How Niche Construction Can Guide Coevolution

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Abstract. Niche construction is the process whereby organisms, through their metabolism, activities, and choices, modify their own and/or each other's niches. Our purpose is to clarify the interactions between evolution and niche construction by focusing on non-linear interactions between genetic and environmental factors shared by interacting species. We constructed a new fitness landscape model termed the NKES model by introducing the environmental factors and their interactions with the genetic factors into Kauffman's NKCS model. The evolutionary experiments were conducted using hill-climbing and niche-constructing processes on this landscape. Results have shown that the average fitness among species strongly depends on the ruggedness of the fitness landscape (K) and the degree of the effect of niche construction on genetic factors (E). Especially, we observed two different roles of niche construction: moderate perturbations on hill-climbing processes on the rugged landscapes, and the strong constraint which yields the convergence to a stable state.

1 Introduction

All living creatures partly modify their own and/or each other's niches as sources of selection through their metabolism, their activities, and their choices. This process is calld "niche construction" [1], and there are many evidences that it has strong effects on the evolution of organisms although it had been neglected for a long time in evolutionary biology.

A typical example of a niche-constructing organism is earthworms that change the structure and chemistry of soils through their burrowing activities. These changes are accumulated over generations, and then bring about different environmental conditions which expose successive population to different selection pressure. This effect is also called "ecological inheritance", which makes the generation inherit both genes and a legacy of modified selection pressures from ancestral organisms. In addition, these changes can affect the other organisms' evolution in the soil. The niche-constructing processes are observed in various taxonomic groups such as bacteria (decomposition of vegetative and animal matter), plants (production of oxygen), non-human animals (nest building) and humans (cultural process) [2].

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 [3]. 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. The niche construction is now getting much attention in the field of artificial life. Taylor presented an individual-based model of niche construction [4]. 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 niche-constructing traits caused an evolution of organism with more genes which implies a continuous increase in the complexity of organisms. These studies describe the basic dynamics of the effects of niche construction within one species.

It is also essential to clarify the effect of the niche construction in the context of the coevolution of multiple species. There are a lot of evidences that the niche-constructing process of one species affected the course of evolution of the other species due to the modifications of the shared environment [2]. For example, many species of birds have evolved to use spider-web silk in their nest construction. Some species of snakes have evolved the behavior of waiting by the trails made by mammalian prey to ambush them. The burrowing behavior of earthworms that we have explained above also provides sites of microbial activity and soil environments for plant species by mixing organic matter in the soils. However, there have been few theoretical or constructive approaches which focused on the universal nature of the coevolutionary dynamics among species under the assumption of the indirect interactions via niche construction and ecological inheritance, although the indirect genetic effects within one species have been discussed [5].

Recently, Hui *et al.* introduced a niche-constructing trait into a lattice model of the evolution of metapopulation [6]. They assumed that there were superior-inferior relationship between several species and the inferior species only conducted niche construction that produces the resources which affect their survival. The result showed that the strength of the effect of interspecific niche construction strongly affects the coexistence of species, and the segregation of species' distribution. However, the results were quite specific to a priori setting of relationships among species and the evolution of the niche-constructing trait itself was not introduced. Thus the general dynamics of indirect interactions among different species sharing the same environment is still unclear.

Our purpose is to clarify the complex relationships between evolution and niche construction by focusing on non-linear interactions between genetic and environmental factors shared by interacting species [8]. For this purpose, we have constructed a new fitness landscape model termed the NKES model by introducing the environmental factors and their interactions with the genetic factors into Kauffman's NKCS model [7]. Then, we conducted the evolutionary experiments based on the hill-climbing and the niche-constructing processes of species on this landscape, in which each species can increase its own fitness by changing not only its genetic factors but also the environmental factors. With experiments using various settings of the ruggedness of fitness landscape and the strength of the effect of niche construction on the fitness of genetic factors, we clarify how niche-constructing behaviors can facilitate the adaptive evolution of interacting species via the shared environment.

2 Model

2.1 NKES fitness landscape

We constructed the NKES model by introducing environmental factors and their interactions with the genetic factors into Kauffman's NKCS model [7]. There are S species who share the same environment of which properties are described as N-length binary values e_i (i=0, ..., N-1). We define e_i as environmental factors which represent abstract conditions of the shared environment such as the chemistry of soil, the temperature, the humidity, the existence of burrows, nests and resources. Each species s_i (i=0, ..., S-1) has N genetic factors represented as binary values $g_{i,j}$ (j=0, ..., N-1).

The fitness of each genetic factor $g_{i,j}$ has epistatic interactions not only with other K genetic factors $g_{i,(j+k) \bmod N}$ (k=1, ..., K) in its own species but also has non-linear interactions with E environmental factors $e_{(j+l) \bmod N}$ (l=0, ..., E-1). The fitness contribution of each genetic factor caused by interactions among genetic and environmental factors is defined in similar manner to the NKCS model. For each $g_{i,j}$, we prepare a lookup table which defines its fitness corresponding to all possible (2^{K+E+1}) combinations of interacting genetic and environmental factors. The value of each fitness in the lookup table is randomly set within the range of $[0.0, 1.0]$. The fitness of each species is regarded as the average fitness over all of its genetic factors. Thus, the parameter K represents the ruggedness of the fitness landscape of each species and E represents the strength of the effect of niche construction on the fitness of genetic factors in this model. Figure 1 shows an example image of this model when N=5, K=1, E=2 and S=3. Each table represents a set of values of genetic or environmental factors, and thin arrows that issue from these values represent the existence of non-linear effects on values of other genetic or environmental factors.

2.2 Evolution and niche construction

In each generation, each species independently chooses the process which yields the best increase in its own fitness from "evolution", "niche construction" or "doing nothing" by using the following procedures: First, we calculate the fitness

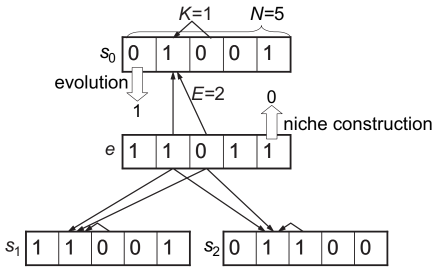


Fig. 1. An example of the NKES model when N=5, K=1, E=2 and S=3.

of the species when a randomly-selected genetic factor is flipped. At the same time, we also calculate its fitness when a randomly-selected environmental factor is flipped. The former value corresponds to the possible result caused by the evolutionary process. The latter corresponds to the possible result by the niche-constructing process, that is, the evolution of the niche-constructing trait which modifies the corresponding environmental factor. Then, the species adopts the process which brings about the best fitness by comparing these two fitness and its current fitness. If the current fitness is the best, it does nothing in this generation. After all species have chosen the processes, they actually conduct the adopted processes at the same time. Note that if more than one species decide to flip the same environmental factor, it is flipped only once in each generation.

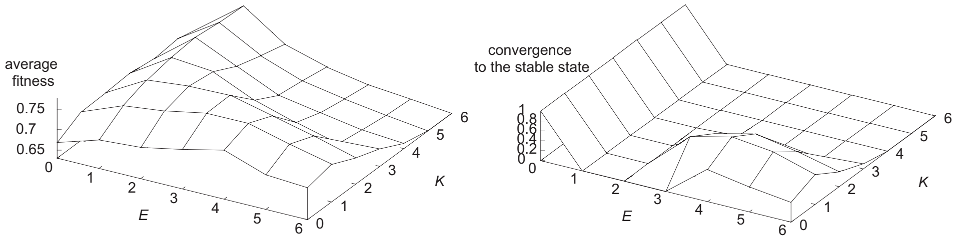
The outlined arrows in Figure 1 represent examples of evolutionary process and niche-constructing process. If one species flips the environmental factor by niche construction, it can change the fitness contributions of the other species' genetic factors, and then can bring about different evolutionary or niche-constructing dynamics of the other species. There are indirect interactions among species via niche constructions instead of the direct interactions among them like the NKCS model.

3 Experimental results

3.1 General analyses

We have conducted experiments using various settings of K and E (N=80 and S=3) for 100000 generations. The initial values of genetic and environmental factors were randomly decided. Firstly, we focus on the effects of K and E on the average fitness among all species. The average fitness does not only represent how the species could evolve on the current environment but also shows how the environment was modified and became better for all species through niche constructions.

Figure 2 (a) shows the average fitness among all species during the last 1000 generations in various cases of K and E. The x and y axes correspond



(a) average fitness (b) convergence to the stable state

Fig. 2. The average fitness and the proportion of the convergence to stable state in various cases of K and E.

to the conditions of K and E, and the z axis represents the average fitness on corresponding conditions. Each value is the average over 20 trials. The first thing we notice is that the average fitness is large (exceeds 0.75) when either K or E is relatively small. In particular, there are two different conditions which created the peaks of the average fitness: the cases when K=4 and E=1 (0.78), and when K=1 and E=4 (0.77). Figure 2 (b) also shows the proportion of trials in which the population completely converged to a stable state, in other words, the fitness of any species can not be improved by neither evolution nor niche construction. There is a peak of the proportion of convergence (0.95) in the latter condition, while it is 0.0 in the former condition. It implies that different dynamics of evolution and niche construction brought about the high average fitness under both conditions.

3.2 Evolutionary dynamics when K=4 and E=1

Here, we investigate in detail the two conditions which brought about the high fitness respectively. First, we focus on the case when K=4 and E=1. In this case, it should be noticed that the average fitness was higher than the corresponding condition without niche construction (K=4 and E=0). When E=0, each species is able to climb the fitness landscape to increase its fitness only by changing its genetic factors, and rapidly gets stuck in the local optimum. Actually, Figure 2 (b) shows that the population always converged to a stable state in all cases of E=0.

However, when E=1, each species can change its fitness landscape by the niche-constructing process. Figure 3 shows a typical transition of the average fitness among species during the first 30000 generations. Note that the transition of the fitness of each species was approximately similar to that of the average fitness but with modest fluctuation. We can see that the species smoothly increased their fitness and fluctuated around 0.78, but they never converged to a stable state.

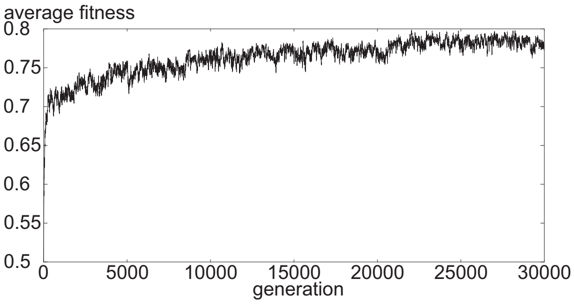


Fig. 3. The transition of the average fitness when K=4 and E=1.

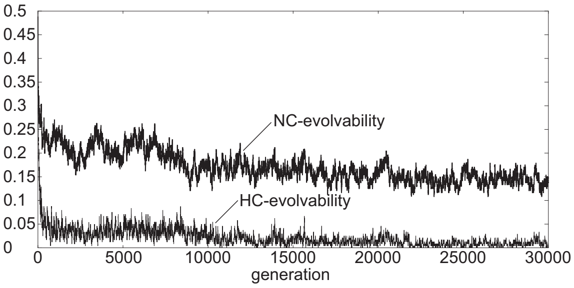


Fig. 4. The transitions of the HC-evolvability (thin line) and NC-evolvability (thick line) when K=4 and E=1.

In this model, the niche construction does not only simply increase the fitness of the performer of the niche construction, but also can change the other species' fitness by changing their fitness landscapes. The difference in the average fitness between with and without niche construction is mainly caused by the latter effect of niche construction. Figure 4 shows the transition of the average evolvability provided by hill climbing (HC-evolvability) and the average evolvability provided by niche construction (NC-evolvability) among species in the same experiment as the one shown in Figure 3. The HC-evolvability (or NC-evolvability) represents the average proportion of genetic (or environmental) factors for each species which can increase its own fitness by flipping them. These indices measure how often each species can apply the evolutionary or niche-constructing process in order to increase its fitness. Figure 4 shows that the NC-evolvability kept a relatively large value, while the HC-evolvability approached to almost 0.0 after the drastic decrease in both indices until a few hundreds generation. This means that the species were almost getting to local optimums, but the continuous niche constructions through generations prevented them from getting stuck in the local

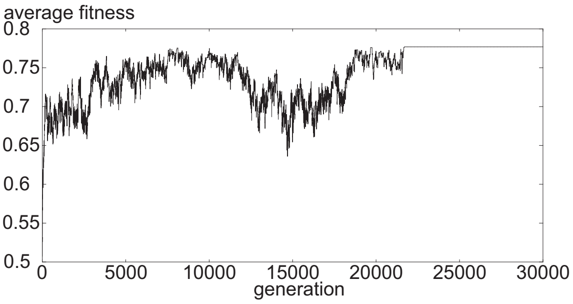


Fig. 5. The transition of the average fitness when K=1 and E=4.

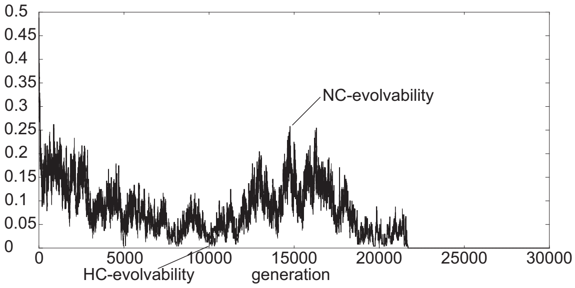


Fig. 6. The transitions of the HC-evolvability (thin line) and NC-evolvability (thick line) when K=1 and E=4.

optimums by slightly changing their landscapes and enabled them to obtain higher fitness regardless of their high ruggedness. Thus, the niche construction worked as a moderate perturbation on the other species' hill-climbing processes in this case.

3.3 Evolutionary dynamics when K=1 and E=4

The other condition which yielded the high average fitness is the case of K=1 and E=4. The important difference compared with the previous condition is that the population converged to a stable state in almost all trials as shown in Figure 2 (b). Figure 5 and 6 show the typical transitions of indices respectively. We observe the average fitness completely converged to 0.78 around 22000th generation after its temporal increase and subsequent decrease from the initial population. Such a temporal decrease is interesting as all species are always trying to increase their own fitness in our model. Also, the transitions of two evolvability in Figure 6 were quite similar though the HC-evolvability was just slightly smaller than the NC-evolvability.

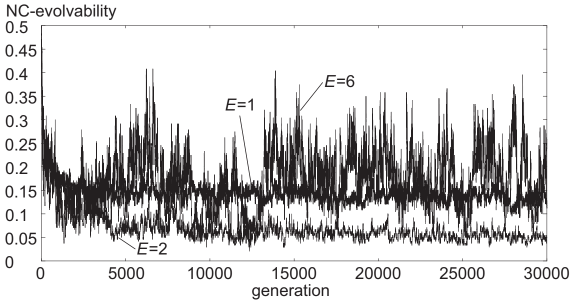


Fig. 7. The transitions of NC-evolvability when K=1, and E=1, 2 and 6.

These phenomena are supposed to occur due to the following reason: As shown in Figure 2 (b), the high average fitness was caused by the convergence to a stable state in this case. It means that the HC-evolvability and NC-evolvability became 0.0 at the same time as shown in Figure 6. Figure 7 shows the transitions of the NC-evolvability when K=1, and E=1, 2 and 6. We see that the NC-evolvability tends to approach to the smaller value in case of E=2 in comparison with the case of E=1. It is because that the strong effects of niche construction on the fitness of genetic factors make the species difficult to improve its fitness by niche construction likewise the species more easily gets stuck in the local optimum on the standard NK fitness landscape as K increases. However, the increase in also E brings about the large fluctuation around the relatively large value in NC-evolvability if E is too large such as the case of E=6 in Figure 7. It is because that as E becomes large, the change in the environmental factor by niche construction of one species more drastically changes the other species' fitness landscapes and draws them back into the bottom of their landscapes. Thus, NC-evolvability frequently approaches to 0.0 when these effects are well-balanced (Figure 6).

Also, as E increases, the transition of HC-evolvability tends to be synchronized with the NC-evolvability as shown in Figure 6, and the fluctuation in HC and NC-evolvability becomes larger as K increases (not shown) because the increase in K makes the species more frequently conduct the niche constructions. Thus, the convergent state occurs the most frequently only when K is small and E is large.

4 Comparison with the NKCS model

Kauffman proposed the NKCS model as a mathematical model designed to investigate the evolutionary dynamics of evolving species in which each species' genetic factor directly affects other species' fitness [7]. In his model, each genetic factor has epistatic interactions not only with other K genetic factors in its own

Table 1. The effect of increase in K, C and E on HC/NC-evolvability in NKCS and NKES model.

	increase in K	increase in C or E
NKCS	decrease in HC-evolvability	increase in the other species' HC-evolvability
NKES	(1) decrease in HC-evolvability (2) increase in the other species' NC-evolvability	(1) decrease in NC-evolvability (2) increase in the other species' NC-evolvability

species but also has interactions with C genetic factors in other S species respectively. It is well known as a good abstract model of directly coevolving species. Here, we compare the evolutionary dynamics of the NKES model with that of the NKCS model so as to clarify how the difference in the structures of (direct or indirect) interactions among species changes the coevolutionary process.

The important fact is that the evolutionary dynamics in the NKES model are quite complex compared with that in the NKCS model. Table 1 shows how HC and NC-evolvability are affected by the increase in the parameters K, C and E in the NKCS or NKES model. In the NKCS model, it is well known that the population tends to rapidly converge to a stable state (ESS condition) when K is relatively large and C is relatively small if the evolutionary processes are conducted in similar manner to that in the NKES model [7]. The typical effects of K and C in the NKCS model become quite simple as shown in Table 1.

In contrast, the effects of K and E in the NKES model are not simple because we have to consider their complex effects on both HC and NC-evolvability. The similar effect of K on the HC-evolvability in the NKCS model also exists in the NKES model. But it brings about the increase in the other species' NC-evolvability because the species frequently conduct niche-constructing behaviors if it is difficult for the species to improve its fitness by evolutionary process. As a result, the population tends to become unstable as K increases. The increase in E also has two different effects on the NC-evolvability as discussed in the previous section, and it make the population stable on the condition that the both effects are well balanced.

As a whole, it should be noticed that the population tends to become completely stable on the opposite condition (K is small and E is large) in the NKES model compared with the condition on which the population rapidly converges to a stable state in the NKCS model (K is large and C is small).

5 Conclusion

We have discussed the universal nature of interactions between evolution and niche construction by using the NKES fitness landscape model. We found that the average fitness among species strongly depends on the ruggedness of fitness landscape (K) and the strength of the effect of niche construction on the genetic factors (E). It should be emphasized that the two qualitatively different roles of niche construction brought about the high average fitness in different conditions. When K is large and E is small, the niche construction by one species works as moderate perturbations on the other species' hill-climbing processes on the highly rugged landscapes, which prevents them from getting stuck in the local optimums. On the other hand, when K is small and E is moderately large, the strong effect of niche constructions on the fitness of genetic factors yields the convergence to a completely stable state which maintain the high average fitness.

There are some examples of the stable and symbiotic relationships among interacting species which mutually modify the shared environment. Some ants have a mutualism with acacia trees [2]. The ants destroy seedlings and attacks mammalian browsers and insect pests. In turn, the acacia provides thorns and nectarines that house and feed the ants. It is also well known that flowering plants have evolved to provide nectar for several insects. The insects attracted by the flowers facilitate pollination process of these plants by providing the movement of pollen while gathering nectar in return. Mutual modification through niche construction is essential for the fitness of both species, which establishes tightly-coupled relationships between the niche-constructing species and environmental factors. In this sense, these types of ecosystems might be explained as the latter case of our experiments (K is small and E is large) rather than the former. We believe that the evolution observed in this case reflects some aspects of the establishment of these tightly-coupled relationships in real biological systems.

Future work includes investigations into the effects of the other parameters on the roles of niche construction and the introduction of the evolution of the network structure among species and environments.

References

1. Odling-Smee, F. J.: Niche Constructing Phenotypes, Plotkin, H. C. (ed), *The Role of Behavior in Evolution*, pp. 73–132, MIT Press (1988).
2. Odling-Smee, F. J., Laland, K. N. and Feldman, M. W.: *Niche Construction -The Neglected Process in Evolution-*, Princeton University Press (2003).
3. Laland, K. N., Odling-Smee, F. J. and Feldman, M. W.: Evolutionary Consequences of Niche Construction: A Theoretical Investigation Using Two-locus Theory, *Journal of Evolutionary Biology*, 9: 293–316 (1996).
4. Taylor, T.: Niche Construction and the Evolution of Complexity, *Proceedings of Artificial Life IX*, pp. 375–380 (2004).
5. Wolf, J. B., Brodie III, E. D., Cheverud, A. J., Moore, A. J. and Wade, M. J., Evolutionary Consequences of Indirect Genetic Effects, *Trends in Ecology and Evolution*, 13: 64–69 (1998).
6. Hui, C., Li, Z. and Yue, D.: Metapopulation Dynamics and Distribution, and Environmental Heterogeneity Induced by Niche Construction, *Ecological Modeling*, 177: 107-118 (2004).
7. Kauffman, S.: *The Origins of Order: Self-Organization and Selection in Evolution*, Oxford University Press (1993).
8. Suzuki, R. and Arita, T.: Evolution and Niche Construction in NKES Fitness Landscape, *Proceedings of the 10th International Symposium on Artificial Life and Robotics*, pp. 493–496 (2005).