Evolution of cooperation

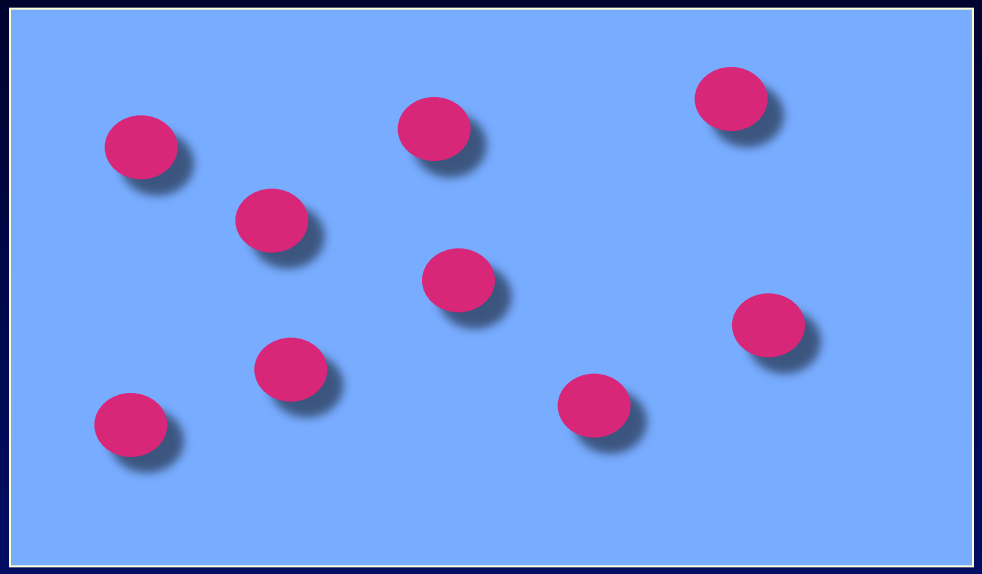
Martin Nowak, Harvard University

bioSpacetime

13700	Universe
4567	Sun
3500	chemical evidence of life on Earth
2100	bacterial fossils (simple multi-cellular)
1800	eucaria
600	complex multi-cellularity
120	insect societies
3	human language

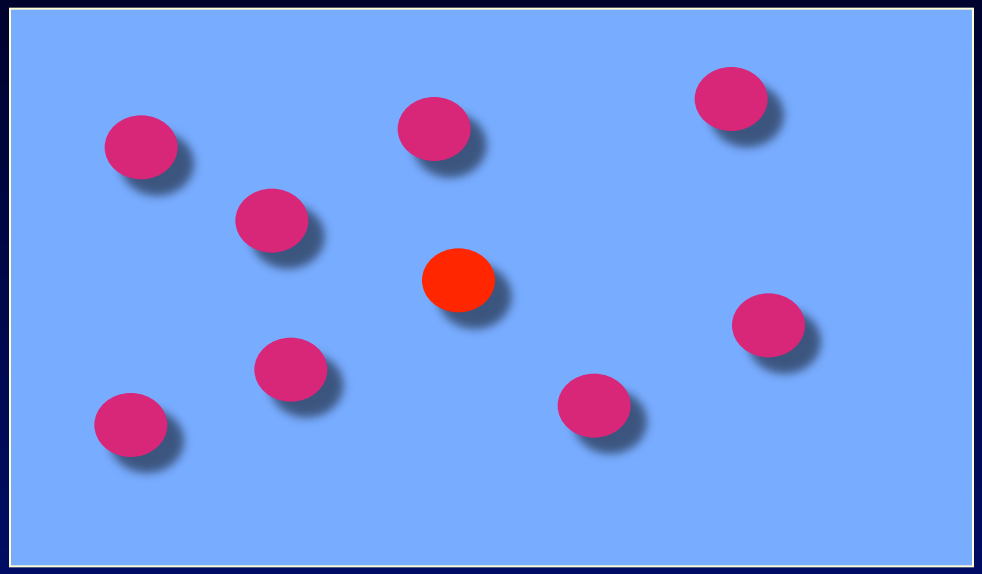
million years ago

What is it that evolves?

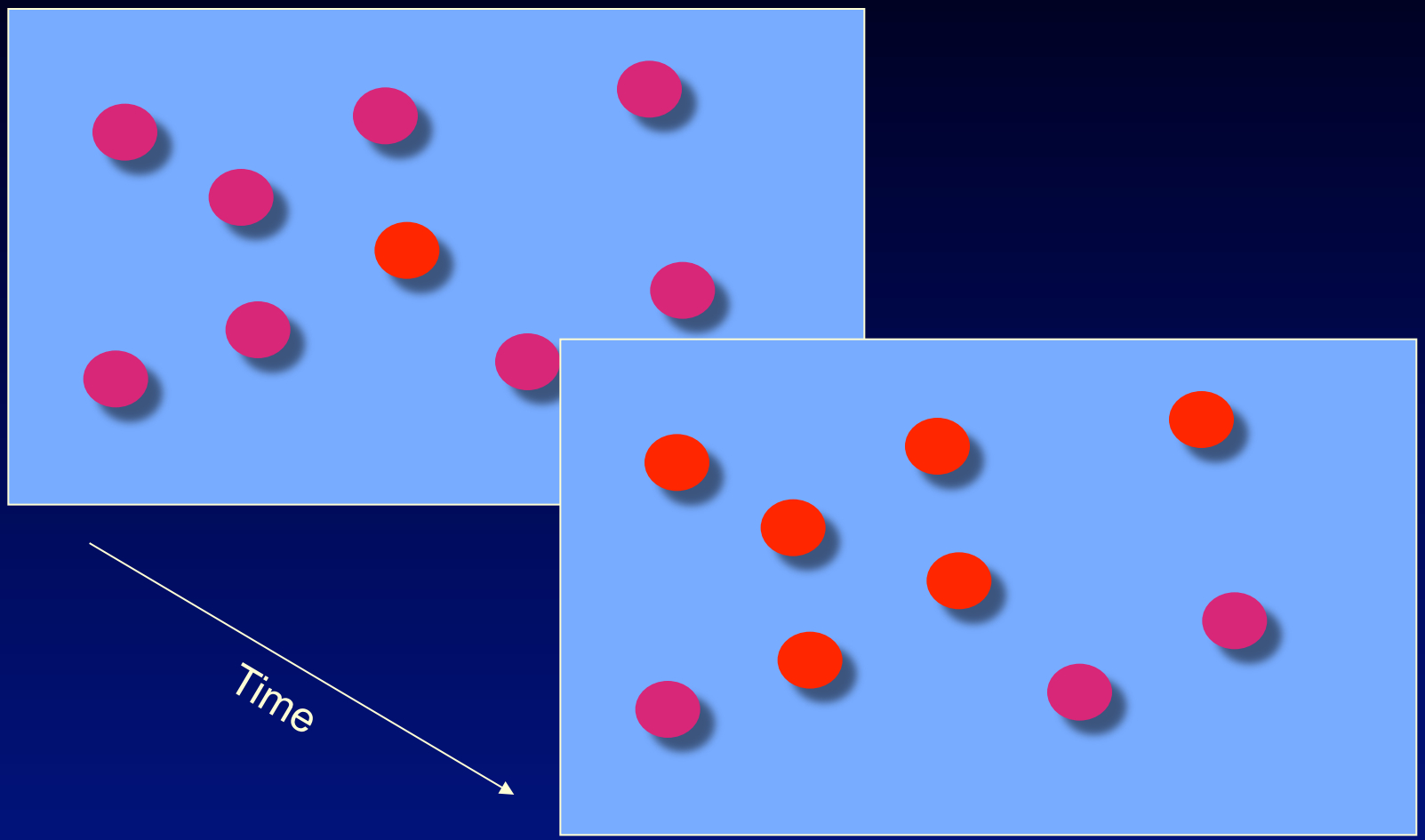


Populations of reproducing individuals

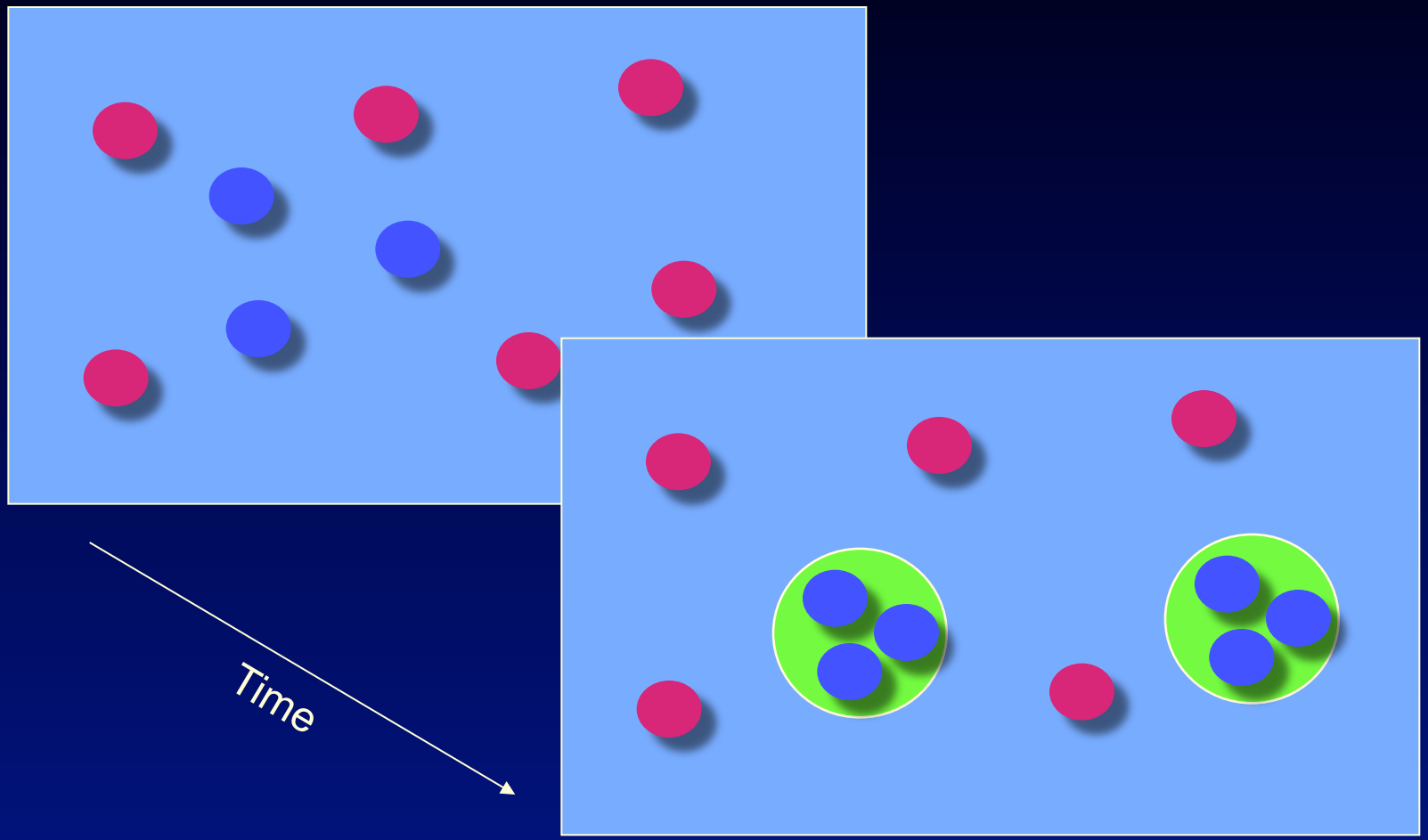
Mutation



Selection



Cooperation



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

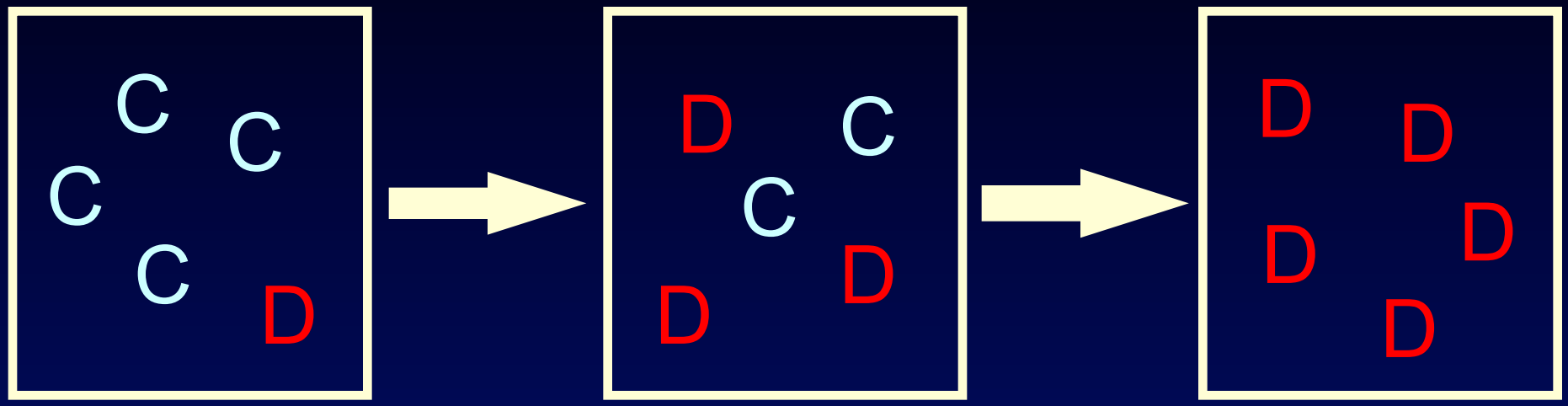
$b > c > 0$

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:

Kin selection
Direct reciprocity
Indirect reciprocity
Spatial selection
Group selection

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

Kin selection

Hamilton's rule

$$r > c / b$$

William Hamilton

r … coefficient of relatedness
c … cost of cooperation
b … benefit of cooperation

Inclusive fitness theory

Direct reciprocity

‘I help you, you help me.’

Robert Trivers, 1971

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, Fudenberg & Maskin

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

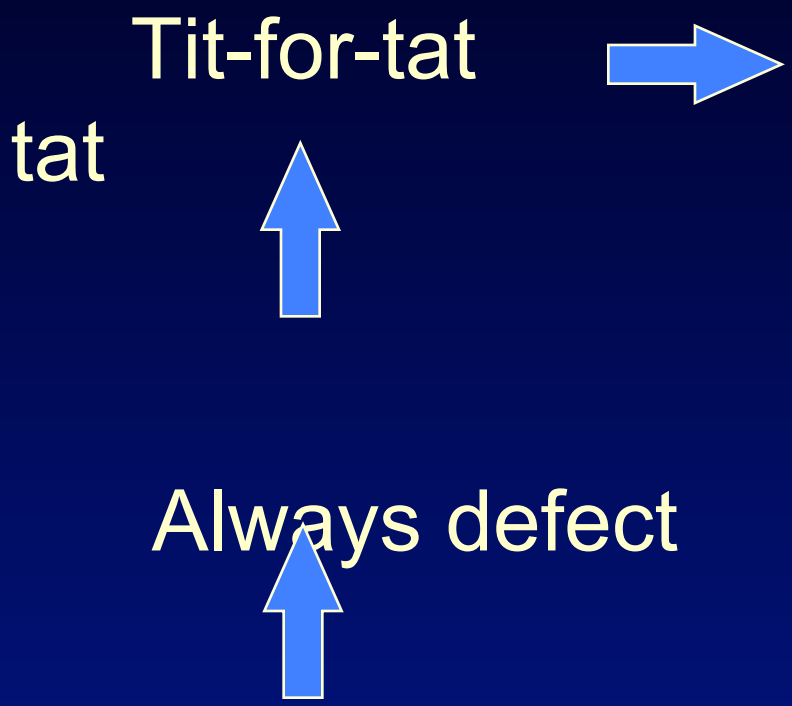
Let natural selection design a strategy

Tit-for-tat

Always defect

Random

Let natural selection design a strategy

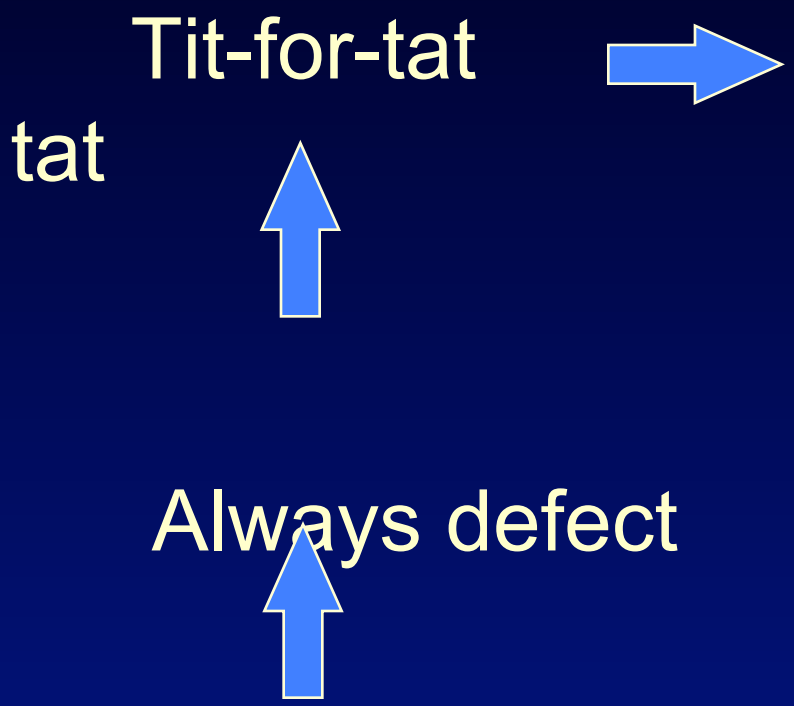


Generous Tit-for-tat

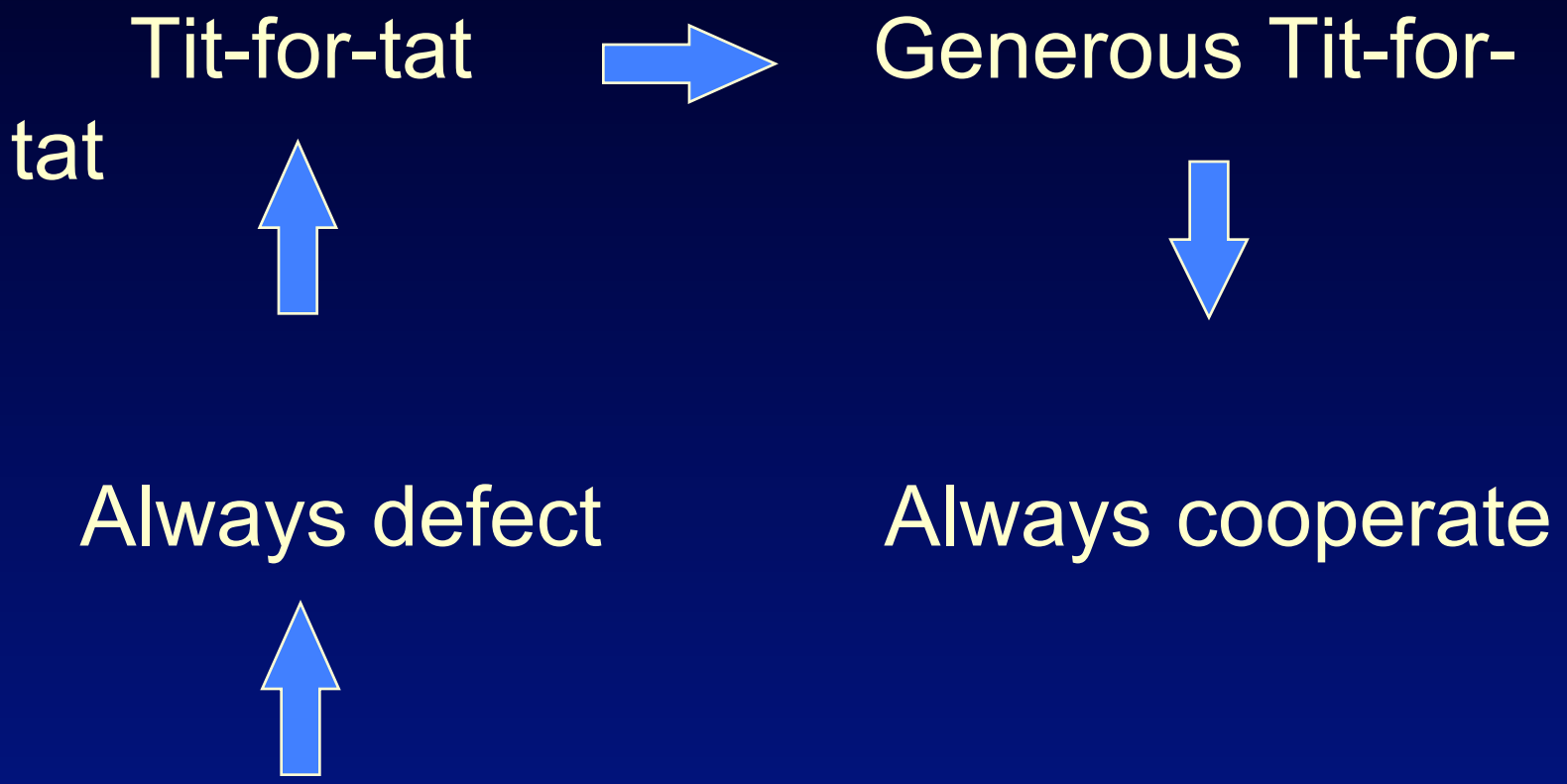
- I start with cooperation.
- If you cooperate, then I will cooperate.
- If you defect, then I will cooperate with a certain probability *(q = 1- c / b).*

Evolution of forgiveness

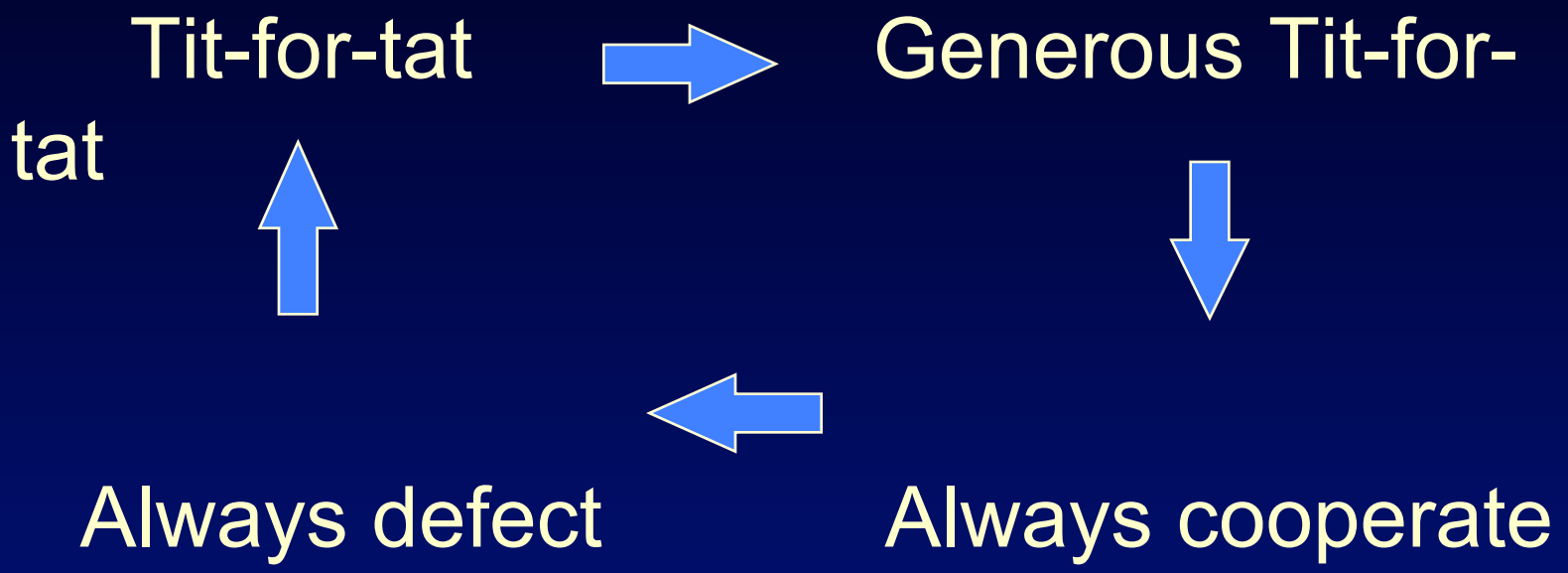
Let natural selection design a strategy



Let natural selection design a strategy

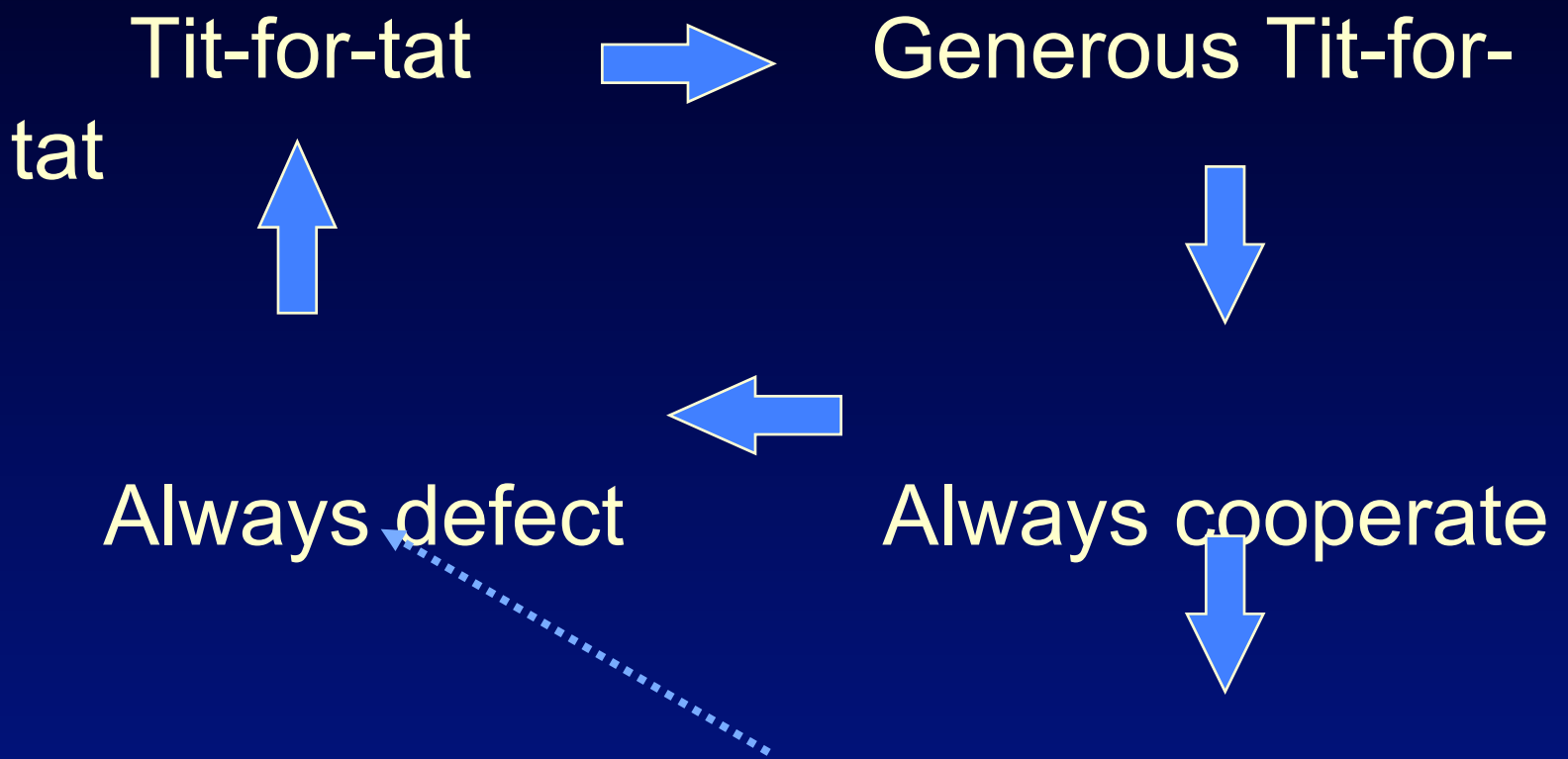


Let natural selection design a strategy



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

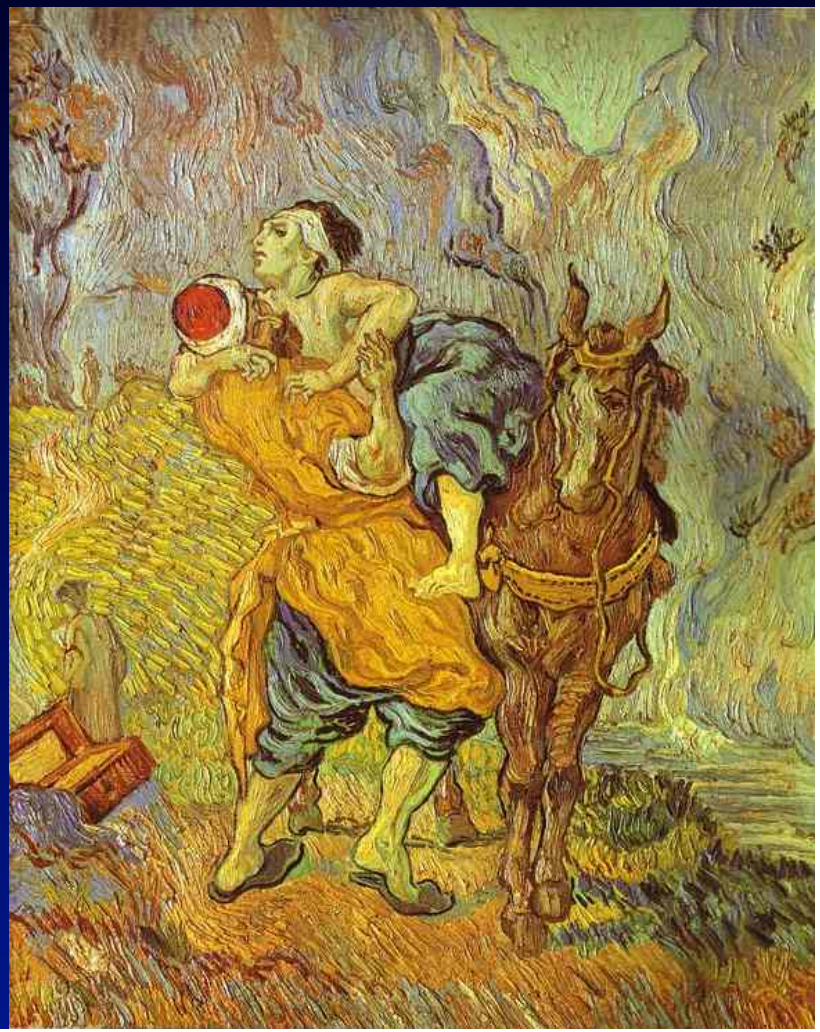
… allows the evolution of cooperation if

$w > c / b$

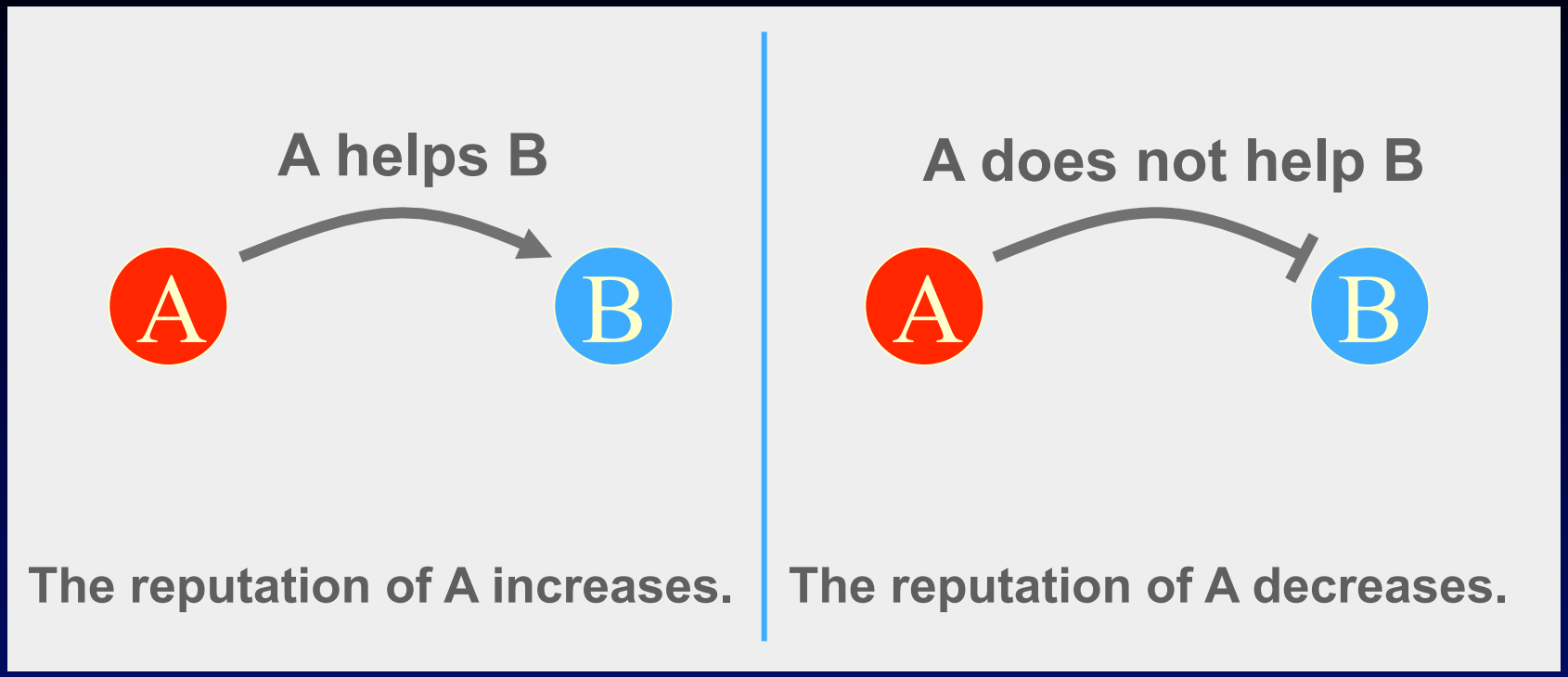
b…benefit
c…cost
w…probability of another round

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

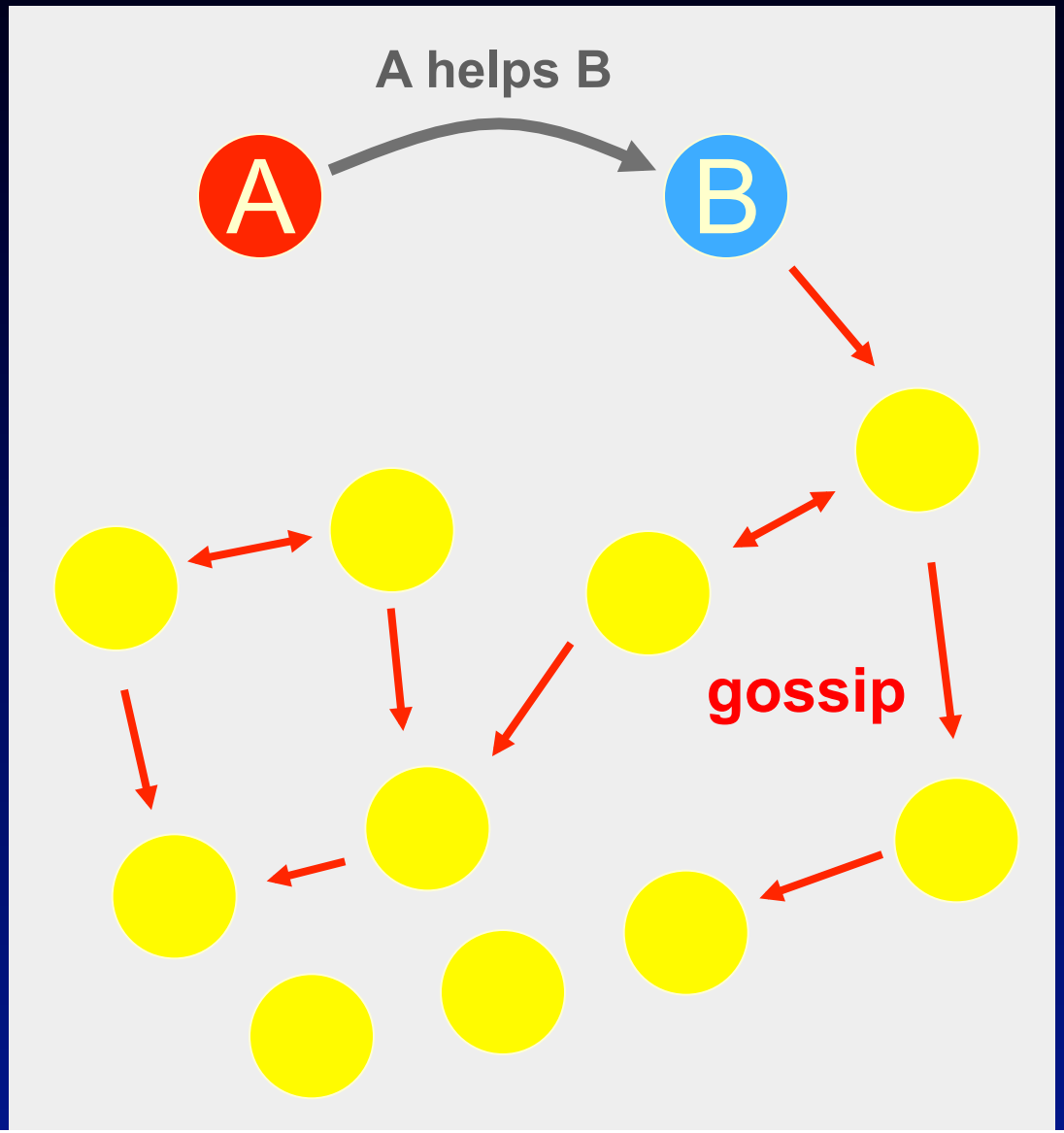
Experimental confirmation:

People help those who help others.

Helpful people have a higher payoff in the end.

Wedekind & Milinski, Science 2000

Gossip spreads reputation



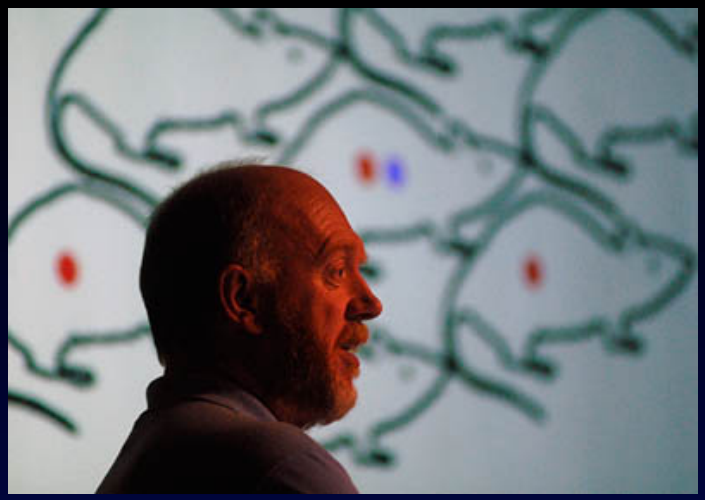
Observers

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.”

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 both social intelligence
and human language.

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

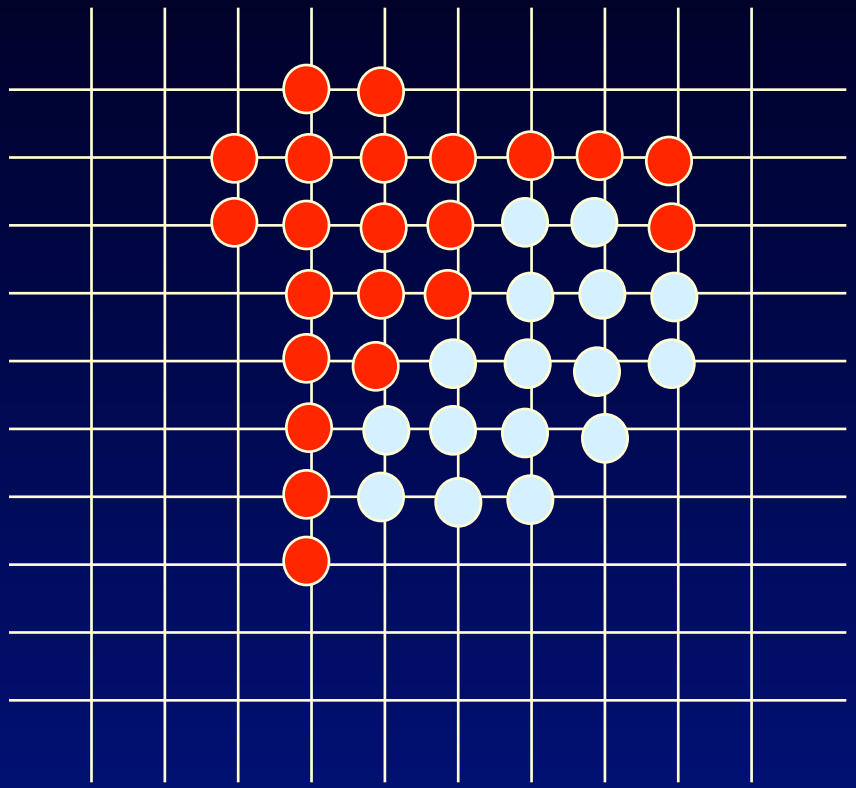
Spatial games

Games on graphs

Games in phenotype space

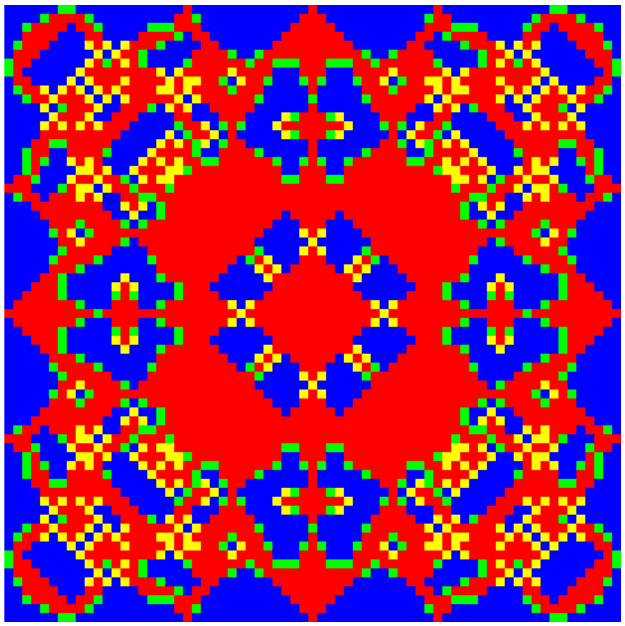
Games on sets

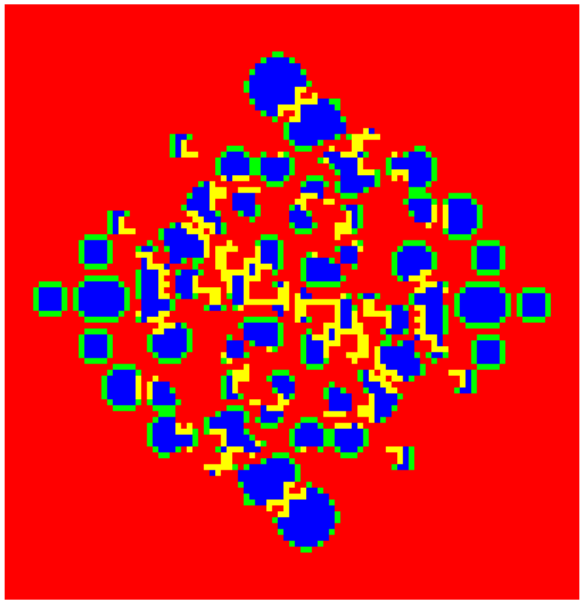
Spatial games

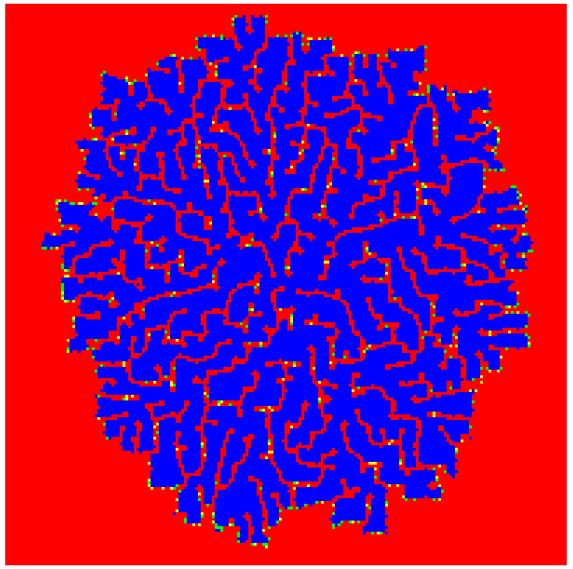


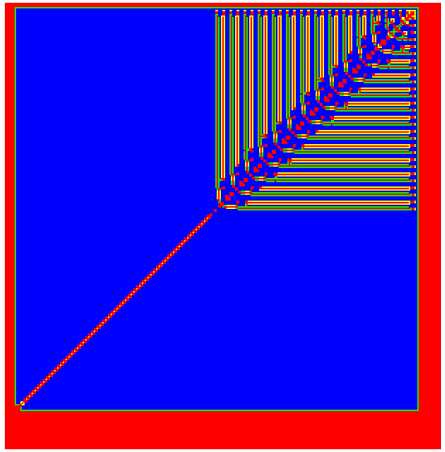
Cooperators
Defectors

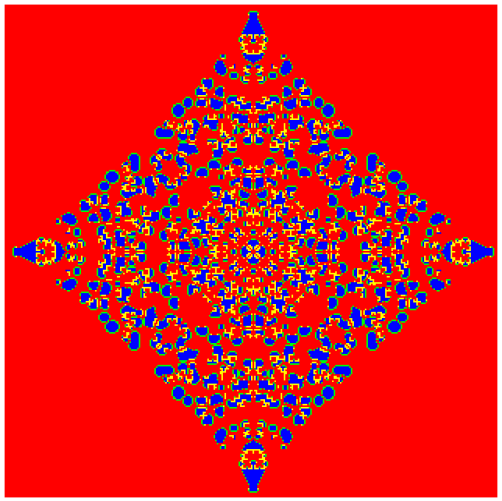
Nowak & May, Nature 1992

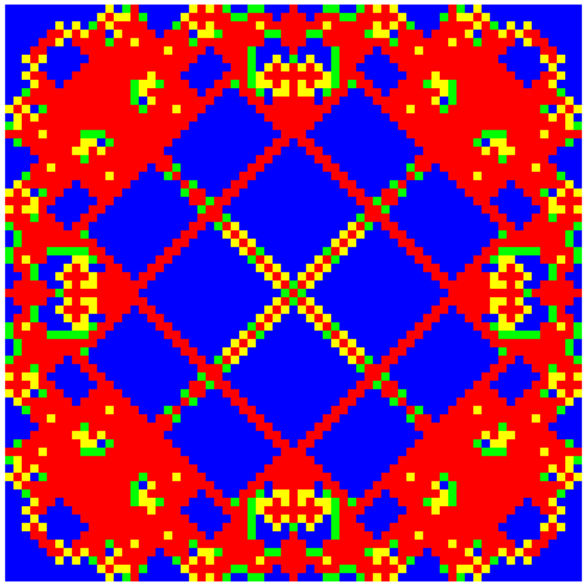




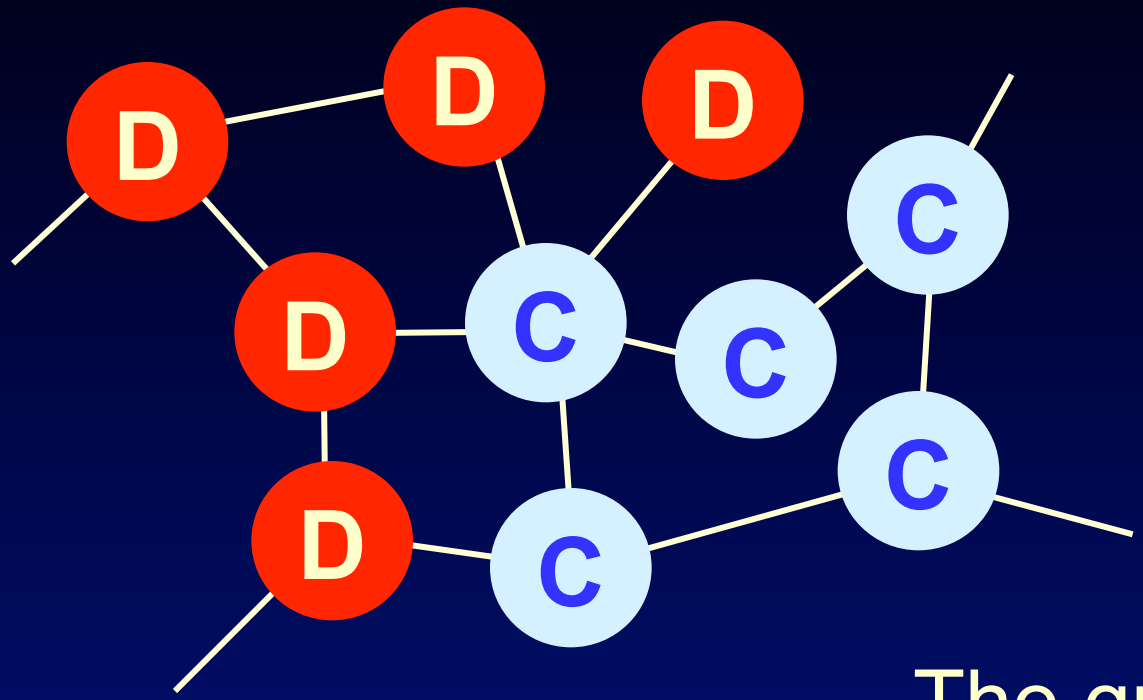








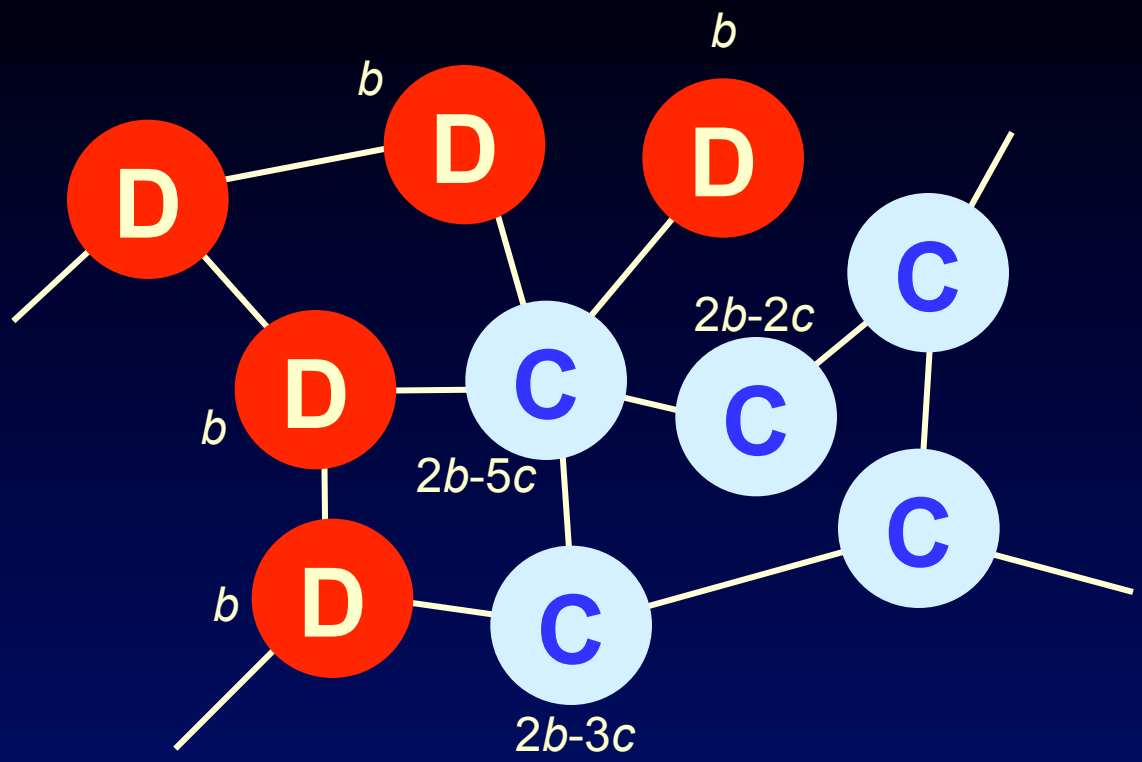
Games on graphs



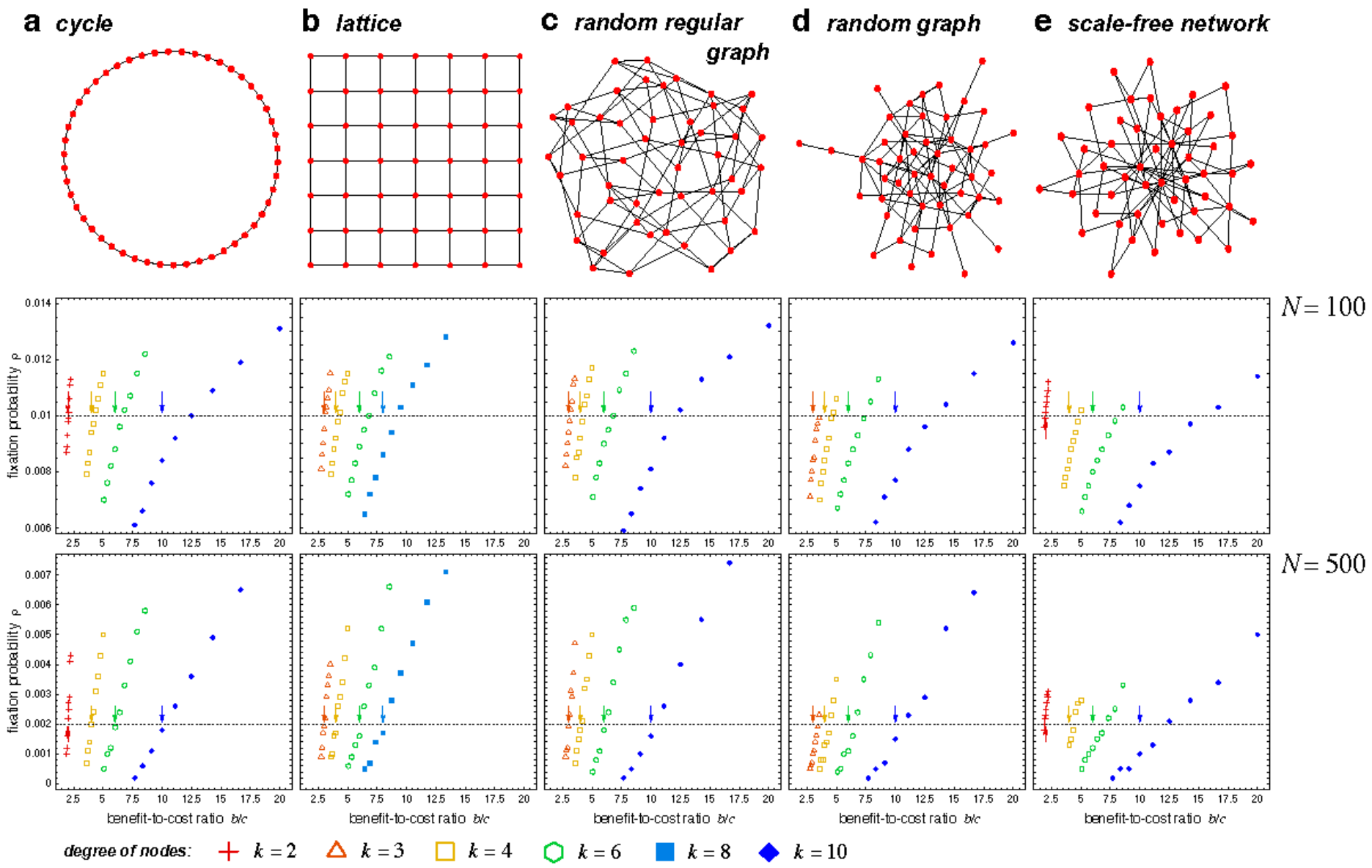
Cooperators
Defectors

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*.



simulations by Christoph Hauert

Graph selection favors cooperation if

$$b / c > k$$

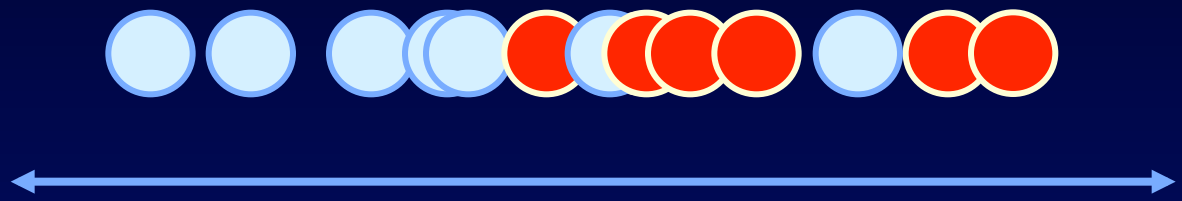
k…(average) number of neighbors

weak selection

Ohtsuki et al, Nature 2006

Games in phenotype space

Cooperation by similarity

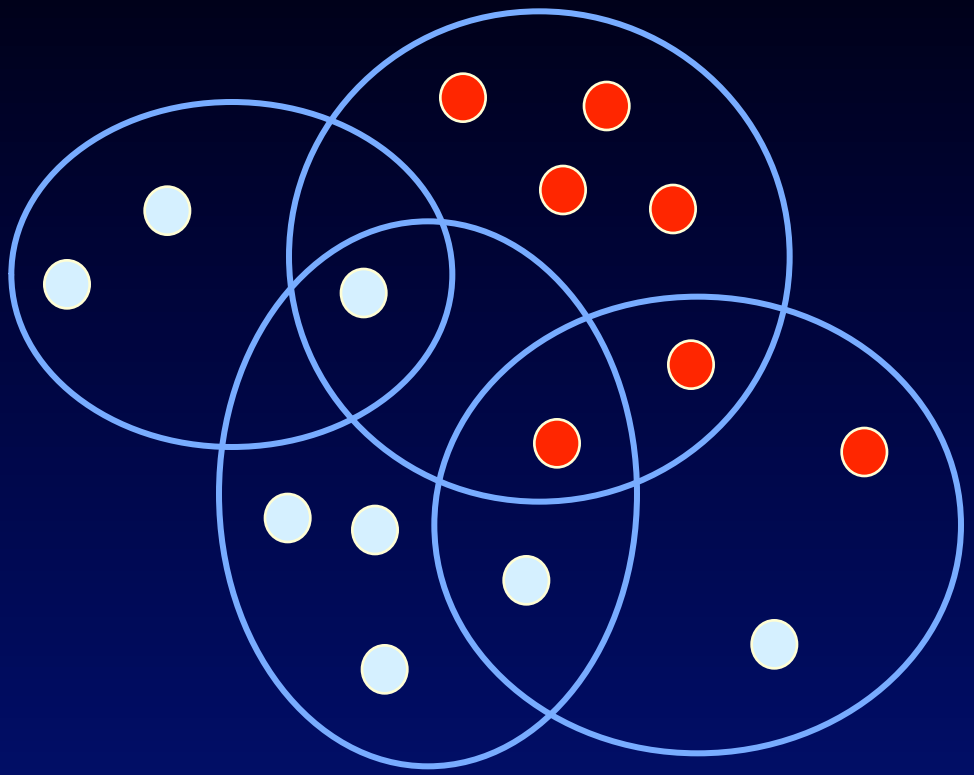


Phenotype space

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

Antal et al, PNAS 2009

Evolutionary set theory



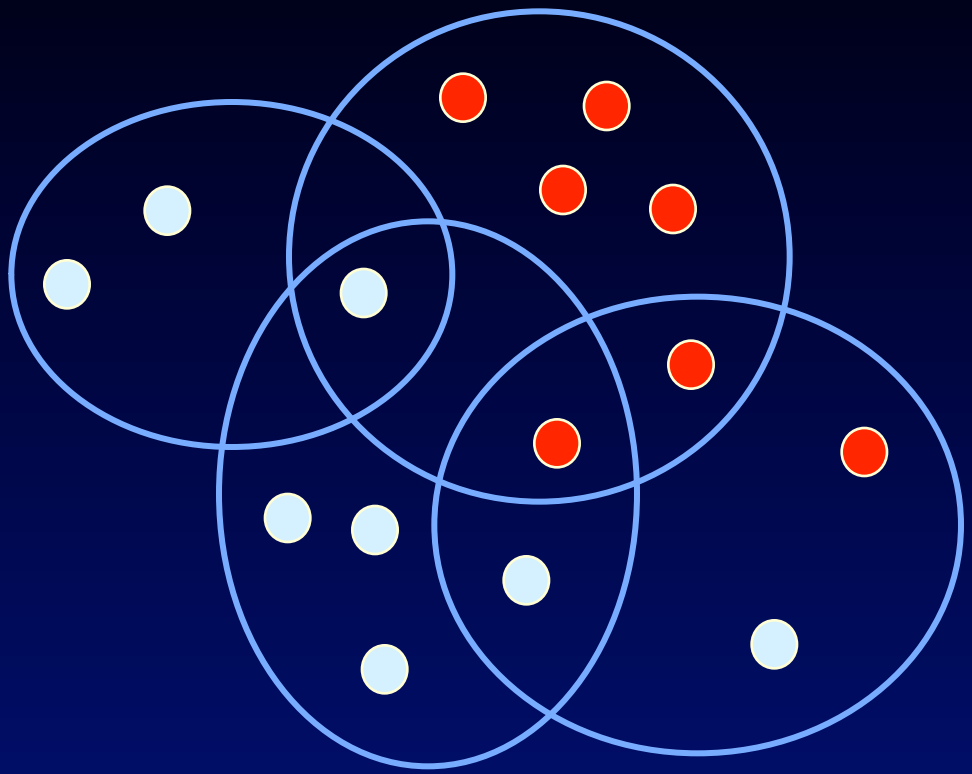
People belong to sets.

People interact with others in the same sets.

People adopt strategy and set membership of successful individuals.

Tarnita et al, PNAS 2009

Evolutionary set theory

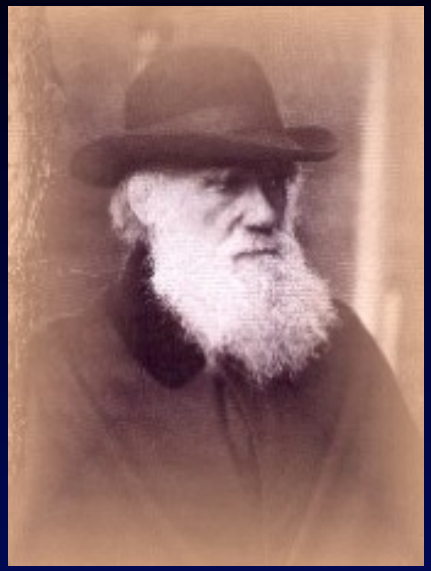


N people
M sets
K set memberships per person
u…strategy mutation rate
v…set mutation rate

$$\frac{b}{c} > 1 + 2\sqrt{\frac{K^*}{M}}$$

Tarnita et al, PNAS 2009

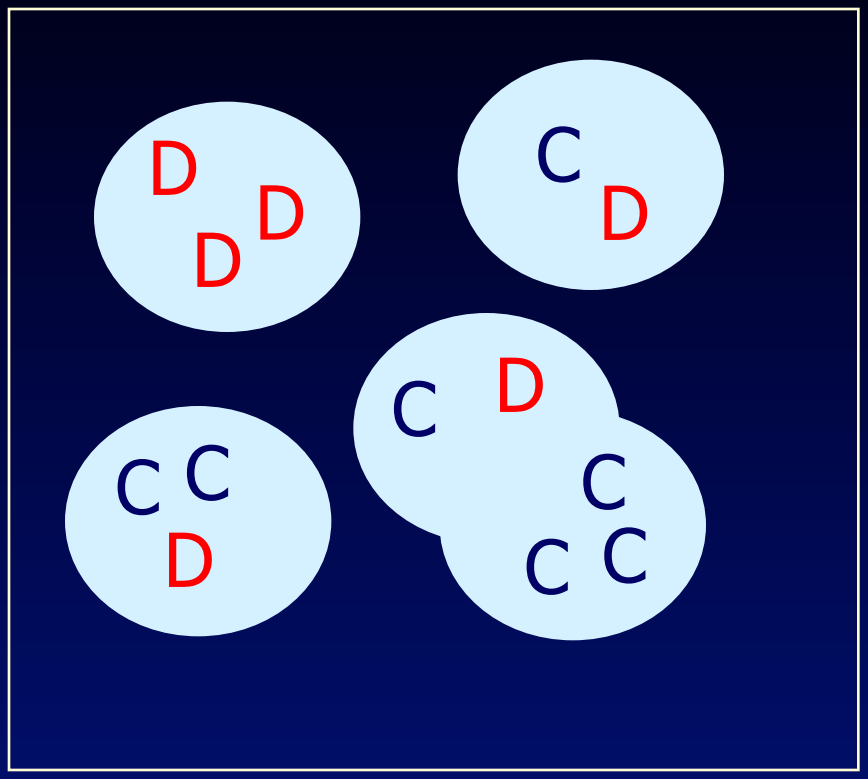
Group selection



‘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.

Traulsen & Nowak, PNAS 2006

Group selection

favors cooperators if

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

n … group size
m … number of groups

Traulsen & Nowak, PNAS 2006

Five mechanisms for cooperation

Kin selection : cooperate with genetic relatives.

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.

Five rules for cooperation

Kin selection : $b / c > 1 / r$ — r…coefficient of relatedness

Direct reciprocity : $b / c > 1 / w$ — w…probability of another round

Indirect reciprocity : $b / c > 1 / q$ — q…probability to know reputation

Spatial selection : $b / c > k$ — k…number of neighbors (for graphs)

Group selection : $b / c > 1 + n / m$ — n…group size; m…number of groups

The “sigma theorem”

For any game

	A	B
A	a	b
B	c	d

In any structured population, A is more abundant than B for weak selection if

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

Tarnita et al, 2009

The critical benefit to cost ratio

	C	D
C	b-c	$-c$
D	b	0

$$\left(\frac{b}{c}\right)^{*} = \frac{\sigma+1}{\sigma-1}$$

Tarnita et al, 2009

Five rules for cooperation

Kin selection : $b / c > 1 / r$ *r*…coefficient of relatedness

Direct reciprocity : $b / c > 1 / w$ *w*…probability of another round

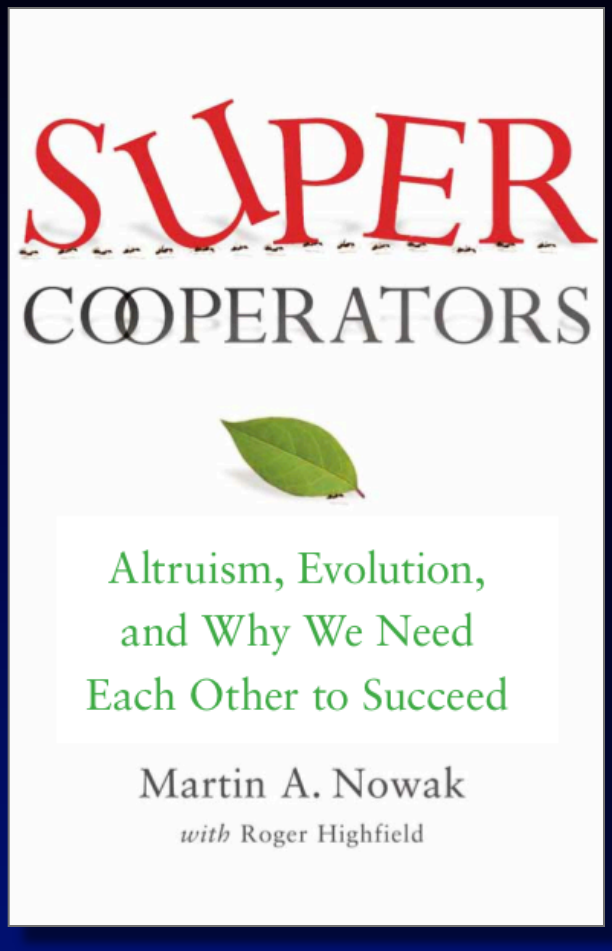
Indirect reciprocity : $b / c > 1 / q$ *q*…probability to know reputation

Spatial selection : $b / c > (s+1)/(s-1)$ s…structure coefficient

Group selection : $b / c > 1 + n / m$ *n*…group size
m…number of groups

Cooperators

- Ben Allen (Harvard)
- Tibor Antal (Edinburgh)
- Peter Blake (Harvard)
- Ivana Bozic (Harvard)
- Anna Dreber (Stockholm)
- Feng Fu (Harvard)
- Drew Fudenberg (Harvard)
- Christoph Hauert (UBC)
- Lorens Imhof (Bonn)
- Erez Lieberman (Harvard)
- Hisashi Ohtsuki (Tokyo)
- David Rand (Harvard)
- Karl Sigmund (Vienna)
- Corina Tarnita (Harvard)
- Christine Taylor (Princeton)
- Arne Traulsen (Ploen)


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

March 2011

Inclusive fitness theory rests on fragile assumptions.

Inclusive fitness theory is not needed to explain the evolution of eusociality (or other social phenomena).

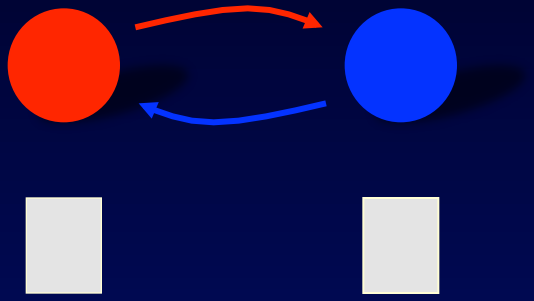
Once "fitness" is calculated every aspect of "relatedness" is included.

Nowak, Tarnita, Wilson, "The evolution of eusociality", Nature 2010

What is inclusive fitness?

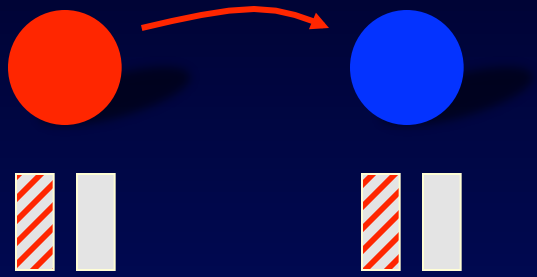
Hamilton: “Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects; unit for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins,....and finally zero for all neighbours whose relationship can be considered negligibly small.”

The standard approach (evolutionary game theory)



interaction
=> payoff
=> fitness
=> reproduction

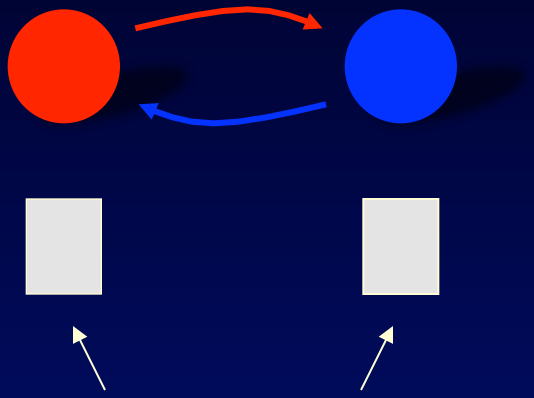
The inclusive fitness approach



only one actor is considered

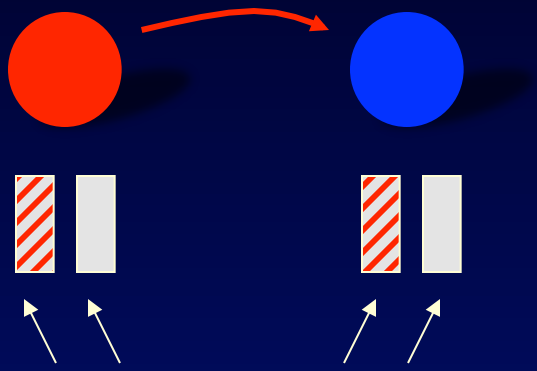
IF = the effect of this action on his own payoff + the effect of this actions on the payoff of others x relatedness

The standard approach for social evolution (evolutionary game theory)

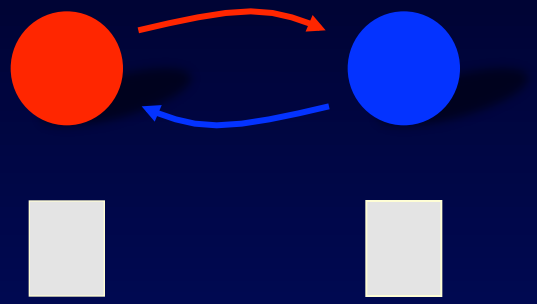


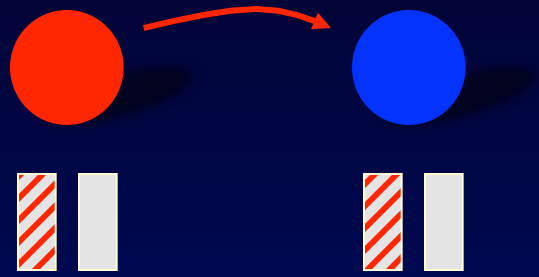
fitness

The inclusive fitness approach:



fitness subdivided into additive components





The two methods cannot be equivalent.

In general it is not possible to decompose fitness
into additive components caused by individual actions.

Inclusive fitness is not simple: