

A minimal model of coevolution between learning and niche construction

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ABSTRACT

Recently, roles of ecological processes such as learning and niche construction in evolution are attracting much attention in evolutionary studies. However, various interactions among ecological processes, including these two, are still poorly understood. The purpose of this study is to clarify self-organizing properties of coevolution between learning and niche construction. We construct a minimal evolutionary model in which individuals can both perform learning and niche construction. We found that there was a clear scale-free property in the distribution of the size of environmental changes. It was also shown that these changes were caused by the increased generic variation of niche-constructing genes, followed by the increase in the phenotypic plasticity. The analyses of effects of ecological inheritance showed that it decreased the speed and size of environmental changes, while maintaining the scale-free property of the whole dynamics.

Categories and Subject Descriptors

I.2.11 [Artificial Intelligence]: Distributed Artificial Intelligence—*multiagent systems*

Keywords

learning, niche construction, coevolution, scale-free, ecological inheritance, artificial life

1. INTRODUCTION

In the standard view of the modern evolutionary synthesis, organisms are regarded as passively evolving entities based on selection and mutations. However, there are two ways, based on ecological activities performed by organisms, for modifying the selection pressure as conceptualized in Fig. 1. One way is for individuals to change their own phenotype, called learning or ontogenetic adaptation. A wide variety of species have abilities to modify their own traits to make themselves more adaptive in their existing environments [1]. The other way is to change their environmental condition,

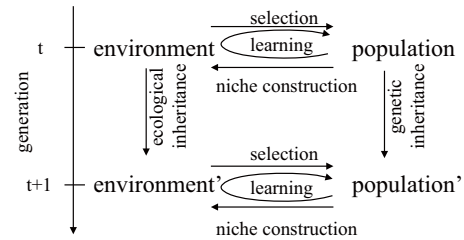


Figure 1: Two processes affecting the selection.

called niche construction [2]. Specifically, niche construction is an ecological process, performed by organisms, that modify their own niches or the niches of others, altering selection pressures through their ecological activities by changing their external environments. It is clear that both processes can interact with each other through changes in the relationship between the environmental conditions and individual phenotypes, suggesting that both processes can co-evolve in complex ways. Although the significance of such interactions has been mentioned in various literatures recently (e.g., [3]), there still have been few computational or mathematical studies that discussed them in detail.

From this viewpoint, we have been constructing and investigating evolutionary models of coevolution¹ of learning and niche-constructing in which individuals can perform both a niche construction of their shared environmental factor and an acquisition of the adaptive phenotype through their lifetime learning (see [4] for detail). We found, when learning and niche construction were conducted sequentially among individuals through their lifetime, that the adaptive benefit of learning and niche construction can emerge dynamically from such interactions, showing that cyclic coevolution of these two ecological behaviors can emerge. However, it was not easy to understand clearly self-organizing properties of the behavior of the model due to its complicated and stochastic nature of ecological interactions in the model.

The purpose of this study is to clarify self-organizing properties of coevolution between learning and niche construction. We construct a minimal model of this coevolutionary process by simplifying our previous model [4]. We assume

¹In this paper, the term “coevolution” refers to the evolutionary process in which multiple traits mutually affect others’ fitness contribution to an individual.

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one-dimensional and toroidal space for both an environmental and a phenotypic states in order to exclude the boundary effects of their space on coevolution. Instead of assuming sequential interactions among individuals, we adopt a simple circular statistics in order to represent a collective effect of niche construction by individuals, and also incorporated an explicit benefit and cost of learning into the model, in order to reduce the stochasticity of the model.

We show that there exists a clear scale-free property in the distribution of the size of environmental changes. We also discuss the statistical tendency of the evolution of both earning and niche construction against the size of environmental change, and their coevolutionary dynamics. We then discuss effects of ecological inheritance on coevolution, which is the inheritance, via an external environment, of one or more natural selection pressures modified by niche-constructing organisms in the previous generations.

2. MODEL

2.1 Overview

Fig. 2 shows an example image of the model. In our model, a state space of an environment shared by all N individuals is represented as a one-dimensional torus with length 1, which abstracts environmental conditions (e.g., directional or coloristic properties of environmental structures, compositions of chemicals in soil). The environmental state at generation t is represented as a real value $e_t (\in [0, 1])$ in this space. We also adopt the same toroidal space for a phenotypic value p of each individual. Each individual have three real-valued genotypes: $gt (\in [0, 1])$ for its innate (or initial) phenotypic value, $gp (\in [0, 1])$ for its phenotypic plasticity and $gn (\in [0, 1])$ for its niche-constructing behavior.

In each generation, first, all individuals perform niche construction according to their gn simultaneously, which moves the shared environmental state e_t toward their own gn . Next, they perform learning in order to make their initial phenotypic value p determined by gt closer to the modified e_t at most gp . Finally, the population evolves under the assumption that the closer p to e_t with the smaller gp brings about higher fitness.

These assumptions correspond to the following example situation: All individuals in a population construct a shared nest and they collect materials of which color (hue) are determined by their niche-constructing trait (gn), affecting the whole color of the nest (e_t). The individuals who have the similar color of their body surface (p) to their nest color tend to survive, because it can reduce predation pressures. They can also make their initial color (gt) more similar to the environmental color (e_t) using their phenotypic plasticity (gp).

We explain details of niche construction, learning, and evolutionary processes in the subsequent sections.

2.2 Niche construction

Each individual performs niche construction to move the current environmental state closer to its own gn . Since the environmental space is toroidal, we use circular statistics to calculate the total effect of niche construction performed

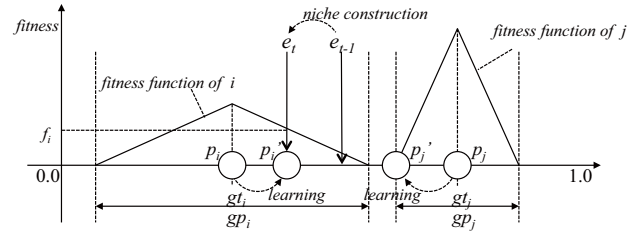


Figure 2: An image of the model, representing two individuals i and j .

by all individuals simultaneously. Specifically, the environmental state e_t after niche construction at generation t is calculated from equations as follows:

$$\vec{\delta e} = \frac{1}{N} \sum_{i=0}^{N-1} \vec{gn}_i, \quad (1)$$

$$\vec{s} = \alpha \vec{e}_{t-1} + (1 - \alpha) \vec{\delta e}, \quad (2)$$

$$\vec{e}_t = \frac{\vec{s}}{2\pi|\vec{s}|}. \quad (3)$$

\vec{gn}_i and \vec{e}_t represent the position vector of gn of the individual i on this circle (gn_i) and that of e_t , respectively, when the toroidal environmental space is represented as a circle whose center is on the origin and circumference is 1. Fig. 3 shows an example calculation of the effect of niche construction performed by two individuals i and j . These equations represent the following situation: the collective effect of the niche-constructing behaviors makes the environmental state closer to the circular average of gns (δe), and its amount of change is negatively related to the circular variance of gns ($1 - |\delta e|$). We adopt this assumption as one of the simplest approximations in which effects of niche-constructing behaviors on the environmental changes are equal among individuals. In addition, the net amount of change in the environmental state is also determined by the parameter α , which corresponds to the degree of ecological inheritance from the previous generation.

2.3 Learning and fitness calculation

After that, each individual i moves its innate (or initial) phenotypic value gt_i closer to e_t at most by its phenotypic plasticity $gp_i/2$. We assume that the individuals that can make their own p the same value as e_t by learning can obtain fitness higher than zero. The actual fitness of the individual i (f_i) is calculated from the equations as follows:

$$f_i = \begin{cases} \frac{4}{gp_i^2} (\frac{gp_i}{2} - d(gt_i, e_t)) & \text{if } d(gt_i, e_t) < \frac{gp_i}{2}, \\ 0 & \text{otherwise,} \end{cases} \quad (4)$$

$$d(x, y) = \begin{cases} |x - y| & \text{if } |x - y| < 0.5, \\ 1 - |x - y| & \text{otherwise.} \end{cases} \quad (5)$$

This means that the fitness function of each individual is hut-shaped, as illustrated in Fig. 2. The center of the hat is located at gt_i , its base length is gp_i and its height is $2/gp_i$. This relationship between the base length and its height represents their trade-off arising from the cost for maintaining

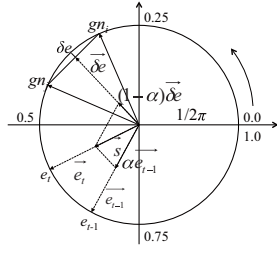


Figure 3: A collective effect of niche construction.

the large phenotypic plasticity. If the plasticity gp_i is large, an individual can adapt to various environmental states obtaining positive fitness while its value is not so large (e.g., the individual i in Fig. 2). On the other hand, an individual that has small gp can only be adaptive in the narrow range of the environmental state while it might earn high fitness if its phenotype is in such a narrow range (e.g., the individual j in Fig. 2).

2.4 Evolutionary process

The evolutionary process is based on a “roulette wheel selection” according to the fitness described above. In addition, for each gene, a mutation occurs with a small probability p_m , which assigns a randomly generated value from a uniform distribution in $[0, 1)$ to the genotypic value.

3. RESULTS

So as to clarify basic behavior of coevolution between learning and niche construction, we conducted evolutionary experiments using the following parameters: $\alpha = 0.0$ (no ecological inheritance), $N = 300$, $p_m = 0.005$. In the initial population, the values of genotypes gt , gp and gn were randomly decided within their domains, and the environmental state e_0 was set to 0.5.

3.1 Basic analyses

Fig. 4 shows an example behavior of the population average of the innate trait value gt and the phenotypic plasticity gp , and the environmental value e_t through 1000 generations in a trial. We see complex behaviors of these values, showing both stable and dynamic transitions repeatedly.

In order to clarify the underlying dynamics in this complex and stochastic evolutionary process, we conducted quantitative analyses summarized in Fig. 5. We focused on the size distribution of changes in the environmental state, measured as follows: We conducted a long-term experiment for 5,000,000 generations, and divided the whole generations into time periods, each in which e_t either increased or decreased monotonously. Note that we made each period as long as possible. For each time period, we defined chg_e as the total amount of change in e_t during that period, and created the frequency distribution of chg_e with the bin size=0.01, as shown in Fig. 5 (a).

When we focus on the distribution within the range of $chg_e < 0.5$, we see its power-law property very clearly. This means that mostly the environmental state e_t was stable while it greatly varied only occasionally. This indicates that the

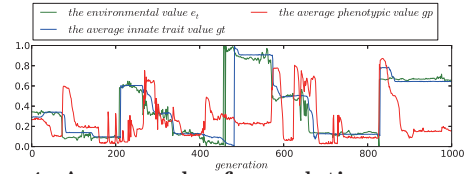


Figure 4: An example of coevolutionary process.

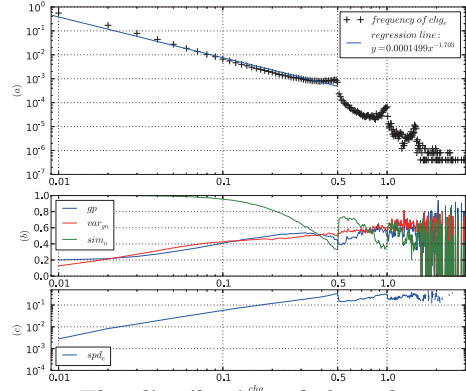


Figure 5: The distribution of chg_e , the average gp , spd_e , var_{gn} and sim_n when $\alpha = 0.0$.

whole population was in a self-organized criticality, implying that this dynamics is a universal phenomenon which can be observed in nature. We also see that chg_e exceeded 0.5, which is the maximal distance between an environmental state and another, because the state space is represented as a one-dimensional torus with the length 1. This is due to the fact that environmental changes explained above toward the same direction (increasing or decreasing) occurred several times sequentially, but such event rarely occurred.

In order to see the evolutionary responses of learning and niche-constructing traits against the different degree of environmental changes, we measured several indices for each time period: the average of the phenotypic plasticity gp , the speed of environmental changes ($spd_e = chg_e / \#$ of generations), the circular variation of gn ($var_{gn} = 1 - |\overrightarrow{\delta e}| (\in [0, 1])$) and the directional similarity between the collective effect of niche construction ($\overrightarrow{\delta e}$) and the environmental state (e_{t-1}) on the circular space ($sim_n = [\cos(\angle(\overrightarrow{\delta e}, \overrightarrow{e_{t-1}})) - 1] / 2 (\in [0, 1])$). We calculated the average values of these indices over time periods for each bin of chg_e in Fig. 5 (a), as shown in Fig. 5 (b and c).

When chg_e was small, both var_{gn} and spd_e was small and sim_n was almost the highest. This means that the niche-constructing genes converged to e_t , keeping the environmental state very stable. In this situation, the phenotypic plasticity evolved to be small due to its explicit cost. As chg_e increased, gp , var_{gn} and spd_e increased, and sim_n decreased. This means that large and fast environmental changes were caused by the increased generic variation of niche-constructing genes, which made the population evolve the large plasticity in order to adapt to such fast and severe variation of e_t .

3.2 Coevolutionary dynamics

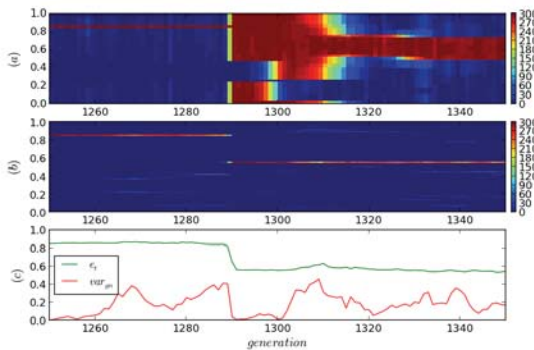


Figure 6: A typical coevolutionary process that caused a drastic change in the environmental state.

In order to clarify the temporal dynamics of coevolution of learning and niche construction that yielded occurrences of large environmental changes, we focused on a hundred generations around the time period in which a typical and large change in the environmental state occurred ($chg_e = 0.3$), as shown in Fig. 6. Fig. 6 (a) shows the temporal changes in the histogram of the feasible phenotypic values through learning process based on phenotypic plasticity. Specifically, for each bin with the size 0.01, we counted the number of individuals of which trait value can be in the corresponding range of the focal bin. Fig. 6 (b) shows the histogram of gn with the bin size = 0.01, respectively. Fig. 6 (c) also shows e_t and the average var_{gn} .

Initially, we see that both e_t and gn converged to around 0.85. We also see that the feasible phenotypic values were distributed around 0.85, which means that the innate traits also converged to around the environmental state and the phenotypic plasticity was small. However, at the same time, we also see that the variance of gn (var_{gn}) sometimes increased due to the nearly-neutral selection pressure on the niche-constructing gene as shown at around the 1,270th and 1,290th generations. When var_{gn} increased to a large value around the 1,290th generation, the environmental state began to change and quickly reached to another value around 0.55. During this process, the individuals whose gn was close to the modified environmental value 0.55 occupied the population. It also should be noted that the feasible phenotypic values widely distributed over both 0.85 and 0.55, meaning that they also had the large plasticity so that they can adapt to both environmental states. After such actively niche-constructing and learning individuals dominated the population, the environmental state became stable again, and thus the innate traits converged to the new environmental state and their plasticity became small. This process is closely related to the cycles observed in [4]. The scale-free distribution of the environmental changes is expected to have emerged from the repeated occurrences of this complex coevolution process of learning and niche construction.

3.3 Effects of ecological inheritance

Finally, we conducted experiments with ecological inheritance. Fig. 7 shows the results of an experiment with $\alpha = 0.9$. The other parameter settings were the same as the ones in the previous experiment. We observed the similar but more smoothed scale-free property of the distribution

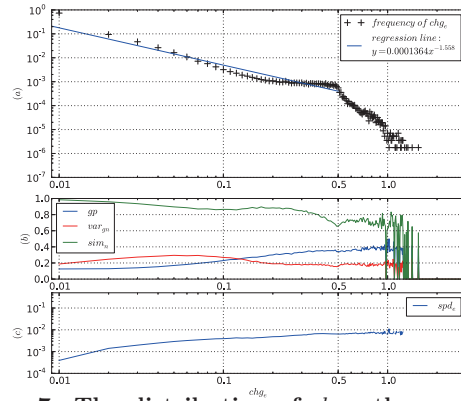


Figure 7: The distribution of chg_e , the average gp , spd_e , var_{gn} and sim_n when $\alpha = 0.9$.

of chg_e , compared with the one in Fig. 5. Also, the frequency of the smallest chg_e ($chg_e < 0.01$) was larger and the maximal chg_e was smaller. This seems to be due to the inertia effect of ecological inheritance, which made e_t stable. Actually, spd_e was much smaller, which also kept the phenotypic plasticity gp smaller. We also see that the peak of var_{gn} at around $chg_e=0.06$, which is also expected to be due to the fact that the large collective effect of niche construction ($|\delta\hat{e}|$) was necessary to change e_t drastically under the strong effect of ecological inheritance.

4. CONCLUSION

We investigated self-organizing properties of coevolution between learning and niche construction by constructing a minimal model in which individuals can both perform learning and niche construction. We found that there was a clear scale-free property in the distribution of the size of environmental changes. It was also shown that these changes were caused by the increased generic variation of niche-constructing genes, followed by the increase in the phenotypic plasticity. The analyses of effects of ecological inheritance showed that it decreased the speed and size of environmental changes, while maintaining the scale-free property of the whole dynamics.

5. ACKNOWLEDGMENTS

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