An Introduction to Evolutionary Game Theory

Mauro Mobilia

Lectures delivered at the Graduate School on Nonlinear and Stochastic Systems in Biology
held in the Department of Applied Mathematics, School of Mathematics
University of Leeds, U.K.

31/03/2009 - 01/04/2009

Evolutionary Game Theory: What is it about?

- Modelling of the animal world
- Description of behavioural science and population dynamics (e.g. in ecology, economics, ...)
- Dynamical version of *classic (rational) game theory*
- Mathematical description of complex phenomena: interacting agents, spatial patterns, noise, non-linearity...

Some of the founders & pioneers:

- John von Neumann & Oskar Morgenstern (1944), “Theory of games and economic behavior”
- John Nash (1994 Nobel prize in Economics) → Nash equilibrium
- John Maynard Smith, “Evolution and the Theory of Games” (1972) → Evolutionary stability

Some books:

- J. Hofbauer & K. Sigmund, “Evolutionary Games and Population Dynamics” (1998)
- M. Nowak, “Evolutionary Dynamics” (2006)
- J. Maynard Smith, “Evolution and the Theory of Games” (1972)

Outline

The goal of these lectures is to give some insight into the ollowing topics:

- Basics of Classic (Rational) Game Theory
- Notion of Nash Equilibrium
- Concept of Evolutionary Stability
- Examples of Popular Games
- Concept of Fitness and Evolutionary Dynamics
- The (deterministic) Replicator Dynamics
- Replicator Equations for 2×2 Games
- Moran Process & Evolutionary Dynamics
- The Concept of Fixation Probability
- Evolutionary Game Theory in Finite Population
- Influence of Fluctuations on Evolutionary Dynamics

Classic (Rational) Game Theory in a Nutshell

Assumptions: complete information and perfect rationality Normal form of classic game is given by the triple $(\{N\},\{\mathscr{E}\},\{A\})$:

- $\{N\} = \{1,2,...,N\}$: set of players
- $\{\mathscr{E}\} = \{\mathbf{e}_1,\mathbf{e}_2,...,\mathbf{e}_Q\}$: same set of Q *pure strategies* for each player
- $\{\mathbf{A}\} = \{\mathbf{A}^{(1)},\mathbf{A}^{(2)},...,\mathbf{A}^{(N)}\}$: set of payoff (utility) functions for each player

Other ingredients:

- Mixed strategies (ME): allow to play each pure strategy $\mathbf{e}_j$ with probability $p_j \Rightarrow$ strategy profile is defined by the simplex $\{S\} = \{\mathbf{p} = (p_1,...,p_Q) : p_j \geq 0$ and $\sum_{j=1}^{Q} p_j = 1\}$
- Assume pairwise contests and symmetry (identical players) $\Rightarrow$ one $(Q \times Q)$ payoff matrix $\mathbf{A} = (A_{ij})$ with $i,j = 1,...,Q$

Player 1 plays $\mathbf{p} \in \{S\}$ against player 2 playing $\mathbf{q} \in \{S\}$:
Payoff of player 1 is $\mathscr{P}_1$ and payoff player 2 is $\mathscr{P}_2$

$$\mathscr{P}_1 = \mathbf{p}.A\mathbf{q}, \quad \mathscr{P}_2 = \mathbf{q}.A^T\mathbf{p}$$

Example 1: Hawks & Doves

- Homogeneous population with individuals competing for their reproductive succcess (food, territory or mates)
- During each contest: individuals compete for resources and can win / lose a fight (possible injury) or run away
- 2 strategies: either Hawk (agressive, escalate) or Dove (avoid fights)

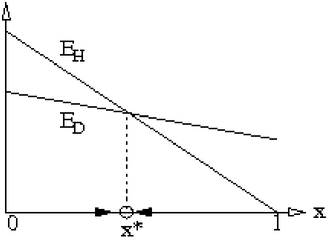
Strategy 1	Strategy 2	Payoff to 1	Because ...
Hawk	Dove	G	Hawk wins & Dove runs
Hawk	Hawk	$\frac{G-C}{2}$	50% chance of win/injury
Dove	Hawk	0	Dove runs away
Dove	Dove	$\frac{G}{2}$	Doves share resources

- For $G=4$, $C=10$, payoff matrix:

$$\mathbf{A} = \begin{array}{c} \\ \textit{Hawk} \\ \textit{Dove} \end{array} \begin{array}{c} \begin{array}{cc} \text{Hawk} & \text{Dove} \end{array} \\ \left(\begin{array}{cc} -3,-3 & 4,0 \\ 0,4 & 2,2 \end{array} \right) \end{array}$$

Example 1: Hawks & Doves (continued)

- Strategies *H* and *D* played with frequencies x and $1-x$, resp.
- Expected payoff H-player is $E_H = -3x + 4(1-x) = 4-7x$
- Expected payoff D-player is $E_D = 0x + 2(1-x) = 2-2x$
- $E_H = E_D$ for $x = x^* = 2/5$
- $x^* = 2/5$ is a *mixed strategy*
- For $x > x^*$: reproductive success of H is *lower* than for the D's. Therefore, the frequency of D's increases and moves towards x^*
- For $x < x^*$: reproductive success of D is *lower* than for the H's. Therefore, the frequency of H's increases and moves towards x^*
- Hence, we call x^* an **evolutionary stable strategy (ESS)**



Nash Equilibrium

What strategy to choose and how to make such a choice?

$$\mathbf{p}.\mathbf{A}\bar{\mathbf{q}} \leq \bar{\mathbf{q}}.\mathbf{A}\bar{\mathbf{q}}, \; \forall \mathbf{p} \neq \bar{\mathbf{q}}$$

$\bar{\mathbf{q}}$ is a Nash equilibrium (NE), or a strategy which is the best reply to itself.
A strict Nash equilibrium (sNE) $\bar{\mathbf{q}}$ is the unique best reply to itself:

$$\mathbf{p}.\mathbf{A}\bar{\mathbf{q}} < \bar{\mathbf{q}}.\mathbf{A}\bar{\mathbf{q}}, \; \forall \mathbf{p} \neq \bar{\mathbf{q}}$$

Every normal form game admits at least one NE (how many of them?)

Problems: Dynamics? How to discriminate between NEs? Rationality seems to restrictive $\rightarrow$ no cooperation
Nonstrict NE are *not* proof against invasion: *invaders may use a strategy doing as well as* $\bar{\mathbf{q}}$ *and may spread (if reproductive advantage),* **unless evolutionary stability strategy (ESS)**

Evolutionary Stability

A strategy is *evolutionary stable* (ESS) if, whenever all members of the population adopt it, no dissident behaviour could invade the population under natural selection

Consider a population in which the majority of the players (fraction $1-\varepsilon$) plays strategy $\mathbf{p}^*$ and a minority, ε plays mutant strategy $\mathbf{p}$.
$\mathbf{p}^*$ is an ESS iff it performs strictly better than the mutant strategy $\mathbf{p}$ against the composed population, i.e.

$$\mathbf{p}^*.\mathbf{A}[(1-\varepsilon)\mathbf{p}^* + \varepsilon\mathbf{p}] > \mathbf{p}.\mathbf{A}[(1-\varepsilon)\mathbf{p}^* + \varepsilon\mathbf{p}]$$

This can be rewritten as

$$(1-\varepsilon)(\mathbf{p}^*.\mathbf{A}\mathbf{p}^* - \mathbf{p}.\mathbf{A}\mathbf{p}^*) + \varepsilon(\mathbf{p}^*.\mathbf{A}\mathbf{p} - \mathbf{p}.\mathbf{A}\mathbf{p}) > 0$$

Thus, 2 conditions:

- NE condition:
  $\mathbf{p}^*.\mathbf{A}\mathbf{p}^* \geq \mathbf{p}.\mathbf{A}\mathbf{p}^*, \forall \mathbf{p} \in S$
- Stability condition:
  if $\mathbf{p}^* \neq \mathbf{p}$ and $\mathbf{p}^*.\mathbf{A}\mathbf{p}^* = \mathbf{p}.\mathbf{A}\mathbf{p}^*$, then $\mathbf{p}^*.\mathbf{A}\mathbf{p} > \mathbf{p}.\mathbf{A}\mathbf{p}, \forall \mathbf{p} \in S$

Evolutionary Stability (continued)

2 conditions for evolutionary stability:

1. NE condition:
   $\mathbf{p}^*.\mathbf{A}\mathbf{p}^* \geq \mathbf{p}.\mathbf{A}\mathbf{p}^*, \forall \mathbf{p} \in S$
2. Stability condition:
   if $\mathbf{p}^* \neq \mathbf{p}$ and $\mathbf{p}^*.\mathbf{A}\mathbf{p}^* = \mathbf{p}.\mathbf{A}\mathbf{p}^*$, then $\mathbf{p}^*.\mathbf{A}\mathbf{p} > \mathbf{p}.\mathbf{A}\mathbf{p}$

(1) says that $\mathbf{p}^*$ is a NE which is **not enough for non-invadibility**: there might be another *alternative best reply* $\mathbf{p}$. In such a case, (2) states that $\mathbf{p}^*$ fares better against $\mathbf{p}$ than $\mathbf{p}$ itself ($\Rightarrow$ **non-invadibility**)

- Strict-NE are ESS (symmetric games)
- All ESS are NEs (but not necessarily strict-NEs)
- A game with 2 pure strategies always has an ESS

How to find an ESS? Necessary condition (for an interior NE) given by the Bishop-Cannings Theorem: If $\mathbf{p}^* = \sum_{i=1}^{Q} p_i \mathbf{e}_i \in \mathrm{int}(S)$ with $p_i \geq 0$ is an interior ESS, then

$$\begin{aligned} \mathbf{e}_1.\mathbf{A}\mathbf{p}^* &= (\mathbf{A}\mathbf{p}^*)_1 = \ldots = (\mathbf{A}\mathbf{p}^*)_i = \ldots = (\mathbf{A}\mathbf{p}^*)_Q = \mathbf{p}^*.\mathbf{A}\mathbf{p}^* \\ p_1 &+ \ldots + p_Q = 1 \end{aligned}$$

Hawks-Doves & game revisited (Example 1)

Hawks & Doves: gain from resources G and cost for injury $C > G$

Payoff matrix: Hawk Dove

$$\mathbf{A} = \begin{matrix} \textit{Hawk} \\ \textit{Dove} \end{matrix} \begin{pmatrix} (G-C)/2 & G \\ 0 & G/2 \end{pmatrix}$$

Mixed strategy $\mathbf{p}^* = (G/C)\mathbf{e_H} + (1 - G/C)\mathbf{e_D}$ is an NE

However, is it an ESS?

With $\mathbf{p} = p\mathbf{e_H} + (1-p)\mathbf{e_D} = (p, 1-p)^T$ we check the conditions for $\mathbf{p}^*$ to be an ESS:

- $\mathbf{p}.\mathbf{A}\mathbf{p}^* = \mathbf{p}^*.\mathbf{A}\mathbf{p}^* = G(1 - G/C)/2, \forall p \in \mathscr{S}$
  Thus, condition 1 (for NE) is satisfied for all $\mathbf{p}$'s with equality

  One has thus to check condition 2 (for stability):

- With $\mathbf{p}.\mathbf{A}\mathbf{p} = (G - Cp^2)/2$ and $\mathbf{p}^*.\mathbf{A}\mathbf{p} = (G^2/2C) + G(1-2p)/2$,
  $\mathbf{p}^*.\mathbf{A}\mathbf{p} - \mathbf{p}.\mathbf{A}\mathbf{p} = \frac{(G-Cp)^2}{2C} > 0$, $\forall \mathbf{p} \neq \mathbf{p}^* \Rightarrow$ stability guaranteed!

Thus, $\mathbf{p}^* = (G/C)\mathbf{e_H} + (1 - G/C)\mathbf{e_D}$ is an ESS for the Hawk-Dove game with $C > G$

Example 2: Prisoner's Dilemma (PD)

Two suspects in a crime are put in separate cells and questioned, they can confess (i.e. cooperation, C) or defect (i.e. remain silent, D)

- If both confess (C C), each is sentenced 3 years (major crime)
- If none confess (D D), each is sentenced 1 year (minor crime because no strong evidences)
- One confess and the other remain silent: C-strategist is used as witness and goes free while the S-strategist is sentenced 5 years
- Payoff matrix for the PD:

$$\mathbf{A} = \begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \left(\begin{array}{cc} 3,3 & 0,5 \\ 5,0 & 1,1 \end{array} \right) \end{array}$$

Defection is the only (strict) Nash equilibrium (i.e. an ESS): D D gives a payoff $(1,1)$. Cooperation gives a higher payoff $(3,3)$, but it is "irrational" because of free ride danger

For each (rational) player it is beneficial to always defect (sNE). However, if both defect they get a payoff 1, less than for mutual cooperation (which gives a payoff 3). *That's the dilemma !*

Example 3: Jean-Jacques Rousseau's stag-hunt game (SHG)

2 individuals can decide to hunt a stag (S) or a hare (H). A hare is worth less than a stag but can be get individually

- If both cooperate to hunt a stag (S S), the payoff is 4
- If one individual chooses to hunt a hare (H), his/her payoff is always 3
- An individual stag-hunter (S) has little chance of success and her/his payoff is 1
- Payoff matrix for the SHG:

$$\mathbf{A} = \begin{array}{c} \\ S \\ H \end{array} \begin{array}{c} \begin{array}{cc} S & H \end{array} \\ \left(\begin{array}{cc} 4,4 & 1,3 \\ 3,1 & 3,3 \end{array} \right) \end{array}$$

There are 2 strict NEs (i.e. ESS): the pure strategies S S, giving payoff $(4,4)$, and H H giving payoff $(3,3)$

S S is *payoff (Pareto) dominant* because $(5,5) > (3,3)$

H H is *risk dominant* ("safer") because it gives a payoff 3 for 2 of the 4 choices (while there is only 1 option out of 4 to get payoff 4)

In addition: the mixed strategy $\mathbf{p} = (2/3)S + (1/3)H = (2/3, 1/3)$ is a nonstrict NE

SH is a coordination game, prototype of the "social contract"

Classic games with 2 pure strategies: summary

Games with 2 pure strategies, $\mathbf{e}_1$ and $\mathbf{e}_2$, and payoff matrix:

$$\mathbf{A} = \begin{array}{c} \mathbf{e_1} \\ \mathbf{e_2} \end{array} \overset{\begin{array}{cc} \mathbf{e_1} & \mathbf{e_2} \end{array}}{\begin{pmatrix} a & b \\ c & d \end{pmatrix}}$$

3 cases:

1. There is one single pure ESS *(e.g. prisoner's dilemma)*
2. Both pure strategies $\mathbf{e_1}$ and $\mathbf{e_2}$ are ESS *(e.g. stag-hunt game)*
3. A mixed strategy is an ESS *(e.g. hawk-dove with $C > G$)*

More precisely:

- If $a > c$, $\mathbf{e_1}$ is ESS (strict-NE)
- If $d > b$, $\mathbf{e_2}$ is ESS (strict-NE)
- If $c > a$, and $b > d$, mixed strategy $\mathbf{p} = p\mathbf{e_1} + (1-p)\mathbf{e_2}$ with $p = \frac{b-d}{b+c-a-d}$ is an ESS (strict-NE)

Evolutionary dynamics & the concept of fitness

Alternative representation in terms of population dynamics: Population of pure strategists with proportion with fraction x_i of $\mathbf{e_i}$-players. In this case, $\mathbf{x} = (x_1, ..., x_i, ..., x_Q)$ is an ESS under the same conditions. In this language $\mathbf{e_i}$-strategists are regarded as individuals of species i

Nash equilibrium and Evolutionary stability are *static* concepts

Evolutionary dynamics relies on the concept of **fitness**:

- Evolutionary "forces": *selection, reproduction, mutation, imitation*
- $\mathbf{x}(t)$ state of population at time t, with $\sum_{i=1}^{Q} x_i = 1$
- Dynamics of the system: $\frac{d}{dt} x_i = F(\mathbf{x})$
- It seems natural to assume that $F(\mathbf{x})$ is a function of the poulation's *fitness*, where
- **Fitness of a species i**, denoted $f_i(\mathbf{x})$, measures the success of reproduction of that species. This quantity depends on the state of the whole population

Goals: Which kind of dynamics? What are the steady states?

Replicator Dynamics

Population of Q different species: $\mathbf{e_1},...,\mathbf{e_Q}$, with frequencies $x_1,...,x_Q$

State of the system described by $\mathbf{x} = (x_1,...,x_Q) \in \mathscr{S}_Q$, where $\mathscr{S}_Q = \{\mathbf{x}; x_i \geq 0, \sum_{i=1}^{Q} x_i = 1\}$

To set up the dynamics, we need a functional expression for the fitness $f_i(\mathbf{x})$

Between various possibilities, a very popular choice is:

$$\dot{x}_i = x_i \left(f_i(\mathbf{x}) - \bar{f}(\mathbf{x}) \right),$$

where, one (out of many) possible choices, for the fitness is the *expected payoff*: $f_i(\mathbf{x}) = \sum_{i=1}^{Q} A_{ij} x_j$

and $\bar{f}(\mathbf{x})$ is the *average fitness*: $\bar{f}(\mathbf{x}) = \sum_i^Q x_i f_i(\mathbf{x})$

This choice corresponds to the so-called **replicator dynamics** on which most of evolutionary game theory is centered

Some Properties of Replicator Dynamics (I)

Replicator equations (REs):

$$\dot{x}_i = x_i\,[(\mathbf{Ax})_i - \mathbf{x}.\mathbf{Ax}]$$

Set of coupled cubic equations (when $\mathbf{x}.\mathbf{Ax} \neq 0$)

Let $\mathbf{x}^* = (x_1^*, ..., x_Q^*)$ be a fixed point (steady state) of the REs

- $\mathbf{x}^*$ can be (Lyapunov-) stable, unstable, attractive (i.e. there is basin of attraction), asymptotically stable=attractor (=stable + attractive), globally stable (basin of attraction is $\mathscr{S}_Q$)
- Only possible interior fixed point satisfies (there is either 1 or 0):

$$(\mathbf{Ax}^*)_1 = (\mathbf{Ax}^*)_2 = ... = (\mathbf{Ax}^*)_Q = \mathbf{x}^*.\mathbf{Ax}^*$$
$$x_1 + ... + x_Q = 1$$

- Same dynamics if one adds a constant c_j to the payoff matrix $\mathbf{A} = (A_{ij})$: $\dot{x}_i = x_i\,[(\mathbf{Ax})_i - \mathbf{x}.\mathbf{Ax}] = x_i\left[(\widetilde{\mathbf{A}}\mathbf{x})_i - \mathbf{x}.\widetilde{\mathbf{A}}\mathbf{x}\right]$, where $\widetilde{\mathbf{A}} = (A_{ij} + c_j)$

Some Properties of Replicator Dynamics (II)

Dynamic versus evolutionary stability: connection between dynamic stability (of REs) and NE/evolutionary stability?
Notions do not perfectly overlap $\Rightarrow$ *Folks Theorem* of EGT:

Let $\mathbf{x}^* = (x_1^*, ..., x_Q^*)$ be a fixed point (steady state) of the REs

- NEs are rest points (of the REs)
- Strict NEs are attractors
- A stable rest point (of the REs) is an NE
- Interior orbit converges to $\mathbf{x}^* \Rightarrow \mathbf{x}^*$ is an NE

- ESSs are attractors (asymptotically stable)
- Interior ESSs are global attractors

Converse statements generally do not hold!

- For 2×2 matrix games $\mathbf{x}^*$ is an ESS iff it is an attractor
- REs with Q strategies can be mapped onto Lotka-Volterra equations for $Q-1$ species: $\dot{y}_i = y_i \left(r_i + \sum_{j=1}^{Q-1} b_{ij} y_j \right)$
- Replicator dynamics is non-innovative: cannot generate new strategies

Replicator Dynamics for 2×2 Games (I)

2 strategies: say A and B
N players: N_A are A-players and N_B are B-players, $N_A + N_B = N$

General payoff matrix:

vs	A	B
A	$1 + p_{11}$	$1 + p_{12}$
B	$1 + p_{21}$	$1 + p_{22}$

where selection $\to p_{ij}$ and the neutral component $\to 1$

Frequency of A and B strategists is resp.

$$x = N_A/N \quad \text{and} \quad y = N_B/N = 1 - x$$

Fitness (expected payoff) of A and B strategists is resp.

$$f_A(x) = p_{11}x + p_{12}(1-x) + 1 \quad \text{and} \quad f_B(x) = p_{21}x + p_{22}(1-x) + 1$$

Average fitness: $\bar{f}(x) = x f_A(x) + (1-x) f_B(x)$

Replicator Dynamics for 2×2 Games (II)

Replicator dynamics:

$$\frac{dx}{dt} = x[f_A(x) - \bar{f}(x)] = x(1-x)[f_A(x) - f_B(x)]$$
$$= x(1-x)[x(p_{11} - p_{21}) + (1-x)(p_{12} - p_{22})]$$

- $xy = x(1-x)$: interpreted as the probability that A and B interact
- $f_A(x) - f_B(x) = x(p_{11} - p_{12}) + (1-x)(p_{12} - p_{22})$: says that reproduction ("success") depends on the difference of fitness

Equivalent payoff matrix ($A_{i1} \to A_{i1} - p_{11}$, $A_{i2} \to A_{i2} - p_{22}$), with $\mu_A = p_{21} - p_{11}$ and $\mu_B = p_{12} - p_{22}$:

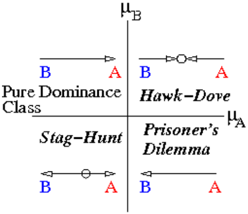
vs	A	B
A	1	$1 + \mu_A$
B	$1 + \mu_B$	1

$$\frac{dx}{dt} = x(1-x)[-x\mu_A + (1-x)\mu_B] = x(1-x)[\mu_B - (\mu_A + \mu_B)x]$$

$\Rightarrow$ For 2×2 games, the dynamics is simple: no limit cycles, no oscillations, no chaotic behaviour

Replicator Dynamics for 2 × 2 Games (III)

$$\frac{dx}{dt} = x(1-x)[\mu_B - (\mu_A + \mu_B)x]$$



1. $\mu_A > 0$ and $\mu_B > 0$: Hawk-Dove game
   $x^* = \frac{\mu_B}{\mu_A + \mu_B}$ is stable (attractor, ESS) interior FP
2. $\mu_A > 0$ and $\mu_B < 0$: Prisoner's Dilemma
   B always better off, $x^* = 0$ is ESS
3. $\mu_A < 0$ and $\mu_B < 0$: Stag-Hunt Game
   Either *A* or *B* can be better off, i.e. $x^* = 0$ and $x^* = 1$ are ESS.
   $x^* = \frac{\mu_B}{\mu_A + \mu_B}$ is unstable FP (non-ESS)
4. $\mu_A < 0$ and $\mu_B > 0$: Pure Dominance Class
   A always better off, $x^* = 1$ is ESS

Some Remarks on Replicator Dynamics

$$\frac{dx}{dt} = x(1-x)[\mu_B - (\mu_A + \mu_B)x]$$

- For x small: $\dot{x} = \mu_B x$
- For $x \approx 1$: $\dot{y} = (d/dt)(1-x) = \mu_A(1-x)$

Thus, the stability of $x^* = 0$ and $x^* = 1$ simply depends on the sign of μ_B and μ_A, respectively

Another popular dynamics is the so-called “adjusted replicator dynamics”, for which the equations read:

$$\frac{dx}{dt} = x\frac{f_A(x) - \bar{f}(x)}{\bar{f}(x)} = x(1-x)\left[\frac{f_A(x) - f_B(x)}{\bar{f}(x)}\right]$$

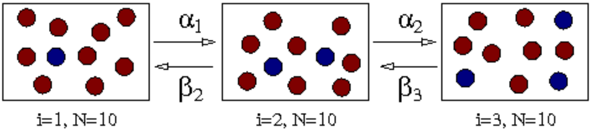
These equations equations share the same fixed points with the REs. In general, replicator dynamics and adjusted replicator dynamics give rise to different behaviours. However, for 2×2 games: same qualitative behaviour

Stochastic Dynamics & Moran Process

Evolutionary dynamics involves a *finite number of discrete individuals*
$\Rightarrow$ "Microscopic" stochastic rules given by the **Moran process**

Moran Process is a Markov birth-death process in 4 steps:
2 species, i individuals of species A and $N-i$ of species B

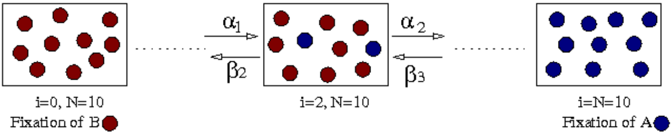
1. An individual A could be chosen for *birth and death* with probability $(i/N)^2$. The number of A remains the same
2. An individual B could be chosen for *birth and death* with probability $((N-i)/N)^2$. The number of B remains the same
3. An individual A could be chosen for *reproduction* and a B individual for *death* with probability $i(N-i)/N^2$. For this event: $i \to i+1$ and $N-i \to N-1-i$
4. An individual B could be chosen for *reproduction* and a A individual for *death* with probability $i(N-i)/N^2$. For this event: $i \to i-1$ and $N-i \to N+1-i$



Stochastic Dynamics & Moran Process

Evolutionary dynamics given by the **Moran process**: Markov birth-death process in 4 steps

There are two absorbing states in the Moran process: all-B and all-A

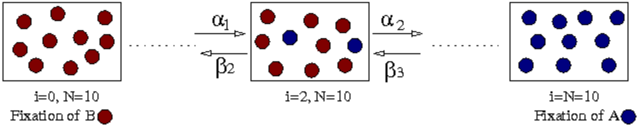


What is the probability F_i of ending in a state with all A ($i = N$) starting from i individuals A? For $i = 1$, F_1 is the “fixation” probability of A

- Transition from $i \to i+1$ given by rate α_i
- Transition $i \to i-1$ given by rate β_i

$$
\begin{aligned}
F_i &= \beta_i F_{i-1} + (1-\alpha_i-\beta_i)F_i + \alpha_i F_{i+1}, \quad \text{for} \quad i = 1, \ldots, N-1 \\
F_0 &= 0 \quad \text{and} \quad F_N = 1
\end{aligned}
$$

Moran Process & Fixation Probability



What is the fixation probability F_1 of A individuals?

$$F_i = \beta_i F_{i-1} + (1-\alpha_i-\beta_i)F_i + \alpha_i F_{i+1}, \quad \text{for} \quad i = 1, ..., N-1$$
$$F_0 = 0 \quad \text{and} \quad F_N = 1$$

Introducing $g_i = F_i - F_{i-1}$ $(i = 1, ..., N-1)$, one notes that $\sum_{i=1}^{N} g_i = 1$ and $g_{i+1} = \gamma_i g_i$, where $\gamma_i = \beta_i/\alpha_i \Rightarrow$ one recovers a classic results on Markov chains: $F_i = \frac{1+\sum_{j=1}^{i-1}\prod_{k=1}^{j}\gamma_k}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}$

$\Rightarrow$ Fixation probability of species A is $F_A = F_1 = \frac{1}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}$

As $i = 0$ and $i = N$ are absorbing states $\Rightarrow$
always *absorption* (all-A or all-B) $\Rightarrow$ Fixation probability of species B is $F_B = 1 - F_{N-1} = \frac{\prod_{k=1}^{N-1}\gamma_k}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}$

Fixation in the Neutral & Constant Fitness Cases

Fixation Probabilities:

$F_A = \frac{1}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}$ and $F_B = F_A \prod_{k=1}^{N-1}\gamma_k$, with $\gamma_i = \beta_i/\alpha_i$

- When $\alpha_i = \beta_i = \gamma_i = 1$, this is the neutral case where there is no *selection* but only *random drift*:
  F_A=F_B=$1/N$
  This means that the chance that an individual will generate a lineage which will inheritate the entire population is $1/N$
- Case where A and B have constant but different fitnesses, $f^A = r$ for A and $f^B = 1$ for B, $\alpha_i = \frac{ri(N-i)}{N(N+(r-1)i)}$ and $\beta_i = \frac{i(N-i)}{N(N+(r-1)i)}$
  Thus, $F_A = \frac{1-r^{-1}}{1-r^{-N}}$ and $F_B = \frac{1-r}{1-r^N}$
  If $r > 1$, $F_A > N^{-1}$ for $N \gg 1$: selection favours the fixation of A
  If $r < 1$, $F_B > N^{-1}$ for $N \gg 1$: selection favours the fixation of B

Evolutionary Games in Finite Populations (I)

Finite population of 2 species: i individuals of species A and $N-i$ individuals of species B interact according to the payoff matrix:

vs	A	B
A	a	b
B	c	d

Probability to draw a A and B is i/N and $(N-i)/N$, respectively $\Rightarrow$

- Probability that a given individual A interacts with another A is $(i-1)/(N-1)$
- Probability that a given individual A interacts with a B is $(N-i)/(N-1)$
- Probability that a given individual B interacts with another B is $(N-i-1)/(N-1)$
- Probability that a given individual B interacts with a A is $i/(N-1)$

The states $i=0$ (All-A) and $i=N$ (All-B) are absorbing

Expected payoff for A and B, respectively:

$$E_i^A = \frac{a(i-1)+b(N-i)}{N-1} \quad \text{and} \quad E_i^B = \frac{ci+d(N-i-1)}{N-1}$$

Evolutionary Games in Finite Populations (II)

$$F_A = \left(1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k\right)^{-1} \text{ and } F_B = F_A \prod_{k=1}^{N-1} \gamma_k, \text{ with } \gamma_i = \beta_i/\alpha_i$$
$$E_i^A = \frac{a(i-1)+b(N-i)}{N-1} \quad \text{and} \quad E_i^B = \frac{ci+d(N-i-1)}{N-1}$$

Expected payoffs $E_i^{A,B}$ are usually interpreted as fitness.

Recent idea (Nowak et al.): Introduce a parameter w accounting for background random drift contribution to fitness f_i^A for A and f_i^B for B

$$f_i^A = 1 - w + wE_i^A \quad \text{and} \quad f_i^B = 1 - w + wE_i^B$$

Average fitness: $\bar{f} = (i/N)f_i^A + (1-(i/N))f_i^B$

Parameter w measures the *intensity of selection*: $w = 0 \Rightarrow$ no selection (only random drift), $w = 1 \Rightarrow$ only selection, $w \ll 1 \Rightarrow$ "weak selection"

Consider a Moran process with frequency-dependent hopping rates:

$$\alpha_i = \frac{f_i^A}{\bar{f}}\left(\frac{i}{N}\right)\left(\frac{N-i}{N}\right) \quad \text{and} \quad \beta_i = \frac{f_i^B}{\bar{f}}\left(\frac{i}{N}\right)\left(\frac{N-i}{N}\right) \Rightarrow \gamma_i = \frac{f_i^B}{f_i^A}$$

Thus, $F_A = 1/\left(1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} (f_k^B/f_k^A)\right)$ and $F_B = F_A \prod_{k=1}^{N-1} (f_k^B/f_k^A)$

Influence of Fluctuations on Evolutionary Dynamics (I)

Fixation Probabilities:

$F_A = \left(1 + \sum_{j=1}^{N-1} \prod_{i=1}^{j} \frac{f_i^B}{f_i^A}\right)^{-1}$ and $F_B = F_A \prod_{i=1}^{N-1} \left(f_i^B / f_i^A\right)$, with

$f_i^A = 1 - w + w\frac{a(i-1)+b(N-i)}{N-1}$ and $f_i^B = 1 - w + w\frac{ci+d(N-i-1)}{N-1}$

Does selection favour fixation of A? Yes, only if $F_A > 1/N$

In the weak selection limit ($w \to 0$):

$F_A \approx \frac{1}{N}\left[1 - \frac{w}{6}\left(\{a+2b-c-2d\}N - \{2a+b+c-4d\}\right)\right]^{-1}$

Thus, $F_A > 1/N$ if $a(N-2)+b(2N-1) > c(N+1)+2d(N-2)$

$N=2$	$b>c$
$N=3$	$a+5b>2(2c+d)$
$N=4$	$2a+7b>5c+4d$
...	...
$N \gg 1$	$a+2b>c+2d$

For large N, $F_A > 1/N$ if $a+2b>c+2d$

Influence of Fluctuations & Finite-Size Effects (II)

In the weak selection limit ($w \to 0$):

$$F_A \approx \frac{1}{N}\left[1 - \frac{w}{6}(\{a+2b-c-2d\}N - \{2a+b+c-4d\})\right]^{-1}$$

For large N, $F_A > 1/N$ if $a+2b > c+2d$

Consequences of finite-size fluctuations?

Reconsider a 2×2 game with $a > c$ and $b < d$ ("Stag-Hunt game"):

- Rational game: all-A and all-B are strict-NE and ESS
- Replicator Dynamics: all-A & all-B attractors and $x^* = \frac{d-b}{a-c+d-b}$ is an unstable interior rest point (NE, but not ESS)
- In finite (yet large) population (stochastic Moran process, weak selection): The condition $a-c > 2(d-b)$ to favour fixation of A leads to $x^* < 1/3$

- If the unstable rest point x^* occurs at frequency $< 1/3$, in a large yet finite population and for $w \ll 1$, selection favours the fixation of A
- Probability that a single A takes over the entire population of $N-1$ individuals B is greater than $1/N$
- This also means that the basin of attraction of all-B is less than $1/3$ (if $x^* < 1/3$)

Influence of Fluctuations & Finite-Size Effects (III)

In the weak selection limit ($w \to 0$, 2 species systems):
$$F_A \approx \frac{1}{N}\left[1 - \frac{w}{6}(\{a+2b-c-2d\}N - \{2a+b+c-4d\})\right]^{-1}$$

Previous result hints that the concept of *evolutionary stability* should be modified to account for finite-size fluctuations $\Rightarrow$ leads to the concept of **ESS**$_N$: *A finite population of B is evolutionary stable is evolutionary stable against a second species A if*

1. The fitness of B is greater than that of A, i.e. $f_i^B > f_i^A$, $\forall i$. This means: “selection opposes A invading B”
2. $F_A < 1/N$, implying that selection opposes A replacing B

This leads to the **criteria for evolutionary stability** of B:

Determinsitic ($N = \infty$)	Stochastic (N finite)
(1) $d > b$ (2) if $b = d$, then $c > a$	$(d-b)N > 2d-(b+c)$ $c(N+1)+2d(N-2) > a(N-2)+b(2N-1)$

Influence of Fluctuations & Finite-Size Effects (III)

In the weak selection limit ($w \to 0$, 2×2 games):

$$F_A \approx \frac{1}{N}\left[1 - \frac{w}{6}\left(\{a+2b-c-2d\}N - \{2a+b+c-4d\}\right)\right]^{-1}$$

Criteria for evolutionary stability of B in a population of size N:

Determinsitic ($N = \infty$)	Stochastic (N finite)
(1) $d > b$ (2) if $b = d$, then $c > a$	$(d-b)N > 2d - (b+c)$ $c(N+1) + 2d(N-2) > a(N-2) + b(2N-1)$

Conditions for evolutionary stability depend on the population size:

B is ESS_N if	$N = 2$	$N \gg 1$ (finite)
Condition (1):	$c > b$	$d > b$
Condition (2):	$c > b$	$x^* = \frac{d-b}{a-c+d-b} > 1/3$

- For small N, the traditional ESS conditions are *neither necessary nor sufficient* to guarantee evolutionary stability
- For large N, the traditional ESS conditions are *necessary but* **not** *sufficient* to guarantee evolutionary stability

Outlook

In this set of lectures dedicated to an introduction to evolutionary game theory, we have discussed

- Some concepts of *classic (rational) game theory* which were illustrated by a series of examples (hawk-doves, prisoner's dilemma and stag-hunt games)
- Notion of evolutionary dynamics via the concept of fitness
- *Replicator dynamics* and discussed its properties: connection between dynamic stability, NEs and ESS
- *Replicator dynamics* for 2×2 games: classification
- Stochastic evolutionary dynamics according to the Moran process
- Fixation probability as a Markov chain problem
- Fixation probability for (a) the neutral case, (b) the case with constant fitness, **(c)** 2×2 **games with finite populations**
- *Influence of fluctuations*: fixation and new criteria for evolutionary stability (ESS_N for 2×2 games)

Outlook

Further topics and some open problems (non-exhaustive list):

- Replicator dynamics for $Q \times Q$ games:
  - For $Q \geq 3$: Replicator equations $\Rightarrow$ cycles, oscillations, chaos ($Q > 3$), ...
  - Spatial degrees of freedom and role of mobility (PDE): pattern formation
  - $Q \times Q$ games with mutations
- Stochastic evolutionary dynamics:
  - Stochastic evolutionary game theory on lattices and graphs
  - Combined effects of mobility, fluctuations, and selection

    For $Q \times Q$ games, with $Q \geq 3$:

  - Diffusion approximation (Fokker-Planck equation)
  - Fixation and extinction times (e.g. as first-passage problems)
  - Generalization of the concept of ESS_N