Three Kinds of Niche Construction

Bendik Hellem Aaby and Grant Ramsey

Niche construction theory concerns how organisms can change selection pressures by altering the feature–factor relationship between themselves and their environment. These alterations are standardly understood to be brought about through two kinds of organism–environment interaction: perturbative and relocational niche construction. We argue that a reconceptualization is needed on the grounds that if a niche is understood as the feature–factor relationship, then there are three fundamental ways in which organisms can engage in niche construction: constitutive, relational, and external niche construction. We further motivate our reconceptualization by showing some examples of organismic activities that fall outside of the current categorization of niche construction, but nonetheless should be included. We end by discussing two objections to niche construction and show how our reconceptualization helps to undercut these objections.

ORCIDs: Aaby, https://orcid.org/0000-0003-2911-1305; Ramsey, https://orcid.org/0000-0002-8712-5521.

1. Introduction

The traditional view of evolution by natural selection is that the environment poses problems for organisms, that these problems act as selection pressures, and that these pressures lead to adaptive evolutionary responses. This view thus regards the environment as an external initiator and prime cause of adaptive evolution (Williams [1966]; Barton and Partridge [2000]). But this view is increasingly being called into question. One important argument takes organisms to be not merely, or not always, passive recipients of environmental challenges (Piaget [1978]; Lewontin [1983]; Levins and Lewontin [1985]; Laland *et al*. [2000]). Instead, organisms can take an active role in their evolutionary fate (Odling-Smee *et al*. [2003]; West-Eberhard [2003]; Odling-Smee [2010]). One way of doing so is by moving around or actively changing themselves or their environment, thereby changing the selection pressures acting on them. This active modification of selection pressures by organisms has been labelled 'niche construction' (Odling-Smee [1988]).

The niche construction perspective thus grew out a dissatisfaction with how evolutionary biology standardly explained adaptation (Lewontin [1983], [1991], [2000];

The British Journal for the Philosophy of Science, volume 73, number 2, June 2022.
© The Authors. Published by The University of Chicago Press for The British Society for the Philosophy of Science. https://doi.org/10.1093/bjps/axz054

Levins and Lewontin [1985]; Godfrey-Smith [1996]; Odling-Smee [1988]; Odling-Smee *et al*. [2003]). This dissatisfaction led to critiques centred on the asymmetrically externalist character of the standard view, which takes organismic adaptations to be explained by environmental properties, while the environmental properties are explained by other sets of properties internal to the environmental system (Godfrey-Smith [1996]; Odling-Smee *et al*. [2003]). Williams ([1992], p. 484) characterized this view as follows:

> Adaptation is always asymmetrical; organisms adapt to their environments, never vice versa. If the environments at the surface of the Earth seem well suited to living organisms, it is simply because those are the environments to which the organisms have adapted.

Lewontin ([1983]), Levins and Lewontin ([1985]) and Odling-Smee ([1988]) argued early on that in many cases, organisms construct their own niches, and their adaptive fit cannot be explained solely with reference to an environment selecting for the organisms that happen to best deal with the environmental problems at hand. Indeed, Lewontin ([2000]) argued that the metaphor of adaptation should be replaced because it carries externalist implications. As the word 'adaptation' stems from the Latin word 'adaptare'—which means 'to make fit'—the implication, according to Lewontin, is that the organism is made to fit into a pre-existing ecological niche (Levins and Lewontin [1985]). Lewontin ([1991]) offered an alternative to externalist adaptationism, which he called constructionism. Lewontin ([2000], pp. 48–9) argued that not only do organism influence the dynamics of the environment, but the environment itself has to be defined relative to an organism: 'The environment of an organism is the penumbra of external conditions that are relevant to it because it has effective interactions with those aspects of the outer world'.

For Lewontin, the possible interactions an organism can have with its physical surroundings is what constitutes its environment. Consequently, the match between organism and environment is explained in terms of organism–environment interactions over time. On this view, organismic activity and reciprocal causation are explanatorily relevant for the explanation of adaptation. Godfrey-Smith ([1996]) calls these constructivist explanations of adaptation.

Inspired by Lewontin,[1] Odling-Smee ([1988]) coined the term 'niche construction'. This term is supposed to pick out the process by which some organisms achieve an adaptive fit through their active modification of the conditions of the environment to better suit their lifestyle or morphology, and of the feedback that this modification generates. Niche construction is thus a causal process capable of generating an organism–environment fit and serves as an alternative explanatory structure, especially in cases where externalist explanations are inadequate or inappropriate.

[1] Schrödinger ([1944]) and Waddington ([1969]) are also important precursors to a more interactionist/constructionist approach to biology.

The concept of niche construction has generated some degree of controversy in evolutionary biology (Laland and Sterelny [2006]; Scott-Phillips *et al.* [2014]). While no one denies that organisms are active and have certain effects on their physical surroundings, many are sceptical about the extent to which such effects can generate persistent and sufficiently strong feedback over generations to have an explanatorily relevant causal influence on evolutionary dynamics (Dawkins [2004]). The divergent views on niche construction fall roughly into two interpretations:

> The Supplementary Interpretation: Niche construction refers to a set of mechanisms (niche construction activities, reciprocal causation, and inclusive inheritance) that explain some cases of adaptation,[2] which are not included in the standard practice of selection-based explanations of adaptations (Godfrey-Smith [1996], p. 131; Odling-Smee *et al.* [2003], p. 371).

> The Revisionary Interpretation: Niche construction refers to an evolutionary process that runs parallel to natural selection, and significantly alters the causal structure of evolution by directing or counteracting the action of natural selection (Laland [2015]; Laland *et al.* [2017]).

In this article, we offer a framework for understanding and distinguishing distinct forms of niche construction. As we will show, this framework best aligns with the supplementary interpretation. Following Schulz ([2014]) and Scott-Phillips *et al.* ([2014]), we hold that there is nothing intrinsic to evolutionary theory that implies that natural selection acts only from the environment to the organism (in other words, natural selection is not exclusively an externalist process). If an organism solves—or dissolves—an adaptive problem by actively modifying the properties of itself or of the environment, or by modifying the way it interacts with the environment, natural selection will select for the traits involved in this modification (so long as there are not countervailing negative consequences). In fact, the two most important and controversial points that niche construction brings to the forefront of evolutionary theory—the active role of the organism in its evolution and how reciprocal causation affects evolutionary trajectories and alters our explanations of adaptations—are perfectly compatible with the principles of natural selection. What the niche construction perspective is not compatible with is an asymmetrical externalist reification of the principles of natural selection.

The primary aim of this article is to argue that the way niche construction is conceptualized in the canonical version of niche construction theory (Laland *et al.* [2000]; Odling-Smee *et al.* [2003]) faces two problems:

(1) It excludes many ways in which organisms can actively modify their relationship with their environment. Importantly, the ways in which organisms can alter their own constitution (and consequently change the selection pressures acting on them) are not included.

[2] We agree with Schulz ([2014]) that the relative frequency of niche construction explanations of adaptations is the most controversial aspect of debates over the role of niche construction in evolutionary theory.

(2) The standard niche construction categories are inconsistent with the standard understanding of a niche. That is, if a niche consists of the feature–factor relationships between organism and environment, and if niche construction is the modification of this relationship by the organism, then the standard niche construction categories (perturbative and relocational) are somewhat arbitrary and do not properly partition the possible forms of niche construction.

In light of this critique, we offer a reconceptualization that captures both the original sentiment of niche construction theory, but also makes room for forms of niche construction that fall outside of canonical niche construction theory but should nonetheless be considered niche construction.

Another aim of this article is to show that niche construction can be seen as a set of resources that supplement evolutionary theory. In so doing, we discuss the two main worries that sceptics have raised in relation to niche construction: its apparent ubiquity and its status as an evolutionary process on par with natural selection. We argue that our reconceptualization of niche construction can help us to better understand the relationship between niche construction and natural selection, and niche construction's place in evolutionary theory.

Before offering our revised niche construction framework, we describe in the following section how niche construction is standardly conceptualized on niche construction theory, and point out some of the problematic aspects that follow from this conceptualization. We then offer our alternative framework and show how it improves on the standard account. At the end of the article, we return to the question of how to understand niche construction in relation to evolutionary theory.

2. Niche Construction Theory

The main reference point for niche construction in the contemporary literature is the writings of Odling-Smee, Laland, and Feldman,[3] especially in their *Niche Construction*: *The Neglected Process in Evolution* ([2003]). We take this as our primary source for the conceptualization of niche construction theory and supplement with other texts when necessary. When we refer to 'niche construction theory' (or 'NCT') in what follows, it is this framework to which we refer.

2.1. The standard account of niche construction

For Odling-Smee *et al*. ([2003]), a niche is 'the sum of all natural selection pressures to which [a] population is exposed' (Odling-Smee *et al*. [2003], p. 40). Defined as

[3] Many of these articles are referenced in this text, but for a full overview of the publications see: <synergy .st-andrews.ac.uk/niche/our-publications/>. The importance of niche construction has been argued for by others, see (Brandon and Antonovics [1996]; Oyama *et al*. [2001]; Lewens [2003]; Sterelny [2003]; Boni and Feldman [2005]; Donohue [2005]; Chiu and Gilbert [2015]; Sultan [2015]).

such, it corresponds to other selection-based conceptualizations of the environment, such as Brandon's ([1990]) definition of the selective environment. The chief motivation behind this selection-based definition is to render the concept of niche—which is primarily understood in ecological terms—into a concept that can capture the evolutionary significance of niches. There are two other important points to note about the definition. First, it is relativistic: 'the selection pressures are only the selection pressures relative to specific organisms [or specific traits of the organism]' (Odling-Smee *et al.* [2003], p. 40). Second, the niche has a dual nature: While it is common in ecology to define an ecological niche as either a portion of a habitat that can sustain a species (Grinnell [1917]; Hutchinson [1957]) or as the role of an organism or species in its biotic environment (Elton [1927]; MacArthur and Levins [1967]), the concept of niche in niche construction theory attempts to capture both of these aspects of the niche. That is, the niche is composed of the selection pressures that relate to the 'lifestyle' or 'occupation' (Ehrlich and Roughgarden [1987]) of the organism and its habitat or 'address' (Odum [1989]). For ease of exposition, Odling-Smee, Laland, and Feldman ([2003]) borrow terminology from Bock ([1980]), who proposed a scheme that decomposes an organism into different subsystems (traits and set of traits) called 'features', and decomposes an organism's environment into different subsystems (environmental variables) called 'factors'. Selection pressures are then understood as factors selecting for features, and niche construction occurs

> [. . .] when an organism modifies the feature–factor relationship between itself and its environment by actively changing one or more of the factors in its environment, either by physically perturbing factors at its current location in space and time, or by relocating to a different space-time address, thereby exposing itself to different factors. (Odling-Smee *et al.* [2003], p. 41)

That is, niche construction happens when organisms are changing selection pressures through the modification of their physical environment or by changing habitats (Laland *et al.* [2016]).

On NCT, an organism may alter the feature–factor relationship in several ways. For Odling-Smee *et al.* ([2003]), the primary ways in which organisms engage in such activities is through perturbative niche construction and relocational niche construction. The former describes cases where organisms change one or more factor in their physical environment, while the latter describes cases where organisms move and thereby expose themselves to different environmental factors. In any given episode, niche construction can, and in practice often will, be both perturbative and relocational.

Further, Odling-Smee *et al.* ([2003]) distinguish two contexts in which niche construction activity occurs: 'inceptive' and 'counteractive' niche construction. Inceptive niche construction occurs when the organism initiates a change in one or more of the factors in its environment, while counteractive niche construction involves counteracting change from the external environment. We thus have four categories of niche construction: inceptive perturbational, counteractive perturbational, inceptive relocational, and counteractive relocational.

Lastly, there is a difference between 'positive' and 'negative' niche construction. This distinguishes cases in which niche construction has beneficial (positive) or detrimental (negative) effects on the niche constructing organism's fitness. The changes to selection pressures brought about by niche construction can be ephemeral or can persist for a long duration. We can expect positive niche construction to spread throughout a population, given that the niche constructing traits have higher fitness values than alternative traits relative to a certain adaptive problem (Schulz [2014]). The effects of niche construction can persist across generations through ecological inheritance. Simply put, it is not only the parental genes an organism inherits, but also the constructed environmental conditions into which it is born. Just as humans inherit (in a legal sense) money or land, so too can organisms inherit the ecological conditions of their parents or other conspecifics. However, niche constructing behaviour can also persist through genetic inheritance. Nest-building birds and web-building spiders do not elaborate on previously built structures, nor do they take previous structures as templates for their creations, and in that sense do not enjoy ecological inheritance. However, they are still engaging in niche construction when they build a nest or web.

2.2. Two problems with the standard account of niche construction

While the standard account of niche construction made progress on how to include the active role of the organism into evolutionary theory, we argue that a reconceptualization is needed. There are two key reasons for this reconceptualization. First, the categories of niche construction given by NCT do not map particularly well onto their conceptualization of the relativistic and interactive nature of an evolutionary niche. Second, their categories leave out of consideration organisms that can change their own phenotypic features and consequently alter the selection pressures acting on them. In the following two subsections, we go through these two problems before offering our expanded conceptualization of the basic kinds of niche construction.

2.2.1. The niche as a result of organism–environment interaction

As we have seen, niche construction theory is presented as an alternative to externalism. The niche is not a pre-existing physical space for the organisms to fit into, but rather the result of the interaction of traits (features) and environmental variables (factors) (cf. Lewontin [1983], [2000]; Odling-Smee *et al*. [2003]). Niche construction occurs when an organism actively changes a factor—or its relationship with factors—in such a way that selection pressures are altered. In this way, organisms are active participants in constructing their adaptive fit, and consequently an explanation of this fit has to refer to the activities of organisms that change the feature–factor relationship (in other words, the selective environment). Changes to the properties of the environment are thus not explained solely by other properties internal to the environment, but also by properties of the organism.

However, if a selection pressure results from the interaction of environmental factors and organismic features, and the niche is defined as the sum of selection pressures acting on a population (as it is in NCT), then organisms can actively change their niche by changing:

(1) traits (features),

(2) environmental variables (factors),

(3) the relation between the features and the factors.

The standard NCT conceptualization allows only for the modification of (2) and a limited set of (3) to count as niche construction. The part of (3) that is included is the modification of the relation between features and factors through relocation in space. However, it is arbitrary to leave out (1) and part of (3), and to do so is inconsistent with NCT's own definition of a niche. We therefore hold that niche construction should be reconceptualized in order to track all aspects of the niche that an organism is capable of modifying—that is, a modification of (1), (2), and (3). To further motivate our claim that niche construction should include modifications of (1)–(3), we will consider in the next subsection some cases of niche construction excluded from NCT, but which fit within an expanded account.

2.2.2. Organisms changing their own features or relations without relocating

Organisms can modify the relationship between features and factors without needing to relocate or alter their features or the factors. For example, take meerkats (*Suricata suricatta*), which have constructed a very peculiar social niche. They have sentries, which are experienced meerkats that keep a lookout for predators while other members gather food. The division of labour and flow of information from sentries to other members of the group alters the epistemic environment of the group (Dugatkin [1997]; Sterelny [2003]). This is a case of 'social' (or 'epistemic') niche construction according to Sterelny ([2003]). However, it is unclear how we should categorize it using the standard niche construction categories. While meerkats surely engage in perturbative niche construction through the creation of their burrows, the information flow through the sentries need not be perturbative or relocational. The meerkat sentry may encourage certain sorts of relocations not possible without it—allowing the other meerkats of its social group to gather food, play, and raise their young without constantly having to be on the lookout for predators—but the information flow itself does not seem to be a relocation as understood by the standard approach to niche construction.

Another example of niche construction falling outside of the NCT framework is how some organisms modify how they experience their environment (Chiu and Gilbert [2015]; Sultan [2015]; Chiu [2019]). For example, an organism can modify how it experiences temperature through a behavioural, morphological, or physiological adjustment in which it modulates the thermal heterogeneity of its environment (Sultan [2015], pp. 74–9). These are cases in which the organism need not change factors or relocate, but it nonetheless changes the relationship between the features and the factors such that the selection pressure is altered.

We label the kind of niche construction characterized by the active modifications of features 'constitutive niche construction'. Godfrey-Smith ([1996], p. 145) saw constitutive niche construction as a potential category of how organisms can be said to construct their environment (or niche) in his *Complexity and Function of Mind in Nature*:

> [. . .] another sense in which organism can be said to construct their environment asserts not a causal, but a constitutive or ontological dependence. Features of the environment which were not physically put there by the organism are nonetheless dependent upon the organism's faculties for their existence, individual identity or structure.[4]

Godfrey-Smith points to what he takes to be a constitutive, and not causal, relationship. But we hold that constitutive niche construction is causal, in that by changing its constitution, the organism changes the causal relations it has with its environment. Recent work (Sultan [2015]; Walsh [2015]; Chiu and Gilbert [2015]) has embraced this mode of niche construction. These are cases in which there is a causal relationship between a change in an organism's form or capacities (its features) and the factors of the environment that it experiences, without there being a change to the environment itself (Walsh [2015], pp. 181–2).

A rich source of examples of this kind of niche construction can be found in the behaviour of sessile organisms. Being limited by an anchoring point, sessile organisms cannot actively move in space, and are often limited to changing their constitution, primarily by the growth and discharging of body parts, in order to solve (or dissolve) certain adaptive problems, such as resource availability (Sultan [2015], pp. 80–4). Arber ([1950], p. 3) made this point in connection to plant behaviour:

> Among plants, form may be held to include something corresponding to behaviour in the zoological field. The animal can do things without inducing any essential change in its bodily structure. When a bird uses its beak to pick up food, the beak remains unchanged. But for most, but not all, plants the only available forms of action are either growth or discarding of parts, both of which involve a change in the size and form of the organism.

Such growth and discarding often occurs in relation to environmental cues, and does so in a flexible way, which is commonly referred to as phenotypic or developmental plasticity (West-Eberhard [2003]; Trewavas [2009]; Sultan [2015]). In relation to

[4] It should be noted, however, that while Godfrey-Smith ([1996], p. 145) alludes to this as a possible way to understand how an organism can be said to construct its environment, he does not ultimately count it as organic construction: 'Organic construction of the environment occurs whenever an organism intervenes in a formerly autonomous process in the physical world, changing their course and upshot'.

the standard approach of niche construction, much of the behaviour in which sessile organism can play an active role in their own evolution therefore falls outside of the categories of niche construction theory.

In light of these problems, we offer a reconceptualization of the basic kinds of niche construction. In the following section, we provide a way of partitioning niche construction into three basic types: constitutive, relational, and external. In Section 4 we consider how this alternative framework is an improvement over that of NCT.

3. Three Kinds of Niche Construction

To clearly grasp the kinds of niche construction that exist and how best to categorize them, consider an FM radio and the ways that it could 'construct its niche'. When turned on, such a radio may receive a signal from a station and convert the electromagnetic waves into sound waves within the range of human hearing. Think of the sound output as the expression of the life of the radio. How does a radio construct its niche and what effect does it have on the outcomes of its life?

The example of the radio will help us to develop a tripartite distinction, to show that there are three fundamentally different forms of niche construction for biological entities.

3.1. Constitutive niche construction

The radio under consideration is constituted in a particular way, and its constitution has an effect on the sound produced. The radio is engineered to receive radio waves in the FM frequency only. Electromagnetic signals outside of that range (AM radio signals, cell phone signals, and so on) are not received and do not affect the sound output—or if the output is affected, it manifests as an unwanted disturbance. The essential parts of the radio—the antenna, circuit board, speaker, power supply—constrain what is possible for the radio to output. There is a wide range of possible frequencies to which a radio can be tuned and the specific constitution of this radio narrows this down. The size and shape of the antenna constrains the space of possible frequencies that can be reliably received, and the electronics are tuned to be sensitive to a narrow band within this space. Furthermore, the acoustic equipment—such as the shape of the speaker and the nature of the amplifier—determine the possible range and characteristics of the sounds (volume, pitch, timbre, and so on). Thus, the very constitution of the radio (in part) determines its niche: its constitution carves out a slice of the world, making this and only this slice matter for the life of the radio.

But if the radio is not a mere passive subject, and is able to change its constitution, then it can construct its niche by changing itself. If it changes the size of its antenna or modifies its circuitry, then it could change its ability to receive signals and convert them into sound. Organisms are in this respect like radios. They are tuned to receive some aspects of the world, while being incapable of receiving others. For bees, ultraviolet light is visible and this has a profound effect on how they perceive flowers. A dog can smell a deer that passed by hours ago, while we are incapable of detecting such diluted smells. Because organisms are dynamic entities, changing from moment to moment, they construct their niche through their behaviour and development. A lion changes its size, strength, and coordination as it matures. Through this maturation, the space of possible prey is transformed. A lion in its prime may be able to take down a healthy mature wildebeest, but an immature lion will be restricted to the young, elderly, or diseased. The development of the lion is thus partly responsible for the construction of its niche.

This form of niche construction is not restricted to animals, and niche construction need not be linked to external movements. It is well known that plants respond to herbivores. For example, some plants will change their physiology in response to the vibrations caused by caterpillar chewing (Appel and Cocroft [2014]). Such a physiological reaction is a form of constitutive niche construction. The plant increases its chemical defences in response to the vibrations, thus changing its selection pressures.

3.2. Relational niche construction

Niches are carved out of the world via the constitutions of organisms, but they are also carved by the relations that the organisms bear to one another and to other factors of the biotic and abiotic environment. These relations can be modified in the absence of the organism transforming its own constitution or the physical conditions of its environment. This form of modification we label 'relational niche construction'. Let's return to the example of the radio to bring this into focus. Consider now a group of radios. These radios are passively receiving FM signals—their behaviour in no way changes the output of the received signals. Nevertheless, the radios can have an effect on one another's life. For example, if one radio is standing before another one, the characteristics of the received signal will be modified, however slightly. If the radios touch their antennae together, the signal reception will change more significantly.

If the radios were equipped with wheels and navigational equipment, they could increase their proximity to the source of the radio signal. This would provide a stronger, clearer signal, though it will not change the source of the signal (and is thus still passive with respect to the signal).

Organisms, especially social organisms, can construct their own niches via relational niche construction. Mice that pile up to keep warm are not keeping warm by changing the temperature of their nest. But they can affect their own rate of heat loss—and the heat loss of their nest mates—just by existing in a particular proximity to others. Alpha males and females in social primate species have significant effects on the behaviour and physiology (stress levels, for instance) of others in the group merely by being present. Their presence may also alter the access to food sources of other members of the group. These alterations are not due to the alphas altering the physical environment, but are instead based on the relation between the alphas and the other members of the group.

A niche is filled with information that organisms can use to solve adaptive problems. For example, some prey prefer to be in a close proximity to their predators, because if they are constantly receiving information about the location of the predator, then they are less susceptible to fatal surprise encounters (Sterelny [2003]). In such cases, prey often move in space in order to keep a steady stream of information about the location of the predator flowing. Such relocational niche construction is best understood in terms of information flow and its consequences. They relocate not to change the world or themselves, but to keep certain channels of information open.

Relational niche construction can also involve relocation for food or mates or nesting sites or any other selection-relevant resource. A deer that moves up the mountain in the summer to dine on rich alpine grass is, via its movement alone, relationally constructing its niche. But the deer is apt to also be actively changing the external environment during its migration. It might, for example, be helping to maintain a system of trails. Let's now consider the idea of constructing the external environment, and how this differs from relational construction.

3.3. External niche construction

Niche construction can involve the modification of the environment, changing not merely the form of interaction with environmental factors, but the very factors themselves. If the radio were able not just to react to the available stations, but to modify them or to create its own, it would be engaging in 'external niche construction'. A group of radios that set up a pirate radio station would be changing the external FM band environment.

The prototypical example of external construction in organisms is beavers building dams (Jones *et al*. [1994], [1997]). Beavers cut down trees to dam rivers. The dams block the passage of water, creating a pond. The beavers then travel around by swimming in the water. The constructed pond exerts selection pressures, selecting for water-related traits like a waterproof coat and webbed feet.

External niche construction is not limited to the modifications of an organism's and its conspecific's own selection pressures, however. Just as the beavers modify their own selection pressures by building a dam, they are modifying the selection pressures of all the fauna and flora in that immediate area. They are creating an environment for aquatic organisms (within the pond) and are making a large area for moisture-loving plants (willow trees, for example) around the pond.

4. Conceptual Improvement on Niche Construction Theory

In the preceding section, we characterized three kinds of niche construction: constitutive, relational, and external. How does this characterization differ from—and why might it be an improvement over—the standard account from niche construction theory? In this section, we discuss how our tripartite characterization improves on the standard categorization.

4.1. Constitutive niche construction

Constitutive niche construction is left out of consideration on the standard account of NCT. The significance for ecology and evolution of the constitution of organisms is by no means overlooked by proponents of NCT (Laland *et al*. [2014]). However, they standardly exclude changes in constitution from niche construction. In Section 2.2 we argued that this was a problem for NCT. Here we provide some further argumentation for taking constitutive niche construction into consideration.

If an organism's niche is defined by the feature–factor relationship between itself and its environment, then a modification of the feature–factor relationship will be an instance of niche construction. As we saw above, there are three ways that the feature–factor relationship can be modified, the first of which involves a change in the features. Thus, if a niche is defined in terms of a feature–factor relationship, and if niche construction is the modification of this relationship, then actively changing the features should be classified as niche construction.

Additionally, many changes to an organism's constitution cannot fully be explained without a reference to the effects (or adaptive consequences) its altered constitution has on the organism–environment interaction. For example, in the case of drought a plant might droop or roll its leaves during the day when the plant experiences the highest rates of transpiration, a phenomenon called wilting (Begg [1980]). At night, with a decline in transpiration, the rolled leaves slowly re-expand (Fang and Xiong [2015]). Cases of constitutive niche construction are not limited to plants and other sessile organisms. Humans, too, can change their constitution in regards to environmental factors. For example, the plasticity involved in muscle growth is influenced by how humans actively engage with certain environmental factors (Gilbert and Epel [2015]).

4.2. Relational niche construction

Relational niche construction is a more expansive concept than NCT's relocational niche construction. Relocational niche construction occurs when organisms alter their spatiotemporal relationship with the external environment. However, organisms can also alter their relationship with other organisms, both conspecifics and heterospecifics. And such alterations do not necessarily involve changes in location. The important changes are those of relationships, not locations. Thus, relational niche construction captures organismic alteration of spatiotemporal relationships to the environment, as well as the alteration of the relationships it has with other organisms.

Habitat selection—the process by which organisms choose areas of their environment where they conduct specific activities (Stamps [2009])—and migration are examples of relocational niche construction. In such cases it is clear that an organism alters its spatiotemporal relation to the external environment and thereby alters its selection pressures. However, a vast array of complex social and inter-organismic behaviour, such as the meerkats' 'social security' niche, social hierarchies in primates, and human domestication of animals and plants consist in a large degree of the alteration of organism–to–organism relationships,[5] and not only the alteration of the organism's spatiotemporal relation to the external environment.

Thus, the NCT concept of relocational niche construction is too narrow. Relocational niche construction is not a basic form of niche construction, but is instead one way of achieving relational niche construction. It is the relations that are fundamental, and while relocating can change relationships, it is not the only way to do so. The gaps in relocational niche construction are particularly apparent when attempting to categorize niche construction via transformations in the flow of information, as in epistemic and social niche construction (Sterelny [2003]).

4.3. External niche construction

While our last category is more of a label change than a conceptual innovation, it seems more appropriate to use 'external' as the label, instead of the NCT's 'perturbative'. These cases are, according to NCT, niche construction activities where there is alteration of the external (or physical) environment. But the concept of perturbation does not by itself distinguish between, for example, the perturbation of physical and social environments. A lone adult lion might challenge an older and weaker male lion for control of its pride and usurp its place as leader of the pride. This is a perturbation of the social structure of the pride, but is not an alteration of the external (or physical) environment as conceived by NCT. It would be a case of relational niche construction. Additionally, an organism can perturb itself: for example, it could estivate or hibernate, where it reduces its metabolic activity and rests for a long period. Such self-directed perturbation would be classified as constitutive niche construction. Perturbation refers to a kind of action, while external refers to what is involved in the action. As such, external niche construction offers a more precise way to pick out and classify niche construction activities involving changes to the external environment.

5. The Status of Niche Construction Theory within Evolutionary Theory

Much of the contemporary literature on niche construction centres on the utility of the niche construction framework. There are several areas in which a niche construction

[5] For a treatment of domestication from a niche construction perspective, see (Zeder [2016]).

perspective appears to clarify or to advance other related topics such as culture, archaeology, primatology, and much more (see Laland and Sterelny [2006]). Other literature, however, directly addresses and critiques niche construction theory. These critiques have been fairly general and focus primarily on how niche construction relates to evolutionary theory. As such, these are worries that any concept of niche construction has to deal with. Before we offer our contribution to these worries, let's briefly go through what we take to be the main criticisms levelled against niche construction.

There are two main lines of critique against niche construction. One concerns the helpfulness of adding niche construction to evolutionary theory, while the other concerns whether niche construction should be understood as a true evolutionary process. The arguments against the helpfulness to evolutionary theory hold that the niche construction framework does not improve on the already existing framework of the modern synthesis. Problems such as the intractability, lack of predictability, and ubiquity of niche construction are their main worries (Sterelny [2001], [2005]; Dawkins [2004]; Brodie [2005]; Griffiths [2005]; Okasha [2005]; Laland and Sterelny [2006]). The arguments over the status of niche construction in evolutionary theory concern scepticism about whether niche construction is, or should be, viewed as a process in addition to standard evolutionary processes such as selection and drift (Scott-Phillips *et al.* [2014]). We will treat these two worries in turn in the next two subsections.

5.1. Is niche construction a helpful addition to evolutionary theory?

One argument against the theoretical value of niche construction is that of Dawkins ([2004]), who argues that it might be better regarded as a background condition than as causal difference maker. The justification given for this is that since evolving systems are so complex, we cannot study them without making simplifying assumptions. Incorporating the feedback—or reciprocal causation—generated by niche construction could very well mean one complication too many. Further, there might be cases in which the apparent niche constructive activity was selected by prior natural selection. As such, the activity that changes selection pressures is a result of natural selection and the explanation of it does not need to be any more complicated (in terms of causal complexity) than what is already available in the standard picture (cf. the extended phenotype, Dawkins [1982]). This is thus an argument that while there is niche construction, it may be best to leave it out of evolutionary models.

There is also the argument that niche construction is so ubiquitous that it should not be identified as a separate phenomenon. The worry about the ubiquity of niche construction stems from the (intentionally) broad definition of niche construction (Laland *et al*. [2016]). All organisms can potentially be considered niche constructors, since the definition requires only that an organism alters selection pressures through environmental modification. Including constitutive niche construction within the scope niche construction appears to make this even worse, as this renders any biotic change into a potential case of niche construction. There appear to be severe consequences of having such an ubiquitous concept at play. First, it appears to render niche construction intractable. Since every selection-relevant interaction counts as niche construction, and since we obviously cannot factor in every interaction into our models, how are we to know what are the important cases of niche construction? Second, the ubiquity of niche construction also seems to marginalize its potency as a causal difference maker in evolution, thus challenging its explanatory significance. Unless we have some sort of demarcation principle between significant and insignificant cases of niche construction, what role can invoking niche construction play in explaining adaptation? What seems to be needed is a way to distinguish significant and insignificant (Matthews *et al.* [2014])and adaptive and accidental (Sterelny [2005]) cases of niche construction, and a way to narrow down the set of behaviours that fall under the rubric of niche construction.

Our response to these worries is that the ubiquity of niche construction is no reason to hold that niche construction is trivial or lacks explanatory relevance, and that the idea that niche construction is a mere background condition is not supported by the importance of niche construction in many evolutionary systems. Consider two central ingredients of evolutionary explanations, selection and drift. Both are ubiquitous. Populations are subject to a multitude of selection pressures. Some of these pressures are so weak that they can be ignored, while others are powerful and can serve in explanations of evolutionary outcomes. Pointing out that selection pressures are ubiquitous does not decrease their importance, much less render them trivial. We hold that just as there are strong selection pressures that we should foreground in our analysis of evolutionary events, while we can safely ignore others, so it is with niche construction. Constructing models always involves simplification and the backgrounding of some factors while foregrounding others. That fact that there will be many forms of niche construction in the background does not mean that all should be relegated to the background.

Drift is also ubiquitous (Ramsey [2013a]), and its evolutionary effect approaches zero as the population size tends toward infinity. Thus, in large populations, especially over short time scales, we could leave drift out of our models. But the ubiquity and at times irrelevance of drift does not mean that it is unimportant. Drift is crucial in understanding the dynamics of small populations, and the ubiquitous drifting of noncoding genes can provide information about such things as divergence times in lineages (for example, Rannala and Yang [2007]).

Drift and selection are thus ubiquitous, but in any evolutionary system, not all drift and selection pressures are equally important. Additionally, we often want to understand the extent to which drift and selection played a role in particular evolutionary events. If we observe that an island population of monkeys has lighter fur than the nearby mainland conspecifics, we can ask if this is an evolutionary response to selection, or if it is drift, or both. Similarly, what is important with niche construction is not whether constitutive, relational, or external niche construction are at play in an evolutionary system, but the relative significance of each in accounting for a particular evolutionary outcome.[6]

We thus hold that like drift and selection and other evolutionary factors, ubiquity does not imply triviality, nor does the fact that niche construction explanations are not always necessary imply that they are never important.

5.2. Is niche construction an evolutionary process?

There is an ongoing debate concerning whether niche construction is a process on par with natural selection (Laland [2015]; Scott-Phillips *et al.* [2014]). While some advocates of the niche construction perspective argue that niche construction is an evolutionary process in its own right—one that biases the action of natural selection by either directing or counteracting its effects (Laland [2015]; Laland *et al.* [2017]), critics have responded by arguing that there are only four 'proper' evolutionary processes: mutation, recombination, natural selection, and drift. The first two are processes that generate phenotypic variation, while the latter two are processes that sort that variation. Niche construction, according to these critics, is one of many factors that can influence either of these processes (Scott-Phillips *et al.* [2014]).

One problem with asking whether niche construction is an evolutionary process is that there is no general agreement concerning what counts as an evolutionary process (Welch [2017]), and even whether we can properly delineate evolutionary causes from other biological or environmental causes (Laland [2015]). Because of this, we think it is more useful to consider in detail how an organism's active modification of its selective environment can be decomposed into an array of different mechanisms, and to couple these with the mechanisms that facilitate an evolutionary response to the organism's activities (in other words, to show how ontogenetic and behavioural mechanisms can have evolutionary—or phylogenetic—effects). In Table 1 we use our tripartite categorization to describe some of the potential mechanisms through which an organism can change the selection pressures acting on it via activities that do not span generations ('intragenerational mechanisms') as well as generation-spanning mechanisms ('intergenerational mechanisms').

Table 1 is meant to do two things. First, it helps to make niche construction more tractable, pointing out mechanisms through which organisms may alter their selection pressures. Second, it highlights the diversity of these mechanisms, and shows that in specific evolutionary systems, and for specific evolutionary questions, we can safely background some of these mechanisms while foregrounding others. A species may be behaviourally plastic without being innovative (Ramsey *et al.* [2007]), and even if it is innovative, we might be able to leave innovations out of the model for our study at hand. Similarly, a species might be innovative without being cultural (Jablonka and Lamb [2005]; Ramsey [2013b]), but even if it is cultural, the culture may not be significant for understanding a particular evolutionary outcome.

[6] We thank one of the reviewers for suggesting that we make this point.

Table 1. Top row: Mechanisms acting within generations that can alter selection pressures. Bottom row: Mechanisms that reach across generations in modifying selection pressures. The list is meant to be illustrative and not exhaustive

	Constitutive	Relational	External
Intragenerational Mechanisms	Phenotypic plasticity, behavioural innovation.	Behavioural placticity, relocation, resource management, social learning.	Ecological engineering; for example, web or nest building. External alterations during an organism's life-history.
Intergenerational Mechanisms	Parental effects (prenatal), including epigenetic inheritance	Behavioural/social and cultural inheritance, parental effects (postnatal).	Ecological inheritance.

We thus see niche construction as a set of mechanisms that yield novel explanatory and theoretical resources involving the active role of organisms in their own evolution. Apprehending the interplay of these mechanisms can result in a more detailed and nuanced understanding of evolutionary dynamics.

6. Conclusion

In this article we offered a reconceptualization of niche construction. We argued that the traditional conceptualization of the basic kinds of niche construction faces two problems. First, if a niche is constituted out of the feature–factor relationship, the basic kinds of niche construction should map onto such an understanding of a niche, and any modification of this relationship should therefore count as niche construction. These modifications can be changes in features, in factors, or in the feature–factor relationship. Second, there is a whole class of cases that are left out of consideration by the standard conceptualization of niche construction. Importantly, organisms can alter their own features, thereby altering their selective environment. To address these problems, we offered our alternative account and identified three corresponding forms of niche construction: constitutive, relational, and external construction. This is an expansion and reworking of the traditional NCT account, which includes only two forms of niche construction, perturbative and relocational.

Drawing out some of the implications of our account, we showed how we can make progress in two common debates in the contemporary literature on niche construction: Its status as an evolutionary process and the question of whether it is a helpful addition to evolutionary theory. For the latter, we showed how both natural selection and drift are ubiquitous, but that this does not undermine their role in our understanding of evolutionary dynamics. Similarly with niche construction, the fact that it is ubiquitous does not undermine its potential for increasing our understanding of evolutionary systems.

On the question of niche construction as a process, we used the tripartite conceptualization to show how the three different types of niche construction activities can be divided into two sets of mechanisms—intragenerational mechanisms and intergenerational mechanism—both of which allow niche construction to have evolutionary effects. By isolating the mechanisms responsible for the occurrence of niche construction, we are hopeful that this will clarify when the niche construction perspective is appropriate and useful.

We hope that our contribution aids further discussion on the fundamental aspects of niche construction and organism–environment interactions more generally, and how it relates to the causal structure of evolutionary theory.

Acknowledgements

An earlier version of this article was presented at the 2019 meetings of the International Society for the History, Philosophy, and Social Studies of Biology and the European Philosophy of Science Association, as well as the 2019 Evolution Evolving conference at Cambridge. We thank the audience members for their helpful feedback. We would also like to thank the members of the Ramsey Lab reading group for carefully reading and commenting on an early version of this article, namely, Stijn Conix, Hugh Desmond, James DiFrisco, Alejandro Gordillo-García, and Charles Pence. Finally, we would like to thank the reviewers and editors of this journal for their helpful suggestions.

Bendik Hellem Aaby
Centre for Logic and Philosophy of Science
KU Leuven
Leuven, Belgium
bendik.aaby@kuleuven.be

Grant Ramsey
Centre for Logic and Philosophy of Science
KU Leuven
Leuven, Belgium
grant.ramsey@kuleuven.be

References

Appel, H. M. and Cocroft, R. B. [2014]: ‘Plants Respond to Leaf Vibrations Caused by Insect Herbivore Chewing’, *Oecologica*, **175**, pp. 1257–66.

Arber, A. [1950]: *The Natural Philosophy of Plant Form*, Cambridge: Cambridge University Press.

Barton, N. and Partridge, L. [2000]: ‘Limits to Natural Selection’, *BioEssays*, **22**, pp. 1075–84.

Bateson, P. [2017]: 'Adaptability and Evolution', *Interface Focus*, **7**, p. 20160126.

Begg, J. E. [1980]: 'Morphological Adaptations of Leaves to Water Stress', in N. C. Turner and P. J. Kramer (*eds*), *Adaptation of Plants to Water and High Temperature Stress*, Toronto: John Wiley, pp. 33–42.

Boni, M. F. and Feldman, M. W. [2005]: 'Evolution of Antibiotic Resistance by Human and Bacterial Niche Construction', *Evolution*, **59**, pp. 477–91.

Bock, W. J. [1980]: 'The Definition and Recognition of Biological Adaptation', *American Zoologist*, **20**, pp. 217–27.

Brandon, R. [1990]: *Adaptation and Environment*, Princeton, NJ: Princeton University Press.

Brandon, R. and Antonovics, J. [1996]: 'The Coevolution of Organism and Environment', in R. Brandon (*ed.*), *Concept and Methods in Evolutionary Biology*, Cambridge: Cambridge University Press, pp. 161–78.

Brodie, E. D. [2005]: 'Caution: Niche Construction Ahead', *Evolution*, **59**, pp. 249–51.

Chiu, L. [2019]: 'Decoupling, Commingling, and the Evolutionary Significance of Experiential Niche Construction', in T. Uller and K. N. Laland (*eds*), *Evolutionary Causation: Biological and Philosophical Reflections*, Cambridge, MA: MIT Press.

Chiu, L. and Gilbert, S. F. [2015]: 'The Birth of the Holobiont: Multi-species Birthing through Mutual Scaffolding and Niche Construction', *Biosemiotics*, **8**, pp. 191–210.

Dawkins, R. [1982]: *The Extended Phenotype: The Gene as the Unit of Selection*, Oxford: Oxford University Press.

Dawkins, R. [2004]: 'Extended Phenotype—but Not Too Extended: A Reply to Laland, Turner, and Jablonka', *Biology and Philosophy*, **19**, pp. 377–96.

Donohue, K. [2005]: 'Niche Construction through Phonological Plasticity: Life History Dynamics and Ecological Consequences', *New Phytologist*, **166**, pp. 83–92.

Dugatkin, L. A. [1997]: *Cooperation among Animals: An Evolutionary Perspective*, Oxford: Oxford University Press.

Ehrlich, P. R. and Roughgarden, J. [1987]: *The Science of Ecology*, New York: Macmillian.

Elton, C. [1927]: *Animal Ecology*, London: Sidgwick and Jackson.

Fang, Y. and Xiong, L. [2015]: 'General Mechanisms of Drought Response and Their Application in Drought Resistance Improvement in Plants', *Cellular and Molecular Life Sciences*, **72**, pp. 673–89.

Gilbert, S. F. and Epel, D. [2015]: *Ecological Developmental Biology: The Environmental Regulation of Development, Health, and Evolution*, Sunderland, MA: Sinauer Associates.

Godfrey-Smith, P. [1996]: *Complexity and the Function of Mind in Nature*, Cambridge: Cambridge University Press.

Godfrey-Smith, P. [2009]: *Darwinian Populations and Natural Selection*, Oxford: Oxford University Press.

Griffiths, P. E. [2005]: 'Review of *Niche Construction*', *Biology and Philosophy*, **20**, pp. 11–20.

Grinnell, J. [1917]: 'The Niche-Relationships of the California Thrasher', *Auk*, **34**, pp. 427–33.

Hutchinson, G. E. [1957]: 'Concluding Remarks: Cold Springs Harbor Symposium', *Quantitative Biology*, **22**, pp. 415–27.

Jablonka, E. and Lamb, M. [2005]: *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioural, and Symbolic Variation in the History of Life*, Cambridge, MA: MIT Press.

Jones, C. G., Lawton, J. H. and Shachak, M. [1994]: 'Organisms as Ecosystem Engineers', *Oikos*, **68**, pp. 373–86.

Jones, C. G., Lawton, J. H. and Shachak, M. [1997]: 'Positive and Negative Effects of Organisms as Physical Ecosystem Engineers', *Ecology*, **78**, pp. 1946–57.

Laland, K. N. [2015]: 'On Evolutionary Causes and Evolutionary Processes', *Behavioral Processes*, **117**, pp. 97–104.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. [1996]: 'On the Evolutionary Consequences of Niche Construction', *Journal of Evolutionary Biology*, **9**, pp. 293–316.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. [1999]: 'Evolutionary Consequences of Niche Construction and Their Implications for Ecology', *Proceedings of the National Academy of Sciences USA*, **96**, pp. 10242–7.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. [2000]: 'Niche Construction, Biological Evolution, and Cultural Change', *Behavioral and Brain Sciences*, **23**, pp. 131–75.

Laland, K. N. and Sterelny, K. [2006]: 'Seven Reasons (Not) to Neglect Niche Construction', *Evolution*, **60**, pp. 1751–62.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. [2005]: 'On the Breadth and Significance of Niche Construction: A Reply to Griffiths, Okasha, and Sterelny', *Biology and Philosophy*, **20**, pp. 37–55.

Laland, K. N., Odling-Smee, J. and Gilbert, S. F. [2008]: 'EvoDevo and Niche Construction: Building Bridges', *Journal of Experimental Zoology Part B*, **310**, pp. 549–66.

Laland, K. N., Sterelny, K., Odling-Smee, J., Hoppitt, W. and Uller, T. [2011]: 'Cause and Effect in Biology Revisited: Is Mayr's Proximate–Ultimate Dichotomy Still Useful?', *Science*, **334**, pp. 1512–6.

Laland, K. N., Odling-Smee, J., Hoppitt, W. and Uller, T. [2013]: 'More on How and Why: Cause and Effect in Biology Revisited', *Biology and Philosophy*, **28**, pp. 719–45.

Laland, K. N., Odling-Smee, J. and Turner, S. [2014]: 'The Role of Internal and External Processes in Evolution', *Journal of Physiology*, **592**, pp. 2413–22.

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E. and Odling-Smee, J. [2015]: 'The Extended Evolutionary Synthesis: Its Structure, Assumptions, and Predictions', *Proceedings of the Royal Society B*, **282**, p. 20151019.

Laland, K. N., Matthews, B. and Feldman, M. W. [2016]: 'An Introduction to Niche Construction Theory', *Evolutionary Ecology*, **30**, pp. 191–202.

Laland, K. N., Odling-Smee, J. and Endler, J. [2017]: 'Niche Construction, Sources of Selection, and Trait Coevolution', *Interface Focus*, **7**, p. 20160147.

Levins, R. and Lewontin, R. C. [1985]: *The Dialectical Biologist*, Cambridge, MA: Harvard University Press.

Lewens, T. [2003]: 'Prospects for an Evolutionary Policy', *Philosophy*, **78**, pp. 495–514.

Lewontin, R. C. [1970]: 'The Units of Selection', *Annual Review of Ecology and Systematics*, **1**, pp. 1–18.

Lewontin, R. C. [1983]: 'Gene, Organism, and Environment', in D. S. Bendall (*ed.*), *Evolution: From Molecules to Men*, Cambridge: Cambridge University Press, pp. 273–85.

Lewontin, R. C. [1991]: *Biology as Ideology: The Doctrine of DNA*, New York: Harper.

Lewontin, R. C. [2000]: *The Triple Helix: Gene, Organism, and Environment*, Cambridge, MA: Harvard University Press.

MacArthur, R. H. and Levins, R. [1967]: 'The Limiting Similarity, Convergence, and Divergence of Coexisting Species', *American Naturalist*, **101**, pp. 377–85.

Matthews, B., De Meester, L., Jones, C. G., Ibelings, B. W., Bouma, T. J., Nuutinen, V., van de Koppel, J. and Odling-Smee, J. [2014]: 'Under Niche Construction: An Operational Bridge between Ecology, Evolution, and Ecosystem Science', *Ecological Monographs*, **84**, pp. 245–63.

Odum, E. P. [1989]: *Ecology and Our Endangered Life-Support Systems*, Sunderland, MA: Sinauer Associates.

Okasha, S. [2005]: 'On Niche Construction and Extended Evolutionary Theory', *Biology and Philosophy*, **20**, pp. 1–10.

Odling-Smee, J. [1988]: 'Niche Constructing Phenotypes', in H. C. Plotkin (*ed.*), *The Role of Behavior in Evolution*, Cambridge, MA: MIT Press, pp. 73–132.

Odling-Smee, J. [2010]: 'Niche Inheritance', in M. Pigliucci and G. Müller (*eds*), *Evolution: The Extended Synthesis*, Cambridge, MA: MIT Press, pp. 175–208.

Odling-Smee, J., Laland, K. N. and Feldman, M. W. [1996]: 'Niche Construction', *American Naturalist*, **147**, pp. 641–8.

Odling-Smee, J., Laland, K. N. and Feldman, M. W. [2003]: *Niche Construction: The Neglected Process in Evolution*, Princeton, NJ: Princeton University Press.

Oyama, S., Griffiths, P. E. and Gray, R. D. [2001]: *Cycles of Contingency: Developmental Systems and Evolution*, Cambridge, MA: MIT Press.

Piaget, J. [1978]: *Behavior and Evolution*, New York: Random House.

Rannala, B. and Yang, Z. [2007]: 'Inferring Speciation Times under an Episodic Molecular Clock', *Systematic Biology*, **56**, pp. 453–66.

Ramsey, G. [2013a]: 'Driftability', *Synthese*, **190**, pp. 3909–28.

Ramsey, G. [2013b]: 'Culture in Humans and Other Animals', *Biology and Philosophy*, **28**, pp. 457–79.

Ramsey, G., Bastian, M. L. and van Schaik, C. [2007]: 'Animal Innovation Defined and Operationalized', *Behavioral and Brain Sciences*, **30**, pp. 393–437.

Schrödinger, E. [1944]: *What Is Life*? Cambridge: Cambridge University Press.

Schulz, A. W. [2014]: 'Niche Construction, Adaptive Preferences, and the Differences between Fitness and Utility', *Biology and Philosophy*, **29**, pp. 315–35.

Scott-Phillips, T. C., Laland, K. N., Shuker, D. M., Dickins, T. E. and West, S. A. [2014]: 'The Niche Construction Perspective: A Critical Appraisal', *Evolution*, **68**, pp. 1231–43.

Stamps, J. [2009]: 'Habitat Selection', in S. A. Levin (*ed.*), *Princeton Guide to Ecology*, Princeton, NJ: Princeton University Press, pp. 38–44.

Sterelny, K. [2001]: 'Niche Construction, Developmental Systems, and the Extended Replicator', in S. Oyama, P. E. Griffiths and R. D. Gray (*eds*), *Cycles of Contingency: Developmental Systems and Evolution*, Cambridge, MA: MIT Press, pp. 331–49.

Sterelny, K. [2003]: *Thought in a Hostile World: The Evolution of Human Cognition*, Malden, MA: Blackwell.

Sterelny, K. [2005]: 'Made by Each Other: Organisms and Their Environment', *Biology and Philosophy*, **20**, pp. 21–36.

Sultan, S. E. [2015]: *Organism and Environment: Ecological Development, Niche Construction, and Adaptation*, Oxford: Oxford University Press.

Trewavas, A. [2009]: 'What Is Plant Behaviour?', *Plant, Cell, and Environment*, **32**, pp. 606–16.

Waddington, C. H. [1969]: 'Paradigm for an Evolutionary Process', in C. H. Waddington (*ed*.), *Towards a Theoretical Biology*, Edinburgh: Edinburgh University Press, pp. 106–23.

Walsh, D. M. [2013]: 'Adaptation and the Affordance Landscape: The Spatial Metaphors of Evolution', in E. Barker, E. Desjardins and T. Pearce (*eds*), *Entangled Life: Organism and Environment in the Biological and Social Sciences*, Dordrecht: Springer, pp. 213–36.

Walsh, D. M. [2015]: *Organisms, Agency, and Evolution*, Cambridge: Cambridge University Press.

West-Eberhard, M. J. [2003]: *Developmental Plasticity and Evolution*, Oxford: Oxford University Press.

Welch, J. J. [2017]: 'What's Wrong with Evolutionary Biology?', *Biology and Philosophy*, **32**, pp. 263–79.

Williams, G. C. [1966]: *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, Princeton, NJ: Princeton University Press.

Williams, G. C. [1992]: 'Gaia, Nature Worship, and Biocentric Fallacies', *The Quarterly Review of Biology*, **67**, pp. 479–86.

Winemiller, K. O., Fitzgerald, D. B., Bower, L. M. and Pianka, E. R. [2015]: 'Functional Traits, Convergent Evolution, and Periodic Tables of Niches', *Ecology Letters*, **18**, pp. 737–51.

Zeder, M. A. [2016]: 'Domestication as a Model System for Niche Construction Theory', *Evolutionary Ecology*, **30**, pp. 325–48.