

Sistemas Dinâmicos

Dinâmica de População e
Epidemiologia

DINÂMICA DE POPULAÇÕES

MODELO MALTHUSIANO

The simplest law

- The simplest law governing the time variation of the size of a population



$$\frac{dN(t)}{dt} = rN(t)$$

- where $N(t)$ is the number of individuals in the population and r is the intrinsic growth rate of the population, sometimes called the *Malthusian parameter*.

Exponential Growth

The solution

The solution to the Malthusian equation is just:

$$N(t) = N_0 e^{rt}$$

- This equation predicts exponential growth.
- Obviously impossible!

How long would take to cover the whole earth with a thin film of *E. coli*?

MODELO DISCRETO

- In the models considered so far, time is continuous.. Quite natural!
- We thus suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defined generations, often regulated by the seasons of the year.
- Flowers, for instance. Certain insects. Fruits. There is no point to speak about continuous time. We rather say "in year one population was N_1 , in year two, N_2 , and so on.
- So, it is natural to consider:

$$\underbrace{N_{t+1} = \alpha N_t}$$

Equivalent to the Malthusian equation

EXEMPLOS

- The history of human population growth

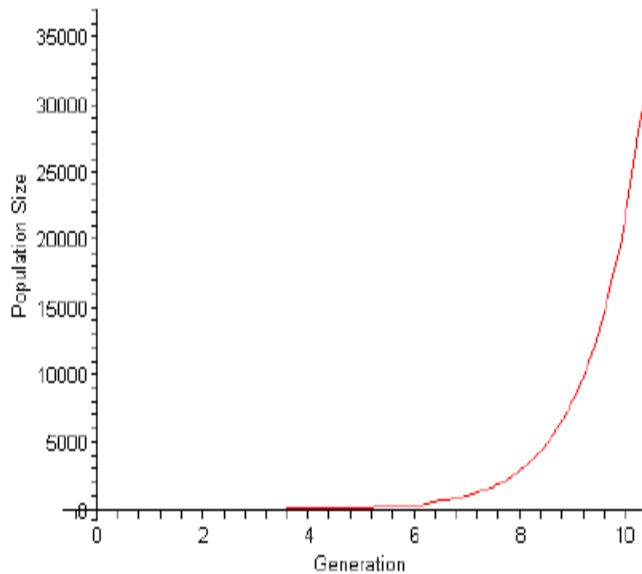
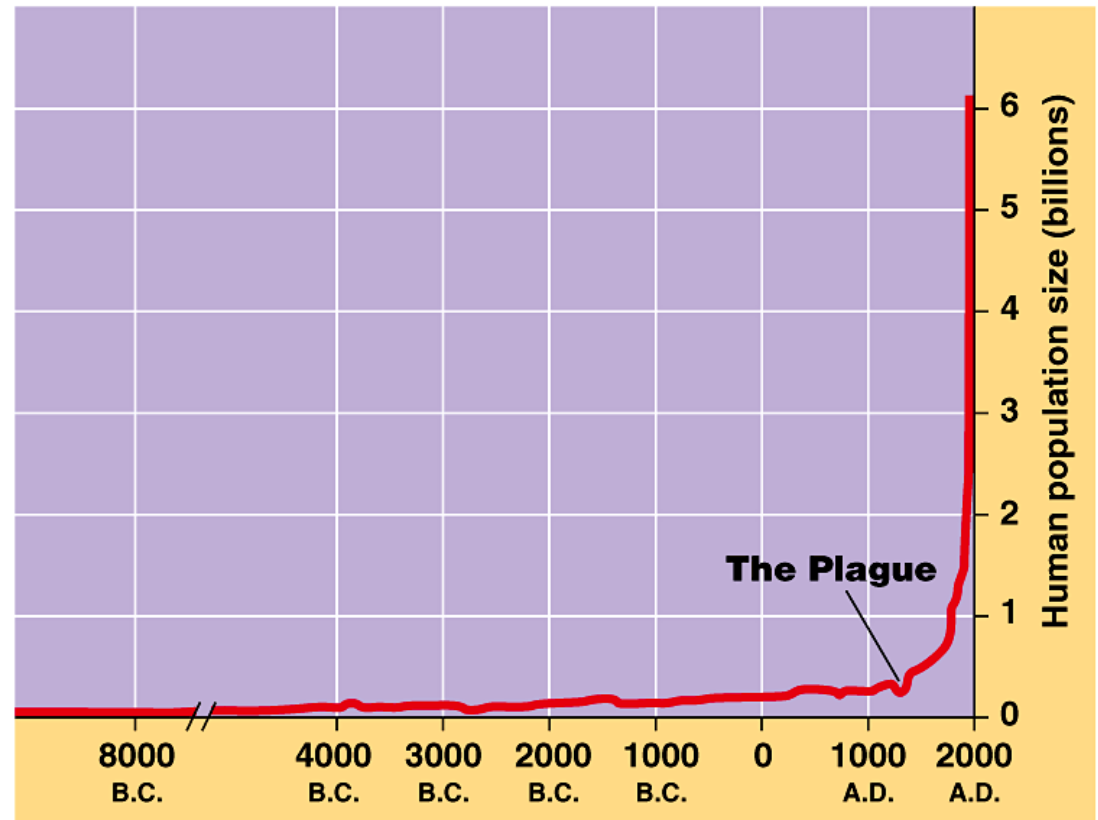
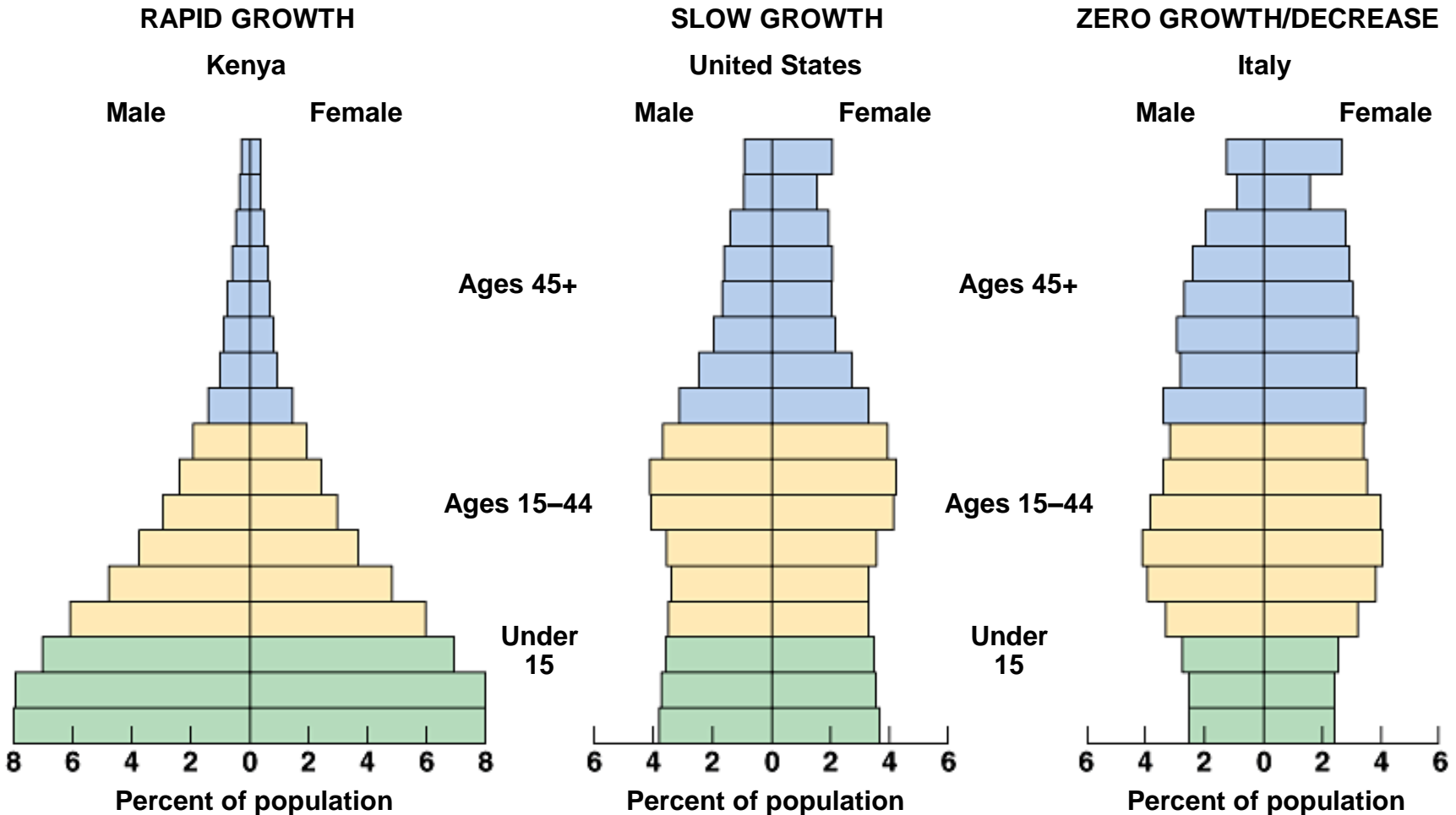


Figura : (*Escherichia coli*) on a Petri dish



- The age structure of a population is the proportion of individuals in different age-groups



Also reveals social conditions, status of women

Figure 35.9B

MODELO LOGISTICO

- We will further postulate that there is an upper limit for the number of beings that can occupy a finite portion of space.
- The simplest way to introduce this mathematically is to modify the Malthusian equation :

$$\frac{dN}{dt} = rN(1 - N/K)$$

- The term $-N^2/K$ is always negative (we assume $K > 0$), \Rightarrow it contributes negatively to $\frac{dN}{dt}$ \Rightarrow it tends to slow down growth.
- For $N/K \ll 1$, we may take $1 - N/K \sim 1$ and we recover the Malthusian equation.

MODELO LOGISTICO

- The quadratic term (rN^2/K) in the logistic equation

$$\frac{dN}{dt} = rN(1 - N/K),$$

models the internal competition in a population for vital resources as:

- Space,
- Food .
- This is called *intra-specific competition*

The constant K that appears in the logistic equation is usually known by *carrying capacity*.

- The carrying capacity is "phenomenological parameter" that depends on the particular environment, on the species and all circumstances affecting population maintenance.

MODELO LOGISTICO

Water lilies on a pond, compete for space:



Trees in the Amazonian forest compete for light:



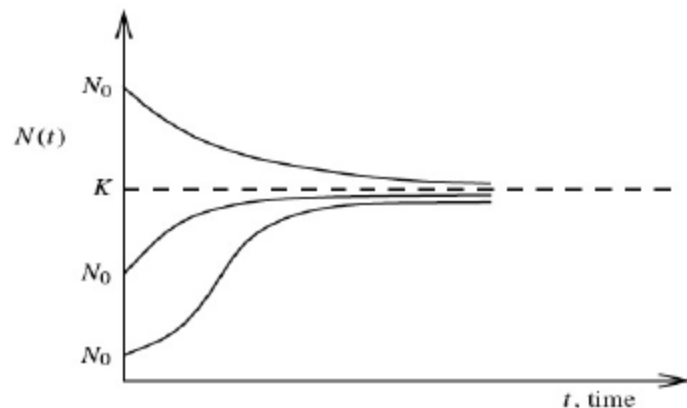
Foto: Ester Melo Nogueira



- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.
- Just take $dt = dN/(rN(1 - n/K))$, integrate both sides and get:

$$N(t) = \frac{N_0 K e^{rt}}{[K + N_0(e^{rt} - 1)]}$$

- Here is a plot of the solution, for different values of N_0 :



Temporal evolution of a population described by solution of the logistic
 Each curve corresponds to a different initial condition. For all initial
 N_0 , $t \rightarrow \infty$, we have $N \rightarrow K$

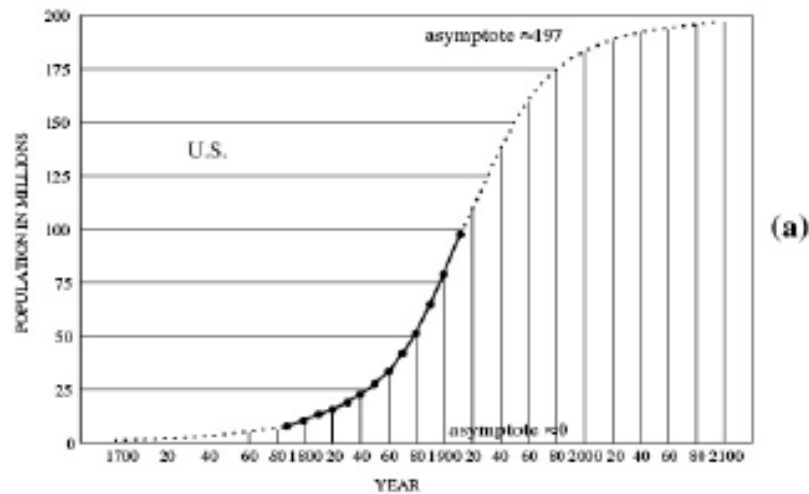


Figura : The population of USA . Until 1920, the growth is well approximated by an exponential.



DUAS FACES DO MODELO LOGISTICO

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

- It's too simple
- It does not model more complex biological facts

So, why should I like the logistic equation?

It's a kind of minimal model whereupon we can build more sophisticated ones.

- To go beyond the logistic, but still in the context of single species dynamics, we consider:

$$\frac{dN(t)}{dt} = \mathcal{F}(N)$$

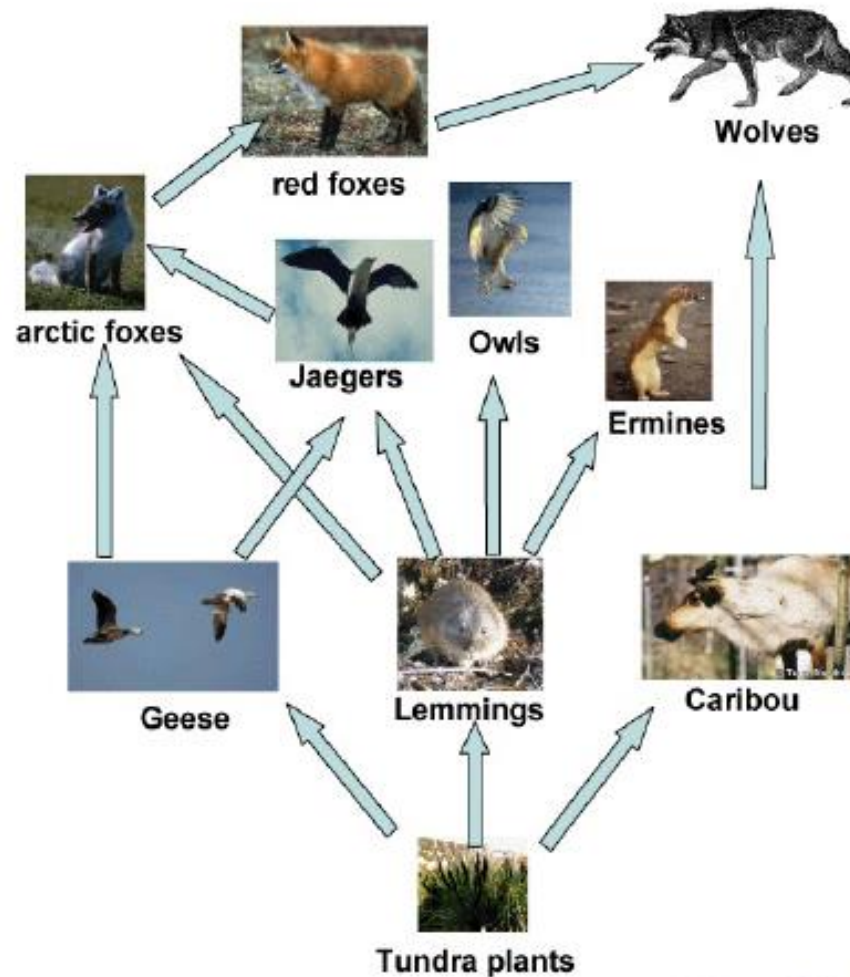
where \mathcal{F} is a given function of N .

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:
 - We look for *fixed points*, N^* , given by $\mathcal{F}(N^*) = 0$.
 - Once N^* have been determined, we study their stability.
 - Try out with any of the previous equations.....
- By these means we get a *qualitative* view of the dynamics.

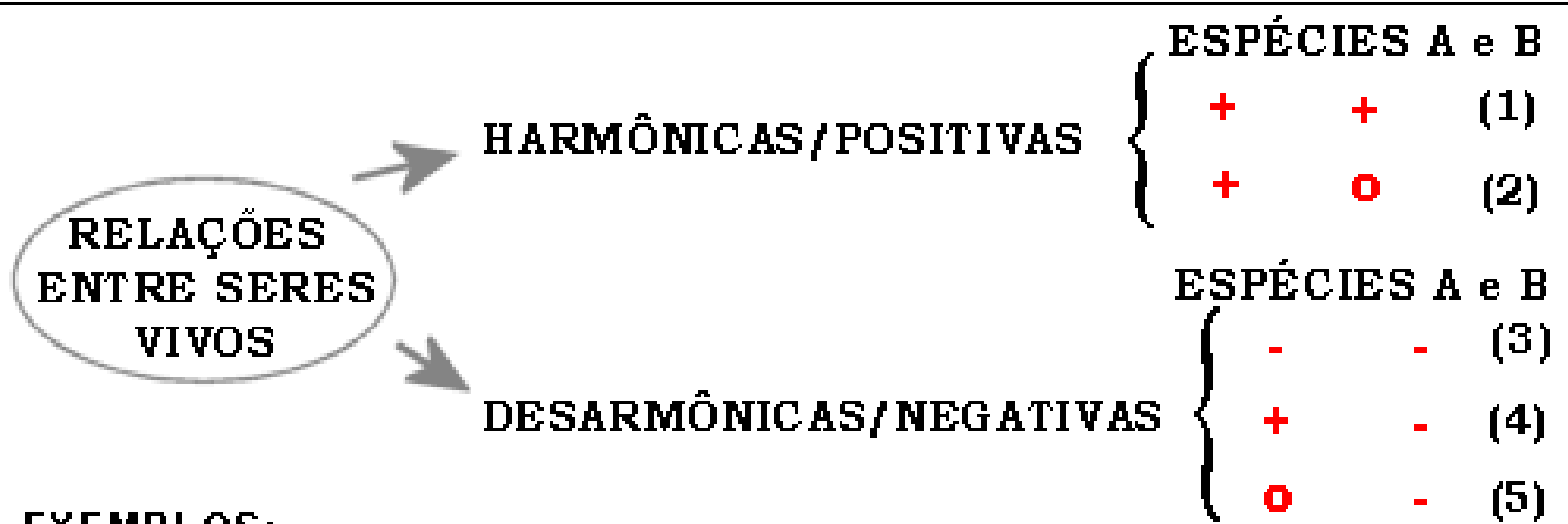
What about interactions?

- Until now we considered populations of different species as independent.
- However, it is a fact that species make part of large interaction networks...
 - Different animals compete for resources
 - Some species are prey on others
- Thus: "*populations are in fact inter-dependent..*".
- The networks involved can be quite complex.

Trophic network, Arctic region



- We saw that populations (animals, plants, bactérias, etc) do live in networks of trophic interactions that might be quite complex .
- Sometimes – as we saw – certain species can be considered effectively non-interacting. But in many instances, not. Let us see the simplest cases of interacting species.
- We begin with just two species.



EXEMPLOS:

- (1) **MUTUALISMO/PROTOCOOPERAÇÃO** > LÍQUENS, CUPIM+PROTOZOÁRIO, BOIS+ANUS
- (2) **COMENSALISMO/INQUILINISMO** > TUBARÃO+REMORA, SAMAMBAIA+BABAÇU,
HOMEM+ENTAMOEBAS COLI
- (3) **COMPETIÇÃO (INTRA E INTERESPECÍFICA)** > HERBÍVOROS DE UM CAMPO
- (4) **PARASITISMO / PREDATISMO** > LOMBRIGA+HOMEM, LEÃO+ZEBRA
- (5) **AMENSALISMO** > ALGAS DINOFLAGELADAS (NEUROTOXINAS)+PEIXES
FUNGOS (ANTIBIÓTICOS) + BACTÉRIAS,

- **Predation** is a widespread interaction between species.
- Ecologically, it is a direct interaction.
- Let us now proceed to describe a mathematical model for it.
- This is known as the *Lotka-Volterra* model.



Vito Volterra (1860-1940), an Italian mathematician, proposed the equation now known as the Lotka-Volterra one to understand a problem proposed by his future son-in-law, Umberto d'Ancona, who tried to explain oscillations in the quantity of predator fishes captured at the certain ports of the Adriatic sea.



Alfred Lotka (1880-1949), was an USA mathematician and chemist, born in Ukraine, who tried to transpose the principles of physical-chemistry to biology. He published his results in a book called "Elements of Physical Biology", dedicated to the memory of Poynting. His results are independent from the work of Volterra.



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Let

- $N(t)$ be the number of predators,
- $V(t)$ the number of preys.

In what follows, a , b , c e d are positive constants

○ number of prey will increase when there are no predators:

$$\frac{dV}{dt} = aV$$

But the presence of predators should lower the growth rate of prey:

$$\frac{dV}{dt} = V(a - bP)$$

and presence of prey will increase the number of predators:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

- We have **nice** equations.
- But we do not know their **solution**.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways
 - Numerical integration. **What's that?**
 - Qualitative analysis. **What's that?**

ANALISE QUALITATIVA

- Let's get back to the equations:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

- The second divided by the first:

$$\frac{dP}{dV} = \frac{P(cV - d)}{V(a - bP)}$$

- So that:

$$\frac{dP(a - bP)}{P} = \frac{dV(cV - d)}{V}$$



$$\frac{dP(a - bP)}{P} = \frac{dV(cV - d)}{V}$$

- Integrate on both sides:

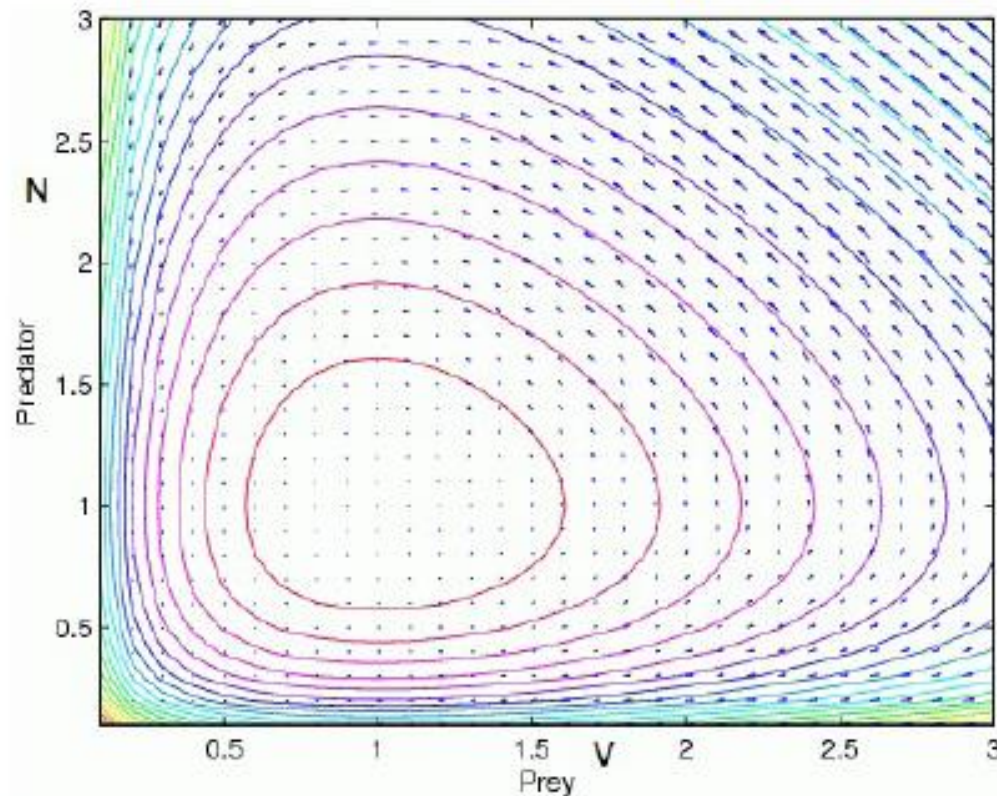
$$a \ln P - bP = cV - d \ln V + H$$

where H is a constant.

- In other words:

$$c\mathbf{V(t)} - b\mathbf{P(t)} + a \ln \mathbf{P(t)} + d \ln \mathbf{V(t)} = H$$

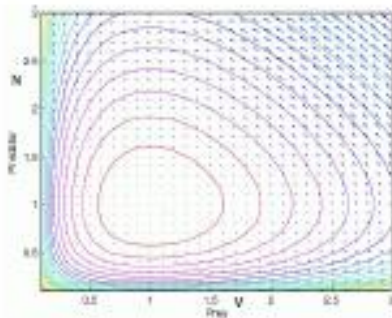
- This is a relation that has to be fulfilled by the solution of the Lotka-Volterra system of equations.
- For a given value of H we can plot on the $P \times V$ plane the geometric locus of the points that obey the above relation. Let's do it!



$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

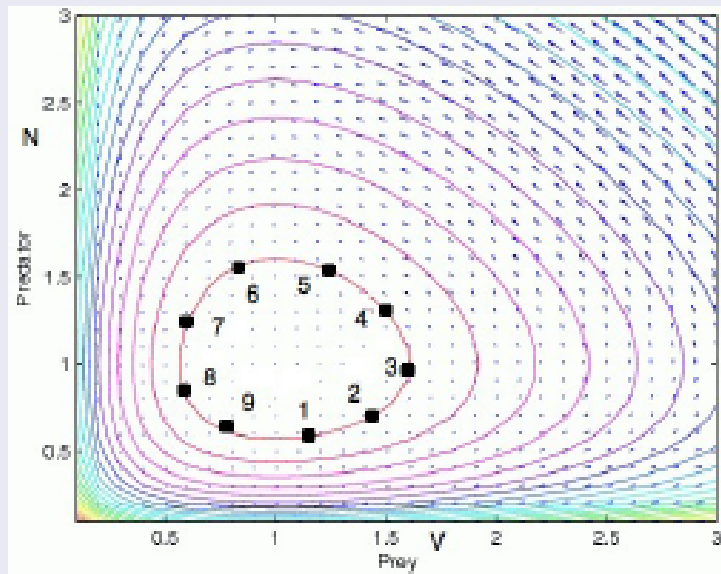
The phase trajectories of the Lotka-Volterra equations, with $a = b = c = d = 1$. Each curve corresponds to a given value of H . The curves obey: $c\mathbf{V}(t) - b\mathbf{P}(t) + a \ln \mathbf{P}(t) + d \ln \mathbf{V}(t) = H$



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In this case, we have *closed orbits*.
- What do they represent?

- Take a point in the phase space.
- It represents a certain number of predators and prey.
- There is a trajectory passing by this point.
- As time passes by, these populations evolve according to the trajectory in phase space.
- After a certain amount of time, they will come back to the initial point.
- This system is periodic.

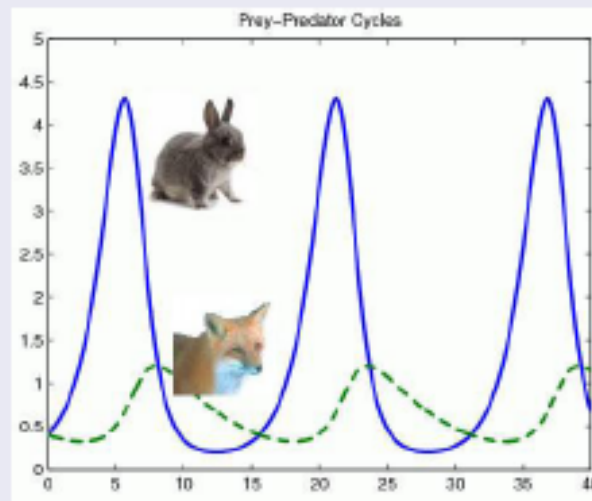
- Ok, the system is **periodic**.
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.
- and from 8 to 3 it increases again
- and so on.

**The number of prey oscillates periodically in time.
and the predators so the same.**

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and **solutions ?**. *The real thing!*
- We can show a plot of them . Where does it come from? Numerical integration.
- Here it is:



- Does the Lotka-Volterra equations describe real situations?
- Partially.
- There are some elements that are clearly not realistic:
 - The growth of prey in the absence of predator is exponential; it does not saturate.
 - No big deal. Just put a logistic term there. We can still have oscillating solutions. Great!
 - On the other hand... the growth rate of the predator is given by $(cV - d)$.
 - The larger V , the higher the rate. This predator is voracious!
 - It would be rather natural to suppose that the conversion rate also saturates. An effect of the predators becoming **satiated**

Host-parasitoid relations

- In close relation to the predator-prey dynamics there is the relation a parasitoid and its host ,
- The parasitoid plays a role analogous to the one of the predator and the host, that of the prey.
- Although these may be seen as different biological interactions, the dynamics is similarly described.
- Note, however, that many insect species have non-overlapping generations.
- which takes us to the realm of discrete-time equations, or coupled mappings.

MODELO DE COMPETIÇÃO

- 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.
- **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:

- 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.

Let N_1 and N_2 be the two species in question.

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..

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

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

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

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.**

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 $1/r_1$.

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

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

The equations in the new variables.

Defining:

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

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

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

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

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

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

We need to study the behavior of their solutions

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

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**.



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



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



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



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

- These are two algebraic equations for $(u_1 \text{ e } u_2)$.
- We **FOUR** solutions. Four 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)*.

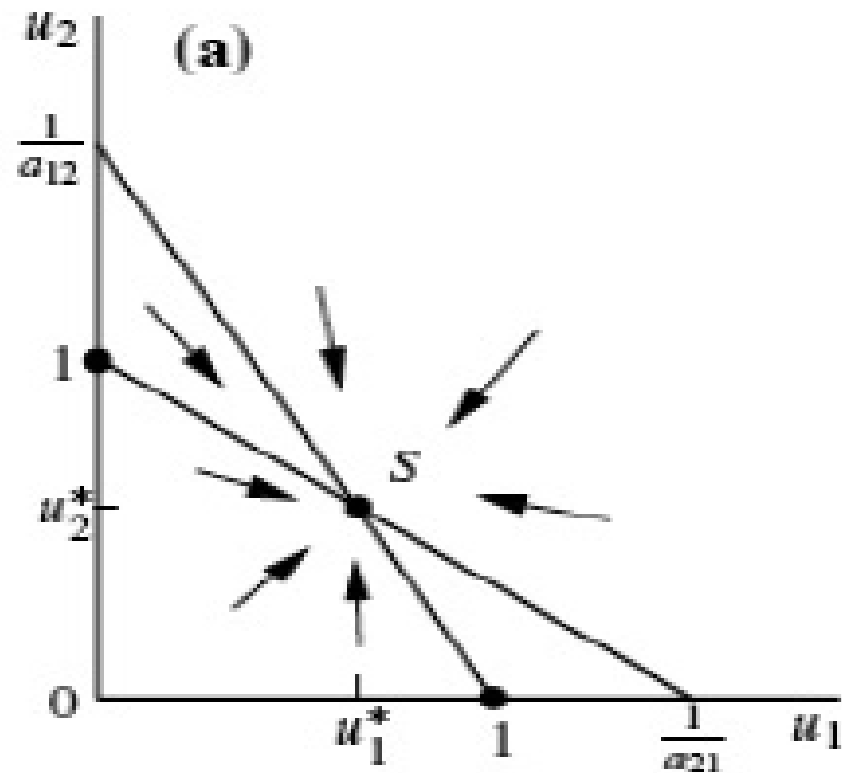


Figura : $a_{12} < 1$ and $a_{21} < 1$. The fixed point u_1^* and u_2^* is stable and represents the coexistence of both species. It is a **global attractor**.

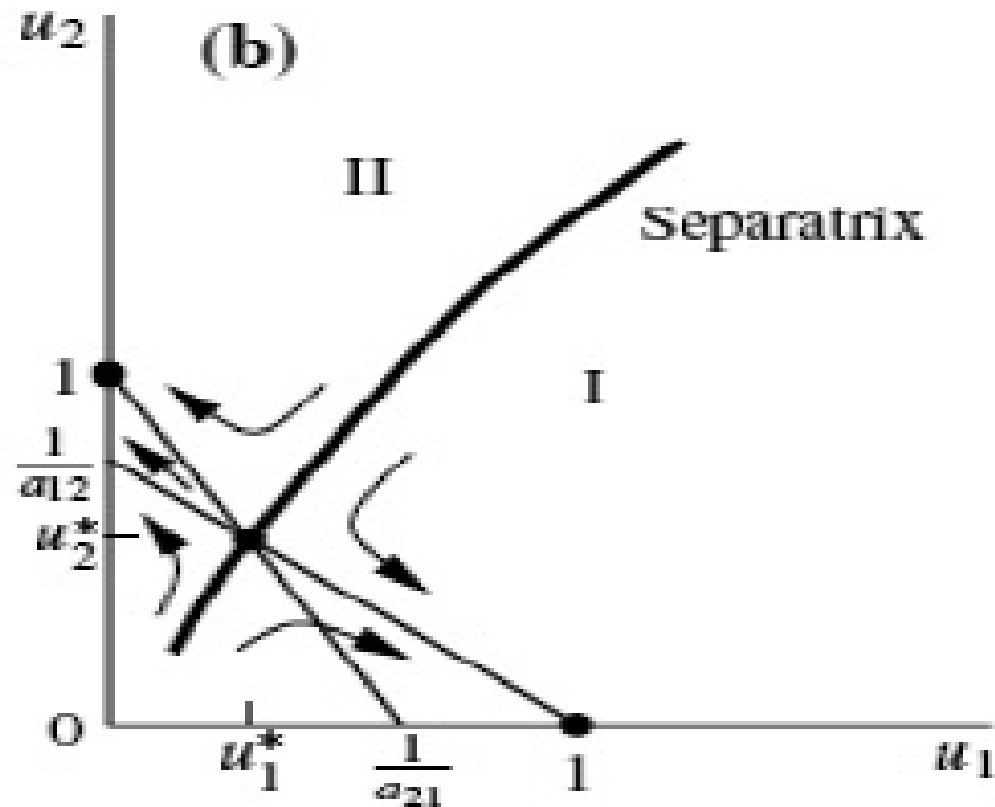


Figura : $a_{12} > 1$ and $a_{21} > 1$. The fixed point u_1^* and u_2^* is unstable. The points $(1, 0)$ and $(0, 1)$ are stable but have *finite basins of attraction*, separated by a *separatrix*. The stable fixed points represent *exclusion* of one of the species.

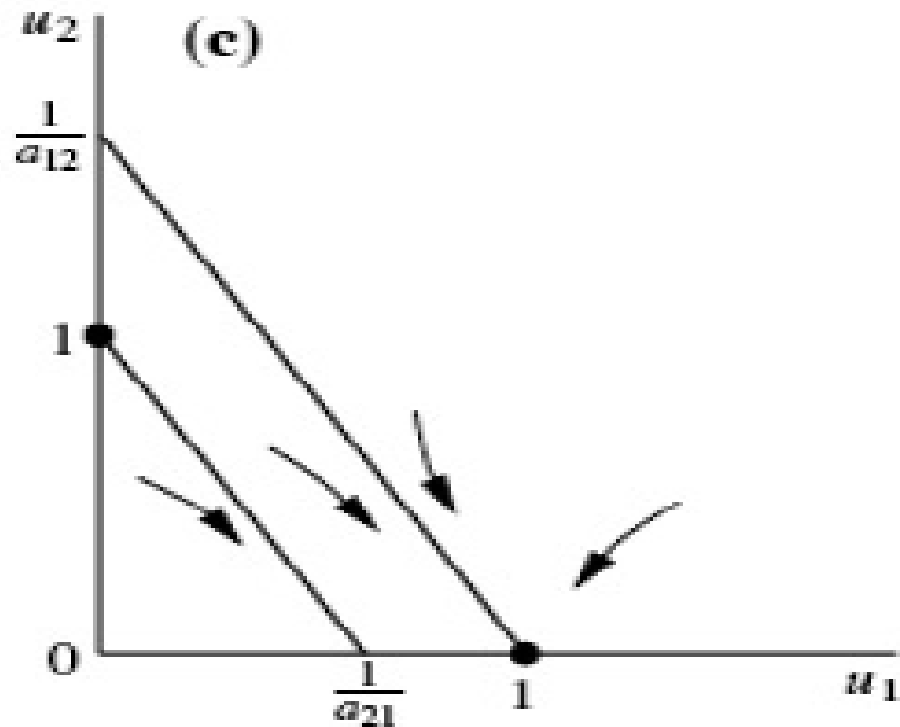


Figura : $a_{12} < 1$ and $a_{21} > 1$. The only stable fixed is $(u_1 = 1, u_2 = 0)$. A global attractor. Species (2) is excluded.

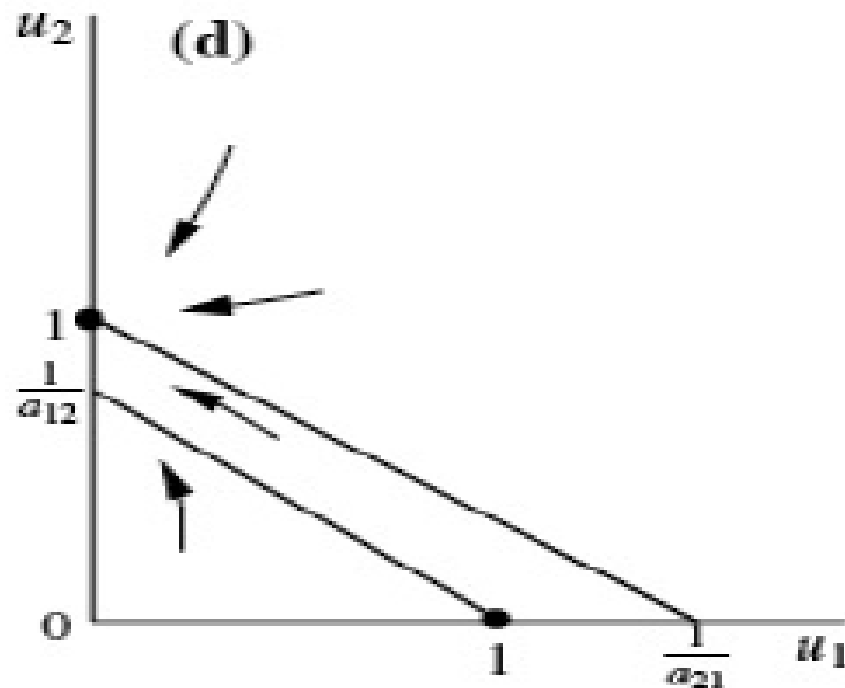
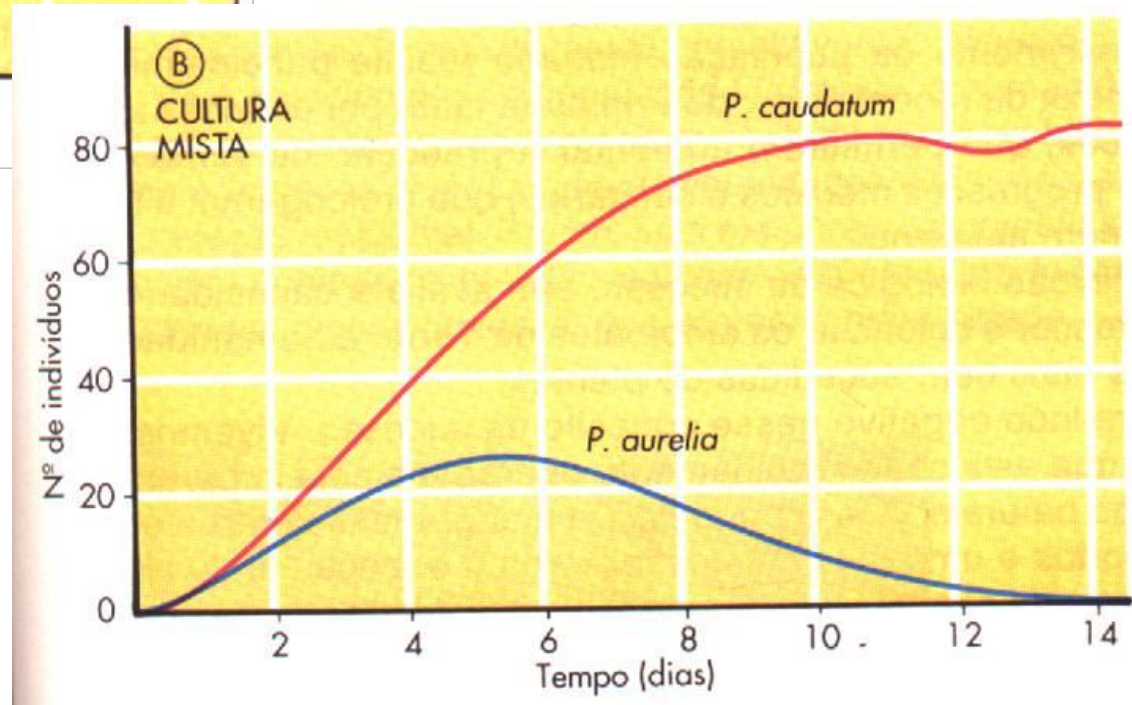
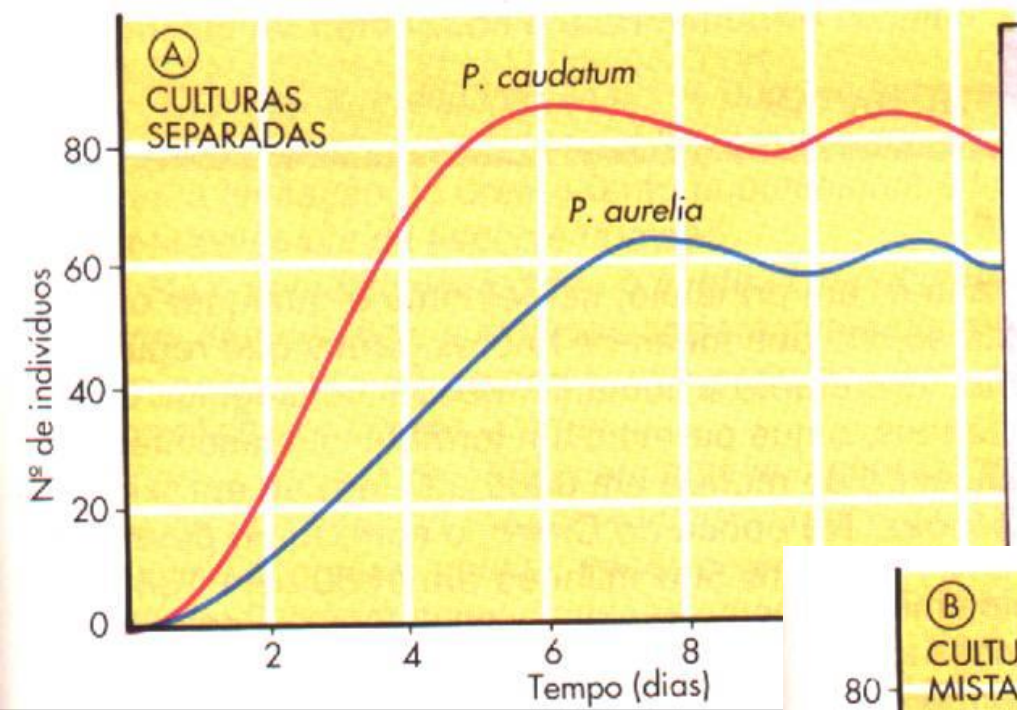


Figura : This case is symmetric to the previous. $a_{12} > 1$ and $a_{21} < 1$. The only stable fixed point is $(u_1 = 1, u_2 = 0)$. A global attractor. Species (1) is excluded

Princípio de Gause ou Princípio da Exclusão Competitiva

- A competição entre duas espécies que exploram o mesmo nicho ecológico pode levar a três diferentes situações:
- A) uma das espécies se extinguir;
- B) uma ou ambas espécies ser expulsa do território;
- C) uma ou ambas espécies adaptarem seus nichos ecológicos em função da competição



SISTEMAS COMPLEXOS

- 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?