Chaos and intermittent instability in ecological systems

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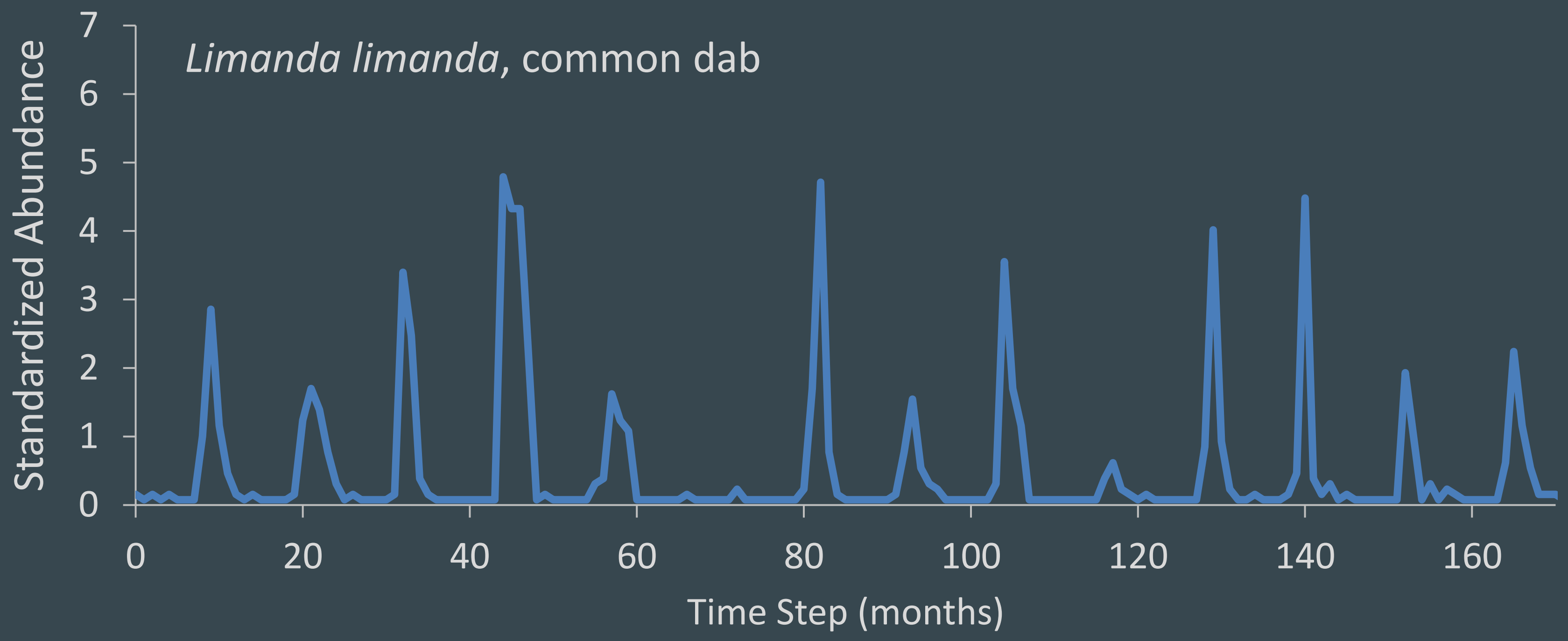
Population fluctuations in nature (historical view)

1. Environmental drivers
2. Population dynamics: density dependence, species interactions
   - Stable equilibrium
   - Regular cycles

Irregular fluctuations/cycles must result from environment, be unpredictable



Origins of chaos in ecology

Science

REPORTS

Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos

Robert M. May[1]

Science 15 Nov 1974:
Vol. 186, Issue 4164, pp. 645-647
DOI: 10.1126/science.186.4164.645

Discrete logistic population model (logistic map)

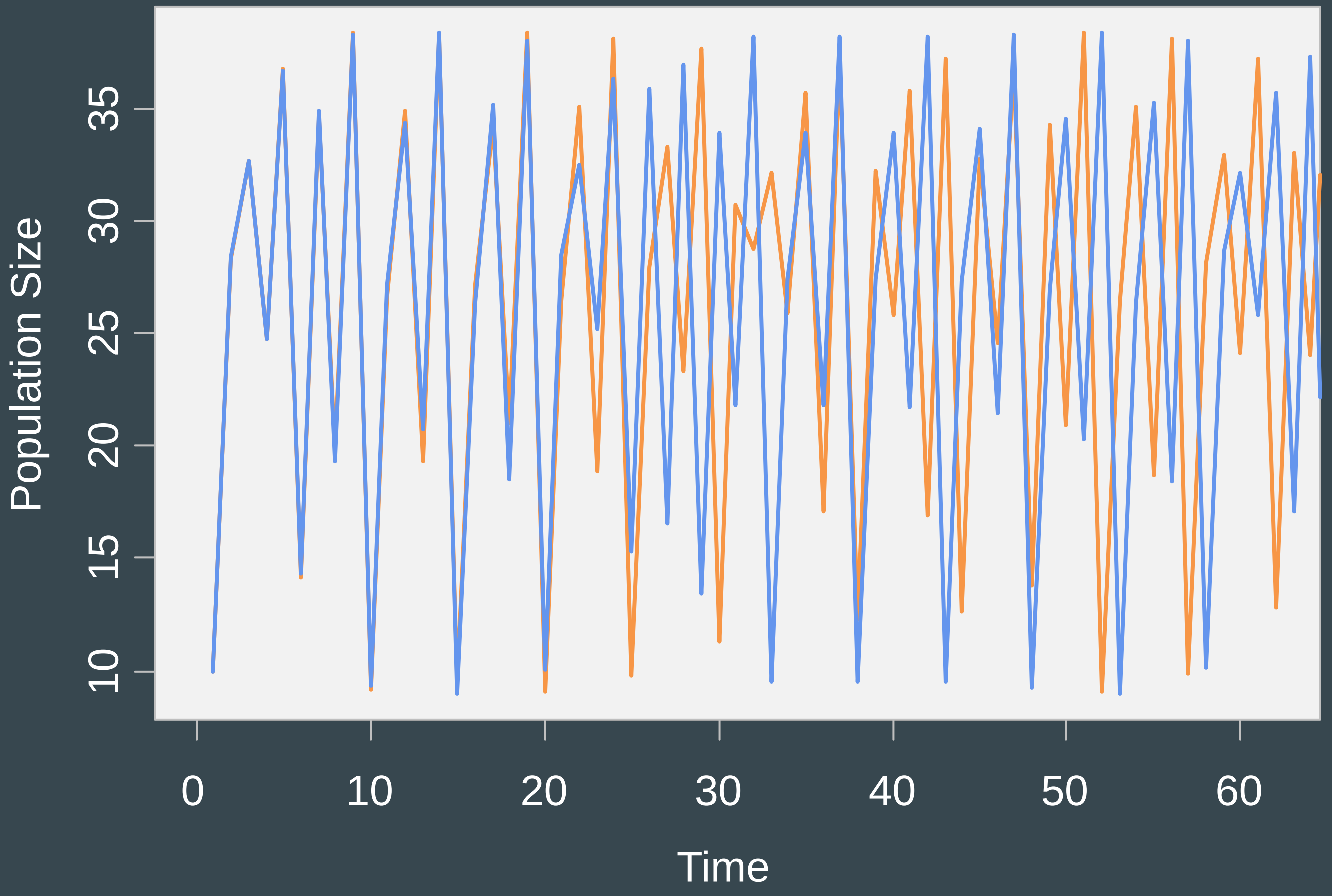
$$N_t = N_{t-1} + N_{t-1} r \left(1 - \frac{N_{t-1}}{K}\right)$$

- Sensitivity to initial conditions
- Bounded, irregular, deterministic oscillations
- No stable equilibria/fixed points
- Short-term predictability, but not long-term (unlike randomness)

Could chaos explain irregular fluctuations in nature?

initial Pop. Size = 10

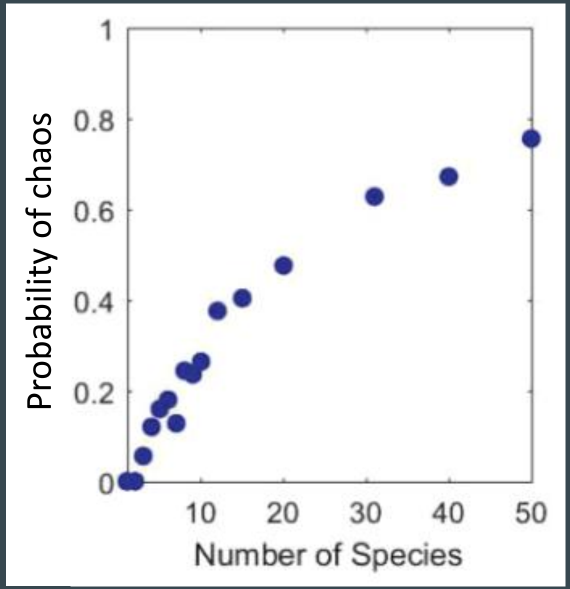
initial Pop. Size = 10.01



What do we know about chaos?

- Numerous theoretical and empirical studies have since been done
- Beyond the 1-d logistic map:
  - Chaos is more likely in more complex (higher-dimensional) systems
    (multiple species, age classes, life histories, populations in space, etc.)
  - Chaos doesn't necessarily depend on (or require high) growth rate
  - Chaos doesn't necessarily result in low pop. sizes (higher extinction risk)

- Chaotic and non-chaotic time series can be impossible to distinguish visually
- Chaos is harder to detect in short, noisy time series

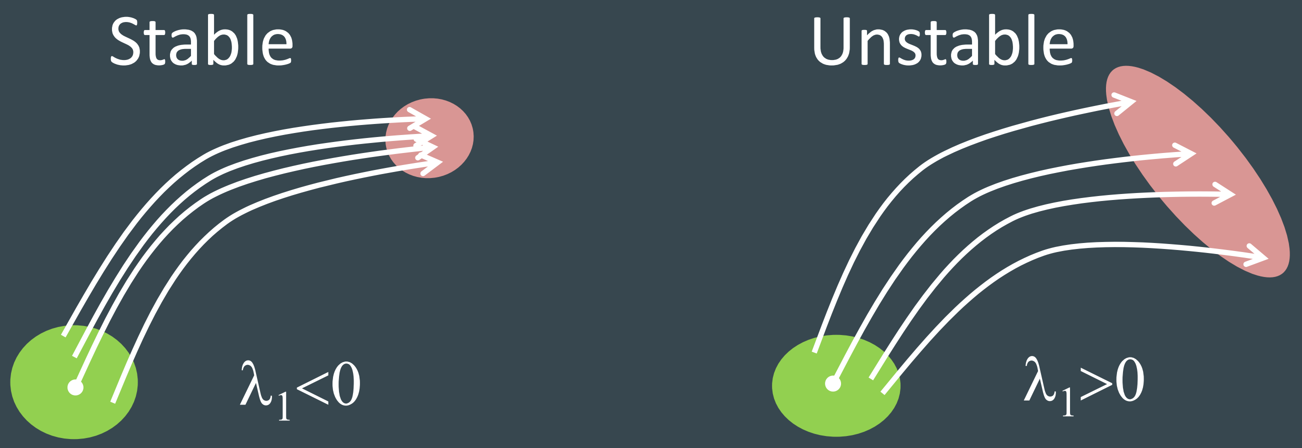


Multi-species Ricker random predator-prey networks

Munch et al. (2019)

Lyapunov exponent (LE)

- Exponential divergence rate, averaged across entire trajectory ($T \rightarrow \infty$)
- LE > 0 indicative of chaos
- Magnitude indicative of forecast horizon (~ 1/LE timesteps)
- There are several different methods for estimating the LE



λ_1= log dominant eigenvalue of Jacobian matrix

Are ecological dynamics chaotic?

- Most recent global meta-analysis found that only 1 out of 634 ecological time series was chaotic (Sibly et al. 2007)
- Similar conclusions have been drawn by other recent papers (Upadhyay et al. 1998, Snell & Serra 1998, Freckleton & Watkinson 2002, Shelton & Mangel 2011, Salvidio 2011)
- Consensus that chaos in ecology is ‘rare’

Ecology Letters, (2007) **10**: 970–976 doi: 10.1111/j.1461-0248.2007.01092.x

LETTER

On the stability of populations of mammals, birds, fish and insects

Richard M. Sibly,[1,2]* Daniel Barker[3], Jim Hone[4] and Mark

Abstract
A key concern for conservation biologists is whether populations of plants and animals are likely to fluctuate widely in number or remain relatively stable around some steady-

extinction. Our estimates of return rates were generally well below the threshold for chaos, which makes it unlikely that chaotic dynamics occur in natural populations – one of ecology’s key unanswered questions.

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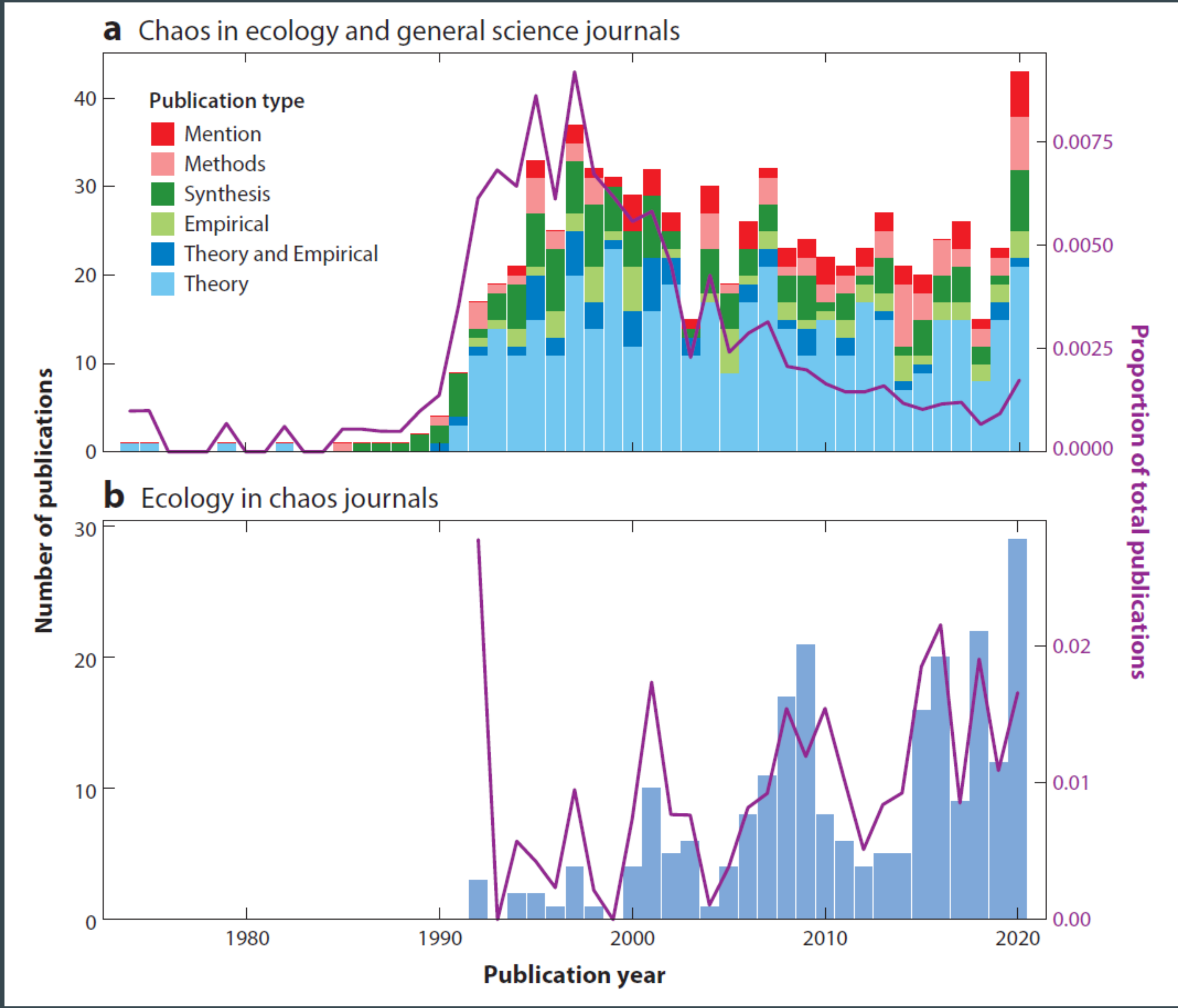
the lower return rates of the large mammals may make them more vulnerable to
extinction. Our estimates of return rates were generally well below the threshold for chaos, which makes it unlikely that chaotic dynamics occur in natural populations – one of ecology’s key unanswered questions.

Keywords
Chaos, contest competition, GPDD, return rate, scramble competition, stability.

Ecology Letters (2007) 10: 970–976

Publications about chaos in ecology



Munch et al. (2022) AREES

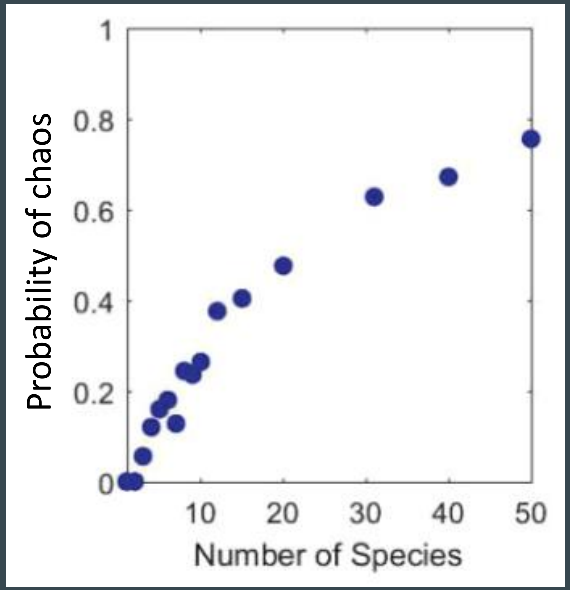
But why should chaos in ecology be rare?

- Nonlinear dynamics are everywhere
- Ecosystems are highly complex and high-dimensional
- Abiotic drivers of ecosystems are themselves chaotic (e.g. the weather)


nature ecology & evolution
ARTICLES
https://doi.org/10.1038/s41559-019-1052-6

Nonlinear population dynamics are ubiquitous in animals

T. J. Clark* and Angela D. Luis

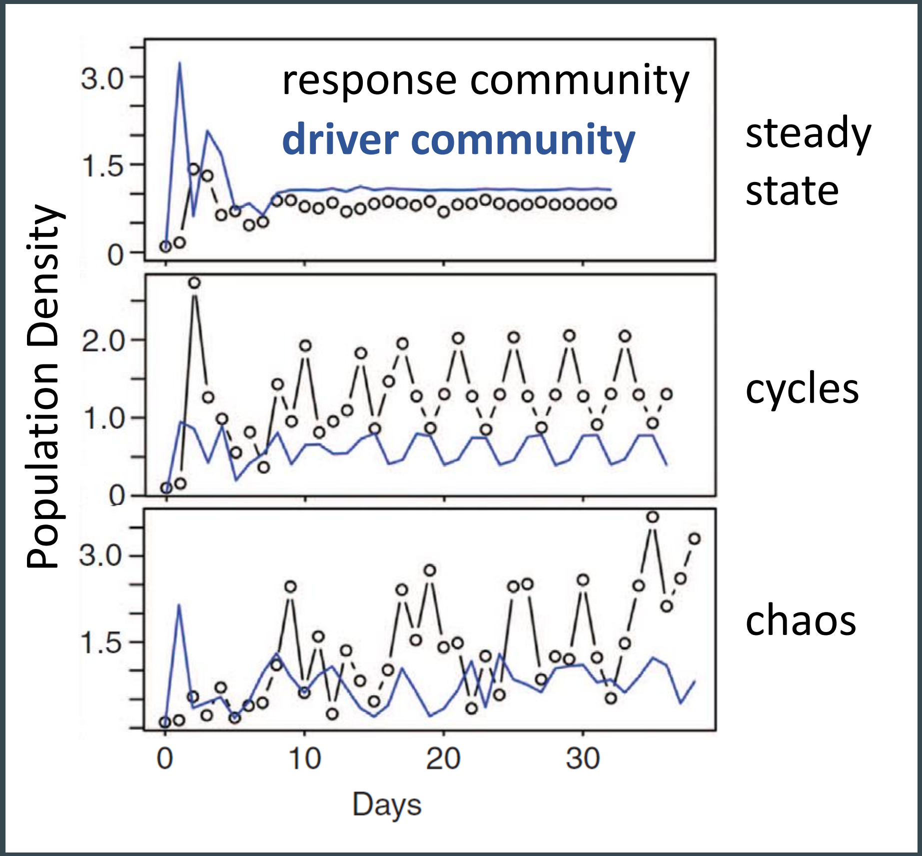


probably accurate

definitely not accurate

Experimental and field demonstrations of chaos

Becks & Arndt 2013



- 3-species microbial communities in chemostat (Becks et al. 2005)
- Flour beetles in lab (Dennis et al. 1997)
- Planktonic community in a mesocosm (Beninca et al. 2008)
- Perennial grasses grown in field (Tilman & Wedin 1991)
- Fennoscandian voles across Europe (Turchin & Ellner 2000)
- Measles dynamics in Africa (Ferrari et al. 2008)
- Rocky intertidal community with intransigent competition (Beninca et al. 2015)

Is it just that chaos is impossible to detect in field data if it's there, or…

nature Vol 435|30 June 2005|doi:10.1038/nature03627

LETTERS

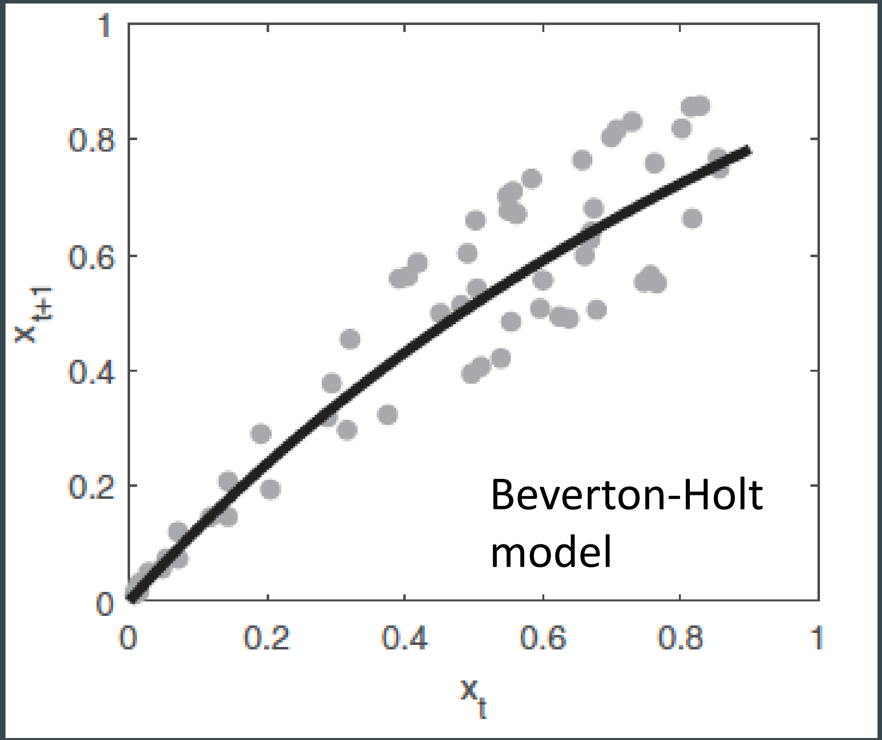
Experimental demonstration of chaos in a microbial food web

Lutz Becks[1]*, Frank M. Hilker[2], Horst Malchow[2], Klaus Jürgens[3,4] & Hartmut Arndt[1]*

Is it just the methods we're using?

- Most meta-analyses fit 1-d parametric models and infer chaos based parameter estimates
- 1-d models treat all higher-dimensional dynamics as noise

$$x_{t+1} = f(x_t)$$



Data are actually generated from a chaotic 2-d predator-prey system

$$x_{t+1} = \frac{r_x x_t(1 - c y_t)}{b + x_t(1 - c y_t)}$$

$$y_{t+1} = r_y y_t(1 - y_t) + f x_t y_t$$

Deterministic chaos in 2-d looks like stable dynamics with noise in 1-d.

Munch et al. (2019)

- Can low-d chaos (e.g. logistic map) explain population fluctuations? No.

Is it just the methods we're using?

- Last meta-analysis to use flexible, higher-dimensional methods was published >25 years ago (Ellner & Turchin 1995)

Evidence for chaos in
- 7 of 31 field time series (23%)
- 3 of 20 experimental time series (15%)

We now have more data and new and improved methods

Vol. 145, No. 3 The American Naturalist March 1995

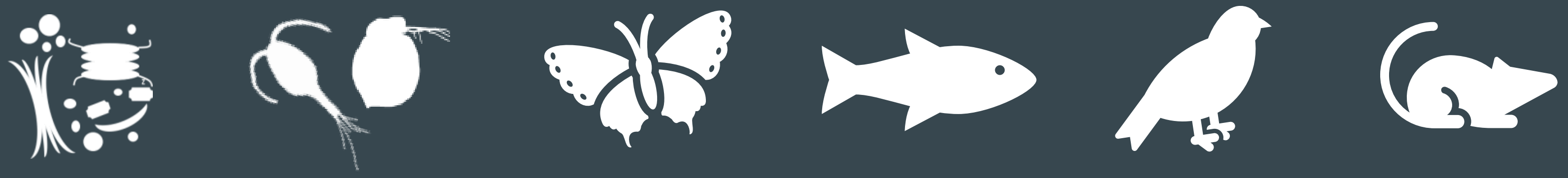
CHAOS IN A NOISY WORLD: NEW METHODS AND EVIDENCE FROM TIME-SERIES ANALYSIS

Stephen Ellner[1,*] and Peter Turchin[2,†]

"… we want to stress that our procedure was biased against finding chaos."
"Our findings of positive Lyapunov exponents in several data sets, despite the biases in our approach, therefore are a strong indication that ecological systems are capable of chaotic behavior."

Our meta-analysis

1. How well do various chaos detection methods work under ecologically realistic conditions (short, noisy data)?
   – Nonparametric, higher-d methods
   – Operate on single time series, substitute lags for unobserved dimensions
2. What happens if we apply the best methods to empirical data from a large number of species around the world?



Rogers et al. (2022) *Nature Ecology & Evolution*

Chaos detection algorithms

Method	
1. Direct estimation of LE	(Rosenstein et al. 1993)
2. Jacobian estimation of LE	(Nychka et al. 1992)
3. Recurrence quantification analysis	(Webber & Zbilut 1994)
4. Permutation entropy	(Bandt & Pompe 2002)
5. Horizontal visibility algorithm	(Luque et al. 2009)
6. Chaos decision tree	(Toker et al. 2020)

Chaos detection algorithms

Method
1. Direct estimation of LE
2. Jacobian estimation of LE
3. Recurrence quantification analysis
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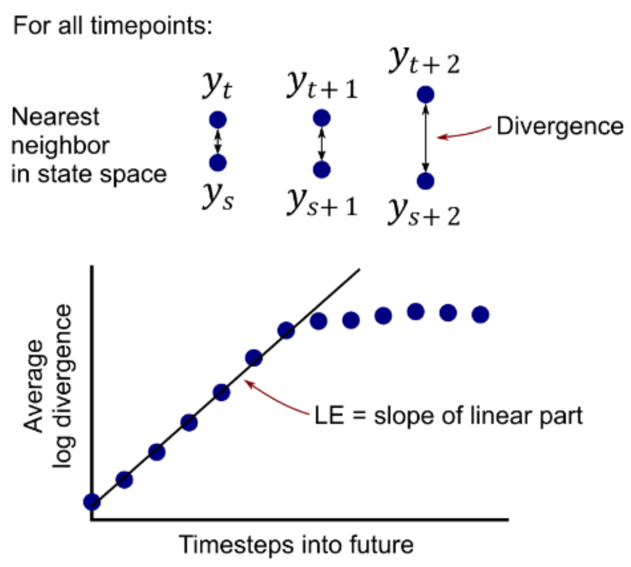
6. Chaos decision tree

Munch et al. (2022) AREES

(a) Direct LE estimation



(b) Jacobian LE estimation

(c) Recurrence Quantification Analysis

(d) Permutation Entropy

Chaos detection algorithms

Method
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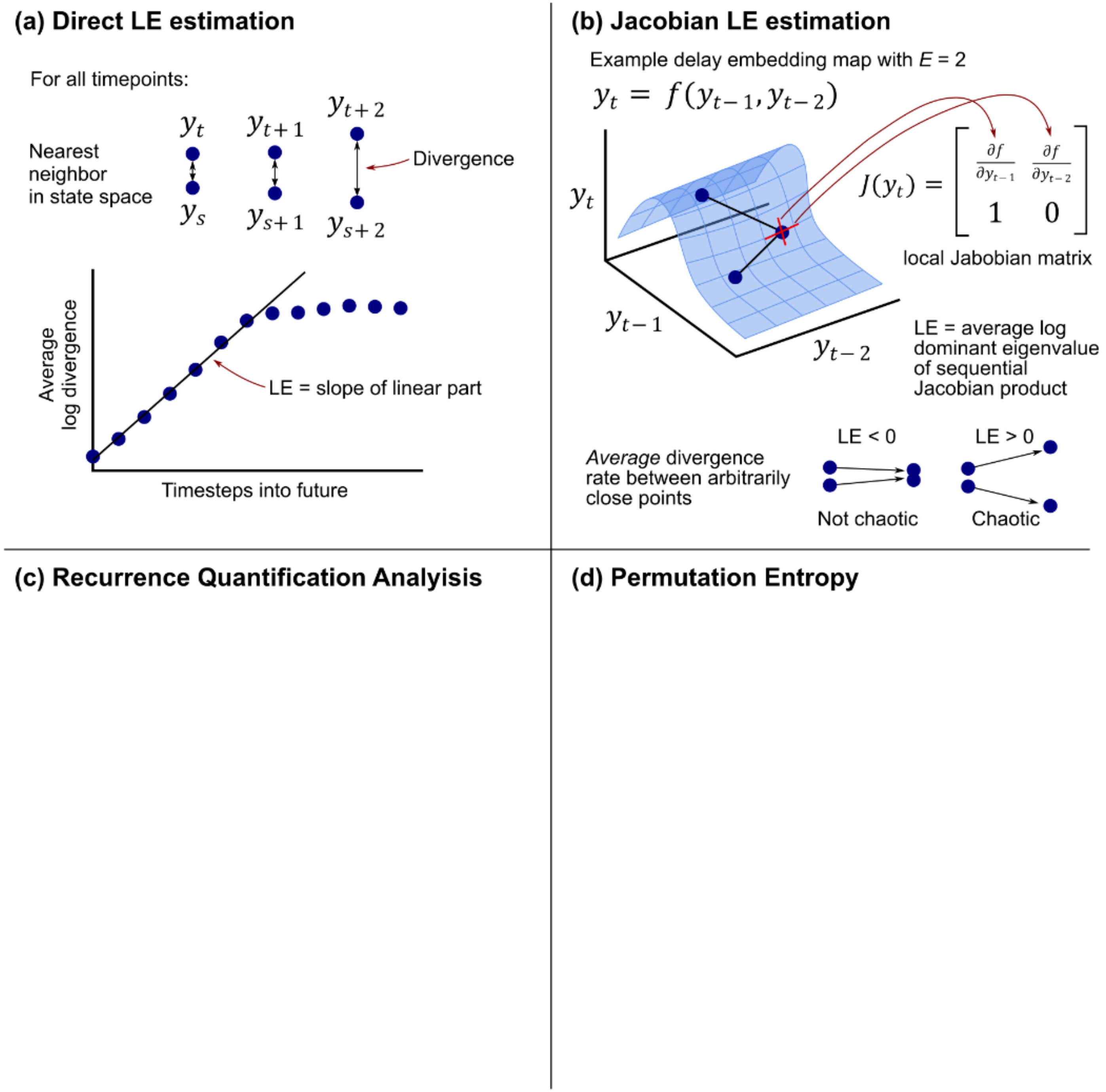

Munch et al. (2022) AREES

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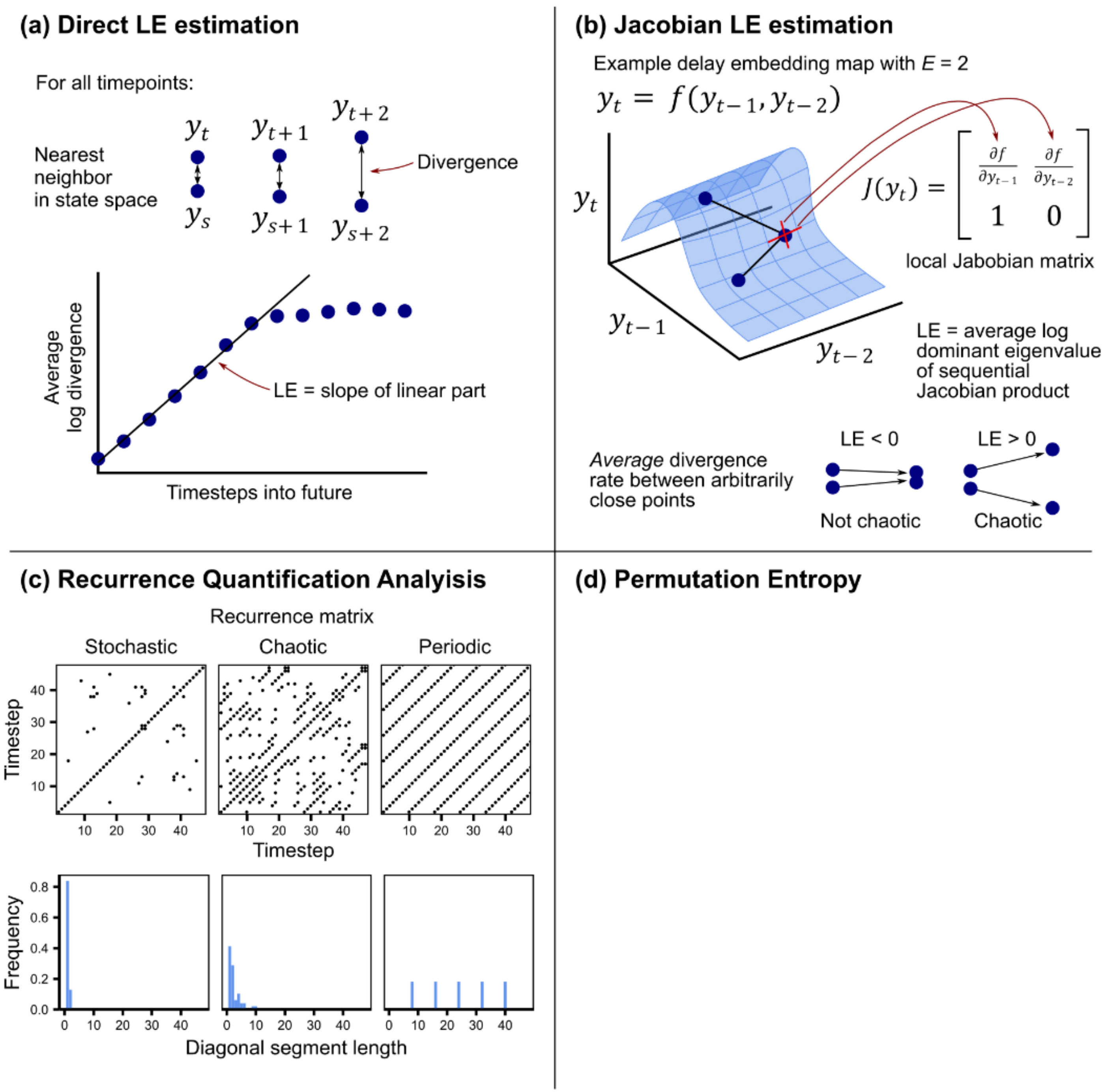

Munch et al. (2022) AREES

Chaos detection algorithms

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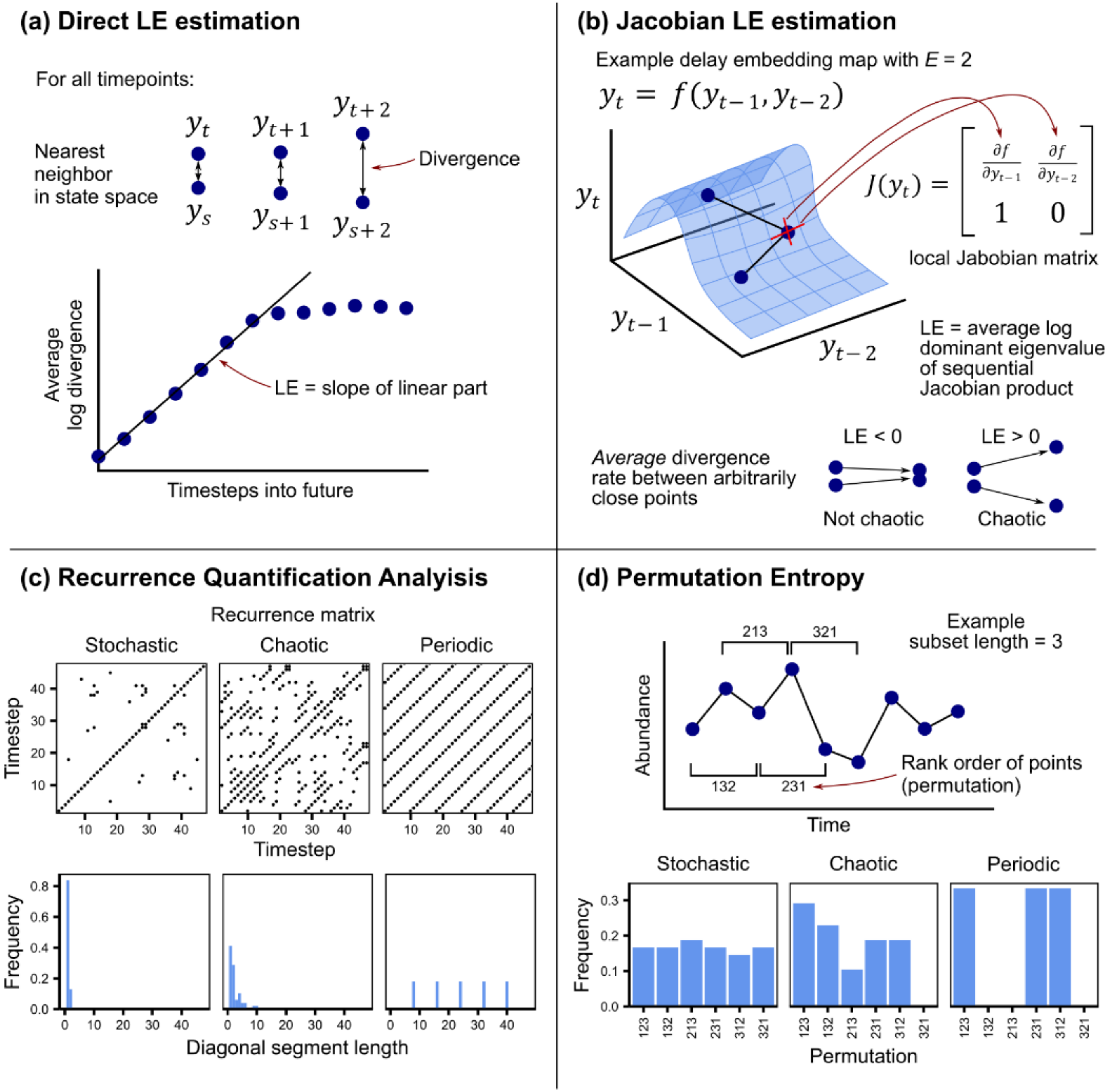


Munch et al. (2022) AREES

Simulation testing

Training/Test dataset

Dynamics	Model	Observation Noise	Time Series Length
Stochastic	WhiteNoise RedNoise RandomWalkTrend RandomWalk Cyclostationary BlueNoise AR1	1% 10% 20% 30%	25 50 75 100 250
Periodic	SineWave Ricker PredatorPrey Logistic8cyc Logistic HostParPar Henon		
Chaotic	Ricker PredatorPrey Poincare Logistic Ikeda HostParPar CubicMap		

- 100 reps for each combination
- 37 different stochastic, periodic, and chaotic models total

Validation dataset #1

Dynamics	Model	Observation Noise	Time Series Length
Stochastic	VioletNoise SinForcedAR1 PinkNoise AR2	1% 10% 20% 30%	25 50 75 100 250
Periodic	Tinkerbell MouseMap Competition		
Chaotic	Tinkerbell MouseMap Competition		

Validation dataset #2

Dynamics	Model	Observation Noise	Process Noise	Time Series Length
Periodic	SeasonalPredPrey NPZ LPA	1% 10% 20% 30%	0% 10% 20% 30%	100
Chaotic	SeasonalPredPrey NPZ LPA			

Simulation results

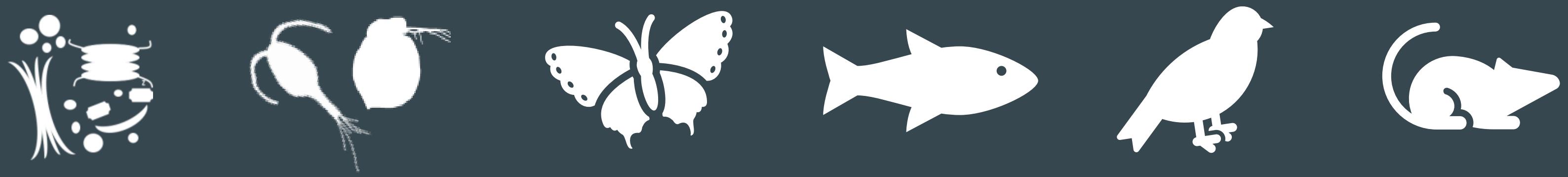
Method	False negative rate	False positive rate
1. Direct estimation of LE	0.08	0.66
2. Jacobian estimation of LE	**0.29**	**0.04**
3. Recurrence quantification analysis	**0.37**	**0.13**
4. Permutation entropy	**0.26**	**0.18**
5. Horizontal visibility algorithm	0.62	0.10
6. Chaos decision tree	0.73	0.02

(Pooled across all test and validation datasets)

- 3 methods were effective classifiers
- Performance similar on test and validation datasets
- Observation and process noise increase false negative rate, but not false positive rate
- Jacobian LE had best performance at short time series lengths

Empirical data

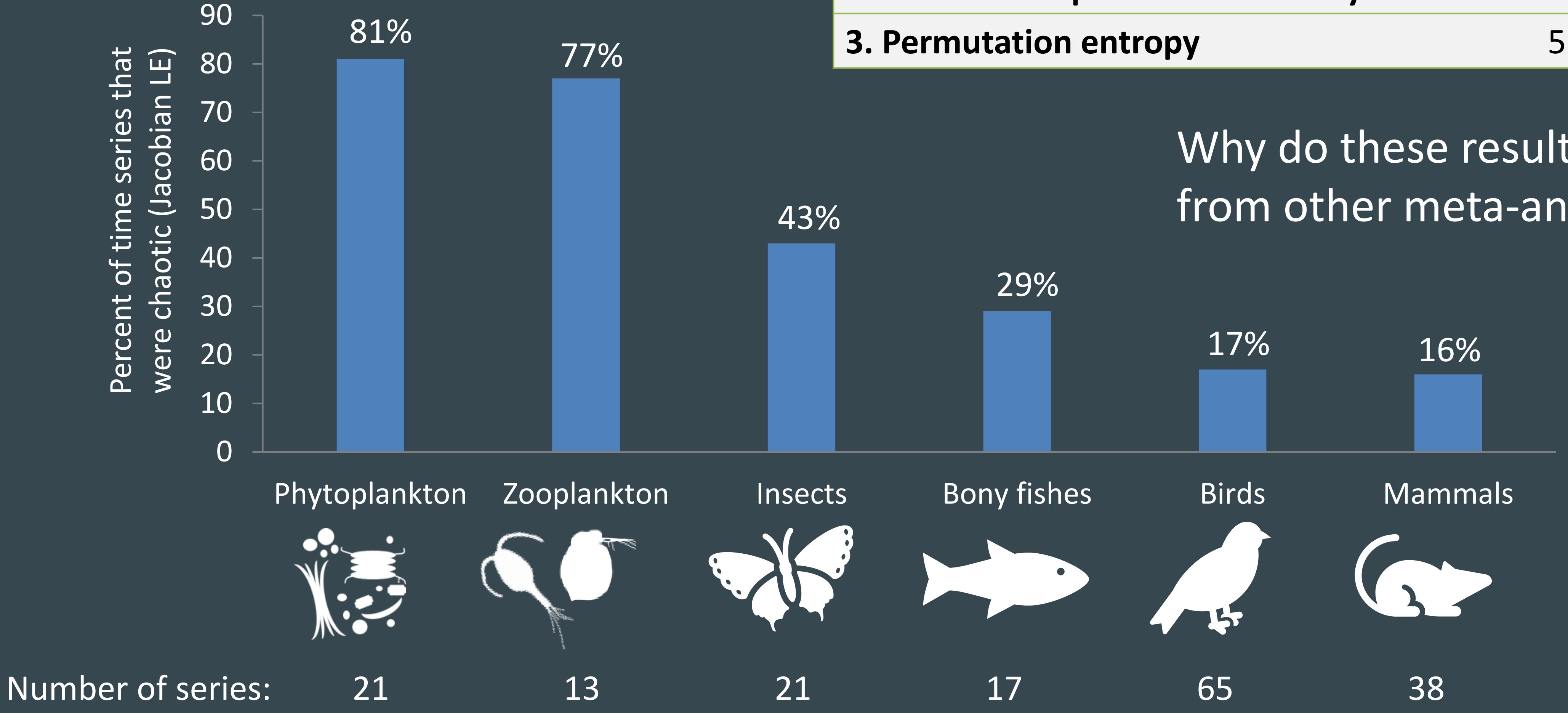
- 172 time series from the Global Population Dynamics Database (GPDD)
  - Field-collected data
  - 138 different taxa
  - 30 to 197 timesteps
  - High-quality subset of the GPDD:
    - length $\geq$30, zeros <60%, missing values <22%, reliability score $\geq$2



Chaos prevalence in the GPDD

- At least 1/3 of time series were chaotic
- Chaos prevalence varied by taxonomic group

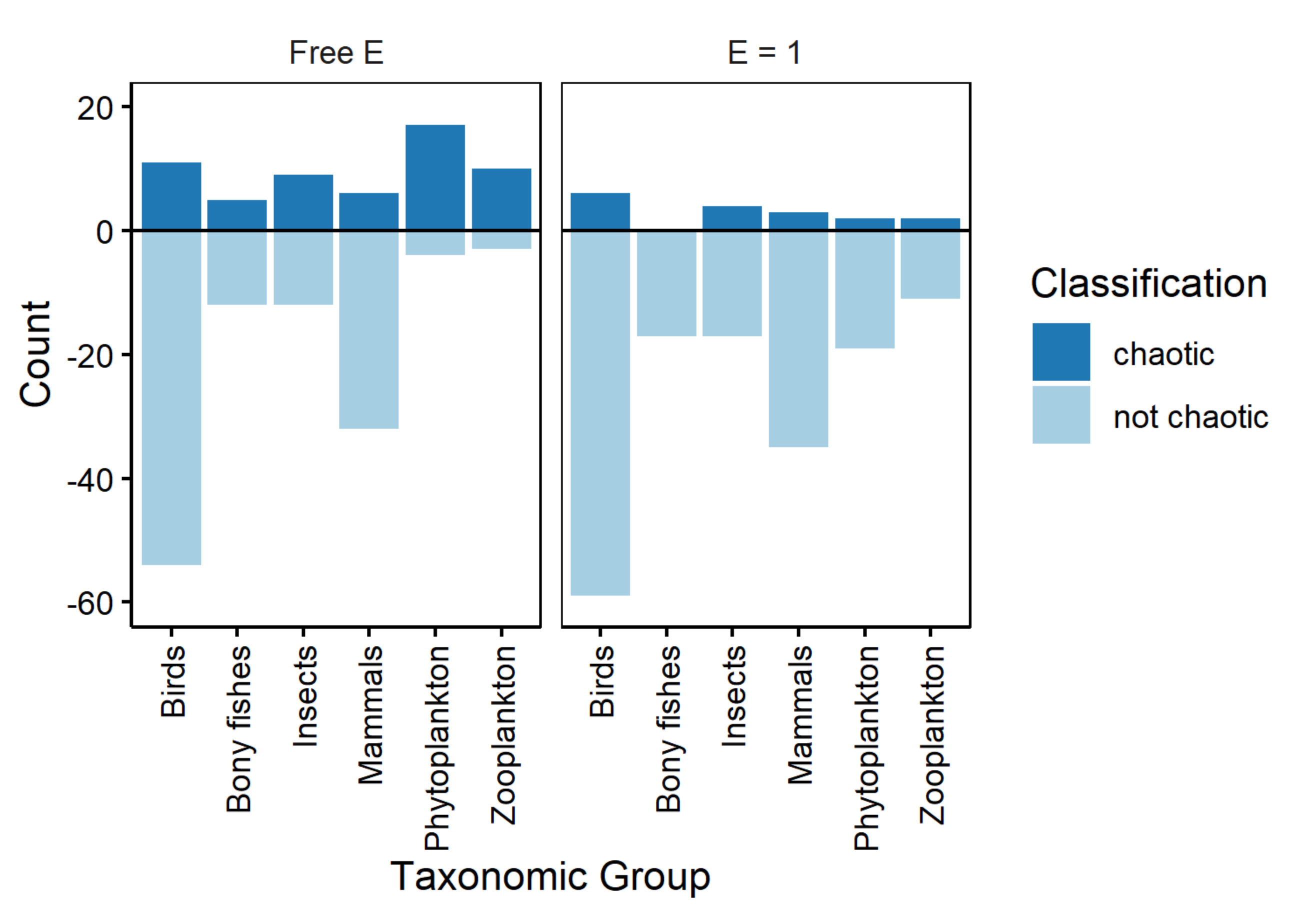
Chaos detection method	GPDD % chaotic (number of series)
1. Jacobian LE	33% (58)
2. Recurrence quantification analysis	42% (74)
3. Permutation entropy	51% (89)



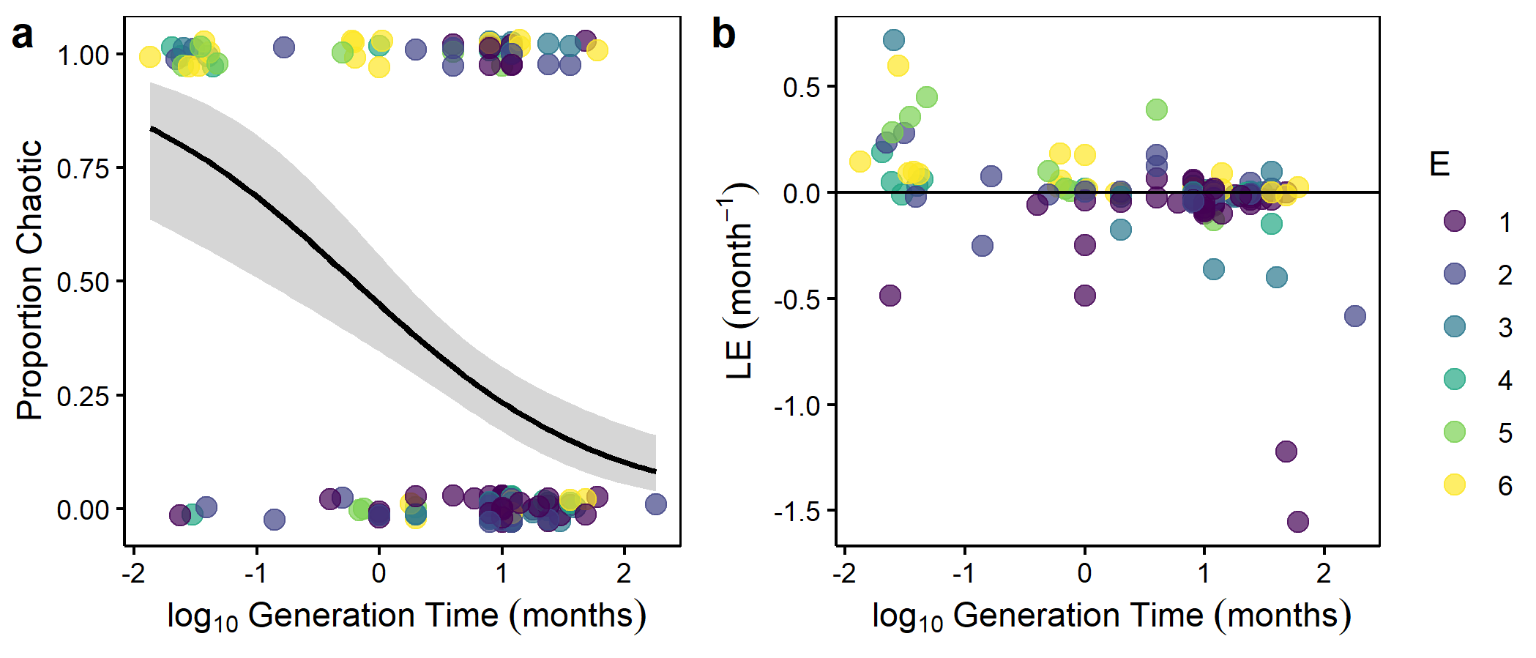
Why do these results differ from other meta-analyses?

Restricted dimensionality reduces ability to detect chaos

- Constraining model used by Jacobian LE to E = 1 (1-d nonparametric model) reduces apparent chaos prevalence to < 10%
- Constraining to 1-d parametric models reduces to < 6%



Chaos more prevalent in shorter-lived species



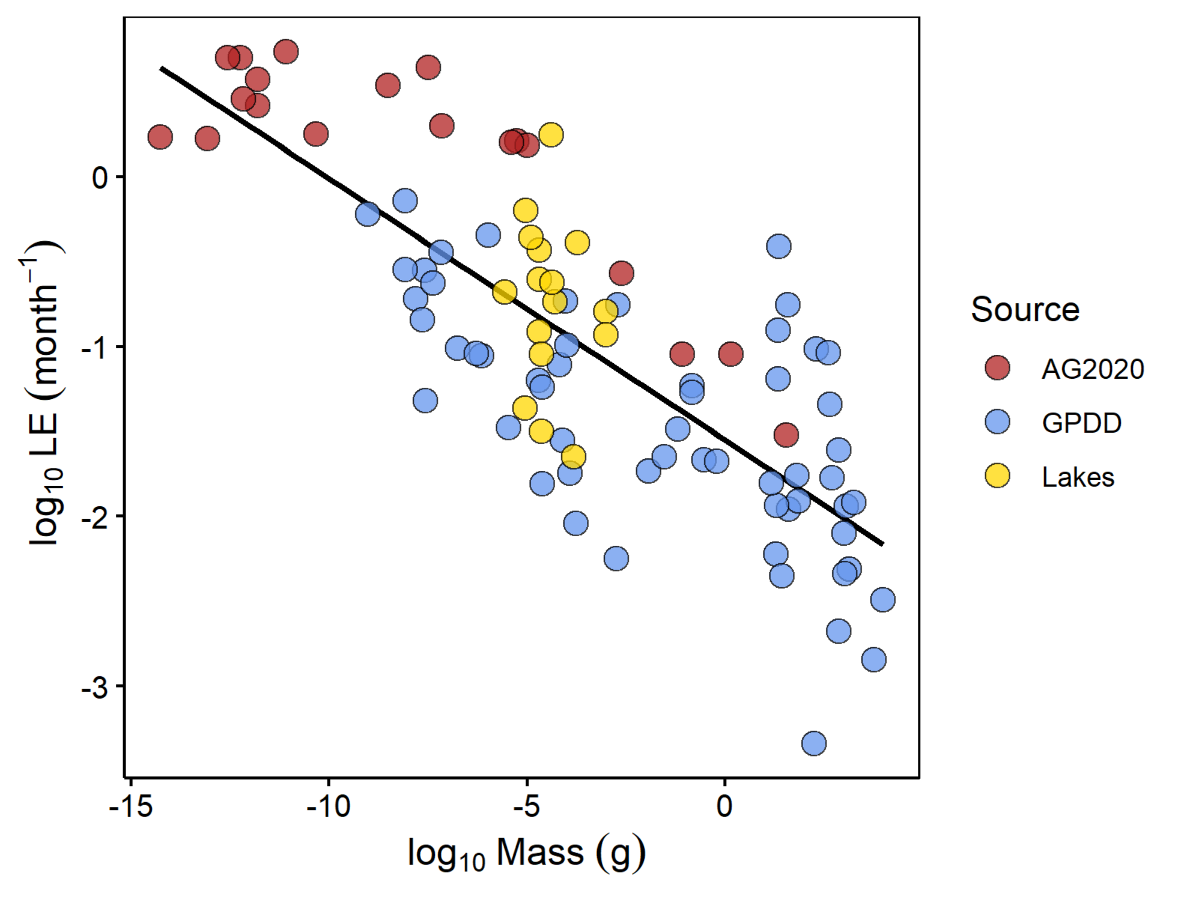
Possibly because long-lived species:

- may be better insulated from chaotic environmental drivers
- have lower average mortality rates, hence potentially weaker interactions with other species (per unit time, but not generation)
- have fewer generations sampled (detection depends on time series length relative to intrinsic time scale)

Positive LEs scale with body size

- Combined results with independently estimated LEs from laboratory and field studies (Anderson & Gilooly 2020)
- Consistent relationship with scaling of about -1/6
- Additional values from lake zooplankton are consistent with this relationship

slope = -0.16



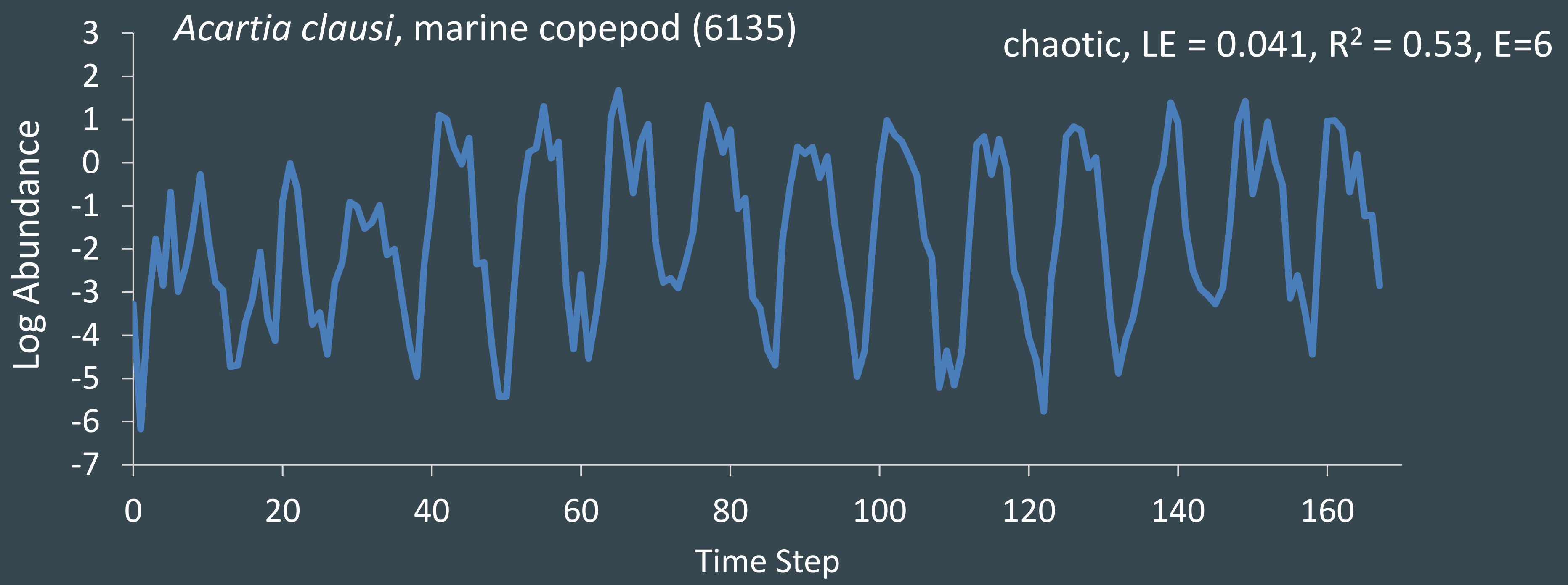
microbes
zooplankton
vertebrates

But is it *really* chaos? Couldn't it just be…

- Noise?
  - Noise increases false negative rate, not false positive
  - Chaotic series are more variable, but not necessarily less predictable
  - Consistent mass scaling with low-noise laboratory studies
- Nonstationarity (e.g. exponential growth)?
  - Median growth rates (around 0) do not differ between chaotic and not chaotic series
  - Most chaotic series do not have a monotonic trend
  - Only few cases of exp. growth misclassified as chaos

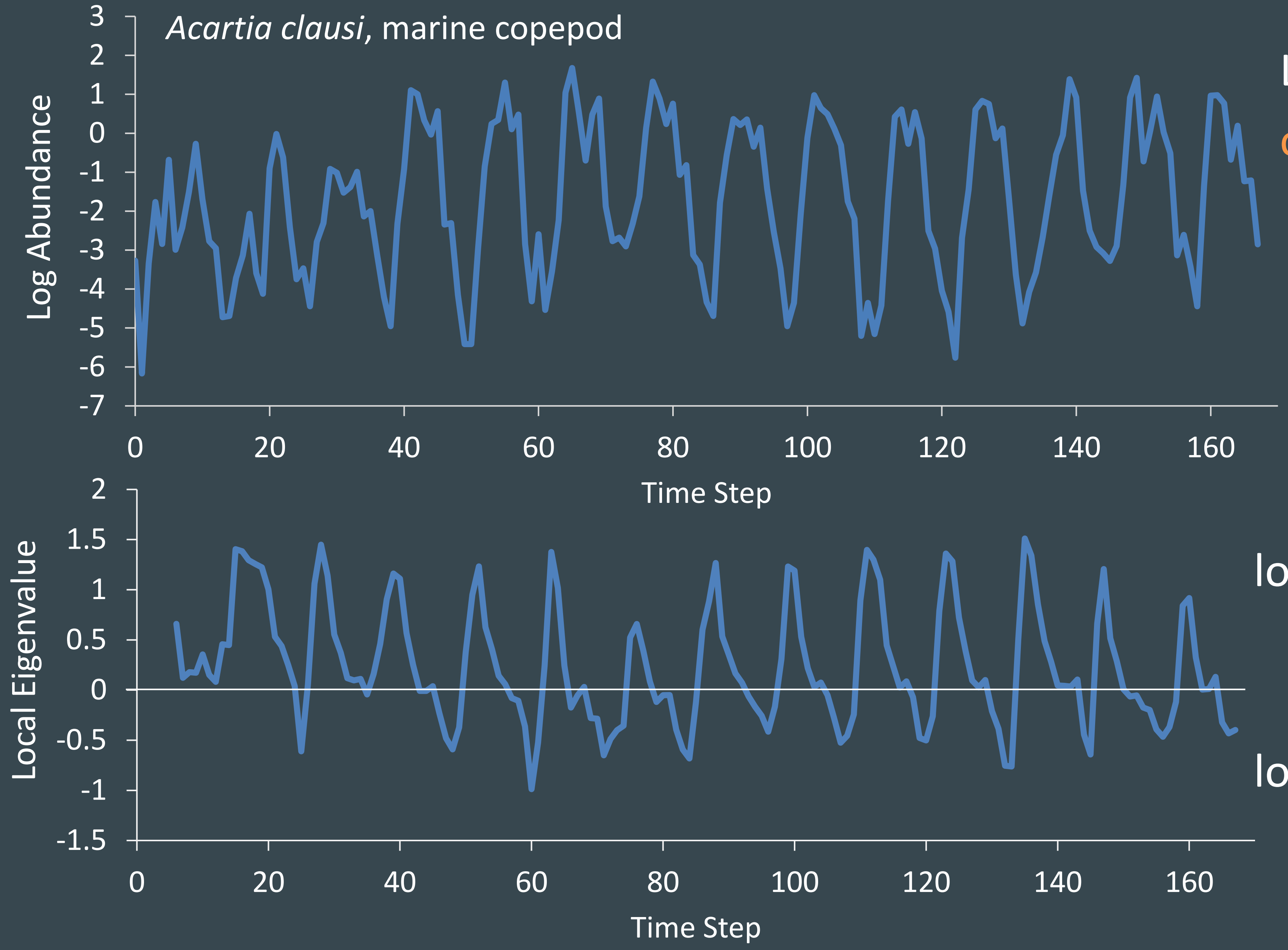
But is it *really* chaos? Couldn't it just be…

- Chaotic advection of marine plankton?
  - 47% of additional lake zooplankton time series were chaotic
  - Time series show persistent seasonal peaks/troughs that are not likely due to advection
  - Consistent mass scaling unlikely to be due to advection



Part 2: Intermittent instability

Global vs. local stability



LE = + 0.041 (chaotic)

overall stability

How widespread is this time-varying local stability and what are these patterns related to?

locally unstable

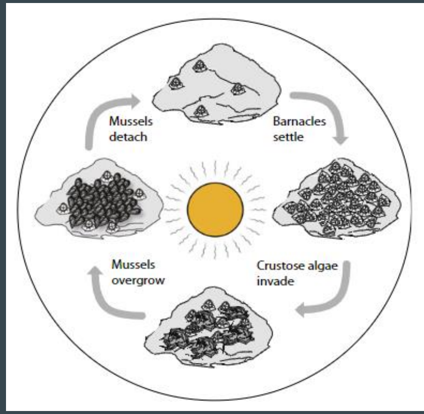
local stability

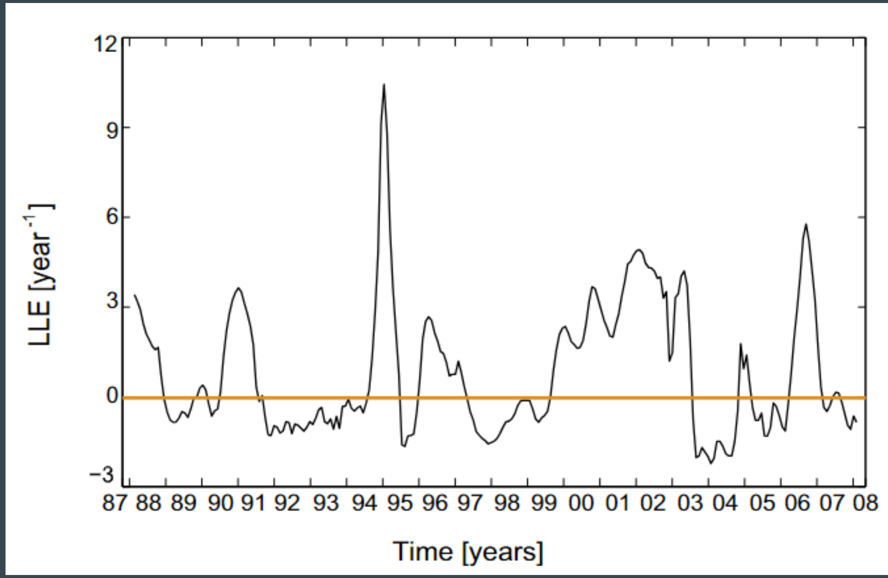
locally stable

Global vs. local stability

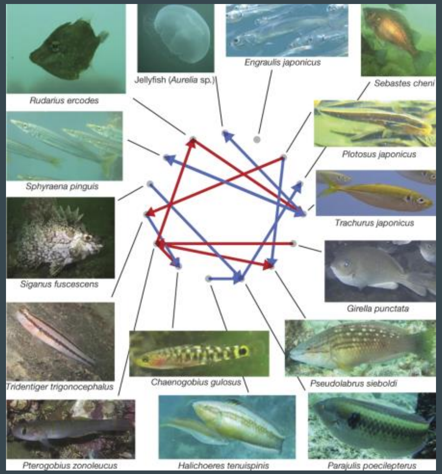
Beninca et al. 2015
New Zealand rocky shore

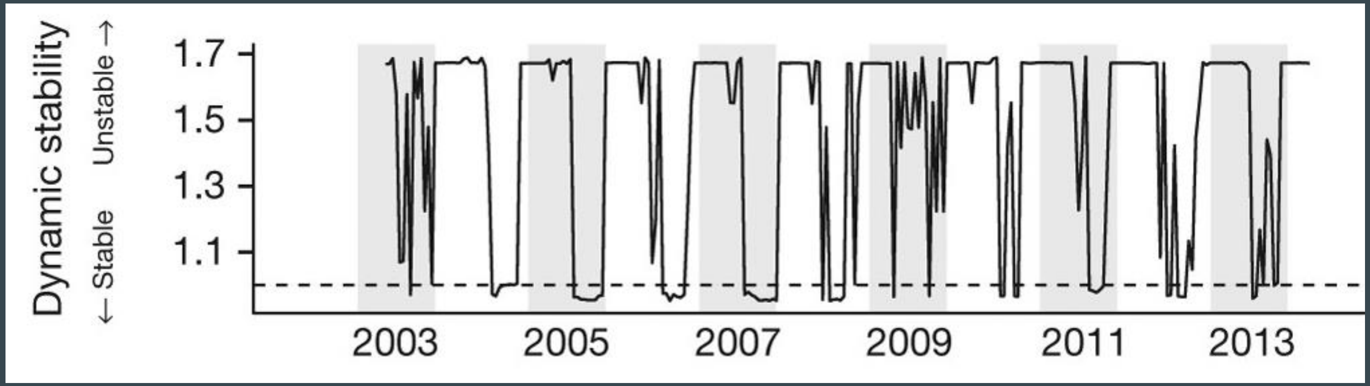
LE ≈ 0





Ushio et al. 2018
Japanese fish
community





Research Approach

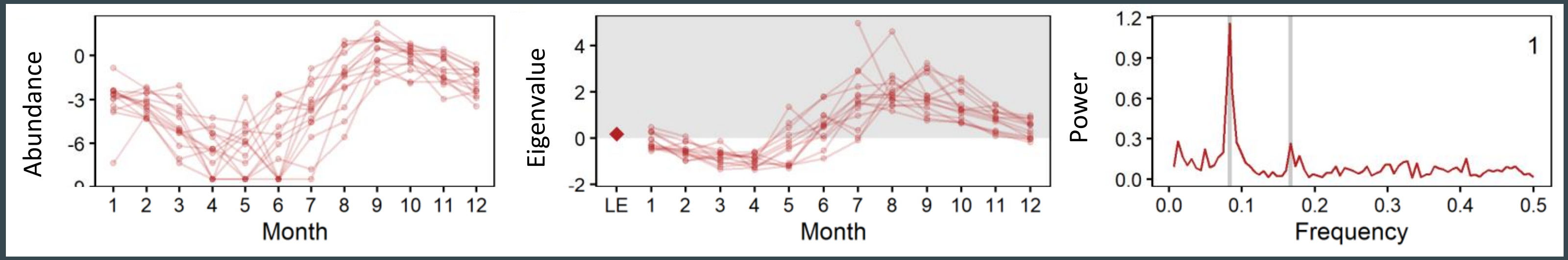
- Assembled monthly plankton time series data from 17 lakes and 4 marine sites (154 species-level time series)
- Used Jacobian method to compute LE and local stability
- We then assessed:
  - prevalence of chaos and seasonal fluctuations in local stability
  - relationship between local stability and predictability
  - across-site variation in LEs and seasonality of local stability
  - how results are affected by level of data aggregation
    - species
    - functional group
    - trophic level (total phytoplankton, total zooplankton)

Rogers et al. (2023) *Ecology Letters*

Local stability sometimes oscillates

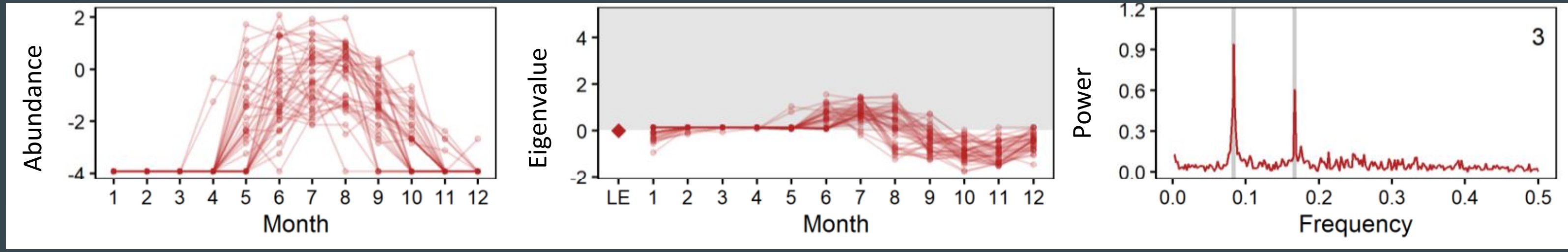
Abundance | Local stability | Local stability (Power spectrum)

Paracalanus parvus
Port Erin Bay



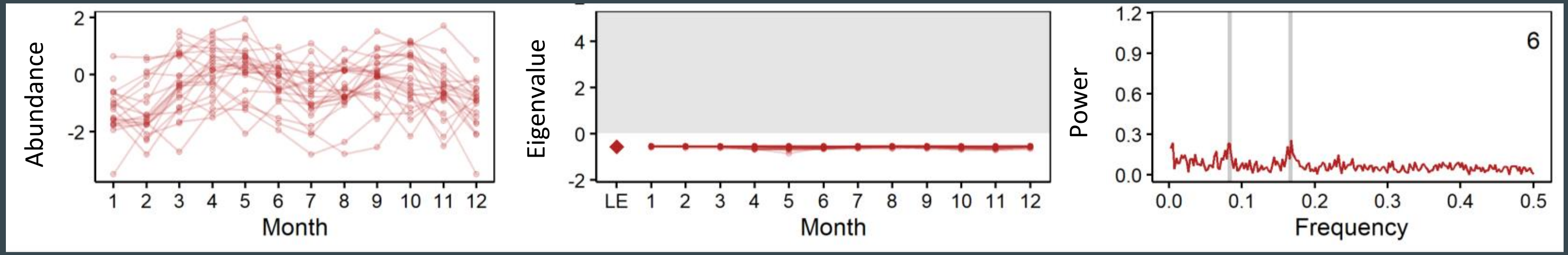
Chaotic (LE = + 0.18)
Local instability
Seasonality

Leptodora kindtii
Lake Müggelsee



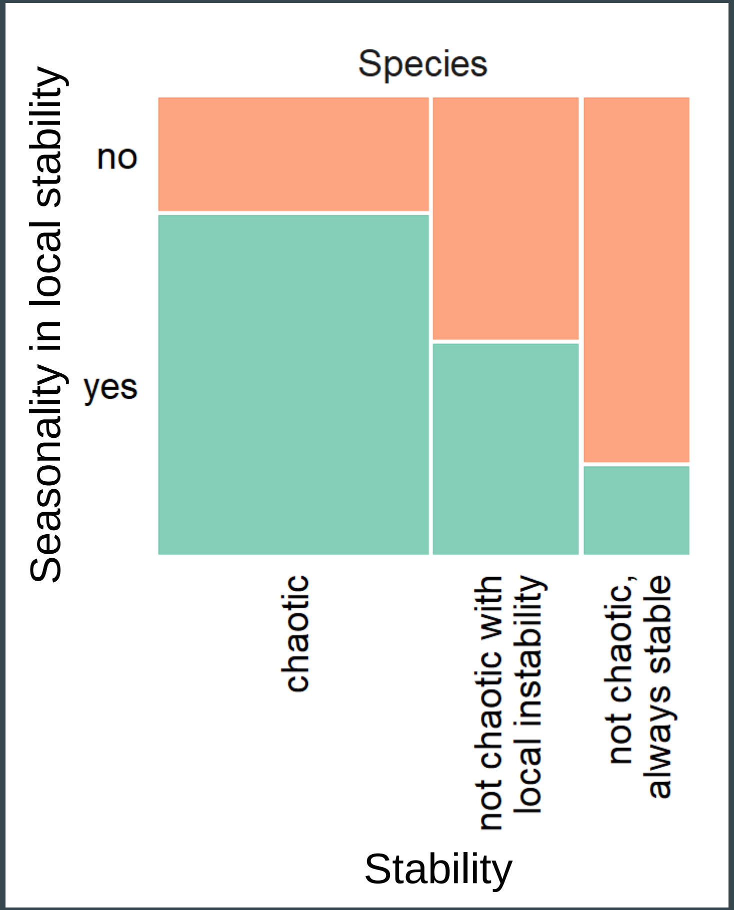
Non-chaotic (LE = − 0.0024)
Local instability
Seasonality

Cyclops prealpinus
Lake Geneva



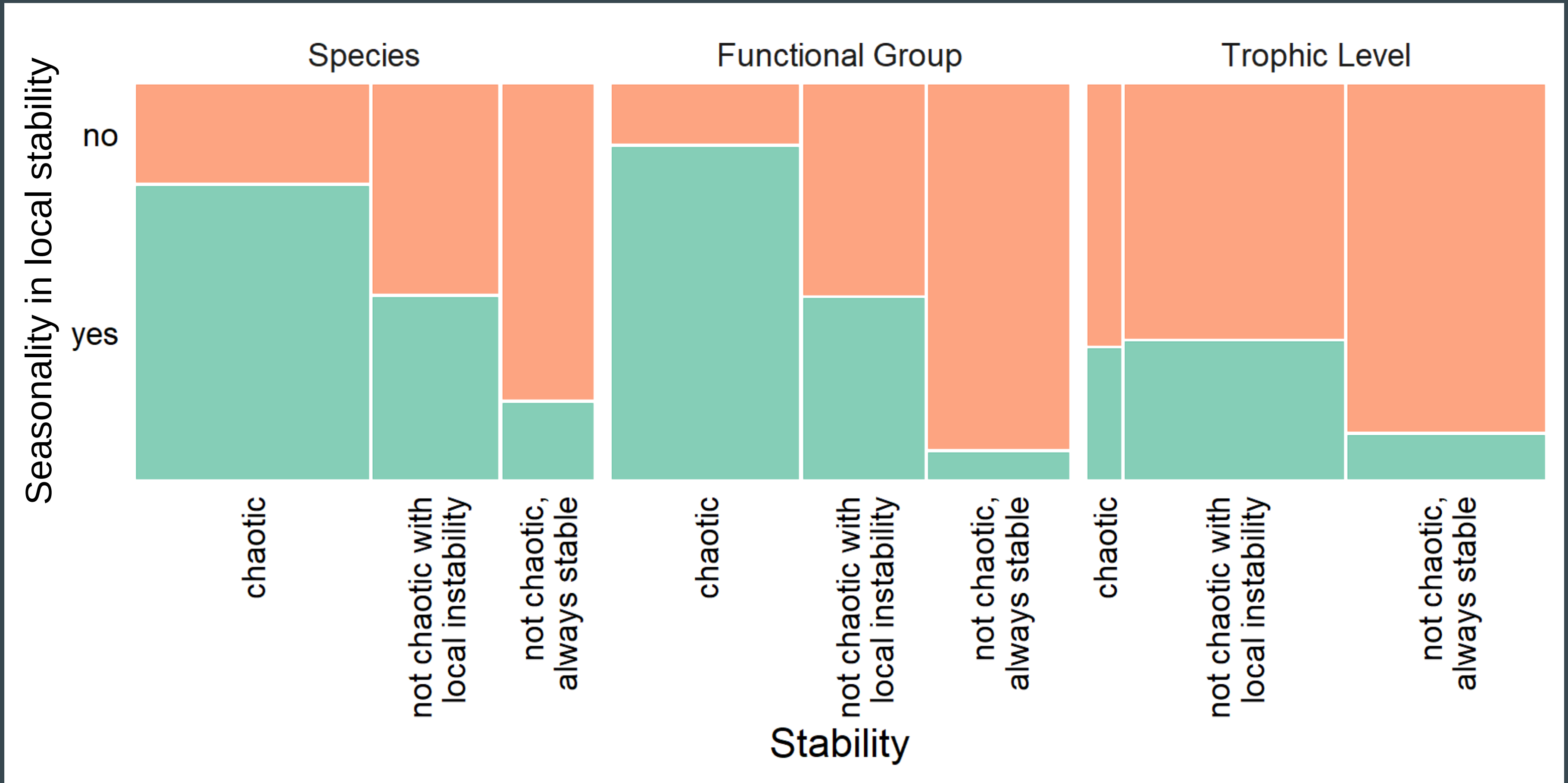
Non-chaotic (LE = − 0.57)
Always locally stable
No seasonality

Summary of stability patterns



- Seasonal oscillations in local stability common in chaotic series, also seen in and non-chaotic (but locally unstable) series

Summary of stability patterns

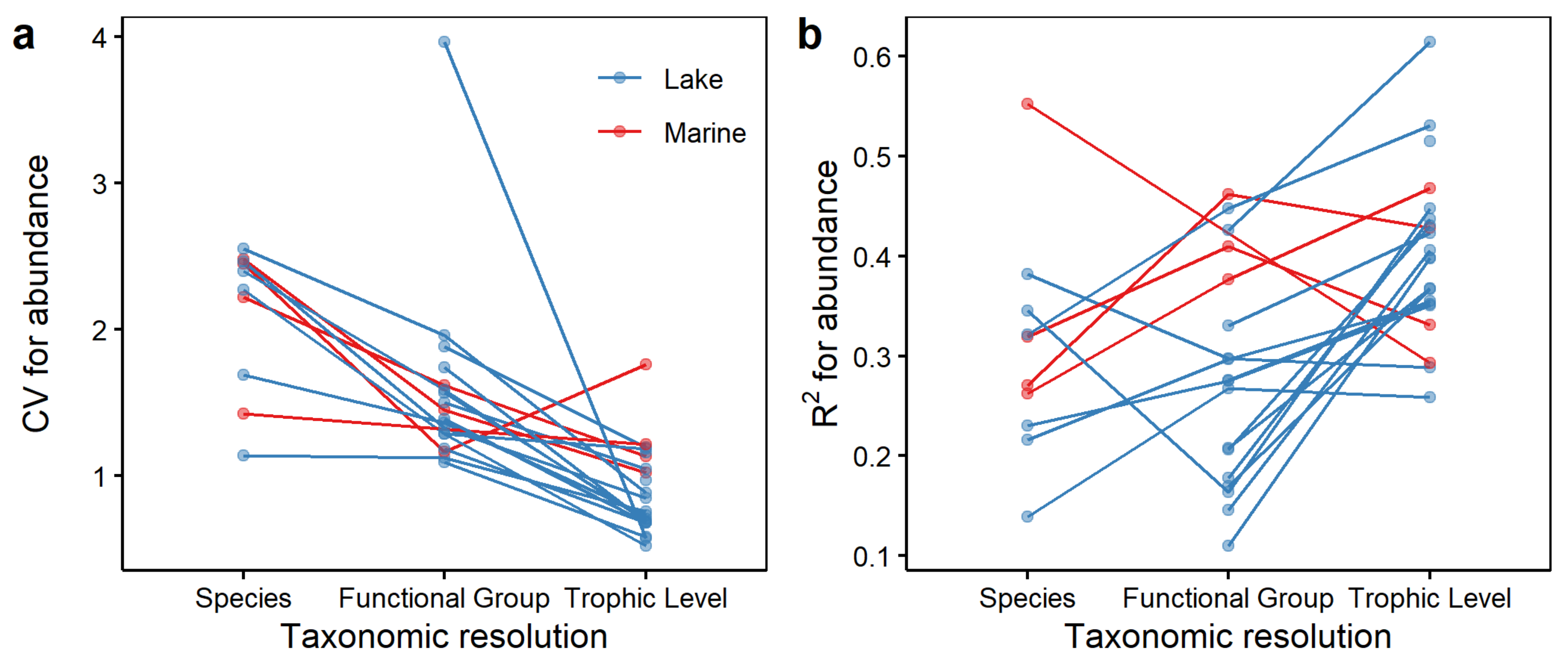


Level of taxonomic aggregation	% chaotic
Species	52%
Functional group	42%
Trophic level	7%

- Chaos detected less frequently with taxonomic aggregation

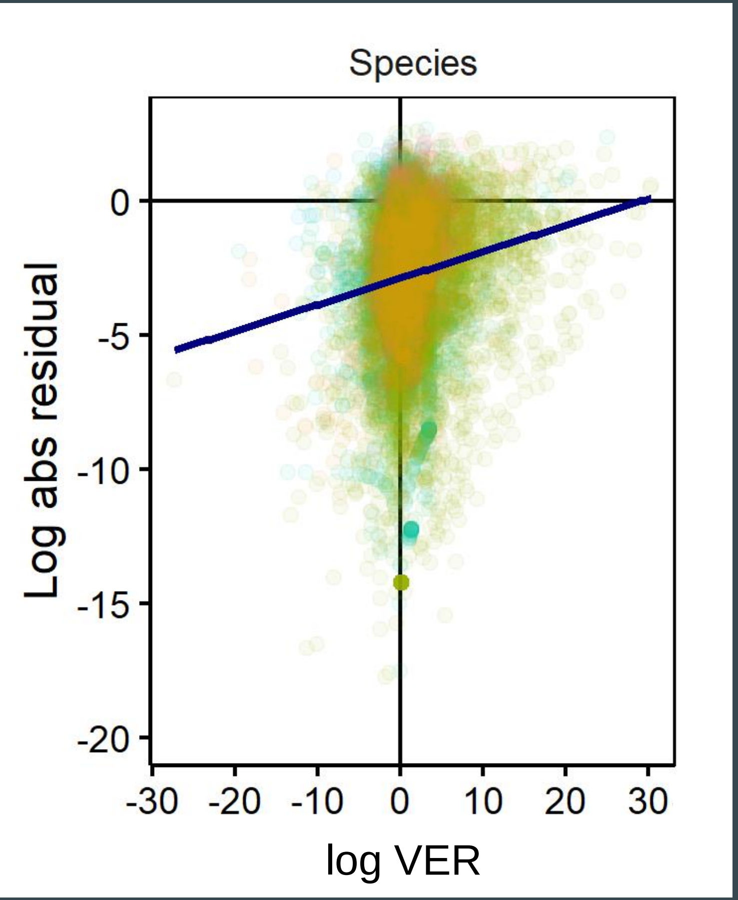
- Seasonal oscillations in local stability common in chaotic series, also seen in and non-chaotic (but locally unstable) series

Aggregates less variable and more predictable



- Increased predictability not expected if species just fluctuating independently
- Suggests species fluctuate out of phase due to dynamics (e.g. complementarity)
- Aggregation smooths over dynamics

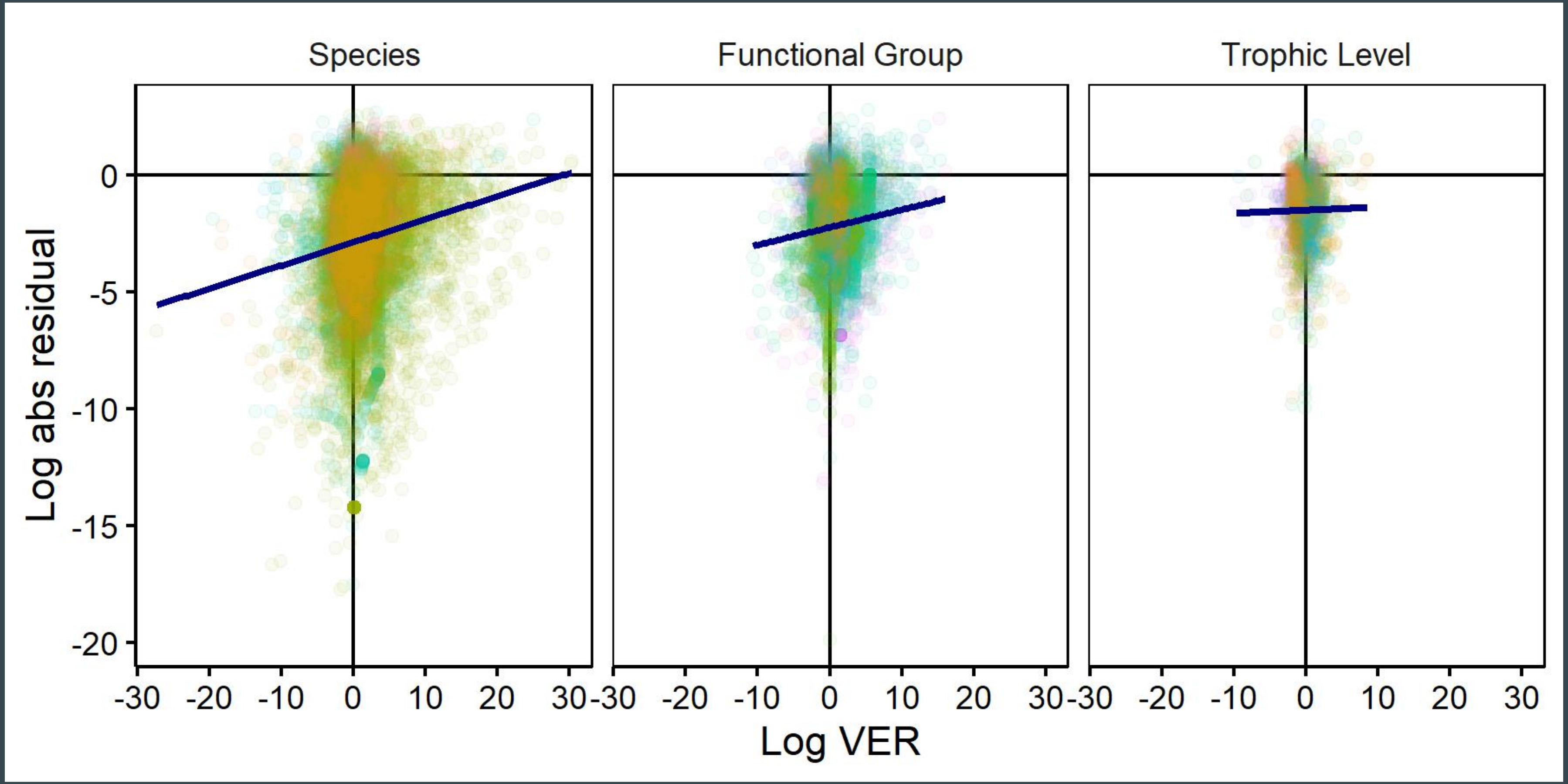
Local instability related to step-ahead prediction error



- Suggests periods of higher/lower forecastability throughout the year

VER = variance expansion ratio:
a less conservative measure of local stability, $tr(J(x_t)J(x_t)^T)$

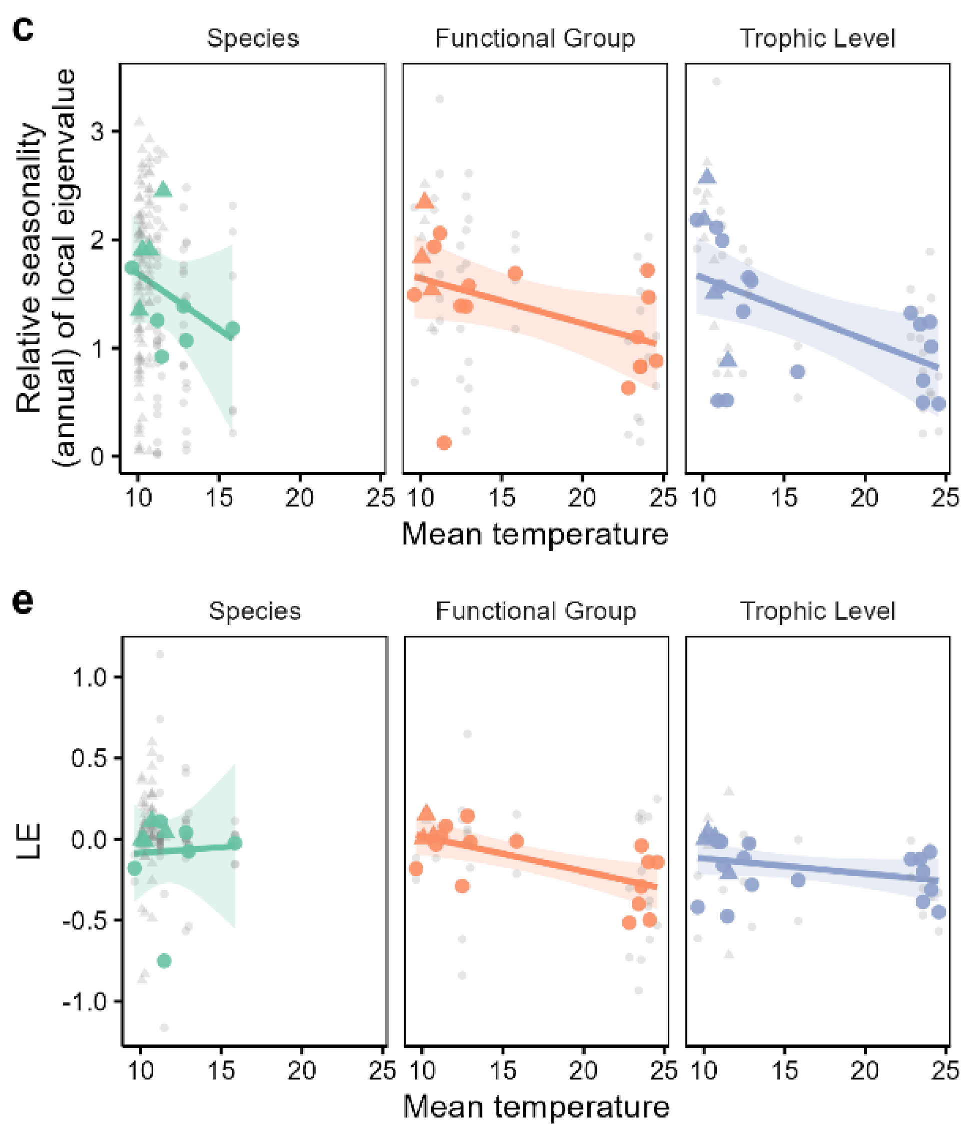
Local instability related to step-ahead prediction error



VER = variance expansion ratio:
a less conservative measure of local stability, $tr(J(x_t)J(x_t)^T)$

Across-site variation in stability

- Sites with lower mean temperature (higher latitude) had:
  - higher relative seasonality in local eigenvalues
  - higher LEs
- Only at coarser taxonomic resolution



Conclusions / Take Aways

- Ecosystems are not 1-d
  - 1-d population models can mischaracterize dynamics, treating complexity as noise
  - May (1976): 1-d models “do great violence to reality”
- Chaos is not ‘rare’
  - Birds and mammals (least chaotic taxa) were 59% of time series analyzed, but are <1% of species on earth; chaos may be considerably more common than ⅓
- Local stability can vary over time
- Implications for management (esp. short-lived species)
  - Short-term forecasting may be feasible, but precise long-term prediction impossible
  - Prediction may be more feasible for taxonomic aggregates
  - Prediction accuracy, sensitivity to change, management efficacy may be greater at certain times of year
  - Re-think use of linear statistical models, 1-d population models, steady-state management policies – is this the best we can do?
  - Perhaps avoid defining objectives in terms of equilibrium conditions, consider index-based management
- Opportunity to use increasing data and modern algorithms to better characterize and understand complex, non-equilibrium, and high-dimensional ecological dynamics

Acknowledgements

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  - NOAA High Performance Computing and Communications
  - SeaGrant number NA19OAR4170353
  - Lenfest Oceans Program

Rogers et al. (2022) Chaos is not rare in natural ecosystems. *Nature Ecology & Evolution*

Rogers et al. (2023) Intermittent instability is widespread in plankton communities. *Ecology Letters*

Munch, Rogers, et al. (2022) Rethinking the prevalence and relevance of chaos in ecology. *Annual Review of Ecology, Evolution, and Systematics*

Thanks for your attention