

Introduction to Evolutionary Games - 4

Escuela de Bioestocástica

Kerlyns Martínez - Nicolás Rivera

Lecture 4: Evolutionary Games

Replicator dynamics

We will study general competition-collaboration dynamics with more than 2 species

- ▶ Denote our species by $1, \dots, m$
- ▶ $x_i(t)$ denotes the abundance of species i , and $x(t)$ denotes the vector $(x_1(t), x_2(t), \dots, x_m(t))$.
- ▶ We consider a payoff matrix A , where A_{ij} is the payoff that receives when i meets j
- ▶ The fitness if species i is given by

$$f_i = \sum_{j=1}^m A_{ij} x_j = (Ax)_i$$

- ▶ then

$$\dot{x}_i = (f_i - \phi)x_i$$

- ▶ Interpretation:
 - ▶ $f_i x_i = \sum_{j=1}^m x_i x_j A_{ij}$ is the amount of fitness that species i gets due to interaction with other species
 - ▶ ϕ only help us to keep the dynamic in the simplex.
- ▶ $\phi = x^T A x = \sum_{ij} x_i x_j A_{ij}$
- ▶ We can write the dynamic as

$$\dot{x}_i = ((Ax)_i - x^T A x) \quad i \in \{1, \dots, m\}$$

- ▶ This is the so-called replicator dynamic... they always stay in the simplex

The two-players game

A two-player game

- ▶ We have two players: the player and the house
- ▶ Each of them has to distribute 1 unit of mass in the m species
- ▶ The house choose a distribution y and the player a distribution x
- ▶ The result of the game is

$$x^T Ay = \sum_{i=1}^m \sum_{j=1}^m x_i y_j A_{ij}$$

- ▶ The goal for the player is to maximise $x^T Ay$

— Nash Equilibrium —

A point y is a Nash Equilibrium if

$$x^T Ay \leq y^T Ay$$

for all $x \in S_m$ (the simplex of m points).

A point y is a **Nash Equilibrium** if

$$x^T A y \leq y^T A y$$

for all $x \in S_m$ (the simplex of m points).

A point y is a **strict Nash equilibrium** if

$$x^T A y < y^T A y$$

for all $x \in S_m$ and $x \neq y$

Example: Consider $A = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$. Then $f_1 = x_1$, and $f_2 = x_2$, $\phi = x^T A x = x_1^2 + x_2^2$, and the whole dynamic is

$$\dot{x}_1 = (x_1 - \phi)x_1$$

$$\dot{x}_2 = (x_2 - \phi)x_2$$

using that $x_1 + x_2 = 1$ we have

$$\dot{x}_1 = x_1(1 - x_1)(2x_1 - 1),$$

thus the equilibrium points are $(1, 0)$, $(0, 1)$ and $(1/2, 1/2)$.

A point y is a **Nash Equilibrium** if

$$x^T A y \leq y^T A y$$

for all $x \in S_m$ (the simplex of m points).

A point y is a **strict Nash equilibrium** if

$$x^T A y < y^T A y$$

for all $x \in S_m$ and $x \neq y$

Now, let's play a game. I am the House and give you a vector y in the simplex S_2 . What do you play in order to maximise $x^T A y = x_1 y_1 + x_2 y_2$?

1. If $y_1 > y_2$ choose $(1, 0)$
2. If $y_1 < y_2$ choose $(0, 1)$
3. if $y_1 = y_2$ choose any vector

We can see that the Nash equilibrium are $(1, 0)$, $(0, 1)$ and $(1/2, 1/2)$. **Why?** Because y is a Nash equilibrium if y is one of the best responses. Moreover, $(1, 0)$ and $(0, 1)$ are strict Nash Equilibrium.

Coincidence?

Theorem

A Nash equilibrium y of the game described by the payoff matrix A , then y is an equilibrium point of the Replicator Dynamic associated with A .

Theorem

A Nash equilibrium y of the game described by the payoff matrix A , then y is an equilibrium point of the Replicator Dynamic associated with A .

Technical Result*:

Theorem

A Nash equilibrium y of the game described by the payoff matrix A , then y is an equilibrium point of the Replicator Dynamic associated with A .

Technical Result*: Moreover, if y is the ω -limit of an orbit in the interior of the simplex S_n , then y is a Nash equilibrium.

Evolutionary Stable State

A point $y \in S_m$ is an evolutionary stable state (ESS) if

$$x^T A x \leq y^T A x, \quad \forall x \neq y \text{ in a neighbourhood of } y,$$

i.e. deviations from y always result in a worse payoff.

An ESS is a Nash Equilibrium, but the converse is not true.

Theorem

If $y \in S_m$ is an ESS, then y is an asymptotically **stable rest point**. Moreover, if $y_i > 0$ for all i , then y is a **globally stable rest point**.

A point $y \in S_m$ is an evolutionary stable state (ESS) if

$$x^T A x \leq y^T A x, \quad \forall x \neq y \text{ in a neighbourhood of } y,$$

i.e. deviations from y always result in a worse payoff.

An ESS is a Nash Equilibrium, but the converse is not true.

Theorem

If $y \in S_m$ is an ESS, then y is an asymptotically **stable rest point**. Moreover, if $y_i > 0$ for all i , then y is a **globally stable rest point**.

- ▶ **rest point**: $y \in S_m$ is a rest point if $f_1(y) = f_2(y) = \dots = f_m(y)$
- ▶ **stable**: if we start the dynamic near y we will go to y
- ▶ **globally**: starting from any point $x(0)$ with $x_i(0) > 0$, then the dynamics converges to y

Examples: Hawks and Doves

Recall the Hawks and Doves dynamic

	H	D
H	$\frac{1-C}{2}$	1
D	0	$1/2$

For extra simplicity, fix $C = 2$, which we know enters in the regime that hawks are a danger for themselves. In this case

	H	D
H	$-\frac{1}{2}$	1
D	0	$1/2$

From the previous class we know that $(x_H, x_D) = (1/C, (C-1)/C)$ is an equilibrium point of this dynamic. In our case it is just $(0.5, 0.5)$

Is $y = (0.5, 0.5)$ a ESS?

	H	D
H	$-\frac{1}{2}$	1
D	0	$1/2$

Is $y = (0.5, 0.5)$ a ESS?

	H	D
H	$-\frac{1}{2}$	1
D	0	$1/2$

We just has to verify that $y^T Ax > x^T Ax$ for all x in a vecinity of y .

Is $y = (0.5, 0.5)$ a ESS?

	H	D
H	$-\frac{1}{2}$	1
D	0	$1/2$

We just has to verify that $y^T A x > x^T A x$ for all x in a vecinity of y .

What is the vecinity of y ? Just take $x = (0.5 + \delta, 0.5 - \delta)$, and let's consider all values $|\delta|$ super small, like smaller than 0.001 (or any small value)

Is $y = (0.5, 0.5)$ a ESS?

	H	D
H	$-\frac{1}{2}$	1
D	0	$1/2$

We just has to verify that $y^T Ax > x^T Ax$ for all x in a vecinity of y .

What is the vecinity of y ? Just take $x = (0.5 + \delta, 0.5 - \delta)$, and let's consider all values $|\delta|$ super small, like smaller than 0.001 (or any small value)

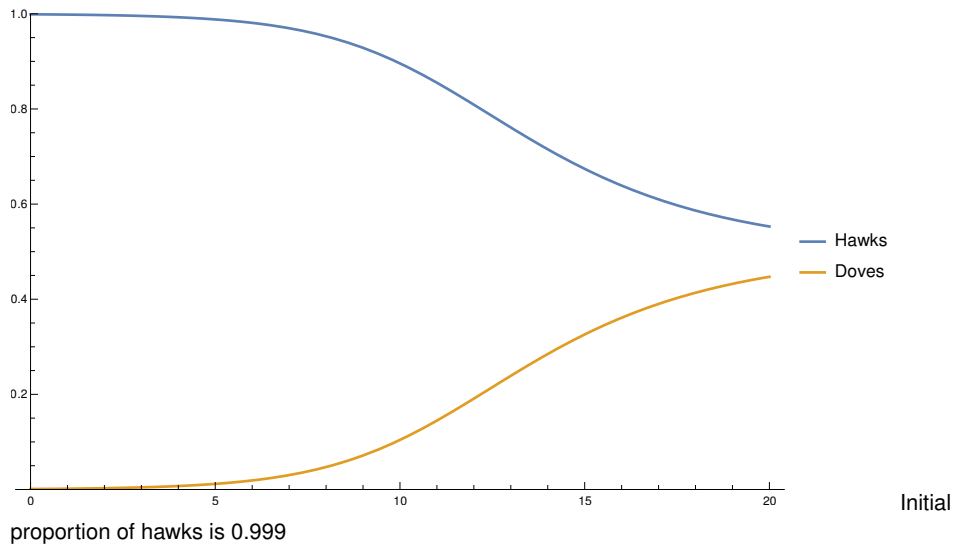
Then, we have

$$y^T Ax - x^T Ax = d^2,$$

which is clearly positive for any δ (and particularly for delta close to 0)

We conclude

1. $(0.5, 0.5)$ is an ESS in the interior of the simplex
2. Then it is a globally stable rest point



Example

Let us consider the payoff matrix

$$A = \begin{bmatrix} 0 & 6 & -4 \\ -3 & 0 & 5 \\ -1 & 3 & 0 \end{bmatrix},$$

Then, an equilibrium point of the replicator equation is $\dot{x}_i = x_i((A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x})$ is

$$\mathbf{x}^* = (1/3, 1/3, 1/3).$$

but it is not an ESS

Dynamics can be complicated

Example

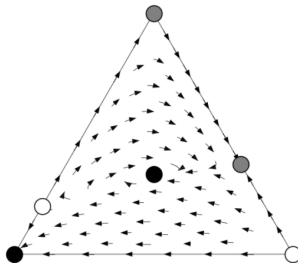
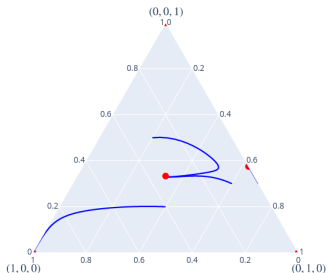
Let us consider the payoff matrix

$$A = \begin{bmatrix} 0 & 6 & -4 \\ -3 & 0 & 5 \\ -1 & 3 & 0 \end{bmatrix},$$

Then, an equilibrium point of the replicator equation is $\dot{x}_i = x_i((Ax)_i - \mathbf{x} \cdot A\mathbf{x})$ is

$$\mathbf{x}^* = (1/3, 1/3, 1/3).$$

but it is not an ESS



Rock-Scissors-Paper and evolutionary games



Wasn't it rock-paper-scissors?

When we establish the order Rock-Scissors-Paper, there is a linearity in terms of the winner per combination:

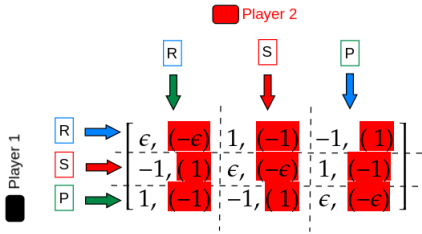
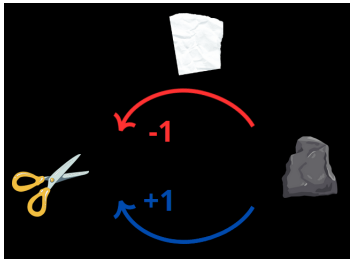


Figure: Cachipún punctuation and payoff matrix

Definition (Zero-sum games)

If the gain of one player is always the loss of the other, i.e. the payoff matrix A is anti-symmetric ($A^T = -A$), then the game is called a **zero-sum game**.

For $\epsilon = 0$, i.e. no reward in case of a tie, the Cachipún game is a zero-sum game, for which we have

$$\mathbf{x} \cdot A\mathbf{x} = 0.$$

Notice that the RSP-payoff matrix is given by:

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

Notice that the RSP-payoff matrix is given by:

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

What are the Nash Equilibria?

Only $(1/3, 1/3, 1/3)$

We can easily write the replicator equation here.
This is an exercise

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

We can easily write the replicator equation here.
This is an exercise

Solution:

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

We can easily write the replicator equation here.
This is an exercise

Solution:

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

We can easily write the replicator equation here.
This is an exercise

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

Solution:

$$\begin{cases} \dot{x}_1 &= x_1(x_2 - x_3) \\ \dot{x}_2 &= x_2(x_3 - x_1) \\ \dot{x}_3 &= x_3(x_1 - x_2) \end{cases}$$

with $(x_1, x_2, x_3) \in S_3$.

Solving the system $\dot{\mathbf{x}}(t) = \mathbf{0}$ gives us the equilibrium points:

$$p_1 = (1, 0, 0)$$

$$p_2 = (0, 1, 0)$$

$$p_3 = (0, 0, 1)$$

$$\hat{\mathbf{x}} = (1/3, 1/3, 1/3).$$

Is some of these points an ESS?

Solving the system $\dot{\mathbf{x}}(t) = \mathbf{0}$ gives us the equilibrium points:

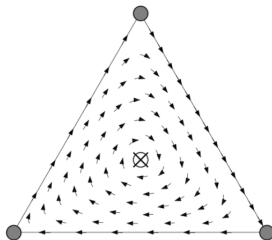
$$p_1 = (1, 0, 0)$$

$$p_2 = (0, 1, 0)$$

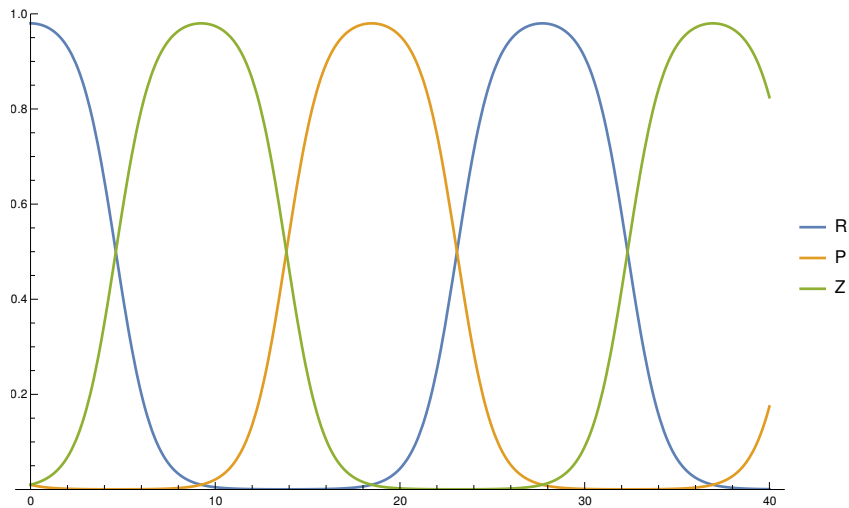
$$p_3 = (0, 0, 1)$$

$$\hat{\mathbf{x}} = (1/3, 1/3, 1/3).$$

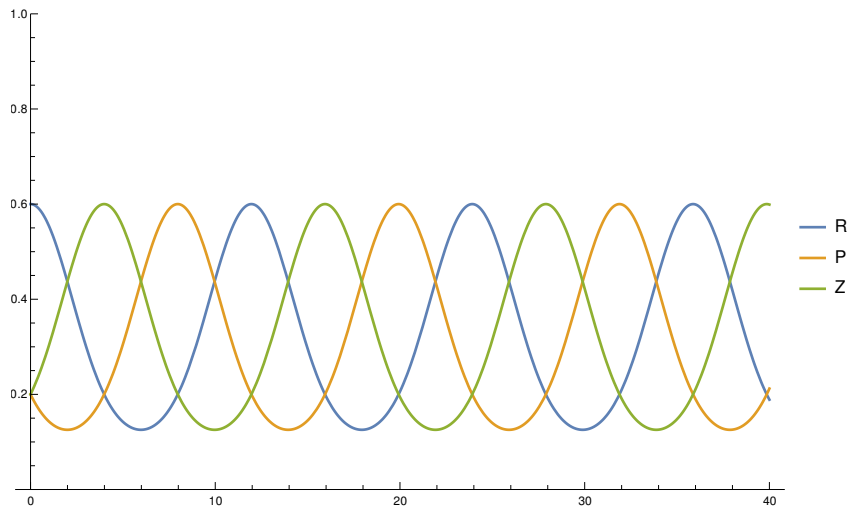
Is some of these points an ESS? The answer is no.



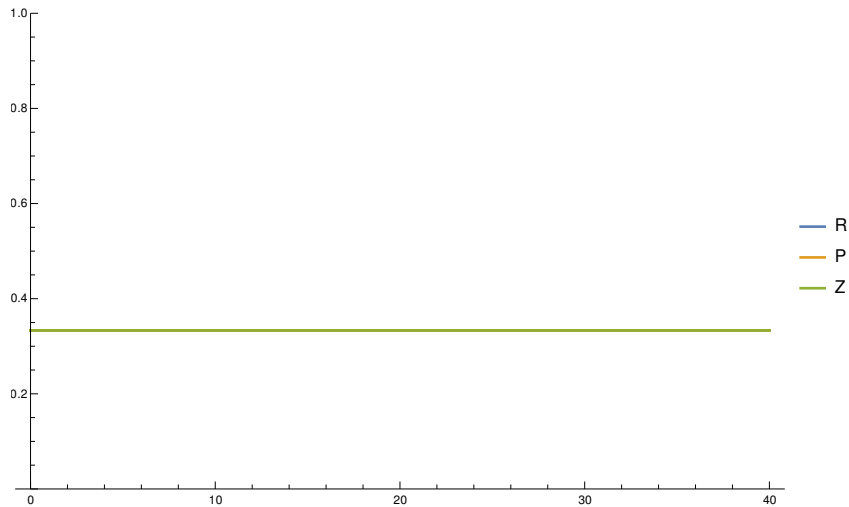
There is no ESS.



$R(0) = 0.98, P(0) = Z(0) = 0.01$



$R(0) = 0.6, P(0) = Z(0) = 0.2$

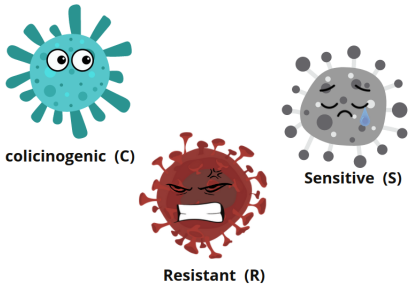


$$R(0) = P(0) = Z(0) = 1/3$$

Rock-scissors-paper is not just a naïve example. This behaviour can be observed also in natural systems, for example, with microbial communities containing toxin-producing (or colicinogenic) *E. coli*. These bacteria can encode the toxin but just a small fraction of them will release the colicin.

In the above example, the cells can be divided in three **types**: resistant cells (R), colicinogenic cells (C) and sensitive cells (S).

- The growth rate of **R** cells will exceed that of **C** cells since they avoid the competitive cost of carrying the col plasmid,
- **R** cells suffer because colicin is also involved in crucial cell functions such as nutrient uptake, so their growth rate will be less than the growth rate of **S** cells.
- colicin-sensitive bacteria are killed by the colicin, although they may occasionally experience mutations that render them resistant to the colicin.



Who would you choose as rock, paper or scissors?

Final words about the course

- ▶ This is just a very basic introduction. There is much more to learn
- ▶ **Some books**
 1. Novak - Evolutionary Dynamics. Very introductory, but a bit too shallow and informal
 2. Hofbauer and Sigmund - Evolutionary Games and Population Dynamics. Much harder, very formal and proof-based
- ▶ There are many resources online, but they are mostly based on the previous books (e.g. same examples etc..)
- ▶ **Numerics**: most software can solve differential equation: e.g. [Mathematica](#), [Matlab](#), probably some library in [R](#), and many libraries in [Python](#)
- ▶ **Stochastic approach**: The fact that the system is stable only means that the abundances are stable. In reality mass is moving quite a lot in a sort of balanced way. If we analyse the movement of one 'particle' it would be a **random processes** jumping between species.
- ▶ **Some prerequisites for self-studying?** More or less the same to study classical mechanics. I reckon
 1. Calculus at Engineering level is probably enough
 2. Linear Algebra
 3. Some knowledge of probability
- ▶ What about the actual values of the rates, payoff matrices, etc? We need data, and there are a lot of statistical problems here. There is a big issue: you can quickly scalate and have a lot of parameters and not a lot of data.
- ▶ All my material is (and I will update a few things) in <https://nnrivera.github.io/teaching/biostochastics2024>