Adaptive metabolic strategies explain diauxic shifts and promote species coexistence

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Leonardo Pacciani, Samir Suweis and Amos Maritan
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Università degli Studi di Padova

Overview

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- Introduction
  - Competitive exclusion principle
  - MacArthur's consumer-resource model

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  - Competitive exclusion principle
  - MacArthur's consumer-resource model
- Adaptive metabolic strategies
  - Diauxic shifts
  - Coexistence violating the exclusion principle

Biodiversity

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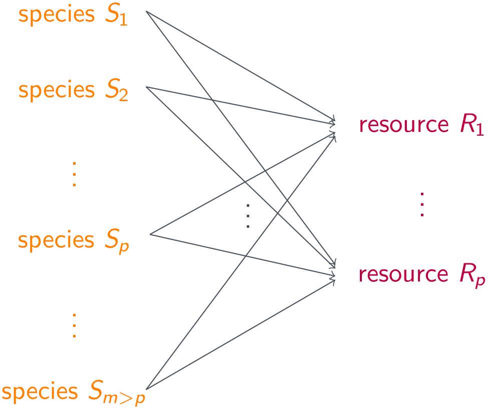
For example: *competitive exclusion principle* (CEP)



species S_1
species S_2
⋮
species S_p
⋮
species $S_{m>p}$
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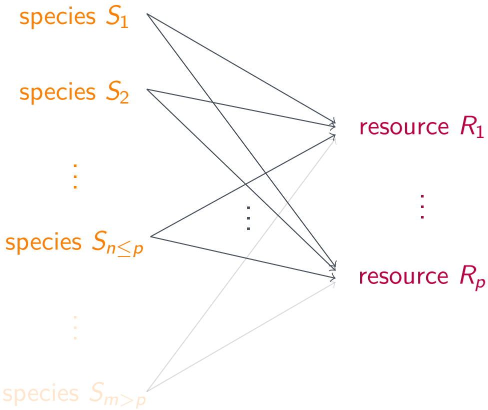
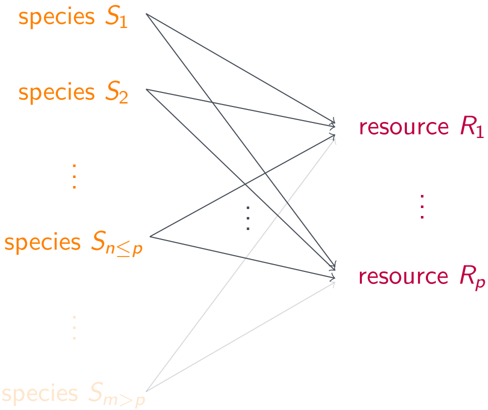
Introduction

Competitive exclusion principle





Problem: there are many known cases where this principle is clearly violated (*paradox of the plankton*)!

For a system of m species and p resources:

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

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

For a system of m species and p resources:

death rate

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

"resource values"

"metabolic strategies"

resource uptake rate, e.g.

$r_i(c_i) = c_i/(K_i + c_i)$

resource supply rate

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

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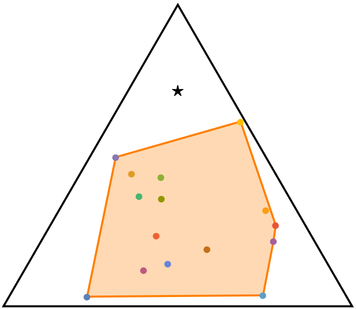

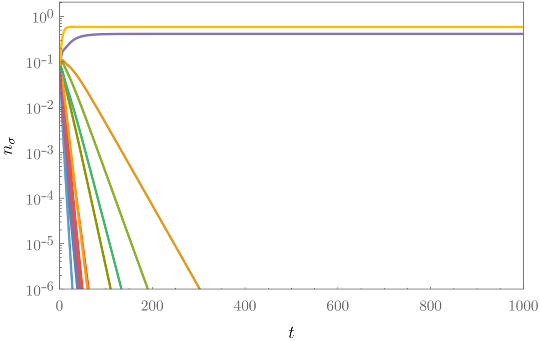

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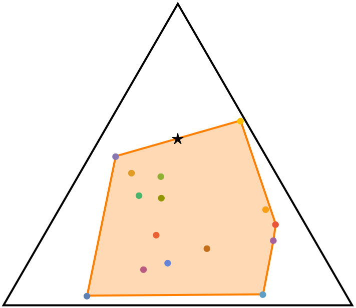

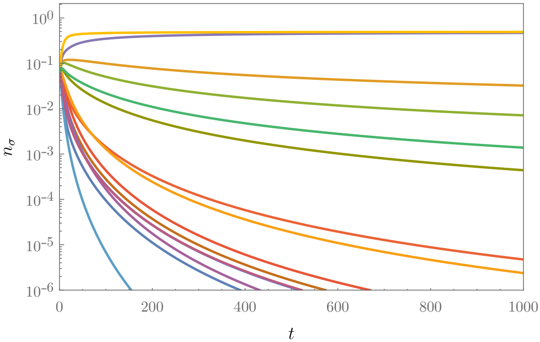

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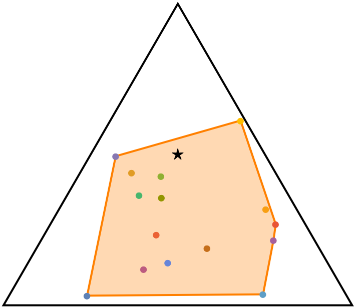

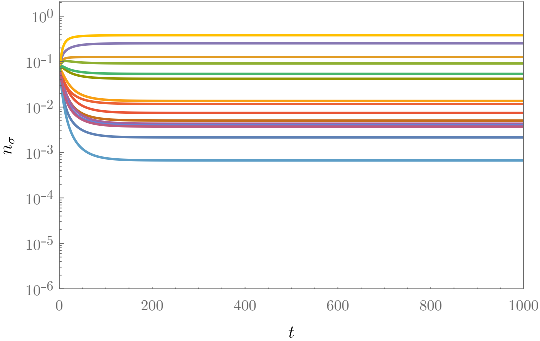

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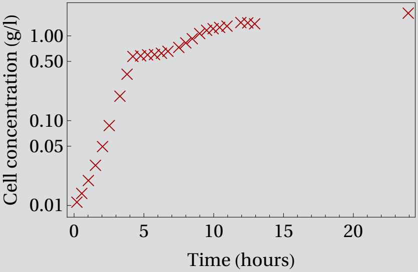
Problem

Since the '40s we know that bacteria can change their metabolic strategies according to environmental conditions (*diauxic shifts*)



Data of the growth of *Klebsiella oxytoca* on glucose and lactose, from D. S. Kompala et al. "Investigation of Bacterial Growth on Mixed Substrates: Experimental Evaluation of Cybernetic Models". In: *Biotechnology and Bioengineering* XXVIII.July (1986), pp. 1044–1055.

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What we can say

It is clear that bacteria can change their metabolic strategies, but a connection with consumer-resource ecological modeling is still missing.

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Our aim

"Promote" $\alpha_{\sigma i}$ to **dynamical variables**, such that the evolution of $\vec{\alpha}_\sigma$ tends to increase its species' relative fitness, measured as its growth rate

$$g_\sigma = \sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i(c_i) \ . \tag{2}$$

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What we will find

We can both explain the existence of diauxic shifts and the coexistence of species against the CEP, in a considerably improved way.

Adaptive metabolic strategies

Adaptive metabolic strategies

If we required only that $\vec{\alpha}_\sigma$ evolves so that g_σ is maximized, we'd obtain:

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We introduce the following requirement:

$$\underbrace{\sum_{i=1}^{p} w_i \alpha_{\sigma i}}_{\text{“resource costs”}} \leq E_\sigma \longrightarrow \text{“maximum energy budget”} \qquad \frac{E_\sigma}{\delta_\sigma} = \mathcal{Q} \ \forall \sigma \ . \tag{4}$$

If we satisfy all these requirements, after some computation we obtain:

$$\dot{\alpha}_{\sigma i} = 2\alpha_{\sigma i}\left[v_i r_i - \Theta\left(\sum_{i=1}^{p}\alpha_{\sigma i} - E_\sigma\right) w_i \frac{\sum_{j=1}^{p} v_j r_j w_j \alpha_{\sigma j}}{\sum_{k=1}^{p} w_k^2 \alpha_{\sigma k}}\right] \;, \qquad (5)$$

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What happens if also these equations are considered?

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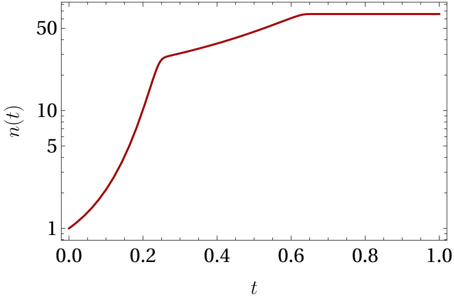

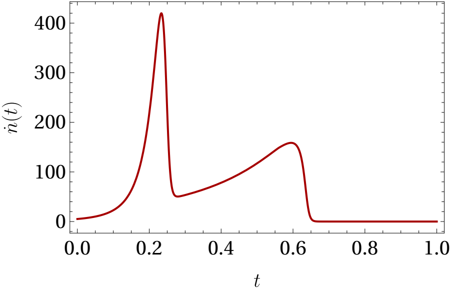

Parameters: $n(0) = 1$, $\vec{c}(0) = (40, 5)$, $\vec{v} = (1, 5)$, $\vec{w} = (1, 1)$, $\vec{\alpha}(0) = (1, 1)$, $E = 10$, $K_1 = K_2 = 1$, $\delta = 0$

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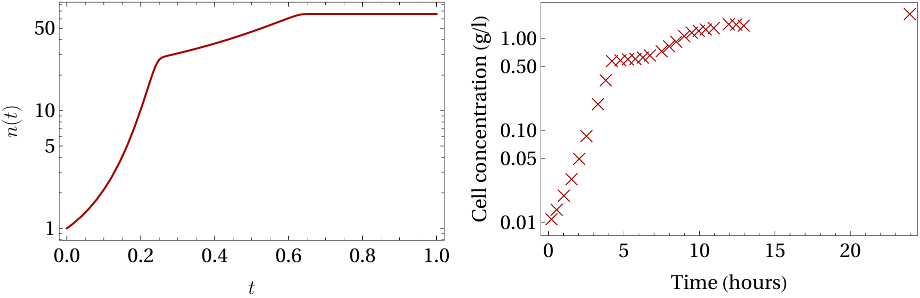

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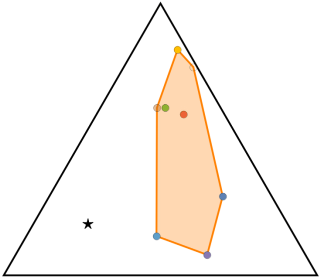

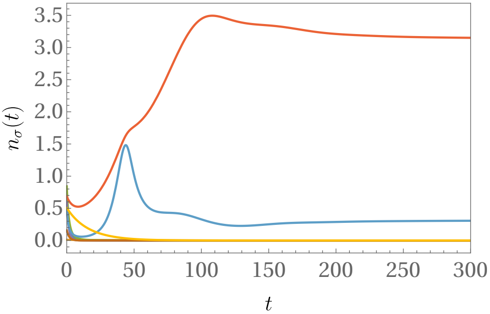

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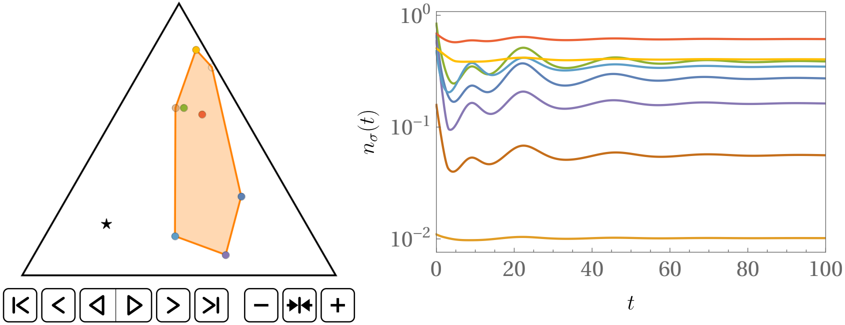

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The requirement $E_\sigma/\delta_\sigma = \mathcal{Q}\ \forall\sigma$ still looks like a very particular situation. Can we do anything better?

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Note

The equations for $\dot{n}_\sigma$ and $\dot{c}_i$ are invariant under the rescaling:

$$\alpha_{\sigma i} \to \lambda\alpha_{\sigma i} \qquad \delta_\sigma \to \lambda\delta_\sigma \qquad s_i \to \lambda s_i \qquad t \to \frac{t}{\lambda} \qquad \forall\lambda \in \mathbb{R}^+ \;, \tag{7}$$

which can then be used to fix the timescale: $1/\tau_\alpha = \delta_\sigma$.

We can then use the following more general constraint:

$$\sum_{\sigma=1}^{m} E_\sigma(t)^2 = mE^2 \qquad \text{with} \qquad E_\sigma(t) = \sum_{i=1}^{p} w_i \alpha_{\sigma i}(t) \ , \tag{8}$$

which consists in limiting an overall average energy budget.

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This way the equation for $\alpha_{\sigma i}$ becomes:

$$\dot{\alpha}_{\sigma i} = 2\alpha_{\sigma i} \left(v_i r_i \delta_\sigma - w_i E_\sigma(t) \frac{\sum_{\tau=1}^{m} \sum_{j=1}^{p} v_j r_j \alpha_{\tau j} \delta_\tau w_j E_\tau(t)}{\sum_{\tau=1}^{m} \sum_{j=1}^{p} \alpha_{\tau j} w_j^2 E_\tau(t)^2} \right) \tag{9}$$

Adaptive metabolic strategies

A more general approach

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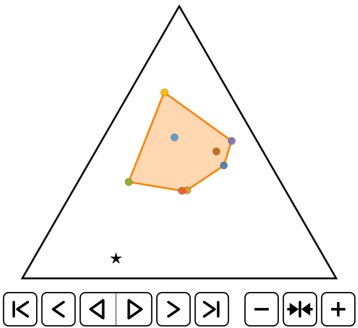

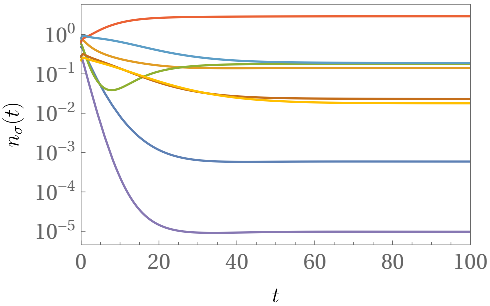

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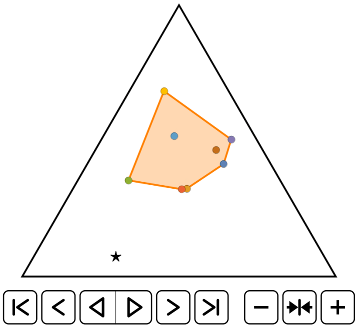

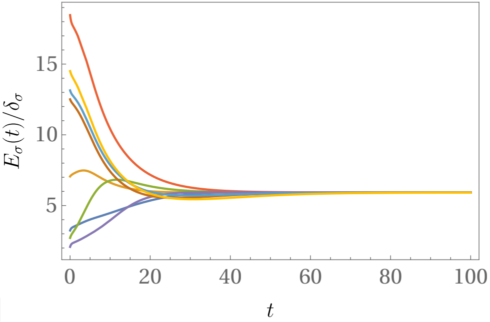

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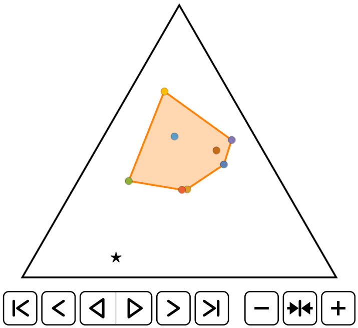

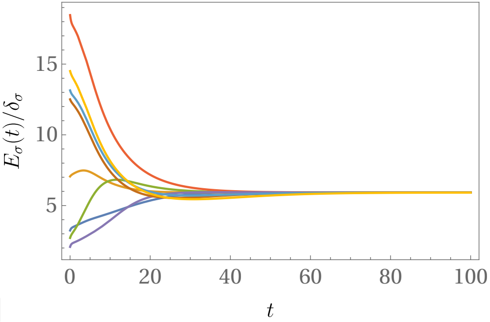

The system finds *spontaneously* the conditions for coexistence!

Conclusions

Take-home message and future perspectives

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Adaptive metabolic strategies + simple assumption (maximization of g_σ):

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Bibliography

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Backup slides

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[2] Gene expression for the synthetization of new enzymes is occurs based on the available resources.

We start from MacArthur's consumer-resource equations, written as

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{p} \alpha_{\sigma i} r_i(c_i) - \delta_\sigma \right) \qquad \dot{c}_i = \frac{1}{\tau_c} \left(s_i - \sum_{\sigma=1}^{m} n_\sigma \alpha_{\sigma i} r_i(c_i) \right) \ , \quad (1)$$

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Adaptive metabolic strategies

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where τ_α is the timescale over wich resources evolve. Since strategies evolve with the same timescale of resources[2] we can set $\tau_c = \tau_\alpha = 1$, so that $\dot{\alpha}_{\sigma i} = \partial g_\sigma / \partial \alpha_{\sigma i}$.

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Requiring that the evolution of $\vec{\alpha}_\sigma$ maximizes g_σ, we can write:

$$\dot{\alpha}_{\sigma i} = \frac{1}{\tau_\alpha} \frac{\partial g_\sigma}{\partial \alpha_{\sigma i}} \ , \qquad (2)$$

where τ_α is the timescale over wich resources evolve. Since strategies evolve with the same timescale of resources[2] we can set $\tau_c = \tau_\alpha = 1$, so that $\dot{\alpha}_{\sigma i} = \partial g_\sigma / \partial \alpha_{\sigma i}$.
We still have to:

- Ensure that any given constraint $\varphi(\vec{\alpha}_\sigma) = 0$ is satisfied

[2] Gene expression for the synthetization of new enzymes is occurs based on the available resources.

Adaptive metabolic strategies

Equation for the metabolic strategies

We start from MacArthur's consumer-resource equations, written as

$$\dot{n}_\sigma = n_\sigma \left(\sum_{i=1}^{p} \alpha_{\sigma i} r_i(c_i) - \delta_\sigma \right) \qquad \dot{c}_i = \frac{1}{\tau_c} \left(s_i - \sum_{\sigma=1}^{m} n_\sigma \alpha_{\sigma i} r_i(c_i) \right) \ , \quad (1)$$

so that the timescale τ_c over which the resources evolve is written explicitly.
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We still have to:

- Ensure that any given constraint $\varphi(\vec{\alpha}_\sigma) = 0$ is satisfied
- $\alpha_{\sigma i}(t) \geq 0 \ \forall t$

[2] Gene expression for the synthetization of new enzymes is occurs based on the available resources.

Adaptive metabolic strategies

Equation for the metabolic strategies

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If we have a constraint $\varphi(\vec{\alpha}_\sigma) = 0$, we can ensure that it is satisfied by removing from $\dot{\alpha}_{\sigma i}$ the component in the direction of $\nabla\varphi$.

Adaptive metabolic strategies

Equation for the metabolic strategies

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In general, if we have the equation $\dot{\vec{x}} = \vec{\nabla} Q(\vec{x})$ and we want $\vec{x}$ to satisfy $\varphi(\vec{x}) = 0$, we can change the equation to:

$$\dot{\vec{x}} = \vec{\nabla} Q(\vec{x}) - \frac{\vec{\nabla}\varphi(\vec{x})}{|\vec{\nabla}\varphi(\vec{x})|} \left(\frac{\vec{\nabla}\varphi(\vec{x})}{|\vec{\nabla}\varphi(\vec{x})|} \cdot \vec{\nabla} Q(\vec{x}) \right) , \tag{3}$$

Adaptive metabolic strategies

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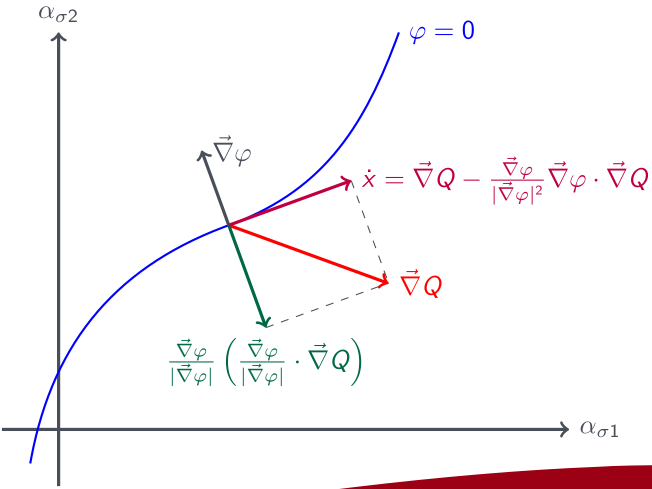
so that:

$$\frac{d\varphi}{dt} = \vec{\nabla}\varphi \cdot \dot{\vec{x}} = \vec{\nabla}\varphi \cdot \vec{\nabla} Q - \frac{|\vec{\nabla}\varphi|^2}{|\vec{\nabla}\varphi|^2} \vec{\nabla}\varphi \cdot \vec{\nabla} Q = 0 , \tag{4a}$$

$$\frac{dQ}{dt} = \vec{\nabla} Q \cdot \dot{\vec{x}} = |\vec{\nabla} Q|^2 - \left(\frac{\vec{\nabla}\varphi}{|\vec{\nabla}\varphi|} \cdot \vec{\nabla} Q \right)^2 \geq 0 . \tag{4b}$$

Adaptive metabolic strategies

Equation for the metabolic strategies



Adaptive metabolic strategies

Equation for the metabolic strategies

If the constraint is of the form $\varphi(\vec{x}) \leq 0$, then we have:

$$\dot{\vec{x}} = \vec{\nabla} Q(\vec{x}) - \Theta(\varphi(\vec{x})) \frac{\vec{\nabla}\varphi(\vec{x})}{|\vec{\nabla}\varphi(\vec{x})|} \left(\frac{\vec{\nabla}\varphi(\vec{x})}{|\vec{\nabla}\varphi(\vec{x})|} \cdot \vec{\nabla} Q(\vec{x}) \right) . \tag{5}$$

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In order to ensure $x_i(t) \geq 0 \ \forall i$ we can write this equation for some auxiliary variables z_i and define $x_i = F(z_i)$ with $F(y) \geq 0 \ \forall y$:

$$\dot{\vec{z}} = \vec{\nabla} Q(\vec{z}) - \Theta(\varphi(\vec{z})) \frac{\vec{\nabla}\varphi(\vec{z})}{|\vec{\nabla}\varphi(\vec{z})|} \left(\frac{\vec{\nabla}\varphi(\vec{z})}{|\vec{\nabla}\varphi(\vec{z})|} \cdot \vec{\nabla} Q(\vec{z}) \right) , \tag{6}$$

$$\dot{x}_i = F'(x_i)^2 \left[\frac{\partial Q}{\partial x_i} - \Theta(\varphi(\vec{x})) \frac{\partial\varphi/\partial x_i}{\sum_j (\partial\varphi/\partial x_j F'(x_j))^2} \sum_j \frac{\partial\varphi}{\partial x_i} \frac{\partial Q}{\partial x_j} F'(x_j) \right] . \tag{7}$$

The simplest choice for F is $F(x) = x^2/2$.

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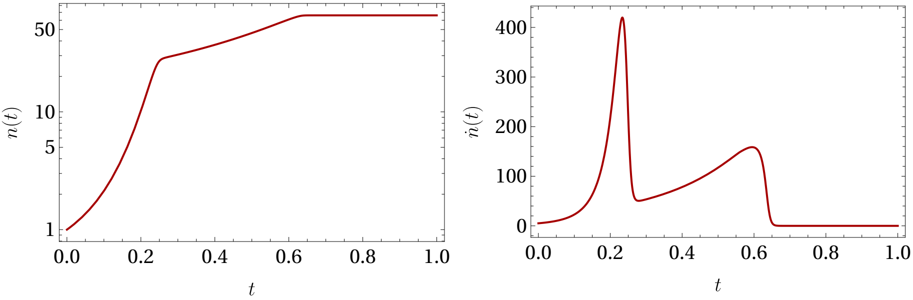
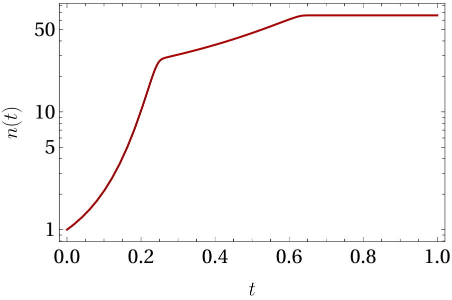
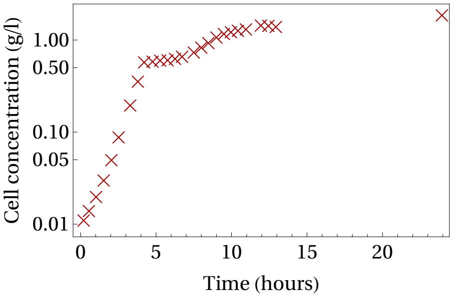


Parameters: $n(0) = 1$, $\vec{c}(0) = (40, 5)$, $\vec{v} = (1, 5)$, $\vec{w} = (1, 1)$, $\vec{\alpha}(0) = (1, 1)$, $E = 10$, $K_1 = K_2 = 1$, $\delta = 0$

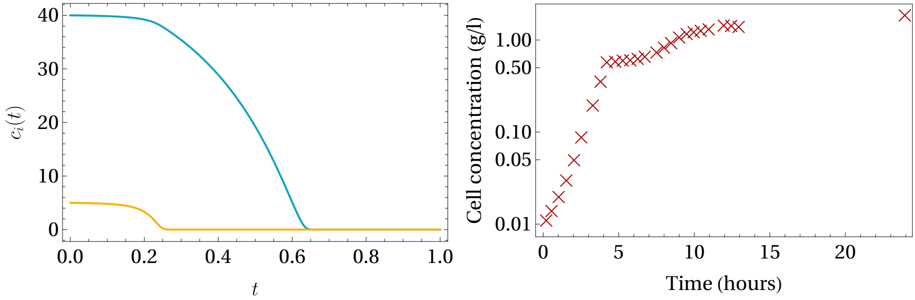




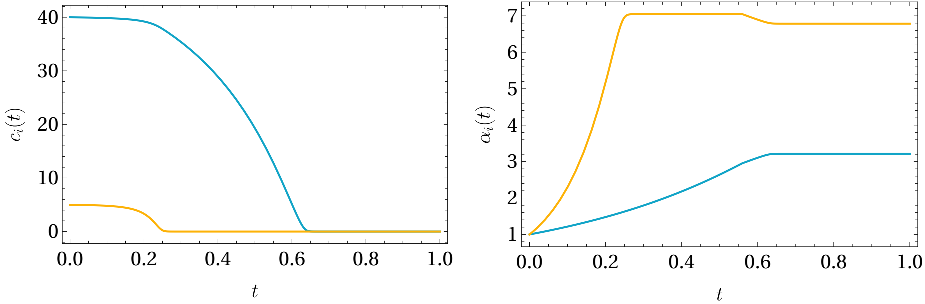
Parameters: $n(0) = 1$, $\vec{c}(0) = (40, 5)$, $\vec{v} = (1, 5)$, $\vec{w} = (1, 1)$, $\vec{\alpha}(0) = (1, 1)$, $E = 10$, $K_1 = K_2 = 1$, $\delta = 0$

Adaptive metabolic strategies

Evolution of resources and metabolic strategies



Parameters: $n(0) = 1$, $\vec{c}(0) = (40, 5)$, $\vec{v} = (1, 5)$, $\vec{w} = (1, 1)$, $\vec{\alpha}(0) = (1, 1)$, $E = 10$, $K_1 = K_2 = 1$, $\delta = 0$



Parameters: $n(0) = 1$, $\vec{c}(0) = (40, 5)$, $\vec{v} = (1, 5)$, $\vec{w} = (1, 1)$, $\vec{\alpha}(0) = (1, 1)$, $E = 10$, $K_1 = K_2 = 1$, $\delta = 0$