

Paper:

Effects of Ecological Inheritance on Coevolution of Cooperative Behaviors and Physically Niche Constructing Behaviors

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Niche construction is a process whereby organisms that modify their own or others' niches through their ecological activities. Recent studies have revealed that changes in social structures of interactions caused by social niche construction of individuals can affect seriously the evolution of cooperation. However, such a social niche also could be changed indirectly by a modification of their physical environment. Our purpose is to clarify the coevolution of cooperative behavior and physically niche-constructing behavior that modifies social niche indirectly. For this purpose, we constructed an evolutionary model in which each individual has not only a strategy for a spatial Prisoner's Dilemma but also has traits for a niche-constructing behavior for modifying its physical environment that can limit social interactions between neighboring individuals. By conducting evolutionary experiments, we show that a cyclic coevolution between cooperative behavior and niche-constructing behavior occurred in the situation with no or low degree of ecological inheritance, in which the constructed niche could not be inherited in succeeding generations at all. Conversely, when the degree of ecological inheritance was high, the evolution of cooperation was promoted by the emerged environmental structure constructed by the evolved niche-constructing behavior. We also show that the condition for each scenario to occur depends on the settings of the payoff parameters as well as the degree of ecological inheritance.

Keywords: evolutionary game theory, ecological inheritance, cooperative behavior, niche construction, coevolution

1. Introduction

1.1. Niche Construction and Ecological Inheritance

Niche construction is known as a process, performed by organisms, that modify their own or the others' niches (selection pressure) through their ecological activities (Fig. 1). The niche-constructing processes are observed in various taxonomic groups such as bacteria (de-

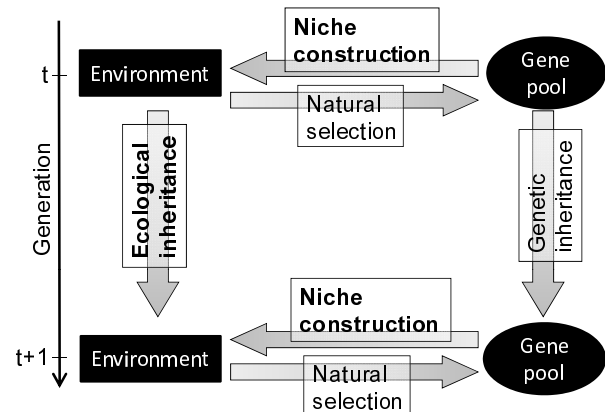


Fig. 1. Diagram of niche construction and evolution.

composition of vegetative and animal matter), plants (production of oxygen), nonhuman animals (nest building) and humans (cultural process) [1]. All living organisms are more or less performing niche constructions, and there are many evidential facts that they have strong effects on the evolution of organisms although they had been neglected for a long time in evolutionary biology.

Niche construction enables organisms to inherit ecologically from their ancestral organisms, as well as genetically. Ecological inheritance is the inheritance, via an external environment, of one or more natural selection pressures modified by niche-constructing organisms in the previous generations. Accumulation of environmental changes due to ecological activities among mass organisms across generations can have a large influence even on global environment (e.g. atmospheric states). It seems to have affected genetic inheritance significantly. For instance, organisms can access and utilize burrows or nests (e.g. beavers' dams) constructed by their ancestors or other organisms in the previous generations, which can affect the evolution of their nest-building behaviors in subsequent generations. Accumulation of environmental changes also can be harmful for some organisms (e.g. accumulation of oxygen which is maladaptive for anaerobic organisms, human environmental pollution). However, mechanisms of effects of ecological inheritance are still poorly understood. We believe that there exist the com-

plex relationships between ecological inheritance system and genetic one.

1.2. Evolution of Cooperation and Social Niche Construction

The evolution of cooperation has been one of the major problems in biology and numerous attempts have been made to find key factors related to the evolution of cooperative behaviors. It has been shown that structures of interactions can affect the evolution of cooperation significantly. As a pioneering study on this effect, Nowak and May showed that the spatial locality facilitates the evolution of cooperation, using a two-dimensional deterministic Prisoner's Dilemma (PD) [2]. This is because cooperators can grow a cluster of their own strategies while defectors cannot on the regular lattice structure of interactions. Furthermore, Nowak discussed network reciprocity, which is a generalization of spatial reciprocity, as one of five mechanisms for the evolution of cooperation [3].

In recent years, extensive studies have been made on coevolution of dynamic network structures of interactions and cooperative behaviors [4–10] in the field of adaptive network that discusses the coevolutionary dynamics of network structures and states of nodes. This is because the structures of existing networks of human interactions are more complex than the ones adopted in classical studies, and dynamically changing. Zimmerman and Eguíluz constructed a model in which the links between mutually defected individuals can be randomly disconnected [10]. 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. Pacheco et al. discussed the coevolution of strategy and structure based on interplay between the active linking process and the strategy updating process [5]. Tanimoto recently discussed a relationship between assortativity (measured as the degree correlation of the connected nodes) in the evolved network and emerging cooperation in the PD, showing that the weak (or strong) dilemma makes the assortativity of emerging networks positive (or negative) [8].

Among these studies, the network structures of interactions could be interpreted as a social niche realized by individuals' behaviors for social interactions. In this sense, the network modification processes explained above correspond to social niche constructions that modify the selection pressure for cooperation, although the procedures for network modification are shared among individuals and do not evolve.

1.3. Evolution of Social Niche Construction

Also, there are studies that focused on the evolution of strategies that modify network structures of interactions. Suzuki et al. constructed an evolutionary model in which each individual not only has a strategy for PD to play with its neighboring individuals on the network, but also has its own strategy for changing its neighboring structure of

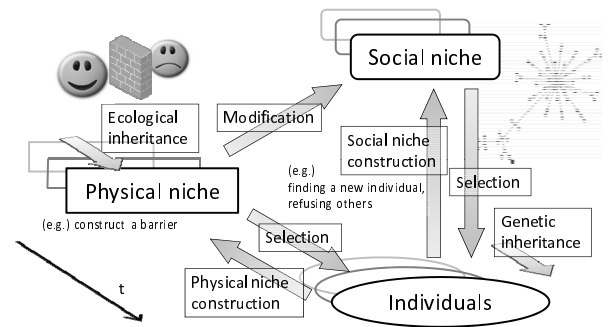


Fig. 2. A relationship among individuals, physical niche and social niche.

the network [7]. They showed that coevolutionary cycles of cooperative behaviors of individuals and their network structures of interactions occur when both the temptation of defect and the cost for playing a game are moderate. This cycle consisted of the following processes: $\dots \rightarrow$ the invasion by isolated defectors $\rightarrow$ the emergence of cooperative clusters $\rightarrow$ the growth of the globally cooperative population $\rightarrow$ the rapid invasion by globally interacting defectors $\rightarrow \dots$.

Segbroeck et al. constructed a model in which each individual has a different strategy (probability) to break links to defectors as well as a strategy for PD [6], and both are allowed to evolve. They reported that the diversity of social reaction promotes cooperation.

Hauert et al. constructed a model of the evolution of cooperation with voluntary participation in public goods game [11] which is equivalent to the n -person PD [12]. In this model, a loner, who does not participate in a game but obtains a fixed payoff, is more adaptive than mutually defected individuals. Thus an unending cycle of the three strategies ($\dots \rightarrow$ cooperators $\rightarrow$ defectors $\rightarrow$ loners $\rightarrow$ cooperators $\rightarrow \dots$) occurred.

Because this type of strategies modifies a local structure of interactions, they can be interpreted as socially niche-constructing traits or genes.

1.4. Effects of Physical Niche Construction on Social Niche and its Evolution

These social niches, however, can be changed not only by direct social actions performed by individuals but also can be changed indirectly by a modification of their physical environment. **Fig. 2** shows an image of the relationship between social niche, physical niche and individuals. A social niche construction corresponds to finding a new individual to interact or refusing the offer from another to interact, for example. Because a physical niche construction can constrain the social niche, it may modify the social niche indirectly. For example, an individual can construct a barrier in order to decrease the chance of encounter with another instead of refusing the interaction with it directly. While previous research has focused on the evolution of social niche construction, there are few

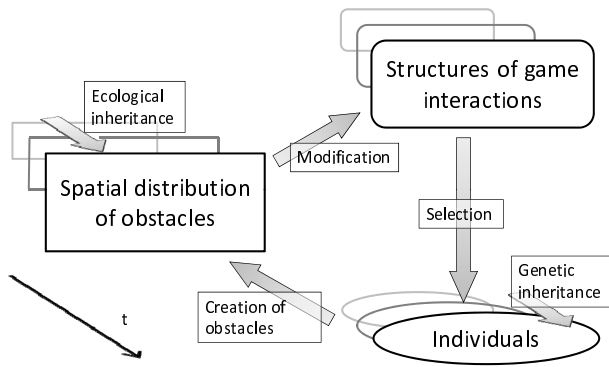


Fig. 3. A conceptual diagram of our model.

studies that focused on the effects of an indirect social niche construction via a physical niche construction on the evolution of cooperative behaviors.

The purpose of this study is to clarify coevolution of physical niche construction and cooperative behaviors via indirect effects of physical niche construction on social niche. For this purpose, we have constructed an agent-based evolutionary model by introducing an environmental factor that can modify structures of interactions into a two-dimensional spatial PD [13]. Fig. 3 shows the relationship between factors that we incorporated into our model from the ones in Fig. 2. The positions of the factors in Fig. 3 correspond to those in Fig. 2. Specifically we have supposed that each individual can place an obstacle, called “peg,” against neighbors that limits interactions with neighbors as a physical niche construction. Individuals have both a gene for strategy of PD and genes to modify their neighboring environment. We have also introduced ecological inheritance in which modified environment is inherited to next generation.

We conducted evolutionary experiments focusing on the effects of the degree of ecological inheritance on evolution, which has not been discussed clearly in the context of the evolution of cooperation. First, we show that a cyclic coevolution between cooperative behavior and niche-constructing behavior occurred in the situation with no or a small degree of ecological inheritance. This cycle turned out to be strongly related to the cycles observed in the prior research mentioned above. Secondly, we also show that when the degree of ecological inheritance was high, physical niche construction evolved but it facilitated the stable evolution of cooperation by creating an adaptive environmental structure that was beneficial for cooperators. However, when the degree of ecological inheritance was excessively high, niche constructing behavior did not evolve. We also report on the effects of the parameters of payoff matrix for the PD on these scenarios.

2. Model

There are toroidal $N = W \times W$ lattice sites and each site contains a single individual as shown in Fig. 4. Each indi-

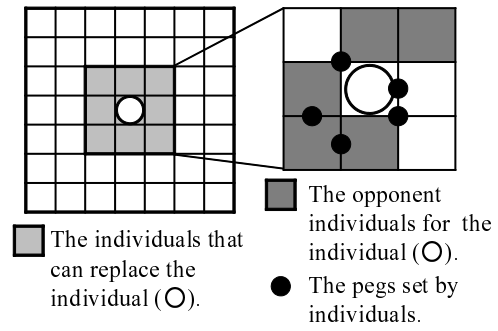


Fig. 4. The spatial locality and the effect of pegs.

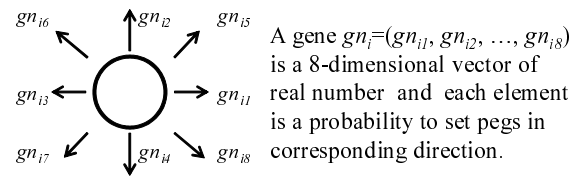


Fig. 5. A gene gn_{ij} that determines niche-constructing behavior.

vidual i ($i = 0, \dots, N - 1$) has a gene gs_i which describes a strategy for the PD game (Cooperate or Defect). It also has a gene gn_{ij} that determines its niche-constructing behavior. Each individual can place an obstacle, called “peg,” between the focal individual and its eight neighboring individuals according to its gn_{ij} respectively (described in detail later). A peg between two individuals limits interactions (playing games) between them. Both individuals can place a peg in between them, but just one peg is allowed to be placed. Thus, an environmental condition is represented as a configuration of pegs over the lattice sites.

Specifically, each generation consists of the four phases defined as follows.

2.1. Niche Construction

Each individual i sets a peg in between its own site and each neighboring site according to $gn_i = \{gn_{ij} \in [0, 1] | j = 1, 2, \dots, 8\}$. gn_{ij} is a probability to set a peg against the neighbor in its corresponding direction j illustrated in Fig. 5. Note that if a peg is already set on the place where an individual try to set, it does nothing.

2.2. Playing Games

In this model, each game is a two-person version of the PD. Each individual plays a PD game with each neighboring individual (Fig. 4 right) only when there is no peg in between the two individuals. They play a game and obtain a payoff of the PD if there is no peg between the focal individual and its neighbor (as a table below). They do not play a game and obtain a constant payoff σ if there is a peg between them.

{	play game:		Cooperate	Defect
		Cooperate	R	S
		Defect	T	P
	no game:	σ		

In this sense, the social niche (the network of interactions) can be modified by the physical niche construction in this model. A set of payoffs must satisfy the inequality $T > R > \sigma > P > S$. This means that the payoff for not playing a game is better than that of a mutual defection in addition to that the payoff satisfies the standard PD condition.

2.3. Genetic Evolution

For each individual, the genetic information in the next generation is replaced by that of the individual with the highest fitness among neighboring individuals and itself (Fig. 4 left). If there are more than one individual whose fitness is the highest in the nine individuals, an individual is randomly selected among them. Note that there is no effect of pegs on this procedure. Also, a genetic mutation can occur with a constant probability for each gene. gs_i inverts with a probability p_s , and gn_{ij} is replaced by a uniform random value in its domain with a probability p_n . The actual updates of the genetic information occur at the same time.

2.4. Ecological Inheritance

Each existing peg is ecologically inherited to the next generation with a probability p_e , which is defined as a parameter that determines the degree of ecological inheritance of the environmental configuration. Otherwise (with the probability $1 - p_e$), the peg is removed from the environment, which reflects external effects on physical niches (e.g. weathering of pegs). If $p_e = 0$, all pegs are removed. If $p_e = 1$, all pegs remain. It should be noted that individuals can place pegs just before interactions even if pegs are removed in this phase.

These phases are conducted repeatedly in the order above.

3. Experimental Results

Basically, we used the following parameters to conduct evolutionary experiments: $W = 40$, $T = 1.2$, $R = 1$, $P = 0.5$, $S = 0.0$, $\sigma = 0.7$ and $p_s = p_n = 0.01$. The initial population was generated on the condition that 0 or 1 is randomly assigned to gs_i , a uniform random value was assigned to gn_{ij} in its domain, and there was no peg in the environment.

3.1. Control Experiments

In order to know basic effects of environmental modification on the evolution of cooperation, we conducted control experiments in which a peg was set in between each

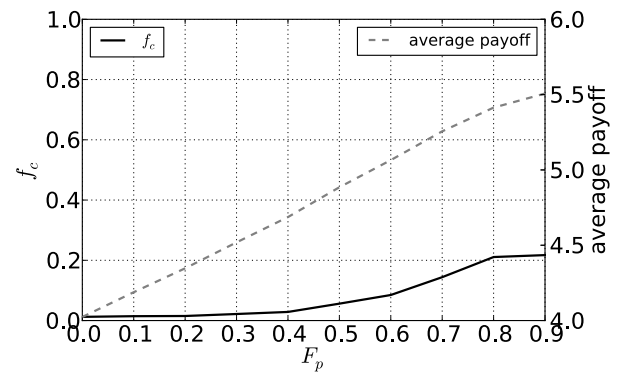


Fig. 6. The results of control experiments with the different F_p .

neighboring individuals with a fixed probability F_p every generation. Note that pegs were not inherited over generations. We conducted experiments through 2,000 generations for each setting of $F_p = 0, 0.1, \dots, 0.9$. We excluded the case with $F_p = 1$ from the experimental condition because all individuals have the same payoff and thus there is no selection pressure for both genes.

Figure 6 shows the average proportion of cooperative individuals f_c among all individuals over 2,000 generations. Each value is the average over 10 trials. We see that f_c increased with F_p . However, it was still a low value (about 0.2 or lower) even in the case of $F_p = 0.9$. Also, the average payoff increased with F_p and was the highest (5.51) when $F_p = 0.9$. This means that the situation with fewer interactions was better for all individuals.

3.2. Effects of the Degree of Ecological Inheritance

First, we discuss the effects of the degree of ecological inheritance p_e on the global behavior of the population. We conducted evolutionary experiments through 2,000 generations for each setting of $p_e = 0, 0.01, 0.02, \dots, 1$. Fig. 7(a) shows the average payoff and f_c . Fig. 7(b) shows f_{nh} of cooperators, f_{nd} of cooperators, f_{nh} of defectors and f_{nd} of defectors. We define f_{nh} as $(1/4N') \sum_i \sum_{j=1,2,3,4} gn_{ij}$ (where N' is population of the focal individuals), which means the average probability to set a peg in a vertical or horizontal direction. We also define f_{nd} as $(1/4N') \sum_i \sum_{j=5,6,7,8} gn_{ij}$, which means the average probability to set a peg in a diagonal direction. Fig. 7(c) shows the average payoff and the proportion of interactions (CC, DD, CD or no game) among all individuals over 2,000 generations. Each value is the average over 10 trials. As we can see from these figures, the degree of ecological inheritance p_e affected significantly the dynamics of population and the average payoff was the largest (5.78) when $p_e = 0.85$ while it was the smallest (5.60) when $p_e = 1.0$.

When $p_e = 0$, all pegs were removed by external effects on physical niches or weathering of pegs. In the cases of such a low degree of ecological inheritance, the average proportion of cooperation was low. It turned out that this

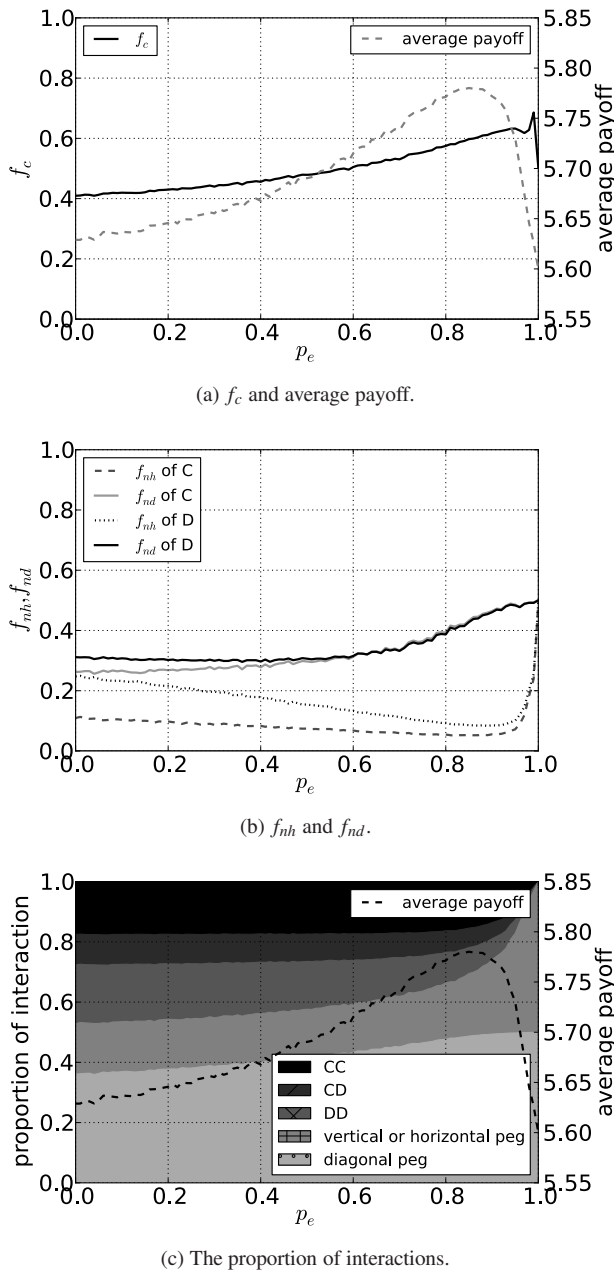


Fig. 7. The effect of p_e on genes and payoff.

is mainly due to the cyclic coevolution of game strategies and niche-constructing strategies, which occurred in parallel (discussed in detail in Section 3.3).

As p_e increased to around 0.85, f_{nd} of both cooperators and defectors slightly increased to around 0.43 from around 0.3 while f_{nh} slightly decreased to around 0.05 (for cooperators) or 0.09 (for defectors) from around 0.11 (for cooperators) or 0.25 (for defectors). This biased niche-constructing behaviors made the proportion of mutual defections decreased, which also made the average payoff the largest when $p_e = 0.85$. This is due to the fact that cooperators could obtain the benefit of adaptive niche construction because constructed environmental structures collapse less frequently (discussed in detail

in Section 3.4).

However, as p_e increased further (above 0.85), both f_{nd} increased slightly to 0.5 while f_{nh} drastically increased to 0.5 from around 0.05 for cooperators and 0.09 for defectors. This is because when p_e was too high, almost all pegs were set and hardly removed. This means that there were few interactions among individuals and there was no selection pressure for game strategies. Therefore, the proportion of each strategy reached 0.5 in the cases with almost complete ecological inheritance.

As a whole, it turned out that ecological inheritance of a niche-constructed environment can strongly affect the evolution of niche construction, and further affects the emergence of cooperative behaviors.

In the following sections, we investigate in detail the two typical scenarios of the evolution process: the cyclic evolution of strategies with the low $p_e = 0.1$ and the emergence of adaptive and stable environmental structures for cooperators with $p_e = 0.85$.

3.3. The Evolution with the Low Degree of Ecological Inheritance ($p_e = 0.1$)

Figure 8 shows a typical transition of f_c , the average payoff, f_{nh} , f_{nd} and the frequency of existing pegs in a trial with $p_e = 0.1$. f_c fluctuated between 0.2 and 0.6 and the average payoff also fluctuated between 5.3 and 6.0 as shown in Fig. 8(a). Fig. 8(b) tells us that f_{nh} and f_{nd} fluctuated under 0.4. f_{nd} for cooperators fluctuated between 0.05 and 0.2, which means that cooperators tended to place fewer pegs than defectors.

These fluctuations were due to the parallel coevolution process in which the three different combinations of game strategies and niche-constructing strategies locally emerged in turns: (1) infrequently niche-constructing (peg-setting) cooperators, (2) infrequently niche-constructing defectors and (3) frequently niche-constructing defectors.

Figure 9 shows a typical distribution of the population when $p_e = 0.1$. We see that there are many clusters of these strategies, and there were more pegs in the inside of the clusters of defectors than the clusters of cooperators or the outside of the clusters of defectors.

Figure 10 also shows a transition of the strategies in a fixed site, roughly showing the temporal dynamics of change in these strategies. A circle marker indicates cooperation and a square marker represent defection. A solid line indicates the average of peg-setting rate in horizontal and vertical directions and a dashed line indicates that in diagonal directions. We see from this figure that the strategies temporally changed in the following order: $\dots \rightarrow$ (1) (e.g. the 237–239 and 257–266th generations) $\rightarrow$ (2) (e.g. the 240–244 and 267–270th generation) $\rightarrow$ (3) (e.g. the 245–254 and 271–272nd generation) $\rightarrow \dots$. This is because clusters of (1) mutually interacting cooperators can be invaded by (2) mutually interacting defectors, but the clusters of (2) can be invaded by (3) niche-constructing defectors because they can avoid mutual defections.

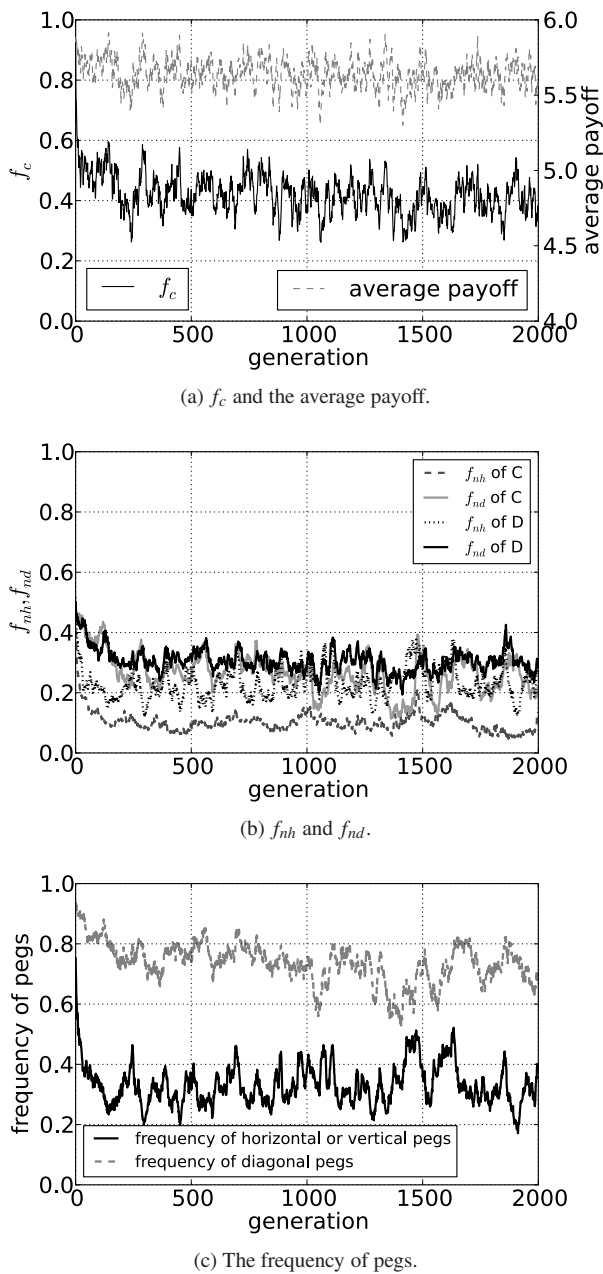


Fig. 8. A typical transition of the situation of $p_e = 0.1$.

The similar cyclic evolution was observed in public good games with volunteering participation [12], because (3) corresponds to loner strategies. It should be noted that the low degree of ecological inheritance contributed to the emergence of this process because game strategies and niche-constructing strategies are tightly related with each other in that the neighboring distribution of pegs around each individual does not reflect ancestral niche-constructing strategy.

3.4. The Evolution with the High Degree of Ecological Inheritance ($p_e = 0.85$)

Next, we focused on experiments with $p_e = 0.85$. We adopted this setting of p_e because the average payoff was

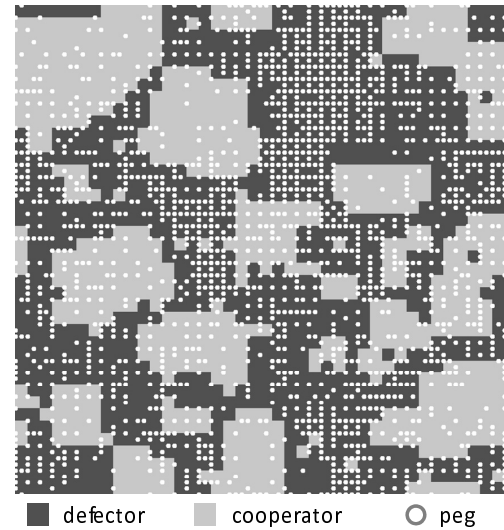


Fig. 9. A typical pattern of the situation of $p_e = 0.1$.

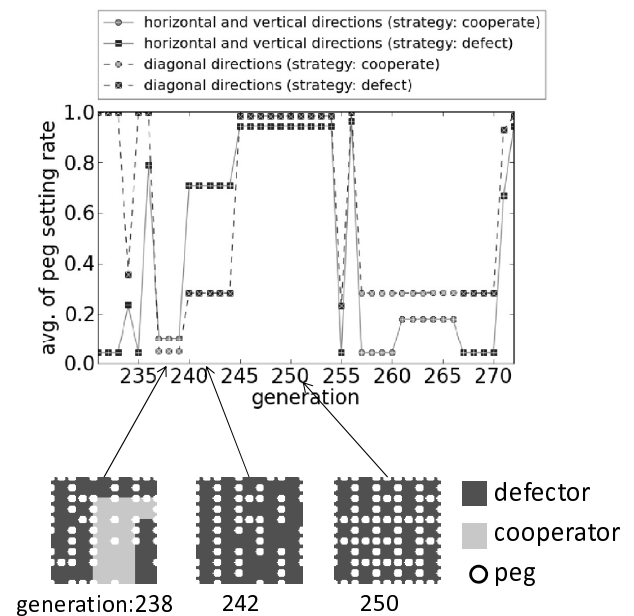


Fig. 10. An individual's gene in the situation of $p_e = 0.1$.

around the largest in this condition. **Fig. 11** shows a typical transition of strategies and payoff. From the initial population, f_c rapidly increased and fluctuated between 0.5 and 0.7 and the average payoff also increased and fluctuated between 5.65 and 5.95 as shown in **Fig. 11(a)**. They correlated strongly with each other. f_c and the average payoff were higher than the highest ones in control experiments. This clearly shows that the evolution of niche constructing behaviors contributed to the evolution of cooperation.

Specifically, the evolution of niche-constructing (peg-setting) behavior constructed the physical niche where cooperators are superior to defectors and promoted the evo-

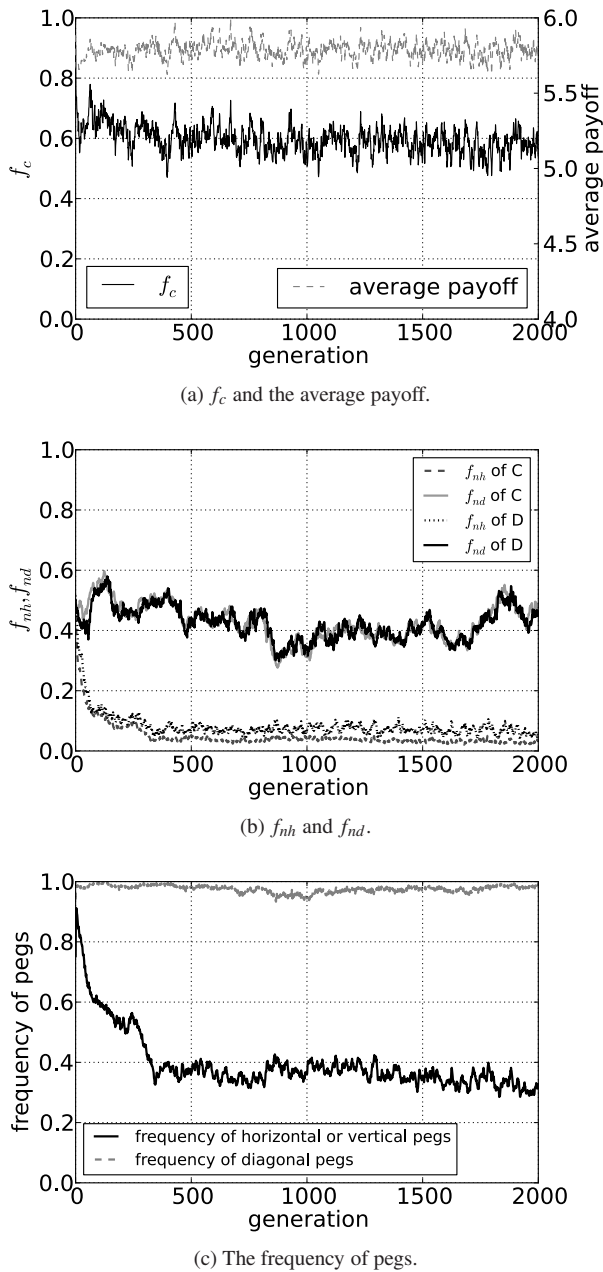


Fig. 11. A typical transition of the situation of $p_e = 0.85$.

lution of cooperative behavior. **Fig. 11(b)** tells us that f_{nd} was significantly higher (around 0.4) than f_{nh} (around 0.1), which means that all individuals evolved to set pegs in diagonal directions more frequently than in vertical or horizontal directions. As a result, the proportion of pegs in diagonal directions fluctuated around 0.95 and that in horizontal or vertical directions fluctuated around 0.4 as shown in **Fig. 11(c)**. The comparison between **Figs. 8** ($p_e = 0.1$) and **11** ($p_e = 0.85$) tell us that the evolution with $p_e = 0.85$ was more stable than that with $p_e = 0.1$.

This situation is thought to be adaptive for cooperators due to the reason as follows. **Fig. 12** shows a typical distribution of the population when $p_e = 0.85$. In this experimental condition, the population is basically composed

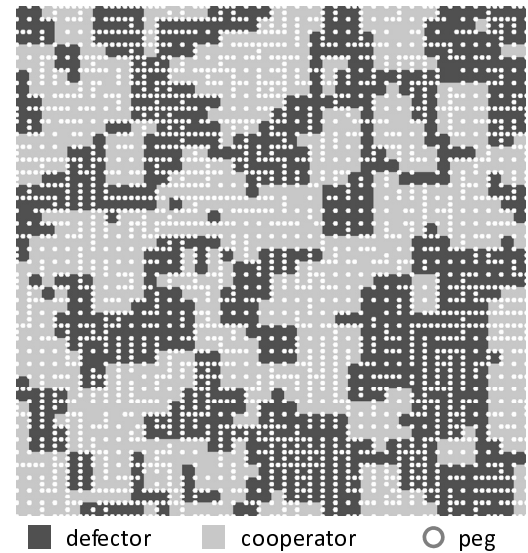


Fig. 12. A typical pattern of the situation of $p_e = 0.85$.

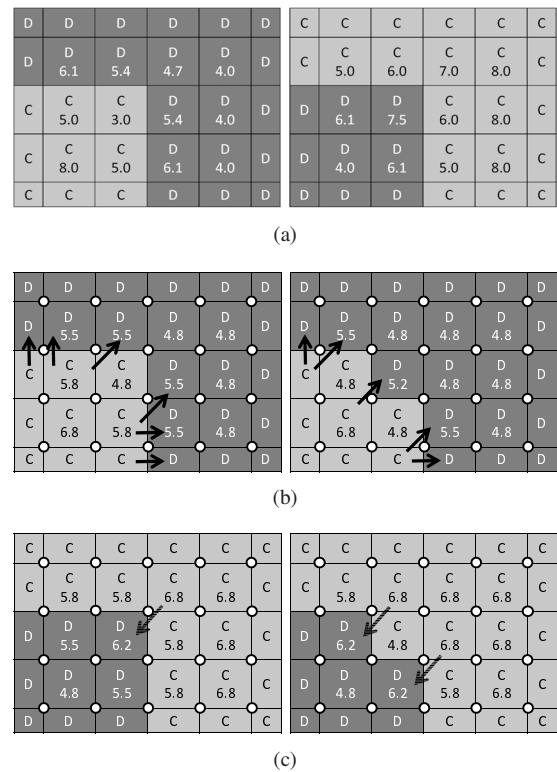


Fig. 13. The effect of diagonal pegs on spread of cooperators.

of large clusters of cooperators in a sea of defectors. We see that the diagonal pegs were set all over the population, while the pegs in horizontal or vertical directions existed sparsely. Here, let us consider the evolutionary process of a cooperator on a boundary of a cooperative cluster in some typical situations: ones in which there are no pegs (**Fig. 13(a)**) and the others in which there are diagonal pegs in all locations (**Figs. 13(b)** and (c)). In the former case, the focal cooperators cannot invade into the neighboring defector. However, the focal cooperators in the latter case can invade into the neighboring defector due to the change in their fitness caused by the limited interac-

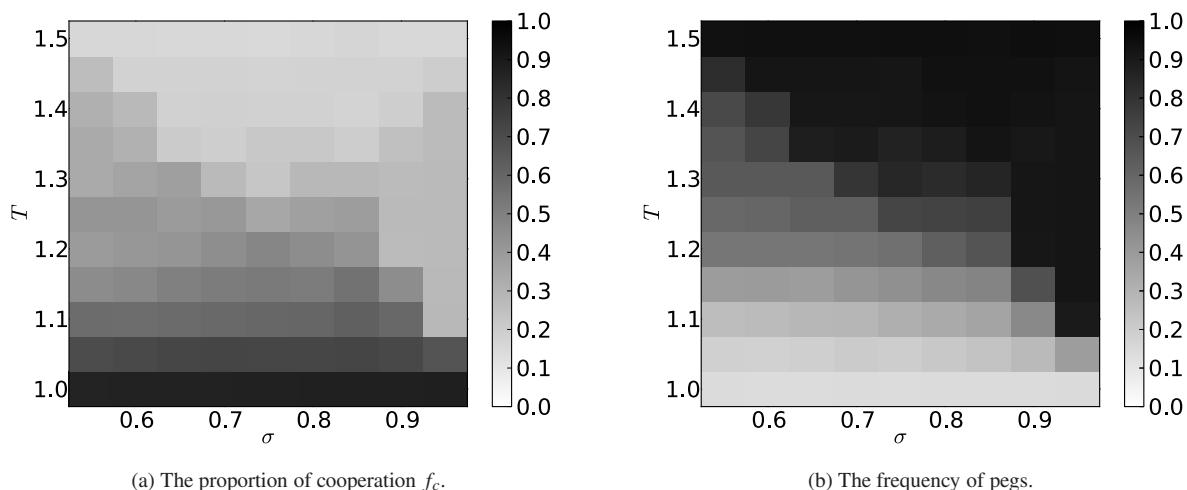


Fig. 14. The effect of T and σ on several indices.

tions between cooperators and diagonally located defectors while keeping the mutual cooperation between horizontal or vertical individuals. This environmental configuration exists across generations due to the high degree of ecological inheritance rate in this setting. Thus, this is expected to be the reason why the emerged niche contributed to the evolution of cooperation. Additional analyses on the correlation between f_c and f_{nd} of cooperators also showed that the change in f_c follows the change in f_{nd} of cooperators, implying that the constructed niche can lead to the emergence of cooperation in succeeding generations.

An expanded cooperative cluster tended to collapse due to an invasion by a mutant defector appeared in the cluster. This mutant defector spreads into the cluster quickly without changing the distribution of niche-constructing genes. This genetic hitchhiking of niche-constructing gene seems to be the reason why there is little difference between f_{nd} of cooperators and that of defectors. In addition, we did not see the evolution of low f_{nd} even though it seems adaptive for the cooperators in cooperative clusters and defectors. This is expected to be due to the fact that the high degree of ecological inheritance masked the expression of the niche-constructing behaviors with low f_{nd} because there existed many diagonal pegs placed by individuals with high f_{nd} through the stable ecological inheritance.

Thus, it turned out that the emergence of cooperation can be facilitated significantly by the evolution of a physical niche construction that creates the social niche beneficial for cooperators if the constructed niche is inherited through generations stably.

3.5. Effects of Payoff Parameters

To understand the effects of payoff parameters on behaviors of our model, we conducted experiments with the settings of $T = 1.0, 1.05, \dots, 1.5$ and $\sigma =$

$0.55, 0.6, \dots, 0.95$. The degree of ecological inheritance was fixed to $p_e = 0.7$. **Fig. 14** shows the average proportion of cooperative strategies and the average frequency of existing pegs over 2,000 generations. Each value is averaged over 10 trials. From **Fig. 14(a)**, low T promoted cooperation.

The analyses clarified that the population tended to evolve to the following four types of individuals depending on the conditions of T and σ : ($T = \text{high}$) actively niche-constructing defectors, ($T = \text{low}$) non niche-constructing cooperators, ($T = \text{intermediate}$ and $\sigma = \text{small}$) actively niche-constructing cooperators in diagonal directions, which was explained in Section 3.4 (e.g. $T = 1.3$ and $\sigma = 0.6$), and ($T = \text{intermediate}$ and $\sigma = \text{high}$) coevolutionary cycles of three strategies, which was explained in Section 3.3.

These results show that the condition for each scenario, explained in the previous sections, to occur depends on the settings of the payoff parameters as well as the degree of ecological inheritance.

4. Conclusion

We have discussed whether and how evolutionary dynamics of physical niche construction contribute to the evolution of cooperative behavior.

We conducted coevolutionary experiments in which each individual has not only a strategy for a spatial Prisoner's Dilemma but also has traits for niche-constructing behavior for modifying its physical environment that can limit social interactions between neighboring individuals. We have shown that the degree of ecological inheritance, which determines how frequently the constructed structure is inherited to the succeeding generation, strongly affected the coevolution of cooperative and niche-constructing behaviors strongly.

When the degree of ecological inheritance was low,

the cyclic coevolution between cooperative and niche-constructing behaviors occurred. This cyclic evolution consisted of invasion processes by the following strategies: niche-constructing defectors, non-niche-constructing cooperators, and non-niche-constructing defectors. This was similar to the cycle observed in public goods games with volunteering participation [12].

In contrast, such a cyclic dynamics did not occur and cooperation was promoted when the degree of ecological inheritance was high. In this situation, the stable environmental structure composed of diagonal pegs enables cooperators to reduce the number of interactions with defectors while keeping that with cooperators moderate. As a result of this modification of the structure of interactions, cooperative clusters could invade into defectors.

However, when the degree of ecological inheritance was excessively high, niche-constructing behavior could not evolve since the accumulated niches masked the selection pressure for any strategies.

We also showed that the condition for each scenario, explained above, to occur depends on the settings of the payoff parameters as well as the degree of ecological inheritance.

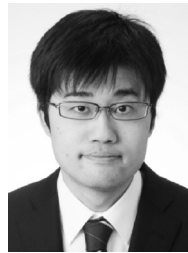
Han et al. constructed a patch occupancy model in which the effect of niche construction accumulates through generations. They found that the three different types of phase-locked patterns emerge depending on the different ecological imprinting processes [14]. Our results also imply that the temporal effects of niche construction.

Future work includes further investigation into effects of different mechanisms of ecological inheritance and different niche-constructing strategies that construct or deconstruct relationships between others on coevolutionary dynamics. Generalization of this model to various network structures would promote a better understanding about coevolution of cooperation and niche construction.

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