Silvia De Monte

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MPI for Evolutionary Biology, Plön, Germany

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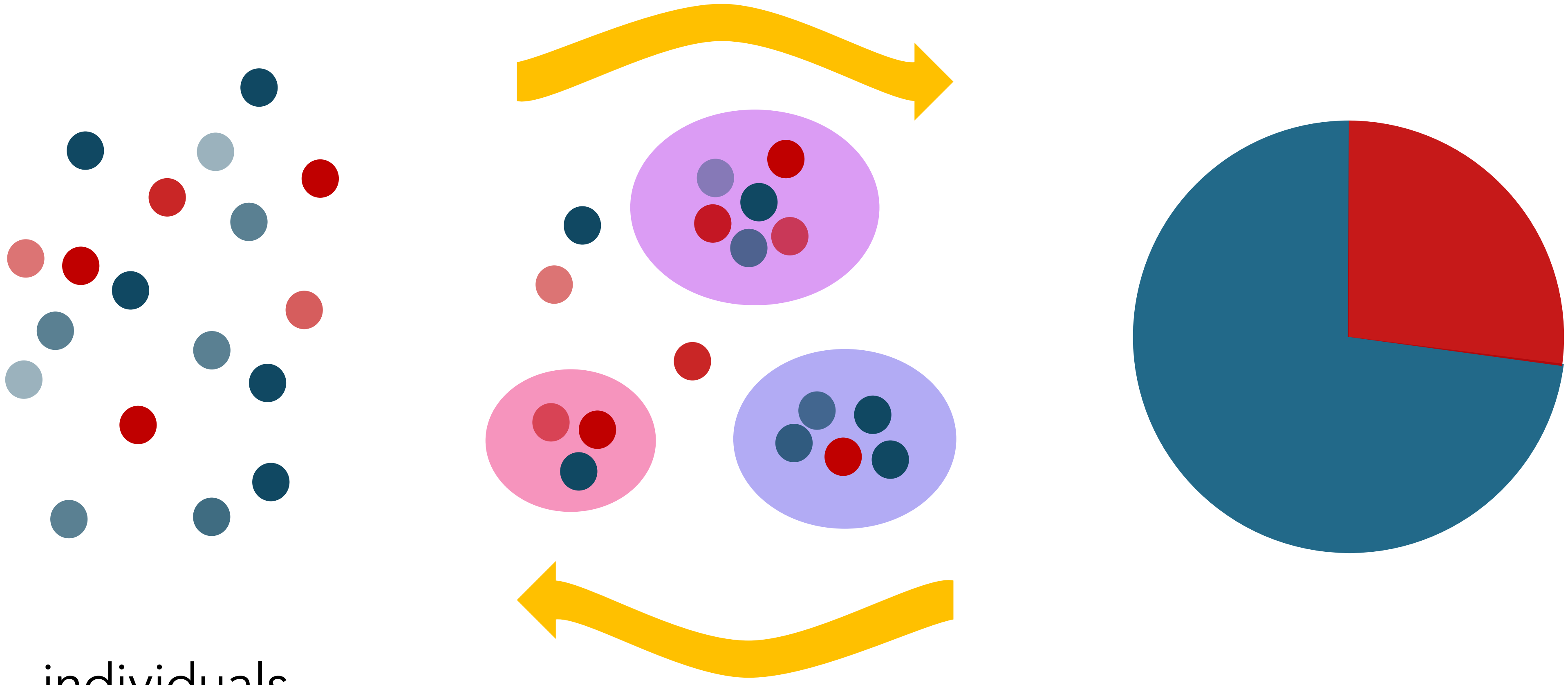
Eco-evolutionary dynamics across levels of organization



individuals
particles

collectives

populations

Plan of the lectures

1. Microbial diversity: how is it quantified, species-symmetric models for community assembly
2. General dynamical properties of species-symmetric models, ecology of non-equivalent species
3. Community evolution under collective-level selection

1. Quantifying and modelling diversity of (microbial) communities

Aussois, June 16, 2025

©Christian Sardet

Microbial communities

They are the object of extensive exploration by high-throughput genomic techniques

They are essential for health, for ecosystem services and for maintaining biotic homeostasis

They can be (to a certain extent) maintained in the lab

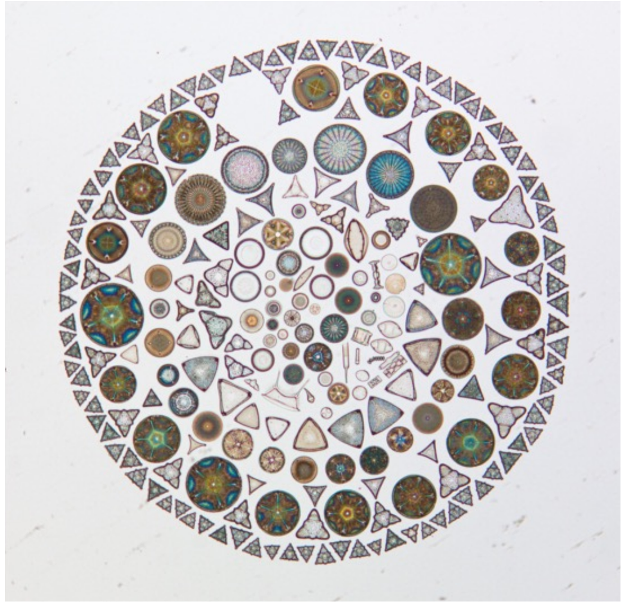
~ 10^{29} cells on Earth, millions of ‘species’, many different kinds of interactions…

Is there anything general to be said about them?

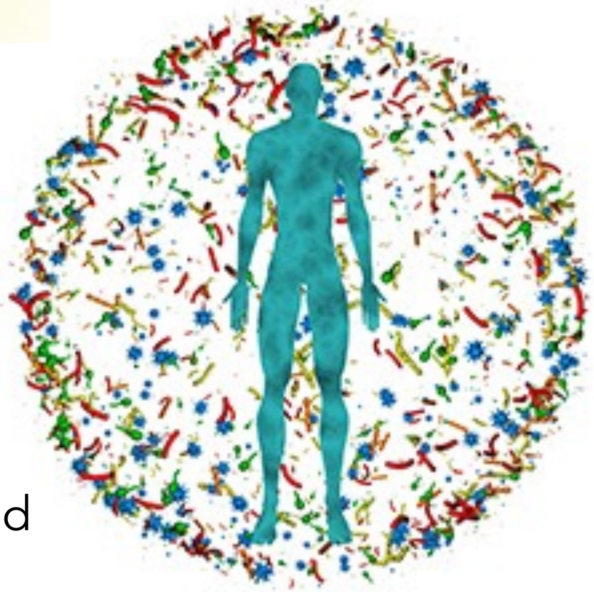
What ecological processes matter in establishing their collective functions?

Microbial communities

soil



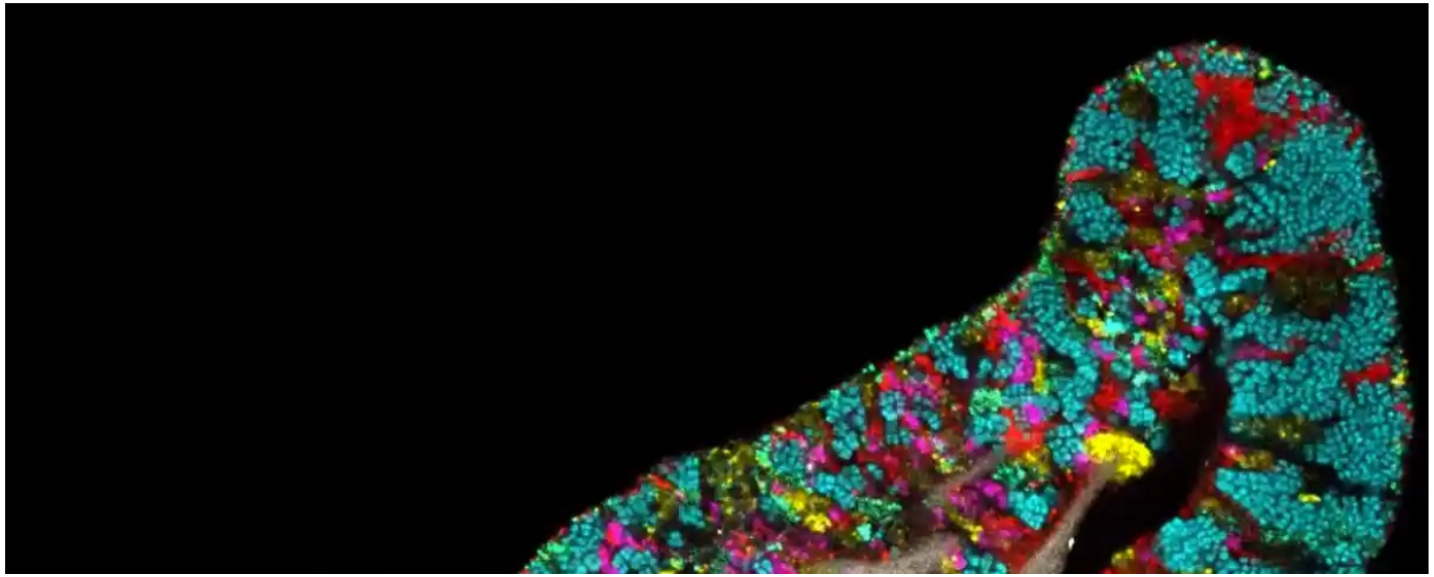
water



Host-associated

Microbes are ‘unknown unknowns’ despite being vital to all life, says study

Understanding these tiny organisms could be crucial to tackling threats such as coronavirus, but new research shows how little we know



Search

The Guardian

For 200 years

International edition

Common features of microbial communities

1. **Diversity**

   Microbial communities pervasively harbour a high genetic diversity

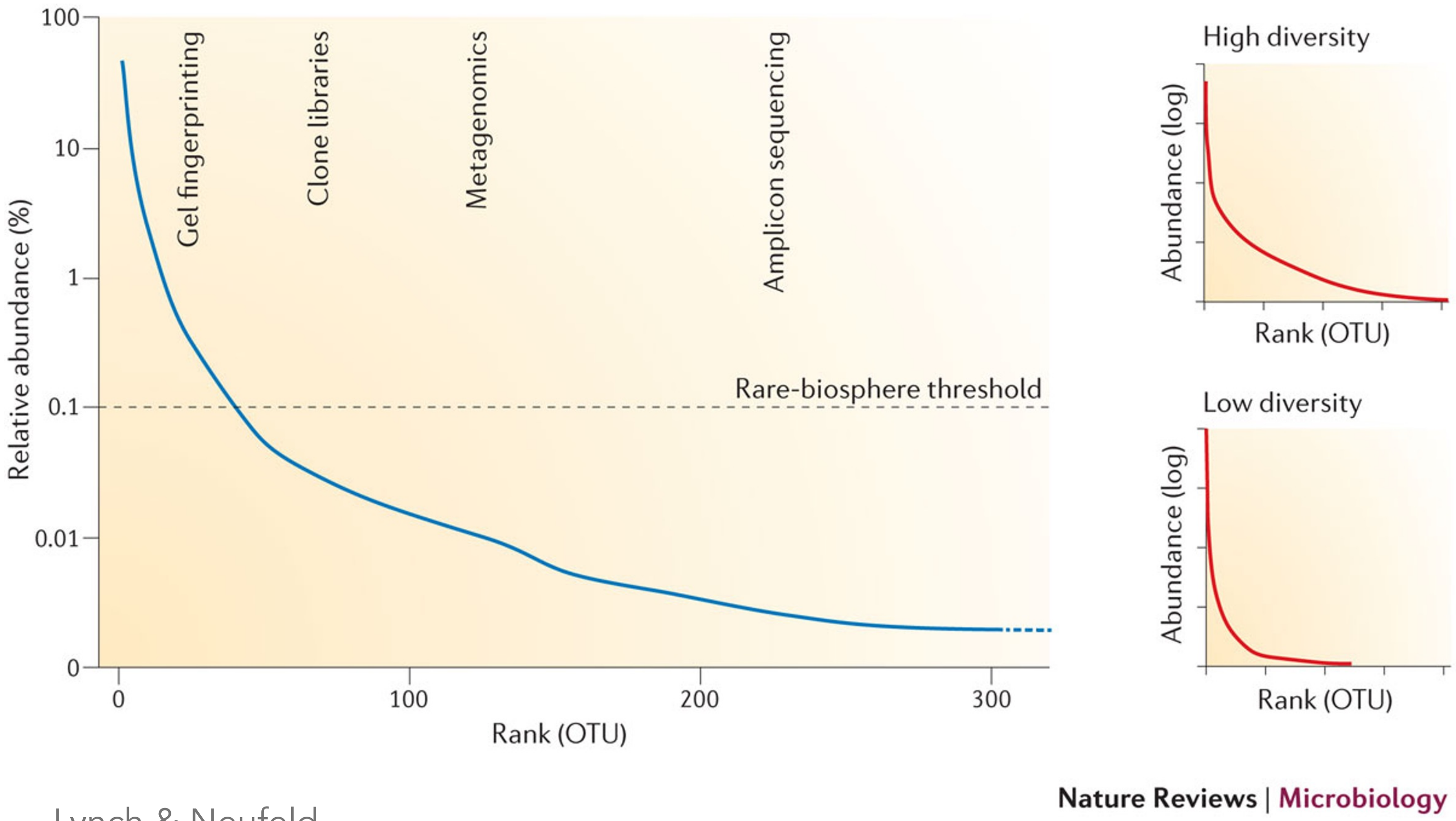
2. **Commonness of rarity**

   Most taxa are rare, few dominate the community

3. **Turnover**

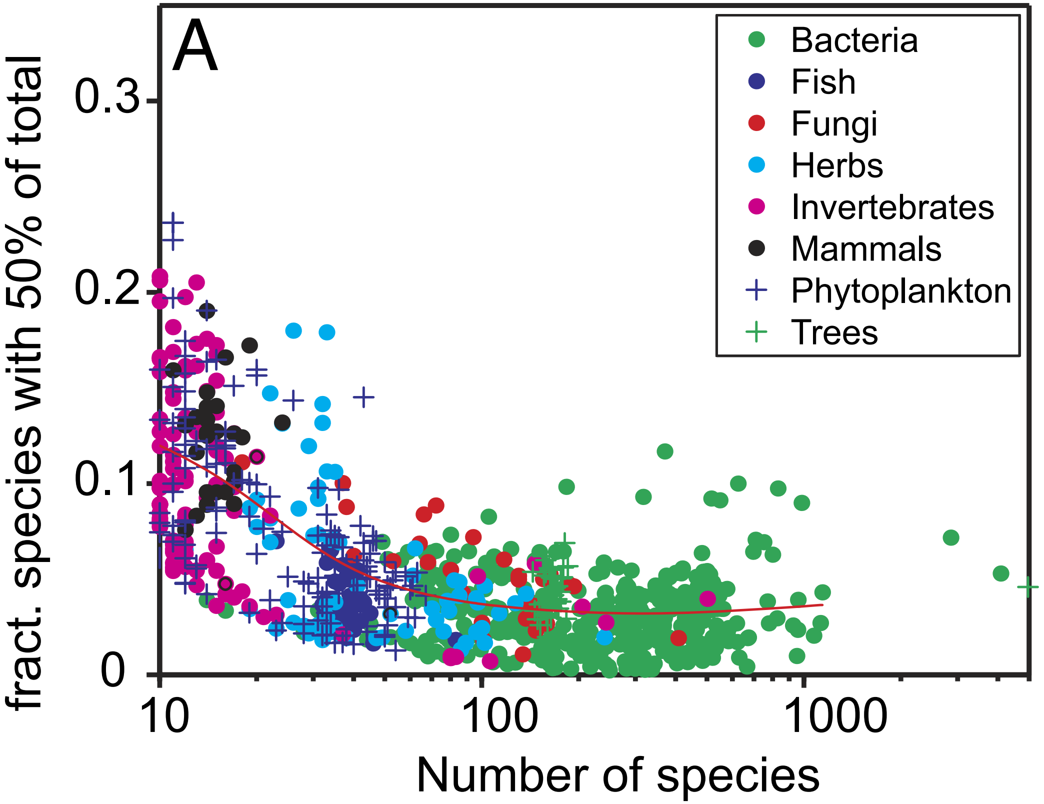
   Species composition changes in time and in space

1. Diversity: the microbial ‘dark matter’



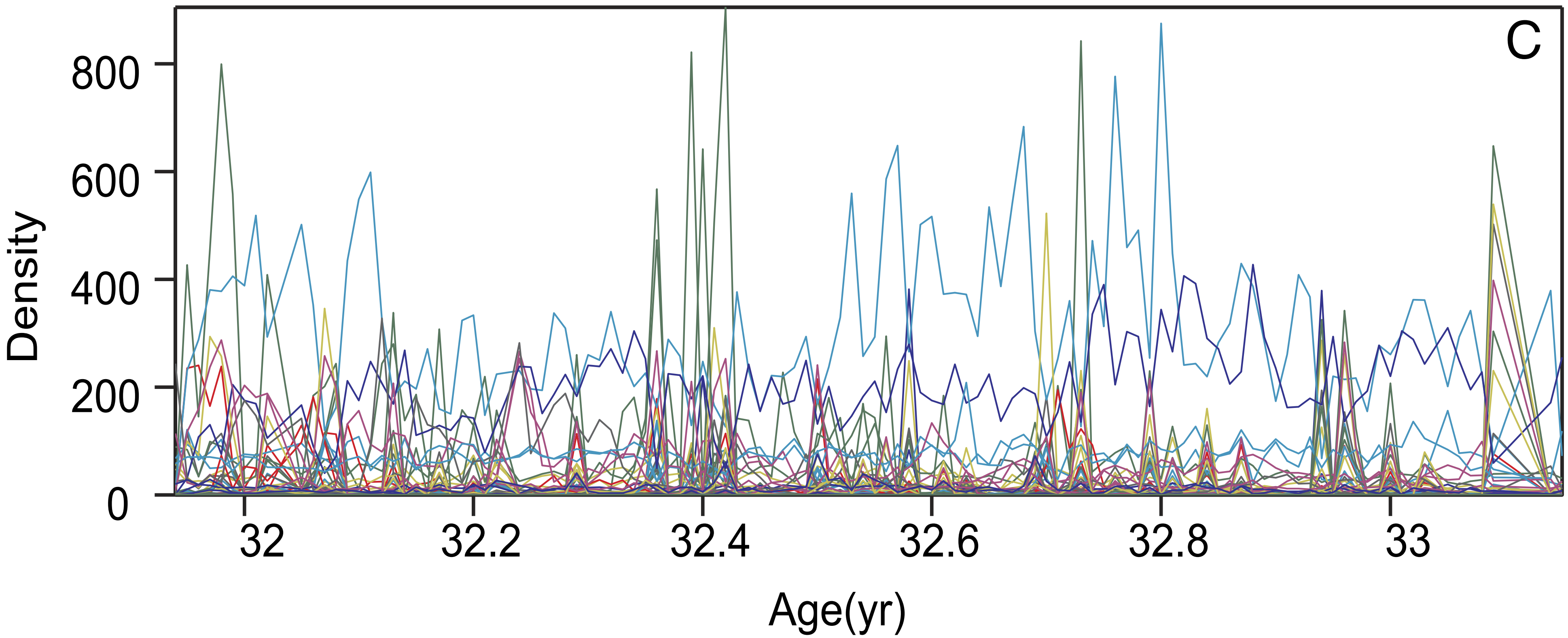
Lynch & Neufeld
Nature Reviews Microbiology (2015)

2. Rarity and dominance



Van Nes et al.
A tiny fraction of all species forms most of nature: Rarity as a sticky state
PNAS 2024

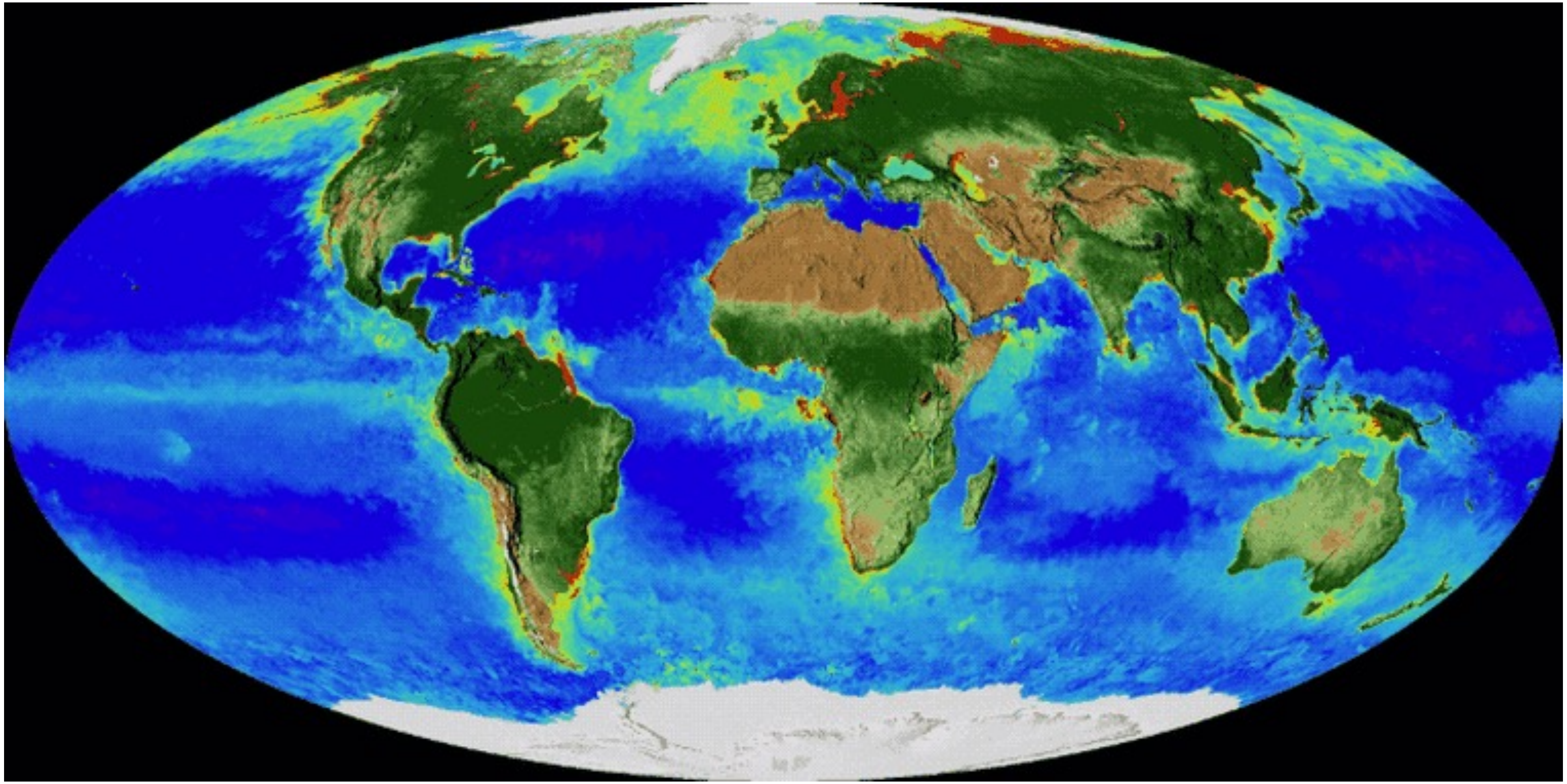
3. Temporal dynamics



Van Nes et al.
A tiny fraction of all species forms most of nature: Rarity as a sticky state
PNAS 2024

Caporaso et al.
Moving pictures of the human microbiome
Genome Biol. (2011)

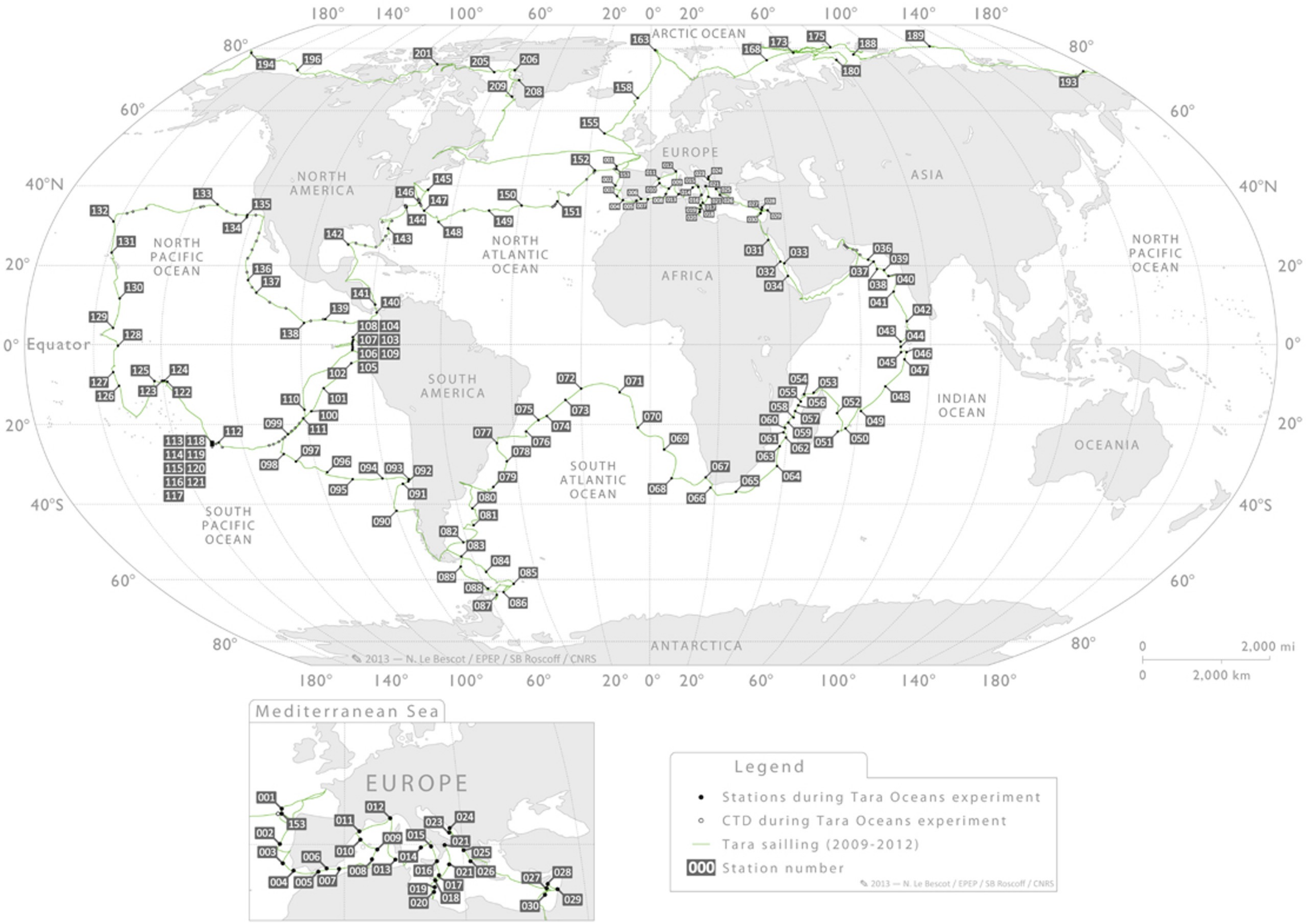
Marine plankton



NASA (Chl, false colours)

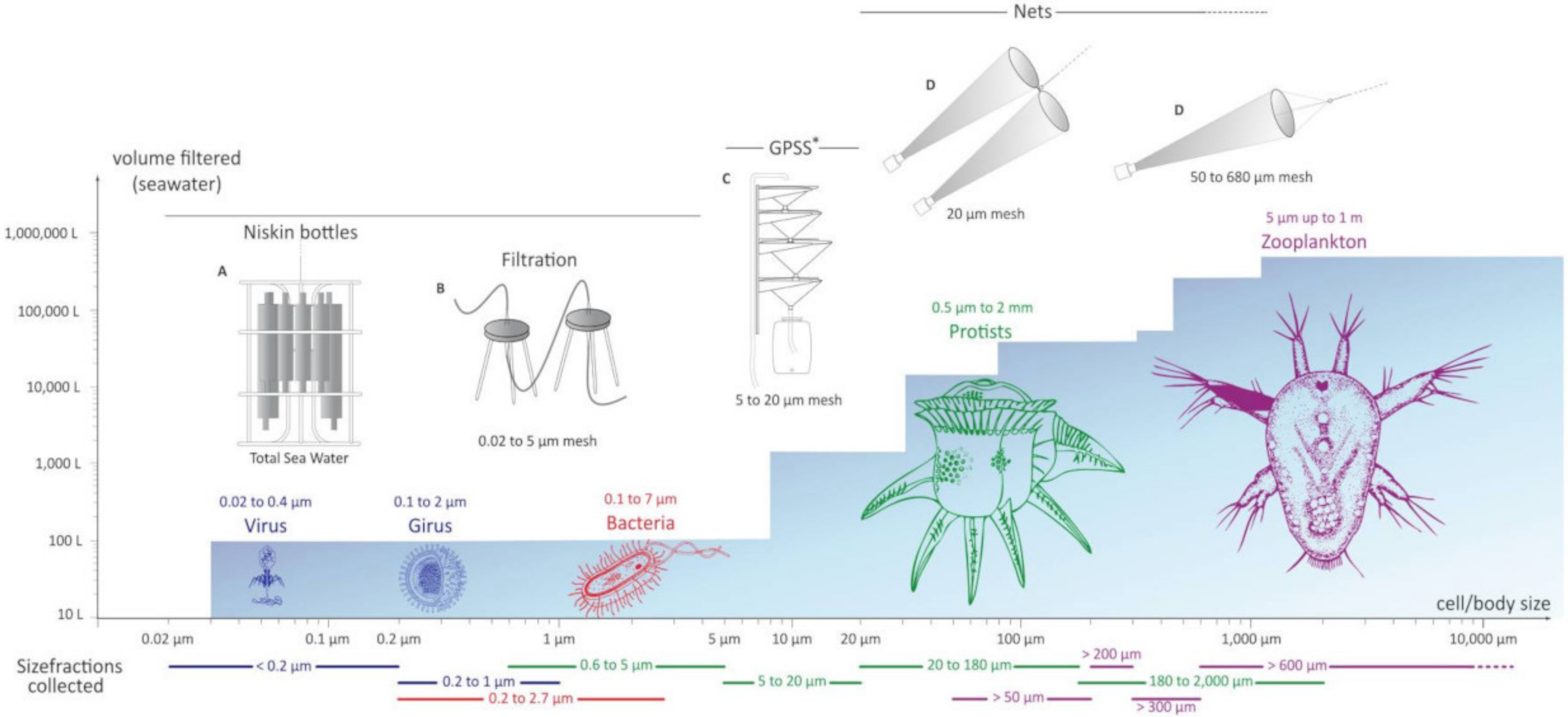
~ 1% of photosynthetic biomass
~ 50% of primary production
~ 85% of pelagic biomass is unicellular

The Tara oceans expedition

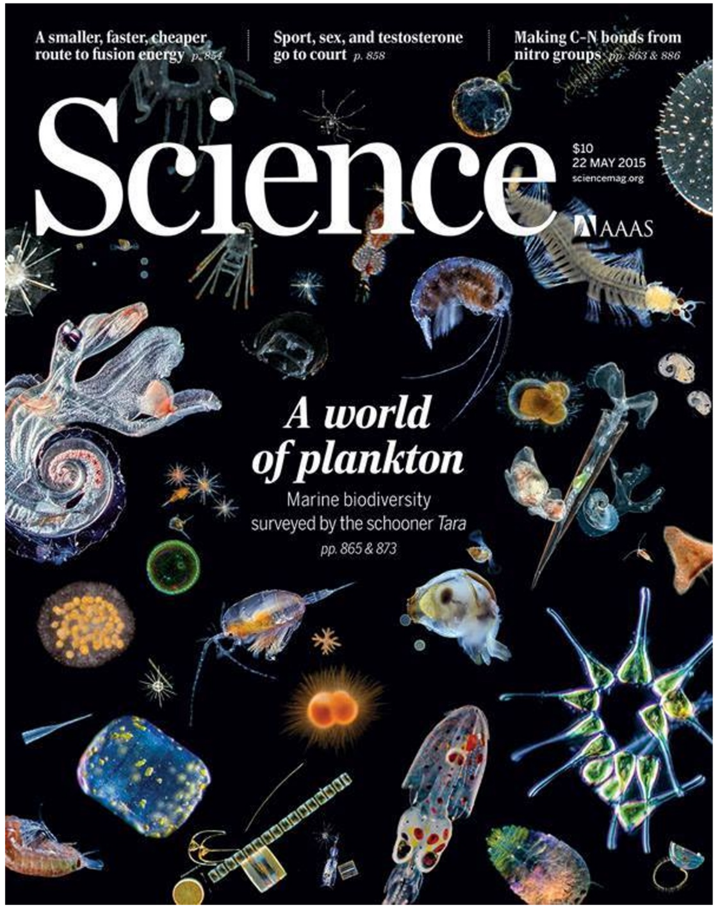


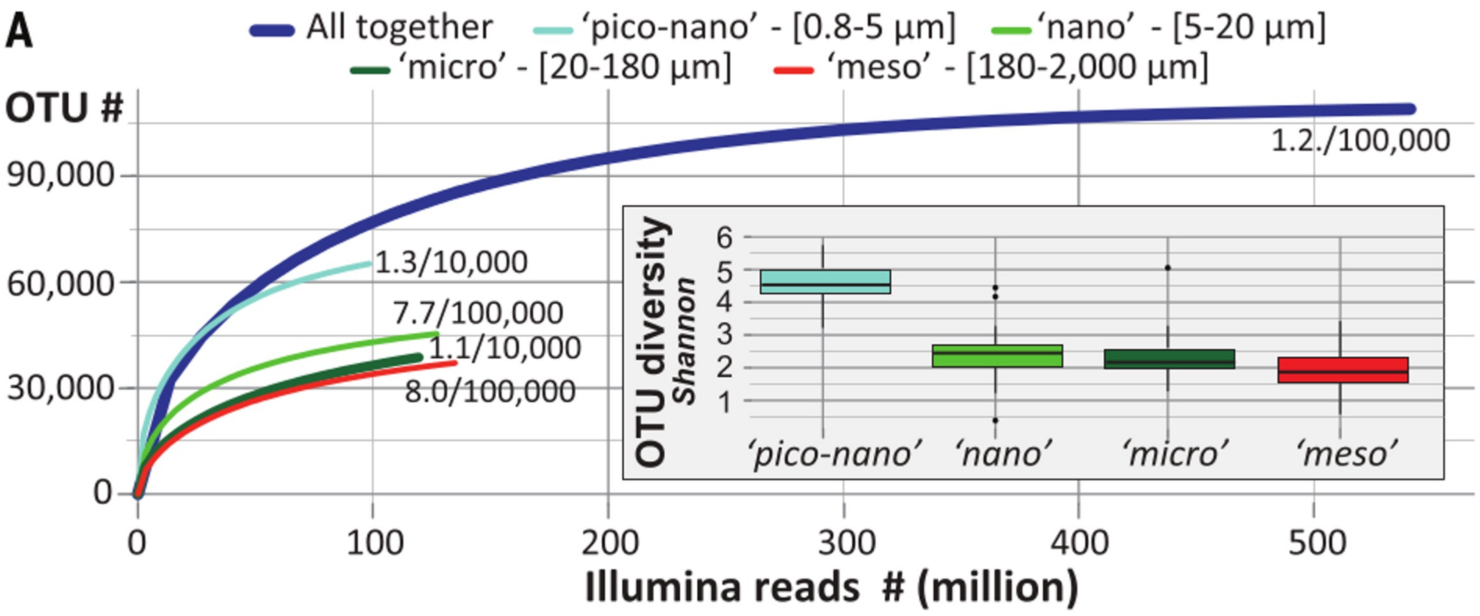
© 2013 — N. Le Bescot / EPEP / SB Roscoff / CNRS

Sampling


Nets
D
D
GPSS*
C
20 µm mesh
50 to 680 µm mesh
volume filtered
(seawater)
Niskin bottles
A
Filtration
B
1,000,000 L
100,000 L
10,000 L
1,000 L
100 L
10 L
Total Sea Water
0.02 to 5 µm mesh
5 to 20 µm mesh
5 µm up to 1 m
Zooplankton
0.5 µm to 2 mm
Protists
0.02 to 0.4 µm
Virus
0.1 to 2 µm
Girus
0.1 to 7 µm
Bacteria
cell/body size
0.02 µm
0.1 µm
0.2 µm
1 µm
5 µm
10 µm
20 µm
100 µm
1,000 µm
10,000 µm
Sizefractions
collected
< 0.2 µm
0.2 to 1 µm
0.2 to 2.7 µm
0.6 to 5 µm
5 to 20 µm
20 to 180 µm
> 50 µm
> 200 µm
180 to 2,000 µm
> 300 µm
> 600 µm

Protist (unicellular eukaryotes) diversity





De Vargas, Audic, Henry, et al.
Eukaryotic plankton diversity in the sunlit global ocean
Science 2015

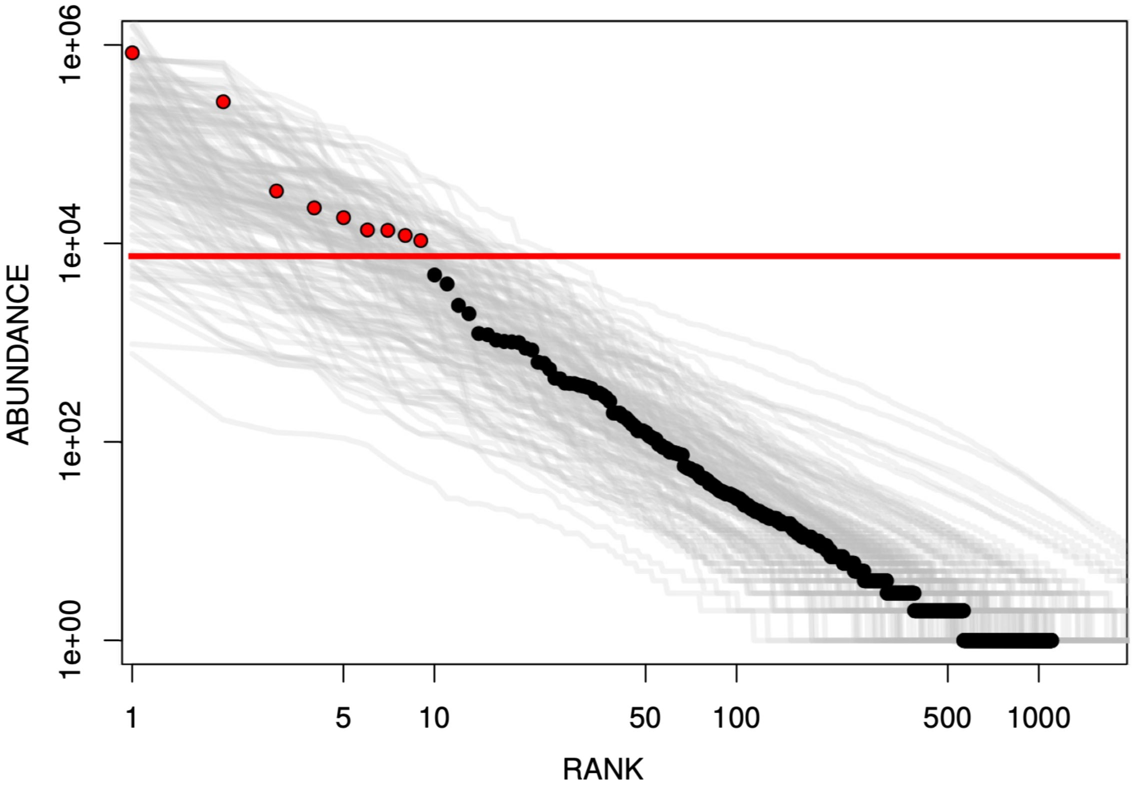
Enrico Ser-Giacomi
(CSIC, Mallorca, Spain)

The distribution of rare plankton

Tara oceans' protist sequences dataset:

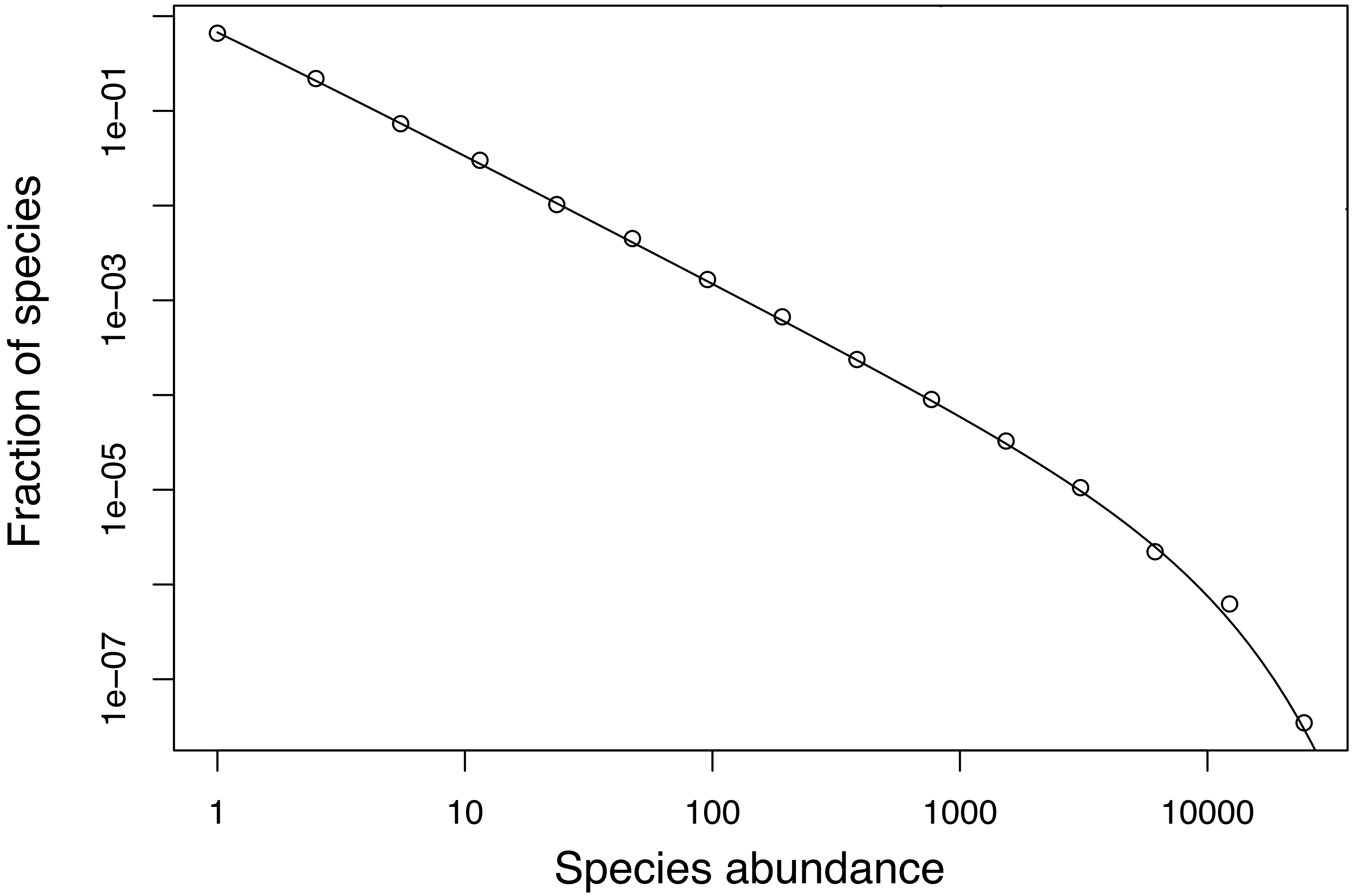
- ~100.000 different OTUs identified, few thousands per sample
- 388 samples in 121 locations (4 size classes)

Lucie Zinger
(IBENS, Toulouse)



Ser Giacomi et al.
Nature Ecology and Evolution (2018)

Species Abundance Distribution (SAD)



A semi-neutral model

Birth & death rates

$$\begin{cases} b_n = b\,n + \chi \\ d_n = d\,n + \mu \end{cases}$$

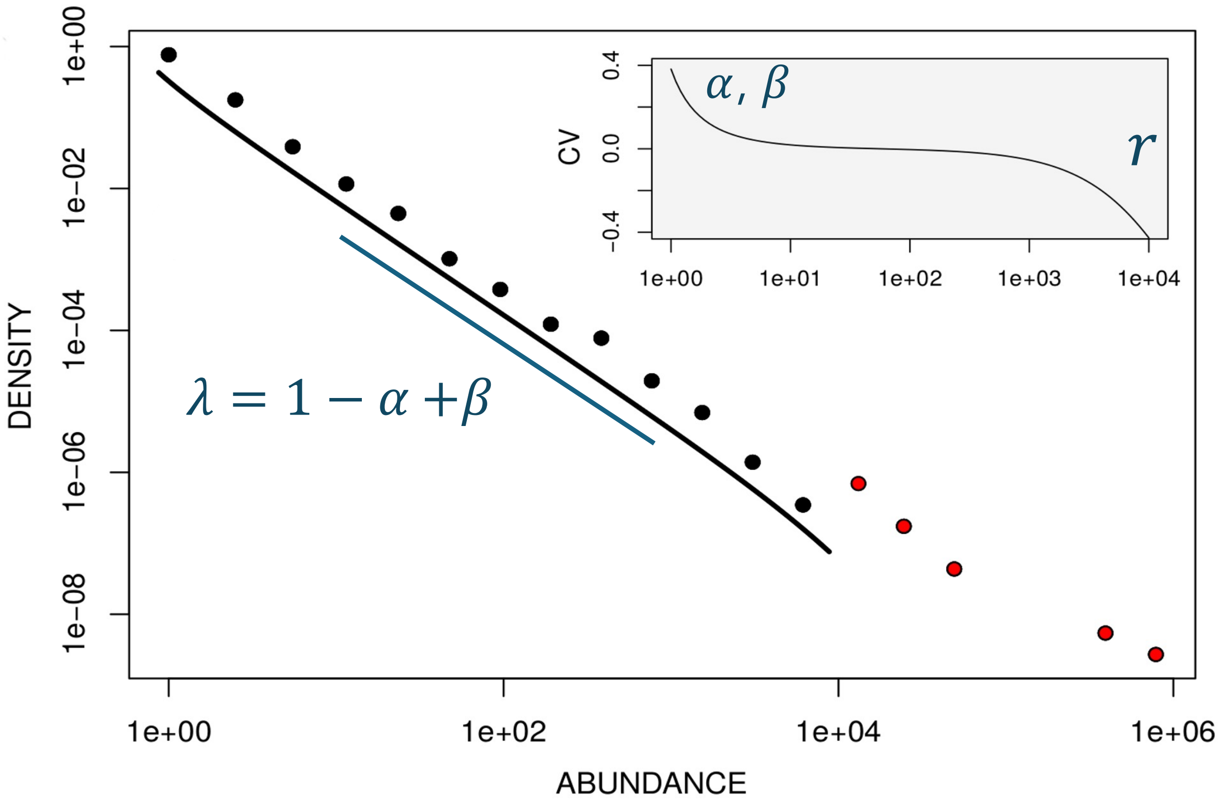
Negative binomial beta distribution:

$$< \phi_n > = \theta \frac{\Gamma(n+\alpha)\Gamma(1+\beta)}{\Gamma(\alpha)\Gamma(n+\beta+1)} e^{-rn}$$

$$\alpha = \frac{\chi}{b} \qquad \beta = \frac{\mu}{d} \qquad r = \frac{b}{d}$$

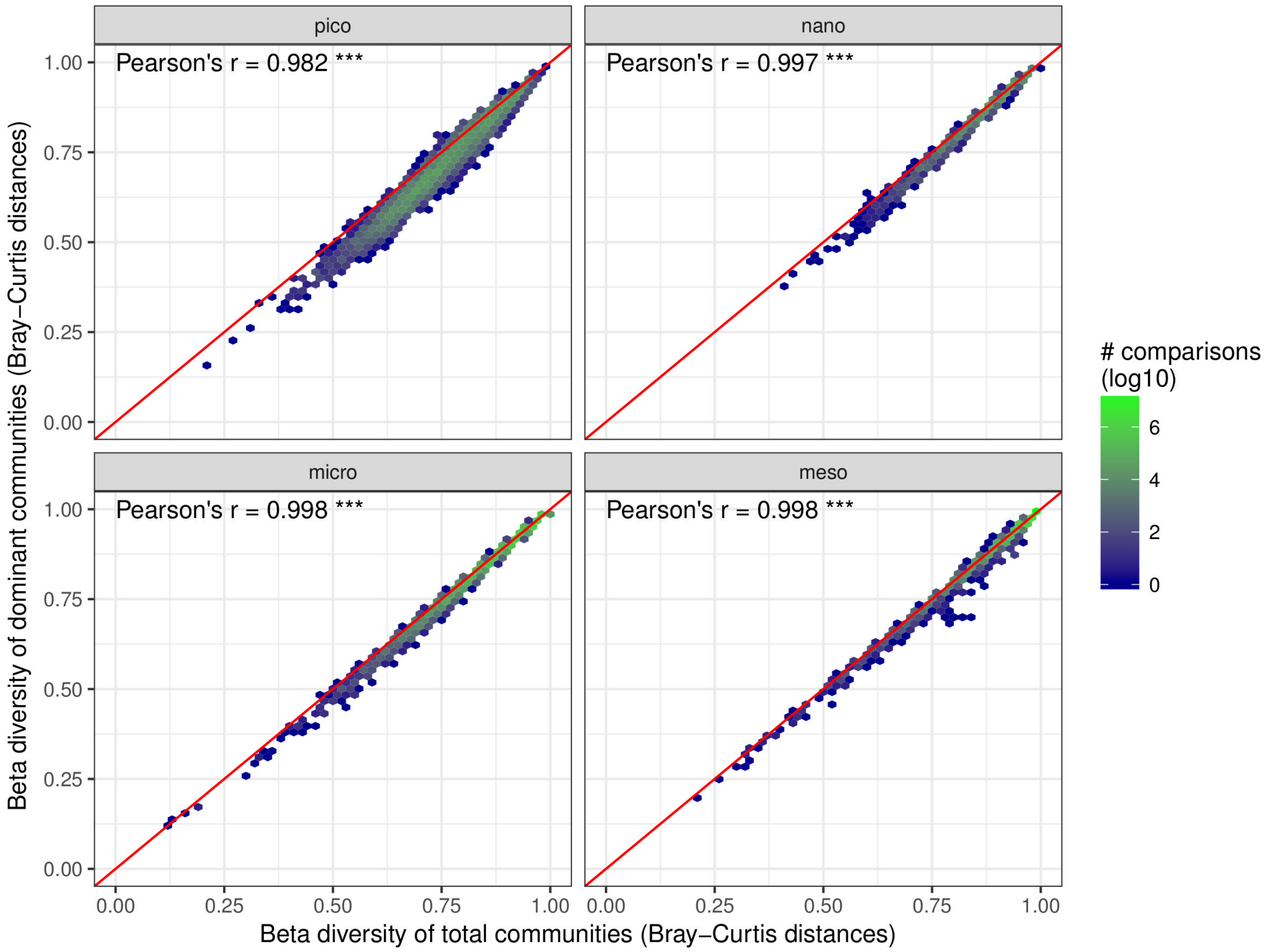
Engen 1978, He 2005

Quantifying variation of SADs

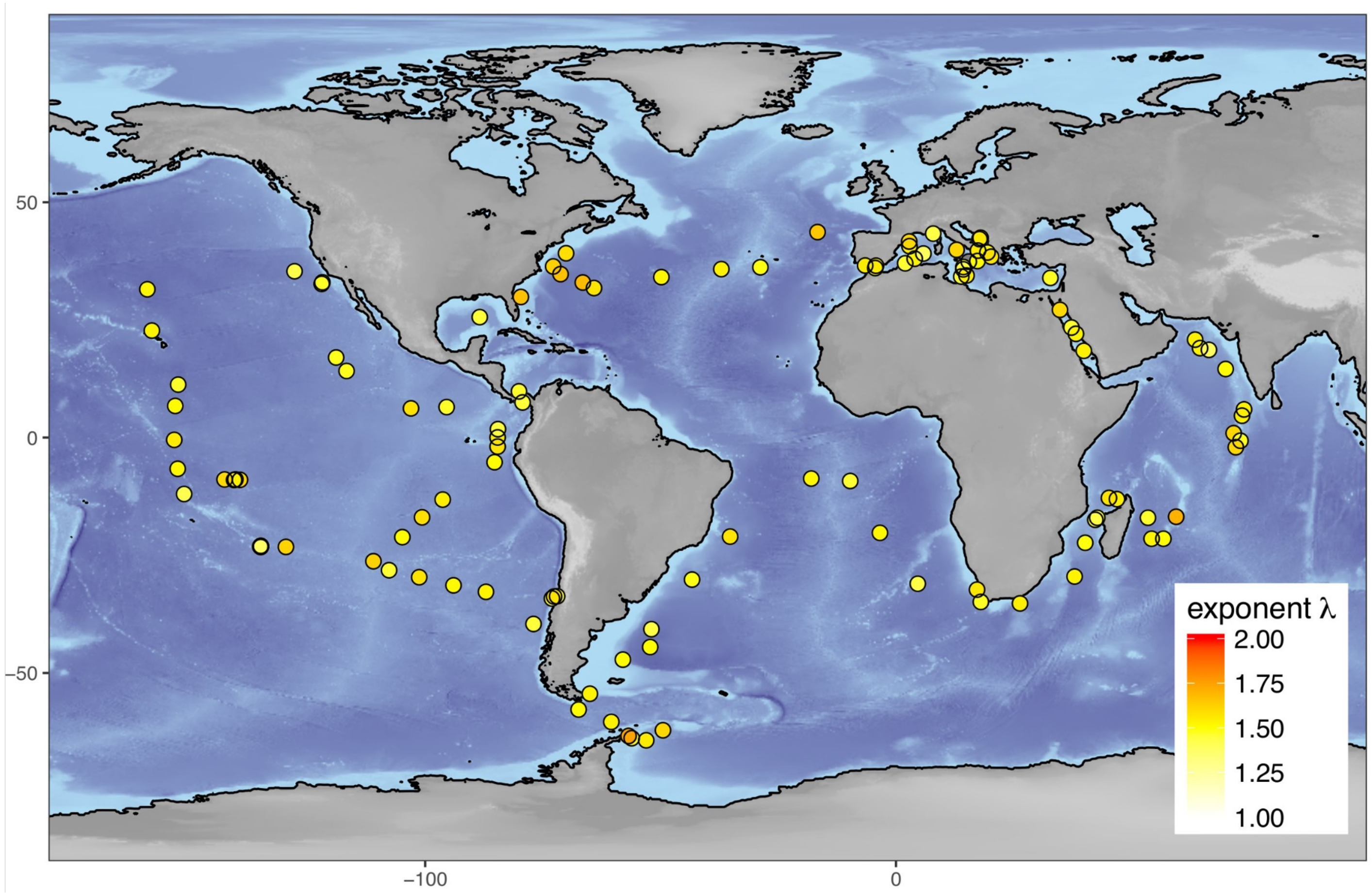


$$< \phi_n >= \theta \frac{\Gamma(n+\alpha)\Gamma(1+\beta)}{\Gamma(\alpha)\Gamma(n+\beta+1)} e^{-rn} \sim e^{-rn} n^{-\lambda}$$

Biogeographical information in 1% abundant OTUs

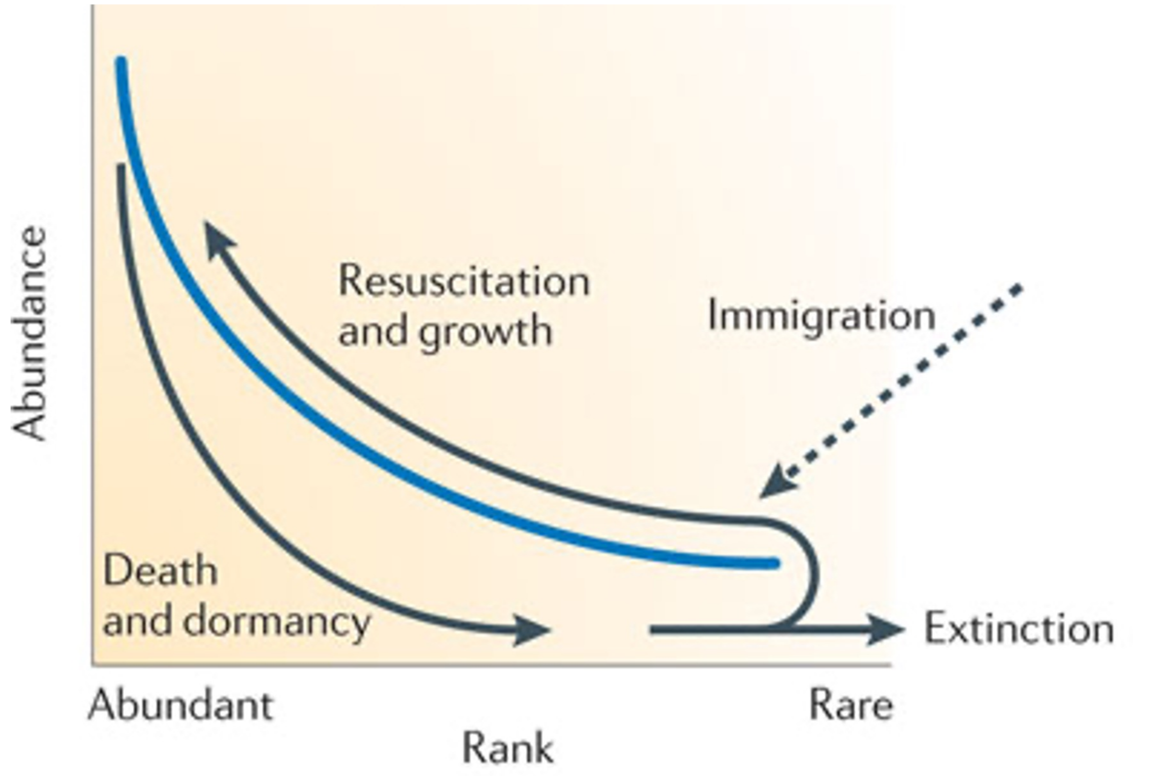


Ubiquitous abundance decay



Abundance decay is dominated by the power-law trend (~ 4 decades)
with exponent $\lambda = 1.53 \pm 0.08$ (CV < 8%)

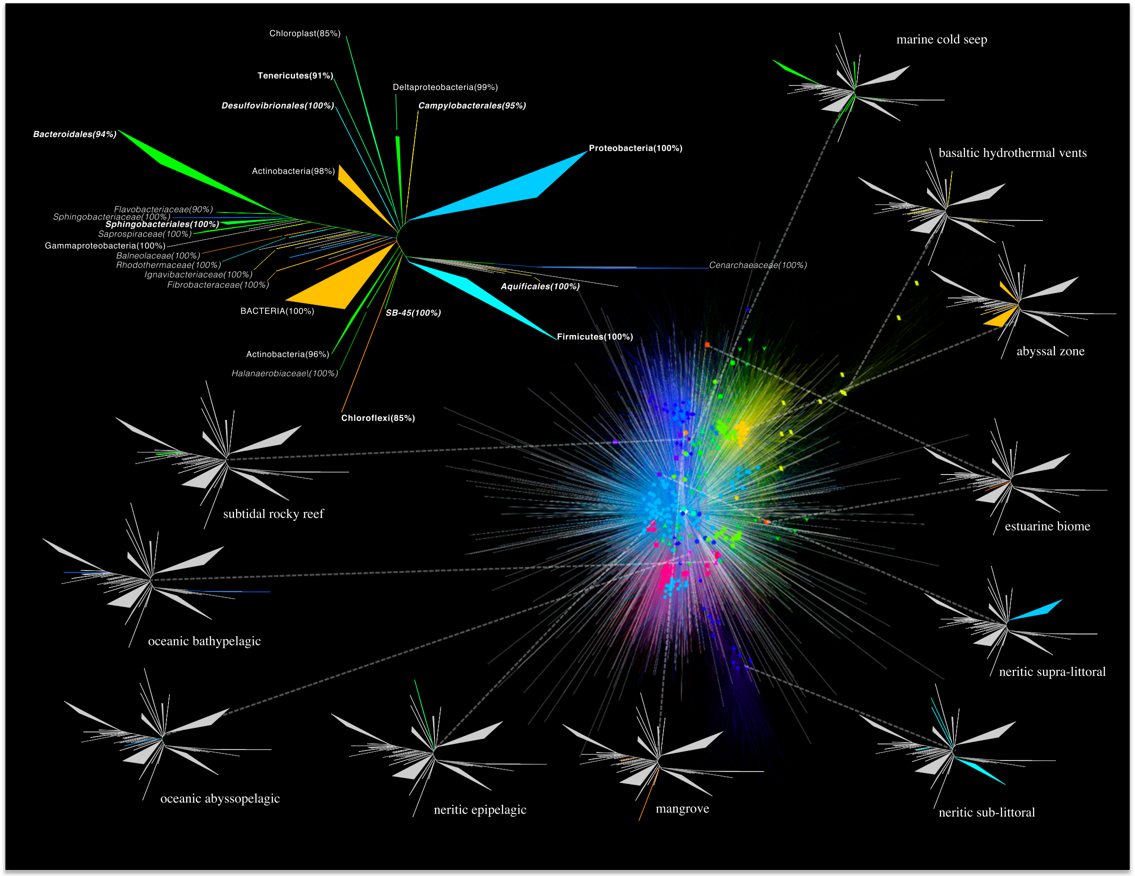
The seed bank hypothesis



Nature Reviews | Microbiology

Lennon & Jones
Nature Reviews Microbiology (2011)

The seed bank hypothesis



Gibbons et al.
Evidence for a persistent microbial seed bank throughout the global ocean
PNAS (2011)

Modelling the dynamics of species-rich communities

Generalized Lotka-Volterra equations

interactions immigration

$$\frac{dx_i(t)}{dt} = r_i x_i(t) \left(1 - x_i(t) - \sum_{j(\neq i)} \alpha_{ij} x_j(t) \right) + \lambda, \quad i = 1, \ldots, S \gg 1$$

$$\forall i : r_i = 1$$

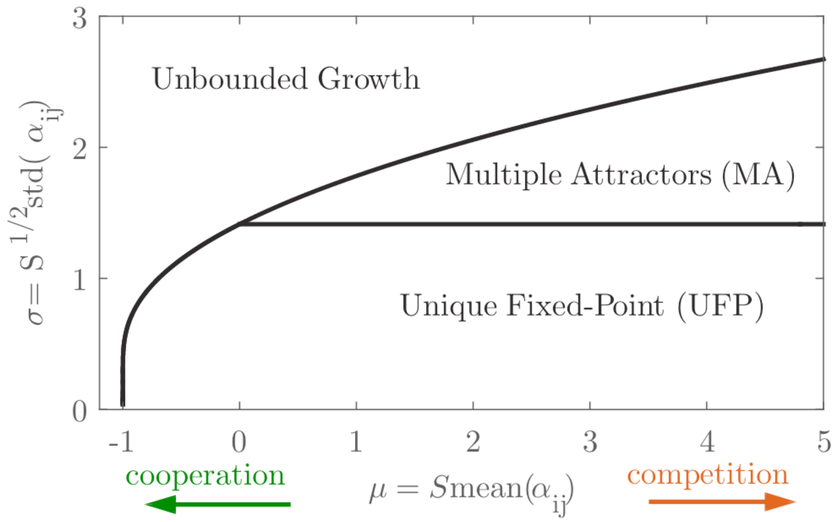
Same maximal net growth rate
and same intra-specific interactions


Emil Mallmin & **Arne Traulsen**
MPI for Evolutionary Biology, Plön

Modelling the dynamics of species-rich communities

Disordered Generalized Lotka-Volterra equations

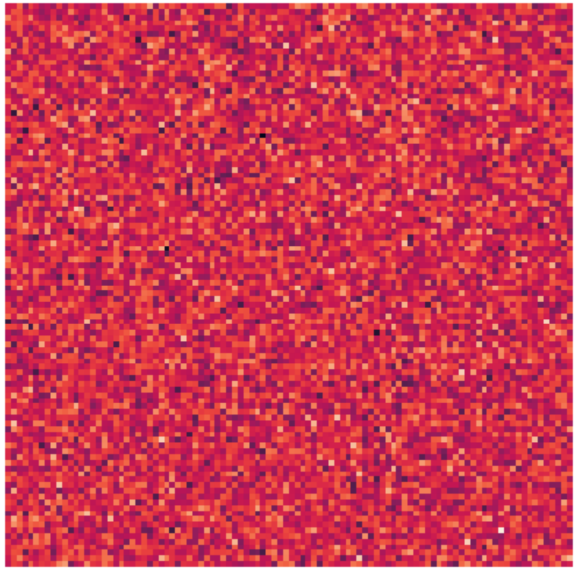
$$\frac{dx_i(t)}{dt} = r_i x_i(t)\left(1 - x_i(t) - \sum_{j(\neq i)} \overset{\text{interactions}}{\alpha_{ij}}\, x_j(t)\right) + \overset{\text{immigration}}{\lambda}, \qquad i = 1, \dots, S \gg 1$$



$\mathbb{E}[\alpha_{ij}]$

$\mathrm{Var}[\alpha_{ij}]$

$\mathrm{Corr}[\alpha_{ij}, \alpha_{ji}]$



G Bunin
Ecological communities with Lotka-Volterra dynamics.
Phys. Rev. E (2017)

Modelling the dynamics of species-rich communities

Disordered Generalized Lotka-Volterra equations

immigration

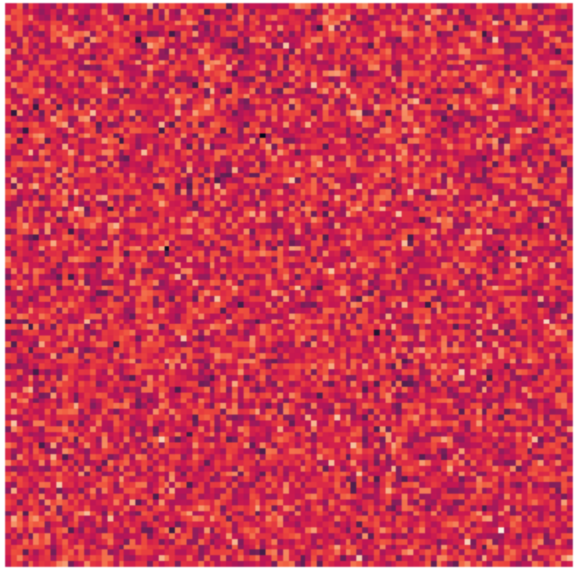
$$\frac{dx_i(t)}{dt} = r_i x_i(t)\left(1 - x_i(t) - \sum_{j(\neq i)} \alpha_{ij} x_j(t)\right) + \lambda, \quad i = 1, \ldots, S \gg 1$$

<u>strong</u> pairwise species interactions

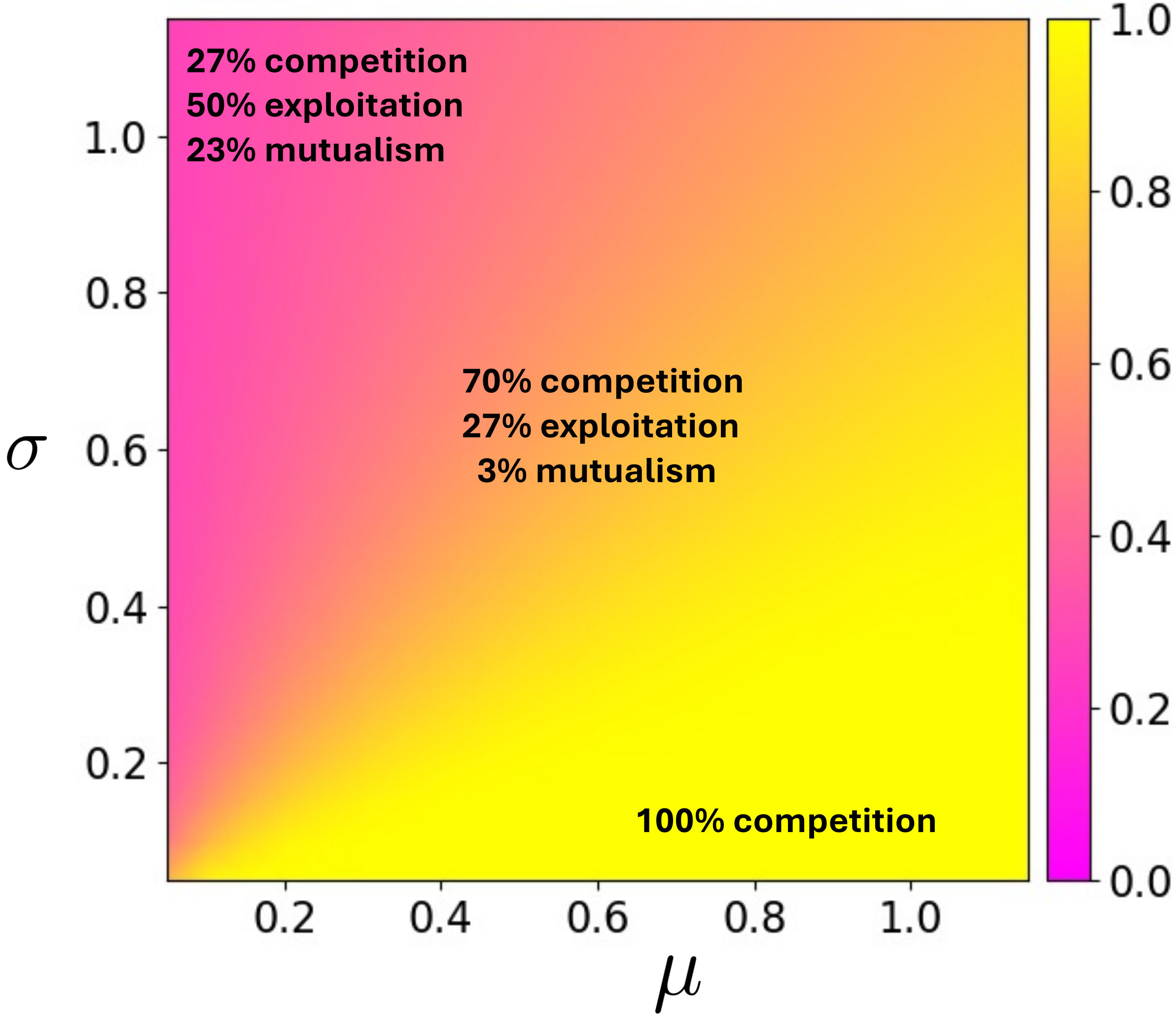
$$\mathbb{E}[\alpha_{ij}] = \mu$$

$$\mathrm{Var}[\alpha_{ij}] = \sigma^2$$

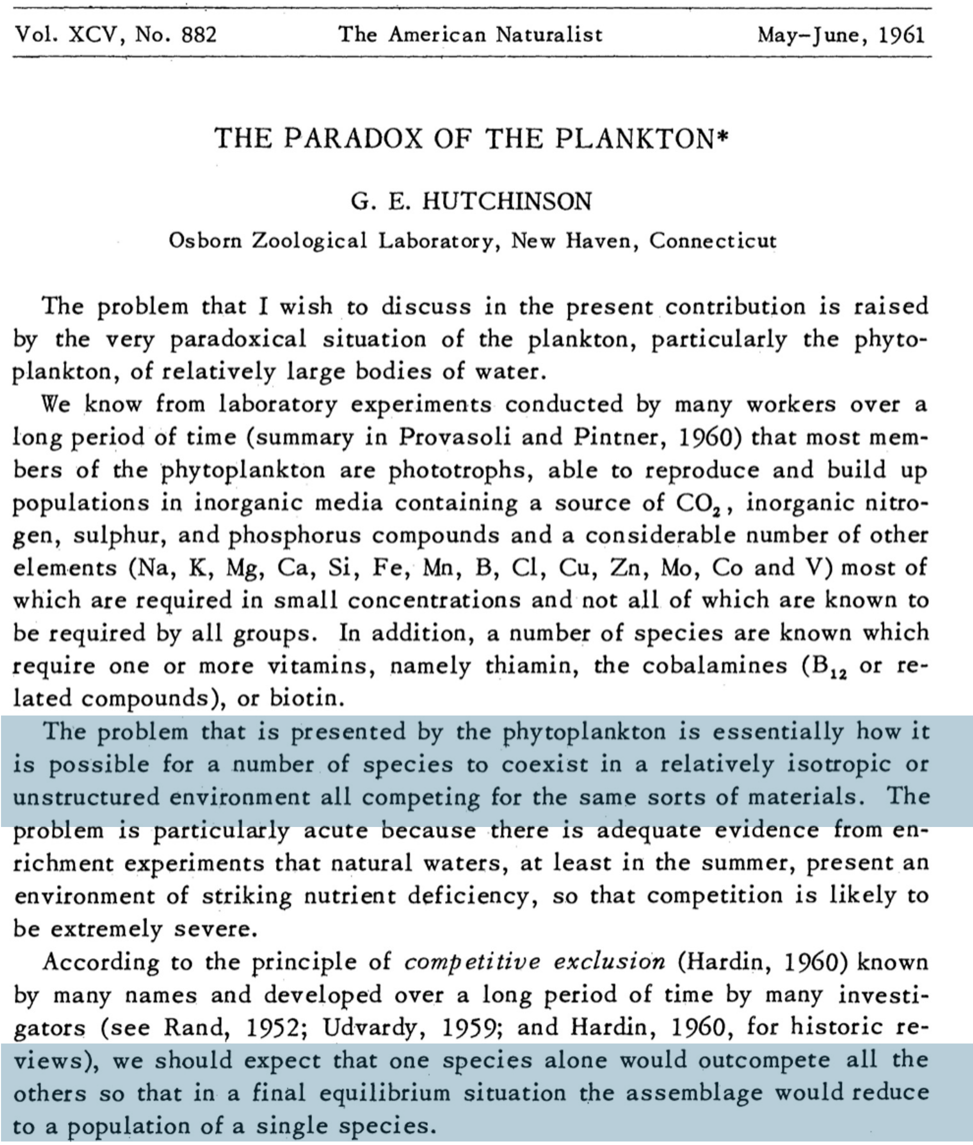
$$\mathrm{Corr}[\alpha_{ij}, \alpha_{ji}] = \gamma = 0$$



Strong interactions



Competition and competitive exclusion



Vol. XCV, No. 882 The American Naturalist May–June, 1961

THE PARADOX OF THE PLANKTON*

G. E. HUTCHINSON

Osborn Zoological Laboratory, New Haven, Connecticut

The problem that I wish to discuss in the present contribution is raised by the very paradoxical situation of the plankton, particularly the phytoplankton, of relatively large bodies of water.

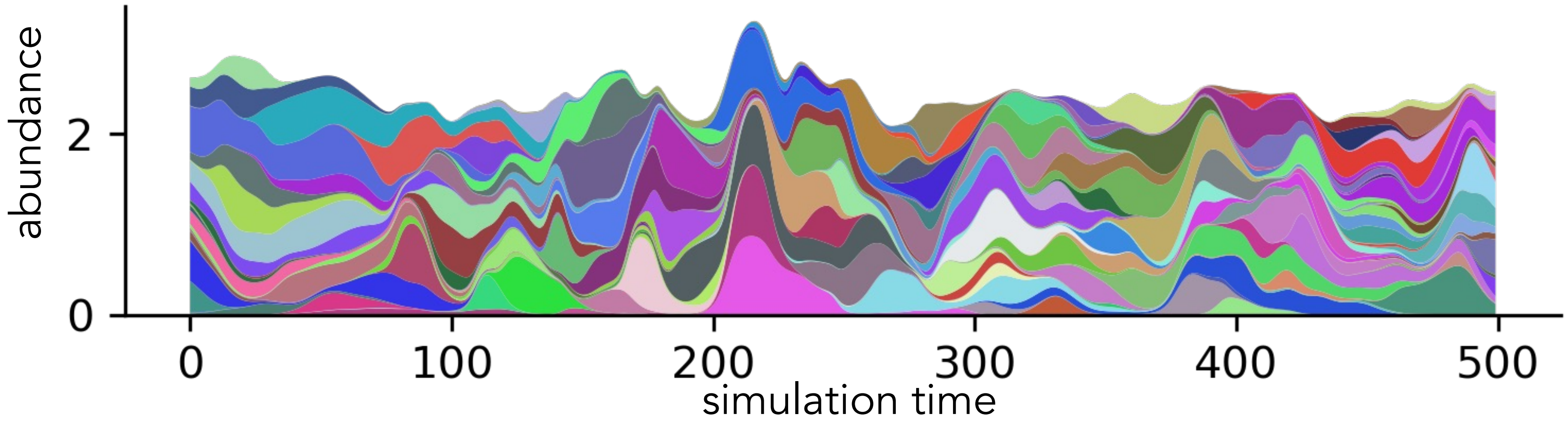
We know from laboratory experiments conducted by many workers over a long period of time (summary in Provasoli and Pintner, 1960) that most members of the phytoplankton are phototrophs, able to reproduce and build up populations in inorganic media containing a source of CO_2, inorganic nitrogen, sulphur, and phosphorus compounds and a considerable number of other elements (Na, K, Mg, Ca, Si, Fe, Mn, B, Cl, Cu, Zn, Mo, Co and V) most of which are required in small concentrations and not all of which are known to be required by all groups. In addition, a number of species are known which require one or more vitamins, namely thiamin, the cobalamines (B_{12} or related compounds), or biotin.

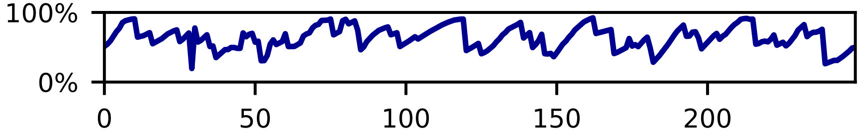
The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials. The problem is particularly acute because there is adequate evidence from enrichment experiments that natural waters, at least in the summer, present an environment of striking nutrient deficiency, so that competition is likely to be extremely severe.

According to the principle of *competitive exclusion* (Hardin, 1960) known by many names and developed over a long period of time by many investigators (see Rand, 1952; Udvardy, 1959; and Hardin, 1960, for historic reviews), we should expect that one species alone would outcompete all the others so that in a final equilibrium situation the assemblage would reduce to a population of a single species.

Competition and diversity drive species turnover

Competition and diversity drive species turnover

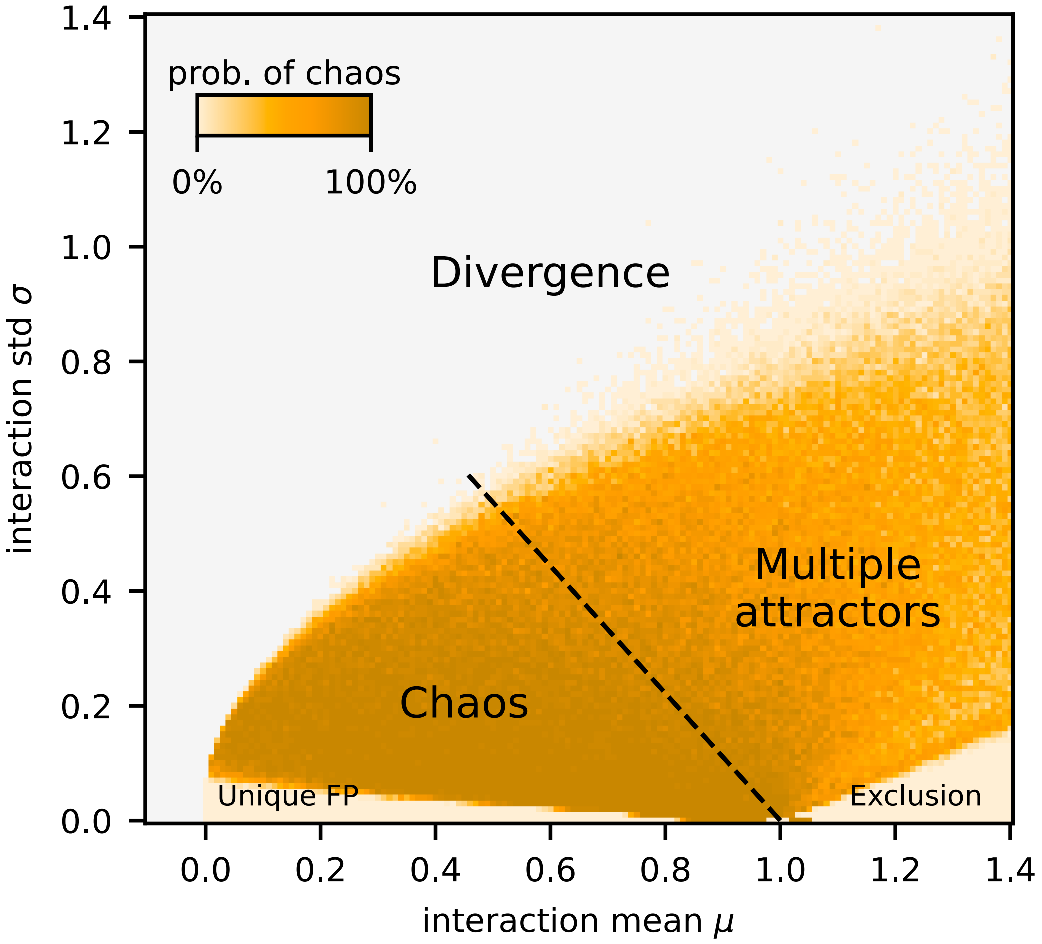




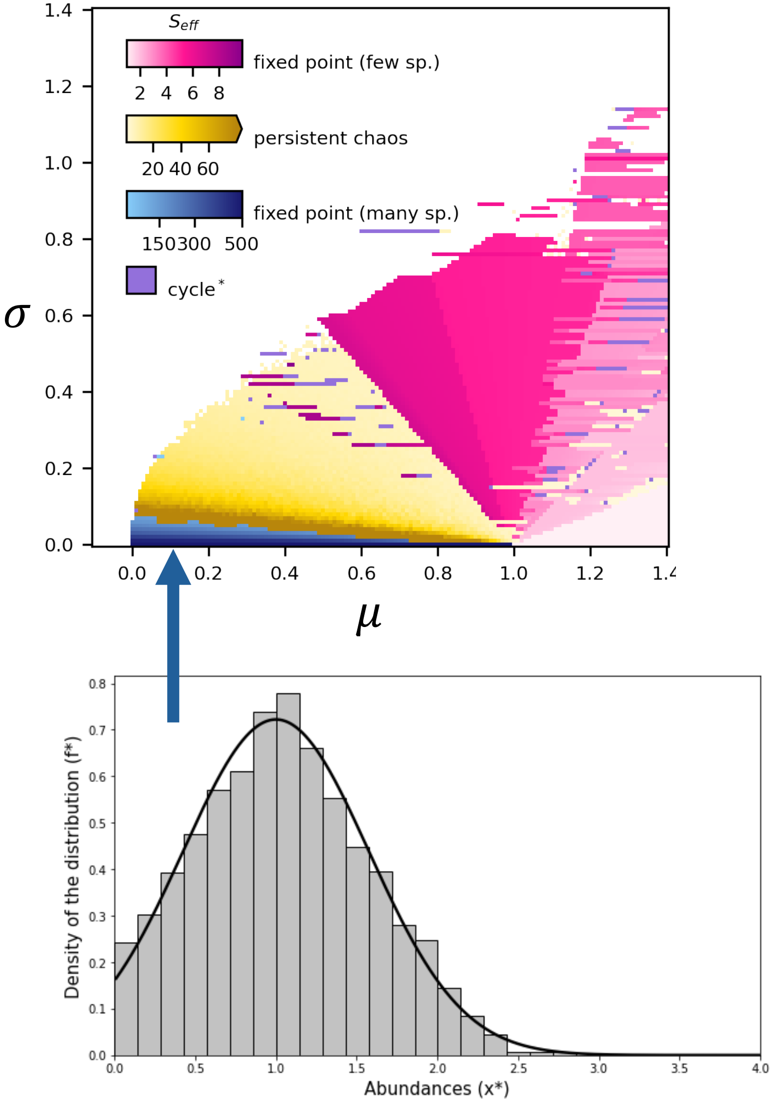
Distance from a few-species equilibrium

At any time, the dominant community is 'effectively' low dimensional
Dominant guilds turn over unpredictably

Chaos is prevalent for intermediate interaction strength and heterogeneity



Species abundance distributions

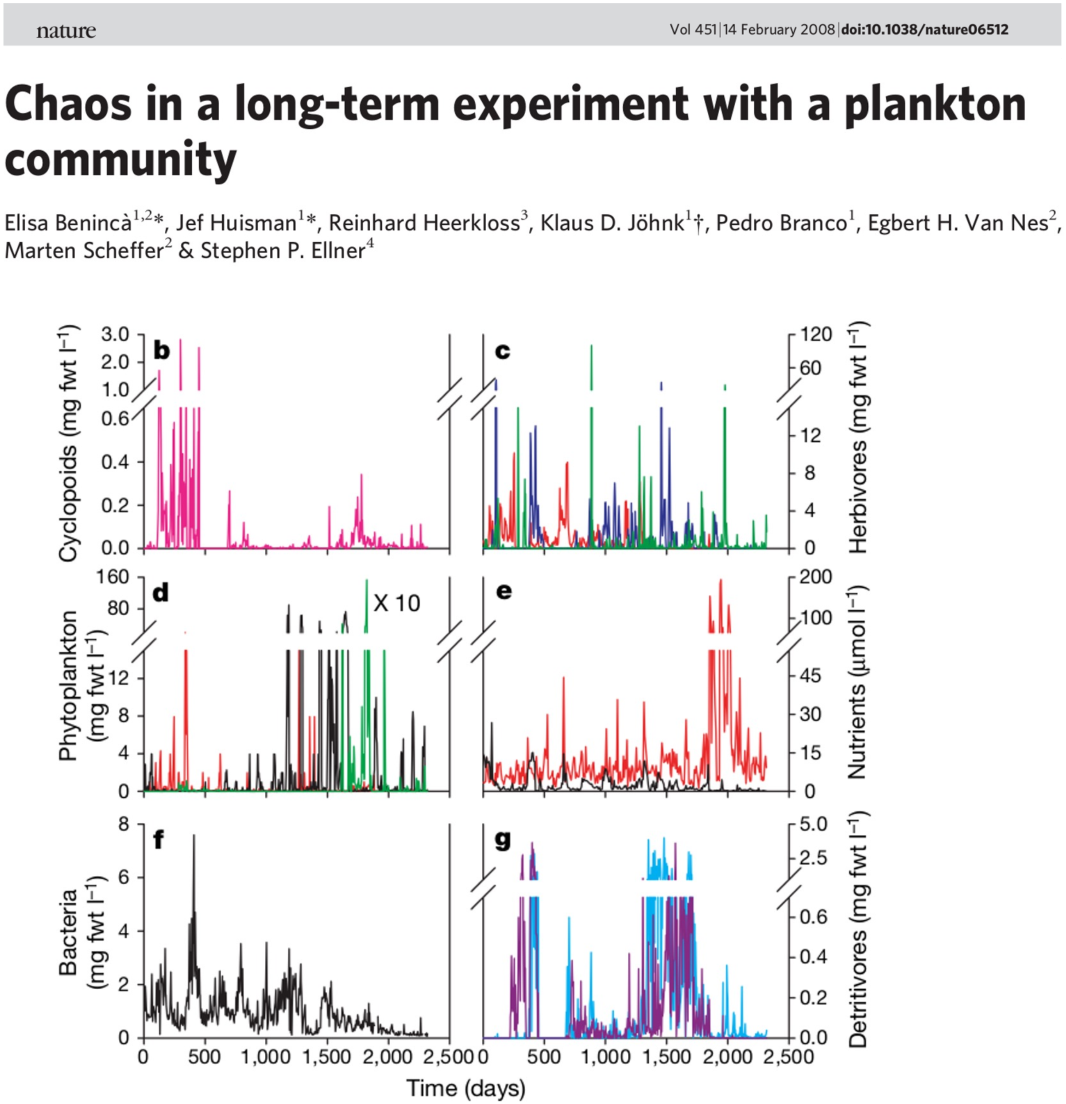


In the **equilibrium phases**, species abundance distributions are either trivial (in the exclusion phases), or resemble a truncated Gaussian distribution (in the high-diversity, unique fixed point phase).

Akijui et al.
Complex systems in Ecology: A guided tour with large Lotka-Volterra models and random matrices
arXiv

Barbier et al.
Generic assembly patterns in complex ecological communities
PNAS (2018)

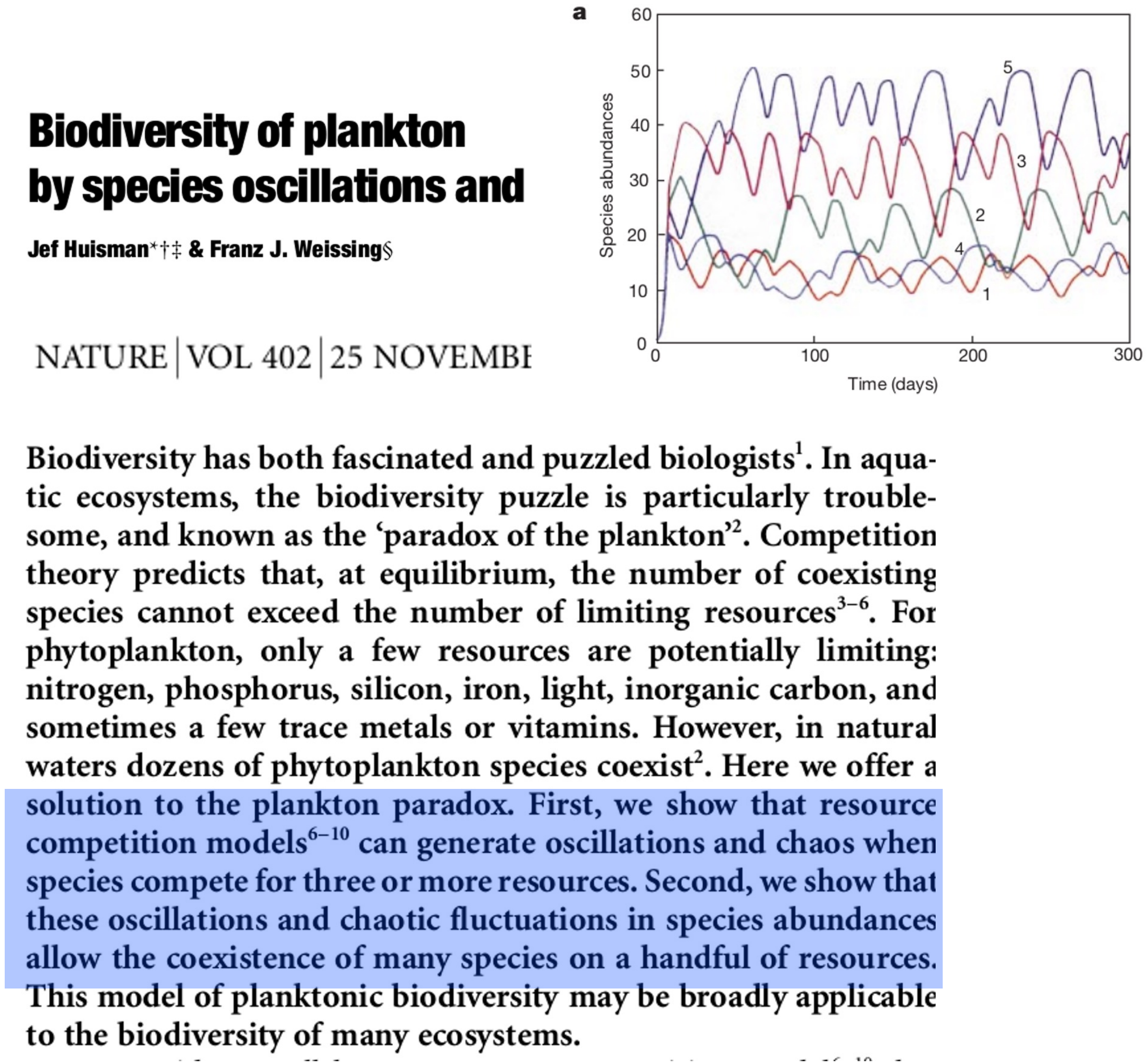
Out-of-equilibrium dynamics and biodiversity



nature Vol 451|14 February 2008|doi:10.1038/nature06512

Chaos in a long-term experiment with a plankton community

Elisa Benincà[1,2]*, Jef Huisman[1]*, Reinhard Heerkloss[3], Klaus D. Jöhnk[1]†, Pedro Branco[1], Egbert H. Van Nes[2], Marten Scheffer[2] & Stephen P. Ellner[4]



Biodiversity of plankton by species oscillations and

Jef Huisman*†‡ & Franz J. Weissing§

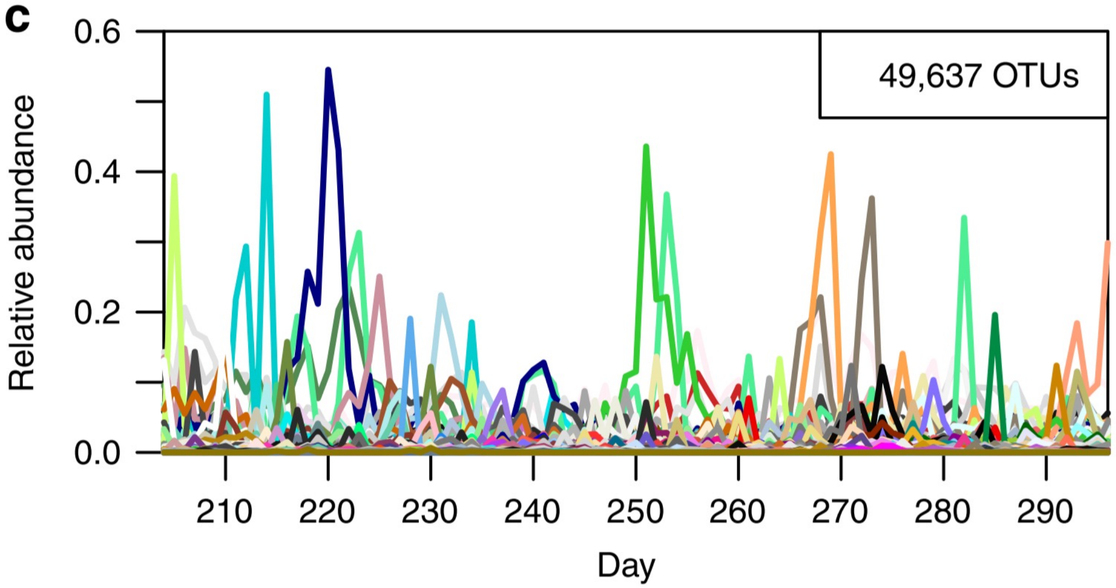
NATURE | VOL 402 | 25 NOVEMB

Biodiversity has both fascinated and puzzled biologists[1]. In aquatic ecosystems, the biodiversity puzzle is particularly troublesome, and known as the 'paradox of the plankton'[2]. Competition theory predicts that, at equilibrium, the number of coexisting species cannot exceed the number of limiting resources[3–6]. For phytoplankton, only a few resources are potentially limiting: nitrogen, phosphorus, silicon, iron, light, inorganic carbon, and sometimes a few trace metals or vitamins. However, in natural waters dozens of phytoplankton species coexist[2]. Here we offer a solution to the plankton paradox. First, we show that resource competition models[6–10] can generate oscillations and chaos when species compete for three or more resources. Second, we show that these oscillations and chaotic fluctuations in species abundances allow the coexistence of many species on a handful of resources. This model of planktonic biodiversity may be broadly applicable to the biodiversity of many ecosystems.

Out-of-equilibrium (chaotic) dynamics in nature

mammals (16%)
birds (18%)
bony fishes (29%)
Insects (43%)
zooplankton (77%)
phytoplankton (81%)

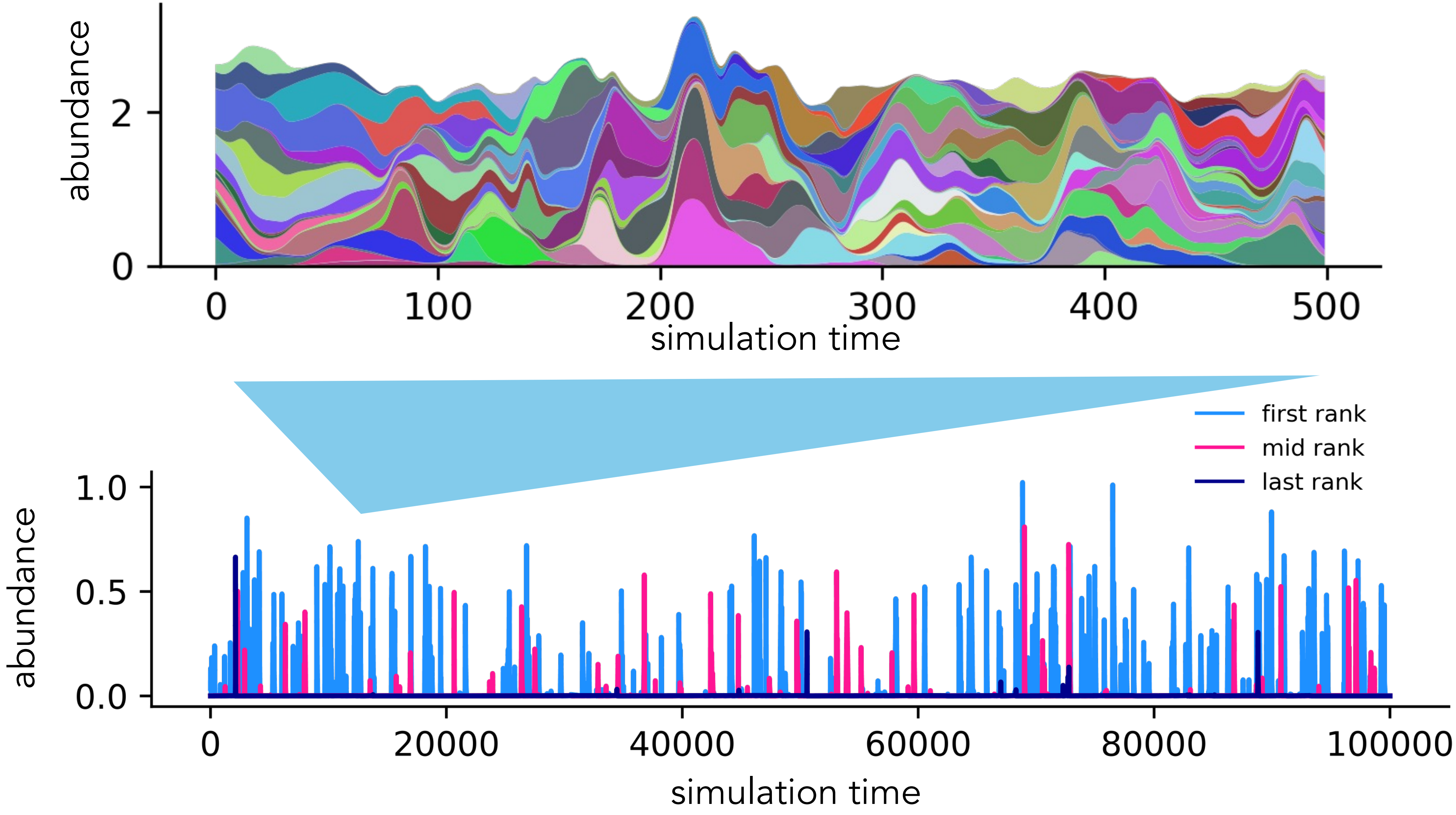
Coastal plankton time-series*



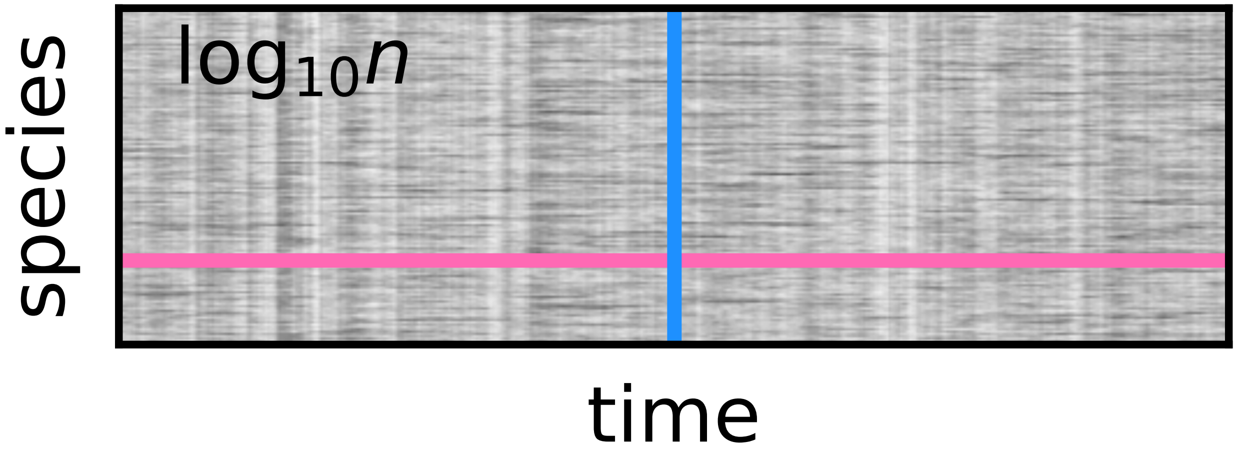
Rogers et al.
Chaos is not rare in natural ecosystems
Nature Ecology and Evolution (2022)

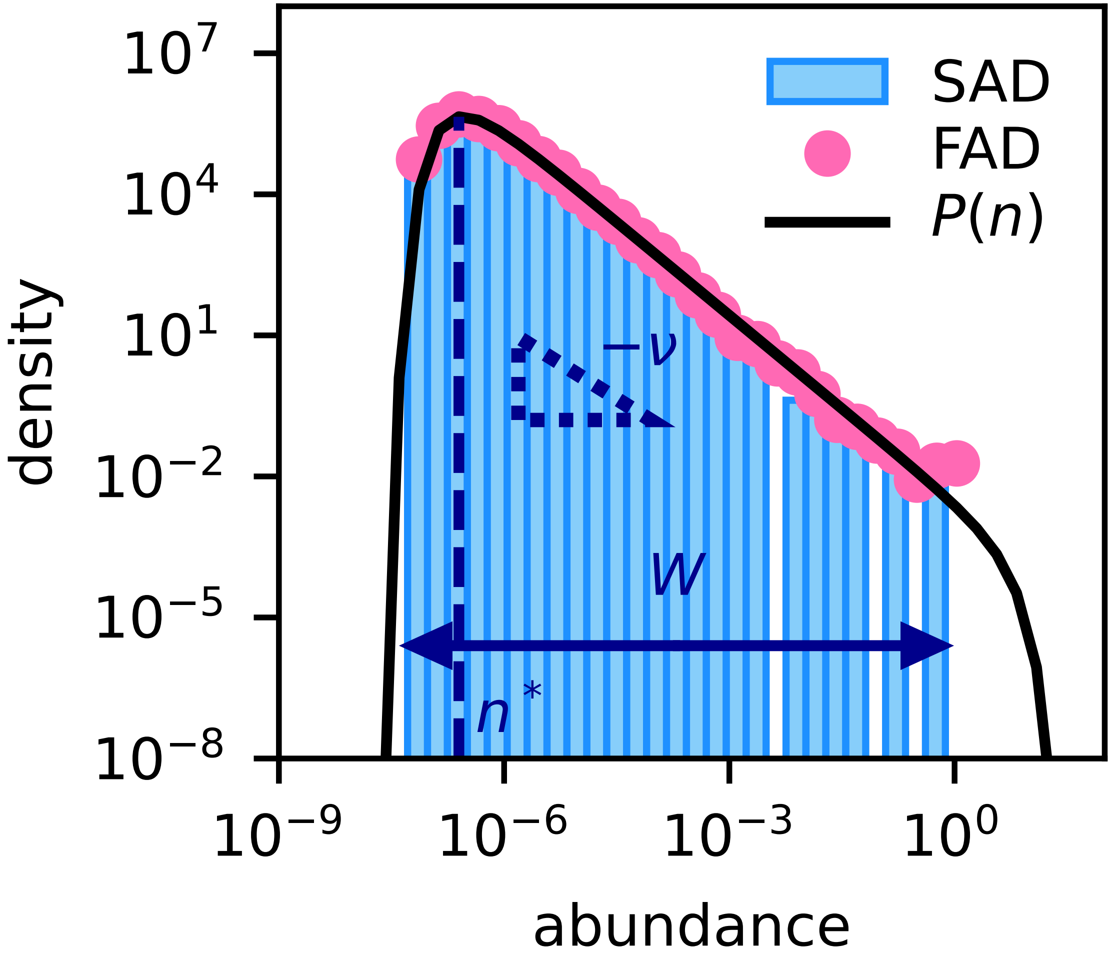
Martin-Platero et al.
High resolution time series reveals cohesive but short-lived communities in coastal plankton
Nature Communications (2018)

Single species have an intermittent dynamics



Distributions of species abundances

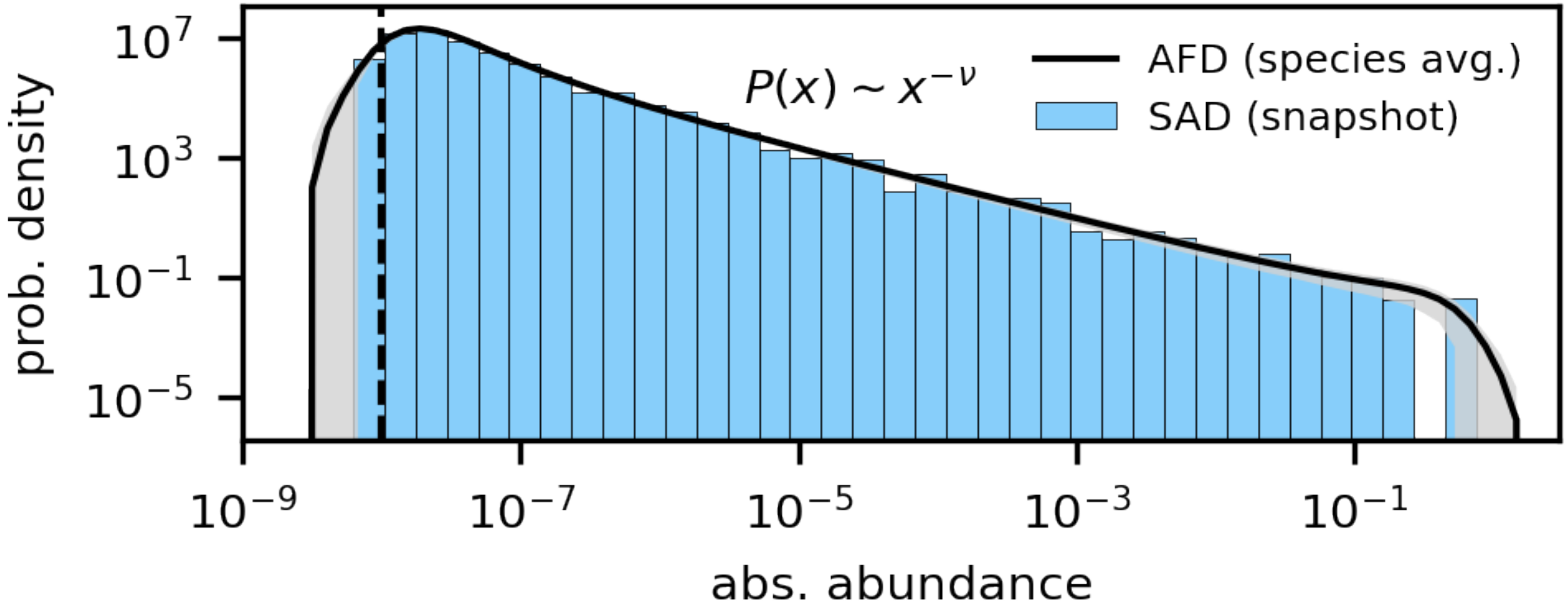




SAD: species abundance distribution (snapshot)

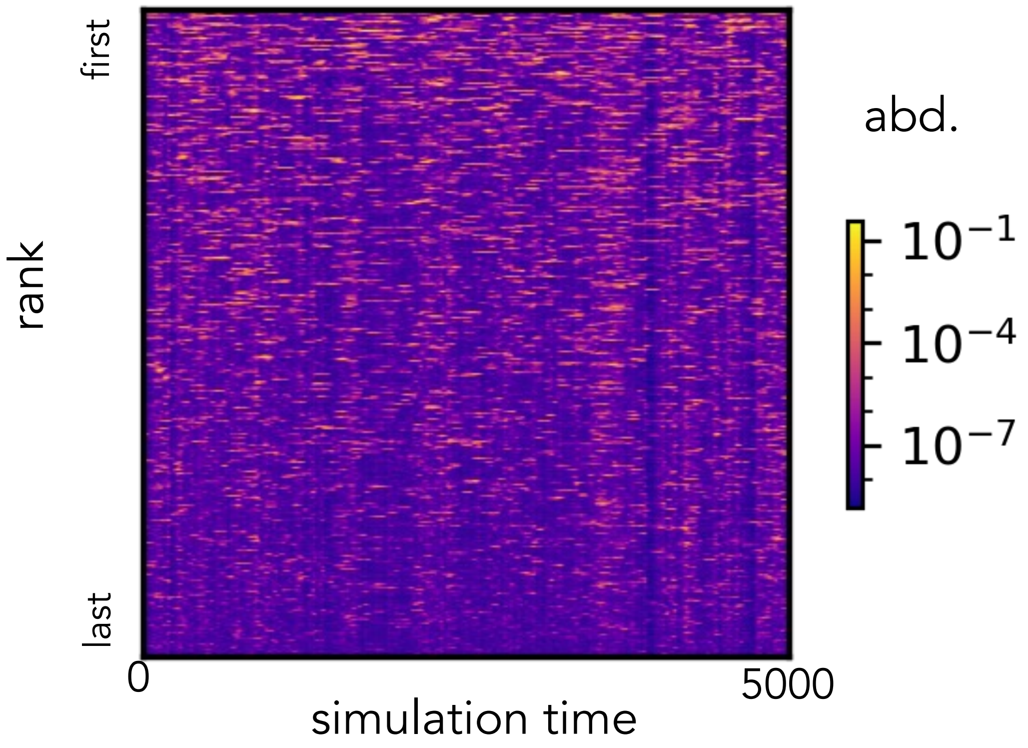
FAD: frequency abundance distribution

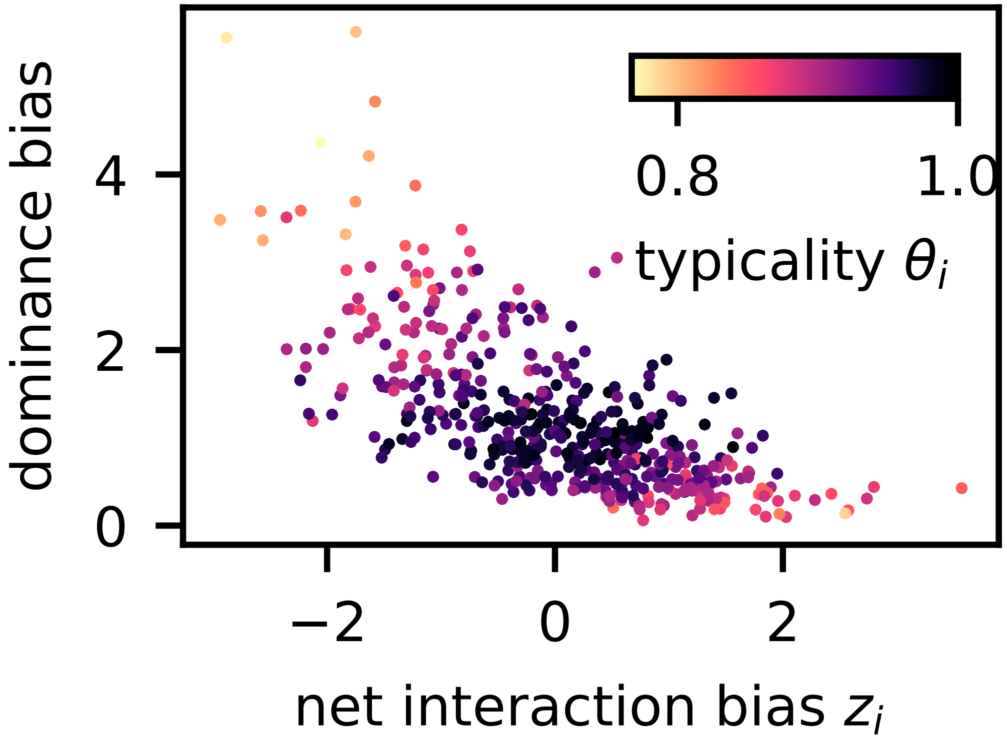
Power-law abundance distributions



Species are largely equivalent in their statistics

Differences between species





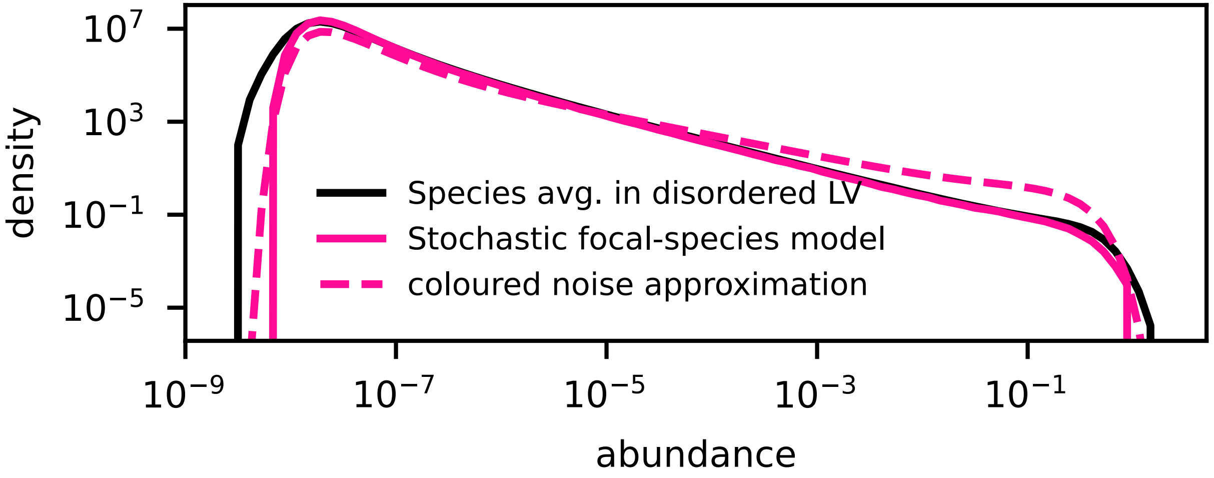
Species-species differences reflect relative rather than absolute interaction strengths

Effective ‘typical’ dynamics

‘Focal species’ model

$$\dot{x}(t) = x(t)\,(g(t) - x(t)) + \lambda$$

$$g(t) = -k + u\,\eta(t) \qquad \langle \eta \rangle = 0, \quad \langle \eta(t)\,\eta(t') \rangle = e^{-|t-t'|/\tau}$$



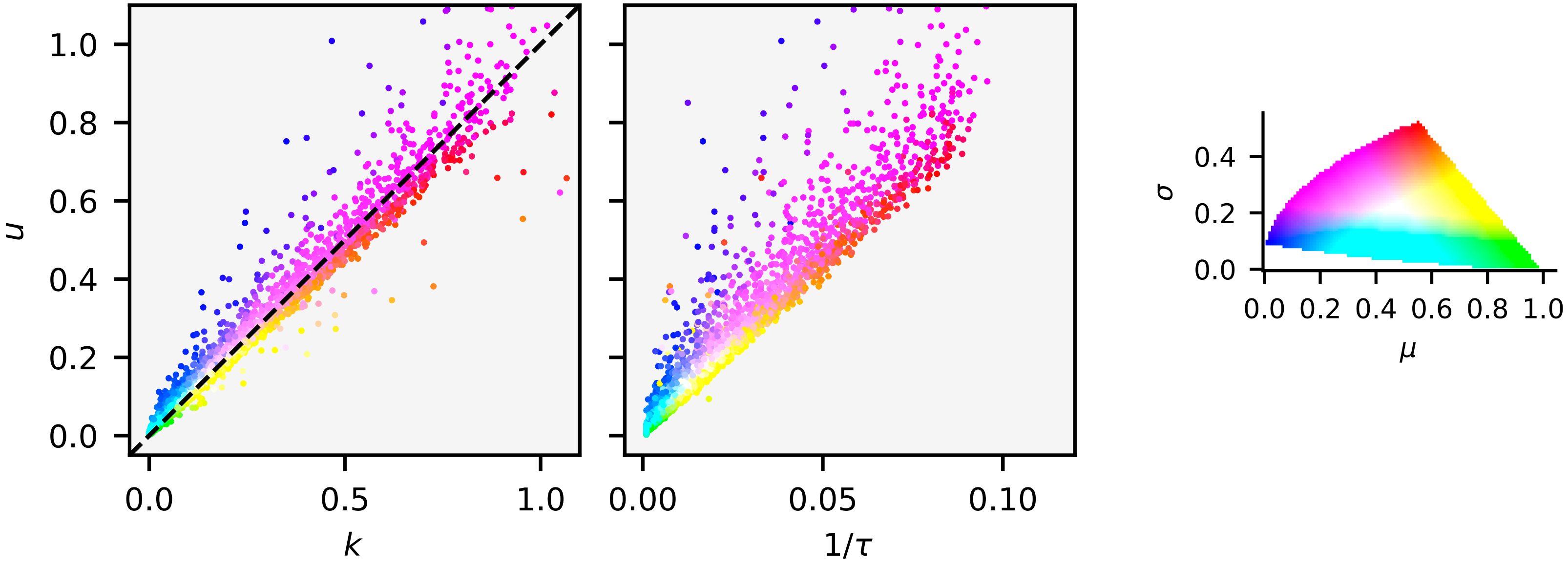
Effective neutrality of the species’ dynamics

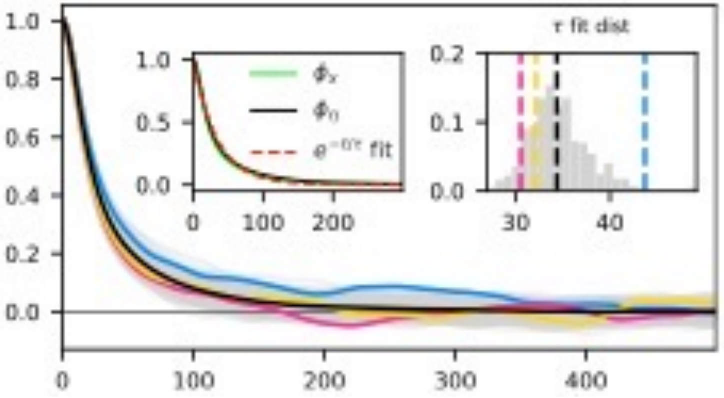
Community-level parameters and observables

$$k = \mu \overline{X} - 1$$

$$u = \sigma \frac{\overline{X}}{\sqrt{S_{\text{eff}}}}$$

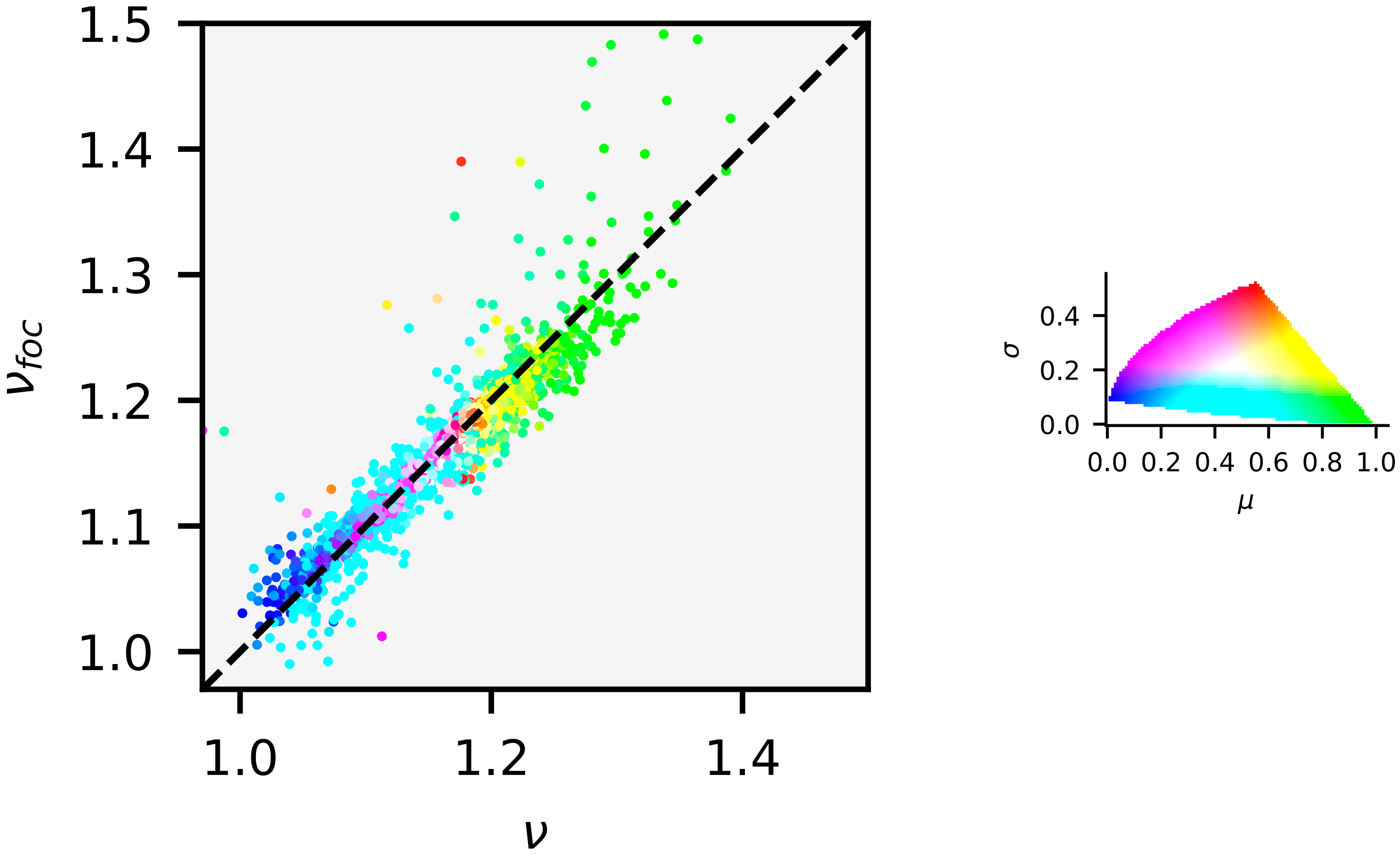
$$S_{\text{eff}}(t) := \frac{1}{\sum_i p_i^2(t)}$$





Power-law exponent

$$\nu = 1 + \frac{k}{u^2\tau}$$



Other single-species effective models

Other single-species models have been proposed to explain the behaviour of many-species GLV equations or to fit observational data

1. Dynamical Mean Field Theory (DMFT)/cavity method

Guy Bunin, Giulio Biroli, Ada Altieri, Tobias Galla, Heyjin Park, Matthieu Barbier

2. Stochastic Logistic Model (SLM)

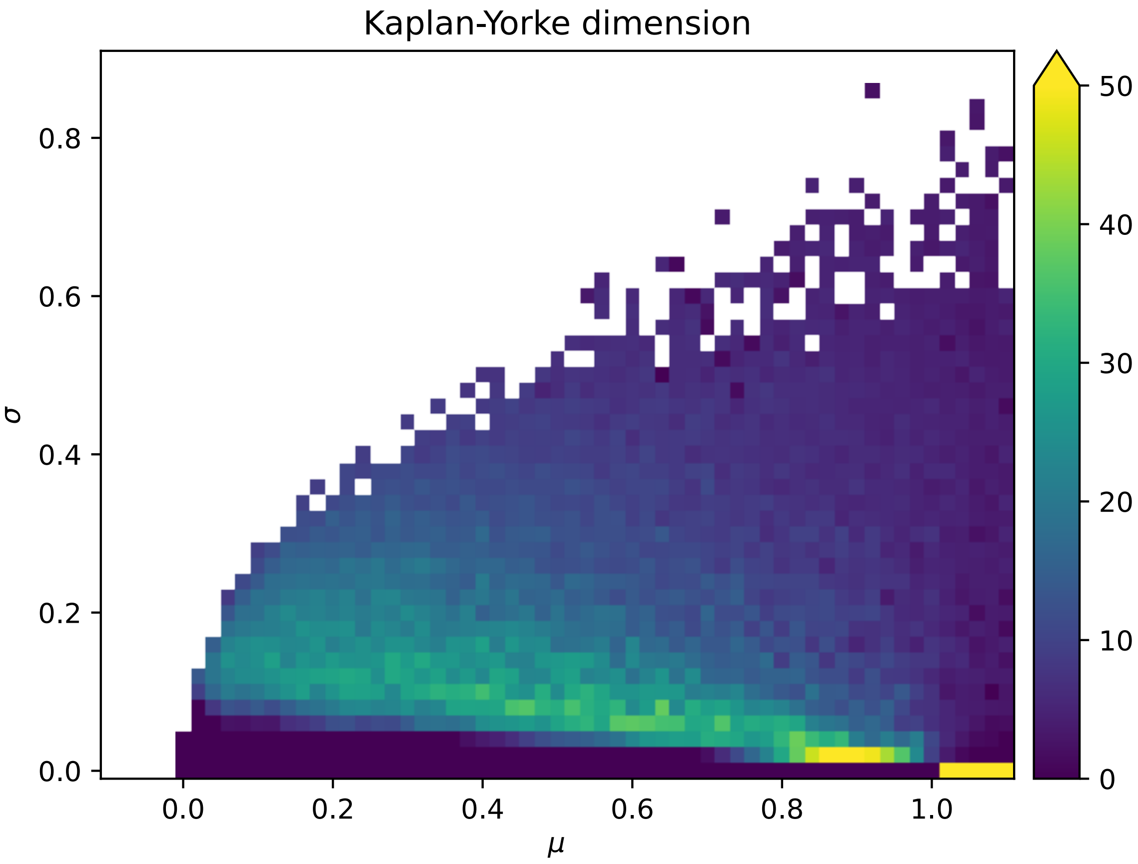
$$\frac{dx_i}{dt} = \frac{x_i}{\tau_i}\left(1 - \frac{x_i}{K_i}\right) + \sqrt{\frac{\sigma_i}{\tau_i}} x_i \xi_i(t)$$

$$\langle \xi_i(t) \xi_j(t') \rangle = \delta_{ij} \delta(t - t')$$

Jacopo Grilli
Macroecological laws describe variation and diversity in microbial communities
Nature Communications (2020)

here, growth rate fluctuations are uncorrelated and the equations are solved close to the equilibrium.

Dimensionality of the chaotic attractor



The chaotic attractor has generally small dimension and a small effective community size

$$S_{\text{eff}}(t) := \frac{1}{\sum_i p_i^2(t)}$$

that increases as interactions weaken

A small number of effective variables are important to describe the community dynamics

Conclusions on unstructured communities

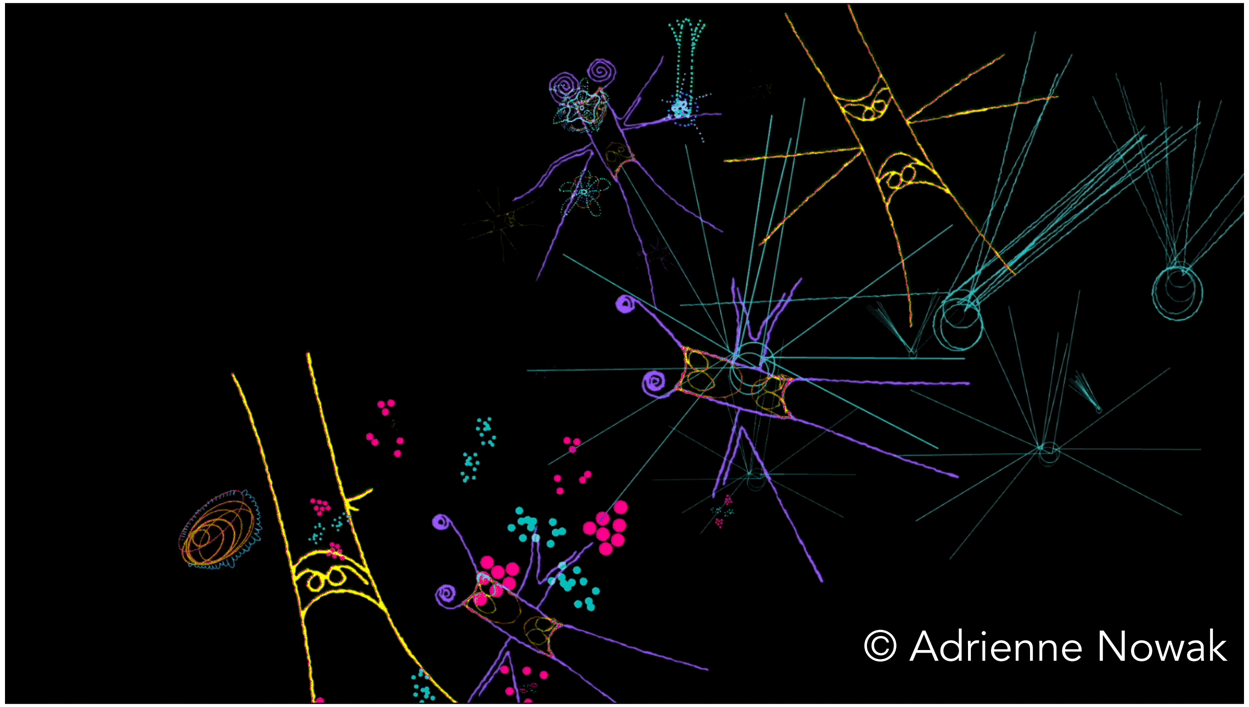
Strong competitive interactions drive exclusion on a short time scale.

In the presence of weak immigration, the community composition wanders between low-dimensional ‘cliques’, and abundant and rare species turn over.

This effectively neutral (*species-symmetric*) behaviour underpins a power-law trend in the rare species’ distribution

The effective dynamics of any species is well approximated by a ‘focal species’ model with a decay trend and correlated effective fluctuations.

E. Mallmin, A. Traulsen, SDM
Chaotic turnover of rare and abundant species in a strongly interacting model community
PNAS (2024)



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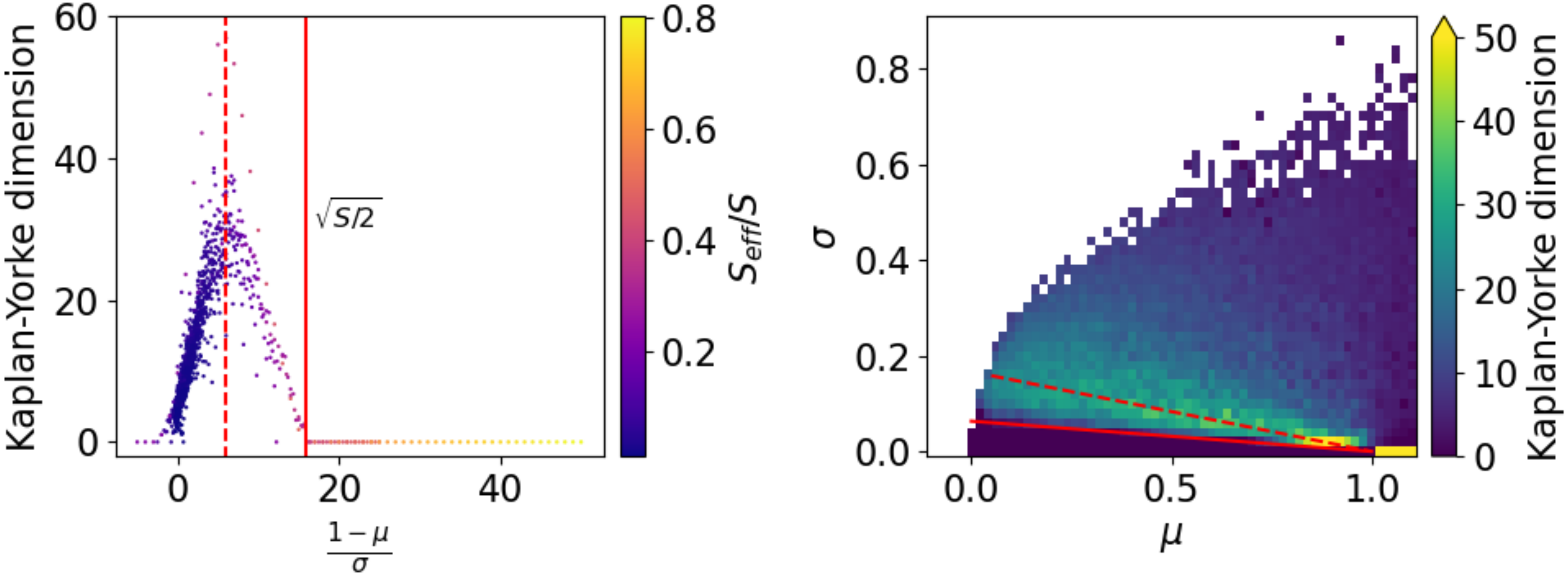
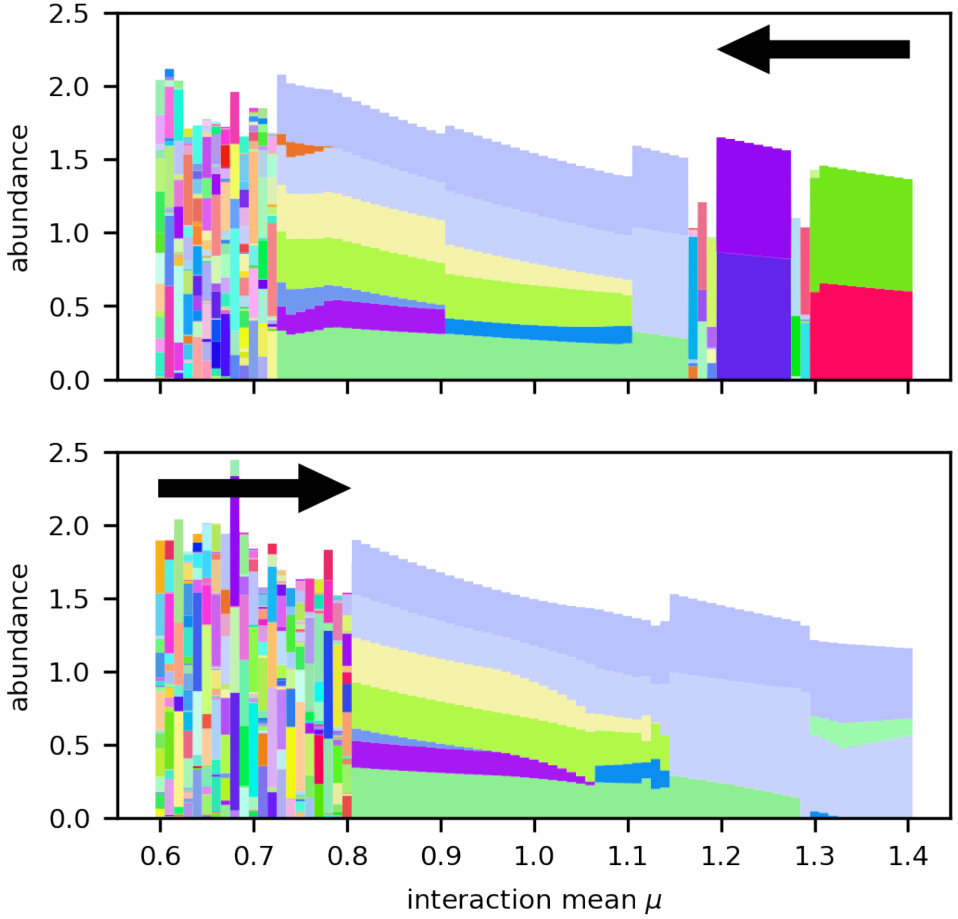
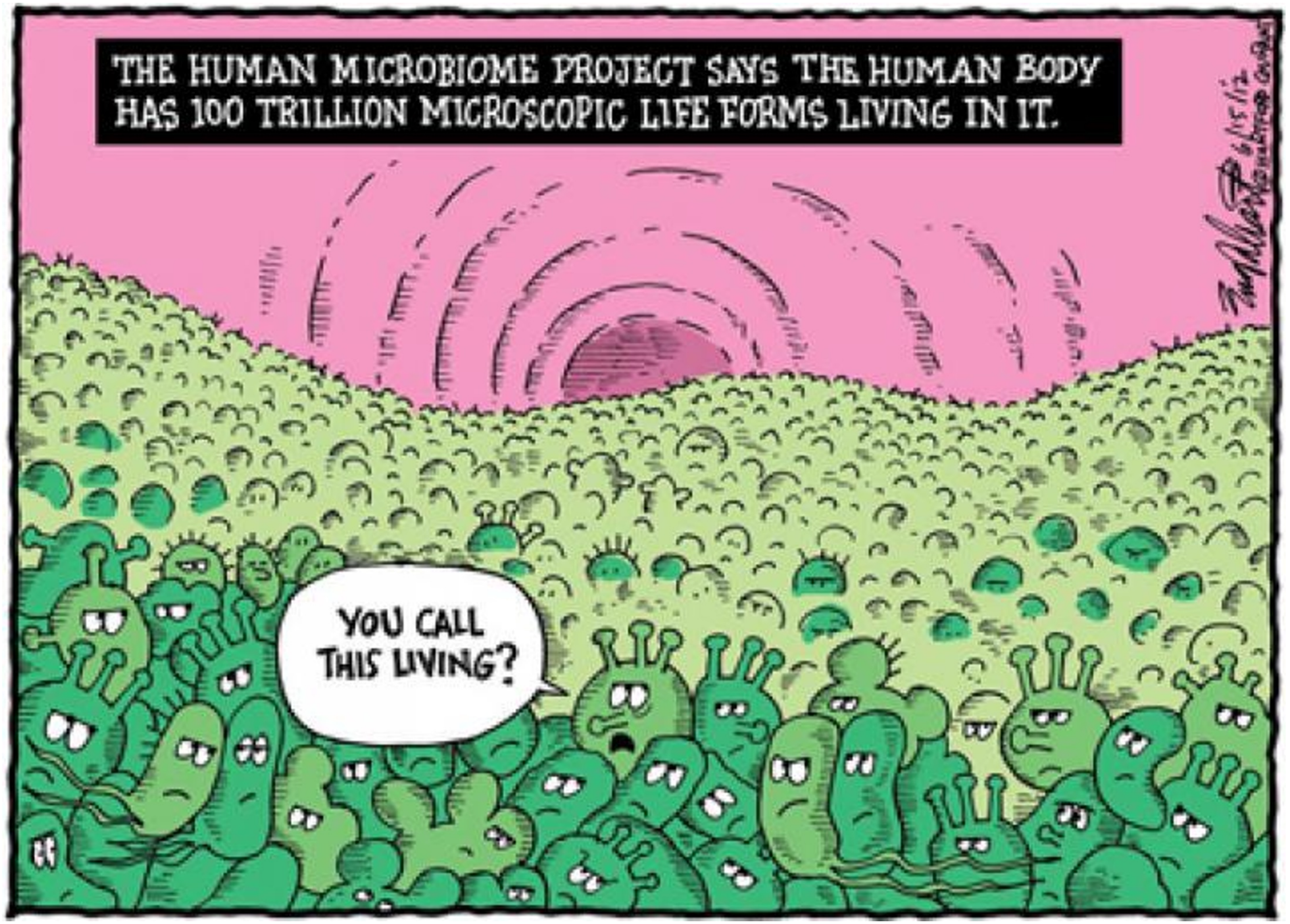
https://iscpif.fr/artex23-prize/

Scaling of attractor dimension

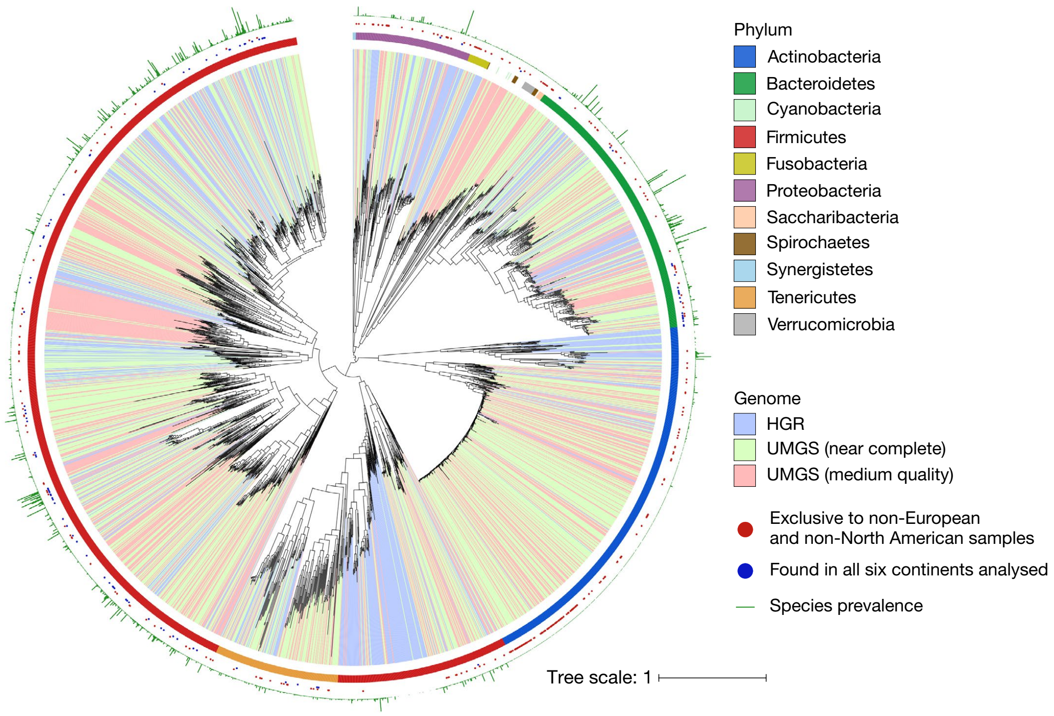


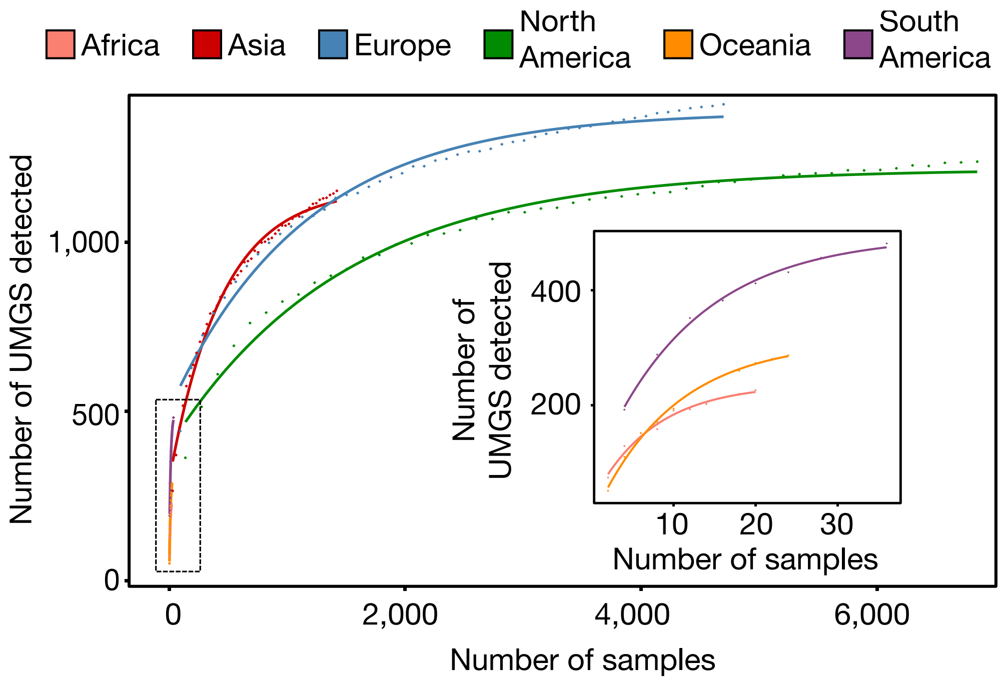

2.5
2.0
1.5
1.0
0.5
0.0
abundance
2.5
2.0
1.5
1.0
0.5
0.0
abundance
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
interaction mean μ

The microbiome



Microbial ‘species’ in the human gut

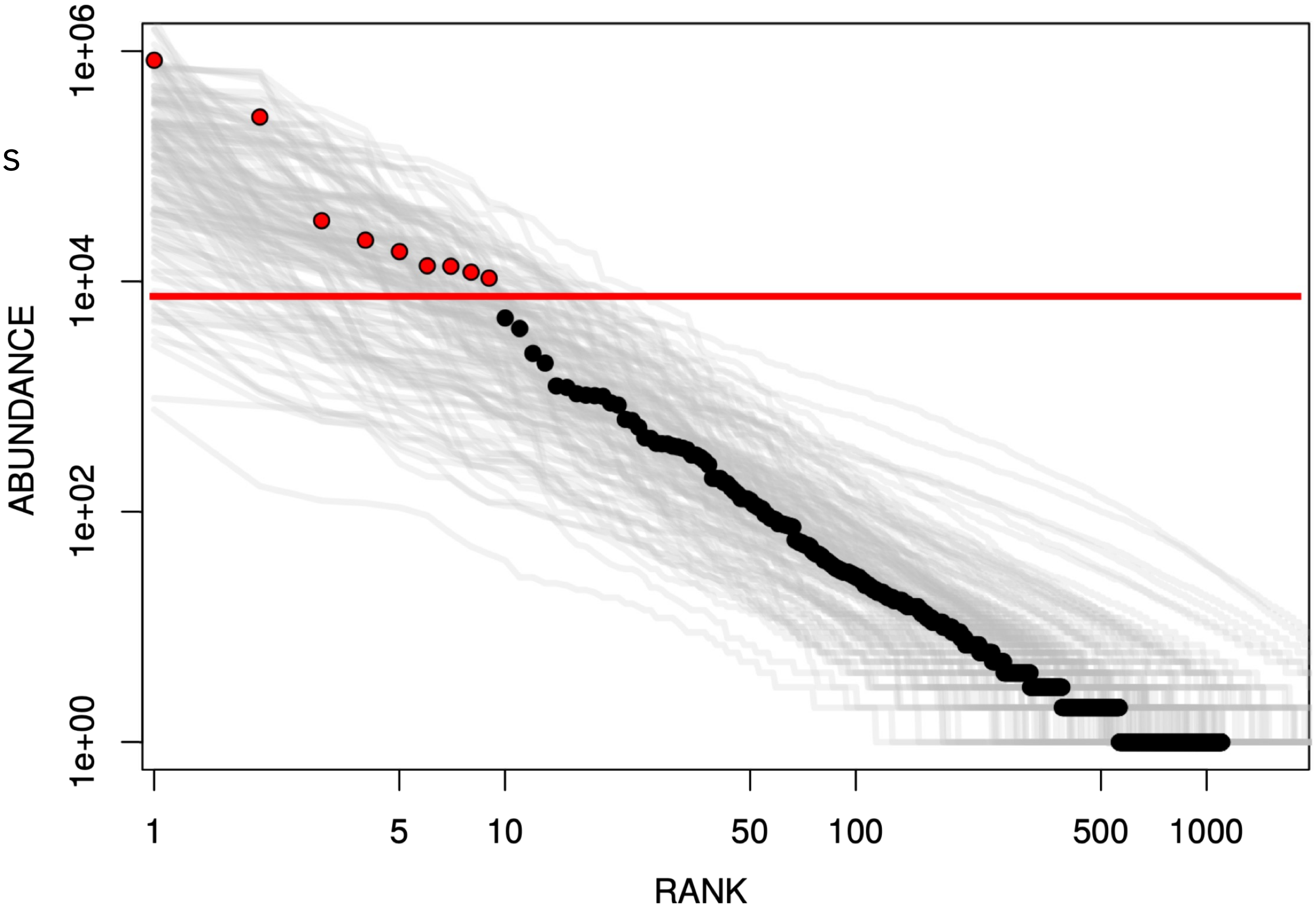




Almeida et al.
A new genomic blueprint of the human gut microbiota
Nature 2019

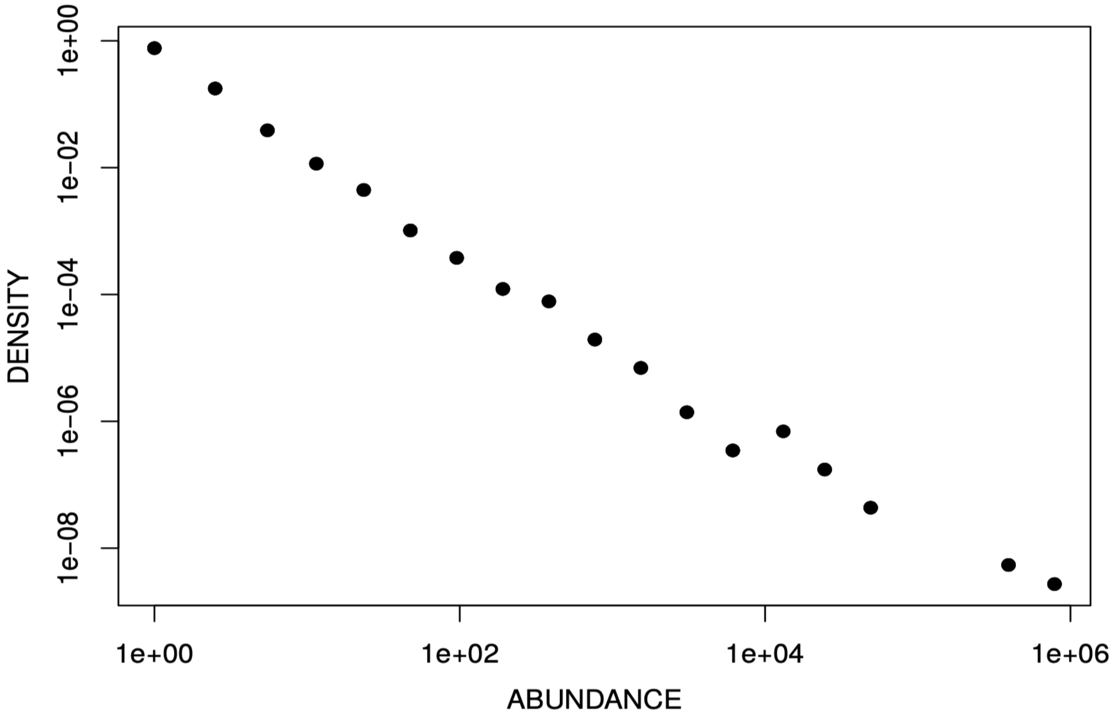
OTUs' rank abundance plots

Dominant species
Idiosyncratic abundances

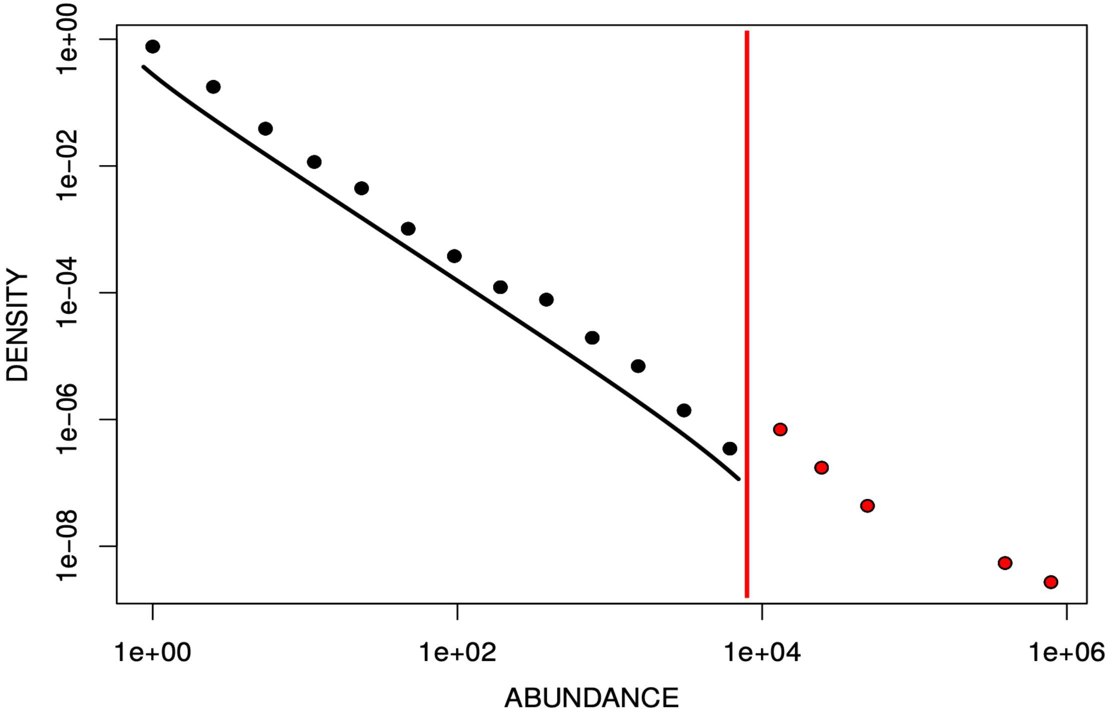


Rare species
Similar decay

For every sample: Species Abundance Distribution



Adaptive fit: distinguish rare and abundant



‘rare’

‘abundant’

A semi-neutral model

Birth & death rates $\begin{cases} b_n = b\,n + \chi \\ d_n = d\,n + \mu \end{cases}$

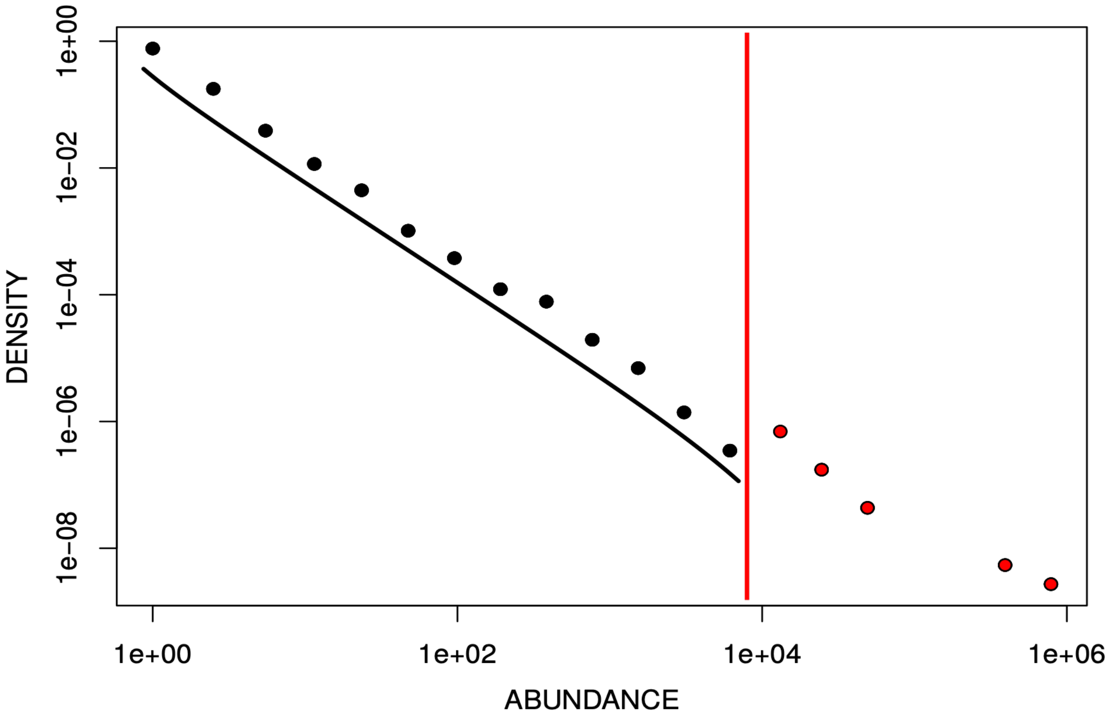
Negative binomial beta distribution:

$$< \phi_n >= \theta \frac{\Gamma(n+\alpha)\Gamma(1+\beta)}{\Gamma(\alpha)\Gamma(n+\beta+1)} e^{-rn}$$

$$\alpha = \frac{\chi}{b} \qquad \beta = \frac{\mu}{d} \qquad r = \frac{b}{d}$$

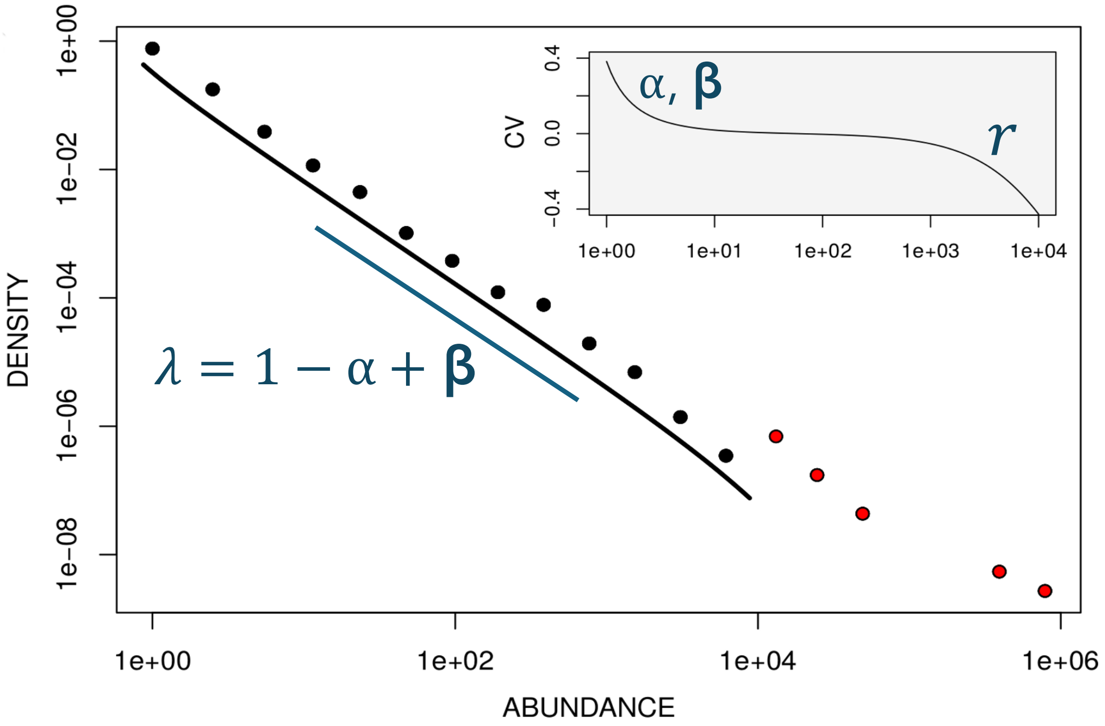
Engen 1978, He 2005

Fitting the distribution



Fit the three parameters r α β

Power-law exponent

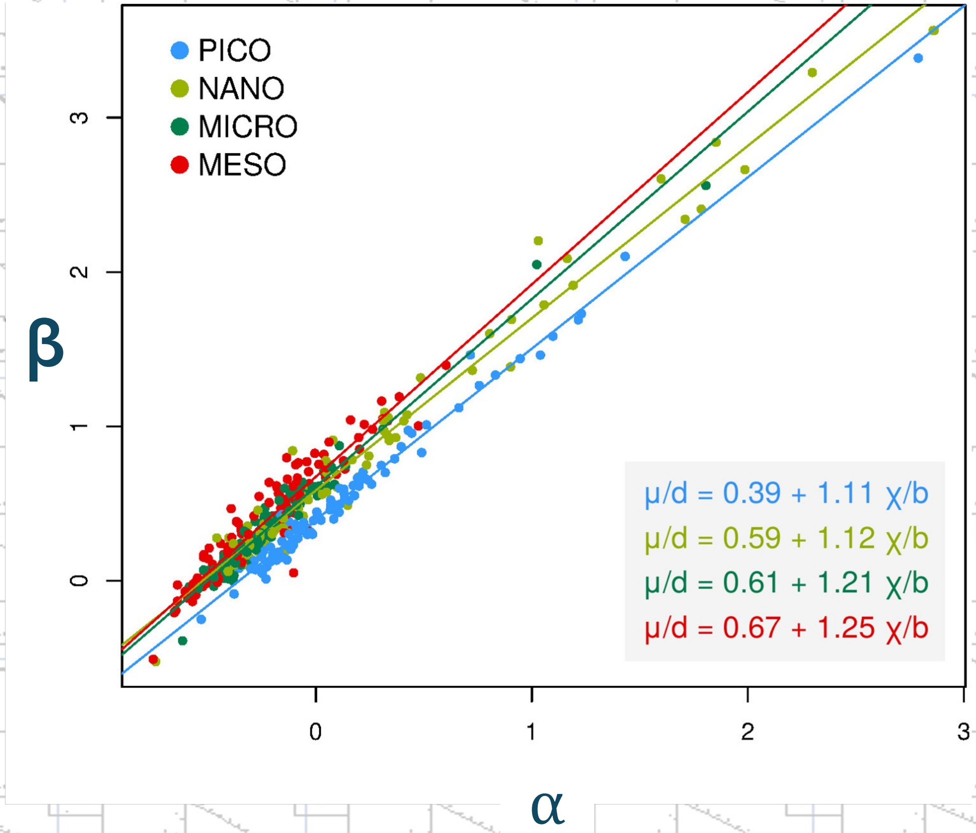


Negative binomial beta distribution:

$$< \phi_n >= \theta \frac{\Gamma(n+\alpha)\Gamma(1+\beta)}{\Gamma(\alpha)\Gamma(n+\beta+1)} e^{-rn} \quad \sim \quad e^{-rn} n^{-\lambda}$$

Engen 1978, He 2005

How much do parameters differ?



372 out of 388 samples fitted by the negative binomial beta distribution

The ‘rare’ component comprises more than 99% of OTUs

‘Demographic’ parameters are different from site to site

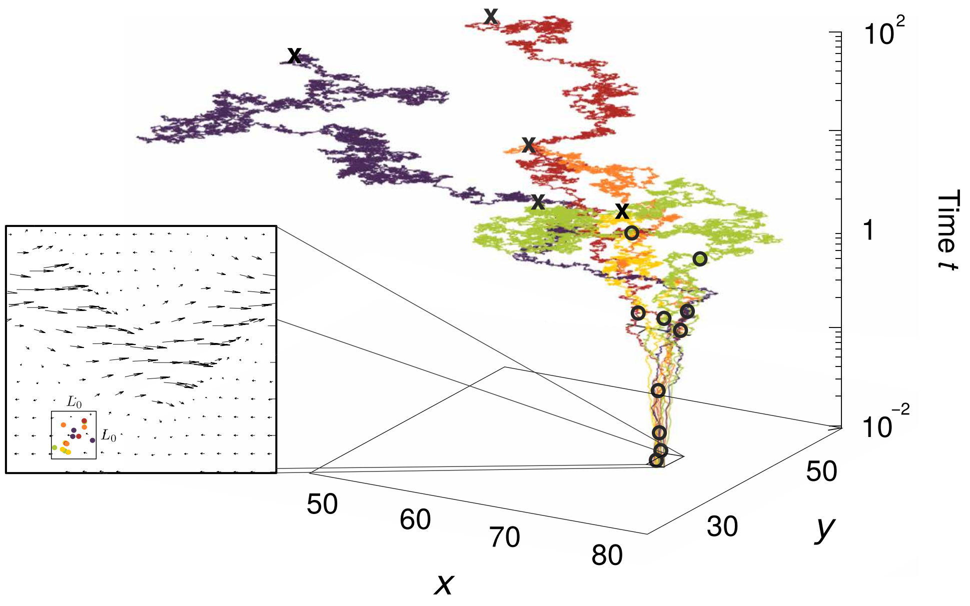
Linear per capita birth comparable to death everywhere

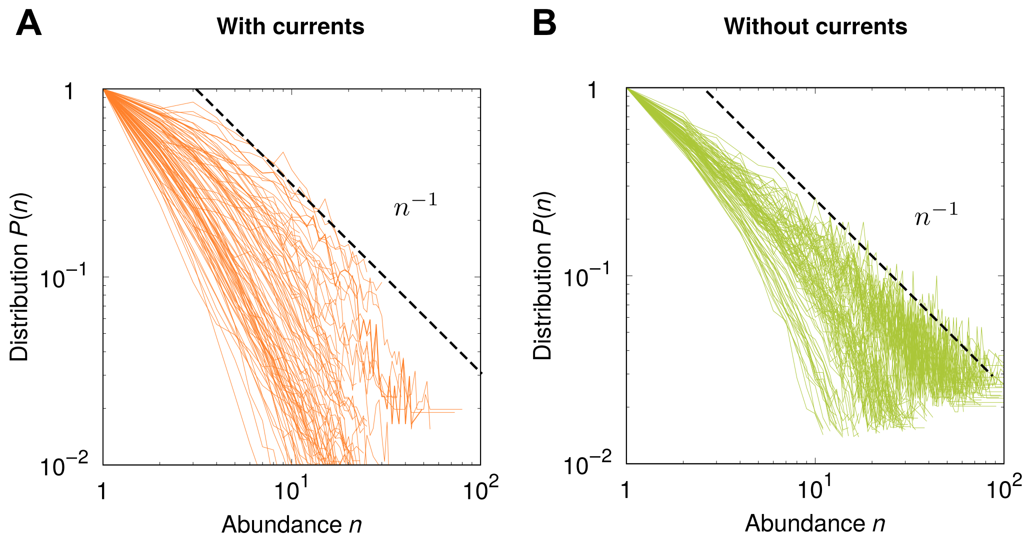
Density-dependent birth and death rates mostly positive

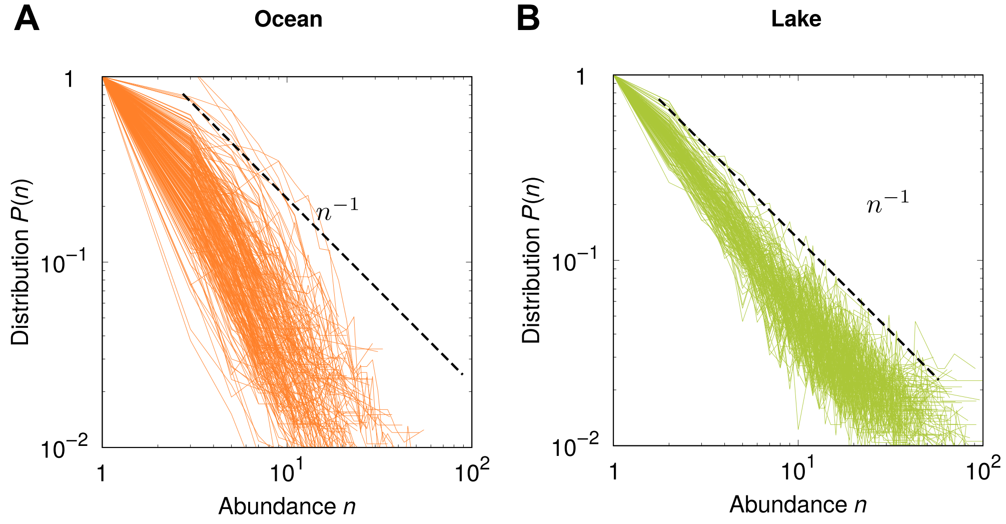
Small but significant variation with size class: abundance decay is slower in smaller organisms

No systematic correlation with environmental variables

The role of transport in abundance distributions

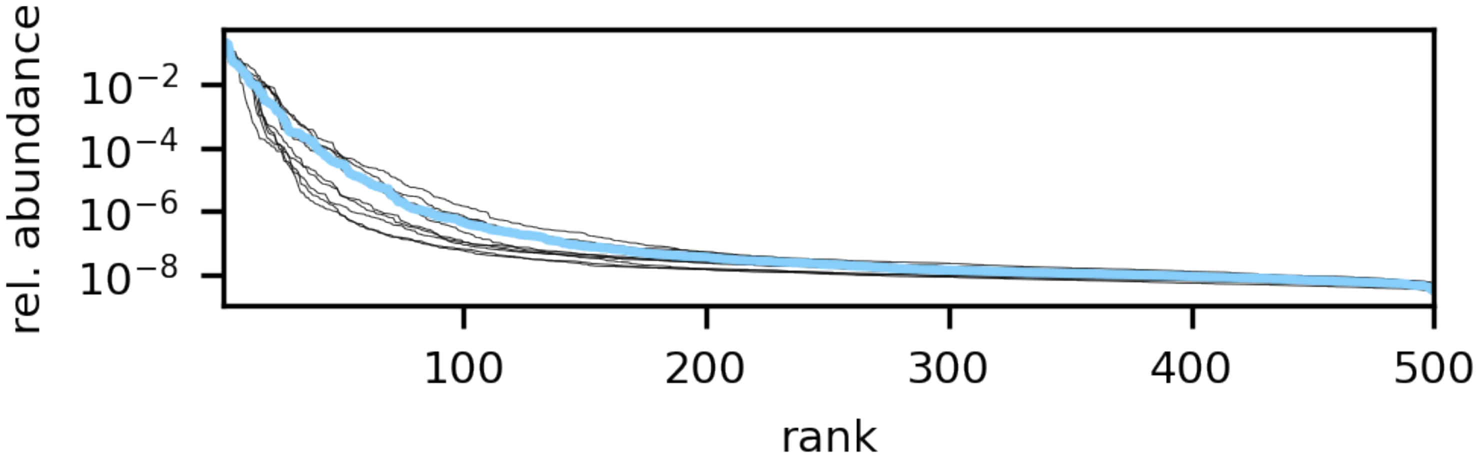




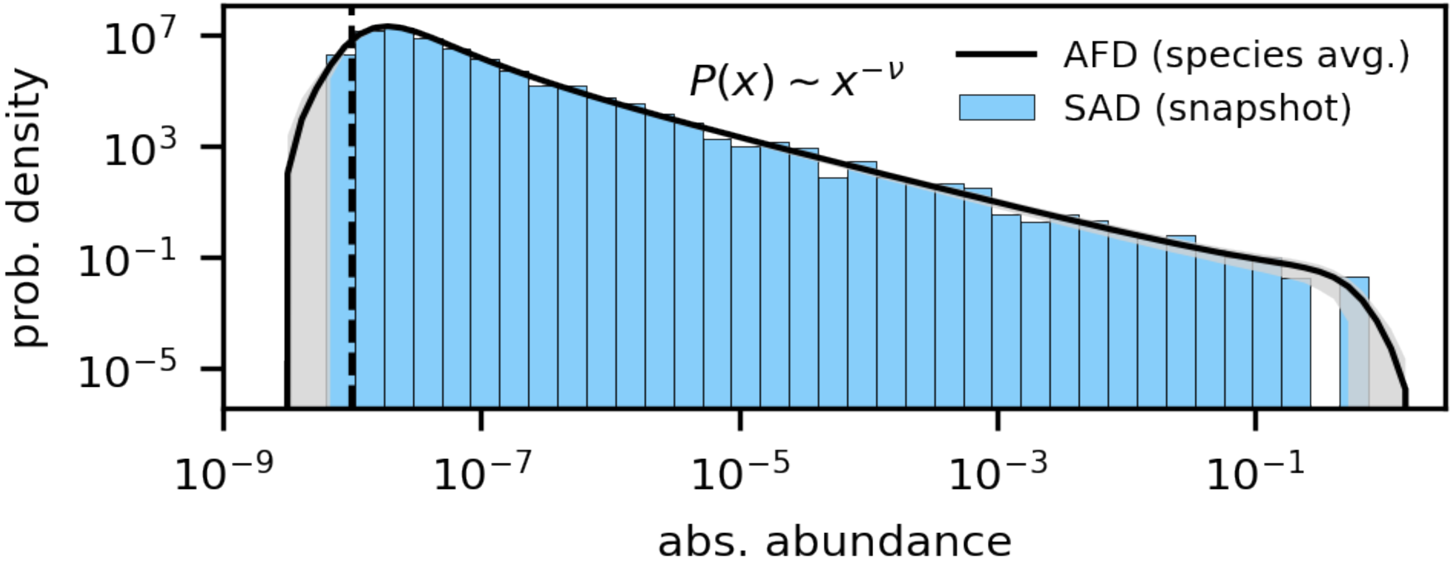


Villa-Martini et al.
Ocean currents promote rare species diversity in protists
Science Advances 2020

Species abundance distributions



In the **chaotic phase**, rank-abundance plots change slightly in time



Species abundance distributions at any time largely overlap with the frequency in time of abundance of any single species (Abundance Frequency Distribution).
$\Longrightarrow$ effective species equivalence

Focal-species model

An approximate, one-species model accounts for this ‘typical’ behaviour

$$\dot{x}(t) = x(t)\,(\mathrm{g}(t) - x(t)) + \lambda$$
$$\mathrm{g}(t) = -k + u\,\eta(t)$$

provided fluctuations in growth rate are chosen as a coloured noise:

$$\langle \eta \rangle = 0, \quad \langle \eta(t)\,\eta(t') \rangle = e^{-|t-t'|/\tau}$$

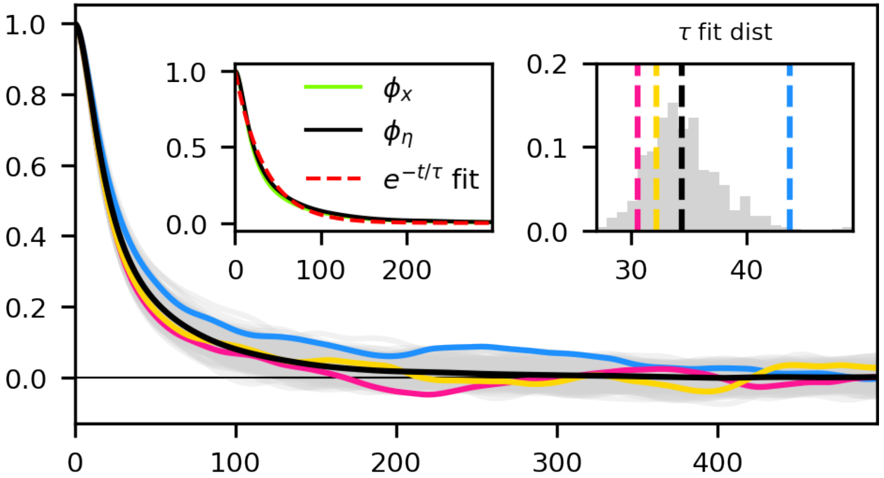
and the parameters k, u, and τ depend on the system’s parameters.

Estimating community-level parameters

Changing the interaction statistics μ and σ therefore affects the features of the effective noise.

It is not possible to solve the equations self-consistently (as in DMFT), but the effective noise parameters can be estimated starting from *community-level observables* derived from the time series: the time-average of the total abundance and of the effective community size:

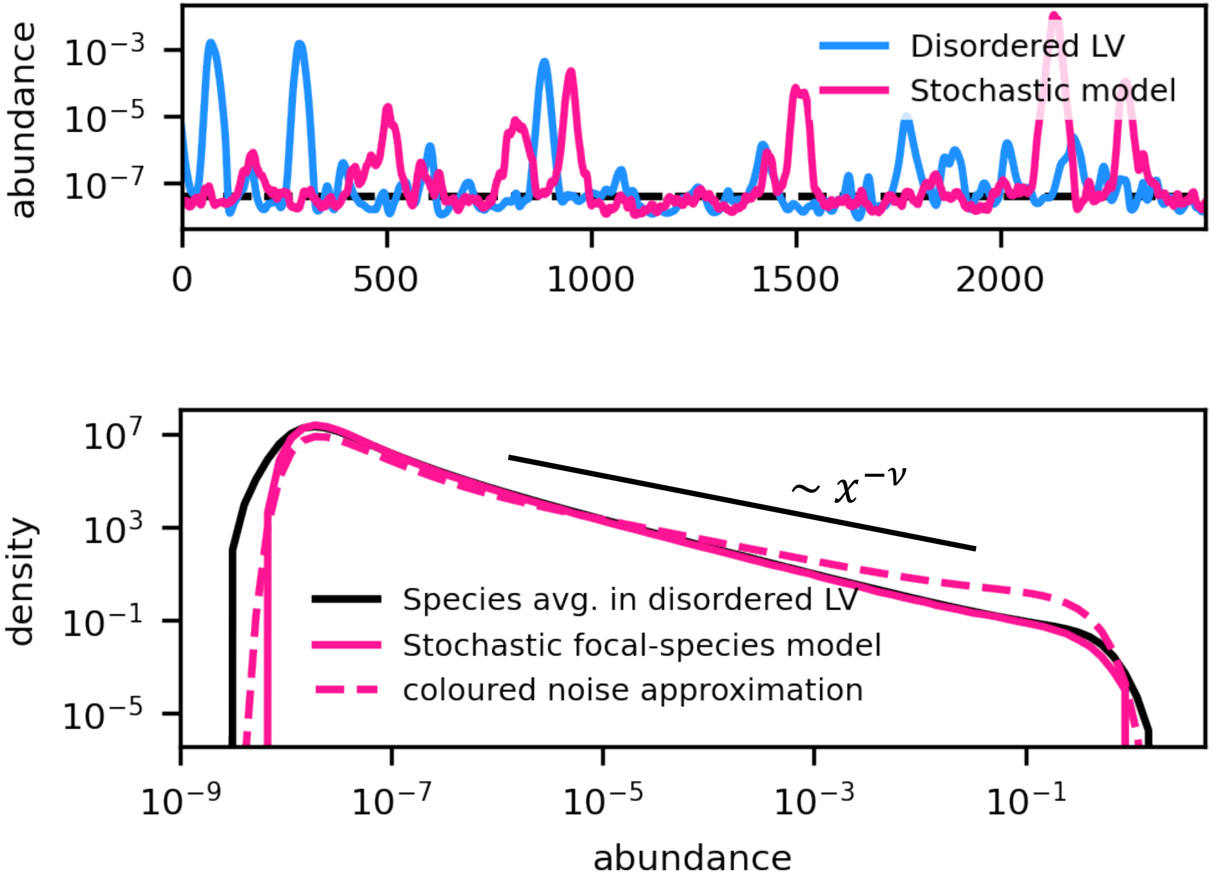
$$k = \mu\overline{X} - 1 \qquad u = \sigma\frac{\overline{X}}{\sqrt{\overline{S}_{\text{eff}}}}$$



The time scale τ corresponds to the autocorrelation of total abundance, which also sets the time scale of ecological turnover

Focal-species vs dGLV models

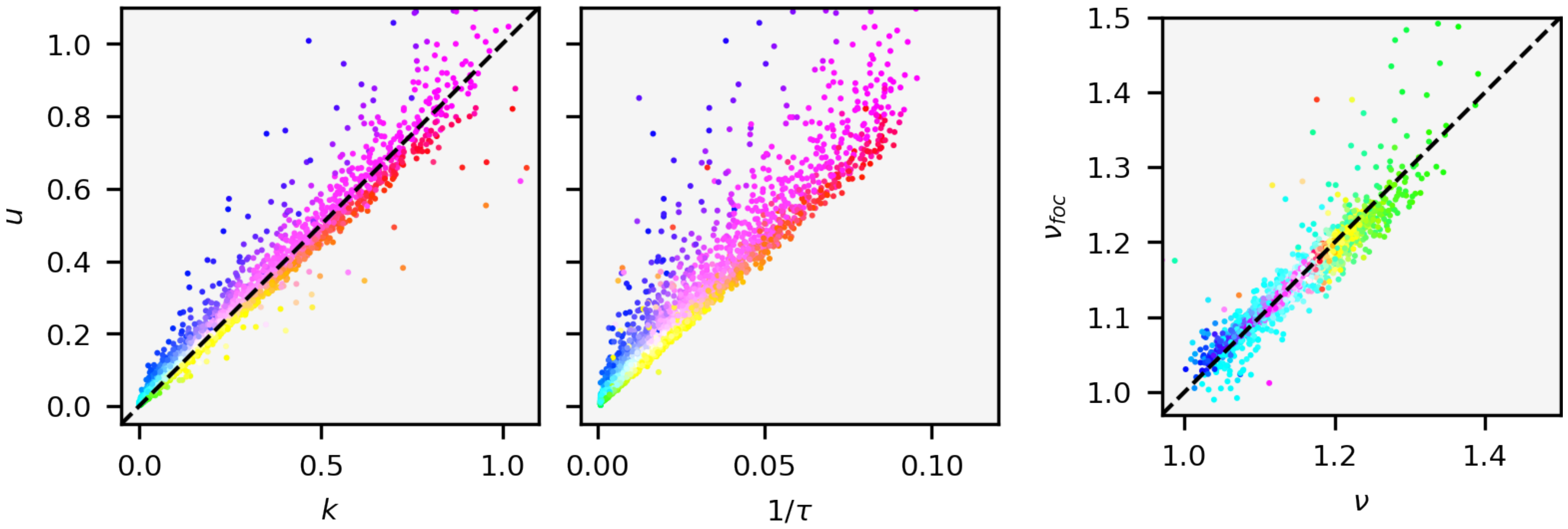
Compare the full system (deterministic, S-dimensional) and of the focal species model (stochastic, one-dimensional)



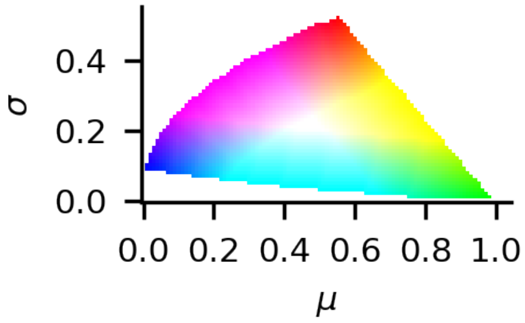
The focal species model can be solved in the limit where turnover time is small or large (unified colours noise approximation), which yields an analytical expression for the slope of the power-law trend

$$\nu = 1 + \frac{k}{u^2\tau}$$

Variation of community-level parameters



Color legend
of chaotic phase



Emergent relationships between community-level parameters result in a small variation of the power-law exponent in the whole chaotic region.

Other single-species effective models

Other single-species models have been proposed to explain the behaviour of many-species GLV equations or to fit observational data

1. Dynamical Mean Field Theory (DMFT)

2. Stochastic Logistic Model (SLM)

$$\frac{dx_i}{dt} = \frac{x_i}{\tau_i}\left(1 - \frac{x_i}{K_i}\right) + \sqrt{\frac{\sigma_i}{\tau_i}} x_i \xi_i(t)$$

$$\langle \xi_i(t) \xi_j(t') \rangle = \delta_{ij} \delta(t - t')$$

Jacopo Grilli
Macroecological laws describe variation and diversity in microbial communities
Nature Communications (2020)

here, growth rate fluctuations are uncorrelated and the equations are solved close to the equilibrium.