14 Decoupling, Commingling, and the Evolutionary Significance of Experiential Niche Construction

Lynn Chiu

1. Introduction

Evolutionary theory is dominated by externalist models, theories, strategies, and metaphors that appeal to the environment to explain adaptive fit, or "good design" (Endler 1986; Godfrey-Smith 1996, 2001; Gould 1977, 2002; Lewontin 2000; Mayr 1982; Walsh 2015; Williams 1966). Externalist explanatory strategies presume that adaptations map onto environmental features. Externalist metaphors speak of traits as "solutions" to environmental "problems" or keys fitted to "fill" an environmental niche or lock.

Richard Lewontin, however, argued that externalism is "bad biology" (Levins and Lewontin 1985; Lewontin 1982, 1983, 2000). Organisms are not "adapted" to environments. Instead, they "construct every aspect of their environment themselves. They are not the passive objects of external forces, but the creators and modulators of these forces" (Levins and Lewontin 1985, 104). The better metaphor for evolution should be "construction," not adaptation.

Lewontin's constructivism has inspired a large and expanding literature on the causal significance of "niche construction" on evolution.[1] However, most followers reject Lewontin's radical ontology of the environment. According to Lewontin, organisms do not just alter the world they occupy, they also change how the world is *experienced*. The niche constructed by the organism is thus not entirely made up by the external world, but by the experiences of the organism as well. Many admirers of Lewontin find it difficult to comprehend or operationalize "experienced niches" as external environments and causes of evolution (Brandon and Antonovics 1995; Godfrey-Smith 1996, 2001; Odling-Smee 1988; Odling-Smee, Laland, and Feldman 2003; Sterelny and Griffiths 1999). They thus opt to identify constructed environments as the intrinsic properties of the external world, albeit those relevant to the organism. An evolutionary theory of niche construction concerns the evolutionary significance of constructed, intrinsically defined environments.

In this chapter, I make the case for the evolutionary significance of "experiential niche construction" (coined by Sultan 2015). I start by arguing that recent analyses that draw on the agency and plasticity of organisms (Walsh 2015; Sultan 2015) can address a major objection against experiential niche construction (Godfrey-Smith 1996, 2001). I then propose a way experiential niche construction is evolutionarily significant. Theories of niche construction that leave out the experiential variety tend to maintain an externalist characterization of natural selection and argue that niche construction feeds into the environmental causes of natural selection. Natural selection, however, does not adapt a population to its environment when different organisms of a population construct and experience different environments. Instead, in these scenarios, the causes of selection are spread across varying organisms and their varying constructed environments. I argue that experiential niche construction helps maintain the spread of selective causes across organism and environment interactions. It thus creates the conditions for a kind of natural selection that is not "externalist."

My approach is pluralistic. Sometimes, natural selection can be heuristically approximated as environmental selection and niche construction contributes to selection's environmental sources. In these scenarios, organisms and environments are "decoupled" causes. Other times, however, natural selection cannot be heuristically treated as environmental selection. This occurs when organisms and environments "commingle" and niche construction *constitutes* the conditions of natural selection. I propose a decoupling/commingling framework that specifies when it is and is not appropriate to heuristically assume that natural selection explanations are externalist.

In the following, I will refer to the external world surrounding the organism, characterized by its intrinsic properties, as the external or physical world or environment. When I am referring to the environment experienced by the organism (which will be determined in part by the properties of the organism), I will qualify the world or environment with terms such as "experienced" or "experiential."

2. Experiential Niche Construction and Its Discontents

According to Lewontin, mainstream evolutionary theory assumes that the environment presents well-defined problems for organisms to solve.

> The word "adaptation" reflects this point of view, implying that the organism is molded and shaped to fit into a preexistent niche, given by the autonomous forces of the environment, just as a key is cut and filed to fit into a lock. (Levins and Lewontin 1985, 98)

He argues that there are two problems with this problem-solution metaphor. The conceptual problem is that organisms do not "fit into a preexistent niche" as the niches of a species come to exist through interactions between organisms and their environments. It is conceptually impossible, then, for a niche to preexist and select organisms. The empirical problem is that niches are not "given by the autonomous forces of the environment" as they are instead determined by the biology of the organism. Organisms create niches by determining what's relevant, by altering properties of the world, by transducing external signals (into different types of signals), or by transforming environmental patterns (Levins and Lewontin 1985, 98–106; Lewontin 2000, 55–68). The properties of environments emerge from interactions with organisms.

The inter-relation between organism and environment is dynamic and dialectical. Lewontin asks us to consider the way plant engineers attempt to improve crop yield by designing (through artificial selection or genetic engineering) leaf phenotypes optimized to a measured microenvironment, for example, the temperature, light exposure, humidity, and oxygen and carbon dioxide concentration around the plant. The problem is that the newly selected leaf morphologies tend to alter the humidity, light, carbon dioxide, and other distribution and create a different, less optimal microenvironment. The plant engineers can intervene again, but only to have the plants change the environment once more. "The plant engineers are chasing not only a moving target but a target whose motion is impelled by their own activities," states Lewontin. "This process is a model for a more realistic understanding of evolution by natural selection" (Lewontin 2001, 57). In the wild, plants are constantly changing the environments as they develop and evolve in response to them, which in turn results in further change to their environments. The properties of organism and environment that emerge through their interactions can propel their future change.

Mediational Niche Construction

Lewontin's examples of niche construction fall under two main categories: physical and experiential niche construction.

Physical Niche Construction (also known as perturbational niche construction or habitat construction) is the causal manipulation of the external world by the organism, changing the environment's intrinsic properties.

Experiential Niche Construction is changes in the environment experienced by the organism without changes to the intrinsic properties of the external world.

There are two types of experiential niche construction:

Relocational Niche Construction (also habitat choice) determines which intrinsic properties of the external world surround an individual.

Mediational Niche Construction determines the relevance, impact, and significance of the external world for the organism. It determines *how* the intrinsic properties of the environment is experienced by the organism.

What I coin "mediational niche construction" is currently an underexplored category.[2] The core question of this paper is whether *mediational* niche construction is a type of niche construction, and if so, whether it has evolutionary significance *qua* niche construction.

Even though relocational and mediational niche construction are both cases of experiential niche construction (they do not change the intrinsic properties of the environment), I single out mediational niche construction as the central concern. Relocational and physical niche construction both determine *which* intrinsic properties surround an organism (the first by choosing an environment, the second by altering an environment). However, mediational niche construction does not alter nor determine which intrinsic properties are around an organism. Instead, it changes the way an organism *experiences* them.[3] Is this niche construction?

Lewontin raises several examples of mediational niche construction. One example is the transduction of temperature into the biochemical signals of organisms such that a one-degree drop in the outside world is experienced as a smaller difference for one organism but a greater difference for another. Another example is the way an organism perceives its environment as resource rich or poor. The perceived scarcity of an environment is relative to the organism's level of fat storage. Yet another example is when the physiology of an organism incorporates rates of change of environmental factors into its experienced environment, thus perceiving and reacting to sudden changes instead of absolute levels.

Mediational niche construction occurs because the organism stands between itself and the world. Through this type of niche construction, states Lewontin, "the common external phenomena of the physical and biotic world pass through a transforming filter created by the peculiar biology of each species, and it is the output of this transformation that reaches the organism and is relevant to it" (Lewontin 2000, 64). It is as if the organism is residing inside a Plato's cave of its own making, "determined by the shadows on the wall, passed through a transforming medium of its own creation" (Lewontin 2000, 64). An organism in its self-created "bubble" is still affected by the physical world, but the effects of the world are distorted and transformed by organismal activities and physiology.

Mediational niche construction was dismissed by philosophers (Godfrey-Smith 1996, 2001) and left out by proponents of NCT (Odling-Smee, Laland, and Feldman 1996; Odling-Smee et al. 2003). In the following, I consider Godfrey-Smith's objections and argue that new developments on mediational niche construction (Sultan 2015; Walsh 2015) can address his concerns.

Godfrey-Smith against Mediational Niche Construction

It is not obvious that mediational niche construction is a type of niche construction. How can *internal* changes within an organism count as changes to the *environment*? Internal changes are usually considered phenotypes under selection, not determinates of selective pressures. That is why some argue that relocational niche construction is actually a phenotype for habitat choice while mediational niche construction is a phenotypic response to environmental pressures (Brandon 1990; Godfrey-Smith 1996, 2001).

Godfrey-Smith suggests that mediational niche construction *as* niche construction might make sense if we adopt one of Lewontin's dialectical principles (found in the conclusion chapter of *The Dialectical Biologist*). Lewontin and colleague Richard Levins have long advocated for a dialectical biology against the "Cartesian" decoupling of causes and effects, parts and wholes, and insides and outsides (Levins and Lewontin 1985; Lewontin and Levins 2007). Organism and environment do not exist independently of each other as causes and effects, they argue, but "interpenetrate," or "commingle." Godfrey-Smith suggests that the dialectical principle that parts do not exist independently of each other can help make a case for mediational niche construction. If we assume that organisms and environments are two parts of a whole and parts do not independently exist, then a change to any part would *logically* (not causally) entail a change in the other parts. The part-whole principle thus explains how an internal change to organisms is a change in their environments.

Applying this dialectical principle to organisms and environments, however, seems to create an undesirable mix of antirealism and intractable holism. The "environment" or "niche" of an organism is not the objectively measurable environment, but something (in part) subjectively constructed by the organism. Furthermore, any change to the organism, the environment, or their relation will count as niche construction, thus trivializing the concept. An all-inclusive notion of niche construction fails to capture the complex and varied relations between organisms and environments that are important for empirical study.

Godfrey-Smith proposes that it is fruitful to just acknowledge physical niche construction as an evolutionarily relevant process and treat mediational niche construction as mere traits undergoing selection. To illustrate, consider two species of bacteria in an environment of toxic molecules. One evolves a different internal physiology such that the chemical is no longer toxic. For instance, the organisms may no longer have the receptors or signaling pathways that react to the chemical in a self-destructive way. The other evolves a mechanism that excretes toxin-degrading enzymes. These are two distinct evolutionary responses to an environmental challenge. The first is a selected internal accommodation to the environment, whereas the second is a selected trait that *also* alters the environment. The second trait changes the environment for future generations to come whereas the descendents of the first are still living with the toxin. Yet for Lewontin, both count as niche construction as the organisms all end up experiencing a nontoxic environment. This coarse-grained dialectical perspective glosses over important differences and outcomes of distinct evolutionary responses.

There are many advantages to a narrower scope of niche construction. First, it gives us a sharper boundary of what counts as niche construction and what does not. Not any change to organism or environment is niche construction. It is clear that the line is drawn at whether organisms alter the intrinsic properties of the external world. Second, we retain a commonsensical notion of the environment as an objective, physical phenomenon instead of constructed experiences. Third, it distinguishes between mere adaptations from those that also alter the external, selective environment.

There is a final reason for discounting mediational niche construction. This phenomenon is not even needed to reject externalism. Godfrey-Smith argues that there are two types of externalist explanations: symmetric and asymmetric. The problem with adaptationist thinking is *asymmetric externalism*, that is, the position that while the environment accounts for organismal evolution, organisms cannot account for changes in the selective environment. Externalism can also be of the symmetric kind, which permits the evolutionary effects of niche construction. As physical niche construction alone rejects asymmetric externalism, leaving out experiential niche construction does not diminish the Lewontinian challenge against what's wrong with externalist thinking.

In sum, contrary to Lewontin's call to replace adaptation with construction, Godfrey-Smith insists that there is a complementary coexistence between the two. "Rather than a replacement, there should be a supplementation. Both adaptation and construction are real relationships that organisms have, in particular instances, to environmental conditions" (Godfrey-Smith 2001, 263). Physical niche construction provides "constructivist" explanations that explain the intrinsic properties of the environment by properties of organisms, whereas natural selection supplies "externalist" explanations that explain the properties of organisms in terms of the intrinsic properties of the environment. Together, they give a fuller picture of how evolution works.

3. New Support for Mediational Niche Construction

Godfrey-Smith's major concern was that mediational niche construction implies holistic intangibility and antirealism about the environment. I argue that recent developments, in particular Denis Walsh's affordance theory of niches and Sonia Sultan's mechanistic account of plastic cue and response systems, provide rich and testable characterizations of mediational niche construction that address each of the challenges. They offer clear-cut distinctions between the various ways affordances or experienced environments can change and explain why experienced environments *are* constructed environments.

Walsh's Affordance Framework

Philosopher Denis Walsh (2012, 2014, 2015) argues that adaptive traits are not evolutionary responses to the external world per se, but responses to opportunities in the environment that appear to the organism *as* opportunities for action. Organisms, as purposeful agents, perceive and respond to opportunities that appear because of what the organism can do and what it aims to do.[4]

An example from Walsh can help clarify how opportunities depend on the goals and capacities of organisms. A stick does not become a tool just because sticks can solve a problem and there are sticks lying around. The problem-solving agent needs to have the capacity to perceive the stick *as* a usable tool that can potentially solve a problem, that is, to experience it as affording a particular type of action that can fulfill a goal. For a hominoid, opposable thumbs and "precision grip" are necessary for the manipulation of handheld tools such as sticks. Without these hand structures, objects in the environment would not seem "grip-able" or "grasp-able" for use. Yet the appearance of precision grip is possibly not the result of direct selection for tool use, and an evolutionary byproduct of bipedalism. The structural changes in feet that enabled hominoids to stand up and run also altered the structures of hands (Rolian, Lieberman, and Hallgrìmsson 2010). These new hand structures opened new possibilities: objects previously inconceivable as graspable are now within "reach." The evolution of precision-grip is a nice example whereby organisms "can make a change in its own form, without affecting the environment, which in turn alters the affordances provided to the organism" (Walsh 2015, 181–182).

According to Walsh, environmental opportunities are *affordances*[5] that appear only when there is a purposeful agent. An affordance exists when the environment is experienced by the agent as having the sorts of properties that can either enable or disrupt it from achieving its goals. An agent responds to these affordances by interacting with them in ways that help attain its goals, either through the exploitation of facilitators or the elimination of obstructions. Affordances are emergent properties of a purposeful agent and its environment. Agents and environment both constitute[6] an agent's affordances, that is, their properties and relations underlie what an environment can afford to an agent.

Walsh thus presents an alternative version of adaptive evolution whereby organisms adapt to affordances: "adaptation is not the process in which the external environment moulds passive form. Rather it is the process by which organisms respond to, and in the process create, their own system of affordances" (Walsh 2015, 164). He proposes a "situated adaptationism" of organisms adapting to affordances. In contrast to a standard evolutionary theory that treats the environment supplying a fixed adaptive landscape that populations climb as they evolve, Walsh proposes a dynamic "affordance landscape" that changes its shape as organisms move across it. A stick that can't be gripped might be an obstacle, but once an organism is able to grip sticks they become tools. The internal change of an organism thus constructed a new environment filled with tools instead of obstacles even though the intrinsic nature of the environment remained unaltered.

Sultan's Cue and Response System

While Walsh provides a conceptual framework for niches as constructed experiences, biologist Sonia Sultan offers an underlying mechanistic framework. Sultan (2015) coined the term "experiential niche construction" and has documented a rich and diverse set of examples from the microbial world to animals and plants. When organisms change, their experience of the environment changes even though the external world remains the same. Some of these changes are achieved by moving around, for instance, to spots where resources are more densely packed (i.e., relocational niche construction). Others are achieved merely by altering how the organism mediates environmental stimuli and signals (i.e., what I refer to as "mediational niche construction").

Cases of experiential niche construction include the construction of perceived resource environments, predator environments, competition environments, and temperature environments. For instance, a resource can be experienced as more or less plentiful depending on the organism's behavior or sensory faculties. The morphology of leaves can alter the perceived density of a plant's photon environment. Root spread and morphology can determine the experienced humidity of the soil.

Phenotypic plasticity, a property of organisms, is a key mechanism of experiential niche construction. Organisms are plastic when they can develop different phenotypes in different environments.[7] More specifically, organisms are *passively* plastic when it is an inevitable result that different conditions (e.g., more nutrition) contribute to different phenotypes (e.g., taller or larger body size). They are *actively* plastic when they have specific mechanisms that allow them to switch to different, and typically adaptive, phenotypes depending on how they receive and process environmental signals. These mechanistic pathways of phenotypic plasticity constitute "cue and response systems," that is, systems that enable the organism to developmentally, physiologically, or behaviorally adjust to perceived environmental information (i.e., cues).

The experienced environment is a combination of "cues" and responses to these cues. What becomes a cue depends on the sensory system and the way the organism conducts its behavior to choose and sample environmental bits and pieces. In these ways, "usable cues are specifically 'constructed' by each organism from the myriad variables in its habitat" (Sultan 2015, 52). Organisms can also sense environmental cues directly from the environment or from themselves (e.g., the chemistry of the tissue, the growth rate of the body, the levels of various internal activities), which often involves feedback loops that further remove the cue from the environmental source. A cue could furthermore be an anticipatory mark of a future condition that has yet to exist, and thus the reaction has little to do with the immediate properties of the current environment. The transduction pathways that lead to responses are also mediated by the organism. Environmental signals are transduced into chemical and cellular interactions. They are mediated by the organism's physiology and behavior at the cellular, tissue, and organ levels, triggering downstream effects that regulate gene expressions or determine physiological responses or social behaviors.

In sum, adaptive interpretations need to distinguish "between traits that comprise functionally adaptive responses to a given environmental challenge and those that instead remediate that challenge" (Sultan 2015, 165). The latter is the effect of experiential niche construction. Experiential niche construction occurs when there are changes in the cues or responses. Cue and response systems "mediate the organism's experience of its external environment. In this sense, plasticity (i.e., aspects of trait expression that change from one environment to another) can be seen as a mode of niche construction that allows the organism to *experience* a different and often more favorable physical and biotic environment, even without altering external conditions as such" (Sultan 2015, 71, original italics).

A New Case for Mediational Niche Construction

These new conceptual and mechanistic developments of mediational niche construction do not suffer from Godfrey-Smith's objections. Godfrey-Smith reconstructed and then rejected Lewontin's argument based on a dialectical principle about parts and wholes. Yet the part-whole principle is not the best dialectical rule to appeal to. Lewontin did not use it to support his claims but instead referred to the separation of causes and effects in his section about niche construction. To Lewontin, the problem with externalism is not that it prohibits organismal sources of environmental change (asymmetric externalism), but that environments are used to explain evolution. Niche construction is supposed to show that environments cannot be prior, explanatory causes of organismal change, not that organisms and environments are both parts of some larger whole.

Walsh and Sultan have each developed a framework that explains why environments cannot be the type of prior causes assumed in externalist thinking. Walsh argued that organisms adapt and respond to organism-mediated affordances. Sultan argued that organisms oftentimes respond to organism-mediated cues through organism-mediated signaling. The external environment underdetermines what would count as an organismal response. Therefore, external environments oftentimes do not serve as a major cause of organismal evolution. Evolution by natural selection is not always a process that adapts organisms *to* environments.

Godfrey-Smith objected that mediational niche construction suffers from holism. This is not the case for Walsh's and Sultan's views. They both clearly dissect the various components of the commingled organism and environment. To Walsh, the organism–environment pair consists of the agent's goals and capacities, the external environment, and the affordances that emerge from the former two. To Sultan, the organism–environment pair consists of the external environment and the organism-mediated cues, transduction pathways, and response. Changes to each component makes different predictions about future evolution. Therefore, it is not the case that any change to any part of the organism–environment system are glossed over as the same type of change.

Finally, Godfrey-Smith worries that mediational niche construction implies an antirealistic position on an organism's "niche" or environment. To Walsh, affordances are not subjective constructs but emergent properties of the organism and its environment. To Sultan, the mechanistic involvement of each aspect of the cue and response system dispels any worries that the experiences of organisms are not objectively measurable properties. The experiential properties of "threatening," "resource-poor," "warm," and so on, that can change when the cue and response system changes are operational because they are features of cues and signals that determine how an organism will react.

There is one more obstacle to overcome. Godfrey-Smith argues that mediational niche construction is just a trait while physical niche construction can also be a cause of natural selection. How can experiential niche construction be a cause of natural selection when there are no changes made to the external environment?

Stotz (2017) argues that *developmental* niche construction should not be conflated with *selective* niche construction. The former occurs when organisms construct their developmental niches, which is "a multi-dimensional space of environmentally induced and developmentally regulated, heritable resources that scaffold development" (Stotz 2017, 2). Developmental niche construction creates new variants. The latter occurs when organisms construct their selective niche, which "is defined by the parameters that determine the relative fitness of competing types in a population" (Stotz 2017, 3). Selective niche construction alters the sources of natural selection.

The types of phenomena described by Sultan and Walsh might seem like developmental niche construction. For instance, one of Sultan's examples is the water flea (*Daphnia sp.*) that plastically morphs into a "defensive" phenotype when exposed to predator cues. This is a classic case instance of a cue-and-response system in action. However, Stotz argues that while the cue is part of the developmental niche, it is not part of the selective niche. Only the predator, characterized by the intrinsic properties of the external world, is part of the selective niche.[8] Contrary to Sultan, cues are not part of the experienced, selective environment.

In response, I argue that a distinction should be made between the causes that make a difference between phenotypic variants (for instance, the causes of developmental niches) and the causes that make a difference to the fitness variables of preexisting variants. The fitness of a trait is context dependent. Cumbersome long claws are fitter when a nutrition source is hidden deep inside a trunk, but they become less fit when the food (e.g., worms) now tends to stay at the surface. A variant can thus have a different fitness value because its context has changed, even though the variant itself is the same. A behavior that alters the context of fitness is selective niche construction because it changes a component of natural selection—differential fitness.

Sultan and Walsh are concerned with cases where the organism constructs its fitness context. For instance, when water fleas are exposed to predator cues, their offspring tend to adopt the acquired "defensive" phenotype even though there are no predators nor cues in the offspring environment. Sultan considers this a case of experiential niche construction, where the parent creates a *less threatening environment* due to the transmission of defensive phenotypes. *If* predators were to appear (suppose the probability of predator encounter is unchanged), the offspring are less vulnerable to their attack (if there is any attack at all, as the predators may be deterred by the defense). While Stotz argues that this is an even stronger mismatch between a developmental response and the selective environment, to Sultan, the developmental response creates a differently experienced environment and thus a different selective environment.

4. Commingling and Decoupling Strategies

In this section, I argue that niche construction theories can differ in their conceptual models about the relation between niche construction and natural selection processes. I will present a heuristic framework that recommends either “decoupling” or “commingling” explanatory strategies depending on the conceptual model. Under this framework, I make a new case for the evolutionary significance of mediational niche construction, one that complements the proposals from Walsh and Sultan.

Niche Construction Theory and Decoupling

Consider the causal commitments of Niche Construction Theory (NCT). NCT is a concrete elaboration of Lewontin’s vision that organisms have an active agency in their own evolution (Day, Laland, and Odling-Smee 2003; Laland 2015; Laland and Sterelny 2006; Odling-Smee 1988; Odling-Smee et al. 1996, 2003). Niche construction, according to NCT, is defined as

> the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other’s niches. Niche construction may result in changes in one or more natural selection pressures in the external environments of populations. (Odling-Smee et al. 2003, 419)

According to proponents of NCT, organisms construct their niches either by changing the properties of the environment surrounding them (perturbation niche construction, or physical niche construction) or by moving to environments with different intrinsic properties (relocation niche construction, the first type of experiential niche construction).

Evolutionary theory is meant to explain the extraordinary match between organism and environment. NCT[9] models niche construction and natural selection as distinct evolutionary processes that can shape this match. These causal processes point in opposite directions: niche construction is a causal process from organism to environment, whereas natural selection points from environment to organism. Separately, niche construction and natural selection can each adjust the complementarity between organisms and environment: one by changing the organisms (natural selection), the other by changing the environment (niche construction). Jointly, niche construction can either reinforce or alter the direction of natural selection through changes to the external environment.

Organisms are not just evolutionary products but also causes of their evolution. A co-evolution between organism and environment is driven by their reciprocal causation (Laland et al. 2012; Laland et al. 2011). When organisms change the environment, the altered environment can be experienced by future generations as an ecological inheritance, either because offspring tend to construct similar environments or inherit a changed environment.

NCT supporters take for granted the assumption that natural selection is a process that adapts organisms to environments.[10] The theory concerns the way intrinsic properties of

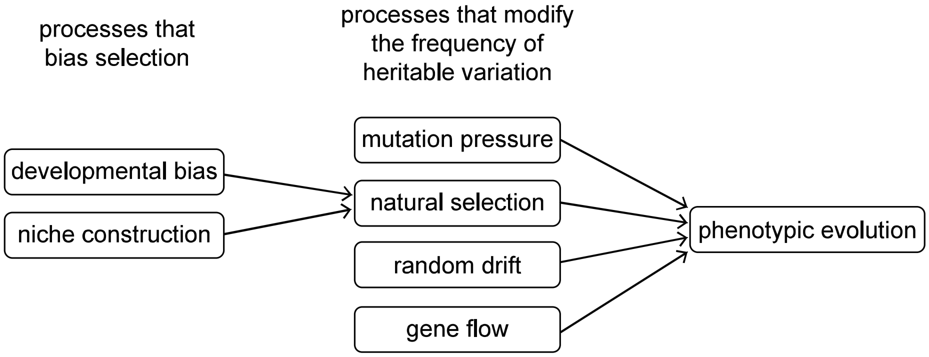

Figure 14.1
Relation between developmental bias, niche construction, and natural selection recreated from Laland et al. (2015).

the environment are manipulated or chosen by organisms, such that niche construction can impose direction and order on these selective pressures.

To further illustrate the NCT conceptual model of niche construction and natural selection, consider the way Laland and colleagues take niche construction and developmental bias as evolutionary processes that bias natural selection (Laland 2015; Laland et al. 2015) (figure 14.1).

Tthe relation between developmental bias and natural selection is usually framed as an *internal versus external* tug-o-war between the relative strength of internalist (developmental bias) and externalist (natural selection) processes in the evolutionary origin of adaptive traits (Amundson 2005; Sansom 2009). Some argue that internal processes constrain the production of possible variants, thus impeding the capacity of selection to build new traits (Gould and Lewontin, 1979). Others argue that internal processes generate novel and adaptive variants, thus rivaling the creativity of selection (Gerhart and Kirschner 2007; Müller and Newman 2003; Walsh 2007). The NCT frames the relation between niche construction and natural selection in a similar way. Proponents argue that niche construction can act against or amplify natural selection. By itself, niche construction can also rival the ability of natural selection to create complementarity between organism and environment.

The conceptual model underlying NCT lines up nicely with Godfrey-Smith's position about the relation between niche construction and natural selection. Both focus on the types of niche construction that pertain to the *intrinsic* properties of their environments, and both endorse an externalist interpretation of natural selection as environmental selection. Even though NCT does not explicitly endorse nor reject mediational niche construction,[11] whereas Godfrey-Smith explicitly dismisses it, both approaches share a similar causal schema of evolutionary causes and processes: organism and environment

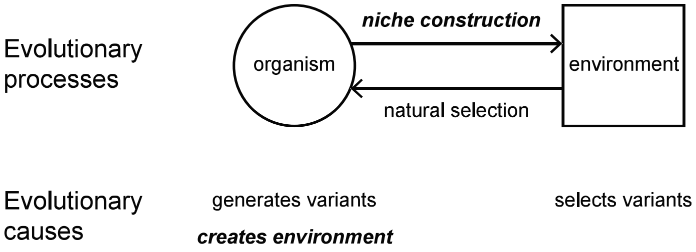

Figure 14.2
Causal Schema of Godfrey-Smith and NCT

are decoupled as cause and effect; niche construction and natural selection are decoupled as distinct causal processes (figure 14.2).

Lewontin and Commingling

In contrast, in a new introduction for his 1983 paper on organisms and environments, Lewontin (2001) proposed a different type of conceptual relation between niche construction and natural selection. He argued that a consequence of niche construction is that *different* types of organisms within the same population will determine *different* types of environments. When organisms have different niches, the selective environment of the entire population is dependent on the specific mixture of constructed environments by actual niche constructing phenotypes. Therefore, as the population evolves, the causes of natural selection simultaneously change.

To Lewontin, when there is intra-population variation in niche construction, natural selection operates in a frequency-dependent-like[12] manner: “the fitness of a genotype is dependent upon the mixture of other genotypes in the population.… It is hopeless to measure the net fitnesses of many genotypes in an immense array of different frequency combinations” (Lewontin 2001, 57). As a consequence, “realistically, selection coefficients are frequency-dependent, and theoretical modeling of the effect of natural selection must use frequency-dependent formulations.” In contrast, the standard model of evolution “assumes constant fitnesses or, at the most, fitnesses that vary with some autonomous extrinsic force or stochastically” (Lewontin 2001, 57).

Lewontin’s conceptual breakthrough is that natural selection *by nature* should be conceptually understood as a type of evolutionary process whereby the fitness differences of phenotypes are in part the result of variation in constructed environments. The central takeaway is that *variation* in niche construction matters for the nature of natural selection. The implications challenge many philosophical characterizations of natural selection, such as the Principle of Natural Selection defended by Brandon (1990). Brandon argues that the selective environment presents a common background condition that supports but does not make a causal difference to variation in fitness. Natural selection occurs only if fitness differences between organismal types are completely accounted for by differences between their internal, intrinsic properties. However, when organisms vary in their constructed niches, differences in fitness are accounted for by both variation in organisms and variation in their constructed niches as well as the interaction between the two.

Intra-population variation in niche construction and plastic response to varying niches have been shown to have many consequences for evolutionary parameters (Saltz and Nuzhdin 2014). An example is social niche construction, where individuals of the same population create different types of social subgroups. Saltz and Foley (2011) studied the role aggressive behaviors play in constructing social groups of fruit flies, and the consequences of these social groups for fitness. Highly aggressive genotypes tend to displace other males, forming a smaller social group with fewer males. The other social groups come to consist of a larger number of less aggressive males. Interestingly, males with genotypes that have higher mating rates after winning a fight thrive only when they are part of the first type of group. The males with genotypes whereby winning or losing does not make a difference thrive when they are in the second type of group. When males of each genotype find themselves in the other group, however, they have lower fitness. The fitness of these fight-related genes are thus dependent on the social context, which in turn are environments constructed by the ration of aggression-related traits. The fight-related genes are not selected against a uniform environment but are against a mixture of environments that depend on the specific composition of the population.[13]

In sum, the conceptual model underlying Lewontin's theory of niche construction does not treat niche construction and natural selection as distinct, decoupled processes. Niche construction is not a prior cause that can incur changes to the environmental causes of natural selection. Instead, variation in niche construction is part of the conditions of natural selection. Niche construction and natural selection are *commingled processes.*

Odling-Smee, Decoupling, and Commingling

Even though NCT assumes the decoupling of niche construction and natural selection, the first model of NCT is compatible with both decoupled and commingled relations between the two processes.

In 1988, John Odling-Smee presented the first model for NCT. His quest was to find a way to measure evolution of the environment so that he could track the co-evolution between organism and environment. The Modern Synthesis does not provide such a measure for two reasons: it defines evolution (of organisms) in terms of gene frequencies, and it uses the environment as a "reference device." A reference device is "the final source of the theory's explanations." When the reference device is the external environment, the environment is the foundational explanation that explains all evolutionary change, including organism–environment co-evolution. In a sense, by explaining co-evolution in terms of the environment (e.g., organisms are selected to respond to and change the environment in a certain way), "co"-evolution is explained away.

Odling-Smee proposed a new reference device to handle the currency of co-evolutionary change—the organism–environment relationship (O_iE_i) or (OE). Co-evolution and evolution of the organism or the environment, respectively, are explained in terms of changes in the (OE) relation. E_i (individual level) or E (population level) is the part of the environment that is relevant to organism perception and action.[14] In Odling-Smee's setup, organisms are purposive agents with the aim to persist and reproduce. They have predictive and decision-making capacities to decide whether to act on themselves, the environments, or on the relation between organisms and environments. The environments, on the other hand, do not have agency, but they can passively change themselves, the organisms, or the relation between organisms and environments. The passive and active actions of organisms and environments are framed in terms of how they contribute to changes in two features of (OE): organism–environment adaptedness and spatio-temporal properties.

Odling-Smee's model is compatible with both decoupling and commingling situations. He identifies the strong causal influence of environments on organisms via changes in (OE)s as natural selection. The strong causal influence of organisms on environments via changes in (OE)s is instead niche construction. The co-evolution between organisms and environments can occur when there is strong bi-directional interaction between natural selection and niche construction via changes to (OE)s. These types of interactions became the sole focus of NCT in later publications with Kevin Laland, Marcus Feldman, and others. A decoupling strategy is appropriate in this case, as the focus is on the reciprocal feedback between the intrinsic properties of organisms and environments.

Odling-Smee's framework also includes the many other types of changes to organisms, environments, and organism–environment relations as a result of changes in (OE). Since Odling-Smee considers (OE) at multiple hierarchical levels from the individual (O_iE_i) to the populational (OE), *prima facie*, a distribution of changes to both Os and Es can create commingling conditions. When some of these varying organism–environment relations determine differences in fitness, then a commingling strategy is more suitable and natural selection is not environmental selection.

The Decoupling/Commingling Framework

To Lewontin, organism and environment do not exist without each other. They "interpenetrate," to use Lewontin's terminology, or in this chapter, "commingle." Instead of treating these relations as ontological properties, I interpret "decouple" and "commingle" as evolutionary scenarios and explanatory strategies. A *decoupling strategy* treats the intrinsic properties of organisms and environments as distinct explanatory entities. It is suitable only if local environments can be reified into a single, causally effective entity that explains organismal evolution, *a decoupled evolutionary scenario*. Natural selection is then an externally driven process that alters organisms. *Commingling strategies* are instead called for when the causes of natural selection are distributed across varying organisms

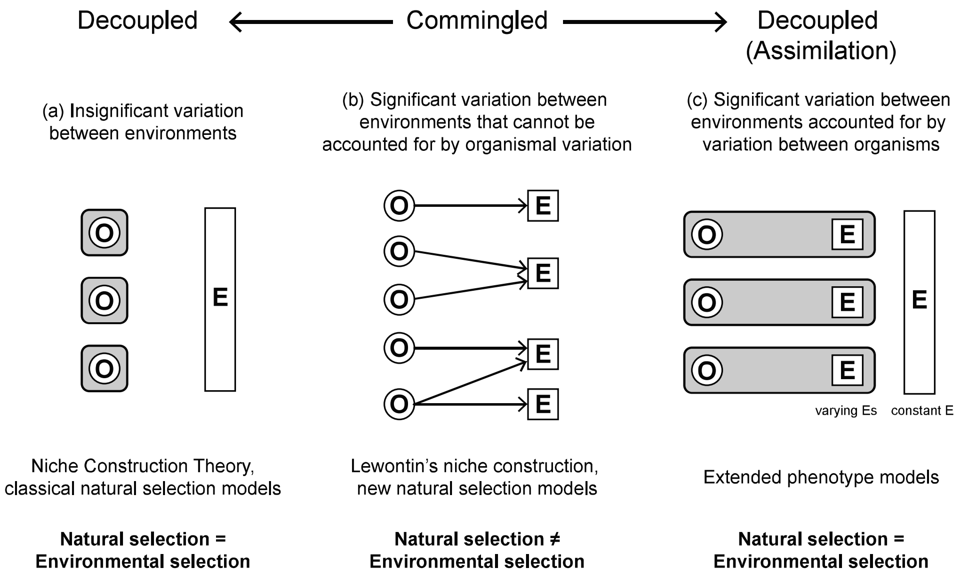

Figure 14.3
The Decoupling/Commingling Framework

and their varying environments, a *commingled evolutionary scenario*. In these cases, the environment cannot be reified into a single explanatory entity. When organisms and environments are commingled, natural selection is not environmental selection (see figure 14.1).

An external environment is a selective environment, that is, the causal source of natural selection, when it is possible to reify a single environment from the local environments different organisms. Emphasis on the intrinsic properties of the world around an organism promotes the reification of the external environment as the selective environment. Physical niche construction and relocational niche construction both determine the intrinsic properties of the external world surrounding an organism or a population of organisms. When the population constructs an environment that is experienced in roughly the same way[15] by all its members, slight variation in local environments is not significant for evolutionary change (figure 14.3a). The selective environment can thus be abstracted into a single causal entity that interacts with the population.

Another way organisms and environments can be "decoupled" is when each type of organism constructs a unique environment that is only experienced by its own type, this is when environmental differences can be entirely accounted for by variation between organismal types (figure 14.3c, "assimilated" into the population). In this, niche construction is an extended phenotype that is subject to natural selection by a wider environmental context. The organisms are not decoupled from their constructed environments, but they are decoupled from the wider selective environment they're embedded in.

However, niche construction can also lead to complex variations in the experienced environments of organisms, preventing the abstraction of local environments into a single, common environment. When variation in constructed environments is significant yet not fully accounted for by differences between individuals (figure 14.3b), the external environment, as a whole, does not have a single explanatory role in natural selection explanations. Instead, the causes of selection are no longer just in the external environment. They are distributed across organisms and environments. When the causes of natural selection are distributed across organism–environment relations, organism and environment are said to be "commingled." In these cases, the difference-makers of fitness are not just the varying organisms but the variation between constructed environments as well. Since the causes of selection are not in the external environment, a "decoupling" heuristic does not capture the causes of selection in these situations. Under a "commingling" scenario, natural selection is the type of process sensitive to the evolving frequencies of constructed environments.

A Different Case for Mediational Niche Construction

Mediational niche construction makes a stronger case for commingling strategies. When organisms vary in mediational niche construction, organism and environment are commingled, yet the commingling conditions of variation between constructed niches are more difficult to cancel out. Contrast the situation with physical niche construction, which can also result in variation in constructed environments. When organisms alter the intrinsic properties of their external world, those properties are *intrinsic* to the environment despite having an organismal origin. That means they are separate from the properties of the organisms. So given enough time, organisms can move about and come to experience the environments constructed by others. The selective environment thus becomes insensitive to population composition as the varying phenotypes eventually experience the same constructed environment.

The different environments caused by mediational niche construction, however, are not easily cancelled out. Mediational niche construction does not leave a mark in the world, and thus variation in created environments is not easily accessible by conspecifics. When two individuals experience the significance of the same environment differently, these differences are not canceled out even if they exchange their spatial locations. Variation in experiential niche construction is more likely to be preserved by the idiosyncratic experiences of individuals. Through mediational niche construction, the same physical world can form different experienced environments for different variants and hence different patterns of selection. The greater the variation in constructed environments, the less impact of the physical world *as is* on relative fitness.

The decoupling/commingling framework is a pluralistic approach that allows both strategies to operate. Which one is appropriate depends on the evolutionary scenarios.

When a decoupling strategy is appropriate, natural selection can be treated as environmental selection and niche construction as the causal contributor to the sources of selection. However, when a commingling strategy is applicable, natural selection supervenes on the varying niche constructing activities and outcomes of organisms. Niche construction is constitutive of natural selection. Mediational niche construction can help retain variation in constructed environments, and thus provides the strongest support for commingling strategies.

5. Conclusion

A common criticism against NCT is that it fails to offer anything new (Gupta, Prasad, Dey, Joshi, and Vidya 2017; Scott-Phillips, Laland, Shuker, Dickins, and West 2014). One of the reasons NCT is seen as rehashing old phenomena is its adoption of decoupling strategies. If environmental selection is still an important actor of adaptive evolution, why would adding organisms as a causal source of the selective environment be considered a conceptual breakthrough? Standard evolutionary thinking already recognizes that environments can be caused by prior organismal activities or that organisms can buffer or strengthen selective pressure by changing their environments (Fisher 1930; see for instance, Mayr 1960).

Mediational niche construction and commingling strategies are some of the unique perspectives NCT can bring to evolutionary thinking (see also Laland et al., this volume). The decoupling/commingling framework proposed in this chapter is an attempt to expand the explanatory strategies that can fall under Niche Construction Theory 2.0. Niche Construction Theory (NCT) adopted decoupling strategies due to their focus on the ways organisms determine the intrinsic properties of their surroundings, either by perturbing the environment or relocating to other environments. But NCT can also take on commingling strategies.

By connecting early theories of niche construction with recent developments on mediational niche construction under a heuristic framework, I have shown that the strongest case for commingling strategies comes from a type of niche construction that occurs without any changes in the intrinsic properties of the environment. When a population of organisms *varies* in their experiences of the environment, the same environment has different relevance, impact, and significance to the organisms, thus creating different patterns of selection. In these cases, organism and environment commingle and the causes of selection are distributed across organism–environment relations. Natural selection is not environmental selection.

Despite Lewontin's original arguments for both, mediational niche construction has been largely neglected in debates over NCT. Perhaps the neglect is part of a heuristic "screening off" strategy to enable productive research (Laland et al. 2011), as many neglected scientific theories and concepts are not empirically refuted but set aside due to pragmatic or conceptual limitations. I argued that Lewontin's niche construction as well as the earliest model of NCT (Odling-Smee 1988) already contain the conceptual resources for commingling strategies. Proponents of NCT may find that revisiting neglected aspects of earlier proposals can gain new currency and viability, affording new avenues for future development and renewed defenses. There is a vast and exciting middle ground of commingled natural selection scenarios to explore.

Acknowledgments

I would like to thank Kevin Laland and Tobias Uller for the opportunity to develop this chapter at the EES workshop at the KLI in Klosterneuberg, Austria. Special thanks to André Ariew, Denis Walsh, Sonia Sultan, John Odling-Smee, Kevin Laland, Tobias Uller, and Jean-François Moreau for valuable feedback and comments on the various versions. Previous versions of this work benefited from the audience of ISHPSSB 2013 at Montpellier, the KLI (in particular, the 2013 cohort) in Austria, the 2nd Toronto Annual Roundtable Meeting 2015 (especially Rasmus Grønfeldt Winther), and members of the ERC-IDEM group at Bordeaux (led by Thomas Pradeu). Parts of the chapter have been developed from the second chapter of my PhD dissertation (University of Missouri). Copyeditor Scott Dyson provided an invaluable service during the initial writing stages. Detailed comments from the three reviewers contributed greatly to the final product, especially the last section. Finally, many thanks to Greg Dupuy for final stylistic comments. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme—grant agreement no. 637647—IDEM.

Notes

1. "Niche construction" was coined by Odling-Smee (1988). The majority of theoretical and empirical work on niche construction is currently developed under the banner of "Niche Construction Theory," spearheaded by John Odling-Smee, Kevin Laland, and Marcus Feldman. It includes hundreds of researchers in a wide range of disciplines. For a list of reseachers under NCT, please consult the St. Andrews website: https://synergy.st-andrews.ac.uk/niche/others-working-with-niche-construction/.

2. In the immediate aftermath of the publication of *Niche Construction: A Neglected Evolutionary Process*, much hair has been split over which phenomena should count niche construction, driven by the worry that the concept would be trivialized if defined too broadly (Archetti 2015; see for instance, Dawkins 2004; Griffiths 2005; Laland 2004; Laland, Odling-Smee, and Feldman 2005; Okasha 2005; Sterelny 2005). However, very few analyses cover the full extent of Lewontin's experiential niche construction. Most leave out mediational niche construction.

3. It is important to clarify that even though mediational niche construction involves the physiological faculties of the organism, it is not *developmental* niche construction: the construction of a developmental environment. Following (Stotz, 2017), our concern here is selective niche construction, the construction of the selective environment.

4. The goal-directedness of organisms does not entail high capacities of cognition or consciousness. Organisms can possess basic goals related to survival and reproduction without consciousness, cognition, or self-awareness, and can select from a repertoire of possible actions without conscious deliberation.

5. "Affordance," or "ecological affordance," is a concept developed by ecological psychologist J. J. Gibson. "The affordances of the environment are what it offers the animal, what it provides or furnishes, for good or ill … I mean by it something that refers to both the environment and the animal … It implies the complementarity of the animal and the environment" (Gibson 1986, 127). There are many opposing interpretations of Gibsonian affordances. Walsh's interpretation, an agency account, is that affordances are emergent properties of the organism–environment system.

6. Walsh distinguishes between a causal and a constitutive relation between organisms and environments. Churchill once remarked "we shape our buildings; thereafter they shape us." This type of niche construction is reciprocal causation between organisms and their environments. Marx, on the other hand, stated "the animal is immediately one with its life activity. It does not distinguish itself from it." This second type of niche construction is instead reciprocal constitution.

7. Plasticity also plays a powerful role in determining the evolutionary outcome of physical niche construction. Organisms have "norms of reaction" that represent their phenotypic responses to different environmental conditions. When organisms alter the properties of their external environment, they supply new environmental cues that can trigger different phenotypic responses. Sultan concludes with at least four evolutionary outcomes of plasticity in physical and experiential niche construction: (1) changed trait expressions in subsequent selection, (2) changed selective pressures on the population, (3) intra-population variation in niche construction, with consequences for evolutionary parameters such as heritability, epistasis, and pleiotropy, and (4) selection of traits that favor the constructed environments (see also Donohue 2005; Saltz and Nuzhdin 2014).

8. "… the cue of the developmental niche to induce the predator-protected morph is not the predator itself but chemicals released by the predator. It is, however, not these so-called kairomones, but the predator itself that is the defining parameter of the selective niche" (Stotz 2017, 3).

9. The primary focus of this chapter is NCT as described in Odling-Smee, Laland, and Feldman 1996, 2003; Laland 2015; Laland et al. 2015.

10. From the very beginning, Odling-Smee was skeptical of Lewontin's claim that adaptation metaphors should be replaced with construction metaphors. "Lewontin is overstating the case slightly. The idea that active organisms construct their own environments does not replace the idea of adaptation. It merely proposes that the adaptive fit which organisms regularly express in their environments could be arrived at by a different route from the one described by the Modern Synthesis" (Odling-Smee 1988, 77).

11. Personal communication with Kevin Laland and John Odling-Smee revealed that the decision to leave out mediational niche construction was largely pragmatic. Doing so allowed them to capture the agency of organisms and implement environmental modification in both experimental and theoretical work. Incidentally, Kevin also revealed that they corresponded frequently with Peter Godfrey-Smith and Richard Lewontin while developing NCT. Peter probably played an active role in their decision to remove mediational niche construction from their analyses.

12. To clarify, Lewontin does not mean to state that all cases of natural selection are frequency dependent or that frequency-dependent selection is natural selection. Nor is he saying that some forms of selection are dependent on the frequency of conspecifics or the environment (e.g., prey, predator, resources). Nor is the point of bringing organisms into selection that selection standards are always relative to a population (i.e., soft selection). Many such forms of frequency-dependent natural selection have long been recognized under standard evolutionary theory, and they do not challenge the conceptual structure of evolution. Many thanks to Kevin Laland and Tobias Uller for pushing me to clarify the difference between Lewontin's notion of frequency-dependent-like natural selection and the more familiar types of frequency-dependent selection.

13. In the wild, the scenario is even more complex. There are multiple dynamic and transient social environments within the same population depending on the composition of aggression-related genotypes and their likelihood of meeting each other. Flies are constantly and freely forming or dissolving social groups. The constructed environments are not entirely unique to the genotypes, as different genotypes can share the same social environment. Furthermore, the non-aggression social groups are quite heterogeneous.

14. The environment variable E is defined in terms of the "observational horizon" (the environment the organism can monitor at a particular space and time) and "action horizon" (the environment the organism can influence at a particular space and time) of an organism.

15. Mediational niche construction does not create commingling between organisms and environments just because it distorts environmental signals. Instead, it creates commingling scenarios because of the variation between the ways the same environment is experienced. Distortion itself is not a sufficient reason to adopt a commingling model. When the constructed experiential environments of all individuals in a population "distort" physical properties in the same way (the physical world has the same relevance, impact, and significance to all individuals regardless of phenotype), there is still a one-to-one mapping between the physical world and the constructed environments (figure 14.3c). In these cases, a decoupling strategy is still apt. Relative fitness can be accounted for in terms of varying phenotypes in a physical world, not an experienced environment.

References

Amundson, R. 2005. *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo*. New York: Cambridge University Press.

Archetti, E. 2015. "Three Kinds of Constructionism: The Role of Metaphor in the Debate over Niche Constructionism." *Biological Theory* 10 (2): 103–115. https://doi.org/10.1007/s13752-015-0205-3.

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

Brandon, R. N., and J. Antonovics. 1995. "The Coevolution of Organism and Environment." In *Concepts, Theories, and Rationality in the Biological Sciences*, edited by G. Wolters, J. G. Lennox, and in collaboration with Peter McLaughlin, 211–232. The second Pittsburgh-Konstanz Colloquium in the Philosophy of Science. University of Pittsburgh, October 1–4, 1993. Pittsburgh: University of Pittsburgh Press.

Dawkins, R. 2004. "Extended Phenotype—But Not Too Extended. A Reply to Laland, Turner and Jablonka." *Biology & Philosophy* 19 (3): 377–396. https://doi.org/10.1023/B:BIPH.0000036180.14904.96.

Day, R. L., K. N. Laland, and F. J. Odling-Smee. 2003. "Rethinking Adaptation: The Niche-Construction Perspective." *Perspectives in Biology and Medicine* 46 (1): 80–95.

Donohue, K. 2005. "Niche Construction through Phenological Plasticity: Life History Dynamics and Ecological Consequences." *New Phytologist* 166 (1): 83–92.

Endler, J. A. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Gerhart, J., and M. Kirschner. 2007. "The Theory of Facilitated Variation." *Proceedings of the National Academy of Sciences of the United States of America* 104 (Suppl 1): 8582–8589. https://doi.org/10.1073/pnas.0701035104.

Gibson, J. J. 1986. *The Ecological Approach to Visual Perception*. New York: Taylor & Francis.

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

Godfrey-Smith, P. 2001. "Organism, Environment, and Dialectics. In *Thinking About Evolution: Historical, Philosophical, and Political Perspectives*, edited by R. S. Singh, C. B. Krimbas, D. B. Paul, and J. Beatty, 253–266. New York: Cambridge University Press.

Gould, S. J. 1977. "Eternal Metaphors of Paleontology." In *Patterns of Evolution as Illustrated by the Fossil Record*, edited by A. Hallam, 1–26. Amsterdam: Elsevier.

Gould, S. J. 2002. *The Structure of Evolutionary Theory*. Cambridge, MA: Belknap Press of Harvard University Press.

Gould, S. J., and R. Lewontin. 1979. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205 (1161): 581–598.

Griffiths, P. 2005. "Review of 'Niche Construction.'" *Biology and Philosophy* 20 (1): 11–20.

Gupta, M., N. G. Prasad, S. Dey, A. Joshi, and T. N. C. Vidya. 2017. "Niche Construction in Evolutionary Theory: The Construction of an Academic Niche?" *Journal of Genetics* 96 (3): 491–504.

Laland, K. N. 2004. "Extending the Extended Phenotype." *Biology & Philosophy* 19 (3): 313–325.

Laland, K. N. 2015. "On Evolutionary Causes and Evolutionary Processes." *Behavioural Processes* 117:97–104. https://doi.org/10.1016/j.beproc.2014.05.008.

Laland, K. N., F. J. Odling-Smee, and M. W. Feldman. 2005. “On the Breadth and Significance of Niche Construction: A Reply to Griffiths, Okasha and Sterelny.” *Biology & Philosophy* 20 (1): 37–55. https://doi.org/10.1007/s10539-004-6834-8.

Laland, K. N., F. J. Odling-Smee, W. Hoppitt, and T. Uller. 2012. “More on How and Why: Cause and Effect in Biology Revisited.” *Biology & Philosophy* 28 (5): 719–745. https://doi.org/10.1007/s10539-012-9335-1.

Laland, K. N., and K. Sterelny. 2006. “Seven Reasons (Not) to Neglect Niche Construction.” *Evolution* 60 (9): 1751–1762. https://doi.org/10.1111/j.0014-3820.2006.tb00520.x.

Laland, K. N., K. Sterelny, F. J. Odling-Smee, W. Hoppitt, and T. Uller. 2011. “Cause and Effect in Biology Revisited: Is Mayr’s Proximate-Ultimate Dichotomy Still Useful?” *Science* 334 (6062): 1512–1516. https://doi.org/10.1126/science.1210879.

Laland, K. N., T. Uller, M. W. Feldman, K. Sterelny, G. B. Müller, A. Moczek, J. Odling-Smee, et al. 2015. “The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions.” *Proceedings of the Royal Society B* 282 (1813): 20151019. https://doi.org/10.1098/rspb.2015.1019.

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

Lewontin, R. 1982. “Organism and Environment.” In *Learning, Development and Culture*, edited by H. C. Plotkin, 151–170. Chichester: Wiley.

Lewontin, R. 1983. “The Organism as the Subject and Object of Evolution.” *Scientia* 118:63–82.

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

Lewontin, R. 2001. “Gene, Organism, and Environment: A New Introduction.” In *Cycles of Contingency: Developmental Systems and Evolution*, edited by S. Oyama, P. E. Griffiths, and R. D. Gray, 55–57. Cambridge, MA: MIT Press.

Lewontin, R., and R. Levins. 2007. *Biology under the Influence: Dialectical Essays on Ecology, Agriculture, and Health*. New York: Monthly Review Press.

Mayr, E. 1960. “The Emergence of Evolutionary Novelties.” In *Evolution after Darwin*, Vol. 1, edited by S. Tax. Chicago: University of Chicago Press.

Mayr, E. 1982. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Harvard University Press.

Müller, G. B., and S. A. Newman. 2003. *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*. Cambridge, MA: MIT Press.

Odling-Smee, F. J. 1988. “Niche-constructing Phenotypes.” In *The Role of Behavior in Evolution*, edited by H. C. Plotkin, 73–132. Cambridge, MA: MIT Press.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman, M. W. 1996. “Niche Construction.” *The American Naturalist* 147 (4): 641–648. https://doi.org/10.2307/2463239.

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

Okasha, S. 2005. “On Niche Construction and Extended Evolutionary Theory.” *Biology & Philosophy* 20 (1): 1–10.

Rolian, C., D. E. Lieberman, and B. Hallgrìmsson. 2010. “The Co-Evolution of Hands and Feet.” *Evolution* 64:1558–1568.

Saltz, J. B., and B. R. Foley. 2011. “Natural Genetic Variation in Social Niche Construction: Social Effects of Aggression Drive Disruptive Sexual Selection in Drosophila Melanogaster.” *The American Naturalist* 177 (5): 645–654.

Saltz, J. B., and S. V. Nuzhdin. 2014. “Genetic Variation in Niche Construction: Implications for Development and Evolutionary Genetics.” *Trends in Ecology & Evolution* 29 (1): 8–14.

Sansom, R. 2009. “The Nature of Developmental Constraints and the Difference-Maker Argument for Externalism.” *Biology and Philosophy* 24 (4): 441–459.

Scott-Phillips, T. C., K. N. Laland, D. M. Shuker, T. E. Dickins, and S. A. West. 2014. “The Niche Construction Perspective: A Critical Appraisal.” *Evolution* 68 (5): 1231–1243.

Sterelny, K. 2005. "Made by Each Other: Organisms and Their Environment." *Biology and Philosophy* 20 (1): 21–36.

Sterelny, K., and P. Griffiths. 1999. *Sex and Death: An Introduction to Philosophy of Biology*. Chicago: University of Chicago Press.

Stotz, K. 2017. "Why Developmental Niche Construction Is Not Selective Niche Construction: And Why It Matters." *Interface Focus* 7 (5): 20160157. https://doi.org/10.1098/rsfs.2016.0157.

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

Walsh, D. M. 2007. "Development: Three Grades of Ontogenetic Involvement." In *Philosophy of Biology*, edited by M. Matthen, C. Stephens, P. Thagard, and J. Woods, 179–200. Amsterdam: Elsevier.

Walsh, D. M. 2012. "Situated Adaptationism." In *The Environment: Philosophy, Science, and Ethics*, edited by W. P. Kabasenche, M. O'Rourke, and M. H. Slater, 89–116. Cambridge, MA: MIT Press. Retrieved from http://www.scopus.com/inward/record.url?eid=2-s2.0-84894865948&partnerID=40&md5=56c1db99e4546bf89d52c3f003353aec.

Walsh, D. M. 2014. "The Affordance Landscape: The Spatial Metaphors of Evolution." In *Entangled Life*, edited by G. Barker, E. Desjardins, and T. Pearce, 213–236. Dordrecht: Springer. https://doi.org/10.1007/978-94-007-7067-6_11.

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

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