds in New Hampshire (1-17%)

rodents in New Mexico (11-37%)

How do these estimates compare
to freshwater plankton communities?



Hampton et al (2006) L&O

Food web studies of plankton communities

Peter/Paul/Tues Lakes in Michigan (Ives et al 2003)

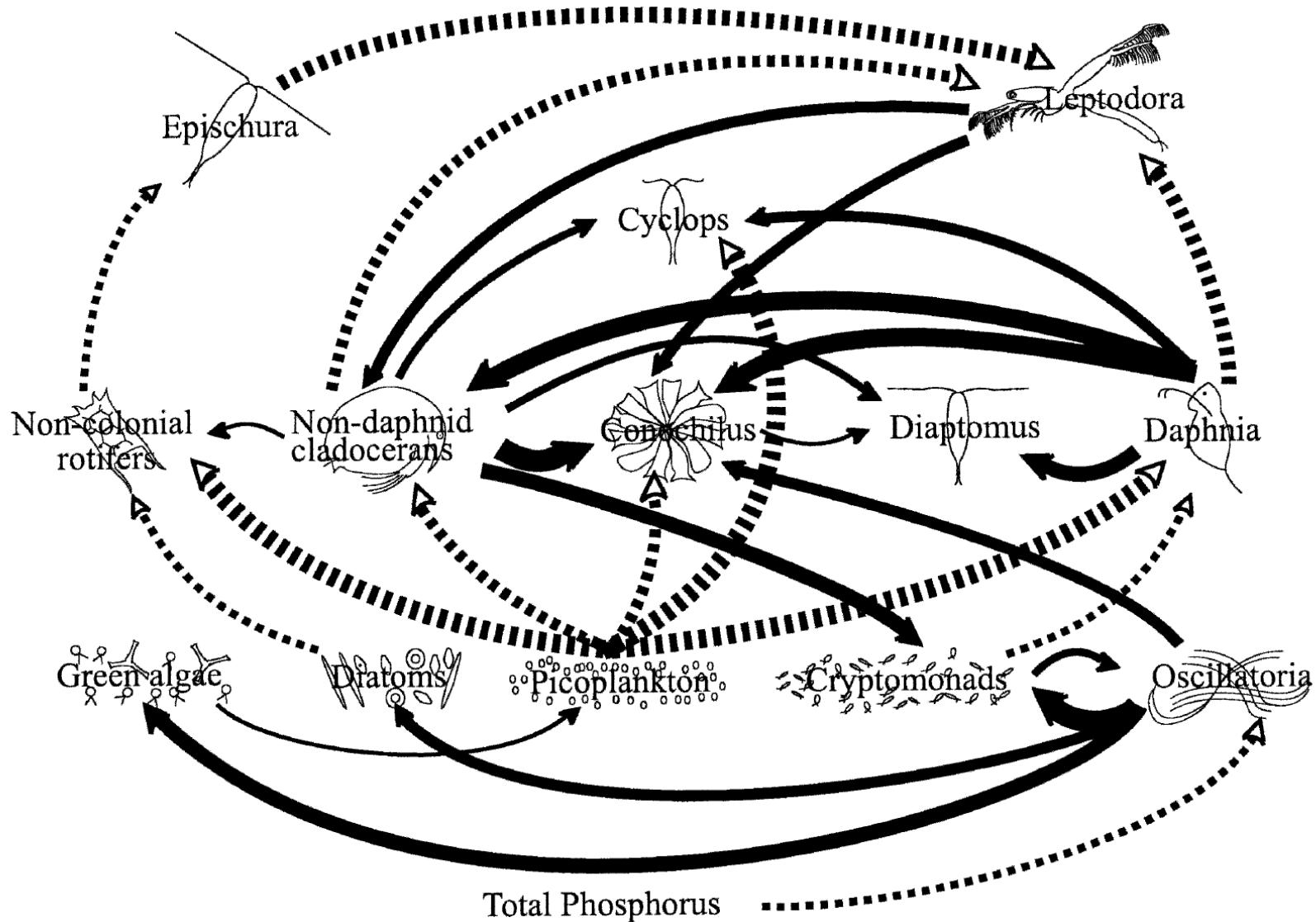
Lake Washington in Washington (Hampton et al 2006)

Okanagan Lake in British Columbia (Schindler et al 2012)

Lake Müggelsee in Germany (Gsell et al 2016)

Lake Aleknagik in Alaska (Carter et al 2017)

**Species interactions in these lakes accounted for
no more than 3% of the total variation**



Hampton et al (2006) L&O

Are *particular interactions* more important?

intra- versus inter-specific?

top-down or bottom-up?

Sensitivity of the proportion

to a change in the effect of species j on species i

$$\frac{\partial \det(\mathbf{B})^2}{\partial \mathbf{B}_{ij}} = \left[2 \det(\mathbf{B})(\mathbf{B}^{-1})^\top \right]_{ij}$$

Sensitivity of the proportion

Density-dependent effects generally most important

Competition plays some role as well

Bottom-up & top-down interactions less important

Are all of these communities *stable*?

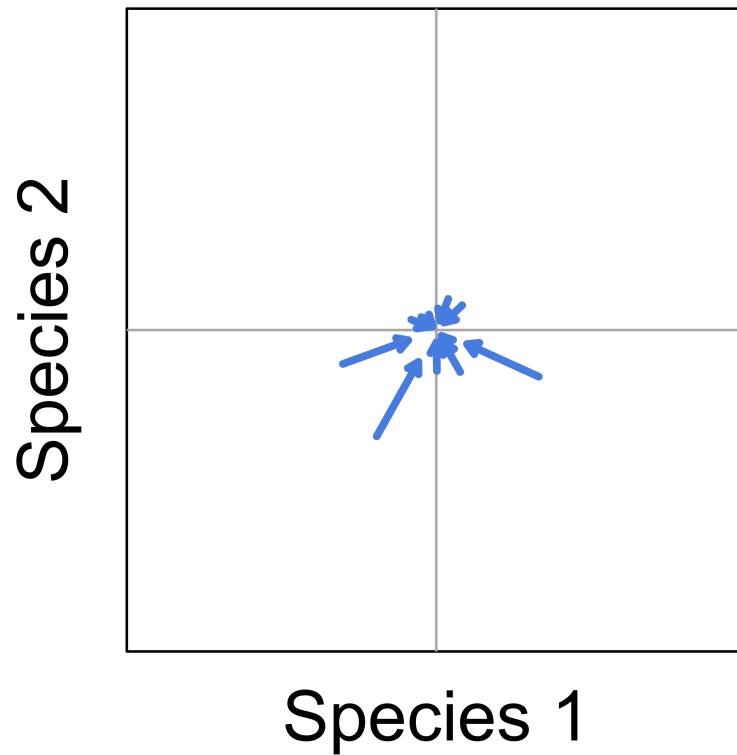
Reactivity

Small perturbations may grow before decaying again

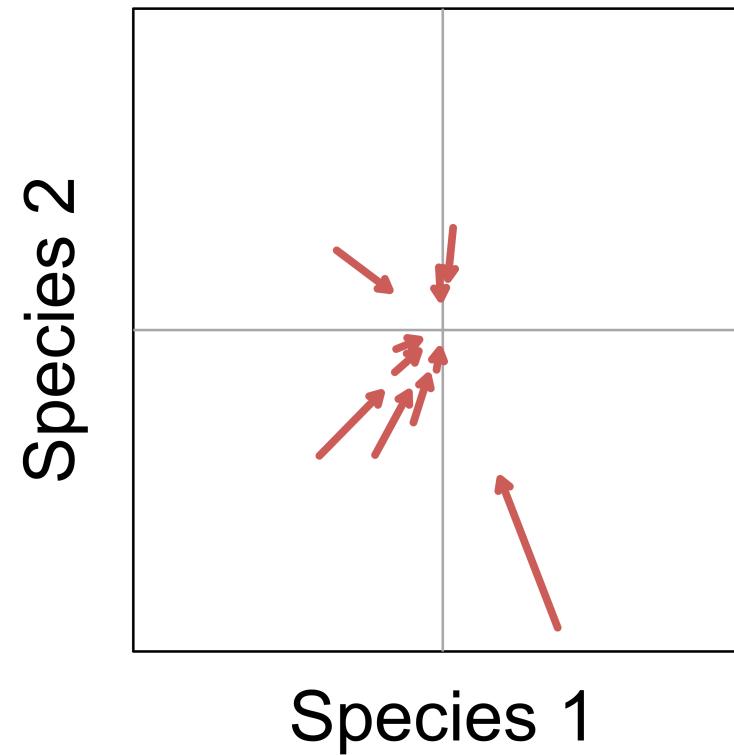
If so, the community is *reactive*

Example of reactivity

Less reactive



More reactive



If $\nu > 0$ the community is reactive

$$\nu = \log \sigma_{\max}(\mathbf{B})$$

$$= \log \|\mathbf{B}\|_2$$

$$= \log \sqrt{\lambda_{\max}(\mathbf{B}^\top \mathbf{B})}$$

(I'm happy to talk about this later)

Some of these are reactive

Peter/Paul/Tues Lakes in Michigan (Ives et al 2003)

Lake Washington in Washington (Hampton et al 2006)

Okanagan Lake in British Columbia (Schindler et al 2012)

Lake Müggelsee in Germany (Gsell et al 2016)

Lake Aleknagik in Alaska (Carter et al 2017)

Predation

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Acknowledgments

Elizabeth "Eli" Holmes (NOAA)

Eric Ward (NOAA)



learn more here