Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

Evolutionary games in finite populations

Niko Beerenwinkel

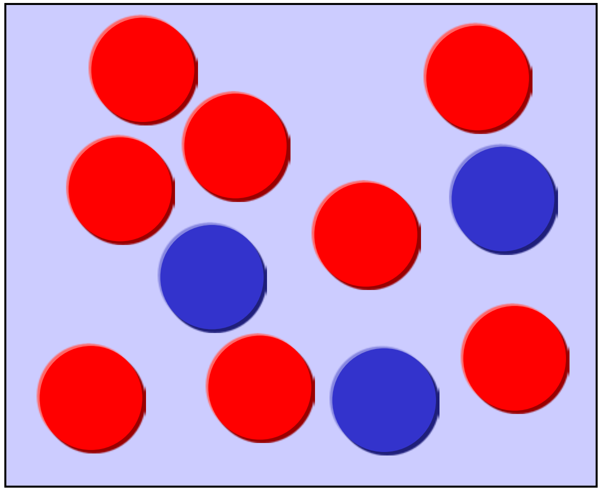
D-BSSE
Department of Biosystems
Science and Engineering

Outline

- Moran process
- Fixation probability
- Evolutionary stability
- Risk dominance
- How can cooperation be established?

Two players in a finite population

- We consider two strategies A and B in a finite population of constant size N.



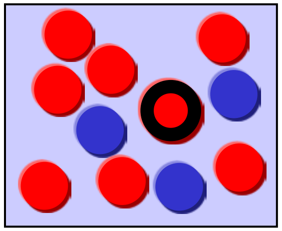
$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}$$

Expected payoff

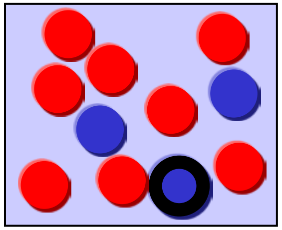
- Let i denote the number of A individuals.
- The expected payoff for A and B, respectively, is

$$\begin{array}{ccc} & A & B \\ A & \multicolumn{2}{c}{\multirow{2}{*}{$\begin{pmatrix} a & b \\ c & d \end{pmatrix}$}} \\ B & & \end{array}$$

$$F_i = \frac{(i-1)a + (N-i)b}{N-1}$$



$$G_i = \frac{ic + (N-i-1)d}{N-1}$$



ETH
Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

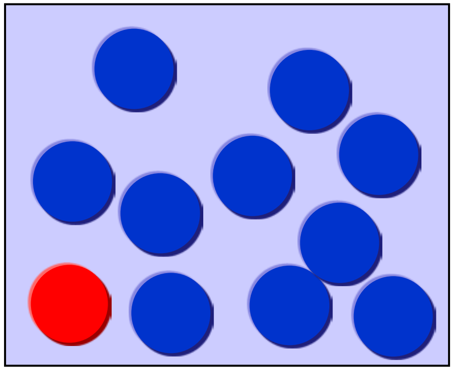
Selection opposing invasion

- We say that *selection opposes A invading B*, if

$$
\begin{aligned}
& F_1 < G_1 \\
\iff \quad & b(N-1) < c + d(N-2)
\end{aligned}
$$

- The condition is independent of a.
- For N = 2, we have b < c.

$$
\begin{array}{c c}
 & \begin{array}{cc} A & B \end{array} \\
\begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix}
\end{array}
$$



Intensity of selection

- Let w denote the intensity of selection and define frequency-dependent fitness for A and B, respectively, as

$$\begin{aligned} f_i &= 1 - w + wF_i \\ g_i &= 1 - w + wG_i \end{aligned}$$

- If w = 0, then the game does not contribute to fitness.
- If w = 1, then fitness is entirely determined by the payoff.
- The limit w $\to$ 0 is referred to as *weak selection*.
- The parameter w cancels out in the deterministic replicator equation, but plays an important role in the stochastic process describing finite populations.

Moran process

- The transition probabilities are

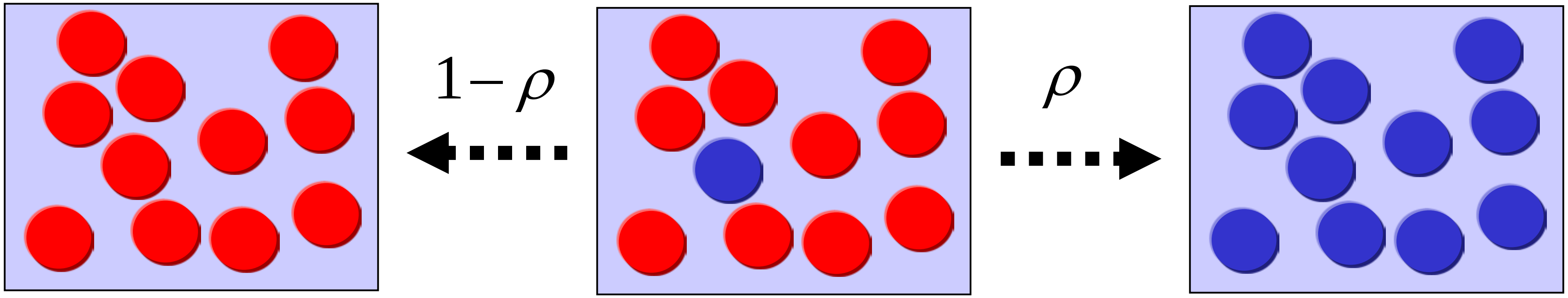
$$P_{i,i+1} = \frac{i f_i}{i f_i + (N-i) g_i} \frac{N-i}{N}$$

$$P_{i,i-1} = \frac{(N-i) g_i}{i f_i + (N-i) g_i} \frac{i}{N}$$

$$P_{i,i} = 1 - P_{i,i+1} - P_{i,i-1}$$

- $P_{0,0} = P_{N,N} = 1$.
- There are two absorbing states, i = 0 and i = N.

Fixation probability



- Because $P_{i,i-1} / P_{i,i+1} = g_i / f_i$, we find

$$\rho_A = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^{k} (g_i / f_i)}$$

Weak selection limit

- Taylor expansion gives, for w $\rightarrow$ 0,

$$\rho_A \approx \frac{1}{N} \frac{1}{1-(\alpha N-\beta)w/6}$$

where α = a + 2b – c – 2d and β = 2a + b + c – 4d.

- If ρ_A > 1/N, we say that *selection favors the fixation of A*.
- This condition is equivalent to αN > β, or equivalently

$$a(N-2)+b(2N-1)>c(N+1)+d(2N-4)$$

- For N = 2, this becomes E(A, B) = b > c = E(B, A).

Weak selection, large population

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}$$

- For large N, the inequality becomes

$$a + 2b \ > \ c + 2d$$

- Suppose a > c and b < d, then both A and B are best replies to themselves.
  - If the frequency of A is high, then A has higher fitness
  - If the frequency of B is high, then B has higher fitness
  - The equilibrium ($F_i = G_i$) relative A-allele frequency is

$$x^* = \frac{d - b}{a - b - c + d}$$

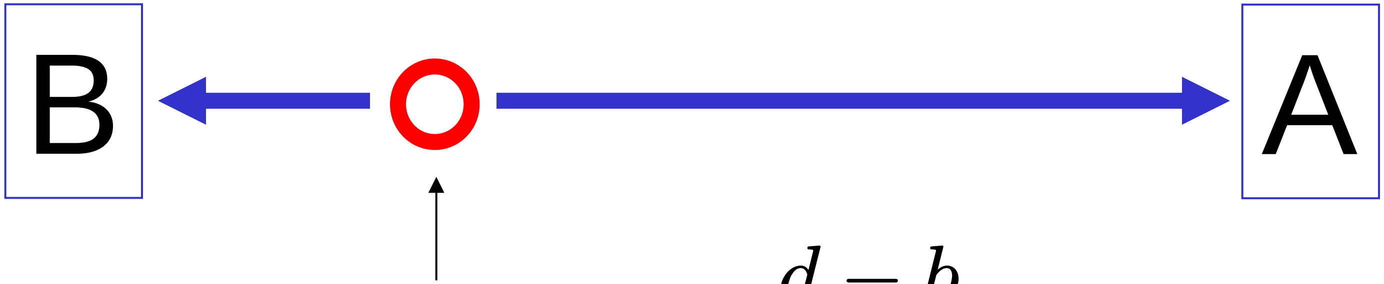
(which is the unstable equilibrium in the replicator equation)

The 1/3 law

- Combining x* and the inequality, we obtain for w $\ll$ 1,

$$\rho_A \;>\; 1/N \qquad\Longleftrightarrow\qquad x^* \;<\; 1/3$$

- If the unstable equilibrium occurs at a frequency smaller than 1/3, then in a large finite population, in the limit of weak selection, selection favors the fixation of A in B.



$$x^* = \frac{d-b}{a-b-c+d}$$

Example

- Consider the evolutionary game $\begin{pmatrix} 5 & 0 \\ 2 & 1 \end{pmatrix}$

- For *N* > 8, fixation of A is favored by selection, because then

$$\rho_A > 1/N \iff 5N - 10 > 4N - 2$$

- But: Selection opposes invasion of B by A, because

$$0 = F_1 < G_1 = 2 + N - 2$$

- Do we consider B evolutionary stable?

Evolutionary stability in finite populations

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}$$

- Recall that B is ESS if
  (i) d > b, or (ii) d = b and a < c.

- **Definition:**
  B is ESS_N if the following two conditions hold:
  1. Selection protects against **invasion**, i.e., a single A mutant has lower fitness in a B population, $F_1 < G_1$, or equivalently

  $$b(N-1) < c + d(N-2)$$

  2. Selection protects against **replacement**, i.e., $\rho_A < 1/N$ for all w > 0. For $w \ll 1$, this condition is equivalent to

  $$a(N-2) + b(2N-1) < c(N+1) + d(2N-4)$$

Small versus large populations

- For N = 2, B is ESS_N if
  1. b < c
  2. b < c

  Thus traditional ESS is neither necessary nor sufficient for ESS_N.

- For large N, B is ESS_N if
  1. b < d
  2. $x^* > 1/3$

  Thus traditional ESS is necessary but not sufficient for ESS_N

Risk dominance

- A is *risk dominant* over B, if $\rho_A > \rho_B$.
- For weak selection, we have

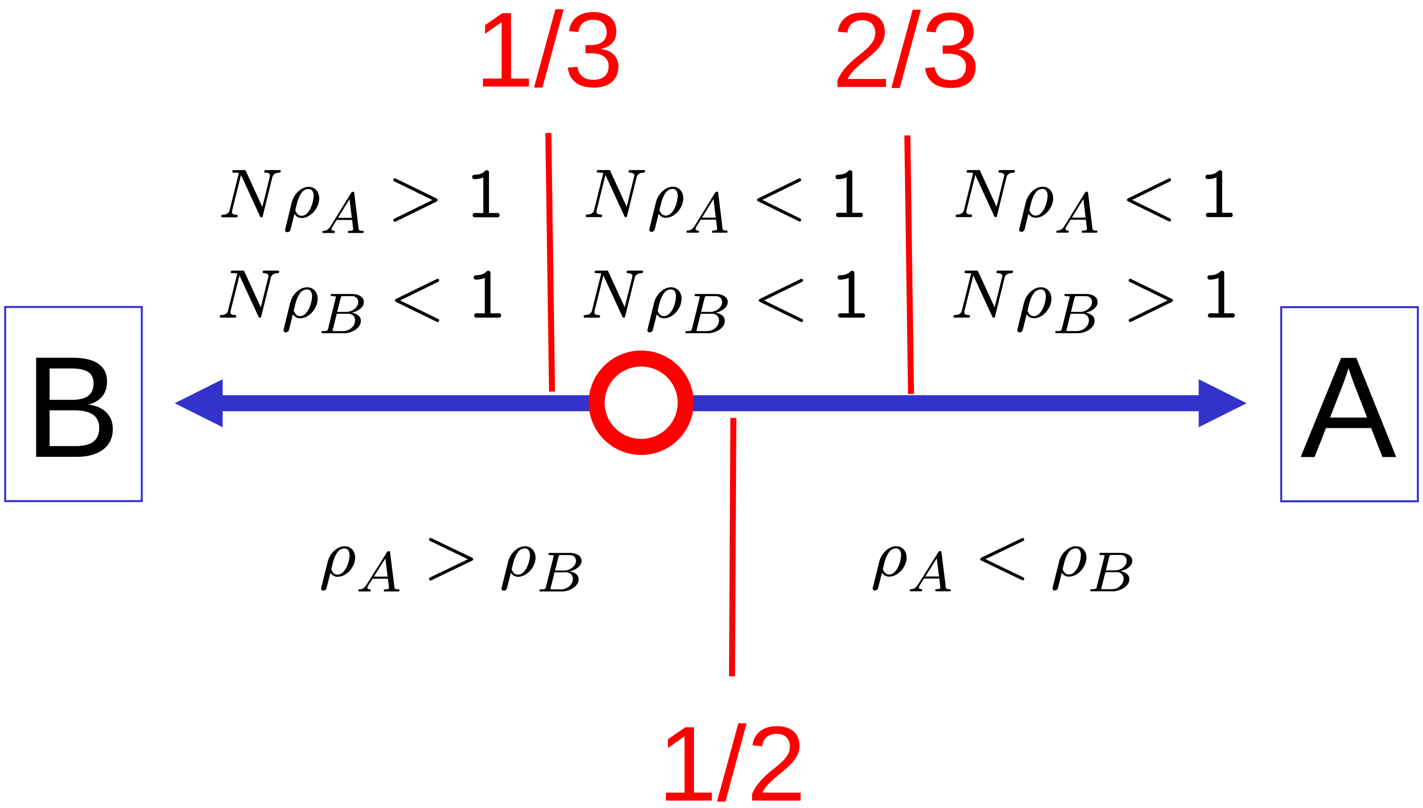
$$\frac{\rho_A}{\rho_B} = \prod_{i=1}^{N-1} \frac{f_i}{g_i} \approx 1 + w\left[N(a+b-c-d)/2 + d - a\right]$$

and $\rho_A > \rho_B$ is equivalent to

$$(N-2)(a-d) > N(c-b)$$

- For large N, we obtain a – d > c – b, or equivalently x* < 1/2.
- If both A and B are strict Nash (a > c and b < d) then the risk dominant strategy has a higher fixation probability.

Risk dominance and the 1/3 law



Recall The Prisoner's Dilemma game

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}$$

$$T > R > P > S \quad \text{and} \quad R > \frac{T+P}{2}$$

- DC: Temptation to defect
- CC: Reward for mutual cooperation
- DD: Punishment for mutual defection
- CD: Sucker's payoff

TFT versus ALLD in the Prisoner's Dilemma

- Recall that T > R > P > S and

$$\begin{array}{cc} & \begin{array}{cc} \text{TFT} & \text{ALLD} \end{array} \\ \begin{array}{c} \text{TFT} \\ \text{ALLD} \end{array} & \begin{pmatrix} mR & S+(m-1)P \\ T+(m-1)P & mP \end{pmatrix} \end{array}$$

  with m the average number of rounds that two players play.
- In an infinite population, if m > (T – P)/(R – P), then each strategy is stable against invasion by the other.

- Can cooperation evolve in a finite population?

TFT versus ALLD in finite populations

- Selection favors the replacement of ALLD by TFT if ρ_{TFT} > 1/N, or equivalently

$$m > \frac{T(N+1) + P(N-2) - S(2N-1)}{(R-P)(N-2)}$$

- For large N, this inequality becomes

$$m > \frac{T + P - 2S}{R - P}$$

- Example: Consider R = 3, T = 5, P = 1, and S = 0.
  - For N = 3, we need m > 10 rounds; for N = 4, we need m > 6 rounds.
  - For large N, we need only m > 3 rounds.

Further reading

- Nowak MA. *Evolutionary Dynamics*, Chapter 7.
- Nowak MA (2006). Five rules for the evolution of cooperation. Science 314:1560.

Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

Evolutionary graph theory

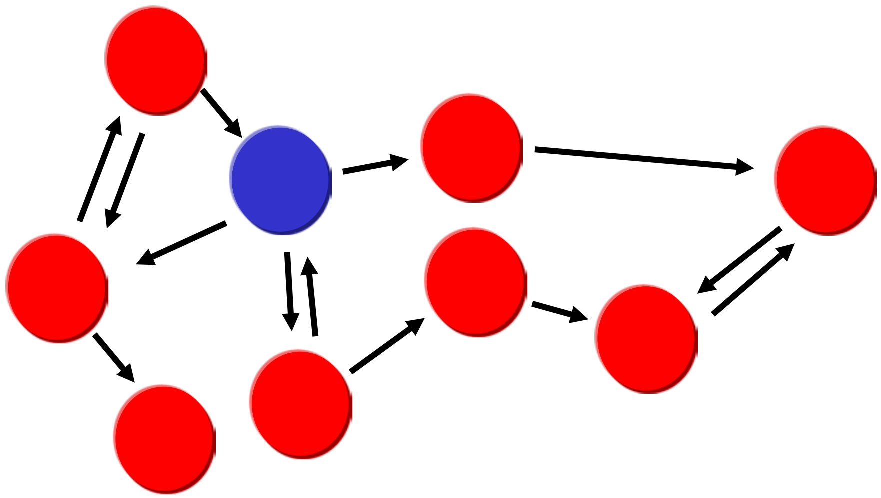
Niko Beerenwinkel

Outline

- Evolution on graphs
- Amplifiers and suppressors of selection
- Games on graphs

Evolution on graphs

- We place individuals on the vertices of a graph.
- The graph represents the structure of the population, e.g., spatial structure or cell differentiation architecture.



- An edge $i \rightarrow j$ means that offspring of i can replace j.

ETH
Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

Stochastic dynamics

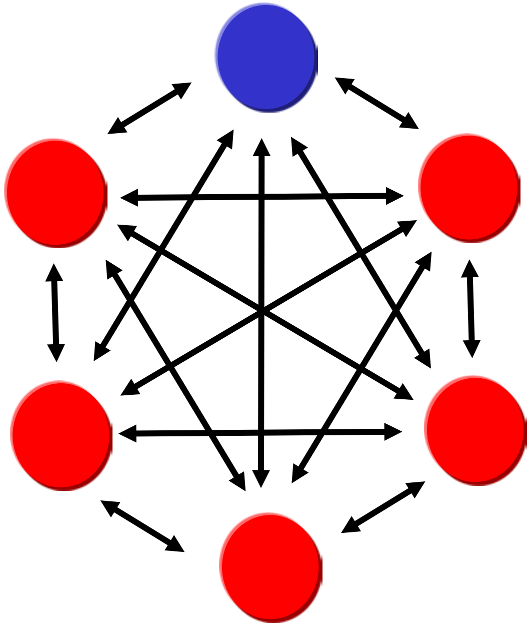
- In each generation, one individual i $\in$ {1, 2, …, N} is chosen randomly for reproduction. Its offspring replaces j with probability w_{ij}. The matrix

$$W = \begin{pmatrix} w_{11} & w_{12} & w_{13} & \cdots & w_{1\,N-1} & w_{1N} \\ w_{21} & w_{22} & w_{23} & \cdots & w_{2\,N-1} & w_{2N} \\ w_{31} & w_{32} & w_{33} & \cdots & w_{3\,N-1} & w_{3N} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ w_{N-1\,1} & w_{N-1\,2} & w_{N-1\,3} & \cdots & w_{N-1\,N-1} & w_{N-1\,N} \\ w_{N1} & w_{N2} & w_{N3} & \cdots & w_{N\,N-1} & w_{N\,N} \end{pmatrix}$$

is a stochastic matrix. It defines a weighted digraph.

Moran process revisited

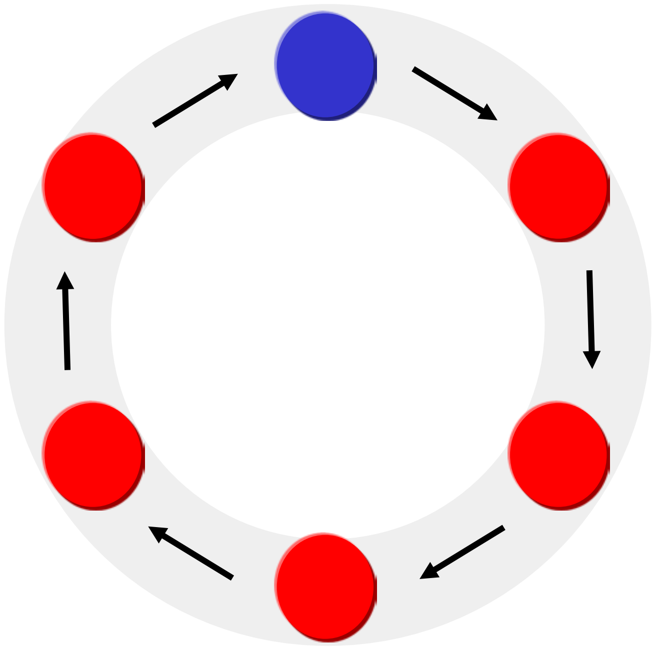
- If w_{ij} = 1/N for all i, j, then the offspring of any one individual can replace any other individual.
- The induced digraph is the complete graph with identical weights.
- The stochastic process on this graph is exactly the Moran process.



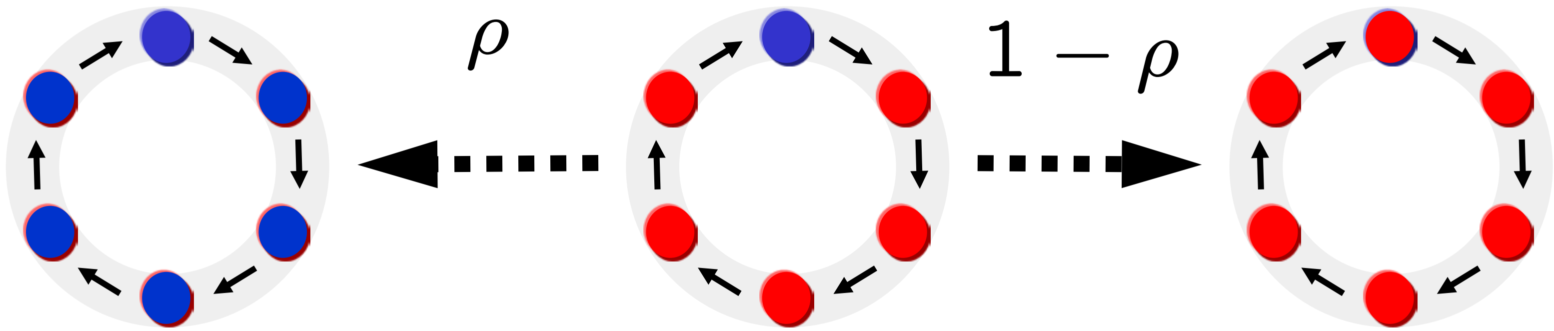
$$\rho = \frac{1 - 1/r}{1 - 1/r^N}$$

The directed cycle

$$\begin{pmatrix} 0 & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & 1 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 1 \\ 1 & 0 & 0 & \dots & 0 & 0 \end{pmatrix}$$



Fixation probability



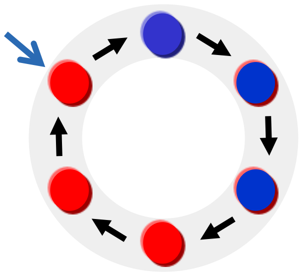
- What is the fixation probability of a mutant that occurs randomly in one of the cells?
- Observation: Starting from one B mutant, only one connected cluster of B mutants can emerge.

ETH
Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

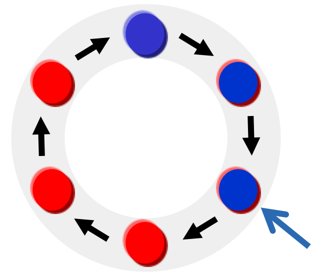
Markov chain on the directed cycle

- Suppose A has fitness 1 and B has fitness r.
- We keep track of the number of B individuals, m:
  - To reduce m by one, the A individual immediately preceding the B cluster must be chosen.



$$P_{m,m-1} = \frac{1}{N - m + rm}$$

  - To increase m by one, the B individual at the end of the cluster has to be chosen.



$$P_{m,m+1} = \frac{r}{N - m + rm}$$

Fixation probability on the directed cycle

- Because

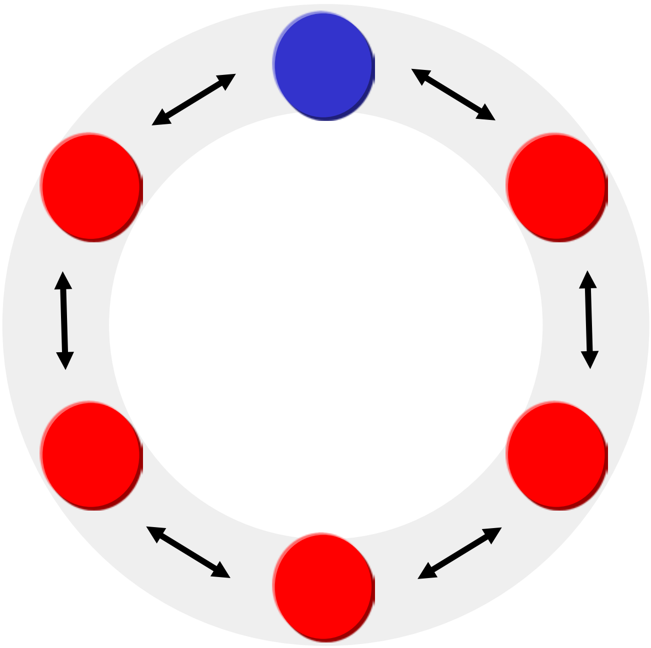
$$\gamma_m = \frac{P_{m,m-1}}{P_{m,m+1}} = \frac{1}{r}$$

the fixation probability on the directed cycle is the same as for the Moran process:

$$\rho = \frac{1 - 1/r}{1 - 1/r^N}$$

The (bidirected or undirected) cycle

$$\begin{pmatrix} 0 & \frac{1}{2} & 0 & \cdots & 0 & \frac{1}{2} \\ \frac{1}{2} & 0 & \frac{1}{2} & \cdots & 0 & 0 \\ 0 & \frac{1}{2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & \frac{1}{2} \\ \frac{1}{2} & 0 & 0 & \cdots & \frac{1}{2} & 0 \end{pmatrix}$$



Fixation probability on the cycle

- We find again

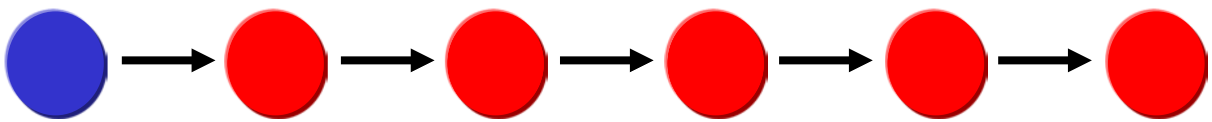
$$P_{m,m-1} = \frac{1}{N - m + rm}$$

$$P_{m,m+1} = \frac{r}{N - m + rm}$$

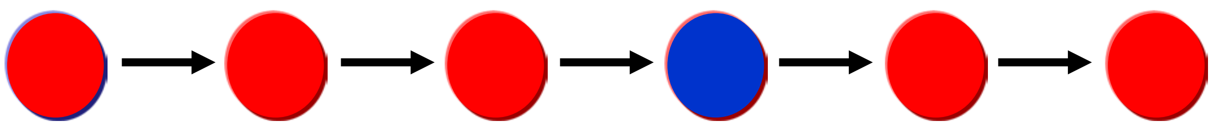
and therefore the same fixation probability

$$\rho = \frac{1 - 1/r}{1 - 1/r^N}$$

In general, the fixation probability depends on the configuration of the population on the graph.

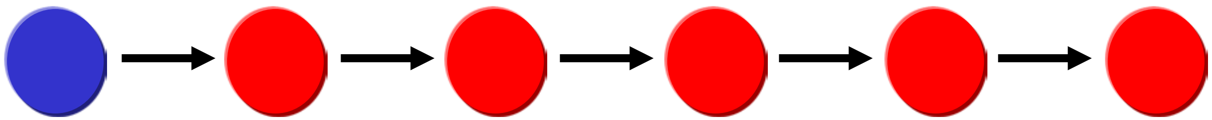


$$\rho = 1$$



$$\rho = 0$$

The line (the linear process)



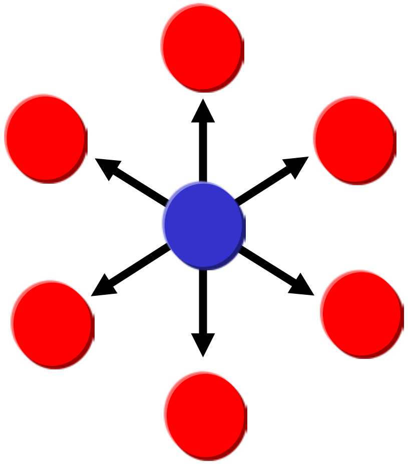
$$\begin{pmatrix} 0 & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & 1 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 1 \\ 0 & 0 & 0 & \dots & 0 & 1 \end{pmatrix}$$

$$\bar{\rho} = \frac{1}{N}$$

for a randomly placed mutant

The burst

$$\begin{pmatrix} 0 & \frac{1}{N-1} & \frac{1}{N-1} & \cdots & \frac{1}{N-1} & \frac{1}{N-1} \\ 0 & 1 & 0 & \ldots & 0 & 0 \\ 0 & 0 & 1 & \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ldots & 1 & 0 \\ 0 & 0 & 0 & \ldots & 0 & 1 \end{pmatrix}$$



$$\bar{\rho} = \frac{1}{N}$$

Amplifiers and suppressors

- We write ρ_G < x (> x, = x) if the (in)equality holds for any configuration of the population, i.e., for any position of the invading mutant on the graph G.
- A graph G is an *amplifier of selection* if, for an advantageous mutant (r > 1), the fixation probability is greater than in the Moran process, $\rho_G > \rho_{Moran}$.
- A graph G is a *suppressor of selection* if, for an advantageous mutant (r > 1), the fixation probability is smaller than in the Moran process, $\rho_G < \rho_{Moran}$.
- Similar definitions apply to disadvantageous mutants (r < 1).
- The strongest suppressors of selection have ρ_G = 1/N, i.e., the fixation probability is completely independent of r.

The isothermal theorem

- Define the temperature of a vertex j as $T_j = w_{1j} + \ldots + w_{nj}$.
- Hot vertices change more often than cold vertices.
- If all vertices have the same temperature, the graph is *isothermal*.

- **Theorem**: $\rho_G = \rho_{Moran}$ if and only if G is isothermal.

- G is isothermal if and only if G is doubly stochastic (that is, all rows and all columns sum to one), because:

$$n = \sum_{i,j} w_{ij} = \sum_j T_j = T\,n \quad \Rightarrow \quad T = 1$$

Proof of the isothermal theorem 1/3

- We describe the configuration of the population on the graph by $v = (v_1, \ldots, v_N)$, where $v_i = 0$ indicates occupation of vertex i by A and $v_i = 1$ occupation by B.
- The number of B individuals is $m = v_1 + \ldots + v_N$.

$$P_{m,m+1} = \frac{r \sum_{i,j} w_{ij} v_i (1 - v_j)}{rm + N - m}$$

$i \rightarrow j$	
B	A

$$P_{m,m-1} = \frac{\sum_{i,j} w_{ij} (1 - v_i) v_j}{rm + N - m}$$

$i \rightarrow j$	
A	B

D-BSSE
Department of Biosystems
Science and Engineering

Proof of the isothermal theorem 2/3

- Now, $\rho_G = \rho_{Moran}$ if and only if

$$\frac{P_{m,m-1}}{P_{m,m+1}} = \frac{1}{r}$$

  for all configurations v.
- This is the case if and only if, for all v,

$$\sum_{i,j} w_{ij}(1 - v_i)v_j = \sum_{i,j} w_{ij}v_i(1 - v_j)$$

Proof of the isothermal theorem 3/3

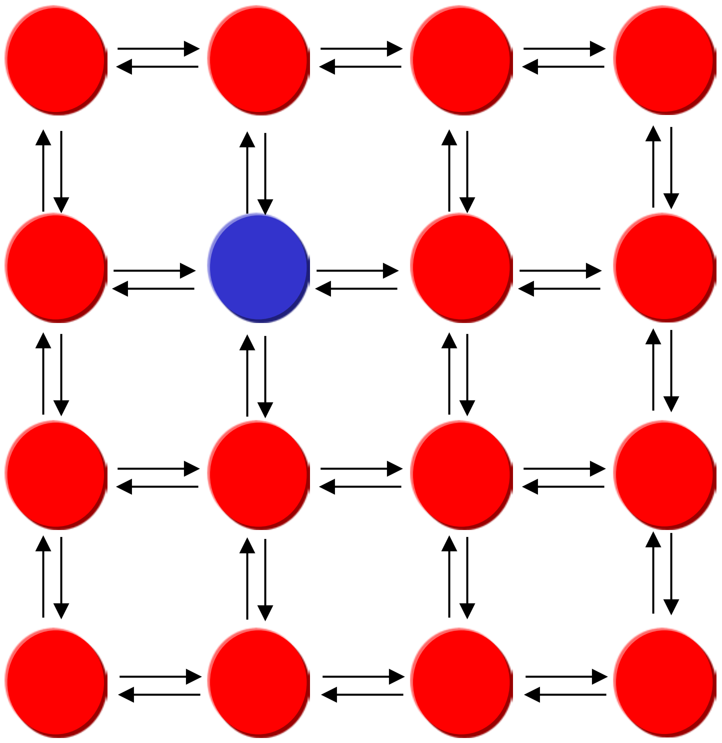
- It is equivalent that the equation holds for all configurations v with $v_k = 1$ and $v_i = 0$ for all $i \neq k$. Thus,

$$1 = \sum_j w_{kj} = \sum_i w_{ik} \quad \text{for all } k$$

i.e., W is doubly stochastic and the corresponding graph is isothermal.

Isothermal graphs

- Directed cycle
- Cycle
- All symmetric graphs, $w_{ij} = w_{ji}$

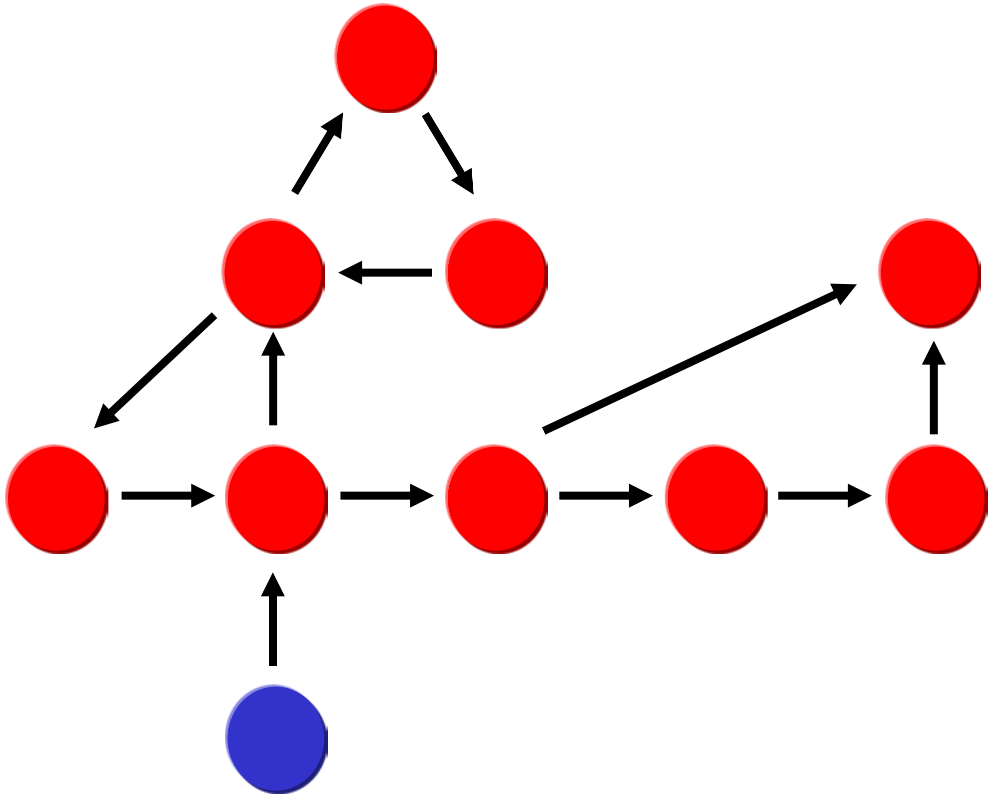


ETH
Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

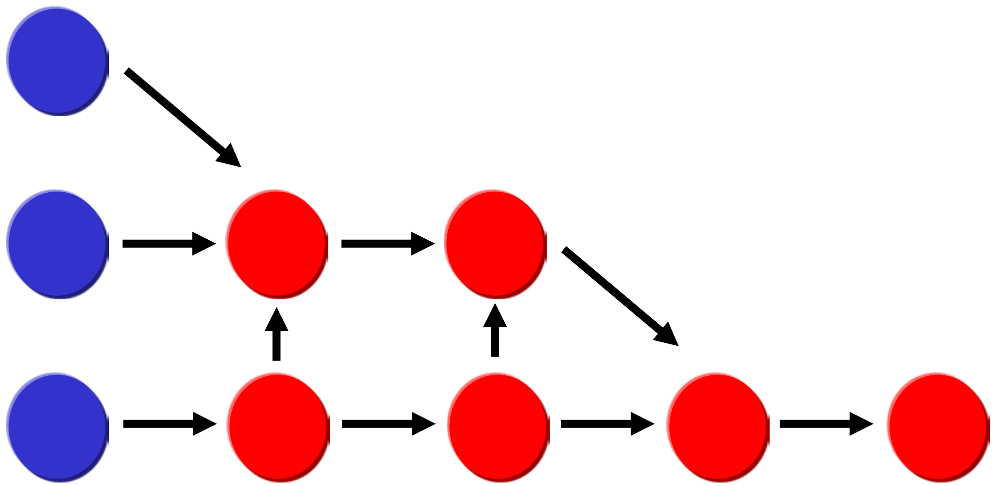
Suppressors of selection

- All one-rooted graphs have the fixation probability ρ = 1/N.



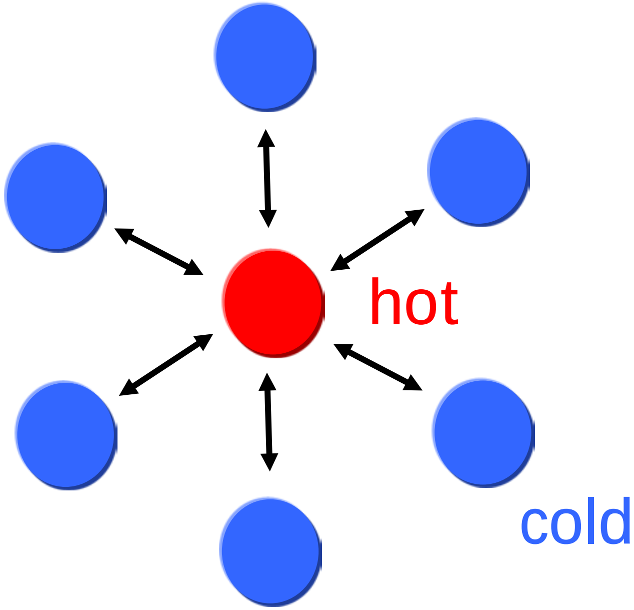
Prevention of fixation

- In graphs with multiple roots, a lineage arising from a single mutant can never reach fixation.



Amplifiers of selection

- The star is an amplifier of selection.

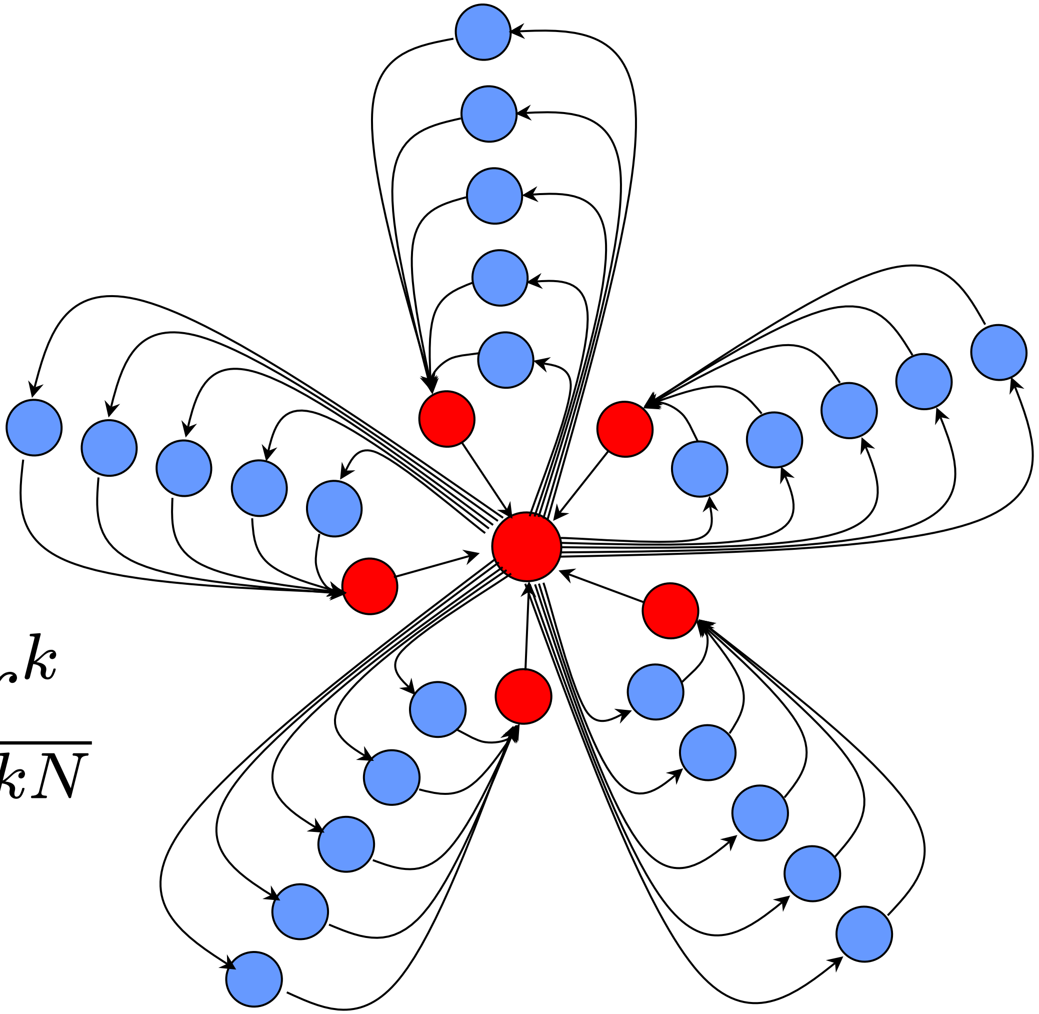


$$\rho = \frac{1 - 1/r^2}{1 - 1/r^{2N}}$$

The superstar is a strong amplifier of selection

l = 5 leaves
m = 5 loops per leaf
k = 3 vertices per loop

$$\lim_{l=m\to\infty} \rho = \frac{1 - 1/r^k}{1 - 1/r^{kN}}$$



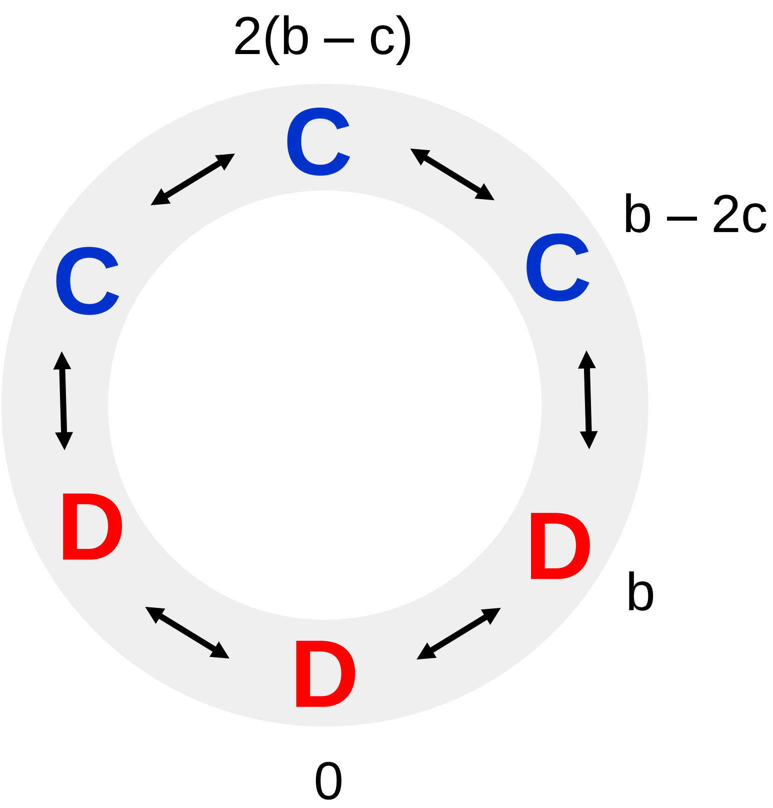
Games on graphs

- We assume that the interaction graph ("who plays with whom?") is identical to the reproduction graph ("whose offspring replaces whom?").
- We consider regular graphs of degree k, i.e., each individual has exactly k neighbors.
- We consider the case of weak selection. Fitness is a constant plus a small contribution from the game.
- We consider cooperators, C, and defectors, D.

Payoff

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}$$

- Cooperators help all neighbors, defectors do not.
- Cooperators pay a cost c for each neighbor; each neighbor of a cooperator receives a benefit b.
- Payoff from all interactions are added up.



"Birth-death" update rule

- Select an individual for reproduction proportional to fitness.
- The offspring replaces a random neighbor.

C ↔ C ↔ C ↔ D ↔ D ↔ D

b – 2c   b

$$\rho_C < \frac{1}{N} < \rho_D \quad \text{for all } b, c$$

“Death-birth” update rule

- Select a random individual to die.
- The neighbors compete for the empty site proportional to their fitness.

$$C \leftrightarrow C \leftrightarrow C \leftrightarrow D \leftrightarrow D \leftrightarrow D$$

2(b – c)   b – 2c   b   0

$$\rho_C > \frac{1}{N} > \rho_D \quad \text{if} \quad b/c > k$$

“Imitation” update rule

- Select a random individual to update its strategy. It will stay with its own strategy or imitate (learn and adopt) a neighbor’s strategy proportional to fitness.

C ↔ **C** ↔ **C** ↔ **D** ↔ **D** ↔ **D**

2(b – c)   b – 2c   b   0

$$\rho_C > \frac{1}{N} > \rho_D \quad \text{if} \quad b/c > k + 2$$

Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

Further reading

- Nowak MA. *Evolutionary Dynamics*, Chapter 8.
- Lieberman E, Hauert C, Nowak MA (2005). Evolutionary dynamics on graphs. Nature 433:312-316.