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CHAPTER

Dialectics That Sweep Away ‘COWDUNG’: The Construction of Evolutionary, Cultural, and Scientific Niches

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Abstract

Developmental geneticist Conrad Waddington and evolutionary biologist Richard Lewontin, two of the pioneers of niche construction theory, were explicit in regarding organisms as co-directing their own evolution. In *The Ethical Animal* (1960), Waddington anticipated features of contemporary cultural evolution theory, including the evolutionary significance of cultural norms. Lewontin was suspicious of evolutionary accounts of human behaviour, which he viewed as governed by political forces and power relations, and in *The Dialectical Biologist* (1985) stressed how scientific enquiry could be biased by politics. Here the authors suggest that Waddington’s emphasis on ethical considerations, and Lewontin’s admonitions concerning sociopolitical interpretation of biological research, remain relevant to the field of cultural evolution, and they review some related scientific controversies. The authors argue that human cultural activities not only construct evolutionary and cultural niches, but also scientific niches. This reasoning applies to both contemporary debates within the evolutionary human sciences and wider evolutionary theory, including niche construction theory itself.

Keywords: [niche construction](#), [cultural evolution](#), [dialectics](#), [scientific ethics](#), [ideology](#), [scientific research programs](#)

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The Ethical Animal and The Dialectical Biologist

Niche construction is the process by which organisms alter the states of their environments, or their relations to them, thereby modifying the conditions that they, and other organisms, experience. Lewontin (1982, 1983, 2000) stressed the symmetry of the interaction between organism and environment (see also Odling-Smee, 1988; Odling-Smee et al., 2003). Niche construction theory is explicit in regarding organisms as co-directing their own evolution, with organisms modifying their environments ('niche construction'), and generating an ecological legacy over time ('ecological inheritance') (Odling-Smee, 1988; Odling-Smee et al., 2003). Through their activities, organisms modify selection acting on themselves and other species that share their environment. Evolution thus entails networks of causation and feedback in which previously selected organisms drive environmental changes, and organism-modified environments subsequently select for changes in organisms.

Niche construction is not restricted to the biological adaptations of organisms, but also stems from their developmental plasticity, their by-products, and their acquired characters. Humans possess a particularly potent capacity for environmental modification, with our niche construction dominated by cultural activities (Laland, 2017; Laland et al., 2000). For this reason, cultural evolution is highly relevant to understanding human biological evolution, and can generate gene-culture coevolution (Boyd & Richerson 1985; Cavalli-Sforza & Feldman, 1973, 1981; Creanza et al., 2017; Feldman & Cavalli-Sforza 1976; Feldman & Laland, 1996).

Although the scientific study of niche construction dates back at least to the early writings of William King on ecological succession in the seventeenth century, it was brought to prominence by the writings of two of the twentieth century's most radical biological thinkers: Conrad Waddington and Richard Lewontin.

In developmental geneticist Waddington's (1960) book, *The Ethical Animal*, he argued that social learning and teaching differentiates humanity from the rest of the animal kingdom and provides our species with a second means of evolutionary change, in addition to biology. While he undoubtedly underestimated the cultural capabilities of other animals, Waddington should be credited for anticipating some key aspects of contemporary cultural evolution theory, including that cultural dynamics could lead to change and adaptation, and drive gene-culture coevolution. However, Waddington also stressed the idea that humans are unique in their capacity to entertain ethical ideas, which he characterized as essential and necessary features of this new mode of evolution. For Waddington, ethics was not a peripheral epiphenomenon of culture but a principal driver of cultural evolution.

Contemporary cultural evolutionary theory broadly concurs with Waddington's conclusion. While cultural traditions are widespread amongst the great apes and found in some other animal taxa too (van Schaik et al., 2003; Whiten et al., 1999, 2017; see Whiten, this volume), humans are especially proficient at teaching, highly disposed towards conformity, and uniquely reliant on norms (Boyd, 2018; Boyd & Richerson, 1985; Castro & Toro, 2004; Csibra & Gergely, 2011; Henrich, 2016; Laland, 2017). Norms go beyond conventions to dictate how individuals in human societies *should* behave, such as how they should build a fire, catch a turtle, or till the soil (Boyd & Richerson, 1985; Henrich, 2016); that is there is an ethical component to group-typical behaviour. Norms go beyond specifying what is the *common* way to behave, to dictating what is the *right* way to behave. Moreover, hominin social life does not merely entail living in groups but also identifying with the group, abiding by its rules, and privileging in-group members (Boyd & Richerson, 1985; Henrich, 2016; Sterelny, 2012). All human societies possess such norms and laws which substantially enhance their capacity for cultural evolution and cooperative endeavour (Boyd & Richerson, 1985; Fehr & Fischbacher, 2003; Henrich, 2016; see Takezawa, this volume).

Norms also specify the consequences of not abiding by the rules (Fehr & Fischbacher, 2003): to do so is not just wrong, or even inappropriate, but frequently *unethical* and can provoke severe punishment. As we shall

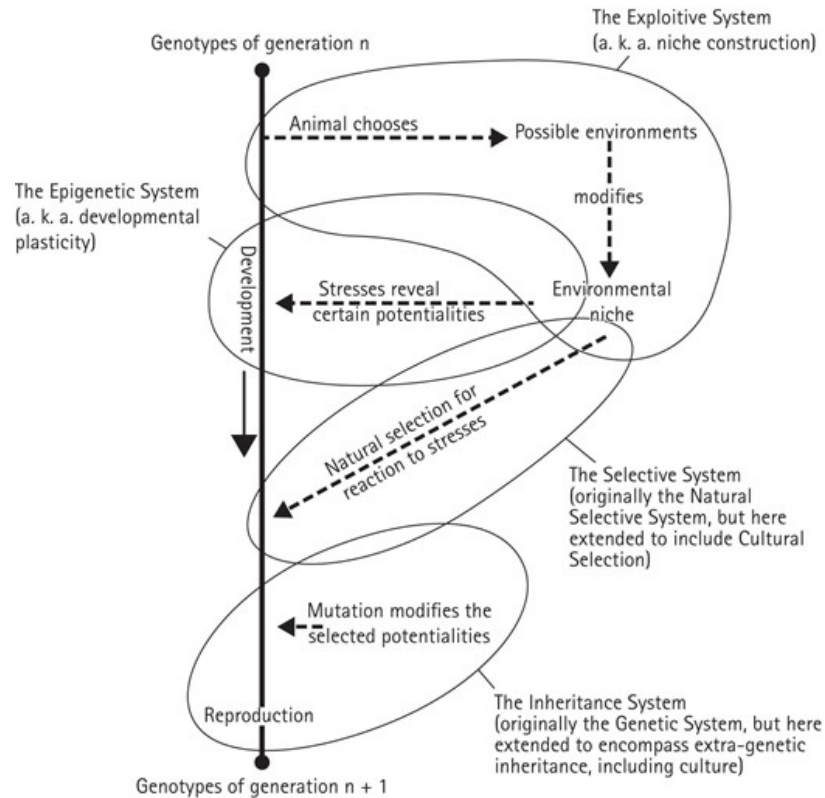
see, scientists are ethical animals too, and there exist discipline-specific norms that regulate, and occasionally stifle, scientific endeavour. Cultural evolution theory is thus highly relevant to understanding the attitudes and practices of contemporary scientists, as well as to shedding light on academic controversies.

Waddington is not generally recognized as a foundational figure in the field of cultural evolution but arguably should be for pioneering a courageous stance that most cultural evolutionists now take for granted. In a nutshell, that position can be summarized as ‘development matters’. The cultural evolutionist stance is the antithesis of biological determinism: it is the idea that culture cannot ultimately be reduced to the dictates of genes. Thus cultural evolution has some level of autonomy from genetic evolution, and hence possesses some capacity to co-direct evolutionary change. However, Waddington’s adherence to that position was far more general than its application to humans.

Waddington (1957, 1959) believed that evolutionary theory as conventionally understood was incomplete and that there are additional processes that are causally important in evolution whose significance remained poorly appreciated. These include what he labelled ‘the epigenetic system’ and ‘the exploitive system’, which in contemporary parlance can be understood as important evolutionary roles for *phenotypic plasticity* and *niche construction*. These developmental processes were important to Waddington because he saw them as feedback systems that codetermine how natural selection (‘the natural selection system’) and inheritance (‘the genetic system’) operate in evolution (see the feedback arrows in Figure 1, based on Waddington, 1959). For Waddington, development was not just a genetically controlled product of evolution, relevant only to ‘proximate’ causation (Mayr, 1961) but also, because of this feedback, an indirect conduit to ‘ultimate’ (evolutionary) causation too (Laland et al., 2011). For example, Waddington’s (1959) idea that differences in developmental responses to stress would generate variation in fitness and thereby alter stress-related selection, is clearly at odds with Mayr’s (1980, p. 9) dogmatic assertion that developmental processes tell researchers ‘absolutely nothing’ about evolution. To quote Waddington’s disciple Mary Jane West-Eberhard (2003): ‘The proximate-ultimate distinction has given rise to a new confusion, namely, a belief that proximate causes of phenotypic variation have nothing to do with ultimate, evolutionary explanation’ (West-Eberhard, 2003, p. 11).

Waddington’s work is currently experiencing something of a renaissance. It was Waddington who first coined the term ‘epigenetics’, and he is widely recognized as a foundational figure for this field (Jablonka, 2017; West-Eberhard, 2003). Waddington’s pioneering experimental work on genetic assimilation was an early demonstration of ‘plasticity led evolution’ (Levis & Pfennig, 2016; West-Eberhard, 2003), and his important contribution to the emergence of niche construction theory is well documented (Odling-Smee et al., 2003; Sultan, 2015). Central to all these ideas is the concept of feedback between multiple processes, possibly operating at different temporal and spatial scales, in dynamical systems. Within the field of cultural evolution, of course, such dynamic feedback is a given.

Figure 1



Waddington's (1959) model of the logical structure of biological evolution, translated into contemporary terminology.

Adapted from Fig. 1 in Waddington. 1959.

Richard Lewontin (1982, 1983, 2000) brought a similar perspective to prominence within evolutionary biology, which may be no coincidence as Waddington and Lewontin are known to have participated in workshops together and most likely shaped each other's thinking (see, for example, *Towards a theoretical biology*, books 1 and 3, edited by Waddington (1968, 1970)). Lewontin's writings also stressed how genes, organisms, and environments are in reciprocal interaction with each other in a way that is both cause and effect. He argued that the legacies of Darwin and Mendel included misleading metaphors that: 'are responsible for certain difficulties in biology, difficulties that prevent us from some kinds of further progress and which keep us locked into a rigid framework of thought about the development and evolution of organisms' (Lewontin, 1983, p. 276). Mendel's view of organisms as the manifestation of autonomous internal 'factors' (i.e. genes) with their own laws, germinated into a post-synthesis metaphor in which ontogeny 'is seen as an unfolding of a form, already latent in the genes, requiring only an original triggering at fertilization and an environment adequate to allow "normal" development to continue' (Lewontin, 1983, p. 276). Likewise, Lewontin regarded Darwin's view of organisms as passive objects moulded by the external force of natural selection as encouraging a conception of evolution in which 'the environment "poses the problem"; the organisms posit "solutions", of which the best is finally "chosen"' (Lewontin, 1983) (In passing, we note that while Lewontin's understanding of Darwin's stance is in line with much Neo-Darwinism, it is at odds with more recent scholarship that views Darwin as embracing a more active role for the organism in evolution; Bradley, 2020).

It is no coincidence that in all his major writings on niche construction without exception, Lewontin stressed that development was not genetically determined. Many of the claims concerning the evolutionary significance of niche construction only make sense under this assumption. Central to the niche-construction perspective has always been a view of developmental processes as open, environmentally

contingent, and self-constructive. Organisms are regarded as influenced, but not determined, by their genes, and their activities are shaped by developmental information-gaining processes as well as by a history of natural selection (Laland & Sterelny, 2006; Lewontin, 1983; Odling-Smee et al., 2003; Sultan, 2015). For researchers sympathetic to this view ('constructive development', Laland et al., 2015) there exists an 'explanatory gap' between the ancestral natural selection that shaped the niche-constructing capabilities and the resulting environmental modification (Laland et al., 2019). One cannot explain, for instance, observed variation in plant-leaf shape solely in terms of genetic variation since, amongst other factors, it is partly shaped by inherited epigenetic marks (Sultan, 2015). More generally, phenotypes are the results of complex interactions between genotype, epigenotype, parental and current environment, learned behaviour, other ontogenetic exploratory and selective processes, as well as developmental noise (Kirschner & Gerhardt, 2005; Lewontin, 2000; Odling-Smee et al., 2003; Sultan, 2017). The characterization of niche construction as an evolutionary process would make little sense if the activities of organisms were entirely genetically determined, since natural selection would fully account for niche construction.

This is a key point for cultural evolutionary theory too, as there would be no need for cultural evolution theory if human behaviour and cognition were genetically determined. Prior natural selection may explain the existence of a *capacity* for learning and culture, but does not explain why individuals in particular populations should, say, consume dairy products or cultivate yams. The ability to learn has been subject to biological (i.e. genetic) evolution and is, at least to some degree, a species-typical universal attribute, but the learned knowledge and behaviour of individual humans is not genetically specified and is shaped primarily by cultural history, rather than biological evolution.

In contrast to Waddington, Lewontin was famously suspicious of all evolutionary accounts of human behaviour. This was in part because he rejected the genetic determinism implicit in much human sociobiology, but also partly because he saw human behaviour as governed by political forces and power relations that evolutionary accounts typically failed to capture (Segerstrale, 1986, 2000). In *The dialectical biologist*, Lewontin, together with Richard Levins, stressed how scientific enquiry was far from immune to this politics (Levins & Lewontin, 1985).

Below we suggest that Waddington's emphasis on ethical considerations, and Lewontin's bio-political stance, remain relevant to the field of cultural evolution, and review some related scientific controversies. We argue that human cultural activities not only construct evolutionary and cultural niches but also scientific niches. This reasoning applies to both contemporary debates within the evolutionary human sciences (Laland & Brown 2011) and wider evolutionary theory, including the niche construction theory itself (Laland et al., 2014, 2015; Wray et al., 2014).

Construction of Evolutionary Niches

Female dung beetles (*Onthophagus spp.*) dig tunnels underneath cowpats, within which they construct brood balls of dung containing a single egg. In doing so, they build a safe, thermally buffered home for their offspring, pre-stocked with the food (i.e. dung) that the emerging larvae will need to complete its development and metamorphosis, including a fecal pellet through which the larvae acquire their mother's gut biota (Hu et al., 2019). The larvae also engage in niche construction, by mixing the dung, repairing the brood ball, and constructing a pupation chamber. Experimental studies show that both maternal and larval niche construction strongly affect larval development, enhancing larval growth and affecting fitness (Schwab et al., 2016, 2017). Their actions generate covariation between diverse niche-constructing traits and other phenotypic characters, including growth, duration of development, and degree of sexual dimorphism. In this manner, niche construction biases the nature of phenotypic variation exposed to natural selection, generating a major axis of covariation with plastically expressed morphological traits. Thus this beetle's niche construction determines the shape of natural selection acting on it by specifying both the targets and the by-products of selection.

Experimental manipulations that either permitted or cancelled the environmental effects of this niche construction also established that the modification of environments by larvae was critically necessary for the maintenance of sexual dimorphism. Larval niche construction was what determined the relationship between key secondary sexual traits (including foreleg size, eye size, and horn size) and fitness. The reason why adult beetle horn size is under sexual selection, as opposed to some other beetle character, is because this trait is unusually sensitive to the way that larval niche construction makes carbon nutrients available to the growing beetle and is thereby an honest signal of beetle quality. Here, niche construction determines what selection occurs, and it is in this sense that we can regard it as an evolutionary cause.

The beetle example has wider implications, including for humans. It suggests that when organisms engage in niche construction, for instance, building nests, digging burrows, or modifying soils, their activities generate regularities in the phenotypic variation exposed to selection, regularities in the fitness of those variants, and regularities in the response to selection (Odling-Smee et al., 2003; Sultan, 2015).

Developmental mechanisms generate consistent patterns in each species' niche construction and in the process produce biased phenotypic variation spanning multiple co-regulated traits. Parallel evolution need not start with similar environments but can be triggered by conserved developmental regularities found in related organisms. This is relevant to humans, where, for instance, consistent cultivation of specific crops has generated parallel evolution of the digestive enzymes of human populations (e.g. increasing copy number of *AMY1*, Perry et al., 2007). In other words, humans do not niche construct at random, but impose direction on their, and on other species', evolution. In this way niche construction is certainly an evolutionary process.

There is now little doubt that human cultural niche construction has co-directed human evolution (Creanza et al., 2017; Laland et al., 2010). Human cultural practices have dramatically modified the selection experienced by human populations, for instance, by facilitating dispersal into new environments with different climates, and through the development of agriculture and the domestication of livestock, which created novel selection on teeth, facial musculature, and digestive enzymes (Feldman & Cavalli-Sforza, 1989; Sabeti et al., 2006; Voight et al., 2006). Over a period of 50,000 years, humans spread from Africa around the globe, experienced an ice age, witnessed rapid increases in population densities, domesticated hundreds of species of plants and animals, and, by keeping animals, experienced a new proximity to animal pathogens (Stringer & Andrews, 2005). Each of these events represents a rapid and major transformation in human selection pressures and resulted in substantive genetic change in human populations (Laland et al., 2010), and virtually all have been self-imposed (O'Brien & Laland, 2012). These events resulted from the flexibility conferred by human cultural niche construction (Odling-Smee et al., 2003).

The possibility that genes and culture might coevolve was first investigated mathematically over 40 years ago by Feldman and coworkers, who devised methods now widely deployed in the fields of *cultural evolution* and *gene–culture coevolution* (a.k.a. *culture–gene coevolution*, *dual–inheritance theory*, and *cultural niche construction*; Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976; Henrich, 2016; Laland et al., 2000). This work established that genes and culture can be modelled as two interacting forms of inheritance, allowing exploration of how learned behaviour coevolves with alleles that affect the expression or acquisition of the behaviour, or whose fitness is affected by the cultural environment.

The approach has been used to explore the adaptive advantages of reliance on learning and culture (Aoki et al., 2016; Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976; Feldman & Laland, 1996; Ram et al., 2018, 2019; Richerson & Boyd, 2005), to investigate the inheritance of behavioural and personality traits (Cavalli-Sforza & Feldman, 1973; Feldman & Ramachandran, 2018; Laland et al., 1995; Otto et al., 1995), and to examine specific topics in human behavioural evolution, such as the evolution of cooperation (Richerson & Boyd, 2005; Richerson et al., 2010, 2016) or Neanderthal extinction (Cohen et al., 2021; Gilpin et al., 2016; Wakano et al., 2018).

There is increasing evidence for gene–culture coevolution in other animals, including nonhuman primates, whales and birds (Whitehead et al., 2019). However, gene–culture coevolution has reached its zenith in humans. Cultural change will typically occur faster than genetic adaptation, and this has allowed cultural niche construction to play a prominent role in human evolution (Creanza et al., 2017). Such studies conclusively demonstrate that genes and culture can coevolve, and that in such interactions culture is not just an outcome but also a potent cause and codirector of evolutionary events.

These gene–culture coevolutionary analyses have established that cultural processes can strongly affect evolutionary rates (Boyd & Richerson, 1985; Creanza & Feldman, 2014; Feldman & Laland, 1996; Laland, 2017). A familiar example is the coevolution of dairy farming and associated consumption of dairy products with alleles of genes that allow adult humans to digest lactose (Bersaglieri et al., 2004; Burger et al., 2007; Feldman & Cavalli-Sforza, 1989; Gerbault et al., 2011; Holden & Mace, 1997; Peng et al., 2012). By constructing a dairying niche, certain human populations induced selection on lactase persistence (*LCT*) alleles.

Lactase persistence is perhaps the best-studied case of gene–culture coevolution, but rapidly accumulating genetic and anthropological data suggest that it is far from unique. Indeed, the example may be broadly representative of a very general pattern of gene–culture coevolution over the last 20,000 years. Recent analyses of human genetic variation suggest that hundreds of genes have been subject to recent positive selection, many apparently in response to human cultural activities (Sabeti et al., 2006; Voight et al., 2006). Gene–culture coevolution may also explain the acceleration in evolutionary rates reported for our species in the last 40,000 years (e.g. Hawkes et al., 2007).

A review compiled data concerning 27 separate genes known to have been subject to recent selection, for which the inferred cultural selection pressure is a change in diet associated with the advent of agriculture (Laland et al., 2010). In addition to those related to dairy products, the list also includes genes expressed in the metabolism of carbohydrates, starch, proteins, lipids, phosphates, plant secondary compounds, and alcohol, as well as jaw muscle fibres and tooth–enamel thickness. Comparative evidence suggests that the cultural change came first, constructing a dietary niche in which genetic change followed (Burger et al., 2007; Holden & Mace, 1997; Laland et al., 2010).

In some West African populations, the practice of cultivating yams has inadvertently generated selection for the haemoglobin S allele that is responsible for sickle cell anaemia, causing it to increase in frequency (Durham, 1991; O'Brien & Laland, 2012). Slash and burn agriculture creates conditions that lead to increased

standing water when it rains, which provides perfect breeding grounds for malaria-carrying mosquitos. The enhanced incidence of malaria, in turn, generates selection for gene variants that in heterozygotes confer resistance to malaria; one of these is the *HbS* allele of the haemoglobin gene. Here cultural activities generated the environmental conditions in which an allele that confers resistance to the disease (i.e. *HbS*) increases in frequency through natural selection. The fact that neighbouring populations with different food-procurement practices do not show the same increase in *HbS* frequency supports the conclusion that the cultural practice (clearing fields to grow crops) was the ultimate force that drove evolution at the haemoglobin gene (Durham, 1991).

Other human populations have constructed an urban niche in which particular diseases thrive. The transition to urban living and associated increases in population density, as well as the spread of pathogens through long-distance trade, and pathogen exposure through animal husbandry and irrigation, are now recognized to have promoted the spread of infectious diseases (Barnes, 2005; Roberts & Buikstra, 2003). For instance, variants of the *SLC11A1* gene are known to be associated with susceptibility to tuberculosis in humans (Bellamy et al., 1998; Li et al., 2006), and are also linked to other infectious diseases such as leprosy, leishmaniasis, and Kawasaki disease (Govoni & Gros, 1998). One study found a highly significant correlation between the frequency of those alleles that confer resistance and the duration of urban settlement—populations with a long history of living in towns are now better adapted to resisting infections that thrive in the urban environment (Barnes et al., 2011).

The studies mentioned above demonstrate that genes and culture can coevolve and that culture is not just an outcome but can be a co-director of the evolutionary process. Thus we suggest that in human evolution our ancestors' cultural practices played an active role in driving genetic change (Henrich, 2016; Laland, 2017). Human cultural niche construction directs human evolution, just as dung beetle niche construction directs dung beetle evolution. This emerging thesis stands in contrast to the historically prevalent narrative depicting hominins as adapting to external conditions, such as climate, predators, or disease, in a manner little different from other organisms (Calvin, 2002; Kurzban, 2011; Owen et al., 2018; Pinker, 2010; Potts, 1996; Potts & Faith, 2015).

Construction of Cultural Niches

The spread of a cultural trait can also create a cultural niche in which another cultural trait can flourish (which others characterize as culture–culture coevolution; Richerson & Boyd, 2005). A good example is provided by the demographic transition. The reduction in birth rate during the demographic transition is often viewed as a paradox because, from a traditional evolutionary perspective, it is difficult to envisage why individuals should prefer to have fewer children. However, cultural niche construction models show that if a cultural norm favouring greater education spreads, a preference for smaller family size follows, allowing the fertility rate to drop (Ihara & Feldman, 2004).

Psychologists and linguists commonly regard the human mind as a symbol-generating and artefact-devising system, as a result of which children develop in a world replete with diverse symbols and artefacts. A child's learning and development both shapes, and is shaped by, this highly constructed cognitive niche (Flynn et al., 2013). Artefacts, physical signs, and symbols built in the environment play important roles in both human development and evolution (Peterson et al., 2018). Niche construction is also now central to several accounts of how language evolved. For instance, Bickerton (2009) describes how our ancestors constructed scavenging niches that required them to communicate in order to recruit sufficient individuals to drive predators away from megafauna corpses. In turn, the use of language constructed a niche in which sophisticated cognition was advantageous. Tomlinson (2015, 2018) makes a related argument concerning the origins of music. Languages and dialects have been shown to function effectively as ethnic markers and

to promote local learning and other parochial tendencies (Kinzler et al., 2009). In turn, imitation, teaching, language diversification, and local conventions all act to ensure that local differences in behaviour among groups can be maintained in the face of the dispersal of individuals (Boyd & Richerson, 1985; Richerson et al., 2016), allowing cultural group selection (where cultural traits rather than genes are selected) to occur (Boyd, 2018; Brown & Richerson, 2014; Henrich, 2016; Richerson & Boyd, 2005; Richerson et al., 2016).

Another example concerns the primary causes of human technological complexity. This issue had proven contentious, with some researchers suggesting that large populations support diverse cultural knowledge (e.g., Henrich, 2004) and others arguing that environmental factors are more important. The paradox is resolved when niche construction is taken into account (Collard et al., 2012; Fogarty & Creanza, 2017). The effects of a changeable environment, to which food gatherers are subject, can be attenuated by the niche-constructing activities of food producers, such as agriculturalists, since on average farming generates more reliable (i.e. less variable) yields. As a result, the effects of environmental fluctuations on cultural complexity are stronger in food-gathering populations and weaker in food-producing populations, while the effect of population size is stronger in producers compared to gatherers.

The niche-construction perspective has proven productive in several other investigations of human social behaviour (Creanza et al., 2017; Kendal et al., 2011), including the extinction of megafauna (Boivin et al., 2016), hunting and gathering (Thompson et al., 2020), and the use of landscapes in Bali (Lansing et al., 2009; Lansing & Fox, 2011) and Polynesia (Quintus & Cochrane, 2018), often entailing complex cascades of ecological and social consequences of crop cultivation. The human transition from hunting and gathering to food production economies provides another case in point (Smith, 2007a,b, 2011, 2016). Archaeological and paleo-environmental records from eastern North America, Amazonia, the Near East, and China, contradict the assumption of traditional explanatory frameworks that environments change and species adapt to such change, and support niche construction theory accounts (Lombardo et al., 2020; Ren et al., 2016; Smith, 2011; Zeder, 2017).

Construction of Scientific Niches

Around the same time that Richard Dawkins introduced the word ‘meme’, Waddington (1977) came up with his own slightly unsettling term for the replicated conventional wisdom of dominant groups—COWDUNG! This graphic metaphor—COWDUNG—stands for Conventional Wisdom of the Dominant Group and is deliberately challenging. ‘Cow dung’ should be taken metaphorically to imply ‘rubbish’, synonymous to the use of ‘crap’ or ‘bullshit’ today. As an outsider to the evolutionary mainstream, Waddington was conscious of how the dominant discourse in scientific fields could be dogmatic. Some of his most radical claims—that epigenetics, plasticity led evolution, and niche construction are important for evolution—are now taken very seriously by the evolutionary biology community, and are perhaps even becoming mainstream. Yet they were certainly not at the time. Indeed, Waddington was cast as a heretic, and excluded from major evolutionary meetings (Peterson, 2016).

Waddington was part of a twentieth-century scientific movement known as ‘organicism’. Organicists held that evolution cannot be understood solely at the level of the gene, nor be adequately described by tracking gene frequencies, but demands consideration of how genotypes develop into phenotypes, and reciprocally, how phenotypes control and regulate gene expression (Peterson, 2016). For Waddington, gene action could only be understood by focusing on gene interactions (what we now call gene regulatory networks, or GRNs), and by recognizing extensive feedbacks with the developmental system (i.e. cell-, tissue- and environment-specific gene expression). Far from being the unrolling of a pre-existing genetic programme, development is a dialogue between the organism, its constituent parts, and the environment (see also Lewontin, 2000).

In the latter half of the twentieth century these views were out of kilter with mainstream evolutionary biology. In the Soviet Union, biologist Trofim Lysenko had adopted a theory of environmentally acquired inheritance, and used his political influence to undermine Mendelian genetics, leading to some geneticists being imprisoned or murdered. The Lysenko affair had incited a backlash in the West against research on environmental influences on heredity and development, leading to an intellectual climate in which research on plasticity or non-genetic inheritance was equated with sympathy for Lysenkoist ideas, and even considered grounds for dismissal from US university positions (Peterson, 2016). While Waddington was no Lamarckian, leading evolutionists marginalized his work as too close to the Lamarckian interpretation of evolution that characterized Lysenkoism.

Waddington put forward 'COWDUNG' as a metaphor for a specific type of cultural trait, namely, a self-sustaining dominant view. The term did not catch on but it nonetheless highlights Waddington's sensitivity to the dangers of scientific fields being trapped by a prevailing mindset. It also illustrates his recognition of the value of alternative perspectives and heterodox views to scientific progress. His choice of acronym leaves no doubt that Waddington believed the dominant group could get it wrong, and that received scientific wisdom could be dogma.

Once again, Richard Lewontin adopted a strikingly similar stance. In *The dialectical biologist*, Lewontin presents dialectics as both a healthy means to foster progress in biological research and a tool to counter scientific dogmatism (Levins & Lewontin, 1985). In *Not in our genes* (Rose et al., 1990) and *Biology as ideology* (Lewontin, 1993), Lewontin exposes many mainstream biological views as heavily influenced by social and political values. In *Biology under the influence* (Lewontin & Levins, 2007), Lewontin stresses how science is heavily influenced by ideology and social context, which can bias the questions asked and methods deployed, in ways that are both good and bad.

Both Waddington and Lewontin were passionate advocates of the scientific method, but their writings, nonetheless, drew attention to how the institutions of science could construct academic niches that perpetuate mainstream views. Philosophers of science refer to such niches as 'paradigms' (Kuhn, 1962) or 'scientific research programs' (Lakatos, 1978), and emphasize how the prevailing dominant mindset can strongly influence the practice of science, shaping the questions asked, the assumptions made, the factors recognized as causes, and the findings considered relevant. Moreover, many contemporary philosophers of science endorse Waddington's and Lewontin's argument that scientific progress requires pluralism, heterodoxy and the willingness to challenge the orthodox or dominant narrative (Barker et al., 2014; Kampourakis & Uller, 2020; Love, 2015; Potochnik, 2017).

More recently, philosophers of science have begun to investigate how ethical norms affect the assessment of theory (e.g. Douglas, 2009), although typically without explicitly recognizing Waddington's (1960) emphasis on scientists as 'ethical animals'. For instance, Douglas (2009) argues that value-free science is impossible, both because the questions being asked in research are always driven by social interests and values that shape the directions science takes, and because scientists commonly rely on their values to plug gaps in empirical data, allowing them to make scientific inferences. It is here that cultural evolutionists may be able to contribute to the philosophy of science, since cultural evolutionists have long been aware of, and studied, how susceptible people are to the norms of their groups (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1973; Fehr & Fischbacher, 2003; Henrich, 2016). From Waddington's perspective, susceptibility to norms leaves scientists vulnerable to 'COWDUNG' (i.e. to potentially fallacious conventional wisdom), and predisposed to regard heterodox scientific theories as not just wrong but as unethical.

Also prominent amongst scientific traditions is the glorification of founders and leading figures, who are commonly presented as heroes, with any weaknesses or failings overlooked or whitewashed. Witness, for instance, the reverence within evolutionary circles afforded to Ronald Fisher, and the associated 'conspiracy of silence' (Gould, 2002, p. 513) concerning his racism and support for eugenics (only acknowledged by the

Society for the Study of Evolution in 2020). Note, too, the outrage expressed when an anthropologist (Fuentes, 2021) dared to point out Charles Darwin's racism and sexism (Whiten et al., 2021). Scientific heroes are, of course, allowed. The problem is that we sometimes glorify them to the level of 'gods', which makes it unacceptable for a student, regular scientist, or researcher in another field, to dare suggest that there might be a better way to think. Scientists often take issue with small ideas, or criticize specific papers, and encourage their students to do the same, but many are wary of challenging truly fundamental assumptions.

Some of the discourse surrounding niche construction theory provides a case in point. This body of work has in general been well received by the human sciences (Ellis, 2015; Flynn et al., 2013; Fuentes, 2017) as well as in ecological developmental biology (Gilbert & Epel, 2015), physiology (Noble, 2017), and other subfields of developmental biology (Kirschner & Gerhardt, 2005). We suggest this is no coincidence, as researchers in these fields generally reject genetic determinism and typically conceive of development as a much more constructive, open-ended process, in line with Lewontin's emphases (1982, 1983). From this perspective, the 'explanatory gap' between ancestral selection and niche-constructing outputs is clear, and it would be a vulgar and naïve simplification to characterize behaviour as genetically determined. For many in these fields, it is no stretch to conceive of niche construction, including cultural niche construction, as eliciting and co-directing natural selection, and in that sense causing evolution.

Conversely, many evolutionary biologists, and perhaps some scientists in other fields such as evolutionary psychology, are aware of environmental influences on phenotypes and reject a simple notion of genetic determinism. Nonetheless a programmed view of development remains widespread. According to this view, developmental processes are controlled by genes, in the form of genetically specified 'switches' or 'reaction norms' that have been shaped by past selection (Dawkins, 1976; Keller, 2010; Laland et al., 2019). If the manner in which organisms engage in niche construction is perceived to be fully explained by earlier natural selection, then niche construction would appear to do no additional explanatory work. From this perspective, which is representative of a number of contemporary evolutionary biologists, the 'explanatory gap' between ancestral selection and niche-constructing outputs may not be apparent. For them, the suggestion that niche construction is an evolutionary process may make little sense; the result has been rather contentious (Scott-Phillips et al., 2014).

Different academic fields are commonly characterized by alternative conceptual frameworks, which channel thinking and encourage some ideas, hypotheses, and perspectives at the expense of others. As we discussed in the preceding section, these prevailing views can be regarded as 'cultural niches', which partly determine the cultural traits that are allowed to flourish. There are undoubtedly multiple issues at stake in the debates over the merits of niche construction theory, including the causal interdependencies of the processes that generate phenotypic variation, differential fitness, and inheritance (Laland et al., 2019; Scott-Phillips et al., 2014; Uller & Helanterä, 2017). Nonetheless, different views of the control of development (i.e. whether it is under genetic or epigenetic control) may strongly influence scientists' response to niche construction theory (Laland et al., 2011, 2015; Lewens, 2019). Likewise, perspectives on development may help to explain whether or not researchers accept important roles for developmental bias, developmental plasticity, and extra-genetic inheritance in the process of evolution (Laland et al., 2011, 2015; Lewens, 2019).

These considerations may help to explain why analyses of niche construction have elicited strongly polarized, and often emotional, responses. Sadly, researchers who think differently from the mainstream are commonly characterized as 'muddled' or deploying 'rhetorical devices', with the 'construction of a conceptual niche' portrayed as a dangerous or exploitative exercise (Gupta et al., 2017; Scott-Phillips et al., 2014) rather than a healthy contribution (Feldman et al., 2017). Dissenting views are subject to personal attacks (see, for instance, the repeated vilification of Waddington as not just wrong but as a 'mystic', by Welch, 2017). Scientists who think differently are characterized as unethical, with their scientific theories framed as 'overclaiming' or 'aggrandizement' (Scott-Phillips et al., 2014). As cultural evolutionary theory

(Boyd & Richerson, 1985; Fehr & Fischbacher, 2003; Henrich, 2016) might anticipate, when scientists violate the norms of how the field is generally understood merely by proposing alternative theories, to many mainstream scientists the writings of the dissenters are not just intellectually wrong but their behaviour is perceived to be morally wrong.

Niche construction theory currently occupies a heterodox position relative to mainstream evolutionary biology, but there is nothing wrong with that. As Waddington and Lewontin stress in their writings, alternative perspectives are of value precisely because they inspire the generation and testing of novel hypotheses, thus opening up new lines of enquiry. Niche construction theory has produced a conceptual niche, but all new theories result in conceptual niches, by generating ideas, insights, and methods that inspire others to use them (Feldman et al., 2017). There is nothing sinister or unusual about that.

Practitioners must be on guard against any suggestion that there is a *right* way to do evolutionary science, or that evolutionists *should* embrace a particular perspective. In particular, we encourage scientists to be wary of castigating the proponents of new or different conceptual frameworks. That is not to suggest that researchers must unthinkingly embrace every hypothesis; clearly there is a need for critical thinking and evidence-based evaluation within academia. Rather, what we discourage is an overly casual and pre-emptive dismissal of radical or unconventional thinking. Many established theories start off as heresy, but without innovation there can be no progress. Evolutionary researchers have every right to think differently from the mainstream, and if they do, to try to convince others of their merits of their theory or approach.

Lewontin's explicitly dialectal stance encourages researchers to present their work as a competing counterpoint to the dominant ideas in the field. Interestingly, he discouraged us from using the term 'dialectic' in our writings on niche construction, for fear that the term carried baggage and might lead to our work being disdained as 'Marxist'. We nonetheless support evolutionary minded researchers who wish to set up their work as a dialectic (Levins & Lewontin, 1985) or expose conventional wisdom as 'COWDUNG' (Waddington, 1977). Pluralism of perspective is critical to the institutions of science. Hopefully, by virtue of being attuned to human sensitivity to norms, cultural evolutionists will be unusually well placed to exhibit tolerance and encourage diversity of thought within their field.

Science itself is a selective process, with well-developed institutions designed to extract useful theory and hypotheses from less useful noise (Hull, 1988). Such institutions are not perfect, since they are 'adaptations' of the cultural evolutionary process, and no adaptations are perfect however they might appear. We encourage researchers to trust in the methodology of science, but to incorporate practices that promote progress. Both theory (e.g., Fisher's 1930 fundamental theory) and empirical work (Kellert et al., 2006; Swartz et al., 2019) have found that the rate of 'adaptation'—here scientific progress—is enhanced by increased diversity. We encourage colleagues and students to be brave and creative, recognizing from the outset that the cultural selection they will face will often be harsh. Challenging core ideas is a high-risk, high-gain strategy, where most new ideas will fail. Some central aspects of niche construction theory germinated at the benign but powerfully intellectual Santa Fe Institute, an environment renowned for its open mindedness and 'big thinking'. The scientific process needs more such safe breeding grounds for innovative and unorthodox ideas. We encourage researchers to view 'thinking differently' to be a virtue, to lay out their reasoning and assumptions clearly, to highlight conceptual differences from the mainstream so that these can be subject to empirical evaluation, and to pursue their hypotheses by whatever means they feel productive. Inspiration can be taken from Waddington and Lewontin, whose initially heterodox ideas have become increasingly valued.

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Note

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