

Constrained proteome allocation affects coexistence in models of competitive microbial communities

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Observation

Microbes are among the most abundant life forms on Earth in terms of biomass. They are found in almost every habitat of our planet, and are characterized by a high biodiversity

- Because of their ubiquity, microbial communities play fundamental roles in countless natural processes of vital importance, from the digestion and overall health of their host organism to the regulation of biogeochemical cycles

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- We still know little about the fundamental mechanisms that regulate microbial communities

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- We are interested in understanding how competition and metabolic interactions allow such systems to maintain the very high level of biodiversity found in nature

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- We can wonder how species uptake and use different resources for growth and proliferation and how these processes affect the dynamics of the entire community.
- Resource uptake is governed by the allocation of the internal resources of the cell like the **proteome** that is the set of proteins expressed by a cell for different tasks.



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Proteome allocation

The proteome of a single microbial species growing on a single resource can be minimally divided into three sectors:

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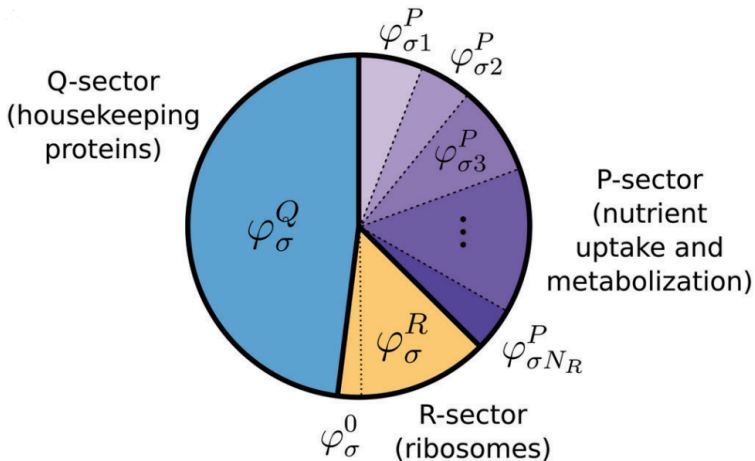
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- One dedicated to nutrient uptake and metabolism ("P-sector") φ^P
- One dedicated to ribosomal proteins responsible for biomass production and growth ("R-sector") φ^R
- One dedicated to housekeeping functions ("Q-sector") which is incompressible φ^Q

Proteome allocation



Some insights on proteome allocation

These fractions are found to be linear w.r.t the growth rate g :

$$\varphi^P = \frac{\rho}{\bar{k}^n} g, \quad \varphi^R = \frac{\rho}{k^t} g + \varphi^0 \quad (1)$$

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- K is the half-saturation constant of the resource and k^n is the "nutritional capacity of the limiting resource. k^t is the "translational capacity" of the microbial species
- φ^0 is the core of φ^R . Ribosomal proteins are present in the cells even when microbes are not growing

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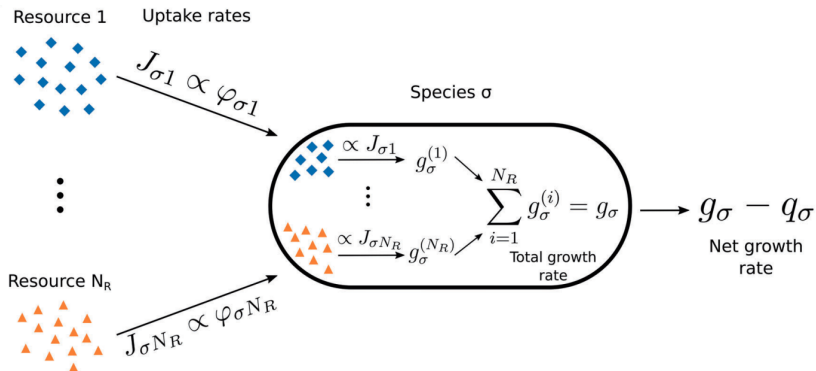
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To ensure that the sum of all the proteome fractions is equal to one we must have:

$$\varphi_{\sigma}^Q + \varphi_{\sigma}^R + \sum_{i=1}^{N_R} \varphi_{\sigma i}^P = 1 \quad (2)$$

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Mc.Arthur consumer resource model

Definition

A community is a set of N_S species that can only uptake some or all of the N_R available resources. Species growth rates are determined by the types and the amount of resources they uptake, and are also regulated by a maintenance cost, indeed species need to uptake a minimum amount of resources in order to survive. Resources can be also thought of as substrates that are supplied to the system with given rates s_i , and they are then eaten.

The model that describes the evolution of both species and resources is the following:

$$\begin{aligned} \dot{m}_\sigma &= m_\sigma (g_\sigma - q_\sigma) & \sigma &= 1, \dots, N_S, \\ \dot{c}_i &= s_i - \sum_{\sigma=1}^{N_S} J_{\sigma i} m_\sigma & i &= 1, \dots, N_R, \end{aligned}$$

Mc.Arthur consumer resource model

The ways in which species uptake resources are encoded in $J_{\sigma i}$ with parameters that are called metabolic strategies. In general $J_{\sigma i} \propto \alpha_{\sigma i}$ where $\vec{\alpha}_{\sigma} = (\alpha_{\sigma 1}, \dots, \alpha_{\sigma N_R})$ is the metabolic strategy of species σ .

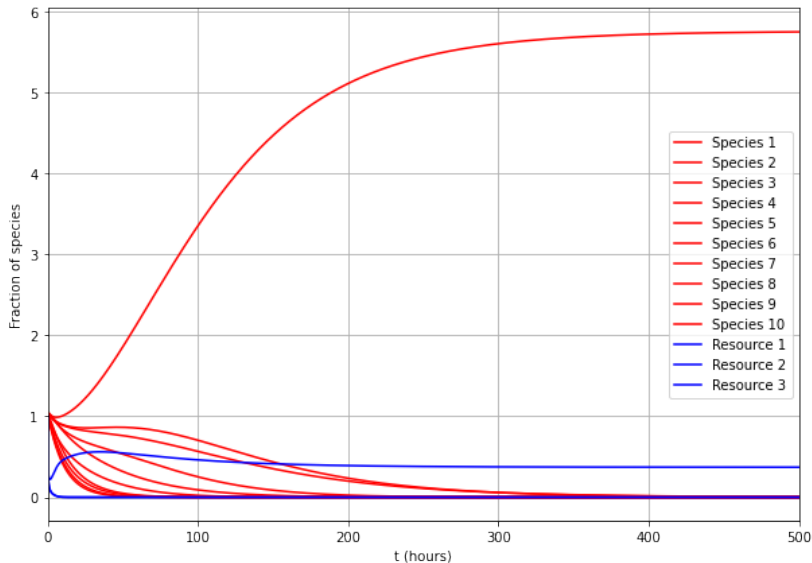
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Observation

In the consumer-resource framework the interactions between species are indirect and mediated by the abundance of resources and the species' resource preferences.

Example $N_S = 10$, $N_R = 3$



Variant of CR model

Definition

In an environment with p resources, only $m \leq p$ species can coexist. This result goes under the name of **competition exclusion principle (CEP)**.

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- One possibility to generalize CR model is to introduce a metabolic trade-off
- The idea is that to consume resources, a species must produce enzymes and metabolites, meaning that it must spend some energy w_i for assimilating a resource i .
- This expense is limited by a total **energy budget** E , which we can assume (for simplicity) to be the same for all species

$$E_\sigma \equiv E \quad \forall \sigma = 1, \dots, N_S$$

Conditions for coexistence

We can add then the following constraint:

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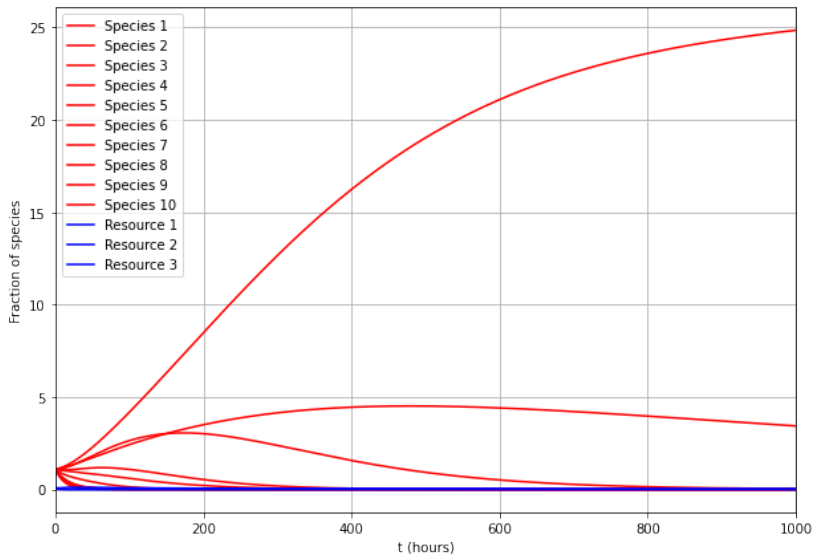
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After some algebra this criterion is translated into:

$$\sum_{\sigma} x_{\sigma}^* \bar{\alpha}_{\sigma i} = \hat{s}_i \quad (4)$$

Where "hat" and "bar" variables are just the original ones but traslated in order to be normalized w.r.t the energy supplies while x_{σ}^* are species at stationarity.

Example with $N_S = 10$ and $N_R = 3$



Coexistence in CR model

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Consumer-proteome-resource model settings

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- The uptake rate $J_{\sigma i}$ is proportional to the proteome fraction $\varphi_{\sigma i} = \varphi_{\sigma i}^P$ allocated by species σ for the uptake and metabolization of resource i : $J_{\sigma i} = \xi_i r_i(c_i) \varphi_{\sigma i}$

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- Each resource contributes to the growth of species σ through a term $g_{\sigma}^{(i)}$ proportional to the uptake rate $J_{\sigma i}$, so that the total growth rate g_{σ} of species σ can be written as the sum of all the terms $g_{\sigma}^{(i)}$. Where in particular $g_{\sigma} = \sum_{i=1}^{N_R} \frac{k_i^n}{\rho_{\sigma}} r_i(c_i) \varphi_{\sigma i}$

Consumer-proteome-resource model

$$\left\{ \begin{array}{l} \dot{m}_\sigma = m_\sigma \left(\sum_{i=1}^{N_R} \frac{k_i^n}{\rho_\sigma} r_i(c_i) \varphi_{\sigma i} - q_\sigma \right) \\ \dot{c}_i = s_i - \xi_i r_i(c_i) \sum_{\sigma=1}^{N_S} \varphi_{\sigma i} m_\sigma \\ \sum_{i=1}^{N_R} \varphi_{\sigma i} \left(1 + \frac{k_i^n}{k_\sigma^t} r_i(c_i) \right) = \Phi_\sigma \end{array} \right.$$

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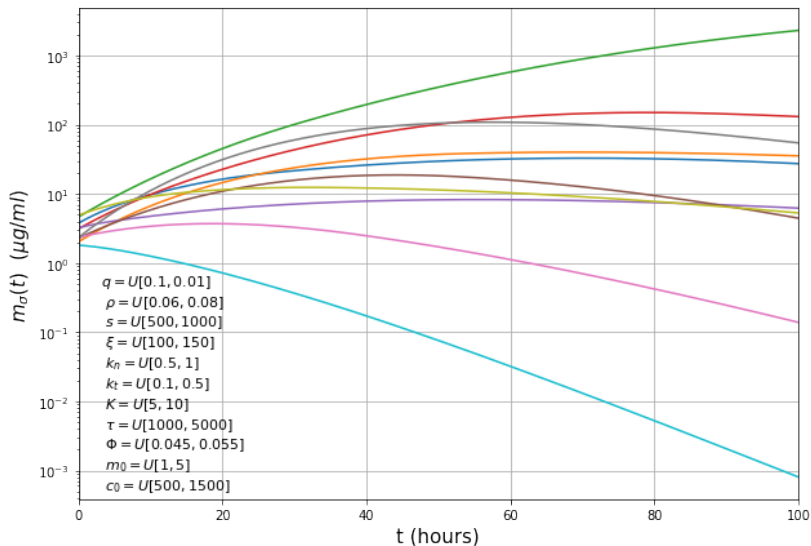
ξ_i can be interpreted as the maximum catalytic rate of the enzyme used to metabolize resource i , and Φ_σ is the total proteome fraction allocated by species σ for metabolism and biomass synthesis, which is fixed. For a species growing on a single resource, we can notice the perbiomass resource uptake rate $\xi r(c) \varphi_\sigma$ and the yield (expressed as biomass per grams of resource), $Y = k^n / \rho \xi$

Consumer-proteome-resource model

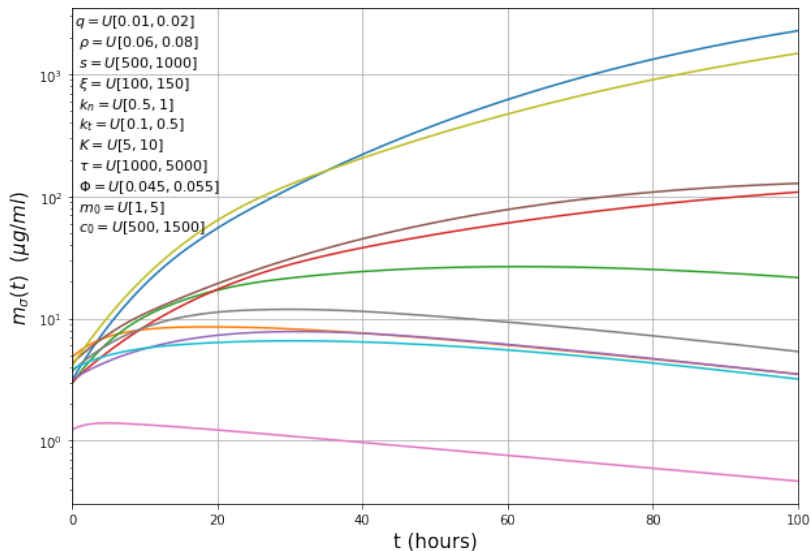
If we add to the previous system of equations the dynamics of the proteome allocations $\varphi_{\sigma i}$ we end up with:

$$\left\{ \begin{array}{l} \dot{m}_{\sigma} = m_{\sigma} \left(\sum_{i=1}^{N_R} \eta_{\sigma i} r_i(c_i) \varphi_{\sigma i} - q_{\sigma} \right) \\ \dot{c}_i = s_i - \xi_i r_i(c_i) \sum_{\sigma=1}^{N_S} \varphi_{\sigma i} m_{\sigma} \\ \dot{\varphi}_{\sigma i} = \varphi_{\sigma i} \left(\frac{\eta_{\sigma i} r_i(c_i)}{\tau_{\sigma}} - \frac{(1 + \gamma_{\sigma i} r_i(c_i))}{\sum_{k=1}^{N_R} \varphi_{\sigma k} (1 + \gamma_{\sigma k} r_k(c_k))^2} \right) \cdot \\ \cdot \left(\sum_{j=1}^{N_R} \varphi_{\sigma j} \left(\frac{\eta_{\sigma j} r_j(c_j)}{\tau_{\sigma}} (1 + \gamma_{\sigma j} r_j(c_j)) + \gamma_{\sigma j} r_j(c_j) \frac{K_j}{(c_j + K_j)^2} \dot{c}_j \right) \right) \end{array} \right.$$

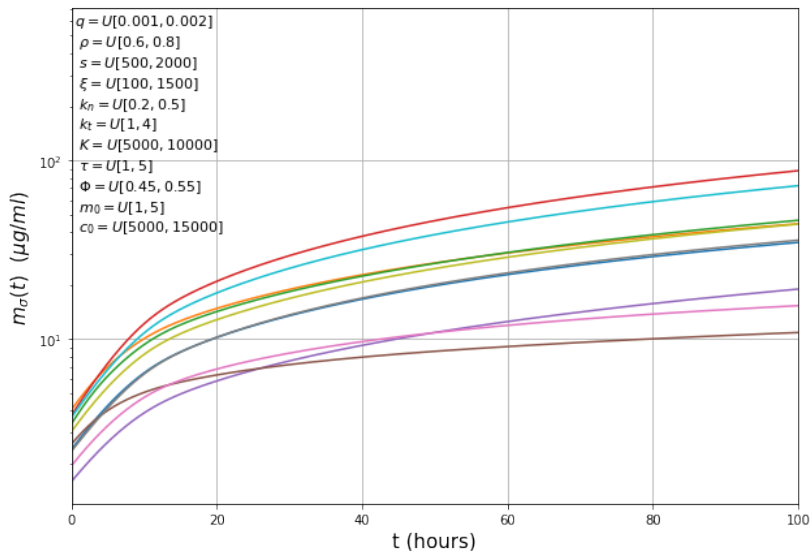
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Conditions for coexistence

We are looking for stationary solutions where all species have non null biomass densities. Doing so yields two necessary conditions for the coexistence of all species when $N_S > N_R$:

- The maintenance cost q_σ of species σ must be proportional to the total proteome fraction allocated for metabolism and growth, i.e. $q_\sigma \propto \Phi_\sigma$, with a species dependent proportionality constant. This requirement is biologically reasonable, since allocating a larger fraction of the proteome to such functions requires additional energy to synthesize the necessary proteins

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- The second condition prescribes that $\vec{\hat{s}}$ must belong to the convex hull of the vectors $\vec{\varphi}_\sigma^*$.

Conditions for coexistence

If we translate the two above mentioned conditions into equations we end up with:

$$q_{\sigma} = \frac{\Phi_{\sigma}}{\rho_{\sigma}(\Theta + 1/k_{\sigma}^t)}$$
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where $\hat{s}_i = \frac{s_i k_i^n / \xi_i}{\sum_{j=1}^{N_R} s_j k_j^n / \xi_j}$, $z_{\sigma} = \frac{m_{\sigma}^* \rho_{\sigma} q_{\sigma}}{\sum_{\lambda} m_{\lambda}^* \rho_{\lambda} q_{\lambda}}$ and $\hat{\varphi}_{\sigma i} = \frac{\varphi_{\sigma i}}{\sum_{j=1}^{N_R} \varphi_{\sigma j}}$

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Parameters exploration

Observation

Because the CPR model is highly non-linear, it is impossible to predict a priori the values of the stationary fractions $\varphi_{\sigma i}$ once all the other parameters are set. However, it is possible to understand how the various parameters affect the dynamics of the system by exploring different regions of the parameter space

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The relevant parameters are the ratios $\gamma_{\sigma i} = k_i^n / k_\sigma^t$ between the nutritional and translational capacities, and the characteristic timescales τ_σ of the adaptive process that maximizes the growth rate g_σ in the dynamics of $\varphi_{\sigma i}$. The time scale τ_σ can be thought as a measure of how fast the regulatory mechanisms of a microbial species can respond to changes in the availability of resources.

$$\tau_{\sigma} \gg 1 \text{ and } \gamma_{\sigma i} \approx 0$$

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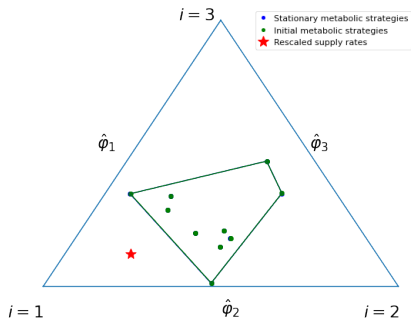
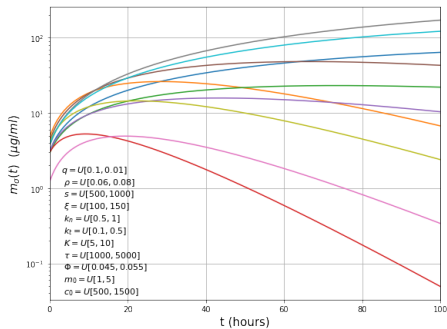
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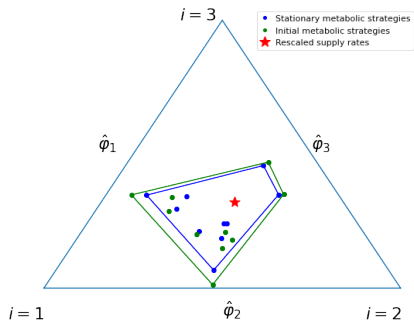
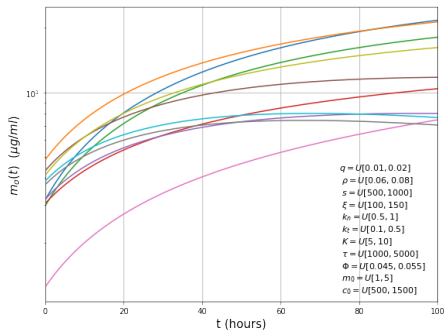
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In this case, the model predicts that the stationary values $\varphi_{\sigma i}^*$ of the rescaled proteome fractions allocated by the species to nutrient uptake and metabolism change negligibly, and therefore all species survive only if the rescaled nutrient supply rate vector \vec{s} lies in the convex hull of the rescaled initial proteome fractions $\vec{\varphi}_{\sigma}$.

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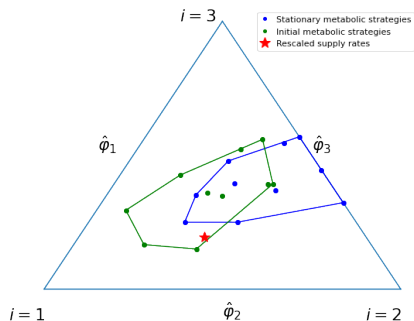
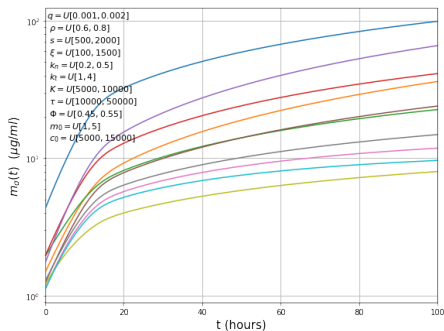
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- If $\vec{\hat{s}}$ lies at an intermediate distance between these two cases, the system can reach diverse stationary states only if the resource supply rates s_i are sufficiently large

For example, multiplying each resource supply rate by a factor $x > 1$, i.e. $s_i \rightarrow xs_i$ we observe a transition between two different states of the system for increasing values of x : when $x \approx 1$, only a few species survive, whereas for larger values of x the stationary biomass densities m_{σ}^* of the other species increase until all of them coexist.



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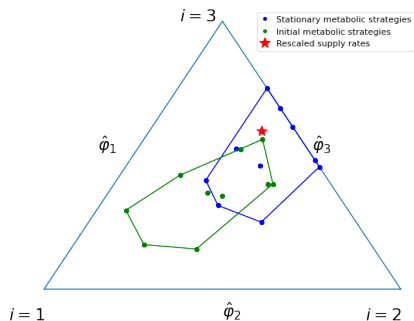
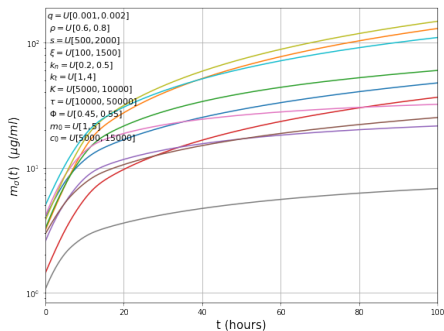


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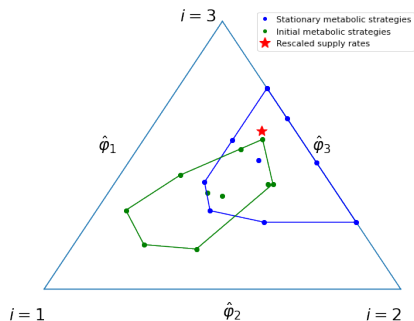
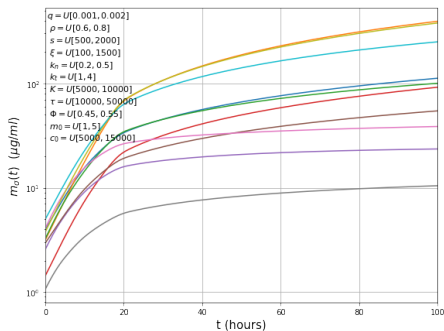


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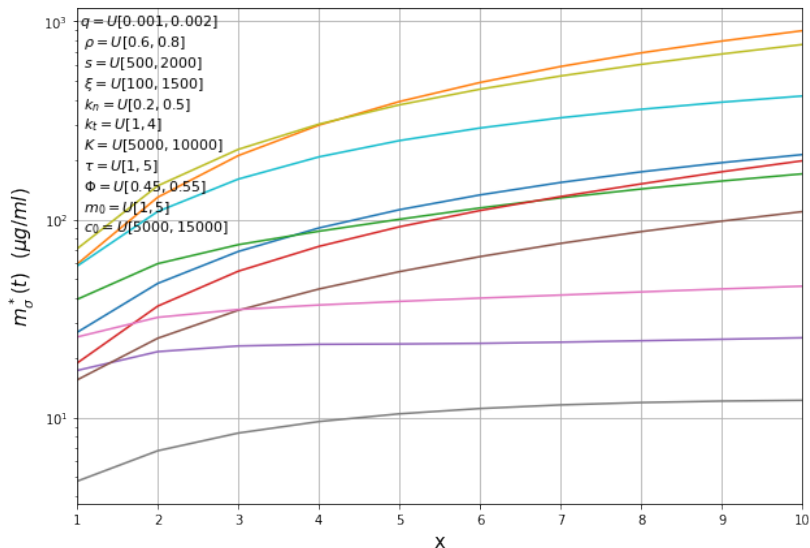
$$\tau_{\sigma} \gg 1 \text{ and } \gamma_{\sigma i} \gtrsim 1, x = 2$$



$$\tau_{\sigma} \gg 1 \text{ and } \gamma_{\sigma i} \gtrsim 1, x = 5$$



$$\tau_\sigma \gg 1 \text{ and } \gamma_{\sigma i} \gtrsim 1$$



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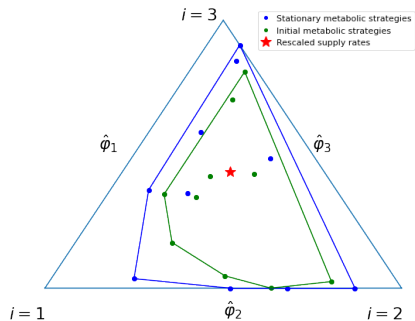
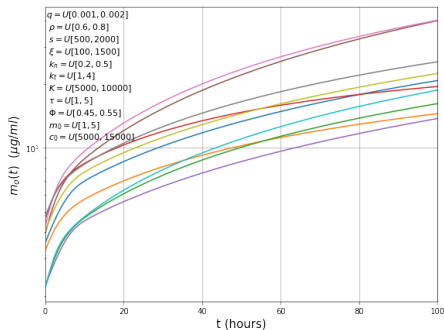
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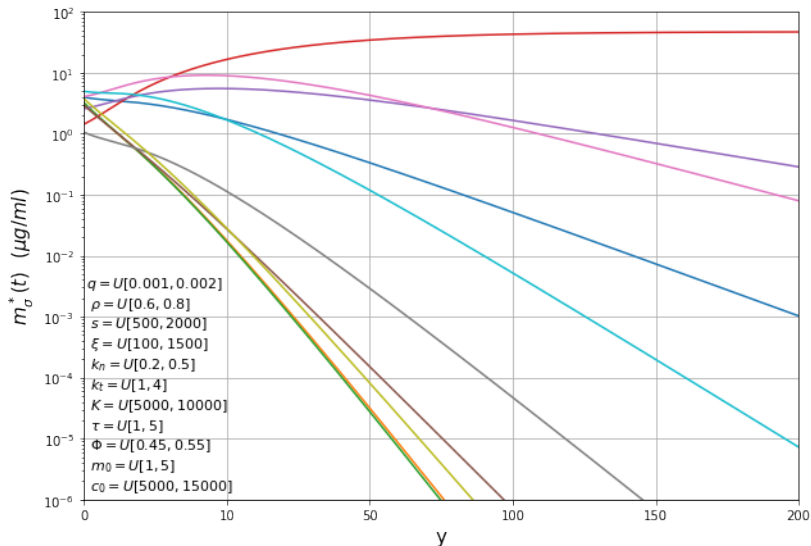
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we will see how species' stationary biomasses change as y increases, and we can see that as species adaptation becomes slower (i.e., for larger y), fewer and fewer species survive in the community.

$$\tau_{\sigma} \ll 1 \text{ and } \gamma_{\sigma i} \gtrsim 1$$



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- 8 "One more thing"

Summing up results

We have shown that the CPR model predicts that high levels of biodiversity can be achieved only if two conditions apply:

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Biological interpretation

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- Fast metabolic adaptation (i.e., the species can switch quickly between different resources) favors coexistence

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"Are there any patterns or considerations that can be done about the dynamics of metabolic strategies by varying the initial conditions of the simulation?"

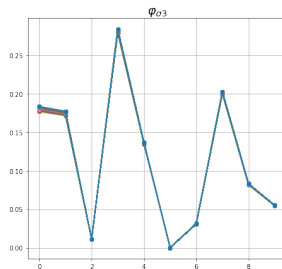
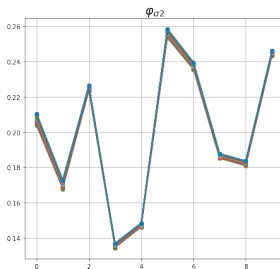
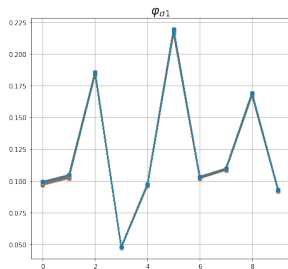
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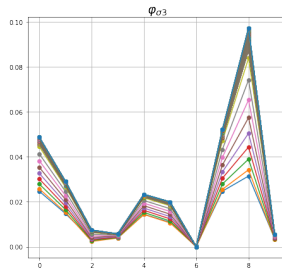
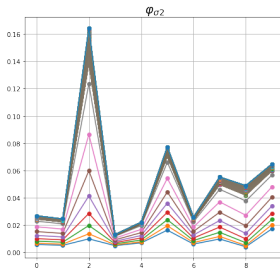
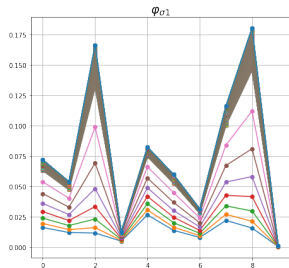
We have explored different approaches:

Dynamics of metabolic strategies, $\tau_\sigma \gg 1$ and $\gamma_{\sigma i} \approx 0$

- We considered separately the evolution of how much all species eat one of the resources $\varphi_{\sigma 1}, \varphi_{\sigma 2}, \varphi_{\sigma 3}$



Dynamics of metabolic strategies, $\tau_\sigma \gg 1$ and $\gamma_{\sigma i} \geq 0$

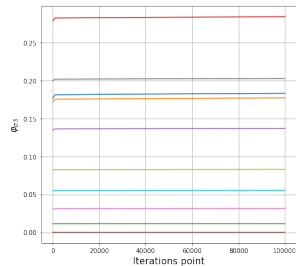
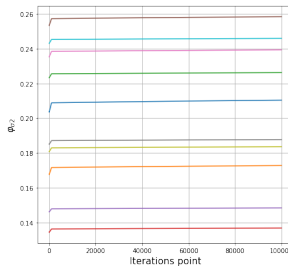
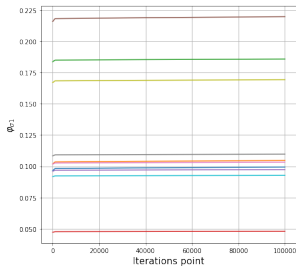


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Dynamics of metabolic strategies, $\tau_\sigma \gg 1$ and $\gamma_{\sigma i} \approx 0$

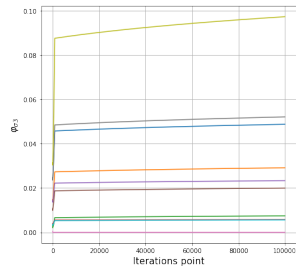
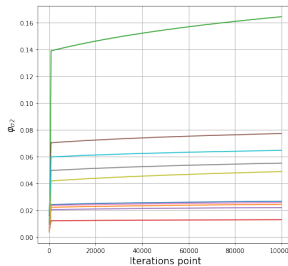
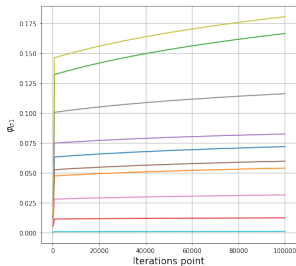


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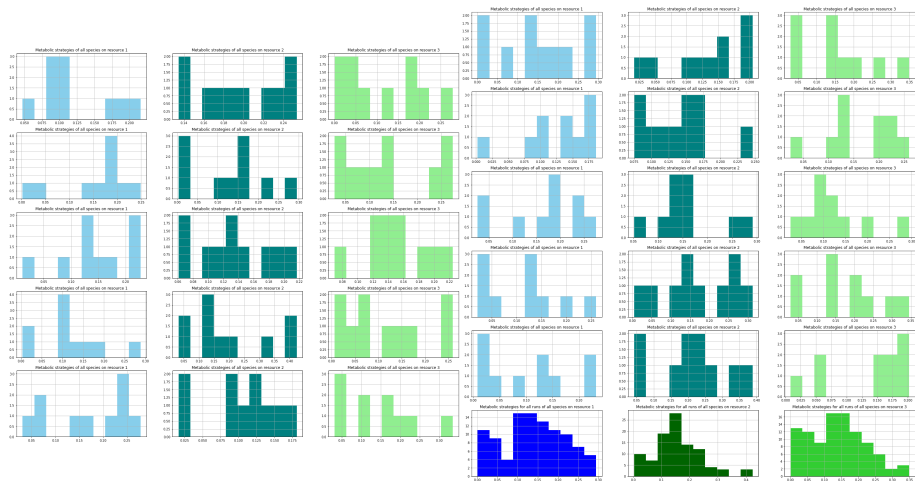
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Dynamics of metabolic strategies, $\tau_\sigma \leq 1$ and $\gamma_{\sigma i} \geq 0$

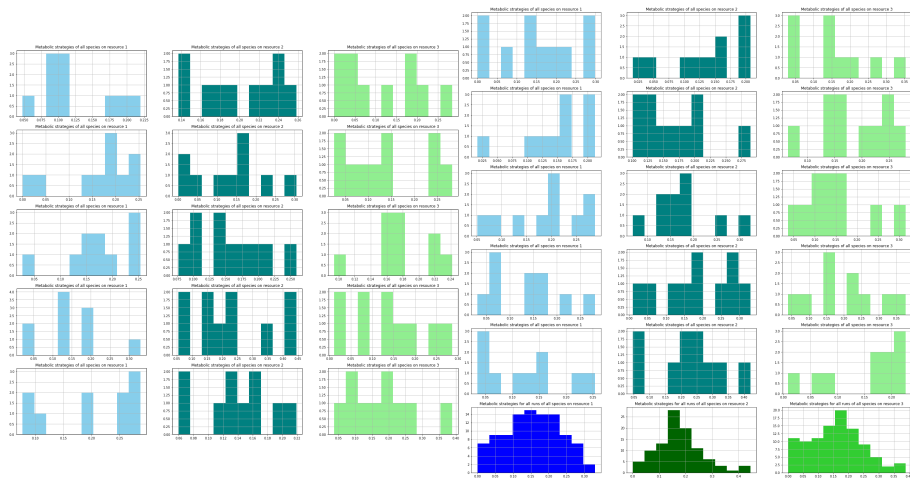


Further exploration about metabolic strategies

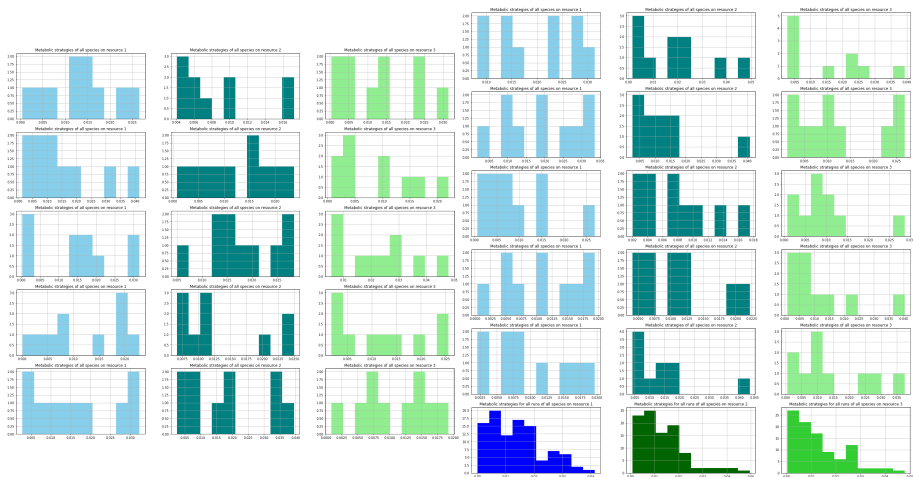
- We decided to exploit the distribution of the metabolic strategies for each resource at the initial and final time of the simulation



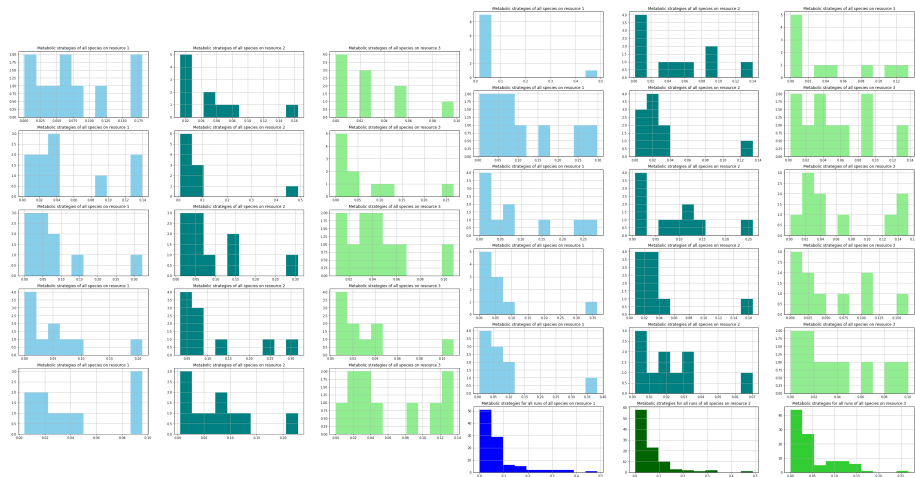
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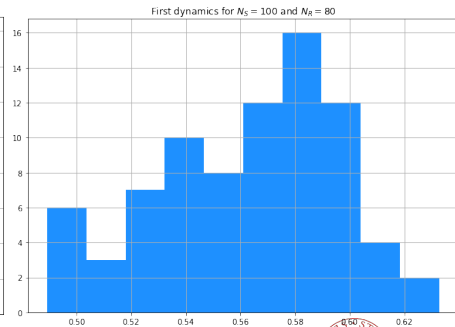
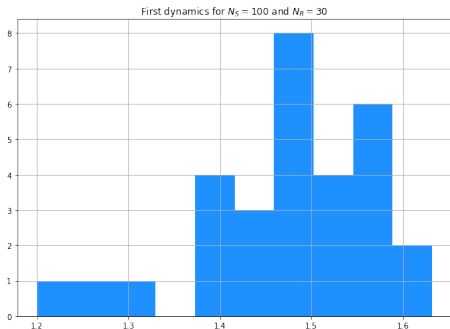


Further exploration about metabolic strategies



Distribution of $\sum_{\sigma=1}^{N_S} \varphi_{\sigma i}$, $\tau_{\sigma} \gg 1$ and $\gamma_{\sigma i} \approx 0$

- Instead of separating the metabolic strategies w.r.t the different resources we marginalized over the species in order to see how much each resource is eaten independently on the consumer

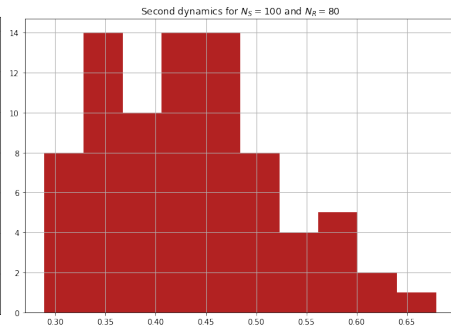
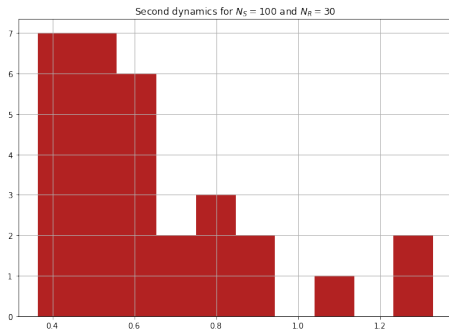


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Distribution of $\sum_{\sigma=1}^{N_S} \varphi_{\sigma i}$, $\tau_{\sigma} \leq 1$ and $\gamma_{\sigma i} \geq 0$



Thanks for your attention!

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