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Conceptual Barriers to Progress Within Evolutionary Biology

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Abstract In spite of its success, Neo-Darwinism is faced with major conceptual barriers to further progress, deriving directly from its metaphysical foundations. Most importantly, neo-Darwinism fails to recognize a fundamental cause of evolutionary change, "niche construction". This failure restricts the generality of evolutionary theory, and introduces inaccuracies. It also hinders the integration of evolutionary biology with neighbouring disciplines, including ecosystem ecology, developmental biology, and the human sciences. Ecology is forced to become a divided discipline, developmental biology is stubbornly difficult to reconcile with evolutionary theory, and the majority of biologists and social scientists are still unhappy with evolutionary accounts of human behaviour. The incorporation of niche construction as both a cause and a product of evolution removes these disciplinary boundaries while greatly generalizing the explanatory power of evolutionary theory.

Keywords Niche construction · Evolutionary biology · Ecological inheritance · Ecosystem ecology · Developmental biology

1 Introduction

On the face of it, evolutionary biology is a thriving discipline: It is built on the solid theoretical foundations of mathematical population biology; it has a rich and productive empirical

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tradition, exploiting an array of effective experimental methods; it is continuously fed by a fertile exchange of hypotheses and data between population geneticists, mathematical biologists, paleontologists, developmental and molecular evolutionists, evolutionary ecologists, and variety of other researchers; and it is the focus of unrivalled scientific interest and excitement.

We suspect that most evolutionary biologists recognise no fundamental problems within their discipline and foresee no major obstacles to future progress. As far as they are concerned, the Evolutionary Synthesis of the 1930s and 1940s established satisfactory foundations for modern evolutionary theory: population genetics is an adequate description of evolutionary dynamics; natural selection is the sole adaptation-generating mechanism of evolutionary change; macroevolution is an extrapolated product of microevolution; and Weismann's barrier, and the early sequestering of the germ line, render most non-genetic influences on development irrelevant to an understanding of evolutionary change.

We view the legacy of Mayr, Dobzhansky and Simpson differently. From our perspective, neo-Darwinism is built on inappropriate metaphysical foundations that provide a suboptimal basis for modern evolutionary biology. Critically, neo-Darwinism fails to recognize a major cause of evolutionary change, which we label "niche construction". We will argue that this failing undermines the potency of evolutionary theory, introduces inaccuracies and reduces its explanatory power. We will suggest that the manner by which evolutionary biology currently depicts what on the surface are simple concepts such as 'change' and 'cause' reflects convention rather than natural truth. These problematic foundations constitute obstacles to further progress within evolutionary biology, and hinder the satisfactory integration of evolutionary biology with neighbouring disciplines, including ecosystem ecology, developmental biology, and the human sciences.

We propose an alternative evolutionary framework, the niche-construction perspective, which directly addresses the conceptual barriers currently confronting evolutionary biology. The niche-construction perspective is not new—it was introduced to evolutionary biology in the 1980s (Lewontin 1982, 1983). But the perspective has gained ground over recent years (Boni and Feldman 2005; Brandon and Antonovics 1996; Laland et al. 1996, 1999, 2001; Lewens 2003; Odling-Smee 1988; Odling-Smee et al. 1996, 2003; Oyama et al. 2001; Sterelny 2003; Donohue 2005).

Niche construction is the process whereby organisms modify their own and/or each others' niches, through their metabolism, their activities, and their choices. For instance, numerous animals manufacture nests, burrows, holes, webs and pupal cases; plants change levels of atmospheric gases and modify nutrient cycles; fungi and bacteria decompose organic matter; bacteria fix nutrients (see Odling-Smee et al. 2003, for a review of this literature). However, the defining characteristic of niche construction is not organism-driven modification of the environment per se, but rather the modification of the relationship between an organism and its relative niche (Odling-Smee 1988).

Advocates of niche-construction are concerned with the causal basis of the organism–environment match and its inherent symmetries, and the active role that organisms play in driving evolutionary and co-evolutionary events. They seek to explain the adaptive complementarity of organism and environment in terms of dynamic, reciprocal interactions between the processes of natural selection and niche construction. 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 theory differs from conventional conceptualisations of evolution. In standard models, leaving aside complications such as co-evolution and habitat selection, adaptation is a process by which natural selection shapes organisms to fit pre-existing environmental "templates". The causal arrow points in one direction only: environments are the source of selection, and they determine the features of living creatures. According to Williams (1992, p. 484): "Adaptation is always asymmetrical; organisms adapt to their environment, never vice versa". This stance is based on some metaphysical assumptions that have underpinned evolutionary thought since the Modern Synthesis. In our view these assumptions are the source of the conceptual barriers that impede further progress in evolutionary biology.

2 Conceptual Barriers to Progress Within Evolutionary Biology

2.1 The Reference Device Problem

Lewontin (1983) drew attention to a problem within evolutionary biology by summarizing standard evolutionary theory as:

$$\frac{dO}{dt} = f(O, E), \tag{1a}$$

$$\frac{dE}{dt} = g(E). \tag{1b}$$

Evolutionary change, *dO/dt*, is assumed to depend on both organisms' states, O, and environmental states, E(1a), but environmental change, *dE/dt,* is assumed to depend on environmental states only (1b). With many caveats and complications (Odling-Smee et al. 2003), organisms are not generally regarded as causing significant changes in their environments. For Lewontin, a more accurate description of how evolution actually works is:

$$\frac{dO}{dt} = f(O, E), \tag{2a}$$

$$\frac{dE}{dt} = g(O, E), \tag{2b}$$

where environmental change also depends on the environment-modifying activities of organisms. Philosopher Godfrey-Smith (1996) drew attention to the same problem by describing standard evolutionary theory as "externalist", by which he meant that it uses the external environment as its 'explanatory reference device'. It seeks to explain the internal properties of organisms, their adaptations, exclusively in terms of external properties, that is natural selection pressures, in their external environments.

The principal point that the conventional approach obscures is that organisms are active, as well as reactive (Waddington 1969; Lewontin 1983). To stay alive organisms must extract resources from their external environments. They are compelled to choose and perturb specific components of their environments, and by doing so, they change some of the selection pressures in their environments. Lewontin's equation (2b) introduces an additional causal arrow into evolutionary biology, which Odling-Smee (1988) labelled "niche construction".

The 'reference device problem', which Odling-Smee et al. (2003) regard as the principle obstacle to progress within evolutionary biology, is that the causal arrow in (2) representing niche construction points in the "wrong" direction, from organisms to environments, and is therefore not compatible with the externalist assumption of standard evolutionary theory. As a result, it is difficult or impossible for evolutionary biologists to describe changes in selection caused by niche-construction as evolutionarily causal. Instead, standard evolutionary theory is forced by its own explanatory reference device to "explain away" all observed instances of niche construction as phenotypic, or extended phenotypic (Dawkins 1982), consequences of prior natural selection. Standard evolutionary theory can recognise niche construction as a consequence of evolution, but it cannot recognise it as a cause.

2.2 The Devaluation of Proximate Causes

Responding to structuralist critics, Harvard evolutionary biologist and Synthesis architect Ernst Mayr (1984,p. 126) wrote:

> All of the directions, controls and constraints of the developmental machinery are laid down in the blueprint of the DNA genotype as instructions or potentialities.

For Mayr, developmental processes cannot be regarded as independent causes of evolutionary events, since their characteristics, including their ability to control and constrain, are themselves fully explained by prior natural selection. If developmental processes direct evolutionary events, this is only the *proximate* manifestation of the *ultimate* cause of natural selection; conversely, those aspects of development that have not been shaped by selection play no evolutionary role.

Mayr was extremely influential in bringing this commonly made distinction between 'proximate' and 'ultimate' causes to prominence within biology. In an article published in 1961, Mayr argued that natural selection should be regarded as the *ultimate* cause of phenotypic characters (Amundson 2005), thereby effectively devaluing so-called proximate causes as explanatory tools within evolutionary biology. Since niche construction includes developmental processes, this stance also prevented evolutionary biologists' from recognising niche construction as an evolutionary process in its own right (Laland and Sterelny 2006).

Instead, niche construction is perceived to have no *independent* evolutionary significance because, to the extent that it is evolutionarily consequential, it is fully explained by a preceding cause, namely preceding natural selection (Dawkins 2004). Niche-construction effects are merely extended phenotypes, and extended phenotypes play the same role in evolutionary biology as ordinary phenotypes, namely to affect the replication potential of the alleles contributing to those phenotypic effects (Dawkins 2004). Similar reasoning underlies the treatment of niche construction as an *indirect genetic effect*, with, for example, a mother's genes affecting her offspring's phenotype by modifying its environment (Wolf et al. 1998). While this stance recognizes that modification of the selective environment does occur, it does not view environmental modification as a process with quasi-independent causal significance. Rather it attributes all causal significance associated with niche-constructing activity to genes or genotypes, that are only present because of prior natural selection.

There are two major problems with this line of reasoning (Laland and Sterelny 2006). First, not all evolutionarily consequential niche construction, nor all development in general, is under genetic control. This is well illustrated by an example from human biology. Adult humans vary in their ability to consume dairy products without sickness as a result of physiological differences in the activity of the enzyme lactase, which relate to genetic variation (Durham 1991). A strong correlation exists across cultures between the presence of the genes for lactose absorption and a history of dairy farming (Ulijaszek and Strickland 1993). This has led to the hypothesis that dairying constructed the selection pressures that led genes for lactose absorption to become common in pastoralist societies. Theoretical analyses provide strong support for this hypothesis and confirm that dairy farming spread before the genes for lactose absorption, not the other way around (Aoki 1986; Feldman and Cavalli-Sforza 1989; Holden and Mace 1997). Dairy farming is apparently an instance of human cultural niche construction that is mediated by cultural processes. There are no genes for dairy farming (using "genes for" in the sense of Dawkins 1976). Genes do not constitute the appropriate level of analysis to explain why individuals in some societies farm cattle and others do not—this is a cultural phenomenon. Yet in spite of the fact that dairy farming is not caused by genes and is not a product of natural selection, it has clearly had evolutionary consequences. Recent findings of mutations that allow lactase persistence in some non-dairying African groups does not fundamentally change this logic (Tishkoff et al. 2006).

Other human genes also appear to have been selected as a direct result of human cultural niche construction, including sickle cell *S* allele, G6PD, TNFSF5, CCR5, AGT, CYP3A and alleles coding for hemoglobin C and Duffly blood groups (Balter 2005). Moreover, analogous examples are found in other species. They all require the modification of selection pressures by niche construction. They do not all require culture (Odling-Smee et al. 2003; Laland and Sterelny 2006).

Even if it were the case that the niche-constructing activities of organisms were under genetic control, it would still not follow that niche construction was a mere effect of the prior selection of these controlling genes. For in many cases these "controlling genes" have themselves been selected as a result of prior niche-constructed changes in selective environments. For example, it is tempting to assume that the 'ultimate' explanation for why earthworms modify soils is that prior selection has furnished them with genes for burrowing, tunnelling, exuding mucous, and so forth. However, it is no more than a convention within evolutionary biology that natural selection should be regarded as the ultimate cause of such phenotypic characters. From the perspective of a philosophical consideration of causation, one might equally argue that the ultimate cause of the selection pressures that favoured earthworm soil processing adaptations is the prior niche constructing activities of ancestral worms, without which there would be no soil environment to act as a source of natural selection (Odling-Smee et al. 2003).

2.3 Misleading Metaphors

Evolutionary theory is often viewed as a fusion of Darwinian and Mendelian insights. Notwithstanding the immense progress that these achievements engendered, Lewontin (1983) argues that the legacies of Darwin and Mendel include 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" (p. 273). Mendel's view of organisms as the manifestation of autonomous internal 'factors' 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" (p. 276). Darwin's view of organisms as passive objects moulded by the external force of natural selection encouraged a conception of evolution in which "the environment 'poses the problem'; the organisms posit 'solutions', of which the best is finally 'chosen' (P276). The metaphor of selection, inspired by the efficacy of artificial selection, continues to encourage a view of organisms as passive objects upon which external forces act. Lewontin argues forcefully that these metaphors are misleading. Similar points have been made by Oyama (1985); Griffiths and Gray (2001, 2004), and others.

3 The Niche Construction Revision

The niche construction perspective differs from the conventional perspective in recognizing two major adaptive processes in evolution, natural selection and niche construction. The perspective also recognizes two general forms of inheritance in evolution, genetic and ecological inheritance. There are two legacies that organisms inherit from their ancestors, genes and modified environments, incorporating modified selection pressures. Ecological inheritance is not a high-fidelity template copying system like genetic inheritance (Dawkins 2004; Sterelny 2001, 2005). Instead, organisms transmit to their offspring, and subsequent descendents, physically altered selective environments, both through actions on their biological and non-biological environments, and by their habitat choices.

The solution to the reference device problem was to change the explanatory reference device. Instead of describing the evolution of organisms relative to natural selection pressures in independent external environments, as in (1), Odling-Smee et al. (2003) describe evolution relative to the "niches", or organism-environment interactive relationships, as in (2). Because niches are defined by two-way interactions between organisms and their environments (Chase and Leibold 2003), this step allowed an "interactionist" (Godfrey-Smith 1996) theory of evolution to be substituted for the standard externalist account. The niche is a neutral explanatory reference device for evolutionary theory that can capture reciprocal causation without imposing any bias either in favour of natural selection and against niche construction, or vice versa. Conceptually it is only necessary to recognise that natural selection pressures are not properties of external environments, but properties of niches.

On the basis of this revised explanatory reference device, all developmental processes that modify the organism–environment relationship are potentially evolutionarily causal. That returns us to Mayr's devaluation of proximate causation in evolution. Niche construction theory replaces both proximate and ultimate causation by 'reciprocal causation' and regards the characteristics of organisms as caused by interacting cascades of selection and construction (Odling-Smee et al. 2003; Laland and Sterelny 2006; see also West-Eberhard 2003), described elsewhere as 'cycles of contingency' (Oyama et al. 2003). The ultimate/proximate dichotomy, and the convention brought to prominence by Mayr, is clearly not the only way to think about causation in biology. The standard view, that niche construction is not a process in evolution because it is determined by prior natural selection, rests on an unstated assumption that the environmental source of prior natural selection is independent of organisms. However, one cannot assume that the ultimate cause of niche construction is prior natural selection by an independent environment if the state of that environment was itself partly caused by prior niche-constructing organisms.

Ultimately, such recursions regress back to the beginning of life. As niche construction is one of the defining features of life (Odling-Smee et al. 2003), there is probably no stage at which we could say natural selection preceded niche construction. From the beginning of life, all organisms have always, in part, modified their selective environments by niche construction, and their ability to do so has always, in part, been a consequence of natural selection. There have probably always been two reciprocal causes in evolution.

This recognition of reciprocal causation in evolution also goes a long way towards addressing Lewontin's concerns regarding the misleading metaphors of unfolding developmental programs, and the externalism of natural selection. " . . . genes, organisms and environments are in reciprocal interaction with each other in such a way that each is both cause and effect in a quite complex, although perfectly analysable, way" (Lewontin 1983,p. 276). Hence, the organism is viewed as both a cause of its own development and a cause of its own selective environment.

From the niche-construction perspective "genes, organisms and environments" are indeed: "in reciprocal interaction with each other". First, niche construction is not only itself a developmental process, but it is to some degree obligate. It follows that development must inevitably modify some selection pressures in environments. Second, because they can niche construct, developing organisms adapt to their environments not only by responding to selection pressures or inputs from their environments, but also by actively choosing and perturbing various components of their developmental environments. Third, niche construction is potentially informed by all the processes that inform development, including learning processes in animals, and cultural processes in humans. Thus, acquired characters play a (non-Lamarckian) role in evolution, by modifying natural selection. Fourth, niche-constructing organisms can introduce feedback in developmental processes, as well as in evolutionary processes. Some of the ways in which a developing organism alters its environment are likely to feed back to affect later stages of its own development (Richardson 1999; Oyama et al. 2001). This idea was originally captured by Waddington (1959) with his concept of an "exploitive system".

All of these changes convert developmental processes from the mere unfolding of genetically guided programs to a process of active "niche regulation". Niche regulation requires developing organisms *partly* to respond to inputs from their developmental environments on the basis of their inherited genes, and *partly* to modify those same developmental environments by their niche-constructing outputs, based on genetically afforded (but not genetically determined) phenotypic plasticity. Hence, from the niche-construction perspective, the key task for any developing organism is the active *regulation* of its inherited 'niche', both by responding to its environment, and by altering its environment, in ways that keep its personal organism–environment relationship continuously adaptive, for the rest of its life.

4 Ramifications of the Niche-Construction Revision for Evolutionary Biology

Many researchers have explored the evolutionary ramifications of niche construction by developing and analyzing mathematical models (Laland et al. 1996, 1999, 2001; Odling-Smee et al. 2003; Ihara and Feldman 2004; Schwilk and Ackerly 2001; Silver and Di Paolo 2006; Borenstein et al. 2006). All such analyses conclude that niche construction is evolutionarily consequential. Typically, population genetic models investigate the dynamics of the joint evolution of environment-altering, niche-constructing traits in organisms and 'recipient traits', whose fitness depends on feedback from natural selection in environments that can be altered by niche construction (Laland et al. 1996, 1999, 2001; Odling-Smee et al. 2003). While the results are usually based on specialized two-locus models, they are consistent with those of related theoretical analyses that employ other mathematical methods, such as quantitative genetic analyses of maternal inheritance and indirect genetic effects (Kirkpatrick and Lande 1989; Mousseau and Fox 1998; Wolf et al. 2000, 1998).

The analyses suggest that the effects of niche construction can override external sources of selection to create new evolutionary trajectories, which lead to the fixation of otherwise deleterious alleles, the support of stable equilibria where none are expected, and the elimination of what would otherwise be stable polymorphisms. Even niche construction that only weakly affects resource dynamics can significantly alter both ecological and evolutionary patterns. This is because traits whose fitness depends on alterable sources of selection co-evolve with traits that alter sources of selection. Such coevolution results in evolutionary dynamics that are very different from what would occur if each trait had evolved in isolation. Other theoretical studies corroborate and extend these findings. For instance, Hui et al. (2004) observed that niche construction profoundly influenced the dynamics, competition, and diversity of metapopulations. Silver and Di Paolo (2006) reported that niche-construction traits can drive themselves to fixation by simultaneously generating selection that favours 'recipient' trait alleles and linkage disequilibrium between niche-construction and recipient trait alleles. Kerr et al. (1999) showed how the magnitude of a tree's impact on the flammable character of its environment affected the evolution of flammability and resistance to fire in resprouting plants.

While most theoretical treatments of niche construction have focused on the selection to which an organism is exposed, Donohue (2005) discusses how niche construction can also influence the expression of phenotypic and genetic variation. Donohue (2005) showed experimentally how niche construction frequently occurs in plants through developmental plasticity, allowing them to determine the selective environments that they or their offspring experience. For instance, seed dispersal ability frequently determines the competitive environment experienced by seeds, seedlings and adult plants. Flowering time determines the seasonal environment that the seeds experience. Germination timing effectively involves habitat choice in plants, since certain environmental conditions must be present to break dormancy, and additional environmental conditions must be present to enable germination after dormancy is broken. For these reasons, it is reasonable to regard traits such as seed dispersal ability, flowering time and germination timing as niche-constructing traits. Donohue also described an experimental study with *Arabidopsis thaliana* showing how two niche-constructing traits—flowering and germination time—influence selection, phenotypic expression and genetic variation, resulting in novel life-history expression, and accounting for variation between spring and winter annual life histories (Donohue 2005).

Mathematical analyses also suggest that ecological inheritance (Odling-Smee 1988, 2003) can generate unusual evolutionary dynamics. Frequently, the evolution of the recipient trait depends on the frequency of the niche-constructing trait over several generations. Theoretical population genetic models have established that processes that carry over from past generations can change the evolutionary dynamic in a number of ways, generating time lags in response to selection of the recipient trait, momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), opposite responses to selection, and sudden catastrophic responses to selection (Feldman and Cavalli-Sforza 1976; Kirkpatrick and Lande 1989; Laland et al. 1996, 1999, 2001; Robertson 1991; Wolf et al. 1998, 2000).

In addition to modifying the environments of populations, niche construction modifies the developmental environments of individuals. Systematic changes in developmental environments may then result in systematic changes to the phenotypic expression of inherited genes. Sometimes niche construction may modify the shape of the relevant norm of reaction, for instance, by reducing the range of developmental environments to which juveniles are exposed (Laland and Sterelny 2006). Nests, burrows, mounds and similar structures all tend to buffer environmental variation, making temperature, humidity, exposure to wind and sunlight more uniform. For example, if in a seabird lineage there is an evolutionary trajectory from ground to burrow nesting, a suite of adaptations of egg and juvenile will no longer be relevant: for instance, there will be no need for camouflaged eggs. If a developmental environment does become more uniform, then alleles that have equivalent phenotypic effects in, say, burrow-rearing environments but not in a broader class of environments, may become selectively equivalent. An allele that is fitter in this narrower class of environments should have its advantage magnified. The heritability of the trait associated with any such allele is also likely to be affected by the reduction in environmental variation.

Conversely, niche construction can result in exposure to a broader range of developmental conditions (Laland and Sterelny 2006). For example, when parents relocate, their offspring are likely to be exposed to novel developmental environments. The new environment will not only be a source of some modified natural selection, but also a determinant of the range of phenotypes exposed to that selection. The modification of reaction norms through the construction of developmental environments may then influence the heritability and response to selection of plastic traits, in some cases exposing genetic variation to selection, in other cases shielding it from selection. Similar arguments have been made with respect to phenotypic plasticity (West-Eberhard 2003). Examples of such phenomena can be found in West-Eberhard (2003) and Donohue (2005).

Niche construction also provides a non-Lamarckian route by which acquired characteristics can influence the selective environment. Acquired characteristics are of particular significance to vertebrate evolution. The Galapagos woodpecker finch provides an example (Odling-Smee et al. 2003). These birds create a woodpecker-like niche by learning to use a cactus spine or similar implement to peck for insects under bark (Tebbich et al. 2001). While true woodpeckers' (Picidae) bills are adaptive traits fashioned by natural selection for grubbing, the woodpecker finch's capacity to use spines to grub for insects is not an adaptation. Rather, this finch exploits a more general and flexible adaptation, namely the capacity to learn the skills necessary to grub in its environment by using cactus spines, or similar implements. The finch's use of spines develops reliably as a consequence of its ability to interact with its environment in a manner that allows it to benefit from its own experience, but this is not guaranteed by the presence of naturally selected genes, nor does it depend on social learning (Tebbich et al. 2001). However, the finch's learning opens up resources in the bird's environment that would be unavailable to it otherwise, and it is therefore an example of niche construction. This niche-constructing behaviour probably created a stable selection pressure that subsequently favoured a bill able to manipulate tools rather than the sharp, pointed bill and long tongue characteristic of most woodpeckers. While the information acquired by individuals through ontogenetic processes cannot be inherited because it is lost when they die, processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction in ways that do modify natural selection.

More generally, any mechanism of phenotypic plasticity in conjunction with reliably present signals from the environment may generate the same niche-constructing activity generation by generation, with evolutionary consequences, without the activity itself being an adaptation, and without the necessity of any tight correspondence between genetic and phenotypic variation (Via et al. 1995; West-Eberhard 2003; Rice 2004).

This route is considerably enhanced by social learning, which allows animals to learn from each other. Hundreds of species of mammals, birds and fishes are now known to learn socially (Zentall and Galef 1988; Heyes and Galef 1996), allowing novel learned traits to sweep through populations, exposing individuals to novel selection pressures. There is already considerable interest among evolutionary biologists in the role that imprinting, song learning, habitat imprinting, cultural transmission and various other forms of learning, play in speciation, the evolution of adaptive specializations, adaptive radiations, the colonization of new habitats, brood parasitism and sexual selection in vertebrates (Aoki et al. 2001; Beltman et al. 2003, 2004; Laland 1994; Kirkpatrick and Dugatkin 1994; Ten Cate and Bateson 1988; ten Cate 2000; West-Eberhard 2003). From the niche-construction perspective, learning in general, and social learning in particular, is likely to exert a widespread influence on animal evolution.

Finally, the significance of acquired characters to evolutionary processes is further amplified with stable trans-generational culture, and it is now widely believed that such characters were probably important to hominid evolution (Cavalli-Sforza and Feldman 1981; Richerson and Boyd 2005). For instance, theoretical analyses by Laland et al. (2001) explored the evolutionary consequences of cultural niche construction. They revealed circumstances under which cultural transmission could overwhelm natural selection, accelerate the rate at which a favoured allele spreads, initiate novel evolutionary events, and possibly trigger hominid speciation. In fact, the analysis found that, because cultural processes typically operate faster than natural selection, cultural niche construction is likely to have more profound consequences than gene-based niche construction.

In summary, there is now strong theoretical and empirical support for the argument that niche construction affects the process of evolution. Such studies refute the charge that niche construction can be neglected because it is intractable. They also negate any suggestion that niche construction is not evolutionarily consequential. The analyses imply that population genetic models that ignore niche construction will frequently generate inaccurate predictions and misleading findings. Niche construction changes the evolutionary process in fundamental ways, (i) by creating an ecological inheritance, (ii) by modifying phenotypes, norms of reaction and heritabilities, and (iii) by allowing acquired characters to play a significant evolutionary role.

5 Ramifications for Other Disciplines

The niche-construction perspective could also bring benefits to other related disciplines, including fields that currently either cannot fully benefit from evolutionary theory because they lie beyond its scope, or are distorted by standard evolutionary theory's limitations. These include ecology, developmental biology and the human sciences.

5.1 Ecology

Elsewhere, we have argued that niche construction has implications for ecosystem-level ecology (Odling-Smee et al. 2003). A key observation is that niche construction can be characterised as the expression of genetically encoded semantic information in constructed components of local environments. As natural selection is a process that results in the acquisition and updating of semantic information through the Darwinian algorithm, it is reasonable to envisage semantic information flowing through entire ecosystems. Niche construction connects the prior expression of semantic information to the subsequent acquisition of semantic information by modifying sources of natural selection in environments, potentially doing so via both biotic and abiotic ecosystem components. As a result the ecological consequences of niche construction may involve chains of events in which information-guided niche construction generates modified natural selection pressures that subsequently cause populations to accrue further information, that subsequently guides additional niche construction.

In discussing the impact of niche construction on ecosystems, Odling-Smee et al. (2003) introduced the concept of *environmentally mediated genotypic associations*, or *EMGA*s. *EMGA*s are indirect but specific connections between distinct genotypes, mediated either by biotic or abiotic intermediate environmental components that have been modified by niche construction. *EMGA*s associate genes in either a single population or multiple populations in ecosystems. Where they arise, the expression of genetic information by niche-constructing organisms in one population can affect the acquisition of genetic information in the same or a second population, through the modification of natural selection. For instance, kelp reduces the impact of waves and currents, maintains water clarity, prevents sediment movement, influences siltation rates and provides a habitat for numerous species that do not feed on kelp (Estes 1995). Kelp genes are indirectly connected to the genes of a multitude of subtidal and intertidal creatures via *EMGA*s springing directly from the consequences of this ecosystem engineering (Jones et al. 1997) rather than from trophic interactions. Thus kelp genes influence the expression of, and selection on, numerous other genes in numerous other species.

Once these points are accepted, several classic problems in ecology begin to be resolved. One problem concerns the relationship between evolution and ecosystem-level ecology. When ecosystems either change or resist change over time are their dynamics partly governed by evolutionary processes? If so, how can evolutionary theory help describe ecosystem dynamics when ecosystems include abiotic components that lack genes or any equivalent heritable information? The presence of abiota in ecosystems appears to rule out the application of evolutionary theory to entire ecosystems; to date, all attempts to understand ecosystems exclusively in terms of bioenergetics, biogeochemistry, or stoichiometry have proved insufficient. Apparently something is left out (Reiners, 1986). But if it is evolution, it is still not clear how the structures and dynamics of ecosystems may indeed depend in part on the evolution of their constituent organisms. Like others before us (Brown 1995; Holt 1995; Jones and Lawton 1995), we think evolution *is* an indispensable co-contributor to any sufficient description of ecosystem dynamics. However, only an evolutionary theory that stresses niche construction can shed light on how ecosystems can be governed by engineering webs of connectivity.

Historically ecologists have finessed this difficulty by partitioning their discipline into population-community ecology, which is able to use evolutionary theory by circumventing abiota, and process-functional ecology, which is able to include abiota by leaving out evolution (O'Neill et al. 1986). This creates a second problem, namely that in spite of repeated attempts these two sub-disciplines are difficult to integrate within a single framework. Many ecologists have recognized this difficulty:

> Recently there has been a fractionation of ecology into its various specialities, thus, potentially at least, reducing the power of the field as a whole to integrate and synthesize to the fullest extent (Likens 1995).
>
> in general, we do not understand how to link organismal activities, population dynamics, and community assemblages to ecosystem processses (Jones and Lawton 1995)

By ignoring niche construction, standard evolutionary theory limits the scope of interactions that are perceived to occur between biotic and abiotic components in ecosystems, and necessarily ignores forms of feedback that probably play a role in co-evolutionary scenarios and ecosystem dynamics. When niche construction is added to evolutionary theory, however, it is possible to explicate, in terms of niche construction, how evolutionary theory can be applied to ecosystems, in spite of the presence of non-evolving abiota, and in a manner that clearly advances and 'evolutionizes' ecosystem-level ecology. By modulating the action of selection on other species, by pumping up abiota into states they would not otherwise occupy, and by modifying downstream selection, niche construction effectively allows semantic information to partly regulate entire ecosystems. Elsewhere we have sketched how these insights can be employed in ecological research, including experimental methods and theoretical modelling (Odling-Smee et al. 2003).

The work of ecologists on “ecosystem engineering” (Jones et al. 1994, 1997), which is a synonym for niche construction, already illustrates the utility of this perspective. Jones et al. point to several ecosystem phenomena that cannot be understood in terms of energy and matter flows only. They emphasize the critical role played by the creation of physical structures and other modifications of their environments by niche-constructing organisms that partly control the distribution of resources for other species in ecosystems. Furthermore, Gurney and Lawton (1996) demonstrated theoretically that the efficacy with which an engineering population niche constructs to degrade a virgin habitat not only determines whether there will be no engineers, a stable population of engineers or population cycles in the frequency of engineering, but also the extent of virgin and degraded habitat.

Evolutionary phenomena associated with niche construction complement and add to Jones et al.’s observations. First, when they engineer, niche-constructing organisms frequently influence their own evolution by modifying their own selective environments, often via EMGAs that include abiotic components, or chains of such components. Second, niche-constructing organisms also influence the evolution of other populations, again often indirectly via EMGAs, and often via intermediary abiotic components. Such interactions may occur between particular species or across entire guilds. Third, through their inceptive niche construction organisms may create new niches for themselves, for example through innovation, or they may relocate to a novel environment, which again will influence the dynamics of their ecosystems (Vitousek 1986). For instance, the effect of improvements in their “paper technology” would appear to have had a massive effect on the geographic distribution, colony size and social complexity of Polistinae wasps (Hansell 1993). Fourth, it is important to recognise that the theoretical tradition in population genetics of finessing intermediary abiotic components in co-evolutionary events, by assuming that the intensity of selection on the biotic sink population is proportional to the frequency of genotypes in the biotic source population, is a distortion imposed for mathematical convenience. We accept the cardinal importance of simplification in theoretical analyses, but there are occasions when such idealization obscures rather than elucidates ecosystem dynamics. Genetic co-evolutionary models that explicitly track intermediary resources are sometimes necessary. Fifth, evolutionary and co-evolutionary events can operate on time scales within the range of ecological temporal scales, which means that the dynamics of abiotic components may reflect gene frequency changes in currently evolving engineering species. Sixth, there may be predictable patterns associated with ecological responses to prior niche construction, such as replacements, competitive exclusions, and invasions, as a function of the characteristics of the niche construction expressed by the incumbent populations in an ecosystem. Based on this reasoning, Odling-Smee et al. (2003) make a number of predictions concerning which species might invade an ecosystem, under what circumstances, and whether the invasion will be benign or malign.

There may also be practical benefits to the niche-construction perspective. Jones et al. (1997) envisaged some utility for an ecosystem-engineering approach to conservation, particularly if it is possible to predict which species will be important ecosystem engineers in which ecosystems (Hui and Yu 2005; Stinchcombe and Schmitt 2006; Crain and Bertness 2006; Wright and Jones 2006). Using a niche construction/ecosystem engineering perspective, Boogert et al. (2006) proposed a number of measures that could be employed to enhance conservation efforts, including: (a) enhancing key engineers’ current activity by supplementing their numbers with introduced members of the same species; (b) enhancing key engineers’ current activity by providing them with the resources necessary for population growth; (c) enhancing key engineers’ current activity by supplementing the ecosystem with introduced members of the same engineering guild (e.g., a different species that engineers in the same manner); (d) artificially manufacturing and introducing the engineered products of the key engineers; and (e) counteracting negative effects and facilitating positive influences of both abiotic and biotic factors that may affect key engineers through trophic or nontrophic links.

5.2 Developmental Biology

The field of evolutionary developmental biology (henceforth Evo Devo) maintains that all complex animals, from flies to humans, share a common "tool kit" of master regulatory genes that govern the formation and patterning of bodies (Gilbert et al. 1996; Gilbert 2003; Carroll 2005). However, there is more to Evo Devo than the differential expression of homologous genes; advocates believe that developmental processes bias and constrain evolutionary pathways (Raff 2000; Arthur 2004). A subset of Evo Devo has given rise to ecological developmental biology, which stresses the roles of developmental plasticity in evolution, especially in the formation and prevention of novelty. Evo Devo has much in common with niche-construction theory (Laland et al. 2008). Both fields maintain that refinements are required in the modern theory of evolution. Many Evo Devo practitioners believe that evolutionary theory is incomplete—or at least, was at the time of the Modern Synthesis and that it is only becoming complete with the insights gained from their own field. Some Evo Devo advocates believe that additional mechanisms to those of neo-Darwinism, mechanisms involved with ontogeny, are required for a full understanding of evolution (Amundson 2005; Raff 2000; Gilbert et al. 1996). Similarly niche-construction advocates are explicit about the need to treat niche construction as both a developmental process and a cause of evolution (Odling-Smee et al. 2003). Both Evo Devo and niche-construction theory 'complain' about the Synthesis' treatment of development as a "black box" (Hamburger 1980) that transforms naturally selected genes into functional phenotypes. Seemingly, evolutionary biologists have given themselves licence to ignore development:

> One consequence of Weismann's concept of the separation of the germline and soma was to make it possible to understand genetics, and hence evolution, without understanding development (Maynard Smith 1982, p. 6).

This treatment has engendered disquiet among development biologists, who stress that one must understand how bodies are built in order to understand how the process of building bodies can be changed (Carroll 2005; Amundson 2005). Evo Devo advocates claim that neo-Darwinism had no theory of macro-variation, but that developmental biology can now supply this essential ingredient (Gilbert 2006). Development-minded evolutionists have argued that developmental processes constitute significant but neglected evolutionary mechanisms in their own right (Gould and Lewontin 1979; West-Eberhard 2003). For instance, micro- and macro-evolutionary patterns are viewed as shaped by developmental constraints (Gould and Lewontin 1979), while developmental plasticity is perceived to provide phenotypic variants that can be later stabilized by genetic networks. "Genes are followers, not leaders" (West-Eberhard 2003).

With striking parallels, advocates of niche construction suggest that it directs, regulates and constrains the action of selection, and is a source of evolutionary innovation (Odling-Smee et al. 2003; Laland et al. 2008). The only major difference between the arguments of the fields of Evo Devo and niche construction is in the domain (internal verses external environment) in which they are deemed to act. Some researchers (Waddington 1959; Lewontin 1983, 2000; West-Eberhard 2003; Jablonka and Lamb 2005) and philosophers of biology (Oyama et al. 2001; Griffiths and Gray 2001) have contributed to both debates. Both disciplines stress that developmental processes are not predictable from the properties of genes, nor well-described as an unfolding of a genetic program (Lewontin 1982, 1983; Gilbert 2006; Raff 2000). Both suggest that the variation needed for evolutionary innovations and novelty can occur without natural selection (Keys et al. 1999; Odling-Smee et al. 2003; West-Eberhard 2004; Sterelny, in press).

There is also a parallel between the emphasis placed on the role of extra-genetic inheritance in evolution by niche construction, and the stress placed by embryologists on additional inheritance systems. For instance, recent years have witnessed the accumulation of empirical support for epigenetic inheritance systems, which transmit phenotypes to daughter cells, and across generations (Bird 2002; Jablonka and Lamb 2005). Bacteria are an essential component of the epigenetic inheritance system in many insects and vertebrates. For instance, Dedeine et al. (2001) found that females of the wasp *Asobara tabida* cannot make their oocytes without products being made from the Wolbachia bacteria stored in them: *A. tabida* treated with antibiotics were unable to produce mature eggs. Similarly, mammalian development is not complete without signals from symbiotic bacteria (Hooper et al. 2001; Xu and Gordon 2003).

Likewise, the incorporation of ecological inheritance into evolutionary biology has consequences for development. In each generation, offspring inherit a local selective environment that has, to an extent, previously been modified, or chosen, by its niche-constructing ancestors. The resulting dual inheritance implies that each offspring must actually inherit an initial organism–environment relationship. In standard evolutionary theory, the development of organisms begins with the inheritance of a "start-up kit" of genes: in niche-construction theory, it begins with the inheritance of a "start-up niche".

Minimally, each start-up niche must include a specific location, in both space and time, typically influenced by parental actions and choices. In many species, parents ensure that some kind of resource package is also present. For example, phytophagous insects typically choose to lay eggs on specific host plants, which subsequently serve as resources for their offspring. In birds and insects, where the egg is the "start-up niche," yolk is provided for embryonic and larval nutrition. Moreover many organisms provide protective chemicals in their start-up kit. These can include antibodies such that the young can survive before their immune systems mature (birds, mammals), compounds that are poisonous or distasteful to predators (moths; Dussourd et al. 1988), or even sun-blocks that protect transparent embryos and larvae from the effects of solar radiation (Goldstone et al. 2006). From the niche-construction perspective, the key task for any developing organism becomes the active *regulation* of its inherited 'niche', by responding to its environment, and by altering its environment, in ways that keep its personal organism–environment relationship continuously adaptive, for the rest of its life.

'Unfolding genetic programs' are rarely acknowledged as affecting developmental environments. However 'niche regulation' involves niche construction that partly destroys the independence of developmental environments from developing organisms. That permits developmental processes to influence evolutionary processes. For example, if most individual organisms in a population inherit the same genes from their ancestors, and if their inherited genes cause most individuals in a population to express similar niche-constructing acts during their development, then it is likely that the activities of developing organisms will sooner or later modify the selective environments of populations. Collectively, developing niche-constructing organisms can act as uni-directional "biological pumps" in their environments, provided they constantly do the same things, to the same components of their environments, generation after generation (Odling-Smee et al. 2003).

In summary, we are not alone in drawing attention to the serious conceptual barriers to any satisfactory integration of development with conventional evolutionary theory (Oyama et al. 2001; West-Eberhard 2003; Amundson 2005). Seemingly, the best that can be achieved within the conventional framework is the accommodation of a ‘watered-down’ version of Evo Devo, a version that abandons any proposals for additional ontogenetic evolutionary mechanisms, that leaves aside any notion that developmental processes can direct evolutionary change, and that regards developmental constraints as manifestations of prior selection. Most fundamentally, it is difficult to reconcile conventional evolutionary thinking with the view that development must be regarded as an evolutionary process; a process that is not fully controlled by genes. Niche construction theory offers the prospect of a richer evolutionary synthesis with development, a synthesis that is consistent with the full gamut of Evo Devo mechanisms, and that does not compromise its conceptual tools (Laland et al. 2008).

5.3 Human Sciences

Odling-Smee et al. (2003) identify two principal reasons why most human scientists find it difficult to make use of evolutionary theory. One is that standard evolutionary theory appears to have too little to offer them. Human scientists are predominantly interested in human behaviour and culture, rather than genes, and as a consequence they have little use for evolutionary theory. The second is that the adaptationist accounts derived from standard evolutionary theory, for example in evolutionary psychology, are regarded by the majority of human scientists as simplified to the point of distortion.

There are two barriers to integration. The first is that standard evolutionary theory recognises only a single role for phenotypes in evolution: diverse phenotypes survive and reproduce differentially relative to natural selection and chance, the fittest passing on their genes to the next generation. Second, standard evolutionary theory recognises only a single evolutionarily significant inheritance system, genetic inheritance. This recognizes that human developmental and cultural processes, including cultural inheritance, contribute to human variation, and therefore to the diversity of human phenotypes subject to selection, but it does not recognize that human cultural processes affect human evolution in any other way. These restrictions minimize the role of developmental and cultural processes in human evolution.

Niche construction removes both these restrictions. It removes the first because niche-constructing phenotypes also construct and modify components of their environments, and in doing so they modify some of the natural selection pressures in their environments that later select them, and their descendents. It removes the second restriction because niche-constructing phenotypes generate a second general inheritance system in evolution, ecological inheritance. Evolution therefore depends on genetic inheritance and ecological inheritance relative to each other (Odling-Smee et al. 2003). In humans, cultural niche-construction contributes directly to ecological inheritance.

In practice, all complex organisms gain the information that guides their niche-constructing activities through several processes including population genetics, ontogenetics, and in humans, cultural processes. Niche construction is therefore guided by semantic information from all the information stores carried by complex phenotypes. In every species, niche construction is informed by naturally selected genes. In most it is also informed by ontogenetic processes, for example, learning in animals. In humans, and a few other species, it is informed by cultural processes as well. Human phenotypes therefore depend on genetic, ontogenetic, and cultural processes operating at distinct, but richly interconnected levels (Odling-Smee 2006).

A consequence of adding niche construction to evolutionary theory is that niche construction permits a non-Lamarckian, yet significant, role for acquired characteristics in evolution. We gave an example earlier, the Galapagos woodpecker finch, which modifies its niche through learned niche construction. In standard evolutionary theory it is of little evolutionary consequence if finches improve their foraging through learning, since all that ultimately counts is the contribution of diverse phenotypes to genetic inheritance. That changes when niche construction and ecological inheritance are added to evolutionary theory. Acquired niche-constructing traits can now modify some of the selection pressures that select for heritable genes. In these Galapagos finches, repeatedly learned tool use probably generated selection in favour of a manipulative beak. In humans, culturally acquired traits are responsible for the modification of selection by cultural niche construction (Laland et al. 2000).

Mathematical analysis has demonstrated that cultural niche construction, guided by culturally transmitted information, is a particularly potent modifier of environments, with major evolutionary and genetic consequences both for humans, and other species in shared ecosystems (Laland et al. 2001; Ihara and Feldman 2004; Boni and Feldman 2005). These analyses suggest that cultural processes can amplify the evolutionary feedback loop that is generated by niche construction (Laland et al. 2001; Odling-Smee et al. 2003). Human evolution may also be unique in that our cultural capacities, and our cultural niche constructing activities, apparently reinforce each other. Trans-generational cultural niche construction modifies environments in ways that favour ever-more culture, causing cultural niche construction to become ever-more powerful (Laland et al. 2000; Odling-Smee et al. 2003; Sterelny 2003; Tomasello et al. 2005).

Niche construction theory may be particularly relevant to the dynamics of cultural traits as the theory can incorporate the effects of the cultural background as a form of constructed niche (Feldman 2008). This is illustrated by a series of theoretical studies of fertility control and the demographic transition. For instance, Ihara and Feldman (2004) examined the effects of a preference for a high or low level of education on the evolution of small family size. They assumed that the average level of education may affect the degree to which traits are transmitted obliquely rather than vertically, for example, from teachers rather than parents to pupils. They found that a preference for small family size can evolve if individuals with few offspring are more likely to transmit their fertility preference to the offspring generation than individuals with a high number of offspring. Similar dynamics relating the education and fertility preference traits were also found under the assumption that the average level of education influences the rate of horizontal transmission of the use of fertility control (Kendal et al. 2005). Here, cultural niche construction facilitates the spread of the use of fertility control, where otherwise fertility selection and conformity would prevent the spread of this trait when rare. Both studies revealed the classic niche-construction characteristic of a time-lag between the increase the average level of education and subsequent decline in fertility; a pattern that is consistent with, and may partially explain, a typical demographic transition. Borenstein et al. (2006) developed a metapopulation cultural niche construction model where the frequency of a trait, such as the preference for a high level of education, affects the construction of a social interaction network, through which other cultural traits may perculate. They found that local between-population cultural niche construction could account for the spread of reduced fertility preference across countries occurs at ever lower levels of development (Bongaarts and Watkins 2005).

There are empirical examples too, where cultural niche construction has induced a genetic response in humans (Odling-Smee et al. 2003). One is provided by a population of yam cultivators in West Africa, who cut clearings in forests to grow crops, with a cascade of consequences (Durham 1991). The clearings increased the amount of standing water, which provided better breeding grounds for mosquitoes and increased the prevalence of malaria. This modified selection pressures in favour of an increase in the frequency of the hemoglobin *S* allele because, in the heterozygous condition, the *S* allele confers protection against malaria. Here, "agri-cultural" niche construction modified selection. The evolutionary change that resulted was adaptive because, in malaria-rife regions being heterozygous for the hemoglobin *S* allele is advantageous. We have already given a second agricultural example, the construction of selection pressures in favour of genes for adult lactose absorption by dairy farmers (see above). There are now a growing number of such examples (Balter 2005).

A candidate example of cultural niche construction affecting cultural processes, and thereby "ratcheting" up the evolution of culture itself, is Aiello and Wheeler's (1995) 'expensive tissue hypothesis'. Aiello and Wheeler claim that cooking by ancestral *homo sapiens* externalized part of the digestive process, which provided a selective environment that favoured a reduction in gut size. This anatomical change then allowed the reallocation of resources over evolutionary time that facilitated an increase in brain size. The cultural niche constructive-activity of cooking may therefore have contributed to the evolution of larger brains by influencing gut size. Bigger brains should then have affected the evolution of human cultural process, for instance, by enhancing the human facility for language (Pinker 1994; Odling-Smee 2006).

Another system that exhibits feedback between human cultural niche construction and genetic selection is the host-parasite relationship between antibiotic treatment and viability selection for antibiotic-resistant bacterial strains. This is an example of inter-specific cultural niche construction. Boni and Feldman (2005) found that the cultural transmission of antibiotic use favours selection of resistant bacterial strains, which in turn can result in cultural selection for the avoidance of antibiotic use. This kind of host behaviour can result in the classic niche-construction phenomenon of maintaining strain polymorphism even in parameter regions where it would not otherwise be expected. Interestingly, the evolution of either the host activity or the parasite strain can be viewed as a niche-constructive activity that modifies the selective environment of the other. Potentially this promotes an arms race between two types of transmitted information, cultural and genetic. Here, the niche constructive effects can be described fully in terms of trait–trait co-evolution as there is no ecological inheritance of a constructed 'resource' that is separate from the cultural or the genetic information transmission systems. The relative frequencies of bacterial resistance and sensitivity are the effective 'resource' influencing the cultural evolution of antibiotic treatment, and visa versa.

6 Conclusion

In this paper we have concentrated on two main points. First, the complementarity of organisms and their environments depend on two reciprocal causes in evolution, natural selection and niche construction. Formal models demonstrate that a revision of evolutionary theory that incorporates natural selection and niche construction could make a considerable difference to our understanding of how evolution works (Odling-Smee et al. 2003). The second point is that a revised evolutionary theory that explicitly includes niche construction and ecological inheritance has the potential to overcome most of the difficulties that are currently impeding the full integration of standard evolutionary theory with other closely related fields in biology. We argued our case with respect to ecosystem ecology, Evo Devo, and the human sciences. We think a revision of evolutionary theory is overdue and that the current outpouring of new data, particularly in molecular biology, will necessitate such a revision, quite soon.

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John Odling-Smee is a Fellow of Mansfield College, Oxford, and is recently retired from the Department of Biological Anthropology at Oxford University. After a late start, he studied psychology at University College London, publishing empirical and theoretical papers, several in collaboration with Henry Plotkin, on animal learning, culture and evolution. He also published an initial article on niche construction in *The Role of Behaviour in Evolution* (1988, MIT Press, edited by Plotkin HC). A Leverhulme Fellowship led to a long-standing collaboration with Laland and Feldman to work on niche construction, culminating in the aforementioned Princeton Monograph.

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Jeremy Kendal is an RCUK Fellow in the Department of Anthropology, University of Durham. After a BSc in Biology from the University of Nottingham and an MSc in Biological Computation from the University of York, he completed his PhD (2003) in animal social learning from the University of Cambridge under the supervision of Kevin Laland. This was followed by postdoctoral positions in Marc Feldman's lab, working on cultural niche construction and the evolution of costly social norms (*Theoretical population biology*, 70), and in Kevin Laland's lab, carrying out experiments and theoretical analysis of the evolution of social learning strategies. His current research interests include social learning, cultural evolution, gene-culture coevolution and cultural niche construction.