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Characterizing the impact of selection on the evolution of cooperation in complex networks

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***Abstract*— Cooperative behaviors are widespread in biological and social populations. Yet the evolution of cooperation is still a puzzle in evolutionary theory. Recent researches have indicated that complex interactions among individuals may promote the evolution of cooperation under weak selection. However, the selection effect on cooperation has not been completely understood. This paper aims to characterize the impact of selection on the emergence of cooperation in evolutionary dynamics on complex networks. By theoretical analysis and numerical simulation, it is found that selection favors defection over cooperation for the birth-death process, while it may favor cooperation over defection for the death-birth process. Furthermore, we come to the condition on which cooperation is dominant over defection. In particular, there exists an optimal selection intensity which favors cooperation the best for the death-birth process. The obtained results indicate that appropriate selection can promote the evolution of cooperation in structured populations under some circumstances.**

I. INTRODUCTION

Evolutionary game theory is a well-known framework for studying the frequency dependent selection in the evolution of human and animal behaviors [1]–[3]. Over the past few decades, evolutionary game theory has been widely applied in various areas, including the evolutionary biology, social behavior analysis, culture evolution and the economics [4]–[8].

The evolution of cooperation is one of the most fundamental challenges in evolutionary game theory [3][7]. Cooperators pay costs and provide benefits to others, while defectors pay no cost and distribute no benefit. According to the Darwin's theory of evolution [9], natural selection will favor defection over cooperation. However, in real-world biological and social systems, cooperative behaviors are ubiquitous [10][11].

The prisoner's dilemma game is one of the most prominent mathematical models to investigate the evolution of cooperation. In the prisoner's dilemma game, a cooperator pays a cost c to distribute a benefit b, where $b > c > 0$, while a defector pays no cost and supplies no benefit. Hence the payoff matrix of the prisoner's dilemma game is given by

$$\begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \quad (1)$$

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It is apparent that defection strictly dominates cooperation in the prisoner's dilemma game. That is, no matter what the opponent's strategy is, defection is the best strategy to obtain more payoff. This payoff matrix can be conveniently rescaled to the following simplified form [21][22]:

$$\begin{pmatrix} 1 & 0 \\ 1+u & u \end{pmatrix}, \quad (2)$$

where $u = c/b$ is called the cost-to-benefit ratio. It is apparently that equation 2 is more simplified and briefly than equation 1 in that equation 2 has one factor.

Recently, evolutionary game dynamics on complex networks is proposed to study the evolution of cooperation in structured populations. In the evolutionary game process, individuals are differed into two types: cooperators C or defectors D. They acquire payoffs by playing the prisoner's dilemma game with other individuals in their neighborhoods. The competitiveness of each individual is measured by its fitness, which is a function of the payoff. A common used formula is

$$\text{Fitness} = 1 - \omega + \omega \times \text{Payoff}. \quad (3)$$

Here ω is called selection intensity, where $0 \leq \omega \leq 1$. The selection intensity characterizes how strong the game is pressuring evolution. For $\omega = 1$, Eq. (3) becomes Fitness=Payoff. That is, individual's fitness is completely determined by its payoff, which is called strong selection. For $\omega \ll 1$, the payoff has little to do with fitness, which is named weak selection. In particular, for $\omega = 0$, all individuals have the same fitness, called neutral drift [12][13].

It has been shown that the selection intensity plays an important role in the evolution of cooperation [12][13]. However, most recent studies investigate the emergence of cooperation only in the special case of weak selection or strong selection [14]–[17]. To fully understand the effect of selection on the evolution of cooperation, it is important and meaningful to further explore the evolutionary game dynamics with any selection intensity instead of the significant cases of strong selection and weak selection.

This paper aims to characterize the effect of selection on the evolution of cooperation in evolutionary game dynamics on complex networks. The main contributions of this paper are in two-folds. Firstly, for the birth-death (BD) process, it is shown that cooperation is never favored over defection for all selection intensity. Secondly, for the death-birth (DB) process, it is found that selection favors cooperation over defection in some networks. Moreover, it is shown that there exists

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an optimal selection intensity which favors cooperation the best. Intuitively, it seems that selection was unfavorable for cooperation. However, the above results clarify the misunderstanding and show that appropriate selection can promote the evolution of cooperation in structured populations under some circumstances.

This rest of this paper is organized as follows. Section II introduces the model of evolutionary game dynamics for the evolution of cooperation. Section III presents the theoretical analysis of the evolutionary game dynamics on some typical graphs. The main results are given in section IV. Some concluding remarks are given in Section V.

II. Model of Networked Evolutionary Game Dynamics

In this section, we introduce the model of evolutionary game dynamics for investigating the evolution of cooperation in complex networks.

Consider a structured population. The interaction structure of the population is characterized by a network, where individuals and their interactions are represented as nodes and links, respectively [18]-[20]. Each individual can be of two strategies: C (cooperation) or D (defection). The payoff matrix of the prisoner's dilemma game is shown as Eq. 2.

The individual acquires sub-payoffs by playing the above game with each of its neighbors. And the total payoff of an individual is the summation of all its sub-payoffs. The fitness of individuals is determined by their payoff according to Eq. (2). It can be observed that the fitness landscape of the population depends completely on the strategy of each individual and the population's structure.

In this paper, two typical updating rules are considered: the BD and DB processes [14]. In each step of the BD process, an individual is selected firstly with a probability proportional to its fitness, and then the selected individual reproduces an offspring to replace one of its neighbors randomly. While in the DB process, the order of birth and death is reversed. In detail, in each step of the DB process, a random individual is selected to die firstly, then one neighbor of the dead individual is selected to reproduce an offspring to replace the dead individual with a probability proportional to its fitness.

The above evolutionary process corresponds to a finite Markov chain with two absorbing states: "all-C" and "all-D". In other words, no matter what the initial state is, under the above evolutionary process, the population will end up with either "all-C" or "all-D". Let ρ_C denote the probability of fixation at "all-C" state, given that a random single C-individual invades a population of D-individuals. Hereafter, we called ρ_C the fixation probability of C in short. Obviously, ρ_C can measure the dominant level of cooperation strategy in the evolutionary process.

Since it is a hard problem to analyze the evolutionary game dynamics on general networks, in this work, we consider the evolution of cooperation on five representative networks, including the complete graph, cycle, star, lattice, and the karate club network, as shown in Fig. 1. The lattice is square and has periodic boundary. The karate club network is a friendship network among 34 members of a university karate club over a period of 2 years. It is a connected, un-weighed and undirected network with 34 nodes and 78 edges [25]. For the complete graph, cycle, and star, the fixation probability ρ_C can be analytically derived. However, for the lattice and karate club network, due to the computation complexity, it is hard to derive the fixation probability ρ_C. Thus, numerical simulations are taken to explore the evolution of cooperation on these two networks.

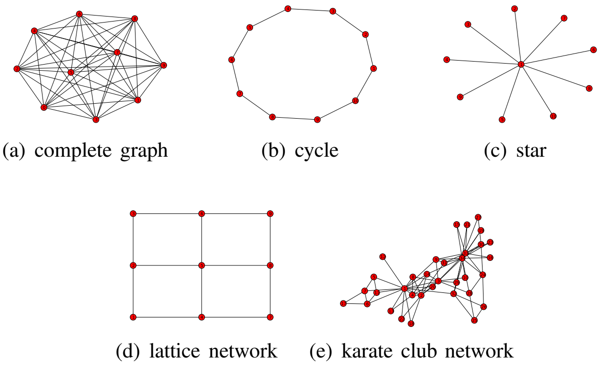


Fig. 1. Some representative network structures. The top row shows the structures of complete graph, cycle and star with the network size $N = 10$. The bottom row depicts the structures of lattice network and the karate club network. The size of the lattice network is $N = 9$, and the karate club network is a connected and undirected network with 34 nodes and 78 edges.

III. Theoretical Analysis

In this section, we derive the fixation probability ρ_C by theoretical methods for the complete graph, cycle, and star for both the BD and DB processes. Based on the fixation probability ρ_C, we can justify the effect of selection ω on the dominant level of cooperation strategy in evolutionary game dynamics on these networks. In the limitation of space, we will only give the formulas below, the similar derivations can be found at [14], [15].

A. Complete Graph

On the complete graph, suppose the number of individuals is N, then any formulations of i C-individuals and $N-i$ D-individuals are equivalent. According to the game interaction, the payoffs of the C-individual and D-individual are respectively

$$\begin{aligned} P(C,i) &= i-1, \\ P(D,i) &= i+u(N-1), \end{aligned} \tag{4}$$

where i is the number of C-individuals in the population. Therefore, the corresponding fitness of the C-individual and D-individual are

$$\begin{aligned} F(C,i) &= 1-\omega+\omega P(C,i), \\ F(D,i) &= 1-\omega+\omega P(D,i). \end{aligned} \tag{5}$$

Let $P(i \to j)$ be the transition probability from i C-individuals to j C-individuals. Denote $\lambda_i = P(i \to i+1)$

and $\mu_i = P(i \to i-1)$. Under both the BD and DB process, the fixation probability of cooperation on complete graphs can be derived as [14][23]

$$\rho_C = 1/(1+\sum_{j=1}^{N-1}\prod_{i=1}^{j}\frac{\mu_i}{\lambda_i}). \quad (6)$$

1) BD Process: For the BD process, the transition probabilities λ_i and μ_i in the complete graphs can be easily derived as

$$\begin{aligned}\lambda_i &= \frac{i(N-i)F(C,i)}{(N-1)(iF(C,i)+(N-i)F(D,i))},\\ \mu_i &= \frac{i(N-i)F(D,i)}{(N-1)(iF(C,i)+(N-i)F(D,i))}.\end{aligned} \quad (7)$$

Substituting Eqs. (4), (5) and (7) into Eq. (6), the fixation probability ρ_C can be got

$$\rho_C = \begin{cases} 0 & \text{for } \omega = 1 \\ \dfrac{1}{1+\sum_{j=1}^{N-1}\prod_{i=1}^{j}\dfrac{\mu_i}{\lambda_i}} & \text{otherwise}\end{cases} \quad (8)$$

where

$$\frac{\mu_i}{\lambda_i} = \frac{1-\omega+\omega(i+u(N-1))}{1+(i-2)\omega}.$$

Based on Eq. (8), the effect of selection intensity w on the evolution of cooperation can be assessed for the BD process on complete graphs.

2) DB Process: In a similar manner, the fixation probability ρ_C for the DB process on complete graphs can be obtained

$$\rho_C = \begin{cases} 0 & \text{for } \omega = 1 \\ \dfrac{1}{1+\sum_{j=1}^{N-1}\prod_{i=1}^{j}\dfrac{\mu_i}{\lambda_i}} & \text{otherwise}\end{cases} \quad (9)$$

where

$$\begin{aligned}\frac{\mu_i}{\lambda_i} &= \frac{iF_CF_D+(N-i-1)F_D^2}{(i-1)F_C^2+(N-i)F_CF_D},\\ F_C &= 1+(i-2)\omega,\\ F_D &= 1+\omega(i-1+u(N-1)).\end{aligned}$$

B. Cycle Graph

Note that if a cycle of D-individuals is invaded by a single C-individual, the C-individuals always form a single connected cluster during the evolutionary process [14]. Thus, the formula (6) is also valid for the evolutionary game dynamics on cycles. Hence, in order to get ρ_C, we only need to calculate the transition probabilities λ_i and μ_i.

1) BD Process: For the BD process on a cycle of size N, an easy derivation of the transition probabilities gives

$$\frac{\mu_i}{\lambda_i} = \begin{cases} \frac{1+2u\omega}{1-\omega} & \text{for } i=1 \\ 1+2u\omega & \text{for } 2\le i\le N-2 \\ 1+\omega+2u\omega & \text{for } i=N-1\end{cases} \quad (10)$$

Substituting the above equation into Eq. (6) yields

$$\rho_C = \begin{cases} \frac{1}{N} & \text{for } w=0 \\ \frac{2u\omega(1-\omega)}{(1+2u\omega)^N+2u\omega^2(1+2u\omega)^{N-2}-2u\omega^2-1} & \text{otherwise}\end{cases} \quad (11)$$

2) DB Process: Similarly, for the DB process on a cycle of size N, the transition probabilities can be obtained as

$$\frac{\mu_i}{\lambda_i} = \begin{cases} \frac{1-\omega+u\omega}{1-\omega} & \text{for } i=1 \\ \frac{(1+2u\omega)(2-\omega+2u\omega)}{2+2u\omega} & \text{for } i=2 \\ \frac{(1+2u\omega)(2-\omega+2u\omega)}{2+\omega+2u\omega} & \text{for } 3\le i\le N-3 \\ \frac{(1+2u\omega)(2+2u\omega)}{2+\omega+2u\omega} & \text{for } i=N-2 \\ \frac{1+\omega+2u\omega}{1+\omega+u\omega} & \text{for } i=N-1\end{cases} \quad (12)$$

Substituting the above equation into Eq. (6) gives

$$\rho_C = \begin{cases} \frac{1}{N} & \text{for } w=0 \\ 0 & \text{for } w=1 \\ \frac{1-\omega+u\omega}{1-\omega}\times\{T_1(\omega,u)+T_2(\omega,u,N)\} & \text{otherwise}\end{cases} \quad (13)$$

where

$$T_1(\omega,u) = \frac{4(1+u\omega)^2(1+\omega)-(1+2u\omega)\omega^2}{4\omega(1-2u)(1+u\omega)^2}$$

and

$$\begin{aligned}T_2(\omega,u,N) &= \frac{(1+2u\omega)^{N-3}(2-\omega+2u\omega)^{N-4}}{(2+\omega+2u\omega)^{N-4}}\\ &\times\left(\frac{(2-\omega+2u\omega)(2+\omega+2u\omega)}{4\omega(2u-1)(1+u\omega)^2}+\frac{2+2\omega+3u\omega}{1+\omega+u\omega}\right)\end{aligned} \quad (14)$$

C. Star

A star of N nodes contains one hub node lying in the center and other $N-1$ leafs connecting only with the hub. The fixation probability of cooperation on a star can be obtained analytically. However, since the derivation is trivial and quite tedious, it is omitted here. The fixation probability of cooperation is directly given in the following.

1) BD Process: For the BD process on a star of size N, the fixation probability of cooperation is given by

$$\rho_C = \frac{(N-1)q_1+r_0}{N\left(\sum_{j=1}^{N-2}q_j(\prod_{i=1}^{j-1}\dfrac{p_i}{r_i})+\prod_{i=1}^{N-2}\dfrac{p_i}{r_i}\right)}. \quad (15)$$

where

$$\begin{cases} p_i = \dfrac{1+\omega((N-1)u+(i-1))}{N+\omega((N-1)u+(j-N))} \\ q_i = \dfrac{N-1+\omega(1-N)}{N+\omega((N-1)u+(i-N))} \\ s_i = \dfrac{(N-1)(1+\omega u)}{(N-1)(1+u\omega)+1-\omega+i\omega} \\ r_i = \dfrac{1-\omega+i\omega}{(N-1)(1+u\omega)+1-\omega+i\omega}\end{cases} \quad (16)$$

2) DB Process: For the DB process on a star of size N, the fixation probability of cooperation is

$$\rho_C = \frac{(N-1)q_1+r_0}{N\left(\sum_{j=1}^{N-2}q_j(\prod_{i=1}^{j-1}\dfrac{p_i}{r_i})+\prod_{i=1}^{N-2}\dfrac{p_i}{r_i}\right)} \quad (17)$$

where

$$\begin{cases} p_i = \dfrac{(N-1)(1-\omega)+(N-i-1)u\omega}{N(1-\omega)+(N-i-1)u\omega} \\ q_i = \dfrac{1-\omega}{N(1-\omega)+(N-i-1)u\omega} \\ s_i = \dfrac{1+u\omega}{N+(N-i)u\omega} \\ r_i = \dfrac{(N-1)+(N-i-1)u\omega}{N+(N-i)u\omega} \end{cases} \tag{18}$$

IV. Numerical Simulations

We have deduced the fixation probability of cooperation ρ_C for three typical networks in Section III. In this section, numerical simulations are taken to validate the above theoretical results. Meanwhile, we also investigate the effect of selection on the evolution of cooperation in another two typical networks—the lattice network and the karate club network by numerical simulations.

A. BD Process

Fig. 2 shows the fixation probability of cooperation ρ_C as a function of selection intensity ω for the BD process on five typical networks in Fig. 1. It is clear to see that the theoretical and simulation results coincide quite nicely in complete network, cycle and star. Moreover, it can be found that, no matter what the graph is, the fixation probability of cooperation ρ_C is monotonically decreasing with the increase of selection intensity ω.

The above results indicate that cooperation is never favored over defection for the BD process on complex networks. Intuitively, these phenomena are caused by the evolutionary rules of the BD process. Note that the BD process contains two steps: firstly an individual is selected with a probability proportional to its fitness, and then the selected individual reproduces an offspring to replace one of its neighbors randomly. At the first step, the individual is selected according to the fitness of all individuals in the population. Hence, selection takes places in a global scope. In this case, if defection is a dominant strategy compared with cooperation, then defection is dominant in a global perspective. According to Eq. (2), the relative fitness of defectors increases with the selection intensity ω. Hence, ρ_C must be decreasing with the increase of ω. That is, selection is unfavorable to the evolution of cooperation for the BD process.

B. DB Process

Fig. 3 shows the variation of the fixation probability ρ_C as a function of the selection intensity ω for the DB process on five typical networks in Fig. 1. Different from the BD process, the effect of selection on the evolution of cooperation depends on the population structure for the DB process. In complete and star graphs, the fixation probability of cooperation ρ_C is monotonically decreasing with the increase of selection intensity ω. However, in cycle, lattice and the karate club network, the fixation probability of cooperation ρ_C firstly increases and then decreases with the increase of ω.

These various phenomena are also resulted from the evolutionary rules of the BD process. Note that the DB process contains two steps: firstly a random individual is chosen to die, and then one neighbor of the dead individual is selected to reproduce an offspring with a probability proportional to its fitness. Compared with the BD updating rule, selection takes effects only in a local neighborhood in the DB process. Therefore, the effect of selection on the fixation probability of cooperation ρ_C is determined not only by the fitness of each individual but also by the structure of population.

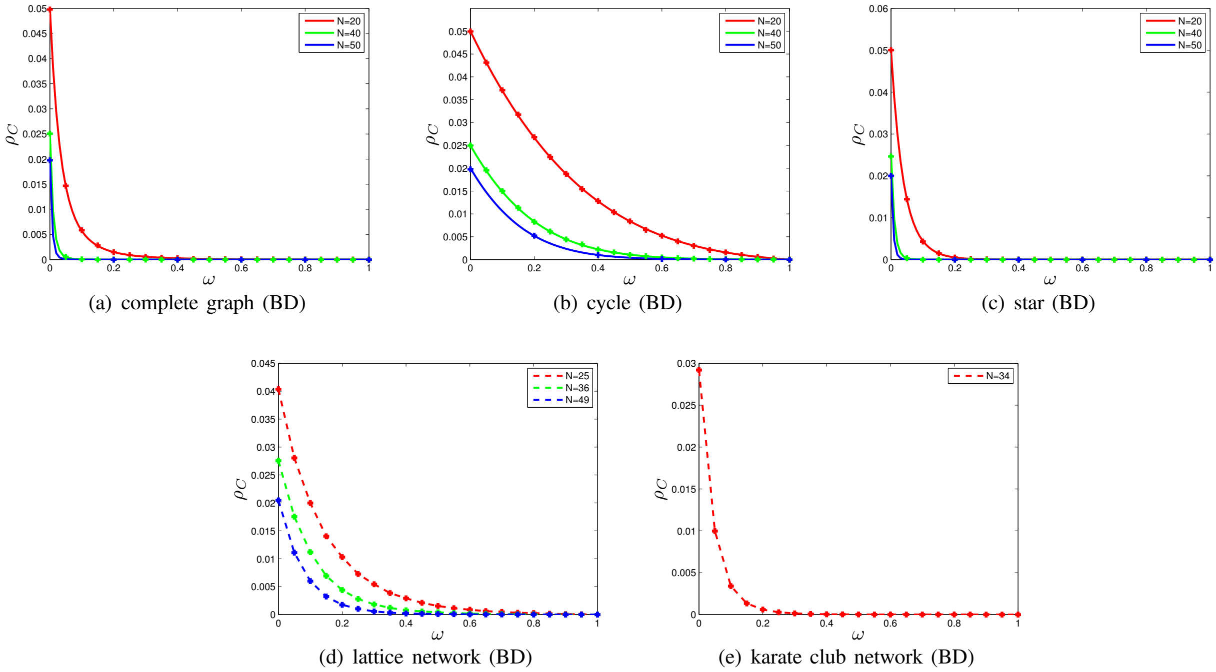
In complete graphs, each node connects with all the other nodes. Hence, the distinction between the local selection in the DB process and the global selection in the BD process is not significant. Therefore, for the DB process on complete graphs, the fixation probability of cooperation ρ_C is monotone decreasing with the selection intensity ω, which is similar in the BD process, as shown in Fig. 2 (a) and Fig. 3 (a).

In the DB process on a star graph, the fixation probability of cooperation ρ_C is also monotone decreasing with the selection intensity ω, as shown in Fig. 3 (c). That is, selection is unfavorable to the evolution of cooperation, as in the BD process. However, in the DB process on star graphs, the fixation probability of cooperation ρ_C decreases slowly and steadily with the selection intensity ω, thus the influence of selection on the emergence of cooperation is not such significant as in the BD process.

In the DB process on cycle graphs, the fixation probability of cooperation ρ_C is not monotonically decreasing with the selection intensity ω. When the selection intensity is close to $\omega_0 \approx 0.71$, the fixation probability ρ_C reaches to its maximum. Meanwhile, when $\omega \in [0, \omega_0]$, ρ_C is monotonically increasing with ω. And when $\omega \in (\omega_0, 1]$, ρ_C is monotonically decreasing with ω. It indicates that appropriate selection intensity can promote the evolution of cooperation in the DB process on cycle graphs.

Like in the cycle graph, the fixation probability of cooperation ρ_C is also firstly increasing with ω and then decreasing with the increase of ω in the lattice network and the karate club network. Therefore, by appropriate choosing the selection intensity ω, we can promote the cooperation level in DB process on the lattice network and the karate club network.

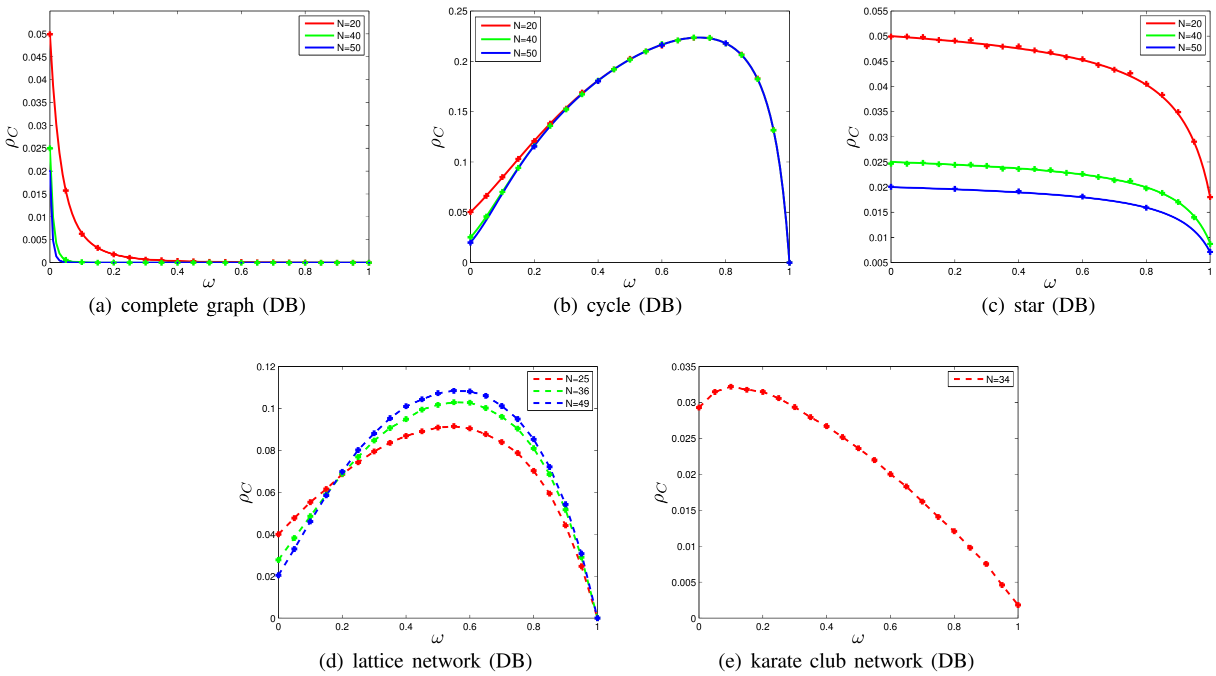
The above simulation results are derived under the condition of $u = 0.1$. However, it is worth noting that the conclusions are also valid for any other cost-to-benefit ratio u. Consider the evolutionary game dynamics on networks. It has shown that cooperation is favored over defection if and only if $\sigma a + b > c + \sigma d$ under weak selection in [15], where a, b, c, d are the payoffs in game (1) and σ is a structural coefficient determined by the population structure and game dynamics. For the DB process, the structural coefficient of complete graph, cycle, star and regular graph of degree k are $\sigma = (N-2)/N$, $\sigma = (3N-8)/N$, $\sigma = 1$ and $\sigma = ((k+1)N - 4k)/((k-1)N)$, respectively. By applying the above condition into the simplified game (3), we can conclude that cooperation cannot favor over defection in complete network and star. However, cooperation can favor over defection for cycle and lattice



(a) complete graph (BD) (b) cycle (BD) (c) star (BD)

(d) lattice network (BD) (e) karate club network (BD)

Fig. 2. The effect of selection on the evolution of cooperation for the BD process in complete graph, cycle, star, lattice and the karate club network. The x-axis is selection strength ω, and the y-axis is the fixation probability ρ_C. The cost-to-benefit ratio is $u = 0.1$, and the network size N is shown in each sub-figure. The points and lines are obtained by simulations and theoretical analysis, respectively. And the dotted lines in (d) and (e) are the direct fit of the simulation points. In the simulation, the fixation probability ρ_C is determined by the proportion of runs where cooperators reached fixation out of 10^6 runs.



(a) complete graph (DB) (b) cycle (DB) (c) star (DB)

(d) lattice network (DB) (e) karate club network (DB)

Fig. 3. The effect of selection on the evolution of cooperation for the DB process in complete graph, cycle, star, lattice and the karate club network. x-axis and y-axis are the selection strength ω and the fixation probability ρ_C, respectively. The cost-to-benefit ratio is $u = 0.1$, and the network size N is shown in each sub-figure. The points and lines are obtained by simulations and theoretical analysis, respectively. And the dotted lines in (d) and (e) are the direct fit of the simulation points. In the simulation, the fixation probability ρ_C is determined by the proportion of runs where cooperators reached fixation out of 10^6 runs.

networks if $u < (N-4)/(2N-4)$ and $u < (N-8)/(4N-8)$, respectively.

In heterogeneous networks, such as the karate club network, it has shown that $b/c > \langle k_{nn} \rangle$ is a condition of favoring cooperation, where $\langle k_{nn} \rangle$ is the mean degree of the nearest neighbors [26]. Therefore, it can be derived that cooperation is favored over defection if $u < 0.1287$ in DB process on the karate club network.

V. Conclusion

In this paper, we have investigated the effect of selection on the evolution of cooperation in evolutionary dynamics on complex networks. The relationship between the fixation probability of cooperation ρ_C and the selection intensity ω have been derived for both the BD and DB processes on some representative networks, including the complete graph, the cycle graph, the star graph, the lattice network and the karate club network. It is shown that cooperation is never favored in the BD process. However, in the DB process on cycles, lattices and the karate club network, it is found that selection can favor cooperation over defection under some conditions. Moreover, there exists an optimal selection intensity which facilitates cooperation the best. The results indicate that appropriate selection may promote the emergence of cooperation in some real-world situations.

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