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### **Outline of the course**

- Day 1: Introduction to Game Theory
- **Day 2: Evolutionary Game Theory**
- Day 3: Games on Networks
- Day 4: Practical challenges and connecting theory to Behavioural Experiments
- Day 5: Final remarks and Project presentations

## **Day 2: Evolutionary Game Theory**

- 1. Evolutionary Stability
- 2. Infinite Populations
- 3. Finite Populations
- 4. Tutorial: how to reproduce an EGT paper

## When you think about Game Theory...





#### games

economy



#### politics

## However, there are many other strategic interactions, and many of them occur in Large populations!













## However, there are many other strategic interactions, and many of them occur in Large populations!





## However, there are many other strategic interactions, and many of them occur in Large populations!



### A change in perspective from individual to population

**Complex individuals - Smaller populations Simpler individuals - Larger populations** 







same species, the winner gains mates, dominance rights, desirable territory, or other advantages that will tend toward transmitting its genes to future generations at higher frequencies than the loser's genes. Consequently, one might

and ask what strategy will be favoured under individual selection. We first consider conflict in species possessing offensive weapons capable of inflicting serious injury on other members of the species. Then we consider conflict in species where serious injury is impossible, so that victory goes to the contestant who fights longest. For each model, we seek a strategy that will be stable under natural selection; that is, we seek an "evolutionarily stable strategy" or ESS. The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur<sup>13</sup> and of Hamilton<sup>14</sup> on the evolution of the sex ratio. Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness.

#### A Computer Model

A main reason for using computer simulation was t test whether it is possible ever

https://blogs.bl.uk/untoldlives/2020/03/john-maynard-smith-evolutionary-biology-and-the-logic-of-animal-conflict.html

#### JOHN MAYNARD SMITH Evolution and the Theory of Games



NOBEL PRIZE

#### THOMAS C. SCHELLING

\*Before Freakonomics and The Tipping Point, there was Micromotives and -BARRY NALEBUFF, coauthor of Thinking Strategically









# Part 1: Evolutionary Stable Strategies (ESS)

## **Evolutionary Stable Strategy (ESS)**

An **Evolutionary Stable Strategy** is an strategy that, if adopted by all individuals of a population, cannot be invaded by alternative or mutant strategies

A strategy S is evolutionary stable if it follows the following 2 conditions for all strategies  $T \neq S$ :

1.  $\Pi(S, S) > \Pi(T, S)$  or

```
2. \Pi(S, S) = \Pi(T, S) and \Pi(S, T) > \Pi(T, T)
```

#### Prisoners Dilemma, T>R, P>S

#### Greed and fear



C.H. Coombs (1973) A reparameterization of the prisoner's dilemma game. Behavioral Science 18:424-428

#### Can C invade a population of D

Assume an infinite population of  $(1 - \epsilon)$  D players and  $\epsilon$  C players

Success of  $\epsilon$  fraction of C in a population with  $(1 - \epsilon)$  D players:  $S(1 - \epsilon) + R\epsilon$ 

Success of  $(1 - \epsilon)$  fraction of D in a population with  $\epsilon$  C players:  $P(1 - \epsilon) + T\epsilon$ 

C players can take over the population when  $S(1 - \epsilon) + R\epsilon > P(1 - \epsilon) + T\epsilon$ 

This happens when either S > P or when S = P, R > T

If C cannot invade, D is an **Evolutionary** Stable Strategy (ESS)



#### ...and inversely, can D invade a population of C

#### Prisoners Dilemma, T>R, P>S

#### Greed and fear



C.H. Coombs (1973) A reparameterization of the prisoner's dilemma game. Behavioral Science 18:424-428

Assume an infinite population of  $(1 - \epsilon)$  C players and  $\epsilon$  D players

Success of  $\epsilon$  fraction of D in a population with  $(1 - \epsilon)$  C players:  $T(1 - \epsilon) + P\epsilon$ 

Success of  $(1 - \epsilon)$  fraction of C in a population with  $\epsilon$  D players:  $R(1 - \epsilon) + S\epsilon$ 

D players can take over the population when  $T(1 - \epsilon) + P\epsilon > R(1 - \epsilon) + S\epsilon$ 

This happens when either T > R or when T = R, P > S

If D cannot invade, C is an **Evolutionary** Stable Strategy (ESS)



























17

















Yes since T > R

D











#### No ESS ?

What about (1/5,4/5)?



#### **Connection between NE and ESS**

Given a symmetric two-player normal-form game  $G = (\{1,2\}, A, u)$  and a mixed strategy s, If s is an ESS then (s, s) is a NE of the game G.

Given a symmetric two-player normal-form game  $G = (\{1,2\}, A, u)$  and a mixed strategy s, If (s, s) is a strict symmetric NE then s is an ESS



## Part 2: Infinite Populations

#### The success of a species depends both on its fitness and its numbers.



### The replicator equation



### The replicator equation









## **Important:** in the following slides we assume the population participates in a 2-player symmetric game.

## Matrix form of expected payoffs

Expected payoff of type of a type *i* in a population with state x

$$(A\mathbf{x})_i = \sum_{j=1}^m a_{ij} x_j$$

Average payoff in the population

$$\boldsymbol{x}^{T} A \boldsymbol{x} = \sum_{i} x_{i} (A \boldsymbol{x})_{i} = \sum_{i,j} a_{ij} x_{i} x_{j}$$

## Nash equilibrium (again...) $G(x_i) = \dot{x}_i = x_i [(Ax)_i - x^T Ax]$

A symmetric  $n \times n$  game has a symmetric NE x if

Where the matrix A is a payoff matrix with element  $A_{ii}$  representing the fitness of strategy iover strategy j.



Every symmetric NE is a rest point of the replicator equation, however, not every rest point of the replicator equation is an NE.

Where the matrix A is a payoff matrix with element  $A_{ii}$  representing the fitness of strategy iover strategy j.

For all  $\hat{x} \neq x$  in some neighbourhood of x (the perturbed state): Equilibrium condition  $\hat{\mathbf{r}}^T A \mathbf{y}$ Stability condition

Where the matrix A is a payoff matrix with element  $A_{ii}$  representing the fitness of strategy iover strategy j.

$$\mathbf{x} \leq \mathbf{x}^T A \mathbf{x}$$

if  $\hat{x}^T A x = x^T A x$  then  $\hat{x}^T A \hat{x} < x^T A \hat{x}$ 

neighbourhood of x (the perturbed state), then

Where the matrix A is a payoff matrix with element  $A_{ii}$  representing the fitness of strategy iover strategy j.

> State x is evolutionary stable if for all  $\hat{x} \neq x$  in some  $\mathbf{x}^T A \mathbf{\hat{x}} > \mathbf{\hat{x}}^T A \mathbf{\hat{x}}$

neighbourhood of x (the perturbed state), then

Where the matrix A is a payoff matrix with element  $A_{ii}$  representing the fitness of strategy iover strategy j.

> State x is evolutionary stable if for all  $\hat{x} \neq x$  in some  $\mathbf{x}^T A \mathbf{\hat{x}} > \mathbf{\hat{x}}^T A \mathbf{\hat{x}}$

Evolutionary stable state extends the concept of ESS to mixed strategies through dynamic stability. That is, a population configuration (state) is stable if, after an infinitesimal change in the population (e.g., the introduction of a mutant), it converges to that state.

Where the matrix A is a payoff matrix with element  $A_{ii}$  representing the fitness of strategy iover strategy *j*.

### Payoff dominance and Risk dominance

A NE is considered **payoff dominant** if it is **Pareto superior** (all other NE provide less payoff to at least one player) to all other NE in the game.

A NE is considered **risk dominant** if it is perceived as "less risky" than all other NE. Risk perception here means that it maximises the expected payoff given the uncertainty about what the opponent(s) might do. It can also be seen as **the equilibria with the largest basin of attraction**.

### **Payoff dominance and Risk dominance**

strategy S.

A strategy S risk dominates a strategy T if the expected payoff for a player i choosing S is bigger than the expected payoff of choosing T, that is  $\Pi_i(p \mid S) > \Pi_i(p \mid T)$ , where p is the is the risk factor of the pure NE (S, S), that is, the probability that an opponent will choose



#### Social dilemma space



T > R > S > P



T > R > P > S



*R*+1




#### **Replicator equation results for all social** dilemmas



#### **Example: The Hawk-Dove game**

#### The Hawk-Dove game

Hawk-Dove Model: Costs and Benefits of Fighting over Resources Payoff' 10 .... ... in fights against: dove hawk. Hawk wins 60% of fights; Hawk always wins; is injured in 50% of fights. **NBMK** dove flees. Payoff: (V-D)/2 Payoff: Dove wins 50% of fights; Dove never wins. is never injured; wastes time. is never injured. CION 6 Payoff: V/2-T Pavoff: 0

\*V = fitness value of winning resources in fight.

D = fitness costs of injury

T = fitness costs of wasting time.

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another <u>dove</u> she also wins 50% of the time (V/2) but only after a period of mutual displays to show of strength (-T). Hawks always win against doves, resulting in a benefit for one (V) and not for the other (0).



The hawk-Dove game ĺS a coordination game formulated by John Maynard Smith and Georg Price. The aim of the game was to understand the resolution of conflicts by fighting in the animal kingdom. The game consists of two players, which each have the choice between two possible actions; either they take time to display (dove) before fighting or they can escalate immediately and fight (hawk). When both players escalate (hawk), they have a 50% risk of being injured (-D/2) and 50% of wining (V/2). When a dove fights

## Example: The Hawk-Dove game - Defection -dominant



# V = 3, D = 2, T = 1 (V > D) $\begin{pmatrix} 0.5, 0.5 & 3, 0 \\ 0, 3 & 0.5, 0.5 \end{pmatrix}$

#### **Example: The Hawk-Dove game - Anticoordination**



# V = 2, D = 3, T = 1 (V < D) $\begin{pmatrix} -0.5, -0.5 & 2, 0\\ 0, 2 & 0, 0 \end{pmatrix}$

#### **Example: The Hawk-Dove game -**Coordination



## V = 3, D = 2, T = -2 (V > D) $\begin{pmatrix} 0.5, 0.5 & 3, 0 \\ 0, 3 & 3.5, 3.5 \end{pmatrix}$



#### **Example: The Hawk-Dove game -Cooperation-dominant**



V = -1, D = 2, T = 0 (V > D) $\begin{bmatrix} -1.5, -1.5 & -1, 0 \\ 0, -1 & -0.5, -0.5 \end{bmatrix}$ 



#### **Rock-Paper-Scissors**



# $\begin{pmatrix} 0.5, 0.5 & 0, 1 & 1, 0 \\ 1, 0 & 0.5, 0.5 & 0, 1 \\ 0, 1 & 1, 0 & 0.5, 0.5 \end{pmatrix}$



#### **Rock-Paper-Scissors**



# $\begin{pmatrix} 0.5, 0.5 & 0, 1 & 1, 0 \\ 1, 0 & 0.5, 0.5 & 0, 1 \\ 0, 1 & 1, 0 & 0.5, 0.5 \end{pmatrix}$

paper



#### Hawk-dove-human Game





#### Other dynamics

Lotka-Volterra (Predator-prey)

**Replicator-mutator equation** 



See <u>http://www.tiem.utk.edu/~gross/bioed/</u> bealsmodules/predator-prey.html

#### Asymmetric Games



**Payoffs A** 

	L	R		т	В
Т	0	-1	L	0	-1
В	Х	-2	R	1	-2

$$\dot{x}_i = x_i [(Ay)_i - x^T Ay]$$
$$\dot{y}_i = y_i [(Bx)_i - y^T Bx]$$

#### Payoffs B

#### Asymmetric Games (see notebook!)



#### Part 3: Finite Populations

#### **Evolution of trust**

https://ncase.me/trust/

#### **Evolutionary dynamics in Finite Populations**





(Agent-based simulation)



**Evolutionary dynamics (\phi)** 

Moran process

Wright-Fisher process







William Hoppitt and Kevin N. Laland

#### **Social Learning**

An Introduction to Mechanisms, Methods, and Models

New behaviour is acquired by observation/imitation



**Social learning** is learning that is facilitated by observation, or interaction with, another individual or its products

**Reinforcement learning** (Bush-Mosteller, Mach-Flach, Roth-Erev, ..., learning automata, Q*learning*) models provide **individual learning by** experience

**Evolutionary dynamics** models use **learning by imitating the best** 











This process can be described by a Markov Chain



**Fermi function** 

$$p \equiv [1 + e^{\beta(f_i(k) - f_j(k))}]^{-1}$$

Assuming 2 strategies C and D in a population of size Z, k C players and Z - k D players

$$T^{+} = (1 - \mu) \frac{Z - k}{Z} \frac{k}{Z} [1 + e^{-\beta (k)}]$$
$$T^{-} = (1 - \mu) \frac{k}{Z} \frac{Z - k}{Z} [1 + e^{\beta (f_{0})}]$$



**Fermi function** 

$$p \equiv [1 + e^{\beta(f_i(k) - f_j(k))}]^{-1}$$

Assuming 2 strategies C and D in a population of size Z, k C players and Z - k D players

$$T^{+} = (1 - \mu) \frac{Z - k}{Z} \frac{k}{Z} [1 + e^{-\beta Q}]$$
$$T^{-} = (1 - \mu) \frac{k}{Z} \frac{Z - k}{Z} [1 + e^{\beta Q}]$$

 $[f_{C}-f_{D}]^{-1} + \mu \frac{Z-k}{7}$  $\int_{C} f_{D} \left[ -f_{D} \right]^{-1} + \mu \frac{1}{Z}$ 

probability that the imitation process occurs and individuals adopting different strategies are selected

> probability of mutating to strategy D



To calculate the fitness we now need to sample without replacement!

For 2-player games, we have:

$$f_D(k) = \frac{k-1}{Z-1} \Pi(D,D) + \frac{Z-k}{Z-1} \Pi(D,C)$$
$$f_C(k) = \frac{k}{Z-1} \Pi(C,D) + \frac{Z-k-1}{Z-1} \Pi(C,C)$$

 $-\Pi(D, C)$ 

To calculate the fitness we now need to sample without replacement!

For n-player games, where N is the size of the group, we have (hypergeometric sampling):

$$f_D(k) = {\binom{Z-1}{N-1}}^{-1} \sum_{j=0}^{N-1} {\binom{k-1}{j}} {\binom{Z-k-1}{N-j-1}} \Pi_D(j)$$
$$f_D(k) = {\binom{Z-1}{N-1}}^{-1} \sum_{j=0}^{N-1} {\binom{k-1}{j}} {\binom{Z-k}{N-j-1}} \Pi_C(j+1)$$

With this we can define the transition matrix T that maps the probabilities of transitioning from a state with k Ds to an adjacent state with k + 1 or k - 1 Ds:

> $T_{i+1,i} = T^ T_{i,i+1} = T^+$  $T_{1,i} = 1 - T^+ - T^-$

## Important indicators

**Gradient of selection** (most likely path for the evolution):

$$G(x) = T^{+}(k) - T^{-}(k) = (1 - \mu)\frac{k}{Z}\frac{Z - k}{Z}\tan h\left(\frac{\beta}{2}[f_{C}(k) - f_{D}(k)]\right) + \mu$$

#### Stationary distribution (the time spent at each state)

with the eigenvalue 1 of the transition matrix.

- The stationary distribution can be computed as the left eigenvector associated

Vasconcelos, V. V., Santos, F. C. & Pacheco, J. M. A bottom-up institutional approach to cooperative governance of risky commons. *Nature Climate Change* **3**, 797–801 (2013).





#### **Evolutionary dynamics**







**Evolutionary dynamics (\phi)** 

Moran process





V = 2, D = 3, T = 1 (V < D)

# $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$

 $Z = 100 \qquad x_i \equiv [k_i/Z]$  $\beta = 1$  $\mu = 0$ 



<i>V</i> = 2, <i>D</i> =	= 3, T = 1 (	(V < D)
(-0.5, 0, 0, 0)	- 0.5 2	2, 0) 0, 0)
$Z = 100$ $\beta = 1$	$x_i \equiv$	$[k_i/Z]$

 $\mu = 1e - 3$ 



V = 2, D = 3, T = 1 (V < D) $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$ 

 $x_i \equiv [k_i/Z]$ Z = 10 $\beta = 1$  $\mu = 0$ 



V = 2, D = 3, T = 1 (V < D)  $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$ 

 $Z = 10 \qquad x_i \equiv [k_i/Z]$  $\beta = 1$  $\mu = 1e - 3$ 



V = 2, D = 3, T = 1 (V < D)

# $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$

 $Z = 100 \qquad x_i \equiv [k_i/Z]$  $\beta = 10$  $\mu = 0$ 

#### Examples: Hawk-Dove: effect of $\beta$ V = 2, D = 3, T = 1 (V < D) $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$ 0.175 0.150 0.125 0.100 0.075 $x_i \equiv [k_i/Z]$ Z = 1000.050 $\beta = 10$ $\mu = 1e - 3$ 0.025 0.000 0.2 0.6 0.8 0.0 0.4 1.0



![](_page_67_Figure_1.jpeg)

V = 2, D = 3, T = 1 (V < D)

# $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$

 $Z = 100 \qquad x_i \equiv [k_i/Z]$  $\beta = 1e - 2$  $\mu = 0$ 

![](_page_68_Figure_1.jpeg)

Examples: Hawk-Dove: effect of  $\mu$ V = 2, D = 3, T = 1 (V < D) $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$  $x_i \equiv [k_i/Z]$ Z = 100 $\beta = 1$  $\mu = 1e - 5$ 1.0

![](_page_69_Figure_1.jpeg)

V = 2, D = 3, T = 1 (V < D)

# $\begin{pmatrix} -0.5, -0.5 & 2, 0 \\ 0, 2 & 0, 0 \end{pmatrix}$

 $Z = 100 \qquad x_i \equiv [k_i/Z]$  $\beta = 1$  $\mu = 1e - 1$ 

![](_page_70_Figure_1.jpeg)

![](_page_71_Figure_1.jpeg)

#### $\rho(1,C) = T^{-}(1)\rho(C,0) + T^{+}(1)\rho(C,2) + (1 - T^{-}(1) - T^{+}(1))\rho(C,1)$

## $\rho(1,C) = \left(\sum_{k=0}^{Z-1} \prod_{i=1}^{k} \frac{T^{-}(i)}{T^{+}(i)}\right)^{-1}$

#### **Fixation probabilities**

We want  $\rho(C,1)$ , the probability that one C can take over a population of D players, which is given by

![](_page_71_Figure_6.jpeg)
# Fixation probabilities, evolutionary robustness and risk dominance

**Fixation probability** (of a single mutant)





$$\sum_{n=1}^{Z-1} \prod_{k=1}^{m} \frac{T^{-}(k)}{T^{+}(k)} \right)^{-1}$$



### **Fixation probabilities and evolutionary robustness**

#### Neutral drift

that does not change the payoff to either player) will eventually replace the entire population with probability  $\rho = \frac{1}{Z}$ ."

#### Survival of the fittest

A deleterious mutation, which is opposed by selection, will fix with probability  $\rho < \frac{1}{7}$ An **advantageous mutation**, which is favored by selection, will fix with probability  $\rho > \frac{1}{7}$ .

Stewart, A. J., & Plotkin, J. B. (2013). From extortion to generosity, evolution in the iterated prisoner's dilemma. Proceedings of the National Academy of Sciences, 110(38), 15348-15353.

"In a finite, homogeneous population of size Z, a newly introduced **neutral mutation** (i.e., a mutation)

#### Prisoners Dilemma, T>R, P>S



Stewart, A. J., & Plotkin, J. B. (2013). From extortion to generosity, evolution in the iterated prisoner's dilemma. Proceedings of the National Academy of Sciences, 110(38), 15348-15353.

#### **Solution concepts ; Evolutionary Robustness**

Remember a *neutral mutation* can replace the entire population with probability  $\rho = -\frac{1}{Z}$ .

A strategy *s*\* is **Evolutionary Robust** against a mutant strategy s' if the latter has a fixation probability of  $\rho \leq \frac{1}{7}$  in a population with  $s^*$ 

In terms of the reduced Markov chain, there are no edges leaving the state  $s^*$  with  $\rho > \frac{1}{7}$ 

In the limit of  $Z \rightarrow \infty$  the condition reduces to the ESS condition





## But, as this can quickly become computationally intractable!







**Evolutionary dynamics (\phi)** 



# Small mutation limit (SML) and dominance between strategies

Under the assumption that **mutations are rare (** $\mu \rightarrow 0$ **)** we always end up in a **monomorphic state** 

This allows us to simplify the transition probabilities to

$$T^{\pm}(k) = \frac{k}{Z} \frac{Z - k}{Z} [1 + e^{\mp \beta (f_a - f_b)}]^{-1}$$
  
And to consider instead the **reduced Mark**  
**the vertices of the simplex**, so that the sy

the following transition probabilities:

$$T_{i,j} = \rho_{ij} / (n_s - 1) \qquad T_{i,i} = 1 - \sum_{\forall j} T_{i,j}$$

**kov chain** which only **contains** system is now characterised by





#### **iScience**



#### Article

EGTtools: Evolutionary game dynamics in Python



Domingos, E. F., Santos, F. C., & Lenaerts, T. (2023). EGTtools: Evolutionary game dynamics in Python. Iscience, 26(4): 106419 <u>https://doi.org/10.1016/</u> <u>j.isci.2023.106419</u>

https://github.com/Socrats/EGTTools

## **EGTtools demo**

Jupyter replicator dynamics Last Checkpoint: 1 minute ago			
File Edit	View Run Kernel Settings Help		
<b>a</b> + %	□ □ ► ■ C → Code ∨ JupyterLab		
[23]:	<pre>import numpy as np # Plotting libraries import matplotlib.pylab as plt # Magic function to make matplotlib inline; other style specs must come AFTER %matplotlib inline # This enables high resolution PNGs. %config InlineBackend.figure formats = {'png', 'svg'}</pre>		
[24]:	<pre>from egttools.analytical import replicator_equation from egttools.analytical.utils import (calculate_gradients, find_roots, check_replicator_stability_pairwise_games from egttools.plotting import plot_gradients</pre>		
[25]:	<pre>#Payoff matrix prisoners dilemma T=7; R=3; P=1; S=0 A=np.array([[R,S],[T,P]])</pre>		
[26]:	<pre>#define a sequence of fractions of cooperators in the population nb_points = 101 strategy_i = np.linspace(0, 1, num=nb_points, dtype=np.float64) #strategy_i</pre>		
[27]:	<pre># Calculate gradient for every population state. gradient_function = lambda x: replicator_equation(x, A) gradients = calculate_gradients(np.array((strategy_i, 1 - strategy_i)).T, gradient_function)</pre>		
[28]:	<pre>#what are the roots (fixed points) of the replicator dynamic in the PD and ae they stable? roots = find_roots(gradient_function, 2, nb_initial_random_points=10, method="hybr") stability = check_replicator_stability_pairwise_games(roots, A, atol_neg=1e-4, atol_pos=1e-4, atol_zero=1e-4) #help(check_replicator_stability_pairwise_games)</pre>		
[22]:	<pre>plot_gradients(gradients[:, 0], figsize=(5,4), fig_title="PD replicator dynamics",</pre>		
	PD replicator dynamics 0.0 -0.2 -0.4 -0.6		





## SCIENTIFIC REPORTS

#### **OPEN**

#### **Computation and Simulation of Evolutionary Game Dynamics in Finite Populations**

Received: 22 October 2018 Accepted: 11 April 2019 Published online: 06 May 2019

Laura Hindersin<sup>1</sup>, Bin Wu<sup>2</sup>, Arne Traulsen <sup>1</sup> & Julian García<sup>3</sup>

The study of evolutionary dynamics increasingly relies on computational methods, as more and more cases outside the range of analytical tractability are explored. The computational methods for simulation and numerical approximation of the relevant quantities are diverging without being compared for accuracy and performance. We thoroughly investigate these algorithms in order to propose a reliable standard. For expositional clarity we focus on symmetric  $2 \times 2$  games leading to onedimensional processes, noting that extensions can be straightforward and lessons will often carry over to more complex cases. We provide time-complexity analysis and systematically compare three families of methods to compute fixation probabilities, fixation times and long-term stationary distributions for the popular Moran process. We provide efficient implementations that substantially improve wall times over naive or immediate implementations. Implications are also discussed for the Wright-Fisher process, as well as structured populations and multiple types.

Theoretical models of evolutionary games in finite populations typically require numerical procedures or simulations<sup>1-5</sup>. This is even the case when analytical results exist, as these are often difficult to interpret or confined to specific limits<sup>6–13</sup>. Simulations as well as numerical approximations are therefore common in the field, but far from being standardised. There are different computational methods to assess the key quantities in evolutionary game dynamics. Here we focus on studying the popular Moran process<sup>6</sup>. The purpose of this paper is to give an overview of such computational methods and to compare their limitations and scalability. We provide algorithms in pseudo-code as well as the source code for all the procedures that we study.

The Moran process<sup>14</sup> and the Wright-Fisher process<sup>15</sup> have become popular models to describe how phenotypes change over time by evolution. Both processes have their roots in population genetics. Only recently, they were introduced to evolutionary game dynamics in finite populations<sup>6,16,17</sup>. In each time step of the *Moran process*,

Hindersin, L., Wu, B., Traulsen, A., & García, J. (2019). Computation and simulation of evolutionary game dynamics in finite populations. Scientific reports, 9(1), 6946.

## **Details on the calculation**

Method	Advantages	Disadvantages
	Wall time is independent of the game	Limited to birth-death processes
Direct	Extendable to other birth-death processes, such as pairwise comparison processes (same complexity)	Not extendable to general graphs
	Wall time is independent of the game	<ul> <li>Strongly limited by population size due to store of transition matrix</li> </ul>
Matrix-based	Extendable to processes with dense transition matrix, such as Wright-Fisher (increased complexity)	
Simulations	Extendable to Fermi and Wright-Fisher	Wall time depends on the game and the selection intensity
	Extendable to games on graphs and multi-player games	Large number of realisations might be nece

Table 1. Overview of the three methods discussed here. This table lists their limitations and possible extensions.







## Mechanisms for the evolution of cooperation









#### Network reciprocity





# Part 4: Tutorial on how to reproduce an EGT paper





@esocrats https://github.com/Socrats







# Questions ?

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