

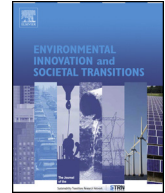


ELSEVIER

Contents lists available at ScienceDirect

Environmental Innovation and Societal Transitions

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



Niche construction, innovation and complexity

Kevin N. Laland*, Neeltje Boogert, Cara Evans

School of Biology, University of St Andrews, St Andrews KY169TS, Scotland, UK

ARTICLE INFO

Article history:

Received 7 February 2013

Received in revised form 15 May 2013

Accepted 2 August 2013

Available online xxx

Keywords:

Cultural niche construction

Ecological inheritance

Evolutionary economics

Legacy effects

Societal transitions

ABSTRACT

Niche construction is the process of environmental modification by organisms. By transforming natural selection pressures, niche construction generates feedback in evolution at various different levels. Niche-constructing species play important ecological roles by creating habitats and resources used by other species and thereby affecting the flow of energy and matter through ecosystems (ecosystem engineering) and can be a source of legacy effects to descendant populations (ecological inheritance). Niche construction theory (NCT) emphasizes how acquired characters play an evolutionary role through transforming selective environments, a point germane to human evolution, where we see extensive environmental modification through cultural practices. Theoretical findings stemming from population-genetic and population-ecology modelling of niche construction suggest that niche construction can be a source of evolutionary innovation and stability, and can generate unusual evolutionary dynamics, such as time-lagged (i.e. inertia, momentum) and autocatalytic responses to selection, and coevolutionary feedback between levels (e.g. gene-culture coevolution). Similar dynamics are predicted in analogous cultural systems subject to human niche construction. Here we present an accessible introduction to NCT and then briefly reflect on how it might be used to study human innovation and complex systems.

© 2013 Elsevier B.V. All rights reserved.

1. An introduction to niche construction theory

A striking feature of the natural world that evolutionary biology sets out to explain is the hand-in-glove complementarity of organisms and their environments. The conventional view of evolution

* Corresponding author. Tel.: +44 133 446 3009.
E-mail address: kn11@st-andrews.ac.uk (K.N. Laland).

is that species, through the action of natural selection, come to exhibit those characteristics that best enable them to survive and reproduce in their environments. Organisms are generally perceived as being moulded by selection to become well adapted to their environments (Fig. 1a). Under this perspective, “adaptation is always asymmetrical; organisms adapt to their environment, never vice versa” (Williams, 1992, p. 484).

In contrast, the niche-construction perspective emphasizes a second route to the adaptive fit or “complementary match” between organism and environment: It places emphasis on the capacity of organisms to modify environmental states (Lewontin, 1983; Odling-Smee, 1988; Odling-Smee et al., 2003), often but not exclusively, in a manner that suits their genotypes (Fig. 1b). Such matches should be thought of as the dynamic products of a two-way process that involves organisms both responding to “problems” posed by their environments through natural selection and setting themselves some new problems by changing environments through niche construction (Lewontin, 1983, 2000; Odling-Smee, 1988). Niche construction theory (NCT) thus treats evolutionary change as ‘reciprocally caused’ (Laland and Sterelny, 2006), with organisms viewed as co-directing their own evolution. To quote Levens and Lewontin (1985, p. 106): “The organism influences its own evolution, by being both the object of natural selection and the creator of the conditions of that selection”.

Niche construction enables and protects our species’ very existence on this planet: Our oxygen-rich atmosphere would not exist if it were not for the niche-constructing cyanobacteria that started to harvest light and release oxygen ca. 3.6 billion years ago (Stal, 2000), and niche-constructing mangroves reduced the damage and number of deaths in Indian coastal villages caused by destructive tsunami waves (Danielsen et al., 2005) and cyclones (Das and Vincent, 2009). Although niche construction is thus all around us, it often occurs in subtler ways, as illustrated by animals building nests and burrows, plants changing levels of atmospheric gases and bacteria fixing nutrients. In fact, all living organisms construct aspects of their world. In doing so they also fashion new agendas, changing the environment in which they and others about them grow, develop, and learn, frequently in ways that revise the pattern of natural selection acting back on their population as well as on other species that cohabit their niche.

This emphasis on the modification of habitat and resources by organisms is shared by ecologists who emphasize the significance of “ecosystem engineering” by which organisms modulate flows of energy and matter through environments (e.g. Cuddington et al., 2007; Jones and Lawton, 1995; Jones et al., 1994, 1997). Such engineering activity can have significant impacts on community structure, composition, and diversity. Young beavers, for example, inherit from their parents not only a local environment comprising a dam, a lake, and a lodge but also an altered community of microorganisms, plants, and animals (Naiman et al., 1988; Wright et al., 2002). In another example, Lill and Marquis (2003) describe how some caterpillars build shelters from leaves and silk, providing a habitat that is colonized by many other insects. They established that removal of caterpillar-built shelters significantly decreased the mean species richness of insects in the trees, whereas trees with artificial shelters mimicking those manufactured by the caterpillars exhibited increased species richness. Here species diversity depends critically on niche construction.

Niche construction can generate long-term effects on ecosystems. For instance, beaver dams deteriorate without beaver activity, but this leads to meadows that can persist for nearly a century and rarely return to the original vegetation (Hastings et al., 2007). Such legacies are known as ‘ecological inheritance’, which comprises modified biotic and abiotic states, bequeathed by niche-constructing organisms to descendant organisms (Odling-Smee et al., 2003), and can be viewed as an additional inheritance system (Fig. 1b). Many of the ecological processes that trigger evolutionary episodes depend on niche construction and ecological inheritance (Odling-Smee, 1988). Ecological inheritance requires intergenerational persistence (often through repeated acts of construction) of whatever physical – or, in the case of humans, cultural – changes are caused by ancestral organisms in the local selective environments of their descendants (Odling-Smee, 2010; Odling-Smee and Laland, 2011). This is relevant to the conservation and management of biodiversity and natural resources. Through their niche construction/ecosystem engineering, organisms produce and destroy habitats and resources for other organisms, generating an additional “engineering web” of connectance and control that regulates ecosystem functioning in conjunction with the well-established webs of trophically-connected

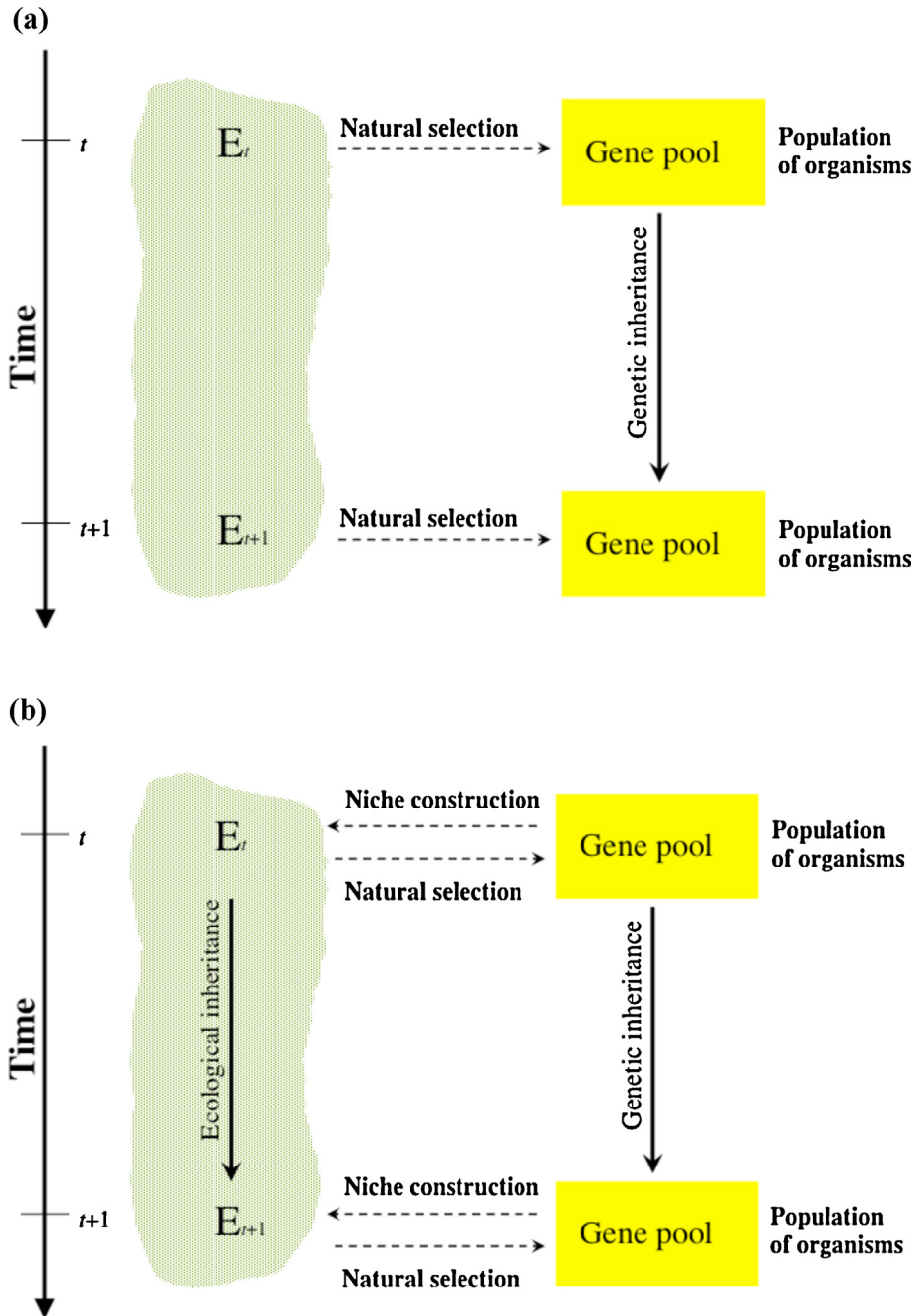


Fig. 1. Two views of evolution. Under the conventional perspective (a), niche construction is recognized as a product of natural selection but not as an evolutionary process. Inheritance is primarily genetic. Under the niche-construction perspective (b), niche construction is recognized as an evolutionary process. Here, ecological inheritance plays a parallel role to genetic inheritance. Taken from [Laland and O'Brien \(2011\)](#) (permission requested).

Table 1

Twelve insights from niche construction theory.

Finding	References
Niche construction can	
1. Fix genes or phenotypes that would, under standard evolutionary theory, be deleterious; support stable polymorphisms where none are expected and eliminate polymorphisms that without niche construction would be stable	Laland et al. (1996, 1999, 2001), Kerr et al. (1999), Creanza et al. (2012)
2. Affect evolutionary rates, both speeding up and slowing down responses to selection under different conditions	Laland et al. (1996, 1999, 2001), Silver and Di Paolo (2006)
3. Cause evolutionary time lags, generate momentum, inertia, and autocatalytic effects. Interactions with evolving environments can produce catastrophic responses to selection, as well as cyclical dynamics	Laland et al. (1996, 1999, 2001), Kerr et al. (1999)
4. Drive niche-constructing traits to fixation by creating statistical associations with recipient traits	Silver and Di Paolo (2006), Rendell et al. (2011a,b)
5. Influence the dynamics, competition, and diversity of meta-populations	Hui et al. (2004), Borenstein et al. (2006)
6. Be favoured, even when currently costly, because of the benefits that will accrue to distant descendants	Lehmann (2007, 2008)
7. Allow the persistence of organisms in currently inhospitable environmental conditions that would otherwise lead to their extinction; facilitate range expansion	Kylafis and Loreau (2008)
8. Regulate environmental states, keeping essential parameters within tolerable ranges	Laland et al. (1996, 1999), Kylafis and Loreau (2008)
9. Facilitate the evolution of cooperative behaviour	Lehmann (2007, 2008), van Dyken and Wade (2012)
10. Drive coevolutionary events, both exacerbate and ameliorate competition, and affect the likelihood of coexistence	Krakauer et al. (2009), Kylafis and Loreau (2011)
11. Affect carrying capacities, species diversity and robustness and macroevolutionary trends	Krakauer et al. (2009)
12. Affect long-term fitness (not just the number of offspring or grand-offspring) by contributing to the long-term legacy of alleles, genotypes, or phenotypes within a population	McNamara and Houston (2006), Lehmann (2007), Palmer and Feldman (2012)

The table is reproduced from [Odling-Smee et al. \(2013\)](#).

organisms. However, environmental changes that exemplify human niche construction, such as habitat degradation, deforestation, industrial and urban development, often destroy the control webs that underlie ecosystems. Fortunately there is scope to use our own niche construction and that of other “key engineering species” ([Boogert et al., 2006](#)) in novel restoration and management methods that complement established conservation strategies ([Laland and Boogert, 2010](#)).

NCT is more than just an alternative perspective; it is a serious body of formal evolutionary theory. Some of the key theoretical findings are summarized in [Table 1](#). One important finding is that niche-constructing traits can drive themselves to fixation by generating statistical associations between niche-constructing alleles and those alleles whose fitness depends on resources modified by niche construction ([Silver and Di Paolo, 2006](#)). The same runaway process can occur even if the niche-constructing trait is a cultural practice, such as the planting of a crop ([Rendell et al., 2011b](#)). This process can be illustrated by the farming practises of West-African people, who cut clearings in forests to grow their yams. When it rains, these clearings inadvertently create puddles that function as breeding grounds for malaria-carrying mosquitos. Exposure to malaria in turn favours the haemoglobin Sickle-cell allele (HbS) that confers resistance to malaria in heterozygote humans. Hence we see a correlation between the frequency of the HbS allele and the amount of rain in those human populations that cultivate crops, but not in adjacent closely-related populations that do not cultivate crops ([Fig. 2a](#)). Here causality flows through the ecosystem, from cultural to genetic and back to cultural processes, and from one species to the next, driven by iterative bouts of niche construction and selection, at multiple levels ([Fig. 2b](#)).

This case study is a plausible example of the kind of phenomena invested in [Rendell et al's \(2011b\)](#) theoretical analysis. Costly cultural practices propagate themselves through inadvertently generating selection for local genotypes with which they are statistically associated and subsequently hitchhiking

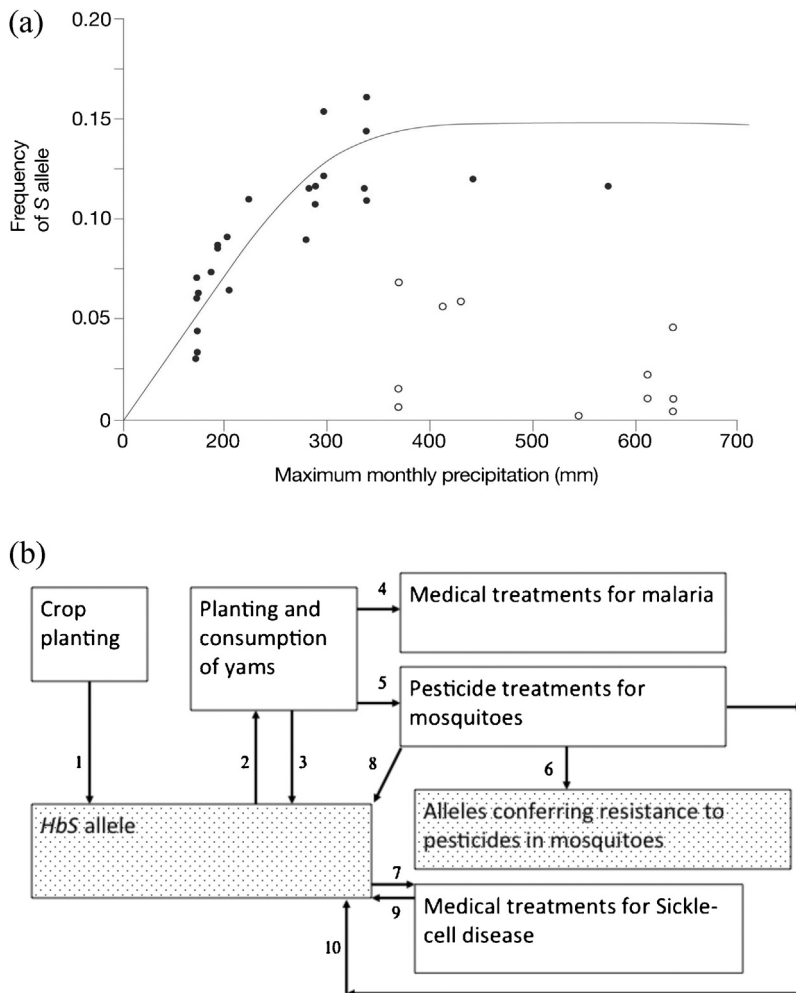


Fig. 2. (a) Populations of Yam cultivators (black circles), but not otherwise adjacent, closely related populations that do not engage in crop planting (open circles) exhibit a positive correlation between the frequency of the sickle-cell allele and the amount of rain. Taken from Durham (1991) (permission requested). (b) Construction chain depicting the causal influences following a cultural niche-constructing practice, here the planting of yams in West Africa. Planting, which involves deforestation, (1) inadvertently promotes the spread of malaria by leaving standing pools of water, leading to selection for the haemoglobin Sickle-cell (*HbS*) allele. The resulting incidence of sickle-cell disease (2) favours the planting of yams and other crops with medicinal benefits, which (3) further promotes the spread of (*HbS*) and (4) scaffolds the development and/or application of medical treatments for malaria, as well as (5) pesticide treatments for mosquitoes, which (6) generates selection for alleles conferring resistance to pesticides in mosquitoes. The spread of sickle cell (7) scaffolds the development and/or application of medical treatments for sickle-cell disease. Pesticide treatment of mosquitoes (8), medical treatment for sufferers of sickle-cell disease (9), and malaria victims (10), affect the intensity of selection on the (*HbS*) allele. Taken from O'Brien and Laland (2012).

to high prevalence in the process. Moreover, the example shows how the niche-construction perspective encourages the tracing of causal influences through ecosystems rather than treating each bout of selection separately, such that the full ramifications of anthropogenic activity can be better understood. More generally, NCT has established that genetic and cultural processes can also affect the rate of change of allelic frequencies in response to selection and greatly influence the pattern and rate of evolutionary processes.

In this article we hope to provide other researchers, particularly those in the human sciences, with a sketch of the new conceptual framework based around NCT. Henceforth we use the term ‘human sciences’ broadly so as to encompass the wide appeal of NCT to all disciplines that seek to understand and address the effects of human agency on both our own, and other species’, physical, developmental and socio-ecological environments. Indeed, many researchers, including some human scientists, have already found this conceptual framework useful. For instance, archaeologist [Smith \(2011\)](#) proposes a cultural niche construction model of initial domestication, which presents a fresh alternative to optimal foraging theory—accounts of the origins of agriculture, and supersedes it in explanatory power. Linguist [Bickerton \(2009\)](#) builds a new account of the evolution of language around NCT. [Collard et al. \(2011\)](#) apply NCT to ethnographic data to explore the causes of cross-cultural variation in the diversity of subsistence toolkits, finding that predictions from NCT provide a good fit to the data, unlike the established theories. Other successes include a suite of novel theoretical and empirical findings related to landform, ecosystem and population dynamics ([Corenblit et al., 2011](#); [Krakauer et al., 2009](#); [Kylafis and Loreau, 2008, 2011](#); [Lehmann, 2008](#); [Post and Palkovacs, 2009](#); [Silver and Di Paolo, 2006](#)), macroevolutionary change ([Erwin, 2008](#)), human cultural evolution and learning ([Laland et al., 2001](#); [Kendal et al., 2011](#)), social systems ([Flack et al., 2006](#); [Ihara and Feldman, 2004](#)), the history of agriculture ([Rowley-Conwy and Layton, 2011](#)) and many other topics.

2. Niche construction theory as a conceptual framework for the human sciences

A focus on niche construction has important implications for how researchers view the relationship between genetic evolution, developmental processes, and cultural change. One implication is that niche-constructing organisms can no longer be treated as merely “vehicles” for their genes ([Dawkins, 1976](#)) because they also modify selection pressures in their own and in other species’ environments. In the process, they can introduce feedback to both ontogenetic and evolutionary (genetic and cultural) processes. Alongside others (e.g. [Bickerton, 2009](#); [Gottlieb, 1998, 2000, 2002](#); [Kendal et al., 2011](#); [Oyama et al., 2001](#); [Plotkin, 2010](#); [Layton, 2010](#)), we have suggested that this active, constructive conception of the role of organisms in evolution, and indeed in ontogeny, fits well with conceptualizations of human agency that are widespread among many disciplines within the human sciences ([Odling-Smee et al., 2003](#); [Laland and O’Brien, 2010](#); [Laland et al., 2000](#); [O’Brien and Laland, 2012](#)). Of course, social scientists do not need to be told that humans build their world. However, they may be less conscious of the fact that other organisms do the same and may, we believe, feel more comfortable with a conceptualization of evolution that, while broadly in accord with the modern synthetic theory, nonetheless has an emphasis that aligns with their own thinking.

A second implication is that there is no requirement for niche construction to result directly from genetic variation in order for it to modify natural selection. Humans can and do modify their environments, largely through cultural processes, and it is this reliance on culture that lends human niche construction a special potency ([Kendal et al., 2011](#); [O’Brien and Laland, 2012](#); [Smith, 2007](#)). However, humans are far from unique in engaging in niche construction: It is a very general process, exhibited by *all* living organisms ([Odling-Smee et al., 2003](#)). Species do not require advanced intellect or sophisticated technology to change their world ([Cuddington et al., 2007](#); [Jones et al., 1994, 1997](#); [Odling-Smee et al., 2003](#)).

The general replacement of a single role for phenotypes in evolution (as gene-carrying vehicles) by the dual role (also encompassing environmental modification and regulation) envisaged by NCT removes from cultural processes any claim to a unique status with respect to their capacity to transform natural selection pressures. Nonetheless, cultural processes provide a particularly powerful engine for human niche construction. Moreover, this dual role for phenotypes in evolution does imply that a complete understanding of the relationship between human genes and cultural processes must acknowledge not only genetic and cultural inheritance but also take account of the legacy of modified selection pressures in environments ([Laland and O’Brien, 2010](#); [Laland et al., 2000](#); [Odling-Smee et al., 2003](#); see [Odling-Smee and Laland, 2011](#), for a discussion of the relationship between ecological and cultural inheritance). Again, it is readily apparent that contemporary humans are born into a massively constructed world, with an ecological inheritance that includes a legacy of houses, hospitals, farms, factories, computers, satellites, and the World Wide Web.

Odling-Smee et al. (2003) describe how humans can acquire the knowledge that is expressed in niche construction through a set of information-acquiring processes operating at three different levels—population genetic, developmental and cultural. The three levels are distinct but interconnected with each interacting with, but not completely determined by, the others. All organisms inherit genetic information from their ancestors, and this is the most fundamental source of information that underpins niche construction. However, some factors in the environment can potentially change many times within the typical lifespan of the animal concerned, and natural selection has selected for processes allowing individuals to adjust on a within-lifetime basis, some of which are adaptations for acquiring knowledge. These secondary sources of information are complementary to the first; for instance, learning allows individual organisms to fine tune their behaviour.

Learning and development can be of considerable importance to evolution because learned knowledge can guide niche construction, the consequences of which can be inherited through ecological inheritance. While the processes underpinning learning have also been shaped by natural selection, leaving some associations formed more readily than others (Garcia and Koelling, 1966), it does not follow that all acquired knowledge is pre-specified by selection, or under genetic control. Processes such as the 'Law of Effect' (Thorndike, 1911), where actions that are followed by a positive outcome are likely to be repeated, while those followed by a negative outcome will be eliminated, can be viewed as learning rules fashioned by selection to ensure that the knowledge we acquire is, with caveats, generally constrained to that which is broadly adaptive. However, our genes specify a tolerance space for our acquired information and less frequently the content within it. That leaves human learning a relatively open program (Mayr, 1997), one capable of introducing novelty into phenotype design space, and of modifying environmental conditions in a manner that potentially generates selective feedback at multiple levels.

This highlights one of the major differences that niche construction makes to the evolutionary process: Acquired characteristics can play a role in evolution through their influence on the selective environment. In humans this ability is facilitated by a further set of processes, such as language, teaching, and prosociality, that collectively underlie cultural processes, enhancing the efficacy of knowledge transfer (Boyd et al., 2011; Dean et al., 2012). Much of human niche construction is guided by socially learned knowledge and cultural inheritance, but the transmission and acquisition of this knowledge is itself dependent on pre-existing information acquired through genetic evolution, complex ontogenetic processes, or prior (a)social learning.

Niche construction modifies selection not only at the genetic level, but at the ontogenetic and cultural levels as well, to facilitate learning and mediate cultural traditions, with consequences that not only feed back to the constructor population, but modify selection for other organisms too. For instance, the construction of towns and cities created new health hazards associated with large-scale human aggregation, such as the rapid and large-scale spread of disease, resulting in epidemics (Diamond, 1997). Humans may either respond to this novel selection pressure, exclusively or in combination (i) through biological evolution, with the selection of resistant genotypes, (ii) at the ontogenetic level, for instance, by developing antibodies that confer some immunity, or (iii) through cultural evolution, for example by creating hospitals, medicines and vaccines (Laland et al., 2000; Laland and Brown, 2006; Odling-Smee et al., 2003).

Where a culturally transmitted response to human niche construction is not possible, perhaps because the population lacks the requisite knowledge or technology, then a genetic response may occur. A familiar example is the coevolution of dairy farming and the allele for adult lactose absorption, where several lines of evidence now support the hypothesis that dairy farming created the selection pressures that favoured this allele in pastoralist populations (Burger et al., 2007; Durham, 1991; Holden and Mace, 1997; Myles et al., 2005; Simoons, 1970). Cultural niche construction can also generate selection on other species, most obviously the domesticates. Beja-Pereira et al. (2003) established that the spread of dairy farming also affected geographical variation in milk protein genes in European cattle breeds, which covary with present day patterns of lactose tolerance in humans.

Recent thinking suggests that this kind of selective feedback from human cultural activities to human genes may be a general feature of human evolution; indeed gene-culture coevolution may even be the dominant form of evolution experienced by our species (Boyd and Richerson, 1985; Feldman and Laland, 1996; Cochran and Harpending, 2009; Laland et al., 2010; Richerson et al., 2010). In the

last few years geneticists have identified several hundred human genes subject to selective sweeps over the last 50,000 years or less. When one considers the functionality of these genes, it would seem many alleles have been favoured as selective responses to human cultural activities.

Humans are also massive constructors of developmental environments. By modifying the world, human niche construction creates artefacts and other externally inherited resources that not only act as sources of biological selection on human genes but shape the learning opportunities and developmental trajectories of recipient organisms within their lifetime (Kendal, 2011). Wheeler and Clark (2008, p. 3564) describe as ‘cognitive niche construction’ the building of ‘physical structures that transform problem spaces in ways that aid (or sometimes impede) thinking and reasoning about some target domain or domains’, and these physical and informational legacies ‘make possible whole new forms of thought and reason’. One obvious example is provided by our educational institutions, practises and artefacts (such as scientific papers) that are passed on across generations and greatly alter individual lifetime learning and thinking. Similar effects can be seen in other animals too. For instance, Fragaszy (2011) describes how capuchin monkeys create learning environments for youngsters, by transforming the environment in a manner that scaffolds their learning, and channels it towards established traditions: Adult bearded capuchins in the savannah of Brazil use large stones as hammers to crack open tough palm nuts that they position on anvils of stone or log surfaces. The hammer stones have a composition that differs from the common sandstone in the area. Adults carry these special hammer stones to the anvil sites and leave them behind after use. As a result, juveniles encountering anvil sites find the tools that were effectively used by adults to crack open the palm nuts, as well as many pieces of cracked shell. These lasting changes to the physical environment, in the form of artefacts left by skilled conspecifics, form the cultural niche that supports the acquisition of technical traditions by juveniles in the same community (Fragaszy, 2011). Social transmission maintained through such inadvertent, or less commonly, advertent, modification of the local environment is surprisingly common: It is known to underlie pine cone opening in black rats (Terkel, 1996), milk-bottle opening in various birds (Sherry and Galef, 1984), the learning of food sites through pheromone trails in ants (Denny et al., 2001), mate-choice copying in egg-dumping fishes (Goldschmidt et al., 1993), and food preference learning through excretory products in rats (Laland and Plotkin, 1991, 1993). However, this facilitation of learning through the construction of developmental environments reaches its zenith in humans (Kendal, 2011; Sterelny, 2012).

Humans, and other animals, can also construct social niches. For example, in an examination of the interaction networks of 32 contemporary foraging societies, Hill et al. (2011) found that enhanced tendencies towards prosociality and cooperation facilitate a social structure that is unique to humans. The hunter-gatherer bands that constitute these diverse populations exhibit high levels of co-residence between non-kin, not found in other primates, engendering high levels of cooperative exchange and innovative information sharing between neighbouring groups. These large interaction networks between non-kin are detected in the archaeological record as early as the middle Pleistocene, in the form of long-distance exchanges of cultural artefacts (McBrearty and Brooks, 2000), and have served to amplify the genetic and cultural evolutionary processes underpinning the spectacular cultural achievements of our species today (Chudek and Henrich, 2011; Hill et al., 2011; Powell et al., 2009; Tomasello, 1999).

Another example is provided by Flack et al. (2006), who deploy network theory to quantify how “policing” (intervening in disputes) by dominant pigtail macaques creates a social niche, stabilizing and integrating macaque societies. Without this policing, societies rapidly fragment. Once again, there is feedback from this social niche construction, potentially at a number of levels.

In summary, advocates of NCT have developed a conceptual framework in which niche construction at multiple levels modifies environmental states, generating selective feedback in various guises. They maintain that this is a useful way of thinking for those social scientists who are evolution friendly but dissatisfied with overly adaptationist and gene-centred approaches. To portray humans as mere gene-carrying vehicles seriously underplays their role in the evolutionary process. Humans are massive constructors of selective and developmental environments, and an accurate depiction of this role calls out for the recognition of niche construction as an evolutionary cause, not just an effect of prior selection. In humans, this is self-apparent: Learning in a culturally constructed environment is a widely

recognized point of emphasis characterizing several fields within the social sciences (Kendal, 2011; Flynn et al., 2013).

3. Significance to the study of innovation and cultural complexity

How can NCT facilitate the study of innovation and social complexity? The previous sections have provided an introduction to the fundamentals of NCT, in the hope that this will provide a platform upon which others with expertise in human innovation and complex systems can seek to address the question directly and substantially. Below we sketch some provisional and general ideas for how NCT might be deployed.

First, NCT has value in drawing attention to the active agency of humans as a source of environmental and social change as well as to the evolutionary, ecological, and social ramifications of human niche construction. A skeptical reader might well respond that it is blindingly obvious that humans manufacture cars, computers and houses and that they plant crops and dam rivers, so how could anybody doubt that we are potent niche constructors? Yet the same can be said for other organisms too. Ecologists and evolutionary biologists have always known that birds build nests, spiders spin webs, coral animals construct reefs, and so forth, but it was not at all obvious that their niche construction was ecologically and evolutionarily consequential. For illustration, who would have imagined that the entire Negev desert ecosystem is critically dependent on the consumption of endolithic lichens by snails (Jones and Shachak, 1990). These tiny creatures have miniscule per capita effects, yet collectively their feeding breaks down desert rocks to generate tonnes of soil annually, upon which higher plant communities thrive, with knock on consequences for many other taxa. And nobody realized, when arctic foxes were introduced on to the Aleutian islands for the fur trade, that their predation on seabirds would have such devastating consequences (Maron et al., 2006). Seabirds feed at sea but typically excrete on land, generating a natural flow of nutrients to the islands. Their guano is potent fertilizer, without which the flora was transformed from lush vegetation to a bleak and barren environment. Decades of ecological and evolutionary research have established that niche construction frequently has these kinds of ecological and evolutionary consequences but, like the snail and seabird guano examples, they are not always immediately obvious. The same lesson applies to human niche construction, where seemingly trivial anthropogenic activity can scale up to dramatic effect.

The potency of niche construction is taken to its pinnacle in humans. The extraordinary cultural capacity of our species has enabled the construction of large-scale, highly cooperative societies, overseen by complex social institutions such as religions and central governments, and coordinated by the social transmission of behavioural norms. Underpinning the human socio-cultural niche is a set of evolved capacities for cultural transmission and learning (Boyd and Richerson, 1985; Dean et al., 2012; Rendell et al., 2011a; Tomasello, 1999), which are considered absent or much reduced in other species. Within this complex social framework, our capacity for technological innovation and environmental reconstruction is bolstered, and can be seen manifest in societal processes such as agriculture and industrialization. Crucially, this culturally constructed matrix, inhabited, inherited and modified by populations over time, acts to reshape selection pressures on ourselves, as well as other species that cohabit our niche.

For instance, the majority of human beings are now living in urbanized, city environments (Crane and Kinzig, 2005), and this increasing trend is set to continue into the future (Angel et al., 2005). Increases in urban population density present both opportunities and challenges for human populations (Bettencourt et al., 2007a). City infrastructure facilitates optimized delivery of services such as education and healthcare (Kates and Parris, 2003), yet accompanying changes in land use and increased green house gas emissions are just two factors that will lead to important yet poorly understood effects on the global environment (Angel et al., 2005; Svirejeva-Hopkins et al., 2004). It is now a global challenge to better understand and quantify the complex and intricate relationship between human society and the natural environment if a sustainable development transition is to be achieved (Kates and Parris, 2003; Parris and Kates, 2003). Researchers studying environmental innovation and societal transitions have emphasized that the role of human agency needs elaboration (Geels, 2011). NCT, in identifying and highlighting how seemingly trivial anthropogenic activity can scale up and generate feedback in a variety of guises, offers researchers an informative framework to employ in

this quest. Additionally, NCT illuminates the extraordinary power of human beings to adapt to and counteract environmental change through innovative cultural niche construction (Laland and Brown, 2006). For example, although there is now consensus that anthropogenic climate change is occurring (Oreskes, 2004), there are also frameworks and measures emerging that provide guidance on regional priorities and adaptive strategies that might counteract future knock-on threats such as food scarcity (Lobell et al., 2008). It is perhaps encouraging that, whilst increases in urbanization exacerbate environmental concerns, our innovative capacity, if measured by rates of patent production and employment in creative sectors, also scales superlinearly with city size (Florida, 2004; Bettencourt et al., 2007a,b).

How can researchers predict whether niche-constructing effects will scale up, over multiple individuals, perhaps multiple populations, and over long periods of time, to generate some sort of feedback without doing the requisite research? Likewise, while it is self-apparent that humans engage in niche construction, the consequences of their activities, in the form of selective feedback at multiple levels (genetic, ontogenetic, cultural) are less transparent. By highlighting the fact that niche construction generates non-trivial feedback in other species, NCT encourages human scientists to consider the possibility, indeed probability, that anthropogenic activity will also generate feedback in various guises, and provides guidelines as to the factors that lead niche construction to scale up to become consequential.

Jones et al. (1994, 1997) discuss several factors that scale up the ecological consequences of niche construction in ecosystems (ecosystem engineering). One is the lifetime per capita activity of individual organisms. Different species of organisms vary hugely in this respect. Boreal forest trees are an example of organisms that have large per capita effects on both hydrology and climate. However, Jones et al. point out that even organisms whose individual impacts on their environments are very small, may nevertheless cause huge ecological effects if they occur in sufficiently high densities, over large enough areas, and for sufficient periods of time. The examples they quote include bog-forming *Sphagnum* mosses, which produce peat that can persist for hundreds or thousands of years after the death of the living moss. Another factor is the length of time a population remains in the same place. Here, the potency of niche construction is a function of its cumulative effects over multiple generations. After a time, the sheer repetition of the same niche-constructing activities can eventually cause a very considerable change in an ecosystem component, for example, the scaled-up contribution of individual photosynthesising micro-organisms to the earth's aerobic atmosphere. Jones et al. also stress the durability of the constructs or artefacts that organisms leave behind after they are dead, or have moved on. Here their examples include beaver dams and termite mounds, which can continue to have considerable ecological consequences long after the constructors have left. Finally, Jones et al. emphasize the number and types of resource flows that are modulated by the niche-constructing activities of a species, and the number of other species that depend on the same flows. The impact of organisms is greatest when the resource flows or abiotic ecosystem components that they modulate are utilized by many other species. For example, in Puerto Rico *Dacryodes excelsa* trees are able to withstand hurricane force winds because their extensive roots and root grafts bind and stabilize bedrock and superficial rocks (Basnet et al., 1993). In this case the trees literally hold the mountainside together, to the benefit of the entire ecosystem. These factors serve to indicate the kind of variables that could operate in a functionally equivalent manner in human societies.

Second, NCT offers conceptual tools for understanding human science phenomena. These range from the overarching conceptual framework sketched above, and in more detail elsewhere (Odling-Smee et al., 2003; O'Brien and Laland, 2012), to established ways of categorizing and organizing cases of niche construction (perturbation vs. relocation, inceptive vs. counteractive, positive vs. negative), to a variety of experimental and theoretical methods for establishing where niche construction is consequential and quantifying its impact (Odling-Smee et al., 2003). These include methods applicable to the human sciences (see Odling-Smee et al., 2003, Chapter 9 or O'Brien and Laland, 2012, for detail). These conceptual tools, whilst designed to promote scientific understanding rather than be applied to manage the environment, nonetheless have implications and outlets that are not entirely abstract. For instance, NCT has already made a modest contribution towards conservation and biodiversity objectives by suggesting novel practical measures that could be implemented to enhance conservation efforts (Boogert et al., 2006; Laland and Boogert, 2010).

In principle the same reasoning that underlies using NCT to devise practical measures to conserve biodiversity could be applied to understand or even facilitate socio-technical transitions. In their article introducing this journal, [van den Bergh et al. \(2011, p. 8\)](#) point out that “transition policy needs to account for . . . network interactions between agents”. This resonates with the emphasis in NCT on the “engineering web” that underlies the stability and dynamics of ecosystems. Niche constructing organisms (frequently inadvertently) generate habitat and resources for other organisms that inhabit their ecosystem, generating an additional web of connectance that supplements the far better studied food webs ([Jones and Lawton, 1995](#)). [Boogert et al. \(2006\)](#) exploit this insight to devise a list of conservation measures. For instance, rather than focusing conservation efforts on charismatic species, keystone species, or top predators, those efforts might be better targeted at the key ecosystem engineers. Practical steps to preserving ecosystem structure and diversity include supplementing the key engineers numbers, either with additional individuals of the same species or with members of the same guild that niche construct in similar ways, reducing predator availability and enhancing prey availability for the key ecosystem engineer, or artificially mimicking its engineering activity. The same reasoning applied to socio-technical transitions would lead researchers to map out a functionally equivalent ‘engineering web’ of transmitted resources, information and services that underpins the relevant societal system, to identify one or more ‘key engineers’ that acts to stabilize the system, and then to take steps to undermine (rather than enhance) their niche constructing activity (which correspond to the reverse of the aforementioned conservation steps).

Third, NCT offers theoretically and empirically derived insights into the dynamics of evolving systems under the influence of niche construction. It is now well established that niche construction can affect evolutionary rates, change evolutionary equilibria, preserve genetic and phenotypic variation, generate time lags in response to selection (with associated momentum, inertia, catastrophic, and cyclical effects), drive niche-constructing traits to fixation in a runaway process, propagate costly traits that have a selective disadvantage in the current generation, allow the persistence of organisms in currently inhospitable conditions, affect carrying capacities, and more (see [Table 1](#)). Scientists working in the human realm can draw from these established findings to better understand the complex dynamics of their own study systems. For illustration, one substantive contribution of NCT to evolutionary theory has been to identify some of the major evolutionary consequences of ecological inheritance. This body of theory demonstrates graphically how legacy effects can build up over time to strongly affect the patterns and rates of change in evolving systems (for instance, many of the theoretical findings specified in [Table 1](#) are the direct consequence of ecological inheritance). Moreover, there is strong theoretical evidence that human cultural processes are capable of generating similar legacy effects in the environment ([Laland et al., 2001](#)), and hence are likely to generate qualitatively similar consequences for the dynamics of human populations. In the light of this body of theory, there is every reason to expect legacy effects to play critical roles in the dynamics of complex systems in general, and human society in particular. For instance, legacy effects might usefully be built into climate change models. [van den Bergh et al. \(2011\)](#) also emphasize how transition policy needs to account for “system failures like lock-in” and “unpredictability and surprise in innovation” (see also [Barbier, 2011](#)). Such phenomena are recognized consequences of legacy effects that have emerged from NCT modelling, and hence this body of theory may potentially suggest explanatory mechanisms for some hitherto puzzling socio-technical transitions.

The father figure of NCT, [Lewontin \(1983\)](#), described the evolution of a population as resembling an individual walking on a trampoline. Each change in the organism, as with each step, inevitably deforms the selective landscape. All living organisms construct aspects of their world, and in doing so they do not just respond to environments by being driven to higher levels of fitness through selection. They also fashion new agendas, changing the environment in which they and others about them grow, develop, and learn, frequently in ways that re-script the pattern of natural selection acting back on their population as well as on other species that cohabit their niche. This metaphor is an apt characterization not only of biological evolution but also of cultural evolution, and hence societal transitions. We are not surprised to learn that innovative technologies frequently suffer from unintended second-order effects, referred to as energy and environmental rebound. We would suggest that such effects are an *inevitable* feature of evolving systems. The specific nature of the rebound is hard to anticipate since

in complex systems it is likely to operate in multiple dimensions. However, the fact that rebound in some form will occur should be expected.

Fourth, we note that there already exists a vibrant field of evolutionary economics, and that evolutionary reasoning has been applied to understand innovations for many years (Nelson and Winter, 1982). Without wishing to undermine the insights already gleaned by drawing inspiration, models and methods from evolutionary biology, NCT potentially offers something different to supplement more established ways of thinking, and take evolutionary economics down new avenues. NCT is, after all, a departure from mainstream evolutionary perspectives. More generally, NCT is viewed by its advocates as contributing to an Extended Evolutionary Synthesis (EES), which takes accounts of recent developments in evolutionary thought, including evo–devo, developmental plasticity, and inclusive inheritance. The EES, while not yet well specified, potentially provides a very different conception of evolution than the traditional neo-Darwinian stance, but one that may prove better suited to understanding human innovation and societal change. One of the defining features of the EES is an emphasis on ‘reciprocal causation’, whereby developmental processes are seen as shaping, as well as shaped by, evolutionary processes. In various guises, advocates of niche construction, evo–devo, developmental plasticity, and inclusive inheritance, emphasize how the activities of organisms modify selective environments or modify the variants subject to selection, thereby influencing evolutionary trajectories (Odling-Smee et al., 2003; West-Eberhard, 2003; Jablonka and Lamb, 2005; Müller, 2007; Pigliucci and Müller, 2010; Danchin et al., 2011; Laland et al., 2011). This seemingly fits well with Ruth et al.’s (2011) emphasis on two-way coupling in models of human and environment system dynamics.

We will illustrate the possible convergence of thinking in the EES and research on innovation and societal transitions with some examples. From the EES perspective, evolutionary innovation is not just a function of ‘requirements’ of selective environments, but also of the evolvability of the organism, which is an intrinsic property of developmental systems and a function of its adaptive plasticity. This implies innovation is not always driven by need, a view that commands some support in the human technological innovation literature (Lane et al., 2009; Johnson, 2010).

Niche construction typically benefits the constructor in the short term, but need not benefit other species that share its ecosystem. For instance, when beavers create lakes by damming-up rivers numerous species of microorganisms, plants and insects die or disperse in the new conditions, whilst other biota rapidly invade and thrive. In the longer term, niche construction activity can accumulate detritus to the point where the local environment becomes uninhabitable and the constructor is forced to disperse. If each form of niche construction is regarded as an evolutionary innovation, then by analogy we would not necessarily expect environmental innovations to be intrinsically good for all. Rather, we would anticipate that there are winners and losers for all innovations, and that the benefits of innovation will change over time. This fits with the suggestion of van den Bergh et al. (2011) that questions a universally positive attitude towards innovation.

Another point of contact concerns transitions. While a rejection of saltationist arguments has been a feature of mainstream evolutionary biology since the 1930s, this is being challenged by insights from evo devo. Recent evidence suggests that developmental processes can construct evolutionary pathways to bring about sudden and dramatic change. This may occur through the elevated mutability of a major regulatory control gene (e.g. the repeated rapid adaptation of sticklebacks to post-glacial lakes through the loss of a pelvic girdle, Chan et al., 2010), or when developmental processes respond phenotypically to environmental challenges with coordinated suites of traits, exposing genetic variation to strong selection (e.g. the rapid adaptation of the house finch in North America, Badyaev, 2009). As societal institutions and other social systems, like developmental processes, are structurally and functionally well-integrated, by analogy, major transitions in society need not await a series of innovations, each of small effect, but may result instead from key innovations or from coordinated flexibility in response to changing conditions.

Also potentially relevant is the observation that from a niche construction perspective, growth is neither solely intrinsic (as economists frequently assume) nor solely extrinsic (as ecologists typically assume). While at any point in time each environment possesses a finite carrying capacity, according to NCT this is a function of the niche-constructing activity of the focal population, who ‘engineer’ additional habitat and resources (Gurney and Lawton, 1996; Odling-Smee et al., 2003). This logic

applies to both populations and commodities, and NCT may prove useful in providing a framework for modelling these interactions.

In sum, NCT is no panacea for difficult theoretical and methodological issues. Nonetheless, its careful application, combined with a detailed understanding of the system at hand, potentially sheds light on a range of phenomena of interest to human scientists, including innovation and complex systems.

Acknowledgements

We are grateful to Claes Anderson, two referees and the members of the Laland Lab for helpful comments. Research supported in part by an ERC Advanced grant to KNL.

References

- Angel, S., Sheppard, S.C., Civco, D.L., Buckley, R., Chabaeva, A., Gitlin, L., Perlin, M., 2005. *The Dynamics of Global Urban Expansion*. Transport and Urban Development Department, The World Bank 1, 3.
- Badyaev, A.V., 2009. Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Philosophical Transactions of the Royal Society Series B* 364, 1125–1141.
- Barbier, E.B., 2011. Transaction costs and the transition to environmentally sustainable development. *Environmental Innovation and Societal Transitions* 1, 58–69.
- Basnet, K., Scatena, F.N., Likens, G.E., Lugo, A.E., 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo experimental forest, Puerto Rico. *Biotropica* 25, 28–35.
- Beja-Pereira, A., Luikart, G., England, P.R., Bradley, D.G., Jann, O.C., Bertorelle, G., Chamberlain, A.T., Nunes, T.P., Metodiev, S., Ferrand, N., Erhardt, G., 2003. Gene–culture coevolution between cattle milk protein genes and human lactase genes. *Nature Genetics* 35, 311–313.
- Bettencourt, L.M., Lobo, J., Helbing, D., Kühnert, C., West, G.B., 2007a. Growth, innovation, scaling, and the pace of life in cities. *Proceedings of the National Academy of Sciences of the United States of America* 104, 7301–7306.
- Bettencourt, L., Lobo, J., Strumsky, D., 2007b. Invention in the city: increasing returns to patenting as a scaling function of metropolitan size. *Research Policy* 36, 107–120.
- Bickerton, D., 2009. *Adam's Tongue: How Humans Made Language, How Language Made Humans*. Hill and Wang, New York.
- Boogert, N.J., Laland, K.N., Paterson, D.M., 2006. The implications of niche construction and ecosystem engineering for conservation biology. *Bioscience* 56, 570–578.
- Borenstein, E., Kendal, J., Feldman, M.W., 2006. Cultural niche construction in a metapopulation. *Theoretical Population Biology* 70, 92–104.
- Boyd, R., Richerson, P.J., 1985. *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.
- Boyd, R., Richerson, P.J., Henrich, J., 2011. The cultural niche: why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences of the United States of America* 108, 10918–10925.
- Burger, J., Kirchner, M., Bramanti, B., Haak, W., Thomas, M.G., 2007. Absence of the lactase-persistence-associated allele in early Neolithic Europeans. *Proceedings of the National Academy of Sciences of the United States of America* 104, 3736–3741.
- Chan, Y.F., Marks, M.E., Jones, F.C., Villarreal Jr., G., Shapiro, M.D., Brady, S.D., Southwick, A.M., Absher, D.M., Grimwood, J., Schmutz, J., Myers, R.M., Petrov, D., Jónsson, B., Schluter, D., Bell, M.A., Kingsley, D.M., 2010. Adaptive evolution of pelvic reduction in sticklebacks by recurrent deletion of a *Pitx1* enhancer. *Science* 327, 302–305.
- Chudek, M., Henrich, J., 2011. Culture–gene coevolution, norm–psychology and the emergence of human prosociality. *Trends in Cognitive Sciences* 15, 218–226.
- Cochran, G., Harpending, H., 2009. *The 10000 Year Explosion*. Basic Books, New York.
- Collard, M., Buchanan, B., Ruttle, A., O'Brien, M.J., 2011. Niche construction and the toolkits of hunter–gatherers and food producers. *Biological Theory* 6 (3), 251–259.
- Corenblit, D., Baas, A.C.W., Bornette, G., Darrozes, J., Delmotte, S., Francis, R.A., Gurnell, A.M., Julien, F., Naiman, R.J., Steiger, J., 2011. Feedback between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews* 106, 307–331.
- Crane, P., Kinzig, A., 2005. *Nature in the metropolis*. *Science* 308, 1225.
- Creanza, N., Fogarty, L., Feldman, M.W., 2012. Models of cultural niche construction with selection and assortative mating. *PLoS One* 7, e42744.
- Cuddington, K., Byers, J.E., Wilson, W.G., Hastings, A., 2007. *Ecosystem Engineers (Vol 4): Plants to Protists*. Academic Press, New York.
- Danchin, E., Charmantier, A., Champagne, F.A., Mesoudi, A., Pujol, B., Blanchet, S., 2011. Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics* 12, 475–486.
- Danielsen, F., Sørensen, M.K., Olwig, M.F., Selvam, V., Parish, F., Burgess, N.D., Hiraishi, T., Karunakaran, V.M., Rasmussen, M.S., Hansen, L.B., Quarto, A., Suryadiputra, N., 2005. The Asian tsunami: a protective role for coastal vegetation. *Science* 310, 643.
- Das, S., Vincent, J.R., 2009. Mangroves protected villages and reduced death toll during Indian super cyclone. *Proceedings of the National Academy of Sciences of the United States of America* 106, 7357–7360.
- Dawkins, R., 1976. *The Selfish Gene*. Oxford University Press, Oxford.
- Dean, L.G., Kendal, R.L., Schapiro, S.J., Thierry, B., Laland, K.N., 2012. Identification of the social and cognitive processes underlying human cumulative culture. *Science* 335, 1114–1118.
- Denny, A.J., Wright, J., Grief, B., 2001. Foraging efficiency in the wood ant (*Formica rufa*): is time of the essence in trail following? *Animal Behaviour* 61, 139–146.

- Diamond, J., 1997. *Guns, Germs and Steel: The Fates of Human Societies*. Norton, New York.
- Durham, W.H., 1991. *Coevolution: Genes, Culture and Human Diversity*. Stanford University Press, Stanford, CA.
- Erwin, D.H., 2008. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology and Evolution* 23, 304–310.
- Feldman, M.W., Laland, K.N., 1996. Gene–culture coevolutionary theory. *Trends in Ecology and Evolution* 11, 453–457.
- Flack, J.C., Girvan, M., de Waal, F., Krakauer, D.C., 2006. Policing stabilizes construction of social niches in primates. *Nature* 439, 426–429.
- Florida, R., 2004. *Cities and the Creative Class*. Routledge, London.
- Flynn, E.G., Laland, K.N., Kendal, R.L., Kendal, J.R., 2013. Developmental niche construction. *Developmental Science* 16, 296–313.
- Fragaszy, D., 2011. Community resources for learning: how capuchin monkeys construct technical traditions. *Biological Theory* 6, 231–240.
- Garcia, J., Koelling, R.A., 1966. Prolonged relation of cue to consequence in avoidance learning. *Psychonomic Science* 4, 123–124.
- Geels, F.W., 2011. The multi-level perspective on sustainability transitions: responses to seven criticisms. *Environmental Innovation and Societal Transitions* 1, 24–40.
- Goldschmidt, T., Bakker, T.C., Feuth-de Bruijn, E., 1993. Selective choice in copying of female sticklebacks. *Animal Behaviour* 45, 541–547.
- Gottlieb, G., 1998. Normally occurring environmental and behavioral influences of gene activity: from central dogma to probabilistic epigenesis. *Psychological Review* 105, 792–802.
- Gottlieb, G., 2000. Environmental and behavioral influence on gene activity. *Current Directions in Psychological Science* 9, 93–97.
- Gottlieb, G., 2002. Developmental–behavioral initiation of evolutionary change. *Psychological Review* 109, 211–218.
- Gurney, W.S.C., Lawton, J.H., 1996. The population dynamics of ecosystem engineers. *Oikos* 76, 273–283.
- Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S., Wilson, W.G., 2007. Ecosystem engineering in space and time. *Ecology Letters* 10, 153–164.
- Hill, K.R., Walker, R.S., Božičević, M., Eder, J., Headland, T., Hewlett, B., Wood, B., 2011. Co-residence patterns in hunter–gatherer societies show unique human social structure. *Science* 331, 1286–1289.
- Holden, C., Mace, R., 1997. Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology* 69, 605–628.
- Hui, C., Li, Z., Yue, D.X., 2004. Metapopulation dynamics and distribution, and environmental heterogeneity induced by niche construction. *Ecological Modelling* 177, 107–118.
- Ihara, Y., Feldman, M.W., 2004. Cultural niche construction and the evolution of small family size. *Theoretical Population Biology* 65, 105–111.
- Jablonka, E., Lamb, M.J., 2005. *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*. The MIT Press, Cambridge, MA.
- Johnson, S., 2010. *Where Good Ideas Come From: A Natural History of Innovation*. Penguin Books, London.
- Jones, C.G., Lawton, J.H. (Eds.), 1995. *Linking Species and Ecosystems*. Chapman and Hall, New York.
- Jones, C.G., Shachak, M., 1990. Fertilization of the desert soil by rock-eating snails. *Nature* 346, 839–841.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Kates, R.W., Parris, T.M., 2003. Long-term trends and a sustainability transition. *Proceedings of the National Academy of Sciences of the United States of America* 100, 8062–8067.
- Kendal, J., Tehrani, J.J., Odling-Smee, F.J., 2011. Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society of London Series B* 366, 785–792.
- Kendal, J.R., 2011. Cultural niche construction and human learning environments: investigating sociocultural perspectives. *Biological Theory* 6, 241–250.
- Kerr, B., Schwilk, D.W., Bergman, A., Feldman, M.W., 1999. Rekindling an old flame: a haploid model for the evolution and impact of flammability in resprouting plants. *Evolutionary Ecology Research* 1, 807–833.
- Krakauer, D.C., Page, K.M., Erwin, D.H., 2009. Diversity, dilemmas and monopolies of niche construction. *American Naturalist* 173, 26–40.
- Kylafis, G., Loreau, M., 2008. Ecological and evolutionary consequences of niche construction for its agent. *Ecology Letters* 11, 1072–1081.
- Kylafis, G., Loreau, M., 2011. Niche construction in the light of niche theory. *Ecology Letters* 14, 82–90.
- Laland, K.N., Boogert, N.J., 2010. Niche construction, co-evolution and biodiversity. *Ecological Economics* 69, 731–736.
- Laland, K.N., Brown, G., 2006. Niche construction, human behavior, and the adaptive-lag hypothesis. *Evolutionary Anthropology* 15, 95–104.
- Laland, K.N., O'Brien, M.J., 2010. Niche construction theory and archaeology. *Journal of Archaeological Method and Theory* 17, 303–322.
- Laland, K.N., O'Brien, M.J., 2011. Cultural niche construction: an introduction. *Biological Theory* 6, 191–202.
- Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 1996. The evolutionary consequences of niche construction. *Journal of Evolutionary Biology* 9, 293–316.
- Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 1999. Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences of the United States of America* 96, 10242–10247.
- Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 2000. Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences* 23, 131–175.
- Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 2001. Cultural niche construction and human evolution. *Journal of Evolutionary Biology* 14, 22–23.
- Laland, K.N., Odling-Smee, F.J., Myles, S., 2010. How culture has shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics* 11, 137–148.
- Laland, K.N., Plotkin, H.C., 1991. Excretory deposits surrounding food sites facilitate social learning of food preferences in Norway rats. *Animal Behaviour* 41, 997–1005.

- Laland, K.N., Plotkin, H.C., 1993. Social transmission of food preferences amongst Norway rats by marking of food sites, and by gustatory contact. *Animal Learning and Behavior* 21, 35–41.
- Laland, K.N., Sterelny, K., 2006. Seven reasons (not) to neglect niche construction. *Evolution* 60, 1751–1762.
- Laland, K.N., Sterelny, K., Odling-Smee, F.J., Hoppitt, W., Uller, T., 2011. Cause and effect in biology revisited: is Mayr's proximate–ultimate distinction still useful? *Science* 334, 1512–1516.
- Lane, D., Maxfield, R., Read, D., van der Leeuw, S., 2009. From population to organization thinking. In: Lane, van der Leeuw (Eds.), *Complexity Perspectives on Innovation and Social Change*. Springer, Purnain and West, Chapter 1.
- Layton, R., 2010. Why social scientists don't like Darwin and what can be done about it. *Journal of Evolutionary Psychology* 8, 139–152.
- Lehmann, L., 2007. The evolution of trans-generational altruism: kin selection meets niche construction. *Journal of Evolutionary Biology* 20, 181–189.
- Lehmann, L., 2008. The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. *Evolution* 62, 549–566.
- Levins, R., Lewontin, R.C., 1985. *The Dialectical Biologist*. Harvard University Press, Cambridge, MA.
- Lewontin, R.C., 1983. Gene, organism and environment. In: Bendall, D.S. (Ed.), *Evolution from Molecules to Men*. Cambridge University Press, Cambridge, pp. 273–285.
- Lewontin, R.C., 2000. *The Triple Helix: Gene, Organism and Environment*. Harvard University Press, Cambridge, MA.
- Lill, J.T., Marquis, R., 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* 84, 682–690.
- Lobell, D.B., Burke, M.B., Tebaldi, C., Mastrandrea, M.D., Falcon, W.P., Naylor, R.L., 2008. Prioritizing climate change adaptation needs for food security in 2030. *Science* 319, 607–610.
- Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C., Buckelew, S.L., 2006. An introduced predator alters Aleutian island plant communities by thwarting nutrient subsidies. *Ecological Monographs* 76, 3–24.
- Mayr, E., 1997. *This is Biology*. Harvard University Press, Cambridge, MA.
- McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39, 453–563.
- McNamara, J.M., Houston, A.I., 2006. State and value: a perspective from behavioural ecology. In: Wells, J.C.K., Strickland, S., Laland, K.N. (Eds.), *Social Information Transmission and Human Biology*. Taylor and Francis, Boca Raton, FL, pp. 59–88.
- Müller, G.B., 2007. *Evo–devo: extending the evolutionary synthesis*. *Nature Reviews Genetics* 8, 943–949.
- Myles, S., Bouzekri, N., Haverfield, E., Cherkaoui, M., Dugoujon, J.-M., Ward, R.D., 2005. Genetic evidence in support of a shared Eurasian–North African dairying origin. *Human Genetics* 117, 34–42.
- Naiman, R.J., Johnston, C.A., Kelley, J.C., 1988. Alterations of North American streams by beaver. *Bioscience* 38, 753–762.
- Nelson, R.R., Winter, S.G., 1982. *An Evolutionary Theory of Economic Change*. Harvard University Press, Cambridge, MA.
- O'Brien, M.J., Laland, K.N., 2012. Genes, culture and agriculture: an example of human niche construction. *Current Anthropology* 53, 434–470.
- Odling-Smee, F.J., 1988. Niche-constructing phenotypes. In: Plotkin, H.C. (Ed.), *The Role of Behavior in Evolution*. MIT Press, Cambridge, MA, pp. 73–132.
- Odling-Smee, F.J., 2010. Niche inheritance. In: Pigliucci, M., Müller, G.B. (Eds.), *Evolution: The Extended Synthesis*. MIT Press, Cambridge, MA, pp. 175–207.
- Odling-Smee, F.J., Laland, K.N., 2011. Ecological inheritance and cultural inheritance: what are they and how do they differ? *Biological Theory* 6, 220–230.
- Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton, NJ.
- Odling-Smee, F.J., Erwin, D.H., Palkovacs, E.P., Feldman, M.W., Laland, K.N., 2013. Niche construction theory: a practical guide for ecologists. *The Quarterly Review of Biology* 88, 3–28.
- Oreskes, N., 2004. The scientific consensus on climate change. *Science* 306, 1686.
- Oyama, S., Griffiths, P.E., Gray, R.D. (Eds.), 2001. *Cycles of Contingency: Developmental Systems and Evolution*. MIT Press, Cambridge, MA.
- Plotkin, H.C., 2010. *Evolutionary Worlds Without End*. Oxford University Press, Oxford.
- Palmer, M.E., Feldman, M.W., 2012. Survivability is more fundamental than evolvability. *PLoS One* 7, e38025.
- Parris, T.M., Kates, R.W., 2003. Characterizing a sustainability transition: goals, targets, trends, and driving forces. *Proceedings of the National Academy of Sciences of the United States of America* 100, 8068–8073.
- Pigliucci, M., Müller, G.B. (Eds.), 2010. *Evolution: The Extended Synthesis*. The MIT Press, Cambridge, MA.
- Post, D.M., Palkovacs, E.P., 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society of London Series B* 364, 1629–1640.
- Powell, A., Shennan, S., Thomas, M.G., 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science* 324, 1298–1301.
- Rendell, L., Boyd, R., Enquist, M., Feldman, M.W., Fogarty, L., Laland, K.N., 2011a. How copying affects the amount, evenness and persistence of cultural knowledge: insights from the social learning strategies tournament. *Philosophical Transactions of the Royal Society of London Series B* 366, 1118–1128.
- Rendell, L., Fogarty, L., Laland, K.N., 2011b. Runaway cultural niche construction. *Philosophical Transactions of the Royal Society of London Series B* 366, 823–835.
- Richerson, P., Boyd, R., Henrich, J., 2010. Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences of the United States of America* 107, 8985–8992.
- Rowley-Conwy, P., Layton, R., 2011. Foraging and farming as niche construction: stable and unstable adaptations. *Philosophical Transactions of the Royal Society of London Series B* 366, 849–862.
- Ruth, M., Kalnay, E., Zeng, N., Franklin, R.S., Rivas, J., Miralles-Wilhelm, F., 2011. Sustainable prosperity and societal transitions: long-term modeling for anticipatory management. *Environmental Innovation and Societal Transitions* 1, 160–165.

- Sherry, D.F., Galef, B.G., 1984. Cultural transmission without imitation: milk bottle opening by birds. *Animal Behaviour* 32, 937–938.
- Silver, M., Di Paolo, E., 2006. Spatial effects favour the evolution of niche construction. *Theoretical Population Biology* 20, 387–400.
- Simoons, F., 1970. Primary adult lactose intolerance and the milking habit: a problem in biological and cultural interrelations. II. A culture historical hypothesis. *American Journal of Digestive Diseases* 15, 695–710.
- Smith, B.D., 2007. Niche construction and the behavioral context of plant and animal domestication. *Evolutionary Anthropology* 16, 188–199.
- Smith, B.D., 2011. A cultural niche construction theory of initial domestication. *Biological Theory* 6, 260–271.
- Stal, L.J., 2000. Cyanobacterial mats and stromatolites. In: Whitton, B.A., Potts, M. (Eds.), *The Ecology of Cyanobacteria: Their Diversity in Time and Space*. Kluwer Academic, London, pp. 61–120.
- Sterelny, K., 2012. *The Evolved Apprentice*. MIT Press, Cambridge, MA.
- Svirejeva-Hopkins, A., Schellnhuber, H.J., Pomaz, V.L., 2004. Urbanised territories as a specific component of the global carbon cycle. *Ecological Modelling* 173, 295–312.
- Terkel, J., 1996. Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In: Heyes, C.M., Galef, B.G. (Eds.), *Social Learning in Animals: The Roots of Culture*. Academic Press, New York, pp. 17–47.
- Thorndike, E.L., 1911. *Animal Intelligence*. Macmillan, New York.
- Tomasello, M., 1999. *The Cultural Origins of Human Cognition*. Harvard University Press.
- van den Bergh, J.C.J.M., Truffer, B., Kallis, G., 2011. Environmental innovation and societal transitions: introduction and overview. *Environmental Innovation and Societal Transitions* 1, 1–23.
- van Dyken, J.D., Wade, M.J., 2012. Origins of altruism diversity II: runaway coevolution of altruistic strategies via “reciprocal niche construction”. *Evolution* 66, 2498–2513.
- West-Eberhard, M.J., 2003. *Developmental Plasticity and Evolution*. Oxford University Press, New York.
- Wheeler, M., Clark, A., 2008. Culture, embodiment and genes: unravelling the triple helix. *Philosophical Transactions of the Royal Society of London Series B* 363, 3563–3575.
- Williams, G.C., 1992. Gaia, nature worship, and biocentric fallacies. *The Quarterly Review of Biology* 67, 479–486.
- Wright, J.P., Jones, C.G., Flecker, A.S., 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132, 96–101.