How ecological inheritance can affect the evolution of complex niche construction in a 2D physical simulation

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Abstract

Niche construction is a process in which organisms modify the selection pressure on themselves and others through their ecological activities. Various evolutionary models of effects of niche construction on evolution have revealed that they bring about unexpected evolutionary scenarios. However, little is still known about how niche-constructing behaviors of complex physical structures (such as nest-building) can emerge through the course of evolution, even though it is one of the most ubiquitous and significant niche-constructing behaviors. Our purpose is to obtain knowledge of the emergence and evolution of physically-grounded niche construction and the effect of its ecological inheritance on evolution. We construct an evolutionary model in which a virtual organism has to arrive at a goal by constructing a physical niche composed of objects in a physically simulated environment. In particular, we focus on effects of the degree of ecological inheritance, which is represented as a weathering probability of ecologically inherited objects from a parent to its offspring. We show that it has a nonlinear effect on the adaptivity of the population. In the case of no ecological inheritance, adaptive niche-constructing behaviors such as valley-filling or ramp-placing strategies emerged, which created complex structures composed of multiple objects. It also turned out that the stable ecological inheritance of constructed structures could increase the adaptivity of the population by allowing an organism to maintain the inherited and adaptive structures while the unstable ecological inheritance rather decreases the adaptivity of the population by making previously adaptive structures maladaptive obstacles.

Introduction

All creatures, to a greater or lesser extent, change their own and others’ niches through their ecological activities, which modify the selection pressure on themselves and others. This process is called “niche construction” (Odling-Smee et al., 2003). The niche construction processes are seen in ecological activities of many species such as plants (photosynthesis), nonhuman animals (nest building) and human. Recently, the niche construction is also recognized as an important factor in considering an open-ended evolution (Taylor, 2015).

A typical example of a niche-constructing organisms are 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 the successive population to different selection pressure. This effect is also called “ecological inheritance”, as it makes the generation inherit a legacy of modified selection pressures from ancestral organisms (Odling-Smee et al., 2003).

The effects of niche construction on evolution have been mainly investigated using both mathematical and simple computational models, in which effects of niche-constructing behaviors are represented as changes in variables that represent the environmental states. The environmental state in Laland et al.’s model of population genetics (Laland et al., 1996) is represented as the amount of resource, which can be directly increased by the niche-constructing behavior. Han et al. extended a version of Laland et al.’s model to a patch occupancy model in which the amount of distributed resources can be modified through niche construction (Han et al., 2009). They showed that three different spatial patterns of metapopulation emerged depending on the different ecological imprint from niche
construction. Suzuki and Arita constructed an evolutionary model into which both learning (change in a phenotypic value) and niche construction (change in an optimal phenotypic value) were incorporated, and reported that a cyclic coevolution of genes for learning and niche construction was observed in the case of the low temporal locality of ecological processes (Suzuki and Arita, 2010). Harvey also constructed a simplified version of the Daisyworld model in order to understand interactions between the environment states (i.e., the temperature of the planet) and organisms (i.e., black and white daisies that increase and decrease the temperature, respectively) (Harvey, 2004). He reported that the homeostasis of the global temperature emerged through the change of the proportion of black and white daisies against the global warming. These studies clarified various effects of niche construction on evolution in the cases when the environmental state is represented as a quantity (e.g., resources, optimal phenotypic values, temperature).

On the other hand, an important feature of niche construction is that it can create physical and complex structures composed of many components, which cannot be represented quantitatively. A nest building is a typical and ubiquitous example of such a behavior. For example, a beaver makes a dam with branches: It stems the flow of a river and have an influence on many organisms (Odling-Sme et al., 2003). Taylor presented an individual-based model of complex niche construction that can make the shape of one-dimensional fitness landscape complex (Taylor, 2004). He showed that the evolved organisms that performed more complex niche constructions had more genes, which implies a continuous increase in the complexity of organisms. Kojima et al. constructed an evolutionary model in which individual has a strategy for a Prisoner’s Dilemma and a trait for creating a physical structure that can limit social interactions between neighboring individuals (Kojima et al., 2014). They found that, when the degree of ecological inheritance was high, a stable pattern of the physical structure emerged. It enabled cooperators to reduce the number of interactions with defectors while keeping that number with cooperators moderate. Although these studies discussed complex or physical niche construction, they are still abstract in the sense that physically-grounded interactions between organisms and environments were not considered.

The purpose of this study is obtaining knowledge of the emergence and evolution of physically-grounded niche construction and the effect of its ecological inheritance on evolution. In particular, we focus on the effects of the degree of ecological inheritance, which could be different due to properties of niches and ecological dynamics. We discuss whether and how complex interaction processes between organisms and environments can bring about non-trivial evolutionary dynamics depending on the different degree of ecological inheritance.

We adopt a model of virtual organisms, which is recognized as a novel platform to discuss recent topics in evolutionary research such as eco-evolutionary feedbacks (Ito et al., in press). We construct an evolutionary model in which a virtual organism has to arrive at a goal by constructing a physical niche composed of some objects. We adopt a physically simulated environment based on a physics engine for 2D games. We show that the degree of ecological inheritance can have a nonlinear influence on the adaptivity of the population, facilitating or retarding the evolution of niche-construction behaviors of complex and physically-grounded structures.

**Model**

**Field and task**

We use the Box2D (Catto, 2016), which is an open source physics engine for 2D games, in order to introduce a physically simulated environment into our model. Box2D can simulate physical interactions between 2D objects such as friction and collision between rigid bodies.

In our model, we assume an x-y coordinate plane that represents a horizontal and vertical space, and there exists gravity along the y-axis toward the bottom. The simulation is updated every infinitesimal time step $dt$ (second). Hence, the physical environment is updated $1/dt$ times in one second. We used the default parameters that define the properties of physical environment with a few modifications\(^1\).

We assumed a $1160 \times 360$ virtual space as shown in Fig. 2. A field consists of squared “field tiles” with a side length of 20. There is a special field tile on the right end of the field, representing a goal. There are two valleys composed of field tiles in the field, and the left one is shallow and wide whereas right one is deep and narrow. The virtual organism is put on a starting point on the left end of the field at first. The task for the organism is to move from the start to the goal as many times as possible within the time limit $T$ seconds under the assumption that the organism is returned to the start after the goal. Specifically, the fitness of the virtual organism is calculated by the following equation (Eq. 1):

$$\text{fitness} = g + \frac{\text{disgoal} - \text{dis}}{\text{disgoal}}, \quad (1)$$

\(^1\)Gravity $g = 9.8 \text{ (m/s)}^2$, density $\rho = 1.0 \text{ (kg/m}^3\text{)}$, coefficient of friction of a virtual organism $\mu_i = 0.7$ and coefficient of friction except for a virtual organism $\mu = 0.3$. 

![Figure 2: The field for fitness evaluation.](image-url)
where $g$ is the number of times for which the virtual organism arrived at the goal, $dis_{goal}$ is the distance between the start and the goal, and $dis$ represents the distance between the goal and the position of the virtual organism at the end of fitness evaluation. Therefore, the more the number of times of arrival at the goal is and closer to the goal at the final step the virtual organism gets, the higher fitness it gets. We expect that a non-niche-constructing organism will get stuck in the first valley because it cannot climb the valley while niche-constructing organisms have a possibility to reach the goal by placing some objects in the field.

**Virtual organism**

In our model, a circular-shaped organism with the radius of 20 can move in the field by rotating its body to the left or right (Fig. 3). It also can place objects\(^\ast\) in the field. This is a niche-constructing behavior in our model in the sense that constructed structures can affect the future adaptivity of the organism. There are two types of objects: “box” with a side length of 16 and “board” which is a $6 \times 60$ rectangle. A virtual organism has two areas around it: the visibility and the motion range of its arm (Fig. 3, right). The visibility is a round shaped region around the organism with the radius of $FV$ and the organism can recognize objects and field tiles within this area. The motion range of its arm is also a round-shaped region with the radius of $L$ and the organism can place objects within this area. Placed object will fall on other objects or field tiles due to the gravity if it is placed in the air. There is no cost for placing objects.

A three-layer neural network, of which weights are defined by the genotypes of an organism, determines the behavior of the organism (Fig. 3, left). We use a sigmoid function as a transfer function in the neural network. The values are inputted to the neural network every time when the physical environment is updated. The following values are inputted to the input layer: the number of field tiles, boxes and boards within the visibility; the relative x-y positions of their center of gravity from the organism; and the number of available objects, which will be explained later.

The output layer consists of one neuron which decides a direction of rotation and five neurons related to placing objects. The first neuron decides which direction the virtual organism rotates and moves. If its output value is higher than 0.5, the clockwise torque $\tau$ of which the magnitude is 100,000 (kgf $\cdot$ m) is applied to the virtual organism, otherwise anti-clockwise torque is applied to it. The second neuron decides whether the virtual organism places an object or not. If its value is larger than 0.5, the virtual organism places the object in the field. The third neuron decides which object the virtual organism places in the field if it does. If its value is higher than 0.5, the virtual organism places a box, otherwise it places a board. The fourth and fifth neurons decide the position on which the virtual organism places the object within the motion range of its arm. The position is represented by the polar coordinates $(r, \theta) = (L \times x_4, 2\pi \times x_5)$, where $x_4$ and $x_5$ represent the fourth and the fifth output values, respectively. The last neuron decides the angle of rotation of the object $\phi = 2\pi \times x_6$, where $x_6$ represents the sixth output value. If the focal object will interfere the existing field tiles or objects in the field, or will be outside of field, the action of placing the object is canceled and nothing happens.

Moreover, the parameter $B$ determines the maximum number of the objects that can exist in the field. It reflects the amount of available resources for niche-constructing behaviors. The organism can make use of the number of available objects for decision making as an input to its neural network.

**Evolution and ecological inheritance**

A virtual organism has synaptic weights of its neural network of which values are determined by its own genes. The population of organisms evolves according to a genetic algorithm. In the initial generation, there are $N$ virtual organisms and the values of their genes are randomly assigned between -1.0 and 1.0. After the fitness evaluation of all organisms, a pair of parents is selected by a roulette-wheel selection in accordance with the fitness. They produce a pair of two offspring with the same genotypes as themselves, and a two-point crossover occurs between -1.0 and 1.0. The off-spring with a probability $PC$. Each gene can mutate with a small probability $PM$. If a mutation occurs, a random number $\in [-DM, DM]$ is added to a value of the gene. This process will be conducted until the number of the offspring reaches $N$.

Furthermore, we introduce an ecological inheritance into the model in order to investigate its effect on the evolution of niche construction. In a pair of the offspring, the environmental state of one parent is inherited to the environment of

\(^{\ast}\)In this paper, the term “objects” represents boxes and boards placed by an organism. It does not include field tiles.
one offspring, and the environmental state of the other parent is also inherited to that of the other offspring. Specifically, each offspring inherits the environmental state of the corresponding parent at the end of its fitness evaluation process. This means that the all objects in the parent’s environment will be copied to the offspring’s environment, keeping their types, positions and rotations the same.

In addition, the degree of such ecological inheritance can vary depending on environmental conditions in the real world. Thus, we also introduce a probability $w_e$ into our model, which represents a probability of weathering of each object. Each inherited object vanishes according to the probability $w_e$. The higher the probability $w_e$ is, the less the virtual organism inherits the objects. We conduct the whole process of evolution and ecological inheritance through $G$ generations.

**Result**

We conducted evolutionary experiments using the following parameters: $N = 50; G = 2,000; dt = 0.02; T = 200; B = 25, 40$ and $55; FV = 500; L = 125, 250$ and $500; we = 10^{-2.0}, 10^{-1.5}, 10^{-1.0}, 10^{-0.5}$ and $10^{-0.0}; PC = 0.7; PM = 0.001$ and $DM = 0.003$. We conducted 10 trials for each combination of the parameters $B, L$ and $we$. This is because $B$ and $L$ are related to the richness of the environment and the basic ability of organisms, respectively. Fig. 4 shows the average fitness over all $(3 \times 3 \times 10)$ trials for each case of $we$. A horizontal axis represents $we$ and the red square represents the average fitness. We used the fitness values of the last 1000 generations for calculating the average fitness in each trial to eliminate effects of initial conditions. We also showed a box plot of each set of 90 trials. We see that the weathering probability $we$ strongly affected the average fitness. There was a statistically significant difference in the fitness distribution among these cases (Kruskal-Wallis test, $H = 81.9, p-value < 1 \times 10^{-3}$).

Here, we particularly focus on the three typical cases of $we$: 0.01, 0.1 and 1.0. In the case of the probability $we = 1.0$, there is no effect of the ecological inheritance because all objects vanish when they are handed over to next generation. On the other hand, the ecological inheritance occurs stably when the probability $we$ is 0.01. When the probability $we$ is 0.1, the ecological inheritance occurs but it is unstable.

In the case of $we = 1.0$, the average fitness was 1.8. It means that a virtual organism arrived at the goal one or two times on average in one trial. On the other hand, the average fitness was about 2.1 when $we$ was 0.01. It indicates that the ecological inheritance of most of the objects from the parental generation contributed to the fitness increase. Comparing with this result, the average fitness was about 0.6 in the case of $we = 0.1$, which also indicates that unstable inheritance of objects can rather decrease the fitness. This implies that the degree of ecological inheritance has a nonlinear effect on the adaptivity of the population.

The high fitness values when $we = 0.01$ and 1.0 were obtained by the evolution of adaptive niche-constructing strategies. Fig. 5 and Fig. 6 show two typical strategies, which were commonly observed in successful trials irrespective of the parameter settings (except for $we = 0.1$). One is a valley-filling strategy that fills a valley with many objects
A typical example of evolution process when $we = 1.0$, $L = 500$ and $B = 25$. (Fig. 5), which allows an organism to pass through the valley. The other is a ramp-placing strategy that creates a ramp of a board, which allows an organism to climb from the bottom of a valley. The former strategy was observed more often than the latter, which implies that the former was more easily acquired through the evolution process due to its simplicity and robustness against external perturbations such as collisions with organisms or other objects, compared with the latter. Fig. 7 shows an example of objects that worked as obstacles, preventing an organism from crossing a valley. We discuss how and why the degree of ecological inheritance affected the evolution of such niche-constructing behaviors in detail.

**Experiments with no ecological inheritance**

($we = 1.0$)

First, we analyze experimental results with the weathering probability $we = 1.0$ as a basic situation in which there is no effect of ecological inheritance. Fig. 8 shows an example evolution process of the fitness (top) and the average number of objects that existed at the end of fitness evaluation in each generation (bottom) in a trial when $L = 500$, $B = 25$ and $we = 1.0$, as a case in which an adaptive structure evolved successfully. While the average fitness was less than 1.0 in the initial generation, it increased to about 3.5 quickly. Then it further increased to about 4.0 at around the 950th generation. There were organisms with very low fitness through experiments. This is because offspring of organisms with higher fitness sometimes cannot reach a goal at all due to the negative effects of genetic operations. The average number of the placed boards was around 24, which is close to the number of available objects $B$ in this case, whereas that of placed boxes was 0. Fig. 9 shows an emerged structure at the 900th (top) and the 2,000th (bottom) generations in the trial in Fig. 8. We see that the organism could pass through valleys by using both valley-filling and ramp-placing strategies with many boards. We also see that the slight changes in the distribution of boards contributed to the fitness increase as mentioned above.

So as to analyze the general tendency of emerged niche-constructing behaviors and their adaptivity, we focus on the average fitness and the average number of the two types of placed objects in various experimental conditions of $B$ and $L$, as shown in Fig. 10. Each point represents the average fitness (color) and the average number of placed boxes (x-axis) and boards (y-axis) during a fitness evaluation process over the last 1000 generations in a single trial. Each subfigure corresponds to the setting of $B$ and each type of marker corresponds to the setting of $L$. We see that the trials in which many objects were placed tended to have the higher fitness, as the example above showed. This indicates that the niche construction, that is, placing many objects, contributed to the adaptivity of the evolved organisms in our model. We also see the virtual organism never arrived at the goal in some trials and thus got a low fitness. In this case, the organisms tended to evolve non-niche-constructing strategies, which do not place any objects at all, because it is better not to place any obstacles in order to get closer to the goal if objects do not contribute to pass through valleys. This strategy is expected to be a sub-optimal in the sense that once such a strategy occupied the population, adaptive niche-constructing strategies rarely evolved.

Next, we focus on the types of the placed objects in the field. It is seen from Fig. 10 that the number of the placed boards was larger than that of placed boxes especially when the fitness was high. The difference in the characteristic of boxes and boards appears to be the cause of this. A box is taller than a board. Thus, it is beneficial to use for filling in valleys. However, at the same time, it can become an...
$B=25$  \hspace{1cm} $B=40$  \hspace{1cm} $B=55$

Figure 10: The fitness and the number of the objects that existed at the end of fitness evaluation when $we = 1.0$.

$B=25$  \hspace{1cm} $B=40$  \hspace{1cm} $B=55$

Figure 11: The fitness and the number of the objects that existed at the end of fitness evaluation when $we = 0.01$.

Obstacle if it exists in front of an organism. On the other hand, a board is flatter than a box and a virtual organism can climb over it, thus, it does not cause such a problem, which allows organisms to obtain the higher fitness when they use boards. Furthermore, it is long enough to create a ramp structure. It is expected that boards were used more frequently than boxes because of these differences in their characteristic. In addition, we also see that the fitness of the trials with $B = 25$ was higher than one with $B = 40$ and 50 in general. This might be because objects tend to become obstacles if too many objects are placed in the field.

**Experiments with stable ecological inheritance** ($we = 0.01$)

Next, we discuss how the evolution of such an adaptive niche construction is affected if constructed structures are inherited to the next generation. Fig. 11 shows the relation between the fitness and the number of the objects that existed at the end of fitness evaluation in the case of stable ecological inheritance: $we = 0.01$. The overall trend did not change compared with Fig. 10, meaning that adaptive organisms tended to have many objects in their field. However, in this case, they inherited most of the objects due to the very low weathering rate, and they tended to add a few boards during their fitness evaluation process. The fitness tended to be higher than the cases with $we = 1.0$, especially when $B$ was large (40 and 55).

Fig. 12 shows a typical example of an evolution process in the case of $L = 125$ and $B = 40$ in which the adaptive structure evolved successfully. The top, middle and bottom panels represent the fitness, the average number of the inherited objects from the previous generation and the average number of the placed objects by an organism at the current generation, respectively. Except for the initial few generations, organisms evolved to place a few boards at each generation, which resulted in the accumulation of many boards in the field. At the last generation, on average, 38.1 boards
and 1.5 boxes were inherited from the previous generation, while 0.3 boards and 0.02 boxes were placed in the field. This means that organisms inherited the nearly maximum number of boards from their parents, and they compensated for the vanished ones by placing a few additional boards. The average fitness reached around 5.0 and this was higher than that of any cases with the probability \( w_e = 1.0 \).

Fig. 13 shows snapshots of the inherited environment in the same trial in Fig. 12. The top, middle and bottom panels represent the inherited environments at the 300th, 400th and 500th generation, respectively. We see that two valley-filling structures of boards were inherited. These structures allowed an organism to pass through the valleys and this is a main reason that this organism obtained the high fitness because it does not need to create such adaptive structures from scratch. We also see that there were a few changes in these structures across generations. This is due to the weathering of a few objects, and the organism maintained adaptive structures by placing additional boards as many as possible in the field. The reason the fitness tended to be high especially when \( B \) was large is expected to be due to the fact that well-organized structures with many objects through ecological inheritance were more adaptive (e.g., easy to pass through, robust against the weathering of objects). Therefore, in the case of stable ecological inheritance, organisms evolved to maintain an inherited adaptive structure composed of many objects.

Experiments with unstable ecological inheritance \( (w_e = 0.1) \)

In this condition, in which 10% of the objects in the previous generation disappear, the fitness was very small in many trials, and the non-niche-constructing strategy evolved in such cases. A cause of it is expected to be large changes in the environmental conditions between generations. Even when adaptive niche-constructing strategies appear and begin to invade into the population, the emerged adaptive structures in the current generation tend to become obstacles (such as shown in Fig. 7) in the subsequent generations because of their irregular shapes due to the high weathering rate. This prevents such adaptive strategies to invade into the population, and further allows non-niche-constructing strategies to evolve.

Fig. 14 shows a typical but a bit complex example of such a situation when \( L = 125, B = 40 \) and \( w_e = 0.1 \). The fitness was high around the initial few generations, meaning that an adaptive niche-constructing strategy evolved. However, the fitness decreased drastically as soon as the organism began not to place objects, and it never increased until the last generation.

Once the adaptive structures emerged and inherited to the next generation, placing more objects might not contribute to the fitness increase or even have a negative effect on the fitness increase. In such a case, there can be no or negative selection pressure to place objects. However, if non-niche-constructing strategies evolved, the adaptive structure became obstacles very quickly in the case of the high weathering rate, which resulted in the rapid fitness decrease, as observed in Fig. 14.

In sum, the unstable ecological inheritance has a negative effect on the evolution of an adaptive niche-constructing be-
Figure 14: A typical example of an evolution process in the case of \( u_{we} = 0.1, L = 125 \) and \( B = 40 \).

behavior by collapsing emerged adaptive niches.

**Conclusion**

In order to clarify the evolutionary dynamics of physical niche-constructing behaviors, we constructed an evolutionary and physically-grounded model of virtual organisms in which an organism has to arrive at the goal by performing a physical niche construction by placing objects in a two-dimensional field with valleys.

The results showed that the degree of ecological inheritance, which is represented as a weathering probability of inherited objects from a parent to its offspring, has a nonlinear effect on the adaptivity of the population. In the case of no ecological inheritance, niche-constructing behaviors such as valley-filling or ramp-placing strategies emerged. Furthermore, the stable inheritance of constructed structures from a parent contributed to the adaptivity of the population by allowing an organism to maintain the inherited and adaptive structures. On the other hand, when constructed structures were unstably inherited, the adaptive structures at a generation tended to become non-adaptive at subsequent generations. This prevents the niche-constructing behavior from evolving and makes the adaptivity of the population lower.

We think that these effects of ecological inheritance on the evolution of niche-constructing behaviors might be one of the typical properties of physical and complex niche construction.

The environmental state in Laland et al.’s model of population genetics (Laland et al., 1996) is represented as the amount of resource, which can be directly increased by the niche-constructing behavior of organisms. They focused on the number of previous generations of niche construction influencing the amount of resource in the current generation, and showed that the increase in the number of previous generation have a simple and monotonous effect on the evolution process, yielding the more considerable time-lag. In contrast, our result implies that such environmental parameters can have more complex effects on the evolution process when there are more complex interactions between organisms and environments.

Future work includes introducing other types of objects and the evolution of object shapes into our model, and conducting evolutionary experiments with different setting of the field.

**References**


