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

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School of Aquatic and Fishery Sciences
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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

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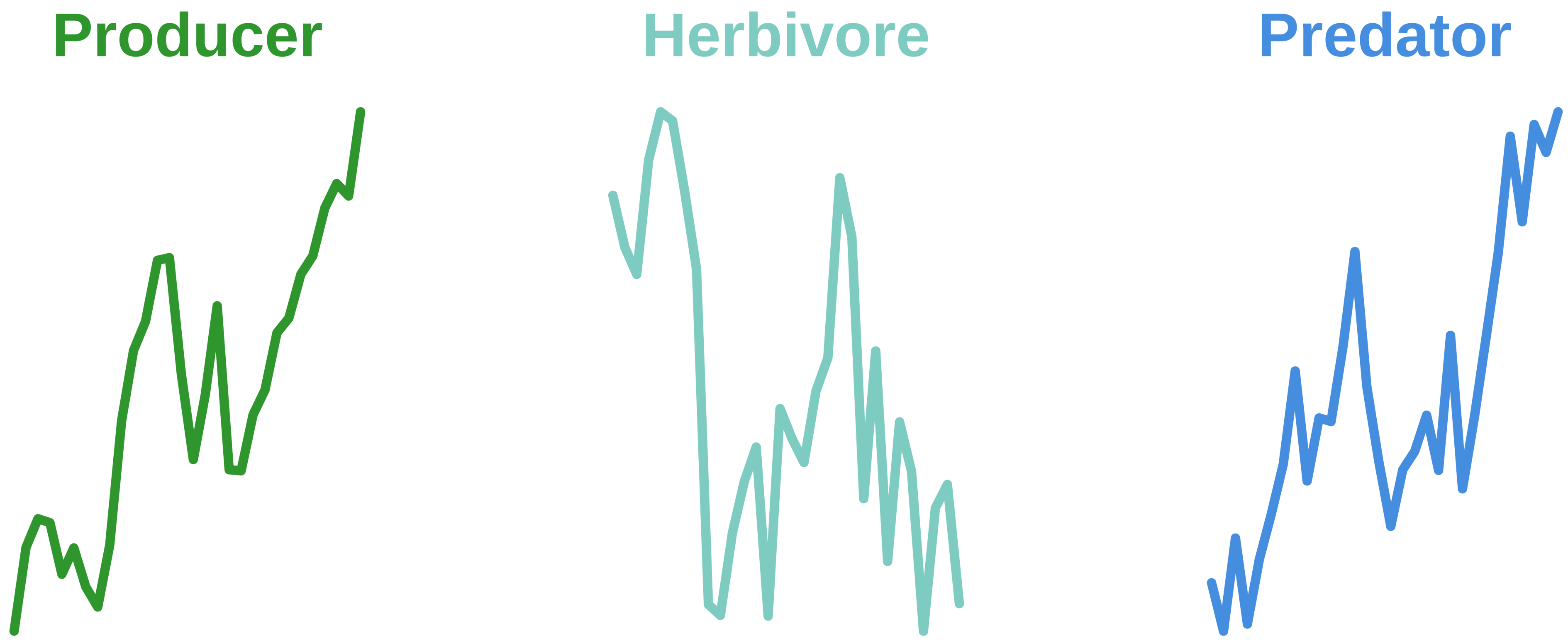
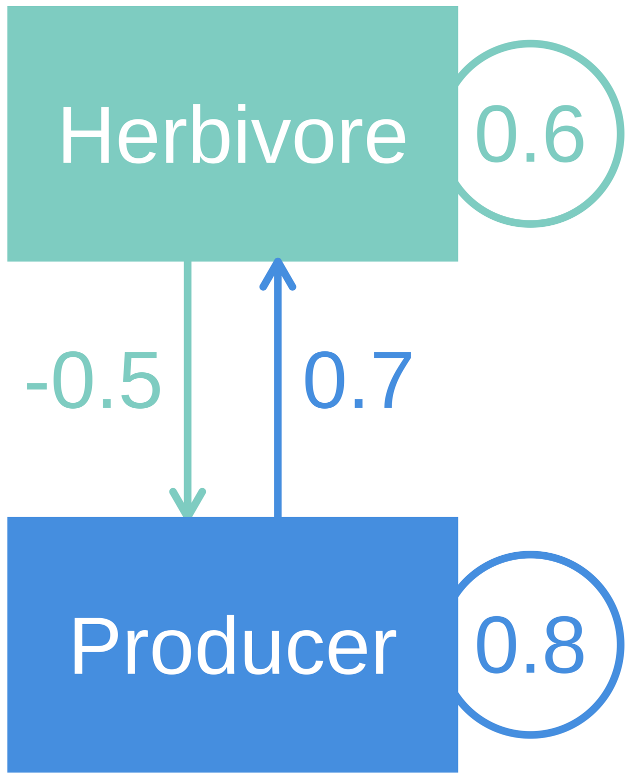
[4]*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California 93101-5504 USA*

We can use time series of abundance...

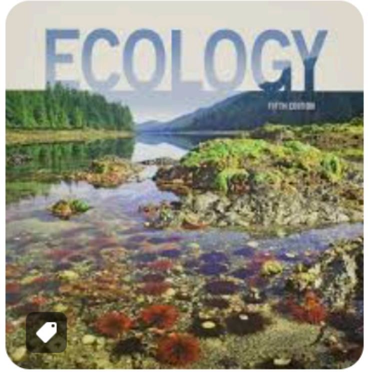


to get intra- & interspecific interaction strengths



How does one do this?!

Let's begin with a model for population size



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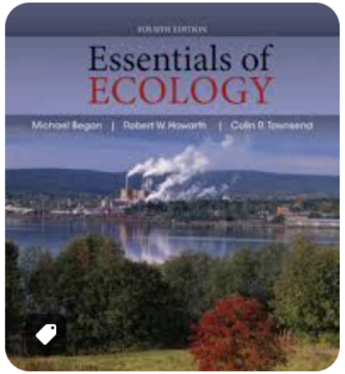
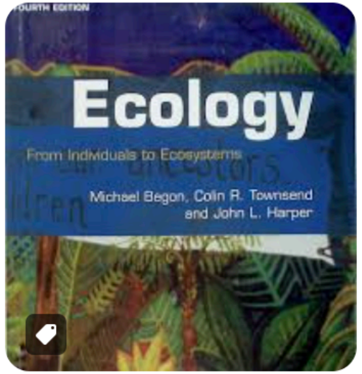
Bowman, William D., Ha...



Wiley

Essentials of Ecology [...



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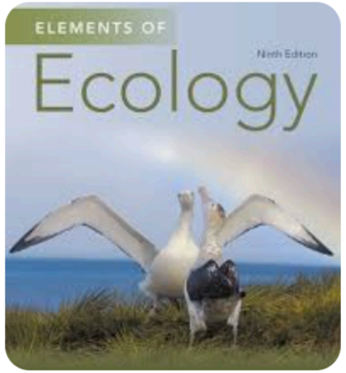
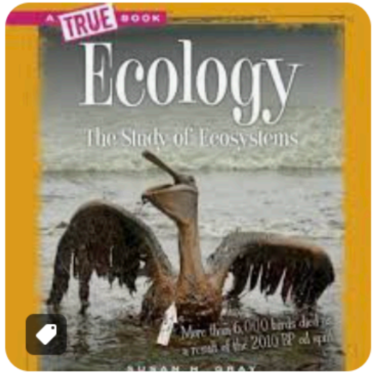
Ecology: From Individua...



Pearson

Elements of Ecology



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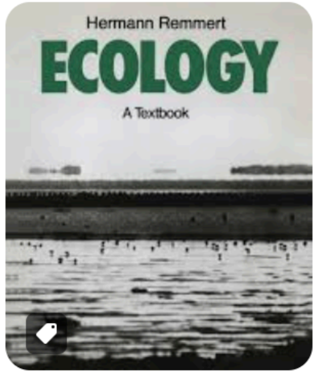
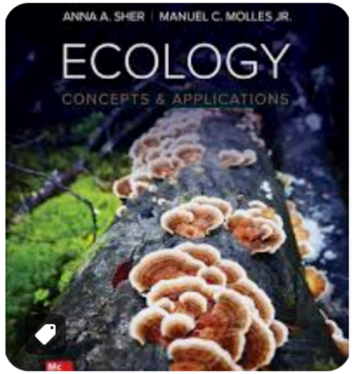
Ecology: The Study of Ec...



SpringerLink

Ecology: A Textbook...



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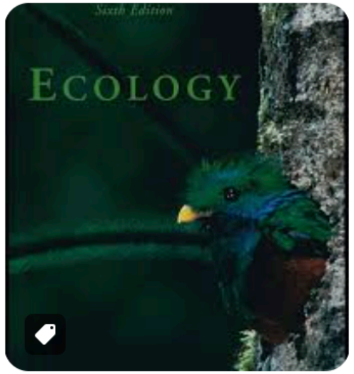
Ecology: Concepts and ...



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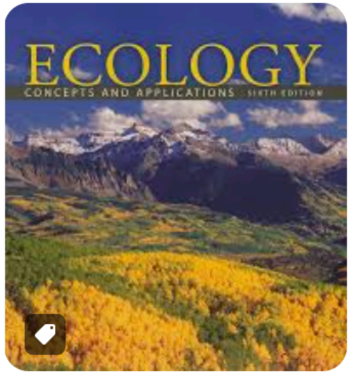
9780321507433: Krebs,...



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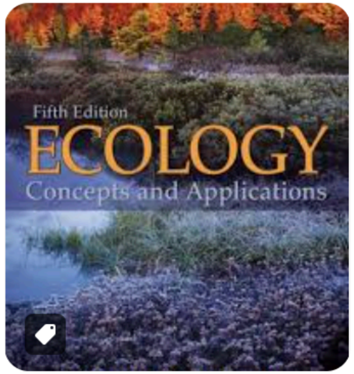
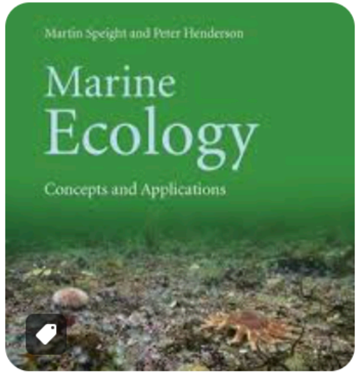
Amazon.com: Ecology: ...



Better World Books

Ecology: Concepts and ...



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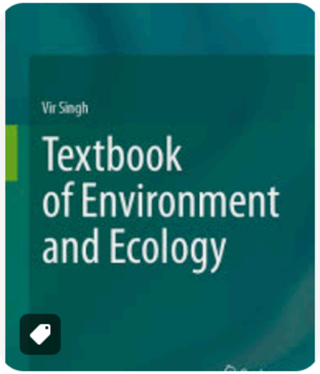
Marine Ecology: Conce...



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Textbook of Environ...

Assumptions 🤔

> The size of a population can change over time
>
> Those changes are density dependent

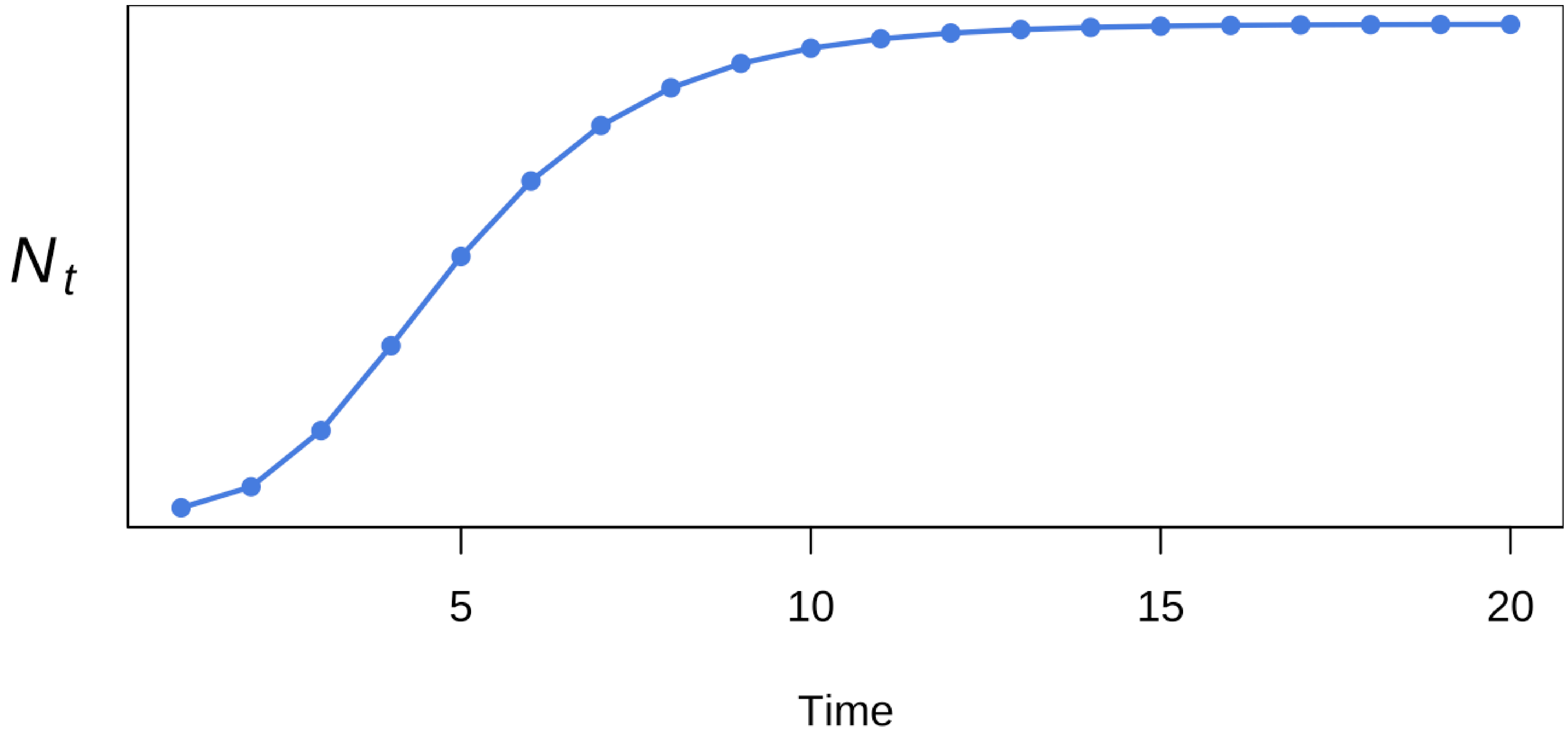
🤓 Discrete-time Gompertz model

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

🙋 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

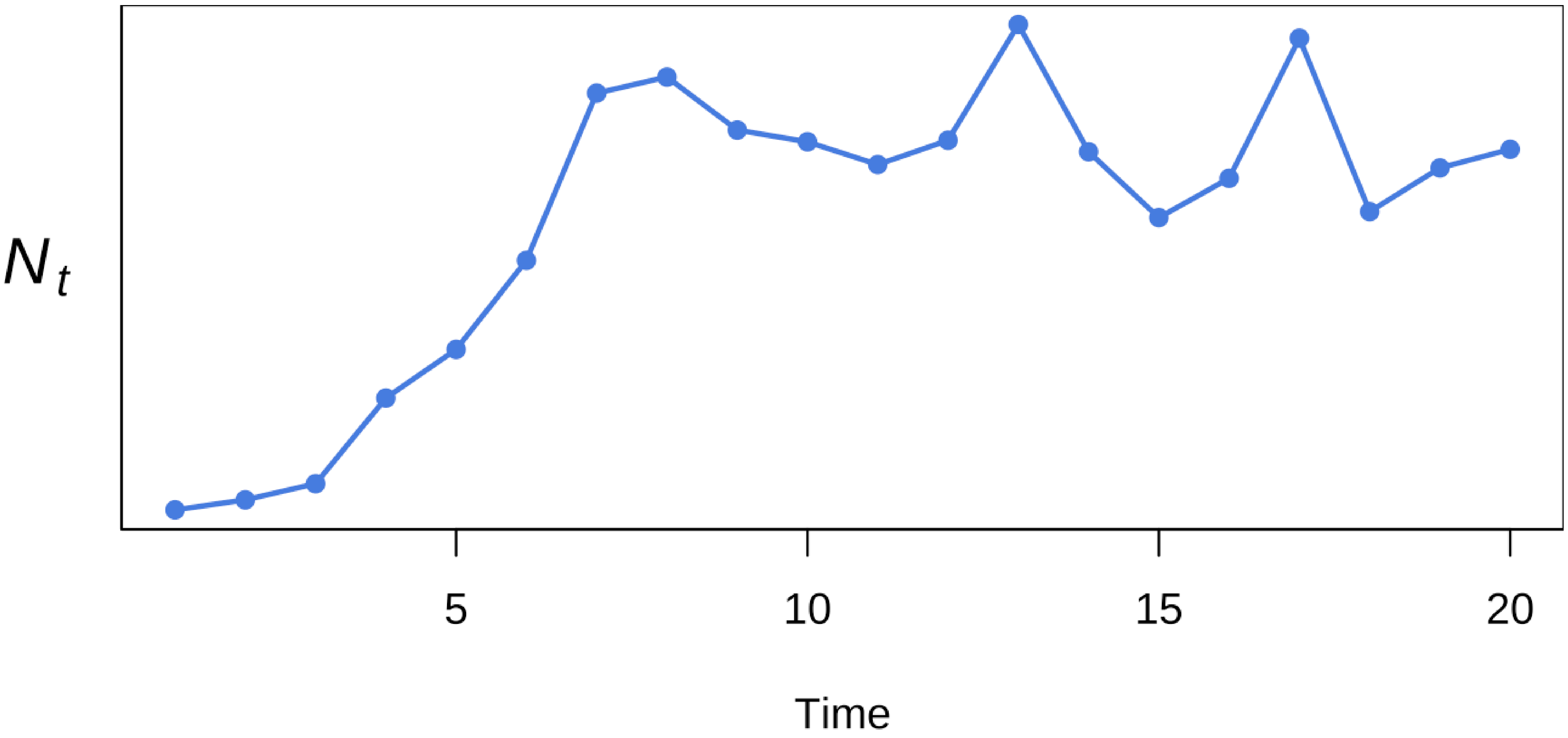
🤓 Discrete-time Gompertz model

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

🙋 In other words

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

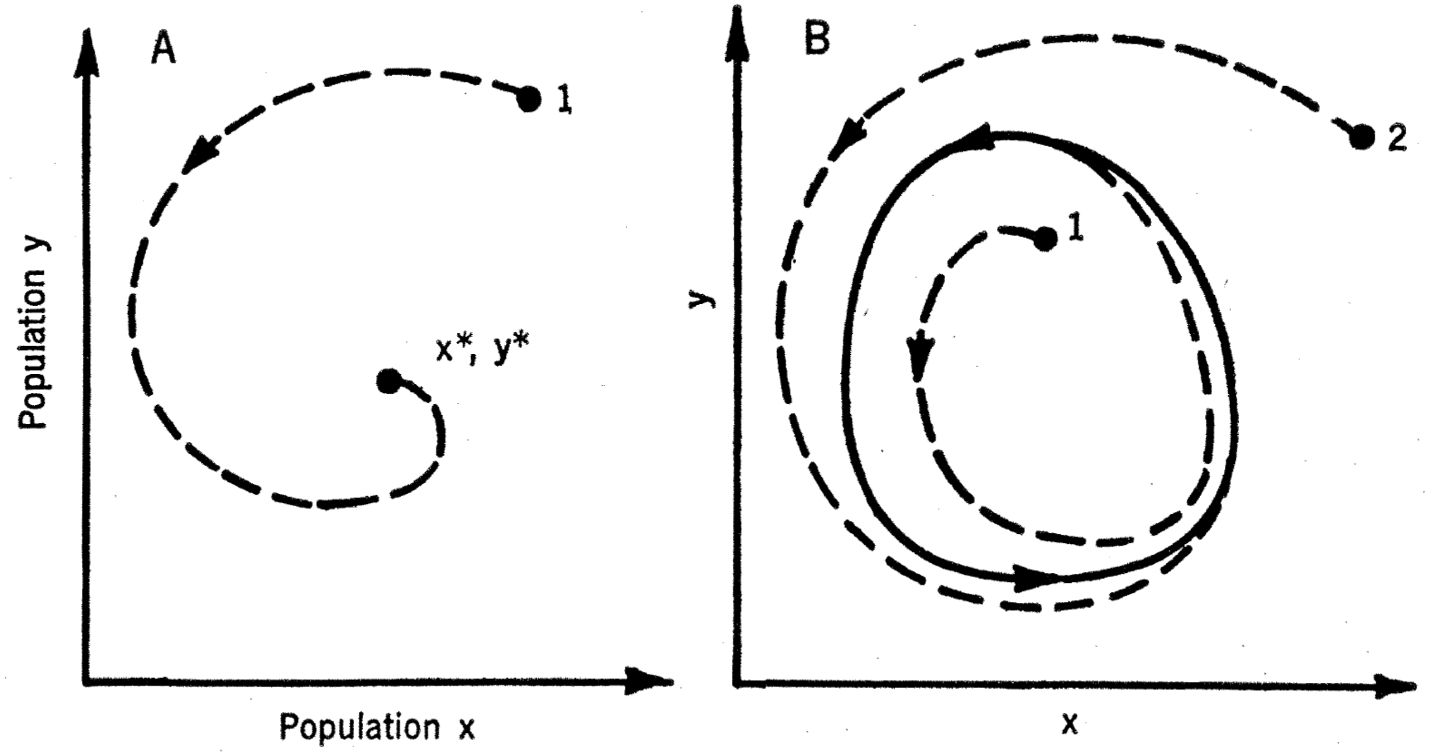
Example of stochastic Gompertz dynamics



Quantifying population stability

Population equilibria

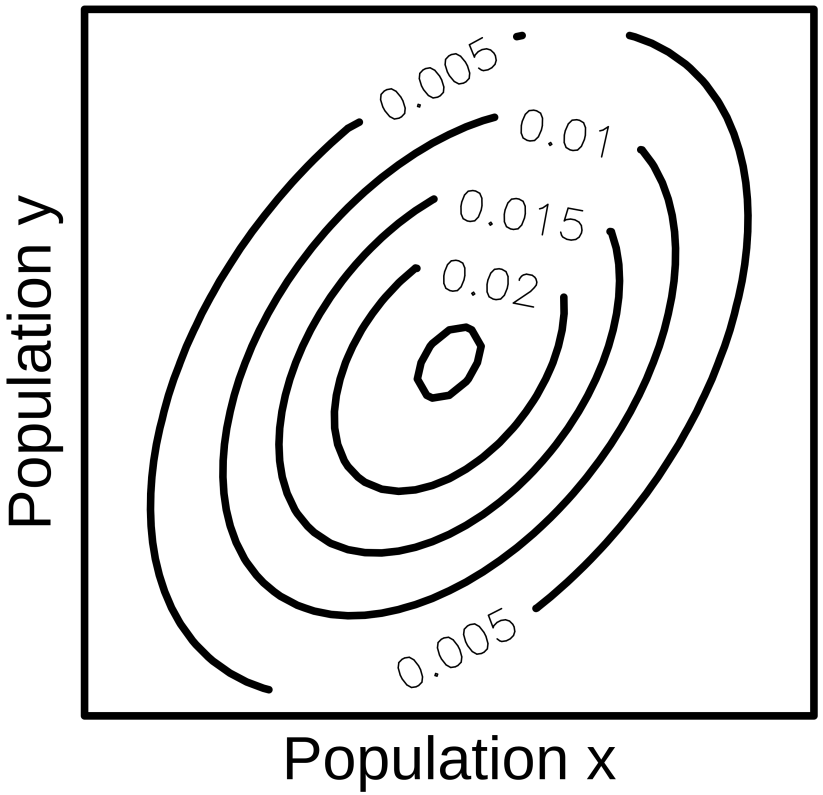
In deterministic models, equilibria are a point or stable limit cycle



May (1972) *Science*

Population equilibria

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



Another look at our Gompertz model

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

Another look at our Gompertz model

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

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

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

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

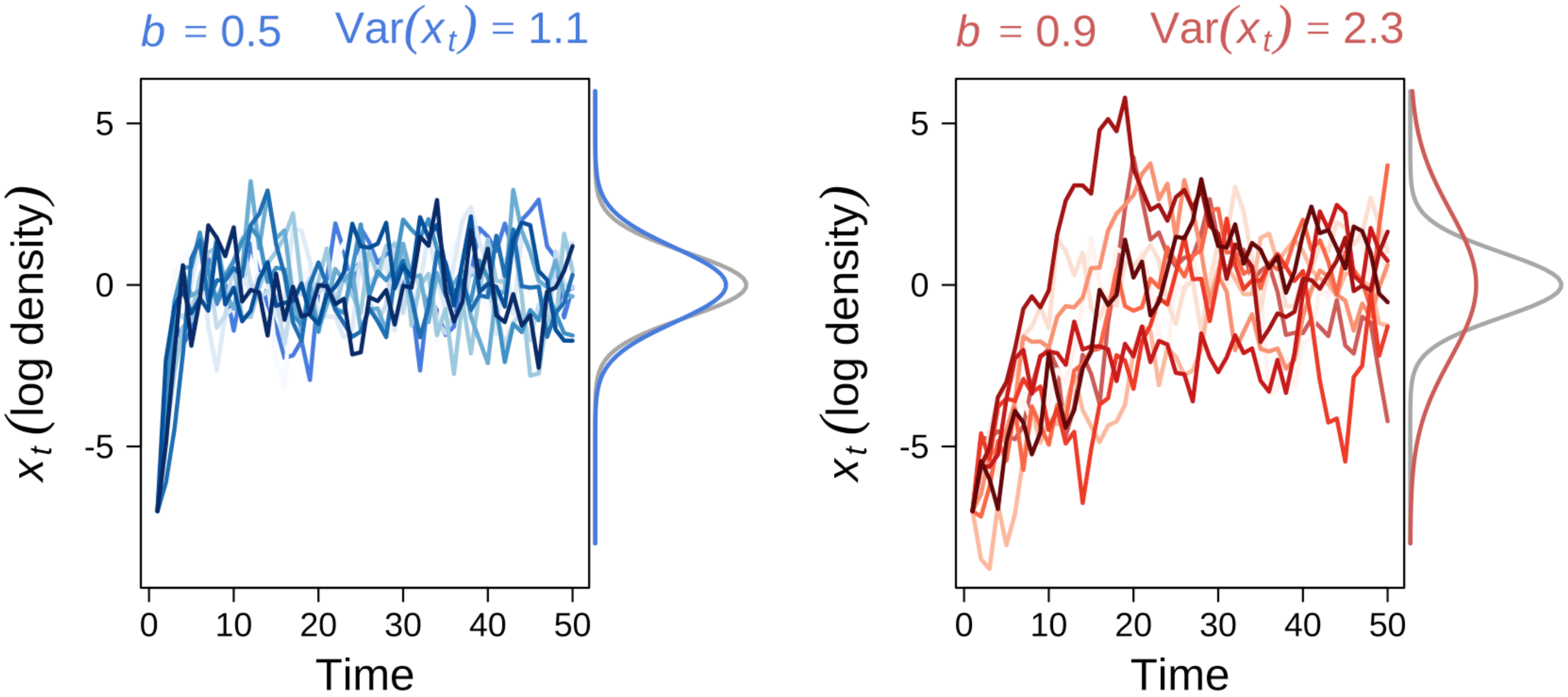
$$stability = \frac{1}{\mathrm{Var}(popn)} = \frac{DD}{\mathrm{Var}(env)}$$

implying a population is more stable when

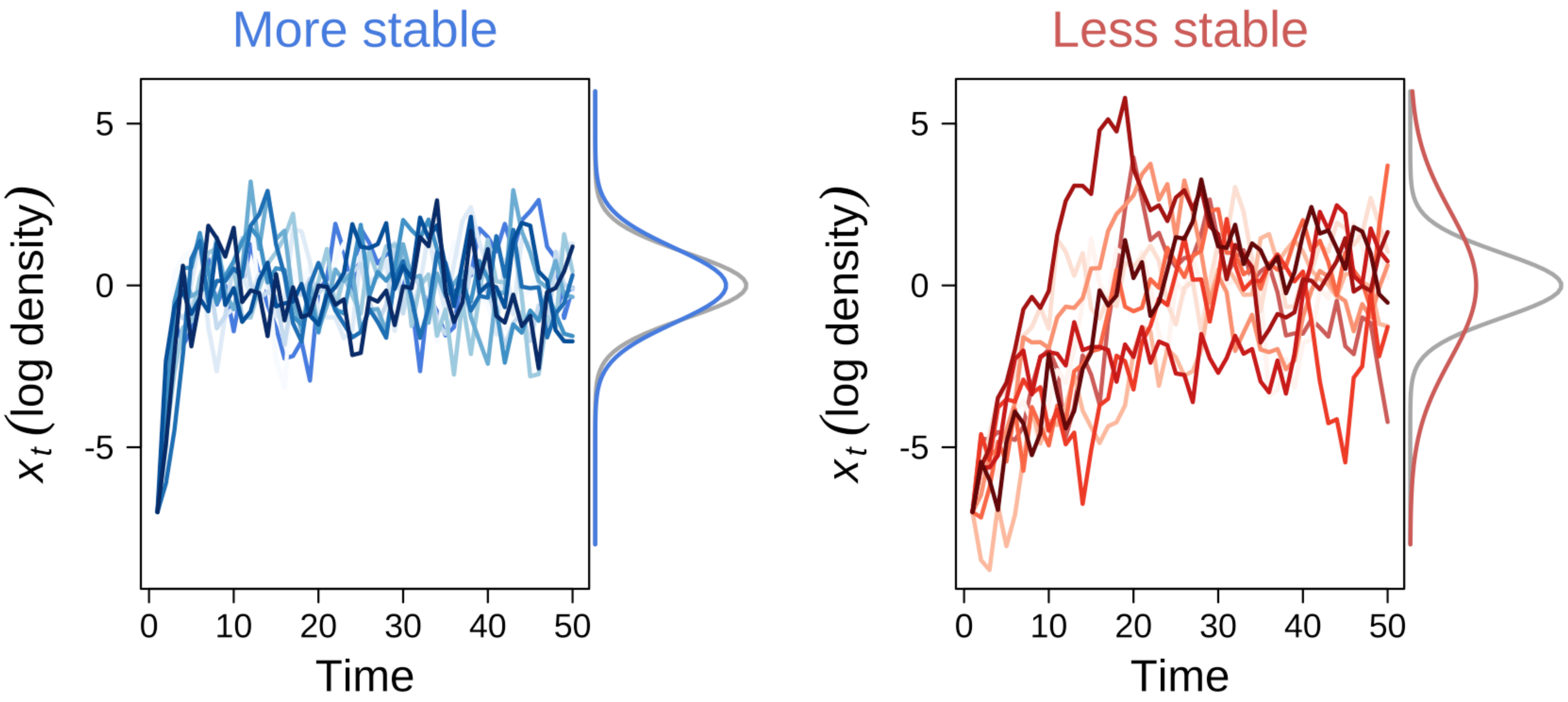
the strength of density-dependence increases

and the environment is less variable

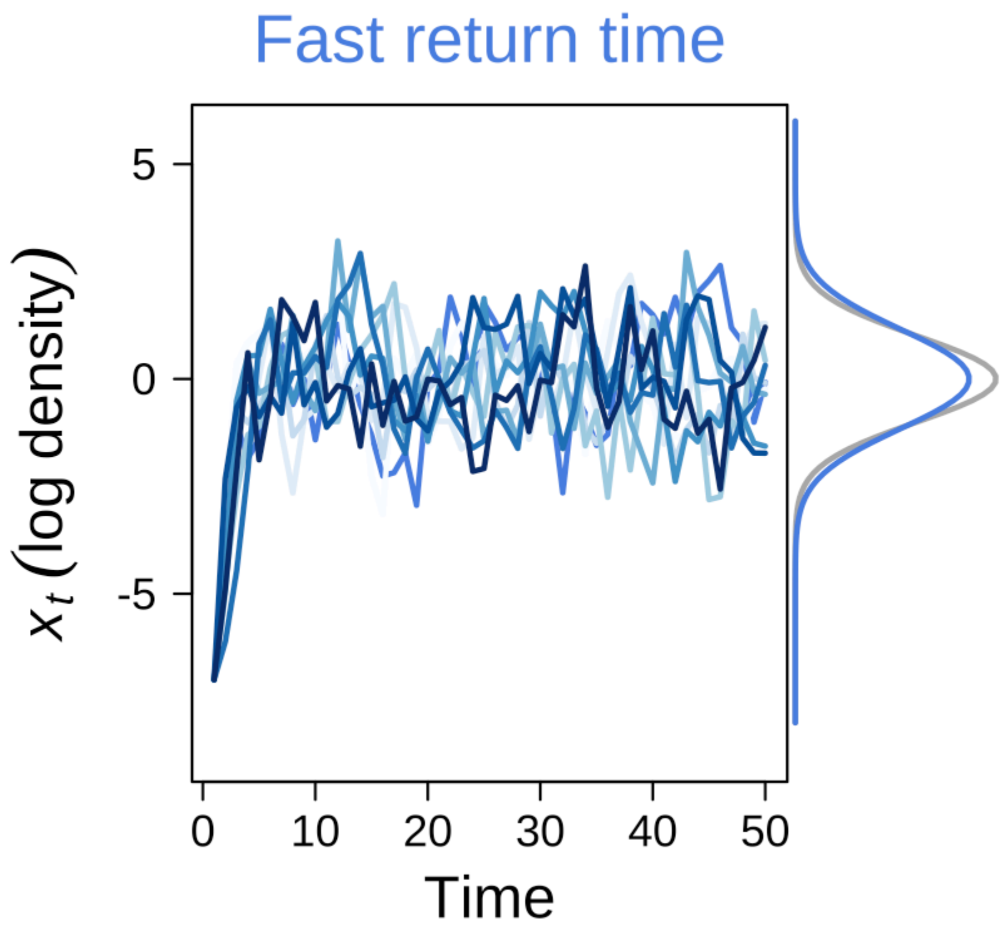
Populations within the same environment

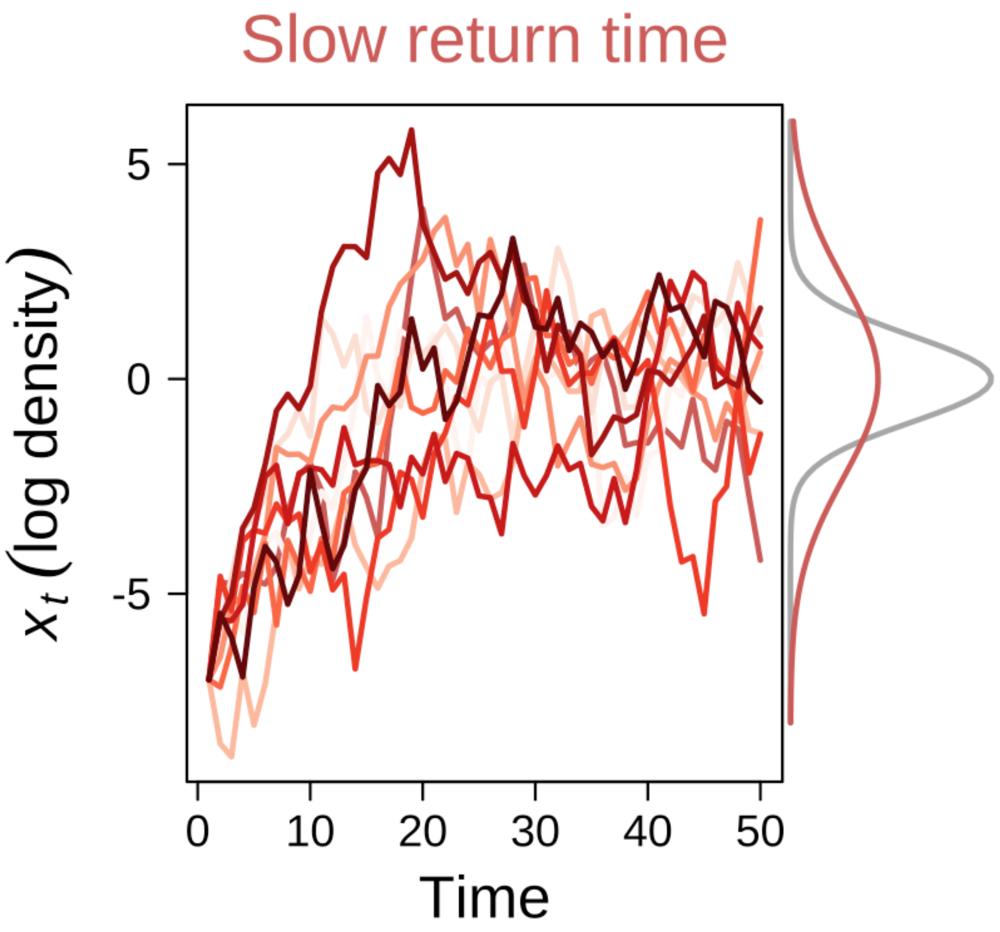


Populations within the same environment



Populations within the same environment

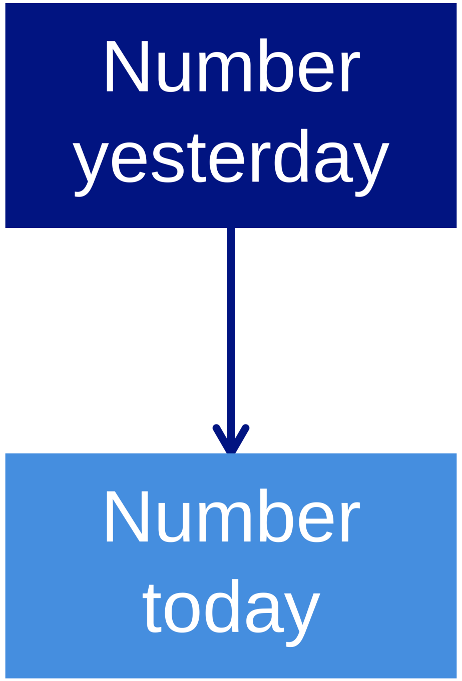




Changes in a community over time

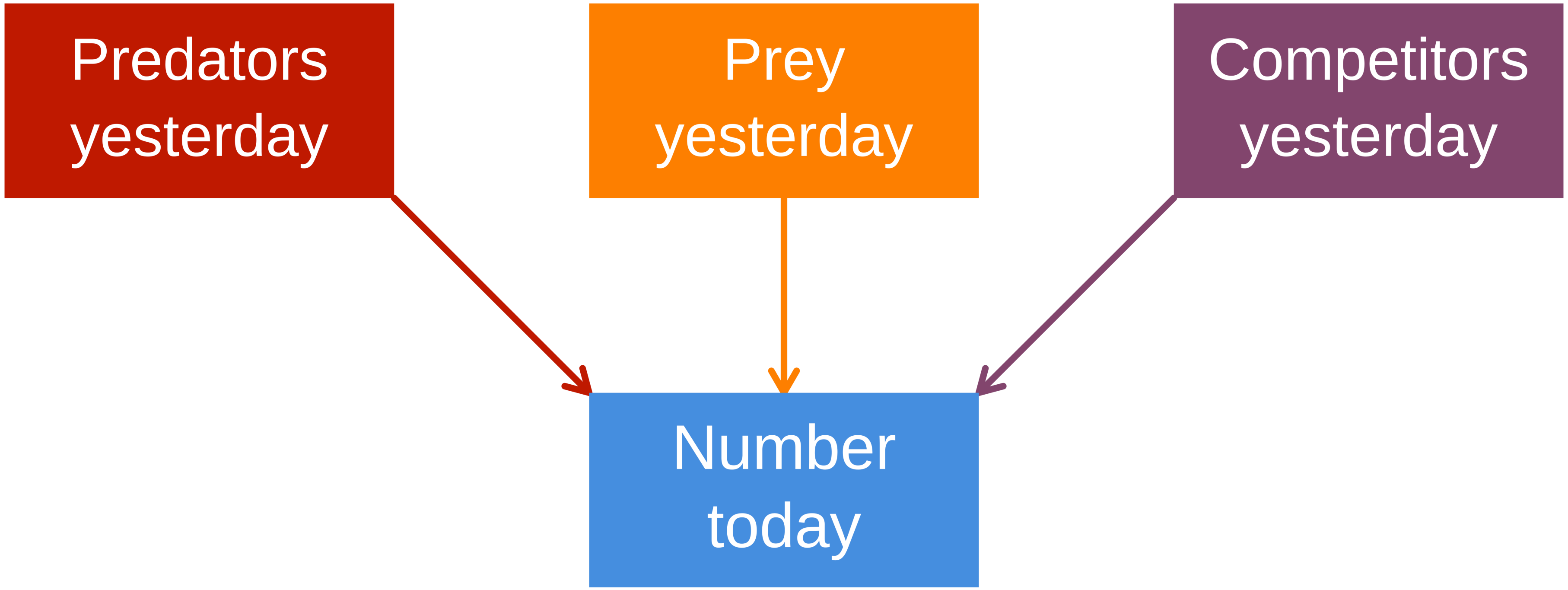
Drivers of community dynamics

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



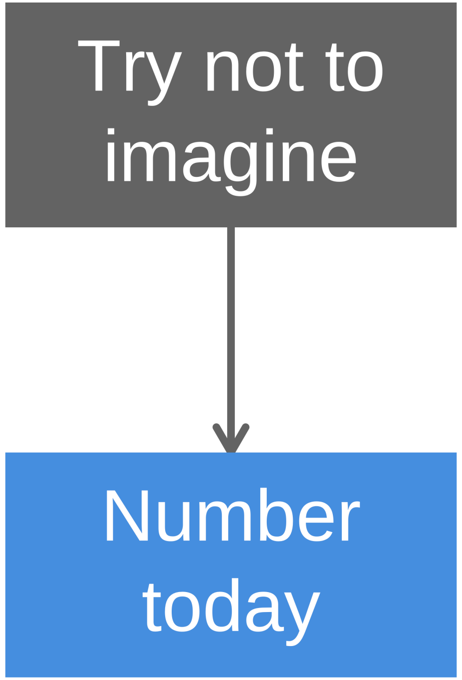
Drivers of community dynamics

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



Drivers of community dynamics

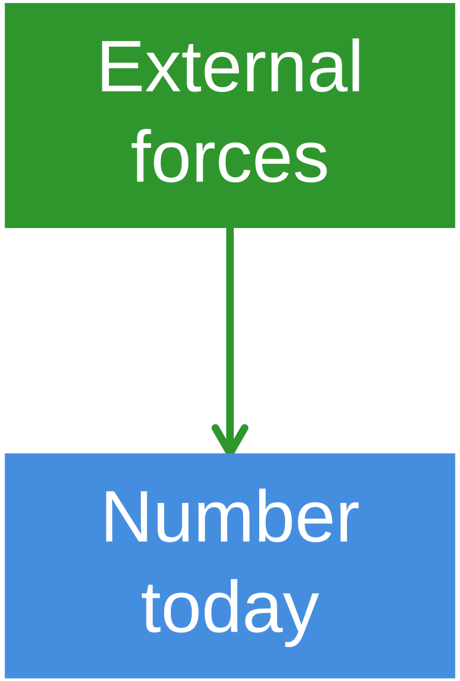
and parasites*, diseases, etc...



*C Wood, pers comm

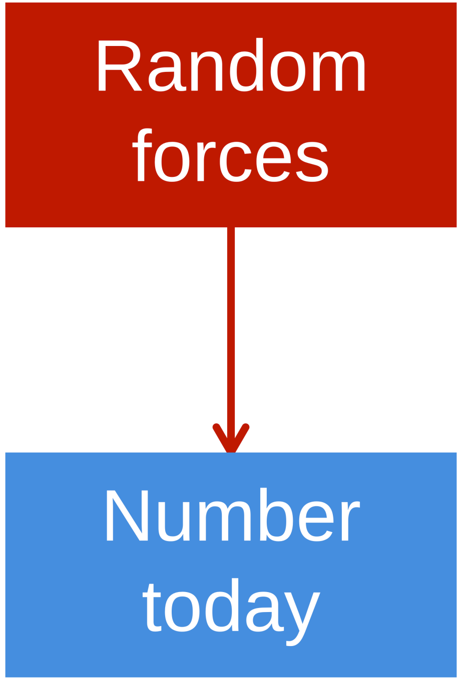
Drivers of community dynamics

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

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

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

(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

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

Recall for a single population

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

(via algebra) the proportion owing to density dependence is

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

Model for community dynamics

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

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

What is the stationary (co)variance?

Stationary variance for a community

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

Stationary variance for a community

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

There's no closed form solution!

Stationary variance for a community

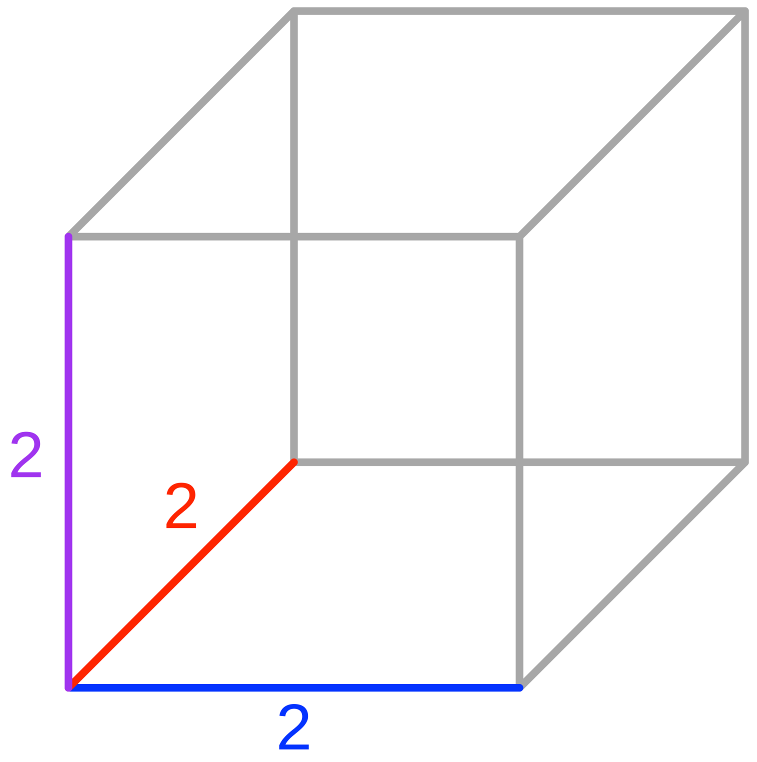
$$\mathrm{Var}(\mathbf{x}_t) = \mathbf{B}\mathrm{Var}(\mathbf{x}_t)\mathbf{B}^\top + \mathbf{C}\mathrm{Var}(\mathbf{z}_{t-h})\mathbf{C}^\top + \mathbf{Q}$$

How "big" are these matrices?

We need some help

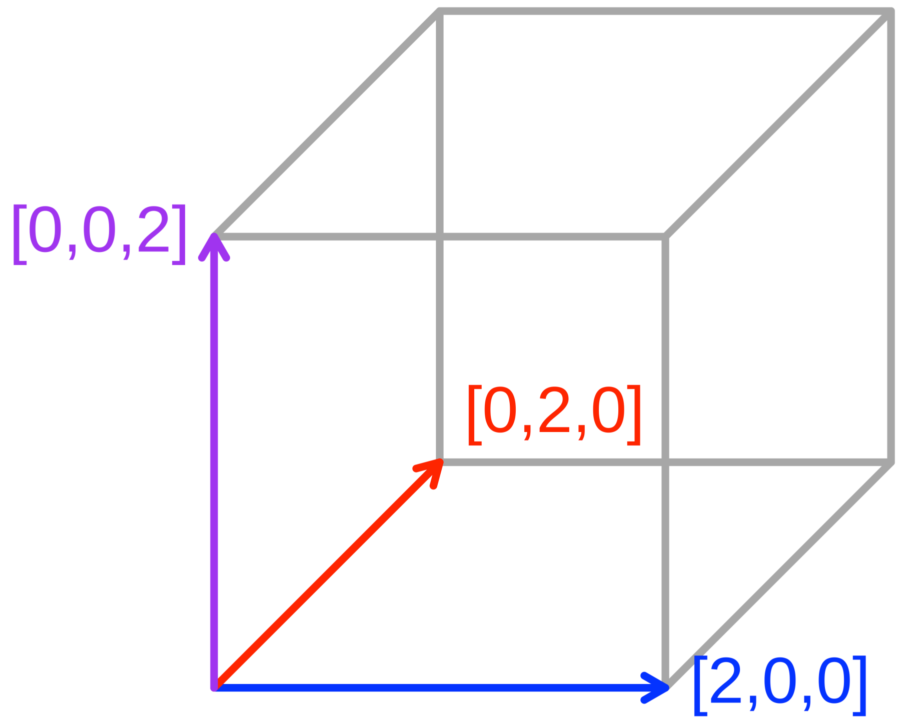
Do you ever reflect on how awesome geometry is?

"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

$$\frac{\det\left[\mathrm{Var}(comm) - \mathrm{Var}(env)\right]}{\det\left[\mathrm{Var}(comm)\right]} = \det(\mathbf{B})^2$$

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%)

Mutshinda et al (2009) *Proc R Soc B*

A previous meta-analysis found

> moths in the United Kingdom (11-54%)
>
> nearshore fishes & inverts in the UK (2-15%)

Mutshinda et al (2009) *Proc R Soc B*

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%)

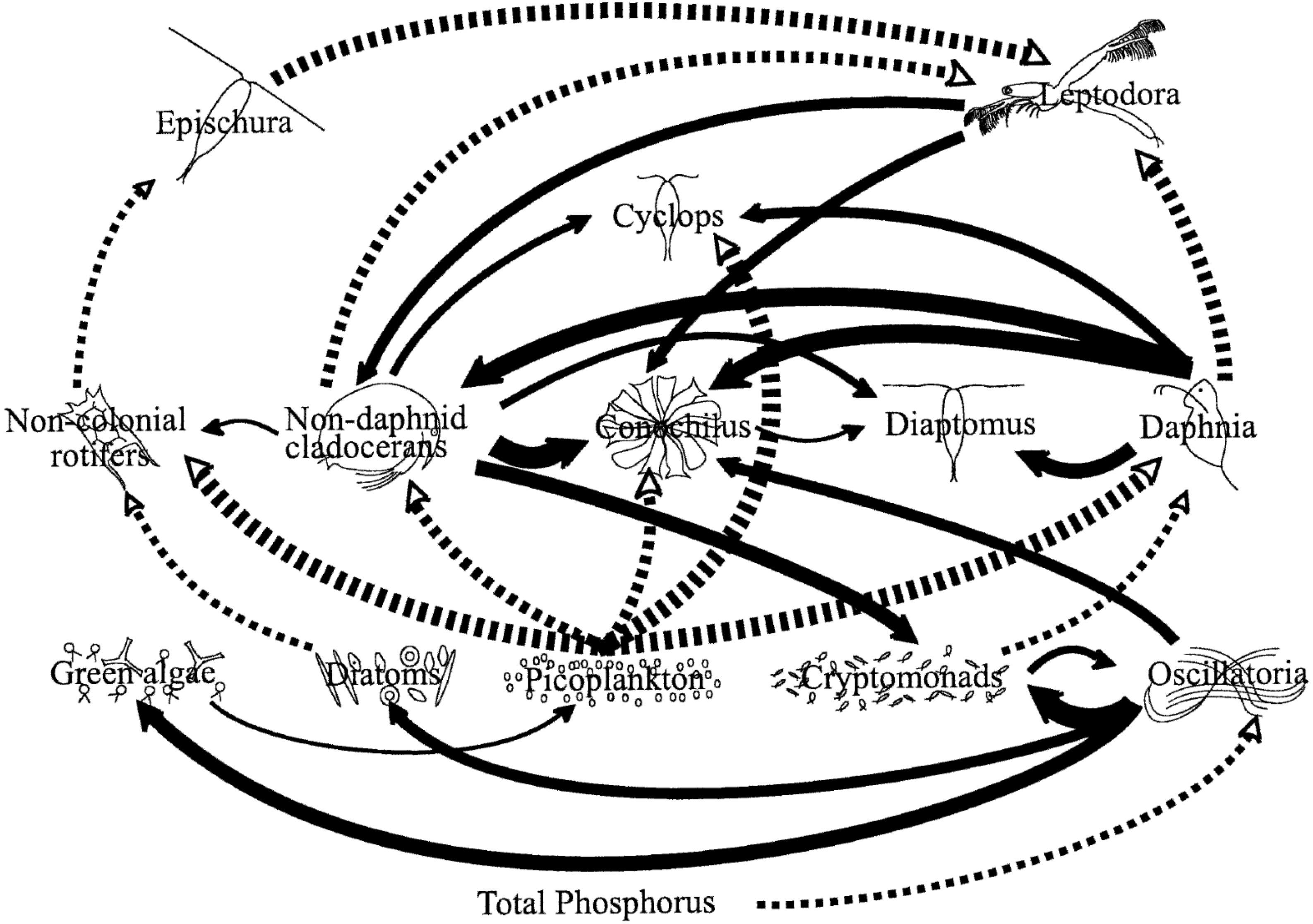
Mutshinda et al (2009) *Proc R Soc B*

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%)

Mutshinda et al (2009) *Proc R Soc B*

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)

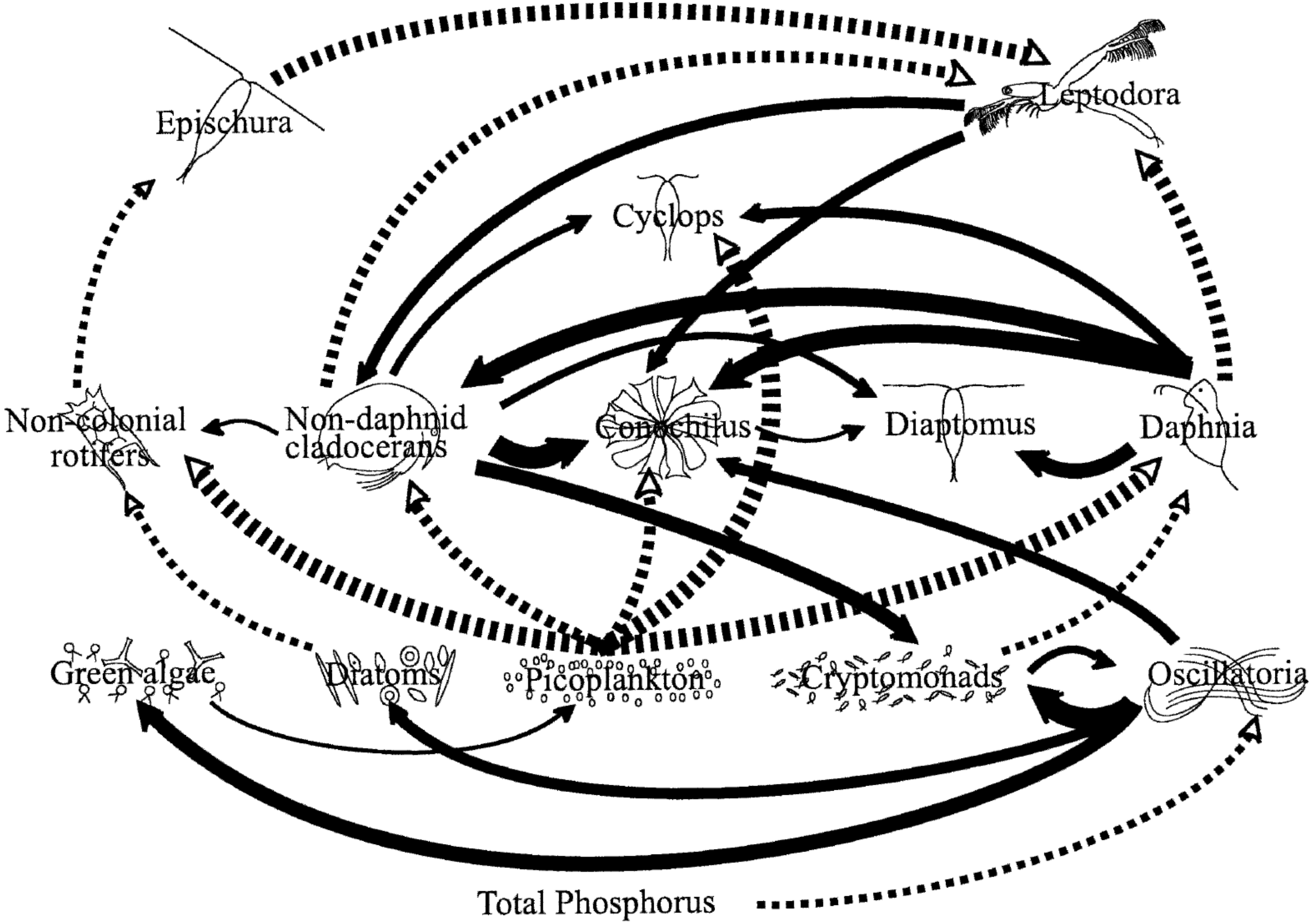
Lake Washington in Washington (Hampton et al 2006)

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

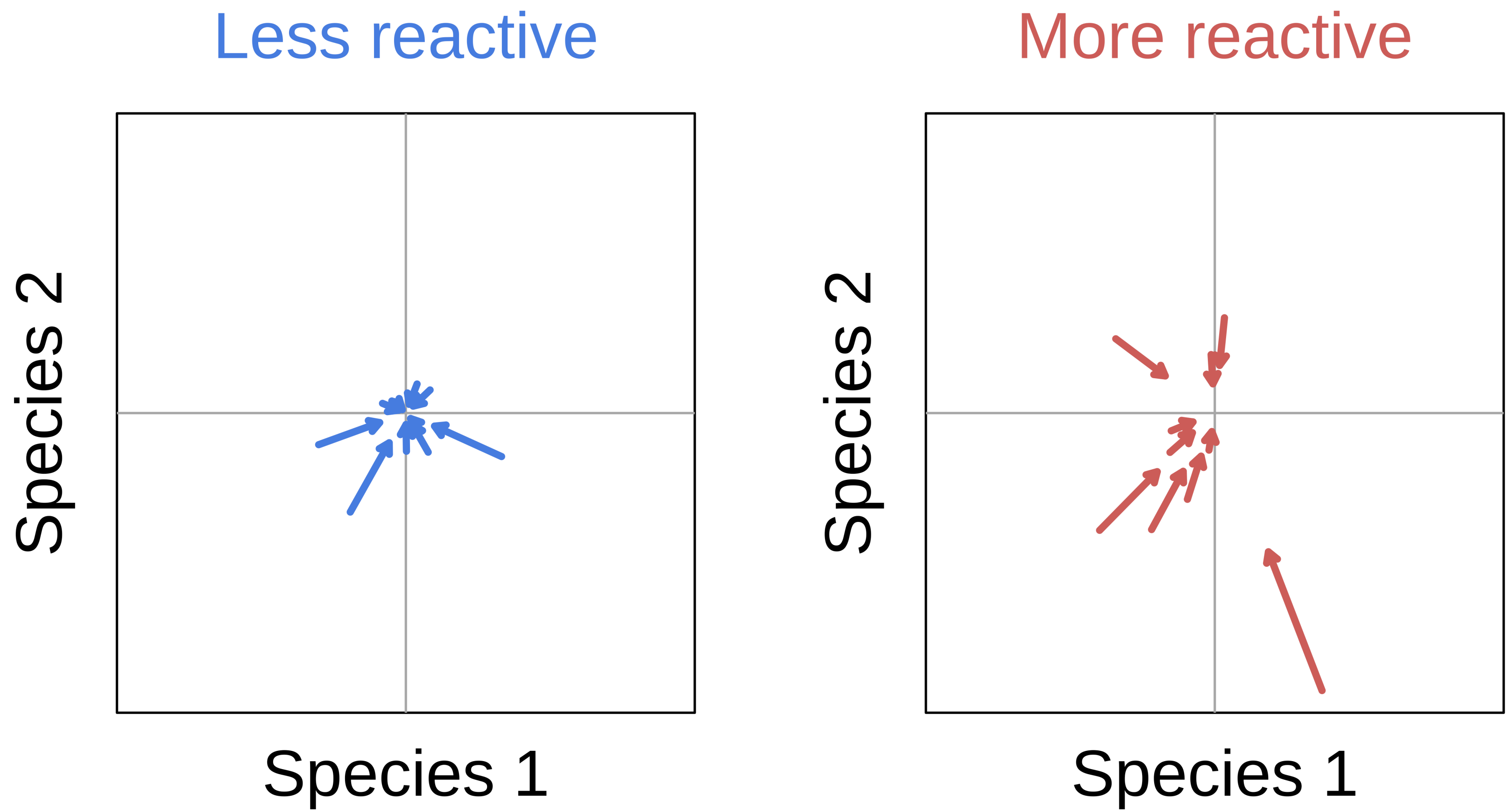
Are all of these communities *stable*?

Reactivity

Small perturbations may grow before decaying again

If so, the community is *reactive*

Example of reactivity



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

Competition

Facilitation

STEEL
VENGEANCE

Acknowledgments

- Elizabeth "Eli" Holmes (NOAA)
- Eric Ward (NOAA)

learn more here