

LETTERS

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

Hisashi Ohtsuki^{1,2}, Christoph Hauert², Erez Lieberman^{2,3} & Martin A. Nowak²

A fundamental aspect of all biological systems is cooperation. Cooperative interactions are required for many levels of biological organization ranging from single cells to groups of animals^{1–4}. Human society is based to a large extent on mechanisms that promote cooperation^{5–7}. It is well known that in unstructured populations, natural selection favours defectors over cooperators. There is much current interest, however, in studying evolutionary games in structured populations and on graphs^{8–17}. These efforts recognize the fact that who-meets-whom is not random, but determined by spatial relationships or social networks^{18–24}. Here we describe a surprisingly simple rule that is a good approximation for all graphs that we have analysed, including cycles, spatial lattices, random regular graphs, random graphs and scale-free networks^{25,26}: natural selection favours cooperation, if the benefit of the altruistic act, b , divided by the cost, c , exceeds the average number of neighbours, k , which means $b/c > k$. In this case, cooperation can evolve as a consequence of ‘social viscosity’ even in the absence of reputation effects or strategic complexity.

A cooperator is someone who pays a cost, c , for another individual to receive a benefit, b . A defector pays no cost and does not distribute any benefits. In evolutionary biology, cost and benefit are measured in terms of fitness. Reproduction can be genetic or cultural. In the latter case, the strategy of someone who does well is imitated by others. In an unstructured population, where all individuals are equally likely to interact with each other, defectors have a higher average payoff than unconditional cooperators. Therefore, natural selection increases the relative abundance of defectors and drives cooperators to extinction. These evolutionary dynamics hold for the deterministic setting of the replicator equation^{27,28} and for stochastic game dynamics of finite populations²⁹.

In our model, the players of an evolutionary game occupy the vertices of a graph. The edges denote links between individuals in terms of game dynamical interaction and biological reproduction. We assume that the graph is fixed for the duration of the evolutionary dynamics. Consider a population of N individuals consisting of cooperators and defectors. A cooperator helps all individuals to whom it is connected. If a cooperator is connected to k other individuals and i of those are cooperators, then its payoff is $bi - ck$. A defector does not provide any help, and therefore has no costs, but it can receive the benefit from neighbouring cooperators. If a defector is connected to j cooperators, then its payoff is bj .

The fitness of an individual is given by a constant term, denoting the baseline fitness, plus the payoff that arises from the game. Strong selection means that the payoff is large compared to the baseline fitness; weak selection means the payoff is small compared to the baseline fitness. The idea behind weak selection is that many different factors contribute to the overall fitness of an individual, and the game under consideration is just one of those factors.

At first, we will study the following update rule for evolutionary dynamics (Fig. 1): in each time step, a random individual is chosen to die, and the neighbors compete for the empty site proportional to their fitness. We call this mechanism ‘death–birth’ updating, because it involves a death event followed by a birth. Later we will investigate other update mechanisms.

Let us explore whether natural selection can favour cooperation on certain graphs. To do this, we need to calculate the probability that a single cooperator starting in a random position turns the whole population from defection to cooperation. If selection neither favours nor opposes cooperation, then this probability is $1/N$, which is the fixation probability of a neutral mutant. If the fixation

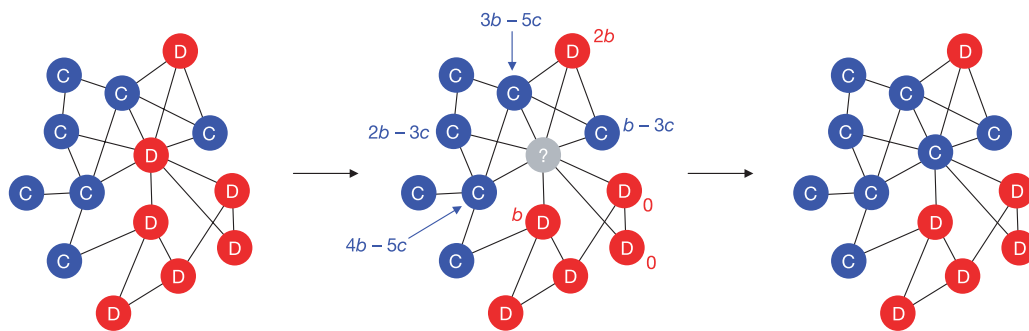


Figure 1 | The rules of the game. Each individual occupies the vertex of a graph and derives a payoff, P , from interactions with adjacent individuals. A cooperator (blue) pays a cost, c , for each neighbour to receive a benefit, b . A defector (red) pays no cost and provides no benefit. The fitness of a player is given by $1 - w + wP$, where w measures the intensity of selection. Strong selection means $w = 1$. Weak selection means $w \ll 1$. For ‘death–birth’

updating, at each time step, a random individual is chosen to die (grey); subsequently the neighbours compete for the empty site in proportion to their fitness. In this example, the central, vacated vertex will change from a defector to a cooperator with a probability $F_C/(F_C + F_D)$, where the total fitness of all adjacent cooperators and defectors is $F_C = 4(1 - w) + (10b - 16c)w$ and $F_D = 4(1 - w) + 3bw$, respectively.

¹Department of Biology, Kyushu University, Fukuoka 812-8581, Japan. ²Program for Evolutionary Dynamics, Department of Organismic and Evolutionary Biology, Department of Mathematics, ³Department of Applied Mathematics, Harvard University, Cambridge, Massachusetts 02138, USA.

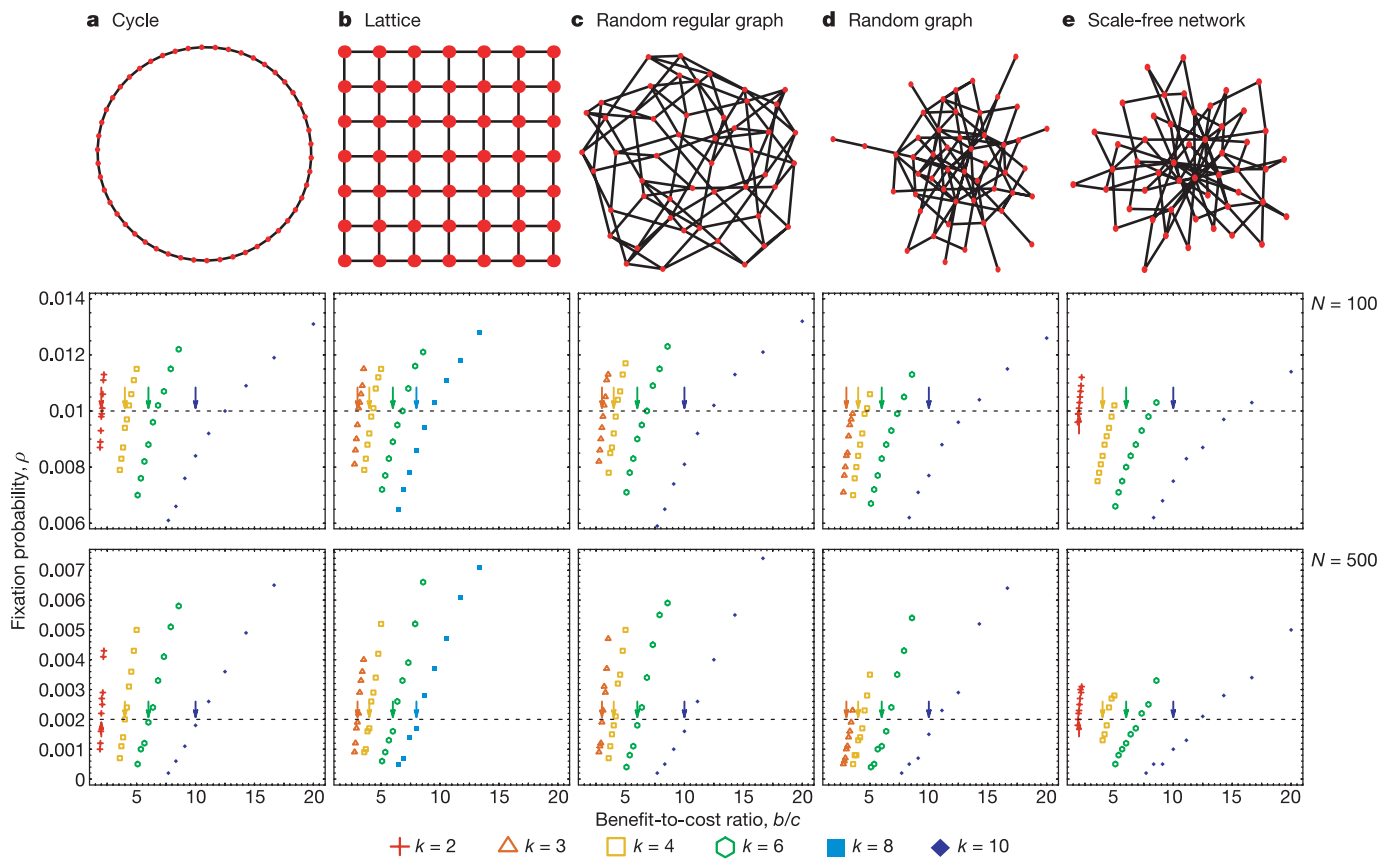


Figure 2 | The simple rule, $b/c > k$, is in good agreement with numerical simulations. The parameter k denotes the degree of the graph, which is given by the (average) number of neighbours per individual. The first row illustrates the type of graph for $k = 2$ (a) and $k = 4$ (b–e). The second and third rows show simulation data for population sizes $N = 100$ and $N = 500$. The fixation probability, ρ , of cooperators is determined by the fraction of runs where cooperators reached fixation out of 10^6 runs under weak selection, $w = 0.01$. Each type of graph is simulated for different (average)

degrees ranging from $k = 2$ to $k = 10$. The arrows mark $b/c = k$. The dotted horizontal line indicates the fixation probability $1/N$ of neutral evolution. The data suggest that $b/c > k$ is necessary but not sufficient. The discrepancy is larger for non-regular graphs (d, e) with high average degree ($k = 10$). This is not surprising given that the derivation of the rule is for regular graphs and in the limit $N \gg k$. Note that the larger population size, $N = 500$, gives better agreement. Interactive online tutorials can be found at <http://univie.ac.at/virtuallabs>.

probability of a single cooperator is greater than $1/N$, then selection favours the emergence of cooperation. We also calculate the fixation probability of a single defector in a population of cooperators, and compare the two fixation probabilities.

The traditional well-mixed population of evolutionary game theory is represented by the complete graph, where all vertices are connected. In this special situation, cooperators are always opposed by selection. This is the fundamental intuition of classical evolutionary game theory. But what happens on other graphs?

Let us first consider a cycle. Each individual is linked to two neighbours. A single cooperator could be wiped out immediately or take over one of its two neighbours. A cluster of two cooperators could expand to three cooperators or revert to a single cooperator. In any case, the lineage starting from one cooperator always forms a single cluster of cooperators, which cannot fragment into pieces. This fact allows a straightforward calculation. We find that selection favours cooperation if $b/c > 2$. This result holds for weak selection and large population size.

Next, we study regular graphs, where each individual has exactly k neighbours. Such graphs include cycles, spatial lattices and random regular graphs. For all such graphs, a direct calculation of the fixation probability is impossible, because a single invader can lead to very complicated patterns: the emerging cluster usually breaks into many pieces, allowing a large number of conceivable geometric configurations. In general, the inherent complexity of games on graphs makes analytical investigations almost always impossible.

Nevertheless, we can calculate the fixation probability of a randomly placed mutant for any two-person, two-strategy game on a regular graph by using pair approximation and diffusion approximation (see Supplementary Information). In particular, we find that cooperators have a fixation probability greater than $1/N$ and defectors have a fixation probability less than $1/N$, if:

$$b/c > k$$

The ratio of benefit to cost of the altruistic act has to exceed the degree, k , which is given by the number of neighbours per individual. This condition is derived for weak selection and under the assumption that the population size, N , is much larger than the degree, k .

We find excellent agreement with numerical simulations (Fig. 2). For a given population size, $b/c > k$ is a necessary condition for selection to favour cooperators. As the population size increases, the discrepancy between $b/c > k$ and the numerical simulations becomes smaller. Moreover, we find that the rule also holds for random graphs²⁵ and scale-free networks^{26,27}, where individuals differ in the number of their neighbours. Here k denotes the average degree of the graph. Scale-free networks fit slightly less well than random graphs, presumably because they have a larger variance of the degree distribution.

The intuitive justification for the $b/c > k$ rule is illustrated in Fig. 3. Consider one cooperator and one defector competing for an empty site. The payoff for the cooperator is $P_C = bq_{C|C}(k-1) - ck$. The payoff for the defector is $P_D = bq_{C|D}(k-1)$. The conditional

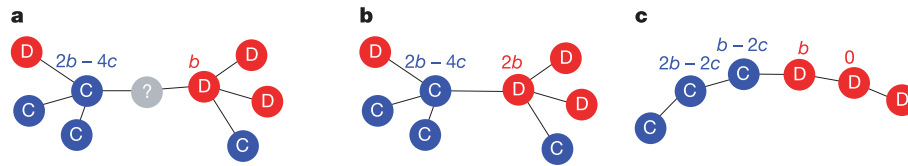


Figure 3 | Some intuition for games on graphs. **a**, For death–birth updating, we must consider a cooperator and a defector competing for an empty site. The pair-approximation calculation shows that for weak selection the cooperator has one more cooperator among its $k - 1$ other neighbours than does the defector. Hence, the cooperator has a higher chance to win the empty site if $b/c > k$. **b**, For birth–death updating, we must consider a cooperator–defector pair competing for the next reproduction event. Again the cooperator has one more cooperator among its $k - 1$ other neighbours than the defector, but the focal cooperator is also a neighbour of the defector.

Hence, both competitors are linked to the same number of cooperators, and therefore the defector has a higher payoff. For birth–death updating, selection does not favour cooperation. **c**, On a cycle ($k = 2$), the situation is simple. A direct calculation, for weak selection and large population size, leads to the following results. For birth–death updating, the boundary between a cluster of cooperators and defectors tends to move in favour of defectors. For death–birth updating, the cooperator cluster expands if $b/c > 2$. For imitation updating, the cooperator cluster expands if $b/c > 4$.

probability to find a cooperator next to a cooperator is $q_{C|C}$ and to find a cooperator next to a defector is $q_{C|D}$. The cooperator pays cost c for all of its k neighbours and receives benefit b from each cooperator among its $k - 1$ neighbours, excluding the contested site. The defector pays no cost, but receives benefit b from each cooperator among its $k - 1$ neighbours, also excluding the contested site. The payoff that comes from the contested site is excluded, because it contributes equally to the cooperator and the defector and therefore cancels out. If $P_C > P_D$, then selection favours the cooperator. Pair-approximation shows that $(k - 1)(q_{C|C} - q_{C|D}) = 1$ for weak selection. Thus, the cooperator has on average one more cooperator neighbour than the defector. Therefore, we obtain $P_C - P_D = b - ck$, which leads to the $b/c > k$ rule.

We have also explored other update mechanisms. Suppose at each time step a random individual is chosen to update its strategy; it will stay with its own strategy or imitate one of the neighbours proportional to fitness. For this ‘imitation’ updating, we find that cooperators are favoured if $b/c > k + 2$. This result can be obtained with an exact calculation for the cycle and with pair approximation for regular graphs. Again, there is good agreement with numerical simulations (Supplementary Fig. 4). Mathematically, imitation updating can be obtained from our earlier death–birth updating by adding loops to every vertex. Therefore, each individual is also its own neighbour. Let us define the connectivity, k , of a vertex as the total number of links connected to that vertex, noting that a loop is connected twice. Then the simple rule $b/c > k$ holds both for the imitation and death–birth updating.

There are also update rules for which selection can never favour cooperators. For example, let us consider ‘birth–death’ updating: at each time step an individual is selected for reproduction proportional to fitness, and the offspring replaces a randomly chosen neighbour. In this case, selection always favours defectors, because only the payoff of individuals right at the boundary between cooperators and defectors matters, and there cooperators are always at a disadvantage (Fig. 3b). In the two other models, the payoffs of individuals that are one place removed from the boundary also play a role, which gives cooperation a chance to survive.

Using a different model, van Baalen and Rand¹¹ have derived a condition for the initial invasion of cooperators. In their model, the vertices of a spatial lattice (or a graph) are either empty or occupied by cooperators or defectors. There are birth, death and migration events. Implicitly, they have shown that without migration a few cooperators can successfully invade a population of defectors if $b/c > k^2/(k - 1)$. The difference between this result and ours is not surprising. The invasion condition of ref. 11 examines whether rare cooperators are able to increase in abundance, whereas our fixation probability includes the whole evolutionary trajectory including the initial invasion and propagation of cooperators as well as the final extinction of defectors. For a comparison of invasion and fixation criteria see Wild and Taylor³⁰.

Thus, we have shown that evolutionary dynamics on graphs can favour cooperation over defection if the benefit to cost ratio, b/c , of the altruistic act exceeds the average connectivity, k . The fewer connections there are, the easier it is for natural selection to promote cooperation. In our present analysis, all connections are equally strong. A next step will be to explore graphs with weighted edges. In social networks, people might have a substantial number of connections, but only very few of them are strong. Hence, the ‘effective’ average degree, k , of many relevant networks could be small, thereby making selection of cooperation on graphs a powerful option.

Our study is theoretically motivated, but has implications for empirical research. For example, one can envisage an experiment where people are asked to play a non-repeated Prisoner’s Dilemma within a given network. Certain network structures should promote cooperative behaviour more than others. In particular, more cooperation should emerge if connectivity is low. Moreover, in certain animal species there exist complicated social networks. Observational studies could reveal how network structure affects the level of cooperation; higher connectivity should reduce cooperation. In this paper, as a logical first step, we have studied the simplest possible interaction between unconditional cooperators and defectors, but in an extended approach, both in terms of theory and experiment, it will be interesting to see which strategies of direct or indirect reciprocity evolve on particular networks.

Finally, we note the beautiful similarity of our finding with Hamilton’s rule¹, which states that kin selection can favour cooperation provided $b/c > 1/r$, where r is the coefficient of genetic relatedness between individuals. The similarity makes sense. In our framework, the average degree of a graph is an inverse measure of social relatedness (or social viscosity). The fewer friends I have the more strongly my fate is bound to theirs.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Supplementary Information

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

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

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 approximation¹ and diffusion approximation², 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

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

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, $N \gg k$, 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

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

The fitness of each B -player is

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

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 $w \ll 1$ 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

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

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

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

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

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

The fitness of each B -player is

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

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

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

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

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

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

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

and

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

We have used the notation

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

From Eq.(12) we have

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

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, $w \ll 1$, 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

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

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

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

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

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

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

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

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,

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

If $k \gg 1$, then inequality (22) leads to $a + 2b > c + 2d$, which is the 1/3 rule³. 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

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

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

$$b/c > k. \quad (26)$$

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

$$f_0 = 1 - w + w(k_{AC} + k_{Bd}). \quad (27)$$

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

$$g_0 = 1 - w + w(k_{Aa} + k_{Bb}). \quad (28)$$

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

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

Similarly, $\rho_B > 1/N$ if

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

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

$$b/c > k + 2. \quad (31)$$

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

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

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

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

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

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

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

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

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* ($k = 8$).

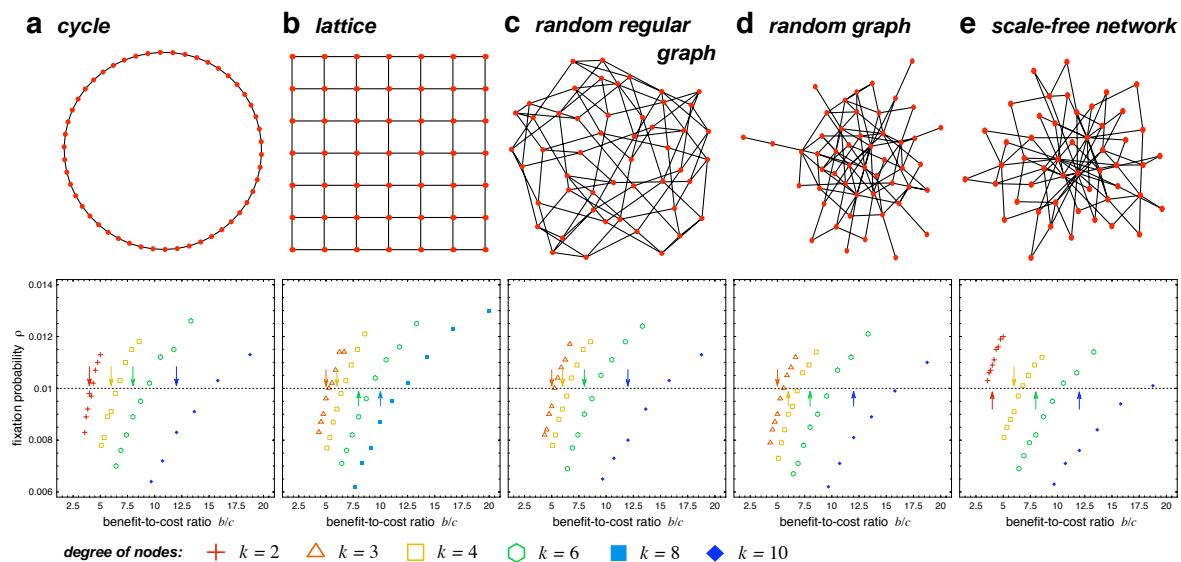


Figure 4: Fixation probability ρ of a single cooperator in the imitation process as a function of the benefit-to-cost ratio b/c under weak selection ($w = 0.01$) for populations of $N = 100$ individuals on various types of graphs with different average numbers of neighbors, k . The top row shows the 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 attachment⁵. 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.

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