

V Southern-Summer School on Mathematical Biology

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Lecture III

São Paulo, January 2016



Outline



Competition

- Consider **competition** between two species.
- We say that two species compete if the presence of one of them is detrimental for the other, and vice versa.
- The underlying biological mechanisms can be of two kinds;
 - ▶ **exploitative competition**: both species compete for a limited resource.
 - ★ Its strength depends also on the resource .
 - ▶ **Interference competition**: one of the species actively interferes in the access to resources of the other .
 - ▶ Both types of competition may coexist.



Models for species in competition

- We are speaking of **inter-specific competition**
- **Intra-specific competition** gives rise to the models like the logistic that we studied in the first lecture.
- In a broad sense we can distinguish two kinds of models for competition:
 - ▶ **implicit**: that do not take into account the dynamics of the resources.
 - ▶ **explicit** where this dynamics is included.
 - ▶ Here is a pictorial view of the possible cases:

Competition

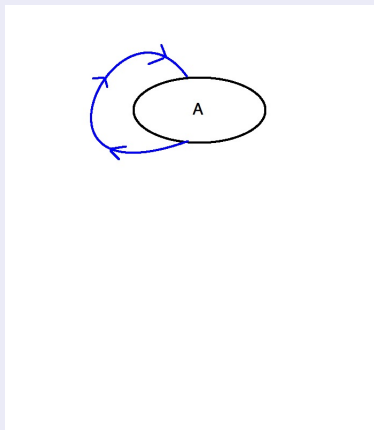


Figura : A single species. Only intra-specific competition indicated by the **blue** arrow

Competition

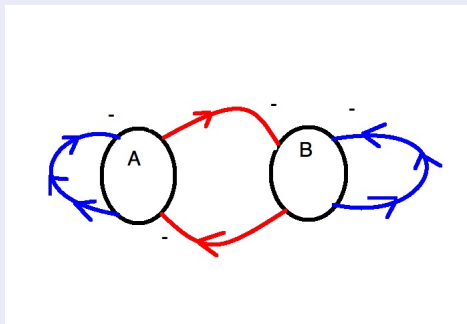


Figura : Two species. Besides intra-specific competition, both species compete. This is an implicit model as we do not even mention the resources. No distinction is made between exploitative or interference competition

Competition

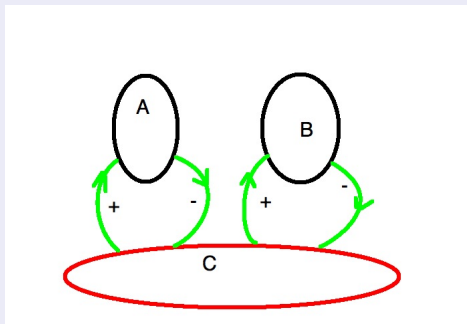


Figura : Two species (**A and B**) that feed on **C**. Intra-specific competition has been omitted, but may exist. Here we have an **explicit** model for **exploitative competition**. A interaction of **A and C** and between **B and C** is usually of the **antagonistic** kind.

Competition

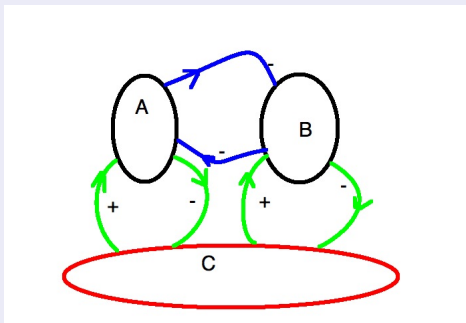


Figura : Two species (**A and B**) that feed on **C** but also interfere. Intra-specific competition has again been omitted, but may exist. We have an **explicit** model with both exploitative and interference competition.

Competition

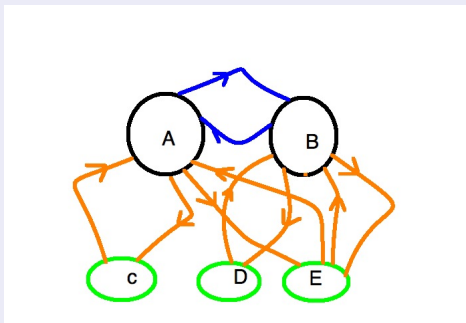


Figura : A model where two species, **A and B**, compete for resources, (**AND**) they have also exclusive resources (**A ↔ C**) e (**B ↔ D**). And interference competition is also indicated.

Mathematical Model

- Let us begin with the simplest case:
 - ▶ **Two species,**
 - ▶ **Implicit competition,**
 - ▶ **intra-specific competition taken into account.**
- We proceed using the same rationale that was used for the predator-prey system.

Lotka-Volterra model for competition

Let N_1 and N_2 be the two species in question.

Lotka-Volterra model for competition

Each of them increases logistically in the absence of the other:

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} \right]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} \right]$$

where r_1 and r_2 are the intrinsic growth rates and K_1 and K_2 are the carrying capacities of both species in the absence of the other..

Lotka-Volterra model for competition

We introduce the mutual detrimental influence of one species on the other:

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - aN_2 \right]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - bN_1 \right]$$

Lotka-Volterra model for competition

Or, in the more usual way :

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right]$$



Lotka-Volterra model for competition

Or, in the more usual way:

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - \overbrace{b_{12}}^{\downarrow} \frac{N_2}{K_1} \right]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - \overbrace{b_{21}}^{\downarrow} \frac{N_1}{K_2} \right]$$

where b_{12} and b_{21} are the coefficients that measure the **strength of the competition between the populations**.

Lotka-Volterra model for competition

This is a Lotka-Volterra type model for competing species. Pay attention to the fact that both interaction terms come in with negative signs. All the constants $r_1, r_2, K_1, K_2, b_{12}$ and b_{21} are positive.

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right]$$

Let's now try to analyze this system of two differential equations .

Analyzing the model I

We will first make a change of variables, by simple re-scalings.

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right]$$

Define:

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right]$$

In other words, we are measuring populations in units of their carrying capacities and the time in units of $1/r_1$.



Analyzing the model II

The equations in
the new variables.

$$\frac{du_1}{dt} = u_1 \left[1 - u_1 - b_{12} \frac{K_2}{K_1} u_2 \right]$$

$$\frac{du_2}{dt} = \frac{r_2}{r_1} u_2 \left[1 - u_2 - b_{21} \frac{K_1}{K_2} u_1 \right]$$

Analyzing the model III

Defining:

$$\frac{du_1}{dt} = u_1 [1 - u_1 - a_{12}u_2]$$

$$a_{12} = b_{12} \frac{K_2}{K_1},$$

$$a_{21} = b_{21} \frac{K_1}{K_2}$$

$$\rho = \frac{r_2}{r_1}$$

$$\frac{du_2}{dt} = \rho u_2 [1 - u_2 - a_{21}u_1]$$

we get these equations.
It's a system of nonlinear ordinary differential equations.

We need to study the behavior of their solutions



Analyzing the model IV

$$\frac{du_1}{dt} = u_1 [1 - u_1 - a_{12}u_2]$$

No explicit solutions!

$$\frac{du_2}{dt} = \rho u_2 [1 - u_2 - a_{21}u_1]$$

- We will develop a *qualitative* analysis of these equations.
- Begin by finding the points in the $(u_1 \times u_2)$ plane such that:

$$\frac{du_1}{dt} = \frac{du_2}{dt} = 0,$$

the **fixed points**.

Analyzing the model V

- $$\frac{du_1}{dt} = 0 \Rightarrow u_1 [1 - u_1 - a_{12}u_2] = 0$$

- $$\frac{du_2}{dt} = 0 \Rightarrow u_2 [1 - u_2 - a_{21}u_1] = 0$$

Analyzing the model V



$$u_1 [1 - u_1 - a_{12} u_2] = 0$$



$$u_2 [1 - u_2 - a_{21} u_1] = 0$$

- These are two algebraic equations for (u_1 e u_2).
- We **FOUR** solutions. Four fixed points.

Fixed points

$$u_1^* = 0$$

$$u_2^* = 0$$

$$u_1^* = 0$$

$$u_2^* = 1$$

$$u_1^* = 1$$

$$u_2^* = 0$$

$$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}}$$

$$u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}}$$

The relevance of those fixed points depends on their **stability**. Which, in turn, depend on the values of the parameters a_{12} e a_{21} . We have to proceed by a phase-space analysis, calculating community matrixes and finding eigenvalues.....take a look at *J.D. Murray (Mathematical Biology)*.

Stability

If $a_{12} < 1$ and $a_{21} < 1$

$$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}}$$

$$u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}}$$

is **stable**.

If $a_{12} < 1$ and $a_{21} > 1$

$$u_1^* = 1 \text{ e } u_2^* = 0$$

is **stable**.

If $a_{12} > 1$ and $a_{21} > 1$

$$u_1^* = 1 \text{ e } u_2^* = 0$$

$$u_1^* = 0 \text{ e } u_2^* = 1$$

are **both stable**.

If $a_{12} > 1$ and $a_{21} < 1$

$$u_1^* = 0 \text{ e } u_2^* = 1$$

is **stable**.

The stability of the fixed points depends on the values of a_{12} and a_{21} .

Phase space

- To have a more intuitive understanding of the dynamics it is useful to consider the trajectories in the phase space
- For every particular combination of a_{12} and a_{21} – but actually depending if they are smaller or greater than 1 – ,we will have a qualitatively different phase portrait.

Phase Space II

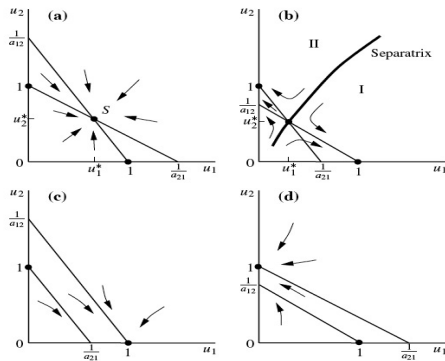


Figura : The four cases. The four different possibilities for the phase portraits.

Coexistence

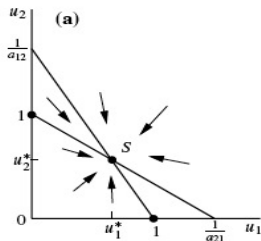


Figura : $a_{12} < 1$ and $a_{21} < 1$. The fixed point u_1^* and u_2^* is stable and represents the coexistence of both species. It is a **global attractor**.

Exclusion

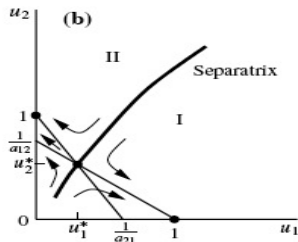


Figura : $a_{12} > 1$ and $a_{21} > 1$. The fixed point u_1^* and u_2^* is unstable. The points (1,0) and (0,1) are stable but have *finite basins of attraction*, separated by a *separatrix*. The stable fixed points represent *exclusion* of one of the species.

Exclusion

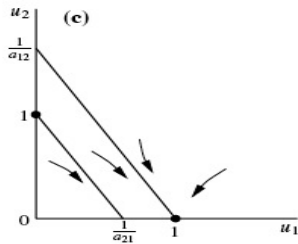


Figura : $a_{12} < 1$ and $a_{21} > 1$. The only stable fixed is $(u_1 = 1, u_2 = 0)$. A global attractor. Species (2) is excluded.

Exclusion

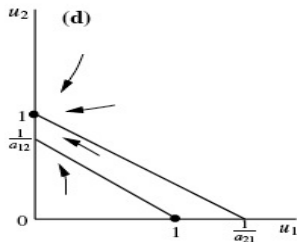


Figura : This case is symmetric to the previous. $a_{12} > 1$ and $a_{21} < 1$. The only stable fixed point is $(u_1 = 1, u_2 = 0)$. A global attractor. Species (1) is excluded



Interpretation of the results

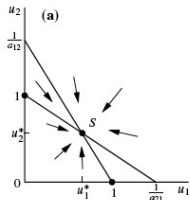
- What is the meaning of these results?
- Let us recall the meaning of a_{12} and a_{21} :

$$\frac{du_1}{dt} = u_1 [1 - u_1 - a_{12}u_2]$$

$$\frac{du_2}{dt} = \rho u_2 [1 - u_2 - a_{21}u_1]$$

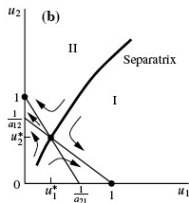
- ▶ a_{12} is a measure of the influence of species 2 on species 1. How detrimental 2 is to 1.
- ▶ a_{21} measures the influence of species 1 on species 2. How detrimental 1 is to 2.
- So, we may translate the results as:
 - ▶ $a_{12} > 1 \Rightarrow$ 2 competes strongly with 1 for resources.
 - ▶ $a_{21} > 1 \Rightarrow$ 1 competes strongly with 2 for resources.
- This leads us to the following rephrasing of the results :

If $a_{12} < 1$ and $a_{21} < 1$
The competition is **weak** and both can coexist.



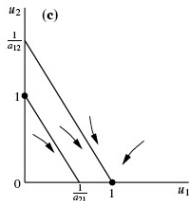
If $a_{12} > 1$ and $a_{21} > 1$

The competition is mutually **strong**. One species always excludes the other. Which one "wins" depends on initial conditions.



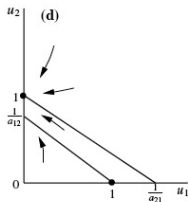
If $a_{12} < 1$ e $a_{21} > 1$

Species 1 is not strongly affected by species 2. But species 2 is affected strongly by species 1. Species 2 is eliminated, and species 1 attains its carrying capacity.



Se $a_{12} > 1$ e $a_{21} < 1$

This is symmetric to the previous case. Species 1 is eliminated and Species 2 attains its carrying capacity



Competitive exclusion

- In summary: the mathematical model predicts patterns of exclusion. Strong competition always leads to the exclusion of a species
- Coexistence is only possible with weak competition.
- The fact that a stronger competitor eliminates the weaker one is known as the **competitive exclusion principle**.



Georgiy F. Gause (1910-1986), Russian biologist, was the first to state the principle of competitive exclusion (1932).

Paramecium

The experiences of G.F. Gause were performed with a protozoa group called *Paramecia*.

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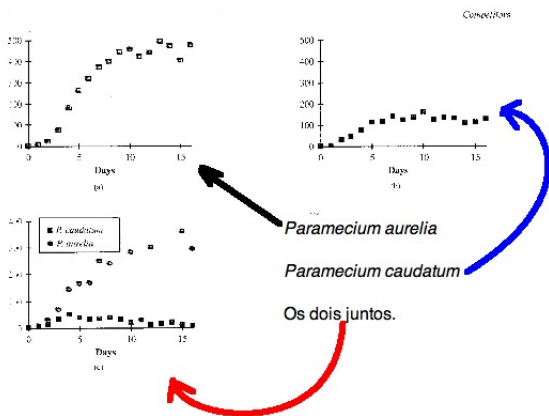
Paramecium

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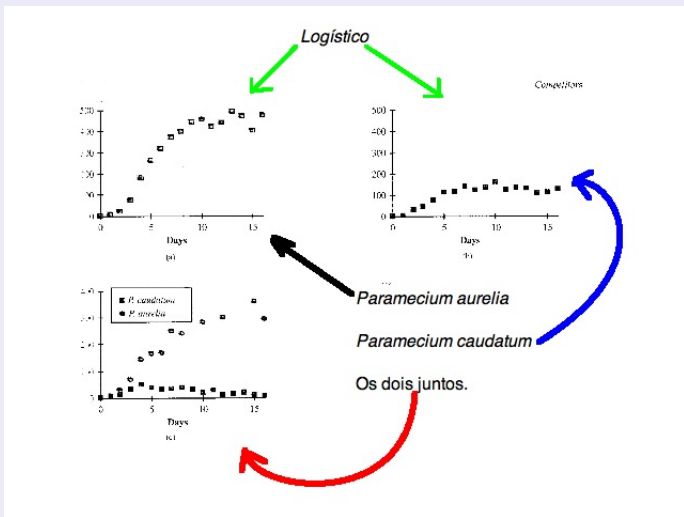
Gause considered two of them: *Paramecium aurelia* e *Paramecium Caudatum*. They were allowed to grow initially separated, with a logistic like growth.

When they grow in the same culture, *P. aurelia* survives and *P. caudatum* is eliminated.

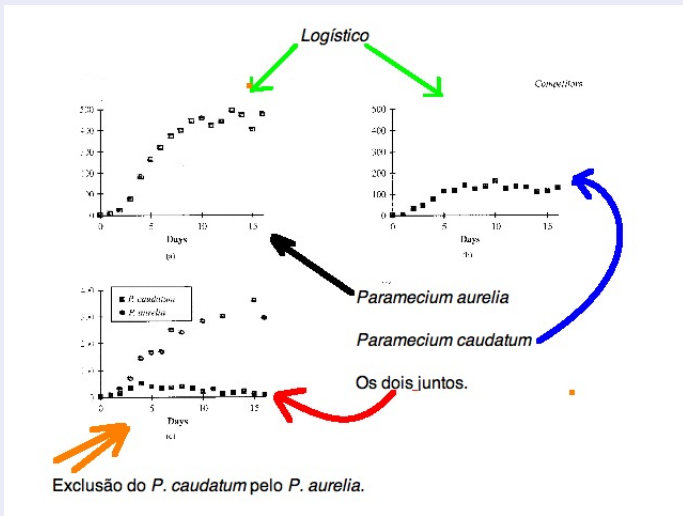
Paramecium



Paramecium



Paramecium



Ants

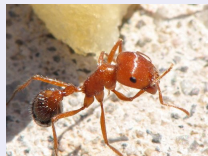


Figura : The Argentinean ant (*Linepithema humile*) and the Californian one (*Pogonomyrmex californicus*)

- The introduction of the Argentinean ant in California had the effect to exclude *Pogonomyrmex californicus*.
- Here is a plot with data....

Ants II

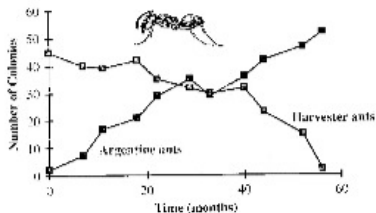
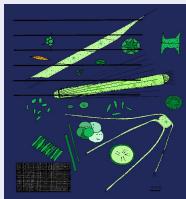


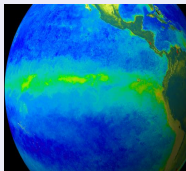
Figura : The introduction of the Argentinean ant in California had the effect of excluding *Pogonomyrmex californicus*

Plankton

In view of the principle of competitive exclusion, consider the situation of *phytoplankton*.



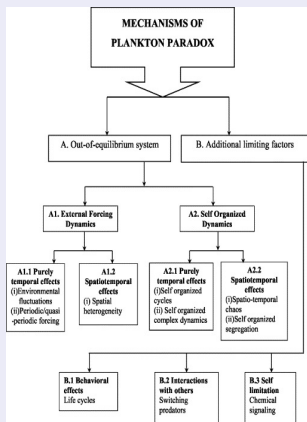
- Phytoplankton are organisms that live in seas and lakes, in the region where there is light.
- You won't see a phytoplankton with naked eye..
- You can see only the visual effect of a large number of them.
- It needs light + inorganic molecules.



The Plankton Paradox

- The plankton paradox consists of the following:
- There are many species of phytoplankton. It used a very limited number of different resources. Why is there no competitive exclusion?

One paradox, many possible solutions



- Competitive exclusion is a property of the fixed points. But if the environment changes, the equilibria might not be attained. We are always in transient dynamics.
- We have considered no spatial structure. Different regions could be associated with different limiting factors, and thus could promote diversity.
- Effects of trophic webs.

References

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- F. Brauer e C. Castillo-Chavez: *Mathematical Models in Population Biology and Epidemiology* (Springer, 2001).
- N.F. Britton: *Essential Mathematical Biology* (Springer, 2003).
- R. May e A. McLean: *Theoretical Ecology*, (Oxford, 2007).
- N.J. Gotelli: *A Primer of Ecology* (Sinauer, 2001).
- G.E. Hutchinson: *An Introduction to Population Ecology* (Yale, 1978).



Online Resources

- <http://www.ictp-saifr.org/mathbio5>
- <http://ecologia.ib.usp.br/ssmb/>

Thank you for your attention