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RESEARCH

Culture and Evolvability: a Brief Archaeological Perspective

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Abstract
Evolvability refers to the capacity, ability, or potential of an organism to generate heritable variation. Under this view, much extragenetic inheritance is regarded not as noise, fine-tuning, or a luxury add-on to genetic inheritance but as an essential tool for short-term adaptation. With respect to humans, the cultural contribution to evolvability is key to understanding evolution. In many instances, cultural inheritance directs genetic inheritance, not the other way around. Culture, being relatively free from the genetic leash, can produce change that genetic inheritance cannot. Soft inheritance—the view that heredity can be changed by an organism's experiences—has been disdained for over a century, but in light of the recent outpouring of data demonstrating extragenetic inheritance, defining evolution only in terms of genetic change ignores half the adaptive process, discarding much of what is interesting and relevant. Archaeologists can play a key role in evolvability research, given their contributions to topics such as niche construction, modularity, mosaic evolution, and developmental bias.

Keywords Developmental bias · Evolvability · Exploratory mechanisms · Extended evolutionary synthesis · Modularity · Mosaic evolution · Niche construction

Introduction

Evolvability is an important yet slippery biological concept, with myriad facets and definitions, which easily leads to misunderstandings (Riederer *et al*., 2022; Sniegowski & Murphy, 2006; Wagner & Altenberg, 1996). Pigliucci (2007, p. 2746) makes this point: "the field is plagued by a variety of hurdles, not the least of which

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there seems to be a variety of (related but not identical) meanings floating around for the word 'evolvability.'" Brown (2014) refers to it as being conceptually confusing. We return to the issue of exactly what evolvability entails in the following section, but one definition that should find a comfortable home in archaeology is "a property of living systems that refers broadly to their capacity, ability, or potential to evolve" (Villegas *et al.*, 2023, p. 35). This equates with "an organism's capacity to generate heritable phenotypic variation" (Kirschner & Gerhart, 1998, p. 8420), rather than having to rely solely on genetic inheritance.

The term evolvability itself has evolved and now is often regarded as a defining concept within both evolutionary developmental biology (Brookfield, 2009; Brown, 2014; Hendrikse *et al.*, 2007; Kirschner & Gerhart, 1998) and the "extended evolutionary synthesis" (EES) (see below) (Laland *et al.*, 2015; Müller, 2007, 2017; Pigliucci, 2008; Pigliucci & Müller, 2010; Wagner & Draghi, 2010). It has also been championed as central to mainstream quantitative genetics (Hansen, 2006; Hansen *et al.*, 2023), molecular evolution, paleontology, and network analysis (Crother & Murray, 2018; Nuño de la Rosa, 2017; Wagner & Draghi, 2010). We believe it should be a key component of archaeological thought too, given the increasing attention paid to the role of such things as stone tools, ceramic vessels, and the like in human evolution (Leonard & Jones, 1987; O'Brien & Holland, 1995). Conversely, we submit that if things such as stone tools and ceramic vessels are *not* regarded as outcomes of adaptive evolution, it is because researchers (*e.g.*, Bamforth, 2002; Gabora, 2006) are operating under a narrow understanding of evolution or adaptation that does not fully recognize the biological significance of cultural adaptation.

Humans, along with many other animals, evolve through both a cultural evolutionary process (Whiten *et al.*, 2011, 2012) and a conventional genetic evolutionary dynamic, with the two processes closely interacting. Here, culture refers to group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted *information*. It encompasses "all that individuals learn from others" and provides a flexible means to adjust to new conditions and thus modify natural selection (Whitehead *et al.*, 2019). However, the vast majority of the literature on evolution and evolvability largely ignores a role for culture. For example, as we point out elsewhere (Laland & O'Brien, 2023), the term goes unmentioned in the leading evolutionary-biology textbook (Futuyma, 2013), which defines evolution as "the origin and subsequent alteration of the frequencies of genotypes from generation to generation within populations" (p. 2) and is explicit in asserting that "the changes in populations that are considered evolutionary "are those that are passed via *the genetic material* from one generation to the next" (p. 2; italics added).

Under this view, cultural inheritance plays little or no causal role in evolution, either because genes are deemed to control almost everything, including culture, or because adaptive change arising through extragenetic processes (any form of heredity that does not involve genetics) is defined as not being a part of evolution. Granted this is an undergraduate textbook, but care should be taken in relying only on a gene-based definition, which is little more than a gussied-up version of the "Weismann barrier," a nineteenth-century genetic principle that hereditary information moves only from genes to body cells, never in reverse. Under this perspective, "adaptation is always asymmetrical; organisms adapt to their environment, never vice versa" (Williams, 1992, p. 484).

In one respect, this is a curious omission, and it biases researchers' understanding of the capacity of organisms, especially humans, to evolve and bring about changes not only in their environments but in themselves as well (Laland & O'Brien, 2011). If, however, one claims that culture cannot evolve, except perhaps in terms of the discredited unilinear schemes proposed by nineteenth-century ethnologists such as Tylor (1871) and Morgan (1877) and which became popular throughout much of the twentieth century (*e.g.*, Carneiro, 1973; Steward, 1956; White, 1959), then the issue is moot. Then there are those—for example, Stephen Jay Gould—who consistently have referred to cultural evolution as merely "cultural change," albeit with an "explosive Lamarckian mode" (Gould, 2002, p. 914). Gould was "convinced that comparisons between biological evolution and human cultural or technological change have done vastly more harm than good—and examples abound of this most common of intellectual traps. Biological evolution is powered by natural selection, cultural evolution by a different set of principles that I understand but dimly" (Gould, 1987, p. 18).

Finally, there are those who hold the view, dating back decades (*e.g.*, Simpson, 1949), that when culture appeared, humans became exempt from further evolution. For example, biologist Ernst Mayr opined that "there's absolutely no chance of the human species evolving. First of all, we can never speciate. We cover every niche, every spot on the earth, so there's no opportunity for isolation. Moreover, I do not feel there's any natural selection in any positive sense going on right now" (Angier, 1997, p. 10). Such an argument raises the question of when in the course of a hominin lineage's history culture became so plastic that it created a shield that natural selection could not penetrate (Lyman & O'Brien, 1998). The answer, of course, is that it never did. Recent studies provide clear evidence for natural selection continuing to operate on humans (Beauchamp, 2016; Stearns *et al.*, 2010), often in pulses (O'Brien *et al.*, 2023), as it has for the last two-million-plus years.

Going hand in hand with the neglect, or denial, of cultural evolution is the fact that within evolutionary biology, gene-centric, Standard evolutionary theory models continue to assume primacy. SET emphasizes that relevant variation arises only through random genetic mutation, relevant inheritance occurs only through DNA, and the natural selection of genetic variation is the sole cause of adaptation (Laland *et al.*, 2015). Traditionalists characterize genetic changes as an essential component of adaptation and speciation, but at best they view extragenetic processes as sometimes playing a bit part—a nonessential "add-on" (Wray *et al.*, 2014)—in how and why organisms evolve.

We agree that genes are important components of adaptation, speciation, and inheritance; how could it be otherwise? Rather, our point is that a gene-centric focus fails to capture all the processes that direct evolution, including how physical development influences the generation of phenotypic variation (developmental bias); how the environment directly shapes organisms' traits (plasticity); how organisms modify environments (niche construction); and how organisms transmit more than genes across generations (Laland *et al.*, 2015). For more traditionally minded researchers, these phenomena are simply *outcomes* of genetic evolution. That standpoint shapes questions and answers alike and leads researchers into viewing some processes as uninteresting transients; into assuming that change must be the result of exogenous triggers; and into thinking that "any and all features of an adapted system should match some feature of an environment that is external and autonomous" (Andersson *et al.*, 2014, p. 155).

Conversely, EES, with its emphasis on the developmental processes that create novel variants, contribute to heredity, generate adaptive fit, and thereby direct the course of evolution, turns the analytical focus to the active and central role that organisms play in shaping not only their own evolution but also the evolution of their evolution. Two features of EES significant to evolvability are *constructive development* and *reciprocal causation.* The former refers to an organism's ability to shape its own developmental trajectory by continually responding to, as well as altering, internal and external states; the latter refers to the idea that developing organisms are not solely products but also *causes* of evolution (Laland *et al.*, 2015).

While the EES has garnered some attention in anthropological and archaeological publications (*e.g.*, Fuentes, 2016; Kissel & Fuentes, 2021; Murray *et al.*, 2021; Piperno, 2017; Zeder, 2016), we could find no references to evolvability, although it is hinted at occasionally (*e.g.*, Andersson *et al.*, 2014). We strongly believe, however, that evolvability can and should be a central focus in all human sciences because "the nature of human culture becomes less mysterious as allied manifestations are charted among non-human animals and early hominins, and inferences drawn about the evolutionary foundations of humanity's distinctive cultural faculties" (Whiten *et al.*, 2011, p. 938). From our perspective, culture should be viewed less as a unique property of our own species and more as a uniquely potent yet general propensity for adaptive plasticity observed in many animals.

Several years ago, we helped introduce "niche construction theory" (NCT) into archaeology specifically (Laland & O'Brien, 2010) and the human sciences generally (Laland & O'Brien, 2011, 2015; see also Smith, 2007a, 2007b). Niche construction is the process whereby organisms, through their activities, interactions, and choices, modify their own and each other's niches, thereby acting as codirectors of their own evolution as well as that of others (Odling-Smee *et al.*, 1996, 2003). Niche construction is a key contributor to evolvability because it creates conditions that lead to "constructing" traits and "recipient" traits being co-expressed (Odling-Smee *et al.*, 2003), making it possible for selection to operate on those traits together, and hence for selection to modify the interactions that support them. As such, niche construction can be viewed as a form of developmental bias that generates clusters of correlated variation among traits (epistasis), making it easier to evolve in some directions than in others. Because it extends and builds on traditional dual-inheritance (genetic and cultural) models of cultural evolution that have provided key insights into human behavior (*e.g.*, Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Laland, 1996), NCT is sometimes referred to as "triple-inheritance theory" (genetic, cultural, and ecological) (Odling-Smee *et al.*, 1996, 2003). NCT is heuristically valuable precisely because it draws our attention to a range of phenomena that are both important and easy to overlook using only standard perspectives (O'Brien & Bentley, 2018).

Mathematical models suggest that niche construction resulting from cultural processes is likely to be even more potent than gene-based niche construction (Laland *et al.*, 2007; Odling-Smee *et al.*, 2003), meaning that cultural niche construction can modify selection on human genes and actually *drive* genetic evolutionary events (Feldman & Laland, 1996; Gerbault *et al.*, 2011; Laland *et al.*, 2001, Laland *et al.*, 2010; Rendell *et al.*, 2011; Richerson *et al.*, 2010). In short, humans are "the ultimate niche constructors" (Odling-Smee *et al.*, 2003)—a perspective that is right at home in archaeology, given its long history of investigating human–land relationships (*e.g.*, Adams, 1962; Flannery, 1969; MacNeish *et al.*, 1972; Steward, 1937; Zubrow, 1971). This recognition on the part of archaeologists undoubtedly led to the recent attention paid to NCT, and we expect the same will be true of evolvability.

NCT was fairly well-known in the biological sciences by the time our original article appeared, alongside several experimental archaeological papers (Bleed & Matsui, 2010; Broughton *et al.*, 2010; Riel-Salvatore, 2010), in a special issue of the *Journal of Archaeological Method and Theory*. Our goal was to show that considerable archaeological thought fits neatly under the NCT banner. Within a few years, there were dozens of articles that used NCT to examine a host of issues both in archaeology (*e.g.*, Bentley & O'Brien, 2019; Boivin *et al.*, 2016; Brock *et al.*, 2016; Collard *et al.*, 2012; Iovita *et al.*, 2021; Murray *et al.*, 2021; O'Brien & Laland, 2012; Riede, 2011, 2019; Riede *et al.*, 2019; Smith, 2007a, 2007b, 2011a, 2011b; Stiner & Kuhn, 2016; Thompson *et al.*, 2021; Veatch *et al.*, 2021; Wollstonecroft, 2011; Zeder, 2016) and in other human sciences (*e.g.*, Creanza *et al.*, 2012; Fuentes, 2016; Kendal, 2011; Kendal *et al.*, 2011; Laland & O'Brien, 2015; Odling-Smee & Turner, 2012; Ready & Price, 2021; Rowley-Conwy & Layton, 2011; Wallach, 2016). Many of those studies were related to plant and animal domestication, which has long been a focus of both archaeology and anthropology (*e.g.*, Binford, 1968; Braidwood, 1960; Flannery, 1973; Gremillion *et al.*, 2014; Hole *et al.*, 1969; Kennett, & Winterhalder, B. (Eds.)., 2006; Manning *et al.*, 2014; O'Brien, 1987; O'Brien & Laland, 2012; Piperno, 2011; Richerson *et al.*, 2001; Rindos, 1984; Zeder, 2012, 2015).

The strong reception that NCT has received in archaeology can also be tied to a dramatic rise in the use of evolutionary principles in archaeology generally, especially given the recognition that artifacts play a significant role in our understanding of evolution. Stone tools and other artifacts, of course, did not exist in a vacuum; rather, they reflect concepts, knowledge, and ideas in human brains and expressed in human behavior. Thus, they were shaped by the same evolutionary processes (*e.g.*, selection and drift) as were the somatic (bodily) features of the makers/users of the artifacts (Dunnell, 1989; Laland, 2004; Leonard & Jones, 1987; O'Brien & Holland, 1995). In other words, "all activities (behaviors) involve artifacts, and so artifacts don't just express behaviors, they are part of it" (O'Brien *et al.*, 2005, p. 240).

Despite the enthusiastic reception that NCT has received in archaeology, there have been fits and starts with successful implementation, some of which seem to stem from an underappreciation for the kinds of data required for NCT to be more than simply a new metaphor for human behavior (Brock *et al.*, 2016; O'Brien & Bentley, 2021; Piperno, 2017; Piperno *et al.*, 2017; Stiner, 2021)—something that archaeology has seen before (Hardesty, 1980). NCT has steep data requirements and thus "is no panacea for difficult theoretical and methodological issues. Put bluntly, it will not 'magic up' answers to challenging and often long-standing puzzles"

(O'Brien & Laland, 2012, p. 462). It can, however, greatly assist us in posing questions that might have escaped attention under standard approaches to the evolution of human behavior (Fuentes, 2016). The same is true for evolvability. While it is no panacea for solving tough problems, it, like NCT, has the ability to lead researchers to pose important questions that might otherwise have escaped attention. Here, archaeology already has a head start. Even though the term does not appear in the archaeological literature, the everyday work of archaeologists is already based on aspects of evolvability, including niche construction, modularity, plasticity, and developmental bias, all which we discuss later.

Our goal in the pages that follow is first to describe and then broaden the concept of evolvability, then show how it can play a key role in how we think about the archaeological record, and then present several examples of how archaeologists have already contributed to the conversation. We make no claim that evolvability should immediately become a central focus of the discipline, but as we noted above, we believe that it *can* lead to fruitful lines of research, just as NCT has in a short time. We see our discussion as more or less a primer on the complex topic of evolvability, leaving it to others to decide its merits (if any) for their own research. For a more detailed treatment of the topic, especially with respect to the evolvability of early hominids, readers might want to refer to Laland and O'Brien (2023).

What Exactly *Is* Evolvability?

Sansom (2008) credits Dawkins (1988) with coining the term "evolvability," although it appears that Scottish biologist Sir J. Arthur Thomson (1931) beat him to the punch a half century earlier (Crother & Murray, 2018). Over the almost one hundred years since Thomson coined the term, there have been countless definitions of evolvability put forward, and if there is one common theme, it would be "the *ability* to evolve" (Crother & Murray, 2018; italics added). There is, however, a subtleness to that definition. All organisms have the potential to evolve, but is it equal across all lifeforms? The answer is decidedly "no" because the potential itself is evolvable.

One way of visualizing the plethora of definitions of evolvability is not to view it as a single idea but rather as "a family of connected but partially distinct ideas under [a] general umbrella" (Pigliucci, 2008, p. 76). Heritability obviously lies at the heart of evolvability because without it (as well as variation and sorting mechanisms), nothing can evolve. Some authors explicitly treat heritability as a measure of evolvability, such as Flatt (2005, p. 306): "the ability of a population to respond to selection," whereas others, such as Griswold (2006), focus on the rate of evolution of a given phenotypic character. Still others define evolvability as "the propensity to evolve novel structures" (Pigliucci, 2008, p. 76).

To many evolutionary geneticists, the capacity to evolve depends largely on how much genetic variation there is in a trait. Hence, evolvability equates not only with the concept of heritability but also with related concepts such as the genetic coefficient of variation (Charlesworth *et al.*, 2017; Houle, 1992). There are advantages to this perspective, including its wide applicability to diverse biological systems, accessibility to measurement, and use in short-term prediction (Brigandt *et al.*, 2023; Hansen, 2006; Nuño de la Rosa, 2017). One drawback, however, is that by tying evolvability to statistical patterns of genetic variation and covariation, we overlook insights into the developmental–mechanistic properties that allow some traits to evolve more readily than others (mosaic evolution). Our view of evolvability transcends genes and refers to any heritable variation, including cultural traits (Laland & O'Brien, 2023; Lyman & O'Brien, 1998). A second, obvious drawback to the standard definition is that it fails to consider how different groups might take different pathways to evolutionary change and adaptation.

Following Jablonka and Lamb (2014), we suggest that extragenetic inheritance should be regarded as an essential tool for short-term adaptation. Different inheritance pathways *complement*, but do not *dominate*, each other (Adrian-Kalchhauser *et al*., 2021), allowing the system as a whole to respond to features in the environment that change at different spatial and temporal scales. Only a subset of epigenetic inheritance has been found to be tightly associated with genetic variation (Jablonka & Lamb, 2014), and the same holds true for cultural variation (Durham, 1991; Hoppitt & Laland, 2013; Laland, 2017; Richerson & Boyd, 2005; Whiten *et al*., 1999). Tight genetic regulation of epigenetic or cultural inheritance would be maladaptive in rapidly changing conditions, given that genetic evolution is too slow to track that change. That is why culture has a degree of autonomy from genetics: the "leash" (Lumsden & Wilson, 1981) can't be too tight, otherwise culture cannot do its evolutionary job.

The Evolution of Evolution

A key question regarding evolvability is whether and how the evolutionary process itself evolves (Kirschner & Gerhart, 1998; Maynard-Smith & Szathmáry, 1995; Pigliucci, 2008; Uller *et al*., 2018). Brookfield (2001, p. R107) framed it this way: "once we think of evolvability as a quantitative trait, merely documenting examples of evolvability is inadequate. We may say that organisms are evolvable, but compared to what? The danger of evolvability becoming a platitude is obvious, unless we have a theory predicting that it will itself evolve."

Given the wide range in lifeforms that exists and has existed—from bacteria, which are microscopic, asexual, ubiquitous, single-cell organisms, to mammals, which are macroscopic, sexual, ecologically constrained, multicellular, and often highly social organisms—is it so difficult to believe that such taxonomic extremes not only evolve in different ways but have evolved the ability to evolve (Kirschner & Gerhart, 1998, 2005; Laland & O'Brien, 2023)? For example, animal design since the pre-Cambrian has involved a succession of new attributes that impacted evolvability, ranging from conserved intercellular signaling pathways and regulatory circuits, to stable body plans, to the evolution of exploratory mechanisms (discussed later) and forms of extragenetic inheritance (Kirschner & Gerhart, 1998, 2005).

The important point—and one that is difficult to overemphasize—is that not only do organisms and their genotypic and phenotypic packages evolve, so too does their *ability* to evolve, with organisms and their traits varying in the extent to which they can generate selectable phenotypic variation, generate fitness difference among heritable phenotypes, and inherit those phenotypes through diverse processes (Endler, 1986). In other words, evolution itself has the capability and ability to evolve. The same is true for culture, the nongenetic inheritance system that can lead to increased evolvability of humans, but we need to make a clear distinction—pointed out by one of our reviewers—between the evolvability of human culture and the evolvability of humans *through* culture. Culture evolves but so, too, do its components such as technology and other aspects of the human-made environment, all of which can make us more evolvable.

Variation and Variability

Underlying many of the debates over evolvability—and often forgotten in archaeology—is the important distinction between *variation* and *variability* (Wagner & Altenberg, 1996), the former being the *actual* current trait differences within a population and the latter the *propensity* of characters to vary (Hansen, 2006; Nuño de la Rosa, 2017; Pigliucci, 2008). If variation is operationalized through the concept of heritability, by contrast variability is typically implemented as mutational effects on diverse traits (Jones *et al.*, 2007). The reasoning here is that the evolvability of traits depends on the probability that the raw material of novel phenotypic variation will be generated through mutation and the extent to which mutations affecting one trait affect, and are affected by, others. We return to this point in the following section.

Although the focus on variability brings advantages with respect to predicting long-term evolutionary change (Houle *et al.*, 2017), in biology it remains tied to genetic change, where a statistical approach provides little insight into the mechanistic bases of the character change and little understanding of how different organisms might evolve in different ways (Cordell, 2002). Whether the focus is on variation or variability, it is difficult to evaluate how the characteristics of cellular, developmental, and physiological mechanisms might affect the quality and quantity of phenotypic variation exposed to natural selection (Kirschner & Gerhart, 1998). For Kirschner and Gerhart, evolutionary change in complex organisms, including humans, occurs primarily through the mix and match of conserved core units—in other words, through alterations in the regulatory control of developmental modules, which channel random mutations into generating adaptively biased patterns of phenotypic variation. Kirschner and Gerhart (2005) argue that animals (and many other organisms too) reduce the number of mutations necessary to produce novel phenotypic traits by generating *adaptively biased* phenotypic variation.

Plasticity and Gene–Culture Co-evolution

To researchers interested in human evolution, gene-centric definitions of evolvability are of limited utility because they overlook the fact that, confronted with new ecological or social challenges, human populations most likely will respond through cultural rather than genetic evolution. Again, if evolvability refers to a *capacity*, or an *ability*, to evolve (Kirschner & Gerhart, 1998), then to ignore culture is to neglect the principal means by which our species, and many others as well, generate adaptive responses (Avital & Jablonka, 2000; Hoppitt & Laland, 2013; Laland, 2017;

Whitehead & Rendell, 2014; Whiten *et al.*, 2017). There is now strong evidence that human evolution, and the evolution of cultural animals in general, has been shaped by a process of *gene–culture coevolution* in which cultural processes facilitate genetic evolution (Feldman & Zhivotovsky, 1992; Henrich, 2016; Laland, 2017; Laland *et al.*, 2010; Richerson *et al.*, 2010; Whitehead *et al.*, 2019), including altering the direction and rate of genetic change. Gene–culture coevolution appears to be a major form of human evolutionary adaptation (Durham, 1991; Feldman & Laland, 1996; Laland *et al.*, 2001, Laland *et al.*, 2010; Richerson *et al.*, 2010), in part because there is reliable transmission of behavioral information (Riede, 2019). The reliability of transmission will differ among traits, but culturally modified selective environments can produce unusually strong selection that is directionally consistent over time (*e.g.*, Bersaglieri *et al.*, 2004). Numerous theoretical studies have found that gene–culture co-evolution is usually faster than conventional biological evolution, in part because cultural evolution occurs at faster rates than biological evolution (Henrich, 2016; Laland, 2017; Laland *et al.*, 2010; Richerson & Boyd, 2005). The contribution of gene–culture coevolution to our ancestors' evolvability was probably initially modest but grew over time, as our cultural capacity was enhanced and our control of the environment increased incrementally (Laland, 2017).

Some of the most compelling examples of plasticity-led evolution (West-Eberhard, 2003) arise as genetic evolutionary responses to the cultural activities of humans (*e.g.*, Laland *et al.*, 2019, 2022; O'Brien & Laland, 2012; Whitehead *et al.*, 2019). For example, Laland *et al.* (2010) collated 27 separate genes in humans believed to have been subject to recent selection and for which the inferred selection pressure was a change in diet associated with the advent of agriculture. In other words, the initial and dominant causal effect is (almost certainly) that culture generated the natural selection of genes, not the other way around, although subsequent feedback from modified genetics to the cultural trait is also likely. The list of genes includes those expressed in lactase persistence; the metabolism of carbohydrates, starch, proteins, lipids, phosphates, plant secondary compounds, and alcohol; and jaw-muscle fiber and tooth-enamel thickness. Laland and colleagues also collated 30 cases of genes that provide some immunity from, or resistance to, disease or pathogens thought to have been promoted by agriculture or other farming practices, with anemia–malaria resistance being one of the more prominent examples (Durham, 1991). These cases, together with many more identified over the last decade, are excellent examples of the contribution of human niche construction to evolvability.

Exploratory Mechanisms

Of all the features that contribute to evolvability, *exploratory mechanisms* are among the most important (Gerhart & Kirschner, 1997; Kirschner & Gerhart, 1998, 2005; West-Eberhard, 2003). These complex *developmental* (key word) systems generate variation by exploring possibilities, largely at random; testing the functionality of variants; and then selecting what appear to be the best solutions for regeneration, all in an iterative developmental process. This process resembles adaptation by natural selection except that it allows for information gained within a lifetime rather than strictly conventional genetic information gained across multiple generations (Laland & O'Brien, 2023). Across a broad range of conditions, especially in the face of unanticipated circumstances, organisms can often produce highly functional responses because their exploratory mechanisms confer the flexibility to render workable otherwise disruptive internal changes. The adaptive immune system provides an obvious example, but there are many more (Gerhart & Kirschner, 1997). Exploratory mechanisms are tolerant of mutation, internal failure, environmental novelty, noise, errors, and injury (Gerhart & Kirschner, 1997; Kirschner & Gerhart, 1998, 2005), and within limits, they are self-correcting in relation to functional demands. They can adapt to evolutionary changes in other parts of the organism—if, for example, sensory fields grow or shrink, and the corresponding cortical areas adjust automatically (Gerhart & Kirschner, 1997).

Diverse biological processes, such as the anatomical organization of the brain, exhibits this form of adaptability. During development, the nervous system generates excess neurons and neuronal connections and then prunes them, retaining only those that are needed. Thus, it is not surprising that the vertebrate brain leans heavily on experience (Gerhart & Kirschner, 1997). Exploratory mechanisms also allow vertebrates to remodel bone and soft tissue in order to respond to various functional demands (Hall, 2015).

Such processes are extremely relevant to the topic of evolvability because they reduce the number of mutational steps necessary for adaptive change. For example, evolutionary modifications of the shape and size of the vertebrate limb are triggered by mutations in bones that do not require additional and matching mutations in muscle, nerve, and vascular systems. The latter ride along for free, since they arise through exploratory mechanisms that search for pathways in which muscles, nerves, and blood vessels automatically adjust to the skeletal structure (Gerhart & Kirschner, 1997; West-Eberhard, 2003). As we will see, these "hitchhikers" play an important role in human evolvability.

Understanding the role of exploratory mechanisms allows us to bypass some of the arguments that have taken place in archaeology (and biology) with respect to selection and intent. For example, Huxley (1956) argued that because cultural evolution was "superorganic"—a term made popular by anthropologist A. L. Kroeber (1917)—and involved the psychosocial realm, it could be directed by human intent alone. In archaeology, intent and adaptation are often seen as being intertwined. They also are invoked as "explanations," being viewed as products of vaguely referenced "selective agents"—elements of the natural or cultural environment that force human groups to change or face decline or extinction (O'Brien & Holland, 1992).

Lest we be misunderstood, certainly a person who, say, sits down to make a ceramic vessel will often have an intended outcome in mind. Decision making serves an important role in introducing variation into a cultural system (O'Brien & Holland, 1992; Rindos, 1989), but as Flannery (1967, p. 122) pointed out, although "individuals *do* make decisions … evidence of these individual decisions cannot be recovered by archaeologists." This does not inevitably produce a conundrum because evolutionary explanations often focus on *why* particular behaviors become fixed, rather than on the sources and kinds of initial variation (Dunnell, 1981). Exploratory mechanisms in diverse organisms can generate developmental biases in the rate of introduction of phenotypic variation, an observation that renders any focus on human “intent” unnecessarily anthropocentric.

Learning as a Key Exploratory Mechanism

Organisms’ reliance on genetic information constitutes a gamble that current environments will resemble past environments, such that traits selected in the past remain adaptive. However, genes can provide only a long-term forecast based on what worked previously. Except for microorganisms, genetic evolution is not fast enough to allow organisms to adjust to sudden or unanticipated changes in conditions. Yet, organisms cannot afford to wait around hoping for a suitable mutation to save them; they need a capability to cope with their changing and variable environment now. For many organisms, especially humans, this is where learning, especially social learning, comes into play. Many animals use social learning—learning by observing, or interacting with, others (Heyes, 1994)—for any number of adaptive purposes (Whiten, 2017). Copying others is itself a set of competing strategies, in that one might preferentially copy by identifying skill level as the main criterion—copy those who are better at something than you are, copy good social learners, or copy those who are successful—whereas others might base their decisions on social criteria—copy the majority, copy kin or friends, or copy older individuals (Kendal *et al.*, 2018). Social learning is *cumulative* over generations, as individuals continue to learn from others, improve on what they learned, and transmit traits to the next generation, where they might be improved again (Boyd & Richerson, 2005; Tennie *et al.*, 2009).

Connected to these points is the issue of what makes cumulative cultural evolution (CCE) an apparently open-ended process in humans (Dean *et al.*, 2014). For example, to the extent that some nonhuman animals are capable of cumulative culture, for example by facing the same problem repeatedly, they are seemingly incapable of producing complex, evolvable traditions as humans do. Pigeons, for example, can cumulatively evolve a behavior and transmit it through social learning (Sasaki & Biro, 2017), but they will rapidly reach an optimum where the trajectory of a cultural lineage is no longer evolvable. Humans seem to be better at getting out of dead ends—“optimization traps”—than other organisms because their traditions are so evolvable, or “open-ended” (Charbonneau, 2015).

In that vein, Derex (2022) makes a useful distinction between what he calls Type 1 CCE and Type II CCE. Both are involved in improving cultural traits, but Type 1 is capable of exploiting only a given set of natural phenomena, whereas Type II recruits *additional* natural phenomena in order to push the improvement process further and/or create new cultural traits, thus escaping optimization traps. Winters (2019) and Charbonneau (2015) argue that this ability is due to the search mechanisms unique to humans, such as the capacity for combinatorial invention. This aspect of evolvability will come up later in our discussion of modularity and mosaic evolution.

Socially acquired knowledge can be adaptive because it skims off what appear to be the best ideas and refines them through a few rounds of cultural and natural selection. As with genetic inheritance, here, too, there is a danger that environmental change will render that information obsolete, but this risk is reduced by the fact that, compared to genetic evolution, cultural evolution samples relatively recent generations iteratively, similar to Bayesian updating (Richerson, 2019). In addition, safeguards evolve, such as the rapid abandonment of outdated or dysfunctional cultural knowledge (Rendell *et al*., 2010). Humans, because of our extremely high degree of phenotypic plasticity, have the unique and useful ability not only to learn from others but to learn exactly *how* and *when* to learn from others—"the social learning of social learning" (Mesoudi *et al*., 2016, p. 215)—which is a key component of human evolvability.

Although the behavioral sciences tend to emphasize social learning, which is not surprising given the extraordinary ability humans have for substantially accumulating and retaining socially learned information over generations (Tennie *et al*., 2009), humans are not purely social learners. Without individual learners to constantly sample the environment and produce updated information useful to the group, it becomes difficult for social learners, who are busy tracking others, to also track environmental change, unless there is extensive copy error (Rendell *et al*., 2010) or recombination of cultural traits (Henrich, 2016). Without a source of variation, agents simply copy themselves into stasis, which potentially is a recipe for disaster in the face of a rapidly changing environment (Aoki *et al*., 2012). Relative to social learning, learning individually is typically a slow process in which agents use trial and error to modify existing behaviors to suit their needs. More commonly, a learner obtains the basic behavior from a parent or master and then begins to tinker with it with no influence from other people. He or she can then pass the behavior on to others—one of the key components of human evolvability.

Invention and Innovation

Phenotypic products that result from learning are *inventions* and *innovations*, which are products of different combinations of individual and social learning. Although the two terms are often used interchangeably, including in the animal-behavior literature (*e.g.*, Reader & Laland, 2003), as this article is targeted to archaeologists, who often make a distinction between the two (see references below), we take a somewhat more conservative position, defining invention as a novelty and innovation as a novelty that has diffused through a population. If an invention does not diffuse, then it is not an innovation. This distinction follows the work of Austrian economist Joseph Schumpeter (1942), and it allows us to keep separate two distinct processes: the production of variants and the subsequent diffusion of a subset of those variants. For humans, invention and innovation are obvious processes for creating new variants (Leonard & Reed, 1993; O'Brien & Holland, 1990, 1995; see papers in O'Brien *et al*., 2010), the vast majority of which spread more quickly than genetic mutations because, again, social learning operates at a faster rate than biological evolution (Feldman & Laland, 1996).

Biologists grappled with the concept of innovation throughout much of the twentieth century, in part because there was no agreed-upon definition (Lyman &

O'Brien, 1998). Mayr (1960, p. 351), for example, defined an innovation as "any newly arisen character, structural or otherwise, that differs more than quantitatively from the character that gave rise to it" or "any newly acquired structure or property which permits the assumption of a new function." A few years later he defined an innovation as "any newly acquired structure or property that permits the performance of a new function, which, in turn, will open a new adaptive zone" (Mayr, 1963, p. 602). On the anthropological side, Durham (1991, p. 24), stated that forces and processes giving rise to cultural innovations have "approximate equivalents" in genetic mutation and biological speciation. Feldman *et al.* (1994, p. 49) noted that the "analogy in culture to mutation in biology is invention and innovation."

We need to insert a caveat because the words "approximate equivalents" and "analogy" are misleading and play into a perspective held not only by some biologists but also by a subsection of the archaeological and cultural-evolution communities (*e.g.*, Bamforth, 2002; Gabora, 2006; Guillo, 2007) that cultural evolution, although analogous to genetic evolution, is not biological evolution (Laland & O'Brien, 2023). The problem lies not with the view that cultural evolution is not genetic evolution; it obviously is not. Rather, the problem lies with the view that cultural evolution is *analogous* to genetic evolution. Again, it is not; for many animals, certainly humans, culture is a vital and central aspect of organic evolutionary adaptability. It is a second inheritance system based on learning from others—what Whiten (2017, p. 1) termed "the extension of biology through culture." And nowhere is that extension more evident than in human evolution.

Cultural Traits and Evolvability

Cultural evolution lies at the heart of human evolvability, and cultural traits are its primary currency. Traits have earned a place of importance in anthropology, with the twentieth century playing witness to dozens if not hundreds of definitions (Driver, 1965; Lyman & O'Brien, 2003; McNett Jr., 1979)—similar to the 300-plus definitions of "culture" that Kroeber and Kluckhohn (1952) cataloged midcentury. Cavalli-Sforza and Feldman (1981, p. 73) defined a cultural trait in terms that are applicable to the archaeological record: "the result of any cultural action (by transmission from other individuals) that can be clearly observed or measured on a discontinuous or continuous scale." This includes innovations, skills, and objects.

Like others (*e.g.*, Krause, 1985; Schiffer & Skibo, 1987), we see analytical value in viewing phenotypic traits as *recipes*, which include the materials (ingredients) required to make something, say, a ceramic vessel, and the behavioral rules (instructions) required to construct and use it. Recipes are often hierarchically structured (Charbonneau, 2015; Lyman & O'Brien, 2003; Mesoudi & O'Brien, 2008; O'Brien *et al.*, 2010), with the finished product comprising several behavioral subroutines—for example, preparation of material, production, and use—each of which in turn can be subdivided into a sequence of constituent lower-level actions required to complete each subroutine. Hierarchical organization is evolutionarily advantageous when subunits are repeated in one or more recipes, as repeated subunits must be learned only once and so reduce the overall costs of learning. This re-use of developmental modules is a general feature of evolution (Kirschner & Gerhart, 2005; West-Eberhard, 2003) but is no less true of behavior that is organized hierarchically, with subroutines and where learning is associated with some degree of both error and cost (*e.g.*, foraging and tool making). If errors are localized, they are far less likely to lead to failure. Given the prevalence of hierarchical learning, we would expect to find evidence of repeated subunits in the archaeological record—for example, where the same technological component is repeated in a single tool (Mesoudi & O'Brien, 2008). Here is where *modularity, mosaic evolution,* and *developmental bias* come into play.

Modularity

Modularity is a concept with a long history in biology (*e.g.*, Bolker, 2000; Bonner, 1988; Lewontin, 1978; Riedl, 1977; Winther, 2001). It refers to the organization of an entity, whether an organism or a clay pot, that favors evolvability by allowing one integrated internal component – a module – to change without interfering with the rest of the entity: "Simultaneous random changes in many parts of a highly integrated structure are not likely to improve its function, as the chance improvement of one part will almost always be swamped by deleterious effects in many other parts. But if the parts are variationally independent, selection gets the chance to tune them one at a time, thereby improving the probability of finding improvements" (Hansen, 2003, p. 84). Jablonski (2022) makes the point that factors that evidently can promote evolvability include modularity, albeit contingent on selection being aligned with either modular structure or morphological integration.

Modularity, at least in concept if not in name, has long been a focus in anthropology (Lyman & O'Brien, 2003) and is playing a growing role in archaeology as we understand more about complex tools (Charbonneau, 2016), which are often "so complex that they have to be dissected into simpler components or aspects for an analysis to be useful" (Cavalli-Sforza & Feldman, 1981, p. 73). This harks back to Clements' (1928) remark that the more complex a trait is, the greater number of "specific elements" it will contain. As Shott and Otárola-Castillo (2022, pp. 80–81) point out, "even the smallest hafted [projectile] point is made up of parts. To its users, the different segments or 'modules' of a point served different purposes and were treated differently. From the perspective of hunters, minimally, tip modules initiated wounds in animal prey, blade modules deepened them, and stems articulated the exposed blade to the composite tool."

Numerous studies have examined modularity in projectile points (*e.g.*, González-José & Charlin, 2012; O'Brien *et al.*, 2014; Smallwood *et al.*, 2019; Smith *et al.*, 2021; Smith & Goebel, 2018). One example is Buchanan *et al.*' (2018) analysis of two readily distinguishable projectile-point types from western North America—Clovis and Folsom—both of which exhibit fluted bases, with the fluting on Folsom points being much more distinctive because of the length of the flutes. Around 12,700–12,600 cal B.P., Clovis points were beginning to be replaced by Folsom points. The elongation of the channel flake in Folsom points could have been a consequence of knappers identifying the benefits of a flute and attempting to augment those benefits by increasing its length (Buchanan *et al.*, 2018).

It had long been assumed that the shape of Folsom points was more standardized than that of Clovis points, but that proposition had never been tested. Buchanan and colleagues used geometric morphometric techniques to capture point shape and then conducted statistical analyses of the variation in Clovis and Folsom bases and blades. Their results demonstrated that Folsom bases and blades were less variable than those on earlier Clovis points, which indicated an increase in point standardization. That the base and blade portions of Folsom points were less integrated than they were in Clovis points lends support to the hypothesis that the separate portions of Folsom points were independent modules, one for precise hafting and the other for penetrating prey. Buchanan and colleagues suggested that several classes of points intended for different functions may have been in use during the Clovis period and that, during the subsequent Folsom period, points may have served exclusively as weapon tips for hunting. This finding forces us to reconsider Shott and Otárola-Castillo's (2022) blanket statement cited earlier that different segments or modules of a point served different purposes and *were treated differently*. It's more accurate to say that in *some* cases they were treated differently, whereas in others, including in the case of Clovis, they were not.

One final note on modularity and evolvability: the difference in complexity of modules. Developmental processes are modular and combinatorial (West-Eberhard, 2003), and the same holds for human developmental processes, including those expressed in the manufacture of artifacts. This combinatory quality is highly relevant to evolvability. A hafted stone hammer, for example, might have several modules—a handle, the join, and the working tip—each of which can evolve in its own way with more or less linkage between component modules. Handles could be made of, say, wood or metal without changing the tip part. In contrast, a house has many more potential modules than does the hammer—beams, walls, flooring, location of windows and entrances, orientation to sun/local winds—and so on. Thus, houses are generally much more evolvable—as technologies—than hammers because there are more combinatorial dimensions. However, there are limits to modularity. No module is entirely autonomous, and an artifact, like an organism, is a mosaic of interacting elements, with some parts more connected than others. For these reasons, some human traits, including cultural traits (lineages/traditions) are themselves more evolvable than others.[1]

Mosaic Evolution

Like modularity, mosaic evolution has long played a significant role in biological evolutionary theory (*e.g.*, Stanley, 1979) and paleoanthropology (*e.g.*, Foley, 2016; Skelton & McHenry, 1998), and it is beginning to play a similar role in archaeology (*e.g.*, Darwent & O'Brien, 2006; Mesoudi & O'Brien, 2008; O'Brien *et al.*, 2010; Prentiss *et al.*, 2016; Smallwood *et al.*, 2019; Smith & Goebel, 2018). Mosaic evolution depends on the presence of modularity so that modules can evolve independently (Carroll, 1997; Foley, 2016). However, as stressed above, not all traits are modular, depending on how tightly integrated its components, and no modules are entirely independent. Where modules are tightly integrated, they may not be able to evolve independently, or may do so only slowly. Also, ancestral selection can favor pleiotropic interactions—one trait affecting multiple traits—that organize phenotypic variation along a small number of major dimensions (Kirkpatrick, 2009). As there is greater variability along the dimension than orthogonal to it, it is easier for the population to evolve in some directions than others.

The *rate* of change in the evolution of one trait can differ from the rate of change in another (Smallwood *et al.*, 2019), which corresponds to a difference in evolvability. "Thus, different traits appear and change at different times, and the rates of evolution vary not just between periods but also between elements of the . . . phenotype" (Foley, 2016, p.12). This is not so different from how rates of change work with the evolution of organisms (Earl & Deem, 2004). To draw a contrast between modularity and lack thereof, let's return to our discussion of the difference between the evolution of Clovis and Folsom points. Recall that the base and blade of Clovis points evolved together, meaning there was greater covariation between the two—weak modularity—whereas the base and blade components of Folsom points exhibited lower covariation—strong modularity—than did Clovis points (Buchanan *et al.*, 2018).

In mosaic evolution, traits can *hitchhike*, which occurs when two or more traits are mechanically linked, for instance, through reliance on shared modules, but only one is being sorted by selection. As a result of the linkage, the "hitchhiker" is also sorted. This is a general issue within evolutionary biology, where selection *for* one character can lead to the selection *of* other mechanistically linked characters. Sober (1984) presents a useful example: balls of four different sizes and colors are inserted into a plastic cylinder that contains four levels, each of which contains holes of equal size. The holes on each level are larger than those on the levels below. The object is to get as many balls as possible to the bottom of the cylinder. Shaking the cylinder distributes the balls to their respective levels. After performing the operation, we notice that all the balls on the bottom level are green and the balls on each of the other levels are also segregated by color. The selection process obviously selected the green balls, so there must be some reason why. In other words, they must have some property that was being selected for. But is that property smallness or greenness? Obviously, it is smallness. There was *selection of* green objects, but no *selection for* greenness. Put another way, we can speak of selection of objects and selection for properties.

An archaeological example is the use of limestone as a temper in ceramic vessels from the American Midwest. Around 200 B.C., some small-scale societies began experimenting with limestone as the primary temper added to clays used to manufacture ceramic cooking and storage containers, and by A.D. 750, limestone had begun to replace grit in many locales. Limestone offers several experimentally demonstrated benefits to vessel manufacture, including easier workability in some (but not all) clays. Increased workability facilitates the creation of larger and thinner vessels (Bebber, 2017). Limestone-tempered vessels are also lighter in weight—4.5% in one unpublished study (M. Bebber, pers. comm.). The question is, which trait was the target of selection? Careful analysis of a variety of evidence, together with applying the principle of parsimony to weed out possible candidates, identified wall thickness as the major target of selection, with clay workability and vessel weight being hitchhikers (Mika *et al.*, 2023). Here, the archaeologist is playing the role of the developmental biologist or evolutionary developmental ("evo-devo") researcher, in identifying the underlying mechanistic detail(s) necessary to specify which trait is "selected for," which trait or traits are the result of "selection of," and, crucially, why these traits are selected together.

Developmental Bias

To place developmental bias in perspective, we have to first introduce the concept of *constraint*, which is one of the most misunderstood, and hence misused, concepts in evolutionary biology (Antonovics & Van Tienderen, 1991; Laland & O'Brien, 2023)—and in archaeology as well. Evolutionary constraints are "restrictions, limitations, or biases on the course or outcome of adaptive evolution. The term usually describes factors that limit or channel the action of natural selection. Constraints occur when a trait is *precluded* from reaching, shifted away from, or slowed down in its approach to a (defined) selective optimum" (Hansen, 2015, p. 1; italics added). However, the concept of "constraint" understood in this way is of limited explanatory value, as it can at best explain why evolution or adaptation has *not* occurred. Quite naturally, evolutionary researchers focus on what they perceive to be the causes of adaptation and diversification rather than on factors that thwart such processes.

Conversely, the term *developmental bias*, which has derived currency in the field of evo-devo, captures the idea that developmental systems tend to generate some characters or trait combinations more readily than others (Uller *et al.*, 2018). It is not simply the inverse of constraint, given that traits arise in a probabilistic rather than an all-or-nothing manner. From an evo-devo perspective, developmental bias partly explains what *does* occur rather than what does not, since it is focused on the variation that is commonly produced. Crucially, it is relevant to explaining adaptive evolution—and not only of neutral traits, as is often assumed. Researchers have established that it is possible to understand some patterns of natural variation, ranging from the number of rodent teeth to the shape of fruit-fly wings, as prevalent because those variants are more likely to arise through developmental processes. This does not mean that there is no role for natural selection but rather that it can operate only on the variation that arises. In other words, selection takes populations along pathways in phenotype space created by the mechanisms of development. This makes developmental bias a much more significant concept in evolutionary explanation than developmental constraint. In the same way that rodents' teeth are developmentally biased to evolve collectively as a unit, and that different features of fruit fly wings are biased to coevolve, so too were the bases and blades of Clovis points.

That said, however, we emphasize that we are not implying that developmental constraint plays *no* role in evolution. Constraint can be viewed as one end of a probabilistic continuum of biased variation, the end at which the probability of certain forms arising is close to zero. For example, Charbonneau (2018, p. 79) asks why a stone trilobate arrowhead—one that has three wings or blades—is not found in the archaeological record and then provides an answer:

> This has to do with the constraints imposed by the conchoidal fracturation process exploited by traditional flintknapping techniques. When a knapper produces such fractures on a core through percussion or pressure, the fissures travel roughly parallel to the surface of the core until they reach one of the core's surfaces. Knapping trilobate arrowheads would necessitate that fractures stop somewhere halfway through the core and then come back toward the hammered platform's surface, which contradicts the physical nature of the fracturing process.

Eren *et al.* (2018, p. 70) put it even more simply: "A knapper cannot strike a spherical flake. Nor can a knapper remove a cylindrical flake from the center of a core." Back to trilobate arrowheads, it's critical to note that the constraint on that form of arrowhead is not universal; they have been found in the archaeological record made from bone, ivory, and metal—but not from stone (Delrue, 2007). This suggests that metal, for example, is more "plastic" than stone, making metal technology potentially more malleable/evolvable than stone-based technology.

Biases can be mechanical, structural, or even cultural and can help explain patterns of parallel cultural evolution observed in the archaeological record (*e.g.*, Adler *et al.*, 2014; Fitzhugh & Chaussonnet, 1994; McGhee, 2018; O'Brien & McGhee, 2020), just as they can account for the parallel evolution of cichlid jaws and butterfly-wing patterns (Laland *et al.*, 2015; Uller *et al.*, 2018). For example, the uniformity in shape of Folsom points from across much of the western United States apparently was the result of strong mechanical biases imposed by preparations for successful fluting (Buchanan *et al.*, 2018). Sometimes, however, there are evolutionary workarounds, which illustrates why the all-or-nothing concept of constraint is suboptimal and developmental bias a more accurate description of the process. Recall our discussion of the evolution of thin-walled cooking vessels in the American Midwest, which is an excellent example of opening up new structural possibilities by changing the "developmental" construction process. Midwestern potters were always experimenting with ways to manufacture thinner-walled cooking vessels. The key was switching to limestone as a temper (Braun, 1983; Hoard *et al.*, 1995), which within several hundred years came to dominate midwestern ceramic recipes (Mika *et al.*, 2023; O'Brien, 1996; O'Brien *et al.*, 1994). This is conceptually similar to the butterfly genus *Heteropsis*, which bucks the general trend in its clade by having evolved the ability to control each eyespot's color independently (Brattstrom *et al.*, 2020). As is often the case, evolution found a work-around.

A third kind of bias is more cognitive. Continuing with our midwestern pottery example, we cannot imagine that decorations engraved or incised in vessel-wall exteriors were mechanically or structurally relevant. We might, however, find that, despite the wide range of decorative variants possible in the world, there are some that the groups using the pots strongly prefer, perhaps because they carry some symbolic significance or act as ethnic markers (Braun, 1991; Braun & Plog, 1982; O'Brien & Holland, 1992). Thus, decorations will be channeled toward a preferred range of variants, and as long as pottery makers remain within the acceptable or appropriate range, their cultural fitness is not affected adversely. But pottery makers who consistently defy the limits of acceptability could plausibly have their biological fitness affected—such as being expelled from a community.

Concluding Remarks

As hopefully is evident by now, our position is that culture evolved as a vehicle for evolutionary adaptation to rapid environmental change (see Laland & O'Brien, 2023 for a more-extensive treatment). We see this in other cultural animals (Aplin, 2019; Avital & Jablonka, 2000; Hoppitt & Laland, 2013; Laland, 2017; Whitehead & Rendell, 2014; Whiten, 2012, 2017), but the cultural component of evolvability hits its stride with humans, who have an ability and capacity for culture, and hence for evolvability, not seen in other organisms. This need not imply that humans are more evolvable than other organisms—other taxa may derive their evolvability from alternative mechanisms, including other forms of extragenetic inheritance. Rather, recent findings from evolutionary biology mean that we should be open to the idea that humans might achieve adaptive solutions faster, or slower, than other species and that human traits will vary in their evolvability too.

As we remarked earlier, evolvability, despite being an "umbrella" for connected but partially distinct ideas (Pigliucci, 2008), has at its core "the ability to evolve" (Crother & Murray, 2018). Instead of waiting for genetic inheritance to (hopefully) find a way out of an environmental jam, organisms, especially cultural organisms, have the potential to generate phenotypic change through a mix of extragenetic and genetic inheritance. For example, recent research has shown the possible effects of dramatic climate change in the Early and Middle Pleistocene, including a depopulation of Europe (Margari *et al.*, 2023) and a 117,000-year bottleneck in Africa and Eurasia that could have resulted in as few as 1280 breeding individuals remaining (Hu *et al.*, 2023). In those cases, genes undoubtedly played a role in hominins' ability to eventually rebound in terms of numbers, but it seems undeniable that extragenetic inheritance played a significant role as well. The important point is not simply that genotypic and phenotypic features evolve—we don't need a concept of evolvability to tell us that. Rather, the important point is that not only do organisms evolve but so too do their *ability* and *capacity* to evolve. Of specific relevance to archaeologists is the recognition that the evolution of culture massively souped-up our species' ability to evolve, both through cultural change itself, where humans solve numerous adaptive problems, and through gene–culture coevolution, which often arises when cultural evolution alone can't do the job (Laland & Brown, 2006).

The explosion of interest in extragenetic, particularly epigenetic, inheritance over recent decades (*e.g.*, Bonduriansky & Day, 2018; Danchin *et al.*, 2019; Jablonka & Lamb, 1995) makes it clear that natural selection operates on epigenetic and cultural variation, just as it does on genetic variation. The SET sees a role for epigenetic and cultural inheritance, but it is a minor one (Wray *et al.*, 2014). Conversely, the EES views genetic, epigenetic, and cultural variation to all be targets of selection (Laland *et al.*, 2014, 2015); they are conjoined, interacting processes that help the organism adapt to changes in the environment, whatever the rate of change.

As animal-behavior researchers have shown over the last several decades, no longer can culture and social learning be viewed as the province of large-brained mammals, including humans, but rather as widespread phenomena across the animal kingdom. We know quite a bit about *how* culture evolved, but we need to ask *why* it evolved in the first place. This question may currently be unanswerable, but significant strides have been made in getting us closer to an answer (Boyd & Richerson, 1985; Henrich 2016). This hinges, though, on a shift in analytical focus from the slowly changing aspects of evolutionary adaptation—and the most stable components of inheritance (genetic processes)—to a focus on the fast-paced aspects of adaptation that diverse forms of evolvability afford (Laland & O'Brien, 2023).

Houle *et al.* (2023, p. 384) believe that "one of the reasons that evolvability research has been and will continue to be productive is that it has provided a theme that unites disparate fields. This unity serves to explain the disposition of geneticists, developmental and systems biologists, and paleontologists to exchange ideas about evolvability." We agree, but don't forget the archaeologists. Who better positioned to take a prominent seat at the table than archaeologists, who have many thousands of years of data that are relevant to the EES? In addition, archaeologists are already predisposed to making significant contributions to the study of human evolvability, given their interest in niche construction, modularity, mosaic evolution, and developmental biases. We noted in our first paper on NCT and archaeology (Laland & O'Brien, 2010) that as much as we hoped that archaeologists would begin to use NCT in their research, we also hoped it would not be an alternative "just-so" evolutionary story nor be so open and vague that it could "explain" any conceivable dataset. To be useful, it must encourage rigorous science. Given the careful thought that archaeologists are putting into not only using NCT but adding to the theory, any fears we had have been largely dispelled. We feel the same about evolvability. All that is required is to keep front and center the view that "not only has life evolved, but life has evolved to evolve" (Earl & Deem, 2004, p. 11536).

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Note 1. We thank one of our reviewers for the excellent examples in this paragraph.

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References

Adams, R. M. (1962). Agriculture and urban life in early southwestern Iran. *Science, 136*, 109–122. http://www.jstor.org/stable/1708435

Adler, D. S., Wilkinson, K. N., Blockley, S., Mark, D. F., Pinhasi, R., Schmidt-Magee, B. A., Nahapetyan, S., Mallol, C., Berna, F., Glauberman, P. J., Raczynski-Henk, Y., Wales, N., Frahm, E., Jöris, O., MacLeod, A., Smith, V. C., Cullen, V. L., & Gasparian, B. (2014). Early Levallois technology and the Lower to Middle Paleolithic transition in the southern Caucasus. *Science, 345*, 1609–1613. https://doi.org/10.1126/science.1256484

Adrian-Kalchhauser, I., Sultan, S. E., Shama, L., Spence-Jones, H., & Tiso, S. (2021). Gene regulation unifies molecular approaches to nongenetic inheritance: Response to Edelaar et al. *Trends in Ecology & Evolution, 36*, 477. https://doi.org/10.1016/j.tree.2021.03.004

Andersson, C., Törnberg, A., & Törnberg, P. (2014). An evolutionary developmental approach to cultural evolution. *Current Anthropology, 55*, 154–174. https://doi.org/10.1086/675692

Angier, N. (1997). Ernst Mayr at 93. *Natural History, 106*(4), 8–11.

Antonovics, J., & Van Tienderen, P. H. (1991). Ontoecogenophyloconstraints? The chaos of constraint terminology. *Trends in Ecology & Evolution, 6*, 166–168. https://doi.org/10.1016/0169-5347(91)90059-7

Aoki, K., Wakano, J. Y., & Lehmann, L. (2012). Evolutionarily stable learning schedules and cumulative culture in discrete generation models. *Theoretical Population Biology, 81*, 300–309. https://doi.org/10.1016/j.tpb.2012.01.006

Aplin, L. M. (2019). Culture and cultural evolution in birds: A review of the evidence. *Animal Behaviour, 147*, 179–187. https://doi.org/10.1016/j.anbehav.2018.05.001

Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge University Press.

Bamforth, D. B. (2002). Evidence and metaphor in evolutionary archaeology. *American Antiquity, 67*, 435–452. https://doi.org/10.2307/1593821

Beauchamp, J. P. (2016). Genetic evidence for natural selection in humans in the contemporary United States. *Proceedings of the National Academy of Sciences, 113*, 7774–7779. https://doi.org/10.1073/pnas.1600398113

Bebber, M. R. (2017). Tempered strength: A controlled experiment assessing opportunity costs of adding temper to clay. *Journal of Archaeological Science, 86*, 1–13. https://doi.org/10.1016/j.jas.2017.08.002

Bentley, R. A., & O'Brien, M. J. (2019). Modeling niche construction in Neolithic Europe. In M. Saqalli & M. Vander Linden (Eds.), *Integrating qualitative and social science factors in archaeological modelling* (pp. 91–108). Springer.

Bersaglieri, T., Sabeti, P. C., Patterson, N., Vanderploeg, T., Schaffner, S. F., Drake, J. A., Rhodes, M., Reich, D. E., & Hirschhorn, J. N. (2004). Genetic signatures of strong recent positive selection at the lactase gene. *American Journal of Human Genetics, 74*, 1111–1120. https://doi.org/10.1086/421051

Binford, L. R. (1968). Post-Pleistocene adaptations. In S. R. Binford & L. R. Binford (Eds.), *New perspectives in archeology* (pp. 313–341). Aldine.

Bleed, P., & Matsui, A. (2010). Why didn't agriculture develop in Japan? A consideration of Jomon ecological style, niche construction, and the origins of domestication. *Journal of Archaeological Method and Theory, 17*, 356–370 http://www.jstor.org/stable/40928423

Boivin, N. L., Zeder, M. A., Fuller, D. Q, Crowther, A., Larson, G., Erlandson, J., Denham, T., & Petraglia, M. D. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences, 113*, 6388–6396. https://doi.org/10.1073/pnas.1525200113

Bolker, J. A. (2000). Modularity in development and why it matters to evo-devo. *Integrative & Comparative Biology, 40*, 770–776. https://doi.org/10.1093/icb/40.5.770

Bonduriansky, R., & Day, T. (2018). *Extended heredity: A new understanding of inheritance and evolution*. Princeton University Press.

Bonner, J. T. (1988). *The evolution of complexity: By means of natural selection*. Princeton University Press.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Boyd, R., & Richerson, P. J. (2005). *The origin and evolution of cultures*. Oxford University Press.

Braidwood, R. J. (1960). The agricultural revolution. *Scientific American, 203*, 131–148.

Brattström, O., Aduse-Poku, K., van Bergen, E., French, V., & Brakefield, P. M. (2020). A release from developmental bias accelerates morphological diversification in butterfly eyespots. *Proceedings of the National Academy of Sciences, 117*, 27474–27480.

Braun, D. P. (1983). Pots as tools. In J. Moore & A. Keene (Eds.), *Archaeological hammers and theories* (pp. 107–134). Academic Press.

Braun, D. P. (1991). Why decorate a pot? Midwestern household pottery, 200 B.C.–A.D. 600. *Journal of Anthropological Archaeology, 10*, 360–397. https://doi.org/10.1016/0278-4165(91)90007-K

Braun, D. P., & Plog, S. (1982). Evolution of 'tribal' social networks: Theory and prehistoric North American evidence. *American Antiquity, 47*, 504–525. https://doi.org/10.2307/280232

Brigandt, I., Villegas, C., Love, A. C., & Nuño de la Rosa, L. (2023). Evolvability as a disposition: Philosophical distinctions, scientific implications. In T. Hansen, D. Houle, M. Pavličev, & C. Pélabon (Eds.), *Evolvability* (pp. 55–72). MIT Press.

Brock, W. A., O'Brien, M. J., & Bentley, R. A. (2016). Validating niche-construction theory through path analysis. *Archaeological and Anthropological Sciences, 8*, 819–837. https://doi.org/10.1007/s12520-015-0257-0

Brookfield, J. F. Y. (2001). Evolution: The evolvability enigma. *Current Biology, 11*, R106–R108. https://doi.org/10.1016/S0960-9822(01)00041-0

Brookfield, J. F. Y. (2009). Evolution and evolvability: Celebrating Darwin 200. *Biology Letters, 5*, 44–46.

Broughton, J. M., Cannon, M. D., & Bartlelink, E. J. (2010). Evolutionary ecology, resource depression, and niche construction theory: Applications to central California hunter–gatherers and Mimbres–Mogollon agriculturalists. *Journal of Archaeological Method and Theory, 17*, 371–421. https://doi.org/10.1007/s10816-010-9095-7

Brown, R. L. (2014). What evolvability really is. *British Journal for the Philosophy of Science, 65*, 549–572. https://doi.org/10.1093/bjps/axt014

Buchanan, B., Andrews, B., O'Brien, M. J., & Eren, M. I. (2018). An assessment of stone weapon tip standardization during the Clovis–Folsom transition in the western United States. *American Antiquity, 83*, 721–734. http://www.jstor.org/stable/26583237

Carneiro, R. I. (1973). Classical evolution. In R. Naroll & F. Naroll (Eds.), *Main currents in cultural anthropology* (pp. 57–121). Appleton-Century-Crofts.

Carroll, R. L. (1997). *Patterns and processes of vertebrate evolution*. Cambridge University Press.

Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton University Press.

Charbonneau, M. (2015). All innovations are equal, but some more than others: (Re)integrating modification processes to the origins of cumulative culture. *Biological Theory, 10*, 322–335.

Charbonneau, M. (2016). Modularity and recombination in technological evolution. *Philosophy & Technology, 29*, 373–392. https://doi.org/10.1007/s13347-016-0228-0

Charbonneau, M. (2018). Technical constraints on the convergent evolution of technologies. In M. J. O'Brien, B. Buchanan, & M. I. Eren (Eds.), *Convergent evolution in stone-tool technology* (pp. 73–89). MIT Press.

Charlesworth, D., Barton, N. H., & Charlesworth, B. (2017). The sources of adaptive variation. *Proceedings of the Royal Society B, 28*, 20162864. https://doi.org/10.1098/rspb.2016.2864

Clements, F. E. (1928). Quantitative method in ethnography. *American Anthropologist, 30*, 295–310. http://www.jstor.org/stable/661339

Collard, M., Buchanan, B., Ruttle, A., & O'Brien, M. J. (2012). Niche construction and the toolkits of hunter–gatherers and food producers. *Biological Theory, 6*, 251–259. https://doi.org/10.1007/s13752-012-0034-6

Cordell, H. J. (2002). Epistasis: What it means, what it doesn't mean, and statistical methods to detect it in humans. *Human Molecular Genetics, 11*, 2463–2468.

Creanza, N., Fogarty, L., & Feldman, M. W. (2012). Models of niche construction with selection and assortative mating. *PLOS ONE, 7*(8), e42744. https://doi.org/10.1371/journal.pone.0042744

Crother, B. I., & Murray, C. M. (2018). Early usage and meaning of evolvability. *Ecology and Evolution, 9*, 3784–3793. https://doi.org/10.1002/ece3.5002

Danchin, E., Pocheville, A., Rey, O., Pujol, B., & Blanchet, S. (2019). Epigenetically facilitated mutational assimilation: Epigenetics as a hub within the inclusive evolutionary synthesis. *Biological Review, 94*, 259–282. https://doi.org/10.1111/brv.12453

Darwent, J., & O'Brien, M. J. (2006). Using cladistics to construct lineages of projectile points from northeastern Missouri. In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory* (pp. 185–208). Aldine.

Dawkins, R. (1988). The evolution of evolvability. In C. G. Langton (Ed.), *Artificial life: The proceedings of an interdisciplinary workshop on the synthesis and simulation of living systems* (pp. 201–220). Addison-Wesley.

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Review, 89*, 284–301.

Delrue, P. (2007). Trilobate arrowheads at ed-Dur (U.A.E., Emirate of Umm al-Qaiwain). *Arabian Archaeology and Epigraphy, 18*, 239–250. https://doi.org/10.1111/j.1600-0471.2007.00281.x

Derex, M. (2022). Human cumulative culture and the exploitation of natural phenomena. *Philosophical Transactions of the Royal Society B, 377*, 20200311. https://doi.org/10.1098/rstb.2020.0311

Driver, H. E. (1965). Survey of numerical classification in anthropology. In D. Hymes (Ed.), *The use of computers in anthropology* (pp. 302–344). Mouton.

Dunnell, R. C. (1981). Comment on "Natural selection, energetics, and 'cultural materialism,'" by R. N. Adams. *Current Anthropology, 22*, 613–614.

Dunnell, R. C. (1989). Aspects of the application of evolutionary theory in archaeology. In C. C. Lamberg-Karlovsky (Ed.), *Archaeological thought in America,* (pp. 35–49). Cambridge University Press.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford University Press.

Earl, D. J., & Deem, M. W. (2004). Evolvability is a selectable trait. *Proceedings of the National Academy of Sciences, 95*, 8420–8427. https://doi.org/10.1073/pnas.0404656101

Endler, J. A. (1986). *Natural selection in the wild*. Princeton University Press.

Eren, M. I., Buchanan, B., & O'Brien, M. J. (2018). Why convergence should be a potential hypothesis for the emergence and occurrence of stone-tool form and production processes: An illustration using replication. In M. J., O'Brien, B. Buchanan, & M. I. Eren (Eds.), *Convergent evolution in stone-tool technology* (pp. 61–71). MIT Press.

Feldman, M. W., & Zhivotovsky, L. A. (1992). Gene-culture coevolution: Toward a general theory of vertical transmission. *Proceedings of the National Academy of Sciences, 89*, 11935–11938. https://doi.org/10.1073/pnas.89.24.11935

Feldman, M. W., & Laland, K. N. (1996). Gene–culture co-evolutionary theory. *Trends in Ecology & Evolution, 11*, 453–457. https://doi.org/10.1016/0169-5347(96)10052-5

Feldman, M. W., Cavalli-Sforza, L. L., & Zhivotovsky, L. A. (1994). On the complexity of cultural transmission and evolution. In G. A. Cowan, D. Pines, & D. Meltzer (Eds.), *Complexity: Metaphors, models, and reality* (pp. 47–64). Addison-Wesley.

Fitzhugh, W. W., & Chaussonnet, V. (1994). Introduction. In W. W. Fitzhugh & V. Chaussonnet (Eds.), *Anthropology of the North Pacific Rim* (pp. 1–24). Smithsonian Institution Press.

Flannery, K. V. (1967). Culture history v. cultural process: A debate in American archaeology. *Scientific American, 217*(2), 119–122.

Flannery, K. V. (1969). Origins and ecological effects of early domestication in Iran and the Near East. In P. J. Ucko & G. W. Dimbleby (Eds.), *The domestication and exploitation of plants and animals* (pp. 73–100). Aldine.

Flannery, K. V. (1973). The origins of agriculture. *Annual Review of Anthropology, 2*, 271–310.

Flatt, T. (2005). The evolutionary genetics of canalization. *Quarterly Review of Biology, 80*, 287–316. https://doi.org/10.1086/432265

Foley, R. A. (2016). Mosaic evolution and the pattern of transitions in the hominin lineage. *Philosophical Transactions of the Royal Society B, 371*, 20150244. https://doi.org/10.1098/rstb.2015.0244

Fuentes, A. (2016). The extended evolutionary synthesis, ethnography, and the human niche: Toward an integrated anthropology. *Current Anthropology, 57*, S13–S26. http://www.jstor.org/stable/26545615

Futuyma, D. J. (2013). *Evolution* (3rd ed.) Sinauer.

Gabora, L. (2006). The fate of evolutionary archaeology: Survival or extinction? *World Archaeology, 38*, 690–696. https://doi.org/10.1080/00438240600963395

Gerbault, P., Liebert, A., Itan, Y., Powell, A., & Currat, M. (2011). Evolution of lactase persistence: An example of human niche construction. *Philosophical Transactions of the Royal Society B, 366*, 863–877. https://doi.org/10.1098/rstb.2010.0268

Gerhart, J., & Kirschner, M. (1997). *Cells, embryos, and evolution*. Wiley.

González-José, R., & Charlin, J. (2012). Relative importance of modularity and other morphological attributes on different types of lithic point weapons: Assessing functional variation. *PLOS ONE, 7*(10), e48009. https://doi.org/10.1371/journal.pone.0048009

Gould, S. J. (1987). The panda's thumb of technology. *Natural History, 96*(1), 14–23.

Gould, S. J. (2002). *The structure of evolutionary theory*. Harvard University Press.

Gremillion, K. J., Barton, L., & Piperno, D. R. (2014). Particularism and the retreat from theory in the archaeology of agricultural origins. *Proceedings of the National Academy of Sciences, 111*, 6171–6177. https://doi.org/10.1073/pnas.1308938110

Griswold, C. K. (2006). Pleiotropic mutation, modularity and evolvability. *Evolution & Development, 8*, 81–93. https://doi.org/10.1111/j.1525-142X.2006.05077.x

Guillo, D. (2007). Is cultural evolution analogous to biological evolution? A critical review of memetics. *Intellectica, 46–47*, 49–68. https://doi.org/10.3406/intel.2007.1277

Hall, B. K. (2015). *Bones and cartilage: Developmental and evolutionary skeletal biology* (2nd ed.). Academic Press.

Hansen, T. F. (2003). Is modularity necessary for evolvability? Remarks on the relationship between pleiotropy and evolvability. *Biosystems, 69*, 83–94. https://doi.org/10.1016/s0303-2647(02)00132-6

Hansen, T. F. (2006). The evolution of genetic architecture. *Annual Review of Ecology, Evolution, and Systematics, 37*, 123–157. http://www.jstor.org/stable/30033829

Hansen, T. F. (2015). Evolutionary constraints. In J. Losos (Ed.), *Oxford bibliographies in evolutionary biology* (pp. 1–28). Oxford University Press. https://doi.org/10.1093/obo/9780199941728-0061

Hansen, T. F., Houle, D., Pavličev, M., & Pélabon, C. (Eds.). (2023). *Evolvability: A unifying concept in evolutionary biology? MIT* Press.

Hardesty, D. L. (1980). The use of general ecological principles in archaeology. *Advances in Archaeological Method and Theory, 3*, 157–187. http://www.jstor.org/stable/20170156

Hendrikse, J. L., Parsons, T. E., & Hallgrímsson, B. (2007). Evolvability as the proper focus of evolutionary developmental biology. *Evolution & Development, 9*, 393–401. https://doi.org/10.1111/j.1525-142x.2007.00176.x

Henrich, J. (2016). *The secret of our success: How culture is driving human evolution, domesticating our species, and making us smarter*. Princeton University Press.

Henrich, J., & McElreath, R. (2012). Dual-inheritance theory: The evolution of human cultural capacities and cultural evolution. In R. Dunbar & L. Barrett (Eds.), *Oxford handbook of evolutionary psychology (pp. 555–557)*. Oxford University Press.

Heyes, H. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews, 69*, 207–231. https://doi.org/10.1111/j.1469-185x.1994.tb01506.x

Hoard, R. J., O'Brien, M. J., Khorasgany, M. G., & Gopalaratnam, V. S. (1995). A materials-science approach to understanding limestone-tempered pottery from the midwestern United States. *Journal of Archaeological Science, 22*, 823–832. https://doi.org/10.1016/0305-4403(95)90011-X

Hole, F., Flannery, K. V., & Neely, J. A. (1969). *Prehistory and human ecology of the Deh Luran Plain: An early village sequence from Khuzistan, Iran*. University of Michigan, Museum of Anthropology, Memoirs No 1.

Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton University Press.

Houle, D. (1992). Comparing evolvability and variability of quantitative traits. *Genetics, 130*, 195–204. https://doi.org/10.1093/genetics/130.1.195

Houle, D., Bolstad, G. H., van der Linde, K., & Hansen, T. F. (2017). Mutation predicts 40 million years of fly wing evolution. *Nature, 548*, 447–450. https://doi.org/10.1038/nature23473

Houle, D., Pélabon, C., Pavličev, M., & Hansen, T. F. (2023). Conclusion: Is evolvability a new and unifying concept? In T. F. Hansen, D. Houle, M. Pavličev, & C. Pélabon (Eds.), *Evolvability* (pp. 373–388). MIT Press.

Hu, W., Hao, Z., Du, P., Di Vincenzo, F., Manzi, G., Cui, J., Fu, Y. X., Pan, Y. H., & Li, H. (2023). Genomic inference of a severe human bottleneck during the Early to Middle Pleistocene transition. *Science, 381*, 979–984.

Huxley, J. S. (1956). Evolution, cultural and biological. In W. L. Thomas (Ed.), *Current anthropology* (pp. 3–25). University of Chicago Press.

Iovita, R., Braun, D. R., Douglass, M. J., Holdaway, S. J., Lin, S. C., Olszewki, D. L., & Rezec, Z. (2021). Operationalizing niche construction theory with stone tools. *Evolutionary Anthropology, 30*, 28–39. https://doi.org/10.1002/evan.21881

Jablonka, E., & Lamb, M. (1995). *Epigenetic inheritance and evolution: The Lamarckian dimension*. Oxford University Press.

Jablonka, E., & Lamb, M. (2014). *Evolution in four dimensions* (revised ed.). MIT Press.

Jablonski, D. (2022). Evolvability and macroevolution: Overview and synthesis. *Evolutionary Biology, 49*, 265–291.

Jones, A. G., Arnold, S. J., & Bürger, R. (2007). The mutation matrix and the evolution of evolvability. *Evolution, 61*, 727–745. https://doi.org/10.1111/j.1558-5646.2007.00071.x

Kendal, J. (2011). Cultural niche construction and human learning environments: Investigating sociocultural perspectives. *Biological Theory, 6*, 241–250. https://doi.org/10.1007/s13752-012-0038-2

Kendal, J., Tehrani, J., & Odling-Smee, F. J. (2011). Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society B, 366*, 785–792. https://doi.org/10.1098/2Frstb.2010.0306

Kendal, R. L., Boogert, N., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. (2018). Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences, 22*, 651–665. https://doi.org/10.1016/j.tics.2018.04.003

Kennett, D. J., & Winterhalder, B. (Eds.). (2006). *Behavioral ecology and the transition to agriculture*. University of California Press.

Kirkpatrick, M. (2009). Patterns of quantitative genetic variation in multiple dimensions. *Genetica, 136*, 271–284. https://doi.org/10.1007/s10709-008-9302-6

Kirschner, M. W., & Gerhart, J. C. (1998). Evolvability. *Proceedings of the Royal Society B, 95*, 8420–8427. https://doi.org/10.1073/pnas.95.15.8420

Kirschner, M. W., & Gerhart, J. C. (2005). *The plausibility of life: Resolving Darwin's dilemma*. Yale University Press.

Kissel, M., & Fuentes, A. (2021). The ripples of modernity: How we can extend paleoanthropology with the extended evolutionary synthesis. *Evolutionary Anthropology, 30*, 84–98. https://doi.org/10.1002/evan.21883

Krause, R. A. (1985). *The clay sleeps*. University of Alabama Press.

Kroeber, A. L. (1917). The superorganic. *American Anthropologist, 19*, 116–213.

Kroeber, A. L., & Kluckhohn, C. (1952). *Culture: A critical review of concepts and definitions* (Vol. 47). Harvard University, Peabody Museum of American Archaeology and Ethnology.

Laland, K. N. (2004). Extending the extended phenotype. *Biology and Philosophy, 19*, 313–325. https://doi.org/10.1023/B:BIPH.0000036113.38737.d8

Laland, K. N. (2017). *Darwin's unfinished symphony: How culture made the human mind*. Princeton University Press.

Laland, K. N., & Brown, G. R. (2006). Niche construction, human behaviour, and the adaptive-lag hypothesis. *Evolutionary Anthropology, 15*, 95–104. https://doi.org/10.1002/evan.20093

Laland, K. N., & O'Brien, M. J. (2010). Niche construction theory and archaeology. *Journal of Archaeological Method and Theory, 17*, 303–322. https://doi.org/10.1007/s10816-010-9096-6

Laland, K. N., & O'Brien, M. J. (2011). Cultural niche construction: An introduction. *Biological Theory, 6*, 191–202. https://doi.org/10.1007/s13752-012-0026-6

Laland, K. N., & O'Brien, M. J. (2015). Niche construction: Implications for human sciences. In R. A. Scott & S. M. Kosslyn (Eds.), *Emerging trends in the social and behavioral sciences*. Wiley. https://doi.org/10.1002/9781118900772.etrds0242

Laland, K. N., & O'Brien, M. J. (2023). The cultural contribution to evolvability. *Paleoanthropology, 2023*(2). https://doi.org/10.48738/2023.iss2.xxx

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (2001). Cultural niche construction and human evolution. *Journal of Evolutionary Biology, 14*, 22–33.

Laland, K. N., Kendal, J., & Brown, G. R. (2007). The niche construction perspective: Implications for evolution and human behaviour. *Journal of Evolutionary Psychology, 5*, 51–66. https://doi.org/10.1556/JEP.2007.1003

Laland, K. N., Odling-Smee, F. J., & Myles, S. (2010). How culture shaped the human genome: Bringing genetics and the human sciences together. *Nature Reviews Genetics, 11*, 137–148. https://doi.org/10.1038/nrg2734

Laland, K., Uller, T., Feldman, M., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E., & Odling-Smee, J. (2014). Does evolutionary theory need a rethink? Yes, urgently. *Nature, 514*, 161–164. https://doi.org/10.1038/514161a

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczec, A., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions, and predictions. *Proceedings of the Royal Society B, 282*, 20151019. https://doi.org/10.1098/rspb.2015.1019

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (2019). Understanding niche construction as an evolutionary process. In T. Uller & K. N. Laland (Eds.), *Evolutionary causation: Biological and philosophical reflections* (pp. 127–152). MIT Press.

Laland, K. N., Oudman, T., & Toyokawa, W. (2022). How learning affects evolution. In M. A. Krause, K. L. Hollis, & M. R. Papini (Eds.), *Evolution of learning and memory mechanisms* (pp. 265–282). Cambridge University Press.

Leonard, R. D., & Jones, G. T. (1987). Elements of an inclusive evolutionary model for archaeology. *Journal of Anthropological Archaeology, 6*, 199–219. https://doi.org/10.1016/0278-4165(87)90001-8

Leonard, R. L., & Reed, H. E. (1993). Population aggregation in the prehistoric American Southwest: A selectionist model. *American Antiquity, 58*, 648–661. https://doi.org/10.2307/282200

Lewontin, R. C. (1978). Adaptation. *Scientific American, 239*, 212–231. http://www.jstor.org/stable/10.2307/24955807

Lumsden, C. J., & Wilson, E. O. (1981). *Genes, mind and culture*. Harvard University Press.

Lyman, R. L., & O'Brien, M. J. (1998). The goals of evolutionary archaeology: History and explanation. *Current Anthropology, 39*, 615–652. https://doi.org/10.1086/204786

Lyman, R. L., & O'Brien, M. J. (2003). Cultural traits: Units of analysis in early twentieth-century anthropology. *Journal of Anthropological Research, 59*, 225–250. https://www.jstor.org/stable/3631642

MacNeish, R. S., Fowler, M. L., García Cook, A., Peterson, F. A., & Neely, J. A. (1972). *The prehistory of the Tehuacán Valley* (Vol. 5). University of Texas Press.

Manning, K. M., Downey, S. S., Colledge, S., Conolly, J., Stopp, B., Dobney, K., & Shennan, S. (2014). The origins and spread of stock-keeping: The role of cultural and environmental influences on early Neolithic animal exploitation in Europe. *Antiquity, 87*, 1046–1059. https://doi.org/10.1017/S0003589X00049851

Margari, V., Hodell, D. A., Parfitt, S. A., Ashton, N. M., Grimalt, J. O., Kim, H., Yun, K. S., Gibbard, P. L., Stringer, C. B., Timmermann, A., & Tzedakis, P. C. (2023). Extreme glacial cooling likely led to hominin depopulation of Europe in the Early Pleistocene. *Science, 381*, 693–699.

Maynard-Smith, J. M., & Szathmáry, E. (1995). *The major transitions in evolution*. Oxford University Press.

Mayr, E. (1960). The emergence of evolutionary novelties. In S. Tax (Ed.), *Evolution after Darwin, vol. 1, The evolution of life* (pp. 349–380). University of Chicago Press.

Mayr, E. (1963). *Animal species and evolution*. Harvard University Press.

McGhee, G. R. (2018). Limits on the possible forms of stone tools: A perspective from convergent biological evolution. In M. J. O'Brien, B. Buchanan, & M. I. Eren (Eds.), *Convergent evolution in stone-tool technology* (pp. 23–46). MIT Press.

McNett, C. W., Jr. (1979). The cross-cultural method in archaeology. *Advances in Archaeological Method and Theory, 2*, 39–76. https://doi.org/10.1023/B:JARE.0000040232.61243.89

Mesoudi, A., & O'Brien, M. J. (2008). The learning and transmission of hierarchical cultural recipes. *Biological Theory* 3, 63–72. https://doi.org/10.1162/biot.2008.3.1.63

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution, 31*, 215–225. https://doi.org/10.1016/j.tree.2015.12.012

Mika, A., Eren, M. I., Meindl, R. S., O'Brien, M. J., & Bebber, M. R. (2023). On the evolution of limestone-tempered pottery in the American Midwest: An experimental assessment of vessel weight and its relationship to other functional/mechanical properties. *Science & Technology of Archaeological Research, 9*, 1–14.

Morgan, L. H. (1877). *Ancient society or researches in the lines of human progress from savagery through barbarism to civilization*. MacMillan.

Müller, G. B. (2007). Evo-devo: Extending the evolutionary synthesis. *Nature Reviews Genetics, 8*, 943–949. https://doi.org/10.1038/nrg2219

Müller, G. B. (2017). Why an extended evolutionary synthesis is necessary. *Interface Focus, 7*, 20170015. https://doi.org/10.1098/rsfs.2017.0015

Murray, J. K., Benitez, R. A., & O'Brien, M. J. (2021). The extended evolutionary synthesis and human origins: Archaeological perspectives. *Evolutionary Anthropology, 30*, 4–7. https://doi.org/10.1002/evan.21837

Nuño De la Rosa, L. (2017). Computing the extended synthesis: Mapping the dynamics and conceptual structure of the evolvability research front. *Journal of Experimental Zoology B, 328*, 395–411. https://doi.org/10.1002/jez.b.22741

O'Brien, M. J. (1987). Sedentism, population growth, and resource selection in the Woodland Midwest: A review of coevolutionary developments. *Current Anthropology, 28*, 177–197. https://www.jstor.org/stable/2743186

O'Brien, M. J. (1996). *Middle Woodland and Late Woodland subsistence and ceramic technology in the Central Mississippi River valley: Selected studies from the Burkemper site, Lincoln County, Missouri.* Illinois State Museum, Reports of Investigations 52.

O'Brien, M. J., & Holland, T. D. (1990). Variation, selection, and the archaeological record. *Archaeological Method and Theory, 2*, 31–79. http://www.jstor.org/stable/40023884

O'Brien, M. J., & Holland, T. D. (1992). The role of adaptation in archaeological explanation. *American Antiquity, 57*, 36–59. https://doi.org/10.2307/2694834

O'Brien, M. J., & Holland, T. D. (1995). Behavioral archaeology and the extended phenotype. In J. M. Skibo, W. H. Walker, & A. E. Nielsen (Eds.), *Expanding archaeology* (pp. 143–161). University of Utah Press.

O'Brien, M. J., & Bentley, R. A. (2018). Dual inheritance, cultural transmission, and niche construction. In J. M. Causadias, E. H. Telzer, & N. A. Gonzales (Eds.), *The handbook of culture and biology* (pp. 179–201). Wiley.

O'Brien, M. J., & Laland, K. N. (2012). Genes, culture, and agriculture: An example of human niche construction. *Current Anthropology, 53*, 434–470. https://doi.org/10.1086/666585

O'Brien, M. J., & McGhee, G. R. (2020). Prehistoric stone projectile points and technological change. In P. Pontarotti (Ed.), *Evolutionary biology* (pp. 229–254). Springer.

O'Brien, M. J., & Bentley, R. A. (2021). Genes, culture, and the human niche: An overview. *Evolutionary Anthropology, 30*, 40–49. https://doi.org/10.1002/evan.21865

O'Brien, M. J., Boulanger, M. T., Buchanan, B., Collard, M., Lyman, R. L., & Darwent, J. (2014). Innovation and cultural transmission in the American Paleolithic: Phylogenetic analysis of eastern Paleoindian projectile-point classes. *Journal of Anthropological Archaeology, 34*, 100–119. https://doi.org/10.1016/j.jaa.2014.03.001

O'Brien, M. J., Duran-Nebreda, S., Vidiella, B., Bentley, R. A., & Valverde, S. (2023). Punctuated equilibrium at fifty: Anything there for evolutionary anthropology? Yes; definitely. *Evolutionary Anthropology* (in press).

O'Brien, M. J., Holland, T. D., Hoard, R. J., & Fox, G. L. (1994). Evolutionary implications of design and performance characteristics of prehistoric pottery. *Journal of Archaeological Method and Theory, 1*, 259–304. https://doi.org/10.1007/BF02231877

O'Brien, M. J., Lyman, R. L., & Schiffer, M. B. (2005). *Archaeology as a process: Processualism and its progeny*. University of Utah Press.

O'Brien, M. J., Lyman, R. L., Mesoudi, A., & VanPool, T. L. (2010). Cultural traits as units of analysis. *Philosophical Transactions of the Royal Society B, 365*, 3797–3806. http://www.jstor.org/stable/20789195

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (1996). Niche construction. *American Naturalist, 147*, 641–648. http://www.jstor.org/stable/2463239

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton University Press.

Odling-Smee, F. J., & Turner, J. S. (2012). Niche construction theory and human architecture. *Biological Theory, 6*, 283–289. https://doi.org/10.1007/s13752-012-0029-3

Pigliucci, M. (2007). Do we need an extended evolutionary synthesis? *Evolution, 61*, 2743–2749. https://doi.org/10.1111/j.1558-5646.2007.00246.x

Pigliucci, M. (2008). Is evolvability evolvable? *Nature Reviews Genetics, 9*, 75–82. https://doi.org/10.1038/nrg2278

Pigliucci, M., & Müller, G. B. (2010). *Evolution: The extended synthesis*. MIT Press.

Piperno, D. R. (2011). The origins of plant cultivation and domestication in the New World tropics: Patterns, process, and new developments. *Current Anthropology, 52*, S453–S470. https://doi.org/10.1086/659998

Piperno, D. R. (2017). Assessing elements of an extended evolutionary synthesis for plant domestication and agricultural origin research. *Proceedings of the National Academy of Sciences, 114*, 6429–6437. https://doi.org/10.1073/pnas.1703658114

Piperno, D. R., Ranere, A. J., Dickau, R., & Aceituno, F. (2017). Niche construction and optimal foraging theory in Neotropical agricultural origins: A re-evaluation in consideration of the empirical evidence. *Journal of Archaeological Science, 78*, 214–220. https://doi.org/10.1016/j.jas.2017.01.001

Prentiss, A. M., Walsh, M. J., Skelton, R. B., & Mattes, M. (2016). Mosaic evolution in cultural frameworks: Skateboard decks and projectile points. In L. M. Straffon (Ed.), *Cultural phylogenetics: Concepts and applications* (pp. 113–130). Springer.

Reader, S. M., & Laland, K. N. (2003). Animal innovation: An introduction. In S. M. Reader & K. N. Laland (Eds.), *Animal innovation* (pp. 3–35). Oxford University Press.

Ready, E., & Price, M. H. (2021). Human behavioral ecology and niche construction. *Evolutionary Anthropology, 30*, 71–83. https://doi.org/10.1002/evan.21885

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T., & Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science, 328*, 208–213. https://doi.org/10.1126/science.1184719

Rendell, L., Fogarty, L., & Laland, K. N. (2011). Runaway cultural niche construction. *Philosophical Transactions of the Royal Society B, 366*, 823–835. https://doi.org/10.1098/rstb.2010.0256

Richerson, P. J. (2019). An integrated Bayesian theory of phenotypic flexibility. *Behavioural Processes, 161*, 54–64. https://doi.org/10.1016/j.beproc.2018.02.002

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. University of Chicago Press.

Richerson, P. J., Boyd, R., & Bettinger, R. L. (2001). Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *American Antiquity, 66*, 387–411. https://doi.org/10.2307/2694241

Richerson, P. J., Boyd, R., & Henrich, J. (2010). Gene–culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences, 107*, 8985–8992. https://doi.org/10.1073/pnas.0914631107

Riede, F. (2011). Adaptation and niche construction in human prehistory: A case study from the southern Scandinavian Late Glacial. *Philosophical Transactions of the Royal Society B, 366*, 793–808. https://doi.org/10.1098/rstb.2010.0266

Riede, F. (2019). Niche construction theory and human biocultural evolution. In A. M. Prentiss (Ed.), *Handbook of evolutionary research in archaeology* (pp. 337–358). Springer.

Riede, F., Hoggard, C., & Shennan, S. J. (2019). Reconciling material cultures in archaeology with genetic data requires robust cultural evolutionary taxonomies. *Palgrave Communications 5*. https://doi.org/10.1057/s41599-019-0260-7

Riederer, J. M., Stefano, T., van Eldijk, T. J. B., & Weissing, F. J. (2022). Capturing the facets of evolvability in a mechanistic framework. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2022.01.004

Riedl, R. J. (1977). A systems-analytical approach to macro-evolutionary phenomena. *Quarterly Review of Biology, 52*, 351–370. http://www.jstor.org/stable/2823251

Riel-Salvatore, J. (2010). A niche construction perspective on the Middle–Upper Paleolithic transition in Italy. *Journal of Archaeological Method and Theory, 17*, 323–355. http://www.jstor.org/stable/40928422

Rindos, D. (1984). *The origins of agriculture: An evolutionary perspective*. Academic Press.

Rindos, D. (1989). Undirected variation and the Darwinian explanation of cultural change. *Archaeological Method and Theory, 1*, 1–45.

Rowley-Conwy, P., & Layton, R. (2011). Foraging and farming as niche construction: Stable and unstable adaptations. *Philosophical Transactions of the Royal Society B, 366*, 849–862. http://www.jstor.org/stable/41441703

Sansom, R. (2008). Evolvability. In M. Ruse (Ed.), *The Oxford handbook of philosophy of biology* (pp. 138–160). Oxford University Press.

Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications, 8*, 15049. https://doi.org/10.1038/ncomms15049

Schiffer, M. B., & Skibo, J. M. (1987). Theory and experiment in the study of technological change. *Current Anthropology, 28*, 595–622. http://www.jstor.org/stable/2743357

Schumpeter, J. A. (1942). *Capitalism, socialism, and democracy*. Harper.

Shott, M. J., & Otárola-Castillo, E. (2022). Parts and wholes: Reduction allometry and modularity in experimental Folsom points. *American Antiquity, 81*, 80–99. https://doi.org/10.1017/aaq.2021.62

Simpson, G. L. (1949). *The meaning of evolution*. Columbia University Press.

Skelton, R. R., & McHenry, H. M. (1998). Trait list bias and a reappraisal of early hominid phylogeny. *Journal of Human Evolution, 34*, 109–113. https://doi.org/10.1006/jhev.1997.0195

Smallwood, A. M., Jennings, T. A., Pevny, C. D., & Anderson, D. G. (2019). Paleoindian projectile-point diversity in the American Southeast: Evidence for the mosaic evolution of point design. *PaleoAmerica, 5*, 218–230. https://doi.org/10.1080/20555563.2019.1600343

Smith, B. D. (2007a). The ultimate ecosystem engineers. *Science, 315*, 1797–1798. https://doi.org/10.1126/science.1137740

Smith, B. D. (2007b). Niche construction and the behavioral context of plant and animal domestication. *Evolutionary Anthropology, 16*, 188–199. https://doi.org/10.1002/evan.20135

Smith, B. D. (2011a). General patterns of niche construction and the management of 'wild' plant and animal resources by small-scale preindustrial societies. *Philosophical Transactions of the Royal Society B, 366*, 836–848. https://doi.org/10.1098/rstb.2010.0253

Smith, B. D. (2011b). A cultural niche construction theory of initial domestication. *Biological Theory, 6*, 260–271. https://doi.org/10.1007/s13752-012-0028-4

Smith, H. L., & Goebel, T. (2018). Origins and spread of fluted-point technology in the Canadian ice-free corridor and eastern Beringia. *Proceedings of the National Academy of Sciences, 115*, 4116–4121. https://doi.org/10.1073/pnas.1800312115

Smith, H. L., Jennings, T. A., & Smallwood, A. M. (2021). Do early Paleoindian point blades carry culturally significant shape information? Modules versus complete points using geometric morphometrics. *Journal of Archaeological Science: Reports, 40*. https://doi.org/10.1016/j.jasrrep.2021.103245

Sniegowski, P. D., & Murphy, H. A. (2006). Evolvability. *Current Biology, 16*, R831–R834. https://doi.org/10.1016/j.cub.2006.08.080

Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus*. MIT Press.

Stanley, S. M. (1979). *Macroevolution: Pattern and process*. Freeman.

Stearns, S. C., Byars, S. G., Govindaraju, D. R., & Ewbank, D. (2010). Measuring selection in contemporary human populations. *Nature Review of Genetics 11*, 611–622. http://doi.org/10.1038/nrg2831

Steward, J. H. (1937). Ecological aspects of Southwestern society. *Anthropos, 32*, 87–104.

Steward, J. H. (1956). Cultural evolution. *Scientific American, 194*(5), 69–80.

Stiner, M. C. (2021). The challenges of documenting coevolution and niche construction: The example of domestic spaces. *Evolutionary Anthropology, 30*, 63–70. https://doi.org/10.1002/evan.21878

Stiner, M. C., & Kuhn, S. L. (2016). Are we missing the "sweet spot" between optimality theory and niche construction theory in archaeology? *Journal of Anthropological Archaeology, 44*, 177–184. https://doi.org/10.1016/j.jaa.2016.07.006

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B, 364*, 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Thompson, J. C., Wright, D. K., & Ivory, S. J. (2021). The emergence and intensification of early hunter–gatherer niche construction. *Evolutionary Anthropology, 30*, 17–27. https://doi.org/10.1002/evan.21877

Thomson, J. A. (1931). Biology and human progress. In W. Rose (Ed.), *An outline of human knowledge* (pp. 203–252). Gollanz.

Tylor, E. B. (1871). *Primitive culture: Researches into the development of mythology, philosophy, religion, art, and culture* (2 vols.). Murray.

Uller, T., Moczek, A. P., Watson, R. A., Brakefield, P. M., & Laland, K. N. (2018). Developmental bias and evolution: A regulatory network perspective. *Genetics, 209*, 949–966. https://doi.org/10.1534/genetics.118.300995

Veatch, E. G., Ringen, E. J., Kilgore, M. B., & Jatmiko. (2021). Using niche construction theory to generate testable foraging hypotheses at Liang Bua. *Evolutionary Anthropology, 30*, 8–16. https://doi.org/10.1002/evan.21878

Villegas, C., Love, A. C., Nuño de la Rosa, L., Brigandt, I., & Wagner, G. P. (2023). Conceptual roles of evolvability across evolutionary biology: Between diversity and unification. In T. F. Hansen, D. Houle, M. Pavličev, & C. Pélabon (Eds.), *Evolvability* (pp. 35–54). MIT Press.

Wagner, G. P., & Altenberg, L. (1996). Complex adaptations and the evolution of evolvability. *Evolution, 50*, 967–976. https://doi.org/10.1111/j.1558-5646.1996.tb02339.x

Wagner, G. P., & Draghi, J. (2010). Evolution of evolvability. In G. B. Müller & M. Pigliucci (Eds.), *Evolution: The extended synthesis* (pp. 379–399). MIT Press.

Wallach, E. (2016). Niche construction theory as an explanatory framework for human phenomena. *Synthese, 193*, 2595–2618. http://www.jstor.org/stable/43921235

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

White, L. A. (1959). *The evolution of culture: The development of civilization to the fall of Rome*. McGraw–Hill.

Whitehead, H., Laland, K. N., Rendell, L., Thorogood, R., & Whiten, A. (2019). The reach of gene–culture coevolution in animals. *Nature Communications, 10*. https://doi.org/10.1038/s41467-019-10293-y

Whitehead, H., & Rendell, L. (2014). *The cultural lives of whales and dolphins*. University of Chicago Press.

Whiten, A. (2012). Social learning, traditions and culture. In J. C. Mitani, J. Call, P. M. Kappeler, J. R. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 681–699). University of Chicago Press.

Whiten, A. (2017). A second inheritance system: the extension of biology through culture. *Royal Society Interface Focus, 7*(5), 20160142. https://doi.org/10.1098/rsfs.2016.0142

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, J., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature, 399*, 682–685. https://doi.org/10.1038/21415

Whiten, A., Hinde, R. A., Laland, K. N., & Stringer, C. B. (Eds.). (2012). *Culture evolves*. Oxford University Press.

Whiten, A., Hinde, R. A., Laland, K. N., & Stringer, C. B. (2011). Culture evolves. *Philosophical Transactions of the Royal Society B, 366*, 938–948. https://doi.org/10.1098/rstb.2010.0372

Whiten, A., Ayala, F. J., Feldman, M. W., & Laland, K. N. (2017). The extension of biology through culture. *Proceedings of the National Academy of Sciences, 114*, 7775–7781. https://doi.org/10.1073/pnas.1707630114

Williams, G. C. (1992). Gaia, nature worship, and biocentric fallacies. *Quarterly Review of Biology, 67*, 479–486. https://doi.org/10.1086/417796

Winters, J. (2019). Escaping optimization traps: The role of cultural adaptation and cultural exaptation in facilitating open-ended cumulative dynamics. *Palgrave Communications, 5*, 149. https://doi.org/10.1057/s41599-019-0361-3

Winther, R. G. (2001). Varieties of modules: Kinds, levels, origins, and behaviors. *Journal of Exploratory Evolution, 291*, 116–129. https://doi.org/10.1002/jez.1064

Wollstonecroft, M. (2011). Investigating the role of food processing in human evolution: A niche construction approach. *Archaeological and Anthropological Sciences, 3*, 141–150. https://doi.org/10.1007/s12520-011-0062-3

Wray, G. A., Hoekstra, H. E., Futuyma, D. A., Lenski, R. E., MacKay, T. F. C., Schluter, D., & Strassmann, J. E. (2014). Does evolutionary biology need a rethink? Counterpoint: No, all is well. *Nature, 514*, 161–164.

Zeder, M. A. (2012). The broad spectrum revolution at 40: Resource diversity, intensification, and an alternative to optimal foraging explanations. *Journal of Anthropological Archaeology, 31*, 241–264. https://doi.org/10.1016/j.jaa.2012.03.003

Zeder, M. A. (2015). Core concepts in domestication research. *Proceedings of the National Academy of Sciences, 112*, 3191–3198. https://doi.org/10.1073/pnas.1501711112

Zeder, M. A. (2016). Domestication as a model system for the extended evolutionary synthesis. *Royal Society Interface Focus, 7*, 20160133. https://doi.org/10.1098/rsfs.2016.0133

Zubrow, E. B. W. (1971). Carrying capacity and dynamic equilibrium in the prehistoric Southwest. *American Antiquity, 36*, 127–138. https://doi.org/10.2307/278666