The Abdus Salam International Centre for Theoretical Physics

Emanuele Pigani

Synergy Summer School 2025

Ischia, 04/07/2025

Complexity and emergence in marine ecosystems seascape: Theory, mechanisms and data

Quantitative Ecology and Evolution Group at ICTP

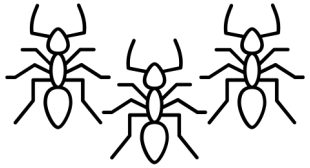
Jacopo Grilli

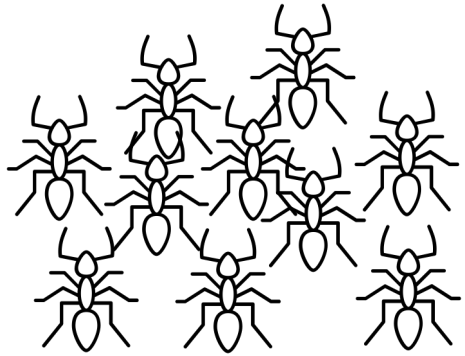
Open positions!

The Abdus Salam International Centre for Theoretical Physics

What is a complex system?

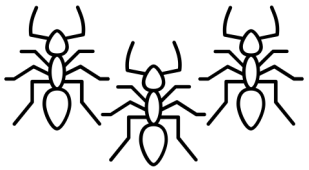
The Physics of Emergence

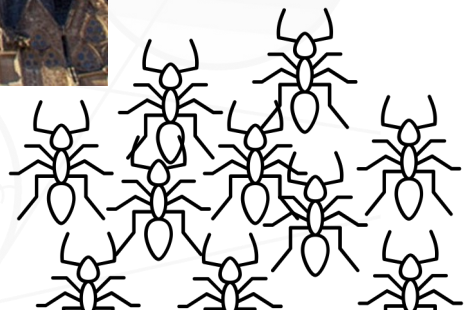




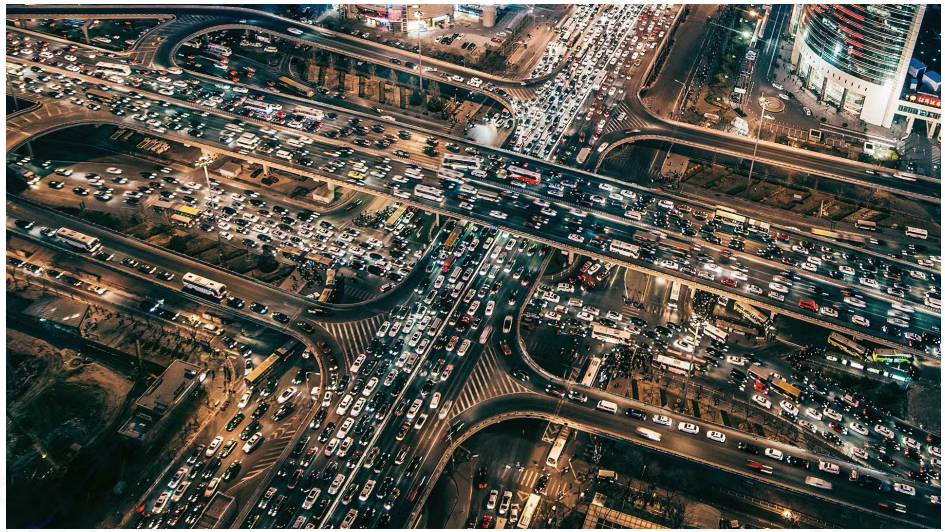
[T. Drayer et al, *PNAS*, 2024]

The Physics of Emergence





Complicated vs Complex

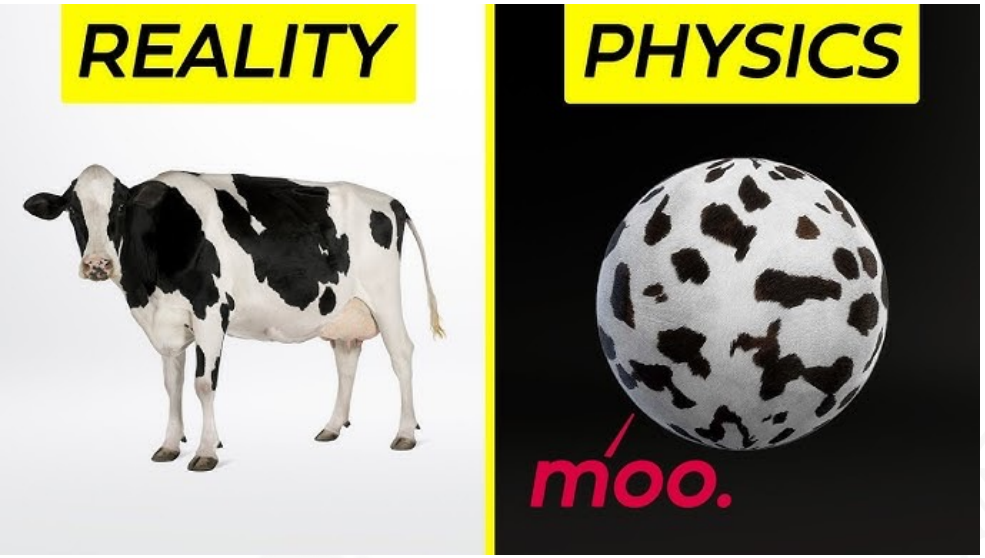


- Causality
- Linearity
- Reducibility
- Locality
- ...

Complex systems require a different approach...

[D. Brockmann, *Complexity Explorables*]

How to study complex systems?



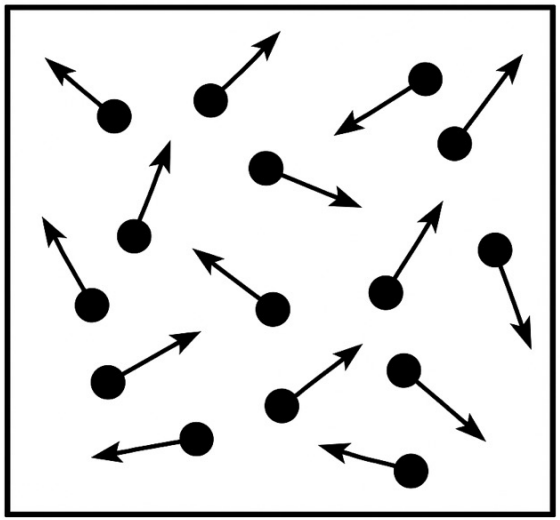
"Make everything as **simple** as possible, but **not simpler**."

A. Einstein

Many Body problems

THE ART OF MAKING THE CORRECT APPROXIMATIONS AND OF LOOKING AT THE RIGHT VARIABLES

- $N = 1$ easy (Newton)
- $N = 2$ feasible
- $N = 3$ challenging
- ...
- $N = 10^3$ almost impossible
- ...
- $N = 10^{23}$ feasible (Statistical Mechanics)



[L. Boltzmann, *Lectures on Gas Theory*, 1896]

Linking Microscopic and Macroscopic states

$N = 2$ dice are rolled. Bet on their sum!

The **identity** of the dice are irrelevant for our **scope**

Micro	Macro
11	2
12 21	3
13 22 31	4
14 23 32 41	5
15 24 33 42 51	6
16 25 34 43 52 61	7
26 35 44 53 62	8
36 45 54 63	9
46 55 64	10
56 65	11
66	12

Bet on the sum for $N = 3,4, \dots, 10^{23}$

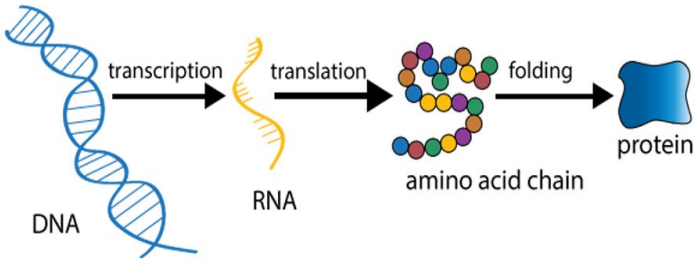
When N is very large, for some **observables**:

- only **few degrees of freedom** may be important;
- some **universal emergent** pattern can exist.

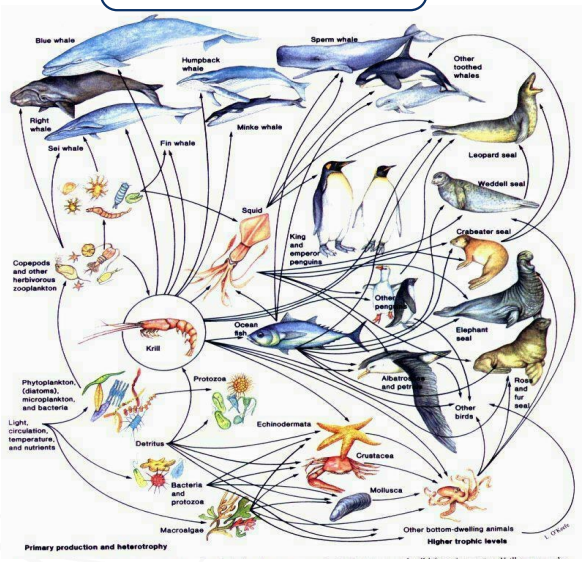
The interplay among three complex systems

Environment

Organisms



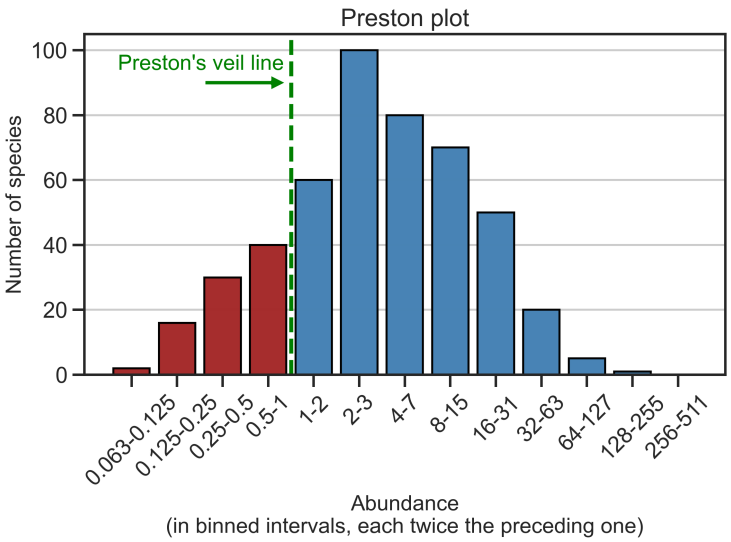
Food webs

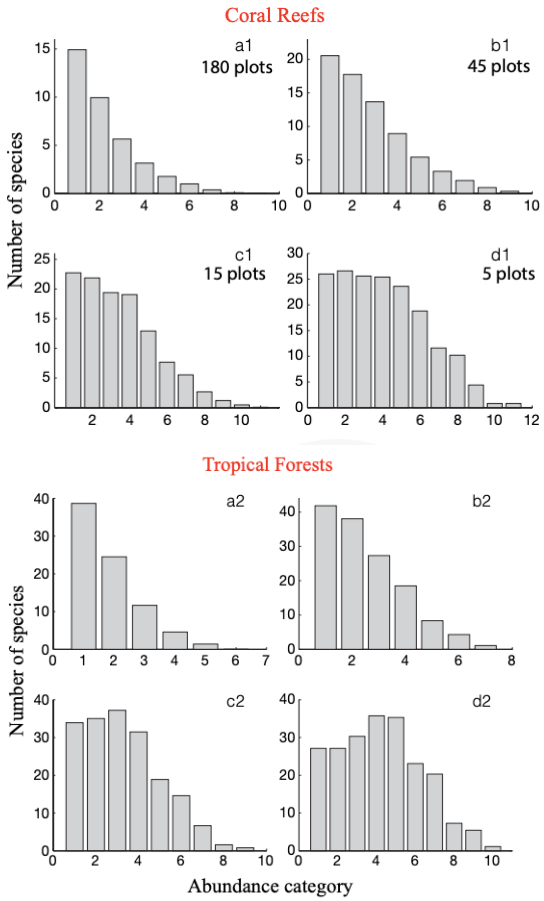


[thanks to DI]

Emergent properties in Ecology

Species Abundance Distribution (SAD)





[Volkov et al., *Nature*, 2007]

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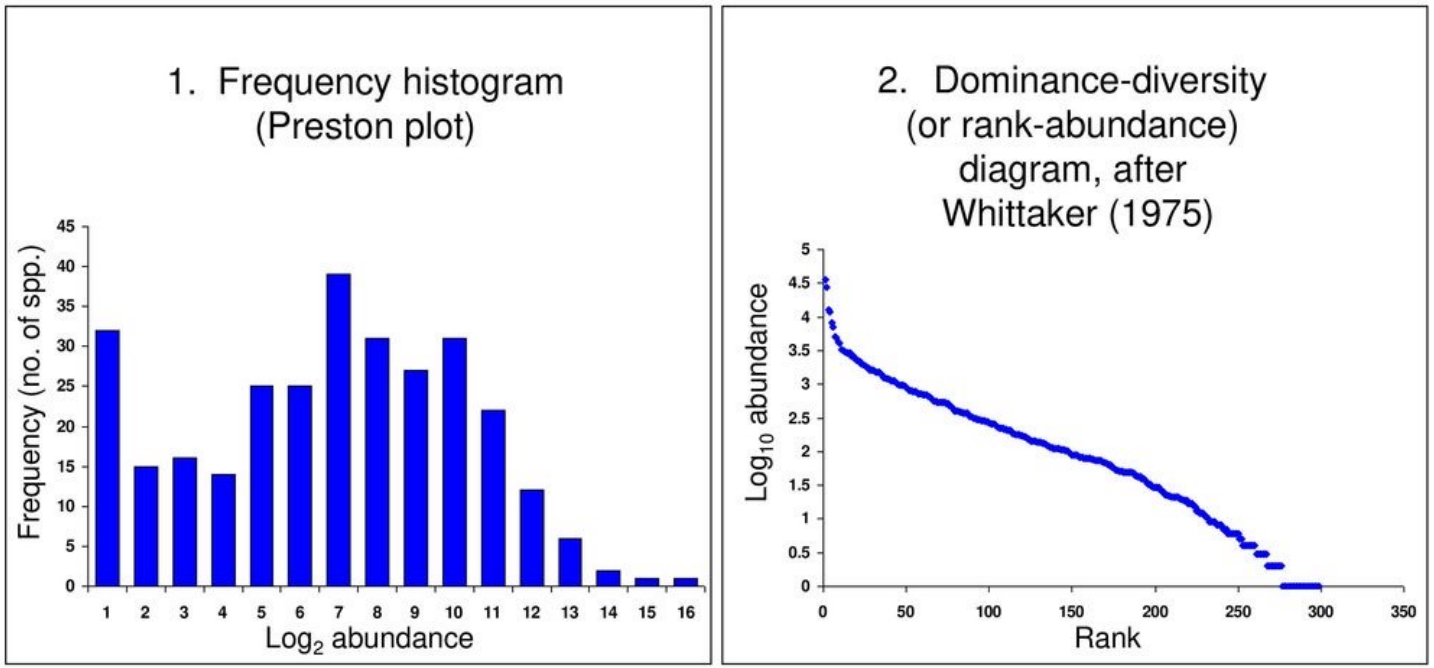

Data from BCI 50-ha Forest Dynamics Plot, Panama; 229,069 individual trees of 300 species; most common species n_{HYBAPR}=36,081; several rarest species n_{RARE}=1

[Volkov et al., *Nature*, 2007]

Emergent properties in Ecology

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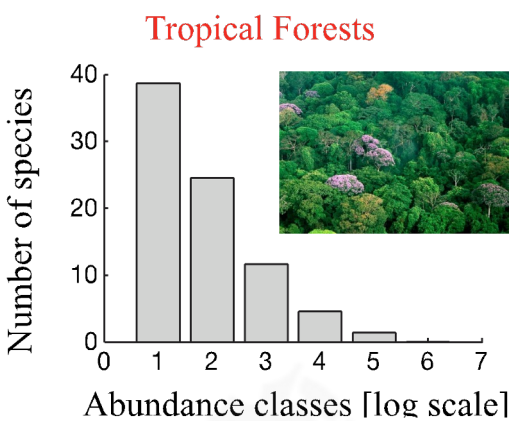
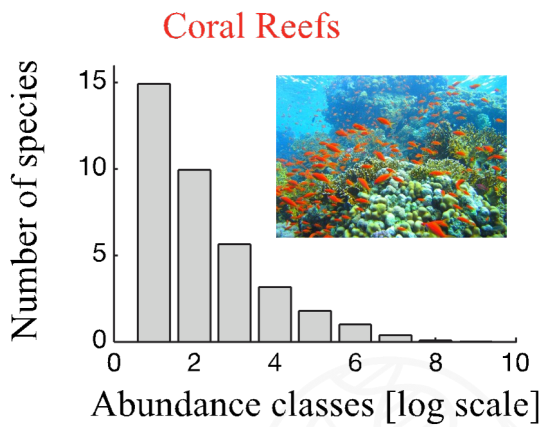
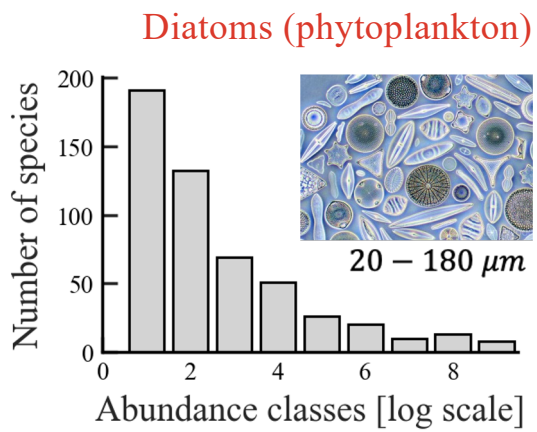


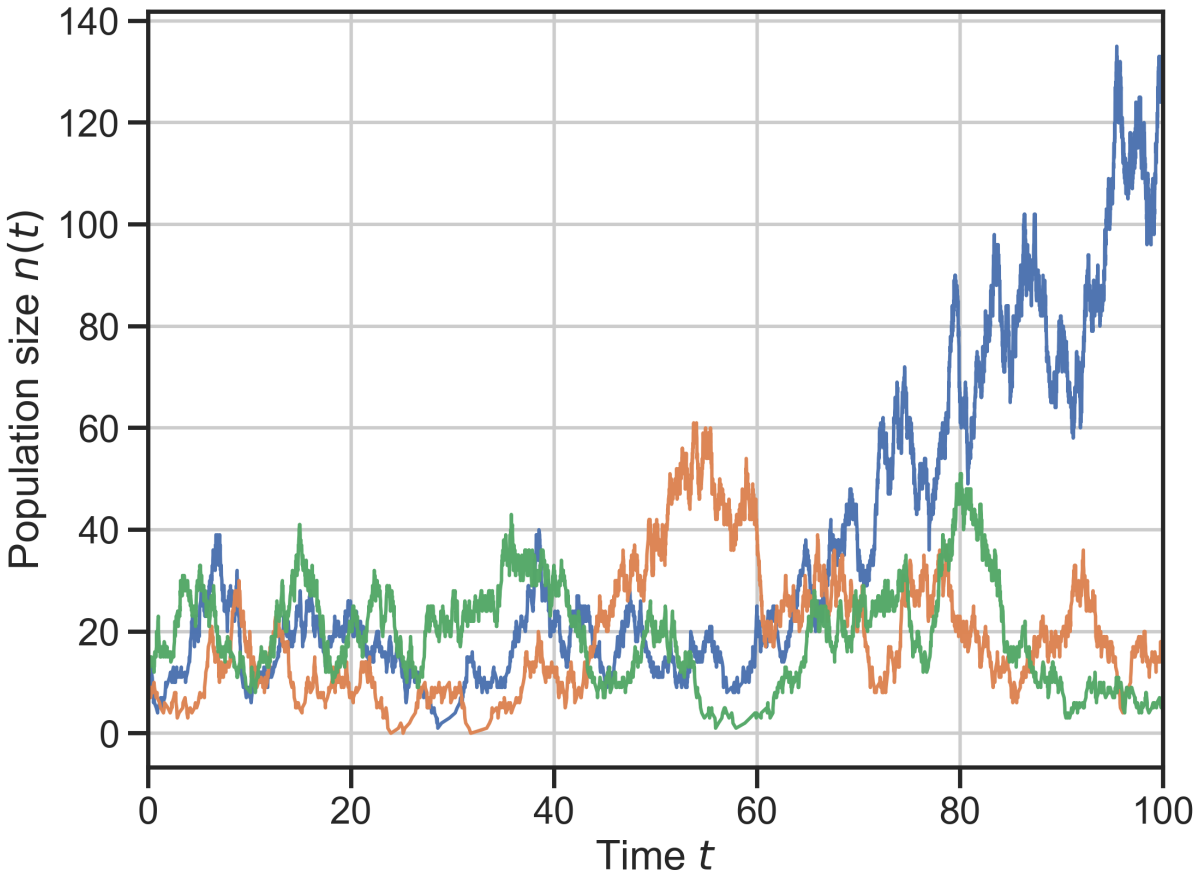




What should we expect **by chance**?
What is a minimal model?

[Volkov et al., *Nature*, 2007; Pigani et al., *Science Advances*, 2024]

Introduction to Neutral Theory



[Volkov et al., *Nature*, 2003; WHITEBOARD]

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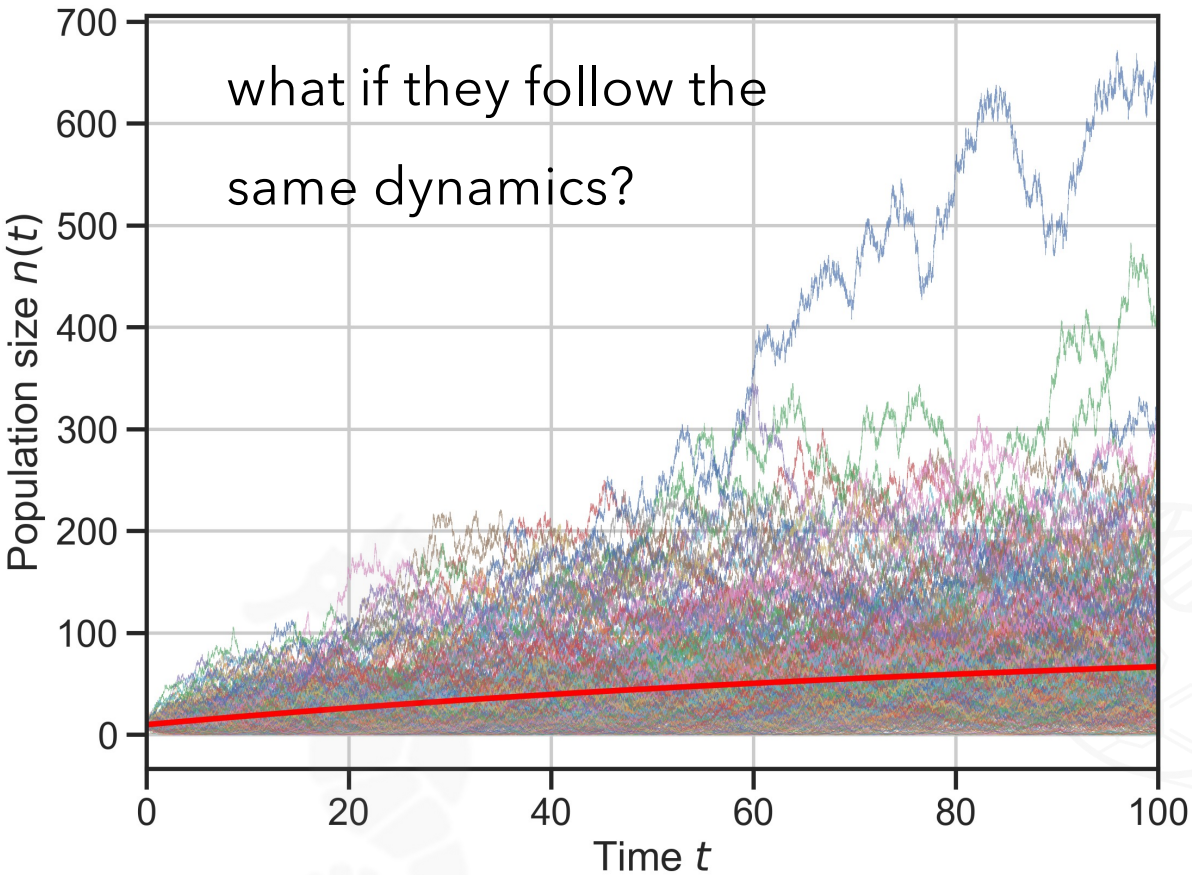


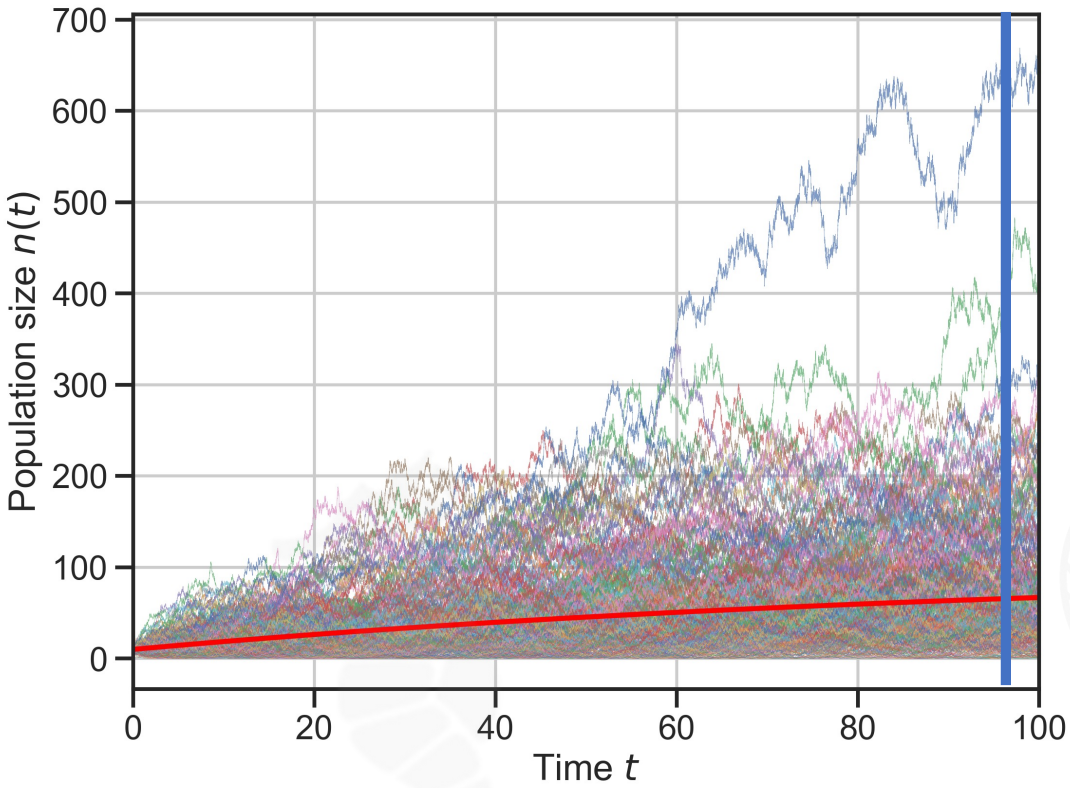
$$\dot{n}_i(t) = \underbrace{r n_i(t) + \nu}_{\text{deterministic}} + \underbrace{\sigma \sqrt{n_i(t)} \eta(t)}_{\text{stochastic}}$$

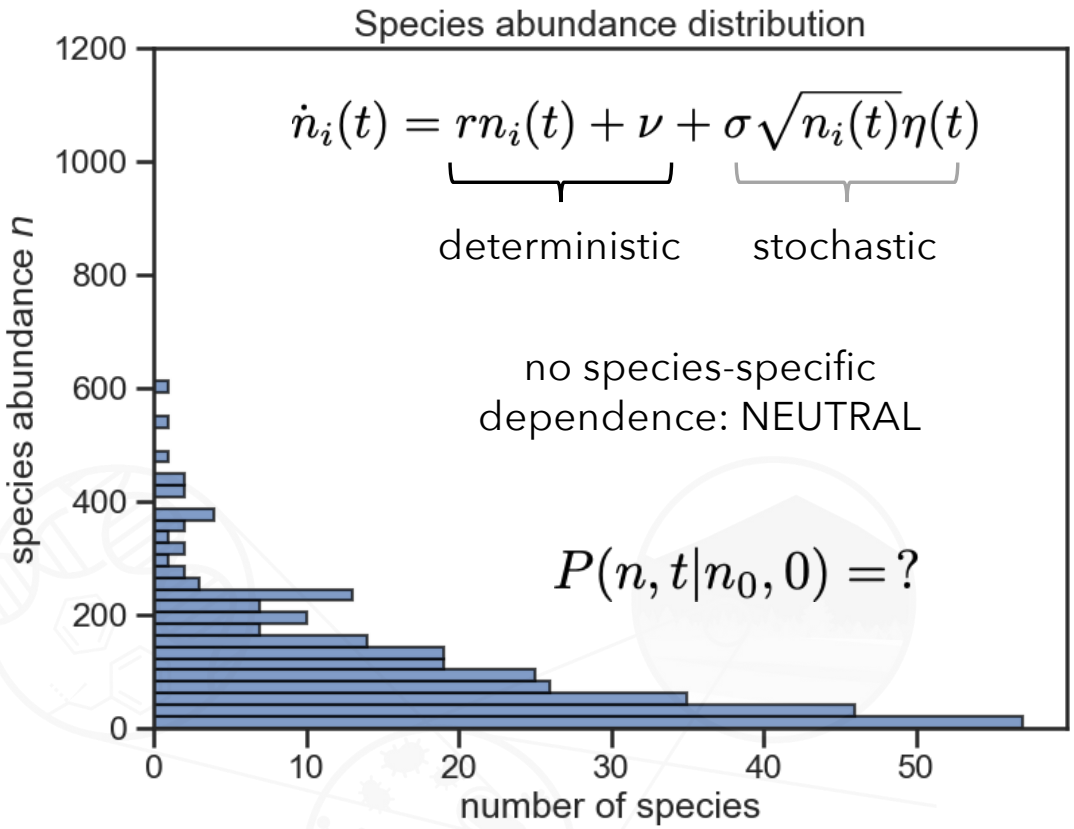
no species-specific dependence: NEUTRAL

$$P(n, t | n_0, 0) = ?$$

[Volkov et al., *Nature*, 2003; WHITEBOARD]

Introduction to Neutral Theory





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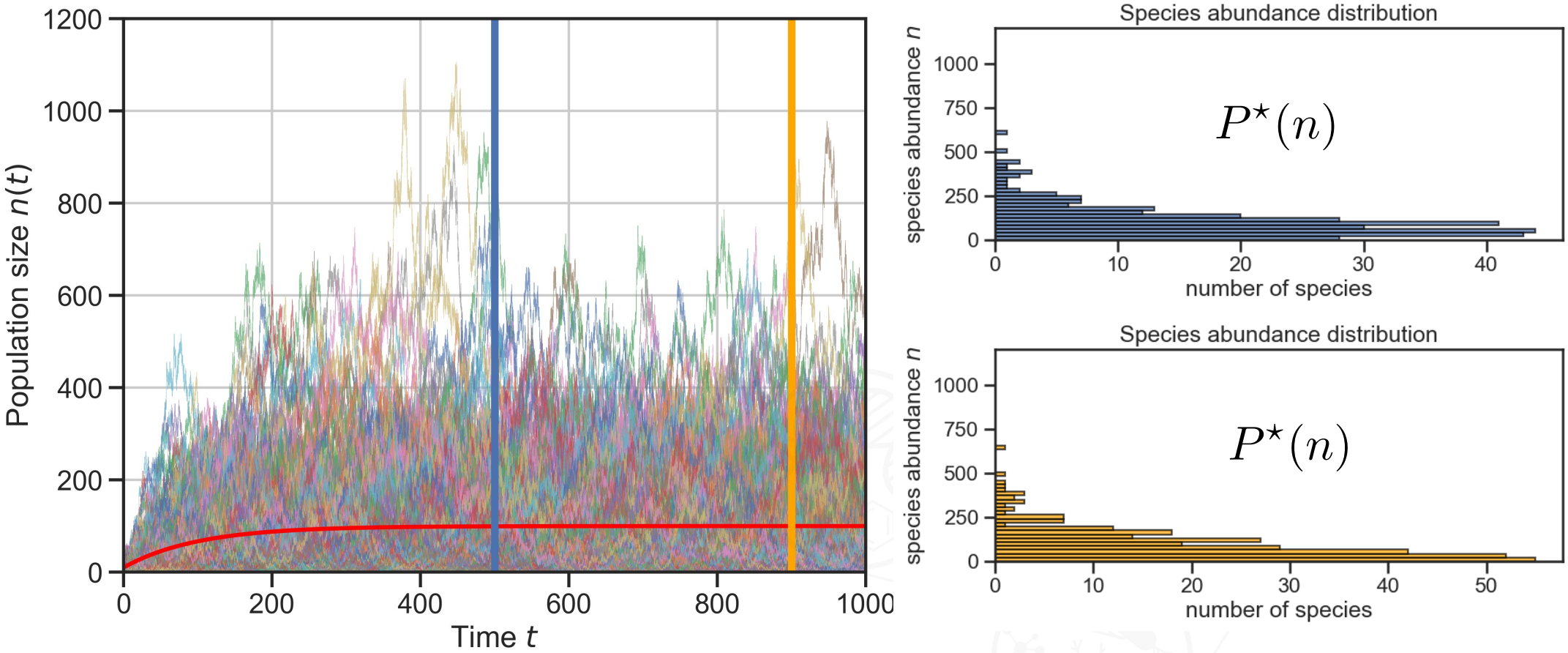
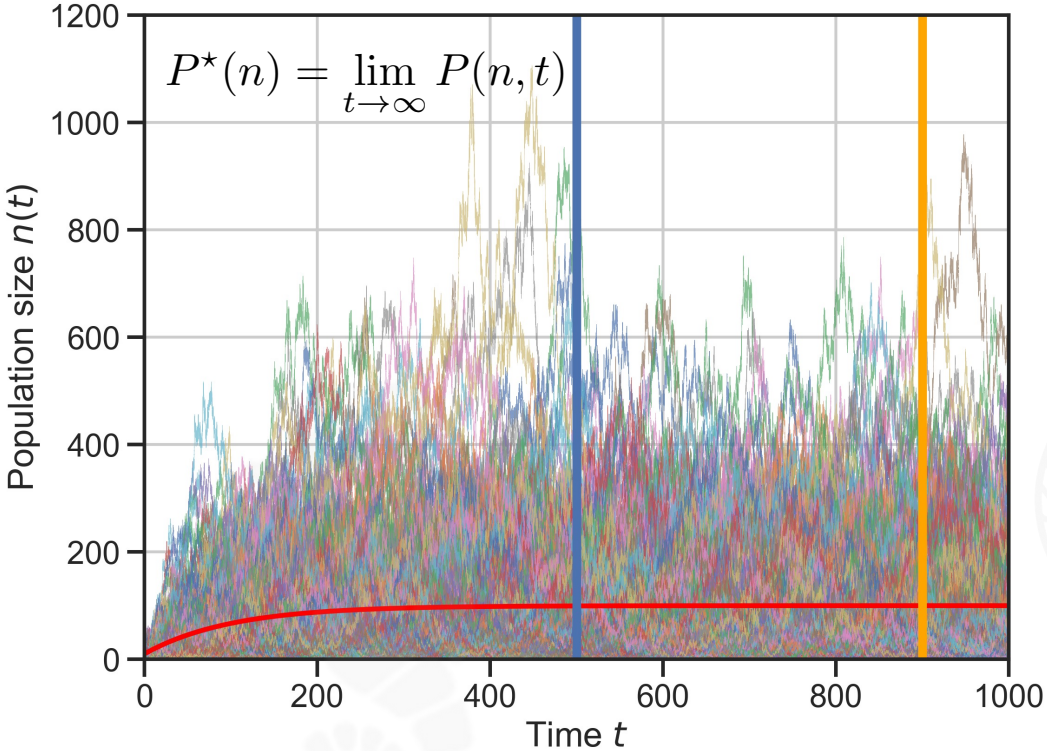
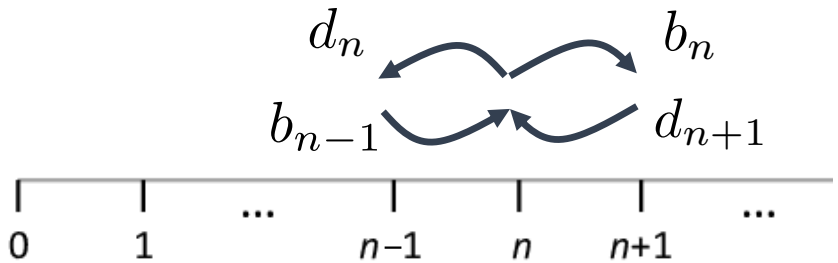


[Volkov et al., *Nature*, 2003; WHITEBOARD]

Introduction to Neutral Theory

birth-death Master Equation $$\frac{dP(n,t)}{dt} = b(n-1)P(n-1,t) + d(n+1)P(n+1,t) - [b(n)+d(n)]\,P(n,t)$$





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Introduction to Neutral Theory

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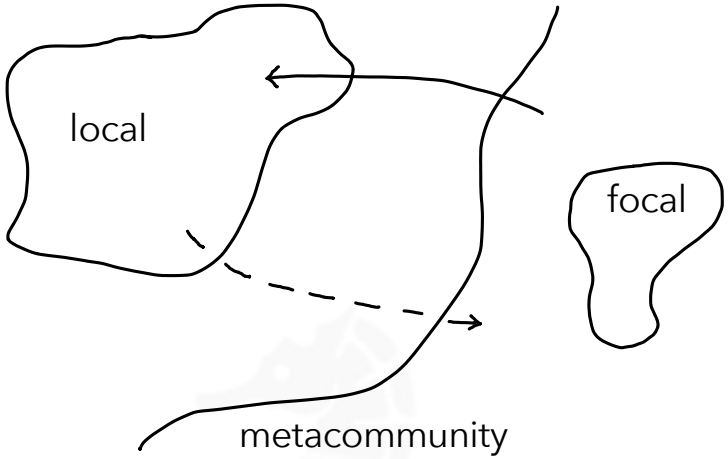
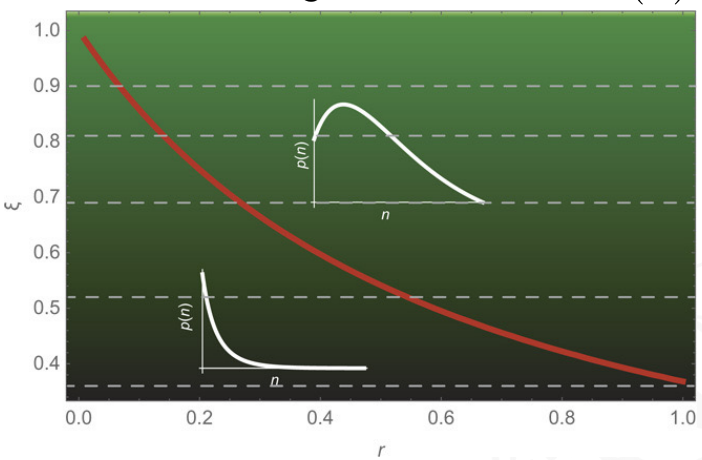


metacommunity (*S species*, N *individuals*)

$$b(n) = b'n(1-\nu) + b'(N-n)\nu\frac{1}{S}$$

$$d(n) = d'n$$

negative-binomial $P^\star(n)$



general case of the Fisher logseries

$$P(n) \sim x^n \frac{1}{n}$$

[Volkov et al., *Nature*, 2003; Tovo et al., *Science* Advances, 2017; WHITEBOARD]

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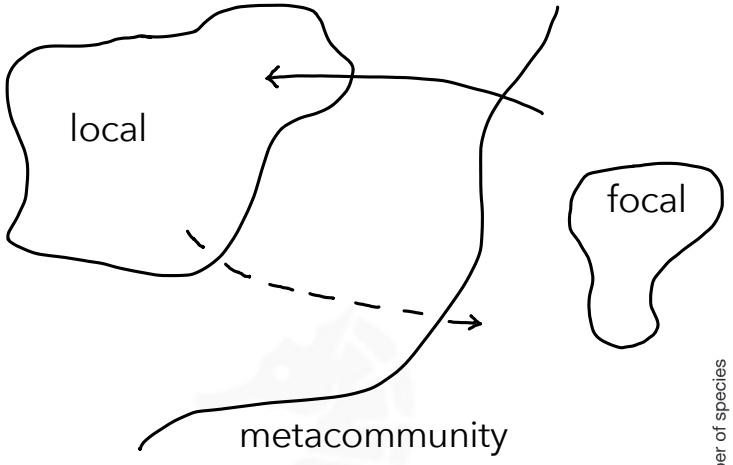

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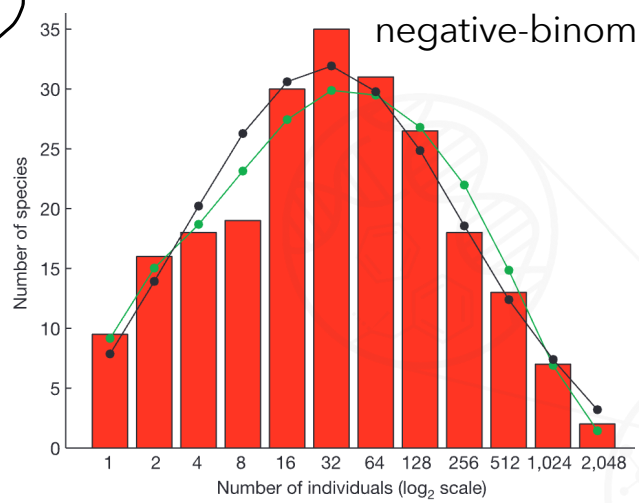

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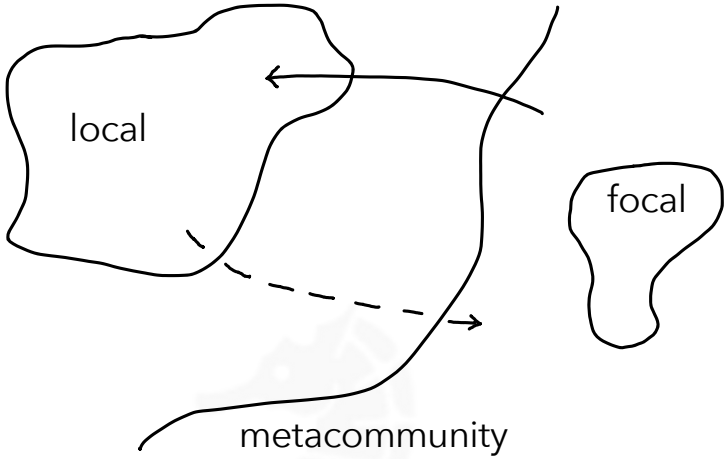


local community (J *individuals*)

$$b(n) = \frac{n}{J}\frac{J-n}{J-1}(1-m) + \frac{n}{J}m(1-y)$$

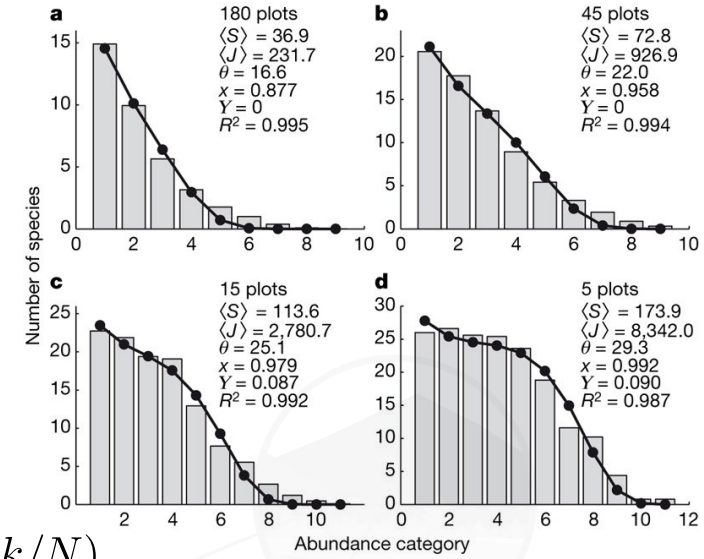
$$d(n) = \frac{n}{J}\frac{J-n}{J-1}(1-m) + \frac{J-n}{J}my$$

$$\downarrow$$

$$P^{\star}\left(n|k/N\right)$$

$$\downarrow$$

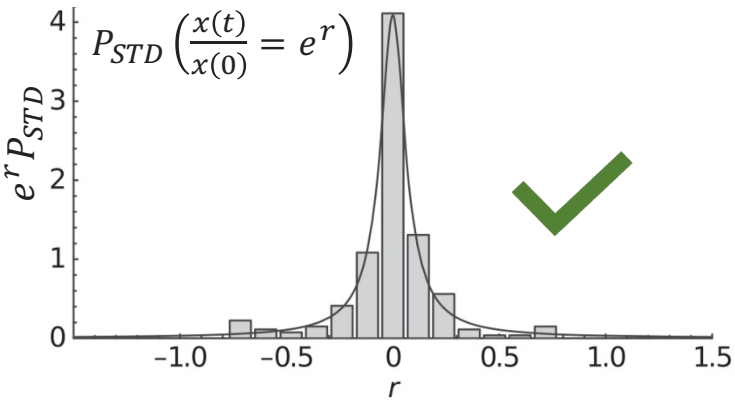
$$P_{local}(n) = \sum_{k=1}^{\infty} P_{meta}(k)P^{\star}\left(n|k/N\right)$$



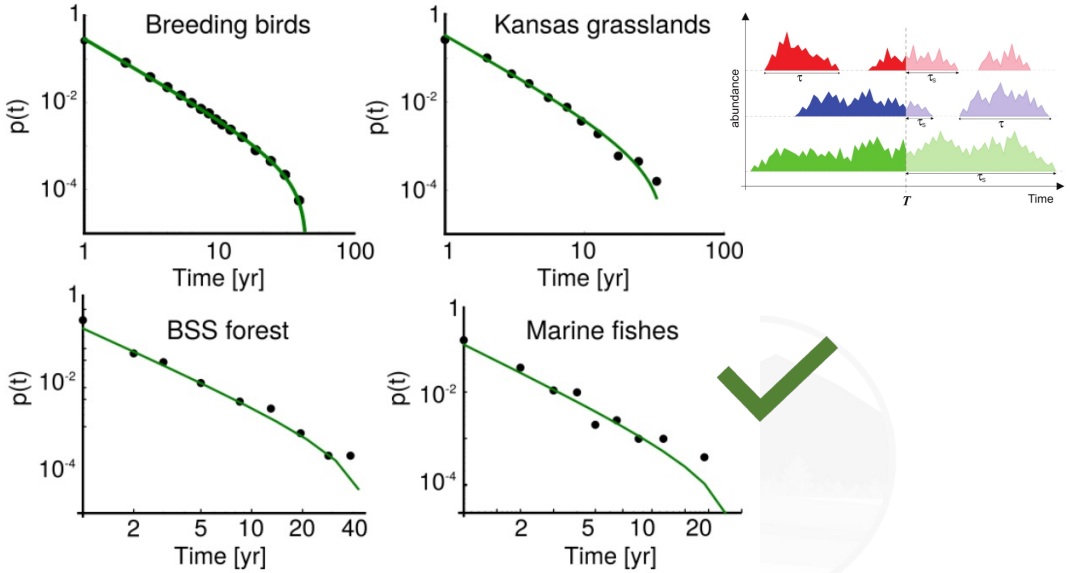
[Volkov et al., *Nature*, 2007; WHITEBOARD]

Other emergent patterns that Neutral Theory can reproduce

Species Turnover Distribution (STD)



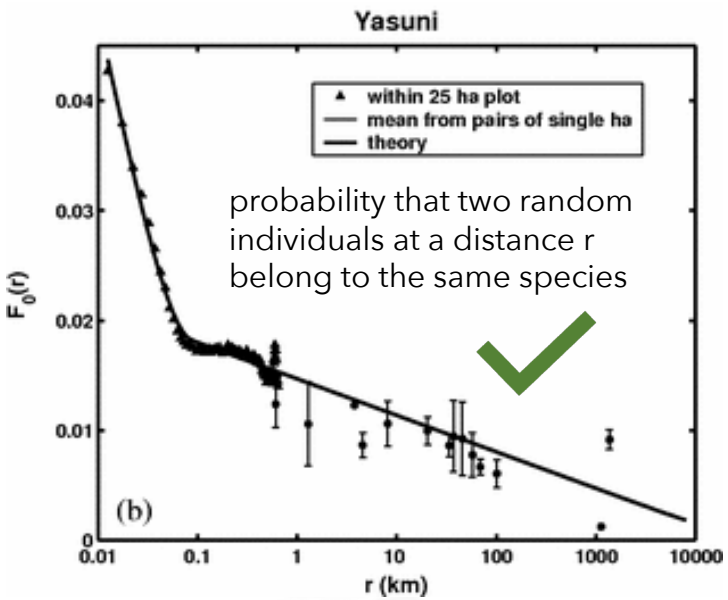
Species-Persistence Time Distribution (SPT)



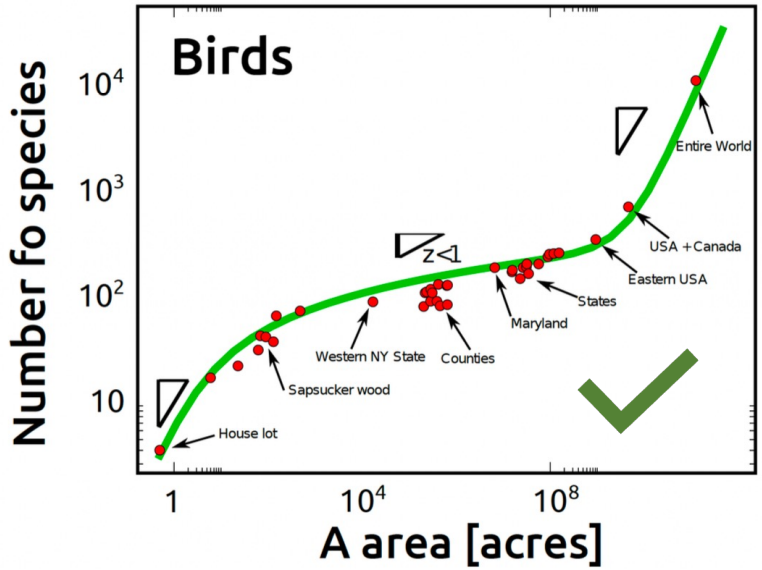
[Azaele et al., *Nature*, 2006; Suweis et al., *Journal of theoretical biology*, 2012]

Other emergent patterns that Neutral Theory can reproduce

β-diversity



Species Area Relationship (SAR)



it fails in many others (which is good)

[Zillio et al., *PRL*, 2005; Grilli et al., *Journal of theoretical biology*, 2012]

Introduction to Neutral Theory

Birth-death Master Equation

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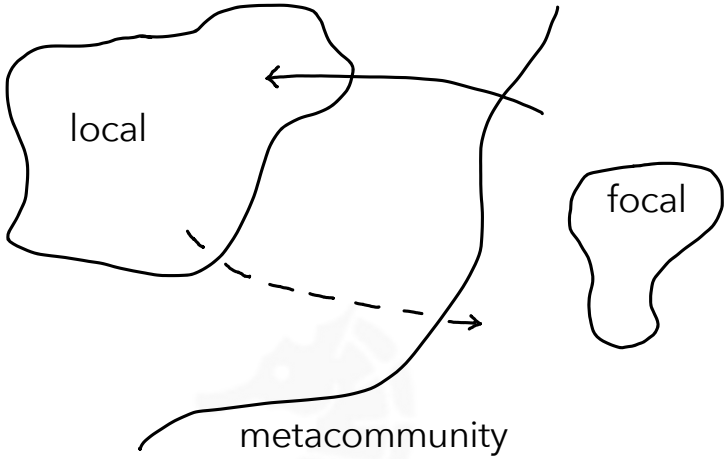
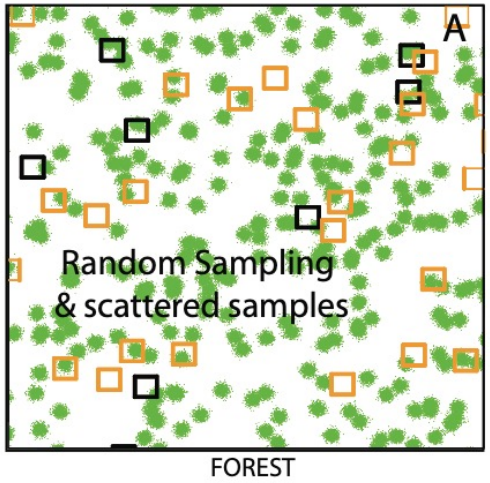
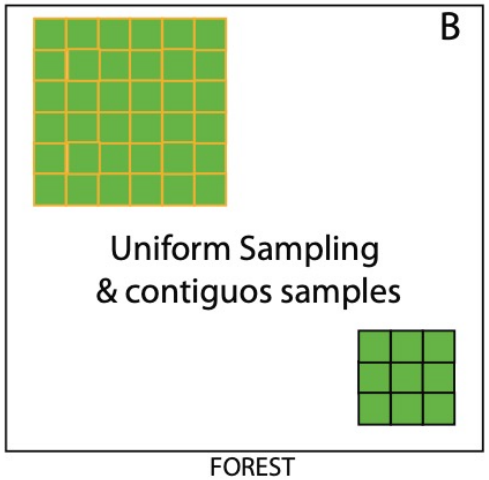


focal community (J *individuals sampled*)

$$P_{\text{focal}}(n) = \sum_{k=1}^{\infty} P_{\text{meta}}(k)\,\text{Binomial}(n \mid k, p = J/N)$$





[Tovo et al., *Science* Advances, 2017; WHITEBOARD]

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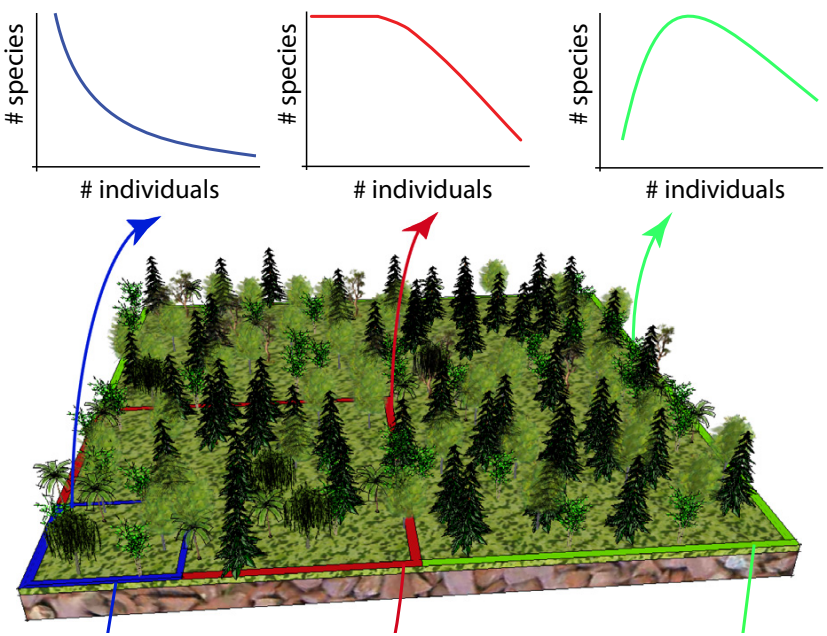

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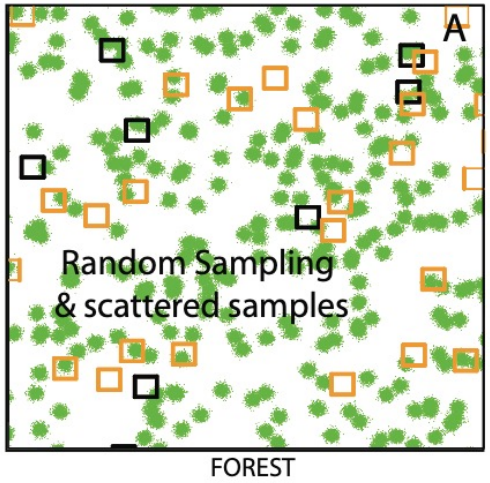
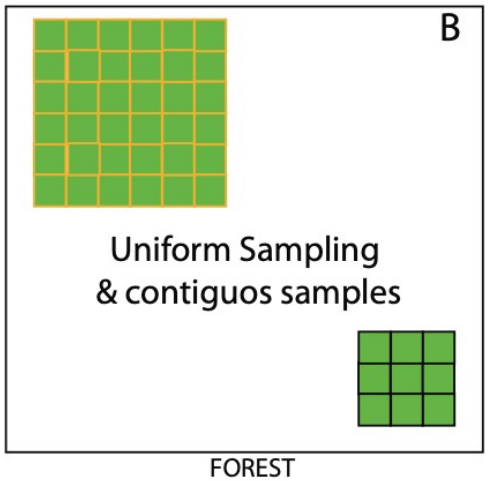




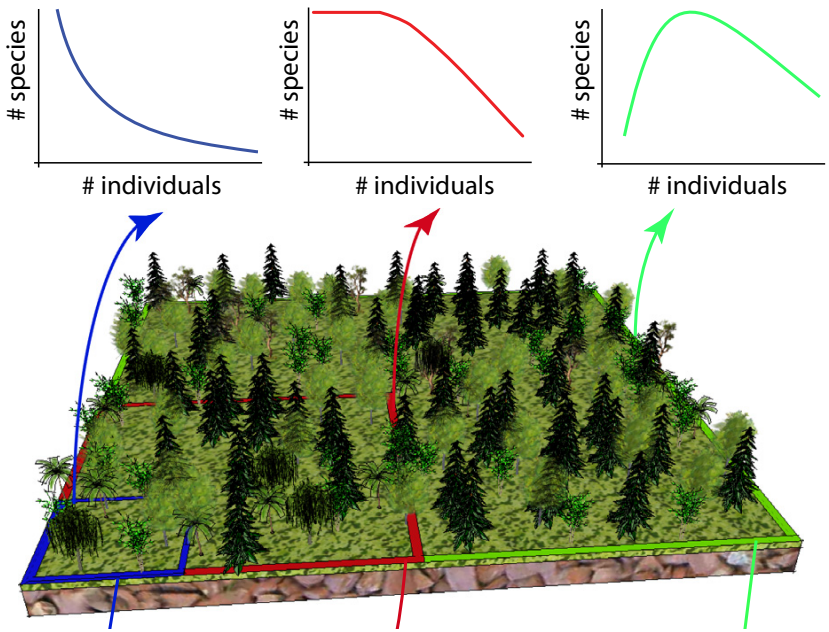
Upscaling Focal Community

The metacommunity follows $P_{meta}(n) = \mathrm{NegBinomial}(n|r,\xi)$

$$P_{\text{focal}}(n) = \sum_{k=1}^{\infty} P_{\text{meta}}(k)\,\mathrm{Binomial}(n \mid k, p = J/N)$$

$$P_{focal}(n) = \mathrm{NegBinomial}(n|r,\xi_p)$$

Self-similarity!



We can predict the number of species at a larger scale

$$r = b_0/b_1$$
$$\xi = 1 - b_1/d_1$$
$$\xi_p = \frac{p\xi}{1-\xi(1-p)}$$

Scaling law

$$\langle S \rangle = S_p \frac{1-(1-\xi)^r}{1-(1-\xi_p)^r}$$

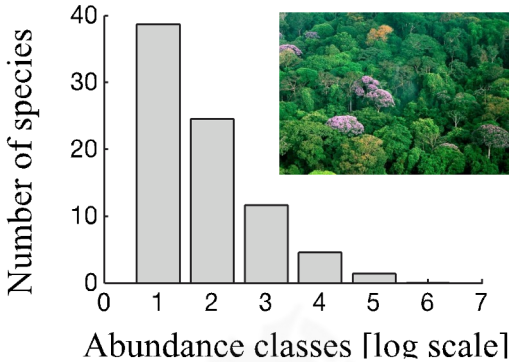
Application: how much we need to sample a forest?

[Tovo et al., *Science* Advances, 2017]

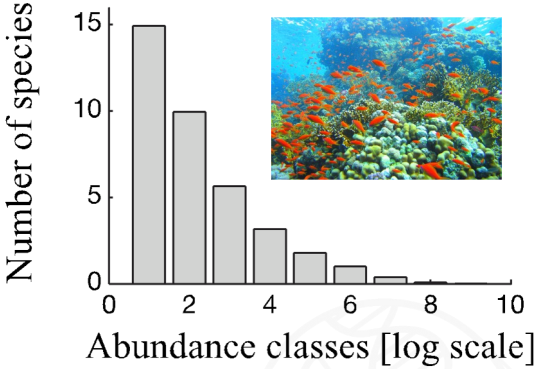
Emergent properties in Ecology

Species Abundance Distribution (SAD)

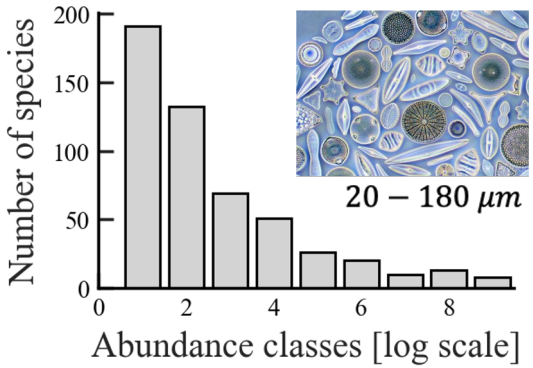
Tropical Forests



Coral Reefs



Diatoms (phytoplankton)



NT reproduces SADs

Can we apply NT and the sampling framework to ocean ecology? What can we learn?

[Volkov et al., *Nature*, 2003; Volkov et al., *Nature*, 2007; Pigani et al., *Science Advances*, 2024]

Niche vs Neutral

$$\dot{n}_i(t) = \underbrace{f_i(\vec{n}(t)|\vec{\alpha}(t))}_{\text{deterministic}} + \underbrace{g_i(\vec{n}(t)|\vec{\beta}(t))\eta_i(t)}_{\text{stochastic}}$$

- **Interactions** are very relevant;
- Stochastic noise is secondary.

$$\dot{n}_i(t) = \underbrace{n_i(t)\left(r_i - \sum_{j=1}^{S} \alpha_{ij} n_j(t)\right)}_{\text{Deterministic, with interactions}}$$

Generalized Lotka-Volterra

- No interactions;
- Stochastic **noise** is very relevant.

$$\dot{n}_i(t) = \underbrace{r n_i(t) + \nu}_{\text{Deterministic, no interactions}} + \underbrace{\sigma\sqrt{n_i(t)}\eta(t)}_{\text{Demographic noise}}$$

Niche vs Neutral

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MacArthur Consumer-Resource Model

- No interactions;
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Phytoplankton?

Niche vs Neutral

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[Hutchinson, *The paradox of the plankton, 1961]*

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*"At nearly all naturally occurring concentrations, the average body-length spacing between individual phytoplankton is such that nutrient depletion zones rarely overlap between neighboring cells, making **direct competition unlikely**, and rapid resource recycling and **physical mixing effectively erase** any depletion-zone **signatures** of **species-specifi**c physiologies."*

[Behrenfeld et al., *Phytoplankton biodiversity and the inverted paradox, 2021]*

General spirit: all models are wrong…

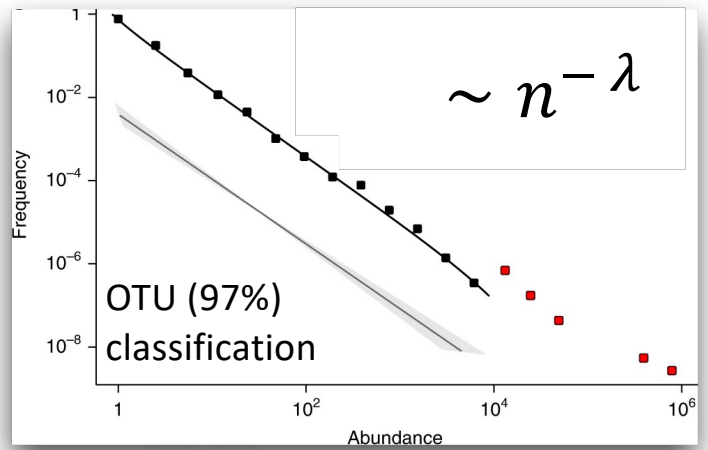
SADs for the plankton in the wild from *Tara Oceans*

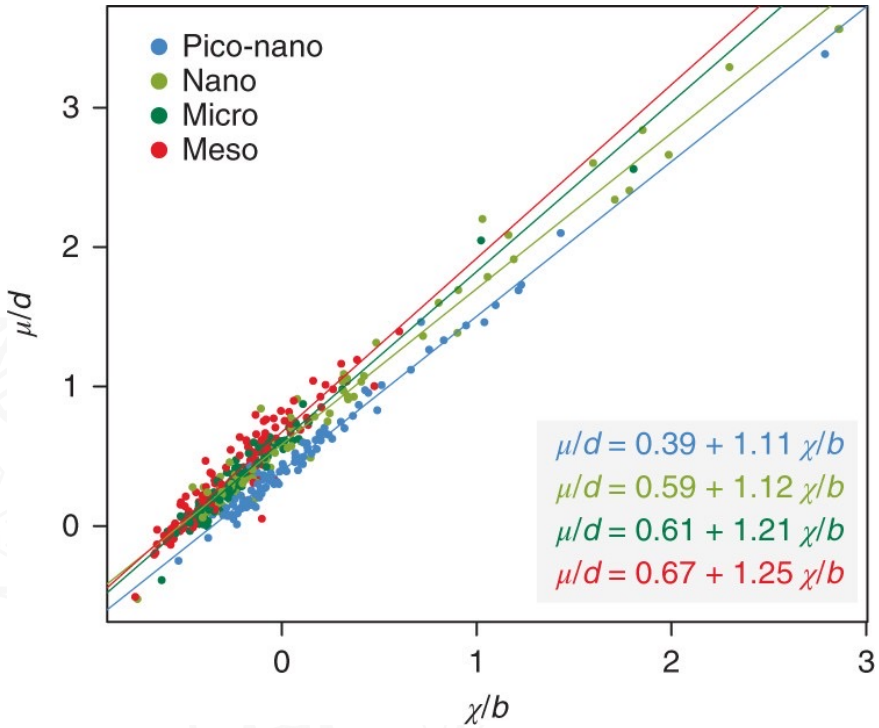
UBIQUITOUS ABUNDANCE DISTRIBUTION OF NON-DOMINANT PLANKTON ACROSS THE GLOBAL OCEAN

Neutral model:

$$\begin{cases} b_n = b\,n + \chi \\ d_n = d\,n + \mu \end{cases} \qquad P(n) \sim n^{-\lambda} e^{-rn}$$

$$\lambda = 1 - \chi/b + \mu/d$$





[Ser-Giacomi et al., Nature ecology & evolution, 2018]

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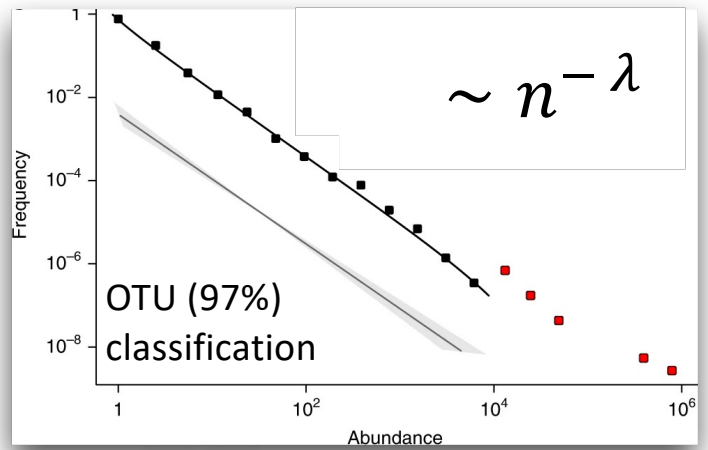
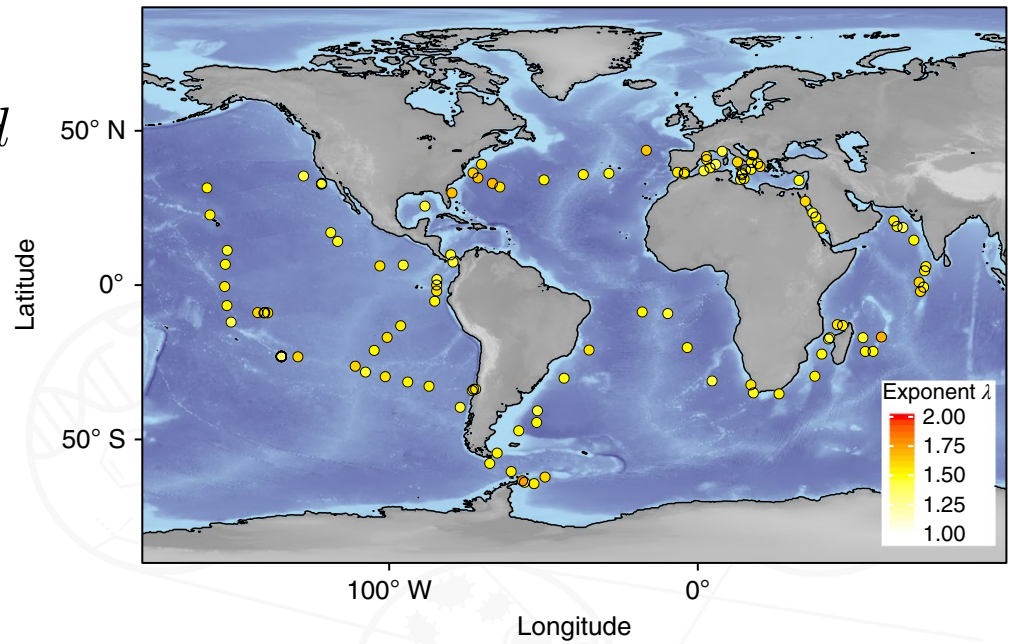
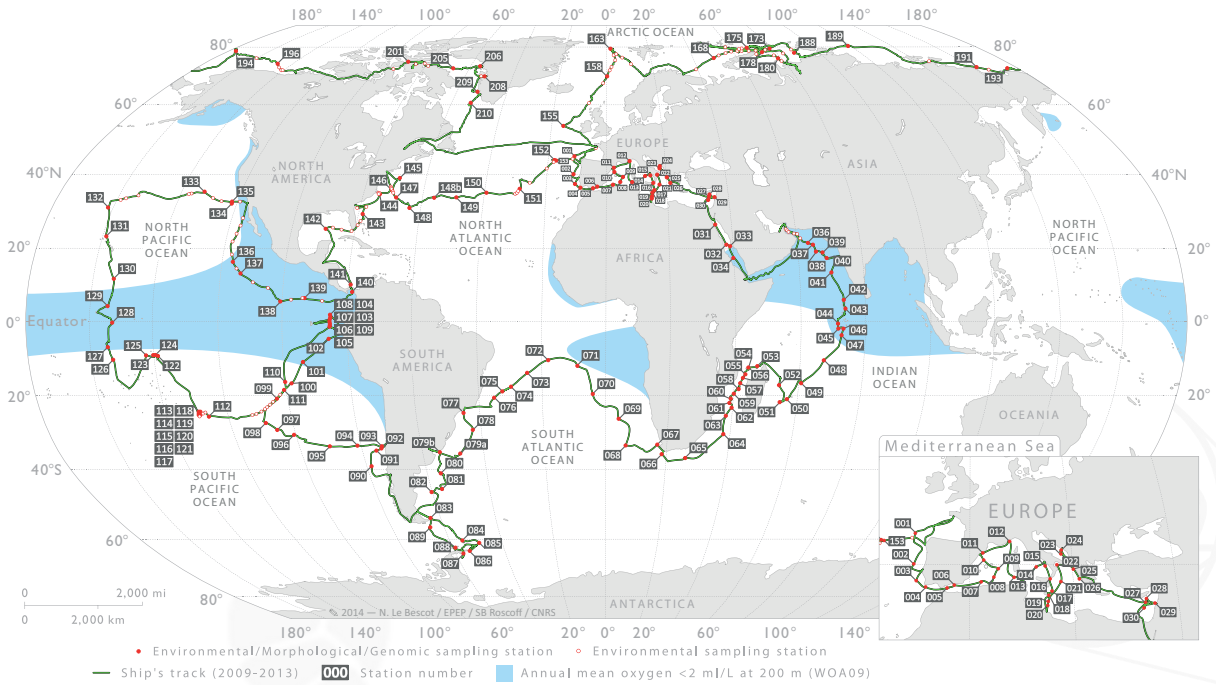


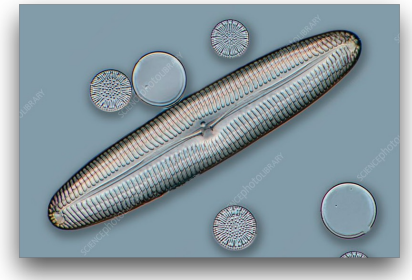


[Ser-Giacomi et al., Nature ecology & evolution, 2018]

Focusing on a single trophic level: Diatoms

Diatoms from the Tara Oceans Dataset



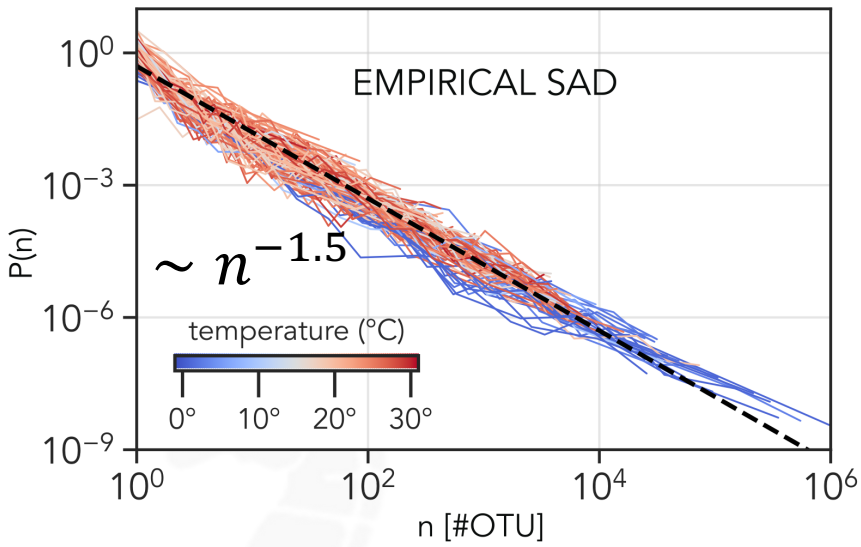


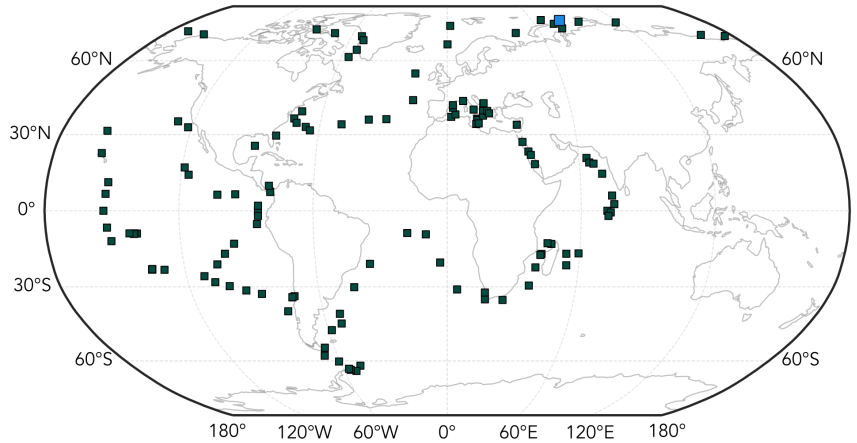
- Unicellular protists;
- >20% of global O_2 production;
- Globally distributed;
- Occupy similar trophic levels despite different life strategies.

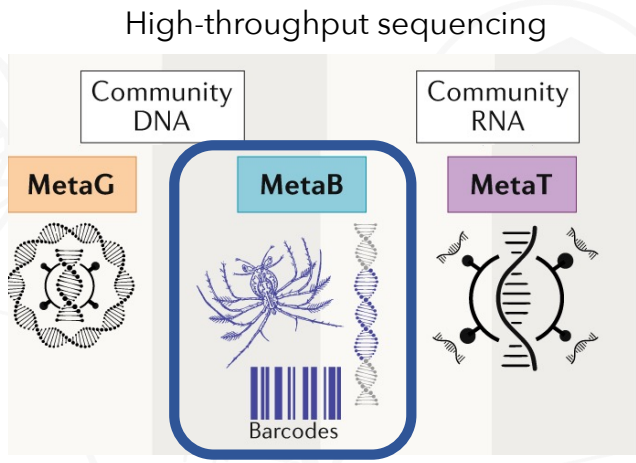
[Bork et al., Science, 2015; Sunagawa et al., *Nature rev. microbiology* 2020]

SADs from *Tara Oceans*

Diatom SADs reveal a similar pattern







[Pigani et al., Science Advances, 2024]

SADs from *Tara Oceans*

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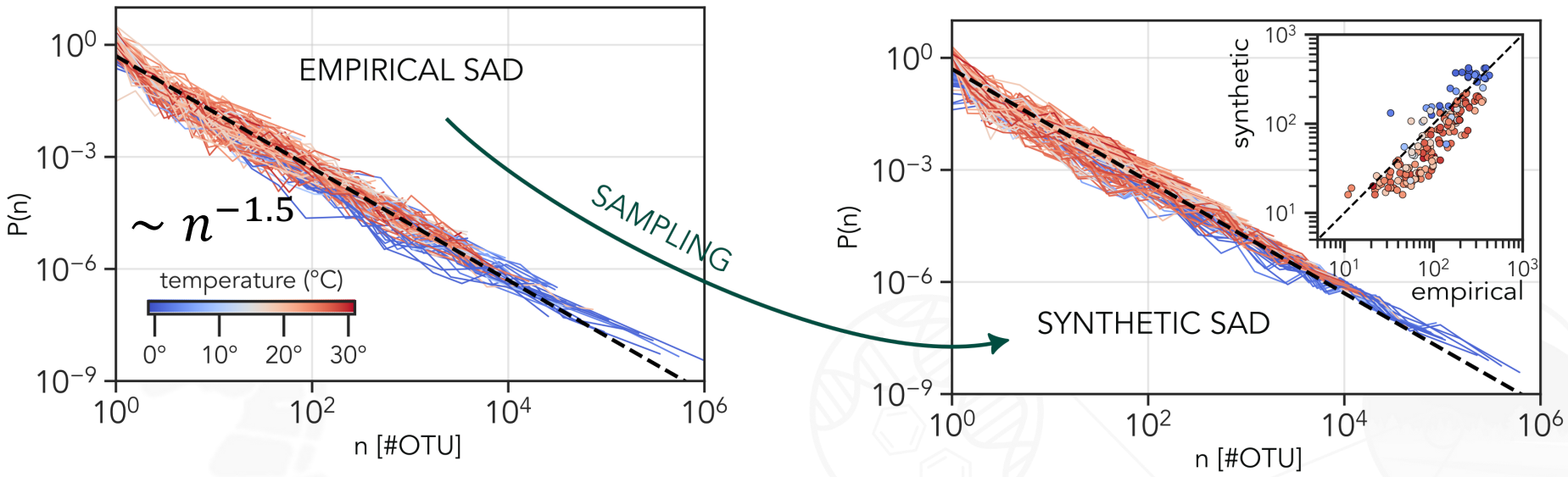
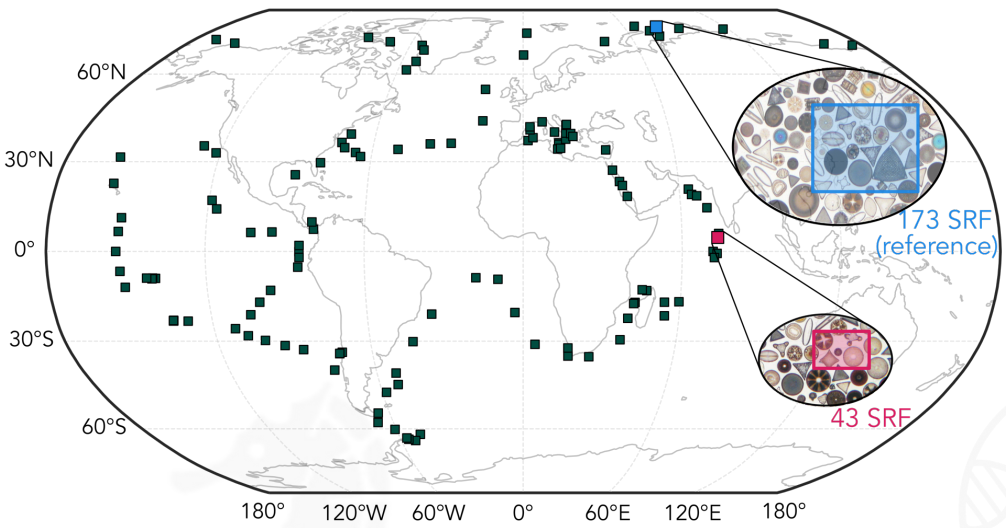


[Pigani et al., Science Advances, 2024]

Test the existence of an **ocean-wide neutral** diatom **metacommunity**



Neutral global metacommunity:

$$\begin{cases} b_n = b\,n + \chi \\ d_n = d\,n + \mu \end{cases} \qquad P(n) \sim n^{-\lambda} e^{-\gamma n}$$

Local sampled communities:

$$SAD_{loc} = \phi(n|\,p, rates)$$

Sampling effort

$$p \ll 1$$

[Pigani et al., Science Advances, 2024]

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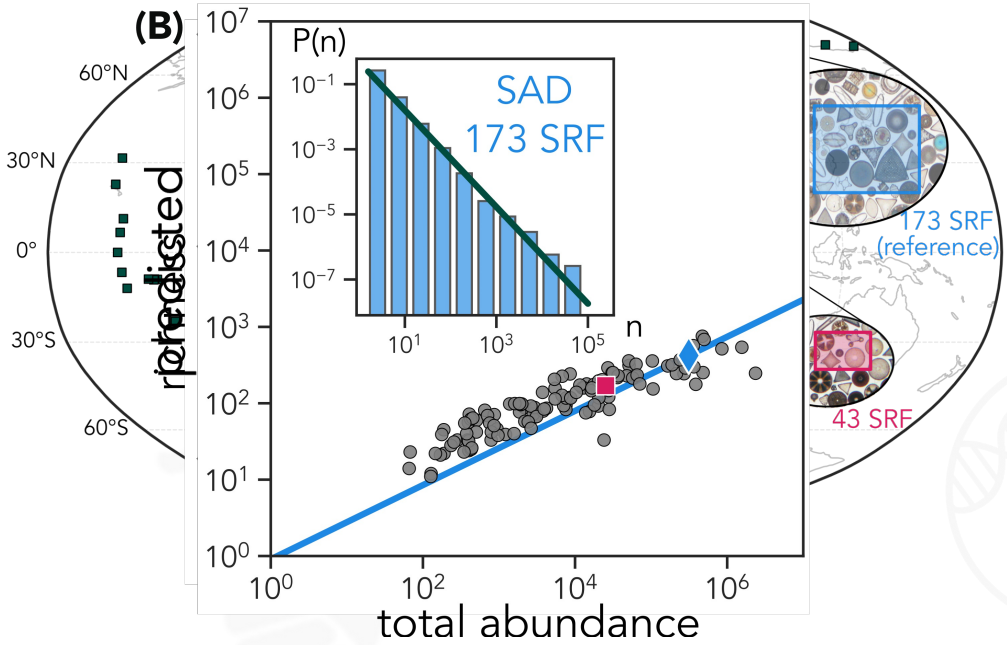

$$\langle S_p \rangle = K(N_{meta}, S_{meta}, \lambda)(N_p)^{\lambda-1}$$

measured local abundance

metacommunity exponent

metacommunity index

expected local richness

comparing with a reference station:

$$\langle S_p \rangle = S_{ref}\left(\frac{N_p}{N_{ref}}\right)^{\lambda-1}$$

[Pigani et al., Science Advances, 2024]

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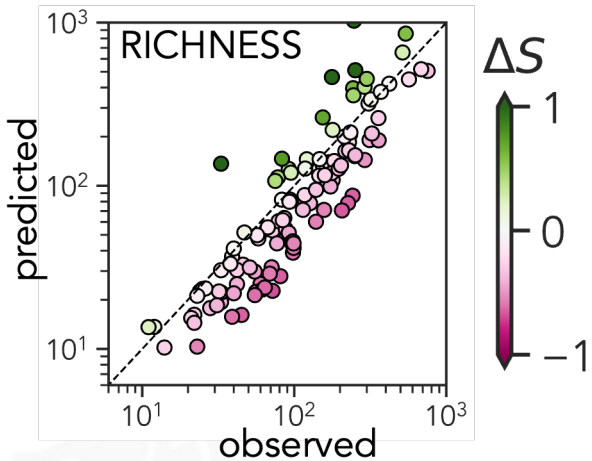
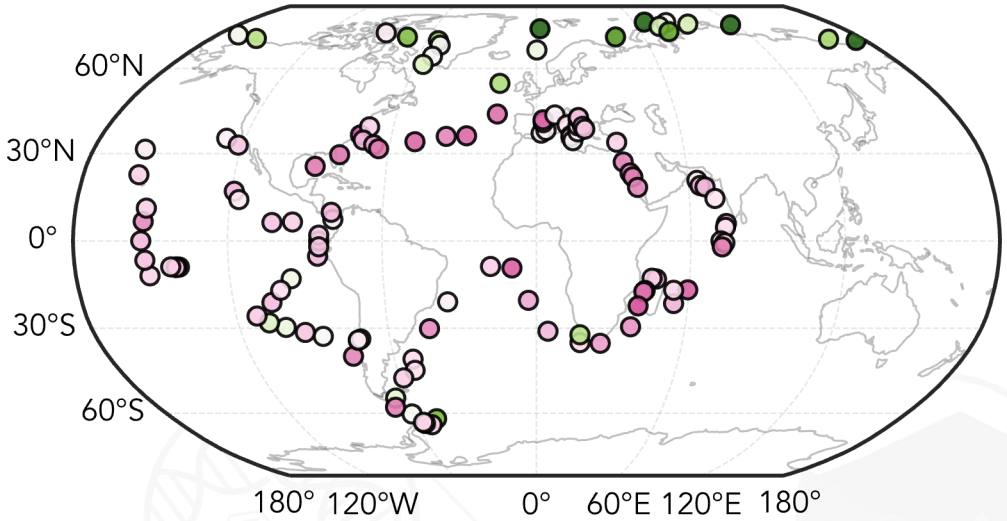


The deviations from the prediction reveal a biogeographical imprinting

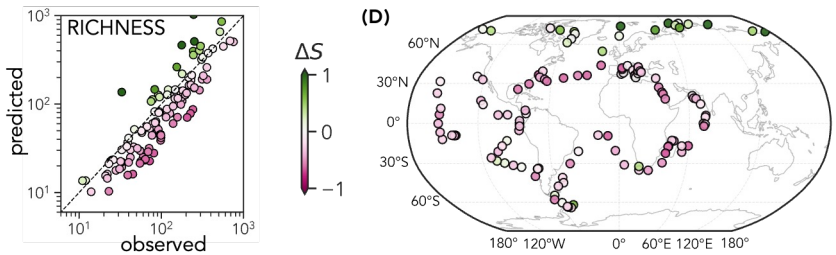


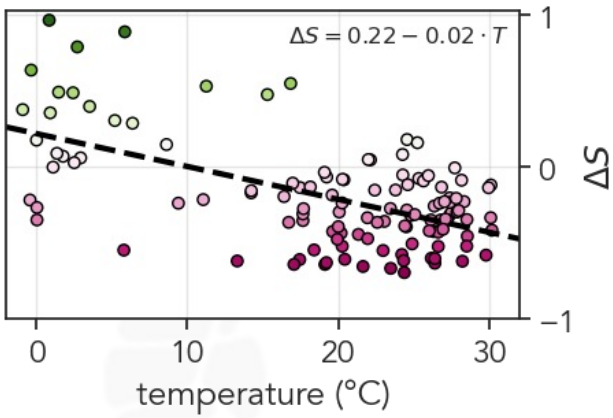
$$\langle S_p \rangle = S_{ref} \left(\frac{N_p}{N_{ref}} \right)^{\lambda - 1}$$

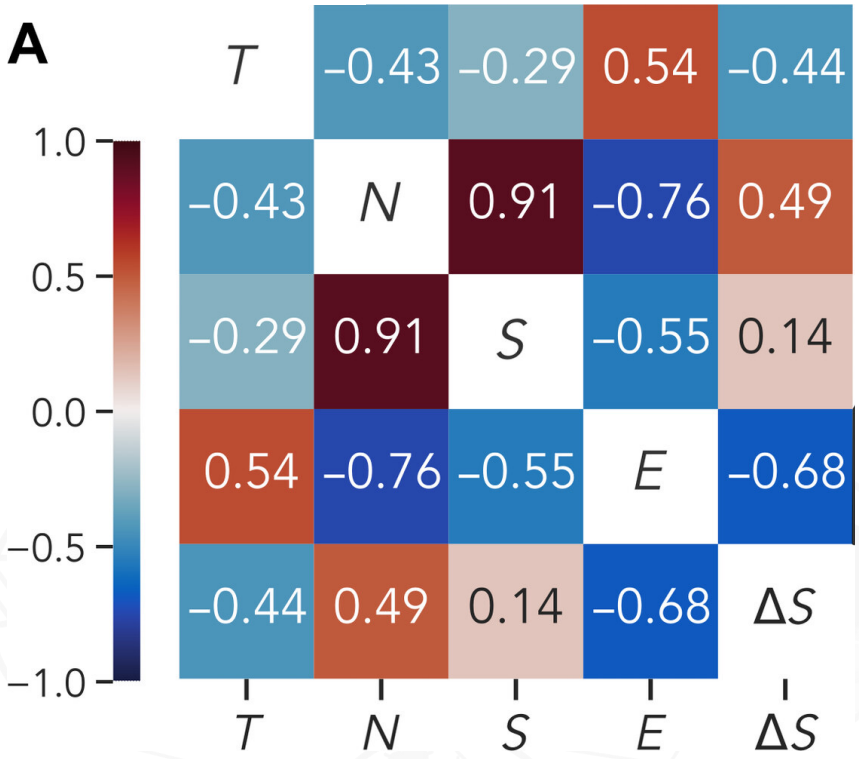
[Pigani et al., Science Advances, 2024]

TEST THE EXISTENCE OF AN OCEAN-WIDE NEUTRAL DIATOM METACOMMUNITY

$$SAD = f(neutral\ sampling) + \Delta f(environment)$$



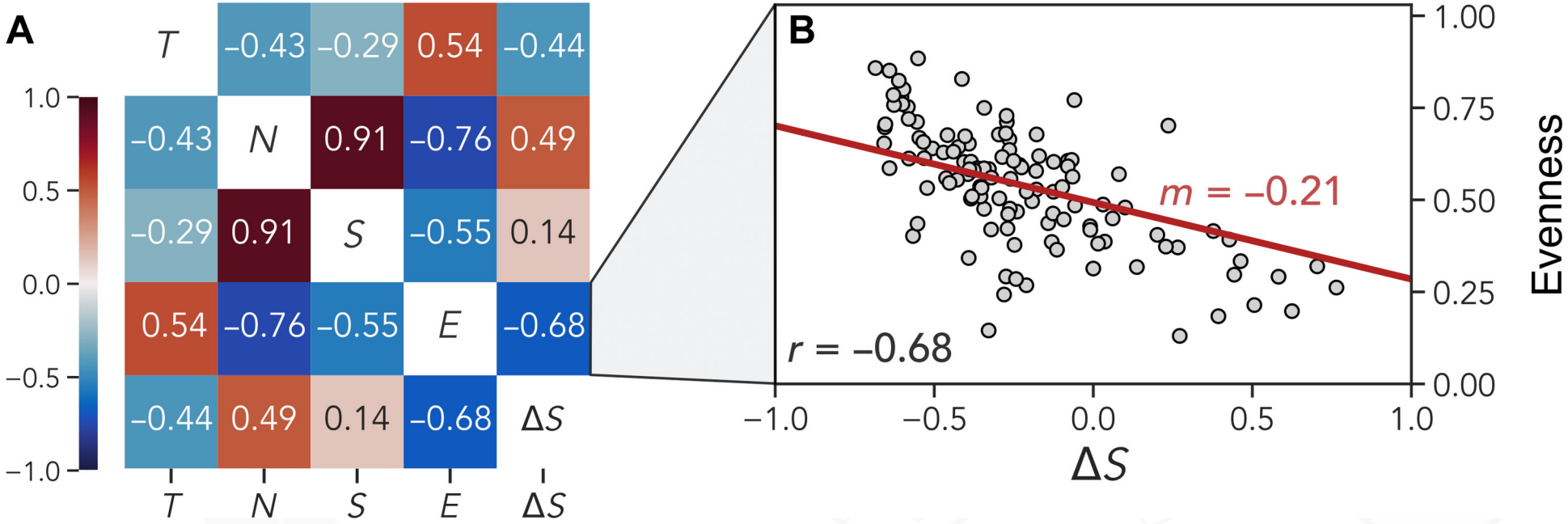




$$E = -\frac{\sum_{i=1}^{S} x_i \log(x_i)}{\log(S)}$$

[Pigani et al., Science Advances, 2024]

Test the existence of an **ocean-wide neutral** diatom **metacommunity**



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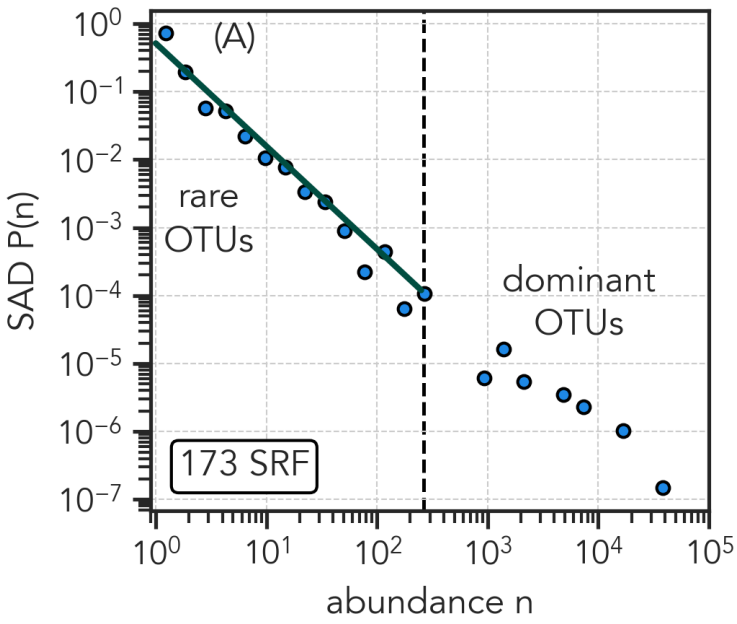
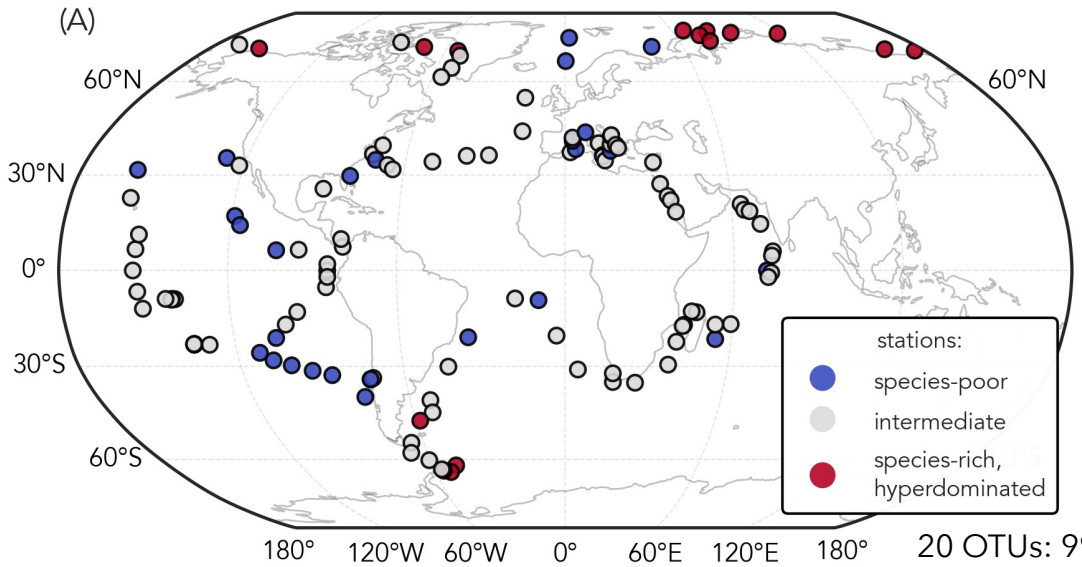
[Pigani et al., Science Advances, 2024]

Test the existence of an **ocean-wide neutral** diatom **metacommunity** for **non-dominant species**



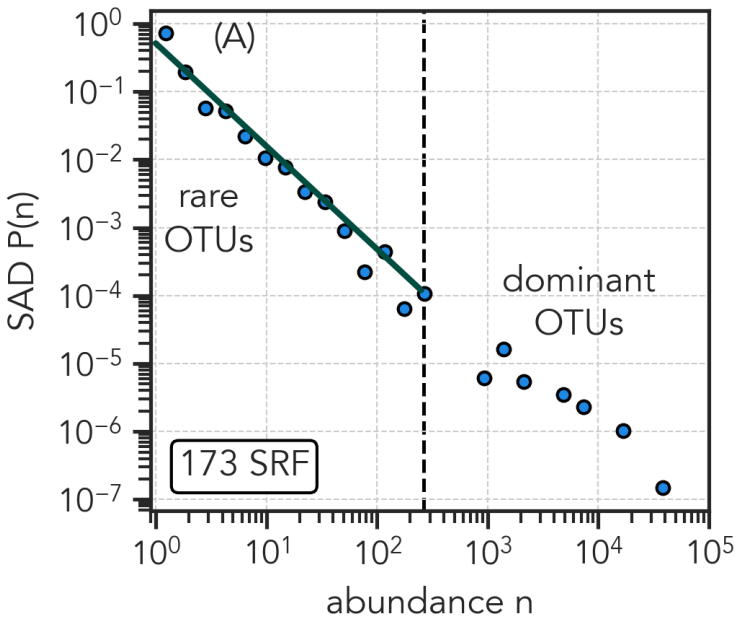


20 OTUs: 99% abundance

$$S_p = K(N_{meta}, S_{meta}, \lambda)(N_p)^{\lambda-1}$$

Biogeographical imprinting **only** on the most abundant species?

Test the existence of an **ocean-wide neutral** diatom **metacommunity** for **non-dominant species**



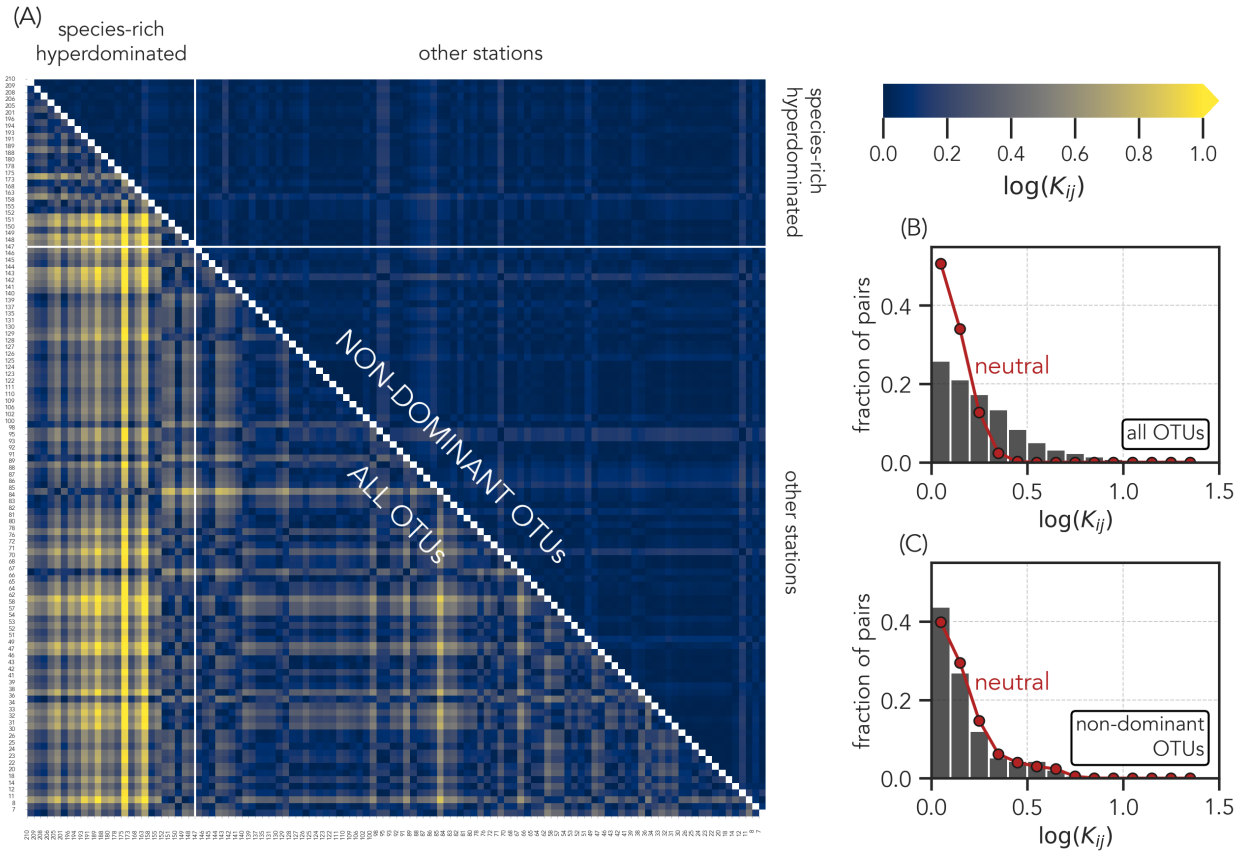
$$S_p = K(N_{meta}, S_{meta}, \lambda)(N_p)^{\lambda-1}$$

For each station: $K_p = S_p/(N_p)^{\lambda-1}$

We define the biodiversity log-ratio distance:

$$\log(K_{ij}) = \left|\log_{10} K_i - \log_{10} K_j\right|$$

Test the existence of an **ocean-wide neutral** diatom **metacommunity** for **non-dominant species**



$$K_p = S_p/(N_p)^{\lambda-1}$$

$$\log(K_{ij}) = |\log_{10} K_i - \log_{10} K_j|$$

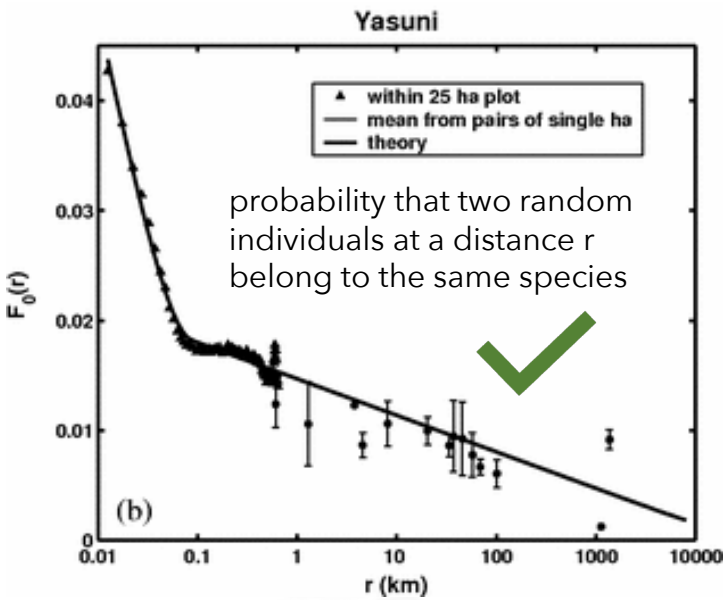
Rare OTUs: compatible with neutral metacommunity;
Dominant OTUs: biogeographical imprinting.

Why?

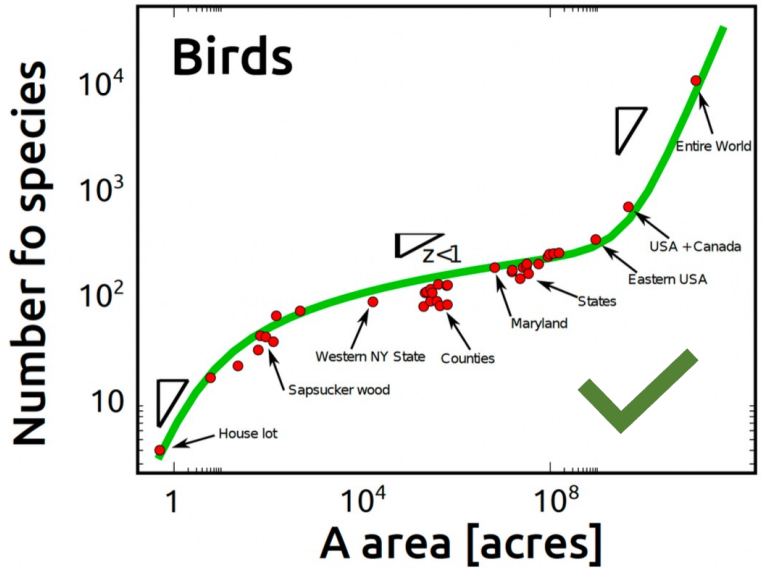
Neutral Theory is a good Wrong (null) model for phytoplankton

Other emergent patterns that Neutral Theory can reproduce

β-diversity



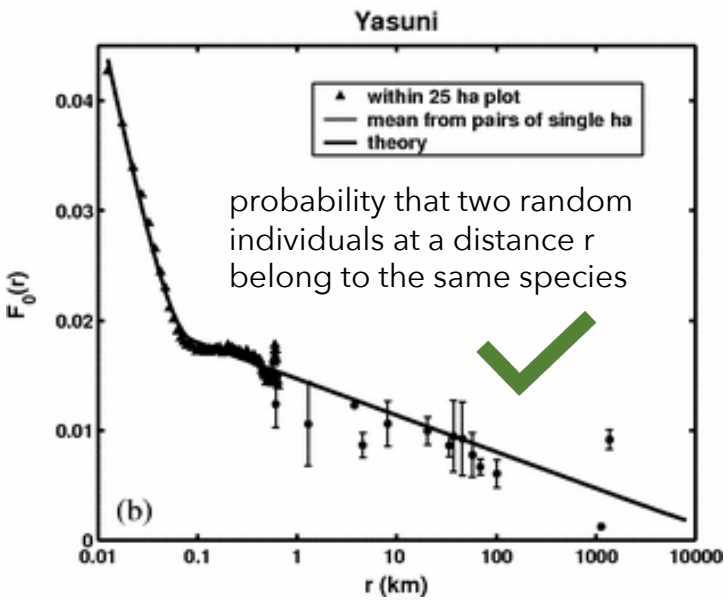
Species Area Relationship (SAR)

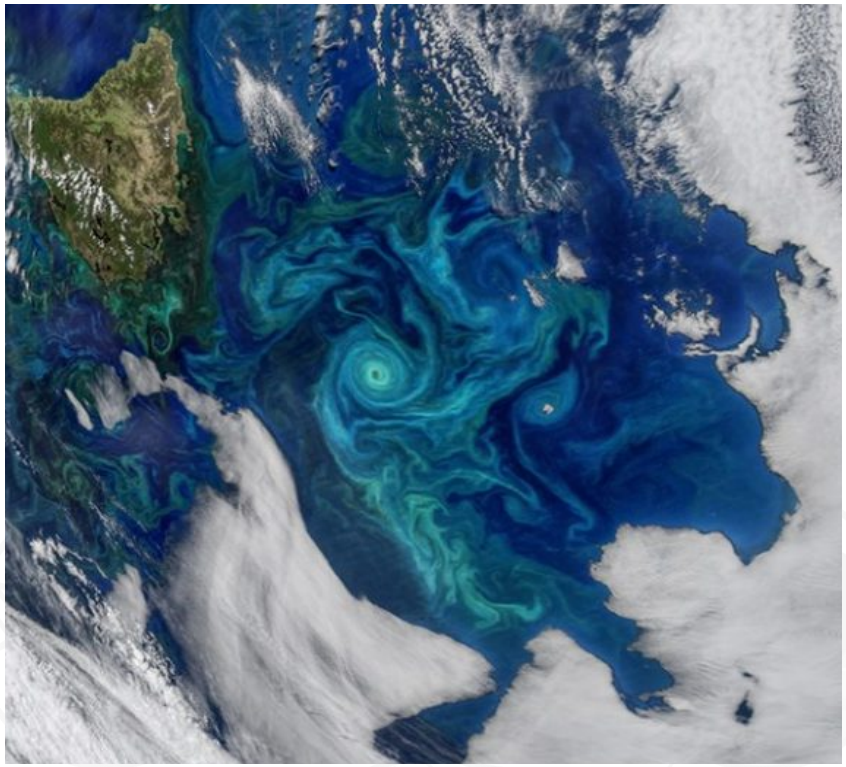


[Zillio et al., *PRL*, 2005; Grilli et al., *Journal of theoretical biology*, 2012]

Other emergent patterns that Neutral Theory can reproduce

B-DIVERSITY



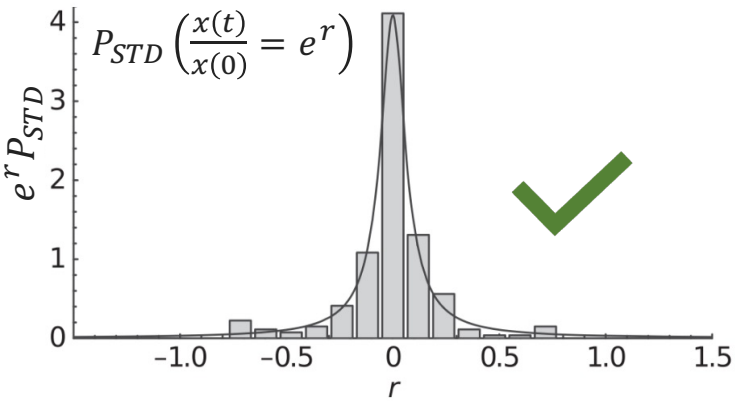


Do they apply also in the ocean?

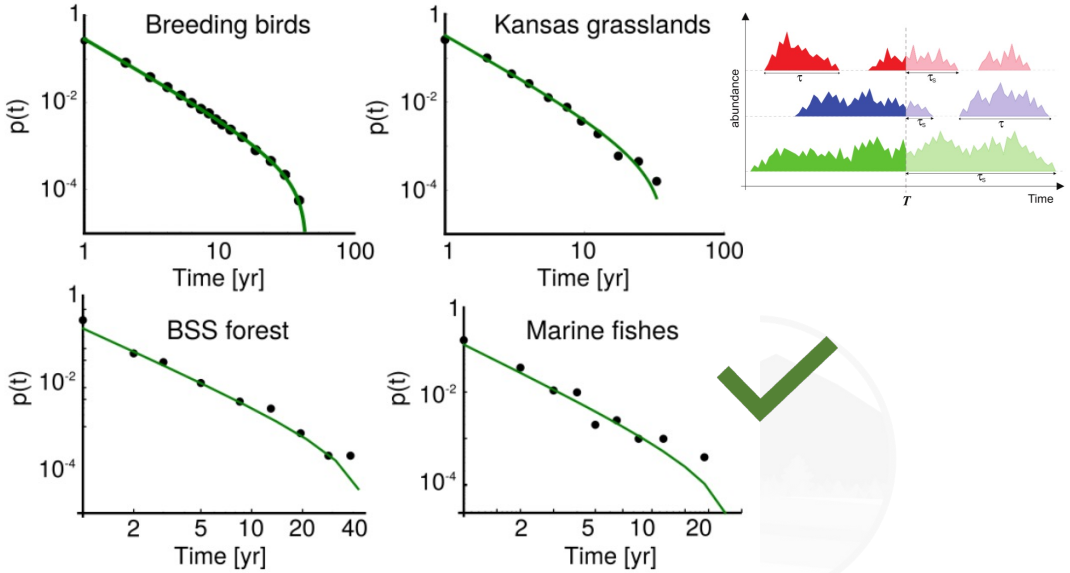
[Zillio et al., *PRL*, 2005; Grilli et al., *Journal of theoretical biology*, 2012]

Other emergent patterns that Neutral Theory can reproduce

Species Turnover Distribution (STD)



Species-Persistence Time Distribution (SPT)



[Azaele et al., *Nature*, 2006; Suweis et al., *Journal of theoretical biology*, 2012]

Other emergent patterns that Neutral Theory can reproduce

Age of a species

How old is a species with relative abundance *x*?

$$a(x) = -2N\frac{x}{1-x}\log x$$

Amazon rainforest

Total number of trees: N ~ 10^{11}

Most abundant species tree: x ~ 10^{-2}

Generation time of trees: ~ 30 years

Age of the most abundant species: ~10^{11} years

Age of the universe: ~10^{10} years , First tree: ~10^{8} years ago

[Kimura, *Molecular Biology and Evolution*, 1983]

Species Persistence Time and the (Inverted) Paradox

Niche vs Neutral

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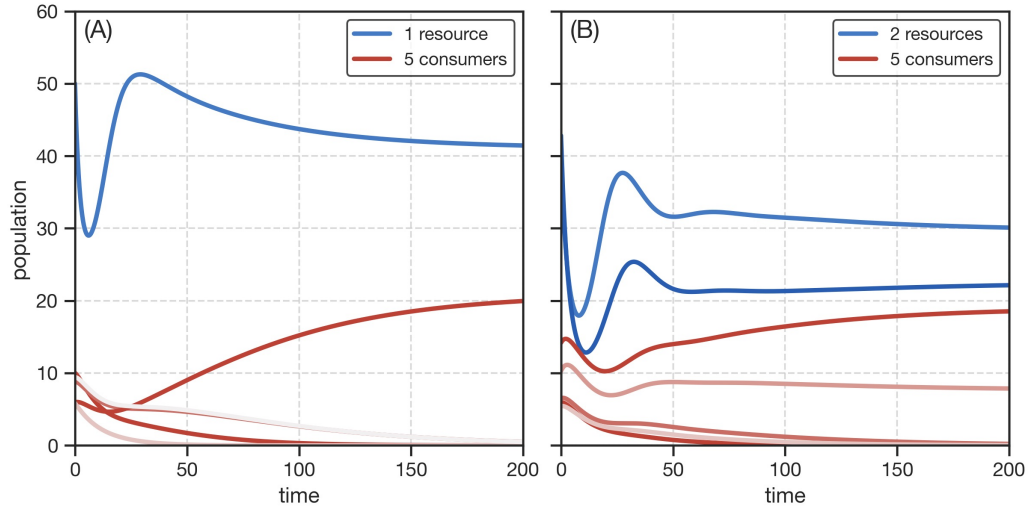

Competitive Exclusion Principle

Species Persistence Time and the (Inverted) Paradox

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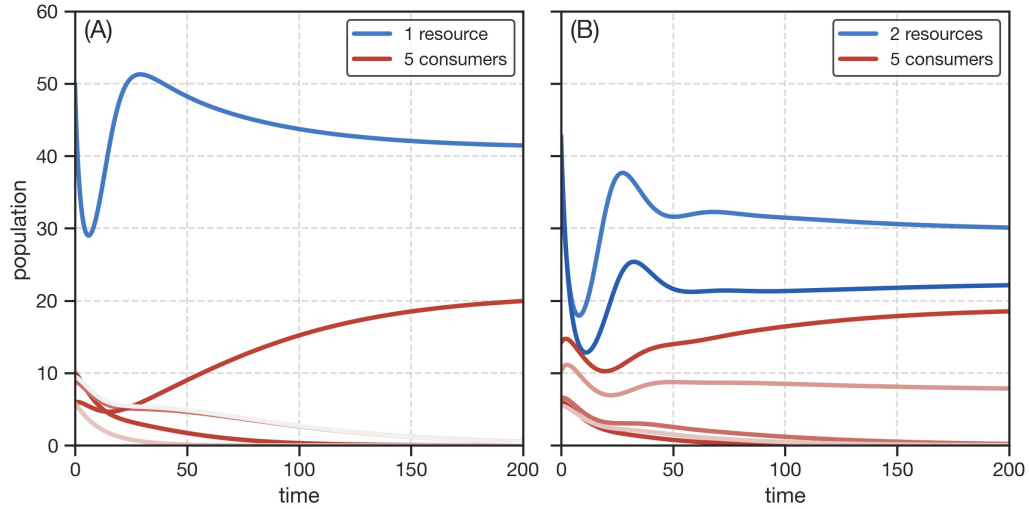

Competitive Exclusion Principle

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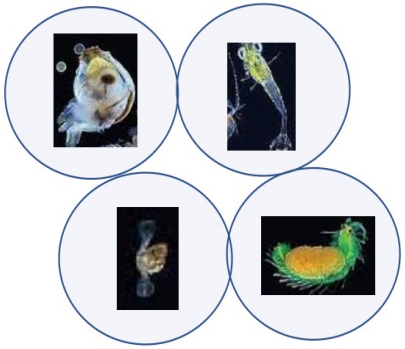
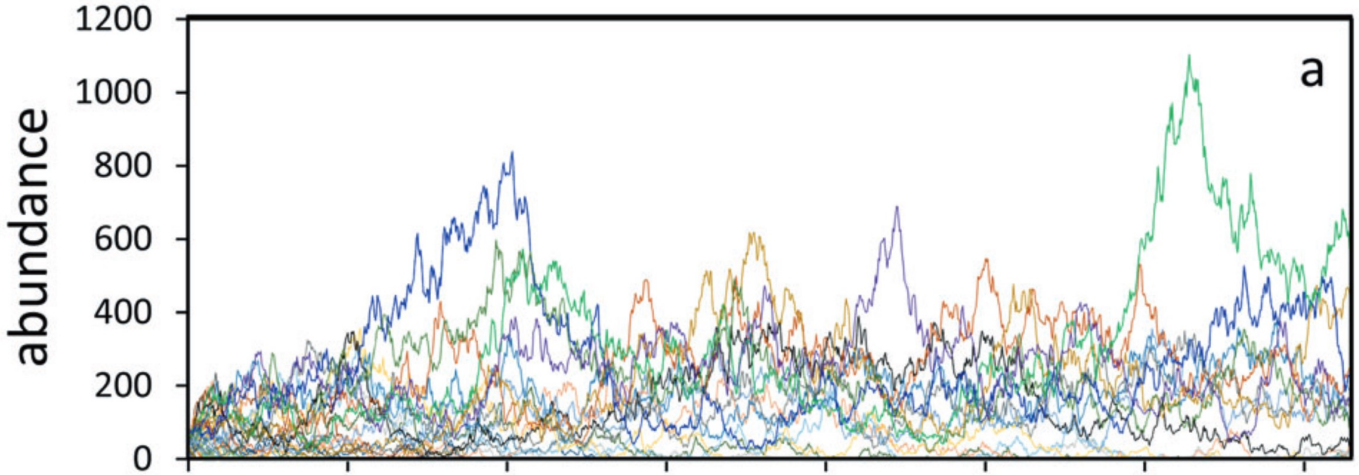


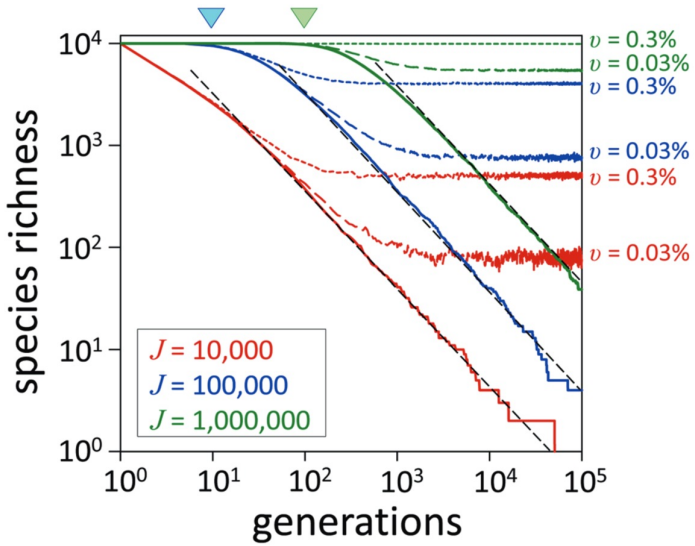


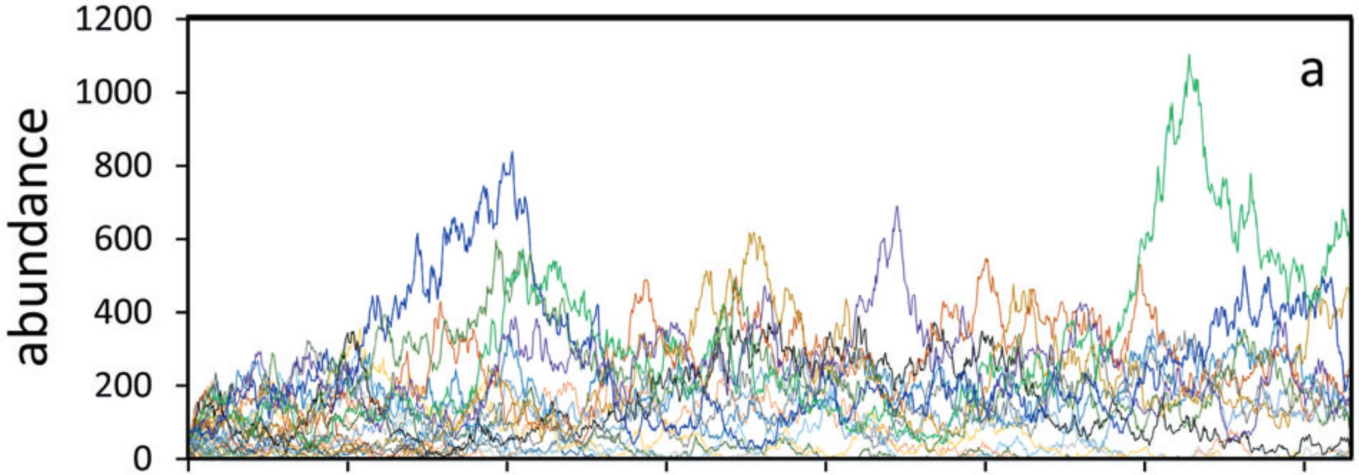
- No interactions;
- Stochastic **noise** is very relevant

*"At nearly all naturally occurring concentrations, the average body-length spacing between individual phytoplankton is such that nutrient depletion zones rarely overlap between neighboring cells, making **direct competition unlikely**, and rapid resource recycling and **physical mixing effectively erase** any depletion-zone **signatures** of **species-specifi**c physiologies."*

[Behrenfeld et al., *Phytoplankton biodiversity and the inverted paradox, 2021*]

Species Persistence Time and the (Inverted) Paradox





homogenized community. With respect to the latter property, typical horizontal eddy diffusion values for the upper ocean are O (10^3 m^2 s^{-1}), implying that the length scale for mixing in 1 day is O (1000 m). Typical number concentrations for phytoplankton of different species in the ocean range from <1 to over 10^5 individuals per milliliter. At these concentrations, extension of our stochastic model results to the population encompassed within a water mass only 1 m deep by 1000 m wide yields an onset time for significant stochastic exclusion of 10^5 to 10^{10} years, comparable to the age of life on Earth (Methods). Recognizing that

Only numerical simulations…
(see notebook)

[Behrenfeld et al., *Phytoplankton biodiversity and the inverted paradox, 2021]*

Species Persistence Time and the (Inverted) Paradox

…But analytical derivation shows the importance of initial conditions!

Voter model: at each time, one individual dies and is replaced

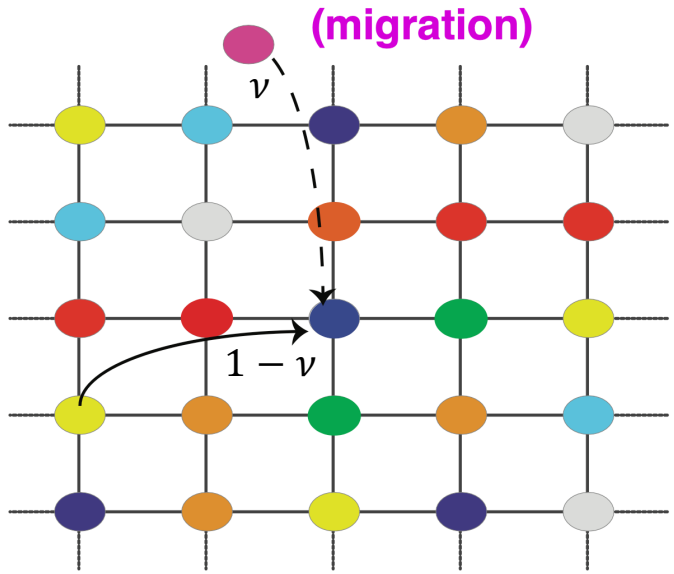
$$b_n = (1-\nu)\frac{J-n}{J}\frac{n}{J-1} + \nu\frac{1}{S}\frac{J-n}{J}\,,$$

$$d_n = (1-\nu)\frac{n}{J}\frac{J-n}{J-1} + \nu\frac{n}{J}\frac{S-1}{S}\,.$$

$\longrightarrow$

$$b_n = \beta_0 + \beta_1 n = \frac{\nu}{S} + \frac{1-\nu}{J}\,n,$$

$$d_n = \delta_1 n = \frac{1}{J}\,n,$$



Probability of being extincted: $n_0 = \frac{J}{S}$

$$P_0(t) = \left(\frac{e^{\nu t} - (1-\nu)}{\nu\, e^{\nu t}}\right)^{-\frac{n_0 \nu}{1-\nu}} \left(\frac{1-e^{\nu t}}{1-\nu-e^{\nu t}}\right)^{n_0}$$

$$\langle S\rangle(t) = S\left[1 - P_0(t)\right]$$

[Volkov et al., *Nature*, 2007]

Species Persistence Time and the (Inverted) Paradox

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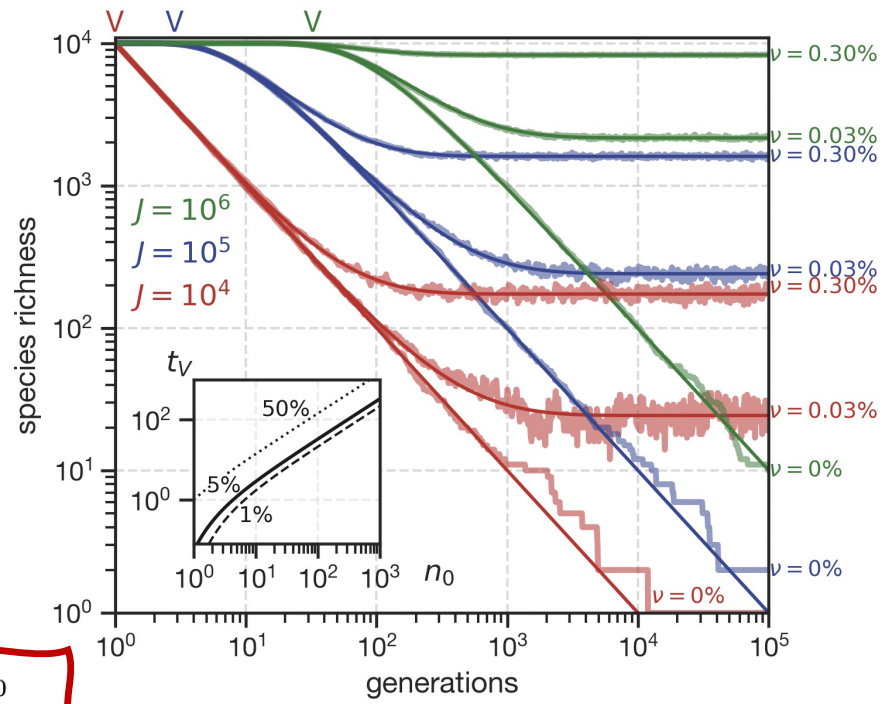
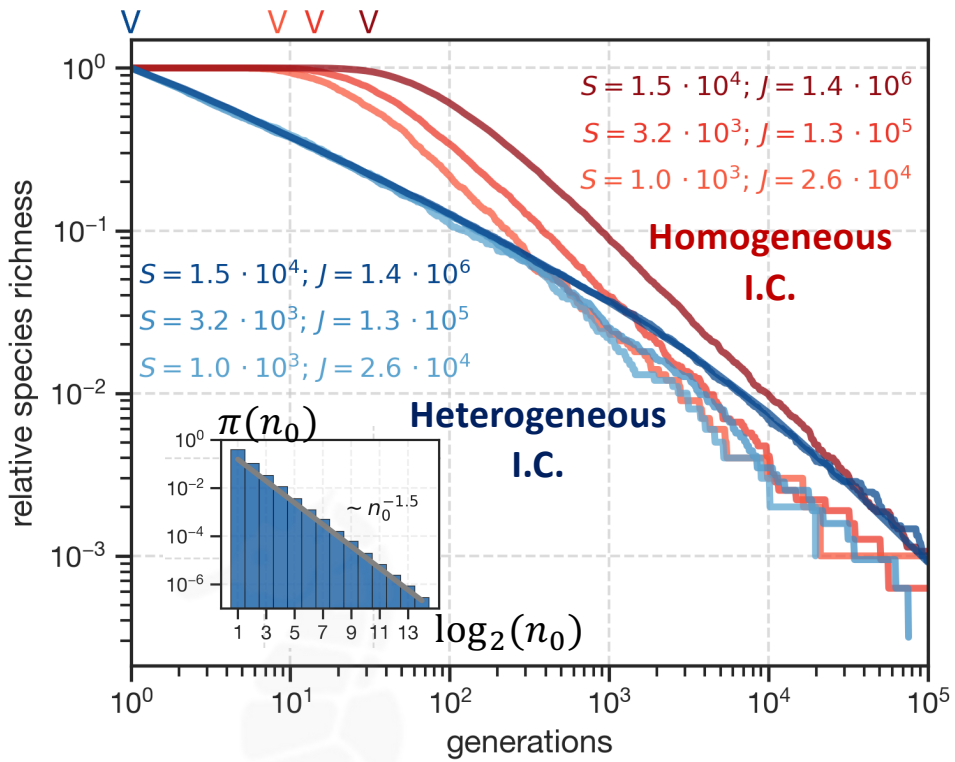
$$\langle S\rangle(t) = S\left[1 - P_0(t)\right]$$

$$t_V(\phi) = \frac{\phi^{1/n_0}}{1-\phi^{1/n_0}}$$



[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

THE EFFECT OF THE RARE BIOSPHERE ON THE INVERTED PARADOX



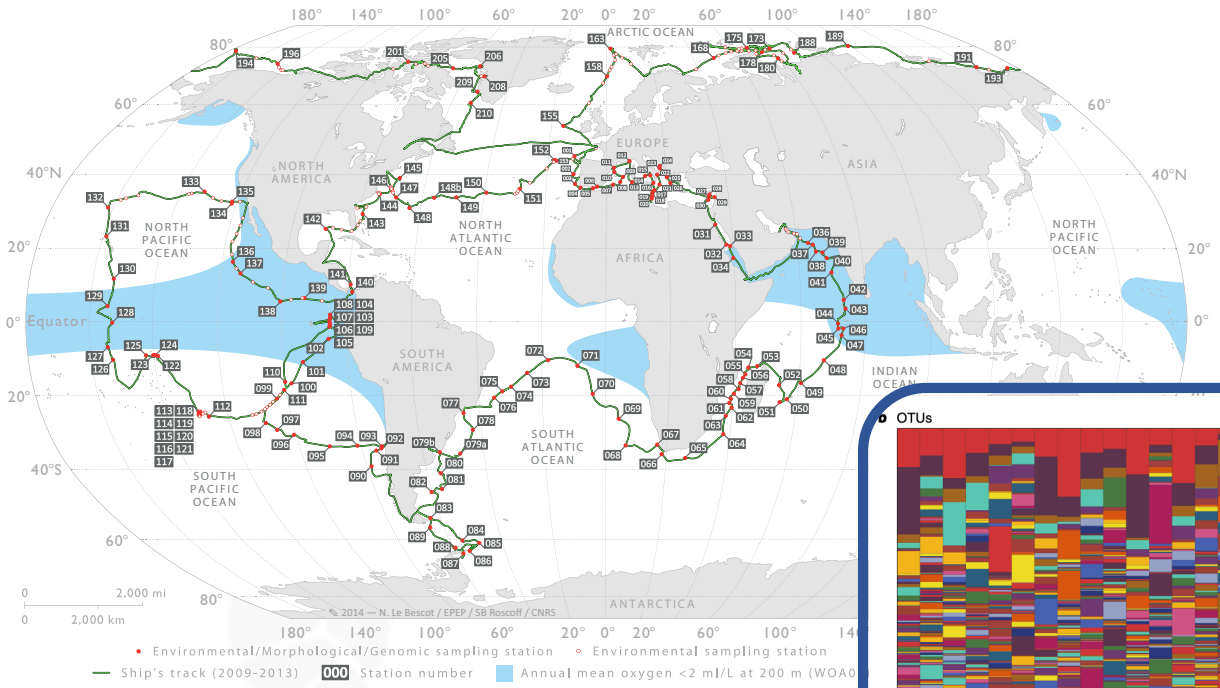
Limits of the inverted paradox:
1) All species with the same initial abundance;
2) Wrong scaling of n_0 ($J >, S =$)

Heterogeneity in abundance distribution solves the inverted paradox

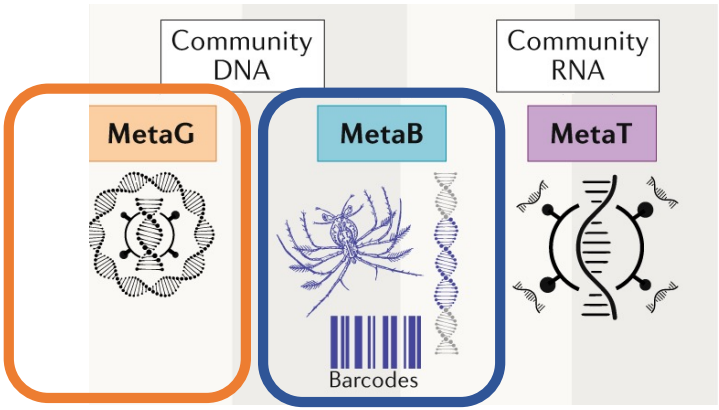
[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

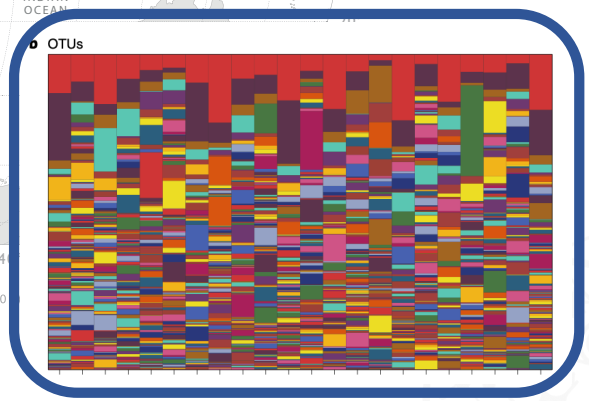
Emergence of Global Functional Neutrality despite non-neutral taxonomy?

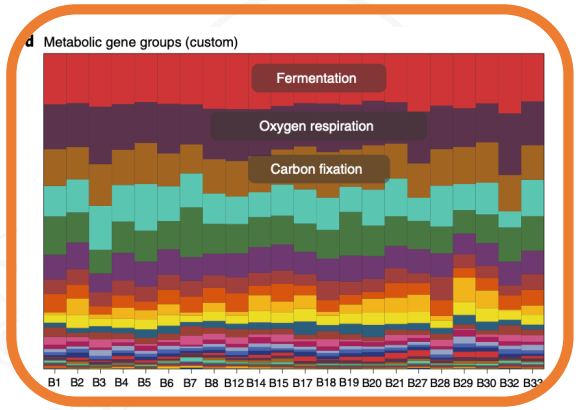
Diatoms from the Tara Oceans Dataset



High-throughput sequencing



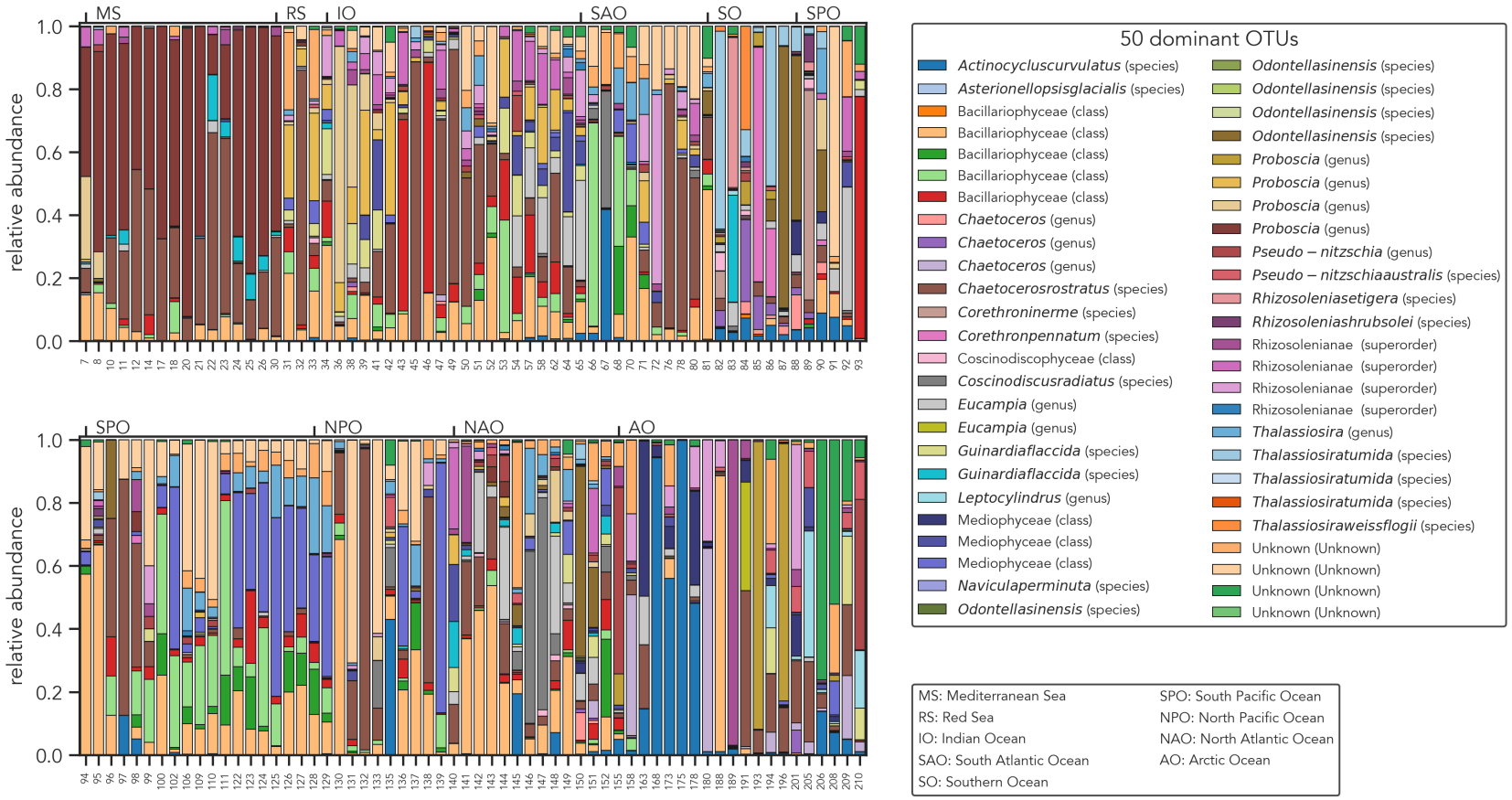




[Sunagawa et al., *Nature rev. microbiology* 2020; Louca et al., *Nature Ecology & Evolution* 2018]

Emergence of Global Functional Neutrality despite non-neutral taxonomy?

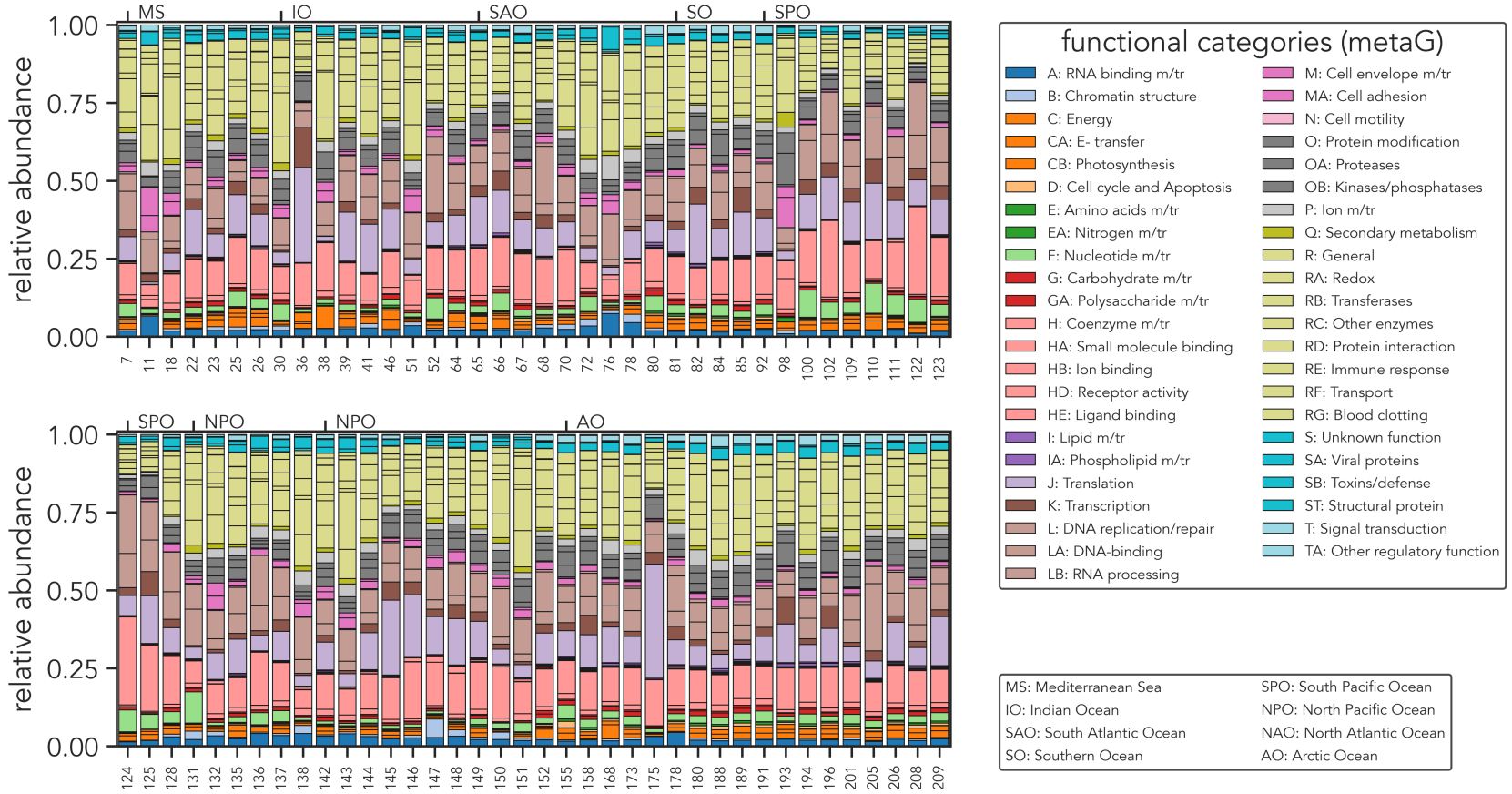
Dominant OTUs display only regional patterns



[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

Emergence of Global Functional Neutrality despite non-neutral taxonomy?

Functional groups are much more stable



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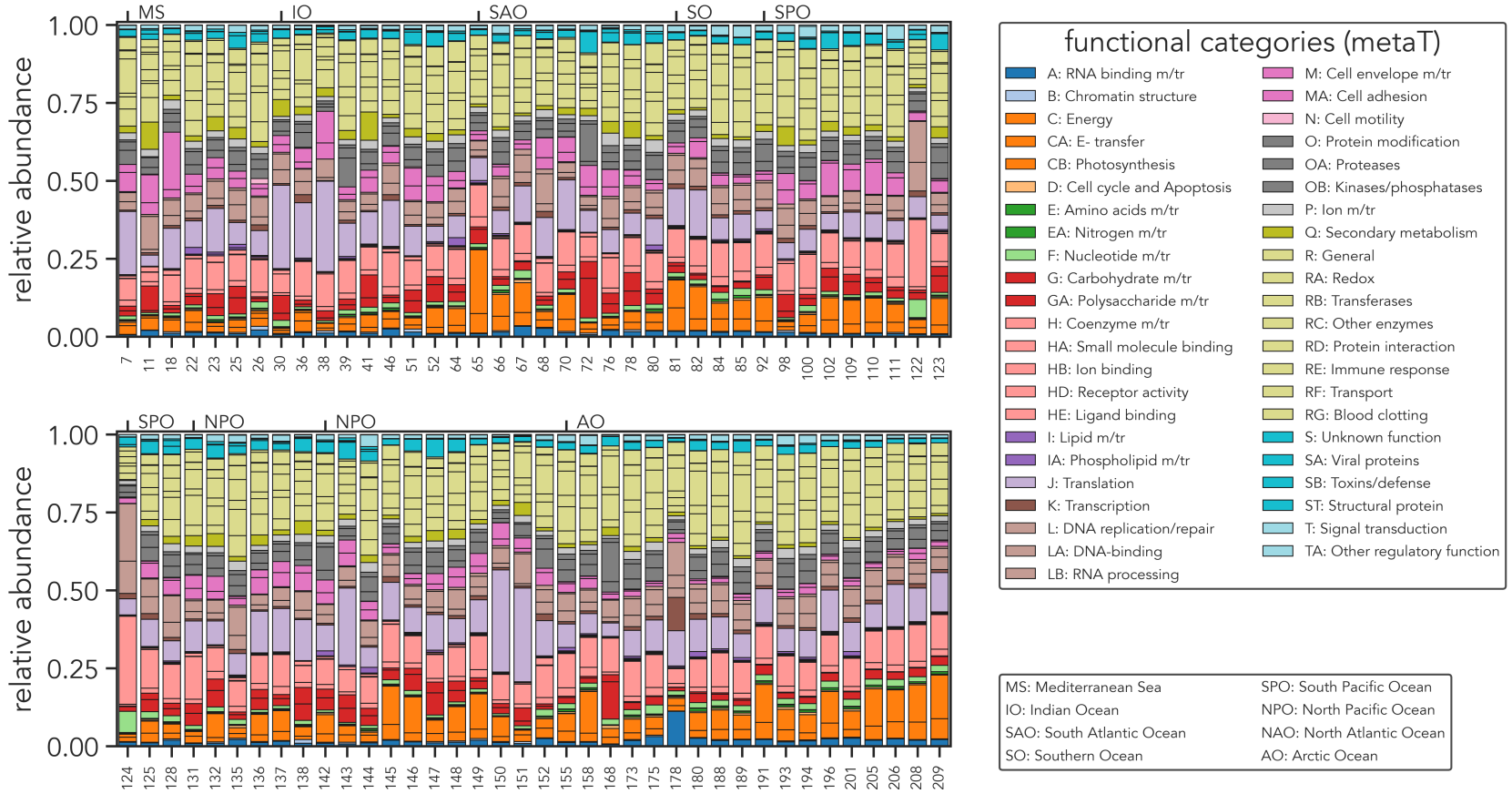
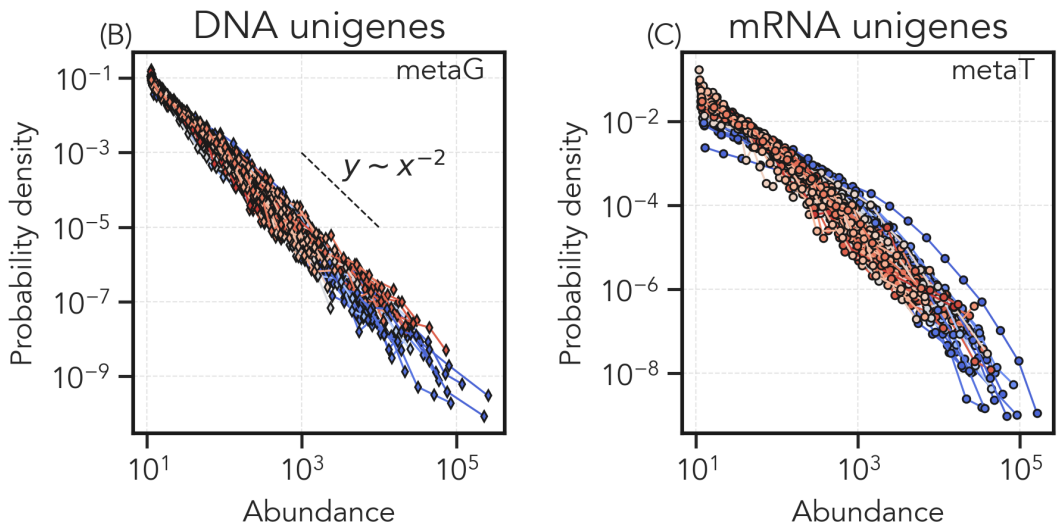


[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

Mechanisms Behind Community Structure and Function

A Null Model for Unigene Dynamics and Expression at the Population Level: Linking Genetic Potential to Expression Patterns



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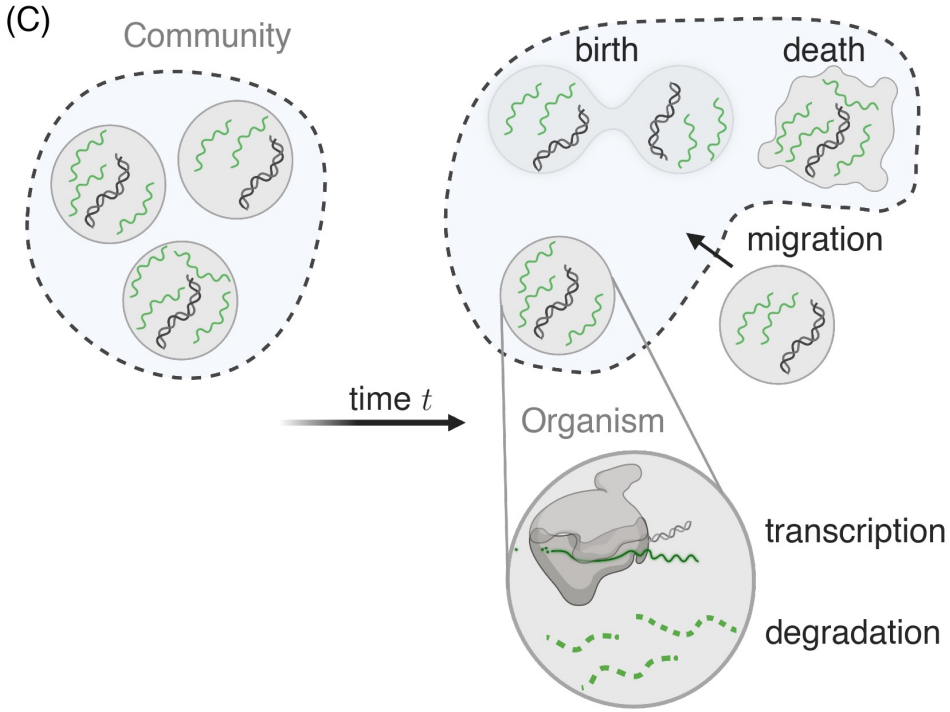

Community dynamics is inherited by DNA unigenes

mRNA undergoes transcription and degradation at a faster time-scale

[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

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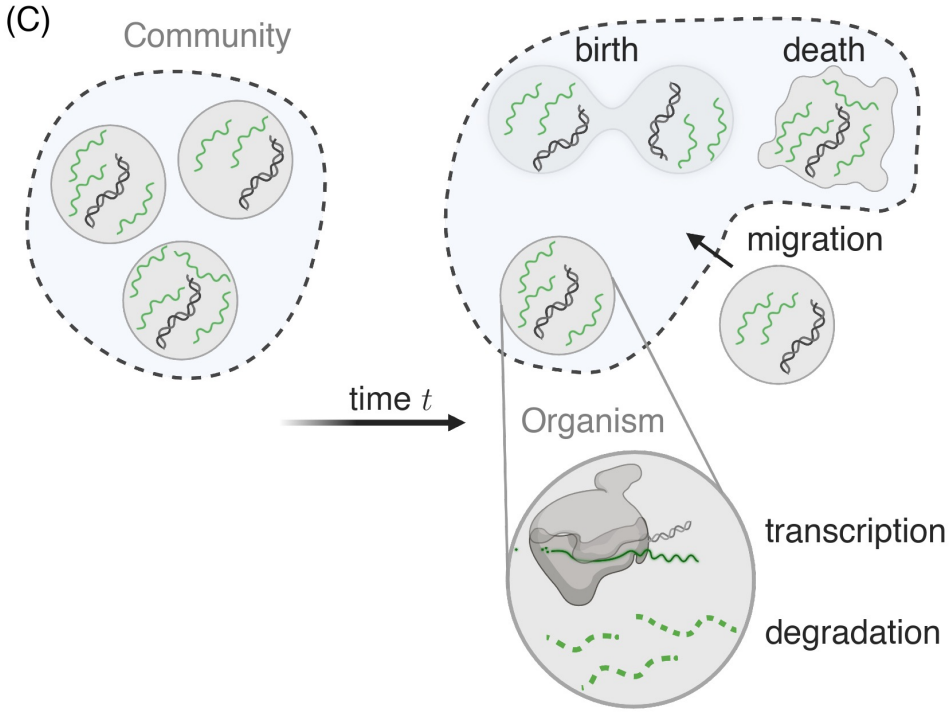

Effective 2-layers model:

$X \xrightarrow{b_1} 2X$ duplication

$\emptyset \xrightarrow{b_0} X$ influx

$X \xrightarrow{d_1 + \frac{d_0}{x}} \emptyset$ deletion

$X \xrightarrow{r} X + Y$ transcription

$Y \xrightarrow{\gamma} \emptyset$ degradation

[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

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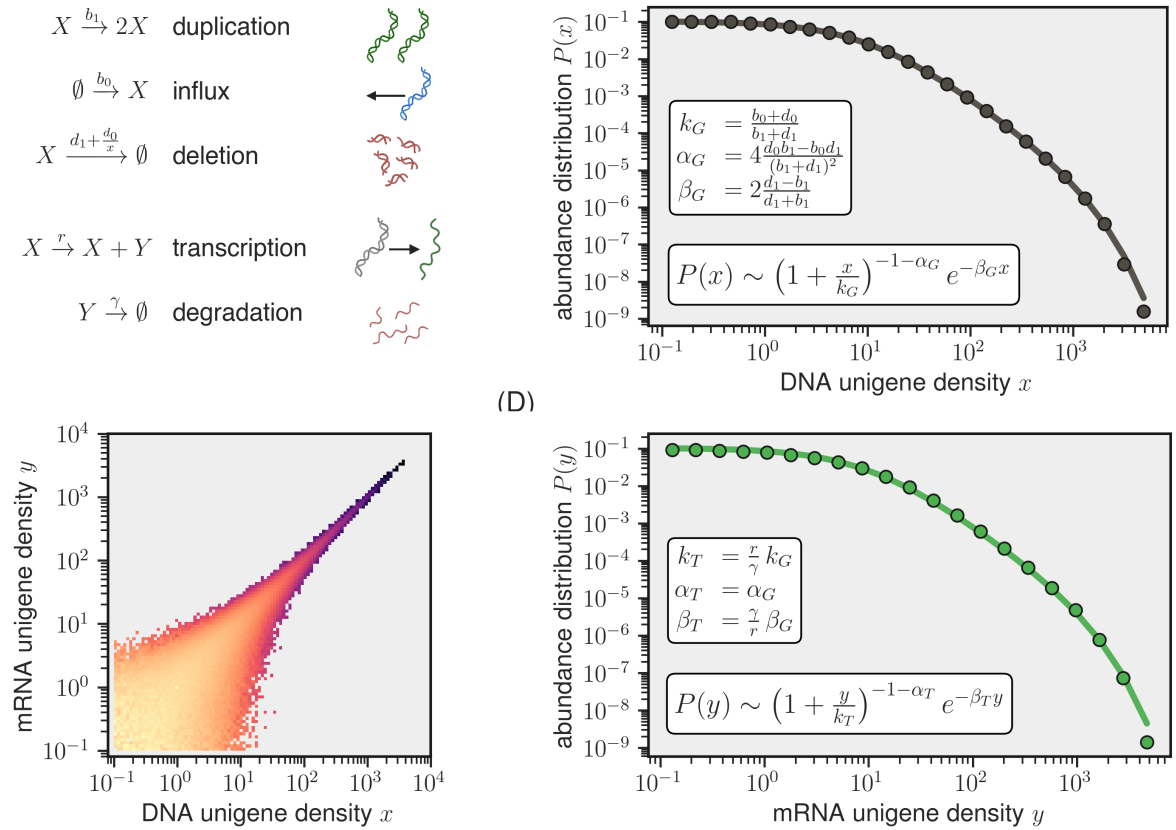
Same stationary distributions

Parameters are rescaled by the transcription efficiency:

$$\eta = \frac{r}{\gamma} = \frac{k_T}{k_G}$$



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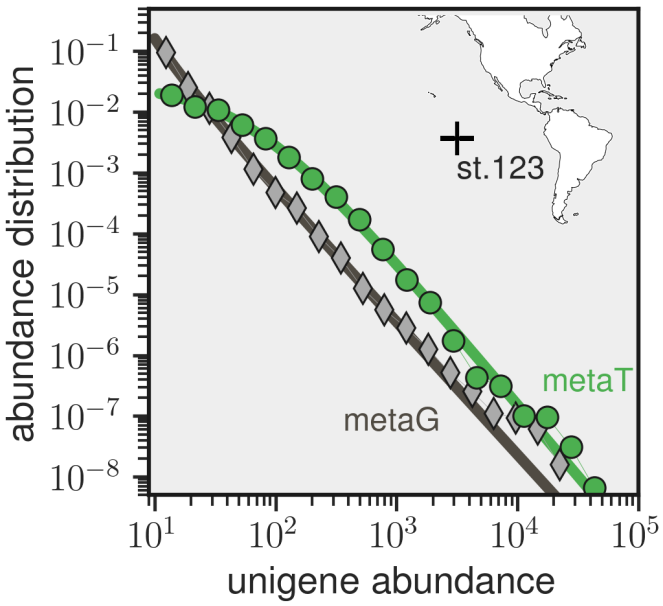

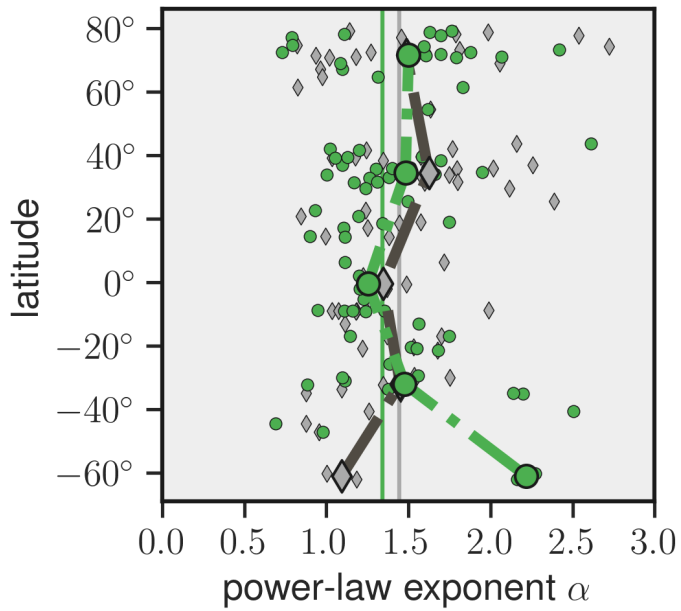

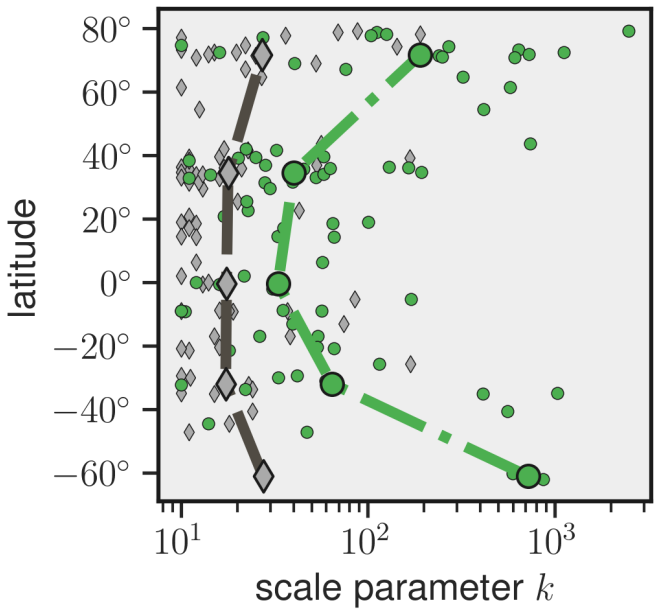

$$P(x) \sim \left(1 + \frac{x}{k_G}\right)^{-1-\alpha_G}$$

$$P(y) \sim \left(1 + \frac{y}{k_T}\right)^{-1-\alpha_T}$$

A.D. test $p > 0.05$:
- 68/77 metaG
- 70/77 metaT

Mechanisms Behind Community Structure and Function

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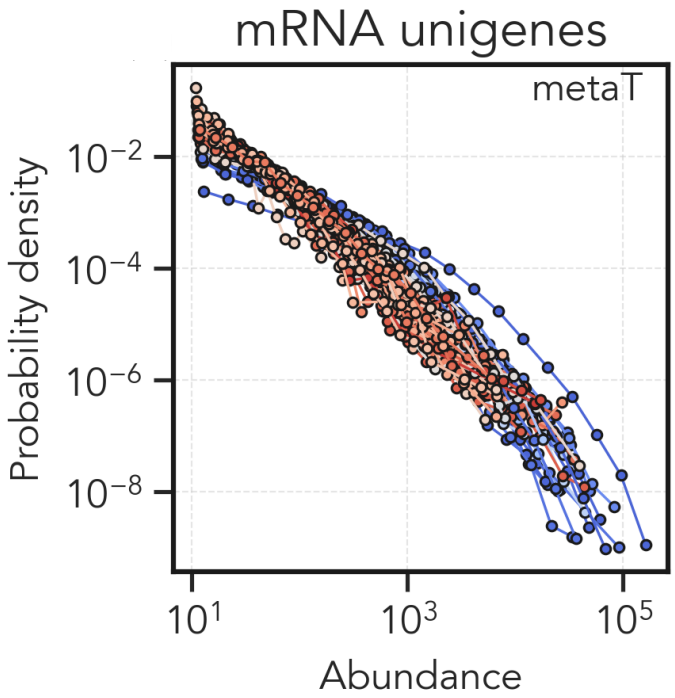

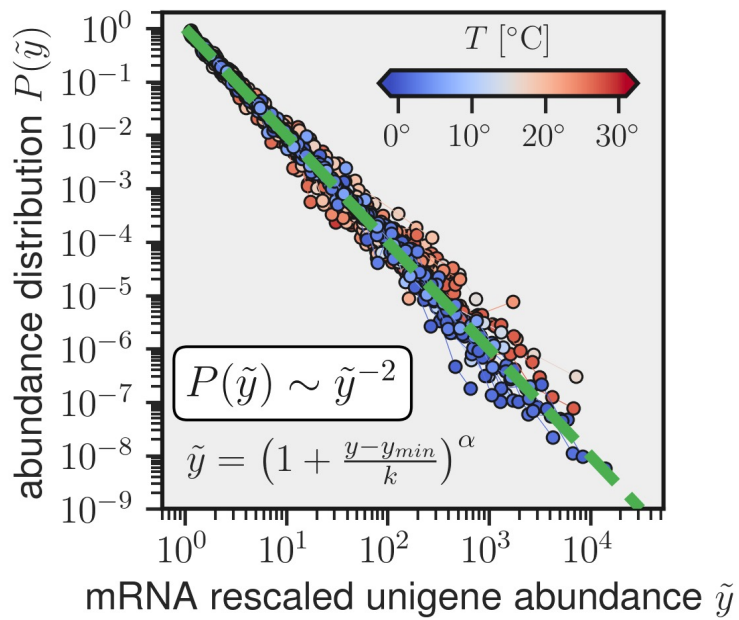

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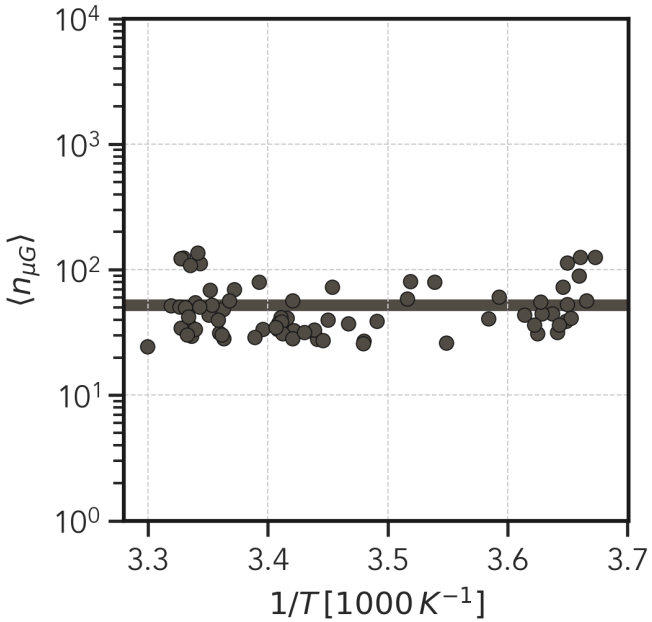
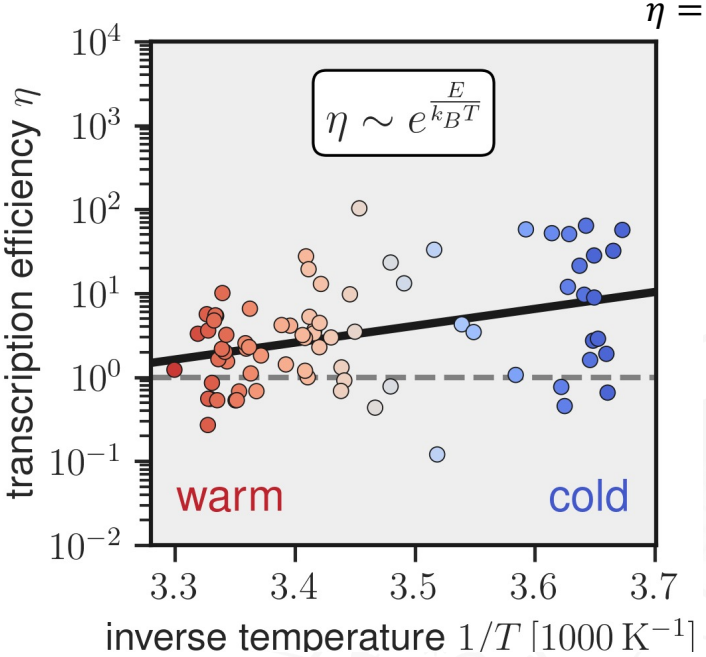


Same dynamics everywhere for metaG.

$$\eta = \frac{r}{\gamma} = \frac{k_T}{k_G}$$



Different functional activity response for metaT.

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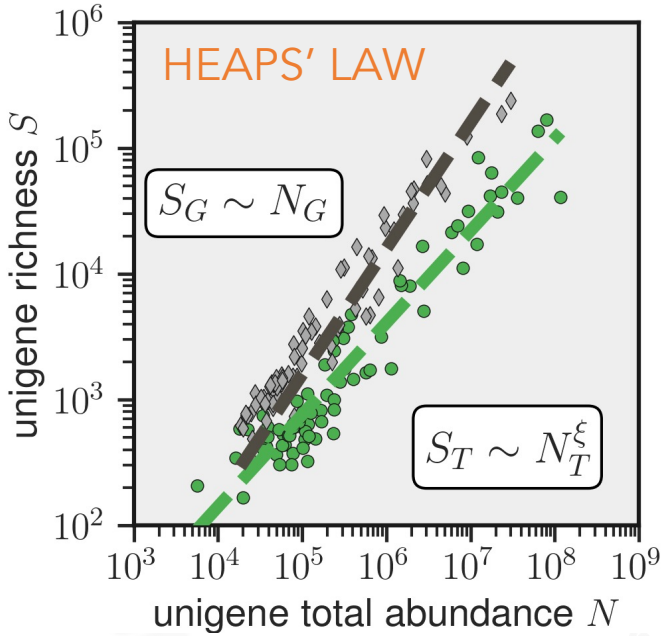


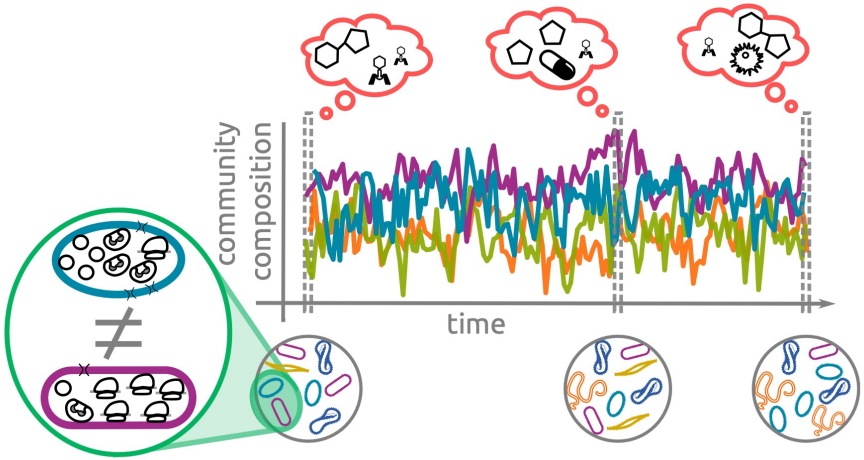
We can **estimate** and give a **meaning** to the sublinear scaling $\xi = \frac{\varepsilon}{E}$

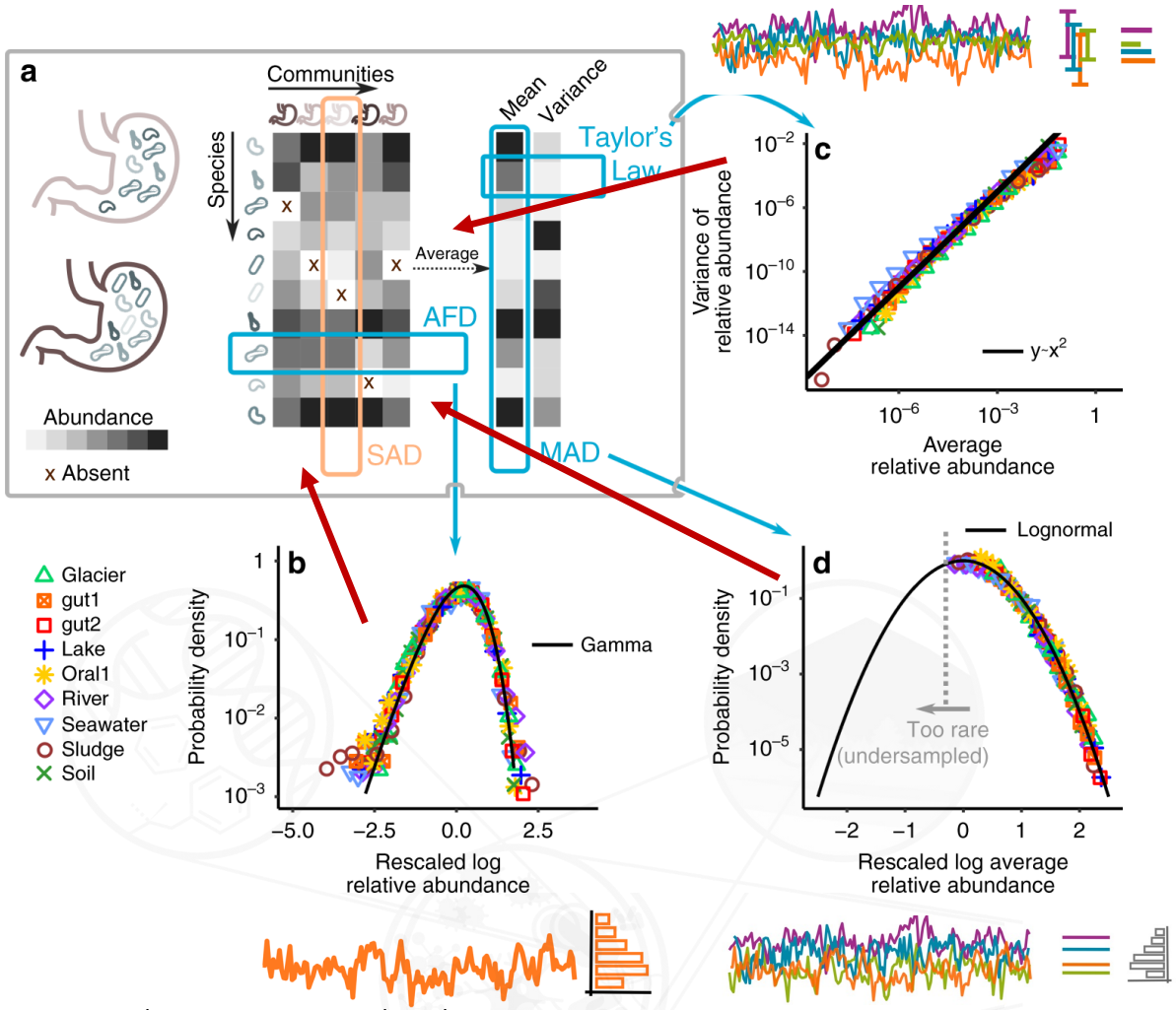
Functional diversity scaling with temperature: $S_T \sim e^{\frac{\varepsilon}{k_B T}}$

Functional activity scaling with temperature: $\eta \sim e^{\frac{E}{k_B T}}$

[Pigani, PhD thesis *Modeling Macroecological Patterns in Marine Ecosystems: From Community Structures to Gene Expressions, 2025*]

An alternative good Wrong (null) model for phytoplankton





The dynamics of communities is **complex**:
- the **environment** is high-dimensional
- **trait space** is high-dimensional

[Grilli, *Nature communications* 2020, Zaoli et Grilli, *Science Advances* 2022; thanks to JG]

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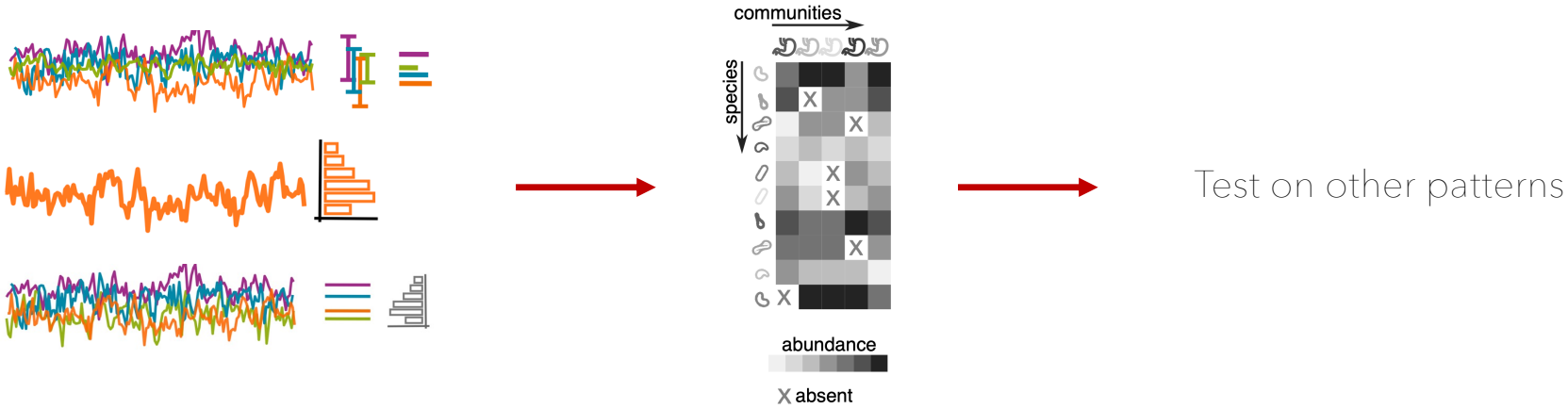

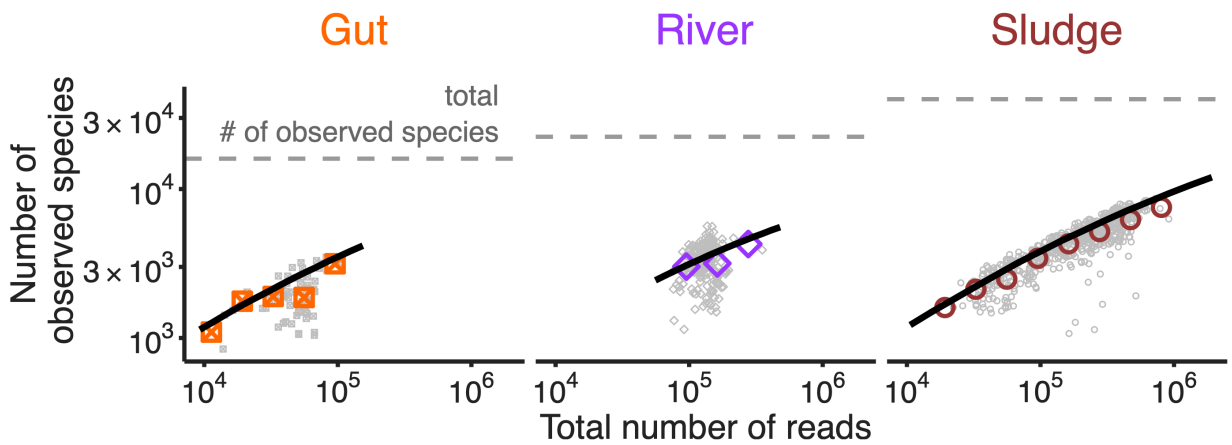

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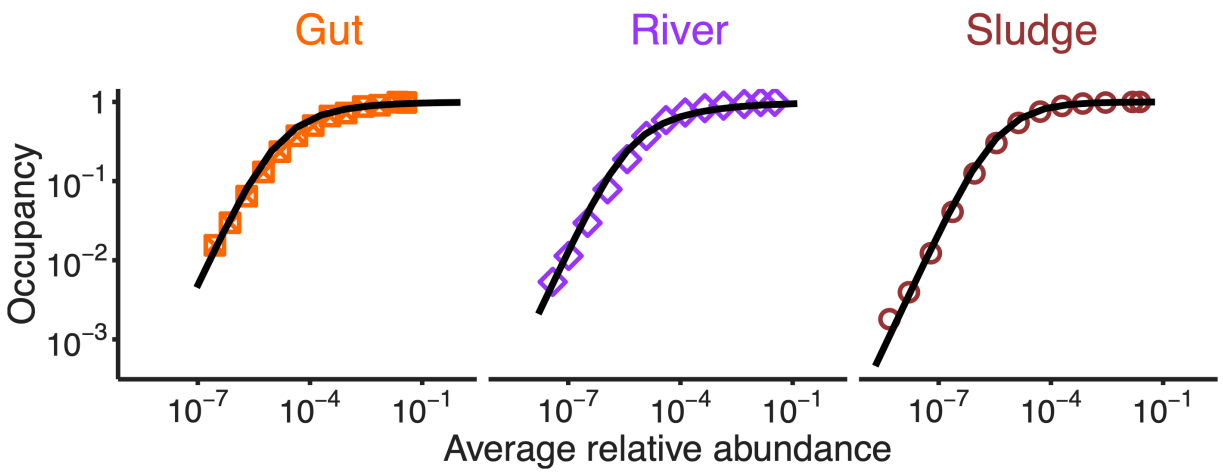
An alternative good Wrong (null) model for phytoplankton

What Dynamics?



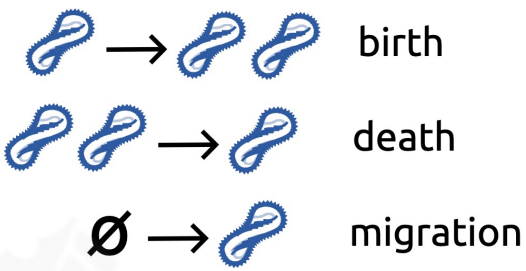
[Grilli, *Nature communications* 2020, Zaoli et Grilli, *Science Advances* 2022; thanks to JG]

An alternative good Wrong (null) model for phytoplankton

deterministic forces

stochastic forces

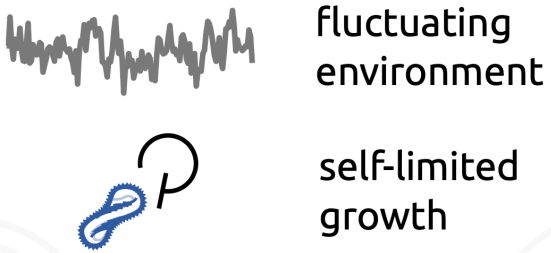
$$\dot{x} = f(x) + \sqrt{D(x)}\xi(t)$$



demographic stochasticity

$$\dot{x} = \frac{1}{\tau}(x^* - x) + \sqrt{\frac{\sigma}{\tau}x}\xi(t)$$

VS



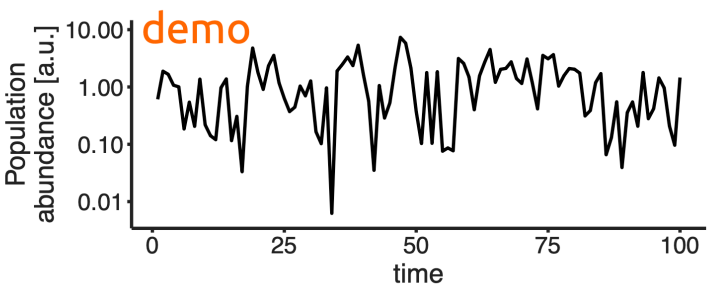
environmental stochasticity

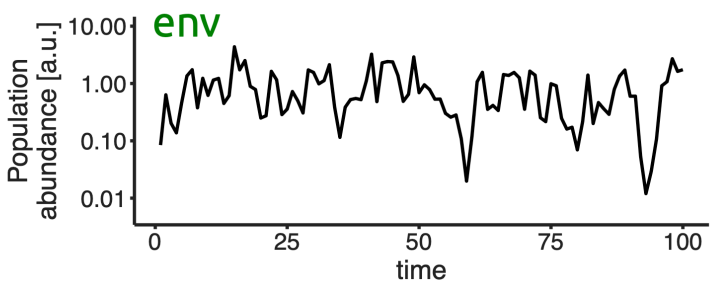
$$\dot{x} = \frac{x}{\tau}\left(1 - \frac{x}{K}\right) + \sqrt{\frac{\sigma}{\tau}x}\xi(t)$$

[Grilli, *Nature communications* 2020, Zaoli et Grilli, *Science Advances* 2022; thanks to JG]

SAD is not enough to discriminate

We need to look at something different



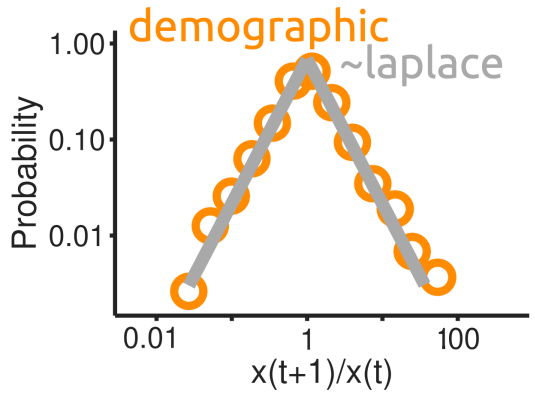


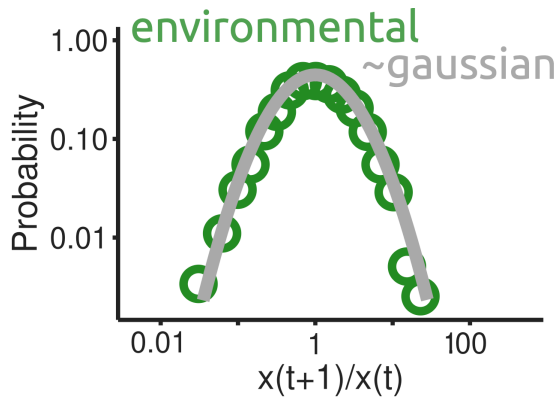
different

$$P(x, t+\tau \,|\, x_0, t)$$

same

$$P^*(x) = \lim_{t\to\infty} P(x, t \,|\, x_0, 0)$$





[Grilli, *Nature communications* 2020, Zaoli et Grilli, *Science Advances* 2022; thanks to JG]

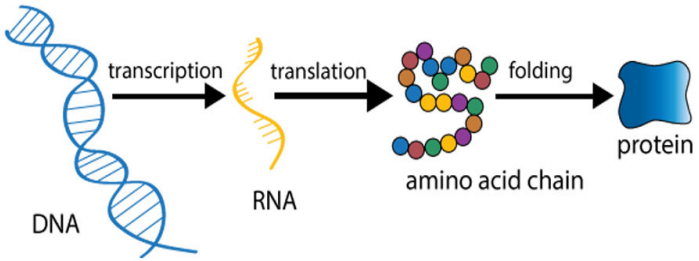
Two examples of good wrong models, but of course…

We miss interactions,
And many other aspects

Environment

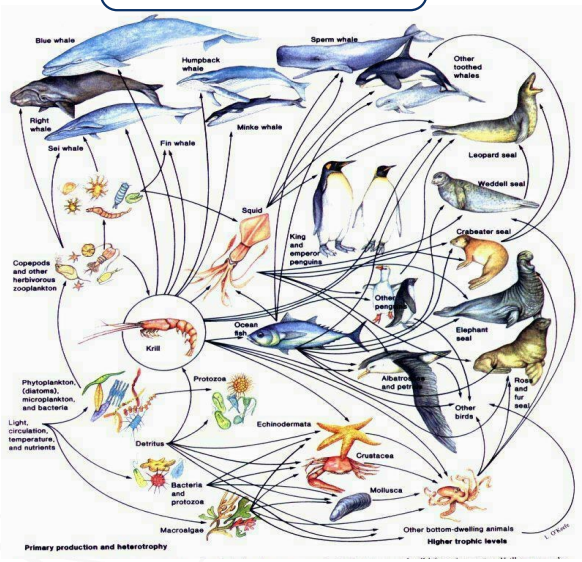
SEASCAPE

Organisms



[thanks to DI]

Food webs



Thank you and thanks to…

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M. Ribera d'Alcalà, A. Maritan, J. Grilli,
K. Simoens, G.V. Visco, L. Campese,
D. Bernardi, E. Ser-Giacomi, B. Hay Mele,
C. Grilletta, F. Ferraro, and many many
others…

Decoding the evolution of anticipation and decision making in uncertain environments

International collaboration funded by the Human Frontier Science Program

Project description

In an international project involving three laboratories with expertise in microbial ecology (Dal Bello lab, Yale, USA), single-cell analyses (McGlynn lab, ELSI, Japan), and theoretical biology (Grilli research group, ICTP, Italy) , we aim to understand how microbes "learn" and anticipate environmental changes, a crucial ability for their survival. We'll investigate diverse microbial species in various environments—from stable to repetitive and random—to determine how much information cells can "remember" based on environmental predictability. We'll explore factors like genome size and growth rates, and use nanoSIMS enabled single-cell observations to track nutrient uptake and understand individuality within populations. By combining our experimental data with mathematical models and evolutionary experiments, we seek to develop a general understanding of learning mechanisms and their limits across the microbial world.

https://github.com/epigani/Synergy-Summer-School-2025