

MacArthur's models in Species ecosystems

Supervisor: Amos Maritan *

Educational Research Project

Alberto Bassi †

August 24, 2022

Abstract

One of the most fascinating challenges in ecosystems' theory is to explain why many species can survive in an environment where there are only few resources available, violating the so-called Competitive Exclusion Principle (CEP). Even though many approaches are possible, enlightening results have been obtained by considering only tiny modifications to MacArthur's Consumer Resource (CR) model taken one at a time, avoiding comprehensive extensions. This work faces this problem, reviewing what has been already done in literature and trying to address new questions.

Contents

1	Introduction	2
2	MacArthur's model	2
3	Adapting strategies	3
4	Constrained Proteome Allocation	3
4.1	Coexistence conditions	5
4.2	Proteome fractions dynamics	5
5	Spatial interactions	7
6	Pathogens	8
7	Conclusion	10
A	Constrained Maximization	12
	References	13

*amos.maritan@unipd.it

†alberto.bassi.3@studenti.unipd.it

1 Introduction

Competitive exclusion principle (CEP) states that in an environment with limited resources at most a number of species which is equal or less the number of resources can coexist. If, for example, we consider an ecosystem consisting of two bacteria and one sugar, we might think that if one of the two species has a slight advantage in consuming the nutrient, then this advantage could lead to the extinction of the less fitting species, meaning that the environment supports only one of the two bacteria. However, many ecosystems violate CEP in Nature, allowing the coexistence of a number of species much greater than number of resources. A famous example is given by Plankton paradox, for it has been observed that the number of plankton species surviving in the oceans is by far larger than the resources available.

MacArthur's consumer resource model is one of the simplest models used to describe the dynamics of a pool of species competing for a limited number of resources. Though, the standard version of this model still predicts CEP. One of the first solutions that has been proposed to violate CEP leads to the introduction of a metabolic constraint: if each species has fixed amount of energy to be spent for metabolism, meaning that the metabolic strategies are constrained, there are solutions with an arbitrary number of coexisting species [1]. However, this solution is evidently fine-tuned, since is very difficult that this strong constraint could be actually held in real ecosystems.

This framework has been further generalized to systems with adapting metabolic strategies [2], for which only an upper bound on the total energy spent by each species is fixed. Moreover, even more realistic biological constraints have been considered, like the total proteome allocation for growth and metabolism [3]. The introduction of an effective carrying capacity term has been investigated [4] recently and brought back to either spatial competitions or Janzen-Connell effects in the presence of auxiliary pathogens species with fast adaptive timescale.

The aim of this project is to review the recent developments in this subject and address new ideas. It should be stressed that all these models share a common factor: CEP violation aims to be explained by the introduction of simple factors, taken one at a time, without taking into account comprehensive models.

2 MacArthur's model

Let us consider an ecosystem of N_S species competing for a limited number of resources N_R . In the absence of a carrying capacity term for resource dynamics, the dynamics is described by the Mac Arthur's model

$$\begin{aligned} \dot{m}_\sigma &= m_\sigma \left(\sum_i \nu_i \alpha_{\sigma i} r(c_i) - q_\sigma \right), \quad (\sigma = 1, \dots, N_S) \\ \dot{c}_i &= S_i - r(c_i) \sum_\sigma \alpha_{\sigma i} m_\sigma, \quad (i = 1, \dots, N_R) \end{aligned} \quad (1)$$

where $\alpha_{\sigma i}$ is the metabolic strategies of species σ w.r.t. resource i , taken as a constant at this stage, which is proportional to the energy spent by that species in uptaking that resource. q_σ is the death rate of species σ . S_i is the constant resource supply rate and $r(c_i) = \frac{c_i}{K_i + c_i}$ is the Monod function, where K_i is resource half saturation constant. Finally, $\nu_i < 1$ is the maximum conversion of resource in biomass coefficient.

Since species cannot consume an unlimited amount of resources, even if they were available, the Monod function has been introduced because the consumption should be saturating with resource concentration.

After a long time, we expect the system to reach stationarity, leading to

$$\sum_i \nu_i \alpha_{\sigma i} r(c_i^*) = q_\sigma \quad (2)$$

and

$$r(c_i^*) \sum_\sigma \alpha_{\sigma i} m_\sigma^* = S_i, \quad (3)$$

where $*$ stands for quantities at stationarity.

Equation 2 is a system of N_S equations in N_R variables, meaning that it can be solved only of $N_S \leq N_R$, leading to CEP.

However, if we add a metabolic constraint the system can explicitly violate CEP. Intuitively, each species has a fixed amount of energy to spend for uptaking resources, therefore allowing us to introduce a constraint on metabolic strategies as

$$\sum_i \alpha_{\sigma i} = E_\sigma. \quad (4)$$

Having this on hands, a possible solution is given by

$$r(c_i^*) = \frac{1}{\nu_i} \frac{q_\sigma}{E_\sigma}, \quad (5)$$

where LHS depends on i , while the RHS depends also on the species. Therefore, in this case coexistence is possible only if, in agreement with metabolic theory of ecology [2], $E_\sigma = Qq_\sigma$. Indeed, let us define the rescaled quantities:

$$x_\sigma = \frac{q_\sigma m_\sigma}{\sum_\rho q_\rho m_\rho}, \quad \hat{s}_i = \frac{S_i \nu_i}{\sum_j S_j \nu_j}, \quad \hat{\alpha}_{\sigma i} = \frac{\alpha_{\sigma i}}{Qq_\sigma}, \quad (6)$$

which all sum to one, meaning that they belong to the $(N_R - 1)$ -dimensional simplex.

If we now sum over σ both sides of the first dynamic equation in Equation 1, we get at stationarity that

$$\sum_\rho q_\rho m_\rho^* = \sum_j S_j \nu_j. \quad (7)$$

Therefore, from Equation 3 it is immediate to obtain

$$\hat{s}_i = \sum_\sigma x_\sigma^* \hat{\alpha}_{\sigma i}. \quad (8)$$

Last equation has a straightforward geometrical interpretation. Since all rescaled quantities sum to one, coexistence is possible only if the rescaled supply rate \hat{s}_i belongs to the convex hull of rescaled metabolic strategies, as it was first shown in [1].

3 Adapting strategies

In the last section, we examined which are the conditions for which Mac Arthur's model leads to a violation of CEP under a strict metabolic constraint. Indeed, the solution found so far is valid only if Equation 4 is exact, that is very unlikely in real ecosystems; if, on the other hand, we had a weaker constraint like $\sum_i \alpha_{\sigma i} \leq E_\sigma$, the dynamics would lead to the extinctions of most of the species [2].

However, if the metabolic strategies were no longer fixed, but could vary in time, this softer metabolic constraint would allow many species to survive, violating CEP. Indeed, even if the rescaled supply rate does not belong to the convex hull of the rescaled metabolic strategies at the beginning of the dynamics, species are able to self-organizing in order to include the rescaled supply rate in their convex hull at stationarity, as it has been shown in [2] and reported in Figure 1.

Since each species has a fixed maximum amount of energy E_σ to spend in resource uptaking, the softer adimensionalized constraint reads

$$\rho(\vec{\alpha}_\sigma(t)) \equiv \sum_i \alpha_{\sigma i}(t)/E_\sigma - 1 \leq 0. \quad (9)$$

The authors of [2] maximized the growth rate as done in Appendix A, given by

$$g_\sigma = \sum_i \nu_i \alpha_{\sigma i} r(c_i) - q_\sigma, \quad (10)$$

under the above constraint, leading to the following dynamics for metabolic strategies

$$\dot{\alpha}_{\sigma i} = \alpha_{\sigma i} \lambda_\sigma \left[\nu_i r(c_i) - \frac{\Theta(\rho(\vec{\alpha}_\sigma))}{\sum_k \alpha_{\sigma k}} \sum_j \nu_j r(c_j) \alpha_{\sigma j} \right], \quad (11)$$

where λ_σ is the learning rate of species.

Equation 11 is not obtained by performing a direct optimization for the dynamics of the metabolic strategies; rather the author considered a positive function $\mathcal{F}(\alpha_{\sigma i}) \geq 0$, such as $x^2/4$, since metabolic strategies could become negative otherwise.

4 Constrained Proteome Allocation

The results of the previous paragraph show that the coexistence of many species and the violation of CEP is possible when allowing the metabolic strategies to adapt in order to maximize the growth rate of each species. However, this solution is not rooted in reasonable biological assumptions.

An step forward is given in [3], where also the allocation of proteome is taken into account, which ultimately is the ensemble of proteins expressed by an organism.

The starting point is the work of Scott et al. [5], which prescribed the division of the proteome of a cell into

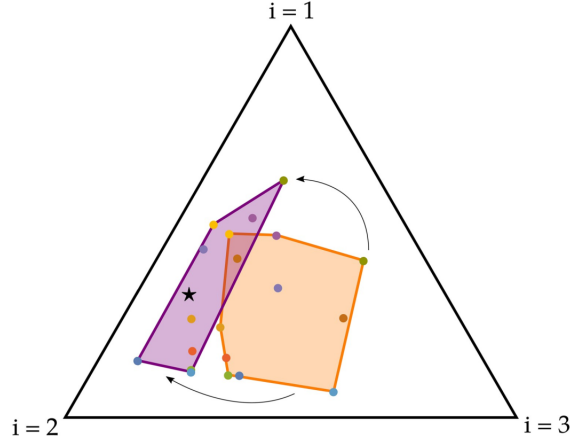


Figure 1: Figure taken from [2] for three resources. Adapting metabolic strategies evolve in order to include the rescaled supply rate at stationarity allowing coexistence of more species than resources.

three sector: P-sector, dedicated to nutrient uptake and metabolism; R-sector, dedicated to biomass production and growth; Q-sector, dedicated to housekeeping functions. Scott et al. showed that these proteome fractions can be practically described by linear functions in the case of one species consuming one resource, such as

$$\varphi^P = \frac{\rho}{k^n r(c)} g, \quad \varphi^R = \frac{\rho}{k^t} g + \varphi^0, \quad (12)$$

where φ^Q has been shown to be incompressible.

In this framework ρ is a conversion factor, g is the growth rate as usual, k^n is the nutritional capacity, which depends on how much energy the resource contains and how efficiently a species can metabolize it and k^t is the translational capacity, which is a measure of how fast a bacterium expresses a gene in order to synthesize proteins. The generalization to many species and resources is straightforward [3], and leads to a constraint on the total proteome fraction, which has to sum to one, while the proteome fractions of *P*–sector depend on the species and the resources and indeed assume the role previously taken by metabolic strategies. We thus have

$$g_\sigma = \sum_i \frac{k_i^n r(c_i)}{\rho_\sigma} \varphi_{\sigma i}^P, \quad \varphi_\sigma^R = \frac{\rho}{k_\sigma^t} g_\sigma + \varphi_\sigma^0; \quad (13)$$

which lead, upon the substitution of the growth rate and the normalization condition

$$\varphi_\sigma^Q + \varphi_\sigma^R + \sum_i \varphi_{\sigma i}^P = 1, \quad (14)$$

to the new constraint

$$\sum_i \varphi_{\sigma i} \left[1 + \frac{k_i^n}{k_\sigma^t} r(c_i) \right] = \Phi_\sigma \equiv 1 - \varphi_\sigma^0 - \varphi_\sigma^Q. \quad (15)$$

Upon the introduction of a maximum catalytic rate ξ_i , which is used to metabolize resource i , MacArthur's model becomes

$$\begin{aligned} \dot{m}_\sigma &= m_\sigma \left[\sum_i \eta_{\sigma i} r(c_i) \varphi_{\sigma i}^P - q_\sigma \right], \\ \dot{c}_i &= S_i - \xi_i r(c_i) \sum_\sigma m_\sigma \varphi_{\sigma i}, \\ \Phi_\sigma &= \sum_i \varphi_{\sigma i} \left[1 + \gamma_{\sigma i} r(c_i) \right], \end{aligned} \quad (16)$$

where we have defined $\eta_{\sigma i} = \frac{k_i^n}{\rho_\sigma}$ and $\gamma_{\sigma i} = \frac{k_i^n}{k_\sigma^t}$.

4.1 Coexistence conditions

We now examine which are the coexistence conditions of the so-called Cosumer Proteome Resource (CPR) model of Equation 16. At stationarity we have

$$\begin{aligned} q_\sigma &= \sum_i \eta_{\sigma i} r(c_i^*) \varphi_{\sigma i}^* , \\ S_i &= \xi_i r(c_i^*) \sum_\sigma m_\sigma^* \varphi_{\sigma i}^* , \\ \Phi_\sigma &= \sum_i \varphi_{\sigma i}^* \left[1 + \gamma_{\sigma i} r(c_i^*) \right] . \end{aligned} \quad (17)$$

If the proteome fractions at stationarity are all strictly positive ($\varphi_{\sigma i}^* > 0$), a possible solution of the third equation in Equation 17 is

$$r(c_i^*) = \left[k_i^n \left(\frac{\Phi_\sigma}{\rho_\sigma q_\sigma} - \frac{1}{k_\sigma^t} \right) \right]^{-1} . \quad (18)$$

If the CEP is violated, with $N_S > N_R$, the only acceptable solution of Equation 18 is when the right hand side is independent on the species, meaning

$$\Theta = \frac{\Phi_\sigma}{\rho_\sigma q_\sigma} - \frac{1}{k_\sigma^t} , \quad (\forall \sigma = 1, \dots, N_S) \quad (19)$$

which put in Equation 18 yields $r(c_i^*) = 1/k_i^n \Theta$, implying that $c_i^* = \frac{K_i}{k_i^n \Theta - 1}$ and since $r(c_i^*) < 1$, eventually leading to $\Theta > \max_i 1/k_i^n$. Equation 19 yield also an expression for the death rate that results to be proportional to Φ_σ as

$$q_\sigma = \frac{\Phi_\sigma}{\rho_\sigma (\Theta + 1/k_\sigma^t)} . \quad (20)$$

If we now define the rescaled quantities, which sum to one with respect of the main indexes, in the spirit of [1, 2] as

$$\begin{aligned} \hat{s}_i &= \frac{S_i k_i^n / \xi_i}{\sum_j S_j k_j^n / \xi_j} , \\ \hat{\varphi}_{\sigma i}^* &= \frac{\varphi_{\sigma i}^*}{\sum_j \varphi_{\sigma j}^*} , \\ z_\sigma &= \frac{m_\sigma^* \rho_\sigma q_\sigma}{\sum_\lambda m_\lambda^* \rho_\lambda q_\lambda} , \end{aligned} \quad (21)$$

from the second of Equation 17, we get

$$\hat{s}_i = \sum_\sigma z_\sigma \hat{\varphi}_{\sigma i}^* , \quad (22)$$

which means that coexistence of more species than resources is possible whenever the the rescaled supply rate belongs to the convex hull of the rescaled proteome fractions at stationarity, exactly as it was in [2] with adapting metabolic strategies and contrary to Posfai et al. work [1], in which coexistence is possible only if this conditions holds from the beginning of the dynamics, due to the static nature of the metabolic strategies in that case.

4.2 Proteome fractions dynamics

From the metabolic constraint of the third equation in Equation 16, it follows that the proteome fractions $\varphi_{\sigma i}$ have to depend on time, as it can be easily seen in the case of one resource. In particular, they depend on the resource availability emphasized by the Monod function, implying that they have to follow an adapting dynamic in order to maintain the proteome constraint.

If we implement an adaptive approach of the proteome fractions in order to maximize the growth rate g_σ under the constraint given by the total proteome fraction allocation, which can be rewritten as follow

$$F_\sigma(\vec{\varphi}_\sigma^P, \vec{c}) = \sum_i \varphi_{\sigma i}^P [1 + \gamma_{\sigma i} r(c_i)] - \Phi_\sigma = 0 , \quad (23)$$

by taking a positive function of the proteome fractions assuring the satisfaction of the feasibility condition $\varphi_{\sigma i} \geq 0$, such as $x^2/4$, we get [3]

$$\dot{\varphi}_{\sigma i}^P = \varphi_{\sigma i}^P \left[\frac{\eta_{\sigma i} r(c_i)}{\tau_\sigma} - \frac{v_{\sigma i}}{\sum_k \varphi_{\sigma k}^P v_{\sigma k}^2} \sum_j \varphi_{\sigma j}^P \left(\frac{\eta_{\sigma j} r(c_j)}{\tau_\sigma} v_{\sigma j} + \gamma_{\sigma j} \frac{K_j}{(c_j + K_j)^2} \dot{c}_j \right) \right] , \quad (24)$$

where τ_σ are the characteristic timescales of proteome fraction dynamics.

For the dynamics given by Equation 24, three regimes are interesting:

- Slow adaptive timescale $\tau \gg 1$ and low quality nutrients $\gamma_{\sigma i} \simeq 0$
In this case, the proteome fitness constraint reduces to that of Posfai

$$\sum_{i=1}^{N_R} \varphi_{\sigma i}^P \simeq \Phi_\sigma. \quad (25)$$

In this regime, which resembles a CR model with metabolic trade-off, the proteome fractions adapt only to maintain the constraint of the total allocation and the adaptive dynamics reduces to

$$\dot{\varphi}_{\sigma i}^P \approx -\varphi_{\sigma i}^P \frac{v_{\sigma i}}{\sum_k \varphi_{\sigma k}^P v_{\sigma k}^2} \sum_j \varphi_{\sigma j}^P \gamma_{\sigma j} \frac{K_j}{(c_j + K_j)^2} \dot{c}_j \approx 0 \quad (26)$$

. Therefore, coexistence is possible only if \vec{s} belongs to the convex hull of the proteome fractions $\vec{\varphi}_\sigma^P$ from the beginning of the dynamics, as shown in Figure 2 and Figure 3.

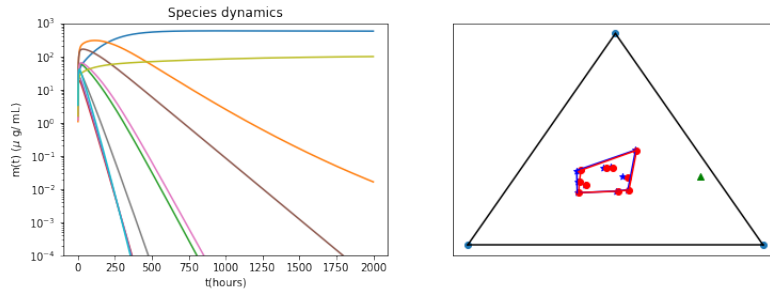


Figure 2: Species dynamics for $\gamma_\sigma \gg 1$ and $\gamma_{\sigma i} \sim O(0.1)$. Since the rescaled supply rate does not belong to the convex hull of metabolic strategies at the beginning of the dynamics, most of the species go extinct.

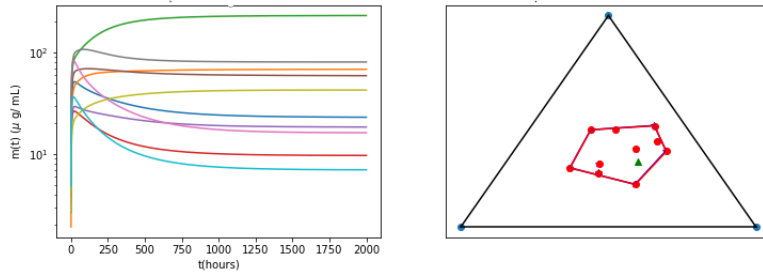


Figure 3: In this case, the rescaled supply rate belongs to the convex hull of rescaled proteome fractions at the beginning of the dynamics and we observe a violation of CEP.

- Slow adaptive timescale $\tau \gg 1$ and high quality nutrients $\gamma \sim O(2)$.
In this case, the dynamics is

$$\dot{\varphi}_{\sigma i}^P \approx -\varphi_{\sigma i}^P \frac{v_{\sigma i}}{\sum_k \varphi_{\sigma k}^P v_{\sigma k}^2} \sum_j \varphi_{\sigma j}^P \gamma_{\sigma j} \frac{K_j}{(c_j + K_j)^2} \dot{c}_j \neq 0, \quad (27)$$

and it is possible for the dynamics of the proteome fractions to move inside the convex hull, if we multiply the supply rate for a factor $x > 1$ sufficiently large, such that we have a supply rate $x\vec{s}$ (which does not affect the rescaled one), as shown in Figure 4 and Figure 5.

- Fast adaptive timescale $\tau \sim O(1)$ and $\gamma \sim O(1)$.

In this case, coexistence is always possible, no matter where the rescaled supply rate lies at the beginning of the dynamics, as shown in Figure 6.

However, as soon as we increase the adaptive timescale τ , by multiplying it for a factor $y > 1$, fewer species are able to survive, as shown in Figure 7

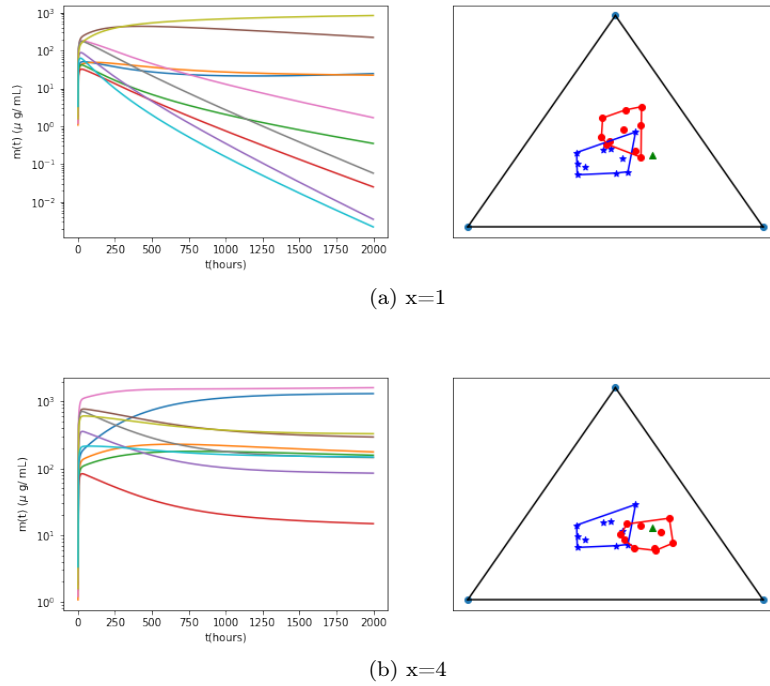


Figure 4: Species dynamics in presence of high quality nutrients and a slow adaptive timescale. We observe coexistence for $x > 1$ sufficiently large.

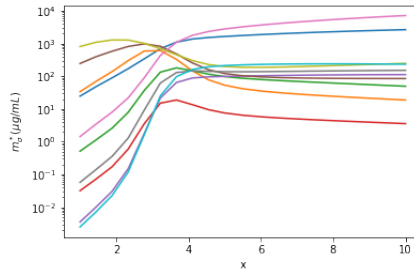


Figure 5: Stationary values of species biomass in function of the rescaling factor for supply rate. We observe a phase transition above the critical value $x \approx 3$.

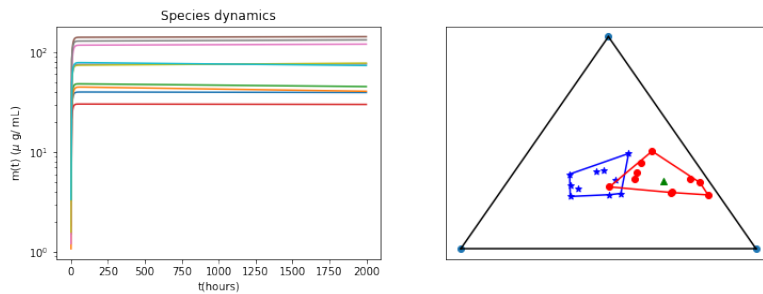


Figure 6: Fast adaptive timescale leads to violation of CEP.

5 Spatial interactions

Now we consider a generalization of the MacArthur's Consumer Resource Models, in which a new term arising from spatial interactions among species is introduced to stabilize the dynamics [4].

If we introduce the gradient of the species biomass and a decaying factor for abiotic resources in the standard

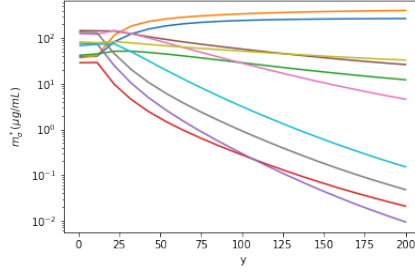


Figure 7: Species biomass at stationarity in function of the multiplicative factor y . If y is sufficiently large, we observe extinctions.

MacArthur's model of Equation 1, by setting $\nu_i = 1$ we have

$$\begin{aligned} \dot{m}_\sigma(\vec{x}) &= m_\sigma(\vec{x}) \left[\sum_i \alpha_{\sigma i} r(c_i(\vec{x})) - q_\sigma \right] - \vec{\nabla} \cdot J_\sigma(\vec{x}, t), \\ \dot{c}_i(\vec{x}) &= \mu_i(\Lambda_i - c_i(\vec{x})) - r(c_i(\vec{x})) \sum_\sigma \alpha_{\sigma i} m_\sigma(\vec{x}), \end{aligned} \quad (28)$$

where $\mu_i \Lambda_i$ and Λ_i correspond respectively to the growth rate and the carrying capacity of the i -th resource. By performing the spatial coarse graining, Equation 28 becomes [4]

$$\begin{aligned} \dot{m}_\sigma &= m_\sigma \left[\sum_i \alpha_{\sigma i} r(c_i) - q_\sigma - \sum_\rho \epsilon_{\sigma \rho} m_\rho \right], \\ \dot{c}_i &= \mu_i(\Lambda_i - c_i) - r(c_i) \sum_\sigma \alpha_{\sigma i} m_\sigma, \end{aligned} \quad (29)$$

meaning that the spatial interaction between species is equivalent to introduce a carrying capacity term equivalent to $\epsilon_{\sigma\sigma}^{-1}$.

If we restrict our attention to the case of one resource, we can analytically study the case when the dynamics Equation 29 leads to a violation of CEP. In [4], the authors obtained that at least $l < N_S$ survive when Λ is greater than a critical supply rate given by

$$\Lambda^{(l)} = \frac{\tilde{r}(\bar{c})}{\mu} \left[A_l^{(c)} \tilde{r}(\bar{c}) - B_l^{(c)} \right] + \frac{k \tilde{r}(\bar{c})}{1 - \tilde{r}(\bar{c})}, \quad (30)$$

where $\tilde{r}(\bar{c}) = \max\{\alpha_\sigma^{-1} | 1 \leq \sigma < l\}$, $A_l^{(c)} = \sum_{j=1}^l \frac{\alpha_j^2}{\epsilon_j}$ and $B_l^{(c)} = \sum_{j=1}^l \frac{\alpha_j}{\epsilon_j}$. A simulation result is shown in Figure 8.

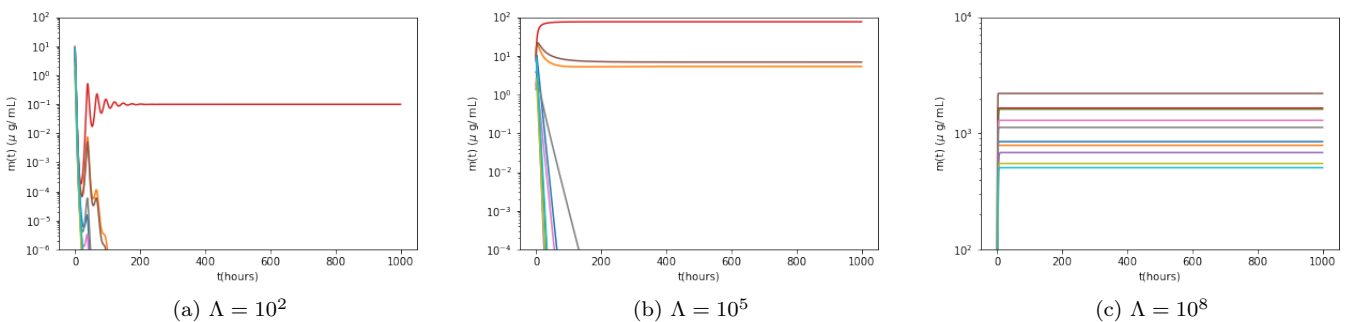


Figure 8: Dynamics of species for $\epsilon \sim O(0.002)$, $\alpha \sim O(2)$, $q_\sigma = 1$, $\mu = 0.001$, $k = 5$ and different values of Λ .

6 Pathogens

The model in Equation 28 may also arise from the presence of pathogens, incorporating the so-called Janzen-Connell effect into MacArthur's dynamics [6, 7].

If we have N_P pathogens and their biomass concentration at time t is denoted with $p_a(t)$, the model becomes

$$\begin{aligned}\dot{m}_\sigma &= m_\sigma \left(\sum_i \alpha_{\sigma i} r(c_i) - q_\sigma - \sum_a A_{\sigma a} p_a \right), \\ \dot{c}_i &= \mu_i(\Lambda_i - c_i) - r(c_i) \sum_\sigma \alpha_{\sigma i} m_\sigma, \\ \dot{p}_a &= \frac{p_a}{\tau} \left(\sum_\sigma B_{a\sigma} m_\sigma - k_a p_a \right),\end{aligned}\tag{31}$$

where the matrix A tells us the degradation of each species due to the interaction with pathogens, while the matrix B accounts the benefits of species to pathogens growth and $1/k_a$ stands for the carrying capacity term for pathogen a .

Pathogens dynamics is determined by the timescale factor γ . If we suppose that this timescale is much faster ($\tau \rightarrow 0$) than species and resources one, pathogens will have reached instantaneous equilibrium with biomass values given by

$$\vec{p}(t) = [K^{(p)}]^{-1} B \vec{m}(t)\tag{32}$$

much time earlier than species and resources ($K^{(p)} = \text{diag}(k_1, k_2, \dots, k_{N_P})$).

In this case, by substitution of the instantaneous values of pathogens biomass, Equation 29 can be recovered by setting

$$\epsilon_{\sigma\rho} = \sum_{a=1}^{N_P} \frac{A_{\sigma a} B_{a\rho}}{k_a}.\tag{33}$$

Let us now examine the two regimes for the specific case of one resource and when A and B are diagonal matrices, meaning that each species has a specific pathogen that affects it, in the limits when τ tends to zero and when it tends to infinity.

- $\tau \rightarrow \infty$

If τ is sufficiently large, then p_σ reaches stationarity long after species and resources dynamics and therefore pathogens act like a renormalization of species death rate, meaning $\tilde{q}_\sigma = q_\sigma + p_\sigma$. The dynamical system becomes

$$\begin{aligned}\dot{m}_\sigma &= m_\sigma \left(\alpha_\sigma r(c) - \tilde{q}_\sigma \right), \\ \dot{c} &= \mu(\Lambda - c) - r(c) \sum_\sigma \alpha_\sigma m_\sigma,\end{aligned}\tag{34}$$

which is exactly the Consumer Resource model with no metabolic trade-off leading to CEP in Equation 1. If we wait a sufficiently long time, we expect the system to reach stationarity, meaning

$$r(c^*) = \frac{\tilde{q}_\sigma^*}{\alpha_\sigma} < 1, \quad \mu(\Lambda - c^*) = r(c^*) \sum_\sigma \alpha_\sigma m_\sigma^*,\tag{35}$$

from which we get $c^* = \frac{\tilde{q}_\sigma k}{\alpha_\sigma - \tilde{q}_\sigma}$ by inversion. Moreover, the metabolic strategies must be proportional and greater than the death rates. From the second of Equation 35, we get $\mu(\Lambda - c^*) = \sum_\sigma \tilde{q}_\sigma m_\sigma^*$.

Let us assume that a species σ reaches a stationary biomass concentration m_σ^* long before its corresponding pathogen; its dynamics becomes

$$\dot{p}_\sigma = \frac{p_\sigma}{\tau} \left(m_\sigma^* - k_\sigma p_\sigma \right).\tag{36}$$

If $m_\sigma = 0$, then the solution is

$$p_\sigma(t) = \frac{\tau p_\sigma(0)}{\tau + k_\sigma p_\sigma(0)t},\tag{37}$$

which decays to zero with inverse power behaviour as $t \rightarrow \infty$. Instead, if $m_\sigma^* \neq 0$, we get

$$p_\sigma(t) = \frac{m_\sigma^* p_\sigma(0) e^{m_\sigma^* t / \tau}}{m_\sigma^* + k_\sigma p_\sigma(0) (e^{m_\sigma^* t / \tau} - 1)},\tag{38}$$

which decays exponentially to the stationary value.

- $\tau \rightarrow 0$

In this case, the dynamics of pathogen is sufficiently fast to adapt instantaneously to the values of the species biomass, meaning we are in the regime of the previous section, so that coexistence l species is possible only when the parameter Λ is larger than a particular threshold $\Lambda^{(l)}$.

Among these two regimes, we expect a phase transition between coexistence of all species and total extinction, as shown by numerical simulations in Figure 9, where we used the parameters of Figure 8 with $\Lambda = 10^8$ which lead to survival of all species in the case no pathogens are present.

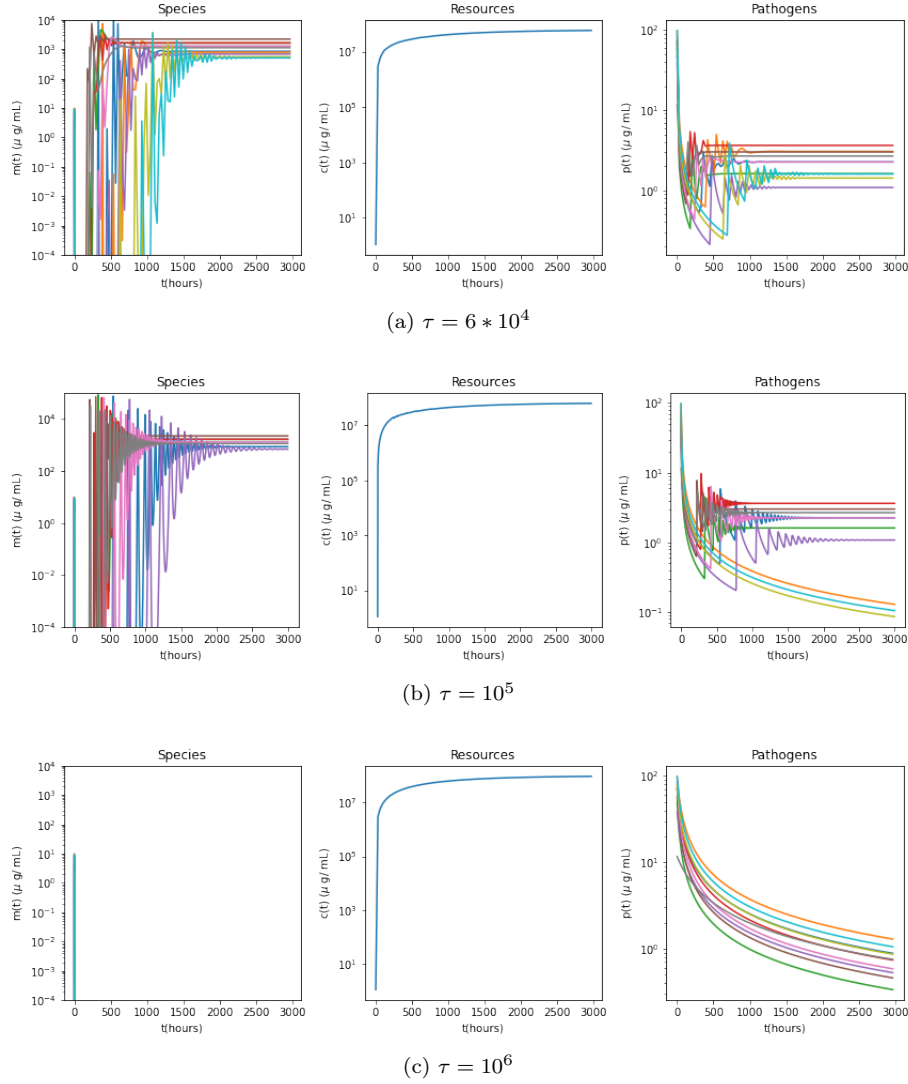


Figure 9: Dynamics of species for $\epsilon \sim O(0.002)$, $\alpha \sim O(2)$, $q_\sigma = 1$, $\mu = 0.001$, $k = 5$, $\Lambda = 10^8$ and different values of the pathogen timescale τ .

In the case, we observe that if τ is low, we are in the conditions of coexistence of all the species, but as soon as τ is becomes increasingly larger, fewer and fewer species are able to survive, until a point where all the species are extinct and resource concentration reaches the carrying capacity Λ . Moreover, numerical analysis confirms our analysis in the case species becomes extinct before pathogens reach stationarity, leading to a inverse power decaying of their concentration.

7 Conclusion

In this essay we have examined how MacArthur's model can be modified to account for the fact that many ecosystems violate CEP in Nature.

First, we have seen that we can add a metabolic constraint in order to make many species coexisting with a limited number of resources, even though this constraint has been recognized to be too strong. To improve the model, metabolic strategies have been allowed to vary in order to satisfy a weaker constraint fixing only the

maximum amount of energy spendable for growth by each species and maximizing its growth rate, leading to a self-adapting strategy that make coexistence of many species possible.

Furthermore, we analysed the case of adapting proteome fractions that root the results on more robust biological assumptions. In all the case we have a very intuitive way to visualize whether the dynamics would lead to extinctions or violation of CEP depending on the position of the rescaled supply rate with respect to the convex hull of rescaled metabolic strategies (or proteome fractions in the context of the CPR model).

Lastly, we analyzed how spatial interactions can be added to the model leading to a dynamics effectively equal to the introduction of a carrying capacity term. In this case, coexistence of a certain number of species is possible whenever the resources supply rate exceeds a certain threshold. Moreover, we have seen how this model is equivalent to the introduction of pathogens in the context of Janzen-Connell effect when the timescale is very fast. This time scale eventually separates a phase in which coexistence is possible to a phase in which all or most of the species are extinct.

Further generalizations can include a studies relating the coexistence conditions to the number of resources available in the environment.

A Constrained Maximization

Let $Q(\vec{x})$ a function to be maximize with respect to \vec{x} , where $\vec{x}(t) \in \mathbb{R}$ is a dynamical variable. The most simple dynamics of \vec{x} which leads to a maximization of Q is simply given by the gradient ascent

$$\dot{\vec{x}} = \vec{\nabla} Q(\vec{x}) , \quad (39)$$

for which it follows that $\dot{Q}(\vec{x}) = \dot{\vec{x}} \cdot \vec{\nabla} Q(\vec{x}) = \left| \vec{\nabla} Q(\vec{x}) \right|^2 \geq 0$.

Now, if we want to impose the dynamics to belong to a strong constraint implicitly given by $\rho(\vec{x}) = 0$, we must subtract from the gradient of Q its component which is parallel to the gradient of ρ , leading to

$$\dot{\vec{x}} = \vec{\nabla} Q(\vec{x}) - \frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \left(\frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \cdot \vec{\nabla} Q(\vec{x}) \right) . \quad (40)$$

Therefore, on the one hand we have

$$\dot{\rho}(\vec{x}) = \dot{\vec{x}} \cdot \vec{\nabla} \rho(\vec{x}) = \vec{\nabla} \rho(\vec{x}) \cdot \vec{\nabla} Q(\vec{x}) - \vec{\nabla} \rho(\vec{x}) \cdot \frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \left(\frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \cdot \vec{\nabla} Q(\vec{x}) \right) = 0 . \quad (41)$$

On the other hand, due to Schwarz's inequality, we have

$$\dot{Q}(\vec{x}) = \dot{\vec{x}} \cdot \vec{\nabla} Q(\vec{x}) = \left| \vec{\nabla} Q(\vec{x}) \right|^2 - \left(\frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \cdot \vec{\nabla} Q(\vec{x}) \right)^2 \geq 0 . \quad (42)$$

If we had a softer constraint of the kind $\rho(\vec{x}) \leq 0$, the dynamics of \vec{x} would be simply modified in

$$\dot{\vec{x}} = \vec{\nabla} Q(\vec{x}) - \Theta(\rho(\vec{x})) \frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \left(\frac{\vec{\nabla} \rho(\vec{x})}{\left| \vec{\nabla} \rho(\vec{x}) \right|} \cdot \vec{\nabla} Q(\vec{x}) \right) , \quad (43)$$

meaning that we would subtract the parallel component of the gradient only when the constraint is not satisfied. This analytic result is emphasised in [Figure 10](#), taken from [\[2\]](#).

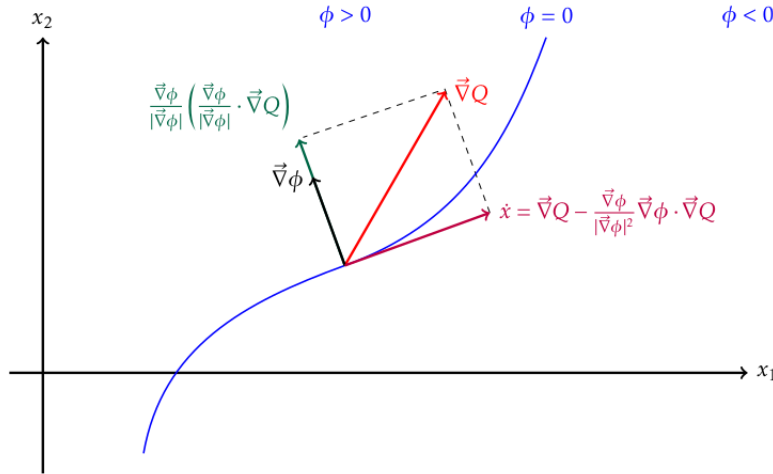


Figure 10: Grafical visualization for constrained maximization of a \mathbb{R}^2 function.

References

- [1] A. Posfai, T. Tallefumier, and NS. Wingreen. Metabolic trade-offs promote diversity in a model ecosystem. *Phys Rev Lett*, page 118, 2017.
- [2] Leonardo Pacciani-Mori, Andrea Giometto, Samir Suweis, and Amos Maritan. Dynamic metabolic adaptation can promote species coexistence in competitive microbial communities. *PLOS Computational Biology*, 2020.
- [3] Leonardo Pacciani-Mori, Samir Suweis, Amos Maritan, and Andrea Giometto. Constrained proteome allocation affects coexistence in models of competitive microbial communities. *The ISME Journal*, 2021.
- [4] Deepak Gupta, Stefano Garlaschi, Samir Suweis, Sandro Azaele, and Amos Maritan. Effective resource-competition model for species coexistence. 2021.
- [5] M. Scott, CW. Gunderson, EM. Mateescu, Z. Zhang, and T. Hwa. Interdependence of cell growth and gene expression. *Science*, 330:1099–1102, 2010.
- [6] Daniel H. Janzen. Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104(940):501–528, 1970.
- [7] Joseph H. Connell. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*, 298:312, 1971.