

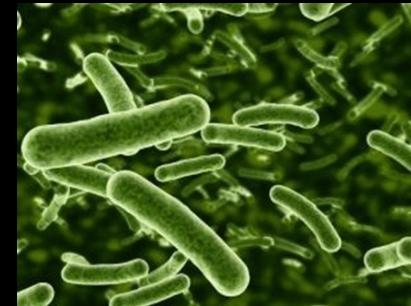
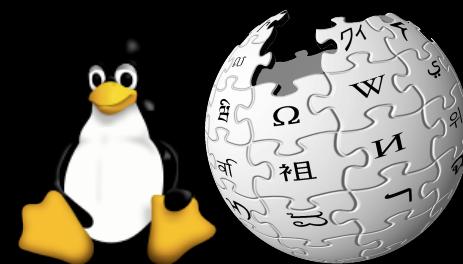


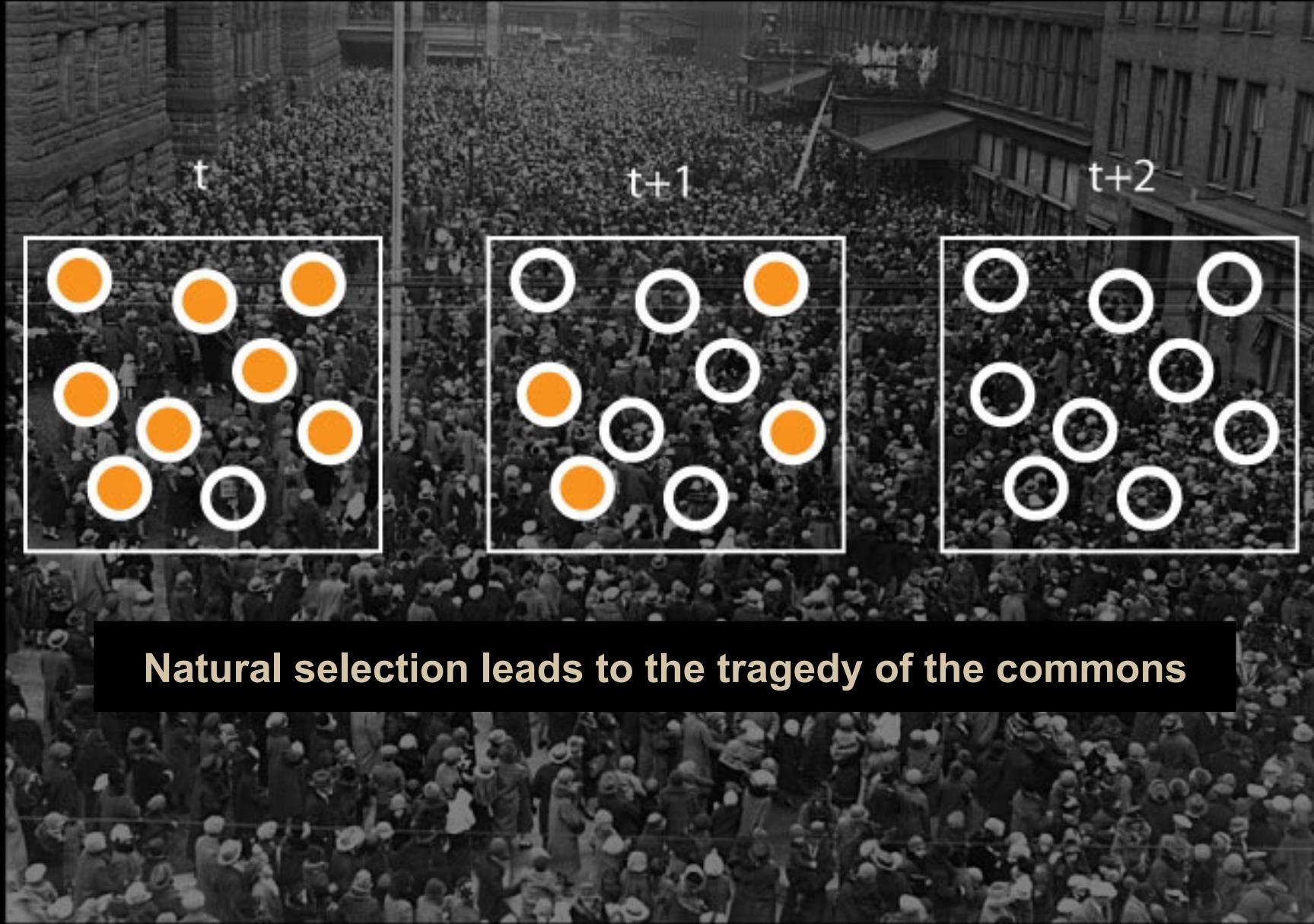
# Games on networks

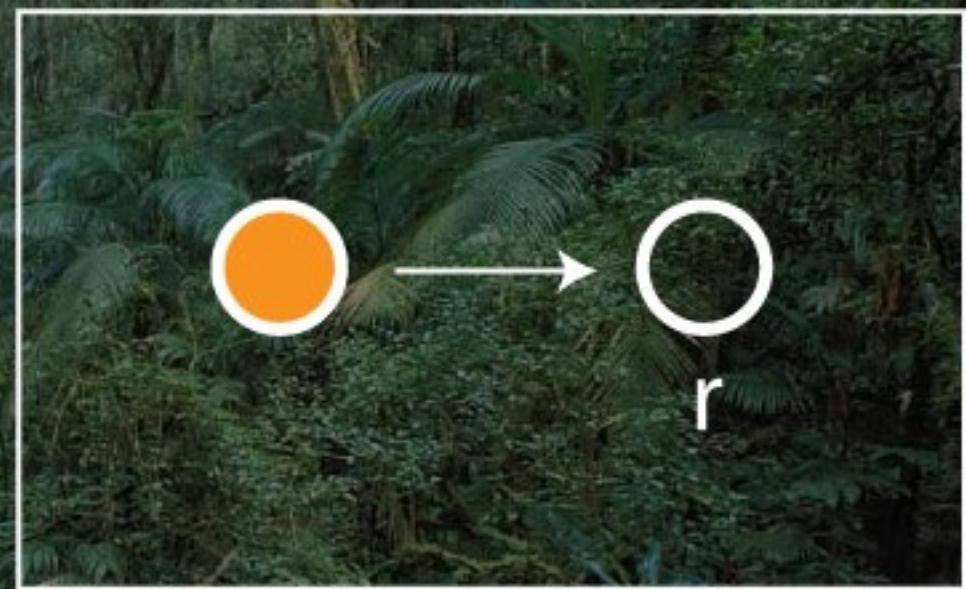




# cooperation at all scales



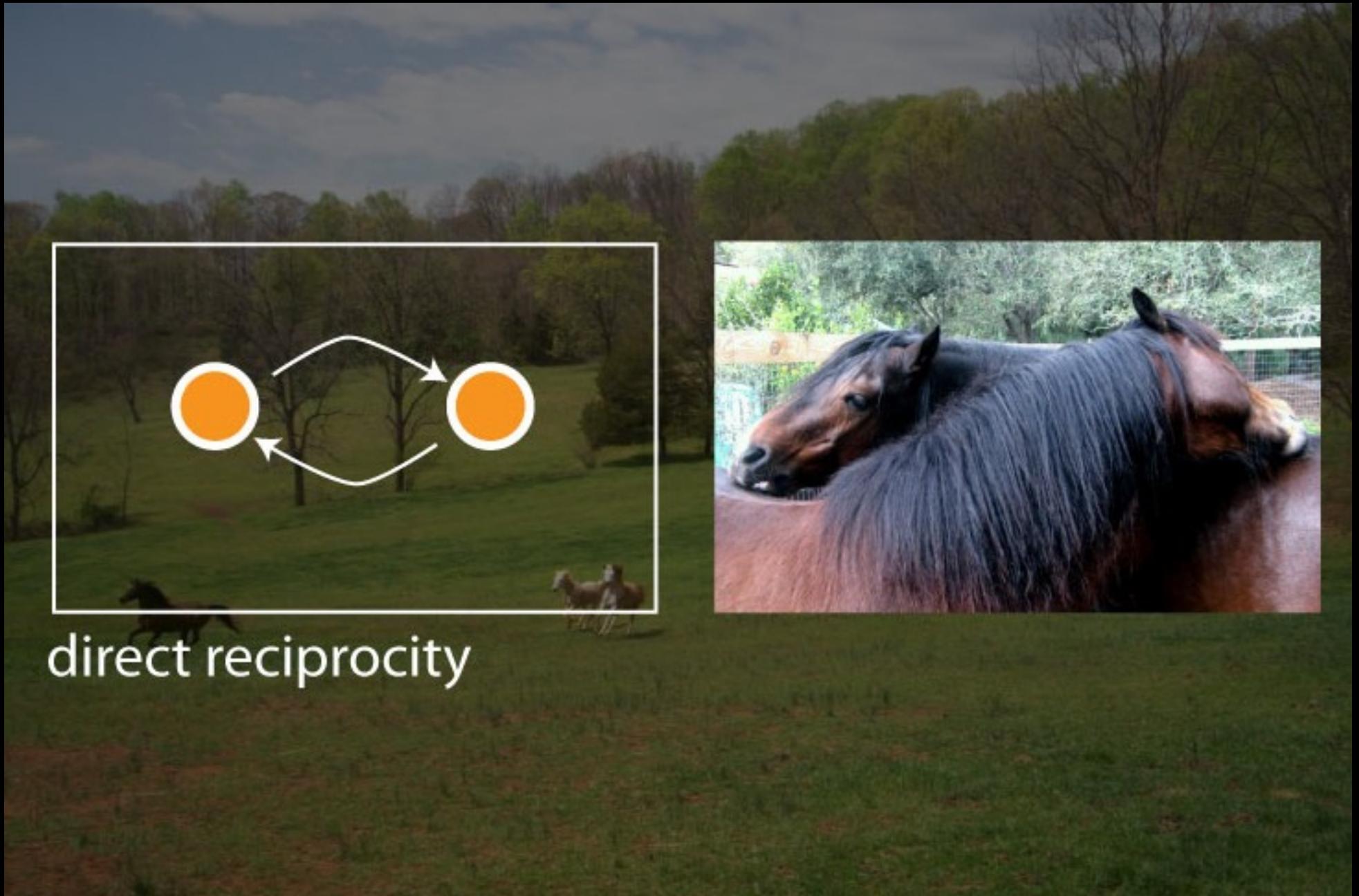




kin selection



Multi-level selection



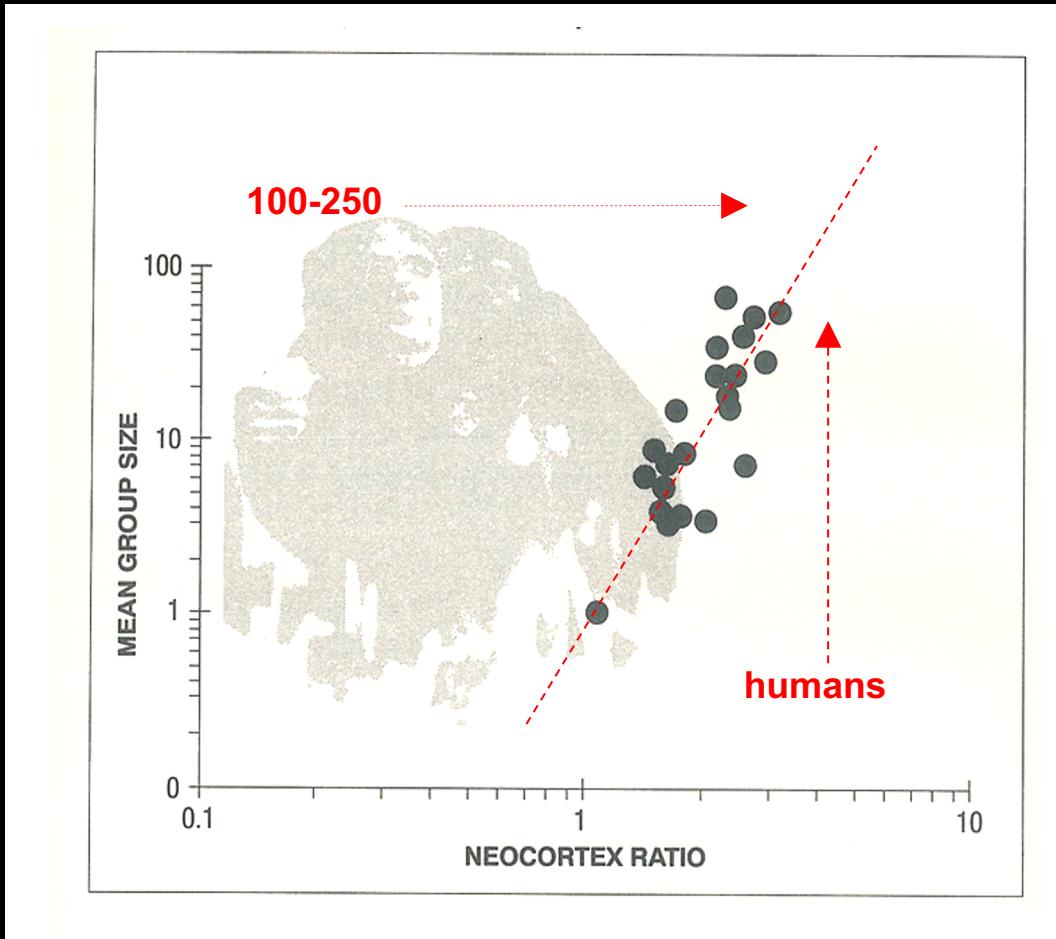
direct reciprocity



# Evolution of social-cognition & cooperation

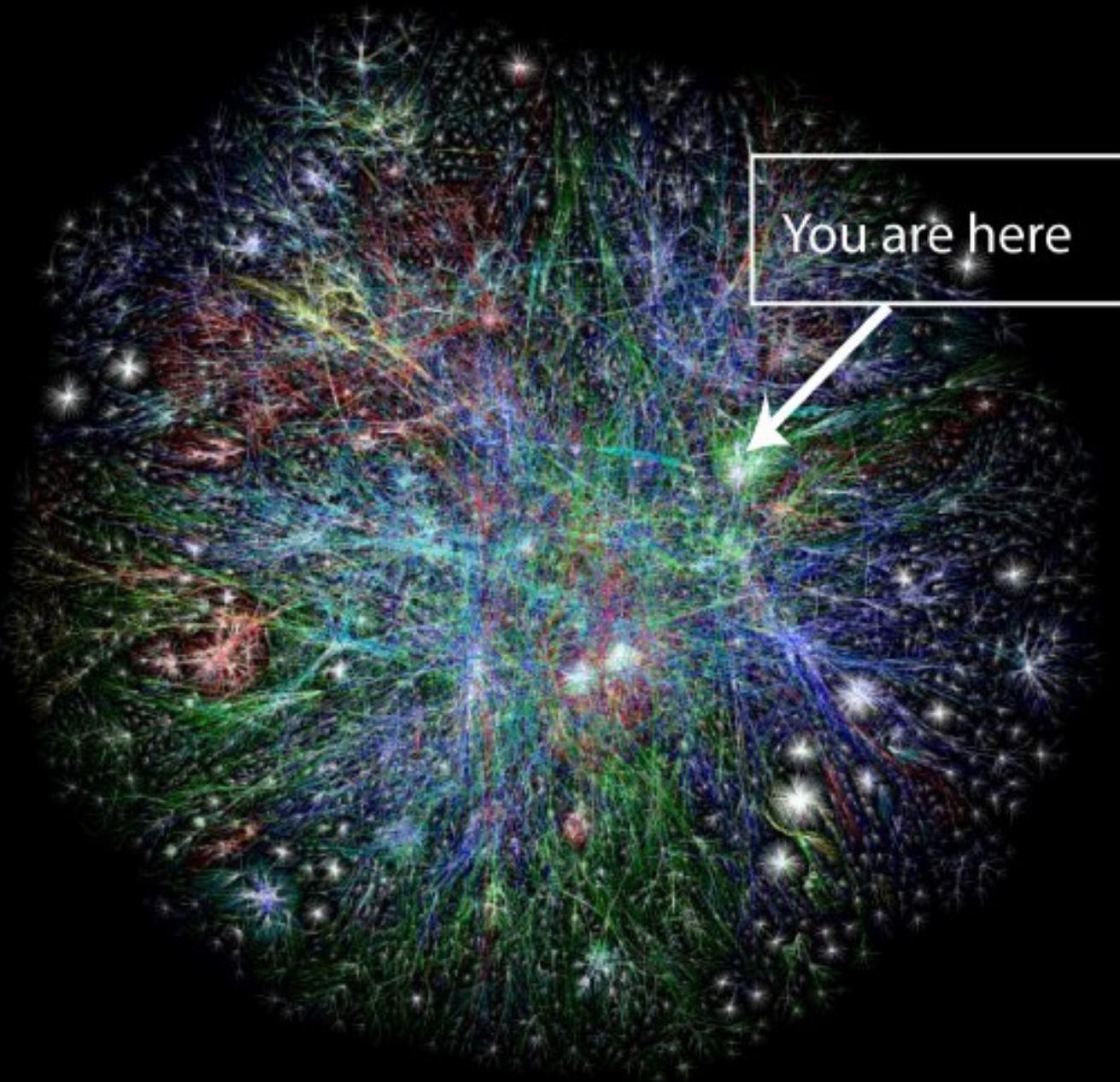
## Co-evolution of different features

- i) Social cognition
- ii) Group size
- iii) Cooperation and social cohesion



# A new evolutionary paradigm

Evolution in networked populations



# Evolution in structured populations

---

***classical social structure metaphor:***

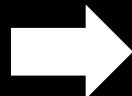
individuals, members of a population, occupy the vertices of a graph or network, whose edges define who interacts with whom.

graphs provide a very convenient means of representing the inter-relations between processes, organisms, organizations, populations or even components of these.

different organisms may be represented by different graphs

the same organisms may be inter-related by means of more than one graph.

# Tools for studying games on graphs



## ❖ competition between cooperators and defectors

numerically :

finite populations;

any kind of network

different intensities of selection (weak to very strong)

[ Abramson, Kuperman, *PRE* 63, 030901(R) (2001) ]

[ Santos, Pacheco, *PRL* 95 (2005) 098104 ]

[ Santos, Pacheco, Lenaerts, *PNAS* 103 (2006) 3490 ]

[ Santos, Pacheco, *J. Evo. Biol.* 19 (2006) 726 ]

## ❖ fixation probabilities

analytically w/ approximations & numerically

weak selection (game is but a small perturbation to fitness)

finite & infinite populations

regular graphs (strictly : trees)

[ Ohtsuki, Hauert, Lieberman, Nowak, *Nature* 441 (2006) 502 ]

[ Ohtsuki, Nowak, *JTB* 243 (2006) 86 ]

[ Pacheco, Ohtsuki, Nowak, *PRL* 98 (2007) 108106 ]

## ❖ Average gradients of selection

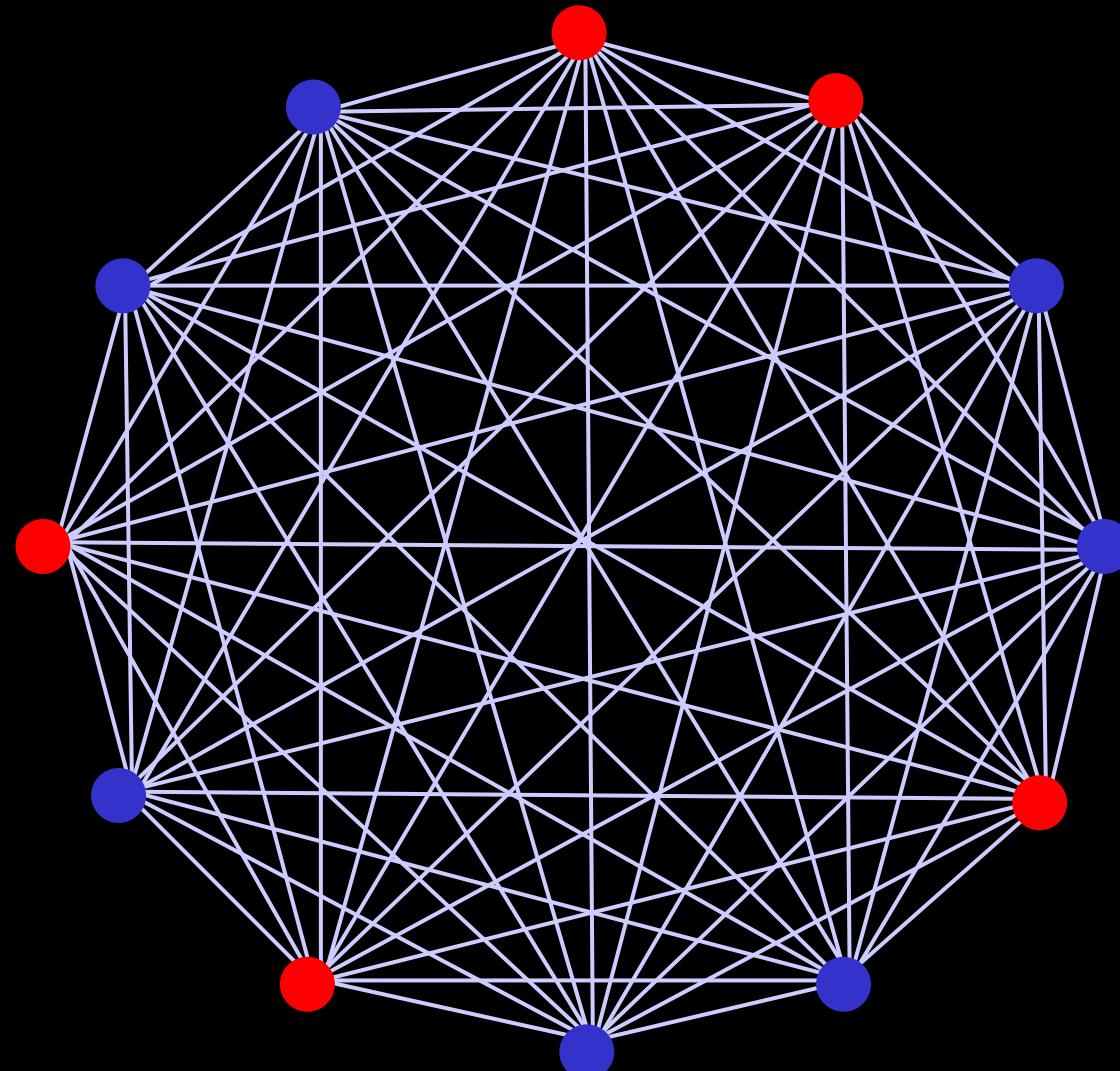
mean-field description of population-wide dynamics

finite populations ; any kind of network ; any intensity of selection

[ Pinheiro, Pacheco, Santos, *PLoS One* 2012 ]

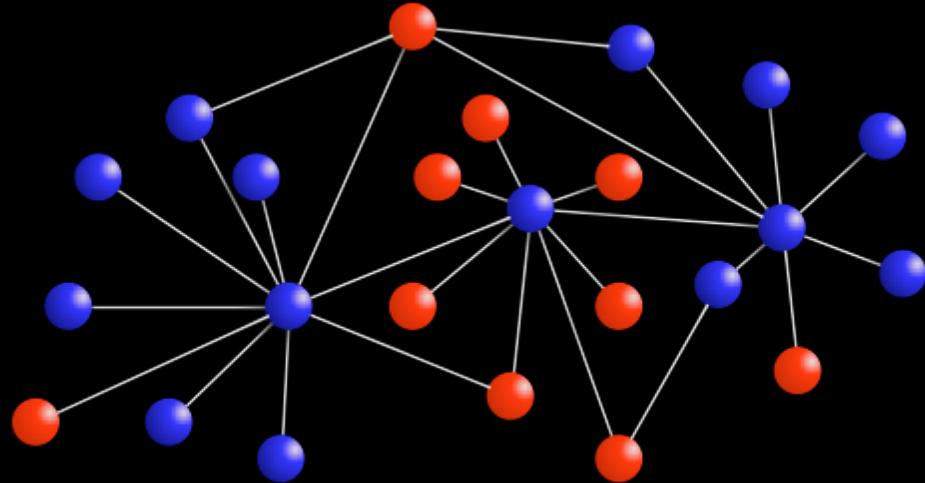
[ Pinheiro, Santos, Pacheco, *New J Phys* 2012 ]

***well-mixed population***  
each individual interacts with ***ALL*** others



→ ***complete graph***

# Multi-agent simulations of social networks

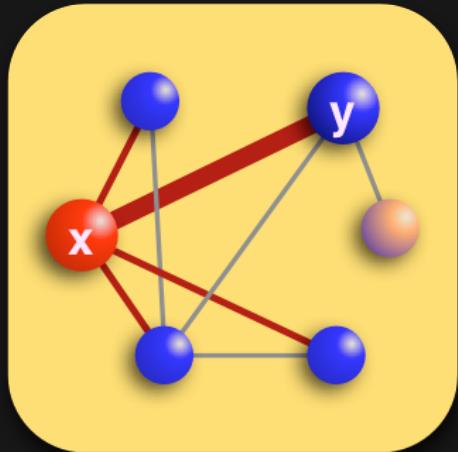


## setup:

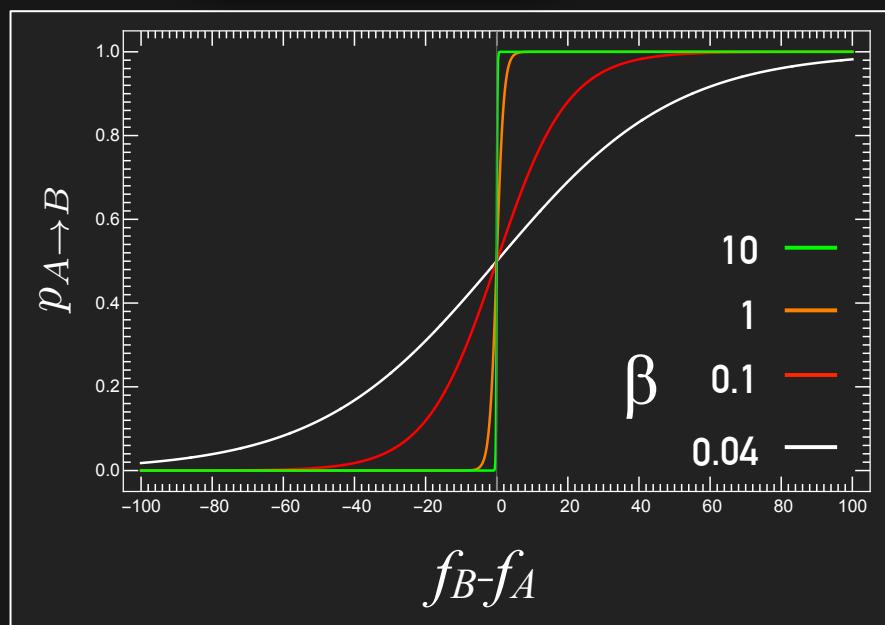
- **Community is defined by a graph static graph**
- **Links define interactions and imitation partners**
- **50% of Ds and 50% of Cs.**
- **evolve for many generations**
- **average over many runs**

# Social learning / Evolution on graphs

*Imagine the simplest form of social learning:*



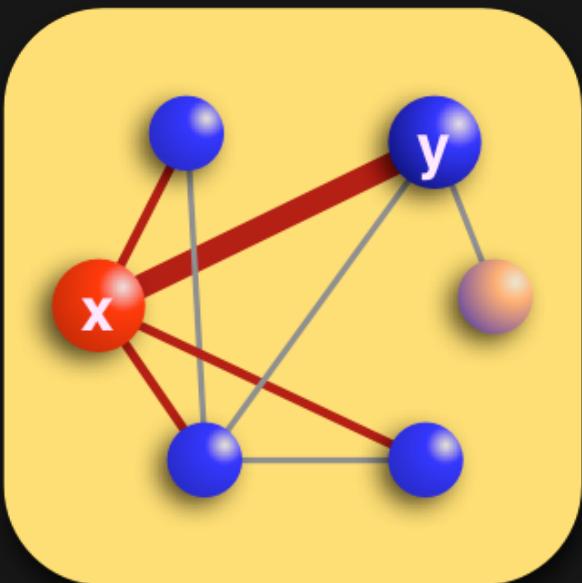
*Imitate a random neighbor with a probability that increases with the fitness difference.*



$$p = \left[ 1 + e^{-\beta(f_B - f_A)} \right]^{-1}$$

# Simulations

*Imagine the simplest form of social learning (alternative):*



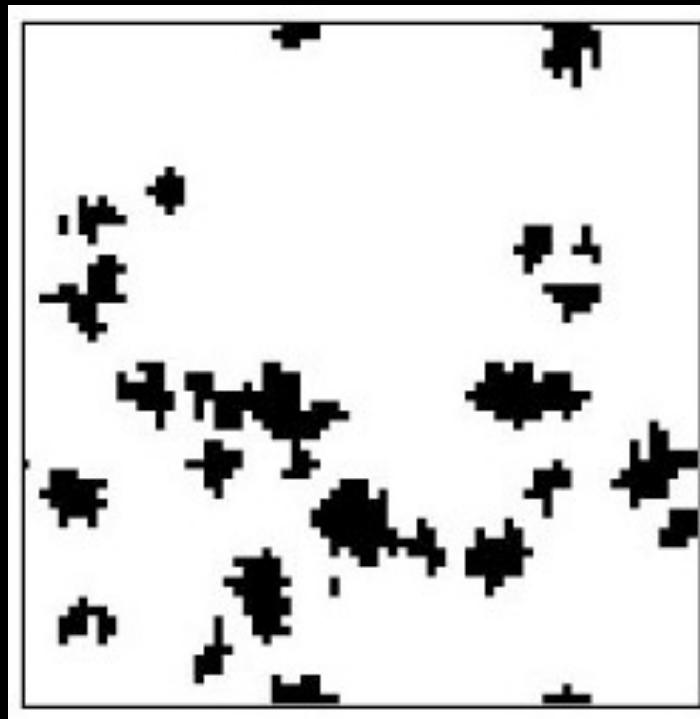
*Imitate a random neighbor with a probability that increases with the fitness difference.*

$$p = \frac{f_B - f_A}{\Delta f_{MAX}}$$

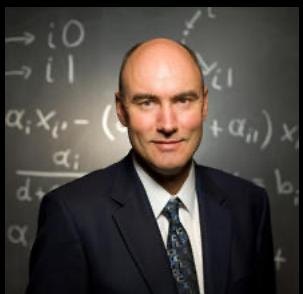
(If  $p < 0$  assume  $p=0$ )

# Cooperation in homogeneous worlds

## Spatial reciprocity



[ Nowak & May, *Nature* 1992 ]

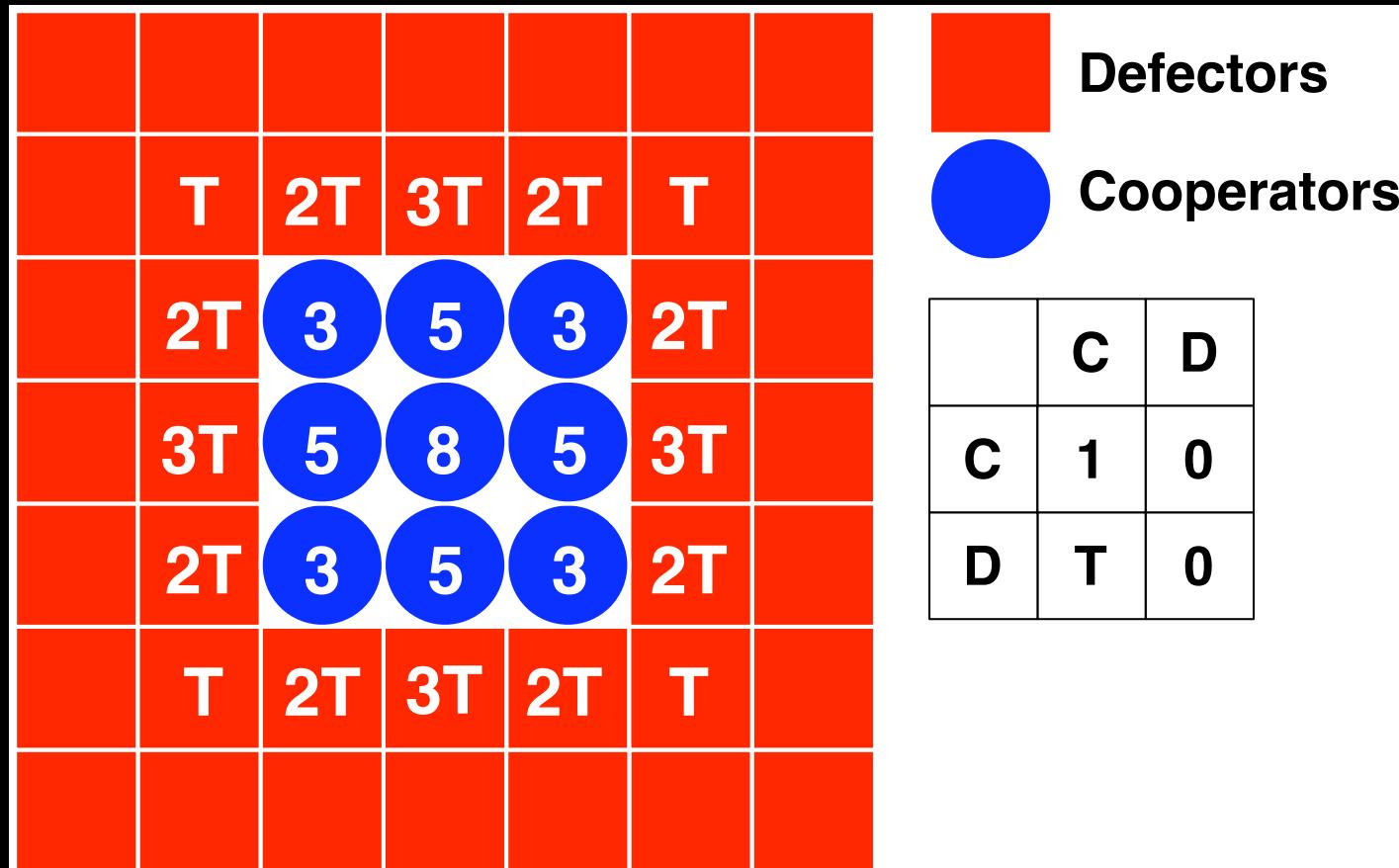


Martin Nowak  
Harvard, USA



Robert May  
Oxford

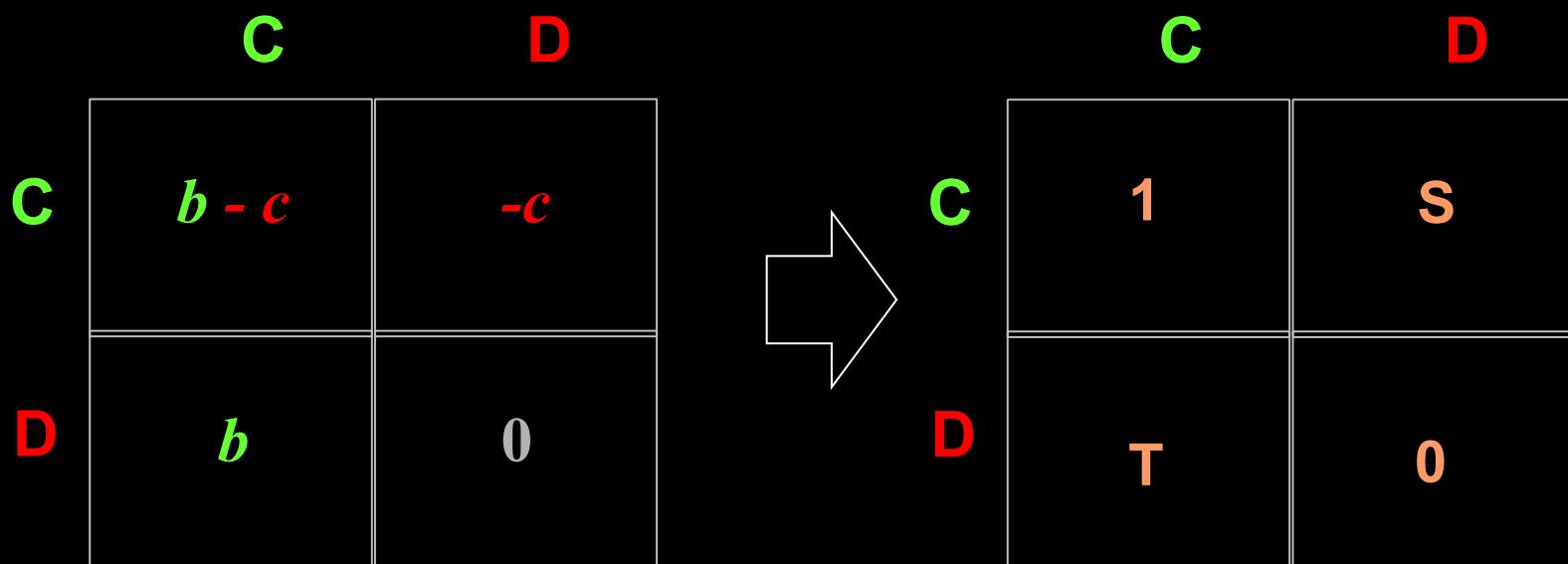
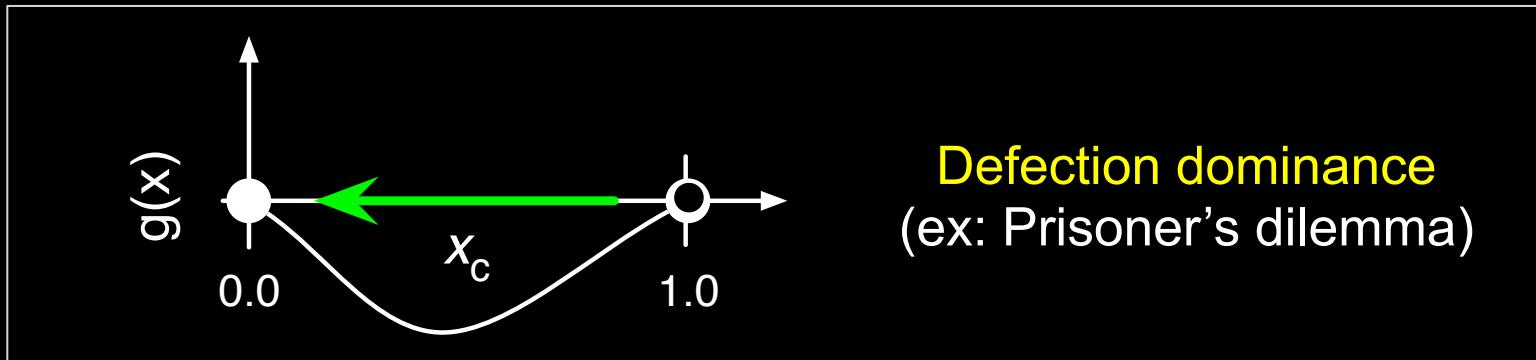
# Cooperation in homogeneous worlds



[ Nowak & May, *Nature* 1992 ]

Is this result valid for any kind of  
cooperation dilemma?

# The calculus of 2-player games



# Different tensions, different dilemmas

**P > S → ( DD is better than CD )**

**one may associate S with fear (of being cheated)**

**T > R → ( DC is better than CC )**

**one may associate T with greed (temptation to cheat)**

we can fix  $R=1$  and  $P=0$ , and vary the intensities of greed and fear at will. as a result, we obtain the most popular social dilemmas of cooperation:

	C	D
C	R	S
D	T	P

# SG: snowdrift game

# SH: stag-hunt game

## **PD: prisoner' s dilemma**

## greed

# fear

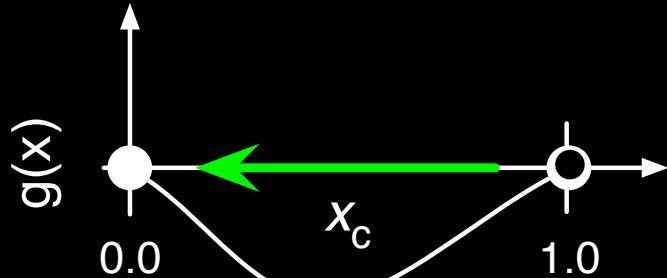
: T > R > S > P

: R > T > P > S

**T > R > P > S**

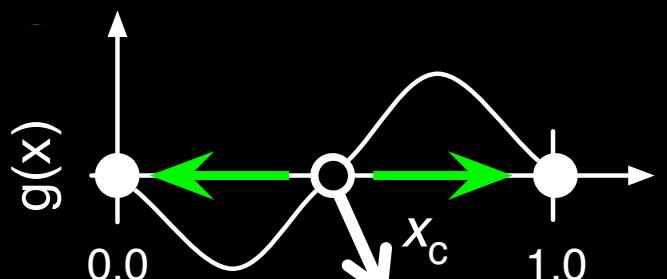
# The calculus of 2-player games

**T > R > P > S**



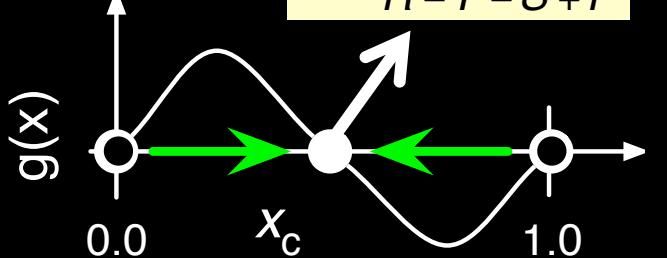
Defection dominance  
(ex: Prisoner's dilemma)

**R > T > P > S**



Bi-stability  
(ex: coordination games,  
stag-hunt game, etc.)

**T > R > S > P**



Co-existence  
(ex: snowdrift, chicken  
games, etc.)

$$x^* = \frac{S - P}{R - T - S + P}$$

## 2D space of 2-person dilemmas

SG: snowdrift game

$$T > R > S > P$$

SH: stag-hunt game

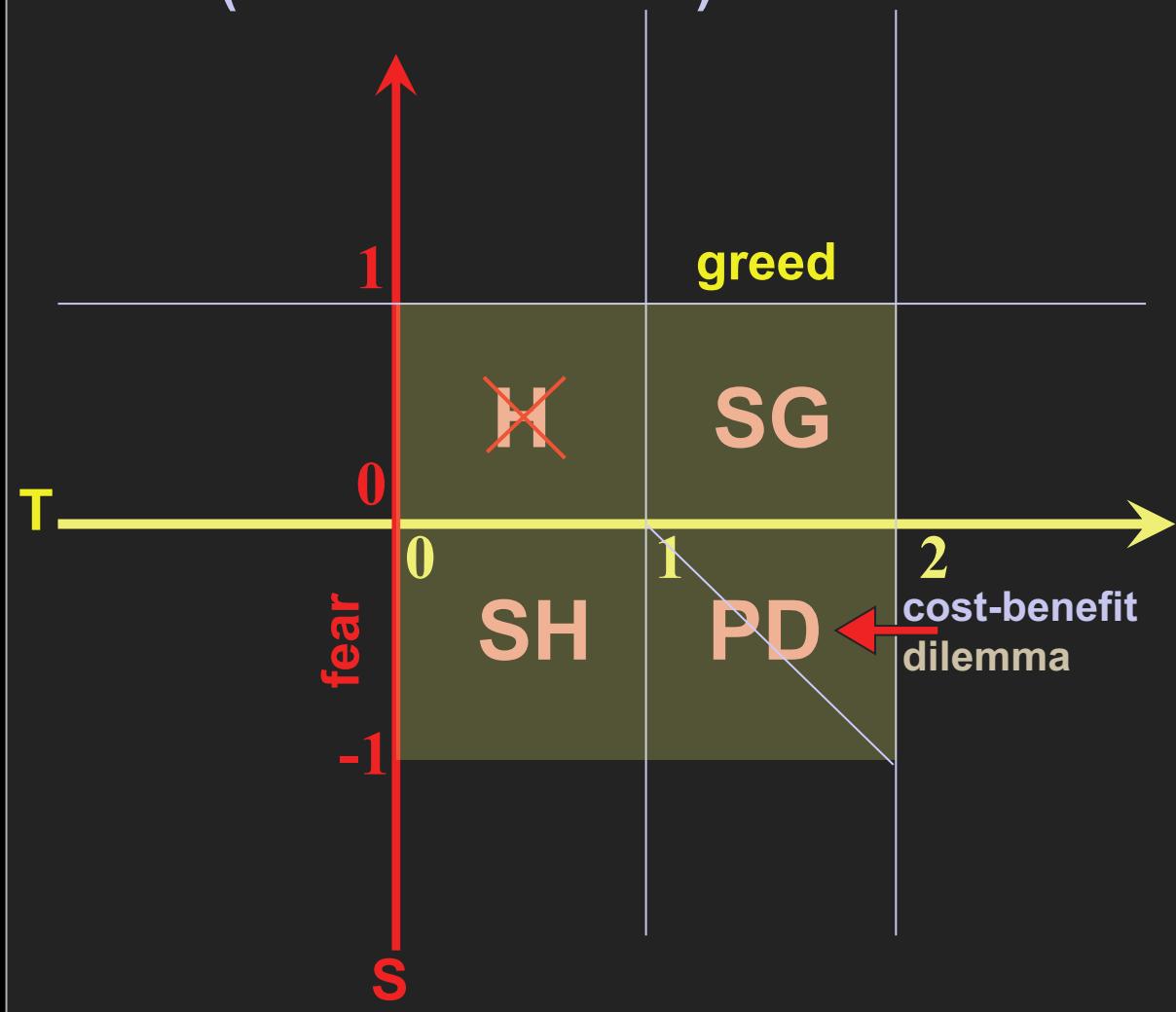
$$R > T > P > S$$

PD: prisoner's dilemma

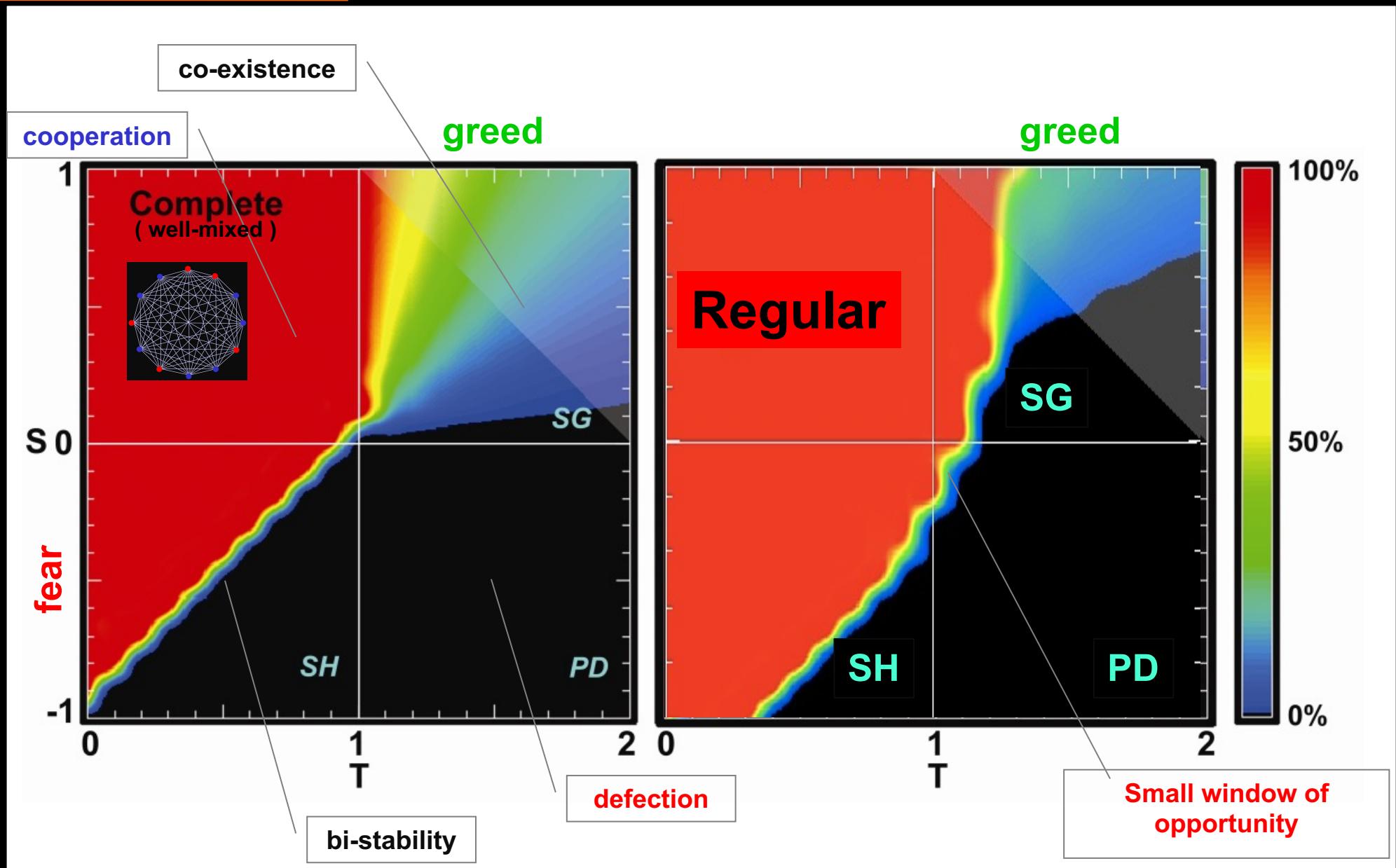
$$T > R > P > S$$

	C	D
C	R	S
D	T	P

$R = 1$  (mutual cooperation)  
 $P = 0$  (mutual defection)

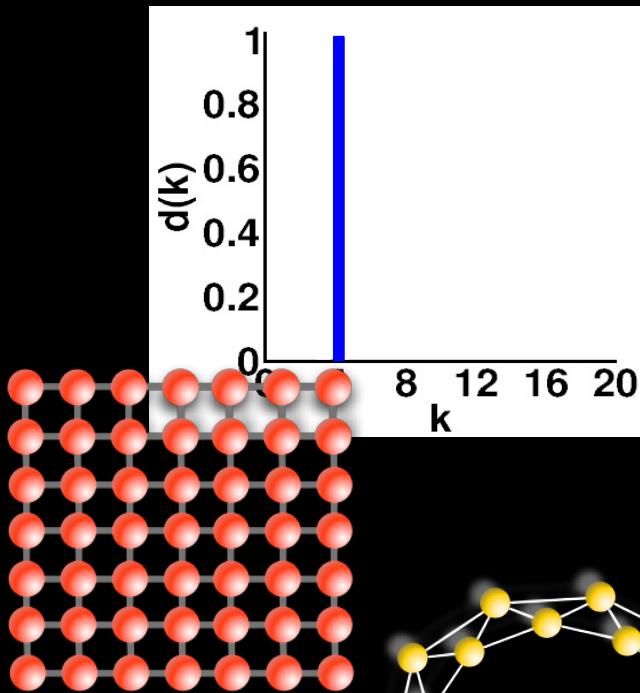


# Cooperation in homogeneous worlds



# What's the role of heterogeneity?

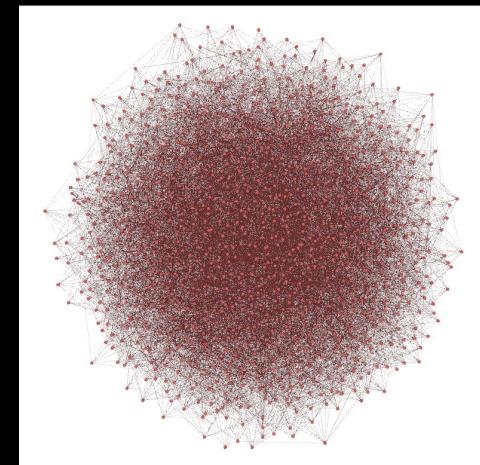
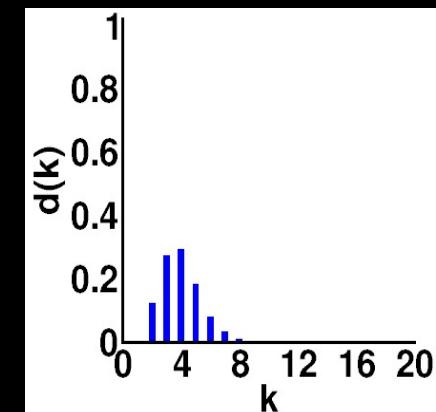
**Homogeneous networks**  
Regular graphs, lattices...



Heterogeneity



**Heterogeneous networks**  
Ex: Random graph

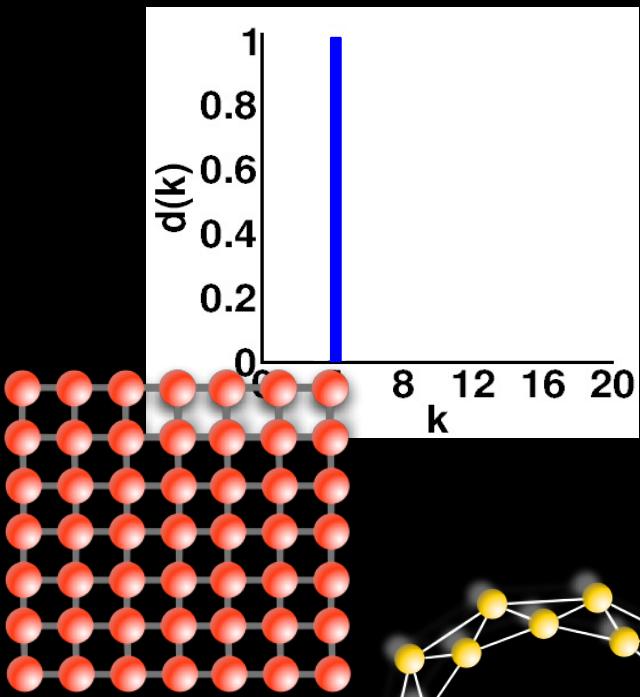


Erdős–Rényi  
model

$k$  = degree = number of connections

# What's the role of heterogeneity?

**Homogeneous networks**  
Regular graphs, lattices...

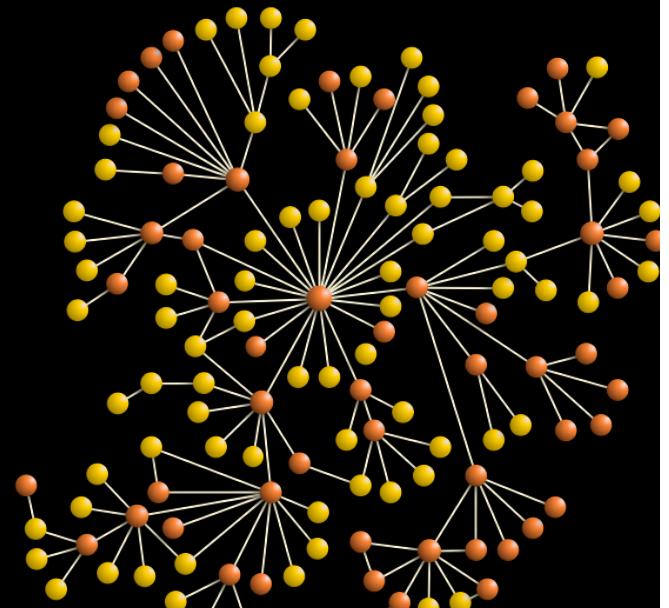
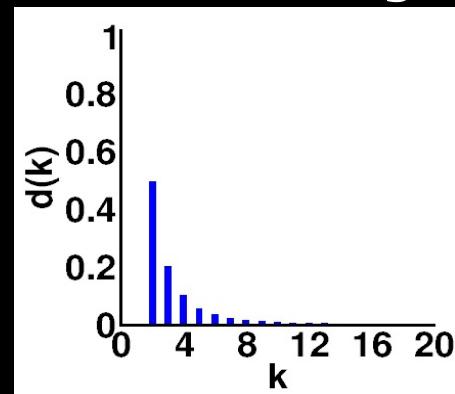


$k$  = degree = number of connections

Heterogeneity



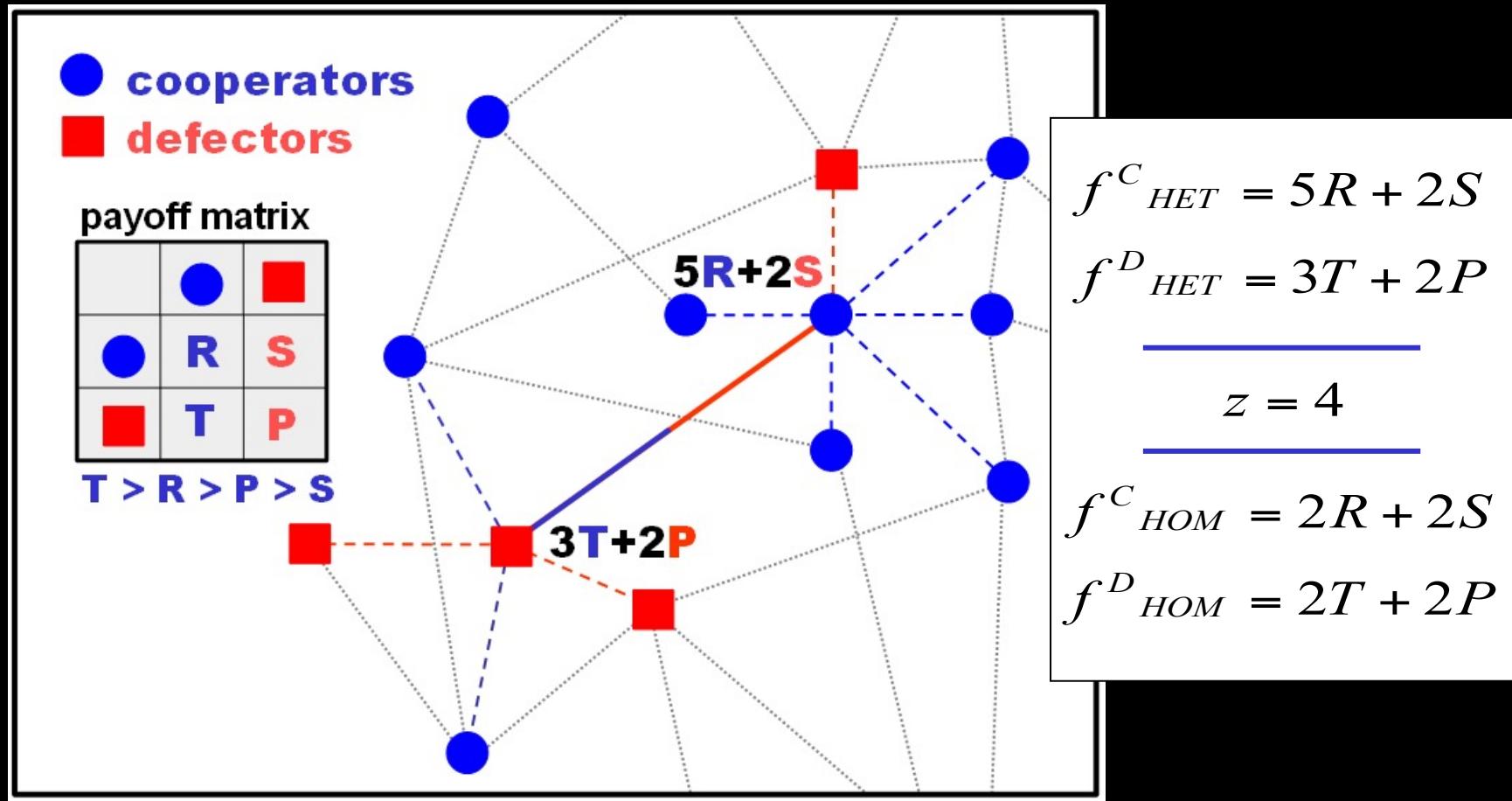
**Heterogeneous networks**  
Ex: Scale-free graph



growth  
+  
preferential  
attachment

Barabási & Albert, Science 1999

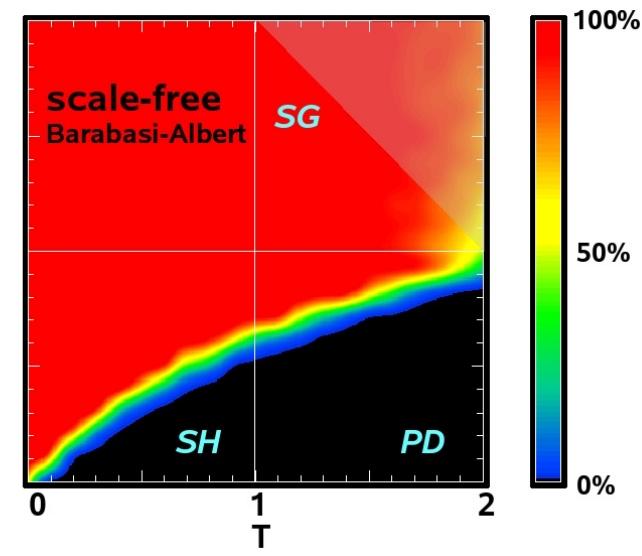
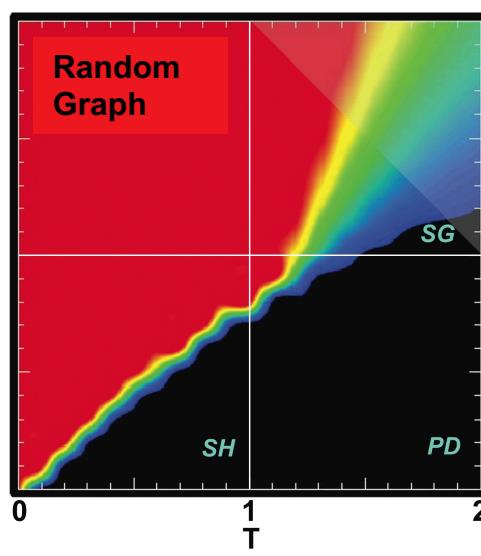
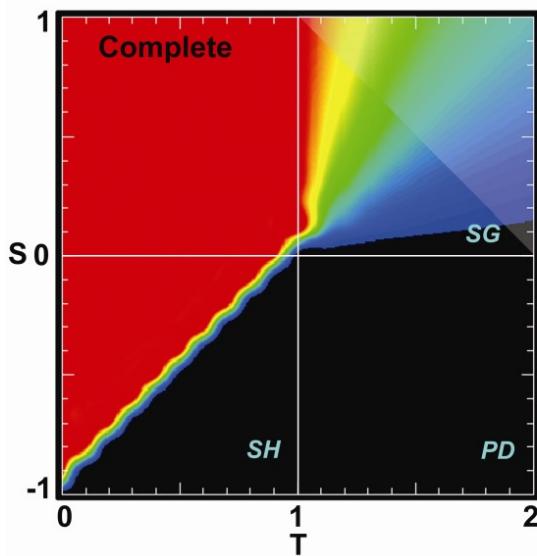
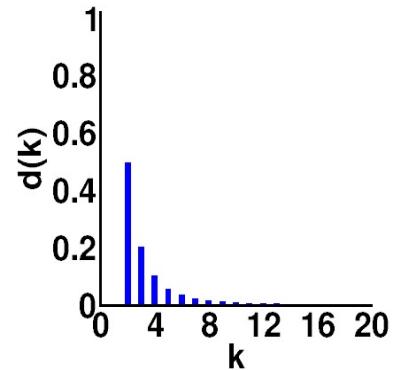
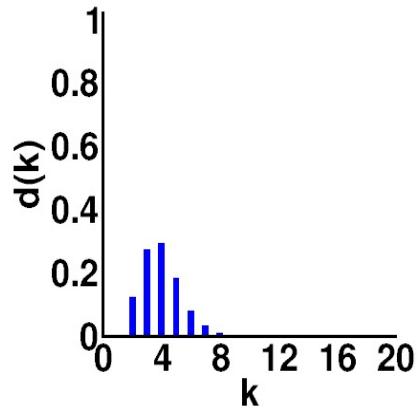
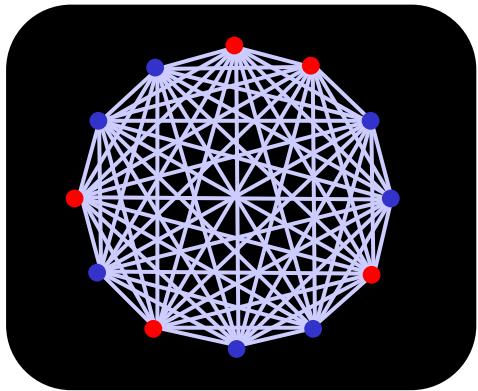
# Heterogeneity: A new route to cooperation?



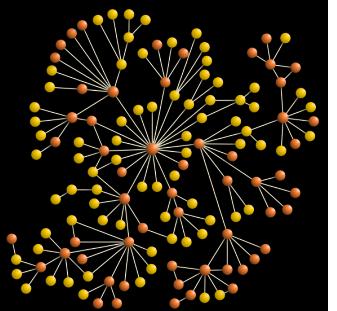
heterogeneity introduces a **connectivity-dependent term** in the **fitness** of each **individual**

**Both Cs and Ds benefit from occupying in highly connected positions**

# Larger the heterogeneity, larger the chances of cooperators



# cooperation on the star(s)

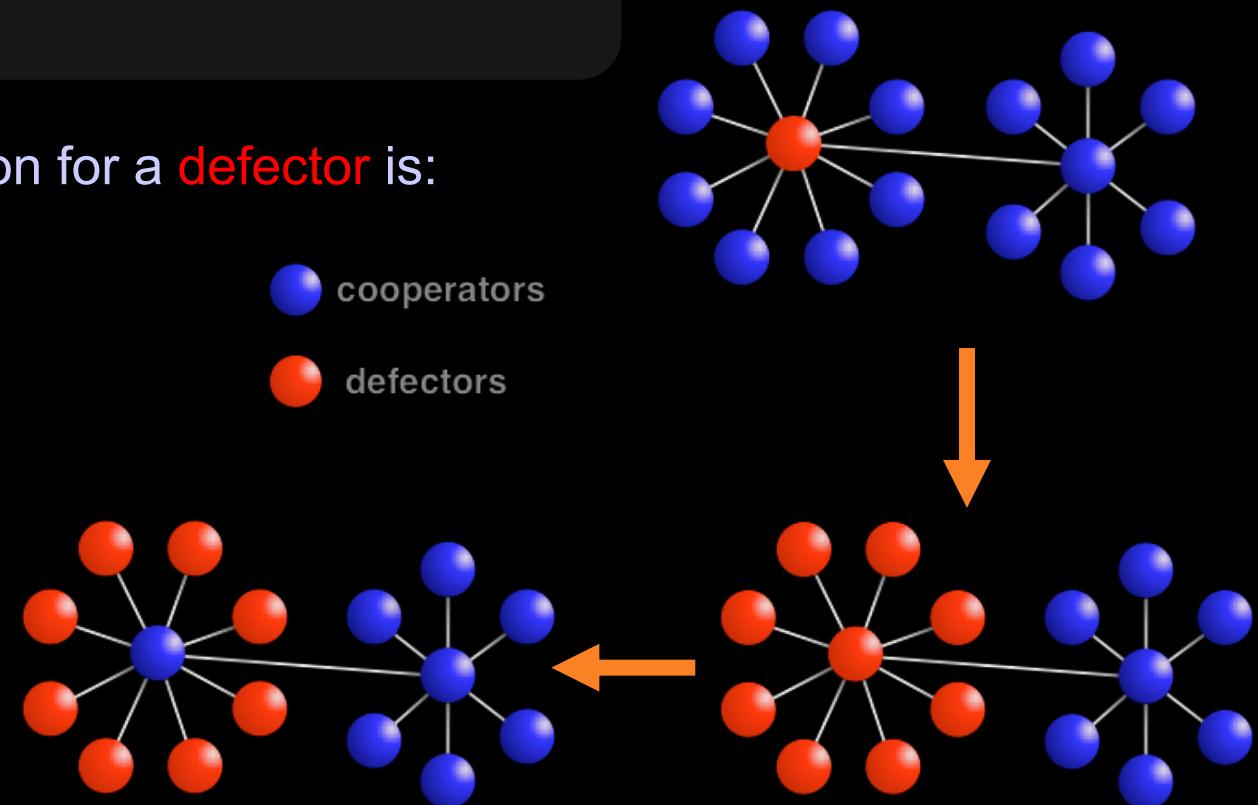


cooperators can dominate if they invade the hubs...

but, how can they get there?

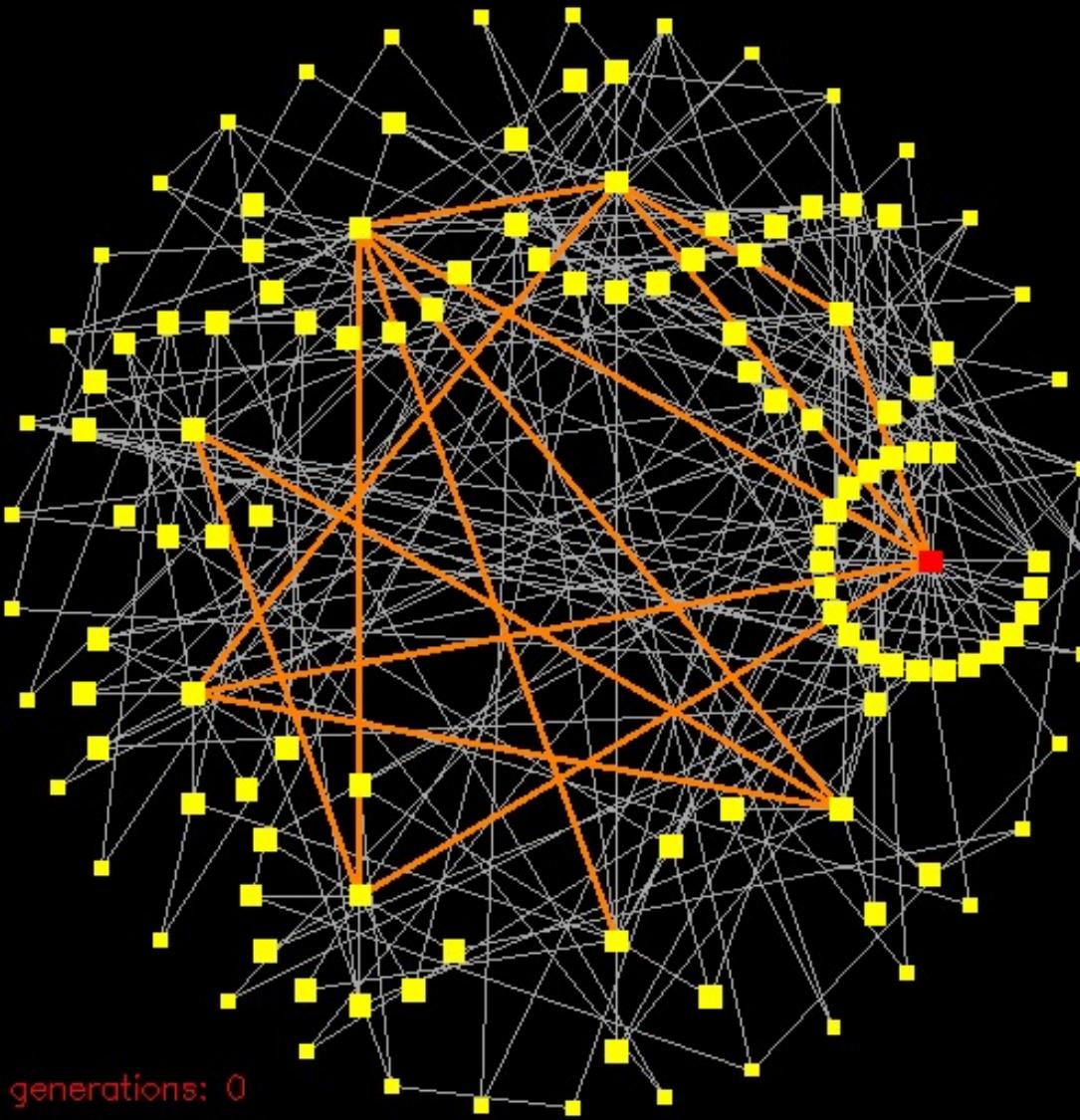
the most advantageous situation for a **defector** is:

- cooperators
- defectors



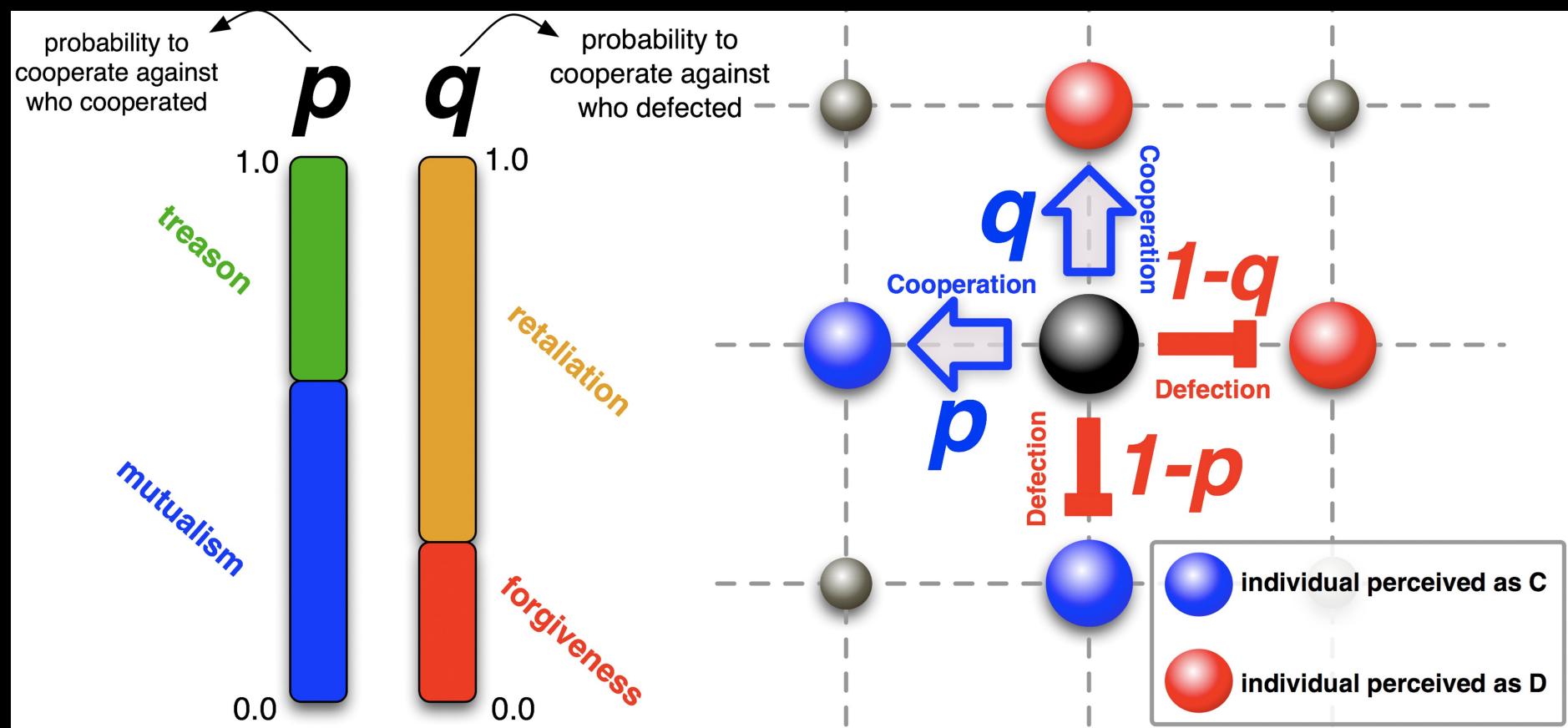
defectors are victims of their own success !!

# league of gentlemen

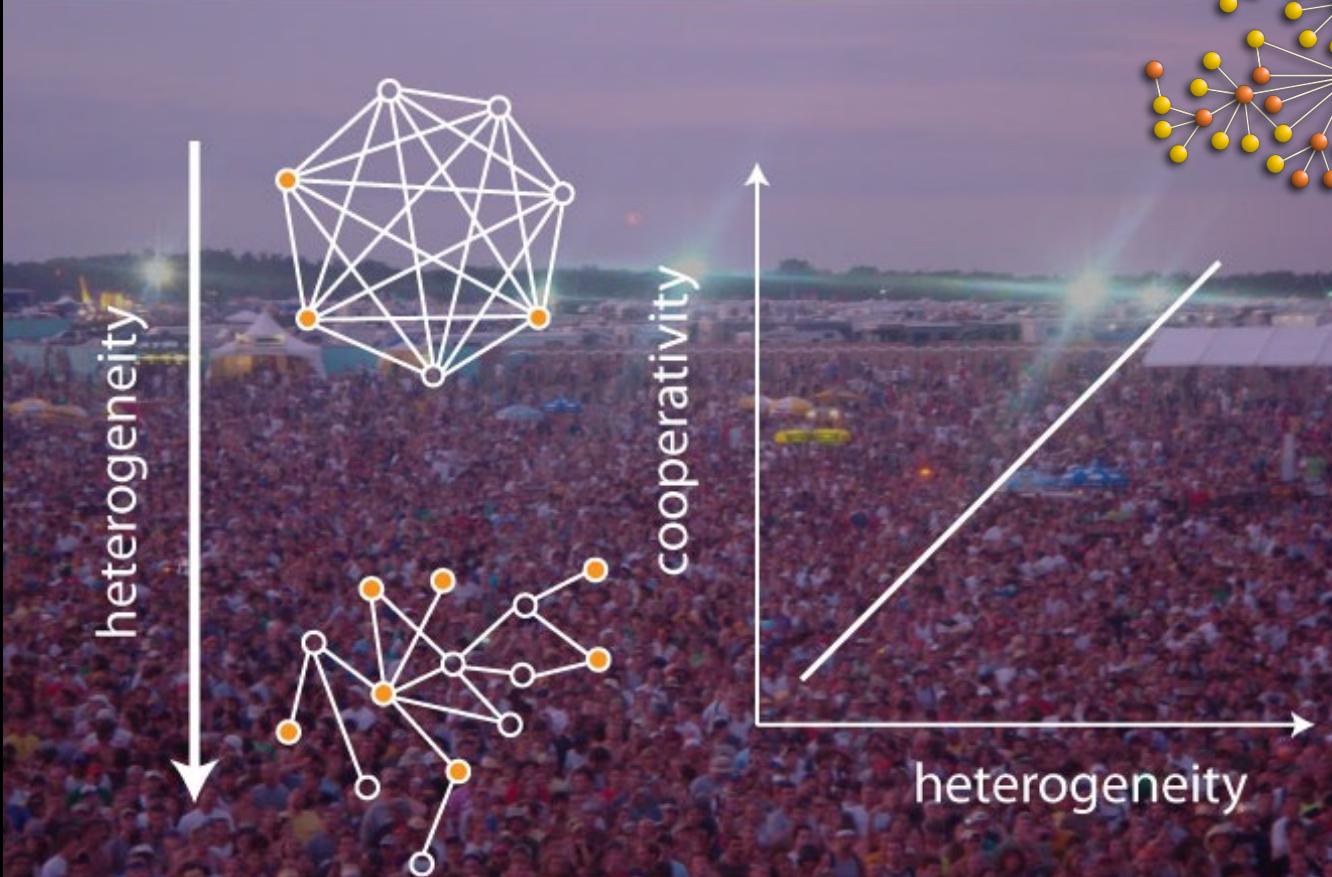


## Side note: Higher cognitive skills in networked populations

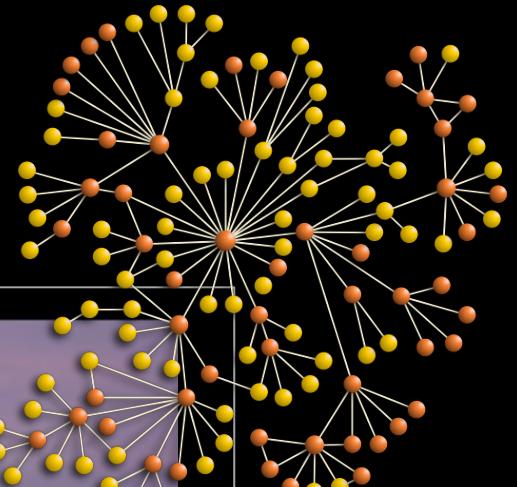
### Evolving higher cognitive skills in complex networks



# Conclusion

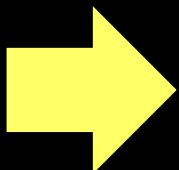


*The topology of real social networks seems to maximize the changes of reaching high levels of cooperation*

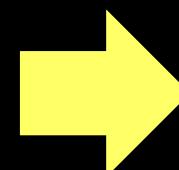


**But.... social networks are not static !!**

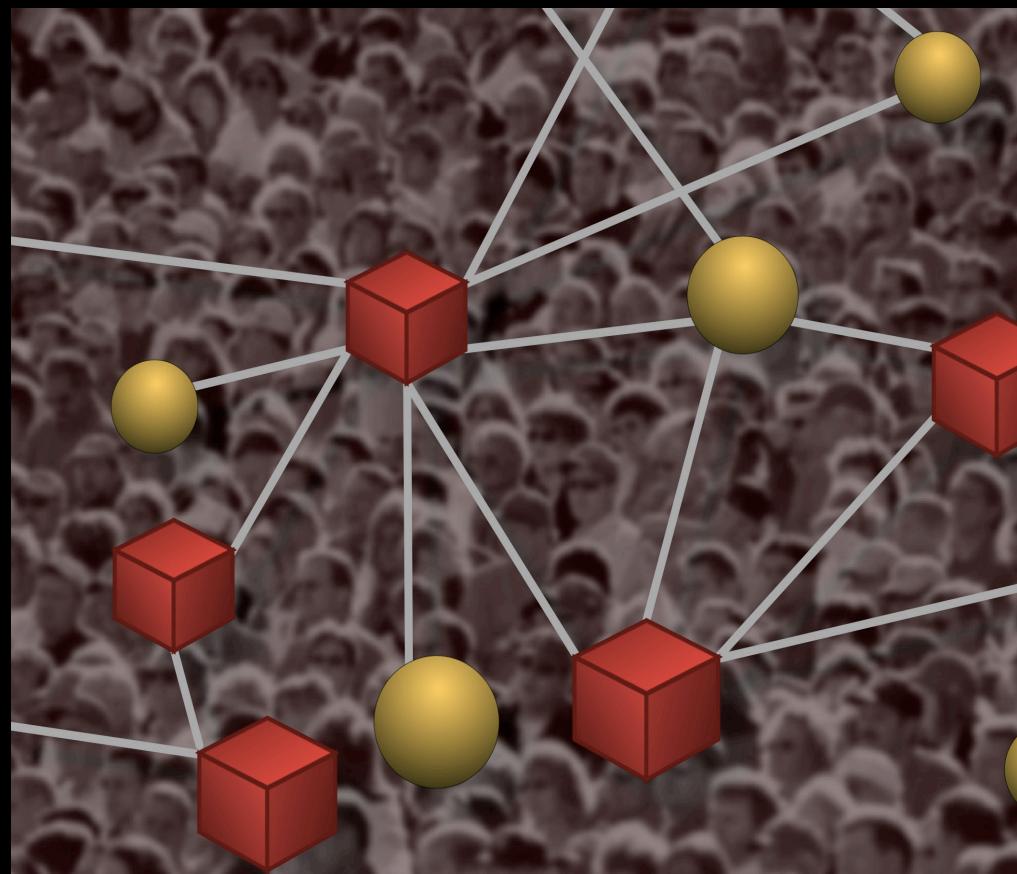
Unsatisfied individuals will tend to  
rewire/remove their connections.



Can we model social  
dynamics in evolving  
networks?



Can we identify a  
possible source of  
topological diversity?



# Adaptive networks

if you have a well-defined behaviour : C or D

*what is your best (most convenient) partner ?*

*for ALL social dilemmas*

**the best partner for any strategy is always a *Cooperator***

*consequently, irrespective of the dilemma :*

Cs look for Cs to cooperate with

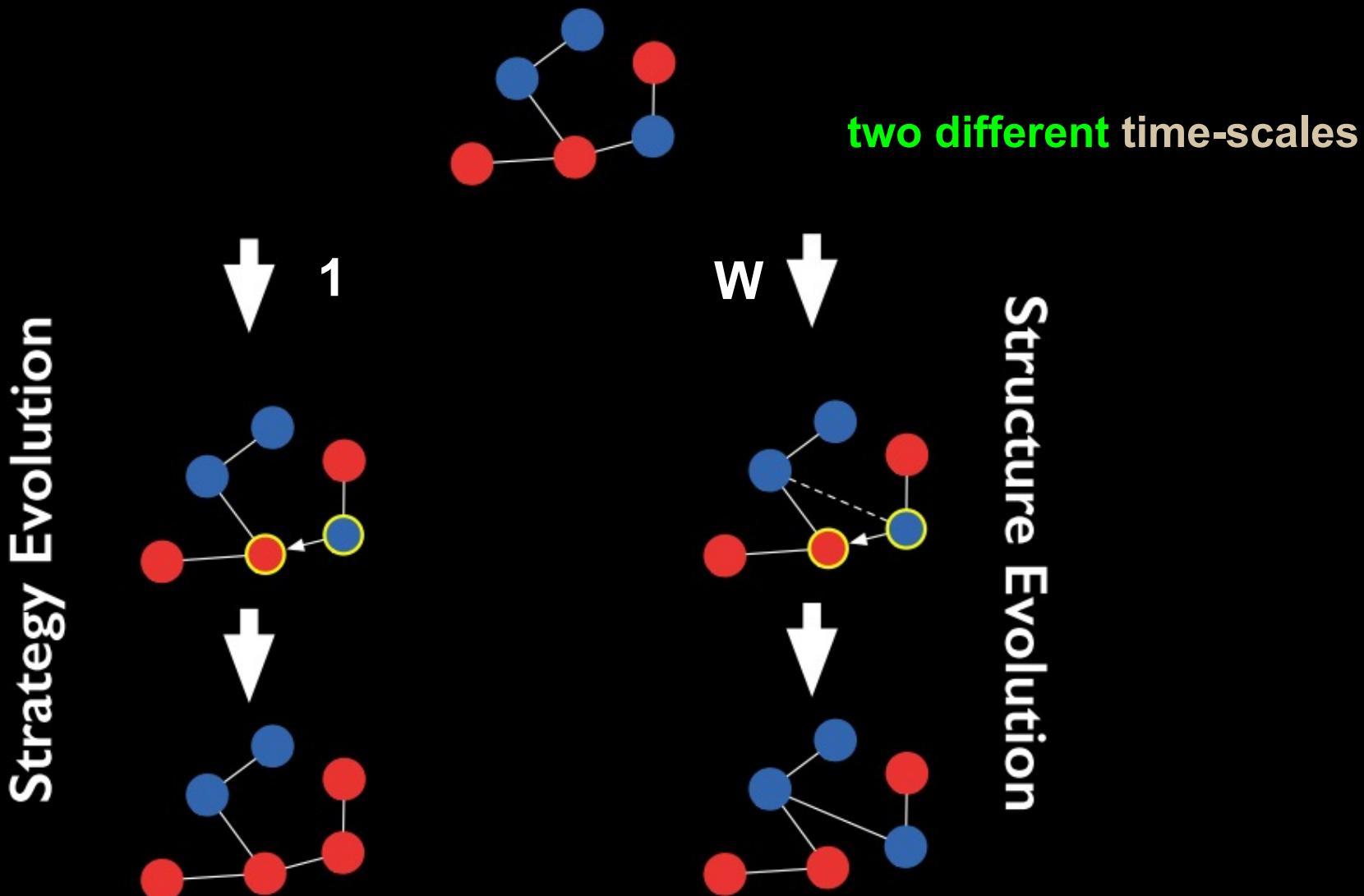
Ds look for Cs to exploit

- Agents can be satisfied or dissatisfied with a link.
- If dissatisfied agents rewire to a random 2nd neighbor

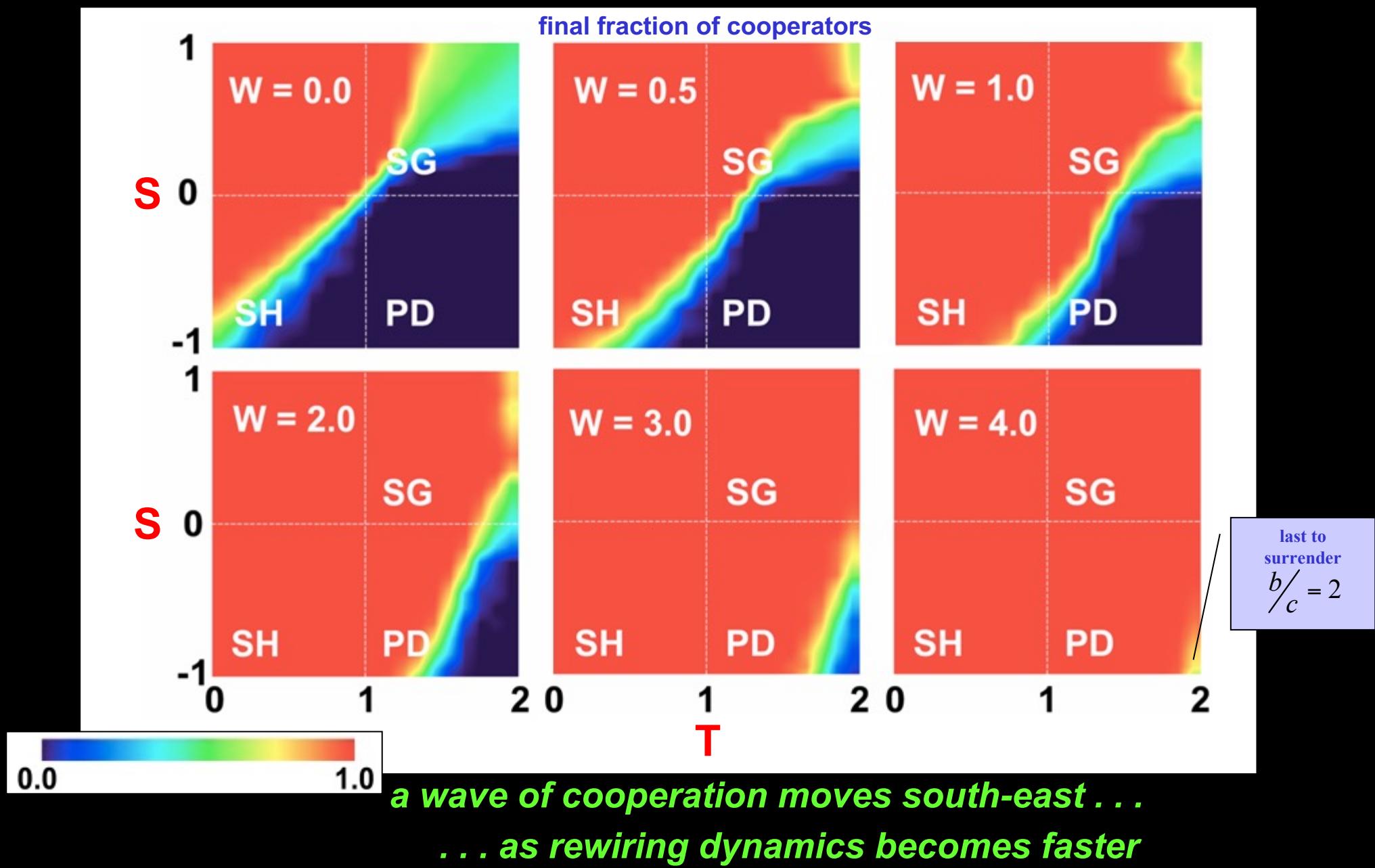
Santos, Pacheco, Lenaerts, PLoS Comput. Biol. (2006).,  
Pacheco, Traulsen , Nowak, Phys. Rev. Lett. (2006) .  
Van Segbroeck, Santos, Lenaerts, Pacheco, BMC Evol Bio (2008).  
...and others.

# Adaptive social networks

Santos, Pacheco, Lenaerts, PLoS Comput. Biol. (2006)  
Pinheiro, Santos, Pacheco, Phys Rev Lett, 2016.



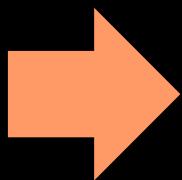
# Evolution of Cooperation in adaptive nets



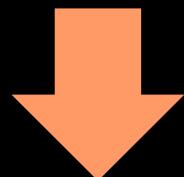
# Co-evolution of strategy and social ties

---

**Cs** look for **Cs** to cooperate with  
**Ds** look for **Cs** to exploit

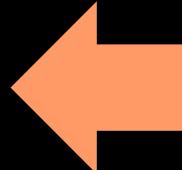


Good guys tend to acquire more links

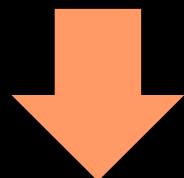


*Real network topologies ?*

*YES !!*

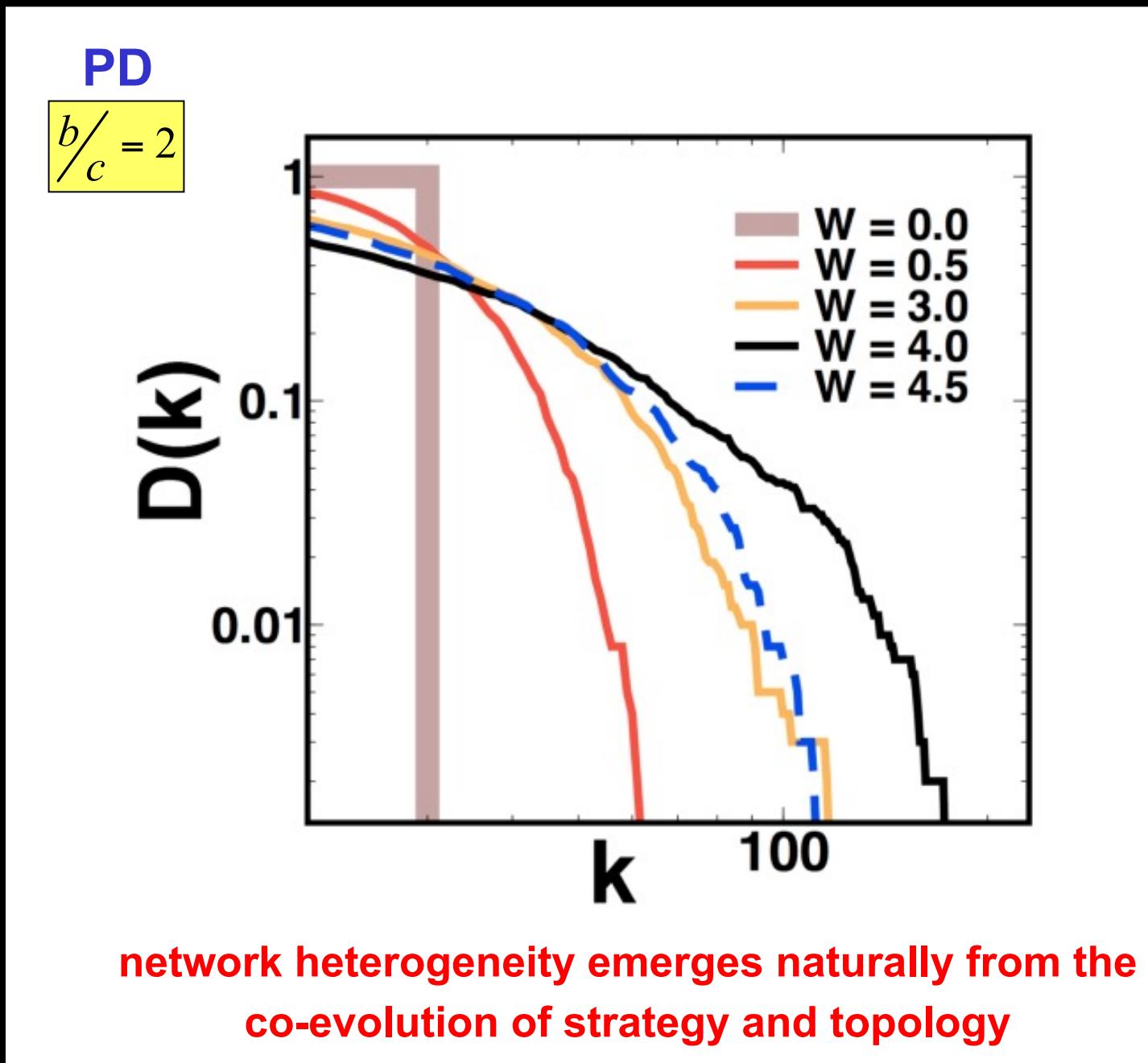


*Heterogeneity & Diversity*



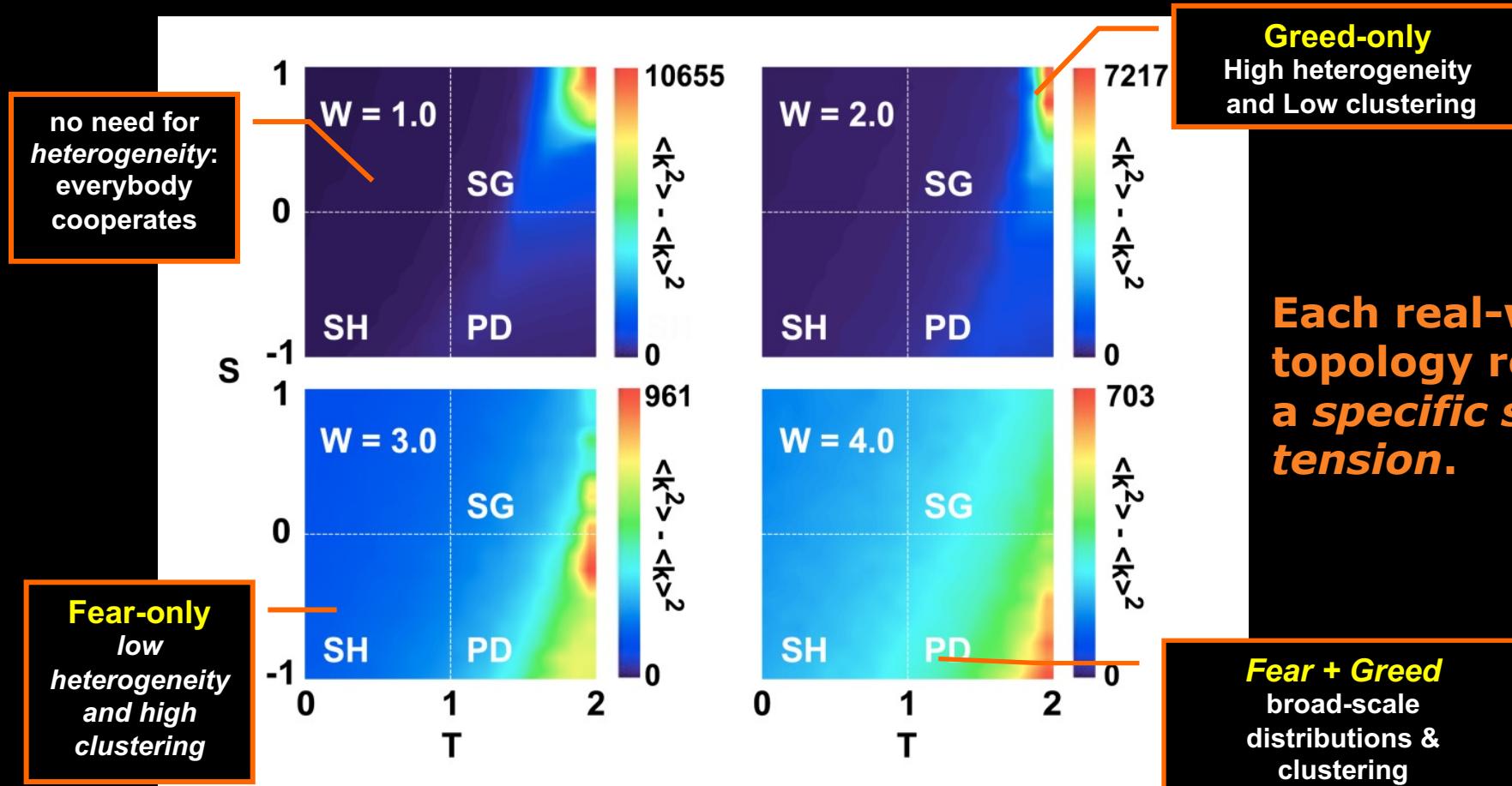
*Cooperation*

# Co-evolution of strategy and social ties

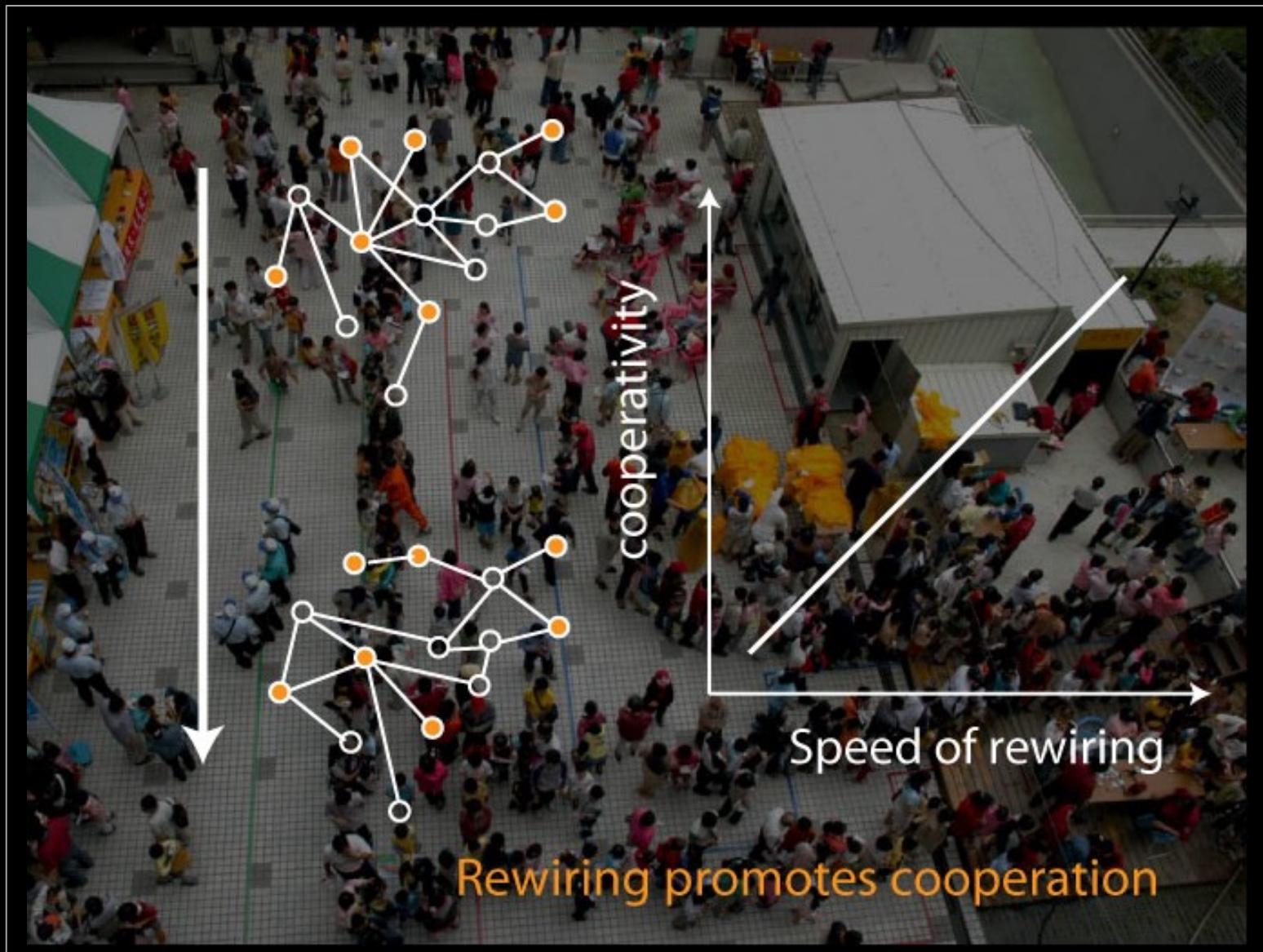


# Different dilemmas lead to different networks

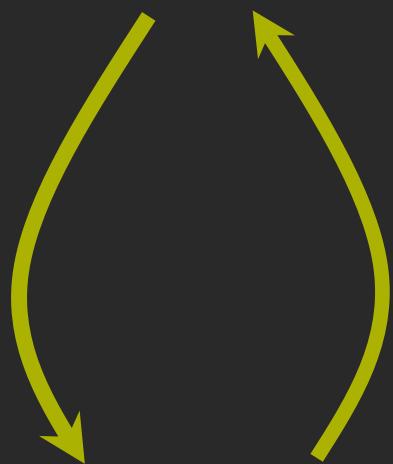
*Variance of the final degree distribution:*



# Conclusion



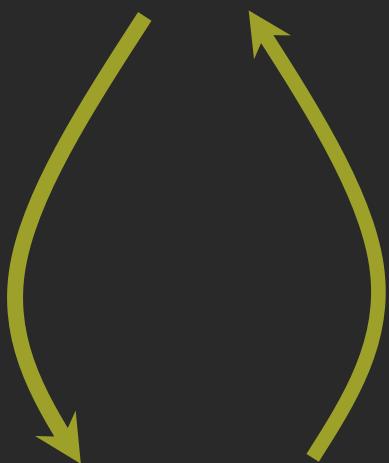
**Collective behavior**



**Social network**

**Cooperation**

**Collective behavior**



**Cooperation**

**Social network  
&**

***Heterogeneity & social diversity***

# Experimental confirmation...

**PNAS**

## Dynamic social networks promote cooperation in experiments with humans

David G. Rand<sup>a,b,1</sup>, Samuel Arbesman<sup>c,d,1</sup>, and Nicholas A. Christakis<sup>c,d,e,f,2</sup>

<sup>a</sup>Program for Evolutionary Dynamics, <sup>b</sup>Department of Psychology, <sup>c</sup>Institute for Quantitative Social Science, and <sup>d</sup>Department of Sociology, Harvard University, Cambridge, MA 02138; and <sup>e</sup>Department of Health Care Policy and <sup>f</sup>Department of Medicine, Harvard Medical School, Boston, MA 02115

Edited by Douglas S. Massey, Princeton University, Princeton, NJ, and approved October 18, 2011 (received for review May 23, 2011)

Human populations are both highly cooperative and highly conditional action, one that occurs via change

**PNAS**

## Static network structure can stabilize human cooperation

David G. Rand<sup>a,b,c,d,1</sup>, Martin A. Nowak<sup>e,f,g</sup>, James H. Fowler<sup>h,i</sup>, and Nicholas A. Christakis<sup>d,j,k,l</sup>

Departments of <sup>a</sup>Psychology, <sup>b</sup>Economics, <sup>c</sup>Sociology, <sup>d</sup>Medicine, and <sup>e</sup>Ecology and Evolutionary Biology, <sup>f</sup>School of Management, <sup>g</sup>Network Science, Yale University, New Haven, CT 06511; <sup>h</sup>Program for Evolutionary Dynamics and Departments of <sup>i</sup>Mathematics, <sup>j</sup>Harvard University, Cambridge, MA 02138; and <sup>l</sup>Medical Genetics Division and <sup>k</sup>Political Science Department, University of California, San Francisco, CA 94143

Edited by Jose A. Scheinkman, Columbia University, New York, NY, and approved October 30, 2014 (received for review January 15, 2014)

The evolution of cooperation in network-structured populations has been a major focus of theoretical work in recent years. When players are embedded in fixed networks, cooperators are more random mixing (41–50) [in contrast to dyadic interactions (51–53)], players can make and break ties, which promotes cooperation experimentally (42).

**ECOLOGY LETTERS**

Ecology Letters, (2011) 14: 546–551 doi: 10.1111/j.1461-0248.2011.01615.

**LETTER**

### Co-evolution of behaviour and social network structure promotes human cooperation

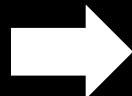
**Abstract**  
The ubiquity of cooperation in nature is puzzling because cooperators can be exploited by defectors. Recent theoretical work shows that if dynamic networks define interactions between individuals, cooperation is favoured by natural selection. To address this, we compare cooperative behaviour in multiple but independent repeated games between participants in static and dynamic networks. In the latter, participants could break their

Katrin Fehl, Daniel J. van der Post and Dirk Semmann\*

Junior Research Group Evolution of Cooperation and Prosocial

(among others)

# Tools for studying games on graphs



## ❖ competition between cooperators and defectors

numerically :

finite populations;

any kind of network

different intensities of selection (weak to very strong)

[ Abramson, Kuperman, *PRE* 63, 030901(R) (2001) ]

[ Santos, Pacheco, *PRL* 95 (2005) 098104 ]

[ Santos, Pacheco, Lenaerts, *PNAS* 103 (2006) 3490 ]

[ Santos, Pacheco, *J. Evo. Biol.* 19 (2006) 726 ]

## ❖ fixation probabilities

analytically w/ approximations & numerically

weak selection (game is but a small perturbation to fitness)

finite & infinite populations

regular graphs (strictly : trees)

[ Ohtsuki, Hauert, Lieberman, Nowak, *Nature* 441 (2006) 502 ]

[ Ohtsuki, Nowak, *JTB* 243 (2006) 86 ]

[ Pacheco, Ohtsuki, Nowak, *PRL* 98 (2007) 108106 ]

## ❖ Average gradients of selection

mean-field description of population-wide dynamics

finite populations ; any kind of network ; any intensity of selection

[ Pinheiro, Pacheco, Santos, *PLoS One* 2012 ]

[ Pinheiro, Santos, Pacheco, *New J Phys* 2012 ]

# escaping the paradox of cooperation

- kin selection

*all in the family . . .*

- multi-level selection

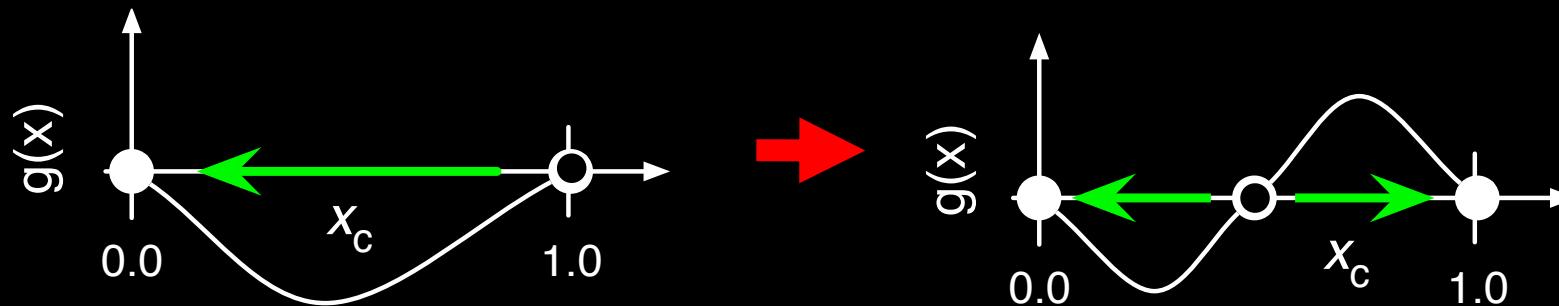
*pick the right team . . .*

- direct & indirect reciprocity

*I scratch your back & you scratch mine . . .*

*I scratch your back & someone else scratches mine . . .*

qualitatively, all these mechanisms transform a  
*Prisoner's Dilemma* into a *Coordination game*



in which *cooperation becomes evolutionary viable*

## *Games on networks → mean field analysis?*

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**Can we show how heterogeneous social structures change the original dilemma to one in which cooperation may thrive?**

**Can we compute the gradient of selection for each network structure?**

# game & network → mean field analysis?

Assuming *infinite* populations

Gradient of selection

$$\dot{x} = x(1-x)(f_C - f_D) = g(x)$$

In finite populations, we can redefine a (discrete) gradient of selection as

$$G(j) = T^+(j) - T^-(j)$$

where  $T^+(x)$  ( $T^-(x)$ ) is the average frequency of transitions increasing (decreasing) the number of Cs for each configuration with  $j$  Cs.

*In networks, this may be tricky to obtain analytically, but possible to address by means of computer simulations...*

# Evolution in finite well-mixed populations in a nutshell

At each time step we have a probability to increase and to decrease the number of cooperators, which is

$$T_j^\pm = \frac{j}{N} \left[ \frac{N-j}{N} \right] \frac{1}{1 + e^{\mp \beta(f_C(j) - f_D(j))}}$$

The equation is displayed within a light yellow box. Below the equation, three boxes are connected by arrows pointing to their respective terms: a blue box labeled "prob select C" points to  $\frac{j}{N}$ ; a red box labeled "prob select D" points to  $\frac{N-j}{N}$ ; and a green box labeled "take-over prob" points to  $\frac{1}{1 + e^{\mp \beta(f_C(j) - f_D(j))}}$ .

(N=population size, j=number of cooperators)

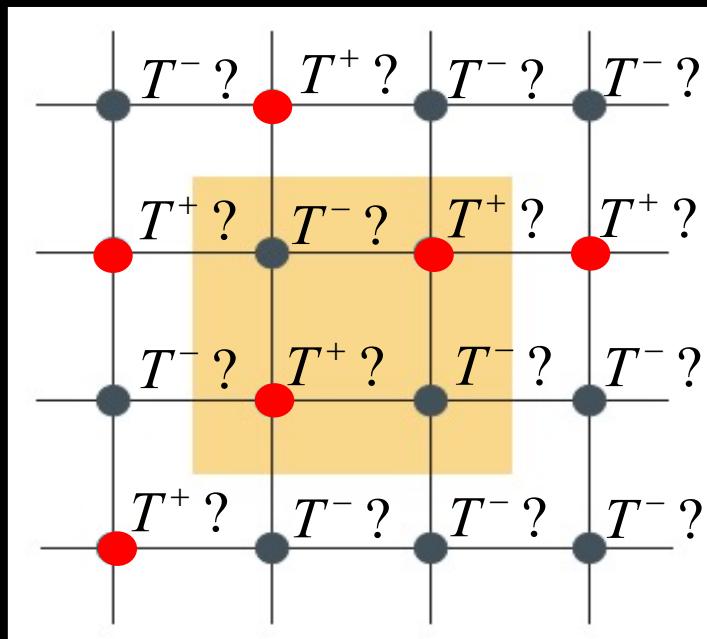
Assuming a finite well-mixed population, our “replicator equation” and gradient of selection is replaced by

$$G(k) \equiv T^+(k) - T^-(k) = \frac{k}{N} \frac{N-k}{N} \tanh \left\{ \frac{\beta}{2} [f_C(k) - f_D(k)] \right\}$$

# Average gradient of selection (AGoS) on networks

in networked (finite) populations, we can redefine an **Average Gradient of Selection (AGoS)** at any time  $t$  of the evolutionary dynamics, as

$$G(j,t) = T^+(j,t) - T^-(j,t)$$

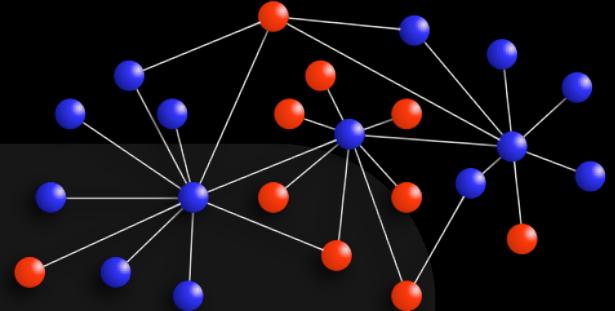


where  $T^+(j)$  [  $T^-(j)$  ] is the average probability of increasing [ decreasing ] the # of Cs for each population configuration with  $j$  Cs.

the  $T^\pm(j,t)$  become context dependent, but now all Cs regain the same average “status” which, however, carries information on the specific network structure.

# Average gradient of selection (AGoS) on networks

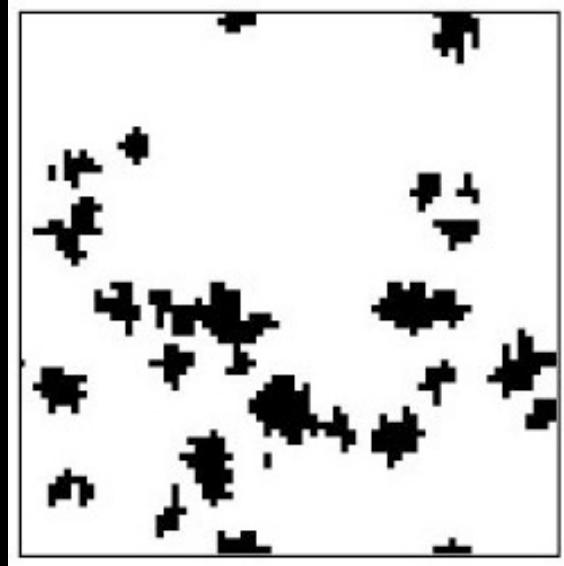
$$G(j,t) = T^+(j,t) - T^-(j,t)$$



## setup:

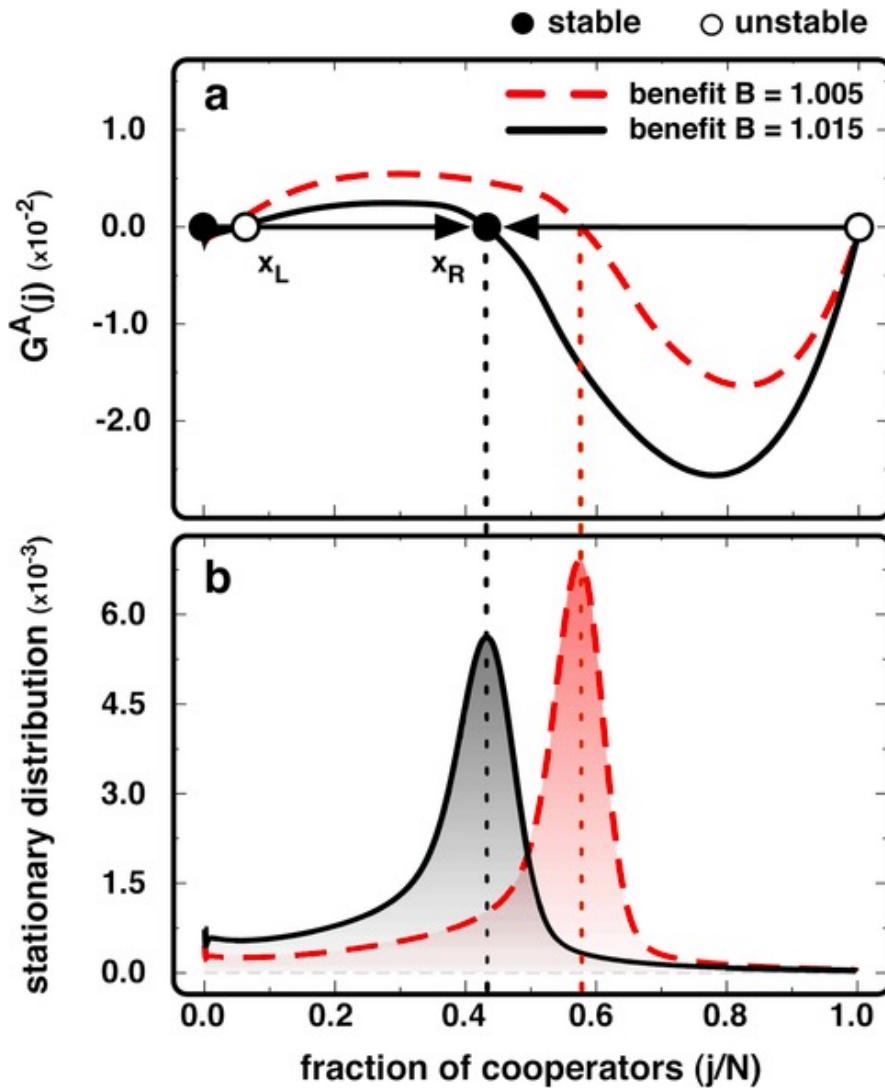
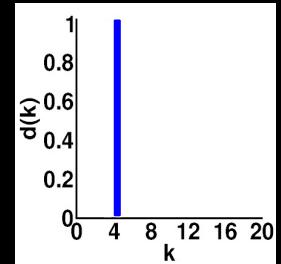
- Evolve for many runs & many generations
- For each time step, record  $G(j,t)=T^+(j,t) - T^-(j,t)$  for a given time  $t$  and  $j$  Cs.
- The **time-independent AGoS( $j$ )** will be given by the average of  $G(t,j)$  over all time-steps.
- The **time-dependent AGoS( $j,t$ )** will be given by the average of  $G(t,j)$  over a single generation ( $N$  updates).

## results – homogeneous networks



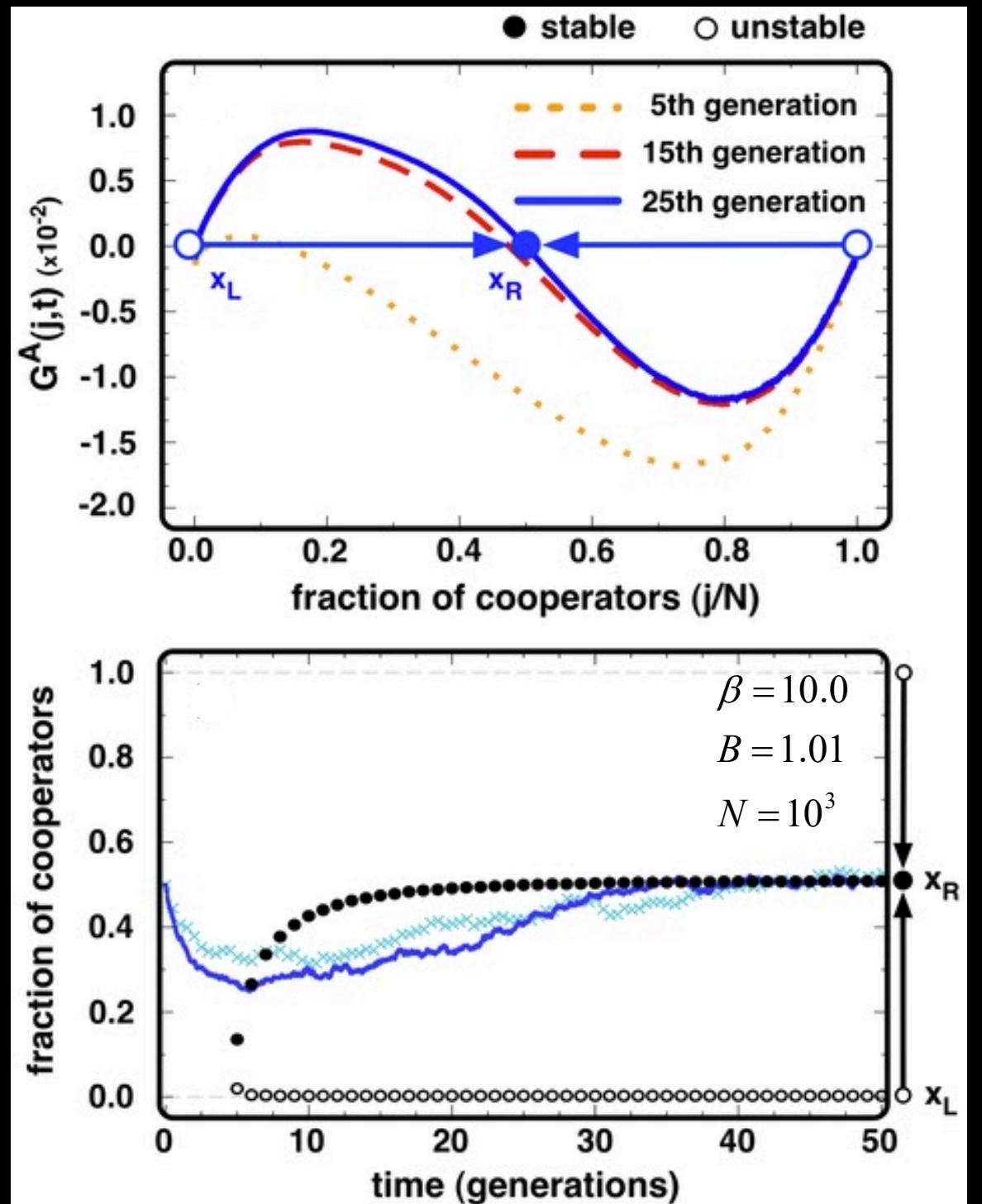
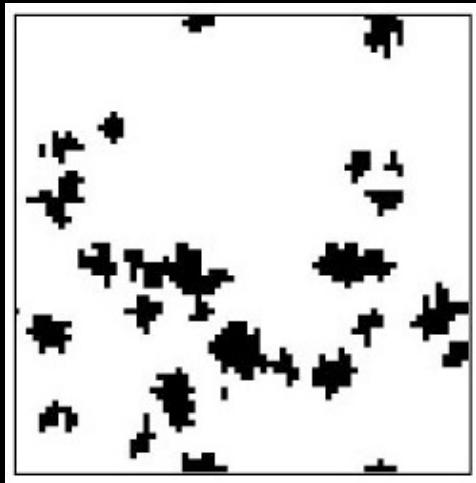
homogeneous networks lead to a scenario characteristic of a **co-existence game**, where clusters of Cs resist the invasion of Ds.

$$T=B, R=1, P=0, S=1-B$$

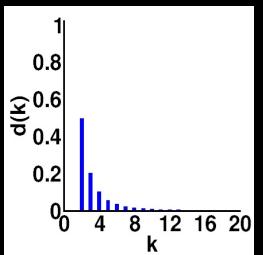


## Time dependence

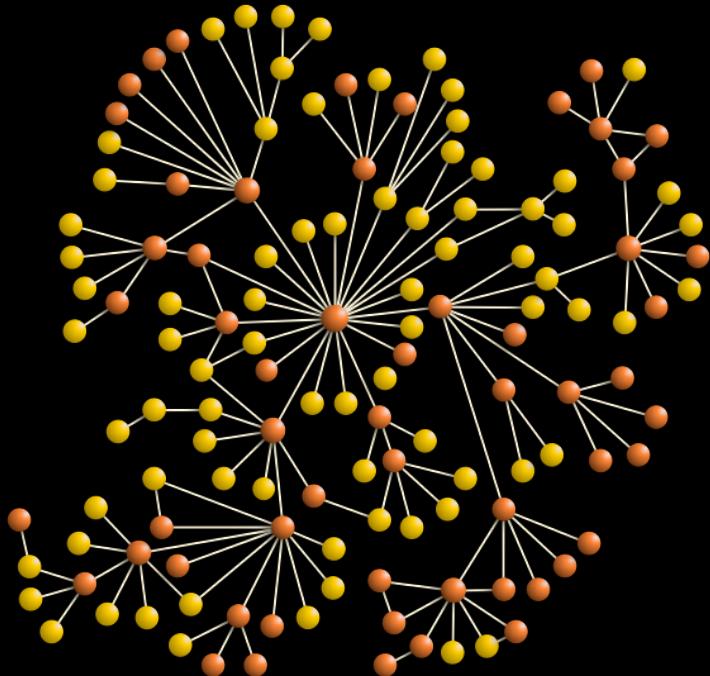
*The “effective game” evolves in time!*



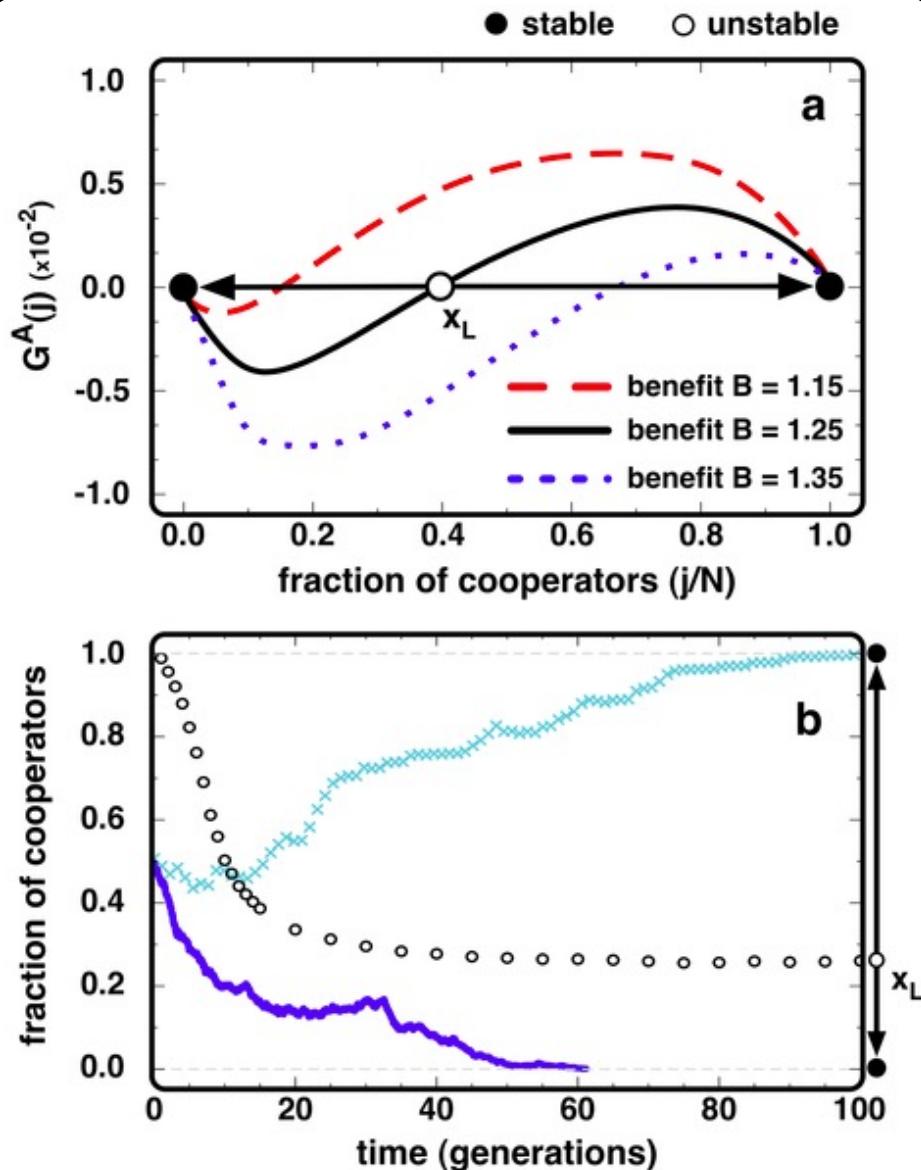
# results: heterogeneous networks



$T=B$ ,  $R=1$ ,  $P=0$ ,  $S=1-B$

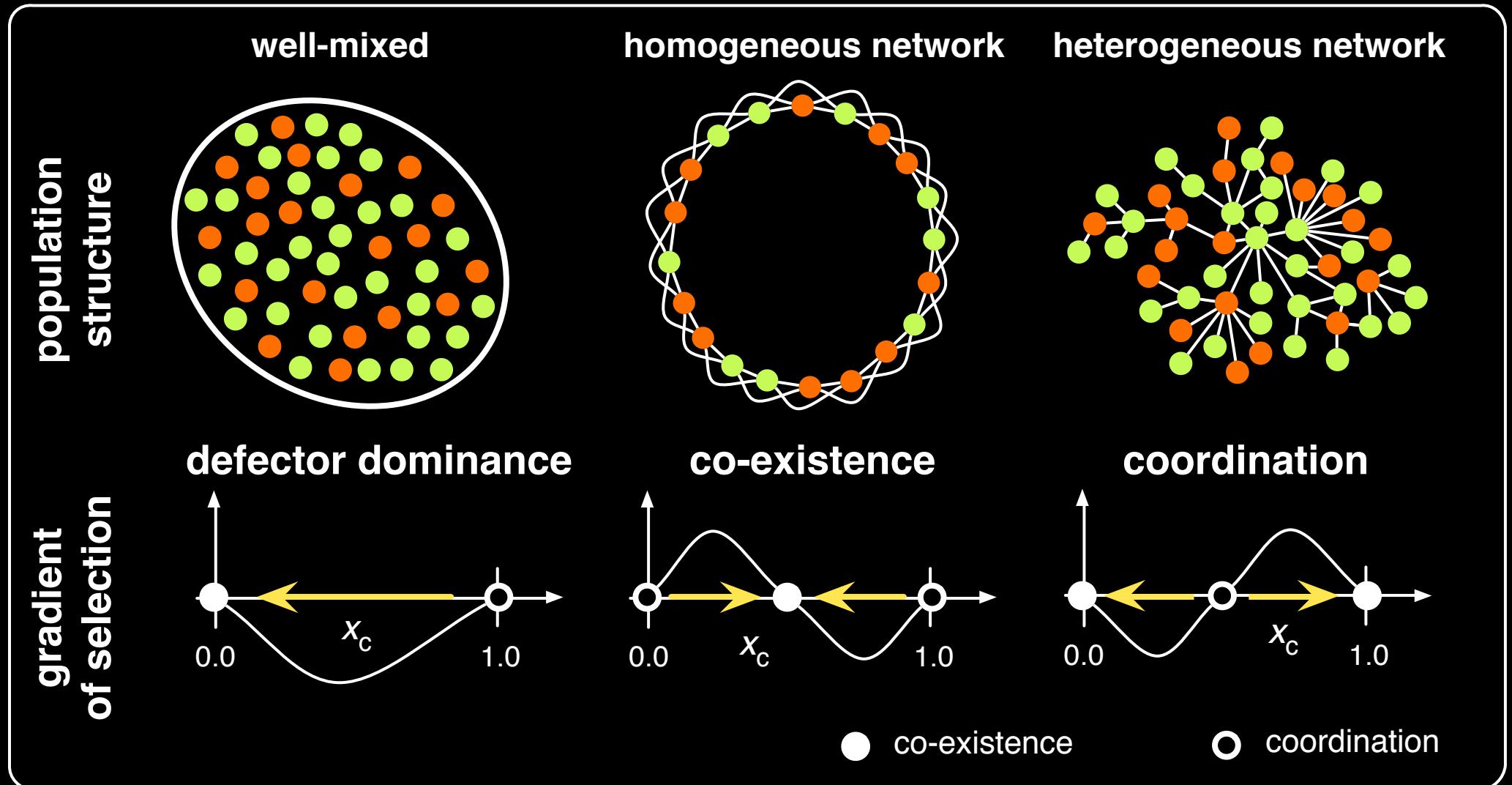


**scale-free networks lead to a scenario characteristic of a coordination game, where **Cs** dominate above the unstable point.**



# From local to global dilemmas in social networks

Social networks transform the “games” we effectively play



*Groups, kin, reciprocity, memory, reputations, moral systems, signals, gossip, networks, etc etc*

Are we missing a lot?

**YES!!!**

*Groups, kin, reciprocity, memory, reputations, moral systems, gossip, networks, etc.*

Are we missing a lot?

**YES!!!**

1. Many of these mechanisms rely on the 2-person nature of cooperative interactions (e.g., direct reciprocity)
2. Can we be more ambitious?