Introduction

Human niche construction in interdisciplinary focus

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Niche construction is an endogenous causal process in evolution, reciprocal to the causal process of natural selection. It works by adding ecological inheritance, comprising the inheritance of natural selection pressures previously modified by niche construction, to genetic inheritance in evolution. Human niche construction modifies selection pressures in environments in ways that affect both human evolution, and the evolution of other species. Human ecological inheritance is exceptionally potent because it includes the social transmission and inheritance of cultural knowledge, and material culture. Human genetic inheritance in combination with human cultural inheritance thus provides a basis for gene–culture coevolution, and multivariate dynamics in cultural evolution. Niche construction theory potentially integrates the biological and social aspects of the human sciences. We elaborate on these processes, and provide brief introductions to each of the papers published in this theme issue.

Keywords: niche construction; gene–culture coevolution; cultural evolution; human evolution

1. INTRODUCTION

Niche-construction theory (NCT) originated as a branch of evolutionary biology that emphasizes the capacity of organisms to modify their environment and thereby influence their own and other species’ evolution [1]. The defining characteristic of niche construction is not the modification of environments per se, but rather organism-induced changes in selection pressures in environments [1]. The effects of niche construction have been documented across a wide range of species including animals manufacturing nests, burrows and webs, and plants modifying nutrient cycles. The papers presented in this special issue explore the phenomenon in Homo sapiens, for whom endogenous causes of evolutionary dynamics are impossible to ignore.

NCT differs from standard evolutionary theory (SET) in recognizing that the evolution of organisms is co-directed by both natural selection and niche construction. While genetic variation is subject to natural selection through differential survival and reproductive success, the selective environments themselves are partly determined by modifications made by niche-constructing organisms. Hence NCT recognizes natural selection and niche construction as reciprocal causal processes in evolution, and treats the adaptations of organisms as products of both processes [2].

Evolution entails networks of causation and feedback in which previously selected organisms drive environmental changes, and organism-modified environments subsequently select for changes in organisms.

NCT provides both a philosophical shift in the way we view and understand evolutionary processes as well as a testable scientific theory. While the effects of niche construction on the evolutionary process have often been neglected in the past, it is also important to note that many aspects of NCT are already incorporated in standard theories of evolutionary biology, ecology, developmental biology and the human sciences. However, rather than aiming just to relabel or reclassify established theories such as gene–culture coevolution or ecosystem engineering, NCT is put to better use when formulating new hypotheses, or building a more general evolutionary framework within which other theories can be subsumed. NCT provides mechanisms by which currently disconnected bodies of theory, such as evolutionary and developmental biology (‘evo-devo’) [1,3,4], or human cultural evolution and structuration theory ([5], see below) can be united [6].

Here, we review the fundamental principles of contemporary NCT, initially in the context of biological evolution, before showing how the theory incorporates cultural evolutionary processes, and how it provides a framework for consilience between the natural and the social sciences [7]. Where appropriate, we give short summaries of each of the contributing papers in this theme issue.

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One contribution of 13 to a Theme Issue ‘Human niche construction’.
2. FUNDAMENTAL PRINCIPLES OF NICHE CONSTRUCTION

An early advocate of the niche construction perspective, Lewontin [8], neatly summarized the differences between standard evolutionary theory and NCT in two pairs of coupled differential equations. His first pair (equations 2.1a,b) summarizes SET:

\[
\frac{dO}{dt} = f(O, E) \quad (2.1a)
\]

and

\[
\frac{dE}{dt} = g(E). \quad (2.1b)
\]

In equation (2.1a), evolutionary change in organisms, \(dO/dt\), depends on both organisms' states, \(O\), and environmental states, \(E\). In equation (2.1b), environmental change, \(dE/dt\), depends exclusively on environmental states. In general, organisms are not treated as the cause of any evolutionarily significant changes in their environments, with the exception of cases such as frequency dependent selection, habitat selection, maternal inheritance and coevolution. Instead adaptive evolutionary change is assumed to be governed exclusively by a single 'causal arrow', natural selection.

However, SET underestimates the significance of the fact that, to stay alive, organisms must be active as well as reactive relative to their environments. Organisms must gain resources from their external environments by genetically informed, or in animals, possibly brain informed, fuel consuming, non-random work [3]. They must perturb specific components of their environments, often at locations chosen by the organisms themselves, and they must excrete detritus to their environments throughout their lives [1]. Organisms are, therefore, compelled to modify some natural selection pressures in their environments by the accumulating consequences of their activities. Lewontin captured this point by his second pair (equations 2.2a,b) of equations that, in effect, summarize NCT:

\[
\frac{dO}{dt} = f(O, E) \quad (2.2a)
\]

and

\[
\frac{dE}{dt} = g(O, E). \quad (2.2b)
\]

In equation (2.2a) change in organisms, \(dO/dt\), is again assumed to depend on both organisms' states and environmental states, but in equation (2.2b) environmental change, \(dE/dt\), is now assumed to depend on both environment states, and the niche-constructing activities of organisms. Therefore, equation (2.2b) introduces the second 'causal arrow' in evolution that Odling-Smee [9] called niche construction.

The philosopher Godfrey-Smith [10] highlighted the same distinction between SET and NCT by describing SET as an 'externalist' theory of evolution. SET is externalist because it seeks to explain the internal properties of organisms, their adaptations, exclusively in terms of properties of their external environments, natural selection pressures. SET is also fully consistent with the traditional view expounded by Mayr [11], who regarded natural selection as the ultimate cause of phenotypic characters [12]. It is a view that devalues so-called proximate causes, including developmental processes such as learning, and human cultural processes in evolutionary biology [13,14]. In SET, niche-construction effects caused by developmental or proximate processes can be regarded as the expression of phenotypic plasticity [15], or sometimes as extended phenotypes [16], but ultimately they still have to be explained by prior natural selection [17].

For many purposes, SET is sufficient, but it is insufficient when genetic selective environments are modified as a function of phenotypic variation derived from so-called proximate processes such as learning. For example, human cultural variation, depending largely on differential social transmission of information through social learning, may result in cultural niche-constructing practices that modify the natural selection of some human genes. As the selected genes may also influence human cultural practices, the assignment of 'causation' becomes complex. NCT replaces SET's dichotomous proximate and ultimate distinction with 'reciprocal causation'. Adaptations of organisms depend on natural selection that is modified by niche construction, and niche construction that is selected by natural selection [1,2]. In this light, niche construction is a mechanism of endogenous causation, reciprocal to natural selection in the evolutionary process.

NCT asserts that, as a consequence of ancestral niche construction, offspring inherit not only genes, but an ecological inheritance, in the form of modified local selective environments relative to genetic fitness. Overall, each offspring actually inherits an initial organism-environment relationship, or 'niche', from its ancestors such that:

\[
N(t) = h(O, E), \quad (2.3)
\]

where \(N(t)\) represents the niche of a population of organisms \(O\) at time \(t\) in an environment \(E\). The dynamics of \(N(t)\) are driven by the interaction of both population-modifying natural selection pressures in \(E\), and by the environment-modifying niche-constructing activities of populations, \(O\) [3].

In effect, this innovation replaces an 'externalist' theory by an 'interactionist' theory of evolution [10]. A niche is a neutral explanatory reference device. It can capture reciprocal causation in evolution without imposing any bias either in favour of natural selection and against niche construction, or vice versa [3]. Conceptually, it permits differential natural selection to be treated no longer as a function of external environments, but, where appropriate, as a function of organism-environment interactions.

In humans, much niche construction is influenced by socially transmitted behaviour This observation provoked Laland et al. [18] to propose a triple inheritance evolutionary framework, delineating genetic, cultural and ecological inheritance systems. Either genetically or culturally influenced behaviours can modify an environmental resource that subsequently
introduces to a human ecological inheritance across generations. In Laland et al.’s models the inherited environmental resource was originally assumed to be a material or energetic resource previously modified by cultural niche construction. The inherited resource might then affect either a human cultural process without having any effect on human genetics, or it could affect the natural selection of human genes including, sometimes, the natural selection of genes that subsequently influenced the expression of human cultural processes [18–20].

Riede [21] in this issue argues that this triple inheritance system (genes, culture and ecology) can provide an effective framework to study archaeological data, and he reviews a variety of cases where archaeology provides signatures of human niche construction activity within this system. A problem with using the archaeological record is that it can be difficult to distinguish causal relationships between niche-constraining traditions and traditions selected as consequences. To overcome this, Riede advocates the use of phylogenetic comparative methods used to study correlated evolution in biology. He demonstrates the potential of this approach in a case study investigating the causal relationships between traditions for reindeer economies and dog use in Late Palaeolithic populations of southern Scandinavia, using a cultural phylogeny derived from artefact traditions.

Recently, Odling-Smee [3,22] suggested that Laland et al.’s triple inheritance system is unnecessarily complicated and constraining. Instead, the original cultural and ecological inheritance systems can be collapsed into a single ecological inheritance system consisting of informatic as well as physical material and energy resources (figure 1). This simplification is consistent with the idea that an individual can inherit both a social and a physical niche that can include culturally transmitted knowledge and behaviours, as well as material culture, providing both culturally modified sources of information and culturally modified physical resources, in an individual’s developmental environment [23,24].

Semantic information in an individual’s inherited niche might take the form of a behaviour, demonstrated by peers or elders, acquired through social learning, such as subsistence practices or social norms. Inherited physical resources could refer to aspects of material culture, for example, nutritional resources or tools, created through hunter-gathering activity or farming. Many inherited niches obviously consist of both informatic and physical resources; for instance, farmed livestock and crops are not just nutritional resources, but also a source of public information concerning subsistence practices.

While the proposed two-track human inheritance system is consistent with Laland et al.’s [18] original triple inheritance model, it is founded on general principles that should apply to all organisms. Informally, evolution based on the transmission of adaptive semantic information or ‘know how’ requires energy and material resources to pay for its physical acquisition, storage (whether it be in RNA, DNA or neurons etc.), use and transmission. Thus, there is a natural delineation between the ecological inheritance of informative and energetic/physical resources. The delineation assumes a working definition of semantic information to be ‘anything that reduces uncertainty about selective environments, relative to the fitness interests of organisms’ [3, p. 184]. In addition, the inherited ecological niche can include epigenetic informatic and physical resources that lie internal to the organism, such as the epigenetic inheritance of DNA methylation patterns or the cytoplasmic inheritance of nutritional resources [14,25]. These ‘evo-devo’ considerations at the cellular level are beyond the scope of this theme issue.

Systematic changes in developmental environments can also result in systematic changes to the phenotypic expression of developing organisms [26]. For example, the construction of a developmental niche may modify the shape of the relevant norm of reaction by reducing the range of developmental environments to which juveniles are exposed [2,6]. Animal burrows and nests typically buffer variation in environmental variables such as temperature and humidity, While human habitation and clothing provide similar roles. Constructed human social environments may also affect behavioural development. For instance, activities such as play and teaching can provide scaffolding for learning [27]. Sterelney [28] in this issue argues that the construction of developmental niche has been critical for the evolution of behavioural modernity in humans. In particular, he asserts that in the context of demographic expansion in the upper Palaeolithic, the construction of structured learning environments, which result in apprentice learning, allows high fidelity cultural transmission of skill sets across generations, resulting in the behaviourally modern cultures.
a two-locus population genetic framework, where a genetic (or cultural) trait at one locus affects the selective environment for recipient genetic (or cultural) traits at the second locus [1,18,29–34]. The research has revealed interesting evolutionary dynamics such as momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), time lags and inertia in response to selection, and sudden catastrophic responses to selection [6,19,29,30,35,36]. The findings have also been consistent with qualitative genetic analysis of indirect genetic effects and maternal inheritance [37–40].

Cultural niche construction can affect either genetic or cultural evolutionary dynamics (or both), depending in part on the relative intensity of selection. Theory suggests that human gene–culture coevolution will typically occur if a genetic selective environment remains stable across sufficient generations for natural selection to act on human genetic variation [1]. Human evolution may be unique insofar as our cultural capacities and adaptive cultural niche-constructing activities reinforce and amplify each other [1,19,41,42]. Thus, the capacities for social, technical or cultural intelligence, such as language and cooperation, have apparently coevolved with the cumulative cultural evolution of technologies and social conventions that these capacities afford [43–45].

In the current issue Rendell et al. [46] use a cellular automaton model to explore local and global spatial effects of cultural niche construction on gene–culture coevolutionary dynamics. Similar to runaway sexual selection, they explore coevolution through ‘hitchhiking’ between cultural transmission of a behaviour (equivalent to the mate preference) that modifies the local selective environment of a genetic trait (equivalent to the preferred trait), even when there is an inherent cost associated with either the cultural trait or the genetic trait. They also examine the unique spatial influence on the evolution, through secondary hitchhiking, of a genetic trait that affects the capacity for cultural niche construction, but bears an inherent cost. The findings show the potential importance of cultural niche construction influencing, for example, genetic evolution of disease resistance and hominid brain size.

Gene–culture coevolutionary dynamics are likely to have been particularly important in recent human evolution by influencing processes such as global dispersal and migration, language evolution, behavioural modernity and sociality, the advent of agriculture, and the evolution of human and domesticate diseases [20,47,48]. This is consistent with evidence for recent and rapid genetic selection, affecting characteristics including skin pigmentation, body shape, dentition, brain function, metabolic efficiency and disease resistance [20,47]. The impact of cultural niche construction and gene–culture coevolutionary dynamics on both human technological and social evolution are considered in the current theme issue.

One of the most powerful examples of such changes is in humans’ exploitation and modification of natural resources. In this issue, Smith [49] draws on a wealth of fascinating examples, largely from North America, to develop a classification of niche-constructing activities, used by small-scale human societies, to produce food and raw material resources from wild flora and fauna. He highlights how the scheme distinguishes particular characteristics of wild taxa that make them likely targets for niche construction, as well as the proactive impact that humans have had on their own subsequent resource selection as a function of yields.

Rowley-Conwy & Layton [50] in this issue contrast the stability of constructed niches by hunter–gatherers with constructed niches during the advent of agriculture. Considering a wide variety of plant manipulation and hunting activity, they show how hunter–gatherers can proactively alter both the ecological stability and evolutionary dynamics of the affected species. The authors examine the role of niche construction in the development and geographical expansion of both cereal and livestock agriculture, and highlight the feedback effects of population expansion on niche instability.

Gerbault et al. [51] in this issue review the current understanding of perhaps the most well-cited case of gene–culture coevolution, that of lactase persistence and dairy farming. Their paper takes an interdisciplinary approach, considering new genetic data, archaeological evidence and simulation modelling to explore how this coevolutionary process took place. Focusing on the European Neolithic transition, including the spread of animal domestication and uptake of dairy farming, Gerbault et al. synthesize these data to give a contemporary explanation for the observed distribution of lactase persistence, highlighting the role of both demography and niche construction.

The role of gene–culture coevolution on the evolution of human sociality is explored in this issue by Gintis [52]. This paper provides a formal argument that culture is not a by-product of genetic evolution, but rather that culturally constituted aspects of the social environment have driven the genetic evolution of predispositions for cognitive features such as prosocial emotions and moral cognition. The paper draws on both theoretical and experimental literature to support the case for the impact of gene–culture coevolution on, for instance, the internalization of norms, altruism and character virtues.

The theme of human sociality is continued in this issue by Ihara [53], who develops a mathematical model to examine how culture-dependent discriminate sociality could have evolved by gene–culture coevolution. Using the scenario of a Hawk–Dove game to elicit resource competition, Ihara shows how a culturally transmitted trait can alter the selective environment to favour the genetic evolution of culture-dependent discriminators that exercise either in-group favouritism or prestige bias as a function of the cultural trait distribution. Ramifications for the evolution of discriminate sociality include the intriguing possibility that the evolution of this capacity in Homo sapiens, but not Neanderthals, contributed to their contrasting fates during the Middle to Upper Palaeolithic transition.

Ihara notes that his model is also consistent with a cultural practice influencing the cultural, rather than genetic, evolution of discriminate sociality. In general, it is probably more common for cultural niche construction to result in a cultural, rather than a genetic...
response. Feasibly, trans-generational cultural niche construction can modify environments in ways that favour ever-more culture, causing cultural niche construction to become ever-more powerful [1,18,23,43,54]. This process may have led to the accumulation of complex social norms and complex cultural knowledge in behaviourally modern humans.

Fast cultural responses to a culturally modified niche can also render genetic responses unnecessary [19]. For example, human-induced pollution may provoke new technology to remove environmental contaminants, thus countering the change in the genetic selective environments for species across relevant ecosystems. Here, the initial detrimental activity could be due to ‘inceptive’ niche construction, while the cultural response is likely to depend on ‘counteractive’ niche construction. Similarly, drug treatments to prevent diseases may relax genetic selection for disease resistance or susceptibility. For instance, Boni & Feldman [55] develop a mathematical model to examine how antibiotic use, favouring selection of resistant bacterial strains, can result in cultural selection for the avoidance of antibiotic use. This example is also notable as a case of interspecific niche construction, as the cultural and genetic evolution of antibiotic use and bacterial strains, respectively, modify the selective environments of one another.

NCT may be particularly relevant to the dynamics of cultural traits because the theory can incorporate the effects of cultural backgrounds, or environments, as components of constructed niches, affecting selection between cultural variants [56]. This point is illustrated by theoretical studies of fertility control and the demographic transition. Ihara & Feldman [31] 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 can affect the degree to which traits are transmitted obliquely rather than vertically, for example, from teachers rather than from 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 are individuals with a high number of offspring. This study revealed the classic niche-construction characteristic of a time-lag between the increase of the average level of education and a subsequent decline in fertility: a pattern that is consistent with, and may partially explain, a typical demographic transition.

In a related study, Borenstein et al. [34] 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 percolate. They found that local between-population cultural niche construction could account for the spread of reduced fertility preference across countries occurring at ever-lower levels of development [57]. Lipatov et al. [58] in this issue distinguish between a social niche, referring to the structure of expected social roles, and a cultural niche, referring to a set of socially transmitted symbolic or meaningful ideas. Drawing on rich ethnographic data relating to a shift from uxorilocal to virilocal marriage practices in early twentieth century Taiwan, they develop a mathematical model to explore the interaction between social structure and cultural ideas. Lipatov et al. show how a disjuncture between practice and belief can be affected by changes in the economy, specifically the proportion of the population wealthy enough to pay the observed brideprice in the virilocal system.

Shennan [59] in this issue chooses to focus on the inheritance of material wealth, such as property, as a constructed niche or resource afforded by private property rights that develop with agriculturalist and pastoralist societies. Shennan explores the influence of this niche on variation and stratification of reproductive strategies, and in addition, uses McNamara & Houston's [60] model for non-genetic inheritance of phenotypic quality to bring insight to the importance of inter-generational transfers of land wealth on long-term reproductive success.

4. INTEGRATING HUMAN, BIOLOGICAL AND SOCIAL SCIENCES

Human and social scientists have been reticent to make use of evolutionary theory in the past for several reasons. One is that human scientists are predominantly interested in human behaviour and culture, rather than genes, and as a consequence they have little use for a standard theory of evolution that is exclusively driven by natural selection acting on genetic variation. A second reason is that an adaptationist account of behaviour derived from SET, for example in evolutionary psychology, is regarded somewhere between oversimplification and misrepresentation [61].

NCT addresses both these issues by accounting for the proactive role of human development and cultural processes in human evolution through the modification and ecological inheritance of selective environments. The inherited selective environment can pertain to any form of ecologically inherited semantic information, including culturally inherited information, as well as physical environments. This enables human scientists to explore human phenotypic variation from the perspective of genetic, ontogenetic and cultural processes operating at distinct, but richly interconnected levels [62], as exemplified in many of the papers in the current issue.

Another source of reticence is the perception among social scientists that evolutionary theory cannot account for cultural diversity, but only for pan-human traits. It is, therefore, unable to offer social scientists any insights into the phenomena that primarily interest them. However, NCT provides a framework for the quantitative examination of cultural diversity through modification of cultural and social selective environments to affect local cultural histories and promote additional cultural diversity, where it is unnecessary to consider genetic fitness consequences [63]. Furthermore, it is now well established that a quantitative evolutionary model can be of great utility to study cultural diversity [56,64–66].

There are also some parallels between the evolutionary framework offered by NCT and some recent

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developments in social theory that have tried to transcend the classic dichotomy between structure (the rules and institutions of societies) and agency (the intentions, motivations and performances of individuals). So-called ‘structuration theory’ [5] is based on a similar premise to niche construction in that it emphasizes that social structures are both the context and the consequences of individual actions. Cultural meanings, moral orders and the distribution of economic and political power constrain agency and inform its goals, but they also depend on it for their reproduction. Humans’ ability to assess the effectiveness of their behaviours (‘reflexive monitoring’) allows them to manipulate and occasionally even to transform structure, which can have intended and unintended consequences for their and others’ future behaviour.

The importance of evaluative and purposeful agency has clear implications for our understanding of human niche construction, as Lansing & Fox [67] discuss in their contribution to this issue. They describe how the engineered landscape of Balinese rice terraces is governed principally by local farming associations responding to the ecologically inherited conflicting interests of water availability and pest control. The development of rice cults has played a crucial role in coordinating farmers’ behaviours, but has also generated a wide range of new cultural representations and paradigms, including the agricultural calendar, cosmological system and religious consciousness.

5. CONCLUSION

We can gain a richer understanding of evolutionary processes by accounting explicitly for phenotypic modification of selective environments that can result in the ecological inheritance of semantic and physical resources (figure 1). Thus, niche construction provides an endogenous causal role in evolution that is reciprocal to that of selection. In recent human evolution, the most potent human contributions to human ecological inheritance have probably occurred through cultural inheritance. If so, that requires the investigation of human evolution in the context of a theory of gene–culture coevolution that explicitly includes cultural niche construction. One potential advantage of combining NCT with gene–culture coevolutionary theory is that it should make gene–culture coevolutionary models more empirically tractable by including NCT’s mechanisms of niche construction and ecological inheritance, both of which are open to investigation [1].

Niche construction provides a powerful framework for bringing together different perspectives on the role of culture as a selective force in human evolution that have developed in recent decades [68]. When framed in terms of SET, these approaches often seem to be in conflict with one another—for example, over the question of the extent to which culture is ‘adaptive’ [69]. In NCT, these differences largely disappear. Rather than focusing on the adaptiveness of cultural behaviours relative to an external environment, NCT recognizes that culture is a crucial part of our ‘ecological inheritance’. Thus, over the last 100 000 years or so, humans have become increasingly reliant on physical and semantic resources that have been shaped by the cultural activities of preceding generations—from domesticated animals and tool-making to writing, the built environment and even religious cosmologies. Such inventions have in various ways both depended on and then subsequently shaped the evolution of genetic and other cultural traits. Niche construction provides a unique paradigm for studying these relationships that explicitly recognizes the reciprocal influences of cultural evolution, cultural evolvability and gene–cultural evolution on one another.

Empirical investigations will not be easy, however. The eco-evolutionary feedbacks generated by cultural niche construction are typically complicated, and they are likely to demand multi-disciplinary approaches [70]. At present, different disciplines, ranging from population geneticists, ecologists and molecular biologists to anthropologists, archaeologists and economists, contribute different datasets and different theoretical interpretations to different arcs of these feedback cycles. In future, a better understanding of human evolution may only be achieved by closer between-discipline cooperation, and the mutual sharing and integration of different bodies of theory from different disciplines [20]. This promises to be an illuminating, though challenging, enterprise. The papers represented in this issue constitute an encouraging start.

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