Evolutionary dynamics in structured populations

SFI CS^3 2026

What is evolution?

- Populations evolve
- Replication, selection, mutation

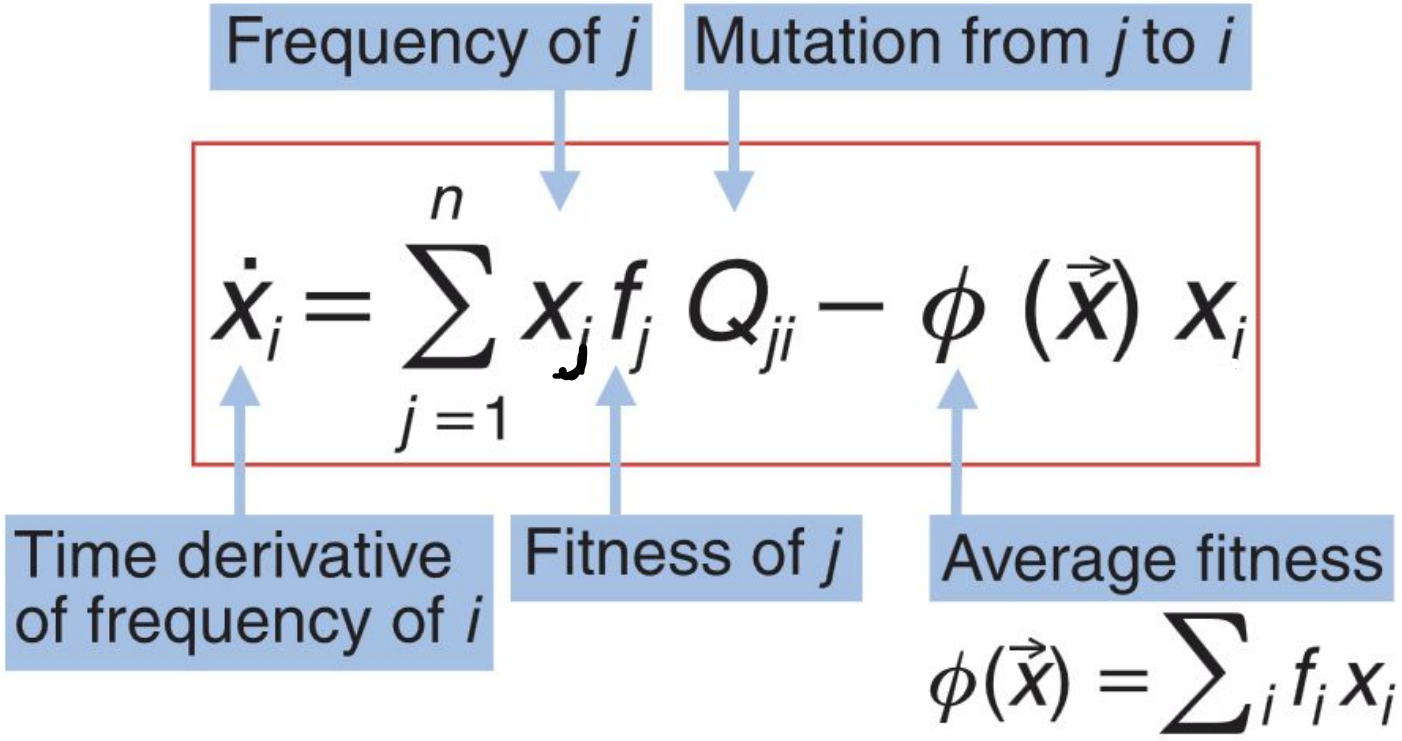
The NASA definition of life, "Life is a self-sustaining chemical system capable of Darwinian evolution" and considered the specific features of the one life we know —Terran life.

- Life is that which evolves

Life forms

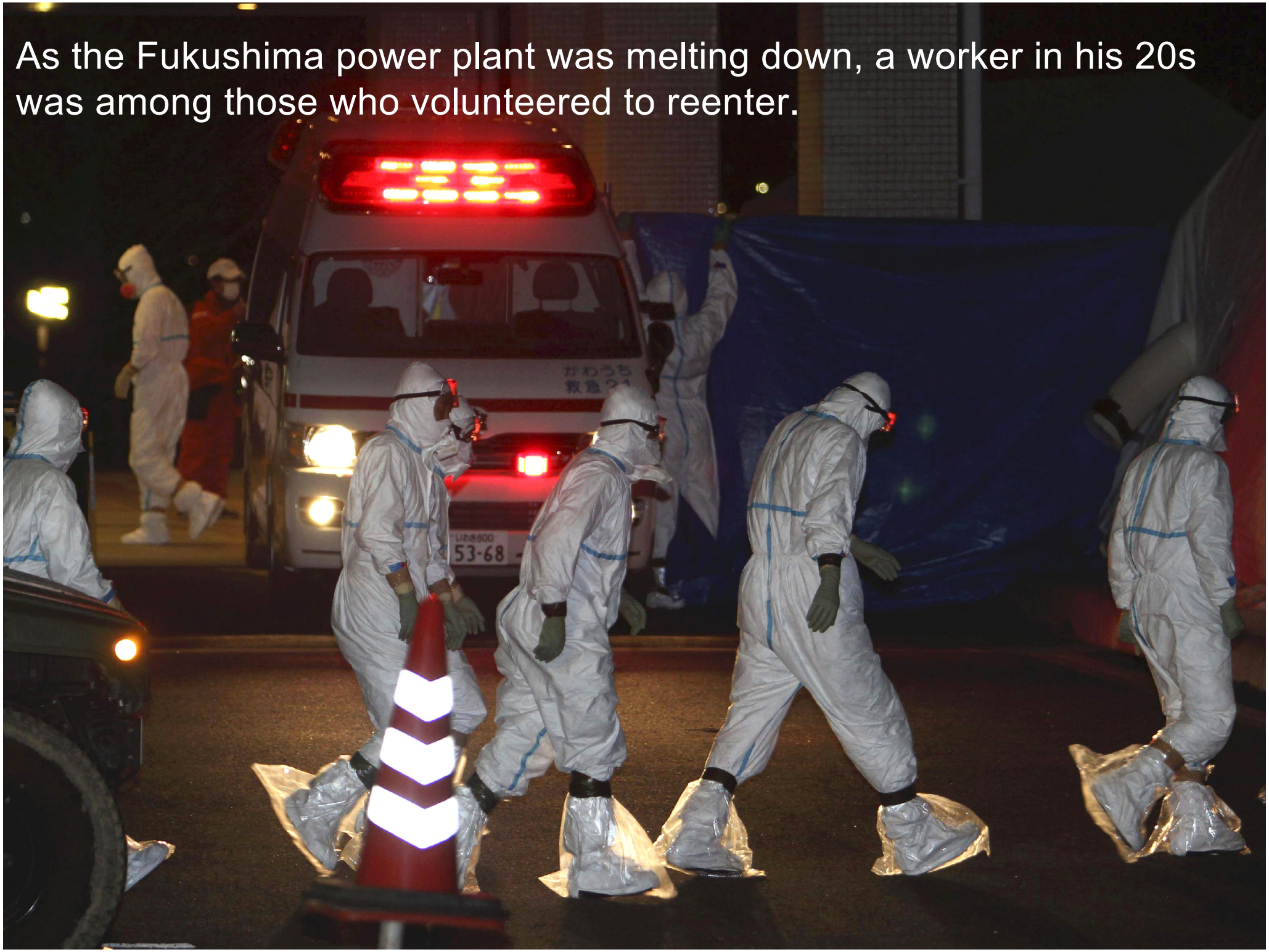
- Genomes
- Cancer
- Infectious diseases
- Language
- Norms
- Behaviors
- Technologies
- Learning
- Businesses
- Cities
- etc.

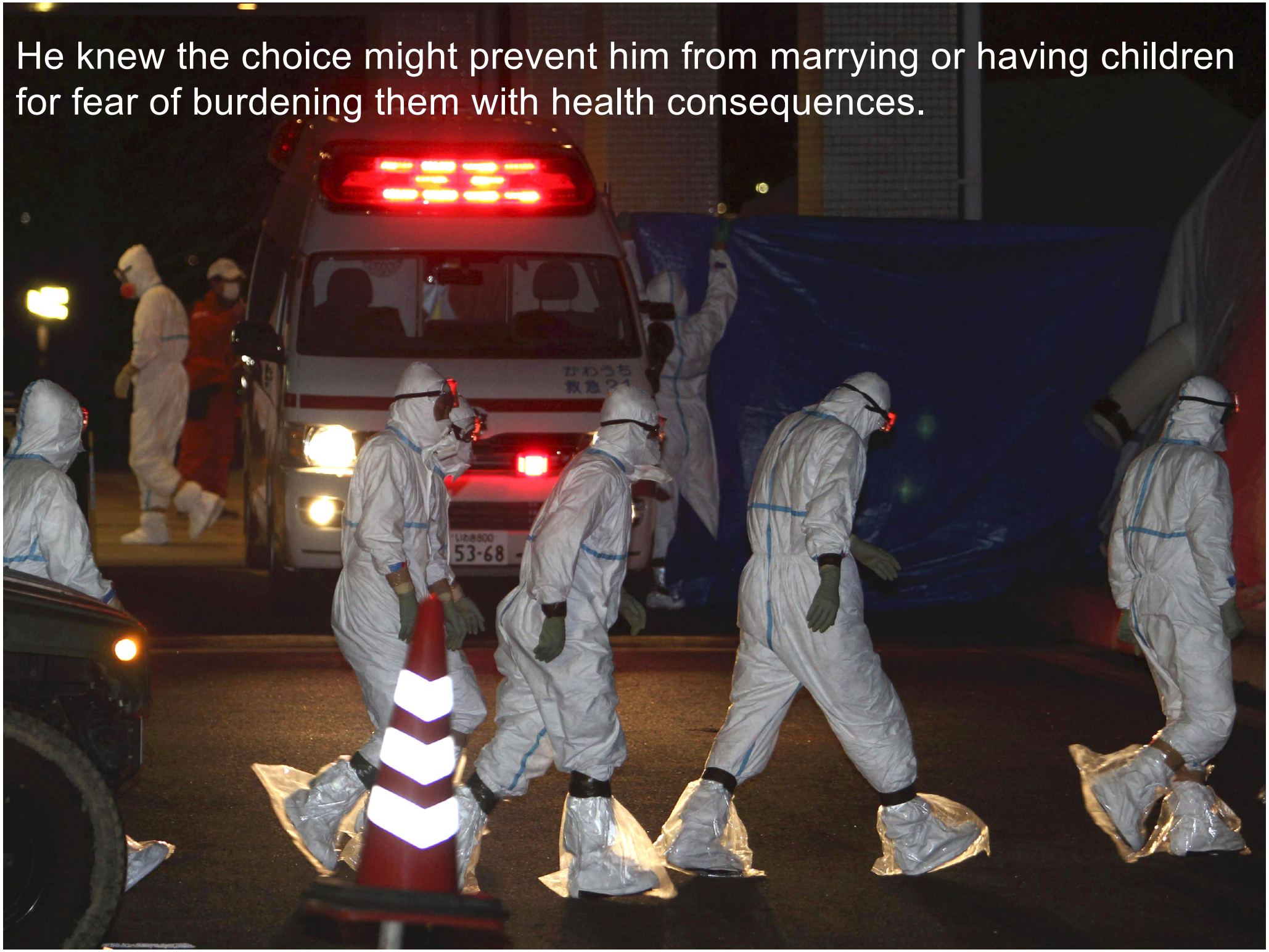
The quasispecies equation

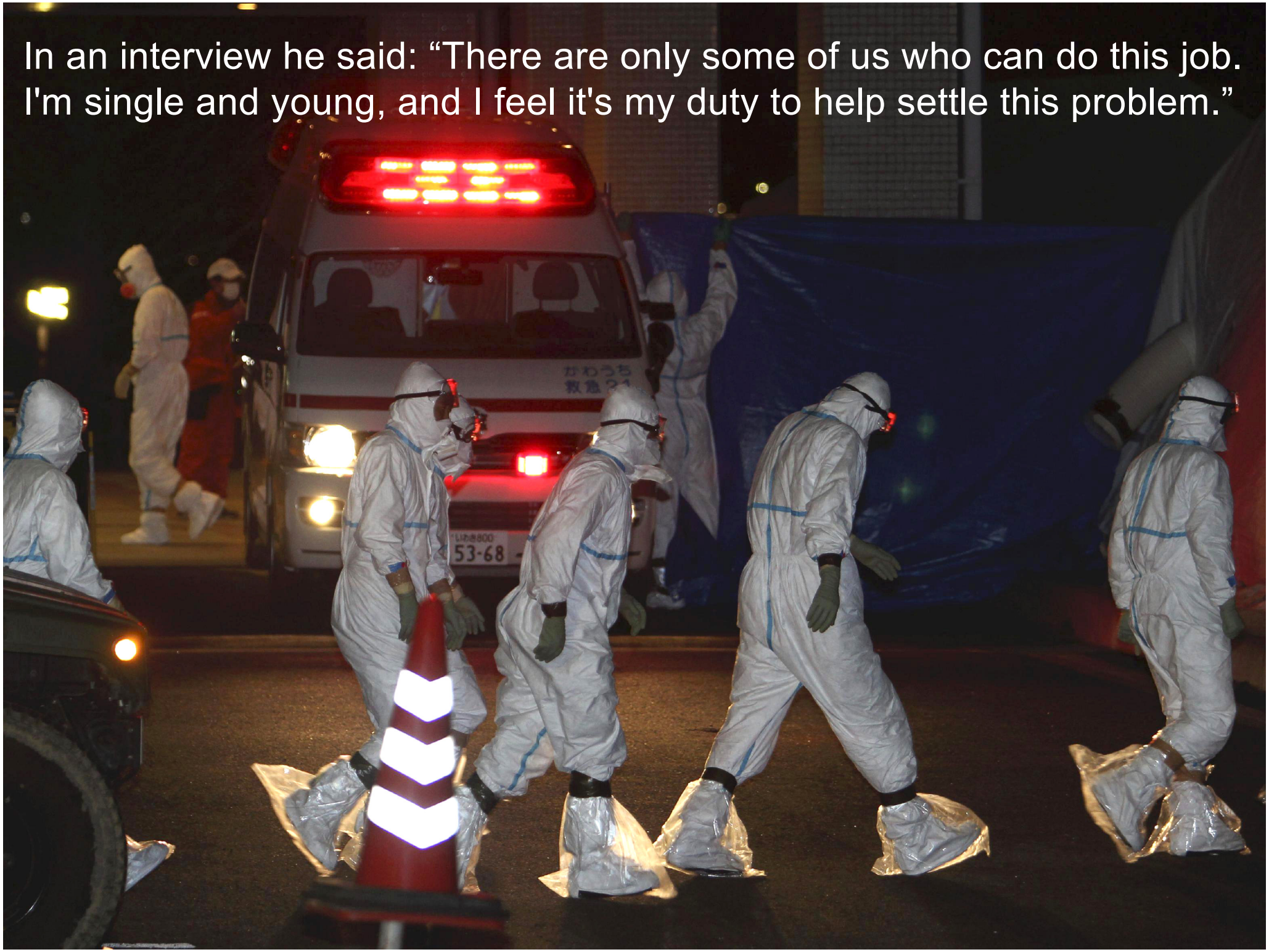


Evolution of cooperation

Martin Nowak, Math 242


As the Fukushima power plant was melting down, a worker in his 20s was among those who volunteered to reenter.


He knew the choice might prevent him from marrying or having children for fear of burdening them with health consequences.


In an interview he said: “There are only some of us who can do this job. I'm single and young, and I feel it's my duty to help settle this problem.”

Wesley Autrey,
the New York Subway Hero

What is cooperation?

Donor
pays a cost, *c*

Recipient
gets a benefit, *b*

Cost and benefit are measured in terms of fitness.
Reproduction can be genetic or cultural.

Prisoner's Dilemma

	I cooperate	I defect
you cooperate	*b* - *c*	- *c*
you defect	*b*	0

you get

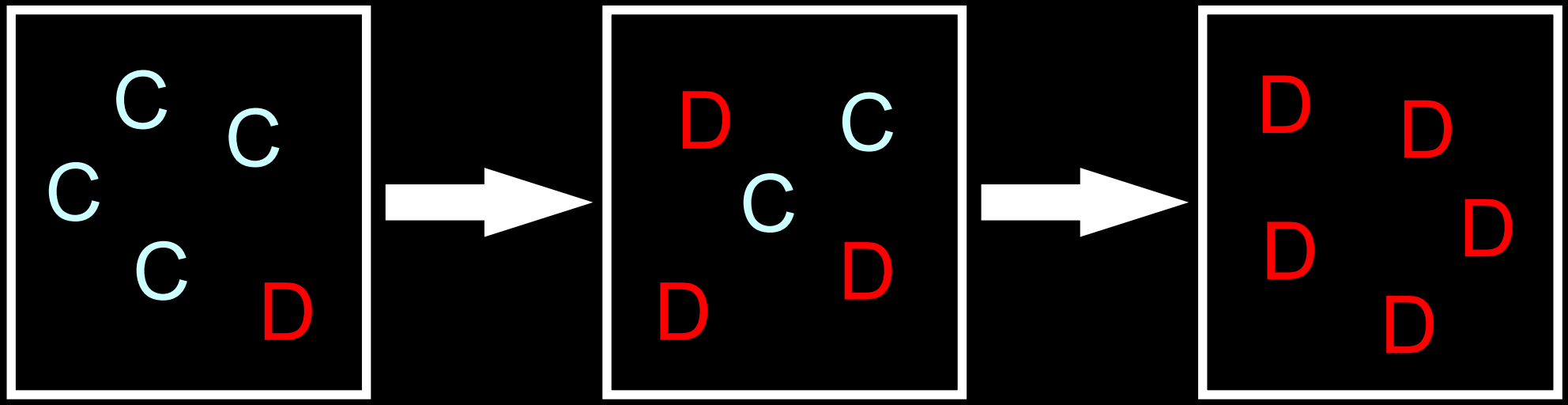
$b > c > 0$

What is the dilemma ?

Two *rational* players defect and end up with a low payoff, 0.

Two *irrational* players might cooperate and receive a higher payoff, $b - c$.

Natural selection chooses defection



In any mixed population, defectors have a higher payoff than cooperators.

Natural selection needs help to favor cooperators over defectors.

Five mechanisms for the evolution of cooperation:

Direct reciprocity
Indirect reciprocity
Spatial selection
Group selection
Kin selection

Direct reciprocity

‘I help you, you help me.’

Repeated Prisoner's Dilemma

Player 1 : C D C D C C C ….

Player 2 : D C D D C C C ….

The Folk theorem

Repeated Prisoner's Dilemma

Player 1 : C D C D C C C ….

Player 2 : D C D D C C C ….

What is a good strategy for playing this game?

Robert Axelrod

Tit-for-tat

- I start with cooperation.
- If you cooperate, then I will cooperate.
- If you defect, then I will defect.

Anatol Rapaport

Tit-for-tat is unforgiving

Errors destroy cooperation

Tit-for-tat : CCCCDCDCDCDDDDDD….
Tit-for-tat : CCCDCDCDCDCDDDDDD….

Let natural selection design a strategy

Random

Let natural selection design a strategy

Always defect

Random

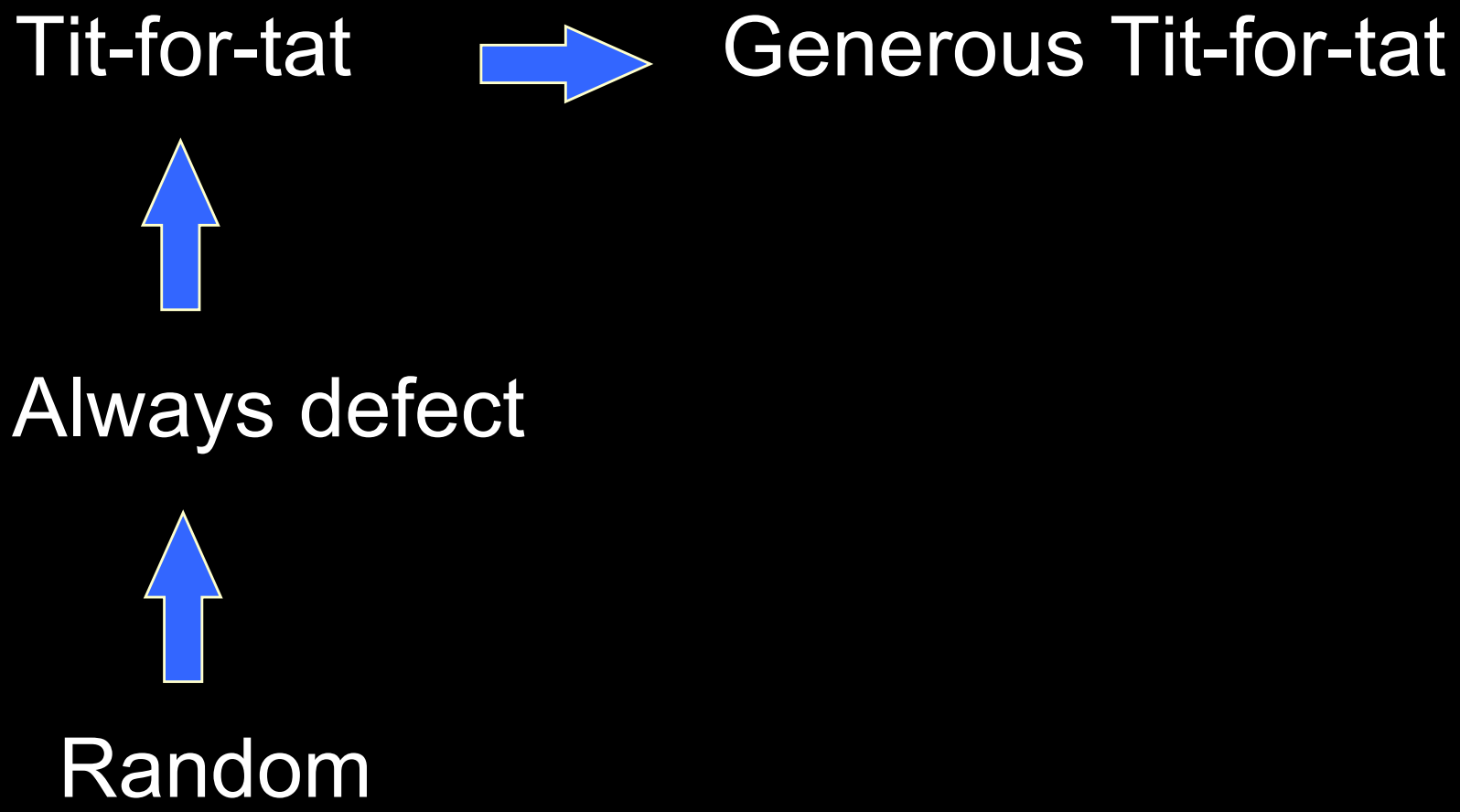
Let natural selection design a strategy

Tit-for-tat

Always defect

Random

Let natural selection design a strategy

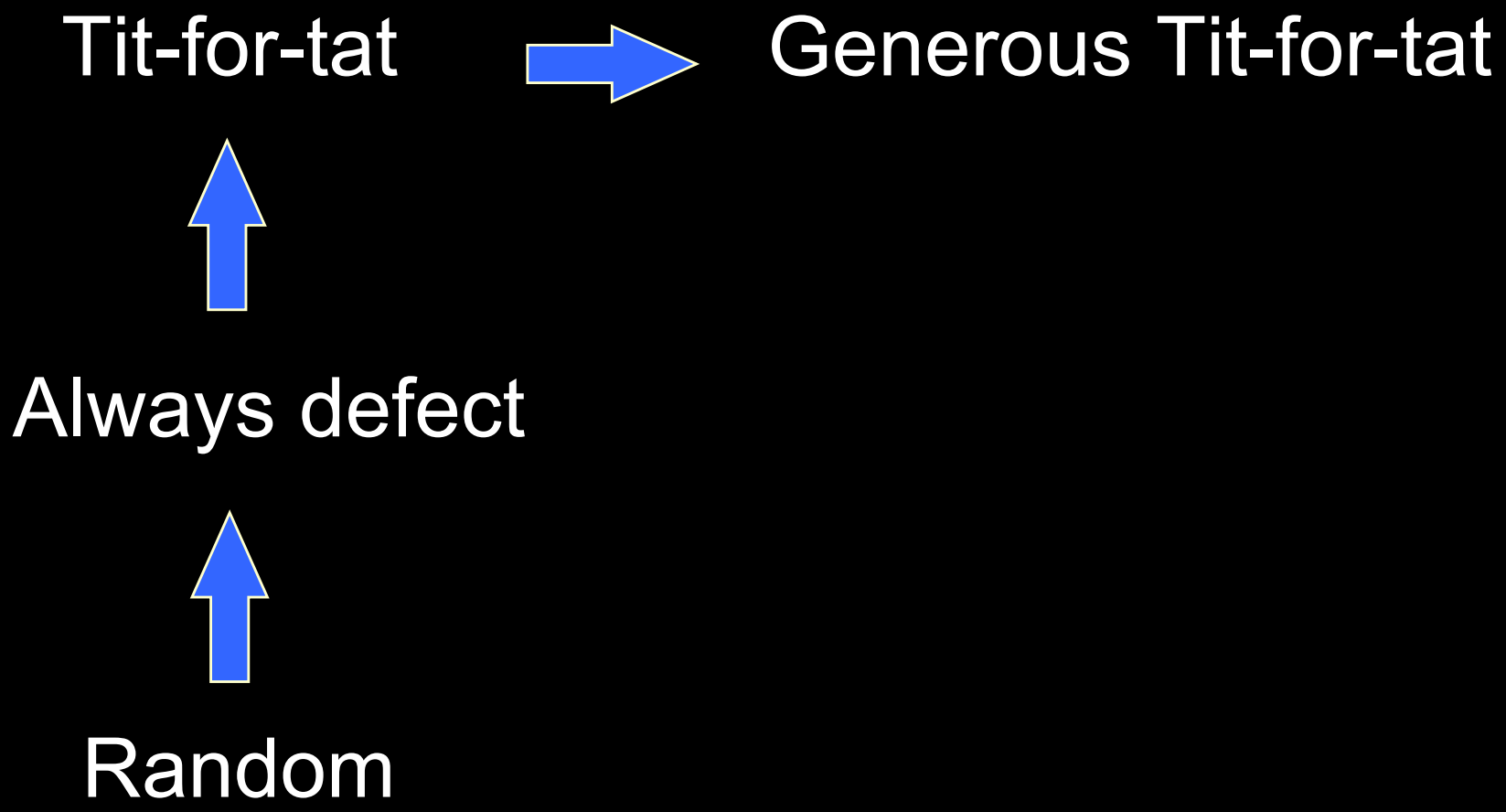


Generous Tit-for-tat

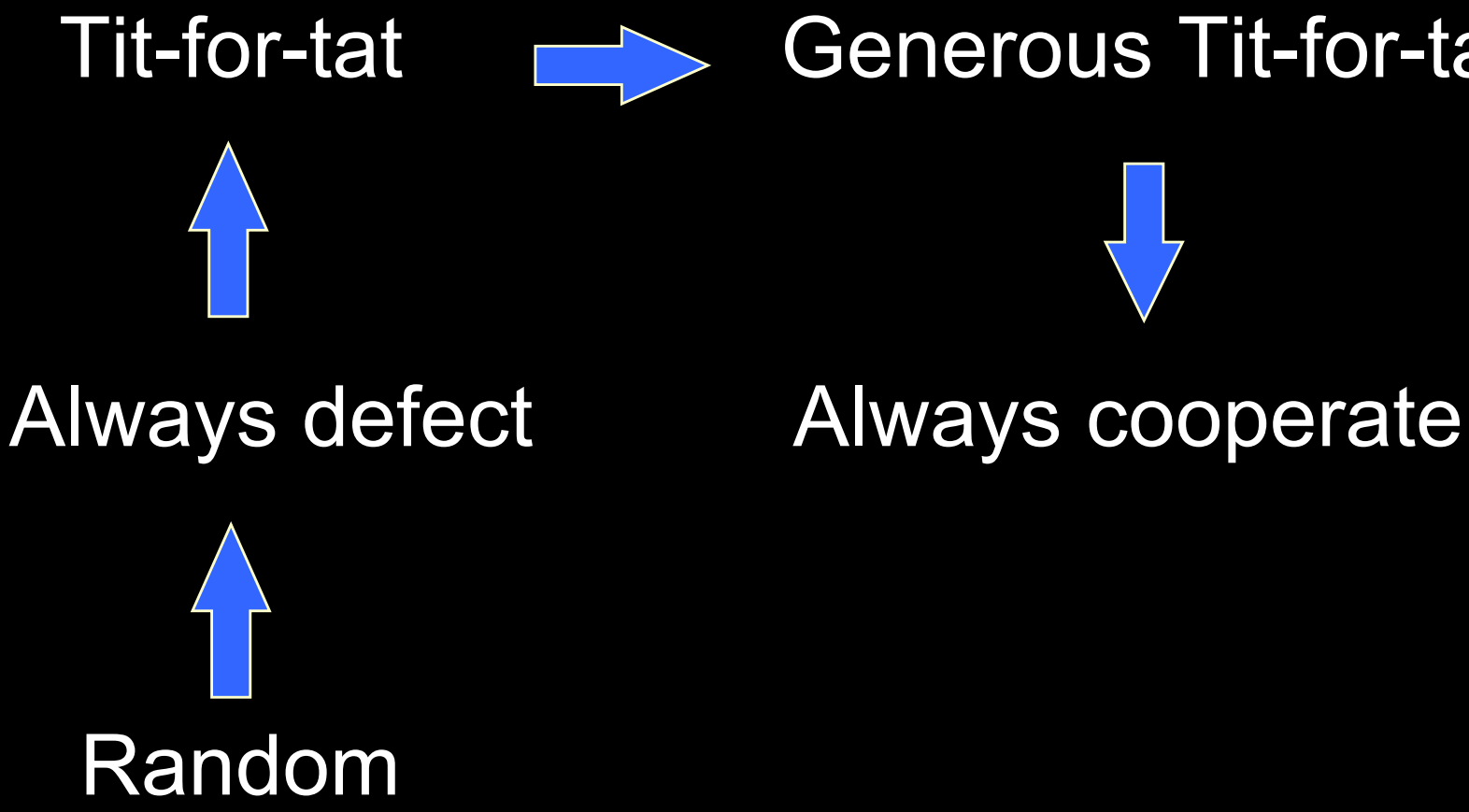
- I start with cooperation.
- If you cooperate, then I will cooperate.
- If you defect, then I will cooperate with a certain probability *(q* = 1- *c / b).*

Evolution of forgiveness

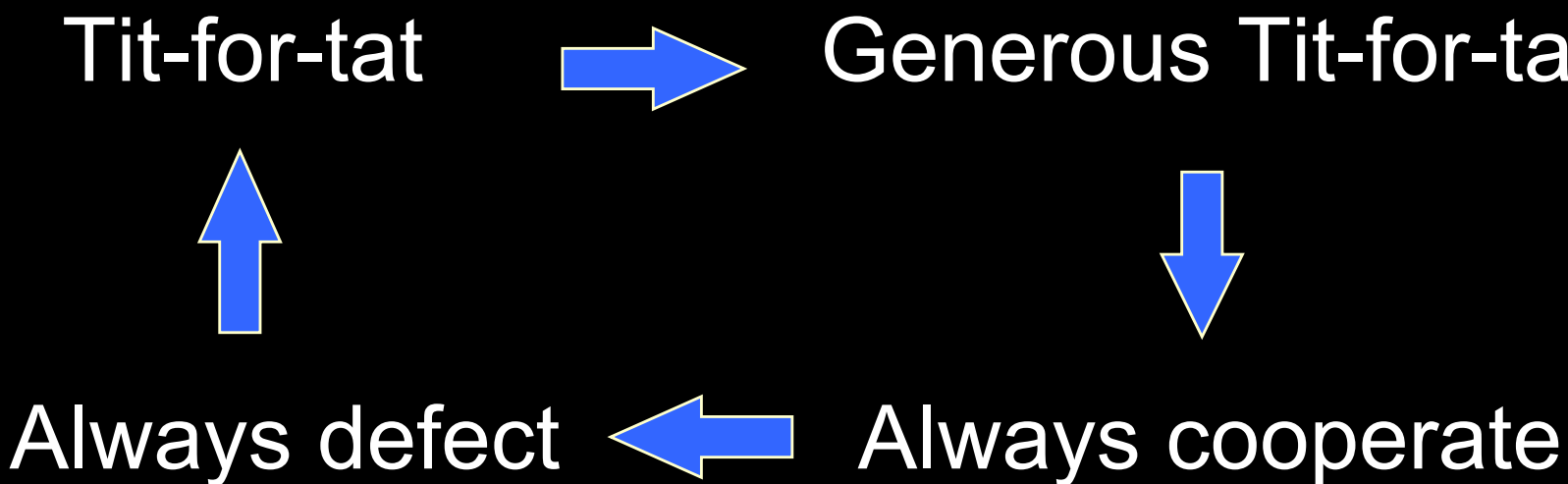
Let natural selection design a strategy



Let natural selection design a strategy

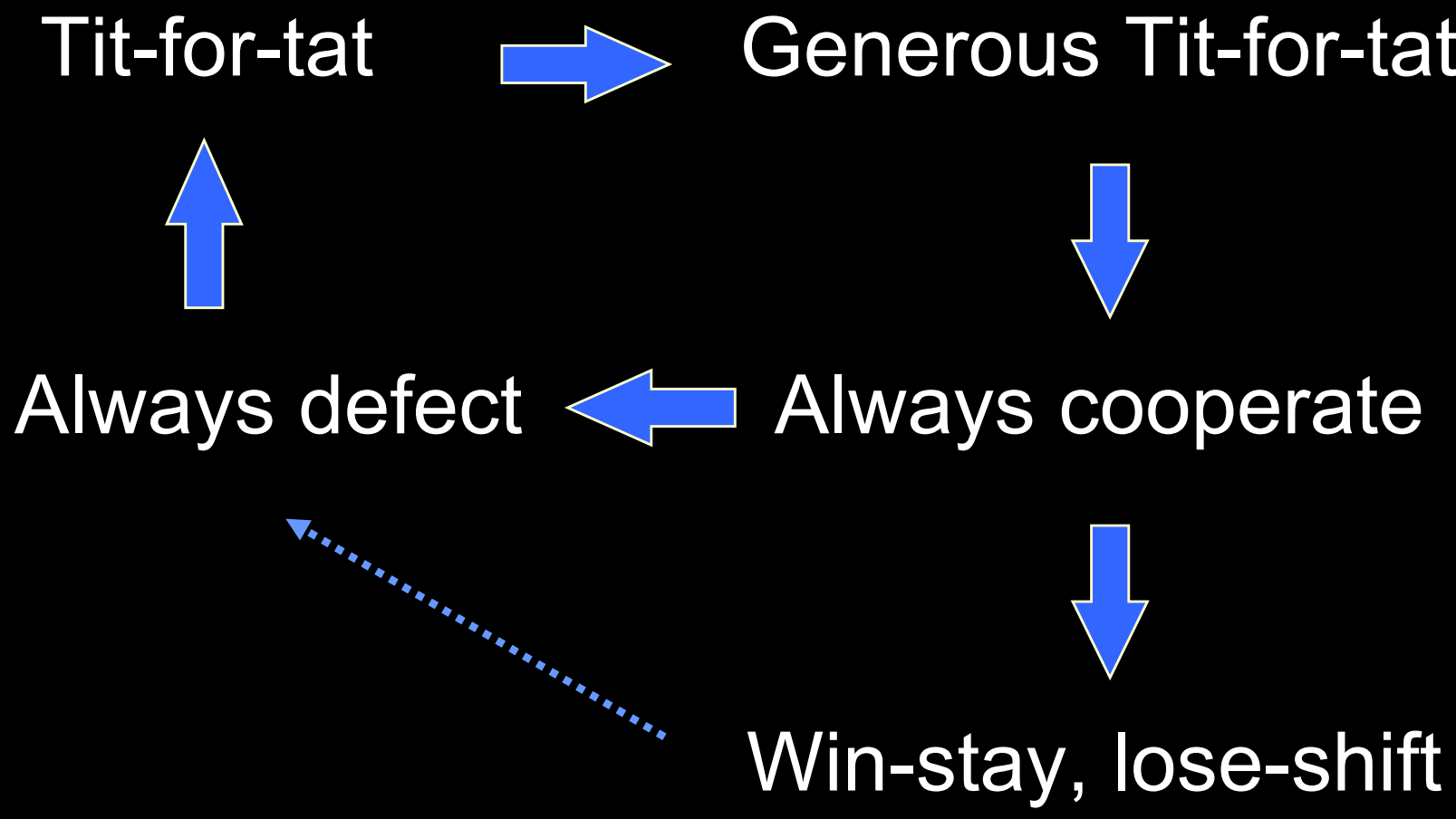


Let natural selection design a strategy



War and peace

Let natural selection design a strategy



Win-stay, lose-shift

- If I am doing well (payoff *b* or *b*-*c*) then I will repeat my move.
- If I am doing badly (payoff 0 or -*c*) then I will change my move.

If b/c<2 then a stochastic variant of WSLS does well (where you return to C after DD only with a certain probability).

Direct reciprocity

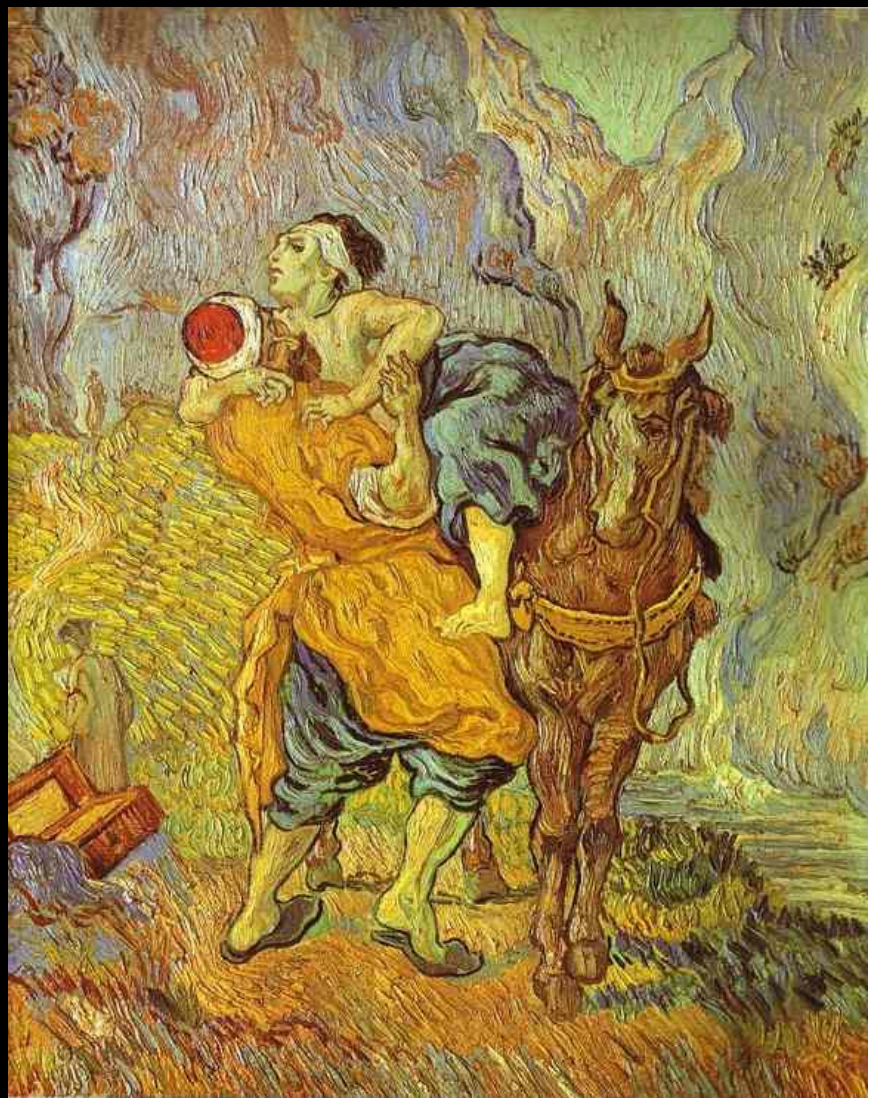
… allows the evolution of cooperation if

$w > c / b$

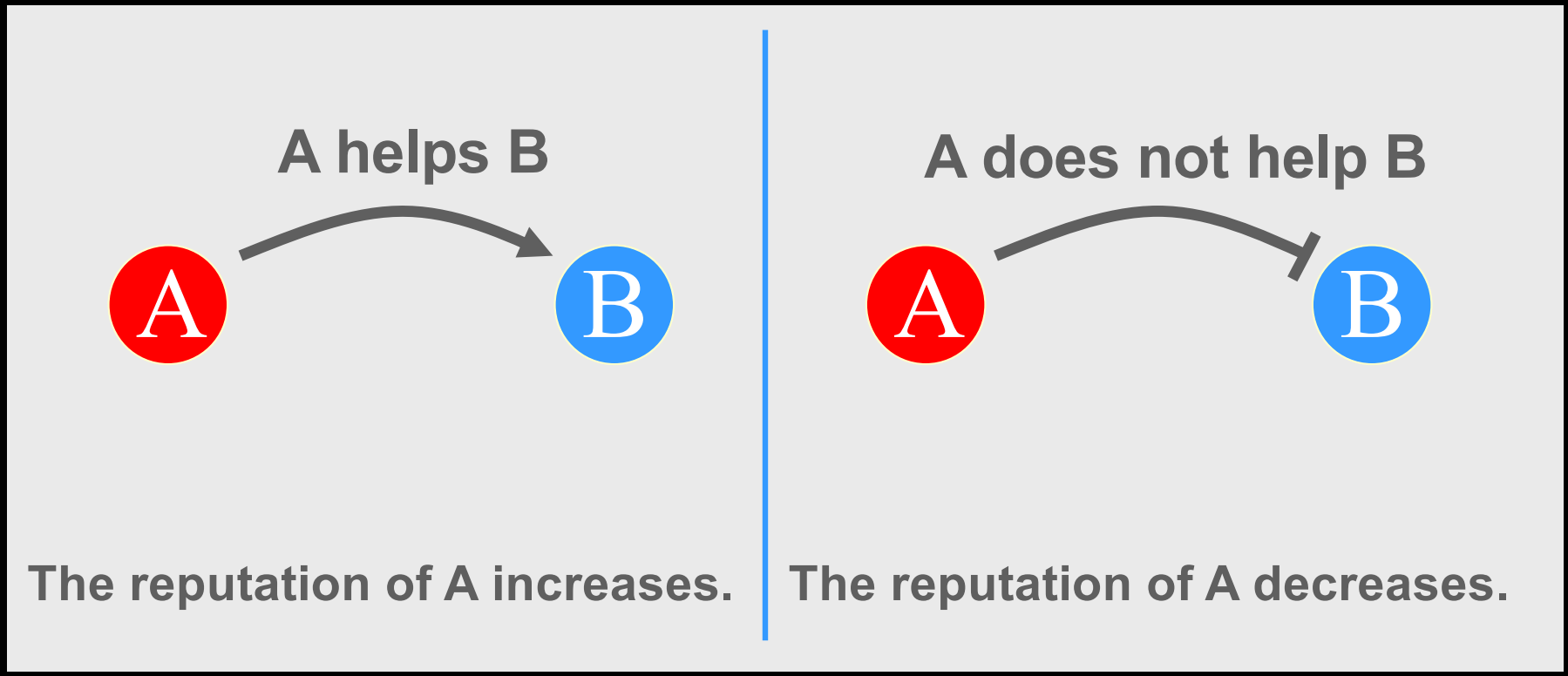
b…benefit
c…cost
w…probability of another round

Indirect reciprocity

‘I help you.
Somebody helps me.’



Indirect reciprocity works via reputation



	donor	recipient	donor's reputation
cooperate	-c	+b	+1
defect	0	0	-1

Nowak & Sigmund, Nature 1998

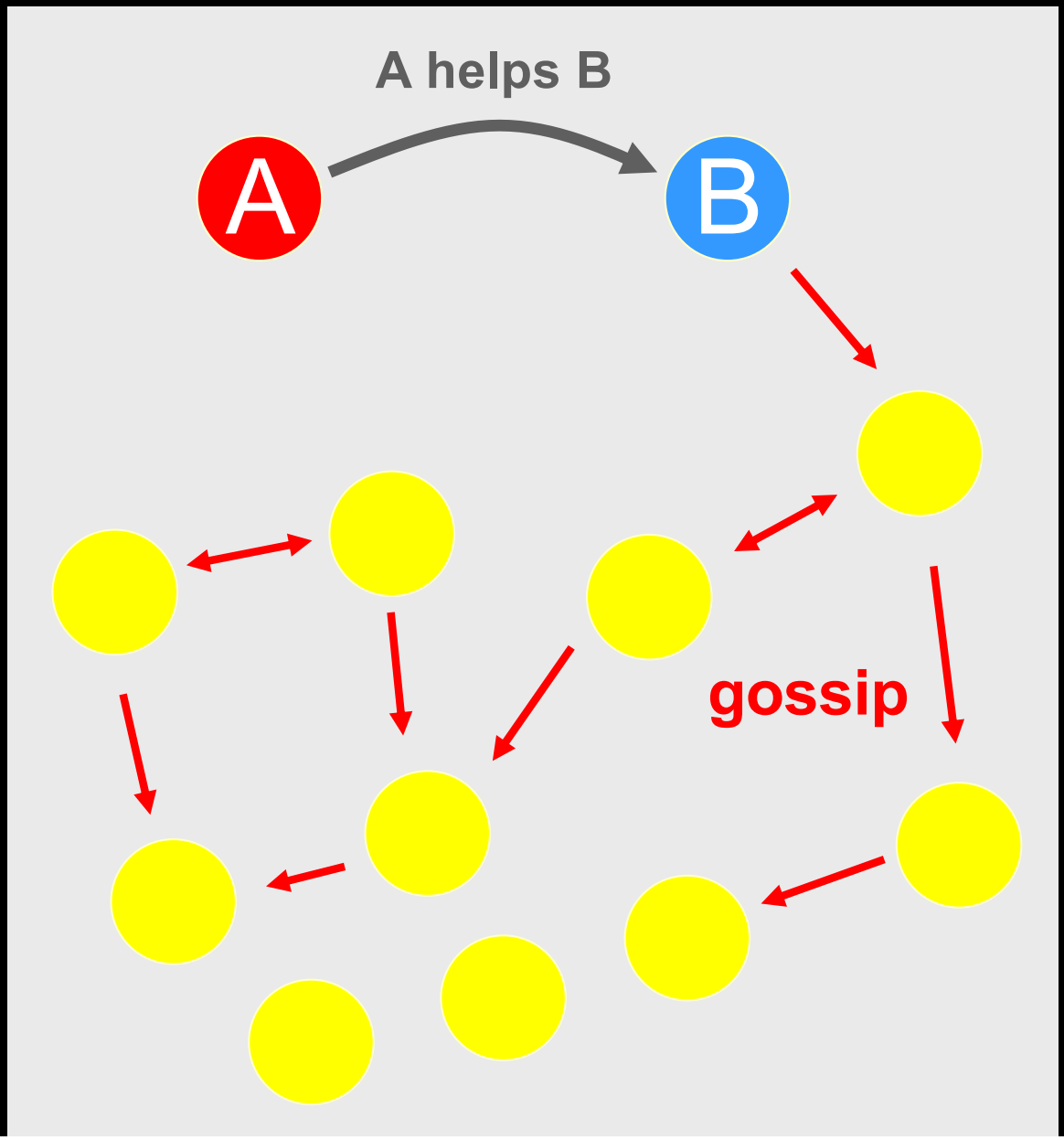
Experimental confirmation:

People help those who help others.

Helpful people have a higher payoff in the end.

Wedekind & Milinski, Science 2000

Gossip spreads reputation



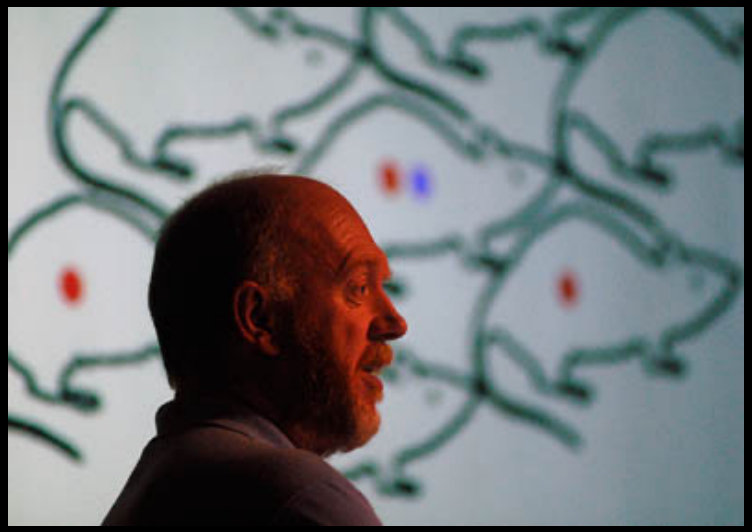
Observers

Rest of the population

Reputation of A is updated.

Games of indirect reciprocity are cognitively demanding; individuals need to monitor the social network of a group.
=> evolution of social intelligence

Individuals must be able to talk to each other about others.
=> evolution of human language



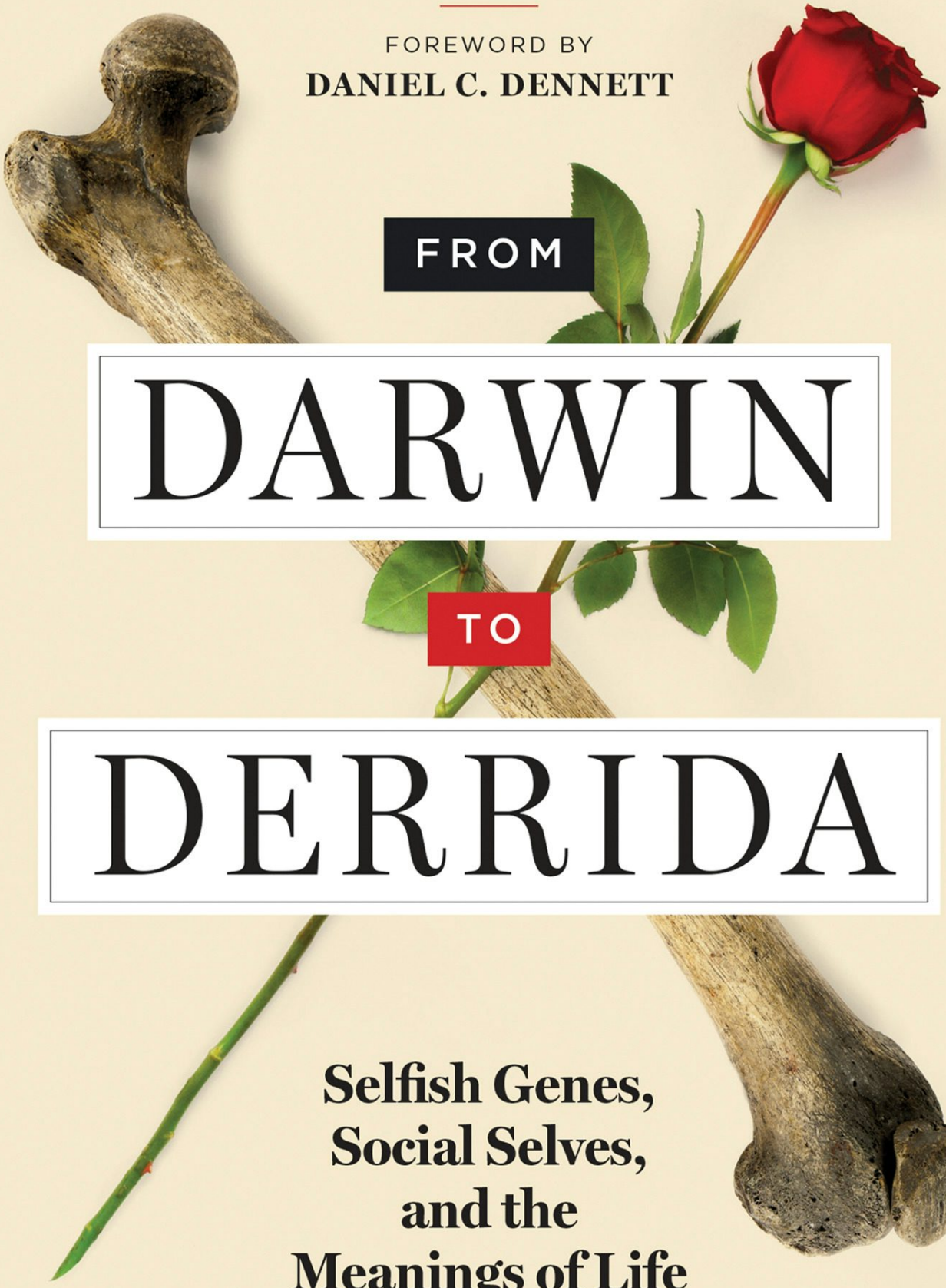
David Haig:

“For direct reciprocity you need a face.

For indirect reciprocity you need a name.”

David Haig

FOREWORD BY
DANIEL C. DENNETT



FROM DARWIN TO DERRIDA

Selfish Genes, Social Selves, and the Meanings of Life

A rule for indirect reciprocity

$$q > c / b$$

q … probability to know someone's reputation

c … cost of cooperation

b … benefit of cooperation

Spatial selection

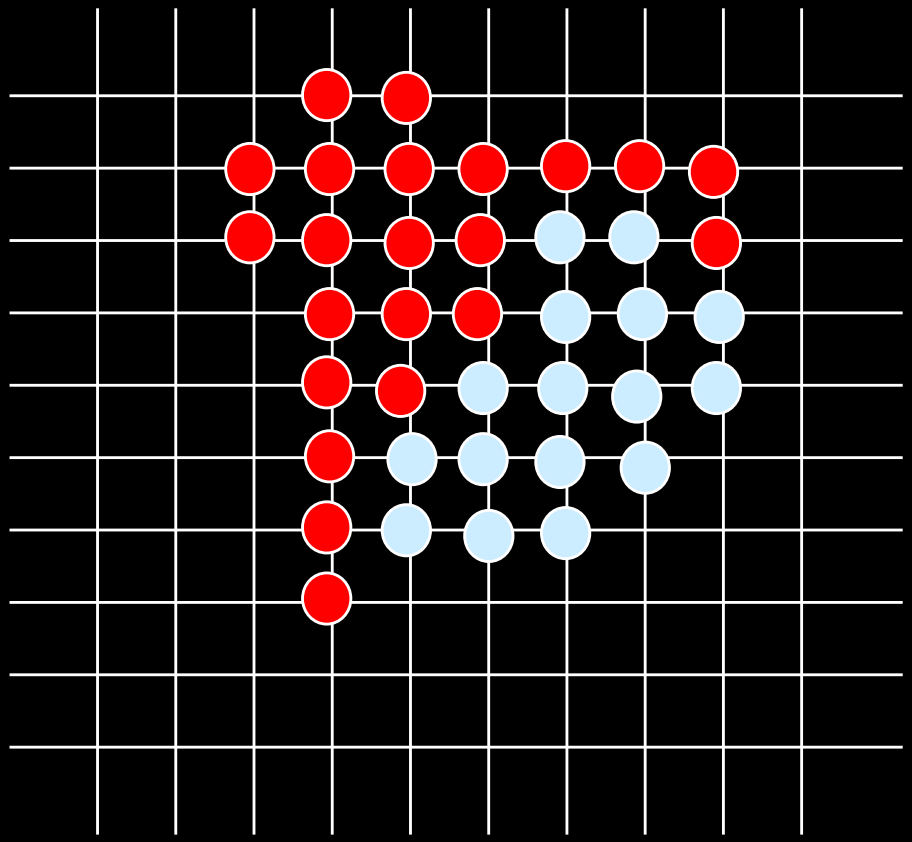
Spatial games

Games on graphs

Games in phenotype space

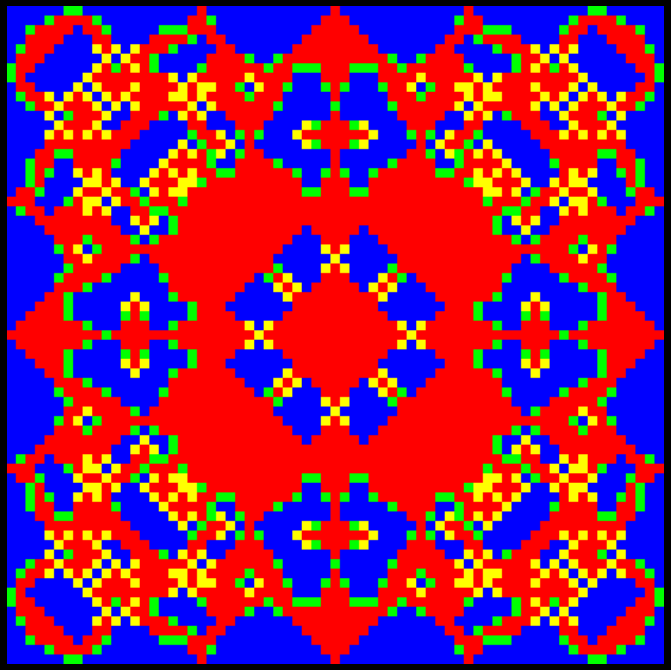
Games on sets

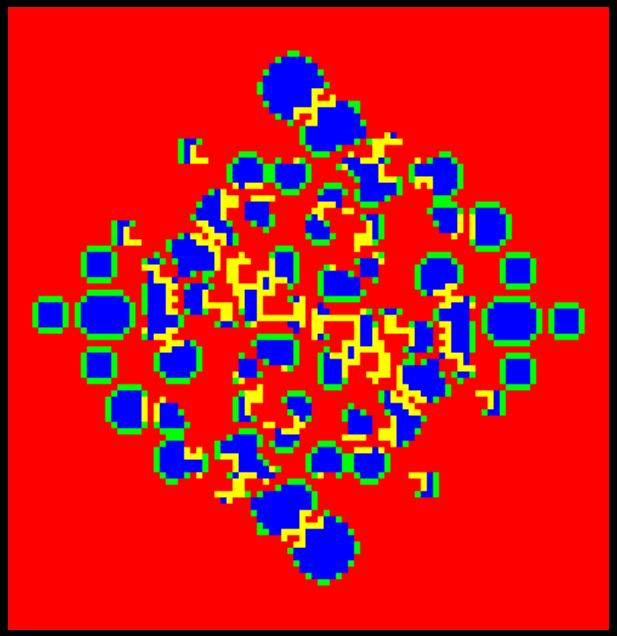
Spatial games

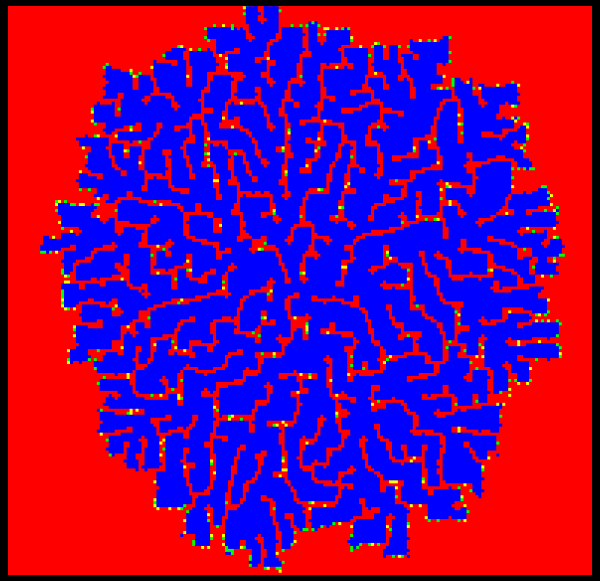


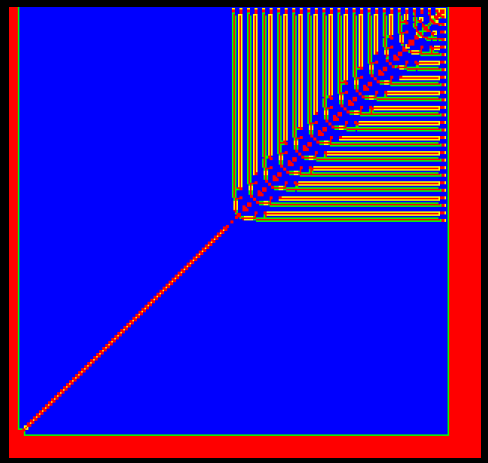
Cooperators
Defectors

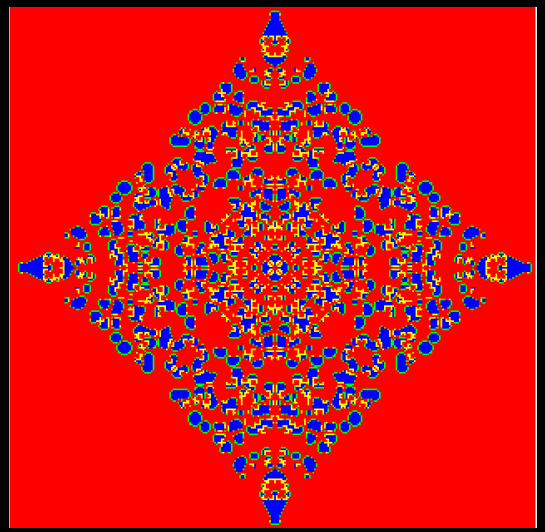
Nowak & May, Nature 1992

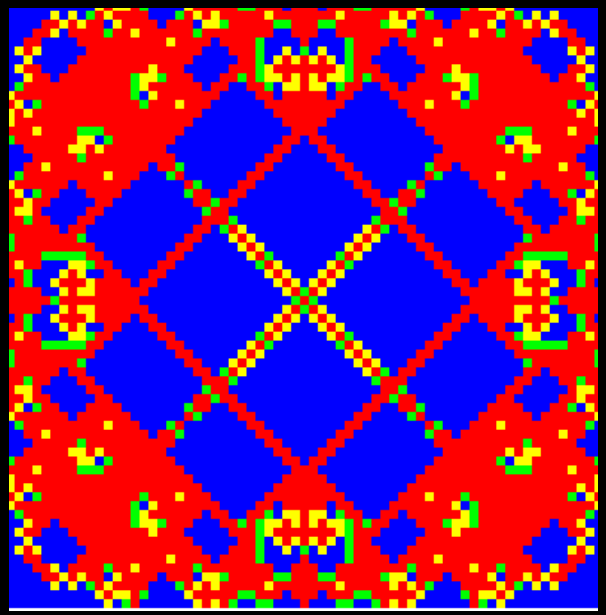




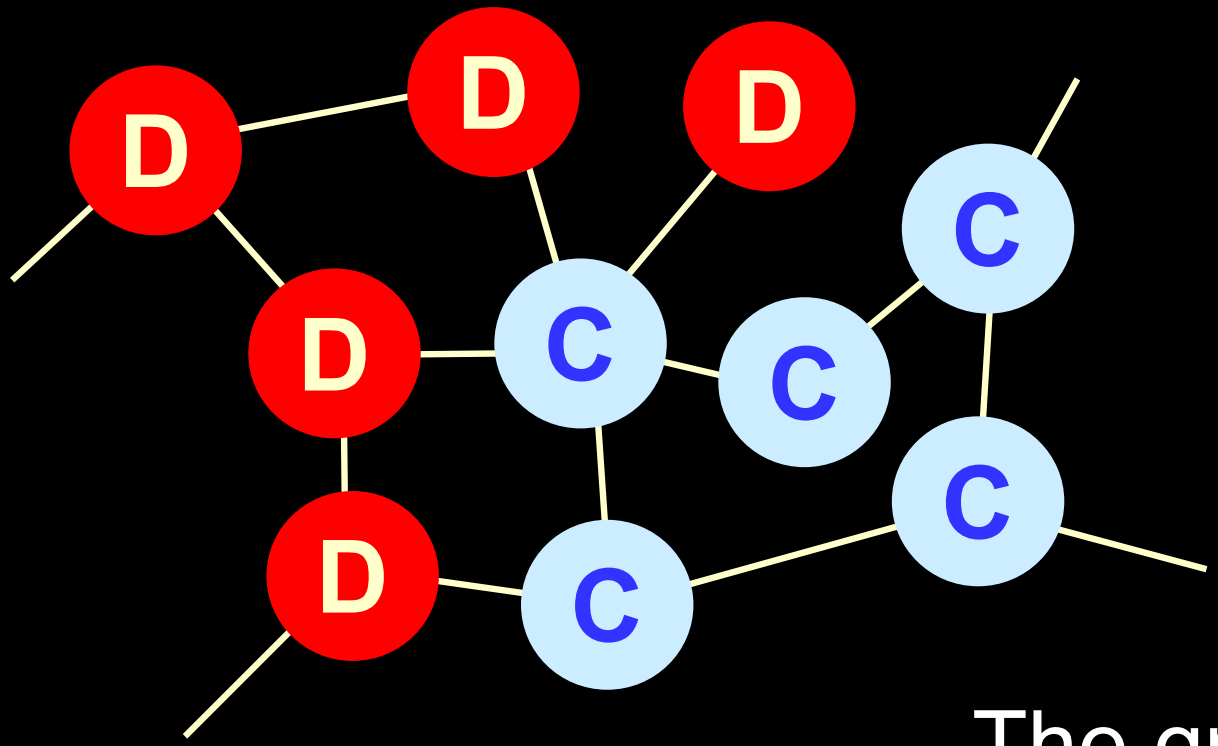








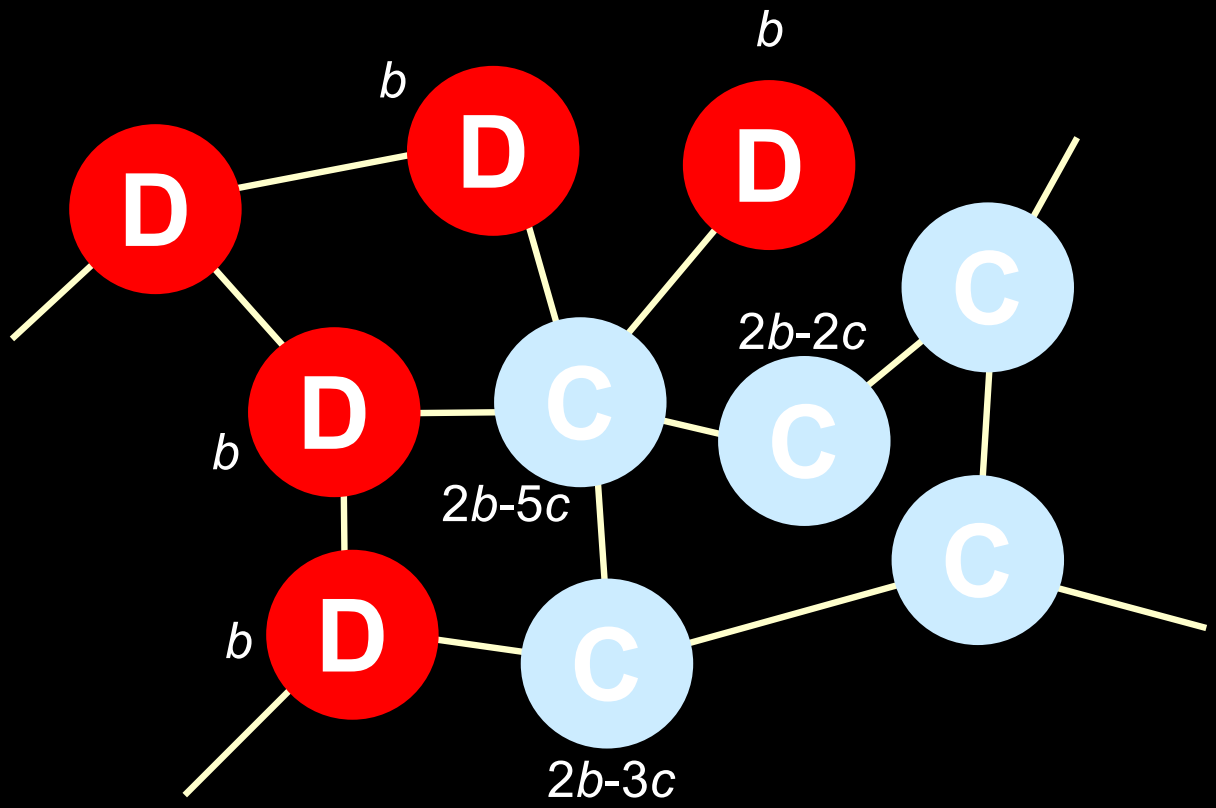
Games on graphs



Cooperators
Defectors

The graph describes
a spatial structure
or a social network.

‘Evolutionary graph theory’ (Lieberman et al, Nature 2005)



Cooperators pay a cost *c*
for each neighbor to receive benefit *b*.

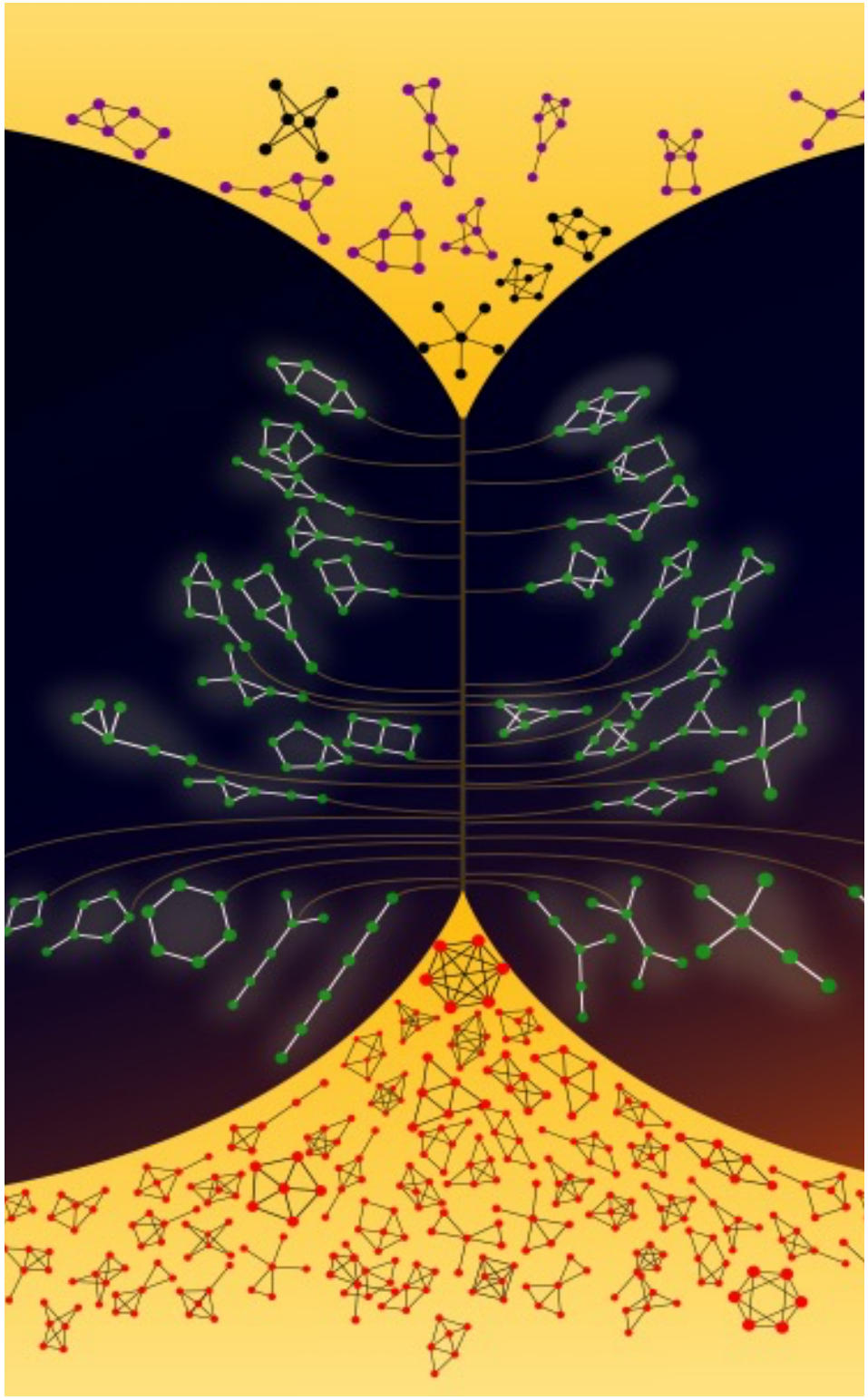
Spatial selection on graphs favors cooperation if

$$b / c > k$$

k…(average) number of neighbors

weak selection

Ohtsuki et al, Nature 2006



LETTER

doi:10.1038/nature21723

Evolutionary dynamics on any population structure

Benjamin Allen[1,2,3], Gabor Lippner[3,4], Yu-Ting Chen[2,3,5], Babak Fotouhi[2,6], Naghmeh Momeni[2,7], Shing-Tung Yau[3,8] & Martin A. Nowak[2,8,9]

Evolution occurs in populations of reproducing individuals. The structure of a population can affect which traits evolve[1,2]. Understanding evolutionary game dynamics in structured populations remains difficult. Mathematical results are known for special structures in which all individuals have the same number of neighbours[3–8]. The general case, in which the number of neighbours can vary, has remained open. For arbitrary selection intensity, the problem is in a computational complexity class that suggests there is no efficient algorithm[9]. Whether a simple solution for weak selection exists has remained unanswered. Here we provide a solution for weak selection that applies to any graph or network. Our method relies on calculating the coalescence times[10,11] of random walks[12]. We evaluate large numbers of diverse population structures for their propensity to favour cooperation. We study how small changes in population structure—graph surgery—affect evolutionary outcomes. We find that cooperation flourishes most in societies that are based on strong pairwise ties.

Ecological and evolutionary dynamics depend on population structure[13–15]. Evolutionary graph theory[1,3,7] provides a mathematical tool for representing population structure: vertices correspond to individuals and edges indicate interactions. Graphs can describe spatially structured populations of bacteria, plants, animals[16], tissue architecture in multi-cellular organisms[17], or social networks[18,19]. Graph topology affects the rate of genetic change[20] and the balance of drift versus selection[1]. The classical setting of a well-mixed population is the complete graph.

Of particular note is the evolution of social behaviour, which can be studied using evolutionary game theory[21–23]. Evolutionary game dynamics, which are tied to ecological dynamics[22], arise whenever reproductive success is affected by interactions with others.

In evolutionary games on graphs[3–8,24,25], individuals interact with neighbours according to a game and reproduce on the basis of payoff (Fig. 1). A central question is to determine which strategies succeed on a given graph. In general, there cannot be a closed-form solution or polynomial-time algorithm for this question, unless it is unexpectedly found that P = NP (polynomial time = nondeterministic polynomial time)[9]. To make progress, one can consider weak selection, meaning that the game has only a small effect on reproductive success. Weak selection results are known for regular graphs, where each individual has the same number of neighbours[3–8]. Evolutionary games on heterogenous (non-regular) graphs have only been investigated using computer simulations[3,24,25], approximations[3,26] and special cases[25,27,28].

We consider games on any weighted graph (Fig. 1a), with edge weights w_{ij}. Individuals are of two types, A and B. The game is specified by a payoff matrix (see Methods). Each individual i plays the game with each neighbour, receiving an edge-weighted average payoff of f_i (Fig. 1b). The reproductive rate of i is $F_i = 1 + \delta f_i$, where $\delta > 0$ is the strength of selection. Weak selection means $\delta \ll 1$; neutral drift, $\delta = 0$, is a baseline.

At each time step, an individual is chosen uniformly at random to be replaced. Its neighbours compete for the vacancy proportionally to their reproductive rates (Fig. 1c). Offspring inherit the type of their parent. This update rule, called death–birth[3], also translates into social settings: a random individual resolves to update its strategy, and adopts one of its neighbours' strategies proportionally to their payoff.

Over time, the population will reach the state of all A or all B. Suppose we introduce a single A at a vertex chosen uniformly at random in a population of B individuals. The fixation probability, ρ_A, is the probability of reaching all A from this initial condition. Likewise, ρ_B is the probability of reaching all B when starting with a single B individual in a population otherwise of A. Selection favours A over B if $\rho_A > \rho_B$.

The outcome of selection depends on the spatial assortment of types, which can be studied using coalescent theory[10,11]. Ancestral lineages are represented as random walks[12]. A step from i to j occurs with probability $p_{ij} = w_{ij}/w_i$, where $w_i = \sum_k w_{ik}$ is the weighted degree of vertex i. The coalescence time τ_{ij} is the expected meeting time of independent random walks started at vertices i and j (Fig. 1d), which can be obtained by solving a system of linear equations (see Methods). We show in the Supplementary Information that, if T is the time to absorption

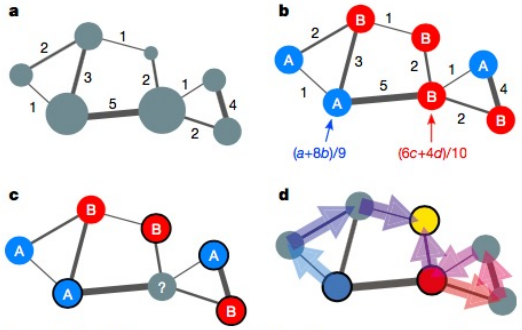


Figure 1 | Evolutionary games on weighted heterogeneous graphs. **a**, Population structure is represented by a graph with edge weights w_{ij}, which are shown next to the edges for this example. **b**, Each individual i plays a game (equation (3) in the Methods) with each neighbour, and retains the edge-weighted average payoff f_i. The reproductive rate of i is $F_i = 1 + \delta f_i$, where δ represents the strength of selection. **c**, For death–birth updating, a random individual i is selected to be replaced (indicated by a '?'); then a neighbour j is chosen with a probability proportional to $w_{ij}F_j$ to reproduce into the vacancy. **d**, The coalescence time[10–13] τ_{ij} is the expected meeting time of random walks from i and j, representing time to a common ancestor (yellow circle).

[1]Department of Mathematics, Emmanuel College, Boston, Massachusetts, USA. [2]Program for Evolutionary Dynamics, Harvard University, Cambridge, Massachusetts, USA. [3]Center for Mathematical Sciences and Applications, Harvard University, Cambridge, Massachusetts, USA. [4]Department of Mathematics, Northeastern University, Boston, Massachusetts, USA. [5]Department of Mathematics, University of Tennessee, Knoxville, Tennessee, USA. [6]Institute for Quantitative Social Sciences, Harvard University, Cambridge, Massachusetts, USA. [7]Department of Electrical and Computer Engineering, McGill University, Montreal, Canada. [8]Department of Mathematics, Harvard University, Cambridge, Massachusetts, USA. [9]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA.

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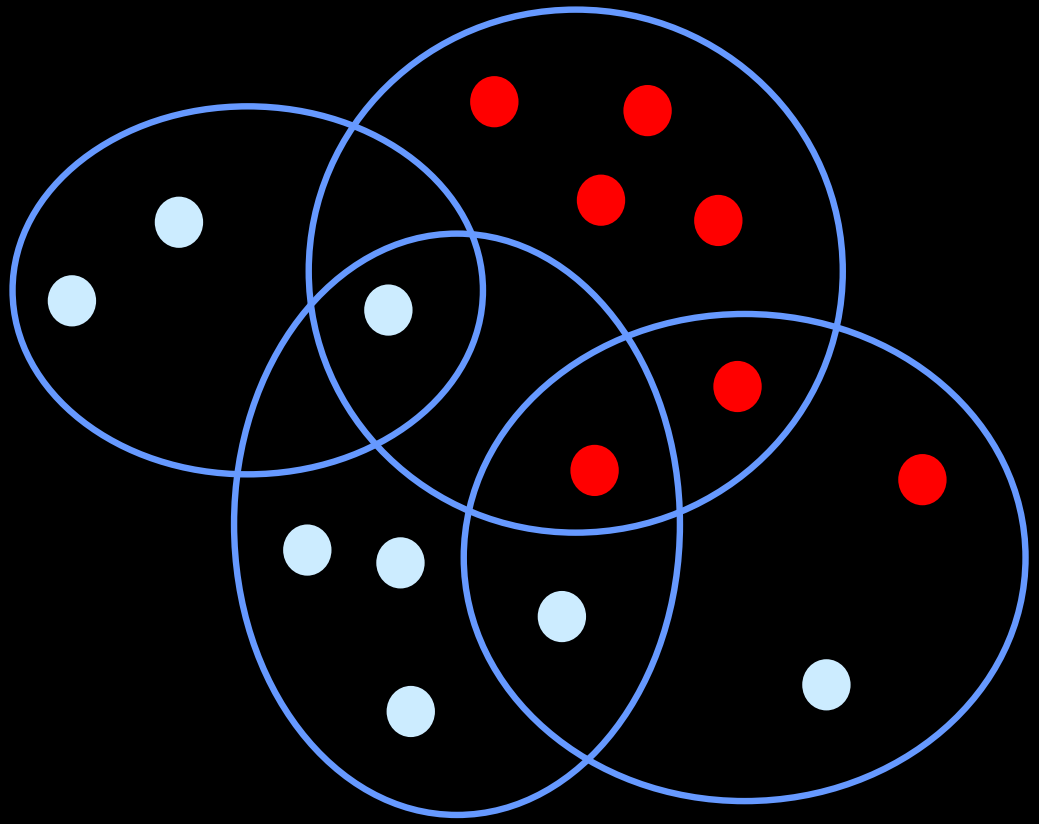
Evolutionary set theory



People belong to sets.

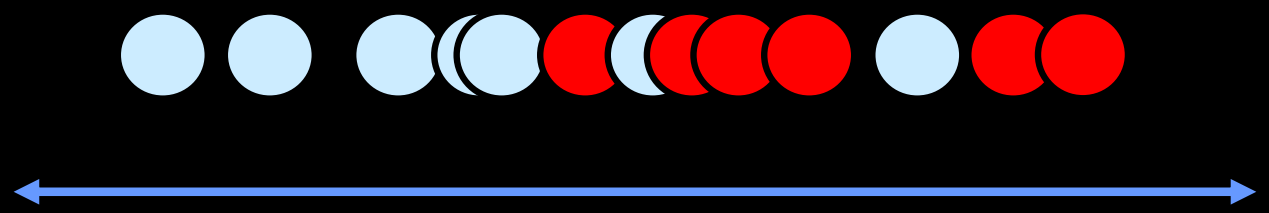
People interact with others in the same sets.

People adopt strategy and set membership of successful individuals.

Tarnita et al, PNAS 2009

Games in phenotype space

Cooperation by similarity / tag based



$$\frac{b}{c} > 1 + \frac{2}{\sqrt{3}}$$

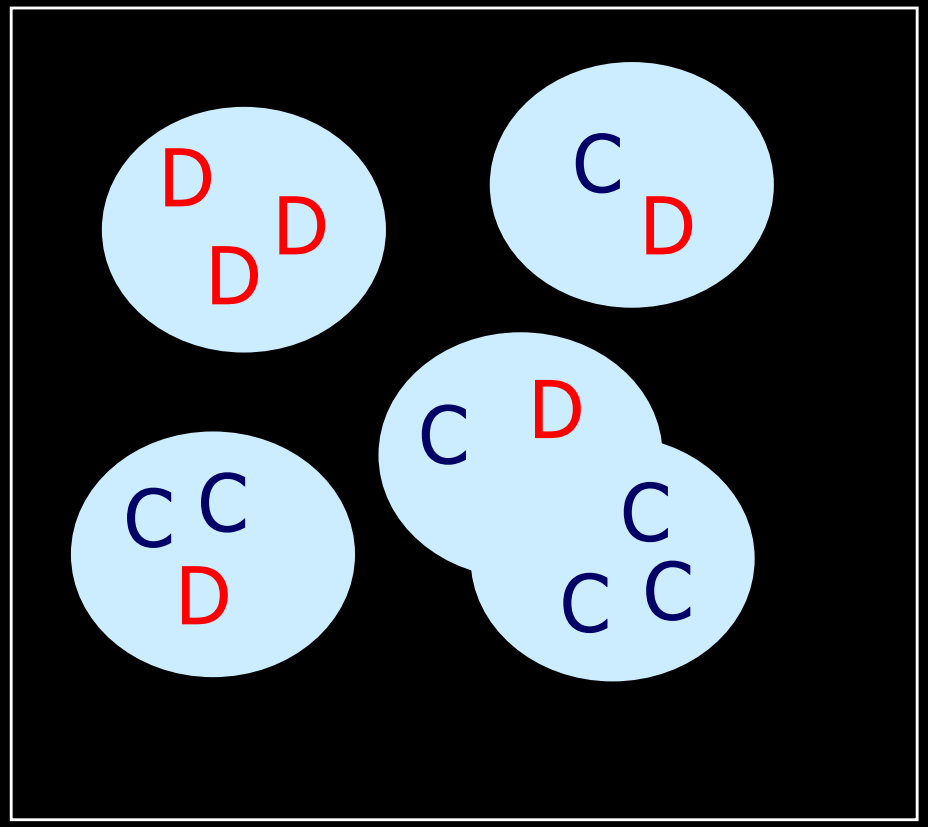
Antal et al, PNAS 2009

Group selection

‘There can be no doubt that a tribe including many members who [...] are always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection.’

Charles Darwin, The Descent of Man, 1871

Group selection



Play the game with others in your group.

Offspring are added to the group.

Groups divide when reaching a certain size.

Groups die.

Group selection

favors cooperators if

$$b / c > 1 + n / m$$

n … group size
m … number of groups

Traulsen & Nowak, PNAS 2006

Kin selection

The interaction occurs between genetic relatives.

‘I will jump into the river to save
2 brothers or 8 cousins’

J.B.S Haldane

Five mechanisms for cooperation

Direct reciprocity : I help you, you help me.

Indirect reciprocity : I help you, somebody helps me.

Spatial selection : Neighbors help each other.

Group selection : groups of cooperators out-compete other groups.

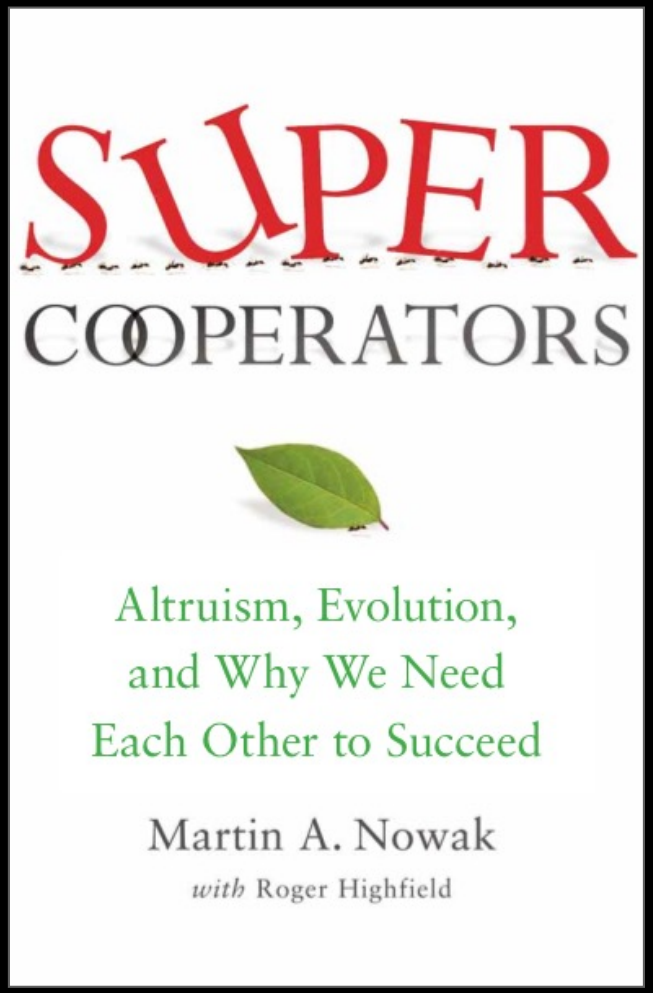
Kin selection : cooperate with genetic relatives.

Direct and indirect reciprocity
are the key components for understanding the evolution of any pro-social behavior in humans.

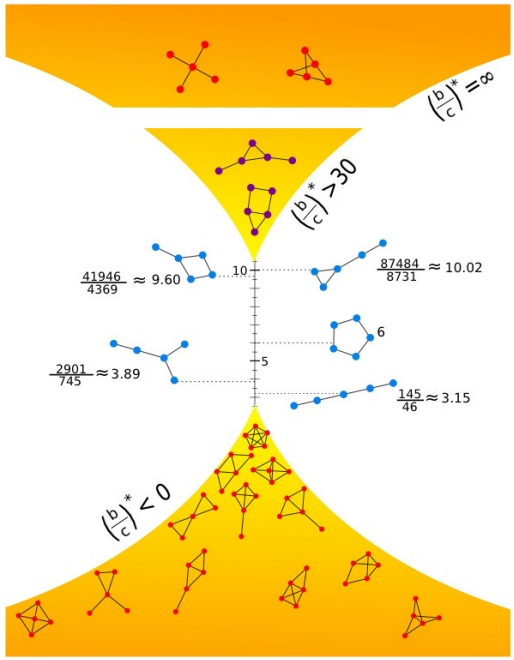
But ‘what made us human’ is
indirect reciprocity,
because it selected for social intelligence and human language.

We must learn global cooperation
…. and cooperation with future generations.

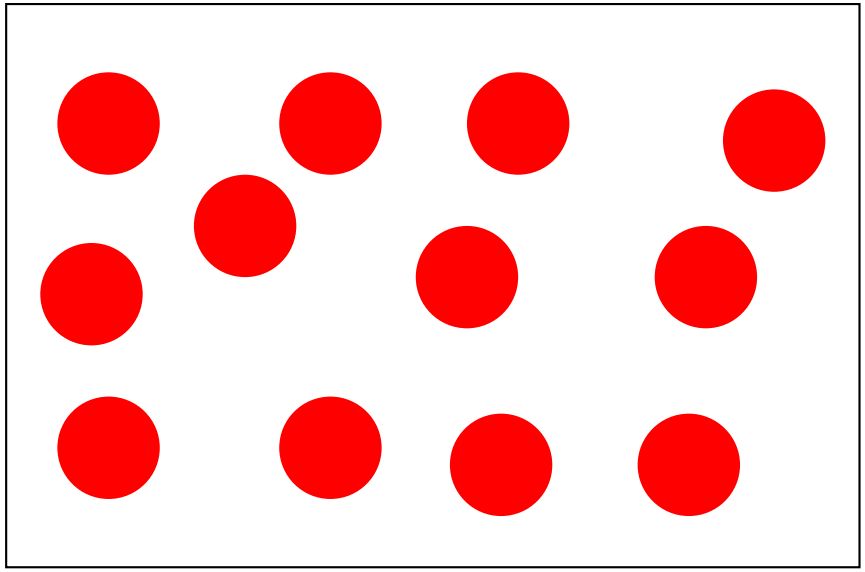
The stability of i-life requires global cooperation
… and cooperation with future generations.


SUPER
COOPERATORS
Altruism, Evolution,
and Why We Need
Each Other to Succeed
Martin A. Nowak
with Roger Highfield

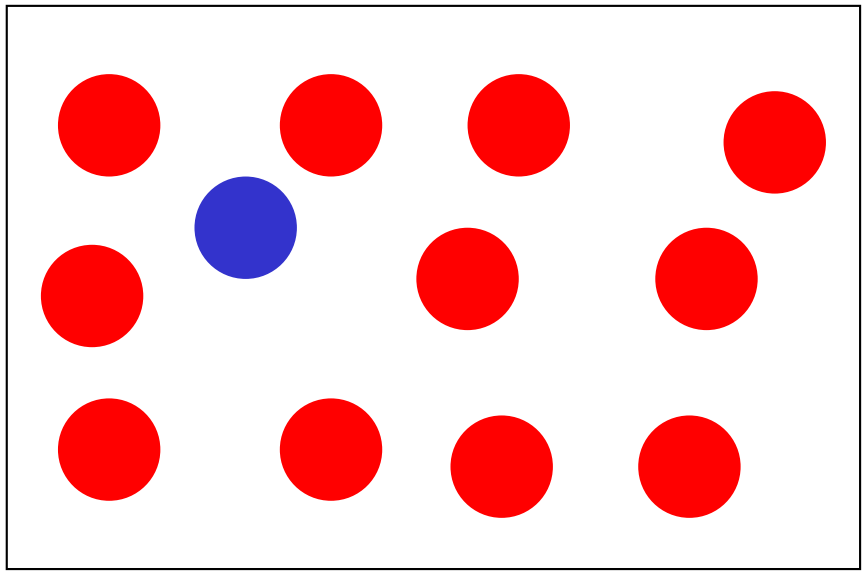
Evolutionary dynamics



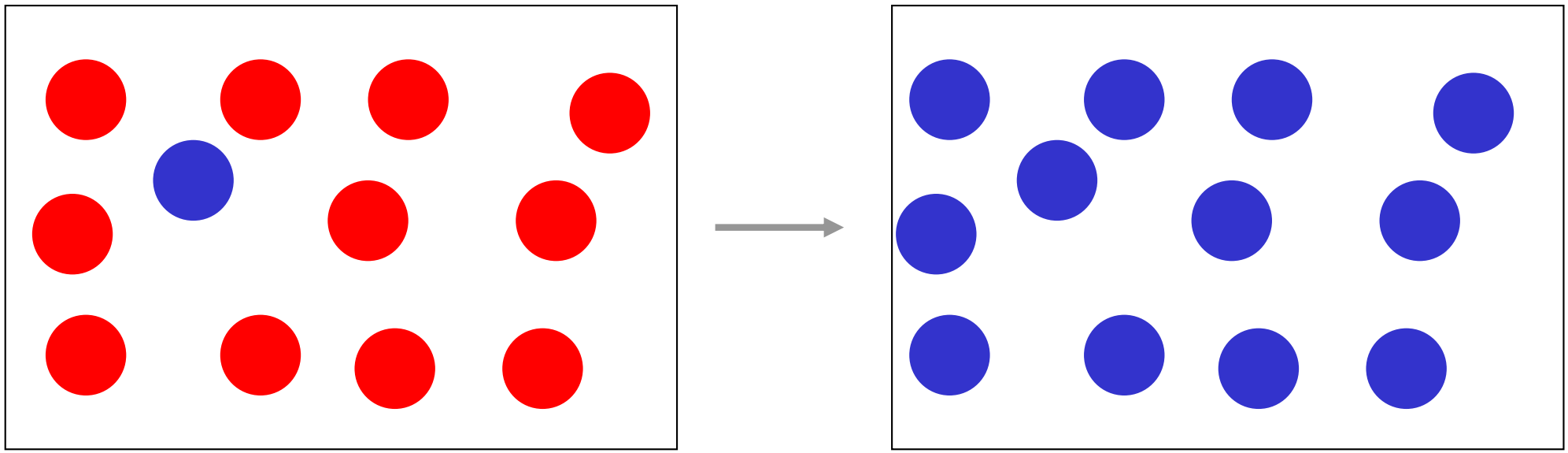
Evolution occurs in populations of reproducing individuals.



mutation



selection

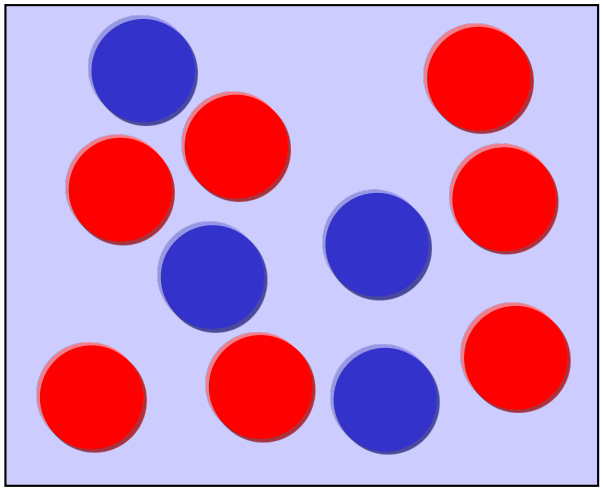


Deterministic

Stochastic

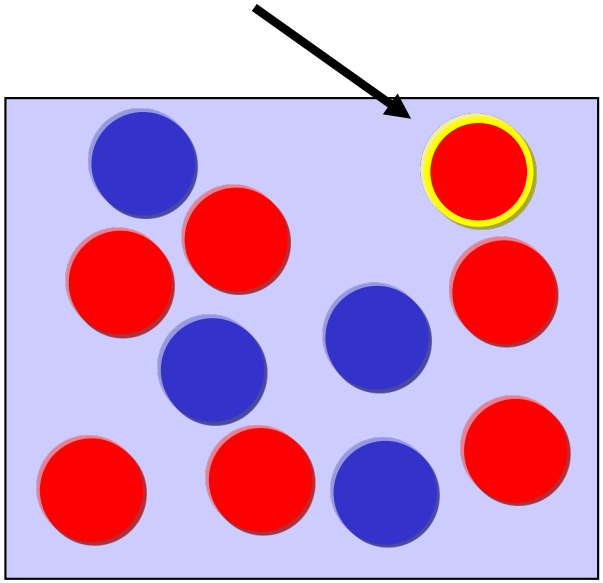
1. Constant selection

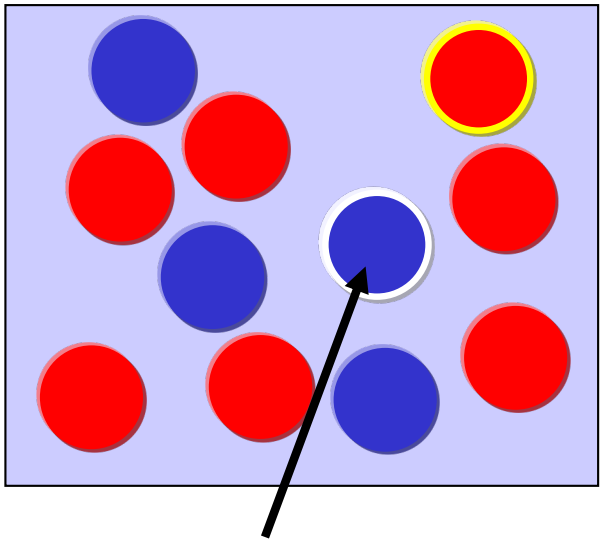
The Moran process



Population of size N

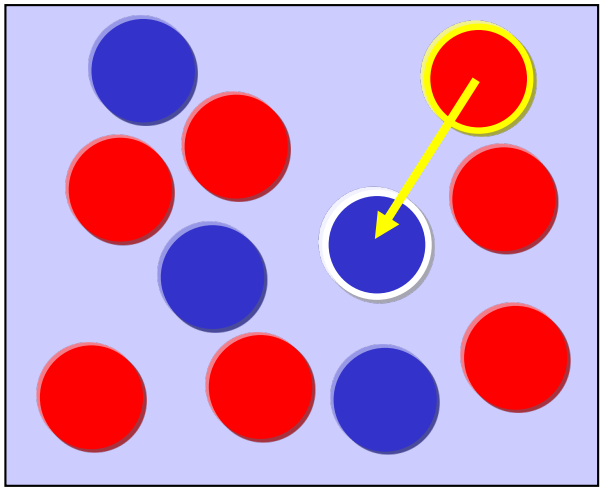
choose an individual for reproduction
(proportional to fitness)

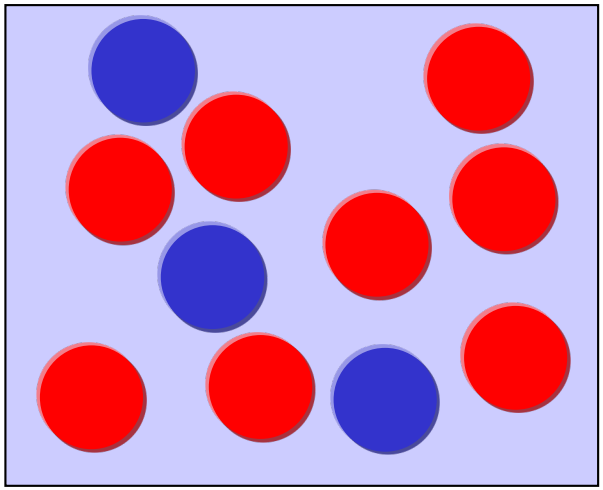




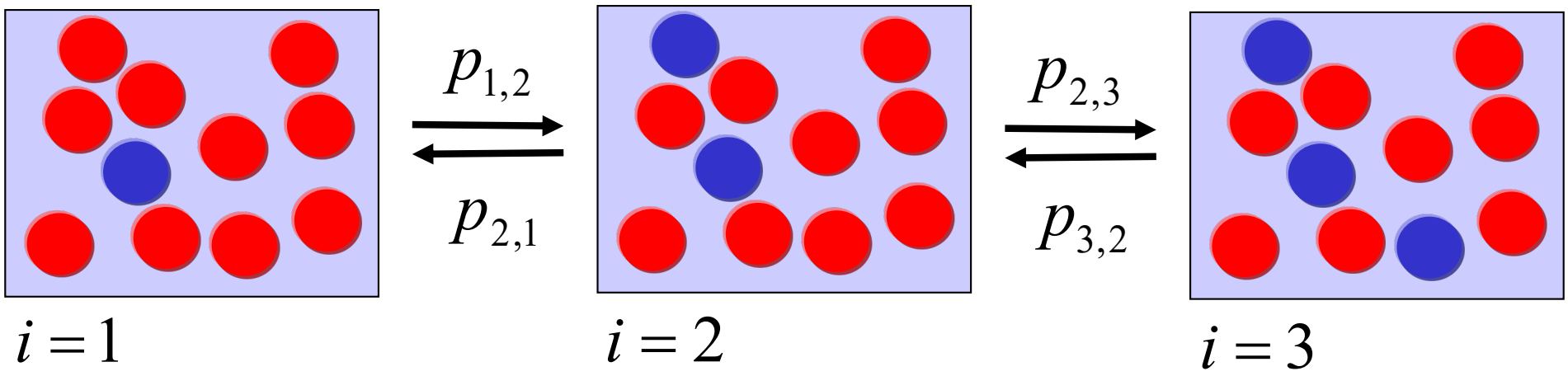
choose one for death

the offspring of the first
replaces the second



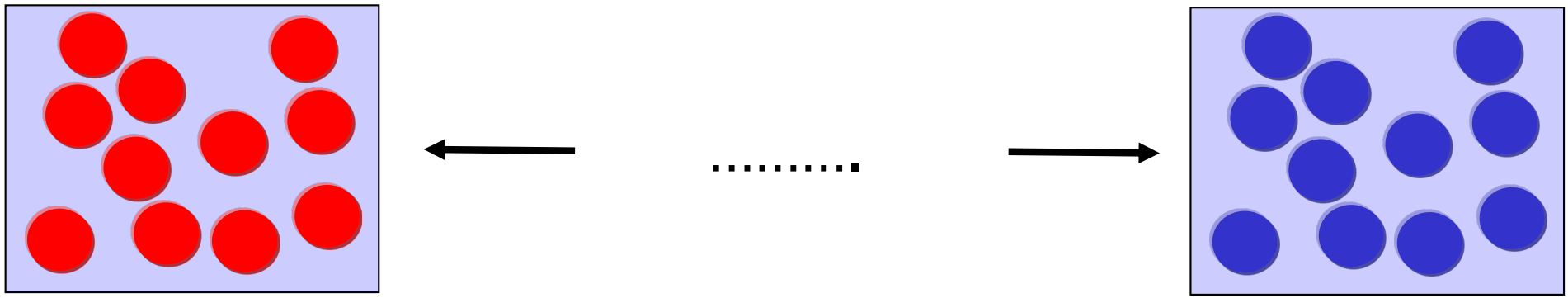


…a birth-death process

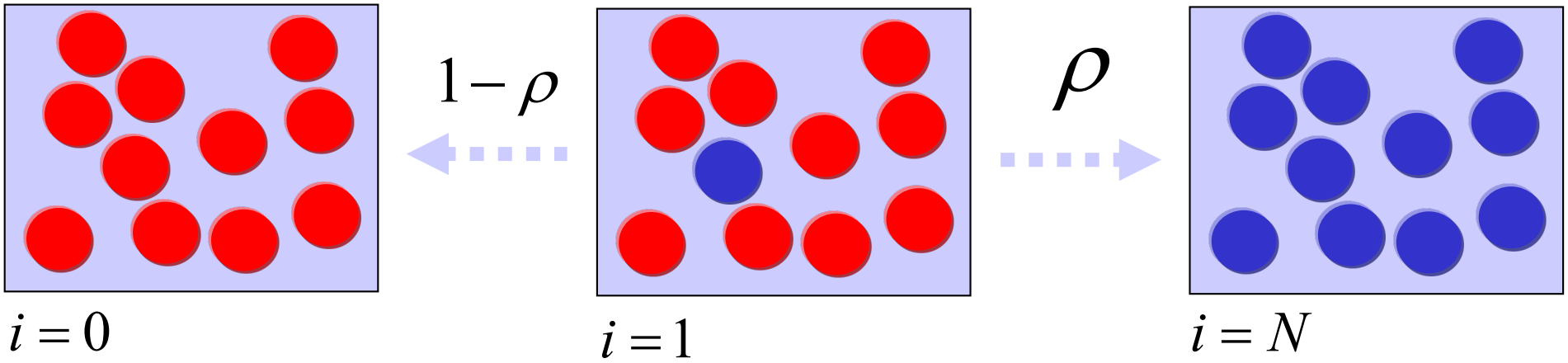


For two types the state space is $i = 0,1,\ldots,N$

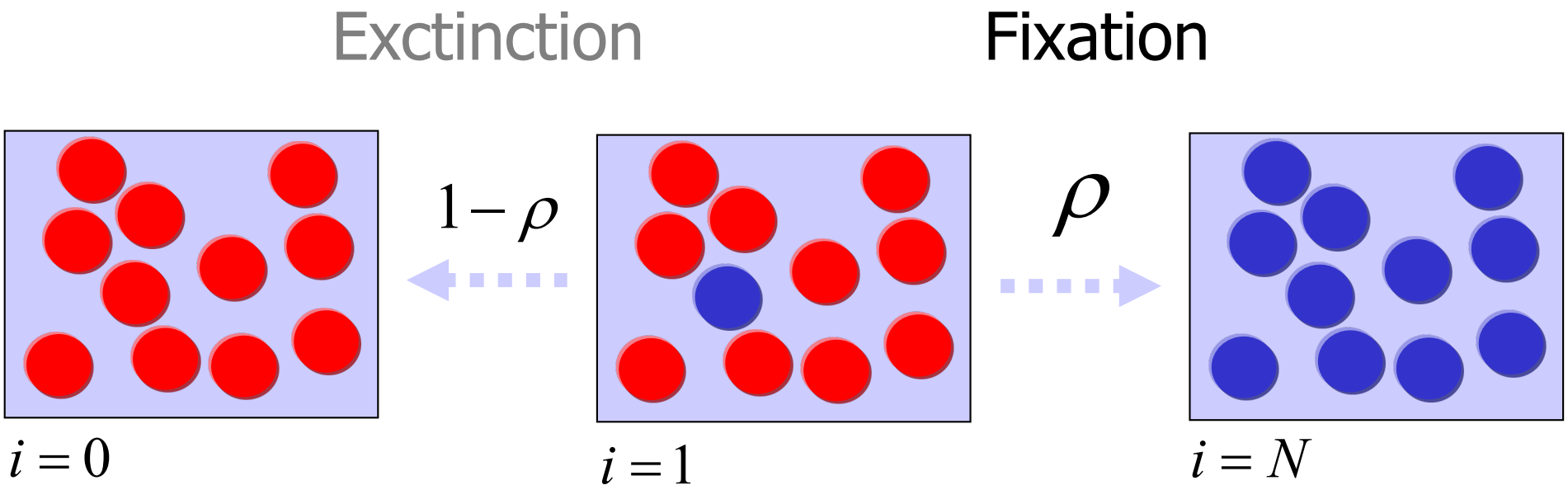
Without mutation: two absorbing states

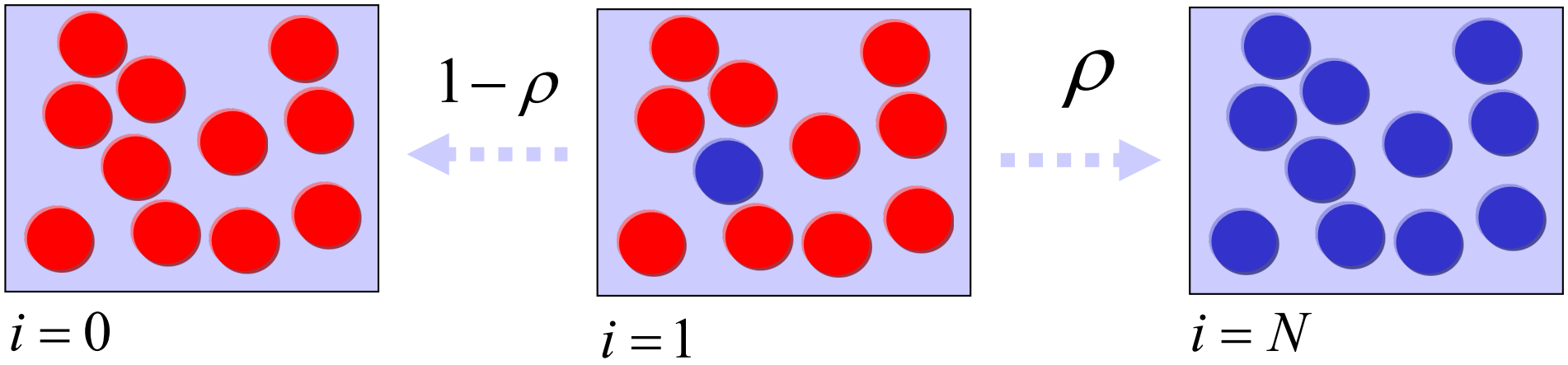


Fixation probability of a new mutant



$$\rho = \Pr(i = 1 \rightarrow i = N)$$

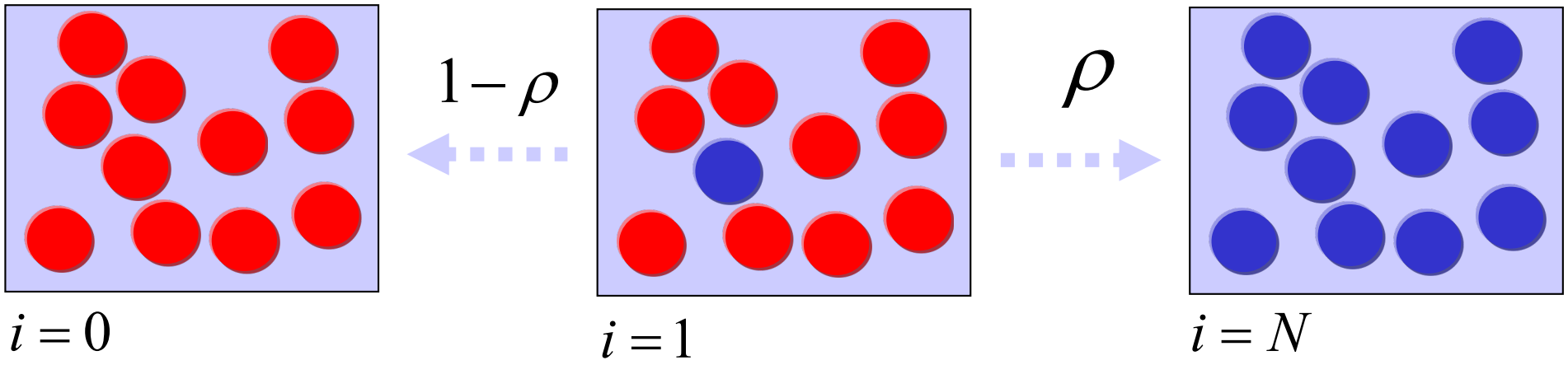

Exctinction
Fixation
$1-\rho$
ρ
$i=0$
$i=1$
$i=N$



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

r … relative fitness of

N … population size



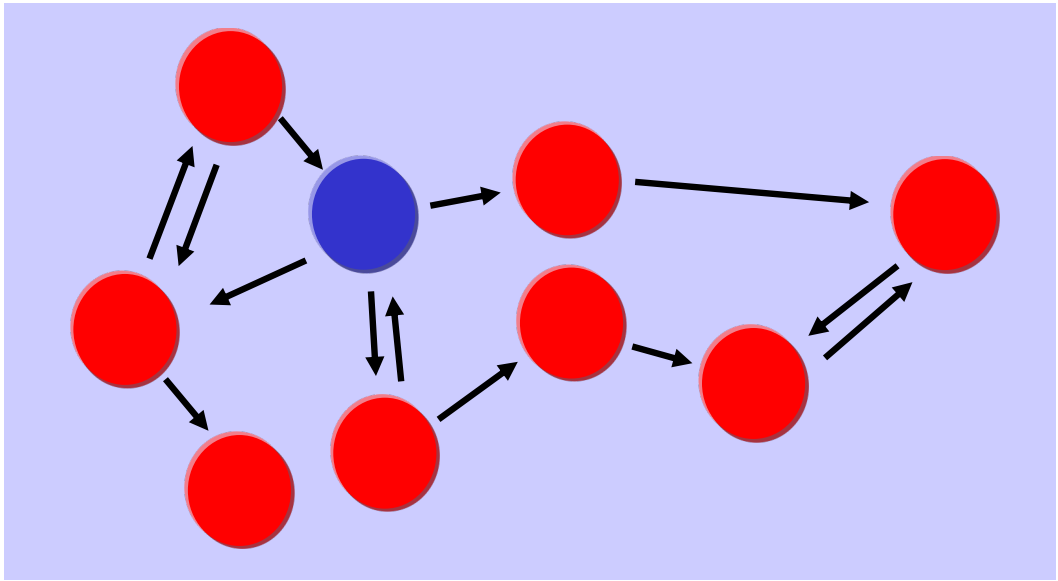
Neutral evolution: $r=1$

$\rho = 1/N$

How does population structure affect natural selection?

Are there suppressors or amplifiers of natural selection?

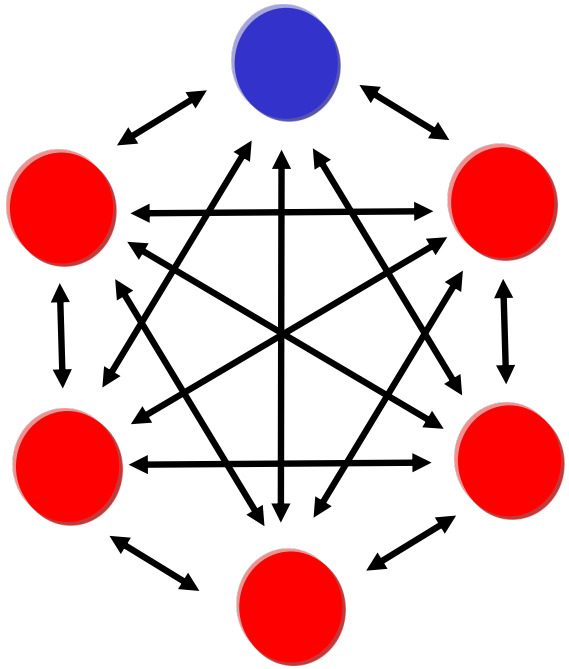
Evolutionary graph theory



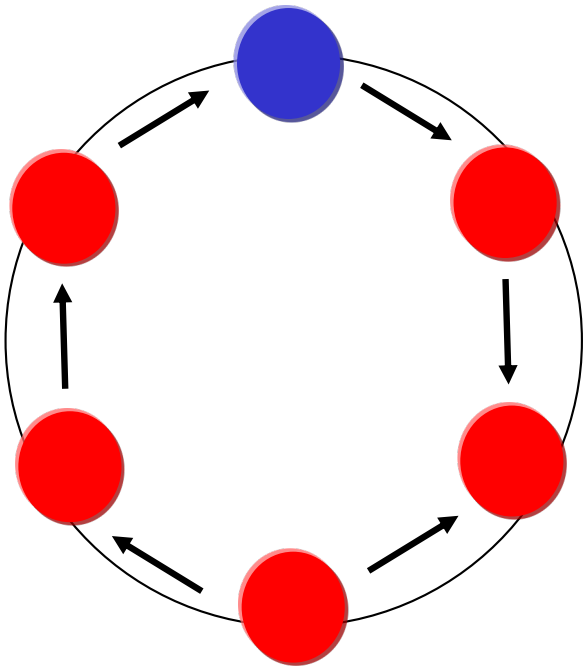
The individuals occupy the vertices of a graph.

The edges determine where to place the offspring.

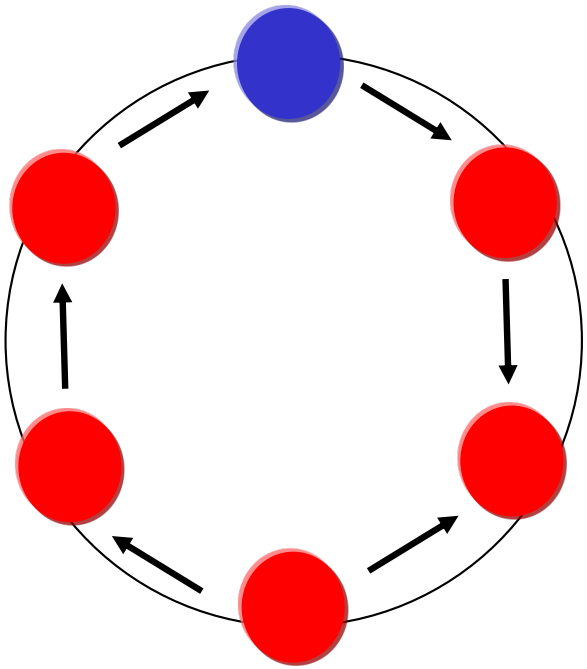
The Moran process is given by the complete graph with identical weights (and self loops).



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

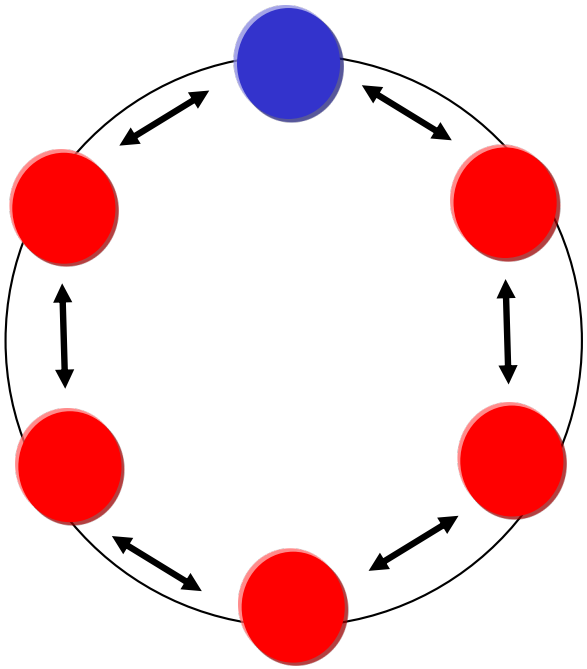


The directed cycle

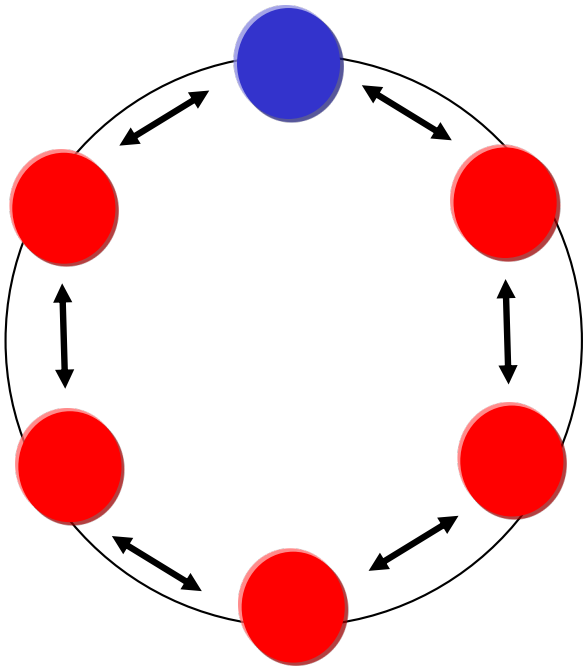


$$\rho = \frac{1 - 1/r}{1 - 1/r^n}$$

The directed cycle has the same fixation probability as the Moran process.



The cycle



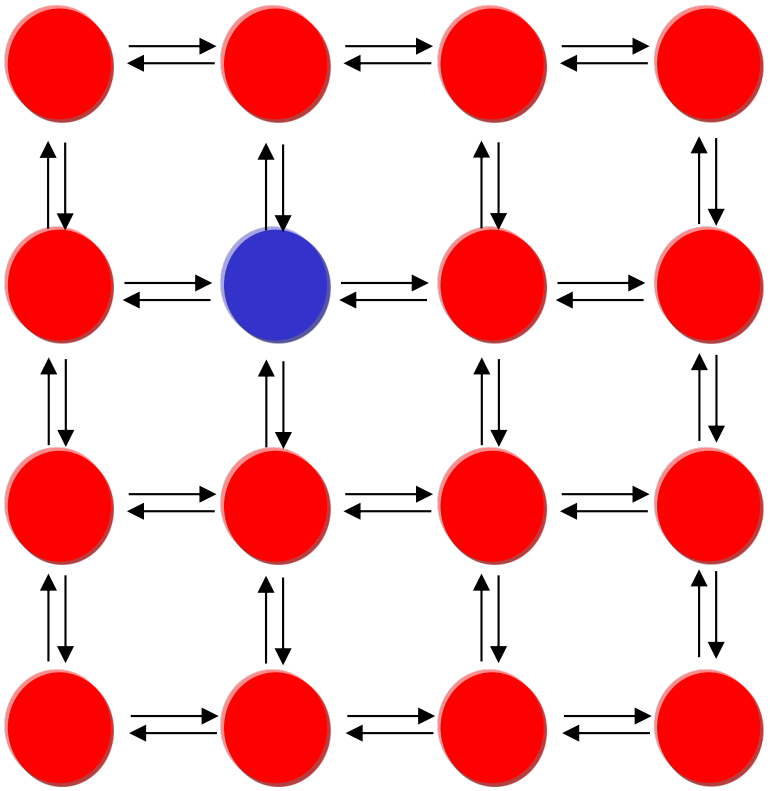
$$\rho = \frac{1 - 1/r}{1 - 1/r^n}$$

The cycle has the same fixation probability as the Moran process.

The temperature of a vertex is the sum of all weights leading into that vertex.

$$T_j = \sum_i w_{ij}$$

The isothermal theorem: if all vertices have the same temperature, then the fixation probability is equivalent to the Moran process.



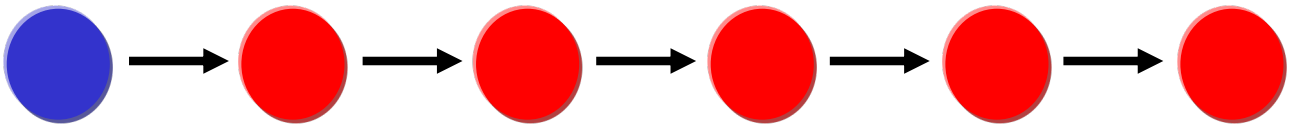
$$\rho = \frac{1 - 1/r}{1 - 1/r^n}$$

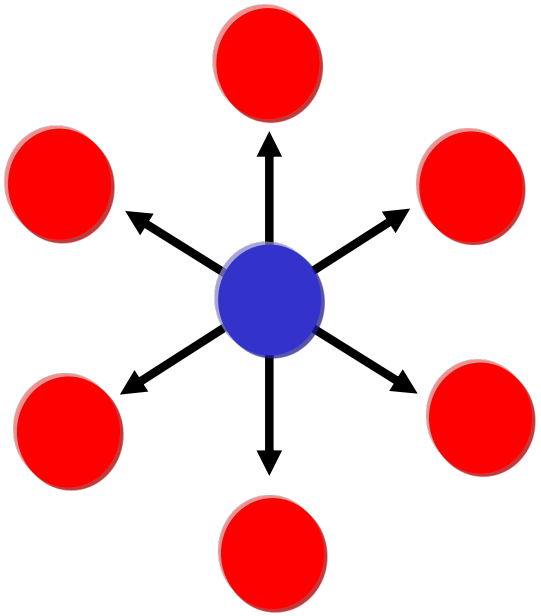
All symmetric graphs have the same fixation probability as the Moran process.

The robust isothermal theorem: if all vertices have approximately the same temperature, then the fixation probability is close to the Moran process.

Some random graph models, including Erdos-Renyi, converge to the same fixation probability as a complete graph.

Suppressors of selection





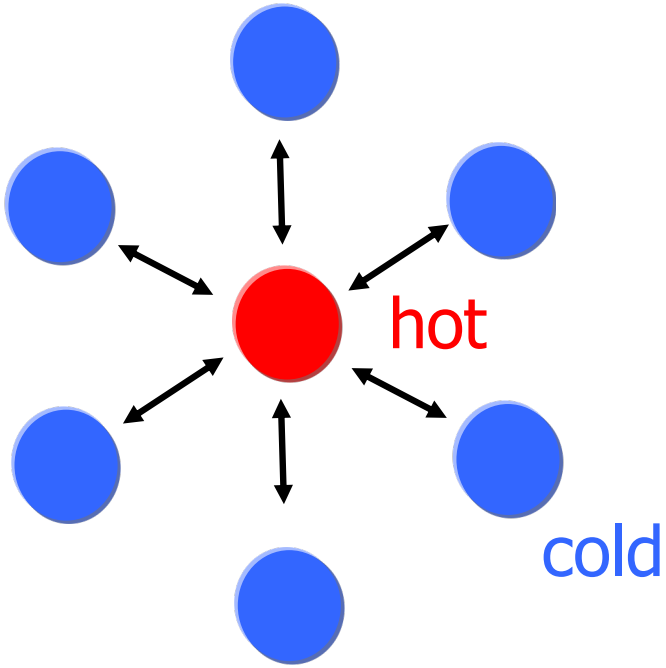
$$\rho = 1/N$$

The line and the burst have fixation probability $1/N$.

Human epithelial tissues and
the hematopoietic system
are suppressors of selection,
thereby reducing the onset of cancer.

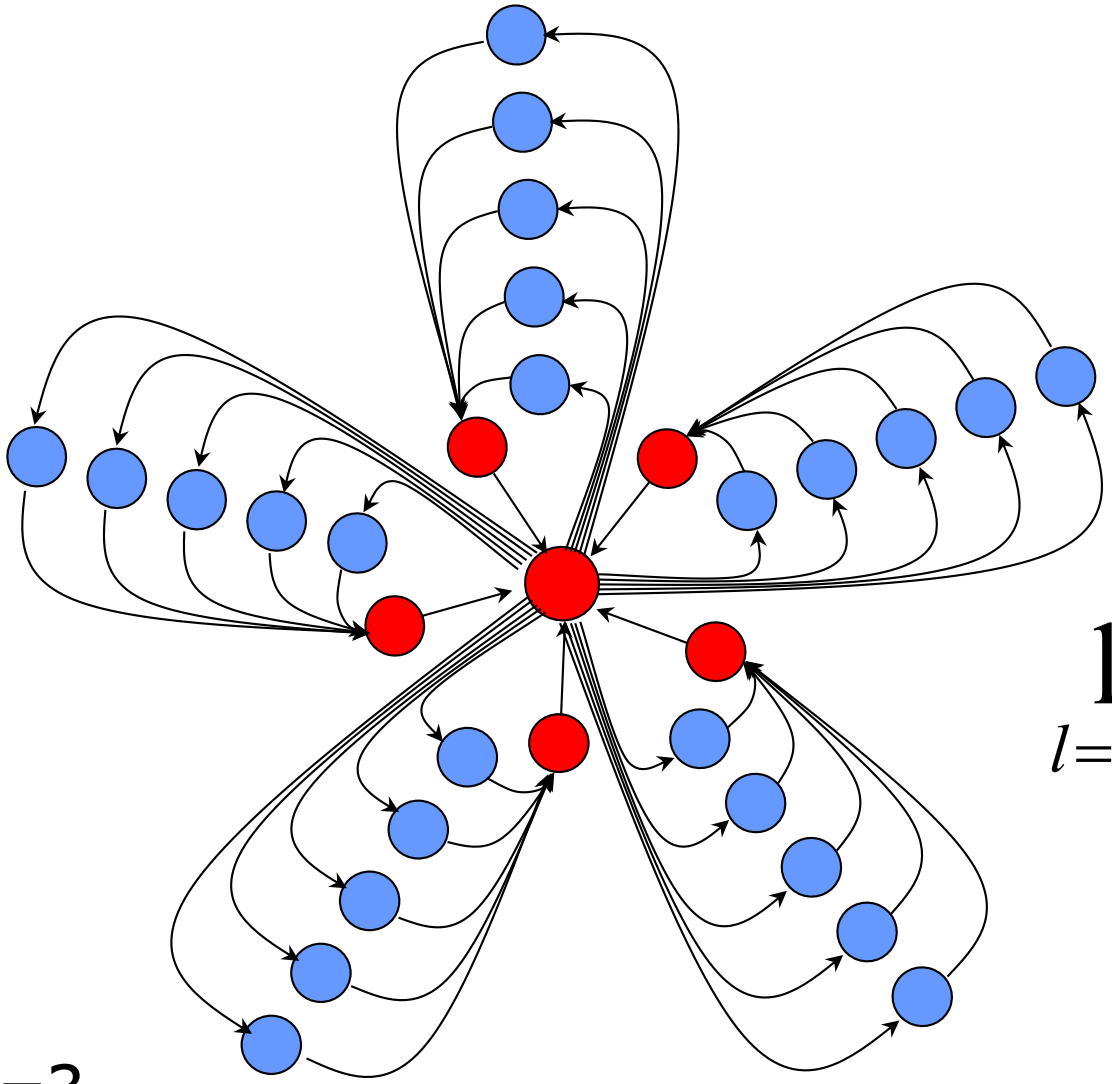
Are there amplifiers of selection ?

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



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

k =3
l =5
m =5

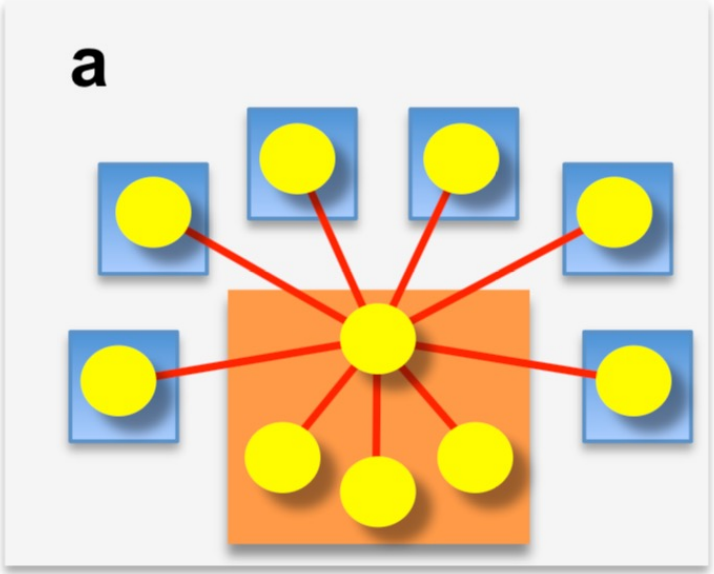
Amplifiers are sensitive to how mutants arise:

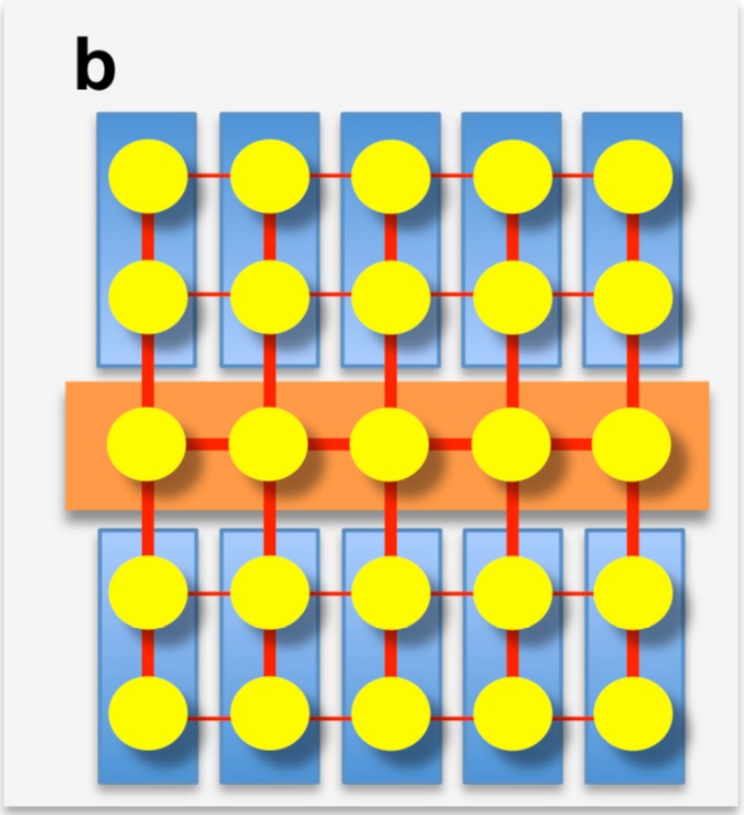
1. uniformly at random

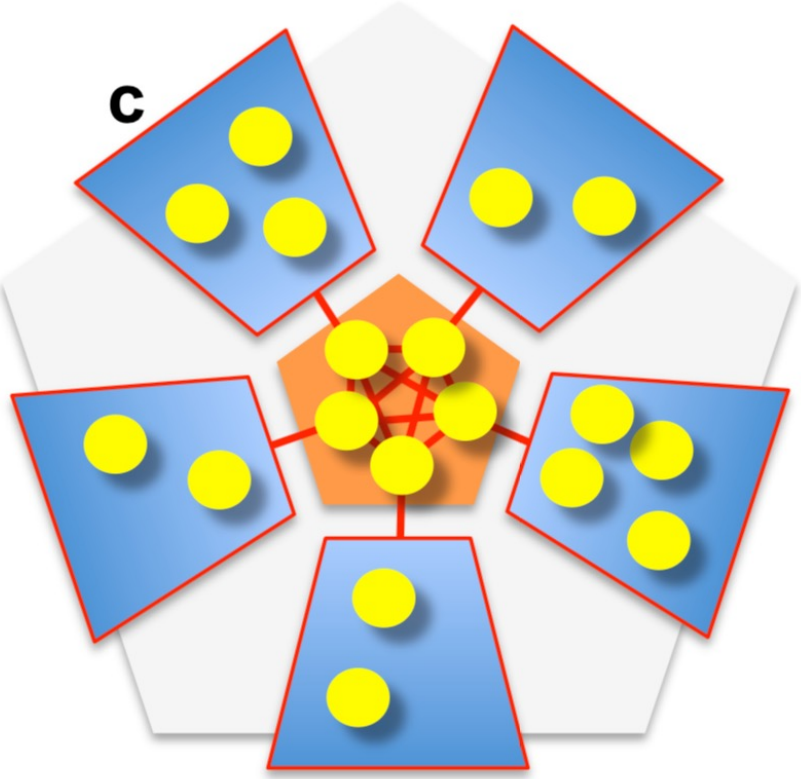
2. during reproductive events

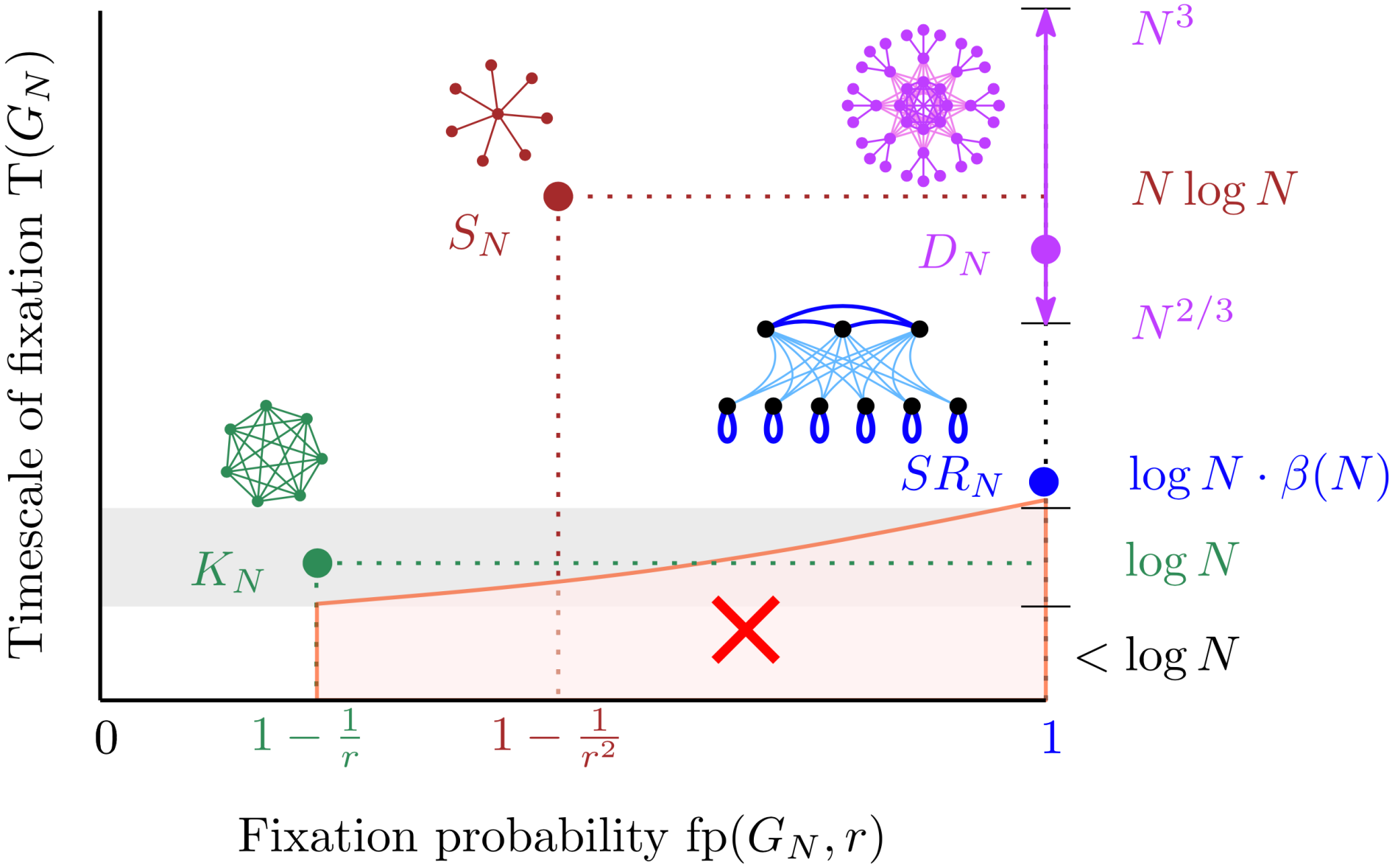
Star and Superstar amplify for 1 but not for 2.

A recent finding: almost any topology can be turned into an arbitrarily strong amplifier by adding weights (and self loops).



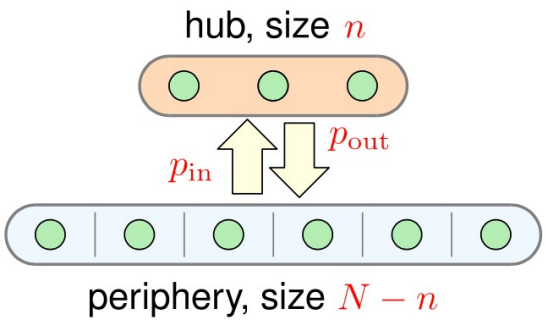





Timescale of fixation $\mathrm{T}(G_N)$
N^3
$N \log N$
$N^{2/3}$
$\log N \cdot \beta(N)$
$\log N$
$< \log N$
S_N
D_N
SR_N
K_N
0
$1 - \frac{1}{r}$
$1 - \frac{1}{r^2}$
1
Fixation probability $\mathrm{fp}(G_N, r)$

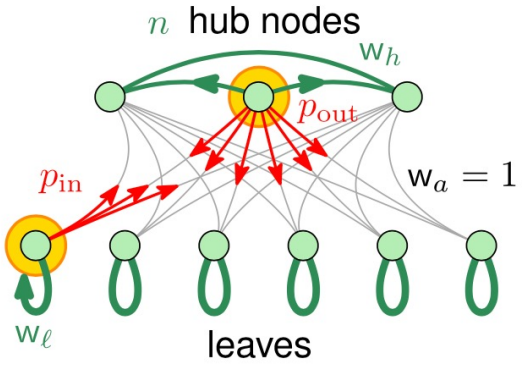
a Selection Reactor

$\mathrm{SR}_N(n, p_{\mathrm{in}}, p_{\mathrm{out}})$



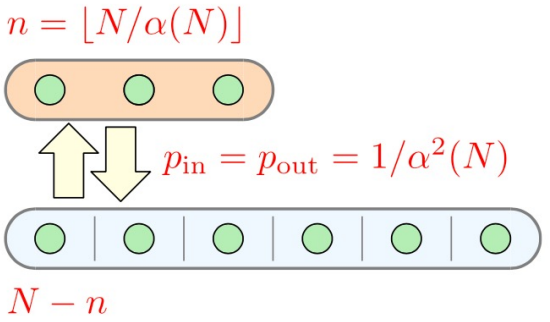
b Graph representation

$\mathrm{SR}^{\mathsf{g}}_N(n, \mathsf{w}_h, \mathsf{w}_\ell)$

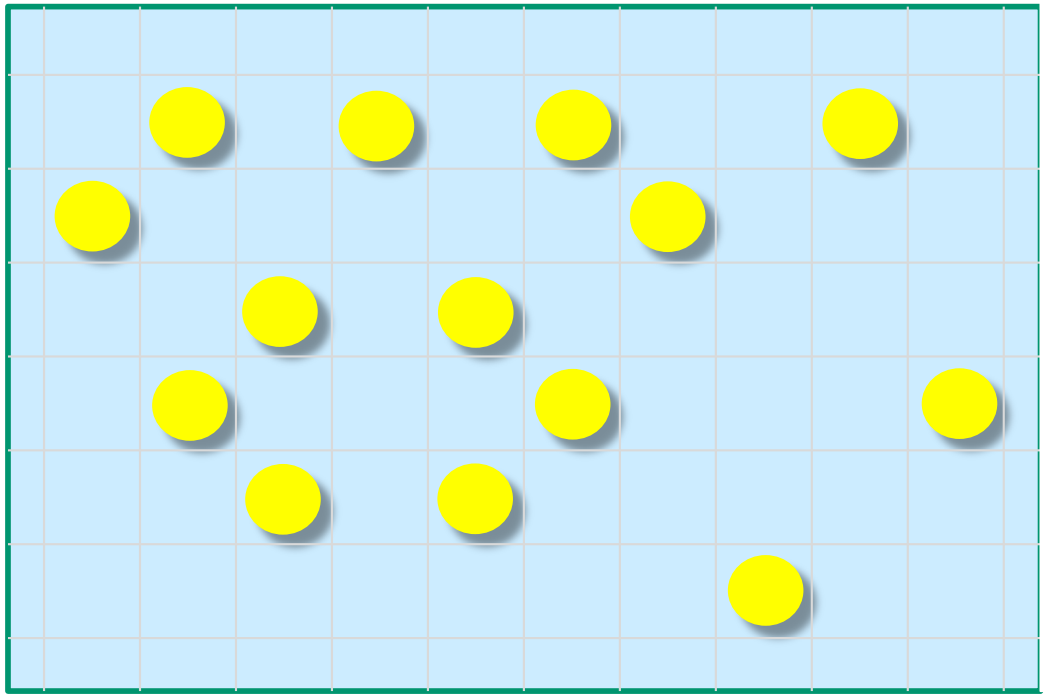


c Specific family

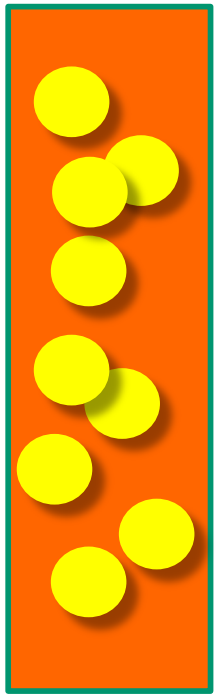
SR^{α}_N



Prechamber ("storage")



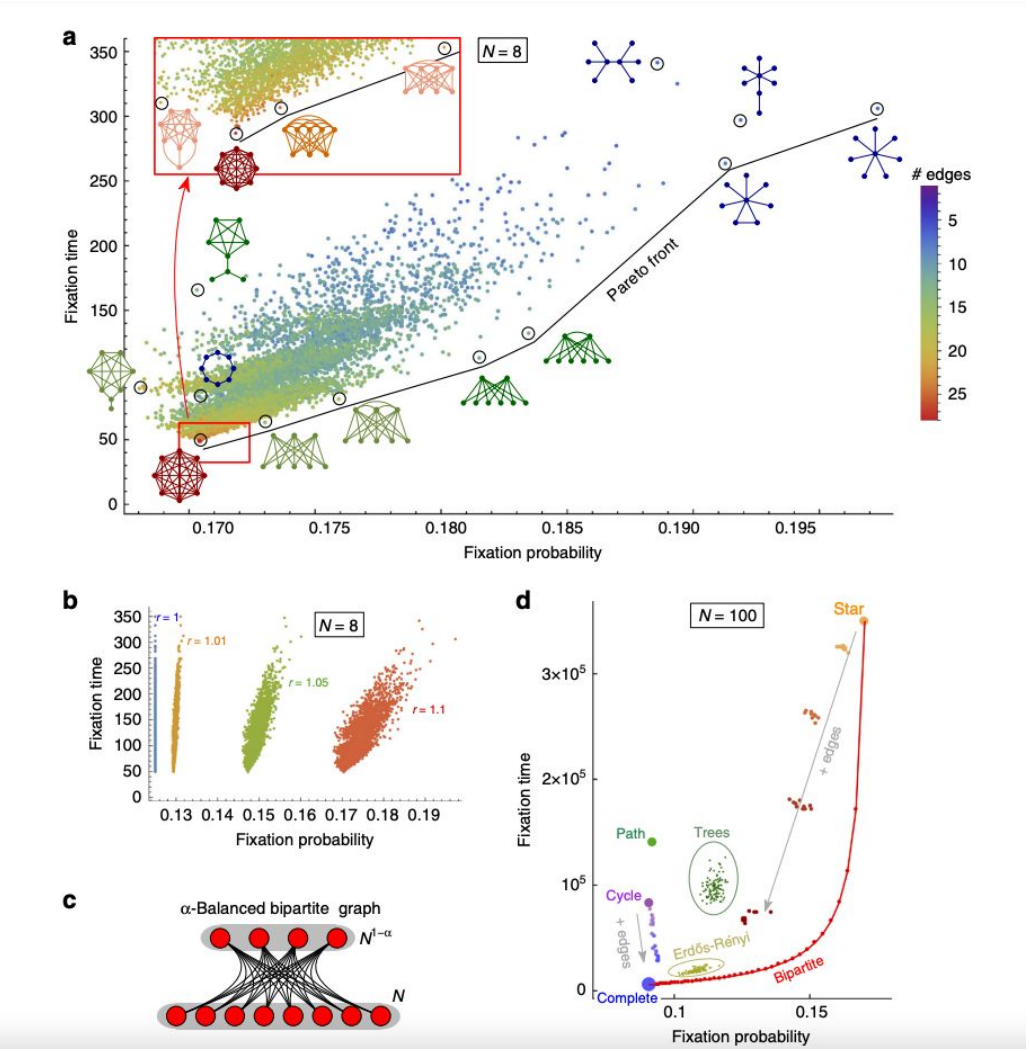
offspring go to main chamber

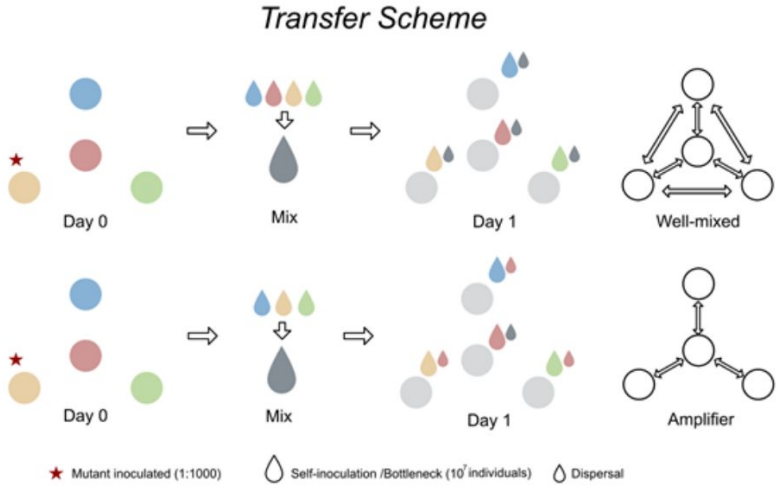


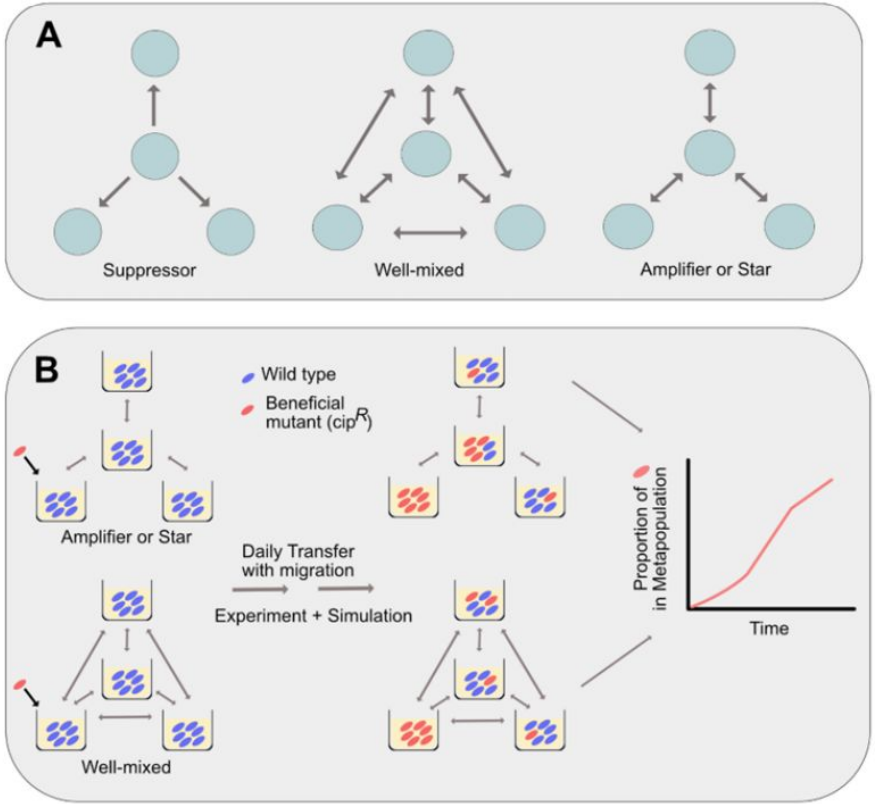
Main Chamber ("CPU")

a well-mixed population

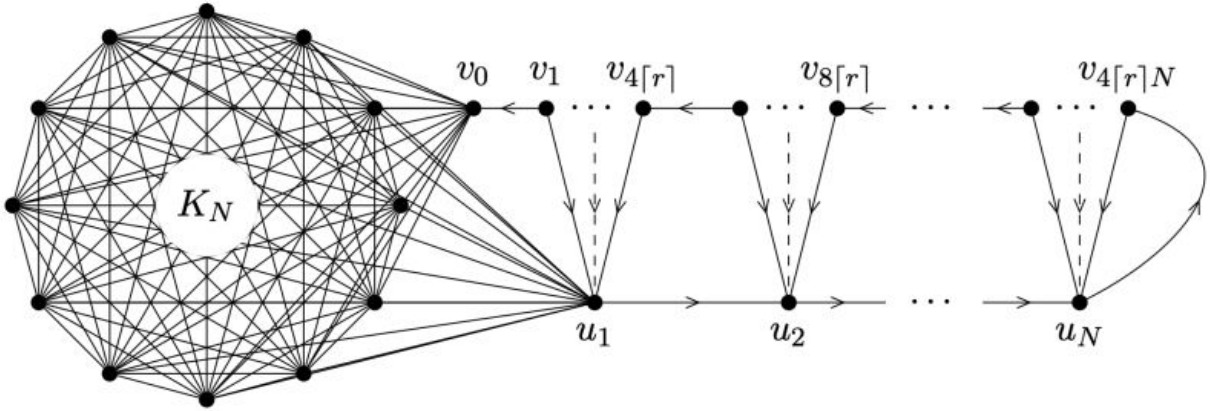
some offspring go back to the prechamber


a
N = 8
Fixation time
Fixation probability
Pareto front
edges
5
10
15
20
25
b
N = 8
r = 1
r = 1.01
r = 1.05
r = 1.1
Fixation time
Fixation probability
c
α-Balanced bipartite graph
N^{1−α}
N
d
N = 100
Star
Path
Trees
Cycle
Erdős-Rényi
Bipartite
Complete
+ edges
+ edges
Fixation time
Fixation probability


Transfer Scheme
Day 0
Mix
Day 1
Well-mixed
Day 0
Mix
Day 1
Amplifier
Mutant inoculated (1:1000)
Self-inoculation /Bottleneck (10^7 individuals)
Dispersal


A
Suppressor
Well-mixed
Amplifier or Star
B
Wild type
Beneficial mutant (cip^R)
Amplifier or Star
Daily Transfer with migration
Experiment + Simulation
Well-mixed
Proportion of in Metapopulation
Time

Some directed graphs have exponentially long fixation time



Theorem. [DGRS '16] D-regular digraphs fixate quickly.

Theorem. [BNT '23+] For *Eulerian* digraph with min degree δ and max degree Δ,

$$r \geq \Delta/\delta \implies \#\text{steps at most } \mathrm{poly}(n).$$

Approximating fixation probabilities in directed graphs

Could try running simulations, but only works if fixation time is short!

Theorem. [BNT '23+] For $r \geq 1$, FPRAS for computing $\mathrm{fp}^r(G)$ if $\mathrm{fp}^{r=1}_{\mathrm{min}}(G) \geq 1/\mathrm{poly}(\mathrm{n})$

2. Non-constant selection

Frequency dependent selection

Evolutionary game theory

Ecology, Infection

Payoff matrix

	A	B
A	a	b
B	c	d

	A	B
A	3	0
B	5	1

	A	B
A	3	0
B	2	2

	A	B
A	0	1
B	5	0

i … A-players

N-i … B-players

Payoff matrix

	A	B
A	a	b
B	c	d

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

Payoff for B: $$G_i = \frac{ci + d(N-i-1)}{N-1}$$

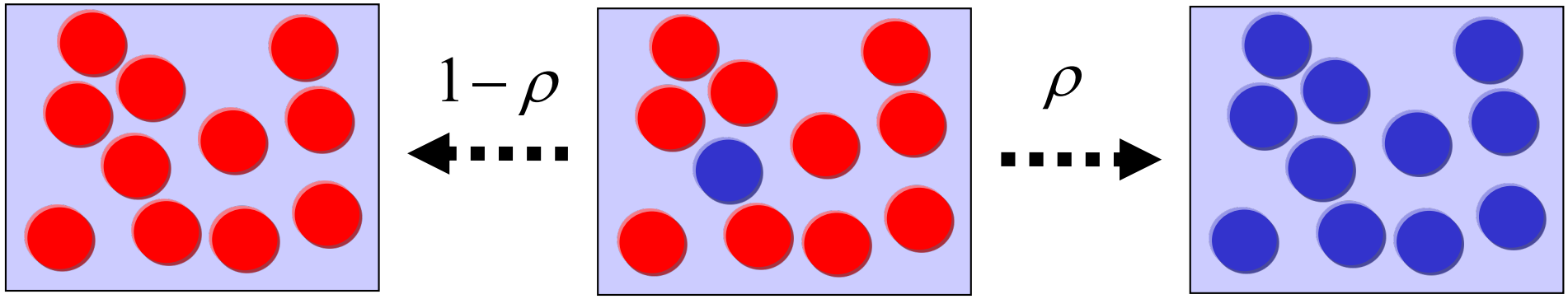
Intensity of selection

Fitness of A: $f_i = 1 + wF_i$

Fitness of B: $g_i = 1 + wG_i$

weak selection: $w << 1$

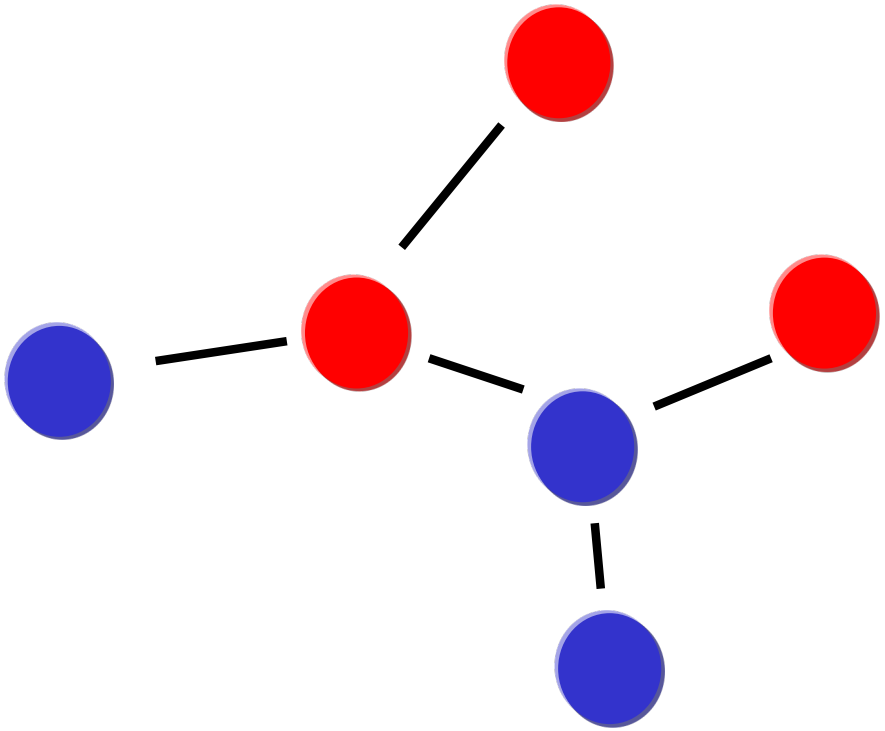
Fixation probability of A



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

If $\rho > 1/N$ then selection favors A replacing B.

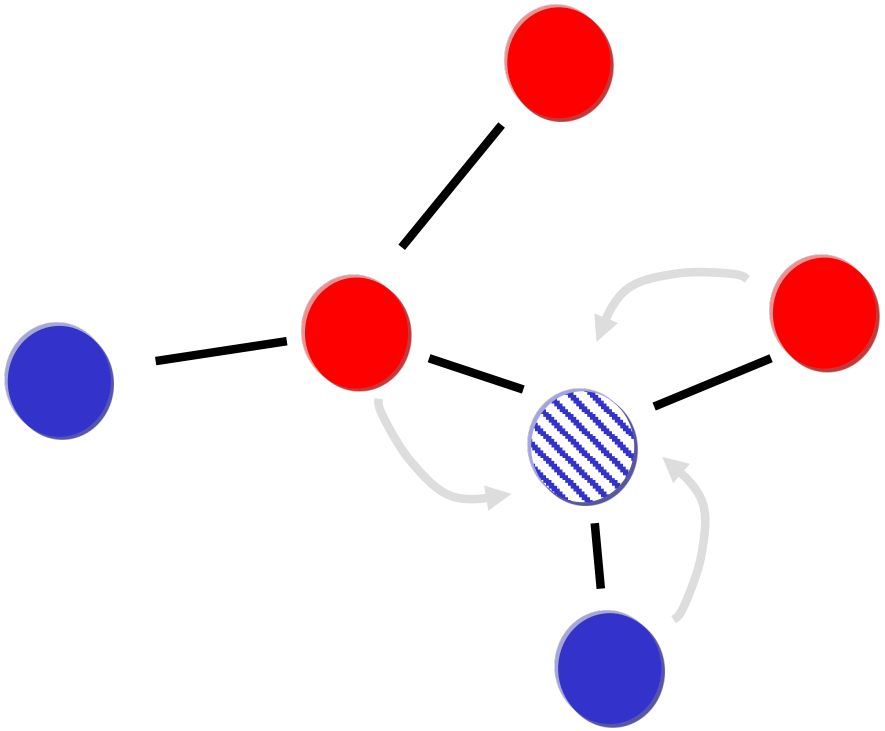
Games on graphs



	A	B
A	a	b
B	c	d

Play the game with your neighbors.

Death-birth updating



1. choose a random individual to die

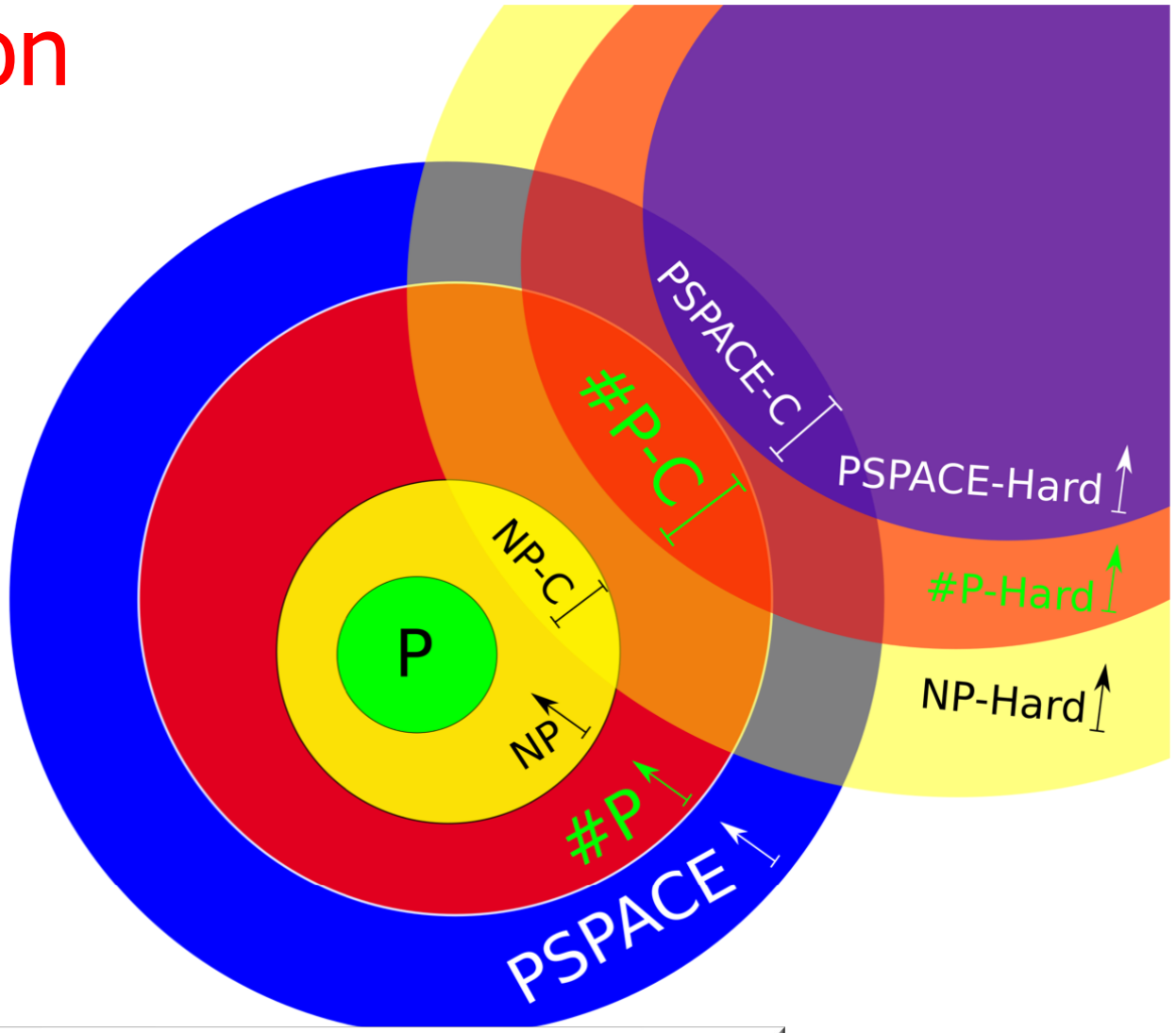
2. the neighbors compete for the empty site proportional to fitness

Evolution of cooperation

	C	D
C	b-c	-c
D	b	0

C…cooperators
D…defectors
b…benefit
c…cost

Games on graphs, in general not weak selection



	Qualitative	Quantitative
Ecological Scenario	NP-complete	#P-complete
Linear fitness	PSPACE-complete	PSPACE-complete
Exponential fitness	P	PSPACE-complete

Maintaining diversity in structured populations

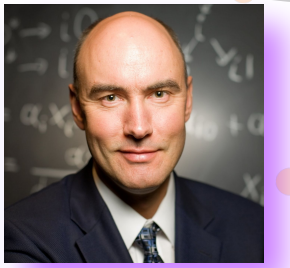
David Brewster
Harvard

Jakub Svoboda
IST Austria (now Dartmouth)

Dylan Roscow
UIUC (now Purdue)

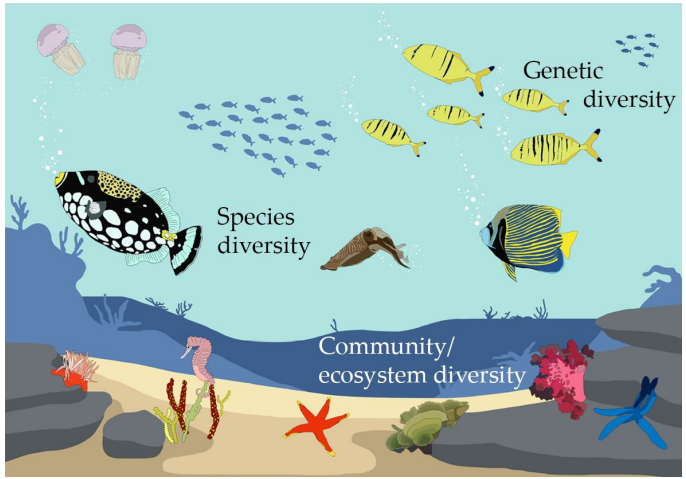
Krish Chatterjee
IST Austria

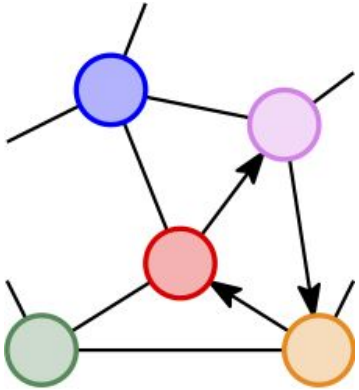
Josef “Pepa” Tkadlec
Charles



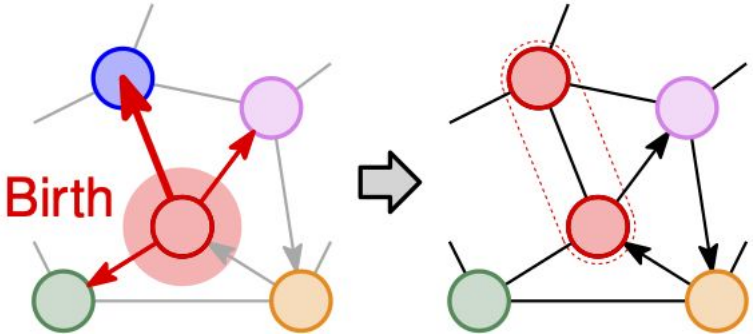
Martin Nowak
Harvard

Diversity

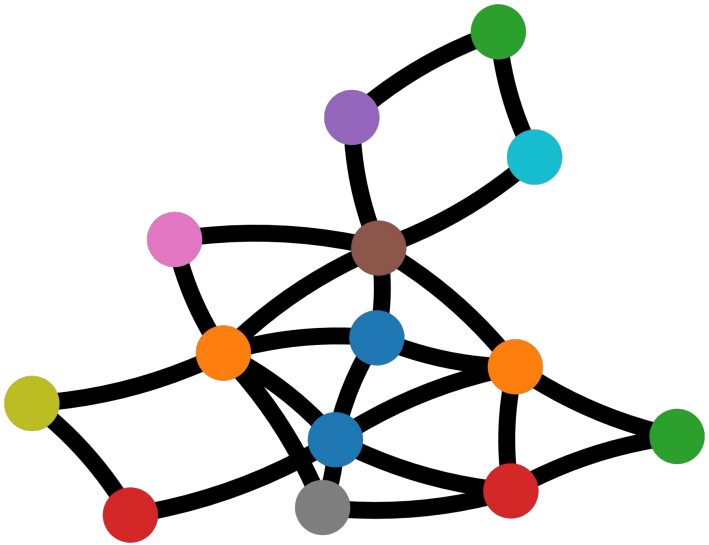

Genetic
diversity
Species
diversity
Community/
ecosystem diversity

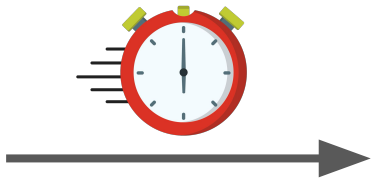


birth-death (bd)

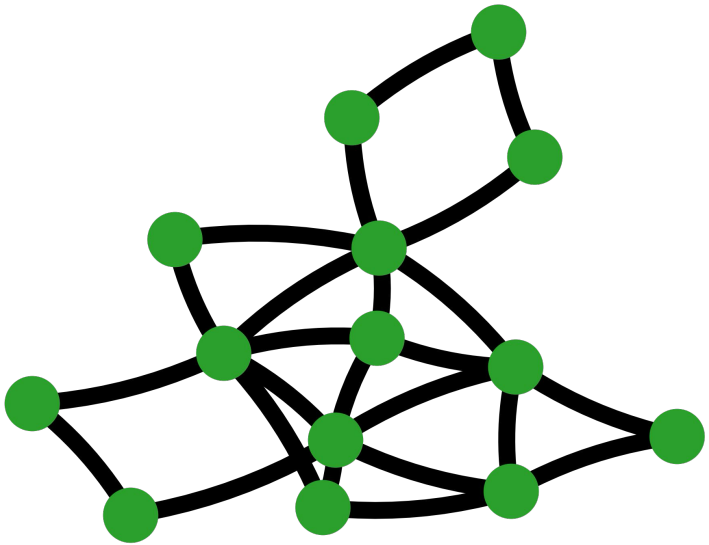


Heterogeneous



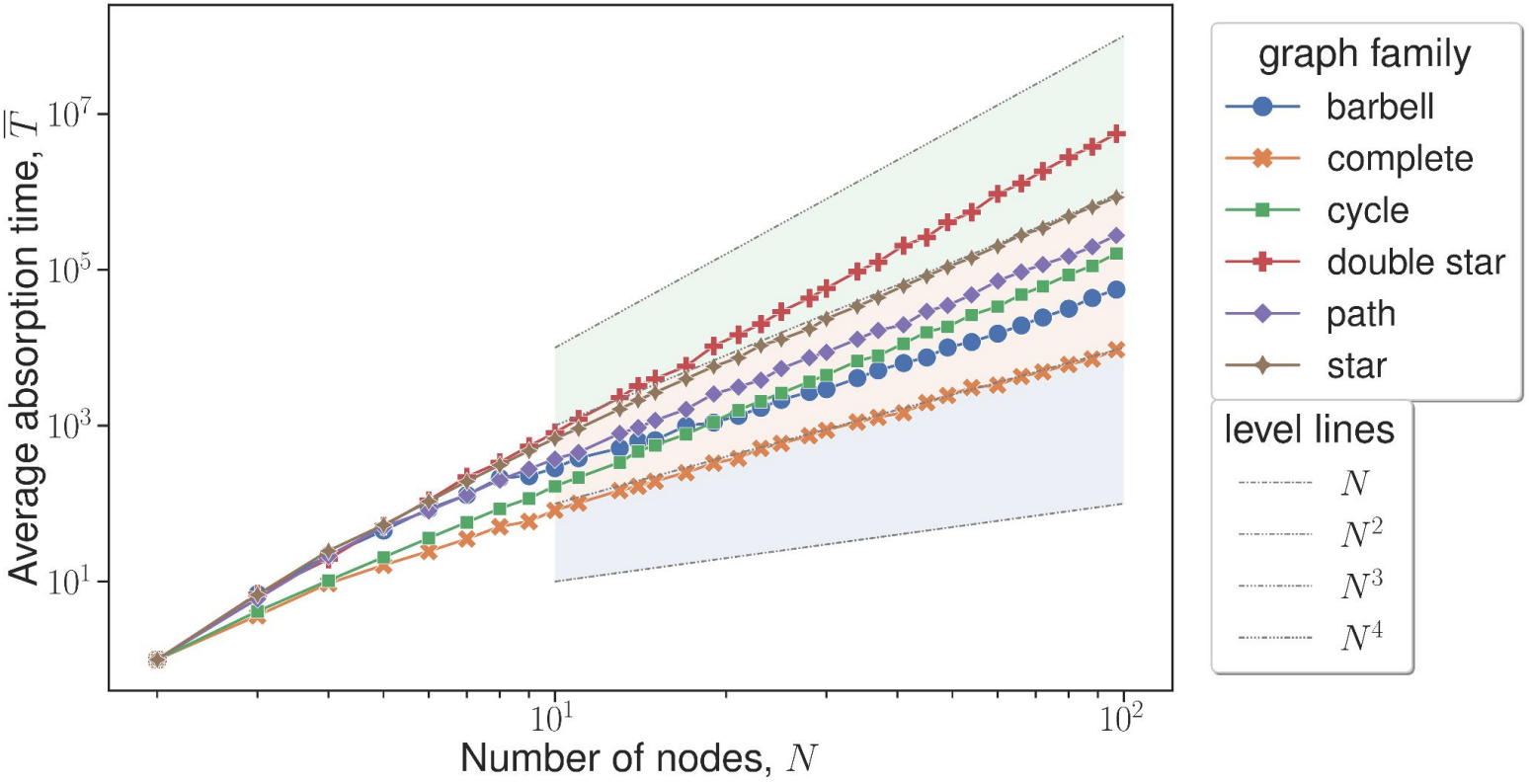


Homogeneous

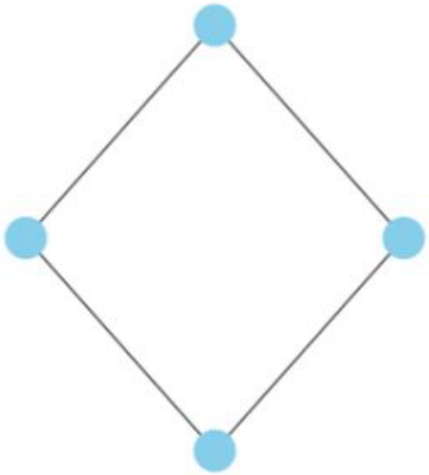


Interactive simulation

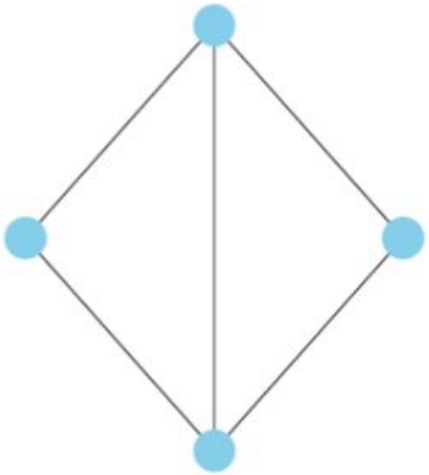
birth-death


Average absorption time, $\overline{T}$
10^7
10^5
10^3
10^1
10^1
10^2
Number of nodes, N
graph family
barbell
complete
cycle
double star
path
star
level lines
N
N^2
N^3
N^4

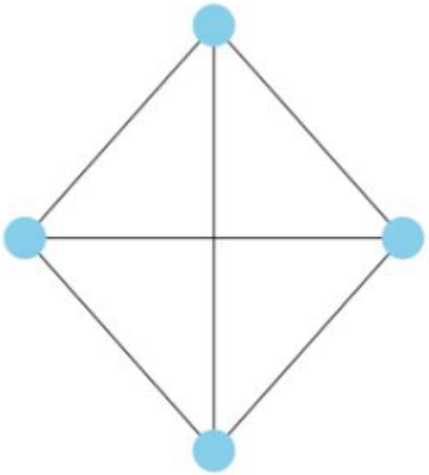
Removing edges, N=4, birth-death



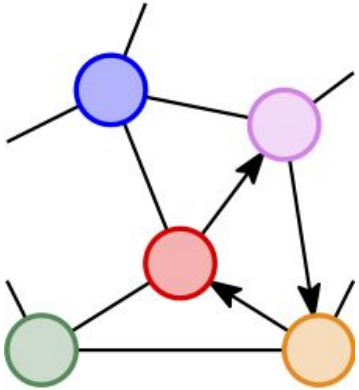
$T = 10$



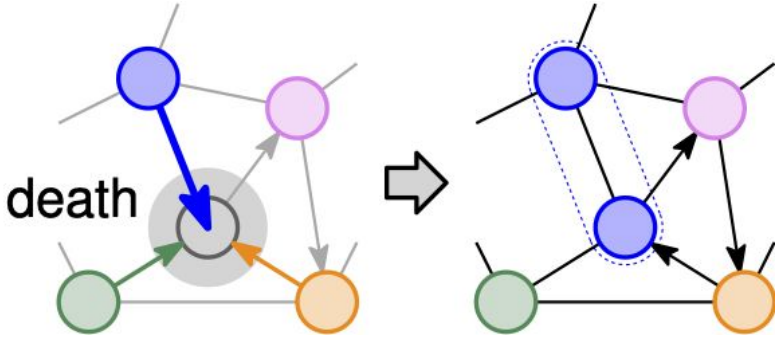
$T = 10.733$



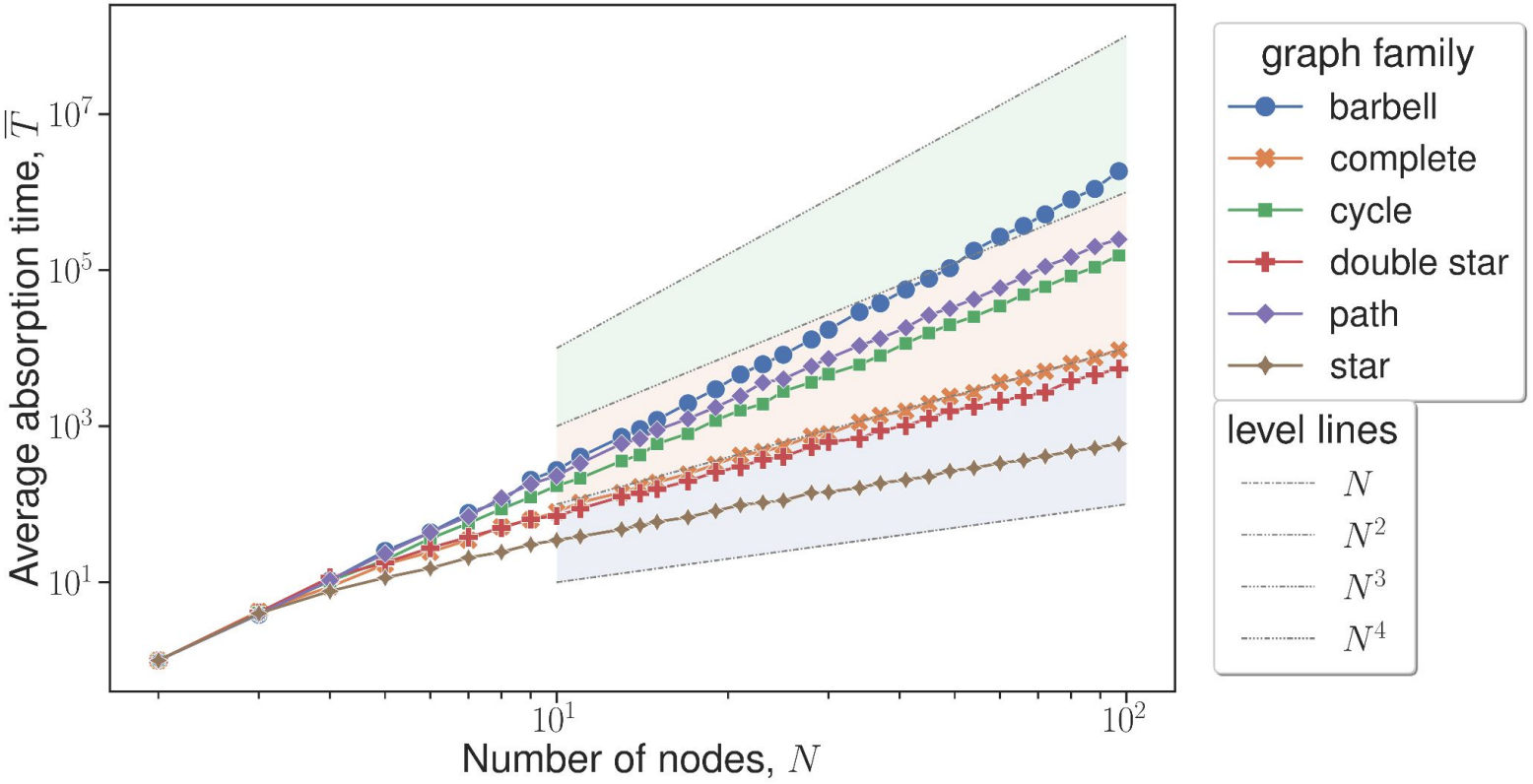
$T = 9$



death-birth (db)



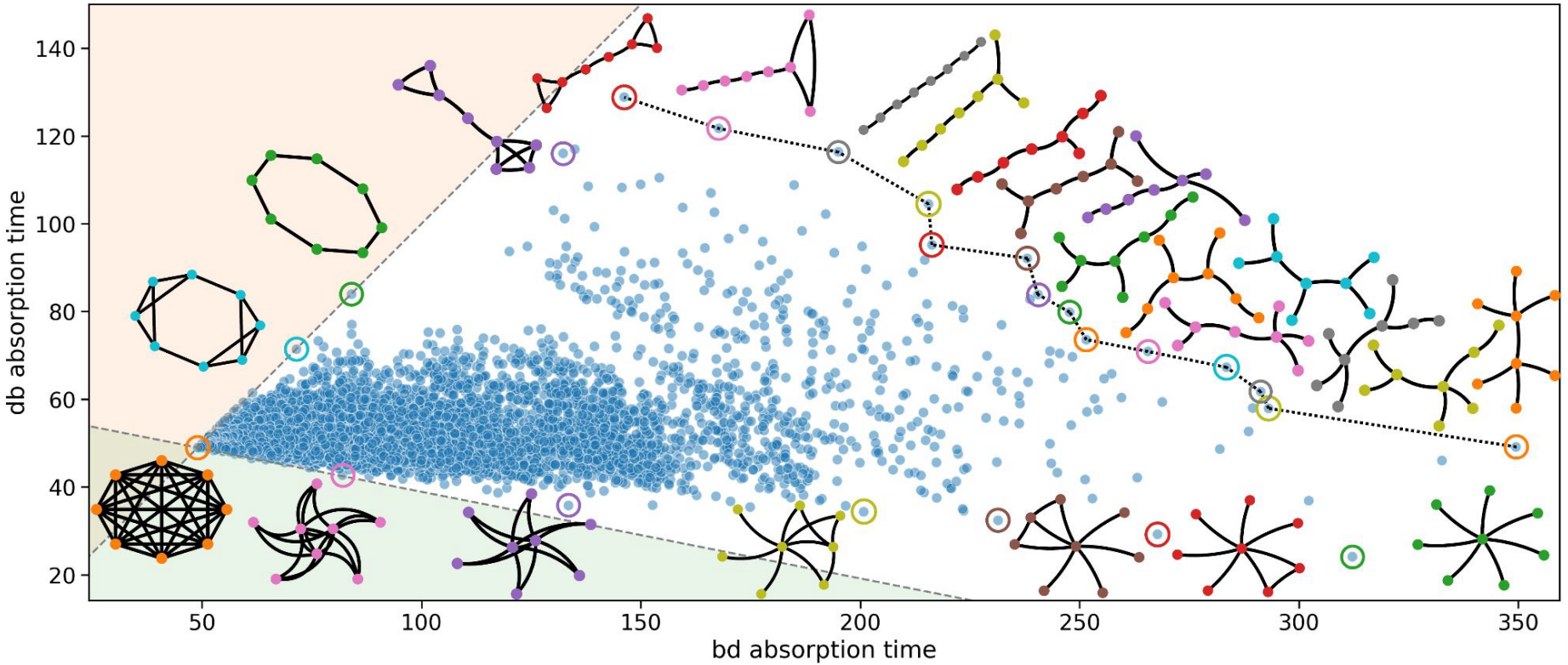
death-birth


Average absorption time, $\overline{T}$
10^7
10^5
10^3
10^1
10^1
10^2
Number of nodes, N
graph family
barbell
complete
cycle
double star
path
star
level lines
N
N^2
N^3
N^4

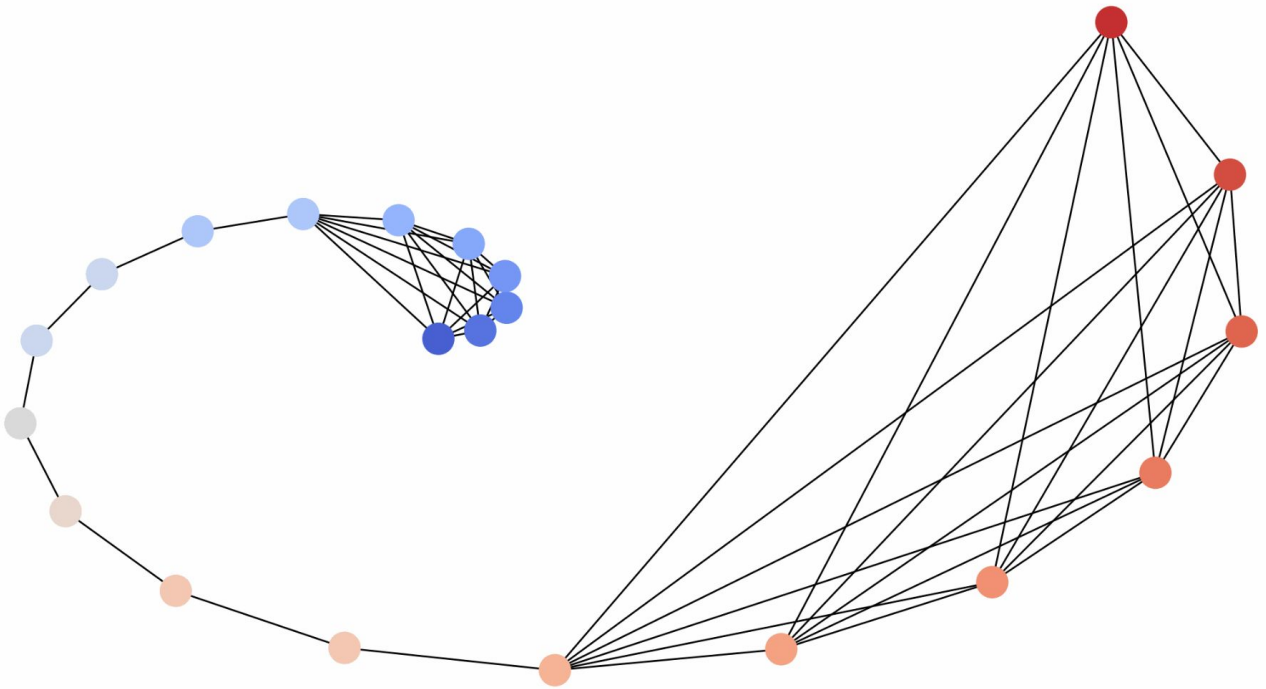
Times

	Graph family	bd time	db time
Undirected	Complete	$\Theta(N^2)$	$\Theta(N^2)$
	Cycle	$\Theta(N^3)$	$\Theta(N^3)$
	Star	$\Theta(N^3)$	$\Theta(N \log N)$
	Double star	$\Theta(N^4)$	–
	Barbell	–	$\Omega(N^4)$
	Undirected graph	$O(N^6 \log N), \Omega(N \log N)$	$O(N^5 \log N), \Omega(N \log N)$
Directed	Contracting star	$2^{\Theta(N \log N)}$	$2^{\Theta(N \log N)}$
	Directed graph	$2^{O(N \log N)}$	$2^{O(N \log N)}, \Omega(N \log N)$

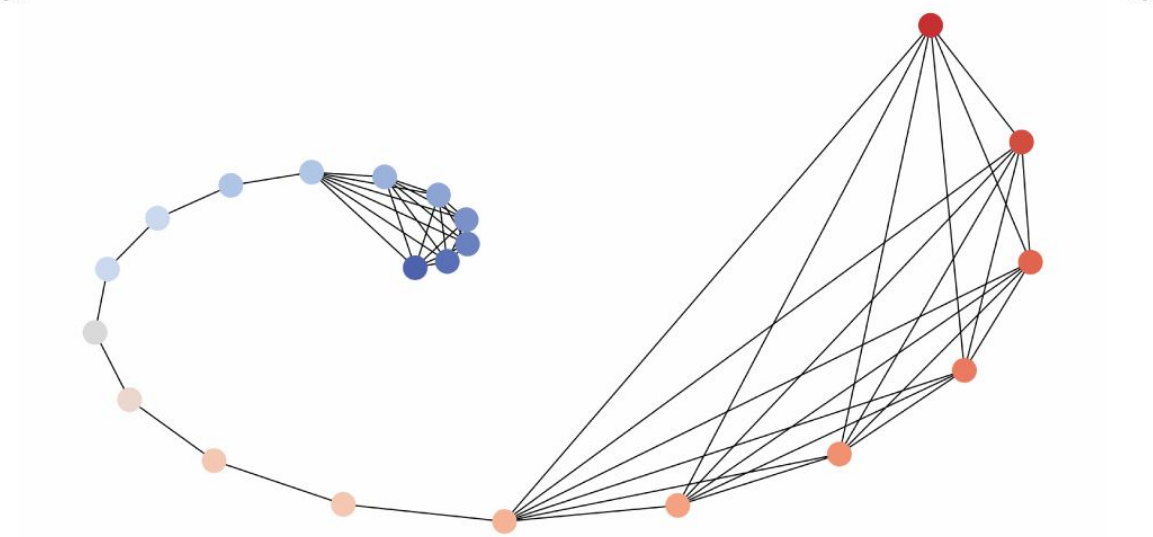
db vs bd, N=8

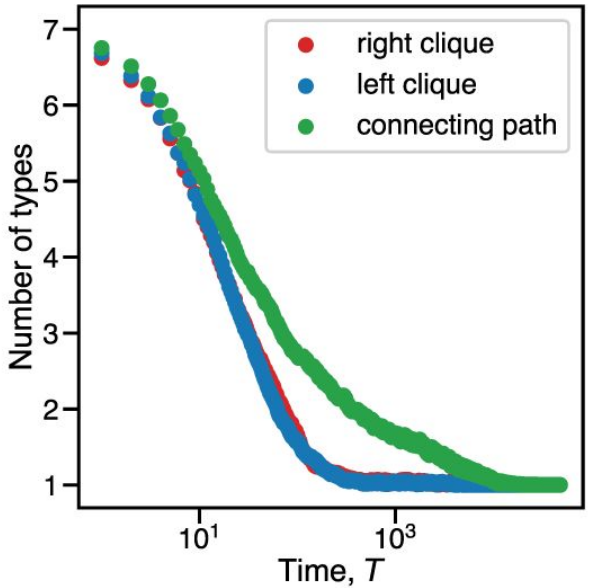

db absorption time
bd absorption time
20
40
60
80
100
120
140
50
100
150
200
250
300
350

Barbell simulation

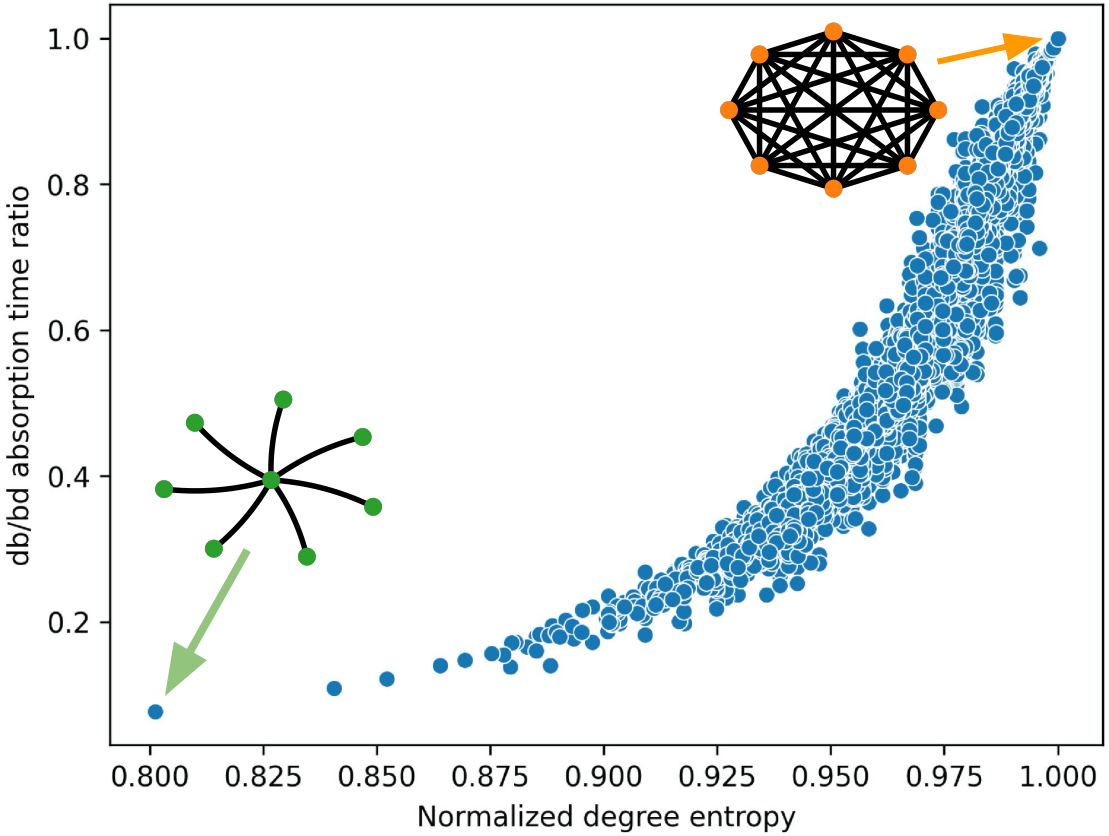


Barbell, N=21, death-birth

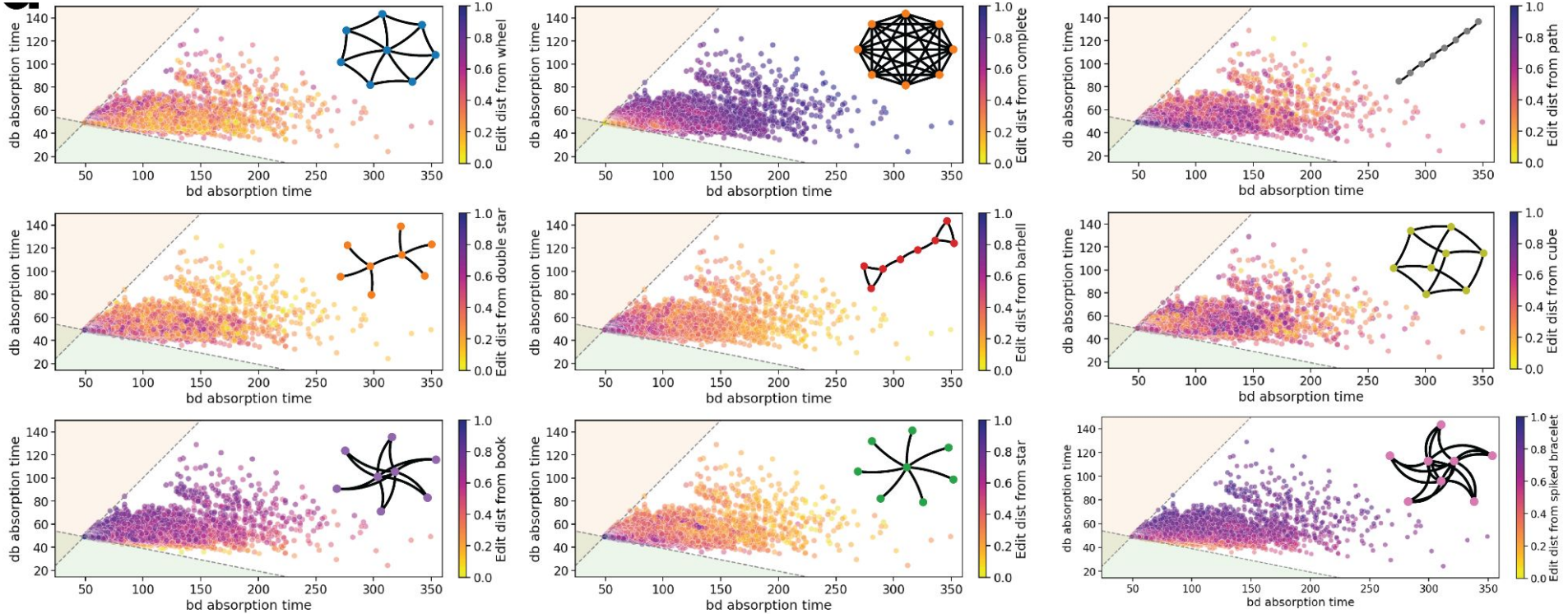


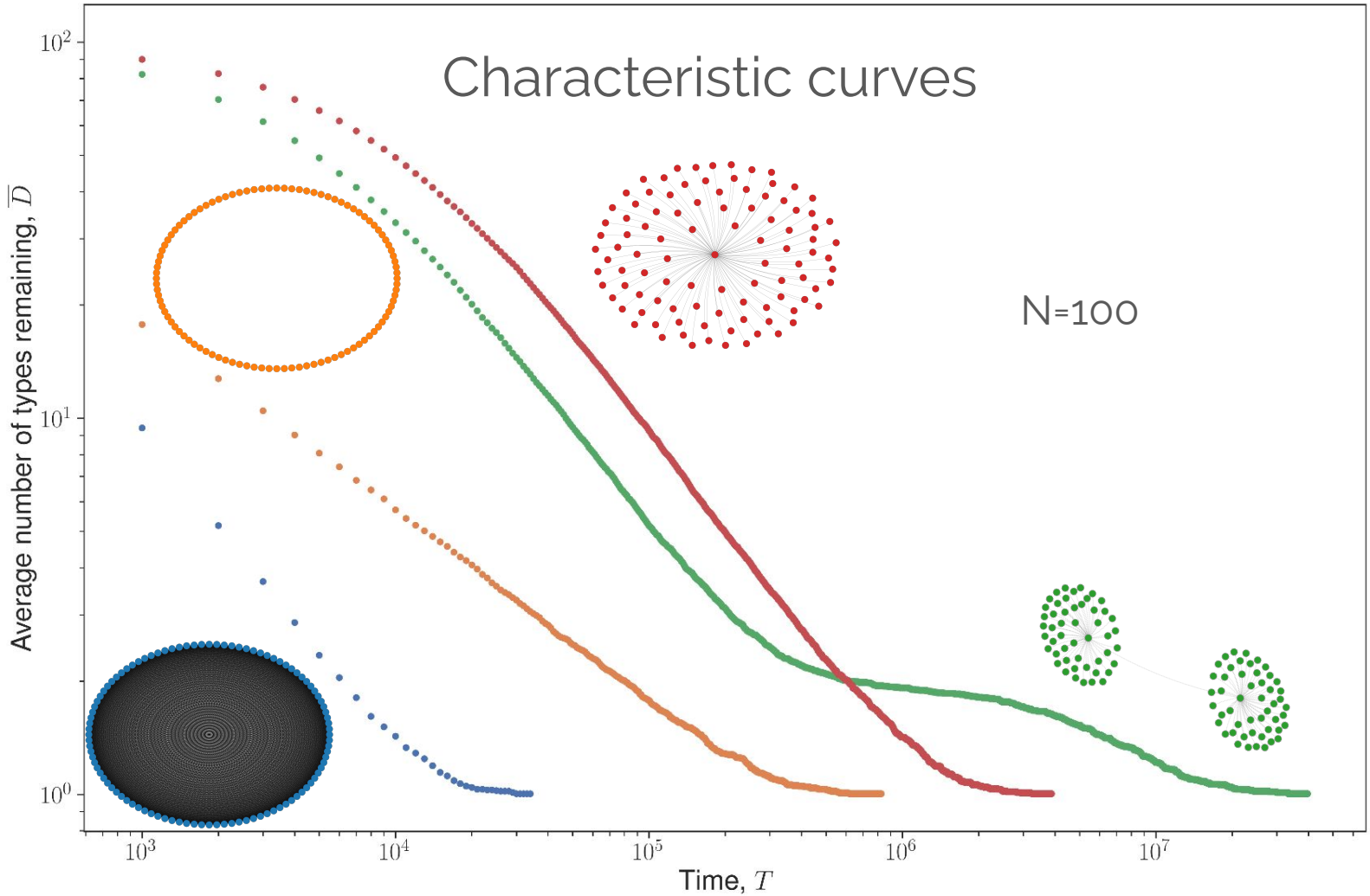


db/bd vs degree entropy, N=8

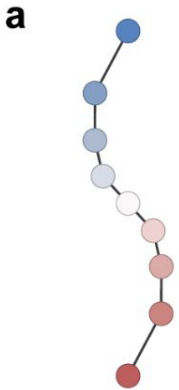


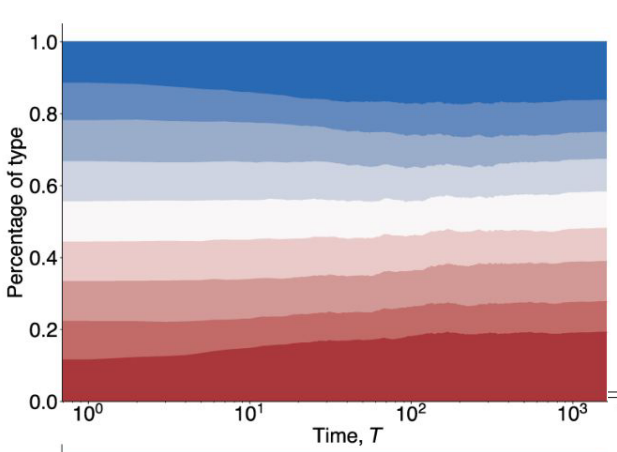
db vs bd, edit distance, N=8

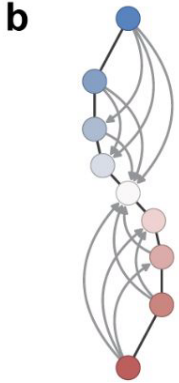


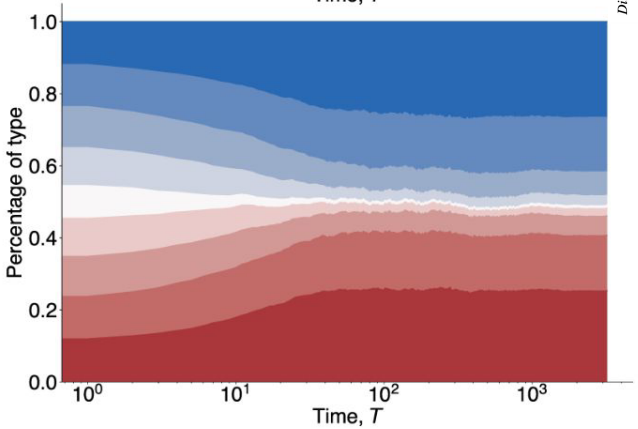

Characteristic curves
N=100
graph family
complete
cycle
double star
star
Average number of types remaining, $\overline{D}$
Time, T
10^2
10^1
10^0
10^3
10^4
10^5
10^6
10^7

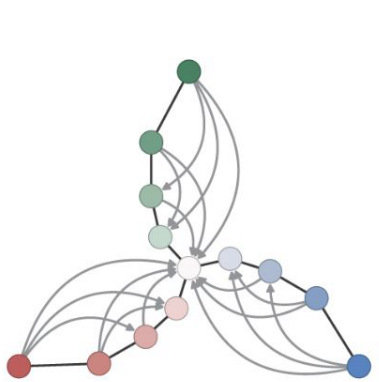
Contracting star, K=3





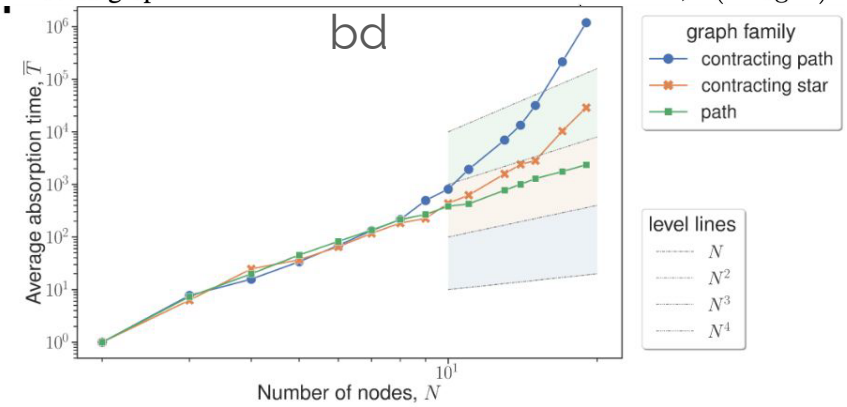






db

	Directed		
Contracting star		$2^{\Theta(N \log N)}$	$2^{\Theta(N \log N)}$
Directed graph		$2^{O(N \log N)}$	$2^{O(N \log N)}$, $\Omega(N \log N)$

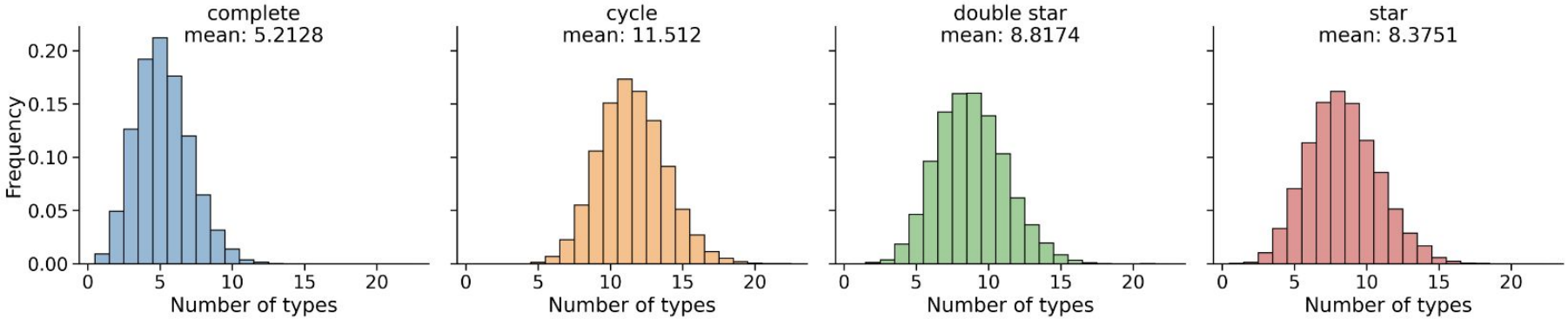


Citation

Brewster, et. al. Maintaining diversity in structured populations. *PNAS Nexus*, 4(8): pgaf252, 2025.

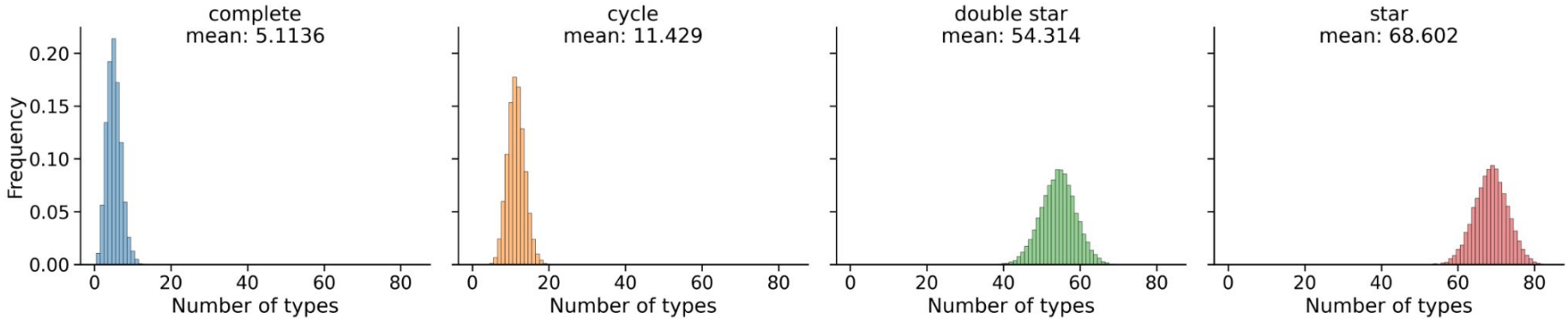
Birth-dependent mutation

$u = 0.01$

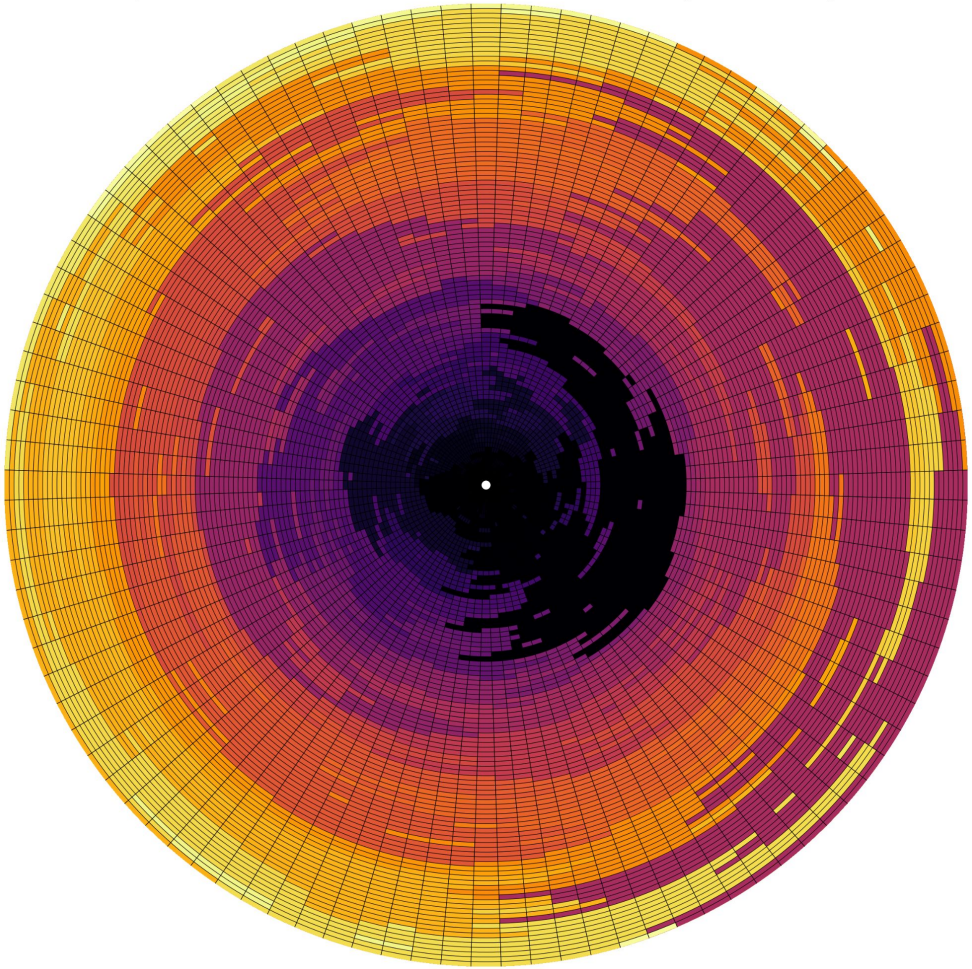


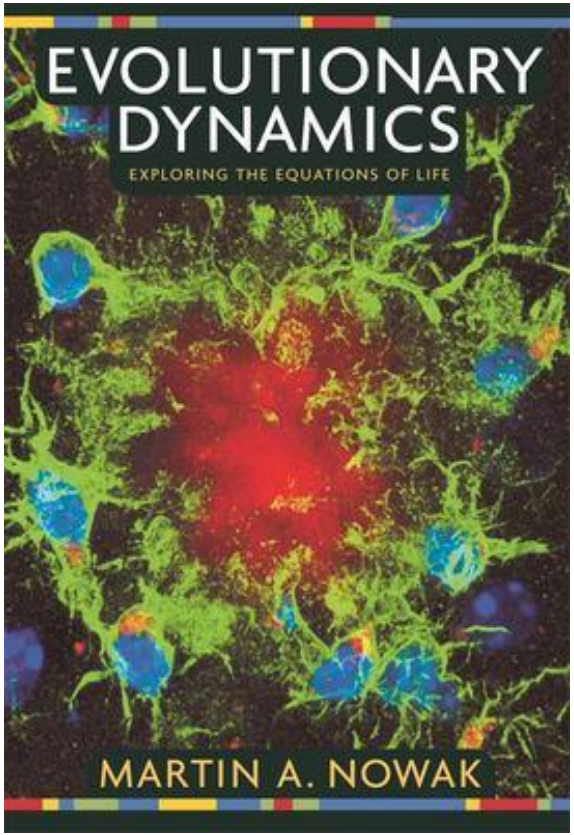
Birth-independent mutation

$u = 0.01$



Cycle N=100, birth mutation rate = 0.01, every 10000 steps

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MARTIN A. NOWAK