Evolution of Diversity and Cooperation

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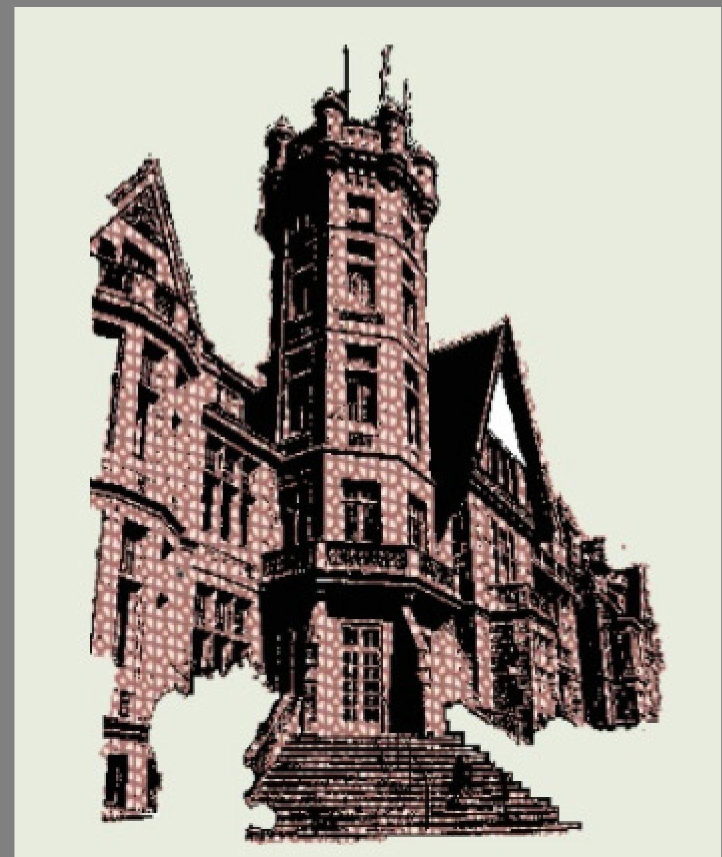


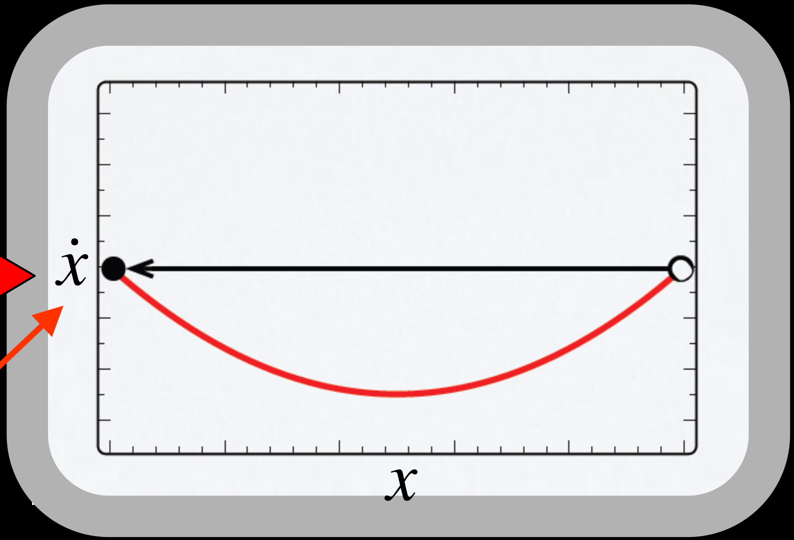
Luis Santaló School, 18th of July, 2013

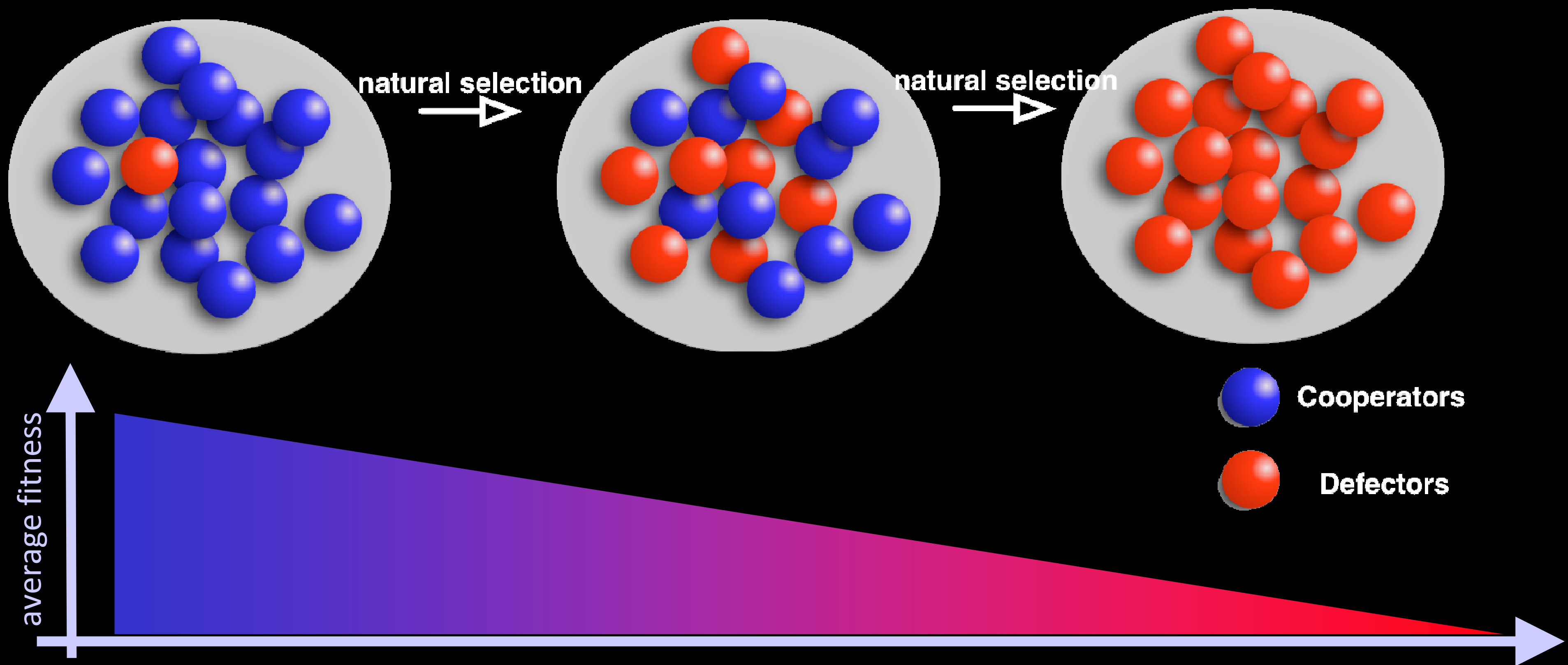
prisoner's dilemma

$$\begin{array}{c|cc} & C & D \\ \hline C & (b-c) & -c \\ D & b & 0 \end{array}$$

$$\dot{x} = x(1-x)\left[f_C(x) - f_D(x)\right]$$

gradient of selection





Kin selection

all in the family . . .

the more individuals ***are related***, the more cooperation is feasible. ***How ?***

r : (genetic) relatedness between individuals → ***your action means r to me; hence, I also get r of what you get;*** then

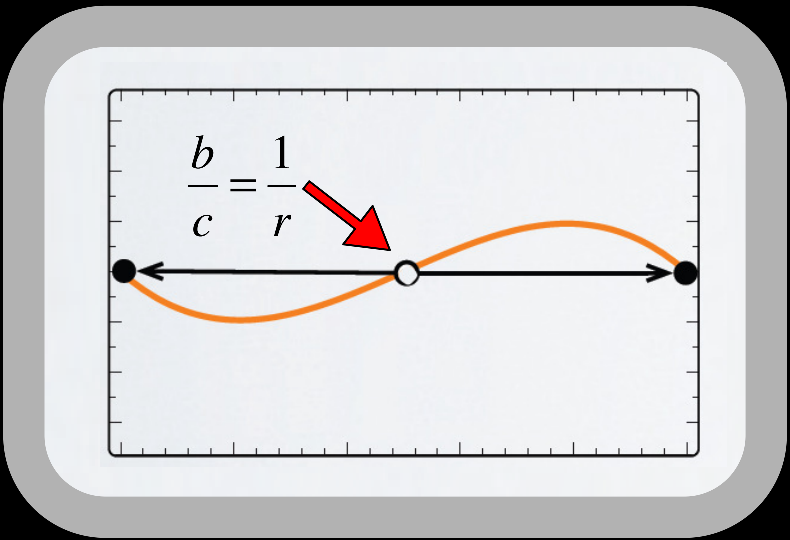
C is an ESS *if* $R > T$

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{cc} C & D \\ \left[\begin{array}{cc} (b-c)(1+r) & -c+br \\ b-cr & 0 \end{array}\right] \end{array}$$

→ ***ESS*** condition for **C** : $\frac{b}{c} > \frac{1}{r}$

this is the famous ***Hamilton's rule of kin-selection***

how does the ***gradient of selection*** look like ?

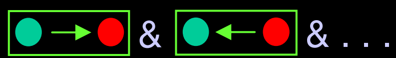


kin selection transforms a ***PD*** into a ***coordination game***

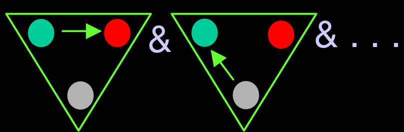
[W. D. Hamilton, J. Theor. Biol. 7, 1 (1964)]

Escaping the paradox of cooperation

- Kin selection — *all in the family . . .*

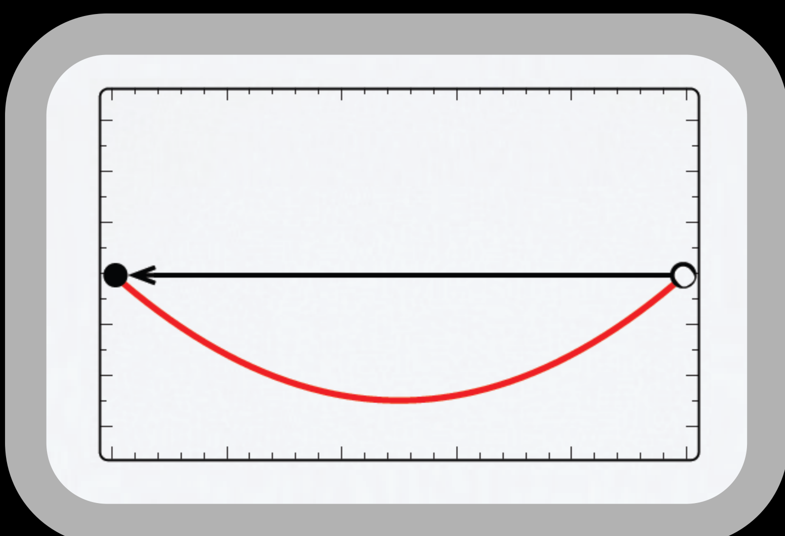


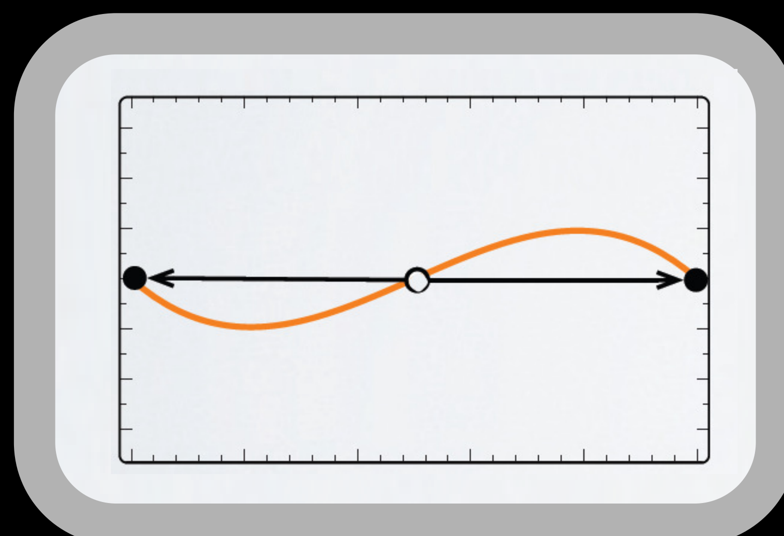
- Direct reciprocity — *I scratch your back & you scratch mine . . .*



- Indirect reciprocity — *I scratch your back & someone else scratches mine . . .*

& evolution of moral systems — *(reputation & the evolution of the concepts of "good" and "evil")*





are we done ?

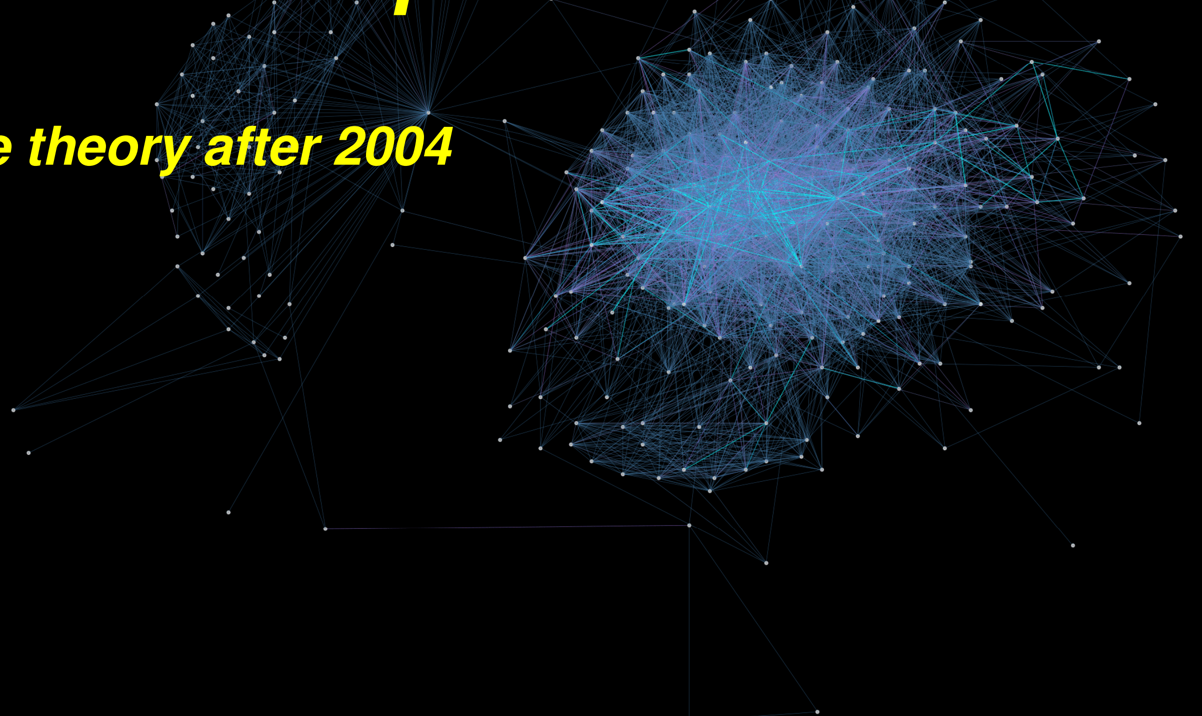
not at all . . . .

Critique 1: Infinite populations?!

Critique 2: Well-mixed populations?!

Evolution in finite populations
Social behavior in complex networks

… Evolutionary game theory after 2004



→ *sample from facebook*

evolution in finite populations in a nutshell

finite populations → countable number of individuals;

Stochastic effects may play an important role.

Finite populations

$\Delta x = 1/Z \neq dx$

Stochastic description

Infinite populations

$\Delta x \rightarrow dx$

Deterministic description

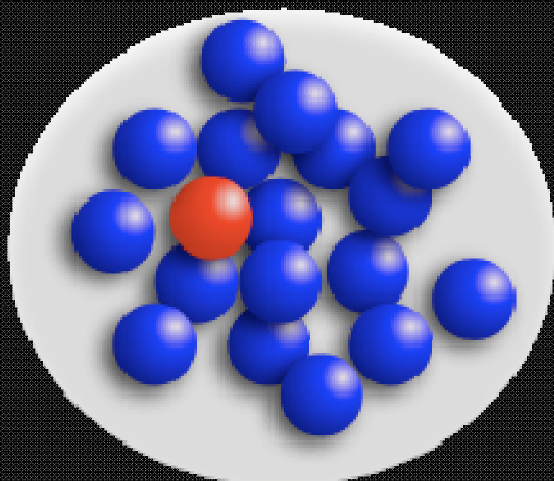
How to formalize the evolutionary dynamics in finite populations?

the replicator equation is no longer valid . . .

evolution in finite populations in a nutshell

Birth-Death processes : *Markov processes which keep population size constant & proceed in discrete time*

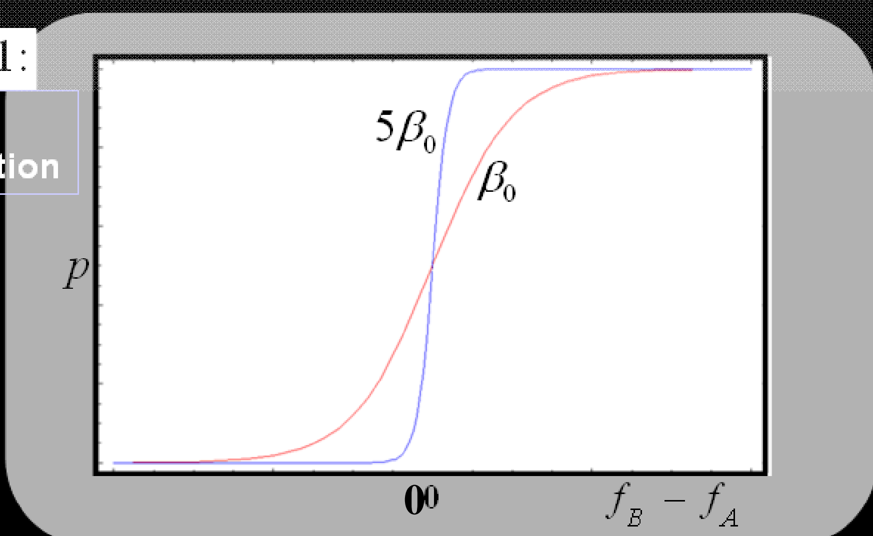
imagine the simplest form of social learning:



Imitate a random individual with a probability that increases with the fitness difference.

$\beta << 1$:

Weak selection



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

Traulsen Nowak, Pacheco, Phys Rev E (2006)

evolution in finite populations in a nutshell

at each time step we may compute the probability to increase and to decrease the number of A's by 1, given by

(Z = population size, *j* = number of A's)

$$T_j^{\pm} = \frac{j}{Z}\frac{Z-j}{Z}\frac{1}{1+e^{\mp\beta(f_A(j)-f_B(j))}}$$

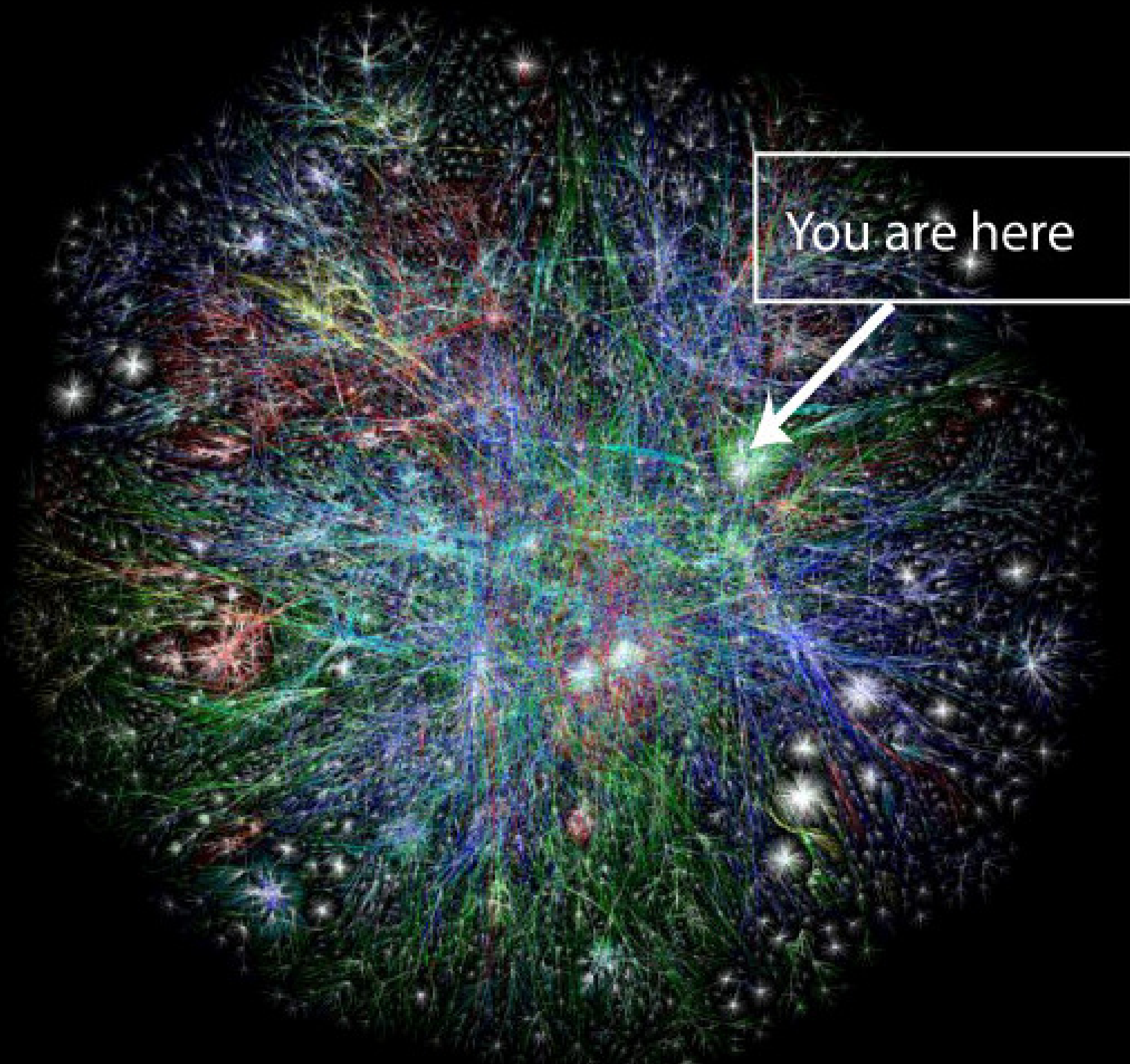
- $\frac{j}{Z}$: prob select A
- $\frac{Z-j}{Z}$: prob select B
- $\frac{1}{1+e^{\mp\beta(f_A(j)-f_B(j))}}$: take-over prob

under these conditions, our gradient of selection now becomes

$$g(k) \equiv T_k^{+} - T_k^{-} = \frac{k}{Z}\frac{Z-k}{Z}\tanh\left\{\frac{\beta}{2}\left[f_A(k)-f_B(k)\right]\right\}$$

when Z >> 1, we recover the replicator dynamics for weak selection ($\beta \ll 1$)

Well-mixed !?



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.

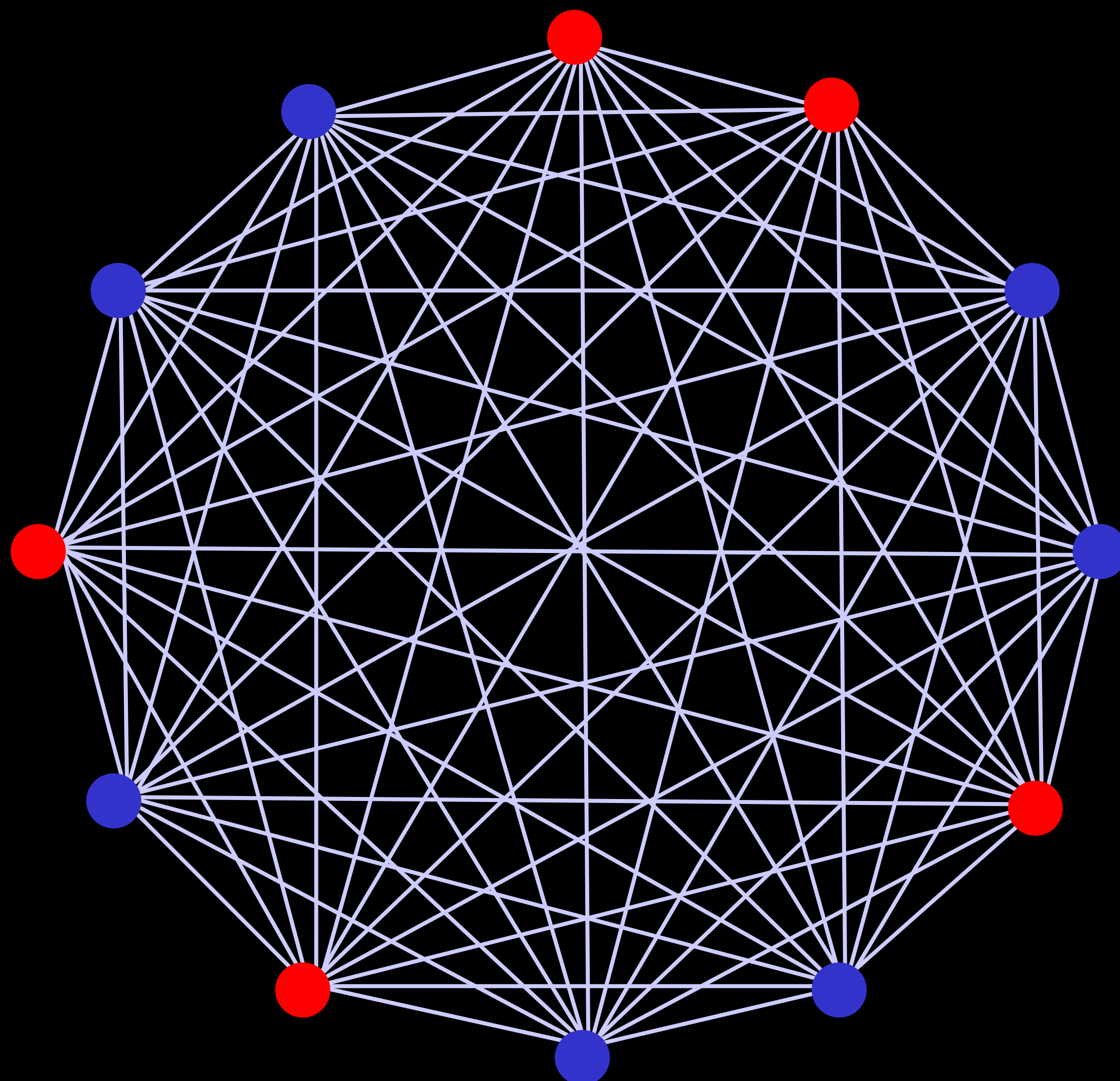
graphs provide a very convenient means of representing the inter-relations between processes, organisms, organizations, populations or even components of these.

different organisms may be represented by different graphs

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

well-mixed but finite population

each individual interacts with *ALL* others



→ ***complete graph***

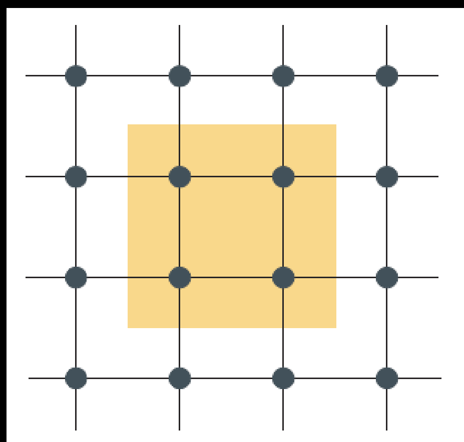
types of graphs

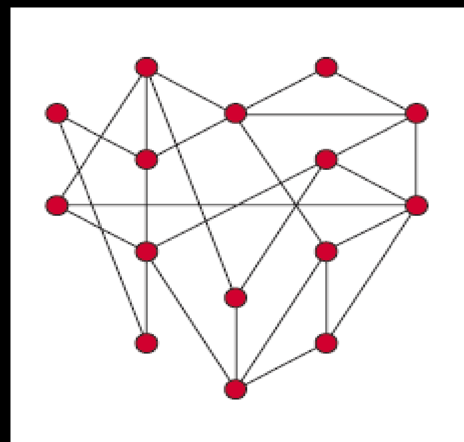
regular graphs

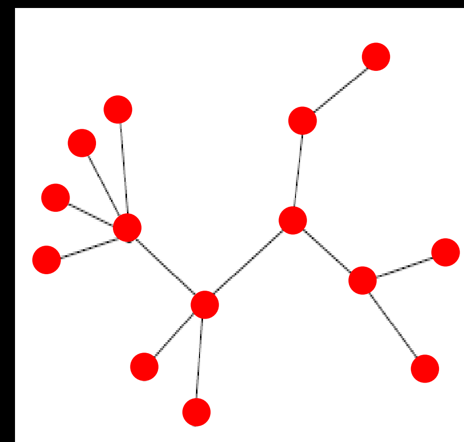
random graphs

trees

2D lattices





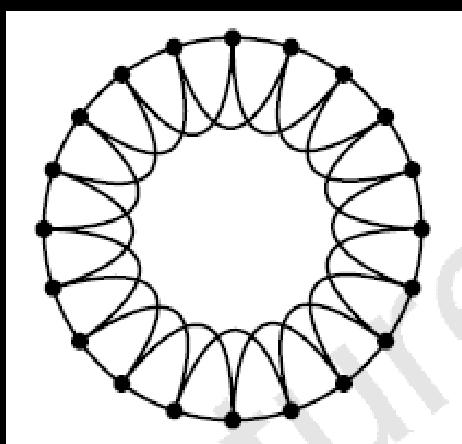


physics

mathematics

comp. science

rings (1D lattices)

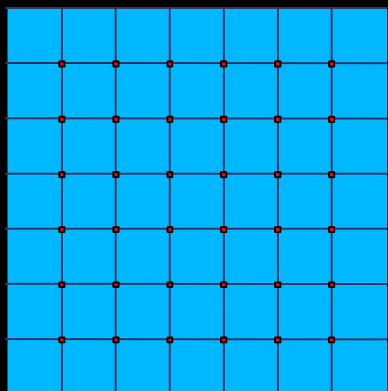


how to characterize a graph ?

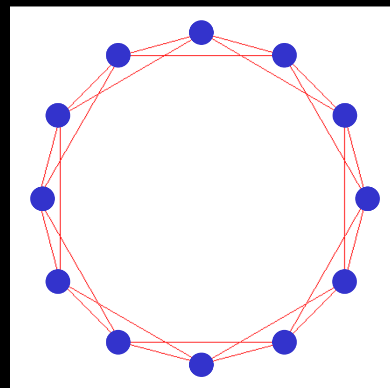
average degree, **degree distribution**, average path length, **cluster coefficient**, degree-degree correlation, **hierarchical structure**, betweeness, …

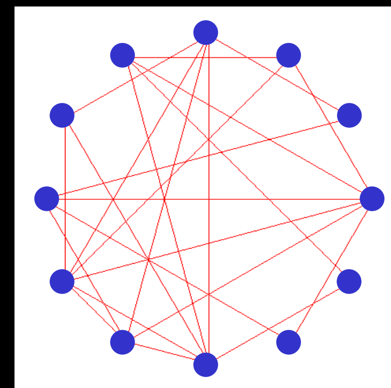
degree distributions

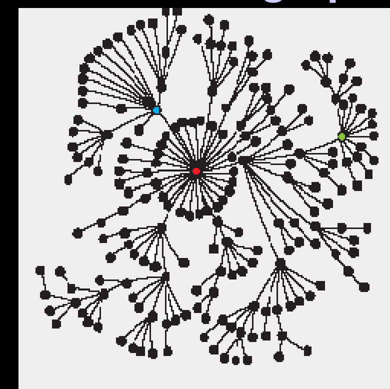
regular lattice | **regular graph** | **random graph** | **scale-free graph**

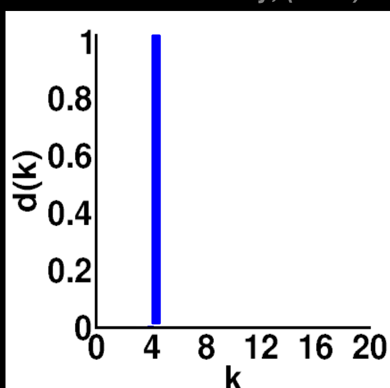


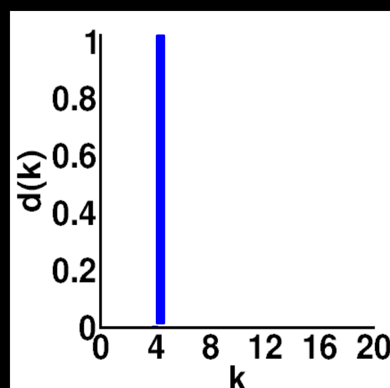
M. Nowak & R. May, *(1992)*

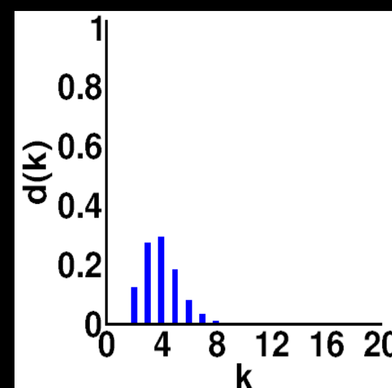


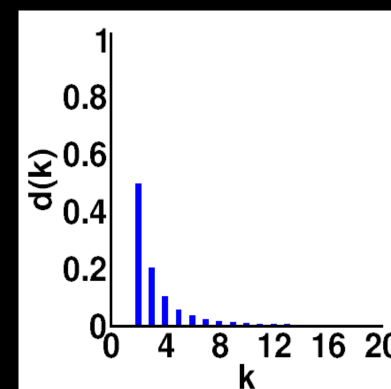










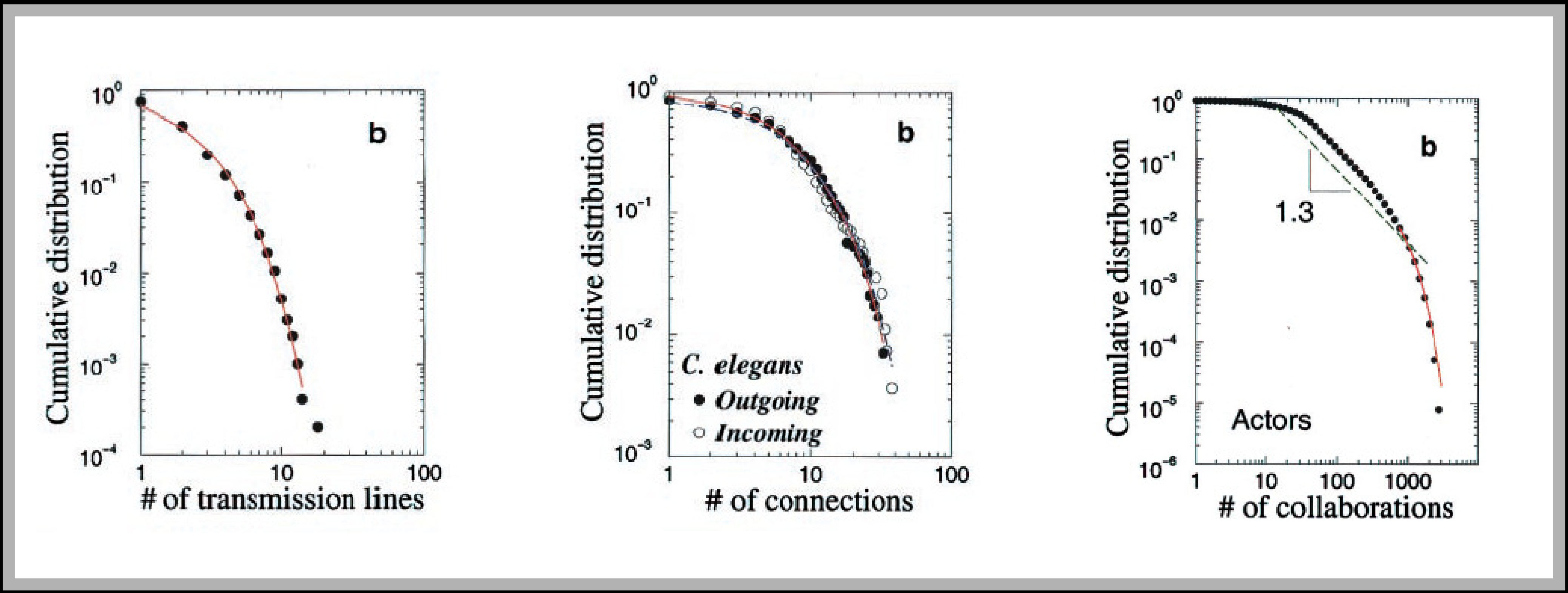


homogeneous graphs | **heterogeneous graphs**

in all graphs $z = \langle k \rangle = 4$ = 2x(ner links) / (ner nodes)

a world of complex ties

technological networks . . . biological networks . . . social networks . . .



(2000)

generally (based on existing empirical analysis of real nets) there are 3 main types of graphs :

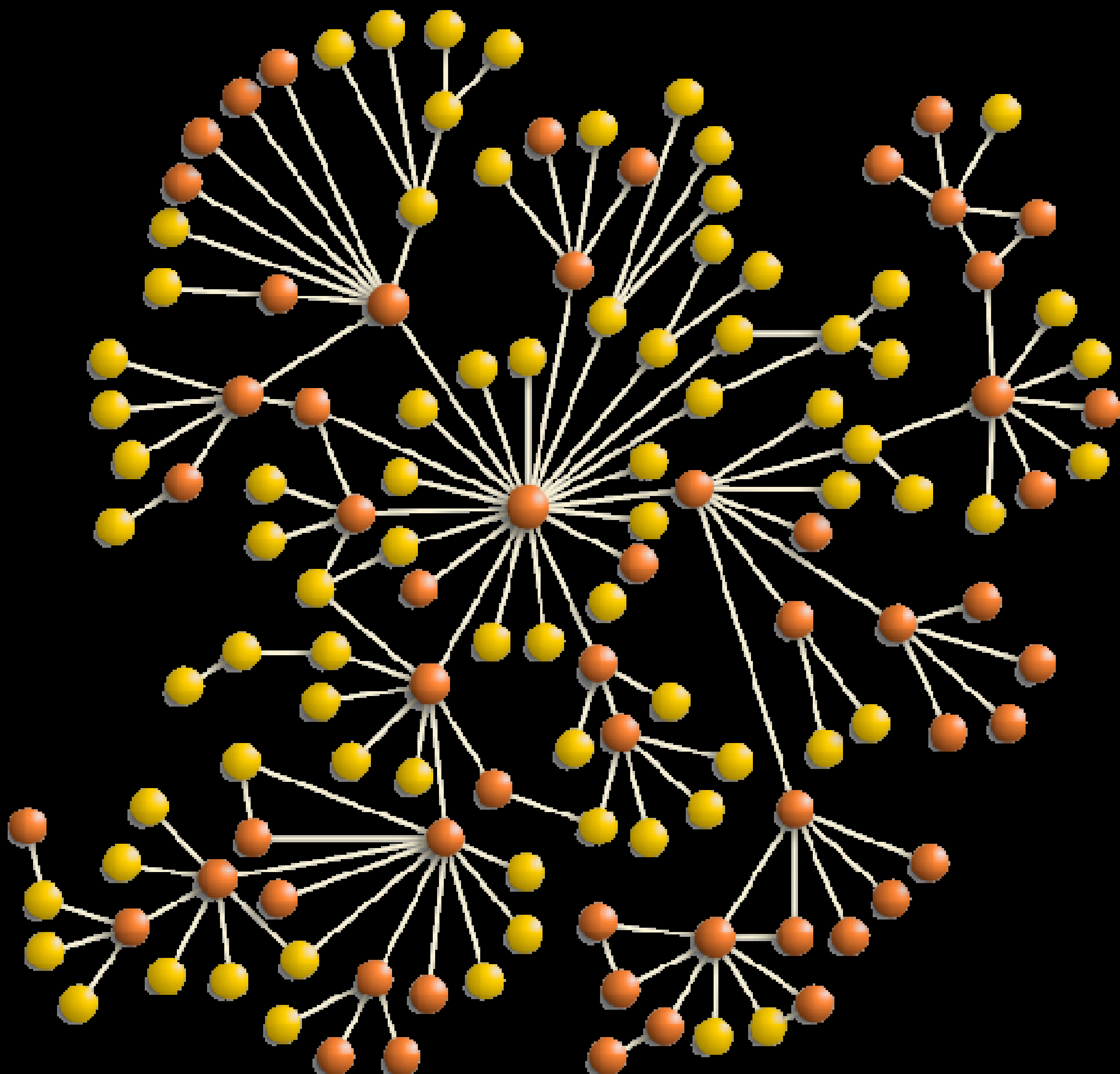
a world of complex ties

single-scale : the individual degrees do not deviate appreciably from the average degree of the graph (type most compatible with a random graph);

broad-scale : degrees span a wider interval, with degree distro falling off exponentially for large k ;

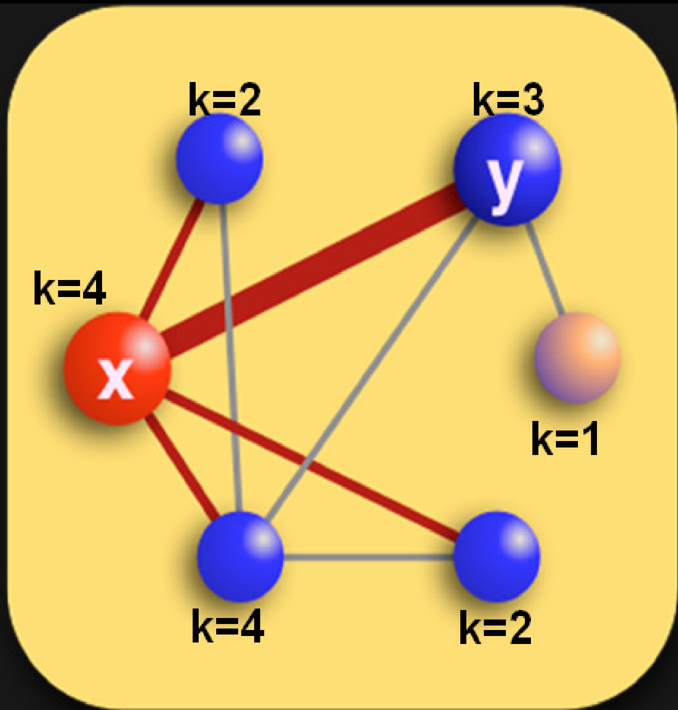
scale-free : those graphs in which the degree-distro decays with a power law (fat tail distros)

scale-free networks & social behavior



- Robust against random attacks
- Fragile against targetted attacks
- Gene regulatory networks
- Protein interaction networks
- Sexual patterns in humans
- Epidemiology
- Opinion dynamics
- what about social behavior?
- what about cooperation ?

evolution on graphs - pairwise comparison update rule



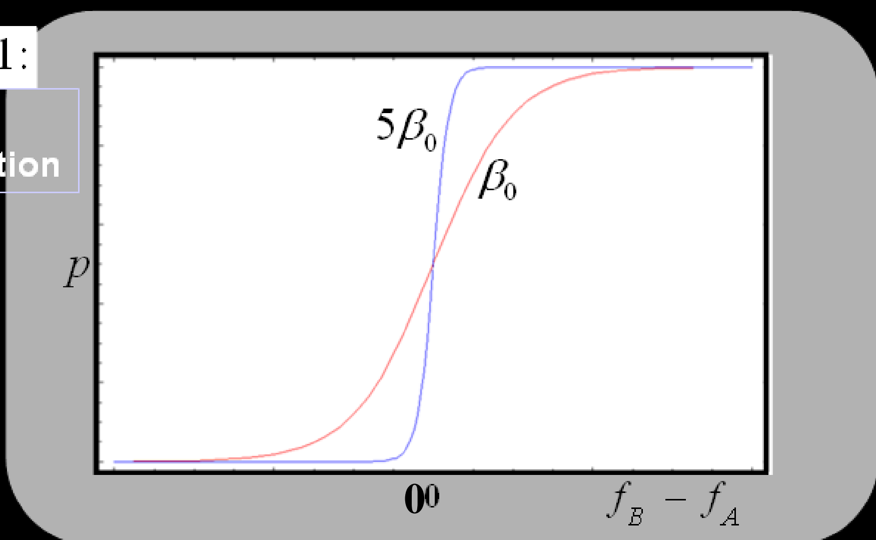
@ every step :

***x* imitates a random neighbor *y* with a probability that increases with the payoff difference.**

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

$\beta << 1:$

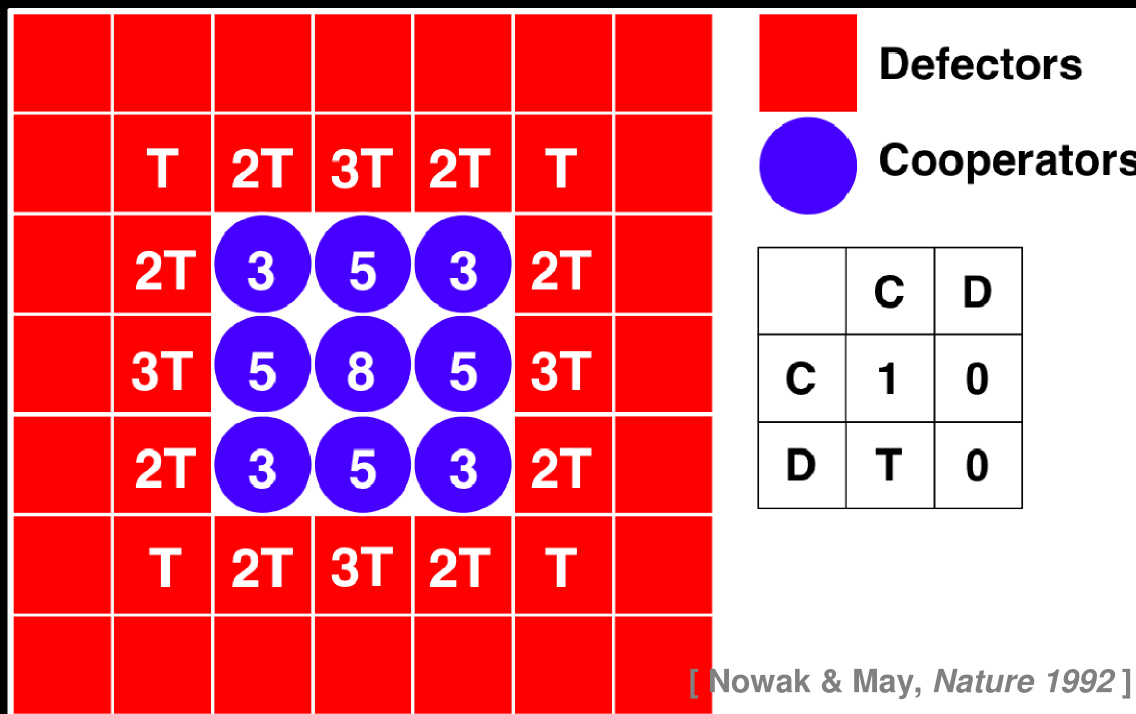
Weak selection



Traulsen Nowak, Pacheco, Phys Rev E (2006)

cooperation in networked populations

entirely different world → *we now have at most 2^N different payoffs, even in a regular graph, where all nodes are topologically equivalent*



	C	D
C	1	0
D	T	0

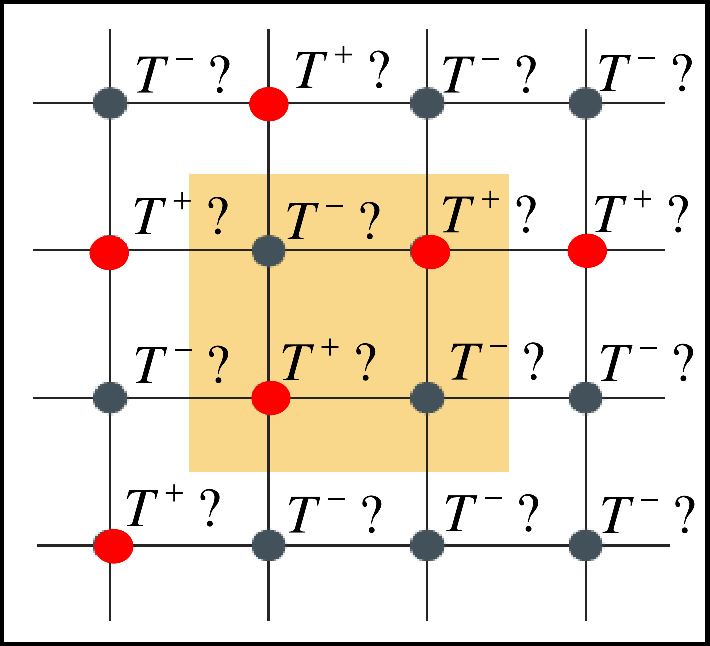
[Nowak & May, *Nature 1992*]

- *when individuals engage in a PD, how does the graph affect the overall dynamics ?*
- *do all graphs affect game dynamics in the same way ?*

gradient of selection 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.*

gradient of selection on networks

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

$$\boldsymbol{G}(j,t) = \boldsymbol{T^{+}}(j,t) - \boldsymbol{T^{-}}(j,t)$$

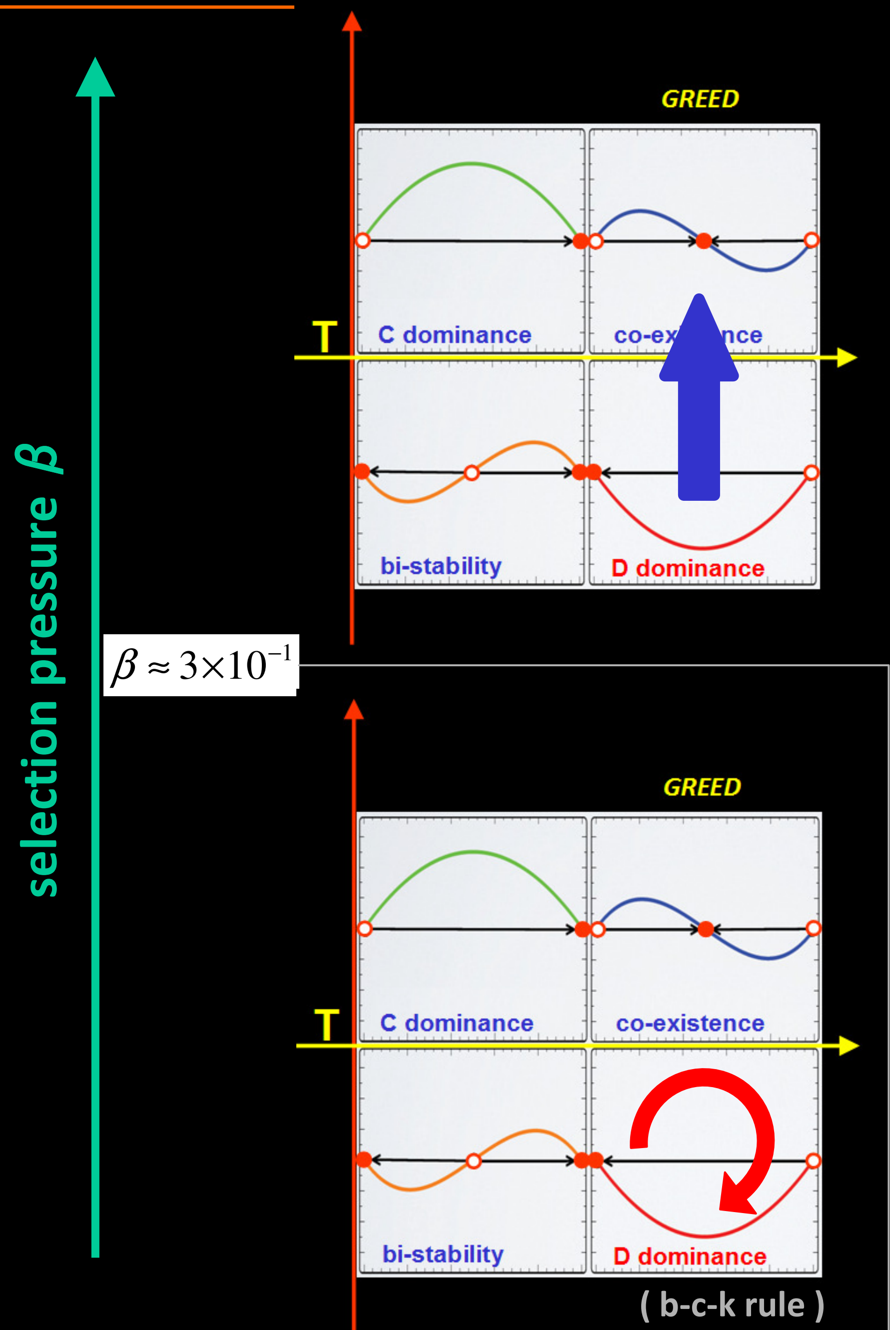
this is as yet impossible to obtain analytically, but possible to compute numerically…

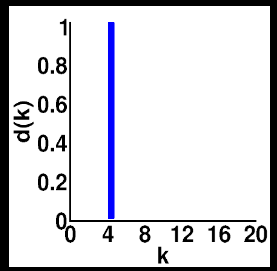
$$T^{\pm}(k,t) = \frac{1}{N}\sum_{i=1}^{\substack{Ds\\Cs}} \frac{1}{k_i}\sum_{m=1}^{\bar{n}_i}\left[1+e^{-\beta(f_m - f_i)}\right]^{-1}$$

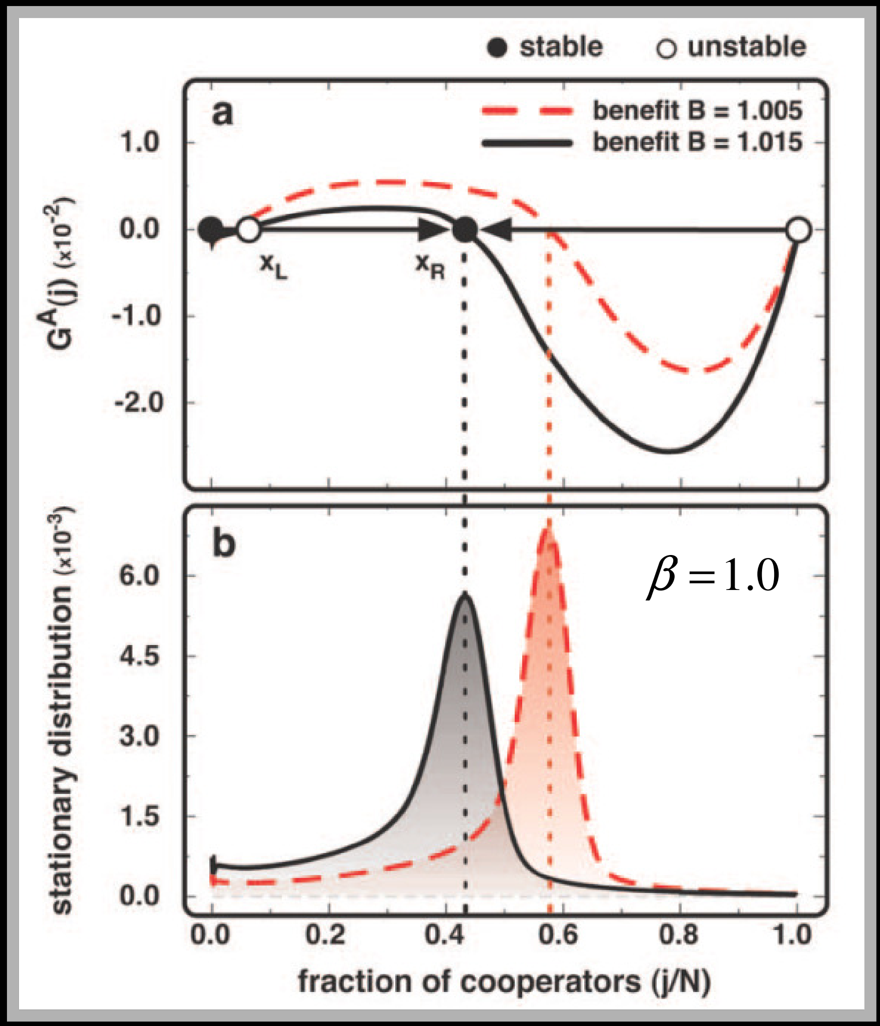
population with a total of *k* *C*s @ time *t*

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

results





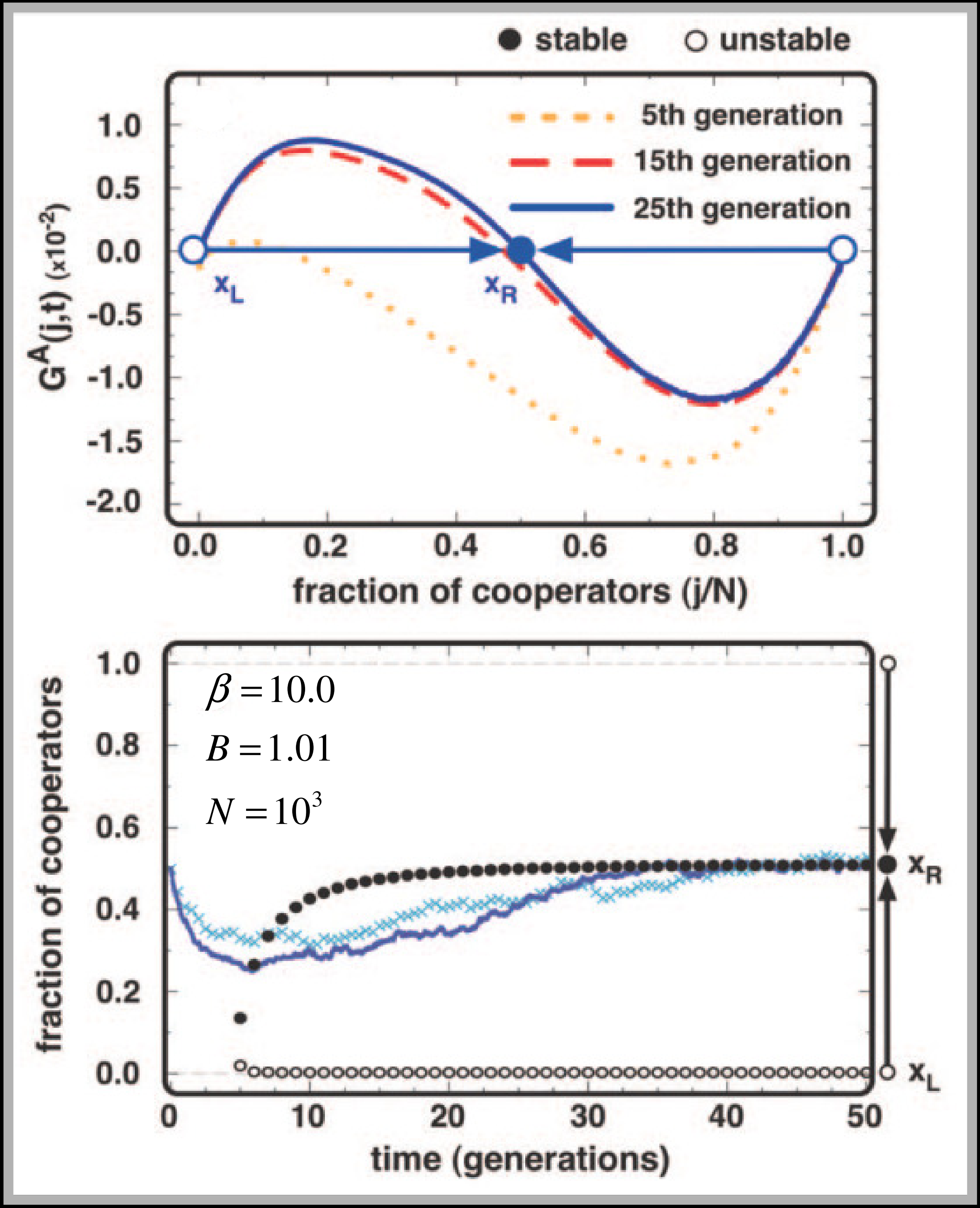


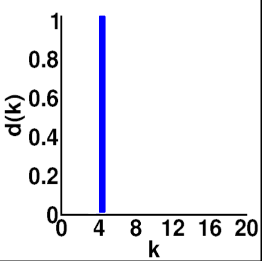
***homogeneous** nets promote the coexistence between Cs & Ds.*

[Pinheiro Santos, Pacheco, 2011]

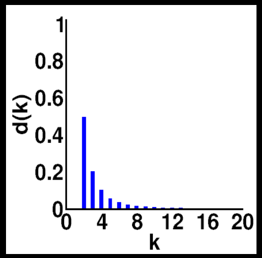
results

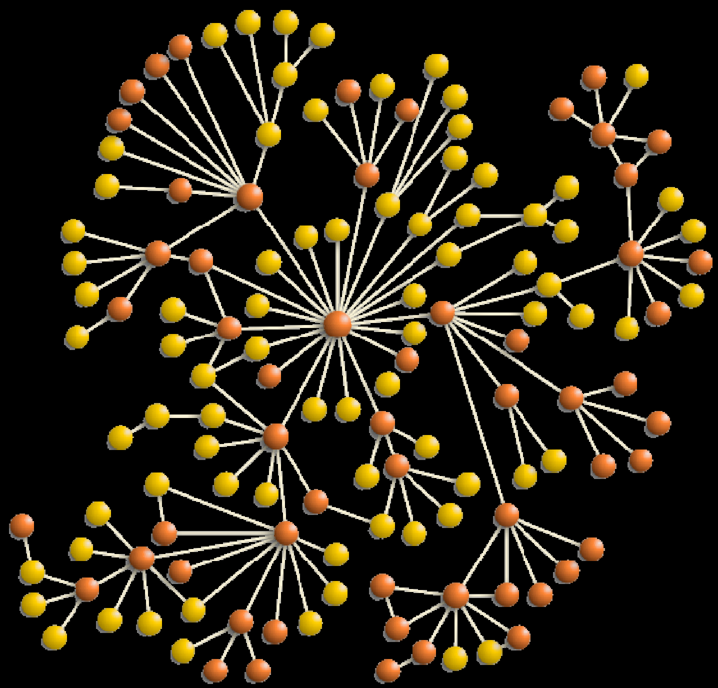
***homogeneous** nets promote the coexistence between **Cs** & **Ds**.*

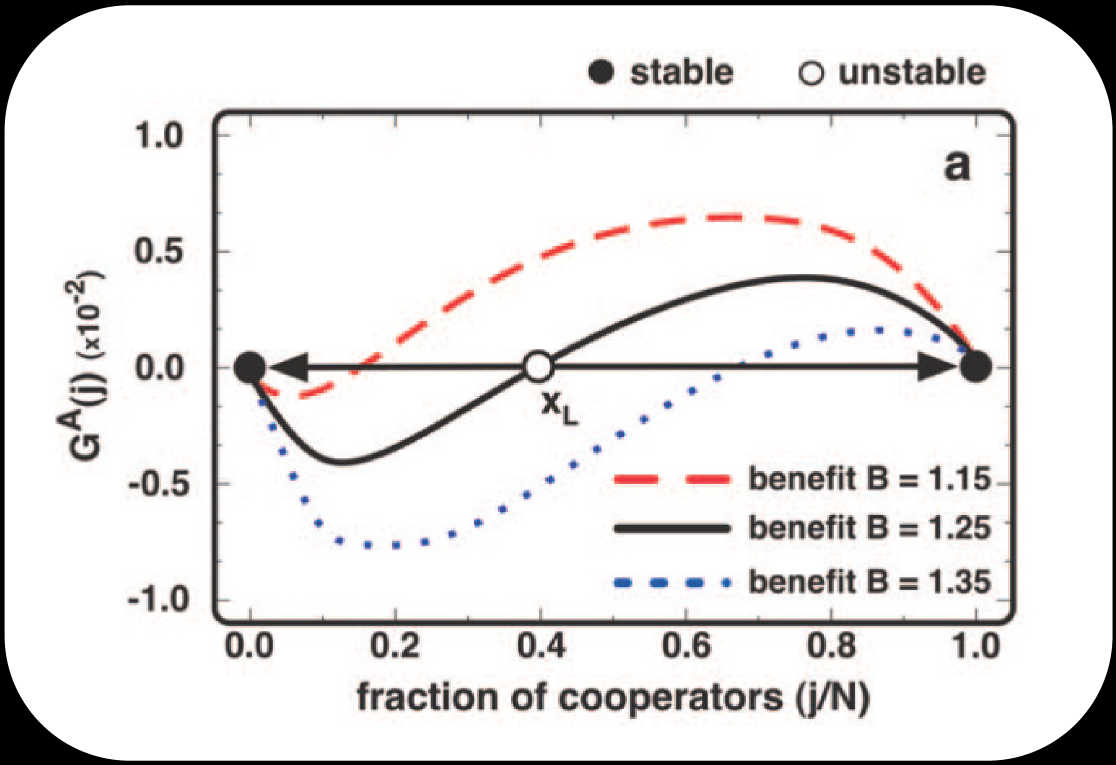




results



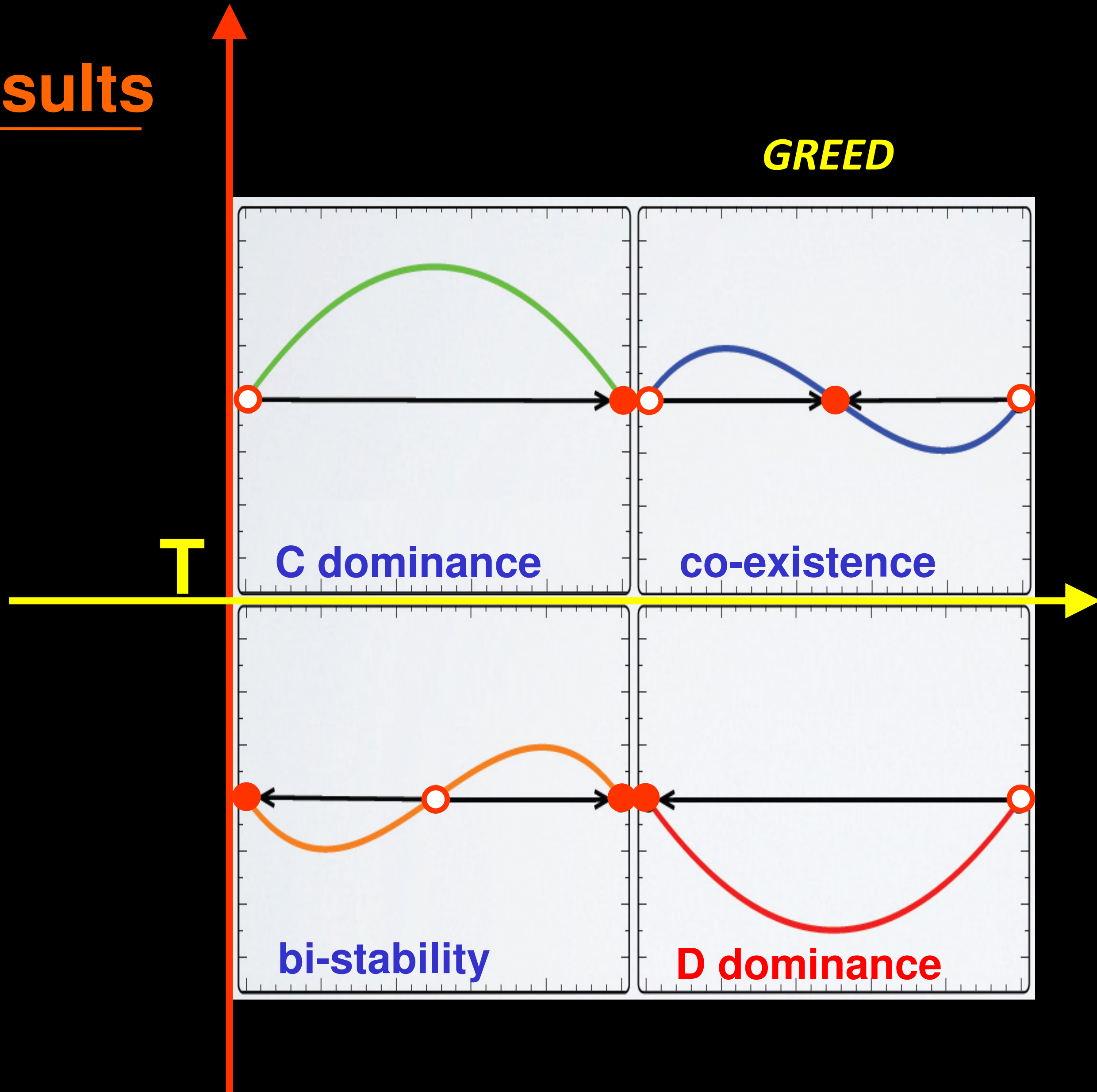




broad-scale (exponental) & scale-free networks lead to a scenario characteristic of a coordination game, where Cs dominate above the unstable point.

[Pacheco, Pinheiro & Santos, PLoS One (2012)]

overall results



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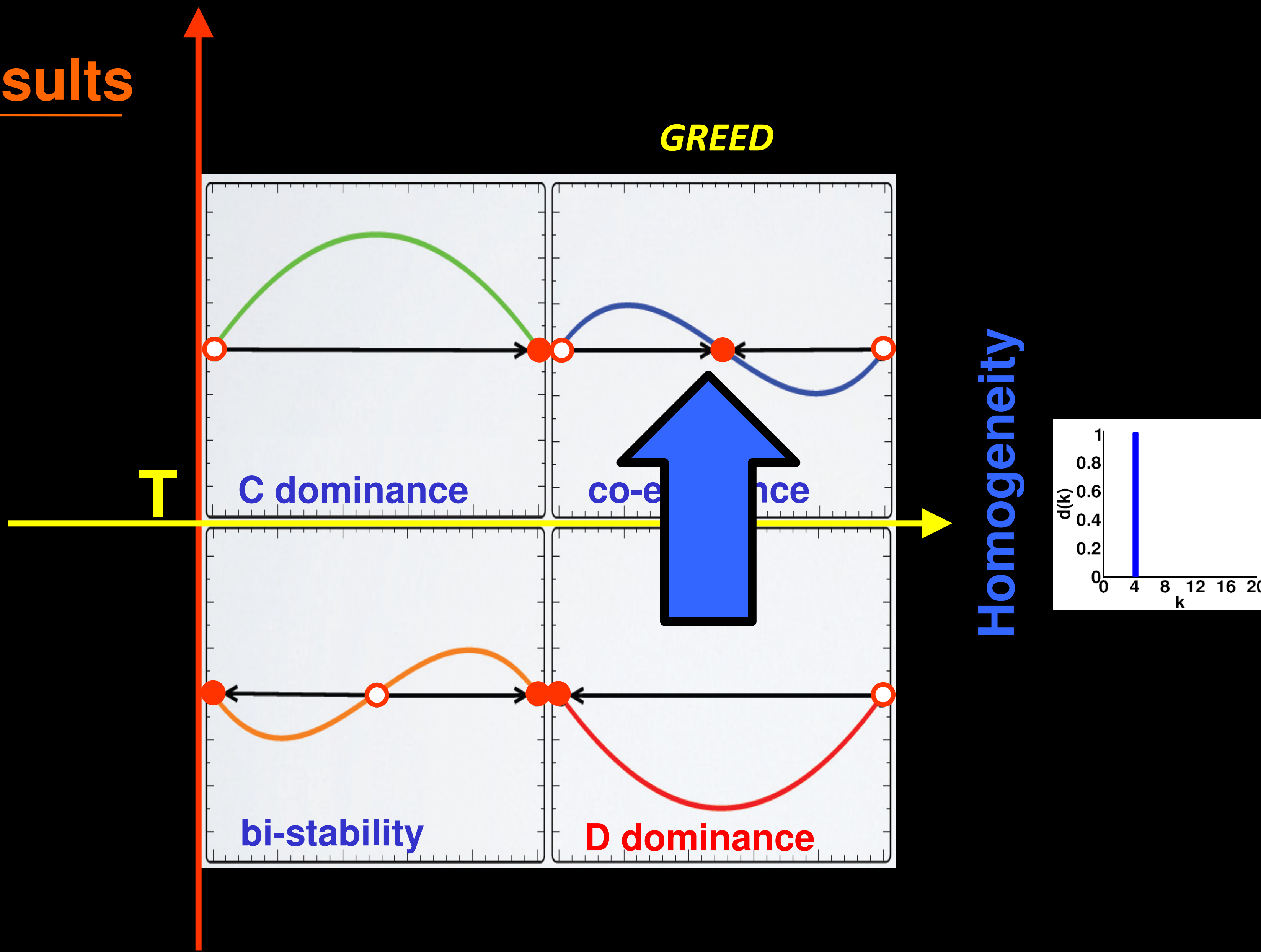
overall results



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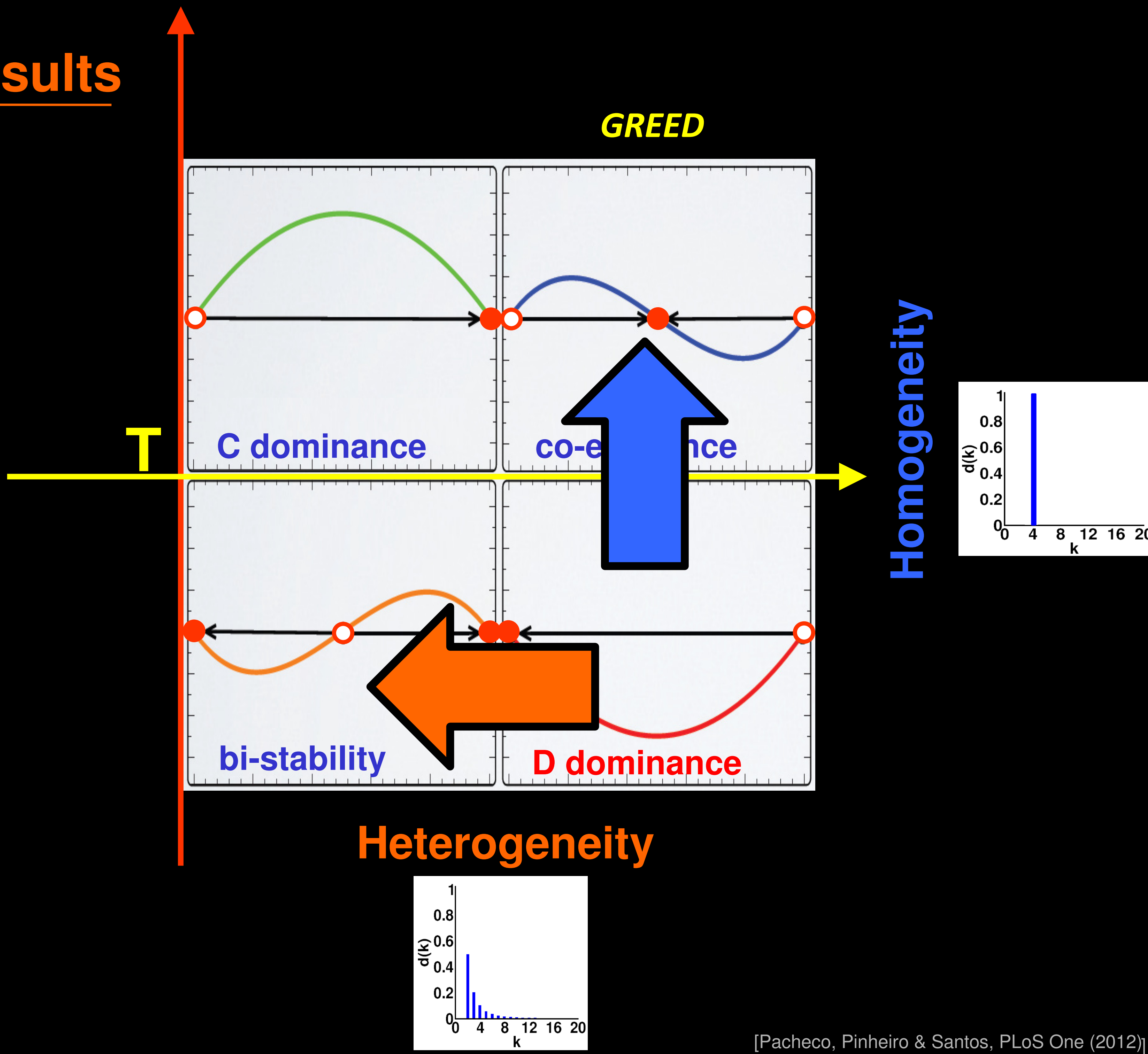
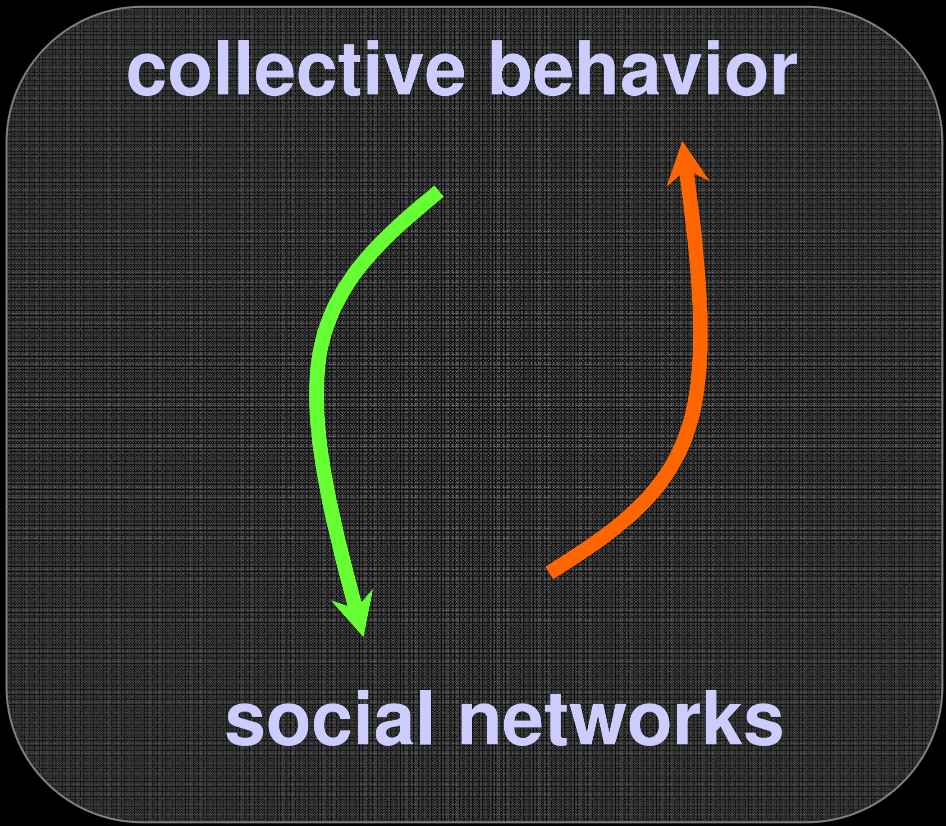


[Pacheco, Pinheiro & Santos, PLoS One (2012)]]

but…. social networks are not static !!

even when individuals remain the same, their connectivity patterns change in time

in fact, games take place on networks that adapt to the behavioural changes of individuals who, in turn, may change their behaviour in response to network changes.



evolutionary games on 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

evolutionary games on adaptive networks

an individual based model of co-evolution of *strategy* & *structure*

- **individuals can be satisfied or dissatisfied with a link**
- **if *satisfied*, they will try to keep the link**
- **if dissatisfied, they may attempt to rewire the link**
- ***link rewiring proceeds to a first neighbor of the previous peer***
- ***conflicts of interest* may occur**

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.

co-evolution of game strategy & network structure

we have *two different* time-scales :

- strategy evolution T_S
- structural evolution T_A

we define the ratio $W = T_S / T_A$

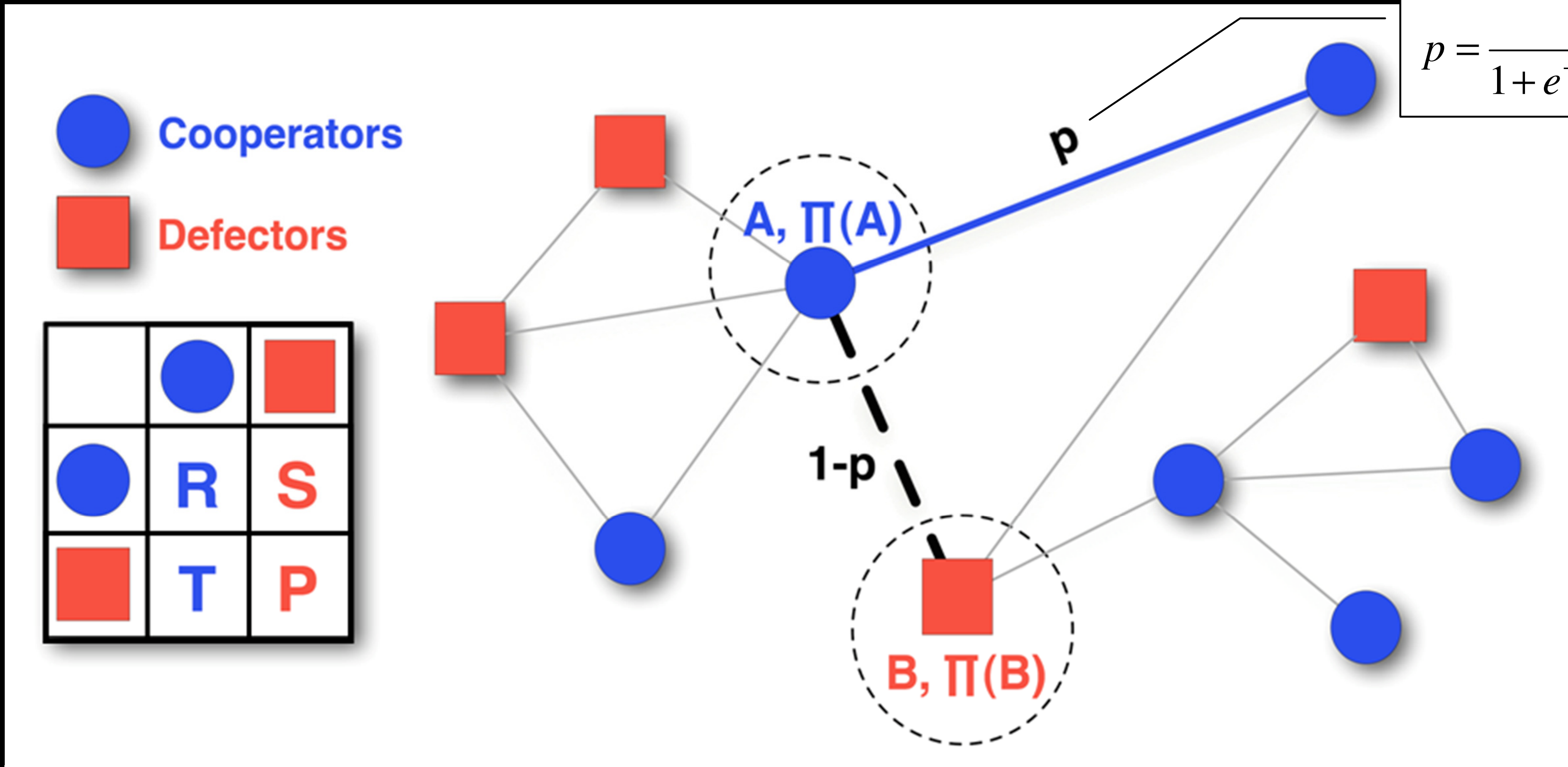
and study co-evolution as a function of W

for ALL social dilemmas ;

features of the model :

- population is constant
- average connectivity remains constant
- graph remains connected

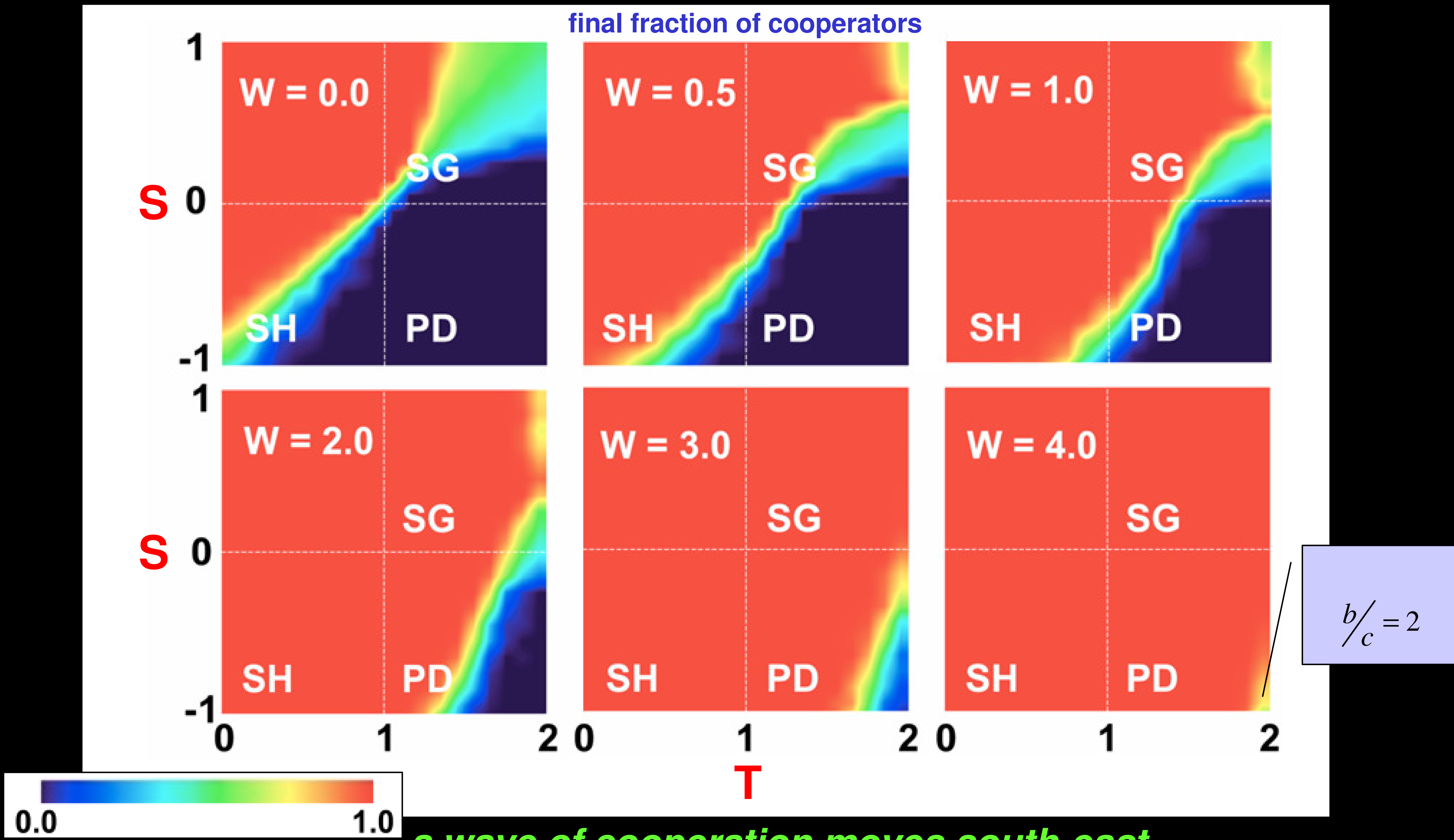
co-evolution of game strategy & network structure



$$p = \frac{1}{1 + e^{-\beta(\Pi_A - \Pi_B)}}$$

- choose A @ random; then choose a neighbour B of A @ random ;
- B is satisfied (A is C) ; A is NOT satisfied (B is D);
- B wants to keep link; A wants to change;
- with probability p A rewires to a neighbour of B ;
- with probability (1-p) B keeps link;
- remember: a neighbour of a defector is "most likely" a cooperator ;

co-evolution of game strategy & network structure



a wave of cooperation moves south-east . . .

. . . as rewiring dynamics becomes faster

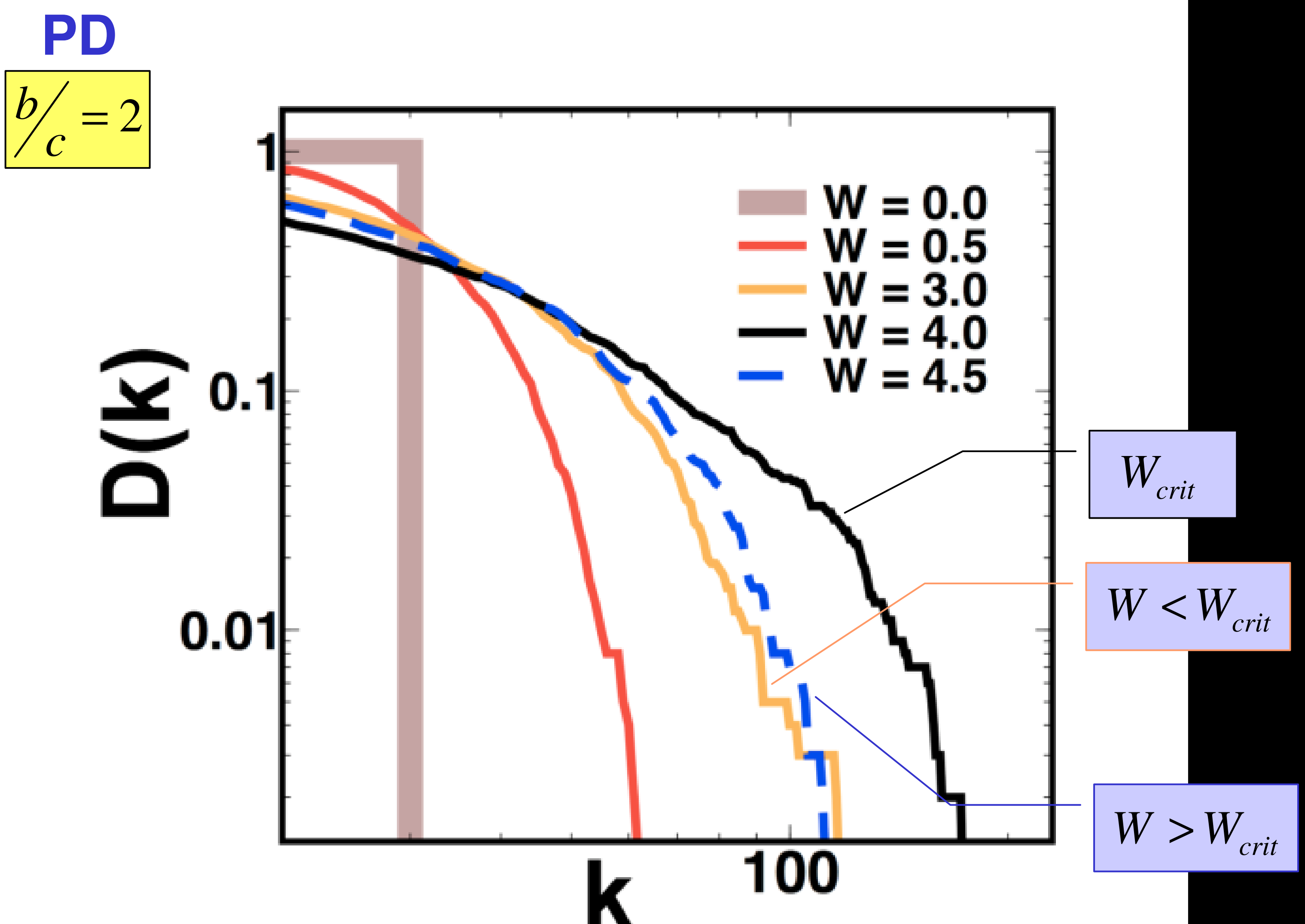
evolutionary games on adaptive networks

OK, cooperation increases, but how do the networks look like ?

networks **exhibit features which depend on the game at stake and on the actual values of the payoff matrix**

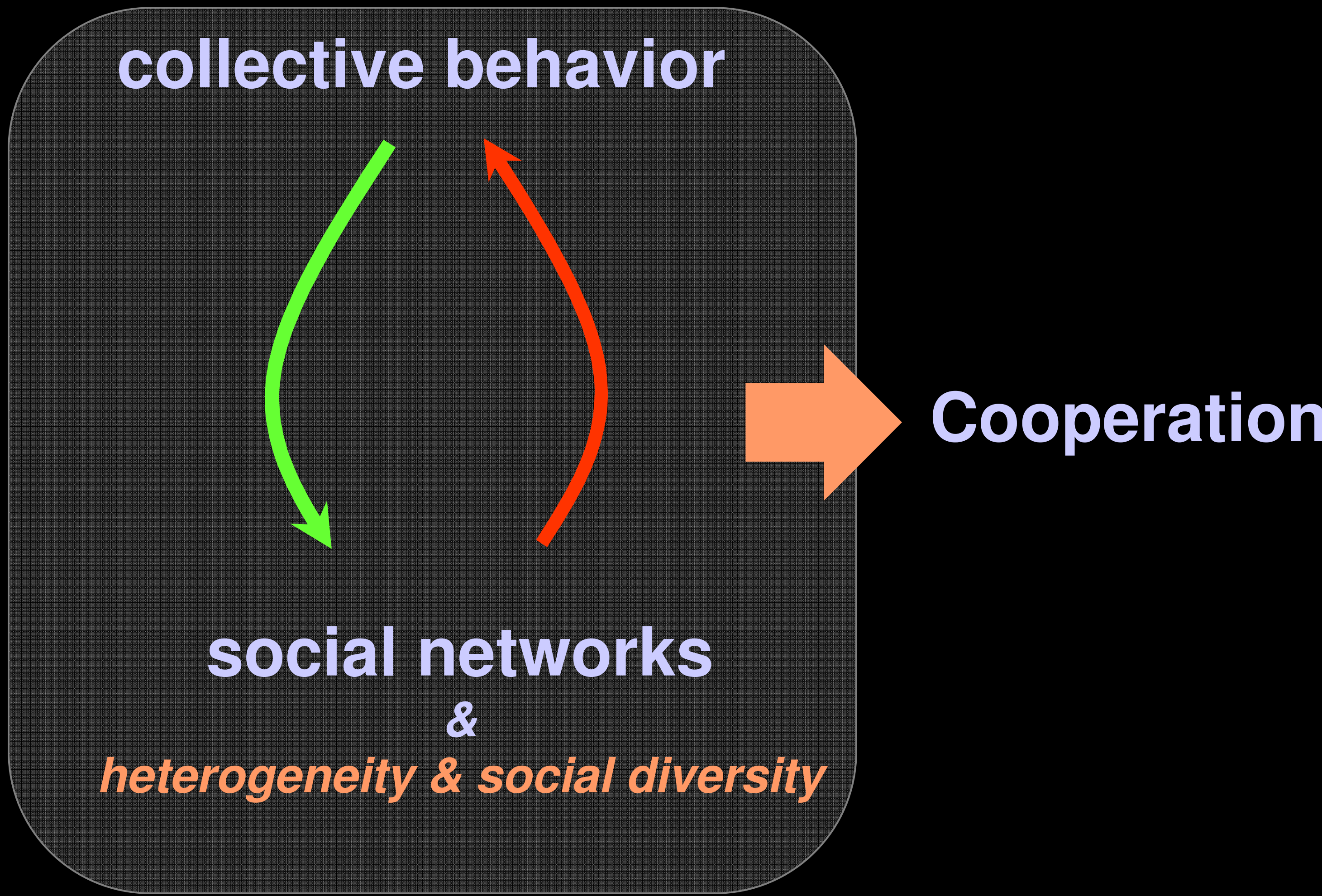
as soon as *C*s get rid of *D*s, netwok heterogeneity gets naturally reduced, as small errors in decision making will help networks to become increasingly random

evolutionary games on adaptive networks



network heterogeneity emerges naturally from the co-evolution of strategy & structure

co-evolution of game strategy & network structure



FC Santos, JM Pacheco, T Lenaerts, PNAS 103 3490-3494 (2006).
FC Santos, MD Santos, JM Pacheco, Nature 454, 213-216 (2008).
And others…

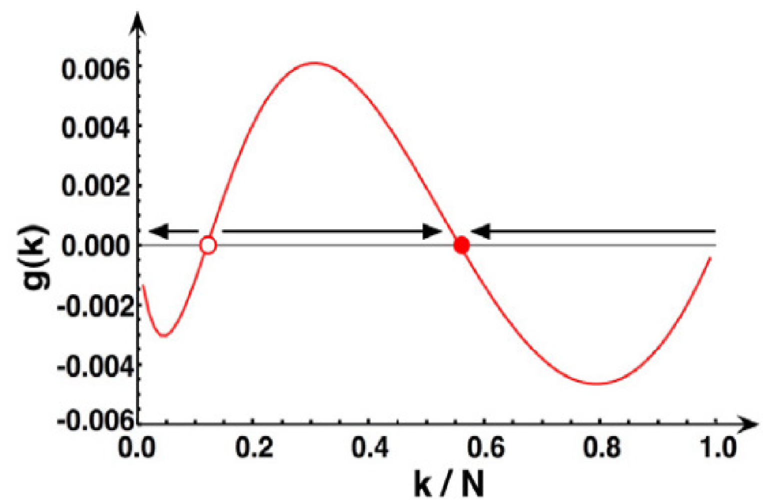
Santos, Pacheco, Lenaerts, PLoS Comput. Biol. (2006).
Pacheco, Traulsen , Nowak, Phys. Rev. Lett. (2006) .
Van Segbroeck, Santos, Lenaerts, Pacheco, Phys Rev Lett (2009)

the role of heterogeneity

- ***network heterogeneity*** **is a natural consequence of evolution**
- ***heterogeneity*** **transforms a *PD* into a *SH*, even for weak selection.**
- **what about N-person games ?**

heterogeneous networks (both static & *dynamic*) lead to

NPD & NSG → NSH



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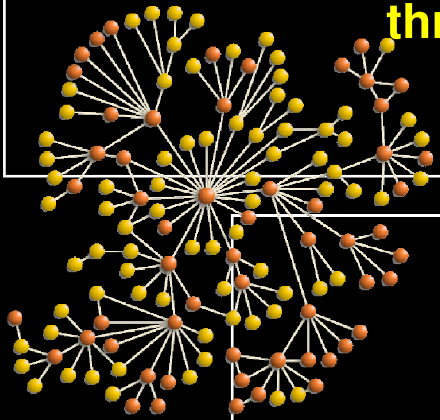
the ubiquity of social diversity

a natural source of diversity

the simple co-evolution of network topology and behaviours leads both cooperation to thrive and to strongly heterogeneous network scenarios



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diversity in the number of interactions

some individuals tend to interact more than others

diversity in social influence

some individuals will be chosen as a role model more often than others

FC Santos, JM Pacheco, Physical Review Letters 95 (2005) 098104

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context dependent contributions

some individuals will contribute more or less depending on their social position and revise their social ties accordingly

FC Santos, MD Santos, JM Pacheco, Nature 454 (2008) 213-216

Pacheco, Pinheiro, Santos, PLoS Comput Bio (2009)

the ubiquity of social diversity

diversity in the way individuals manage their social ties

diversity in individual responses to adverse social ties promotes cooperation

S. Van Segbroeck, F.C. Santos, T. Lenaerts, J.M. Pacheco. Phys Rev Lett,102 058105, 2009.

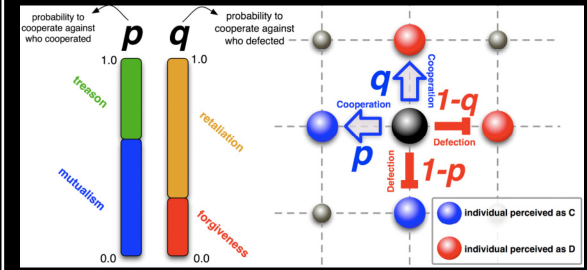
diversity of signals promotes cooperation

cooperators may easily find a suitable secret handshake whenever they have a rich portfolio of signals to pick from

FC Santos, JM Pacheco, B Skyrms, Journal of Theoretical Biology 274 (1) 30-35 (2011).

diversity in individual cognition promotes cooperation

whenever *Cs* & *Ds* react differently to different neighbours based on past experience, cooperation blooms



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the ubiquity of social diversity

diversity in learning rates

some tend to change their behavior more swfitly than others

A. Szolnoki, M. Perc, and G. Szabó, Eur. Phys. J. B, 2008

globalization and human cooperation

individuals that often participate in culturally diverse interaction groups, tend to be more cooperative (experimental result)

Buchan et al. , PNAS 2009

solving the climate change probem

individuals cooperate more when they play different roles in deciding to cooperate or not in taming the planet's climate

Santos & Pacheco, PNAS 2011

the ubiquity of social diversity

***diversity* in many of its forms appears to be a fundamental mechanism towards cooperation**

Evolution of Diversity and Cooperation

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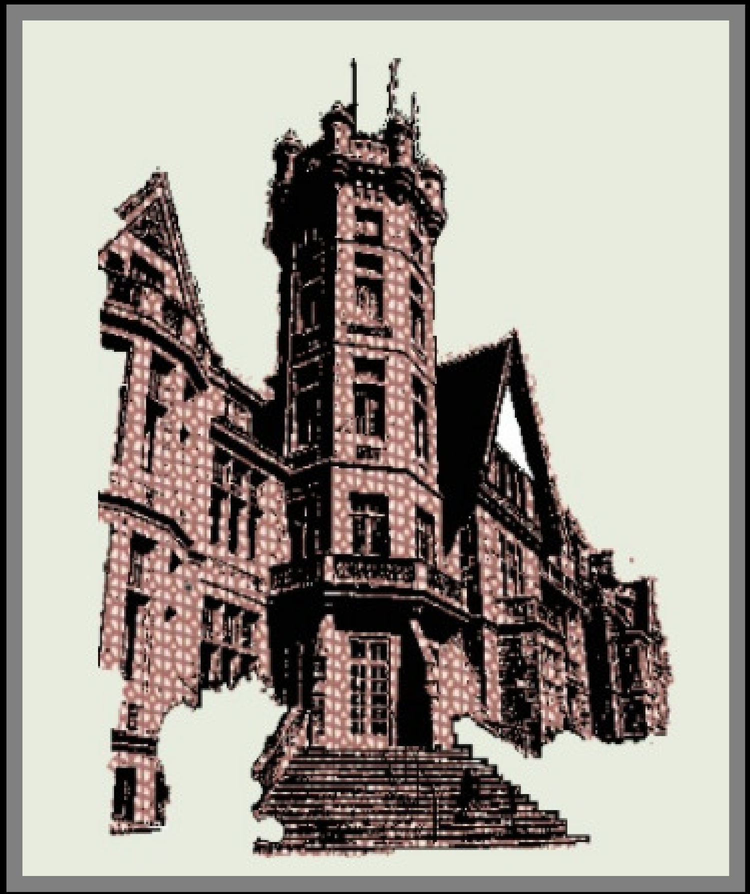

Luis Santaló School, 19th of July, 2013