

Evolution of multiplayer cooperation on graphs

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Abstract

There has been much interest in studying evolutionary games in structured populations, often modelled as graphs. However, most analytical results so far have only been obtained for two-player or additive games, while the study of more complex multiplayer games has been usually tackled by computer simulations. Here we investigate evolutionary multiplayer games in regular graphs updated with a Moran process. Using a combination of pair approximation and diffusion approximation, we obtain an analytical condition for cooperation to be favored by natural selection, given in terms of the payoffs of the game and a set of structure coefficients. We show that, for a large class of cooperative dilemmas, graph-structured populations are stronger promoters of cooperation than populations lacking spatial structure. Computer simulations validate our results, showing that the complexity arising from many-person social interactions and spatial structure can be often captured by analytical methods.

Introduction

Graphs are a natural starting point to assess the role of population structure in the evolution of cooperation. Vertices of the graph represent individuals, while links (edges) define interaction and dispersal neighborhoods. Classical models of population structure, such as island models [1,2] and lattices [3,4], often developed before the current interest in complex networks [5,6], can all be understood as particular instances of graphs [7,8]. More recently, the popularity of network theory has fueled a renewed interest in evolutionary dynamics on graphs, specially in the context of social behaviors such as cooperation and altruism [7–21].

When selection is weak on two competing strategies, such that fitness differences represent only a small perturbation of a neutral evolutionary process, a surprisingly simple condition for one strategy to dominate the other, known as the “sigma rule”, holds for a large variety of graphs and other models of spatially structured populations [22]. Such condition depends not only on the payoffs of the game describing the social interactions, but also on a number of “structure coefficients”. These coefficients are functions of demographic parameters of the spatial model and of its associated update protocol, but they are independent of the payoffs. In the case of two-player games, the sigma rule depends on a single structure coefficient σ . The larger this σ , the greater the ability of spatial structure to promote the evolution of cooperation or to choose efficient equilibria in coordination games [22]. Partly for this reason, the calculation of structure coefficients for different population structures and demographic scenarios has attracted increasing interest during the last years [8, 21–27].

Despite the theoretical and empirical importance of two-player games, many social interactions involve the collective action of more than two individuals. Examples range from bacteria producing extracellular compounds [28–31] to human social dilemmas [32–36]. In these situations, the evolution of cooperation is better modeled as a multiplayer game where individuals obtain their payoffs from interactions with more than two players [37–42]. Multiplayer games can be also embedded in graphs, assuming for example that nodes represent not only individuals playing games but also games played by individuals [43–45].

Most previous studies on the effects of graph structure on multiplayer game dynamics have relied on computer simulations [45]. However, similar to the two-player case, some analytical progress can be made if selection is assumed to be weak. In the multiplayer case, the sigma rule depends no longer on one, but on up to $d - 1$ structure coefficients, where d is the number of players [46]. Although exact formulas for structure coefficients of multiplayer games can be obtained for relatively simple models such as cycles [47], analysis has proved elusive in more complex population structures, including regular graphs of arbitrary degree. Indeed, extending analytical results on evolutionary two-player games on graphs to more general multiplayer games is still considered to be an open problem in evolutionary graph theory [48].

Here, we contribute to this body of work by deriving approximate analytical expressions for the structure coefficients of regular graphs updated with a Moran death-Birth model, and hence for the condition of one strategy to dominate another according to the sigma rule. We show that regular graphs updated with a death-Birth Moran process always promote cooperation with respect to the baseline case of a well-mixed population, and that this is so for a large class of games modeling cooperative dilemmas. Computer simulations confirm our analytical predictions, showing that our results remain valid with parameter values going beyond the assumptions of our approximations.

Methods

We consider stochastic evolutionary dynamics on a graph-structured population of size N . Each individual is located in the vertex of a regular graph of degree k . Individuals obtain a payoff by interacting with their k neighbors in a d -person symmetric game (i.e., $d = k + 1$). If j co-players play A , a focal A -player obtains a_j whereas a focal B -player obtains b_j , as indicated in the following payoff table:

| Opposing A -players | 0 | 1 | ... | j | ... | $d - 1$ |
|-----------------------|-------|-------|-----|-------|-----|-----------|
| payoff to A | a_0 | a_1 | ... | a_j | ... | a_{d-1} |
| payoff to B | b_0 | b_1 | ... | b_j | ... | b_{d-1} |

The effective payoff affecting the stochastic evolutionary dynamics is given by $1 + w \times \text{payoff}$, where the parameter w measures the intensity of selection.

We model the stochastic evolutionary dynamics as a Markov process on a finite space state where a state S corresponds to a given composition of the population, i.e., which vertices are A and which are B . More specifically, we consider a Moran death-Birth process [12, 14, 49] according to which, each time step: (i) a random individual is chosen to die, and (ii) its neighbors compete to place a copy of themselves in the new empty site with probability proportional to their effective payoff. Without mutation, such Markov process has two absorbing states: that where all vertices are occupied by A -players and that where all vertices are occupied by B -players. Let us denote by ρ_A the fixation probability of a single A -player in a population of B -players, and by ρ_B the fixation probability of a single B -player in a population of A -players. We take the comparison of fixation probabilities, i.e.

$$\rho_A > \rho_B, \tag{1}$$

as a measure of evolutionary success [50] and say that A is favored over B if condition (1) holds.

Under weak selection, i.e., $w \rightarrow 0$, the condition for A to be favored over B holds if the sigma rule for multiplayer games [46] is satisfied, i.e., if

$$\sum_{j=0}^{d-1} \sigma_j f_j > 0. \quad (2)$$

Here, $\sigma_0, \dots, \sigma_{d-1}$ are the d structure coefficients (constants that depend on the population structure and on the update dynamics), and the quantities f_0, \dots, f_{d-1} , given by

$$f_j = a_j - b_{d-1-j}, \quad j = 0, 1, \dots, d-1, \quad (3)$$

are differences between payoffs, which we will refer to in the following as the “gains from flipping”. The gains from flipping capture the change in payoff experienced by a focal individual playing B in a group where j co-players play A when all players simultaneously switch strategies (so that A -players become B -players and B -players become A -players). It turns out that the payoffs of the game only enter into condition (1) via the gains from flipping (3), as the structure coefficients are themselves independent of a_j and b_j .

Structure coefficients are uniquely determined up to a constant factor. Setting one of these coefficients to one thus gives a single structure coefficient for $d = 2$ [22]. For $d > 2$, and in the usual case where structure coefficients are nonnegative, we can impose $\sum_{j=0}^{d-1} \sigma_j = 1$ without affecting the selection condition (2). For our purposes, this normalization turns out to be more useful than setting one coefficient to one, as it allows us to rewrite the sigma rule (2) as

$$\sum_{j=0}^{d-1} \varsigma_j f_j = \mathbb{E}[f(J)] > 0, \quad (4)$$

where $f(j) \equiv f_j$, and J is the random variable with probability distribution prescribed by the “normalized structure coefficients” $\varsigma_j = \sigma_j / \sum_{i=0}^{d-1} \sigma_i$. In light of condition (4), the sigma rule can be interpreted as stating that strategy A is favored over B if the expected gains from flipping are greater than zero when the number of co-players J is distributed according to the normalized structure coefficients. From this perspective, different models of population structure lead to different normalized structured coefficients and hence to different expected gains from flipping, which in turn imply different conditions for strategy A to be favored over B in a given multiplayer game [47]. For instance, the baseline case scenario of a large well-mixed population updated with either a Moran or a Wright-Fisher process leads to normalized structure coefficients given by [39, 40]:

$$\varsigma_j^{\text{W}} = \begin{cases} \frac{N}{d(N-1)} & \text{if } 0 \leq j \leq d-2 \\ \frac{N-d}{d(N-1)} & \text{if } j = d-1 \end{cases}. \quad (5)$$

A normalized sigma rule such as the one given by Eq. (4) holds for many spatial models and associated updating protocols [46, 47]. Here, we focus on the case of regular graphs updated with a Moran death-Birth process. We provide exact expressions for the case of cycles for which $k = 2$. For $k \geq 3$ the structure coefficients are difficult to calculate exactly. We bypass these difficulties by using a combination of pair approximation and diffusion approximation [14] together with mathematical identities involving polynomials in Bernstein form [41, 51]. Our approach implicitly assumes that graphs are equivalent to Bethe lattices (or Cayley trees) with a very large number of vertices ($N \gg k$). In addition, weak selection intensities ($w \ll 1$) are also required for an implicit argument of separation of timescales to hold. In order to validate our approximations, we implemented a computational model that simulates a Moran death-Birth process in

three different regular graphs (the cycle, the random regular graph, and the lattice) with different degrees. We run two sets of 10^7 realizations for each of the three types of graphs selected, each with different degrees, $k \in \{2, 3, 4, 6, 8, 10\}$. In the first set, cooperation is the mutant strategy and in the second one defection is the mutant. A single realization of the simulation starts with the mutant placed in a randomly selected vertex. The graph is then updated until the mutant has reached fixation or extinction. The fixation probability is then estimated as the average of all the realizations where the mutant succeeded in invading the wild-type.

Results

Structure coefficients for regular graphs

The simplest case of a regular graph is the cycle, for which $k = 2$. In this case, we find the following exact expressions for the structure coefficients (S1 Text, Section 1):

$$\zeta_0^G = \frac{1}{2(N-2)}, \quad \zeta_1^G = \frac{1}{2}, \quad \zeta_2^G = \frac{N-3}{2(N-2)}. \quad (6)$$

For $k \geq 3$, we make use of pair approximation and diffusion approximation, and find that the structure coefficients for regular graphs of degree $k \geq 3$ can be written as (S1 Text, Section 2)

$$\zeta_j^G = \frac{(k-2)^{k-1-j}}{k^2(k+1)(k+2)} \sum_{\ell=0}^{k-1} (k-\ell) \{ [k^2 - \ell(k-2)] v_{\ell,j,k} + [2k + \ell(k-2)] \tau_{\ell,j,k} \}, \quad (7)$$

where

$$\tau_{\ell,j,k} = \binom{k-1-\ell}{k-j} \frac{k-2}{(k-1)^{k-1-\ell}} + \binom{\ell}{k-1-j} \frac{1}{(k-1)^\ell},$$

and

$$v_{\ell,j,k} = \binom{k-1-\ell}{k-1-j} \frac{1}{(k-1)^{k-1-\ell}} + \binom{\ell}{k-j} \frac{k-2}{(k-1)^\ell}.$$

These expressions are nontrivial functions of the degree of the graph k and thus difficult to interpret. For instance, for $k = 3$, we obtain $\zeta^G = \left(\frac{7}{144}, \frac{31}{144}, \frac{61}{144}, \frac{45}{144} \right)$.

Containment order and promotion of cooperation in multiplayer social dilemmas

The previous results hold for any symmetric multiplayer game with two strategies. To investigate the evolution of multiplayer cooperation, we label strategy A as ‘‘cooperate’’, strategy B as ‘‘defect’’, and assume that, irrespective of the focal player’s strategy, the payoff of a focal player increases with the number of co-players that choose to cooperate, i.e.,

$$a_{j+1} \geq a_j \text{ and } b_{j+1} \geq b_j \text{ for all } j. \quad (8)$$

This restriction on the payoffs is characteristic of ‘‘cooperation games’’ in which playing A is beneficial to the group but might be costly to the individual [47]. Well-known multiplayer games belonging to this large class of games include different instances of volunteer’s dilemmas [52, 53], snowdrift games [54], stag hunts [55], and many other instances of public, club, and charity goods games [56].

We are interested in establishing whether graph-structured populations lead to structure coefficients that make it easier to satisfy the normalized sigma rule (4) than well-mixed populations (the baseline case scenario

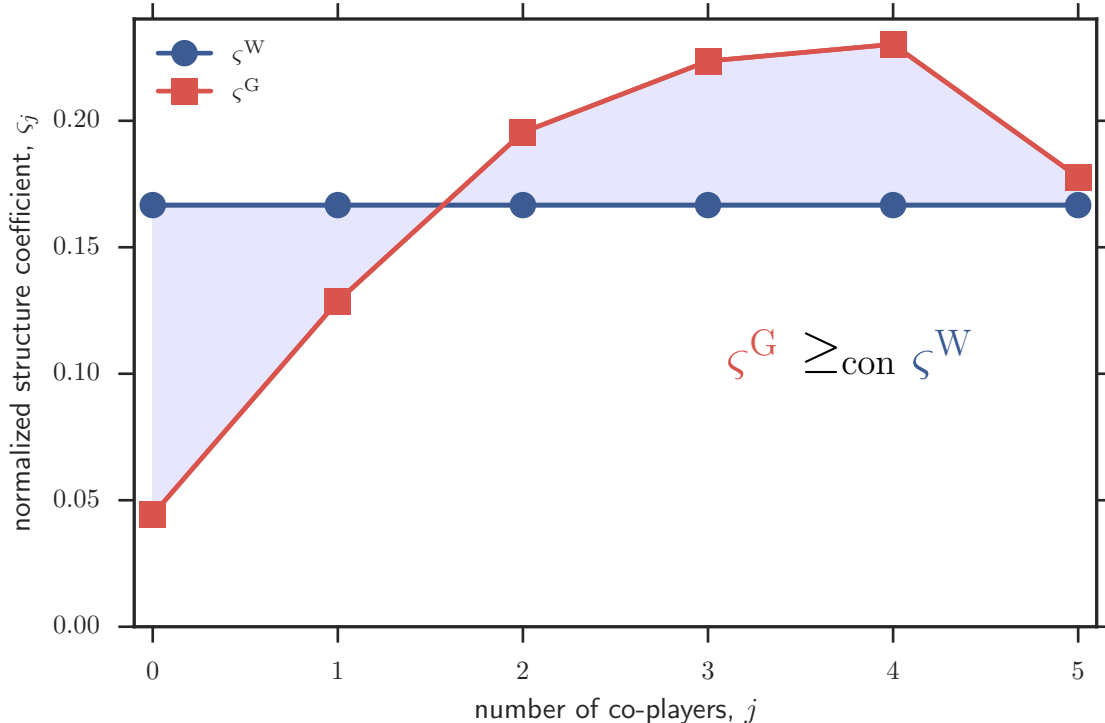


Figure 1. Structure coefficients and containment ordering. Normalized structure coefficients ζ_j for large ($N \rightarrow \infty$) regular graphs of degree $k = 5$ updated with a Moran death-Birth process (ζ^G ; red squares) and well-mixed populations with $d = 6$ (ζ^W ; blue circles). Since $\zeta^G - \zeta^W$ has one sign crossing from $-$ to $+$, the graph is greater in the containment order than the well-mixed population (denoted by $\zeta^G \geq_{\text{con}} \zeta^W$). Consequently, if the sigma rule holds for a well-mixed population, then it also holds for a graph-structured population for any cooperation game fulfilling condition (8).

of a population with no spatial structure) for any cooperation game satisfying condition (8). In other words, we ask whether a graph is a stronger promoter of cooperation than a well-mixed population; technically, this is equivalent to ask whether a graph is greater or smaller than a well-mixed population in the so-called “containment order” [47]. A simple sufficient condition for this is that the difference in normalized structure coefficients, $\zeta^G - \zeta^W$ has exactly one sign change from $-$ to $+$ [47]. This can be verified for any $N > 3$ in the case of cycles ($k = 2$) by inspection of equations (5) and (6). For large regular graphs of degree $k > 2$ and hence multiplayer games with $d > 3$ players, we checked the condition numerically by comparing equations (5) and (7) for $k = 3, \dots, 100$. We find that $\zeta^G - \zeta^W$ always has a sign change from $-$ to $+$ and hence that regular graphs promote more cooperation than well-mixed populations (Fig. 1).

Examples

Collections of two-player games. As a consistency check, let us consider the case where individuals play two-player games with their k neighbors and collect the payoffs of the different interactions. The two-player

game is given by the payoff matrix

$$\begin{array}{cc} & \begin{array}{c} A \quad B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix}. \end{array} \quad (9)$$

The payoffs for the resulting multiplayer game, which are just the sum of payoffs of the pairwise games, are then given by $a_j = j\alpha + (k-j)\beta$ and $b_j = j\gamma + (k-j)\delta$. The sigma rule (4) can hence be written as

$$k(\beta - \gamma)(\alpha - \beta + \gamma - \delta) \sum_{j=0}^k \zeta_j^G j > 0. \quad (10)$$

We can show that (S1 Text, Section 4)

$$\sum_{j=0}^k \zeta_j^G j = \mathbb{E}[J] = \frac{k+1}{2}, \quad (11)$$

so that condition (10) is equivalent to

$$(k+1)\alpha + (k-1)\beta - (k-1)\gamma - (k+1)\delta > 0,$$

i.e., the sigma rule previously established for pairwise games in regular graphs [cf. Eq. (24) in the Supplementary Material of Ref. [14]]. For a pairwise donation game (for which $\alpha = \mathcal{B} - \mathcal{C}$, $\beta = -\mathcal{C}$, $\gamma = \mathcal{B}$, $\delta = 0$, where \mathcal{B} and \mathcal{C} are respectively the benefit and cost of donation) this reduces to the famous $\mathcal{B}/\mathcal{C} > k$ rule [7, 14, 16].

Linear games and additive prisoner’s dilemma. Suppose now that a_j and b_j are both linear functions of j . We can thus write

$$\begin{aligned} a_j &= -\mathcal{C} + \frac{\mathcal{B} + \mathcal{D}}{k} j, \\ b_j &= \frac{\mathcal{B}}{k} j, \end{aligned} \quad (12)$$

for some parameters \mathcal{B} , \mathcal{C} , and \mathcal{D} . When $\mathcal{B} > \mathcal{C} \geq 0$, Eq. (12) can be interpreted in terms of a social dilemma where strategies A and B correspond to “cooperate” and “defect”, as follows. Cooperators pay each a cost \mathcal{C} in order to provide a benefit \mathcal{B}/k to each of their co-players; defectors receive the benefits but pay no cost. In addition to the benefit \mathcal{B}/k , cooperators also get an additional bonus \mathcal{D}/k per other cooperator in the group. This bonus can be positive or negative.

For such linear games, and by making use of Eq. (11), the sigma condition simplifies to

$$\frac{2\mathcal{B} + \mathcal{D}}{\mathcal{B} + \mathcal{C}} > \frac{2k}{k+1}. \quad (13)$$

When there is no bonus ($\mathcal{D} = 0$) the game is an additive prisoner’s dilemma [57] and we recover the condition

$$\mathcal{B}/\mathcal{C} > k. \quad (14)$$

In the limit of large k , the sigma condition becomes $\mathcal{D} > 2\mathcal{C}$.

Volunteer's dilemma. As an example of a nonlinear cooperation game, consider the volunteer's dilemma [52, 58]. In such a game, one volunteer can produce a public good of value \mathcal{B} at a personal cost \mathcal{C} . Payoffs are then given by $a_j = \mathcal{B} - \mathcal{C}$ for all j , $b_0 = 0$, and $b_j = \mathcal{B}$ for $j > 0$. The sigma condition, Eq. (4), for the volunteer's dilemma on a graph reduces to

$$\mathcal{B}/\mathcal{C} > 1/\zeta_k^G.$$

For the cycle, we thus find

$$\mathcal{B}/\mathcal{C} > \frac{2(N-2)}{N-3},$$

which in the limit of large N reduces to $\mathcal{B}/\mathcal{C} > 2$. For large regular graphs of degree $k \geq 3$, our approximations lead to

$$\mathcal{B}/\mathcal{C} > \frac{(k-1)^2 - (k-1)^{1-k}}{k(k+1)(k-2)}.$$

These conditions contrast with that for a large well mixed population, which is given by $\mathcal{B}/\mathcal{C} > k+1$ (Fig. 2) and with that of an additive prisoner's dilemma on a graph, given by (14).

Suppose now that the cost of producing the public good is shared among volunteers [53]. Payoffs are then given by $a_j = \mathcal{B} - \mathcal{C}/(j+1)$, $b_0 = 0$ and $b_j = \mathcal{B}$ for $j > 0$. In this case the sigma rule simplifies to

$$\mathcal{B}/\mathcal{C} > \frac{1}{\zeta_k^{G,k}} \sum_{j=0}^k \frac{\zeta_j^G}{j+1}.$$

This leads to

$$\mathcal{B}/\mathcal{C} > \frac{5N-6}{2(N-2)}$$

in the case of a finite cycle of size N and $\mathcal{B}/\mathcal{C} > 5/2$ for a large cycle. Contrastingly, in a well-mixed population,

$$\mathcal{B}/\mathcal{C} > \sum_{j=0}^k \frac{1}{j+1}.$$

Fig. 2 shows these different critical benefit-to-cost ratios for different values of the degree of the graph k .

Computer simulations

Simulation results are in good agreement with analytical predictions (Fig. 3). Some discrepancies between the numerical results and the analytical predictions stem from the fact that pair approximation is formulated for graphs containing no loops such as Cayley trees. As all graphs explored in the simulations but the cycles ($k = 2$) do contain loops, such discrepancies are expected. On the other hand, our analytical predictions appear to be a lower bound as they systematically underestimate the results of the simulations.

Discussion

We provided an analytical approximation for the structure coefficients of a regular graph, which together with the payoffs from the game determine when a strategy is more abundant than another in the limits of weak selection and weak mutation. Such condition is valid for any symmetric multiplayer game, including the

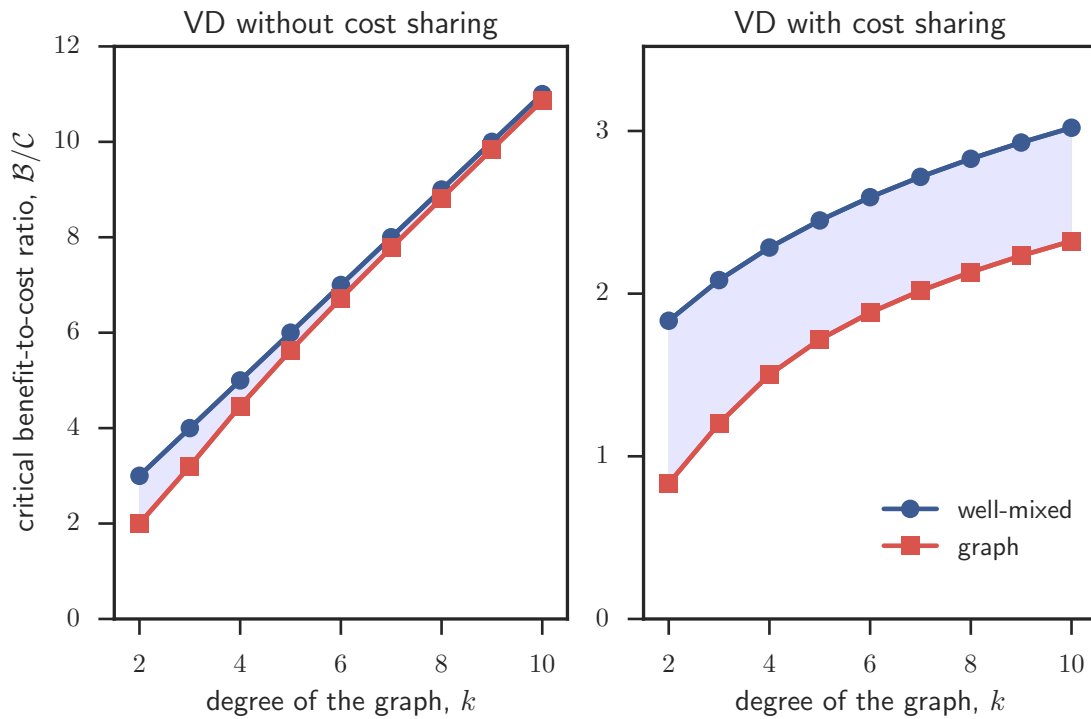


Figure 2. Critical benefit-to-cost ratios for the volunteer's dilemma. Critical benefit-to-cost ratios below which cooperation is not promoted for the volunteer's dilemma (VD) without cost sharing (*left panel*) and with cost sharing (*right panel*) on large graphs (*red squares*) and well-mixed populations (*blue circles*).

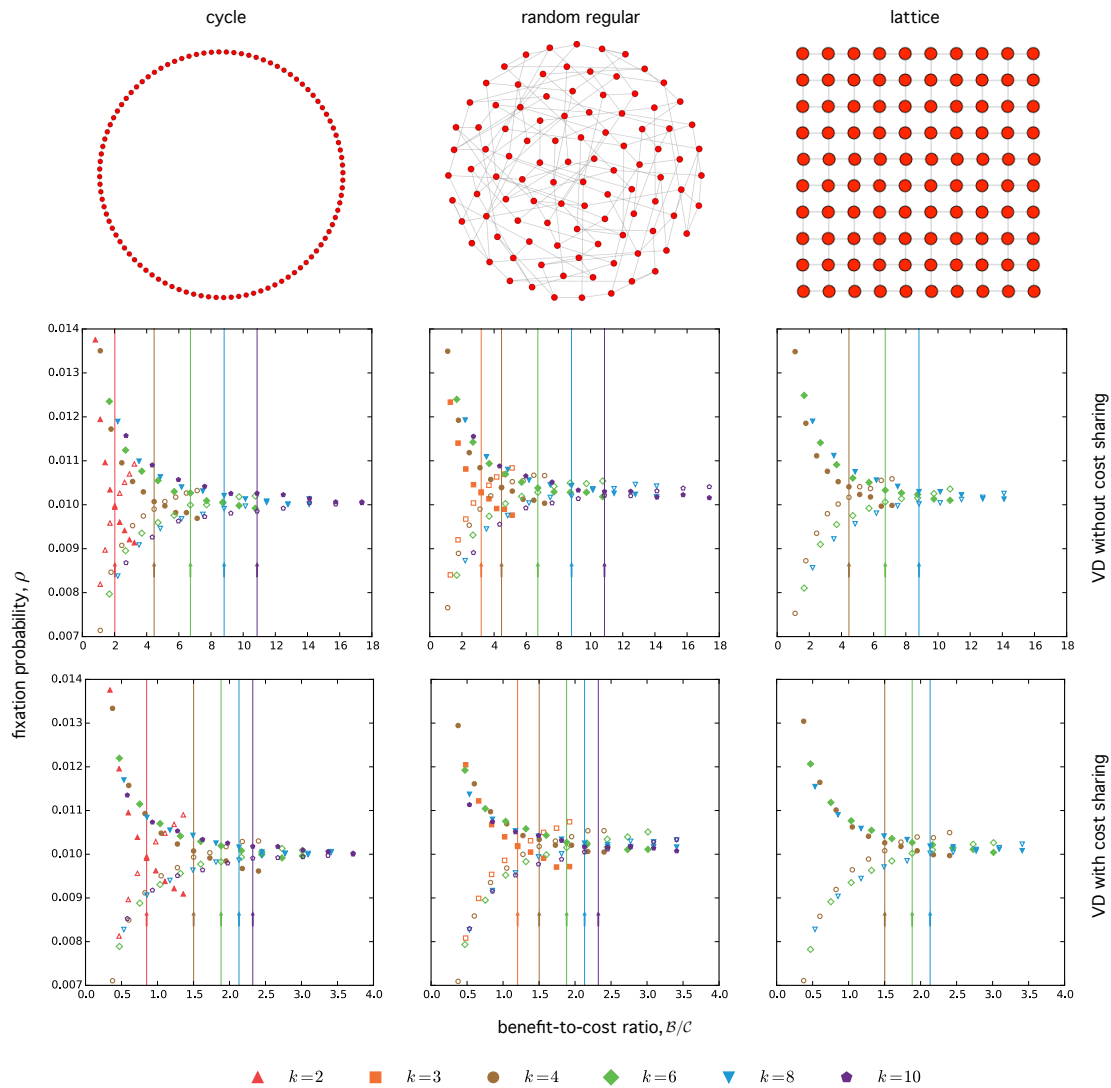


Figure 3. Fixation probabilities of cooperator and defector mutants. Simulations start from either a single cooperator mutant (*empty symbols*) or a single defector mutant (*full symbols*). Analytical predictions (*arrows*) agree well with the numerical results for small degree k of the graph, but they systematically underestimate the numerical results for larger degree k . The figure also shows that the intersection of the two fixation probabilities does not necessarily coincide with the fixation probability under neutrality, $1/N$ (Population size $N = 100$, intensity of selection $w = 0.01$, payoff cost $C = 1.0$).

volunteer’s dilemma [52, 53, 58] and other multiplayer social dilemmas discussed in the recent literature [38, 41, 54, 55, 59]. The condition can be used to determine the specific conditions (in terms of the degree of the graph and the parameters of the game, such as payoff costs and benefits) under which cooperation will thrive. The structure coefficients also provide a way of comparing the graph with other population structures, such as the well-mixed population. In particular, we established that a graph updated with a death-Birth process always promotes cooperation with respect to the baseline scenario of a well-mixed population for a large class of cooperation games, hence extending previous results on two-player games [7, 14, 16] to the more general case of multiplayer games.

We assumed that a focal player obtains its payoff from a single multiplayer game with its k immediate neighbors. This is in contrast with a common assumption of many studies of multiplayer spatial and network games in which a focal player’s total payoff is the sum of payoffs obtained in $k + 1$ different games, one “centered” in the focal player itself and the other k centered in its neighbors [43–45]. As a result, focal players interact not only with first-order but also with second-order neighbors, which leads to more intricate structure coefficients. For example, in this case the structure coefficients of a cycle are given by [47, 60]

$$\zeta_0^{G^*} = \frac{N + 1}{3(2N - 3)}, \zeta_1^{G^*} = \frac{2N - 1}{3(2N - 3)}, \zeta_2^{G^*} = \frac{N - 3}{2N - 3}. \quad (15)$$

These values are different from those we calculated under the assumption that individuals play a single game with first-order neighbors, given by Eq. (6). For $N > 4$, the structure coefficients fulfill $\zeta^G \geq_{\text{con}} \zeta^{G^*}$, meaning that our assumption of payoffs from a single game leads to more promotion of cooperation. This observation is in line with previous results for pairwise games on graphs suggesting that the condition for the evolution of cooperation is optimized when interaction and replacement neighborhoods coincide [61], which corresponds to our assumption of individuals playing a single game.

We used pair approximation and diffusion approximation to find approximate values for the structure coefficients, but other approaches can be used to estimate them. In particular, the sigma rule can be written in terms of selection coefficients (dependent on the payoffs of the game and the demographic parameters of the model) and expected coalescence times under neutrality [cf. Eq. (24) in Ref. [62]], which would allow to make use of coalescent theory [63] to obtain exact analytical expressions for the structure coefficients. However, such expected coalescence times can be difficult to obtain exactly [62, 64]. Alternatively, for small graphs, the sigma rule and hence the structure coefficients can be explicitly calculated from the transition matrix of the evolutionary process [cf. Appendix C of Ref. [26]]. Finally, we note that even in cases for which the structure coefficients are difficult to obtain by purely analytical means, they can be estimated numerically, either indirectly (by estimating the expected times to coalescence) or directly (by computing and comparing fixation probabilities).

We modelled social interactions as multiplayer matrix games with two discrete strategies (A and B) and obtained our results by assuming that selection is weak (w is small). Alternatively, one could model the same multiplayer game but assume instead that players play two similar mixed strategies z and $z + \delta$, where z and $z + \delta$ refer to the probability of playing A for each strategy, and δ is small [56, 65]. In such “ δ -weak selection” scenario [65, 66], and for any number of players, only one structure coefficient is needed to identify conditions under which a higher probability of playing A is favored by natural selection. For transitive graphs of size N and degree k , such structure coefficient is given by [7, 25]

$$\sigma = \frac{(k + 1)N - 4k}{(k - 1)N}.$$

Exchanging the structure coefficient σ by the “scaled relatedness coefficient” κ of inclusive fitness theory via

the identity $\kappa = (\sigma - 1)/(\sigma + 1)$ [62], we obtain [16]

$$\kappa = \frac{N - 2k}{k(N - 2)}.$$

With such value, recent results on multiplayer discrete games in structured populations under δ -weak selection [56] can be readily applied to show that, for all cooperation games as we defined them and for a death-Birth protocol, A is favored over B more easily for a graph-structured population than for a well-mixed population, as long as $N > k + 1$. This illustrates a case where predictions using different methodologies and sets of approximations qualitatively coincide.

To sum up, we have shown that even for multiplayer games on non-trivial graphs, which are routinely analyzed by simulation only, some analytical insight can be generated. One important message is that the evolutionary dynamics and the underlying structure cannot be fully disentangled, as both affect the structure coefficients.

Supporting Information

S1 Text

Supplementary Methods.

References

1. Wright S. Evolution in Mendelian Populations. *Genetics*. 1931;16:97–159.
2. Rousset F. Genetic structure and selection in subdivided populations. Princeton, NJ: Princeton University Press; 2004.
3. Malécot G. Heterozygosity and relationship in regularly subdivided populations. *Theoretical Population Biology*. 1975;8(2):212–241.
4. Nowak MA, May RM. Evolutionary games and spatial chaos. *Nature*. 1992;359:826–829.
5. Albert R, Barabási AL. Statistical mechanics of complex networks. *Review of Modern Physics*. 2002;74:47–97.
6. Boccaletti S, Latora V, Moreno Y, Chávez M, Hwang DU. Complex Networks: Structure and Dynamics. *Physics Reports*. 2006;424:175–308.
7. Taylor PD, Day T, Wild G. Evolution of cooperation in a finite homogeneous graph. *Nature*. 2007;447(7143):469–472.
8. Débarre F, Hauert C, Doebeli M. Social evolution in structured populations. *Nature Communications*. 2014;5(3409).
9. Abramson G, Kuperman M. Social games in a social network. *Physical Review E*. 2001;63:030901.
10. Ebel H, Bornholdt S. Coevolutionary games on networks. *Physical Review E*. 2002;66:056118.

11. Holme P, Trusina A, Kim BJ, Minnhagen P. Prisoner's Dilemma in real-world acquaintance networks: Spikes and quasiequilibria induced by the interplay between structure and dynamics. *Physical Review E*. 2003;68:030901(R).
12. Lieberman E, Hauert C, Nowak MA. Evolutionary dynamics on graphs. *Nature*. 2005;433:312–316.
13. Santos FC, Pacheco JM. Scale-free networks provide a unifying framework for the emergence of cooperation. *Physical Review Letters*. 2005;95:098104.
14. Ohtsuki H, Hauert C, Lieberman E, Nowak MA. A simple rule for the evolution of cooperation on graphs. *Nature*. 2006;441:502–505.
15. Tomassini M, Luthi L, Giacobini M. Hawks and Doves on small-world networks. *Physical Review E*. 2006 Jan;73(1):016132.
16. Lehmann L, Keller L, Sumpter DJT. The evolution of helping and harming on graphs: the return of the inclusive fitness effect. *Journal of Evolutionary Biology*. 2007;20:2284–2295.
17. Szabó G, Fáth G. Evolutionary games on graphs. *Physics Reports*. 2007;446:97–216.
18. Ohtsuki H, Nowak MA, Pacheco JM. Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs. *Physical Review Letters*. 2007;98:108106.
19. Wu B, Zhou F, Luo Q, Wang L, Traulsen A. Evolution of cooperation on stochastic dynamical networks. *PLoS One*. 2010;5:e11187.
20. Buesser P, Peña J, Pestelacci E, Tomassini M. The influence of tie strength on evolutionary games on networks: An empirical investigation. *Physica A: Statistical Mechanics and its Applications*. 2011;390(23–24):4502–4513.
21. Allen B, Nowak MA. Games on graphs. *EMS Surveys in Mathematical Sciences*. 2014;1(1):113–151.
22. Tarnita CE, Ohtsuki H, Antal T, Fu F, Nowak MA. Strategy selection in structured populations. *Journal of Theoretical Biology*. 2009;259:570–581.
23. Nathanson CG, Tarnita CE, Nowak MA. Calculating evolutionary dynamics in structured populations. *PLoS Computational Biology*. 2009;5(12):e1000615.
24. Nowak MA, Tarnita CE, Antal T. Evolutionary dynamics in structured populations. *Philosophical Transactions of the Royal Society B*. 2010;365:19–30.
25. Allen B, Nowak MA, Dieckmann U. Adaptive dynamics with interaction structure. *American Naturalist*. 2013;181(6):E139–E163.
26. McAvoy A, Hauert C. Structure coefficients and strategy selection in multiplayer games. *Journal of Mathematical Biology*. 2015;p. 1–36.
27. McAvoy A, Hauert C. Structural symmetry in evolutionary games. *Journal of The Royal Society Interface*. 2015;12(111).
28. Griffin AS, West SA, Buckling A. Cooperation and competition in pathogenic bacteria. *Nature*. 2004;430:1024–1027.

29. Xavier JB, Foster KR. Cooperation and conflict in microbial biofilms. *Proceedings of the National Academy of Sciences USA*. 2007;104(3):876–881.
30. Gore J, Youk H, van Oudenaarden A. Snowdrift game dynamics and facultative cheating in yeast. *Nature*. 2009;459:253–256.
31. Li XY, Pietschke C, Fraune S, Altrock PM, Bosch TCG, Traulsen A. Which games are growing bacterial populations playing? *Journal of The Royal Society Interface*. 2015;12(108).
32. Gordon HS. The Economic Theory of a Common-Property Resource: The Fishery. *The Journal of Political Economy*. 1954;62:124–142.
33. Hardin G. The tragedy of the commons. *Science*. 1968;162:1243–1248.
34. Taylor M. *The Possibility of Cooperation*. Cambridge University Press; 1987.
35. Ostrom E. *Governing the commons: The evolution of institutions for collective action*. Cambridge Univ. Press; 1990.
36. Milinski M, Semmann D, Krambeck HJ, Marotzke M. Stabilizing the Earth’s climate is not a losing game: Supporting evidence from public goods experiments. *Proceedings of the National Academy of Sciences USA*. 2006;103:3994–3998.
37. Broom M, Cannings C, Vickers GT. Multi-player matrix games. *Bulletin of Mathematical Biology*. 1997;59(5):931–952.
38. Hauert C, Michor F, Nowak MA, Doebeli M. Synergy and discounting of cooperation in social dilemmas. *Journal of Theoretical Biology*. 2006;239:195–202.
39. Kurokawa S, Ihara Y. Emergence of cooperation in public goods games. *Proceedings of the Royal Society B*. 2009;276:1379–1384.
40. Gokhale CS, Traulsen A. Evolutionary games in the multiverse. *Proceedings of the National Academy of Sciences USA*. 2010;107:5500–5504.
41. Peña J, Lehmann L, Nöldeke G. Gains from switching and evolutionary stability in multi-player matrix games. *Journal of Theoretical Biology*. 2014;346:23–33.
42. Gokhale CS, Traulsen A. Evolutionary multiplayer games. *Dynamic Games and Applications*. 2014;4:468–488.
43. Santos FC, Santos MD, Pacheco JM. Social diversity promotes the emergence of cooperation in public goods games. *Nature*. 2008;454:213–216.
44. Peña J, Rochat Y. Bipartite graphs as models of population structures in evolutionary multiplayer games. *PLoS ONE*. 2012;7(9):e44514.
45. Perc M, Gómez-Gardeñes J, Szolnoki A, Floría LM, Moreno Y. Evolutionary dynamics of group interactions on structured populations: A review. *Journal of The Royal Society Interface*. 2013 Mar;10(80).
46. Wu B, Traulsen A, Gokhale CS. Dynamic properties of evolutionary multi-player games in finite populations. *Games*. 2013;4(2):182–199.

47. Peña J, Wu B, Traulsen A. Ordering structured populations in multiplayer cooperation games. *Journal of the Royal Society Interface*; (13):20150881.
48. Shakarian P, Roos P, Johnson A. A review of evolutionary graph theory with applications to game theory. *Biosystems*. 2012;107:66–80.
49. Hindersin L, Traulsen A. Most undirected random graphs are amplifiers of selection for Birth-death dynamics, but suppressors of selection for death-Birth dynamics. *PLoS Computational Biology*. 2015;11:e1004437.
50. Tarnita CE, Taylor PD. Measures of relative fitness of social behaviors in finite structured population models. *The American Naturalist*. 2014;184(4):477–488.
51. Farouki RT. The Bernstein polynomial basis: A centennial retrospective. *Computer Aided Geometric Design*. 2012;29:379–419.
52. Diekmann A. Volunteer's Dilemma. *Journal of Conflict Resolution*. 1985;29:605–610.
53. Weesie J, Franzen A. Cost sharing in a Volunteer's Dilemma. *Journal of Conflict Resolution*. 1998;42:600–618.
54. Souza MO, Pacheco JM, Santos FC. Evolution of cooperation under N-person snowdrift games. *Journal of Theoretical Biology*. 2009;260:581–588.
55. Pacheco JM, Santos FC, Souza MO, Skyrms B. Evolutionary dynamics of collective action in N-person stag hunt dilemmas. *Proceedings of the Royal Society B*. 2009;276:315–321.
56. Peña J, Nöldeke G, Lehmann L. Evolutionary dynamics of collective action in spatially structured populations. *Journal of Theoretical Biology*. 2015;382:122–136.
57. van Veelen M. The replicator dynamics with n players and population structure. *Journal of Theoretical Biology*. 2011;276:78–85.
58. Archetti M. Cooperation as a volunteer's dilemma and the strategy of conflict in public goods games. *Journal of Evolutionary Biology*. 2009;11:2192–2200.
59. Bach LA, Helvik T, Christiansen FB. The evolution of N-player cooperation - threshold games and ESS bifurcations. *Journal of Theoretical Biology*. 2006 Jul;238:426–434.
60. van Veelen M, Nowak MA. Multi-player games on the cycle. *Journal of Theoretical Biology*. 2012;292:116–128.
61. Ohtsuki H, Pacheco JM, Nowak MA. Evolutionary graph theory: Breaking the symmetry between interaction and replacement. *Journal of Theoretical Biology*. 2007;246:681–694.
62. Van Cleve J. Social evolution and genetic interactions in the short and long term. *Theoretical Population Biology*. 2015;103:2–26.
63. Wakeley J. *Coalescent theory: an introduction*. Roberts and Company Publishers; 2008.
64. Ladret V, Lessard S. Fixation probability for a beneficial allele and a mutant strategy in a linear game under weak selection in a finite island model. *Theoretical Population Biology*. 2007;72(3):409–425.

65. Traulsen A. Mathematics of kin- and group-selection: formally equivalent? *Evolution*. 2010;64:316–323.
66. Wild G, Traulsen A. The different limits of weak selection and the evolutionary dynamics of finite populations. *Journal of Theoretical Biology*. 2007;247:382–390.

Supplementary Methods: Evolution of multiplayer cooperation on graphs

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1 Structure coefficients for the cycle ($k = 2$)

We start by considering the case $k = 2$, i.e., the cycle. Here the state space of the Markov process is captured by the number of the mutants. The Moran process on the cycle is a birth-death process, with a tridiagonal transition matrix as the Moran process in a well-mixed population [1]. Analytical expressions for the fixation probabilities and hence for the structure coefficients can then be obtained exactly.

In the limit of weak selection and for a death-Birth update rule, we obtain the following expression:

$$\frac{\rho_A}{\rho_B} \approx 1 + \frac{w}{2} \{a_0 + (N-2)a_1 + (N-3)a_2 - (N-3)b_0 - (N-2)b_1 - b_2\}.$$

The condition $\rho_A > \rho_B$ is hence given by

$$(a_0 - b_2) + (N-2)(a_1 - b_1) + (N-3)(a_2 - b_0) > 0,$$

from which we identify the structure coefficients:

$$\sigma_0 = 1, \sigma_1 = N-2, \sigma_3 = N-3.$$

As we assume $N > 3$, the structure coefficients are nonnegative. Normalizing the structure coefficients we obtain the values given by Eq. (6) in the main text.

2 Structure coefficients for regular graphs with $k \geq 3$

We obtain the structure coefficients by finding an approximate expression for the comparison of fixation probabilities, $\rho_A > \rho_B$. To estimate these fixation probabilities, we follow closely the procedure used in Ref. [2], based on a combination of pair approximation and diffusion approximation.

2.1 Pair approximation

Let us denote by p_A and p_B the global frequencies of types A and B ; by p_{AA} , p_{AB} , p_{BA} and p_{BB} the frequencies of AA , AB , BA , and BB pairs; and by $q_{X|Y}$ the conditional probability of finding an X -player given that the adjacent node is occupied by a Y -player, where X and Y stand for A or B . The crucial assumption of pair approximation is that higher-order of moments can be simply approximated by moments of pairs. In particular, we assume that the following set of equations:

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

hold, implying that the system can be described by only two variables: p_A and p_{AA} . In the following, we write down the changing rate of p_A and p_{AA} under the assumptions of pair approximation. Then, we assume that selection is weak and that a separation of timescales hold in order to reduce the dimension of the system of equations. Finally, we employ a diffusion approximation to get the equation that governs the fixation probabilities.

2.2 Updating a B -player

A B -player is chosen to die with probability p_B ; its k neighbors compete for the vacant vertex proportionally to their effective payoffs. Denoting by k_A and k_B the number of A and B players among these k neighbors, the frequency of such configuration is given by

$$\binom{k}{k_A} q_{A|B}^{k_A} (1 - q_{A|B})^{k - k_A}.$$

The effective payoff of each A -player connected by an edge to the dead B -player is given by

$$f_A = 1 + w\pi_A^B,$$

where

$$\pi_A^B = \sum_{j=0}^{k-1} \binom{k-1}{j} q_{A|A}^j (1 - q_{A|A})^{k-1-j} a_j$$

is the average payoff to an A -player with one B co-player and $k - 1$ other players, each of which has an independent probability $q_{A|A}$ of playing A .

Likewise, the effective payoff of each B -player connected by an edge to the dead B -player is given by

$$f_B = 1 + w\pi_B^B,$$

where

$$\pi_B^B = \sum_{j=0}^{k-1} \binom{k-1}{j} q_{A|B}^j (1 - q_{A|B})^{k-1-j} b_j$$

is the average payoff to a B -player with one B co-player and $k - 1$ other players, each of which has an independent probability $q_{A|B}$ of playing A .

The probability that one of the A -players replaces the vacant spot left by the dead B -player is given by

$$\frac{k_A f_A}{k_A f_A + k_B f_B} = \frac{k_A}{k} + w \frac{k_A(k - k_A)}{k^2} \mathcal{S}_B + \mathcal{O}(w^2),$$

where

$$\mathcal{S}_B = \pi_A^B - \pi_B^B.$$

Hence, the frequency p_A of A -players in the population increases by $1/N$ with probability

$$\begin{aligned} \Pr\left(\Delta p_A = \frac{1}{N}\right) &= p_B \sum_{k_A=0}^k \binom{k}{k_A} q_{A|B}^{k_A} (1 - q_{A|B})^{k - k_A} \frac{k_A f_A}{k_A f_A + k_B f_B} \\ &= p_B \left\{ q_{A|B} + w \frac{k-1}{k} q_{A|B} (1 - q_{A|B}) \mathcal{S}_B + \mathcal{O}(w^2) \right\} \\ &= p_{AB} \left\{ 1 + w \frac{k-1}{k} q_{B|B} \mathcal{S}_B + \mathcal{O}(w^2) \right\}. \end{aligned} \quad (1)$$

2.3 Updating an A -player

An A -player is chosen to die with probability p_A . There are k_A A -players and k_B B -players in the neighborhood of the vacant node. The frequency of this configuration is

$$\binom{k}{k_A} q_{A|A}^{k_A} (1 - q_{A|A})^{k - k_A}.$$

The effective payoff of each neighboring A -player is

$$g_A = 1 + w\pi_A^A,$$

where

$$\pi_A^A = \sum_{j=0}^{k-1} \binom{k-1}{j} q_{A|A}^j (1 - q_{A|A})^{k-1-j} a_{j+1}$$

is the average payoff to an A -player with one A co-player and $k - 1$ other players, each of which has an independent probability $q_{A|A}$ of playing A .

Likewise, the effective payoff to each neighboring B -player is given by

$$g_B = 1 + w\pi_B^A,$$

where

$$\pi_B^A = \sum_{j=0}^{k-1} \binom{k-1}{j} q_{A|B}^j (1 - q_{A|B})^{k-1-j} b_{j+1}$$

is the average payoff to a B -player with one A co-player and $k - 1$ other players, each of which has an independent probability $q_{A|B}$ of playing A .

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

$$\frac{k_B g_B}{k_A g_A + k_B g_B} = \frac{k_B}{k} + w \frac{k_B (k - k_B)}{k^2} \mathcal{S}_A + \mathcal{O}(w^2),$$

where

$$\mathcal{S}_A = \pi_B^A - \pi_A^A.$$

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

$$\begin{aligned} \Pr\left(\Delta p_A = -\frac{1}{N}\right) &= p_A \sum_{k_B=0}^k \binom{k}{k_B} q_{A|A}^{k-k_A} (1 - q_{A|A})^{k_B} \frac{k_B g_B}{k_A g_A + k_B g_B} \\ &= p_A \left\{ q_{B|A} + w \frac{k-1}{k} q_{A|A} (1 - q_{A|A}) \mathcal{S}_A + \mathcal{O}(w^2) \right\} \\ &= p_{BA} \left\{ 1 + w \frac{k-1}{k} q_{A|A} \mathcal{S}_A + \mathcal{O}(w^2) \right\}. \end{aligned} \quad (2)$$

2.4 Separation of time-scales

Let us now suppose that one replacement event takes place in one unit of time, so that the time derivative of p_A is given by

$$\dot{p}_A = \frac{1}{N} \Pr\left(\Delta p_A = \frac{1}{N}\right) - \frac{1}{N} \Pr\left(\Delta p_A = -\frac{1}{N}\right).$$

Using Eq. (1) and (2) we obtain, to first order in w :

$$\begin{aligned} \dot{p}_A &= \frac{1}{N} p_{AB} \left\{ 1 + w \frac{k-1}{k} q_{B|B} \mathcal{S}_B \right\} - \frac{1}{N} p_{BA} \left\{ 1 + w \frac{k-1}{k} q_{A|A} \mathcal{S}_A \right\} \\ &= \frac{w p_{AB}}{N} \frac{k-1}{k} \mathcal{S}(p_A) \end{aligned} \quad (3)$$

where

$$\mathcal{S}(p_A) = q_{B|B} \mathcal{S}_B + q_{A|A} \mathcal{S}_A.$$

The time derivative of p_{AA} is given by (cf. Eq. (12) of the Supplementary Material of Ref. [2])

$$\dot{p}_{AA} = \frac{2}{kN} p_{AB} [1 + (k-1)(q_{A|B} - q_{A|A})] + \mathcal{O}(w).$$

For weak selection ($w \ll 1$) the local density of players, p_{AA} , equilibrates much more quickly than the global density, p_A . Therefore, the dynamical system rapidly converges onto the slow manifold. Setting $\dot{p}_{AA} = 0$ and defining

$$r = \frac{1}{k-1},$$

we obtain

$$\begin{aligned} q_{A|A} - q_{A|B} &= r, \\ q_{B|B} - q_{B|A} &= r, \end{aligned}$$

and hence

$$\begin{aligned} q_{A|A} &= p_A + r(1 - p_A) = r + (1 - r)p_A, \\ q_{A|B} &= (1 - r)p_A, \\ q_{B|A} &= (1 - r)(1 - p_A), \\ q_{B|B} &= r p_A + (1 - p_A) = r + (1 - r)(1 - p_A). \end{aligned}$$

2.5 Polynomials in Bernstein form

From Eq. (3), \dot{p}_A is proportional to

$$\begin{aligned} \mathcal{S}(p_A) &= q_{B|B} \mathcal{S}_B(p_A) + q_{A|A} \mathcal{S}_A(p_A) \\ &= [r p_A + (1 - p_A)] \mathcal{S}_B(p_A) + [p_A + r(1 - p_A)] \mathcal{S}_A(p_A), \end{aligned} \quad (4)$$

which is a polynomial of degree k in p_A . We find it convenient to write such polynomial in Bernstein form [3].

To do so, we make use of the following identities:

$$\begin{aligned} \sum_{j=0}^m \binom{m}{j} [r + (1-r)x]^j [(1-r)(1-x)]^{m-j} c_j &= \sum_{j=0}^m \binom{m}{j} x^j (1-x)^{m-j} \sum_{\ell=0}^{m-j} \binom{m-j}{\ell} r^\ell (1-r)^{m-j-\ell} c_{j+\ell} \\ \sum_{j=0}^m \binom{m}{j} [(1-r)x]^j [1 - (1-r)x]^{m-j} c_j &= \sum_{j=0}^m \binom{m}{j} x^j (1-x)^{m-j} \sum_{\ell=0}^j \binom{j}{\ell} r^\ell (1-r)^{j-\ell} c_{j-\ell} \\ x \sum_{j=0}^{m-1} \binom{m-1}{j} x^j (1-x)^{m-1-j} c_j &= \sum_{j=0}^m \binom{m}{j} x^j (1-x)^{m-j} \frac{j c_{j-1}}{m}, \\ (1-x) \sum_{j=0}^{m-1} \binom{m-1}{j} x^j (1-x)^{m-1-j} c_j &= \sum_{k=0}^m \binom{m}{j} x^j (1-x)^{m-j} \frac{(m-j) c_j}{m}. \end{aligned}$$

where $c_{k-1} = c_{k+1} = 0$.

Applying these to (4) and simplifying, we obtain

$$\mathcal{S}(p_A) = \sum_{j=0}^k \binom{k}{j} p_A^j (1-p_A)^{k-j} e_j,$$

where

$$e_j = \frac{rj c_{j-1} + (k-j) c_j + j d_{j-1} + r(k-j) d_j}{k}, \quad (5)$$

and

$$c_j = \sum_{\ell \geq 0} \binom{k-1-j}{\ell} r^\ell (1-r)^{k-1-j-\ell} a_{j+\ell} - \sum_{\ell \geq 0} \binom{j}{\ell} r^\ell (1-r)^{j-\ell} b_{j-\ell}, \quad (6)$$

$$d_j = \sum_{\ell \geq 0} \binom{k-1-j}{\ell} r^\ell (1-r)^{k-1-j-\ell} a_{j+1+\ell} - \sum_{\ell \geq 0} \binom{j}{\ell} r^\ell (1-r)^{j-\ell} b_{j+1-\ell}. \quad (7)$$

2.6 Diffusion approximation

Within a short interval, Δt , we have (cf. Eq. (18) in the Supplementary Material of Ref. [2])

$$\begin{aligned} \mathbb{E}[\Delta p_A] &\approx \frac{w p_{AB}}{N} \frac{k-1}{k} \mathcal{S}(p_A) \Delta t \equiv m(p_A) \Delta t \\ \text{Var}[\Delta p_A] &\approx \frac{2}{N^2} p_{AB} \Delta t \equiv v(p_A) \Delta t. \end{aligned}$$

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

$$m(y) \frac{d\rho_A(y)}{dy} + \frac{v(y)}{2} \frac{d^2 \rho_A(y)}{dy^2} = 0,$$

with boundary conditions $\rho_A(0) = 0$ and $\rho_A(1) = 1$.

We thus have

$$\rho_A(y) = \frac{\int_0^y Q(x)dx}{\int_0^1 Q(x)dx}, \quad (8)$$

where

$$Q(x) = \exp\left(-\int^x 2\frac{m(z)}{v(z)}dz\right) = \exp\left(-\frac{Nw(k-1)}{k}\int^x \mathcal{S}(z)dz\right),$$

which involves the indefinite integral of $\mathcal{S}(z)$. To evaluate this, we make use of the formula for the indefinite integral of a polynomial in Bernstein form (cf. p. 391 of Ref. [3]), according to which

$$\int^x \mathcal{S}(z)dz = \sum_{\ell=0}^{k+1} \binom{k+1}{\ell} x^\ell (1-x)^{k+1-\ell} \left(\frac{1}{k+1} \sum_{k=0}^{\ell-1} e_k\right) + \text{constant}.$$

Taylor expanding Eq. (8) and assuming that $w \ll 1$, we obtain

$$\rho_A(y) \approx y + \frac{wN(k-1)}{k} \left(y \int_0^1 \int_0^x \mathcal{S}(z)dzdx - \int_0^y \int_0^x \mathcal{S}(z)dzdx\right). \quad (9)$$

where

$$\begin{aligned} \int_0^1 \int_0^x \mathcal{S}(z)dzdx &= \frac{1}{(k+2)(k+1)} \sum_{\ell=0}^{k+1} \sum_{j=0}^{\ell-1} e_j, \\ \int_0^y \int_0^x \mathcal{S}(z)dzdx &= \frac{1}{(k+1)(k+2)} \sum_{s=0}^{k+2} \binom{k+2}{s} y^s (1-y)^{k+2-s} \left(\sum_{q=0}^{s-1} \sum_{j=0}^{q-1} e_j\right), \end{aligned} \quad (10)$$

are obtained by making use of the formula for the definite integral of a polynomial in Bernstein form (cf. p. 391 of Ref. [3]).

If the initial value $y = 1/N$, i.e., there is only one A -type mutant, and population size N is large, Eq. (10) can be approximated by

$$\frac{e_0}{2N^2}.$$

The fixation probability, Eq. (9), can then be written as

$$\begin{aligned}
 \rho_A &\approx \frac{1}{N} + \frac{wN(k-1)}{k} \left(\frac{1}{N} \frac{1}{(k+2)(k+1)} \sum_{\ell=0}^{k+1} \sum_{j=0}^{\ell-1} e_j - \frac{e_0}{2N^2} \right) \\
 &= \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \left(\sum_{\ell=0}^{k+1} \sum_{j=0}^{\ell-1} e_j - (k+2)(k+1) \frac{e_0}{2N} \right) \\
 &= \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \left(\sum_{\ell=0}^k \sum_{j=0}^{\ell} e_j - (k+2)(k+1) \frac{e_0}{2N} \right) \\
 &= \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \left(\sum_{j=0}^k (k+1-j)e_j - (k+2)(k+1) \frac{e_0}{2N} \right) \\
 &= \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \left(\sum_{j=1}^k (k+1-j)e_j + (k+1)e_0 \left(1 - \frac{k+2}{2N} \right) \right).
 \end{aligned}$$

If $k \ll N$, then $(k+2)/(2N) \ll 1$ and we finally obtain

$$\rho_A \approx \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \sum_{j=0}^k (k+1-j)e_j. \quad (11)$$

2.7 Sigma rule and structure coefficients

By Eq. (11), the fixation probability of a mutant A is greater than neutral if $\sum_{j=0}^k (k+1-j)e_j > 0$. In the following, we simplify $\sum_{j=0}^k (k+1-j)e_j$. By Eq. (5), the coefficients e_j are linear in c_j and d_j . Furthermore, c_j and d_j are linear in the payoff entries a_j and b_j (cf. Eq. (6) and (7)). Thus $\sum_{j=0}^k (k+1-j)e_j$ is also linear in the payoff entries, meaning that there exist α_j and β_j such that

$$\sum_{j=0}^k (k+1-j)e_j = \sum_{j=0}^k (\alpha_j a_j + \beta_j b_j),$$

and so

$$\rho_A \approx \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \sum_{j=0}^k (\alpha_j a_j + \beta_j b_j).$$

We need to calculate is α_j and β_j . In particular, for a multiplayer game with only $a_i = 1$ and all the other entries being zero, we have

$$\sum_{j=0}^k (k+1-j)e_j^i = \alpha_i.$$

Such condition can be written as

$$\begin{aligned}
 \sum_{j=0}^k (k+1-j)e_j^i &= \frac{r}{k} \sum_{j=0}^k (k+1-j)j c_{j-1}^i + \frac{1}{k} \sum_{j=0}^k (k+1-j)(k-j)c_j^i \\
 &+ \frac{1}{k} \sum_{j=0}^k (k+1-j)j d_{j-1}^i + \frac{r}{k} \sum_{j=0}^k (k+1-j)(k-j)d_j^i \\
 &= \frac{r}{k} \sum_{j=0}^k (k-j)(j+1)c_j^i + \frac{1}{k} \sum_{j=0}^k (k+1-j)(k-j)c_j^i \\
 &+ \frac{1}{k} \sum_{j=0}^k (k-j)(j+1)d_j^i + \frac{r}{k} \sum_{j=0}^k (k+1-j)(k-j)d_j^i \\
 &= \frac{1}{k} \sum_{j=0}^{k-1} (k-j) [r(j+1) + (k+1-j)] c_j^i \\
 &+ \frac{1}{k} \sum_{j=0}^{k-1} (k-j) [(j+1) + r(k+1-j)] d_j^i.
 \end{aligned}$$

Since $a_j = \delta_{i,j}$ and $b_j = 0$ for all j ranging from 0 to k , and by Eq. (6) and (7), we have

$$c_j^i = \begin{cases} \binom{k-1-j}{i-j} r^{i-j} (1-r)^{k-i-1} & : j \leq i \\ 0 & : j > i \end{cases}, \quad d_j^i = \begin{cases} \binom{k-1-j}{i-j-1} r^{i-j-1} (1-r)^{k-i} & : j \leq i-1 \\ 0 & : j > i-1 \end{cases}$$

and $d_j^0 = 0$ for every $0 \leq j \leq k-1$. Hence

$$\begin{aligned}
 \alpha_i &= \sum_{j=0}^k (k+1-j)e_j^i \\
 &= \frac{1}{k} \sum_{j=0}^k (k-j) [r(j+1) + (k+1-j)] \binom{k-1-j}{i-j} r^{i-j} (1-r)^{k-1-i} \\
 &+ \frac{1}{k} \sum_{j=0}^k (k-j) [(j+1) + r(k+1-j)] \binom{k-1-j}{i-j-1} r^{i-j-1} (1-r)^{k-i}.
 \end{aligned}$$

Similarly, letting the payoff entries be $b_j = \delta_{j,i}$ and $a_j = 0$ leads to

$$\begin{aligned}
 \beta_i &= -\frac{1}{k} \sum_{j=0}^k (k-j) [r(j+1) + (k+1-j)] \binom{j}{j-i} r^{j-i} (1-r)^i \\
 &- \frac{1}{k} \sum_{j=0}^k (k-j) [(j+1) + r(k+1-j)] \binom{j}{j-i+1} r^{j-i+1} (1-r)^{i-1}.
 \end{aligned}$$

By symmetry, the fixation probability of a single B mutant is given by

$$\rho_B \approx \frac{1}{N} + \frac{w(k-1)}{(k+2)(k+1)k} \sum_{k=0}^k (\alpha_j b_{k-j} + \beta_j a_{k-j}).$$

Therefore, $\rho_A > \rho_B$ is equivalent to

$$\sum_{j=0}^k (\alpha_j a_j + \beta_j b_j) > \sum_{j=0}^k (\alpha_j b_{k-j} + \beta_j a_{k-j})$$

or

$$\sum_{j=0}^k \sigma_j (a_j - b_{k-j}) > 0.$$

where

$$\sigma_j = \alpha_j - \beta_{k-j}.$$

Collecting terms, we finally obtain

$$\sigma_j = \frac{(k-2)^{k-1-j}}{k(k-1)} \sum_{\ell=0}^{k-1} (k-\ell) \{ [k^2 - \ell(k-2)] v_{\ell,j,k} + [2k + \ell(k-2)] \tau_{\ell,j,k} \},$$

where

$$\begin{aligned} \tau_{\ell,j,k} &= \binom{k-1-\ell}{k-j} \frac{k-2}{(k-1)^{k-1-\ell}} + \binom{\ell}{k-1-j} \frac{1}{(k-1)^\ell}, \\ v_{\ell,j,k} &= \binom{k-1-\ell}{k-1-j} \frac{1}{(k-1)^{k-1-\ell}} + \binom{\ell}{k-j} \frac{k-2}{(k-1)^\ell}. \end{aligned}$$

3 Sum of structure coefficients

The leading order of the fixation probability difference under weak selection can be written as

$$\rho_A - \rho_B \approx w \frac{(k-1)}{(k+2)(k+1)k} \sum_{j=0}^k \sigma_j (a_j - b_{k-j}). \quad (12)$$

In particular, this is true for a game with $a_j = 1$ and $b_j = 0$ for all j . The leading order of the fixation probability difference of this multiplayer game is

$$\rho_A - \rho_B \approx w \frac{(k-1)}{(k+2)(k+1)k} \sum_{j=0}^k \sigma_j. \quad (13)$$

The fixation probability of strategy A is identical to that of the pairwise game

$$\begin{array}{cc} & \begin{array}{c} A \quad B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} \frac{1}{k} & \frac{1}{k} \\ 0 & 0 \end{pmatrix}, \end{array} \quad (14)$$

since the accumulated payoff of strategy A is always 1 and that of strategy B is always 0. The same applies to the fixation probability of strategy B . This is exactly the multiplayer game defined above. For this pairwise game, we have that (see Eqs. (19) and (21) in the Supplementary Material of Ref. [2])

$$\rho_A \approx \frac{1}{N} + \frac{w}{6k} [(k^2 + 2k + 1)a + (2k^2 - 2k - 1)b - (k^2 - k + 1)c - (2k^2 + k - 1)d].$$

By symmetry:

$$\rho_A \approx \frac{1}{N} + \frac{w}{6k} [(k^2 + 2k + 1)d + (2k^2 - 2k - 1)c - (k^2 - k + 1)b - (2k^2 + k - 1)a].$$

Therefore, for the pairwise game described in Eq. (14), we have that

$$\rho_A - \rho_B \approx w. \quad (15)$$

Comparing Eqs. (13) and (15), and by the uniqueness of the Taylor expansion, we conclude that

$$\sum_{j=0}^k \sigma_j = \frac{k(k+1)(k+2)}{k-1}. \quad (16)$$

4 A useful identity

If individuals play the pairwise game

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} \end{array}$$

with each neighbor, then the payoffs for the corresponding multiplayer game in a graph are given by $a_j = j$ and $b_j = 0$. If we consider the difference in fixation probabilities resulting from the pairwise game, and by Eq. (21) in the Supplementary Material of Ref. [2], we have

$$\rho_A - \rho_B \approx w \frac{k+1}{2}. \quad (17)$$

Now consider the difference in fixation probabilities arising from the equivalent multiplayer version. Replacing the payoffs $a_j = j$ and $b_j = 0$ into Eq. (12) leads to

$$\rho_A - \rho_B \approx w \frac{(k-1)}{(k+2)(k+1)k} \sum_{i=0}^k \sigma_j j. \quad (18)$$

Since, by virtue of Eq. (16), the normalized structured coefficients satisfy

$$\varsigma_i = \frac{\sigma_i}{\sum_j \sigma_j} = \frac{k-1}{(k+2)(k+1)k} \sigma_i,$$

Eq. (18) becomes

$$\rho_A - \rho_B \approx w \sum_{i=0}^k \varsigma_j j. \quad (19)$$

Comparing Eq. (17) and (19), we hence obtain

$$\sum_{j=0}^k \varsigma_j j = \frac{k+1}{2}.$$

References

1. Karlin S, Taylor HMA. A First Course in Stochastic Processes. 2nd ed. London: Academic; 1975.
2. Ohtsuki H, Hauert C, Lieberman E, Nowak MA. A simple rule for the evolution of cooperation on graphs. *Nature*. 2006;441:502–505.
3. Farouki RT. The Bernstein polynomial basis: A centennial retrospective. *Computer Aided Geometric Design*. 2012;29:379–419.