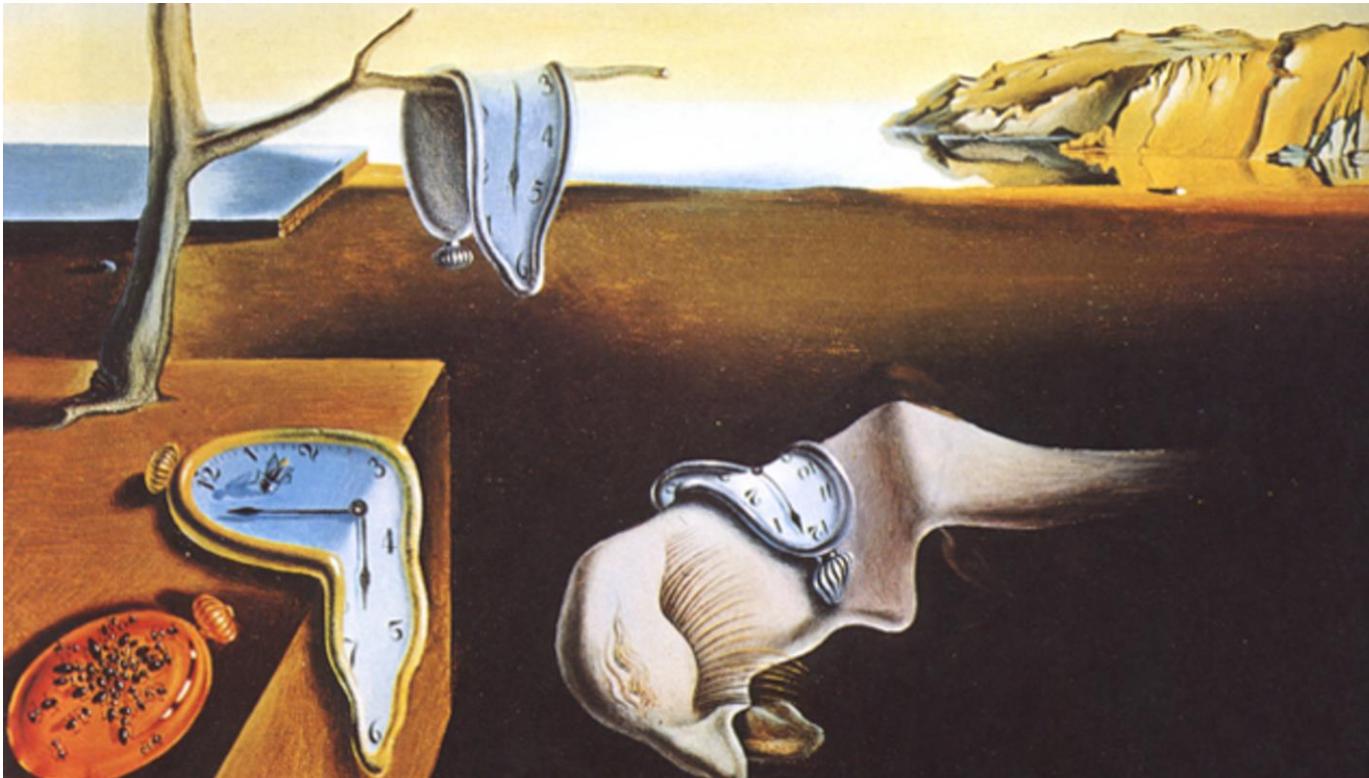


# Biodiversity patterns across space and time



Federico Riva, PhD

McGill, BIOL 310

February 9<sup>th</sup>, 2022

[federicoriva@cunet.carleton.ca](mailto:federicoriva@cunet.carleton.ca)

<https://github.com/FedericoRiva>

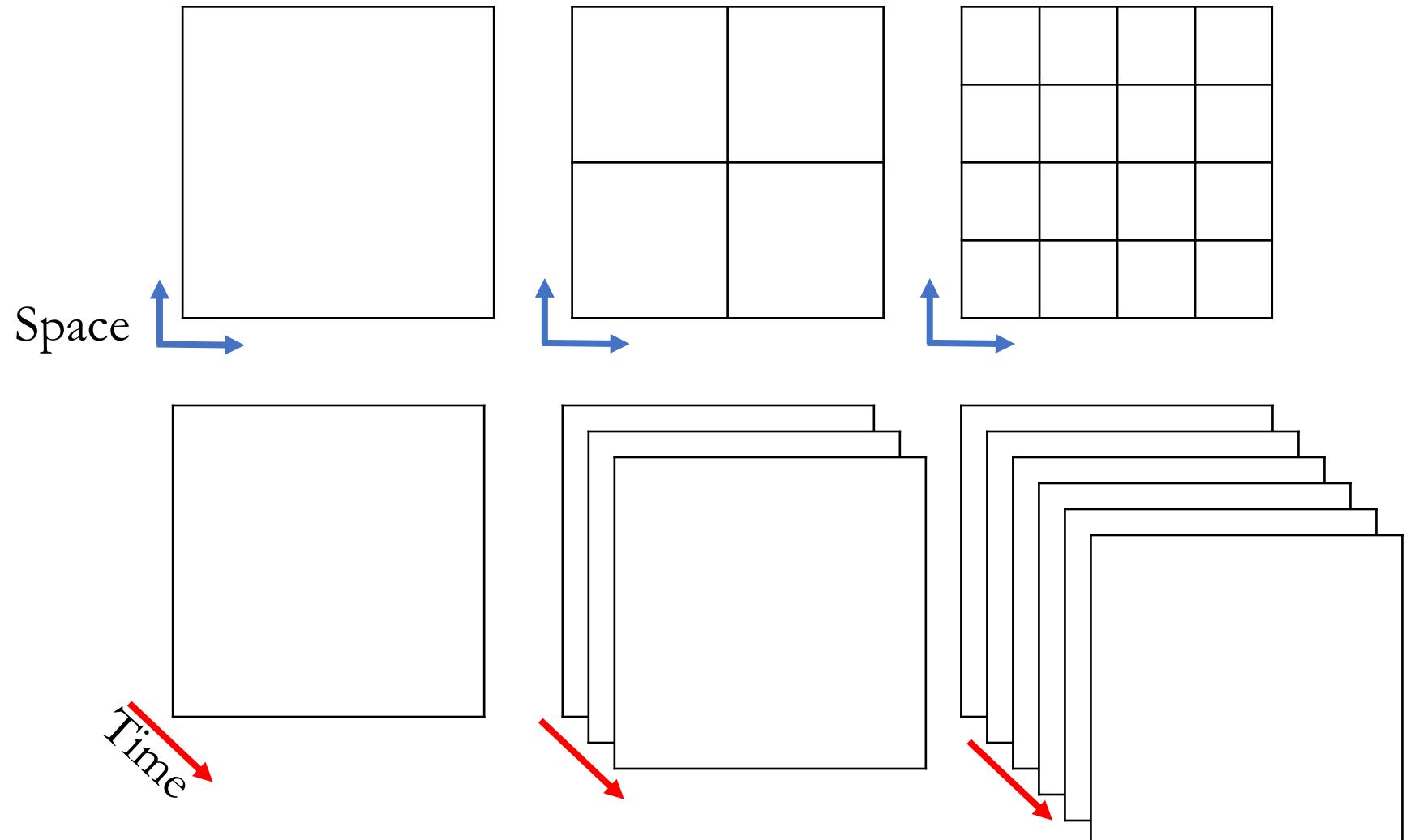
 @riva\_ecology

# Summary

- Defining scales
- The complexity of natural systems
- Scales in ecology and conservation
  - History of research on scales
  - Theory to understand biodiversity in space and time
  - The role of scales in solving long-standing debates
  - Applied implications
- Conclusions
  - How to deal with scales in your own work
  - R workshop

“In ecology, scale usually refers to the spatial and temporal dimensions of a pattern or process”

Spatial scale



Temporal scale

Resolution

Today, my goal is convincing you that the spatial and temporal scales of your analysis are crucial to interpreting your findings

**Complexity in ecology:  
why we need scales to begin with**

Trends in Ecology & Evolution

CellPress  
REVIEWS

Opinion

## Protecting Biodiversity (in All Its Complexity): New Models and Methods

nature  
ecology & evolution

ARTICLES

<https://doi.org/10.1038/s41559-021-01644-4>



**Ecological network complexity scales with area**

# ECOGRAPHY

Forum

Future restoration should enhance ecological complexity and emergent properties at multiple scales

PNAS

Proceedings of the  
National Academy of Sciences  
of the United States of America

Key

Home

Articles

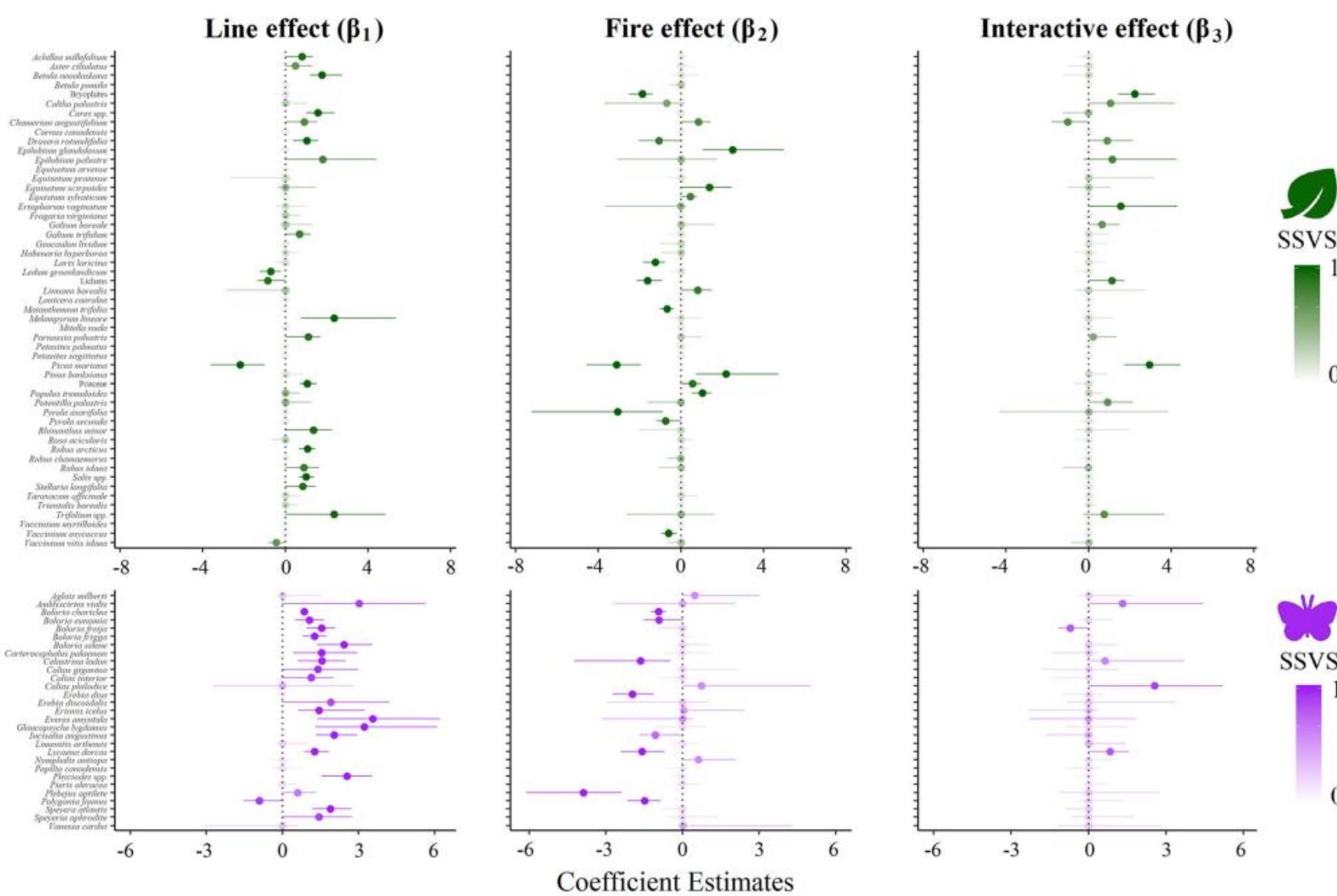
Front Matter

News

Podcasts

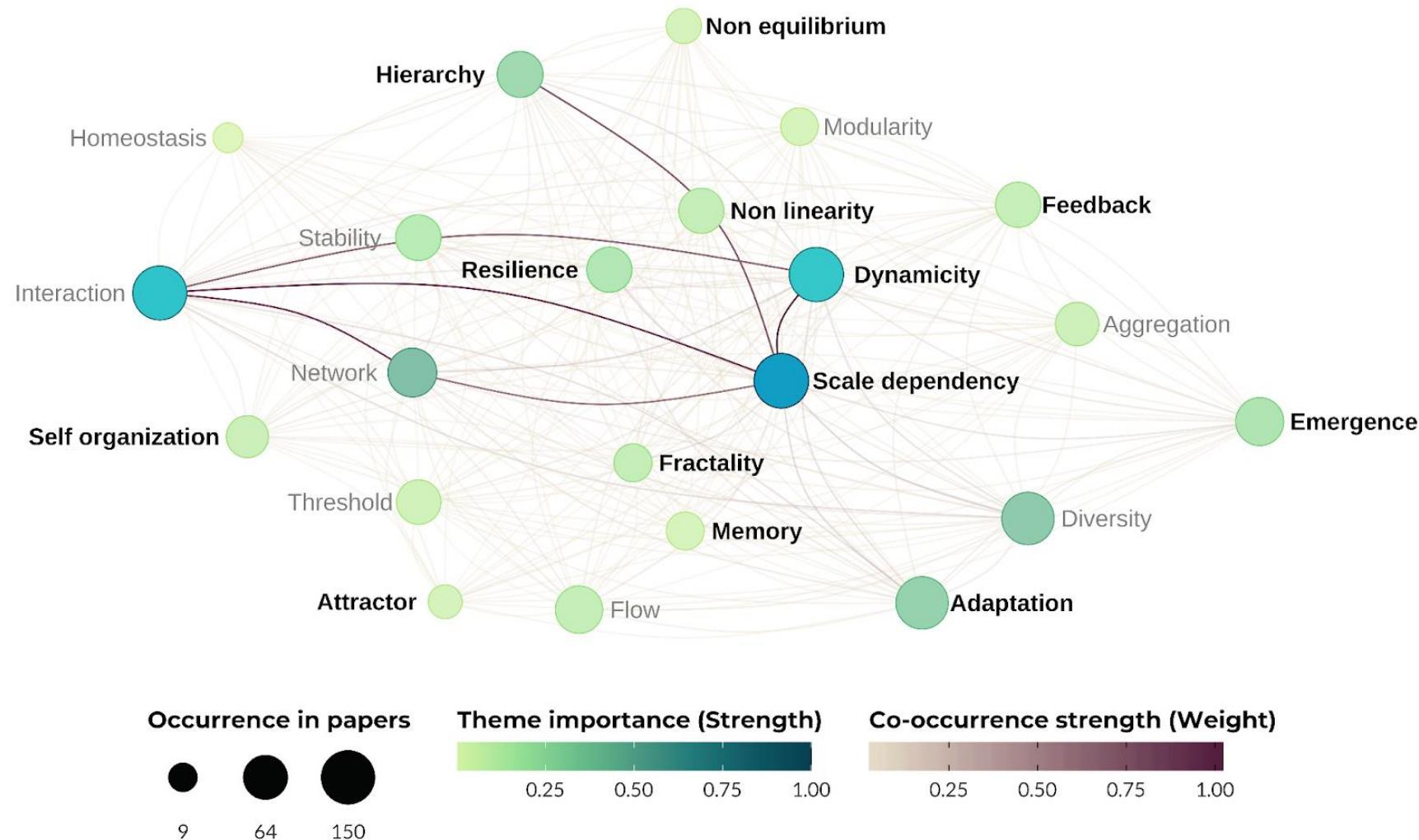
RESEARCH ARTICLE

Multiscale structural complexity of natural patterns

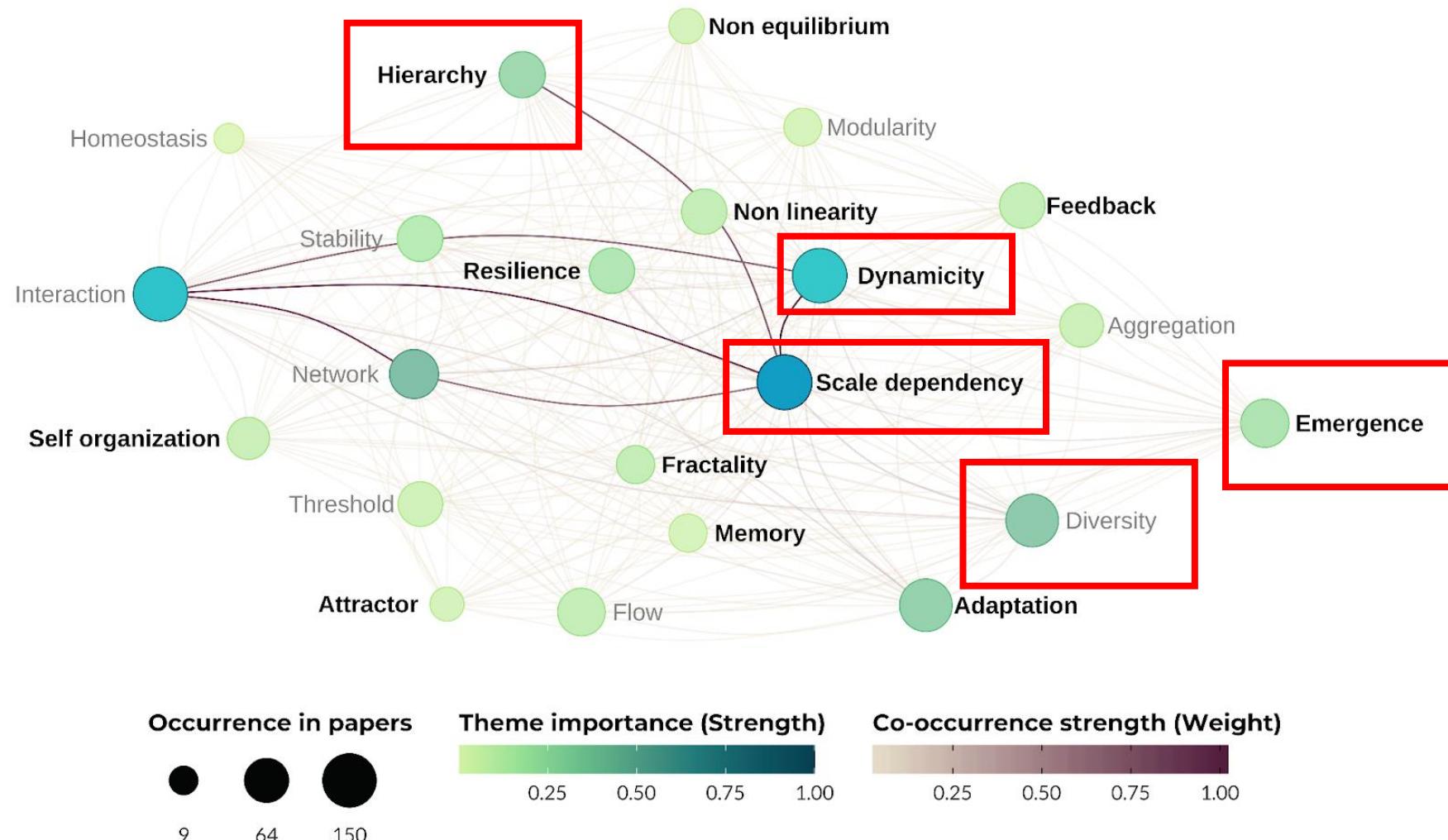


**Figure 3.** Posterior median estimates and highest posterior density (HPD) intervals estimated using single-species GLMMs predicting responses to cutlines ( $\beta_1$ ), wildfire ( $\beta_2$ ), and their interactive effects ( $\beta_3$ ). Interactive effects represent deviations from expected additive effects of line and fire effects in burned cutlines. Colors represent the results of stochastic search variable selection (SSVS) performed on individual model parameters, with darker colors presenting higher likelihood of effect. Posterior median estimates of each parameter, HPD intervals, and SSVS visualized in Figure 3 are provided in electronic supplementary material (ESM1).

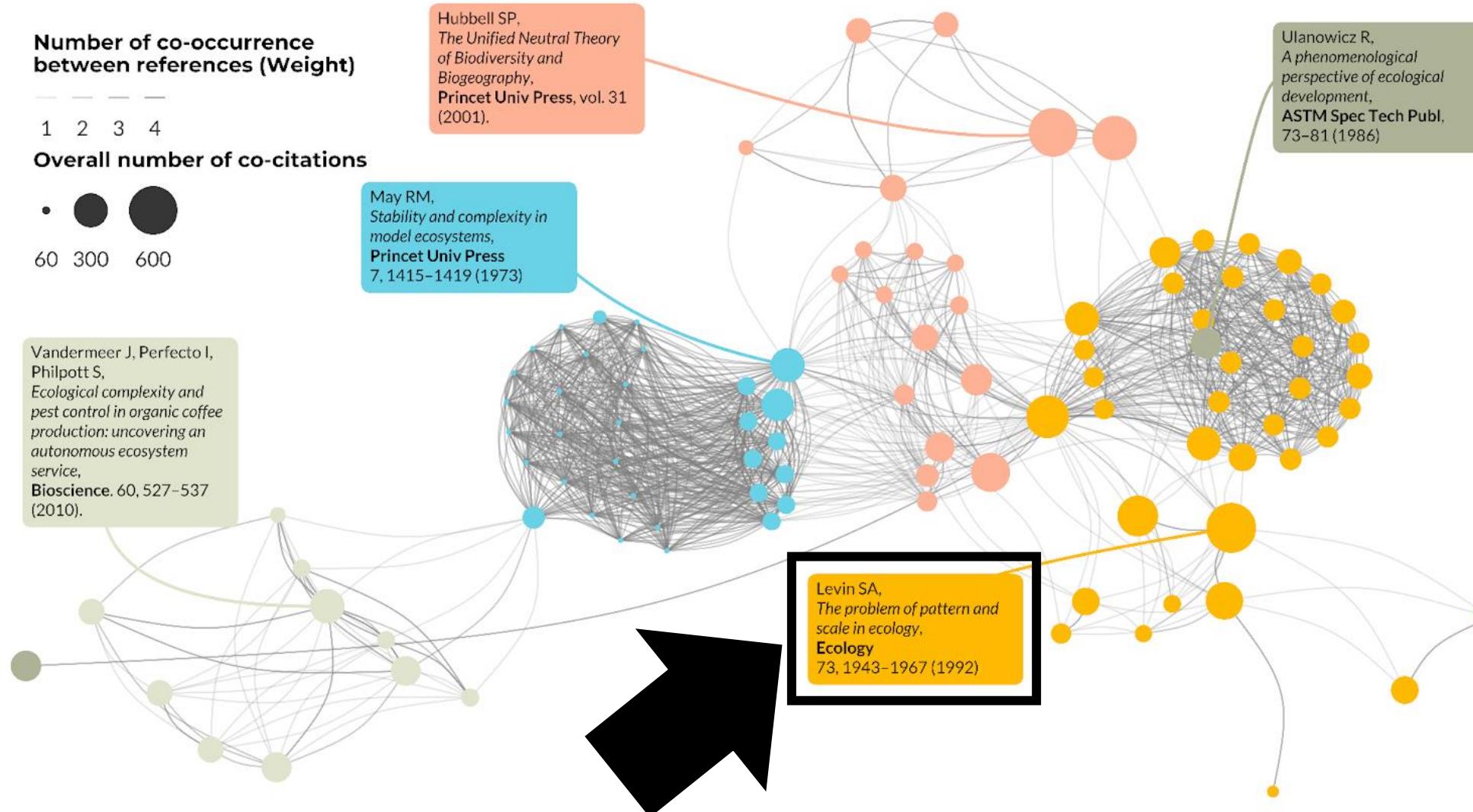
# Natural systems are prototypical complex adaptive systems



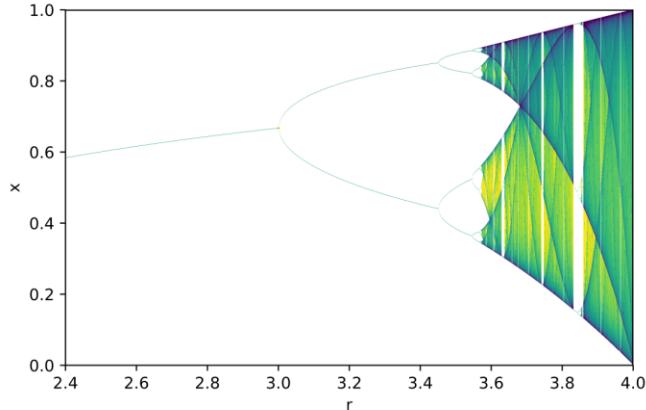
# Natural systems are prototypical complex adaptive systems



# How do we deal with this complexity?



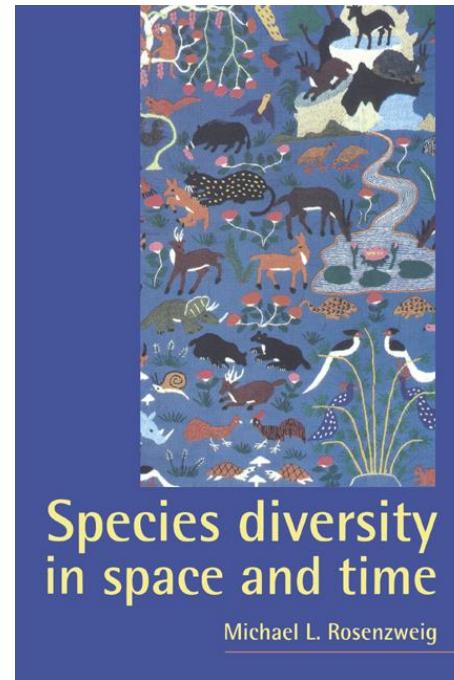
# Hard theory



$$x_{n+1} = rx_n(1 - x_n)$$

May 1976  
Rosen 2000  
Kuhn 1970  
...

# Macroecology



...

Rosenzweig 1995  
Hubbell 2001  
Brown 1995

# Scales

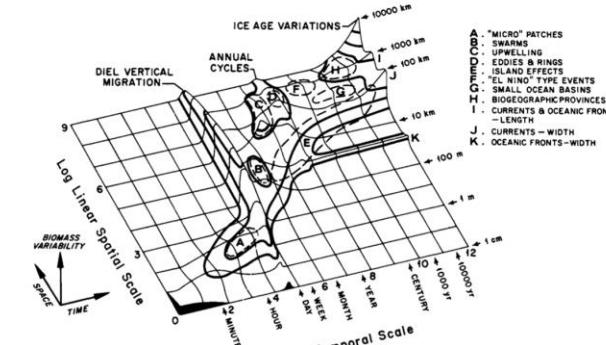


FIG. 3. Stommel diagram of spatial and temporal scales of zooplankton biomass variability (from Haury et al. 1978).

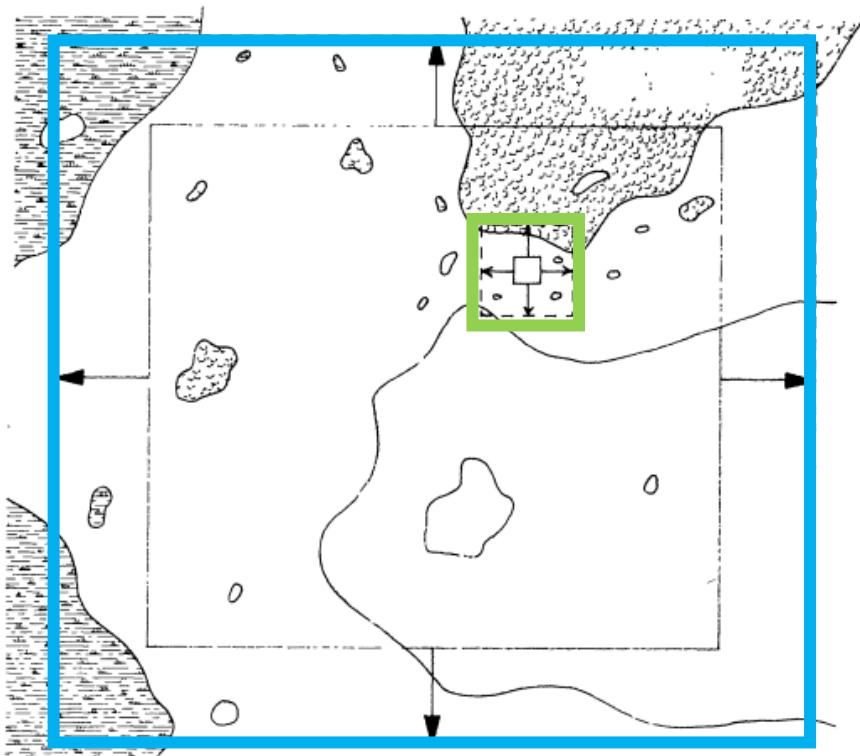
Levin 1992  
Allen and Starr 1982  
Wu and Loucks 1995  
...

Natural systems span multiple, interconnected levels of biological organization and change dynamically through space and time

Focusing on meaningful scales (spatial and temporal observational units) simplifies this complexity, resulting in tractable scenarios

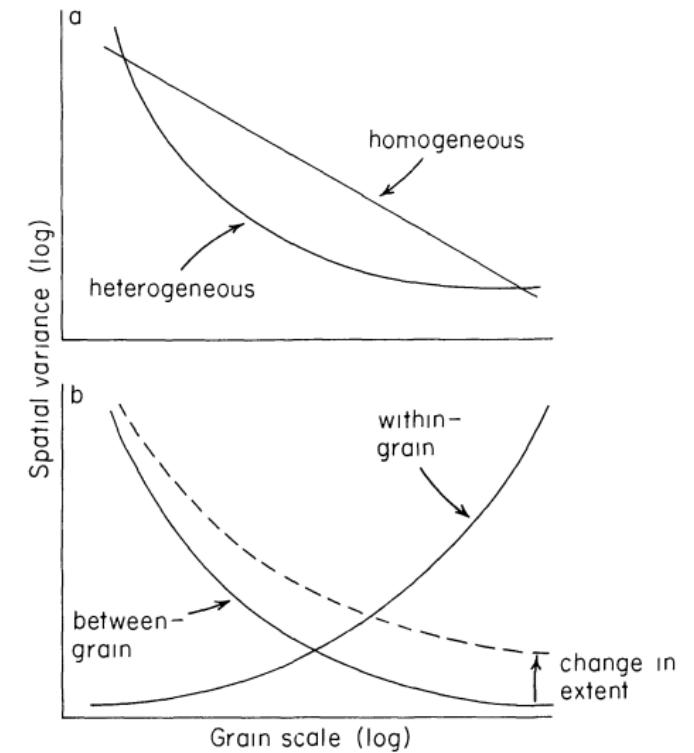
**Growing awareness of the  
importance of scales**

# Wiens 1989 – Space



**Fig. 1.** The effects of changing the grain and extent of a study in a patchy landscape. As the extent of the study is increased (large squares), landscape elements that were not present in the original study area are encountered. As the grain of samples is correspondingly increased (small squares), small patches that initially could be differentiated are now included within samples and the differences among them are averaged out.

## Grain vs. extent



**Fig. 2.** (a) As the grain of samples becomes larger, spatial variance in the study system as a whole decreases, albeit differently for homogeneous and heterogeneous areas. This is related to the within- and between-grain (sample) components of variation. (b) With increasing grain scale, less of the variance is due to differences between samples and more of the overall variation is included within samples (and therefore averaged away). An increase in the extent of the investigation may increase the between-grain component of variance by adding new patch types to the landscape surveyed (Fig. 1), but within-grain variance is not noticeably affected.

# Levin 1992 – Space and time

## THE PROBLEM OF PATTERN AND SCALE IN ECOLOGY

THE ROBERT H. MACARTHUR AWARD LECTURE  
Presented August 1989  
Toronto, Ontario, Canada

by

SIMON A. LEVIN

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003 USA, and  
Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853-2701 USA



Simon A. Levin  
MacArthur Award Recipient

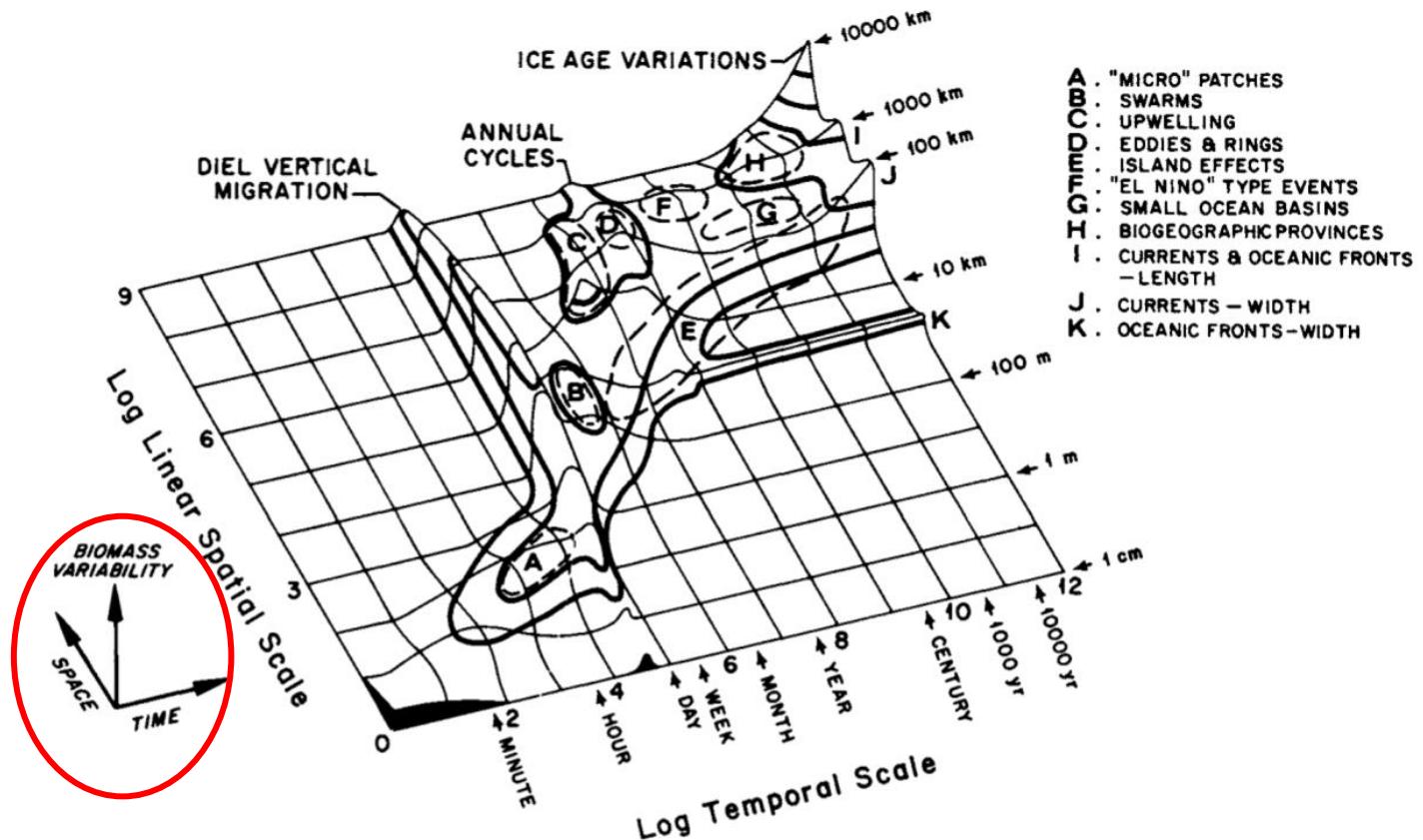


FIG. 3. Stommel diagram of spatial and temporal scales of zooplankton biomass variability (from Haury et al. 1978).

# Levin 1992 – Space and time

## THE PROBLEM OF PATTERN AND SCALE IN ECOLOGY

THE ROBERT H. MACARTHUR AWARD LECTURE  
Presented August 1989  
Toronto, Ontario, Canada

by

SIMON A. LEVIN

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003 USA, and  
Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853-2701 USA



Simon A. Levin  
MacArthur Award Recipient

## MACARTHUR AWARD LECTURE

1957

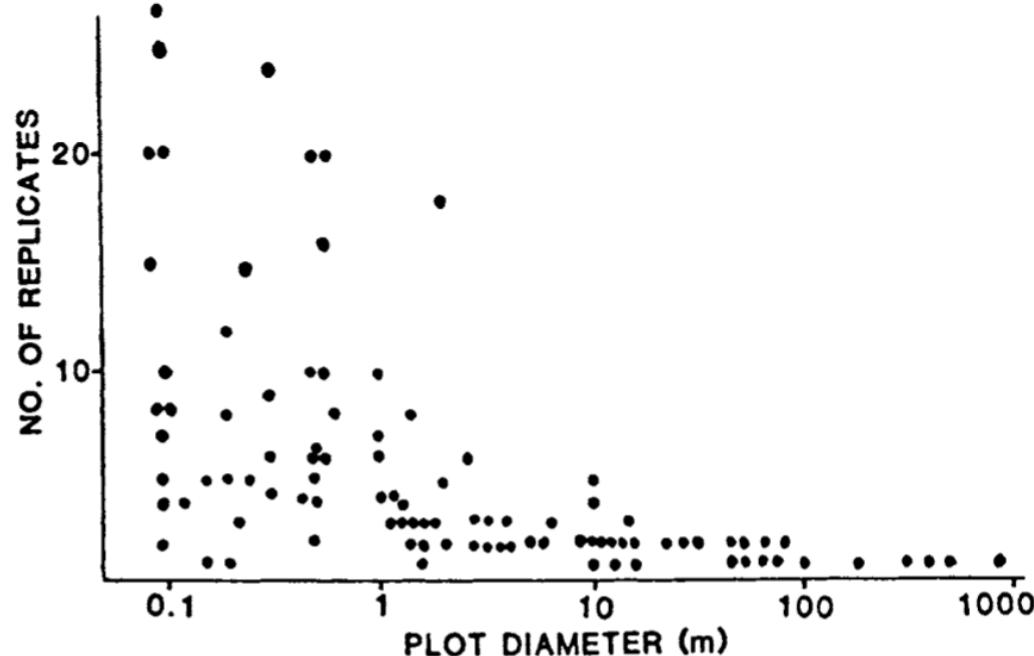
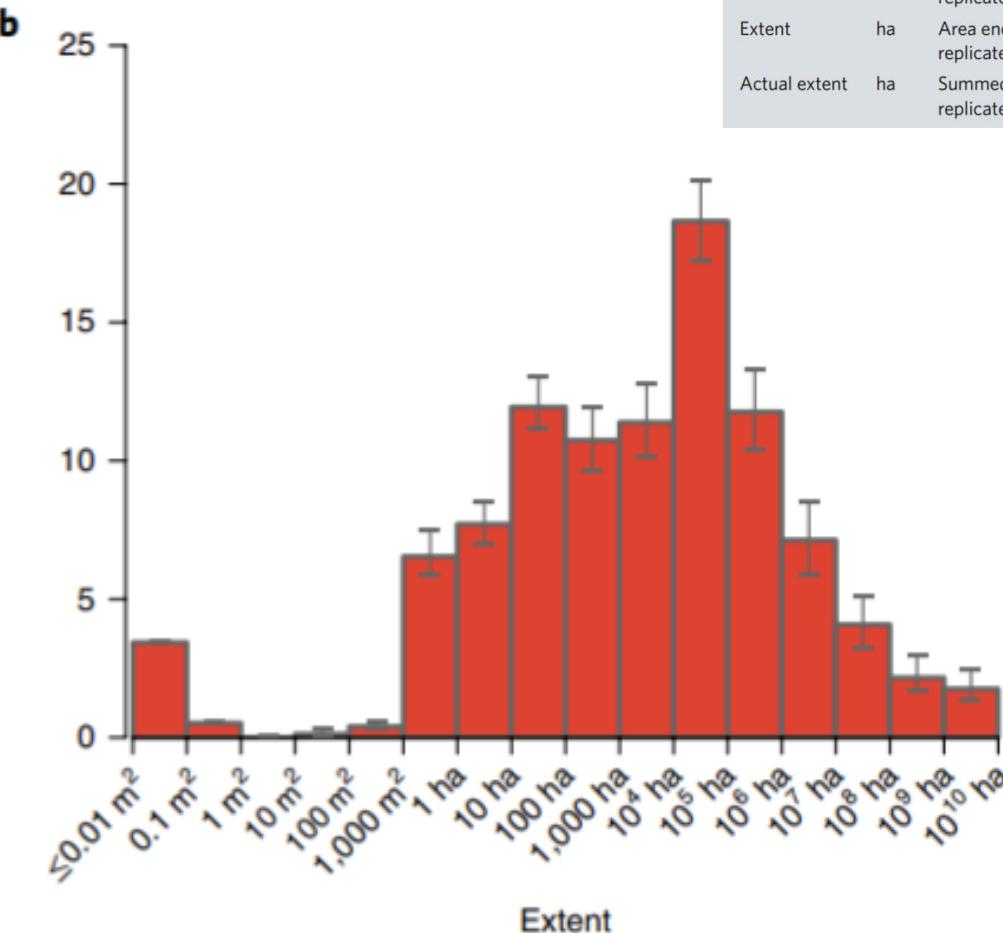
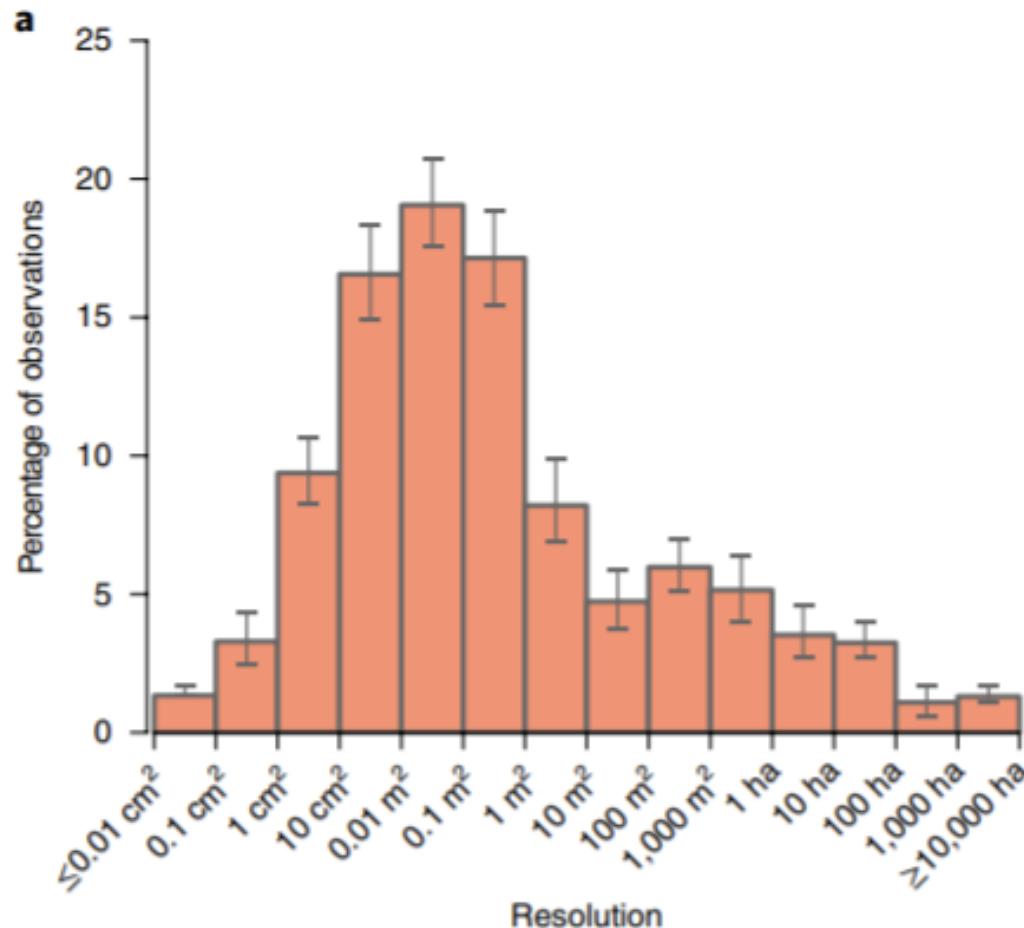


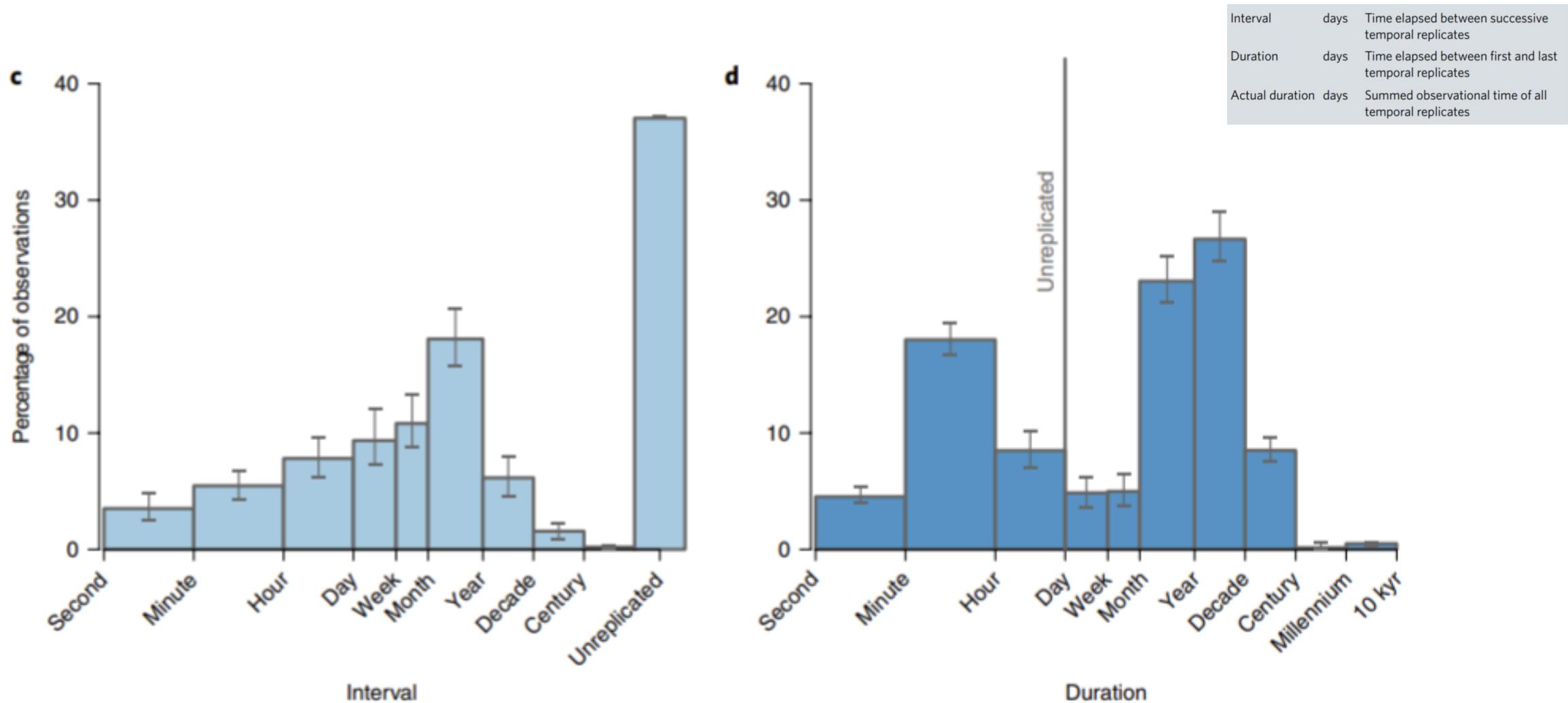
FIG. 14. Size and number of replicates in experimental community ecology. Each point is taken from a different paper published in *Ecology*. Every paper from January 1980 to August 1986 was included if it involved experimental manipulation of resources or populations “in order to learn about community dynamics or community properties” (from Kareiva and Anderson 1988).

# Estes et al. (2018) – after 30+ years, our perspective is still very biased towards short studies, small spatial resolutions



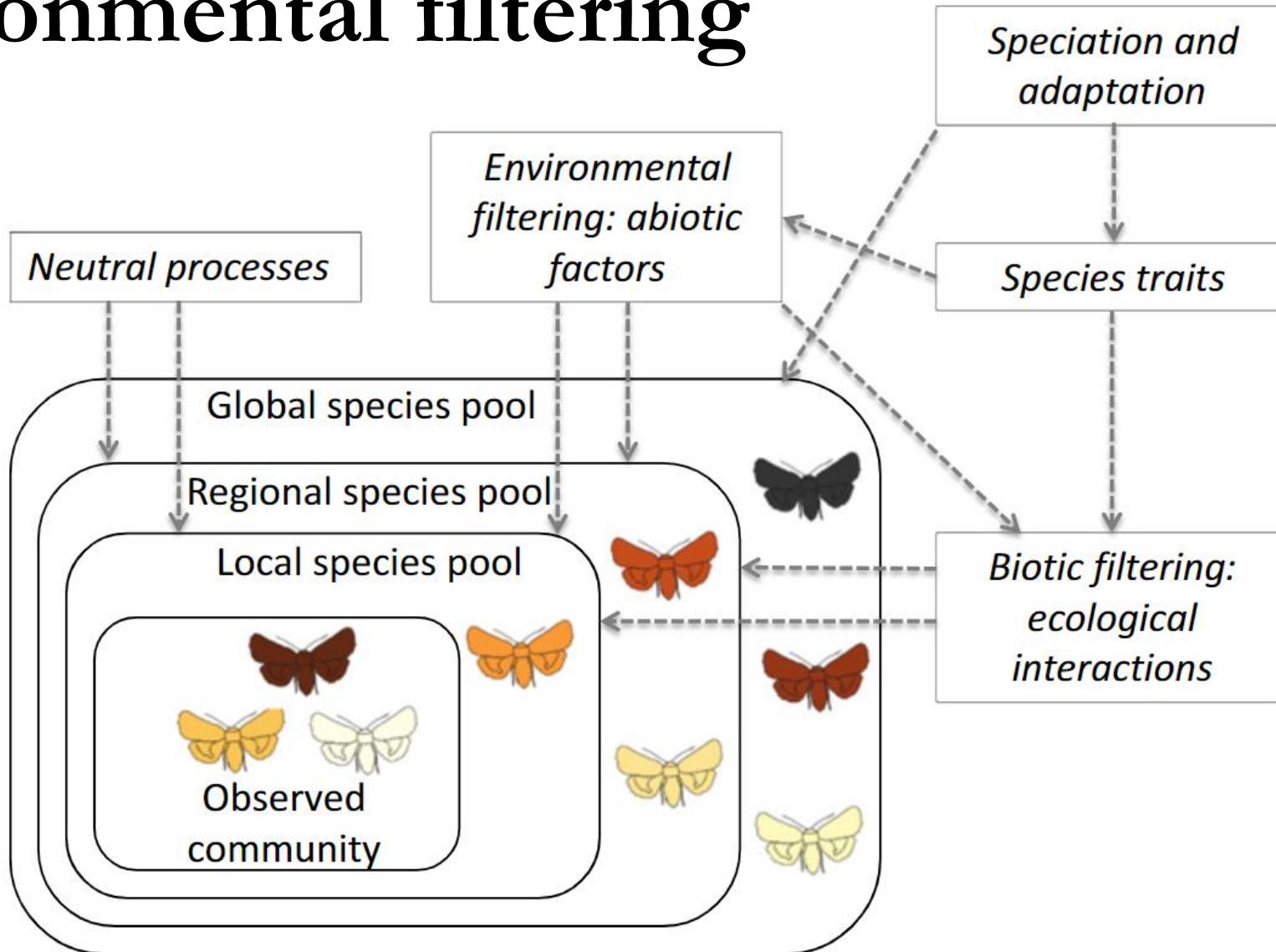
Resolution	m <sup>2</sup>	Area of an individual spatial replicate (for example, plot)
Extent	ha	Area encompassed by all spatial replicates
Actual extent	ha	Summed area of all spatial replicates

# Estes et al. (2018) – after 30+ years, our perspective is still very biased towards short studies, small spatial resolutions



Theoretical paradigms that  
incorporate scales in the study  
of biodiversity

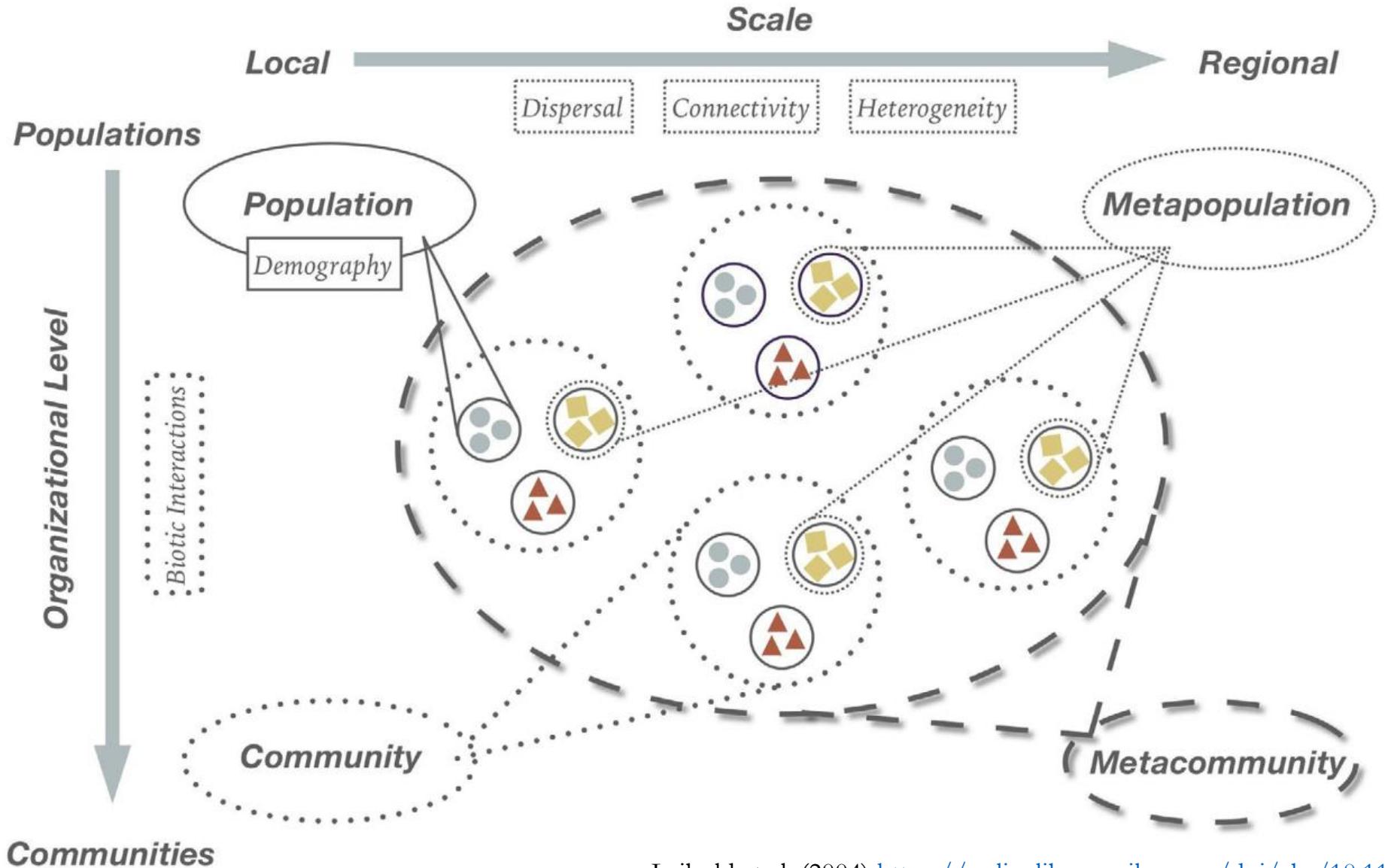
# Environmental filtering



Ovaskainen et al. (2017) <https://onlinelibrary.wiley.com/doi/10.1111/ele.12757>

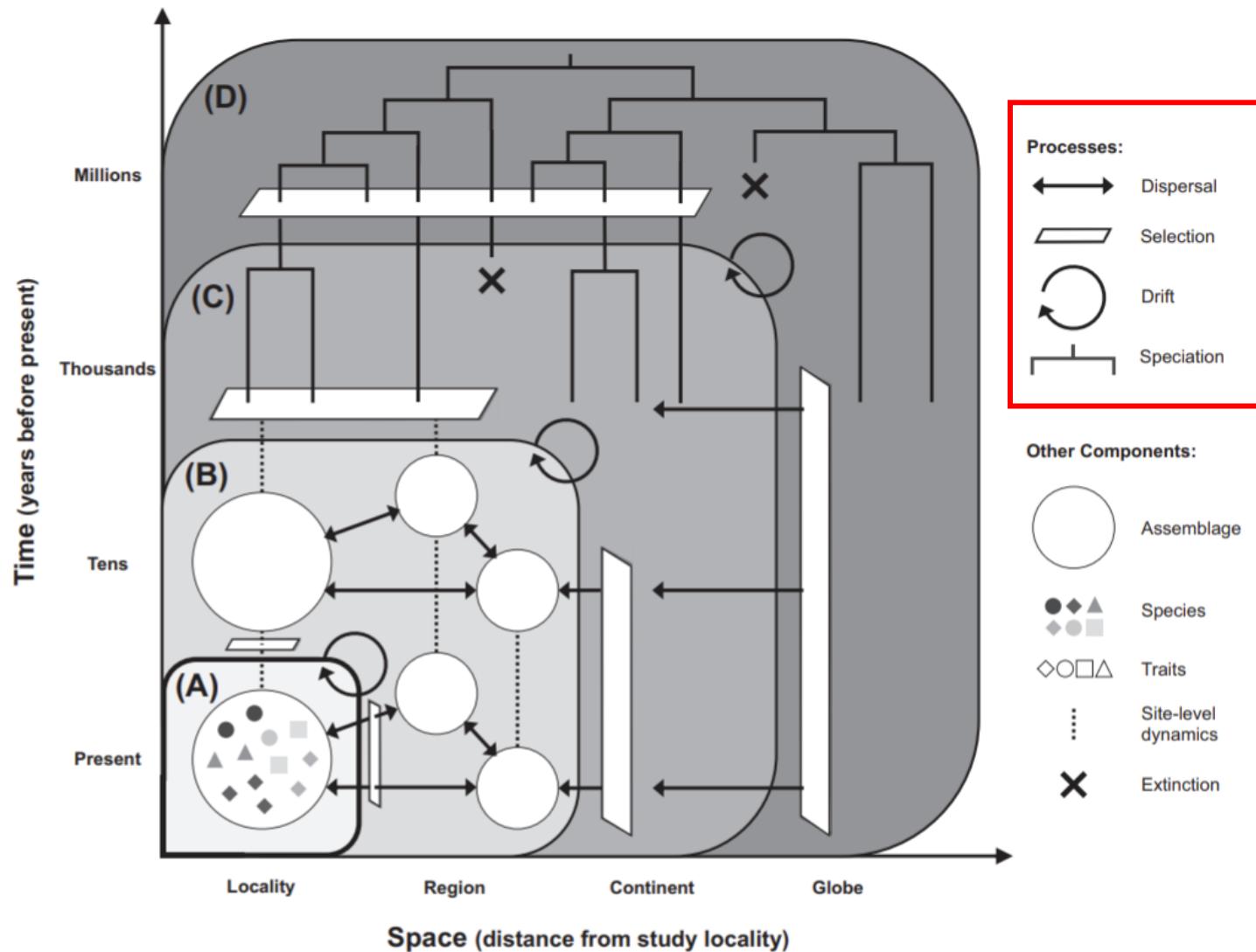
Kraft et al. (2015) <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12345>

# Metacommunity theory



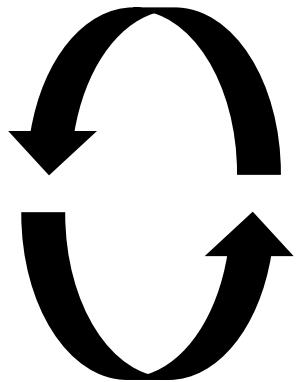
Leibold et al. (2004) <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2004.00608.x>  
Chase et al. (2020) <https://nyaspubs.onlinelibrary.wiley.com/doi/10.1111/nyas.14378>

# The Theory of Ecological Communities



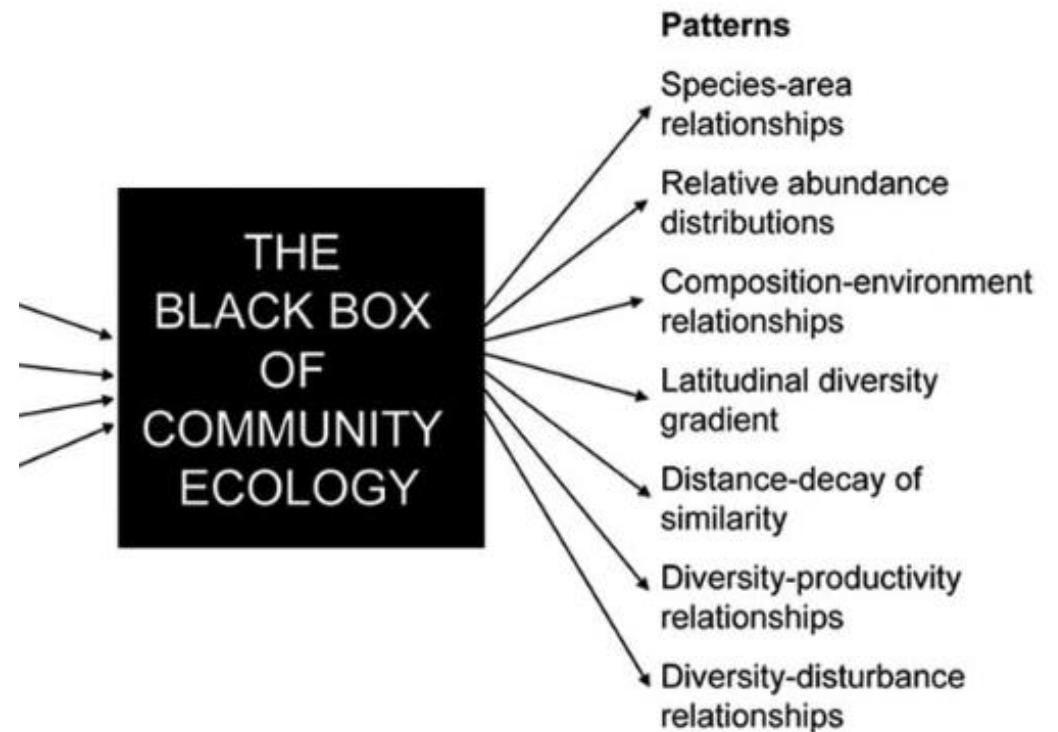
## **Population genetics**

- Selection
- Drift
- Mutation
- Gene flow



## **Community ecology**

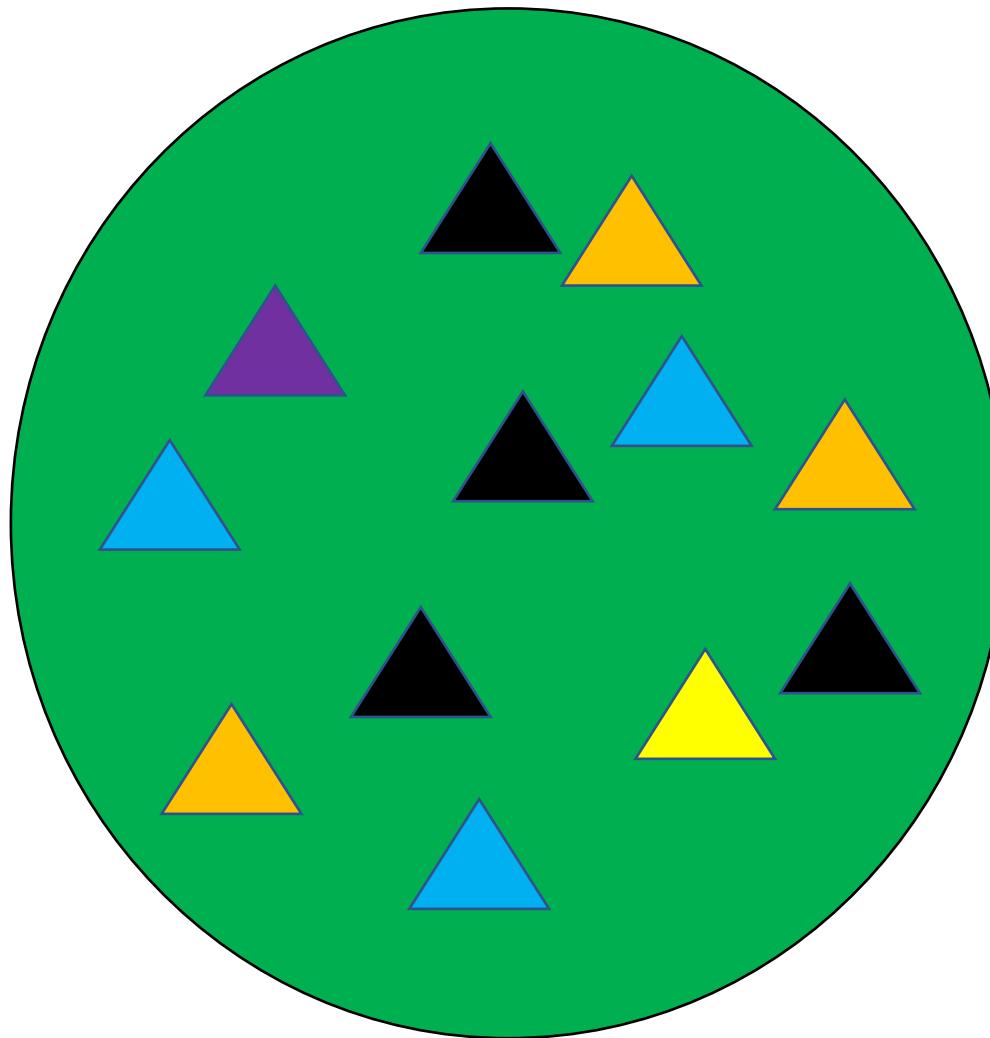
- Selection
- Drift
- Speciation
- Dispersal



More or less explicitly, most theoretical paradigms developed to address biodiversity patterns have to tackle the concept of spatial and temporal scales

Yes, but

# The concept of ecological community



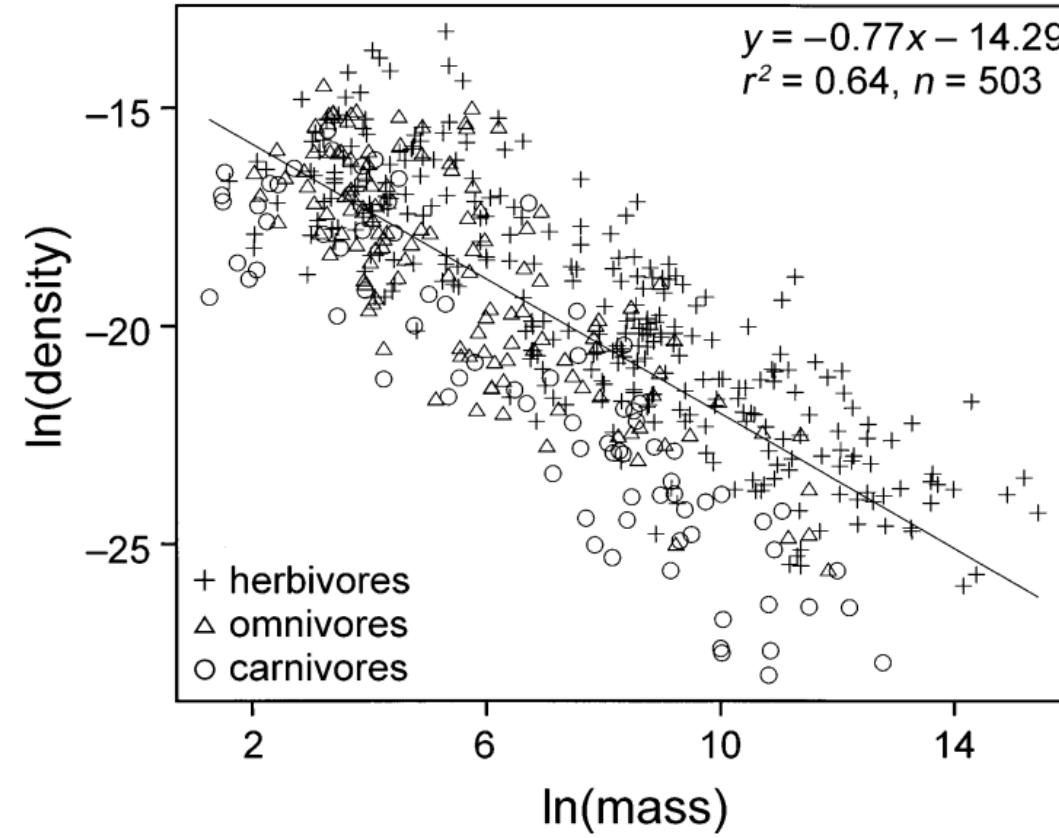
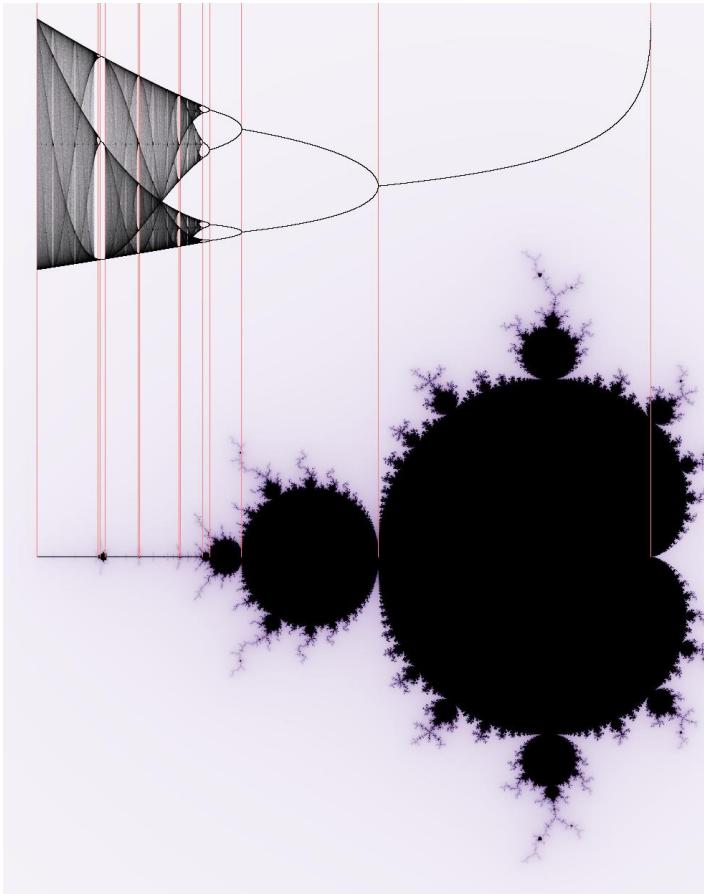
$N$  species  
at a site  $s$ ,  
at time  $t$

# Disintegration of the ecological community

**ABSTRACT:** In this essay, I argue that the seemingly indestructible concept of the community as a local, interacting assemblage of species has hindered progress toward understanding species richness at local to regional scales. I suggest that the distributions of species within a region reveal more about the processes that generate diversity patterns than does the co-occurrence of species at any given point. The local community is an epiphenomenon that has relatively little explanatory power in ecology and evolutionary biology. Local coexistence cannot provide insight into the ecogeographic distributions of species within a region, from which local assemblages of species derive, nor can local communities be used to test hypotheses concerning the origin, maintenance, and regulation of species richness, either locally or regionally. Ecologists are moving toward a community concept based on interactions between populations over a continuum of spatial and temporal scales within entire regions, including the population and evolutionary processes that produce new species.

# Also, some processes do not change with scales

E.g., fractals (self-similarity across different scales) and metabolic constraints

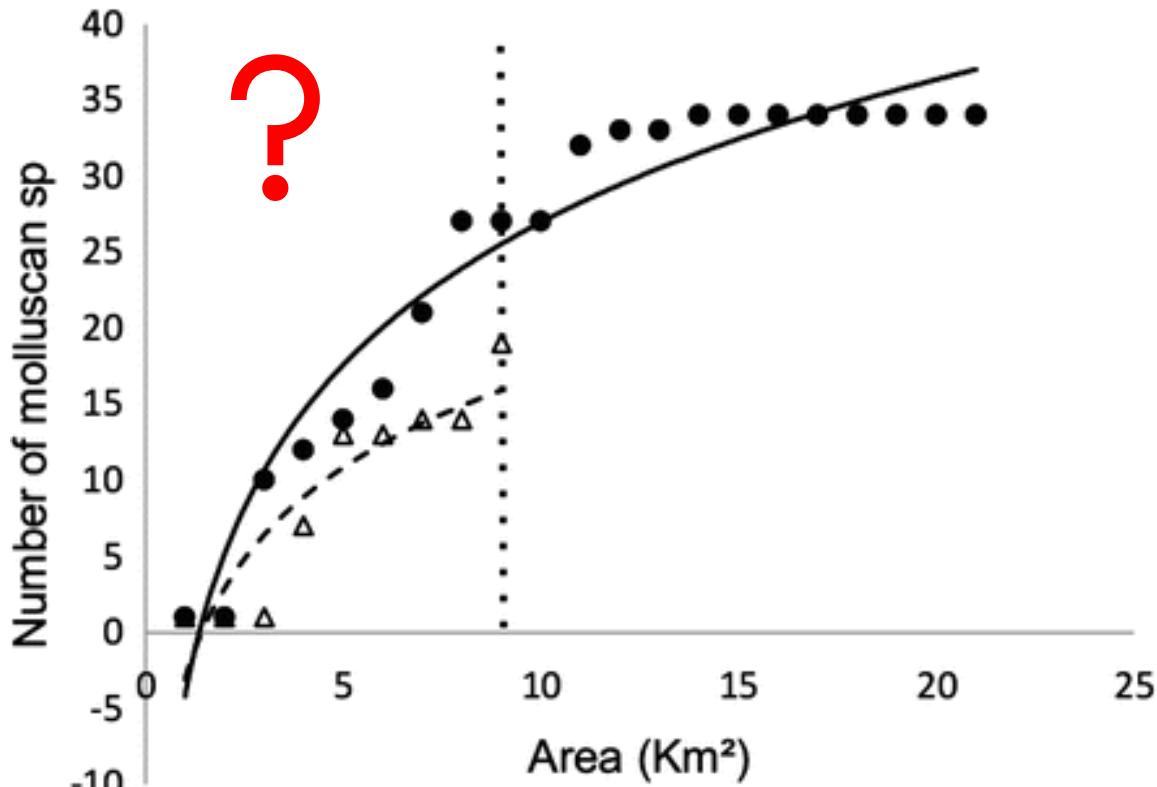


<https://commons.wikimedia.org/wiki/File:Verhulst-Mandelbrot-Bifurcation.jpg>

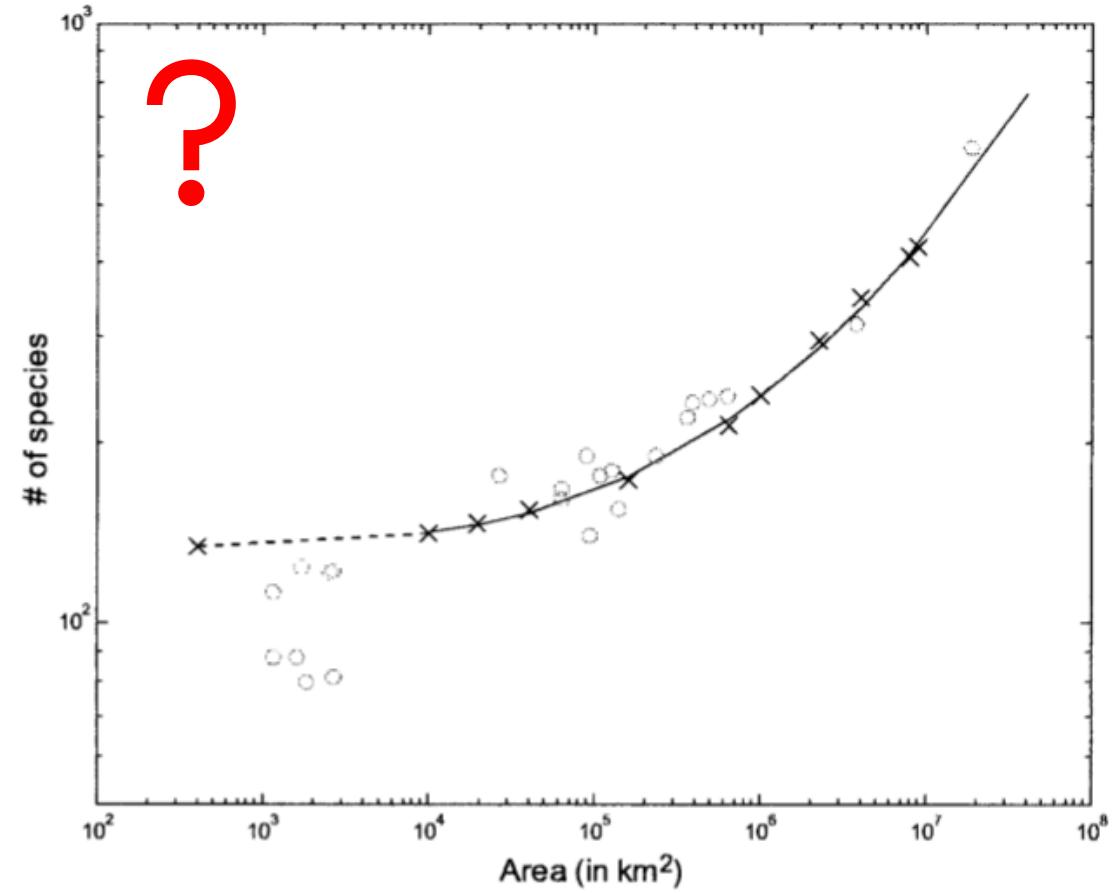
Brown et al. (2004) [https://www.esa.org/history/Awards/papers/Brown\\_JH\\_MA.pdf](https://www.esa.org/history/Awards/papers/Brown_JH_MA.pdf)  
Halley et al. (2004) <https://pdodds.w3.uvm.edu/files/papers/others/everything/halley2004a.pdf>

# Scales as a mediator of contrasting perspectives

# Species-area relationship

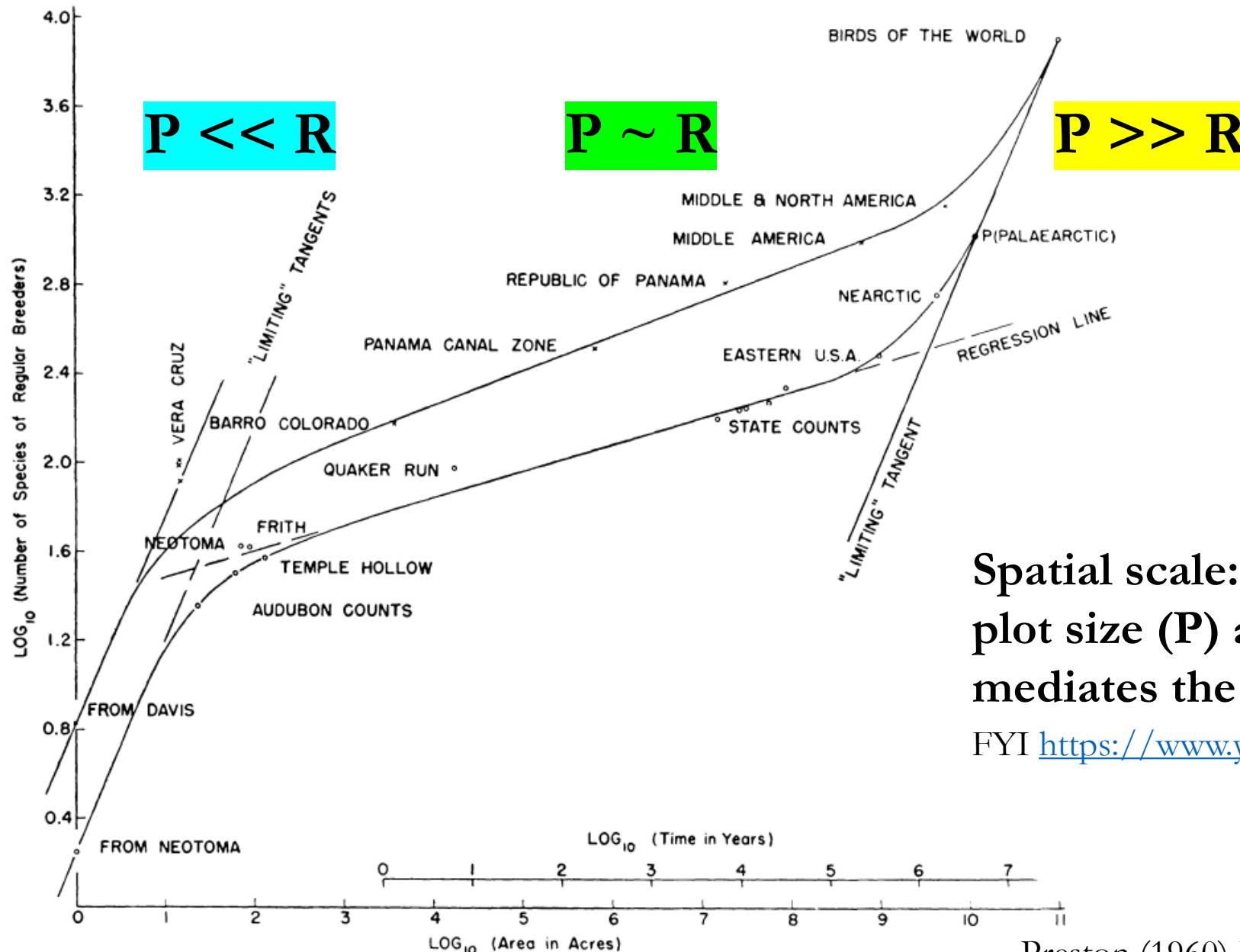


McGill and Collins



Pruden and Leighton (2018) [https://link.springer.com/chapter/10.1007/978-3-319-73795-9\\_7](https://link.springer.com/chapter/10.1007/978-3-319-73795-9_7)

McGill and Collins (2003) <https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.499.9375&rep=rep1&type=pdf>



Spatial scale: the relationship between plot size (P) and the range of species (R) mediates the species-area relationship

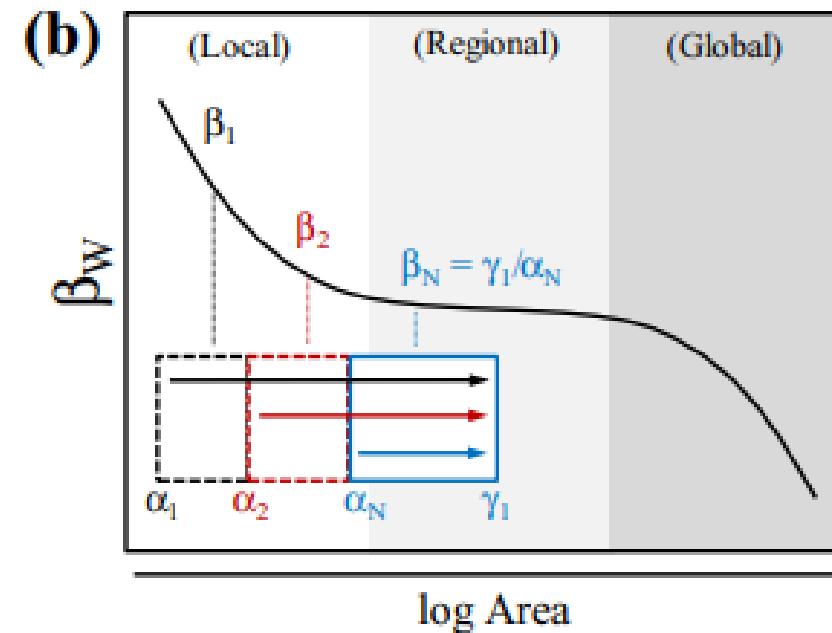
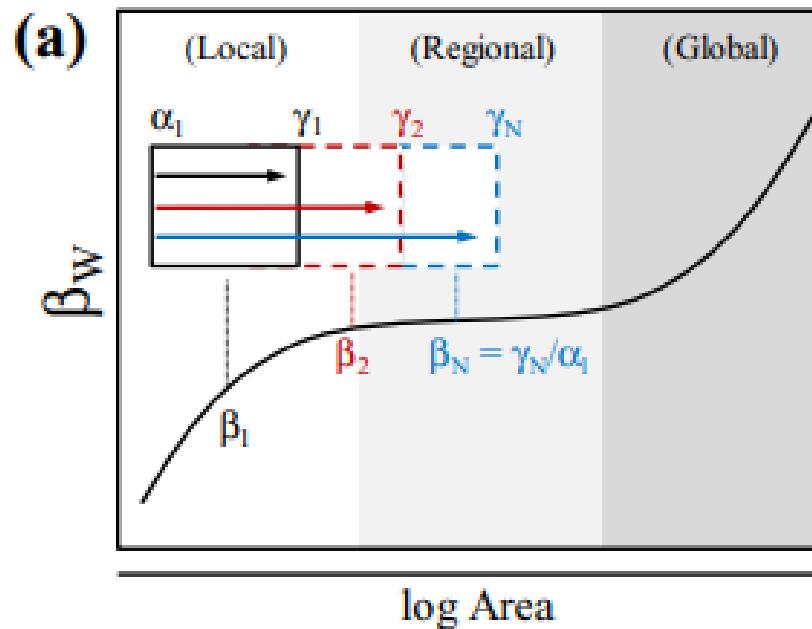
FYI <https://www.youtube.com/watch?v=YfbKYKPUzdo>

# Beta diversity (species turnover)

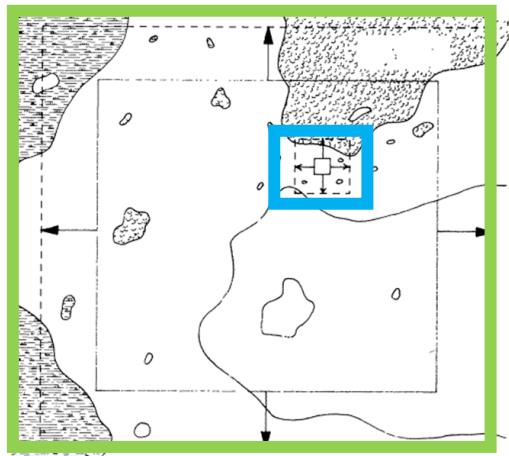
Whittaker's multiplicative beta:  $\text{Alpha} * \text{Beta} = \text{Gamma} \leftrightarrow \text{Beta} = \text{Gamma} / \text{Alpha}$

Alpha = species in a community

Gamma = species in a region

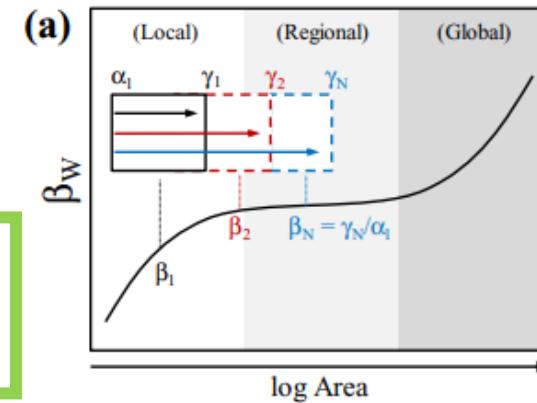


# Wiens 1989 – grain vs extent

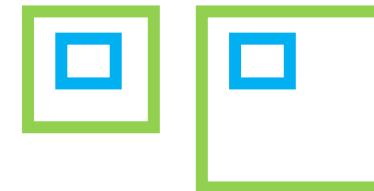


Whittaker's beta diversity  
(multiplicative partitioning)

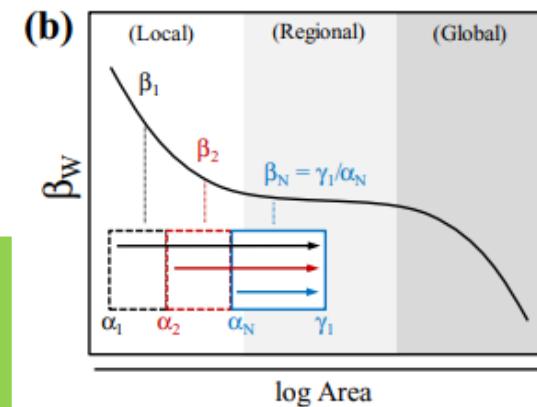
**(a)**



Fixed grain,  
varying extent



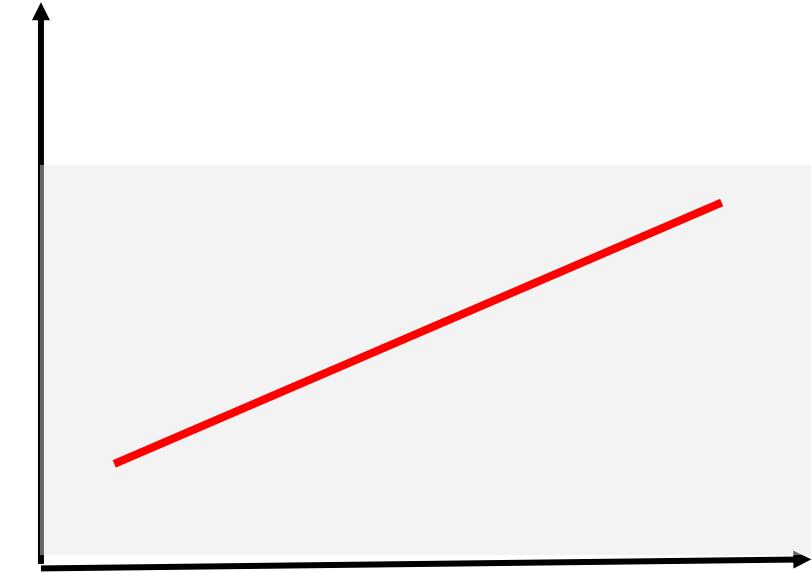
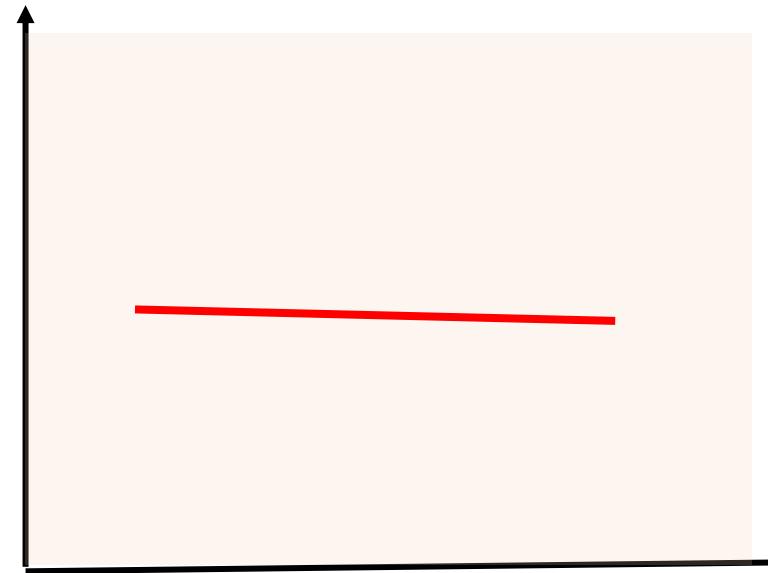
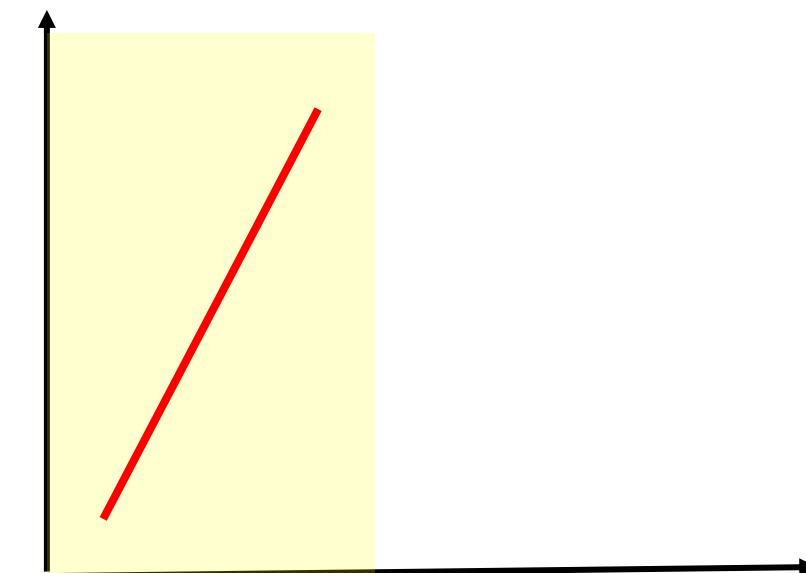
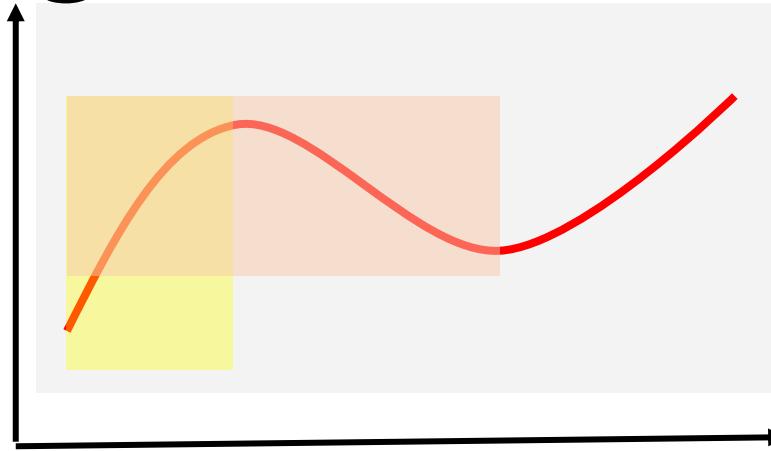
**(b)**

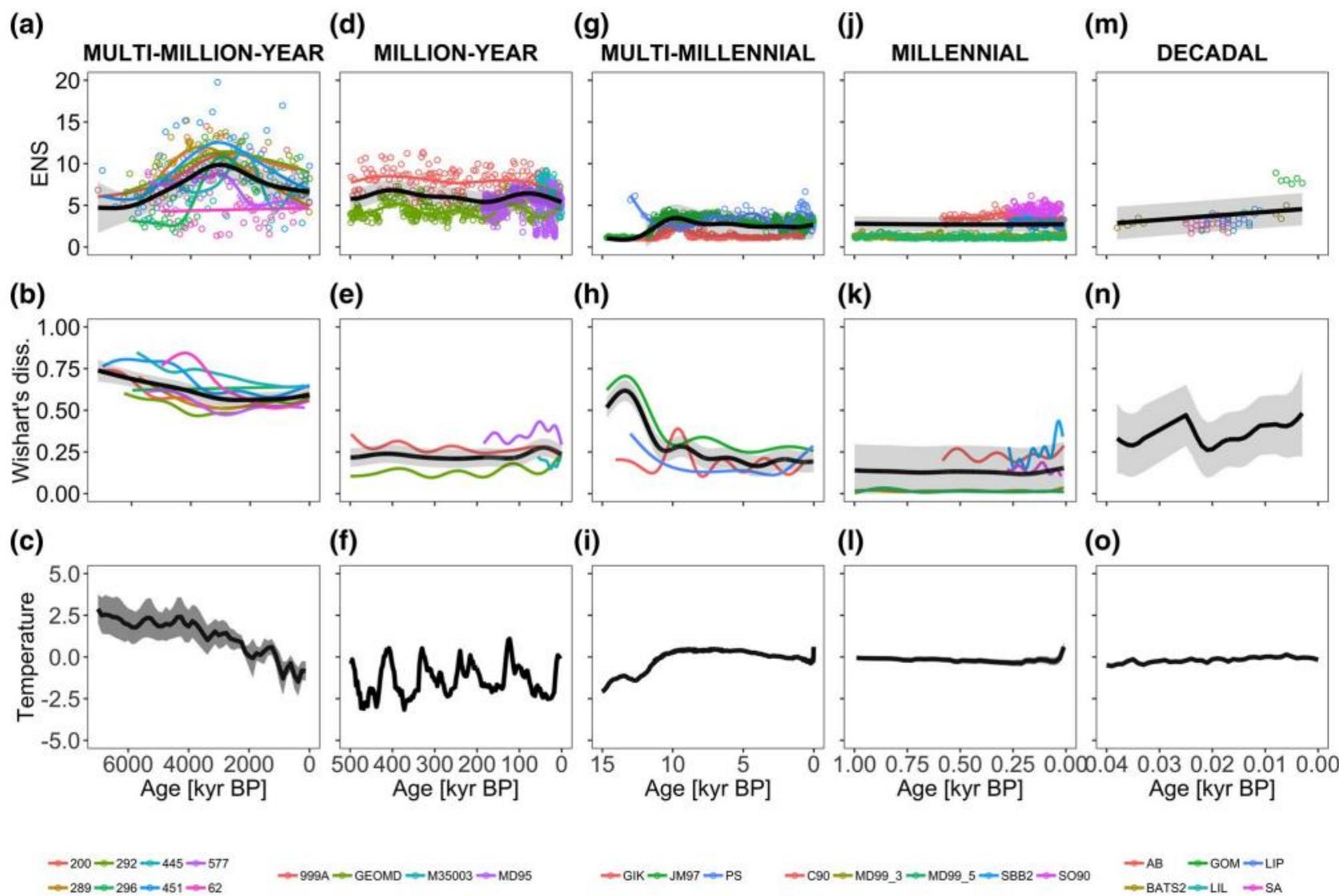


Varying grain,  
fixed extent



# Biodiversity change in time

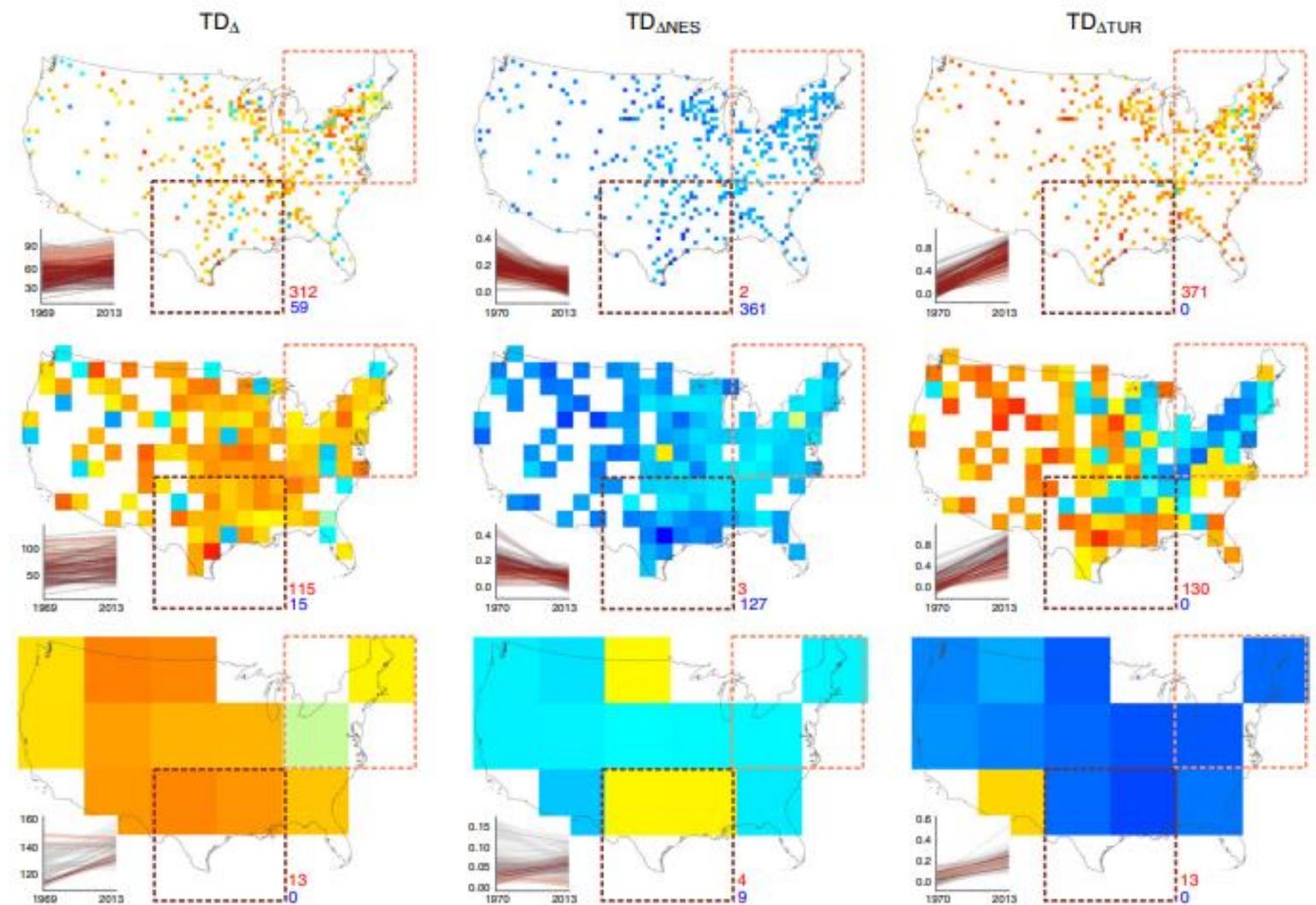




**FIGURE 5** Temporal trends of foraminifera biodiversity over different time periods (as in Figure 2) as effective number of species (upper panels) and Wishart's dissimilarity (mid panels) in relation to temperature (bottom panels). Colours represent different sites, which are listed in the Supporting Information Appendix S1: Table S1. Black solid lines are general trends ( $\pm 95\%$  confidence intervals) calculated using generalized additive models (GAMs) [Colour figure can be viewed at [wileyonlinelibrary.com](https://wileyonlinelibrary.com)]

# Trends in biodiversity change with spatial scales

... Scales shown, from top to bottom, are 50 km, 200 km, 800 km. Fitted positive and negative slopes indicate increases and declines in taxonomic diversity ( $\text{TD}\Delta$ , left panel), temporal nestedness of taxonomic diversity ( $\text{TD}\Delta\text{NES}$ , middle panel), and temporal turnover of taxonomic diversity ( $\text{TD}\Delta\text{TUR}$ , right panel). Red and blue numbers indicate the number of grid cells for which these trends were positive and negative, respectively. Insets show the fitted slopes between the respective measure of change (y-axis) and time (x-axis; calendar year) for the cell inside the brown (brown lines) or beige (beige lines) quadratic regions.



# Temporal cycles, biodiversity, and abundance

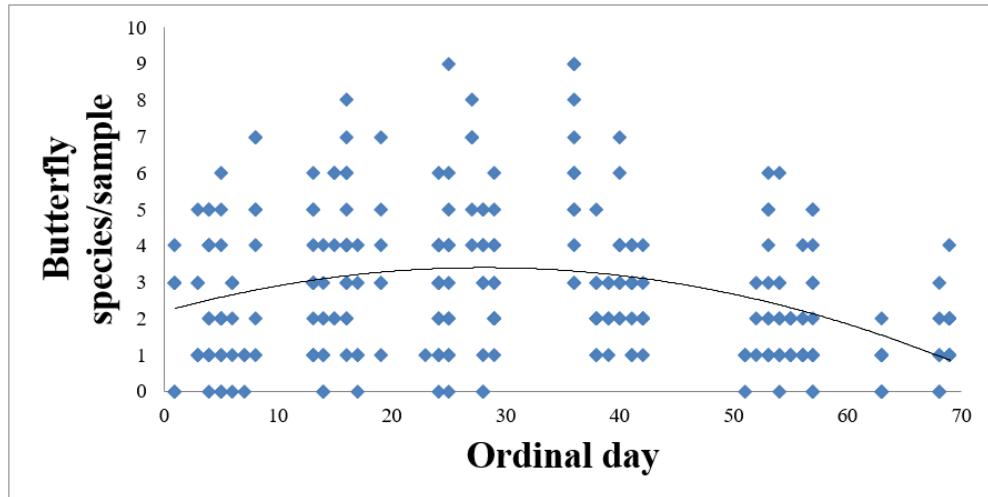
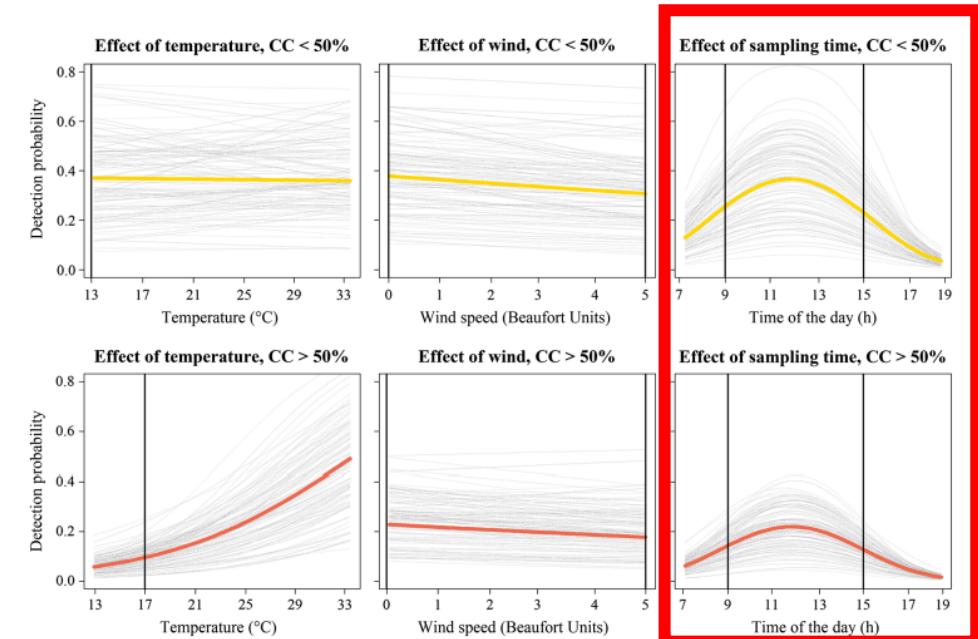
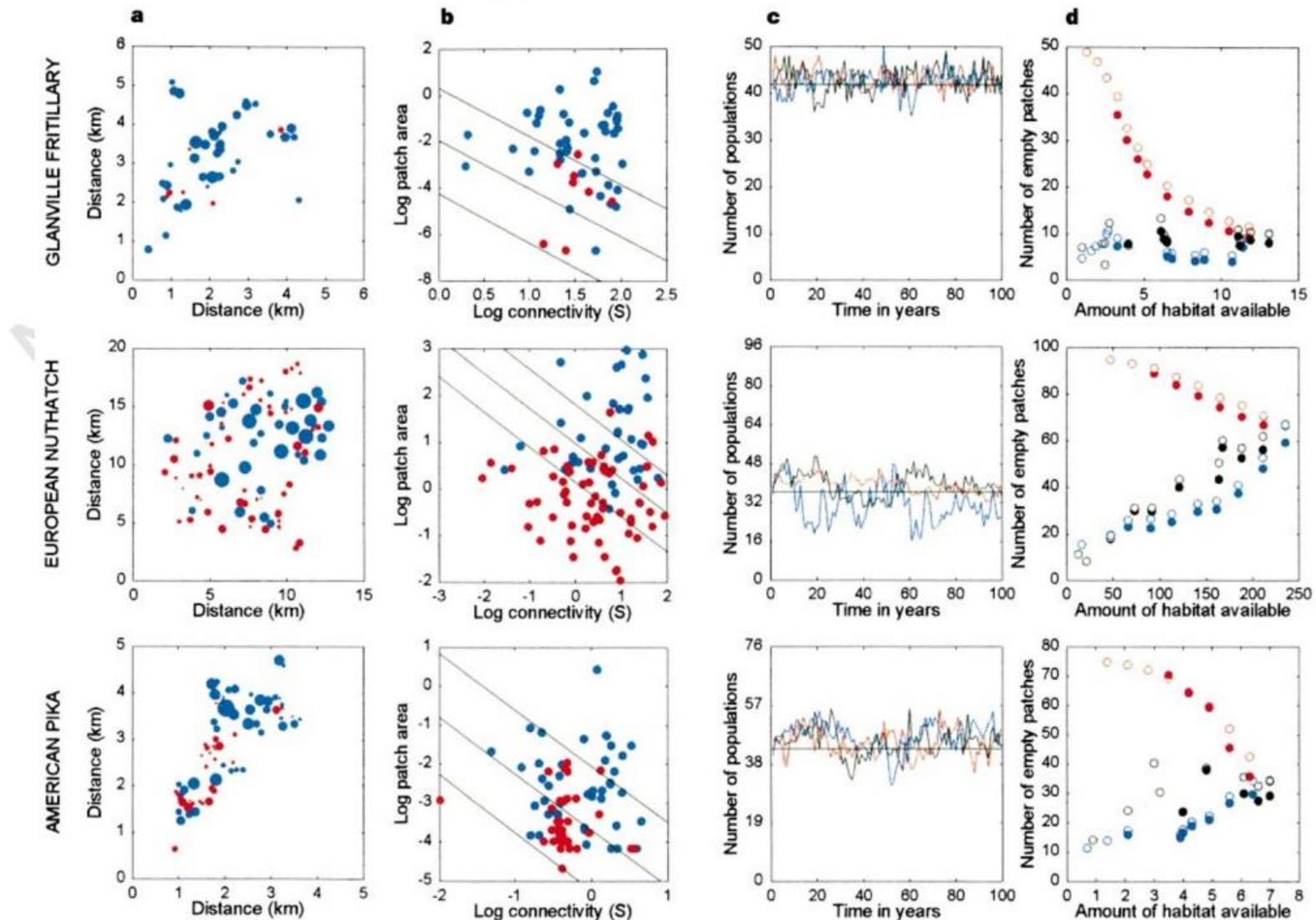


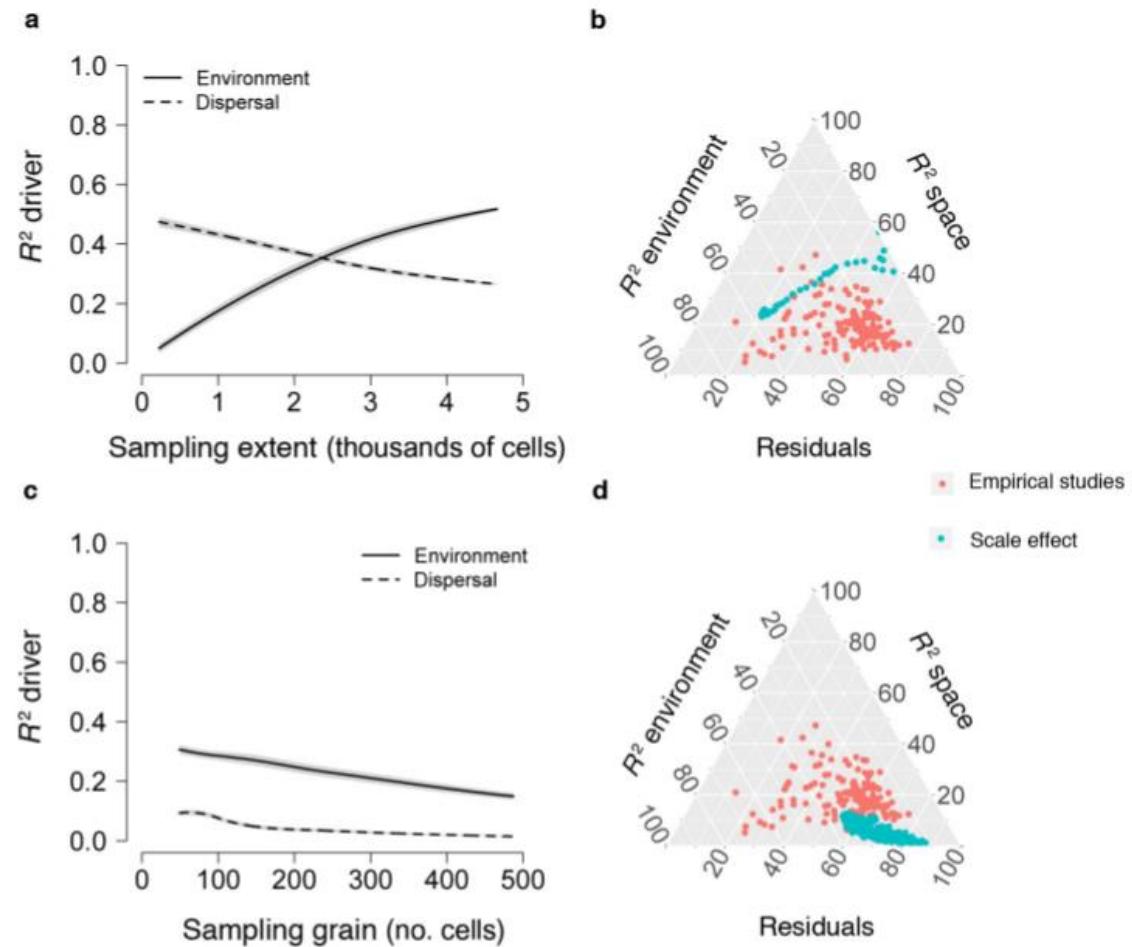
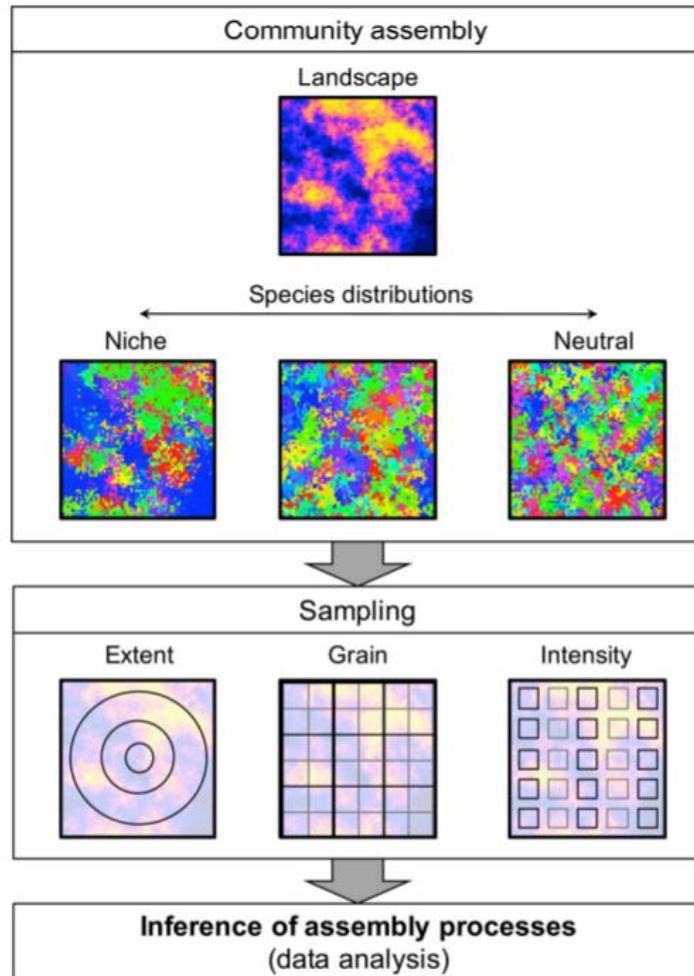
Figure 6: Number of butterfly species observed per sample ( $n = 275$ ) between June 14<sup>th</sup> (ordinal day = 1) and August 24<sup>th</sup> (ordinal day = 69). Diversity of butterflies peaks around the second week of July. A quadratic function is fitted to represent the unimodal diversity trend.



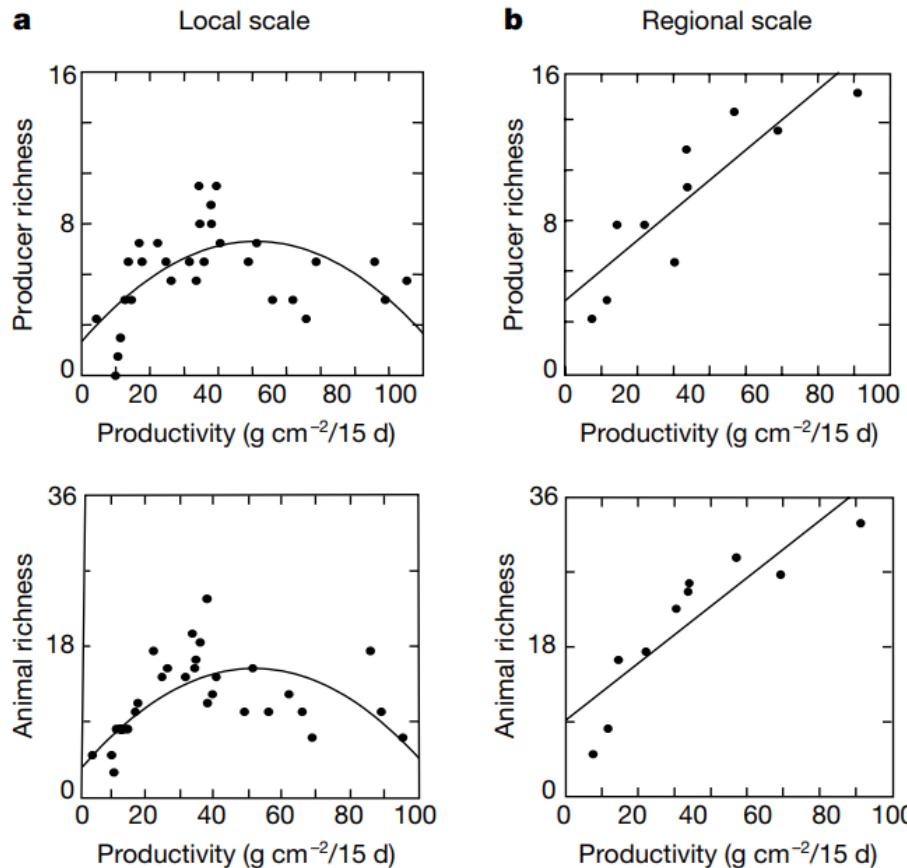
# Metacommunity dynamics



# Assembly processes in metacommunities



# Productivity-diversity relationship



**Figure 1** Results from the survey of pond species diversity relative to *in situ* primary productivity at local and regional scales. Top panels, producers (vascular plants and macroalgae); bottom panels, benthic animals (insects, crustaceans, amphibians, and so on). **a**, Local, within-pond, species diversity ( $N = 30$ ). Both relationships are significantly unimodel ( $P < 0.05$ ) (see text for explanation of statistical methodology). The line

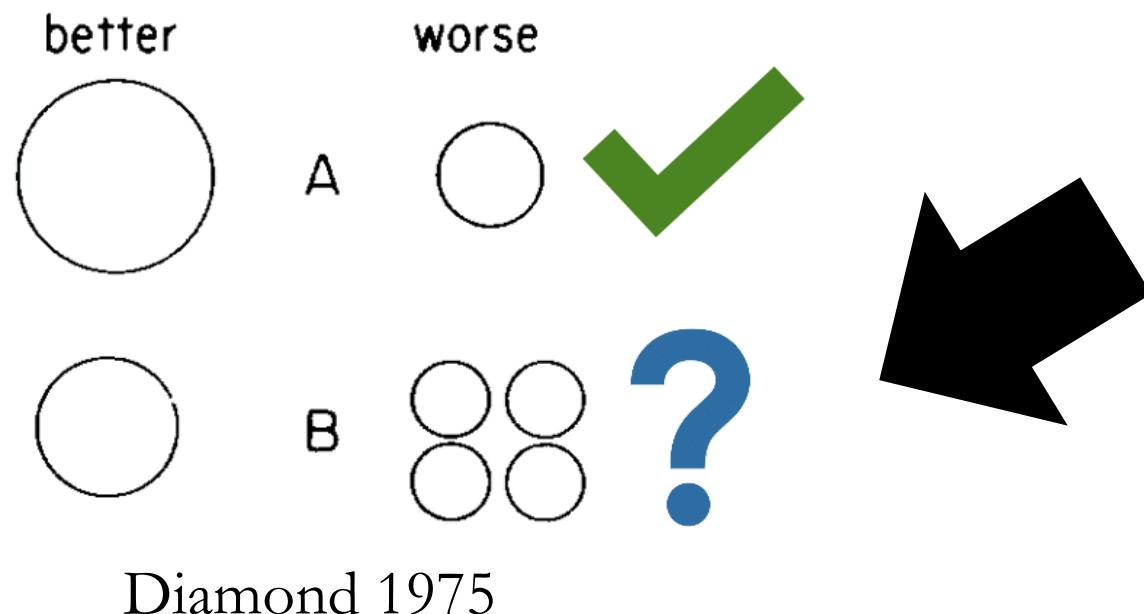
represents the estimated quadratic function. **b**, Regional, within-watershed, species diversity. For both producers (regression:  $N = 10, R^2 = 0.74, P < 0.001$ ) and benthic animals (regression:  $N = 10, R^2 = 0.75, P < 0.001$ ) regional species diversity was linearly related to primary productivity.

Scales often explain why we get different results  
when answering the same questions

# Applications in conservation

# Example 1: Single Large Or Several Small (SLOSS)?

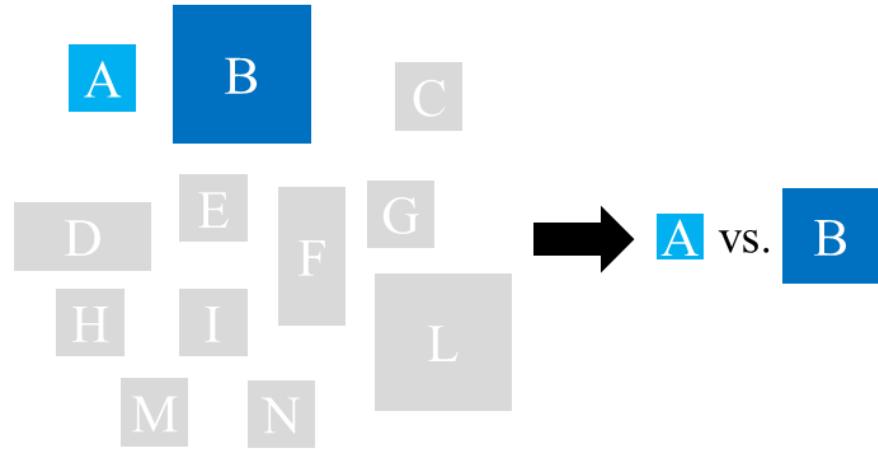
If I have the resources to protect 100 ha of forests, will biodiversity be higher in one 100-ha patch, or ten 10-ha patches?



“Like previous reviews, I found that SS > SL dominates empirical findings”  
Fahrig 2020

Diamond 1975

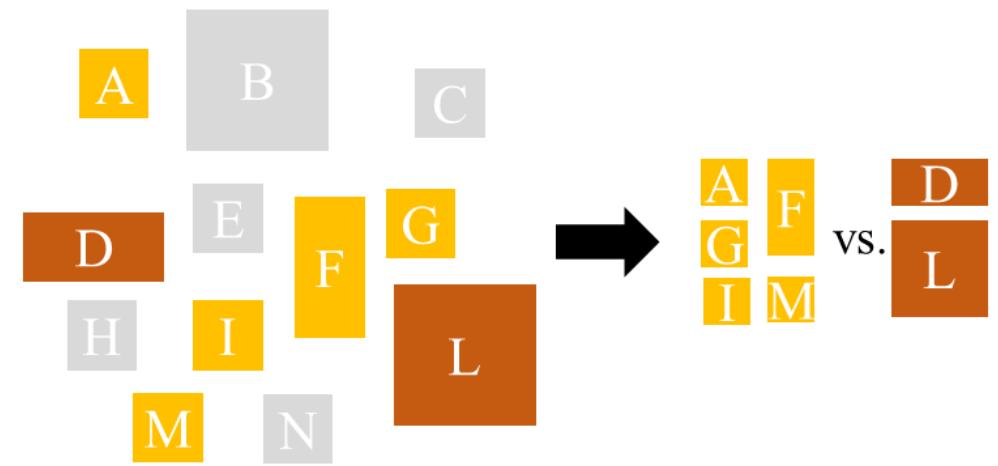
## Patch scale



Comparing two patches

- Same number of patches
- Different area

## Landscape scale

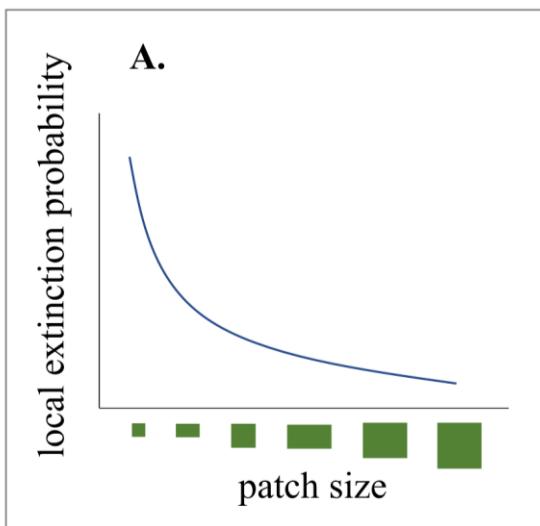


Comparing two sets of patches

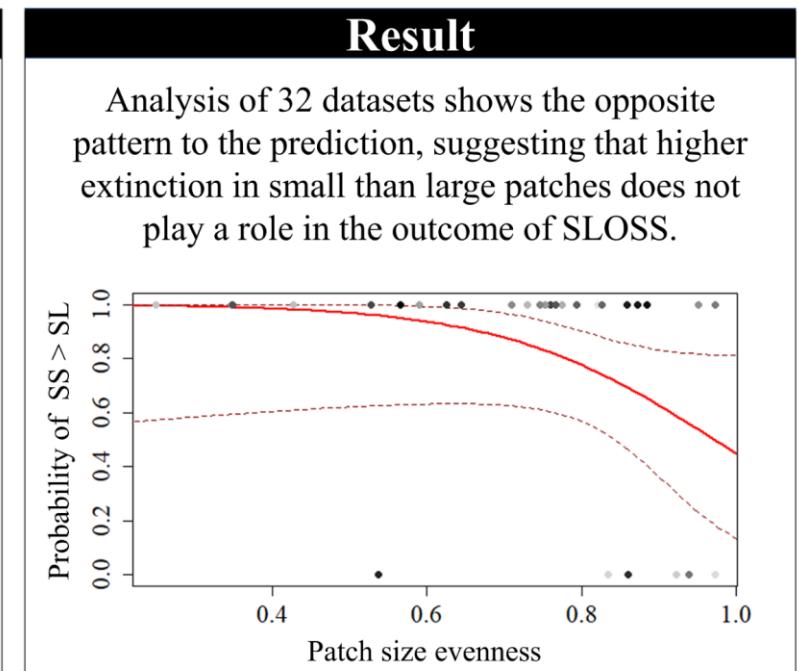
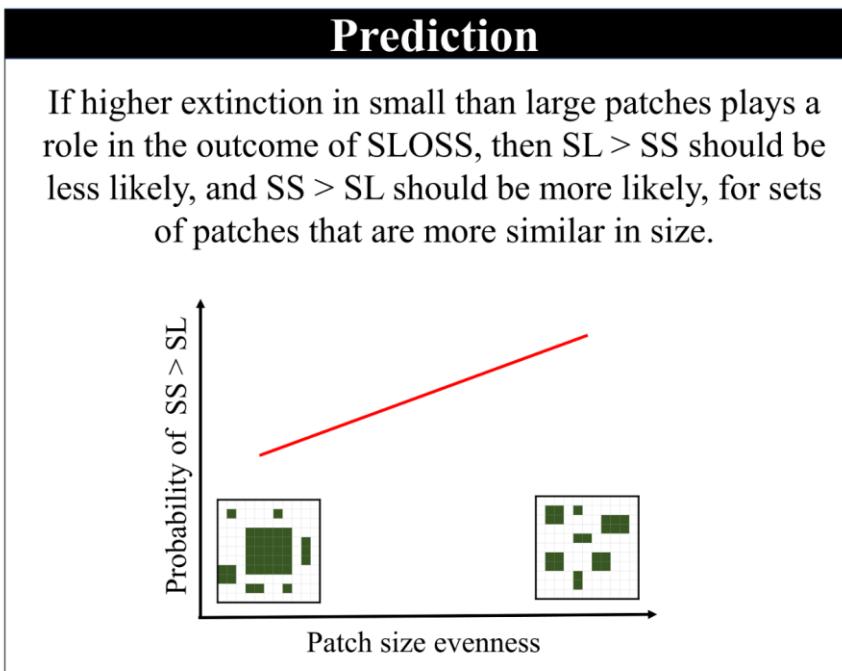
- Same area
- Different number of patches

# Extinction risk, patch size, and the landscape scale

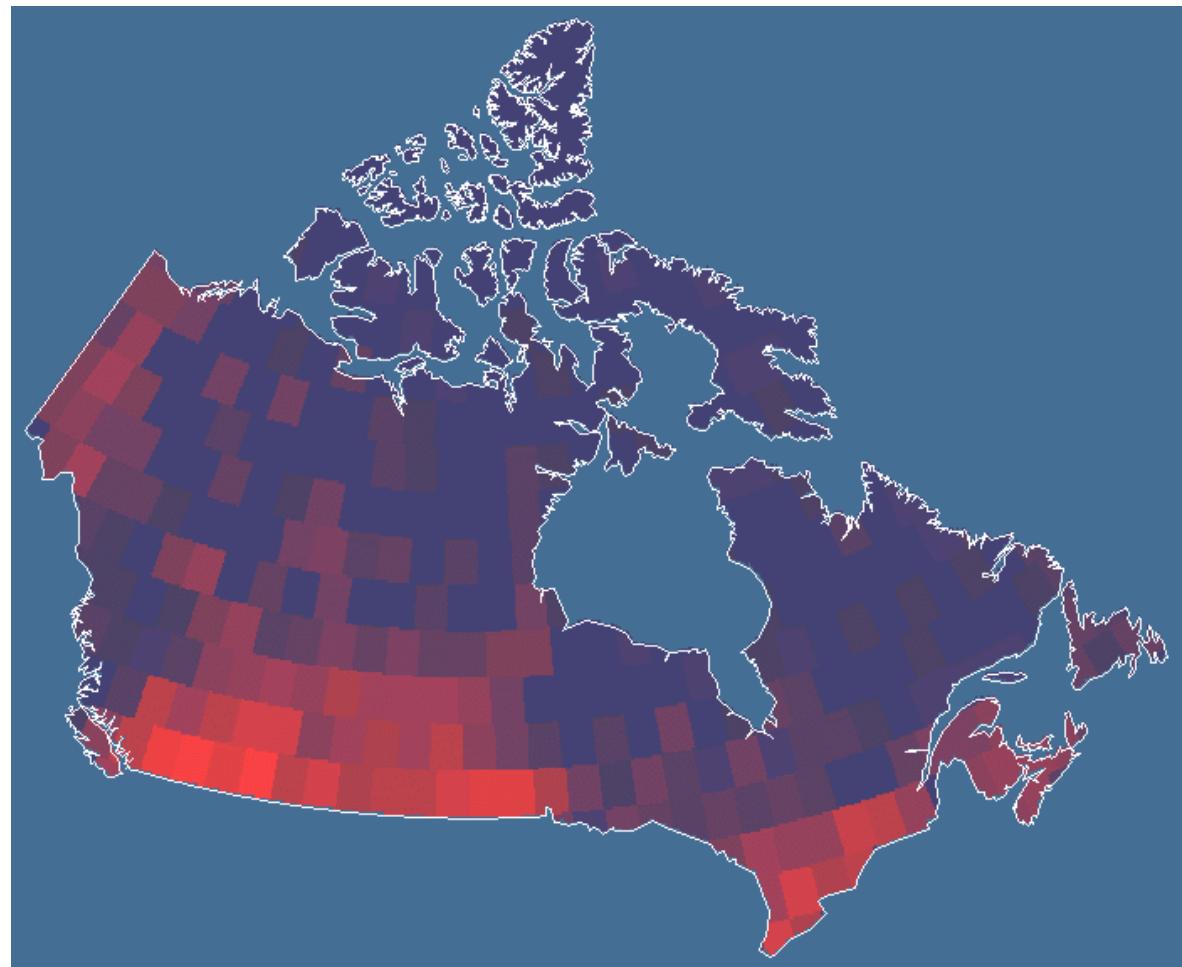
## Patch scale



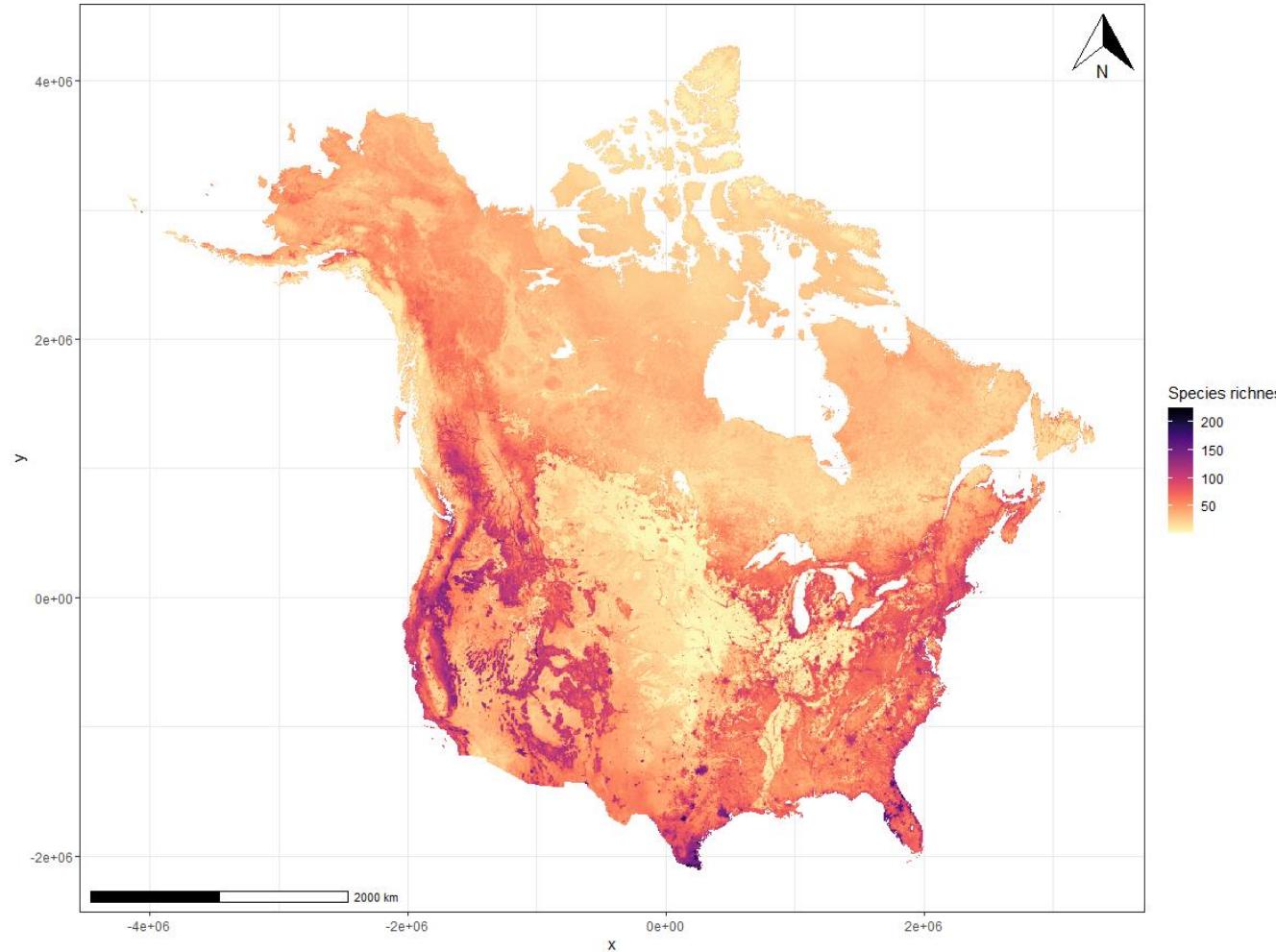
## Landscape scale



# Example 2: Big data and remote sensing

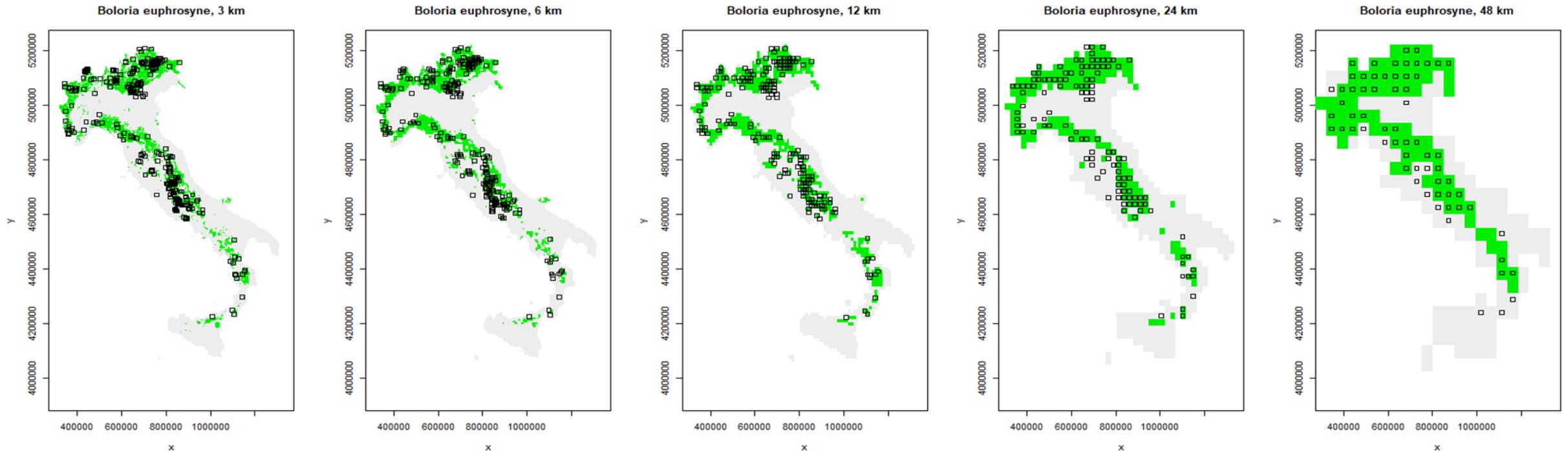


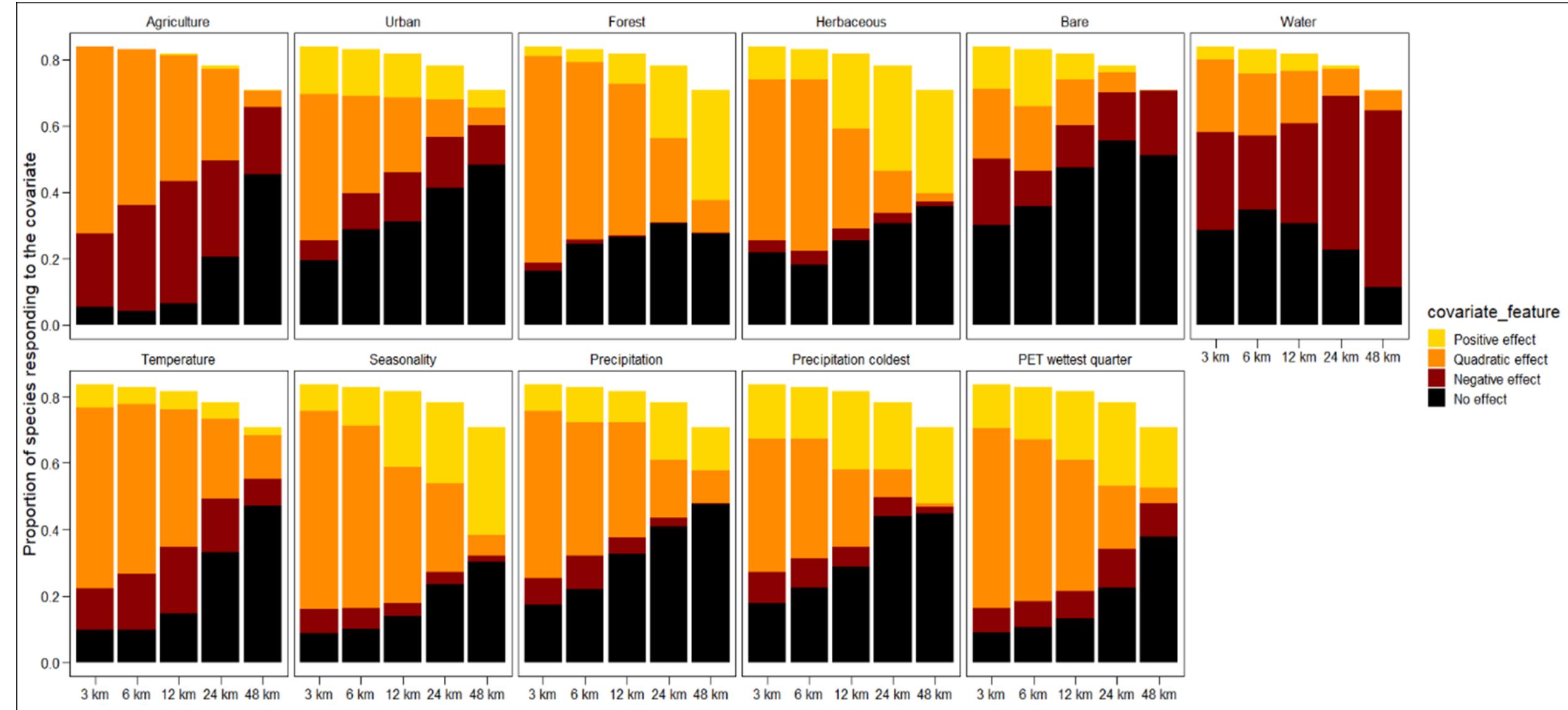
Kerr 2001: <https://www.ecologyandsociety.org/vol5/iss1/art10/>  
371 cells, 2 degrees ( $\sim 200$  km) grain



Riva et al. (in prep)  
2.3 million cells, 5-km grain

# Grain affects the relationship between species distribution and the environment

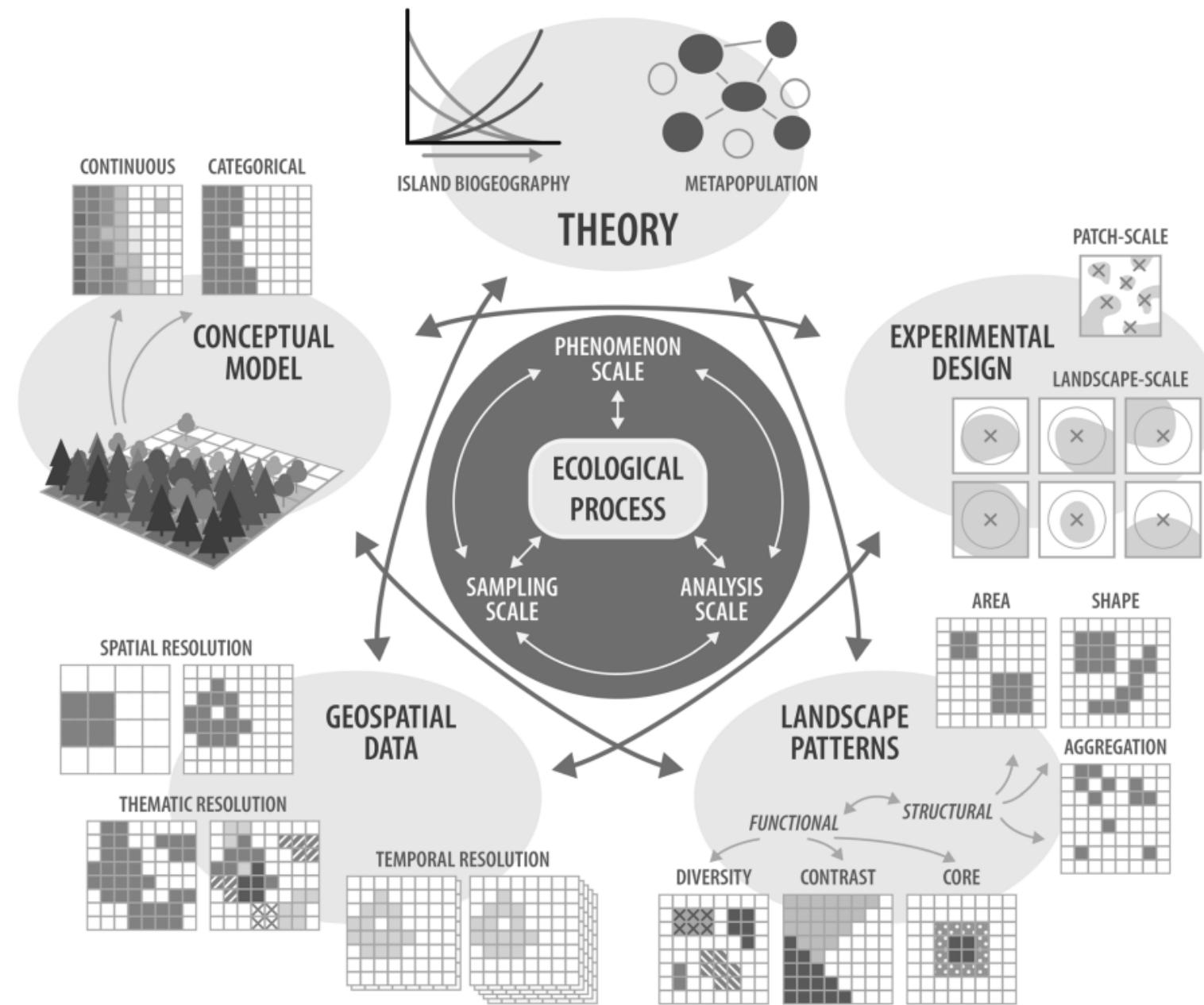


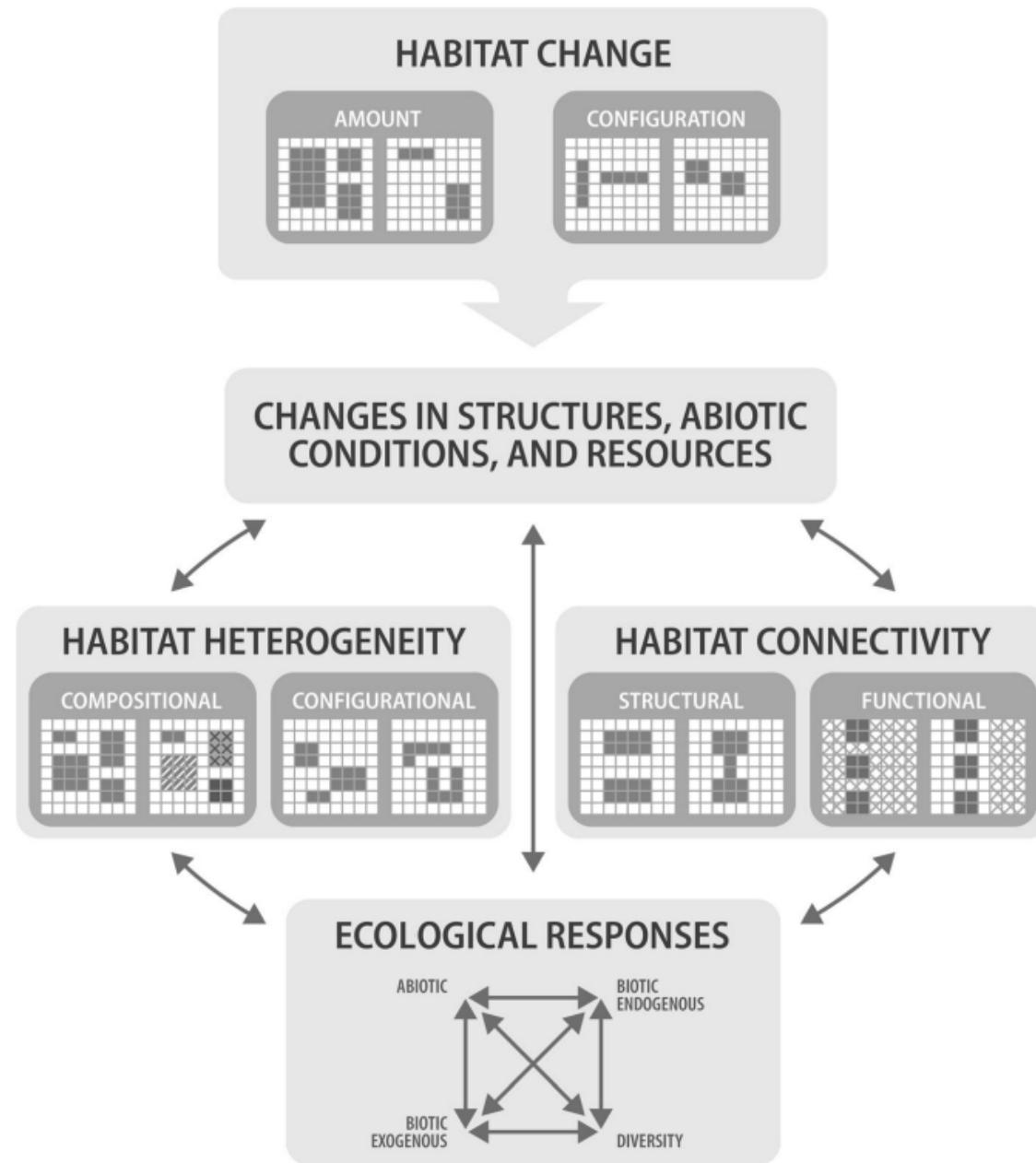


# Conclusions

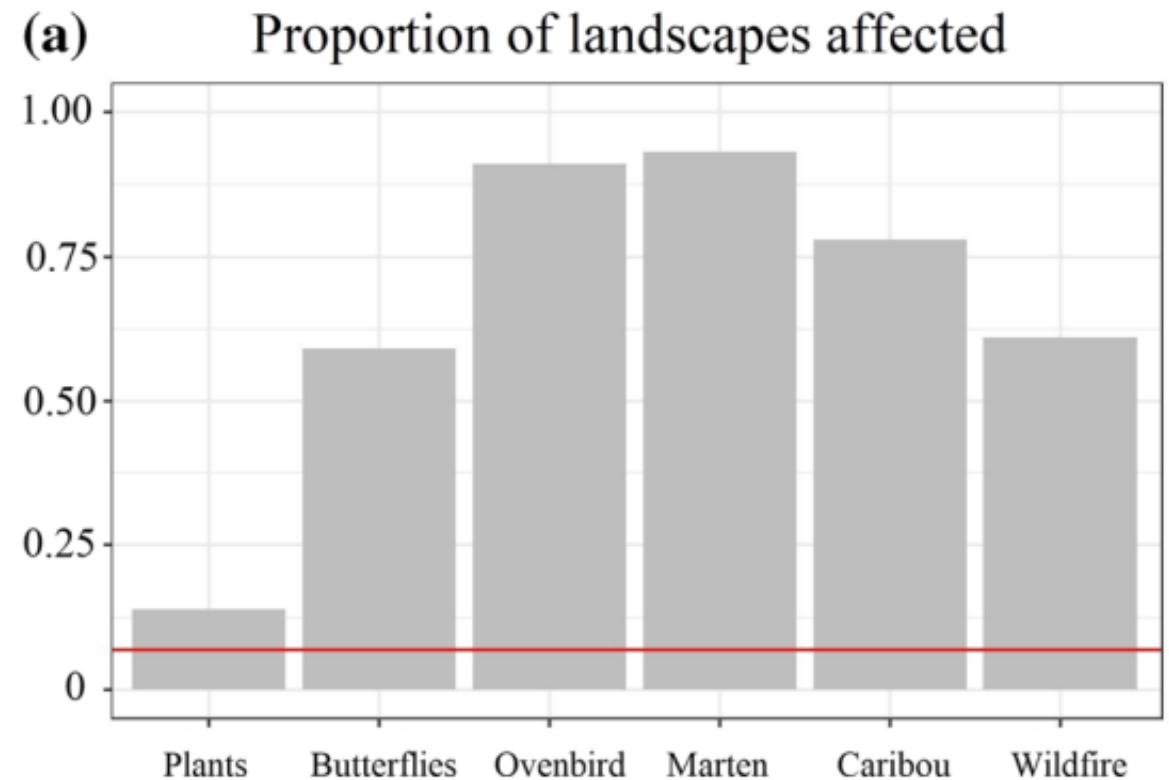
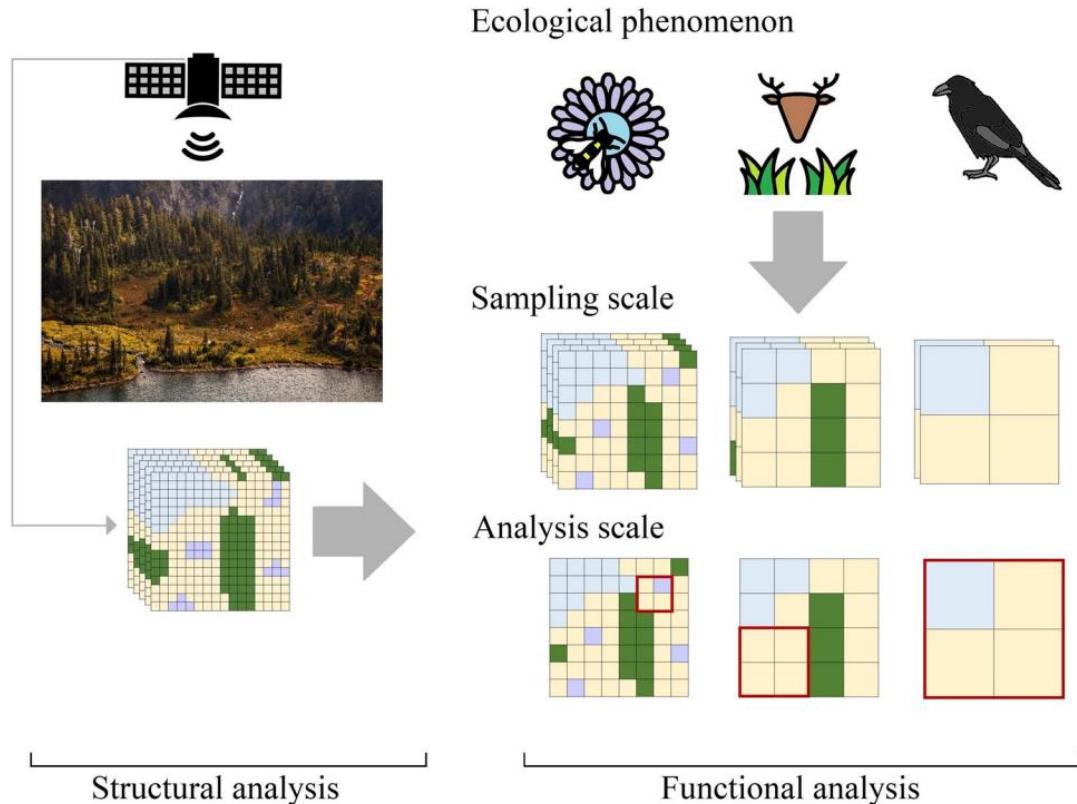
# Scales matter – what can we do?

- Always think about the ecological process of interest
  - E.g., for conservation, are you interested in large scale, regional patterns, or in *in situ* protection and management of species?
  - Why are you designing an analysis at a given spatial and temporal scale?
  - Taxonomic scales, other scales?
- How can scales affect your conclusion, and why?





# Measuring functional habitat loss



# McGill University, BIOL 310 - Scaling in ecology

Riva, Federico

03/02/2022

## Introduction

This is a tutorial complementing the lecture on scales, available at <https://github.com/FedericoRiva>. We will focus on three main parts: 1) spatial data preparation; 2) scale dependency in species rarity; and 3) scale dependency in biodiversity trends

## Spatial data preparation

```
# set up
# packages needed in the tutorial
packages = c("data.table", "raster", "sp", "maptools", "dplyr", "vegan")

# load the packages; if missing, install & load
package.check <- lapply(
  packages,
  FUN = function(x) {
    if (!require(x, character.only = TRUE)) {
```