IX Southern-Summer School on Mathematical Biology

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Lecture III
1 Competition
Outline

1. Competition

2. Mathematical Model
Outline

1. Competition
2. Mathematical Model
3. Interpretation!
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1. Competition
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4. Protozoa, ants and plankton!
Outline

1 Competition

2 Mathematical Model

3 Interpretation!

4 Protozoa, ants and plankton!

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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.
Let us begin with the simplest case:

- Two species,
- Implicit completion model,
- 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:

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\frac{dN_1}{dt} = r_1 N_1 \left[ 1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right]
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\[
\frac{dN_2}{dt} = r_2 N_2 \left[ 1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right]
\]

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

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

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

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

Define:

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

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

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

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

The equations in the new variables.
Analyzing the model III

\[ \frac{du_1}{d\tau} = u_1 [1 - u_1 - a_{12}u_2] \]

\[ \frac{du_2}{d\tau} = \rho u_2 [1 - u_2 - a_{21}u_1] \]

Defining:

\[ a_{12} = b_{12} \frac{K_2}{K_1}, \]
\[ a_{21} = b_{21} \frac{K_1}{K_2} \]
\[ \rho = \frac{r_2}{r_1} \]

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

\[
\frac{du_1}{d\tau} = u_1 [1 - u_1 - a_{12} u_2] \\
\frac{du_2}{d\tau} = \rho u_2 [1 - u_2 - a_{21} u_1]
\]

No explicit solutions!

We will develop a **qualitative** analysis of these equations.

Begin by finding the points in the \((u_1 \times u_2)\) plane such that:

\[
\frac{du_1}{d\tau} = \frac{du_2}{d\tau} = 0,
\]

the **fixed points**.
Analyzing the model V

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

\[
\frac{du_2}{d\tau} = 0 \Rightarrow u_2 [1 - u_2 - a_{21} u_1] = 0
\]
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 \((u_1, u_2)\).
We FOUR solutions. Four fixed points.
Fixed points

\begin{align*}
  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}}
\end{align*}

The relevance of those fixed points depends on their stability. Which, in turn, depend on the values of the parameters $a_{12}$ and $a_{21}$. 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

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

<table>
<thead>
<tr>
<th>Condition</th>
<th>Fixed Points</th>
<th>Stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_{12} &lt; 1$ and $a_{21} &lt; 1$</td>
<td>$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}}$, $u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}}$</td>
<td>stable</td>
</tr>
<tr>
<td>$a_{12} &gt; 1$ and $a_{21} &gt; 1$</td>
<td>$u_1^* = 1$ and $u_2^* = 0$</td>
<td>both stable</td>
</tr>
<tr>
<td>$a_{12} &lt; 1$ and $a_{21} &gt; 1$</td>
<td>$u_1^* = 1$ and $u_2^* = 0$</td>
<td>stable</td>
</tr>
<tr>
<td>$a_{12} &gt; 1$ and $a_{21} &lt; 1$</td>
<td>$u_1^* = 0$ and $u_2^* = 1$</td>
<td>stable</td>
</tr>
</tbody>
</table>
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.
Figura: The four cases. The four different possibilities for the phase portraits.
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.
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.
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 $a_{21}$:

\[
\frac{du_1}{d\tau} = u_1 [1 - u_1 - a_{12}u_2]
\]

\[
\frac{du_2}{d\tau} = \rho u_2 [1 - u_2 - a_{21}u_1]
\]

- $a_{12}$ 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 where performed with a protozoa group called *Paramecia*.
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The experiences of G.F. Gause where performed with a protozoa group called *Paramecia*. Gause considered two of them: *Paramecium aurelia* e *Paramecium Caudatum*. They where 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 aurelia

Paramecium caudatum

Os dois juntos.
Paramecium

Logístico

Paramecium aurelia

Paramecium caudatum

Os dois juntos.
Paramecium

Exclusão do *P. caudatum* pelo *P. aurelia*.

*Logístico*

*Paramecium aurelia*

*Paramecium caudatum*

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

Online Resources

- http://ecologia.ib.usp.br/ssmb/

Thank you for your attention