

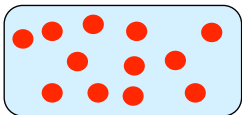
Cooperation and construction

Corina E. Tarnita

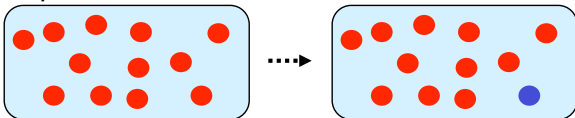
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Evolution

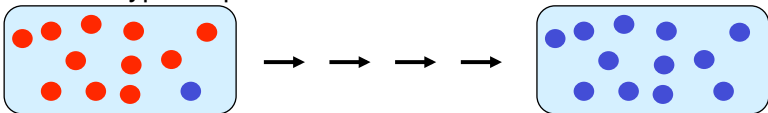
- A population of reproducing individuals



- Reproduction occurs with mistakes \Rightarrow Mutation



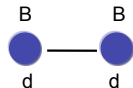
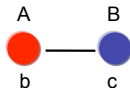
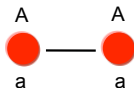
- Different types reproduce at different rates \Rightarrow Selection



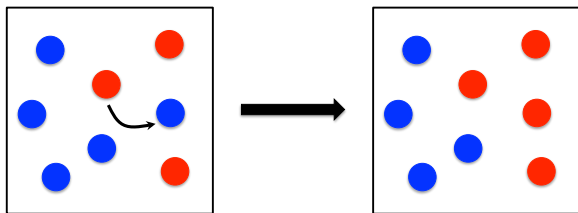
Evolutionary games

- The fitness of individuals is not constant, but depends on the composition of the population.

$$\begin{array}{c} A \\ B \end{array} \begin{pmatrix} A & B \\ a & b \\ c & d \end{pmatrix}$$



Evolutionary games – updating



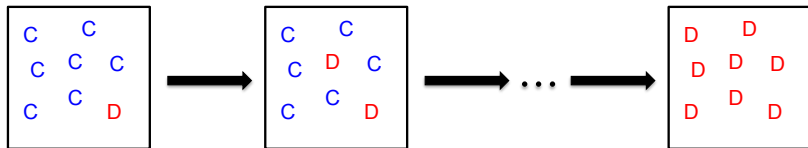
- An individual is picked to die (or to imitate) at random;
- An individual is chosen to reproduce (or to be imitated) proportional to payoff.

Evolution of cooperation – simplified PD

	<i>Cooperator</i>	<i>Defector</i>
<i>Cooperator</i>	$b - c$	$-c$
<i>Defector</i>	b	0

where $b > c > 0$.

Natural selection chooses defection



In a well-mixed population, defectors will always have a higher payoff than cooperators.

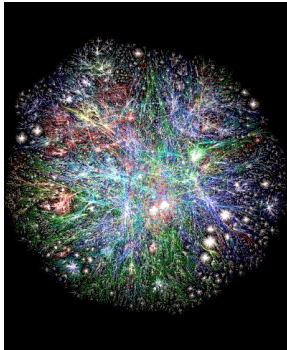
Mechanisms for the evolution of cooperation

- Direct reciprocity
- Indirect reciprocity
- Structure
- Kin selection
- Group (multi-level) selection

Why are we interested in structure?

- Because evolutionary processes tend to occur in structured populations.

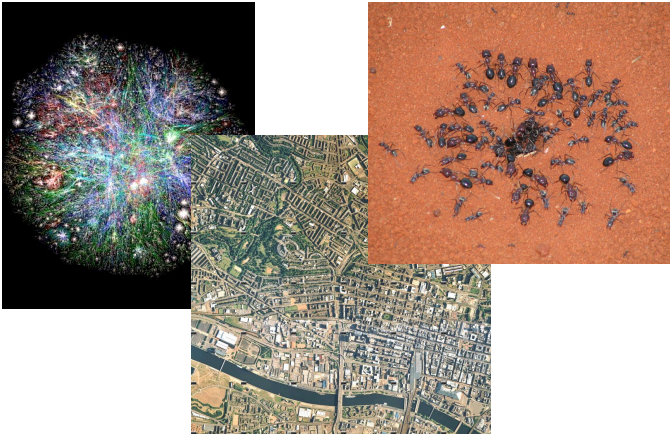
Structure



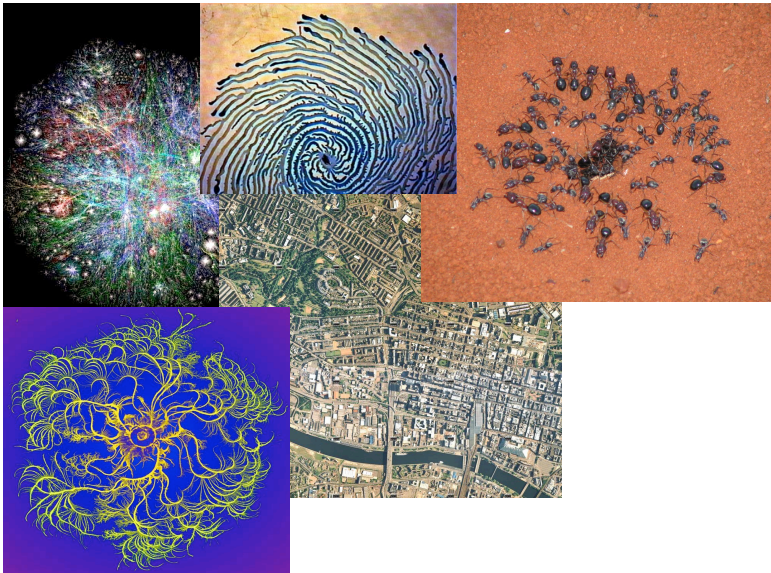
Structure



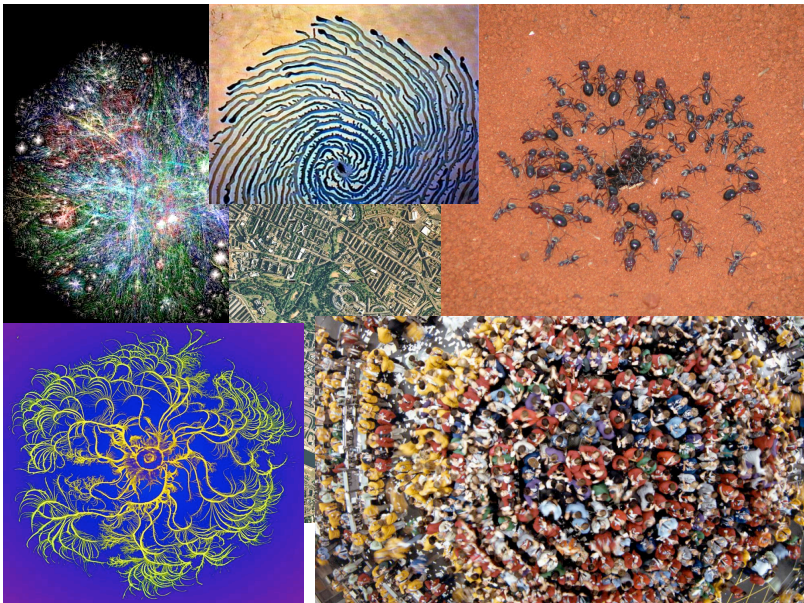
Structure



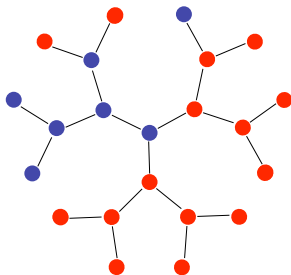
Structure



Structure



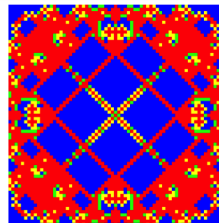
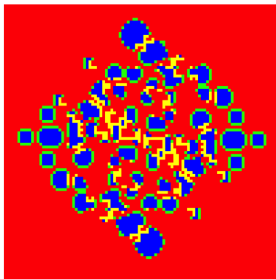
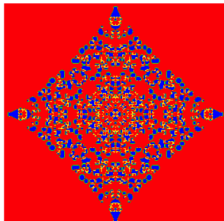
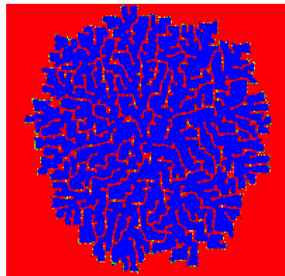
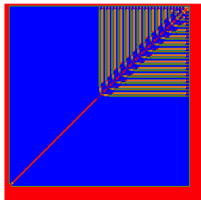
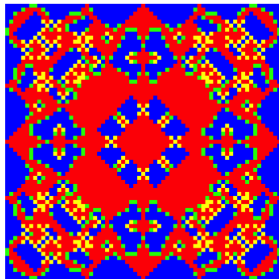
Games on fixed graphs



- Individuals interact and compete only with neighbors.
- for $N \gg k$, $b/c > k$

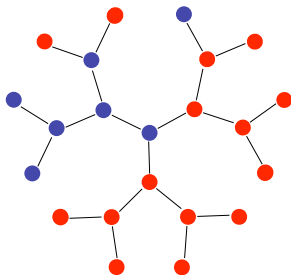
(Ohtsuki et al, *Nature* 2006, Taylor et al, *Nature* 2007)

Spatial kaleidoscopes



(Nowak and May, *Nature* 1992)

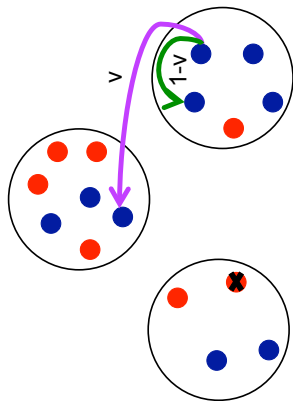
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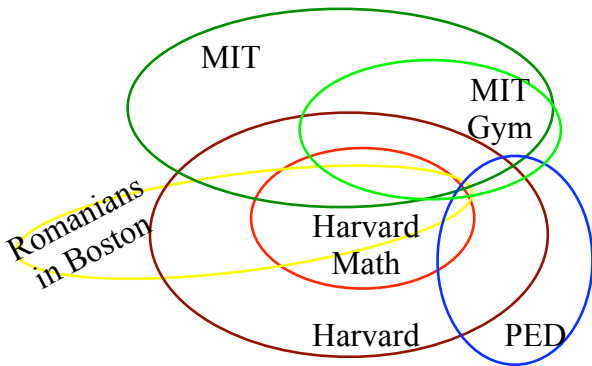
(Ohtsuki et al, *Nature* 2006, Taylor et al, *Nature* 2007)

Games on islands



- individuals play with group members games that can be different from those played with outsiders
- one individual is picked to die (change strategy) at random
- and one individual is picked to reproduce (become a role-model) proportional to payoff
- strategy and set membership are both imitated (with respective mutation probabilities u and v)

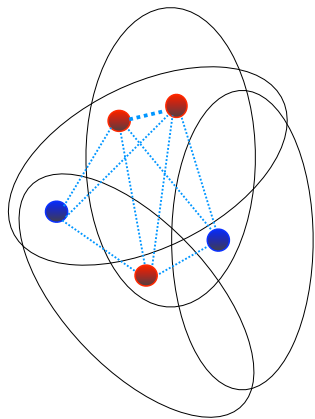
"No man is an island."



Potential questions to address with this framework

- alignment of interests
- different games in different sets
- creation of hype
- environment/time - dependent hierarchy of sets
- time-constraint conflicts

Evolutionary Dynamics on Sets



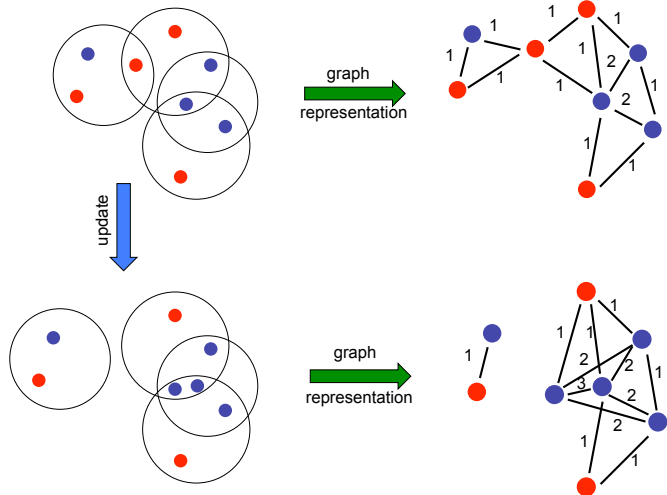
- N individuals are distributed into M sets.
- Each individual interacts with others who are in the same set.
- Two individuals interact as many times as they have sets in common.

(Tarnita et al, *PNAS* 2009)

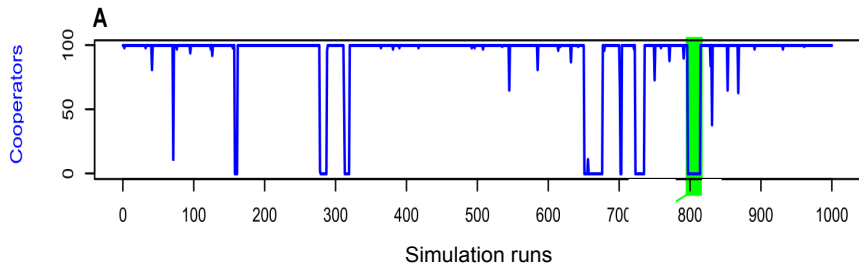
Selection and mutation

- Successful individuals are more likely to be imitated.
- Strategy and set memberships are both imitated.
- An individual inherits the **strategy** of the parent with probability $1 - u$; with probability u he picks a random strategy.
- An individual inherits the **set memberships** of the parent with probability $1 - v$; with probability v he picks a random set configuration.

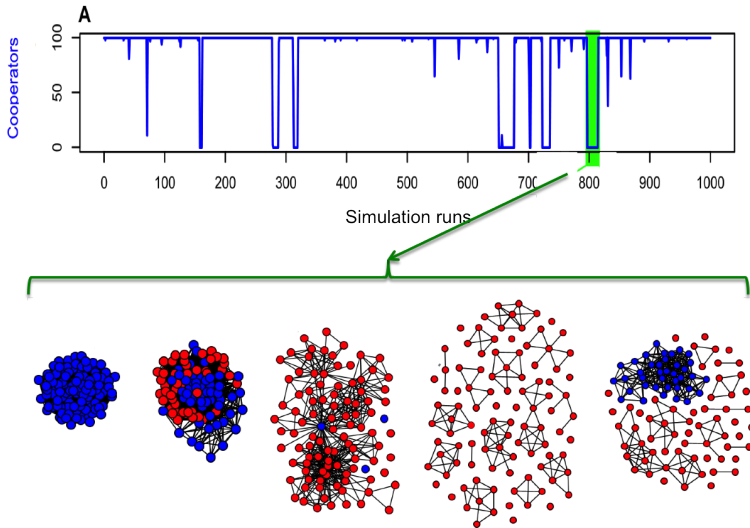
Dynamical Graph Theory



Dynamical Graph Theory



Cooperators build; defectors fragment



Evolution of cooperation – the critical b/c

$$\frac{b}{c} > \frac{1 - \bar{G}}{G - \bar{G}}$$

- for ‘islands’:

$$G = \Pr(s_i = s_j \mid i \text{ and } j \text{ are on the same island})$$

$$\bar{G} = \Pr(s_i = s_k \mid i \text{ and } j \text{ are on the same island})$$

- in general, for overlapping sets:

$$G = \frac{\langle w_{ij} \mathbf{1}_{s_i=s_j} \rangle_0}{\langle w_{ij} \rangle_0}$$

$$\bar{G} = \frac{\langle w_{ij} \mathbf{1}_{s_j=s_k} \rangle_0}{\langle w_{ij} \rangle_0}$$

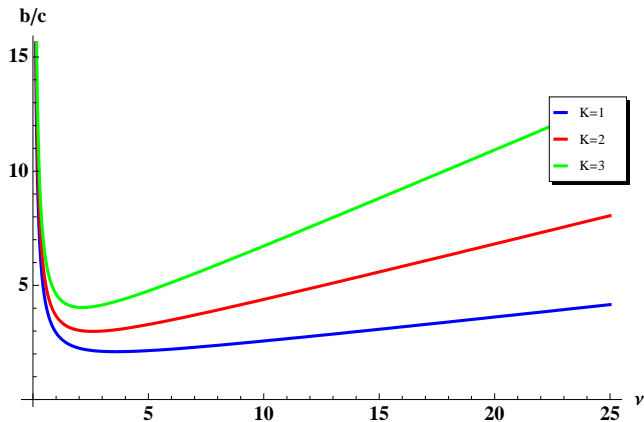
- For N large and $u \rightarrow 0$ we have

$$\frac{b}{c} > \frac{K}{M-K}(\nu + 2) + \frac{M}{M-K} \frac{\nu^2 + 3\nu + 3}{\nu(\nu + 2)}$$

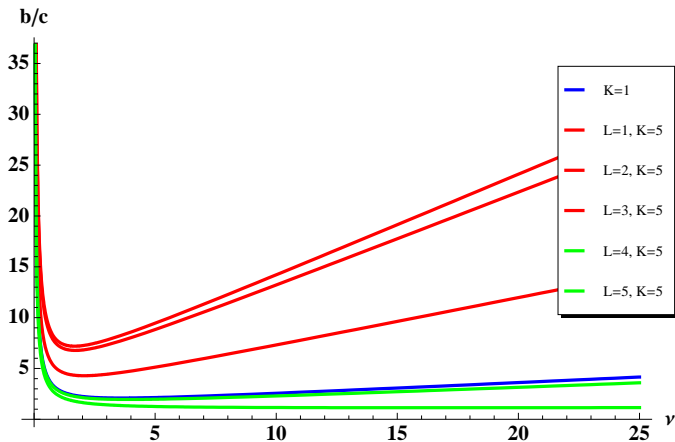
where $\nu = 2Nv$ is twice the number of set mutants in a generation and M is the total number of sets. We introduced the additional assumption that each individual belongs to exactly $K \leq M$ sets.

(Tarnita et al, *PNAS* 2009)

Critical ratios for $K=1$, $K=2$ and $K=3$ ($M=10$)



A simple alignment of interests



Conclusions

- The sets framework is an example of dynamical graphs: the interaction network changes as a consequence of the evolutionary dynamics
- Cooperators build the network and defectors fragment it
- The sets promote the evolution of cooperation but the more sets we allow for each individual the harder it is to get cooperation
- Unless there is conditional behavior: I cooperate only if we have at least L sets in common.

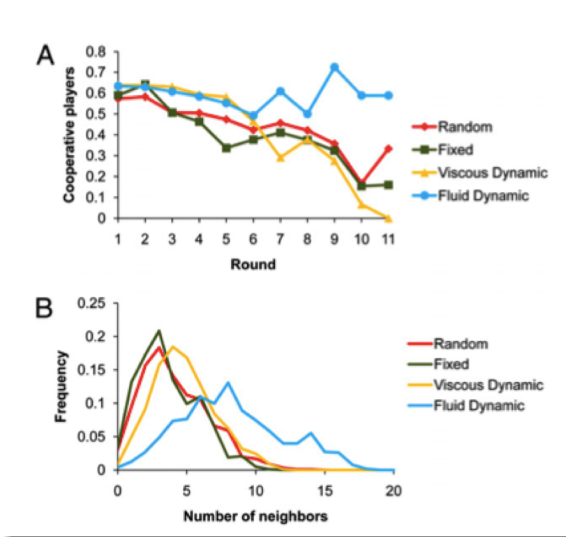
Dynamical networks: second approach

- Strategy updates are independent of graph updates.
- With probability $1/(1 + p)$ a strategy update occurs
 - One individual is picked at random to die and the entire population competes proportional to payoff to replace it as before.
- With probability $p/(1 + p)$ a graph update occurs
 - Two individuals are picked at random and the connection between them is updated (links can be made or broken depending on the strategies of the two players)
- Cooperation evolves if

$$b/c > 1/p$$

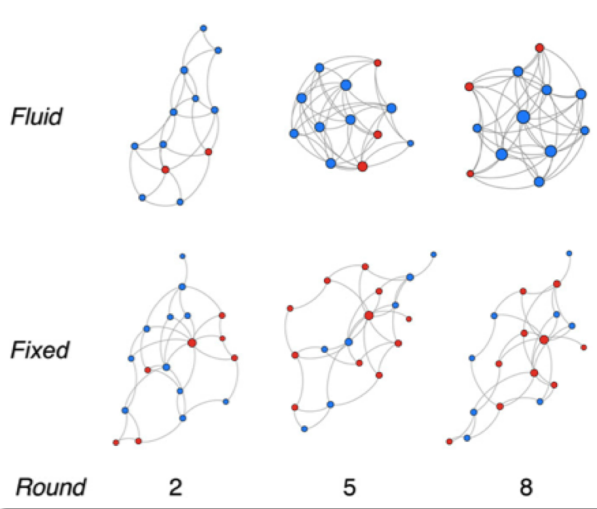
(very approximately)

Experiments: the more dynamical, the better



(Rand et al, *PNAS* 2011)

Experiments: fluid versus fixed



(Rand et al, *PNAS* 2011)

General effect of population structure

General Games ... on any population structure

Theorem. For any structured population and any update rule satisfying mild conditions, in the limit of weak selection, there exists a σ intrinsic to the model and to the dynamics*, such that for any game $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ between two strategies A and B , the condition that strategy A is favored over B is

$$\sigma a + b > c + \sigma d$$

(*i.e. σ depends on the population structure, the population size, the mutation rates etc., but not on the game)

(Tarnita et al, *JTB* 2009)

Prisoner's Dilemma

$$\begin{array}{cc} & C & D \\ C & \left(\begin{array}{cc} 3 & 0 \end{array} \right) \\ D & \left(\begin{array}{cc} 5 & 1 \end{array} \right) \end{array}$$

- Cooperation is favored over defection if

$$3\sigma + 0 > 5 + \sigma$$

which is

$$\sigma > 2.5$$

Coordination games

$$\begin{array}{cc} & \begin{array}{c} A \\ B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} 3 & 0 \\ 2 & 2 \end{pmatrix} \end{array}$$

- A is Pareto efficient because $3 > 2$.
- B is risk-dominant because $3 + 0 < 2 + 2$.
- However, a structured population can select for the Pareto equilibrium if

$$3\sigma + 0 > 2 + 2\sigma$$

which is

$$\sigma > 2$$

Corollary: Connection to the Prisoner's Dilemma

In the limit of weak selection, for the purpose of establishing strategy dominance, it suffices to study simpler games, given by only one parameter (eg. the Prisoner's Dilemma with the single parameter b/c).

$$\sigma = \frac{(b/c)^* + 1}{(b/c)^* - 1}$$

Multiple strategies: $n = 3$ is the general case

- The σ -theorem can be generalized to several strategies: if the game is played in a population where each player uses one of n strategies; the payoff matrix is $A = [a_{ij}]$. Then, strategy k is favored by selection if

$$\underbrace{\sigma_1 a_{kk} + \bar{a}_{k*} - \bar{a}_{*k} - \sigma_1 \bar{a}_{**}}_{\text{pairwise risk-dominance}} + \sigma_2 \underbrace{(\bar{a}_{k*} - \bar{a})}_{\text{risk-dominance}} > 0$$

where

$$\begin{aligned}\bar{a}_{**} &= \frac{1}{n} \sum_i a_{ij} & \bar{a}_{k*} &= \frac{1}{n} \sum_i a_{ki} \\ \bar{a}_{*k} &= \frac{1}{n} \sum_i a_{ik} & \bar{a} &= \frac{1}{n^2} \sum_{i,j} a_{ij}\end{aligned}$$

- Different measures of strategy success: are they equivalent?
- Inclusive fitness as accounting method and measure of strategy success
- Inclusive fitness and kin selection