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The Cultural Contribution to Evolvability

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ABSTRACT

Evolvability is an emerging, synthetic topic that is making an impact in a variety of evolutionary fields. Although several definitions of evolvability have earned currency, most share a focus on the capacity or potential of systems to evolve. The suggestion that this capacity depends in part on the complexity of an organism's development, and hence that different organisms evolve in fundamentally different ways, is a key point of contention in debates over the importance of evolutionary developmental biology and the merits of an extended evolutionary synthesis, both of which afford evolvability an important role. Here we make the case that the cultural contribution to evolvability is key to understanding human evolution in part because cultural inheritance can oftentimes direct genetic inheritance, and thereby can produce change that genetic inheritance cannot. We also suggest that evolvability can help researchers—certainly paleoanthropologists, given their control over long time spans of human evolution—to pose questions that perhaps otherwise would have escaped attention.

INTRODUCTION

Evolvability is an important emerging concept within the evolutionary sciences (Hansen et al. 2023). Although defined in numerous ways (Pigliucci, 2007; Riederer et al., 2022), for our purposes evolvability is "a property of living systems that refers broadly to their capacity, ability, or potential to evolve" (Villegas et al., 2023) and largely equates with "the ability of a biological system to produce phenotypic variation that is both heritable and adaptive" (Payne and Wagner, 2019: 24). We agree with Pigliucci (2008: 76) that we are not dealing with a single view of evolvability but with "a family of connected but partially distinct ideas under the general umbrella of evolvability." All ideas (definitions), however, have three features in common: (1) heritable phenotypic variation is the essential raw material of evolution; (2) unless a system has the potential to produce variation that is beneficial (adaptive) at least in *some* environments (which might eventually change), adaptation by natural selection is impossible; and, (3) the definition is broad enough to apply to fields as different as population genetics and molecular biology (Payne and Wagner, 2019).

Evolvability plays an interesting role in contemporary debates over the structure of evolutionary theory (Laland et al., 2014, 2015; Wray et al., 2014). On the one hand, evolvability is widely regarded as a core, and perhaps the defining, concept within evolutionary developmental biology (Kirschner and Gerhart, 1998; Hendrikse et al., 2007; Brown, 2014) and the extended evolutionary synthesis (Pigliucci, 2008; Pigliucci and Müller, 2010; Laland et al., 2015). On the other hand, it is also championed as central to mainstream quantitative and population genetics (Hansen, 2006) as well as to molecular evolution, paleontology,

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and network analysis (Wagner and Draghi, 2010; Nuño de la Rosa, 2017; Crowther and Murray, 2018; Brigandt et al., 2023). Topics such as modularity, robustness, bias/constraint, and the genotype–phenotype map are tackled by different fields under the umbrella of evolvability research.

Currently, despite recognition that in addition to standard genetic evolution, humans—and many other animals—also evolve through a cultural evolutionary process (Whiten et al., 2011), and that countless organisms are currently evolving in direct response to anthropogenic change, much of the literature on evolution and evolvability ignores a role for culture. For example, it is not mentioned in a leading evolutionary biology undergraduate textbook, which defines evolution as "the origin and subsequent alteration of the frequencies of genotypes from generation to generation within populations" 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" (Futuyma, 2013: 2; italics added). 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 "Weissmann 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: 484).

This gene-centric and adaptationist perspective, which has dominated evolutionary science for much of the last century, is being increasingly challenged (e.g., Avital and Jablonka, 2000; Kirschner and Gerhart, 2005; Müller, 2007; Pigliucci and Müller, 2010; Jablonka and Lamb, 2014; Laland et al., 2014, 2015; Fuentes, 2017; Danchin et al., 2019). Over the past several decades, evidence for culture—at least when broadly defined—has emerged through scientific investigations of a wide array of animals (Avital and Jablonka, 2000; Hoppitt and Laland, 2013; Galef and Whiten, 2017) including insects (Leadbeater and Dawson, 2017). The alternative to the gene-centered/adaptationist perspective, the view that we advocate is that an "organism influences its own evolution, by being both the object of natural selection and the creator of the conditions of that selection" (Levins and Lewontin, 1985: 106).

Despite the preponderance of evidence from the biological world for the significant role of cultural inheritance, there are claims—thankfully, few—that cultural evolution is not even evolution, except perhaps in a broad, metaphorical sense (e.g., Bamforth, 2002; Gabora, 2006), and that only genes matter when we talk about units of transmission. Gould (1987: 18), for example, noted that:

> "I am 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."

This reminds us of what anthropologist Berthold Laufer (1918: 90) said about cultural evolution over a century ago:

> "the theory of cultural evolution [is] to my mind the most inane, sterile, and pernicious theory ever conceived in the history of science (a cheap toy for the amusement of big children)."

We obviously do not agree, nor do we agree with the related view that cultural evolution, although analogous to genetic evolution, is not biological evolution (Guillo, 2007). The problem lies not with the view that cultural evolution is not genetic evolution; it obviously is not. The problem lies with the flawed view that cultural evolution is *analogous* to genetic evolution. Again, it is not; for many animals, culture is a vital and central aspect of biological evolution. It is a second inheritance system based on learning from others—what Whiten (2017: 1) termed "the extension of biology through culture." And nowhere is that extension more evident than in human evolution.

To date, cultural evolvability has played a relatively minor role in paleoanthropological research, but we think it can play an even more-significant role, in that paleoanthropologists and related researchers are not simply consumers of evolutionary knowledge but also have a key role to play in devising new theory, given their ever-growing understanding of chronology, paleoclimate, hominid morphology and function, tool use, social learning and transmission, and how our ancestors exploited their environments (e.g., Bednarik, 2014; Brown et al., 2009, 2012; Whiten et al., 2009; Coward and Grove, 2011; Eren et al., 2011; Shea, 2011; Stout, 2011; d'Errico and Banks, 2013; Richerson and Boyd, 2013; Hecht et al., 2014; Henke and Tattersall, 2015; Marean, 2015; Marean et al., 2015; Morgan et al., 2015; Tennie et al., 2016; Stout and Hecht, 2017; Potts et al., 2018; Galway-Withem and Stringer, 2019; Stout et al., 2019; Brumm et al., 2021; Schwartz, 2022). These are key components of our ability to understand the evolvability of humans and the contribution that culture makes to it.

In the sections that follow, we first define culture, then define evolvability, pointing out that whereas narrow statistical–genetic views offer limited traction for researchers, broader definitions derived from evolutionary developmental biology can usefully be extended to encompass adaptability arising through culture. We go on to discuss exploratory mechanisms, which are complex information-gaining forms of developmental plasticity that confer considerable adaptability on the organism, one example of which is learning and culture. We stress how the capacity of humans both to respond to, and create, changing environments is heavily reliant on learning and culture and argue that the primary function of culture, as well as some other forms of extra-genetic inheritance, is to allow organisms to adjust to rapidly changing features of their environment. In the final sections we spell out a few of the implications of cultural evolvability for conservation and sustainability science.

The careful reader will note that our primary emphasis throughout the paper is on the species *Homo sapiens*, which, depending on how it—as well as other species in the genus *Homo* (Collard and Wood, 2015)—is defined, evolved in Africa roughly 250,000–300,000 years ago (Richter et al., 2017; Schlebusch et al., 2017). We focus on that species in part because of space limitations and in part because so much more is known about that species than about earlier hominins. Our emphasis, however, should not be taken as suggesting that the contribution that culture makes to human evolvability began around that date (see Antón and Snodgrass, 2012). Strong evidence indicates that culture played a significant role in the evolvability of other, earlier species of the tool-producing genus *Homo,* which date back to as early as 2.8 million years ago (Villmoare et al., 2015; Kimbel and Villmoare, 2016; Schlebusch et al., 2017; Thompson et al., 2019), and potentially the evolvability of even earlier hominids (e.g., Bramble and Lieberman, 2004; Harmand et al., 2015; Zink and Lieberman, 2016; Lieberman, 2018).

WHAT EXACTLY IS CULTURE?

The term "culture" has a long career in the behavioral sciences, with little consensus on how to define it. For example, Kroeber and Kluckhohn (1952) cataloged an incredible 300 definitions of human culture in the early 1950s, with many more appearing since then. One often-cited definition that dominated much of twentieth-century anthropology, and still does in some quarters, is that culture is humankind's "extrasomatic means of adaptation" (White, 1959: 8). In other words, culture is viewed primarily as an adaptive mechanism that comes along in a time of need and helps organisms to adjust. This was the central tenet of much of mid-century anthropology (e.g., Steward, 1955), processual archaeology of the 1960s and 1970s (e.g., Binford, 1968), and paleoanthropology of the same period (e.g., Butzer, 1977; Issac, 1972).

Our definition of culture, shared by an increasing number of behavioralists (see chapters in Whiten et al., 2012), is different in that it is based on learning via cultural transmission, not strictly on environmental adaptation but also on adaptability. 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). Culture appears to play an increasingly significant role in human adaptability, with genetic change largely and increasingly peripheral (Waring and Wood, 2021).

Just as genes are units of transmission, so too are cultural traits, which reflect behavioral characteristics of the individuals or groups exhibiting them (Lyman and O'Brien, 1998, 2003; O'Brien et al., 2010). Once transmitted, cultural traits serve as units of replication in that they can be modified as part of an individual's cultural repertoire through processes such as recombination (new associations with other cultural traits), loss (forgetting), or partial alteration (incomplete learning, personal experience, or forgetting components) within an individual's mind (Eerkens and Lipo, 2005). In this respect, cultural traits play a role roughly analogous to, but not identical to (Andersson, 2011), genes, in that organisms replicate them, but the cultural traits themselves, conceived as ideas in the minds of individuals (Lyman and O'Brien, 2003), are also replicators (Hull, 1981; Dawkins, 1982).

The human capacity for adaptation through culture does more than just allow humans to adjust to novel circumstances; it also ramps up our species' ability to modify and regulate the environment:

> "organisms [are] not just adapted to their ecological environments but also [are] adapting their environments to themselves. In the end, it becomes impossible to decouple these processes" (Andersson et al., 2014: 156).

As Lewontin (1983: 280) put it, "organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world." In so doing, organisms direct their own evolution, often but not exclusively in a manner that suits their genotypes, contributing to their own evolvability by setting their own evolutionary agenda (O'Brien and Laland, 2012).

Humans, as they have for millennia, manifestly transform the planet in nonrandom ways—urbanization and deforestation, for example—in the process altering the form and rate of change of natural selection operating in natural systems and also making available new forms of energy that ultimately translate into an enhanced potential for change in other species. These considerations have implications for sustainability and biodiversity in that the capacity of other species to respond to human impacts depends in part on their own extragenetic inheritance systems, including culture. Instead of being recent, these impacts have a deep history in human evolution (Judson, 2017; Thompson et al., 2021).

UNDERSTANDING EVOLVABILITY

A key question within evolvability research is whether and how the evolutionary process itself evolves (Maynard-Smith and Szathmáry, 1995; Kirschner and Gerhart, 1998; Pigliucci, 2008; Uller et al., 2018). After all, bacteria are microscopic, asexual, single-cell organisms, whereas, say, mammals are macroscopic, sexual, multicellular, and often highly social organisms. Is it implausible that such taxonomic extremes evolve in different ways? Animal design since the pre-Cambrian seems to have 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 and forms of extragenetic inheritance. The suggestion that the capacity of a biological system for evolutionary change depends in part on the complexity of the focal organism's development is a key point of contention within the field. Different positions with respect to this issue are reflected in how evolvability is defined and studied.

To many evolutionary geneticists, the capacity to evolve hangs largely on how much "additive genetic variation" there is in a trait of interest; hence, evolvability equates to the concept of heritability or to related concepts such as the genetic coefficient of variation (Houle, 1992; Charlesworth et al., 2017). The advantages of this perspective include its wide applicability to diverse biological systems, accessibility to measurement, and use in short-term prediction (Hansen, 2006; Nuño de la Rosa, 2017; Brigandt et al., 2023). One potential 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, the hallmark of *mosaic evolution* (Carroll, 1997), which plays a significant role in paleoanthropological research (e.g., Skelton and McHenry, 1998; Foley, 2016). A second potential drawback is that it fails to consider how taxonomic groups might take quite distinctly different pathways to evolutionary change and adaptation.

Underlying many of the debates over evolvability is the important distinction between *variation* and *variability* (Wagner and Alternberg, 1996), the former being the actual current trait differences within a population and the latter the *propensity* of characters to vary (Hansen, 2006; Pigliucci, 2008; Nuño de la Rosa, 2017). 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 is critically dependent on the probability that the raw material of novel genetic variation will be generated through mutation and the extent to which mutations affecting one trait affect, and are affected by, others (*epistatic interactions*).

Although the focus on variability brings advantages with respect to predicting long-term evolutionary change (Houle et al., 2017), it suffers from many of the same deficiencies as the focus on genetic variation and adaptation. This construal of evolvability, like the preceding one, 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. Whether the focus is on genetic variation or on genetic variability, it remains 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 and Gerhart, 1998).

To researchers with an interest in human evolution, such definitions might appear to be of limited utility for at least two reasons. First, at least for members of our genus, the primary dimension of human evolution and adaptation is our unparalleled capacity for culture. Like many other animals, humans acquire knowledge and skills from other individuals and adjust their behavior and cognition in light of the cultural wisdom accumulated over generations (Henrich et al., 2016; Mesoudi and Thornton, 2018). Today, such accumulation is evident within our lifetimes, as exemplified by digital technology and genetic engineering (Valverde et al., 2022). Confronted with new ecological or social challenges, human populations most likely will respond through cultural rather than genetic evolution. Evolvability refers to a *capacity* to evolve, so to ignore culture is to neglect the principal means by which our species, and many others, generate adaptive responses (Avital and Jablonka, 2000; Hoppitt and Laland, 2013; Whitehead and Rendell, 2014; Laland, 2017; Whiten et al., 2017; Aplin, 2019).

Second, even if a conservative line is taken that restricts evolution to genetic change—a position with which we obviously disagree—there nonetheless 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 can influence genetic evolution (Laland et al., 2010; Richerson et al., 2010; Henrich, 2016; Laland, 2017; Whitehead et al., 2019), including altering the direction and rate of genetic change. Some of the most compelling examples of plasticity-led evolution (West-Eberhard, 2003) arise as genetic evolutionary responses to the cultural activities of humans and other animals (Laland et al., 2019, 2022; Whitehead et al., 2019).

Fortunately, there exists a view of evolvability that potentially offers traction for students of human evolution—one that has emerged from evolutionary developmental biology (Müller, 2007). Recall from earlier discussion Kirschner and Gerhart's (1998: 8420) definition of evolvability as "an organism's capacity to generate heritable phenotypic variation." Here, "organism" should be read as a *population* of organisms, and hence evolvability remains a population-level property. Although Kirschner and Gerhart assume that genetic variation underlies heritable phenotypic variation, their definition leaves open the possibility of cultural evolution contributing to evolvability. Moreover, they stress the need "to look beyond the quantity of sequence variation" (Kirschner and Gerhart, 1998: 8421) in order to understand patterns of trait evolution. For Kirschner and Gerhart, evolutionary change in complex organisms 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. In contrast to simple (e.g., unicellular) organisms, complex multicellular animals possess a number of mechanistic features that both undermine the lethality of mutations by making them workable and reduce the number of mutations necessary to produce novel phenotypic traits by generating adaptively biased phenotypic variation. This is highly relevant to humans and, in fact, underlies our capacity for learning and culture.

EVOLVABILITY AND EXPLORATORY MECHANISMS

Prominent among evolvability-enhancing features are "exploratory mechanisms" (Gerhart and Kirschner, 1997; Kirschner and Gerhart, 1998, 2005; West-Eberhard, 2003), which are complex developmental systems that operate by generating variation—that is, by exploring possibilities largely at random, testing the functionality of variants, and selecting the best solutions for regeneration, in an iterative developmental process. The process resembles adaptation by natural selection except that it allows for ontogenetic information gained within a lifetime rather than only conventional genetic information gained across multiple generations.

Diverse biological processes function in this way. For example, the adaptive immune system generates antibodies and T-cells with initially random variation, then multiplies and refines those that bind successfully to antigens, with a memory of effective molecules retained (Klenerman, 2017). Similarly, the nervous system generates excess neurons, excess neuronal connections, and excessively distributed neuronal connections through random exploration and then prunes these, retaining solely those that are required. Much of the patterning in the brain depends on the use of functional interactions by exploratory mechanisms in order to sort out connectivity. The final anatomy of vertebrate brains thus depends heavily on experience (Gerhart and Kirschner, 1997).

The remodeling of bone and soft tissue such as muscles and tendons is also known to be responsive to functional demands (Hall, 2015), and these processes have also been characterized as reliant on this "somatic [bodily] selection" (West-Eberhard, 2003). Such processes are relevant to the topic of evolvability because they reduce the number of mutational steps necessary for adaptive change. For example, evolutionary modifications of the vertebrate limb shape and size are triggered by mutations that modify bone condensations and do not require additional and matching mutations in muscle, nerve, and vascular systems. The latter ride along for free—they hitchhike—given that they arise through exploratory mechanisms through which muscles, nerves, and blood vessels automatically adjust to the skeletal structure.

Organisms face challenges that arise not only from the external environment but also from large numbers of individual-specific internal failures in somatic genome, epigenome, and microbiome that are too numerous or unique to be anticipated by genetically coded plasticity. As a result, across a broad range of conditions, organisms are often capable of producing highly functional responses because their exploratory mechanisms confer the flexibility to render workable otherwise disruptive internal changes. As a consequence, exploratory mechanisms are tolerant of mutation, internal failure, environmental novelty, noise, errors, and injury (Gerhart and Kirschner, 1997; Kirschner and Gerhart, 1998, 2005). Within limits, they are self-correcting anatomically 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 and Kirschner, 1997).

CULTURAL EVOLVABILITY AND LEARNING

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, the long-term forecast that genes "provide" is based on what worked in the past. Except for microorganisms, genetic evolution is not usually fast enough to allow organisms to adjust to sudden or novel 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 environment now. That is where culture, and its attendant process, learning, come into play, especially with respect to humans (Potts, 1999).

One concept that is central to many studies of learning and behavior is the distinction between *individual learning* and *social learning* (Boyd and Richerson, 1985). We know humans are neither purely individual learners nor purely social learners, neither of which "can operate in isolation to produce the impressive array of cultural behaviors humans exhibit" (Eerkens and Lipo, 2007: 242). Rather, certain conditions, real or perceived, dictate which type of learning might be more useful in a particular situation (Mesoudi, 2011). The behavioral sciences tend to emphasize social learning, which is not surprising given the extraordinary ability humans have for substantially accumulating, and importantly, retaining adaptive socially learned information over generations (Tomasello et al., 1993; Tennie et al., 2009), but this focus overlooks the fact that whereas social learning spreads behaviors, it depends on individual learning to generate them in the first place. In other words, there needs to be at least a few "producers" to supply information to all the "scroungers" (Giraldeau and Caraco, 2000; Mesoudi, 2008).

Learning individually is a process in which agents use trial and error to modify existing behaviors or to try out novel behaviors for the first time. Exploratory mechanisms are relevant here because some animal learning—including human learning—operates on exploratory and selective principles. Agents learn about their world in multiple ways, but the primary mechanism by which they acquire behavior is "operant," also referred to as "instrumental," conditioning (Staddon, 2016). This type of trial-and-error learning occurs through reinforcement, in which the positive or negative experiences that follow their actions provide agents with a mechanism for the selection of appropriate behavior. Actions followed by pleasant consequences are repeated, whereas those followed by unpleasant consequences (e.g., punishment) are not.

In his classic study of animal behavior based on rewards and punishment—usually referred to as *operant conditioning*—B.F. Skinner (1938) stressed three general features of animal learning: (1) animals are frequently active, and hence are continuously emitting behavior; (2) emitted behaviors have consequences that influence the frequency with which they are repeated; and, (3) the effects of these consequences are influenced by the animal's motivational state and the environment. The first of these, though rarely emphasized, is important—learned behavior is often the result of an exploratory search conducted over multiple trials, through which individuals hone their behavior to exploit their environment. The initial exploratory component to learning generates behavioral variability, from among which the most effective actions are retained. Generating behavior in this way leads to extraordinary flexibility—agents can learn to produce a wide range of functional behaviors in even highly novel contexts. Learning is adaptive partly because evolution has granted agents the autonomy to seek out high-fitness behavioral outcomes and to forestall activities that might negatively impact their survival and reproduction (Pulliam and Dunford, 1980; Staddon, 2016).

As opposed to individual learning, social learning—that is, learning by observing or interacting with others (Heyes, 1994)—enables an agent to examine and filter the behaviors of others and adopt those that appear to have the highest payoffs (utility) (Rendell et al., 2010; Kline, 2015; O'Brien, 2019). Social learning is widespread among animals, including invertebrates (Avital and Jablonka, 2000; Hoppitt and Laland, 2013; Whitehead and Rendell, 2014; Laland, 2017; Whiten, 2017; Whiten et al., 2017; Aplin, 2019), and compared to individual learning alone, social learning is less costly in terms of time and/or energy (Morgan et al., 2011). Theoretical analyses and experimental studies show that social learning (sometimes in conjunction with individual learning) is more efficient—for example, at finding food or avoiding predation—than individual learning alone. That is because when agents learn socially, the aforementioned "exploratory search" is effectively expanded to encompass the trials and associated experiences of multiple individuals. This strategy allows one to filter behaviors and adopt those that have the highest payoff—or at least appear to. This applies to humans (Rendell et al., 2010) as well as other organisms (Hoppitt and Laland, 2013).

Agents—human and nonhuman—acquire socially learned knowledge through *emulation*—copying the result of an action sequence—and *imitation*—copying the form of an action (Whiten et al., 2009). Both have been identified in the archaeological record, including the Middle Stone Age record at the Early/Middle Stone Age site of Kathu Pan in the Northern Cape of South Africa (Wilkins, 2018). These and other forms of social learning open doors to dietary information, feeding techniques, predator recognition and avoidance methods, songs, calls, and mate-choice preference (Hoppitt and Laland, 2013; Whiten, 2017; Oudman et al., 2020). Learning from others is itself a set of competing strategies in that one might preferentially copy someone based on that individual's apparent skill level (copy those who are better at something than you are, copy good social learners, copy those who are successful, and so on), whereas others might base their decisions on social criteria (copy the majority, copy kin or friends, copy older individuals). Some researchers (e.g., Tennie et al., 2020) make a distinction between low-fidelity social learning, which supplements individual learning but may not involve reliable transmission, and high-fidelity social learning, including such things as imitation and teaching, which often does lead to reliable transmission. Tennie and colleagues argue that only high-fidelity social learning can support cumulative culture.

Although we embrace a broad definition of culture, and while we recognize that our position is not universal, with some preferring more stringent definitions that restrict culture to our own species (see chapters in Laland and Galef, 2009), our arguments about the contribution of "cultural" processes (broadly characterized) to evolvability apply to many animal species, irrespective of how they are labeled. Certainly, unique features of human culture allow for forms of adaptability that are rare or absent in other animal social learners, but regardless, social learning allows individuals to adjust their behavior to the social and physical environment, to accumulate knowledge, and to pass it across generations.

By copying others, agents acquire up-to-date and typically (but not always) positive adaptive knowledge.[1] This is why "culturally organized groups appear to solve adaptive problems more readily than individuals through the compounding value of social learning and cultural transmission in groups" (Waring and Wood, 2021: 1). There are numerous scientific reports of learned behaviors spreading through animal populations, some through transmission and some through low-fidelity copying. Familiar examples include food washing in macaques (Kawai, 1965), termiting in chimpanzees (Goodall, 1986), and the transmission of songs in birds and whales (Marler and Tamura, 1964; Whitehead and Rendell, 2014). These observations are bolstered by experimental demonstrations of social learning, including cross-fostering studies in great tits and blue tits, in which birds raised by the other species shift numerous aspects of their behavior toward that of their foster parent, including the height in trees at which they forage; choice of prey, calls, and songs; and mate choice—traits long assumed to be genetically specified (Slagsvold and Wiebe, 2007, 2011; Slagsvold et al., 2013). The point is, humans are far from alone in using learning and culture to meet challenges, although, again, there are clear differences. As a colleague of ours noted, "chimps, birds, and ants don't have electricity, nuclear warheads, and GPS systems (yet)."

Culturally acquired knowledge is highly adaptive because it skims off the best ideas from a pool of local individuals and refines them through a few generations of selection. As for genetic inheritance, here, too, there is a danger that environmental change will render that information obsolete. Many animals have evolved safeguards, such as the rapid abandonment of outdated or dysfunctional cultural knowledge. For example, red-winged blackbirds copy feeding conspecifics except when they exhibit an aversive reaction to the food (Mason and Reidinger, 1982), and insects and birds copy the nest-site decisions of successful but not unsuccessful individuals, be they of the same or different species (Sarin and Dukas, 2009; Seppänen et al., 2011). Although there is no guarantee that such safeguards will evolve and always work, particularly in humans, nonetheless that mix of recency and population-based reliability helps to ensure that cultural knowledge is typically productive (Richerson and Boyd, 2005).

THE ROLE OF CULTURE IN EVOLUTIONARY ADAPTATION

All culture-bearing animals become locally adapted through a combination of natural and cultural selection. In killer whales, for example, populations exhibit socially learned specializations on particular prey (e.g., fish, dolphins, and pinnipeds) that have favored population-specific morphology and digestion, known as "ecotypes" (Foote et al., 2016; Hoelzel and Moura, 2016). Here, socially learned dietary traditions have initiated and modified the selection of genes, leading to morphologies and physiologies that match the whales' learned habits.

In humans, the use of symbols and invention of language and writing substantially enhanced the volume and accuracy of culturally transmitted knowledge (Richerson and Boyd, 2005; Jablonka and Lamb, 2014; Laland, 2017; Kissel and Fuentes, 2021), not to mention the speed at which it can be transmitted. In an evolutionary short period of 50,000–200,000 years, humans spread from Africa around the globe (Stringer and Galway-Witham, 2018), experienced an ice age, witnessed rapid increases in population densities, domesticated hundreds of species of plants and animals, and, by keeping animals, experienced a new proximity to animal pathogens (Stringer and Andrews, 2005; O'Brien and Laland, 2012). Each of these events represented a rapid and major transformation in human selection pressures that resulted in substantive genetic change in human populations, and virtually all events have been self-inflicted, made possible through the evolvability conferred by culture and social learning (Laland et al., 2010).

Nowhere has gene–culture co-evolution happened faster than within societies that domesticated animals and plants, which substantially modified selection on alleles expressed in the ability of humans to process novel diets and, at least potentially, to resist inadvertently produced disease. Among the most familiar examples are the geographic distribution of two alleles—one providing an ability to tolerate lactose (Gerbault et al., 2011) and the other providing protection against the deadly disease malaria (Durham, 1991). These culturally induced disruptions of the ecosystem had recursive effects on the human genotype. In addition, agricultural practices led to greater consumption of starch, protein, lipids, alcohol, and phosphate, generating selection for alleles that metabolize these foods more efficiently (Laland et al., 2010)—a point supported by extensive gene–culture coevolutionary theory (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985).

Such examples reveal how culture commonly operates as a fast-response capability, through which diverse animals survive and adapt to novel, changing, and/or challenging conditions. Subsequently, the more slowly acting genetic system may stabilize culturally mediated evolutionary responses. Animal culture often buys time for the focal organisms to evolve complementary genetic adaptations. For example, killer whales have evolved population-specific morphology and digestion (Morin et al., 2010; Riesch et al., 2012; Foote et al., 2016), but that was only after cultural transmission allowed them to exploit fish, cetacean, or pinniped diets. Likewise, human populations possess digestive enzymes that allow them to break down dairy products, starch, and protein in their diets, but alleles enhancing these physiological capabilities spread only after cultural knowledge allowed human populations to exploit novel foods (Laland et al., 2010; O'Brien and Laland, 2012; Laland, 2017). Culture, then, can be thought of as the rapid-response team, with genes being the reinforcement.

Living organisms possess other systems that help them cope with environmental change. Developmental plasticity allows individual organisms to *update* their inherited genetic information and produce a phenotype suited to current conditions using cues extracted from the external environment (West-Eberhard, 2003; Moczek et al., 2011). Such systems are evolutionary adaptations that allow for fine-tuning of the phenotype (Sultan, 2016). However, it is misleading to characterize culture as no more than developmental (or phenotypic) plasticity, as culture possesses adaptive potentialities that extend beyond such fine-tuning. Culture is an information-gaining and sometimes adaptation-generating process.[2] Although commonly adaptive, developmental plasticity can be highly idiosyncratic and specific as developmental adjustments each rely on the environmental experiences of a single individual, at a particular time and place.

Culture, by contrast, is a population-based phenomenon, where pooling information allows the sharing of knowledge across individuals and the accumulation of wisdom over generations. In other words, the larger human groups became, the more information, including kinship information, could be stored in the collected minds of its individuals (Powell et al., 2009)—the adaptive memory of crowds (O'Brien and Bentley, 2023). Alternatively, the smaller groups became, the more likely knowledge would have been lost (Henrich, 2004). Cultural knowledge can be repeatedly refined and extended, to build understanding, behaviors, and artifacts with the design properties of adaptations. Most other forms of developmental plasticity rely on genetic evolution to change beyond their current sensitivity to the evolutionary-anticipated environment, and hence evolve comparatively slowly. In contrast, cultural information can be modified within biological generations, tested for functionality, and then rapidly disseminated.

There is another side to the adaptive memory of crowds. From the beginning, the human brain has been energetically expensive, primarily because it takes a lot of energy to "think." The modern brain makes up only two percent of human body weight, but it consumes about twenty percent of energy input (Raichle and Gusnard, 2002). Thus, there must be direct benefits from possessing a more-expensive brain, which ultimately translate into ecological, social, and cultural strategies for accruing energy more efficiently. The heavy metabolic and neurological costs associated with encephalization (Bednarik, 2014) may also help to explain a reported substantial reduction in endocranial volume 45,000–40,000 years ago, which led to a ten percent reduction in size by the start of the Neolithic period, some 12,000 years ago. This decrease might be accounted for by various means of storing memory outside the brain, including ornamentation and cave painting (Henshilwood et al., 2002, 2011; Brumm et al., 2021; Bacon et al., 2023)

The bottom line is this—once the shift to the symbolic information-processing mode occurred,

> “the metabolically expensive human brain found itself working on a new and different processing algorithm: one that was less dependent on the sheer volume of brain tissue than on the specific nature of the operations and connections within it. A more efficient algorithm may have permitted a reduction in the quantity of energy-hungry brain tissue, while simultaneously making possible a qualitative leap in processing power” (Tattersall 2017:8).

Thus, there may have been a feedback loop between an increase in social learning and a decrease in brain size. Speech, and later language, facilitated social learning, eventually leading to other means of learning such as outward signaling using personal ornamentation and painting information on cave walls. The emergence of this symbolic material culture represented

> “a threshold in the evolution of our species. Artifacts with a functional value that lies in the informational realm are proxies for the presence of language and, thus, of the fundamental aspects of human cognition as we know it” (Hoffman et al., 2018: 1).

CULTURE AND THE PACE OF EVOLUTIONARY CHANGE

The pace of evolutionary change experienced by our lineage is reported to have accelerated over time (Hawks et al., 2007), which is neither coincidental nor unconnected to our capacity for culture. Several theoretical studies have concluded that gene–culture co-evolution is typically faster than conventional biological evolution, in part because cultural evolution occurs at faster rates than biological evolution (Richerson and Boyd, 2005; Henrich, 2016; Laland, 2017). The contribution of gene–culture coevolution to our adaptive evolution was probably initially modest but grew over time, as our cultural capacity increased and our control of the environment went up incrementally (Laland, 2017).

Eventually, culture began to take over and rapidly provided our ancestors with food-procurement and survival behaviors, such as how to access nutrient-rich foods, build a fire, or make a weapon. Through culture, hominin populations were able to exploit their environments with greater efficiency. However, by changing their environments at accelerated rates, our ancestors increasingly set themselves, and their descendants, challenges to which they sometimes adapted biologically. The result was higher rates of morphological evolution in humans compared to other mammals, with human genetic evolution reported as accelerating more than a hundredfold over the last 40,000 years (Hawks et al., 2007; Cochran and Harpending, 2009). In the modern era, cultural evolution dominates almost completely. Cultural practices often set adaptive problems for humans but then, at least in the short-term, they solve them through further cultural activity, all before biological evolution gets moving.

IMPLICATIONS FOR THE FUTURE

Not all organisms are cultural, of course, but all possess some form of fast-response adaptive machinery. Which capacity organisms rely on to solve their adaptive challenges depends on numerous factors. Complex animals commonly respond to novel challenges through learning and have less need than many other organisms to adapt through the selection of epigenetic variation. In contrast, plants, being incapable of learning, are often forced to rely on epigenetic inheritance mechanisms to cope with novel circumstances such as drought or toxins (He and Li, 2018). In other instances, organisms adjust to change through the rapid adaptation of symbiotic microorganisms living in their guts and other parts of their bodies, which are passed across the generations in a variety of ways. For example, Neolithic dogs responded to a starch-rich diet by expanding symbiotic bacterial functionalities devoted to breaking down starch, thus allowing the dogs to extract energy from novel agricultural foods (Rampelli et al., 2021). Selection for an increase in copy number of the dogs’ own starch-digesting genes occurred only much later, probably thousands of years after the adoption of the novel diet. Thus, extragenetic inheritance (at least much of it) is best regarded not as noise, fine-tuning, or luxury “add ons” (Wray et al., 2014) but as essential tools for short-term adaptation.

Different inheritance pathways complement each other (Adrian-Kalchhauser et al., 2021), but it does not follow that epigenetic inheritance is under genetic control. Only a subset of epigenetic variation has been found to be tightly associated with genetic variation (Jablonka and Lamb, 2014; Bonduriansky and Day, 2018; Anastasiadi et al., 2021), and the same holds true for cultural variation (Durham, 1991; Whiten et al., 1999; Richerson and Boyd, 2005; Hoppitt and Laland, 2013; Laland, 2017). Tight genetic regulation of extragenetic inheritance would be maladaptive in rapidly changing conditions because genetic evolution is too slow to track that change. That is why culture has a degree of autonomy from genetics: The “leash” (Lumsden and Wilson, 1981) cannot be too tight, otherwise culture cannot do its evolutionary job.

The sheer potency of human culture has broad implications for evolvability. We rarely tie culture to these implications, at least not directly, but from its inception, our species has been transforming landscapes, in the process dramatically altering ecosystems and changing species compositions through a combination of environmental alteration, climate change, urbanization, pollution, habitat destruction, predation, competition, introductions, and extinctions (Boivin et al., 2016; Ellis, 2018; Kemp et al., 2020; Thompson et al., 2021). And this is occurring rapidly and in nonrandom ways, all of which destroy the engineering control webs that underlie ecosystems (Boogert et al., 2006; Schielke et al., 2012). Our global impact is now so devastating that scientists have marked it as an ongoing geological event, the Anthropocene, and speak of mass extinction (Ellis, 2018; Gibbard et al., 2022). However, it is not our rapid genetic change that is threatening the biosphere with extinction but rather our rapid cultural evolution and associated technological development—what we might term "runaway evolvability."

Other species may struggle, but, given that population growth rates are a standard measure of absolute fitness (Endler, 1986), our burgeoning population numbers imply that humanity adapts to the self-imposed changes in conditions with little trouble. That is because humans possess a uniquely powerful culture that both elicits environmental change *and* enables our rapid accommodation to it. Our ability to cause, and to survive, the Anthropocene both result directly from our extraordinary evolvability. That is not to suggest that cultural adaptations will always prove adaptive (Richerson and Boyd, 2005); in the longer-term, cultural innovations—for example, the use of fossil fuels—may have negative ramifications even for us. However, natural selection is famously "myopic," and traits need only confer short-term benefits to evolve.

That humans should rely on the rapid-response component of their evolvability to cope with changing conditions is, of course, hardly surprising. Perhaps less intuitive is the expectation that other species should rely on their own rapid-response capabilities to escape the dangers of anthropogenic change. However, a sizable fraction of other species, including primates (Fuentes and Hockings, 2010; Fuentes et al., 2016), are unable to cope with the serious transformations of their environment that human beings have imposed, and many have gone extinct before natural selection can craft new adaptations. Other species have evolved solutions through genetic change, which has led, for example, to slower growth in fishes, smaller tusks in elephants, and increased recombination rates and polyploidy in domesticated plants (Alberti, 2015; Zeder, 2017; Otto, 2018).

The process by which a population is saved from extinction through genetic evolution is known as "evolutionary rescue" (Carlson et al., 2014), but rescue can come through other ways as well (O'Dea et al., 2016; Feiner et al., 2021). Understanding the processes that lead to adaptation in fast-changing environments is of critical importance to attempts to conserve biodiversity, yet the role that extragenetic inheritance mechanisms play in that process is much neglected (O'Dea et al., 2016) because of the historical focus on slowly changing and slowly adapting genetic systems. This has misled many of us into thinking that genetic evolution is the only pathway out of trouble that organisms can take. It is not, and nor, we submit, is it the most likely pathway, except for microorganisms. All species must have a rapid-response capability of some form, be it through reliance on learning, epigenetics, symbionts, or some other mechanism. It is here, rather than through genetic evolution, that conservation and sustainability researchers should look for the immediate responses of most other organisms. Genetic change is likely to be secondary.

Researchers are starting to emphasize how epigenetic modifications in response to environmental change can generate novel phenotypic variation that can be subject to natural selection, resulting in an increase in the evolutionary potential of the population (O'Dea et al., 2016). For example, there is now good evidence—particularly in plants, insects, and nematodes—that the selection of epigenetic-mediated phenotypic variation can provide populations with the resilience to persist through periods of environmental change as well as to facilitate genetic adaptation over longer time frames—a phenomenon known as "epigenetic buffering" (Houri-Zeevi and Rechavi, 2017; Stajic and Jansen, 2021).

Other forms of extragenetic inheritance can play the same buffering role. Although researchers have thus far stopped short of describing the process of adaptation through the selection of extragenetic variation as a component of evolvability, that is a clear implication. Evidence is starting to emerge that many animals are learning socially to escape the impacts of climate change. For example, there is strong evidence that moose and bighorn sheep (Jesmer et al., 2018), as well as several large migratory species of birds such as geese, storks, and cranes (Sutherland, 1998; Oudman et al., 2020), are now adjusting their migration pathways and feeding and breeding site choices through social learning. Countless organisms have quickly modified their behavior to keep out of trouble—for example, commensals and inquilines that are able to thrive in an urban environment, or birds and animals that are able not only to avoid colliding with buildings or windfarms but to repopulate urban areas in light of substantial automobile noise abatement (Alberti, 2015; Zeder, 2017; Otto, 2018; Derryberry et al., 2020; Feiner et al., 2020)—and it is highly plausible that social learning is playing a central role in such adjustments.

There is another, more indirect route by which human culture has impacted our own and other species' evolvability. Controlled fire—"a breakthrough adaptation in human evolution" (Brown et al., 2009: 859)—began sometime between 1.5 million and 0.4 million years ago (Wrangham, 2009; Hlubik et al., 2019), becoming habitual around 350,000 years ago in Israel and the Levant (Schimelmitz et al., 2014). The significance of this is generally thought to relate to the invention of cooking, which allowed our ancestors to predigest their food and thereby extract more energy from their diets, but there is an alternative view that centers around evolvability:

> "The concept of a long prehistory of fire moves away from viewing technology as an endowment made possible by favorable genetic mutations and toward a more complex view that looks at the interplay between genetics and culture in driving hominin evolution" (Chazan, 2017: S357).

There are, however, other results of the invention of controlled fire that may ultimately prove far more profound, and they certainly play a significant role in human cultural evolvability. As Wiessner (2014) notes, fire altered anatomy, particularly brain size and gut volume; protected early humans from predators; and, provided a new context for social interaction when food was brought to a central site for cooking. Landscapes modified through burning (Bliege Bird et al., 2008), together with higher caloric returns from cooked foods, lowered both the costs of foraged foods and the costs of sharing. Finally, firelight altered circadian rhythms and extended the day (Burton, 2011), which freed time for social interaction that did not conflict with subsistence work.

Controlled fire also led directly to the large-scale burning of fossil fuels such as coal, gasoline, and oil to generate heat and light as well as to smelt iron, power combustion engines and turbines, fix nitrogen, and manufacture fertilizers (Judson, 2017). Our control of fire and associated activities released a vast bank of hitherto untapped energy stored deep in the ground into the biosphere. Although the energetic constraints on evolutionary change are rarely considered, it is a truism that populations cannot evolve without the energy to reproduce. Early anthropologists knew that, including White (1943), who saw energy capture as the driver of cultural evolution. This is an outdated notion, of course—that energy capture "allows" "an extraordinary flowering of culture" (Linton, 1938: 245)—but nonetheless human control of fire and exploitation of fossil fuels not just underpinned massive growth in human populations but in the entire biosphere (Judson, 2017). The use of fire and subsequent exploitation of this new energy supply was central to the origins of agriculture and triggered profound transformations in human life-history strategies, massive changes in diet, a shift from hunting and foraging to sedentary agricultural forms of subsistence, the products of which were far-higher crop yields; enormously larger human populations; massive populations of cows, pigs, dogs, and chickens; and exposures to new infectious burdens (O'Brien and Laland, 2012; Wells and Stock, 2020).

Moreover, human control of fire and the exploitation of hitherto untapped energy stores has had similar impacts on other species, changing ecological and social systems going back several hundred thousand years (Thompson et al., 2021). For example, the transport of fire from one region to another allowed Australian hunter–gather communities to increase resource productivity by promoting landscapes with diverse successional stages in which small game flourish, in the process triggering ecological cascades (Thompson et al., 2021). Controlled burning created legacy effects that increased over time, as revealed by the preference of contemporary hunter–gatherers to hunt and forage in regions with long histories of fire modification (Thompson et al., 2021). In more recent times, control of fire has provided much of the raw energy that fuels the current avalanche of evolutionary responses in animals, plants, and microorganisms to human activity.

The focus has been on how humans trigger evolutionary responses through modifying selection, but they have also indirectly provided the energy that underpins evolutionary change. The newly emerging food webs are ultimately powered by energy stores released through human niche construction. Disturbingly, if the construction of the biosphere has depended on repeated energy expansions (Judson, 2017), this implies that the vanishing of an energy source as we use up fossil fuels could cause a corresponding contraction in the biosphere and perhaps a dramatic reduction in global evolution rates. Recognizing the direct and indirect roles that cultural processes play in underpinning the evolvability of humans and other animals is not only central to developing a truer understanding of the evolution of our Pleistocene ancestors but might be critical to conservation and sustainability goals.

CONCLUSION

Culture can no longer be regarded as the province of humans, apes, or large-brained mammals but as widespread phenomena across the animal kingdom. This generality demands a rethink. Why did culture evolve? What job does it do in evolution? Irrespective of whether we are correct in our claim that culture evolved as a vehicle for evolutionary adaptation to rapid environmental change, there is now extensive evidence that culture commonly fulfills this function (Boyd and Richerson, 1985; Avital and Jablonka, 2000; Whiten, 2012, 2017; Hoppitt and Laland, 2013; Whitehead and Rendell, 2014; Laland, 2017; Aplin, 2019).

Few researchers, particularly biologists, can be unaware of the explosion of interest in epigenetic inheritance over recent decades, and huge literatures have also amassed on other aspects of extragenetic inheritance, including diverse parental effects, the inherited microbiome, and animal cultures (Jablonka and Lamb, 1995, 2014; Bonduriansky and Day, 2018; Danchin et al., 2019). It is now clear that natural selection operates on epigenetic and cultural variation, just as it does on genetic variation, although the roles that extragenetic inheritance plays in evolution are not restricted to being a target of selection (Shea et al., 2011). "Soft inheritance"—the view that heredity can be changed by an organism's experiences—has been tarred with a disreputable stain for over a century, but now its time has come (Jablonka and Lamb, 2014; Bonduriansky and Day, 2018).

In the light of the outpouring of new data on heredity, it is possible to understand that adaptation in biological systems arises through selection operating on different temporal scales and on diverse forms of inheritance extending beyond genes. Historically, evolutionary researchers have tended to focus on the slowly changing aspects of evolutionary adaptation and the most stable components of inheritance (genetic processes). However, any restriction of the definition of evolution to genetic change crudely carves in half the adaptive process, discarding much that is interesting and relevant. The time has come to recognize culture's credentials as a central component of animal evolvability.

ENDNOTES

[1] We say "but not always" because although cumulative culture allows members of a group to incorporate behavioral features that have positive utility, if the members read the social and/or physical environment incorrectly, are using outdated information, or the environment suddenly changes, the features can take on negative utility

(Castro and Toro, 2004: 10235). Enquist et al. (2007: 728) introduced the notion of a critical social learner, which "allows culture to be adaptive under most circumstances. Individuals adopting this strategy first try social learning and then resort to individual learning if the solution obtained by social learning proves unsatisfactory."

[2] Here we refer to a cultural adaptation, that is, a trait with design properties refined through a process of the selection of cultural variation.

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STATEMENT ON USE OF AI

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