An Introduction to Evolutionary Game Theory: Lecture 2

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

Outline

The goal of this lecture is to give some insight into the following topics:

- Some Properties of the 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

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*: $f_i(\mathbf{x}) = \sum_{j=1}^{Q} A_{ij} x_j$

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 the 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 the 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 $\mu_B = p_{12} - p_{22}$:

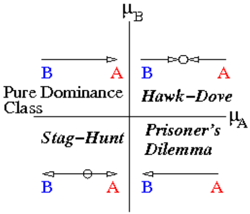
vs	A	B
A	1	$1+\mu_A$
B	$1+\mu_B$	1

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

$\Rightarrow$ 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:

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

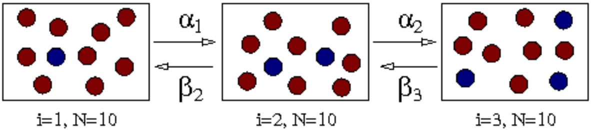
These equations equations share the same fixed points with the REs. In general, replicator dynamics and adjusted replicator dynamics give rise to different behaviours. However, for 2×2 games: same qualitative behaviour

Stochastic Dynamics & Moran Process

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

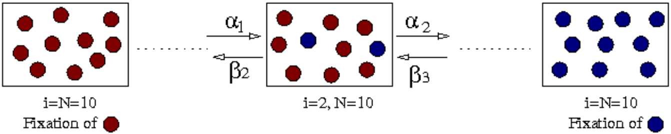
Moran Process is a Markov birth-death process in 4 steps:
2 species, i individuals of species A and $N-i$ of species B

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 $N-i \to N+1-i$



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

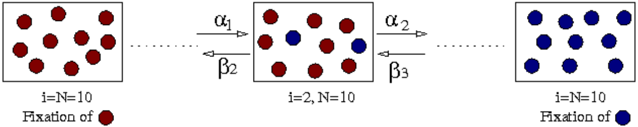
There are two absorbing states in the Moran process: all-B and all-A



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

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



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:

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

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

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

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

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

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 ($w \to 0$):

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

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 $1/N$

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

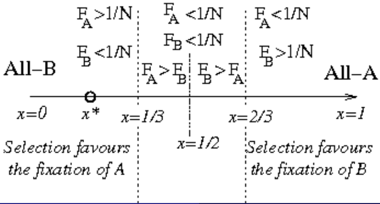
$$F_A \approx \frac{1}{N}\left[1 - \frac{w}{6}\left(\{a+2b-c-2d\}N - \{2a+b+c-4d\}\right)\right]^{-1}$$

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 $x^* < 1/3$



Influence of Fluctuations & Finite-Size Effects (III)

In the weak selection limit ($w \to 0$, 2 species systems):

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

Previous result hints that the concept of *evolutionary stability* should be modified to account for finite-size fluctuations $\Rightarrow$ leads to the concept of $\mathbf{ESS}_N$: *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) $d > b$	$(d-b)N > 2d - (b+c)$
(2) if $b = d$, then $c > a$	$c(N+1) + 2d(N-2) > a(N-2) + b(2N-1)$

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