Ecological Network Dynamics and Fluctuations Favour Species Coexistence in Ecological Communities

L. Pacciani Mori[1,3], A. Giometto[2], F. Ferraro[1], S. Azaele[1], A.Maritan[1,] S.Suweis [1]

[1]Università di Padova
[2] Cornell University
[3] University of California, San Diego

&thanks for inspiring discussions @LIPh Lab

www.liphlab.com

**ELLIIT Symposium
"Network Dynamics and Control" 20-22
September**

ELLIIT
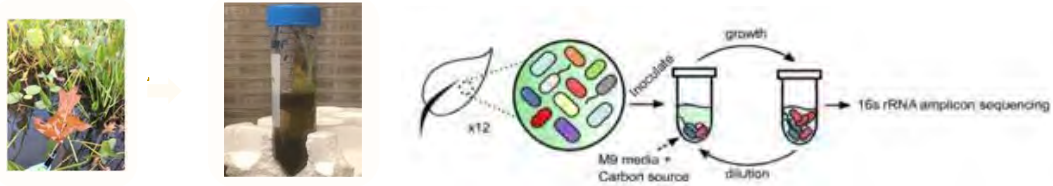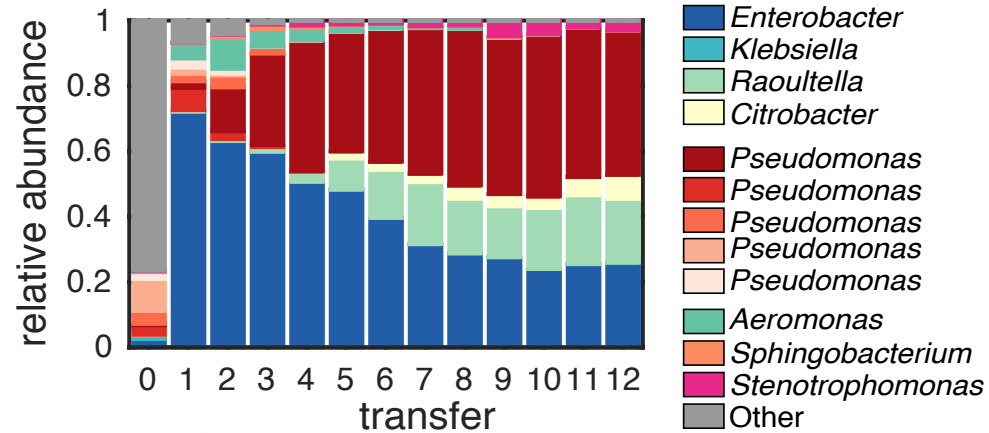
UNIVERSITÀ
DEGLI STUDI
DI PADOVA

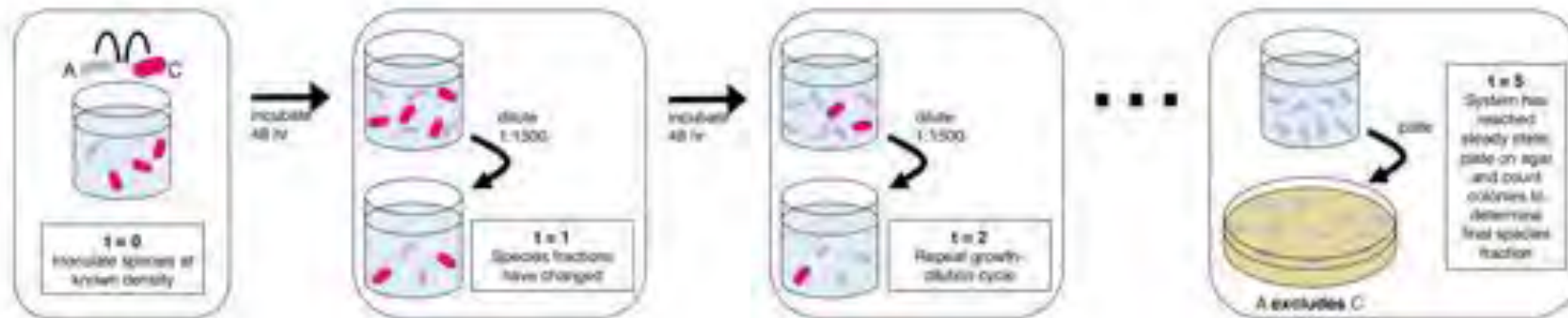@SamirSuweis

How many species can coexist?

The paradox of Plankton, Hutchinson 1961

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

Ecological Niches & Competition Exclusion Principle

Friedman et al., *Nature Ecology and Evolution*, 2017

Consumer resource models

MacArthur model, 1970

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i(c_i) - \delta_\sigma \right)$$

$$\dot{c}_i = s_i - \sum_{\sigma=1}^{m} n_\sigma \alpha_{\sigma i} r_i(c_i)$$

$$\sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i^*(c_i) = \delta$$

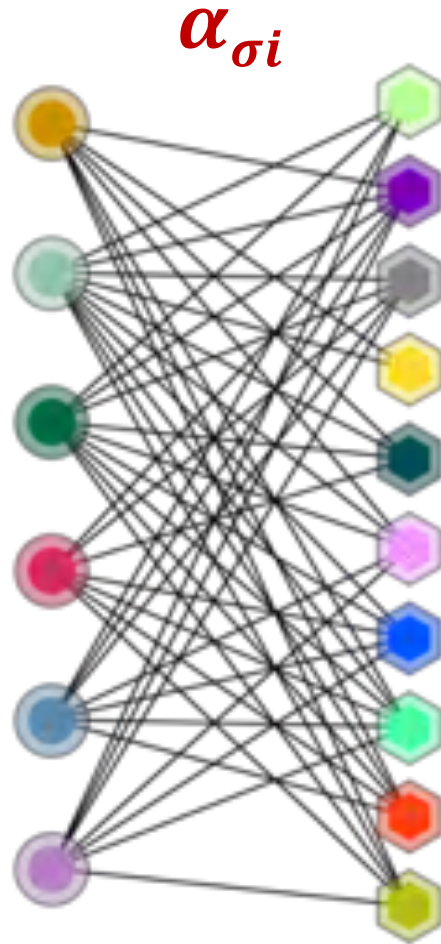## Competition Exclusion Principle

These are *m* equations in *p* variables

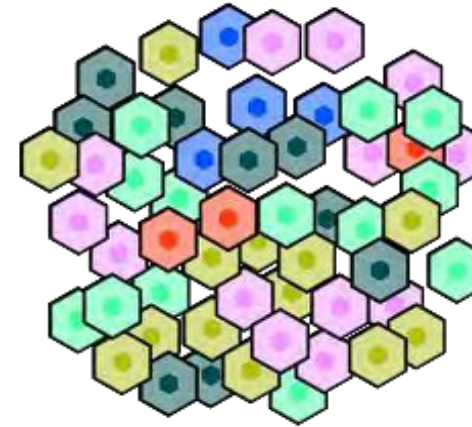If *m>p:* no solution for the system
It solvable only if *m≤p*

The Competitive
Exclusion Principle

(CEP – Hardin 1961,…)

Species-Resource Bipartite Network
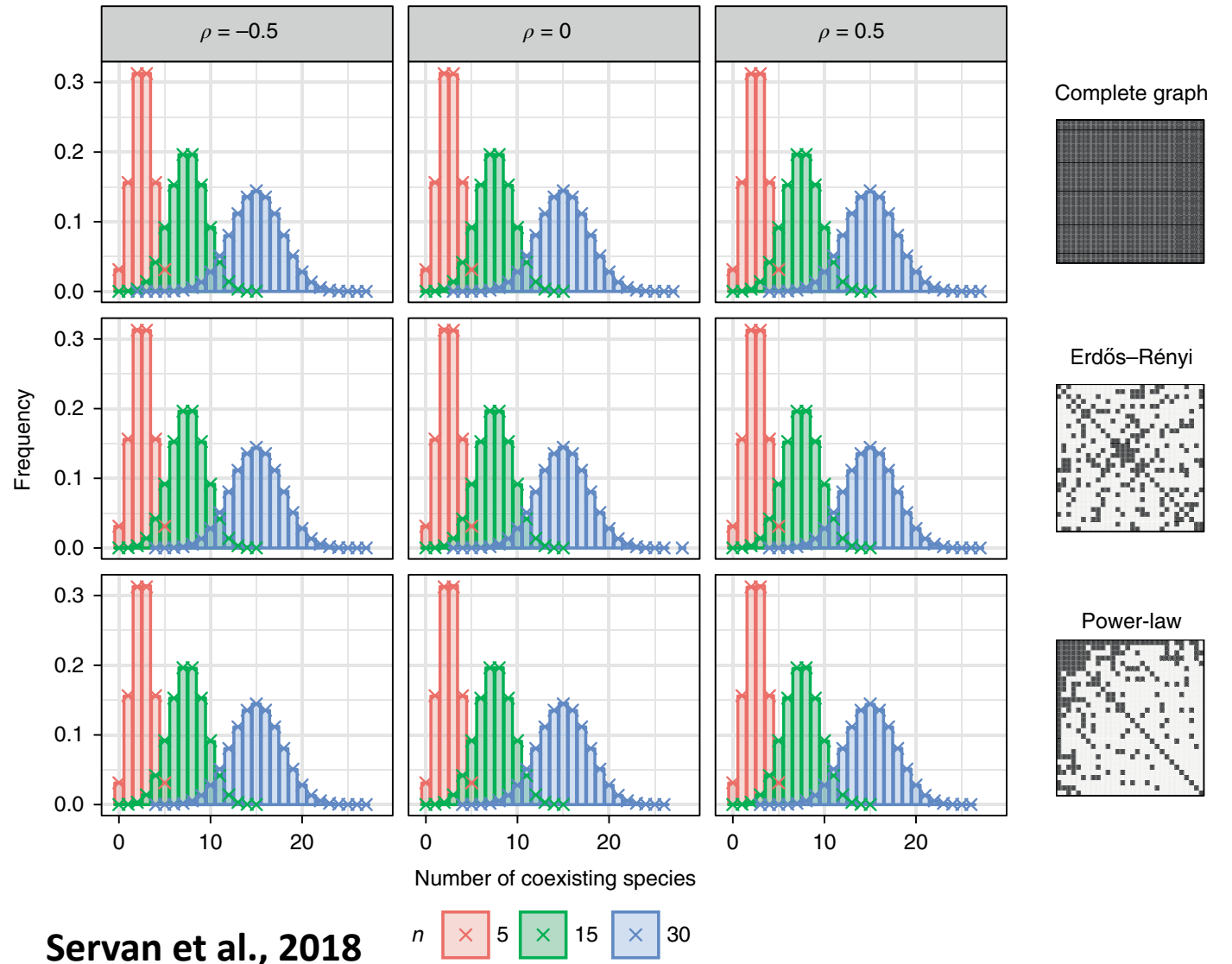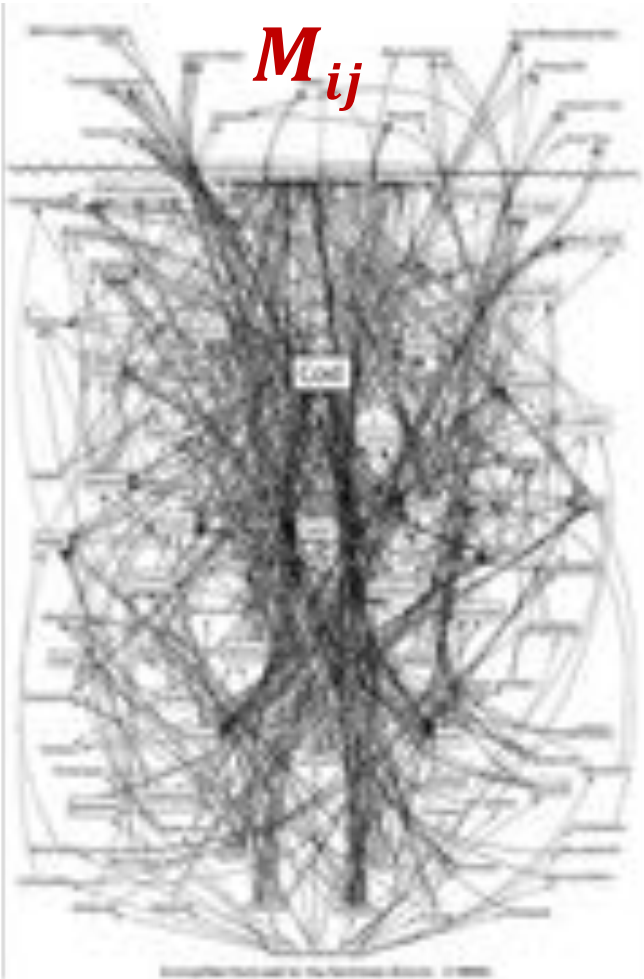
Generalized Lotka-Volterra Equations

$$\frac{dx_i}{dt} = x_i \left(\alpha_i - \sum_{j}^{S} M_{ij} x_j \right) \equiv f_i(\vec{x})$$

M_{ij}

Servan et al., 2018

Complexity-Stability Paradox

NATURE VOL. 238 AUGUST 18 1972
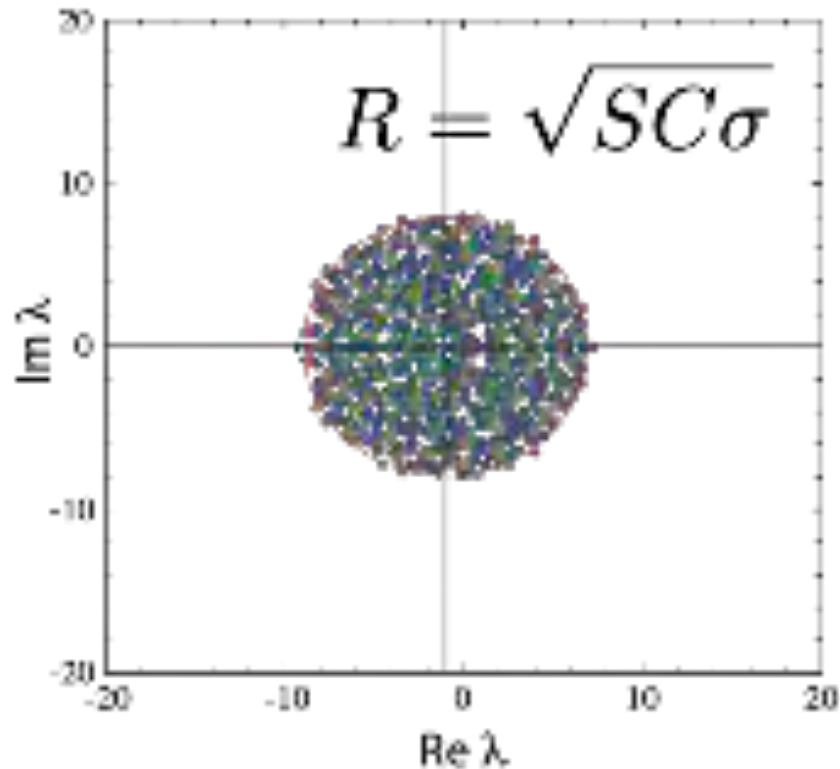
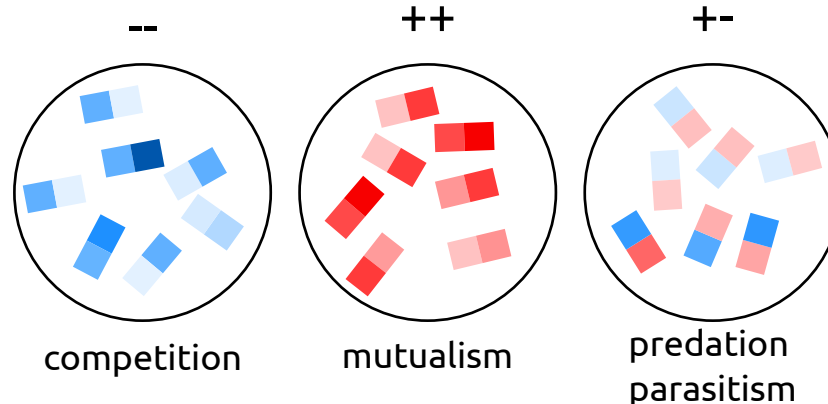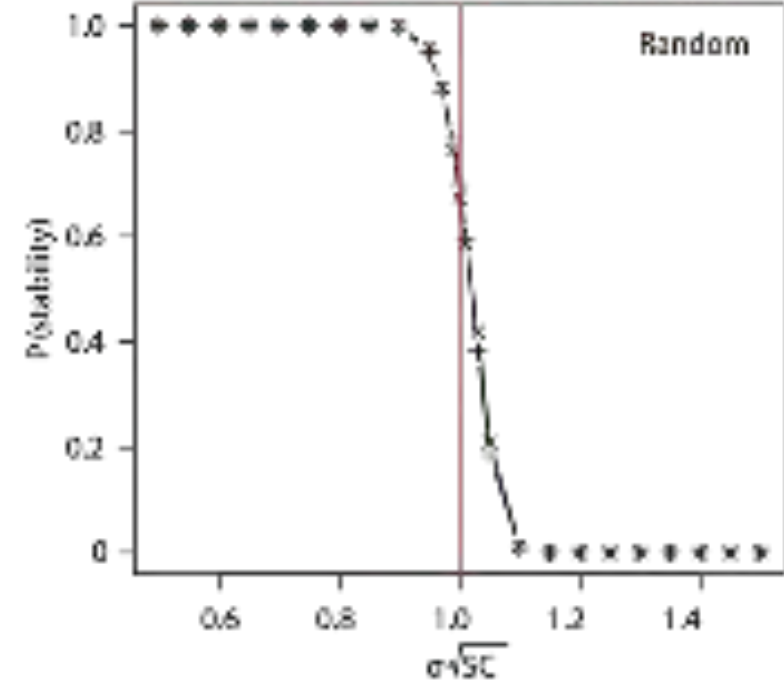**R. May**

GENERAL

Will a Large Complex System be Stable?

$$\delta \dot{\mathbf{n}} = \Phi \delta \mathbf{n}$$

$$\phi_{ij} \sim \mathcal{N}(0, \sigma)$$

$$\Phi_{ii} = -1$$

$$R = \sqrt{SC}\sigma$$

Critical "Phase Transition"

Random

competition   mutualism   predation parasitism
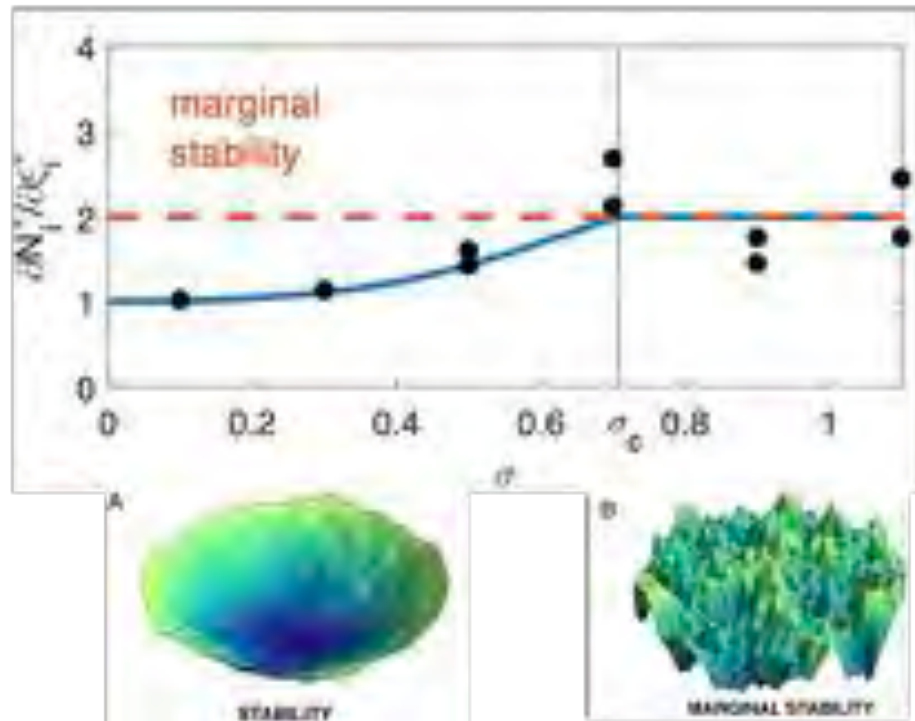
--   ++   +-

Allesina & Tang, 2012

Random Matrix / Spin Glass / Cavity / DMFT

Marginally Stable Equilibria in Critical Ecosystems

Giulio Biroli[a,b,], Guy Bunin[c], Chiara Cammarota[d]
[a]Institut de physique théorique, Université Paris Saclay, CEA, CNRS,

$$\frac{dN_i}{dt} = -N_i\left[\nabla_{N_i}V_i(N_i) + \sum_{j,(j\neq i)}\alpha_{ij}N_j\right] + \sqrt{N_i}\eta_i(t) + \lambda$$

Editors' Suggestion

Properties of Equilibria and Glassy Phases of the Random Lotka-Volterra Model with Demographic Noise

Ada Altieri[1,5] Felix Roy[2,1] Chiara Cammarota[3,4] and Giulio Biroli[1]

Breakdown of Random-Matrix Universality in Persistent Lotka-Volterra Communities

Joseph W. Baron[1,*] Thomas Jun Jewell[2] Christopher Ryder[2] and Tobias Galla[1,2,†]

Generalized Lotka-Volterra Equations with Random, Nonreciprocal Interactions: The Typical Number of Equilibria

Valentina Ros
Université Paris-Saclay, CNRS, LPTMS, 91405 Orsay, France

Felix Roy and Giulio Biroli

Guy Bunin and Ari M. Turner
Department of Physics, Technion-Israel Institute of Technology, Haifa 32000, Israel

Phase transition to chaos in complex ecosystems with non-reciprocal species-resource interactions
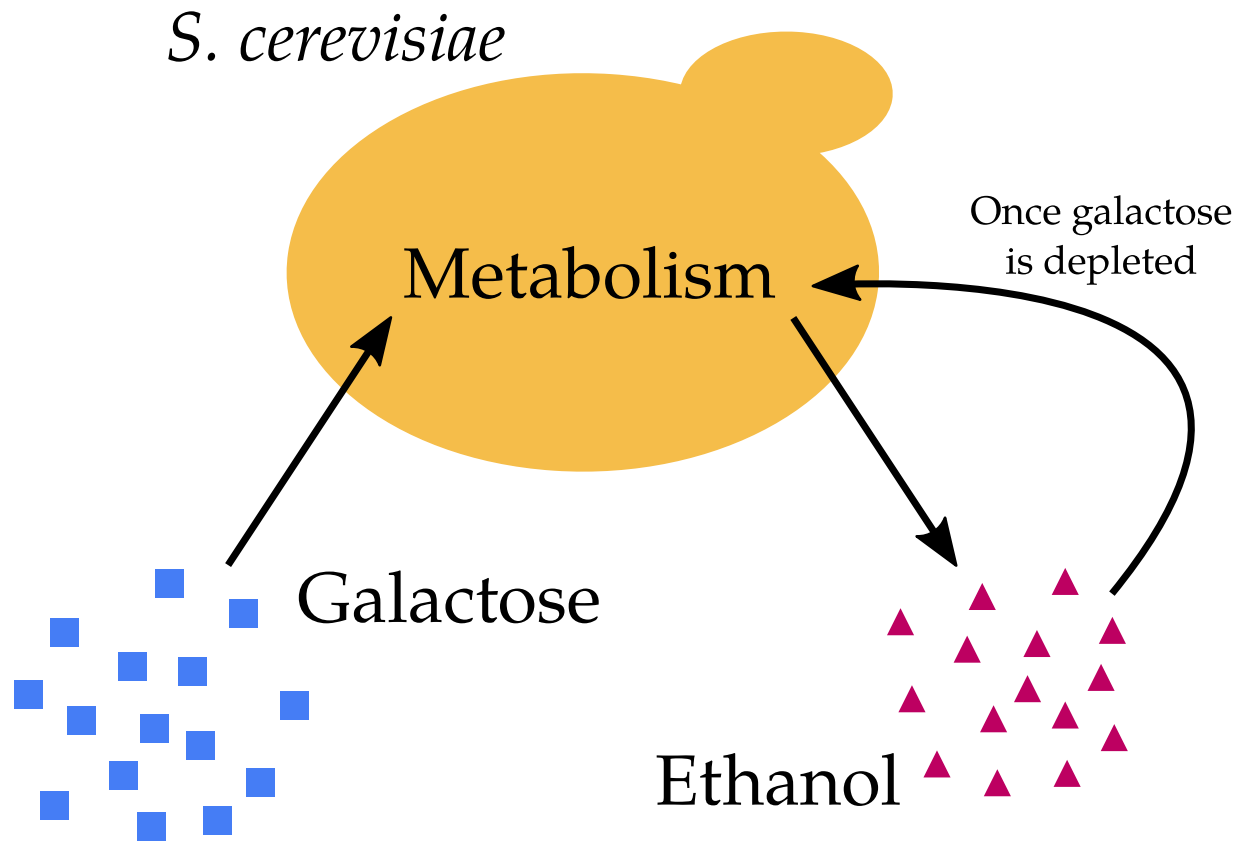
Emmy Blumenthal,[1,2,*] Jason W. Rocks,[1,2,†] and Pankaj Mehta[1,2,‡]
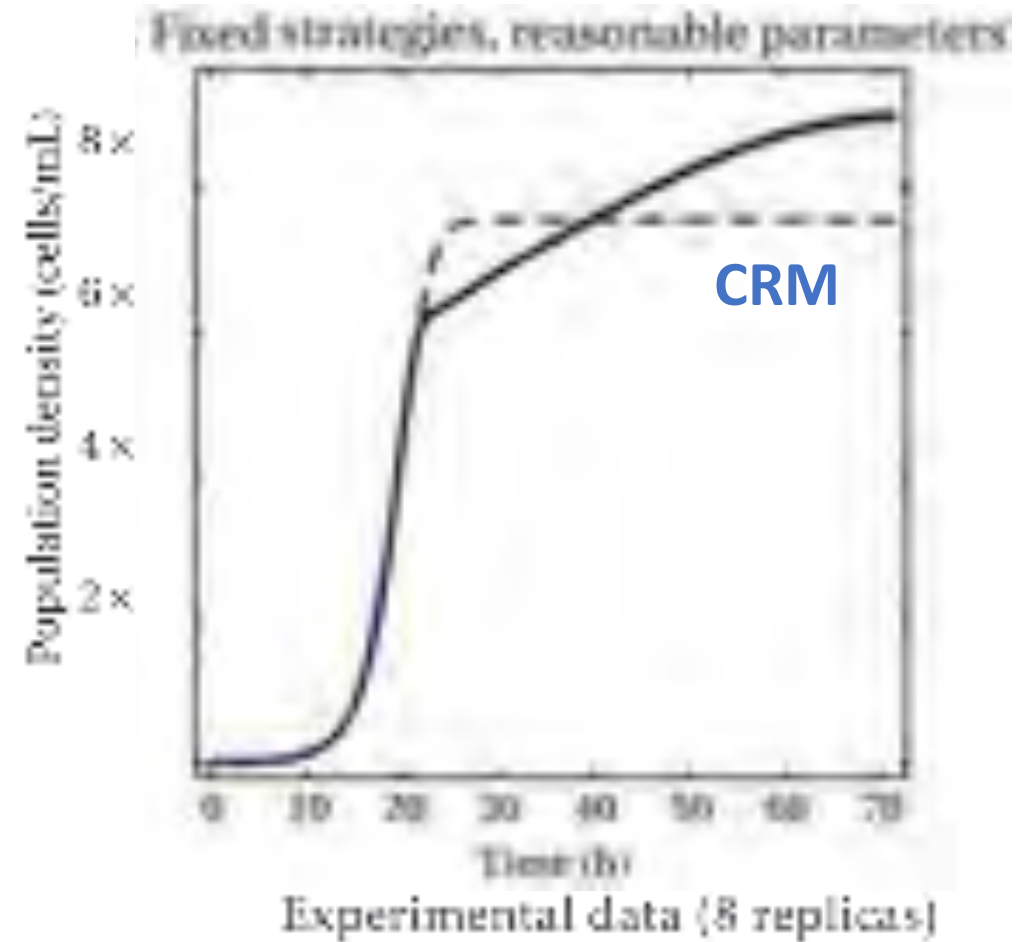[1]*Department of Physics, Boston University, Boston, MA 02215, USA*

BUT ... species interactions are not quenchd, but dynamics

Experimental evidence: quantitative description of diauxic shift

S. cerevisiae

Metabolism

Galactose

Ethanol

Once galactose is depleted

Schematic representation of the yeast used in the experiment

Fixed strategies, reasonable parameters

CRM

Population density (cells/mL)

Time (h)

Experimental data (8 replicas)
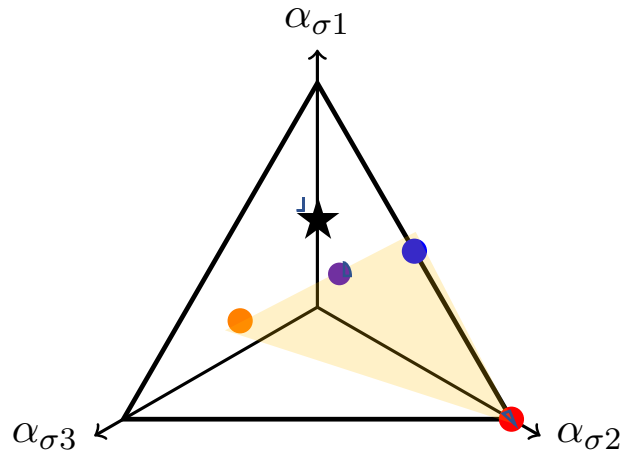
Time dependent interactions in Consumer Resource Models (CRM)

Energy Constraint in CRM

Adding a total energy budget E (independent of species)

$$\sum_{i=1}^{p} \alpha_{\sigma i} = E \implies \text{All species survives if} \quad n_1\vec{\alpha}_1 + \cdots + n_m\vec{\alpha}_m = \frac{E}{\delta}\vec{s}$$

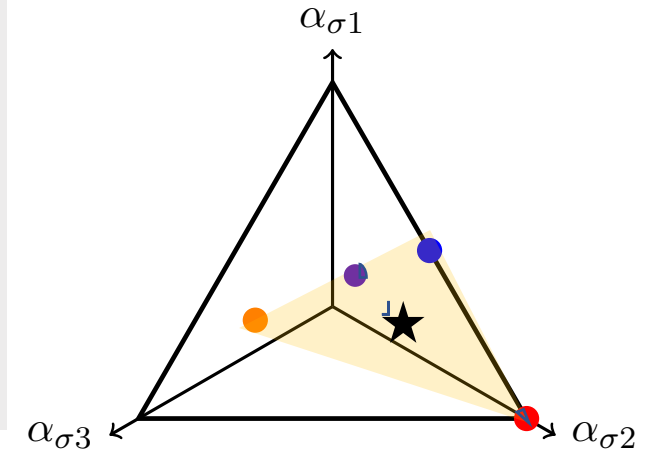*(Posfai et al, PRL 2017)*

After rescaling:

Geometrical Interpretation

Red species eats only nutrient 2,
Blue one feeds equally upon 1 and 2;
Orange-violet species uses all resources

★ = supply rate (**s**)

Only m ≤ 3 species coexist: at least one extinction – CEP is recovered

All species coexist, but with soft bound (≤ E) or species dependent budget (E$_\sigma$), CEP is recovered

Bridging the cellular and ecological scale…

Communities' structure is influenced by the metabolism of microbial species

- The abundance of microbial species correlate well with their metabolic function
(Damian et al., Nat. Microbiol. 2018)
- Microbial communities assemble in "metabolic blocks" specialized in particular metabolic functions, and this simple arrangement allows prediction of community composition
(Enke *et al., Curr. Biol.* 2019)

The functions performed by a species depend on the proteins it is producing.
The balance between the functions depend on how the proteome of a species is allocated.

?

?

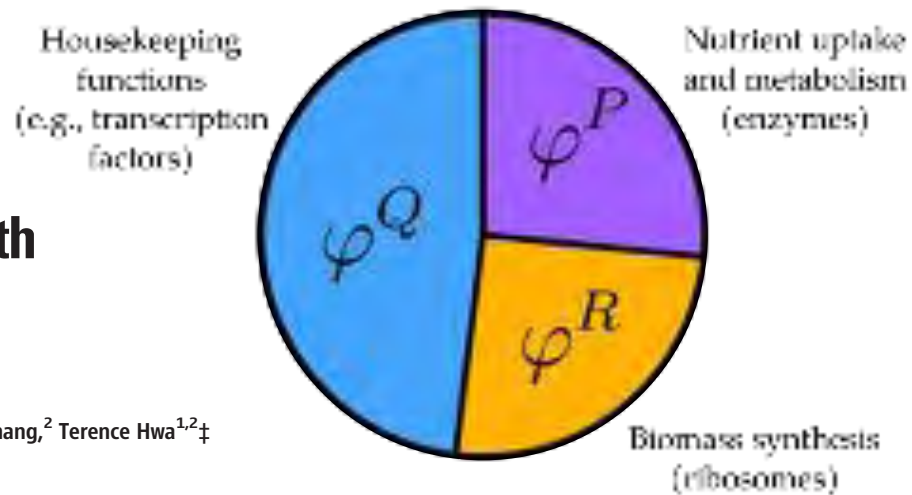$$\sum_{i=1}^{p} \alpha_{\sigma i} \leq E_{\sigma}^{*}$$

How does allocation of the proteome affect the dynamics of microbial communities?
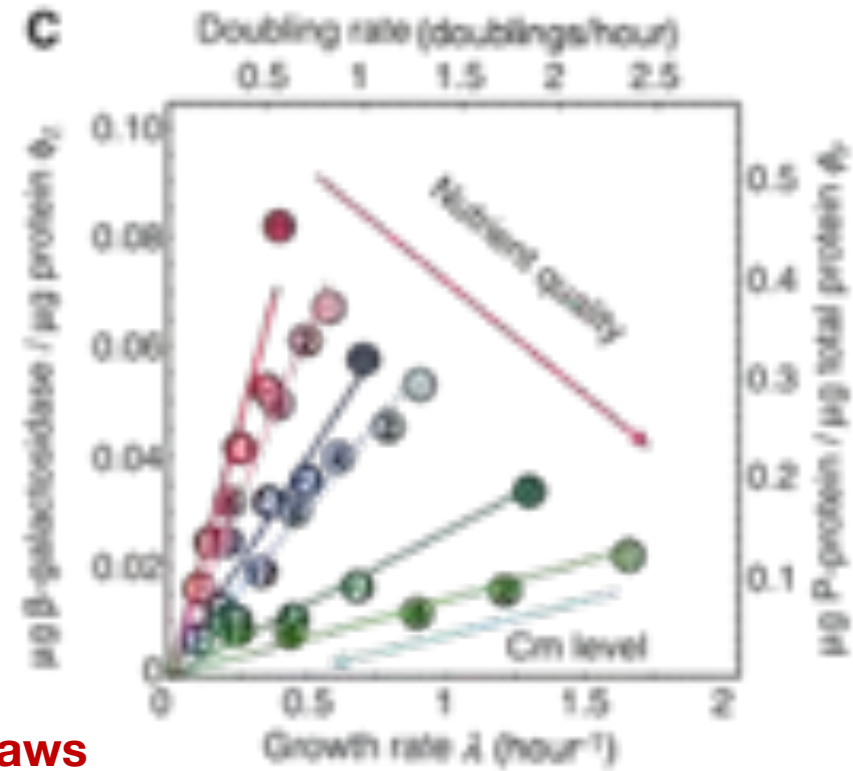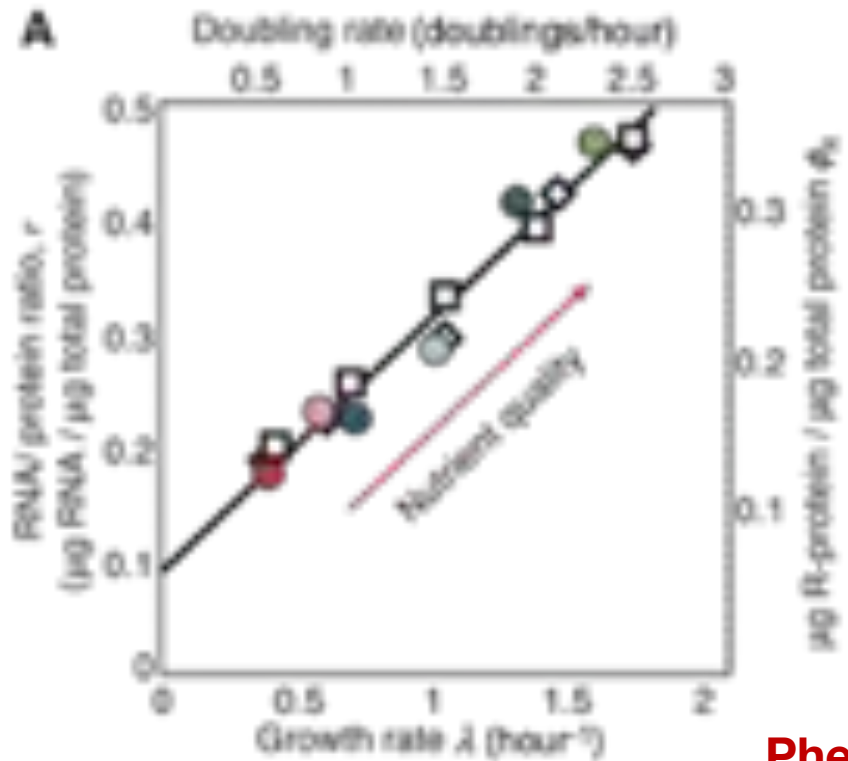
Proteome allocations: experimental facts

Interdependence of Cell Growth and Gene Expression: Origins and Consequences

Matthew Scott,[1]*† Carl W. Gunderson,[2]* Eduard M. Mateescu,[1] Zhongge Zhang,[2] Terence Hwa[1,2]‡

Proteome allocations: experimental facts
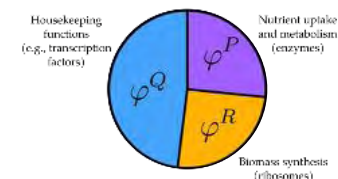

Phenomenological laws

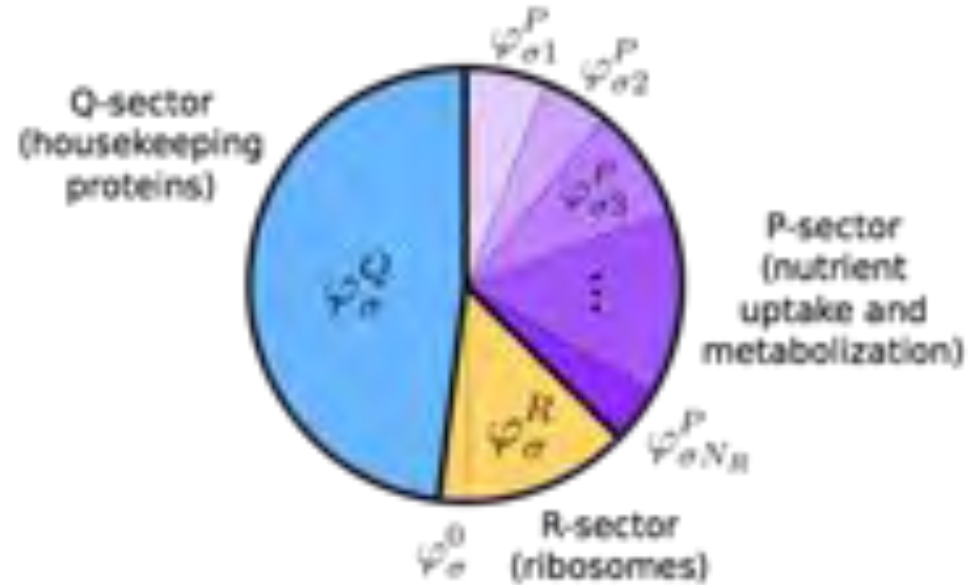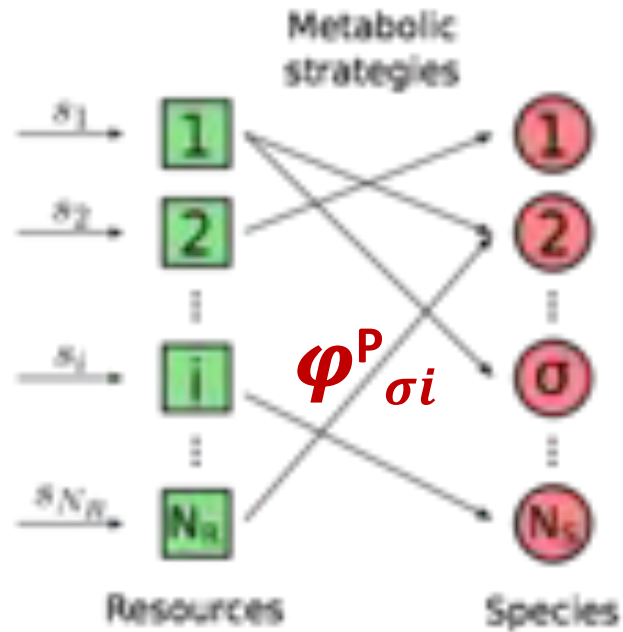$$\varphi^R = \varphi^0 + \frac{\rho}{\kappa^t} g$$

$$\varphi^Q = const$$

$$\varphi^P = \frac{\rho}{\kappa^n} g$$

$$\varphi^Q + \varphi^R + \varphi^P = 1$$

Scott, …, Hwa, Science 2010

Generalization of Hwa phenomenological laws for N_R resources and N_P species

$$\varphi^P_{\sigma i} := \varphi^P_{\sigma i} = \frac{\rho_\sigma}{\overline{\kappa}^n_i(c_i)} g^{(i)}_\sigma$$

$$\varphi^R_\sigma = \frac{\rho_\sigma}{\kappa^t_\sigma} g_\sigma + \varphi^0_\sigma$$

$$\sum_{i=1}^{N_R} g^{(i)}_\sigma = g_\sigma$$

$$\varphi^P_\sigma + \varphi^R_\sigma + \varphi^Q_\sigma = 1$$

$$\Downarrow$$

$$\sum_{i=1}^{N_R} \varphi_{\sigma i} \left[1 + \frac{\overline{\kappa}^n_i(c_i)}{\kappa^t_\sigma} \right] = 1 - \varphi^Q_\sigma - \varphi^0_\sigma := \Phi_\sigma$$

From proteome allocation to consumer resource equations

Resource 1

Uptake rates

$J_{\sigma 1} \propto \varphi_{\sigma 1}$

Species σ

$\propto J_{\sigma 1}$ $g_\sigma^{(1)}$

$\propto J_{\sigma N_R}$ $g_\sigma^{(N_R)}$

$$\sum_{i=1}^{N_R} g_\sigma^{(i)} = g_\sigma$$

Total growth rate

$g_\sigma - q_\sigma$

Net growth rate

$$\varphi^P = \varphi$$

Resource N_R

$J_{\sigma N_R} \propto \varphi_{\sigma N_R}$
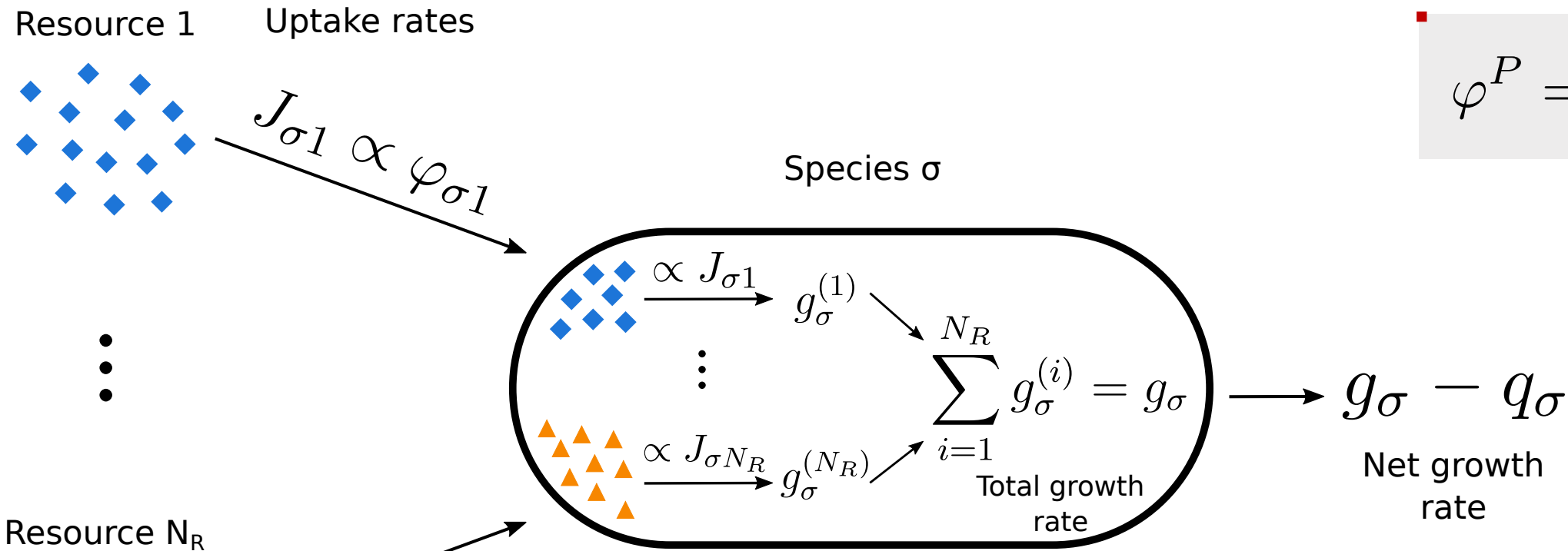
$$\dot{m}_\sigma = m_\sigma (g_\sigma - q_\sigma)$$
$$\dot{c}_i = s_i - \sum_{\sigma=1}^{N_S} J_{\sigma i} m_\sigma$$

$$\sum_{i=1}^{N_R} \varphi_{\sigma i} \underbrace{[1 + \gamma_{\sigma i} r_i(c_i)]}_{variable} = \underbrace{\Phi_\sigma}_{fixed} \qquad \Rightarrow \qquad \varphi_{\sigma i} \; \textbf{\textit{must}} \; \textbf{be variables}$$

Consumer Resource Model with constraint proteome allocation

$$\sum_{i=1}^{N_R} \varphi_{\sigma i} \underbrace{[1 + \gamma_{\sigma i} r_i(c_i)]}_{\text{variable}} = \underbrace{\Phi_\sigma}_{\text{fixed}}$$

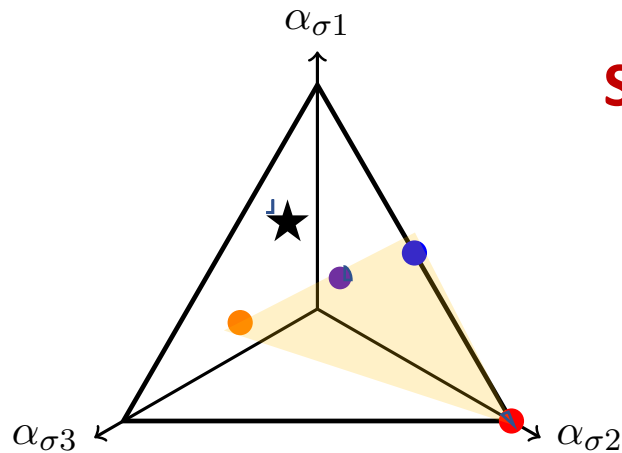**→** **Dynamic consumer-resource network** **→** **Optimization with constraint**

$$\dot{\vec{\varphi}}_\sigma = \frac{1}{\tau_\sigma} \vec{\nabla}_\varphi g_\sigma$$

$$F_\sigma(\vec{\varphi}_\sigma, \vec{c}) := \sum_{i=1}^{N_R} \varphi_{\sigma i} [1 + \gamma_{\sigma i} r_i(c_i)] - \Phi_\sigma$$

Adaptive Framework

Each species changes its metabolic allocation so to maximize its growth rate g_σ. τ_σ = adaptation velocity

$$\dot{\vec{\varphi}}_\sigma = \frac{1}{\tau_\sigma} \vec{\nabla}_\varphi g_\sigma - \frac{\vec{\nabla}_\varphi F_\sigma}{(\vec{\nabla}_\varphi F_\sigma)^2} \left(\frac{1}{\tau_\sigma} \vec{\nabla}_\varphi g_\sigma \cdot \vec{\nabla}_\varphi F_\sigma + \dot{\vec{c}} \cdot \vec{\nabla}_c F_\sigma \right)$$
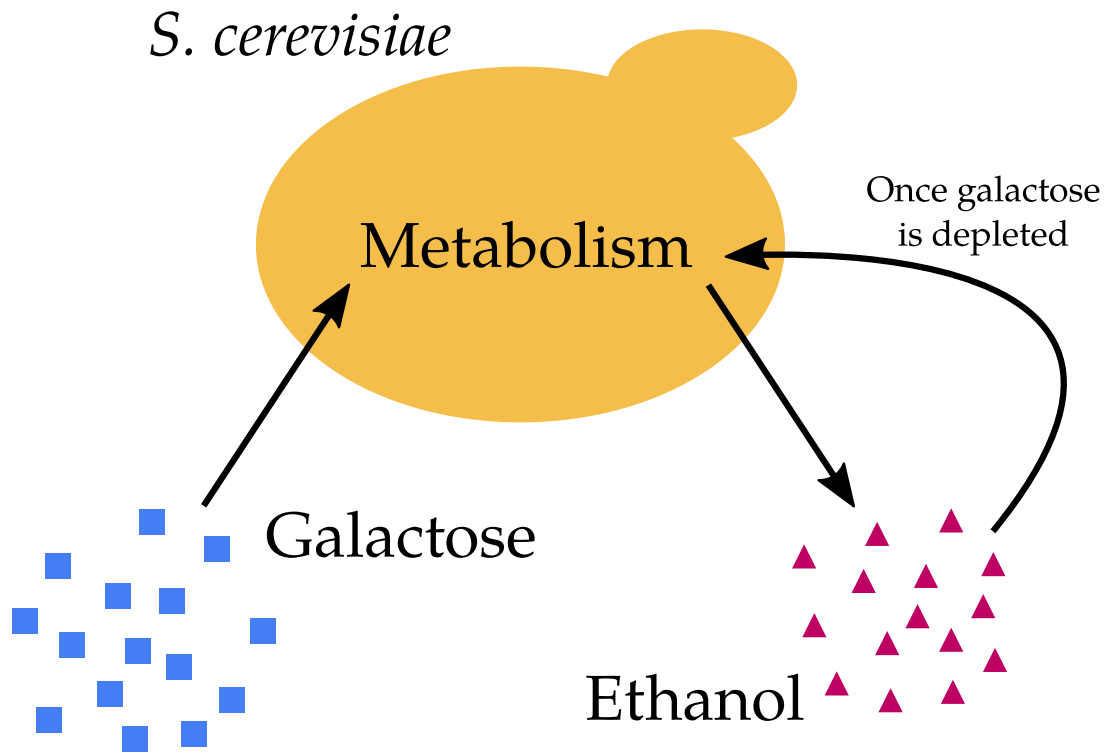
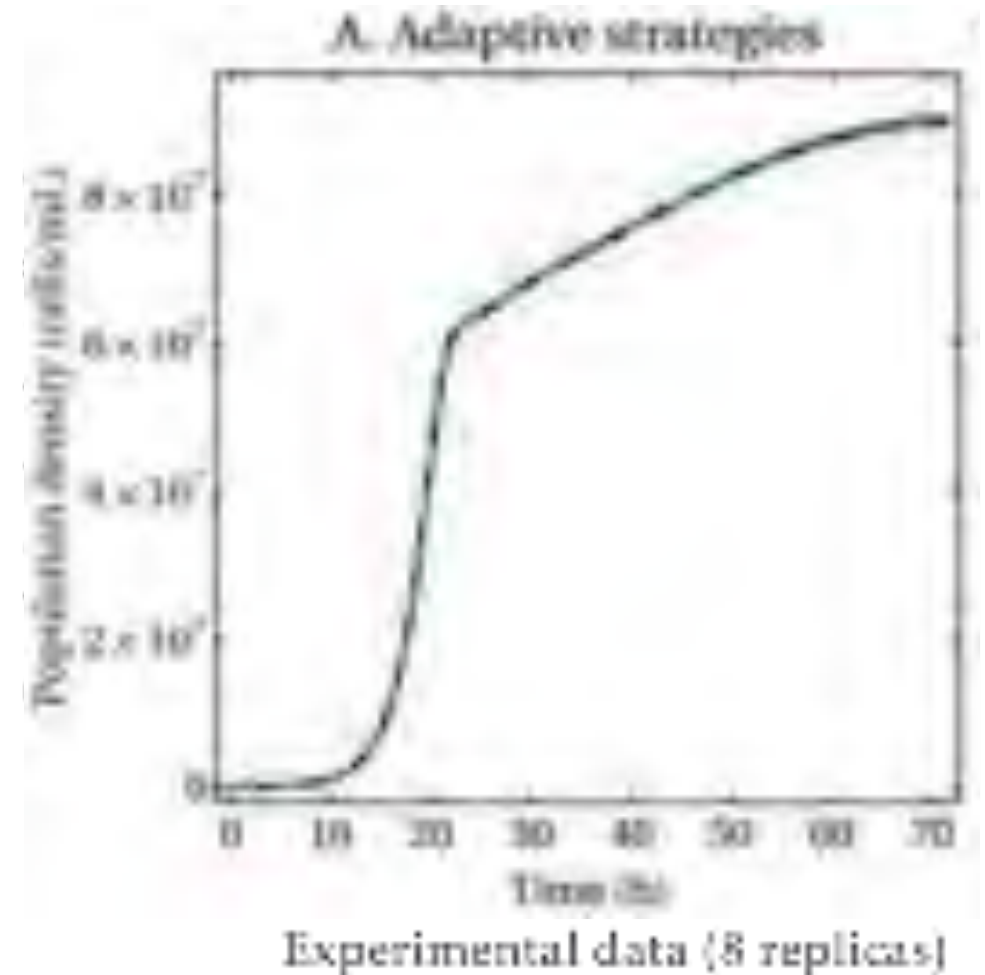

Species coexist if + Constraint (biological meaningful)

$$\hat{s}_i = \sum_{\sigma=1}^{N_S} z_\sigma \hat{\varphi}_{\sigma i}^*$$

$$q_\sigma = \frac{\Phi_\sigma}{\rho_\sigma (\Xi - 1/\kappa_t^\sigma)}$$

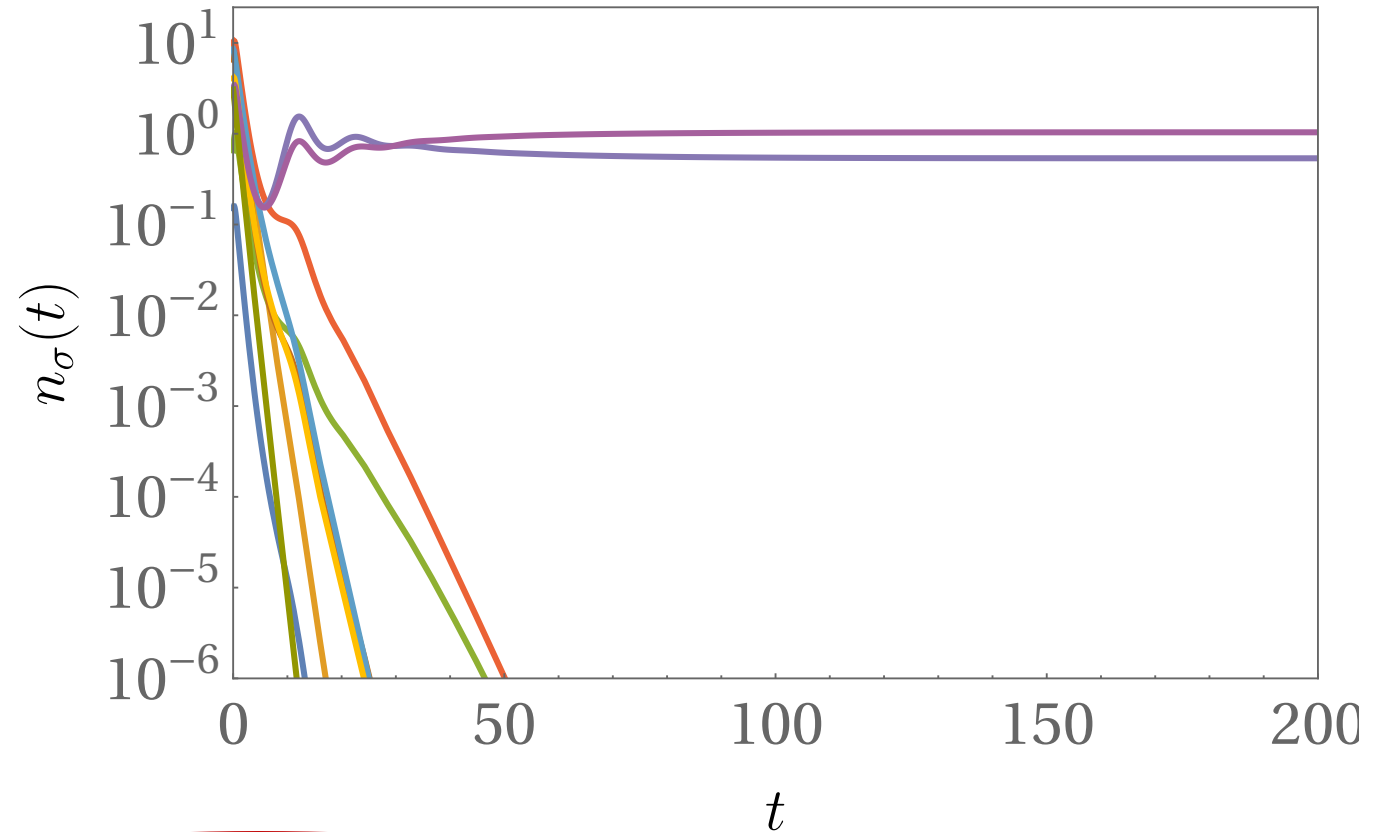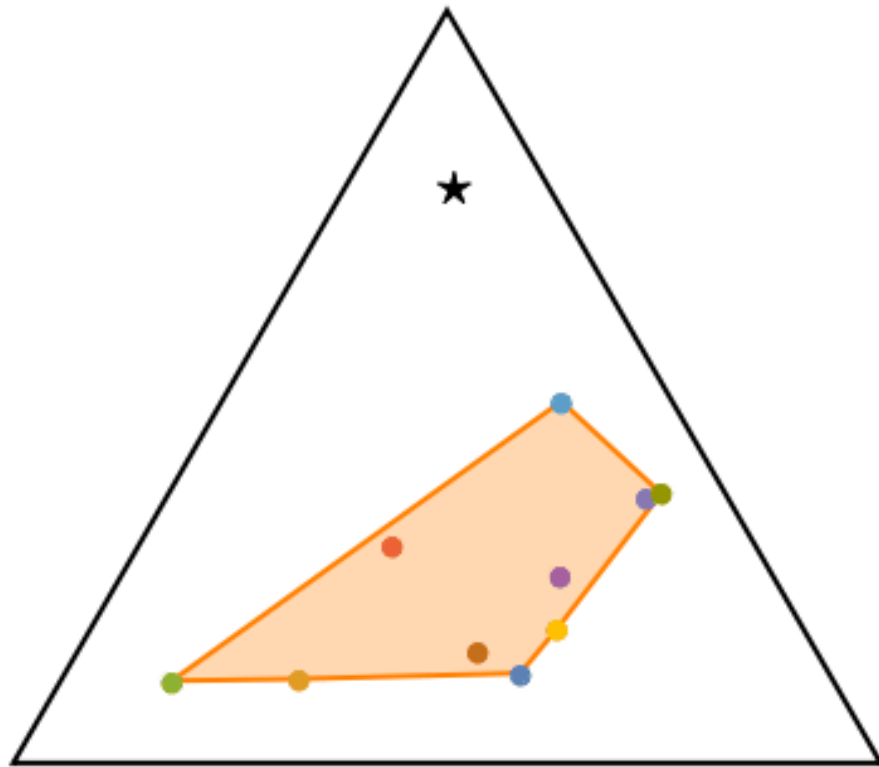# Result 1: Dynamic Consumer-Resources network can reproduce diauxic shift

S. cerevisiae

Metabolism

Galactose

Ethanol

Once galactose is depleted

Schematic representation of the yeast used in the experiment

A. Adaptive strategies

Population density (cells/ml)

8×10^7

6×10^7

4×10^7

2×10^7

0

0   10   20   30   40   50   60   70

Time (h)

Experimental data (8 replicas)

L. Pacciani Mori et al., Plos Comp. Biology 2020

Effect of adaptation on species coexistence

Static metabolic strategies

Fixed metabolic strategies

Result 2: adaptation may favour species coexistence

2/4) When multiple species and resources are considered, the model naturally violates the Competitive Exclusion Principle:
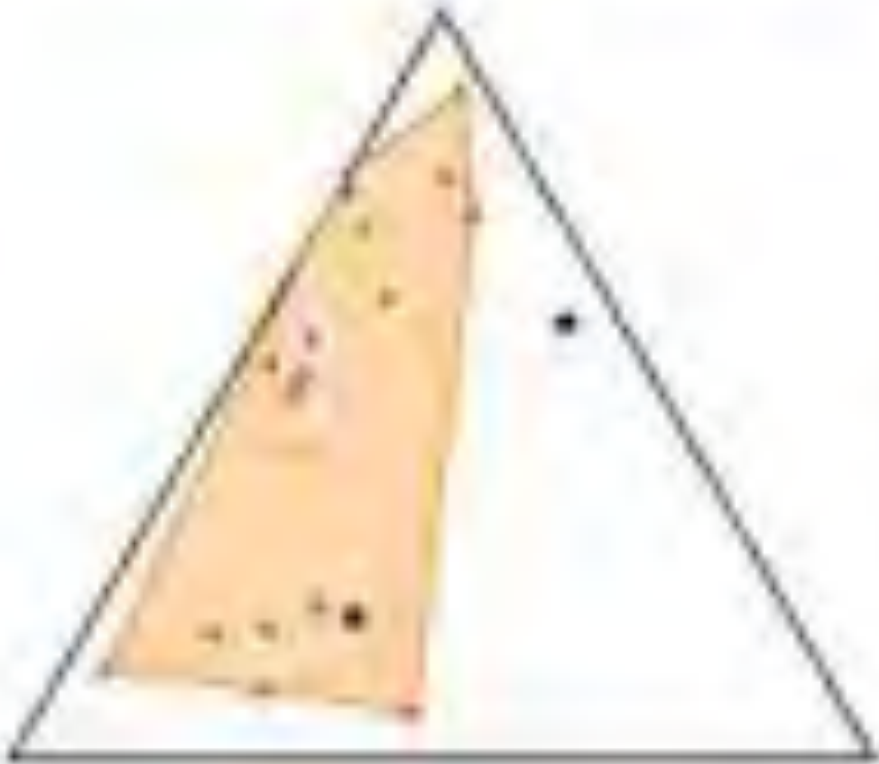

**Dynamics of
Consumer-resources network**
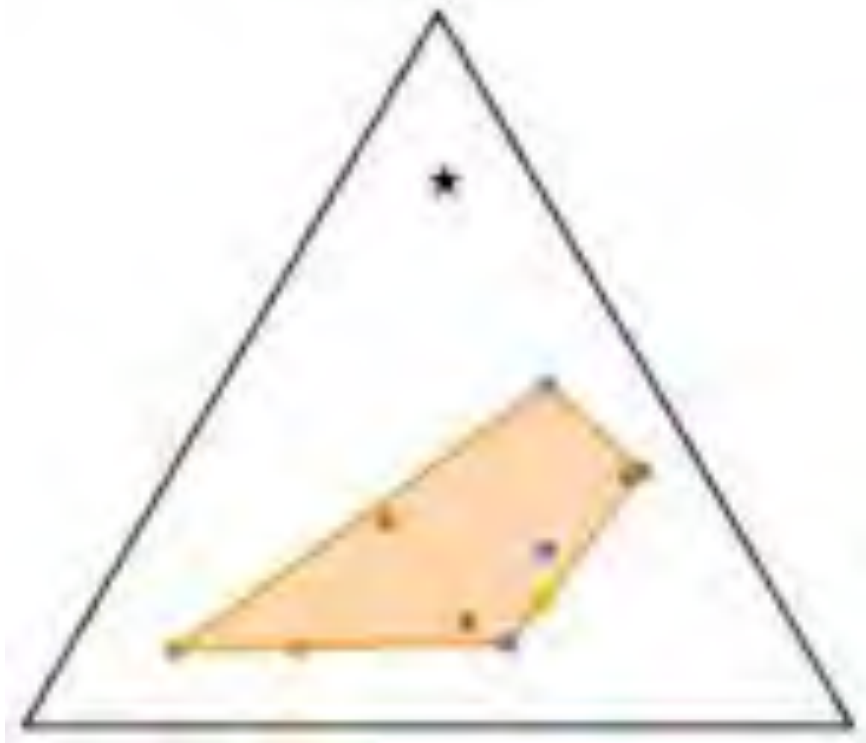
L. Pacciani Mori et al., Plos Comp. Biology 2020
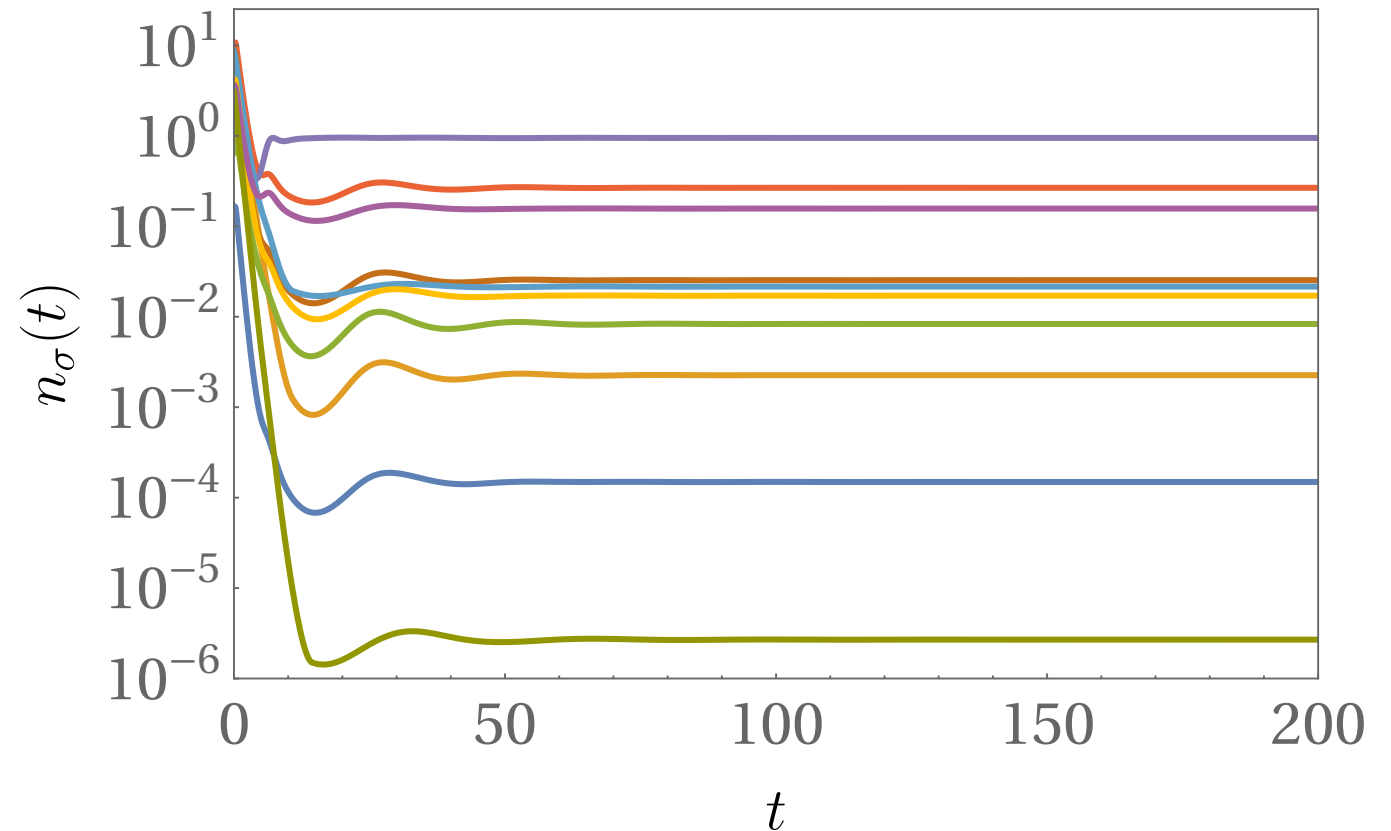
Result 3: increase of community resilience

Perturbation of the supply rate (e.g. changes in time) lead to extinction in the absence of adaptation.
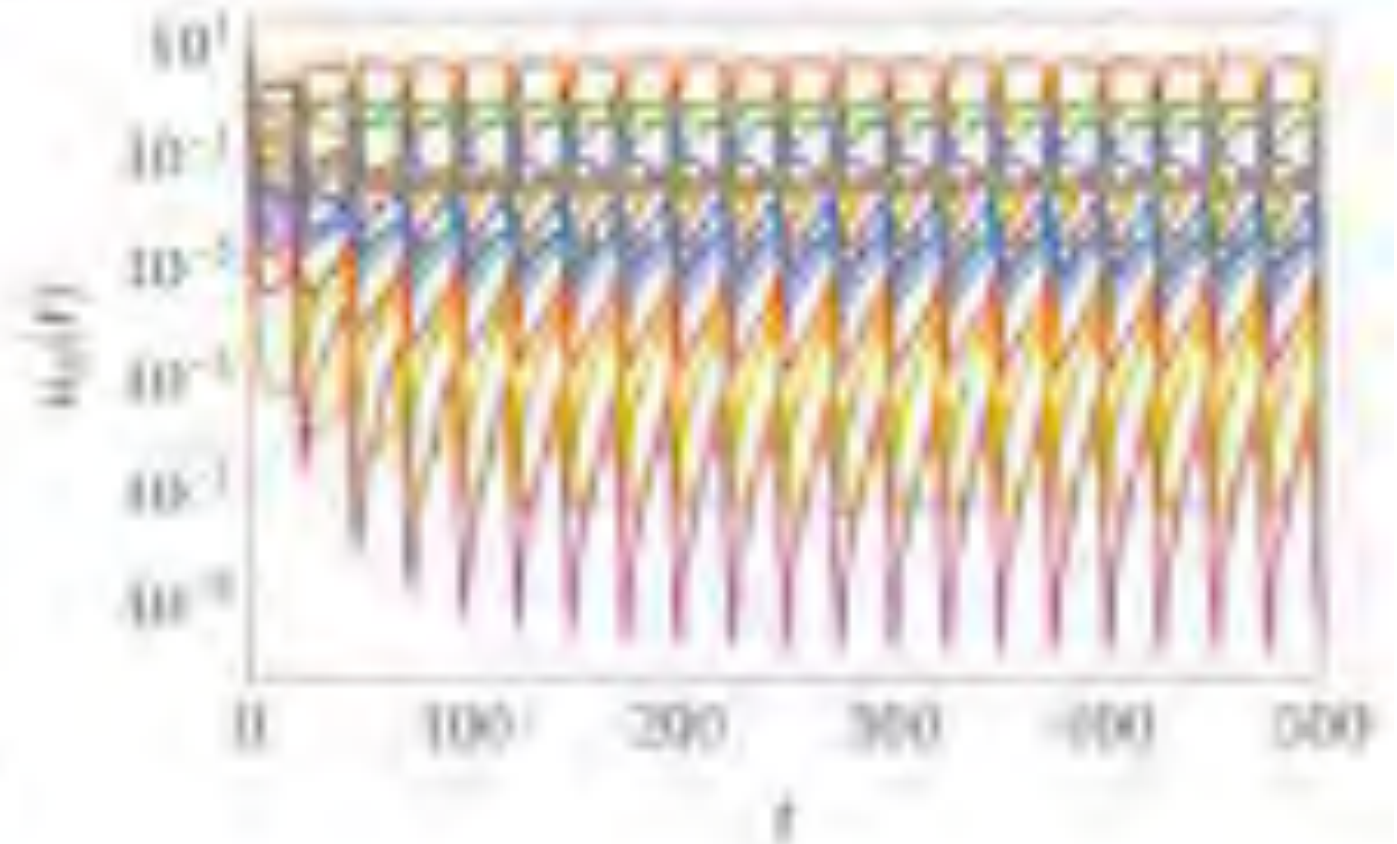
L. Pacciani Mori et al., Plos Comp. Biology 2020

Fixed metabolic strategies, $\tau_{in} = 20$, $\tau_{out} = 5$
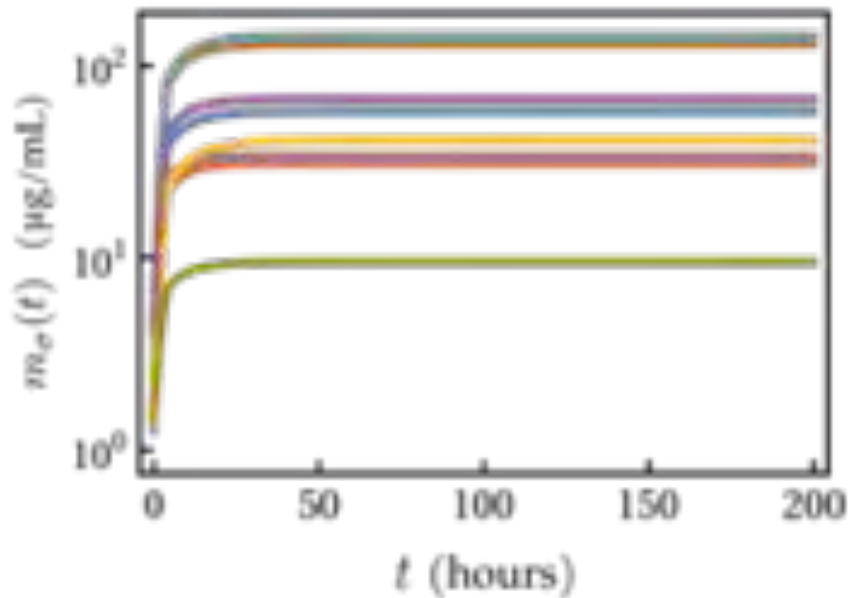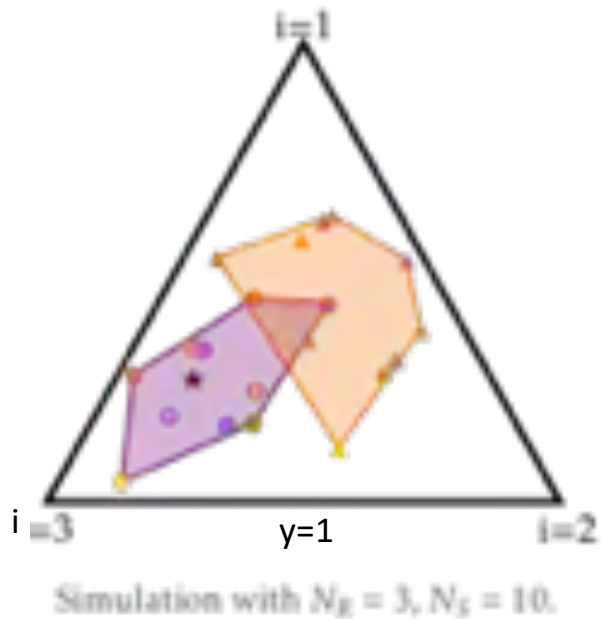
Result 4: increase of community resilience

3/4) When environmental conditions are variable (i.e. the nutrient supply rates change in time) using adaptive α_{ij} leads to more stable communities
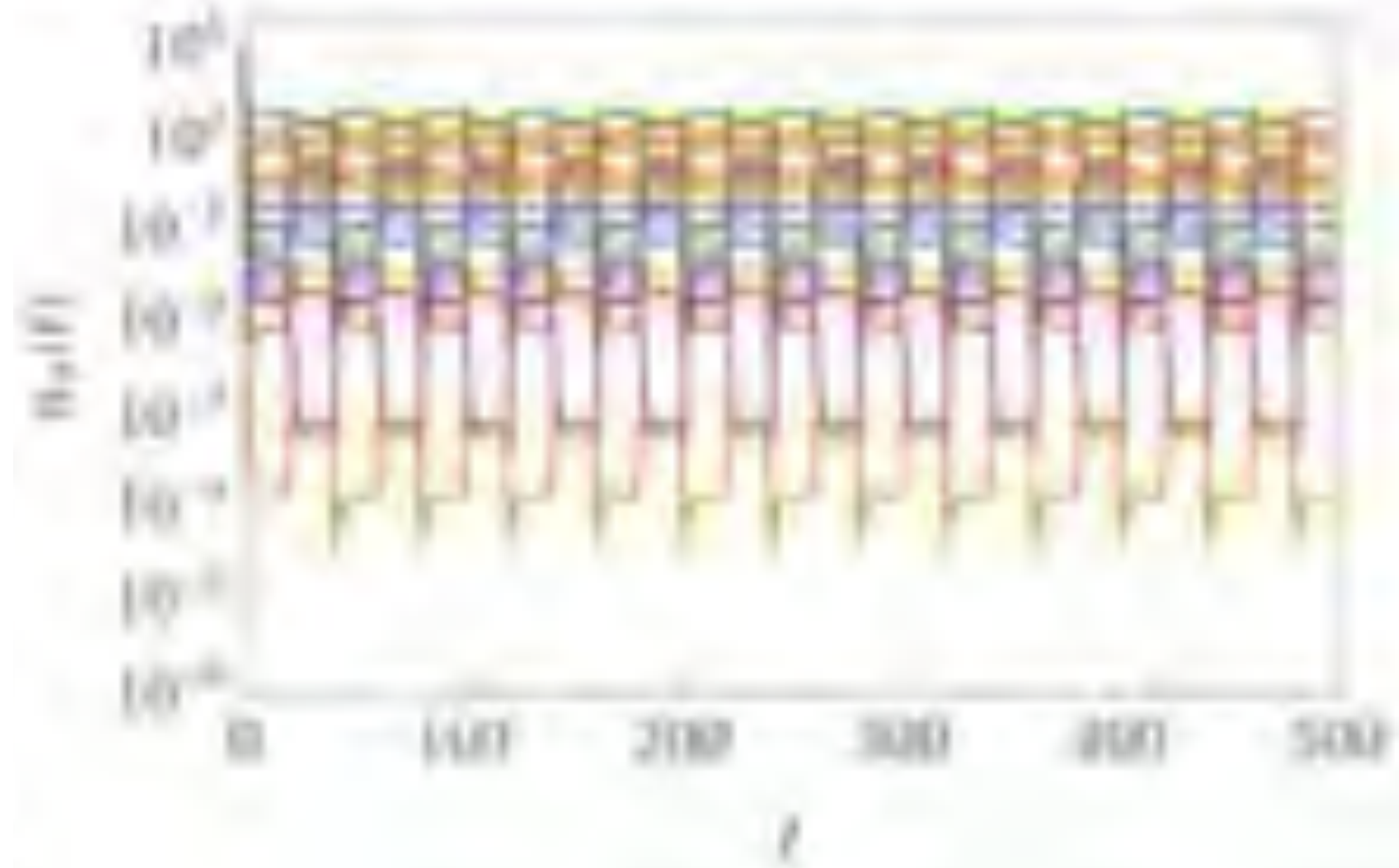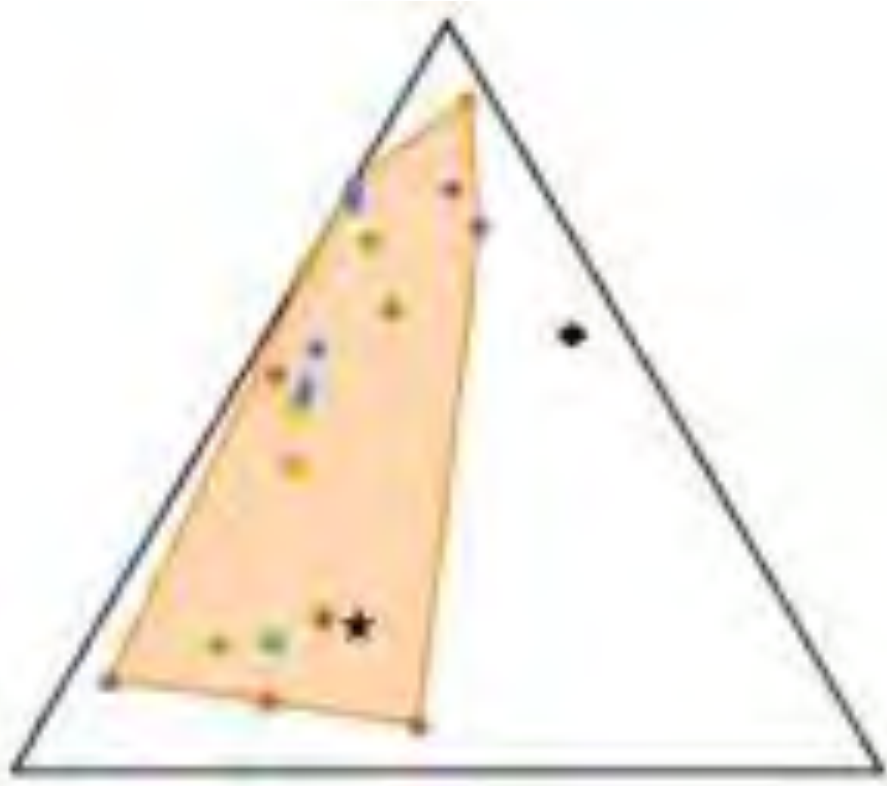
**Dynamics of
Consumer-resources network**

Importance of adaptation velocity

4/4) Fast adaptation (i.e., τ_σ small) always favors coexistence, while slower adaptation does not
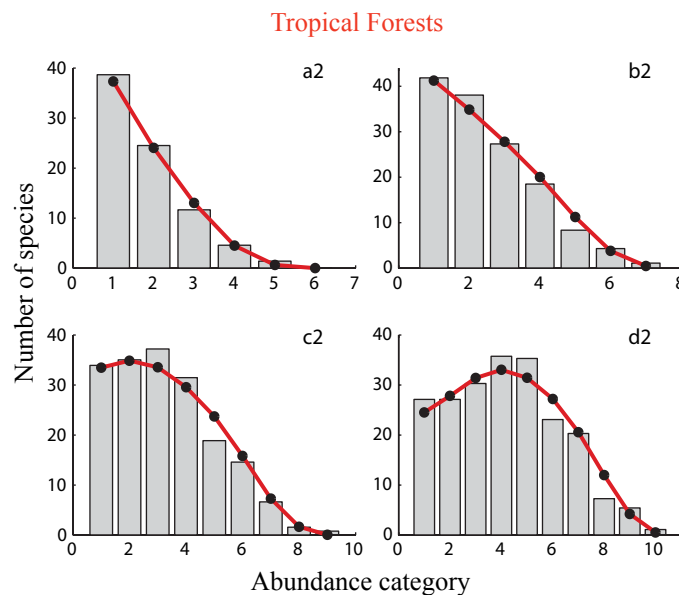

Simulation with $N_g = 3$, $N_\xi = 10$.
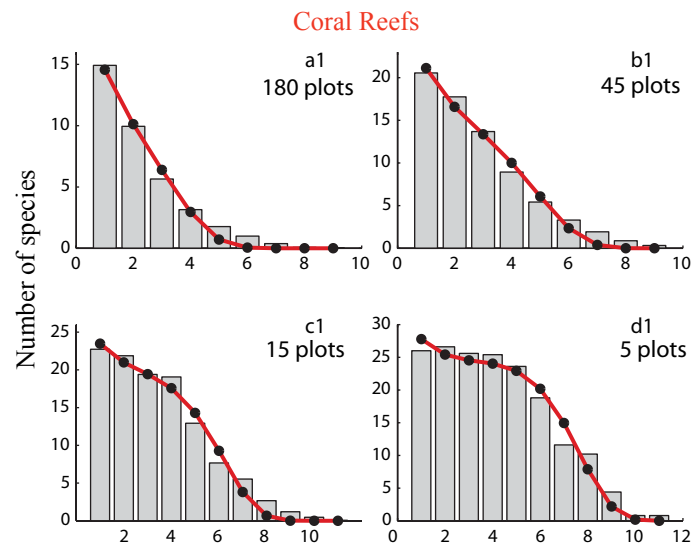
$$\dot{\vec{\varphi}}_\sigma = \frac{1}{\tau_\sigma}\vec{\nabla}_\varphi g_\sigma$$

$\tau_\sigma \rightarrow y*\tau_\sigma$

L. Pacciani-Mori et al., ISME Journal, 2021
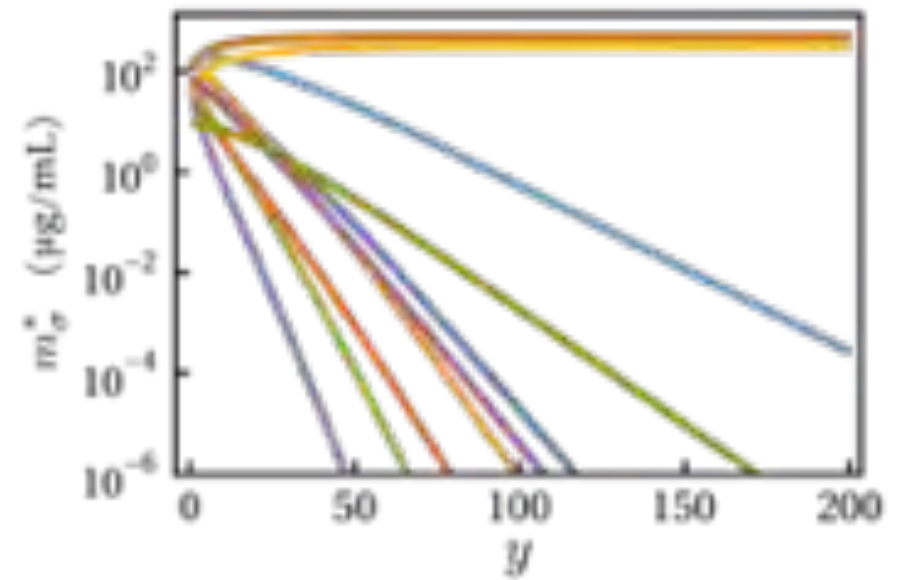
Generalized Lotka Volterra (GLV) and connection with microbiome ecological data.
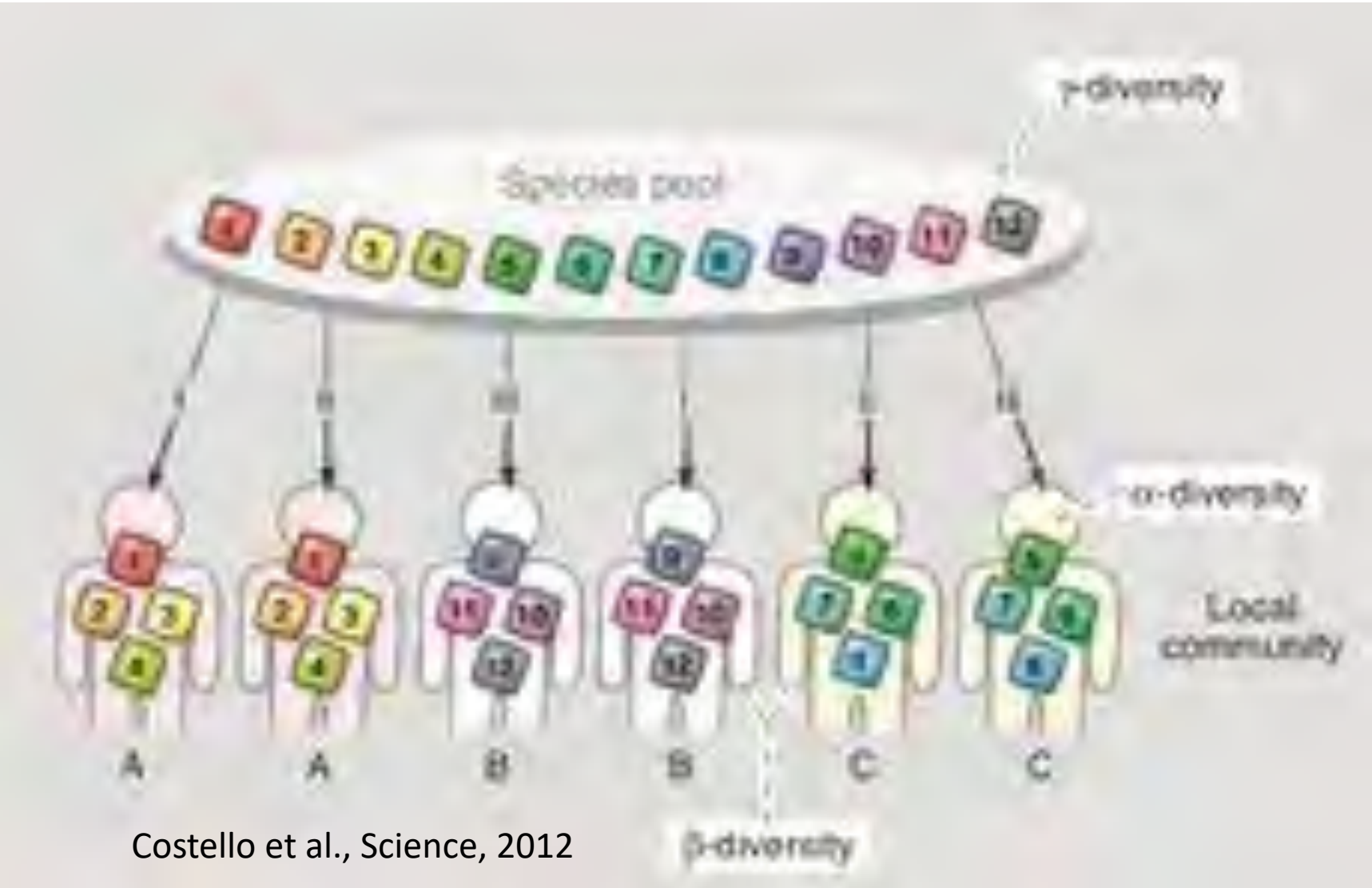
Species Abundance Distribution (SAD or RSA)

SAD is a Gamma distribution

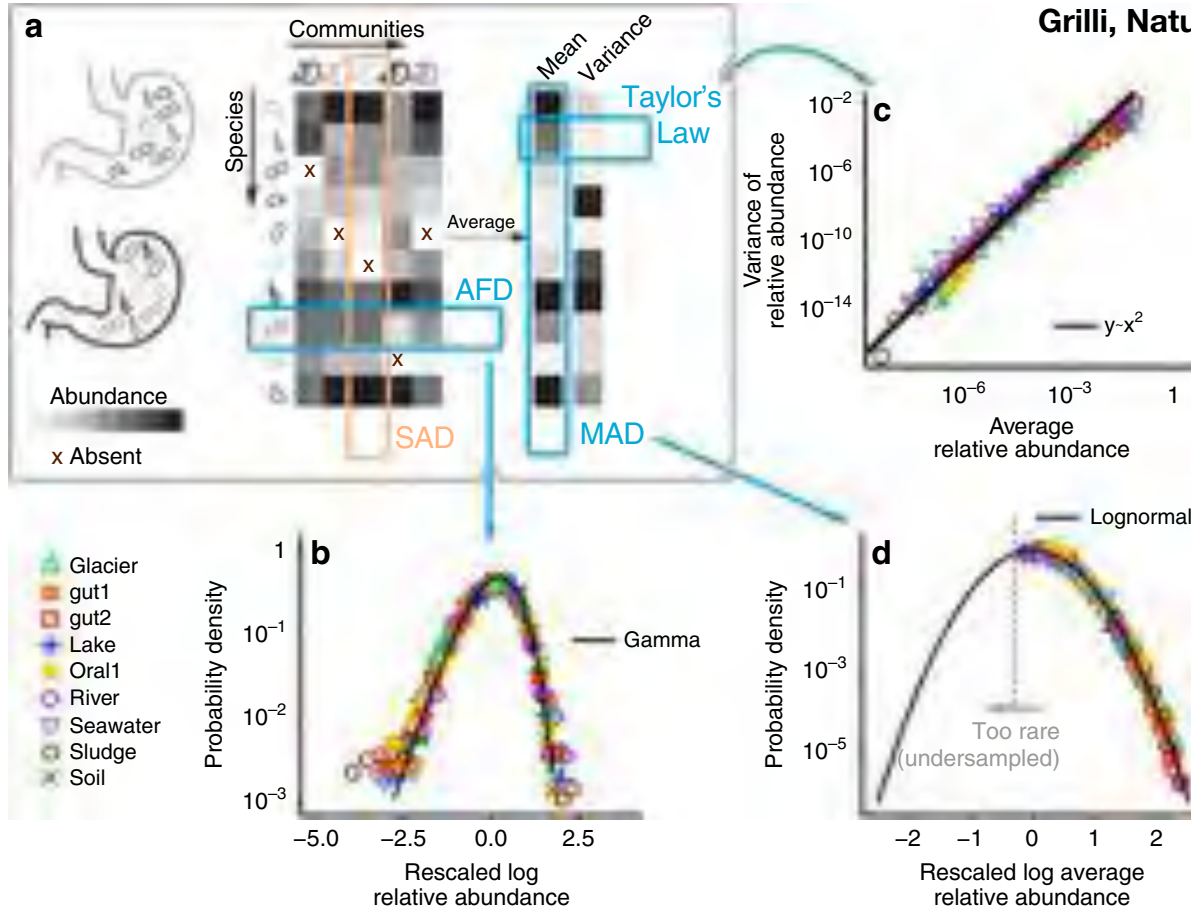$$P_{\mathrm{RSA}}(x) = \frac{(D\tau)^{-b/D}}{\Gamma(b/D)} x^{b/D-1} e^{-x/D\tau}$$

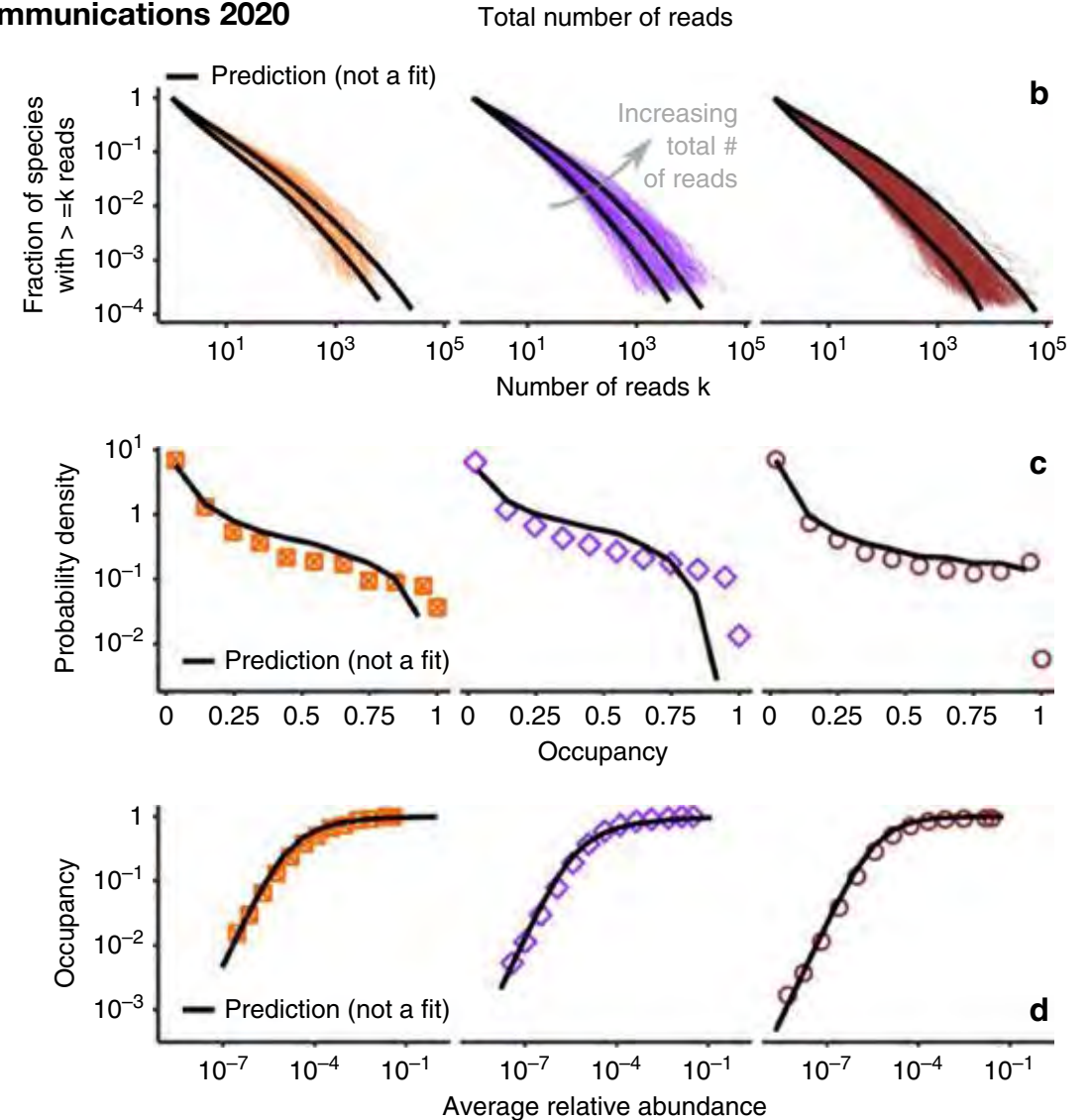Volkov et al., Nature 2003

Azaele et al., Nature 2005

Ecology of the Microbiomes

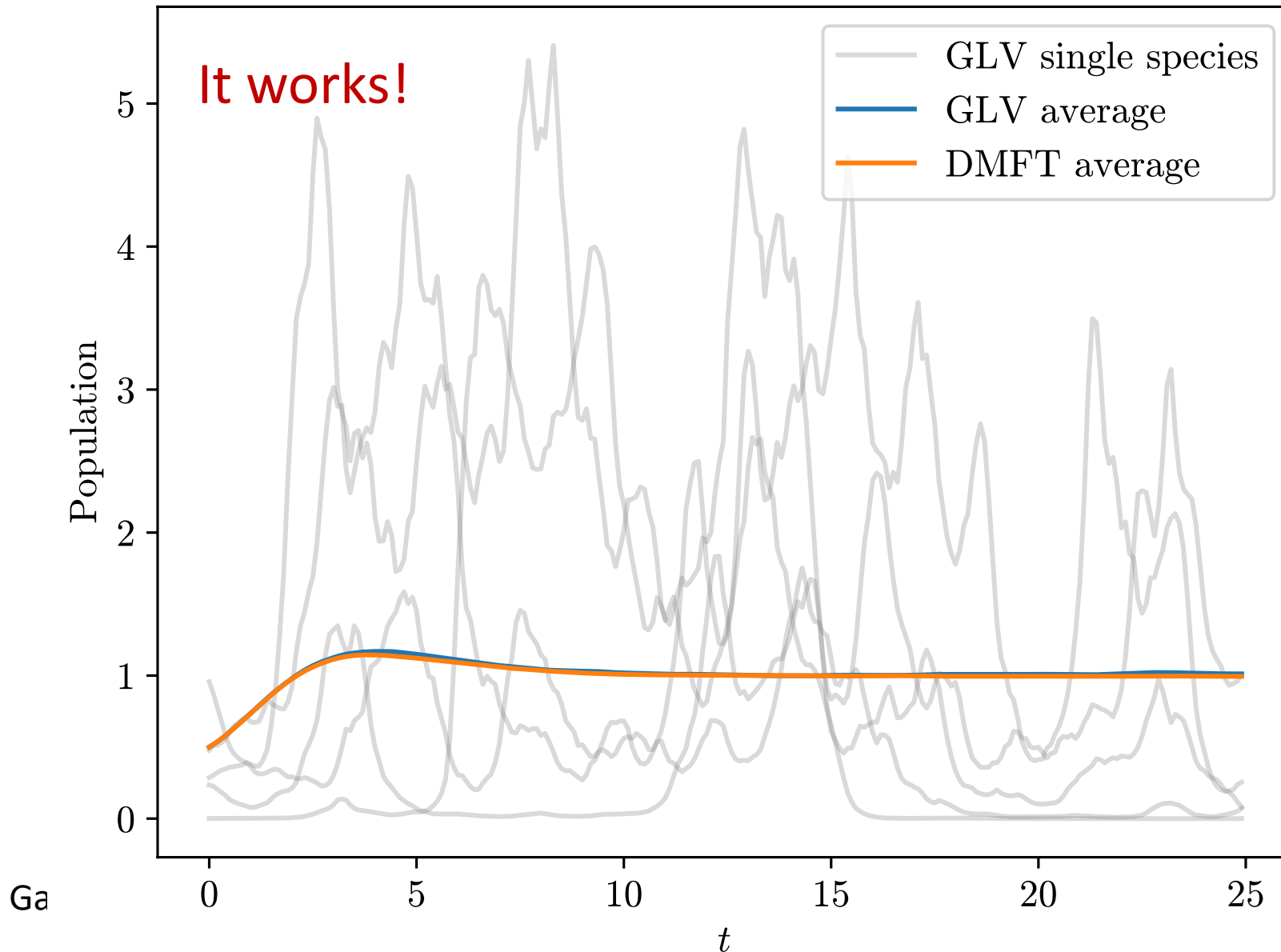Costello et al., Science, 2012

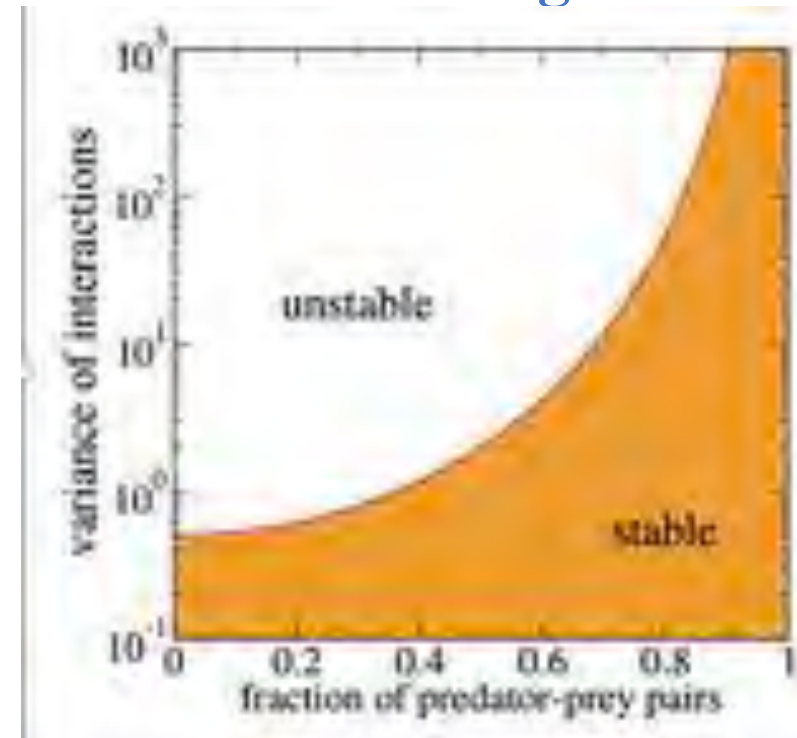# Macro-Ecological Patterns in Microbiomes

Grilli, Nature Communications 2020

$$\frac{dx_i}{dt} = \underbrace{\frac{x_i}{\tau_i}\left(1 - \frac{x_i}{K_i}\right)}_{Logistic\ Growth} + \underbrace{\sqrt{\frac{\sigma_i}{\tau_i}}x_i\xi_i}_{Env.\ Noise}$$
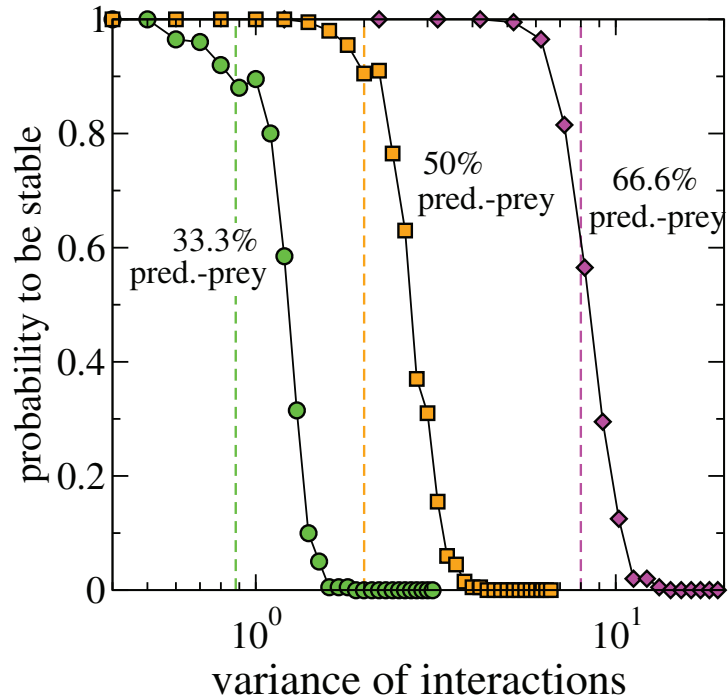
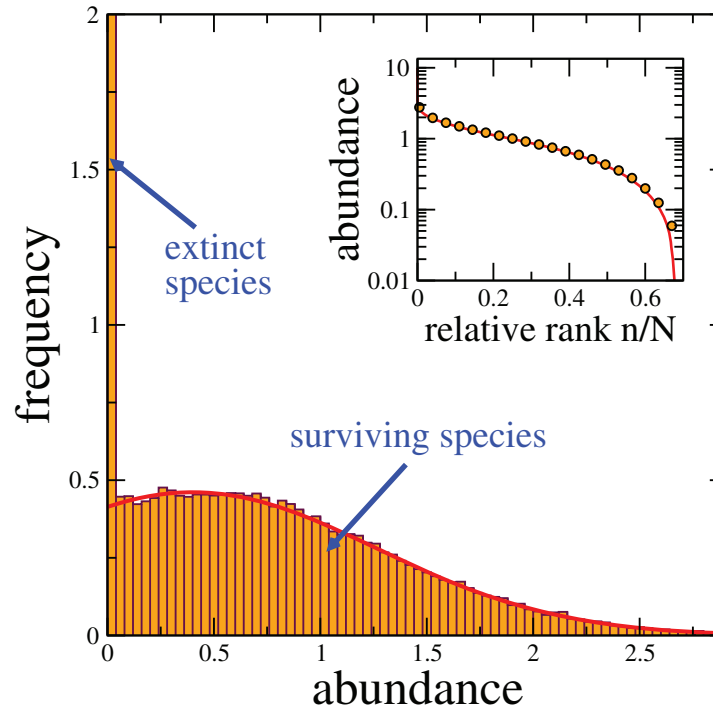# Dynamical Mean Field Theory
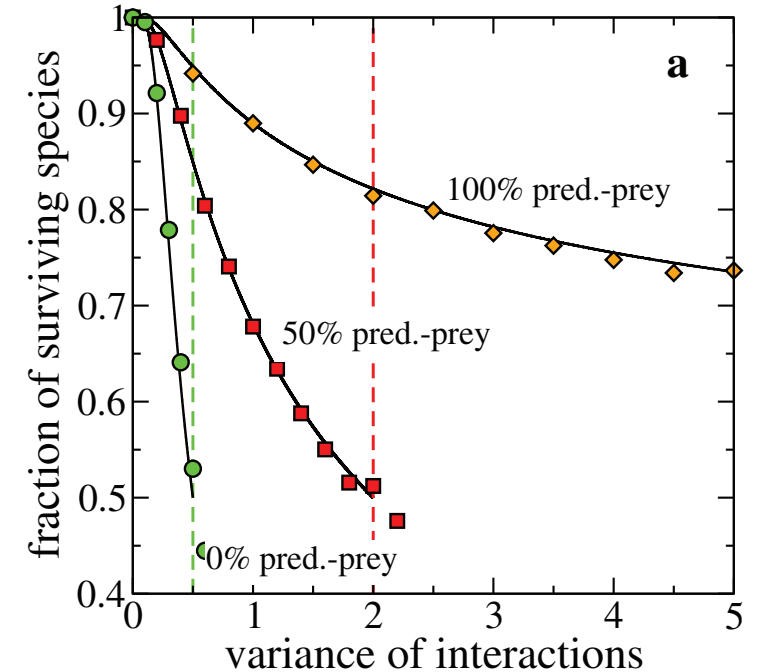

It works!

Full G
Random
Inter

P

Ga

Results for Fixed Interactions...

Complexity Stability Paradox
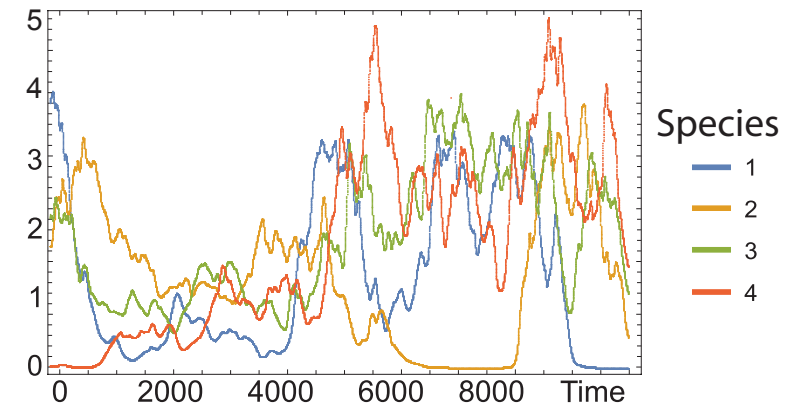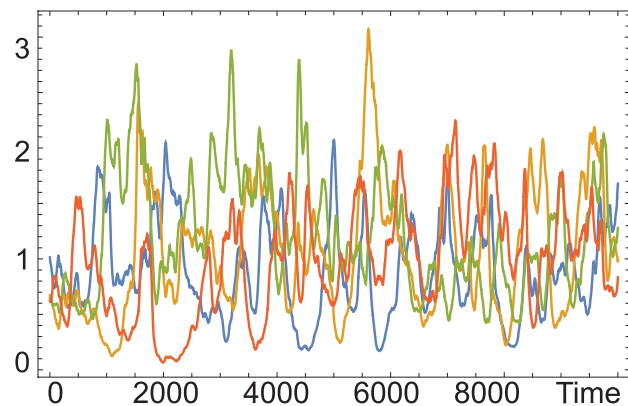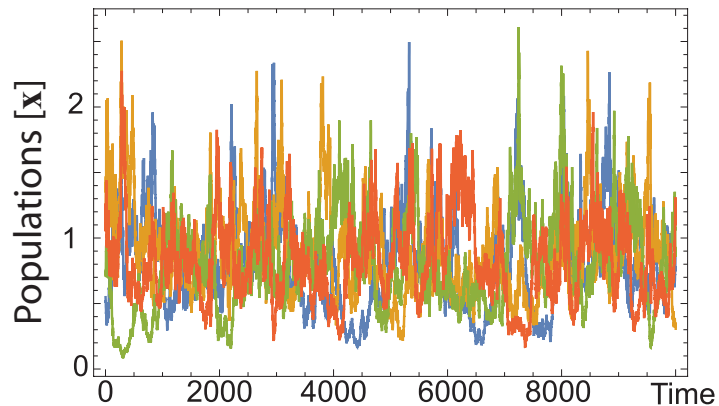
Truncated Gaussian SAD

Extinctions

Galla, EPL, 2018

GLV with Time Correlated Stochastic Interactions

$$\dot{x}_i(t) = r_i x_i(t) \left[1 - x_i(t)/K_i + \sum_{j \neq i} \alpha_{ij}(t) x_j(t) + h_i(t) \right]$$

$$\alpha_{ij}(t) = \mu/S + \sigma z_{ij}(t)/\sqrt{S} \qquad \overline{z_{ij}(t)z_{ij}(t')} = P(\Delta t | \tau) = \frac{1+2\tau/\tau_0}{2\tau} e^{-\Delta t/\tau}$$
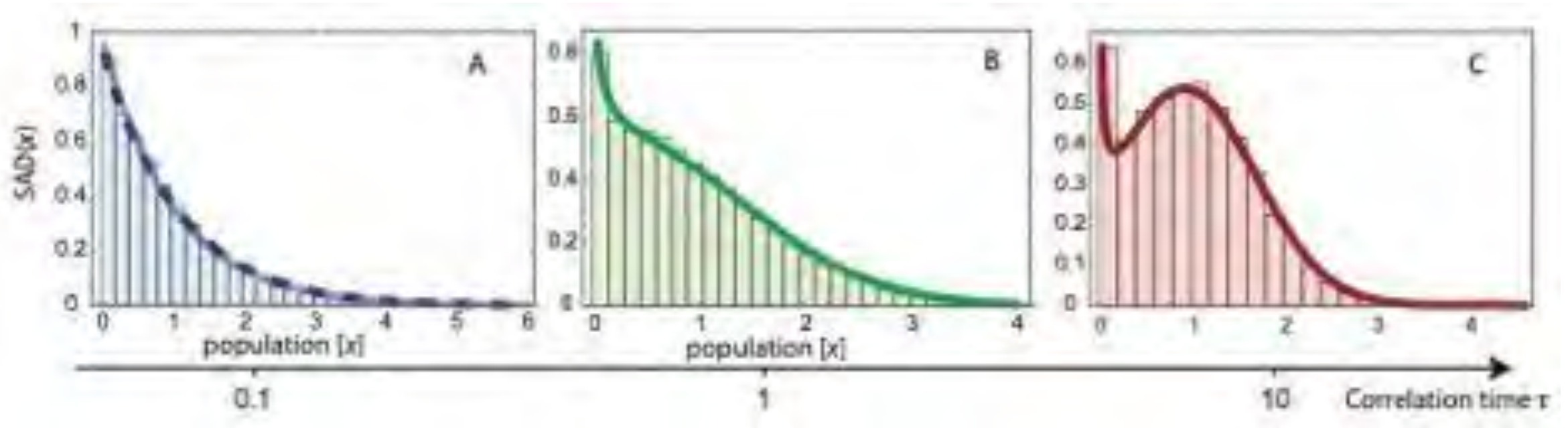
SAD for GLV with time dependent interactions
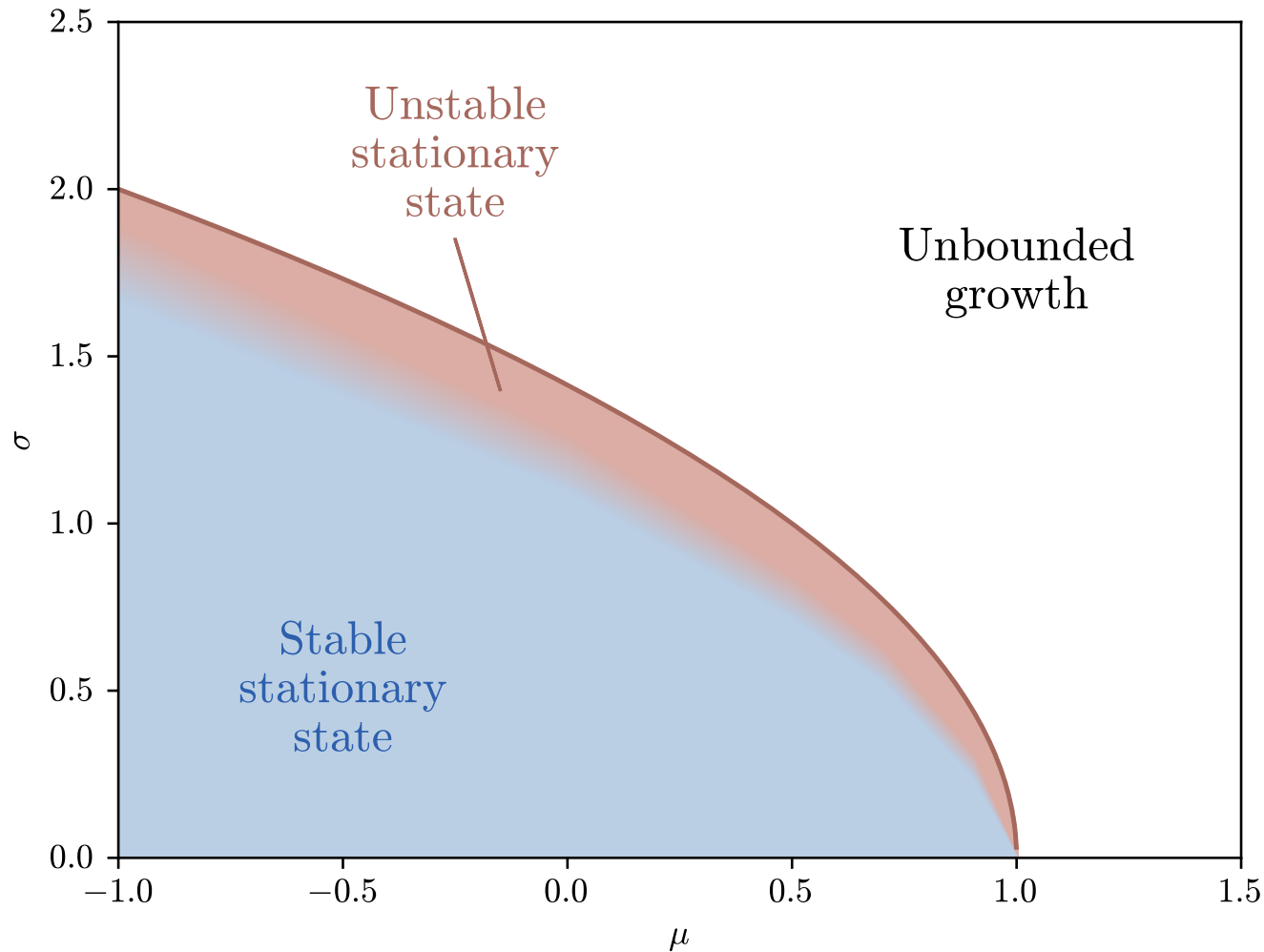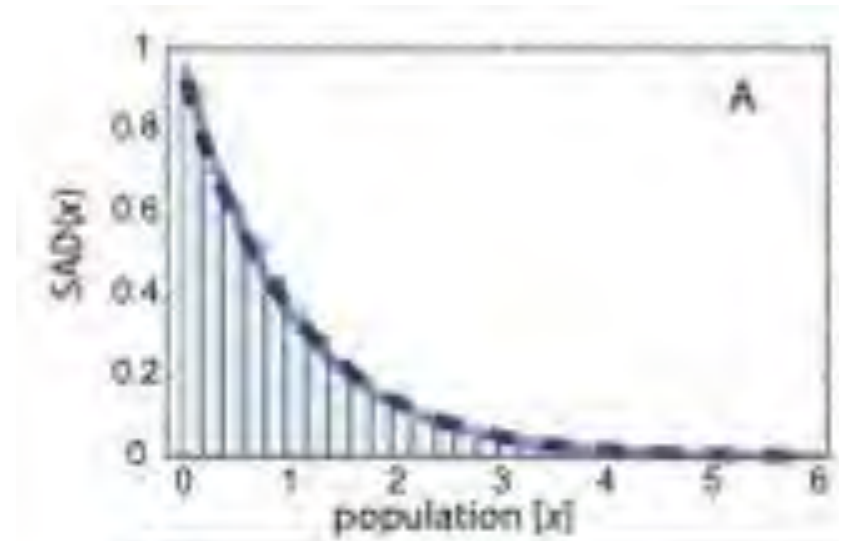

DMFT + UCNA

$$P_\tau^*(x) = \frac{x^{-1+\delta_\tau}}{Z} \left(\frac{1}{\bar{\tau}} + x \right) e^{-\frac{x}{D} - \frac{\bar{\tau}}{2D}(x-\bar{x})^2}$$

Suweis, Arxiv, 2023

Phase diagram for GLV with time dependent interactions in the limit $\tau \to 0$

SAD is a Gamma distribution

$$P_0^*(x) = \frac{\beta^\delta}{\Gamma(\delta)} x^{-1+\delta} e^{-\beta x}$$

Conclusions and future perspectives

Adding network dynamics and fluctuations favour species coexistence in ecological communities for both CRM and GLV models

In CRM this time dependency of interactions arises from proteome allocations law in relation to the species growth rate.

In GLV adding temporal fluctuations in species interaction networks allows species coexistence also for large systems and explain SAD

Combine quenched correlated interactions among species + temporal fluctations → CRM with GLV network dynamics.

Study effect of sparsity on the specie interactions networks

Large system population dynamics with non-Gaussian interactions

Sandro Azaele[1,2,3] and Amos Maritan[1,2,3]

Questions?

Thanks for your attention
&
thanks to all collaborators!

@SamirSuweis

L. Pacciani-Mori, A. Giometto, S. Azaele, A. Maritan,
G. Nicoletti, F. Ferraro

REFERENCES:

L. Pacciani-Moril, A. Giometto, S. Suweis, A. Maritan,
Dynamic metabolic adaptation can promote species coexistence in competitive microbial communities (2020),
Plos Computational Biology

L. Pacciani-Moril, S. Suweis, A. Maritan, A. Giometto, *Constrained proteome allocation affects species coexistence in models of competitive microbial communities* (2021), **ISME journal**

S. Suweis, S. Azaele, F. Ferraro, A. Maritan, *Generalized Lotka-Volterra Systems with Time Correlated Stochastic Interactions* ***Arxiv*** (2023)