Evolution and Niche Construction in NKES Fitness Landscape

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Abstract

Niche construction is known as the process whereby organisms, through their metabolism, their activities, and their 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 have constructed a new fitness landscape model termed NKES model by introducing the environmental factors and their interactions with the genetic factors into Kauffman's NKCS model. Then, we conducted the evolutionary experiments based on the hill-climbing and the niche-constructing processes of species on this landscape. Experimental 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 the fitness of genes (E). Especially, we observed two different roles of niche construction which brought about the high average fitness. One of the roles prevents the species from getting stuck in the local optimums when K is large and E is small. The other role yields the completely stable state which maintains the high average fitness when K is small and E is large.

Keywords: NKES fitness landscape, niche construction, ecological inheritance, epistasis, artificial life.

1 Introduction

Organisms can modify their own and / or each other's niches (sources of selection) through their metabolism, their activities, and their choices. This process is calld "niche construction", and there are many evidences that it has strong effects on the evolution of organisms in various taxonomic groups although it had been neglected for a long time in evolutionary biology [1]. A typical example of niche-constructing organism is earthworms that change the structure and chemistry of soils through their burrowing behaviors. 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.

The effects of niche construction on evolution have been mainly investigated in 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 [2]. They have shown that niche construction and ecological inheritance yield unexpected results such as the maintenance of polymorphisms, evolutionary momentum and so on. However, previous studies were based on simplified cases as described above despite the fact that real biological systems are more complex in the sense that existing species have mutually affected their courses of evolutions by niche-constructing their shared environment, although only a few individual-based models which focused on the perturbational effects of niche constructions were investigated recently [3].

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. For this purpose, we have constructed a new fitness landscape model termed NKES model by introducing the environmental factors and their interactions with the genetic factors into Kauffman's NKCS model [4]. 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. Based on 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 NKES model by introducing environmental factors and their interactions with the genetic factors into Kauffman's NKCS model. There are S species who share the same environment of which properties are described as N-length binary values e_i (i=0, $\cdots$, 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 burrow or nest and so on. Each species s_i (i=0, $\cdots$, S-1) has N genetic factors which are represented as binary values $g_{i,j}$ (j=0, $\cdots$, N-1).

The fitness of each genetic factor $g_{i,j}$ has epistatic interactions not only with other K genetic factors $g_{i,j+kmodN}$ (k=1, $\cdots$, K) in its own species but also has non-linear interactions with E environmental factors e_i (i=0, $\cdots$, 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 $[0.0, 1.0]$. 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 the value of genetic or environmental factors, and thin arrows that issue from these values represent the existence of non-linear interactions with 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 of the species when randomly selected one genetic factor is flipped. At the same time, we also calculate its fitness when randomly selected one environmental factor is flipped. The former value corresponds to the expected result caused by the evolutionary process and the latter corresponds to that by the niche-constructing process. 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 some 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, this 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 NKCS model.

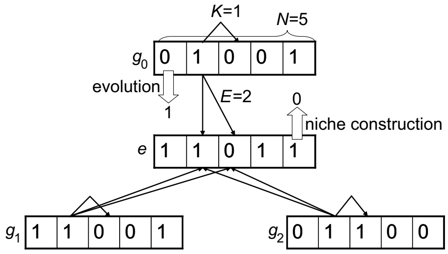

Figure 1: An example of NKES model when N=5, K=1, E=2 and S=3.

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. This index does not only represents how the species could evolve on the current environment but also shows how the environment was modified and become better for all species through niche constructions.

Figure 2 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 to the conditions of K and E, and the z axis represents the average fitness on corresponding conditions. Each value is the averages 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 brought about 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 3 also shows the proportion of trials in which the population completely converged to the stable state (the condition that 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 the two conditions which brought about the high fitness respectively in detail. First, we focus on the case when K=4 and E=1. In this case, it should be noticed that the average fitness

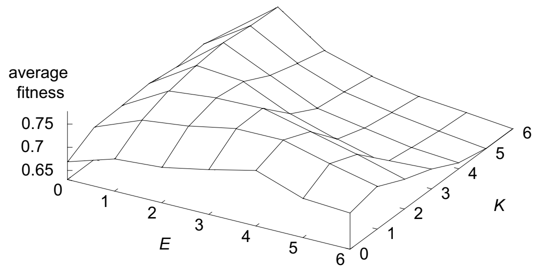

Figure 2: The average fitness in various cases of K and E.

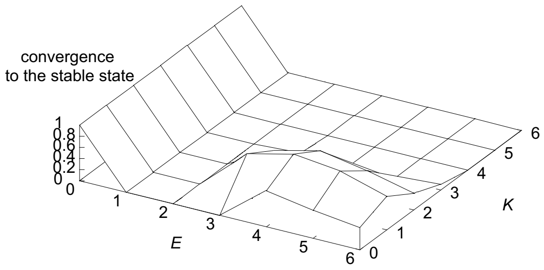

Figure 3: The proportion of the convergence to stable state in various cases of K and E.

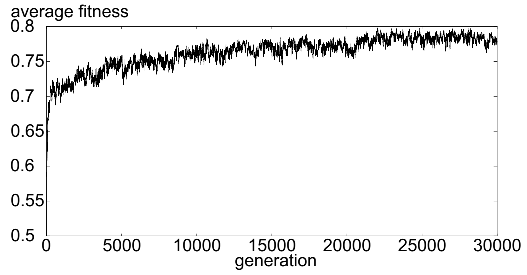

Figure 4: The transition of the average fitness when K=4 and E=1.

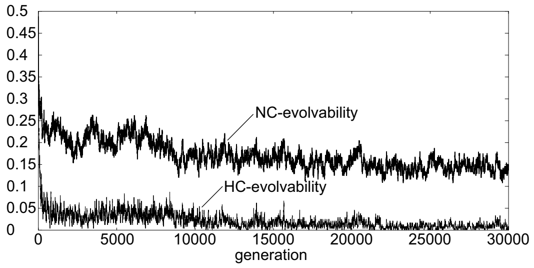

Figure 5: The transitions of the HC-evolvability (thin line) and NC-evolvability (thick line) when K=4 and E=1.

was higher than the corresponding condition without niche construction (K=4 and E=0). When E=0, the evolution of each species rapidly gets stuck in the local optimum because each species is able to climb the fitness landscape to increase its fitness only by changing its genetic factors (not shown). Actually, Figure 3 shows that the population always converged to the 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 4 shows a sample 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, although it tended to fluctuate around the average fitness. We can see that the species gradually and smoothly increased their fitness and fluctuated around 0.78, but they never converged to the stable state.

In this model, the niche construction does not only simply increase the fitness of performer of the niche construction, but also can decrease 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 5 shows the transition of the evolvability provided by hill climbing (HC-evolvability) and the evolvability provided by niche construction (NC-evolvability) in the same experiment as Figure 4. 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 5 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 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 the stable state in almost all trials as shown in Figure 3. Figure 6 and 7 show the sample transitions of indices respectively. We observe the average fitness completely converged to 0.78 around 22000th generation after its temporal increase and sub-

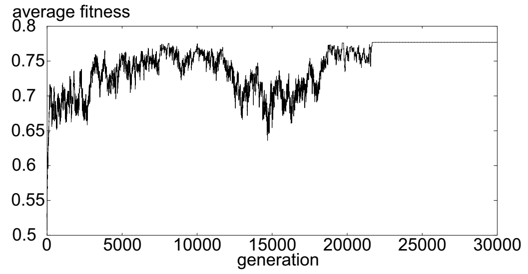

Figure 6: The transition of the average fitness when K=1 and E=4.

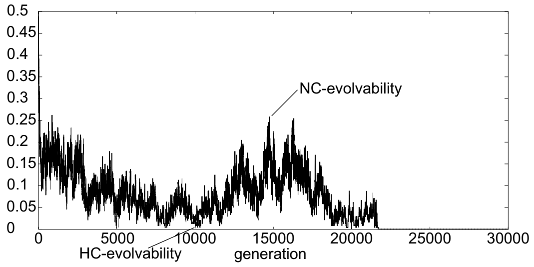

Figure 7: The transitions of the HC-evolvability (thin line) and NC-evolvability (thick line) when K=1 and E=4.

sequent decrease from the initial population. Such a temporal decrease is interesting because all species are always trying to increase their own fitness in our model. Also, the transitions of two indices in Figure 7 were quite similar and the HC-evolvability was just slightly smaller than the NC-evolvability.

These phenomena are supposed to occur due to the reason as follows: As shown in Figure 3, the high average fitness was caused by the convergence to the 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 7. When K=1, the NC-evolvability tends to approach to the smaller value as E increases (not shown). 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. Simultaneously, the increase in E also brings about the large fluctuation around the relatively large value in NC-evolvability (not shown). 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. Also, when E is large, the transition of HC-evolvability tends to be synchronized with the NC-evolvability as shown in Figure 7, and the fluctuation in HC and NC-evolvability becomes larger as K increases (not shown). Thus, the convergent state occurs the most frequently only when K is small and E is large. In addition, the temporal decrease in the average fitness in this case is supposed to be caused by the strong perturbational effects of niche construction as described above.

4 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 perturbation 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 large, the strong effect of niche constructions on the fitness of genetic factors yields the convergence to the completely stable state which maintain the high average fitness. Future work includes investigations into the effects of the other parameters on the roles of niche construction and the introduction of learning into the model.

Acknowledgements

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