Evolutionary graph theory: Breaking the symmetry between interaction and replacement

Hisashi Ohtsuki[a,b,*], Jorge M. Pacheco[a,c], Martin A. Nowak[a,d]

[a]*Program for Evolutionary Dynamics, Harvard University, Cambridge MA 02138, USA*
[b]*Department of Biology, Faculty of Sciences, Kyushu University, 6-10-1 Hakozaki, Fukuoka 812-8581, Japan*
[c]*Centro de Física Teórica e Computacional, Departamento de Física da Faculdade de Ciências, P-1649-003 Lisboa Codex, Portugal*
[d]*Department of Organismic and Evolutionary Biology, Department of Mathematics, Harvard University, Cambridge, MA 02138, USA*

Abstract

We study evolutionary dynamics in a population whose structure is given by two graphs: the interaction graph determines who plays with whom in an evolutionary game; the replacement graph specifies the geometry of evolutionary competition and updating. First, we calculate the fixation probabilities of frequency dependent selection between two strategies or phenotypes. We consider three different update mechanisms: birth–death, death–birth and imitation. Then, as a particular example, we explore the evolution of cooperation. Suppose the interaction graph is a regular graph of degree h, the replacement graph is a regular graph of degree g and the overlap between the two graphs is a regular graph of degree l. We show that cooperation is favored by natural selection if $b/c > hg/l$. Here, b and c denote the benefit and cost of the altruistic act. This result holds for death–birth updating, weak-selection and large population size. Note that the optimum population structure for cooperators is given by maximum overlap between the interaction and the replacement graph ($g = h = l$), which means that the two graphs are identical. We also prove that a modified replicator equation can describe how the expected values of the frequencies of an arbitrary number of strategies change on replacement and interaction graphs: the two graphs induce a transformation of the payoff matrix.
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1. Introduction

Evolutionary game theory is a general description of evolutionary dynamics whenever the fitness of individuals is not constant but frequency dependent (Maynard Smith, 1982; Nowak and Sigmund, 2004; Nowak, 2006). Many concepts of evolutionary game theory have their equivalent formulations in mathematical ecology (May, 1973; Hofbauer and Sigmund, 1998). The classical approach to evolutionary game dynamics is given by the replicator equation, which describes deterministic evolutionary dynamics in infinitely large populations (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980; Weibull, 1995; Hofbauer and Sigmund, 1998, 2003; Nowak and Sigmund, 2004). More recently there have been many investigations into stochastic evolutionary game dynamics of finite populations (Nowak et al., 2004; Taylor et al., 2004; Wild and Taylor, 2004; Imhof et al., 2005; Traulsen et al., 2005; Antal and Scheuring, 2006; Antal et al., 2006; Imhof and Nowak, 2006; Traulsen et al., 2006a–c; Fudenberg et al., 2006; Traulsen et al., 2007).

Evolutionary graph theory (Lieberman et al., 2005; Ohtsuki et al., 2006) is a powerful new method to study the effect of population structure or social networks on evolutionary dynamics. This approach is based on the long standing interest of how spatial effects influence evolutionary and ecological dynamics (Levin and Paine, 1974; Nowak and May, 1992; Ellison, 1993; Durrett and Levin, 1994; Hassell et al., 1994; Killingback and Doebeli,

*Corresponding author. Department of Biology, Faculty of Sciences, Kyushu University, 6-10-1 Hakozaki, Fukuoka 812-8581, Japan. Tel.: +81 92 642 2641; fax: +81 92 642 2645.

E-mail address: ohtsuki@bio-math10.biology.kyushu-u.ac.jp (H. Ohtsuki).

1996; Nakamaru et al., 1997, 1998; Tilman and Karieva, 1997; Szabó and Töke, 1998; van Baalen and Rand, 1998; Eshel et al., 1999; Liggett, 1999; Irwin and Taylor, 2001; Hauert et al., 2002; Szabó and Hauert, 2002; Le Galliard et al., 2003; Hauert and Doebeli, 2004; Ifti et al., 2004; May, 2006). Spatial games can lead to evolutionary kaleidoscopes, deterministic chaos as well as the stable coexistence of cooperators and defectors in the Prisoner's Dilemma (Nowak and May, 1992, 1993). For games on graphs we have found a very simple rule that specifies evolution of cooperation: if the benefit-to-cost
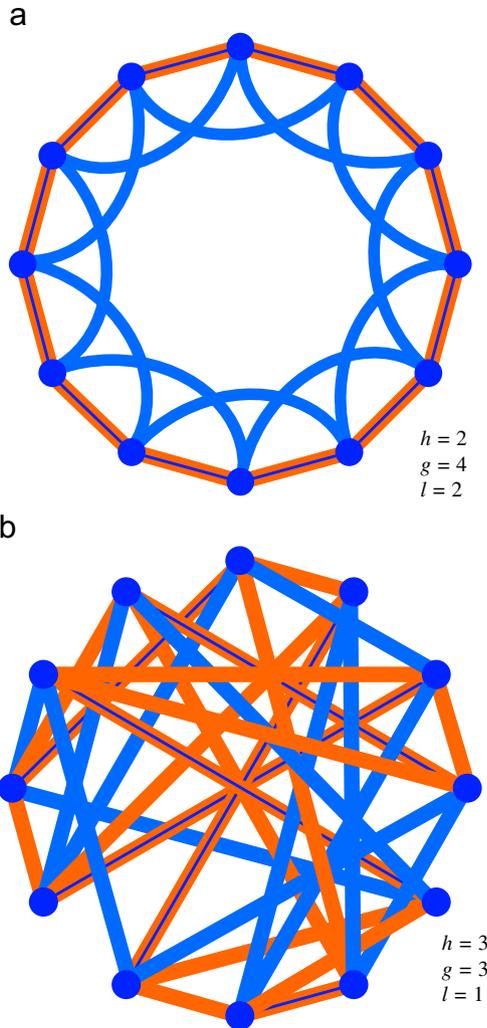

Fig. 1. Possible graph layouts: (a) case when $h = l = 2$ and $g = 4$. The interaction graph H corresponds to the cycle drawn with thick orange lines. The overlap graph L (drawn with thin blue lines) corresponds to the same cycle (full overlap, $L = H$). Finally, the replacement graph G adds to the overlap graph the links drawn with thick blue lines, resulting in a regular graph with $g = 4$ (thin and thick blue lines). (b) the lower panel shows an example in which all graphs are homogeneous random graphs such that $h = g = 3$ and $l = 1$. We use the same color codes as before. Since graphs G and H are both connected, exchanging their roles leads to another possible construction which, as discussed in the main text, leads to the same results for **DB** updating in what concerns the fixation probability of a given trait in this population structure ($h = g$), as opposed to the graphs in (a), where the exchange of G and H would lead to different theoretical predictions ($h \neq g$), as nicely demonstrated in Figs. 2 and 3 below.

ratio of an altruistic act exceeds the average number of neighbors, $b/c > k$, then selection on graphs favors cooperators (Ohtsuki et al., 2006). This phenomenon is called 'network reciprocity'.

Here we extend our investigations of evolutionary graph theory by placing the members of a population on the vertices of two graphs. The interaction graph, H, determines who-meets-whom in an evolutionary game. The replacement graph, G, specifies evolutionary updating. Both graphs have the same vertices. Each vertex is occupied by one individual. There are no empty vertices. The population size and therefore the number of vertices of each graph is given by N. The graphs H and G may differ in their edges. For the analytic calculations we only consider (random) regular graphs, which are defined by the property that all vertices have the same degree (= number of edges). The degrees of H and G are, respectively, given by h and g. For analytical treatment we require $g \geqslant 3$ throughout the paper.

The intersection of the sets of edges of graphs H and G defines the graph L. We only consider situations where L is again a random regular graph. The degree of L is given by l. Note that l cannot be larger than h or g. Therefore, we have $l \leqslant \min\{h, g\}$. Fig. 1 shows two examples.

Note that our analytic methods can only deal with regular graphs. Therefore, in this paper we restrict our attention to regular graphs. In a previous study, however, we have observed that the analytic results for regular graphs are also good approximations for non-regular graphs, such as random graphs and scale-free networks (Ohtsuki et al., 2006).

This paper is organized as follows. Section 2 describes our basic model. In Section 3 we study stochastic game dynamics on replacement and interaction graphs for finite populations and show numerical simulations for the Prisoner's Dilemma. These simulations further validate the nature of the approximations used in our analytical treatment. Section 4 investigates replicator dynamics on these graphs, which can be obtained by taking the infinite-population limit. Discussion and conclusions are provided in Section 5.

2. The basic model

Let us consider a 2×2 game with two pure strategies, A and B. The payoff matrix of the game is given by

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

The entries represent the payoffs for the row player. Each individual uses either strategy A or B. We do not consider mixed strategies.

Individuals play the game with all of their h neighbors in the interaction graph, H. These interactions determine the

total payoff, P, of each player. The fitness is given by

$$F = 1 - w + wP. \tag{2}$$

Here, $0 \leqslant w \leqslant 1$ represents the relative contribution of the game to fitness. If $w = 1$ then the payoff is equal to fitness. This is the case of 'strong selection'. If $w = 0$ then the game is irrelevant to fitness; all players have the same fitness. This is the case of 'neutral drift'. Throughout this paper we study the case $w \ll 1$, which is the limit of 'weak-selection' (Nowak et al., 2004).

Studying this limit can be justified in two different ways. First, in most real life situations we are involved in many different games, and each particular game only makes a small contribution to our overall performance. Second, weak-selection leads to analytic insights which are not possible for strong selection. Numerical simulations suggest that these results are usually good approximations for larger values of w (Ohtsuki et al., 2006). When studying finite populations in Section 3, we require that the population size, N, fulfills the inequalities $N \gg \max\{h, g\}$ and $N \ll 1/w$ (Traulsen et al., 2006b). For infinite populations, studied in Section 4, we take the limit $N \to \infty$, keeping w fixed ($w \ll 1$).

The evolutionary dynamics are determined by the 'update-rules' which govern how the population changes over time. As in previous papers (Ohtsuki et al., 2006; Ohtsuki and Nowak, 2006a, b), we consider three different update rules:

- *Birth–death* (*BD*) *updating*: An individual is chosen for reproduction proportional to fitness; the offspring replaces at random one of the g neighbors on the replacement graph.
- *Death–birth* (*DB*) *updating*: A random individual is chosen to die; the g neighbors of the replacement graph compete for the empty site proportional to their fitness.
- *Imitation* (*IM*) *updating*: A random player is chosen for updating his strategy; he either adopts a strategy of one of the g neighbors in the replacement graph or remains with his own strategy, proportional to fitness.

An elementary step of updating is an event where an individual is potentially replaced by another individual (or where an individual potentially changes his strategy). Reproduction can be genetic or cultural (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). Strategies breed true: we do not explicitly consider mutations. But we calculate the probability that a resident population is invaded and replaced by a mutant strategy.

The evolutionary outcomes are dependent on the updating rules. Our three updating rules are only a small subset of the possible dynamics on graphs. For example, some rules might use synchronous updating but others asynchronous updating (Nowak and May, 1992, 1993; Nowak et al., 1994). The **BD**, **DB**, and **IM** updating rules assume 'fertility-selection' where the payoffs of the game affect the fertility (reproductive success) of players.

However, one can also imagine 'viability-selection' where the payoffs affect the survival of players. For instance, in the score-dependent viability model of Nakamaru et al. (1997, 1998) and Nakamaru and Iwasa (2005, 2006), an individual is chosen to die according to his payoff (strictly speaking, a candidate is randomly chosen and he can die according to his payoff) and then one of the neighbors takes over the vacancy at random (while their so-called 'score-dependent fertility model' corresponds to our **DB** updating). This subtle change can lead to very different dynamics on graphs. We will discuss the effect of different updating rules in Section 5.

3. Fixation probabilities for games on replacement and interaction graphs

One of the most important quantities in stochastic game dynamics is the fixation probability, defined as the probability that a mutant invading a population of $N - 1$ resident individuals will produce a lineage which takes over the whole population (Nowak et al., 2004; Taylor et al., 2004; Imhof and Nowak, 2006). We denote the fixation probability of strategy A in a B-population by ρ_A. We denote the fixation probability of strategy B in an A-population by ρ_B.

The fixation probability of a neutral mutant is given by the inverse of the population size, $1/N$. If $\rho_A > 1/N$, then natural selection favors the fixation of strategy A.

In frequency dependent selection, $\rho_A > 1/N$ does not necessarily imply that $\rho_B < 1/N$ (Nowak et al., 2004). We are also interested in deriving conditions for $\rho_A > \rho_B$, which means that the fixation of A is more likely than the fixation of B. Under recurrent but rare mutations, if $\rho_A > \rho_B$ then strategy A dominates the population more often than strategy B (Fudenberg et al., 2006).

To estimate the fixation probabilities we use diffusion theory (Kimura, 1962; Crow and Kimura, 1970; Ewens, 2004). For analytical convenience we assume that the population size, N, satisfies $N \gg \max\{h, g\}$ and $N \ll 1/w$, where $w \ll 1$ is the intensity of selection. Let x_X denote the global density of strategy X ($= A$ or B). Let T_A^+ (T_A^-) be the probability that the number of A-strategists increases (decreases) by one in an elementary step of updating. These probabilities are defined as

$$T_A^+ = \text{Prob}\left(\Delta x_A = \frac{1}{N}\right), \quad T_A^- = \text{Prob}\left(\Delta x_A = -\frac{1}{N}\right). \tag{3}$$

We assume that N updating steps occur per unit time ($\Delta t = 1/N$). In this sense, the unit of time is considered to be one generation. The probability $\phi_A(y_A)$ that strategy A ultimately takes over the whole population, when its initial frequency is y_A, is given as the solution of the following backward Kolmogorov equation (Ewens, 2004)

$$0 = m(y)\frac{\mathrm{d}\phi_A(y)}{\mathrm{d}y} + \frac{v(y)}{2}\frac{\mathrm{d}^2\phi_A(y)}{\mathrm{d}y^2}. \tag{4}$$

Here, the mean of the increment of x_A per unit time, $m(x_A)$, is given by

$$
\begin{aligned}
m(x_A) &= \frac{\mathrm{E}[\Delta x_A]}{\Delta t} \\
&= \frac{\mathrm{E}[\Delta x_A]}{1/N} \\
&= N\left\{ \left(\frac{1}{N}\right) \mathrm{Prob}\left(\Delta x_A = \frac{1}{N}\right) \right. \\
&\quad \left. + \left(-\frac{1}{N}\right) \mathrm{Prob}\left(\Delta x_A = -\frac{1}{N}\right) \right\} \\
&= T_A^+ - T_A^-.
\end{aligned}
\tag{5}
$$

The variance of the increment of x_A per unit time, $v(x_A)$, is given by

$$
\begin{aligned}
v(x_A) &= \frac{\mathrm{Var}[\Delta x_A]}{\Delta t} \\
&= \frac{\mathrm{E}[(\Delta x_A)^2] - (\mathrm{E}[\Delta x_A])^2}{1/N} \\
&\approx N \cdot \mathrm{E}[(\Delta x_A)^2] \quad (\text{since } (\mathrm{E}[\Delta x_A])^2 = O(w^2)) \\
&= N\left\{ \left(\frac{1}{N}\right)^2 \mathrm{Prob}\left(\Delta x_A = \frac{1}{N}\right) \right. \\
&\quad \left. + \left(-\frac{1}{N}\right)^2 \mathrm{Prob}\left(\Delta x_A = -\frac{1}{N}\right) \right\} \\
&= \frac{T_A^+ + T_A^-}{N}.
\end{aligned}
\tag{6}
$$

From Eq. (4), the fixation probability is calculated as $\rho_A = \phi_A(1/N)$. Hence, we need to calculate T_A^+ and T_A^-.

However, the state of the population cannot be fully described by global densities of strategies, x_A and x_B. A particular configuration of the population corresponds to a two-coloring of the vertices. Each vertex can be occupied either by an A or a B individual. There are 2^N possible configurations on a graph, which is a huge number for large N. Therefore, in order to calculate T_A^+ and T_A^-, we must make approximations. Here, we adopt the pair-approximation method (Matsuda et al., 1987; Nakamaru et al., 1997, 1998; Keeling, 1999; Haraguchi and Sasaki, 2000; van Baalen, 2000) in order to describe the local configurations of strategies on graphs. Pair-approximation considers not only frequencies of strategies, but also frequencies of (connected) strategy-pairs which enables us to estimate the correlation of strategies in two adjacent nodes. We must take into account that we have three different types of pairs: pairs connected only through the replacement graph, those connected only through the interaction graph, and those connected through both graphs. We label each of them (G), (H), or (L), respectively.

Let $q_{X|Y}$ denote the conditional probability that the focal node is occupied by strategy X $(= A$ or $B)$ given that strategy Y $(= A$ or $B)$ occupies an adjacent node. This conditional probability depends on the type of edges connecting X and Y. Therefore, we need to distinguish

$q_{X|Y}^{(G)}$, $q_{X|Y}^{(H)}$, and $q_{X|Y}^{(L)}$. In the weak-selection limit, we expect these 'local' frequencies to equilibrate much faster than global frequencies of strategies, x_X. Hence, we are able to decouple the dynamics of local frequencies and that of global frequencies. In other words, the system reaches a local steady state while the global frequencies remain constant.

We first derive differential equations for the local frequencies, $q_{X|Y}$. In order to do so, we count the increase and/or decrease of the number of $X - Y$ pairs for each type of edges, (G), (H), and (L). Eqs. (A.1) in Appendix A show the dynamics of $q_{X|Y}^{(G)}$, $q_{X|Y}^{(H)}$, and $q_{X|Y}^{(L)}$ for **BD** updating. For **DB** and **IM** updating we have the same equations as Eqs. (A.1) except for different constants in front of the equation, which does not change the position of equilibrium. Hence from Eqs. (A.1), the steady state values of the local frequencies are given by

$$
q_{A|A}^{(G)} = q_{A|A}^{(L)} = \frac{g-2}{g-1}x_A + \frac{1}{g-1}, \quad q_{A|A}^{(H)} = x_A,
$$

$$
q_{B|A}^{(G)} = q_{B|A}^{(L)} = \frac{g-2}{g-1}x_B, \quad q_{B|A}^{(H)} = x_B,
$$

$$
q_{A|B}^{(G)} = q_{A|B}^{(L)} = \frac{g-2}{g-1}x_A, \quad q_{A|B}^{(H)} = x_A,
$$

$$
q_{B|B}^{(G)} = q_{B|B}^{(L)} = \frac{g-2}{g-1}x_B + \frac{1}{g-1}, \quad q_{B|B}^{(H)} = x_B
\tag{7}
$$

for all three updating mechanisms.

An intuitive interpretation of Eqs. (7) is as follows. It is obvious that correlations between two adjacent nodes build up only through reproduction, and not through interaction. Consequently, we obtain no local correlations through interaction—only edges, (H). Hence, the local frequency of strategy X, $q_{X|Y}^{(H)}$, is equal to its global frequency, x_X. Regarding the other edges, (G) and (L), with probability $1/(g-1)$ a player shares a common ancestor with his neighbor. With the remaining probability, $(g-2)/(g-1)$, his neighbor is a random individual.

Assuming that local frequencies are at steady state, we can now calculate the dynamics of global frequencies: that is, we can calculate T_A^+ and T_A^-. The details of the calculation are shown in Appendix A. Then by solving Eq. (4) we derive the fixation probabilities, ρ_A and ρ_B. For **BD** updating we obtain

$$
\rho_A > 1/N \iff (gh + l)(a - c) > (2gh - l)(d - b)
\tag{8}
$$

and

$$
\rho_A > \rho_B \iff a + b > c + d.
\tag{9}
$$

For **DB** updating we obtain

$$
\begin{aligned}
\rho_A > 1/N \iff & g^2 h(a + 2b - c - 2d) \\
& + gl(2a - 2b + c - d) \\
& + l(a - b - c + d) > 0
\end{aligned}
\tag{10}
$$

and

$$\rho_A > \rho_B \iff (gh + l)(a - d) > (gh - l)(c - b). \quad (11)$$

For **IM** updating we obtain

$$\rho_A > 1/N \iff (g + 2)gh(a + 2b - c - 2d)$$
$$+ gl(2a - 2b + c - d)$$
$$+ 3l(a - b - c + d) > 0 \quad (12)$$

and

$$\rho_A > \rho_B \iff (gh + l + 2h)(a - d) > (gh - l + 2h)(c - b). \quad (13)$$

All results hold for weak-selection, $w \ll 1$, and large population size, $N \gg h, g \geqslant l$. Moreover, we need $Nw \ll 1$. Note that we always have $g \geqslant 3$.

There is an exceptional case in which we do not require $Nw \ll 1$ for the results (8)–(13) to hold. We show in Appendix A that if $a - c = b - d$ holds then Eqs. (8)–(13) remain true for any values of Nw as long as $w \ll 1$ and $N \gg h, g \geqslant l$ are satisfied. The condition $a - c = b - d$ is called 'equal gains from switching' (Nowak and Sigmund, 1990).

3.1. The limit of well-mixed populations

Nowak et al. (2004) studied evolutionary game dynamics in finite and well-mixed populations. For the 2×2 game given by Eq. (1), they found that for large population size and weak-selection, the following results hold:

$$\rho_A > 1/N \iff a + 2b > c + 2d, \quad (14)$$

$$\rho_A > \rho_B \iff a + b > c + d. \quad (15)$$

These results, which hold for the well-mixed population, are obtained from our results for the three different update rules on replacement and interaction graphs (8)–(13) in three different limiting cases: (i) $g \gg h$; (ii) $h \gg g$, and (iii) $l \to 0$. All three update rules, **BD**, **DB**, and **IM**, lead to the results of the well-mixed population (14) and (15) for any of the three limits (i)–(iii). Therefore, the population becomes essentially well-mixed if the degree of the overlap, l, becomes small relative to either h or g.

3.2. The Prisoner's Dilemma

As a particular example, we explore the interaction between cooperators and defectors. Let us study a simplified Prisoner's Dilemma given by two parameters. A cooperator, C, pays a cost c for every edge, and the partner of this edge receives a benefit b. Defectors, D, pay no cost and distribute no benefits. We assume $b > c$ otherwise cooperation has no net benefit. The payoff matrix becomes

$$\begin{array}{cc} & A \quad B \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \rightarrow \begin{array}{cc} & C \quad D \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix}. \end{array} \quad (16)$$

For **BD** updating, we find from Eqs. (8)–(9) that for any b and c we have $\rho_C < 1/N$ and $\rho_C < \rho_D$. Therefore, selection never favors cooperators.

For **DB** updating, we find from Eq. (10) that $\rho_C > 1/N$ if

$$\frac{b}{c} > \frac{hg}{l}. \quad (17)$$

The same condition implies that $\rho_C > \rho_D$.

For **IM** updating, we find from Eq. (12) that $\rho_C > 1/N$ if

$$\frac{b}{c} > \frac{h(g + 2)}{l}. \quad (18)$$

The same condition implies that $\rho_C > \rho_D$.

Inequalities (17) and (18) suggest that the optimum configuration for evolution of cooperation is $h = g = l$. The degree l of the overlap should be as large as possible, while the degrees h and g should be as small as possible. This optimum is reached when the replacement graph and the interaction graph are identical. In this limit we recover our previous condition, $b/c > k$ (using $k = h = g = l$) (Ohtsuki et al., 2006). Any deviation from the identity between the interaction and the replacement graphs makes evolution of cooperation more difficult. Note that cooperation is never favored if the overlap between interaction and replacement graph is empty ($l = 0$).

Note that for **DB** updating the critical threshold condition (17) is symmetric in the degrees of the replacement and interaction graph, g and h. Therefore, a highly connected replacement graph (large g) and a sparsely connected interaction graph (small h) have the same threshold as the reverse situation (for a fixed overlap l). The symmetry is broken for **IM** updating. Here it is better to have a smaller degree for the interaction graph than for the replacement graph.

For a general 2×2 game with payoff matrix given by (1), we can prove that the degrees of the replacement and interaction graphs play a symmetric role in Eq. (10) for **DB** updating if and only if $a - c = b - d$ holds, which is the condition for 'equal gains from switching' (Nowak and Sigmund, 1990). We can easily confirm that the Prisoner's Dilemma game with the payoff matrix (16) satisfies this condition.

Strictly speaking pair-approximation is only valid for infinite Bethe lattices (or Cayley trees) where each node has exactly the same number of links and there are no loops or leaves. The performance of pair-approximation and its limitation have been studied by several authors (Matsuda et al., 1992; Harada and Iwasa, 1994; Nakamaru et al., 1997, 1998; Keeling, 1999; van Baalen, 2000). Under weak-selection, Ohtsuki et al. (2006) found that pair-approximation

is in excellent agreement with computer simulations for random regular graphs and other structures.

3.3. Numerical simulations on random regular graphs

We will now test our analytic results with numerical simulations on random regular graphs. The procedure to generate those graphs is straightforward: given values of h, g, l, we start by constructing a random regular graph (Santos et al., 2005) of degree g, ensuring that it is connected. Subsequently, we augment this graph by increasing the connectivity of all nodes by $h - l$, such that G has connectivity g, while H has connectivity h and L has connectivity l. In general, it is not always possible to generate a graph in this way, due to the stochastic nature of the construction algorithm. However, the algorithm for generation of each homogeneous random graph (Santos et al., 2005) is very efficient, and a few attempts have proven sufficient for generating the plethora of graphs that we used to compute the fixation probabilities by means of numerical simulations.

Players interact on H and reproduce on G. We consider only two update rules for reproduction: **DB** and **IM**, since, for weak-selection, the **BD** update rule never provides an evolutionary advantage for cooperators in the Prisoner's Dilemma. The fitness of each individual is related to its payoff by Eq. (2). In all numerical simulations, we use $w = 0.1$. We start by stipulating given values for the connectivities (h, g, l), as well as for the cost to benefit ratio c/b. Subsequently we generate 3000 graphs G and H compatible with the fixed (h, g, l), and run 5000 simulations for each graph, reaching a grand total of 15 000 000 simulations for each set of parameters (N, h, g, l, b, c).

Simulations always start with a population consisting of only defectors and a single randomly placed cooperator. Its location is changing from simulation to simulation. By changing the initial location of the cooperator and by changing the specific graph realization for given (h, g, l), we compute the average fixation probability of a single cooperator in a population of defectors. Simulations stop when one of the two absorbing states is reached: either 100% cooperators (fixation) or 100% defectors (extinction). We scan regions of the ratio c/b in order to find the critical value below which cooperators become advantageous mutants. We consider populations of size $N = 100$ and 500. Therefore, we have $Nw = 10$ and 50. Remember that for games of 'equal gains from switching', such as the Prisoner's Dilemma (16), our analytical predictions (8)–(13), hence the conditions (17), (18), are valid for any values of Nw, as long as $w \ll 1$ and $N \gg h, g \geqslant l$ hold.

The results are shown in Figs. 2 and 3 for the **DB**-updating and in Figs. 4 and 5 for the **IM**-updating. Excellent agreement with the theoretical predictions is obtained. In particular, the numerical simulations confirm the invariance of the condition above for **DB**-updating upon exchange of h and g (cf. Fig. 2), showing also how this symmetry is broken under **IM**-updating (cf. Fig. 4).
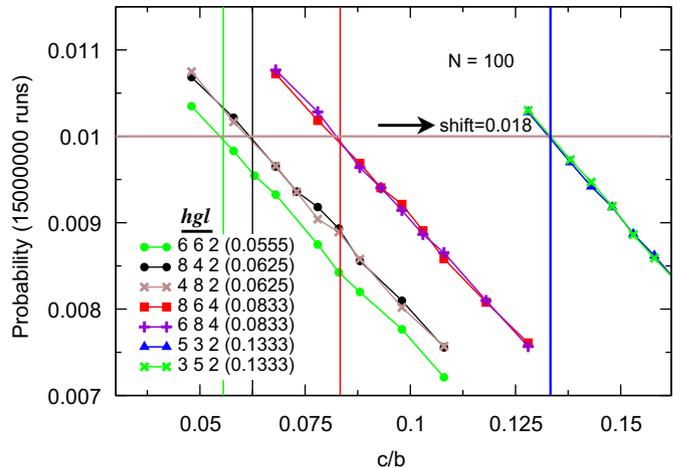

Fig. 2. Results for the fixation probability under **DB**-updating. For a population size of $N = 100$, and for each combination of values (h, g, l), we ran 15 000 000 simulations starting from a single cooperator immersed in a sea of defectors. We did so for different values of the ratio c/b. For each value, we computed the fixation probability as the ratio between those runs in which the system reached 100% cooperators and the total number of runs. Each symbol represents one such calculation, whereas the lines provide a guide to the eye. The crossing between the vertical lines (each with a color corresponding to a different combination of (h, g, l)) and the horizontal line at $p = \frac{1}{100}$ indicate the values associated with the theoretical predictions. In all cases the numerical results have been systematically shifted by a constant factor of 0.018 towards higher values of c/b in order to bring theory and computer simulations into agreement. This shift depends on the population size, decreasing with increasing N (see main text for details).
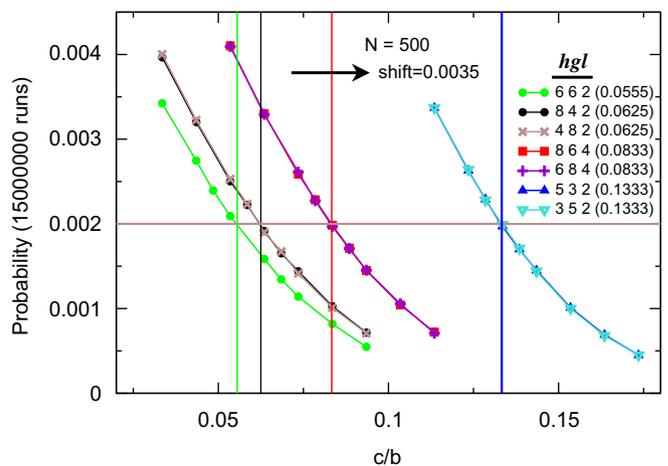

Fig. 3. Results for the fixation probability under **DB**-updating. This figure shows the same results as Fig. 2 but for a population size of $N = 500$. In all cases the numerical results have been systematically shifted by a constant factor of 0.0035 towards higher values of c/b in order to bring theory and computer simulations into agreement. This shift depends on the population size, decreasing with increasing N (see main text for details).

Yet, for **IM**-updating, new combinations of h and g lead to the same threshold condition, a feature nicely corroborated by the results of computer simulations.

A perfect agreement between theory and computer simulations would imply that the simulation results cross the $1/N$ horizontal line exactly at the point where this line
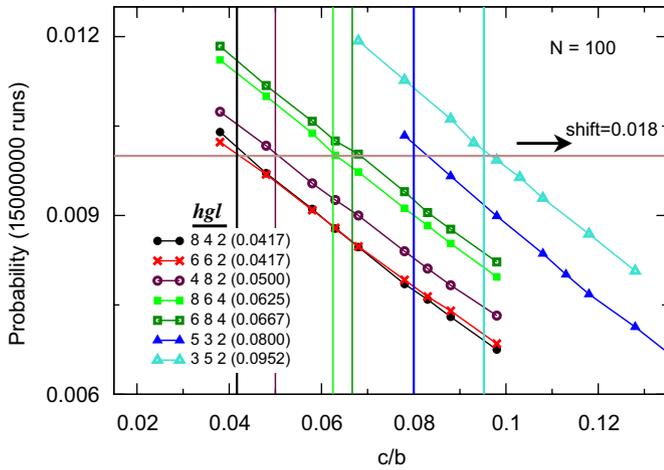
Fig. 4. Results for the fixation probability under **IM**-updating. The population size is $N = 100$. The same simulation conditions employed in Fig. 2 also apply here. The only change occurs in what concerns the update rule which, as predicted theoretically, leads to a different relation for the critical ratio c/b below which a cooperator mutant becomes advantageous in a population of defectors. Similarly to Fig. 2, all numerical results have been shifted by the same constant amount of 0.018, which improves the agreement between theoretical predictions and numerical results. Note, however, that comparison with Fig. 2, the agreement is not as good, suggesting that the size-dependent correction term is different for **IM**-updating.
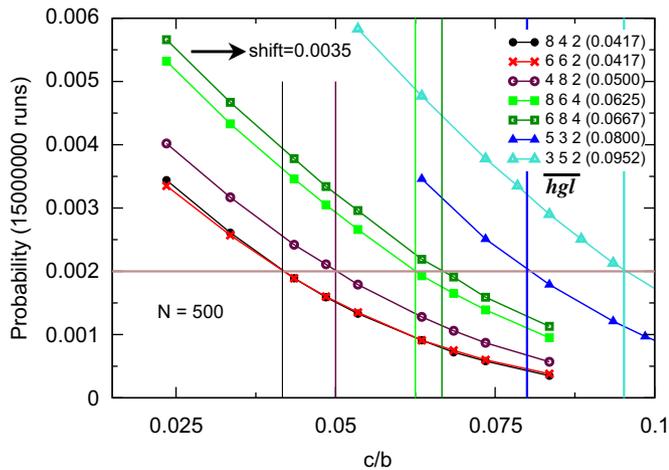

Fig. 5. Results for the fixation probability under **IM**-updating. This figure shows the same results as Fig. 4 but for a population size of $N = 500$. In all cases the numerical results have been systematically shifted by a constant factor of 0.0035 towards higher values of c/b in order to bring theory and computer simulations into agreement. This shift depends on the population size, decreasing with increasing N (see main text for details).

crosses each appropriate vertical line. What we observe for $N = 100$ is a rigid shift of ≈ 0.018 towards lower values of c/b between the simulation results and the theoretical predictions (note the numerical shift of data by this amount in Figs. 2 and 4). This constant shift turns out to be a population size-effect. For $N = 500$ (Figs. 3 and 5), we find

an entirely equivalent scenario with a reduced shift of 0.0035.

In other words, as the population size increases, the agreement between the pair-approximation-based predictions and computer simulations improves in the Prisoner's Dilemma (16). For a given finite value of N we need b/c to be slightly larger than the thresholds (17) and (18).

4. The replicator equation for games on replacement and interaction graphs

In the limit of $N \to \infty$ with $w \ll 1$ held constant, we obtain deterministic game dynamics on our two graphs. The key equation will be a replicator equation with a modified payoff matrix. We note that this deterministic equation gives a good approximation for the stochastic process on two graphs with large population size $N \gg \max\{h, g\}$ and weak-selection $w \ll 1$ when $Nw \gg 1$ holds.

Consider a game with n strategies, $i = 1, \ldots, n$. The payoff for strategy i versus strategy j is a_{ij}. The payoff matrix is given by $A = (a_{ij})$. Let x_i denote the global frequency of strategy i. We have $\sum_{i=1}^{n} x_i = 1$. In a well-mixed population, strategy i meets strategy j with probability x_j. The average payoff of an i-player is given by $\sum_{j=1}^{n} a_{ij}x_j = e_i \cdot Ax$, where e_i is the ith unit column vector, $x = (x_1, \ldots, x_n)^T$, and the dot denotes inner product. From this we obtain the replicator equation in a well-mixed population as

$$\dot{x}_i = x_i(e_i \cdot Ax - x \cdot Ax). \tag{19}$$

Here $x \cdot Ax = \sum_{i=1}^{n} (e_i \cdot Ax)x_i = \sum_{i,j=1}^{n} a_{ij}x_i x_j$ is the average payoff of the population (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998). This equation is defined on the simplex $S_n = \{(x_1, \ldots, x_n) \mid x_1 + \cdots + x_n = 1, x_i \geqslant 0\}$. Each face of the simplex is invariant under the dynamics.

If, however, the population is structured according to the two graphs, the probability that strategy i meets strategy j is no longer equal to x_j. We will show that the replicator equation on graphs has the form:

$$\dot{x}_i = x_i[e_i \cdot (A + B)x - x \cdot (A + B)x]. \tag{20}$$

The matrix $B = (b_{ij})$ contains the effect of local interactions. The matrix B is calculated from A and satisfies $x \cdot Bx = 0$.

Consider the $n \times n$ game with payoff matrix $A = (a_{ij})$. Each individual plays the game with h neighbors on the interaction graph, H, and gains a total payoff which translates into biological fitness by Eq. (2). The reproduction of strategies occurs on the replacement graph G. We consider the same update rules as before. We assume that an individual updates its strategy on average once per unit time. We also assume weak-selection, $w \ll 1$. We require $g \geqslant 3$ throughout our calculation.

First, we estimate the local frequencies of strategies in a given environment, using the pair-approximation method. Let $q_{i|j}$ denote the conditional probability that the focal node is occupied by strategy i given strategy j is in an

adjacent node. For each of three different types of edges, (G), (H) and (L), we consider such probabilities, denoted by $q_{i|j}^{(G)}$, $q_{i|j}^{(H)}$ and $q_{i|j}^{(L)}$, respectively. Then the equilibrium values of these probabilities are calculated as (see Appendix A)

$$q_{i|j}^{(G)} = q_{i|j}^{(L)} = \frac{g-2}{g-1}x_i + \frac{1}{g-1}\delta_{ij}, \quad q_{i|j}^{(H)} = x_i. \qquad (21)$$

Here δ_{ij} is one if $i = j$ and zero otherwise.

Let T_i^+ (T_i^-) denote the probability that the number of i-strategists increases (decreases) by one in an elementary step of updating. From

$$\dot{x}_i \approx \frac{\mathrm{E}[\Delta x_A]}{\Delta t} = T_i^+ - T_i^-, \qquad (22)$$

we obtain the equations for the rate of change of global frequencies, which have the form of a replicator equation on graphs.

For **BD** updating we obtain

$$\dot{x}_i = \frac{w(g-2)(gh-2l)}{g(g-1)} \cdot x_i[e_i \cdot (A+B)x - x \cdot (A+B)x] \\ + O(w^2), \qquad (23)$$

where $B = (b_{ij})$ is given by

$$b_{ij} = \frac{l(a_{ii} + a_{ij} - a_{ji} - a_{jj})}{gh - 2l}. \qquad (24)$$

By re-scaling the time and neglecting w^2 and higher order terms we obtain

$$\dot{x}_i = x_i[e_i \cdot (A+B)x - x \cdot (A+B)x]. \qquad (25)$$

For **DB** updating, we also recover this form after neglecting a constant, but in this case the matrix B is given by

$$b_{ij} = \frac{l\{(g+1)a_{ii} + a_{ij} - a_{ji} - (g+1)a_{jj}\}}{g^2h - gl - 2l}. \qquad (26)$$

Similarly, for **IM** updating the matrix B is given by

$$b_{ij} = \frac{l\{(g+3)a_{ii} + 3a_{ij} - 3a_{ji} - (g+3)a_{jj}\}}{g^2h - gl - 6l + 2gh}. \qquad (27)$$

In each of three different limits: (i) $g \gg h$; (ii) $h \gg g$, and (iii) $l \to 0$, the correction term b_{ij} in Eqs. (24), (26), (27) vanishes to zero and we obtain the standard replicator equation describing a well-mixed population.

4.1. Prisoner's Dilemma

We study the Prisoner's Dilemma (16) using the replicator equation on graphs, (20).

For **BD** updating, we find that defectors always dominate cooperators, as predicted for a well-mixed population. For **DB** updating, cooperators dominate defectors if

$$\frac{b}{c} > \frac{hg}{l}. \qquad (28)$$

In this case, 'network reciprocity' favors cooperators over defectors: the relative abundance of cooperators converges

to unity from any initial fraction. Interestingly, the condition (28) is exactly the same as the one for $\rho_C > 1/N$ (Eq. (17)).

For **IM** updating, the equivalent condition is found to be

$$\frac{b}{c} > \frac{h(g+2)}{l} \qquad (29)$$

which is the same as Eq. (18).

4.2. The Snow-drift game

The Snow-drift game is given by the payoff matrix

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{cc} C \qquad D \\ \begin{pmatrix} b - \dfrac{c}{2} & b - c \\ b & 0 \end{pmatrix}. \end{array} \qquad (30)$$

Two drivers are trapped on either side of a snow drift. Cooperation means getting out of the car and shovel. Defection means to remain in the car and let the other driver shovel. The benefit of getting home is b, which is larger than the cost of shoveling, c. If both cooperate the cost is halved for each person. If both defect neither can go home, and both drivers obtain zero payoff (Hauert and Doebeli, 2004).

In a well-mixed population, the traditional replicator Eq. (19) predicts stable coexistence of cooperators and defectors at an equilibrium where the relative abundance of cooperators is given by $x_C^* = 1 - [c/(2b - c)]$.

Let us consider the Snow-drift game played on graphs. We use the replicator equation on graphs (20). From Eqs. (24), (26), and (27) the matrix B is calculated as

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{cc} C \qquad D \\ \begin{pmatrix} 0 & \chi \\ -\chi & 0 \end{pmatrix}. \end{array} \qquad (31)$$

For **BD** updating, we obtain

$$\chi = \frac{l(2b - 3c)}{2(gh - 2l)}. \qquad (32)$$

For **DB** updating, we obtain

$$\chi = \frac{l\{(2 + 2g)b - (3 + g)c\}}{2(g^2h - gl - 2l)}. \qquad (33)$$

For **IM** updating, we obtain

$$\chi = \frac{l\{(6 + 2g)b - (9 + g)c\}}{2(g^2h - gl - 6l + 2gh)}. \qquad (34)$$

We can show that the existence of the fixed point is not affected by the graph structure, but its location changes. From Eq. (31) it is obvious that cooperation is favored on graphs compared to well-mixed populations if and only if χ is positive. For **BD** updating this condition is $b/c > \frac{3}{2}$. For **DB** and **IM** updating this condition is always satisfied whenever $g \geq 3$ and $l > 0$. If there is no overlap between
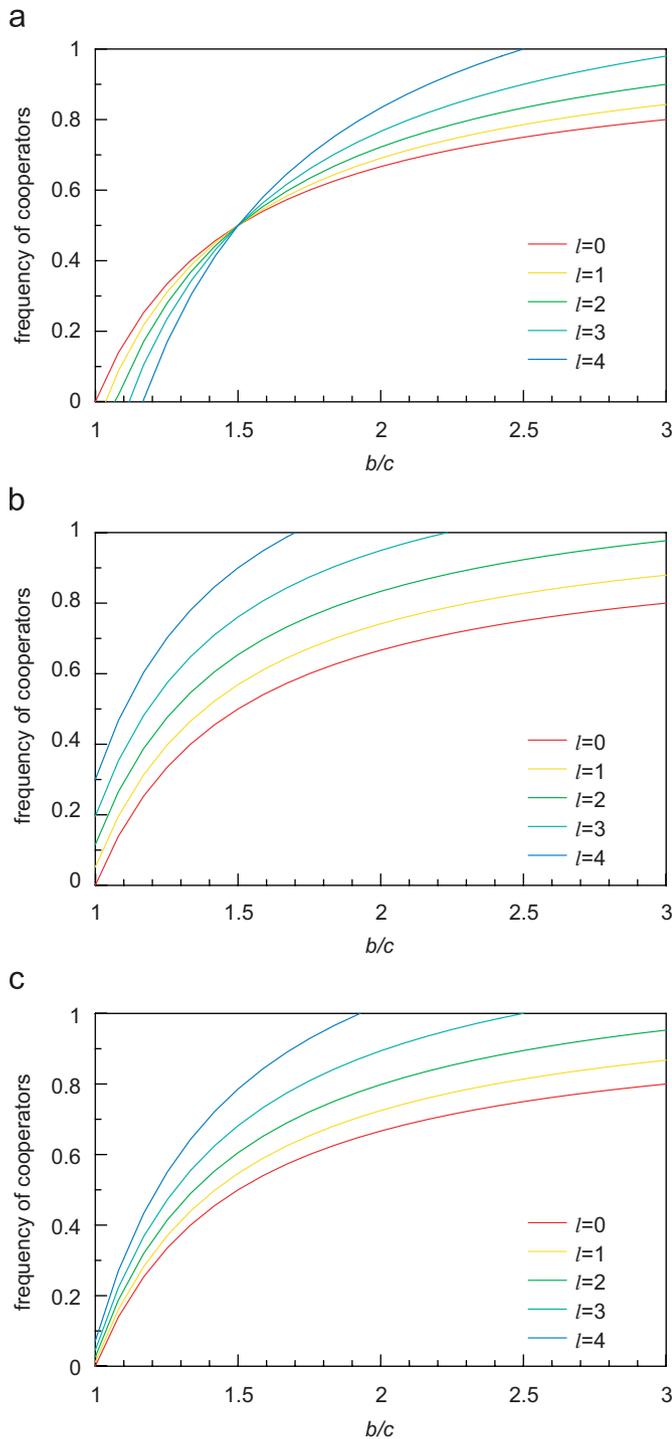
a

b

c

Fig. 6. The frequency of cooperators at the equilibrium in the Snow-drift game played on graphs for (a) **BD**; (b) **DB**, and (c) **IM** updating. The x-axis represents the benefit-cost ratio of cooperation, b/c. The degrees of replacement graph and interaction graph are fixed as $g = h = 4$. We change the degree of overlap from $l = 0$ to $l = 4$. (a) When $b/c > \frac{3}{2}$ graph structure favors cooperation for increasing overlap l. When $b/c < \frac{3}{2}$, on the other hand, the opposite is observed. (b,c) The larger the overlap l between replacement graph and interaction graph, the more cooperation is favored in **DB** and **IM** updating.

replacement graph and interaction graph (i.e. $l = 0$) then χ is equal to zero, which leaves the dynamics unchanged with respect to that in a well-mixed population.

Figs. 6a–c show the equilibrium-frequency of cooperators over the benefit-to-cost ratio, b/c, for each of three update rules. We observe that for fixed g and h the effect of spatial structure becomes more prominent with increasing degree of overlap, l.

5. Discussion

In the prisoner's dilemma, **BD**-updating never confers an evolutionary advantage to cooperators, even in the imit of weak-selection. For **DB** and **IM** updating, cooperators can be favored over defectors by 'network reciprocity'. Cooperators in clusters earn a higher payoff than defectors, and therefore the cluster can expand. In Ohtsuki and Nowak (2006a) an intuitive explanation has been proposed for the difference in behavior associated with these two classes of updating, which stems from the fact that both **DB** and **IM** explore a larger neighborhood than **BD** updating. In fact, under **DB** and **IM** updating the neighbors of a dying/learning individual, who themselves are not direct neighbors of each other, compete for reproduction. This favors the assortative correlation between cooperators, thereby enhancing the survival chances of cooperators. In contrast, under **BD** updating a player competes against his immediate neighbors with whom he played the Prisoner's Dilemma. In this case the advantage of a cooperator resulting from the assortativeness is exactly canceled out by the benefit a defector receives from the cooperator, thus cooperation never evolves (see also Taylor, 1992; Wilson et al., 1992).

Nakamaru et al. (1997, 1998) and Nakamaru and Iwasa (2005, 2006) compared fertility-selection and viability-selection. In their score-dependent fertility model, a random death is followed by reproduction with selection. In their score-dependent viability model, a selective death is followed by a random birth. For the Prisoner's Dilemma on one- and two-dimensional lattices, Nakamaru et al. (1997, 1998) found that the former is more favorable to cooperation than the latter (we note that the citation of the results of Nakamaru et al., 1997, 1998 in Ohtsuki and Nowak, 2006a was mistakenly reversed). The observation by Nakamaru et al. is due to the same reason as the difference between **BD** and **DB** updating. In the score-dependent fertility model, neighbors opposite to the empty site compete, while in the score-dependent viability model only direct neighbors compete for survival.

In view of this argument, we expect that neither the order of birth and death nor the distinction between fertility-selection and mortality-selection yields a critical difference. We note that in our **BD**, **DB** and **IM** updating rules, and Nakamaru et al's two selection mechanisms, either birth or death event is under selection and the other is a random process. A crucial difference stems from the fact whether the second part of the update rule is affected by payoff or purely random. Cooperation

is favored only when a random step is followed by a selective step.

Recently, we have studied the role of population structure in finite (Ohtsuki et al., 2006) and infinite populations (Ohtsuki and Nowak, 2006b), for the case where $k = h = g = l$. It is therefore worth investigating the consequences of the present study in the light of these previous findings. For **DB** updating, natural selection will favor cooperators whenever the condition $b/c > k$ is satisfied, a result which assumes that graphs are regular, although numerical simulations have shown that the applicability of this result extends beyond the theoretical assumptions (Ohtsuki et al., 2006). In practice, this rule means that smaller connectivities k favor cooperators, in the sense that smaller clusters of co-operators can play a role at the start of the evolutionary process. Interestingly, for the **DB** updating, our present results $b/c > hg/l$ show that cooperation is maximally favored whenever $h = g = l = k$ (since $g \geqslant l$ and $h \geqslant l$, always). In other words, even when we separate the interaction from the replacement graph, cooperation is maximized whenever the two actually coincide, in which case we recover the $b/c > k$-rule. In retrospect, this result is intuitive. For the Prisoner's Dilemma, the only means of cooperators to fare better than defectors is to successfully assortate and to use clustering to collect the benefits from cooperative interactions. Clearly, assortation is maximal through the replacement graph, since cooperators breed cooperators and defectors breed defectors. Consequently, in order for cooperators to benefit from such assortation, the overlap between H and G has to be maximal, and this leads to $k = h = g = l$.

Note that $b/c > hg/l$ is symmetric in g and h. Therefore, it does not matter whether the interaction graph has high connectivity and the replacement has low connectivity or vice versa. This symmetry is broken for **IM** updating, which leads to $b/c > h(g + 2)/l$. This result is also easy to understand: as opposed to **DB** updating, for **IM** updating the strategy of the focal individual also competes for 'remaining' in place. This affects exclusively the replacement graph G. Moreover, one can picture the alluded competition of the own strategy with the others to remain 'in place' as if the replacement graph would exhibit an additional 'loop' emerging from the focal individual and ending in the same focal individual. This loop, which does not overlap with H, leads to an effective connectivity of G which becomes $(g + 2)$. Remarkably, this is precisely the result given by Eq. (18).

So far we have discussed evolutionary dynamics for the special case of the Prisoner's Dilemma. Our results, however, extend to other 2×2 games in finite populations, as well as to $n \times n$ games in infinite populations. In this respect, it is noteworthy that our results, for weak-selection (for other intensities, cf. Traulsen et al. 2006a, b) also lead to the so-called $\frac{1}{3}$-rule in appropriate limits (Nowak et al., 2004). For example, for **DB** updating the general condition

for $\rho_A > 1/N$ implies

$$
\begin{aligned}
g^2 h(a + 2b - c - 2d) + gl(2a - 2b + c - d) \\
+ \, l(a - b - c + d) > 0.
\end{aligned}
\tag{35}
$$

Surprisingly, this condition is equivalent to asking that the abundance of strategy A increases at frequency $x_A = \frac{1}{3}$ in the replicator equation on graphs, Eq. (20), given the local configuration of strategies on graphs is at the steady state given by Eq. (7).

In infinite, structured populations, and in the limit of weak-selection, strategies evolve according to a replicator equation. The effect of population structure is to induce a transformation of the payoff matrix. Once such a transformation is performed, then evolution proceeds 'as if' the population were well-mixed (unstructured). This remarkable result also shares many of the peculiarities already found for the case where the replacement and interaction graphs are identical (Ohtsuki and Nowak, 2006b). In particular, the transformation of the payoff matrix is of the form (for the case of 2×2 games)

$$
\begin{array}{c}
\begin{array}{cc} & A \quad B \end{array} \\
\begin{array}{c} A \\ B \end{array}
\begin{pmatrix} a & b \\ c & d \end{pmatrix}
\end{array}
\quad \rightarrow \quad
\begin{array}{c}
\begin{array}{cc} & A \quad\;\; B \end{array} \\
\begin{array}{c} A \\ B \end{array}
\begin{pmatrix} a & b + \chi \\ c - \chi & d \end{pmatrix}.
\end{array}
\tag{36}
$$

The specific form of χ depends on the update rule (cf. Eqs. (24, (26), and (27)). Yet, irrespective of the update rule, the population structure affects only the off-diagonal terms of the payoff matrix, that is, population structure only affects the interactions between different strategies. Therefore, a transformed replicator equation can describe evolutionary dynamics on replacement and interaction graphs.

In the present paper we have studied fixed regular graphs. Future directions should include evolutionary dynamics on graphs of subdivided populations (Maruyama, 1970; Slatkin, 1981; Barton, 1993), heterogenous graphs (Antal et al., 2006; Santos et al., 2006b), complex networks (Nakamaru and Levin, 2004; Santos et al., 2005, 2006a; Santos and Pacheco, 2005; May, 2006), and dynamic networks (Bala and Goyal, 2000; Mohtashemi and Mui, 2003; Pacheco et al., 2006; Santos et al., 2006c).

Acknowledgments

Appendix A

In this Appendix, we study the general case of a $n \times n$ game whose payoff matrix is given by $A = (a_{ij})$. Subsequently, we consider the particular case of $n = 2$, that is, 2×2 games, and derive both the replicator equation for the frequencies of strategies in infinite populations, as well as the fixation probabilities of strategies for finite populations.

We use the following notations. x_i represents the global frequency of strategy i. x_{ij} represents the global frequency of i–j pairs. Since we have three different types of pairs, (G), (H), and (L) as in the main text, we must consider $x_{ij}^{(G)}$, $x_{ij}^{(H)}$, and $x_{ij}^{(L)}$ separately. The conditional probability that the focal node is occupied by strategy i given strategy j is next is denoted by $q_{i|j}$. Similarly to pair-frequencies, we have $q_{i|j}^{(G)}$, $q_{i|j}^{(H)}$, and $q_{i|j}^{(L)}$. In the pair-approximation we neglect the effect from nodes that are two or more steps away from the focal one. We shall frequently make use of the following identities: $q_{i|j}^{(*)} = x_{ij}^{(*)}/x_j$ and $x_{ij} = x_{ji}$, where $(*)$ is a wild-card for (G), (H), and (L).

A.1. BD updating

First we study **BD** updating. We determine the rate of change in the number of i–j pairs of the three different types of pair-frequencies. Using $q_{i|j}^{(*)} = x_{ij}^{(*)}/x_j$ we obtain

$$\frac{\mathrm{d}q_{i|j}^{(G)}}{\mathrm{d}t} = \frac{1}{g}\left[2\delta_{ij} + \sum_k q_{i|k}^{(G)}\{(g-l-1)q_{k|j}^{(G)} + lq_{k|j}^{(L)}\} \right.$$
$$\left. + \sum_k \{(g-l-1)q_{i|k}^{(G)} + lq_{i|k}^{(L)}\}q_{k|j}^{(G)} - 2gq_{i|j}^{(G)} \right] + O(w),$$

$$\frac{\mathrm{d}q_{i|j}^{(H)}}{\mathrm{d}t} = \frac{1}{g}\left[\sum_k q_{i|k}^{(H)}\{(g-l)q_{k|j}^{(G)} + lq_{k|j}^{(L)}\} \right.$$
$$\left. + \sum_k \{(g-l)q_{i|k}^{(G)} + lq_{i|k}^{(L)}\}q_{k|j}^{(H)} - 2gq_{i|j}^{(H)} \right] + O(w),$$

$$\frac{\mathrm{d}q_{i|j}^{(L)}}{\mathrm{d}t} = \frac{1}{g}\left[2\delta_{ij} + \sum_k q_{i|k}^{(L)}\{(g-l)q_{k|j}^{(G)} + (l-1)q_{k|j}^{(L)}\} \right.$$
$$\left. + \sum_k \{(g-l)q_{i|k}^{(G)} + (l-1)q_{i|k}^{(L)}\}q_{k|j}^{(L)} - 2gq_{i|j}^{(L)} \right]$$
$$+ O(w). \tag{A.1}$$

Here $O(w)$ represents terms which scale as w^n $(n \geqslant 1)$. From Eqs. (A.1) the equilibrium values of conditional probabilities $q_{i|j}^{(*)}$ are calculated, leading to Eq. (21).

Let T_i^+ (T_i^-) be the probability that the number of i-strategists increases (decreases) by one in an elementary step of **BD** updating. After some algebra we have

$$T_i^+ + T_i^- = \frac{2(g-2)}{g-1}x_i(1-x_i) + O(w),$$

$$T_i^+ - T_i^- = \frac{w(g-2)(gh-2l)}{g(g-1)}x_i[e_i \cdot (A+B)x$$
$$- x \cdot (A+B)x] + O(w^2), \tag{A.2}$$

where $B = (b_{ij})$ is given by Eq. (24). In infinite populations $\dot{x}_i$ is given by $T_i^+ - T_i^-$. Hence, neglecting higher order terms with respect to w and re-scaling the time we obtain the replicator equation on graphs, Eq. (20).

Consider a game with $n = 2$ strategies in finite populations ($N < \infty$). We rename strategies $i = 1$ and 2, A and B. For payoffs we substitute a, b, c, and d for a_{11}, a_{12}, a_{21}, and a_{22}, respectively. From Eq. (A.2) we have

$$m(x_A) = \frac{\mathrm{E}(\Delta x_A | x_A)}{\Delta t} = T_A^+ - T_A^-$$
$$= \frac{w(g-2)}{g(g-1)}x_A(1-x_A)(\alpha x_A + \beta) + O(w^2),$$

$$v(x_A) = \frac{\mathrm{var}(\Delta x_A | x_A)}{\Delta t} = \frac{1}{N}(T_A^+ + T_A^-)$$
$$= \frac{2(g-2)}{N(g-1)}x_A(1-x_A) + O(w), \tag{A.3}$$

where

$$\alpha = (gh - 2l)(a - b - c + d),$$

$$\beta = la + (gh - l)b - lc - (gh - l)d. \tag{A.4}$$

Solving the backward Kolmogorov equation (4) gives us

$$\phi_A(y_A) = \begin{cases} \int_{\xi_+(0)}^{\xi_+(y_A)} \mathrm{e}^{-z^2}\,\mathrm{d}z \Big/ \int_{\xi_+(0)}^{\xi_+(1)} \mathrm{e}^{-z^2}\,\mathrm{d}z & \text{if } \alpha > 0, \\[2mm] \dfrac{1 - \mathrm{e}^{-Nw\beta y_A/g}}{1 - \mathrm{e}^{-Nw\beta/g}} & \text{if } \alpha = 0, \\[2mm] \int_{\xi_-(0)}^{\xi_-(y_A)} \mathrm{e}^{z^2}\,\mathrm{d}z \Big/ \int_{\xi_-(0)}^{\xi_-(1)} \mathrm{e}^{z^2}\,\mathrm{d}z & \text{if } \alpha < 0, \end{cases} \tag{A.5}$$

where

$$\xi_+(x) \equiv \sqrt{\frac{Nw}{2\alpha g}}(\alpha x + \beta) \quad \text{and} \quad \xi_-(x) \equiv -\sqrt{\frac{Nw}{-2\alpha g}}(\alpha x + \beta). \tag{A.6}$$

From $\rho_A = \phi_A(1/N)$ we obtain ρ_A. For $Nw \ll 1$, Eq. (A.5) is simplified to

$$\phi_A(y_A) \approx y_A + \frac{Nw}{6g}y_A(1-y_A)(\alpha + 3\beta + \alpha y_A). \tag{A.7}$$

We can calculate ρ_B in a similar manner. Assuming $Nw \ll 1$, from Eq. (A.7) we obtain

$$\rho_A \approx \frac{1}{N} + \frac{w(N-1)}{6Ng}\left(\alpha + 3\beta + \frac{\alpha}{N}\right),$$

$$\frac{\rho_A}{\rho_B} \approx 1 + \frac{w(N-1)h}{2}(a+b-c-d). \tag{A.8}$$

Therefore we obtain Eqs. (8), (9) in the main text.

From Eq. (A.5), we see that when $\alpha = 0$, or equivalently when $a - c = b - d$, the inequalities $\rho_A > 1/N$ and $\rho_A > \rho_B$ hold for any values of Nw if and only if $\beta > 0$. Therefore, if $a - c = b - d$ holds, Eqs. (8), (9) are valid not only for

$Nw \ll 1$ but also for any Nw values. Note that we always need weak-selection, $w \ll 1$, and large population size, $N \gg h, g \geqslant l$.

A.2. **DB** and **IM** updating

Next we study **DB** and **IM** updating. For convenience we herein introduce an updating rule called 'generalized imitation (**GIM**)' updating with resistance $r \geqslant 0$. This is a generalization of **DB** and **IM** updating in the main text. Under this rule a random player is chosen for updating her strategy, and she either adopts a strategy of one of her g neighbors connected via the replacement graph or remains with the same strategy, proportionally to fitness with her own payoff weighted as r, whereas all her neighbours have their payoffs weighted with weight 1. Without resistance ($r = 0$) we recover the original **DB** updating. Choosing $r = 1$ gives us the **IM** updating. Below we will study this **GIM** updating with resistance r.

As in calculations for **BD** updating, we first explore the dynamics of local frequencies of strategies. The resulting equations turn out to be the same as Eq. (A.1) except that $1/g$'s in the r.h.s's of Eq. (A.1) has to be replaced by $1/(g+r)$'s. As a result, we recover Eq. (21) as defining the equilibrium local frequencies.

Given this fact, we can calculate T_i^+ and T_i^- as follows:

$$T_i^+ + T_i^- = \frac{2g(g-2)}{(g+r)(g-1)} x_i(1-x_i) + O(w),$$

$$T_i^+ - T_i^- = \frac{w(g-2)\{g^2h - gl - 2l + 2r(gh - 2l)\}}{(g+r)^2(g-1)}$$
$$\times x_i[\mathbf{e_i} \cdot (\mathbf{A} + \mathbf{B})\mathbf{x} - \mathbf{x} \cdot (\mathbf{A} + \mathbf{B})\mathbf{x}] + O(w^2), \tag{A.9}$$

where $\mathbf{B} = (b_{ij})$ is given by

$$b_{ij} = \frac{l\{(g+1+2r)a_{ii} + (1+2r)a_{ij} - (1+2r)a_{ji} - (g+1+2r)a_{jj}\}}{g^2h - gl - 2l + 2r(gh - 2l)}. \tag{A.10}$$

In infinite populations $\dot{x}_i = T_i^+ - T_i^-$ holds. By neglecting higher order terms with respect to w and by re-scaling the time, we obtain the replicator equation on graphs as in the main text.

For finite populations, let us study the 2×2 game with strategies A and B with payoff matrix given by Eq. (1). From (A.9) we obtain

$$m(x_A) = T_A^+ - T_A^- = \frac{w(g-2)}{(g+r)^2(g-1)} x_A(1-x_A)$$
$$\times (\alpha'x_A + \beta') + O(w^2),$$

$$v(x_A) = \frac{1}{N}(T_A^+ + T_A^-) = \frac{2g(g-2)}{N(g+r)(g-1)}$$
$$\times x_A(1-x_A) + O(w), \tag{A.11}$$

where

$$\alpha' = \{g^2h - gl - 2l + 2r(gh - 2l)\}(a - b - c + d),$$

$$\beta' = (gl + l + 2rl)a + \{g^2h - gl - l + 2r(gh - l)\}b$$
$$- (l + 2rl)c - \{g^2h - l + 2r(gh - l)\}d. \tag{A.12}$$

Solving the backward Kolmogorov equation (4) gives us

$$\phi_A(y_A) = \begin{cases} \int_{\xi_+(0)}^{\xi_+(y_A)} e^{-z^2} dz \Big/ \int_{\xi_+(0)}^{\xi_+(1)} e^{-z^2} dz & \text{if } \alpha' > 0, \\ \dfrac{1 - e^{-Nw\beta'y_A/g(g+r)}}{1 - e^{-Nw\beta'/g(g+r)}} & \text{if } \alpha' = 0, \\ \int_{\xi_-(0)}^{\xi_-(y_A)} e^{z^2} dz \Big/ \int_{\xi_-(0)}^{\xi_-(1)} e^{z^2} dz & \text{if } \alpha' < 0, \end{cases} \tag{A.13}$$

where

$$\xi_+(x) \equiv \sqrt{\frac{Nw}{2\alpha'g(g+r)}}(\alpha'x + \beta') \quad \text{and} \quad \xi_-(x)$$
$$\equiv -\sqrt{\frac{Nw}{-2\alpha'g(g+r)}}(\alpha'x + \beta'). \tag{A.14}$$

From $\rho_A = \phi_A(1/N)$ we obtain ρ_A. For $Nw \ll 1$, Eq. (A.13) is approximated by

$$\phi_A(y_A) \approx y_A + \frac{Nw}{6g(g+r)} y_A(1-y_A)(\alpha' + 3\beta' + \alpha'y_A). \tag{A.15}$$

We can calculate ρ_B in a similar manner. Assuming $Nw \ll 1$, from Eq. (A.15) we obtain

$$\rho_A \approx \frac{1}{N} + \frac{w(N-1)}{6Ng(g+r)}\left(\alpha' + 3\beta' + \frac{\alpha'}{N}\right),$$

$$\frac{\rho_A}{\rho_B} \approx 1 + \frac{w(N-1)}{2(g+r)}$$
$$\times [(gh + l + 2rh)(a-d) - (gh - l + 2rh)(c-b)]. \tag{A.16}$$

Hence for **GIM** updating with resistance r we have

$$\rho_A > 1/N \iff (g+2r)gh(a + 2b - c - 2d)$$
$$+ gl(2a - 2b + c - d)$$
$$+ (1+2r)l(a - b - c + d) > 0 \tag{A.17}$$

and

$$\rho_A > \rho_B \iff (gh + l + 2rh)(a - d) > (gh - l + 2rh)(c - b). \tag{A.18}$$

By substituting 0 or 1 for r we obtain results for **DB** or **IM** updating, Eqs. (10)–(13).

From Eq. (A.13), it is easy to see that when $\alpha' = 0$, or equivalently when $a - c = b - d$, the inequalities $\rho_A > 1/N$ and $\rho_A > \rho_B$ hold for any Nw if and only if $\beta' > 0$. Thus, if $a - c = b - d$ holds, Eqs. (A.17), (A.18) remain true for any Nw values. We note that we always need weak-selection, $w \ll 1$, and large population size, $N \gg h, g \geqslant l$.

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