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Eco-Evo-Devo in the Adaptive Evolution of Artificial Creatures Within a 3D Physical Environment

Siti Aisyah Binti Jaafar *, Reiji Suzuki and Takaya Arita

Graduate School of Informatics, Nagoya University, Furo-cho, Chikusa-ku, Nagoya 464-8601, Aichi, Japan; reiji@nagoya-u.jp (R.S.); arita@nagoya-u.jp (T.A.)

* Correspondence: binti.jaafar.siti.aisyah.v4@s.mail.nagoya-u.ac.jp

Abstract: Eco-evo-devo is an interdisciplinary field integrating ecology, evolutionary biology, and developmental biology. Niche construction refers to the phenomenon where organisms alter selection pressures through ecological activities, and ecological inheritance is the consequence of niche construction, passed down through generations. Development encompasses the process by which an organism grows and changes its form and behavior throughout its lifetime. Despite emerging research on eco-evo-devo, the evolution of organisms involving complex physical structures remains underexplored. We aim to explore interactions between these components in the evolution of the adaptive morphology and behavior of artificial creatures. We constructed an evolutionary model where a population of rigid-bodied creatures must cross two valleys to reach a goal, using morphological development and object construction in a 3D physical environment. We found that the evolution of both lifetime development (LD) and niche construction (NC) showed complementary roles, with LD contributing to crossing one valley and NC the other. Regarding ecological inheritance (EI), we observed how NC adapts to the presence of inherited objects by placing fewer objects to construct structures. On the other hand, a large percentage of EI can cause obstacles to form, which hinders the population from moving towards the target and facilitates non-adaptive morphology, making the evolution unsuccessful.

Keywords: eco-evo-devo; development; niche construction; ecological inheritance; artificial creatures; 3D multi-agent simulation

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1. Introduction

Eco-evo-devo is an interdisciplinary field that integrates ecology, evolutionary biology, and developmental biology. Niche construction refers to the phenomenon in which organisms alter the selection pressures on themselves and others through their ecological activities [1]. Ecological inheritance encompasses the consequences of niche construction that are passed down through generations. Development, on the other hand, involves the process by which an organism grows and changes its form and behavior throughout its lifetime.

Development plays a crucial role in the evolution of organisms by influencing how the agents grow, adapt, and interact with their environments over time (e.g., developmental plasticity [2,3]). For example, the plasticity-first hypothesis proposes that when an environment changes, phenotypes that were previously hidden and evolved neutrally in a stable environment are expressed through developmental plasticity. Subsequently, the invasion of the adaptive phenotypes among them into the population precedes and promotes genetic evolution [3]. In evolutionary computation, Miras et al. (2021) concluded that in robot

evolution characterized by phenotypic plasticity, traits suited to early life environments are favored, supporting the plasticity-first hypothesis that emphasizes the importance of early adaptive traits for survival [4].

In the context of artificial life and evolutionary robotics, development typically refers to the processes by which an agent's morphology and behavior change throughout its lifetime. The roles of development in evolution have been demonstrated in many recent studies. Higashinaka et al. (2024) found that the developmental plasticity of flexible two-dimensional voxel-type virtual creatures that evolved neutrally exhibited diverse morphological and behavioral patterns when the environment changed [5]. Furthermore, they found that in cases where the evolutionary process was accelerated, adaptive morphology and behavior emerged by utilizing existing morphology and plasticity to adapt to new environments. They argue that this phenomenon aligns with the concepts of the plasticity-first hypothesis and exaptation.

A study by Gupta (2021) found that environmental complexity fosters the evolution of morphological intelligence in embodied agents. This was evidenced by their ability to facilitate the learning of novel tasks [6]. Another example is Kriegman et al.'s study on the evolution of virtual creatures with morphological development in an evolutionary environment of 3D voxel-type soft robots, where morphology (i.e., the shape of the voxels) can change through their lifetime [7]. They found that creatures exhibited various morphologies and behaviors throughout their lifetime. Among them, individuals that expressed adaptive morphologies and behaviors (e.g., rotation with rounded shapes in a locomotion task) via their lifetime evolved. Then, these adaptive traits subsequently progressed in a more stable and robust direction in response to variations.

Niche construction plays an important role in evolution by allowing organisms to actively modify their own and others' environments, thereby influencing evolutionary processes. A typical example of niche-constructing behavior that leads to phenotypic adaptations is seen in woodpeckers (*Picidae*) [8]. These birds peck holes in trees, and the inherited consequences (i.e., holes in trees) of this behavior result in adaptations such as a lengthened, strengthened, and sharply pointed bill. As mentioned above, environmental modifications by organisms lead to inherited ecological changes, further driving evolutionary adaptations in subsequent generations.

In addition, previous research has also indicated that complex niche construction can significantly contribute to open-ended evolutionary processes in physically grounded environments, such as the long-term embodied evolution of robots [9]. These studies specifically explored how ecological inheritance affects the evolution of complex niche-constructing behaviors in a 2D physical simulation. Their findings suggest that niche-constructing activities can lead to increasingly sophisticated and adaptive behavior over time, resulting in highly adaptable and resilient robotic systems capable of continuous evolution and improvement in response to changing environmental conditions.

Another criterion of niche construction is that it can lead to both positive and negative effects on niche-constructing organisms. Coninx (2023) shed light on the darker side of niche construction, revealing that organisms can modify environmental features in ways that may be harmful to them. Some alterations due to niche construction can pose new challenges that genetic adaptation cannot address quickly enough, leading to serious consequences for the organisms. This study suggested that much faster local adaptations are needed to address these issues. Hence, niche construction not only provides a positive mechanism for the interplay between organisms and their environment but also poses challenges and can negatively impact the adaptability of organisms [10].

The mutual relationship between development and niche construction in evolution has been emphasized in various biological and theoretical studies, highlighting the importance of these components in the evolution of organisms. According to Lala (2024), niche construction creates new selection pressures, leading to adaptive trait changes and allowing the same species to exhibit different characteristics based on the environments shaped by their activities [11]. Trappes (2022) demonstrates that individuals adjust their phenotypes in response to the environment and act as agents of evolution, influencing selection pressures and resources for new phenotypic variation [12]. Additionally, more studies have discussed how the evolution of niche construction significantly affects the traditional understanding of phenotypic evolution [1,13].

In the context of computational approaches to evolution, the discussion on the dynamics of the coevolution of development and niche construction is still very limited. Nisioti (2023) suggested that niche construction in simulated environments with diverse niches and evolving populations promotes adaptability, finding that populations adapt to their preferred niches, increase plasticity, and maintain high evolvability [14]. This suggests that niche construction promotes adaptability and results in various types of plasticity. Suzuki and Arita (2010) suggested that when comparing cases of different temporal localities of ecological processes, the adaptive benefit of learning behaviors and niche construction can change, and this significantly affects their coevolutionary dynamics [15].

Our aim is to understand how niche construction and development coevolve in the presence of ecological inheritance within a complex environment, focusing on their effects on emerging adaptive morphology and behavior in artificial creatures. Despite increasing interest in this biological topic, as explained above, the coevolution of niche-constructing behaviors and the development of complex physical structures remains underexplored. Therefore, we constructed an evolutionary model of a rigid-bodied creature in a 3D multiagent environment with a simple task: crossing two valleys to reach a goal. We used HyperNEAT [16] to evolve the genotype, represented by the Compositional Pattern Producing Network (CPPN) of the creatures, focusing on their morphological development and behavioral generation during developmental events.

We introduced two types of developmental processes. One is lifetime development (LD), where creatures can grow and change their form throughout their lifetime. The other is initial development (ID), where the developmental events occur only at the initial timestep. Niche construction (NC) was implemented by enabling the construction of blocks to be evolvable in the environment. We also introduced ecological inheritance (EI), which allows a certain percentage of niche-constructed blocks to be inherited into the environment in the next generation. We conducted several experiments by explicitly enabling and disabling these components and discussed how they mutually interact through their evolutionary process, resulting in diverse types of morphological and behavioral patterns of artificial creatures.

This paper is structured as follows: Section 1 provides an overview of the background and significance of the study. Section 2 details the evolutionary model employed in our research. Section 3 outlines the experiments conducted and presents the results obtained from the analysis. Finally, Section 4 concludes the paper by summarizing the key findings and discussing their implications for future research.

2. Model

We developed an evolutionary framework for artificial creatures within a 3D multiagent environment based on the Python module-based physics engine PyBullet [17] to discuss eco-evo-devo in the emerging morphology and behavior of artificial creatures.

2.1. Field and Task

Multiple rigid-bodied artificial creatures composed of several blocks are evaluated simultaneously in a large flat space with two valleys within a 3D virtual environment. Figure 1i illustrates a snapshot of the field used for fitness evaluation. The artificial creatures are initially arranged in a straight line with a distance of 30 units between each to minimize interactions for simplicity. There exists a long target block (grey) beyond the valleys. The initial distance from the creatures to Valley 1 is 15 units, to Valley 2 is 38 units, and to the target block is 50 units. The creatures are tasked with locomoting toward the target block by crossing both Valley 1 and Valley 2. A snapshot of the population moving towards the target to complete the tasks is shown in (ii).

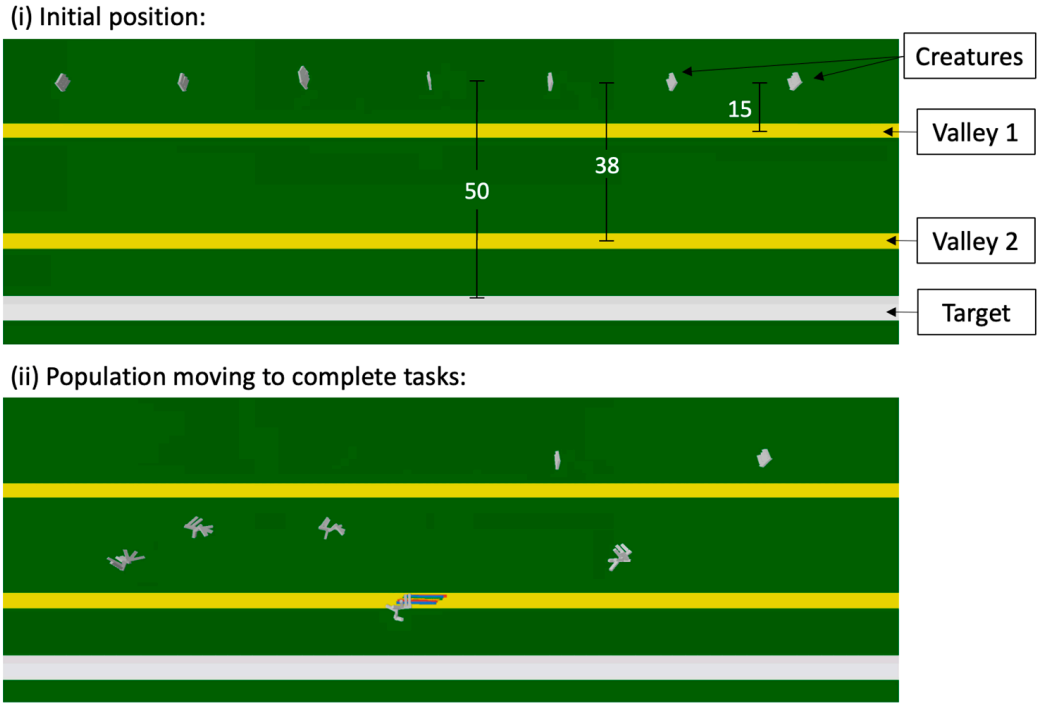


Figure 1. Top view of the field for fitness evaluation showing the environment and task. (**i**) The initial position of the population of creatures and (**ii**) the creatures moving towards the target block. The rainbow-colored blocks represent the NC blocks placed by a creature in the valley.

Fitness is measured by the distance traveled from the starting point to the target and is calculated using the following equation:

$$fitness = \begin{cases} 50 - d_{io} & , \quad d_{io} < 50 \\ 0 & , \quad d_{io} \geq 50 \end{cases}, \tag{1}$$

In this equation, d_{io} represents the final distance between a creature's center node and the nearest point on the target surface, measured at the end of the fitness evaluation. The constant value 50 reflects the initial distance between these points. For each creature, d_{io} is calculated from the center node to the nearest point on the surface of the target block (Figure 2i). Creatures can engage in niche construction by placing blocks in the valley area (ii), which will be explained further in Section 2.4.

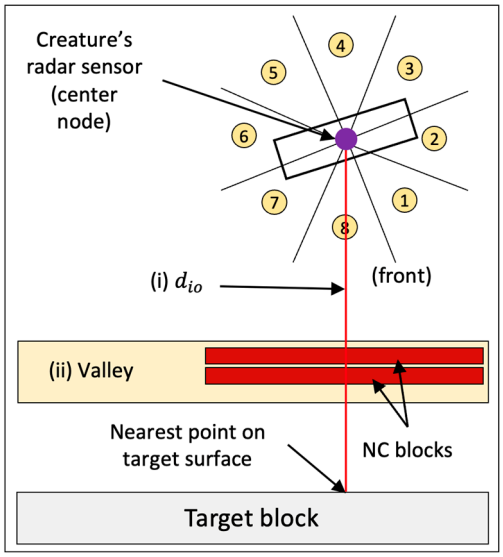


Figure 2. Illustrations of creatures approaching the target block, demonstrating (**i**) d_{io}, between the creature's center node and the nearest point on the target block's surface, the mechanism of the radar sensor (purple node), and (**ii**) the placement of NC blocks in the valley by the creature.

2.2. Development

In this model, each creature is assigned a lifetime represented by timesteps (T). Throughout this lifetime, developmental events can occur at specific timesteps, as illustrated in Figure 3. The timing of these events depends on the experimental settings, such as initial development (ID) or lifetime development (LD), as well as the individual's genotype.

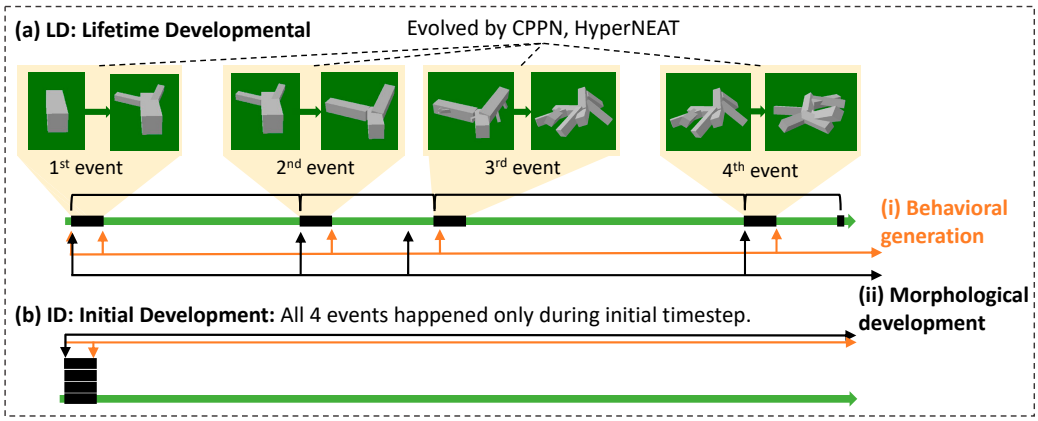


Figure 3. The lifetime of a creature through a repeating process that involves two key steps: (**i**) behavioral generation through connection weight settings and (**ii**) morphological development that takes place via new block additions. In (**a**) LD, a maximum of 4 events can occur at any time according to CPPN output, while in (**b**) ID, the occurrence of 4 events is fixed during initial timesteps only.

The development of an artificial creature involves morphological changes through the growth and addition of new body parts during its lifetime, controlled by neural network outputs. We assume that a single large Compositional Pattern Producing Network (CPPN), which is the creature's genotype, represents two sub-networks, as shown in Figure 4a-iv for determining the morphological development and (b-ii) for the behavior generation process. Each CPPN is a neural network that maps input into output values. These CPPNs utilize various activation functions, including sine, cosine, Gaussian, and sigmoid functions, to create geometric patterns (a-v).

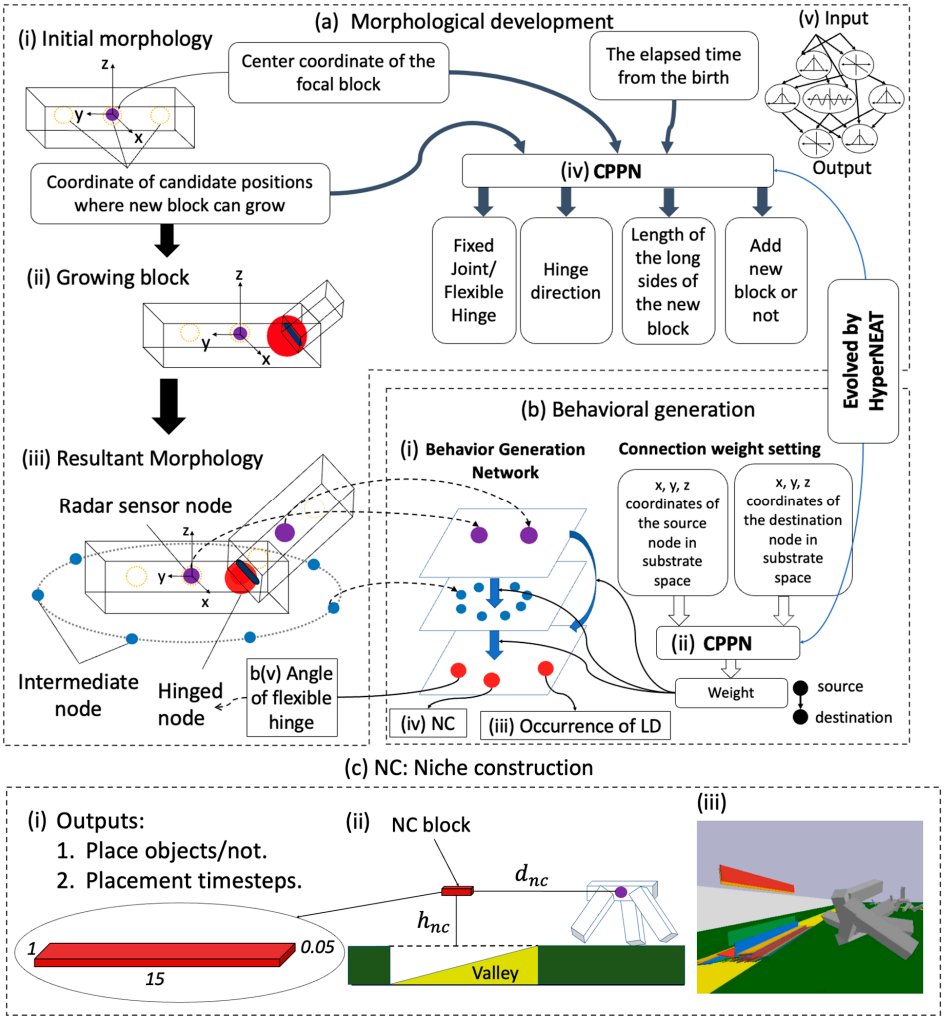


Figure 4. (**a**) The morphological development of a creature, which proceeds from (**i**) the initial morphology, to (**ii**) the growth of a new block, resulting in (**iii**) the resultant morphology showcasing a fully developed new block, all occurring within a single developmental event evolved by (**iv**) the CPPN and (**v**) the example of the CPPN with its activation functions. (**b**) The behavioral generation, where the CPPN is then employed to calculate the connection weights for nodes in the three-layer behavioral generation network in substrate space. (**c**) NC: Niche construction is one of the outputs of the behavioral generation network, where creatures are able to place objects into the environment under certain conditions, demonstrating the niche-constructing behavior.

The initial body of a creature consists of a single block positioned at the origin (a-i). As development proceeds, the creature becomes composed of rectangular blocks interconnected via hinges (a-iii). The creature's morphology can develop up to four times throughout its lifetime (Figure 3). The specific timesteps at which these developments occur are determined by the behavior generation network, as explained in more detail in Section 2.3. Each developmental event involves adding a new block to each candidate position (yellow circle) on the existing body blocks, with each block having three candidate positions.

The genotype, represented by the CPPN (Figure 4a-iv), receives three inputs: (1) the elapsed time since birth, (2) the central coordinate of the focal block in the substrate space, and (3) the coordinate of a potential position on the focal block. This leads to four outputs: (1) a determination of whether a new block should be added, (2) the length of the long sides of the new block, (3) the hinge direction, and (4) a decision between a fixed hinge or a flexible joint. The size of each new block gradually increases from 0 to a specified length until the developmental event concludes. This process consists of a total of 500 steps for

each developmental event. An example shown in (i–iii) illustrates how the process begins with a single block as the initial morphology (i). Subsequently, a new block develops at the right candidate position (ii), creating additional candidate positions for further blocks to grow in subsequent developmental events (iii).

2.2.1. Lifetime Development (LD)

To investigate the effects of lifetime development on the evolution of creatures, we introduced two types of developmental processes: lifetime development (LD) and initial development (ID), as shown in Figure 3. This comparative approach enables us to examine the evolution of niche construction and development in the presence or absence of lifetime development capabilities. In LD, the timing of these events is determined by the behavioral generation network (Figure 4b-i). This ability to modify form during a creature's lifetime facilitates morphological adaptation to environmental conditions and helps overcome obstacles.

2.2.2. Initial Development (ID)

In the case of ID, creatures can develop their morphology only at the beginning four times (Figure 3b). Consequently, creatures maintain a constant morphology that is established at the start of their lifetime and remains unchanged until the end.

2.3. Behavioral Generation

The behavior generation process, illustrated in Figure 4b, controls the movement of creatures through the manipulation of flexible hinges. The genotype CPPN (b-ii) builds this behavioral generation network (b-i), which is updated in response to the creature's morphological changes. The network structure comprises three layers: input, intermediate, and output. The CPPN is a neural network that computes input coordinates into output values, which is the connection weight between each layer of the behavioral generation network (b-ii). This application of the CPPN is based on that in the HyperNEAT [16].

Each block features a centrally positioned radar sensor (a-iii), depicted in purple, along with a corresponding radar node that gathers sensory information from the substrate space (b-i). The mechanism of the radar sensor is illustrated in Figure 2, where the radar sensor is configured with eight segments. Using the distance obtained from the calculation of d_{io} (i), the relative angle between the creature's front direction to d_{io} was calculated to determine which of the eight segments d_{io} falls into. As shown in the example in Figure 2, d_{io} falls into segment eight and the value is then stored in the radar list at the corresponding segment index. This radar data are then used as input for the behavior generation network to compute the angle of the creature's flexible hinges (b-v) for movement generation. Each hinge connecting the blocks is associated with a corresponding hinge node (red), along with several intermediate nodes distributed throughout the creature in the substrate space (a-iii).

We propose that the radar, intermediate, and hinge nodes are situated in the input, intermediate, and output layers of the behavioral generation network, respectively. For example, in the network illustrated in (b-i), there are two radar sensor nodes (input layer), seven intermediate nodes (intermediate layer), and three nodes in the output layer: one hinge node, one NC node, and one LD node. Connections are established among the nodes across the input–intermediate, intermediate–output, and input–output layers. Each connection has its own weight, determined by the genotype CPPN, which receives the coordinates of the source and destination node pairs within the substrate space. Nodes in the output layer provide various outputs, including hinge angles (b-v), the timing of lifetime development (LD) events (i.e., identifying when developmental changes occur) (b-iii), and NC strategies (i.e., decisions on whether to place objects and at which timesteps) (b-iv). Consequently, the behavioral generation network can produce (1) diverse behavioral

patterns in the creature, (2) evolve NC behavior, and (3) evolve lifetime developmental events according to the sensory input received from the radars.

2.4. Niche Construction (NC)

Niche construction (NC) allows creatures to modify their own selection pressures by altering the environment during their lifetime. We implement NC by allowing each creature to alter its environment through the placement of objects in the valley. Figure 4c–ii illustrates that NC blocks can be placed at a distance of 5 units from the center node of the creature toward the nearest point on the target's surface (Figure 2). The NC blocks will be placed from a height of 2, allowing blocks to be constructed on top of each other during niche construction. To maintain simplicity, we implemented a single type of NC block with a length of 15, a height of 0.05, and a width of 1. Due to the elongated shape of the NC block, when blocks are placed in the valley area, their orientation is fixed to align parallel to the valley, as shown in Figure 2ii. We experimented with several block shapes, including cubes; however, the resulting structures became overly complex for the artificial creatures to navigate effectively. Consequently, we opted for the current type of blocks, allowing for more consistent stacking and easier traversal of the valleys. This ensures that the constructed NC structures remain within the valley, preventing the formation of obstacles.

The (1) decision to place objects and (2) the placement timesteps are determined by the behavioral generation network (Figure 4c-i). Object placements can occur every 20 timesteps, determined by the output of the NC node in the behavior generation network. Additionally, the construction of NC structures is restricted to the valley areas to prevent them from becoming potential obstacles when placed elsewhere. This restriction is necessary because the emergence of NC behavior during the initial evolutionary stage is still robust, and such obstacles can greatly affect the evolution of niche construction and development later in the process.

2.5. Evolution

We adopted the excessive elitism method, by modifying elitism in NEAT without speciation and fitness sharing. This method, as described in [18], preserves many of the best-performing individuals as elite across generations, ensuring diversity while reducing evaluation costs in this complex evolutionary process.

In a single population of N individuals without speciation, the M best-fit individuals are preserved from one generation to the next. These elite genotypes maintain their fitness values in the next generation, eliminating the need for re-evaluation. Therefore, in each generation, $N—M$ new individuals need fitness evaluation (or all N individuals in the initial generation), which is conducted simultaneously in a field environment. For the next generation, elitism is first applied by preserving the M best individuals and their fitness values from the current population. Then, to generate the remaining $N—M$ individuals, parents are selected from the entire current population using roulette wheel selection based on fitness values. Each selected parent's genotype is copied and undergoes mutation to create an offspring's genotype. This parent selection and genetic operation process is repeated $N—M$ times. We adopted a mutation process to the genotype (i.e., the CPPN), such as adding or removing nodes and connections, modifying weights, and changing activation functions within the CPPN composition structure, as used in the HyperNEAT algorithm [16]. This approach enhances diversity and improves population fitness while reducing computational costs by replacing only a few individuals with offspring in each generation. We conduct the whole process of evolution through G generations and R trials.

The pseudocode, as shown in Figure 5, outlines the implementation of the coevolution of development, niche construction, and ecological inheritance using the specified experimental parameters for the experiment.

```
(Initialization)
Initialize basic configuration settings for NEAT
Initialize the basic parameters for the model: N, G, T, R and P
Initialize the list of genomes, the list of the fitness values, and the list of NC blocks
For each generation:
    (Initialization for fitness evaluation)
    Connect to PyBullet
    Load environmental field objects (URDF files)
    Set gravity and simulation parameters
    Load inherited positions of NC blocks from the previous generation (if they exist)
    For each of the N-M genomes whose fitness are not evaluated:
        Create an individual and initialize its base block in the field
        Set up a neural network for the genome
    (Fitness evaluation)
    For each time step:
        For each individual in the field:
            (Handle developmental events based on ID or LD cases)
            If the developmental process = ID:
                If the step = 0:
                    Repeat four times:
                        (developmental process)
                        Repeat for 20 developmental steps:
                            Activate neural network to determine target positions for growth of new body parts
                            Generate new parts based on CPPN output: Length, flexible joints/ fixed hinge
                            Update the neural network according to the current individual structure
            else (LD):
                If the developmental event is activated according to the neural network output:
                    Conduct the process defined in (developmental process) above
        For each individual in the field:
            (Movement)
            CPPN outputs the desired angle of motion for flexible joints
            Movements of joints were activated based on the angles provided by CPPN outputs
        For each individual in the field:
            (Niche construction)
            If the position of the focal individual is near the valley area:
                The individual places NC blocks based on CPPN output
    Assign the fitness value (distance to the goal) to each individual
    (Selection and reproduction based on the excessive elitism)
    Select the best M individuals and directly copy both their genotypes and fitness values to the next generation
    Repeat N-M times:
        Select two parent individuals randomly using the roulette wheel selection method from all evaluated N individuals
        Reproduce an offspring genotype from these two using crossover and mutation, and put it into the next generation
    (Ecological Inheritance)
    Randomly select which NC blocks will be carried over to the next generation, preserving its position and direction, based on the percentage of inheritance (P), and update the list of NC blocks
```

Figure 5. Pseudocode for the evolutionary algorithm utilized in the experiment, which co-evolves development, niche construction, and ecological inheritance based on the specified experimental parameters.

3. Experiments and Results

We carried out evolutionary experiments by utilizing the HyperNEAT algorithm through the PUREPLES Python library. To enhance computational efficiency and tailor the implementation to our specific evolutionary framework, we modified several key parameters from the default configuration. We modified the related settings regarding fitness evaluation, speciation, and fitness-sharing processes to implement the excessive elitism method. For more details, see reference [18]. We conducted evolutionary experiments using the following parameters: G = 1500; R = 10; T = 20,000; P = 20, 40, 60, 80, and 100; N = 95; M = 83; and $N - M$ = 12.

Before the main experiments, we evolved a population on a flat surface without valleys to evolve basic locomotion toward a target. We found that creatures with small body sizes (2.5–5 blocks) exhibited effective mobility on flat surfaces. This evolved population served as the initial population for all experimental cases described in Table 1. This ensured that the population could already move towards the target without valleys. We focused on how development and niche construction evolve to adapt to the presence of valleys in the environment, which act as obstacles to reaching the target, as exhibited in Figure 1.

Table 1. List of experimental cases and the presence of development, niche construction, and ecological inheritance in the co-evolution. ✓ represents the existence of the corresponding process.

Case	Development (ID/LD)	Niche Construction (NC)	Ecological Inheritance (EI)
Initial development (ID)	ID	✕	✕
Lifetime development (LD)	LD	✕	✕
Initial development + Niche construction (ID + NC)	ID	✓	✕
Lifetime development + Niche construction (LD + NC)	LD	✓	✕
Lifetime development + Niche construction + Ecological inheritance (LD + NC + EI)	LD	✓	✓

In this study, we investigated the evolutionary dynamics of developmental processes and niche construction and their mutual relationships, by focusing on several cases involving these components. We conducted five distinct cases, as shown in Table 1. First, we examined the case (ID) where we only assumed initial development (ID). Next, we analyzed the case (LD) where lifetime development was assumed. Following this, we explored the case (ID + NC) where niche construction was enabled and evolved alongside initial development. Then, we evolved niche construction with lifetime development in another case (LD + NC). Finally, we evolved NC and LD with EI in another case (LD + NC + EI).

3.1. Evolutionary Dynamics of Development and Niche Construction Under Different Conditions

Figure 6 shows the evolution of fitness across 10 trials for case ID (i), LD (ii), ID + NC (iii), and case LD + NC (iv). We captured the phenotypes of the best-evolved creatures from the best trial (Figure 7i,ii). Additionally, we tracked the evolution of morphology by plotting the average number of body blocks across generations (iii), which were calculated at the end of each generation. For cases involving niche construction, such as case (ID + NC) and (LD + NC), we investigated the evolution of niche construction by analyzing the average number of blocks placed in Valley 1 and Valley 2 throughout the generations (iv).

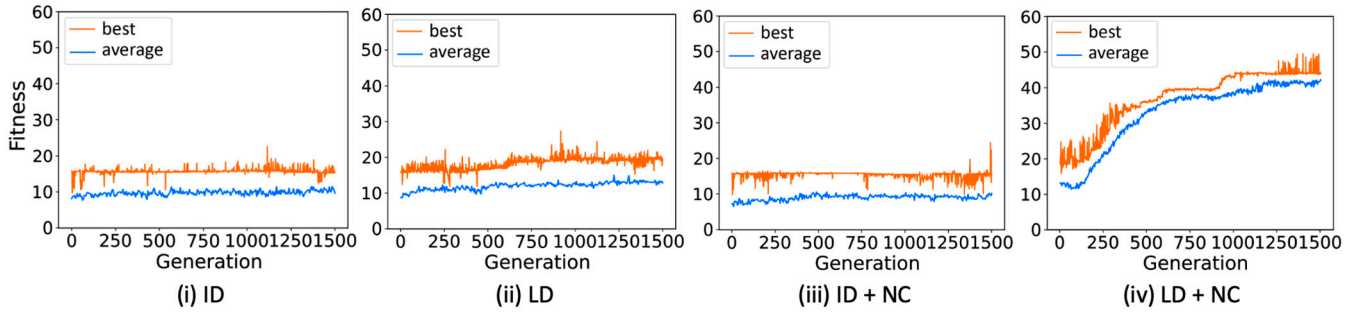


Figure 6. The evolution of fitness over 10 trials is shown, with orange representing the best fitness in each trial and blue indicating the average fitness for cases (**i**) ID, (**ii**) LD, (**iii**) ID + NC, and (**iv**) LD + NC.

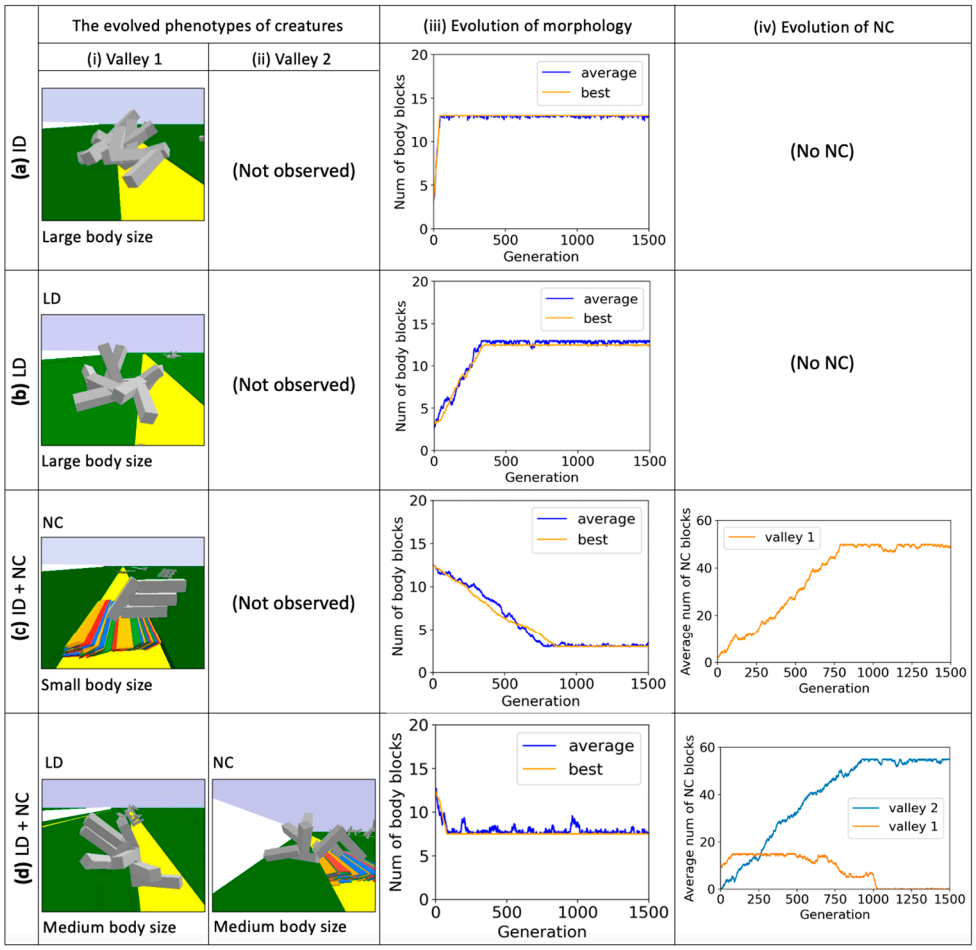


Figure 7. This diagram summarizes the evolution of development and niche construction for each case, where it shows snapshots of the evolved phenotype of the best creatures for cases (**a**) ID, (**b**) ID, (**c**) ID + NC, and (**d**) LD + NC at (**i**) Valley 1 and (**ii**) Valley 2. (**iii**) The evolution of morphology is shown by plotting the average (blue) and best (orange) number of body blocks throughout 1500 generations. (**iv**) The evolution of NC is plotted for Valley 1 (orange) and Valley 2 (blue) throughout 1500 generations. Supplementary Videos showing the behavior of the best creatures in each case, as shown in (**i**), can be found at: https://figshare.com/s/200a85f3552830815e97 (accessed on 26 December 2024).

The data demonstrate a significant increase in fitness when LD and NC evolved together, reaching maximum values in most trials, indicating successful locomotion across both valleys to reach the target. Conversely, fitness remained consistently low in cases ID and ID + NC, indicating a failure to cross Valley 1. However, the fitness for case LD, was

slightly higher than that of case ID, indicating the ability to cross Valley 1 but an inability to move further. In the following sections, we will conduct a comprehensive comparison of these cases.

3.1.1. Evolutionary Dynamics Under the Initial Development (ID) Condition

We first investigated the evolution of creatures with only initial development (ID). The best fitness, in this case, showed a stagnation at around 15, indicating that creatures only traveled from the initial position toward Valley 1. This fitness is similar to that of the initial population (Figure 6i), indicating almost no fitness improvement. This stagnation is due to creatures rapidly developing a large body size (about 12.5 blocks) early on, which limited their ability to move on a flat surface toward Valley 1 (Figure 7a).

The tendency for the number of blocks to rapidly increase by repeating developmental events at the beginning merely created a large and complex structure with many blocks, which was a suboptimal solution. This dominated the population and prevented it from evolving more adaptive and sophisticated behaviors. When creatures adopted a large body size made of many blocks, it often became too complicated for them to move, even on a flat surface. This can cause some agents to struggle with effective locomotion, as shown in the snapshots (i,ii). We expect that when creatures are unable to change their phenotype during their lifetime, it influences their morphology and behavior to be non-adaptive to the environment.

3.1.2. Evolutionary Dynamics Under the Lifetime Development (LD) Condition

We then focused on the case of lifetime development (LD), where creatures could modify their morphology during their lifetime. The best fitness reached around 20, higher than the 15 observed in the ID case (Figure 6ii). Although the final body size of the evolved creatures was similar to the ID case (around 12.5), the number of blocks increased gradually alongside the increase in fitness (Figure 7b-iii).

This gradual increase suggests the emergence of a longer-term adaptation process through the experiments, demonstrating the difference from case ID in their adaptation strategy. We observed that creatures traveled to Valley 1 and evolved to develop a large body size of about 12.5 blocks (around the 400th generation). The creatures evolved to develop larger body sizes, enabling them to utilize multiple body parts for climbing out of Valley 1 rather than becoming trapped. However, these larger morphologies resulted in complex phenotypes that impaired locomotion on flat surfaces after crossing Valley 1 (b-ii), consequently hindering progress toward Valley 2. This resulted in a fitness plateau at around 20 (Figure 6ii). Therefore, the evolved lifetime development allowed creatures to use a larger body size at the valley position while maintaining a smaller body size to move on the flat surface beforehand.

3.1.3. Evolutionary Dynamics Under the Initial Development (ID) and Niche Construction (NC) Condition

We next investigated the coevolution of niche-constructing behavior (NC) with initial development (ID) to examine whether NC could enable creatures to reach Valley 2, which was previously unattainable. As shown in Figure 6iii, the best fitness stagnated at around 15. This is because many creatures were stuck in Valley 1 (Figure 7c-ii). The evolution of morphology (c-iii) revealed that the best-performing creatures evolved small body sizes (2.5–5 blocks) during initial development, facilitating efficient movement on flat surfaces. Unlike in the ID case, these creatures maintained their compact morphology for better movement rather than developing larger bodies at the initial stage. When reaching Valley 1, they used NC and constructed structures to cross the valley. However, the small body size made it difficult to move across the uneven structures in the valley. In Valley 1,

the number of placed NC blocks gradually increased from around 1–2 to 50 blocks by the 800th generation (c-iv). As shown in (c-ii), this quantity sufficiently filled Valley 1 without overflow, demonstrating that NC evolved to adapt to the depth of the valley. This influenced the evolution of development by making the body size smaller for ease of motion on flat surfaces, but this size, while suitable for such environments, made it challenging to navigate through the blocks placed in the valley.

3.1.4. Evolutionary Dynamics Under the Lifetime Development (LD) and Niche Construction (NC) Condition

We then focused on the coevolution of lifetime development (LD) and niche construction (NC) to examine their combined effects on the adaptability of creatures in this environment. The best fitness, in this case, reached the maximum value of 50 in most trials (Figure 6iv), demonstrating successful locomotion across both valleys. The creatures initially evolved to maintain small body sizes while moving toward Valley 1 (Figure 7d). To cross Valley 1, the creatures utilized developmental events to achieve medium-sized bodies (7.5–10 blocks) (d-iii). The developmental event enabled valley crossing through a specific mechanism: the force generated by growing new body parts against the ground created a leaping motion (d-i). After crossing, they successfully moved across the flat surface and headed towards Valley 2. In Valley 2, they used NC to fill the valley with objects, facilitating the crossing (d-iii). The creatures then successfully moved on the flat surfaces heading toward the target by utilizing their medium body size.

The analysis of the NC block placement revealed that niche-constructing behavior initially occurred in Valley 1, with creatures placing around 15–20 blocks per generation (d-v). This construction pattern appeared to promote the evolution of smaller body sizes, enhancing mobility toward the valley in subsequent generations. However, this behavior only appeared at the initial evolutionary stage and disappeared around the 1000th generation. The frequency of niche-constructing behavior then gradually increased at Valley 2, with creatures consistently placing around 50–60 blocks by the 1000th generation. This indicates a complex mutual interaction between niche construction and development throughout their coevolution. In conclusion, evolution with niche construction significantly influences the adaptability of the morphology and behavior of creatures to achieve higher fitness successfully.

3.2. Evolution of Lifetime Development (LD) and Niche Construction (NC) with Ecological Inheritance (EI)

We incorporated ecological inheritance (EI) into experiments, whereby objects placed through niche construction activities were carried over to the environment in the next generation. In each case of *P*, we coevolved both lifetime development (LD) and niche construction (NC). The results for the average best fitness from 10 trials are shown in Figure 8i. To observe the evolution of lifetime development, we analyzed the evolved phenotypes of the best creatures in Valley 1 and Valley 2 (ii,iii). Additionally, we analyzed the evolution of niche construction by plotting the average of NC blocks placed by the current creatures for both valleys, as depicted in Figure 9.

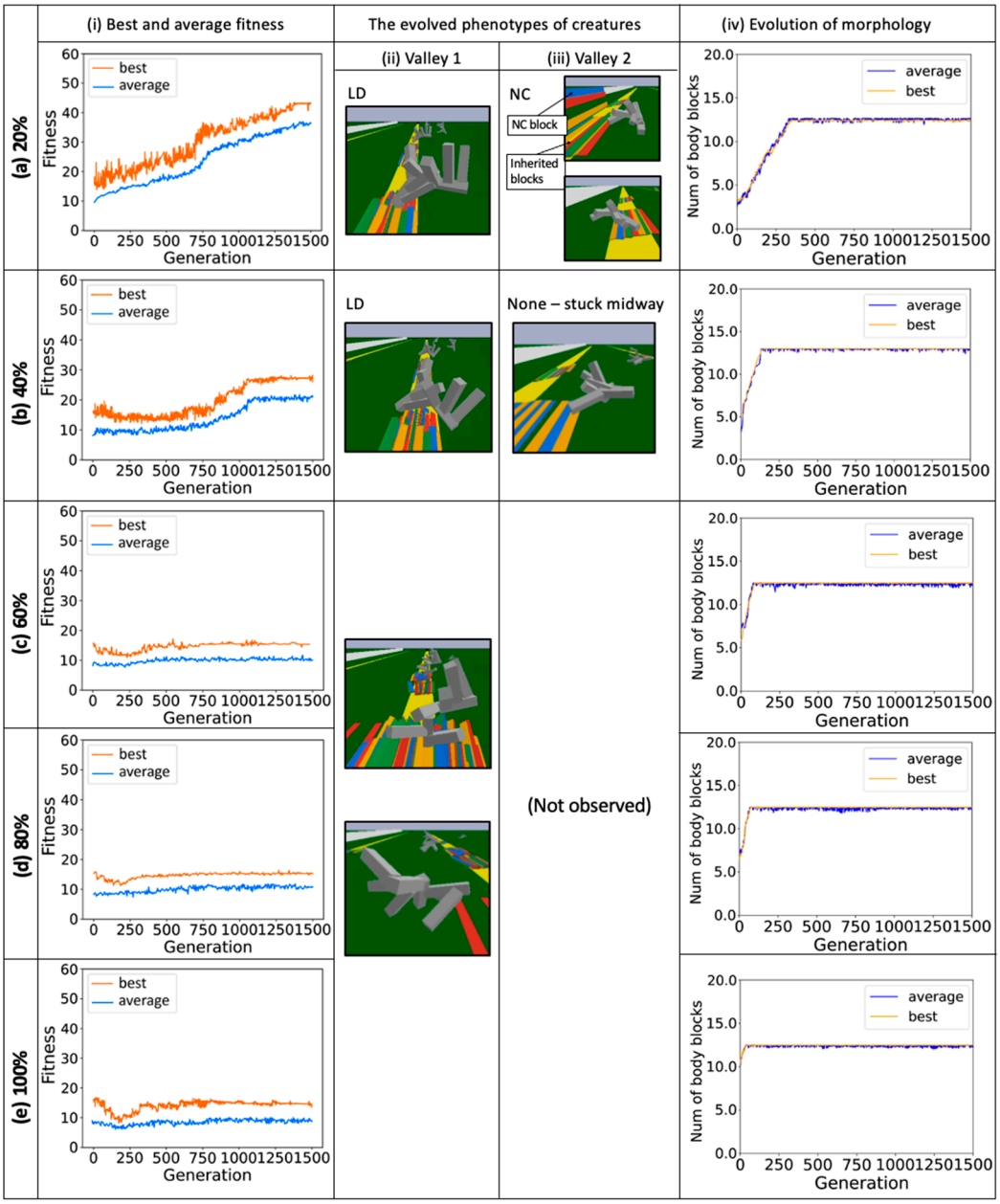


Figure 8. This diagram illustrates (**i**) best and average fitness, (**ii**) the evolved phenotype of creatures in valley 1 and (**iii**) valley 2, followed by (**iv**) the evolution of morphology for each case.

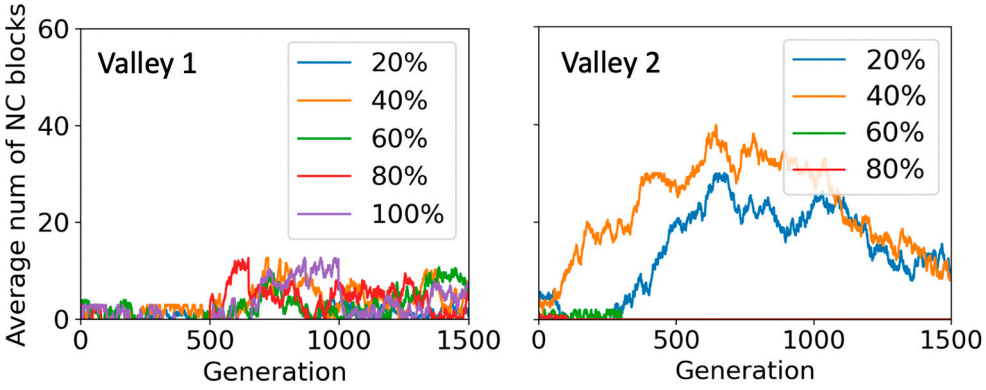


Figure 9. The evolution of niche construction for each case of EI where it shows the average number of blocks placed by NC in both Valley 1 (**left**) and Valley 2 (**right**).

We first examined the case with the lowest percentage of EI ($P = 20$). This configuration yielded the highest fitness among all cases of EI (Figure 8a-i), with creatures achieving around 45 in most trials. These results demonstrate that creatures successfully crossed Valley 1 but frequently became stuck in Valley 2 (a-iii), contrasting with the LD + NC case without EI. The evolved creatures initially maintained small body sizes for efficient movement across flat surfaces toward Valley 1 (a-ii). Subsequently, they utilized LD to leap across Valley 1, developing larger morphologies (around 12.5 blocks) (a-iv).

The niche-constructing behavior adapted to ecologically inherited structures in Valley 2. Around the 500th generation, creatures began to evolve strategic block placement in Valley 2 (a-iii), reaching an average placement of about 25 blocks per generation by around the 700th generation. Then, towards the end of the experiments, the creatures adapted to placing fewer blocks in Valley 2 (Figure 9 (right) (blue)). This behavioral adaptation appears to be an evolutionary response to the accumulation of inherited structures. The reduction in block placement represented an adaptive strategy that prevented excessive structure accumulation in Valley 2, which could otherwise form obstacles. However, due to their large body size, it was difficult for them to move forward after crossing (iii). From this, we can observe that the presence of EI affected the evolution of niche construction and development in this case.

In the case of $P = 40$, we observed evolutionary patterns similar to those in the $P = 20$ case. However, the fitness converged to around 25–30 (Figure 8b). The creatures in this configuration were unable to cross Valley 2, with locomotion typically getting stuck midway through the valley (b-iii). While creatures successfully approached Valley 2 and engaged in block placement (Figure 9 (right—orange curve)), their forward progression was impeded. This limitation appears to result from excessive block accumulation in Valley 2, caused by the high inheritance rate, which constrained the adaptive adjustment of block placement patterns. This also negatively affected the evolution of locomotion behavior toward Valley 2 when they adapted large body sizes (around 12.5 blocks) (b-iv).

For evolution with $P = 60$, 80, and 100, the best fitness values remained stagnant at around 15 from the beginning until the final generation (Figure 8a). The analysis revealed that the majority of creatures became stuck in Valley 1. The creatures evolved to obtain large body sizes (around 12.5 blocks), which made it difficult to move on flat surfaces (c-i). The evolution of a large body size was facilitated by the formation of obstacles in Valley 1 due to the niche construction and the high percentage of EI during initial generations (b). However, the blocks in Valley 1 had accumulated excessively due to the large percentage of inheritance.

Theoretically, in cases with high ecological inheritance, the rapid accumulation of NC structures occurs in Valley 1. This environmental modification selects for creatures with larger and more complex developmental mechanisms capable of traversing these accumulated structures. However, such increased phenotypic complexity that emerged under these selective pressures subsequently constrains the evolution of locomotion patterns, preventing creatures from reaching Valley 2. Consequently, this process results in the evolution of less adaptive morphology and behavior.

In conclusion, in these experiments, the ecological inheritance had more or less negative effects on the adaptive evolution of artificial creatures in terms of fitness. However, it should be noted that the evolution with lower percentages, $P = 20$ and 40, had achieved higher fitness than those with higher EI percentages (Figure 8i). In the former cases, the niche-constructing behavior could evolve to balance the number of placed blocks and inherited blocks, which maintained the adaptive structures in Valley 2. In the latter cases, creatures tended to be less adaptive and evolved into larger and more complex morphologies. This is due to less adaptive NC behavior, where creatures continue to place blocks

despite the presence of inherited blocks, leading to the accumulation of blocks as obstacles. This can also be reflected as negative NC behavior, which emerges when the evolution of niche construction cannot adapt quickly to the environment, leading to increased environmental challenges and resulting in the evolution of less adaptive morphology and behavior in creatures. This highlights the importance of maintaining a balance between ecological inheritance and adaptability, as excessive reliance on inherited traits can hinder the evolution of effective responses to new environmental pressures.

The vanished blocks during the ecological inheritance process symbolize a form of decay. Consequently, a decreasing EI parameter value corresponds to scenarios involving a more frequent decay of blocks. Alternatively, other implementations of decay processes could be explored, such as breaking blocks into multiple smaller pieces or reducing their size. The effects of these different types of decay processes could significantly impact the evolutionary dynamics, presenting an opportunity for future research.

4. Conclusions

We proposed a coevolutionary model integrating niche construction and morphological development to investigate the evolution of adaptive morphology and behavior in artificial creatures within a 3D multi-agent environment. We developed an evolutionary framework in which a population of creatures must cross two valleys to reach a goal, utilizing developmental events and the construction of objects. We introduced ecological inheritance to examine the effects of the inheritance of constructed objects in the environment.

The analysis of the LN + NC case revealed complementary roles between niche construction and morphological development in successfully evolved creatures. Specifically, LD evolved to facilitate crossing Valley 1, while niche construction evolved to facilitate crossing Valley 2. We also observed mutual interactions among them through evolution, such that niche-constructing structures facilitated the development of intermediate body sizes for creatures during the earlier evolutionary stages but disappeared later.

To systematically organize our findings, we present a structured summary of the key experimental observations and their broader implications in Table 2. As shown in the table, our findings can be categorized into two major aspects: (1) the relationship between lifetime development and niche construction, and (2) the effects of ecological inheritance on evolutionary dynamics. For each finding, we identified broader implications for understanding the evolution of complex adaptive systems.

Table 2. Summary of key observations from this study and their broader implications with analogous cases in nature.

Key Findings	Broader Implications	Analogous Cases in Nature
Relationship between Lifetime Development (LD) and Niche Construction (NC)		
Adaptive evolution where LD enabled crossing Valley 1 through morphological changes, while NC facilitated crossing Valley 2 through constructed structures.	The importance of complementary roles and sequential adaptation between development and niche construction in the evolution of complex traits.	Beavers: physical development within the lodge under parental care before acquiring dam-building capabilities [19]. Plants: rapid growth to compete for sunlight, subsequently altering soil composition [20].
The presence of blocks in Valley 1 facilitated the evolution of intermediate body sizes during early developmental stages.	The importance of niche-constructed environments in early developmental evolution.	
Effects of Ecological Inheritance (EI) on Evolutionary Dynamics		
With lower EI, creatures evolutionarily adapted by successfully adjusting their body size and the number of block placements.	When the accumulation of environmental modifications through niche construction is small enough, adaptive evolution is possible.	Evolution of termite mound-building behavior [21]. The resilience of coral reefs to human impacts [22].
With higher EI, bodies evolved to become more complex due to excessive blocks in Valley 1, preventing crossing of Valley 2.	Excessive environmental modifications through niche construction can hinder adaptive evolution.	Mass extinction of corals caused by thermal stress due to climate change [23]. Environmental pollution by human cultural activities.

The sequential adaptation pattern—morphological development preceding niche construction during an organism's lifetime—appears to share commonalities with developmental and behavioral patterns in biological systems. For example, this pattern may be similar to behavioral development in beavers (*Castor fiber* L.), where individuals initially undergo physical development within the lodge under parental care before acquiring dam-building capabilities that enable environmental modification [19]. These habitat-modifying activities can alter aquatic environments through the creation of ponds, which serve as ecological niches for various species and contribute to water flow regulation. This is also evident in examples such as plants that grow rapidly to compete for sunlight, subsequently altering soil composition [20]. These instances illustrate that growth is often a prerequisite for niche construction in real ecology.

Both niche-constructing behavior and morphological development showed distinct evolutionary patterns under different degrees of ecological inheritance. In cases with lower EI percentages (P = 20 and 40), niche-constructing behavior evolved to reduce the frequency of block placement, representing an adaptive response to accumulated environmental modifications. This suggests that if the degree of changes in the environment is small enough, positive niche-constructing behavior can evolve by maintaining a balance between the current and previous effects of niche construction in the environment. This adaptive pattern aligns with our observation in Table 2 that when the accumulation of environmental modifications through niche construction is small enough, adaptive evolution is possible. The evolution of termite mound-building behavior represents a natural example of such adaptive responses, where colonies successfully adjust their construction behavior in response to existing structures. Similarly, the resilience of coral reefs to human impacts [22] demonstrates how ecosystems can adaptively respond when environmental modifications occur at a manageable rate.

With larger percentages of EI (P = 60, 80 and 100), we observed substantially different patterns. The accumulation of NC structures and inherited blocks led to the evolution of larger morphologies, resulting in increased phenotypic complexity that impaired locomotion efficiency. It also hindered adaptive adjustments for constructing NC structures, which accumulated to form obstacles. This behavior emerged when the environment changed too quickly due to the high percentage of the ecological inheritance of blocks, increasing the environmental challenges. These results indicate that rapid environmental changes induced by high inheritance rates promoted the evolution of maladaptive developmental patterns. As noted in Table 2, excessive environmental modifications through niche construction can hinder adaptive evolution. This is analogous to natural cases where rapid environmental changes overwhelm species' adaptive capabilities, as seen in the mass extinction of corals caused by thermal stress due to climate change [23] and environmental pollution caused by human cultural activities.

These findings indicate that varying degrees of ecological inheritance have distinct effects on the evolution of niche construction and development. This highlights the intricate interplay between niche construction and development as influenced by ecological inheritance. As summarized in Table 2, our experimental results demonstrate how the degree of ecological inheritance can either facilitate or hinder adaptive evolution, depending on the rate of environmental change. This perspective aligns with the Triadic Niche Construction Hypothesis (TNCH) [24], which proposes that human evolution accelerated through interactions between ecological modifications (through tool use), cognitive developments (new capabilities), and neural changes (brain expansion)—each domain constructing its own niche and influencing the others. While our study focuses on physical domains of morphological development and environmental structures rather than cognitive domains, including brain development and informational environments, our experimental results

with artificial creatures demonstrate the possible scenario of interactions among these processes: when ecological inheritance was maintained at appropriate levels (low EI cases), creatures successfully adapted their niche-constructing behavior to the inherited environmental modifications, demonstrating the positive feedback loop between environmental modification and adaptive development proposed by TNCH. However, our observation that excessive ecological inheritance (high EI cases) can impair adaptive evolution also extends the TNCH framework by highlighting the importance of balanced interactions between ecological inheritance and developmental plasticity. This experimental model thus offers a valuable framework for understanding how the dynamic interplay between niche construction, development, and ecological inheritance shapes evolutionary trajectories.

Future work will investigate the evolution of development and niche construction in cooperative tasks that promote increased interactions among creatures within the population. Enhanced interaction may foster either cooperative behaviors, such as the shared utilization of NC structures for valley crossing, or competitive strategies, including blocking through NC structure placement. These social dynamics could lead to the emergence of more diverse morphology and behavior in creatures. Furthermore, future studies will incorporate increasing environmental complexity by including resource limitations for niche construction, allowing for the exploration of how development and niche construction adapt to resource availability.

Supplementary Materials: The following supporting information can be downloaded at: Source code: https://doi.org/10.6084/m9.figshare.27100309 (accessed on 26 December 2024); Supplementary Videos: Morphological changes and patterns of locomotion of best individual in each case—https://figshare.com/s/200a85f3552830815e97 (accessed on 26 December 2024).

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