

# Niche construction and conceptual change in evolutionary biology

Tobias Uller and Heikki Helanterä

Paper accepted in *the British Journal for the Philosophy of Science*

## 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.

### 1. *Introduction*

### 2. *Selective niche construction*

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

2.2 *Selective niche construction interpreted as compatible with the received view*

2.3 *A fault line in interpretative understanding*

### 3. *Developmental niche construction*

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

3.2 *Developmental niche construction interpreted as compatible with the received view*

25                   3.3 A fault line in interpretative understanding

26           4.    *Understanding the fault line*

27                   4.1 Causation in evolving systems

28           5.    *Anomalies, communication failure and conceptual change*

29           6.    *References*

30

31

## 1. Introduction

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

45           Our aim in this paper is to substantiate the reasons for these differences in interpretation. We begin  
46   by introducing two recognised concepts of niche construction that emphasize different components of the  
47   evolutionary process. The first, which we will refer to as ‘*selective niche construction*’, describes how persistent  
48   modification of environments affects the fitness of the constructing agent and its descendants. The second,  
49   ‘*developmental niche construction*’, describes how niche construction, in the form of non-genetic resources  
50   contributed by parents and constructed by the developing individual, enable the generation and maintenance  
51   of heritable phenotypic variation. These concepts have been advanced in different fields of biology, but their

52 evolutionary implications are increasingly discussed together (e.g., Laland *et al.* [2008]; [2015]; Bateson and  
53 Gluckman [2011]; Chiu and Gilbert [2015]; Sultan [2015]; Watson *et al.* [2016]; an early synthetic treatment is  
54 Waddington [1959]).

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

66

67

## 2. Selective Niche Construction

68 The term niche construction was coined by Odling-Smee in a seminal contribution published in [1988]<sup>1</sup>. In  
69 Odling-Smee's version, which built on work by Waddington (e.g., [1959]) and Lewontin (e.g., [1983]), niche  
70 construction is particularly evolutionarily important when modified environments persist, such that niche  
71 constructing activity in generation  $t$  causes a selective pressure in some later generation  $t+n$ . Odling-Smee  
72 ([1988]) dubbed this ecological inheritance, and defined it as 'any case in which organisms encounter a  
73 modified feature-factor relationship between themselves and their environment [i.e., a matching of phenotype  
74 and environment] where the change in selective pressure is a consequence of prior niche construction by

---

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

75 parents or other ancestral organisms'. This definition remains in later works on niche construction (e.g., p. 42  
76 in Odling-Smee *et al.* [2003]). If we take 'selective pressure' to represent factors external to organisms that  
77 affect their fitness, the definition of ecological inheritance does not demand that the modified environment has  
78 an effect on phenotype, only that it affect survival or reproduction. For example, by dispersing (a form of niche  
79 construction as defined by Odling-Smee *et al.* [2003]), individuals may become exposed to a new predator but  
80 not show any phenotypic responses to that predator (i.e., the cause of differential survival is not a cause of  
81 phenotype)<sup>2</sup>.

82

### 83 2.1 Selective niche construction interpreted as a challenge to the received view

84 Niche construction and ecological inheritance introduce a second causal arrow to the evolutionary dynamics,  
85 from the population to their environment (Fig. 1). Lewontin ([1983]) used two coupled differential equations  
86 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  
87 first equation describes evolutionary change in phenotype as a function of the environment and the second  
88 change in environment as a function of phenotype. Lewontin's interpretation was demanding for the dominant  
89 framework because it described the match between organism and environment as the consequence of two,  
90 inter-linked but different, processes; populations adapting phenotypically to their environment through  
91 natural selection, and populations adapting the environment to their phenotypes through niche construction  
92 (Fig. 1). Thus, whereas the explanandum of 'standard evolutionary theory' and niche construction theory is  
93 typically the same (e.g., the complementarity of organism and environment), they differ in that niche  
94 construction theory introduces an additional explanans in the form of features of the environment that are  
95 there because of the activities of ancestors.

96

97 [insert figure 1 about here]

98

---

<sup>2</sup> Ecological inheritance may of course affect both fitness and parent-offspring resemblance (i.e., heredity). This is discussed in more detail later in the paper.

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

117

## 118           2.2 Selective niche construction interpreted as compatible with the received view

119 There are, however, alternative ways to accommodate niche construction and ecological inheritance that do  
120 not present any problems for the standard framework. A minimal accommodation of selective feedback  
121 through niche construction is to account for the relationship between the population composition at time  $t$  and  
122 selection on descendant populations at time  $t+n$ . As Lewontin himself noted ([1983], [2001], p. 65), this bears  
123 similarities to more standard scenarios where fitness depends on the population composition of phenotypes.  
124 In co-evolution between species, selection on one population is a function of the phenotypes of a different  
125 population. In co-evolution between the sexes, females generate selection on males and *vice versa*. In

126 frequency-dependent selection, the fitness of an individual depends on the frequency of its own phenotype and  
 127 the frequencies of other phenotypes. Each form of co-evolution can include biotic or abiotic intermediates, for  
 128 example resources needed to maintain high-quality territories.

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

138 There is now a substantial literature using mathematical modelling and experimental methods to  
 139 understand the evolutionary implications of selective niche construction. Such papers often refer to the  
 140 feedback between ecological resources and evolving populations as ‘eco-evolutionary dynamics’ (Pelletier *et al.*  
 141 [2009]). Although the focus is more on the evolution of species interactions than on the co-evolution of  
 142 organisms and their abiotic environments, the similarities in logic and methodology (e.g., use of coupled  
 143 equations) indicate that the evolutionary ecology community has taken on board the central argument that  
 144 selective feedback matters<sup>3</sup>. However, in contrast to niche construction advocates, papers on eco-evolutionary  
 145 dynamics typically do not make claims about conceptual change and, by and large, appear to embrace the gene-  
 146 centric perspective on evolution. In fact, some major reviews in the field omit any mentioning of the term ‘niche  
 147 construction’ and do not cite the literature that use this term (e.g., Pelletier *et al.* [2009]; Travis *et al.* [2014]; a  
 148 notable example of a paper that instead cross-cites extensively is Post and Palkovacs [2009]).

---

<sup>3</sup> 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 co-evolution between organisms involving abiotia (i.e., niche construction = eco-evolutionary dynamics in Matthews *et al.* ([2014])) would approach trait co-evolution in the case of the beaver (i.e., niche construction ≠ eco-evolutionary dynamics in Matthews *et al.* ([2014])).

149

150

### 2.3 A fault line in interpretative understanding

151 That two such different interpretations of the theoretical status of selective niche construction co-exist points  
 152 towards the existence of a fault line in interpretative understanding. Following Waddington, Lewontin and  
 153 Odling-Smee, one interpretation is that at least two processes in evolution, natural selection and niche  
 154 construction, together produce a systematic bias in favour of adaptation. In contrast, interpretation of selective  
 155 niche construction within the contemporary genetic theory of evolution keeps natural selection as the only  
 156 cause of systematic bias in favour of adaptation, and makes the niche construction concept appear superfluous  
 157 or even misleading.

158

159

## 3. Developmental Niche Construction

160 The definition of ecological inheritance means that niche construction theorists tend to view effects of the  
 161 environment on phenotypes as important in evolution insofar as it generates directionality of selective  
 162 pressures (Odling-Smee [2010]). Yet, another consequence of modification of the environment by ancestors is  
 163 that it can affect features in the constructor and its descendants, in the case of the latter influencing the parent-  
 164 offspring resemblance<sup>4</sup>. While the term inheritance is typically restricted to the passing of genes from one  
 165 generation to the next, some biologists and philosophers have argued for a more inclusive concept of  
 166 inheritance that includes parental transference of non-genetic developmental resources, including modified  
 167 features of the environment (e.g., Oyama [2000]; Griffiths and Gray [1994]; Stotz [2010]; Jablonka and Lamb  
 168 [2014]).

169 The set of ecological and social circumstances that is inherited from parents are sometimes referred to as  
 170 the *ontogenetic niche* or the *developmental niche* (West and King [1987]; Badyaev and Uller [2009]; Griffiths  
 171 and Stotz [2013]). Developmental niches do not exist 'out there' for organisms to fit into, they are

---

<sup>4</sup> As pointed out above, the concept of ecological inheritance as defined by Odling-Smee does not refer to parent-offspring similarity in phenotype ([1988], 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], p181, see also Laland *et al.* [2008]; Flynn *et al.* [2013])

172 (re)constructed each generation as parents transfer a variety of resources and modify the environment of  
173 offspring, who accommodate these factors into their own development. For example, mothers determine many  
174 features of the environment for their offspring by choosing where and when to nest, and social interactions  
175 between parents and offspring after hatching or birth are important for the development of species-typical  
176 features as well as for maintaining heritable differences between families (Uller [2012]). Similarly, plants  
177 modify the development of their offspring by changing the timing of seed dispersal and features of the seed  
178 coat (Donohue [2009]). Offspring are not passive recipients of whatever parents pass on; they actively respond,  
179 sometimes resulting in repeated interactions with phenotypic effects in both generations.

180

### 181 3.1 Developmental niche construction interpreted as a challenge to the received view

182 An inclusive notion of inheritance appears challenging for the received view, which separates the inheritance  
183 of features from the development of features. When heredity is equated with transmission of genes,  
184 evolutionary change can be represented as transgenerational change in gene frequency. But if genes are not  
185 privileged as causes of heredity, phenotypic evolution may also occur through persistent changes to the  
186 developmental niche, that is, through epigenetic, social, and environmental mechanisms. This may raise  
187 concerns about the validity, or at least completeness, of evolutionary models whose currency is restricted to  
188 one out of possibly many sources of heredity, some of which may qualify formally as inheritance systems (Shea  
189 [2011]). Furthermore, a broader notion of inheritance appears to grant the possibility that development can  
190 direct evolutionary change through biased acquisition and transmission of features, which makes natural  
191 selection but one of several causes of adaptive change.

192 With an inclusive notion of inheritance, explaining the complementarity between organisms and  
193 environment requires us to work through a sequence of events in which developmental niche construction is  
194 both a cause and a consequence of evolution (Fig. 2). For example, individuals may exploit a new food resource  
195 by behavioural innovation (i.e., within-generation plasticity). If offspring learn how to forage by observing and  
196 imitating parents (i.e., a form of non-genetic inheritance), the new behavior may persist, with more or less  
197 fidelity, down generations. If individuals that make use of the new resource have higher fitness, the result of  
198 natural selection should be increased canalization of the behaviour's acquisition in ontogeny, and hence a more



199 reliable inheritance (Badyaev and Uller [2009]). Although this process likely would involve genetic changes,  
200 gene-frequency change follows the acquisition and inheritance of the novel behavior, and the latter therefore  
201 provide part of the explanation for why the population adapts to the new resource (e.g., Baldwin [1896]; review  
202 in West-Eberhard [2003]). This is not a hypothetical mechanism for adaptive divergence. For example, cross-  
203 fostering of chicks between great tits and blue tits demonstrate that imitation of parents can contribute to  
204 reliable inheritance of 'species-typical' foraging behaviours (Slagsvold and Wiebe [2011]).

205

206 [insert figure 2 about here]

207

### 208 3.2 Developmental niche construction interpreted as compatible with the received view

209 Evolutionary biologists are of course aware that parents contribute more than genes to their offspring (and  
210 later generations), and they have devised a number of ways to investigate its evolutionary implications. A  
211 shared feature of these approaches is that they consider the mechanism, and sometimes the content, of non-  
212 genetic inheritance a property of genotypes. For example, using the statistical framework of quantitative  
213 genetics, theoreticians have shown that effects of the social environment on phenotype can affect the rate and  
214 direction of evolution (reviewed in Wade [1998]; Hadfield [2012]). These models work by separating genetic  
215 and non-genetic causes of parent-offspring resemblance, which makes it possible to derive evolutionary  
216 trajectories for populations under particular assumptions about the architecture of genetic and non-genetic  
217 effects and the form of selection<sup>5</sup>. Other models have explored the evolution of the developmental niche itself.  
218 A large literature on the evolution of parental care (Clutton-Brock [1991]; Royle *et al.* [2012]) has been followed  
219 by more recent models that address when non-genetic, for example epigenetic, transmission is adaptive. By  
220 recognizing that several mechanisms can carry information about local conditions, researchers have identified  
221 under what conditions inheritance should be context-dependent and what is the optimal fidelity of  
222 transmission (e.g., Rivoire and Leibler [2014]; Leimar and McNamara [2015]; English *et al.* [2015]; Uller *et al.*  
223 [2015]).

---

<sup>5</sup> 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]).

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

236           What about cultural evolution? Mechanisms of cultural inheritance are often granted a comparably  
237 generous autonomy from genes, such that the content of cultural representations is independent of the  
238 underlying genetics. In dual inheritance models, cumulative phenotypic evolution occurs via two transmission  
239 channels, one genetic and one cultural, which affect the features of the next generation (Richerson and Boyd  
240 [2005]). In contrast to genetic inheritance, the mechanisms of cultural inheritance may not reduce to simple  
241 copying but, by specifying rules for cultural transmission, theoreticians can make use of the same mathematical  
242 tools as models that rely on genetic inheritance alone (e.g., population or quantitative genetics; Cavalli-Sforza  
243 and Feldman [1981]; Boyd and Richerson [1985]). Researchers disagree on how autonomous cultural and  
244 genetic channels of transmission are and, indeed, the extent to which cultural evolution is Darwinian (e.g.,  
245 Cladiere *et al.* [2014]; see Lewens [2015]). The details of this fall beyond the scope of this paper, and here it is  
246 sufficient to point out that one interpretation of non-genetic, including cultural, mechanisms of inheritance is  
247 that the mechanism, even if not the content, is under genetic ‘control’, which make them candidate adaptations  
248 brought about by natural selection (e.g., Dawkins [1982]; Dickins and Rahman [2012]). In other words, natural

---

<sup>6</sup> In this the logic of models of the evolution of non-genetic inheritance (e.g., Leimar & 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 (e.g., Laland *et al.* [1996]).

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

254

### 255 3.3 A fault line in interpretative understanding

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

263

## 264 4. Understanding the fault line

265 Since Waddington, Lewontin and Odling-Smee initially emphasized the importance of selective feedback it has  
266 arguably become a mainstream part of evolutionary biology<sup>7</sup>. A similar case could be made for developmental  
267 niche construction, as it is captured in models of parental effects, epigenetic inheritance and so on.  
268 Nevertheless, the debate regarding the evolutionary implications of selective and developmental niche  
269 construction has not subsided (e.g., for a recent exchange regarding the selective interpretation, see Scott-  
270 Phillips *et al.* [2014], and for the developmental interpretation see Dickins and Rahman [2012] and the  
271 response by Mesoudi *et al.* [2013]; see also Laland *et al.* [2014] and Wray *et al.* [2014]). This suggests that the  
272 underlying reasons for the differences in interpretative understanding are not trivial and that they may go  
273 unrecognized by many practicing biologists. Here we attempt to shed some light on the nature of the fault line.

---

<sup>7</sup> 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]).

274 We show that, contrary to how some, perhaps most, evolutionary biologists interpret the situation (e.g., Wray  
 275 *et al.* [2014]), the disagreement is not primarily due to a perceived lack of attention to niche construction  
 276 phenomena. Instead, the debate reflects that biologists hold a variety of views on causation in evolving systems.

277

#### 278 4.1 Causation in evolving systems

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

294 To understand the rationale for these interpretations of selective and developmental niche construction,  
 295 recall that evolution by natural selection requires the following three conditions: variation in characters among  
 296 members of a population, that some variants leave a greater number of descendants than others, and that  
 297 offspring resemble their parents (e.g., Lewontin [1970]; Godfrey-Smith [2009])<sup>8</sup>. Such summaries state the

---

<sup>8</sup> Darwin's 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.' (Darwin [1859], pp. 489-490).

298 necessary conditions for evolution by natural selection. But they do not specify how variation, differential  
299 fitness, and heredity are conceptually related; how autonomous the processes that generate them are, for  
300 example. Nor do they specify how the processes should be construed.

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

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

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

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

349 The quasi-independence of phenotypic variation, differential fitness and inheritance is deeply  
350 entrenched in contemporary evolutionary biology. But it is a convenient heuristic and not a logical necessity,

---

<sup>9</sup> 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]).

351 and it may or may not accurately capture biological reality. To sketch an alternative account, let us begin with  
352 an example that is a paradigm of quasi-independence.

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

357 This evolutionary account bears all the hallmarks of quasi-independence; the mutation was presumably  
358 random and it is passively passed on to offspring at reproduction. The offspring reliably develop pale coats  
359 when they receive the mutated allele, and their pale colour is the cause of their high survival relative to dark  
360 mice on sandy soils. Nevertheless, we may shift our evolutionary explanandum from the colour of the coat to  
361 the complementary fit between the mice's colour and their environment. Whereas quasi-independence applies  
362 to the former, it does not obviously do so for the latter. Although it is true that the mice cannot change the  
363 colour of their coat, they can change the fitness consequences of their colour by choosing where to live (e.g., by  
364 dispersing), how to live (e.g., by becoming more risk-averse), and how to raise their offspring (e.g., by  
365 constructing safer nests and raising offspring to become risk-averse too). These characters, which affect the  
366 developmental and selective niches of the coat colour phenotype, may be adaptive but they were not originally  
367 selected to enable a match between coat colour and environment, which is the explanandum. Furthermore, in  
368 contrast to coat colour, these behaviours may not map straightforwardly onto any particular genetic variant.  
369 Instead, behavioural types are often constructed in ontogeny through bouts of causal interactions between the  
370 environment the individual experiences (e.g., predation attempts) and how it responds in terms of changes in  
371 physiology, behavior, and so on (e.g., behaving cryptically) (Lickliter and Harshaw [2010]). Fit, that is surviving,  
372 mice are those mice for which there is a match between the context that makes a particular phenotype become  
373 expressed and the context that makes this phenotype functional (Badyaev [2011]).

374 Spelled out this way, it is not obvious which part of the explanation of the complementarity between  
375 organism and environment that refers to causes of variation in phenotype versus causes of variation in fitness.  
376 The processes that produce recurrent phenotypes and the processes that produce recurrent selection are  
377 intimately intertwined. Some biologists suspect that this is the rule rather than the exception, and have  
378 amassed a large number of empirical examples demonstrating that individuals respond to their environment

379 during ontogeny, and that these responses shape future experiences and environments for the individuals  
380 themselves and their descendants in ways that affect their survival and reproduction (Sultan [2015]). The  
381 significance of this in terms of evolutionary causation is that the mechanisms by which individuals interact with  
382 their surroundings (i.e., proximate causes; Mayr [1961]), contribute to the directionality of evolution typically  
383 aggregated under the label natural selection.

384       One response to this account is to grant that the causes of variation and fitness are intertwined, but to  
385 argue that what matters in the long run are the genetic variants that ensure transgenerational stability in  
386 organism-environment relations. Thus, the high-fidelity replication of genes keeps inheritance quasi-  
387 independent of development and selection, and this is ultimately what justifies the gene-centric perspective.  
388 Indeed, the separation of development and inheritance has been hailed as one of the most important conceptual  
389 contributions to evolutionary theory (Mayr [1981]). It is evident why; quasi-independence effectively limits  
390 what causes of development will also count as causes of evolution. But inheritance does not need to be  
391 conceptualized as transmission (Müller-Wille and Rheinberger [2012]). If heredity instead is interpreted as  
392 recurrence of developmental process (Oyama [1985]; Griffiths and Gray [1994]), developmental causes  
393 become evolutionary causes not by their survival through a static channel of transmission<sup>10</sup>, but insofar as they  
394 are recurrent. Thus, the properties of inheritance mechanisms become evolving features and these properties  
395 are what may grant certain mechanisms (e.g., genetic inheritance) special evolutionary significance (Shea *et al.*  
396 [2011]; Shea [2011]). On this account, representing inheritance and development as a genotypic reaction norm  
397 is unsatisfactory because this does not address how novel interactions arise in development or how those  
398 interactions evolve to become dependencies for the reliable inheritance of species-typical features (Badyaev  
399 and Uller [2009]; Uller [2012]).

400       In summary, we suggest that the fault line in interpretative understanding of niche construction is  
401 underpinned by different assumptions regarding the autonomy of the sets of causes or processes that embody  
402 the principles of variation, differential fitness and heredity. Assuming quasi-independence leads naturally to a  
403 marginalization of selective and developmental niche construction and the view that natural selection is the  
404 only source of adaptive organism-environment relations in evolution. Rejecting quasi-independence, on the

---

<sup>10</sup> Or, in the case of dual inheritance models, two or more channels of transmission.



405 other hand, leads to an appreciation of the importance of development and may reveal that specific adaptations  
406 results from both natural selection and niche construction<sup>11</sup>.

407

## 408 5. Anomalies, communication failure and conceptual change

409 The existence of these alternative ways to accommodate niche construction raises the question of the benefits  
410 of conceptual change. Are alternative perspectives superfluous when there are no data incompatible with the  
411 existing framework? Anomalous data are the fundamental driver of conceptual change in Kuhn's description  
412 of scientific revolutions (Kuhn [1962]). Empirical observations are sometimes presented as anomalies in the  
413 niche construction literature. For example, Turner ([2000]) considers earth worms an anomaly because they  
414 maintain a physiology suited for an aquatic life-style despite being terrestrial<sup>12</sup>. The reason for this, according  
415 to Turner, is that earth worms, by their burrowing behavior, modify the soil to suit their ancestral physiology,  
416 thereby effectively eliminating selection on features that would reduce water loss. Although this example bears  
417 the signature of an anomaly, evolutionary biologists can be quick to point out that this could be interpreted as  
418 an ancestral behavior (e.g. burrowing) that merely facilitated colonization of land. This is not obviously  
419 different from, say, the reasons that larger mammals are more likely to expand into cool climates because of  
420 their lower surface area to volume ratio. Over the past decades, the niche construction literature has grown to  
421 encompass many taxonomically diverse examples like the earthworms and, as a consequence, evolutionary  
422 biologists today are much more aware of the breadth and extent of niche construction in nature (Sultan [2015]).  
423 Nevertheless, the examples do not appear to generally be considered true anomalies for evolutionary theory,  
424 but rather as surprising discoveries of phenomena already known to exist elsewhere (e.g., in humans).

425 Faced with a lack of anomalies, evolutionary biologists may have difficulties understanding why the  
426 facts of niche construction should be accompanied by conceptual change, even if they do recognize both the  
427 selective and developmental consequences of niche construction as being evolutionarily important. In the  
428 absence of empirical demonstration of an unambiguous anomaly, especially scientists who expect that

---

<sup>11</sup> Specifying alternative accounts of evolutionary causation goes beyond the scope of this paper and we do not wish to pigeonhole those who argue for conceptual change into any particular representation.

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

429 conceptual frameworks are replaced through falsification may not perceive the need for alternative  
 430 perspectives. For example, in a recent exchange in *Nature*, the lack of data that disprove the gene-centric  
 431 perspective was invoked to argue against the value of specifying alternative conceptual frameworks in  
 432 evolutionary biology (Wray *et al.* [2014]). Similar arguments are made specifically against the value of niche  
 433 construction concepts (Scott-Phillips *et al.* [2014]).

434         One problem with these responses is that, as a theory of scientific change, falsification alone is a poor  
 435 representation of how science works. Neither the gene-centric evolutionary theory nor its alternatives  
 436 constitute single testable theories, but are rather ways of thinking that stimulate generation and interpretation  
 437 of specific theories. Some perspectives on scientific change put less emphasis on anomalies and more on the  
 438 process underlying progressive problem-shifts (Lakatos [1978]; Chang [2013]). A problem-shift is progressive  
 439 if the revised framework makes predictions that increase the framework's empirical content. On this view,  
 440 conceptual frameworks may be revised in response to new problems and research questions, and not only  
 441 anomalous data. Specification of alternative conceptual frameworks therefore becomes a fundamental feature  
 442 of scientific change (in Lakatos' words 'it is only constructive criticism which, with the help of rival research  
 443 programs, can achieve real successes'; Lakatos and Musgrave [1970], p. 179). At least some biologists who  
 444 argue that niche construction should motivate conceptual change in evolutionary theory explicitly identify  
 445 development of multiple, co-existing, conceptual frameworks as an important task for scientists (Laland *et al.*  
 446 [2014], [2015])<sup>13</sup>.

447         We suggest that the niche construction controversies should be understood as attempts to develop  
 448 alternative research programmes, not in response to anomalous data, but motivated by a belief that the scope,  
 449 structure, and content of the dominant research programme is too limited. These include the logic of the gene-  
 450 centric model of evolution (e.g., conceptual problems with notions of the genome as a program), the limited  
 451 breadth of phenomena that are considered to be causes of evolution (e.g., the proximate-ultimate distinction  
 452 (Mayr [1961]) appears to rule out behavior and development as evolutionary causes), and the perceived  
 453 limitation of standard evolutionary theory when applied to human evolution, in particular culture. The  
 454 phenomena of niche construction thus act as a vehicle of conceptual change by drawing attention to alternative

---

<sup>13</sup> This is not only true of critics of gene centric perspectives: Gardner & Welch ([2011], p.10) make a similar point in their defense of selfish gene theory.

455 ways to describe the evolutionary process, and not as anomalous observations that falsify existing theory. As  
456 alternative interpretations appear in the scientific literature, conceptual change is naturally resisted by the  
457 majority of researchers in the core of the field, who share the dominant perspective and will interpret the facts  
458 and novel predictions of niche construction within their existing conceptual framework.

459 Evolutionary theory may be particularly prone to clashes between scientific world views because its  
460 practitioners come from many different fields within, and even outside of, biology. However, if we are right in  
461 our interpretation of recent exchanges over niche construction, communication failure is only partially a result  
462 of disciplinary differences in conceptual frameworks; it may also reflect different beliefs about how science  
463 progresses. Perspectives on scientific progress cut across disciplines<sup>14</sup> but are rarely made explicit in debates  
464 among scientists. Thus, the possibility to represent and interpret the same data within frameworks that make  
465 different assumptions about causality and different perspectives on the value of alternative conceptual  
466 frameworks are both sources of communication failure. If we consider the niche construction perspectives as  
467 attempts to formulate alternative research programmes, their constructive evaluation should be on the basis  
468 of their ability to stimulate new questions and predict patterns and phenomena that would otherwise appear  
469 surprising; not on the basis of the perceived explanatory sufficiency of the majority view of evolutionary theory.  
470 Those arguing for more substantial conceptual change must strive towards showing that rejecting quasi-  
471 independence lead to a more theoretically and empirically progressive research programme than the  
472 contemporary genetic representation of biological evolution.

473

474 *Tobias Uller*475 *Department of Biology, Lund University, Sölvegatan 37, 22362 Lund, Sweden*476 *Department of Zoology, University of Oxford, South Parks Rd, OX1 3PS, Oxford, UK*477 *tobias.uller@biol.lu.se*

478

479 *Heikki Helanterä*

---

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

480 Centre of Excellence in Biological Interactions, Department of Biosciences, University of Helsinki, POB  
 481 65, Viikinkaari 1, FI00014, Finland  
 482 [heikki.helantera@helsinki.fi](mailto:heikki.helantera@helsinki.fi)  
 483

## 484 Acknowledgements

485 TU is grateful to John Odling-Smee and Kevin Laland for many enlightening discussions and to Rosamond and  
 486 John Odling-Smee for their hospitality. He is also grateful to Kevin Laland, Marcus Feldman, Lucy Odling-  
 487 Smee, and Doug Erwin for an invitation to the workshop *Frontiers in niche construction: From theory to*  
 488 *application in the biological and social sciences* at the Santa Fe Institute, which provided the impetus for this  
 489 paper. Jonathan Birch, Andy Gardner, Kevin Laland, John Odling-Smee, Thom Scott-Phillips, Richard Watson  
 490 and two anonymous reviewers provided helpful comments on the paper. We are grateful to the Royal Society  
 491 of London, the Knut and Alice Wallenberg Foundations, the Academy of Finland, the Kone Foundation, and the  
 492 John Templeton Foundation (grant no: 60501) for funding.

493

494

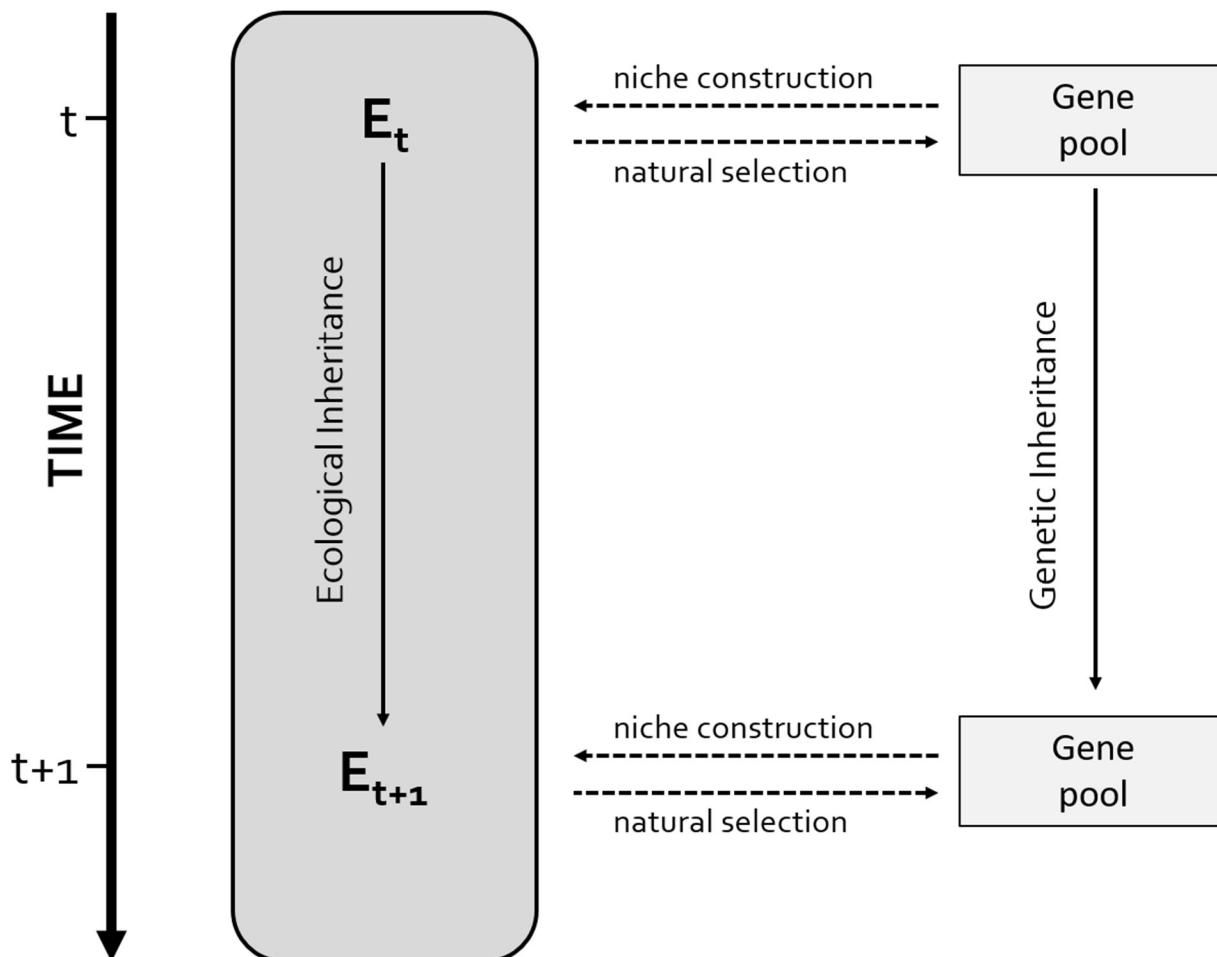
## 495 References

- 496 Anton, S. C., Potts, R. and Aiello, L. C. [2014]: 'Evolution of Early Homo: An Integrated Biological Perspective',  
 497 *Science*, **345**, 1236828.  
 498 Arnold, S. J. [1983]: 'Morphology, Performance and Fitness', *American Zoologist*, **2**, pp. 347-61.  
 499 Badyaev, A. V. [2011]: 'Origin of the Fittest: Link between Emergent Variation and Evolutionary Change as a  
 500 Critical Question in Evolutionary Biology', *Proceedings of the Royal Society B: Biological Sciences*, **27**,  
 501 pp. 1921-9.  
 502 Badyaev, A. V., and Uller, T. [2009]: 'Parental Effects in Ecology and Evolution: Mechanisms, Processes and  
 503 Implications', *Philosophical Transactions of the Royal Society B: Biological Sciences*, **36**, pp. 1169-77.  
 504 Baldwin, J. M. [1896]: 'A New Factor in Evolution', *American Naturalist*, **3**, pp. 441-51.  
 505 Bateson, P. and Gluckman, P. [2011]: *Plasticity, Robustness, Development and Evolution*, New York, NJ:  
 506 Cambridge University Press.  
 507 Boivin, N. L. Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., Denham, T. and Petraglia, M. D.  
 508 [2016]: 'Ecological Consequences of Human Niche Construction: Examining Long-Term  
 509 Anthropogenic Shaping of Global Species Distributions', *Proceedings of the National Academy of*  
 510 *Sciences USA*, **11**, pp. 6388-96.  
 511 Boyd, R. and Richerson, P. J. [1985]: *Culture and the Evolutionary Process*, Chicago, IL: University of Chicago  
 512 Press.  
 513 Cavalli-Sforza, L. L. and Feldman, M. W. [1981]: *Cultural Transmission and Evolution: a Quantitative Approach*,  
 514 Princeton NJ: Princeton University Press.  
 515 Chang, H. [2012]: *Is Water H<sub>2</sub>O? Evidence, Realism and Pluralism*, New York: Springer Science & Business  
 516 Media.

- 517 Chiu, L. and Gilbert, S. F. [2015]: 'The Birth of the Holobiont: Multi-Species Birthing Through Mutual  
518 Scaffolding and Niche Construction', *Biosemiotics*, **8**, pp. 191-210.
- 519 Claidière, N., Scott-Phillips, T. C. and Sperber, D. [2014]: 'How Darwinian is Cultural Evolution?', *Philosophical  
520 Transactions of the Royal Society of London B*, **36**, 20130368.
- 521 Clutton-Brock, T. H. [1991]: *The Evolution of Parental Care*, Princeton, NJ: Princeton University Press.
- 522 Dawkins, R. [1982]: *The Extended Phenotype. The Long Reach of the Gene*, Oxford, UK: Oxford University Press.
- 523 Dawkins, R. [2004]: 'Extended Phenotype - But not too Extended. A Reply to Laland, Turner and Jablonka',  
524 *Biology and Physiology*, **1**, pp. 377-96.
- 525 Day, T., and Bonduriansky, R. [2011]: 'A Unified Approach to the Evolutionary Consequences of Genetic and  
526 Nongenetic Inheritance', *American Naturalist*, **17**, pp. E18-36.
- 527 Dickins, T. E. and Barton, R. A. [2013]: 'Reciprocal Causation and the Proximate-Ultimate Distinction', *Biology  
528 and Philosophy*, **2**, pp. 747-56.
- 529 Dickins, T. E. and Rahman, Q. [2012]: 'The Extended Evolutionary Synthesis and the Role of Soft Inheritance in  
530 Evolution', *Proceedings of the Royal Society B: Biological Sciences*, **27**, pp. 2913-21.
- 531 Donohue, K. [2009]: 'Completing the Cycle: Maternal Effects as the Missing Link in Plant Life Histories',  
532 *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **36**, pp. 1059-74.
- 533 English, S., Pen, I. R., Shea, N. and Uller, T. 'The Adaptive Value of Non-Genetic Inheritance in Plants and  
534 Insects', *Plos One*, **1**, E0116996.
- 535 Flynn, E. G., Laland, K. N., Kendel, R. L., and Kendal, J. R. [2013]: 'Developmental Niche Construction',  
536 *Developmental Science*, **1**, pp. 296-313.
- 537 Ghalambor, C. K., McKay, J. K., Carroll, S. P. and Reznick, D. N. [2007]: 'Adaptive versus Non-Adaptive  
538 Phenotypic Plasticity and the Potential for Contemporary Adaptation in New Environments',  
539 *Functional Ecology*, **2**, pp. 394-407.
- 540 Godfrey-Smith, P. [2009]: *Darwinian Populations and Natural Selection*, New York: Oxford University Press.
- 541 Gottlieb, G. [1992]: *Individual Development and Evolution. The Genesis of Novel Behavior*, New York: Oxford  
542 University Press.
- 543 Griffiths, P. E., and Gray, R. D. [1994]: 'Developmental Systems and Evolutionary Explanation', *Journal of  
544 Philosophy*, **9**, pp. 277-304.
- 545 Griffiths, P. and Stotz, K. [2013]: *Genetics and Philosophy. An Introduction*, New York, NJ: Cambridge University  
546 Press.
- 547 Hadfield, J. [2012]: 'The Quantitative Genetic Theory of Parental Effects', in N. Royle, P. Smiseth and M.  
548 Kölliker (eds), *Evolution of Parental Care*, New York: Oxford University Press, pp. 268-284.
- 549 Haig, D. [2007]: 'Weismann Rules! OK? Epigenetics and the Lamarckian Temptation', *Biology and Philosophy*,  
550 **2**, pp. 415-28.
- 551 Hoekstra, H. E., Hirschmann, R. J., Bunday, R. A., Insel, P. A., Crossland, J. P. [2006]: 'A Single Amino Acid  
552 Mutation Contributes to Adaptive Beach Mouse Color Pattern', *Science*, **31**, pp. 101-4.
- 553 Jablonka, E. and Szathmáry, E. [1995]: 'The Evolution of Information Storage and Heredity', *Trends in Ecology  
554 and Evolution*, **1**, pp. 206-11.
- 555 Jablonka, E. and Lamb, M. [2005]: *Evolution in Four Dimensions. Genetic, Epigenetic, Behavioral and Symbolic  
556 Variation in the History of Life*, Cambridge, MA: MIT Press.
- 557 Jablonka, E. and Lamb, M. [2014]: *Evolution in Four Dimensions. Genetic, Epigenetic, Behavioral and Symbolic  
558 Variation in the History of Life, 2<sup>nd</sup> edition*, Cambridge, MA: MIT Press.
- 559 Kuijper, B. and Hoyle, R. B. [2015]: 'When to Rely on Maternal Effects and When on Phenotypic Plasticity?',  
560 *Evolution*, **6**, pp. 950-68.
- 561 Kuhn, T. S. [1962]: *The Structure of Scientific Revolutions*, Chicago, IL: Chicago University Press.
- 562 Lakatos, I. [1978]: *The Methodology of Scientific Research Programmes*, J. Worrall and G. Currie (eds), New  
563 York, NJ: Cambridge University Press.
- 564 Laland, K. N., and O'Brien, M. J. [2011]: 'Cultural Niche Construction: an Introduction', *Biological Theory*, **6**, pp.  
565 191-202.
- 566 Laland, K. N., Odling-Smee, F. J. and Feldman, M. W. [1996]: 'The Evolutionary Consequences of Niche  
567 Construction: a Theoretical Investigation Using Two-Locus Theory', *Journal of Evolutionary Biology*,  
568 **9**, pp. 293-316.
- 569 Laland, K. N., Odling-Smee, F. J. and Feldman, M. W. [1999]: 'Evolutionary Consequences of Niche Construction  
570 and Their Implications for Ecology', *Proceedings of the National Academy of Sciences USA*, **96**, pp.  
571 10242-7.

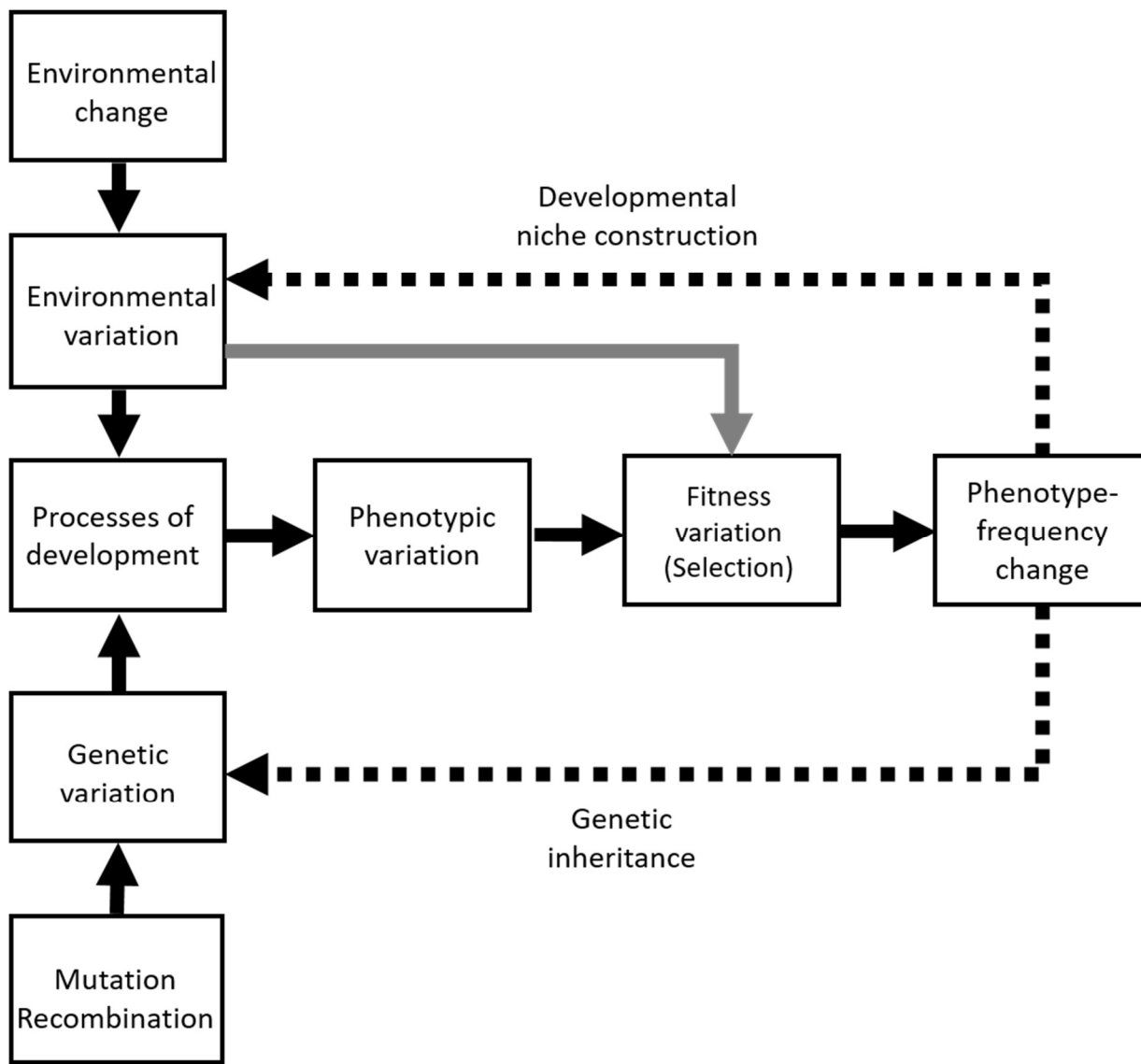
- 572 Laland, K. N., Odling-Smee, F. J. and Gilbert, S. F. [2008]: 'Evodevo and Niche Construction: Building Bridges',  
573 *Journal of Experimental Zoology*, Part B, 310B, pp. 549-66.
- 574 Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E. and Odling-Smee, F. J.  
575 [2014]: 'Does Evolutionary Theory Need a Rethink?', *Nature*, **51**, pp. 161-4.
- 576 Laland, K. L., Uller, T., Feldman, M., Sterelny, K., Müller, G.B., Moczek, A., Jablonka, E. and Odling-Smee, F. J.  
577 [2015]: 'The Extended Evolutionary Synthesis: Its Structure, Core Assumptions, and Predictions',  
578 *Proceedings of the Royal Society of London*, **28**, pp. 20151019.
- 579 Laland, K. L., Odling-Smee, F. J. and Endler, J. 'Niche Construction, Sources of Selection and Trait Co-Evolution',  
580 *Royal Society Interface Focus*, in press.
- 581 Lande, R. [2009]: 'Adaptation to an Extraordinary Environment by Evolution of Phenotypic Plasticity and  
582 Genetic Assimilation', *Journal of Evolutionary Biology*, **2**, pp. 1435-46.
- 583 Leimar, O. and McNamara, J. M. ([2015]). The Evolution of Transgenerational Integration of Information in  
584 Heterogeneous Environments', the *American Naturalist*, **185**, pp. E55-69.
- 585 Lewens, T. [2015]: *Cultural Evolution*, New York: Oxford University Press.
- 586 Lewontin R. C. [1970]: 'The Units of Selection', *Annual Review of Ecology and Systematics*, **1**, pp. 1-18.
- 587 Lewontin, R. C. [1983]: Gene, Organism, and Environment, in D. S. Bendall (ed.) *Evolution from Molecules to*  
588 *Men*, New York, NJ: Cambridge University Press, pp. 273-85.
- 589 Matthews, B., De Meester, L., Jones, C., Ibeling, B., Bouma, T., Nuutinen, V., Van De Koppel, J. and Odling-Smee,  
590 F. J. [2014]: 'Under Niche Construction: an Operational Bridge between Ecology, Evolution, and  
591 Ecosystem Science', *Ecological Monographs*, **8**, pp. 245-63.
- 592 Maynard Smith, J. and Szathmáry, E. [1995]: the *Major Transitions on Evolution*, New York: Oxford University  
593 Press.
- 594 Maynard-Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D. and  
595 Wolpert, L. [1985]: 'Developmental Constraints and Evolution: a Perspective from the Mountain Lake  
596 Conference on Development and Evolution', *Quarterly Review of Biology*, **6**, pp. 265-87.
- 597 Mayr, E. [1961]: 'Cause and Effect in Biology', *Science*, **13**, pp. 1501-6.
- 598 Mayr E. [1980]: 'Some Thoughts on the History of the Evolutionary Synthesis', in E. Mayr, W. B. Provine (eds),  
599 *The Evolutionary Synthesis*, Cambridge, MA: Harvard University Press, pp. 1-48.
- 600 Mayr, E. [1982]: *The Growth of Biological Thought. Diversity, Evolution and Inheritance*, Cambridge, MA: The  
601 Belknap Press of Harvard University Press.
- 602 Mcadam, A. G., Garant, D. and Wilson, A. J. [2014]: 'The Effects of Others' Genes: Maternal and Other Indirect  
603 Genetic Effects', in A. Charmantier, D. Garant and L. E. B. Kruuk (eds), *Quantitative Genetics in the Wild*  
604 New York: Oxford University Press.
- 605 Mesoudi, A., Blanchet, S., Charmantier, A., Danchin E., Fogarty, L., Jablonka, E., Laland, K. N. *et al.* [2013]: 'Is  
606 Non-Genetic Inheritance Just a Proximate Mechanism? A Corroboration of the Extended Evolutionary  
607 Synthesis', *Biological Theory*, **7**, pp. 189-95.
- 608 Moore, A. J., Brodie III, E. D. and Wolf, J. B. [1997]: 'Interacting Phenotypes and the Evolutionary Process. I.  
609 Direct and Indirect Genetic Effects of Social Interactions', *Evolution*, **5**, pp. 1352-62.
- 610 Mousseau, T. A. and Fox, C. W. [1998]: *Maternal Effects as Adaptations*, New York: Oxford University Press.
- 611 Müller-Wille, S. and Rheinberger, H.-J. [2012]: *A Cultural History of Heredity*, Chicago, IL: University of Chicago  
612 Press.
- 613 Odling-Smee, F. J. [1988]: 'Niche Constructing Phenotypes', in H. C. Plotkin (ed.), *The Role of Behavior in*  
614 *Evolution*, Cambridge MA: MIT Press, pp. 73-132.
- 615 Odling-Smee, F. J. [2010]: 'Niche Inheritance', in M. Pigliucci and G.B. Müller (eds), *Evolution. The Extended*  
616 *Synthesis*, Cambridge MA: MIT Press, pp. 175-208.
- 617 Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. [2003]: *Niche Construction. The Neglected Process in*  
618 *Evolution*, Princeton, NJ: Princeton University Press.
- 619 Oyama S. [2000]: *A Systems View of the Biology-Culture Divide*, Durham, NC: Duke University Press.
- 620 Oyama, S. [1985]: *The Ontogeny of Information. Developmental Systems and Evolution* (Second Edition 2000),  
621 Durham, NC: Duke University Press.
- 622 Oyama, S., Griffiths, P. E. and Gray, R. D. [2001]: *Cycles of Contingency. Developmental Systems and Evolution*,  
623 Cambridge MA: MIT Press.
- 624 Pelletier, F., Garant, D. and Hendry, A. P. [2009]: 'Eco-Evolutionary Dynamics', *Philosophical Transactions of*  
625 *the Royal Society B: Biological Sciences*, **364**, pp. 1483-9.

- 626 Pigliucci, M. [2001]: *Phenotypic Plasticity. Beyond Nature and Nurture*, Baltimore, ML: The John Hopkins  
 627 University Press.
- 628 Post D. M., Palkovacs E. P. [2009]: 'Eco-Evolutionary Feedbacks in Community and Ecosystem Ecology:  
 629 Interactions between the Ecological Theatre and the Evolutionary Play', *Philosophical Transactions of  
 630 the Royal Society B: Biological Sciences*, **36**, pp. 1629-40.
- 631 Richerson, P. J. and Boyd, R. [2005]: *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago,  
 632 IL: University of Chicago Press.
- 633 Rivoire, O. and Leibler, S. [2014]: 'A Model for the Generation and Transmission of Variations in Evolution',  
 634 *Proceedings of the National Academy of Sciences of the United States of America*, **111**, pp. E1940-9.
- 635 Royle, N. J., Smiseth, P. T., Kölliker, M. [2012]: *The Evolution of Parental Care*. Chicago, IL: University of Chicago  
 636 Press.
- 637 Scott-Phillips, T. C., Dickins, T. E. and West S. A. [2011]: 'Evolutionary Theory and the Ultimate-Proximate  
 638 Distinction in the Human Behavioral Sciences', *Perspectives on Psychological Science*, **6**, pp. 38-47.
- 639 Scott-Phillips, T. C., Laland, K. N., Shuker, D. M., Dickins, T. E. and West, S. A. [2014]: 'The Niche Construction  
 640 Perspective: a Critical Appraisal', *Evolution*, **6**, pp. 1231-43.
- 641 Shea, N. [2011]: 'Developmental Systems Theory Formulated As a Claim About Inherited Representations',  
 642 *Philosophy of Science*, **7**, pp. 60-82.
- 643 Shea, N., Pen, I., and Uller, T. [2011]: 'Three Epigenetic Information Channels and Their Different Roles in  
 644 Evolution', *Journal of Evolutionary Biology*, **2**, pp. 1178-87.
- 645 Slagsvold T. and Wiebe K. L. [2011]: 'Social Learning in Birds and Its Role in Shaping a Foraging Niche',  
 646 *Philosophical Transactions of the Royal Society B: Biological Sciences*, **36**, pp. 969-77.
- 647 Smiseth, P. T., Wright, J. and Kölliker, M. [2008]: 'Parent-Offspring Conflict and Co-Adaptation: Behavioural  
 648 Ecology Meets Quantitative Genetics', *Proceedings of the Royal Society of London B*, **27**, pp. 1823-30.
- 649 Stotz, K., [2010]: 'Human Nature and Cognitive-Developmental Niche Construction', *Phenomenology and the  
 650 Cognitive Sciences*, **9**, pp. 483-501.
- 651 Sultan, S. E. [2015]: *Organism and Environment. Ecological Development, Niche Construction and Adaptation*,  
 652 New York: Oxford University Press.
- 653 Travis, J., Reznick, D., Bassar, R. D., López-Sepulcre, A., Ferriere, R. and Coulson, T. [2014]: 'Do Eco-Evo  
 654 Feedbacks Help Us Understand Nature? Answers from Studies of the Trinidadian Guppy', *Advances in  
 655 Ecology*, **5**, pp. 1-40.
- 656 Turner, J. S. [2000]: *The Extended Organism*. Cambridge, MA: Harvard University Press.
- 657 Uller, T. [2008]: 'Developmental Plasticity and the Evolution of Parental Effects'. *Trends in Ecology &  
 658 Evolution*, **2**, pp. 432-8.
- 659 Uller, T. [2012]: 'Parental Effects in Development and Evolution', in N. Royle, P. Smiseth and M. Kölliker (eds),  
 660 *Evolution of Parental Care*, New York: Oxford University Press, pp. 247-66.
- 661 Uller, T., English, S. and Pen, I. [2015]: 'When Does Natural Selection Favour Incomplete Epigenetic Resetting  
 662 in Germ Cells?', *Proceedings of the Royal Society of London B*, **28**, 20150682.
- 663 Waddington, C. H. [1959]: 'Evolutionary Systems - Animal and Human', *Nature*, **18**, pp. 1634-8.
- 664 Wade, M. [1998]: 'The Evolutionary Genetics of Maternal Effects', in T.A. Mousseau and C.W. Fox (eds),  
 665 *Maternal Effects As Adaptations*, New York: Oxford University Press, pp. 5-21,
- 666 Walsh, D. M. [2015]: *Organism, Agency, and Evolution*, New York, NJ: Cambridge University Press.
- 667 Watson, R. A., Mills, R., Buckley, C. L., Kouvaris, K., Jackson, A., Powers, S. T., Cox, C., Tudge, S., Davies, A.,  
 668 Kounios, L. and Power, D. [2016]: 'Evolutionary Connectionism: Algorithmic Principles Underlying  
 669 the Evolution of Biological Organization in Evo-Devo, Evo-Eco and Evolutionary Transitions',  
 670 *Evolutionary Biology*, in press.
- 671 West, M. J. and King, A. P. [1987]: 'Settling Nature and Nurture into an Ontogenetic Niche', *Developmental  
 672 Psychobiology*, **2**, pp. 549-62.
- 673 West-Eberhard, M. J. [2003]: *Developmental Plasticity and Evolution*. Oxford University Press, New York, NY.
- 674 Wray, G. A., Futuyma, D. J., Lenski, R. E., Mackay, T. F. C., Schluter, D., Strassman, J. E. and Hoekstra, H. E.  
 675 [2014]: 'Does Evolutionary Theory Need a Rethink? No, All Is Well', *Nature*, **514**, pp. 161-4.
- 676
- 677



679  
 680 Fig. 1. Graphical representation of an evolutionary process involving both natural selection and niche  
 681 construction. Organism-environment complementarity arises because of reciprocal causation between the  
 682 processes that make organisms modify their selective environments and natural selection in those  
 683 environments, whereby individuals with particular phenotypes suited to the constructed conditions leave  
 684 more descendants. Redrawn from Odling-Smee *et al.* ([2003]).  
 685





686  
 687 Figure 2. A developmental perspective on the relationships between environment, genes, phenotype and  
 688 selection. Both environmental (i.e., non-genetic) and genetic variation can initiate phenotypic evolution and  
 689 developmental niche construction and genetic inheritance together contribute to heredity. Adaptive evolution  
 690 proceeds through repeated bouts of reciprocal causation between developmental plasticity, processes of  
 691 inheritance, and natural selection. The grey arrow represents the effects of selective niche construction,  
 692 discussed in the previous section. Figure modified from West-Eberhard ([2003], p.142).

693