Evolutionary Dynamics, Games and Graphs

Barbara Ikica
Supervisor: prof. dr. Milan Hladnik
Faculty of Mathematics and Physics, University of Ljubljana
18 June 2015
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.
- **Stochastic models:**
  - evolutionary graph theory:
    - amplifiers of random drift,
    - amplifiers of selection,
    - the replicator equation on graphs.
Overview

- **Deterministic models:**
  - the replicator equation,
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.

- **Stochastic models:**
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.

- **Stochastic models:**
  - evolutionary graph theory:
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.

- **Stochastic models:**
  - evolutionary graph theory:
    - amplifiers of random drift,
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.

- **Stochastic models:**
  - evolutionary graph theory:
    - amplifiers of random drift,
    - amplifiers of selection,
Overview

- **Deterministic models:**
  - the replicator equation,
  - Nash equilibria and evolutionary stability,
  - permanence and persistence.

- **Stochastic models:**
  - evolutionary graph theory:
    - amplifiers of random drift,
    - amplifiers of selection,
    - the replicator equation on graphs.
Deterministic models

State of the population (with $n$ species):

$$\Delta_n := \left\{ \mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n : x_i \geq 0 \text{ in } \sum_{i=1}^{n} x_i = 1 \right\}$$

Fitness (reproductive success) of the $i$-th species: $f_i(\mathbf{x})$
Replicator dynamics

The replicator equation

\[ \dot{x}_i = x_i (f_i(x) - \bar{f}(x)), \quad i = 1, 2, \ldots, n \]

Average fitness: \( \bar{f}(x) = \sum_{i=1}^{n} f_i(x) x_i \)
Replicator dynamics

The replicator-mutator equation

\[ \dot{x}_i = x_i \left( f_i(x) - f_i(x) \sum_{j \neq i}^n q_{ij} \right) + \sum_{j \neq i}^n x_j f_j(x) q_{ji} - x_i \bar{f}(x), \quad i = 1, 2, \ldots, n \]

Average fitness: \( \bar{f}(x) = \sum_{i=1}^n f_i(x) x_i \)
Replicator dynamics

The replicator equation

\[ \dot{x}_i = x_i (f_i(x) - \bar{f}(x)), \quad i = 1, 2, \ldots, n \]

Average fitness: \[ \bar{f}(x) = \sum_{i=1}^{n} f_i(x) x_i \]
Game theory in replicator dynamics

Strategies:

\[ \Delta_N := \left\{ \mathbf{p} = (p_1, p_2, \ldots, p_N) \in \mathbb{R}^N : p_i \geq 0 \text{ in } \sum_{i=1}^{N} p_i = 1 \right\} \]

Payoff matrix: \[ U = [u_{ij}]_{i,j=1}^{N} \]
Game theory in replicator dynamics

Strategies:

\[ \Delta_N := \left\{ p = (p_1, p_2, \ldots, p_N) \in \mathbb{R}^N : p_i \geq 0 \text{ in } \sum_{i=1}^{N} p_i = 1 \right\} \]

Payoff matrix: \[ U = [u_{ij}]_{i,j=1}^{N} \]

Expected payoff of a \( p \)-strategist against a \( q \)-strategist:
\[ p \cdot U q \]
Game theory in replicator dynamics

How to incorporate a game?

1. $i$-th species ($x_i$) $\sim \rightarrow \ p^i$
Game theory in replicator dynamics

How to incorporate a game?

1. \(i\)-th species \((x_i)\) \(\sim\) \(\rightarrow\) \(p^i\)
2. \(A = [a_{ij}]_{i,j=1}^n, a_{ij} = p^i \cdot U p^j\)
Game theory in replicator dynamics

How to incorporate a game?

1. $i$-th species $(x_i) \leadsto p^i$
2. $A = [a_{ij}]_{i,j=1}^n$, $a_{ij} = p^i \cdot U p^j$
3. $f_i(x) = (Ax)_i = \sum_{j=1}^n p^i \cdot U p^j x_j$
Game theory in replicator dynamics

How to incorporate a game?

1. $i$-th species ($x_i$) $\sim$ $p^i$
2. $A = [a_{ij}]_{i,j=1}^{n}$, $a_{ij} = p^i \cdot U p^j$
3. $f_i(x) = (Ax)_i = \sum_{j=1}^{n} p^i \cdot U p^j x_j$

The replicator equation

\[ \dot{x}_i = x_i (f_i(x) - \bar{f}(x)), \quad i = 1, 2, \ldots, n \]

Average fitness: \( \bar{f}(x) = \sum_{i=1}^{n} f_i(x) x_i \)
Game theory in replicator dynamics

How to incorporate a game?

1. $i$-th species $(x_i) \rightarrow p^i$

2. $A = [a_{ij}]_{i,j=1}^n$, $a_{ij} = p^i \cdot U p^j$

3. $f_i(x) = (Ax)_i = \sum_{j=1}^n p^i \cdot U p^j x_j$

The linear replicator equation

\[
\dot{x}_i = x_i ((Ax)_i - x \cdot Ax), \quad i = 1, 2, \ldots, n
\]

Average fitness: $\bar{f}(x) = x \cdot Ax$
Nash equilibria and evolutionary stability

(Symmetric) Nash equilibrium

A strategy \( \hat{p} \in \Delta_N \) such that for all \( p \in \Delta_N \),

\[
\hat{p} \cdot U\hat{p} \geq p \cdot U\hat{p}.
\]
Nash equilibria and evolutionary stability

(Symmetric) Nash equilibrium

A strategy \( \hat{p} \in \Delta_N \) such that for all \( p \in \Delta_N \),

\[
\hat{p} \cdot U\hat{p} \geq p \cdot U\hat{p}.
\]

Evolutionary stable strategy

A strategy \( \hat{p} \in \Delta_N \) such that for all \( p \in \Delta_N \setminus \{\hat{p}\} \),

\[
\hat{p} \cdot U(\varepsilon p + (1 - \varepsilon)\hat{p}) > p \cdot U(\varepsilon p + (1 - \varepsilon)\hat{p})
\]

holds for all sufficiently small \( \varepsilon > 0 \).
Nash equilibria and evolutionary stability

**Theorem**

A strategy $\hat{p}$ is an ESS iff (for $0 < \varepsilon < \bar{\varepsilon}$) the following two conditions are satisfied:

- **equilibrium condition**: $\hat{p} \cdot U\hat{p} \geq p \cdot U\hat{p}$ for all $p \in \Delta_N$,
- **stability condition**: if $p \neq \hat{p}$ and $p \cdot U\hat{p} = \hat{p} \cdot U\hat{p}$, then $\hat{p} \cdot Up > p \cdot Up$. 
Nash equilibria and evolutionary stability

(Symmetric) Nash equilibrium

A strategy \( \hat{p} \in \Delta_N \) such that for all \( p \in \Delta_N \),

\[
\hat{p} \cdot U\hat{p} \geq p \cdot U\hat{p}.
\]

Evolutionary stable strategy

A strategy \( \hat{p} \in \Delta_N \) such that for all \( p \in \Delta_N \setminus \{\hat{p}\} \),

\[
\hat{p} \cdot U(\varepsilon p + (1 - \varepsilon)\hat{p}) > p \cdot U(\varepsilon p + (1 - \varepsilon)\hat{p})
\]

holds for all sufficiently small \( \varepsilon > 0 \).
Nash equilibria and evolutionary stability

(Symmetric) Nash equilibrium

A state of the population \( \hat{x} \in \Delta_n \) such that for all \( x \in \Delta_n \),

\[
\hat{x} \cdot A\hat{x} \geq x \cdot A\hat{x}.
\]
Nash equilibria and evolutionary stability

(Symmetric) Nash equilibrium

A state of the population \( \hat{x} \in \Delta_n \) such that for all \( x \in \Delta_n \),

\[
\hat{x} \cdot A\hat{x} \geq x \cdot A\hat{x}.
\]

Evolutionary stable state

A state of the population \( \hat{x} \in \Delta_n \) such that for all \( x \neq \hat{x} \) in a neighbourhood of \( \hat{x} \) in \( \Delta_n \),

\[
\hat{x} \cdot Ax > x \cdot Ax.
\]
Equilibria of the linear replicator equation
The Hawk–Dove Game

\[
\begin{bmatrix}
H & D & T \\
H & \frac{G-C}{2} & G & \frac{G(C-G)}{2C} \\
D & 0 & \frac{G}{2} & \frac{G(C-G)}{2C} \\
T & \frac{G(G-C)}{2C} & \frac{G(G+C)}{2C} & \frac{G(C-G)}{2C}
\end{bmatrix}
\]
The Hawk–Dove Game

\[
\begin{bmatrix}
H & D & T \\
H & \frac{G-C}{2} & G & \frac{G(C-G)}{2C} \\
D & 0 & \frac{G}{2} & \frac{G(C-G)}{2C} \\
T & \frac{G(G-C)}{2C} & \frac{G(G+C)}{2C} & \frac{G(C-G)}{2C} \\
\end{bmatrix}
\]
The Rock–Scissors–Paper Game

\[
A = \begin{bmatrix}
R & S & P \\
R & 0 & 1 + \varepsilon & -1 \\
S & -1 & 0 & 1 + \varepsilon \\
P & 1 + \varepsilon & -1 & 0
\end{bmatrix}
\]

Permanence

A dynamical system on $\Delta_n$ is \emph{permanent} if there exists a $\delta > 0$ such that $x_i = x_i(0) > 0$ for $i = 1, 2, \ldots, n$ implies

$$\lim \inf_{t \to +\infty} x_i(t) > \delta$$

for $i = 1, 2, \ldots, n$. 
Permanence and persistence

Persistence

A dynamical system on $\Delta_n$ is persistent if $x_i = x_i(0) > 0$ for $i = 1, 2, \ldots, n$ implies

$$\limsup_{t \to +\infty} x_i(t) > 0$$

for $i = 1, 2, \ldots, n$. 

\[ \varepsilon = -0.5 \]
Permanence and persistence

**Strong persistence**

A dynamical system on $\Delta_n$ is **strongly persistent** if

$x_i = x_i(0) > 0$ for $i = 1, 2, \ldots, n$ implies

$$\lim \inf_{t \to +\infty} x_i(t) > 0$$

for $i = 1, 2, \ldots, n$. 

---

Stochastic models

- Evolutionary graph theory
- Amplifiers of random drift
- Amplifiers of selection
- The replicator equation on graphs

Deterministic models

- The replicator equation
- Nash equilibria and evolutionary stability

---

$\varepsilon = 0$
Index theory

Saturation

An equilibrium $p$ of the replicator equation

$$\dot{x}_i = x_i(f_i(x) - \bar{f}(x)), \quad i = 1, 2, \ldots, n,$$

is saturated if $f_i(p) \leq \bar{f}(p)$ holds for all $i$ with $p_i = 0$. 
Index theory

Saturation

An equilibrium \( p \) of the replicator equation

\[
\dot{x}_i = x_i (f_i(x) - \bar{f}(x)), \quad i = 1, 2, \ldots, n,
\]

is saturated if \( f_i(p) \leq \bar{f}(p) \) holds for all \( i \) with \( p_i = 0 \).

General index theorem for the replicator equation

There exists at least one saturated equilibrium for the replicator equation. If all saturated equilibria \( p \) are regular, i.e. \( \det J\hat{f}(p) \neq 0 \), the sum of their Poincaré indices \( \sum_p i(p) \) is \((-1)^{n-1} \), and hence their number is odd.
Index theory

Saturation

An equilibrium \( \mathbf{p} \) of the linear replicator equation

\[
\dot{x}_i = x_i \left( (A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x} \right), \quad i = 1, 2, \ldots, n,
\]

is saturated if \( (A\mathbf{p})_i \leq \mathbf{p} \cdot A\mathbf{p} \) holds for all \( i \) with \( p_i = 0 \).

General index theorem for the replicator equation

There exists at least one saturated equilibrium for the replicator equation. If all saturated equilibria \( \mathbf{p} \) are regular, i.e. \( \det \hat{J}\mathbf{f}(\mathbf{p}) \neq 0 \), the sum of their Poincaré indices \( \sum_{\mathbf{p}} i(\mathbf{p}) \) is \((-1)^{n-1}\), and hence their number is odd.
Index theory

Saturation

An equilibrium $\mathbf{p}$ of the linear replicator equation

$$\dot{x}_i = x_i((Ax)_i - x \cdot Ax), \quad i = 1, 2, \ldots, n,$$

is saturated if $(Ap)_i \leq p \cdot Ap$ holds for all $i$ with $p_i = 0$.

(Symmetric) Nash equilibrium

A state of the population $\mathbf{p} \in \Delta_n$ such that for all $\mathbf{x} \in \Delta_n$,

$$\mathbf{x} \cdot Ap \leq p \cdot Ap.$$
Evolutionary graph theory
Evolutionary graph theory

\[
\frac{r_i}{\sum_{k=1}^{S} n_k r_k}
\]
Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$

Deterministic models
- The replicator equation
- Nash equilibria and evolutionary stability
- Permanence and persistence

Stochastic models
- Evolutionary graph theory
  - Amplifiers of random drift
  - Amplifiers of selection
  - The replicator equation on graphs
Evolutionary Dynamics, Games and Graphs

Barbara Ikica

Deterministic models
The replicator equation
Nash equilibria and evolutionary stability
Permanence and persistence

Stochastic models
Evolutionary graph theory
Amplifiers of random drift
Amplifiers of selection
The replicator equation on graphs

Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$
Fixation probability $\rho_G$

The Moran process in a homogeneous population

Consider a complete graph with $N$ vertices and identical edge weights. The corresponding fixation probability of a single mutant with relative fitness $r \neq 1$ (in a population of residents with fitness 1) is given by

$$\rho_M := \frac{1 - 1/r}{1 - 1/r^N}.$$

If $r = 1$, $\rho_M = 1/N$. 
Fixation probability $\rho_G$

Classification of graphs according to $\rho_G$

1. If $\rho_G = \rho_M$, then the graph $G$ is $\rho$-equivalent to the Moran process; it has the same balance of selection and random drift.
Fixation probability $\rho_G$

Classification of graphs according to $\rho_G$

1. If $\rho_G = \rho_M$, then the graph $G$ is $\rho$-equivalent to the Moran process; it has the same balance of selection and random drift.

2. A graph $G$ is an amplifier of selection if

$$\rho_G > \rho_M \text{ for } r > 1 \text{ and } \rho_G < \rho_M \text{ for } r < 1.$$
Fixation probability $\rho_G$

Classification of graphs according to $\rho_G$

1. If $\rho_G = \rho_M$, then the graph $G$ is $\rho$-equivalent to the Moran process; it has the same balance of selection and random drift.

2. A graph $G$ is an amplifier of selection if $\rho_G > \rho_M$ for $r > 1$ and $\rho_G < \rho_M$ for $r < 1$.

3. A graph $G$ is an amplifier of random drift if $\rho_G < \rho_M$ for $r > 1$ and $\rho_G > \rho_M$ for $r < 1$. 
$\rho$-equivalence to the Moran process

The isothermal theorem

A graph $G$ is $\rho$-equivalent to the Moran process if and only if it is isothermal.
Amplifiers of random drift

Construction of amplifiers of random drift

Suppose $1/N \approx 0$. Choose a fitness $r > 1$ and a constant $\rho \in (1/N, \rho_M)$ or, alternatively, a fitness $r < 1$ and a constant $\rho \in (\rho_M, 1/N)$. There exists a graph $G$ on $N$ vertices such that $\rho_G = \rho$. 

\[
\rho_G(N-1) := \frac{N-1}{r} - \frac{1}{r} \leq \rho.
\]
Amplifiers of random drift

Construction of amplifiers of random drift

Suppose $1/N \approx 0$. Choose a fitness $r > 1$ and a constant $\rho \in (1/N, \rho_M)$ or, alternatively, a fitness $r < 1$ and a constant $\rho \in (\rho_M, 1/N)$. There exists a graph $G$ on $N$ vertices such that $\rho_G = \rho$.

$$\rho_G(N_1) := \frac{N_1}{N} \frac{1 - 1/r}{1 - 1/r^{N_1}}.$$
Amplifiers of selection

Theorem

Let $G_{(L,C,D)}$ be a superstar with $D > 2$. In the limit as $L$ and $C$ tend to infinity, for $r > 1$,

$$1 - \frac{1}{r^4(D-1)(1-1/r)^2} \leq \rho \leq 1 - \frac{1}{1+r^4D},$$

and for $0 < r < 1$,

$$\rho \leq ((1/r)^4 T)^{-\delta+1}.$$

Here, $T$ and $\delta > 1$ are appropriately chosen natural numbers with $T$ satisfying $(D - 1)(1 - r)^2 \leq T \leq D$. 
0 < r < 1:
\[ \rho \leq \left( \frac{1}{r} \right)^4 T^{\delta+1} \]
\[ (D - 1)(1 - r)^2 \leq T \leq D \]

r > 1:
\[ 1 - \frac{1}{r^4(D - 1)(1 - 1/r)^2} \leq \rho \leq 1 - \frac{1}{1 + r^4D} \]
Evolutionary game theory on graphs

**Strategies:** $R_1, R_2, \ldots, R_n$; **payoff matrix:** $A = [a_{ij}]_{i,j=1}^n$
Evolutionary game theory on graphs

**Strategies:** $R_1, R_2, \ldots, R_n$; **payoff matrix:** $A = [a_{ij}]_{i,j=1}^n$

**Graphs:** $N$ vertices, undirected and unweighted edges, $k$-regular
Evolutionary game theory on graphs

**Strategies:** \( R_1, R_2, \ldots, R_n; \) **payoff matrix:** \( A = [a_{ij}]_{i,j=1}^n \)

**Graphs:** \( N \) vertices, undirected and unweighted edges, \( k \)-regular
Evolutionary game theory on graphs

**Strategies:** $R_1, R_2, \ldots, R_n$; **payoff matrix:** $A = [a_{ij}]_{i,j=1}^n$

**Graphs:** $N$ vertices, undirected and unweighted edges, $k$-regular
Evolutionary game theory on graphs

**Strategies:** $R_1, R_2, \ldots, R_n$; **payoff matrix:** $A = [a_{ij}]_{i,j=1}^n$

**Graphs:** $N$ vertices, undirected and unweighted edges, $k$-regular

**Payoff** of a $R_i$-strategist with $k_j$ neighbouring $R_j$-strategists:

$$F_i = \sum_{j=1}^n k_j a_{ij}$$
Evolutionary game theory on graphs

**Strategies:** $R_1, R_2, \ldots, R_n$; **payoff matrix:** $A = [a_{ij}]_{i,j=1}^n$

**Graphs:** $N$ vertices, undirected and unweighted edges, $k$-regular

**Payoff** of a $R_i$-strategist with $k_j$ neighbouring $R_j$-strategists:

$$F_i = \sum_{j=1}^{n} k_j a_{ij}$$

**Fitness** of a $R_i$-strategist:

$$f_i = 1 - w + wF_i, \quad w \in [0, 1]$$

**intensity of selection**
Evolutionary game theory on graphs

Let $x_i(t)$ denote the expected frequency of $R_i$-strategists at time $t \geq 0$.

The replicator equation on graphs

Suppose $k > 2$ and $N \gg 1$. In the limit of weak selection, $w \to 0$, the following equation can be derived to describe evolutionary game dynamics on graphs.

$$
\dot{x}_i = x_i \left( ((A + B)x)_i - x \cdot (A + B)x \right), \quad i = 1, 2, \ldots, n.
$$

Here, the elements of the matrix $B = [b_{ij}]_{i,j=1}^n$ are given by

$$
b_{ij} = \frac{a_{ii} + a_{ij} - a_{ji} - a_{jj}}{k - 2}.
$$