How Spatial Locality Can Affect the Evolution of Niche Construction

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Abstract

Niche construction is a process whereby organisms that modify their own or the others' niches through their ecological activities. It is getting much attention in evolutionary studies but still poorly understood. Our purpose is to clarify the effects of spatial locality of niche construction on the evolution of the niche-constructing trait. Especially, we focus on the evolution of negative niche construction that reduces the fitness of niche-constructing individuals themselves. We constructed an evolutionary model by introducing a negative niche-construction of cooperative individuals that reduces their payoff values into Nowak and May's spatial model of the evolution of strategies for Prisoner's Dilemma. We found that the evolution of negative niche-constructing trait is drastically affected by the degree of spatial locality of niche construction. When the locality of niche construction was high, the small number of cooperative and negative niche-constructing individuals could survive due to the unexpected effect of negative niche construction, that is the stabilization of their local environments. When the locality of niche construction was sufficiently low or completely global, the negative niche-constructing trait counterintuitively became dominant in the population of cooperative individuals by changing the global property of the population such as the robustness against invasion by mutant individuals.

Introduction

Niche construction (Odling-Smee, 1988) is known as a process, performed by organisms, that modify their own or the others' niches[1] through their ecological activities. The niche-constructing processes are observed in various taxonomic groups such as bacteria (decomposition of vegetative and animal matter), plants (production of oxygen), nonhuman animals (nest building) and humans (cultural process) (Odling-Smee et al., 2003). All living organisms are more or less performing niche constructions, and there are many evidences that they have strong effects on the evolution of organisms although they had been neglected for a long time in evolutionary biology.

A typical example of niche construction is nest-building behaviors by animals. It is a well known fact that a lot of animals build their nests for various kinds of adaptive reasons (Odling-Smee et al., 2003). For example, some nests protect their inhabitants from being attacked by predators such as beaver's dams, and other ones help their inhabitants with their predation behaviors such as spider's webs. These are called positive niche constructions in the sense that they increase the adaptivity of the niche-constructing individuals themselves by modifying the environmental factors. On the contrary, the negative niche construction refers to the process that reduces the fitness of the niche-constructing individuals themselves. The evolutionary significance of negative niche construction is one of the controversial issues in evolutionary ecology. For example, an autotoxicity, that is a self-destruction of organisms through the production of chemicals by themselves, is ubiquitous phenomena in plants (Singh et al., 1999). An environmental pollution caused by human cultural activities is also an example of the negative niche construction.

The theoretical investigations into the effects of niche construction on evolution have been based mainly on the population genetics. For instance, Laland *et al.* constructed two-locus models, in which one locus affects the niche-constructing behavior which produces the resources in the environments and the fitness of the other locus is affected by the amount of accumulated resources (Laland et al., 1996). They also introduced the ecological inheritance into their models in which the current amount of resources not only depends on the niche construction of the current individuals but also depends on the results of niche construction in previous generations. The results showed that niche construction and ecological inheritance yield unexpected results such as the maintenance of polymorphisms and the evolutionary momentum. Also, the niche construction is now getting much attention in the field of artificial life. Recently, Suzuki and Arita discussed the universal nature of the coevolutionary dynamics among species under the assumption of the indirect interactions via niche construction and ecological inheritance (Suzuki and Arita, 2005). They constructed a

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[1] In this paper, the term *niche* refers to *evolutionary niche* defined by Odling-Smee *et al.*, that means the sum of all the natural selection pressures to which the population is exposed (Odling-Smee et al., 2003).

fitness landscape model termed NKES model by introducing the environmental factors and their interactions with the genetic factors into Kauffman's NKCS model. Results showed that the average fitness among species strongly depends on the ruggedness of the fitness landscape and the degree of the effect of niche construction on genetic factors.

When we discuss on the evolutionary dynamics of a niche-constructing trait, it is one of the essential points whether it can modify the selection pressures locally or globally. For example, if the effect of niche construction of an organism is spatially local, it is supposed that the positive niche construction can invade the population because it brings about the difference in the fitness between the positive niche-constructing individuals and the other non-niche-constructing individuals in distant locations. Taylor presented an individual-based model of spatially local niche construction (Taylor, 2004). In his model, the fitness of each individual is determined by other neighbors' gene expressions in its local environment. The results showed that the complex changes in the environmental states by the evolution of the niche-constructing traits caused an evolution of organism with more genes, which implies a continuous increase in the complexity of organisms.

However, if the effect of niche construction of an organism is completely global, it is not always clear that such a niche-constructing trait can evolve even when it is positive. It is because that the niche construction equally increases or decreases the individuals' fitness regardless of their niche-constructing traits. By using the same model as explained above, Laland *et al.* also pointed out that the evolution of the globally niche-constructing trait can not be affected by the evolutionary process of the other trait of which fitness is determined only by the results of niche construction by all individuals, if there is no linkage disequilibrium among these traits. Although these results clearly showed that the locality of the effect of niche construction is a key factor to understand the evolution of niche construction, as far as we know, there are still no studies that discussed the evolutionary dynamics of niche-constructing trait by comparing the cases with or without the locality of the effect of niche construction.

Our purpose is to clarify the effects of the spatial locality of niche construction on the evolution of the niche-constructing trait. Especially, we focus on the evolution of negative niche-constructing trait due to the following reasons: It is reasonable to suppose that the positive niche-constructing trait can invade the population if its effect is spatially local as explained before. However, counter-intuitively, there exist some examples of negative niche-constructing traits in our real-world, but their evolutionary dynamics are poorly understood.

We have constructed an evolutionary model of spatial niche construction by introducing a niche-constructing behavior that modifies the payoff matrix into Nowak and May's spatial model of the evolution of the strategy for the Prisoner's Dilemma (PD) (Nowak and May, 1992). It is well known that their model generates a large variety of qualitatively different patterns of cooperative and defect individuals depending on the payoff values of the PD game. In our model, individuals are placed on a two dimensional space, and they conduct PD games with their nearest individuals by using the payoff matrix of which its payoff values are modified by the niche constructions performed by neighboring individuals. With experiments based on the various settings of the degree of the spatial locality of niche construction, we show that the evolutionary dynamics of niche-constructing trait is drastically affected by its spatial locality.

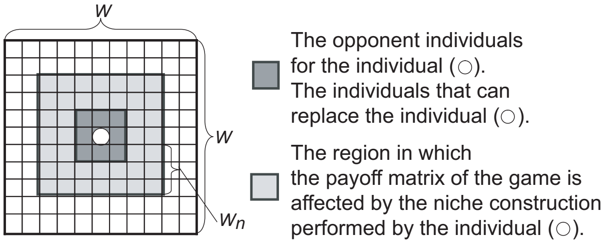

Figure 1: The spatial locality in our model.

Model

There are toroidal $N = W \times W$ lattice sites and each site contains a single individual as shown in Figure 1. Each individual i (i=0, $\cdots$, N-1) has a gene gs_i which describes a strategy for the PD game (Cooperate: 1, Defect: 0). We adopted these simple strategies because the effects of niche construction (positive or negative) are clear and easy to analyze. It also has a gene gn_i which determines whether it performs a niche-constructing behavior (1) or not (0). Here, we introduce an abbreviation for each combination of genes of the individual as follows: DX – (gs_i=0, gn_i=0), DN – (gs_i=0, gn_i=1), CX – (gs_i=1, gn_i=0) and CN – (gs_i=1, gn_i=1). So as to focus on the evolution of niche-constructing trait of cooperative individuals, we assume that there was an epistatic relationship between the expression of gs_i and that of gn_i. The expression of the defect strategy represses the expression of the niche-constructing trait. That is, the individual performs niche construction only when gs_i=gn_i=1.

The environmental state of the site occupied by the individual i is defined as R_i, which is the proportion of niche-constructing individuals among the neighboring $(2W_n + 1)^2$ individuals (including the individual i itself) as shown in Figure 1. R_i is calculated as follows:

$$R_i = \frac{1}{(2W_n + 1)^2} \times \sum_{i \in neighbors(i)} gn_i \times gs_i, \qquad (1)$$

where W_n is the degree of the spatial locality of the effect of

Table 1: A payoff matrix of Prisoner's Dilemma.

Opponent Player	Cooperate	Defect
Cooperate	$(R+\alpha \times R_i, R+\alpha \times R_i)$	(S, T)
Defect	(T, S)	(P, P)

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

niche construction and $neighbors(i)$ is a set of neighboring $(2W_n+1)^2$ individuals.

Each individual i conducts PD games represented by Table 1 against nearest 8 individuals. Note that α is a constant which determines the type and strength of the effect of niche construction. If α is positive, the niche construction becomes positive for cooperative and niche-constructing (CN) individuals in the sense that they can receive larger payoff values when they played against cooperative strategies. If α is negative, the niche construction becomes negative for them in the sense that they can receive smaller payoff values. Also, When W_n is the largest (W_n=$(W-1)/2$), no explicit selection pressure affects on the evolution of gn_i in the sense that all cooperative individuals always share the same payoff values regardless of the values of their gn_i. In addition, gn_i is always completely neutral gene among defect individuals.

The average payoff over all games is treated as the fitness of each individual. The evolutionary process is conducted as follows: For each individual, if there are individuals in the neighboring 8 sites that have higher fitness than itself, its genes are replaced by the genes whose fitness is the highest among neighbors. Next, the mutation which flips the value of gene occurs with a probability p_m on all genes of all individuals respectively.

Experimental results

Basic analyses

We have conducted evolutionary experiments using the following parameters: W=51, R=1, P=S=0, p_m=0.0015, T=1.62 and α=-0.3, so as to investigate the evolution of negative niche construction. We adopted the condition P=S for simplicity, but none of the results are changed qualitatively if P is positive and sufficiently small. The initial population was generated on condition that each value of gs_i was assigned 1 with a probability 0.8 (otherwise it was assigned 0), and each value of gn_i was randomly assigned 0 or 1. Note that our model exhibits basically similar behavior to Nowak and May's (Nowak and May, 1992) when α= 0.0.

Firstly, we discuss the effects of W_n on the global behavior of the population. We conducted evolutionary experiments through 5000 generations for each setting of W_n= 1, 3, 5, $\cdots$, 25. Figure 2, 3 and 4 show the average proportion of cooperative individuals (f_c) and the average proportion of niche-constructing individuals (f_n) among all individuals over 5000 generations. f_{cn} is the average proportion of CN individuals among cooperative (CN and CX) individuals. Each value is the average over 20 trials. The reason that we focus on f_{cn} is that it clearly reflects how the selection pressure affects the evolution of niche-constructing trait because it can be expressed only in cooperative individuals in this model.

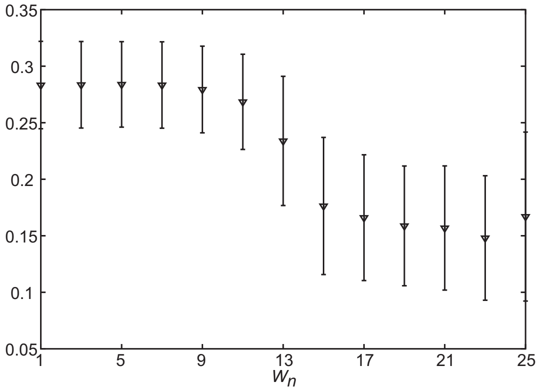

Figure 2: Effects of W_n on f_c.

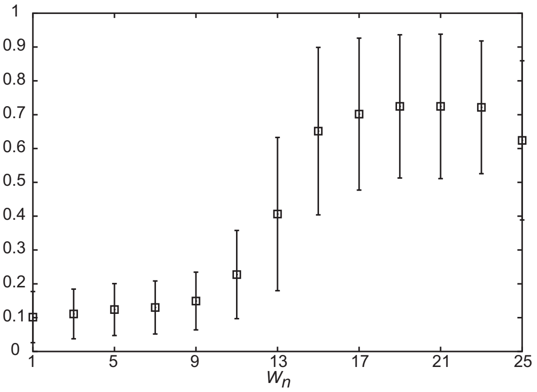

Figure 3: Effects of W_n on f_n.

These figures show that the strong spatial locality of the effect of niche construction facilitated the evolution of cooperation as a whole. f_c was the largest (0.283) when W_n=1 while it was the smallest (0.148) when W_n=23. There are clearly two opposite evolutionary dynamics of niche-constructing trait depending on W_n. The non-niche-constructing (CX and DX) individuals became dominant in the population when $W_n \leq 11$. f_n was the smallest (0.102) and f_{cn} was also the smallest (0.004) when W_n=1. Oppositely, the niche-constructing (CN and DN) individuals tended to become dominant when $W_n \geq 15$. f_n was the largest (0.721) and f_{cn} was also the largest (0.768) when W_n=23. In the former case, it should be noticed that the

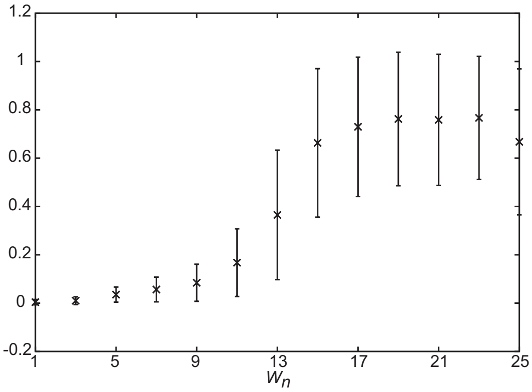

Figure 4: Effects of W_n on f_{cn}.

small number of CN individuals could survive in the cooperative individuals despite the fact that their negative niche construction reduces the fitness of the neighboring cooperative individuals themselves. In the latter case, it also should be noticed that f_n and f_{cn} exceeded 0.5 that is the expected value when gn_i evolved by genetic drift only. It means that a positive selection pressure on the negative niche-constructing trait counterintuitively existed, and the CN individuals were dominant in cooperative individuals. Especially, it is interesting that the evolution of the niche-constructing trait occurred even when W_n=25, in which there are no explicit selection pressures on the niche-constructing trait.

In addition, we have conducted control experiments on the evolution of positive niche constructing trait by changing α to a positive value 0.3 (not shown). In this case, a niche construction can always increase the fitness of cooperative (CN and CX) individuals. When W_n=1, 3 and 5, f_n exceeded 0.95 and f_c also exceeded 0.75. As W_n increased, both f_n and f_c gradually decreased, and finally f_n became around 0.5 and f_c became around 0.6 when W_n=25. These results clarified that the positive niche-constructing trait can almost completely occupy the population when its effect is spatially local, but it can not occupy more than a half of the population when its effect is global. Thus, we can say that whether the effect of niche construction is positive or negative can strongly affect its evolutionary dynamics.

Evolutionary dynamics with the high spatial locality of negative niche construction

As shown above, the evolutionary dynamics of niche-constructing trait was drastically affected by the spatial locality of the effect of niche construction. Next, we investigate in detail the evolutionary dynamics of negative niche construction.

First, we focus on the condition that the spatial locality of niche construction is maximal. Figure 5 is an example of the distribution of individuals when W_n=1. We see a lot of small clusters of CX individuals in the population of defect (DX and DN) individuals. In this case, the evolutionary pattern of the population was chaotic throughout generations as Nowak and May pointed out (Nowak and May, 1992). The clusters of CX individuals repeated the cycle of expansion, collision with each other, and fragmentation.

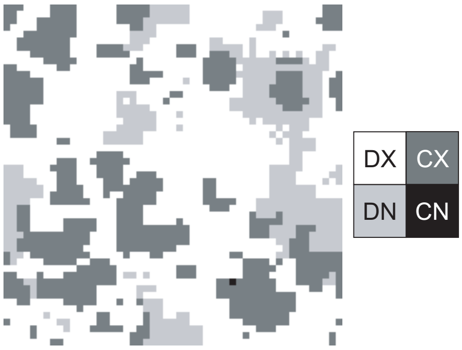

Figure 5: Distribution of individuals when W_n=1.

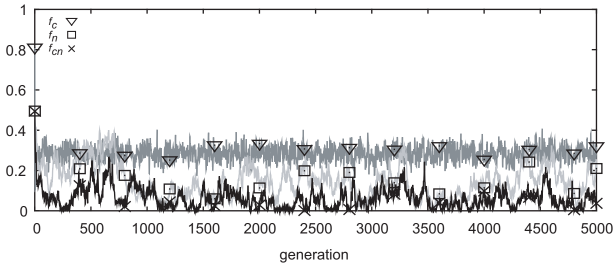

Figure 6: The evolution of f_c, f_n and f_{cn} when W_n=7.

The transitions of the global indices were stable in contrast. f_c remained around 0.28 with small fluctuations and f_{cn} almost always remained 0.0 (not shown). It shows that cooperative individuals evolved not to perform negtive niche constructions. As we defined, the niche construction reduces the fitness of the cooperative individuals. The actual amount of reduction (R_i) is proportional to the proportion of the CN individuals in neighboring $(2W_n+1)^2$ sites. Thus, the smaller W_n is, the stronger the effect of negative niche-construction performed by the CN individual itself becomes. In this case, the negative effect was too strong for CN individuals to invade the population of defect individuals.

As W_n increased, the clusters of CN individuals began to appear. Figure 6 shows a typical transition of f_c, f_n and f_{cn} when W_n=7. In this case, f_{cn} fluctuated between 0.0 and 0.2. Figure 7 is the distribution of individuals at the 500th generation. We see a few clusters of CN individuals that existed stably over many generations without collision with the other chaotically moving clusters of CX individuals.

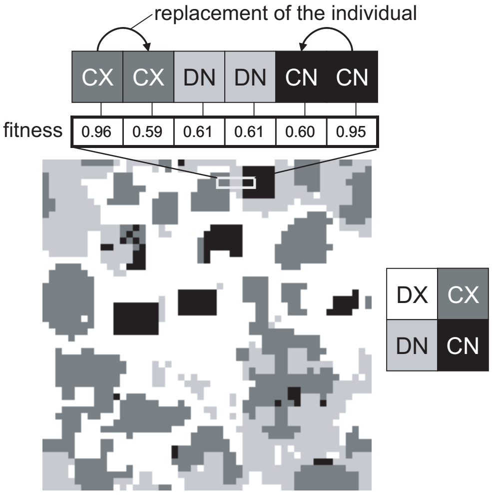

Figure 7: Distribution of individuals at the 500th generation when W_n=7.

Such stable existence of CN individuals with small W_n was caused by the unexpected effect of the negative niche construction, that is the stability against invasion by other cooperative individuals. For example, the cluster of CN individuals that exists on the upper side of the lattice sites in Figure 7 is quite stable. In this case, the CX cluster on the immediate left of the CN cluster can not approach to the CN cluster because the DN individuals between these two clusters can not be replaced by neighboring cooperative individuals. Figure 7 also shows the fitness distribution around these clusters. We pick up the fitness distribution of a horizontal part of these clusters for simplicity. Each value of the table corresponds to the fitness of the individual on the corresponding site and each arrow represents the replacement of the individual which will occur in generation change. It shows that the fitness of the neighboring CN and CX individuals is not higher than those of DN individuals due to the reduction of the fitness caused by the effect of negative niche constructions. The CX cluster can not invade the DN individuals although the CN cluster can not grow any larger at the same time. This situation makes the CN cluster stable because if cooperative clusters get too close with each other, they tend to be collapsed due to the invasion by the defect individual that exists between them. The same discussion holds true at all edges of the CN cluster. Thus, the CN clusters can survive and remain stable at the same position until a mutant DN individual appears inside of it even in the negative and locally niche-constructing population.

These effects of the negative niche construction on the CN individuals became small as W_n increased. It is because that the increase in W_n brought about the decrease in the direct effect of negative niche construction on the CN individuals themselves as explained before. Thus, the CN clusters tended to grow larger and collide with the other clusters likewise the CX clusters. In contrast, the effect of negative niche construction by CN individuals on the other neighboring CX clusters increased as W_n increases. As a result, the selection pressure on the niche-constructing trait became small, and f_n and f_{cn} became close to 0.5 when W_n=13. At the same time, f_c became small due to the increase in the total amount of the effect of negative niche construction caused by the increase in the number of CN individuals.

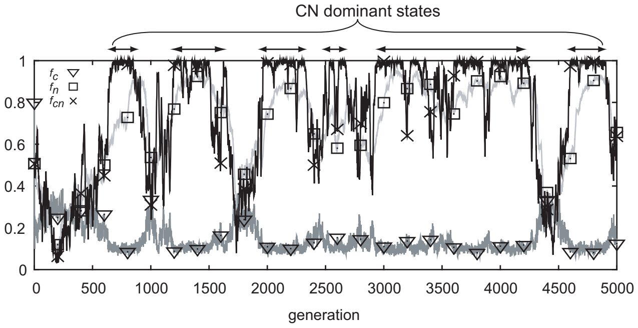

Figure 8: The evolution of f_c, f_n and f_{cn} when W_n=25.

In addition, we can also see from Figure 6 that f_n generally tended to follow the transition of f_{cn} despite that the niche-constructing gene was completely neutral among defect individuals that occupied more than 70 % of the whole population. In this model, a mutant DN or DX individual that appear inside of the clusters of cooperative individuals can rapidly invade these clusters and gradually spread over the defect population. Because these mutant individuals basically have the same gn_i as that of the members of the cooperative clusters, f_n tended to be close to f_{cn} in general.

Evolutionary dynamics with the low spatial locality of negative niche construction

Next, we clarify the evolutionary dynamics of the population with the low spatial locality of negative niche construction. Here, we focus on the case that the effect of niche construction is completely global, in which there were no explicit selection pressures on the niche constructing trait.

Figure 8 shows the typical transitions of indices when W_n=25. From the initial generation, we see that the transition of these indices were quite unstable until around 600th generation. f_c fluctuated around 0.3, and f_n and f_{cn} also widely fluctuated between 0.01 and 0.69. Next, both f_n and f_{cn} began to increase and f_{cn} rapidly approached to almost 1.0 while f_c decreased to around 0.1. This *CN dominant* state, in which the CN individuals were dominant in cooperative (CX and CN) individuals, stably continued until around the 800th generation. Subsequently, f_{cn} and f_n rapidly decreased and the population turned back to the unstable state as observed around the initial generations. Generally, the CN dominant state and the unstable state occurred alternately as shown in this figure, and the number of generations in which the population was in the CN dominant state was larger than that in which the population was in the unstable state. As a result, the average f_n and f_{cn} exceeded 0.5 that is the expected value when gn_i evolved only by genetic drift. Thus, we can say that the dominance of the negative niche-constructing trait in this case is mainly due to the stable transitions of the population after it entered into the CN dominant state.

The stability of the population in the CN dominant state is supposed to be due to the topological properties of the population caused by the strong effects of negative niche construction of CN individuals. Figure 9 is the distribution of individuals in the 3144th generation. This is an example of the population in the CN dominant state. We see that there are only a few large clusters of CN individuals in Figure 9. In this case, tiny clusters of cooperative individuals can not survive regardless of their location due to the decrease in their fitness caused by the global niche construction of the dominant CN individuals. This negative effect of niche construction brought about the decrease in the total number of cooperative individuals. At the same time, the existing relatively large clusters of CN individuals can increase their size slowly. It is because that the decrease in the fitness caused by the global and negative niche construction is not so large as to strongly prevent these CN clusters from invading the DN or DX individuals in their neighboring sites in this case. The fitness distribution around CN clusters in Figure 9 shows that the large CN cluster on the upper side of the lattice sites can increase its size in generation change. When a mutant DN individual appeared inside of them, they were divided into several small CN clusters and some of them begin to grow again.

These topological properties brought about the robustness of the whole population against invasion by the CX individuals generated by mutations, due to the reasons as follows: First, the decrease in f_c in the CN dominant state represses invasion by mutant CX individuals. In this model, cooperative individuals can survive only when they appear immediate next to the cooperative individuals. It means that the probability of survival of mutant cooperative individuals is correlated with f_c. Second, if a mutant CX individual appears inside of the large cluster of CN individuals, it can not always occupy the cluster. It is because that the individuals inside of a cooperative cluster tend to have the same fitness, while the replacement of the individuals occurs only when there exist more adaptive neighboring individuals in this model. Third, even when a cluster of CX individuals appears in the population by chance, it often disappear due to the effect of global and negative niche construction if they are too small. Figure 10 also shows the average proportion of sites on which the replacement of individuals occurred (f_r) in the same experiment as Figure 8. We can see that the speed of evolution in the CN dominant state (0.2) was approximately three times slower than that in the unstable state (around 0.6).

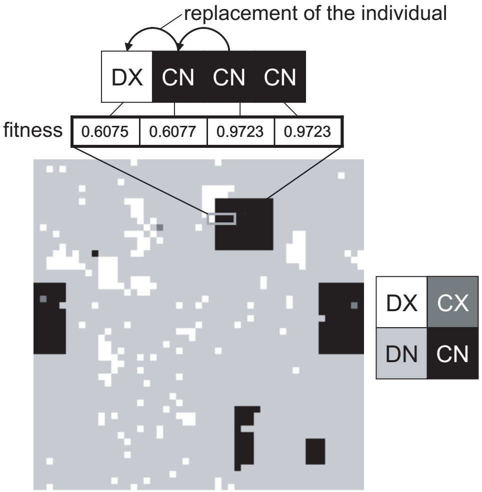

Figure 9: Distribution of individuals at the 3144th generation when W_n=25.

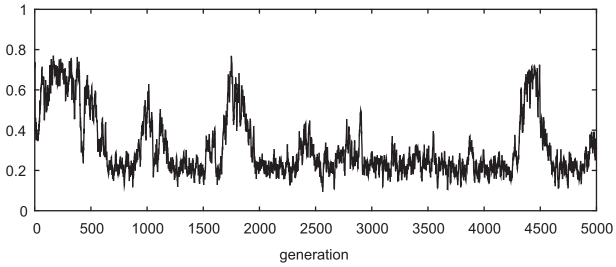

Figure 10: The evolution of f_r when W_n=25.

This scenario can occur if the spatial locality of the effect of niche construction is sufficiently low. As Figure 3 and 4 show, the average f_n and f_{cn} were large when $W_n \geq 15$. We can also see that the average f_n and f_{cn} were the highest when W_n=23. It is supposed to be due to the fact that the existence of the small locality contributed to the stable domination by CN individuals without changing the basic property of the globally niche-constructing population.

Conclusion

We have discussed the evolutionary dynamics of niche construction by focusing on the spatial locality of the effect of negative niche construction. By conducting the experiments of the spatial evolution of Prisoner's Dilemma strategies in which the cooperative individuals perform niche constructions that reduce the payoff values of neighboring cooperative individuals, we found that the evolutionary scenario of the negative niche-constructing trait was drastically affected by the locality of the effects of niche construction. Also, the spatial locality of the effect of niche construction facilitated the evolution of cooperative behaviors in general.

Finally, we summarize our findings as follows: When the locality of the niche construction is high, a negative niche-constructing trait can not become dominant in the population. However, the small number of the negative niche-constructing individuals can exist if the negative niche construction increases the stability of the local environment. In our model, such stability was obtained by the effect of negative niche construction that enabled the clusters of niche-constructing individuals to avoid attacks from the non-niche-constructing individuals by decreasing their fitness. This type of the adaptive property of negative niche construction partly corresponds to the autotoxicity by plants in the sense that these species are supposed to avoid intra-specific competition by producing autotoxins (Singh et al., 1999). That is, the negative niche construction in our model corresponds to the increase in the amount of autotoxins produced by plants.

On the other hand, when the locality of the negative niche construction is sufficiently low or global, there are no direct selection pressures on the evolution of the niche-constructing trait. However, even in such a situation, the evolutionary dynamics of the niche-constructing trait shows unexpected results if the niche construction affects the global property of the population. In our model, the increase in the proportion of negative niche-constructing trait increases the robustness against invasion by mutants and slows down the speed of evolution by changing the topological property of the whole population. As a result, the negative niche construction tended to become dominant even when the effect of niche construction was completely global. The control experiments have shown that these properties of the evolutionary dynamics of negative niche construction are different from those of positive niche construction.

The Gaia theory proposes that organisms contribute to self-regulating feedback mechanisms that have kept the Earth's surface environment stable and habitable for life (Lovelock, 2000). The daisy world model have shown that such a self-regulating mechanism can occur if there exist competitions between two opposite niche-constructing traits that affect the local property of the environment toward opposite directions. Our results partly implies that such mechanisms can be strongly affected by the degree of spatial locality of niche construction, and complex evolutionary dynamics can occur even when the effect of niche construction is completely global if the niche constructing traits have some effects on the property of the global environment.

Future work includes further investigations into the evolutionary dynamics when the different kinds of niche construction that modify the payoff matrix in different ways.

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