

Effect of mortality selection on the emergence of cooperation with network dynamics

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Abstract. Most previous studies have focused on the effect of fertility selection on the evolution of cooperation. In fact, the payoff to an individual is in terms of the effect on fitness including survival and fecundity. In this paper, we introduce a model of strategy evolution with network dynamics based on mortality selection. The intensity β of mortality selection has a nontrivial role in the evolution of both cooperation and network structure. At a defector's temptation $b = 1$, the system gains its maximal cooperation level at $\beta \rightarrow \infty$. Increasing b decreases β_{\max} for the maximal cooperation level. For network structure, the average degrees of strategists and the self-organization of clusters are investigated to understand the connections of strategists and their effects on cooperation level. Furthermore, we introduce the cooperating k -core to describe the tight level of the cooperator cluster. Cooperation is enhanced by forming a tight cooperating k -core at moderate β , but there is a collapse of the cooperating k -core when β is too large. The results indicate that cooperators outside the cooperating k -core play an important role in maintaining that core to ensure a high cooperation level. So the formation and maintenance of the cooperating k -core coordinate with each other at maximum cooperation level at a specific value of β .

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1. Introduction

The evolution of life is full of fierce struggles and the fittest one has the most powerful ability to survive. Yet cooperative phenomena are common between unrelated individuals as well as related individuals [1]. Then one problem arises: how the fierce struggles of life affect the evolution of cooperation. Evolutionary game theory [2]–[4] has proved to be a competent tool for studying the evolution of altruistic behavior under natural selection. The prisoner’s dilemma (PD) [5] has become the general metaphor for the evolution of cooperative behavior between unrelated individuals. In this game, pairwise interactions are carried out between two players who decide simultaneously to cooperate or to defect. They will both collect the payoff R and P for mutual cooperation and mutual defection, respectively. Otherwise, the cooperator will get the payoff S facing a defector, who gets the payoff T instead. In the PD game, the payoffs satisfy $T > R > P > S$ and $2R > T + S$. It immediately follows that rational players are always better off defecting regardless of the opponent’s decision and the dilemma arises because mutual cooperation gives higher cumulative payoffs than mutual defection does. So the evolution of cooperation needs, for supporting the cooperation to withstand the invasion of defection, specific mechanisms such as direct reciprocity [5], indirect reciprocity [6], group selection [7], network reciprocity [8]–[11], noise [12]–[14], social diversity [15, 16] and so on (more references in the review [17]).

In biology, an altruist pays a cost c for its opponent to receive a benefit b_0 , while a nonaltruist pays nothing and only receives the benefit. As is customary in the literature, we can make an identification between biological benefits and PD payoffs by letting $T = b_0$, $R = b_0 - c$, $P = 0$ and $S = -c$. In the evolutionary game theory setting, the payoff to an individual is generally in terms of the effect on fitness including survival and fecundity [5]. However, most previous works focused on fecundity selection, where an altruist enhances the reproductive probability of another individual at expense of its own and the fittest phenotypes spread over the population. Recently, finite systems evolving under the stochastic death–birth process [4] have been studied widely. In the death–birth Moran process [19], an individual is randomly eliminated and another individual is chosen for reproduction in proportion to its fitness. On static networks, it is reported that cooperation is viable in the death–birth Moran process only if the average degree (number of neighbors) $\langle k \rangle$ of the network satisfies $\langle k \rangle < b_0/c$ [18]. Similar results are also reported in [20] on a stochastic nongrowth network evolution model, in which the

offspring inherits a strategy of its parent and definitely links to its parent. However, both results are in line with Hamilton's rule of kin selection [1], [21]–[23], that is, frequent kin interactions promote cooperation. In fact, this parent–offspring link leads assortative players to be closer and disassortative players to be alienated, which is an implicit assumption for network reciprocity.

On the other hand, there are only a few works about the effect of mortality selection on the evolution of cooperation. An iterated PD game on a lattice-structured population has been derived analytically and numerically in [24]. More recently, Wang *et al* have presented a global payoff-based strategy updating model to study cooperative evolution in the snow-drift game [23], [25]–[29] on complex networks [27]. We plan to discuss the self-organization of players with network dynamics under mortality selection. At present, the dynamical coevolution of individual strategies and network structure has been discovered with many insights into dynamical features and strategy dynamics [30]–[35]. Here, we present a coevolution model based on mortality selection without an inheritance mechanism to study the evolution of cooperation as well as network dynamics. The effects of selection intensity on the evolution of cooperation as well as network structure are discussed thoroughly. We are interested in knowing what intensity can improve cooperation the most and what the corresponding network structure is. Surprisingly, the results show us that cooperators can self-organize to a cluster and withstand the invasion of defectors by forming a firm cooperating core. The population needs a certain intensity of selection to form a firm cooperating core. However, when the intensity is too strong, the cooperating core will collapse, which leads the population to lower and lower cooperation levels. Our results may provide many more insights for understanding the coevolution of strategy and network structure under natural selection.

2. Model

To explore the effect of mortality selection, we maintain and evolve a population composed of N pure strategists on a network. Initially, the population is linked by a random network with the average degree $\langle k \rangle$ and behaves as cooperators and defectors with equal probability. Each individual i interacts with all its neighbors in pairwise encounters and collects a total payoff stored in π_i . According to previous works, we adopt the common payoff matrix, letting $T = b$, $R = 1$, $P = S = 0$, which preserves the essential characteristics of PD [8]. The stochastic death–birth process in our model is conducted as follows:

- (i) *Mortality selection*: Choose an individual for death with probability inversely proportional to its fitness and remove it together with all its links.
- (ii) *Reproduction*: Introduce a new individual with random strategy and link it to other $\langle k \rangle$ existing nodes randomly.

In our model, we do not consider any inheritance mechanism and regard mortality selection as the primary effect on the evolution. The fitness is chosen to be an exponential function of the payoff, given as $F_i = \exp(\beta * \pi_i)$ [36], where parameter β measures the intensity of selection. Thus the instantaneous mortality of an individual decreases exponentially with its total payoff:

$$M_i = 1/F_i = \exp(-\beta * \pi_i). \quad (1)$$

Here, parameter β can take any positive value. When $\beta = 0$, all the processes in our model are totally random, resulting in no change of the frequency of cooperators. It is a neutral drift, which

can be considered as a background case. For small β , it is a weak selection and the exponential function can be approximated by a linear function. For large β , there is an intensive effect of mortality selection on the evolution of cooperation and the individual with lowest payoff is selected to die out definitely as is the case in [27].

In our simulation, each time step consists of N two-step circular procedures and the system reaches a steady state within several time steps. Equilibrium frequencies of cooperators (ρ_c) are averaged over 1000 time steps after a transient of 10000 time steps. Each datum is an ensemble average over 100 independent simulations. All the following results are simulated with the system size $N = 1000$ and the initial average degree $\langle k \rangle = 6$.

3. Results

3.1. Effect of selection intensity on cooperation level

At first, we investigate how the macroscopic behavior of the system depends on the incentive b to defect. In the case of random mixing as well as random networks, which are our initial states, the system satisfies the mean-field approximation. Based on the classical mean-field theory, the average mortality of cooperators is

$$\begin{aligned} M_C &= \sum_{k_C=0}^{\langle k \rangle} \frac{\langle k \rangle!}{k_C!k_D!} \rho_c^{k_C} (1 - \rho_c)^{k_D} \exp(-\beta * k_C) \\ &= (1 + (\exp(-\beta) - 1)\rho_c)^{\langle k \rangle} \end{aligned} \quad (2)$$

and that of defectors is

$$\begin{aligned} M_D &= \sum_{k_C=0}^{\langle k \rangle} \frac{\langle k \rangle!}{k_C!k_D!} \rho_c^{k_C} (1 - \rho_c)^{k_D} \exp(-\beta * k_C b) \\ &= (1 + (\exp(-\beta * b) - 1)\rho_c)^{\langle k \rangle}, \end{aligned} \quad (3)$$

where k_C (k_D) is the number of cooperative (defective) neighbors and we assume that the number of neighbors for every individual remains $\langle k \rangle$. Population dynamics gives

$$\frac{\partial \rho_c}{\partial t} = \frac{1}{N} \frac{(1 - \rho_c)M_D - \rho_c M_C}{(1 - \rho_c)M_D + \rho_c M_C}, \quad (4)$$

which indicates that ρ_c will stabilize at a certain value smaller than $1/2$ at the arbitrary intensity of selection β as $M_D < M_C$, that is, $b > 1$.

However, as shown in figure 1(a), the equilibrium cooperation frequency ρ_c can be larger than $1/2$ when b is a little larger than 1. Figure 1(a) shows the equilibrium frequencies of cooperators ρ_c as a function of b for different values of the selection intensity β . In the equilibrium state, ρ_c is independent of the initial state and decreases monotonically as b increases for any β . One can find that at a low intensity of selection, the system will be stable at states with almost equal cooperators and defectors as the initial states. On increasing the selection intensity, the mortality selection will promote the cooperation level when $b < 1.2$ but suppress the cooperation otherwise. Especially at $b = 1$, where the defection has no advantage

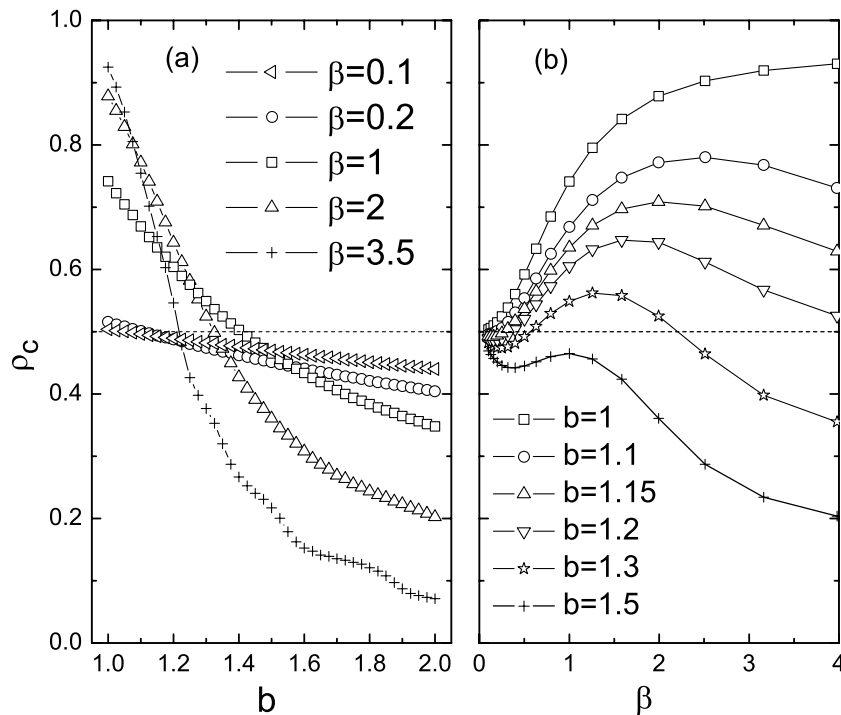


Figure 1. (a) Frequencies of cooperators ρ_c as a function of the temptation to defect b for different values of β . (b) Frequencies of cooperators ρ_c as a function of the selection intensity β with various values of the temptation to defect b . The system parameters are $N = 1000$ and $\langle k \rangle = 6$.

compared to cooperation, the mortality selection will enhance cooperation as the intensity β is strengthened. But the cooperation level will instead decrease more abruptly with higher β .

We also find that the selection intensity β affects the cooperation level significantly. The dependence of ρ_c on β for different values of temptation b to defect is plotted in figure 1(b). The figure shows that the mortality selection can enhance cooperation at a certain range of β when $b < 1.5$. Here, we denote as β_{\max} the value of selection intensity for maximum ρ_c . When $b = 1$, the cooperation level increases monotonically asymptotically to a maximum ρ_c at $\beta_{\max} \rightarrow \infty$, where the individual with lowest payoffs is selected for mortality definitely. As long as $b > 1$, there is a clear maximum ρ_c at intermediate β . Moreover, β_{\max} decreases as b increases. When b is large enough, the maximum ρ_c occurs at low β , and then the mortality selection cannot enhance cooperation any more. These phenomena indicate that there exists some competition between the cooperation-enhancing mechanism and the temptation to defect in our evolving system. When b is small, an appropriate β adapts the ability of cooperators standing up against the spiteful defectors to the maximum, similar to the effects of noise and disorder in nonlinear systems [37, 38]. But defection will completely outcompete cooperation when b is large enough.

3.2. Effect of selection intensity on network structure

The simulation results give us much more information about the dynamics of strategy evolution as well as network structure than the random mixing case, which drives us to investigate the last

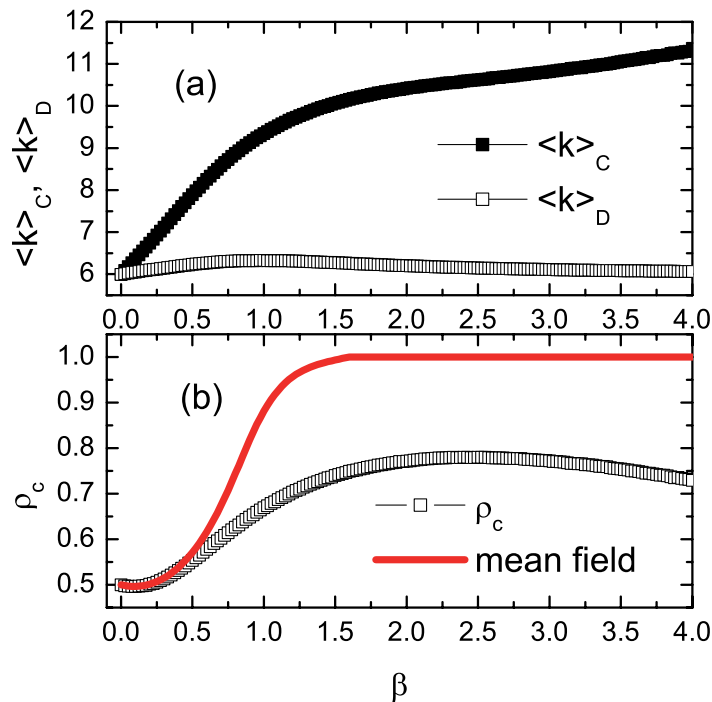


Figure 2. (a) Average degree of cooperators and defectors as a function of selection intensity. (b) Equilibrium cooperation frequency ρ_c as a function of β for the simulation and mean-field analysis with data of the average degree of both strategists derived from the simulation. The system parameters are $b = 1.1$, $\langle k \rangle = 6$ and $N = 1000$.

two assumptions:

- (i) the average degrees of cooperators and defectors are the same, and
- (ii) they are randomly connected.

In our model, a cooperator distributes a benefit to support each neighbor for survival, while a defector spreads out no benefit to his neighbors. The individual's total payoff determines one's instantaneous mortality. So the mortality of individuals with different behavior will have different effects on the fitness of their neighbors. Generally, the neighbors of cooperators will have more of a chance to survive than those of defectors. On the other hand, if a cooperator is selected to die, the benefit to its neighbors will disappear simultaneously, while the survival of a defector has no effect on its neighbors. Thus mortality selection will influence the connections between these two strategists significantly.

Note that the average degree $\langle k \rangle$ of the network can change during the death–birth process, although the degrees of new individuals equal the average degree of the initial network. But individuals with lower degree are more often selected to die, which increases $\langle k \rangle$ in the process. Figure 2(a) shows that under mortality selection the average degree of cooperators will increase monotonically with the selection intensity β , while that of defectors almost holds the average degree of the initial network.

Then the simulated average degrees of both strategists are applied in the mean-field formula to calculate the ρ_c for each β . In formulae (2) and (3), we replace $\langle k \rangle$ by simulated

average degrees $\langle k \rangle_C$ and $\langle k \rangle_D$ for cooperators and defectors, respectively. Thus, the equilibrium cooperation level ρ_c can be calculated by

$$\rho_c = \frac{M_D}{M_D + M_C}, \quad (5)$$

which is derived from equation (4). In figure 2(b), we find that the simulated and analytical results are in agreement at $\beta < 0.5$, but gradually deviate when β increases. The comparison tells us that in the region of low intensity of mortality selection both cooperators and defectors are almost connected randomly as the initial state and a slight increase in ρ_c is due to the fact that cooperators will get more neighbors than defectors. On the other hand, the deviation of simulated and mean-field results at $\beta > 0.5$ indicates that the connections between the two strategists are not random any more. The defectors will struggle to survive by getting more cooperative neighbors than the randomly connected case, which limits the cooperation level consequently. What is more, there is a maximum ρ_c at an intermediate value of β . By increasing selection intensity β , defectors will recapture some advantages even though cooperators get more and more neighbors.

On the other hand, cooperators also need more cooperative neighbors to survive under a large intensity of mortality selection. It will be difficult for cooperators isolated from other cooperators to survive and only cooperators who connect together can struggle for life. So the two kinds of strategists will never be connected randomly like the initial case any more. Cooperators will aggregate to form a common cooperator cluster (CC) and the defectors will be partitioned apart. Here, the cluster is the connected component and the cooperator cluster or defector cluster (DC) is the connected component fully occupied by cooperators or defectors, respectively. Figure 3(a) shows us that there is only one CC but more and more DCs as long as $\beta > 0.5$, although the defector number becomes smaller. This indicates that the average size of CC increases rapidly to the number of cooperators in the population, while that of DC gets smaller and smaller and decreases to almost 1 eventually as shown in figure 3(b). The increasing average size of CCs shows that cooperators get closer and closer. The cluster number of nodes (including cooperators and defectors) as a function of β also tells us that all defectors gather around cooperators to form a common cluster along with congestion of cooperators.

3.3. Introduction of cooperating k -core and its function

How can defectors recapture the advantage under the condition that cooperators get more and more neighbors when selection intensity β is large enough? In order to answer this, we first investigate what kind of connection there is among all cooperators after they have assembled together. Apparently, when β becomes larger, cooperators will struggle to get more and more cooperative neighbors, who are in the common CC with them. So the CC will become tighter on increasing β . To characterize the tight level of CC here, we introduce a cooperating k -core [39], which can be obtained in the following way:

- (i) firstly, find all connected components of cooperators;
- (ii) for each cooperative component, remove all individuals whose number of cooperative neighbors is less than k ;
- (iii) some of the remaining individuals may remain with less than k cooperative neighbors; then remove these individuals, and so on, until no further removal is possible.

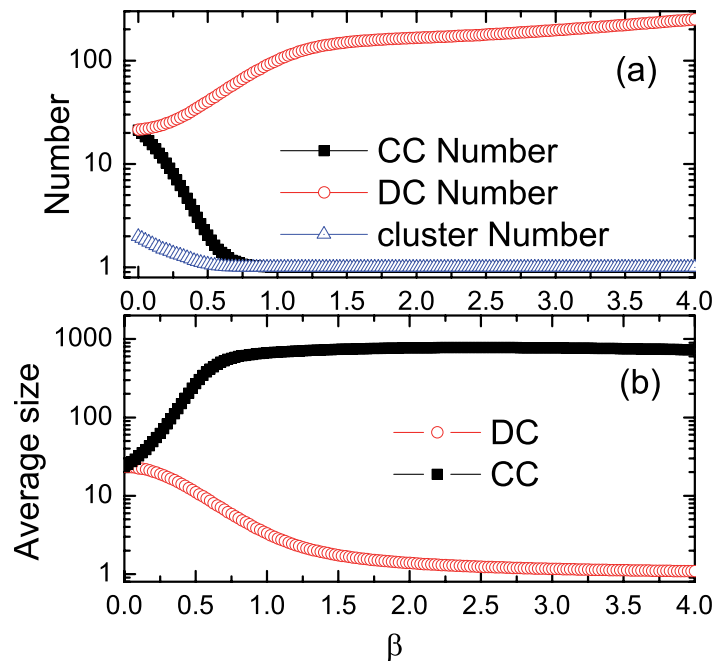


Figure 3. (a) Cluster numbers as a function of selection intensity β with $b = 1.1$. When $\beta = 0$, there is no difference between these two kinds of strategists and mortality selection has no substantial effect on network structure. The number of CCs is equal to that of DC for the case of $\beta = 0$. For $\beta > 0$, CC number is always smaller than DC number. With increasing β , the CC number decreases, while the DC number increases. The cluster number of individuals (including cooperators and defectors) decreases quickly to 1 with increasing β , which indicates that cooperators form a common cluster and all defectors surround this cluster to form an all-connected network. (b) Average size of DCs and CCs as a function of β . The system size is $N = 1000$.

Thus, every cooperator in the cooperating k -core has at least k cooperative neighbors who are also in that cooperating k -core. The larger the k , the tighter the cooperating k -core. Especially, the cooperating 1-core is equivalent to CC. On the other hand, if one cooperator in the cooperating k -core is eliminated, some cooperators will hold only $k - 1$ cooperative neighbors in this cooperating k -core and they will be excluded outside this core. So the death of one cooperator will decrease the size of the core he belonged to previously. Sometimes the k -core may even be turned into a $(k - 1)$ -core.

At $b = 1$, cooperators will outcompete defectors by forming a firm cooperating k -core. An increase in intensity β eases the formation of the cooperating k -core; hence mortality selection will enhance cooperation more and more as the intensity β is strengthened. This mechanism leads the system to maximum cooperation level at a strong intensity of selection. With increasing b , defectors who benefit more from cooperators can struggle to survive even though they lose certain cooperative neighbors. Under this condition, cooperators need more cooperative neighbors to prevent the tendency of dying out and then CC becomes tighter. Increase in intensity β eases the formation of the cooperating k -core but also exerts more pressure on cooperators outside that k -core, leading to different cooperation levels. When b is small but

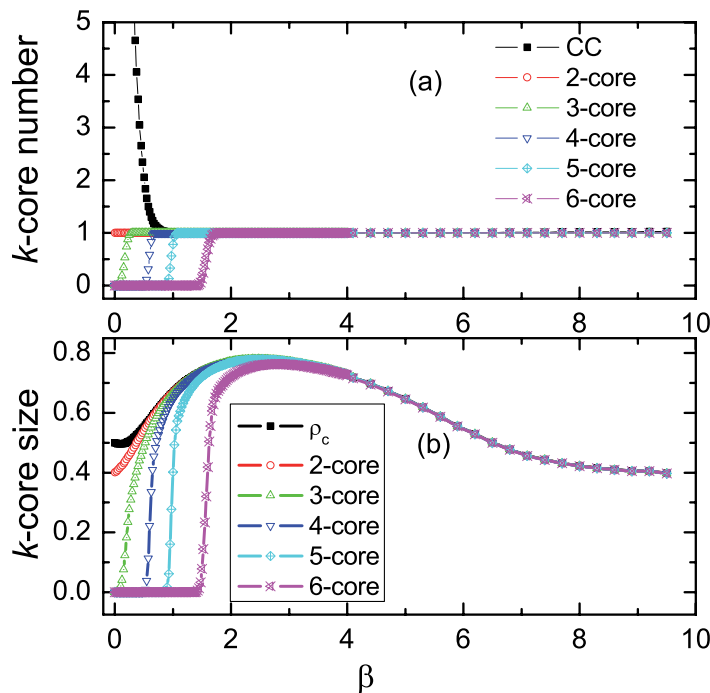


Figure 4. (a) Cooperating k -core number as a function of β . At low β , there is more than 1 CC (also 1-cores). For $k > 1$, there is always only one cooperating k -core, and the emergence of a cooperating k -core with larger k needs larger β . (b) Cooperating k -core size as a function of β . We can always find the cooperating 2-core and 3-core at any value of β . But the cooperating k -core with $k > 3$ forms only when $\beta > 0.5$. Especially when the size of the cooperating k -core is near ρ_c , the cooperating $(k + 1)$ -core forms. At the system value of $\langle k \rangle = 6$, the maximum k for the cooperating k -core is 6.

larger than 1, the cooperators need to form a k -core of mutualistic symbioses and some noise to protect this k -core. With intermediate values of β , a firm cooperating k -core can form and a few cooperators outside the cooperating k -core survive due to a little noise of mortality selection.

Now, let us study the network structure of cooperators dependent on the selection intensity β . Figure 4 shows the evolution of cooperating k -core dependent on β . There is always only one cooperating k -core with $k > 1$ (figure 4(a)). The cooperating k -core with larger and larger k emerges along with increasing β , which indicates that only one of the CCs gets tighter and tighter. At the condition with $\langle k \rangle = 6$, the tightest CC is the cooperating 6-core. When $\beta > 1.5$, the cooperating 6-core forms. Figure 4(b) shows us the cooperating k -core size dependent on β . We find that for moderate β , the size of any core increases with β and the cooperating $(k + 1)$ -core forms after the size of cooperating k -core approaches ρ_c . The larger the β , the more cooperators are included in a cooperating k -core and the less the cooperators outside the cooperating k -core can survive. For large β , it is also shown that the size of the cooperating 6-core and ρ_c increase to the maximum at $\beta = 2.5$. With β increasing further, both ρ_c and the size of the cooperating 6-core decrease, but the fraction of cooperators outside this core still decreases.

At the same time, figure 5(a) shows that p_{out} continuously decreases after the cooperating 6-core forms. Here we refer to p_{out} as the fraction of cooperators outside the cooperating

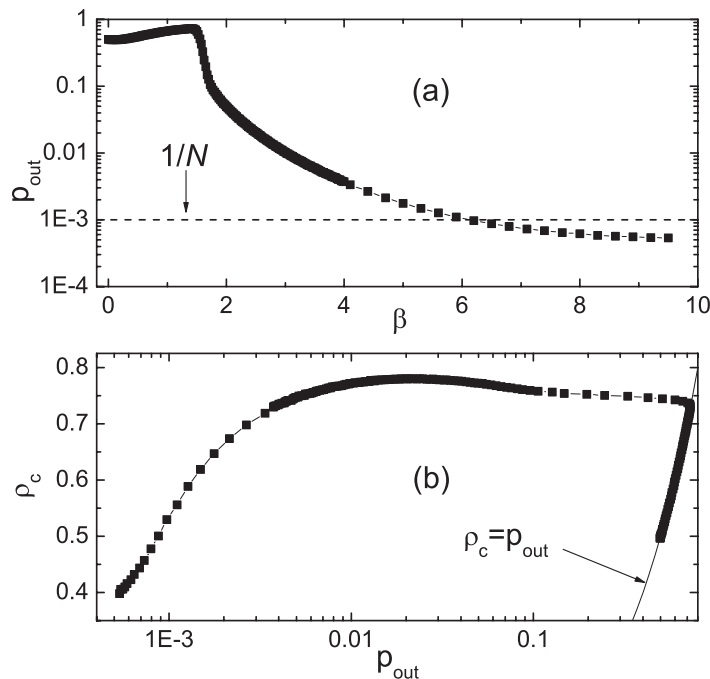


Figure 5. (a) p_{out} as a function of β . At $\beta > 6.1$, $p_{\text{out}} < 0.001 = 1/N$, which means that almost all cooperators merge together by forming a cooperating 6-core at a large intensity of mortality selection. (b) ρ_c as a function of size p_{out} of cooperators outside the cooperating 6-core for large β . The maximum ρ_c occurs at $p_{\text{out}} \simeq 0.02$.

6-core. p_{out} becomes less and less, although ρ_c still increases with β . It can be found that the population reaches some maximal cooperation level at $p_{\text{out}} \simeq 0.02$ as shown in figure 5(b). Note that, in figure 5(b), there are two different values of ρ_c when $p_{\text{out}} > 0.5$. This shows that $\rho_c = p_{\text{out}}$ for lower values in this range, which indicates that the cooperating 6-core has not formed yet, corresponding to low β . Increasing β increases p_{out} as well as ρ_c . After p_{out} becomes a maximum, the cooperating 6-core occurs. Then p_{out} decreases promptly, although the cooperation keeps a high level. At very large β , there is almost no cooperator outside that core eventually when $p_{\text{out}} \simeq 0.001 = 1/N$ in this system with $N = 1000$. Under this condition, the system will go through the collapse of the cooperating k -core. It seems that the population needs a certain fraction of cooperators outside this tightest core to obtain a maximal cooperation level. To sum up, the cooperating k -core needs a certain β to get tighter and tighter CCs for cooperators' survival but also needs some cooperators outside the core to protect this core. This phenomenon is somewhat like the case of noise and disorder in nonlinear systems.

3.4. Dynamics of strategy evolution and cooperating k -core size

To investigate the collapse of the cooperating k -core, we further study the dynamical process of cooperator aggregation with various β . At every time step, if there exists a cooperating k -core with $k \geq \langle k \rangle \rho_c b$, that is, the average payoff for defectors in the random mixing case, these cooperators can exist together to form a firm component. They protect each other so that the system can maintain a high cooperation level. Thus cooperation is enhanced.

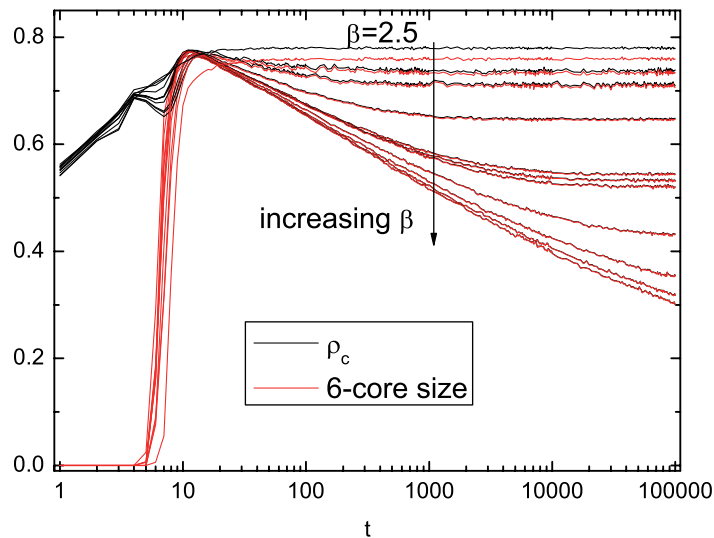


Figure 6. Transient evolution of the frequencies of cooperators ρ_c (black line) and the size of the cooperating 6-core (red line) with various values of the selection intensity $\beta = [2.5, 3.8, 4.2, 5, 6, 6.1, 6.2, 7, 8, 9, 10]$. The temptation to defect is $b = 1.1$. At $\beta \simeq 2.5$, both ρ_c and the cooperating 6-core size increase rapidly and are stable at the maximal level. For the case with $\beta > 2.5$, they reach their own vertices and then decrease logarithmically to a different level with different times for different values of β . The larger the β , the more time it takes for collapse and the lower the cooperation level that the system will be stable at.

Here we analyze the average dynamical processes at various β , as shown in figure 6. Their starting transient dynamics are all similar. In all cases, ρ_c increases with the size of the cooperating 6-core at the beginning. At the same time, the number of cooperators outside the cooperating 6-core decreases rapidly. At moderate selection intensity $\beta = 2.5$, the system is stable at the maximal level after it reaches the vertex. For any intensity $\beta > 2.5$, both ρ_c and the size of cooperating 6-core increase rapidly to a close vertex. After that, they both go through a transient time of logarithmic decrease. What is more, increasing β prolongs the dropping time and leads the system to a lower cooperation level.

Note that figure 5 in the last subsection has shown us that there are fewer cooperators outside the cooperating 6-core with larger β . In other words, the condition at larger β is hard for cooperators outside the cooperating 6-core to survive, and only cooperators in the cooperating 6-core can struggle for life. Once the selection intensity β exceeds a certain value, the cooperating 6-core goes through a little collapse, which decreases ρ_c . In this case, cooperators gain more payoffs than defectors by forming a cooperating 6-core and there are a few cooperators outside this core. This process enhances cooperation at the beginning. When the cooperation level arrives at the vertex, every existing defector will have more payoffs than cooperators in the cooperating 6-core. Under this condition, once the new incoming defector is introduced with a payoff larger than 6, the cooperating 6-core becomes unstable. If one of the cooperators in this 6-core dies, the cooperating 6-core will collapse in a cascading way.

As a result, the condition of a few cooperators outside the cooperating k -core will limit the cooperation level.

Therefore, the formation and maintenance of the cooperating k -core coordinate to maximum cooperation level at a specific value of β . Additionally, it is more difficult for cooperators outside the cooperating k -core to survive when the temptation b is higher, so that cooperators outside the cooperating k -core will extinguish at a lower β , resulting in lower β_{\max} .

4. Summary

In summary, we have introduced a model of strategy evolution with network dynamics based on mortality selection. Our results indicate that the intensity β of mortality selection has a nontrivial role on the evolution of cooperation as well as network structure. At temptation $b = 1$, defectors do not have any advantage and cooperators outcompete defectors at any β . The system gains its maximal cooperation level at $\beta \rightarrow \infty$. For moderate b , the maximal cooperation level occurs at moderate β . Increasing b decreases β_{\max} . The average degrees of cooperators and defectors are investigated to understand the connections of strategists and their effects on cooperation level. We have also investigated the cluster organization of different strategists under various intensities β of mortality selection.

Furthermore, we have introduced the cooperating k -core to describe the effect of selection intensity β on cooperation level and network structure with $b = 1.1$. We have found that cooperation is enhanced by forming a tight cooperating k -core at moderate β and there is a collapse of the cooperating k -core at large β . The results indicate that cooperators outside the cooperating k -core are important in maintaining that core and further ensure a high cooperation level. Hence the formation and maintenance of the cooperating k -core coordinate to maximum cooperation level at a specific value of β .

Here we only consider the effect of mortality selection with network dynamics. In fact, an individual's payoff from interaction in a game is in terms of the effect on fitness including survival as well as fecundity. So the combination of mortality and fertility needs to be investigated for the evolution of cooperation and network structure as well. We have also found that mortality selection played an unusual role in the enhancement of cooperation with the existence of strategy inheritance. However, the condition in that case is much more complicated and we will study this further in greater detail in our future work.

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