

Ubiquitous abundance decay in the rare biosphere of marine plankton

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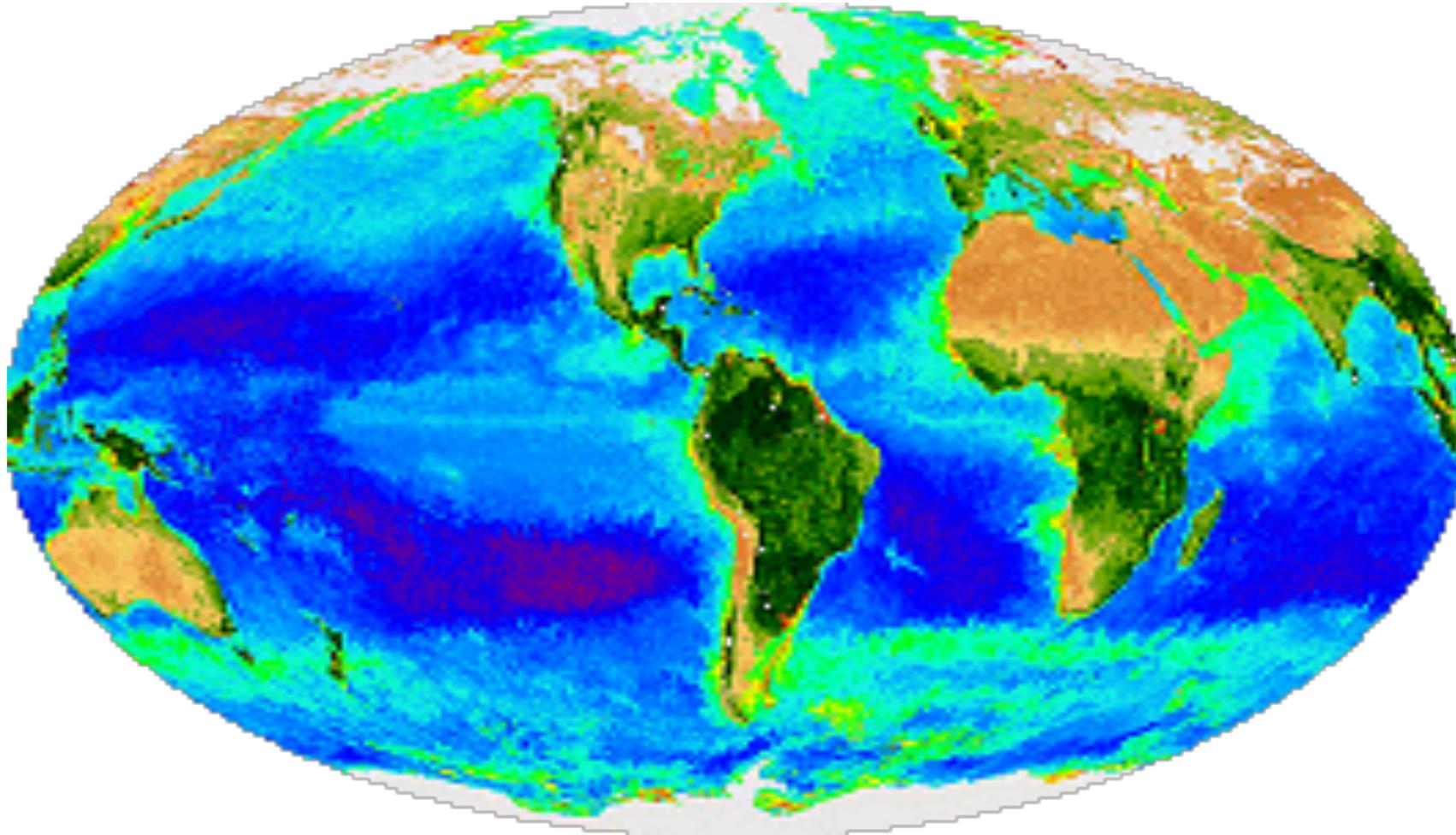
Colomba de Vargas, Roscoff, France

Eric Karsenti, EMBL, Heidelberg, Germany & IBENS, Paris, France

Chris Bowler, IBENS, Paris

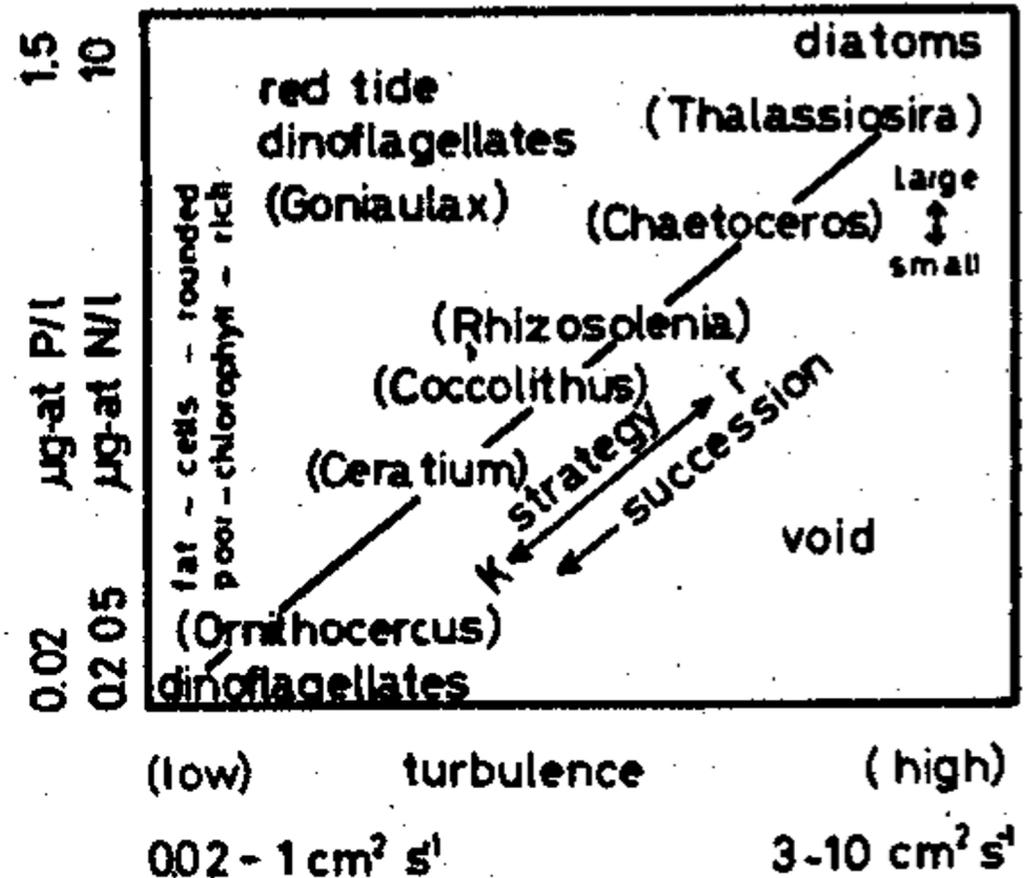
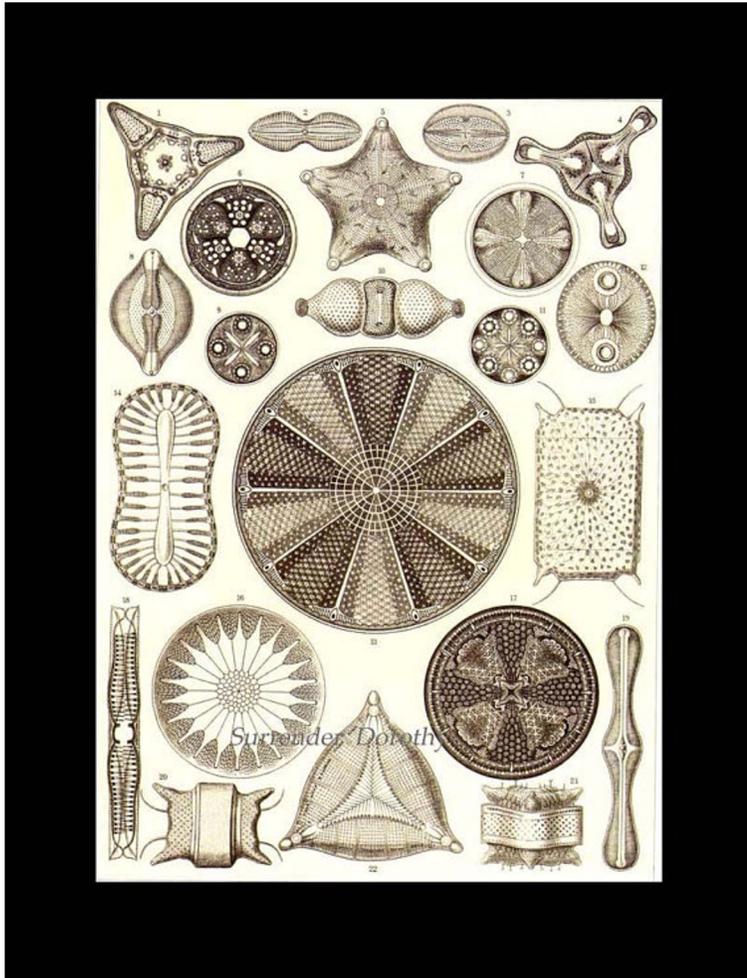
Rencontre de La chaire MMB, March 12, 2020

Marine plankton communities in a dynamic seascape



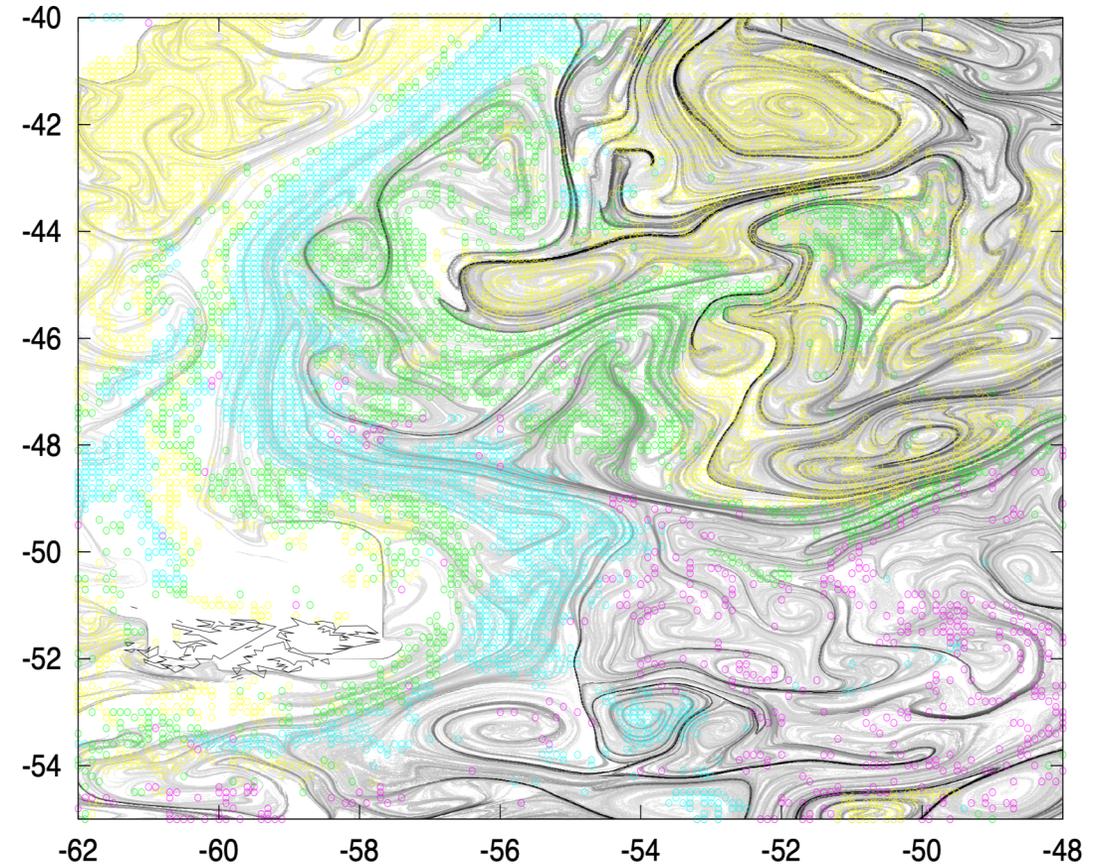
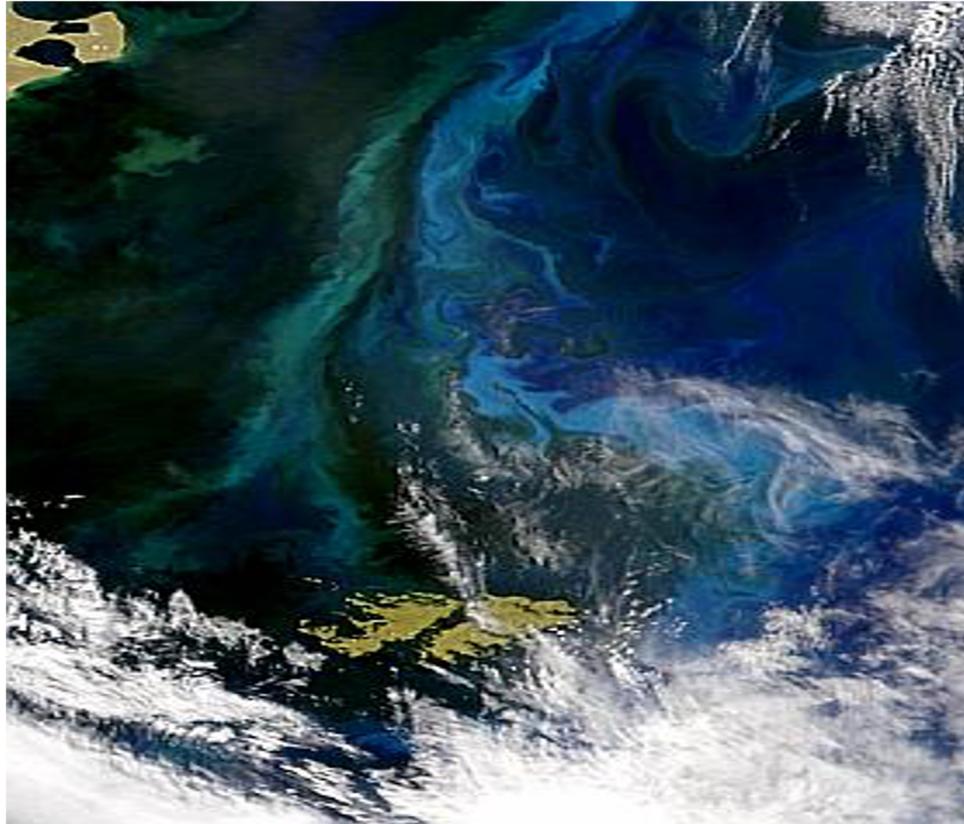
SeaWiFS ocean color data: Chlorophyll concentration

Plankton diversity and physical forcings



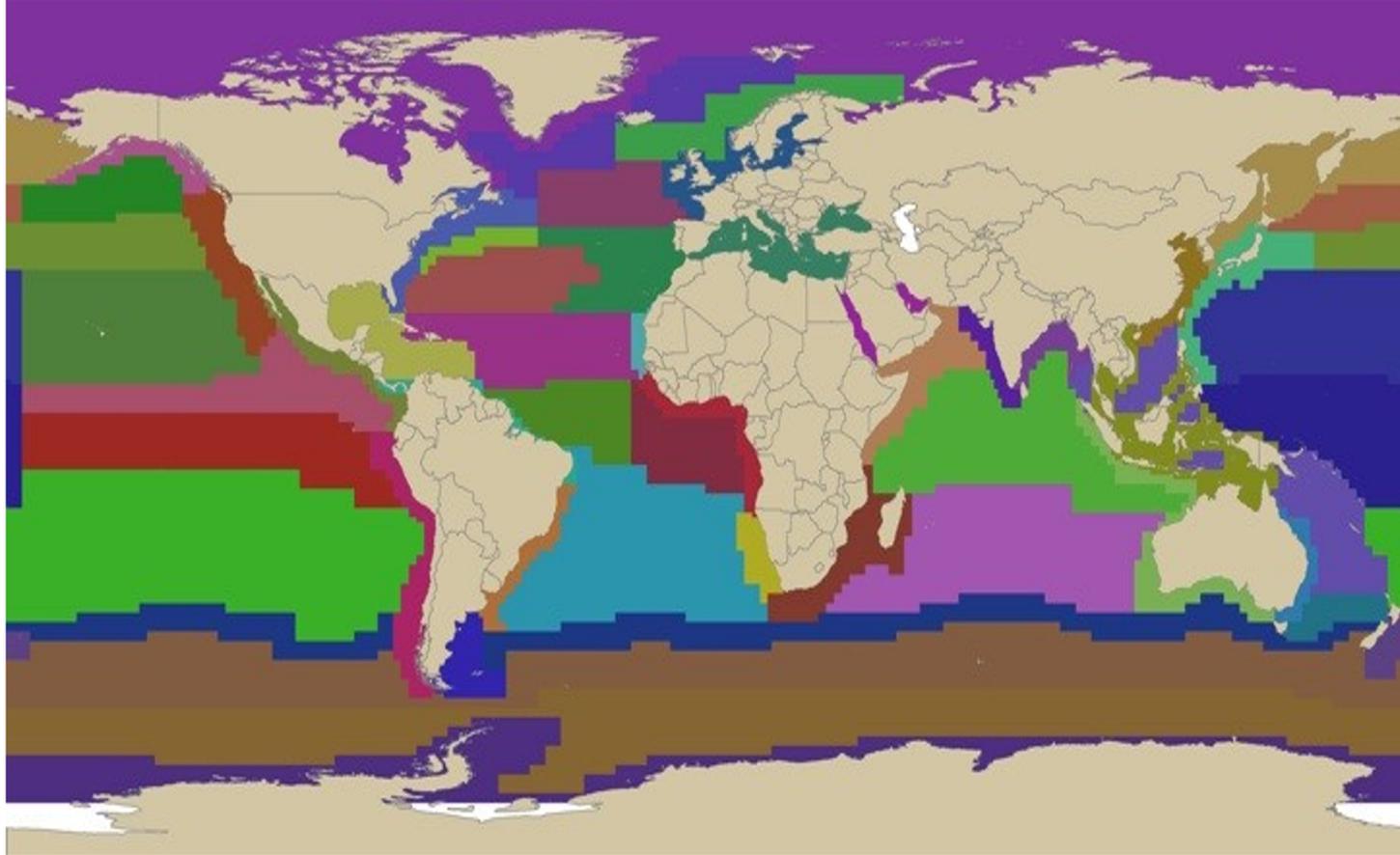
Life-Forms of Phytoplankton As Survival Alternatives in An Unstable Environment
Ramon Margalef, Oceanologica Acta (1978)

Mesoscale variability of plankton communities



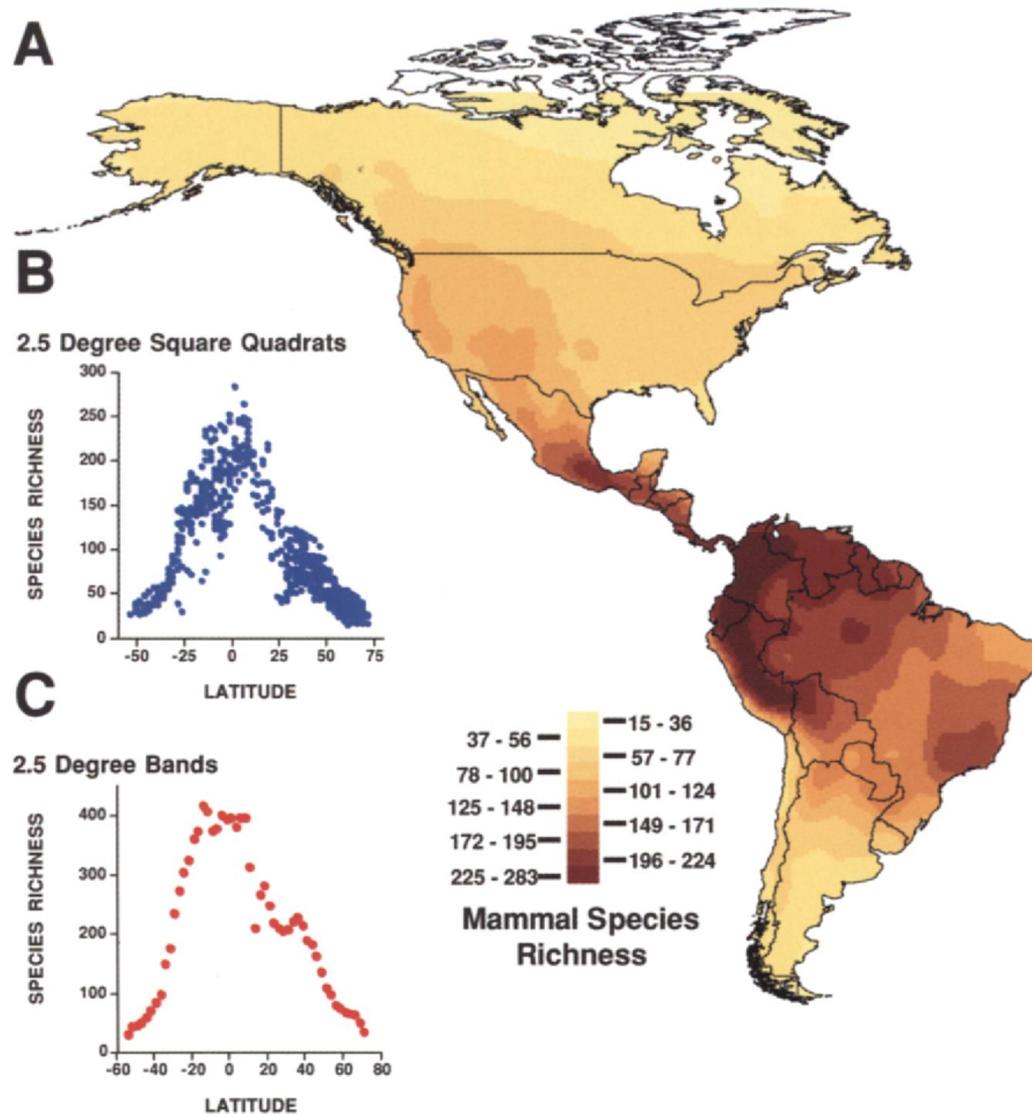
Fluid dynamical niches of phytoplankton types
D'Ovidio, De Monte et al. PNAS 2010

Marine biogeography

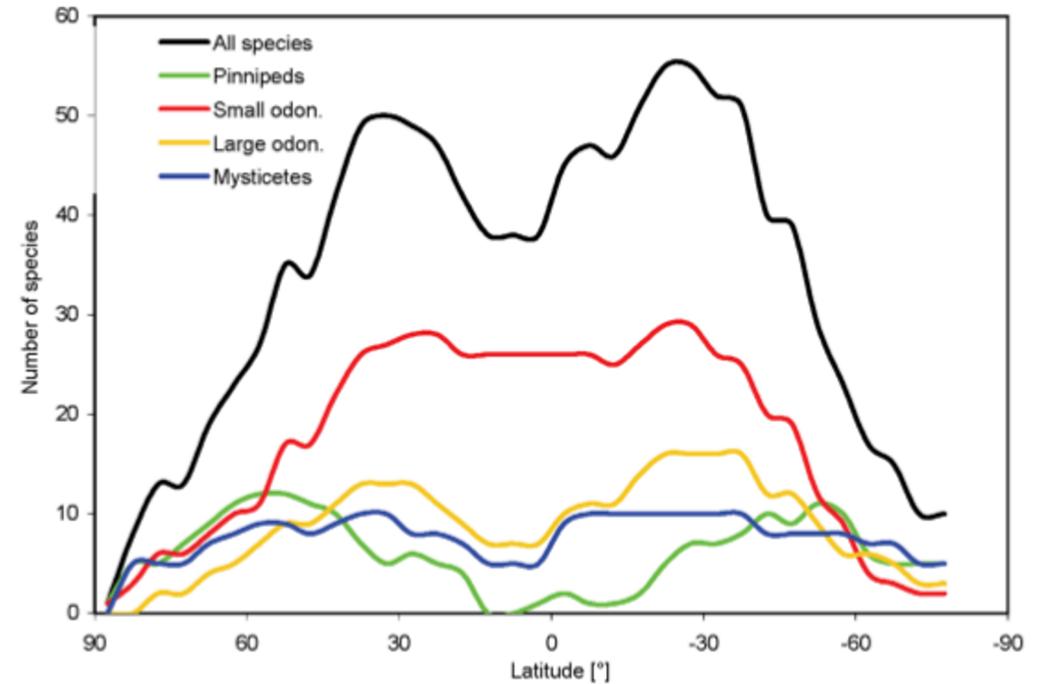


Ecological Geography of the Sea
Alan Longhurst, Academic Press (1998)

Macroecological patterns of diversity

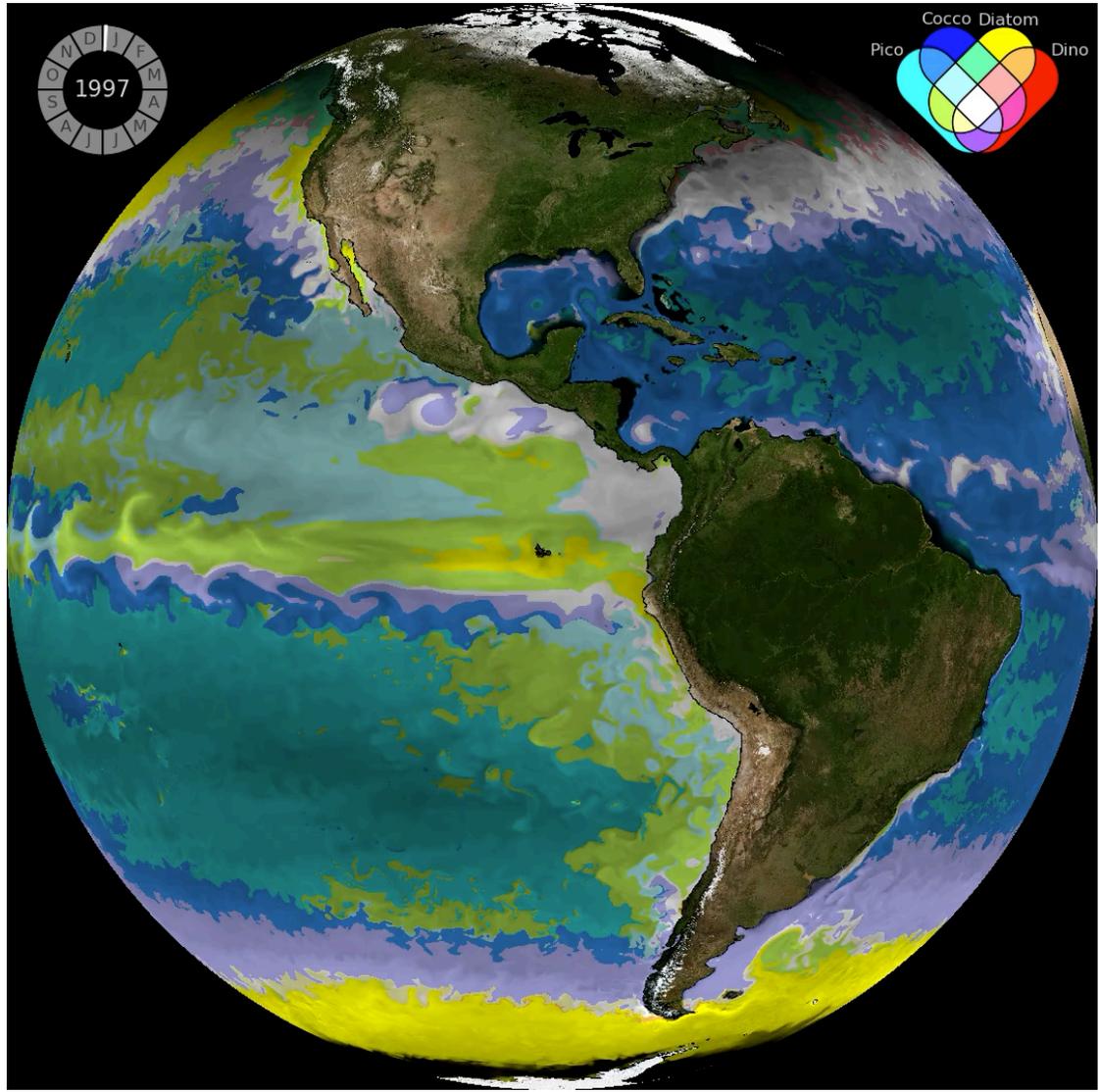


Willig, Ann Rev Ecol Evol Syst (2003)

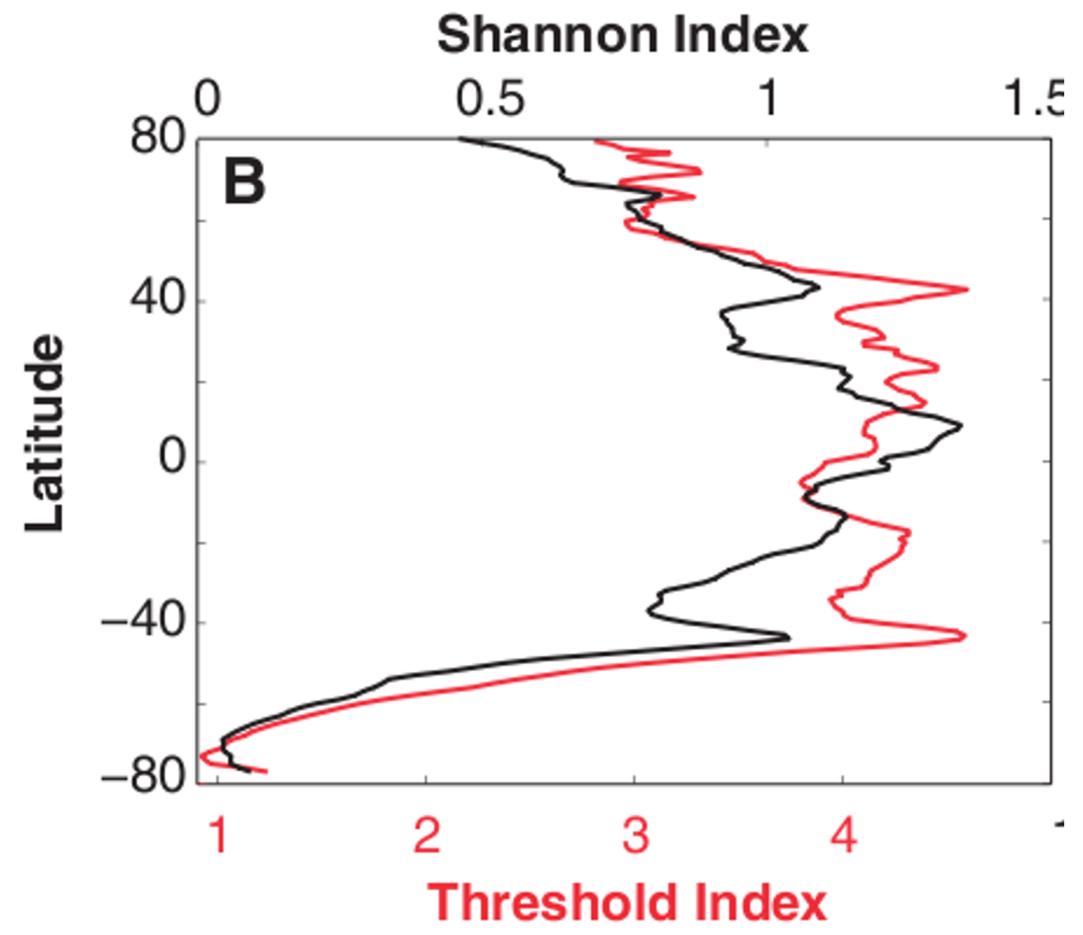


Kasner et al., PLoS One (2011)

Spatio-temporal variability of marine plankton

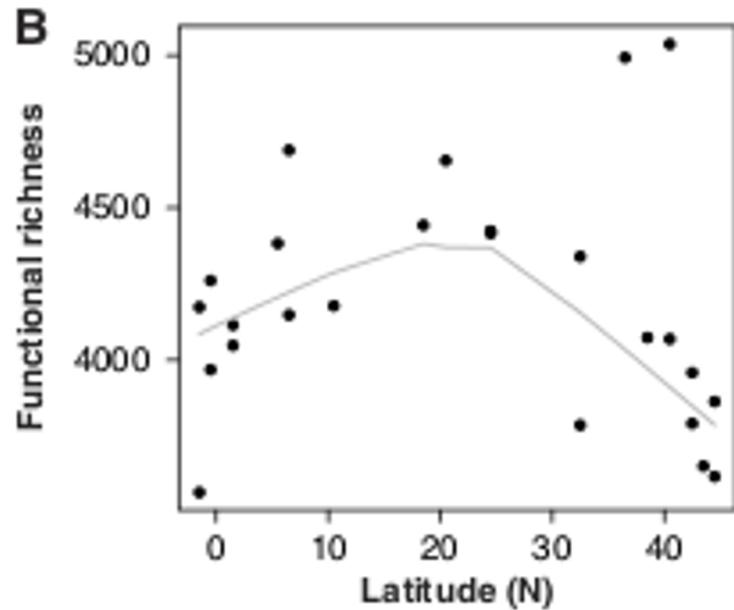


DARWIN model MIT (Mick Follows)

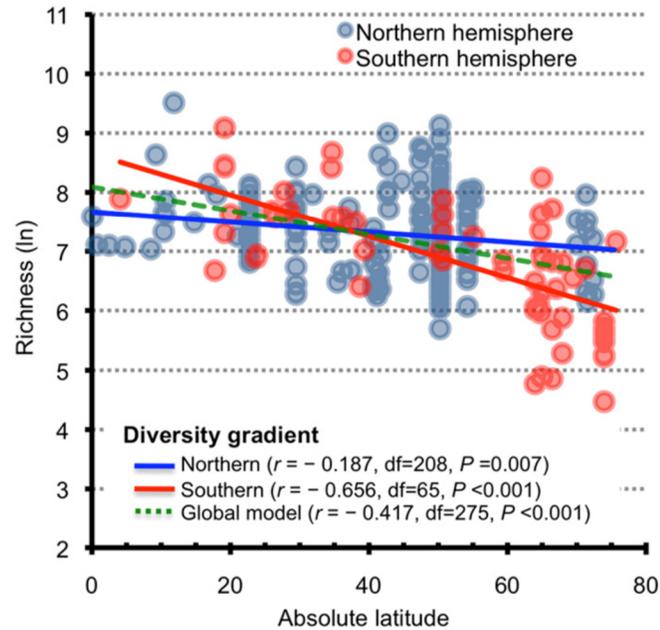


Barton et al., Science (2010)

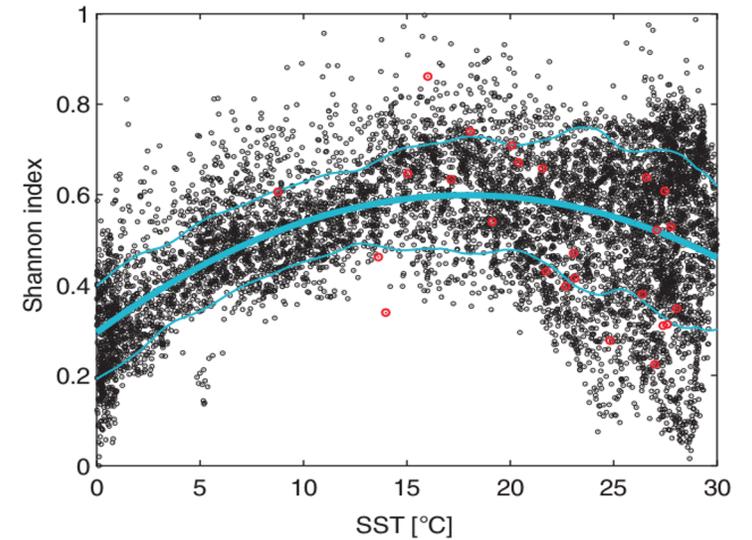
Patterns of diversity of marine plankton



Raes et al. Mol Syst Biol (2011)



Sul et al. PNAS (2013)



De Monte et al. ISME J. (2013)



Plankton protist communities

Tara oceans: Global-scale sampling with uniform protocol



Barcodes: V9 of 18S rRNA gene

388 samples of plankton communities in 121 different locations in the world ocean, covering 8 oceanic regions

4 organisms' size classes: pico-nano (0.8-5 μm), nano (5-20 μm), micro (20-180 μm), meso (108-2000 μm)

Different methods of sequence clustering/taxonomic resolution: Swarms and OTUs (UCLUST 95% and 97%)

Physico-chemical (temperature, salinity, nutrients, etc.) and biological (Chl, ocean colour, diversity, etc.) context

- ~150.000 different OTUs identified, few thousands per sample
- 388 samples in 121 locations

De Vargas, Audic, Henry, et al.

Eukaryotic plankton diversity in the sunlit global ocean

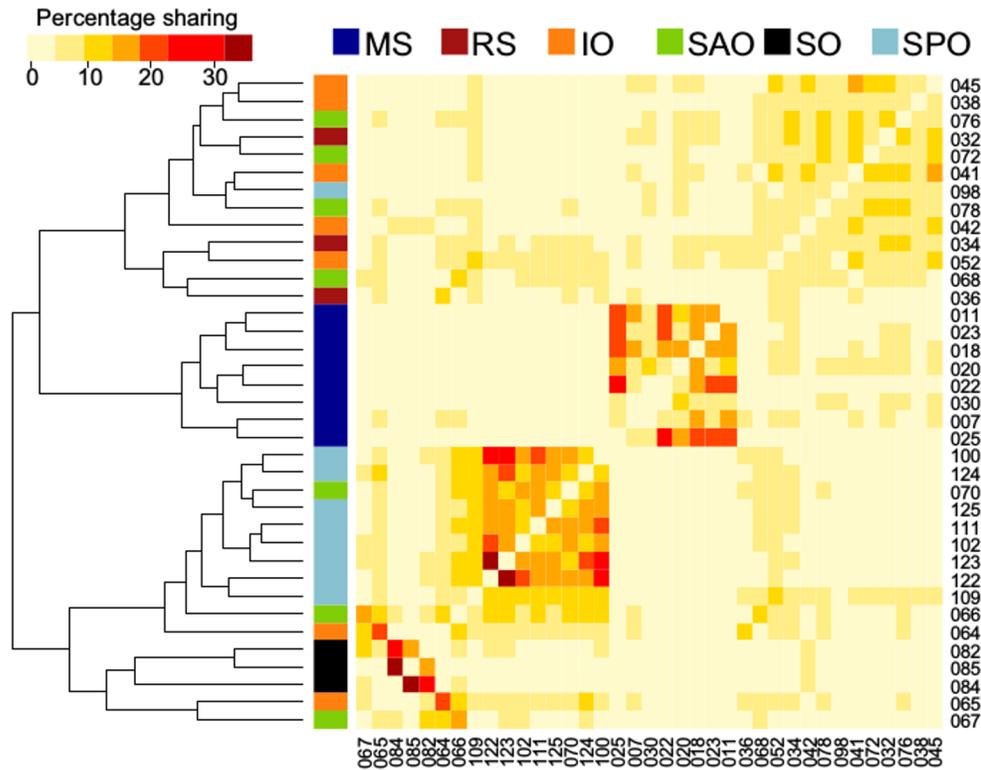
Science 2015



Plankton protist communities

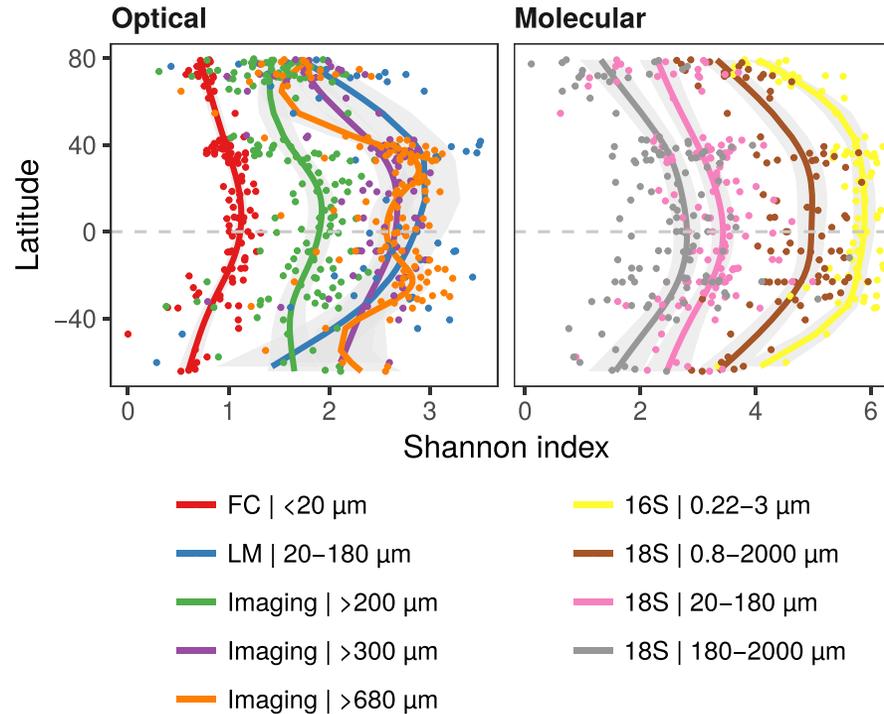


Community composition differs from site to site (average Jaccard index < 0.15)
 OTUs display biogeographical patterns



Malviya et al. PNAS (2016)

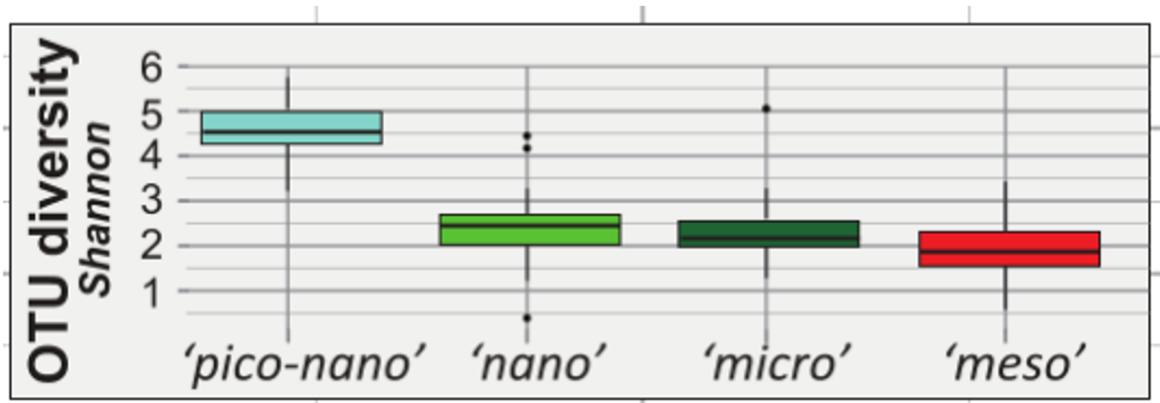
Latitudinal Diversity Gradients



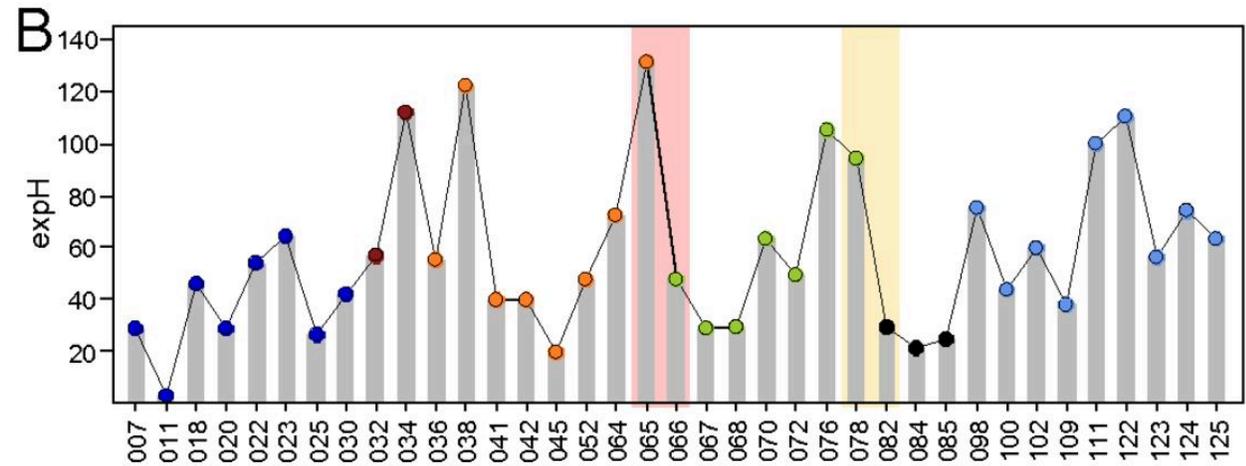
F. Ibarbalz, L. Zinger, IBENS, Paris
 + more from Paris, Villefranche-sur-Mer, Roscoff,
 Zürich, Ohio, Kyoto, Naples, Maine
 Cell (2019)



Plankton protist communities



De Vargas, Audic, Henry, et al. Science 2015



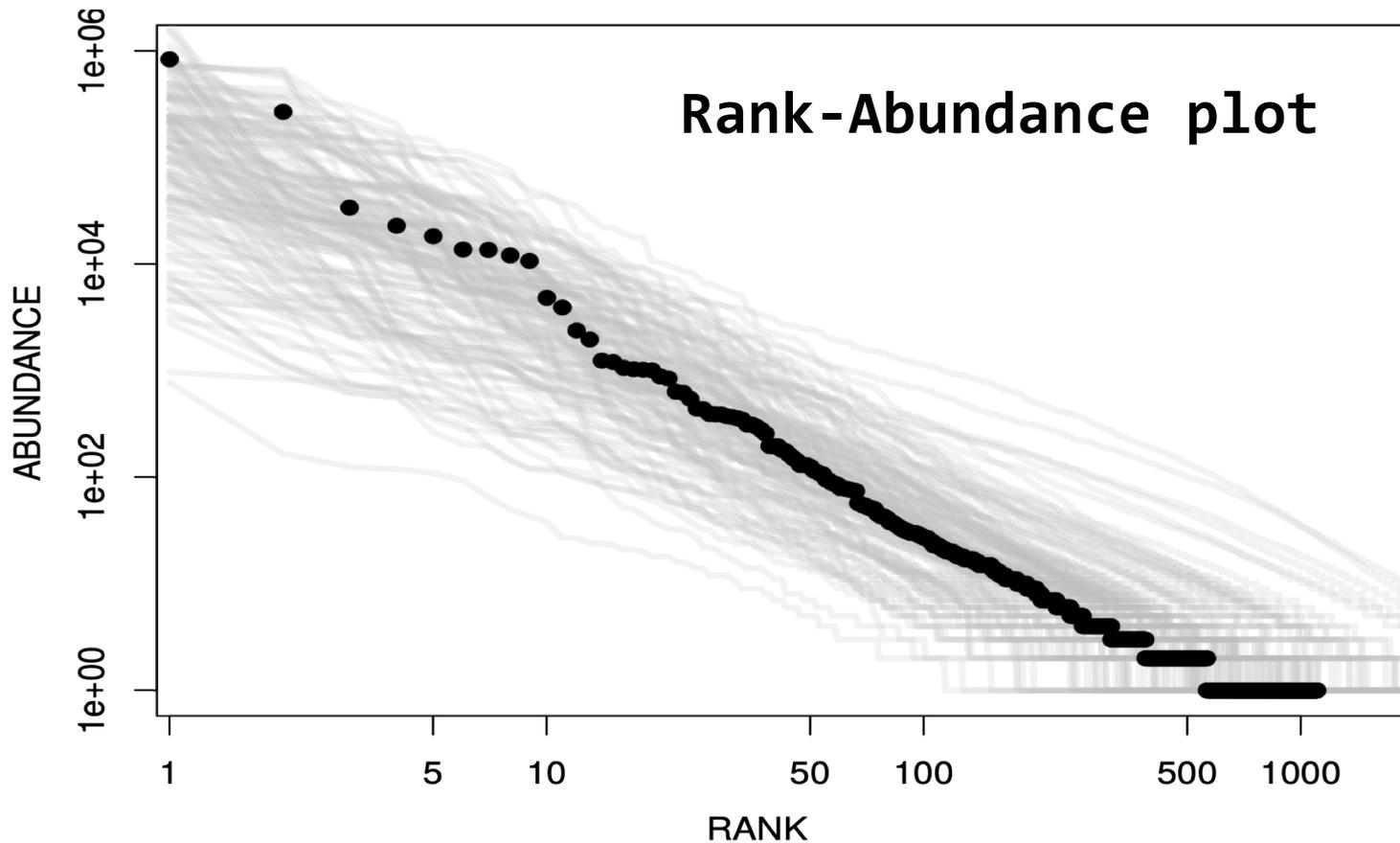
Carradec et al. Nature Comm 2018

Measuring community diversity

Ecological community characterized by:

K species of abundance (n_1, \dots, n_K)

$$N = \sum n_i \text{ organisms}$$



Diversity indicators:

Species richness K

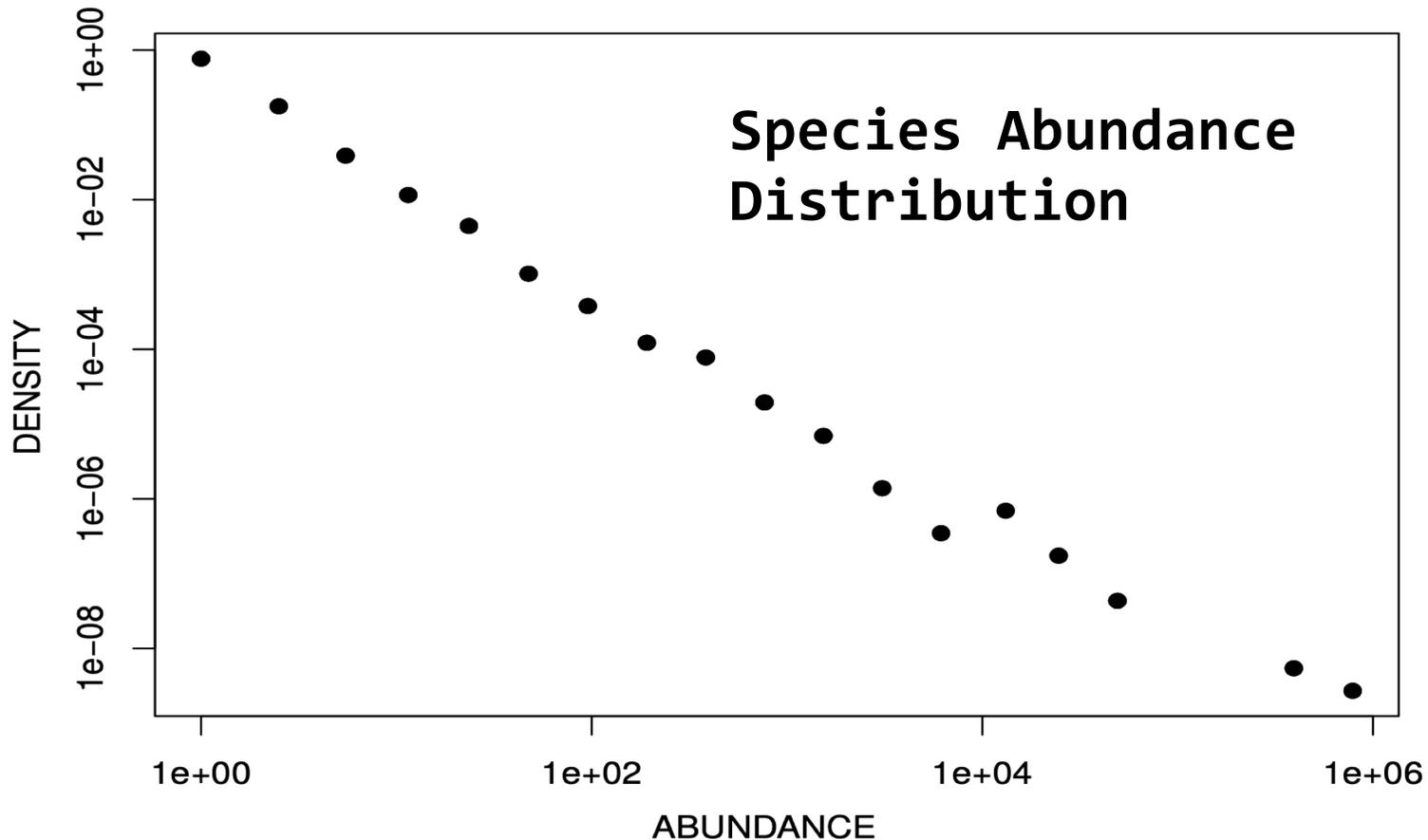
Shannon Index $H = \sum n_i \log n_i$

Measuring community diversity: SAD

Ecological community characterized by:

K species of abundance (n_1, \dots, n_K)

$$N = \sum n_i \text{ organisms}$$



Fit with theoretical models to determine the qualitative shape of the distribution

Empirical vs theoretical SADs

Theoretical models based on mechanistic or statistical hypotheses predict different functional forms for the abundance distributions. The most commonly used are (Poisson) lognormal and log-series.

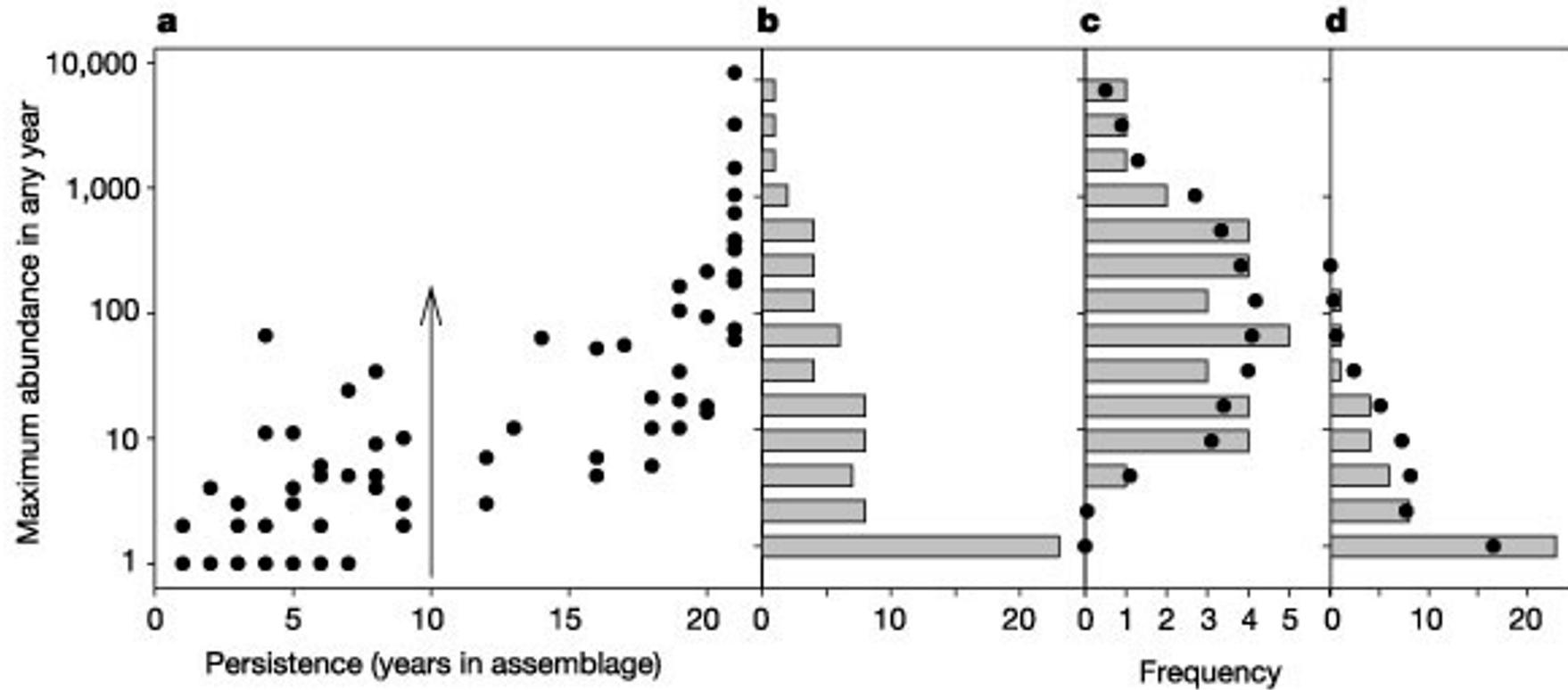
Fitting empirical distributions has led to inconclusive results as to the underlying mechanisms.

Problems with model-fitting:

1. different hypotheses give rise to the same distributions
2. there are parameter values for which different distributions are indistinguishable
3. based on the hypothesis that all members of the community obey the same ecological process

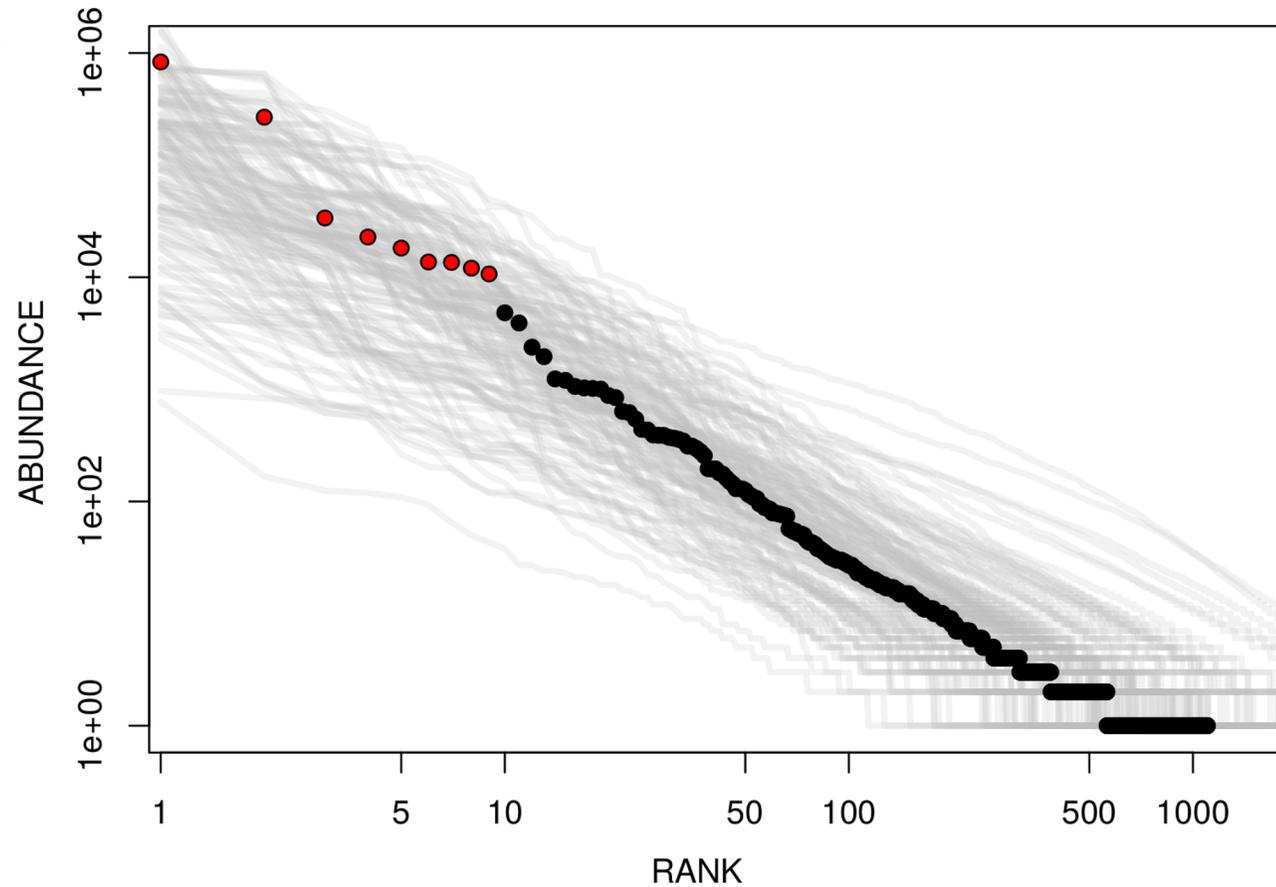
Community decomposition

Endemic and 'visitor' species obey different distributions



Magurran & Henderson, Nature (2003)

Plankton protist communities



Huge number of rare species

Regular abundance decay for rare species

Variability of abundant species

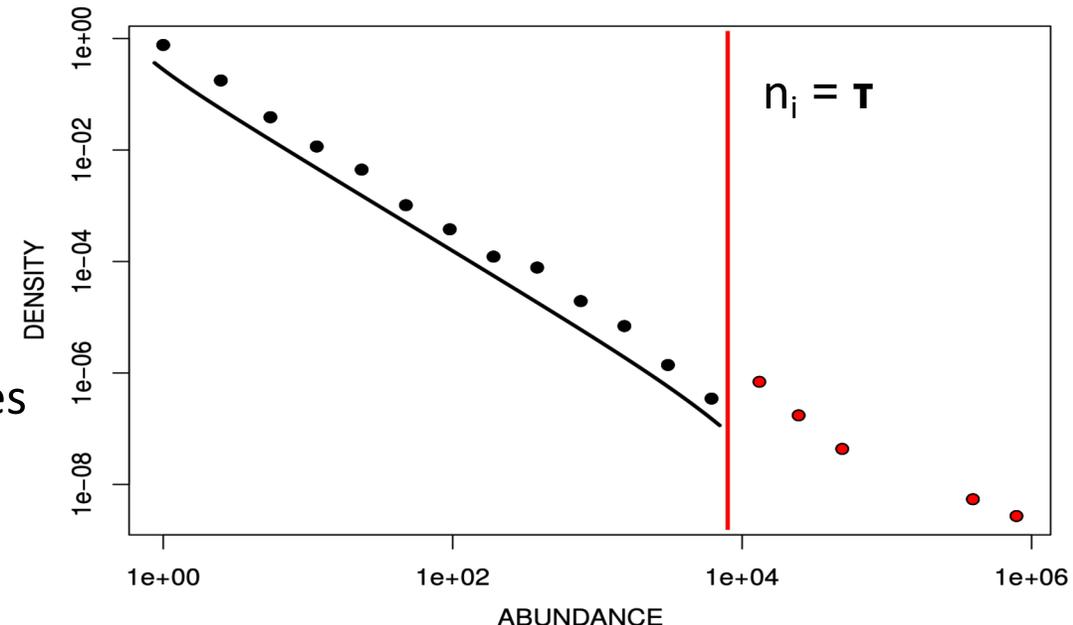
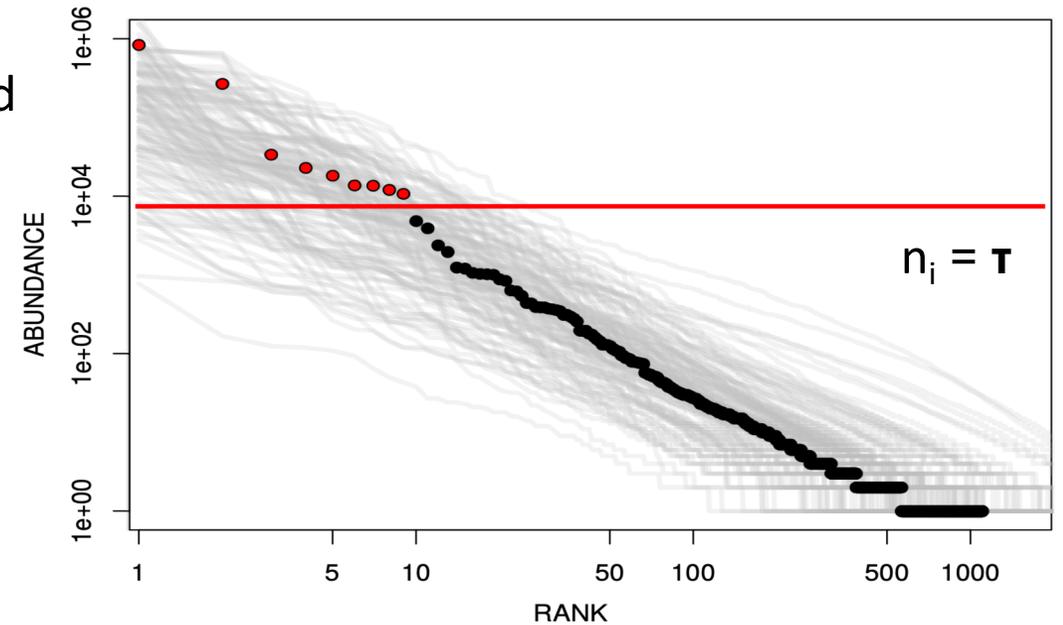
Adaptive algorithm for community decomposition

Aim: identify the largest community component that is well fitted by a family of distributions.

1. Set an abundance threshold τ for abundances (take only $10^2 < n_i \leq \tau$)
2. Maximize the likelihood τ to fit the data below the threshold and compute p-value
3. Loop on τ and choose the largest value of τ for which the data represent a random realization of the fitting distribution (p-value ≥ 0.1)

→ Identification of **abundant** and **non-abundant** OTUs

→ Quantitative comparison of best-fit parameters among samples



Neutral, density-dependent model for community assembly

Birth & death rates

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

Negative binomial beta distribution:

$$\langle \phi_n \rangle = \theta \frac{\Gamma(n + \alpha) \Gamma(1 + \beta)}{\Gamma(\alpha) \Gamma(n + \beta + 1)} e^{-rn} \quad \alpha = \frac{\chi}{b} \quad \beta = \frac{\mu}{d} \quad r = \frac{b}{d}$$

Neutral, density-dependent model for community assembly

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

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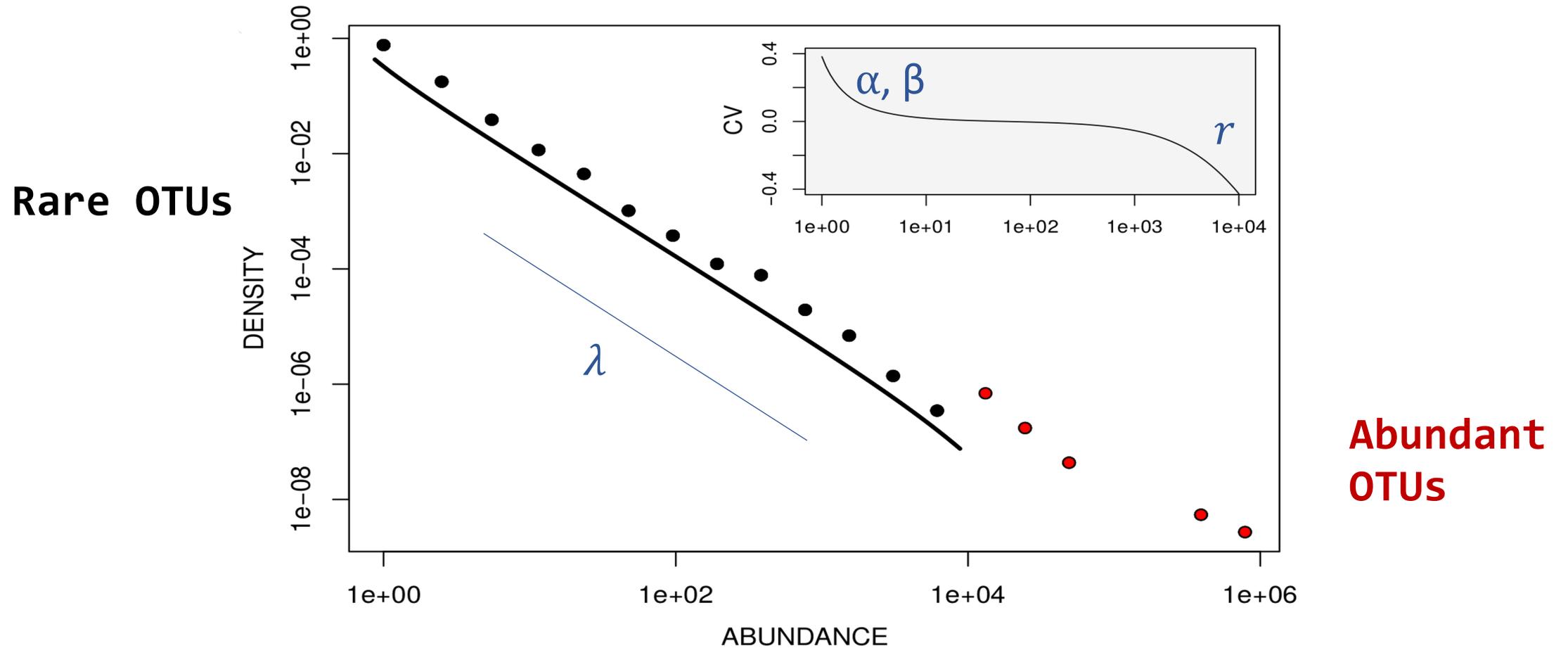
$$\langle \phi_n \rangle = \theta \frac{\Gamma(n + \alpha) \Gamma(1 + \beta)}{\Gamma(\alpha) \Gamma(n + \beta + 1)} e^{-rn}$$

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

$$\sim e^{-rn} n^{-\lambda}$$

$$\lambda = 1 - \alpha + \beta$$

Fit to empirical distributions



Quantifying variation of rare protist diversity

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

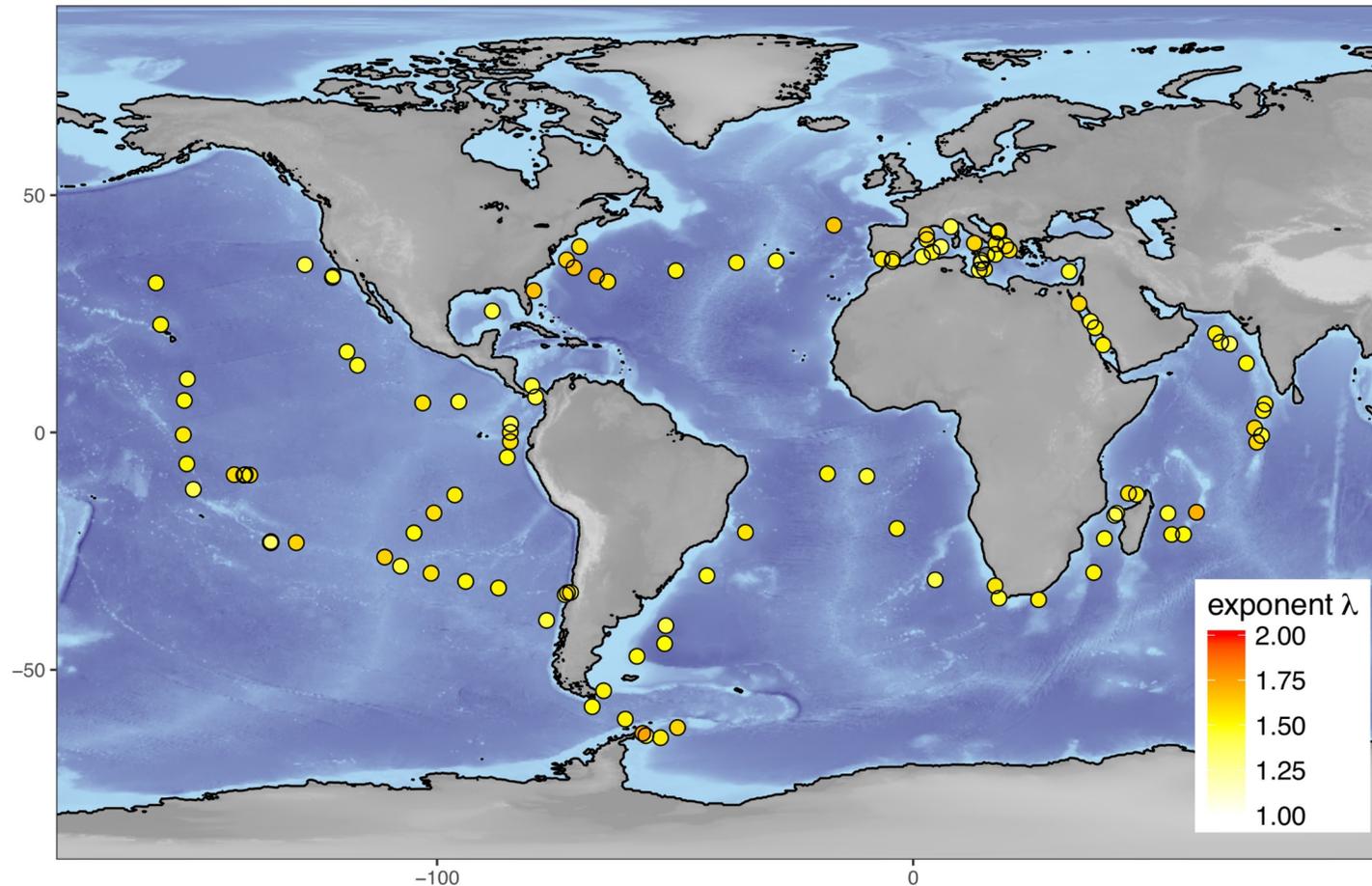
The non-dominant component comprises more than 99% of OTUs

Abundance decay is dominated by the power-law trend (~ 4 decades)

$$\lambda = 1.53 \pm 0.08 \quad (\text{CV} < 8\%)$$

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

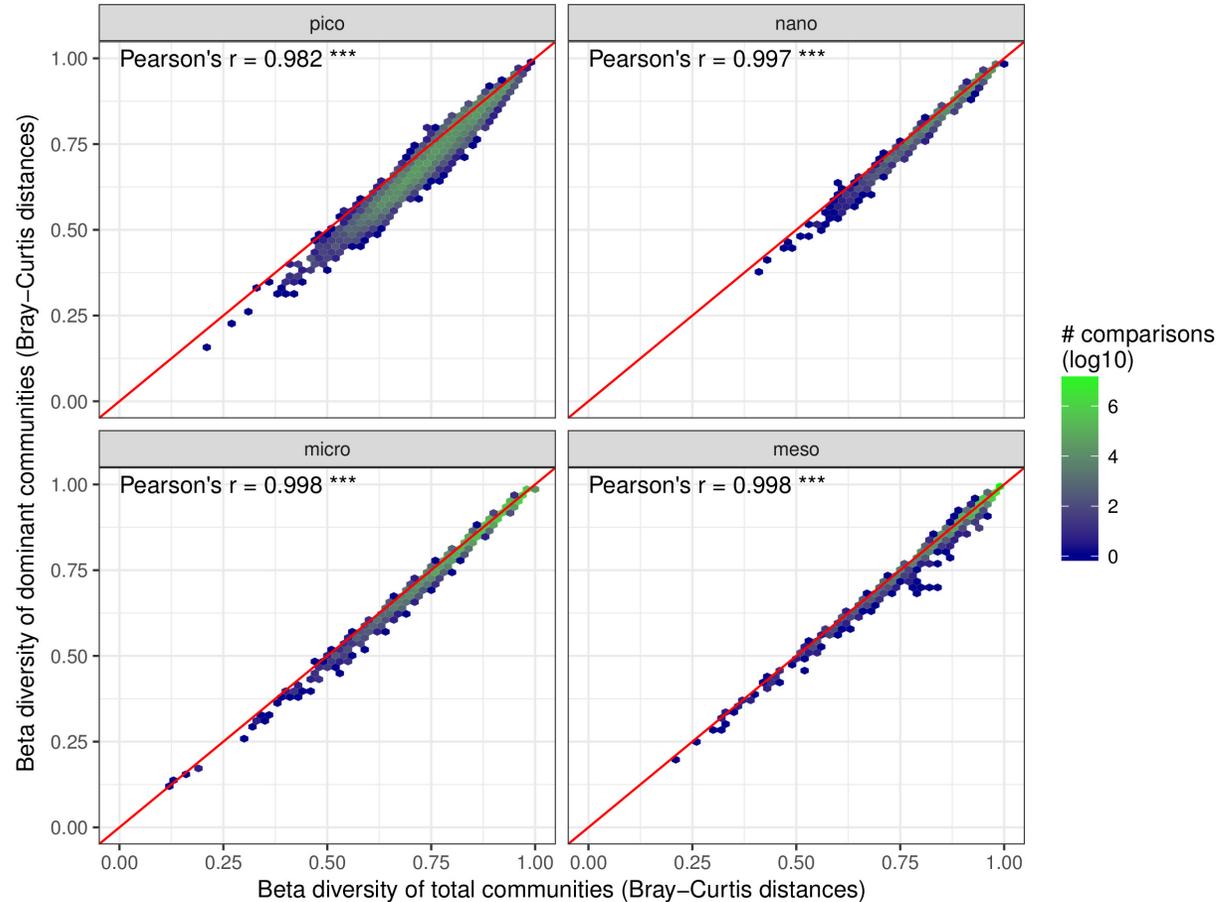
Spatial variation of best-fit parameters



Variation of best-fit parameters of the same amplitude as contextual parameters, but no systematic co-variation.

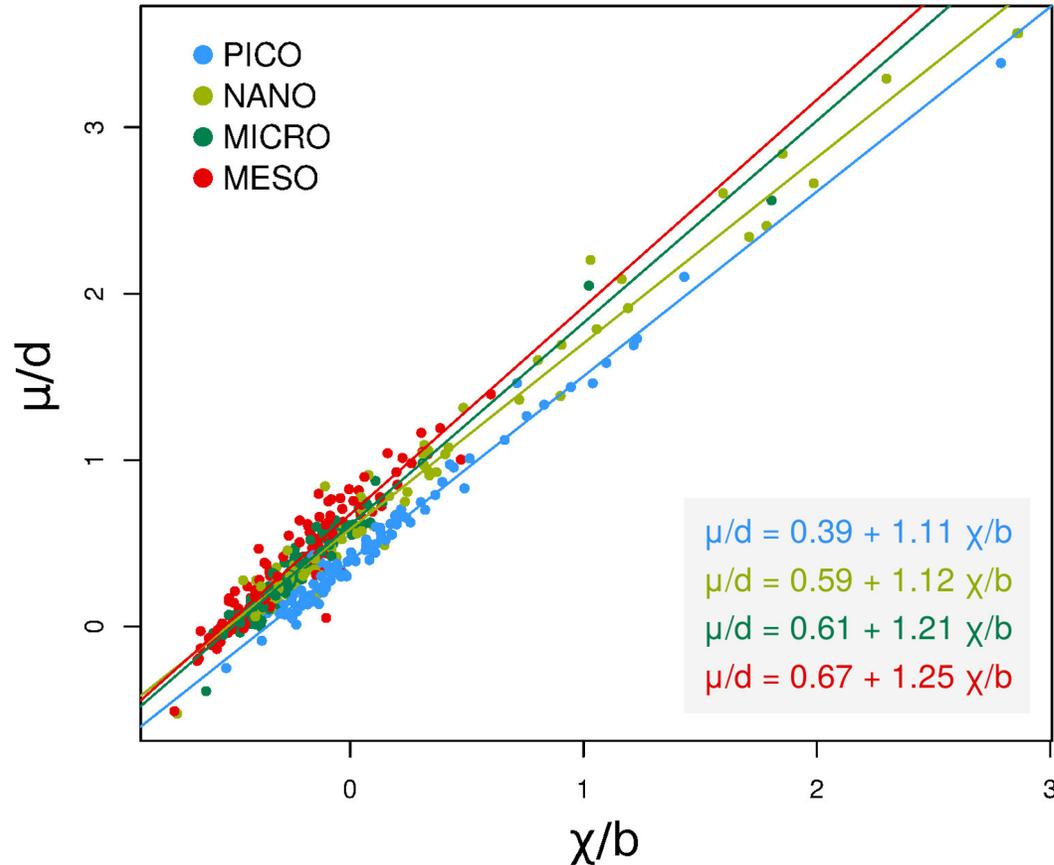
➡ Ubiquitous distribution of rare species

Non-abundant OTUs and biogeography



Spatial information on community diversity is concentrated in the 1% most abundant species

Ecological basis of the statistical regularity



$$r = \frac{b}{d}$$
$$\lambda = 1 - \frac{\chi}{b} + \frac{\mu}{d}$$

Non-abundant OTUs:

Local balance of linear birth and death

Strong correlation of density/dispersal-dependent corrections

Equivalence of non-abundant species

Plankton species differ substantially in their local growth rates ('fitness')

Abundant species are directly engaged in competition, and shape biogeography

Non-abundant species are likely non-growing, locally non-adapted, sharing ecological histories with similar spatio-temporal statistics

→ 'effective' neutrality

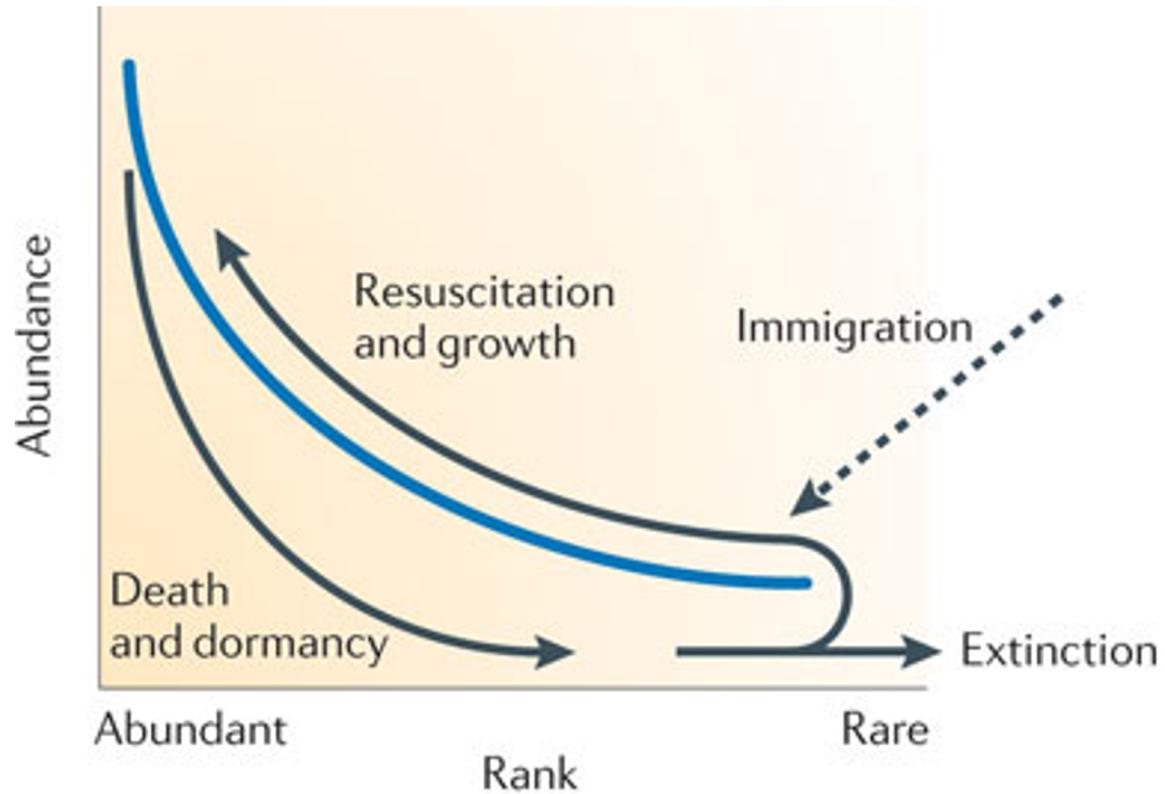
Is a neutral model the best to describe plankton communities?

Effective neutrality in a niche model

Matthieu Baron, ENS Physics, Paris

Giulio Biroli, ENS Physics, Paris

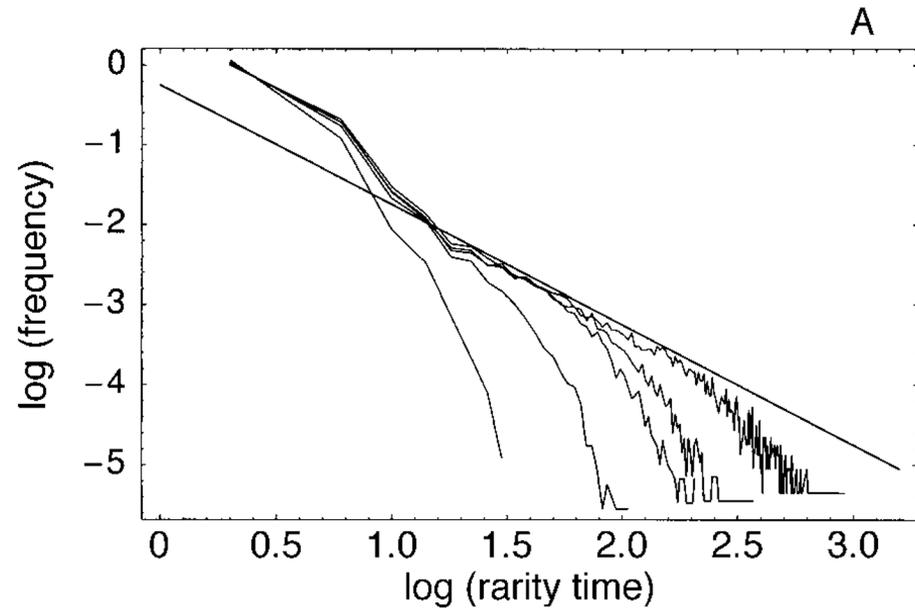
Microbial seed bank



Nature Reviews | **Microbiology** 9, 119-130 (2011)

Microbial seed banks: the ecological and evolutionary implications of dormancy
Jay T. Lennon & Stuart E. Jones

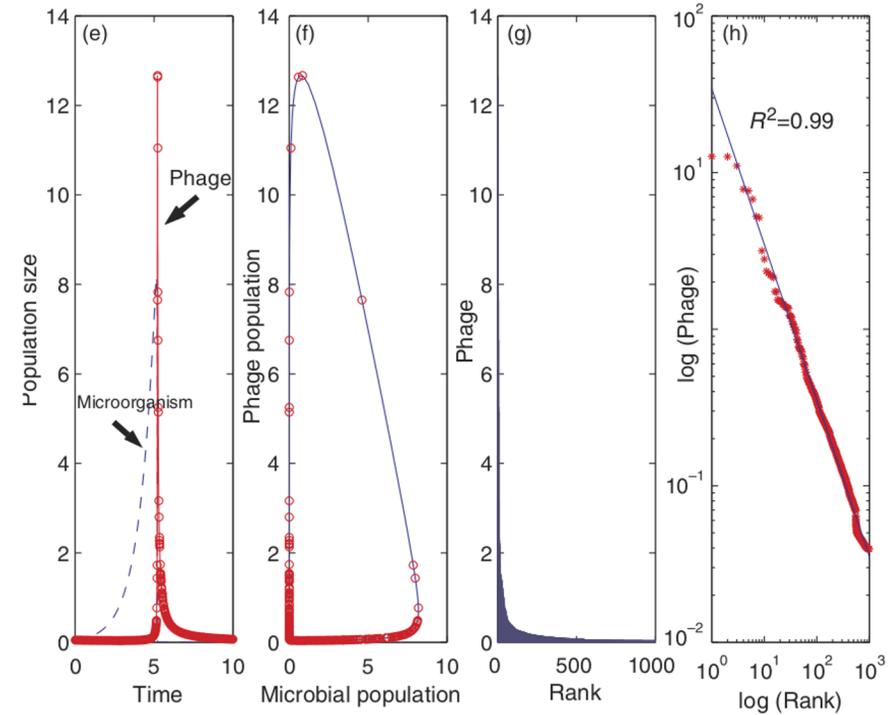
Temporal intermittency



UNIVERSAL POWER LAWS GOVERN INTERMITTENT RARITY IN COMMUNITIES OF INTERACTING SPECIES

REGIS FERRIERE^{1,2,4} AND BERNARD CAZELLES^{1,3}

Ecology, 80(5), 1999, pp. 1505–1521
© 1999 by the Ecological Society of America



Power law rank–abundance models for marine phage communities

Karl Heinz Hoffmann¹, Beltran Rodriguez-Brito^{2,3}, Mya Breitbart⁴, David Bangor^{2,3}, Florent Angly², Ben Felts³, James Nulton³, Forest Rohwer^{2,5} & Peter Salamon³

FEMS Microbiol Lett **273** (2007) 224–228

Model for ecosystem dynamics

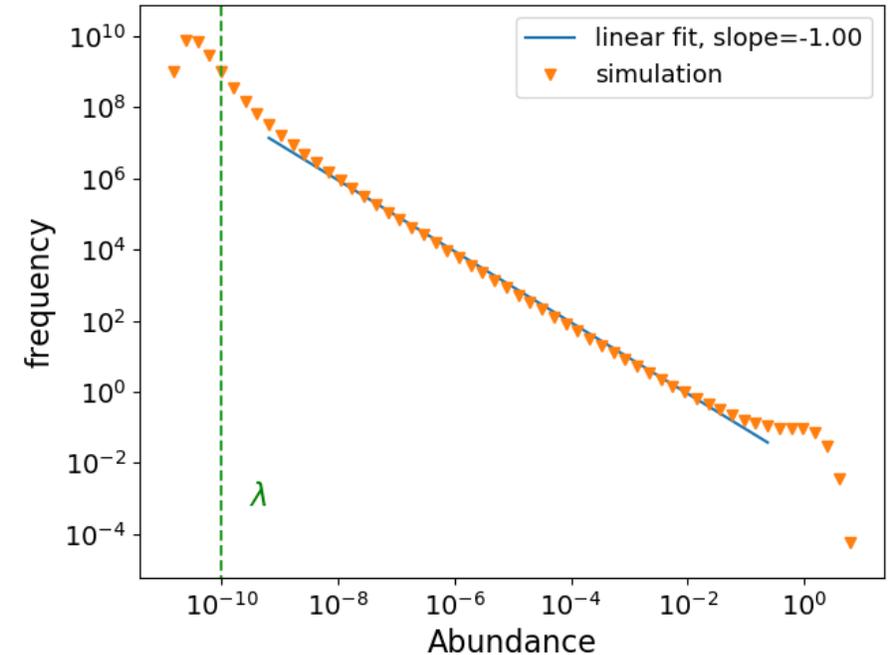
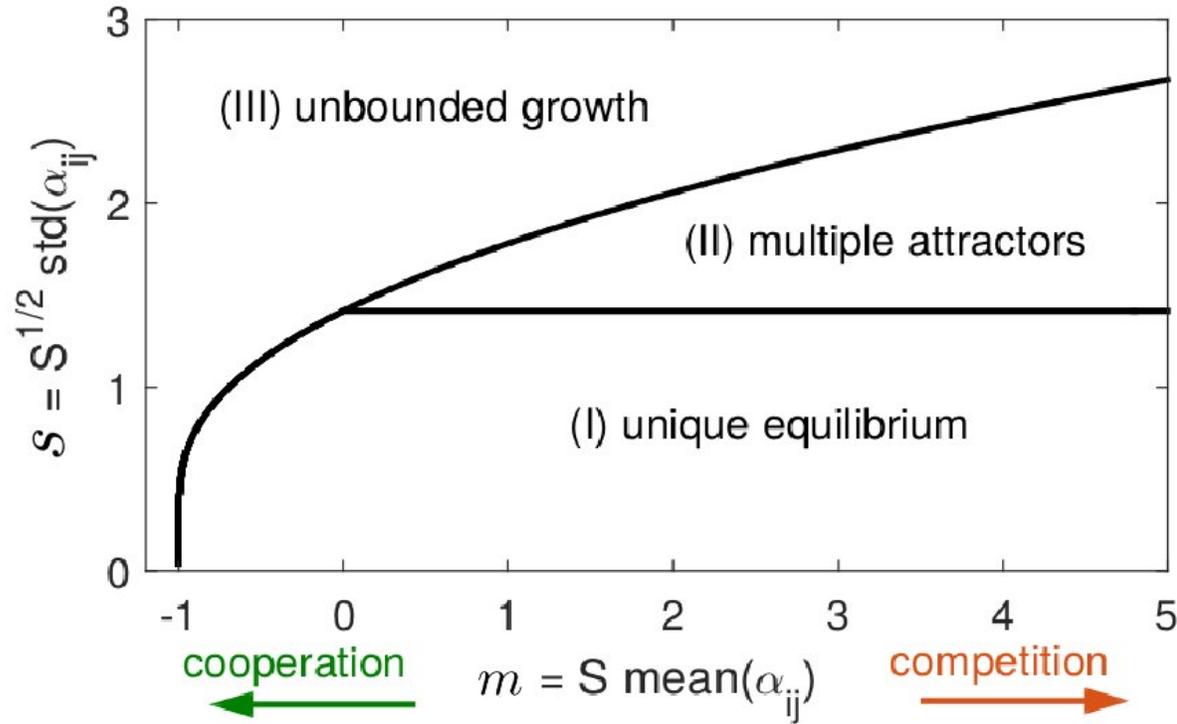
Generalized Lotka-Volterra equations:

$$\frac{dN_i}{dt} = \lambda + N_i(1 - N_i) - \sum_{j=1}^S \alpha_{ij} N_i N_j$$

1. Species have a logistic growth
2. Species interact (their growth depends on the density of other species)
3. Immigration

The interaction parameters are randomly chosen from a Gaussian distribution of average μ and standard deviation σ

Phase diagram for weak interactions



The chaotic regime produces SADs with a power law of exponent 1

Roy et al.

Numerical implementation of dynamical mean field theory for disordered systems:

application to the Lotka-Volterra model of ecosystems

Journal of Physics A: Mathematical and Theoretical (2019)

Open questions

Is plankton different from other microbial communities?

Lucie Zinger, IBENS

To what extent plankton species are 'equivalent'?

Giulio Biroli, Dept. of Physics, ENS

What is the role of ocean transport?

Francesco d'Ovidio, LOCEAN; Mick Follows, MIT

What are the best descriptors of diversity in plankton communities?

Arne Traulsen, MPI Evolutionary Biology, Plön, Germany

**Looking for a post-doc to work at the Max Planck
Institute of Evolutionary Biology, Plön, Germany**



Thank you