Adaptive metabolic strategies:

an (apparently) simple and effective answer to many challenging problems in ecology and microbiology

The physics of complex systems IV: from Padova to the rest of the world and back

Leonardo Pacciani Mori
leonardo.pacciani@phd.unipd.it
December 20th, 2018

Università degli Studi di Padova

Introduction: theoretical ecology

Introduction: theoretical ecology

- Fairly recent discipline (born in 1972 from an article by Robert May)

Introduction: theoretical ecology

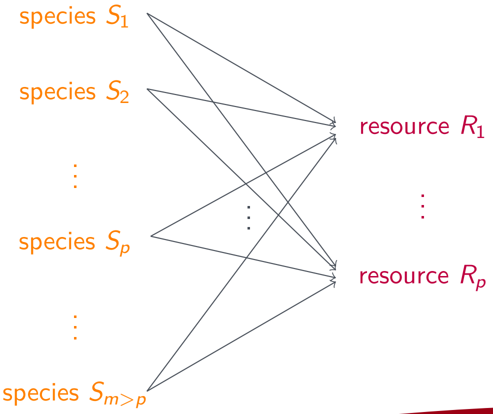
- Fairly recent discipline (born in 1972 from an article by Robert May)
- Many open problems

Introduction: theoretical ecology

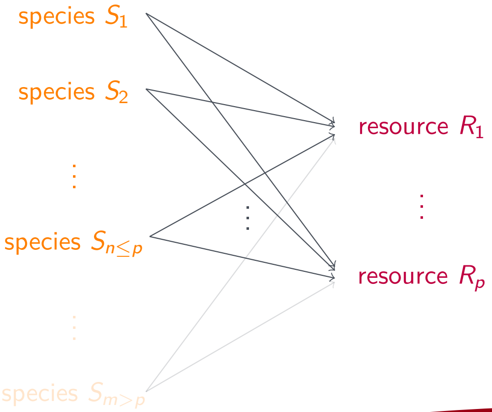
- Fairly recent discipline (born in 1972 from an article by Robert May)
- Many open problems
  - "Competitive Exclusion Principle" (CEP): the number of competing coexisting species in an ecosystem is limited by the number of available resources.

Introduction: theoretical ecology

- Fairly recent discipline (born in 1972 from an article by Robert May)
- Many open problems
  - "Competitive Exclusion Principle" (CEP): the number of competing coexisting species in an ecosystem is limited by the number of available resources.



- Fairly recent discipline (born in 1972 from an article by Robert May)
- Many open problems
  - "Competitive Exclusion Principle" (CEP): the number of competing coexisting species in an ecosystem is limited by the number of available resources.



Introduction: experimental ecology

Introduction: experimental ecology

UNIVERSITÀ DEGLI STUDI DI PADOVA

From an experimental point of view, the situation is very complicated:

Introduction: experimental ecology

From an experimental point of view, the situation is very complicated:

1. It is *very* difficult to monitor **whole** ecosystems in the field
   - We may not be able to detect all the species in it
   - Some species may enter or exit during the experiment

Introduction: experimental ecology

From an experimental point of view, the situation is very complicated:

1. It is *very* difficult to monitor **whole** ecosystems in the field
   - We may not be able to detect all the species in it
   - Some species may enter or exit during the experiment
2. There are *a lot* of factors that cannot be controlled
   - Immigrant or emigrant species
   - Climate and weather
   - Interaction between species

Introduction: experimental ecology

From an experimental point of view, the situation is very complicated:

1. It is *very* difficult to monitor **whole** ecosystems in the field
   - We may not be able to detect all the species in it
   - Some species may enter or exit during the experiment
2. There are *a lot* of factors that cannot be controlled
   - Immigrant or emigrant species
   - Climate and weather
   - Interaction between species

In the last decades *microbial ecosystems* are increasingly being used as a testing ground for ecolgical models:

Introduction: experimental ecology

From an experimental point of view, the situation is very complicated:

1. It is *very* difficult to monitor **whole** ecosystems in the field
   - We may not be able to detect all the species in it
   - Some species may enter or exit during the experiment
2. There are *a lot* of factors that cannot be controlled
   - Immigrant or emigrant species
   - Climate and weather
   - Interaction between species

In the last decades *microbial ecosystems* are increasingly being used as a testing ground for ecolgical models:

1. They are easier (but not necessarily easy *per se*) to manage in the lab

Introduction: experimental ecology

UNIVERSITÀ DEGLI STUDI DI PADOVA

From an experimental point of view, the situation is very complicated:

1. It is *very* difficult to monitor **whole** ecosystems in the field
   - We may not be able to detect all the species in it
   - Some species may enter or exit during the experiment
2. There are *a lot* of factors that cannot be controlled
   - Immigrant or emigrant species
   - Climate and weather
   - Interaction between species

In the last decades *microbial ecosystems* are increasingly being used as a testing ground for ecolgical models:

1. They are easier (but not necessarily easy *per se*) to manage in the lab
2. Their understanding has very important applications

The context of our work

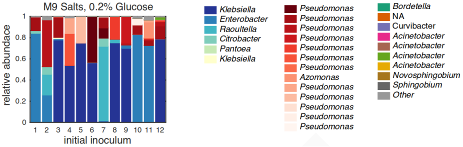
"Competitive Exclusion Principle" (CEP): there are *many* known cases in nature where this principle is *clearly* violated.

The context of our work

Università degli Studi di Padova

"Competitive Exclusion Principle" (CEP): there are *many* known cases in nature where this principle is *clearly* violated.

1. Bacterial community culture experiments

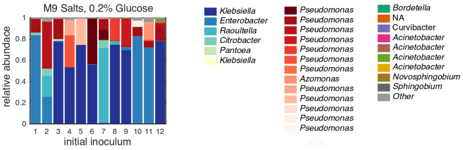


From Goldford et al. 2018

The context of our work

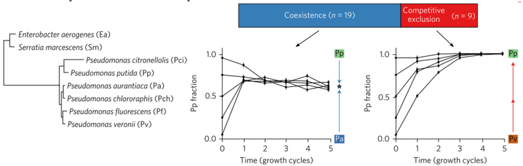
"Competitive Exclusion Principle" (CEP): there are *many* known cases in nature where this principle is *clearly* violated.

1. Bacterial community culture experiments



From Goldford et al. 2018

2. Direct bacterial competition experiments



From Friedman et al. 2017

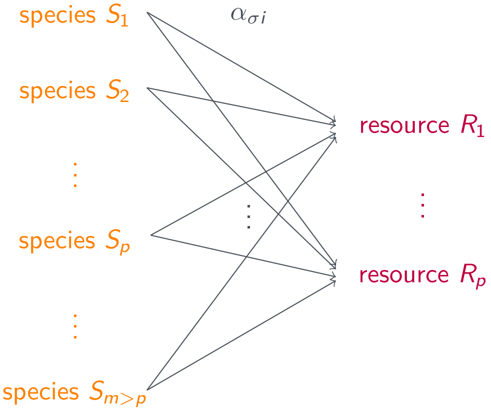
Modeling ecological competition

Modeling ecological competition

Since the '70s, the main mathematical tool used to model competitive ecosystems has been *MacArthur's consumer-resource model*.

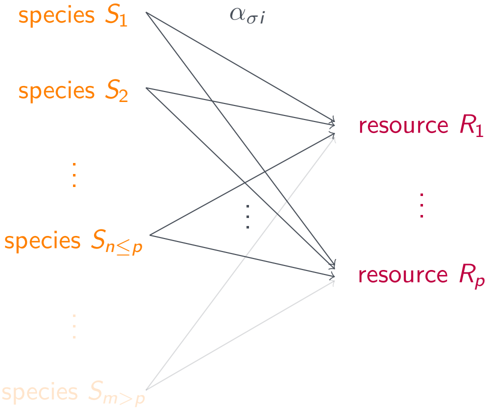
Modeling ecological competition

Since the '70s, the main mathematical tool used to model competitive ecosystems has been *MacArthur's consumer-resource model*.



Modeling ecological competition

Since the '70s, the main mathematical tool used to model competitive ecosystems has been *MacArthur's consumer-resource model*.



As it is, the model reproduces the CEP. In order to violate it, very special assumptions or parameter fine-tunings are necessary (Posfai et al. 2017).

Our work

Our work

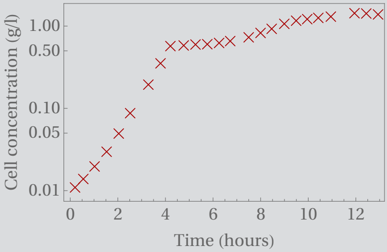
In the literature of consumer-resource models $\alpha_{\sigma i}$ are always considered as fixed parameters that do not change over time.

Our work

In the literature of consumer-resource models $\alpha_{\sigma i}$ are always considered as fixed parameters that do not change over time.

Problem ⚠

In many experiments *diauxic shifts* have been observed (Monod 1949)!



Growth of *Klebsiella oxytoca* on glucose and lactose. Data taken from Kompala et al. 1986, figure 11.

Our work

In the literature of consumer-resource models $\alpha_{\sigma i}$ are always considered as fixed parameters that do not change over time.

Our work in one sentence

We have modified MacArthur's consumer-resource model so that the metabolic strategies evolve over time.

Our work

In the literature of consumer-resource models $\alpha_{\sigma i}$ are always considered as fixed parameters that do not change over time.

Our work in one sentence

We have modified MacArthur's consumer-resource model so that the metabolic strategies evolve over time.

How?

Adaptive framework: each species changes its metabolic strategies in order to increase its own growth rate; adaptation velocity is measured by a parameter d.

What we have found

What we have found

Using adaptive metabolic strategies allows us to explain many experimentally observed phenomena, that span from the single species to the whole community!

What we have found

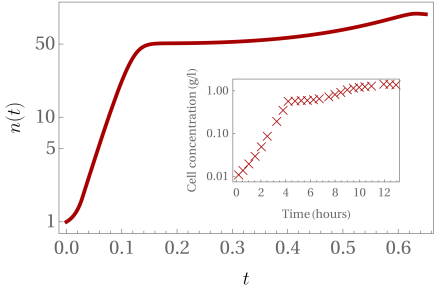
Using adaptive metabolic strategies allows us to explain many experimentally observed phenomena, that span from the single species to the whole community!

1/4) With one species and two resources, the model reproduces diauxic shifts:

What we have found

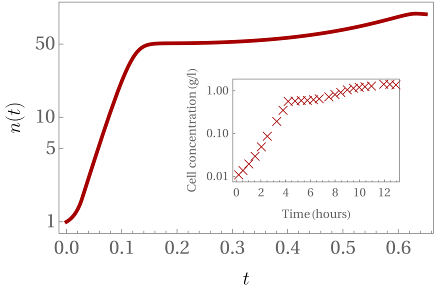
Using adaptive metabolic strategies allows us to explain many experimentally observed phenomena, that span from the single species to the whole community!

1/4) With one species and two resources, the model reproduces diauxic shifts:



Using adaptive metabolic strategies allows us to explain many experimentally observed phenomena, that span from the single species to the whole community!

1/4) With one species and two resources, the model reproduces diauxic shifts:



Notice

We can explain the existence of diauxic shifts with a completely general model, neglecting the particular molecular mechanisms of the species' metabolism.

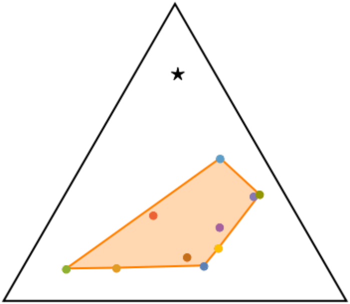
What we have found

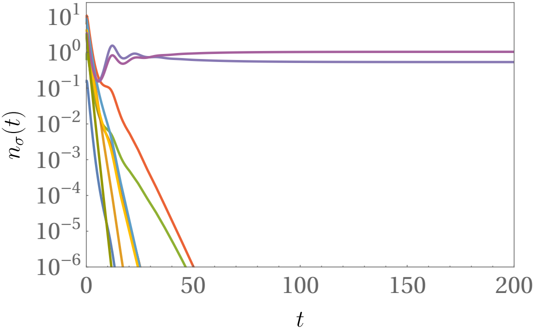
2/4) When multiple species and resources are considered, the model naturally violates the Competitive Exclusion Principle:

What we have found

Università degli Studi di Padova

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



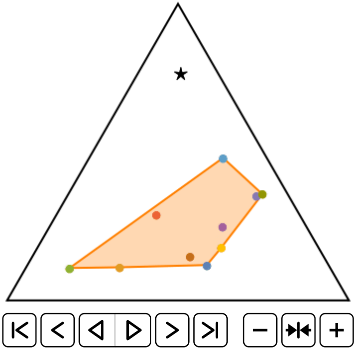


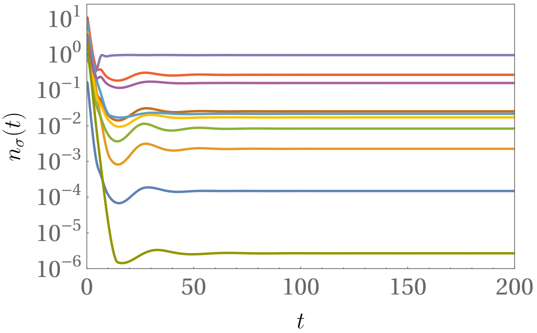
Fixed metabolic strategies

What we have found

Università degli Studi di Padova

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





Adaptive metabolic strategies

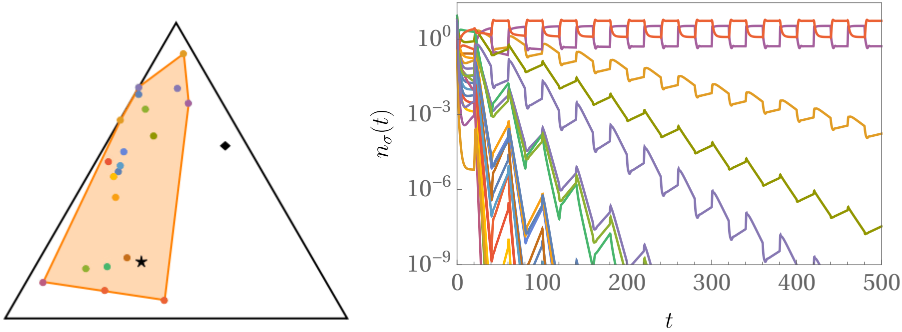
What we have found

Università degli Studi di Padova

3/4) When environmental conditions are variable (i.e. the nutrient supply rates change in time) using adaptive $\alpha_{\sigma i}$ leads to more stable communities:

Università degli Studi di Padova

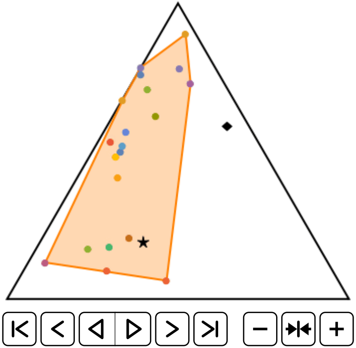
3/4) When environmental conditions are variable (i.e. the nutrient supply rates change in time) using adaptive $\alpha_{\sigma i}$ leads to more stable communities:

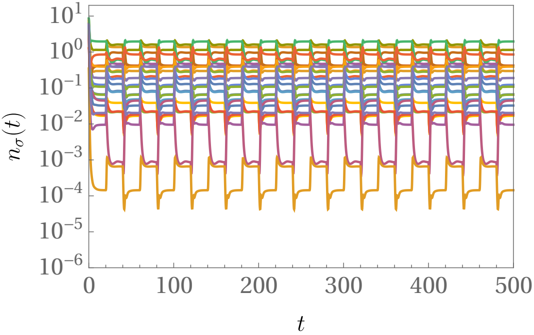


Fixed metabolic strategies, $\tau_{\text{in}} = \tau_{\text{out}} = 20$

What we have found

3/4) When environmental conditions are variable (i.e. the nutrient supply rates change in time) using adaptive $\alpha_{\sigma i}$ leads to more stable communities:

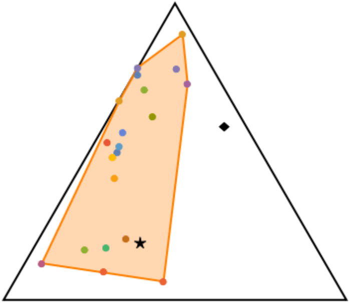


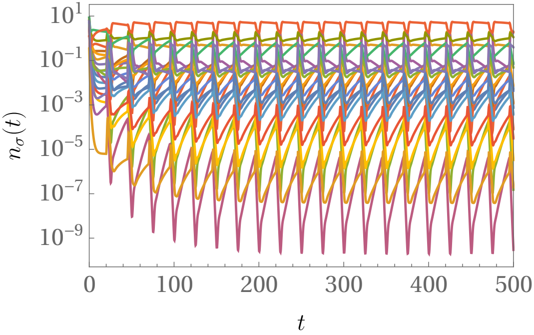


Adaptive metabolic strategies, $\tau_{\text{in}} = \tau_{\text{out}} = 20$

What we have found

3/4) When environmental conditions are variable (i.e. the nutrient supply rates change in time) using adaptive $\alpha_{\sigma i}$ leads to more stable communities:

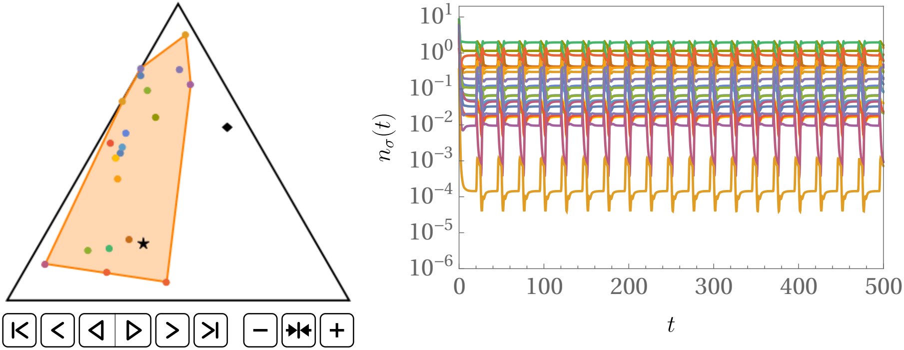




Fixed metabolic strategies, $\tau_{\text{in}} = 20$, $\tau_{\text{out}} = 5$

Università degli Studi di Padova

3/4) When environmental conditions are variable (i.e. the nutrient supply rates change in time) using adaptive $\alpha_{\sigma i}$ leads to more stable communities:



Adaptive metabolic strategies, $\tau_{\text{in}} = 20$, $\tau_{\text{out}} = 5$

What we have found

Adaptation velocity d is a crucial element of the model.

What we have found

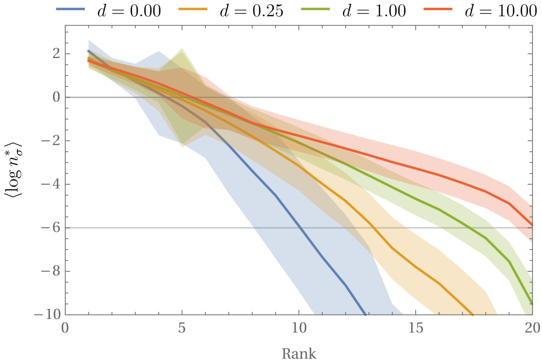
Adaptation velocity d is a crucial element of the model.

4/4) If adaptation is sufficiently slow there can be extinction and the Competitive Exclusion Principle can be recovered.

Università degli Studi di Padova

Adaptation velocity d is a crucial element of the model.

4/4) If adaptation is sufficiently slow there can be extinction and the Competitive Exclusion Principle can be recovered.



20 species, 3 resources

Conclusions and future developments

Conclusions

Using adaptive metabolic strategies in consumer-resource models allows us to explain lots of different experimentally observed phenomena.

Conclusions and future developments

Conclusions

Using adaptive metabolic strategies in consumer-resource models allows us to explain lots of different experimentally observed phenomena.

Future developments

Conclusions and future developments

Università degli Studi di Padova

Conclusions

Using adaptive metabolic strategies in consumer-resource models allows us to explain lots of different experimentally observed phenomena.

Future developments

- Understand more deeply the role of adaptation velocity d: could it be the key element to predict competition outcome?

Conclusions and future developments

Conclusions

Using adaptive metabolic strategies in consumer-resource models allows us to explain lots of different experimentally observed phenomena.

Future developments

- Understand more deeply the role of adaptation velocity d: could it be the key element to predict competition outcome?
- Design and perform experiments to verify the predictions

References

Friedman, Jonathan et al. (2017). "Community structure follows simple assembly rules in microbial microcosms". In: *Nature Ecology and Evolution* 1.5, pp. 1–7.

Goldford, Joshua E. et al. (2018). "Emergent simplicity in microbial community assembly". In: *Science* 361.6401, pp. 469–474.

Kompala, Dhinakar S. et al. (1986). "Investigation of bacterial growth on mixed substrates: Experimental evaluation of cybernetic models". In: *Biotechnology and Bioengineering* 28.7, pp. 1044–1055.

Monod, Jacques (1949). "The Growth of Bacterial Cultures". In: *Annual Review of Microbiology* 3.1, pp. 371–394.

Posfai, Anna et al. (2017). "Metabolic Trade-Offs Promote Diversity in a Model Ecosystem". In: *Physical Review Letters* 118.2, p. 28103.

Backup slides

Details of the model

Details of the model

The equations that define MacArthur's consumer-resource model are the following:

Details of the model

Università degli Studi di Padova

The equations that define MacArthur's consumer-resource model are the following:

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

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

Details of the model

Università degli Studi di Padova

The equations that define MacArthur's consumer-resource model are the following:

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

resource degradation rate

Details of the model

Università degli Studi di Padova

We can require that $\alpha_{\sigma i}$ evolves so that $g_\sigma = \sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i(c_i)$ is maximized by means of a simple "gradient ascent" equation:

Details of the model

We can require that $\alpha_{\sigma i}$ evolves so that $g_\sigma = \sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i(c_i)$ is maximized by means of a simple "gradient ascent" equation:

$$\dot{\alpha}_{\sigma i} = \frac{1}{\tau_\sigma} \cdot \frac{\partial g_\sigma}{\partial \alpha_{\sigma i}} = d\delta_\sigma v_i r_i \qquad \text{where} \qquad \frac{1}{\tau_\sigma} = d\delta_\sigma \tag{2}$$

Details of the model

UNIVERSITÀ DEGLI STUDI DI PADOVA

We can require that $\alpha_{\sigma i}$ evolves so that $g_\sigma = \sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i(c_i)$ is maximized by means of a simple "gradient ascent" equation:

$$\dot{\alpha}_{\sigma i} = \frac{1}{\tau_\sigma} \cdot \frac{\partial g_\sigma}{\partial \alpha_{\sigma i}} = d\delta_\sigma v_i r_i \qquad \text{where} \qquad \frac{1}{\tau_\sigma} = d\delta_\sigma \tag{2}$$

Problem ⚠

As it is, eq (2) does not prevent $\alpha_{\sigma i}$ from growing indefinitely!

Details of the model

We can require that $\alpha_{\sigma i}$ evolves so that $g_\sigma = \sum_{i=1}^{p} v_i \alpha_{\sigma i} r_i(c_i)$ is maximized by means of a simple "gradient ascent" equation:

$$\dot{\alpha}_{\sigma i} = \frac{1}{\tau_\sigma} \cdot \frac{\partial g_\sigma}{\partial \alpha_{\sigma i}} = d\delta_\sigma v_i r_i \qquad \text{where} \qquad \frac{1}{\tau_\sigma} = d\delta_\sigma \tag{2}$$

Problem ⚠

As it is, eq (2) does not prevent $\alpha_{\sigma i}$ from growing indefinitely!

Solution

We must introduce some constraint in the resource uptake: the metabolic strategies $\alpha_{\sigma i}$ must be somehow limited.

Details of the model

Università degli Studi di Padova

Our choice:

$$\underbrace{\sum_{i=1}^{p} w_i \alpha_{\sigma i}}_{\text{“resource costs”}} := E_\sigma(t) \leq \mathcal{Q}\delta_\sigma \tag{3}$$

Details of the model

Università degli Studi di Padova

Our choice:

$$\underset{\substack{\big\downarrow \\ \text{“resource costs”}}}{\sum_{i=1}^{p} w_i \alpha_{\sigma i}} := E_\sigma(t) \leq \mathcal{Q}\delta_\sigma \tag{3}$$

Final equation (after some work):

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

Details of the model

Università degli Studi di Padova

Our choice:

$$\underbrace{\sum_{i=1}^{p} w_i \alpha_{\sigma i}}_{\text{"resource costs"}} := E_\sigma(t) \leq \mathcal{Q}\delta_\sigma \tag{3}$$

Final equation (after some work):

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

Attention ⚠

We have also made sure that $\alpha_{\sigma i}(t) \geq 0 \; \forall t$.