On the emergence of cooperation

in social and biological systems

José A. Cuesta

Grupo Interdisciplinar de Sistemas Complejos
Universidad Carlos III de Madrid
Spain

A basic unsolved question

1 July 2005

Science

Vol. 309 No. 5731
Pages 1–204 $10

125 Questions:
WHAT DON'T WE KNOW?

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WHAT DON'T WE KNOW?

Special Section

How Did Cooperative Behavior Evolve

When Charles Darwin was working out his grand theory on the origin of species, he was perplexed by the fact that animals from ants to people form social groups in which most individuals work for the common good. This seemed to run counter to his proposal that individual fitness was key to surviving over the long term.

By the time he wrote *The Descent of Man*, however, he had come up with a few explanations. He suggested that natural selection could encourage altruistic behavior among kin so as to improve the reproductive potential of the "family." He also introduced the idea of reciprocity: that unrelated but familiar individuals would help each other out if both were altruistic. A century of work with dozens of social species has borne out his ideas to some degree, but the details of how and why cooperation evolved remain to be worked out. The answers could help explain human behaviors that seem to make little sense from a strict evolutionary perspective, such as risking one's life to save a drowning stranger.

Animals help each other out in many ways. In social species from honeybees to naked mole rats, kinship fosters cooperation: Females forgo reproduction and instead help the dominant female with her young. And common agendas help unrelated individuals work together. Male chimpanzees, for example, gang up against predators, protecting each other at a potential cost to themselves.

Generosity is pervasive among humans. Indeed, some anthropologists argue that the evolution of the tendency to trust one's relatives and neighbors helped humans become Earth's dominant vertebrate: The ability to work together provided our early ancestors more food, better protection, and better childcare, which in turn improved reproductive success.

However, the degree of cooperation varies. "Cheaters" can gain a leg up on the rest of humankind, at least in the short term. But cooperation prevails among many species, suggesting that this behavior is a better survival strategy, over the long run, despite all the strife among ethnic, political, religious, even family groups now rampant within our species.

Evolutionary biologists and animal behavior researchers are searching out the genetic basis and molecular drivers of cooperative behaviors, as well as the physiological, environmental, and behavioral impetus for sociality. Neuroscientists studying mammals from voles to hyenas are discovering key correlations between brain chemicals and social strategies.

Others with a more mathematical bent are applying evolutionary game theory, a modeling approach developed for economics, to quantify cooperation and predict behavioral outcomes under different circumstances. Game theory has helped reveal a seemingly innate desire for fairness: Game players will spend time and energy to punish unfair actions, even though there's nothing to be gained by these actions for themselves. Similar studies have shown that even when two people meet just once, they tend to be fair to each other. Those actions are hard to explain, as they don't seem to follow the basic tenet that cooperation is really based on self-interest.

The models developed through these games are still imperfect. They do not adequately consider, for example, the effect of emotions on cooperation. Nonetheless, with game theory's increasing sophistication, researchers hope to gain a clearer sense of the rules that govern complex societies.

Together, these efforts are helping social scientists and others build on Darwin's observations about cooperation. As Darwin predicted, reciprocity is a powerful fitness tactic. But it is not a pervasive one.

Modern researchers have discovered that a good memory is a prerequisite: It seems reciprocity is practiced only by organisms that can keep track of those who are helpful and those who are not. Humans have a great memory for faces and thus can maintain lifelong good—or hard—feelings toward people they don't see for years. Most other species exhibit reciprocity only over very short time scales, if at all.

Limited to his personal observations, Darwin was able to come up with only general rationales for cooperative behavior. Now, with new insights from game theory and other promising experimental approaches, biologists are refining Darwin's ideas and, bit by bit, hope that one day they will understand just what it takes to bring out our cooperative spirit.

–ELIZABETH PENNISI

Why do we dream?
Freud thought dreaming provides an outlet for our unconscious desires. Now, neuroscientists suspect that brain activity during REM sleep—when dreams occur—is crucial for learning. Is the experience of dreaming just a side effect?

JUPITER IMAGES

Why are there critical periods for language learning?
Monitoring brain activity in young children—including infants—may shed light on why children pick up languages with ease while adults often struggle to learn train station basics in a foreign tongue.

Do pheromones influence human behavior?
Many animals use airborne chemicals to communicate, particularly when mating. Controversial studies have hinted that humans too use pheromones. Identifying them will be key to assessing their sway on our social lives.

CORBIS

continued >>

How do general anesthetics work?
Scientists are chipping away at the drugs' effects on individual neurons, but understanding how they render us unconscious will be a tougher nut to crack.

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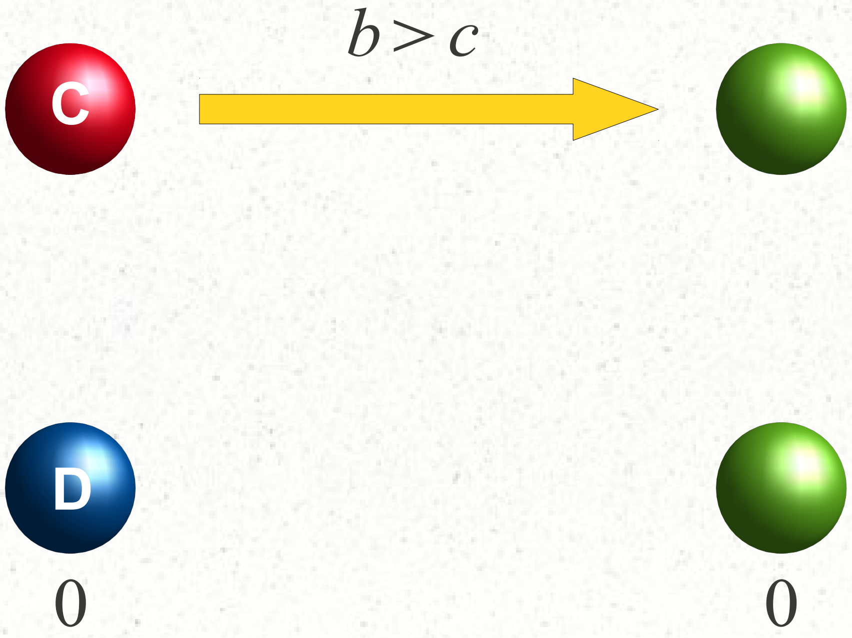
The problem



$b > c$

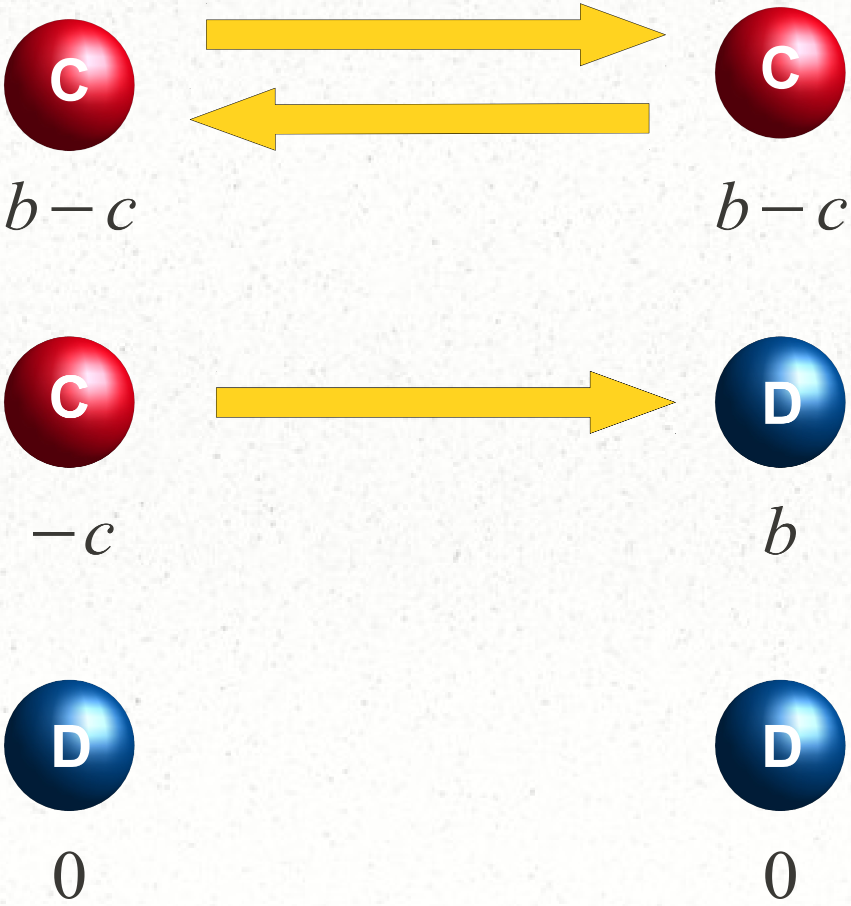
C

D

0

0

The problem

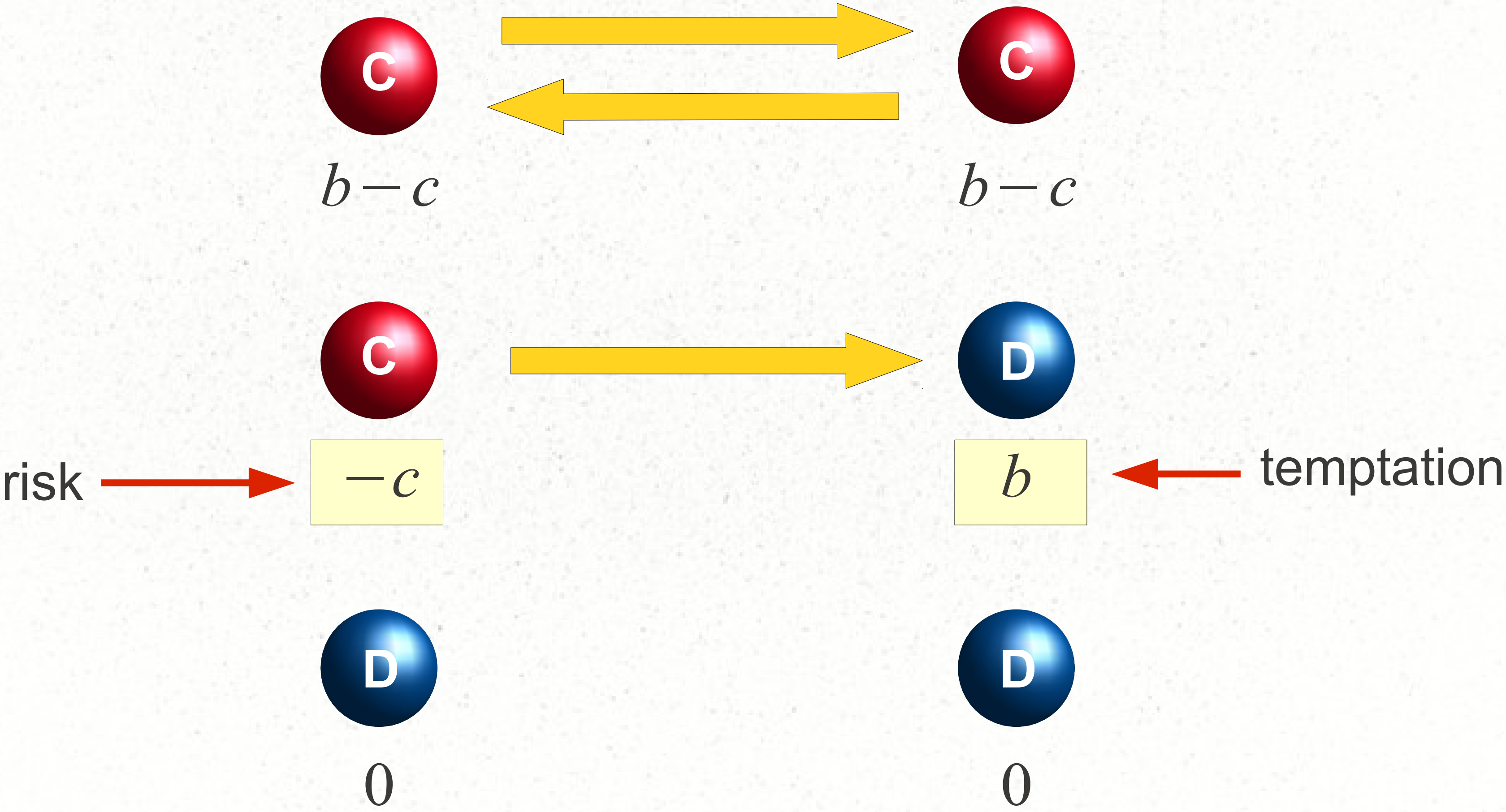


$b-c$ $b-c$

$-c$ b

0 0

The problem



C C

$b-c$ $b-c$

C D

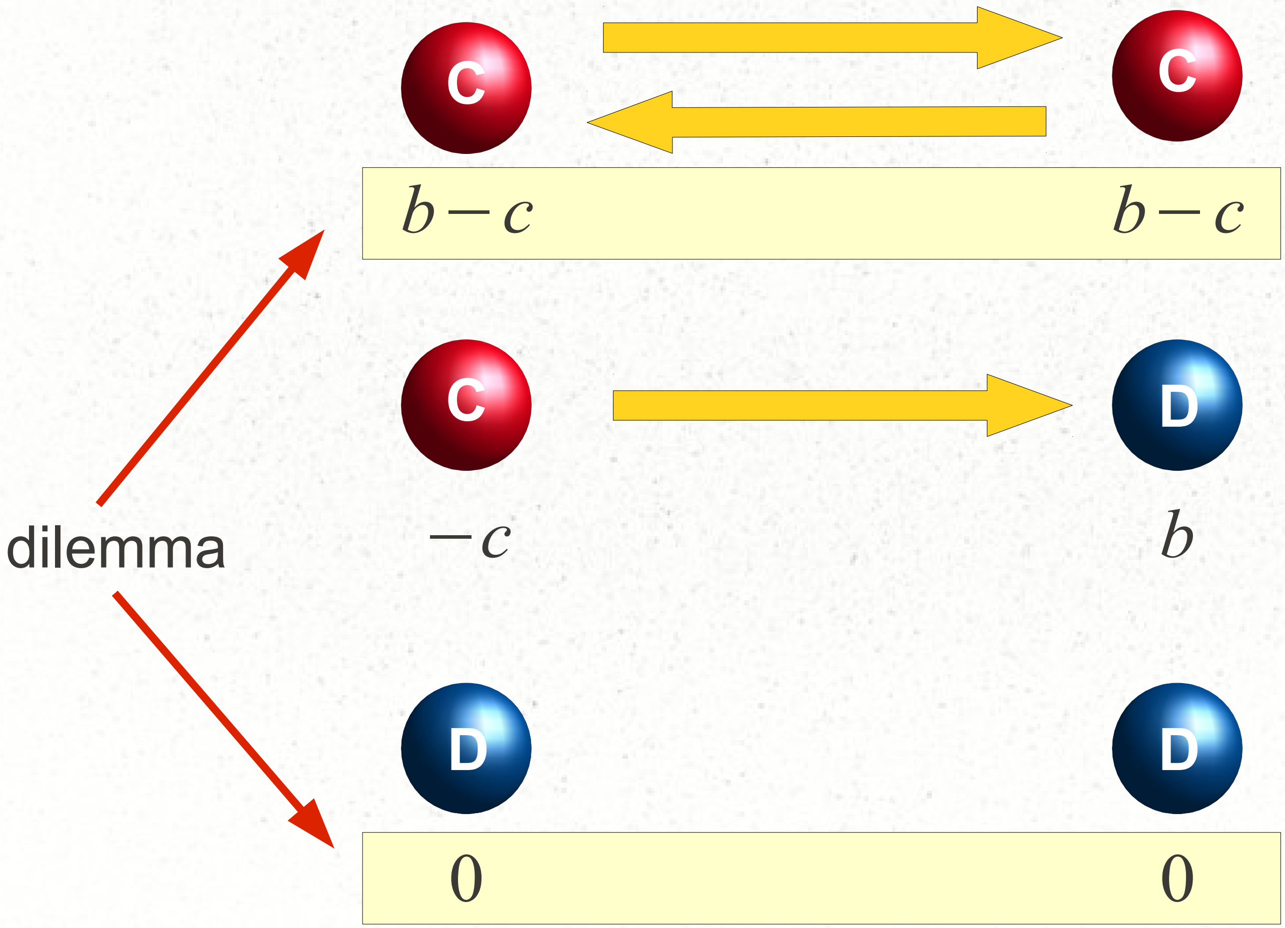
risk $-c$

b temptation

D D

0 0

The problem



$b-c$ $b-c$

$-c$ b

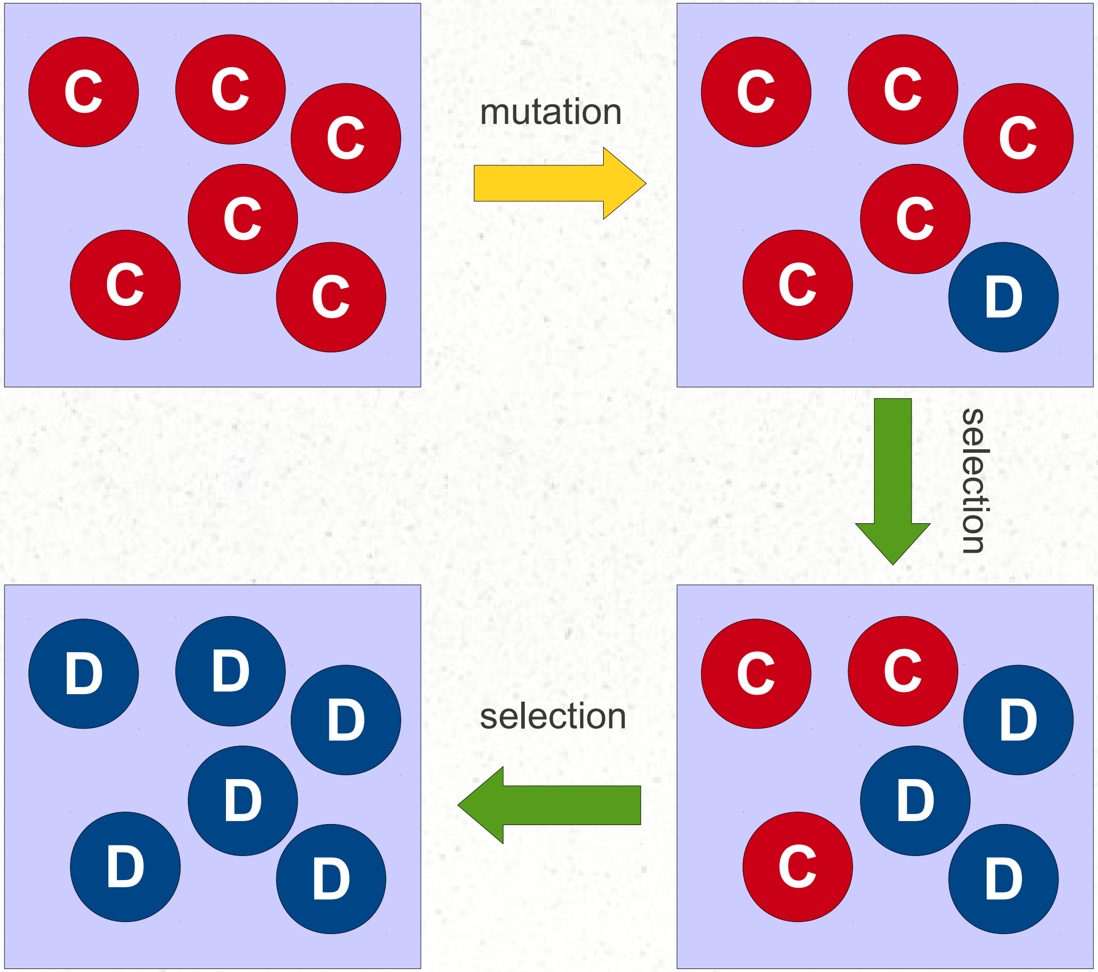
dilemma

0 0

The problem

> *He who was ready to sacrifice his life […] would often leave no offspring to inherit his noble nature. […] Therefore, it hardly seems probable, that the number of men gifted with such virtues […] could be increased through natural selection, that is, by the survival of the fittest […].*
>
> Charles Darwin, *The Descent of Man,* 1871

The problem


C
C
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mutation
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selection
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selection
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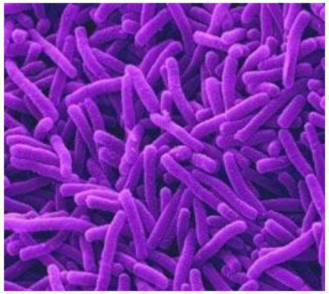
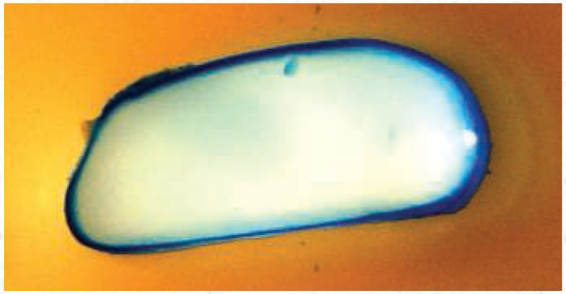
D

Why is it a problem?



quorum sensing



yeast cells in ethanol

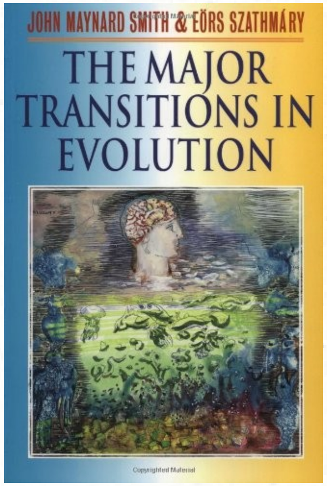
ants

baboons

hunter-gatherers

rescue

Why is it so important?



replicating molecules → populations of molecules in compartments

individual replicators → chromosomes

RNA world → DNA and proteins *(genetic code)*

prokaryotes → eukaryotes

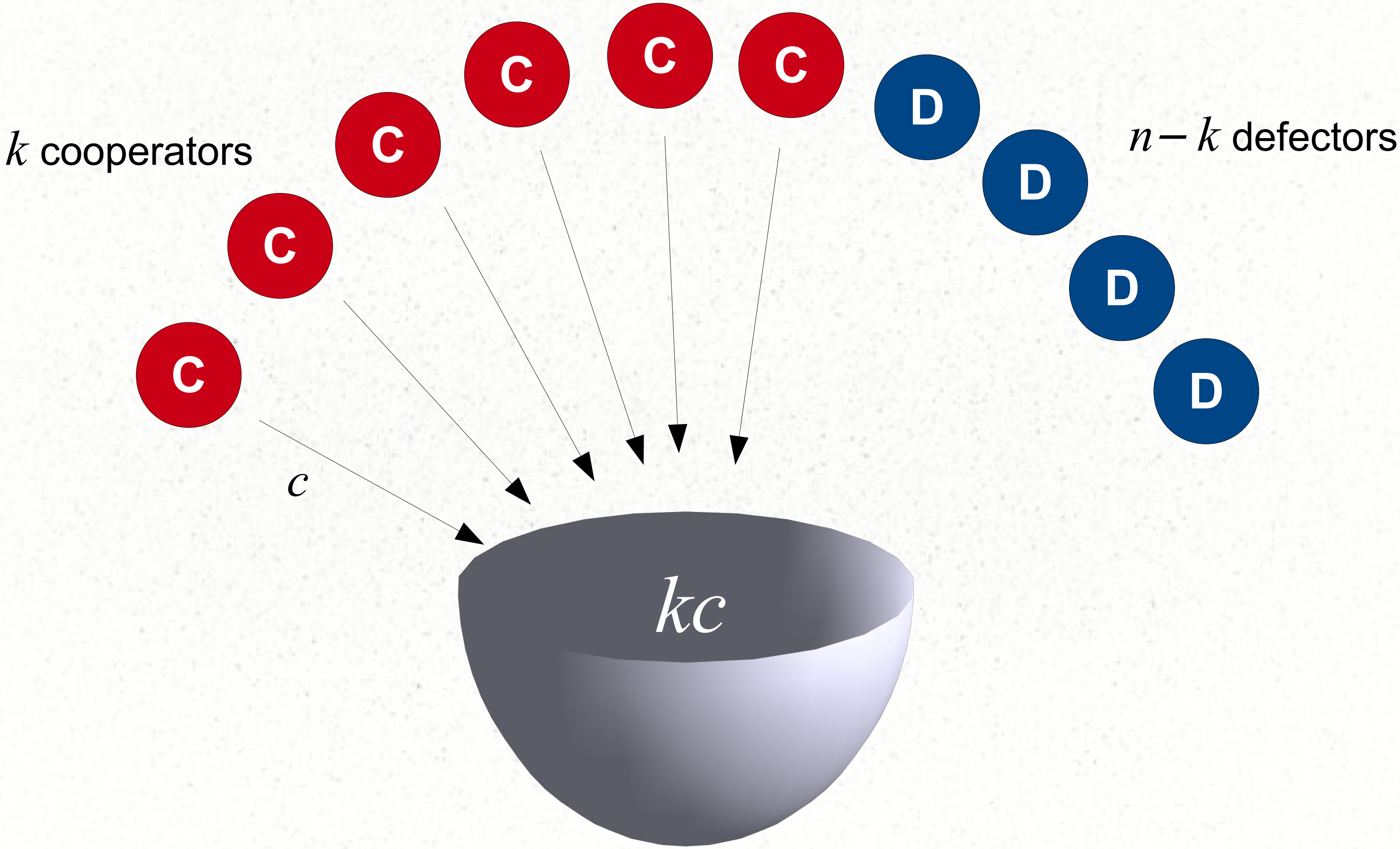
asexual clones → sexual populations

single-celled organisms → multicellular organisms *(cell differentiation)*

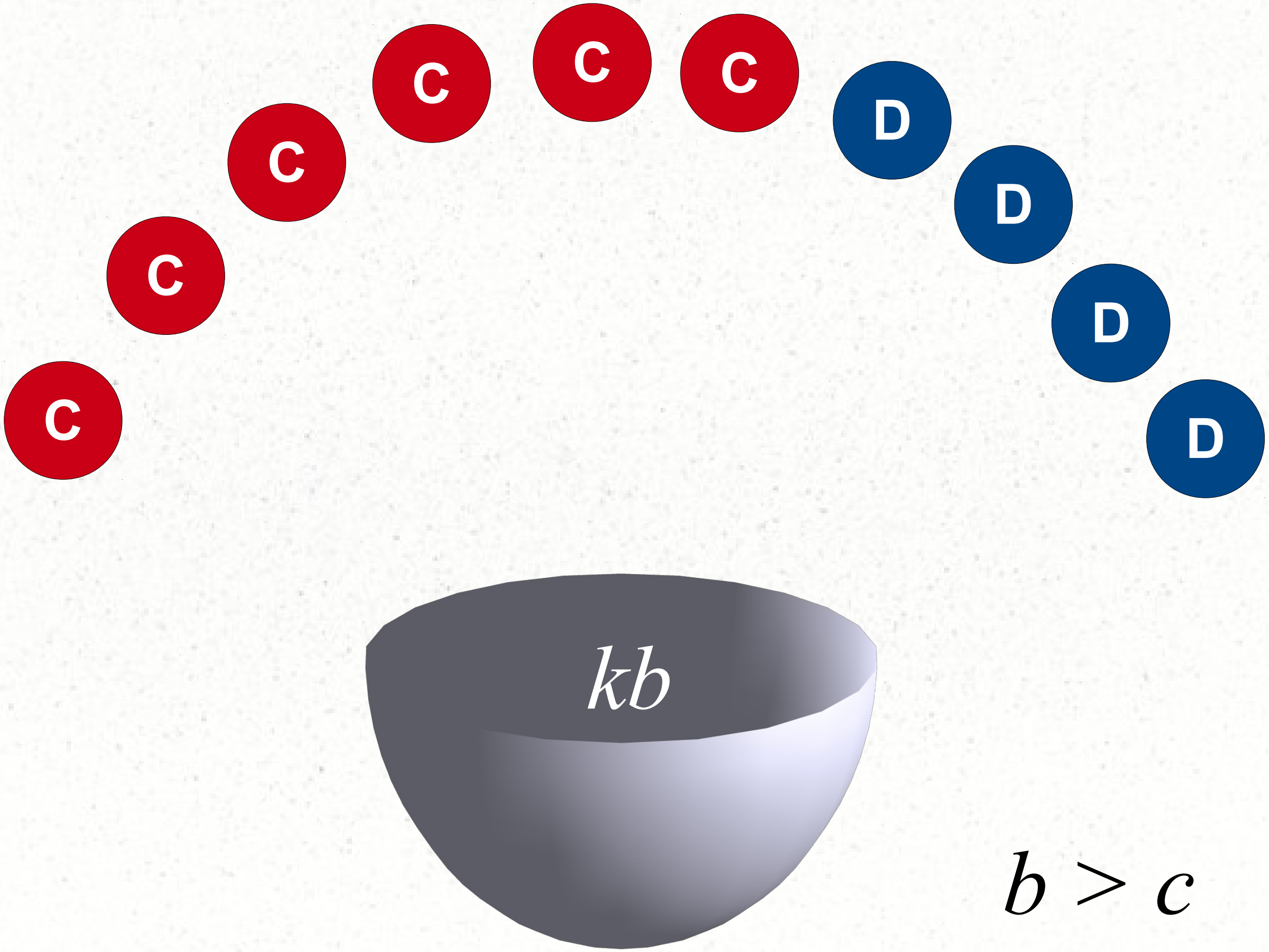
individuals → social colonies *(nonbreeding castes)*

primate societies → human societies *(language)*

Public goods game

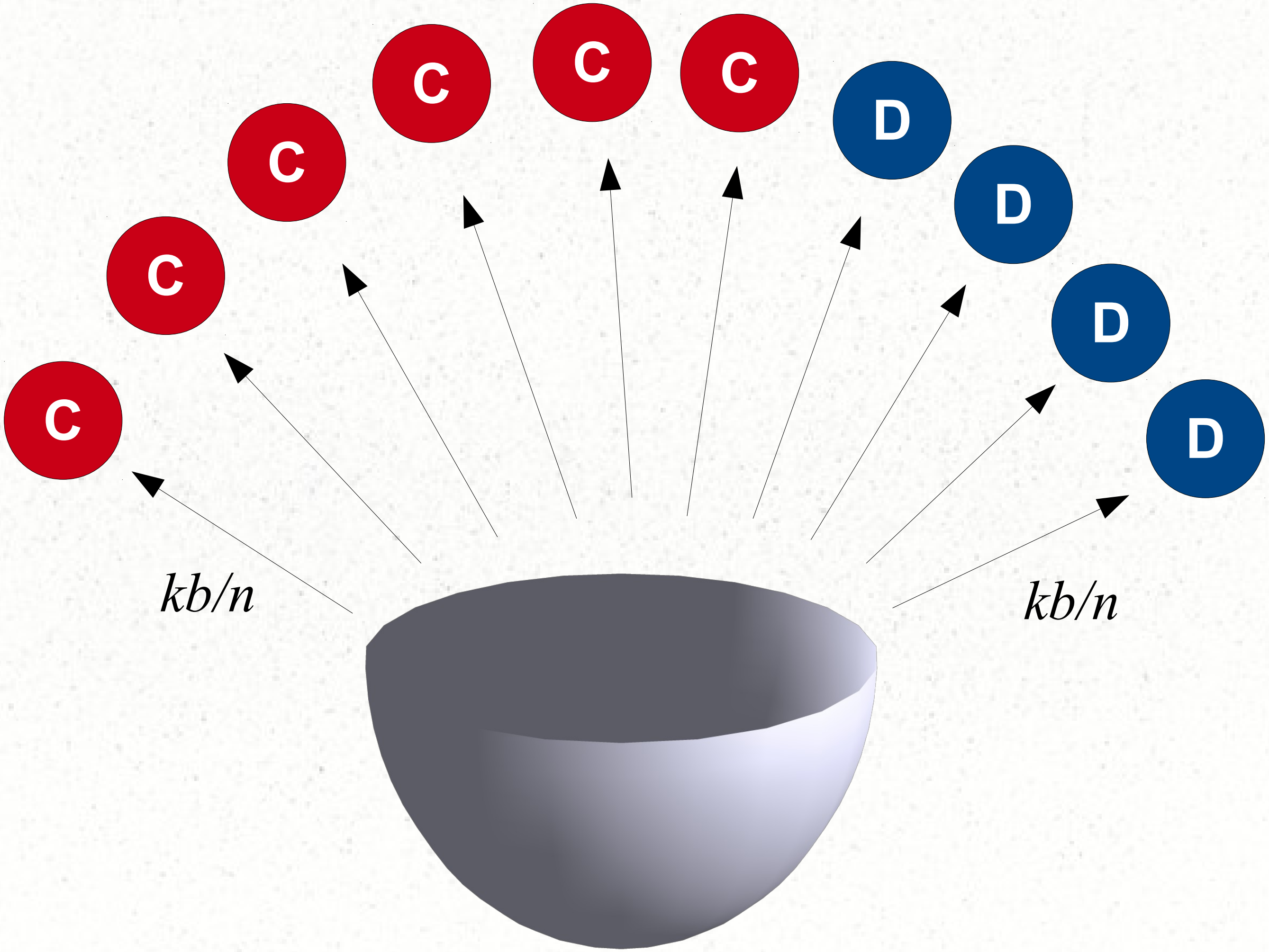


Public goods game



$b > c$

Public goods game



Public goods game

$$\Pi_C(k) = k\frac{b}{n} - c, \qquad k = 1, \ldots, n$$

$$\Pi_D(k) = k\frac{b}{n}, \qquad k = 0, \ldots, n-1$$

$n = 2$ → Prisoner's dilemma

Public goods game

	self	others
Π_C	$\frac{b}{n} - c$	$(k-1)\frac{b}{n}$
Π_D	0	$k\frac{b}{n}$

$\frac{b}{n} - c < 0$ → strong altruism

$\frac{b}{n} - c > 0$ → weak altruism

A basic mechanism: assortment

Fletcher & Doebeli, Proc. R. Soc. B (2009) 276, 13–19

	self	**others**
Π_C	$\frac{b}{n} - c$	$e_C \frac{b}{n}$
Π_D	0	$e_D \frac{b}{n}$

e_C → average no. of cooperators in a cooperator's environment

e_D → average no. of cooperators in a defector's environment

A basic mechanism: assortment

Fletcher & Doebeli, Proc. R. Soc. B (2009) 276, 13–19

	self	**others**
Π_C	$\frac{b}{n}-c$	$e_C\frac{b}{n}$
Π_D	0	$e_D\frac{b}{n}$

cooperation spreads iff

$$(e_C+1)\frac{b}{n}-c>e_D\frac{b}{n} \quad \Leftrightarrow \quad \boxed{e_C-e_D>\frac{c\,n}{b}-1}$$

Ex. 1: well-mixed populations

$$\boxed{e_C - e_D > \frac{c\,n}{b} - 1}$$

- Well-mixed population with fraction of cooperators x

$$e_C = e_D = x(n-1)$$

cooperation emerges iff $\frac{b}{n} > c$ (weak altruism)

Ex. 2: extreme assortment

$$\boxed{e_C - e_D > \frac{c\,n}{b} - 1}$$

- Cooperators interact only with cooperators
- Defectors interact only with defectors

$$e_C = n - 1 \qquad e_D = 0$$

cooperation emerges iff $b > c$

Ex. 3: overdispersion of cooperators

$$\boxed{e_C - e_D > \frac{c\,n}{b} - 1}$$

- Every group can contain only 1 cooperator

$$e_C = 0 \qquad e_D = 1$$

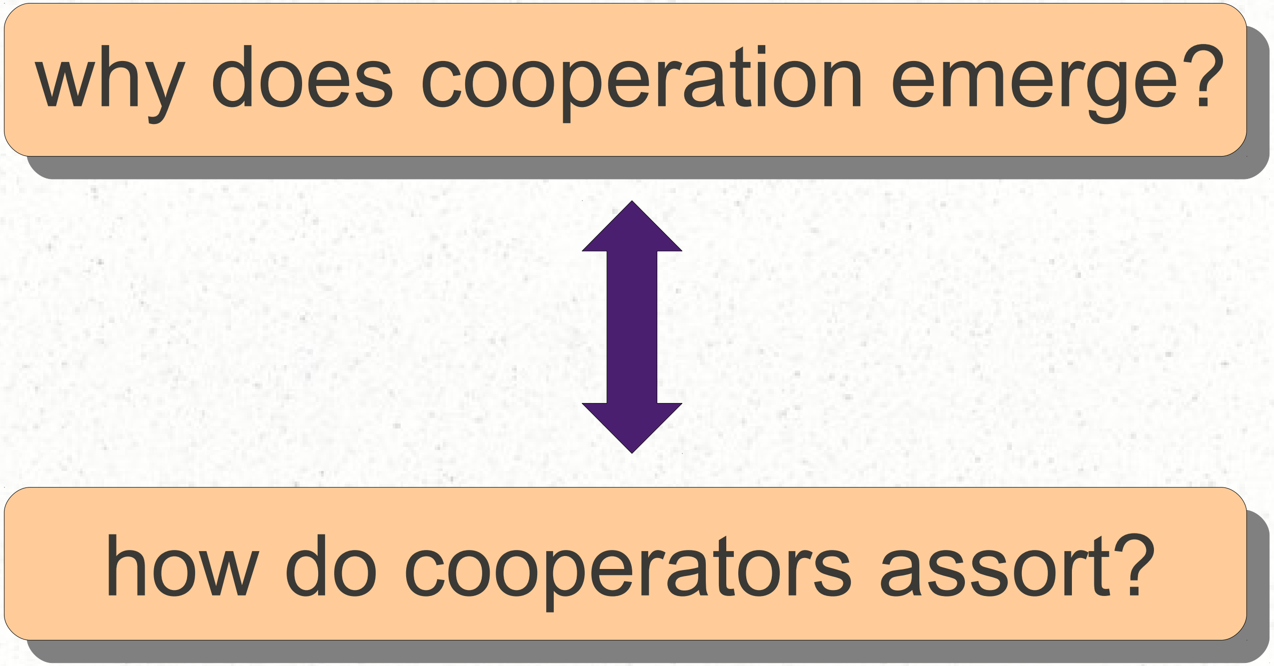
cooperation cannot emerge

Hamilton's rule

$$r\,b > c\,, \qquad r = \frac{e_C - e_D + 1}{n}$$

- r was termed “relatedness” by Hamilton (1964)
- Extreme assortment: $r = 1$
- Overdispersion of cooperators: $r = 0$

A problem shift

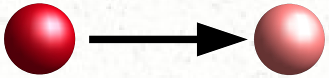


why does cooperation emerge?

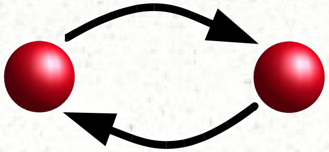
how do cooperators assort?

Five mechanism of assortment

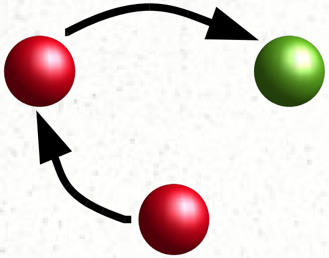
Nowak, Science (2006) 314, 1560–1563



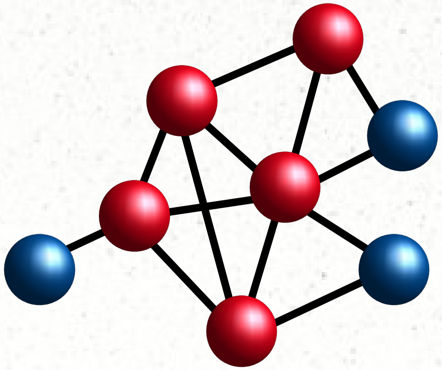
kin selection



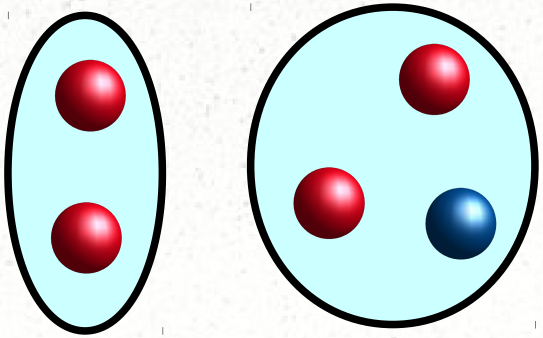
direct reciprocity



indirect reciprocity

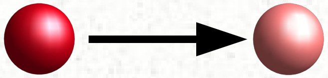


population structure



group selection

Kin selection



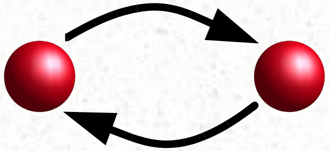
> *I will jump into the river to save two brothers or eight cousins.*
>
> J. B. S. Haldane

Hamilton's rule:

$$\boxed{r\,b > c}$$

relatedness $\begin{cases} \text{brothers: } r = 1/2 \\ \text{cousins: } r = 1/8 \end{cases}$

Direct reciprocity



Repeated Prisoner's dilemma: players play once more with probability w

retaliator → C C C … C C D D … D …
opponent → C C C … C $\underset{(n)}{\text{D}}$ X X … X …

$$\left.\begin{aligned} \Pi(D_n) &= \frac{1-w^n}{1-w}(b-c)+bw^n \\ \Pi(D_\infty) &= \frac{1}{1-w}(b-c) \end{aligned}\right\} \quad \Pi(D_\infty)-\Pi(D_n)=w^n\frac{wb-c}{1-w}$$

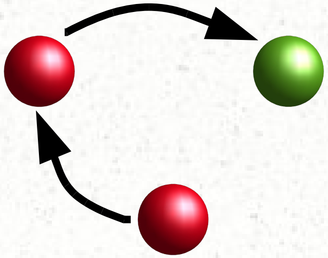
$$\boxed{wb>c}$$

Axelrod's tournaments

Axelrod (1984) *The evolution of cooperation* (Basic Books)

- 13 (first tournament) and 62 (second tournament) strategies, plus RANDOM, played 200 iterations of the repeated PD
- Absolute winner: Tit-for-tat (TFT), by Rapoport:
    - Start cooperating
    - Do what your opponent did in the previous round
- Good strategies are:
    - **Nice**: start cooperating
    - **Provocable**: retaliate after being defected
    - **Forgiving**: help restoring cooperation
    - **Simple**: behavior easy to understand

Indirect reciprocity

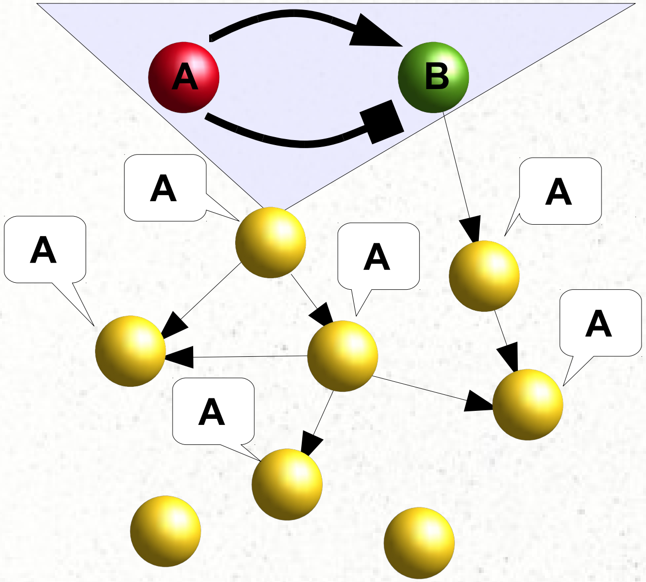


- Assortment achieved through signaling
- Problem: fake signals

eastern coral snake
(venomous)

false coral snake
(non-venomous)

Reputation



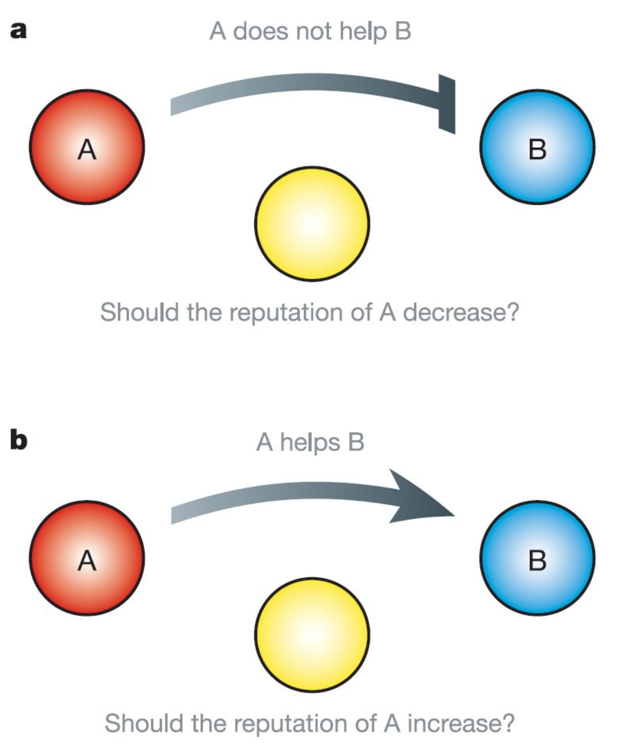
q → probability to be aware of opponent's reputation

	C	D
C	$b-c$	$-c(1-q)$
D	$b(1-q)$	0

$$b-c>b(1-q) \quad \Rightarrow \quad \boxed{q\,b>c}$$

Emergence of moral rules

Brandt & Sigmund (2004) J. Theor. Biol. **231**, 475-486



$A = \{\mathrm{C}, \mathrm{D}\}$ actions

$R = \{\mathrm{G}, \mathrm{B}\}$ reputations

$S = \{R^2 \to A\}$ strategies

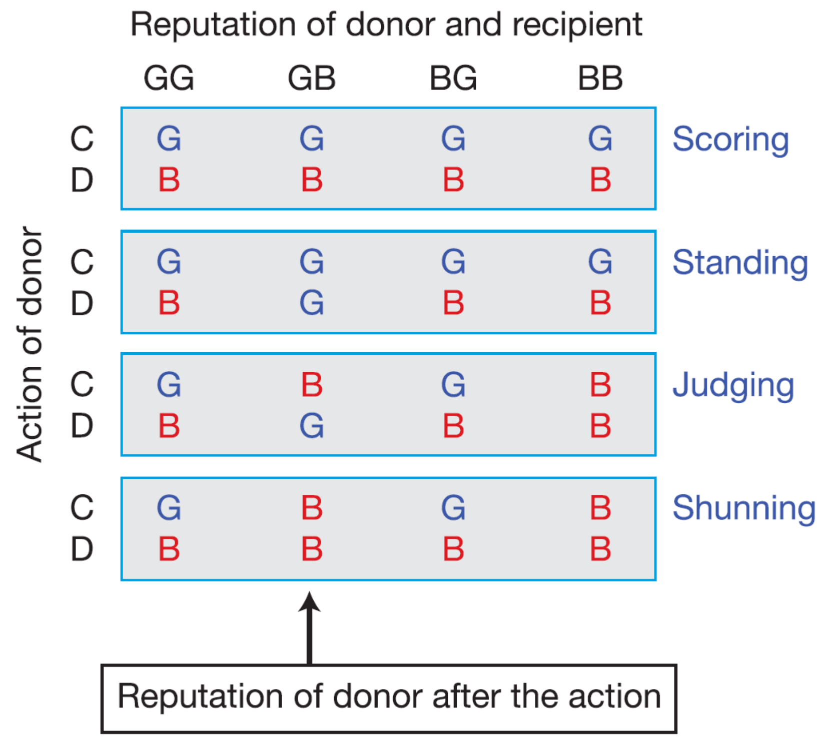
$M = \{A \times R^2 \to R\}$ moral systems

$|S| = 2^4 = 16$ $|M| = 2^8 = 256$

$$|S \times M| = 2^{12} = 4096$$

Emergence of moral rules

Brandt & Sigmund (2004) J. Theor. Biol. **231**, 475-486



Action of donor	Reputation of donor and recipient				
	GG	GB	BG	BB	
C	G	G	G	G	Scoring
D	B	B	B	B	
C	G	G	G	G	Standing
D	B	G	B	B	
C	G	B	G	B	Judging
D	B	G	B	B	
C	G	B	G	B	Shunning
D	B	B	B	B	

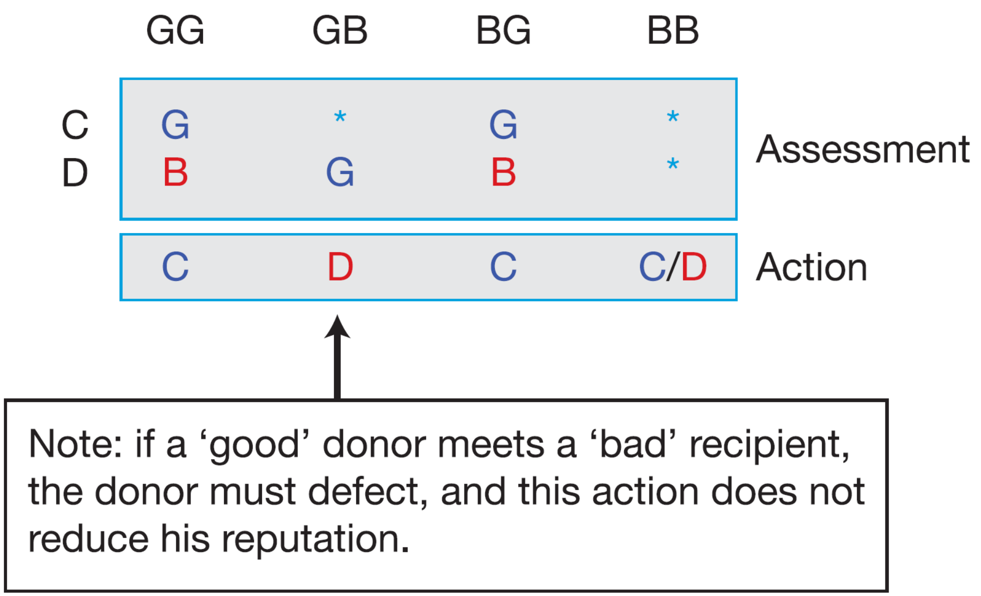
Reputation of donor after the action

moral assessment of an action

Emergence of moral rules

Ohtsuki & Iwasa (2004) J. Theor. Biol. **231**, 107-120

leading eight (uninvadable)

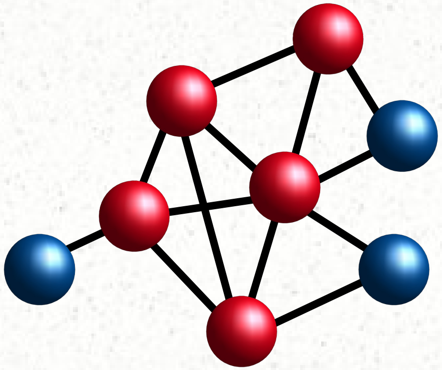


	GG	GB	BG	BB	
C	G	*	G	*	Assessment
D	B	G	B	*	
	C	D	C	C/D	Action

Note: if a ‘good’ donor meets a ‘bad’ recipient, the donor must defect, and this action does not reduce his reputation.

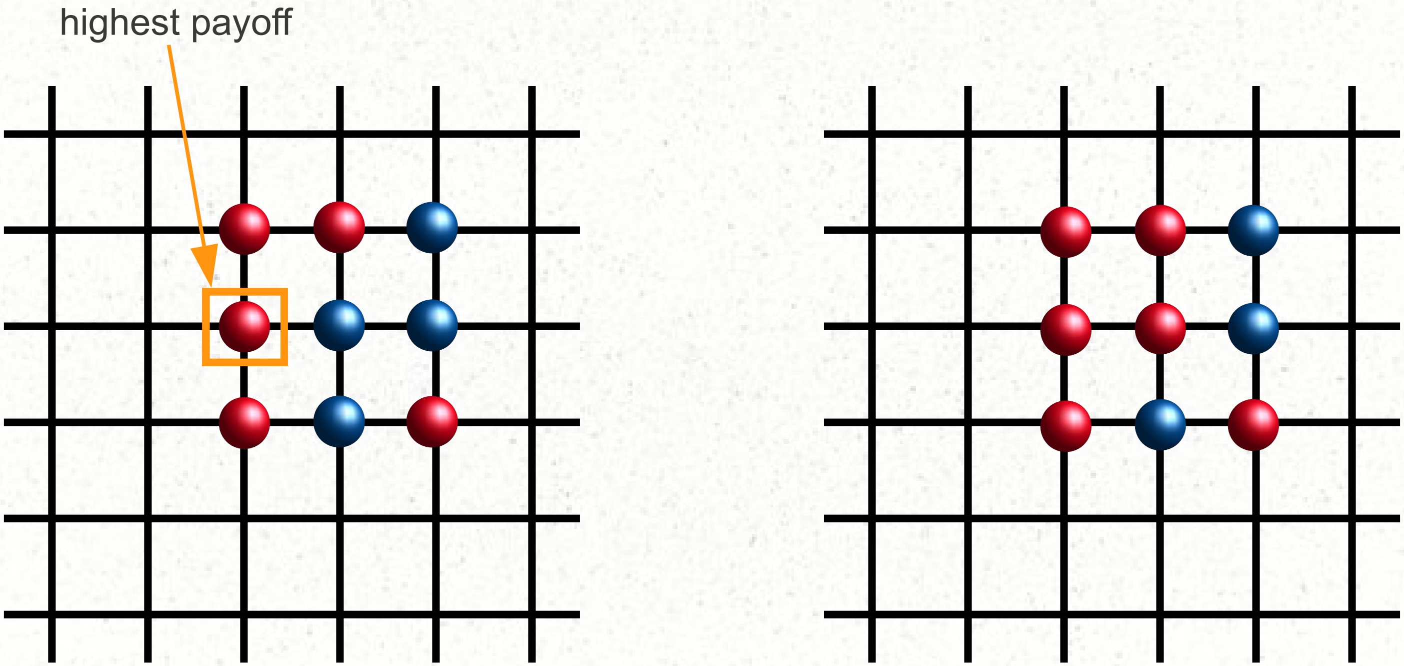
Population structure

Nowak & May (1992) Nature **359**, 826-829



- Assortment through interaction with neighbors in a network
- Includes spatial as well as social assortment
- Requires a dynamics inducing clustering of cooperators

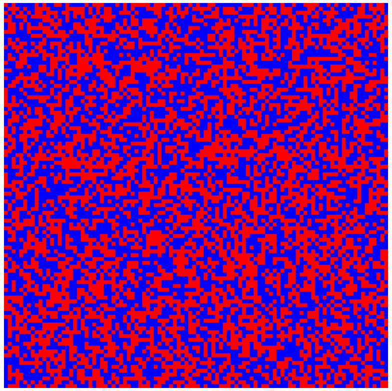
Population structure



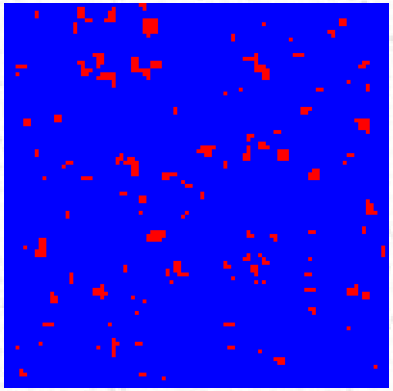
unconditional imitation

Population structure

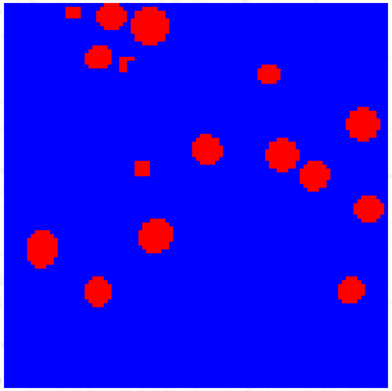
$b = 1.2 \quad c = 0.2$



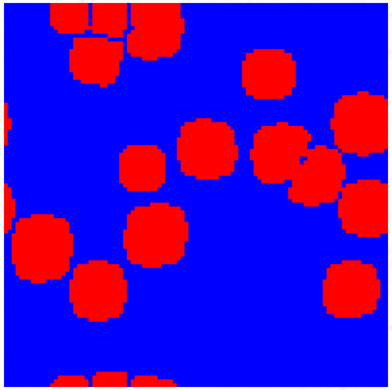
t = 0



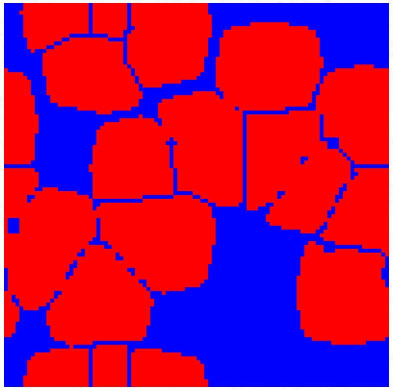
t = 1



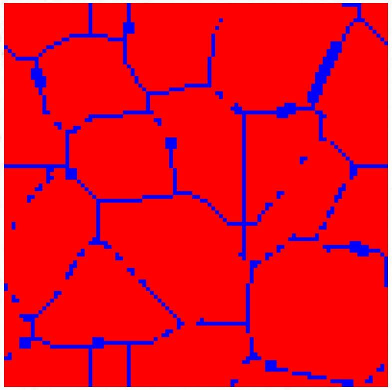
t = 4



t = 9



t = 18



t = 35

Population structure

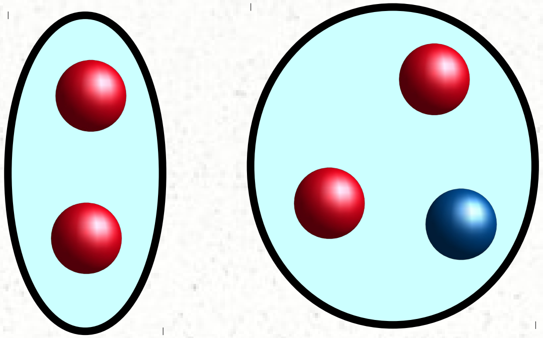
- No general rule (depends on the specific dynamics)
  Roca, Cuesta, Sánchez, Phys. Life Rev. (2006) **6**, 208-209

- An empirical rule in a very specific context:
  Ohtsuki et al., Nature (2006) **441**, 502-505

$$\boxed{b > c\, n}$$

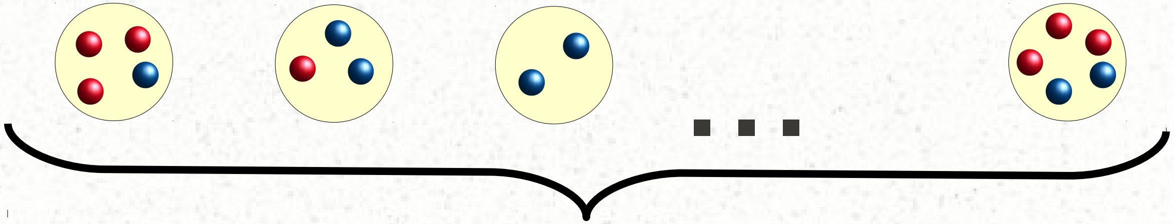
average number of neighbors

Group selection



- First step in a hierarchy of multilevel selection
- Individuals reproduce
- Selection acts upon groups

Group selection



m groups

- Individuals reproduce proportional to payoff
- Payoff of a group with k cooperators = $k(b–c)$ regardless of size
- Payoff of a cooperator in a group of size s and k cooperators = $[(k/s)b–c]/[b–c]$
- Groups of size $>n$ split replacing a randomly selected group
- Under specific assumptions, cooperation spreads if

$$\boxed{b > c(1+n/m)}$$

Conclusions

- Emergence of cooperation underlies the increasing complexity direction of evolution
- Major transitions in evolution are related to the appearance of a collective behavior triggered by cooperation
- The basic motor for the emergence of cooperation is assortment of cooperators
- There are at least five basic mechanisms inducing assortment of cooperators
- All five yield a Hamilton rule for the threshold of benefit-to-cost necessary for cooperation
- Other mechanisms not explored here: intervention of third parties