

QLS 2021/2022

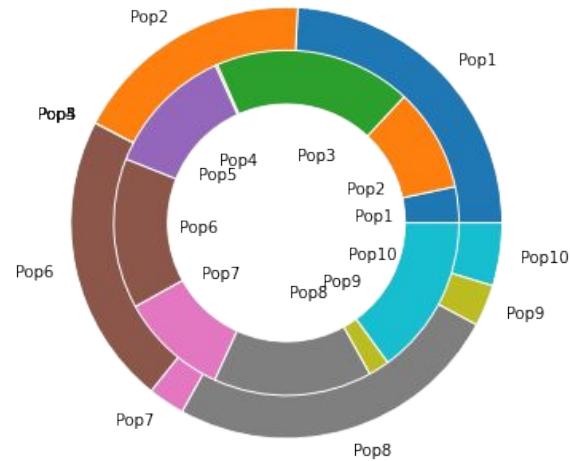
Spatial ecology for territorial populations

Benjamin G. Weiner, Anna Posfai, and Ned S. Wingreen

THE MODEL: GENERAL OVERVIEW

In this work it's presented an ecological model that allows to describe simple spatial structures. The main features are:

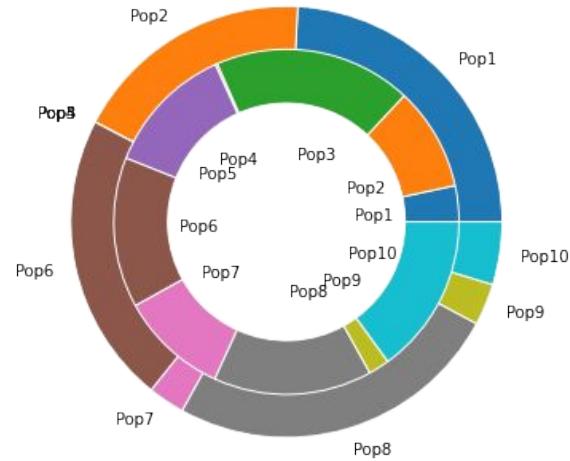
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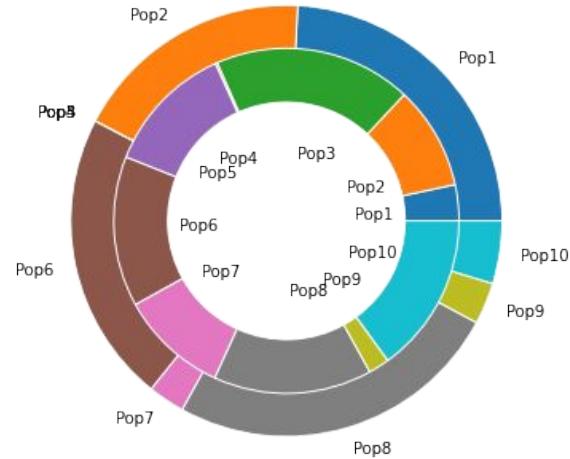
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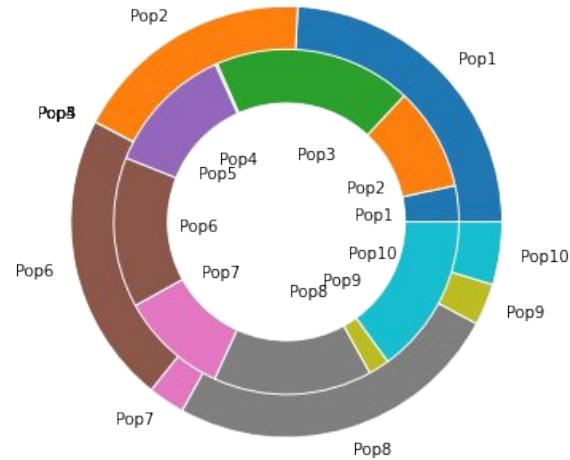
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3. Each species occupies a **segment of the ring** whose **size** is given by its **population** n_σ



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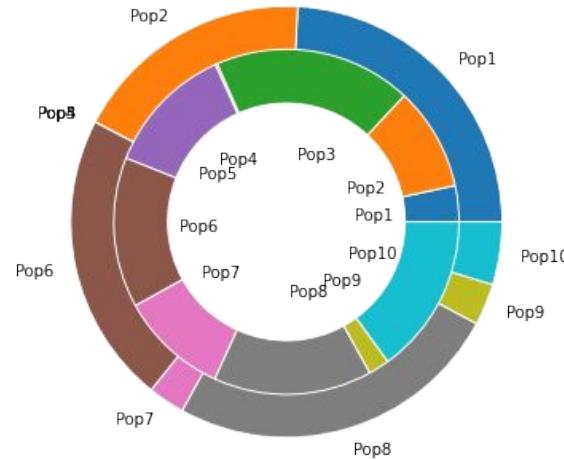
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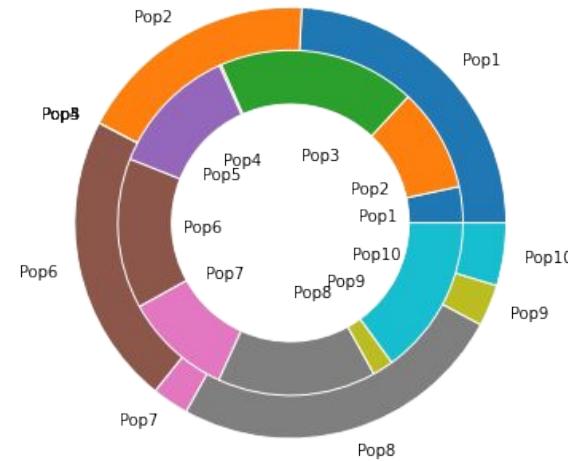
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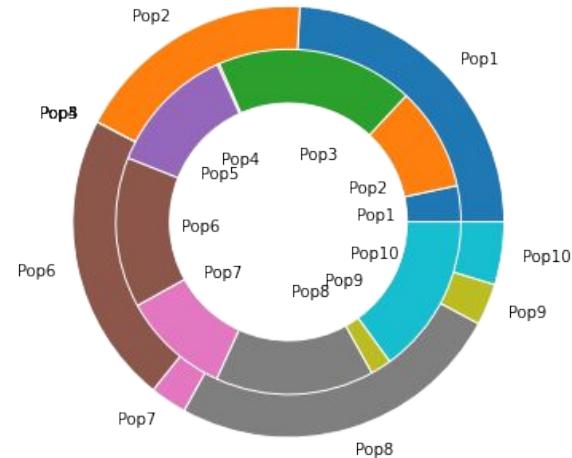
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 6. The nutrients diffuse in space with time according to a differential equation
 7. The space dimension L and consequently the **total population remains constant in time**



THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

This equation tells how the nutrients' abundance change in time

THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

$c_{\sigma i}$ indicates the abundance
of the nutrient i consumed by
the population σ

THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

S_i indicates the supply rate of the i -th nutrient, i.e. the rate at which the resource is injected into the environment

THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

This term quantifies the speed at which the resource i resource is consumed by the population sigma. $\alpha_{\sigma i}$ represents the metabolic strategy of a particular pair of resource–population (a deeper explanation will be given later)

THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

D is the constant diffusion rate at which the resources spread in the territory

THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

The nutrients spread is influenced by the spatial distribution of them at the current time, which is quantified by the second derivative of the abundance w.r.t. the space

THE MODEL: RESOURCES

$$\frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2}$$

- $c_{\sigma i}$: nutrient i abundance distribution in the territory occupied by the population σ
- S_i : supply rate of the i -th resource
- $\alpha_{\sigma i}$: metabolic strategy of the pair σi
- D : diffusion rate

THE MODEL: STATIONARITY

The differential equations for the dynamics of the nutrients are too complex to simulate numerically



Given the fact that nutrients processing is generally much faster than
species growth, we can assume **timescale separation**



$$\frac{\partial c}{\partial t} = 0$$

**QUASI-STATIONARY
APPROXIMATION FOR
NUTRIENTS**

THE MODEL: RESOURCES

What remains is a second order differential equation in space, which can be solved analytically, returning:

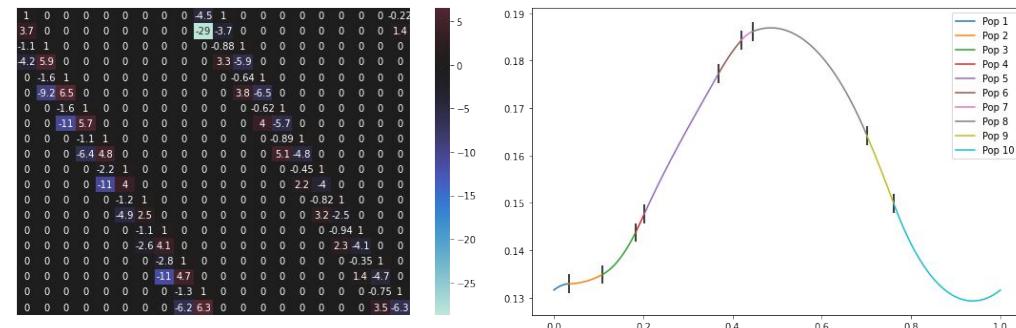
$$c_{\sigma i} = \frac{S_i}{\alpha_{\sigma i}} + A_{\sigma i} \exp \left(x \sqrt{\frac{\alpha_{\sigma i}}{D}} \right) + B_{\sigma i} \exp \left(-x \sqrt{\frac{\alpha_{\sigma i}}{D}} \right)$$

The expression above returns the spatial function that describes the distribution of the nutrient i in the territory occupied by the population σ

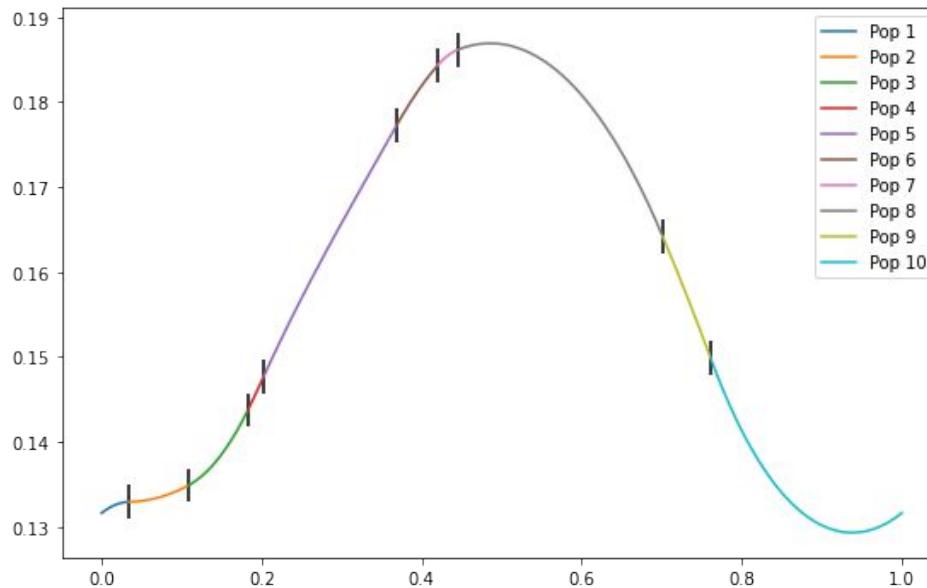
THE MODEL: RESOURCES

$$c_{\sigma i} = \frac{S_i}{\alpha_{\sigma i}} + A_{\sigma i} \exp\left(x\sqrt{\frac{\alpha_{\sigma i}}{D}}\right) + B_{\sigma i} \exp\left(-x\sqrt{\frac{\alpha_{\sigma i}}{D}}\right)$$

The integration constants $A_{\sigma i}$ $B_{\sigma i}$ are fixed by the physical constraints of the system. In particular the nutrients distributions have to be continuous and differentiable in any point, also in the conjunction between the areas occupied by different populations



THE MODEL: RESOURCES



THE MODEL: POPULATIONS

$$\frac{dn_\sigma}{dt} = \sum_i \alpha_{\sigma i} \left(v \int_0^{n_\sigma} c_i(x) dx \right) - \delta n_\sigma$$

This equation tells how the species populations change in time

THE MODEL: POPULATIONS

$$\frac{dn_\sigma}{dt} = \sum_i \alpha_{\sigma i} \left(v \int_0^{n_\sigma} c_i(x) dx \right) - \delta n_\sigma$$

n_σ is the population of the species σ , and also corresponds to the fraction of the territory occupied by such a species

THE MODEL: POPULATIONS

$$\frac{dn_\sigma}{dt} = \sum_i \alpha_{\sigma i} \left(v \int_0^{n_\sigma} c_i(x) dx \right) - \delta n_\sigma$$

Conversion rate between nutrients consumption
and population /occupied territory increase

THE MODEL: POPULATIONS

$$\frac{dn_\sigma}{dt} = \sum_i \alpha_{\sigma i} \left(v \int_0^{n_\sigma} c_i(x) dx \right) - \delta n_\sigma$$

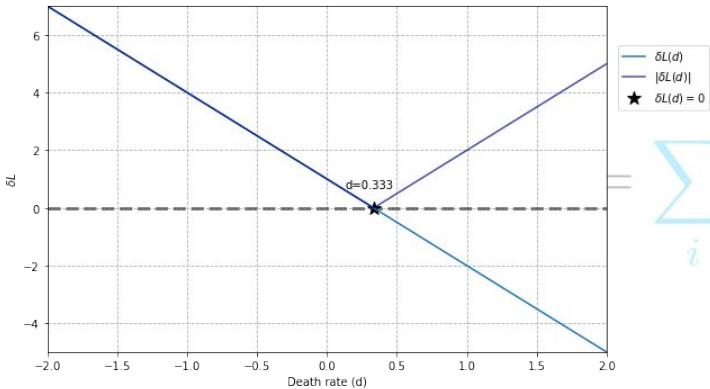
The integral return the quantity of nutrient i contained in the territory of species σ . By multiplying for the metabolic strategies and summing over all the nutrients, we have the growth rate of the species

THE MODEL: POPULATIONS

$$\frac{dn_\sigma}{dt} = \sum_i \alpha_{\sigma i} \left(v \int_0^{n_\sigma} c_i(x) dx \right) - \delta n_\sigma$$

It is the term related to the decreasing of the species abundance due to the death of some individuals, i.e. the negative growth

THE MODEL: POPULATIONS



The death rate is a fundamental parameter in the simulation. It's possible to see that it has to be tweaked perfectly in order to have a constant total population in the territory.

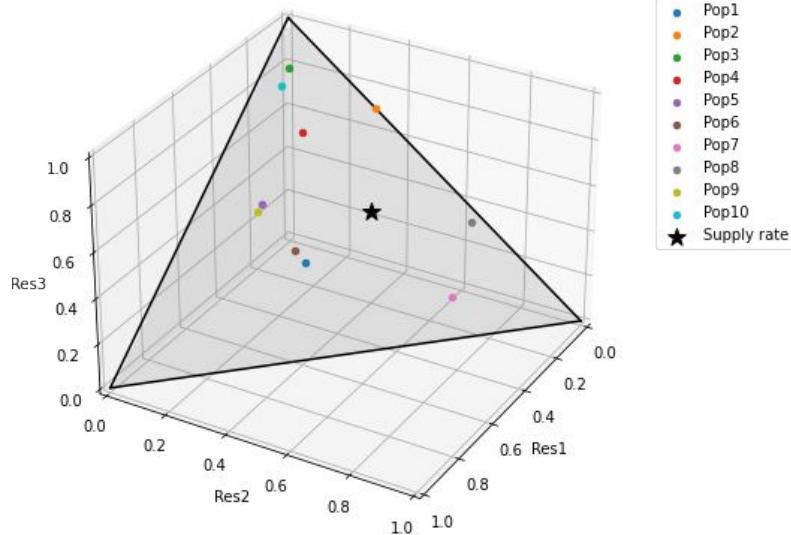
δn_σ

Find δ such that $\sum_{\sigma} \frac{dn_{\sigma}}{dt} = 0$

It can be shown that it has to be equal to $\frac{1}{p}$ with p the number of nutrients.

Even small variations make the system diverge (or vanish).

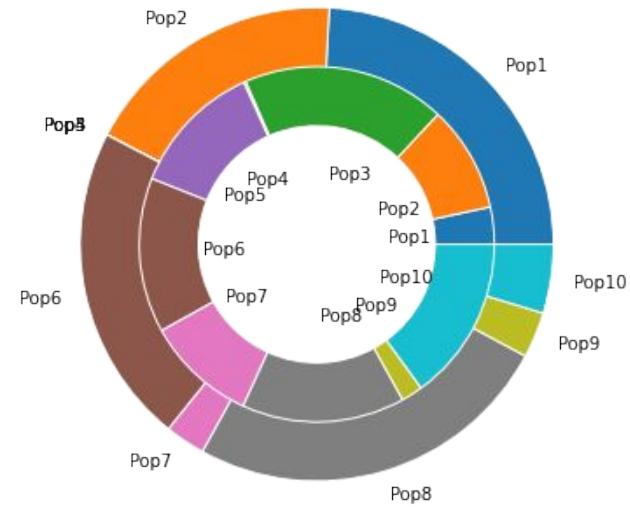
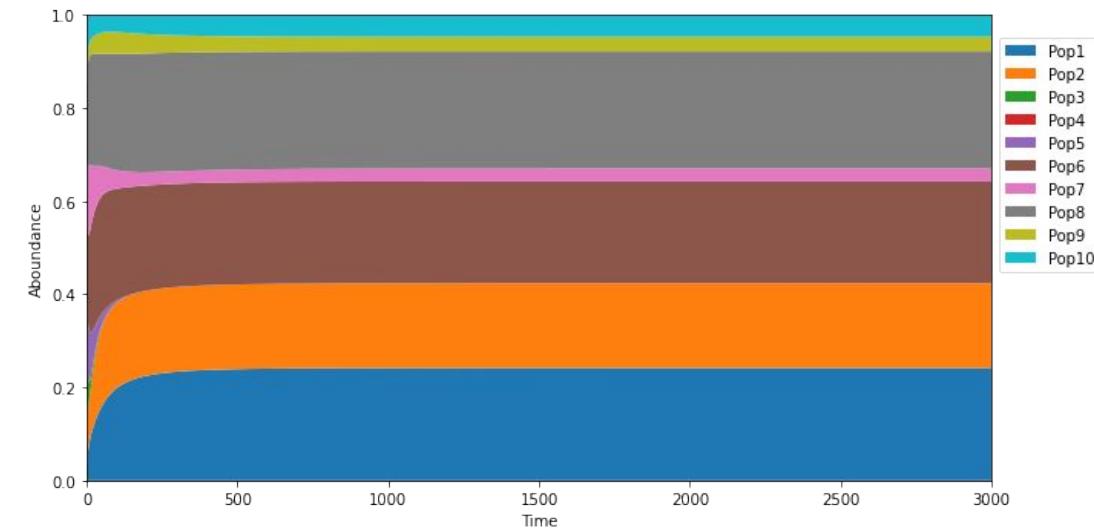
THE MODEL: METABOLIC TRADEOFF



$$\sum_i \alpha_{\sigma i} = E$$

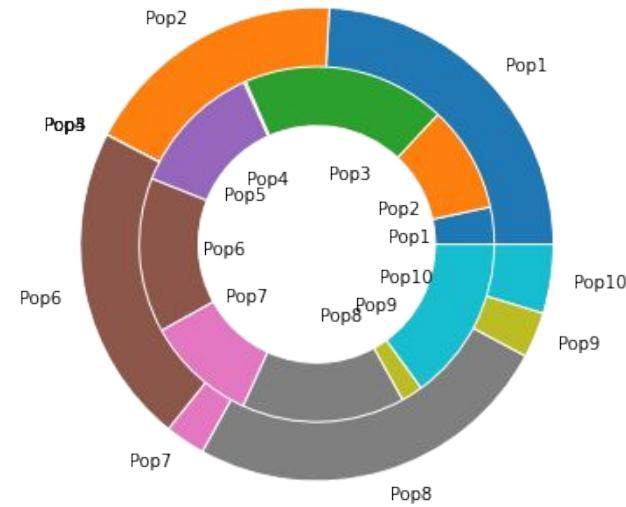
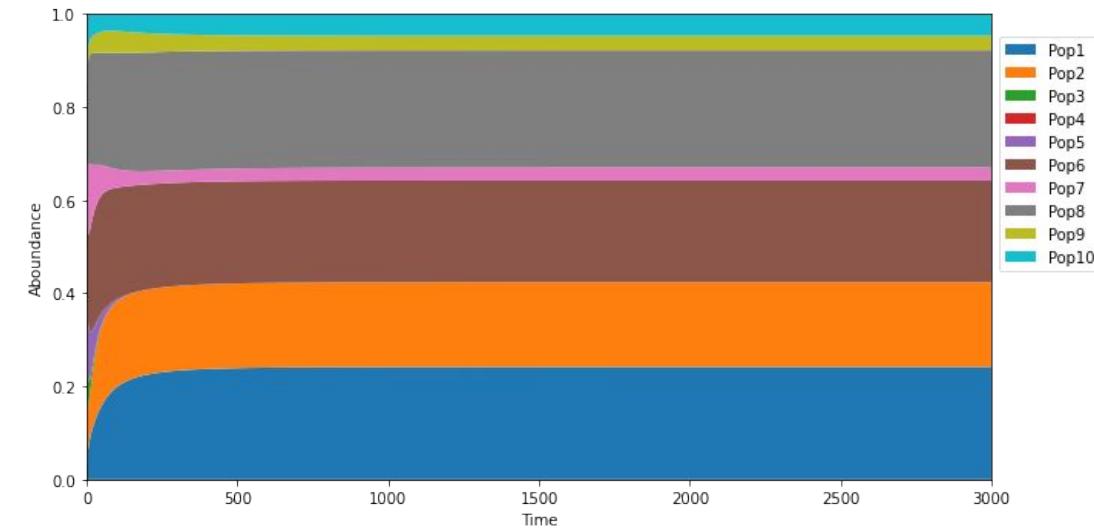
The metabolic constraint forces the alphas to lie in $p-1$ dimensional simplex.
It derives from the observation that every living organism has a fixed quantity of energy to invest into metabolic dynamics.

COMPLETE SIMULATION

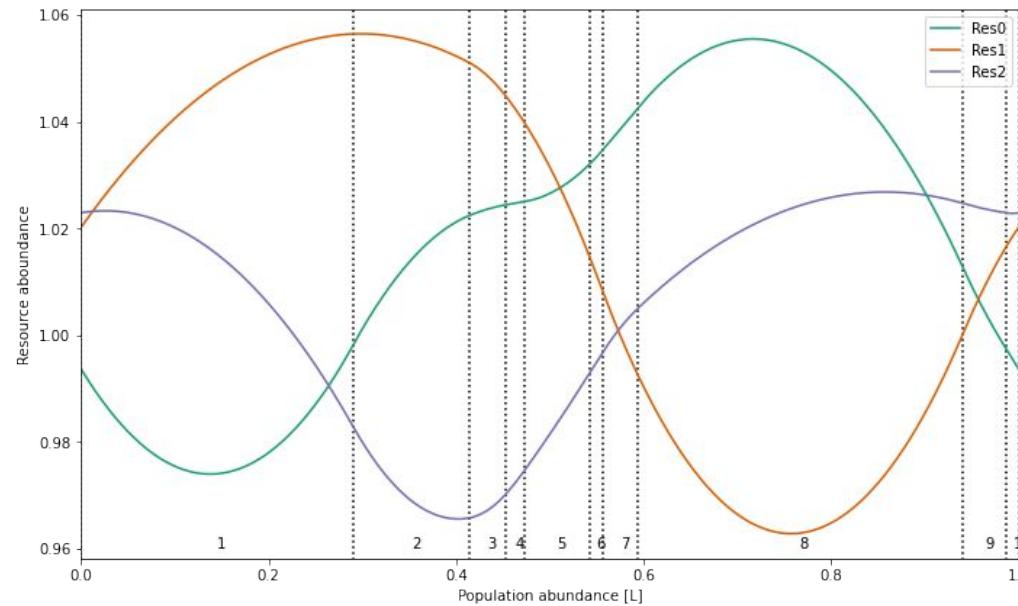


COMPLETE SIMULATION

CEP violated!!!



COMPLETE SIMULATION

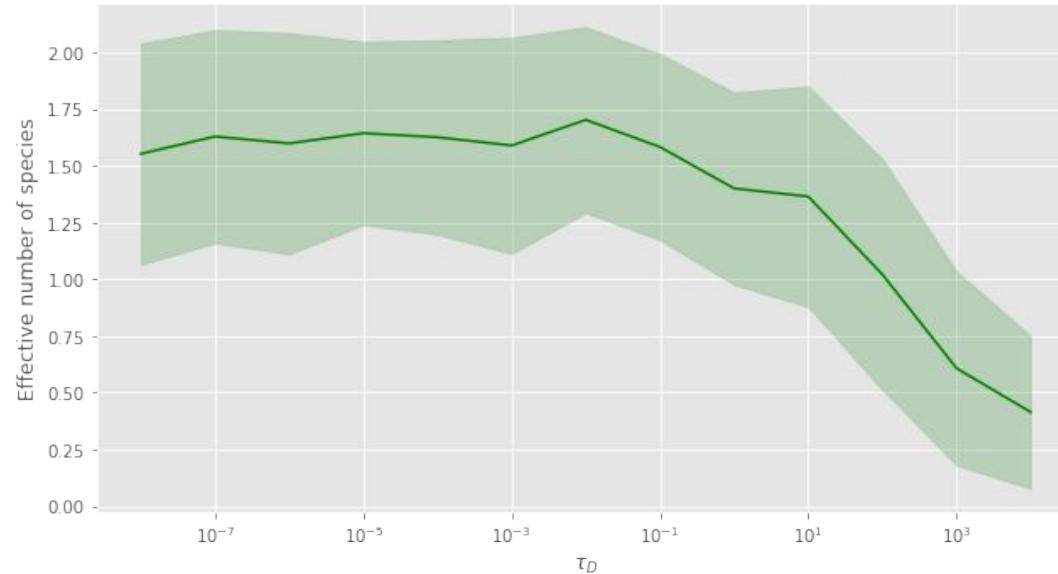


VARIATION OF THE DIFFUSION RATE

Effective number of species: it is defined as the Shannon entropy of the population densities

$$H = - \sum_{\sigma} p_{\sigma} \log p_{\sigma}$$

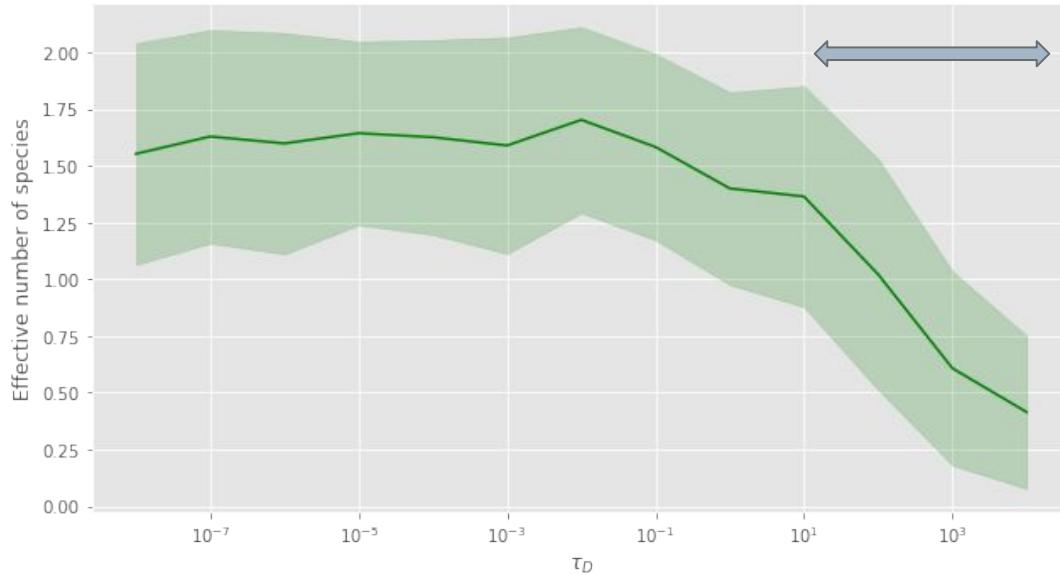
It allows to quantify the biodiversity of the system without setting an arbitrary threshold to state if a species is extinct or not.



$$\tau_D = \frac{LE}{D}$$

Diffusion time, the time required for nutrients to diffuse a distance L relative to the uptake time. It is inversely proportional to the Diffusion Rate

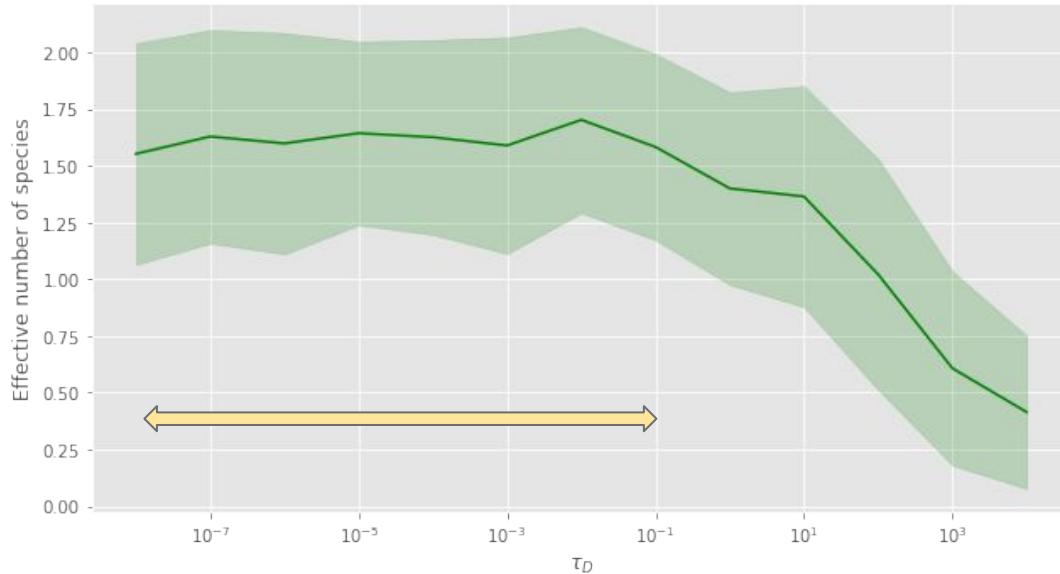
VARIATION OF THE DIFFUSION RATE



The biodiversity of the system decreases as the diffusion rate increase

For small values of D , the nutrients spread in the territory with a timescale comparable to the one of the species growth, and so the spatial features of the system are relevant.

VARIATION OF THE DIFFUSION RATE



The biodiversity of the system decreases as the diffusion rate increase

For large values of D , the nutrients spread very fast, and the concentration of each one is almost constant in each point of the space in every instant.

In the limit of , $D \rightarrow \infty$ we talk about WELL MIXED CASE

NULL MODEL: WELL-MIXED CASE

Spatial $\xrightarrow{D \rightarrow \infty}$ Well-Mixed

$$\begin{cases} \frac{\partial c_{\sigma i}}{\partial t} = S_i - \alpha_{\sigma i} c_{\sigma i} + D \frac{\partial^2 c_{\sigma i}}{\partial x^2} \\ \frac{dn_{\sigma}}{dt} = \sum_i \alpha_{\sigma i} \left(v \int_0^{n_{\sigma}} c_i(x) dx \right) - \delta n_{\sigma} \end{cases}$$

$\xrightarrow{D \rightarrow \infty}$

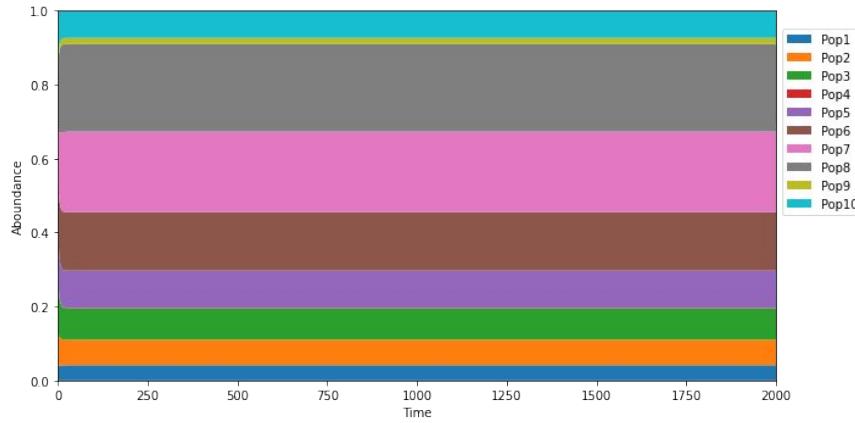
Applying
expansions and
approximations

$$\frac{\partial c_i}{\partial t} = S_i \left(\sum_{\sigma} n_{\sigma} \alpha_{\sigma i} \right) r_i(c_i)$$

QUASI-STATIONARY
APPROXIMATION

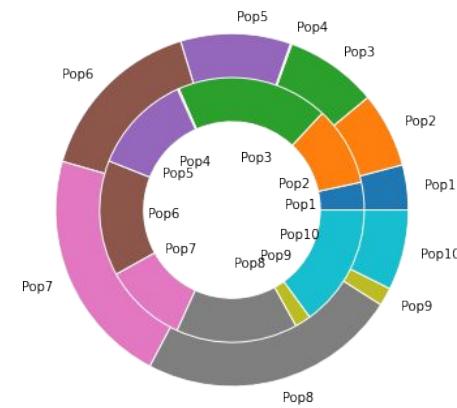
$$\frac{dn_{\sigma}}{dt} = \left(\sum_i \alpha_{\sigma i} \frac{S_i}{\sum_{\gamma} \alpha_{\gamma i} n_{\gamma}} - \delta \right) n_{\sigma}$$

NULL MODEL: WELL-MIXED CASE



In general the *typical timescale* for the population dynamics in the *well-mixed case* is much faster than the one of the *spatial case*

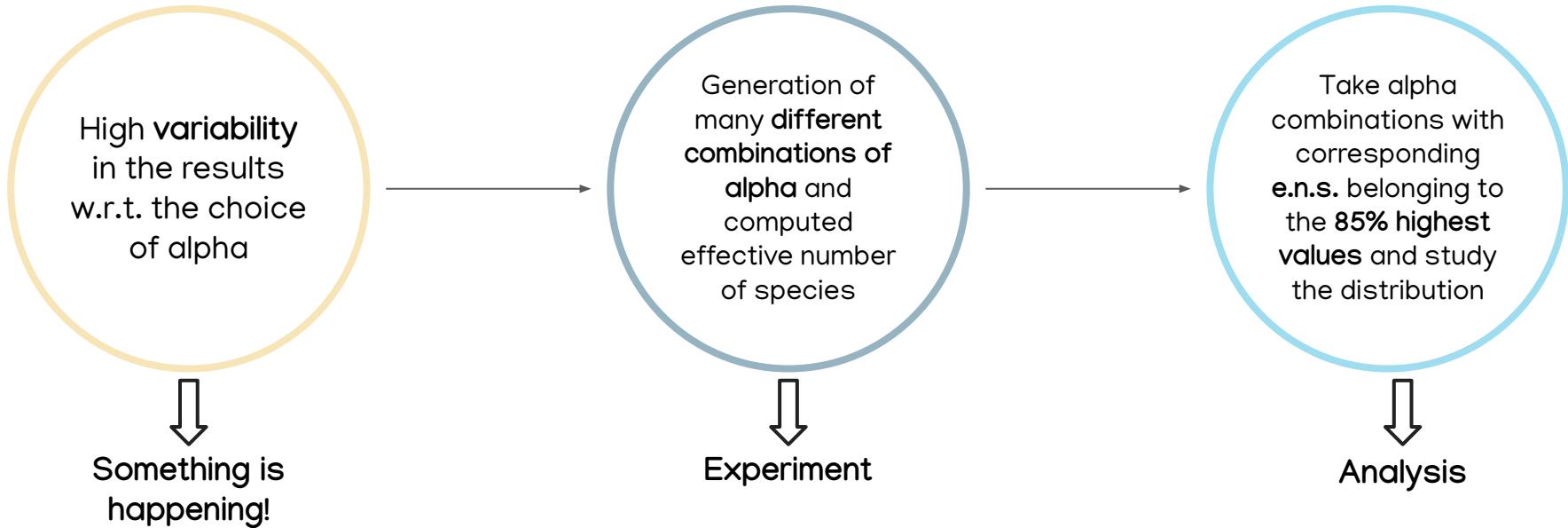
If the *metabolic tradeoff condition holds*, typically all or almost all the species survive asymptotically, and this leads to an high biodiversity degree



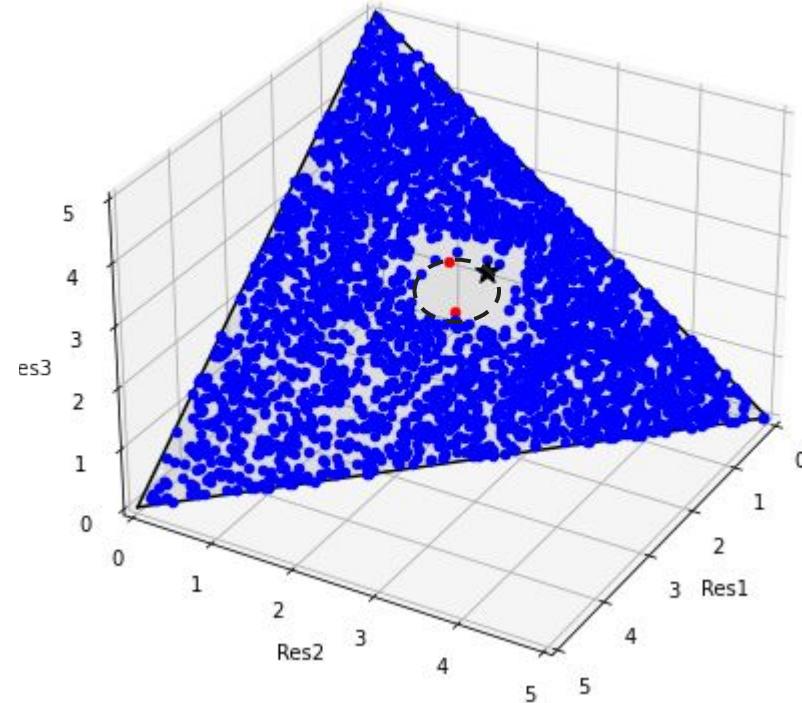


**Before the comparison, one
more ingredient ...**

OLIGOTROPHS



OLIGOTROPHS

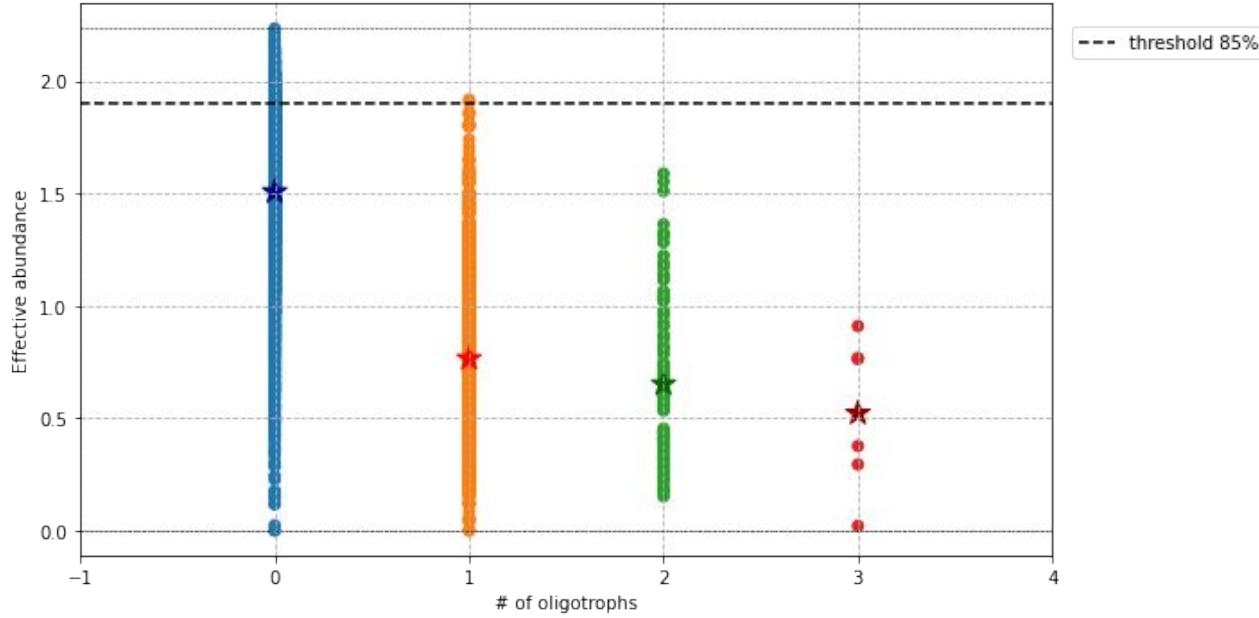


*Inside the region delimited by the dashed line,
there are almost no points*

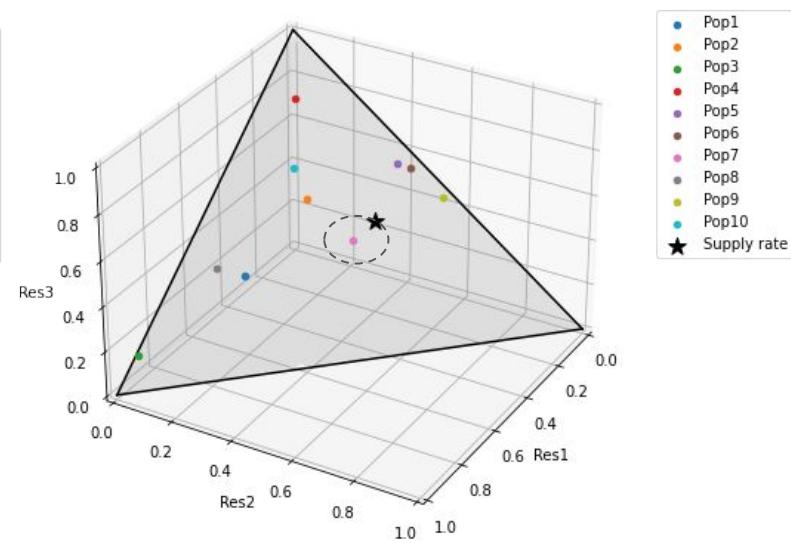
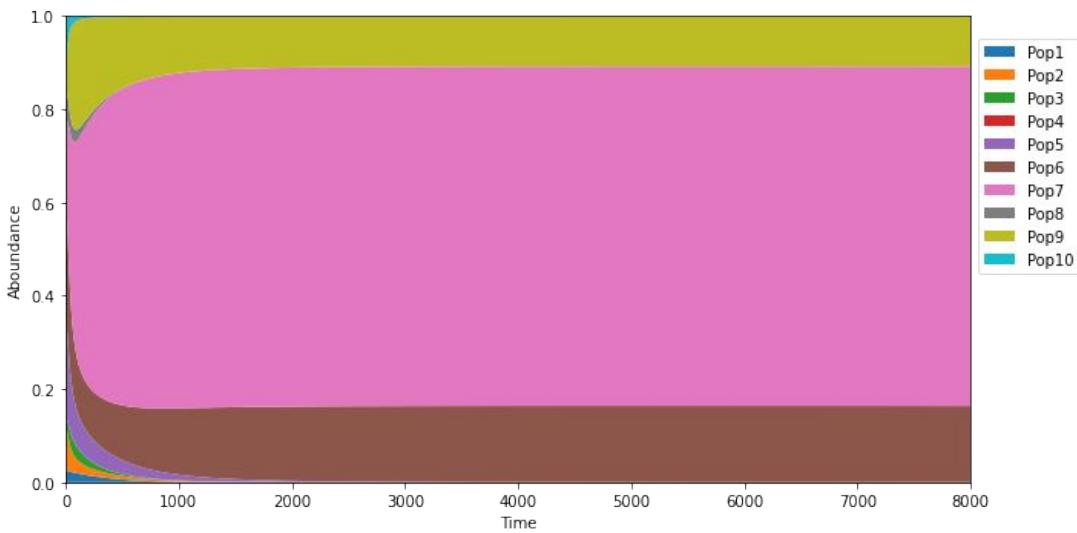
Oligotrophs: they are species able to survive also at minimum total nutrient level, and in such a way they drive other competitors to extinction. This property is mathematically given by the formula below

$$\sum_i \frac{S_i}{\alpha_{\sigma i}} < \frac{p}{E}$$

OLIGOTROPHS

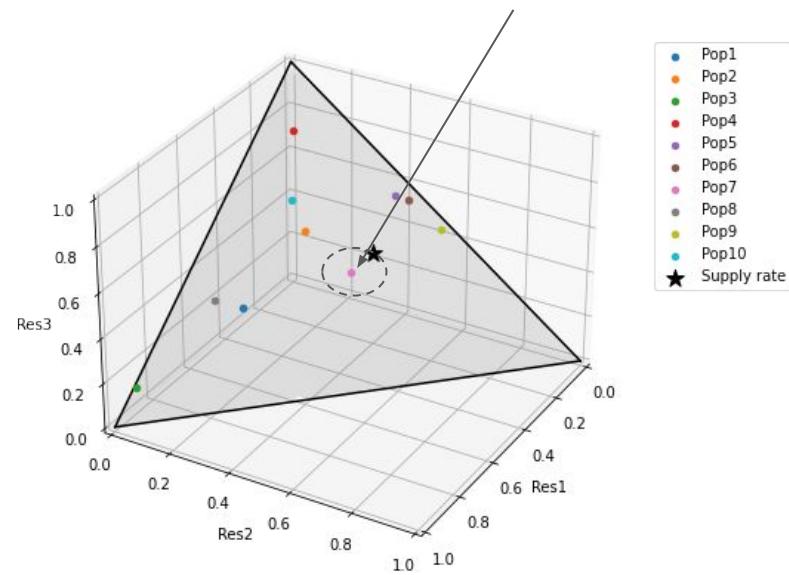
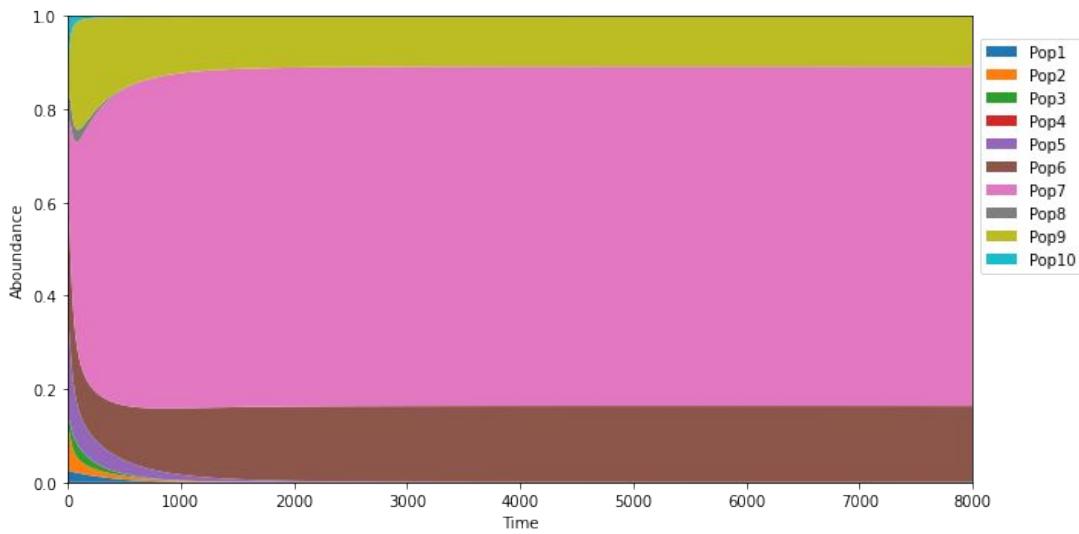


OLIGOTROPHS



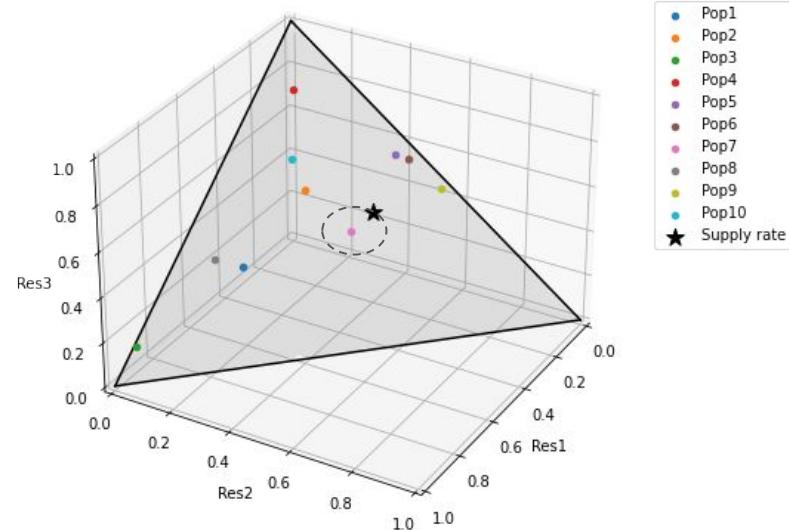
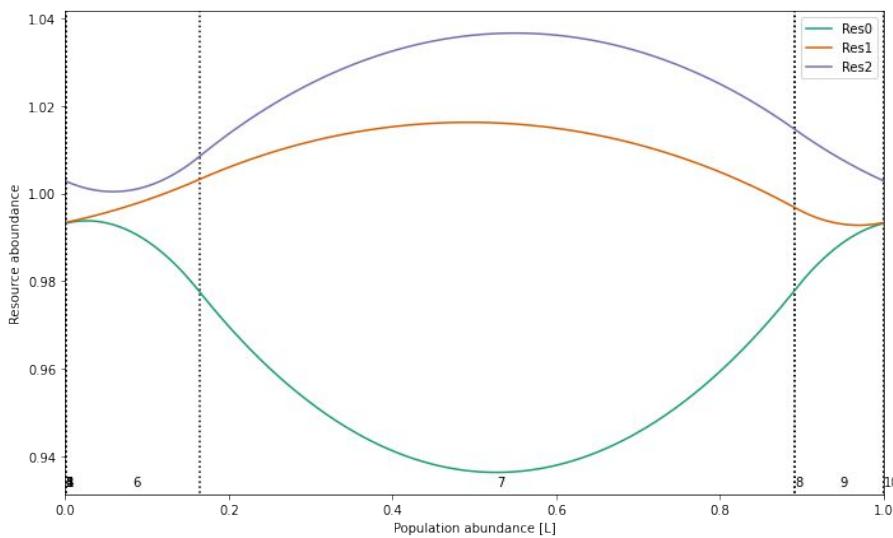
OLIGOTROPHS

Species 7 is an oligotroph



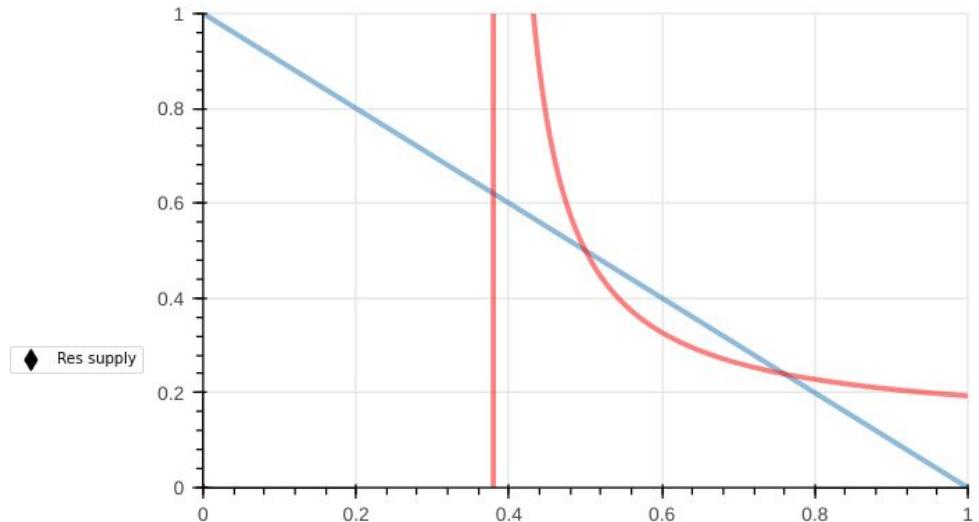
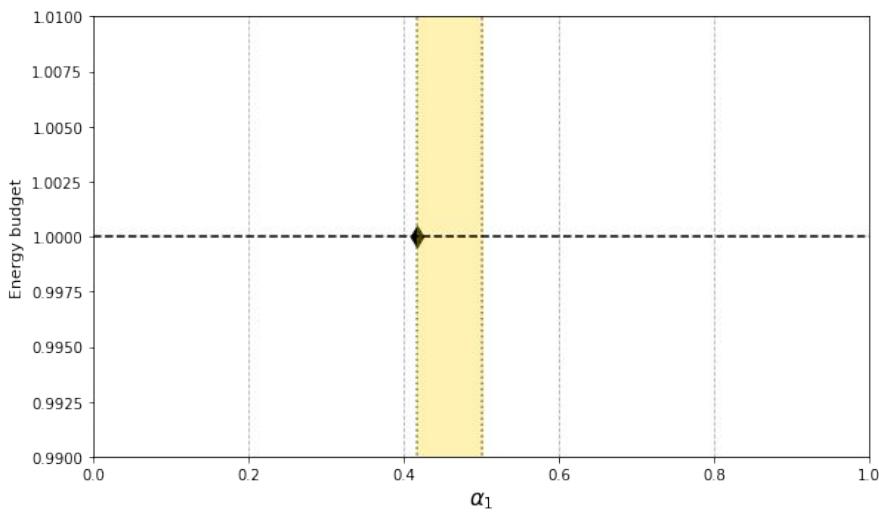
OLIGOTROPHS

The majority of the resources have flowed in the area
occupied by species 7 !



OLIGOTROPHS with 2 nutrients

In the case of 2 nutrients is easier to determine the position of the oligotrophs region because it's possible to solve analytically the system of equations.



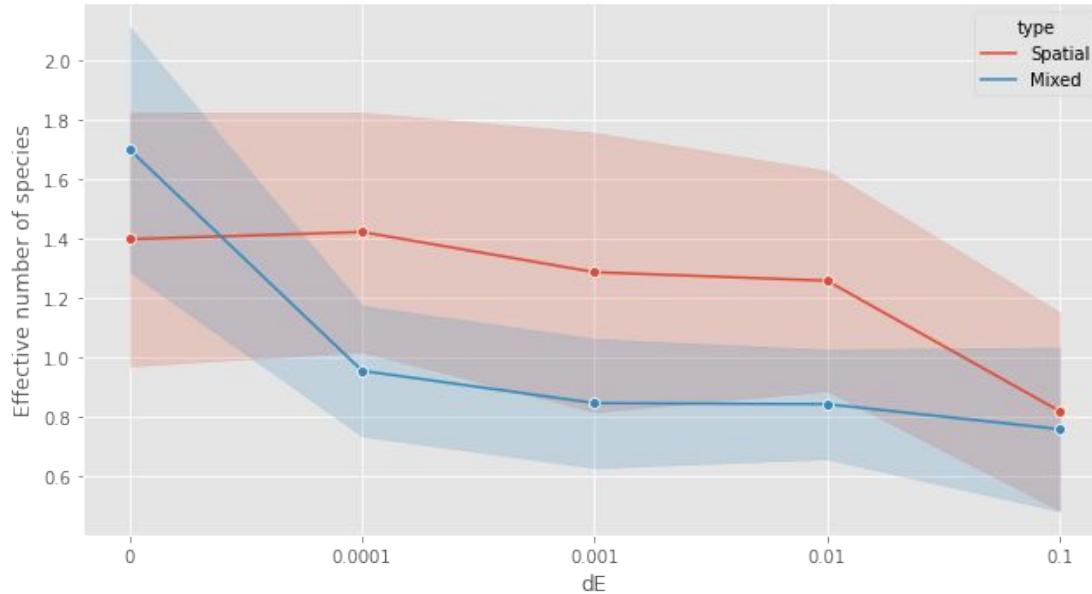
UNEQUAL ENERGY BUDGET

The condition for which the sum of the metabolic strategy coefficients should be equal to a constant E allows the violation of the CEP and the resulting increase of the system's biodiversity. Now we want to explore what will happen if this condition is relaxed and each population is characterized by a specific value of E . In particular we want:

$$\sum_i \alpha_{\sigma i} = E_{\sigma} \quad E_{\sigma} \sim \mathcal{N}(E, dE)$$

We want now to study the different behaviour of systems following the spatial model and the well-mixed one

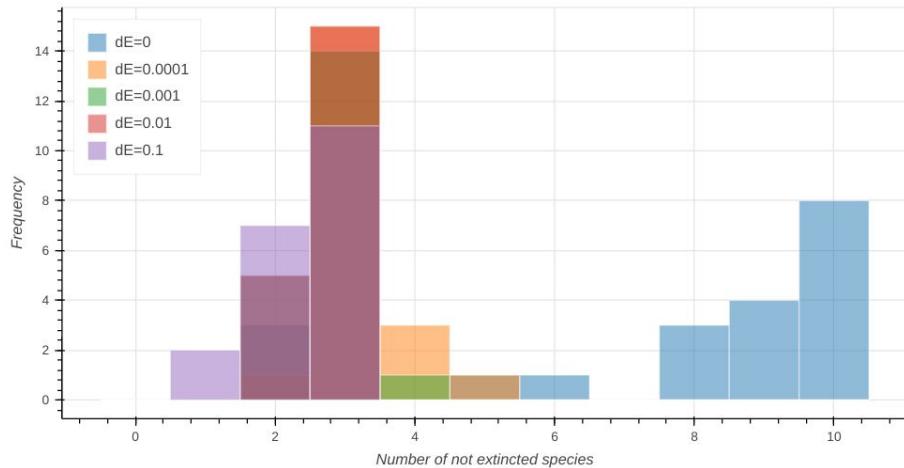
UNEQUAL ENERGY BUDGET



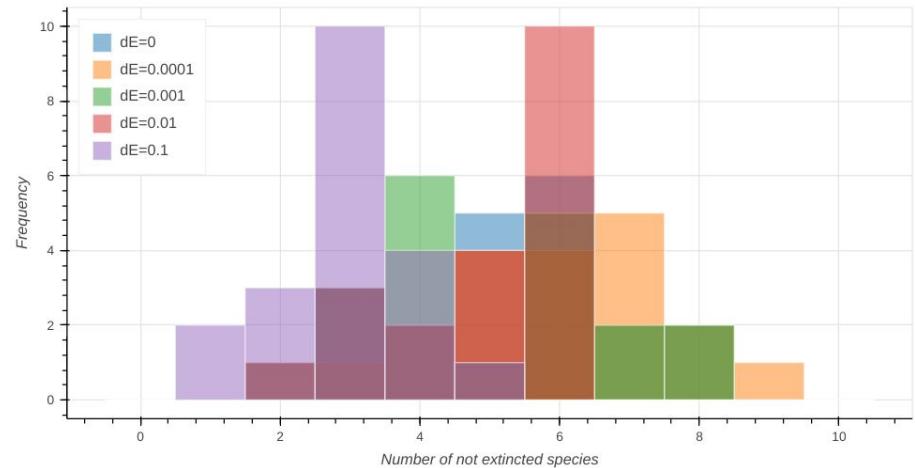
- For $dE=0$ the well-mixed case leads to a greater biodiversity
- As soon as dE becomes different from 0 the e.n.s. relative the the well-mixed case drastically drops.
- The spatial case biodiversity is almost constant for a wide range of dE
- For too large values of dE also the spatial system starts to fail
- The variability of the spatial case is significantly greater than the one of the well-mixed case, probably due to phenomenon of the oligotrophs

UNEQUAL ENERGY BUDGET

Well-mixed

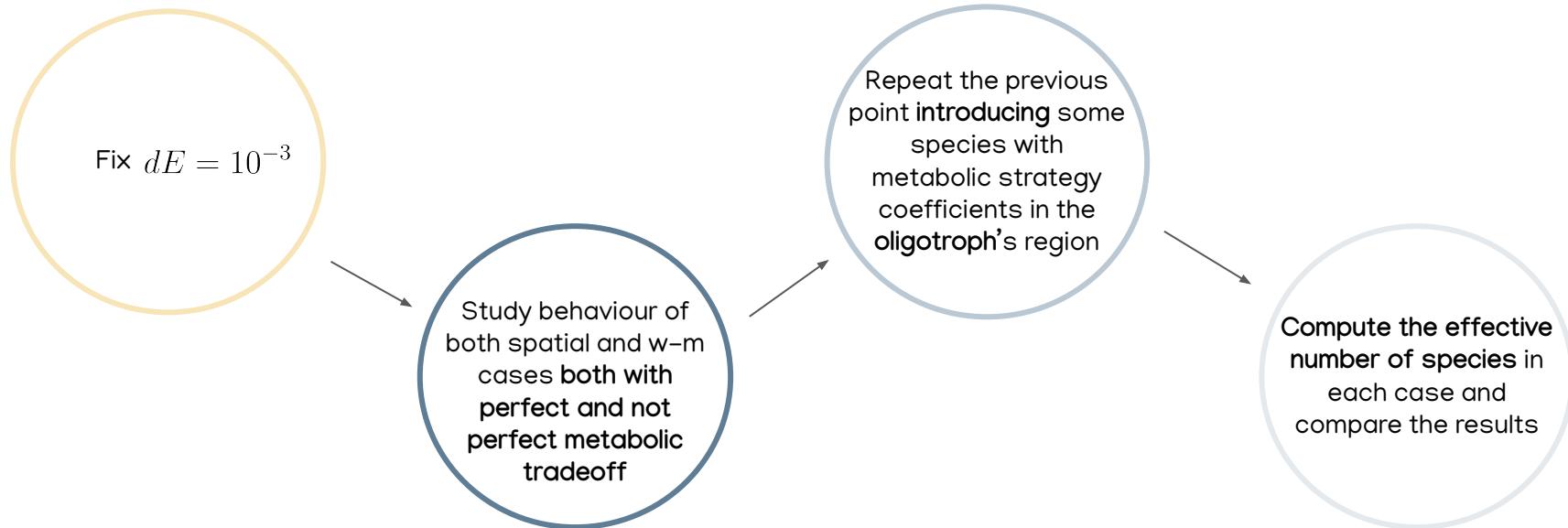


Spatial

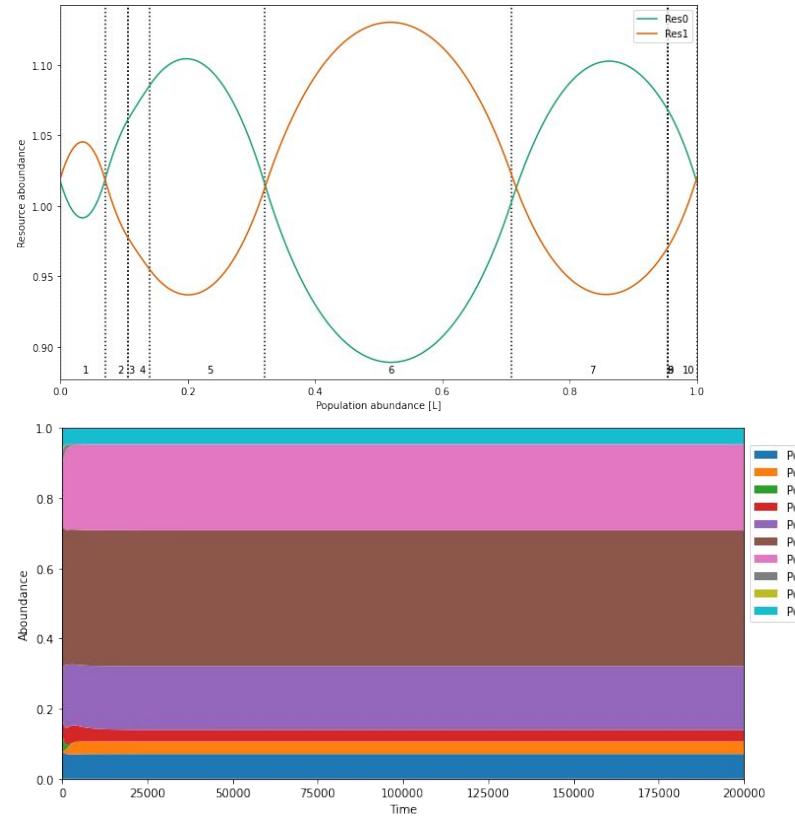
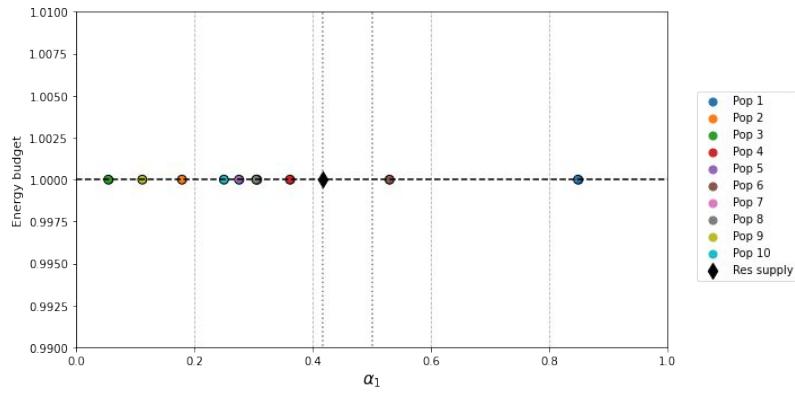


UNEQUAL ENERGY BUDGET

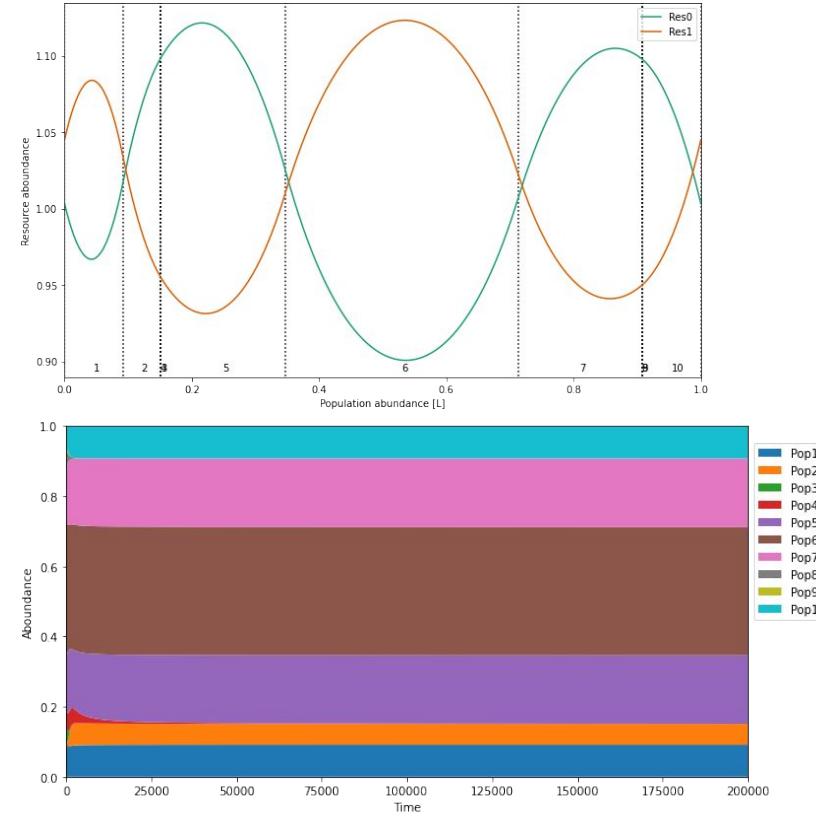
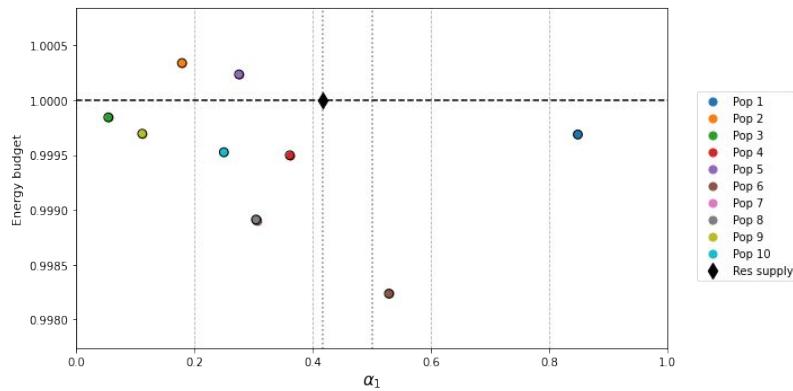
2 nutrients and presence of oligotrophs



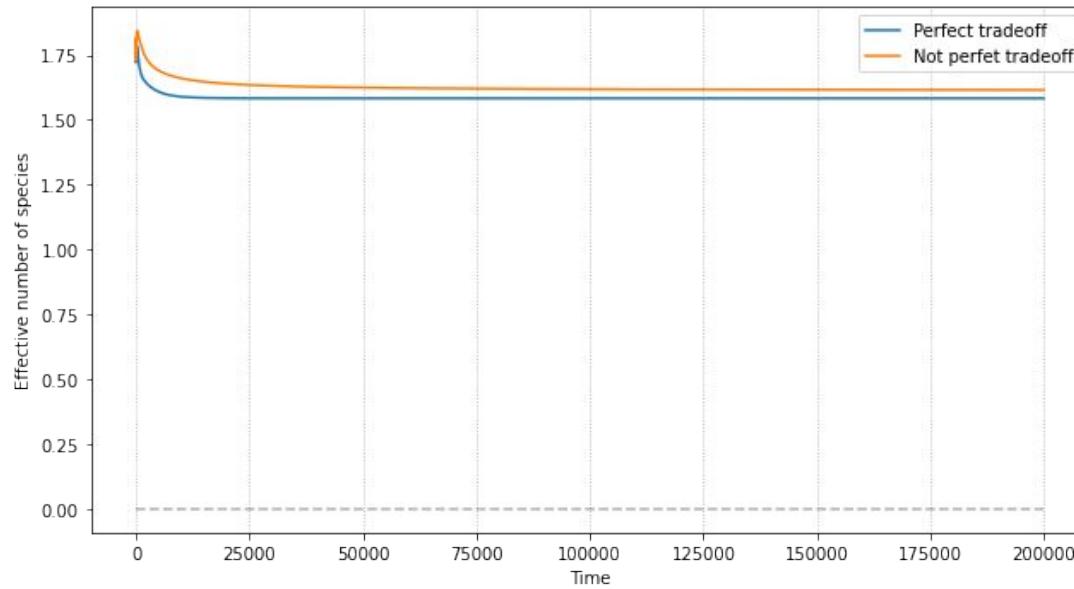
SPATIAL CASE: PERFECT METABOLIC TRADEOFF



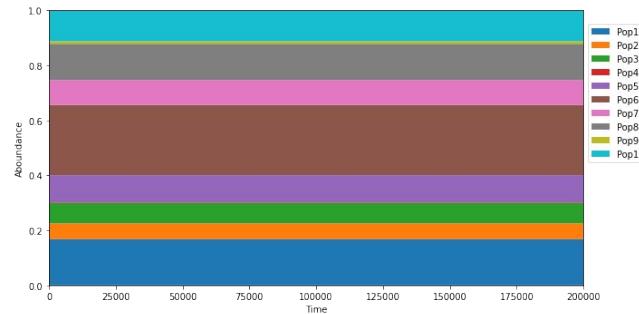
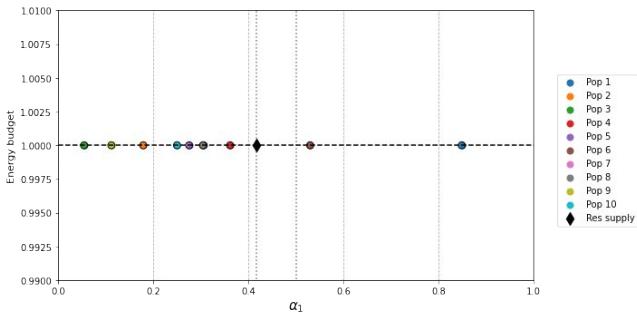
SPATIAL CASE: NOT PERFECT METABOLIC TRADEOFF



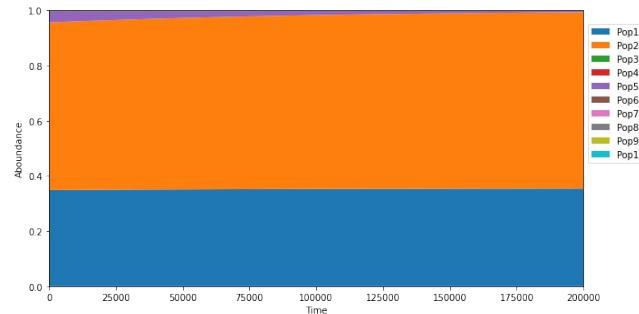
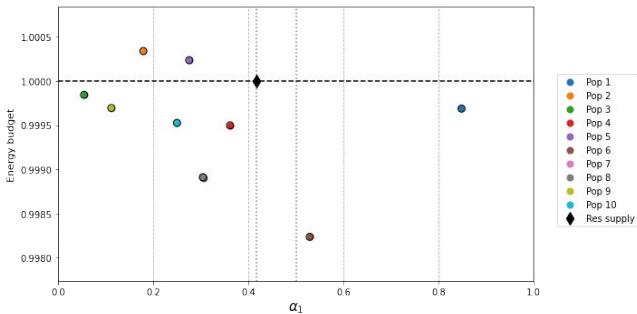
SPATIAL CASE: COMPARISON



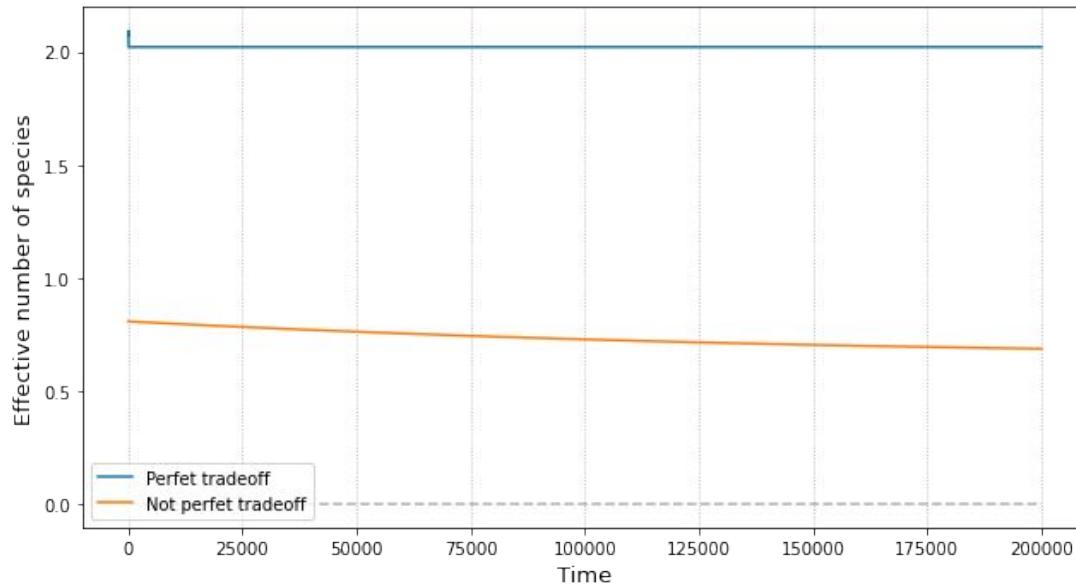
WELL-MIXED CASE



Not perfect
metabolic
tradeoff

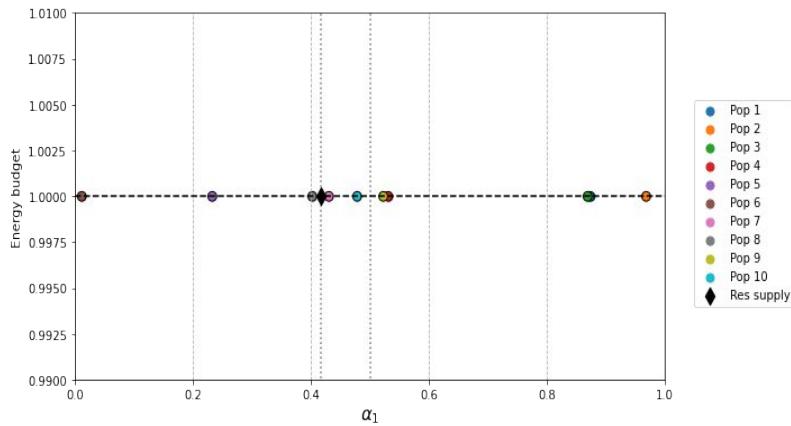


WELL-MIXED CASE: COMPARISON

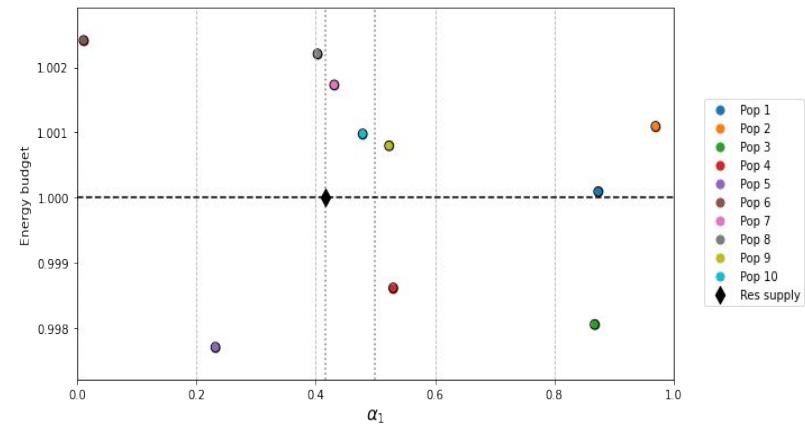


INTRODUCTION OF OLIGOTROPHS

Perfect metabolic tradoff



Not perfect metabolic tradoff

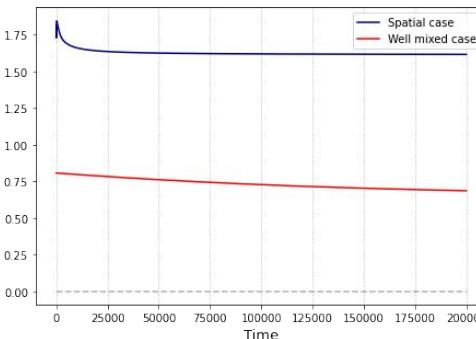
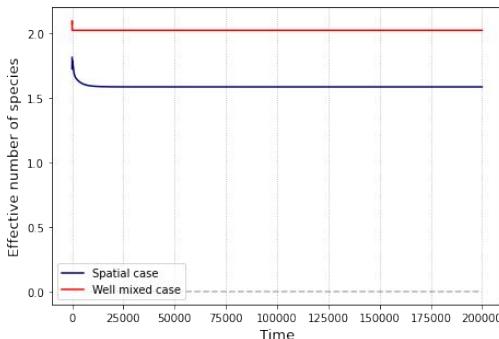


COMPARISON

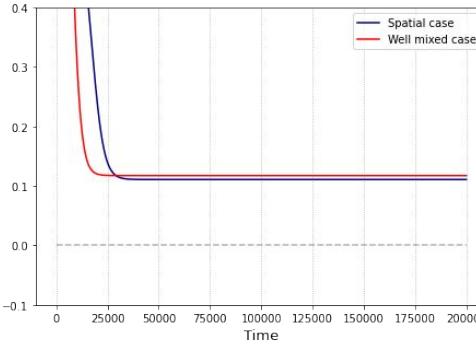
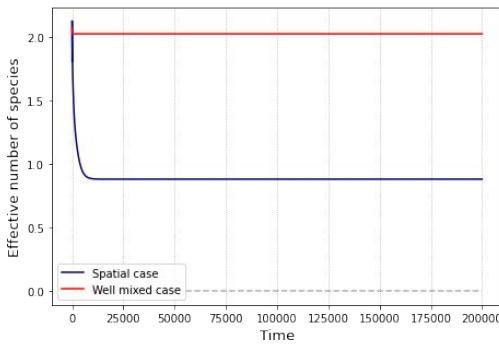
Perfect metabolic tradeoff

Not perfect metabolic tradeoff

No oligotrophs

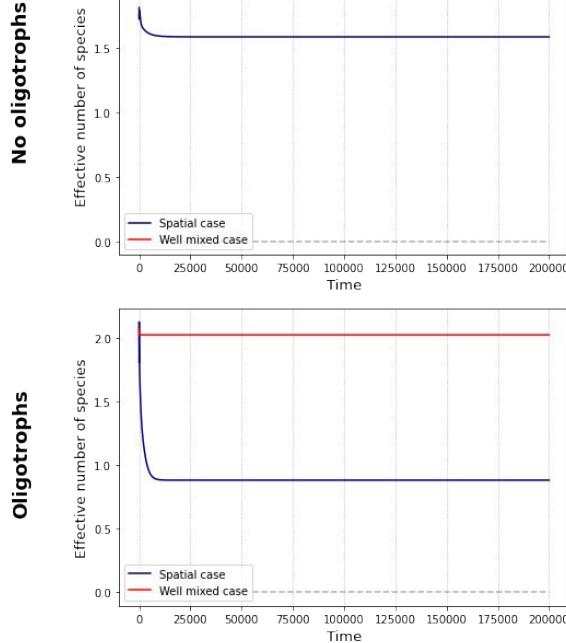


Oligotrophs

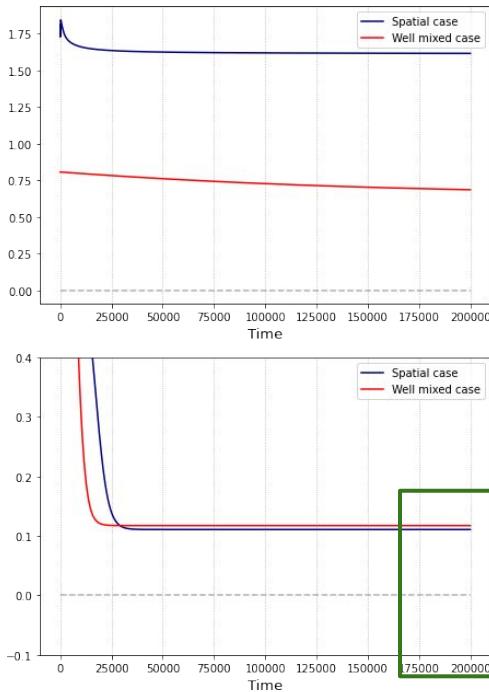


COMPARISON

Perfect metabolic tradeoff



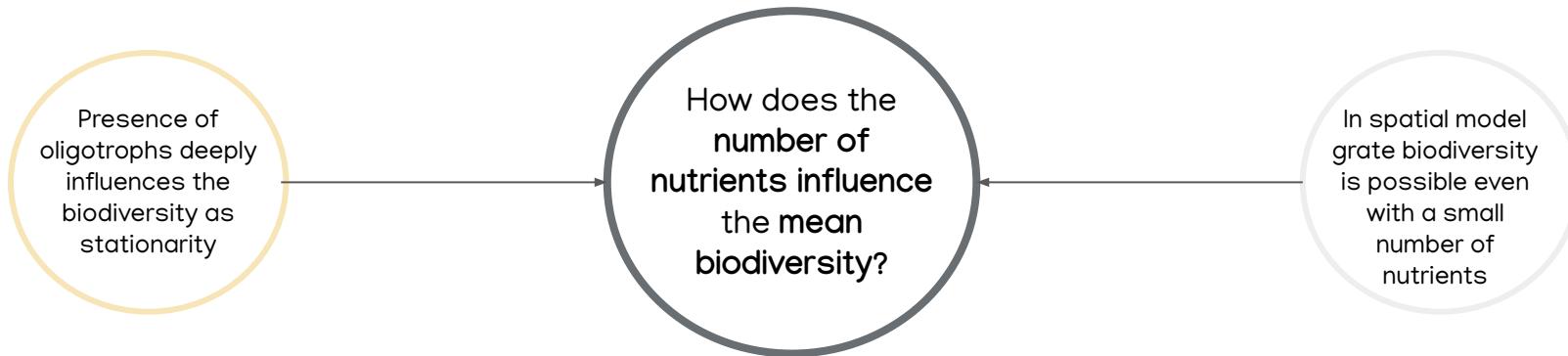
Not perfect metabolic tradeoff



In this case the w-m model surpasses, even if very lightly, the spatial case



VARIATION OF NUMBER OF NUTRIENTS



VARIATION OF NUMBER OF NUTRIENTS

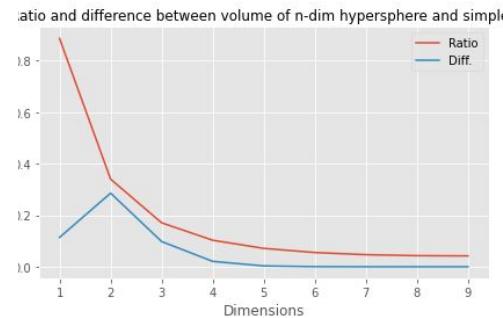
ANSATZ: the oligotroph's region in the metabolic strategies plane can be approximated as an hypersfere with diameter equal to the distance between the center of the corresponding hyper pyramid and the point corresponding to the supply rate d

Diameter		Volume
$d = \vec{S} - \vec{c} $		$V = \int_{\mathcal{C}} dV$
$c_i = \frac{E}{p} \quad i = 1, \dots, p$		$\mathcal{C} = \{x_i, i = 1, \dots, p - 1 : \sum_i x_i^2 < d/2\}$

VARIATION OF NUMBER OF NUTRIENTS

From math, the ratio between the volume of the hyperpyramid and the hypersphere decreases as the number of dimension in which they leave increase

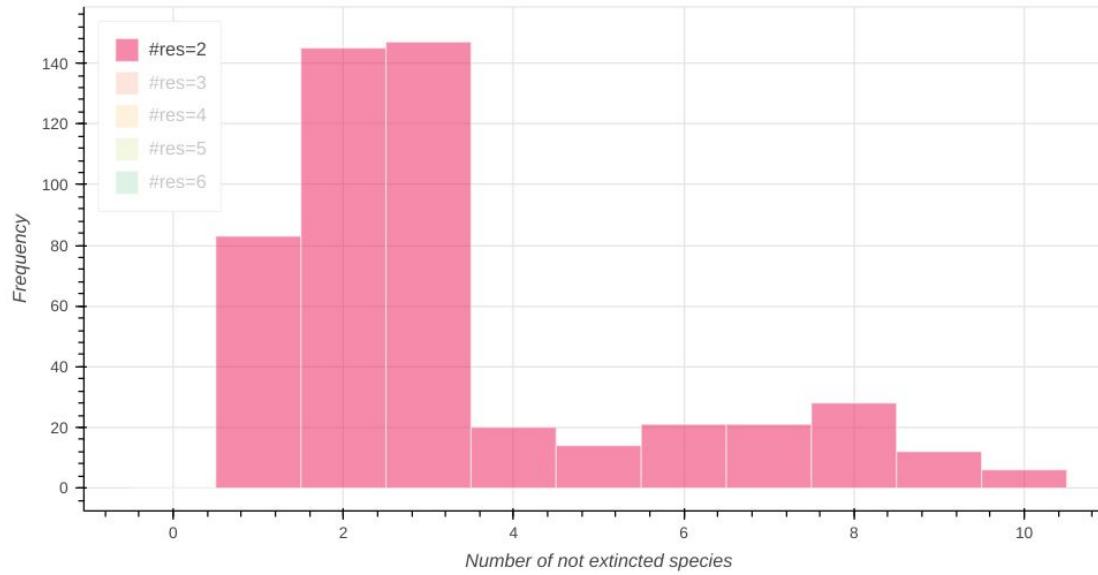
In our case the number of dimensions correspond to $p-1$



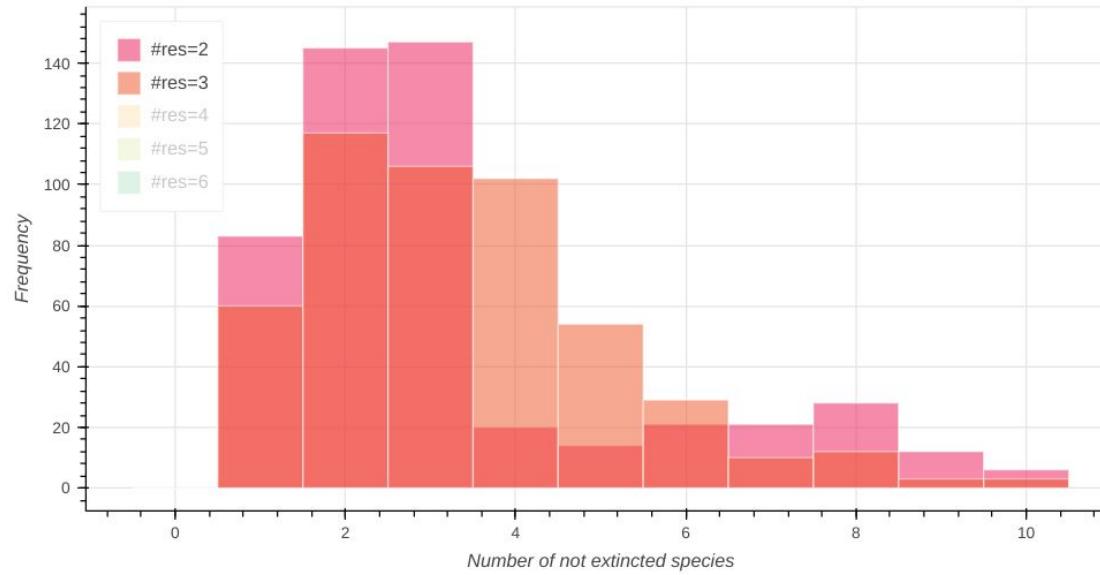
The probability that a random metabolic strategy lying in the $p-1$ dimensional simplex falls in the metabolic region is proportional to the ratio between the hypersphere and the simplex

The occurrence of an oligotroph becomes rarer as the number of nutrients increases, and so the biodiversity should increase

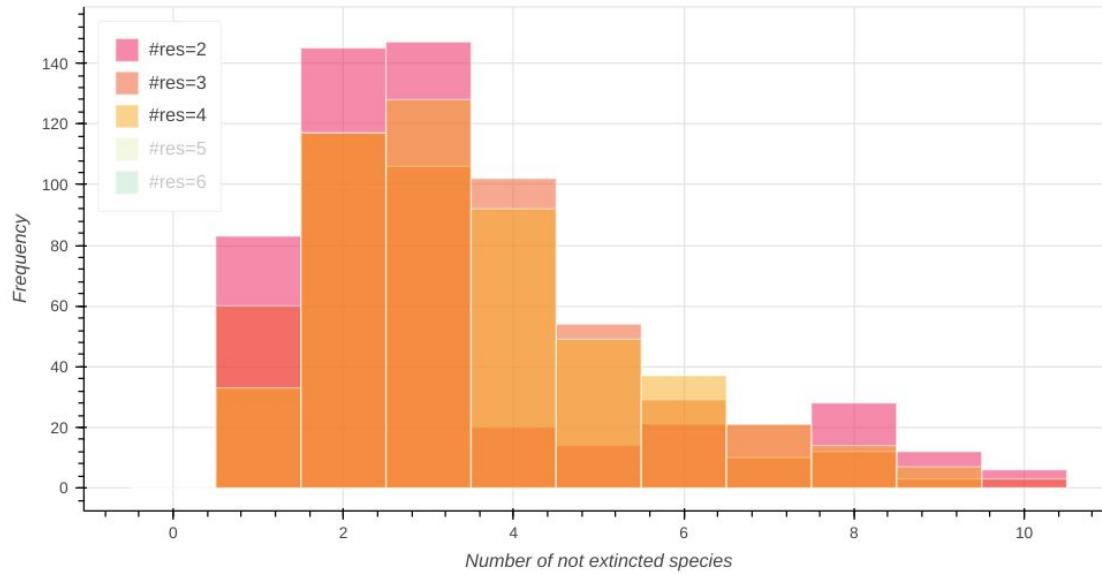
VARIATION OF NUMBER OF NUTRIENTS



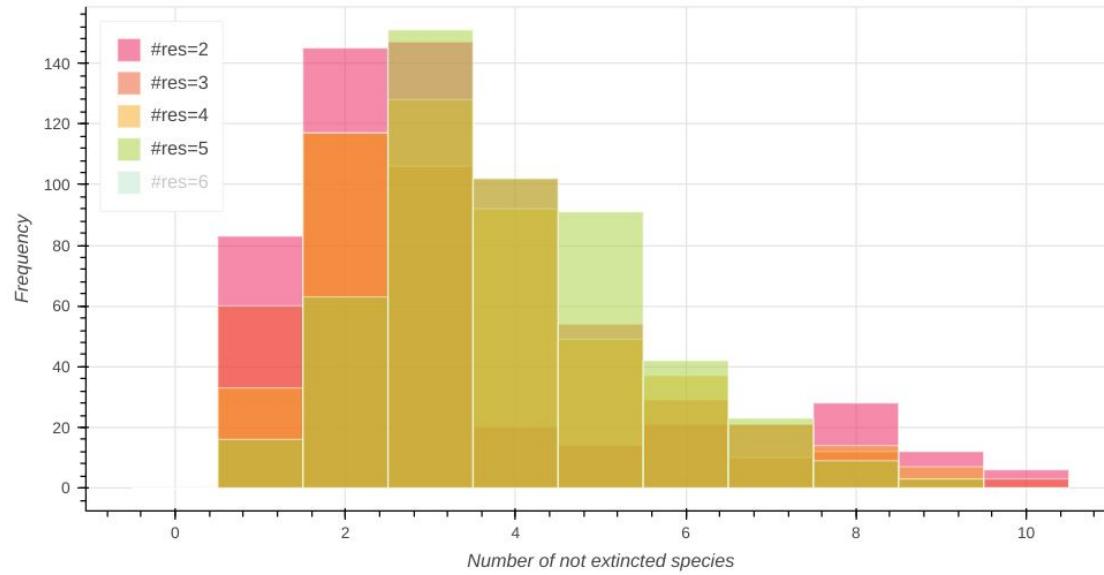
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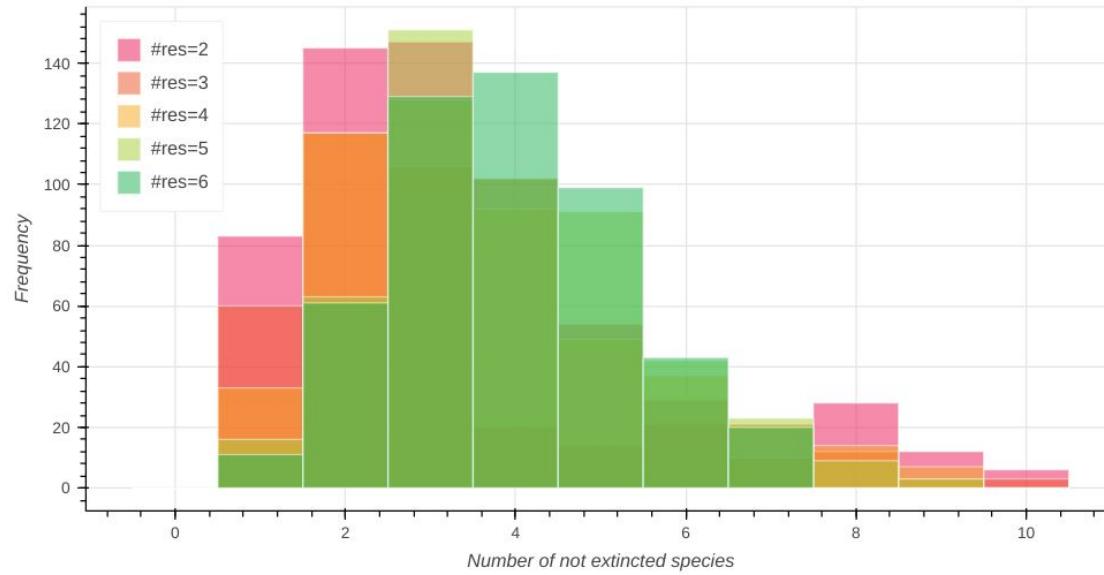
VARIATION OF NUMBER OF NUTRIENTS



VARIATION OF NUMBER OF NUTRIENTS

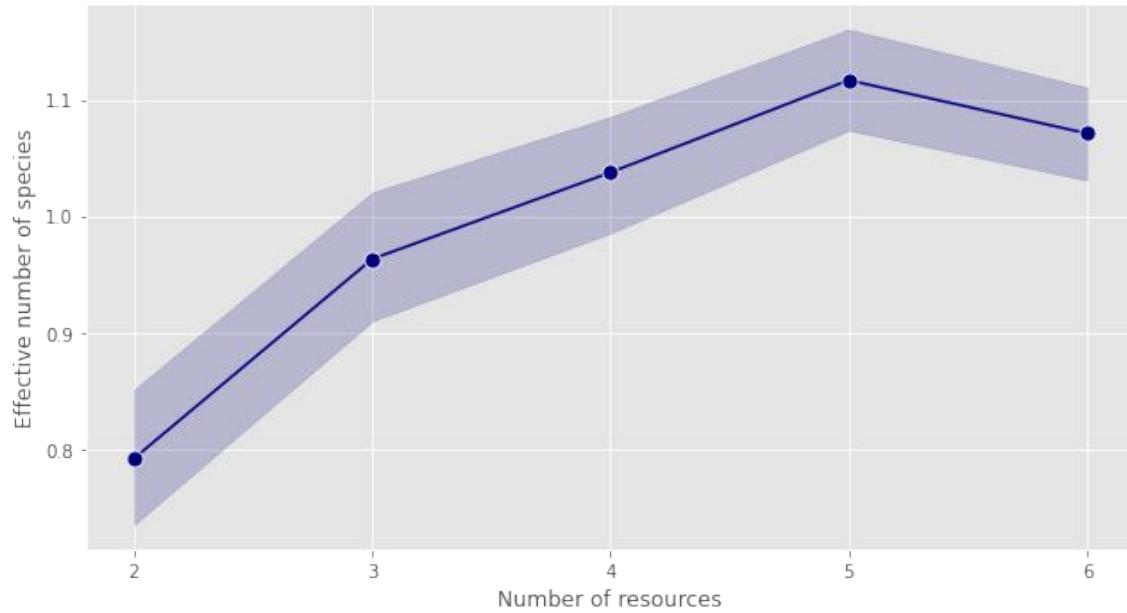


VARIATION OF NUMBER OF NUTRIENTS



VARIATION OF NUMBER OF NUTRIENTS

As expected as
the number of
nutrients
increase, also
the biodiversity
increase



CONCLUSIONS

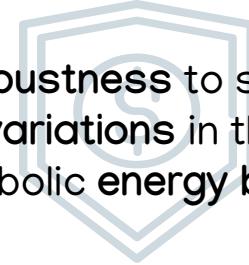
In general reduced mean biodiversity w.r.t. well mixed case



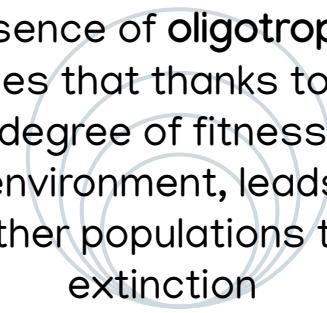
Small diffusion rates reduce mean biodiversity



Robustness to small variations in the metabolic energy budget



Presence of oligotrophs, species that thanks to their high degree of fitness with the environment, leads the other populations to extinction



THANKS!

KPI OVERVIEW

▲ PEOPLE

Is the closest planet of all

▲ SALES

Mars is a cold place

▲ MARKET

Jupiter is a gas giant



458K

Neptune is the farthest

7,520,000\$

Has a beautiful name

86%

Mars is a cold place

OUR TEAM



AMANDA RICHARDS

You can replace the image on the screen with your own



JENNIFER ADAMS

You can replace the image on the screen with your own

A PICTURE IS WORTH MORE THAN A THOUSAND WORDS



AWESOME WORDS

ICON PACK



RESOURCES

PHOTOS

- Cute girl with her hairstyle
- Front view of business people talking
- Girl
- Front view of business woman talking at phone

VECTORS

- Colorful weekly schedule template with flat design

ICON PACK

- Business Icon Pack

ALTERNATIVE RESOURCES

PHOTOS

- Men shaking hands
- Thoughtful young man sitting near laptop against wall with notes
- Cheerful colleagues looking at project on laptop in office
- Smiling couple sitting at desk with laptops against wall with notes
- Colleagues happy to work together
- Adult women working on new project together
- Businesswoman posing outdoors with tablet ad notepad
- Front view of businesswoman working on laptop in the office
- Group of businesspeople making plans on energy saving at workplace

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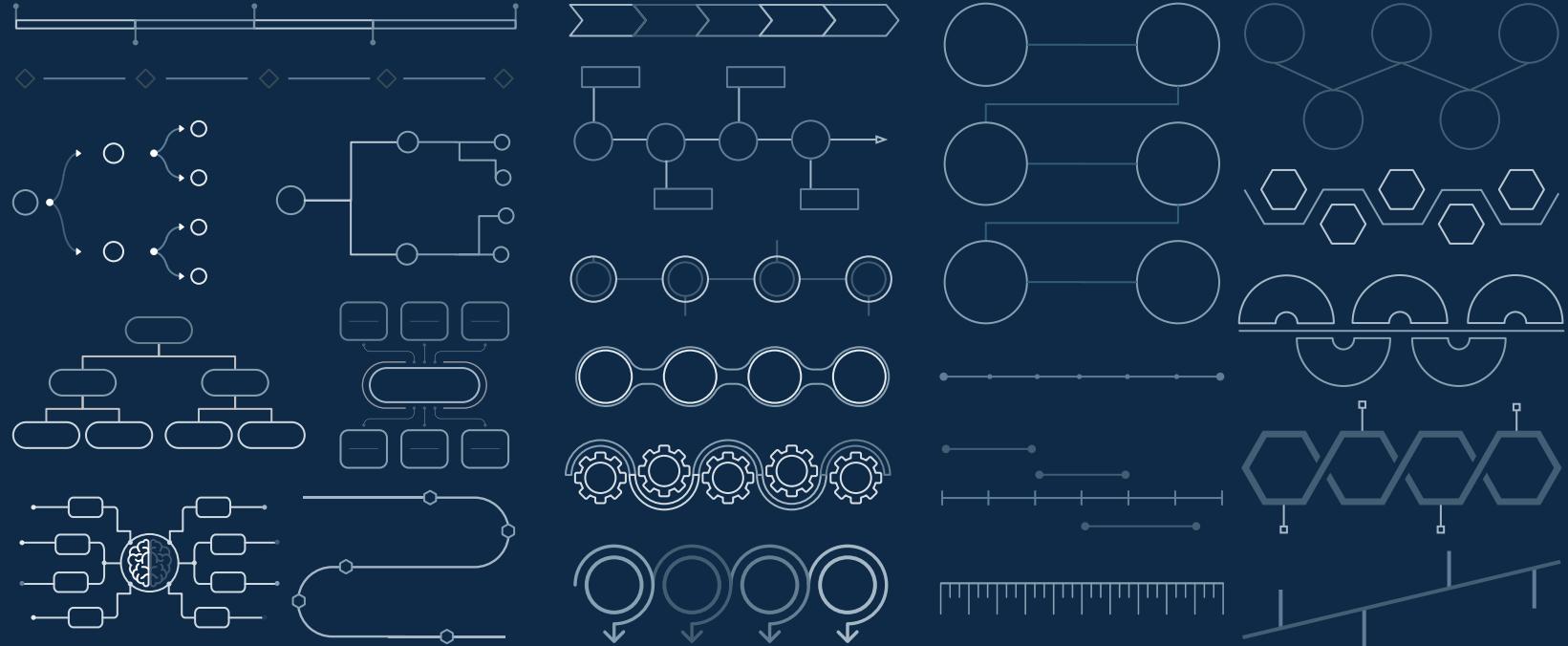
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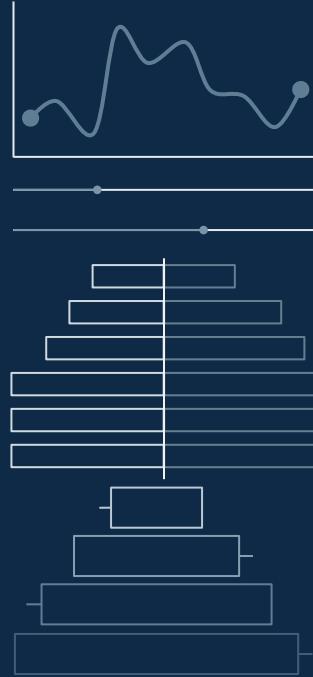
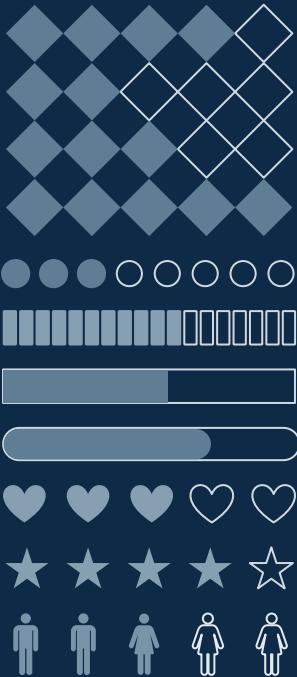
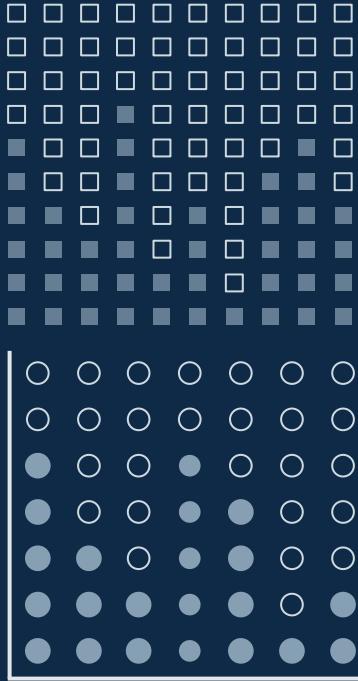
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