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Niche Construction and Conceptual Change in Evolutionary Biology

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ABSTRACT

The theoretical status of 'niche construction' in evolution is intensely debated. Here we substantiate the reasons for different interpretations. We consider two concepts of niche construction brought to bear on evolutionary theory; one that emphasizes how niche construction contributes to selection and another that emphasizes how it contributes to development and inheritance. We explain the rationale for claims that selective and developmental niche construction motivate conceptual change in evolutionary biology and the logic of those who reject these claims. Our analysis shows how the contention arises from alternative assumptions regarding the causal independence of the processes that generate variation, differential fitness and inheritance.

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1 Introduction

Biologists differ on what processes they consider fundamental for evolution. Whereas virtually everyone would include natural selection on this list, intense debate surrounds the evolutionary status of the causal effects that organisms have on their environments, known as niche construction (Odling-Smee *et al.* [2003]; Scott-Phillips *et al.* [2014]). Are these effects simply 'add-ons' to evolutionary theory or are there reasons to interpret niche construction in a different light; one that would make it a central preoccupation by evolutionary biologists? Some highly influential biologists (for example, Waddington [1959]; Lewontin [1983]; Odling-Smee *et al.* [2003]) have answered in the affirmative, concluding that niche construction makes the standard representation of phenotypic evolution in terms of genetic mutation, drift, and selection problematic. Nevertheless, niche construction has not entered textbooks on evolution (Laland *et al.* [2015]), and the claim that niche construction has implications for the structure of evolutionary theory has been passionately rejected by members of the same scientific community (for example, Dawkins [2004]; Haig [2007]; Dickins and Rahman [2012]; Scott-Phillips *et al.* [2014]; Wray *et al.* [2014]). As a consequence, parallel literatures have arisen (Matthews *et al.* [2014]) between which communication is limited and sometimes strained.

Our aim in this article is to substantiate the reasons for these differences in interpretation. We begin by introducing two recognized concepts of niche construction that emphasize different components of the evolutionary process. The first, which we will refer to as 'selective niche construction', describes how persistent modification of environments affects the fitness of the constructing agent and its descendants. The second, 'developmental niche construction', describes how niche construction, in the form of non-genetic resources contributed by parents and constructed by the developing individual, enable the generation and maintenance of heritable phenotypic variation. These concepts have been advanced in different fields of biology, but their evolutionary implications are increasingly discussed together (for example, Laland *et al.* [2008], [2015]; Bateson and Gluckman [2011]; Chiu and Gilbert [2015]; Sultan [2015]; Watson *et al.* [2016]; an early synthetic treatment is Waddington [1959]).

The article is structured as follows. We first explain the rationale for claims that selective and developmental niche construction should bring about conceptual change in evolutionary biology, and the reasons why some reject these claims. This reveals that the niche construction concepts are used by advocates to describe biological evolution in ways that make how organisms work explanatorily relevant for how they evolve, whereas interpretation of the same concepts within the standard, genetic, representation of evolution maintains natural selection as the only explanation for the adaptive fit between organism and environment. We then go on to suggest that the two representations of evolving systems reflect underlying assumptions regarding the autonomy of the conditions for natural selection, that is, the processes that produce variation, differential fitness, and inheritance. We conclude by discussing some sources of communication failure surrounding the niche construction literatures, and suggest that these partly reflect that scientists hold different views on how formulation of alternative conceptual frameworks contribute to scientific progress.

2 Selective Niche Construction

The term 'niche construction' was coined by Odling-Smee in his seminal ([1988]).[1] In Odling-Smee's version, which built on work by Waddington ([1959]) and Lewontin ([1983]), niche construction is particularly evolutionarily important when modified environments persist, such that niche constructing activity in generation t causes a selective pressure in some later generation $t+n$. Odling-Smee ([1988]) dubbed this ecological inheritance, and defined it as 'any case in which organisms encounter a modified feature-factor relationship between themselves and their environment [that is, a matching of phenotype and environment] where the change in selective pressure is a consequence of prior niche construction by parents or other ancestral organisms'. This definition remains in later works on niche construction (for example, Odling-Smee *et al.* [2003], p. 42). If we take 'selective pressure' to represent factors external to organisms that affect their fitness, the definition of ecological inheritance does not demand that the modified environment has an effect on phenotype, only that it affect survival or reproduction. For example, by dispersing (a form of niche construction as defined by Odling-Smee *et al.* [2003]), individuals may become exposed to a new predator but not show any phenotypic responses to that predator (that is, the cause of differential survival is not a cause of phenotype).[2]

2.1 Selective niche construction interpreted as a challenge to the received view

Niche construction and ecological inheritance introduce a second causal arrow to the evolutionary dynamics, from the population to their environment

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[1] Odling-Smee *et al.* ([2003], p. 419) define niche construction as 'the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches'. They refer to an 'evolutionary niche' as the sum of all selective pressures acting on a population. In this article we avoid the term 'evolutionary niche' because it may give the impression that only the selective interpretation of niche construction has evolutionary consequences.

[2] Ecological inheritance may of course affect both fitness and parent–offspring resemblance (that is, heredity). This is discussed in more detail later in the article.

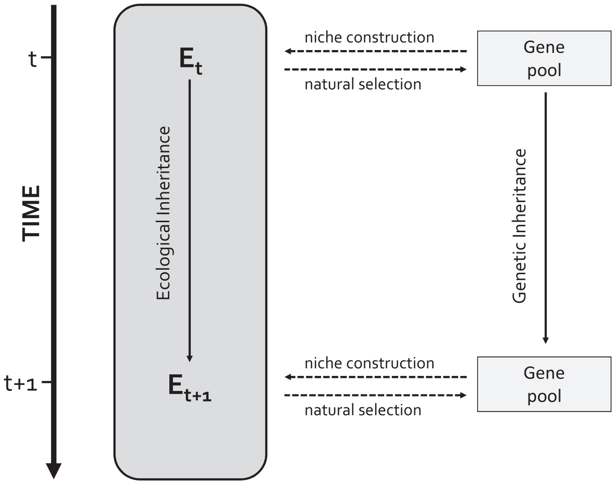

Figure 1. Graphical representation of an evolutionary process involving both natural selection and niche construction. Organism–environment complementarity arises because of reciprocal causation between the processes that make organisms modify their selective environments and natural selection in those environments, whereby individuals with particular phenotypes suited to the constructed conditions leave more descendants. Redrawn from (Odling-Smee *et al.* [2003]).

(Figure 1). Lewontin ([1983]) used two coupled differential equations to make this point: $dO/dt = f(O, E)$ and $dE/dt = g(O, E)$, where O stands for organism and E for environment. The first equation describes evolutionary change in phenotype as a function of the environment and the second change in environment as a function of phenotype. Lewontin's interpretation was demanding for the dominant framework because it described the match between organism and environment as the consequence of two, inter-linked but different, processes; populations adapting phenotypically to their environment through natural selection, and populations adapting the environment to their phenotypes through niche construction (Figure 1). Thus, whereas the explanandum of 'standard evolutionary theory' and niche construction theory is typically the same (for example, the complementarity of organism and environment), they differ in that niche construction theory introduces an additional explanans in the form of features of the environment that are there because of the activities of ancestors.

The diagram in Figure 1 is an important heuristic tool in selective niche construction theory because it illustrates the 'reciprocal causation' (Laland *et al.* [2011]) leading up to the complementarity between organism and its surroundings. To explain any particular fit between organism and environment, we need to work through a sequence of events in which niche construction alternates between cause and effect of evolution. To take a familiar example, consider beavers and their dams. To explain why beavers appear to be so well adapted to permanent bodies of water, we also need to explain the origin of dam building and the persistence of dams and lodges down generations as these rely on the actions of the beavers themselves. Similarly, in humans, the causes of the origin and maintenance of cultural practices will often enter explanations for why humans are well suited to their environments (Laland and O'Brien [2011]). More generally, when environments are constructed, a satisfactory evolutionary explanation for phenotypic divergence, convergence, and adaptation may need to include the causes of (persistent) selection. For selective niche construction advocates, the natural starting point for evolutionary analysis is open; it could be natural selection or it could be niche construction. Furthermore, because natural selection and niche construction have been intertwined throughout the evolutionary history of a species, the directionality imposed by niche construction on the evolutionary process is considered to be not only non-random but perhaps even systematically biased towards producing adaptive effects (Odling-Smee *et al.* [2003]; Laland *et al.* [forthcoming]). Thus, it is not *a priori* obvious if natural selection or niche construction should be assigned a privileged explanatory role in the evolution of the complementary fit between organism and environment.

2.2 Selective niche construction interpreted as compatible with the received view

There are, however, alternative ways to accommodate niche construction and ecological inheritance that do not present any problems for the standard framework. A minimal accommodation of selective feedback through niche construction is to account for the relationship between the population composition at time t and selection on descendant populations at time $t+n$. As Lewontin ([1983], [2001], p. 65) himself noted, this bears similarities to more standard scenarios where fitness depends on the population composition of phenotypes. In coevolution between species, selection on one population is a function of the phenotypes of a different population. In coevolution between the sexes, females generate selection on males and *vice versa*. In frequency-dependent selection, the fitness of an individual depends on the frequency of its own phenotype and the frequencies of other phenotypes. Each form of co-evolution can include biotic or abiotic intermediates, for example, resources needed to maintain high-quality territories.

Modelling how ancestors modify the selective pressures of descendants is possible by adopting a similar logic. An early model by Kevin Laland and colleagues (Laland *et al.* [1996]) treated both the niche constructing and focal phenotypes as genetic characters, that is, two loci, here referred to as E and A, respectively. This makes it possible to model the coevolution of niche constructing and 'recipient' traits by specifying how a resource, R, which causes selection on locus A, is affected by allele frequencies at locus E in past generations. Evolutionary biologists can recognize such models as a form of trait coevolution, but with the unusual feature that traits expressed in ancestors affect selection on contemporary populations. The resulting dynamics reveal non-trivial results with respect to, for example, the time it takes for a population to adapt and the frequency of genotypes and phenotypes at evolutionary equilibrium (Laland *et al.* [1996], [1999]).

There is now a substantial literature using mathematical modelling and experimental methods to understand the evolutionary implications of selective niche construction. Such papers often refer to the feedback between ecological resources and evolving populations as 'eco-evolutionary dynamics' (Pelletier *et al.* [2009]). Although the focus is more on the evolution of species interactions than on the coevolution of organisms and their abiotic environments, the similarities in logic and methodology (for example, use of coupled equations) indicate that the evolutionary ecology community has taken on board the central argument that selective feedback matters.[3] However, in contrast to niche construction advocates, papers on eco-evolutionary dynamics typically do not make claims about conceptual change and, by and large, appear to embrace the gene-centric perspective on evolution. In fact, some major reviews in the field omit any mentioning of the term 'niche construction' and do not cite the literature that use this term (for example, Pelletier *et al.* [2009]; Travis *et al.* [2014]; a notable example of a paper that instead cross-cites extensively is Post and Palkovacs [2009]).

2.3 A fault line in interpretative understanding

That two such different interpretations of the theoretical status of selective niche construction co-exist points towards the existence of a fault line in interpretative understanding. Following Waddington, Lewontin, and Odling-Smee, one interpretation is that at least two processes in evolution, natural selection and niche construction, together produce a systematic bias in favour of adaptation. In contrast, interpretation of selective niche construction within the contemporary genetic theory of evolution keeps natural selection

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[3] In their taxonomy of fields that deal with feedback in ecological and evolutionary systems, Matthews *et al.* ([2014]) restricts the use of 'eco-evolutionary dynamics' to cases involving at least two organisms. Although this means that selective niche construction theory and eco-evolutionary dynamics are not completely overlapping, it does not mean that they occupy different conceptual spaces. For example, the model of Laland *et al.* ([1996]) appears consistent with how a researcher that normally models coevolution between organisms involving abiota (that is, niche construction = eco-evolutionary dynamics in (Matthews *et al.* [2014]) would approach trait coevolution in the case of the beaver (that is, niche construction $\neq$ eco-evolutionary dynamics in (Matthews *et al.* [2014]).

as the only cause of systematic bias in favour of adaptation, and makes the niche construction concept appear superfluous or even misleading.

3 Developmental Niche Construction

The definition of ecological inheritance means that niche construction theorists tend to view effects of the environment on phenotypes as important in evolution insofar as it generates directionality of selective pressures (Odling-Smee [2010]). Yet, another consequence of modification of the environment by ancestors is that it can affect features in the constructor and its descendants, in the case of the latter influencing the parent–offspring resemblance.[4] While the term inheritance is typically restricted to the passing of genes from one generation to the next, some biologists and philosophers have argued for a more inclusive concept of inheritance that includes parental transference of non-genetic developmental resources, including modified features of the environment (for example, Griffiths and Gray [1994]; Oyama [2000a]; Stotz [2010]; Jablonka and Lamb [2014]).

The set of ecological and social circumstances that is inherited from parents is sometimes referred to as the ‘ontogenetic niche or the developmental niche’ (West and King [1987]; Badyaev and Uller [2009]; Griffiths and Stotz [2013]). Developmental niches do not exist ‘out there’ for organisms to fit into, they are (re)constructed each generation as parents transfer a variety of resources and modify the environment of offspring, who accommodate these factors into their own development. For example, mothers determine many features of the environment for their offspring by choosing where and when to nest, and social interactions between parents and offspring after hatching or birth are important for the development of species-typical features as well as for maintaining heritable differences between families (Uller [2012]). Similarly, plants modify the development of their offspring by changing the timing of seed dispersal and features of the seed coat (Donohue [2009]). Offspring are not passive recipients of whatever parents pass on; they actively respond, sometimes resulting in repeated interactions with phenotypic effects in both generations.

3.1 Developmental niche construction interpreted as a challenge to the received view

An inclusive notion of inheritance appears challenging for the received view, which separates the inheritance of features from the development of features.

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[4] As pointed out above, the concept of ecological inheritance as defined by Odling-Smee ([1988]) does not refer to parent–offspring similarity in phenotype (Odling-Smee *et al.* [2003]). However, more recently Odling-Smee and colleagues have been considering ‘niche construction theory (to apply) to development as well as evolution by substituting niche inheritance for genetic inheritance’ (Odling-Smee [2010], p. 181; see also Laland *et al.* [2008]; Flynn *et al.* [2013]).

When heredity is equated with transmission of genes, evolutionary change can be represented as transgenerational change in gene frequency. But if genes are not privileged as causes of heredity, phenotypic evolution may also occur through persistent changes to the developmental niche, that is, through epigenetic, social, and environmental mechanisms. This may raise concerns about the validity, or at least completeness, of evolutionary models whose currency is restricted to one out of possibly many sources of heredity, some of which may qualify formally as inheritance systems (Shea [2011]). Furthermore, a broader notion of inheritance appears to grant the possibility that development can direct evolutionary change through biased acquisition and transmission of features, which makes natural selection but one of several causes of adaptive change.

With an inclusive notion of inheritance, explaining the complementarity between organisms and environment requires us to work through a sequence of events in which developmental niche construction is both a cause and a consequence of evolution (Figure 2). For example, individuals may exploit a new food resource by behavioural innovation (that is, within-generation plasticity). If offspring learn how to forage by observing and imitating parents (that is, a form of non-genetic inheritance), the new behaviour may persist, with more or less fidelity, down generations. If individuals that make use of the new resource have higher fitness, the result of natural selection should be increased canalization of the behaviour's acquisition in ontogeny, and hence a more reliable inheritance (Badyaev and Uller [2009]). Although this process likely would involve genetic changes, gene-frequency change follows the acquisition and inheritance of the novel behaviour, and the latter therefore provide part of the explanation for why the population adapts to the new resource (for example, Baldwin [1896]; review in West-Eberhard [2003]). This is not a hypothetical mechanism for adaptive divergence. For example, cross-fostering of chicks between great tits and blue tits demonstrate that imitation of parents can contribute to reliable inheritance of 'species-typical' foraging behaviours (Slagsvold and Wiebe [2011]).

3.2 Developmental niche construction interpreted as compatible with the received view

Evolutionary biologists are of course aware that parents contribute more than genes to their offspring (and later generations), and they have devised a number of ways to investigate its evolutionary implications. A shared feature of these approaches is that they consider the mechanism, and sometimes the content, of non-genetic inheritance a property of genotypes. For example, using the statistical framework of quantitative genetics, theoreticians have shown that effects of the social environment on phenotype can affect the

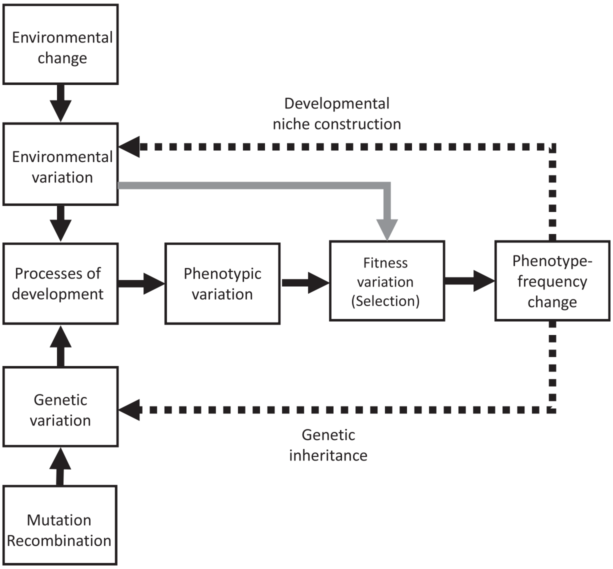

Figure 2. A developmental perspective on the relationships between environment, genes, phenotype, and selection. Both environmental (that is, non-genetic) and genetic variation can initiate phenotypic evolution and developmental niche construction and genetic inheritance together contribute to heredity. Adaptive evolution proceeds through repeated bouts of reciprocal causation between developmental plasticity, processes of inheritance, and natural selection. The grey arrow represents the effects of selective niche construction, discussed in the previous section. Figure modified from (West-Eberhard [2003], p. 142).

rate and direction of evolution (reviewed in Wade [1998]; Hadfield [2012]). These models work by separating genetic and non-genetic causes of parent–offspring resemblance, which makes it possible to derive evolutionary trajectories for populations under particular assumptions about the architecture of genetic and non-genetic effects and the form of selection.[5] Other models have explored the evolution of the developmental niche itself. A large literature on the evolution of parental care (Clutton-Brock [1991]; Royle *et al.* [2012]) has been followed by more recent models that address when non-genetic, for example, epigenetic, transmission is adaptive. By recognizing that several mechanisms can carry information about local conditions, researchers have identified under what conditions inheritance should be context-dependent and what is the optimal fidelity of transmission (for example, Rivoire and

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[5] These models are not restricted to interactions between parents and offspring and belong to a broader category often referred to as 'indirect genetic effects' models (Moore *et al.* [1997]; McAdam *et al.* [2014]).

Leibler [2014]; English *et al.* [2015]; Leimar and Mcnamara [2015]; Uller *et al.* [2015]).

At first sight these models appear at odds with the standard conceptual framework, which equates inheritance with gene transmission. However, interpreting the non-genetic causes of phenotype to be under genetic control makes this body of work compatible with the core features of the genetic representation. For example, in their important paper exploring the evolutionary implications of non-genetic inheritance, Day and Bonduriansky ([2011]) distinguish between genetic inheritance and inheritance of 'the interpretative machinery', suggesting that the authors follow tradition in considering genes to be informationally (and perhaps causally) privileged in development and evolution. Furthermore, models often assign genes 'for' non-genetic mechanisms of inheritance to study how the latter evolve.[6] In this sense, models of (environmentally responsive) non-genetic inheritance can be understood as an extension of standard models of plasticity (where plasticity is conceptualized as a genotype norm of reaction; Pigliucci [2001]), an interpretation that is often explicit in the literature on parental effects (for example, Mousseau and Fox [1998]; Smiseth *et al.* [2008]; Uller [2008]; Kuijper and Hoyle [2015]).

What about cultural evolution? Mechanisms of cultural inheritance are often granted a comparably generous autonomy from genes, such that the content of cultural representations is independent of the underlying genetics. In dual inheritance models, cumulative phenotypic evolution occurs via two transmission channels, one genetic and one cultural, which affect the features of the next generation (Richerson and Boyd [2005]). In contrast to genetic inheritance, the mechanisms of cultural inheritance may not reduce to simple copying but, by specifying rules for cultural transmission, theoreticians can make use of the same mathematical tools as models that rely on genetic inheritance alone (for example, population or quantitative genetics; Cavalli-Sforza and Feldman [1981]; Boyd and Richerson [1985]). Researchers disagree on how autonomous cultural and genetic channels of transmission are and, indeed, the extent to which cultural evolution is Darwinian (for example, Claidière *et al.* [2014]; see Lewens [2015]). The details of this fall beyond the scope of this article, and here it is sufficient to point out that one interpretation of non-genetic, including cultural, mechanisms of inheritance is that the mechanism, even if not the content, is under genetic 'control', which make them candidate adaptations brought about by natural selection (for example, Dawkins [1982]; Dickins and Rahman [2012]). In other words, natural

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[6] In this the logic of models of the evolution of non-genetic inheritance (for example, Leimar and Mcnamara [2015]; English *et al.* [2015]) is similar to how population genetic models of selective niche construction assigns genes for the niche constructing and recipient traits (for example, Laland *et al.* [1996]).

selection can produce new channels of transmission of information (Jablonka and Szathmáry [1995]; Maynard-Smith and Szathmáry [1995]). But on the standard interpretation, this does not violate the role of natural selection on genetic variation as the only (ultimate) explanation for adaptation as long as there is an evolutionary story in which the new channel's ability to transmit adaptively relevant information is the result of inclusive fitness benefits conferred in the past (for example, Scott-Phillips *et al.* [2011]).

3.3 A fault line in interpretative understanding

Similarly to the situation for selective niche construction, there appears to be a fault line in interpretative understanding of developmental niche construction. Under one interpretation developmental niche construction is argued to motivate conceptual change in evolutionary biology, by broadening the concept of inheritance and enable development to produce a systematic bias on evolution in favour of adaptation. Yet, interpreted within the received view developmental niche construction keeps the structure of evolutionary theory intact, with inheritance remaining a matter of transmission through discrete channels and natural selection (on genes or other stably transmitted entities) ultimately responsible for adaptation.

4 Understanding the Fault Line

Since Waddington, Lewontin, and Odling-Smee initially emphasized the importance of selective feedback it has arguably become a mainstream part of evolutionary biology.[7] A similar case could be made for developmental niche construction, as it is captured in models of parental effects, epigenetic inheritance, and so on. Nevertheless, the debate regarding the evolutionary implications of selective and developmental niche construction has not subsided. (For a recent exchange regarding the selective interpretation, see (Scott-Phillips *et al.* [2014]), and for the developmental interpretation, see (Dickins and Rahman [2012]) and the response by Mesoudi *et al.* ([2013]); see also (Laland *et al.* [2014]; Wray *et al.* [2014]).) This suggests that the underlying reasons for the differences in interpretative understanding are not trivial and that they may go unrecognized by many practicing biologists. Here we attempt to shed some light on the nature of the fault line. We show that, contrary to how some, perhaps most, evolutionary biologists interpret the situation (for example, Wray *et al.* [2014]), the disagreement is not primarily

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[7] Those who argue that niche construction should motivate conceptual change are well aware that selective niche construction has been widely studied. For example, Odling-Smee and colleagues mention many different theoretical approaches and devote a substantial part of their book to previous empirical work (Odling-Smee *et al.* [2003]).

due to a perceived lack of attention to niche construction phenomena. Instead, the debate reflects that biologists hold a variety of views on causation in evolving systems.

4.1 Causation in evolving systems

A shared feature of the selective and developmental niche construction literature is that adaptive evolution is described as a reciprocally caused process (Figures 1 and 2). Natural selection and niche construction, the latter through its effects on variation, selection and inheritance, are concurrent processes that share responsibility for the complementary fit between organism and environment. In contrast, in the genetic theory of evolution natural selection alone is responsible for adaptation. This structural feature of evolutionary theory can be maintained even if niche construction is acknowledged as important in evolution. As will be explained below, this is because the consequences of selective and developmental niche construction are interpreted within a conceptual framework where variation, differential reproduction, and inheritance are autonomous processes. This results in a model of causation that makes the directionality imposed on the evolutionary process by niche construction explained in terms of natural selection in the past. Rather than being an evolutionary cause or process, niche construction becomes a subordinate concept in an evolutionary explanation where natural selection on genetically inherited traits retains its privileged role as the only cause of sustained adaptive change. For example, the beaver's impact on its environment, which both maintains the adaptive value of its phenotype and may bias further evolution, is itself an adaptation brought about by selection on genetic variation for dam building and other behavioural characters.

To understand the rationale for these interpretations of selective and developmental niche construction, recall that evolution by natural selection requires the following three conditions: variation in characters among members of a population, that some variants leave a greater number of descendants than others, and that offspring resemble their parents (for example, Lewontin [1970]; Godfrey-Smith [2009]).[8] Such summaries state the necessary conditions for evolution by natural selection. But they do not specify how variation, differential fitness, and heredity are conceptually related; how autonomous the processes that generate them are, for example. Nor do they specify how the processes should be construed.

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[8] Darwin's ([1859], pp. 489–90) own summary reads: 'These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms'.

The Modern Synthesis achieved both of these objectives. Its main heuristic advantage is that it postulates variation, differential fitness, and inheritance as quasi-independent processes (Badyaev [2011]; Walsh [2015]). By quasi-independence we mean that the internal structure or behaviour of a process is unaffected by what it is being fed by other processes. To illustrate, imagine that three people are to paint a house. The first person goes to the store to buy the paint, the second mixes the paint, and the third does the painting. Further imagine that each person receives instructions separately and independently. Although the decisions that go into the buying and mixing of the paint affect the colour of the house, buying and mixing do not influence how the house is painted. The same applies to the three components of adaptive evolution in the Modern Synthesis. Variable rates of survival among individuals with different features determine what features will occur in the next generation. However, selection does not affect the process of inheritance; inheritance is merely the passing on of whatever genes were selected, typically following Mendelian rules. The variation that fuels evolution is similarly autonomous. Mutations occur randomly with respect to their consequences for development and fitness, and the acquisition of new variants does not change how variation is transmitted down generations. Each step determines (partly) the inputs for the next step, but not how those inputs will be processed.

Quasi-independence makes it possible to describe evolution in terms of an ordered set of processes. Individual development produces variation at the population level; differences among variants in survival or reproduction produce selection at the population level; the process of inheritance passes on the means of development, and results in heritability at the population level. Representing evolution as an ordered set of independent processes effectively reduces the role of development since only those developmental causes that survive selection and inheritance become evolutionary causes (Badyaev [2011]; Walsh [2015]). If inheritance is a process separated from development, any organismal features that persist for a sufficient number of generations will become explained in terms of the mechanism of transgenerational transmission (which in the Modern Synthesis was equated with genes). Adding mechanisms by which parents influence the development of their offspring does not change the genetic content that is inherited, it merely changes the environmental context in which those genes will be expressed.

Quasi-independence greatly facilitates building mathematical models of evolution since it can justify avoiding phenotypes altogether. Consider population genetic models of niche construction or eco-evolutionary dynamics. These models include selective feedback but leave quasi-independence intact. The sustained directional effect on evolution comes from a sustained directional effect of niche constructing activities and ecological inheritance. The capacity for niche construction and ecological inheritance are evolved features. But if these are to systematically improve the fit between organism and environment, the genetic representation requires them to be explained in terms of past natural selection on genetic variation. Without an evolutionary explanation based on natural selection of genes, the positive effects of niche construction on adaptation would be fortuitous, and without genetic control of niche construction activities those effects would not be persistent and evolve. Thus, any sustained direction on adaptation to which niche construction contributes is ultimately reduced to natural selection of genetic variation.[9]

Quantitative genetic models of parental effects also retain the quasi-independence assumption. The additive genetic variance transmitted from one generation to the next is not affected by how phenotype was translated into fitness, nor does it affect how the genotype will be translated into phenotype in the next generation (Arnold [1983]). Parental effect models therefore effectively represent non-genetic inheritance as an environment, affected by activities of parents, in which the components of 'hard' inheritance (that is, genes) are expressed. The mechanisms involved in developmental niche construction are evolved features. But if environments are construed by parents to systematically improve performance, or offspring respond appropriately to those environments, this is ultimately to be explained in terms of selection of genetic variation. Consequently, those who grant that 'genes may be followers rather than leaders in adaptive evolution' (West-Eberhard [2003]) may nevertheless ascribe the ability of plasticity to contribute constructively to evolution in terms of past selection of genes (for example, Ghalambor *et al.* [2007]), a view that appears consistent with plasticity being a relatively minor 'add-on' (Wray *et al.* [2014]) to evolutionary theory.

The quasi-independence of phenotypic variation, differential fitness, and inheritance is deeply entrenched in contemporary evolutionary biology. But it is a convenient heuristic and not a logical necessity, and it may or may not accurately capture biological reality. To sketch an alternative account, let us begin with an example that is a paradigm of quasi-independence.

Beach mice are pale mice that live on sand dunes in Florida. Their pale colour is due to a single nucleotide substitution in the melanocortin-1 receptor (Hoekstra *et al.* [2006]). This allele is likely bad for mice in ancestral habitats, which means the allele is usually rare. However, carriers are less visible to predators on sand dunes so that the mutation, and the white mice, have increased in frequency in this habitat.

This evolutionary account bears all the hallmarks of quasi-independence; the mutation was presumably random and it is passively passed on to offspring at reproduction. The offspring reliably develop pale coats when they

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[9] If the effects of niche construction have not been shaped by natural selection they may still bias evolution by limiting adaptation, analogous to how developmental constraints typically are perceived (Maynard-Smith *et al.* [1985]).

receive the mutated allele, and their pale colour is the cause of their high survival relative to dark mice on sandy soils. Nevertheless, we may shift our evolutionary explanandum from the colour of the coat to the complementary fit between the mice's colour and their environment. Whereas quasi-independence applies to the former, it does not obviously do so for the latter. Although it is true that the mice cannot change the colour of their coat, they can change the fitness consequences of their colour by choosing where to live (for example, by dispersing), how to live (for example, by becoming more risk-averse), and how to raise their offspring (for example, by constructing safer nests and raising offspring to become risk-averse too). These characters, which affect the developmental and selective niches of the coat colour phenotype, may be adaptive but they were not originally selected to enable a match between coat colour and environment, which is the explanandum. Furthermore, in contrast to coat colour, these behaviours may not map straightforwardly onto any particular genetic variant. Instead, behavioural types are often constructed in ontogeny through bouts of causal interactions between the environment the individual experiences (for example, predation attempts) and how it responds in terms of changes in physiology, behaviour, and so on (for example, behaving cryptically) (Lickliter and Harshaw [2010]). Fit, that is surviving, mice are those mice for which there is a match between the context that makes a particular phenotype become expressed and the context that makes this phenotype functional (Badyaev [2011]).

Spelled out this way, it is not obvious which part of the explanation of the complementarity between organism and environment that refers to causes of variation in phenotype versus causes of variation in fitness. The processes that produce recurrent phenotypes and the processes that produce recurrent selection are intimately intertwined. Some biologists suspect that this is the rule rather than the exception, and have amassed a large number of empirical examples demonstrating that individuals respond to their environment during ontogeny, and that these responses shape future experiences and environments for the individuals themselves and their descendants in ways that affect their survival and reproduction (Sultan [2015]). The significance of this in terms of evolutionary causation is that the mechanisms by which individuals interact with their surroundings (that is, proximate causes; Mayr [1961]), contribute to the directionality of evolution typically aggregated under the label natural selection.

One response to this account is to grant that the causes of variation and fitness are intertwined, but to argue that what matters in the long run are the genetic variants that ensure transgenerational stability in organism–environment relations. Thus, the high-fidelity replication of genes keeps inheritance quasi-independent of development and selection, and this is ultimately what justifies the gene-centric perspective. Indeed, the separation of development and inheritance has been hailed as one of the most important conceptual contributions to evolutionary theory (Mayr [1980]). It is evident why; quasi-independence effectively limits what causes of development will also count as causes of evolution. But inheritance does not need to be conceptualized as transmission (Müller-Wille and Rheinberger [2012]). If heredity instead is interpreted as recurrence of developmental process (Griffiths and Gray [1994]; Oyama [2000b]), developmental causes become evolutionary causes not by their survival through a static channel of transmission, but insofar as they are recurrent.[10] Thus, the properties of inheritance mechanisms become evolving features and these properties are what may grant certain mechanisms (for example, genetic inheritance) special evolutionary significance (Shea [2011]; Shea *et al.* [2011]). On this account, representing inheritance and development as a genotypic reaction norm is unsatisfactory because this does not address how novel interactions arise in development or how those interactions evolve to become dependencies for the reliable inheritance of species-typical features (Badyaev and Uller [2009]; Uller [2012]).

In summary, we suggest that the fault line in interpretative understanding of niche construction is underpinned by different assumptions regarding the autonomy of the sets of causes or processes that embody the principles of variation, differential fitness, and heredity. Assuming quasi-independence leads naturally to a marginalization of selective and developmental niche construction and the view that natural selection is the only source of adaptive organism–environment relations in evolution. Rejecting quasi-independence, on the other hand, leads to an appreciation of the importance of development and may reveal that specific adaptations result from both natural selection and niche construction.[11]

5 Anomalies, Communication Failure, and Conceptual Change

The existence of these alternative ways to accommodate niche construction raises the question of the benefits of conceptual change. Are alternative perspectives superfluous when there are no data incompatible with the existing framework? Anomalous data are the fundamental driver of conceptual change in Kuhn's description of scientific revolutions (Kuhn [1962]). Empirical observations are sometimes presented as anomalies in the niche construction literature. For example, Turner ([2000]) considers earthworms an anomaly because they maintain a physiology suited for an aquatic lifestyle despite

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[10] Or, in the case of dual inheritance models, two or more channels of transmission.

[11] Specifying alternative accounts of evolutionary causation goes beyond the scope of this article and we do not wish to pigeonhole those who argue for conceptual change into any particular representation.

being terrestrial.[12] The reason for this, according to Turner, is that earthworms, by their burrowing behaviour, modify the soil to suit their ancestral physiology, thereby effectively eliminating selection on features that would reduce water loss. Although this example bears the signature of an anomaly, evolutionary biologists can be quick to point out that this could be interpreted as an ancestral behaviour (for example, burrowing) that merely facilitated colonization of land. This is not obviously different from, say, the reasons that larger mammals are more likely to expand into cool climates because of their lower surface area to volume ratio. Over the past decades, the niche construction literature has grown to encompass many taxonomically diverse examples like the earthworms and, as a consequence, evolutionary biologists today are much more aware of the breadth and extent of niche construction in nature (Sultan [2015]). Nevertheless, the examples do not appear to generally be considered true anomalies for evolutionary theory, but rather as surprising discoveries of phenomena already known to exist elsewhere (for example, in humans).

Faced with a lack of anomalies, evolutionary biologists may have difficulties understanding why the facts of niche construction should be accompanied by conceptual change, even if they do recognize both the selective and developmental consequences of niche construction as being evolutionarily important. In the absence of empirical demonstration of an unambiguous anomaly, especially scientists who expect that conceptual frameworks are replaced through falsification may not perceive the need for alternative perspectives. For example, in a recent exchange in *Nature*, the lack of data that disprove the gene-centric perspective was invoked to argue against the value of specifying alternative conceptual frameworks in evolutionary biology (Wray *et al.* [2014]). Similar arguments are made specifically against the value of niche construction concepts (Scott-Phillips *et al.* [2014]).

One problem with these responses is that, as a theory of scientific change, falsification alone is a poor representation of how science works. Neither the gene-centric evolutionary theory nor its alternatives constitute single testable theories, but are rather ways of thinking that stimulate generation and interpretation of specific theories. Some perspectives on scientific change put less emphasis on anomalies and more on the process underlying progressive problem-shifts (Lakatos [1978]; Chang [2012]). A problem-shift is progressive if the revised framework makes predictions that increase the framework's empirical content. On this view, conceptual frameworks may be revised in response to new problems and research questions, and not only anomalous data. Specification of alternative conceptual frameworks therefore becomes a

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[12] 'Earthworms [. . .] have no business living where they do, because they are physiologically quite unsuited for terrestrial life' (Turner [2000], p. 99).

fundamental feature of scientific change (in Lakatos' words, 'it is only constructive criticism which, with the help of rival research programs, can achieve real successes'; Lakatos [1980], p. 179). At least some biologists who argue that niche construction should motivate conceptual change in evolutionary theory explicitly identify development of multiple, co-existing, conceptual frameworks as an important task for scientists (Laland *et al.* [2014], [2015]).[13]

We suggest that the niche construction controversies should be understood as attempts to develop alternative research programmes, not in response to anomalous data, but motivated by a belief that the scope, structure, and content of the dominant research programme is too limited. These include the logic of the gene-centric model of evolution (for example, conceptual problems with notions of the genome as a program), the limited breadth of phenomena that are considered to be causes of evolution (for example, the proximate–ultimate distinction (Mayr [1961]) appears to rule out behaviour and development as evolutionary causes), and the perceived limitation of standard evolutionary theory when applied to human evolution, in particular culture. The phenomena of niche construction thus act as a vehicle of conceptual change by drawing attention to alternative ways to describe the evolutionary process, and not as anomalous observations that falsify existing theory. As alternative interpretations appear in the scientific literature, conceptual change is naturally resisted by the majority of researchers in the core of the field, who share the dominant perspective and will interpret the facts and novel predictions of niche construction within their existing conceptual framework.

Evolutionary theory may be particularly prone to clashes between scientific world views because its practitioners come from many different fields within, and even outside of, biology. However, if we are right in our interpretation of recent exchanges over niche construction, communication failure is only partially a result of disciplinary differences in conceptual frameworks; it may also reflect different beliefs about how science progresses. Perspectives on scientific progress cut across disciplines but are rarely made explicit in debates among scientists.[14] Thus, the possibility to represent and interpret the same data within frameworks that make different assumptions about causality and different perspectives on the value of alternative conceptual frameworks are both sources of communication failure. If we consider the niche construction perspectives as attempts to formulate alternative research programmes, their

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[13] This is not only true of critics of gene centric perspectives: Gardner and Welch ([2011], p. 10) make a similar point in their defence of selfish gene theory.

[14] One possible place to look: niche construction has been enthusiastically received by some researchers who study human evolution (for example, Anton *et al.* [2014]; Boivin *et al.* [2016]), but some of the most vocal critics also come from these disciplines (for example, Dickins and Barton [2013]; Scott-Phillips *et al.* [2014]).

constructive evaluation should be on the basis of their ability to stimulate new questions and predict patterns and phenomena that would otherwise appear surprising; not on the basis of the perceived explanatory sufficiency of the majority view of evolutionary theory. Those arguing for more substantial conceptual change must strive towards showing that rejecting quasi-independence lead to a more theoretically and empirically progressive research programme than the contemporary genetic representation of biological evolution.

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