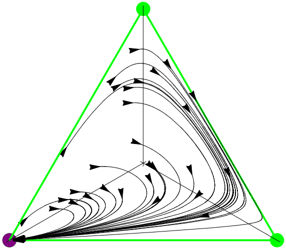
Evolutionary Dynamics, Games and Graphs



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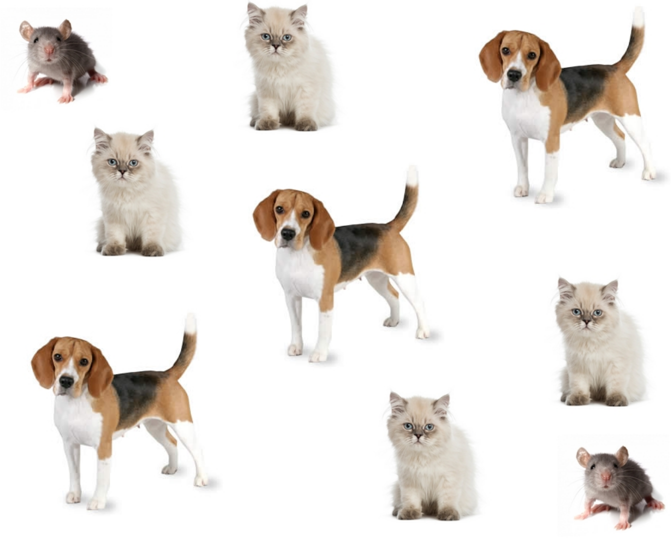

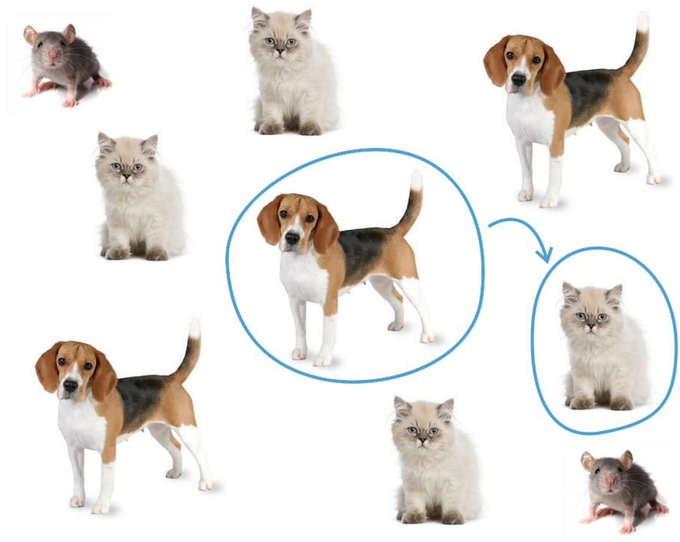

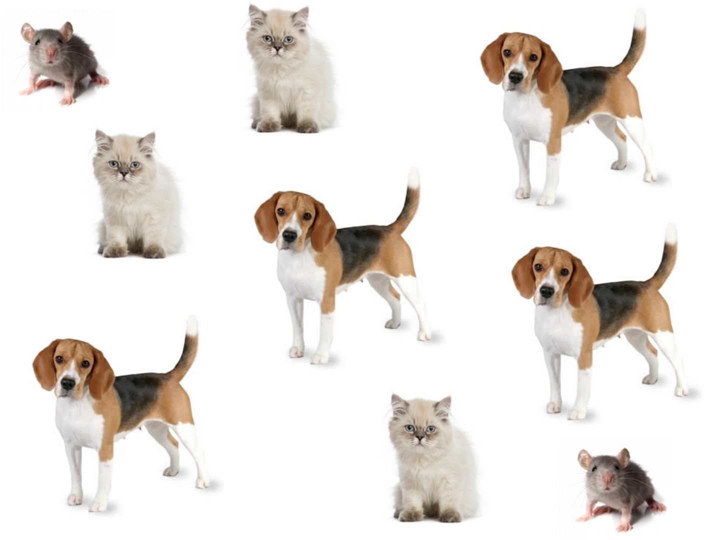

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  - Nash equilibria and evolutionary stability,
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- **Stochastic models**:
  - evolutionary graph theory:
    - amplifiers of random drift,
    - amplifiers of selection,
    - the replicator equation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

Deterministic models

State of the population (with n species):

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

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

Replicator dynamics

The replicator equation

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

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

Replicator dynamics

The replicator-mutator equation

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

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Game theory in replicator dynamics

Strategies:

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

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

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Expected payoff of a $\boldsymbol{p}$-strategist against a $\boldsymbol{q}$-strategist: $\boldsymbol{p} \cdot U \boldsymbol{q}$

Game theory in replicator dynamics

How to incorporate a game?

1. i-th species (x_i) $\rightsquigarrow$ $\boldsymbol{p}^i$

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The linear replicator equation

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

Average fitness: $\bar{f}(\boldsymbol{x}) = \boldsymbol{x} \cdot A\boldsymbol{x}$

Nash equilibria and evolutionary stability

(Symmetric) Nash equilibrium

A strategy $\hat{\boldsymbol{p}} \in \Delta_N$ such that for all $\boldsymbol{p} \in \Delta_N$,

$$\boxed{\hat{\boldsymbol{p}} \cdot U\hat{\boldsymbol{p}} \geq \boldsymbol{p} \cdot U\hat{\boldsymbol{p}}}.$$

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Evolutionary stable strategy

A strategy $\hat{\boldsymbol{p}} \in \Delta_N$ such that for all $\boldsymbol{p} \in \Delta_N \backslash \{\hat{\boldsymbol{p}}\}$,

$$\boxed{\hat{\boldsymbol{p}} \cdot U\big(\varepsilon\boldsymbol{p} + (1-\varepsilon)\hat{\boldsymbol{p}}\big) > \boldsymbol{p} \cdot U\big(\varepsilon\boldsymbol{p} + (1-\varepsilon)\hat{\boldsymbol{p}}\big)}$$

holds for all sufficiently small $\varepsilon > 0$.

Nash equilibria and evolutionary stability

Theorem

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

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

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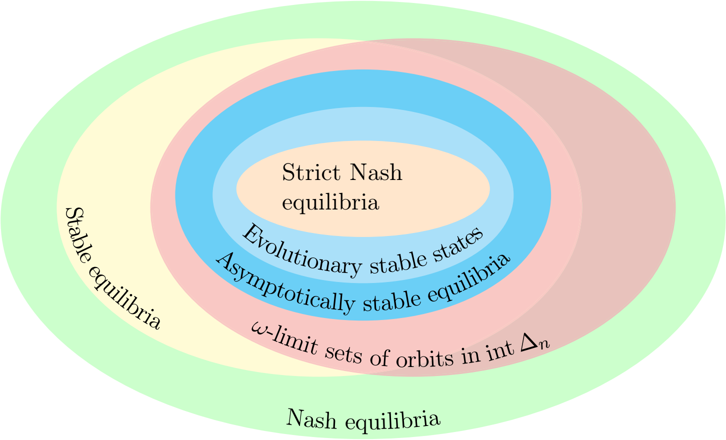
Evolutionary stable state

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

$$\boxed{\hat{\boldsymbol{x}} \cdot A\boldsymbol{x} > \boldsymbol{x} \cdot A\boldsymbol{x}}.$$

Equilibria of the linear replicator equation



The Hawk–Dove Game

$$
\begin{array}{c} \\ H \\ D \\ T \end{array}
\begin{array}{c}
\begin{array}{ccc} H & D & T \end{array} \\
\begin{bmatrix}
\frac{G-C}{2} & G & \frac{G(C-G)}{2C} \\
0 & \frac{G}{2} & \frac{G(C-G)}{2C} \\
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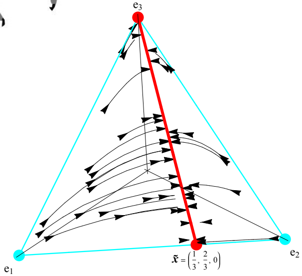


The Rock–Scissors–Paper Game

$$A = \begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{bmatrix} 0 & 1+\varepsilon & -1 \\ -1 & 0 & 1+\varepsilon \\ 1+\varepsilon & -1 & 0 \end{bmatrix} \end{array}$$

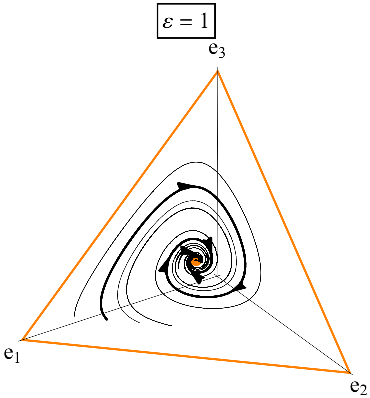
Permanence and persistence

Permanence

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

$$\boxed{\liminf_{t\to+\infty} x_i(t) > \delta}$$

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



Permanence and persistence

Persistence

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

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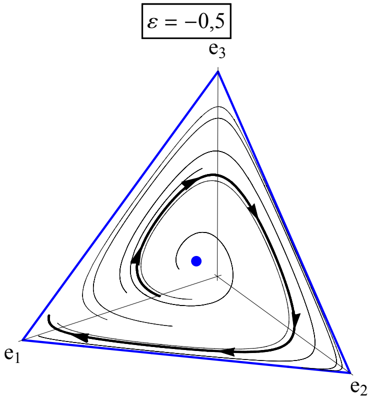

Permanence and persistence

Strong persistence

A dynamical system on Δ_n is *strongly persistent* if $x_i = x_i(0) > 0$ for $i = 1, 2, \dots, n$ implies

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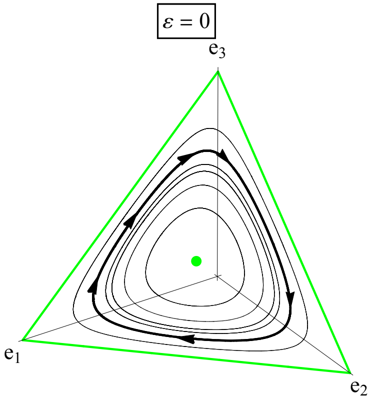

Index theory

Saturation

An equilibrium $\boldsymbol{p}$ of the replicator equation

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

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

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General index theorem for the replicator equation

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

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

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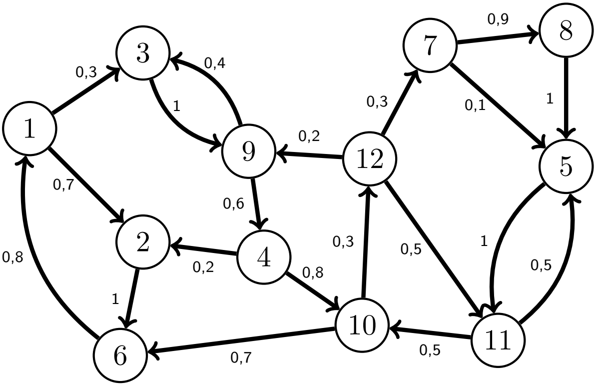
Evolutionary graph theory



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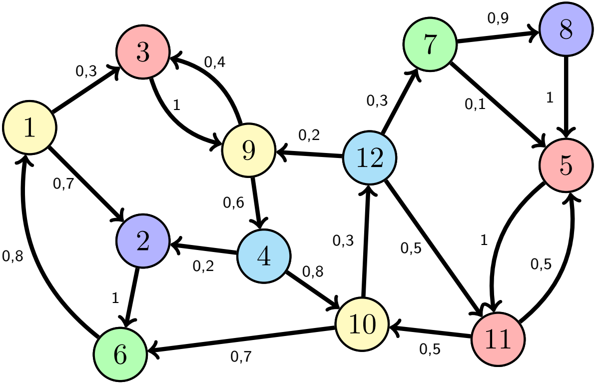
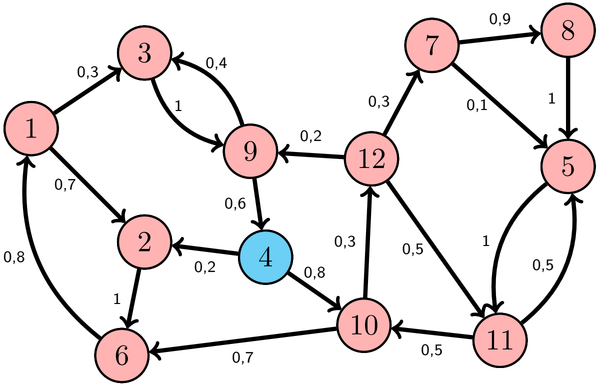


$$\frac{r_i}{\sum_{k=1}^{S} n_k r_k}$$

Fixation probability ρ_G



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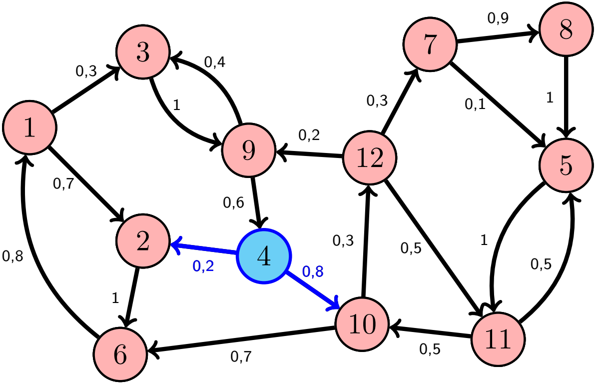

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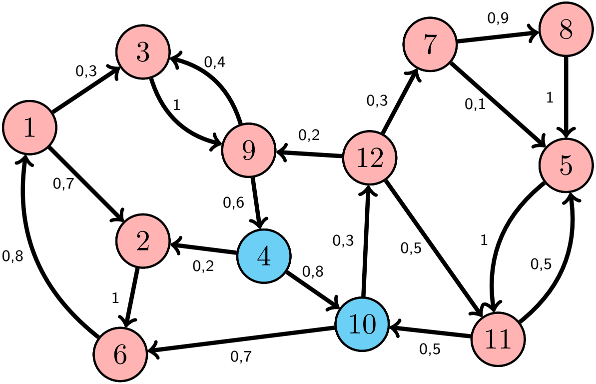

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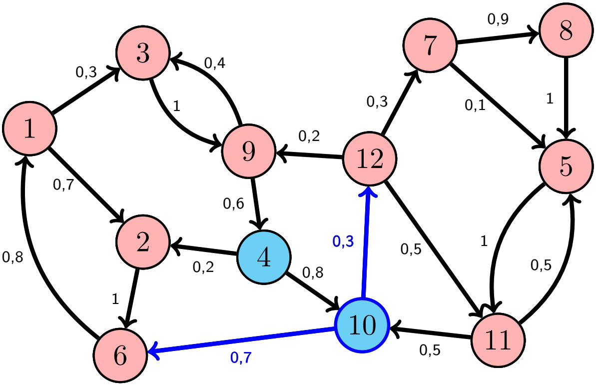

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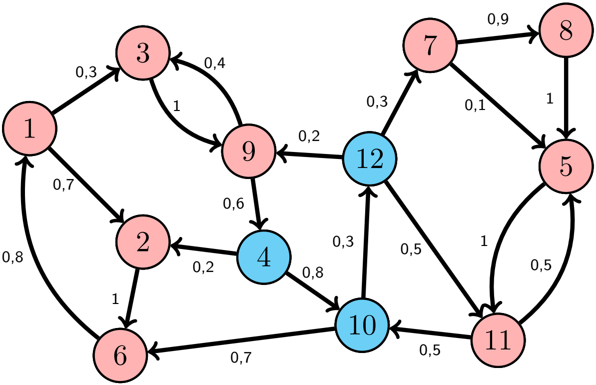

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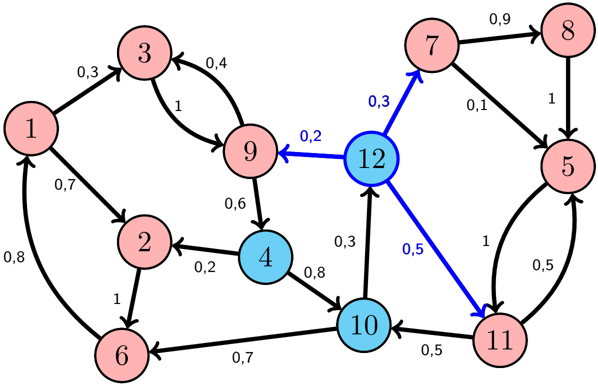

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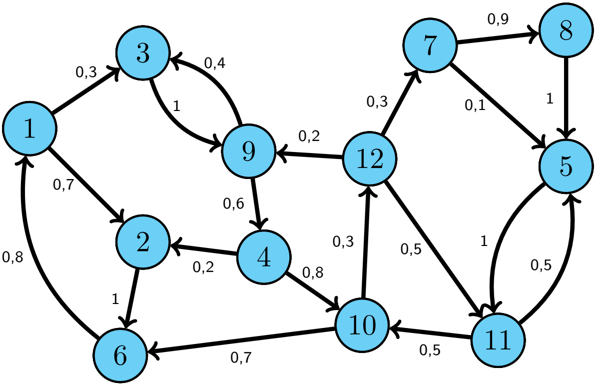

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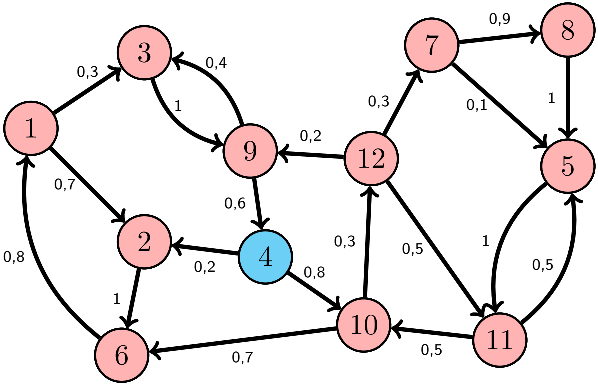

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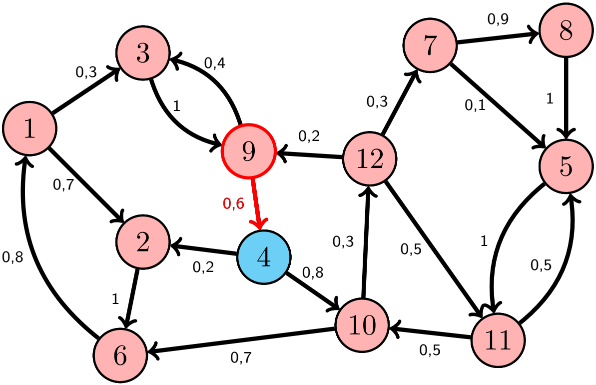

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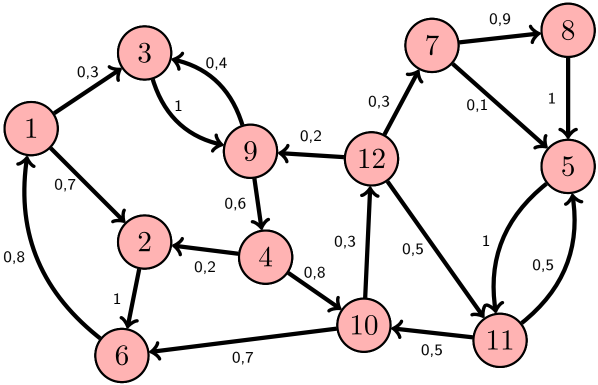

Fixation probability ρ_G

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

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

If $r = 1$, $\boxed{\rho_M = 1/N}$.

Fixation probability ρ_G

Classification of graphs according to ρ_G

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

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

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

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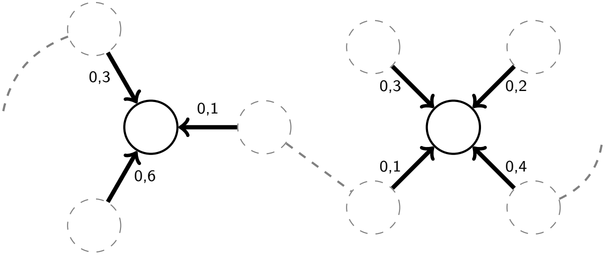
ρ-equivalence to the Moran process

The isothermal theorem

A graph G is ρ-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 $\rho_G = \rho$.

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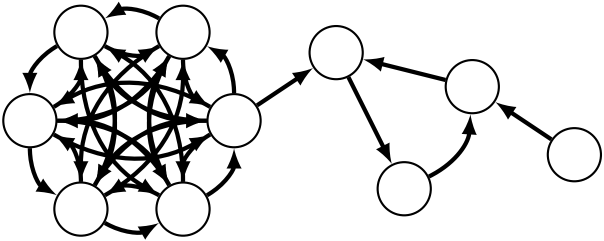


$$\rho_G(N_1) := \frac{N_1}{N} \frac{1 - 1/r}{1 - 1/r^{N_1}}.$$

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 $r > 1$,

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

and for $0 < r < 1$,

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

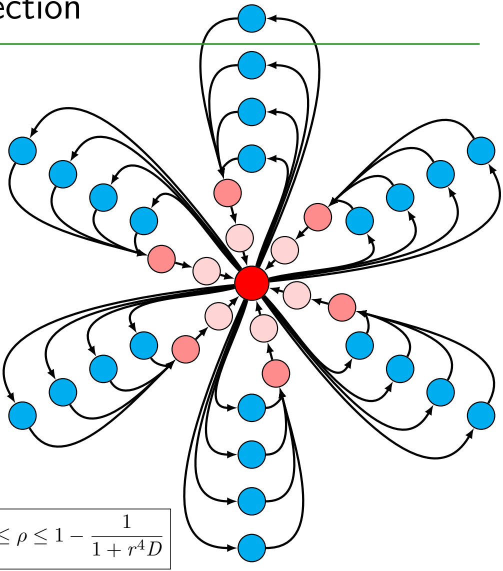
Here, T and $\delta > 1$ are appropriately chosen natural numbers with T satisfying $(D-1)(1-r)^2 \leq T \leq D$.

Amplifiers of selection

$0 < r < 1:$

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

$$(D-1)(1-r)^2 \leq T \leq D$$



$r > 1:$

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

Evolutionary game theory on graphs

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

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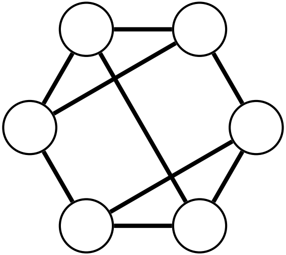
Graphs: N vertices, undirected and unweighted edges, k-regular



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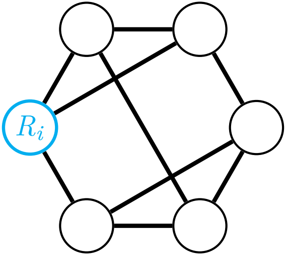

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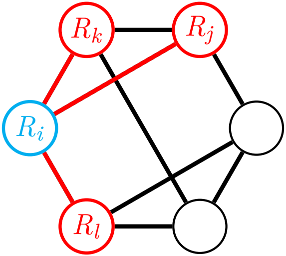

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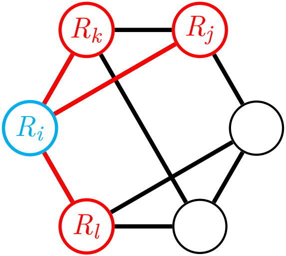

Payoff of a R_i-strategist with k_j neighbouring R_j-strategists:

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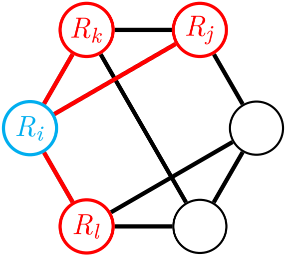

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Fitness of a R_i-strategist: $\boxed{f_i = 1 - w + wF_i}$, $w \in [0, 1]$ **intensity of selection**

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.

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

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

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