

Human culture is uniquely open-ended rather than uniquely cumulative

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Theories of how humans came to be so ecologically dominant increasingly centre on the adaptive abilities of human culture and its capacity for cumulative change and high-fidelity transmission. Here we revisit this hypothesis by comparing human culture with animal cultures and cases of epigenetic inheritance and parental effects. We first conclude that cumulative change and high transmission fidelity are not unique to human culture as previously thought, and so they are unlikely to explain its adaptive qualities. We then evaluate the evidence for seven alternative explanations: the inheritance of acquired characters, the pathways of inheritance, the non-random generation of variation, the scope of heritable variation, effects on organismal fitness, effects on genetic fitness and effects on evolutionary dynamics. From these, we identify the open-ended scope of human cultural variation as a key, but generally neglected, phenomenon. We end by articulating a hypothesis for the cognitive basis of this open-endedness.

The difference between humans and other species has occupied human thought for millennia¹. Early arguments hinged on whether other animals (henceforth ‘animals’) possessed a soul, consciousness or rationality. Even after the acceptance of biological evolution, a clear basis for human uniqueness was not forthcoming. Darwin himself, writing for an audience sceptical of the continuity between human and animal minds, emphasized the similarities between human and animal cognition², arguing that “the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind”³. Since Darwin, various features of human cognition have been identified as unique to our species, including language, toolmaking, self-awareness and theory of mind. However, forms of these behaviours have been documented in other species, particularly primates, cetaceans and corvids^{4–11}.

Emphasis has recently shifted from specific cognitive abilities to a phenomenon they enable: culture¹². That is, human global success stems from adaptation through culture^{13,14}, whereas other dominant taxa, such as ants, spread by radiating into many thousands of genetically adapted species¹⁵. Genes remain critical to human adaptation, both by facilitating culture and by interacting with culture to reshape the genetic basis of human psychology¹⁶. However, this emphasis on culture raises the questions of what is special about human culture and how human cognition supports this. Two such hypotheses

have received considerable attention (although alternatives have been proposed^{17–22}). One is that human culture is particularly notable because, similar to genetic inheritance, it is cumulative^{23,24}, enabling it to accumulate adaptive knowledge over time. As a result, human cultures consist of highly complex and effective behaviours, whereas animal cultures, unable to accumulate, are much simpler. However, it remains unclear why human culture can accumulate. To this end, the second hypothesis identifies our capacity for stable, high-fidelity transmission as the enabling cognitive factor behind cumulative cultural change^{23,25}. For instance, imitation, teaching and language are all fidelity-enhancing traits present in humans but less so in other species¹¹, where the lower fidelity of cultural transmission causes innovations and refinements to be lost from the population, preventing accumulation (though see ref. 26). Cumulative cultural evolution and high-fidelity transmission thus form a pair, which explain the basis of human uniqueness.

Despite the success of these hypotheses, they are challenged by recent findings (as discussed below), and so alternative explanations are needed. The past few decades have also seen a growing body of evidence for forms of non-genetic inheritance, such as epigenetic inheritance and parental effects²⁷ (see Box 1 for an overview). These have a wide taxonomic distribution and mirror cultural inheritance in various ways; nonetheless, they have not enabled any species to

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BOX 1

Non-genetic inheritance

Darwin and other early evolutionists did not understand the mechanism of biological inheritance^{27,99,224}. Yet within a century, genetic inheritance had been discovered and came to be regarded as the sole inheritance system common to all life^{27,225–232}. This understanding of inheritance was hugely productive: a formal body of evolutionary theory based on genes emerged^{100,232–235} and the application of this theory across biological fields created the “Modern Synthesis”²³⁶. Later, inclusive fitness and kin selection were invoked to explain animal social behaviour, and this drove the development of the gene’s-eye view of evolution^{71,237–239}. The success of gene-based evolutionary theory has supported the centrality of genetic inheritance, and it remains at the heart of the contemporary understanding of evolution^{27,227,230,231}. Despite this success, non-genetic inheritance—inheritance defined as the transmission of a trait from one organism to another—has been known to science for decades^{27,142,240}. Here we focus on three broad categories: cultural inheritance, epigenetic inheritance and parental effects (for a broader discussion of the role of development in phenotypic evolution, see ref. 241).

Cultural inheritance is the transmission of behaviours and beliefs through interaction between individuals^{59,242}. Cultural inheritance has long been known to be ubiquitous in humans and was a key part of Darwin’s thinking in the *Descent of Man*³, but only in the past few decades has its presence in other species become appreciated. Although human-like culture is rare, cultural transmission is now known to be common across both vertebrates and invertebrates, with transmitted information including dietary and mating preferences, hunting and foraging techniques, and knowledge about resource locations and richness^{58,106,108,243–250}.

Epigenetic inheritance is the transmission of gene regulatory information across generations separately from the DNA

sequence^{89,251–253}. It involves multiple different biochemical mechanisms, including DNA methylation, cytoplasmic RNA and histone modification⁸⁹. It has been documented in vertebrates, invertebrates, fungi, plants and unicellular organisms^{142,254–259}. Although many epigenetic marks are reset every generation (particularly in mammals⁹²), the extent to which resetting occurs varies along the genome as well as among species^{253,260}. For instance, in mammals, paternal epigenetic marks are not passed on to the zygote, but maternal epigenetic marks often are²⁶¹, whereas the reverse is true in zebrafish^{262,263}. More broadly, epigenetic inheritance is relatively common in plants, fungi, nematodes and, particularly, unicellular organisms^{90,255,260}.

Parental effects include cases of non-genetic inheritance that do not have a basis in epigenetic or cultural mechanisms and typically occur between parents and their offspring¹⁰⁴. Examples include the inheritance of some food preferences via amniotic fluid or breast milk consumption or exposure to maternal faeces^{102,264}, and the inheritance of gut microbiome composition via the offspring’s passage through the vagina¹⁸³, all of which occur routinely across mammalian taxa.

The increasing recognition of these non-genetic modes of inheritance has generated debate over whether genetic inheritance is the primary mechanism of inheritance or one mechanism among many^{27,196,226}. It has also been suggested that non-genetic inheritance challenges the gene-based modern synthesis, and instead an “extended evolutionary synthesis”^{142,196,226,254,265–269} is needed. Such claims are controversial, and it is debated whether the success of gene-based evolutionary theory negates the need for such an extension^{196,241,270–275}.

achieve the same ecological dominance as humans. Thus, they offer another means to identify the basis of human uniqueness: whatever are the features of human culture that enabled our global dominance, they must be diminished not only in animal cultures but also in other forms of non-genetic inheritance.

Here we provide an analysis of the unique features of human culture through comparison with animal cultures and other forms of non-genetic inheritance. Our goal is to refine our knowledge of what makes human culture, and hence humans, so unusual. We first evaluate the importance of cumulative change and stable, high-fidelity transmission, and we conclude that the importance of both is challenged by recent results and other forms of inheritance. We then consider the inheritance of acquired characters, the pathways of inheritance, the non-random generation of variation and the scope of heritable variation. We separately consider effects on organismal fitness, genetic fitness and evolutionary dynamics (Boxes 2–4). Our analysis concludes that the most distinctive feature of human culture is its enormous scope for transmitting evolutionarily novel variation, whereas animal cultures, epigenetics and parental effects all have circumscribed domains in terms of the information they can carry (see Fig. 1 for a visual summary). Human culture is thus distinguished by its open-endedness. We argue that this is key to its adaptive quality and articulate a hypothesis for the neural and cognitive basis of this open-endedness.

Cumulative change

As with genetic change, or geological erosion and orogeny, human culture changes cumulatively. Indeed, the accumulation of human

culture is observable within a single lifetime and far outstrips the rate of genetic change²⁸, producing technologies beyond the means of any single individual, be they powerful computers²⁹ or systems of musical notation³⁰. Such accumulation is also manifested in language change, generating mutually unintelligible dialects in just a few centuries^{31–33}. Until relatively recently, cumulative cultural change was thought to be absent in animals^{23,34}. Although there was evidence of directionless vocal turnover, similar to human language, in both birds^{35–37} and whales^{38–41}, there were no known examples of an animal behaviour cumulatively increasing in its complexity or efficacy.

This has recently changed. The collection of additional data on animal vocalizations has made clear that they change cumulatively. For instance, long-term data collection shows that humpback whale songs oscillate in complexity⁴², and those of savannah sparrows have cumulatively increased in their salience⁴³. Indirect evidence for cumulative technological evolution is also known. For instance, regional designs of varying complexity were documented in the *Pandanus* leaf tools of the New Caledonian crow⁴⁴ and were hypothesized to represent a history of unobserved cumulative change⁴⁴. Similar observations have been made regarding termite fishing techniques across chimpanzee communities, including complex combinations of multiple elements within some groups⁴⁵. Human attempts at termite fishing and other chimpanzee behaviours have shown that they are challenging to re-invent, again consistent with the accumulation of innovations⁴⁶, although such evidence is highly indirect and potentially misleading.

Other studies have directly documented cumulative improvements in efficiency. Experimental work with homing pigeons found that

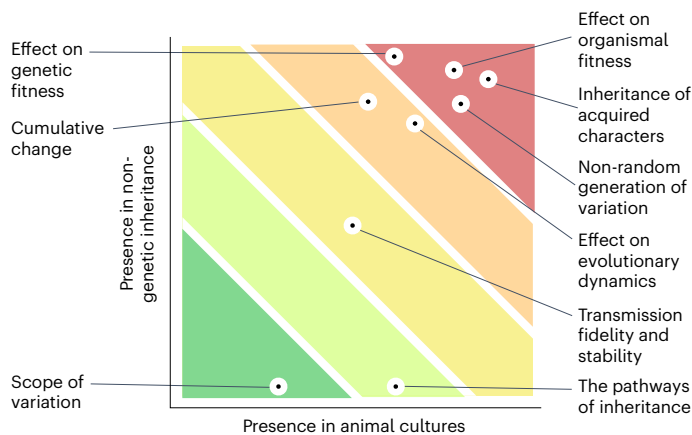


Fig. 1 | The scope of variation is human culture's most distinctive feature.

A visual summary of the conclusion of this review. Considered features are placed according to their presence in animal cultures (x axis; left indicates low, right indicates high) and non-genetic forms of inheritance (y axis; bottom indicates low, top indicates high). Features placed in the lower-left, green region are the most distinctive of human culture and are potential causes of its unique adaptive qualities. Features placed in the upper-right, red region are common to human culture, animal cultures and non-genetic modes of inheritance and so are unlikely to explain human uniqueness. Note that the placement of features is a subjective summary of our argument and is not explicitly quantified; rather, the purpose of this figure is to summarize our conclusions visually.

groups in which individuals were replaced over time converged on more efficient routes than those taken by lone or paired pigeons⁴⁷ (Fig. 2a). Similarly, translocated herds of ungulates cumulatively adjusted their migratory patterns to take advantage of the timing of plant growth⁴⁸. The relatively recent discoveries of these cases suggests that the historical focus on complexity over efficiency may have hindered the identification of cumulative cultural change in other species^{49–52}.

Epigenetic inheritance is also known to result in cumulative change. For example, the water nymph *Daphnia cucullata* can plastically develop an armoured helmet in response to cues of predation risk⁵³, making them harder to swallow (Fig. 2b). The helmet is both heritable and cumulative; offspring of mothers exposed to the cues develop larger helmets than those whose mothers were not exposed, and offspring whose mothers and grandmothers were exposed to the cues develop larger helmets still⁵³. The result is that, in the presence of predators, helmet size grows cumulatively over multiple generations.

Cumulative epigenetic inheritance enables the desert locust, *Schistocerca gregaria*, to switch between its green, solitary and yellow-and-black, gregarious morphs. The triggers are visual, olfactory and tactile indications of high population density that lead to changes in epigenetic gene regulation⁵⁴. Although single individuals can begin the transition from solitary to gregarious in just a few hours, the full suite of changes to morphology, neurochemistry and physiology develop cumulatively across multiple generations of high population density⁵⁵.

Parental effects can also accumulate, because they allow a parent's genes to influence their offspring. As offspring are likely to have similar genetic variants to their parents, this generates 'momentum' whereby the phenotypic effect of a novel mutation can grow cumulatively over generations⁵⁶. That parental effects can transmit the effects of genes across multiple generations has been documented in the herb *Campanulastrum americanum*, where seed size and life history traits, such as the number of days to germination, are affected by the maternal genotype in addition to the offspring plant's own genotype⁵⁷.

Transmission fidelity and stability

Human culture is commonly thought to involve uniquely high-fidelity transmission^{16,23,25,34}, which facilitates the accumulation of complex

BOX 2

Non-genetic inheritance and organismal fitness

Human cultural traits can be associated with variation in fitness. Consider, for example, the belief that children can have multiple fathers (partible paternity), which is common in several South American societies. Children with multiple 'fathers' receive more food provisioning and have higher chances of survival to reproductive age than children with only one recognized father^{276,277}. Proponents of the 'cultural niche' theory have argued that culture is so strongly associated with fitness that humans cannot survive without it^{13,147,195}. A recent case illustrates this vividly: a group of four children (one of whom was an infant) survived for 40 days in the Colombian Amazon by relying on traditional knowledge after a plane crash. As members of the Indigenous Huitoto group, they had been taught how to find food, construct shelter and avoid danger in the Amazon. Without this knowledge they would almost certainly have perished.

Human culture is not unique in its fitness effects, however²⁴¹. For example, resistance to herbivory in the wild radish (*Raphanus raphanistrum*) is epigenetically inherited^{53,197,278}. Plants attacked by caterpillars increase the quantities of chemical repellents in newly formed leaves, deterring herbivores, which enables them to produce a greater number of seeds, thus increasing their fitness. Moreover, the offspring of attacked plants also show elevated defences (in terms of repulsive chemicals as well as the number of trichomes per leaf), and caterpillars that feed on them grow more slowly^{53,197,278}. Thus, the fitness of wild radish seedlings is affected by epigenetically inherited factors and not just by their genome and environment.

An example of parental effects affecting organismal fitness involves telomere length²⁷⁹. Telomeres are highly conserved repetitive sequences of DNA at the ends of chromosomes. They protect chromosomes, are involved in organismal ageing and so are likely to have strong fitness consequences. Variation in telomere length is known to be highly heritable, with non-genetic factors passed on via the mother explaining ~45% of the variation²⁷⁹. Another example, in mice, involves differences in microbiota that were observed to have effects on the levels of immunoglobulin A—an antibody critical to mucosal immunity—indicating important effects on fitness¹²².

Culturally transmitted traits also have fitness effects in non-human taxa. Many such behaviours in animals involve food, such as seed extraction in capuchins¹⁸⁵. Given the importance of foraging to survival, these behaviours are likely to have fitness consequences. Elsewhere, the failure of male regent honeyeaters to culturally inherit their species-typical song was associated with lower fitness because song is used to attract a mate²⁸⁰. More generally, increasing evidence suggests that socially inherited information has major effects on species viability, with implications for how species adapt to anthropogenic environments and conservation^{281,282}.

bodies of knowledge. One hypothesis posits that humans are uniquely capable of imitation, the ability to copy actions, whereas other animals are limited to simpler forms of learning^{34,58,59}. Another hypothesis is that humans are uniquely capable of transmitting know-how, the knowledge of how to do something, whereas other animals only transmit knowledge of where to be and what objects to interact with^{60–62}. Despite many

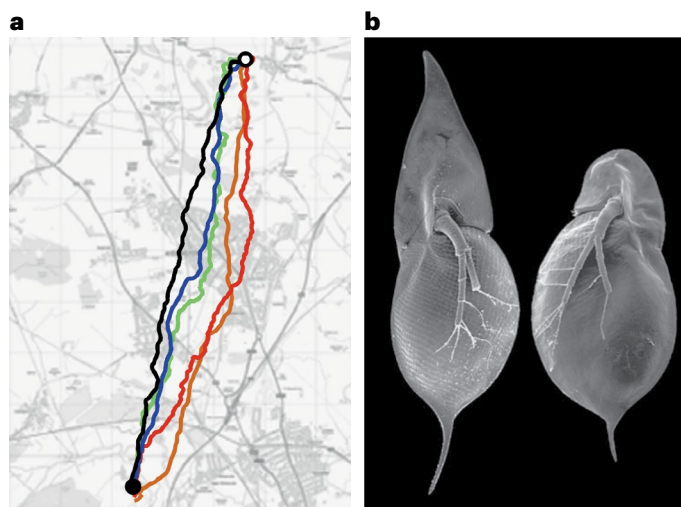


Fig. 2 | Examples of cumulative change beyond human culture. a, The cumulative improvement of route efficiency by groups of homing pigeons. The routes, from initial and inefficient to eventual and efficient, are orange, red, green, blue and black. **b,** Scanning electron micrographs of *Daphnia cucullata* with and without an armoured helmet. The epigenetic development of the helmet occurs over multiple generations. Images reproduced with permission from: **a**, ref. 47, Springer Nature Limited, map image: OS data © Crown copyright and database right (2017); **b**, ref. 53, Springer Nature Limited.

experiments, the limits of animal transmission remain unclear, and these hypotheses are contested⁴⁶. Indeed, recent studies suggest that animals can in fact socially transmit know-how; both chimpanzees^{63,64} and bees⁶⁵ are capable of learning from conspecifics how to operate puzzle boxes that they are unable to solve themselves⁶⁶ (though see refs. 67,68).

Another approach is to measure transmission stability⁴⁶. The stability of genes, which have been characterized as “replicators” and “immortal”^{69,70}, is argued to be central to their evolutionary importance⁷¹. Moreover, studying stability can identify the fidelity of cultural transmission, even if its psychological basis remains unclear. Such studies can also use data on cultural traditions in wild animal populations and permit comparisons across modes of inheritance despite the mechanistic differences.

Many human cultural practices endure (with various degrees of change) for thousands of years. For instance, a phylogenetic analysis of Indo-European folktales found that some originated over 5,000 years ago in the Bronze Age^{72,73}. Similarly, a study of 172 Native American societies found that many practices, such as political or kinship systems, are better predicted by cultural history than by local ecological conditions⁷⁴. The stability of human culture may be due to psychological biases such as conformist transmission⁷⁵. However, although evidence for conformist transmission has been documented^{76,77}, recent theory suggests that it cannot reliably stabilize traditions^{78–81}.

Animal cultures can also be highly persistent. For instance, song syllables in the swamp sparrow are stable enough to last for many centuries⁸². Among chimpanzees, an analysis of long-term data showed that group-specific differences in grooming postures are stable for at least 12 years, even in the face of changes in group composition⁸³. Similarly, a study of meerkats found that troops maintained different wake-up times for at least a decade, despite group turnover and overlapping ranges⁸⁴. Removal and replacement experiments in the bluehead wrasse, *Thalassoma bifasciatum*, have demonstrated that mating sites persist as traditions even as the environment changes to favour other sites^{85,86}. Finally, some animal traditions, particularly primate tool use, leave an archaeological record⁸⁷, and evidence extends chimpanzee nut cracking to at least 4,300 years ago⁸⁸.

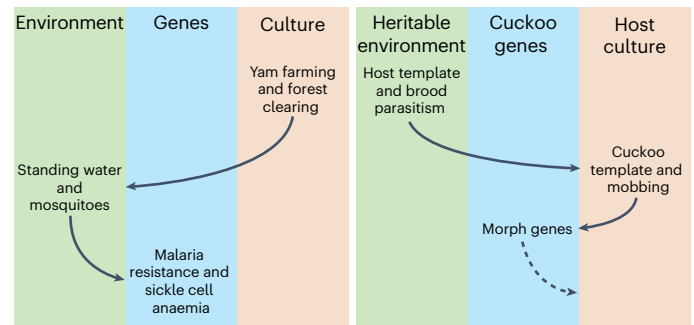


Fig. 3 | Two cases of interactions between genetic evolution and other forms of inheritance. The arrows represent causal influence. Left, the evolution of malaria resistance in humans. The cultural practice of yam farming caused the appearance of standing water and mosquitoes, which generated selection that drove the spread of malarial resistance, but also an increased risk of sickle-cell anaemia²²³. Right, cuckoo–host coevolution. Cuckoos inherit their host template by imprinting on their natal environment. Hosts respond to parasitism by mobbing cuckoos, and the hosts’ cuckoo template is culturally inherited. This generates selection that drives the evolution of different cuckoo morphs. The genetic cuckoo morphs and cultural host mobbing templates continue to coevolve (as indicated by the dashed arrow). See Box 3 for further discussion.

These cases may appear to fall short of the stability of human culture. However, animal studies tend to use more conservative definitions of stability. For instance, the ancient folktales have changed so dramatically as to be unrecognizable to a regular reader, and only through sophisticated phylogenetic methods can such stability be identified^{72,73}. Meanwhile, animal studies focus on cases where behaviours are transmitted with minimal change.

The stability of epigenetic inheritance varies greatly across cases. One mechanism of epigenetic inheritance is the addition of methyl groups to DNA, which alters gene expression and can be transmitted to offspring⁸⁹. It has been found that half of methylable DNA sites in plants lost their methylation within five generations^{90,91}. Similarly, in mammals, most epigenetic marks are reset every generation⁹². However, such epigenetic resetting may be an evolved policy given the involvement of epigenetics in organismal development, and instability may not be inevitable. For instance, epigenetic marks affecting eye colour in *Drosophila* were found to be stable across 50 generations—the full duration of the study⁹³. Similarly, a study of the epigenetic inheritance of preference for an odorant by *Caenorhabditis elegans* found that transmission continued for 40 generations—again, the full duration of the study⁹⁴. Notably, multiple epigenetic mechanisms exist⁹⁵, and stability arose only if five successive generations were consistently exposed to the odorant⁹⁴. A study of the parasitic flatworm *Schistosoma mansoni* also found differential stability of epigenetic marks depending on how they were induced⁹⁶. This variability has led to the distinction between short-lived “intergenerational epigenetic inheritance” and longer-lasting “transgenerational epigenetic inheritance”⁸⁹.

Parental effects can also be long lasting. An extreme case is the inheritance of domesticated fungus among leafcutter ants. Newly hatched queens take a small amount of fungus from their maternal nest and carry it in their infrabuccal pocket as they found a new colony⁹⁷. Genetic analyses of the fungus suggest that some fungal lineages have been genetically isolated from wild populations, and therefore continually transmitted by ants, for millions of years⁹⁸.

Alternative hypotheses for the uniqueness of human culture

The above evidence suggests that multigenerational accumulation and stability, often argued to be unique to human culture and responsible for our ecological success, are in fact common to human culture,

BOX 3

Non-genetic inheritance and genotype fitness

In addition to changing fitness at the level of an organism (Box 2), human culture can affect the fitness of specific genotypes. This can result in genetic change driven by cultural factors, referred to as gene–culture coevolution^{13,16,223,243,283,284}. One example is the genetic evolution of risk factors for sickle-cell anaemia in humans following the cultural evolution of forest clearing and yam cultivation (Fig. 3). In this case, the culturally transmitted practice of yam farming, which involves clearing areas of forest, led to standing bodies of water following rainfall, which became breeding grounds for mosquitoes that transmit malaria. This increased the prevalence of malaria and, in turn, increased the fitness of heterozygote individuals with the *HbS* allele, who have resistance to the malarial pathogen, while *HbS* homozygote individuals suffer from anaemia²²³.

Interactions between genetic and cultural evolution are not limited to humans¹⁰. For instance, culturally inherited mate-choice preferences can change the relationship between male quality and mating success²⁸⁵ which alters sexual selection and produces new dynamics influenced by culturally transmitted preferences^{286,287}. The cultural inheritance of birdsong alters the dynamics of genotypes that influence song acquisition and preference^{288,289}. It can also lead to the evolution of brood parasitism and facilitate speciation^{290,291}. Finally, theory suggests that the social transmission of prey recognition among predators greatly facilitates the evolution of aposematism by accelerating the rate at which predators learn to avoid unpalatable prey²⁹². This conclusion is supported by data from blue tits and great tits; in these birds, the cultural inheritance of prey recognition increased the fitness of bright warning colorations in unpalatable prey species²⁹³.

Similar effects are seen for other modes of inheritance as well. The interactions between cuckoos—parasitic birds that lay their eggs in nests of other species—and their hosts is a particularly elaborate example of how parental effects can change the fitness of genotypes (Fig. 3). Cuckoo host preference is heritable because young cuckoos

imprint on their natal environment and, as adults, use this to guide their search for host nests²⁹⁴. As a result, although the territories of female cuckoos include different possible hosts, matrilineal maintain distinct preferences for a specific habitat²⁹⁵ and host species²⁹⁶. Host parents will mob (that is, attack) adult cuckoos to deter parasitism²⁹⁷, and to avoid mobbing, cuckoo species have evolved different morphs: a rufous morph and a grey morph that resembles a sparrowhawk²⁹⁸. To effectively target mobbing, hosts culturally inherit their cuckoo template by watching the mobbing behaviour of conspecifics, allowing them to strategically defend against the more prevalent local cuckoo morph²⁴⁷. In turn, this creates strong balancing selection on the genotypes that contribute to the cuckoo morph²⁴⁷. The fitness of different cuckoo genotypes thus depends on their parentally transmitted host preference and the culturally inherited cuckoo template of the hosts.

Another example concerns maternally inherited cytoplasmic genes, which reside outside of the cell nucleus and distort sex ratios in many species of plants and invertebrates²⁹⁹. In some cases, the sources of the cytoplasmic genes are bacteria that enter cells and are then passed on to offspring in the cytoplasm. As they cannot be passed on by males (who do not contribute cytoplasm to the offspring), the bacterial DNA has evolved to kill male offspring^{299,300}. The cytoplasmic genes increase the evolutionary fitness of female offspring (and surviving male offspring) by increasing access to resources³⁰¹ and reducing crowding, or indirectly by reducing inbreeding³⁰².

Non-genetic forms of inheritance can also render fitness-relevant genetic variation fitness-neutral. For instance, Furrow and Feldman³⁰³ considered a population evolving in a fluctuating environment, into which heritable epigenetic regulation of the genome was allowed to invade. They showed that epigenetic regulation can evolve and even replace genetic transmission as the means of evolution. Having been made redundant, genetic variants that once followed environmental states instead reached fixation.

animal culture, epigenetic inheritance and parental effects. Although cumulative changes in animal cultures may often emphasize efficiency rather than complexity, this is not true for epigenetic inheritance and parental effects. In addition, human culture may not be more stable than animal cultures, and the stability of epigenetic inheritance is probably an evolvable property. Collectively, this evidence suggests that the key to human uniqueness lies elsewhere, and we now review four alternative explanations: the inheritance of acquired characters, the pathways of inheritance, the non-random generation of variation and the scope of heritable variation. We consider three additional phenomena in Boxes 2–4: effects on organismal fitness, genetic fitness and evolutionary dynamics.

The inheritance of acquired characters

The immutability of the germ line was a key discovery in modern evolutionary theory, creating a distinction between the heritable genotype and the plastic phenotype^{99–101}. Human culture breaks this dichotomy, being both heritable and plastic; nonetheless, this does not distinguish human culture from other forms of non-genetic inheritance. For instance, the epigenetic inheritance of olfactory preference in *C. elegans*, mentioned above, starts with the first generation of individuals acquiring the preference during their lifetime⁹⁴. Parental effects also allow the inheritance of acquired characters—for example, in rabbits’

inheritance of food preferences via exposure to maternal faeces¹⁰². The food preferences of the mother reflect both inherited influences and responses to food sources she encountered in her lifetime. Also, some female birds place antibodies in their egg yolks, thereby transmitting pathogen resistance to their offspring¹⁰³. These antibodies originate in the mother’s acquired phenotype following pathogen exposure, but they are nonetheless heritable^{104,105}.

The inheritance of acquired characters is also common in animal cultures. For example, female *Drosophila melanogaster* copy the mate choices of other females¹⁰⁶, and demonstrator flies can even induce a preference for low-quality males¹⁰⁶, a phenomenon also observed in the lekking sage grouse *Centrocercus urophasianus*¹⁰⁷. Mate-choice copying has also been shown in fish^{108–110}, birds^{111–113} and rats¹¹⁴. The inheritance of acquired food preferences has been experimentally documented in vervet monkeys, where whole groups learned to eat food of a particular colour and this preference was continued by their offspring, even though alternative coloured foods were available¹¹⁵.

The pathways of inheritance

Genetic material is typically passed vertically, from parents to offspring, although horizontal transmission between individuals of the same generation may occur^{116,117}. However, human cultural transmission is routinely horizontal, oblique (from older individuals other than

BOX 4

Non-genetic inheritance and evolutionary dynamics

Human cultural transmission leads to much faster phenotypic evolution than would be possible under purely genetic evolution^{28,243}. One way it can do this is by allowing heritable phenotypic change to occur without genetic change or even reproduction: cultural practices can be altered through experience and subsequently propagated via horizontal/oblique transmission (see ‘The inheritance of acquired characters’ and ‘The pathways of inheritance’). Indeed, one of the leading explanations for the evolution of human culture is its ability to produce more rapid adaptation than genetic evolution³⁰⁴. There are extensive data showing rapid behavioural, linguistic, cognitive and technological change in humans resulting from culturally transmitted information, with no compelling evidence for causally relevant genetic change, via either the DNA sequence or its expression^{14,305}. However, the rapid spread of behaviours via cultural transmission is not restricted to humans, and the diffusion of novel behaviour patterns, related to foraging, predator identity and evasion, mate choice, and a variety of other functions, is widespread in animals^{58,245}. For instance, lobtail fishing in whales was first observed in 1980, but just 20 years later it was being performed by a third of the humpback population¹²⁴.

Even when evolution involves genetic change, its rate can be increased by cultural inheritance, both in humans and in other species¹⁰. To illustrate, consider the case where selection on a gene is a co-evolutionary response to a culturally inherited trait. Because cultural traits can spread quickly, they can become widespread while a genetic response has barely begun. As a result, selection on genetic variation can be extremely strong and accelerate the spread of a genetic change. This supports the argument that culture has ‘ramped up’ human evolution³⁰⁶, with a large number of human genes related to cultural practices (such as dietary choices, cooking, farming, large-scale group living and migration) showing

evidence of having been under strong selection over the past 100,000 years²⁸⁴.

The inclusion of parental effects in evolutionary models also produces more rapid phenotypic change than would be predicted by purely genetic models⁵⁶. This occurs for two reasons: (1) parental effects allow the transmission of some acquired characters, which both increases the heritable variation available for selection to act on and, where this variation is non-random, drives populations in a particular direction; and (2) parental effects allow genetic change to have a cumulative effect over time, so phenotypic change can continue for multiple generations following a single genetic change. Supporting the predictions of these models, a study comparing the fit of the purely genetic breeder’s equation with models including parental effects to the evolution of *Campanulastrum americanum* under artificial selection found that the models including parental effects enabled much better predictions of the rate of phenotypic evolution than the standard breeder’s equation³⁰⁷.

Similar results hold true for epigenetic inheritance. For instance, theory suggests that epigenetic adaptation can displace genetic adaptation, precisely because the biased variation it produces allows more rapid adaptation than does genetic change^{303,308}. Such rapid epigenetic change can be observed in transitions between the solitary and gregarious morphs of the desert locust, *Schistocerca gregaria*. Single individuals can initiate the transition via plasticity, and behavioural changes appear in just a few hours. However, the full suite of changes, including changes in morphology, neurochemistry and physiology, requires multiple generations⁵⁵ and relies on changes to heritable epigenetic factors⁵⁴. In this case, the epigenetic inheritance of biased variation allows complex morph transitions to occur much faster than under genetic evolution, and beyond the scope of individual plasticity.

parents) or reversed (from offspring to parents). For example, knowledge of how to use local plants for food or medicine among the Tsimané of Bolivia is primarily obliquely transmitted¹¹⁸, and singing and dancing skills in the Aka of the Central African Republic and Republic of Congo exhibit horizontal transmission¹¹⁹, as do textile-making techniques and designs among Iranian tribal groups¹²⁰.

By virtue of their relationship with genetic transmission, epigenetic inheritance and parental effects are constrained to be mostly vertical. However, there are exceptions. For instance, body size in the fly *Telostylinus angusticollis* is influenced by non-genetic factors in semen that persist within the bodies of females and affect offspring sired by subsequent (that is, different) males, a phenomenon known as telegony¹²¹. In mice, the gut microbiome is typically transmitted via vertical parental effects, but horizontal transmission can occur via co-housing¹²².

As with human culture, non-vertical transmission is a feature of animal cultures. For instance, by observing conspecifics, archer fish socially acquire the ability to shoot down fast-moving, flying insects with jets of water propelled from their mouth¹²³. The cumulative cultural evolution of effective ungulate migration routes (see ‘Cumulative change’) involves mass horizontal transmission across entire herds⁴⁸. Wild humpback whales socially learn the lobtail feeding technique¹²⁴, but maternal behaviour does not enhance transmission, suggesting transmission is horizontal. Indeed, humpback whales do not begin lobtail feeding until after weaning, when they no longer preferentially associate with their mothers. Finally, ecological modifications can facilitate broad-ranging cultural inheritance. For instance, many male

fishes build nests, and females’ choice of nest in which to lay their eggs is influenced by the eggs of other females already in the nest, with popular nests becoming increasingly successful^{125–127}.

Despite these similarities, human culture may make unusual use of transmission pathways at larger scales. For instance, in many species, mother–offspring vertical transmission will be promoted by limited positive interactions with other individuals. This has been documented in primates¹²⁸, including the transmission along wild chimpanzee matrilineal lines of moss-sponging¹²⁹. Human societies, by contrast, have different structures, including positive between-group interactions, that facilitate intergroup cultural transmission^{130,131}. These extended networks appear to be critical to cultural adaptation¹³², with larger populations supporting more complex culture^{133–135} and partially connected networks often outperforming fully connected networks^{136,137}. Nonetheless, animal groups vary in size, yet similar patterns have not been reported. Some evidence suggests that group size correlates with cultural repertoire size in chimpanzees¹³⁸. However, this study only counted females, who migrate between groups, thereby shuffling regional practices and inflating cultural repertoire sizes. Moreover, it did not consider Ngogo, the largest known chimpanzee group, which nonetheless has a small cultural repertoire¹³⁹. It is thus unclear whether intra- and intergroup transmission networks constrain animal cultures.

The non-random generation of variation

Whether heritable variation was random was an important question in Darwin’s time⁹⁹. In particular, theories of orthogenesis argued that

internal factors drove species in particular directions, leading ultimately to their extinction¹⁴⁰. Although it is now understood that genetic mutation is largely random (though see refs. 141,142), this is not the case for human culture, where variants are generated through invention, with organisms drawing on their prior experience to develop effective ways to deal with their environments^{143–145}. For instance, King Sejong the Great of Korea, having observed the difficulties of writing Korean in the logographic Hanja derived from Chinese characters, designed a new writing system, Hangul, in 1443¹⁴⁶. Hangul, which is much easier to learn than Hanja and has been argued to be the most logical of all writing systems, became the official script of the Korean language in the late nineteenth century.

Despite such cases, the cultural niche theory argues that much of human cultural variation is generated randomly¹⁴⁷, with individuals typically only partially understanding the cultural traits they rely on. As a consequence, cultural adaptation arises from selective processes, such as the selective copying of successful individuals^{76,148–151} or cultural group selection^{13,152}. In support of this, interviews with Hadza bowyers suggest they have only partial knowledge of the mechanics governing bow function and design¹⁵³. Similarly, in an experiment where participants were asked to place weights on a wheel to maximize its speed down a ramp, causal understanding did not aid the evolution of effective designs¹⁵⁴. Nonetheless, in both cases individuals did have some knowledge of the task at hand and used this to guide decisions, albeit in imperfect ways. Moreover, other experiments, some using the same tasks, suggest that causal understanding is involved in the cumulative evolution of effective solutions^{18,19,155}. Human culture thus probably reflects a combination of random guesses, exploratory trial-and-error and theory-driven design.

Non-random cultural variation has also been found in other species. For instance, long-term observations of wild chimpanzees have revealed many instances of adaptive innovation¹⁵⁶. For example, the use of leaf sponges to collect mineral-rich water is common in chimpanzees¹⁵⁷, but in Budongo Forest, Uganda, the discovery of a new watering hole led to two individuals inventing moss-sponging¹⁵⁸, a more effective technique¹⁵⁹. This innovation later spread through the group via social learning and has since persisted^{129,158}. Random cultural variation has also been documented in animals—for instance, in corvid species in the Aesop's Fable paradigm in which rocks must be dropped into water to raise the water level and retrieve a floating worm¹⁶⁰. Thus, animal cultural variation, similar to human cultural variation, can reflect a mix of insight and trial-and-error.

Epigenetic inheritance and parental effects are also associated with non-random variation. For example, the water nymph *Daphnia cucullata* develops armoured helmets (see 'Cumulative change') as a non-random response to chemical cues released by conspecifics that indicate the presence of predators^{53,161}. Parental effects can also generate non-random variation, such as when maternal antibodies are transmitted via the egg yolk¹⁰³; the antibodies are not acquired at random but are present because the parent encountered a relevant pathogen. Indeed, the adaptive value of these non-genetic inheritance systems is due to their ability to transmit information corresponding to specific environmental features, a necessarily non-random phenomenon.

The scope of heritable variation

There seems to be little limit on what can be acquired and transmitted in human culture. From complex technologies and epic poems to geographical knowledge and codes of etiquette, human culture contains it all. This open-endedness greatly facilitated the geographic expansion of our species. For instance, humans relied on novel cultural practices to spread from Africa into the Arctic Circle in just a few tens of thousands of years, and with little genetic change^{162,163}. Cultural adaptations among historical Netsilik Inuit populations included making harpoons and leisters from bone, horn and antler; making warm and waterproof clothing from caribou and seal skin; and detailed knowledge of snow

and ice¹⁶⁴. We continue to see open-endedness in the modern era, with the dramatic effects of industrialization, electricity and computers. These changes have sometimes confronted biological constraints, such as when the cultural evolution of sea voyaging exposed the human inability to synthesize ascorbic acid (vitamin C), leading to increased scurvy^{165,166}. Nonetheless, such obstacles have rarely been insurmountable, and in the case of scurvy, citrus juice was discovered to be an effective remedy. Currently, bionic prosthetic limbs are being used to restore missing limbs and augment individuals with additional fingers or arms¹⁶⁷. Although humans have not evolved a third arm, we are nonetheless sufficiently flexible to learn to use one.

Despite this flexibility, there are detectable constraints that shape human culture. For example, languages become increasingly regular over time^{168,169}. Such phenomena have been documented across tasks in laboratory experiments^{170–173}, where they are described as inductive biases^{174,175}. However, although these biases are detectable, they are not strong enough to prevent humans from engaging in highly unintuitive behaviours. For instance, in an experimental study of the cultural evolution of sorting algorithms, payoff-biased copying overwhelmed inductive biases and facilitated the spread of unintuitive solutions such as 'gnome sorting'¹⁷⁶, in which a two-item sub-list is first sorted, and the remaining items are then sequentially sorted into it. Thus, although the scope of human culture may not be truly limitless, the range of variation that can be transmitted is exceptionally broad.

Compared with human cultural variation, the scope of epigenetically heritable variation and parental effects is greatly circumscribed²⁷. For instance, epigenetic changes can allow *Daphnia cucullata* to develop an armoured helmet⁵³, but other defences are not possible through epigenetic change alone. This is because the effects of epigenetic marks depend on available genetic variation, with epigenetic factors regulating the expression of existing genes. Instances of novel phenotypes resulting from environmentally induced epigenetic changes are known and are commonly referred to as cryptic genetic variation (that is, genetic variation that was already present but not expressed in the phenotype¹⁷⁷). Examples include Waddington's experimental study of *Drosophila melanogaster*, in which embryonic heat shocks led to the development of crossveinless wings¹⁷⁸. Other studies have found cryptic genetic variation in scutellar bristle number and photoreceptor patterning¹⁷⁷. Thus, although epigenetic plasticity can produce novelties, and this is of evolutionary importance^{179–182}, such novelties are typically rather modest adjustments of existing phenotypes and not the radically unprecedented behaviours that characterize human culture. Indeed, relative to epigenetically mediated phenotypic plasticity, learned behaviour is sometimes referred to as hyperplastic¹⁸¹.

Similar constraints to those of epigenetic inheritance exist in parental effects. For instance, although the immune system and microbiome can flexibly respond to environmental conditions and these responses are heritable^{103,183}, this kind of inheritance is limited to phenotypic effects that can result from the information stored in the immune system and microbiome. These systems are thus open-ended only within a relatively circumscribed domain. Other cases of parental effects, similar to epigenetic inheritance, are limited by their close relationships with available genetic material, such as where parental effects amplify the effect of a mutation¹⁰⁴.

Even as a more detailed appreciation of animal cultures has developed, it is clear that they do not have the same scope as human culture. For instance, animal cultures are dominated by behaviours related to food and its extraction, such as the transmission of food preferences in rats¹⁸⁴, seed extraction in capuchins¹⁸⁵, lobtail feeding in humpback whales¹²⁴ and termite fishing in chimpanzees⁴⁵. By contrast, the contents of human cultures are more diverse, including moralized norms, rules and rituals that regulate behaviour, often in arbitrary ways, along with punishments for rule breakers¹⁸⁶. Animal cultures do have some arbitrary traditions, including hand-clasp grooming in chimpanzees⁸³ and eye-poking in capuchins¹⁸⁷. Communication

systems are another example; the specific sounds or gestures do not matter provided their meaning is shared. Although evidence for vocal or gestural learning in primates is limited^{188,189}, it has been documented in some mammals and birds^{190,191}, suggesting that their communication systems are group-wide cultural traits. Moreover, the fact that bird and whale vocalizations can cumulatively evolve^{42,43} indicates a somewhat open-ended system. However, similar to the immune system yet unlike human culture, this is constrained to a specific domain. This domain specificity may reflect that these behaviours (communication and grooming) involve the direct coordination of individuals and can be acquired through repeated interactions¹⁸⁸, without the need for moralized norms or punishment of deviants.

Another test of the scope of animal culture involves raising an animal among humans and observing how much of human culture they can acquire. Many such studies were conducted in the latter half of the twentieth century, including attempts to teach chimpanzees a human language^{192–194}. Although it was found that many species can learn to use a few tens of symbols to communicate basic goals and to respond to simple requests, the results fall far short of a typical human language, lacking syntax and grammar among many other features¹¹. Thus, although animal cultures, along with epigenetic inheritance and parental effects, allow the inheritance of phenotypic variation, they are constrained in a way that human cultures are not.

Discussion

We have reviewed a wide range of factors to identify how human culture differs from animal cultures and from other modes of non-genetic inheritance. Specifically, we first argued that cumulative change and transmission stability are not as characteristic of human culture as previously suggested^{1,12–14,16,23–25,34,195} and so are unlikely to explain the adaptive propensity of human culture. We then considered a range of other hypotheses (see also Boxes 2–4). In most cases, human culture exhibits similar properties to animal cultures and other forms of non-genetic inheritance (see Fig. 1 for a summary). However, the most distinctive feature of human culture, which has hitherto been relatively unexplored, is its comparatively open-ended capacity for generating heritable variation. That is, many modes of inheritance involve the stable transmission of non-random, acquired variation that accumulates over time and flows along non-vertical pathways. However, these modes are typically limited to particular kinds of variation, such as songs or antibodies, or those that are supported by the regulation of existing genetic variation. Indeed, the scopes of epigenetic inheritance and parental effects are sufficiently dependent on available genetic variation that novel heritable traits usually depend on genetic change (but see Laland et al. in ref. 196). For instance, epigenetic factors typically switch between previously evolved alternatives, be they desert locust morphs⁵⁴, *Daphnia* helmets⁵³ or wild radish trichome density¹⁹⁷. By contrast, human culture is much less constrained and can be characterized as open-ended.

Although we suggest that the broad scope of human culture has been underexplored, some studies have identified open-endedness as an important factor^{51,198,199}. For instance, it has been suggested that although animal cultures can cumulatively increase the efficiency with which they exploit natural phenomena, only human cumulative culture is able to expand to exploit new phenomena²⁰⁰. Other work has explored how human culture is enhanced by recombination^{17,201} and the ability to avoid getting stuck at local optima²⁰. Although such work does not evaluate alternative hypotheses or draw on literature concerning epigenetic inheritance or parental effects, it is nonetheless consistent with our position that open-endedness, as opposed to cumulativity or stability, is the key distinction between human and animal cultures, as well as other modes of non-genetic inheritance.

This limited scope of epigenetic, parental and animal-cultural variation masks the capacity of these systems for cumulative change and has contributed to the perception that, among non-genetic biological

processes, cumulative change is unique to our species' culture. The distinction between open-ended cumulative change being rare, and any capacity for cumulative change being rare, is important because broad acceptance of the latter hypothesis led to theories focusing on specific features of human cultural transmission that enable cumulative change^{16,23,25,34}. However, as discussed above, such theories remain contested^{46,66,202,203}. Indeed, we suggest that such theories will probably never fully succeed because human culture is not unique in its mere capacity for cumulative change. Instead, we suggest that it may be more fruitful to explore why human culture can accumulate in a uniquely open-ended fashion.

How best to assess cultural open-endedness across species? One approach is to map out the scope of inheritance systems through long-term observations and by testing what can or cannot be transmitted (for example, refs. 204,205). However, such a top-down approach is likely to be extremely time consuming given the variety of cultural traits and the potentially slow pace of cultural change. Instead, we suggest a bottom-up approach in which how inheritance systems store information is used to understand and predict the kinds of variation they can support. That is, we suggest drawing on cognitive science to inform our understanding of the limits cultural inheritance²⁰⁶. For instance, differences between the scope of human culture and that of animal cultures and other modes of non-genetic inheritance may result from how individuals mentally represent actions and their goals. It is well established that complex action sequences are represented hierarchically; that is, an overarching goal is broken (or 'chunked') into a series of sub-goals, each of which can consist of its own series of steps, sub-steps and so on^{207–210}. Such a system uses working memory resources more efficiently than non-hierarchical representations²¹¹. This approach has been used to describe dust bathing in birds²¹², nettle folding in gorilla foraging²¹³, human memory of short stories²¹⁴ and how humans sort items¹⁷⁶. In particular, the songs of humpback whales, which evolve cumulatively in their complexity⁴², are hierarchically composed of themes and smaller phrases²¹⁵. Such cumulatively evolving animal vocalizations may prove a useful model system for the role of hierarchical representation in cultural change.

Neurological evidence supporting this hypothesis has identified a rostral-caudal axis of the frontal lobe involved in the representation of actions. Critically, the patterning of activity along this axis matches the hierarchical arrangement of sub-goals^{216–218}, with caudal activity associated with concrete steps and action execution, while rostral activity corresponds to abstract, higher-level goals. Further support comes from the observation that damage to points along this axis leads to impairments at the corresponding level of abstraction²¹⁹. Of particular importance to theories of cultural evolution, the same system appears to represent the individual's own actions and goals as well as those of others that they observe^{220–222}. It turns goals into a hierarchy of steps and actions that can be executed, as well as inferring the hierarchy and goals behind another individual's actions. It is thus well positioned to explain the differing scopes of human and animal cultures.

A system for the hierarchical representation of actions can differ across species in a multitude of different ways that can be identified both behaviourally and neurologically. For instance, given that they support working memory²¹¹, effective representations can be detected by improved performance when hierarchical representations are possible. Cross-species work could also assess the number of nested levels that can be represented, the maximum number of steps at any level, the ability to adjust plans when a particular step fails, how long representations can be held in working memory and the accuracy of representations constructed through observation. In particular, the open-ended, cumulative evolution of hierarchical songs, but not other behaviours, in whales and songbirds may prove a useful entry. All this work would contribute to a cognitive basis for the causes of culture in humans and other species, as well as why our species is uniquely cultural and our culture so adaptive. Nonetheless, such considerations

have been hindered by strong emphases on cumulative change and transmission stability as the distinctive features of human culture. Whether our particular hypothesis is correct or not, we suggest that such emphases may no longer be warranted and that greater insight may be gained by considering alternative explanations for the unique adaptiveness of human culture.

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