

Adaptive consumer-resource models can explain diauxic shifts and the violation of the Competitive Exclusion Principle

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ABSTRACT

Competitive ecosystems are most commonly described mathematically using MacArthur’s consumer-resource model, leading to the “Competitive Exclusion Principle” which limits the number of coexisting competing species to the number of available resources. Nevertheless, several empirical evidences – such as bacterial community cultures – show that this principle is violated in real ecosystems. Another experimental evidence involving microbial populations that cannot be explained in this framework is the existence of diauxic (or polyauxic) shifts in microbial growth curves. By introducing adaptive metabolic strategies whose dynamics tends to maximize species’ relative fitness, we can explain both these empirical evidences. Moreover, we show that adaptation velocity plays a fundamental role in determining the outcome of competition.

INTRODUCTION

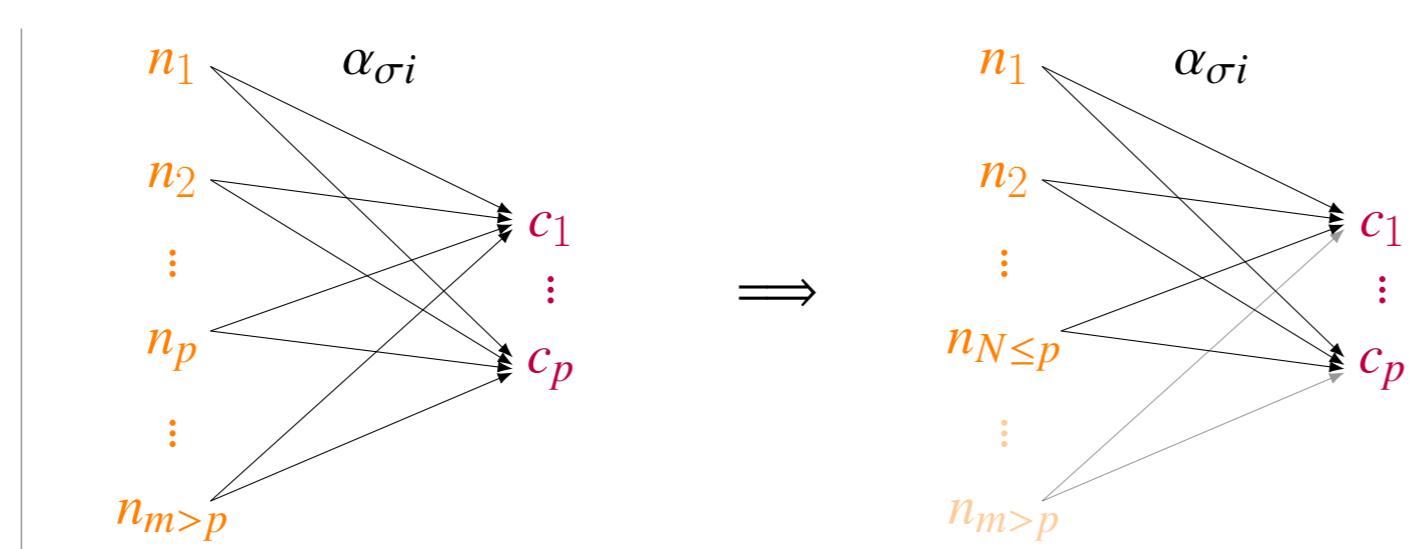
One of the most fascinating aspects of nature is biodiversity: even though empirically we observe that the world is made of very complex and diverse communities, from a theoretical point of view we are still unable to understand how this is possible. Considering competitive ecosystems, for example, the so-called “Competitive Exclusion Principle” (CEP) [5] states that if m consumers compete (with no predation between them) for p resources, then they may coexist only if $m \leq p$, otherwise at least $m - p$ of them will go to extinction. However, even if the CEP holds in many mathematical models of species abundance dynamics [9, 1] there are many known cases in nature where the CEP is clearly violated [6, 3, 4]. It is clear, therefore, that we are missing something essential in order to explain the high biodiversity observed in many ecological communities.

MAIN OBJECTIVES

Competitive ecosystems are generally described mathematically using MacArthur’s consumer-resource model [8, 2], which prescribes that for a system of m species and p resources the population density $n_\sigma(t)$ of species σ and the concentration $c_i(t)$ of resource i evolve following (1) and (2), where $r_i(c_i) = c_i/(K_i + c_i)$ and $K_i > 0$. As it is, the model reproduces the CEP.

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

$$\dot{c}_i = s_i - \sum_{\sigma=1}^m n_\sigma \alpha_{\sigma i} r_i(c_i) \quad (2)$$



In the literature the “metabolic strategies” $\alpha_{\sigma i}$ (i.e. the rates at which species σ uptakes resource i) have always been treated as fixed parameters, but since the 1940s we have *incontrovertible* experimental evidence [10] that microbes’ metabolic strategies *can* and *do* change over time according to their surrounding environmental conditions. The main objective of this work is therefore to modify MacArthur’s consumer-resource model so that metabolic strategies evolve in time according to an appropriate dynamics.

MATERIALS AND METHODS

We use an adaptive framework: we require that each metabolic strategy $\tilde{\alpha}_\sigma$ evolves in order to maximize its own species’ growth rate $g_\sigma = \sum_{i=1}^p v_i \alpha_{\sigma i} r_i(c_i)$. This can be achieved by requiring that metabolic strategies follow a simple “gradient ascent” equation:

$$\dot{\alpha}_{\sigma i} = d \delta_\sigma \frac{\partial g_\sigma}{\partial \alpha_{\sigma i}}, \quad (3)$$

where $d > 0$ is the “adaptation velocity”. However, microbes have limited amounts of energy that they can use for metabolism, so we must introduce some constraint in Eq. (3). We thus require that $\sum_{i=1}^p w_i \alpha_{\sigma i}(t) := E_\sigma(t) \leq E_\sigma^*$ where $E_\sigma^* = Q \delta_\sigma$ (and $Q > 0$) is the maximum total resource uptake rate of species σ ; the parameters w_i are called “resource costs”. If we do so, and we also prevent $\alpha_{\sigma i}$ from becoming negative, we obtain:

$$\dot{\alpha}_{\sigma i} = \alpha_{\sigma i} d \delta_\sigma \left[v_i r_i - \Theta \left(\sum_{i=1}^p w_i \alpha_{\sigma i} - Q \delta_\sigma \right) \frac{w_i}{\sum_{k=1}^p w_k^2 \alpha_{\sigma k}} \sum_{j=1}^p v_j r_j w_j \alpha_{\sigma j} \right] \quad (4)$$

where Θ is Heaviside’s step function.

RESULTS

Using this adaptive framework allows the model to take into account several experimentally observed phenomena. In particular, we are able to explain the existence of diauxic shifts [10] and the fact that the CEP can be violated. Furthermore d turns out to be crucial, as it is the parameters that determines the actual outcome of competition: fast adaptation leads to coexistence, while slow adaptation can lead to competitive exclusion.

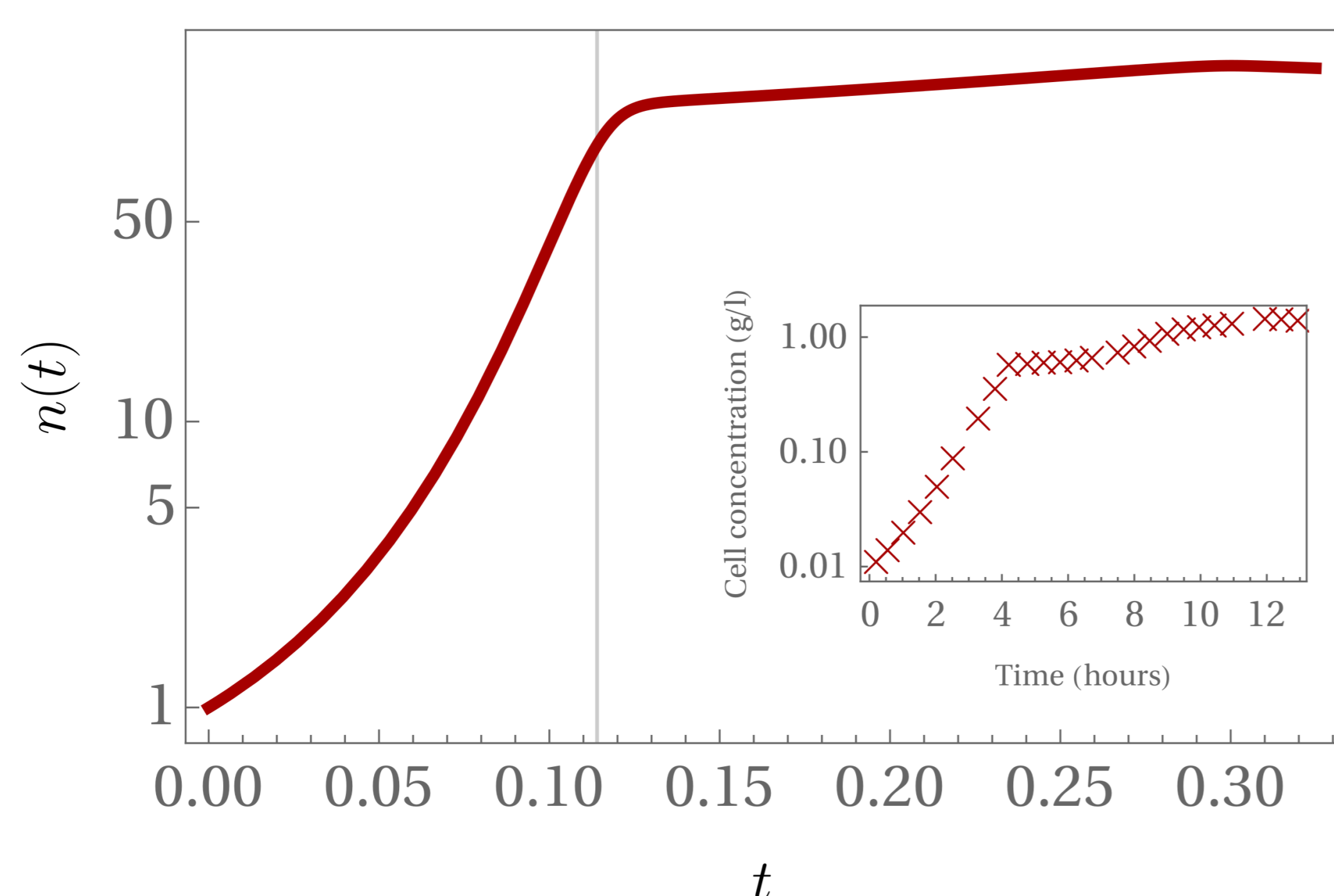


Figure 1: Growth of the population over time using (1), (2) and (4) for a system with $m = 1$ and $p = 2$. In this case we have used $n(0) = 1$, $\vec{c}(0) = (40, 5)$, $\vec{s} = (0, 0)$, $\vec{v} = (2, 25)$, $\vec{w} = (1, 4)$, $\vec{\alpha}(0) = (1, 1)$, $\vec{K} = (1, 3)$, $Q = 25$ and $\delta = 1$; time is in arbitrary units. The grey vertical line corresponds to \bar{t} , the estimate given by the model of the instant at which the diauxic shift occurs (in this case we have $\bar{t} \approx 0.114$). Inset: Data of experimental measurements of the growth of *Klebsiella oxytoca* on glucose and lactose, taken from [7, figure 11] for comparison only (the parameters have *not* been set in order to reproduce the data).

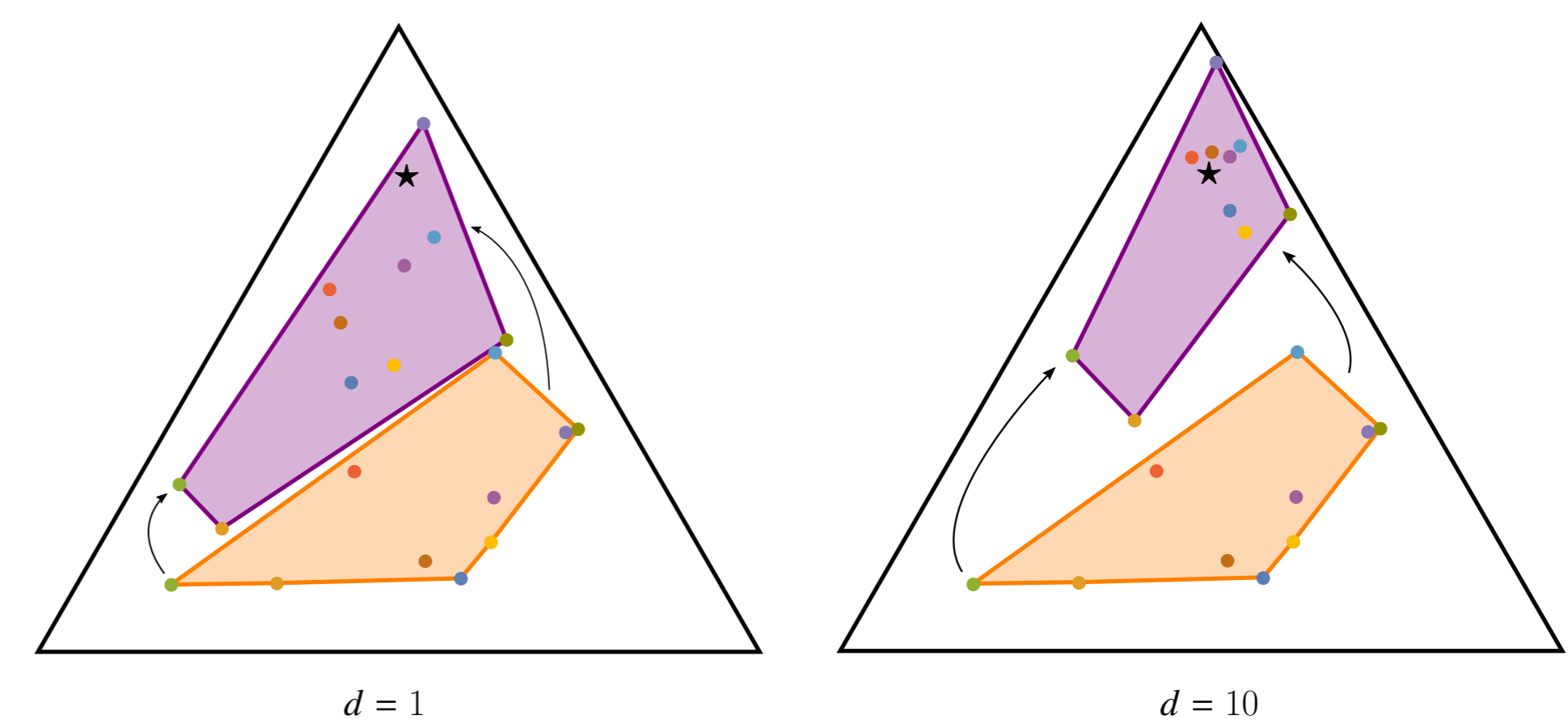


Figure 2: Comparison between the initial (orange) and final (purple) convex hull of the rescaled metabolic strategies $\hat{\alpha}_{\sigma i} := w_i \alpha_{\sigma i} / (Q \delta_\sigma)$ (colored dots) when they are allowed to evolve, for a system with $p = 3$ and $m = 10$. In this simulation we have considered a system with $m = 10$, $p = 3$, $Q = 2$, $\delta_\sigma \in \mathcal{U}[1, 1.5]$ (with \mathcal{U} the uniform distribution), $E_\sigma(0) \in \mathcal{U}[0, Q \delta_\sigma]$, $v_i \in \mathcal{U}[1, 2]$, $w_i \in \mathcal{U}[0, v_i Q]$, $n_\sigma(0) \in \mathcal{U}[0, 1]$, $c_i(0) \in \mathcal{U}[0, 1]$, $K_i \in \mathcal{U}[1, 5]$. We have drawn $s_i \in \mathcal{U}[0, 5]$ and $\alpha_{\sigma i}(0)$ so that $\sum_{i=1}^p w_i \alpha_{\sigma i}(0) = E_\sigma(0)$. Heaviside’s step function has been approximated with the smooth function $\Theta(x) = 1/(1 + \exp(-x \cdot 10^{10}))$. It can be shown analytically that in general \vec{s} (with $s_i := v_i \alpha_{\sigma i} / \sum_{j=1}^p v_j \alpha_{\sigma j}$) and $\vec{\alpha}_\sigma$ must lie on a $(p - 1)$ -dimensional simplex (so in this case on a triangle, which is the black triangle shown in the figure), and that coexistence is possible only when \vec{s} belongs to the convex hull of $\vec{\alpha}_\sigma$. As we can see, in the final state the system has put itself in the right conditions for coexistence, since $\vec{\alpha}_\sigma$ have “incorporated” the rescaled nutrient supply rate vector \vec{s} (black star) in their convex hull. Furthermore, fast adaptation ($d = 10$) allows the rescaled metabolic strategies to arrange themselves so that \vec{s} lies in a more central position of their convex hull.

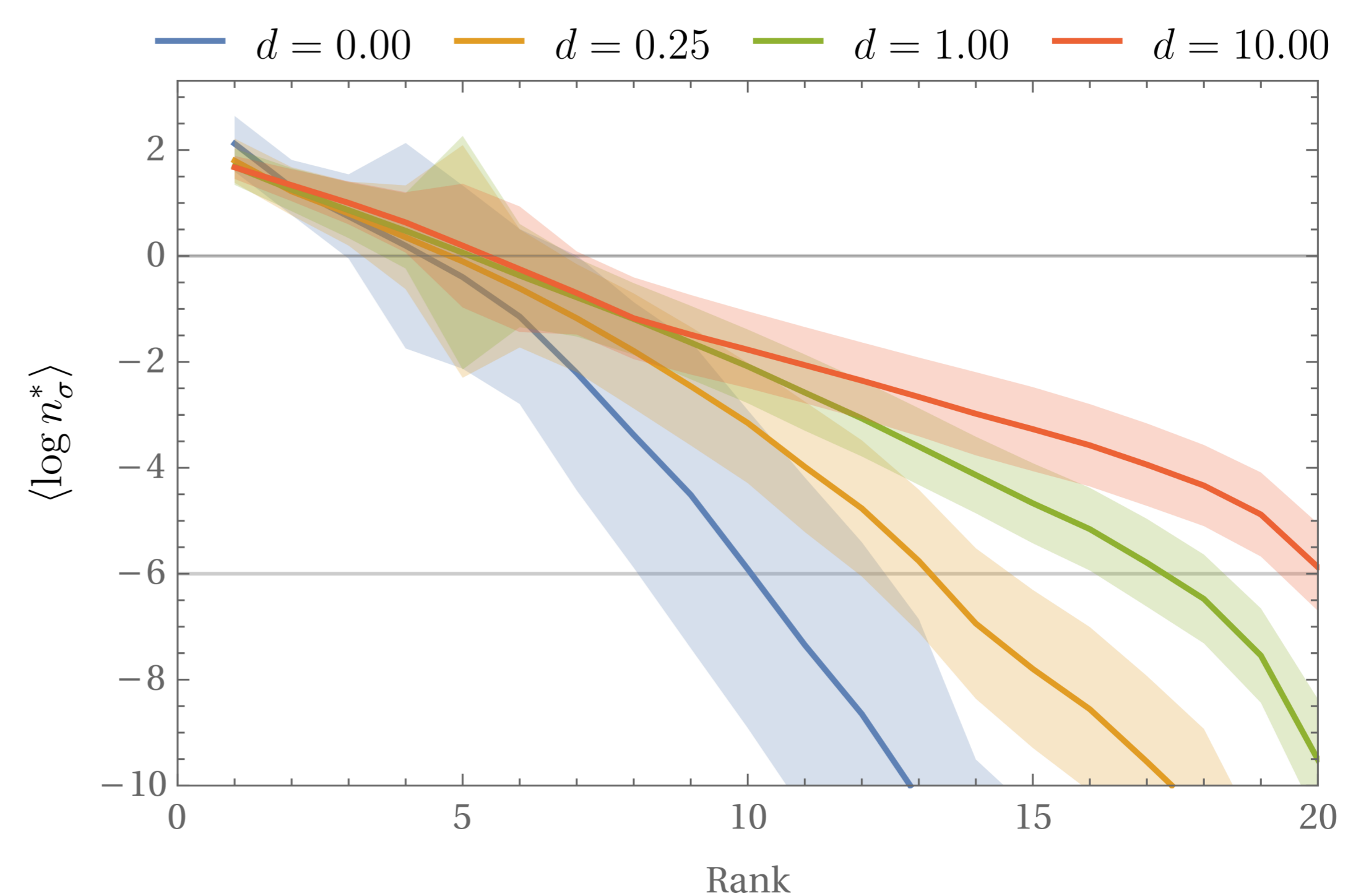


Figure 3: Relative abundance distribution of the logarithm of the stationary populations for different adaptation velocities. We have used $m = 20$, $p = 3$, $Q = 2$, $\delta_\sigma \in \mathcal{U}[0, 5]$, $E_\sigma(0) = Q \delta_\sigma$ (because this way the CEP can be violated also when the metabolic strategies are fixed, i.e. $d = 0$), $v_i \in \mathcal{U}[0, 1]$, $w_i \in \mathcal{U}[0, v_i Q]$. For each value of d we have performed 100 iterations, each with its own $n_\sigma(0) \in \mathcal{U}[0, 10]$, $c_i(0) \in \mathcal{U}[0, 10]$ and $K_i \in \mathcal{U}[1, 10]$, then we have computed the logarithm of the stationary values of the species’ populations and ordered them by rank. The opaque bands represent one standard deviation. As we can see, as d increases the relative abundance distribution tends to be more even, while it is steeper for slower adaptation velocities; therefore, if we set an extinction threshold there will always be a value of d under which an increasing fraction of the species will go to extinction. For example, if we set an extinction threshold at $\log n_\sigma^* = -6$ (horizontal line in the plot) we can see that with $d = 0$ approximately half of the species in the system will go extinct, while with $d = 10$ almost all of them will survive.

CONCLUSIONS

If we introduce in a MacArthur’s consumer-resource model adaptive metabolic strategies evolving so that each species’ growth rate is maximized, then we can explain using the same theoretical framework phenomena observed experimentally from the single species to the community level. Furthermore, with this hypothesis we can naturally violate the CEP without any strong assumption on the parameters of the model, but at the same time we can explain why competitive exclusion still happens in some cases.

FORTHCOMING RESEARCH

Given the results of this work, forthcoming research will focus on bringing together theory and empirical observation, i.e. designing and performing experiments that can validate or reject the model.

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