Evolutionary Dynamics in Finite Populations

Supratim Sengupta

Department of Physical Sciences

IISER Kolkata

Outline

- Evolution in Finite Populations
    - Evolution via mutation without selection
    - Evolution via selection without mutation
    - Evolution with mutation *and* selection

- Evolutionary Games in Finite, *well-mixed* Populations

- Evolutionary Games in *Structured* Populations

Darwinian Evolution

- Mutation acts randomly to produce new variants
- Selection acts on those variants to preferentially select the ones with higher fitness

Evolution is a stochastic process

Higher fitness individuals are ***not guaranteed*** to take over the population

but

more likely *to do so than dictated by chance*.

Quasi-Species Equation: Evolution with Mutation *and* selection

M. Eigen

$$\frac{dx_i}{dt} = \sum_{j=1}^{N} x_j f_j q_{ji} - \phi x_i$$

Constant Fitness

$$\phi = \sum_{i=1}^{N} f_i x_i$$

Average Fitness

P. Schuster

Limiting Cases

Mutation *without* selection: $\frac{dx_i}{dt} = \sum_{j=1}^{N} x_j q_{ji} - \phi x_i$ when $f_i = 1$ for all i

Selection *without* mutation (Error-free replication): $q_{ji} = \delta_{ji} \Rightarrow \frac{dx_i}{dt} = x_i(f_i - \phi)$

Competition between 2 types

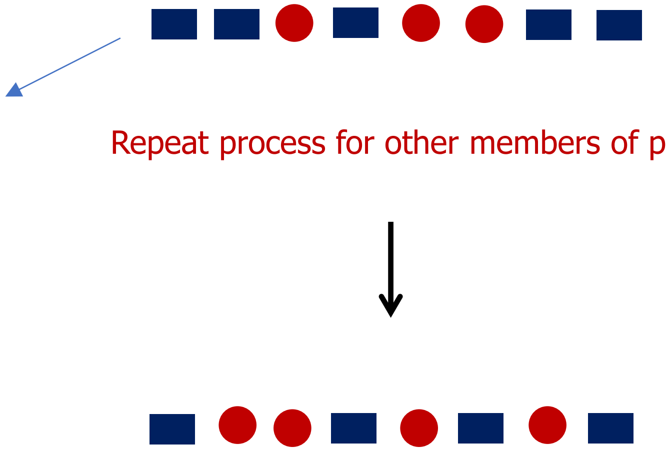
$$\boxed{\frac{dx_A}{dt} = x_A(1-x_A)(f_A - f_B)}$$

Useful in describing evolution of population of sequences where

- ❖ Variations between sequences arise as a result of errors during replication
- ❖ Presence of replication errors shifts the equilibrium from a pure state (survival of the fittest) to a mixed state where multiple quasi-species can coexist
- ❖ The equilibrium state does not necessarily maximize average fitness

Pictorial representation of evolution by mutation without selection

■ A-type ● B-type



Time

Time=t

Check type **A** or **B**

Pick Random members

Check if RN < u1, if true mutate A to B. If False, leave A unchanged

Repeat process for other members of population

Time=t+1

#A	**#B**
nA	**nB**
nA-1	**nB+1**

Evolution via mutation without selection : Algorithm

```
Divide population of size N equally between two types of individuals A and B represented by the numbers 0 & 1
Define mutation rates u1 and u2
Start loop over generations (total =T)
        Start loop over entire population (size=N)
          Check if the individual chosen is of type 0 or type 1
            If type 0, mutate individual from 0 to 1 with probability u1
                  Pick a random number r between 0 and 1
                  If r < u1, mutate individual from 0 to 1, else leave unchanged
            If type 1, mutate individual from 1 to 0 with probability u2
                  Pick a random number r between 1 and 0
                  If r < u2, mutate individual from 1 to 0, else leave unchanged
        Close loop over population
Calculate frequency of type 0 and type 1 in the population
Record generation versus frequency data
Close loop over generations
```

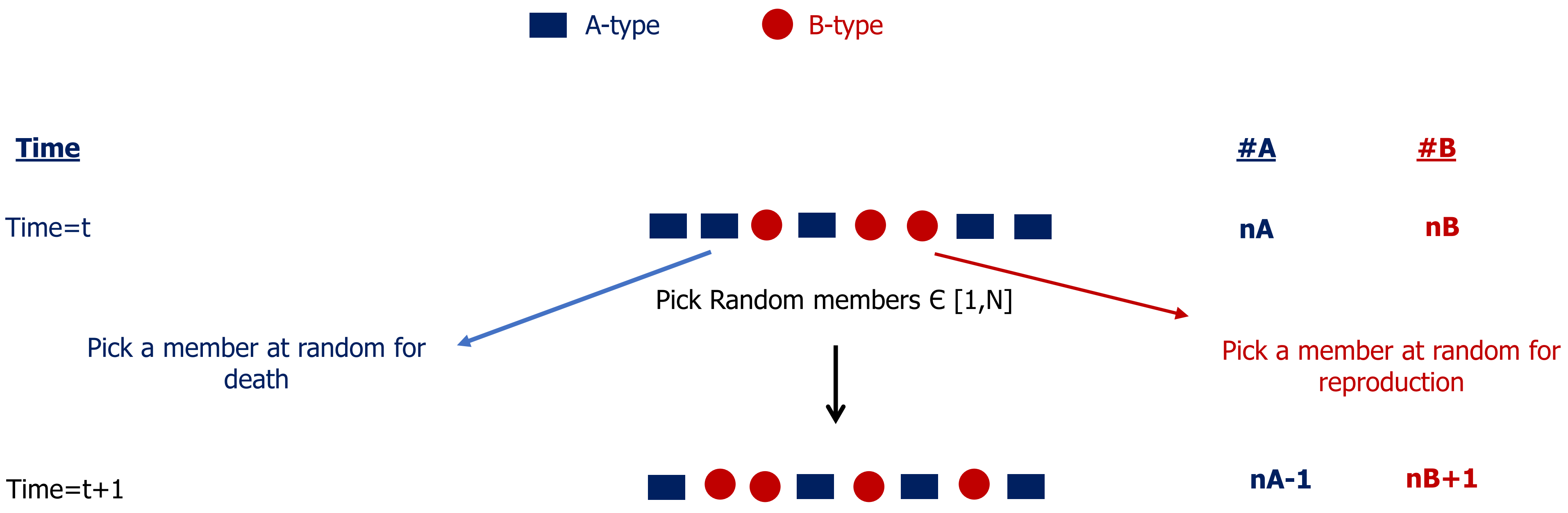
Practice Assignment

Run simulations using u1=0.003 and u2=0.001 for 3 different population sizes N=100, 1000, 10000

Verify if the equilibrium value for frequency of type 0 and type 1 matches with theoretical predictions

Genetic Drift: Neutral Evolution

What is the outcome of evolution of a population of 2 species having the ***same*** fitness?



GenDrift-global.nlogo

Two Absorbing States: A only or B only

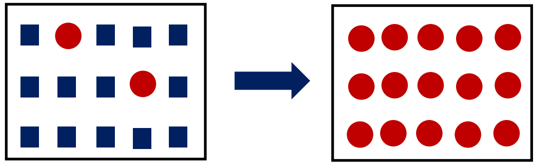
How does the final state of the population depend on the initial fraction of A and B ?

Moran Process

Assume two types of individuals A and B in the population of N individuals, both types having the *same* fitness.

In every generation, one individual is picked at random for reproduction and another individual is picked at random for death.

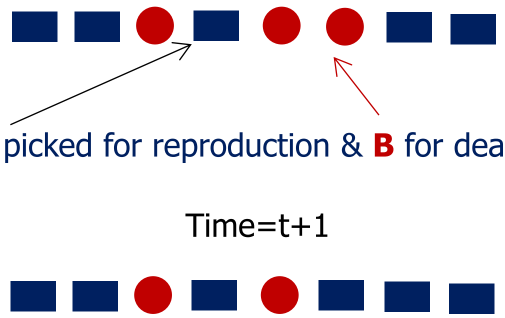
Question: What is the ***fixation probability*** of **B** ?



Fixation Probability of B: Probability that the frequency of **B** increases from an initial value of **i/N** to a final value of 1 i.e. the final population consists entirely of **B**

■ A-type ● B-type

Time=t

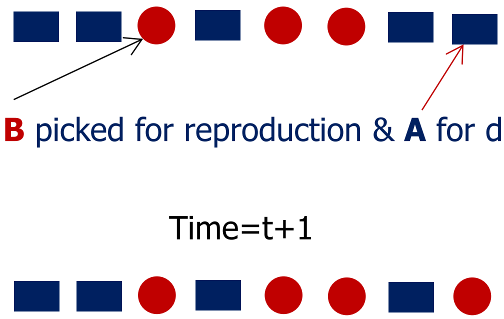


A picked for reproduction & **B** for death

Time=t+1

Probability = $p_{i,i+1}$

Time=t

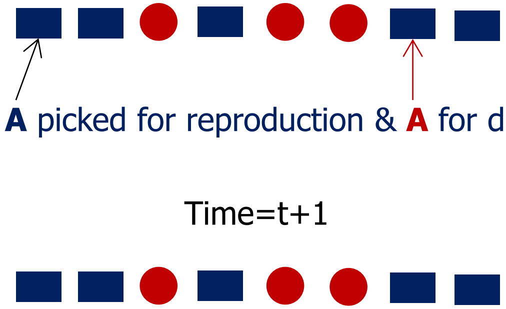


B picked for reproduction & **A** for death

Time=t+1

Probability = $p_{i,i-1}$

Time=t



A picked for reproduction & **A** for death

Time=t+1

Probability = $p_{i,i}$

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

Difference between Invasion and Fixation

Invasion is a special case of Fixation

In *deterministic* simulations involving the replicator equation,

Invasion by type A ➔ frequency of A increases from a very small fraction $x=\varepsilon << 1$ ➔ $x=1$

Fixation of A ➔ frequency of A increases from any x ➔ $x=1$

In *stochastic* simulations like evolution by Moran process

Invasion by type A ➔ frequency of A increases from $x=1/N$ ➔ $x=1$

Fixation of A ➔ frequency of A increases from any x (such that $0 < x=\#A/N < 1$) ➔ $x=1$

NOTE

The inability of A to *invade* a population of B does not mean that A cannot get *fixed* in the population if its initial frequency is sufficiently large.

Neutral Evolution via Moran Process in Finite Populations

No. of A players = **i;** No. of B players = **N-i.** Also **assume A and B has the same fitness**

Prob. of choosing A for both death and reproduction = (i/N)^2

Prob. of choosing B for both death and reproduction = ((N-i)/N)^2

Prob. of choosing A for reproduction and B for death = {i/N}{(N-i)/N}= **$p_{i,i+1}$**

Prob. of choosing B for reproduction and A for death = {(N-i)/(N)}{i/N}= **$p_{i,i-1}$**

Define: $\gamma_i = \frac{p_{i,i-1}}{p_{i,i+1}} = \frac{\beta_i}{\alpha_i}$ $y_i = x_i - x_{i-1}$

If x_i is the fixation probability of A's starting from a state with #A=i

$$x_i = x_i p_{i,i} + x_{i-1} p_{i,i-1} + x_{i+1} p_{i,i+1} \Longrightarrow y_{i+1} = \gamma_i y_i$$

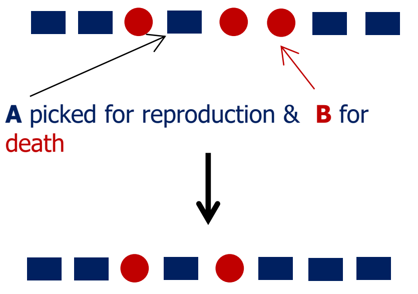
$$\sum_{i=1}^{N} y_i = x_N - x_0 = 1$$

$$y_{i+1} = \gamma_i y_i \Longrightarrow \sum_{i=1}^{N} y_i = x_1(1+\gamma_1+\gamma_2\gamma_1+.......+\gamma_{N-1}.....\gamma_1) \Longrightarrow x_1 \equiv \rho_C = \frac{1}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k} = \frac{1}{N}$$

$$y_{i+1} = \gamma_i y_i \Longrightarrow x_i = x_1(1+\gamma_1+\gamma_2\gamma_1+...+\gamma_{i-1}..\gamma_1) \Longrightarrow x_i = \frac{1+\sum_{j=1}^{i-1}\prod_{k=1}^{j}\gamma_k}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k} = \frac{i}{N}$$

Pictorial algorithm for the Simulation of **Moran Process**: Neutral Evolution Case

■ A-type ● B-type



Time			**#A**	**#B**
Time=t	Pick Random members Suppose RN1=6 ; RN2=4	■ ■ ● ■ ● ● ■ ■ **A** picked for reproduction & **B** for death	nA	nB
Time=t+1		■ ■ ● ■ ● ■ ■ ■	nA+1	nB-1

Repeat above steps as many times until #A=N or #B=N

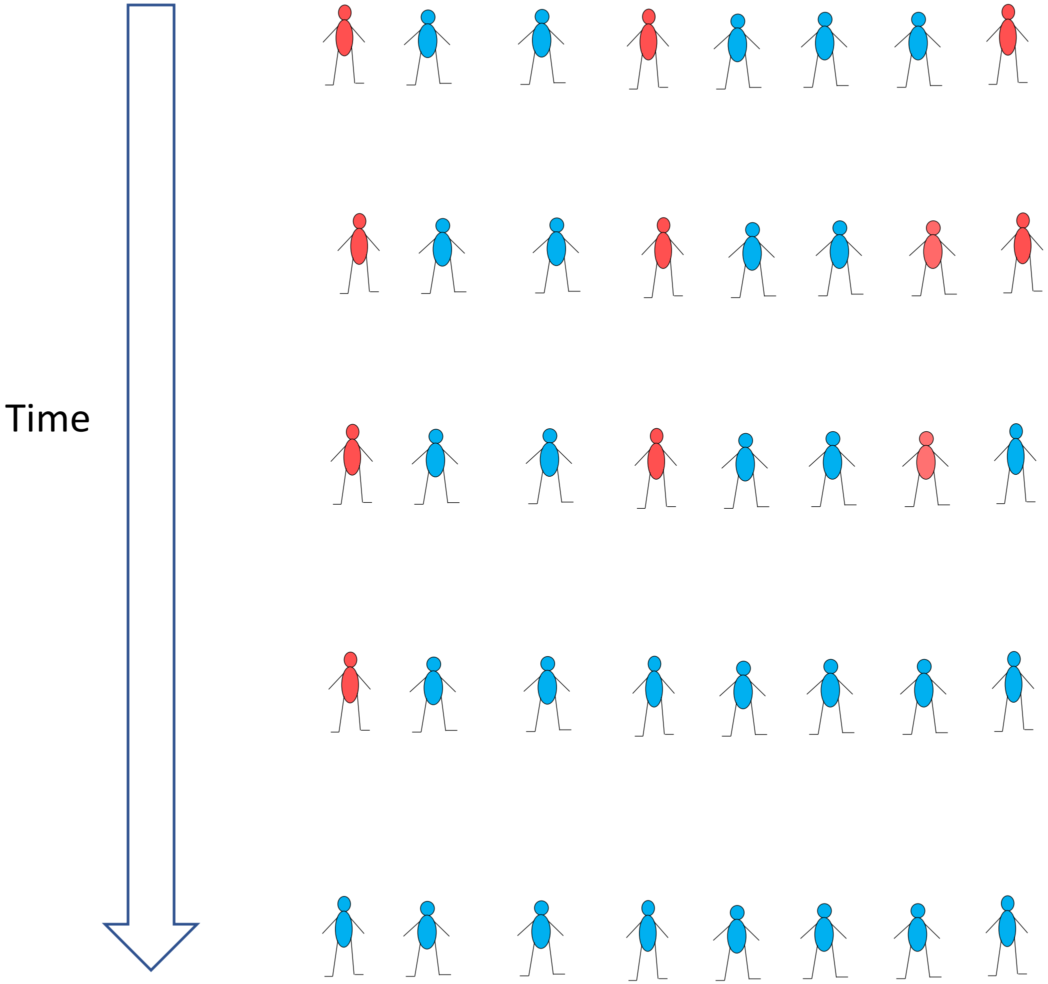
Repeat simulation with same initial condition NT times to determine ρ_A and ρ_B

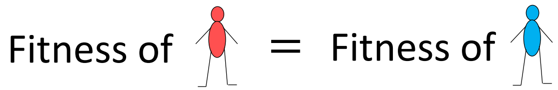
Invasion probability of A: $\rho_A \equiv x_1 = \frac{1}{N};$

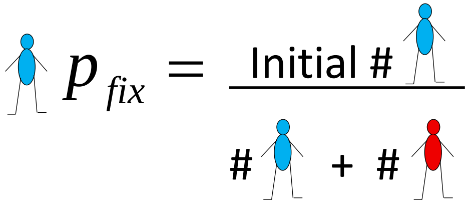
Invasion probability of B: $\rho_B \equiv 1 - x_{N-1} = \frac{\prod_{k=1}^{N-1}\gamma_k}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k} = \frac{1}{N};$

For the Neutral Evolution Case, invasion probability of a single mutant is inversely proportional to population size

Neutral Evolution: A simple model without mutation




Fitness of 🔴 = Fitness of 🔵


$$🔵\ p_{fix} = \frac{\text{Initial \# 🔵}}{\text{\# 🔵 + \# 🔴}}$$

Evolution with selection via Moran Process

Reproduction: Occurs with probability proportional to the fitness of the agent

Death: Occurs at random, independent of the fitness of the agent

$$p_{i,i+1} = \underbrace{\left(\frac{ri}{ri+1(N-i)}\right)}_{\text{Prob. of picking A for reproduction}}\underbrace{\left(\frac{N-i}{N}\right)}_{\text{Prob. of picking B for death}}$$

$$p_{i,i-1} = \underbrace{\left(\frac{(N-i)1}{ri+1(N-i)}\right)}_{\text{Prob. of picking B for reproduction}}\underbrace{\left(\frac{i}{N}\right)}_{\text{Prob. of picking A for death}}$$

$$\gamma_i = \frac{p_{i,i-1}}{p_{i,i+1}} = \frac{1}{r}$$

$$x_i = \frac{(1-\frac{1}{r^i})}{(1-\frac{1}{r^N})}$$

For r> 1; as N➔ ∞ $x_1 \equiv \rho_A \simeq 1 - \frac{1}{r}$

Invasion Probabilities for N=100

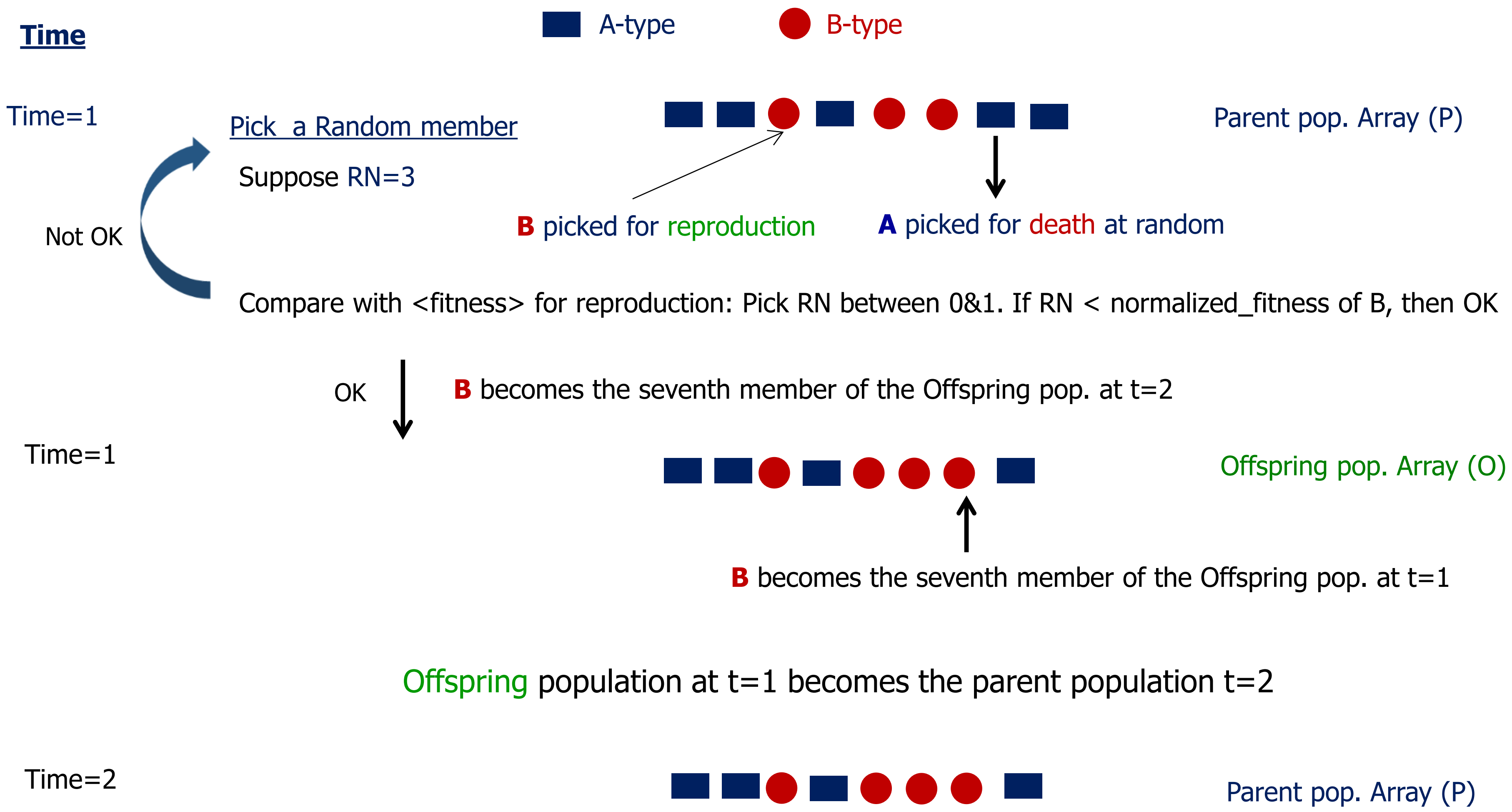
r	$x_1 \equiv \rho_A$
2	0.5
1.01	0.016
1	0.01

r	$x_1 \equiv \rho_A$
0.99	0.0058
0.9	0.000003

➔ **Invasion by a selectively advantageous mutant is not guaranteed even for large population sizes**

Pictorial representation of selection without mutation: Fixation of an ad/disadvantageous mutant

Evolution by Moran Process



<u>**Time**</u>

■ A-type ● B-type

Time=1

<u>Pick a Random member</u>

Suppose RN=3

■ ■ ● ■ ● ● ■ ■ Parent pop. Array (P)

B picked for reproduction

A picked for death at random

Not OK

Compare with <fitness> for reproduction: Pick RN between 0&1. If RN < normalized_fitness of B, then OK

OK

B becomes the seventh member of the Offspring pop. at t=2

Time=1

■ ■ ● ■ ● ● ● ■ Offspring pop. Array (O)

B becomes the seventh member of the Offspring pop. at t=1

Offspring population at t=1 becomes the parent population t=2

Time=2

■ ■ ● ■ ● ● ● ■ Parent pop. Array (P)

Repeat above steps to generate the parent population t=3 and so on

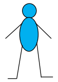
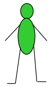
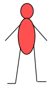
Note: If fitness of A is r1 and fitness of B is r2,

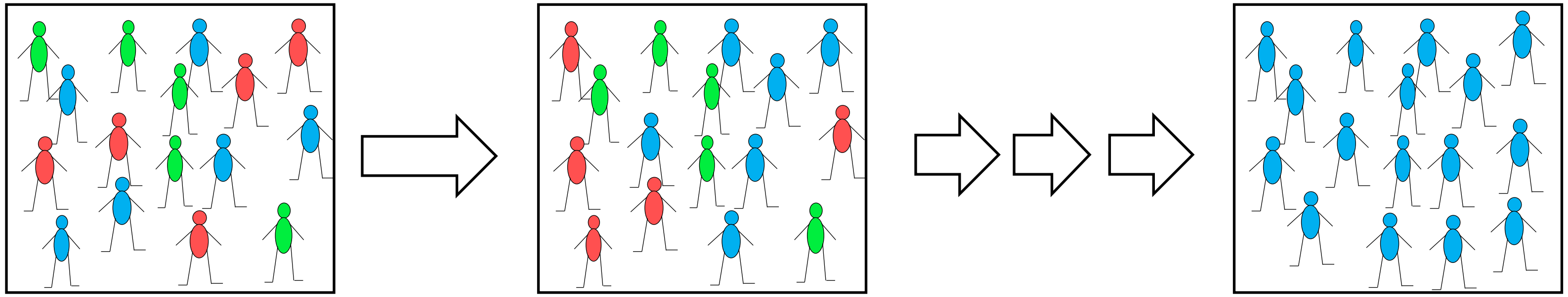
normalized_fitness_of_**A**=r1/(r1+r2); normalized_fitness_of_**B**=r2/(r1+r2)

Different possible outcomes of Evolution

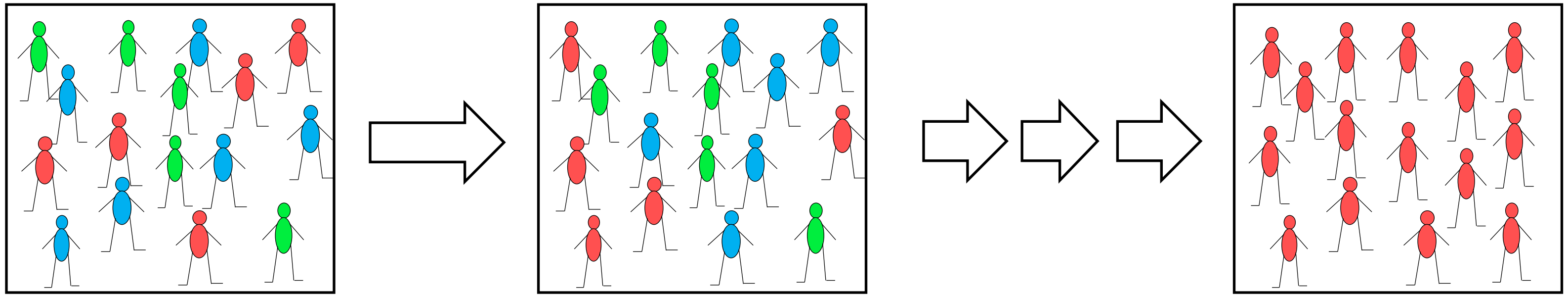
No mutation

Selection with probability *proportional* to Fitness

Fitness of  > Fitness of  > Fitness of 



Alternative outcome

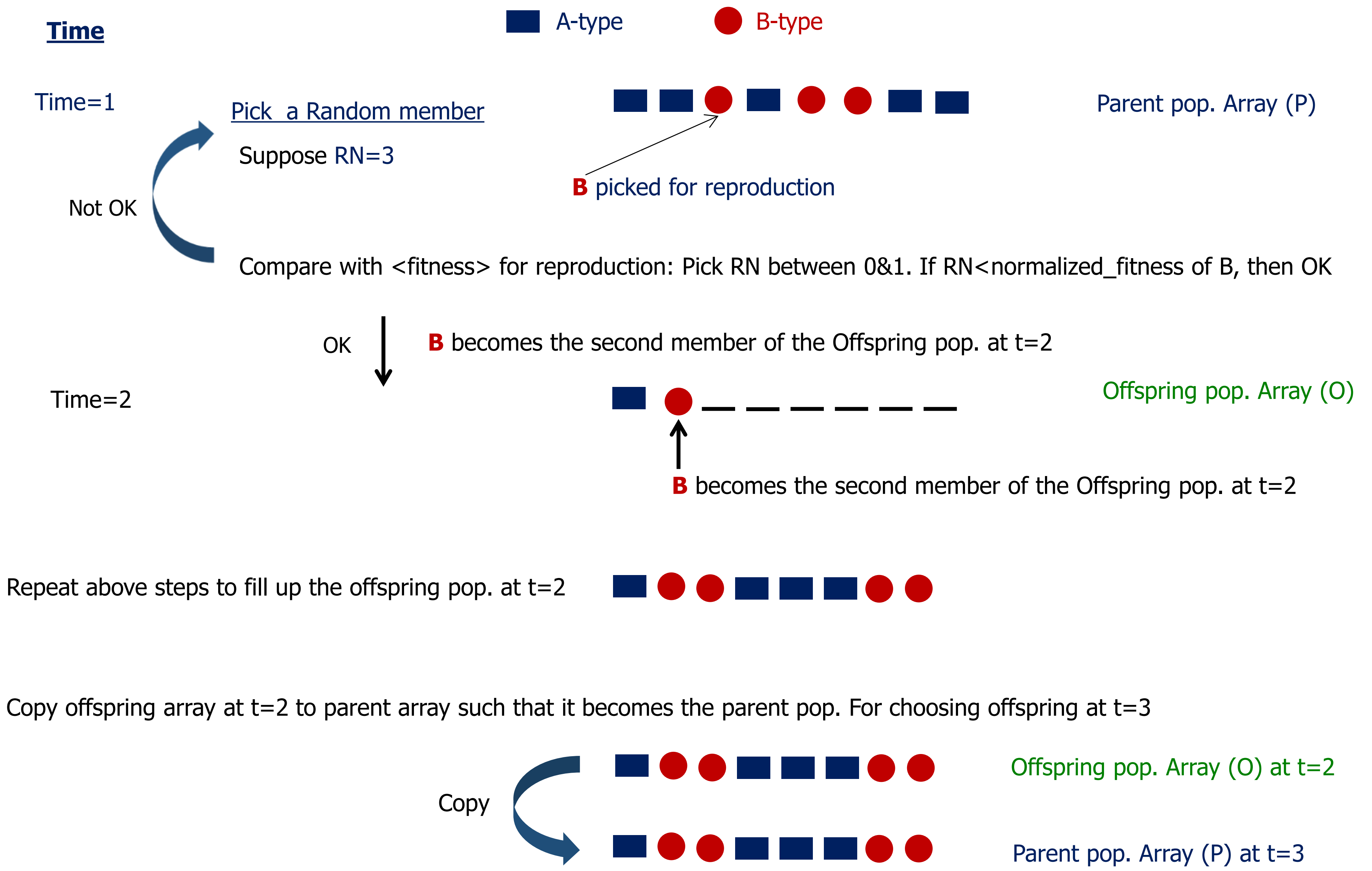


Algorithm for Moran Process

```
Create an array for the population of size N. The array P should initially contain 1 type 0 and N-1 type 1
  Start loop over trials (Nt)
                Generate a uniformly distributed random number RN1 lying between 1 and N
                The corresponding member in the population array i.e. P[RN1] is marked for death
                  Generate another uniformly distributed random number RN2 lying between 1 and N
                    Generate a random number z between 0 and 1
                      If P[RN2]=0 and $z < r/(r+1)$ replace P[RN1] by 0
                      If P[RN2]=1 and $z < 1/(r+1)$ replace P[RN1] by 1
                  Else Generate new RN2 by picking a random no. between 1 and N
                Repeat last 3 steps till a suitable individual is found for reproduction
           Calculate frequency of type 0 and type 1 in the population.
        Repeat above steps for next generation; Continue iterations until freq. of type 0 is either 0 or 1
    Write frequencies of type 0 and type 1 vs time in a file for any one trial
  Close loop over trials
Calculate fixation probability of type0 by counting how many times type 0 gets fixed in the population.
```

Pictorial representation of selection ***without*** mutation: Fixation of an ad/disadvantageous mutant

Wright- Fischer process: Evolution by updating whole population every generation



Time

■ A-type ● B-type

Time=1

Pick a Random member

Suppose RN=3

■ ■ ● ■ ● ● ■ ■ Parent pop. Array (P)

B picked for reproduction

Not OK

Compare with <fitness> for reproduction: Pick RN between 0&1. If RN<normalized_fitness of B, then OK

OK

B becomes the second member of the Offspring pop. at t=2

Time=2

■ ● _ _ _ _ _ _ Offspring pop. Array (O)

B becomes the second member of the Offspring pop. at t=2

Repeat above steps to fill up the offspring pop. at t=2 ■ ● ● ■ ■ ■ ● ●

Copy offspring array at t=2 to parent array such that it becomes the parent pop. For choosing offspring at t=3

■ ● ● ■ ■ ■ ● ● Offspring pop. Array (O) at t=2

Copy

■ ● ● ■ ■ ■ ● ● Parent pop. Array (P) at t=3

Quasi-Species Equation: Evolution with Mutation *and* selection


M. Eigen

$$\frac{dx_i}{dt} = \sum_{j=1}^{N} x_j f_j q_{ji} - \phi x_i$$

Constant Fitness

$$\phi = \sum_{i=1}^{N} f_i x_i$$

Average Fitness


P. Schuster

Limiting Cases

Mutation *without* selection: $\frac{dx_i}{dt} = \sum_{j=1}^{N} x_j q_{ji} - \phi x_i$ when $f_i = 1$ for all i

Selection *without* mutation (Error-free replication): $q_{ji} = \delta_{ji} \Rightarrow \frac{dx_i}{dt} = x_i(f_i - \phi)$

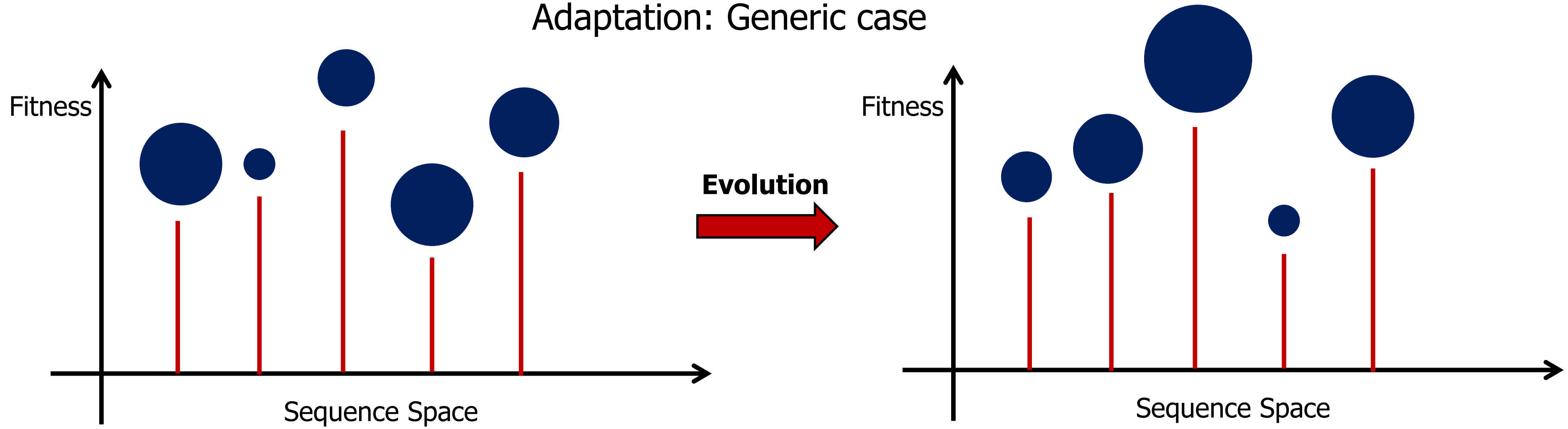
Competition between 2 types

$$\boxed{\frac{dx_A}{dt} = x_A(1 - x_A)(f_A - f_B)}$$

Useful in describing evolution of population of sequences where

- ❖ Variations between sequences arise as a result of errors during replication
- ❖ Presence of replication errors shifts the equilibrium from a pure state (survival of the fittest) to a mixed state where multiple quasi-species can coexist
- ❖ The equilibrium state does not necessarily maximize average fitness

Adaptation: Generic case

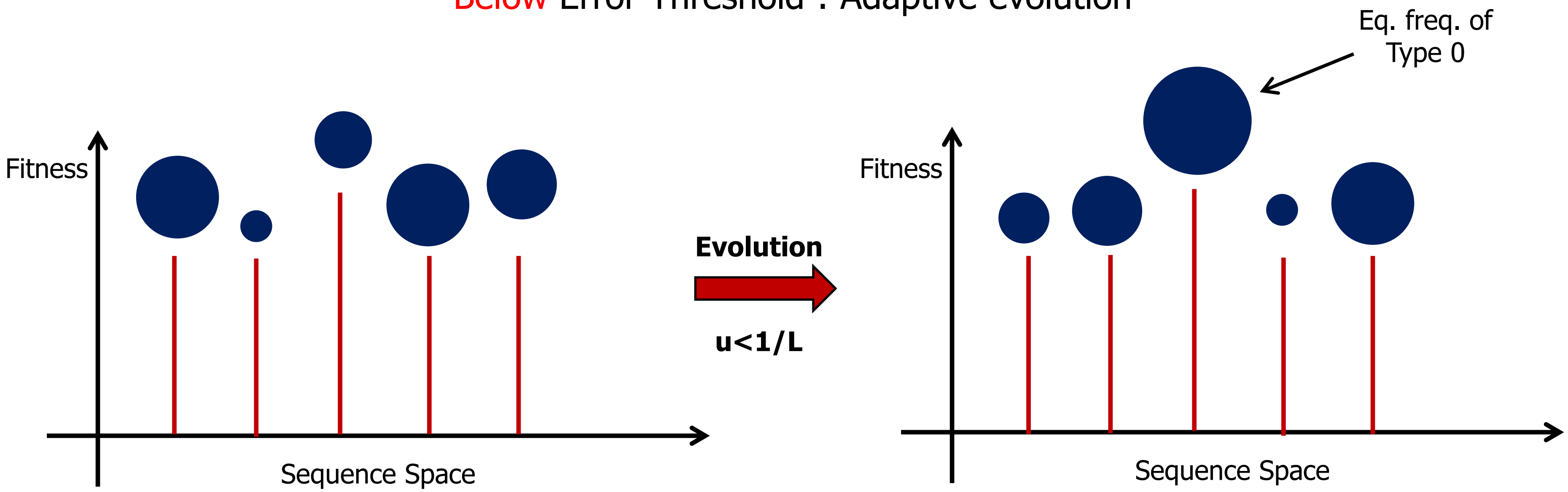


Initial population distribution

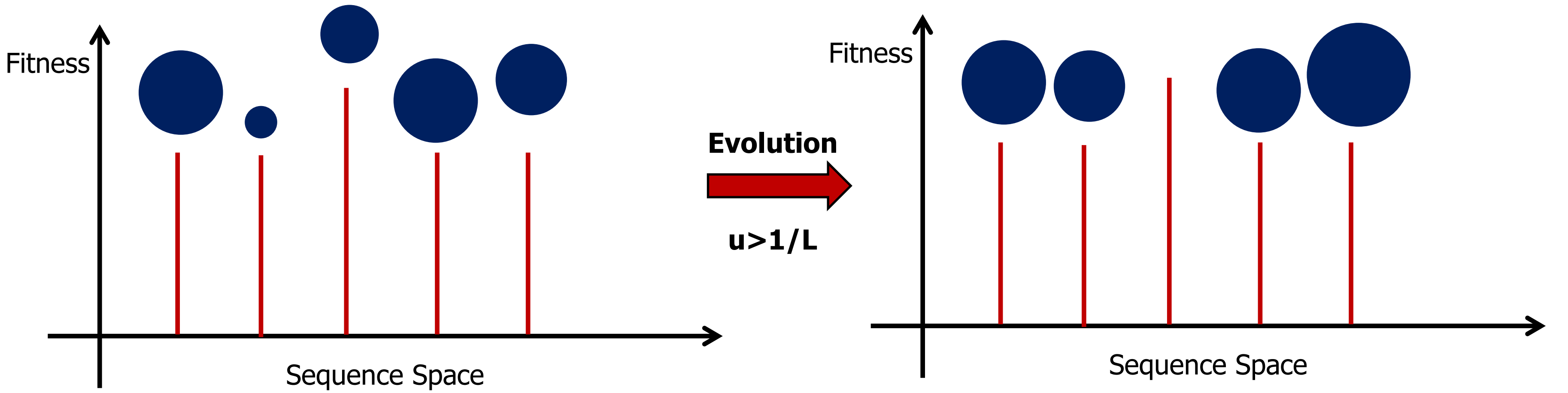
Well adapted population clustered around the peak

Size of the circles represent the frequency of the corresponding sequence in the population

Below Error Threshold : Adaptive evolution



Above Error Threshold : Non-adaptive evolution



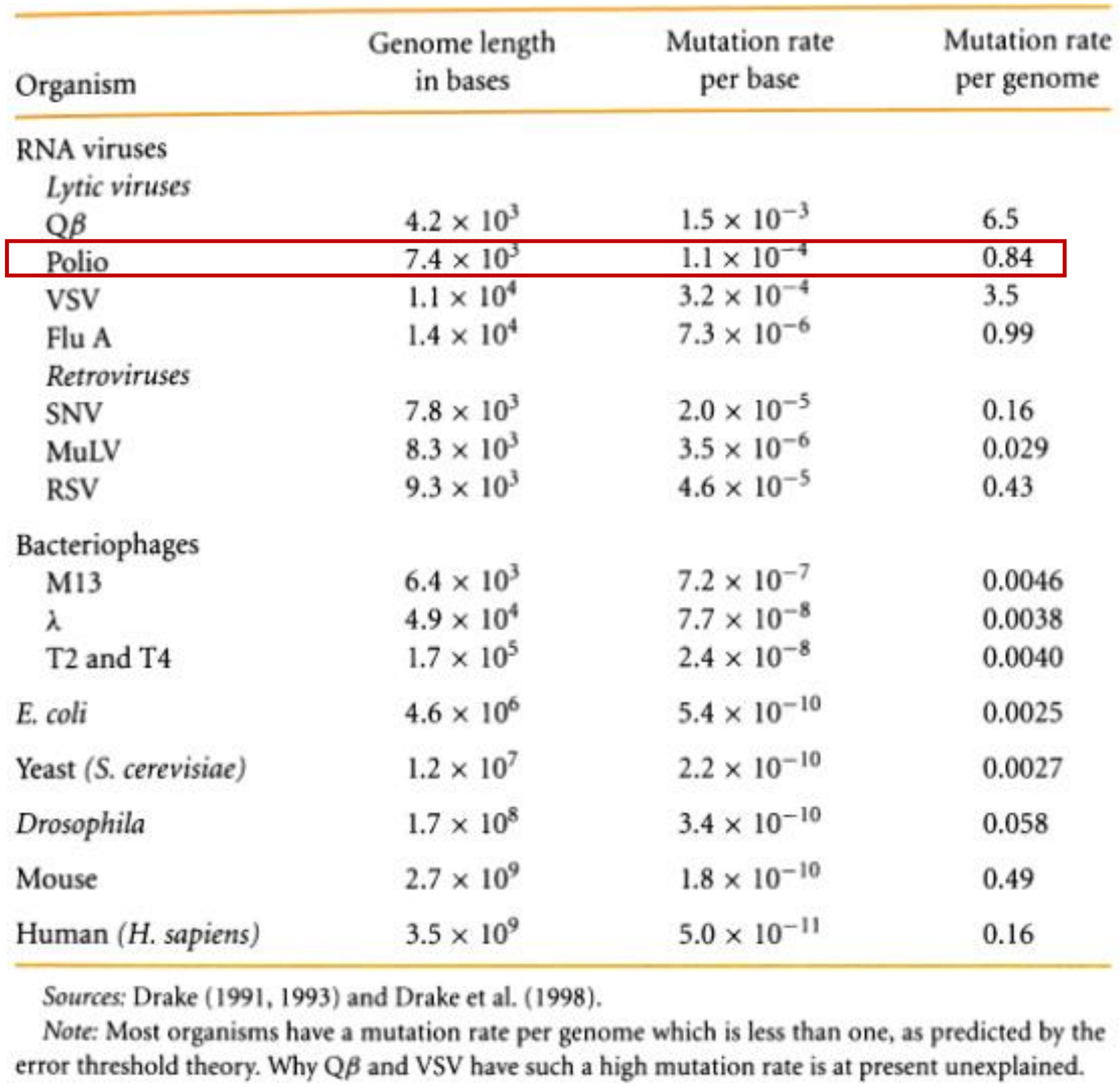
Fittest Sequence Type (Type 0) lost from the population

Eigen's Paradox

- For a replicating molecule to be viable and not be subject to mutational degradation (i.e. evade the error threshold problem), *its sequence length should be small*.
- For a replicating molecule to encode enzymes (i.e. to be functional), *its sequence length should be substantially large*.

How can functional molecules with long sequences survive in the population?

How does Mutation Rate per site (u) across organisms compare with the Error Threshold ($1/L$) ?



Organism	Genome length in bases	Mutation rate per base	Mutation rate per genome
RNA viruses			
Lytic viruses			
Qβ	4.2×10^3	1.5×10^{-3}	6.5
Polio	7.4×10^3	1.1×10^{-4}	0.84
VSV	1.1×10^4	3.2×10^{-4}	3.5
Flu A	1.4×10^4	7.3×10^{-6}	0.99
Retroviruses			
SNV	7.8×10^3	2.0×10^{-5}	0.16
MuLV	8.3×10^3	3.5×10^{-6}	0.029
RSV	9.3×10^3	4.6×10^{-5}	0.43
Bacteriophages			
M13	6.4×10^3	7.2×10^{-7}	0.0046
λ	4.9×10^4	7.7×10^{-8}	0.0038
T2 and T4	1.7×10^5	2.4×10^{-8}	0.0040
E. coli	4.6×10^6	5.4×10^{-10}	0.0025
Yeast (*S. cerevisiae*)	1.2×10^7	2.2×10^{-10}	0.0027
Drosophila	1.7×10^8	3.4×10^{-10}	0.058
Mouse	2.7×10^9	1.8×10^{-10}	0.49
Human (*H. sapiens*)	3.5×10^9	5.0×10^{-11}	0.16

Sources: Drake (1991, 1993) and Drake et al. (1998).

Note: Most organisms have a mutation rate per genome which is less than one, as predicted by the error threshold theory. Why Qβ and VSV have such a high mutation rate is at present unexplained.

Note: Organisms remain viable only if uL<1

For polio virus: uL=0.814

RNA virus Error Catastrophe

- Anti-viral effect manifest by enhanced mutagenesis of the Polio virus genome

High mutation rates ➔ loss of viability of the Polio virus genome

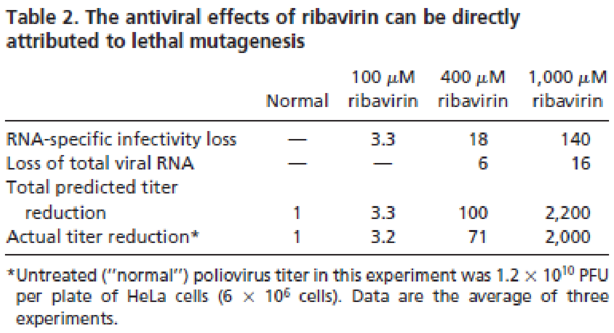


Table 2. The antiviral effects of ribavirin can be directly attributed to lethal mutagenesis

	Normal	100 μM ribavirin	400 μM ribavirin	1,000 μM ribavirin
RNA-specific infectivity loss	—	3.3	18	140
Loss of total viral RNA	—	—	6	16
Total predicted titer reduction	1	3.3	100	2,200
Actual titer reduction*	1	3.2	71	2,000

*Untreated ("normal") poliovirus titer in this experiment was 1.2 × 10^{10} PFU per plate of HeLa cells (6 × 10^6 cells). Data are the average of three experiments.

- Polio viruses reside near the edge of the Error Threshold

Modest (less than 2-fold) increase in mutation rate ➔ 50% of the viral population becomes unviable

4-fold increase in mutation rate ➔ 95% of the viral population becomes unviable.

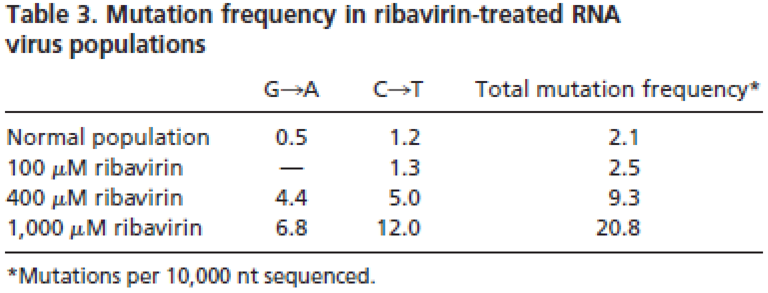
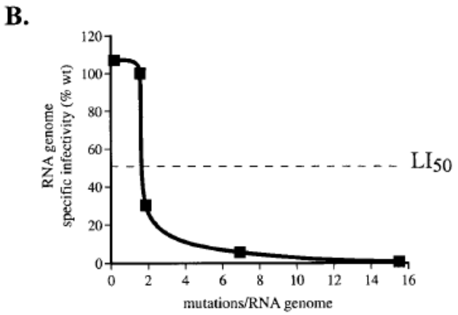


Table 3. Mutation frequency in ribavirin-treated RNA virus populations

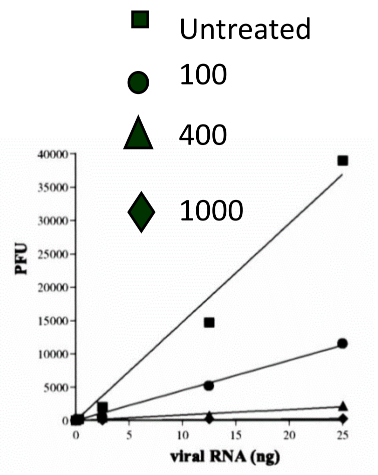
	G→A	C→T	Total mutation frequency*
Normal population	0.5	1.2	2.1
100 μM ribavirin	—	1.3	2.5
400 μM ribavirin	4.4	5.0	9.3
1,000 μM ribavirin	6.8	12.0	20.8

*Mutations per 10,000 nt sequenced.



- High mutation rate produces Polio-virus mutants having low infectivity

The amount of infectious virus genomes in the population is reduced several fold as concentration of Ribavarin increases.



Ref.: Crotty, Cameron, Andino; PNAS 98, 6895-6900 (2001)

PFU: plaque forming unit

1'st lecture: Key Results

$\rho_A \equiv x_1 = \frac{1}{N};$ Neutral Fixation probability of A starting from an initial configuration with a **single** A

Competition between two types A and B with **different** fitness

Higher fitness type is ***not guaranteed*** to take over the population

but

more likely *to do so than dictated by chance.*

$$x_1 \equiv \rho_C = \frac{1}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}$$

$$x_i = \frac{1+\sum_{j=1}^{i-1}\prod_{k=1}^{j}\gamma_k}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}\gamma_k}$$

$$\gamma_i = \frac{p_{i,i-1}}{p_{i,i+1}} = \frac{\beta_i}{\alpha_i}$$

References

Nowak, M; Evolutionary Dynamics: Exploring the equations of life; Belknap Press (2006)

Traulsen, A. & Hauert, C. Stochastic evolutionary game dynamics; Rev. Nonlinear Dynam Complex. 2, 25–61 (2009).

Evolution with *Frequency-dependent* Fitness

Individuals have ***fixed strategies*** that are known to other individuals in the population.

Random interactions occur with other individuals (including those belonging to the same type)

In the Biological Context

strategy ⟷ ***phenotype*** and **payoff** ⟷ ***fitness***

Fitness is a measure of reproductive success

A component of ***Fitness*** of an individual is determined by the ***cumulative*** payoff to that individual resulting from the encounter with other individuals of the same type as well as different types.

The population is *updated* every generation when individuals reproduce with

Probability ***proportional to*** fitness

George Price

Evolutionary Games in N➔∞ limit: A quick review

$$\frac{dx_i}{dt} = x_i(f_i - \phi)$$

John Maynard-Smith

Competition between different types of individuals with frequency-dependent fitness can be thought of as a game in which each type employs a distinct strategy and gets a certain payoff in an encounter with another individual.

Fitness is a measure of reproductive success and **strategies** that yield higher cumulative **payoff**, reproduce at a faster rate.

Consider a population with two types of individuals **A** and **B** whose fitness are $\mathbf{f_A}$ and $\mathbf{f_B}$ respectively.

Assuming ***linear*** dependence of fitness on frequencies $\mathbf{x_A}$, $\mathbf{x_B}$;

$\mathbf{f_A} = a\,\mathbf{x_A} + b\,\mathbf{x_B}$

$\mathbf{f_B} = c\,\mathbf{x_A} + d\,\mathbf{x_B}$

➔ $$f_i(\vec{x}) = M_{ij}x_j$$

Can be written in matrix notation as **f** = **Mx, f**=[$\mathbf{f_A}$, $\mathbf{f_B}$]; **x**=[$\mathbf{x_A}$, $\mathbf{x_B}$]

where **M** is the payoff matrix.

$$\mathbf{M=}\begin{array}{c|cc} & \mathbf{A} & \mathbf{B} \\ \hline \mathbf{A} & a & b \\ \mathbf{B} & c & d \end{array}$$

E(A,A)=a : Payoff to **A** when it interacts with another A

E(A,B)=b : Payoff to **A** when it interacts with **B**

E(B,A)=c : Payoff to **B** when it interacts with **A**

E(B,B)=d : Payoff to **B** when it interacts with another **B**

Replicator Dynamics

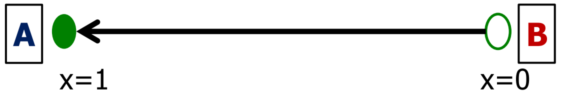
$$\dot{x}_A = x_A(1\text{-}\, x_A)[(a-b-c+d)x_A + b - d]$$

$$M=\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array}$$

Harmony game:

Case 1: a>c; b >d ➔ Payoff to **A** > Payoff to **B** : **A** dominated **B** **i.e. A is a Nash**

Only one stable equilibrium solution exists.



PD game:

Case 2: a<c; b<d ➔ Payoff to **B** > Payoff to **A** : **B** dominates **A** **i.e B is a Nash**

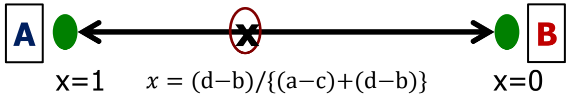
Only one stable equilibrium solution exists.

Stag-Hunt game/ Coordination game:

Case 3: a>c; b<d ➔ $x = 0, 1, (\mathrm{d-b})/\{(\mathrm{a-c})+(\mathrm{d-b})\}$

3 equilibrium solution exists; **A** and **B** are ***bistable***, mixed-state solution is ***unstable***.

Both A and B are Nash

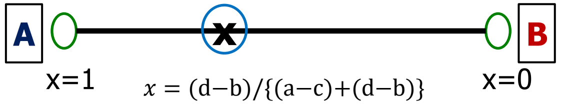


Chicken game/ Snowdrift game:

Case 4: a<c; b>d ➔ $x = 0, 1, (\mathrm{d-b})/\{(\mathrm{a-c})+(\mathrm{d-b})\}$

Only one stable equilibrium solution exists. ***A*** & ***B*** stably co-exist. **Neither A nor B is a Nash**

x=0, 1 are ***unstable*** equilibrium solutions.



Cooperation and Conflict

©Bill Watterson

A fundamental problem in evolution

Altruistic behaviour comes at a ***cost***

but

Selfish behaviour does ***not*** entail a cost

How do we explain the survival of altruistic agents?

Behaviour affecting Evolution of Cooperation & Conflict

How does individual “behaviour” evolve during a social conflict?

How is evolution of our “behaviour” affected by

- Size and underlying structure of the social network in which we are embedded
- The nature and behaviour of connected neighbours
- The economic and social environment
- Individual aspiration levels

Big Questions

☐ How do individuals incorporate these factors into their learning strategies?

☐ How do these factors shape collective (population-level) outcomes ?

☐ Can we socially engineer situations where cooperation thrives?

Evolution of Cooperation

What Don't We Know?

At *Science*, we tend to get excited about new discoveries that lift the veil a little on how things work, from cells to the universe. That puts our focus firmly on what has been added to our stock of knowledge. For this anniversary issue, we decided to shift our frame of reference, to look instead at what we *don't* know: the scientific puzzles that are driving basic scientific research.

We began by asking *Science*'s Senior Editorial Board, our Board of Reviewing Editors, and our own editors and writers to suggest questions that point to critical knowledge gaps. The ground rules: Scientists should have a good shot at answering the questions over the next 25 years, or they should at least know how to go about answering them. We intended simply to choose 25 of these suggestions and turn them into a survey of the big questions facing science. But when a group of editors and writers sat down to select those big questions, we quickly realized that 25 simply wouldn't convey the grand sweep of cutting-edge research that lies behind the responses we received. So we have ended up with 125 questions, a fitting number for *Science*'s 125th anniversary.

First, a note on what this special issue is not: It is not a survey of the big societal challenges that science can help solve, nor is it a forecast of what science might achieve. Think of it instead as a survey of our scientific ignorance, a broad swath of questions that scientists themselves are asking. As Tom Siegfried puts it in his introductory essay, they are "opportunities to be exploited."

We selected 25 of the 125 questions to highlight based on several criteria: how fundamental they are, how broad-ranging, and whether their solutions will impact other scientific disciplines. Some have few immediate practical implications—the composition of the universe, for example. Others we chose because the answers will have enormous societal impact—whether an effective HIV vaccine is feasible, or how much the carbon dioxide we are pumping into the atmosphere will warm our planet, for example. Some, such as the nature of dark energy, have come to prominence only recently; others, such as the mechanism behind limb regeneration in amphibians, have intrigued scientists for more than a century. We listed the 25 highlighted questions in no special order, but we did group the 100 additional questions roughly by discipline.

Our sister online publications are also devoting special issues to *Science*'s 125th anniversary. The Science of Aging Knowledge Environment, SAGE KE (www.sageke.org), is surveying several big questions confronting researchers on aging. The Signal Transduction Knowledge Environment, STKE (www.stke.org), has selected classic *Science* articles that have had a high impact in the field of cell signaling and is highlighting them in an editorial guide. And *Science*'s Next Wave (www.nextwave.org) is looking at the careers of scientists grappling with some of the questions *Science* has identified.

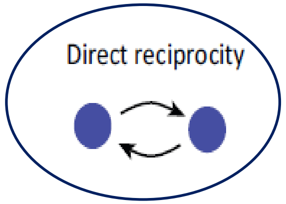
We are acutely aware that even 125 unknowns encompass only a partial answer to the question that heads this special section: What Don't We Know? So we invite you to participate in a special forum on *Science*'s Web site (www.sciencemag.org/sciext/eletters/125th), in which you can comment on our 125 questions or nominate topics we missed—and we apologize if they are the very questions you are working on.

—DONALD KENNEDY AND COLIN NORMAN

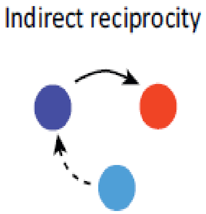
Contents >> NEWS

See also Editorial on p. 19 and www.sciencemag.org/sciext/125th

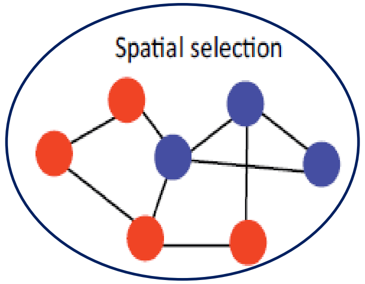
Mechanisms for sustaining Cooperation



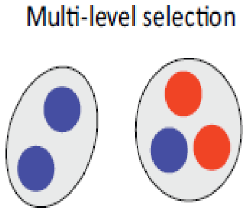
Tit-for-tat strategies that utilize past strategy of interacting partner



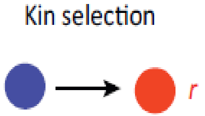
Strategies based on reputation of interacting partner



Strategies adapted to structured populations that facilitates more cooperative interactions through clustering



Group selection



Interaction and cooperation with related individuals promote spread of cooperation : Hamilton’s rule

Nowak; *Science* (2006)

Rand & Nowak
Trends in Cognitive Sciences (2013)

Nash Equilibrium

A strategy is said to be a *Nash Equilibrium* if the person adopting the strategy cannot increase his payoff by changing to a different strategy.

A is a ***strict*** Nash Equilibrium if $a > c$

A is a Nash Equilibrium if $a \geq c$

B is a strict Nash Equilibrium if $d > b$

B is a Nash Equilibrium if $d \geq b$

$$M = \begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array}$$

Evolutionarily Stable Strategies (ESS)

Consider a large population of individuals employing strategy A. If a mutant employing strategy B is introduced into the population, **can the mutant invade the population consisting primarily of A-type players?**

In the *infinitely large population size limit*, let the number of B mutants (invaders) be infinitesimally small with frequency given by $x_B = \varepsilon$. Frequency of **A's**: $x_A = 1 - \varepsilon$

$f_A = a\,(1-\varepsilon) + b\,\varepsilon$; $f_B = c\,(1-\varepsilon) + d\,\varepsilon$

B cannot invade A only if $f_B < f_A$ i.e. $a\,(1-\varepsilon) + b\,\varepsilon > c\,(1-\varepsilon) + d\,\varepsilon$

Since ε is very small, neglecting terms of order ε gives **$a>c$**

If however, $a=c$, $f_A > f_B$ gives **$b>d$**

Condition for A to be an ESS in infinite population limit: **$a>c$ or if $a=c$, $b>d$**

Key Questions

How is the concept of an ESS modified for *finite* populations?

↓

How does population size affect the survival of *cooperative* strategies ?

Games in Finite Populations

For the Payoff Matrix **M=** $\begin{array}{c|cc} & C & D \\ \hline C & a & b \\ D & c & d \end{array}$

b<c and a>d

No. of C players = **i**

No. of D players = **N-i**

Prob. that C interacts with another C = (i-1)/(N-1)

Prob. that C interacts with another D = (N-i)/(N-1)

Prob. that D interacts with another C = i/(N-1)

Prob. that D interacts with another D = (N-i-1)/(N-1)

Expected payoff to C when it interacts with C = a(i-1)/(N-1)

Expected payoff to C when it interacts with D = b(N-i)/(N-1)

Total expected payoff for C : $\mathbf{F_i = (a(i-1)+b(N-i))/(N-1)}$

Total expected payoff for D : $\mathbf{G_i = (ci+d(N-i-1))/(N-1)}$

Define fitness of **C** as : $f_i = 1- w + w F_i$; fitness of **D** as : $g_i = 1- w + w G_i$

w ➔ intensity of selection

w=1 ➔ strong selection; fitness completely determined by interactions

w=0 ➔ no selection between C & D

w<<1 ➔ weak selection

Revisiting the ESS condition for large populations

When can a population of D-type players avoid being invaded by a single mutant C-type?

Selection opposes C invading D: Fitness of a single C-type < Fitness of (N-1) D-types

$f_1 < g_1$ ➔ $\boxed{b(N-1) < c + d(N-2)}$ ➔ For N>>1: **b < d** **;** For N=2: b<c ⟺

Infinite population result

D is an ESS iff:

d<b **or** if b=d, a<c

$$M=\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{bmatrix} a & b \\ c & d \end{bmatrix} \end{array}$$

When can a population of C-type players avoid being invaded by a single mutant D-type?

Selection opposes D invading C: Fitness of a single D-type < Fitness of (N-1) C-types

$g_{N-1} < f_{N-1}$ ➔ $\boxed{c(N-1) < b + a(N-2)}$ ➔ For N>>1: **c < a;** For N=2: c<b ⟺

Infinite population result

C is an ESS iff:

a<c **or** if a=c, b>d

Essential to consider fixation probability in finite populations to determine the ESS

$\rho_C > \frac{1}{N} \Rightarrow$ Selection favours C replacing D

$\rho_C < \frac{1}{N} \Rightarrow$ Selection opposes C replacing D

Moran Process in Games in Finite Populations

C's and D's are picked for reproduction with a probability proportional to their mean fitness and for death randomly.

Probability of picking **C** for reproduction and **D** for death : $p_{i,i+1} \equiv \alpha_i = \left(\frac{i\,f_i}{if_i + (N-i)\,g_i}\right)\left(\frac{N-i}{N}\right)$

Probability of picking **D** for reproduction and **C** for death : $p_{i,i-1} \equiv \beta_i = \left(\frac{(N-i)\,g_i}{if_i + (N-i)\,g_i}\right)\left(\frac{i}{N}\right)$

$$\gamma_i = \frac{\beta_i}{\alpha_i} = \frac{g_i}{f_i}$$

$$\rho_C = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^{k} \frac{g_i}{f_i}} \qquad \rho_D = \frac{\prod_{i=1}^{N-1} \frac{g_i}{f_i}}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^{k} \frac{g_i}{f_i}} \qquad \frac{\rho_D}{\rho_C} = \prod_{i=1}^{N-1} \frac{g_i}{f_i}$$

In the limit w→0, $\rho_C > \frac{1}{N}$ leads to the inequality

$\boxed{a(N-2) + b(2N-1) > c(N+1) + d(2N-4)}$ which in the limit $N>>1$,reduces to $\boxed{a + 2b > c + 2d}$

For fixed, a,b,c,d, the above inequality gives a lower bound on the population size N

$\boxed{N > N_c}$ $$N_C = \frac{2a + b + c - 4d}{a + 2b - c - 2d}$$

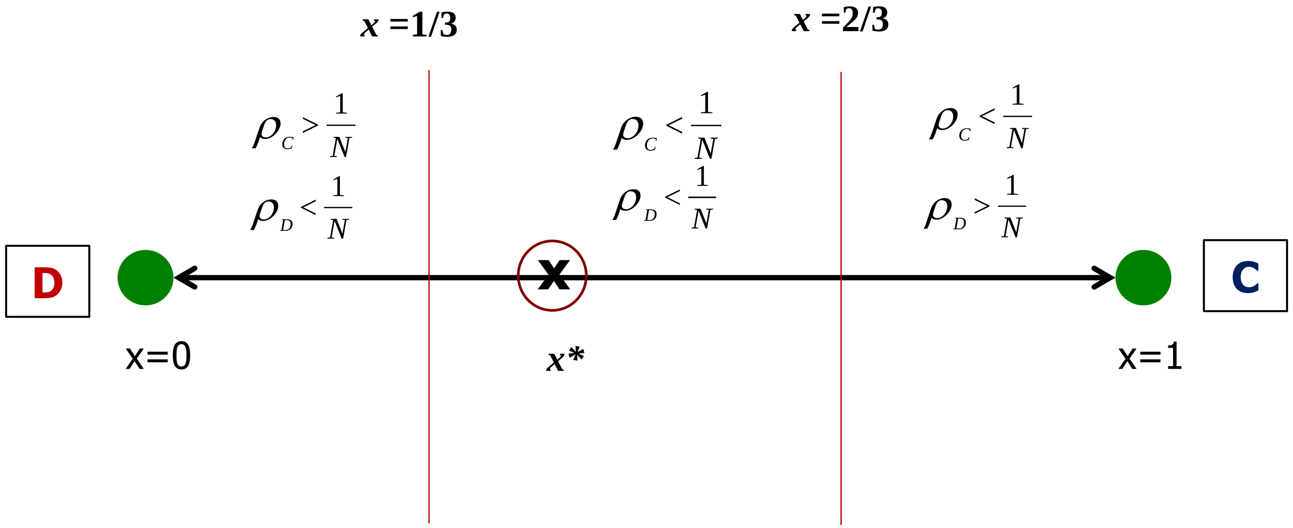
Nc is the *minimum* size of the population necessary for selection to favour fixation of cooperators

1/3 Law: Condition for the invasion probability of C **>** *neutral* invasion probability

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

$$x^* = \frac{d - b}{a - c + d - b} \quad \Rightarrow x^* < \frac{1}{3}$$

Condition on the mixed state equilibrium frequency obtained from replicator dynamics



Risk Dominance in Evolutionary Games

Risk Dominance: If both **C** and **D** is a strict Nash Equilibrium in the conventional sense i.e. if a>c and d>b then which strategy has a higher fixation probability ?

$$\frac{\rho_D}{\rho_C} = \prod_{i=1}^{N-1} \gamma_i = \prod_{i=1}^{N-1} \frac{g_i}{f_i}$$

$$w << 1: \quad \gamma_i \simeq 1 - w(F_i - G_i) + o(w^2)$$

$$\frac{\rho_D}{\rho_C} = \prod_{i=1}^{N-1} (1 - w(F_i - G_i)) \simeq 1 - w \sum_{i=1}^{N-1} (F_i - G_i)$$

$$\sum_{i=1}^{N-1} (F_i - G_i) = \sum_{i=1}^{N-1} ui + v \qquad u = \frac{(a-b-c+d)}{N-1}; \qquad v = \frac{-a+bN-dN+d}{N-1}$$

$$\frac{\rho_D}{\rho_C} = 1 - \frac{w}{2} X; \quad \boxed{X = (a+b-c-d)N - 2a + 2d} \quad \boxed{X > 0 \Rightarrow \rho_C > \rho_D}$$

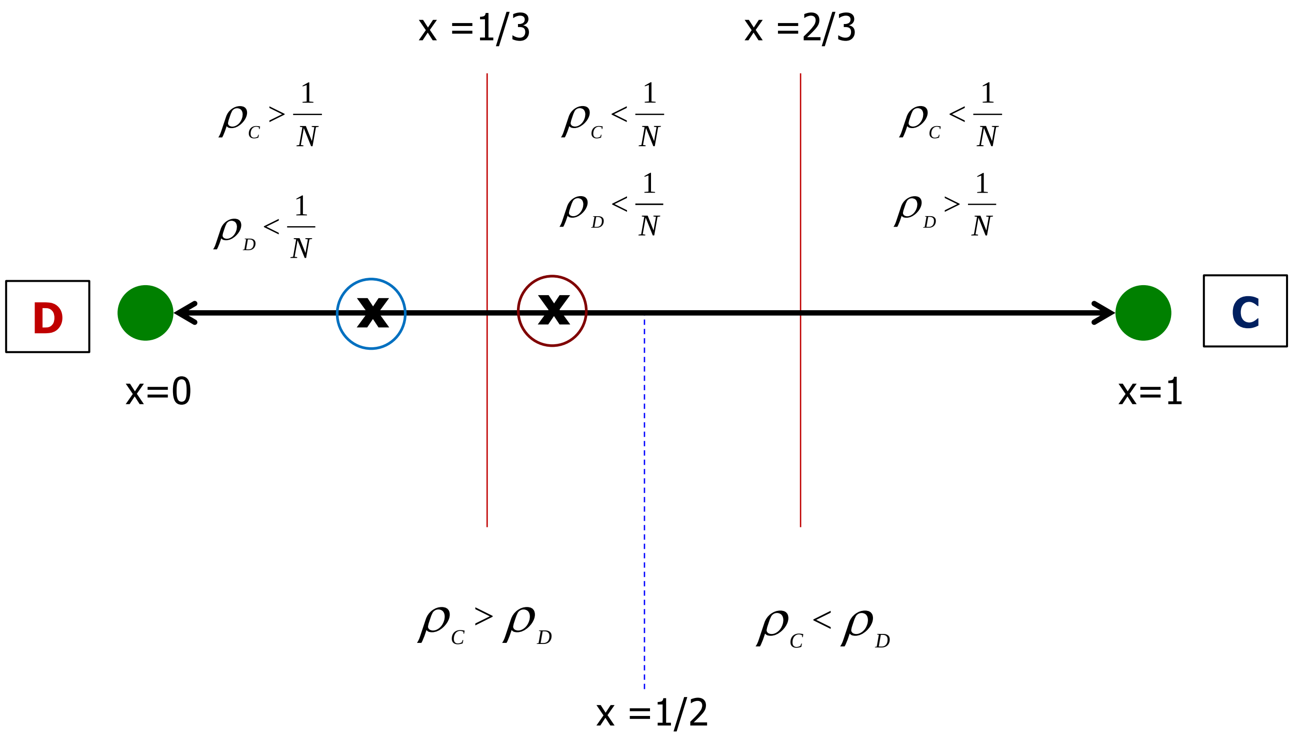
$$N >> 1: X > 0 \Rightarrow \boxed{a + b > c + d} \qquad x^* = \frac{d-b}{a-c+d-b} \Rightarrow x^* < \frac{1}{2}$$

$$M = \begin{array}{c|cc} & C & D \\ \hline C & a & b \\ D & c & d \end{array}$$

Risk Dominance: If both **C** and **D** is a strict Nash Equilibrium in the conventional sense i.e. if a>c and d>b then which strategy has a higher fixation probability ?

Fixation Probabilities and the 1/3 Law for w<<1 and N>>1

⊗ -- Unstable mixed state equilibrium



C is Risk Dominant if $\rho_C > \rho_D$ ➔ **a + b > c + d** when w<<1 and N>>1

D is Risk Dominant if $\rho_D > \rho_C$

- A strategy is Risk Dominant if the total payoff for that strategy is larger than the total payoff for every other strategy.
- The Risk Dominant strategy has a greater fixation probability in the limit **w<<1** and **N>>1**

Evolutionary Stability in Finite Populations

If a>c and b>d, **C** is a strict Nash equilibrium as well as an ESS and selection will always favour fixation of **C** and oppose fixation of **D** in a finite population of any size.

If a>c and b<d, both **C** and **D** is an ESS. According to the *infinite population* analysis, a small fraction of **C** mutants cannot invade a population consisting predominantly of **D** players.

What happens for finite populations ?

Condition for a strategy to be an ESS has to be modified for *finite* populations.

In a *finite* population of size N, a strategy **C** is an ***ESSN*** if

(i) A single mutant of any other strategy has lower fitness than **C**

(ii) The fixation probability of *every other strategy* must be smaller than the neutral fixation probability **and** the fixation probability of **C** must be larger than the neutral fixation probability

C is an ***ESSN*** if $G_{N-1} < F_{N-1}$ and $\rho_C > \frac{1}{N}$ and $\rho_D < \frac{1}{N}$

D is an ***ESSN*** if $F_1 < G_1$ and $\rho_D > \frac{1}{N}$ and $\rho_C < \frac{1}{N}$

Evolutionary Stability in Finite Populations: Examples

For D to be an ESS:

Selection opposes C invading D: Fitness of a single C-type < Fitness of (N-1) D-types

$$f_1 < g_1 \quad \rightarrow \quad \boxed{b(N-1) < c + d(N-2)}$$

Selection opposes C replacing D: $\rho_C < \frac{1}{N}$

$$\boxed{a(N-2) + b(2N-1) < c(N+1) + d(2N-4)} \quad \text{for } w<<1$$

$$M= \begin{array}{c|cc} & C & D \\ \hline C & a & b \\ D & c & d \end{array}$$

For N>>1: **b < d** and **a+b<c+d**

For N=2: $f_1 < g_1$ → b<c and $\rho_C < \frac{1}{2}$ → b<c

Examples

$$M= \begin{array}{c|cc} & C & D \\ \hline C & 20 & 0 \\ D & 17 & 1 \end{array}$$

Infinite population inference

Both C & D are an ESS

$f_1 < g_1$ → -15<N

$\rho_C < \frac{1}{N}$ → N<53

In finite populations

D is an ESS only for N<53

$$M= \begin{array}{c|cc} & C & D \\ \hline C & 1 & 28 \\ D & 2 & 30 \end{array}$$

Infinite population inference

Only D is an ESS

$f_1 < g_1$ → N>15

$\rho_C < \frac{1}{N}$ → N>17

In finite populations

D is an ESS only for N>17

Fixation Probability and Risk Dominance using the Fermi update rule

Payoff Comparison **method of population update**

Blume 1993, Szabo & Toke 1998
Traulsen, Pacheco, Nowak 2007

$$P(C \to D) = \frac{1}{1 + e^{-w(F_D - F_C)}}$$

C : Focal player
D : Role model

Limiting case: $\boldsymbol{w} \to \infty$, If $F_D > F_C$, C is replaced by D with probability 1

If $F_D < F_C$, C is retained with probability 1

$$p_{i,i+1} \equiv \alpha_i = \left(\frac{i}{N}\right)\left(\frac{1}{1+e^{-w(F_i - G_i)}}\right)\left(\frac{N-i}{N}\right)$$

Probability of choosing C for reproduction

$$p_{i,i-1} \equiv \beta_i = \left(\frac{N-i}{N}\right)\left(\frac{1}{1+e^{-w(G_i - F_i)}}\right)\left(\frac{i}{N}\right)$$

Probability of choosing D for reproduction

$$\gamma_i = \frac{\beta_i}{\alpha_i} = e^{-w(F_i - G_i)}$$

$$\frac{\rho_D}{\rho_C} = \prod_{i=1}^{N-1} \gamma_i = \prod_{i=1}^{N-1} e^{-w(F_i - G_i)} = e^{-w \sum_{i=1}^{N-1} (F_i - G_i)} = e^{-\frac{w}{2}X}$$

Valid for **all** selection strengths

$$X = (a+b-c-d)N - 2a + 2d > 0 \Rightarrow \rho_D < \rho_C$$

$$\boxed{N >> 1 : X > 0 \Rightarrow a+b > c+d}$$

Fixation Probability calculation using the Fermi update rule

$$\rho_C = \frac{1}{1+\sum_{k=1}^{N-1}\prod_{i=1}^{k}\gamma_i} = \frac{1}{1+\sum_{k=1}^{N-1}\prod_{i=1}^{k}e^{-w(F_i-G_i)}}$$

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{bmatrix} a & b \\ c & d \end{bmatrix} \end{array}$$

If a - c = b - d → Payoff difference is the same regardless of which strategy one of the players unilaterally switch from

$$\rho_C \equiv x_1 = \frac{1}{1+\sum_{k=1}^{N-1}e^{-wvk}} = \frac{1-e^{-wv}}{1-e^{-Nwv}}$$

➔ Invasion probability of **C**

$$x_i = \frac{1-e^{-wvi}}{1-e^{-wvN}}$$

compare

⟺

$$x_i = \frac{(1-\frac{1}{r^i})}{(1-\frac{1}{r^N})}$$

Equivalent to fixation probability in the constant selection case with $r = e^{wv}$

↓

Fixation probability starting from a state with *i* C’s

TFT can Invade ALLD in a Finite Population

For the Payoff Matrix

$$\mathbf{M} = \begin{array}{c|cc} & \text{TFT} & \text{ALLD} \\ \hline \text{TFT} & ma & b+(m-1)d \\ \text{ALLD} & C+(m-1)d & md \end{array}$$

No. of TFT players = **i**

No. of ALLD players = **N-i**

c>a>d>b $\quad m = \dfrac{1}{1-\delta}$

According to the *infinite population* analysis, for m > (c-d)/(a-d), both TFT and ALLD are an ESS and each strategy is stable against invasion by either strategy.

In finite populations, **TFT** can get fixed in the population even if $F_{TFT} < G_{ALLD}$ provided $\rho_{TFT} > \dfrac{1}{N}$

If F_i and G_i is the fitness of **i** **TFT** and (**N-i)** **ALLD** players,

$$F_i = \frac{ma(i-1)+(b+(m-1)d)(N-i)}{N-1} \qquad G_i = \frac{(c+(m-1)d)i+md(N-i-1)}{N-1}$$

$F_1 = F_{TFT} = b+(m-1)d$ and $G_1 = G_{ALLD} = (c+(m-1)d + md(N-2))/(N-1)$

For w→0 and fixed N, $\rho_{TFT} > \dfrac{1}{N}$ gives a lower bound on m: $m > \dfrac{c(N+1)+d(N-2)-b(2N-1)}{(a-d)(N-2)}$

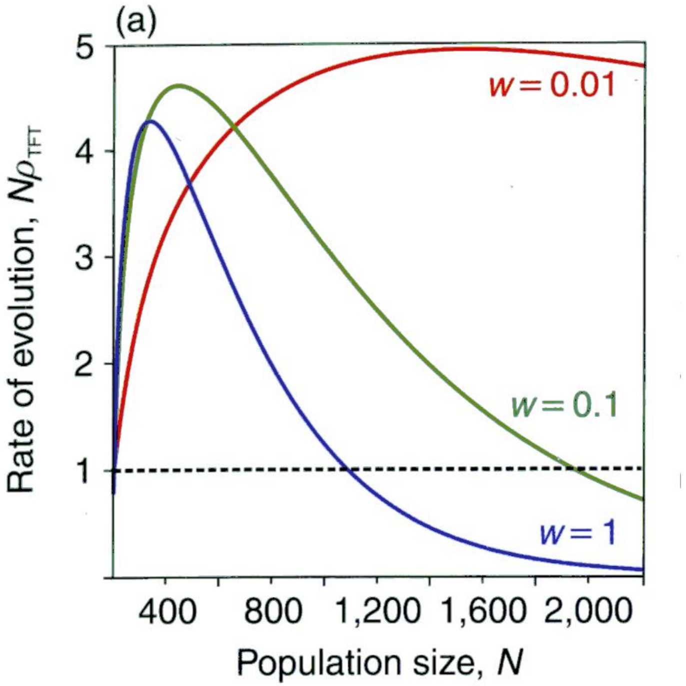
When N=2, m>∞, When N=3: m>10 When N=4: m>6

For N>>1, lower bound on m: $m > \dfrac{c+d-2b}{(a-d)} \Rightarrow m > 3$ when a=3, b=0, c=5, d=1

For fixed m, $\rho_{TFT} > \frac{1}{N}$ gives a *lower bound* on N:

$$\boxed{N > \frac{2ma + b + c - 2d(m+1)}{ma + 2b - c - d(m+1)}}$$

For fixed **m=10** : N > 3 (if a=3,b=0,c=5,d=1)



Structure of an agent-based simulation (ABS) of evolutionary games on networks

- **Initial configuration:** Specify initial distribution of different strategies on a network
- **Payoff calculation:** Interaction and payoff calculation for every member of the population
- **Strategy update:** Update the strategies of the agents using specified deterministic or stochastic update rules

Spatial Games

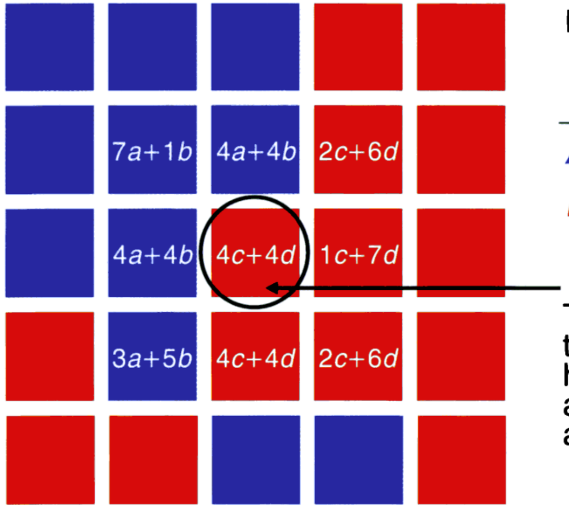
Rules for *Deterministic* Spatial Games

1. The payoff to each player is given by the total payoff obtained by playing each of its eight neighbours.

2. **Rules for updating a cell are deterministic**: The focal (central) cell is replaced either by itself or one of the eight neighbouring cells (Moore neighbourhood) **depending on which has the highest payoff.**

3. All cells are updated *simultaneously* (synchronous updating)

4. Periodic boundary condition is used to ensure all cells are treated in the same way and there are no boundary effects.



Payoff matrix:

	A	*B*
A	*a*	*b*
B	*c*	*d*

The focal cell will be taken over by whoever has the highest payoff among the 8 neighbors and the cell itself

🟦 Cooperator 🟥 Defector

Nowak 2006

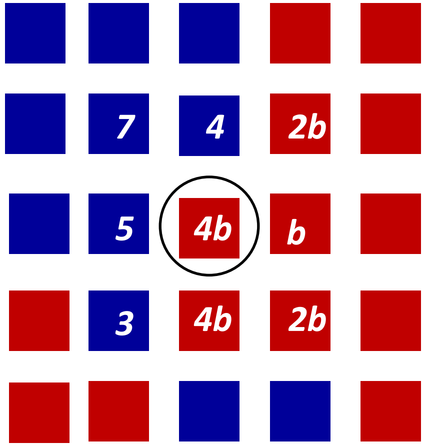
b-Measure of benefit gained from *exploiting* an *altruistic* partner relative to the benefit gained from *cooperating* with an *altruistic* partner

The survival of a cell depends on its own strategy, the strategy of its eight neighbours as well as the strategies of their neighbours
➔ 25 cells in all

As $\varepsilon \rightarrow 0$, the focal cell (D) has a total payoff = 4b since it is surrounded by 4 C's and 4 D's.

If **4b>7**, central cell remains a Defector in the next generation

If **4b<7**, central cell transforms from Defector to Cooperator in the next generation



a=1,b=0,c=b,d=ε

Spatial Games

Algorithm for *Stochastic* Spatial Games

1. The payoff to each player is given by the total payoff obtained by playing each of its eight neighbours.

2. Rules for updating a cell are stochastic:

- The fitness of all altruists (fC) and all selfish (fD) agents in the neighbourhood of each focal player is separately calculated.

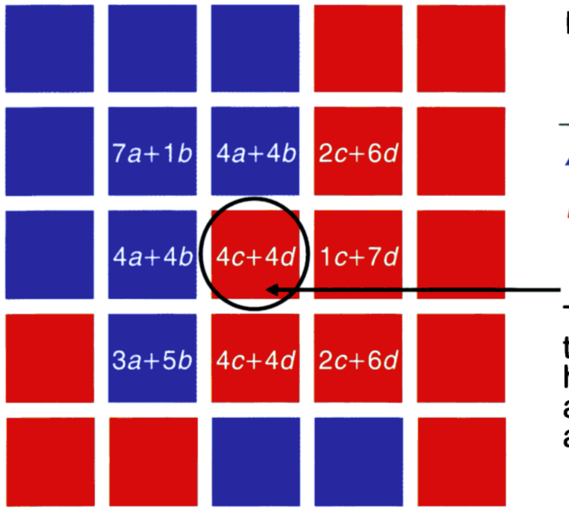
- The fractional fitness of the altruists (**FC**) and selfish agents **(FD)** is calculated by dividing fC and fD by the total fitness (fC+fD). **FC**=fC/(fC+fD) etc

- Generate random number (RN) between 0 & 1.

```
IF RN <minimum(FC,FD)
        replace focal cell with C if FC<FD
                              with D if FD<FC
ELSE
        replace focal cell with C if FC>FD
                              with D if FD>FC
```

3. All cells are updated *simultaneously* (synchronous updating)

4. Periodic boundary condition is used to ensure all cells are treated in the same way and there are no boundary effects.



Payoff matrix:

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

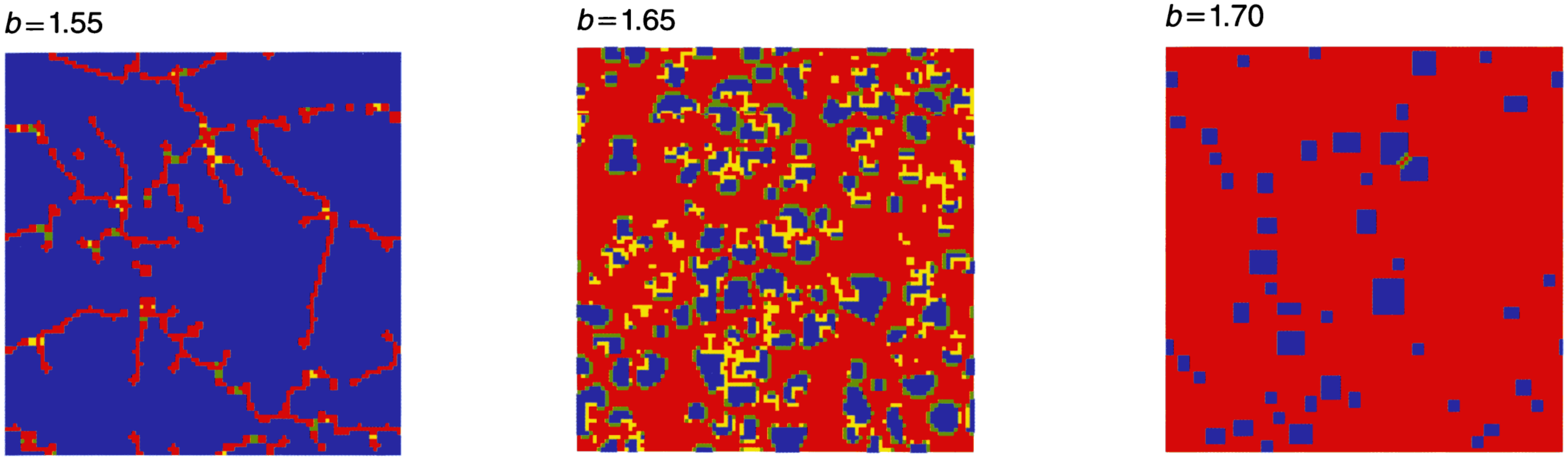
The focal cell will be taken over by whoever has the highest payoff among the 8 neighbors and the cell itself

🟦 Cooperator 🟥 Defector

Nowak 2006

b-Measure of benefit gained from *exploiting* an *altruistic* partner relative to the benefit gained from *cooperating* with an *altruistic* partner

Altruism.nlogo



Colour Code:

Blue : C that was C earlier.

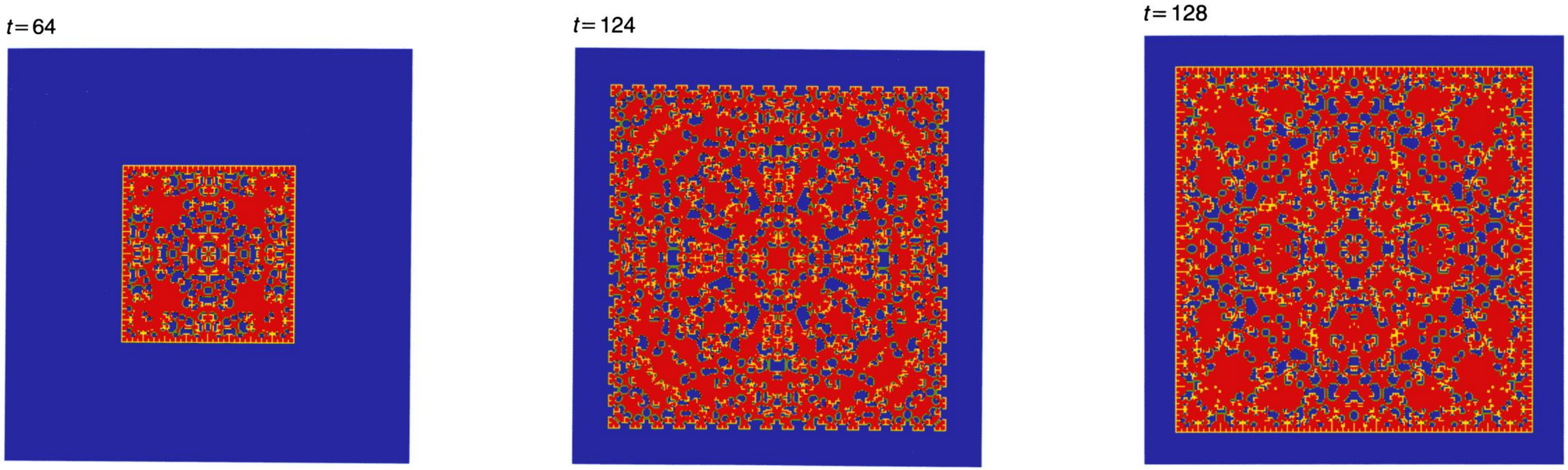
Green: C that was D earlier.

Red: D that was D earlier.

Yellow: D that was C earlier

Nowak 2006

Time evolution for b=1.65

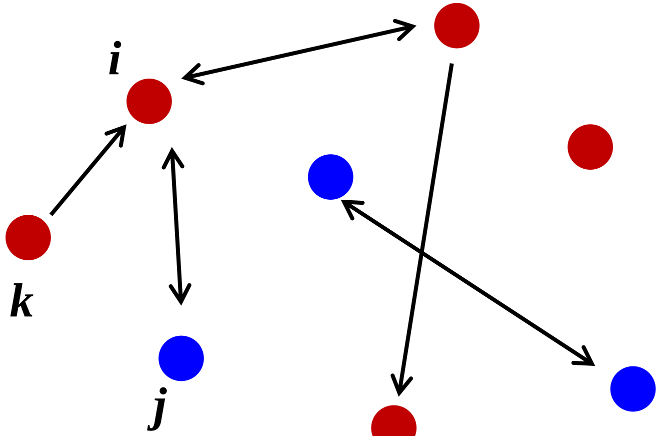


Nowak 2006

Evolutionary Graph Theory

Questions

- How does the fixation probability of a mutant change when the population is structured i.e. only certain members of the population can replace others during the course of evolution.
- If a structured population is represented by a graph, with vertices representing members and edges representing interaction between corresponding members, is it possible to characterize ***all*** graphs that have the ***same*** evolutionary dynamics.
- Can certain structured populations increase the fixation probabilities of advantageous mutants ?
- Can certain structured populations eliminate the effect of selection ?



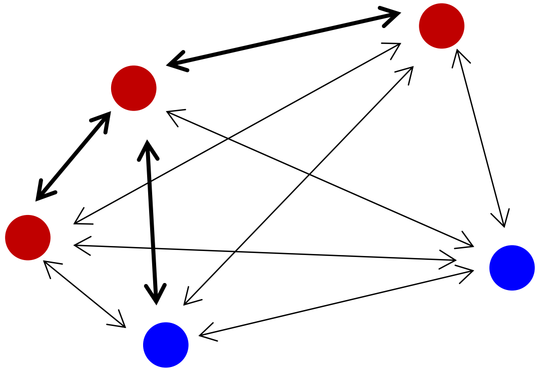
Structured Population

Not all vertices are connected by an edge

The edges can have different weights

i can replace j and j can replace i

k can replace i but i cannot replace k



Unstructured Population

There is an edge between ***any*** two vertices

All edges have the ***same*** weight

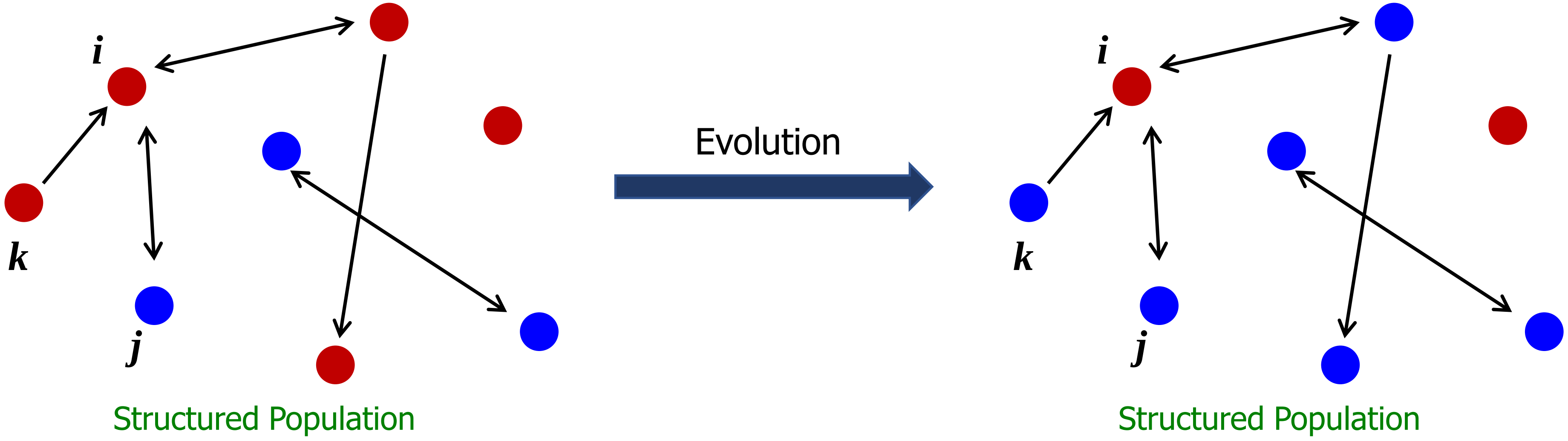
Formulating Evolution on Networks

A graph (network) can be completely specified by a stochastic matrix $W=[w_{ij}]$

$W=[w_{ij}]$ is an N x N stochastic matrix that determines the probability of replacing the j'th member of the population by the i'th member.

$w_{ij}=0$ if there is no directed edge *from* **i** *to* **j** ➔ offspring of i ***cannot*** replace j

$$\sum_{j=1}^{N} w_{ij} = 1$$ since the i'th member picked for reproduction has to replace someone



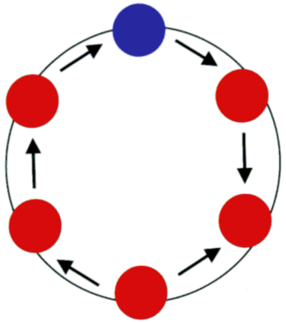
Structured Population

Structured Population

Population composition changes as the population evolves but the rules for replacement via the Moran process remain the same.

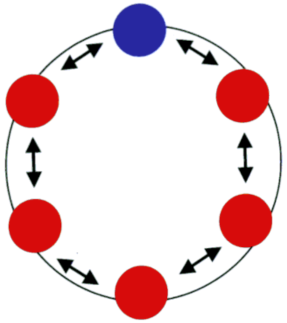
Fixation Probability of a mutant that arises in a structured population

$$W=\begin{bmatrix} 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$



Directed Cycle

$$w=\begin{bmatrix} 0 & \frac{1}{2} & 0 & 0 & 0 & \frac{1}{2} \\ \frac{1}{2} & 0 & \frac{1}{2} & 0 & 0 & 0 \\ 0 & \frac{1}{2} & 0 & \frac{1}{2} & 0 & 0 \\ 0 & 0 & \frac{1}{2} & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & \frac{1}{2} & 0 & \frac{1}{2} \\ \frac{1}{2} & 0 & 0 & 0 & \frac{1}{2} & 0 \end{bmatrix}$$



Cycle

The i’th member can only be replaced by the member preceding it i.e the (i-1)th member.

Fitness of B (blue) = r
Fitness of A (red) = 1

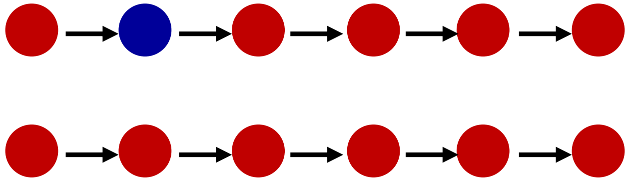
Due to the nature of the structured population (only nearest neighbour replacements are allowed), there can be only one cluster of B’s. Fragmentation of clusters into two or more sub-clusters is not possible.

$$\rho_B = \frac{1}{1+\sum_{k=1}^{N-1}\prod_{i=1}^{k}\gamma_i} = \frac{1-1/r}{1-1/r^N}$$

Fixation probability of B on a directed cycle is identical to the fixation probability of B in the Moran process (unstructured population)

Fixation probability of a mutant randomly placed on a "Line" graph

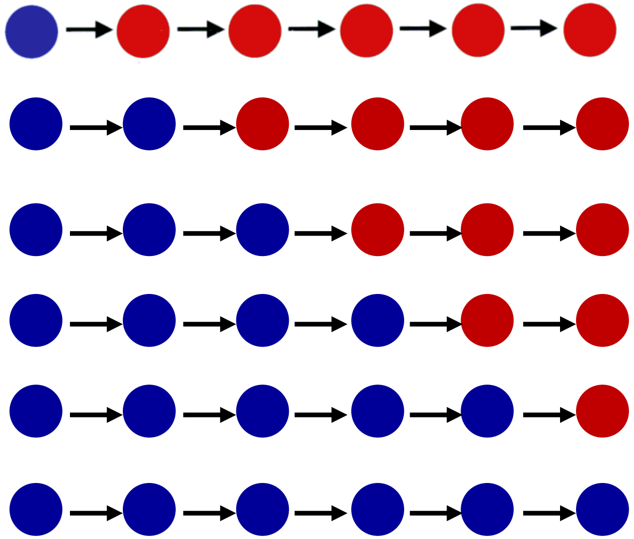
Line



Rules of Replacement: Every member is replaced only by the member preceding it. The last member replaces itself.

If the mutant B arises at any position other than the first position in the line, it will be replaced by A and become extinct.

Probability that B arises in any positions from i=2…N is (N-1)/N since there are N-1 such positions.



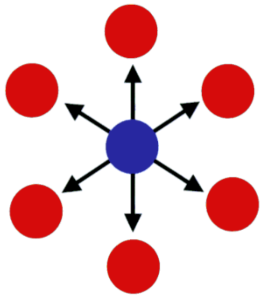
Probability that B appears in position 1: 1/N

The mutant B will definitely be fixed if it arises in position 1

Fixation probability of B: $\rho_B = \dfrac{1}{N}$

Fixation probability differs from the Moran process and is independent of the fitness of members.

Invasion probability of a mutant randomly placed on a “Burst” graph



Burst

Rules of Replacement: Every member is replaced only by the member at the centre with equal probability. The central member *cannot* be replaced by any other peripheral member or itself.

If the mutant B arises at any position other than the ***central*** position in the star, it will be replaced by the A at the centre and become extinct.

Probability that B arises in any positions from i=2…N
is (N-1)/N since there are N-1 such positions.

Probability that B appears in the central position: 1/N

The mutant B will definitely be fixed if it appears at the centre of the star

Invasion probability of B: $\rho_B = \dfrac{1}{N}$

Invasion is *independent* of the fitness of members and equivalent to that of a neutral mutant in the Moran process.

Both the “Line” and ”Burst” graphs are suppressors of selection

Graphs which are suppressors or amplifiers of selection

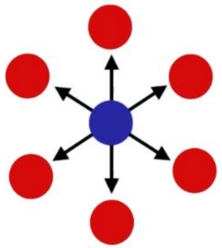
$$\rho_B = \frac{1-1/r}{1-1/r^N}$$ Invasion probability of a single mutant with a relative fitness ***r*** in a Moran process

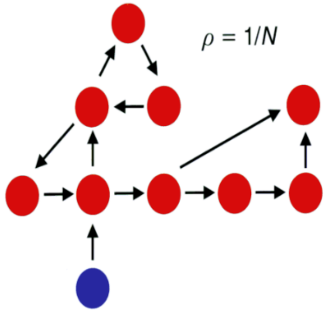
If the fixation probability of a single mutant with a relative fitness r on the *structured graph* G is ρ_G

If $\rho_G > \rho_B$ when r>1 ➔ G is an amplifier of selection. G favours selection over drift

If $\rho_G < \rho_B$ when r>1 ➔ G is an suppressor of selection. G favours drift over selection

If $\rho_G = \frac{1}{N}$ when r>1 ➔ G is the strongest possible suppressor of selection.





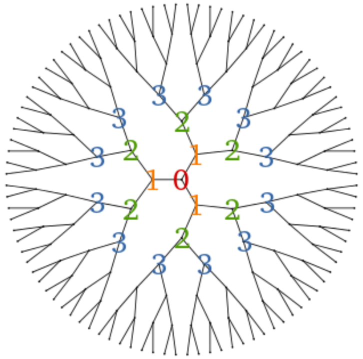
All Graphs with a ***single root*** have the same invasion probability: $\rho_G = \frac{1}{N}$

Evolution of Cooperation on Graphs

Constraints on the Theoretical Formulation

- Caley Tree/Bethe Lattice
  - *Regular* graph with each node having **k** neighbours
  - Graph does not have any loops

Image Source: Wikipedia



Caley Tree/Bethe Lattice with k=3

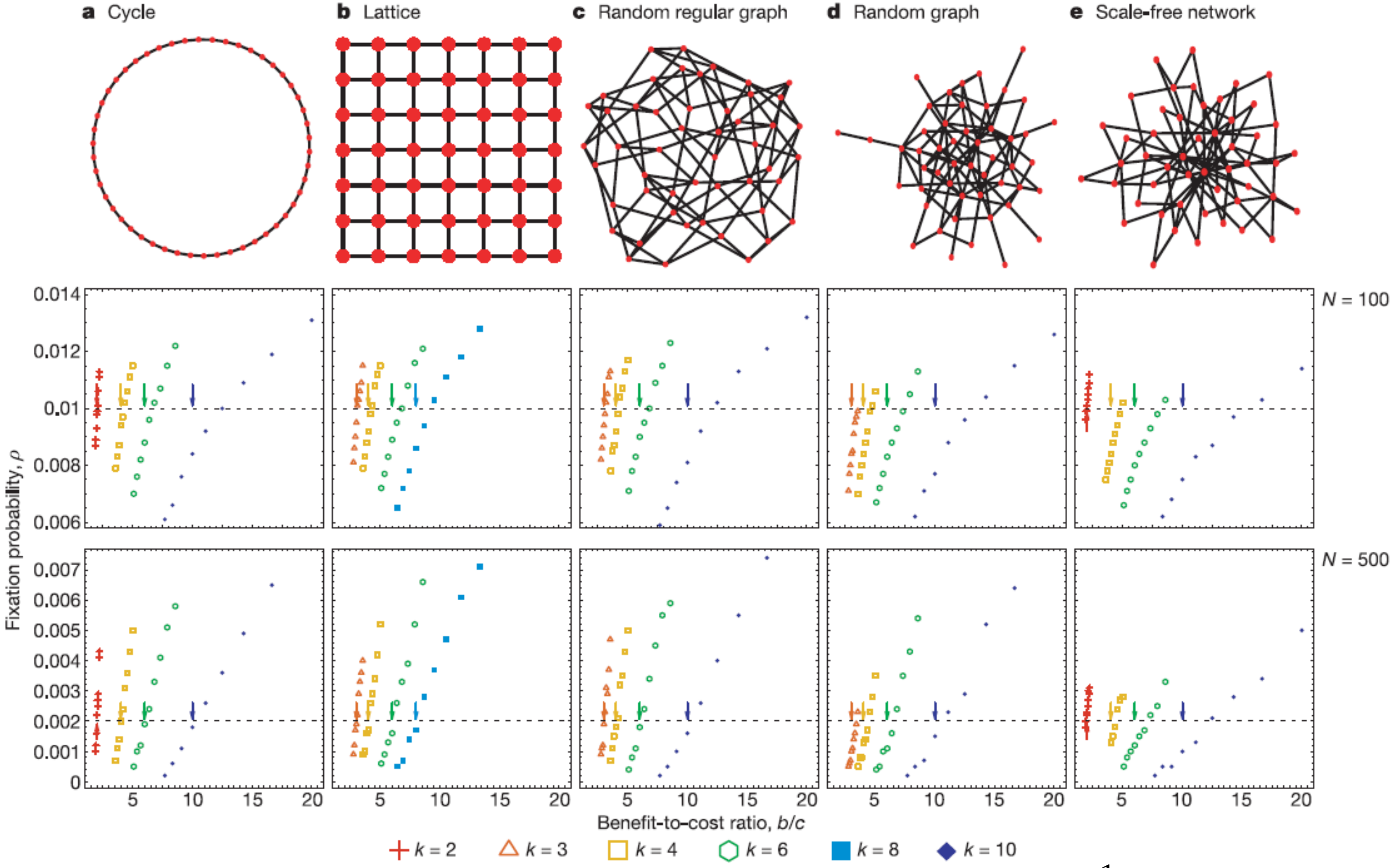
- Theoretical analysis valid for
  - N>>k
  - Weak selection limit holds i.e. w<<1 when separation of time-scales is possible
  - Uses the pair approximation which is valid only for Bethe lattices i.e. graphs without any loops.

Pair Approximation ➔ frequencies of larger clusters obtained from pair frequencies

Condition for Spread of Cooperation on Networks

Ohtsuki *et al.* A simple rule for evolution of cooperation on graphs and social networks; Nature 441 (2006) 502

Birth-Death (BD) updating: $\rho_D > \frac{1}{N} > \rho_C$ ➔ Selection never favours fixation of cooperators



Arrow indicates b/c=k. Theoretical Prediction : b/c > k ➔ $\rho_C > \frac{1}{N} > \rho_D$

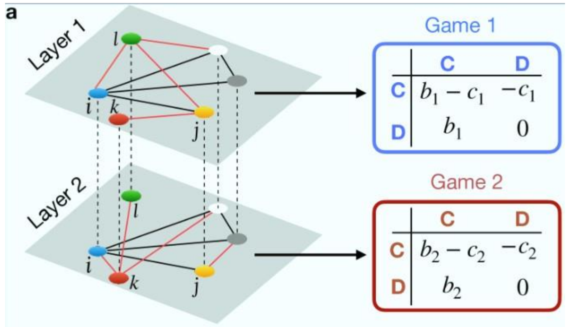
- ❖ Discrepancy with theoretical prediction observed for *non-regular* graphs
- ❖ Discrepancy increases with increasing k but decreases with increasing N

Realm of Possibilities: A biased sample

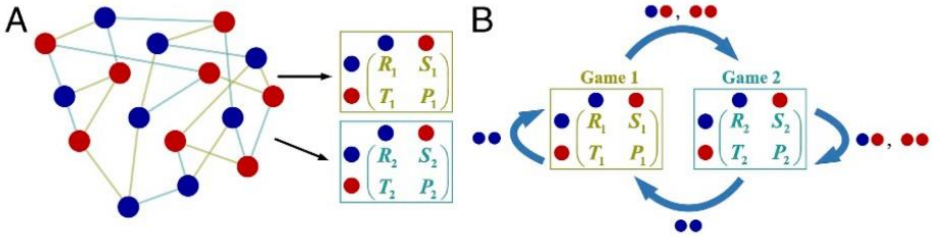
- Role of different forms of learning during strategy update
  - Social Learning
  - Bayesian Learning
  - Reinforcement Learning
  - Heterogeneous learning strategies

Pathak, Verma, Ram and SS; *Proc. Royal Society B* (2020)
Anuran Pal and SS; Chaos (2022)
Patra, SS, Paul, Chakraborty, NJP (2024)
Amit Basak and SS; PLoS Computational Biology (2024)

- Multiple games on multiplex networks



- Switching between different games: Stochastic games on networks



Hilbe et al. Nature (2018)
Su et al. ; *PNAS* (2019)

The possibilities are only limited by your imagination…….