

Evolutionary Stability and the Evolution of Cooperation on Heterogeneous Graphs

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Abstract Recent studies have revealed that graph heterogeneity can considerably affect evolutionary processes and that it promotes the emergence and maintenance of cooperation in social dilemmas. In this paper, we analytically derive the evolutionary dynamics and the evolutionarily stable strategy (ESS) condition for 2×2 games on heterogeneous graphs based on "pairwise comparison" updating. Using pair approximation, we introduce a new state variable to measure the evolutionary process. In the limit of weak selection, we show that the evolutionary dynamics can be approximated as a replicator equation with a transformed payoff matrix, and the ESS condition depends on both the mean value and the variance of the degree distribution. These results are subsequently applied to the Prisoner's Dilemma game and the Stag Hunt game. In both games, we find that the variance plays a determinant role in the evolution of cooperation: Cooperative strategy cannot evolve in regular graphs, but it is favored by natural selection in strongly heterogeneous graphs.

Keywords Graph heterogeneity · Evolutionary dynamics · ESS · Cooperation

1 Introduction

Understanding the evolution of cooperation is a fundamental problem in evolutionary biology and social science [3, 16]. It is well known that in a well-mixed popula-

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tion where all individuals have the same chance of interacting with one another, natural selection favors defectors over cooperators [16]. However, in more realistic populations, different individuals interact with different subsets of the whole population. This type of structure can be described by means of complex networks (or graphs), in which players of an evolutionary game occupy the vertices of a graph, and the edges denote the links between individuals [15,30]. Recent developments in statistical physics have shown that most real-world networks of contacts are highly heterogeneous, and many of them are conjectured to be scale-free, where the degree distributions exhibit power-law characteristics (e.g., computer networks and biological networks) [1,2,4,6,9].

A great deal of research has revealed that graph heterogeneity dramatically enhances cooperation in complex networks [27-29], in particular for scale-free networks [11,20, 23,24,26,31]. In 2 × 2 social dilemma games, such as the Prisoner's Dilemma, increasing heterogeneity not only catalyzes the emergence of cooperation but also changes the direction of the evolutionary process such that cooperators can resist the invasion of defectors [21,22,27,29]. Most of these studies considered so-called "pairwise comparison" updating, i.e., an individual randomly chooses one of its neighbors and imitates the strategy of the neighbor with a probability depending on their payoff difference [21-24,27-29,31]. Although the degree distributions, network clusterings or payoff structures in these models are different, one of the main reasons behind the increase of cooperators, which ensures their long-term success in the evolutionary process (see [20] for a review).

Recently, Ohtsuki et al. [17-19] developed a theoretical model to investigate evolutionary games on regular graphs. They described the evolutionary process by using pair approximation and obtained the replicator equation on graphs in the limit of weak selection. They then applied their results to several examples (e.g., the Prisoner's Dilemma game, the Stag Hunt game and the Hawk Dove game) and showed that "pairwise comparison" updating can never favor cooperation in 2×2 social dilemma games. However, Ohtsuki et al.'s model is based on regular graphs only and therefore cannot explain how cooperation prevails in heterogeneous graphs. Thus, a greater challenge is to incorporate the graph heterogeneity into the evolutionary dynamics and establish a relation between the evolution of cooperation and the graph heterogeneity.

In this paper, we derive the evolutionary dynamics for 2×2 games on heterogeneous graphs based on "pairwise comparison" updating. The paper is organized as follows. Section 2 defines games on graphs and introduces pair approximation for heterogeneous graphs. Section 3 derives the evolutionary dynamics under "pairwise comparison" updating. In the limit of weak selection, the evolutionary dynamics can be approximated as a modified replicator equation that involves both the mean value and the variance of the degree distribution. Section 4 applies these results to the Prisoner's Dilemma game and the Stag Hunt game. In both games, the variance of the degree distribution plays a key role in the evolution of cooperation. We show that cooperative strategy cannot evolve in regular graphs but is favored by natural selection in strongly heterogeneous graphs. These predictions are compared with numerical simulations for random graphs and scale-free graphs. Section 5 discusses the main results.

2 Model

2.1 Games on Graphs

Consider a directed graph with *N* vertices. We label these *N* vertices as vertex 1, vertex 2, ..., vertex *N*, respectively, and the degree of vertex *i* is denoted by k_i for i = 1, 2, ..., N. The average degree of the graph, denoted by *z*, is then written as $z = \sum_{i=1}^{N} k_i/N$. The degree distribution of a graph, denoted by p(k), gives the frequency of vertices with degree *k* (for k = 1, 2, ...). Therefore, the average degree could also be expressed as $z = \sum_k kp(k)$. In a graph, if there exists an edge between two vertices *i* and *j* for $1 \le i, j \le N$, 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.

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

Suppose that the individual at each vertex uses either strategy A or strategy B in interactions with all of its neighbors. We denote the strategy of the individual at vertex i by s_i with $s_i \in \{A, B\}$ for i = 1, 2, ..., N. The fitness of individual i is the sum over all interactions with its k_i neighbors.

Notice that the total number of directed edges in the graph is zN, and the proportion of the directed edges starting from individuals who use strategy A out of the total directed edges, denoted by ϕ_A , is given by $\phi_A = \sum_{s_i=A} k_i/zN$. In particular, if $k_i = z$ for all i = 1, 2, ..., N (i.e., a regular graph), then ϕ_A exactly represents the frequency of strategy A in the population.

2.2 Pair Approximation

Under pair approximation, the conditional probability that a neighbor of an arbitrary Y individual is an X individual $(X, Y \in \{A, B\})$ is derived from the frequencies of AA, AB, BA and BB pairs [10,17]. Denote the number of directed edges (i, j) with $s_i = X$ and $s_j = Y$ by $\Phi_{XY} = \sum_{s_i=X} k_{i,Y}$, where $k_{i,Y}$ is the number of vertex *i*'s neighbors with strategy Y. Thus, the proportion of directed edges with strategy pair (X, Y) in the total set of directed edges is $\phi_{XY} = \Phi_{XY}/(\Phi_{AA} + \Phi_{AB} + \Phi_{BA} + \Phi_{BB}) = \Phi_{XY}/zN$. Furthermore, the conditional probability that a neighbor of a vertex with strategy X is a Y-individual is given by $q_{Y|X} = \sum_{s_i=X} k_{i,Y} / \sum_{s_i=X} k_i$. Interestingly, $\phi_{XY} = q_{Y|X}\phi_X$ for any $X, Y \in \{A, B\}$. This implies that, under pair approximation, a heterogeneous graph is characterized by the variables $\phi_X, q_{Y|X}$ and ϕ_{XY} , where $X, Y \in \{A, B\}$. Notice that these variables satisfy identities as follows

$$\phi_A + \phi_B = 1,$$

$$q_{A|X} + q_{B|X} = 1,$$

$$\phi_{XY} = q_{Y|X}\phi_X,$$

$$\phi_{AB} = \phi_{BA},$$
(2)

and the entire system can be described by only two variables, ϕ_A and ϕ_{AA} [10].

3 Evolutionary Stability

3.1 Pairwise Comparison Updating

In this paper, we consider so-called "pairwise comparison" updating [17–19]. In each time step, one individual is chosen at random, and then, one of its neighbors is chosen. The first individual will adopt the strategy of the second individual with a probability that is given by $(1 + \exp(-\omega(f_2 - f_1)))^{-1}$, where ω measures the intensity of selection, and f_1 and f_2 are the fitness of the first individual and the second individual, respectively [17–19,21,22,27–29]. For $\omega \to 0$, selection is weak and individual fitness is only a small perturbation to the neutral drift. In contrast, for $\omega \to +\infty$, selection is strong, and an updating individual always imitates the neighbor with a higher fitness and never imitates the neighbor with a lower fitness. The case of strong selection has been studied by many authors [21,22,27–29]. In this paper, we consider weak selection.

3.2 Evolutionary Dynamics

If a *B* individual with degree *k* is randomly chosen to update, the probability that this individual has exactly k_A neighbors with strategy *A* and k_B neighbors with strategy *B* is $\frac{k!}{k_A!k_B!}(q_{A|B})^{k_A}(q_{B|B})^{k_B}$, and its fitness is given by $f_0 = k_A a_{21} + k_B a_{22}$. Let f_A denote the fitness of its *A* neighbors. Under pair approximation, $f_A = (z-1)(q_{A|A}a_{11}+q_{B|A}a_{12})+a_{12}$. Thus, the probability that the change of ϕ_A exactly equals $\Delta \phi_A = k/zN$ in one time step is

$$\Pr\left(\Delta\phi_{A} = \frac{k}{zN}\right) = p(k)\phi_{k,B}$$

$$\times \sum_{k_{A}+k_{B}=k} \frac{k!}{k_{A}!k_{B}!} (q_{A|B})^{k_{A}} (q_{B|B})^{k_{B}} \frac{k_{A}}{k} \frac{1}{1 + \exp\left(-\omega\left(f_{A} - f_{0}\right)\right)},$$
(3)

and the probability that the change of ϕ_{AA} exactly equals $\Delta \phi_{AA} = 2k_A/zN$ is

$$\Pr\left(\Delta\phi_{AA} = \frac{2k_A}{zN}\right) = \sum_{k \ge k_A} \left[p(k)\phi_{k,B} + \frac{k!}{k_A!(k-k_A)!} (q_{A|B})^{k_A} (q_{B|B})^{k-k_A} \frac{k_A}{k} \frac{1}{1 + \exp(-\omega(f_A - f_0))} \right],$$
(4)

where $\phi_{k,B}$ denotes the proportion of vertices with degree k that are using strategy B.

Similarly, if an *A* individual with degree *k* is randomly chosen to update, the probability that this individual has k_A A neighbors and k_B *B* neighbors is $\frac{k!}{k_A!k_B!}(q_{A|A})^{k_A}(q_{B|A})^{k_B}$, and its fitness is written as $g_0 = k_A a_{11} + k_B a_{12}$. Let g_B denote the fitness of its *B* neighbors, where $g_B = (z - 1)(q_A|Ba_{21} + q_B|Ba_{22}) + a_{21}$. Then, the probability that the change of ϕ_A exactly equals $\Delta \phi_A = -k/zN$ is

$$\Pr\left(\Delta\phi_{A} = -\frac{k}{zN}\right) = p(k)\phi_{k,A}$$

$$\times \sum_{k_{A}+k_{B}=k} \frac{k!}{k_{A}!k_{B}!} (q_{A|A})^{k_{A}} (q_{B|A})^{k_{B}} \frac{k_{B}}{k} \frac{1}{1 + \exp(-\omega(g_{B} - g_{0}))}.$$
(5)

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and the probability that the change of ϕ_{AA} exactly equals $\Delta \phi_{AA} = -2k_A/zN$ is

$$\Pr\left(\Delta\phi_{AA} = -\frac{2k_A}{zN}\right) = \sum_{k \ge k_A} \left[p(k)\phi_{k,A} \\ \times \frac{k!}{k_A!(k-k_A)!} (q_{A|B})^{k_A} (q_{B|B})^{k-k_A} \frac{k-k_A}{k} \frac{1}{1 + \exp(-\omega(g_B - g_0))} \right],$$
(6)

where $\phi_{k,A} = 1 - \phi_{k,B}$ denotes the proportion of vertices with degree *k* that are using strategy *A*.

In summary, from Eqs. (3)–(6), the time derivatives of ϕ_A and ϕ_{AA} can be written as

$$\frac{\mathrm{d}\phi_A}{\mathrm{d}t} = \sum_{k=1}^{N-1} \frac{k}{zN} \Pr\left(\Delta\phi_A = \frac{k}{zN}\right) - \sum_{k=1}^{N-1} \frac{k}{zN} \Pr\left(\Delta\phi_A = -\frac{k}{zN}\right),\tag{7}$$

$$\frac{\mathrm{d}\phi_{AA}}{\mathrm{d}t} = \sum_{k_A=1}^{N-1} \frac{2k_A}{zN} \Pr\left(\Delta\phi_{AA} = \frac{2k_A}{zN}\right) - \sum_{k_A=1}^{N-1} \frac{2k_A}{zN} \Pr\left(\Delta\phi_{AA} = -\frac{2k_A}{zN}\right). \tag{8}$$

3.3 Local Equilibrium

Under weak selection $\omega \to 0$, Eqs. (3)–(6) can be approximated as

$$\Pr\left(\Delta\phi_{A} = \frac{k}{zN}\right) = \frac{1}{2}p(k)\phi_{k,B}q_{A|B}\left[1 + \frac{\omega}{2}(f_{A} - l_{B})\right] + O(\omega^{2}),$$

$$\Pr\left(\Delta\phi_{AA} = \frac{2k_{A}}{zN}\right) = \frac{1}{2}\sum_{k\geq k_{A}}p(k)\phi_{k,B}\frac{k!}{k_{A}!k_{B}!}(q_{A|B})^{k_{A}}(q_{B|B})^{k_{B}}\frac{k_{A}}{k} + O(\omega),$$

$$\Pr\left(\Delta\phi_{A} = -\frac{k}{zN}\right) = \frac{1}{2}p(k)\phi_{k,A}q_{A|B}\left[1 + \frac{\omega}{2}(g_{B} - h_{A})\right] + O(\omega^{2}),$$

$$\Pr\left(\Delta\phi_{AA} = -\frac{2k_{A}}{zN}\right) = \frac{1}{2}\sum_{k\geq k_{A}}p(k)\phi_{k,A}\frac{k!}{k_{A}!k_{B}!}(q_{A|A})^{k_{A}}(q_{B|A})^{k_{B}}\frac{k_{B}}{k} + O(\omega),$$
(9)

where $h_A = (k - 1)(q_{A|A}a_{11} + q_{B|A}a_{12}) + a_{12}$ is the fitness of a *B* individual's *k* degree *A* neighbor and $l_B = (k - 1)(q_{A|B}a_{21} + q_{B|B}a_{22}) + a_{21}$ is the fitness of an *A* individual's *k* degree *B* neighbor. Applying Eq. (9), Eqs. (7)–(8) can then be simplified as

$$\frac{\mathrm{d}\phi_A}{\mathrm{d}t} = \frac{\omega}{2zN} \times \sum_{k=1}^{N-1} kp(k) \left[\phi_{k,B} q_{A|B}(h_A - l_B) - \phi_{k,A} q_{B|A}(g_B - h_A) \right] + O(\omega^2), \quad (10)$$

$$\frac{\mathrm{d}\phi_{AA}}{\mathrm{d}t} = \frac{1}{zN} \times \sum_{k=1}^{N-1} p(k) \left[\phi_{k,B} q_{A|B}(kq_{A|B} + q_{B|B}) - \phi_{k,A} q_{A|A} q_{B|A}(k-1) \right] + O(\omega). \quad (11)$$

In addition, $\phi_{k,A}$ and $\phi_{k,B}$ in Eqs. (10)–(11) are also variables of time *t*. For each degree *k*, the time derivative of $\phi_{k,A}$ is given by

$$\frac{d\phi_{k,A}}{dt} = \frac{1}{Np(k)} \operatorname{Pr}\left(\Delta\phi_{k,A} = \frac{1}{Np(k)}\right) - \frac{1}{Np(k)} \operatorname{Pr}\left(\Delta\phi_{k,A} = -\frac{1}{Np(k)}\right)$$
$$= \frac{\phi_{AB}}{N\phi_A\phi_B} (\phi_A - \phi_{k,A}) + O(\omega).$$
(12)

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Notice that the dynamics of ϕ_{AA} and $\phi_{k,A}$ include the term ω^0 , in the limit of weak selection (i.e., $\omega \to 0$), and ϕ_{AA} and $\phi_{k,A}$ should be considered to be fast variables compared with ϕ_A [10,17–19]. To be precise, the dynamical system quickly converges onto a slow manifold at a rate of order ω^0 , where, on this manifold, the global frequency ϕ_A is regarded as constant (because it changes at a rate of order ω) and the evolution of local frequencies ϕ_{AA} and $\phi_{k,A}$ is described by Eqs. (11)–(12). From Eq. (12), $\phi_{k,A}$ converges to $\phi_A + O(\omega)$ for any $0 < \phi_A < 1$ (i.e., $d\phi_{k,A}/dt = 0$). Therefore, Eq. (11) can be simplified as

$$\frac{\mathrm{d}\phi_{AA}}{\mathrm{d}t} = \frac{\phi_{AB}}{zN} \left[1 + (z-1)(q_{A|B} - q_{A|A}) \right] + O(\omega). \tag{13}$$

As shown in [17], Eq. (13) converges to $d\phi_{AA}/dt = 0$. Thus, the local equilibrium on this slow manifold satisfies $d\phi_{AA}/dt = 0$ and $d\phi_{k,A}/dt = 0$. From $d\phi_{k,A}/dt = 0$, we obtain

$$\phi_A - \phi_{k,A} = O(\omega), \tag{14}$$

and from $d\phi_{AA}/dt = 0$ and Eq. (14), we obtain

$$(z-1)(q_{A|A} - q_{A|B}) = 1 + O(\omega).$$
(15)

In addition, from Eqs. (2) and (15), the equilibrium local frequency $q_{A|A}$ is calculated as

$$q_{A|A} = \phi_A + \frac{1 - \phi_A}{z - 1} + O(\omega).$$
(16)

3.4 Evolutionary Stability

We now derive the evolutionary dynamics of the global frequency ϕ_A . Because ϕ_{AA} and $\phi_{k,A}$ converge to the local equilibrium at a rate of order ω^0 (which is faster than ϕ_A), we could substitute $q_{A|A}$ and $\phi_{k,A}$ in Eq. (10) with the equilibrium local frequencies of Eqs. (14)–(16). From $\phi_{k,B}q_{A|B} = \phi_{k,A}q_{B|A} = \phi_{AB}$, Eq. (10) becomes

$$\frac{\mathrm{d}\phi_A}{\mathrm{d}t} = \frac{\omega\phi_{AB}}{N} \left[(z-1) \left(q_{A|A}a_{11} + q_{B|A}a_{22} - q_{A|B}a_{21} - q_{B|B}a_{12} \right) + a_{12} - a_{21} \right] + \frac{\omega\phi_{AB}\mathrm{var}(k)}{2zN} \left(q_{A|A}a_{11} + q_{B|A}a_{22} - q_{A|B}a_{21} - q_{B|B}a_{12} \right) + O(\omega^2), \quad (17)$$

and from Eqs. (15)–(16), we finally obtain

$$\frac{\mathrm{d}\phi_A}{\mathrm{d}t} = \frac{\omega}{2zN} \frac{z-2}{z-1} \phi_A(1-\phi_A) \times \left[\phi_A(z-2)(a_{11}+a_{22}-a_{21}-a_{12})\left(2z+\frac{\mathrm{var}(k)}{z-1}\right) + a_{11}\left(2z+\frac{\mathrm{var}(k)}{z-1}\right) - a_{22}(z-1)\left(2z+\frac{\mathrm{var}(k)}{z-1}\right) + a_{12}\left(2z(z-1)+\mathrm{var}(k)\frac{z-2}{z-1}\right) - 2za_{21}\right] + O(\omega^2),$$
(18)

where var(k) is the variance of the degree distribution p(k). Eq. (18) is called the *global dynamics* of the evolutionary dynamics on the graph [18,19]. Interestingly, Eq. (18) has the form of a replicator equation [7] with a transformed payoff matrix

$$\begin{pmatrix} a_{11} & a_{12} + \alpha \\ a_{21} - \alpha & a_{22} \end{pmatrix},$$
(19)

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where

$$\alpha = \frac{\beta a_{11} + a_{12} - a_{21} - \beta a_{22}}{\beta (z - 2)},$$

$$\beta = 1 + \frac{\operatorname{var}(k)}{2z(z - 1)}.$$
(20)

It is evident that the global dynamics Eq. (18) have two boundary equilibria $\phi_A = 0$ and $\phi_A = 1$, which correspond to all individuals adopting strategy *B* and all individuals adopting strategy *A*, respectively. As pointed out by Ohtsuki and Nowak [18, 19], evolutionary stability on graphs can be derived from the transformed payoff matrix (19). If $a_{11} > a_{21} - \alpha$, then the boundary equilibrium $\phi_A = 1$ is locally asymptotically stable, which means that rare *B* mutants are selected against in an *A* population. In this case, *A* is an evolutionarily stable strategy (ESS) when compared to *B*. Conversely, if $a_{11} < a_{21} - \alpha$, then *B* mutants can invade the *A* population, and therefore, *A* is not evolutionarily stable.

In general, the heterogeneity of a graph can be measured by the variance of its degree distribution var(k) [10,13]. If the graph is homogeneous (i.e., var(k) = 0), then $\alpha = (a_{11} + a_{12} - a_{21} - a_{22})/(z-2)$, and the ESS condition of strategy A (i.e., $a_{11} > a_{21} - \alpha$) is

$$(z-1)a_{11} + a_{12} > (z-1)a_{21} + a_{22}.$$
(21)

This agrees with the results of Ohtsuki and Nowak [18,19] for regular graphs. Alternately, if the graph is strongly heterogeneous (i.e., $var(k) \gg 1$), then $\alpha = (a_{11} - a_{22})/(k - 2)$. Thus, *A* is evolutionarily stable if and only if

$$(z-1)a_{11} > (z-2)a_{21} + a_{22}.$$
(22)

Ohtsuki and Nowak [19] gave a geometrical interpretation of Eq. (21), and we next provide an intuition for Eq. (22). In a strong heterogeneous graph, whether a *B* mutant can spread depends crucially on whether it can successfully invade an *A* hub [23,28]. Let us consider two connected *k* degree ($k \gg z$) vertices *i* and *j*, where *i* is an *A* resident and *j* is a *B* mutant (see Fig. 1b, where the two vertices are specified by the double-headed arrow). As discussed in Sect. 3.2, evolutionary dynamics on graphs have two timescales. On a fast timescale, a local equilibrium is formed around the *B* mutant, and, on a slow timescale, the global frequency ϕ_A is changing. From Eq. (15), after the local equilibration process, the *B* mutant, whose one neighbor is already *A*, has on average (k - 1)/(z - 1) *B* neighbors among its k - 1 other neighbors (see Fig. 1). Thus, the payoff of the *B* mutant at the local equilibrium is

$$a_{21} + \frac{k-1}{z-1}a_{22} + \frac{(k-1)(z-2)}{z-1}a_{21},$$
(23)

and the payoff of the A resident is

$$a_{12} + (k-1)a_{11}. \tag{24}$$

For $k \gg z$, the comparison of two payoffs, (23) and (24), immediately leads to the ESS condition Eq. (22). In particular, both conditions (21) and (22) converge to $a_{11} > a_{21}$ for $z \rightarrow +\infty$. This makes sense because a well-mixed population can be approximately described by a highly connected graph [18,19].



Fig. 1 A geometrical interpretation of the ESS condition in **a** a regular graph and **b** a heterogeneous graph. Both graphs have mean degree z = 3. *A* individuals and *B* individuals are denoted by *blue balls* and *red balls*, respectively. Payoffs are shown next to the individuals. **a** At the local equilibrium, the *B* mutant (specified by the *double-headed arrow*) whose one neighbor is already *A* has on average one *B* neighbor among its two other neighbors. Thus, it can successfully invade the *A* neighbor if $2a_{21} + a_{22} > 2a_{11} + a_{12}$ [i.e., Eq. (22)]. **b** At the local equilibrium, the *B* mutant (specified by the *double-headed arrow*) whose one neighbors among its six other neighbors. Thus, it can successfully invade the *A* neighbors. Thus, it can successfully invade the *A* neighbors. Thus, it can successfully invade the *A* hub if $4a_{21} + 3a_{22} > 6a_{11} + a_{12}$ [i.e., Eq. (23)] (Color figure online)

4 Examples

4.1 The Prisoner's Dilemma Game

In this example, we consider the interaction between cooperators and defectors in a simplified Prisoner's Dilemma (PD) game [16, 17]. A cooperator (denoted by C) pays a cost c for every neighbor, and each of its neighbors receives a benefit b. A defector (denoted by D) pays no cost and distributes no benefit. The payoff matrix is then given by

$$\begin{array}{ccc}
C & D \\
C & \left(\begin{array}{ccc}
b - c & -c \\
b & 0 \end{array} \right).
\end{array}$$
(25)

Under the payoff matrix (25), the global dynamics Eq. (18) is written as

$$\frac{d\phi_C}{dt} = \frac{\omega}{2zN} \frac{z-2}{z-1} \phi_C (1-\phi_C) \left(b \frac{\operatorname{var}(k)}{z-1} - c(2z^2 + \operatorname{var}(k)) \right),$$
(26)

and the ESS condition of cooperation is

$$\frac{b}{c} > (z-1)\left(\frac{2z^2}{\operatorname{var}(k)} + 1\right).$$
(27)

It is easy to check that $d\phi_C/dt > 0$ (for any $0 < \phi_C < 1$) if and only if Eq. (27) is satisfied. Therefore, cooperation is an ESS that implies that selection favors the increase of cooperation almost always.

Under "pairwise comparison" updating, Ohtsuki et al. [17–19] indicated that defectors always win over cooperators in regular graphs (i.e., $d\phi_C/dt < 0$ for any $0 < \phi_C < 1$ when var(k) = 0). However, our result shows that cooperators could dominate defectors if the graph is strongly heterogeneous. Because the right hand of Eq. (27) is decreasing in var(k), graph heterogeneity in general promotes the evolution of cooperation (see Fig. 2). In particular, if $var(k) \gg 1$, the ESS condition becomes b/c > z - 1. This condition is even



Fig. 2 Simulation results for the evolution of ϕ_C in (**a**) scale-free graphs (z = 10, generated according to [4]) and **b** random graphs (z = 14, generated according to [14]) with different heterogeneities. Each data point is plotted using the average of 10⁵ simulations (based on 10² graphs and 10³ simulations per graph). In each simulation, we run "pairwise comparison" updating for $10 \times N$ time steps (i.e., each individual updates on average 10 times) starting from $\phi_C = 0.5$, and we record ϕ_C in the last step. **a** The variances of the *red points* and the *blue points* are var(k) = 187 and var(k) = 275, respectively. The *dashed lines* represent the theoretical predictions of b/c such that $d\phi_C/dt = 0$ [i.e., Eq. (27)]. (**b**) The variances of the *red points* and the *blue points* are var(k) = 15 and var(k) = 18, respectively. Again, the *dashed lines* represent the theoretical predictions of b/c such that $d\phi_C/dt = 0$. These figures show clearly that graphs with higher heterogeneities promote cooperation better (Color figure online)

weaker than the "simple rule" for the evolution of cooperation on graphs, which says that selection favors cooperation if b/c > z [10,17].

4.2 The Stag Hunt Game

As a second example, we consider a Stag Hunt game given by the payoff matrix

$$\begin{array}{ccc}
S & H \\
S & \begin{pmatrix} a & 0 \\
H & \begin{pmatrix} 1 & 1 \end{pmatrix}
\end{array}$$
(28)

In the game, two individuals can either jointly hunt a stag (denoted by S) or individually hunt a hare (denoted by H). We assume that the parameter a satisfies 1 < a < 2. In this case, both strategies S and H are strict Nash equilibria, where the cooperative strategy S is Pareto-efficient and the self-safety strategy H is risk dominant.

In a well-mixed population, "pairwise comparison" updating can be approximately described by the canonical replicator dynamics when selection is weak [32]. Because the risk-dominant strategy always has a larger basin of attraction under the replicator dynamics, if individuals choose their initial strategy randomly, the population will eventually converge to the noncooperative strategy H [7].

For the payoff matrix Eq. (28), the global dynamics Eq. (18) is written as

$$\frac{\mathrm{d}\phi_S}{\mathrm{d}t} = \frac{\omega}{N} \frac{z-2}{z-1} \phi_S (1-\phi_S) \left(a(z-2)\beta\phi_S - (z-a-1)\beta - 1 \right). \tag{29}$$

It is easy to verify that the two boundary equilibria $\phi_S = 0$ and $\phi_S = 1$ are locally asymptotically stable, and Eq. (29) also has an unstable interior equilibrium at

$$x^* = \frac{1}{a} - \frac{a - 1 - 1/\beta}{a(z - 2)}.$$
(30)

Thus, the sizes of the basins of attraction of strategies S and H under Eq. (29) are $1 - x^*$ and x^* , respectively.



Fig.3 Simulation results for the evolution of ϕ_S in scale-free graphs with different heterogeneities. 1100 scale-free graphs with z = 16 and $\operatorname{var}(k) \in [1700, 2700]$ are generated according to [4]. We run 10^3 simulations on each graph, where, in each simulation, the population updates on average 3×10^5 time steps (i.e., each individual updates on average 10 times) starting from $\phi_S = 0.5$. **a** The *i* – th data point is the average ϕ_S of the graphs with variances in the interval $[1700 + 100 \times (i - 1), 1700 + 100 \times i], i = 1, \ldots, 10$. The *dashed line* represents the theoretical prediction of $\operatorname{var}(k)$ such that $d\phi_S/dt = 0$ at 1/2 (i.e., $x^* = 1/2$). **b** ϕ_S in the 1100 scale-free graphs. Again, the *dashed line* represents the theoretical prediction of $\operatorname{var}(k)$ such that $d\phi_S/dt = 0$ at 1/2 (i.e., the cooperative strategy has a larger basin of attraction)

In a regular graph where $\beta = 1$, we always have $x^* > 1/a$, i.e., the basin of attraction of *H* is even larger than in a well-mixed population [18]. However, from Eq. (30), the size of the basin of attraction of *H* decreases to (z - a - 1)/a(z - 2) as β goes to infinity. In this limit, the cooperative strategy *S* has a larger basin of attraction if z < 2/(2 - a). This implies that graphs with low mean degree *z* and high heterogeneity var(*k*) favor the evolution of cooperation (see Fig. 3).

5 Discussion

In this paper, we derive evolutionary dynamics on heterogeneous graphs. We use a new state variable, ϕ_A (i.e., the proportion of directed edges starting from *A* individuals out of the total directed edges), to measure the evolution of strategy *A* instead of the frequency of *A* individuals. The reason is twofold. On the one hand, in a spatial game where individuals only play with their neighbors, the influence of strategy *A* depends on how often individuals have *A* neighbors. In a regular graph where all vertices have the same degree, this probability is positively related to the frequency of *A* individuals. Therefore, it is natural to describe the evolution of strategy *A* by its frequency [15, 17-19, 30]. However, in a heterogeneous graph, a high frequency of *A* individuals does not always imply that individuals are more likely to meet *A* neighbors. In this case, ϕ_A rather than the frequency of *A* is a sensible measurement for the influence of strategy *A* in the evolutionary process [10]. On the other hand, two core concepts of the pair approximation, the frequency of pairs XY (i.e., ϕ_{XY}) and the conditional probability that a neighbor of an *X* individual is using strategy *Y* (i.e., $q_{Y|X}$), are perfectly linked by ϕ_A (*X*, *Y* \in {*A*, *B*}). Under pair approximation, we show that evolutionary games on a heterogeneous graph can be characterized by only two variables, ϕ_A and ϕ_{AA} .

When selection is weak, we find that ϕ_{AA} evolves much faster than ϕ_A , and a local equilibrium is formed before ϕ_A is changing. From Eq. (15), at a local equilibrium, a k degree A individual has on average k/(z-1) more A neighbors than a k degree B individual, and a k degree B individual has on average k/(z-1) more B neighbors than a k degree A individual. Thus, "pair comparison" updating together with weak selection can give rise to homophily, which is the tendency to interact with others of similar strategy [8, 12]. Both

theoretical and empirical studies have highlighted that homophily (or assortative matching) can preserve cooperation in social dilemmas because a cluster of cooperators has a higher average payoff than a cluster of defectors [5,25]. Ohstuki et al. [17–19] indicated that this would be the key reason that spatial structure promotes cooperation. However, our results cannot be easily extended to the situation of strong selection because the calculation of local equilibrium depends crucially on the separation of fast and slow variables.

By using the local equilibrium condition, we derive the time evolution of ϕ_A . Interestingly, the evolutionary dynamics on a heterogeneous graph are represented by a modified replicator equation (although ϕ_A does not represent the frequency of *A*). Furthermore, the ESS condition can be obtained directly from the transformed payoff matrix (19). We show that the evolutionary stability of a strategy depends on both the mean value and the variance of the degree distribution. These results are then applied to the Prisoner's Dilemma game and the Stag Hunt game.

Many recent studies have observed that graph heterogeneity enhances cooperation in the Prisoner's Dilemma [21,22,27,29]. Our analysis provides insight for understanding these results. Equation (27) shows that the variance of the degree distribution plays a determinant role in the evolution of cooperation. In regular graphs where var(k) = 0, cooperation cannot evolve. In large scale-free graphs where $var(k) \rightarrow \infty$, selection favors cooperation if the benefit-to-cost ratio is larger than z - 1. The reason behind this is that, at a local equilibrium, the average number of C(D) neighbors of a k-degree C(D) individual is linearly increasing with k. Therefore, C hubs usually have higher payoff than D hubs, which ensures the long-term success of cooperation in the evolutionary process. Furthermore, Eq. (27) implies that heterogeneous graphs with low mean degree and high variance are better for the evolution of cooperation. Thus, it is not a surprise that scale-free graphs promote cooperation better than small-world graphs and random graphs [20] (see also Fig. 2).

Like the Prisoner's dilemma game, the Stag Hunt game also describes a conflict between social cooperation and self-safety. If an individual hunts a stag, it must have the cooperation of the other individual to succeed. In contrast, an individual can get a hare by itself, but a hare is worth less than a stag. Ohtuski and Nowak [18] noted that under "pairwise comparison" updating, the basin of attraction of Stag in a regular graph is always smaller than in a well-mixed population (i.e., a regular graph inhibits cooperation). However, our study shows that its size increases with the variance of the degree distribution, and the basin of attraction of Stag could be larger than Hare if the graph is strongly heterogeneous. This supports the simulation results of Santo et al. [27,29] that showed that graph heterogeneity promotes the evolution of cooperation in the Stag Hunt game.

Our study analyzes the effect of graph heterogeneity on "pairwise comparison" updating. A further question is then whether our results hold for other update rules, such as Birth-Death (BD), Death-Birth (DB) and imitation (IM) updating [17–19]. Recent studies have shown that graph heterogeneity does not change the evolutionary results of BD and DB updating: BD updating can never favor cooperation [17] and DB updating favors cooperation if b/c > z [10]. Why does graph heterogeneity affect the condition for the evolution of cooperation under pairwise comparison, but not under DB and BD? Because individuals who have the chance to birth in DB and BD updating need not be direct neighbors of each other, as their (excepted) fitness is decided by local density $q_{X|Y}$ only [10,17]. Notice that $q_{X|Y}$ equilibrates independently of var(k) in the limit of weak selection (see Eq. (15) and [10]), and DB and BD updating, two connected individuals are chosen to compare their fitness. In a heterogeneous graph, the fitness difference between two connected low-degree individuals mainly depends on the payoff that they obtained from their direct interaction. In contrast, the fitness difference

between two connected high-degree individuals mainly depends on the payoff that they obtained from their other neighbors. Thus, under "pairwise comparison" updating, the payoff matrix (1) should be modified by a factor that includes the graph heterogeneity parameter var(k) in order to measure the weight of the direct interaction between two individuals [see the transformed payoff matrix (19)]. Because graph heterogeneity weakens (enhances) the role of direct interaction between two connected high (low)- degree individuals in general, we can expect that the evolutionary result of IM updating on a heterogeneous graph is different from that of a regular graph because the individual that is chosen to update has to compare its payoff with neighbors [17–19].

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