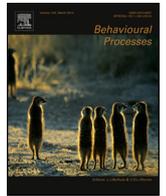




Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



On evolutionary causes and evolutionary processes

Kevin N. Laland*

School of Biology, University of St Andrews, United Kingdom

ARTICLE INFO

Article history:
Available online xxx

Keywords:
Causation
Evolutionary process
Niche construction
Developmental bias
Reciprocal causation

ABSTRACT

In this essay I consider how biologists understand 'causation' and 'evolutionary process', drawing attention to some idiosyncrasies in the use of these terms. I suggest that research within the evolutionary sciences has been channeled in certain directions and not others by scientific conventions, many of which have now become counterproductive. These include the views (i) that evolutionary processes are restricted to those phenomena that directly change gene frequencies, (ii) that understanding the causes of both ecological change and ontogeny is beyond the remit of evolutionary biology, and (iii) that biological causation can be understood by a dichotomous proximate–ultimate distinction, with developmental processes perceived as solely relevant to proximate causation. I argue that the notion of evolutionary process needs to be broadened to accommodate phenomena such as developmental bias and niche construction that bias the course of evolution, but do not directly change gene frequencies, and that causation in biological systems is fundamentally reciprocal in nature.

This article is part of a Special Issue entitled: In Honor of Jerry Hogan.

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A volcano erupts, generating extreme environmental conditions. Magma and hot gasses pour out of the mountainside, and every living creature that the lava stream crosses is demolished. Such eruptions are amongst the most destructive natural disasters known to science. Yet even here we see the evidence of evolutionary adaptation. For instance, an underwater volcano in Guam has been erupting since 2004, and investigations of the marine life near it have revealed unusual varieties of fish, shrimp, crabs and limpets, including several newly identified species (Green, 2009). These organisms thrive in hot water with strong chemicals, for instance, they possess anatomical adaptations that allow them to survive in extremely high sulphide concentrations (Moyes and Schulte, 2007). Seemingly, a history of volcanic eruption in the vicinity has caused evolutionary change by leading to the natural selection of organisms able to tolerate or exploit the severe ecological states created.

In common parlance we would feel entirely comfortable speaking of the volcano causing evolution, yet neither volcanoes, nor any other environmental change, are formally recognized as causes of evolutionary change in evolutionary biology textbooks. This is not to suggest that evolutionary biologists fail to appreciate the causal link between environmental change and organismal change: of course they do. That relationship has been well-established

since Darwin (1859). Yet the evolutionist would typically make a distinction between those processes that bring about changes in environmental conditions (amongst which they would include volcanic eruptions) and those processes that bring about lasting and heritable changes in organisms through modifying gene frequencies (where volcanoes do not show). For the evolutionary biologist, the *real cause* of those organismal adaptations for tolerance to extreme temperatures and chemical environments is natural selection. Other direct causes of evolution are also recognized, and include random genetic drift, gene flow and mutation. But volcanic eruptions, like all other phenomena that modify the circumstances in which organisms live, are not viewed as evolutionary causes: rather they are background conditions.

This distinction between a *phenomenon that causes an evolutionary process to occur* and a *direct evolutionary cause or process itself*, is a subtle but important one. Volcanic eruptions do not cause organismal change directly (if selections were impeded, for instance, though the absence of heritable variation, no organismal change would arise): rather, they create the conditions under which natural selection may (or may not) ensue.

Note, this is a different description of causality from that found in common parlance, or even in other domains of science. If a nail is hit with a hammer we describe the hammer as the direct cause of the nail entering the wood. It would seem strange to describe the impact of the hammer as a background condition to the nail's momentum. To my knowledge, physicists see no need to distinguish, as categorically different, hammer-moving processes

* Tel.: +44 01334463009.
E-mail address: kn1@st-andrews.ac.uk

from wood-entering processes. Likewise, we would not be optimistic about the chances of the defendant in the dock receiving a 'not guilty' verdict if their defense was based on the argument that they did not cause the death of the victim that they shot – that was the bullet – they only pulled the trigger. In common parlance, the layperson might well describe the volcano as the cause of the Loihi shrimp's unusual physiology, but the professional evolutionist, whilst recognizing the causal connection, would typically not. Perhaps philosophers would point to other differences between these examples, but it is my contention that they are not to be distinguished on logical grounds, but rather by scientific convention.

The convention within evolutionary biology is to distinguish evolutionary processes from the causes or modulators of those processes. A volcanic eruption, like all environmental change, can trigger an evolutionary event to occur, or transform the course of pre-existing evolutionary events, but this does not make it an evolutionary process in itself. Any suggestion that environmental events are evolutionary processes would, it is generally argued, conflate causes of changes in background conditions with the evolutionary processes by which organic changes occur (Scott-Phillips et al., 2014). Eruptions are ecological, not evolutionary, events. They might initiate or change a response to selection, by modifying the relative fitnesses of alternative genotypes, but (even granting that they are indirectly causal) it would be a logical error to view volcanoes as direct causes of evolutionary change. Likewise, population size might modulate the action of genetic drift, but this does not make it an evolutionary process: rather, it is a modulator, or background condition.

I see considerable merit in the aforementioned distinction, but nonetheless suspect that it is more problematical than it first appears. Recently, I have argued that discipline-based scientific fields frequently emerge that by default do not treat potentially relevant phenomena as causes, leading to the neglect of relevant processes (Laland et al., 2011, 2013a,b). A good example is provided by Ernst Mayr's, and the other architects of the Modern Synthesis', 'black boxing' of development (Hamburger, 1980; Amundson, 2005; Laland et al., 2011). Such 'black boxing' or 'screening off' of a phenomenon, and exiling its study to an adjacent discipline, is often initially useful, and may be necessary to make scientific progress. It is only a problem if and when it becomes dogma. I suspect that this has happened with Mayr's (1961) distinction between proximate and ultimate causation: an initially useful heuristic (i.e. that proximate and ultimate explanations are not competing alternatives) has degenerated into a convention (e.g. where developmental processes are seen as irrelevant to evolution), leading to unhelpful divisions between academic fields of enquiry (e.g. the weak link between evolutionary and developmental biology; West-Eberhard, 2003; Amundson, 2005; see Laland et al., 2011, 2013a,b for discussion).

In one sense this screening off of fields of enquiry by researchers might be regarded as inevitable, or perhaps even desirable. To understand a bewilderingly complex and changing world, scientists must devise conceptual tools that render their business more manageable. They assume that, at least for the kinds of questions in which they are interested, with their associated temporal and spatial scales, it is reasonable to treat certain processes, and certain kinds of variation, as relatively unimportant. This allows them to hold certain aspects of the world constant, to treat them as 'context', and to explore the causal structure of the phenomena of interest relative to that context. All scientists do this – although I suspect, few do so deliberately; rather these fundamental assumptions are commonly accepted with little reflection. Accordingly, scientific disciplines effectively become 'clubs' in which like-minded researchers share some consensus over what is, and what is not, reasonably treated as cause and context.

Consider Hutchinson's (1957) famous metaphor of the 'evolutionary play in the ecological theatre'. What does this metaphor imply? To me, it implies that environments are 'out there' – that they are the background, the context, the theater, in which the great evolutionary drama ensues, and where natural selection might perhaps be conceived as the casting director, eliminating or keeping for the next 'showing' a given species of 'actor'. This separation of organism and environment is well-recognized by both biologists and philosophers of biology, and countless researchers have taken issue with it (Barker et al., 2014; Bateson, 1988; Gottlieb, 1992; Keller, 2010; Lewontin, 1983, 2000; Odling-Smee et al., 2003; Oyama, 1985; Oyama et al., 2001). Evolutionary biologists are primarily interested in understanding organismal change and diversity, not ecological change. At the time of the forging of the Modern Synthesis, understanding ecological change was regarded as broadly outside the remit of evolutionary biology – that is ecologists' job (Mayr, 1982). Of course, the last few decades have witnessed the emergence of evolutionary ecology (Ford, 1964; Roughgarden, 1979), whilst the study of eco-evolutionary feedbacks is an exciting recent development (Post and Palkovacs, 2009; Loreau, 2010). Nonetheless, it remains the case today that for the vast majority of evolutionary biologists, the causes of changes in selection pressures are not generally the focus of enquiry, except in some special cases, such as sexual selection. Typically, the selection pressures are taken as the starting point for evolutionary analysis (Endler, 1986a).

Feeding into this division of labor was another longstanding assumption, only recently challenged by evidence for rapid evolution (Kingsolver et al., 2001; Hairston et al., 2005; Ellner et al., 2011), that ecological and evolutionary processes operate of different temporal and spatial scales (Lewontin, 1982, 1983, 2000; Levins and Lewontin, 1985; O'Neill et al., 1986). This assumption was embraced by ecologists and evolutionary biologists alike, in no small part for its convenience (O'Neill et al., 1986). It meant that ecosystem ecologists could disregard evolutionary events as something that likely happened a long time ago, and hence did not need to be considered in their analyses of ecological processes (O'Neill et al., 1986). It also meant that evolutionary biologists could disregard the changes that organisms manifestly brought about in their environments as local and temporary, and hence unlikely to scale up, across populations and over evolutionary timeframes, to be evolutionarily important. One ramification is that evolutionary biologists rarely ask "where do the selection pressures come from?"

The distinction between ecological and evolutionary causes is a scientific convention born through historical accident, rather than from some fundamental truth about how causation operates in the natural world. The forging of the Modern Synthesis in the early part of the 20th century, with its integration of Darwinian natural selection, population-level thinking and Mendelian inheritance, led to the widespread adoption of several core assumptions (Mayr, 1982; Futuyma, 1998). These assumptions included: that new phenotypic variation is a consequence of genetic mutations; that most favorable mutations have small phenotypic effects, which result in gradual phenotypic change; that inheritance is genetic; and that natural selection is the sole explanation for the adaptive match between organisms and their environments. This geocentric stance led to the view that evolution could appropriately be defined as "a change in the genetic composition of populations" (Dobzhansky, 1937, p. 11), and that it could be studied without reference to mechanisms of development (Mayr, 1982). If evolution is characterized as change in gene frequencies over time, then it is perhaps natural to define evolutionary processes as phenomena that directly bring about changes in gene frequencies. Four such evolutionary processes are widely recognized – selection (natural and sexual), drift, mutation and gene flow – and accordingly they are the only accepted direct causes of evolutionary change.

Now imagine a world in which organisms could not tolerate the high sulphur concentrations, or endure the extreme temperatures, and hence could not adapt to volcanoes. Such limitations are far from implausible – indeed they are inevitable: all organisms have their physiological tolerances, and cannot survive outside their fundamental niche, and likewise all the biochemical processes necessary for life are critically contingent on suitable environmental conditions. Under such circumstances, the resulting pattern of evolution – the organismal diversity we see in the world – would depend in part on the nature of the physiological and biochemical tolerances possessed by organisms. Should we think of these tolerances as evolutionary causes? The conventional wisdom is not to do so – rather these are viewed as constraints (Maynard-Smith et al., 1985). Such phenomena do not cause evolution, since they do not directly change gene frequencies, they merely shut out some hypothetical areas of phenotype space as ‘out of bounds’ to selection, drift, and so forth. Constraints are not, as generally conceived, causes of evolution – rather they are causes of the absence of evolution. Constraints might, for instance, explain why adaptation has not occurred in a given circumstance, or why phenotypes are not globally optimal. Yet selection, drift, mutation and gene flow would remain the only widely recognized evolutionary processes, and developmental and physical constraints would most commonly be viewed as providing limited restrictions on their action. On this view, constraints might explain, say, why pigs cannot fly, since there exist severe size and weight limitations on animals that can get airborne (Haldane, 1985), but the dazzling diversity of life is testimony to the fact that the phenotype space open to recognized evolutionary processes is vast. This conception, which remains the dominant view within evolutionary biology, is that while constraints might impose modest limitations on selection, it is selection and the other evolutionary processes that explain the rich tapestry of life. Constraints would certainly be recognized as a non-trivial part of the causal explanation for a given pattern of taxonomic diversity. Yet, to put it in statistical terms, I suspect that for most evolutionists it is selection and drift that are conceived of as accounting for the vast bulk of variation in organismal form.

But what if the constraints were sometimes so potent, regular and systematic that they shaped the course of evolution? What if there were severe limitations on those phenotypes that were physiologically plausible? What if there were only certain ways of building bodies? Then, rather than thinking of selection as free to traverse a vast empty chasm of morphospace, it would be channeled along those limited and narrow pathways that were opened up by the processes of development (Gould, 2000). Under such circumstances, a sizeable portion of the variation in organismal form would be explained by developmental ‘constraints’. Indeed, if that were the case the very term ‘constraint’ would be highly misleading. Developmental processes would be the creative element in evolution, demarcating which forms would occur and which would not, and accounting for why organisms possess the characters that they do. Selection, drift and the like would play a more restricted explanatory role than currently recognized. Given its channeling or directing role, some researchers would argue that we should call such events a ‘developmental bias’, rather than a constraint (Arthur, 2004, 2011; Brakefield, 2006, 2011; Müller, 2007). Note, such developmental bias would be a phenomenon that specified the pattern of phenotypic variation and change in the world, not to mention frequently providing a mechanistic account of the origins of that variation, but yet nonetheless did not meet current definitions of an evolutionary process. It would seem that contemporary evolutionary biology does not provide us with adequate conceptual tools specifying how to think about the causal role of phenomena like developmental bias.

Developmental bias is real. For example, virtually all mammals, from mice to giraffes, possess seven cervical vertebrae (in

contrast to reptiles and birds, which vary enormously in their number of vertebrae), despite considerable variation in neck length, and despite evidence that extra cervical vertebrae allow greater flexibility of the neck (Arthur, 2011). It would seem that mammalian development largely precludes the production of variants with more or fewer vertebrae, but readily allows for vertebrae of different lengths. Hence while neck length may be determined by selection, whether the evolved changes are achieved through changes in the number or length of vertebrae depends on the developmental system (Arthur, 2011). Another example concerns segment number in centipedes, where in every one of more than a 1000 species of geophilomorphs the number of leg-bearing segments is an odd number (Minelli and Bortolotto, 1988). This is thought to result from a mechanism of segment development that brings about a bias against the production of even numbered leg-bearing segments (Arthur, 2011). Likewise, in other taxa, some limb or digit numbers are probabilistically more likely than others (Arthur, 2004, 2011; Galis et al., 2010).

Artificial selection experiments on *Bicyclus* butterfly eyespots, combined with evo-devo mechanistic analyses, provide further compelling evidence for developmental bias (Beldade et al., 2002; Allen et al., 2008). Such experiments have established that it is easier to select for both anterior and posterior eyespots to get bigger, or for both to get smaller, than to select for opposite changes in the two pairs of eyespots, leading to a bias for strong positive correlation in eyespot size. Moreover, selection on eyespot color was unable to make one pair of eyespots more gold and the other more black, leading to a bias toward covariation in eyespot color. Similarly, Arthur (2011) points out that there are more than 50 independent origins of legless tetrapods, but only a single (or at most two) incidences of the origin of shelled tetrapods, arguing that the relative frequency of these two types of tetrapod body plan lies not in the relative frequencies with which the selective advantages of a shell and the loss of legs occur, but rather in a bias in the developmental system, such that some kinds of variation are common, others exceedingly rare.

Importantly, developmental bias goes beyond recognition that some phenotypes may be less likely to originate than others. In fact, a major shift in thinking compared to the original Modern Synthesis is that biased phenotypic variation can be channeled or directed by the processes of development toward functional goals, a phenomenon known as *facilitated variation* (Kirschner and Gerhart, 2005; Gerhart and Kirschner, 2007, 2010). The theory of facilitated variation provides a framework for understanding how random genetic variation is transformed by developmental processes into functional phenotypic variation (Kirschner and Gerhart, 2005; Gerhart and Kirschner, 2007, 2010). It suggests that the development and functioning of phenotypic traits occurs through the operation of a number of conserved core processes (e.g. gene regulation, information retrieval from the genome, eukaryotic cellular processes, cell-cell signaling, and muscle-, neural-, and vascular system development), which can be combined in various ways (“weak linkage”) to generate functional phenotypic variation. Core processes are so called because they are highly conserved phylogenetically, as are the underlying genes expressed in these processes. Developmental plasticity results, in part, because of the capacity of some core processes for exploratory behavior, which enables somatic selection of more functional states. Exploratory behavior is defined as ‘adaptive behavior of certain cellular and developmental core processes, wherein they generate many... specific outcome states, any of which can be stabilized selectively by other kinds of agents’ (e.g. nerve axons contacting distant target cells) (Kirschner and Gerhart, 2005). Neural, muscular, and vascular systems all select and stabilize certain states over others following periods of exploratory behavior. Thus somatic selective processes stabilize those states that are most appropriate in the

current conditions (eliminating those that are not). In this manner developmental processes adapt to local demands without genetic change. This ontogenetic adaptability is exploited in evolution when genetic changes harness, fix or stabilize pre-existing tried-and-tested phenotypic variants to generate adaptive innovation at the level of the phenotype. The logic is highly consistent with West-Eberhard's (2003) claim that 'genes are followers, not leaders, in evolution' (although I anticipate that genes will sometimes be leaders too). The significance of the theory of facilitated variation stems from its potential to explain how small, random genetic changes can elicit substantial, well-integrated and often adaptive innovations in the phenotype.

These observations provide empirical support for Gould and Lewontin's (1979) claim that organisms are "so constrained by phyletic heritage, pathways of development and genetic architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs". Some researchers have argued on theoretical grounds that developmental bias should be regarded as the rule, rather than the exception, in nature (e.g., Arthur, 2011), although the prevalence of developmental bias in nature remains largely uncharted. What is undeniable is that more and more examples of developmental bias are continually coming to light, and the phenomenon increasingly garners attention.

Developmental processes are not only manifest in morphological characteristics but in behavior and other outputs expressed in the external environments. For instance, organisms construct nests, burrows, mounds, webs, and dams, they deposit detritus, modify soils and chemical environments, they select habitat and essential resources, they move in space (e.g. migration), and they leave ecological legacies for future generations. In all these ways, organisms modify environmental conditions, and thereby change the selection pressures to which they, their descendants, and other organisms that inhabit their local environments, are exposed (Odling-Smee et al., 1996, 2003). What if the developmental bias were expressed in the environment? Then there would be a systematic bias to the way organisms modify selection pressures, and a resultant systematic bias to the selection generated. This is the argument at the heart of niche construction theory (Odling-Smee et al., 2003).

Niche construction refers to the process whereby the metabolism, activities, and choices of organisms modify or stabilize environmental states, and thereby affect selection acting on themselves and other species (Odling-Smee et al., 2003; see also Lewontin, 1983, 2000). Niche construction also influences development, and constitutes an important way in which environmental factors stabilize normal development (Badyaev and Uller, 2009). *Ecological inheritance* refers to the accumulation of environmental changes, such as altered soil, atmosphere or ocean states that previous generations have brought about through their niche-constructing activity, and that influence the development of descendant organisms (Odling-Smee et al., 2003; Erwin, 2008).

Niche construction is both universal to, and obligate for, living creatures. Living organisms are far-from-equilibrium systems relative to their physical or abiotic surroundings. They can only survive by constantly exchanging energy and matter with their environments. Organisms feed on molecules rich in free energy, using the harvested energy to do work, and generating outputs largely in the form of molecules that are poor in free energy. Such work is necessary to allow organisms to produce and maintain a specified orderliness, be it inside their bodies or in their external environments. In order to survive, organisms must act on their environments and, by doing so, must change them. One consequence of this imperative is that all living organisms *must* engage in niche construction—that is, they must modify their environment to some degree, however small-scale and transient. One ramification

of the fact that niche construction ultimately functions to harvest energy is that niche construction cannot be random, since random niche-constructing acts could not provide organisms with a basis for sustained life (Odling-Smee et al., 2003, chapter 4).

The directionality of niche construction results from the expression of genetic and acquired (e.g. learned, brain-based) semantic information: information specifying how organisms should operate in their local environments in order to satisfy their requirements. This information would be eradicated, by selection, or through learning, if its average effect on fitness was negative. It follows that niche construction is a selective process (albeit very different in form to natural selection), since it requires an ability on the part of organisms to discriminate, and actively sort between environmental resources, and hence to change the physical state of some factors in their environments in beneficial ways (Odling-Smee et al., 2003).

This reasoning, which derives directly from the laws of thermodynamics (Odling-Smee et al., 2003; Laland et al., in press), implies that organisms must modify environmental states in a systematic and directional way. For instance, niche construction disproportionately generates environmental states that are likely to match – that is, be coherent and integrated with – the constructing organism's phenotype and its developmental needs, or those of its descendants. These environments are therefore adaptive for the constructor or its descendants, at least in the short-term (Odling-Smee et al., 2003).

Standard evolutionary theory tacitly assumes that environmental states modified by organisms are not systematically different from environments that change through processes independent of organismal activity. On the basis of this assumption, the construction of nests, mounds, burrows and dams can be treated as just like the volcanic eruption: it is a background condition to selection, rather than an evolutionary process in its own right (Scott-Phillips et al., 2014). However, there are strong grounds for thinking that niche construction is qualitatively different from environmental change that occurs independently of organismal activity (Odling-Smee et al., 2003, 2013). Niche construction is guided by (genetic and/or acquired) information, and thereby generates nonrandom environmental change, frequently driving environments into states that could not otherwise occur (Odling-Smee et al., 2003, 2013). Moreover, unlike environmental change stemming from independent events (e.g., climate), here ecological, even abiotic, variables are tied to rates of niche construction, often over multiple generations. Evolutionary models have established that the resulting dynamics are quite distinct from either cases where each trait is considered in isolation or conventional coevolution scenarios (Laland et al., 1996, 1999; Lehmann, 2008; Krakauer et al., 2009; Loreau, 2010). This directional or systematic quality has led to the argument that niche construction should be regarded as, not just an ecological but also, an evolutionary process (Odling-Smee et al., 2003).

The argument that developmental bias, developmental plasticity and facilitated variation play important, but poorly recognized, evolutionary roles have in common the view that developmental processes systematically channel the generation of phenotypic variants along certain pathways, and thereby bias the direction and rate of evolution by, in part, determining the variants that are subject to selection (Arthur, 2004; Brakefield, 2006; Kirschner and Gerhart, 2005; Müller, 2007; West-Eberhard, 2003). Niche construction theory makes a related argument: it emphasizes how developing organisms modify external environments in a manner that systematically biases the selection pressures acting on the constructing population, their descendants, and other populations (including other species) that inhabit their local environment (Odling-Smee et al., 2003). Both of these arguments fall foul of current conceptions of an evolutionary process, since neither

developmental bias or niche construction directly modifies gene frequencies. This makes it harder to view such phenomena as genuine evolutionary causes.

For illustration, consider the evolution of adult lactose tolerance in humans. All human babies, but only some adults, exhibit lactose tolerance. The frequency of alleles for adult lactose absorption within a culture correlates with whether that culture has a history of dairy farming (Ulijaszek and Strickland, 1993; Durham, 1991). Such data suggest that in those populations that adopted dairy farming, and hence came to rely upon dairy products throughout life, lactose tolerant alleles were selected (Feldman and Cavalli-Sforza, 1989; Durham, 1991; Holden and Mace, 1997; Tishkoff et al., 2007). The standard neo-Darwinian account of this is that dairy farming changed the local ecology, creating a lactose-rich nutritional environment that favored genetic variants that thrive in this new ecology. On this view, niche construction is no different to environmental change more generally: it can elicit natural selection by generating covariance between specific genotypes and fitness, but it is not an evolutionary process (Scott-Phillips et al., 2014).

What this account misses is that the adoption of dairy farming has not only caused this particular evolutionary episode (in fact, generating selection for adult lactose tolerance on multiple independent occasions) but is a manifestation of a general propensity of human cultural niche-constructing practices to modify diets and thereby bias selection pressures (Voight et al., 2006; Wang et al., 2006; Nielsen et al., 2007; Laland et al., 2010). Human cultural activities over the last 15,000 years, through the domestication of plants and animals, have systematically generated selection for countless alleles, for instance, expressed in the digestion of not just milk and dairy products, but also the metabolism of carbohydrates, starch, proteins, lipids, phosphates, alcohol, and the detoxification of numerous plant secondary compounds (Laland et al., 2010). Human diets have changed in a directional manner, almost certainly becoming more diverse, and better able to metabolize a broader range of food substances. The standard evolution perspective treats niche construction as a background condition, and regards the evolution of lactose absorption as an isolated event, equivalent to a lactose-rich asteroid crashing into the planet. But, like the aforementioned examples of developmental bias, niche construction is doing more than that – it is imposing a pattern on the course of human evolution. What is more, self-induced changes in diet are just the tip of the iceberg (Laland et al., 2010), and over the last 50,000 years, and perhaps longer, human cultural niche construction has almost certainly imposed directional selection on our immunity to disease, our nervous system and brain functioning, our learning, our skeletal development, and more (Feldman and Laland, 1996; Kumm et al., 1994; Laland et al., 1995, 2010; Richerson et al., 2010).

I utilize a human example here solely because it is particularly well-studied and data rich, but the same logic applies to other species. For instance, in standard evolutionary accounts, termites evolve to become adapted to the mound that they construct in a manner no different from how the aforementioned *Loihi* shrimps adapted to the high sulphide concentrations following volcanic eruptions. Yet I view these cases as fundamentally different. Volcanic eruptions are idiosyncratic events, independent of organisms' actions, whereas termites construct and regulate their nests and mounds in a repeatable, directional manner consistent with their survival and reproductive needs (themselves shaped by past selection). For instance, the fungus cultivating *Macrotermes* maintain the temperature and humidity of their nest within tight adaptive bounds, and constantly remodel the mound structure to tap the wind and thereby power air-conditioning through the vents of the nest (Turner, 2000). Such niche construction acts to impose patterning and directionality on evolution through the systematic, nonrandom modification of environments. Variation in termite

behavior and morphologies reflects variation in termite mound building.

I characterize such niche construction as an evolutionary process (rather than, say, referring to it as phylogenetic inertia) because the selection pressures it generates are directional, orderly and often highly consistent amongst unrelated organisms. Build a nest, and an organism creates selection pressures for the nest to be defended, maintained, regulated, and improved upon in design, as well as for others to steal it, destroy it, squat in it, or dump eggs in it. Such adaptive responses evolve time and time again, generating signatures of environmental change that are quite distinct from processes independent of the organism, to produce parallel evolution in independent lineages, and often long-term trends, in ways that are potentially probabilistically predictable (Odling-Smee et al., 2003, 2013; Laland et al., 2008). There are (as yet largely un-deciphered) laws of niche construction, and hence stochastic regularities to how selective environments will change over time, and their future decoding potentially boosts the predictive power of evolutionary biology. The same applies to developmental bias, where regularities of organismal development generate consistent, and potentially stochastically predictable, patterns to the phenotypic variants generated in particular environmental conditions, and hence subject to selection (Arthur, 2004, 2011; Kirschner and Gerhart, 2005; Müller, 2007; West-Eberhard, 2003). Drawing on a distinction made by philosopher Sober (1984), a deeper understanding of ecology and developmental biology provides 'source laws' for natural selection, which will complement those 'consequence laws' currently studied through population genetics (Endler, 1986b). In the longer term, a broader conception of the causes of evolution, drawing on insights into the developmental origins of variation and the ecological sources of selection, will surely pave the way to a stronger explanatory and predictive science.

Yet, once again, a scientific convention proves an impediment. Historically, evolutionarily minded researchers have tended to characterize culture as constrained by genes to operate like a (proximate) switch (akin to the buttons on a jukebox) to shift behavior and cognition from one pre-established program to another, with each context-dependent strategy fashioned by natural selection (Wilson, 1975, 1978; Lumsden and Wilson, 1981; Tooby and Cosmides, 1992). Many evolutionary psychologists and other nativists assume that natural selection fashions both how and what humans learn (Scott-Phillips et al., 2011), such that cultural transmission is 'under genetic control' (Dickins and Rahman, 2012). Following Mayr (1961), cultural transmission has been widely regarded by evolutionists as a proximate mechanism that fine-tunes behavior in a manner little different from any other aspect of plasticity. The same reasoning applies more generally to all forms of plasticity, which are commonly regarded as solely products of evolution, controlled by genes to allow for adaptive fine-tuning of organismal form. However, the aforementioned data strongly suggest that culture is doing much more than this: human cultural niche construction is not just a proximate mechanism, it is driving directional change in biological evolution. Likewise, many researchers now believe that plasticity is setting the evolutionary agenda (West-Eberhard, 2003; Pfennig et al., 2010; Moczek et al., 2011).

Recent articles drawing attention to problems with Mayr's (1961) distinction between proximate and ultimate causation (Hogan, 1994; Dewsbury, 1999; West-Eberhard, 2003; Thierry, 2005; Hogan and Bolhuis, 2009; Laland et al., 2011, 2013a,b; Watt, 2013) (amongst other concerns), take issue with Mayr's repeated equation of development with the solely proximate, and his subsequent insistence that development is irrelevant to evolution. Mayr's term 'ultimate causation' is problematical both because it is ambiguous, simultaneously seeking to encapsulate both the

'function' of a character and its 'evolutionary history', and because 'ultimate cause' is frequently equated with function, which is not a cause (Hogan, 1994; Laland et al., 2013a,b). In spite of these concerns, the proximate–ultimate causation dichotomy remains widely deployed across the evolutionary sciences.

This dichotomous way of thinking about biological causation has had its uses, but is now proving counterproductive, and needs to be replaced. Developing organisms are not solely products, but are also causes, of evolution (Bateson and Gluckman, 2011; Oyama et al., 2001; Laland and Sterelny, 2006; Laland et al., 2011, 2013a,b). Biological causation is fundamentally reciprocal in nature. Organisms co-direct the rate and direction of evolution through nonrandom generation of phenotypic variants (developmental bias) and nonrandom generation of selection (niche construction). The complementary match between organism and environment arises not from selection alone, but through interactions between natural selection and internally and externally expressed constructive development. Even though organisms regularly 'adapt' environments to suit themselves (Turner, 2000; Odling-Smee et al., 2003), the current conceptual framework makes it hard to view niche construction as an evolutionary cause, since it is viewed as a proximate mechanism.

The same conventions hinder recognition of the role of developmental plasticity in evolution (West-Eberhard, 2003). There is now extensive data suggesting that environmentally-induced phenotypes can subsequently be stabilized and fine-tuned across generations by selection of standing genetic variation, previously cryptic genetic variation, or newly arising mutations. Developmental plasticity, and subsequent genetic accommodation, can therefore facilitate rapid adjustment to diverse conditions and trigger subsequent selection on reaction norms (Schlichting and Pigliucci, 1998; West-Eberhard, 2003; Pfennig et al., 2010; Moczek et al., 2011). Consistent with these arguments, plasticity within lineages often parallels variation between lineages, while in some taxa more plastic clades are found to be more speciose than sister clades that lack plasticity (Pfennig et al., 2010). Yet plasticity is not typically recognized as a cause of evolutionary change, largely because it is perceived as a proximate mechanism, a product of natural selection.

Those same conceptual barriers also hinder recognition of mutational biases as shaping evolution: biases in the introduction of variation constitute a prior bias on the course of evolution (Stoltzfus, 2012). They are a specific form of developmental bias. The fact that niche construction, developmental plasticity and even patterns of mutation may have been shaped by prior selection does not negate their playing an evolutionary role, once causation is recognized to be reciprocal. Developmental processes are underdetermined by prior selection, and hence evolutionary causation mediated by bouts of niche construction and developmental bias cannot be reduced to selection alone.

If my arguments are sound then developmental bias and niche construction each impose directionality on the evolutionary process, and potentially help evolutionary researchers to understand trends and patterns in data. Yet they remain largely unrecognized as evolutionary processes largely because of scientific conventions, that (i) constrain evolutionary processes to those phenomena that directly change gene frequencies, (ii) treat understanding the causes of ecological change as beyond the remit of evolutionary biology, and (iii) view biological causation dichotomously, with developmental processes perceived as solely relevant to proximate causation.

There is a pressing need to think about evolutionary causes and evolutionary processes differently. In particular, the evolutionary sciences require a broader conceptualization of what qualifies as an evolutionary process. Such a broader conception was proposed by John Endler in 1986, who devised an admirable scheme that

recognized several classes of evolutionary process. These, included processes that 'generate variation', 'restrict the kinds of variant which are either possible or likely', 'change the frequencies of variants', and 'improve an organism's fit with the environment' (Endler, 1986b). Unfortunately, Endler's scheme has not yet been widely adopted. I would choose to broaden Endler's category of processes that restrict the kinds of variant to 'processes that bias selection', since selection cannot only be biased by restriction on organismal variation, but also through biases in selection environments. Niche construction and developmental bias would then fit into this category. A failure to recognize these factors as evolutionary processes leads to an inaccurate and impoverished account of evolutionary dynamics.

Many eminent scientists and philosophers of biology have characterized science as an evolutionary process (Popper, 1979; Hull, 1982; Plotkin, 1994). To the extent that it is, I believe that it is subject to its own developmental biases. Conceptual frameworks channel thinking along particular lines, encouraging researchers to consider some hypotheses but not others. For instance, it is surely no coincidence that, following the emergence of the Modern Synthesis that emphasized gradualistic change, at a time when population genetics and ecology were largely independent fields, for decades evolutionary biologist rarely went out and measured rates of natural selection (Endler, 1986a). When ecologically-minded pioneers, such as Bernard Kettlewell, EB Ford, Arthur Cain and Philip Sheppard were measuring natural selection in natural populations of moths, butterflies and snails in the 1950s and 60s, population geneticists (who historically had studied selection in the laboratory) were slow to appreciate the significance of this work, because they thought that traits such as color polymorphisms were unlikely to be important to fitness (Endler, personal communication). Some other eminent evolutionary biologists also shared this attitude. For instance, Mayr (1942, p. 32) writes: "The variation in color patterns, such as bands in snails and spot patterns in lady beetles are, by themselves, obviously of very insignificant selective value". Lande and Arnold's (1983) classic paper on the measurement of selection changed this mindset, by placing the study of selection in an ecological context.

The manner in which evolutionary biologists have investigated niche construction has been similarly channeled by the dominant manner of thinking. As a result, there exists extensive work investigating the evolution of niche-constructing activities, spanning several decades, and across many scientific fields, but until recently little consideration of the ecological and evolutionary consequences of niche construction. With the exception of some isolated pockets of theory, scientific interest in such questions really took off with key publications on ecosystem engineering (Jones et al., 1994, 1997) and niche construction (Odling-Smee et al., 1996, 2003). Ecologists had neglected the manner in which organisms provide habitat and resources for other organisms, and the way in which these interactions can generate webs of connectance that underpin ecosystems (Jones et al., 1994, 1997), largely because the dominant externalist convention was to reduce ecosystems to food webs, leaving out the abiota (O'Neill et al., 1986). Likewise, evolutionary biologists had neglected how niche-constructing traits resulting from byproducts, acquired characters, the collective actions of ecological communities, and ecological legacies, can drive evolutionary and coevolutionary episodes, primarily because the dominant 'extended phenotype' perspective (Dawkins, 1982) drew attention to the adaptations of individual organisms (Odling-Smee et al., 2003, 2013). It is far more obvious that the beaver's dam is evolutionarily and ecologically important than that the beaver's dung is. Yet the dramatic ecological effects of seabird guano on the Aleutian islands were highlighted through the introduction of arctic foxes, who devastated the seabird population, without whose guano lush vegetation was transformed into a

bleak wilderness (Croll et al., 2005). That such byproducts can also have evolutionary consequences is strongly suggested by the use of fecal remains to communicate dietary preferences, information about dominance, reproductive state, and so forth (e.g. Laland and Plotkin, 1991, 1993). These kinds of feedbacks and spillover effects are increasingly being recognized as ecologically and evolutionarily important (Odling-Smee et al., 2013).

The same holds for acquired characters. Social learning is now known to be ubiquitous in animals, with thousands of reports of novel behavior (related to diet choice, foraging skills, anti-predator behavior, etc.) spreading through animal populations through learning, in hundreds of species, including primates, cetaceans, rodents, many other mammals, birds, reptiles, fishes, insects and cephalopods (Day et al., 2003; Jablonka and Lamb, 1995; Coolen et al., 2005; Boogert et al., 2006, 2008; Leadbeater and Chittka, 2007; Laland et al., 2011; Hoppitt and Laland, 2013). There is even evidence for active teaching in some species, including ants, bees, meerkats and pied babblers (Hoppitt et al., 2008). This social transmission has been found to affect the evolution of a variety of animals, in different ways. For example, mate-choice copying, where the choice of mating partner is influenced by the mate choices of other individuals, is found in *Drosophila*, fishes, birds, and mammals (Hoppitt and Laland, 2013), song learning affects the frequency of alleles that influence song acquisition and preference (Lachlan and Slater, 1999), promotes the evolution of brood parasitism (Beltman et al., 2003), and facilitates speciation (Beltman et al., 2004), and the socially transmitted mobbing of brood parasites by host birds affects the balance of costs to benefits in the evolution of parasitism (Thorogood and Davies, 2012). It would consequently be a mistake to assume that acquired characters are only relevant to human evolution.

Of course, all conceptual frameworks, including those that I myself advocate, channel thinking, and all will eventually be superseded. However, for the moment there is much useful mileage to be had by thinking more deeply about developmental bias, niche construction, and reciprocal causation, and by revisiting the meanings of evolutionary causes and evolutionary processes.

Acknowledgements

This essay is dedicated to Jerry Hogan, who is one of a surprisingly small number of people who have both appreciated the importance of, and thought clearly about, biological causation. I am grateful to John Endler for helpful discussion and to two referees for useful feedback.

References

- Allen, C.E., Beldade, P., Zwaan, B.J., Brakefield, P.M., 2008. Differences in the selection response of serially repeated color pattern characters: standing variation, development, and evolution. *BMC Evol. Biol.*, <http://dx.doi.org/10.1186/1471>.
- Amundson, R., 2005. *The Changing Role of the Embryo in Evolutionary Thought*. Cambridge University Press, Cambridge.
- Arthur, W., 2004. *Biased Embryo and Evolution*. Cambridge University Press, Cambridge.
- Arthur, W., 2011. *Evolution: A Developmental Approach*. Wiley-Blackwell, New York.
- Badyaev, A.V., Uller, T., 2009. Parental effects in ecology and evolution: mechanisms, processes and implications. *Philos. Trans. R. Soc. B* 364, 1169–1177.
- Barker, G., Desjardins, E., Pearce, T. (Eds.), 2014. *Entangled Life. Organism and Environment in the Biological and Social Sciences*. Springer, New York.
- Bateson, P., 1988. The active role of behaviour in evolution. In: Ho, Fox (Eds.), *Evolutionary Processes and Metaphors*. Wiley-Blackwell, New York.
- Bateson, P., Gluckman, P., 2011. *Plasticity, Robustness, Development and Evolution*. Cambridge University Press, Cambridge.
- Beldade, P., Koops, K., Brakefield, P.M., 2002. Developmental constraints versus flexibility in morphological evolution. *Nature* 416, 844–847.
- Beltman, J.B., Haccou, P., ten Cate, C., 2004. Learning and colonization of new niches: a first step towards speciation. *Evolution* 58, 35–46.
- Beltman, J.B., Haccou, P., ten Cate, C., 2003. The impact of learning foster species' song on the evolution of specialist avian brood parasitism. *Behav. Ecol.* 14, 917–923.

- Boogert, N.J., Reader, S.M., Laland, K.N., 2006. The relationship between social rank, neophobia and individual learning ability in starlings (*Sturnus vulgaris*). *Anim. Behav.* 72, 1229–1239.
- Boogert, N.J., Reader, S.M., Hoppitt, W.J.E., Laland, K.N., 2008. The origin and spread of innovations in starlings. *Anim. Behav.* 75, 1509–1518.
- Brakefield, P., 2006. Evo-devo and constraints on selection. *Trends Ecol. Evol.* 21, 362–368.
- Brakefield, P., 2011. Evo-devo and accounting for Darwin's endless forms. *Philos. Trans. R. Soc. B* 366, 2069–2075.
- Coolen, I., Ward, A.J.W., Hart, P.J.B., Laland, K.N., 2005. Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behav. Ecol.* 16, 865–870.
- Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M., Byrd, G.V., 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307, 1959–1961.
- Darwin, C., 1859. *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London (1st ed. reprinted Penguin Books, London; 1968).
- Day, R.L., Coe, R.L., Kendal, J.R., Laland, K.N., 2003. Neophilia, innovation and social learning: a study of intergeneric differences in Callitrichid monkeys. *Anim. Behav.* 65, 559–571.
- Dawkins, R., 1982. *The Extended Phenotype*. Oxford University Press, Oxford.
- Dewsbury, D., 1999. The proximate and the ultimate: past, present, and future. *Behav. Processes* 46, 189–199.
- Dickins, T., Rahman, Q., 2012. The extended evolutionary synthesis and the role of soft inheritance in evolution. *Proc. R. Soc. B*, <http://dx.doi.org/10.1098/rspb.2012.0273>.
- Dobzhansky, T., 1937. *Genetics and the Origin of the Species*. Columbia University Press, New York.
- Durham, W.H., 1991. *Coevolution: Genes, Culture and Human Diversity*. Stanford University Press, Stanford, CA.
- Ellner, S., Geber, M.A., Hairston, N.G., 2011. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol. Lett.* 14, 603–614.
- Endler, J.A., 1986a. *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ.
- Endler, J.A., 1986b. The newer synthesis? Some conceptual problems in evolutionary biology. *Oxford Surv. Evol. Biol.* 3, 224–243.
- Erwin, D.H., 2008. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends Ecol. Evol.* 23, 304–310.
- Feldman, M.W., Cavalli-Sforza, L.L., 1989. On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In: Feldman, M.W. (Ed.), *Mathematical Evolutionary Theory*. Princeton University Press, Princeton, NJ, pp. 145–173.
- Feldman, M.W., Laland, K.N., 1996. Gene–culture coevolutionary theory. *Trends Ecol. Evol.* 11, 453–457.
- Ford, E.B., 1964. *Ecological Genetics*. Methuen, London.
- Futuyma, D.J., 1998. *Evolutionary Biology*, 3rd ed. Sinauer, Sunderland, MA.
- Galis, F., Arntzen, J.W., Lande, R., 2010. Dollo's law and the irreversibility of digit loss in *Bachia*. *Evolution* 64, 2466–2476.
- Gerhart, J.C., Kirschner, M.W., 2007. The theory of facilitated variation. *Proc. Natl. Acad. Sci. U.S.A.* 104, 8582–8589.
- Gerhart, J.C., Kirschner, M.W., 2010. Facilitated variation. In: Pigliucci, M., Mueller, B.G. (Eds.), *Evolution: The Extended Synthesis*. MIT Press, Boston, MA.
- Gottlieb, G., 1992. *Individual Development and Evolution. The Genesis of Novel Behavior*. Oxford University Press, Oxford.
- Gould, S.J., 2000. *The Structure of Evolutionary Theory*. Belknap Press, New York.
- Gould, S.J., Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm. A critique of the adaptationist programme. *Proc. R. Soc. B* 205, 581–598.
- Green, J., 2009. *Volcanoes Around the World*. PowerKids Press, New York.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., Fox, J.A., 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8, 1114–1127.
- Haldane, J.B.S., 1985. *On Being the Right Size and Other Essays*. Oxford University Press, Oxford.
- Hamburge, V., 1980. Embryology and the modern synthesis in evolutionary theory. In: Mayr, Provine (Eds.), *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Cambridge University Press, Cambridge, pp. 97–112.
- Hogan, J.A., 1994. The concept of cause in the study of behavior. In: Hogan, J.A., Bolhuis, J.J. (Eds.), *Causal Mechanisms of Behavioural Development*. Cambridge University Press, Cambridge, pp. 3–15.
- Hogan, J.A., Bolhuis, J.J., 2009. The development of behavior: trends since Tinbergen. In: Bolhuis, J.J., Verhulst, S. (Eds.), *Tinbergen's Legacy: Function and Mechanism in Behavioral Biology*. Cambridge University Press, Cambridge, pp. 82–106.
- Holden, C., Mace, R., 1997. Phylogenetic analysis of the evolution of lactose digestion in adults. *Hum. Biol.* 69, 605–628.
- Hoppitt, W.J.E., Laland, K.N., 2013. *Social Learning: An Introduction to Mechanisms, Methods, and Models*. Princeton University Press, Princeton, NJ.
- Hoppitt, W.J.E., Brown, G., Kendal, R.L., Rendell, L., Thornton, A., et al., 2008. Lessons from animal teaching. *Trends Ecol. Evol.* 23, 486–493.
- Hull, D.L., 1982. The naked meme. In: Plotkin, H.C. (Ed.), *Learning, Development, and Culture*. Wiley, Chichester, pp. 273–327.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427.
- Jablonka, E., Lamb, M., 1995. *Epigenetic Inheritance and Evolution: Lamarckian Dimension*. Oxford University Press, Oxford.

- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Keller, E.F., 2010. The Mirage of a Space between Nature and Nurture. Duke University Press, Durham, NC.
- Kingsolver, J.G., et al., 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157, 245–261.
- Kirschner, M., Gerhart, J., 2005. The Plausibility of Life: Resolving Darwin's Dilemma. Yale University Press, New Haven, CT.
- Krakauer, D.C., Page, K.M., Erwin, D.H., 2009. Diversity, dilemmas, and monopolies of niche construction. *Am. Nat.* 173, 26–40.
- Kumm, J., Laland, K.N., Feldman, M.W., 1994. Gene–culture coevolution and sex ratios: the effects of infanticide, sex-selective abortion, and sex-biased parental investment on the evolution of sex ratios. *Theor. Popul. Biol.* 46, 249–278.
- Lachlan, R.F., Slater, P.J.B., 1999. The maintenance of vocal learning by gene–culture interaction: the cultural trap hypothesis. *Proc. R. Soc. B* 266, 701–706.
- Laland, K.N., Plotkin, H.C., 1991. Excretory deposits surrounding food sites facilitate social learning of food preferences in Norway rats. *Anim. Behav.* 41, 997–1005.
- Laland, K.N., Plotkin, H.C., 1993. Social transmission of food preferences amongst Norway rats by marking of food sites, and by gustatory contact. *Anim. Learn. Behav.* 21, 35–41.
- Laland, K.N., Sterelny, K., 2006. Seven reasons (not) to neglect niche construction. *Evolution* 60, 1751–1762.
- Laland, K.N., Kumm, J., Feldman, M.W., 1995. Gene–culture coevolutionary theory: a test case. *Curr. Anthropol.* 36, 131–156.
- Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 1996. On the evolutionary consequences of niche construction. *J. Evol. Biol.* 9, 293–316.
- Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 1999. Evolutionary consequences of niche construction and their implications for ecology. *Proc. Natl. Acad. Sci. U.S.A.* 96, 10242–10247.
- Laland, K.N., Odling-Smee, F.J., Gilbert, S.F., 2008. EvoDevo and niche construction: building bridges. *J. Exp. Zool.* 310B, 549–566.
- Laland, K.N., Odling-Smee, F.J., Myles, S., 2010. How culture has shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* 11, 137–148.
- Laland, K.N., Sterelny, K., Odling-Smee, F.J., Hoppitt, W., Uller, T., 2011. Cause and effect in biology revisited: is Mayr's proximate–ultimate dichotomy still useful? *Science* 334, 1512–1516.
- Laland, K.N., Odling-Smee, J., Hoppitt, W., Uller, T., 2013a. More on how and why: cause and effect in biology revisited. *Biol. Philos.* 28, 719–745.
- Laland, K.N., Odling-Smee, J., Hoppitt, W., Uller, T., 2013b. More on how and why: a response to commentaries. *Biol. Philos.* 28, 793–810.
- Laland, K.N., Odling-Smee, F.J., Turner, S., 2014. The role of internal and external constructive processes in evolution. *J. Physiol.* 592, 2413–2422.
- Lande, R., Arnold, S.J., 1983. The measurement of selection on correlated characters. *Evolution* 37, 1210–1226.
- Leadbeater, E., Chittka, L., 2007. Social learning in insects – from miniature brains to consensus building. *Curr. Biol.* 16, R323–R325.
- Lehmann, L., 2008. The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. *Evolution* 62, 549–566.
- Lewins, R.C., Lewontin, R.C., 1985. *The Dialectical Biologist*. Harvard University Press, Cambridge, MA.
- Lewontin, R.C., 1982. Organism and environment. In: Plotkin, E.C. (Ed.), *Learning, Development and Culture*. Wiley-Blackwell, New York.
- Lewontin, R.C., 1983. Gene, organism and environment. In: Bendall (Ed.), *Evolution from Molecules to Men*. Cambridge University Press, Cambridge.
- Lewontin, R.C., 2000. *The Triple Helix: Gene, Organism, and Environment*. Harvard University Press, Cambridge, MA.
- Loreau, M., 2010. From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis. Princeton University Press, Princeton, NJ.
- Lumsden, C.J., Wilson, E.O., 1981. *Genes, Mind and Culture*. Harvard University Press, Cambridge, MA.
- Maynard-Smith, J., Burian, R., Kaufman, S., Alberch, P., Campbell, J., et al., 1985. Developmental constraints and evolution. *Quat. Rev. Biol.* 60, 265–287.
- Mayr, E., 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.
- Mayr, E., 1961. Cause and effect in biology. *Science* 134, 1501–1506.
- Mayr, E., 1982. *The Growth of Biological Thought: Diversity, Evolution and Inheritance*. Belknap Press, New York.
- Minelli, A., Bortolotto, S., 1988. Myriapod metamerism and arthropod segmentation. *Biol. J. Linn. Soc.* 33, 323–343.
- Moczek, A.P., Sultan, S., Foster, S., Ledon-Rettig, C., Dworkin, I., et al., 2011. The role of developmental plasticity in evolutionary innovation. *Proc. R. Soc. B* 278, 2705–2713.
- Moyes, C., Schulte, J., 2007. *Principles of Animal Physiology*, 2nd ed. Pearson, New York.
- Müller, G., 2007. Evo-devo: extending the evolutionary synthesis. *Nat. Rev. Genet.* 8, 943–950.
- Nielsen, R., Hellmann, I., Hubisz, M., Bustamante, C., Clark, A.G., 2007. Recent and ongoing selection in the human genome. *Nat. Rev. Genet.* 8, 857–868.
- Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 1996. Niche construction. *Am. Nat.* 147, 641–648.
- Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. *Niche Construction: The Neglected Process in Evolution*. Monographs in Population Biology, 37, Princeton University Press, Princeton, NJ.
- Odling-Smee, F.J., Erwin, D., Palkovacs, E., Feldman, M., Laland, K.N., 2013. *Niche construction theory: a practical guide for ecologists*. *Quat. Rev. Biol.* 88, 3–28.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H., 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, NJ.
- Oyama, S., 1985. *The Ontogeny of Information*. Cambridge University Press, Cambridge.
- Oyama, S., Griffiths, P.E., Gray, R.D. (Eds.), 2001. *Cycles of Contingency: Developmental Systems and Evolution*. MIT Press, Cambridge.
- Pfennig, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D., et al., 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* 25, 459–467.
- Plotkin, H.C., 1994. *Darwin Machines and the Nature of Knowledge*. Penguin, New York.
- Popper, K., 1979. *Objective Knowledge: An Evolutionary Approach*. Oxford University Press, Oxford.
- Post, D.M., Palkovacs, E.P., 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. B* 364, 1629–1640.
- Richerson, P., Boyd, R., Henrich, J., 2010. Gene–culture coevolution in the age of genomics. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8985–8992.
- Roughgarden, J., 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan Publishing, New York.
- Schlichting, C.D., Pigliucci, M., 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer, Sunderland, MA.
- Scott-Phillips, T., Dickins, T., West, S., 2011. Evolutionary theory and the ultimate–proximate distinction in the human behavioural sciences. *Psychol. Sci.* 6, 38–47.
- Scott-Phillips, T., Laland, K.N., et al., 2014. The niche construction perspective: a critical appraisal. *Evolution*, <http://dx.doi.org/10.1111/evo.12332>.
- Sober, E., 1984. *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. University of Chicago Press, Chicago.
- Stoltzfus, A., 2012. Constructive neutral evolution: exploring evolutionary theory's curious disconnect. *Biol. Direct* 7, 35.
- Thierry, B., 2005. Integrating proximate and ultimate causation: just one more go! *Curr. Sci.* 89, 1180–1183.
- Thorogood, R., Davies, N.B., 2012. Cuckoos combat socially transmitted defences of reed warbler hosts with a plumage polymorphism. *Science* 337, 578–580.
- Tishkoff, S.A., et al., 2007. Convergent adaptation of human lactase persistence in Africa and Europe. *Nat. Genet.* 39, 31–40.
- Tooby, J., Cosmides, L., 1992. The psychological foundations of culture. In: *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford University Press, Oxford, pp. 137–159.
- Turner, J.S., 2000. *The Extended Organism: The Physiology of Animal-built Structures*. Harvard University Press, Cambridge, MA.
- Ulijaszek, S.J., Strickland, S.S., 1993. *Nutritional Anthropology: Prospects and Perspectives*. Smith-Gordon, London.
- Voight, B.F., Kudaravalli, S., Wen, X., Pritchard, J.K., 2006. A map of recent positive selection in the human genome. *PLoS Biol.* 4, e72.
- Wang, E.T., Kodama, G., Baldi, P., Moyzis, R.K., 2006. Global landscape of recent inferred Darwinian selection for *Homo sapiens*. *Proc. Natl. Acad. Sci. U.S.A.* 103, 135–140.
- Watt, W., 2013. Causal mechanisms of evolution and the capacity for niche construction. *Biol. Philos.* 28, 757–766.
- West-Eberhard, M.J., 2003. *Developmental Plasticity and Evolution*. Oxford University Press, Oxford.
- Wilson, E.O., 1975. *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, MA.
- Wilson, E.O., 1978. *On Human Nature*. Harvard University Press, Cambridge, MA.