Combining evolutionary games with network formation explains emergence of cooperation in biology

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Outline of the talk

- Basics on Game Theory
- Basics on Evolutionary Games
- Development of the Replicator Equation on Graphs (RE-G)
- Results on $(N, 2)$-games
- Experiments and Simulations
- Modeling the Formation of Bacterial Networks
- Conclusions and Future Directions

Non-cooperative games (1/2)

- **Game theory deals with decision making in systems where more than one rational agent are involved**
- A rational agent is called **player**
- Decisions are called **strategies**
- At the end of the game, each player earns a **payoff**

Non-cooperative games (2/2)

- The game structure (players, strategies, payoffs) is known to all players
- Each player adopts a strategy wishing to maximize his payoff
- Decisions are made without interaction between players (communications and coalitions are forbidden, non transferable payoffs)
- The payoff of a player depends on his strategy, but also on the strategies of the others!

The Prisoners' dilemma game (1/2)

- Two players (the thieves)
- Two strategies: confess (C), not confess (NC)
  - Confess is a non cooperative behavior
  - Not confess is a cooperative behavior
- Payoffs (years in jail, minimization problem):

		Player2 C	*Player2* NC
Player1	*C*	2	0
Player1	*NC*	3	1

Many people say that the best strategy is to confess (C)...

The Prisoners' dilemma game (2/2)

		Player2		
		C		NC
	C	$2, 2$	$\Leftarrow$	$0, 3$
Player1		$\Uparrow$		$\Uparrow$
	NC	$3, 0$	$\Leftarrow$	$1, 1$

...but a deeper investigation shows that it's better for both not to confess (NC)!

- Arrows represent the preferences of rational players
- (C, C) is said to be a **pure Nash equilibrium***
- Nash equilibrium is the n-uple of strategies such that no player has anything to gain by changing only his own strategy unilaterally

**J.F. Nash was awarded with the Noble Prize in 1994 thanks to his huge contribution to game theory*

The Rock - Scissor - Paper game

		Player2		
		R	S	P
	R	$0, 0$	$1, -1$	$-1, 1$
Player1	S	$-1, 1$	$0, 0$	$1, -1$
	P	$1, -1$	$-1, 1$	$0, 0$

- Some games have no pure Nash equilibria!
- Randomization is the key to be successful
- A player can play a certain strategy with a particular probability
- The probability density function is called **mixed strategy**
- Nash demonstrated that every game has at least one Nash equilibrium in the set of mixed strategies

Basics on Evolutionary Game Theory

- Infinite population of equal individuals (players or **replicators**)
- Each individual exhibits a certain phenotype (= it is preprogrammed to play a certain strategy)
- An individual asexually reproduces himself by replication. Offspring will inherit the strategy of parents

Nature favors the fittest

- Two replicators are randomly drawn from the population. Only one of them can reproduce himself
- They play a game in which strategies are the phenotypes
- Fitness of a replicator is evaluated like for game theory!
- The fittest is able to reproduce himself. The share of population with that phenotype will increase

Natural selection!

The replicator equation

$$\dot{x}_s = x_s(p_s(x) - \phi(x))$$

- x_s is the share of population with strategy s
  $0 \leq x_s \leq 1$, $\sum_s x_s = 1 \ \forall t \geq 0$
- $p_s(x) = e_s^T Bx$ is the payoff obtained by a player with strategy s
- $\phi(x) = x^T Bx$ is the average payoff obtained by a player
- B is the payoff matrix

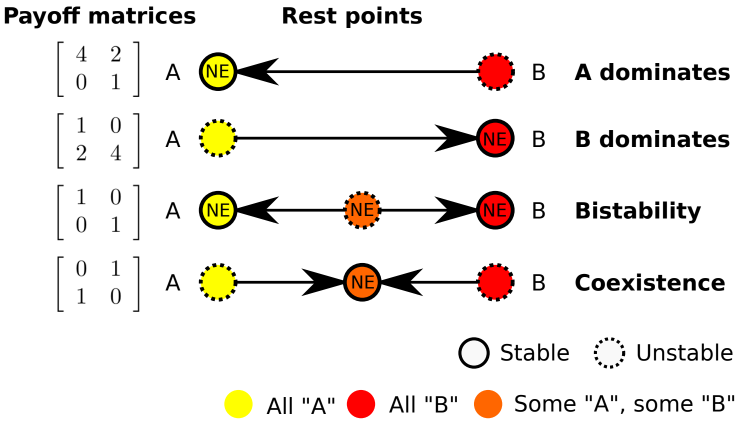
- All Nash equilibria are rest points
- Lyapunov stable rest points are Nash equilibria

The replicator equation is equivalent to Lotka-Volterra equation!

Weibull, J.W., 1995. Evolutionary Game Theory. MIT Press

Hofbauer J., Sigmund K., 1998. Evolutionary games and population dynamics, Cambridge University Press

Properties of the replicator equation



Marginal stability and existence of infinite equilibria are also possible, e.g with payoff matrices $[a\ b; a\ b]$.

...but in real world situations, things are different!

Indeed:

- The population of individuals can be finite
- In general, players aren't preprogrammed to play a pure strategy; they can be "mixed" (i.e. they can be partially cooperator and partially defector, selfish and altruist...)
- Population has a structure: an individual can meet only his neighbors
- Individuals are described by vertices of a graph, edges are the connections between them. $A = \{a_{v,w}\}$ is the adjacency matrix of the graph

Extensions of the replicator equation to networks

- The replicator equation on graphs has been obtained for networks with infinite vertices
- It has also been studied with infinite networks of fixed degree (each vertex has the same number of connections)
- Algorithmic approaches have been used to model finite population showing cooperative behavior (Prisoners' dilemma game) in discrete time

Ohtsuki, H., Nowak, M.A., 2006. The replicator equation on graphs. J. Theor. Biol., Vol. 243, N. 1, pp. 86-97

Szabó G., Fáth G., 2007. Evolutionary Games on Graphs. Physics Reports, Vol. 446, pp. 97-216

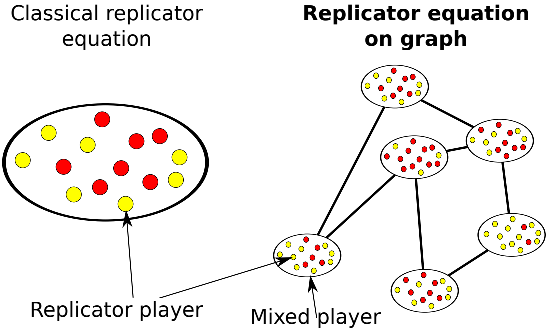
Gómez-Gardeñes, I. Reinares, A. Arenas and L.M. Floría, 2012. Evolution of Cooperation in Multiplex Networks,

Scientific Reports, Vol. 2, n. 620

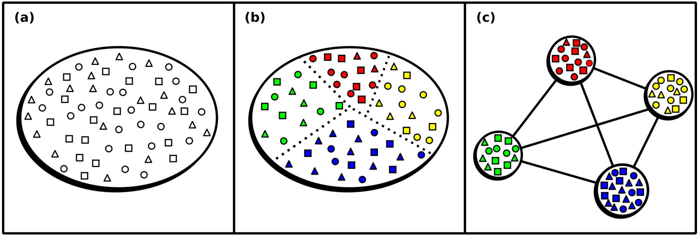
Our idea for a replicator equation on graphs

Each circle or cluster or tangle of relationships is linked by infinite strands to infinite circles or clusters or tangles (C. E. Gadda, Meditazione Milanese, 1974)

Main idea A mixed player is an infinite population of replicators!



Step 1. From the RE to the multipopulation RE



a) The population is well mixed and the individuals differ only for the chosen pure strategy (mean field approach)
b) The population is splitted in subpopulations with different characteristics (not the strategies)
c) The subpopulations are organized as the vertices of a fully connected graph

Modeling phase: preliminaries

- $x_{v,s}$ is the share of replicators in subpopulation v choosing strategy s
- $\mathbf{x}_v = [x_{v,1} \ \dots \ x_{v,M}]^T$ is the strategy distribution of subpopulation v
- $p_{v,s} = \boldsymbol{\pi}_v(\mathbf{e}_s, \mathbf{x}_{-v})$[1] is the average payoff earned by a replicator of subpopulation v with pure strategy s ($\mathbf{e}_s$ is the s-th standard versor of $\mathbb{R}^M$)
- $\phi_v = \boldsymbol{\pi}_v(\mathbf{x}_v, \mathbf{x}_{-v}) = \sum_{s=1}^{M} x_{v,s} p_{v,s}$ is the average payoff earned by a replicator of subpopulation v

[1] In general, $\boldsymbol{\pi}_v(\mathbf{x}_v, \mathbf{x}_{-v})$ is the payoff earned by the mixed player v when he plays strategy $\mathbf{x}_v$.

The multipopulation replicator equation provides a solution

- The multipopulation replicator equation describes how the game strategies evolve in subgroups of the population identified by specific characteristics (not the strategies)

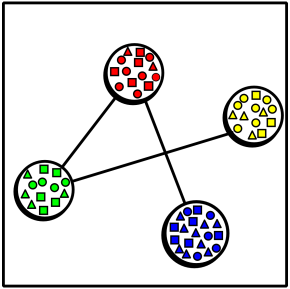
$$\dot{x}_{v,s}(t) = x_{v,s}(t)(p_{v,s}(t) - \phi_v(t))$$

- The replicators of a vertex play games only with the replicators of different vertices
- If the strategy s is better than the average the share of population that uses s increases in time ($p_{v,s}(t) - \phi_v(t) > 0$); it decreases otherwise.

In our model these subgroups are the individuals!

Weibull, J.W., 1995. Evolutionary Game Theory. MIT Press

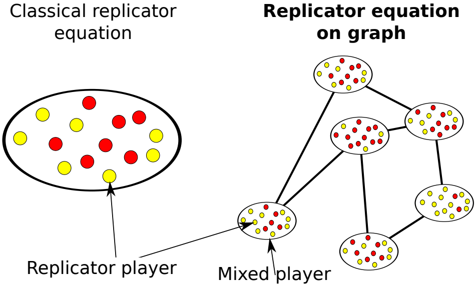
Step 2. The multipopulation RE on graphs



- The subpopulations are organized as the vertices of a generic finite graph and each vertex behaves as a population player
- The replicators of a vertex play 2-players games with the replicators of all the other vertices connected to him

Calculate the payoffs of the vertex players

Step 3. Calculate the payoffs (1/3)



- A vertex player interprets all his neighbors as an "average player"
- This game is equivalent to a N-players M-strategies game

Step 3. Calculate the payoffs (2/3)

The payoffs depend on the adjacency matrix $\mathbf{A} = \{a_{v,w}\}$ of the graph.

- Payoff obtained by player v when players use pure strategies $s_1, \ldots, s_N$ is a *tensor*:

$$\bar{\pi}_v^{\mathcal{G}}(s_1, \ldots, s_N) = \mathbf{e}_{s_v}^T \mathbf{B}_v \left(\frac{1}{d_v} \sum_{v=1}^{N} a_{v,w} \mathbf{e}_{\mathbf{s_w}} \right)$$

- When strategy distributions $\mathbf{x}_v$ are known for each vertex player, then the average payoff can be evaluated as follows:

$$\pi_v^{\mathcal{G}} = \sum_{s_1=1}^{M} \cdots \sum_{s_N=1}^{M} \left(\prod_{w=1}^{N} x_{w,s_w} \right) \bar{\pi}_v^{\mathcal{G}}(s_1, \ldots, s_N).$$

Jackson M. O., Zenou Y., 2014. Games on Networks, Handbook of Game Theory, Vol. 4, Peyton Young and Shmuel Zamir, eds., Elsevier Science

Step 3. Calculate the payoffs (3/3)

The extension to the mixed strategy set allows to evaluate the following payoff functions:

- Payoff obtained by player v with pure strategy s:

$$p^{\mathcal{G}}_{v,s} = \mathbf{e}_s^T \mathbf{B}_v \mathbf{k}_v$$

- Average payoff obtained by player v:

$$\phi^{\mathcal{G}}_v = \mathbf{x}_v^T \mathbf{B}_v \mathbf{k}_v$$

where

$$\mathbf{k}_v = \frac{1}{d_v} \sum_{v=1}^{N} a_{v,w} \mathbf{x}_w$$

Multipopulation RE + graph payoffs → RE on graphs

$x_{v,s}$ is the probability that player v will play strategy s

or

the probability that a replicator inside v is preprogrammed to use pure strategy s. Then, the replicator equation on graphs (RE-G) is:

$$\dot{x}_{v,s} = x_{v,s}(p^{\mathcal{G}}_{v,s} - \phi^{\mathcal{G}}_{v})$$

The Cauchy problem:

$$\begin{cases} \dot{x}_{v,s} = x_{v,s}(p^{\mathcal{G}}_{v,s} - \phi^{\mathcal{G}}_{v}) \\ x_{v,s}(t = 0) = c_{v,s} \end{cases} \quad \forall v \in \mathcal{V}, \quad \forall s \in \mathcal{S},$$

Madeo D., Mocenni C., Game interactions and dynamics on networked populations, IEEE Transactions on Automatic Control, (accepted with revisions), 2014

Relationship to the standard RE

Theorem

Let $\mathbf{X}(t)$ be the unique solution of the Cauchy problem of RE-G where $x_{v,s}(0) = c_s\ \forall v$. Assume also that $\mathbf{A}$ is stochastic and $\mathbf{B}_v = \mathbf{B}\ \forall v$. Let $\mathbf{y}(t)$ be the unique solution of the Cauchy problem, with $y_s(0) = c_s$. Then, $\mathbf{x}_v(t) = \mathbf{y}(t)\ \forall v, \forall t \geq 0$.

The Theorem states that the standard replicator equation can be obtained as a special case of the proposed extended version on networks, provided that initial conditions and payoff matrices are the same for all vertices.

The equation for $(N, 2)$-games

The payoff matrix for 2-strategies games is:

$$\mathbf{B}_v = \begin{bmatrix} b_{v,1,1} & b_{v,1,2} \\ b_{v,2,1} & b_{v,2,2} \end{bmatrix}.$$

Let $\sigma_{v,1} = b_{v,1,1} - b_{v,2,1}$, $\sigma_{v,2} = b_{v,2,2} - b_{v,1,2}$ and $\mathbf{k}_v(\mathbf{y}) = [k_{v,1}(\mathbf{y}) \; k_{v,2}(\mathbf{y})]^T$, then the RE-G reads:

$$\dot{y}_v = y_v(1 - y_v)f_v(\mathbf{y}), \qquad (1)$$

where

$$f_v(\mathbf{y}) = \sigma_{v,1}k_{v,1}(\mathbf{y}) - \sigma_{v,2}k_{v,2}(\mathbf{y}). \qquad (2)$$

- $\sigma_{v,1}$ and $\sigma_{v,2}$ represent the gains obtained by pure strategies
- $k_{v,s}$ is related to the number of players connected to v using s

Structure of NE and stationary point sets

$$\Theta^{NE} = \Big\{ \mathbf{y}^* \in [0,1]^N : ((y_v^* = 0 \wedge f_v(\mathbf{y}^*) \leq 0) \vee (y_v^* = 1 \wedge f_v(\mathbf{y}^*) \geq 0) \vee (f_v(\mathbf{y}^*) = 0)) \ \forall v \Big\},$$

$\Theta^{NES} = \Theta^{NE}$ where strict inequalities hold

$$\Theta^* = \Big\{ \mathbf{y}^* \in [0,1]^N : y_v^* = 0 \vee y_v^* = 1 \vee f_v(\mathbf{y}^*) = 0 \ \forall v \Big\}$$

1. The set of pure steady states $\Theta^p = \{0,1\}^N \subseteq \Theta^*$
2. $\Theta^m = (0,1)^N \cap \Theta^*$ is the set of interior steady states. Notice that $\Theta^m \subseteq \Theta^{NE}$
3. All other steady states are classified as pure/mixed and their set is $\Theta^{mp} = \Theta^* \setminus (\Theta^p \cup \Theta^m)$

Stability of pure stationary points

Theorem

Let $\mathbf{y}^* \in \Theta^p$. Then, the following statements are equivalent:

(a) $(\sigma_{v,1}k_{v,1}(\mathbf{y}^*) \leq \sigma_{v,2}k_{v,2}(\mathbf{y}^*) \wedge y_v^* = 0) \vee$
$(\sigma_{v,1}k_{v,1}(\mathbf{y}^*) \geq \sigma_{v,2}k_{v,2}(\mathbf{y}^*) \wedge y_v^* = 1)\ \forall v$

(b) $\lambda_v(\mathbf{J}(\mathbf{y}^*)) \leq 0\ \forall v$

(c) $\mathbf{y}^* \in \Theta^{NE}$

Corollary

Let $\mathbf{y}^* \in \Theta^p$. Then, the following statements are equivalent:

(a') $((\sigma_{v,1}k_{v,1}(\mathbf{y}^*) < \sigma_{v,2}k_{v,2}(\mathbf{y}^*) \wedge y_v^* = 0) \vee$
$(\sigma_{v,1}k_{v,1}(\mathbf{y}^*) > \sigma_{v,2}k_{v,2}(\mathbf{y}^*) \wedge y_v^* = 1))\ \forall v$

(b') $\lambda_v(\mathbf{J}(\mathbf{y}^*)) < 0\ \forall v$

(c') $\mathbf{y}^* \in \Theta^{NES}$

Some remarks to Theorem

1. Equivalence between (b)/(b') and (c)/(c') implies that:

every pure Nash equilibrium is Lyapunov stable

every pure strict Nash equilibrium is asymptotically stable

2. By definition of $\sigma_{v,1}$, $\sigma_{v,2}$ and $k_{v,s}(\mathbf{y}^*)$ we have that:

the steady state corresponding to a pure Nash equilibrium is stable if for each vertex v the total gain of players in his neighborhood choosing pure strategy s_v is the highest

Stability of mixed stationary points

Theorem

Suppose that $\sigma_{v,1} = \sigma_1$ *and* $\sigma_{v,2} = \sigma_2$ $\forall v$ *with* $sign(\sigma_1) = sign(\sigma_2) \neq 0$. *Then there always exists a steady state* $\mathbf{y}^* \in \Theta^m$ *such that* $y_v^* = \frac{\sigma_2}{\sigma_1+\sigma_2}$ $\forall v$. *Moreover,* $\lambda(\mathbf{J}(\mathbf{y}^*)) = \frac{\sigma_1\sigma_2}{\sigma_1+\sigma_2}\lambda(\mathbf{A})$.

The payoff matrices satisfying the hypotheses of Theorem 3 describe games where *coexistence* ($\text{sign}(\sigma_1) < 0$) or *bistability* ($\text{sign}(\sigma_1) > 0$) occur.

Some remarks to Theorem

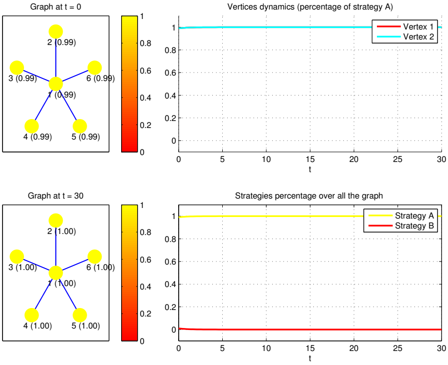
1. The adjacency matrix **A** of an undirected graph with no self-edges is symmetric, has real spectrum and null trace. The Perron-Frobenius theorem states that the largest eigenvalue of **A** is non-negative. Null trace implies that there must exist at least one non positive eigenvalue. From Theorem 3 follows that the same property holds for the spectrum of the Jacobian matrix $\mathbf{y}^*$. Then,

all the elements of Θ^m are saddle points

2. In the graph context coexistence or bistability are feasible only along the stable manifold of the saddle point

Bistable payoff matrix (1/4)

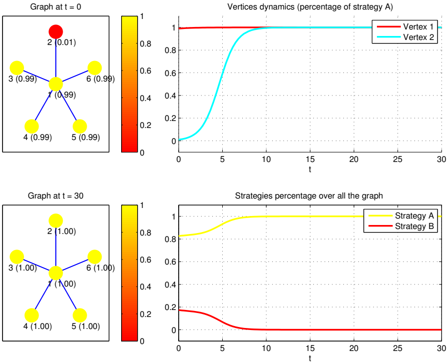
$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$



Since all vertices are the same at initial time, then evolution is equivalent to the standard replicator equation

Bistable payoff matrix (2/4)

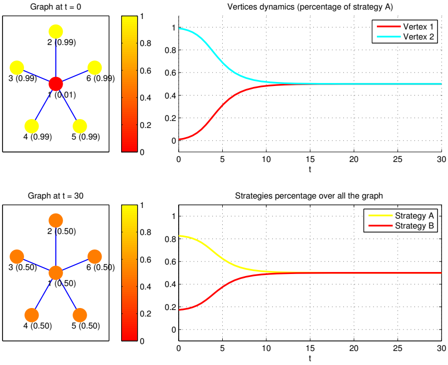
$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$



Network is resistant to the mutator

Bistable payoff matrix (3/4)

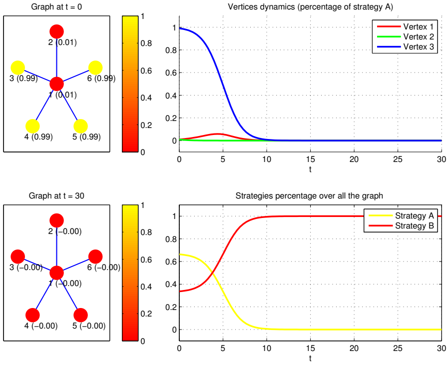
$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$



The mutator is stronger thanks to his connections. We have a diffusive process and the coexistence of strategies

Bistable payoff matrix (4/4)

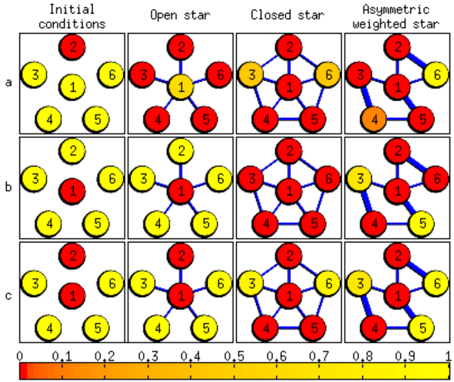
$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$



The central mutator is helped by another mutator. They impose their strategy to all the population!

The non strict prisoners' dilemma game

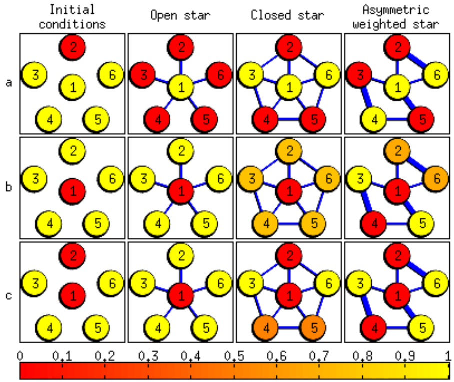
$$B = \begin{bmatrix} 1 & 0 \\ 1.5 & 0 \end{bmatrix}$$



Resilience of cooperation in non strict Prisoners' dilemma

Coexistence of strategies

$$B = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$$



The attractive mixed Nash equilibrium of RE is not homogeneously stable in the RE-G

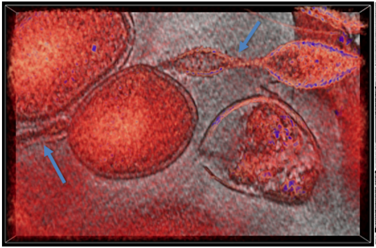
Bacterial networks: motivation and assumptions (1/2)

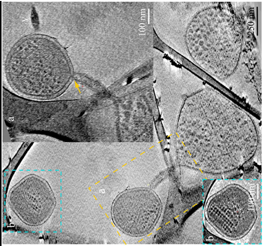
Biological evolution is driven more by symbiotic or cooperative relationships than competition between species: eukaryotic cells originated as communities of interacting entities (symbiogenesis) (Lynn Margulis, 1967)

- Cellular cooperation has been necessary for the evolution towards multicellular organisms
- New metagenomics data from environmental microbial communities (e.g. Wrighton et al. (2012); Kantor et al. (2013)) is showing that novel, small microorganisms lack the full metabolic potential to have a truly independent lifestyle

Bacterial networks: motivation and assumptions (2/2)

- Linking genomics and imaging (Comolli and Banfield (2014)), one novel nanoarchaea named ARMAN has been found establishing connections with archaea of different species
- Microbes of different classes or species may lack the full metabolic potential necessary for survival under certain (averse) conditions





Madeo D., Comolli L. and Mocenni C., Emergence of microbial networks as response to hostile environments, Frontiers in Microbiology, Nature Publishing Group, in press. 2014

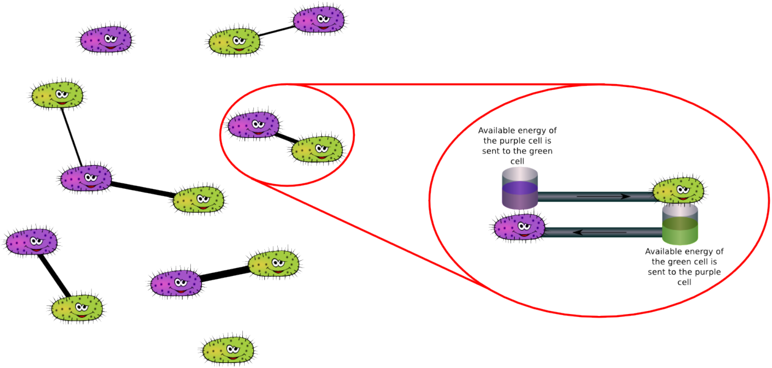
Modeling bacterial connection

- N bacteria are present in the space
- Bacteria are subdivided into $D \geq 2$ subclasses
- Bacteria want to create links to exchange matter and information such as genetic material, proteins, metabolic intermediates, etc. (behavioral strategies)
- Two bacteria of the same class do not link together
- Each bacterium has a finite amount of transferable energy
- Energy transfer is dissipative (a part of the energy is lost due to the distance between two bacteria)

Basics and notation

- $\mathcal{V}$ is the set of all considered bacteria ($|\mathcal{V}| = N$);
- $\mathcal{V}_1 \subset \mathcal{V}$ and $\mathcal{V}_2 \subset \mathcal{V}$ are the subclasses, where $\mathcal{V} = \mathcal{V}_1 \cup \mathcal{V}_2$ and $\mathcal{V}_1 \cap \mathcal{V}_2 = \emptyset$;
- $\rho_{v,w} > 0$ is the distance between bacteria v and w;
- $T_v > 0$ is the maximum amount of energy that organism v can transfer to others.

Energy transfer



The mechanism of connection

- The establishment of a connection between two individuals is modeled by an evolutive game
- The strategies available to each player consist of the will of being connected to another player
- The number of feasible strategies to each player corresponds to the number of bacteria different from itself: $N-1$
- Due to dissipation, connections are possible only under a threshold distance μ
- An individual v is effectively connected to another individual w if and only if w is also willing to be connected to v

From the RE-G to the formation of connections

The RE-G reads

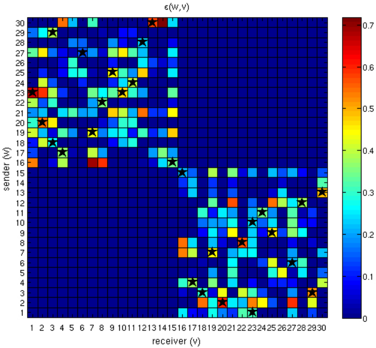
$$\dot{x}_{v,s_v} = x_{v,s_v}(p^{\mathcal{G}}_{v,s_v} - \phi^{\mathcal{G}}_v)$$

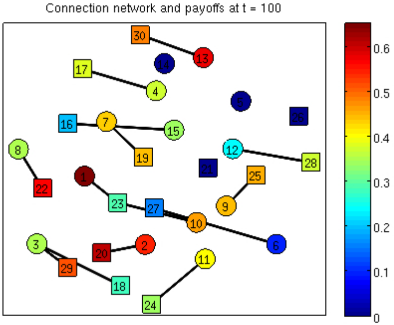
Given the solution of the RE-G, we built the effective connection graph $\mathcal{G}^E(t)$ by definining its adjacency matrix $\mathbf{A}^E(t) = \{a^E_{v,w}(t)\}_{v,w\in\mathcal{V}}$ as follows:

$$a^E_{v,w}(t) = \begin{cases} 1 & \text{if } x_{v,s_v}(t) > \eta \wedge x_{w,s_w}(t) > \eta \\ 0 & \text{otherwise} \end{cases}$$

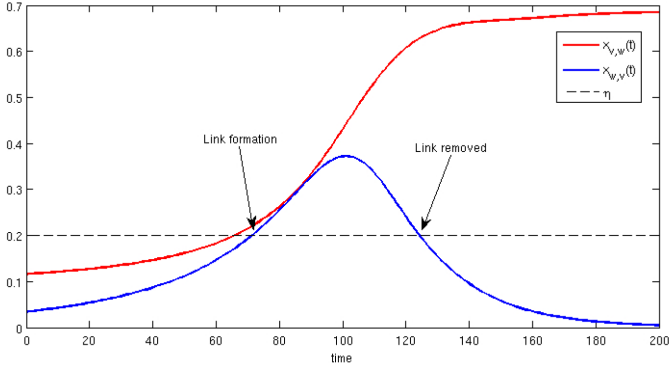
where $s_v = w$, $s_w = v$ and $\eta \in [0, 1]$ is a threshold.

Effective network formation

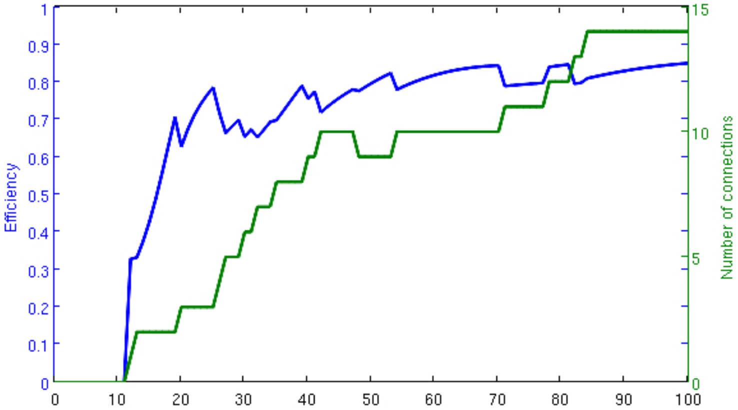




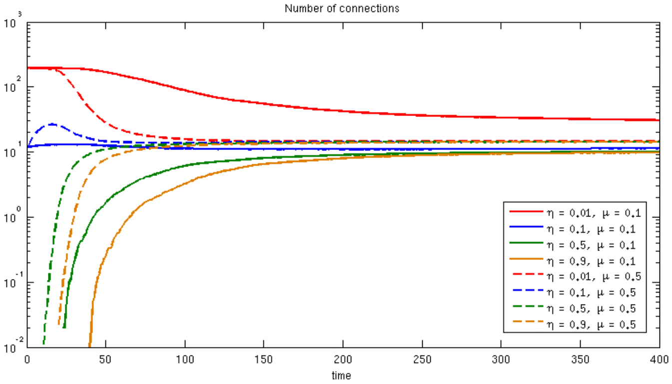
Formation of stable links



System efficiency and number of links over time



Asymptotic network



The asymptotic network does not depend on the distance (except for very small ones) and threshold parameters: it is a stable intrinsic property of the model

Conclusions and Future Work

Model construction. The theoretical formulation of the RE-G provides a new way for

- describe decisions and dynamical interactions among individuals in a society
- obtaine a general framework to derive suitable equations of such interactions and analyze their properties

Network reconstruction. Solving inverse problems on the basis of RE-G allows to

- explain mechanisms arising in real world phenomena. E.g. it has been observed that genes responsible for the cellular cooperation necessary for multicellularity are also the genes that malfunction in cancer cells (Davies and Lineweaver, 2011)
- optimize the network and the decision problem (game) to solve consensus and synchronization problems