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Coevolution of cooperation and network structure under natural selection

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Abstract – A coevolution model by coupling mortality and fertility selection is introduced to investigate the evolution of cooperation and network structure in the prisoner's dilemma game. The cooperation level goes through a continuous phase transition *vs.* defection temptation b for low mortality selection intensity β and through a discontinuous one for infinite β . The cooperation level is enhanced most at $\beta \approx 1$ for any b . The local and global properties of the network structure, such as cluster and cooperating k -core, are investigated for the understanding of cooperation evolution. Cooperation is promoted by forming a tight cooperating k -core at moderate β , but too large β will destroy the cooperating k -core rapidly resulting in a rapid drop of the cooperation level. Importantly, the infinite β changes the normalized sucker's payoff S from 0 to $1 - b$ and its dynamics of the cooperation level undergoes a very slow power-law decay, which leads the evolution into the regime of neutral evolution.

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Introduction. – Evolutionary game theory [1–4], first introduced by Maynard Smith, has proved to be a competent tool in studying the evolution of altruistic behavior under natural selection, due to the fundamental description of frequency-dependent selection. For unrelated individuals, the prisoner's dilemma (PD) [5,6] has become the general metaphor. This game carries out a pairwise interaction between two players each deciding simultaneously to cooperate or to defect. Mutual cooperation and defection will offer both reward R and punishment P , respectively. Otherwise, the cooperator will get the sucker's payoff S facing a defector who gets temptation T instead. In PD game, the payoffs are arranged as $T > R > P > S$ and $2R > T + S$. It immediately follows that it is always better to defect regardless of the opponent's decision and the dilemma lies in that mutual cooperation gives higher cumulative payoffs than mutual defection does.

Early pioneering numerical work was implemented with imitation dynamics of the PD game in two-dimensional square lattices [7]. Each individual would play PD game with its grid neighbors, record its total score, and then

copy the strategy of its highest-scoring neighbor for the next round. In this setting, cooperators could form clusters to resist invasion by defectors at their borders. As inspired by the network science [8] in the last decade, the studies of evolutionary games have shifted from on regular grid to on complex networks, which can be considered as a step towards more realistic conditions. Variations in topology and strategy update mechanism have since been extensively studied [9–12].

Recently the finite systems evolving under stochastic death-birth Moran process [13–15], where an individual is randomly eliminated and another individual is chosen for reproduction proportionally to its fitness, have been studied widely. It is reported that cooperation is viable in this process only if the average degree (number of neighbors) $\langle k \rangle$ of the network satisfies $\langle k \rangle < b_0/c$ [15] on static networks, where a cooperator pays a cost c for its opponent to receive a benefit b_0 , while a defector pays nothing and just receives the benefit. Similar results are also reported in refs. [16,17] on a coevolution model, where 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 [16–20], that is frequent kin interactions promote cooperation.

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A lot of works have focused on fertility selection [16–20]. However, the payoff to an individual is in terms of the effect in fitness including survival and reproduction [6] generally. There are only a few works [21–23] about the effect of mortality selection on the evolution of cooperation. For instance, iterated prisoner’s dilemma game on a lattice-structured population has been derived analytically and numerically in ref. [21]. On the other hand, coevolution of individual strategies and network structure has been studied extensively and discovered with many insights of dynamical features and strategy dynamics [24–31]. Under the simple coevolution rule, the formation of cooperator groups has been recognized to be paramount for cooperation enhancement [32–34]. Our previous work [34] proposed a coevolution model which was based on mortality selection without inheritance mechanism. We showed that with a certain range of the intensity, cooperators can self-organize to a cluster and withstand the invasion of defectors by forming a firm cooperating core.

In this letter, we investigate a more realistic coevolution model with mortality selection and fertility selection to understand their cooperativity and competition for the evolution of cooperation. We want to know if these two cooperation-promoting mechanisms can coexist and reinforce cooperators’ survival ability and fertility so as to enhance cooperation further. We show that the coupling of them is nontrivial and can induce much more complicated dynamics. Here, we study their cooperativity and competition by varying the intensity of mortality selection. We show that the cooperation level goes through a continuous phase transition *vs.* defection temptation for low mortality selection intensity, but a discontinuous one for infinite intensity. The local and global properties of the network structure, such as cluster and cooperating k -core, are introduced to understand the underlying mechanism for cooperation enhancement. Our simulation indicates that the cooperating k -core and the cooperation level will breakdown at large intensity, while the cooperation level will decay in a power-law way at infinite intensity, which implies, as an important result, that the infinite intensity of mortality selection leads the evolution into the regime of neutral evolution [35,36].

Coevolution model under natural selection. –

In this coevolution model, we maintain the population size N in the stochastic death-birth process. In most cases, the system size is set as $N=1000$, except for the conditions near the critical point, where we simulate with N from 10^4 to 10^5 . Initially, the population are located on a random network with average degree $\langle k \rangle = k_0 = 6$ and they act as cooperators and defectors with identical probability. At each time each individual i gathers its payoff π_i by interacting pairwise with all its neighbors. As advised by previous works, the common payoff matrix is set as $T = b$, $R = 1$, $P = S = 0$ [7]. We simply suppose that an individual i ’s fertility probability

is proportional to its payoff, while its mortality probability is negative-exponentially proportional to its payoff as $\exp(-\beta * \pi_i)$ [37].

The parameter β measures the intensity of mortality selection and can take any positive value. $\beta = 0$ means no mortality selection and individuals have the identical probability to be eliminated. For small β , it is weak selection and the exponential function can be approximated by a linear function, which is also adopted by fertility selection. In this case, both mortality and fertility selections acting on individual level can be well described by mean-field analysis which just acts on species. For large β , an intensive effect of mortality selection is imposed on the evolution of cooperation and individuals’ fates are now distinguished remarkably. Specially, in the extreme case of $\beta = \infty$, the individual with lowest payoff is selected to be death definitely, which is somehow treated as deterministic process similar to that in ref. [22].

The coevolution dynamics of strategy and network structure are performed by the procedure consisting of the following stochastic death-birth process:

i) Fertility selection. An individual is selected for reproduction with its fertility probability. The offspring inherits the strategy of its parent and links to its parent certainly. Then, the offspring attaches to other $k_0 - 1$ nonparent nodes randomly.

ii) Mortality selection. An individual is selected to die out with its mortality probability and removed from the network together with all its links.

Accordingly, the network is dynamically created and evolved, and is not a preexisting space to be colonized but an ever-changing web. This implies that local topological properties, such as clustering coefficient [10], gradient and topology potential [11], are not necessarily the mechanisms for promoting cooperation. Therewith, owing to the global selections of both mortality and fertility, cluster of both strategists and cooperating k -core introduced in refs. [34,38] can be employed to study the coevolution dynamics of cooperation as well as global features of network.

In our simulation, the timescale is such that an average number of N death and reproduction events occur in one time step. At small β , 100 time steps are sufficient for the system properties to reach the stationary state, including cooperation density as well as network structure. The stationary fraction of cooperators ρ_C and the properties of network structure are determined by averaging over 1000 time steps after transients of 10000 time steps are discarded. The results presented below are obtained from ensemble averages over 100 independent simulations.

Results. –

Coevolution dynamics of the cooperation level. We start by presenting results of the cooperation level ρ_C as a function of the temptation b for various values of β as shown in fig. 1(a). ρ_C always decreases monotonically with increasing b for any β . At $\beta = 0$ as the case in [17], the

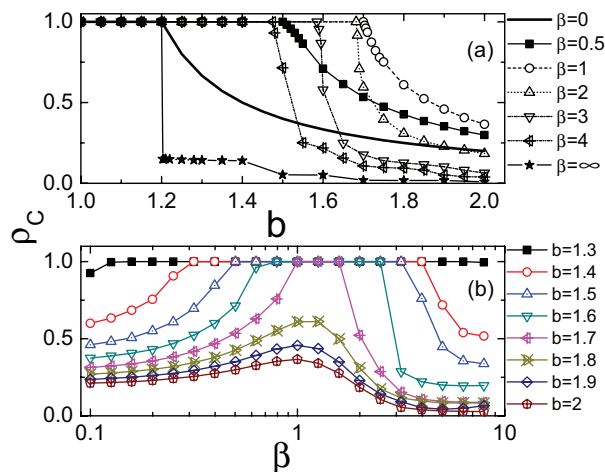


Fig. 1: (Color online) (a) Density of the cooperators ρ_C in dependence on temptation b at various values of mortality selection intensity β . At $b=1.2$, the system goes through a continuous phase transition for $\beta=0$ and a discontinuous phase transition for $\beta=\infty$, where the individual with lowest payoff dies out definitely. At $\beta=1$, the cooperation level is promoted most for any b . For the simulation at the critical value of b for each β , the system size ranges from 10^4 to 10^5 . (b) Density of cooperators ρ_C as a function of β with various values of temptation b .

cooperation level is given by

$$\rho_C = \begin{cases} 1, & b < 1.2, \\ \frac{1}{5(b-1)}, & b > 1.2, \end{cases} \quad (1)$$

so the system goes through a continuous phase transition from absorbing state (all cooperators) to coexistence at $b=1.2=1+1/(\langle k \rangle - 1)$, that is the network reciprocity in agreement with Hamilton's rule of kin selection. When β is small, the weak mortality selection helps cooperators to evolve under fertility selection. The low intensity of mortality selection makes the cooperator hubs' payoff larger than the defector hubs' one by eliminating the low-payoff cooperators surrounding defector hubs, resulting in more fertility of cooperator hubs than defector ones. Thus, the cooperation level ρ_C is enhanced. Increasing β up to about 1, ρ_C is enhanced most and the critical value for continuous transition is also increased to $b \approx 1.7$. At the same time, the dropping rate of ρ_C after critical b increases with β due to its effect of payoff amplification in the expression of mortality selection.

When β is larger than 1, mortality selection will be the main effect on competition among the population. Cooperators will self-organize into some special pattern like cooperating k -core to survive as in the case in [34]. Although cooperators with higher payoff get more chance to reproduce offsprings, their offsprings also need to get high payoff to survive and then support parents survival and reproduction further. Anyway, the results show that higher intensity β of mortality selection exerts more

pressure on cooperators, resulting in lower cooperation level ρ_C and critical b for transition. Payoff amplification of β in mortality selection still steepens the dropping of cooperation level *vs.* b .

At the extreme case of $\beta=\infty$, there will be a discontinuous phase transition from all cooperators to all defectors and the critical b is reduced back to 1.2 as in the case of $\beta=0$. Here, the individual with lowest payoff dies out definitely. At $b < 1.2$, fertility selection fixes cooperation even with so strong mortality selection because of the network reciprocity [17], without which the population falls into whole defection for $b > 1.2$ (more details will be discussed in the last section of results). In the latter condition, fertility selection is totally disregarded and mortality selection has become the primary factor in the evolution.

We then investigate the dependence of the cooperation level on the mortality selection intensity β as shown in fig. 1(b). In agreement with the results shown in fig. 1(a), ρ_C increases to maximum around $\beta=1$, and drops down as β gets too large for any value of b . From this viewpoint, intermediate β coordinates with the fertility selection for enhancing cooperation at most independently of temptation b . Note that at $b=1.8$, the cooperation level ρ_C at $\beta=1$ almost equals that at $\beta=1.26$. We will focus on the case of $b=1.8$ and discuss the relationship between cooperation evolution and network dynamics in the next subsection.

Coevolution dynamics of network structure. The information of the average degrees is important for understanding the equilibrium value of ρ_C as a function of β . Owing to the individual-based mortality selection, the dynamics of average degrees are long-time correlated. So we resort to the numerical simulation (fig. 2(a)), which shows that intensity β exerts almost no influence over the average degree of defectors $\langle k_D \rangle$ while the one of cooperators $\langle k_C \rangle$ increases with β slowly up to $\beta \approx 1$ and then booms up. The reason lies in that defectors have no payoff effect for their neighbors, while cooperators have a great influence on the payoff of their neighbors and significantly affect the mortality as well as fertility of their neighbors. Another fact is that cooperators with few neighbors are more likely to be eliminated. Especially in the case with large β , every individual needs to struggle to get links with cooperators for survival, which results in a rapid increase of $\langle k_C \rangle$. At the same time, the rapid drop of the cooperation level ρ_C for large β leads $\langle k_C \rangle$ to grow further.

The correlation of these two populations is also required to understand the evolution of cooperation. Let $\langle k_{XY} \rangle$ denote the average number of Y neighbors for X -player and $q_{X|Y}$ the conditional probability to find an X -player given that the adjacent node is occupied by a Y -player. At $\beta=0$ as the case in [17], $\langle k_{CC} \rangle$ is equal to the mean-field value $1+(k_0-1)\rho_C$ and one link larger than $\langle k_{CD} \rangle$ due to the very parent-offspring link (fig. 2(b)). So the individuals are randomly connected. With increasing β ,

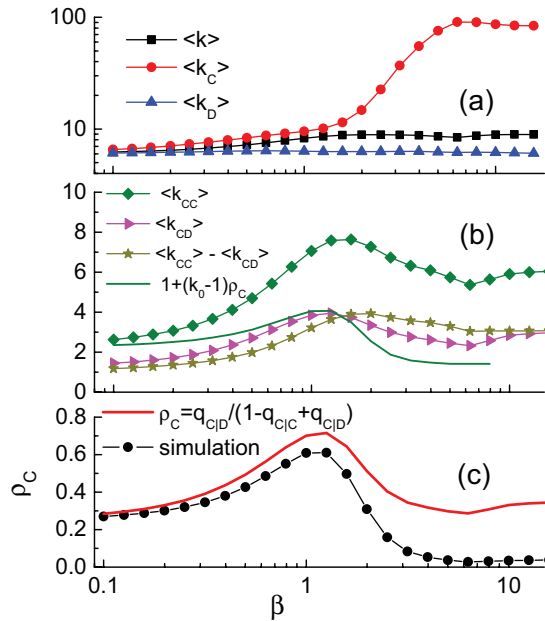


Fig. 2: (Color online) (a) The average degree of nodes $\langle k \rangle$, cooperators $\langle k_C \rangle$ and defectors $\langle k_D \rangle$ vs. β , respectively. $\langle k_C \rangle$ goes through a rapid rise for β ranging from 2 to 7, while $\langle k_D \rangle$ almost keeps initial value 6. (b) $\langle k_{CC} \rangle$ and $\langle k_{CD} \rangle$ and their difference vs. β . At $\beta = 0$, $\langle k_{CC} \rangle$ is one larger than $\langle k_{CD} \rangle$ due to the very parent-offspring link. With increasing β , both $\langle k_{CC} \rangle$ and $\langle k_{CD} \rangle$ increase to maximum near $\beta = 1$. The line is the mean-field value of $\langle k_{CC} \rangle$ for random connection. (c) ρ_C vs. β for the simulation and mean-field value using the data local connection information shown in (a) and (b). The parameter of the game is $b = 1.8$.

all individuals get closer to cooperators and both $\langle k_{CC} \rangle$ and $\langle k_{CD} \rangle$ increase up to maximum near $\beta = 1$, although $\langle k_C \rangle$ grows more rapidly for $\beta > 1$. It means more and more defectors get around cooperators. But cooperators also struggle to get more cooperative neighbors to survive, which leads $\langle k_{CC} \rangle$ to be larger than the mean-field value. The larger β is, the wider the difference grows. Anyway, these information of local connections can be used to infer the cooperation level ρ_C as a function of β for $\beta < 1$ pretty well as shown in fig. 2(c). Nonetheless, mortality selection gradually differentiates individuals' fate by their payoffs even though they are the same strategists, resulting in the larger and larger deviation of mean-field prediction [17] from simulation (fig. 2(c)). For $\beta > 1$, the cooperation level drops down to almost extinction, while the mean field predicts that the cooperation level maintains at a moderate value.

The global properties of the network structure, such as cluster of nodes and strategists and cooperating k -core [34], may shed some light on understanding the cooperation level. The cluster of nodes is the connected component of nodes and the cooperator cluster (CC) or defector cluster (DC) is the connected component fully occupied by cooperators or defectors, respectively. As β is large, defectors struggle to survive by getting more

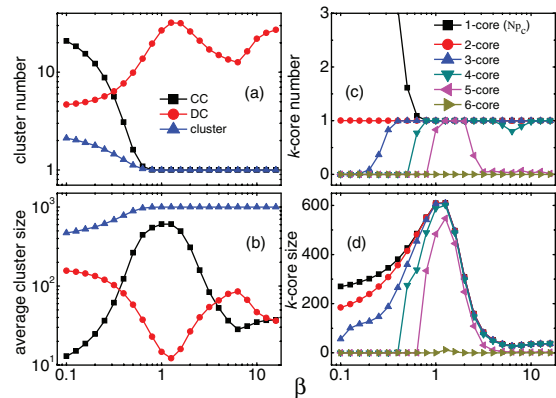


Fig. 3: (Color online) (a) Numbers of CC, DC and node cluster vs. β , respectively. With increasing β , the CC number and cluster number decline to 1 simultaneously. (b) The average size of CC, DC and cluster as a function of β , respectively. (c) The cooperating k -core number vs. β . Although there is more than one 1-cores (also CCs) at low β , there is only one k -core with $k > 1$. Note that there is almost no cooperating 6-core at the system with $k_0 = 6$. (d) The cooperating k -core size vs. β . The size of the cooperating k -core with all k gets to the maximum at $\beta = 1.26$. The parameter of the game is $b = 1.8$.

and more cooperative neighbors, while cooperators struggle for life by connecting together. Apparently, it will be difficult for the isolated cooperators to survive as well as to reproduce. Thus, cooperators assemble in a cooperator cluster and defectors surround cooperators. Increasing β induces the congestion of cooperators as well as that of nodes clusters (fig. 3(a)). At the same time, the sole CC alienates defectors and the DC number increases gradually until β increases up to 1.26. It is worth remarking that the mean-field analysis predicts the simulation result of ρ_C relatively well in this range of β (fig. 2(c)). For $\beta > 1.26$, the cooperation level ρ_C begins to drop rapidly and then defectors get more chance to link with each other, resulting in the decline of the DC number and in the increase of the DC average size (fig. 3(b)). On the other hand, fig. 3(c) shows us that the cooperating k -core with larger k emerges at larger β and disappears at smaller β . Cooperating k -core describes the tight level of CC. Here, $k_0 = 6$ limits the tightest CC to be the cooperating 6-core. But in the case of $b = 1.8$, just the cooperating 5-core exists at the range of β from 0.8 to 3, where ρ_C increases to maximum and begins to drop down. What makes sense is that cooperation level is still promoted most at $\beta = 1.26$ where the cooperating k -core size with k up to 5 gets to maximum as shown in fig. 3(d). When $\beta > 1.26$, the payoff amplification effect in mortality selection destabilizes the cooperating k -core and causes its collapse.

The effects of mortality selection on the dynamics. Interestingly, intensity β also makes sense in the dynamics. There is a lot of noise in the evolution at low β . Figure 4(a) shows that there is a large fluctuation of the cooperation

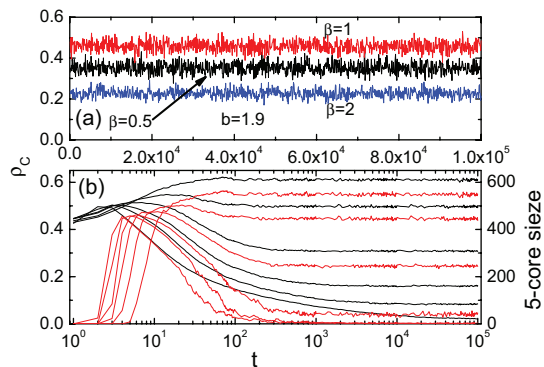


Fig. 4: (Color online) (a) Typical temporal evolution of ρ_C for $b=1.9$ at $\beta=0.5, 1, 2$ in one-time simulation. (b) The transient evolution of ρ_C (black line) and the size of the cooperating 5-core (red line) with various values of $\beta = [1.26, 1.59, 2.0, 2.51, 3.16, 10]$, corresponding lines from top to bottom. The larger β is, the more rapidly both ρ_C and cooperating 5-core size increase in the beginning, the earlier they get to vertexes and the lower cooperation level the system will be stabilized at. The parameter of the game is $b=1.8$.

level ρ_C , but the system reaches the steady state quickly and gets the highest cooperation level at $\beta=1$. With increasing β , the process becomes more and more determinate but the steady state needs more and more time to reach. We further analyze the average dynamical processes at various β as shown in fig. 4. When the cooperating 5-core emerges, a large β will hamper cooperators outside the cooperating 5-core to survive, and only cooperators in the cooperating 5-core could struggle for life. At this condition, cooperators gain more payoffs than defectors by forming a cooperating 5-core and there are a few cooperators outside this core. This process enhances cooperation at the beginning. After the cooperation level arrives at the vertex, defector's reproduction capacity will surpass its mortality and cooperators will be selected out to die with more probability. If one of the cooperators in this 5-core dies out, the cooperating 5-core will collapse down in a cascading way. At moderate selection intensity $\beta=1.26$, the system is stable at the maximal level after it reaches the vertex. Once the selection intensity β exceeds 1.26 , the cooperating 5-core goes through a little collapse, which decreases the cooperation level ρ_C . Thus, for any intensity $\beta > 1.26$, both ρ_C and the cooperating 5-core size increase rapidly to a lower vertex and then they both go through a transient time of prompt decreasing. What is more, increasing β prolongs the dropping time and leads the system to a lower cooperation level. Importantly, increasing β disrupts the cooperating 5-core rapidly, which results in a rapid drop of ρ_C , although there are some cooperators surviving outside the cooperating 5-core.

In the extreme case of $\beta = \infty$ as shown in fig. 5(a), ρ_C shows a power-law decay *vs.* time. Note that the values shown in fig. 1(a) for large β with $b > 1.2$ are the transient cooperation density not the equilibrium ones. The system may go into the absorbing state without any cooperator,

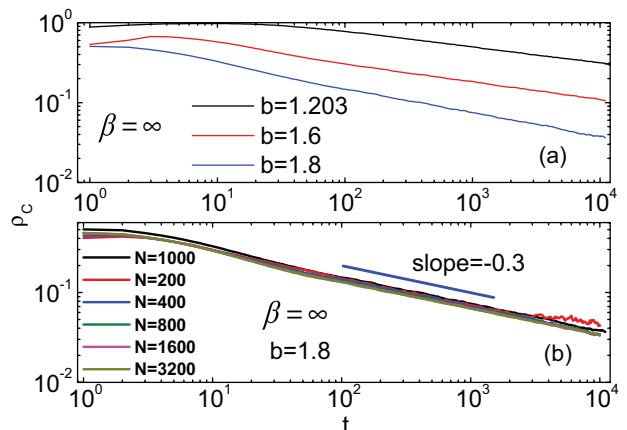


Fig. 5: (Color online) (a) Temporal evolution of ρ_C for $\beta = \infty$ at various b . The cooperation density shows a power-law decay at $b > 1.2$. (b) The power-law decay of the cooperation density at $\beta = \infty$ and $b=1.8$ is independent of the system size.

but the process needs enormous time which is unreachable now. If so, this discontinuous phase transition from all cooperators to all defectors corresponds to the classic PD game with normalized sucker's payoff $S=1-b$ on dynamical network without mortality selection [17], which is in consistency with the simple rule $\langle k \rangle < b/(b-1)$ for network reciprocity [15]. Thus, mortality selection with infinite intensity transforms the payoff matrix [27] by changing S from 0 to $1-b$. Notice that here $\langle k \rangle$ evolves with network dynamics as shown in fig. 2(a) and $\langle k \rangle$ is replaced by the initial value k_0 in the simple rule of network reciprocity.

What is more, the power-law decay of the cooperation level (fig. 5(a)) implies that the mean extinction time T has a power-law dependence on the system size N , $T \sim N^\gamma$. Due to the unreachable time cost for extinction time, we plotted the dynamics of ρ_C with various system size as shown in fig. 5(b). Excluding the finite-size effect, the dynamics are nearly the same for different system size. In the case of $b=1.8$, $\rho_C \propto t^\alpha$ with $\alpha = -0.3$. When the system is going into extinction of cooperators, $\rho_C = 1/N$ at $t=T$. Thus the mean extinction time T is proportional to a power-law function of the system size, like $T \propto N^{-1/\alpha} = N^\gamma$. This process corresponds to the so-called neutral evolution apart from Darwinian evolution [35,36,39]. Neutral evolution signals dominant influences of stochastic effects that occur from the unavoidable stochasticity of death and birth events and the finiteness of populations. In our case, $\beta = \infty$ minimizes the stochastic effect of the death event, but leads the evolution to the neutral regime. We argue that the space viscousness may play an important role in this abnormal result. Anyway, as for the dynamics, this discontinuous phase transition is distinct from the classic PD game without mortality selection in [17].

Summary. – Here we propose a very simple coevolution model of cooperation evolution with network

dynamics composed of mortality and fertility selections. Our study shows that the cooperation level ρ_C goes through a continuous phase transition *vs.* b for finite β and a discontinuous one for infinite β . The cooperation level is enhanced most at $\beta \approx 1$ for any temptation b . Connectivity and global properties of the network structure such as clusters and cooperating k -core have been investigated for understanding the cooperation level ρ_C as a function of β . As β increases to the optimal cooperation level, all cooperators gather together to form a cooperator cluster and all defectors surround this cluster to form a node cluster of the whole population. After that, increasing β tightens the cooperator cluster to promote the cooperation level and gives rise to a cooperating k -core with larger and larger k . However, too large β destroys the cooperating k -core rapidly which results in a rapid drop of ρ_C and invalids the mean-field prediction completely after ρ_C rises to the maximum. The critical value of b at $\beta = \infty$ is the same as that in the case $\beta = 0$, whose transition corresponds to the classic PD game with normalized sucker's payoff $S = 1 - b$ on a dynamical network without mortality selection [17]. This result indicates that infinite mortality selection can transform the payoff matrix such as parameter S by changing from 0 to $1 - b$. What is more, the dynamics of ρ_C undergoes a power-law decay, which is considered as the so-called neutral selection usually induced by large stochasticity of basic events of death and birth and the finiteness of population.

In future work, we will devote to the description of the collapse dynamics of the cooperating k -core and exploration of the mechanisms to preserve the cooperating k -core. More importantly, our simple coevolution model may pave the way for future studies in this field by being extended. For example, including the inheritance of successful relationships of parent's neighbors as well as a strategy will promote the cooperation level further.

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