Cyclic coevolution of cooperative behaviors and network structures

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This paper aims at understanding coevolutionary dynamics of cooperative behaviors and network structures of interactions. We constructed an evolutionary model in which each individual not only has a strategy for prisoner's dilemma to play with its neighboring members on the network, but also has a strategy for changing its neighboring structure of the network. By conducting evolutionary experiments with various settings of the payoff matrix, we found that the coevolutionary cycles of cooperative behaviors of individuals and their network structures repeatedly occurred when both the temptation to defect and the cost for playing a game were moderate.

I. INTRODUCTION

Prisoner's dilemma (PD) has been widely studied for evolution of cooperation in various scientific fields [1]. A spatial locality has been introduced into evolutionary models as more realistic and ecologically plausible situations of interactions. It is often said that the regular spatial locality facilitates the evolution of cooperation and also brings about the higher degree of diversity in comparison with nonspatial models [2–5]. It is because cooperators can grow a cluster of their own strategies while defectors cannot. Nowak and May adopted a two-dimensional deterministic PD model which consists of the always cooperating or defecting strategies [2]. They observed chaotically varying spatial arrays, in which both strategies persist in shifting patterns when the payoff value for the temptation to defect is modest. Grim reported that a strategy, which is twice as generous as the "GTFT" (cooperates on the first round, cooperates with the probability of 1/3 when the opponent defected on the previous round, otherwise does whatever its opponent did) turned out to be optimal with a two-dimensional spatialization of a stochastic iterated PD model [3]. Suzuki and Arita investigated how local interactions among individuals affect the benefit and the cost of learning through the evolutionary experiment of two-dimensional iterated PD game strategies of which the phenotypic plasticity were able to evolve [6,7]. They reported that a cooperative population more easily emerged through the interaction between evolution and learning called the Baldwin effect [8] as the degree of the spatial locality became large.

The structures of existing networks of human interactions are more complex than the ones adopted in the studies above and have several complex properties such as the small-world [9] or the scale-free [10]. There are a lot of discussions on the evolution of cooperation on the complex network structures [11–15]. For example, Watts showed that the small-world properties can facilitate the emergence of cooperation in the evolution of generalized tit-for-tat strategies on α graphs [11]. Masuda showed the negative effects of the participation costs on the emergence of cooperation on scale-free networks [14]. On the other hand, Ohtsuki *et al.* pointed out that whether cooperative strategies occupy the population or not depends on the relationship between the payoff values of the game and the average degree regardless of the actual topologies of the network [15].

These studies are based on the fixed and static networks of interactions. However, in a real world, it is plausible that the cooperative behaviors and the network structures can coevolve by affecting their evolutionary dynamics mutually. Zimmerman constructed a model in which the neighboring network structure of an individual can be changed according to the result of the games with neighbors in addition to the evolution of the PD strategies [16]. Specifically, they adopted a simple rule that the links between mutually defected individuals were rewired with other randomly selected individuals. They found that the emergence of the cooperative leader who had the largest payoff in the cluster of cooperative agents brought about the global cooperation. Luthi adopted another rewiring rule with which each agent decides whether it rewires links with defectors or not by comparing its payoff with the fixed threshold. They showed that the clusters of cooperative strategies emerged and defectors were isolated when the value of the threshold was modest [17]. Also, Pacheco *et al.* discussed the coevolution of strategy and structure based on interplay between the active linking process and the strategy updating process [18]. These studies clarify a strong impact, which the evolution of network structures has on the evolution of cooperation. Nevertheless, the clarification is based on the strong assumption that all agents adopt the same fixed rule for rewiring. It must be

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TABLE I. Set of genetic information.

Gene\Value	0	1
g_{pd}	Defect	Cooperate
g_{na}	Does nothing	Creates a new link with a randomly selected individual
g_{ns}	Does nothing	Removes all links with the individuals with the same action
g_{nd}	Does nothing	Removes all links with the individuals with the different action

recognized that each agent has its own strategy for modifying its neighboring network.

Also, Hauert *et al.* and Szabó *et al.* constructed several models of the evolution of cooperation with voluntary participation in public goods games [19,20]. In their model, each agent takes one of three strategies: cooperator, defector, and loner (who does not participate in a game but obtains a fixed payoff). It was shown that the unending cyclic evolution of these strategies occurred in a large well-mixed population. They also reported that the evolutionary dynamics of the strategies depended on the fixed structures of interactions and it resulted in the spatiotemporal patterns on the spatially local environments. In addition, the hierarchical evolution of metalevel decision making strategies (such as the coevolution of actions and imitation rules) was recently discussed by Chavalarias [21].

The purpose of this study is to understand coevolutionary dynamics of cooperative behaviors and network structures of interactions. We constructed an evolutionary model in which each individual not only has a strategy for PD to play with its neighboring members on the network, but also has a strategy for changing its neighboring structure of the network. By conducting evolutionary experiments, we observed coevolutionary cycles of cooperating behaviors and the network structures.

II. MODEL

N individuals are represented as nodes in the network and each (nondirectional) link between the two nodes represents that a PD game will be conducted between the two individuals. Each individual has the information of the four genes as illustrated in Table I. g_{pd} represents a strategy for the PD game (defect: 0, cooperate: 1). A set of g_{na}, g_{ns}, and g_{nd} (0 or 1, respectively) represents the strategy for modifying its neighboring network structure.

Each step consists of the three phases defined as follows.

(1) In this model, each game is a two-person version of the prisoner's dilemma game. The players obtain the payoffs defined in Table II depending on the pair of their actions. Note that the σ is a constant which decides the relative difference in the payoff between the individual who played a game and the individual who did not play. Each individual plays PD games against all neighboring (directly connected) individuals, respectively, and obtains payoffs. The total payoff is taken as the fitness of each individual.

(2) For each individual, if there are any neighboring individuals whose fitness is higher than that of the individual itself, the genetic information of the focal individual is replaced by that of the neighboring individual with the highest fitness. If there is more than one individual whose fitness is the highest among neighbors, an individual is randomly selected from them. During this process, the inversion of each genetic value occurs with a probability p_m, respectively. Note that the actual updates of the genetic information occur at the same time.

(3) Each individual modifies its neighboring network structure by using the results of actions in phase 1 and its current network modifying strategies. If $g_{ns}=1$, the individual removes all links with the individuals whose action is the same as that of the individual itself. If $g_{nd}=1$, the individual removes all links with the individuals whose action is different from that of the individual itself. In addition, if $g_{na}=1$, the individual creates a new link with a randomly selected individual who was not connected with itself in phase 1.

These steps are conducted repeatedly [23]. Note that the modified order of phases "3-1-2" is also plausible in that the evolution takes place after both genes are expressed in each step. However, the actual process of evolution with this order is basically the same as that of the original one except for the initial step if we assume that each agent modifies the network depending on the results of games in the previous time step.

III. RESULTS

We conducted evolutionary experiments using the following parameters: $N=1000$ and $p_m=0.005$. We adopted the condition for the payoff matrix $R=1.0$ and $P=S=0.0$ for simplicity, which is often adopted in other studies ([2], for example). The initial population was generated on the condition that each value of genes was randomly assigned 0 or 1, and the network was the one-dimensional regular network in which each individual was connected with six neighboring individuals.

A. General analyses

We conducted experiments using various settings of the parameters for the payoff matrix T and σ, and found that

TABLE II. Payoff matrix of Prisoner's dilemma.

Player\Opponent	Cooperate	Defect
Cooperate	$(R-\sigma, R-\sigma)$	$(S-\sigma, T-\sigma)$
Defect	$(T-\sigma, S-\sigma)$	$(P-\sigma, P-\sigma)$

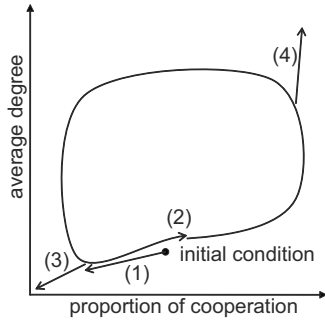(Player's score, opponent's score) $T>R>P>S$.

FIG. 1. Typical evolutionary scenario of the population.

these parameters strongly affect the evolutionary dynamics of the population. Figure 1 illustrates typical evolutionary pathways which were characterized by the transition of the average proportion of cooperative strategies and the average degree of the individual.

Starting from the initial population, (1) both indices rapidly decreased to the small values due to the invasion by isolated defectors. The decrease in the average degree is due to the asymmetry between the creating and destructing process of the links in that each agent can create only a link per step while it can remove an arbitrary number of links. Next, the population exhibited (2) the cyclic transitions in which both indices repeated the increase and subsequent decrease alternately. However, the cycles were transient stable, then the population converged to the state in which both indices were quite (3) small or (4) large. Once the population converged to case (3), almost all individuals had the strategies that did not connect with the other individuals by themselves, and the population never returned to case (2). On the other hand, in case (4), the temporal decrease in the proportion of cooperation was observed, and the population occasionally returned to case (2).

How long and often each pathway appears depends on the experimental conditions of T and σ. Figure 2 shows (i) the average proportion of cooperative strategies, (ii) the average degree, and (iii) the frequency of the occurrence of the cycles (explained later) through 500 steps in various cases of T and σ, respectively. The x and y axes correspond to the conditions of T and σ, and the z axis represents each value of the index on the corresponding condition. Each value is the average over 20 trials where each index has been averaged over 500 successive time steps without the lead-in time.
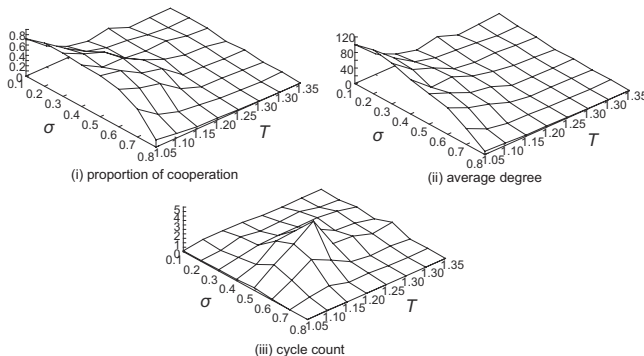
The first thing we notice is that the average proportion of cooperation was the largest (0.83) when T was the smallest (1.05) and σ was relatively small (0.3) as shown in Fig. 2(i). The population often showed the trajectory (4) and the average degree became large. It is clear that the smaller T becomes, the larger the proportion of cooperation becomes because T defines the benefit of the success in the defection. A smaller σ is beneficial for cooperators in that it reduces the cost for playing a game, but it also reduces the payoff difference between the mutual defection and not to play a game. Due to the balances of these two different effects of σ, the proportion of cooperation was supposed to be the largest when σ was relatively small. On the other hand, the population quickly showed the trajectory (3) and converged when both parameters were sufficiently large.

Also, we see that the proportion of cooperation was relatively large when both parameters were moderate. In these conditions, the coevolutionary cycles (2) were frequently observed. Figure 2(iii) shows the average count of the cycles. Actually, we counted the occurrence of a cycle as follows: We divided the trajectory space in quarters using (0.3, 20) so as to accurately count the occurrences of cycles which will be discussed later. We specifically adopted the relatively smaller values in order to detect the rapid decrease in both indices during the cycle explained later. Then, we counted when the trajectory went through four areas counterclockwise, starting from the bottom left area. We see that there is a peak of the cycle count and the value became the largest, 4.9, when $T=1.20$ and $\sigma=0.5$. These cycles often continued over 500 steps around this condition.

This cycle composed of the processes in which the three different strategies alternately dominated the population is as follows: Starting from the sparsely connected population in which the strategy D110 occupied the whole population, the small cluster of cooperative strategies C100 could gradually grow and occupied the population. Note that the first character in the strategy represents the strategy for the game g_{pd} [C=cooperate (1), D=defect (0)], and the other three bits represent the network modifying strategy: g_{na}, g_{ns}, and g_{nd}, respectively. The C100s continued to increase the average degree, and then the network became globally connected. In such a situation, the defectors D100 rapidly occupied the population without changing the network structure. Finally, the population returned to the population of the D110s which removed the links with defectors.

B. Effects of changes in environmental settings

These results were based on the particular environmental setting on which we could clearly observe the cyclic coevolution of cooperative behaviors and network structures. It is important to investigate the effects of other environmental settings on the evolutionary dynamics. We conducted additional experiments in which there were variations in the settings or the network modifying rule as follows: (1) $N=2000$ (twice the default setting), (2) $p_m=0.05$ (ten times larger than the default setting), (3) $P=0.1$ ($P>S$), (4) an empty initial network (no links), (5) a random initial network (in which two nodes are connected with the probability

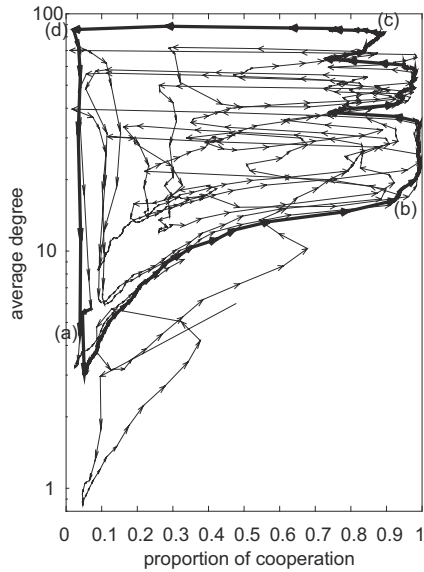FIG. 2. Effects of T and σ on several indices.

FIG. 3. Cycles of the proportion of cooperation and the average degree when $T=1.20$ and $\sigma=0.5$. The four typical steps [(a) 389, (b) 415, (c) 462, and (d) 471] are indicated and the transition from the 389 to the 471 step is drawn in a thick line, which are discussed in Sec. III C.

0.06), and (6) the limited removal of links (the removal of at most K links in each step). In each case, the other settings are the same as the ones adopted in the original experiments, and we mainly focused on the effects of these changes in the case of $T=1.2$ and $\sigma=0.5$ in which the cyclic behaviors were observed the most frequently in the original settings.

First, we changed several settings of the parameters (1, 2, and 3). In case (1) $N=2000$, there were no significant differences in the global behaviors of the population compared with those with the default setting. On the other hand, the cyclic behaviors were observed in several trials also in case (2) $p_m=0.05$, but the population quickly converged to the defectors from the initial condition in more than half of the trials. It is supposed to be due to the fact that the clusters of cooperators are difficult to grow from the initial population because of the invasion by mutant defectors that appeared frequently with such a high mutation rate. In case (3) $P=0.1$, the cyclic behaviors more quickly transited to the convergent state that consisted of the defectors in comparison with those in the original setting; but there were no significant differences in the basic dynamics of the cycles.

We also conducted experiments with different settings of initial network structures or network modifying rules [(4)–(6)]. In case (4) an empty initial network and (5) a random initial network, both changes in the initial topology slightly increased the frequency of the rapid convergence of the population to the defectors. It is because that the locality of the regular network in the default initial setting facilitated the stable survival of the cooperators from the initial condition. However, once cyclic behaviors appeared, they were the same ones as observed in the case with the default setting.

In case (6), each agent removes only several links to agents with the same (different) action. Specifically, each agent can remove at most K links in each step. If the number
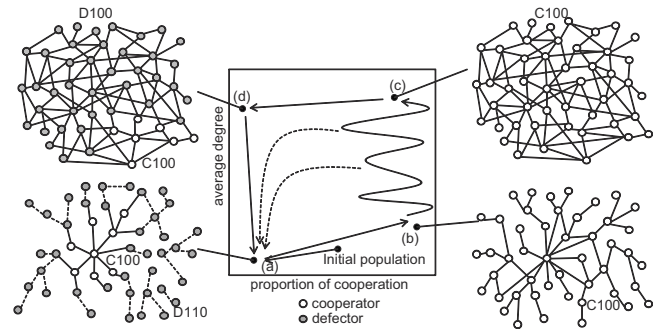
of candidate links (L) is smaller than K, the agent removes all of them. Otherwise, it removes K links which are selected randomly from the L links. We conducted experiments with $K=10$. In this limited case, the evolutionary dynamics generally became slow compared with the original case. The similar cyclic transitions of strategies as explained in the paper appeared but the average degree of state (a) and (c) became higher and higher through the repeated occurrences of the cycles. These are due to the fact that the decrease in the average degree during the transition from state (c) to (d) became smaller than its increase during the transition from state (a) to (c) because of the limitation of the removal of the links. As a whole, we can say that the observed scenario of the cyclic coevolution was generally robust against the changes in environmental settings.

C. Coevolutionary cycles of cooperative behaviors and network structures

In the previous section, we observed the coevolutionary cycles of cooperation and network structures when T and σ were moderate. Previous discussions on the evolution of cooperation often focused on the condition in which cooperative behavior successfully occupies the population. However, the cooperative relationships are not always permanently maintained in real personal relationships. It is an essential aspect of the real cooperative relationships that they can suddenly collapse and then another new cooperative relationship emerges. It is expected that the observed cycles in our model reflect such a dynamic property of the real cooperative networks. Thus we investigate in detail the emergent mechanism of these coevolutionary cycles.

Figure 3 is an example trajectory of the population on the space of the proportion of cooperation and the average de-
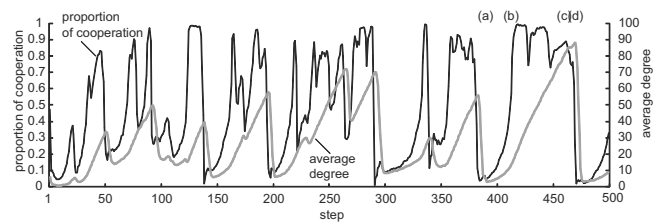

FIG. 4. The dynamics of the coevolutionary cycles. Figures on the left and right side illustrate the typical population in each state.

FIG. 5. Evolution of the proportion of cooperation and the average degree.
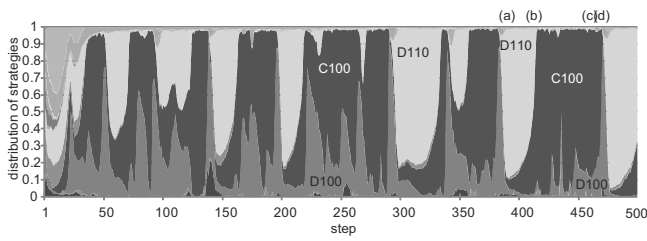
FIG. 6. Evolution of the distribution of strategies.

gree when $T = 1.20$ and $\sigma = 0.5$. Note that the y axis is in logarithmic scale because the peak value of the average degree varies widely among cycles. Although there were a large amount of fluctuations in the indices, a cycle can be typically divided into the four processes as shown in Fig. 4. The example images of the network in the typical four states [(a)–(d)] are shown at the same time. Figures 5 and 6 show the transition of both indices and the distribution of the strategies through generations in the same experiment as in Fig. 3, respectively. Figure 7 also shows the transition of the average clustering coefficient and the interface density. The former is normalized with that of a random network with the same number of links and the same number of the individuals that connect with more than two individuals. The latter is the proportion of links that connect individuals with different strategies for the prisoner's dilemma.

Here, we explain the typical dynamics of the cycles by focusing on the transition from the 389 to the 480 step. At around the 389 step (a), the population consisted of a large number of D110s as illustrated in Fig. 4(a). They remove links with defectors and connect to a randomly selected individual at each step. Because most of the population were defectors, they were repeating the rewiring with randomly selected defectors every step [the dotted lines in Fig. 4(a)].

Figures 8 and 9 show the degree distribution and the correlation between the average fitness and the degree of individuals in the typical four states, respectively. Although the average degree of the defectors in Fig. 8(a) was smaller than those in the other states, their degree distribution fitted well with the Poisson distribution (with the average degree being 3) because the network of D-D links was close to an Erdos-Renyi network. As we see from these figures, there were a lot of defect individuals with a small number of links and the fitness of the defectors tended to become small as their degree increased.

At the same time, there were a relatively small number of C100s. Although the fitness of the cooperators also tended to become smaller as their degree increased, we also see that
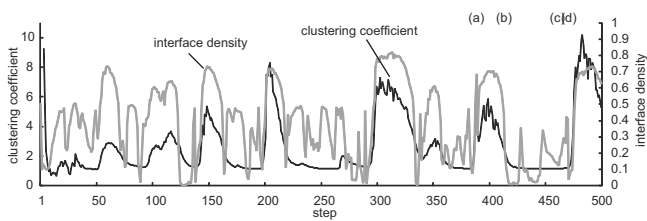

FIG. 7. Evolution of the average clustering coefficient and the interface density.
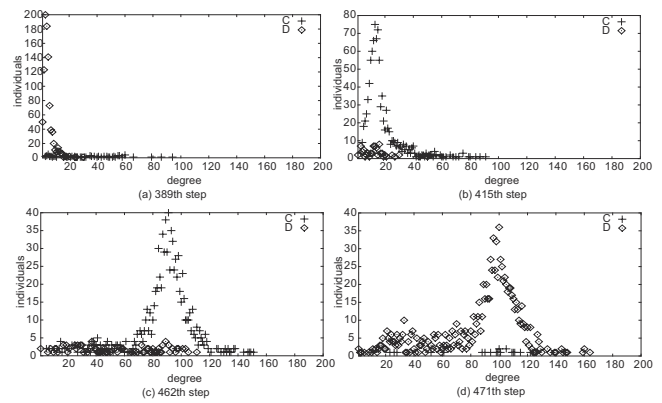

FIG. 8. Degree distribution.

the average fitness was around 2.0 among the individuals whose degree was 11 and 35. These intermediately connected and cooperative strategies formed a cooperative cluster in which they play a hublike role in that they are connected with a lot of cooperators with the small number of links. These clusters are basically robust because the genes of peripheral individuals are always replaced by those of the hublike individuals of which the fitness is high due to the mutual cooperation. Furthermore, the clusters can gradually increase their size by invading the D110s that connected with the cluster of cooperators by chance. Actually, as shown in Fig. 7, we see that the clustering coefficient and the interface density increased around step (a) in which the proportion of the cooperative strategies began to increase. This means that the number of the D-D links rapidly decreased due to the invasion by the D110s, and at the same time, the highly clustered cooperators C100s successfully survived and began to connect with the defectors. As a result, the proportion of cooperative strategies gradually increased, and the average degree slowly increased. In addition, the individuals with $g_{nd} = 1$ such as C101 did not appear in this process, although it seems beneficial for cooperators to remove links with the defectors voluntarily so as to avoid being exploited. However, in this model, they remove the links to the opponents with different action regardless of their success in the invasion into the opponents. This makes them difficult to form
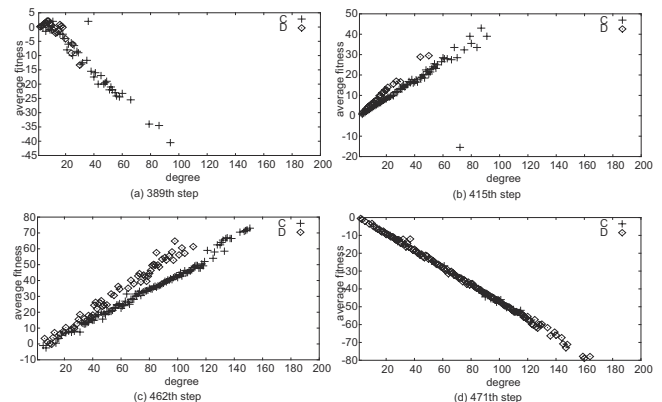

FIG. 9. Correlation between the average fitness and the degree of individuals. Each y value represents the average fitness among individuals whose degree is the same as the x value.

the clusters of cooperators compared with C100s.

The population was occupied by the cooperative strategies at around the 415 step (b) as illustrated in Fig. 4(b). In such a situation, the fitness has a positive relationship with the degree as shown in Fig. 9(b). Thus the C100s could stably add links with each other at every step, and then the whole population became highly connected at around the 462 step (c) as illustrated in Fig. 4(c). During this process, we often observed the temporal invasions by D100s as shown in Fig. 6, which made the interface density fluctuate.

In Fig. 9(b), we see that the higher the degree of the agent was, the higher fitness it had. It means that, among the existing individuals on the network of state (b) in Fig. 4(b), the cooperative agents with a lower degree tended to be invaded by the defectors because of their lower fitness compared to those with a higher degree. This is also similar in the state (c) except for the increase in the fitness and degree due to the increase in the number of C-C links. However, the clustering coefficient became smaller through the transition from state (b) to (c) because the cooperators connected with randomly chosen individuals. This makes it easier for defectors to invade the whole population because the network becomes globally connected. Finally, the whole population was rapidly occupied by D100s without changing the average degree, and it became highly connected and defect-oriented at around the 471 step as illustrated in Fig. 4(d).

In the population of the highly connected and defectors, it is more adaptive not to play a game than to receive the punishment of mutual defection as shown in Fig. 9(d). Thus the individuals with the strategy D110s appeared. They were basically mutants of D100s. They can occupy the population quickly because they obtain higher scores by removing links with defect strategies, and further connecting randomly selected individuals so as to spread into the remaining cluster of D100 individuals. As a result, the average degree rapidly decreased, and the population returned to state (a) at around the 480 step. During this process, the C110s did not appear because they were not able to form a cluster of cooperators

because they removed C-C links, and thus are easily dominated by defectors.

IV. CONCLUSION

We have discussed the coevolutionary dynamics of cooperative behaviors and network structures of interactions. We constructed an evolutionary model in which each individual not only has a strategy for the prisoner's dilemma to play with its neighboring members on the network, but also has a strategy for changing its neighboring structure of the network. By conducting evolutionary experiments, we observed coevolutionary cycles of cooperative behaviors of individuals and their network structure of interactions when the temptation to defect and the cost for playing a game were moderate. In addition, the behaviors of the strategy D110 in our model partly corresponds to the loner in Hauert and Szabó's models [19,20], and our results show that such a cyclic mechanism can also occur in the context of the coevolution of cooperative behaviors and network structures.

It should be emphasized that the observed coevolutionary dynamics implies the dynamic aspect of the emergence and collapse of cooperative networks in a real world as follows: In the population of isolated individuals, the small clusters of the cooperative relationships can gradually grow and occupy the whole population. However, as the cooperative relationships get matured in that individuals become highly connected, the network tends to be infested with free-riders. The invasion by the free-riders into the individuals with higher degree yields the mutually defecting population, and finally the whole network collapses. We believe that our findings can help further understanding of dynamic aspects of the cooperative behaviors in real biological systems. Future work includes the experiments and analyses with the iterated games or other genetic representations of network modifying strategies such as an addition of a link to a friend of a friend [22].

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