Effects of Temporal Locality of Ecological Processes
on Coevolution of Learning and Niche Construction

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Abstract

Roles of ecological processes in evolution are attracting much attention in evolutionary studies. Learning and niche construction are regarded as ecological processes that can affect the course of evolution directly or indirectly. However, the effects of mutual interactions between them on evolution are still poorly understood. Our purpose is to provide insight into the coevolutionary dynamics of learning and niche construction. For this purpose, we constructed a simple individual-based model 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. In particular, we focus on the effects of the temporal locality of ecological processes, which is the degree of simultaneous occurrence of ecological processes performed by individuals. We report that a cyclic coevolution of genes for learning and niche construction can occur when the temporal locality of ecological processes is low.

Introduction

In the standard view of the modern evolutionary synthesis, organisms are basically regarded as passively evolving entities based on selection and mutations. However, there are two ways, based on ecological activities, for modifying the selection pressure as conceptualized in Fig. 1. One is for individuals to change their own phenotype called learning, and the other is to change their environmental condition, called niche construction (Odling-Smee et al., 2003). Recently, the roles of these ecological processes in evolution are attracting much attention in evolutionary studies called Evo-devo (West-Eberhard, 2003) or Eco-devo (Gilbert and Epel, 2009).

A wide variety of species have abilities to modify their own traits to make themselves more adaptive in their existing environments. It has been controversial how this ecological process, called individual learning, or ontogenetic adaptation based on phenotypic plasticity, can affect evolution indirectly. Since Hinton and Nowlan's pioneering work (Hinton and Nowlan, 1987), ALife researchers have focused on the Baldwin effect (Baldwin, 1896; Weber, 2003), which is typically interpreted as a two-step evolution of the genetic
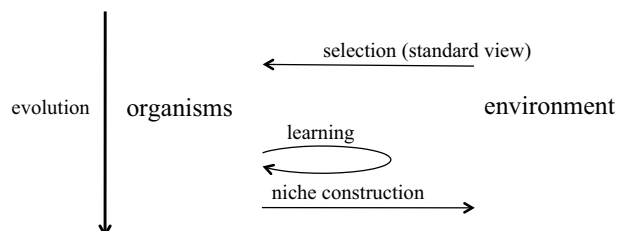

Figure 1: Two processes affecting the selection.

acquisition of a learned trait without the Lamarckian mechanism (Turney et al., 1996). An important finding is that the balances between the benefit and cost of learning can modify the shape of the fitness landscape, and can either accelerate or decelerate adaptive evolution (Paenke et al., 2009). A recent study has also discussed effects of the ruggedness of the fitness landscape (Suzuki and Arita, 2007). This study showed that if the shape of the fitness landscape is rugged, the learning can bring about a complex three-step evolution through the Baldwin effect.

Niche construction is another 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 (Odling-Smee et al., 2003). Such 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).

Recently, conditions for niche-constructing traits to evolve have been analyzed using theoretical or constructive approaches, in some cases leading to stable polymorphism (Laland et al., 1996), co-evolutionary dynamics of multiple species induced by their niche constructions (Suzuki and Arita, 2005), and so on. Self-regulation mechanisms of the environment caused by niche-constructing behaviors of individuals has also been investigated using several versions of the Daisyworld model (Harvey, 2004; Dyke, 2008).

So far, the effects of individual learning and niche con-

struction on evolution have typically been analyzed separately. We can interpret them as different processes in that the former is a change in the phenotype of the learning individual itself and the latter is the change in the surrounding environment of the niche-constructing individual. However, it is clear that both processes can interact indirectly 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. That is, a niche construction can change an environmental factor, which can in turn modify the selection pressures on individuals that share the modified environment. Such an environmental change can further affect their learning process. Both gene-culture coevolution and language evolution appear to exemplify such situations, in that their mutual interactions were implicitly incorporated. In addition, it was recently pointed out that evolutionary developmental biology and niche-construction theory have much in common, in that both place emphasis on the role of ontogenetic processes in evolution, despite independent intellectual origins (Laland et al., 2008). However, as far as we know, there are still few approaches that have focused on interactions between learning and niche construction explicitly, in spite of their importance as ecological activities that can affect evolution.

Locality of ecological processes is an important factor for evolution of ecological traits in general, because it can affect the difference in the fitness between the performing individuals and the other individuals. One can distinguish two different kinds of locality: spatial and temporal locality of ecological processes. For example, it has been reported that the strong spatial locality of the effects of niche construction can contribute to the evolution of niche-constructing traits (Suzuki and Arita, 2006; Silver and Di Paolo, 2006), because it leads to difference in the fitness between the niche-constructing individuals and other, non-niche-constructing, individuals in distant locations. Temporal locality of ecological processes has received much less attention.

Our purpose is to consider whether and how learning and niche construction can interact with each other (Suzuki and Arita, 2009). For this purpose, we construct a simple individual-based evolutionary model in which the individuals can perform both a niche construction of their shared environmental factors and acquire an adaptive phenotype through their lifetime learning. Especially, we focus on the temporal locality of ecological processes, which is defined as the degree of simultaneous occurrence of ecological processes performed by individuals. There could be two extreme situations. One is a case in which individuals perform their ecological activities one by one, and the other is a case in which all individuals perform their ecological processes at the same time. The former corresponds to the situation in which the temporal locality is lowest, and the latter corresponds to when temporal locality is highest. It is

not clear what aspects of these situations will contribute to the evolution of learning and niche construction. Through computational experiments with these two types of ecological processes, we show that temporal locality can strongly affect the evolutionary dynamics of learning and niche construction. Especially, we show that a cyclic coevolution of genes for niche construction and learning may occur in experiments with serial processes of ecological activities.

Model

Environment and genetic description of individuals

In our model, an environmental state shared by all N individuals is represented as a single real value e ($\in [0, 1]$). Each agent has a real-valued phenotype p ($\in [0, 1]$) whose initial value is determined by its genotype g_p ($\in [0, 1]$). The fitness contribution of p depends on e, and is determined by the following triangular shaped function $f(p, e)$:

$$f(p, e) = \begin{cases} 1 - |p - e|/L & \text{if } |p - e| \leq L, \\ 0 & otherwise. \end{cases} \quad (1)$$

Fig. 1 shows an example situation of the model. This function has a peak value 1 at e. Its value decreases linearly from the peak, and reaches 0 when the distance between p and e becomes L. Thus, the closer each agent's p is to e, the more fit it is.

Learning and niche construction

Each agent also has real-valued genes for learning g_l ($\in [0, 1]$) and niche construction g_n ($\in [-1, 1]$).

A learning process of each individual moves its phenotypic value p closer to e by (at most) g_l so as to increase its fitness contribution. Note that we assume that g_l can take a positive value because learning is a process that can increase the current fitness in general. The actual phenotypic value of an agent after its learning process p' is calculated from the equations as follows:

$$p' = \begin{cases} e & \text{if } |e - p| < g_l, \\ p - sgn(p - e) \times g_l & otherwise. \end{cases} \quad (2)$$

$$sgn(x) = \begin{cases} 1 & \text{if } x > 0, \\ 0 & \text{if } x = 0, \\ -1 & \text{if } x < 0. \end{cases} \quad (3)$$

This means that if the distance between the phenotype p of the focal individual and the environmental value e is smaller than its g_l, it can make its own p the same value as e completely. Otherwise, it can move its own p closer to e by g_l.

In addition, each individual can perform either positive or negative niche construction, which means that a niche construction can increase or decrease the fitness of the performing individual. This is because that niche construction is not always beneficial for performing individuals (i.e., there may
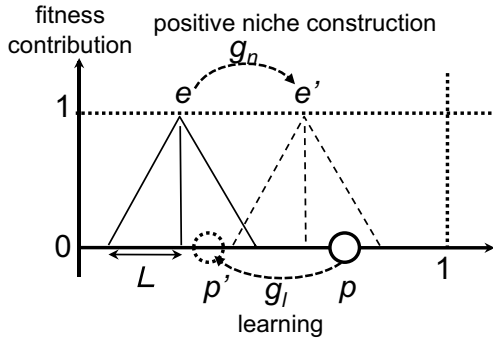
Figure 2: A learning and a niche construction in the proposed model.

Serial ecological processes (low temporal locality)

Parallel ecological processes (high temporal locality)

Figure 3: Serial and parallel processes of ecological activities. "L" or "N" represents an occurrence of learning or niche construction performed by an individual with the corresponding ID.

be environmental pollution). If g_n of an individual is positive (or 0), its niche construction is positive and the actual environmental value e' after its niche-constructing process is calculated from the equation as follows:

$$e' = \begin{cases} p & \text{if } |e - p| < g_n, \\ e - sgn(e - p) \times g_n & otherwise. \end{cases} \quad (4)$$

On the other hand, if its g_n is negative, its niche construction is negative, and e' is calculated as follows:

$$e_{temp} = e - sgn(e - p) \times g_n, \quad (5)$$
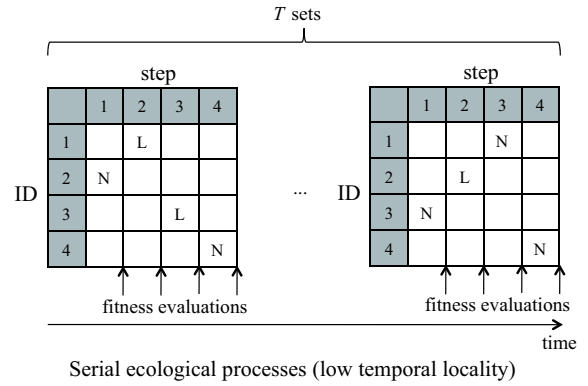
$$e' = \begin{cases} 0 & \text{if } e_{temp} < 0, \\ e_{temp} & 0 \leq e_{temp} \leq 1, \\ 1 & \text{if } e_{temp} > 1. \end{cases} \quad (6)$$

When g_n is positive, a niche construction moves e closer to its p (at most) by g_n. That is, a positive niche-constructing process is basically similar to a learning process except that it shifts the environmental value e rather than its own phenotype p. On the other hand, if g_n is negative, it makes e more distant from its p by $|g_n|$ within the range of the domain of $e \in [0, 1]$. If g_n is negative and p is exactly the same as e, we randomly add g_n or -g_n to e.
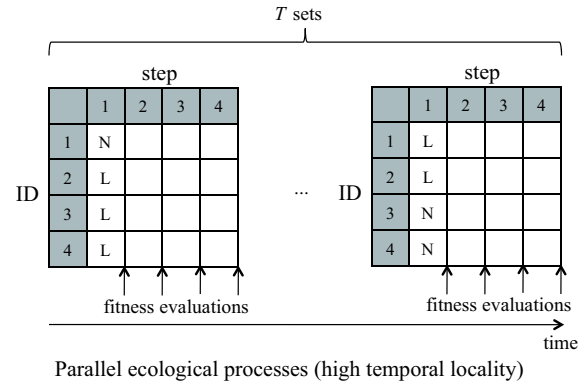
Ecological processes and evolution

In each generation, there are T sets of ecological processes, in each of which there are N steps. In each set, the individuals randomly decide which kind of ecological process to perform. We assume the two extreme types of temporal locality of ecological processes as follows:

Serial processes (low temporal locality) The individuals perform ecological processes serially in each set as shown in Fig. 3. In each set, an individual who has not done its ecological process yet in the current set is randomly selected and performs an ecological process. After the

phenotypic value of the learning individual or the environmental value is modified, the fitness contribution of all individuals' phenotype are evaluated independently. This situation corresponds to the low temporal locality of ecological processes.

Parallel processes (high temporal locality) All individuals perform ecological processes at the same time at the initial step in each set as shown in Fig. 3. Before they actually modify the phenotypic and environmental values, they determine the amount of change in them using the current environmental value. Then, they update their phenotypic values, and the average amount of change in the environmental value determined by niche-constructing individuals is added to the current value. This situation corresponds to the high temporal locality of ecological processes.

The final fitness of each individual is defined as the average fitness contribution evaluated in all $T \times N$ steps. The evolutionary process is based on a "roulette wheel selection" according to fitness. For each gene, a mutation occurs with a

small probability p_m, which randomly determines its genotypic value.

The model incorporates a mechanism called ecological inheritance. This means that an environmental state can be passed on to the next generation. In this model, the value of e at the last step in the previous generation is used as the initial value in each generation.

Results

Serial processes of ecological activities

We examined evolution based on serial processes of ecological activities. We conducted evolutionary experiments for 2000 generations using the following parameters: N=250, T=300, L=0.1, p_m=0.05. In the initial population, the values of genotypes g_p, g_l and g_n were randomly decided within their domains, and the environmental state e was set to the intermediate value 0.5.

So as to clarify a possible dynamics of interactions between learning and niche-constructing processes, we focused on the evolutionary trajectory of g_l and g_n shown in Fig. 4. The horizontal axis is the average g_n and the vertical axis is the average g_l among all individuals at each generation. Although there were large fluctuations, we could see a cyclic evolutionary behavior of both indices, in which four typical states from (i) to (iv) (in Fig. 4) were traversed in a clockwise fashion. This means that the evolutionary trend of learning behaviors was strongly affected by existing niche-constructing behaviors and vice versa. Essentially, this evolutionary scenario was observed when N and T were relatively large and L was sufficiently small.

More detailed analyses, described later, clarified that the transitions between these states shown in Fig. 4 could be summarized as follows: (i) $\rightarrow$ (ii) the nearly neutral evolution of niche-constructing behavior, which brought about large fluctuations of the environmental state, (ii) $\rightarrow$ (iii) the adaptive evolution of learning behavior in dynamically changing environment, (iii) $\rightarrow$ (iv) the adaptive evolution of positively niche-constructing behavior, which made the environment stable, and (iv) $\rightarrow$ (i) the adaptive evolution of non-learnable individuals due to the implicit cost of learning (a kind of over-learning) in the stable environment. This cyclic behavior implies that the change in the stability of the environmental state arising from positive and negative niche constructions dynamically altered the balances between benefit and cost of learning behaviors. So as to clarify the universal mechanism of interactions between learning and niche construction inherent in this behavior, we investigated in more detail the dynamics of the observed evolutionary process by focusing on the effects of the environmental changes on evolution, and on the benefit and cost of learning.
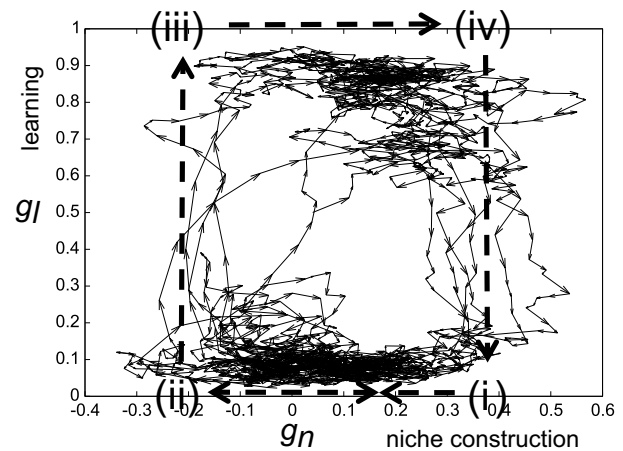

Figure 4: An example evolution of the average g_l and g_n through 2000 generations in the case of serial processes of ecological activities.

The detailed analyses of coevolution of learning and niche construction

Fig. 5 shows the evolution of the average and standard deviation of g_n, g_l, g_p and e through the initial 1000 generations in the same experiment as that shown in Fig. 4. Each value of g_n, g_l and g_p is derived from the values of all individuals in each generation, which means that their standard deviation represents their genetic variation in the population. Each value of e is derived from the values in all steps in each generation, which means that its standard deviation represents its temporal variation through steps in the generation.

Let us start from a situation around the state (i) near the 500th generation in Fig. 4 in which positively niche-constructing but non-learnable individuals dominated the population. As shown in Fig. 5, the standard deviation of g_p was relatively small (less than 0.2), which means that most individuals had basically the same, intermediate phenotypic value g_p. In this situation, there was nearly neutral selection pressure on the niche-constructing gene g_n because it could increase or decrease the fitness contribution of all individuals' phenotypes equally. Thus, the average g_n reached 0.0 and fluctuated around it because of the relatively small population size.

When the average g_n became negative as in the state (ii) at around the 600th generation, the environmental state e began to fluctuate by often taking either extreme value 0.0 or 1.0 and its standard deviation increased to higher values (around 0.4). Note that collective behaviors with positive and negative niche construction tend to make the environment state stable and unstable, respectively. In this case, the learnable individuals became adaptive because they can catch up with such environmental changes through their learning processes. Thus, the individuals with larger g_l and negative g_n
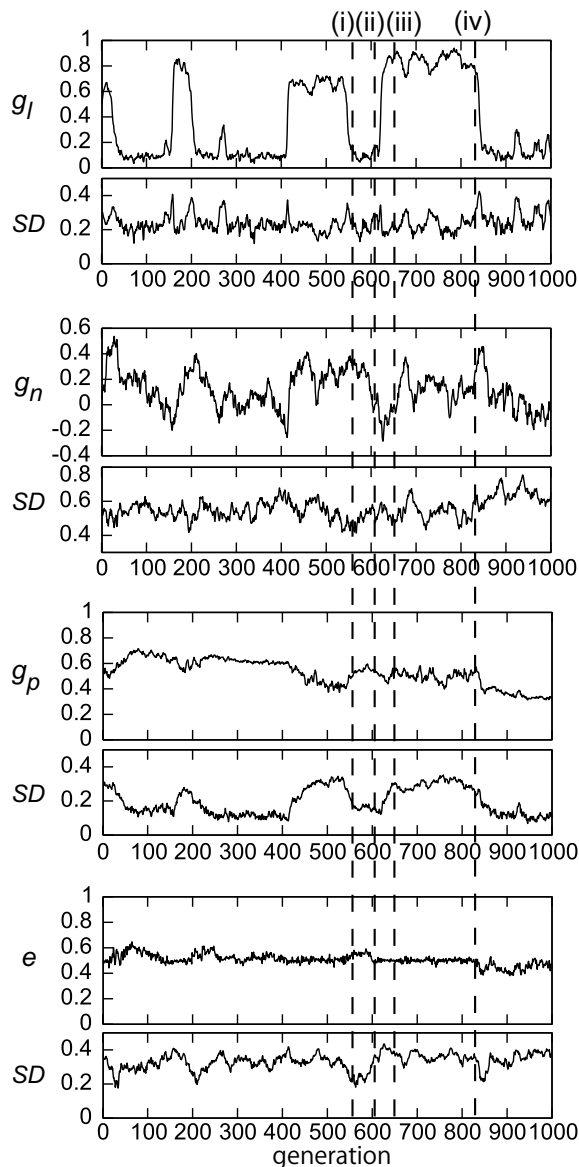
Figure 5: The evolution of the average and standard deviation of g_l, g_n, g_p and e through the initial 1000 generations in the case of serial processes of ecological activities.

rapidly occupied the population by keeping and even decreasing the stability of the environment. As a result, the average g_l increased quickly, and the population reached the state (iii) at around the 650th generation.

In the state (iii), individuals were changing their own phenotypic values dynamically so as to keep them closer to the fluctuating environmental values, which brought about a large variation among their phenotypic values. In such a situation, the positively niche-constructing individuals occupied the population because they can keep the environmental values close to their own phenotypes dynamically changed

by learning. Thus, the population reached the state (iv) at around the 840th generation. During this period, the standard deviation of g_p remained high because learning reduced the selection pressure on the initial phenotypic values. This effect of learning on genetic evolution is sometimes called a hiding effect (Mayley, 1997).

Finally, when the number of such individuals increased enough, the standard deviation of the environmental value began to decrease and the environmental value come to fluctuate around the intermediate value (around 0.5) as a result of a "tug-of-war" between positively niche-constructing individuals. It should be noticed that the environmental value still takes the extreme values 0.0 or 1.0 even in this situation. If individuals with the larger g_l modify their own phenotype to either extreme value, that individual's fitness tends to become quite small in the remaining steps because the environmental value stays around the intermediate value or sometimes takes the other extreme value. Such a negative effect, caused by a kind of over-learning, could be interpreted as an implicit cost of learning, in that the learning behavior made the individual's fitness smaller than the one's with less ability to learn, even under the assumption of no explicit cost of learning, such as an energetic cost for performing the learning behavior itself. On the other hand, the individuals with the smaller g_l and the intermediate g_p can obtain relatively high fitness consistently by keeping its phenotypic value around the intermediate value. Thus, these positively niche-constructing individuals without learning could occupy the population quickly by keeping or even increasing the environmental stability. As a result, the population got back to the state (i).

Parallel processes of ecological activities

We also conducted the experiments under the condition of parallel processes of ecological activities. The experimental setting was the same as the one in the previous section except for updating process. Fig. 6 shows the evolutionary trajectory of g_l and g_n in an example trial, and Fig. 7 shows the evolution of the average and standard deviation of g_n, g_l, g_p and e through initial 1000 generations.

Fig. 6 clearly shows that the evolutionary dynamics of the population was quite different from the one with serial processes. There was no clear correlation between the genes for learning and niche-constructing traits. More specifically, Fig. 7 shows that g_n largely fluctuated between -0.2 and 0.2 through generations, which means that the evolution of niche-constructing trait was neutral in this case. This is expected to be due to the fact that niche-constructing behavior by an individual was cancelled, on average, by niche-constructing behaviors of others performed in parallel. Because this neutral evolution made the environment unstable, the learning behavior was always beneficial, and thus g_l stayed around 0.6, as shown in Fig, 7.

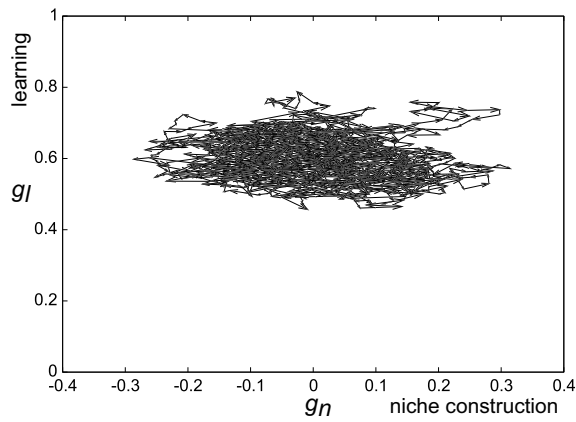As a whole, under the condition of parallel processes of

Figure 6: An example evolution of the average g_l and g_n through 2000 generations in the case of parallel processes of ecological activities.

ecological activities, there is basically no selection pressure on the niche-constructing trait, but its neutral evolution can cause selection pressure on the learning trait.

Conclusion

We studied the general nature of coevolution of learning and niche construction by using a simple evolutionary model of learning and niche-constructing genes. By comparing the cases with different temporal locality of ecological processes, we found that the adaptive benefit of learning and niche construction can change, and this strongly affects their coevolutionary dynamics. In the case of the low temporal locality of ecological processes, the positive effect of niche-construction directly affected the adaptivity of the niche-constructing individuals, which brought about a cyclic coevolution of genes for learning and niche construction. The detailed analyses showed that the changes in the stability of the environmental state arising from positive and negative niche constructions is a key factor that dynamically determines the benefit and cost of learning behaviors. On the other hand, in the case of the high temporal locality, the neutral evolution of niche-constructing traits led to adaptive evolution of the learning trait.

One of the controversial topics that relates to this discussion is the interaction between evolution and learning in the context of language evolution, in that the fitness of each individual is determined by its linguistic niche composed of the other individuals' linguistic abilities based on learning. Yamauchi showed that the accumulated linguistic information through an ecological inheritance masks selection pressure on the innate linguistic traits acquired through the Baldwin effect (Yamauchi, 2007). Suzuki and Arita also showed that the Baldwin effect can occur repeatedly on dynamically changing fitness landscapes (linguistic niches) which arise from communicative interactions among individuals, and
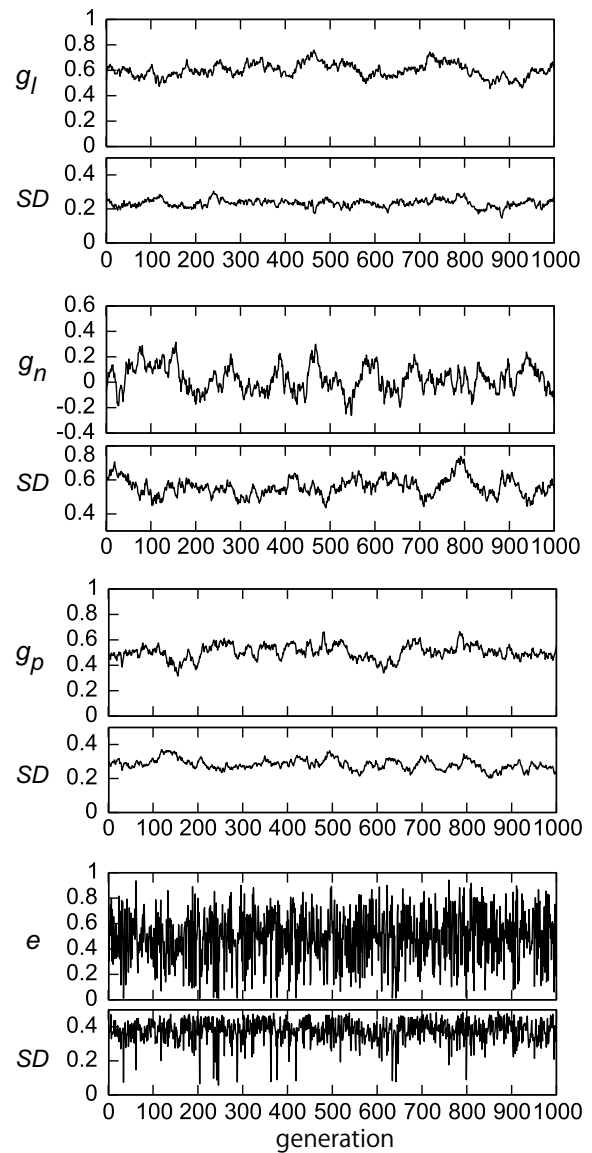

Figure 7: The evolution of the average and standard deviation of g_l, g_n, g_p and e through the initial 1000 generations in the case of parallel processes of ecological activities.

facilitates genetic evolution as a whole (Suzuki and Arita, 2008).

If we regard the horizontal axis in Fig. 2 as a space of possible language and each agent has a specific language determined by its p, the value of the environmental state e can be regarded as the most adaptive language due to the accumulation of its linguistic resources, which can contribute to its fitness increase, for example. In this case, a learning behavior corresponds to the process in which each agent changes its own language to a more adaptive one in its current linguistic environment, and a positive or negative niche construction corresponds to the production of linguistic re-

sources which can make its own language more or less adaptive. Our results with the low temporal locality of ecological activities imply that the intrinsic dynamics of coevolution of the abilities of learning language and constructing linguistic niche can bring about the dynamic and diverse aspects of language evolution even without any effects from external environments.

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