

# *Ecological Inheritance and Cultural Inheritance: What Are They and How Do They Differ?*

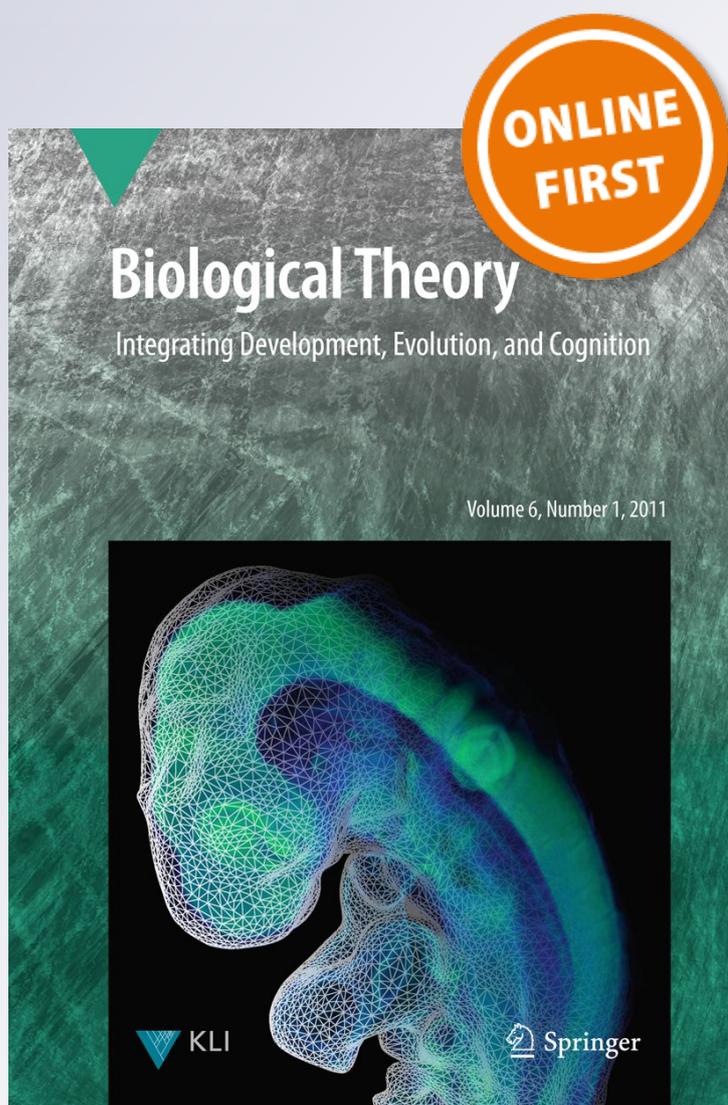
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# Ecological Inheritance and Cultural Inheritance: What Are They and How Do They Differ?

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**Abstract** Niche construction theory (NCT) is distinctive for being explicit in recognizing environmental modification by organisms—niche construction—and its legacy—ecological inheritance—to be evolutionary processes in their own right. Humans are widely regarded as champion niche constructors, largely as a direct result of our capacity for the cultural transmission of knowledge and its expression in human behavior, engineering, and technology. This raises the question of how human ecological inheritance relates to human cultural inheritance. If NCT is to provide a conceptual framework for the human sciences, then it is important that the relationship between these two legacies is clear. We suggest that cultural processes and cultural inheritance can be viewed as the primary means by which humans engage in the universal process of niche construction.

**Keywords** Cultural inheritance · Ecological inheritance · Legacy effects · Niche construction

When organisms modify the selective environment of their descendants, they leave an ecological inheritance (Odling-Smee 1988; Odling-Smee et al. 2003). In the case of humans, we also leave culturally constructed legacies to future generations. Here we consider the relationship

between human ecological inheritance and human cultural inheritance. We begin by discussing niche construction.

The niche-construction perspective was introduced to evolutionary biology in the 1980s by Richard Lewontin (1982, 1983, 2000) and has grown over the last three decades into a multidisciplinary movement (Odling-Smee 1988; Odling-Smee et al. 1996, 2003; Laland et al. 2000, 2004, 2010; Ihara and Feldman 2004; Flack et al. 2006; Laland and Sterelny 2006; Erwin 2008; Kylafis and Loreau 2008, 2011; Lehmann 2008; Krakauer et al. 2009; Post and Palkovacs 2009; Corenblit et al. 2011; Kendal et al. 2011). Niche construction is the process whereby organisms, through their metabolism, activities, and choices, modify their own and/or each others' niches (Odling-Smee et al. 2003). For instance, many species of animals manufacture nests, burrows, holes, webs, and pupal cases; algae and plants change levels of atmospheric redox states and modify nutrient cycles; fungi and bacteria decompose organic matter; and bacteria fix nutrients and excrete compounds that alter the environment. Organisms also relocate in space and thereby modify the niche relationships that both they, and other organisms, experience.

The niche-construction perspective within evolutionary biology is of value to the extent that it draws attention to the active, constructive capabilities of living organisms and to the many, and often neglected, forms of feedback that flow from these, be they to developmental, ecological, evolutionary, or sociocultural processes (Odling-Smee et al. 2003; Laland and Sterelny 2006).

The simple, expedient revision of evolutionary theory endorsed by niche constructionists calls for an explicit recognition of niche construction as an evolutionary process in its own right (Odling-Smee 1988; Odling-Smee et al. 1996, 2003). That is, niche construction is treated as an evolutionary cause rather than a mere effect, or product,

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of prior natural selection. Certainly the niche-constructing capabilities of living organisms are recognized as being shaped by natural selection, but these capabilities are viewed as underdetermined by naturally selected genes and equally fashioned by a myriad of other processes, including development, learning, and culture. Hence, the hand-in-glove complementarity of organism and environment is regarded as being brought about by two co-causal processes: (1) natural selection, which shapes organisms to be suited to environments, and (2) niche construction, through which organisms shape environments to states that are suited to their biology (and less frequently to states that are not).

Adaptation is typically viewed in evolutionary biology as a process by which natural selection shapes organisms to fit preexisting environments (Godfrey-Smith 1996). It is common to view natural selection as the *cause* of adaptive organismal change and the environment as providing the *context* in which selection, drift, mutation, and other evolutionary processes change gene frequencies. In contrast, niche construction theory (NCT) views the adaptive complementarity of organism and environment as *always* involving dynamic, reciprocal interactions between the processes of natural selection and niche construction, through which organisms modify environmental states (Lewontin 1983; Odling-Smee et al. 2003; Laland et al. 2011).

The distinctive features of the niche-construction perspective are drawn out by explicit comparison with the manner in which standard evolutionary theory treats environmental modification by organisms. The latter is most clearly encapsulated in Dawkins' (1982) concept of the "extended phenotype." Dawkins describes the evolution of, for instance, beaver dam building, or caddis fly larvae houses, as occurring in an identical manner to any beaver or caddis fly phenotype—that is, selection favors dam- or house-building alleles over their alternatives. For Dawkins, the fact that these adaptations happen to be expressed outside the organism's body, and in the external environment, does not change the manner in which they could have evolved. From this perspective, the evolutionarily significant consequences of beaver dam building are restricted to changes in the probability that genes expressed in dam building will be passed on to the next generation. For us, this is unsatisfactory because it ignores additional complex feedbacks that affect selection and hence evolution. These omissions impose constraints on the utility of the extended-phenotype concept and render it of limited practical use to the human sciences. Five points are worth making along this line.

First, the beaver's dam and lodge create a lake and influence river flow, dramatically changing the beaver's local environment, including nutrient cycling, decomposition

dynamics, the structure of the riparian zone, and plant and community composition and diversity (Naiman et al. 1988). It follows that dam building must also influence selection, acting on many other beaver traits that contribute to subsequent beaver evolution. The extended-phenotype stance, in restricting evolutionary feedback to the alleles underlying niche-constructing behavior, may be adequate as a conceptual simplification with which to understand the *evolution of niche-constructing traits*, but it does not encompass the complexity of *the evolutionary and ecological consequences of niche construction*, given that it ignores the additional forms of feedback that flow to the constructor and to other populations whose environments its niche-constructing activity influences. Conversely, NCT highlights these phenomena (e.g., Corenblit et al. 2009).

Second, and particularly germane to the focus of this article, the environmental modifications produced by niche-constructing organisms may persist for longer than the individual constructors, continuing to modulate the impact of these effects on subsequent generations of the population. This legacy is referred to as an *ecological inheritance* (Odling-Smee 1988) and is similar to what is described in ecology as "legacy effects" (Cuddington 2012, this issue) or "historical contingency," with the caveat that the focus is on the modification of descendants' selection pressures rather than on resources. For example, modified selection pressures will remain in the beaver's environment as long as the dam, lake, and lodge remain; dams are frequently maintained or reconstructed by families of beavers for decades (Naiman et al. 1988) and have effects that last for centuries or longer (Hastings et al. 2007). Likewise, the changes that earthworm activities produce in the soil can last many generations and build up over time (Jones et al. 1994; Odling-Smee et al. 2003), as can termite activities (Odling-Smee and Turner 2012, this issue). At the extreme, niche-constructing activities, such as sediment bioturbation or the accumulation of shell beds, can accumulate over geological time, modulating macro-evolutionary patterns and diversity (Erwin 2008; Corenblit et al. 2011). This temporal dimension to niche construction, in shaping inherited patterns and intensities of selection experienced by distant descendants, is missing from the extended-phenotype perspective, yet formal population-genetic models have established that it can strongly affect the evolution of the constructor population (Laland et al. 1996, 1999, 2001; Silver and Di Paolo 2006; Lehmann 2008).

Third, although by-products—characters not directly favored by selection for their current function—could in principle be characterized as "extended phenotypes," Dawkins (1982, p. 234) is explicit in stating that this is "not profitable." For Dawkins, extended phenotypes are best regarded as adaptations, and all of his examples fall

into this category. Conversely, NCT emphasizes that niche construction also incorporates evolutionary by-products (Odling-Smee et al. 2003; Laland 2004; Post and Palkovacs 2009). Often the by-products of niche construction are generated by *obligate* rather than *facultative* niche construction—for example, the nonadaptive detritus by-products of the adaptive metabolisms of organisms. Nevertheless, they can still impact many other species, and the ecological spillovers they cause can impact entire ecosystems (Odling-Smee et al. 2003; Erwin 2008; Post and Palkovacs 2009; Corenblit et al. 2011). This broad characterization is vital because the ecological and evolutionary consequences that flow from niche-constructing by-products are likely to be as substantial as those flowing from niche-constructing adaptations.

Fourth, and again of particular significance to understanding human niche construction, because extended phenotypes are restricted to biological adaptations, they automatically exclude from consideration virtually all aspects of niche construction that include use of acquired knowledge—for example, knowledge resulting from human learning and culture. This is an important limitation because very little human niche construction can accurately be characterized as extended phenotypic. Most instances of human-induced habitat modification, from digging ditches to climate change, are the products or by-products of cultural knowledge, acquired and socially transmitted by humans and expressed in their use of technology and engineering (Laland and O'Brien 2012, this issue; Smith 2012, this issue; Sterelny 2012). In contrast, NCT emphasizes how knowledge acquired by organisms can trigger ecological cascades and drive evolutionary episodes. This is of particular relevance for understanding human anthropogenic change within ecosystems. Clearly it is acquired knowledge that underpins urbanization, deforestation, agricultural practices, and the majority of major human impacts on the environment. Such processes undoubtedly precipitate evolutionary episodes in humans and in other species, including domesticated plants and animals (Beja-Pereira et al. 2003; Smith 2011).

We cannot assume that human-modified selective environments can be treated as equivalent to independent sources of selection, as for instance those that arise from geological or climatic change, given that there may be selective feedback to the constructing population of a form that influences its constructing behavior. Take, for example, a dairy-farming niche that creates the conditions that favored the spread of alleles facilitating adult lactose persistence, although the consumption of dairy products is more likely in individuals already possessing the lactose-tolerant genotype (Gerbault et al. 2011; O'Brien and Laland 2012). Similarly, crop planting has apparently inadvertently promoted insect-propagated diseases, such as

malaria, in many human populations, generating selection for resistant alleles (Durham 1991; Laland et al. 2010; O'Brien and Laland 2012) and triggering further human niche construction, such as the widespread use of chemical insecticides. Hence anthropogenic change leads to the type of eco-evolutionary feedbacks and feed-forwards recognized by ecologists (Schielke et al. 2012, this issue) but here underpinned by cultural learning.

Fifth, extended phenotypes are properties of individuals, not of collections of individuals, yet some forms of niche construction are the results of actions by many populations, even many species (Kylafis and Loreau 2008). For instance, the extended-phenotype model is frequently not a good description of the role of bioturbators, both because many effects are probably not adaptations and because sediment is typically a collective, co-constructed product rather than an individual product that may comprise the by-products of several species' niche-constructing activities (Lohrer et al. 2004; Meysman et al. 2006; Corenblit et al. 2011). Such diffuse activities also mean that it can be difficult to trace niche construction back to single individuals, species, or even clades. Once again, this is relevant to considerations of human niche construction, where almost all human artifacts, constructions, and engineering are the product of multiple individuals' activities.

Because niche construction is such a pervasive process, it may help to indicate its limits by citing some examples of what is not niche construction. Its most important limitation is that it is possible for environment-altering organisms to cause ecological changes in ecosystems without causing any evolutionary changes. If, for example, ecosystem-engineering organisms (Jones et al. 1994, 1997; Cuddington et al. 2007) change ecological components in ecosystems without legating any modified selection pressures to any population in their ecosystems, then their environment-altering activities are not niche construction. To qualify as niche construction it is necessary that the ecological changes they cause also change at least one natural selection pressure, for at least one recipient population in an ecosystem, with at least one evolutionary consequence. Unlike ecosystem engineering, niche construction must be evolutionarily as well as ecologically consequential (Odling-Smee 2010).

Other examples are more obvious and less fundamental. Relocative niche construction, for instance, refers to organisms actively moving in space, choosing or biasing the direction and distance they travel and often choosing the time (e.g., the season) when they travel (Odling-Smee et al. 2003; Piersma and van Gils 2011), all of which is likely to cause the modification of natural selection pressures by niche construction. However, if organisms are displaced by passive dispersal mechanisms, their relocation is not niche construction. Because passive and active

dispersal can co-occur, it may sometimes be hard to disentangle these two kinds of relocation, but only one kind is niche construction.

Over and above these structural limitations, we encourage a pragmatic stance that restricts consideration of niche construction to cases where it is *useful* to emphasize that construction. To consider a specific example, local fluctuations in ambient temperature caused by the movement of homeothermic organisms are, for many species that share a habitat, so trivial that they can be ignored. However, Lewontin (1982, p. 160) points out that “we do not live in the outside air, but literally in an atmospheric shell of our own manufacture” and that “small organisms like fleas or other ectoparasites live completely immersed in that boundary layer.” For such creatures, the temperature exchange of their hosts cannot be disregarded. More generally, whether, say, discarded shells or hoof prints need to be treated as an instance of niche construction depends on whether the shells or indented soils provide resources for other organisms and accrue in space and time to affect selection pressures on descendant populations.

A final important point is that, for the *evolution of niche-constructing traits*, the appropriate focus is on adaptations and on the direct and indirect fitness benefits accrued to niche constructors as a result of modifying their environment. However, for both *the ecological and the evolutionary consequences of niche construction*, analysis must include the many important consequences that flow from time-lagged effects, by-products, acquired characters, collective activity, and so forth. Analysis of human impacts on their environment, as well as much of human evolution, falls into the latter category and is therefore likely to benefit from a niche-construction perspective.

### What is Ecological Inheritance?

When niche construction is added as a co-causal process in evolution, it not only contributes to the adaptations of organisms but also generates ecological inheritances whenever the environmental consequences of the prior niche-constructing activities of organisms—for example, the presence of burrows, mounds, and dams or, on a larger scale, changed atmospheric states, soil states, substrate states, or sea states (Meysman et al. 2006; Erwin 2008)—persist or accumulate in environments as modified natural selection pressures, either relative to successive generations of organisms in the niche-constructing population or in other populations. Beaver offspring inherit from their parents not just a local environment comprising a dam, lake, and lodge but also a dramatically altered community of microorganisms, insects, plants, and animals that thrive in beaver-modified, but not virgin, environments (Naiman

et al. 1988; Wright et al. 2002). It is the totality of all of these environmental changes and not just the immediate constructions that we regard as ecological inheritance.

It will be immediately apparent that ecological inheritance is very different from genetic inheritance (Odling-Smee 1988, 2009). First, ecological inheritance is transmitted by organisms through the modification of an external environment; it is not transmitted by reproduction. Second, ecological inheritance is not fundamentally reliant on discrete replicators nor on any kind of ecological replication process other than repetitive niche construction. Typically, it depends on organisms bequeathing altered selective environments to their offspring by, often repeatedly, choosing or physically perturbing, and frequently maintaining, biological or nonbiological components of their environments. However, those environmental components include other living organisms, which obviously do possess their own genetic and ecological inheritance systems. Third, in sexual populations, genes are transmitted by two parents only, on a single occasion only, to each offspring. In contrast, an ecological inheritance is continuously transmitted by multiple organisms to multiple other organisms, within and between generations, throughout the lifetimes of organisms. Fourth, ecological inheritance is not always transmitted by genetic relatives. It can be transmitted by other organisms in shared ecosystems that must be ecologically related but need not be genetically related to the organisms receiving the inheritance.

There is, however, a complementary relationship between ecological inheritance and genetic inheritance (see below). If a selection pressure is modified by a niche-constructing population, and if it is subsequently transmitted to descendant organisms by means of ecological inheritance, then it will change the fitness value of whatever genes or DNA sequences were previously selected by the unmodified version of that same selection pressure, positively or negatively. It should also change the value of whatever selection differential (or coefficient) is used to describe the intensity of that selection. Both changes are potentially measurable. The logic is similar to that which applies to artificial selection. The only difference is that instead of the artificial modification of a selection pressure for  $n$  generations by a human experimenter, the changes are caused by the natural modification of a natural selection pressure by the niche-constructing activities of organisms, and are then inherited, through an ecological inheritance, for  $n$  generations of a population.

### The Significance of Ecological Inheritance

Population-genetic models show that the explicit inclusion of ecological inheritance in NCT affects the dynamics of the evolutionary process. For example, niche construction

can generate ecological inheritances to the point where modified natural selection overrides independent sources of selection and drives populations down alternative evolutionary trajectories. Legated niche construction can initiate novel evolutionary episodes; it can influence the amount of genetic variation carried by populations; and it can generate unusual dynamics such as time lags and momentum effects (Laland et al. 1996, 1999, 2001; Schwilk and Ackerly 2001; Hui et al. 2004; Ihara and Feldman 2004; Borenstein et al. 2006; Silver and Di Paolo 2006; Lehmann 2008). Niche construction also has considerable potential to influence empirical work. For example, Shavit and Griesemer (2011, p. 315) argue that researchers cannot afford to ignore it:

In the field, biodiversity researchers cannot establish rigorous protocols to revisit species localities if they assume a locality is not partly constructed by its occupying species... it is actually the failure to consider niche construction that undermines research on practical grounds.

#### Transmission Channels and Niche Inheritance

NCT is also relevant to developmental processes because it substitutes *niche inheritance* for genetic inheritance. If in each generation each individual offspring inherits not only genes relative to its selective environment but also an ecological inheritance, in the form of a modified local selective environment relative to its genes, then each offspring must actually inherit an initial organism–environment relationship, or niche, from its ancestors (Odling-Smee 1988; Odling-Smee et al. 2003).

Previously, one of us (Odling-Smee 2010) elaborated on how various diverse inheritance systems can be viewed as components of this niche inheritance. Two dimensions are particularly useful (Odling-Smee 2007). One concerns the relationship between internal and external environments of organisms. It demarcates the two transmission channels through which the two principal components of niche inheritance, genetic and ecological, are inherited (Table 1). A second dimension stems from the relationship between the two principal kinds of resources that organisms inherit—“algorithmic information,” previously less accurately referred to as “semantic information”—and energy and material resources. Algorithmic information was first defined and described by Chaitin (1987). In organisms it typically comprises the structural and functional information, or “know-how,” underpinning the adaptations of organisms.

The first transmission channel comprises the direct connection between the internal environments of parent organisms and the internal environments of their offspring

**Table 1** Niche inheritance (after Odling-Smee 2010)

Transmission channel	What is transmitted?	Type of inheritance system
Internal environment	Algorithmic information	Genetic inheritance Epigenetic inheritance Maternal effects
	Energy/matter	Cytoplasmic inheritance Other maternal effects
External environment	Algorithmic information	Changed informational Environments Cultural knowledge Behavioral traditions Language
	Energy/matter	Ecological inheritance of modified selective and developmental environments

through reproduction. It is reducible to the mechanisms of cell division and cell fusion, and it relates to any kind of inheritance that travels between organisms, directly during reproduction. The second transmission channel connects possibly multiple ancestral niche-constructing organisms to multiple descendant organisms indirectly, through the modification of selection pressures in external environments. Any kind of inheritance that does not travel between organisms, from cell to cell directly, is treated as this second type of inheritance. The second channel comprises an ecological inheritance, from organism to environment and back to organism. These definitions imply that it is easy to demarcate the internal and external environments of organisms, but this is not always true (see Odling-Smee [2010] for further discussion).

The relationship between information and energy and matter is also sometimes difficult to demarcate (Bergstrom and Lachmann 2004; Odling-Smee 2010; Bergstrom and Rosvall 2011). The distinction between algorithmic information versus energy and matter in biology relates fundamentally to the definitions and origin of life. To survive and reproduce, organisms must import energy and materials from, and must return detritus to, their environments. However, organisms can do neither of these things unless they are adapted to their environments, and that requires them to be sufficiently “informed” a priori by adaptive algorithmic information. Organisms cannot be sufficiently informed a priori, however, unless they, or their ancestors, also possess sufficient energy and material resources a priori to pay for the physical acquisition, storage, use, and transmission of adaptive semantic information.

By algorithmic information we mean *anything that reduces uncertainty about selective environments, relative to the fitness interests of organisms* (Odling-Smee 2010).

When encoded in the genome, algorithmic information is meaningful only relative to particular selection pressures in the particular environments of particular organisms. Equally, environmental resources, whether positive (e.g., food) or negative (e.g., predators), can serve only as natural selection pressures, relative to the specific needs and traits of specific organisms. However, this definition is neutral with respect to the physical basis of the memory systems that carry semantic information within and between organisms. Carriers of algorithmic information include DNA, RNA, several other types of molecules, brains, language, and many artifacts (e.g., computers). In the case of cultural knowledge, the algorithmic information is stored in brains and in various other cultural repositories (e.g., books, computers) and is meaningful relative to ancestral cultural selection pressures (although here there is also the possibility of misinformation). All that matters in evolution is that the algorithmic information carried by any physical carrier can potentially influence the fitness of organisms.

As Table 1 highlights, both types of transmission channel comprise both types of resources. Historically, evolutionary biologists have emphasized that the internal channel relies on genetic inheritance. Recently, however, there has been increasing recognition that internal inheritance also comprises other forms of algorithmic information, including epigenetic and maternal inheritance as well as the transfer of energy and matter—for example, in the cytoplasm or through other maternal effects. In insects and birds, eggs supplied by mothers to their offspring carry some energy and matter resources in the form of cytoplasm and protein in yolks as well as genetically encoded algorithmic information (Sapp 1987; Amundson 2005).

Similarly, algorithmic information, as well as physical resources, can be transmitted through the external environment. Algorithmic information is transmitted when, as a result of the niche-constructing activities of an organism, an ecological inheritance is generated that includes other organisms in an environment that are likewise the inheritors of, and carriers of, algorithmic information, or when it comprises physical resources that have been modified to convey algorithmic information. In the former case, these other organisms could belong to the same population as the niche-constructing organisms or to different populations in a shared, modified environment.

Unlike abiota, however, other organisms always contain two kinds of resources themselves, physical resources and algorithmic information. Thus, if a resource is another organism, it might act solely as a physical resource, say a food item, for a niche-constructing organism. Alternatively, it might act as an information resource. For example, a niche-constructing organism may “manipulate” another organism (e.g., the brood parasitism of cuckoos [Davies

et al. 1998], where the host species is manipulated into investing in the cuckoo chick by the deceptive similarity of the legated cuckoo egg and chick to that of the host) or “copy” the algorithmic information carried in either the genome or the brain of another organism by “communicating” with it (e.g., social learning in animals [Fragaszy and Perry 2003; Hoppitt and Laland 2008]). Although we initially modeled ecological inheritance exclusively as a physical resource (Laland et al. 1996, 1999), that restriction is neither necessary nor desirable. Ecological inheritance can refer to both physical and algorithmic resources because both can be modified by niche construction, although we note that the subsequent dynamics may differ in the two cases. Hence, both internal and external channels transmit both physical and informational resources between organisms and between generations.

In principle, it is also possible, although difficult, to describe the complementary relationship between genetic inheritance (internal channel) and ecological inheritance (external channel) in terms of mutual information. The change in the fitness of a gene caused by the modification of a natural selection pressure is potentially measurable in standard ways and can be treated as equivalent to a change in the algorithmic informational value of the gene. Conversely, the capacity of that modified selection pressure to change the algorithmic informational value of that gene should itself equate to the complement of the algorithmic informational value of the change in the gene's fitness (Bergstrom and Lachmann 2004). This step is seldom likely to be necessary in practice. Its theoretical value lies in indicating the intimacy of the complementary relationship between genetic inheritance (internal channel) and ecological inheritance (external channel) in evolution. They work relative to each other.

### Some Complexities

Finally, we end this section by noting that our use of the term “inheritance” in “ecological inheritance” relates to a more colloquial rather than scientific conception of inheritance. Strictly speaking, ecological inheritance does not satisfy all the conventional conditions of a biological inheritance system (Sterelny 2001). For example, ecological inheritance is not fundamentally a high-fidelity replicator system unless it comprises the genetics of another co-evolving population. However, we persist with the term for two reasons. First, ecological inheritance matches very effectively how most people conceive of inheritance, that is, it fits with the colloquial use of the term, nicely encompassing both inherited knowledge and inherited property. Second, as described above, although ecological inheritance need not rely on replication, many of the modified selection pressures that descendant organisms

inherit through ancestral niche construction stem from living creatures with their own inheritance systems, including algorithmic informational components of both genetic and cultural inheritance, and many inherited environmental resources persist for long periods because they are regularly and consistently maintained through “instructions” encoded in those inheritance systems.

Consider the ant–fungus mutualism exhibited by many attine ants (more than 200 species), for which the agriculture exhibited by more than 40 species of leaf-cutter ants is the most famous (Hölldobler and Wilson 1995). In all these cases, the ants actively propagate, nurture, and defend the fungus in their nests in return for nutrients. Prior to her nuptial flight, the leaf-cutter queen takes up some of the fungus in her mouth, and when she reaches her new chamber spits it out (Hölldobler and Wilson 1995). Here, the fungus constitutes an ecological inheritance, but one with its own inheritance system, which the ants actively propagate. Moreover, this mutualism is further complicated by two other organisms, a fungal parasite (*Escovopsis*) frequently also found in the nest, which the ants inadvertently cultivate, and *Pseudonocardia* bacterial species that reside inside the ants and assist in defending the fungus from the parasite through the production of secondary metabolites (Currie et al. 2006). These two organisms are part of the leafcutter ants' ecological inheritance.

More generally, virtually every creature that manufactures a nest, burrow, mound, or any kind of artifact, and thereby constructs a resource that comprises an ecological inheritance for its descendants, also creates a home for numerous other organisms, including parasites and inquilines, which also comprise a part of that ecological inheritance. Moreover, to the extent that any act of niche construction leads directly or indirectly to a change in the species composition of the local ecological community that descendant organisms experience, it generates an ecological inheritance with its own set of built-in inheritance systems. That ecological inheritance can even be held inside the organism. Bacteria are an essential component of the epigenetic inheritance system in many animals and can be regarded as a component of ecological inheritance, despite the fact that they are stored internally. Ley et al. (2006) have shown that human babies acquire their gut microbial communities from the vagina and the feces of their mothers early in life. Babies born through Caesarian section have an altered colonization pattern compared with vaginally delivered babies. Of course, whether those aspects of the ecological inheritance are experienced as an evolutionary inheritance or merely as a developmental inheritance will depend on the temporal scales of reproduction of the organisms concerned. For these reasons, ecological inheritance frequently shares with strict

inheritance systems the property of being reproduced repeatedly through time.

### What is Cultural Inheritance?

Historically, anthropologists have characterized culture in a broad, inclusive manner. The most famous definition, dating back to Tylor (1871, p. 1) describes it as “that complex whole which includes knowledge, belief, art, morals, custom and any other capabilities and habits acquired by man as a member of society.” This amorphous definition, however, is not particularly conducive to scientific analysis. Human culture has proven a difficult concept to pin down, and there exists little definitional consensus within the social sciences, and frequently little appetite for definition (Kroeber and Kluckhohn 1952; Keesing 1974; Durham 1991). Cultural evolutionists have taken a more pragmatic line. For instance, according to Richerson and Boyd (2005, p. 5), “Culture is information capable of affecting individuals' behavior that they acquire from members of their species through teaching, imitation, and other forms of social transmission.” Something like this definition will do for our purposes, provided we recognize that the information referred to is algorithmic information and that it includes learned knowledge, beliefs, values, and attitudes, which are expressed in behavior, artifacts, and technology.

*We define as cultural niche construction that subset of niche construction that is the expression of culturally learned and transmitted knowledge* (as opposed to individually learned or genetic information). Although not all human niche construction is cultural niche construction, the vast bulk of the impact that human beings have made on this planet has undoubtedly resulted directly from socially transmitted knowledge. We all acquire knowledge and skills from other people. We express that knowledge in our behavior, engineering, and technology, in the process modifying our environments in a myriad of ways, from tending crops to burning fossil fuels (Laland and O'Brien 2010, 2012, this issue; Fogarty and Feldman 2012, this issue; Smith 2012, this issue). And, we build on that reservoir of shared algorithmic information iteratively, manufacturing ever more efficient and diverse solutions to life's challenges and ever more advanced technology, which frequently translates into ever more dramatic impacts on our environments (Sterelny 2012).

In *The Origin of Species*, Darwin presented extensive evidence for *variation* in the characteristics of individuals within a species, for *competition* among individuals for survival and reproduction, and for the *inheritance* of characteristics in the next generation. Culture equally exhibits these characteristics, spawning extensive discussion of the

parallels between the processes of biological evolution and cultural change (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Mesoudi et al. 2004, 2006; Mesoudi 2011). If culture exhibits variation, if these variants compete with differential fitness, and if the variants are inherited, then cultural evolution must ensue.

This is important for at least two reasons. First, as outlined by Laland and O'Brien (2012, this issue), when they engage in niche construction, humans potentially modify two kinds of selective processes (Laland et al. 2000, 2001; Laland and Brown 2006; Kendal 2012, this issue)—natural selection and what is often referred to as “cultural selection” (Cavalli-Sforza and Feldman 1981). We can define the latter as collective decisions that construct and bias the learning environments for other humans (Boyd and Richerson 1985; Laland et al. 2000; Odling-Smee et al. 2003). Second, because of differences in the transmission process, cultural inheritance is very different from genetic inheritance. For example, unlike genetic inheritance but like ecological inheritance, cultural inheritance is continuously transmitted by multiple human beings, to multiple other human beings, within and between generations, through an external environment, by a number of different routes, such as learning obliquely from the previous generation, learning horizontally from siblings, friends, or peers, copying the behavior with the highest payoff, or conforming to the majority behavior (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland 2004).

Cultural inheritance can also generate different selective outcomes in culturally different human populations (Laland et al. 2010), and it is clearly capable of the stable transmission of algorithmic information in the form of cultural knowledge, in successive human generations. Several studies have found that the attitudes of parents and offspring are rather similar and maintain that the most obvious explanation for this is that children learn attitudes socially (Boyd and Richerson 1985). For example, a study of Stanford University students revealed that religious and political attitudes were strongly consistent between parents and offspring (Cavalli-Sforza et al. 1982). The same has been reported for nonindustrial societies. Among Aka pygmies, an African group of hunter-gatherers, there was evidence for the transgenerational transmission of many customs (Hewlett and Cavalli-Sforza 1986), and among horticulturists in the Democratic Republic of Congo, the young acquire knowledge about foods primarily from their parents (Aunger 2000). Similarly, in Bolivian Amazon populations, the transmission of ethnobotanical knowledge and skills in general was found to occur from the older to the younger generation (Reyes-Garcia et al. 2009). These data are reinforced by historical records, which report the consistent use of farming practices, modes of subsistence, social systems, and social preferences over centuries or

even millennia (Durham 1991; Diamond 1997). In anthropology, these are referred to as *traditions* (Brown 1984)—a term that is beginning to find wide acceptance in biology (e.g., Fragaszy and Perry 2003; Whiten et al. 2011; Fragaszy 2012, this issue).

Cultural inheritance does not comprise only the transmission of brain-based knowledge through teaching and social learning. The algorithmic informational component of culture also obviously comprises a broad range of external memory stores that today include books, papers, photographs, diagrams, movies, and computer-based records, expressed not just in tools and engineering works but also in laws, norms, conventions, and institutions. There is also a widely recognized physical (energy and matter) component to cultural inheritance, as individuals inherit money, houses, property, land, and so forth.

However, the energy/matter-based, culturally generated, external-channel legacy of humans goes far beyond those resources transferred in wills. Generations of humans also inherit culturally modified rural and urban environments—fields of crops, terraces, artificial lakes, canals, roads, schools, hospitals, factories, police forces, electricity grids, waste products, and pollution. We also inherit a world of our making, complete with dogs, wheat, dairy cows, nectarines, and countless genetically modified types of grapes and without dodos, woolly mammoths, and the numerous other species left extinct by human activities. This is both our ecological and our cultural inheritance.

A broad characterization of culture also opens up the possibility of culture in other animals, and indeed traditions for exploiting prey or food sites, tool use, and vocalizations, are reported in a variety of animals, including fish, birds, cetaceans, and nonhuman primates (e.g., Fragaszy and Perry 2003; Laland and Galef 2009; Fragaszy 2012, this issue). Social transmission is widespread in animals because copying is adaptive under a broad range of conditions, largely because demonstrator animals pre-filter behavior, performing a subset of high-payoff behavioral options (Rendell et al. 2010). Fragaszy (2012, this issue) discusses how the physical traces that other organisms leave in their environment (for instance, discarded nut shells or stone hammers), can support behavioral traditions (e.g., nutcracking in capuchin monkeys). Thus the legacy of inherited physical resources may be vital to the stable transmission of algorithmic cultural information.

## Summary

It should be apparent that we view cultural inheritance as a component of ecological inheritance. Not all human niche construction is cultural niche construction, and not all human ecological inheritance is cultural inheritance, yet in

both cases the vast bulk of it is. Cultural processes and cultural inheritance can be viewed as the primary means by which humans engage in the universal process of niche construction, leaving universal ecological inheritances. However, it is precisely because of our uniquely potent cultural knowledge that we humans can be characterized as “the ultimate niche constructors” (Smith 2007). We transform environments on unprecedented scales, frequently destroying the natural control webs stemming from the niche-constructing/ecosystem-engineering activities of its constituent organisms that are vital to the functioning of ecosystems (Jones et al. 1994, 1997), with important implications for conservation (Boogert et al. 2006; Crain and Bertness 2006).

When we engage in niche construction, like other organisms, we modify both selective and developmental environments for ourselves, our offspring, and other organisms that inhabit our planet. However, we shape developmental environments in an astonishingly diverse range of ways, from constructing schools to promote our children’s learning to using propaganda to manipulate others into buying our products, voting for our candidate, or fighting in our wars (Kendal 2012, this issue). In this way, we fashion the course of cultural evolution for our own species. Moreover, we deliberately shape ecological environments, by imposing artificial selection, or through direct genetic modification, to fashion the course of biological evolution for numerous other species. In these respects, human cultural niche construction is unique.

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