FIVE RULES FOR THE EVOLUTION OF COOPERATION

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OUTLINE

- Natural selection
- Kin selection
- Direct reciprocity
- Indirect reciprocity
- Network reciprocity
- Group selection
- Mathematical framework

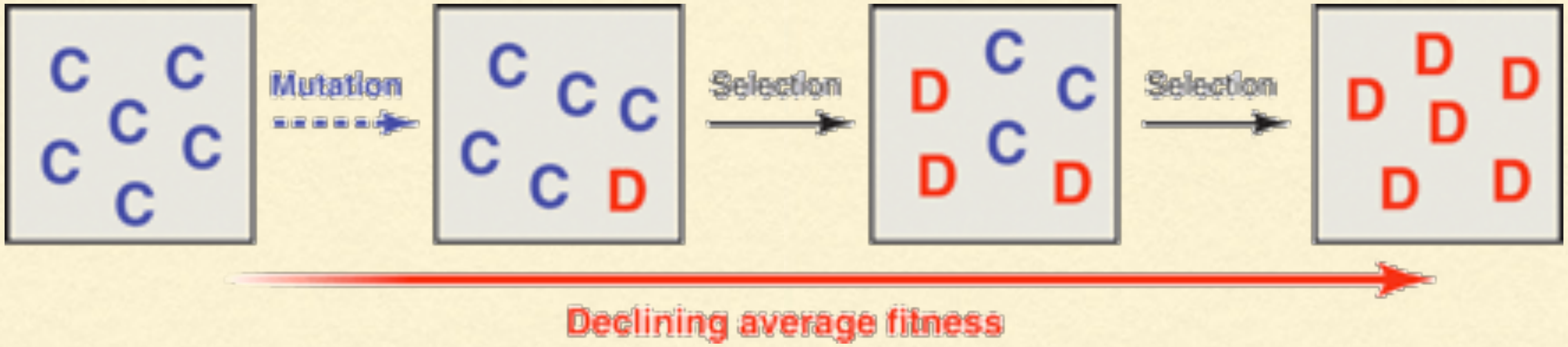
NATURAL SELECTION

- A cooperator is someone who pays a cost, c, for another individual to receive a benefit, b.
- A defector has no cost and does not deal out benefits.
- Cost and benefit are measured in terms of fitness.

PRISONERS' DILEMMA

	C	D
C	b-c	-c
D	b	0

$b>c>0$



- i cooperators and N – i defectors
- $f_C = [b(i - 1)/(N - 1)] - c$
- $f_D = bi/(N - 1)$

KIN SELECTION

"I will jump into the river to save two brothers or eight cousins."

–J.B.S. Haldane, 1930s

- the coefficient of relatedness, r, must exceed the cost-to-benefit ratio of the altruistic act:

$$r > c/b$$

DIRECT RECIPROCITY

- It is unsatisfactory to have a theory that can only explain cooperation among relatives.
- repeated Prisoner's Dilemma (repeated encounters between the same two individuals)

- tit-for-tat
- generous-tit-for-tat (cooperates although you have defected with probability $1 - c/b$)
- win-stay, lose-shift

- Direct reciprocity can only lead to the evolution of cooperation if the probability, w, of another encounter between the same two individuals exceeds the cost-to-benefit ratio of the altruistic act:

$$w > c/b$$

INDIRECT RECIPROCITY

- Direct reciprocity relies on repeated encounters between the same two individuals, and both individuals must be able to provide help.

- Randomly chosen, pairwise encounters, where the same two individuals need not meet again.
- One individual acts as donor the other as recipient. The donor can decide whether or not to cooperate.
- Indirect reciprocity can only promote cooperation if the probability, q, to know someone's reputation exceeds the cost-to-benefit ratio of the altruistic act:

$$q > c/b$$

NETWORK RECIPROCITY

- A cooperator pays a cost, c, for each neighbor to receive a benefit, b.

- Defectors have no costs, and their neighbors receive no benefits.

- The benefit-to-cost ratio must exceed the average number of neighbors, k, per individual:

$$b/c > k$$

GROUP SELECTION

- Cooperators help others in their own group. Defectors do not help.
- Individuals reproduce proportional to their payoff.
- Offspring are added to the same group.
- If a group reaches a certain size it can split into two.

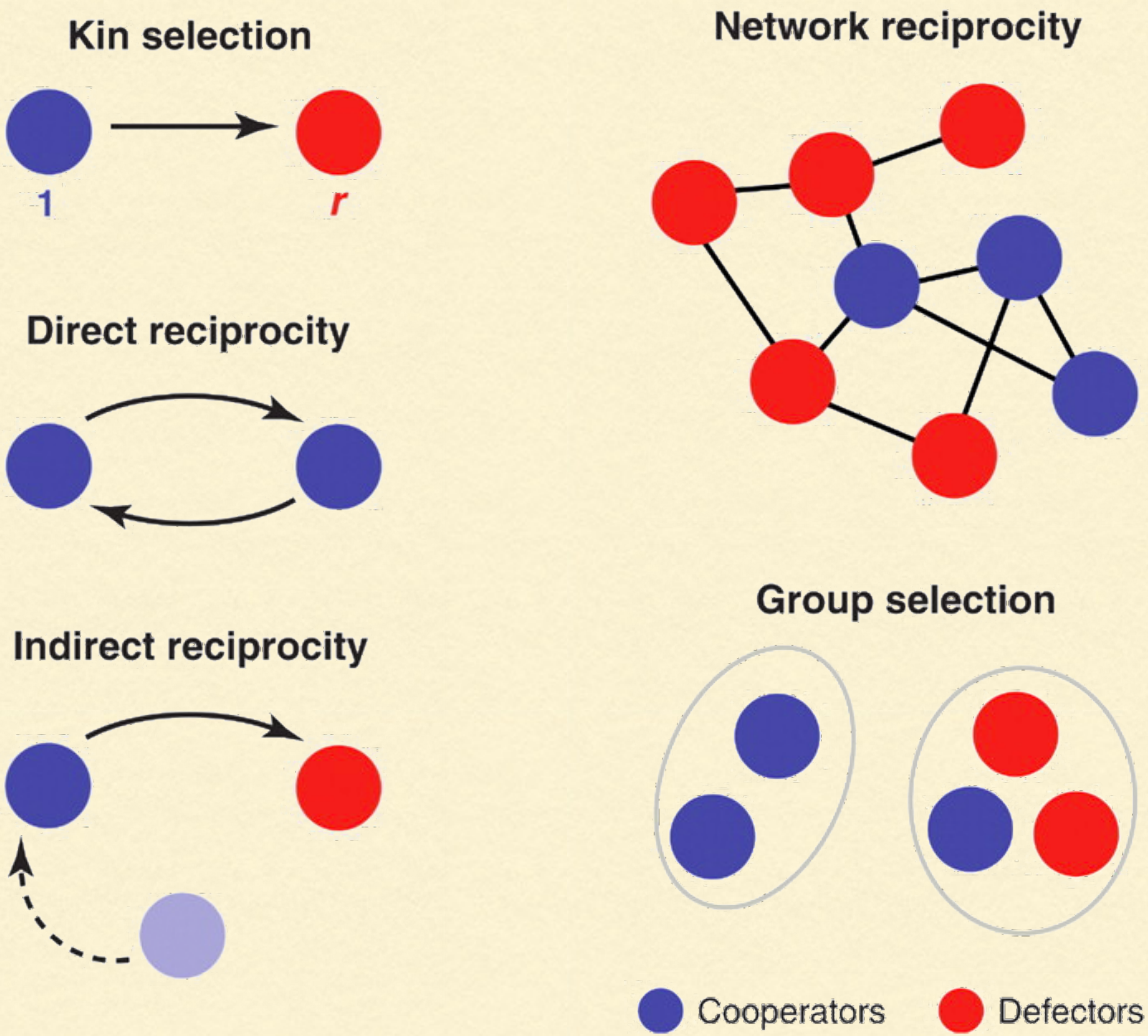
- only individuals reproduce, but selection emerges on two levels.

- In particular, pure cooperator groups grow faster than pure defector groups, while in any mixed group defectors reproduce faster than cooperators.

- if n is the maximum group size and m the number of groups, then group selection allows evolution of cooperation provided

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

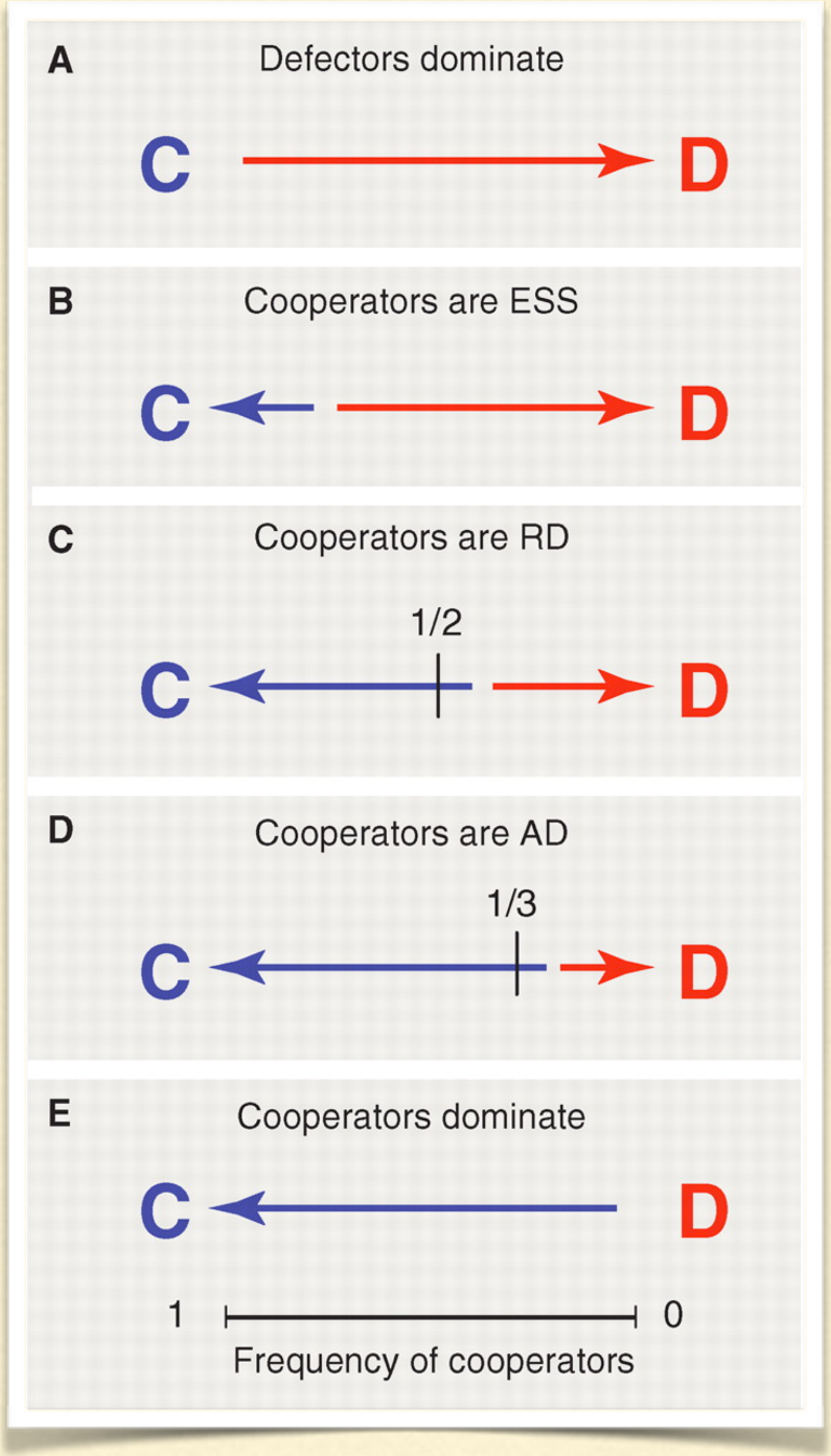
Smaller group sizes and larger numbers of groups favor cooperators


Kin selection
1
r
Direct reciprocity
Indirect reciprocity
Network reciprocity
Group selection
Cooperators
Defectors

MATHEMATICAL FRAMEWORK

$$
\begin{array}{c c}
 & \begin{array}{cc} C & D \end{array} \\
\begin{array}{c} C \\ D \end{array} & \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix}
\end{array}
$$

$\alpha > \gamma$	evolutionarily stable strategy (ESS)
$\alpha + \beta > \gamma + \delta$	risk-dominant (RD)
$\alpha + 2\beta > \gamma + 2\delta$	advantageous (AD)



	Payoff matrix	Cooperation is … ESS	RD	AD	
Kin selection	$\begin{array}{ccc} & C & D \\ C & (b-c)(1+r) & br-c \\ D & b-rc & 0 \end{array}$	$\frac{b}{c}>\frac{1}{r}$	$\frac{b}{c}>\frac{1}{r}$	$\frac{b}{c}>\frac{1}{r}$	r…genetic relatedness
Direct reciprocity	$\begin{array}{ccc} & C & D \\ C & (b-c)/(1-w) & -c \\ D & b & 0 \end{array}$	$\frac{b}{c}>\frac{1}{w}$	$\frac{b}{c}>\frac{2-w}{w}$	$\frac{b}{c}>\frac{3-2w}{w}$	w…probability of next round
Indirect reciprocity	$\begin{array}{ccc} & C & D \\ C & b-c & -c(1-q) \\ D & b(1-q) & 0 \end{array}$	$\frac{b}{c}>\frac{1}{q}$	$\frac{b}{c}>\frac{2-q}{q}$	$\frac{b}{c}>\frac{3-2q}{q}$	q…social acquaintanceship
Network reciprocity	$\begin{array}{ccc} & C & D \\ C & b-c & H-c \\ D & b-H & 0 \end{array}$	$\frac{b}{c}>k$	$\frac{b}{c}>k$	$\frac{b}{c}>k$	k…number of neighbors $H=\frac{(b-c)k-2c}{(k+1)(k-2)}$
Group selection	$\begin{array}{ccc} & C & D \\ C & (b-c)(m+n) & (b-c)m-cn \\ D & bn & 0 \end{array}$	$\frac{b}{c}>1+\frac{n}{m}$	$\frac{b}{c}>1+\frac{n}{m}$	$\frac{b}{c}>1+\frac{n}{m}$	n…group size m…number of groups

THANKS