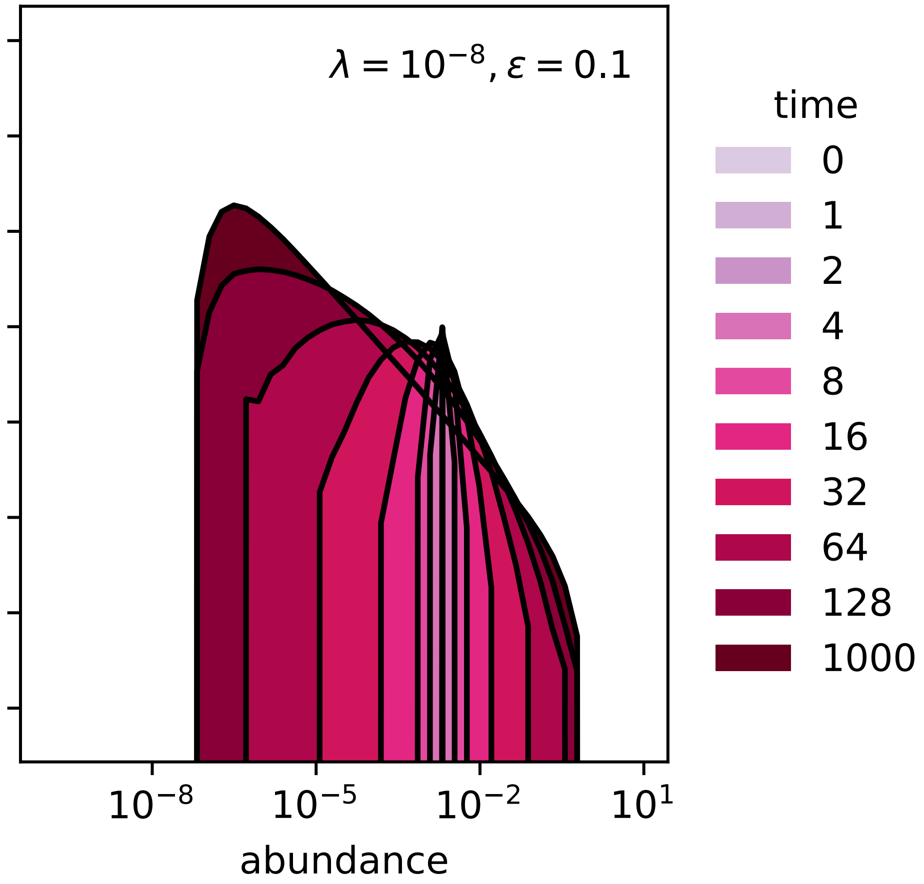
2. Abundance distributions and dynamics with and without species symmetry



Aussois, June 17, 2025

Abundance distributions

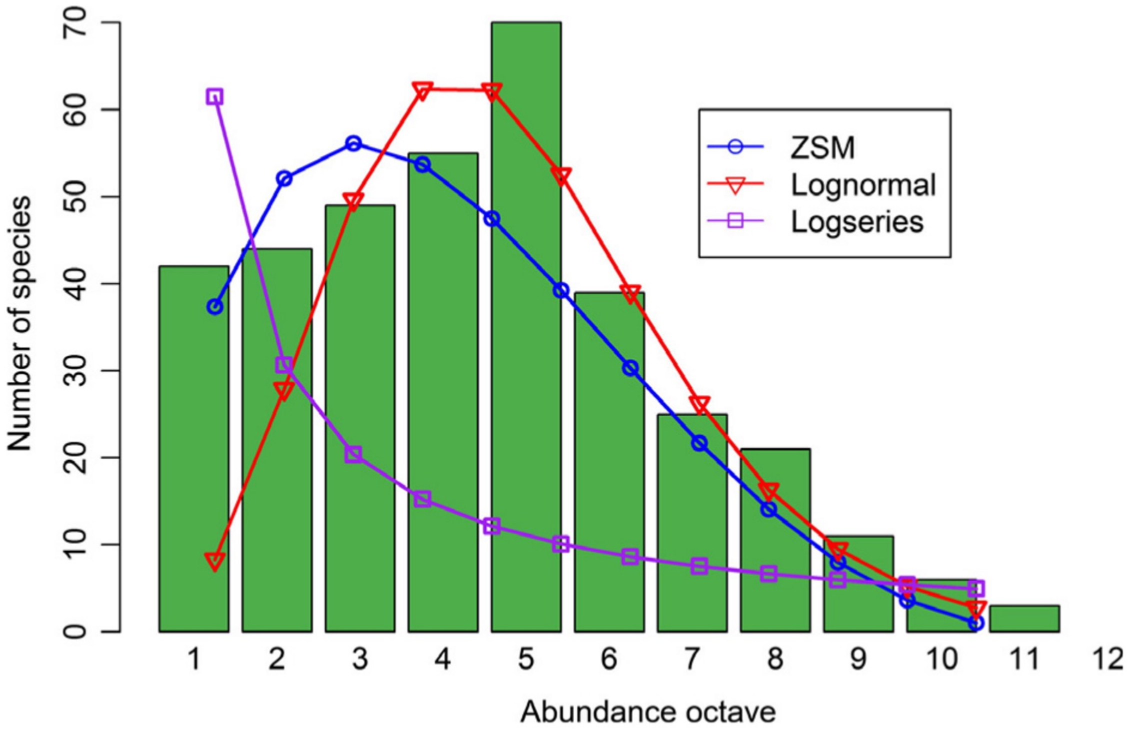
Diversity is best studied by looking at the identity and abundance of species

Statistical properties of abundance distributions reflect demographic processes

The hope is therefore to be able to tell processes apart by looking at the corresponding distributions

A large number of models exist, based on different hypotheses on, for instance, species symmetry, degree of competition, importance of finite-size fluctuations/drift, dispersal.

Fitting abundance distributions



Ecology and Evolution

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REVIEW

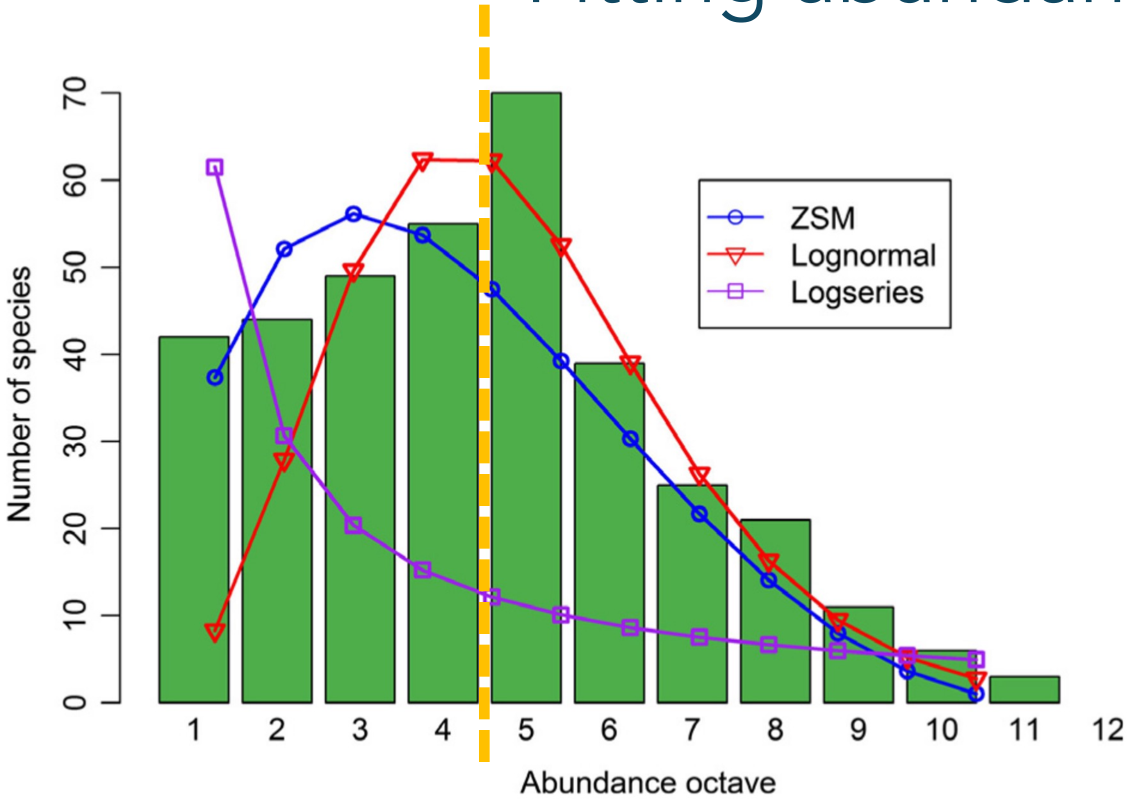
Neutral theory and the species abundance distribution: recent developments and prospects for unifying niche and neutral perspectives

Thomas J. Matthews[1,2] & Robert J. Whittaker[1,3]

Long-lasting debate on the functional form of SADs.

Problem: ecologically different modelling hypotheses produce the same class of distributions, and, vice-versa, different distributions can become qualitatively similar in certain limits.

Fitting abundance distributions


Preston's veil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REVIEW

Neutral theory and the species abundance distribution: recent developments and prospects for unifying niche and neutral perspectives

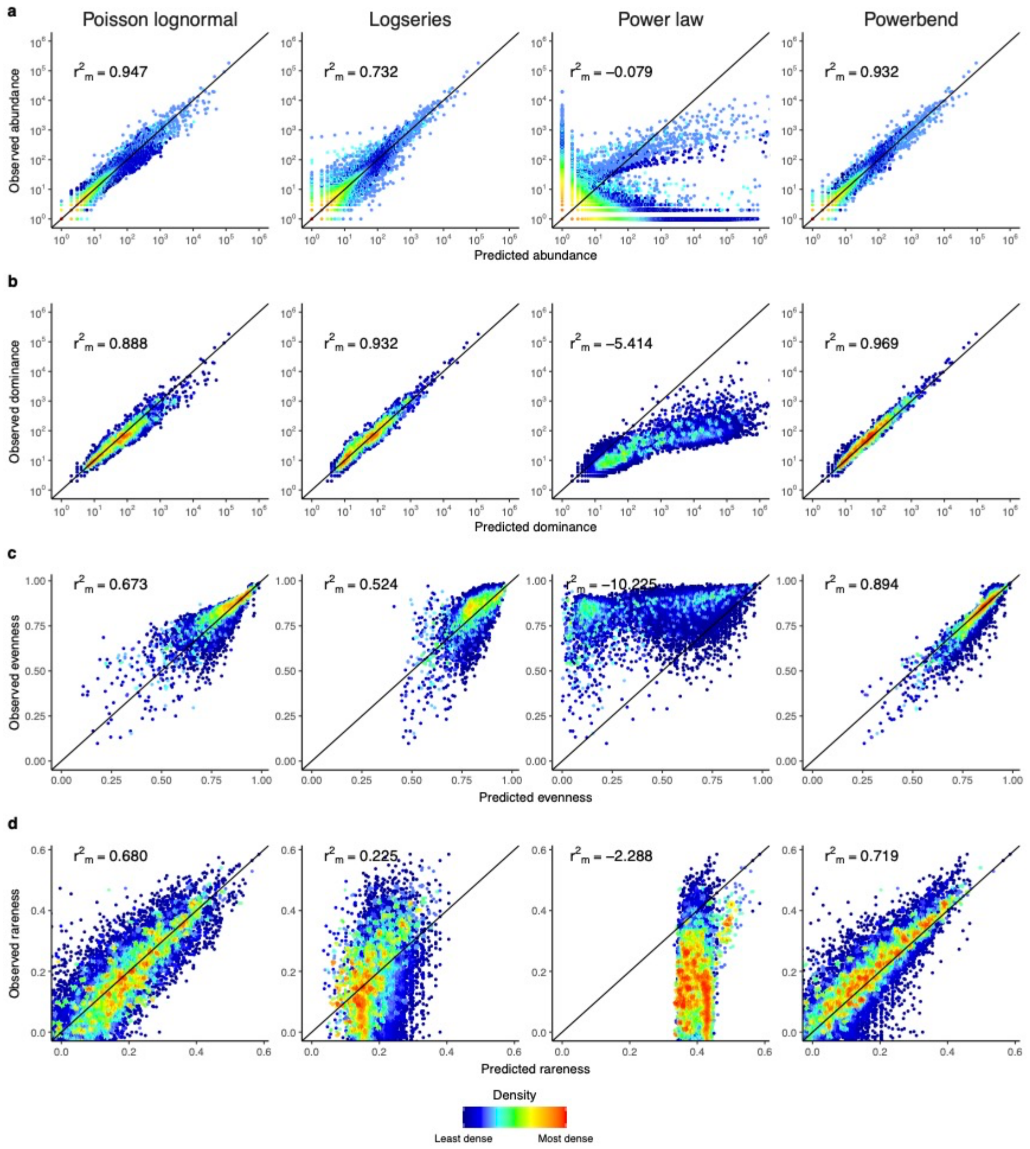
Thomas J. Matthews[1,2] & Robert J. Whittaker[1,3]

Long-lasting debate on the functional form of SADs.

Problem: ecologically different modelling hypotheses produce the same class of distributions, and, vice-versa, different distributions can become qualitatively similar in certain limits.

Sampling blurs things further.

Universal law of abundance decay

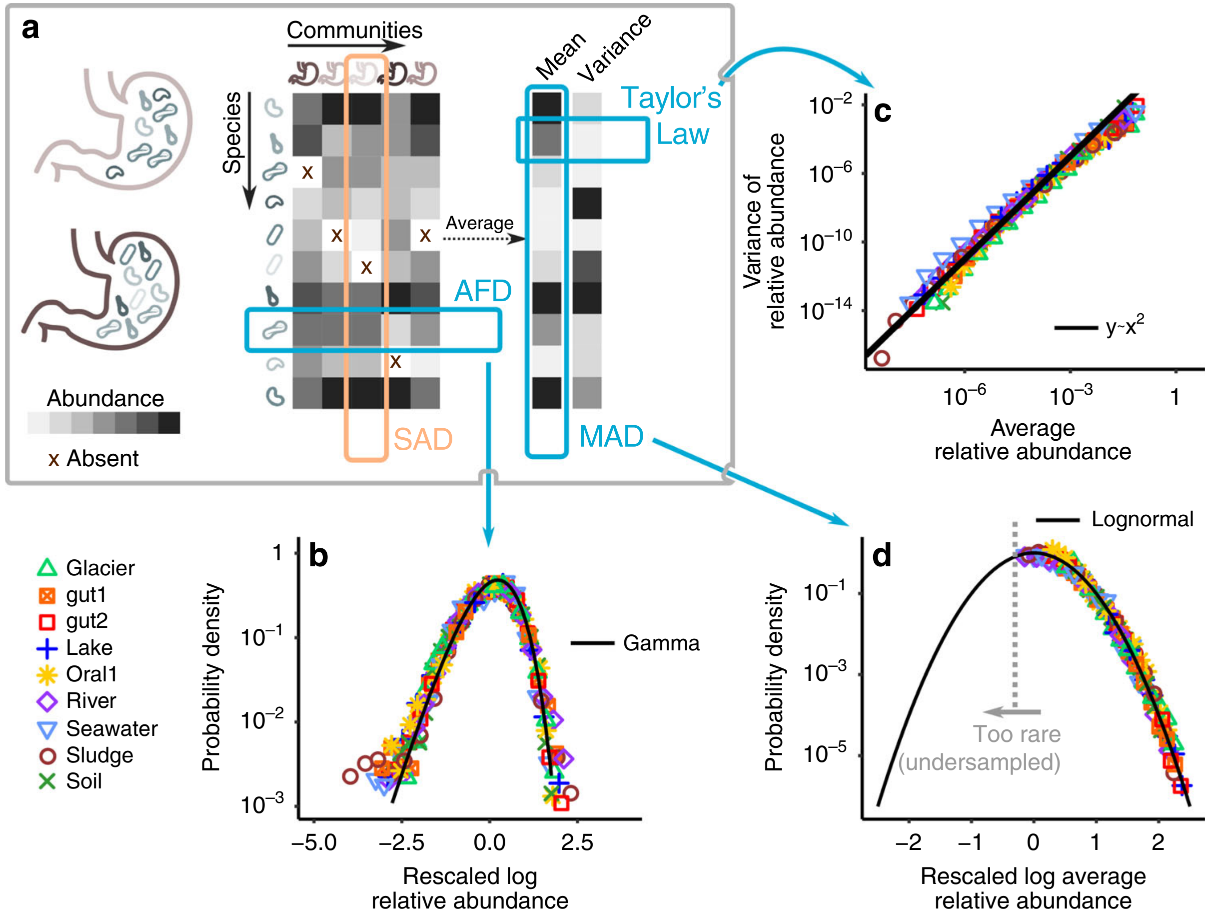


13.819 animal and plant communities
15.329 microbial communities

'Powerbend' $e^{-rn}n^{-\lambda}$ fits the SADs best when sampling is modelled

Gao et al.
The powerbend distribution provides a unified model for the species abundance distribution across animals, plants and microbes
Nature Comm (2025)

Distributions of microbial abundance fluctuations



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

What are the key features of species abundance distributions?

What ecological factors shape them?

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

A general model with fluctuating growth rates and regulation

Species growth rate can fluctuate due to (effective) environmental fluctuations, and abundances are capped by interactions within the same species and with the rest of the community

Abundance

$$\dot{n}_i(t) = n_i(t)[r_i(t) - \overset{\text{Community limitation}}{\mu N(t)} - \overset{\text{Self limitation}}{\varepsilon n_i(t)}] + \overset{\text{Immigration}}{\lambda}$$

Fitness

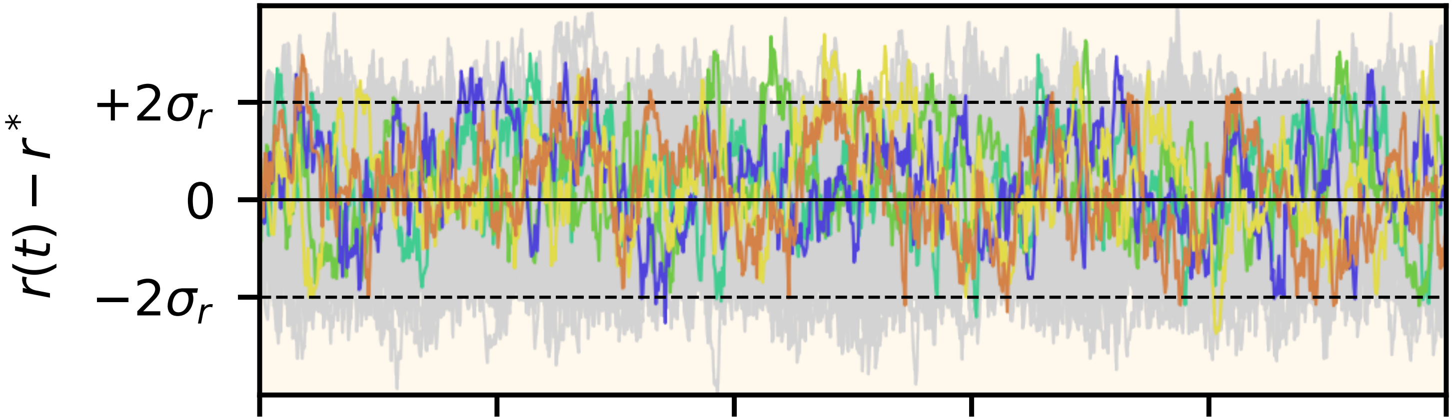
$$\tau \dot{r}_i(t) = -(r_i(t) - r_i^*) + \sqrt{\gamma}\,\dot{W}_i(t)$$

$\gamma := 2\sigma_r^2\tau$ Time scale of exclusion

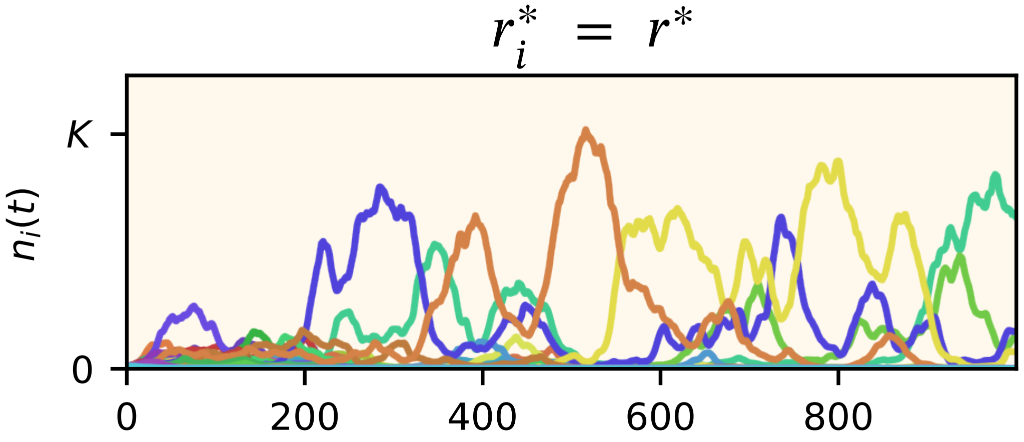
‘Neutral’ case

$$\dot{n}_i(t) = n_i(t)[r_i(t) - \mu N(t)]$$

Same community-level regulation and time average of fluctuations



‘Neutral’ case: transient and asymptotic dynamics

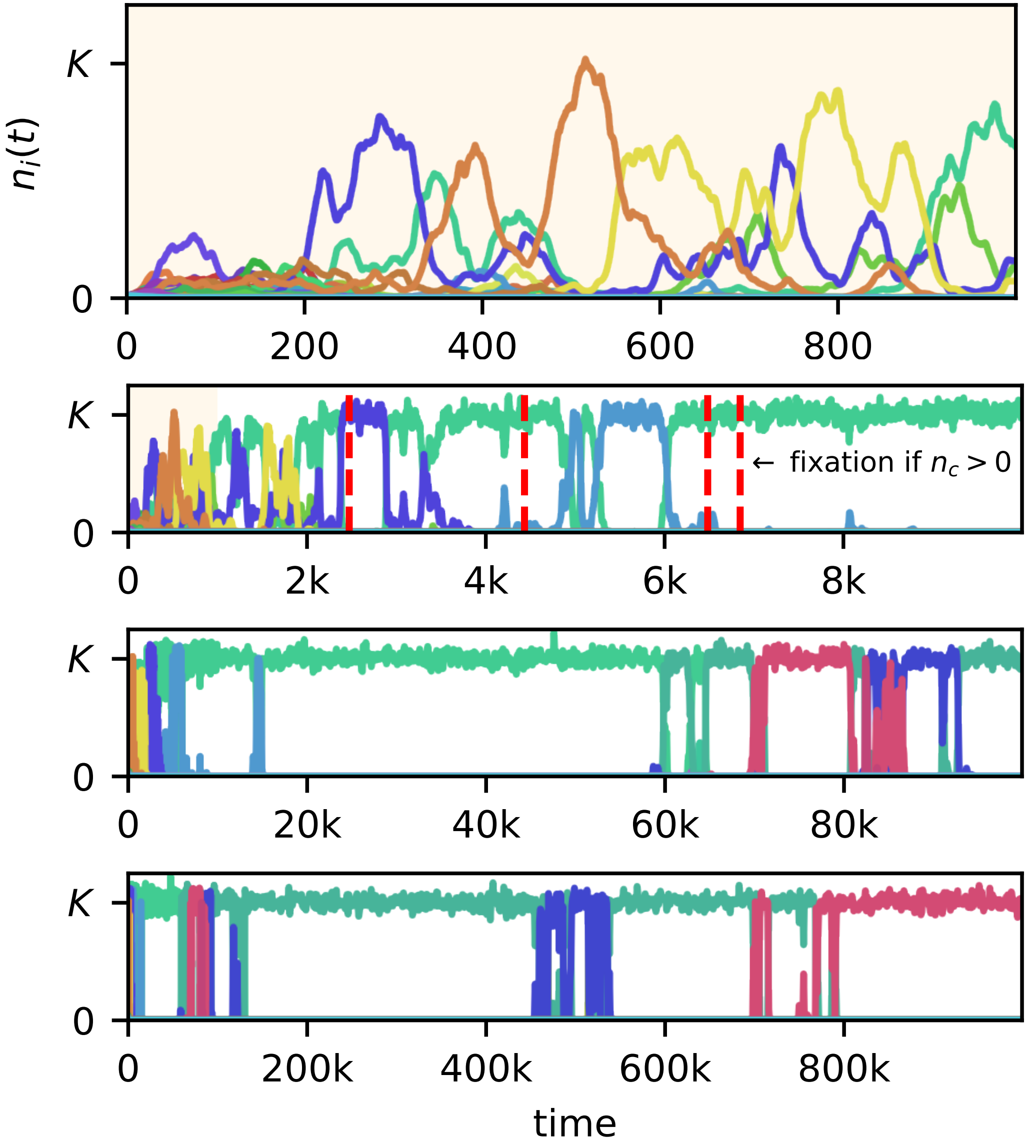


Community diversity rapidly increases and species turn over

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

‘Neutral’ case: transient and asymptotic dynamics

$$r_i^* = r^*$$



Community diversity rapidly increases and species turn over

but eventually one species excludes all the others on the timescale $\ln(S)/\gamma$

Mapping into the random energy model

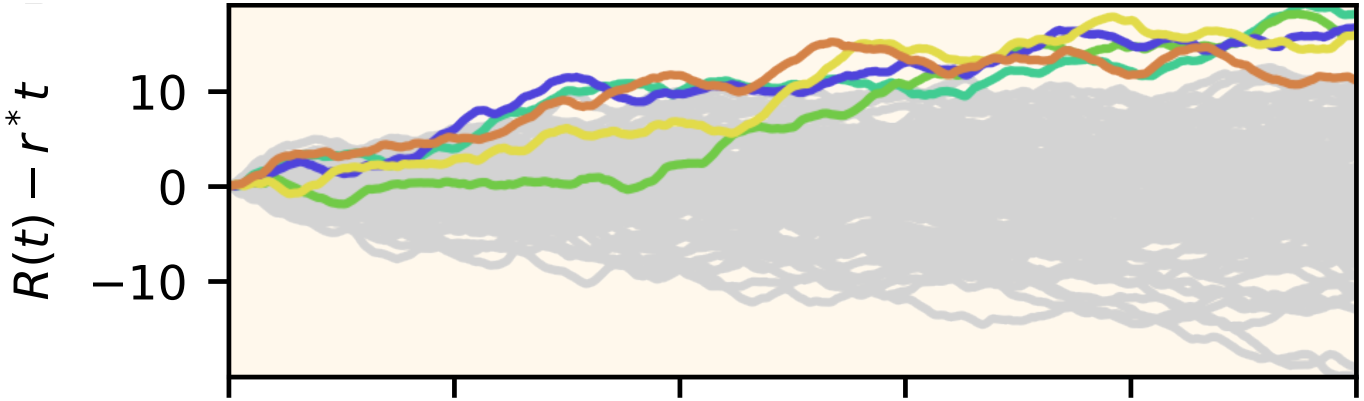
Formal solution of the associated replicator equation

$$p_i(t) = \frac{p_i(0)e^{R_i(t)}}{Z(t)}$$

The time-integrated fitnesses

$$R_i(t) := \int_0^t \mathrm{d}t' \, r_i(t')$$

diverge at rate γ



The time scale of 'condensation' (i.e. fixation of one species) is $t_c \sim \frac{\ln S}{\gamma}$

Time-average neutrality and stabilization

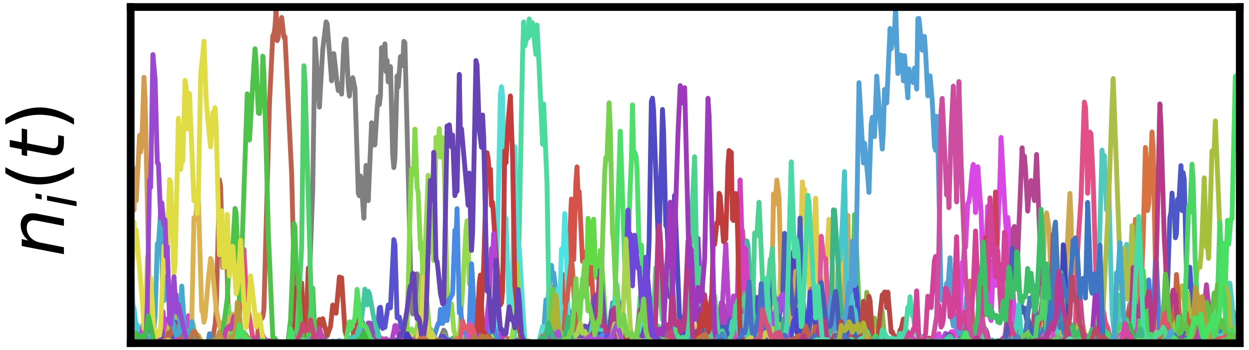
Self-limitation

$$\dot{n}_i(t) = n_i(t)[r_i(t) - \mu N(t) - \varepsilon n_i(t)] + \lambda$$

Immigration

Species-independent average fitness

$$r_i^* = r^*$$



Species coexist virtually forever with a perpetual temporal turnover

Approximation and an effective description

The (nondimensional) stationary solution depends mostly on two ratios of three compound parameters

$$\hat{\gamma} = \frac{\gamma}{r*}, \quad \hat{\varepsilon} = \frac{K\varepsilon}{r*}, \quad \hat{\lambda}_{\text{tot}} = \frac{S\lambda}{Kr*}$$

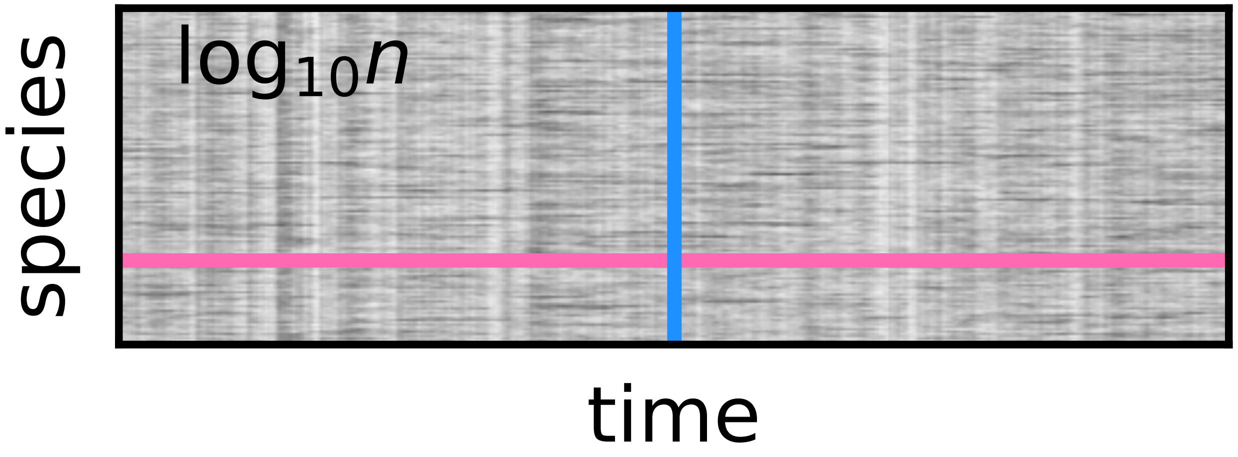
A ‘focal-species’ effective model captures the shape of such abundance distributions

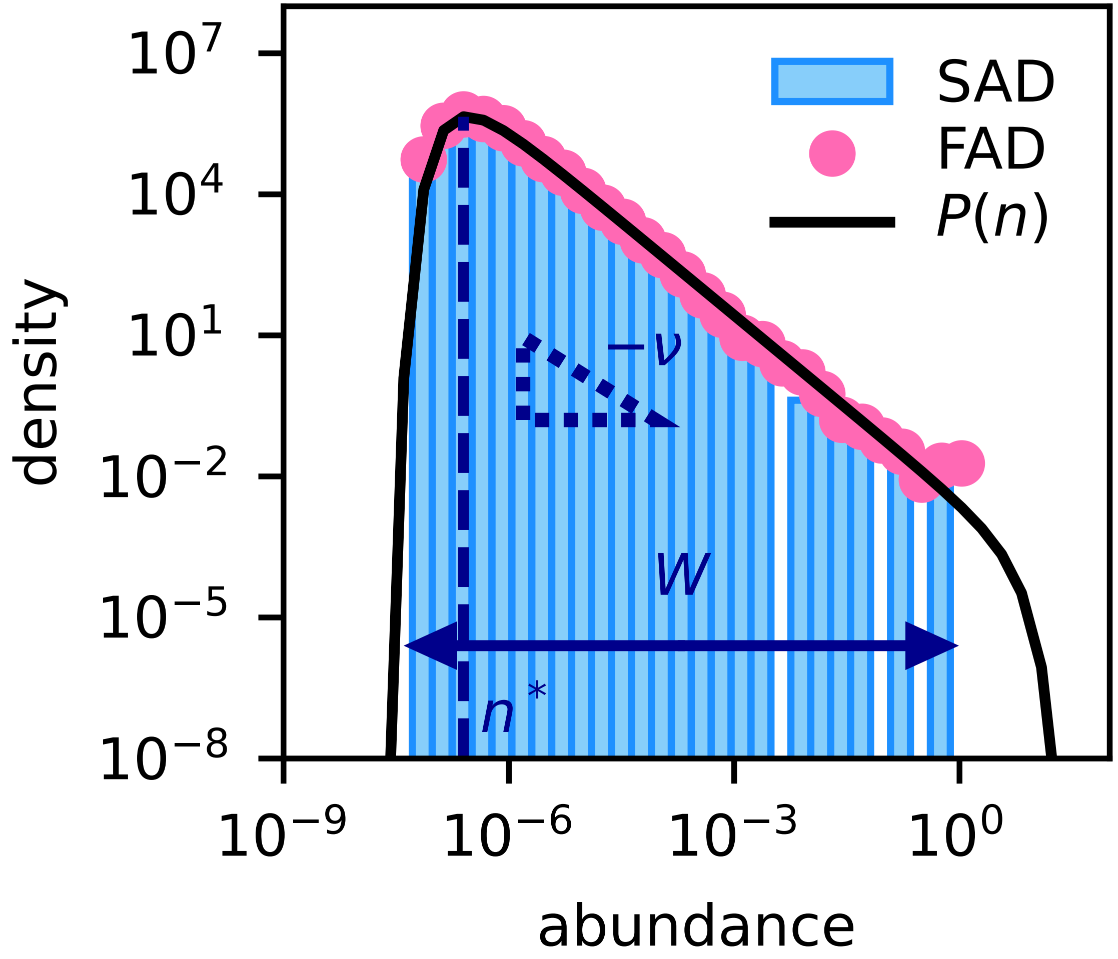
$$\dot{n} = n(r_{\text{eff}}(t) - \varepsilon n) + \lambda$$

$$P(n) \propto n^{-\nu} e^{-\frac{2}{\gamma_{\text{eff}}}(\varepsilon n + \lambda / n)}$$

$$\nu = 1 - \frac{2r^*_{\text{eff}}}{\gamma_{\text{eff}}}$$

Distributions of species abundances

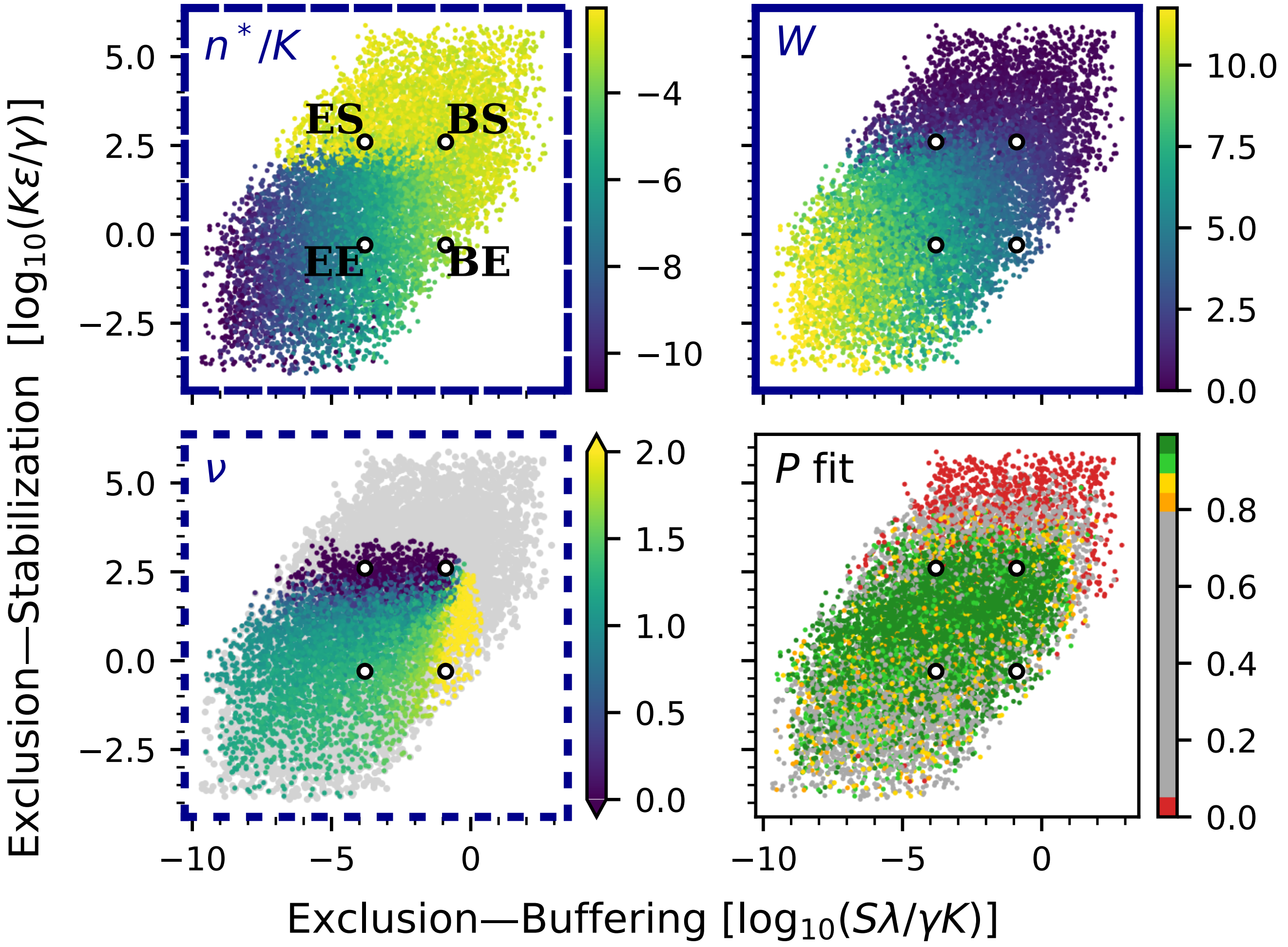


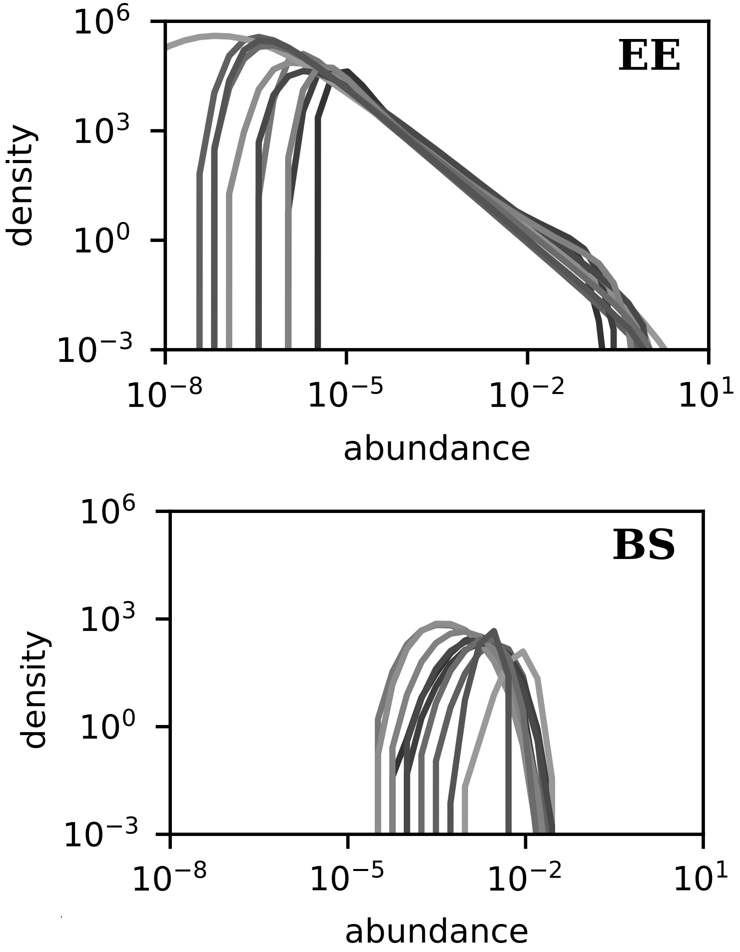


SAD: species abundance distribution (snapshot)

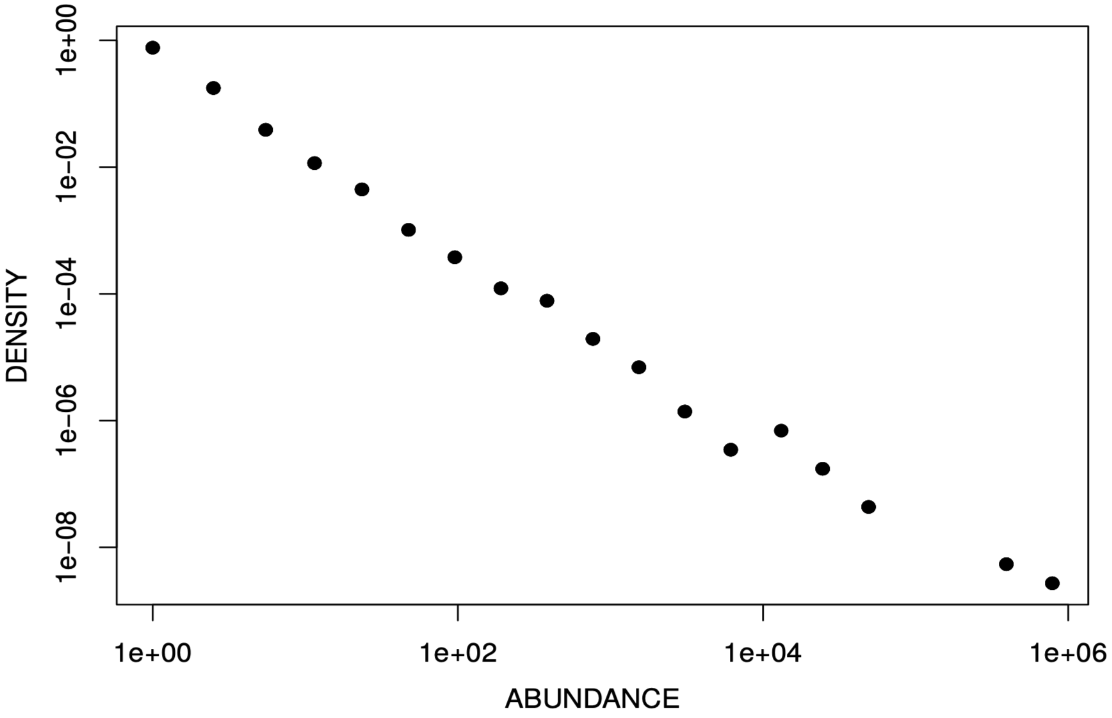
FAD: frequency abundance distribution

Distributions for time-average neutral communities

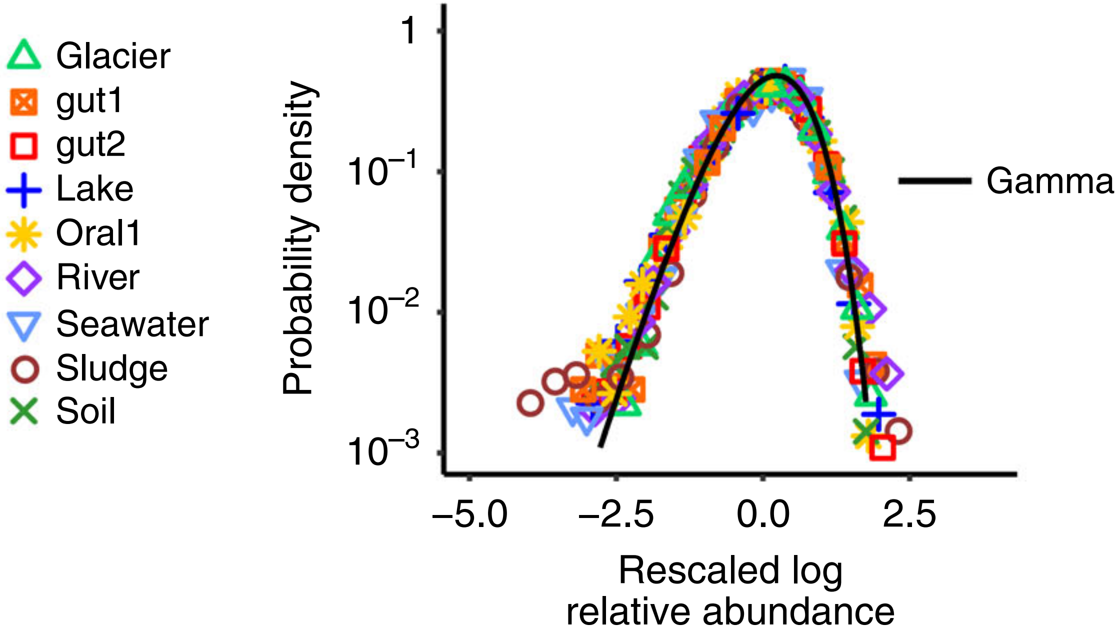




Empirical observations: SADs and AFDs

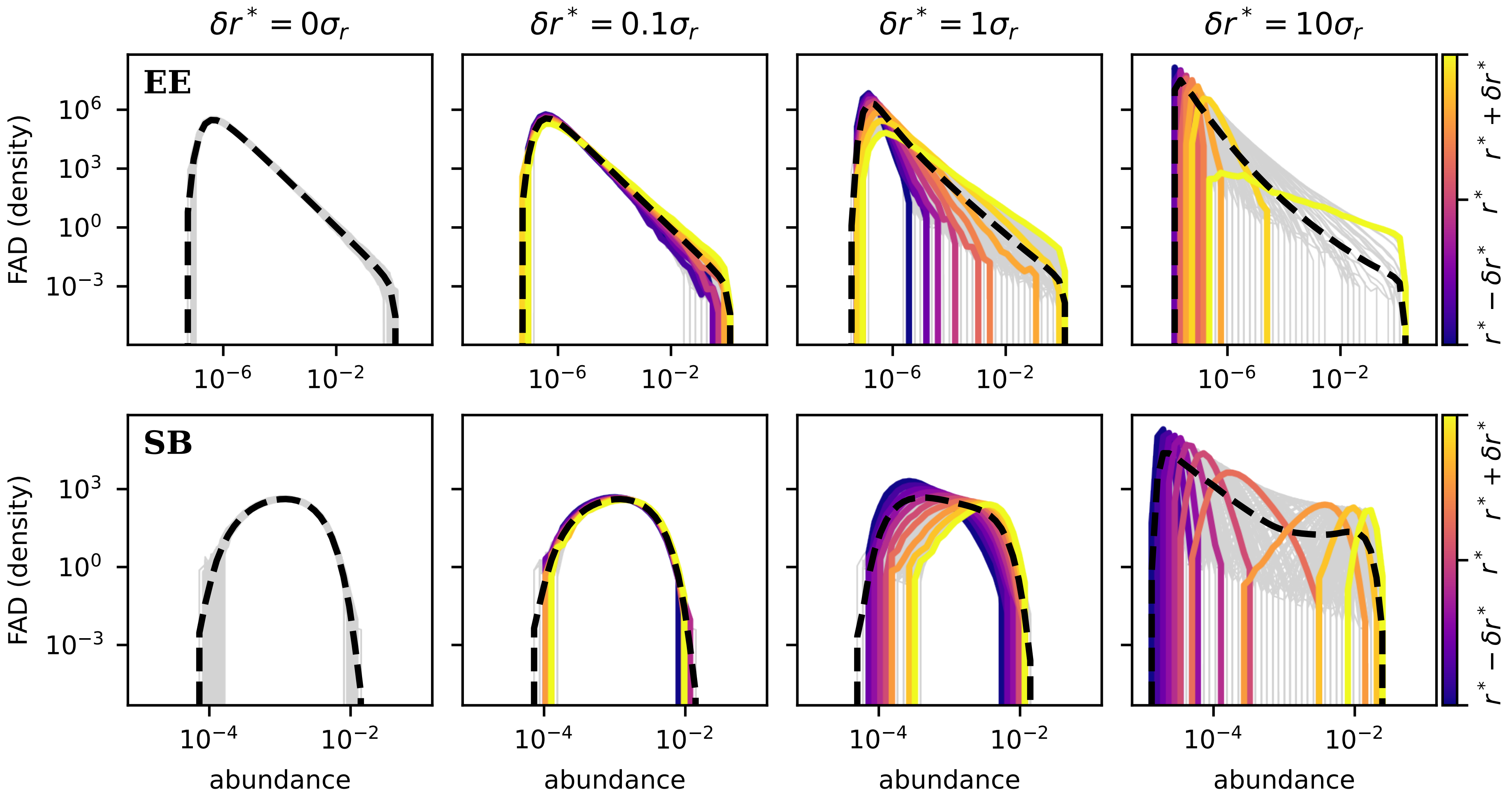


Internship of Fabio Rivellini



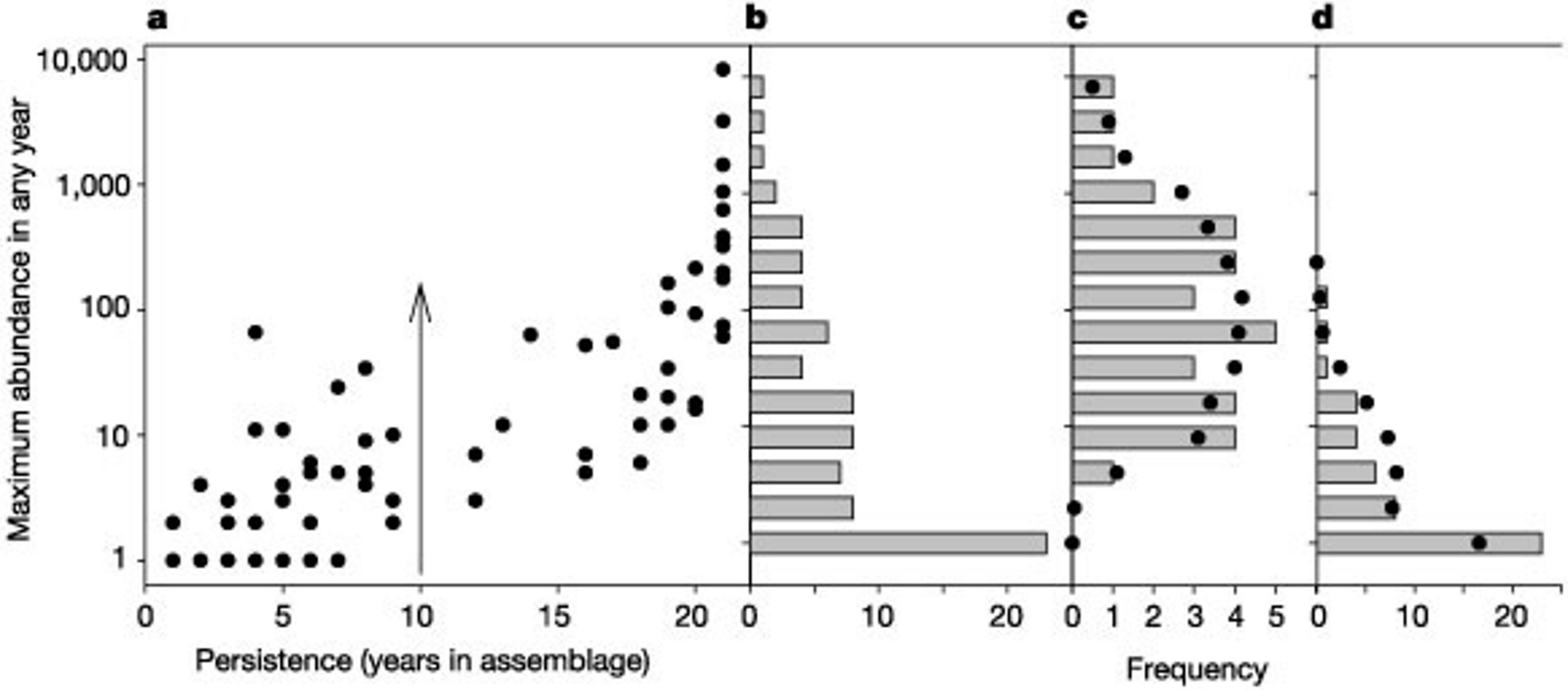
Grilli
Macroecological laws describe variation and diversity
in microbial communities
Nature Communications 2020

Distributions for heterogeneous communities



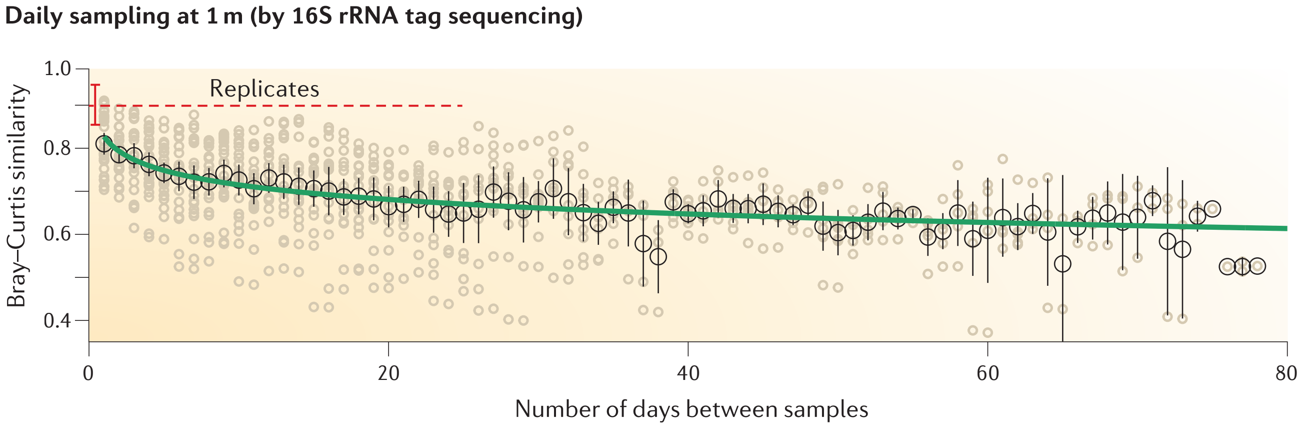
Single species are still described by the focal species model, but with varying parameters

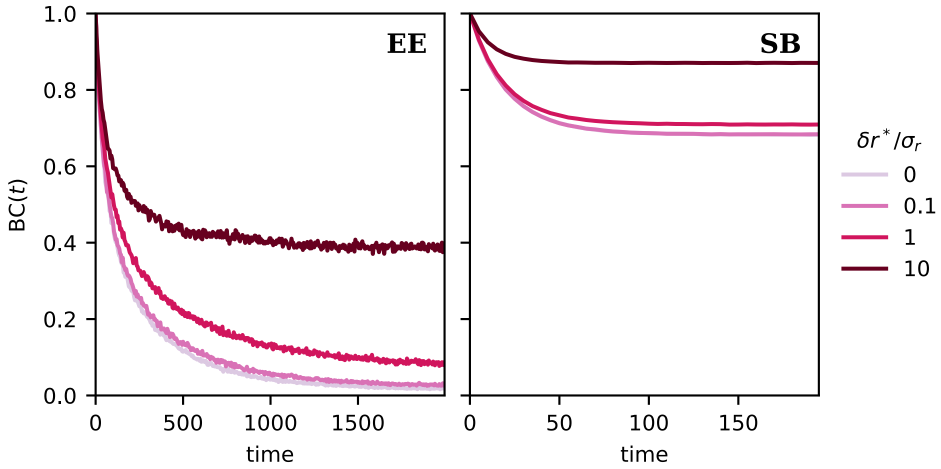
Empirical observations: frequent and occasional species



Magurran & Henderson
Explaining the excess of rare species in natural species abundance distributions
Nature 2003

Empirical observations: temporal turnover





Fuhrmann et al.
Marine microbial community dynamics and their ecological interpretation
Nature Reviews Microbiology 2015

Conclusions

The combination of fitness fluctuations (that yield growing inequalities in integrated fitness), buffering (that prevents extinction) and limitation (that bounds abundances) generically constrains abundance distributions.

A number of features of empirical observations (snapshot and time-resolved) are retrieved with a stylized model that encompasses those features.

In such model, the shape of the abundance distributions mostly depends on just two parameter combinations, that quantify the relative strength of limitation and of buffering relative to the exclusion time scale.

This pinpoints the limitations of resolving ecological processes from fitting abundance distributions, but also to the possible use of quantitative variation to distinguish different ecological regimes.

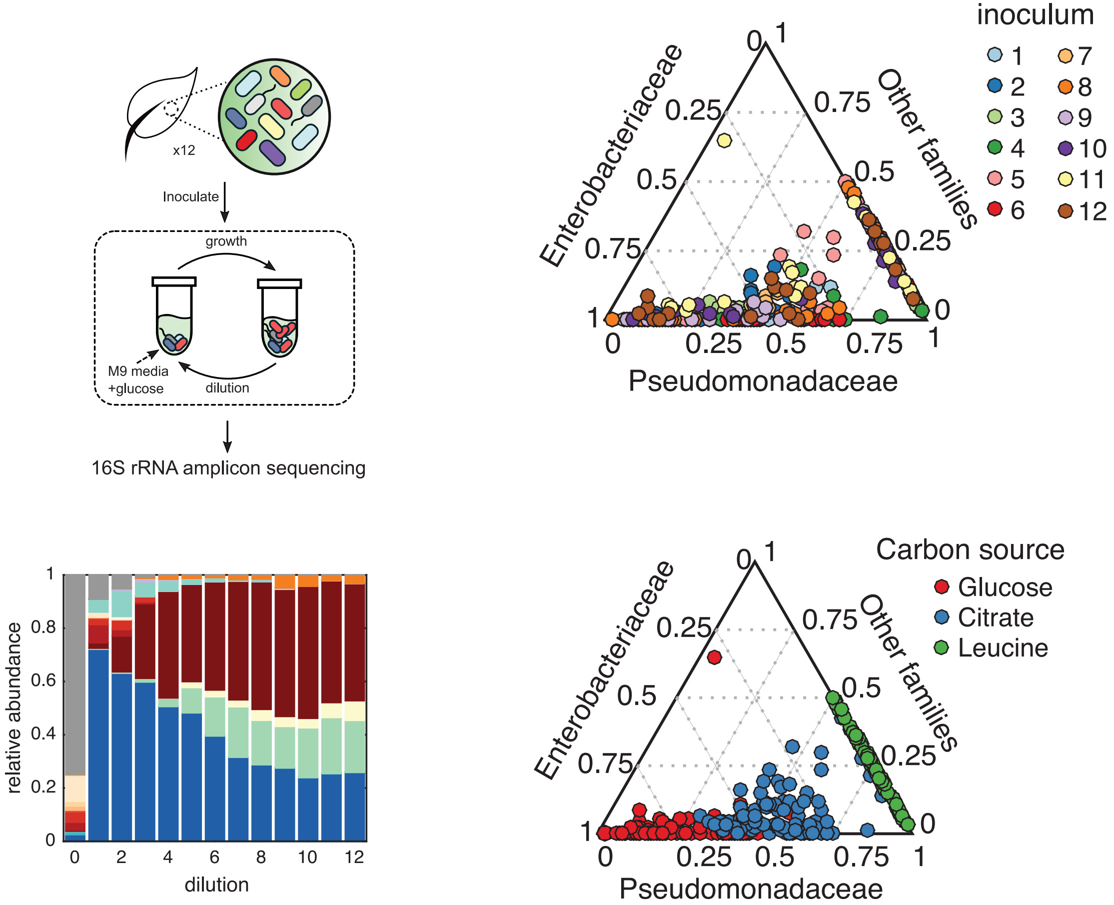
Emil Mallmin, Arne Traulsen, SDM
Fluctuating growth rates link turnover and unevenness in species-rich communities
https://arxiv.org/pdf/2505.01376

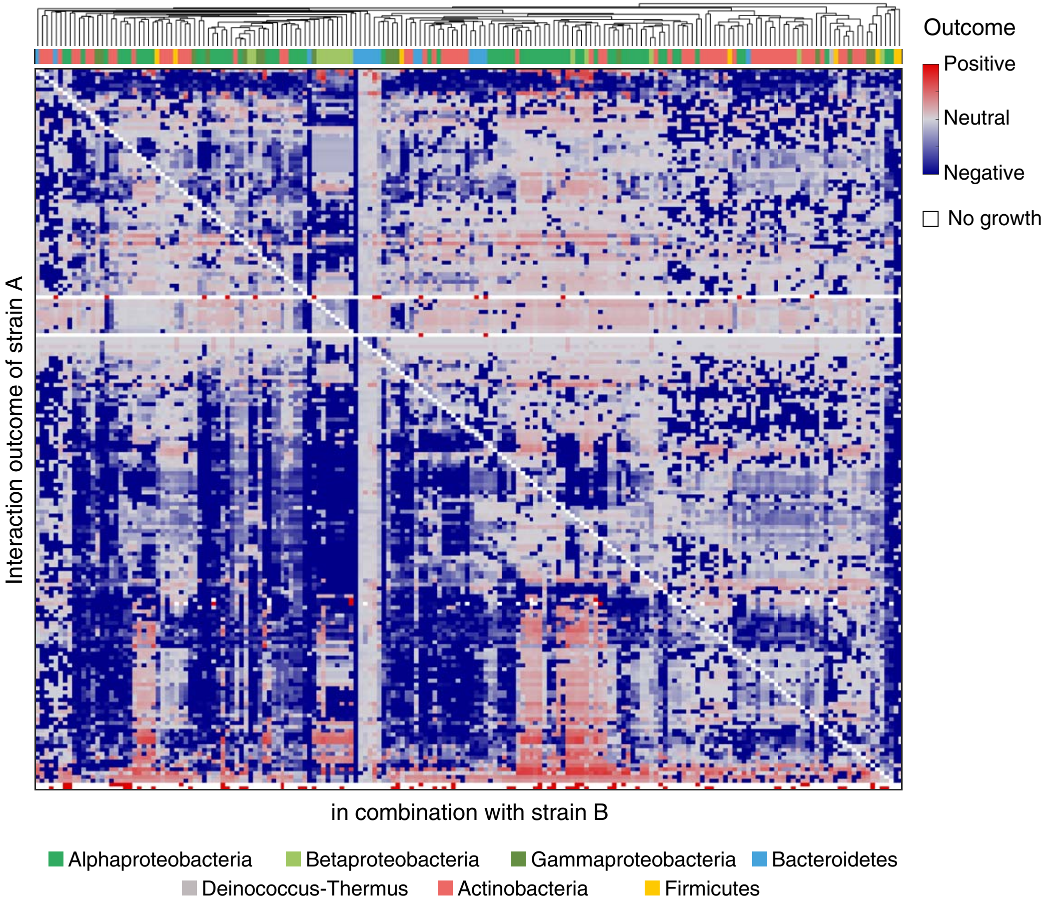
Random ecosystems with structure

Juan Giral-Martinez
(IBENS et INTP)

Matthieu Barbier
(INTP, CIRAD, Montpellier)

Species are often clustered into functional groups





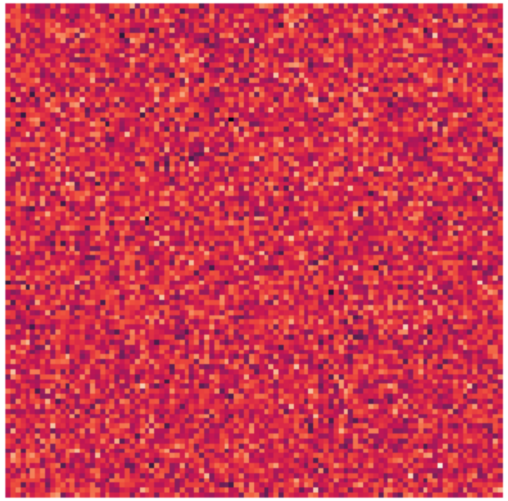
Goldford et al.
Emergent simplicity in microbial community assembly
Science (2018)

Schëfer, Pacheco et al.
Metabolic interaction models recapitulate leaf microbiota ecology
Science (2023)

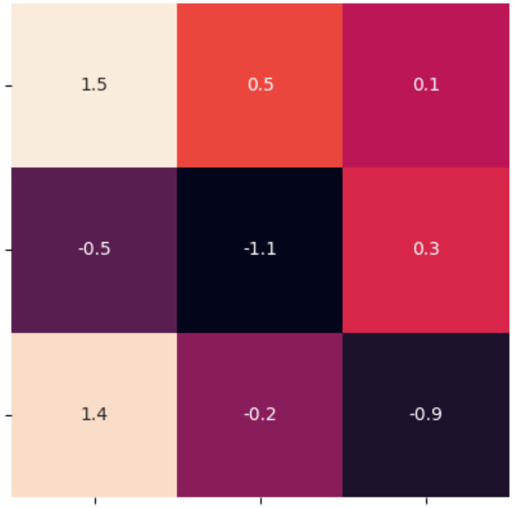
Disordered generalized LV equations with structure

$$\frac{dx_i(t)}{dt} = r_i x_i(t) \left(1 - x_i(t) + \sum_j \alpha_{ij} x_j(t) \right)$$

$$\alpha_{ij} =$$



$$+$$



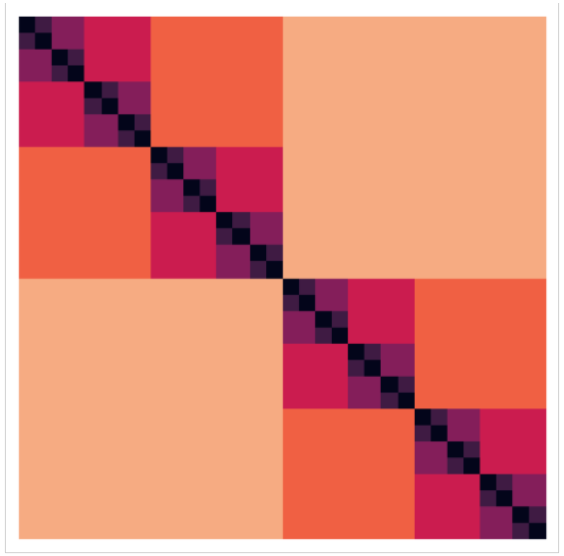
1.5	0.5	0.1
-0.5	-1.1	0.3
1.4	-0.2	-0.9

$$\mathbb{E}[\alpha_{ij}] = \frac{\mu}{S} \qquad \mathbb{V}[\alpha_{ij}] = \frac{\sigma^2}{S}$$

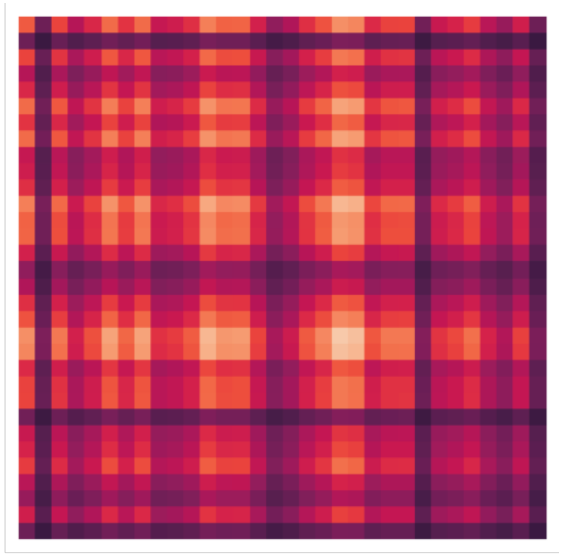
Types of structure

1.5	0.5	0.1
-0.5	-1.1	0.3
1.4	-0.2	-0.9

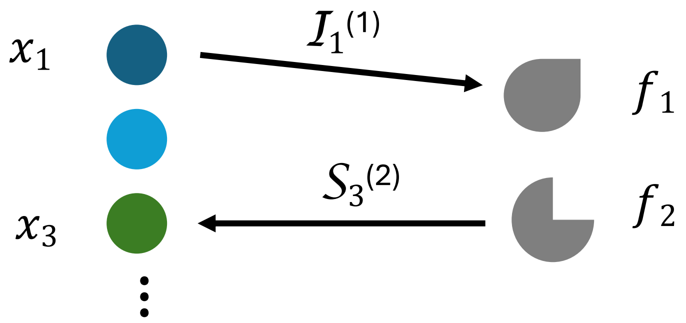
Group structure



Nested structure (e.g. phylogenies)



Competition for one resource

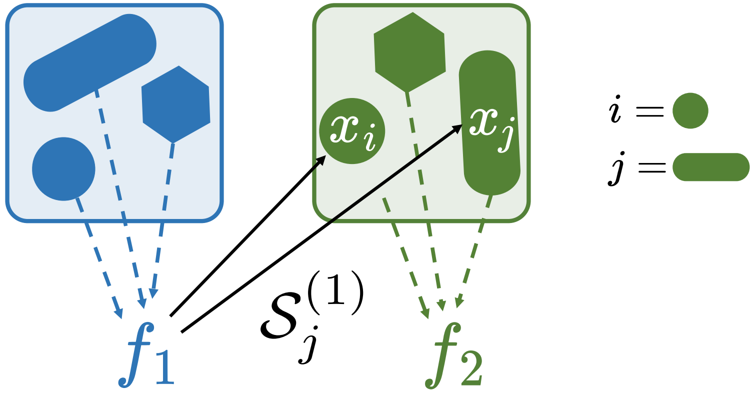


$\mathcal{I}_i^{(\lambda)}$ impact traits

$\mathcal{S}_i^{(\lambda)}$ sensitivity traits

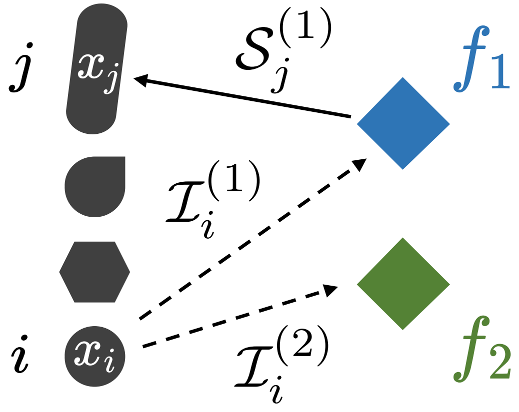
Examples of structuring interactions

Two functional groups



$$\mathcal{I}_i^{(\lambda)} = 1$$

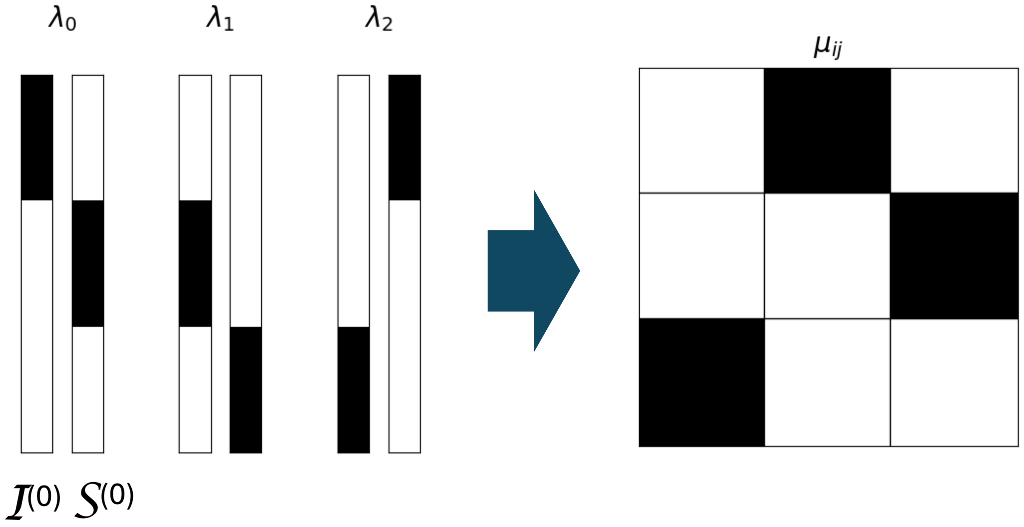
Consumer-resource



Structured random interaction matrix

functions’ index

$\lambda = 1 \ldots n_F$



$$\mu_{ij} = \frac{1}{S}\sum_{\lambda} \mathcal{S}_i^{(\lambda)} \mathcal{I}_j^{(\lambda)}$$

$$A_{ij} = \mu_{ij} + \frac{\sigma}{\sqrt{S}} z_{ij}$$

σ measures the weight of the random versus structured component of interactions

‘Structured’ DMFT

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i \left[1 - x_i + \sum_\lambda u_i^{(\lambda)} f_\lambda(t) + \sigma \zeta_i(t) \right]$$

$$f_\lambda(t) = \frac{1}{S} \sum_i v_i^{(\lambda)} x_i(t)$$

$$C(t,t') = \overline{x_i(t) x_i(t')}$$

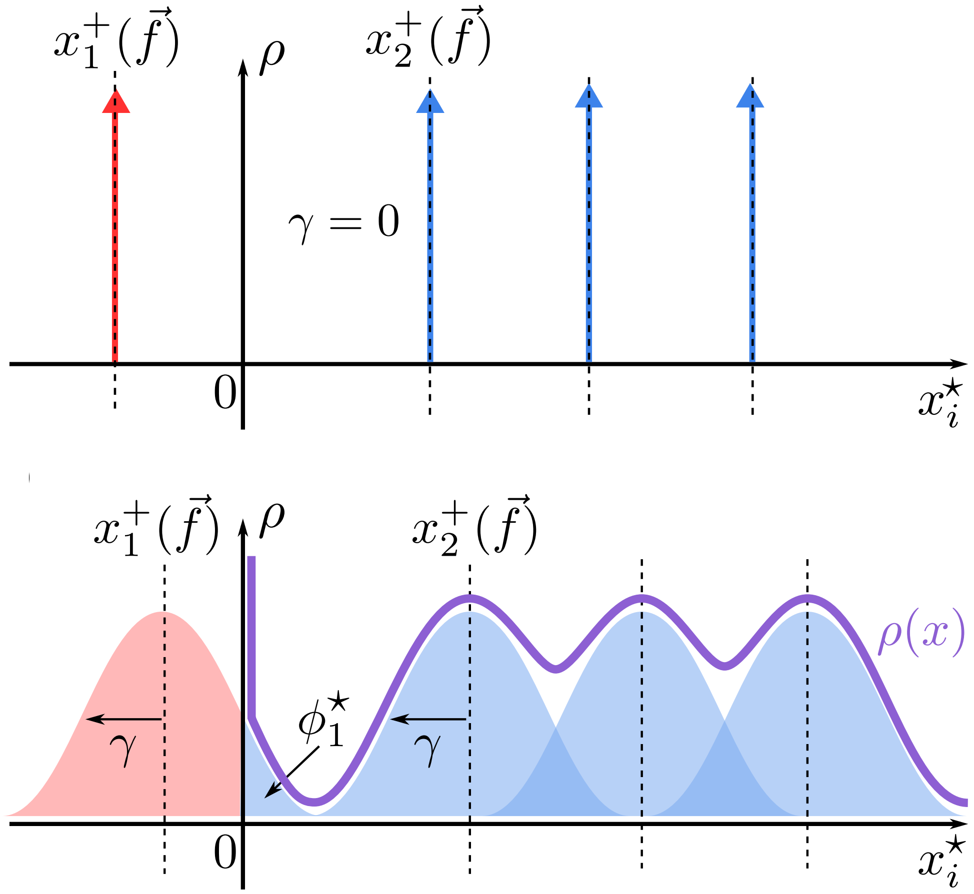
$n_F + 1$ mesoscopic degrees of freedom

At equilibrium, these are coupled by community-level self-consistent relations

$$f_\lambda^\star = \frac{\gamma}{S} \sum_i \mathcal{I}_i^{(\lambda)} \; \omega_1\left(\frac{x_i^+}{\gamma}\right)$$

$$1 = \frac{\sigma^2}{S} \sum_i \omega_2\left(\frac{x_i^+}{\gamma}\right)$$

Equilibrium SADs



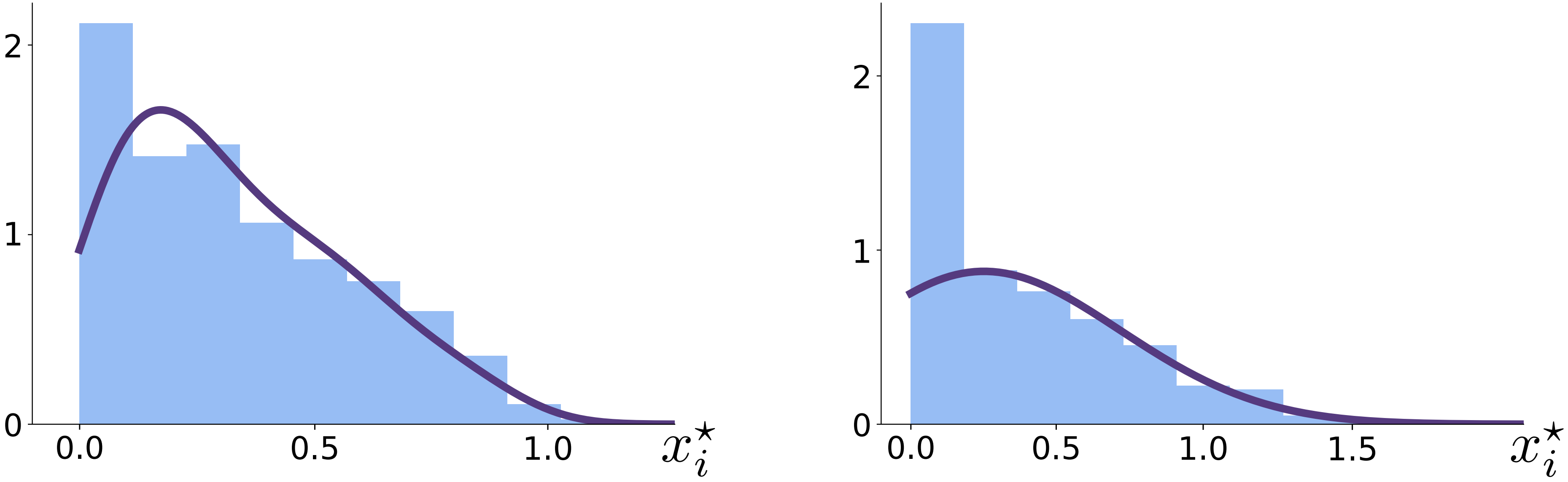
$$x_i^+ = 1 + \sum_\lambda \mathcal{S}_i^{(\lambda)} f_\lambda^\star$$

$$x_i^\star = \max\left(0, x_i^+ + \gamma \xi_i^\star\right)$$

$$\gamma = \sigma \sqrt{C^\star}$$

The combination of structure and disorder can create virtually any shape of the species abundance distribution.

Trait structure propagates to the SAD



Power-law distributed response traits give rise to power-law SADs for small randomness, but for strong randomness the Gaussian shape supersedes.

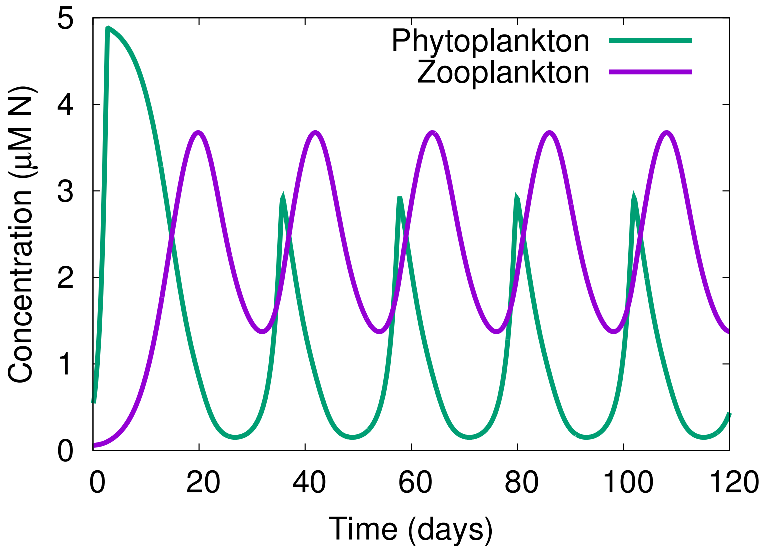
Group structure and out-of-equilibrium dynamics

Ecosystems with a small number of functional classes (macroscopic degrees of freedom) are predicted to easily produce oscillations

$$\frac{dN}{dt} = -\frac{\mu_{P,max} N}{N + K_N} P + I_{N,tot}$$

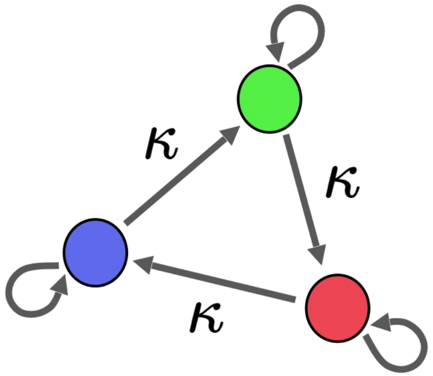
$$\frac{dP}{dt} = \frac{\mu_{P,max} N}{N + K_N} P - m_P P - \frac{\mu_{Z,max} P}{P + K_P} Z$$

$$\frac{dZ}{dt} = \frac{\mu_{Z,max} P}{P + K_P} Z - m_Z Z - d_Z(Z) Z$$

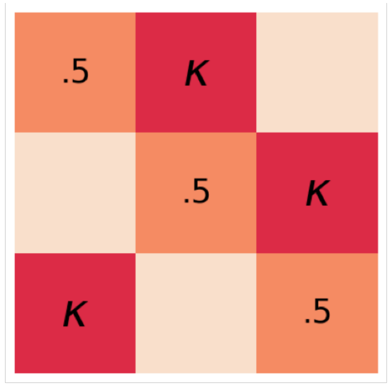


Omta et al.
Trophic model closure influences ecosystem response to enrichment
Ecological Modelling (2023)

Dynamics

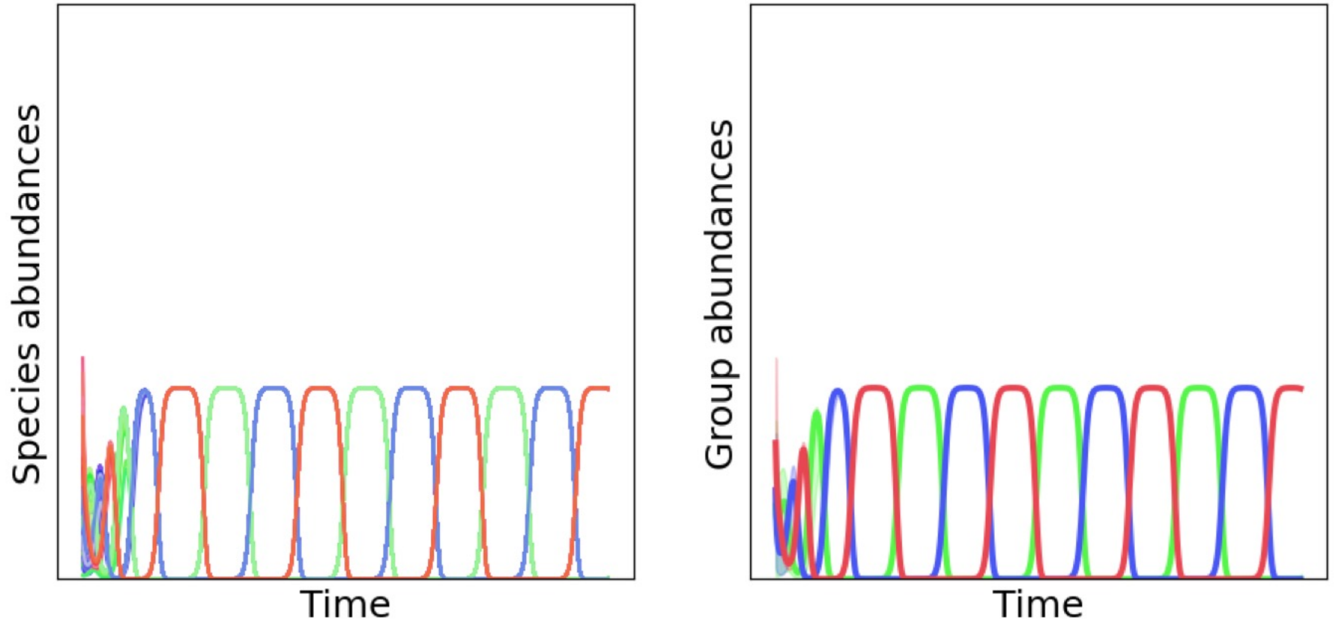


(Rock-paper-scissors)



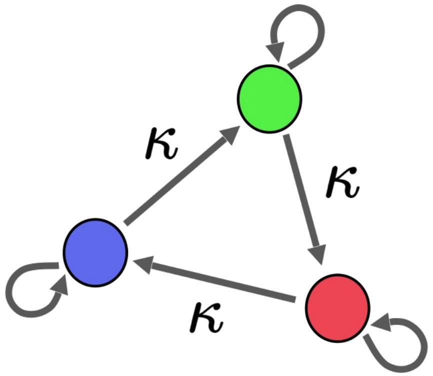
.5	κ	
	.5	κ
κ		.5

(structural matrix)

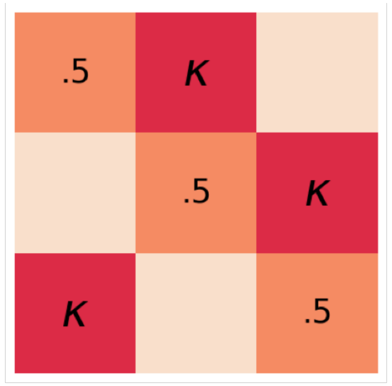


$$\sigma = 0$$

Dynamics

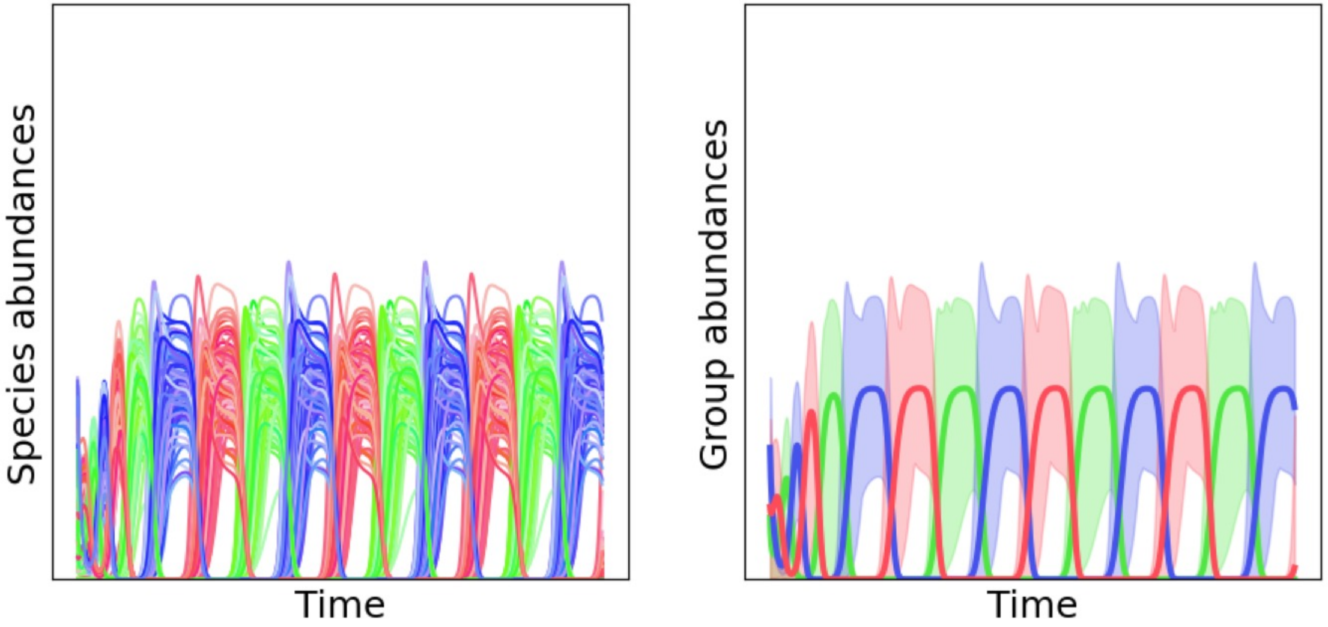


(Rock-paper-scissors)



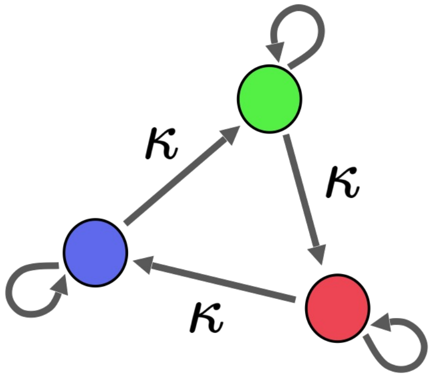
.5	κ	
	.5	κ
κ		.5

(structural matrix)

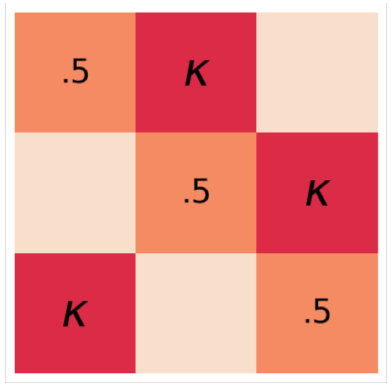


$$\sigma = 0.3$$

Dynamics

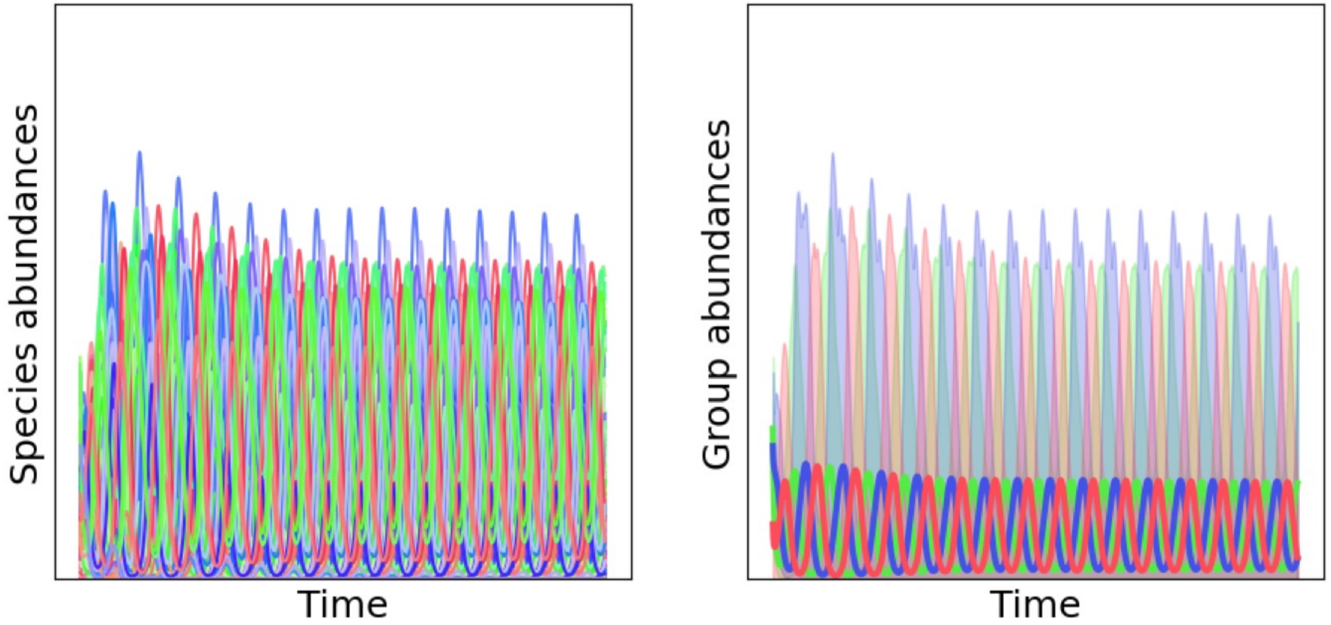


(Rock-paper-scissors)



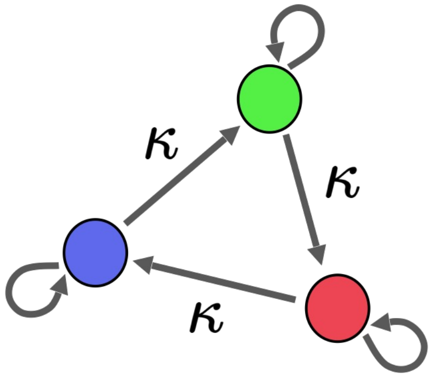
.5	κ	
	.5	κ
κ		.5

(structural matrix)

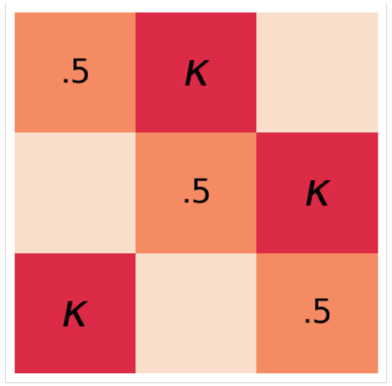


$$\sigma = 0.95$$

Dynamics

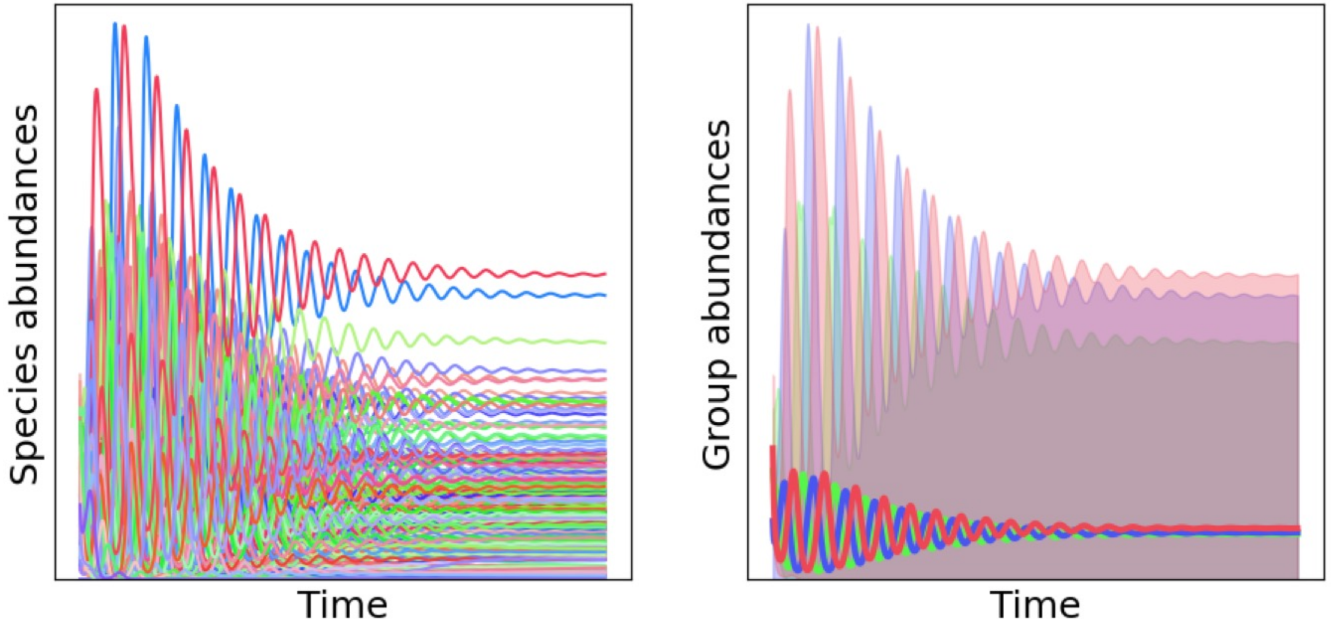


(Rock-paper-scissors)



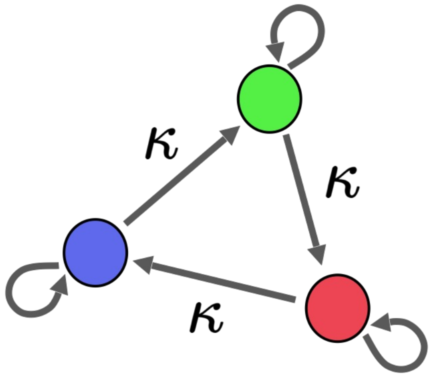
.5	κ	
	.5	κ
κ		.5

(structural matrix)

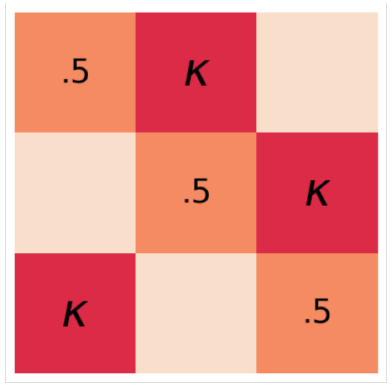


$$\sigma = 1.05$$

Dynamics

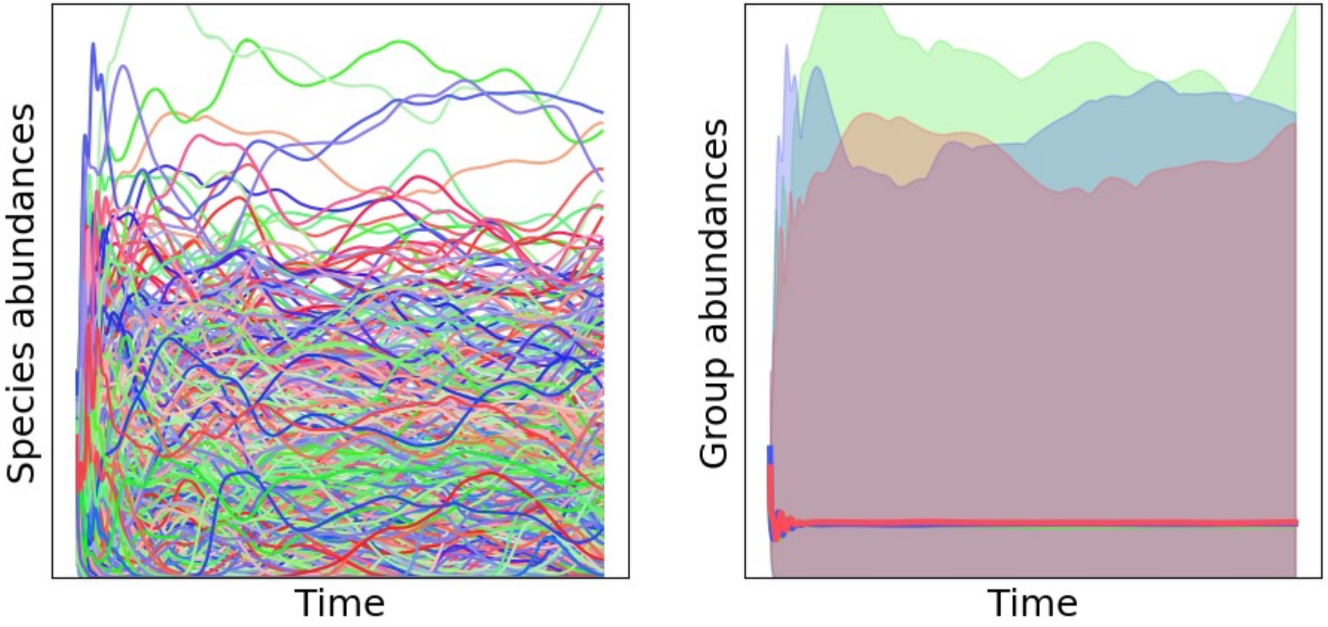


(Rock-paper-scissors)



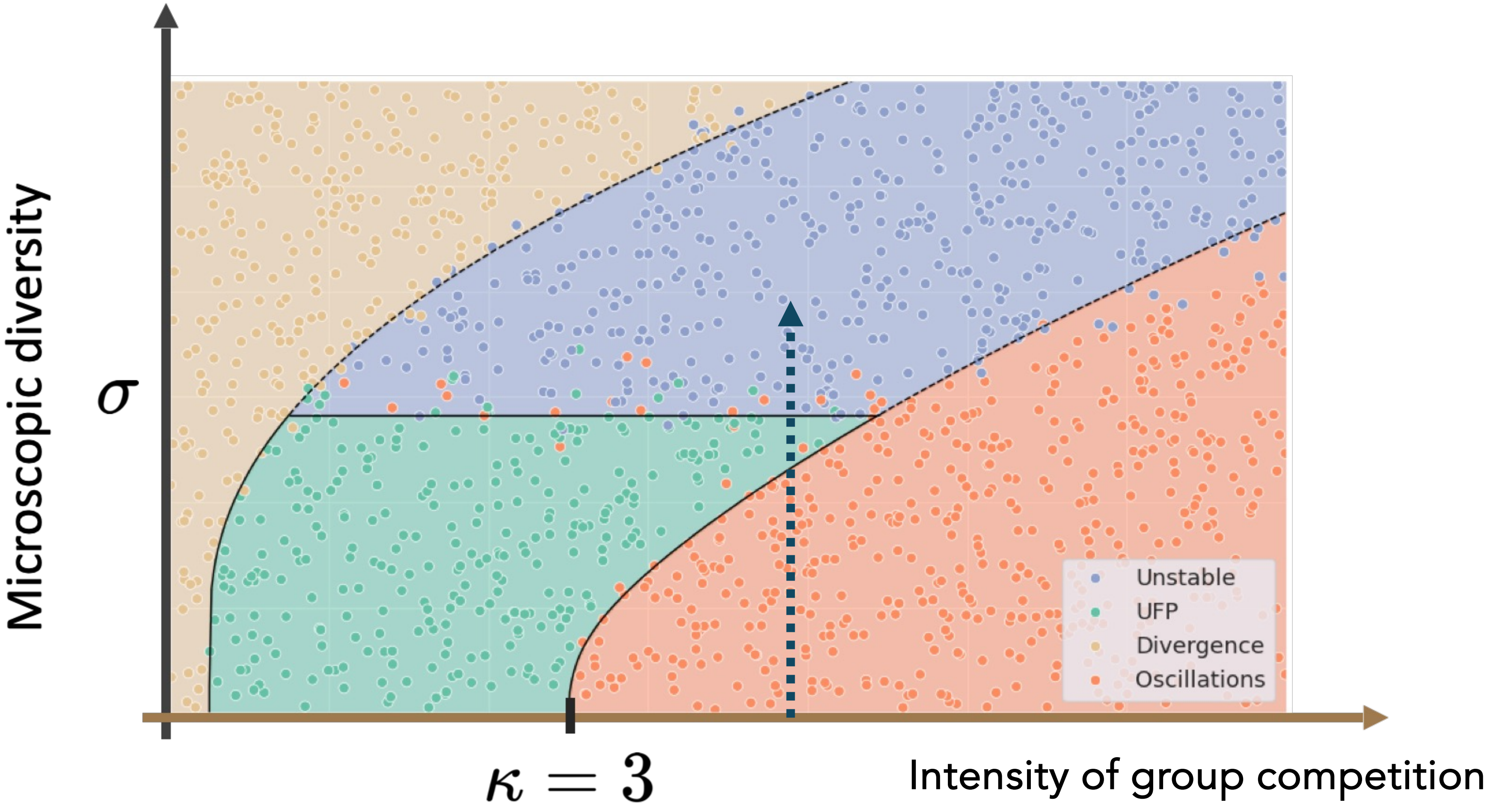
.5	κ	
	.5	κ
κ		.5

(structural matrix)

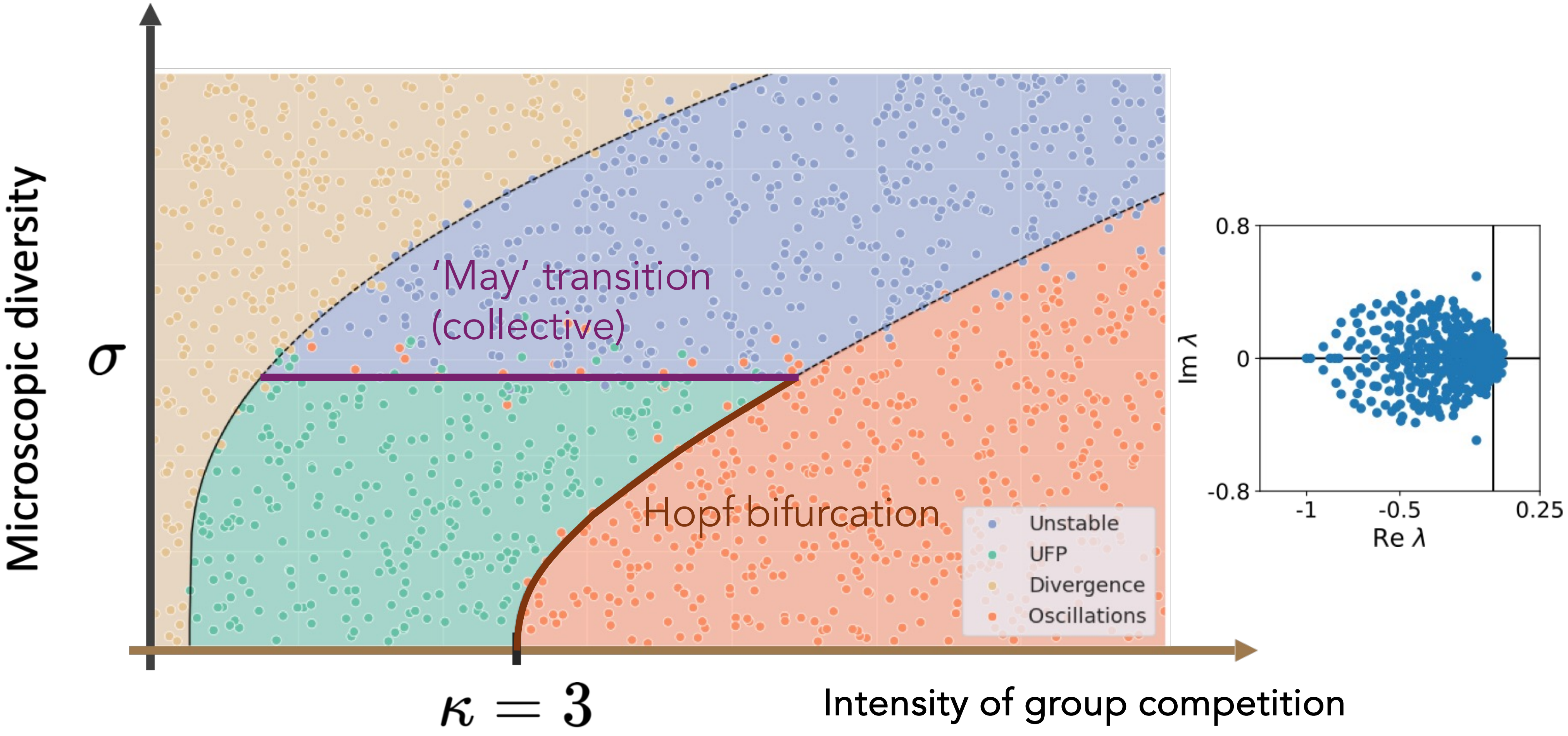


$$\sigma = 1.5$$

Diversity and stability



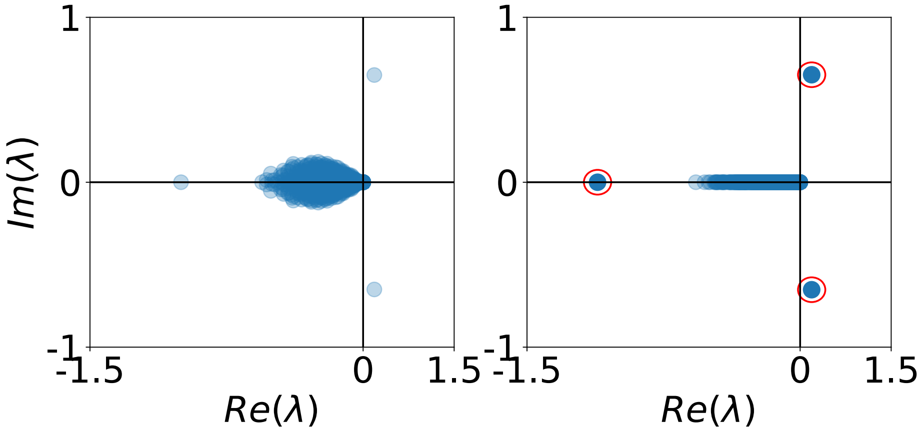
Diversity and stability



Coherent loss of stability of the fixed point

Pseudo-Jacobian

$$\mathcal{J}_{ij} = -x_i^\star \left(\delta_{ij} - \mu_{ij}\right) \qquad x_i^\star = \max\left(0, x_i^+ + \gamma \xi_i^\star\right)$$

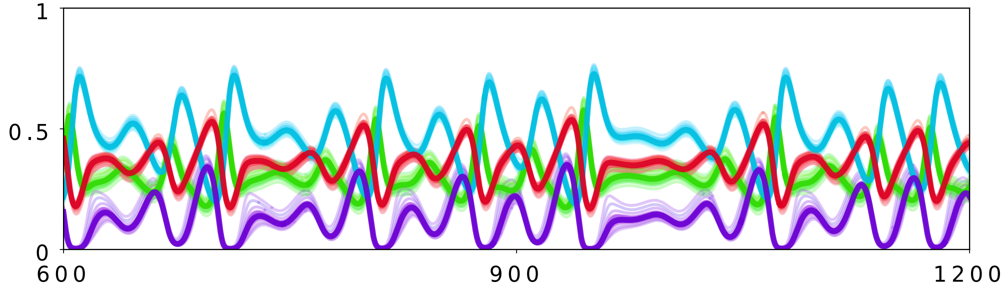


The outlier eigenvalues of the pseudo-Jacobian are the same as the Jacobian, but depend on disorder only through the equilibrium abundances.
They shift to the left when disorder increases.

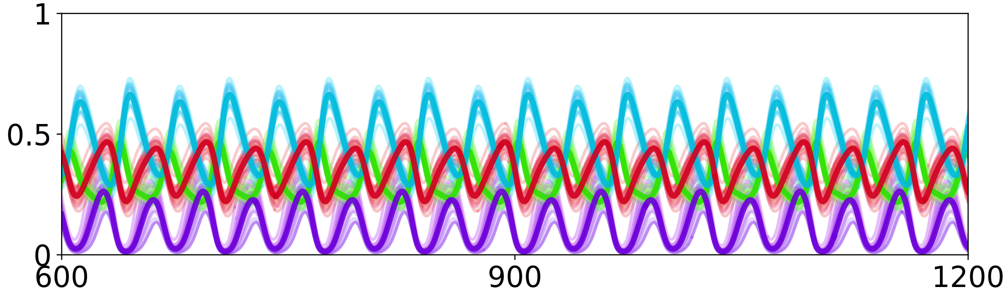
As the time scales associated with the microscopic variables spread out, the macroscopic and microscopic oscillations are simultaneously suppressed

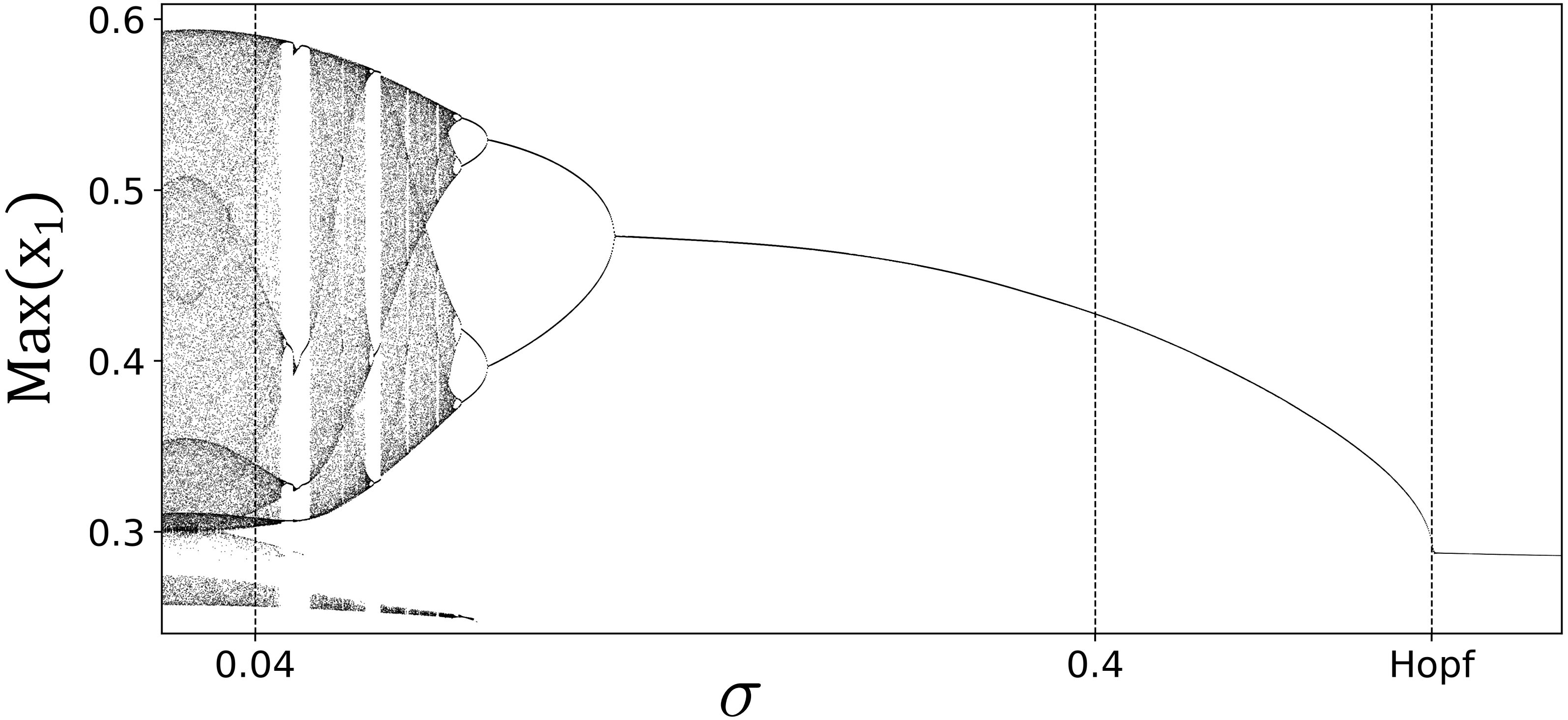
Low-dimensional chaos and randomness

$\sigma = 0.04$

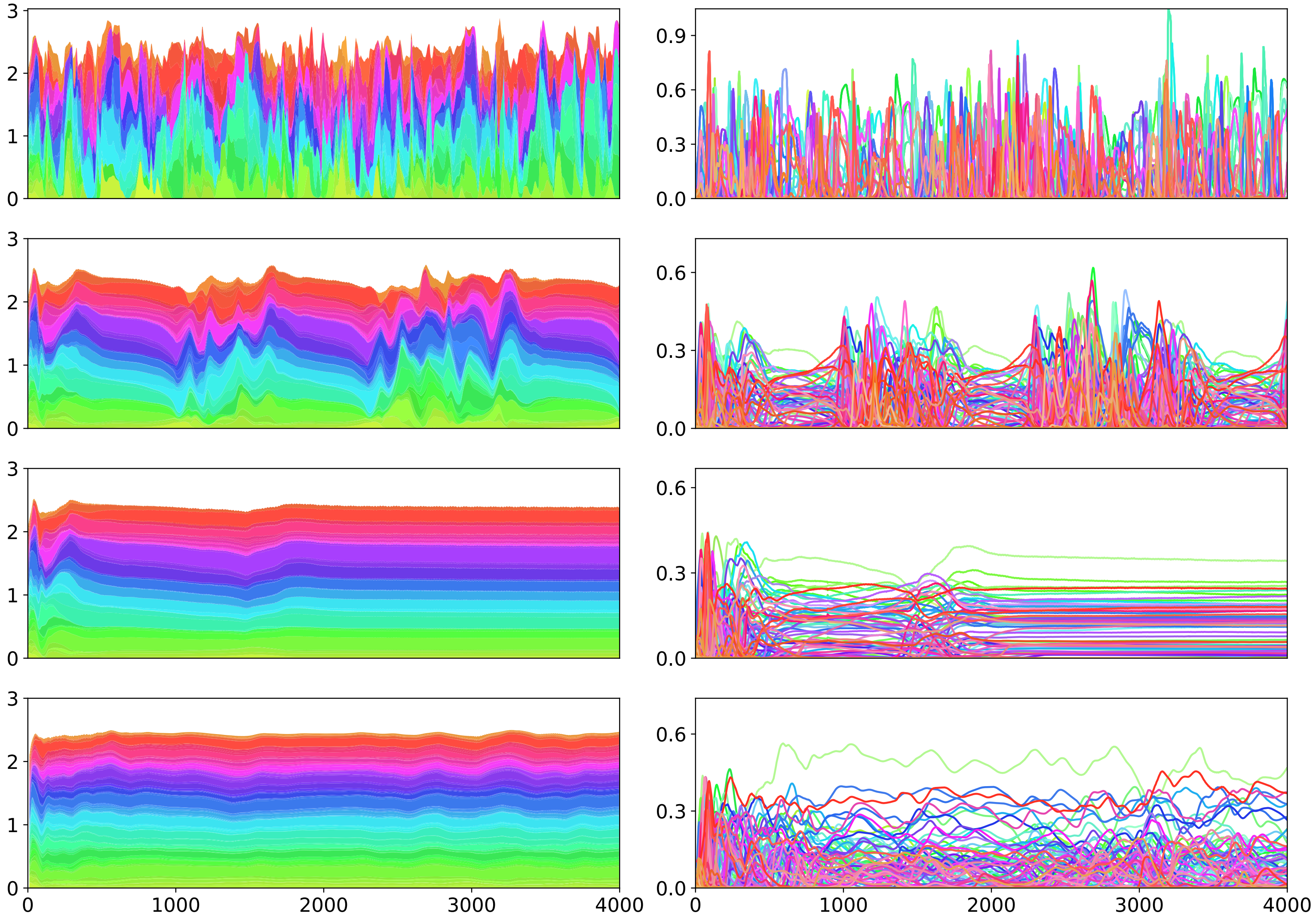


$\sigma = 0.4$





High-dimensional chaos and randomness



Conclusions on the interplay of structure and randomness

Structure and randomness overlap simply at equilibrium, where the system is described by mesoscopic variables that combine them.

Equilibria can lose stability through both collective transitions and low-codimension bifurcations.

When the structured dynamics is out-of-equilibrium, dephasing of species oscillations within functional groups induces community stabilization for intermediate disorder.

How to evaluate the degree of randomness in real ecosystems?

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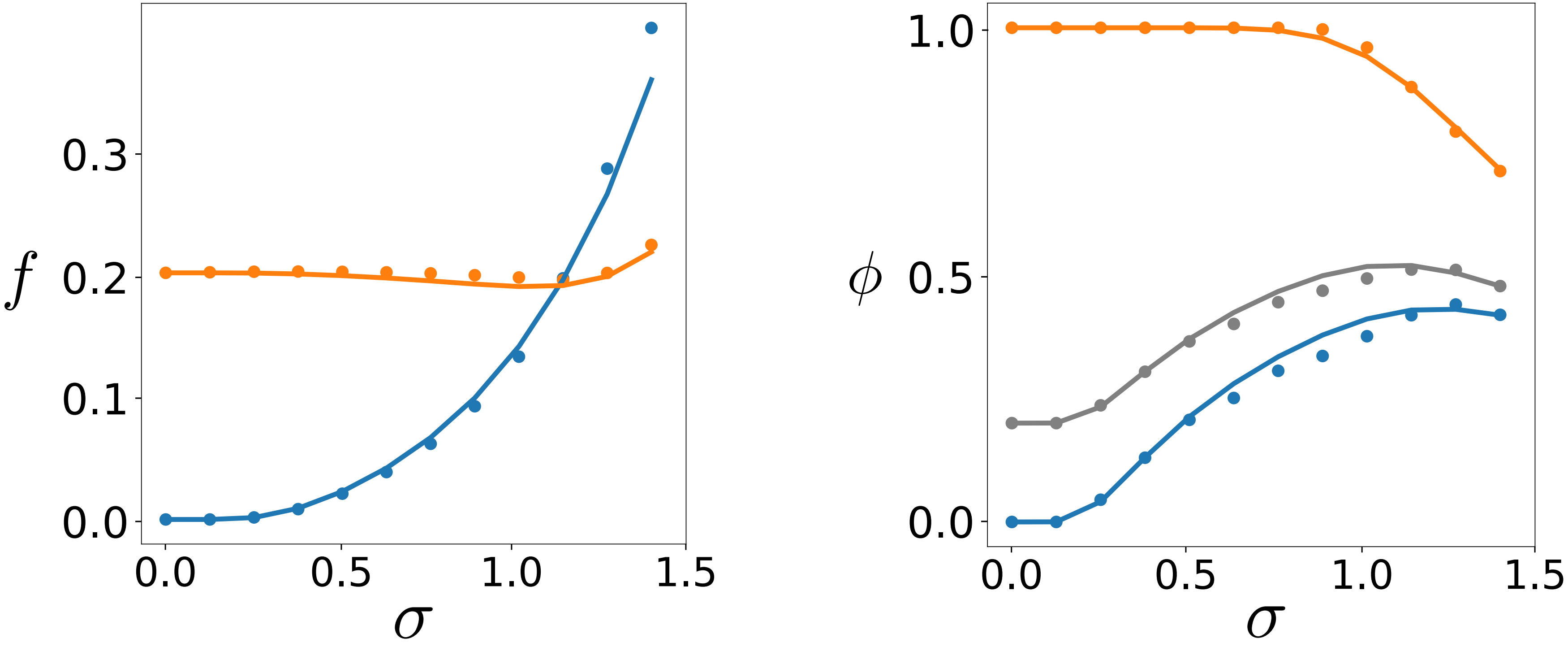

f
0.3
0.2
0.1
0.0
0.0
0.5
1.0
1.5
σ
ϕ
1.0
0.5
0.0
0.0
0.5
1.0
1.5
σ