Evolution of Cooperation in a Heterogeneous Graph: Fixation Probabilities under Weak Selection

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Abstract

It has been shown that natural selection favors cooperation in a homogenous graph if the benefit-to-cost ratio exceeds the degree of the graph. However, most graphs related to interactions in real populations are heterogeneous, in which some individuals have many more neighbors than others. In this paper, we introduce a new state variable to measure the time evolution of cooperation in a heterogeneous graph. Based on the diffusion approximation, we find that the fixation probability of a single cooperator depends crucially on the number of its neighbors. Under weak selection, a cooperator with more neighbors has a larger probability of fixation in the population. We then investigate the average fixation probability of a randomly chosen cooperator. If a cooperator pays a cost for each of its neighbors (the so called fixed cost per game case), natural selection favors cooperation if the benefit-to-cost ratio is larger than the average degree. In contrast, if a cooperator pays a fixed cost and all its neighbors share the benefit (the fixed cost per individual case), cooperation is favored if the benefit-to-cost ratio is larger than the harmonic mean of the degree distribution. Moreover, increasing the graph heterogeneity will reduce the effect of natural selection.

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Introduction

Evolution of cooperation is one of the most important theoretical questions in evolutionary biology and social biology [1–4]. In the framework of evolutionary game theory, cooperation has been studied in a variety of game theoretical models such as the Prisoner’s Dilemma [1–3]. It is well known that in unstructured populations, natural selection favors defectors over cooperators [2–3]. This means that in a population where all individuals have the same chance to interact with each other, defectors will have a higher average payoff than cooperators (i.e. natural selection will increase the relative abundance of defectors and drive cooperators to extinction). However, in more realistic populations, different individuals interact with different subsets of the whole population. This kind of structure can be described by means of complex networks (or graphs), in which players of an evolutionary game occupy the vertices of a network, and the edges denote the links between individuals in terms of game dynamical interaction.

A great deal of research has been devoted to explain the influence of network structure on the evolution of cooperation. Pioneering work by Nowak and May [5] unveiled that a spatial lattice where each player interacts only with his/her four (or eight) immediate neighbors is a viable mechanism for the emergence of cooperation. The success of their model has attracted considerable attention, subsequent studies including not only theoretical investigations [6–14] but also economic experiments [15–17]. In these studies, the spatial structure retains homogeneity (or regularity) since every individual is topologically identical to any other individual in the population. However, empirical evidence shows that most networks related to interactions in the real world are heterogeneous in that some individuals have many more neighbors (i.e. have higher degree) than others [18–23]. Representative networks include the random network [24–25], Small-World network [26–27] and scale-free network [28–29]. Many recent researches have revealed that graph heterogeneity dramatically enhances cooperation in complex networks [30–36], in particular for the scale-free network [37–42]. Although there are many differences in the models considered in this literature (e.g. different update rules, payoff structure, network clustering, etc.), one of the main reasons behind the increase of cooperation levels in the scale-free network is that hubs are usually occupied by cooperators, which ensures their long term success in the evolutionary process. The same occurs when the network structure is coevolving together with the strategy dynamics [43–48]. If neighboring pairs of cooperators are more stable than pairs that include at least one defector, cooperators are more likely to have higher degree, which gives rise to highly cooperative heterogeneous networks.

Recently, Ohtsuki et al. [49] extended the approach of Nowak and May [3] and developed a theoretical model based on the simplified Prisoner’s Dilemma (PD) game to investigate the evolution of altruistic cooperation on a graph (or a social network) where a donor pays a cost, c, for the recipient to get a benefit, b. They alleged that natural selection favors the emergence of cooperation if the benefit of the altruistic act, b, divided by the cost, c, exceeds the average degree of the graph, k, i.e. $b/c > k$. 
They considered a population of $N$ individuals consisting of cooperators and defectors (where the population size $N$ is fixed), and assumed that: (i) a cooperator helps all individuals to whom it is connected, i.e. if a cooperator is connected to $k$ other individuals and $i$ of those are cooperators, then its payoff is $b(i,k)-c(k)$; (ii) a defector does not provide any help, but it can receive the benefit from neighboring cooperators, i.e. if a defector is connected to $j$ cooperators, then its payoff is $b(j)$; (iii) the fitness of an individual is given by its baseline fitness plus the payoff, where strong (weak) selection means that the payoff is large (small) compared to the baseline fitness; and (iv) for the evolutionary dynamics, in each time step, a random individual is chosen to die, and the neighbors compete for the empty site proportional to their fitness (this process is called ‘death-birth’ updating). Ohtsuki et al.’s theoretical results show that if all individuals have the same number of neighbors, denoted by $k$, then the fixation probability of a single cooperator exactly equals $1/N$ if there is no selection, and, under weak selection, it is larger than $1/N$ if $b/c > k$.

However, Ohtsuki et al.’s theoretical analysis [49] is based only on a regular graph where all vertices have the same degree. Numerical simulations in their paper show that the fixation probabilities of cooperators in heterogeneous graphs deviate from the theoretical prediction. Thus, a more challenging question is to derive the relation between the fixation probability and the graph heterogeneity. In general, the heterogeneity of a graph (or a social network) can be described by the mean and variance of its degree distribution [34,50]. The degree distribution of a graph, denoted by $p(k)$, gives the frequency of vertices with degree $k$ for $k=1,2,\cdots$, or, alternatively, $p(k)$ is the probability that a randomly chosen individual has exactly $k$ neighbors.

In this paper, we develop and analyze the connection between $p(k)$ and the fixation probabilities of cooperators when selection is weak that provides a new theoretical explanation for the effect of graph heterogeneity on the evolution of cooperation.

### Methods

Consider a connected graph with $N$ vertices and with degree distribution $p(k)$. Similar to Ohtsuki et al. [49], the individual at each vertex is either a cooperator in interactions with all of the neighbors or a defector. We label these $N$ vertices as vertex 1, vertex 2, $\cdots$, vertex $N$, respectively, and the degree of vertex $i$ is denoted by $k_i$ for $i=1,2,\cdots,N$. For an individual at vertex $i$, its degree $k_i$ can be also expressed as $k_i=k_{i,C}+k_{i,D}$ where $k_{i,C}$ is the number of its neighbors with strategy $C$ (cooperation) and, similarly, $k_{i,D}$ the number of its neighbors with strategy $D$ (defection) (see Figure 1). The average degree of the graph, denoted by $\langle k \rangle$, is given by $\langle k \rangle = \sum_{i=1}^{N} k_i/N$, or $\langle k \rangle = \sum_{k} kp(k)$. On the other hand, the strategy of the individual at vertex $i$ is denoted by $s_i$ with $s_i \in \{C,D\}$ for $i=1,2,\cdots,N$, i.e. if this individual is a cooperator (or a defector), then $s_i=C$ (or $s_i=D$).

In our model, if there exists an edge between two vertices $i$ and $j$ for $1\leq i\leq j \leq N$, then we use $(i,j)$ to denote a directed edge from vertex $i$ to vertex $j$. For the interaction between two individuals at vertices $i$ and $j$, we consider the two directed edges $(i,j)$ and $(j,i)$ equivalent. Notice that the total number of the directed edges in the graph is $2N$. Thus, the proportion of the directed edges starting from the cooperators in the total directed edges, denoted by $\phi_C$, can be given by $\phi_C = \sum_{k_i} k_i/2N$, i.e. $\phi_C$ denotes a ratio of the total number of cooperators to the total number of directed edges. Similarly, the proportion of directed edges starting from the defectors, denoted by $\phi_D$, is $\phi_D = \sum_{k_i} k_i/2N = 1-\phi_C$. It is easy to see that if $k_i=k$ for all $i=1,2,\cdots,N$ (i.e. all vertices have the same degree), then $\phi_C$ exactly represents the proportion of cooperators in the population (i.e. the frequency of strategy $C$ in the population). For a general heterogeneous graph, we will use the time evolution of $\phi_C$ to measure the evolution of cooperation.

We also assume that an individual is randomly chosen to die, and its neighbors compete for the empty site proportional to their fitness, i.e. the ‘death-birth’ updating process [49,51–52]. For a randomly chosen defector, let $f_C$ denote the fitness of its $C$-neighbors and $f_D$ the fitness of its $D$-neighbors. These are given by $f_C=(1-\omega)+\omega h_C$ and $f_D=(1-\omega)+\omega h_D$, respectively, where the parameter $\omega$ measures the intensity of selection with $0 \leq \omega \leq 1$ [49,51–52], and $h_C$ ($h_D$) is the expected payoff of its $C$-neighbors ($D$-neighbors). Similarly, for a randomly chosen cooperator, let $g_C$ denote the fitness of its $C$-neighbors and $g_D$ the fitness of its $D$-neighbors, which are $g_C=(1-\omega)+\omega l_C$ and $g_D=(1-\omega)+\omega l_D$, respectively, where $l_C$ ($l_D$) is the expected payoff of its $C$-neighbors ($D$-neighbors).

For the expected payoffs of both $C$- and $D$-individuals, two cases are considered in our model, called the fixed cost per game and the fixed cost per individual, respectively [33]. For the fixed cost per game, a cooperator pays a cost $c$ for each of its neighbors to get a benefit $b$ [49]; and for the fixed cost per individual, a cooperator with $k$ neighbors pays a cost $c/k$ for each of its neighbors to get a benefit $b/k$, i.e. a cooperator will provide a combined fixed cost $b$ to all its neighbors and pay a fixed cost $c$ equally shared by all its neighbors [33]. Notice also that the conditional probability that a neighbor of a $Y$-individual is a $X$-individual is given by $q_{X|Y}=\sum_{s_i=Y} k_i/\sum_{s_i=Y} k_i$ for $X,Y\in\{C,D\}$. Thus, for a randomly chosen $D$-individual with degree $k$, the expected payoffs of its $C$- and $D$-neighbors are $h_C=(1-\omega)+\omega q_Ch_Cb$ and $h_D=(1-\omega)+\omega q_Dh_Db$, respectively, in the case of fixed cost per game. In the case of fixed cost per individual, these expected payoffs are $h_C=(1-\omega)+\omega q_Cvh_Cb$ and $h_D=(1-\omega)+\omega q_Dvh_Db$, respectively, where $vb=\sum_{k} (b/k)p(k)$ is the expected benefit from a $C$-neighbor (see Supporting Information S1).

Similarly, for a randomly chosen $C$-individual with degree $k$, the expected payoffs of its $C$- and $D$-neighbors are $l_C=(1-\omega)+\omega q_Clh_Cb+b$ and $l_D=(1-\omega)+\omega q_Dlh_Db+b$, respectively, in the case of fixed cost per game, and $l_C=(1-\omega)+\omega q_Cvl_Cb+b/k$ and $l_D=(1-\omega)+\omega q_Dvl_Db+b/k$, respectively, in the case of fixed cost per individual (see Supporting Information S1).

If a defector with degree $k$ is randomly chosen to die, then the probability that this individual has exactly $k_C$ neighbors with strategy $C$ and $k_D$ neighbors with strategy $D$ is $\phi_C^k(1-\phi_C)^{k-D}$. Thus, the probability that the change of $\phi_C$ equals exactly $\Delta \phi_C = k/N$ in one time step is

**Figure 1.** The vertices and degrees in a heterogeneous graph. The $N$ vertices are labeled vertex 1, vertex 2, $\cdots$, vertex $N$. The degree of vertex $i$ is $k_i$, and $k_i=k_{i,C}+k_{i,D}$ where $k_{i,C}$ is the number of $C$-neighbors and $k_{i,D}$ the number of $D$-neighbors.

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Figure 2. Effect of an individual’s degree on the fixation probability under neutral selection. The scale-free network (generated according to (28)) and the random graph (generated according to (62)) are used to test the effect of graph heterogeneity on neutral selection (ω = 0). For each of these two graphs, the total population size is \( N = 1000 \) and the fixation probability of a single cooperator is measured using the fraction of runs where cooperators reached fixation out of \( 3 \times 10^6 \) runs (based on \( 10^3 \) graphs and \( 3 \times 10^4 \) runs per graph). The simulation results are plotted in Figure 2A for the scale-free network and in Figure 2B for the random graph. For both Figures 2A and 2B, the \( x \)-axis denotes the number of a single cooperator’s neighbors and the \( y \)-axis the fixation probability of cooperation. In each of Figures 2A and 2B, the three solid lines represent the theoretical predictions of fixation probabilities for three average degrees, where \( z = 4, 6, 8 \) in Figure 2A and \( z = 10, 20, 30 \) in Figure 2B, and diamonds, squares and triangles denote the simulation results. It is clear that the simulation results match the theoretical prediction well.

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We next derive the time evolution of \( \varphi_C \) under weak selection. Weak selection means that the payoff from the game represents only a small contribution to fitness [2]. In a heterogeneous graph, this requires that the payoff for the player with highest degree is small compared to the baseline fitness, i.e., \( \omega k_\text{max} \ll 1 \), where \( k_\text{max} = \max \{ k_i | i = 1, \ldots, N \} \). In the limit of weak selection, the expected change of \( \varphi_C \), denoted by \( \Delta \varphi_C \), in the time interval \( (t, t+\Delta t) \) is approximated by \( \varphi_C(1-\varphi_C) N/2 \) for the fixed cost per game and \( \varphi_C(1-\varphi_C)(vb-c)/N(z-1) \) for the fixed cost per individual (this follows from Eq. 1 in Supporting Information S1). For both cases, the variance of \( \varphi_C \) is \( \text{Var}[\varphi_C] = 2E[k^2](z-2)\varphi_C(1-\varphi_C)/N^2 z^2(z-1) \) (see also Supporting Information S1). So, from the theory of diffusion approximation [33], if the initial value of \( \varphi_C \) is \( s \) (with \( 0 < s \ll 1 \)), then the fixation probability of cooperation, denoted by \( \rho(s) \), is

\[
\rho(s) = s + \frac{1}{1 + \gamma_d} \omega N \frac{1}{2} \omega N (b - c) s (1 - s)
\]

for the case of fixed cost per game, and, similarly,

\[
\rho(s) = s + \frac{1}{1 + \gamma_d} \omega N \frac{1}{2} \omega N (b - c) s (1 - s)
\]

for the case of fixed cost per individual (the mathematical proofs of these two equations are shown in Supporting Information S1). In both Eq. (3) and Eq. (4), \( \gamma_d \) is the square of the relative deviation of the degree distribution (i.e. \( \gamma_d = \text{Var}[k]/z^2 \)) where \( \text{Var}[k] = E[k^2] - N^{-1} \). This provides a measure of heterogeneity for the graph.

Results

It is easy to see that for both Eq. (3) and Eq. (4), if \( \omega = 0 \), then \( \rho(s) = s \). That is, under neutral selection, the fixation probability of a single cooperator with degree \( k \) exactly equals \( k/N \). To test the effect of graph heterogeneity on neutral selection, two graphs are considered in Figure 2; namely, the scale-free network and the random graph. The simulation results match the theoretical prediction well: if there is no selection, then the fixation probability of a single cooperator is uniquely determined by the number of its neighbors. In a heterogeneous graph, if there is no selection, then the fixation probability of a single cooperator with degree \( k \) is larger (less) than \( 1/N \) if \( k > z \) (\( k < z \)). This implies that the condition that the fixation probability of a randomly chosen cooperator is larger (or less) than \( 1/N \) cannot be used as a criterion to estimate whether cooperation will be favored by natural selection in a general heterogeneous graph, the degree of the cooperator must also be considered. This is different from the situation for a homogeneous graph [49].

When there is weak selection (i.e. \( \omega > 0 \) but \( \omega k_\text{max} \ll 1 \)), the term \( \omega N (b - c) s (1 - s) / (2 + \gamma_d) \) in Eq. (3) denotes the effect of natural selection on cooperation for the case of fixed cost per game. In particular, cooperation will be favored by natural selection (i.e.
should also hold in general: the fixation probability of a single cooperator is larger than $1/N$ if $b/c$ is larger than the average degree of the graph. Later, Tomohiko [54] provided a more accurate approximation based on the average degree of the nearest neighbors. In this paper, we find that the fixation probability of a cooperator depends crucially on its degree. In our theoretical framework, a new state variable $\theta_C$ is used to measure the time evolution of cooperation in a heterogeneous graph, which is the proportion of the total degree of cooperators in the total directed edges, instead of the frequency of cooperators in the population.

If all individuals have the same number of neighbors, then $\theta_C$ equals the frequency of cooperators and so Ohtsuki et al.'s method is a special case of our model. On the other hand, for the expected payoff of an individual, two cases are considered, called the fixed cost per game and the fixed cost per individual, respectively. In the case of fixed cost per game, a cooperator pays a cost for each of its neighbors to get a benefit; and in the case of fixed cost per individual, a cooperator pays a cost if any of its neighbors to get a benefit $b/k$, i.e. a cooperator will provide a fixed benefit $b$ to its all neighbors and pay a fixed cost $c$ equally shared by its all neighbors. For the evolution of cooperation in a heterogeneous graph, our main results show that (i) under neutral selection, the fixation probability of a single cooperator depends linearly on the number of its neighbors, i.e. the more neighbors a single cooperator has, the larger its fixation probability; (ii) under weak selection, cooperation is favored by natural selection if the benefit-to-cost ratio, $b/c$, is larger than the average degree, $z$, in the case of fixed cost per game or if the benefit-to-cost ratio, $b/c$, is larger than the harmonic mean of the degree distribution, $1/v$, in the case of fixed cost per individual; and (iii) the heterogeneity of a graph is measured by $\gamma_d$, and the effect of selection will decrease with the increase of $\gamma_d$.

Our analysis provides an insight for understanding the evolution of cooperation in a heterogeneous graph. In the case of fixed cost per game, Ohtsuki et al.'s simple rule [49] is still valid on average. However, numerical simulations in their paper show that the
The vertical dashed line represents the harmonic mean of degree distribution, a single cooperator with $z$ neighbors in SW-I, SW-II and RD are shown in Figure 4A. For $z = 4, 6, 8$, the harmonic means of the degree distribution are $1/v \approx 3.90$, 5.90 in SW-I, 1/v $\approx 3.53$, 5.51, 7.51 in SW-II, and 1/v $\approx 3.00$, 4.82, 6.83 in RD, respectively. The vertical dashed line represents the harmonic mean of degree distribution, 1/v, for each of $z = 4, 6, 8$, where the red, green and blue vertical dashed lines correspond to SW-I, SW-II and RD, respectively. Figure 4B shows the simulation results for the fixation probability of a single cooperator with $4z$ neighbors in 5F. For $z = 8,12,16$, the harmonic means of the degree distribution are $1/v \approx 5.72$, 8.76, 11.83, respectively. The vertical dashed line represents the harmonic mean of degree distribution, 1/v, where the blue, green and red vertical dashed lines correspond to $z = 8,12,16$, respectively. In both Figures 4A and 4B, the y-axis denotes the benefit-to-cost ratio, $b/c$, the x-axis denotes the fixation probability, and the horizontal dash-point line denotes the fixation probability of a single cooperator under neutral selection (i.e. $\omega = 0$) which is $\epsilon/2N$. The fixation probability of a single cooperator is measured using the fraction of runs where cooperators reached fixation out of $5 \times 10^5$ runs (based on $10^3$ graphs and $5 \times 10^6$ runs per graph). Both Figures 4A and 4B show that the theoretical predictions present a good approximation to the numerical results. doi:10.1371/journal.pone.0066560.g004

Figure 4. Effect of the fixed cost per individual on the fixation probability under the weak selection. Four heterogeneous graphs, SW-I (the Small-World graph generated according to [27] with rewiring probability 0.1), SW-II (the Small-World graph generated according to [27] with rewiring probability 1), RD (random graph generated according to [62]) and SF (scale-free graph generated according to [28]) are used to test the theoretical predictions. Simulation results for the fixation probability of a single cooperator with $z$ neighbors in SW-I, SW-II and RD are shown in Figure 4A. For $z = 4, 6, 8$, the harmonic means of the degree distribution are $1/v \approx 3.90$, 5.90 in SW-I, 1/v $\approx 3.53$, 5.51, 7.51 in SW-II, and 1/v $\approx 3.00$, 4.82, 6.83 in RD, respectively. The vertical dashed line represents the harmonic mean of degree distribution, 1/v, for each of $z = 4, 6, 8$, where the red, green and blue vertical dashed lines correspond to SW-I, SW-II and RD, respectively. Figure 4B shows the simulation results for the fixation probability of a single cooperator with $4z$ neighbors in 5F. For $z = 8,12,16$, the harmonic means of the degree distribution are $1/v \approx 5.72$, 8.76, 11.83, respectively. The vertical dashed line represents the harmonic mean of degree distribution, 1/v, where the blue, green and red vertical dashed lines correspond to $z = 8,12,16$, respectively. In both Figures 4A and 4B, the y-axis denotes the benefit-to-cost ratio, $b/c$, the x-axis denotes the fixation probability, and the horizontal dash-point line denotes the fixation probability of a single cooperator under neutral selection (i.e. $\omega = 0$) which is $\epsilon/2N$. The fixation probability of a single cooperator is measured using the fraction of runs where cooperators reached fixation out of $5 \times 10^5$ runs (based on $10^3$ graphs and $5 \times 10^6$ runs per graph). Both Figures 4A and 4B show that the theoretical predictions present a good approximation to the numerical results. doi:10.1371/journal.pone.0066560.g004

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Graph heterogeneity should be one of the most important characteristics of natural and social networks. Our study analyzes the effect of graph heterogeneity under weak selection only, and a further question is how to explain the effect of strong selection. Evolution of cooperation under strong selection in a heterogeneous graph have been considered by several authors [30–34,55–58]. Unfortunately, our theoretical methods cannot be easily extended to the situation with strong selection. In fact, it has been shown that analytical predictions obtained in the pair approximation leads to an apparent contradiction with simulation results even in regular graphs [11,59–61]. In our opinion, other theoretical methods such as the "macro-dynamics" approach developed by Pinheiro et al. [57–58] are then better able method to explain the evolution of cooperation under strong selection in a heterogeneous graph.

Supporting Information

Supporting Information S1 Supporting Information (containing one table) for Evolution of cooperation in a heterogeneous graph: Fixation probabilities under neutral selection.

(PDF)

Author Contributions

Conceived and designed the experiments: CL BZ RC YT. Performed the experiments: CL. Analyzed the data: CL BZ RC YT. Contributed reagents/materials/analysis tools: CL. Wrote the paper: CL BZ RC YT.
References

1. Axelrod R (1984) The Evolution of Cooperation. New York:Basic Books.
2. Nowak MA (2006) Evolutionary Dynamics. Cambridge:Harvard University Press.
3. Nowak MA, Sigmund K (2007) How population cohere: Five rules for cooperation. In MayR, editor. Theoretical Ecology: Principle and Applications (Third Edition). Oxford:Oxford University Press.
4. Sherratt TN, Wilkinson DM (2009) Big Questions in Ecology and Evolution. Oxford:Oxford University Press.
5. Nowak MA (1992) Evolutionary games and spatial chaos. Nature 359: 826–829.
6. Nowak MA, May RM (1993) The spatial dilemmas of evolution. International Journal of Bifurcation and Chaos 3: 35–78.
7. Nowak MA, Bonhoeffer S, May RM (1994) Spatial games and the maintenance of cooperation. Proceedings of the National Academy of Sciences of the USA 91: 4877–4881.
8. Szabö G, Tóke C (1998) Evolutionary Prisoner’s Dilemma game on a square lattice. Physical Review E 58: 69–73.
9. Szabó G, Hauert C (2002) Phase transitions and volunteering in spatial public goods games. Physics Review Letters 89: 118101.
10. Hauert C, Doebeli M (2004) Spatial structure often inhibits the evolution of cooperation in the snowdrift game. Nature 428: 634–643.
11. Szabó G, Fath G (2007) Evolutionary games on graphs. Physics Reports 446: 97–216.
12. Wang Z, Wang, Yin ZY, Xia CY (2012) Inferring reputation promotes the evolution of cooperation in spatial social dilemma games. PLoS ONE 7: e49218.
13. Shigaki K, Tanimoto J, Wang Z, Koboko S, Hagishima A, et al. (2012) Referring to the social performance promotes cooperation in spatial prisoner’s dilemma games. Physics Review E 86: 031141.
14. Wang Z, Szolnoki A, Perc M (2012) If players are sparse social dilemmas are too. Importance of percolation for evolution of cooperation. Scientific Reports 2: 960.
15. Traulsen A, Semmann D, Sommerfeld RD, Krambeck HJ, Milinski M (2010) Human strategy updating in evolutionary games. Proceedings of the National Academy of Sciences of the USA 91: 4877–4881.
16. Grujic J, Fosco C, Araujo L, Cauesta JA, Sánchez A (2010) Social experiments in the mesoscale: Humans playing a spatial Prisoner’s Dilemma. PLoS ONE 5: e13749.
17. Grujic J, Roh T, Semmann D, Milinski M, Traulsen A (2012) Consistent strategy updating in spatial and non-spatial behavioral experiments does not promote cooperation in social networks. PLoS ONE 7: e47710.
18. Albert R, Jeong H, Barabási AL (1999) Internet: Diameter of the world-wide web. Nature 401: 130–131.
19. Amaral LA, Scala A, Barthélémy M, Stanley HE (2000) Classes of small-world networks. Proceedings of the National Academy of Sciences of the USA 97: 11149–11152.
20. Jeong H, Tombor B, Albert R, Oltvai ZN, Barabási AL (2000) The large-scale organization of metabolic networks. Nature 407: 651–654.
21. Liljeros F, Edling CR, Amaral LAX, Stanley HE, Aberg Y (2001) The web of human sexual contacts. Nature 411: 907–908.
22. Dorogovtsev SN, Mendes JFF (2003) Evolution of Networks: From Biological Nets to the Internet and WWW. Oxford:Oxford University Press.
23. Jackson MO (2008) Social and Economic Networks:Princeton:Princeton University Press.
24. Erdős P, Rényi A (1960) On the evolution of random graphs. Publications of the Mathematical Institute of the Hungarian Academy of Sciences 5: 17–61.
25. Newman MEJ, Strogatz SH, Watts DJ (2001) Random graphs with arbitrary degree distribution and their applications. Physical Review E 64: 026118.
26. Watts DJ, Strogatz SH (1998) Collective dynamics of small-world networks. Nature 393: 440–442.
27. Watts DJ (1999) Small Worlds. Princeton:Princeton University Press.
28. Barabási AL, Albert R (1999) Emergence of scaling in random networks. Science 15: 509–512.
29. Albert R, Barabási AL (2002) Statistical mechanics of complex networks. Reviews of Modern Physics 74: 47–98.
30. Santos FC, Pacheco JM, Lenaerts T (2006) Evolutionary dynamics of social dilemmas in the structured heterogeneous populations. Proceedings of the National Academy of Sciences of the USA 103: 1490–1494.
31. Santos FC, Rodrigues JF, Pacheco JM (2006) Graph topology plays a determinant role in the evolution of cooperation. Proceedings of the Royal Society B: Biological Sciences 273: 51–55.
32. Fu F, Liao LH, Wang L (2007) Evolutionary Prisoner’s Dilemma on heterogeneous Newman-Watts small-world network. The European Physical Journal B 56:367–372.
33. Santos FC, Santos MD, Pacheco JM (2008) Social diversity promotes the emergence of cooperation in the public goods game. Nature 454: 215–216.
34. Devlin S, Treloar T (2009) Evolution of cooperation through the heterogeneity of random networks. Physical Review E 79: 016107.
35. Pacheco JM, Pinheiro FL, Santos FC (2009) Population structure induces a symmetry breaking favoring the emergence of cooperation. PLoS Computational Biology 5: e1000596.
36. Santos FC, Pinheiro FL, Lenaerts T, Pacheco JM (2012) The role of diversity in the evolution of cooperation. Journal of Theoretical Biology 299: 88–96.
37. Szolnoki A, Perc M, Danku Z (2008) Towards effective payoffs in the prisoner’s dilemma game on scale-free networks. Physica A 387: 2075–2082.
38. Assenza S, Gómez-Gardeñes J, Latora V (2008) Enhancement of cooperation in highly clustered scale-free networks. Physical Review E 78: 017101.
39. Poncele J, Gómez-Gardeñes J, Moreno Y, Flora LM, Moreno A (2009) Cooperative scale-free networks despite the presence of defector hubs. Europhysics Letters 88: 38003.
40. Poncela J, Gómez-Gardeñes J, Moreno Y, Flora LM (2010) Cooperation in the Prisoner’s Dilemma game in random scale-free graphs. International Journal of Bifurcation and Chaos 20: 849–857.
41. Tanimoto J, Yamauchi A (2010) Does “game participation cost” affect the advantage of heterogeneous networks for evolving cooperation? Physica A 389: 2204–2209.
42. Perc M, Gómez-Gardeñes J, Szolnoki A, Flora LM, Moreno Y (2013) Evolutionary dynamics of group interactions on structured populations: a review. Journal of The Royal Society Interface 10: 20120997.
43. Zimmermann MG, Eguíluz V, San Miguel M (2004) Coevolution of dynamical rules and interactions in dynamic networks. Physical Review E 69: 066102(R).
44. Pacheco JM, Traulsen A, Nowak MA (2006) Coevolution of strategy and structure in complex networks with dynamical linking. Physical Review Letters 97: 238103.
45. Szolnoki A, Perc M, Danku Z (2008) Making new connections towards cooperation in the Prisoner’s Dilemma game. Europhysics Letters 84: 50007.
46. Perc M, Szolnoki A (2010) Coevolutionary games–A mini review. Biosystems 99: 109–125.
47. Zhang CY, Zhang JL, Xie GM, Wang L, Perc M (2011) Evolution of interactions and cooperation in the spatial Prisoner’s Dilemma game. PLoS ONE 6: e26724.
48. Seghbrock SV, Santos FC, Lenaerts T, Pacheco JM (2011) Selection pressure transforms the nature of social dilemmas in adaptive networks. New Journal of Physics 13: 013007.
49. Ohtsuki H, Hauert C, Lieberman E, Nowak MA (2006) A simple rule for the evolution of cooperation on graphs and social networks. Nature 441: 502–505.
50. Newman M, Barabási AL, Watts DJ (2006) The Structure and Dynamics of Networks.Princeton:Princeton University Press.
51. Ohtsuki H, Nowak MA (2006) The replicator equation on graphs. Journal of Theoretical Biology 243: 68–97.
52. Ohtsuki H, Nowak MA (2009) Evolutionary stability on graphs. Journal of Theoretical Biology 251: 698–707.
53. Ewens WJ (2004) Mathematical Population Genetics: I. Theoretical Introduction. Berlin:Springer.
54. Tomohako K (2011) A condition for cooperation in a game on complex networks. Journal of Theoretical Biology 269: 221–233.
55. Gómez-Gardeñes J, Campillo M, Flora LM, Moreno Y (2007) Dynamical organization of cooperation in complex topologies. Physical Review Letters 98: 108103.
56. Wang Z, Szolnoki A, Perc M (2012) Evolution of public cooperation on interdependent networks: The impact of biased utility functions. Europhysics Letters 97: 48001.
57. Pinheiro FL, Santos FC, Pacheco JM (2012) How selection pressure changes the nature of social dilemmas in structured populations. New Journal of Physics 14: 073035.
58. Pinheiro FL, Santos FC, Pacheco JM (2012) From local to global dilemmas in social networks. PLoS ONE 7: e32114.
59. Szabó G, Vukov J, Szolnoki A (2005) Phase diagrams for an evolutionary prisoner’s dilemma game on two-dimensional lattices. Physical Review E 72: 047107.
60. Vukov J, Szabó G, Szolnoki A (2006) Cooperation in the noisy case: Prisoner’s dilemma game on two types of regular random graphs. Physical Review E 73: 067103.
61. Szabó G, Vukov J, Szolnoki A (2009) Selection of noise level in strategy adoption for spatial social dilemmas. Physical Review E 80: 056112.