

Generalized reciprocity in spatially structured populations

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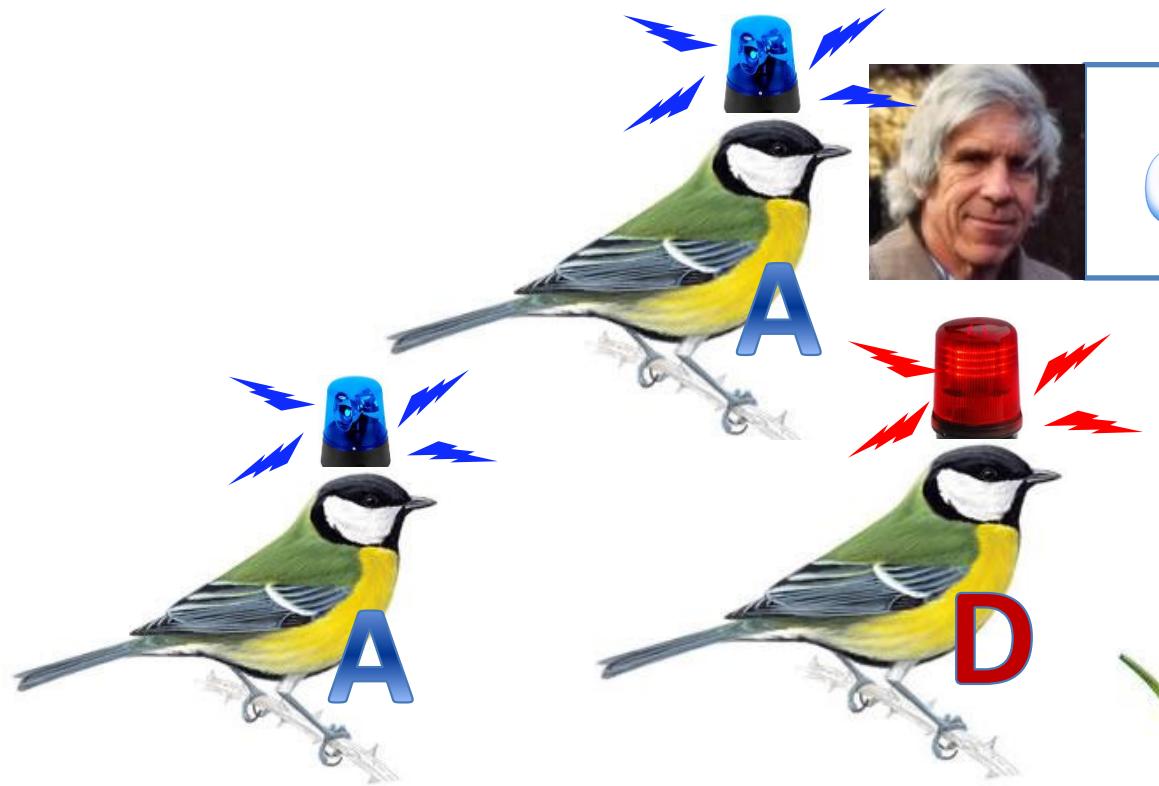
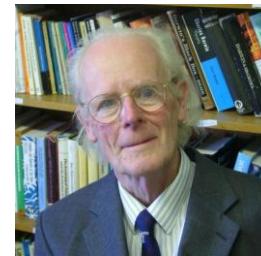
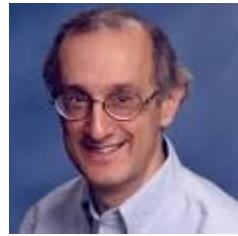
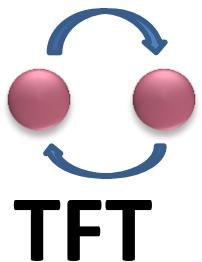


*“A **hydrogen bomb** is an example of mankind’s enormous capacity for friendly cooperation. Its construction requires an intricate network of human **teams**, all working with a single minded devotion towards a common goal. Let us pause and savor in the glow of self-congratulation we deserve for belonging to such an **intelligent** and **sociable** species.”*



Altruism

??



$$c < r b$$



Spatial reciprocity Network reciprocity



letters to nature

Spatial structure often inhibits the evolution of cooperation in the snowdrift game

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Understanding the emergence of cooperative behaviour in evolutionary biology¹. Evolution has become a powerful framework with which to tackle many problems in biology. Two simple games have attracted theoretical and experimental studies: the Prisoner's Dilemma, the non-cooperative game², and the Snowdrift game (also known as the hawk-dove game)³. In the Prisoner's Dilemma, the non-cooperative strategy, which is evolutionarily unstable, which has inspired many extensions that enable cooperation to persist. In particular, on the basis of spatial models of the Prisoner's Dilemma, it is widely accepted that spatial structure promotes the evolution of cooperation^{4–8}. However, such general predictions can be made for the

Evolutionary games and spatial chaos

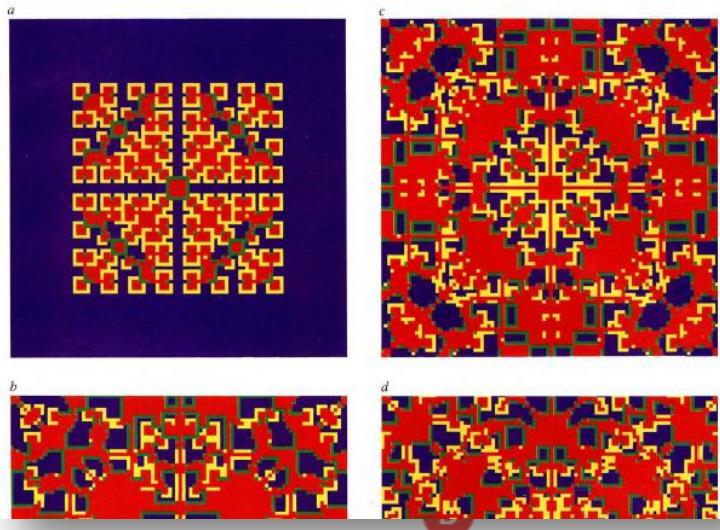
Martin A. Nowak & Robert M. May

LETTERS TO NATURE

fraction, f_C , shown in Fig. 2a is found for essentially all starting proportions and configurations for these b values.

Figure 3 is perhaps more in the realm of aesthetics than biology. Again $2 > b > 1.8$, but now we begin ($t = 0$) with a single D at the centre of a 99×99 lattice of Cs. Figure 3a shows the consequent symmetrical pattern 30 time-steps later, and Fig. 3b, c and d shows three successive patterns at $t = 217, 219$ and 221 after the pattern has reached the boundary (which happens at $t = 49$). These patterns, each of which can be characterized in fractal terms, continue to change from step to step, unfolding a remarkable sequence, dynamic fractals. The patterns show

every lace doily, rose window or Persian carpet you can imagine. As Fig. 2b shows, the asymptotic fraction of C is as for the chaotic pattern typified by Figs 1b and 2a. Many of the dynamic features of the symmetric patterns illustrated in Fig. 3 can be understood analytically. In particular, we can make a crude estimate of the asymptotic C fraction, f_C , for such very large symmetric patterns. This approximation is shown by the dashed horizontal line in Fig. 2b, and it agrees with the numerical results significantly better than we would have expected. Why the approximation also works for the irregular, spatially chaotic patterns (Fig. 2a) we do not know.



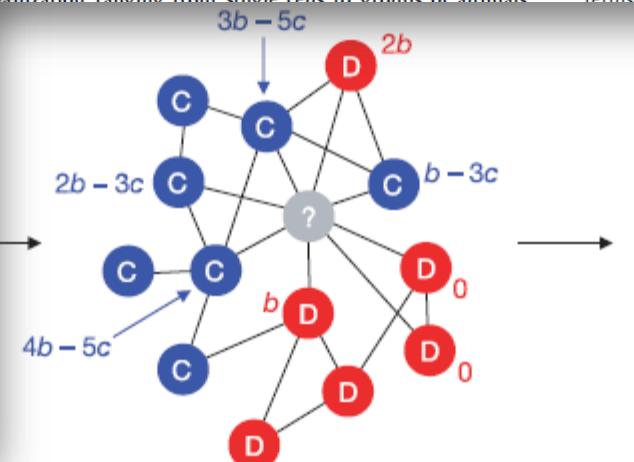
LETTERS

A simple rule for the evolution of cooperation on graphs and social networks

Hisashi Ohtsuki^{1,2}, Christoph Hauert², Erez Lieberman^{2,3} & Martin A. Nowak²

A fundamental aspect of all biological systems is cooperation. Cooperative interactions are required for many levels of biological organization, ranging from single cells to groups of animals^{1–4}.

In our



Indirect reciprocity

Large-scale cooperation among humans can be understood as resulting from networks of indirect reciprocity.

[R. Alexander, 1987]

“what comes around goes around”

Boyd & Richerson (1989):

Groups of size n are sampled from a large population and interact repeatedly. Probability w that the group persists for one more generation.

Upstream TFT: cooperate if individual ‘upstream’ cooperated before.

Downstream TFT: cooperate if individual ‘downstream’ cooperated before.

ALLD: Always defect.

Indirect reciprocity is unlikely to be important unless interacting groups are fairly small.

Indirect reciprocity

Nowak & Roche (2007):

Continuous strategies:

q : probability to initiate

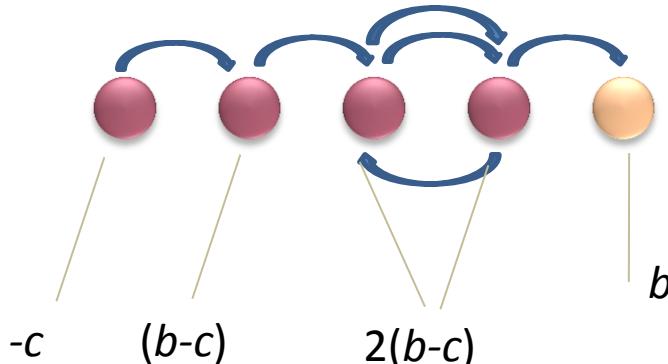
p : probability to pass on

*“Upstream reciprocity alone does **not** lead to the evolution of cooperation, but it can evolve and increase the level of cooperation if it is linked to [...] spatial reciprocity.”*

imitation updating



Generalized reciprocity



ORIGINAL ARTICLE

Evolution (2012)

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THE EVOLUTION OF GENERALIZED RECIPROCITY ON SOCIAL INTERACTION NETWORKS

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Evolutionary dynamics:

- + discrete strategies: **A D**
- + fitness dependent reproduction
- + offspring randomly placed on graph

cognitively simple

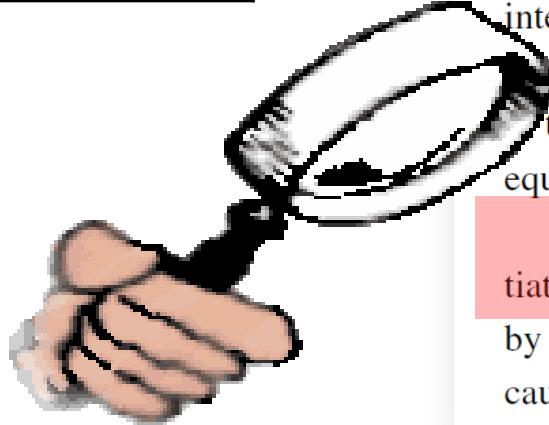


without kin assortment



Assumption 1: perfect genetic linkage

		Initiate
		Yes No
Reciprocate	Yes	A L
	No	S D



accumulated by reciprocal altruists is therefore given by

$$\pi_A = E[(n + n'_i)(b - c)(k_i + 1) - n b], \quad (2)$$

where n is the expected number of times that the focal individual initiates cooperation, and n'_i denotes the expected number of times that individual i is hit for the first time by a sequence of altruistic interactions that originated elsewhere on the network. Without loss of generality, we choose $n = 1$ in the analytical treatment of the model. As elsewhere in this manuscript, the expectation in equation (2) is taken over all positions in the network.

If we conservatively assume that only reciprocal altruists initiate cooperation, then the expected payoff of defectors is given by $\pi_D = b \bar{n}'$, where $\bar{n}' = E[n'_i] = f_t/(1 - f_t)$. This follows because every sequence that is initiated by a reciprocal altruist must

Assumption 2: discrete strategies

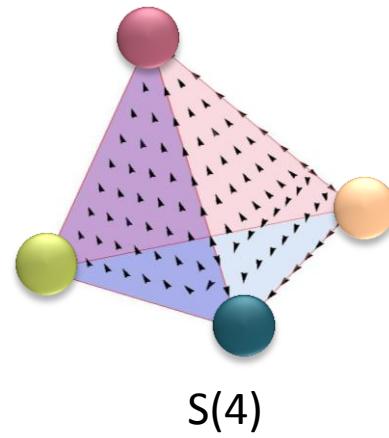
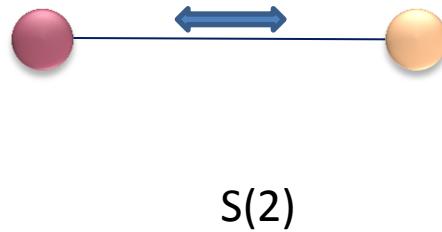
		Yes No
Reciprocate	A	D



$P_{\text{(reciprocate)}}$	r
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Assumption 1: perfect genetic linkage

		Initiate	
		Yes	No
Reciprocate	Yes	A	L
	No	S	D



Generalized reciprocity on the cycle

Average payoff of strategy X

$$\Pi_{\bar{X}} = \left(\frac{s}{N} \Pi_{X|S} + \frac{a}{N} \Pi_{X|A} \right) \frac{1}{x}$$

$$\Pi_{A|S} = \frac{a+l}{N-1} \sum_{j=1}^{a+l} j \varphi_j \frac{a}{a+l} (b-c)$$

$$\Pi_{A|A} = \sum_{j=1}^{a+l} \left(\frac{j-1}{3} + \frac{j^2+j-2}{6} \frac{a-1}{a-1+l} \right) \tilde{\varphi}_j (b-c) - c$$

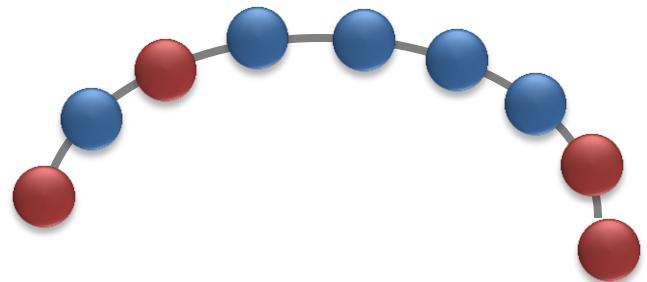
⋮

How frequently do we get segments with j individuals in a row?

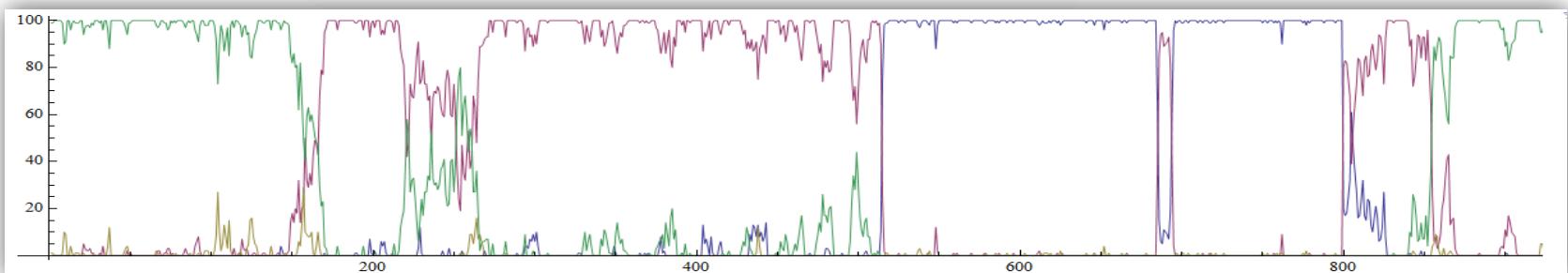
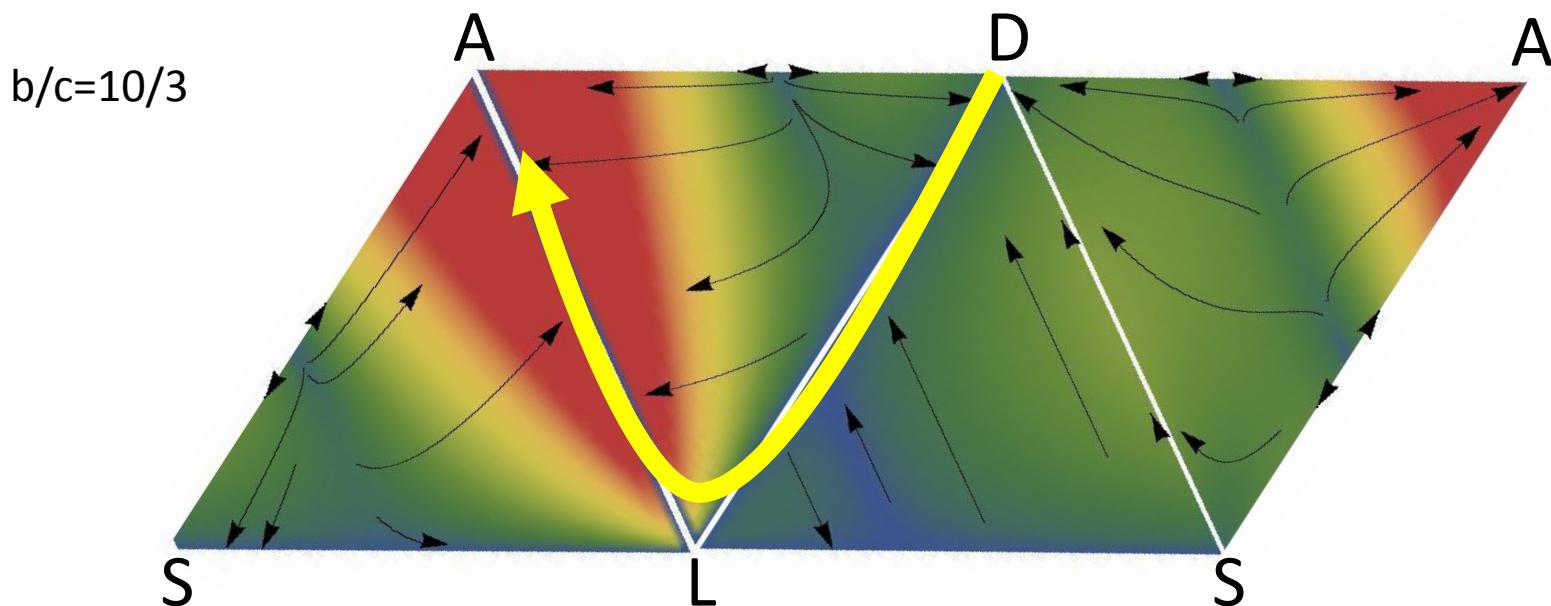
$$\varphi_j = \frac{\sigma_j}{\sum_{i=1}^{a+l} \sigma_i}, \quad \sigma_j = \frac{N}{(a+l-j)!} \prod_{k=1}^{a+l-j} (N-j-k-1)$$

		Initiate	
	Yes	No	
Yes	A	L	
No	S	D	

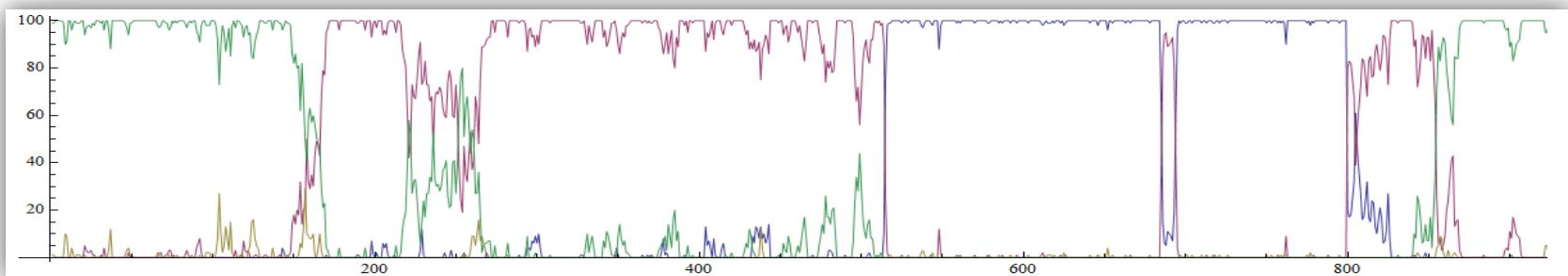
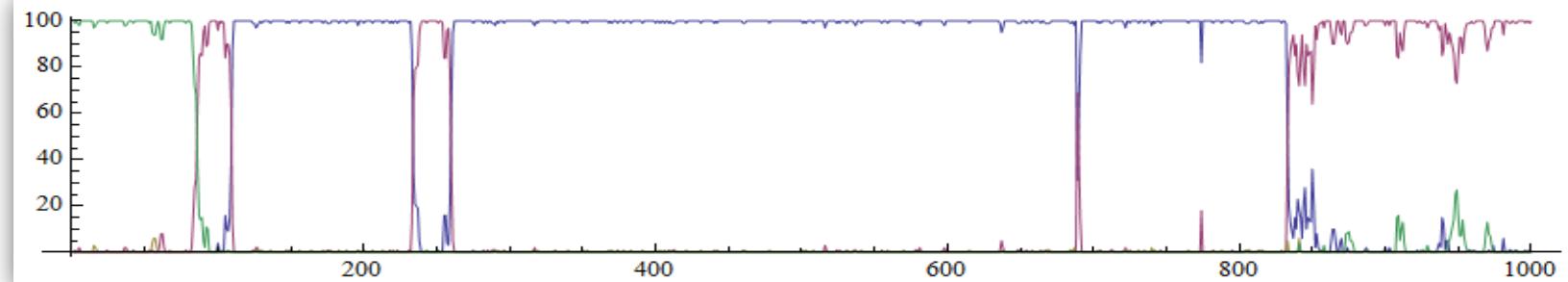
Reciprocate



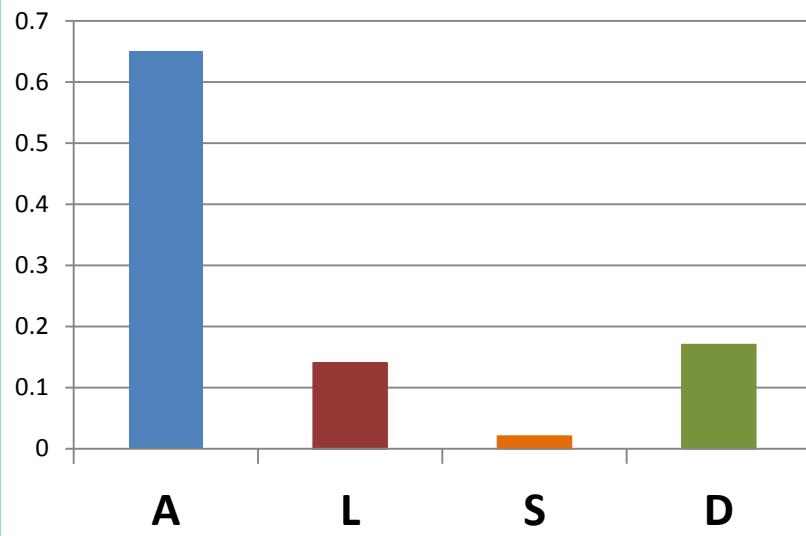
Generalized reciprocity on the cycle

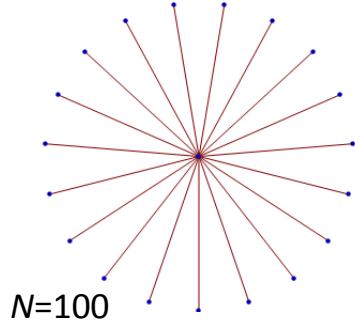


Generalized reciprocity on the cycle

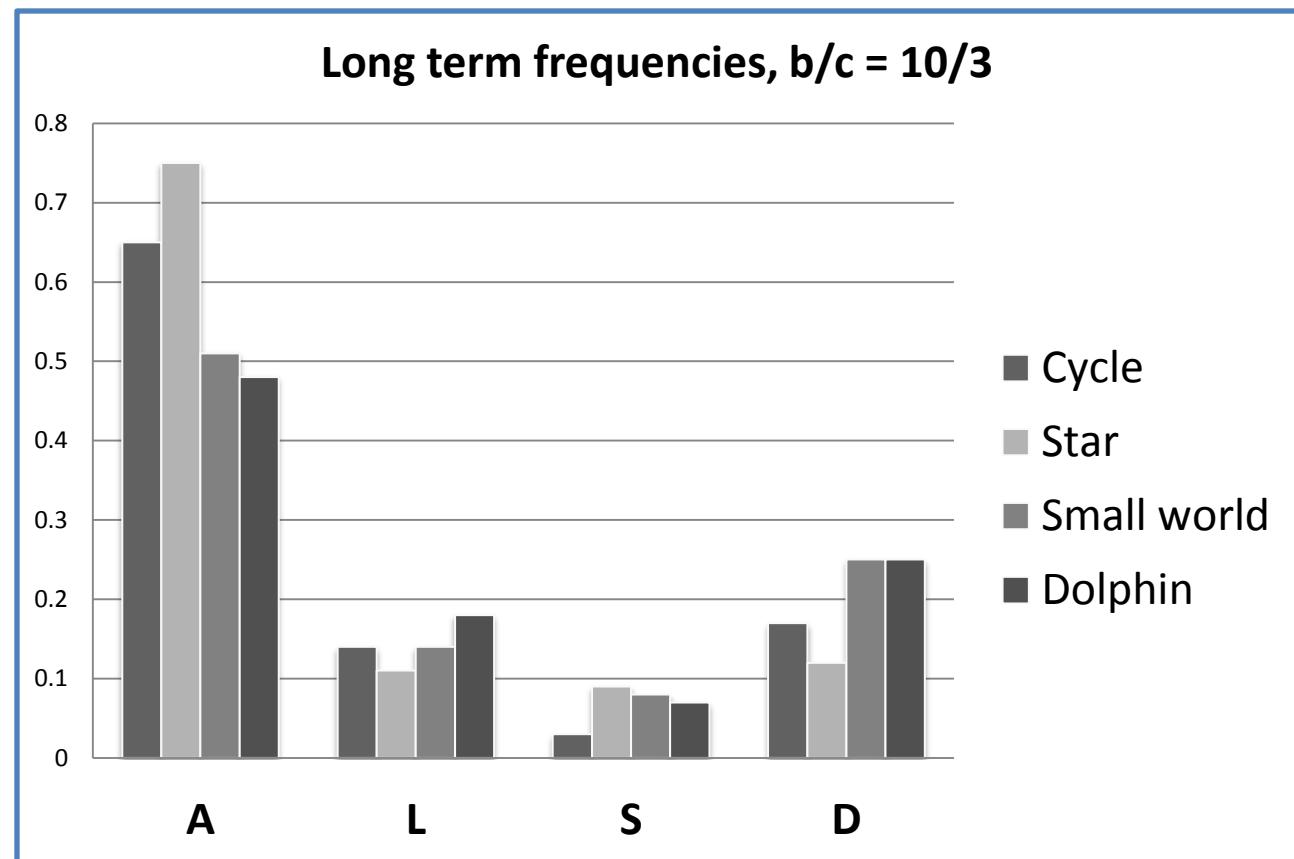
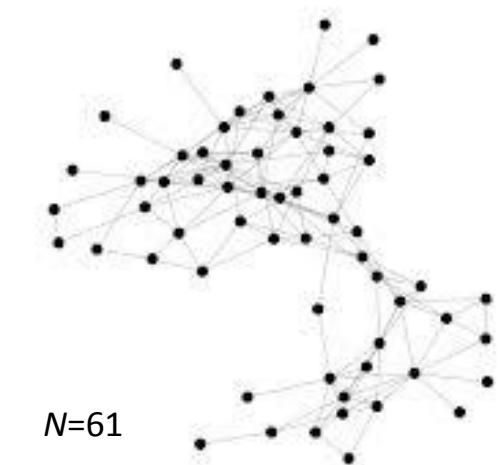
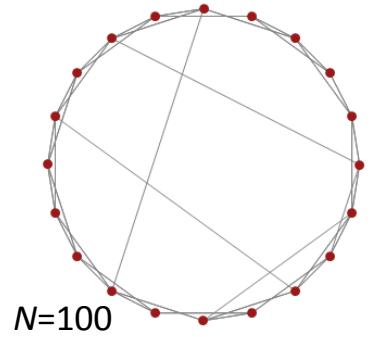


Long term frequency
cycle $b/c = 10/3$

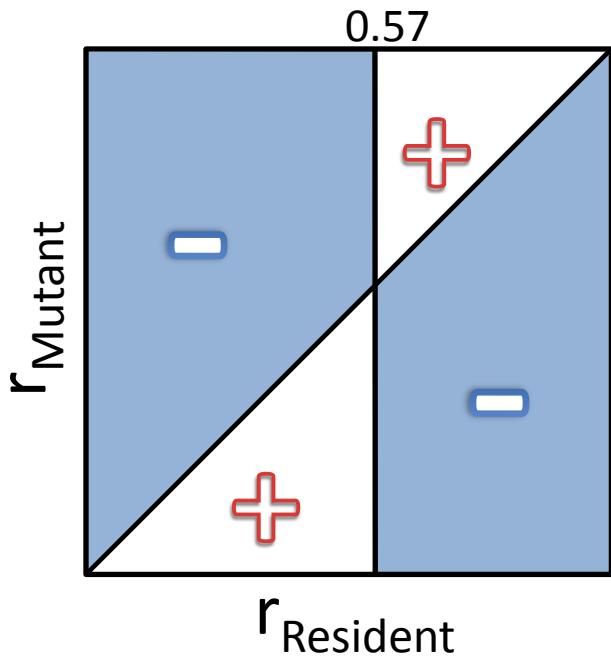




.. and on other graphs



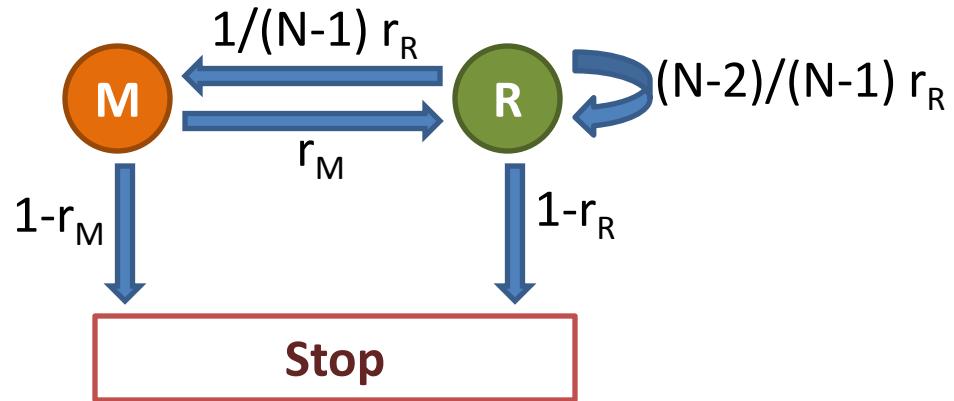
Continuous case



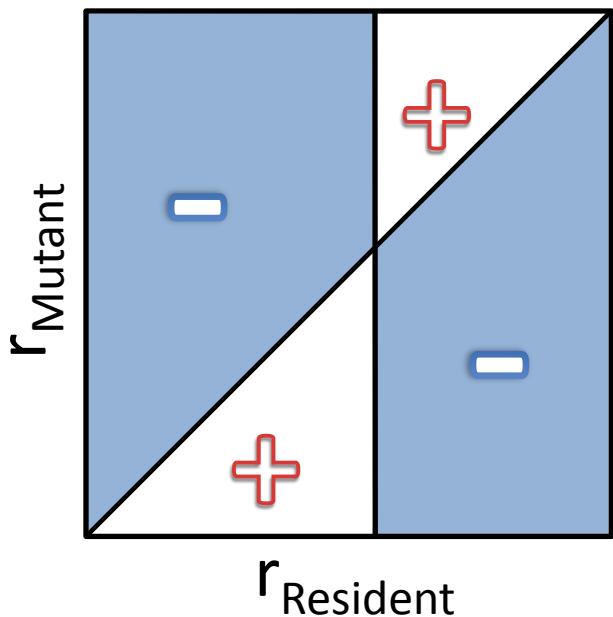
Cycle: $b/c = 10/3$

r : probability to reciprocate

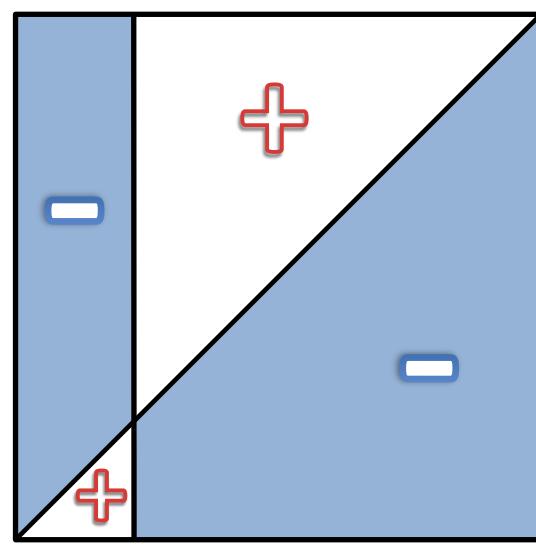
Initial growth rate starting with a single mutant?



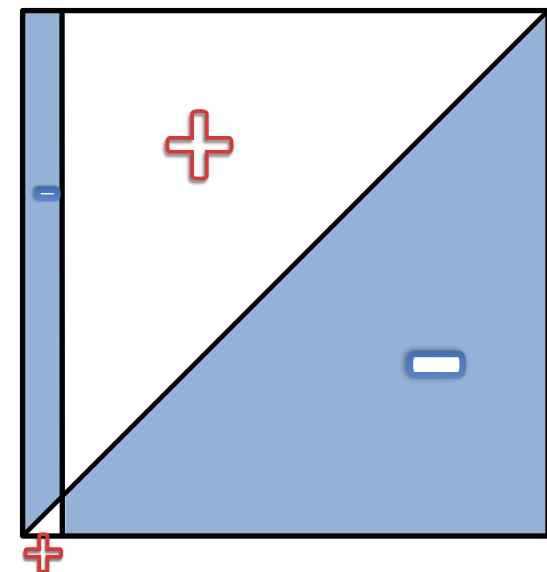
Continuous case



Cycle: $b/c = 10/3$

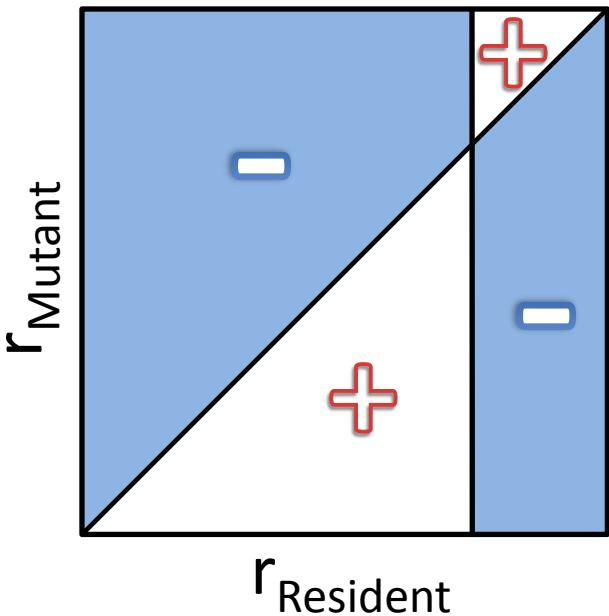


$b/c = 10/1$

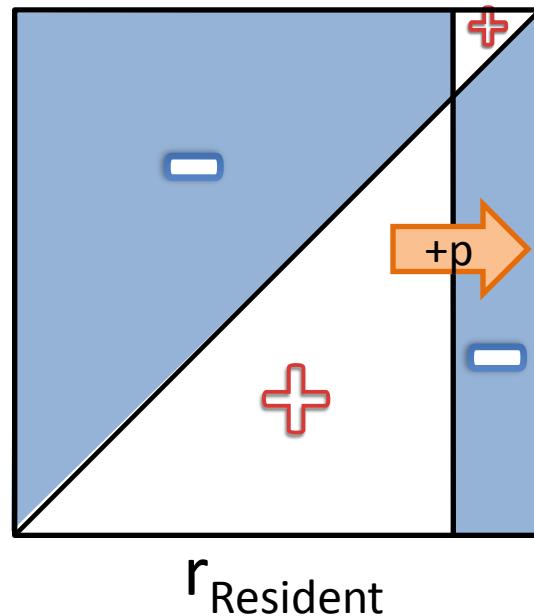


$b/c = 100/1$

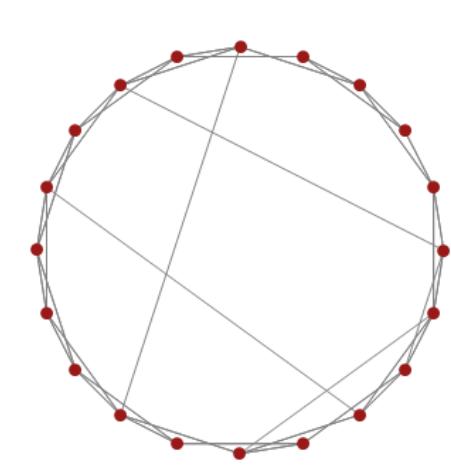
Continuous case



1D lattice: $b/c = 10/3$
 $k=4, p=0$

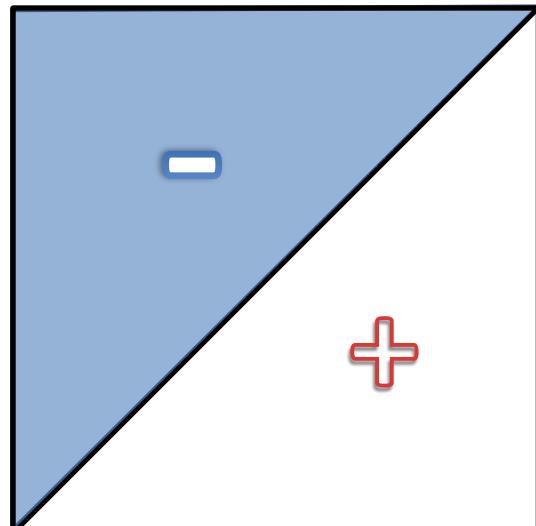


Small world: $b/c = 10/3$
 $k=4, \underline{p=0.1}$



Continuous case

r_{Mutant}



Star: $b/c = 10/3$

$N=100$

r_{Resident}



Dolphin: $b/c = 10/3$

$N=61$

r_{Resident}

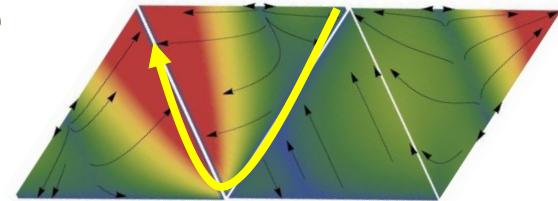
Generalized Reciprocity

Discrete strategies without genetic linkage

sparse graphs

neutral path to altruism

high rates of reciprocation



Continuous strategies

evolution of cooperation requires

extreme population structure

extreme b/c ratio

perturbations

