

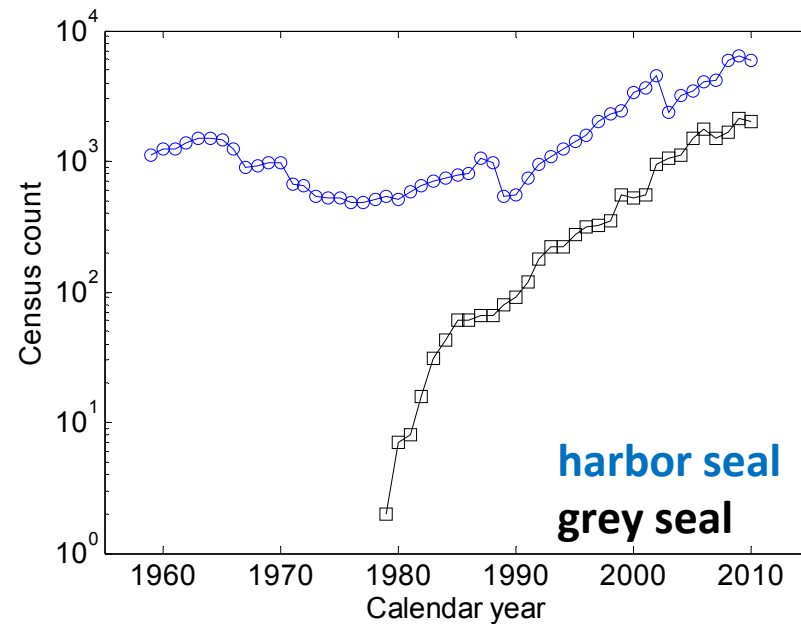
Making histories:

fluctuations in replicate
closed ecosystems



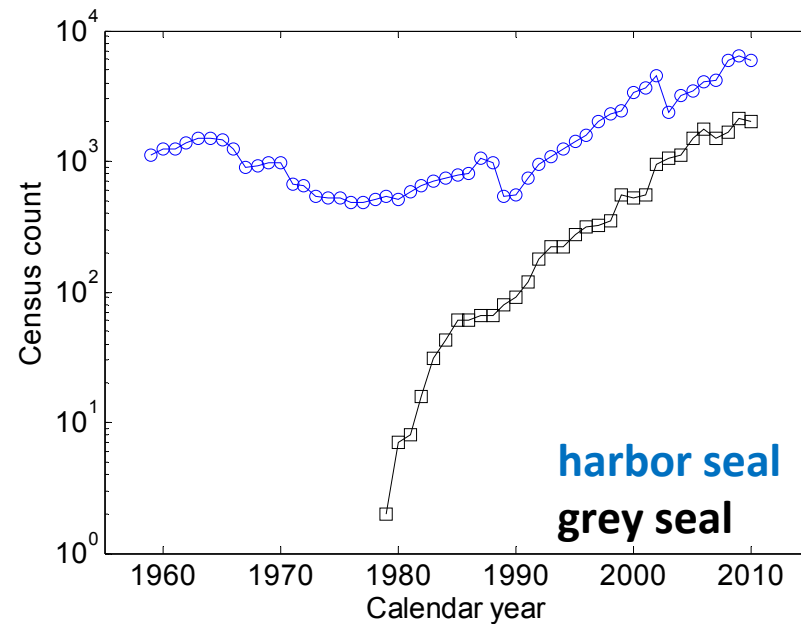
Doeke Hekstra,
The Rockefeller University

Ecology – a brief introduction



Each is a **unique** realization of a **stochastic, contingent** process.

Ecology – a brief introduction



Each is a **unique** realization of a **stochastic, contingent** process.



Often cannot redo
the experiment

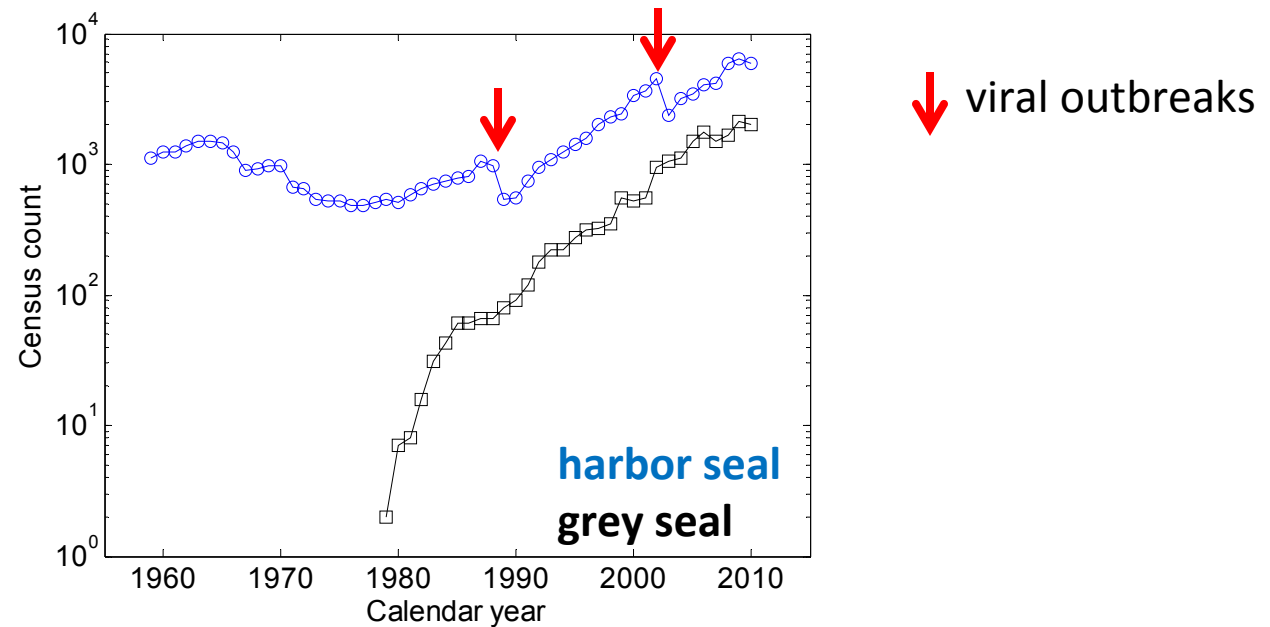


Random effects:
genes, phenotypes,
encounters with
predator, prey, mates,
weather, invasion



Some random events
change long-term
dynamics

Ecology – a brief introduction



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Some random events
change long-term
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Question

Are fluctuations in ecosystems entirely idiosyncratic?

Can we even study ecological fluctuations?

Variability across realizations?

Role of species interactions?

Temporal structure?

Can we study fluctuations in ecology?

We need:

1. Statistics: many replicate systems
2. Long time series: short generation times
3. Control of external sources of noise
 - initial conditions
 - boundary conditions

=> Need microbes in the lab.

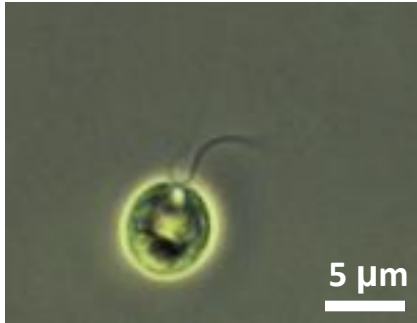
Can we study fluctuations in ecology?

We need:

1. Statistics: many replicate systems
2. Long time series: short generation times
3. Control of external sources of noise
 - initial conditions
 - boundary conditions
4. Minimal perturbation

Even the best experimental microbial systems (chemostats, serial transfer) are not suitable for this.

A model closed ecosystem



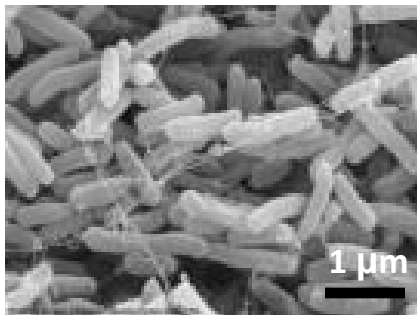
Chlamydomonas reinhardtii

Algae (chlorophyll)

Each

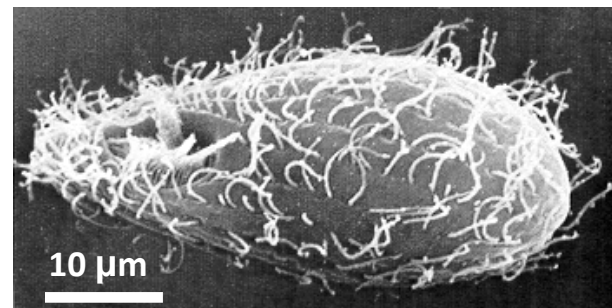
- Grows in chemically defined media
- Motile
- Genetically tractable

Together: coexistence for >3 years (>50%)



Escherichia coli

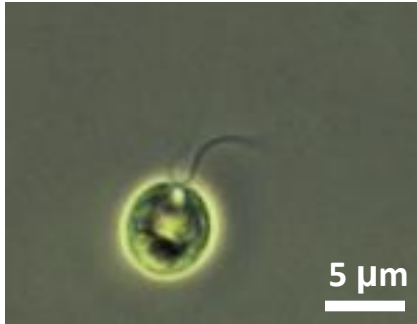
Bacteria (RFP)



Tetrahymena thermophila

Ciliates (YFP)

A model closed ecosystem



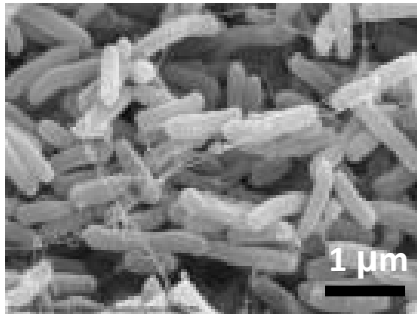
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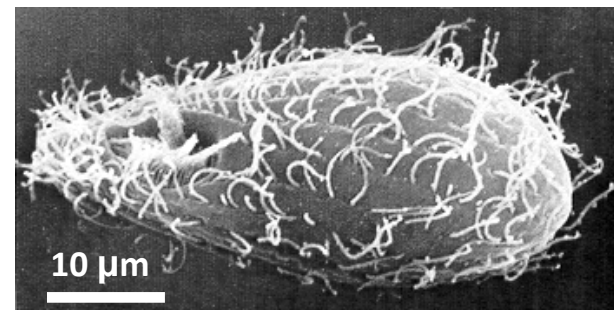
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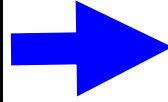
Escherichia coli

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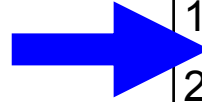


Time (s)	A	B	C
0	1	0	0
1	0	1	0
2	2	1	1
3	1	0	0
...	...	...	...

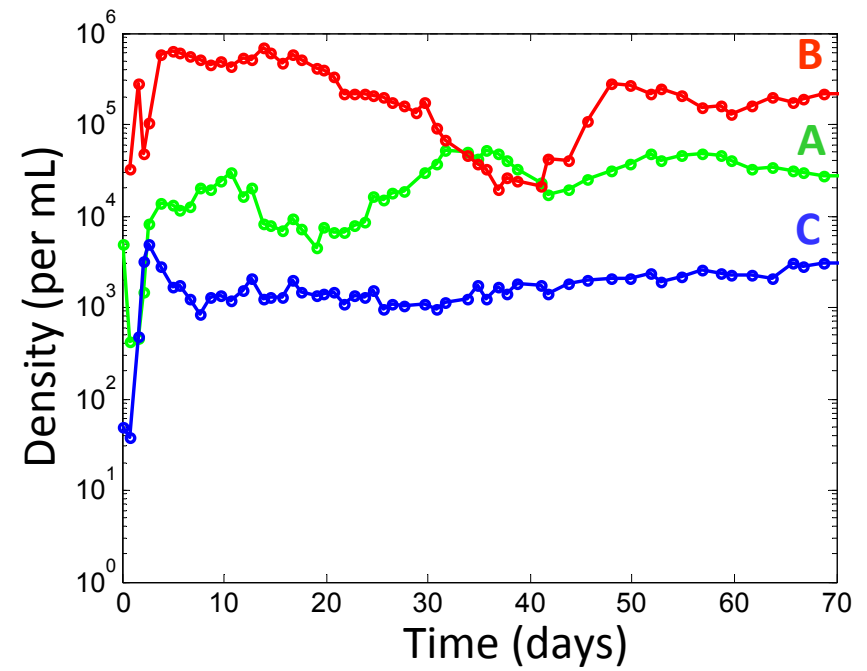
Fluorescence emission --
Single Plane Illumination Microscopy

One local density measurement:

3,000-5,000 images taken 1/sec.



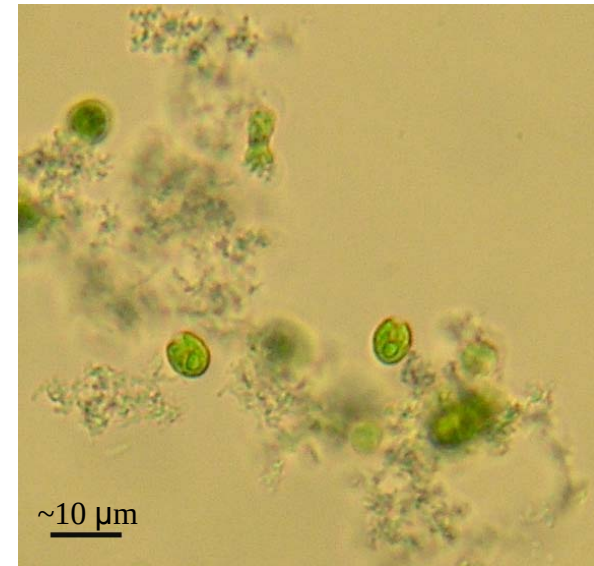
Time (s)	A	B	C
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Spatial heterogeneity

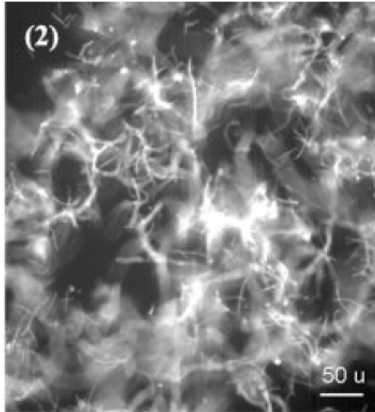


Large scale . . .

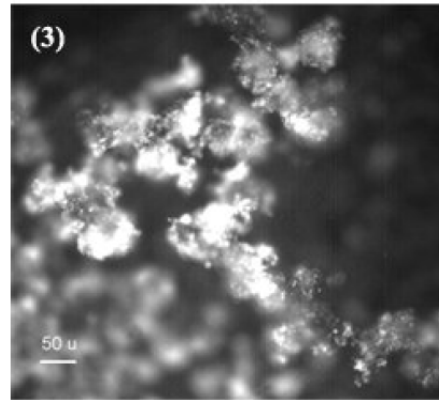


and small scale.

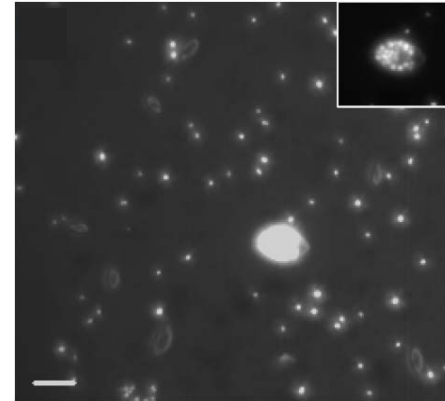
Phenotypic heterogeneity



filamentous *E. coli*,

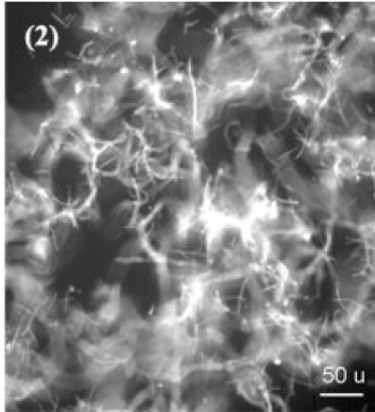


3D structures (*E. coli*)

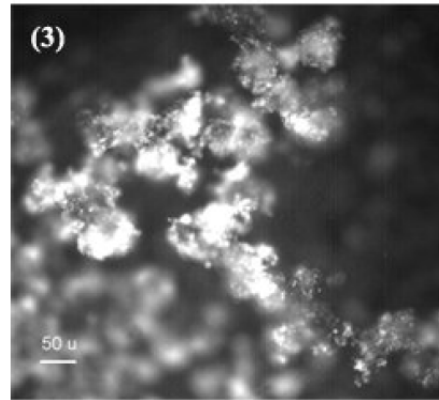


Alga-eating *Tetrahymena*

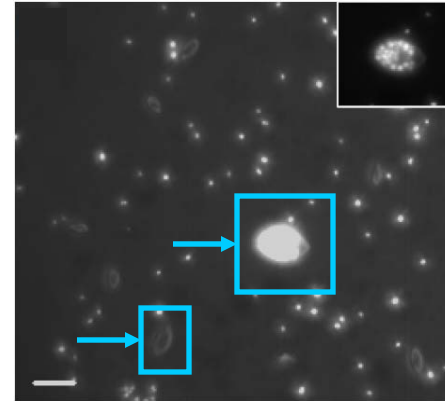
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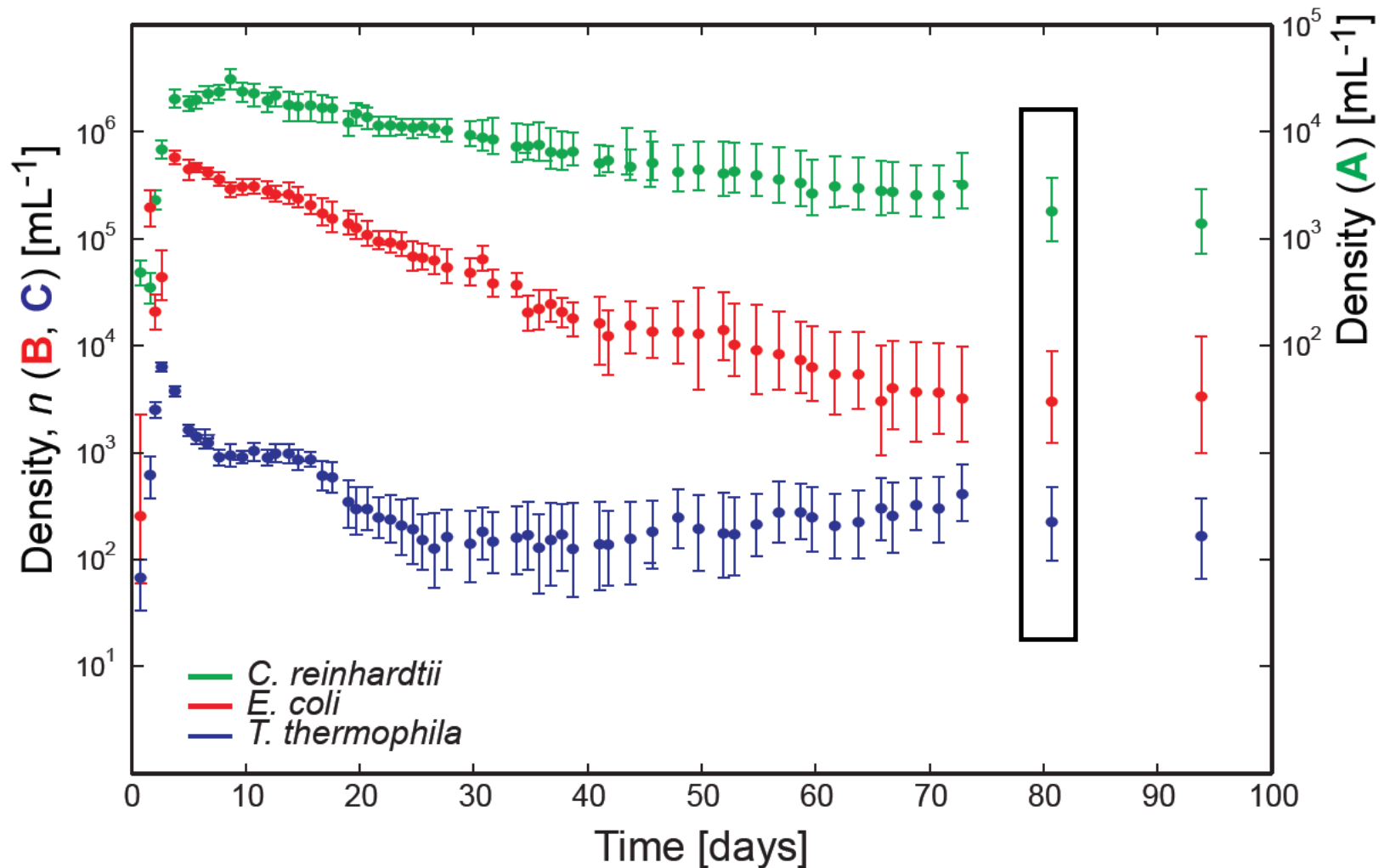
3D structures (*E. coli*)



Alga-eating *Tetrahymena*

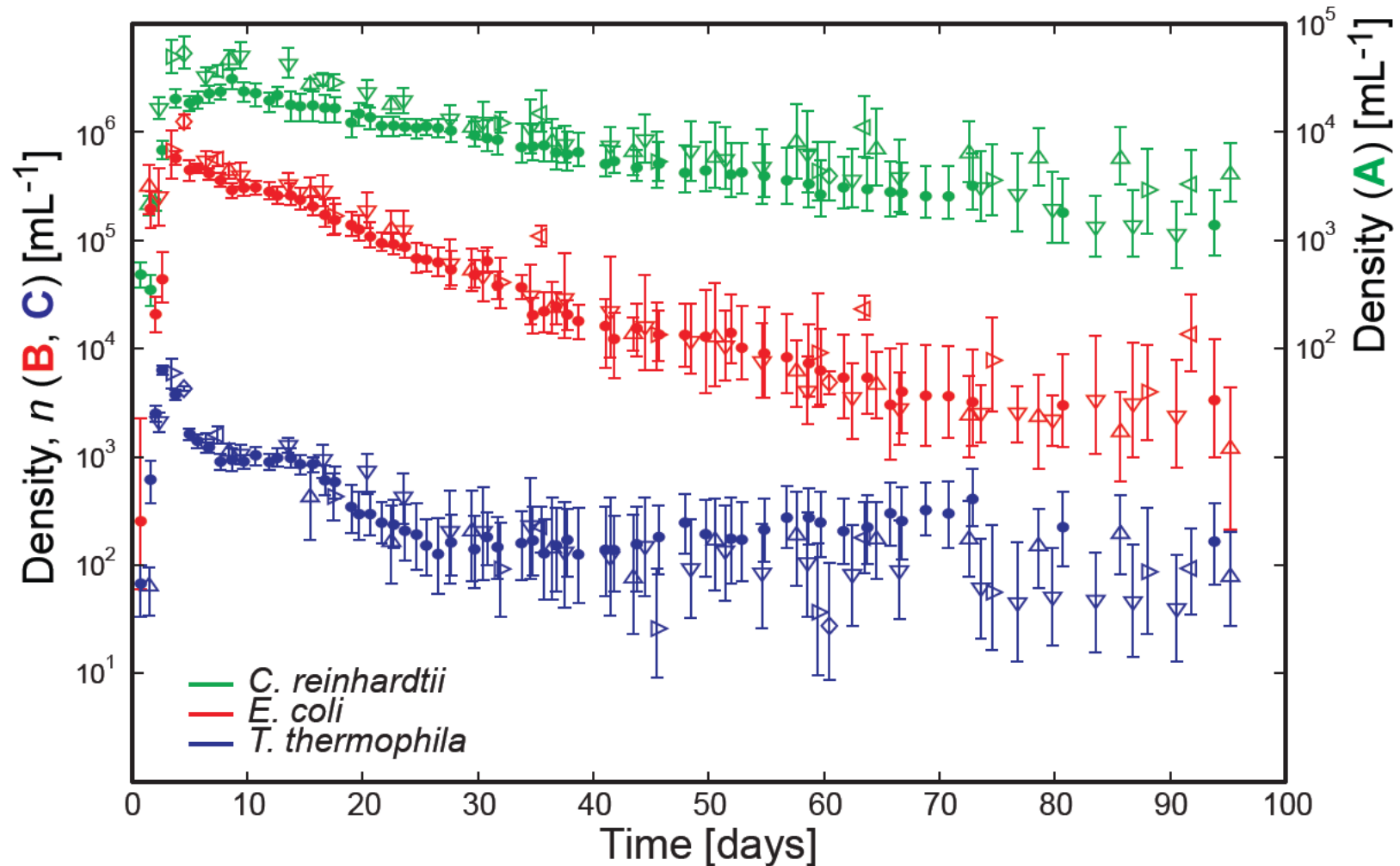
A complex system:
Likely much more is unobserved.

Reproducible average dynamics?



Experiment 1: filled circles (•).

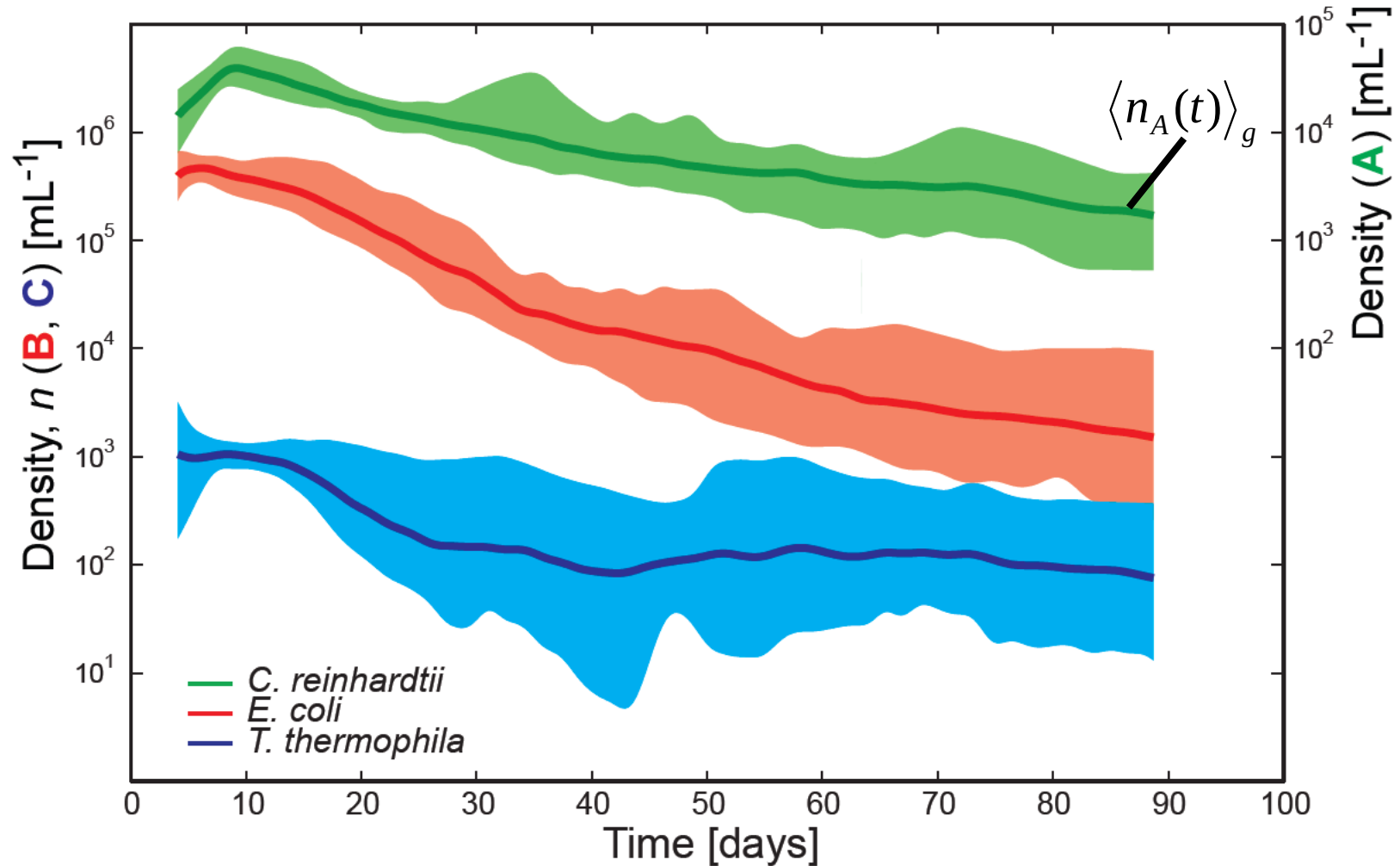
Reproducible average dynamics



Experiment 1: filled circles (•).

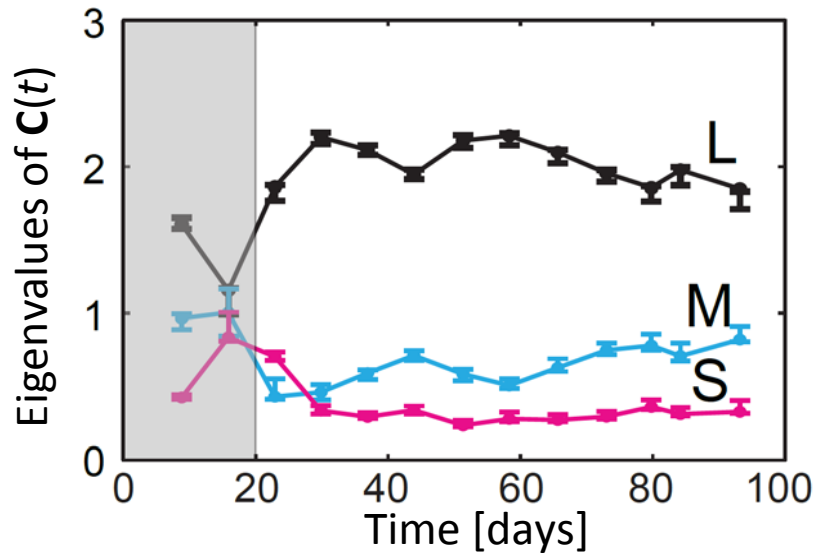
Experiment 2: (∇ , $\triangle$, $\triangleright$, $\triangleleft$, $\diamond$): five more sets of 8-10 systems each.

Reproducible average dynamics



$\langle n_A(t) \rangle_g$: geometric mean

Variability across replicate ecosystems

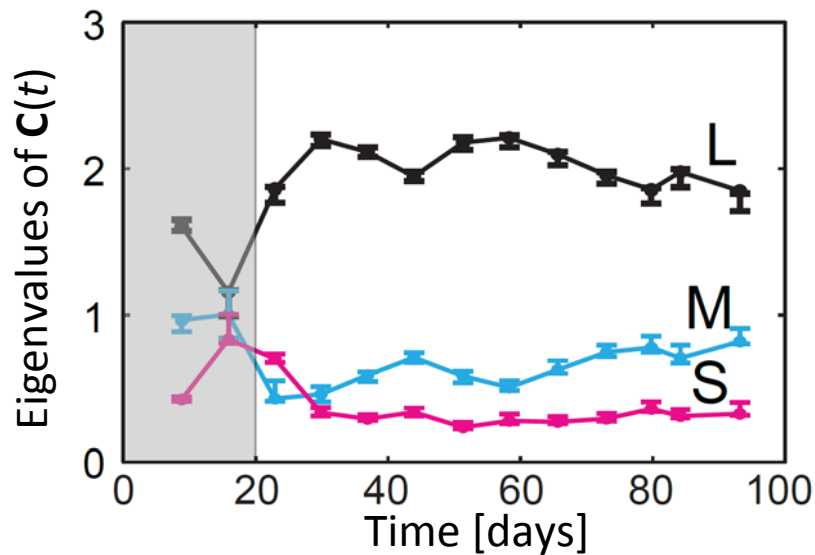


$$c_{ij} = \frac{\text{Cov}(\log n_i(t), \log n_j(t))}{\sigma(\log n_i(t)) \cdot \sigma(\log n_j(t))}$$

Eigenvalues of C :

Fairly stable and reproducible.

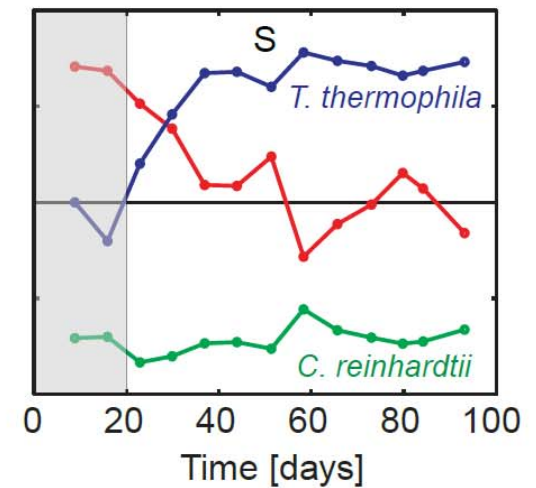
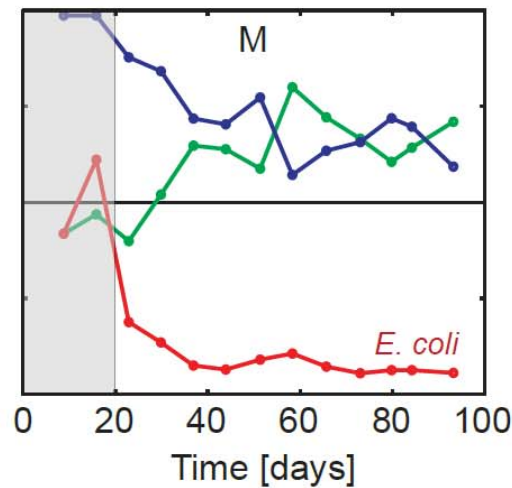
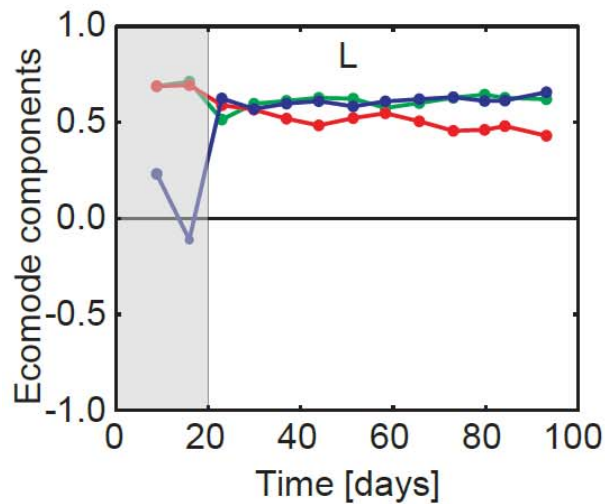
Variability across replicate ecosystems



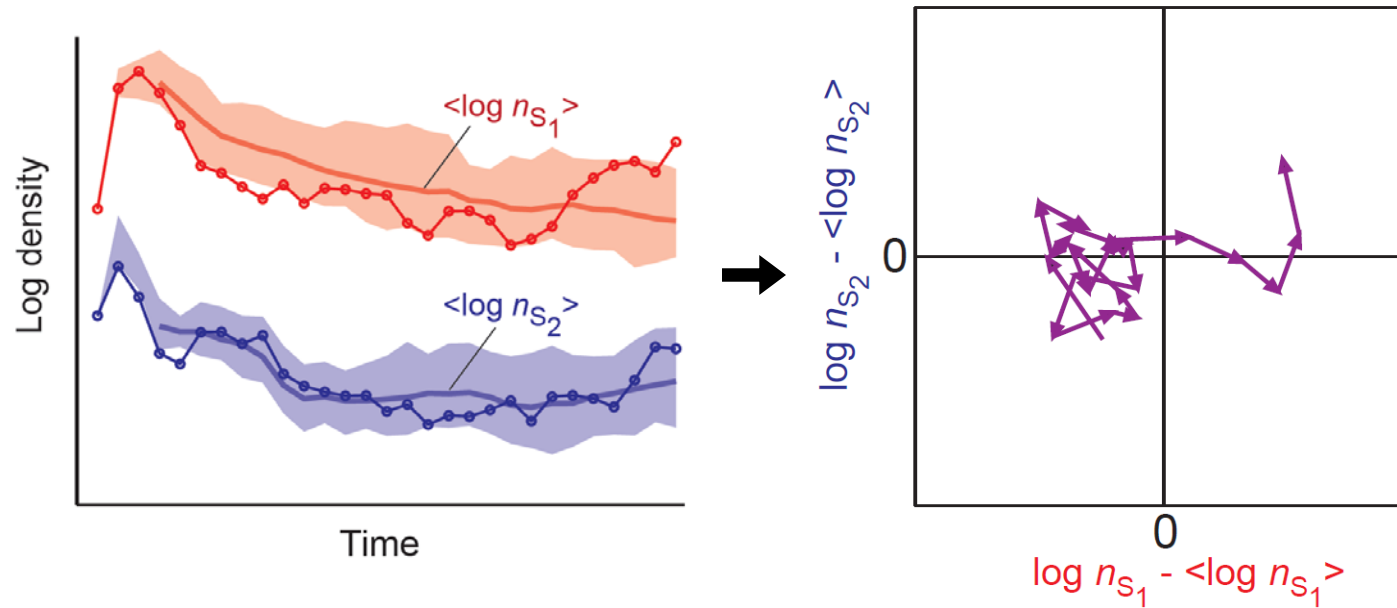
Eigenvectors: **ecomodes**

- stable
- reproducible

properties of ecological variability



Long-term variability and species interactions

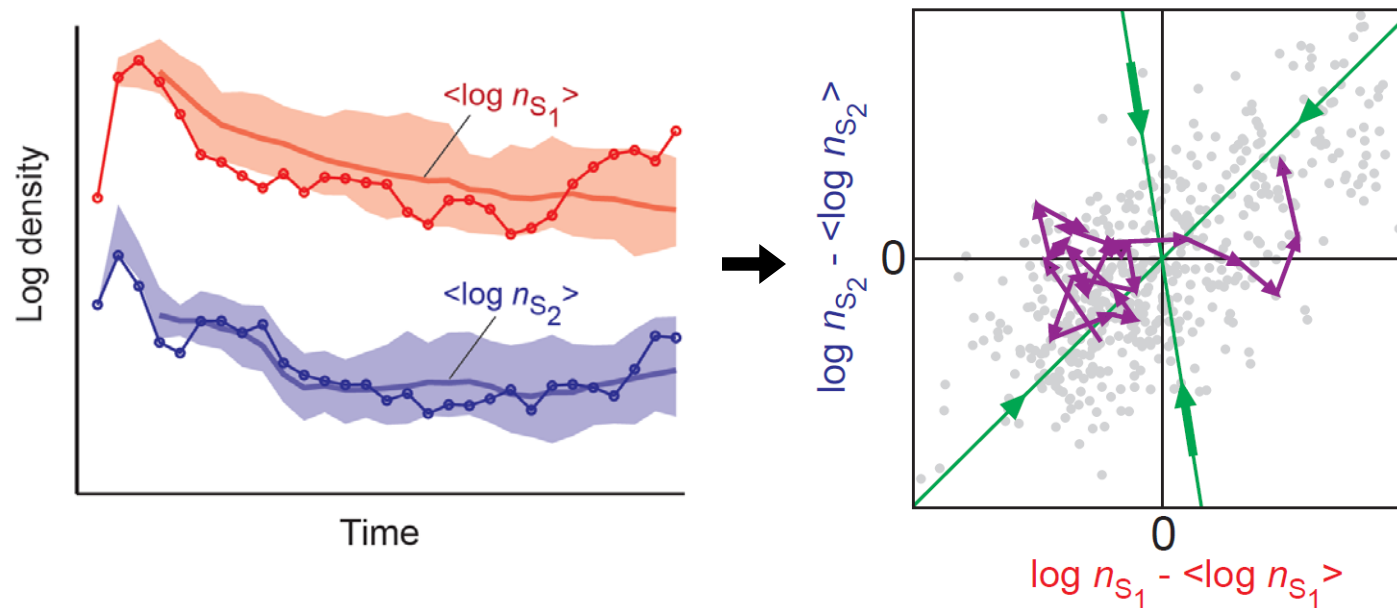


Two toy species

“interaction”: correlated changes in density

Analogy: Particle diffusing in a well (damped, Ornstein-Uhlenbeck process)

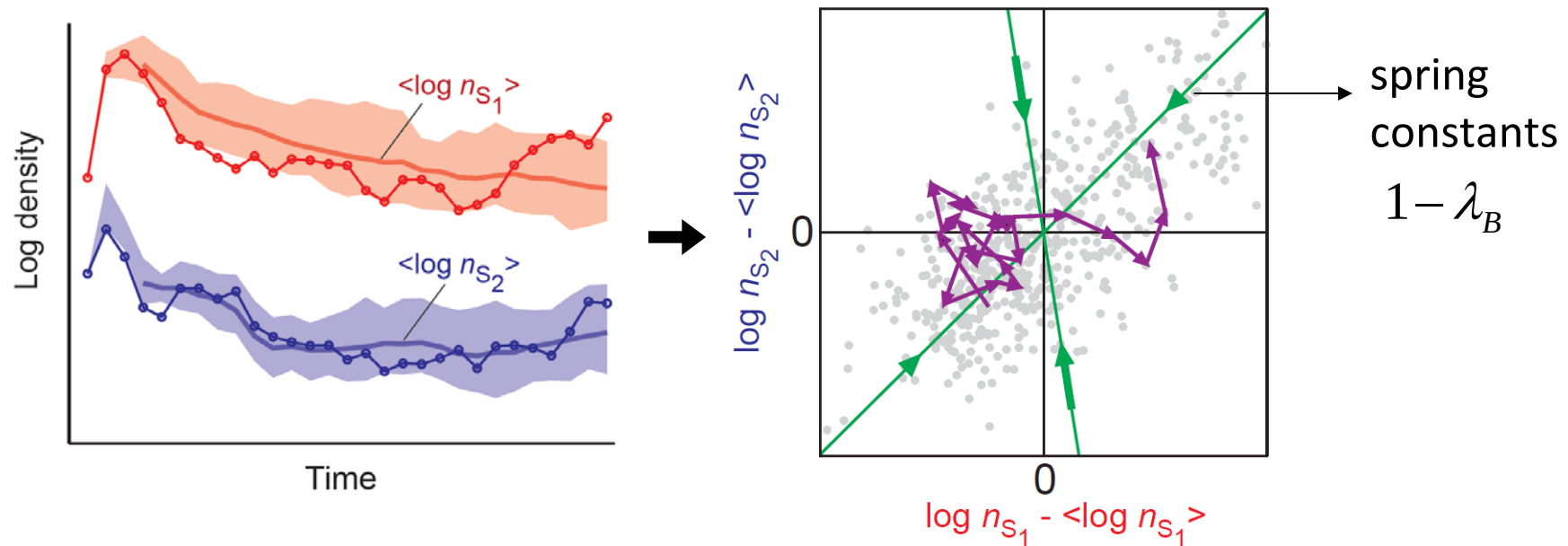
Long-term variability and species interactions



$$\text{Regression: } \log \frac{\mathbf{n}(t + \Delta t)}{\langle \mathbf{n}(t + \Delta t) \rangle_g} = \mathbf{B} \log \frac{\mathbf{n}(t)}{\langle \mathbf{n}(t) \rangle_g} + \text{noise}$$

$\langle n(t) \rangle_g$: geometric mean

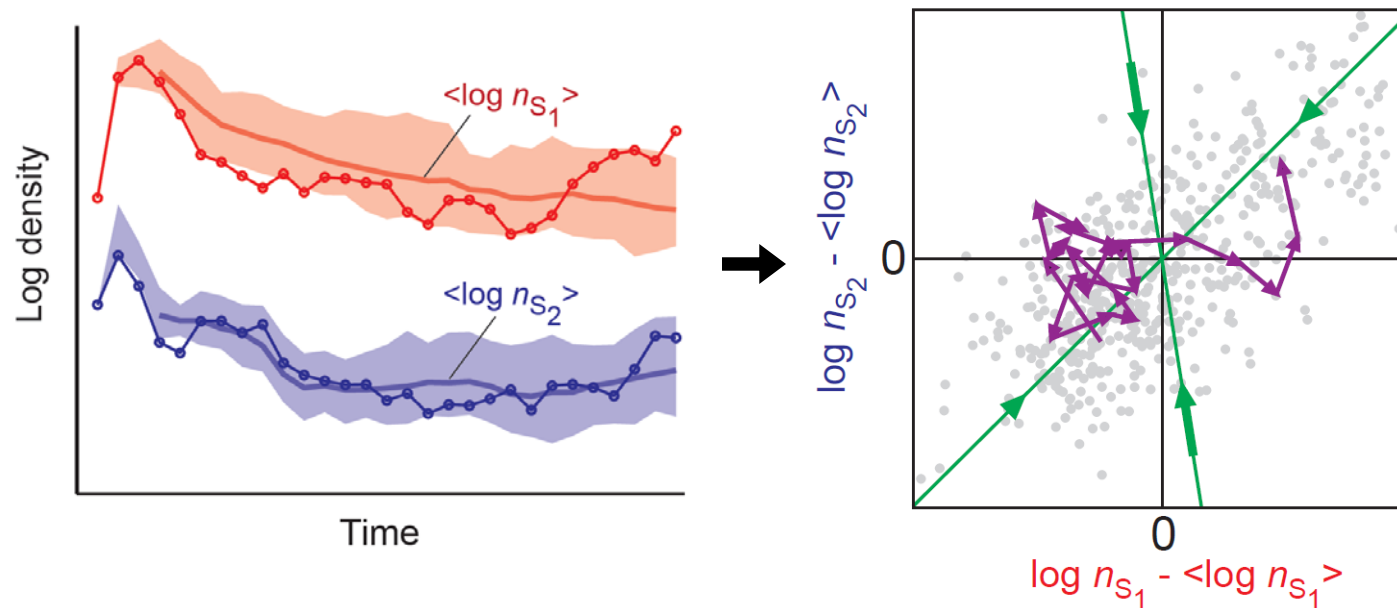
Long-term variability and species interactions



Regression:
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If no long-term memory and oscillations,
variance accumulates along directions with small $1 - \lambda_B$

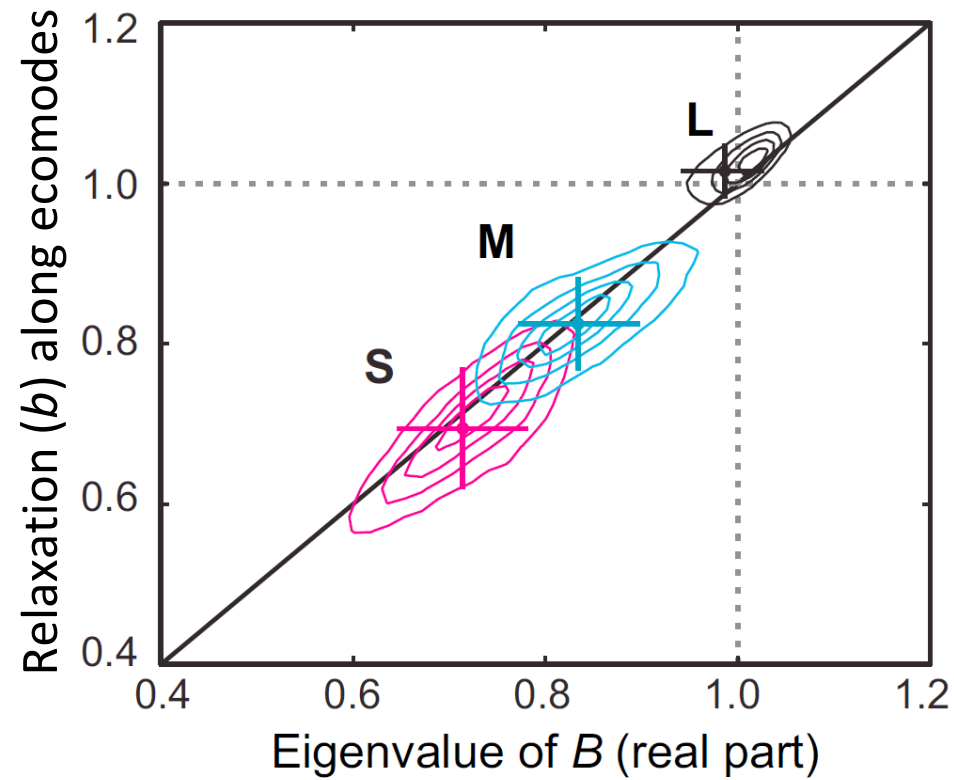
Long-term variability and species interactions



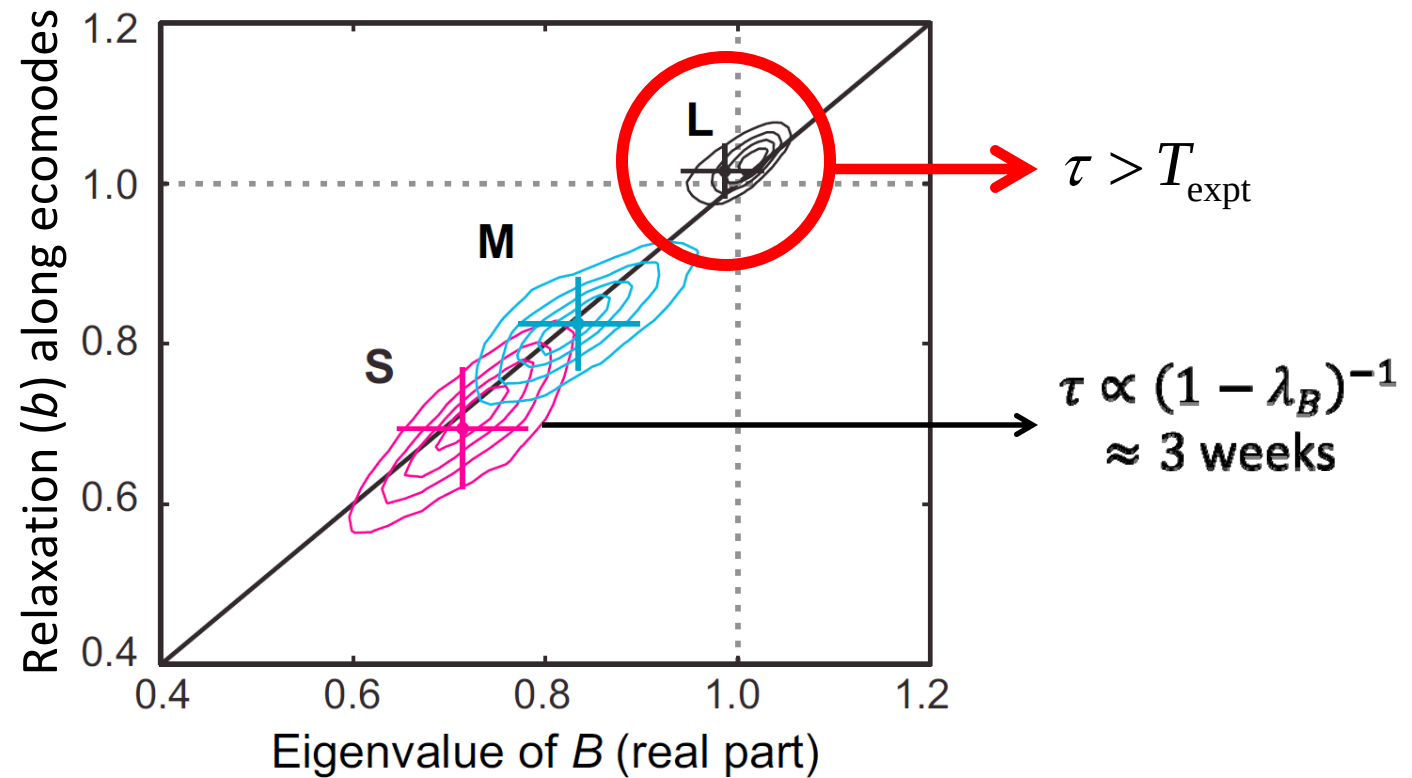
Regression:
$$\log \frac{\mathbf{n}(t + \Delta t)}{\langle \mathbf{n}(t + \Delta t) \rangle} = \mathbf{B} \log \frac{\mathbf{n}(t)}{\langle \mathbf{n}(t) \rangle} + \text{noise}$$

Relaxation rate $\approx (1 - \lambda_B) \Delta t^{-1}$

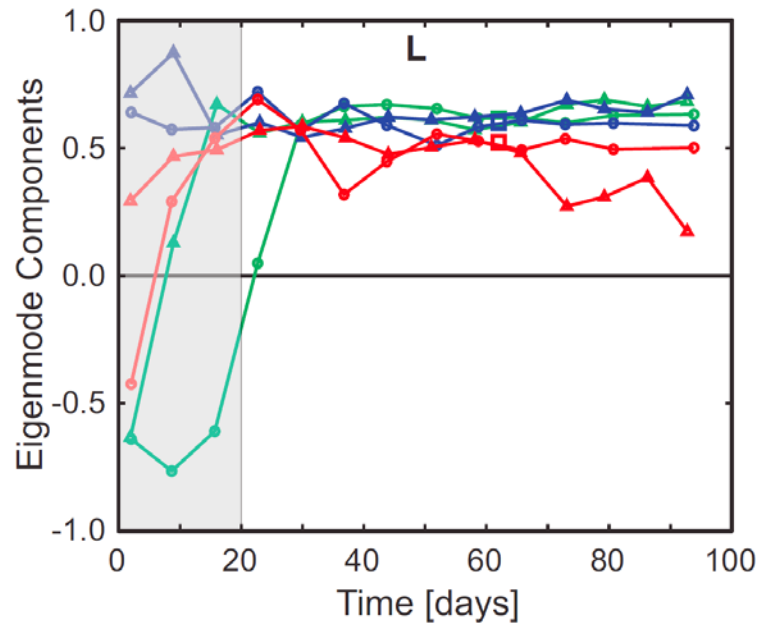
Do ecomodes reflect species interactions?



Do ecomodes reflect species interactions?



What does this mean for dynamics?



The large (L) ecomode:

Non-stationary fluctuations along a collective mode dominate variability in population dynamics

What kind of non-stationarity?

Growth rate fluctuations, $\delta r = r - \langle r \rangle$,

for each species:

- $\sigma(\delta r)$ is limited and stable
- δr shows little autocorrelation

$$\log \frac{n(t)}{\langle n(t) \rangle_g} = \log \frac{n(0)}{\langle n(0) \rangle_g} + \Delta t \sum_t \delta r$$

⇒ Temporal fluctuations of $\log n(t)$ should resemble **random walks**.

– geometric random walks for $n(t)$ –

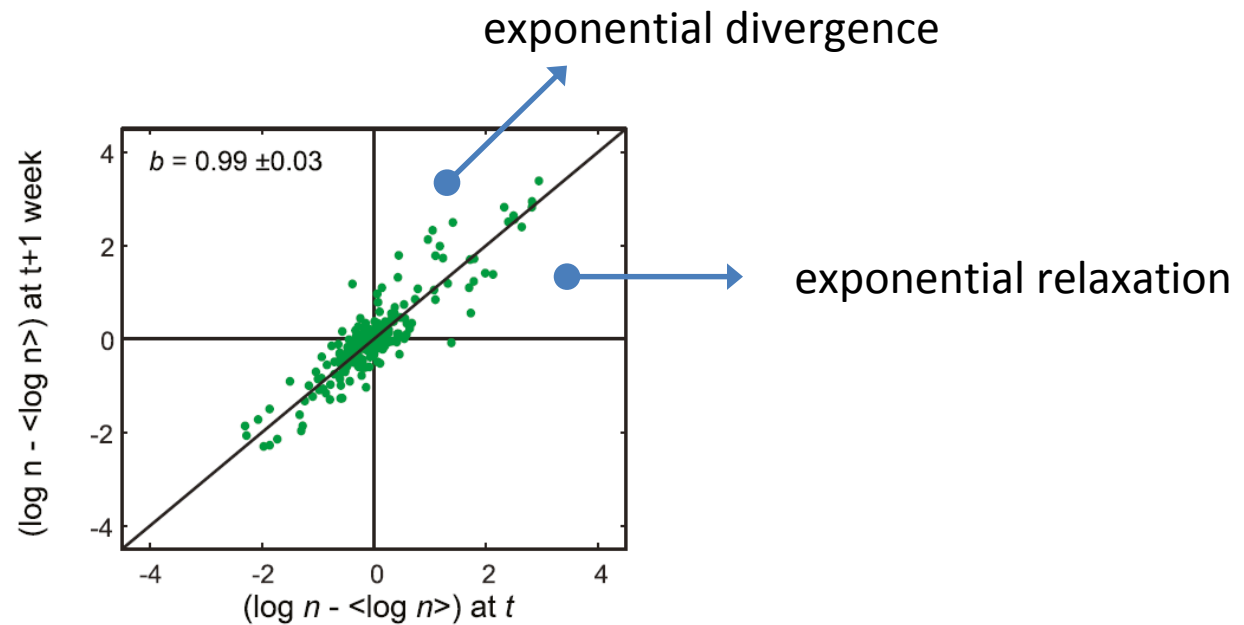
Temporal fluctuations

Random walks satisfy in addition:

1. Lack of reversion to the mean
2. Linear growth of variance with time
3. Scaling of the power spectrum

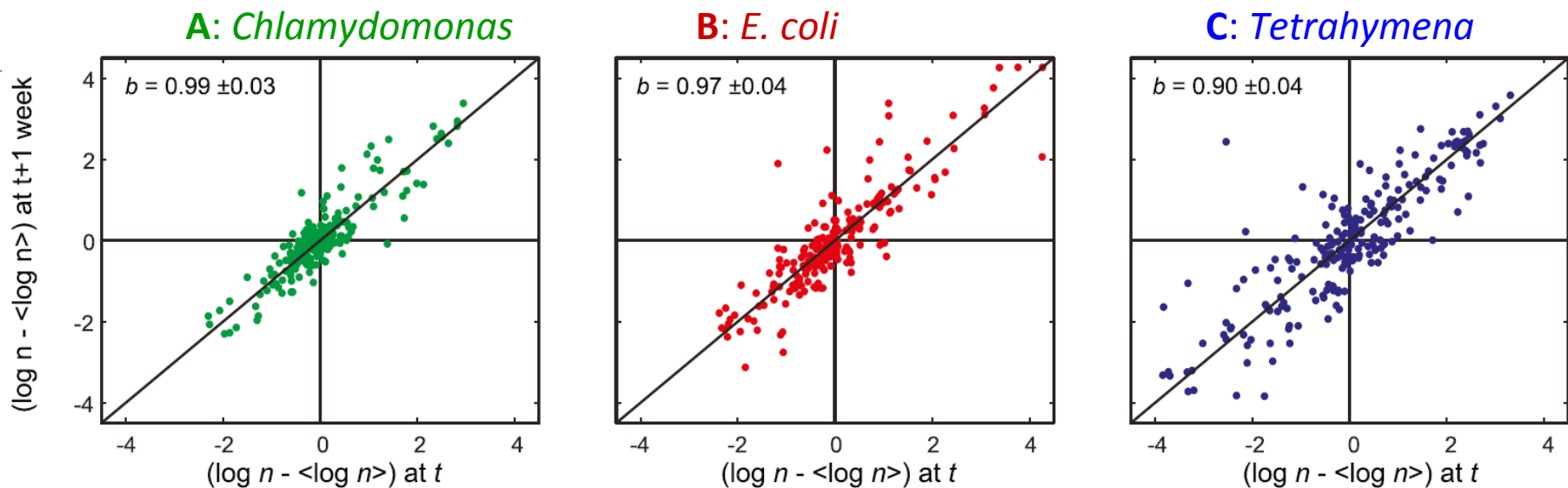
Temporal fluctuations

1. Lack of (exponential) reversion to the mean



Temporal fluctuations

1. Lack of (exponential) reversion to the mean



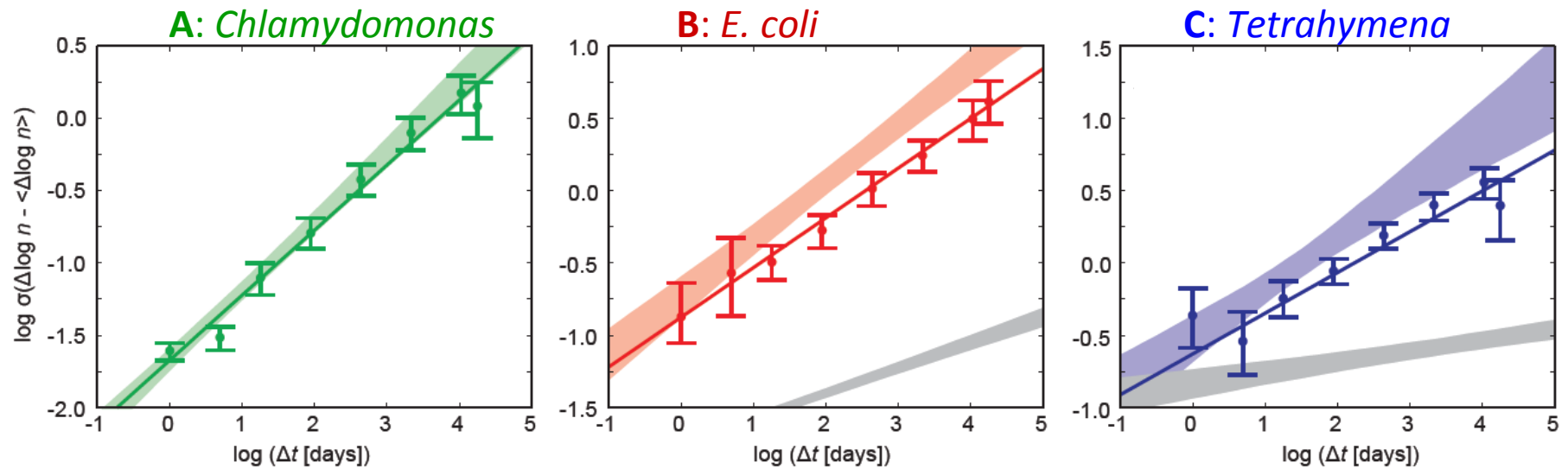
Temporal fluctuations

1. Lack of reversion to the mean
2. **Linear growth of variance with time**

$$\text{Var} \left(\log \frac{n(t + \Delta t)}{n(t)} \right) \propto \Delta t$$

Temporal fluctuations

1. Lack of reversion to the mean
2. **Linear growth of variance with time**

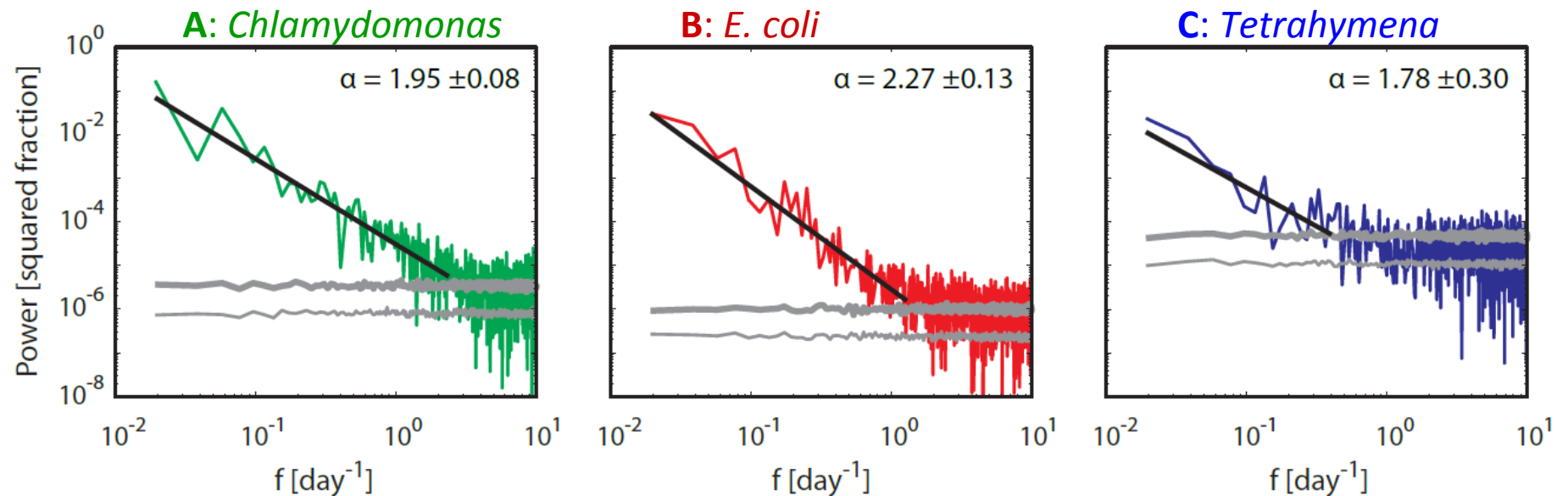


$$\text{Var} \left(\log \frac{n(t + \Delta t)}{n(t)} \right) \propto \Delta t$$

Temporal fluctuations

1. Lack of reversion to the mean
2. Linear growth of variance with time
3. **Scaling of power spectrum for individual time series**
with exponent $\alpha = 2$.

$$S(f) \propto f^{-\alpha}$$



Take home message...

- Replicate closed ecosystems allow us to separate idiosyncratic from statistical properties of dynamics.
 - Fluctuations show reproducible features: ecomodes.
 - Ecomodes reflect species interactions.
 - The large ecomode dominates and results in scaling laws.
-

Acknowledgements

Stanislas Leibler (Rockefeller University, IAS)

Seppe Kuehn and Zak Frentz (Rockefeller University)

Members of the “Laboratory of Living Matter”, past & present

Remi Monasson and Simona Cocco (IAS/ENS)

Yifan Liu (Allis Lab, RU; now at MSU)

[Read more](#)

Hekstra, D.R., and S. Leibler, *Cell* **149** (5): 1164-1173, (2012).

Further Questions

Consequences for evolution?

- Is fitness as growth rate averaged over possible histories relevant?
- Outcome of competition between phenotypes?

Stochastic “architecture”?

- Dominant sources of randomness?
- Noise propagation through the ecosystem?

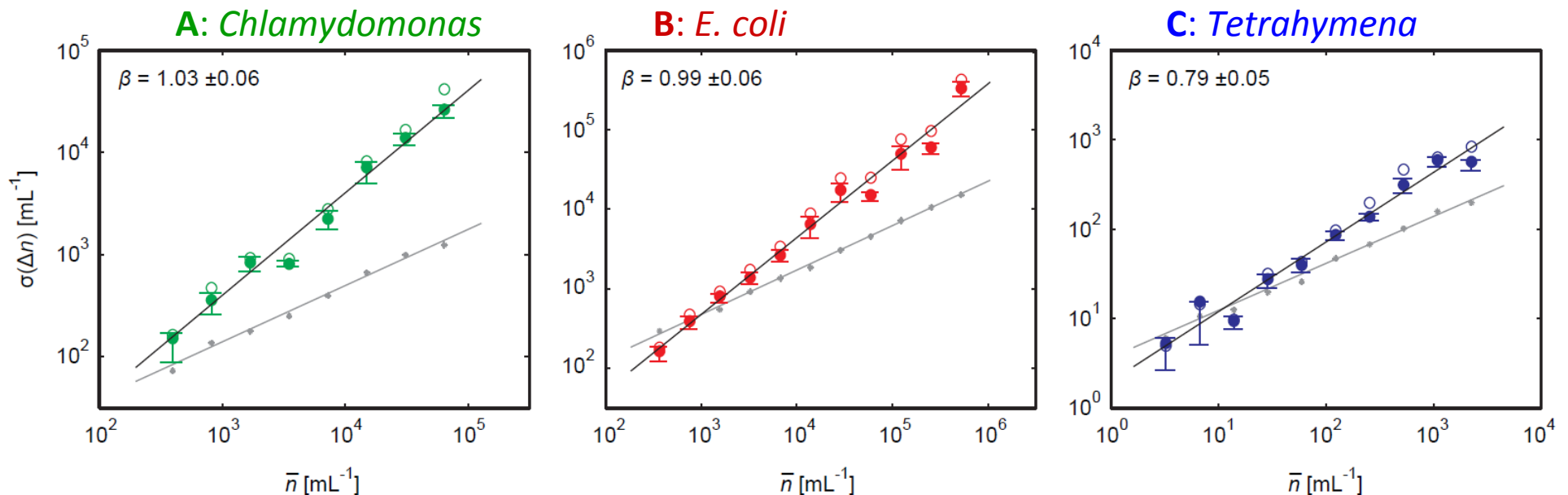
Can we selectively “excite” ecomodes?

- Relation of ecomodes to nutrient cycling?
 - Impulse-response properties?
-

Variability across replicate ecosystems

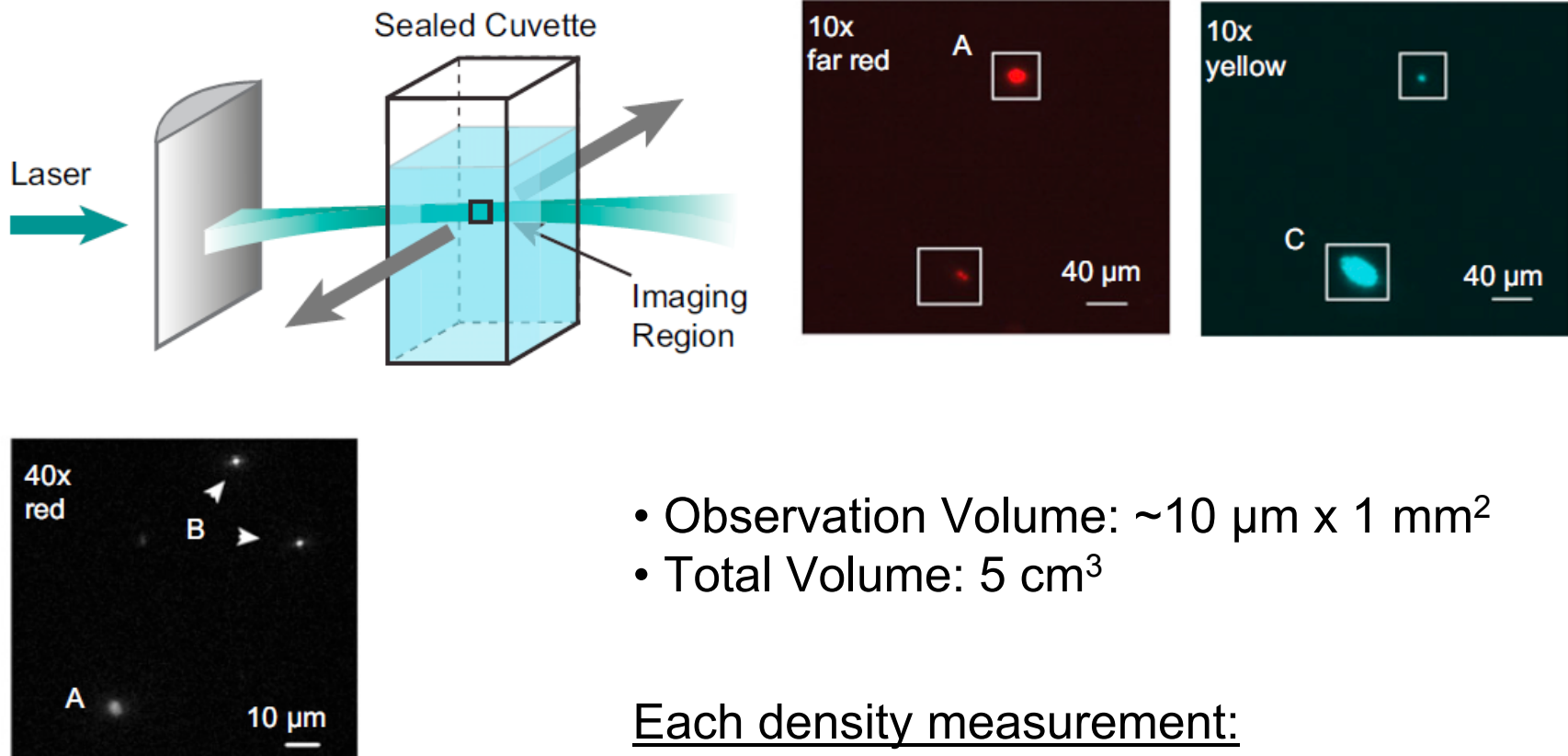
Why look at $\log(n)$?

$$\sigma(n) \propto n^{1.0} \Rightarrow \sigma(\log n) \propto n^{0.0}$$



Statistics over 279 weekly intervals (!)

Selective Plane Illumination Microscopy



- Observation Volume: $\sim 10 \mu\text{m} \times 1 \text{ mm}^2$
- Total Volume: 5 cm^3

Each density measurement:

- Expose 35 ms per second (lights off)
- $\sim 3,000$ - $5,000$ images (~ 1 hour)