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

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Supplementary Information

Consider a game between two strategies, A and B, with the general payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}. \tag{1}$$

A population of fixed size N is distributed over the vertices of a graph. All vertices of the graph are occupied by individuals who use either strategy A or B. The payoff of each individual is the sum over all interactions with its neighbors. Each vertex is connected to k other vertices; this number denotes the degree of the graph.

We study three different update rules. First, we consider 'death-birth' (DB) updating: in each time step a random individual is chosen to die; subsequently the neighbors compete for the empty site proportional to their fitness. Second, we consider imitation (IM) updating: in each time step a random individual is chosen to evaluate its strategy; it will either stay with its own strategy or imitate a neighbor's strategy proportional to fitness. Third, we consider 'birth-death' (BD) updating: in each time step an individual is chosen for reproduction proportional to fitness; the offspring replaces a random neighbor. In an unstructured population, these three update mechanism generate almost equivalent evolutionary dynamics, but for games on graphs they lead to very different outcomes.

Using a combination of pair approximation[1] and diffusion approximation[2], we derive the fixation probability, ρ_A, which represents the probability that a single A player starting in a random position on the graph (with $N-1$ many B players occupying the remaining positions) generates a lineage of A

players that takes over the entire population. If $\rho_A > 1/N$, then selection favors the fixation of A. We can also compare the two fixation probabilities, ρ_A and ρ_B.

Having derived the conditions for the general game, we will then examine the fixation probabilities, ρ_C and ρ_D, for cooperators, C, and defectors, D, in a Prisoner's Dilemma given by the payoff matrix

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}.$$

The parameters b and c denote the benefit for the recipient and the cost for donor of an altruistic act.

For DB updating, we find that $\rho_C > 1/N > \rho_D$ if $b/c > k$. For IM updating, we find that $\rho_C > 1/N > \rho_D$ if $b/c > k+2$, where k is the degree of the graph. For BD updating, we obtain that $\rho_D > 1/N > \rho_C$ always holds, and therefore selection cannot favor cooperation in this case.

These results hold for large population size, $N >> k$, and weak selection. Moreover, pair approximation is formulated for Bethe lattices (or Cayley trees), which are regular graphs without any loops. Therefore, some discrepancy with numerical simulations on graphs with loops is expected.

1 'Death-birth' (DB) updating

Let p_A and p_B denote the frequencies of A and B in the population. Let p_{AA}, p_{AB}, p_{BA} and p_{BB} denote the frequencies of AA, AB, BA and BB pairs. Pair approximation means that the frequencies of larger clusters are derived from the frequencies of pair. Let $q_{X|Y}$ denote the conditional probability to find an X-player given that the adjacent node is occupied by a Y-player. Here, both X and Y stand for A or B.

The identities

$$\begin{aligned} p_A + p_B &= 1 \\ q_{A|X} + q_{B|X} &= 1 \\ p_{XY} &= q_{X|Y} \cdot p_Y \\ p_{AB} &= p_{BA} \end{aligned} \tag{2}$$

imply that the whole system can be described by only two variables, p_A and $q_{A|A}$, in pair approximation.

Each player derives a payoff from interaction with all its neighbors. At each time step, a random player is chosen to die. The neighbors compete for the empty site proportional to their fitness. First we calculate the probabilities that the variables p_A and p_{AA} change during one time step.

1.1 Updating a B-player

A B player is eliminated with probability p_B. Its k neighbors compete for the vacancy. Let k_A and k_B denote the numbers of A and B players among these k neighbors. We have $k_A + k_B = k$. The frequency of such a configuration is $(k!/k_A!k_B!)\ {q_{A|B}}^{k_A} {q_{B|B}}^{k_B}$. The fitness of each A-player is

$$f_A = (1-w) + w\Big[(k-1)q_{A|A} \cdot a + \{(k-1)q_{B|A} + 1\} \cdot b\Big]. \tag{3}$$

The fitness of each B-player is

$$f_B = (1-w) + w\Big[(k-1)q_{A|B} \cdot c + \{(k-1)q_{B|B} + 1\} \cdot d\Big]. \tag{4}$$

The parameter w represents the intensity of selection. If $w = 1$ then the fitness is identical to payoff; this is the case of strong selection. If $w << 1$ then the payoff from the game represents only a small contribution to the fitness; this is the case of weak selection.

The probability that one of the A-players replaces the vacancy is given by

$$\frac{k_A f_A}{k_A f_A + k_B f_B}.$$

Therefore, p_A increases by $1/N$ with probability

$$\text{Prob}\Big(\Delta p_A = \frac{1}{N}\Big) = p_B \sum_{k_A + k_B = k} \frac{k!}{k_A! k_B!}\ {q_{A|B}}^{k_A} {q_{B|B}}^{k_B} \frac{k_A f_A}{k_A f_A + k_B f_B}. \tag{5}$$

Regarding pairs, the number of AA-pairs increases by k_A and therefore p_{AA} increases by $k_A/(kN/2)$ with probability

$$\text{Prob}\Big(\Delta p_{AA} = \frac{2k_A}{kN}\Big) = p_B \frac{k!}{k_A! k_B!}\ {q_{A|B}}^{k_A} {q_{B|B}}^{k_B} \frac{k_A f_A}{k_A f_A + k_B f_B}. \tag{6}$$

1.2 Updating an A-player

An A player is eliminated with probability p_A. There are k_A A-players and k_B B-players in the neighborhood of the vacancy. As before, we have $k_A + k_B = k$. The frequency of this configuration is $(k!/k_A!k_B!)\ {q_{A|A}}^{k_A} {q_{B|A}}^{k_B}$. The fitness of each A-player is

$$g_A = (1-w) + w\Big[\{(k-1)q_{A|A} + 1\} \cdot a + (k-1)q_{B|A} \cdot b\Big]. \tag{7}$$

The fitness of each B-player is

$$g_B = (1-w) + w\Big[\{(k-1)q_{A|B} + 1\} \cdot c + (k-1)q_{B|B} \cdot d\Big]. \tag{8}$$

The probability that one of the B-players replaces the vacancy is given by

$$\frac{k_B g_B}{k_A g_A + k_B g_B}.$$

The vacancy is replaced by a B-player and therefore p_A decreases by $1/N$ with probability

$$\text{Prob}\Big(\Delta p_A = -\frac{1}{N}\Big) = p_A \sum_{k_A+k_B=k} \frac{k!}{k_A! k_B!}\, {q_{A|A}}^{k_A} {q_{B|A}}^{k_B} \frac{k_B g_B}{k_A g_A + k_B g_B}. \tag{9}$$

Regarding pairs, the number of AA-pairs decreases by k_A and therefore p_{AA} decreases by $k_A/(kN/2)$ with probability

$$\text{Prob}\Big(\Delta p_{AA} = -\frac{2k_A}{kN}\Big) = p_A \frac{k!}{k_A! k_B!}\, {q_{A|A}}^{k_A} {q_{B|A}}^{k_B} \frac{k_B g_B}{k_A g_A + k_B g_B}. \tag{10}$$

1.3 Diffusion approximation

Let us now suppose that one replacement event takes place in one unit of time. The time derivatives of p_A and p_{AA} are given by

$$\begin{aligned} \dot{p}_A &= \frac{1}{N} \cdot \text{Prob}\Big(\Delta p_A = \frac{1}{N}\Big) + \Big(-\frac{1}{N}\Big) \cdot \text{Prob}\Big(\Delta p_A = -\frac{1}{N}\Big) \\ &= w \cdot \frac{k-1}{N} p_{AB}(I_a a + I_b b - I_c c - I_d d) + O(w^2) \end{aligned} \tag{11}$$

and

$$\begin{aligned} \dot{p}_{AA} &= \sum_{k_A=0}^{k} \frac{2k_A}{kN} \cdot \text{Prob}\Big(\Delta p_A = \frac{2k_A}{kN}\Big) + \sum_{k_A=0}^{k} \Big(-\frac{2k_A}{kN}\Big) \cdot \text{Prob}\Big(\Delta p_A = -\frac{2k_A}{kN}\Big) \\ &= \frac{2}{kN} p_{AB}\Big[1 + (k-1)(q_{A|B} - q_{A|A})\Big] + O(w). \end{aligned} \tag{12}$$

We have used the notation

$$\begin{aligned} I_a &= \frac{k-1}{k} q_{A|A}(q_{A|A} + q_{B|B}) + \frac{1}{k} q_{A|A}, \\ I_b &= \frac{k-1}{k} q_{B|A}(q_{A|A} + q_{B|B}) + \frac{1}{k} q_{B|B}, \\ I_c &= \frac{k-1}{k} q_{A|B}(q_{A|A} + q_{B|B}) + \frac{1}{k} q_{A|A}, \\ I_d &= \frac{k-1}{k} q_{B|B}(q_{A|A} + q_{B|B}) + \frac{1}{k} q_{B|B}. \end{aligned} \tag{13}$$

From Eq.(12) we have

$$\begin{aligned} \dot{q}_{A|A} &= \frac{d}{dt}\Big(\frac{p_{AA}}{p_A}\Big) \\ &= \frac{2}{kN} \frac{p_{AB}}{p_A} \Big[1 + (k-1)(q_{A|B} - q_{A|A})\Big] + O(w). \end{aligned} \tag{14}$$

Remember that the system is described by p_A and $q_{A|A}$. Rewriting the r.h.s's of Eq.(11) and Eq.(14) as functions of p_A and $q_{A|A}$ yields the closed dynamical system:

$$\begin{aligned} \dot{p}_A &= w \cdot F_1(p_A, q_{A|A}) + O(w^2), \\ \dot{q}_{A|A} &= F_2(p_A, q_{A|A}) + O(w). \end{aligned} \tag{15}$$

For weak selection, $w << 1$, the local density of players, $q_{A|A}$, equilibrates much more quickly than the global density, p_A. Therefore, the dynamical system rapidly converges onto the slow manifold, defined by $F_2(p_A, q_{A|A}) = 0$, or more explicitly,

$$q_{A|A} = p_A + \frac{1}{k-1}(1 - p_A). \tag{16}$$

Using Eq.(2) we obtain

$$\begin{aligned} q_{A|A} - q_{A|B} &= \frac{1}{k-1}, \\ q_{B|B} - q_{B|A} &= \frac{1}{k-1}. \end{aligned} \tag{17}$$

Therefore, among the $k-1$ neighbors, an A player has on average one more A neighbors than a B player has A neighbors. In other words, Eq.(17) specifies the amount of positive correlation between adjacent players that is generated by the evolutionary dynamics. As shown in the main text (and below) this relationship leads directly to the rule $b/c > k$.

Instead of studying a diffusion process with respect to two random variables, p_A and $q_{A|A}$, we now assume, that the relationship given by Eq.(16) always holds. Hence, we study a one dimensional diffusion process of the random variable p_A.

Within the short time interval, Δt, we have

$$\begin{aligned} \mathrm{E}[\Delta p_A] &\simeq w \cdot \frac{k-2}{k(k-1)N}\, p_A(1-p_A)(\alpha p_A + \beta)\Delta t \quad \Big(\equiv m(p_A)\Delta t\Big), \\ \mathrm{Var}[\Delta p_A] &\simeq \frac{2}{N^2}\frac{k-2}{k-1}\, p_A(1-p_A)\Delta t \quad \Big(\equiv v(p_A)\Delta t\Big). \end{aligned} \tag{18}$$

Here

$$\begin{aligned} \alpha &= (k+1)(k-2)(a-b-c+d), \\ \beta &= (k+1)a + (k^2-k-1)b - c - (k^2-1)d. \end{aligned} \tag{19}$$

The fixation probability, $\phi_A(y)$ of strategy A with initial frequency $p_A(t=0) = y$, satisfies the following differential equation:

$$0 = m(y)\frac{d\phi_A(y)}{dy} + \frac{v(y)}{2}\frac{d^2\phi_A(y)}{dy^2}. \tag{20}$$

Since w is very small, we have

$$\phi_A(y) = y + w \cdot \frac{N}{6k} y(1-y)\big[(\alpha + 3\beta) + \alpha y\big] \tag{21}$$

as an approximate solution.

1.4 Fixation probabilities

The fixation probability of a single A player in a population of $N-1$ B players is given by $\rho_A = \phi_A(1/N)$. For large N, we have $\rho_A > 1/N$ if and only if $\alpha + 3\beta > 0$, which is equivalent to

$$(k^2+2k+1)a + (2k^2-2k-1)b > (k^2-k+1)c + (2k^2+k-1)d. \tag{22}$$

Similarly, $\rho_B > 1/N$ is equivalent to

$$(k^2+2k+1)d + (2k^2-2k-1)c > (k^2-k+1)b + (2k^2+k-1)a. \tag{23}$$

For $k=2$, both the expectation and variance in Eq.(18) are zero. Therefore, the above calculation only makes sense for $k \geq 3$. A separate exact calculation for the cycle shows, however, that inequalities (22) and (23) also hold for $k=2$.

From Eq.(21), we can also calculate the ratio of the fixation probabilities,

$$\frac{\rho_A}{\rho_B} = 1 + w \cdot \frac{N-1}{2}\{(k+1)a + (k-1)b - (k-1)c - (k+1)d\}. \tag{24}$$

If $k \gg 1$, then inequality (22) leads to $a + 2b > c + 2d$, which is the $1/3$ rule[3]. This rule works as follows. Consider a game between two strategies, A and B, which are best replies to themselves: $a > c$ and $d > b$. In this case, the replicator equation has an unstable equilibrium at $x^* = (d-b)/(a-b-c+d)$ denoting the frequency of A. If $x^* < 1/3$, then in an unstructured population (described by a complete graph) the fixation probability ρ_A will be greater than $1/N$ for weak selection and sufficiently large population size, N. The calculation shown here has extended the $1/3$ rule to any graphs with sufficiently large N.

1.5 The rule $b/c > k$

Let us now consider a game between cooperators, C, and defectors, D. The benefit of cooperation is b and the cost is c. The payoff matrix takes the form

$$\begin{array}{c} \\ A \\ B \end{array}\begin{array}{c} \begin{array}{cc} A & B \end{array} \\ \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \rightarrow \begin{array}{c} \\ C \\ D \end{array}\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}. \tag{25}$$

Substituting those payoff values into inequalities (22) and (23) leads to the conclusion that if $b/c > k$ then $\rho_C > 1/N > \rho_D$. Vice versa, we have if $b/c < k$ then $\rho_C < 1/N < \rho_D$. Therefore, cooperation is favored (for weak selection and large population size) if and only if

$$b/c > k. \tag{26}$$

2 Imitation (IM) updating

Let us now study a different update rule. In any one time step, a random individual is chosen to compare its payoff with those of its neighbors. The individual stays with its own strategy or imitates a neighbor's strategy proportional to the payoff. In contrast to 'death-birth' (DB) updating, here the payoff of the individual that is being updated also matters. We expect that this effect will introduce an advantage for defectors, because defectors at the boundary of a cluster have a higher payoff than cooperators at the boundary and therefore defectors are less likely to change their strategy.

The fitness of a B-player with k_A many A-players and k_B many B-players in its neighborhood is given by

$$f_0 = 1 - w + w(k_A c + k_B d). \tag{27}$$

The probability that the B player will adopt strategy A is given by

$$\frac{k_A f_A}{k_A f_A + k_B f_B + f_0}.$$

The fitness of an A-player with k_A many A-players and k_B many B-players in its neighborhood is given by

$$g_0 = 1 - w + w(k_A a + k_B b). \tag{28}$$

The probability that the A-player will adopt strategy B is given by

$$\frac{k_B g_B}{k_A g_A + k_B g_B + g_0}.$$

Taking these two modifications into account, a similar calculation as in Section 1 leads to the following result: $\rho_A > 1/N$ if

$$(k^2 + 4k + 3)a + (2k^2 + 2k - 3)b > (k^2 + k + 3)c + (2k^2 + 5k - 3)d. \tag{29}$$

Similarly, $\rho_B > 1/N$ if

$$(k^2 + 4k + 3)d + (2k^2 + 2k - 3)c > (k^2 + k + 3)b + (2k^2 + 5k - 3)a. \tag{30}$$

Returning to the Prisoner's Dilemma, given by payoff matrix (25), we find that $\rho_C > 1/N > \rho_D$ if

$$b/c > k + 2. \tag{31}$$

If instead $b/c < k + 2$ then $\rho_D > 1/N > \rho_C$.

3 'Birth-death' (BD) updating

Finally, we consider the following update rule: in each time step an individual is selected for reproduction proportional to fitness. The offspring replaces a randomly chosen neighbor.

In order to derive the transition probabilities of p_A and p_{AA} we need to specify not only who reproduces but also the local configuration of the reproducing individual. The probability that an A-player who has k_A many A-neighbors and k_B many B-neighbors is selected for reproduction is proportional to

$$\left[p_A \frac{k!}{k_A! k_B!}\, {q_{A|A}}^{k_A} {q_{B|A}}^{k_B}\right] \cdot \left[1 - w + w(k_A a + k_B b)\right]. \tag{32}$$

The first term is the frequency of such a configuration. The second term denotes the fitness of the A-player. If one of the B-neighbors is replaced, then the number of A-players increases by one and the number of AA-pairs increases by $1 + (k-1)q_{A|B}$. Similarly, the probability that a B-player who has k_A many A-neighbors and k_B many B-neighbors is selected for reproduction is proportional to

$$\left[p_B \frac{k!}{k_A! k_B!}\, {q_{A|B}}^{k_A} {q_{B|B}}^{k_B}\right] \cdot \left[1 - w + w(k_A c + k_B d)\right]. \tag{33}$$

If one of the A-neighbors is replaced, then the number of A-players decreases by one and the number of AA-pairs by $(k-1)q_{A|A}$.

A similar calculation as in Section 1 leads to the following result: $\rho_A > 1/N$, if

$$(k+1)a + (2k-1)b > (k+1)c + (2k-1)d. \tag{34}$$

Moreover, $\rho_B > 1/N$, if

$$(k+1)d + (2k-1)c > (k+1)b + (2k-1)a. \tag{35}$$

Applying inequalities (34) and (35) to the Prisoner's Dilemma payoff matrix (25), we find that $\rho_D > 1/N > \rho_C$ always holds for any choice of cost and benefit, $b > c > 0$. Thus, selection never favors cooperators for BD updating.

4 Computer simulations

The different network structures are generated with either $N = 100$ or $N = 500$ nodes and then initialized with all defectors except for a single cooperator placed in a random location. At each time step, a randomly chosen individual is updated according to two different rules.

In Figure 2 (main paper), we simulate death-birth (DB) updating. A random individual is chosen to die. The neighbors compete for the empty site proportional to their payoff. In Figure 4 (online), we simulate imitation (IM) updating. A random individual is chosen to update its strategy. It will keep its current strategy or imitate a neighbor's strategy proportional to payoff. For IM updating, the payoff of the focal individual also plays a role.

For each simulation run, the respective update steps are repeated until either cooperators have vanished or reached fixation. The fixation probability ρ_C of cooperators is determined by the fraction of runs where cooperators reached fixation out of 10^6 runs. The network structure was re-generated every 10^3 runs to prevent any spurious results based on one particular realization of a specific network type.

Cycles: On cycles, individuals interact with their $k/2$ nearest neighbors on either side. Consequently, odd degrees are not possible.

Lattices: The three regular lattices in two dimensions are considered: triangular, hexagonal and square. On square lattices we consider the standard neighborhoods, *von Neumann* ($k = 4$) and *Moore* ($k = 8$).

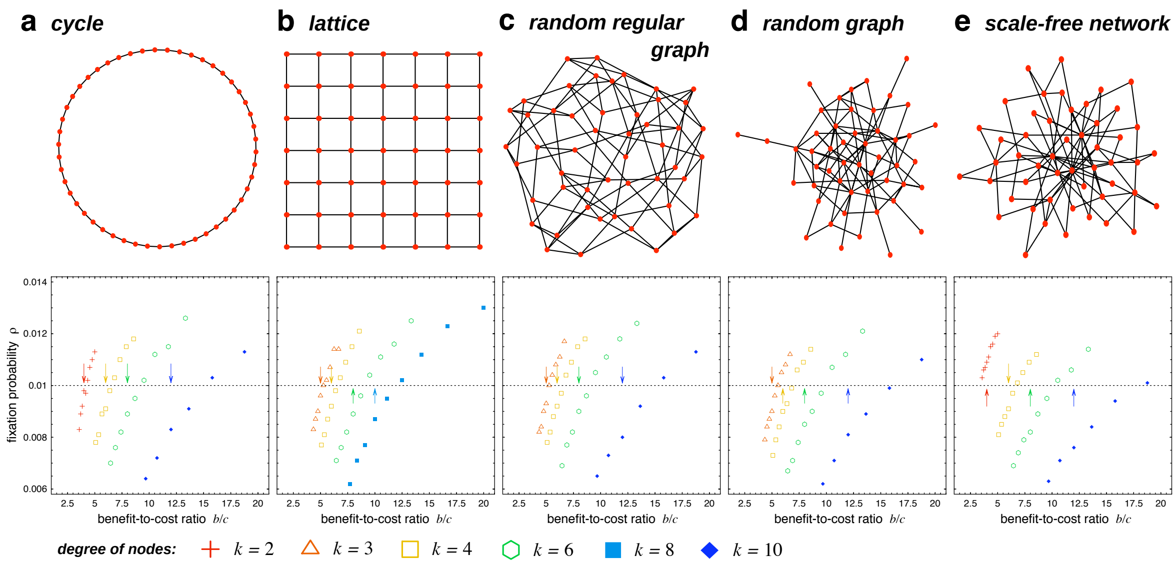

Figure 4: Fixation probability ρ of a single cooperator in the imitation process as a function of the benefit-to-cost ratio b/c under weak selection ($w = 0.01$) for populations of $N = 100$ individuals on various types of graphs with different average numbers of neighbors, k. The top row shows the structure of the graph for $k = 2$ (a) and (on average) $k = 4$ (b-e). The bottom row depicts simulation data for the fixation probability, ρ, of cooperators as determined by the fraction of runs where cooperators reached fixation out of 10^6 runs. In every time step, a focal site is randomly selected and adopts a neighboring strategy with a probability proportional to the neighbors' payoff *or* keeps its strategy proportional to the focal individual's payoff. The arrows mark $b/c = k + 2$ and the dotted line indicates the fixation probability $1/N$ under neutral evolution.

Random-regular-graphs: For random regular graphs (RRG), the links between nodes are randomly drawn under the constraint that every node ends up with an equal number of links, k. Locally a RRG is similar to a tree (or Bethe lattice) because the average loop size increases with N (Ref 4). Note that the results from pair-approximation are exact for Bethe lattices but because of boundary problems they are unsuitable for simulations and RRG's serve as suitable substitutes. In order to ensure connectedness of the network, every node is first linked to a random node of the already connected ones.

Random-graphs: Random graphs (RG) are generated in much the same way as RRG, but relaxing the constraint that every node has the same number of links to having k links on average. As for RRG, we first need to make sure that the graph is connected. In a second step two randomly drawn nodes are linked. The second step is repeated until the desired average connectivity is reached.

Scale-free networks: Scale-free networks are generated according to the method of preferential attachment[5]. This leads to a degree distribution of $P(k) = 2m^2k^{-3}$ with $k \geq m$ and an average connectivity of $\langle k \rangle = 2m$ (see Ref 6).

For interactive online tutorials illustrating the dynamics of cooperation and defection on graphs and social networks see Ref. 7.

References

[1] Matsuda, H., Ogita, N., Sasaki, A. & Satō, K. Statistical mechanics of population: The lattice Lotka-Volterra model. *Prog. Theor. Phys.* **88**, 1035-1049 (1992).

[2] Crow, J. F. & Kimura, M. *Introduction to Population Genetics Theory* (Harper & Row, New York, 1970).

[3] Nowak, M. A., Sasaki, A., Taylor, C. & Fudenberg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646-650 (2004).

[4] Bollobás, B. *Random Graphs* (Academic Press, New York, 1995).

[5] Albert, R. & Barabási, A.-L. Statistical mechanics of complex networks. *Rev. Mod. Phys.* **74**, 47-98 (2002).

[6] Klemm, K. & Eguíluz, V. M. Growing scale-free networks with small-world behavior. *Phys. Rev. E* **65**, 057102 (2002).

[7] Hauert, C. VirtualLabs: Interactive tutorials on evolutionary dynamics, *http://www.univie.ac.at/virtuallabs* (2005).