Cultural Evolution

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Article Contents

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Cultural evolution is the idea that cultural change, that is changes in socially acquired information such as knowledge or beliefs, constitutes a Darwinian evolutionary process that shares fundamental similarities with (but also some differences to) genetic evolution. While parallels between cultural and biological change have been drawn ever since Darwin provided his theory of evolution, it is only in the last few decades that this parallel has been fully pursued. Models, experiments and fieldwork has probed the details of how individuals learn from one another within societies (cultural microevolution), while comparative phylogenetic methods have been used to reconstruct long-term cultural change and diversity over long timescales (cultural macroevolution). Key topics include language, cooperation, technology, innovation, migration and religion. The theory and field of cultural evolution can link the biological and social sciences by providing an evolutionarily based theory of cultural change and diversity.

Introduction

Cultural evolution is both a theory and a field of study. The theory of cultural evolution is that cultural change constitutes a Darwinian evolutionary process, sharing fundamental similarities with (but also some differences to) genetic evolution. *Cultural change* (and *culture* more generally) here refers to information that is passed from one individual to another nongenetically, via *social learning* mechanisms such as imitation or spoken and written language. In nonhuman species, examples of culture include migration routes, nesting site locations and foraging techniques, all of which may be learned from conspecifics. Human culture encompasses all the knowledge, beliefs, values and customs that we learn from others, whether it is our parents, peers, teachers or indirect routes such as books and the internet.

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What does it mean to say that this body of socially learned information 'evolves'? Darwin, with little knowledge of genetics or Mendelian inheritance, provided a mechanism-neutral theory of evolution in *The Origin of Species* (Darwin, 1859) that he applied to biological organisms. Darwin noted that individuals within a species vary; that this variation is passed from parents to offspring at birth; and that some variants are more likely to be passed on than others. Over time, this creates 'descent with modification': the gradual change and adaptation of species to their environments along branching lineages of descent.

In these generic terms, the same evolutionary processes also describe cultural change. Individuals vary in their socially learned information; this variation is passed from individual to individual via social learning; and some socially learned variants are more likely to be passed on than others. While the basics are the same, the details are different. For example, we can immediately see that there is a difference in the pathways of inheritance: while genes are inherited from parents to offspring at birth (at least in sexually-reproducing organisms like us), cultural variants can be inherited from multiple sources (peers, teachers, books, etc.) throughout the lifetime.

Darwin's notion of descent with modification can also be applied to culture. Over time, the contents of culture adapt to the environments in which individuals live. Branching lineages of cultural descent emerge. Darwin (1871) himself recognised this as having occurred in language change (a particular kind of cultural change) in *The Descent of Man*. Different Indo-European languages, from Hindi to English, are the surviving tips of cultural lineages that can be traced back to the same common ancestral language that existed in the distant past, just like extant species represent the surviving tips of genetic lineages that all share a common ancestor. Again, there are differences: there is more cross-lineage borrowing in language evolution than in species evolution, although not nearly enough to destroy the signature of history (Bouckaert *et al.*, 2012; Pagel, 2009).

The field of cultural evolution uses the insight that culture can be described as an evolutionary process to improve our understanding of cultural change. As already noted, Darwin himself hinted that this could be done. But it is only in the last few decades that scholars have pursued the parallel between genetic and cultural evolution seriously (Mesoudi, 2017). This began in the 1980s when researchers used population genetic-style mathematical modelling methods to ask how different learning biases affect large-scale patterns of cultural change and diversity (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981), paralleling how population geneticists linked the mechanisms of genetics to macro-evolutionary biological change in the early twentieth century. In the 1990s and 2000s, researchers used phylogenetic methods, originally developed in biology to reconstruct the evolutionary history of species, to reconstruct the history of cultural phenomena including marriage and wealth customs (Fortunato *et al*., 2006; Holden and Mace, 2003), languages (Gray and Jordan, 2000; Pagel, 2009) and artefacts (O'Brien *et al*., 2001). In parallel, empirical data on social learning was obtained from the lab (McElreath *et al*., 2005; Mesoudi and Whiten, 2008) and the field (Henrich and Henrich, 2010; Hewlett *et al*., 2011), and models were combined with data to explore historical dynamics (Turchin, 2003; Turchin *et al*., 2013). There has also been an explosion of research into the cultural abilities of nonhuman species, not just other apes but in various species of mammals, birds, insects and fish (Hoppitt and Laland, 2013; Leadbeater and Chittka, 2007; Thornton and Clutton-Brock, 2011; Whiten, 2017). All of these lines of research have grown in both number of findings and sophistication of methods.

The following sections provide brief overviews of the broad topics of evolutionary origins of culture and cultural evolution, cultural microevolution, cultural macroevolution and gene-culture coevolution. A few common specific topics are then covered, including language, cooperation, technology, innovation, migration and religion. Finally, the implications of cultural evolution for the biological and the social sciences are discussed.

The Evolution of Cultural Evolution

Not all species possess the capacity for cultural evolution. Many species get along fine with just genetic evolution. Others combine genetic adaptation with individual learning processes such as classical or operant conditioning to survive. But comparative research in the last few decades has revealed that culture, in the sense of social learning from conspecifics, is found in a surprisingly wide range of species (Hoppitt and Laland, 2013; Leadbeater and Chittka, 2007; Thornton and Clutton-Brock, 2011; Whiten, 2017). Bees communicate the location of food via their waggle dance; fish follow each other to feeding sites; birds learn each others' songs and migration routes; and various species learn from conspecifics how to use tools to extract resources from their environments. In some species, this social learning generates *cultural traditions* or between-group variation in behaviour resulting from social learning. Examples include tool use behaviours such as nut-cracking in chimpanzees, which varies across populations in Africa in a way not explicable by genetic variation or individual learning opportunities (Whiten, 2017). A further distinction is *cumulative culture*, in which cultural traits are improved over successive generations to eventually result in products that could not have been invented by a single individual alone (Tennie *et al*., 2009). Arguably, only humans have cumulative culture in this sense; a single chimpanzee could plausibly invent nut-cracking alone, whereas a single human could not invent a computer or discover quantum physics without 'standing on the shoulders' of prior generations (although see Mesoudi and Thornton, 2018).

All of these cases – social learning between individuals, geographically patterned cultural traditions, and multi-generational cumulative culture – constitute cultural evolution of different kinds. It is instructive to ask how these phenomena evolved, and what their adaptive benefits are. Individual (asocial) learning evolved to deal with environmental change occurring within lifetimes that cannot be tracked or predicted directly by genes. Social learning likely evolved because it avoids the potential costs of individual learning (Boyd and Richerson, 1985); for example, learning from another individual what food is safe to eat is much less risky than blindly trying out all potential foods in your environment. However, this generates a 'producer-scrounger' dilemma (Rogers, 1988). If social learning is less costly than individual learning, then social learning will dominate the population. When the environment changes, social learning will be less useful because everyone will be copying out-dated information; instead, individual learning will be more effective as it directly samples the environment and gives the new, optimal behaviour. At equilibrium, individual and social learning will coexist, but this mixed equilibrium will have mean fitness no higher than that of 100% individual learning (Rogers, 1988). Social learning in this simple sense may then be described as 'parasitic' – social learners are parasitising the hard-won information acquired by individual learners – and does nothing to enhance a population's mean fitness.

Subsequent theoretical work showed that social learning *can* increase mean population fitness when it makes individual learning less costly or more accurate, or when culture is cumulative (Boyd and Richerson, 1995). In the latter case, social learning allows individuals to learn from others what they could not learn alone. Cumulative cultural evolution, however, also requires high-fidelity social learning and favourable group structure (e.g. multiple individuals from whom to learn) to emerge (Kempe *et al*., 2014).

Linking the comparative evidence and theoretical results, we can posit that low-fidelity social learning which supports noncumulative culture is widespread because of its immediate individual-level benefits (exploiting others' more-costly individual learning), but does not enhance a species' overall ecological success. Cumulative cultural evolution requires high-fidelity social learning making it less likely to evolve, but when it does evolve it enhances a species' ecological success beyond what individual learning alone can provide. This perhaps explains why cumulative cultural evolution seems to have evolved only once, in hominins, and has led to our species' spectacular ecological success. However, exactly what socio-cognitive mechanisms permit cumulative cultural evolution, and why this happened in the hominin lineage specifically, are open questions.

Cultural Microevolution

Cultural microevolution describes the individual-level processes that determine cultural change within populations over short time periods. Typically, this involves specifying how people learn from each other via social learning. Theoretical modelling suggests that social learning is most adaptive when it is selective, that is when individuals do not blindly copy others at random, but rather target specific classes of others from whom to copy, or use particular cues, or copy particular kinds of traits (Kendal *et al*., 2018; Laland, 2004). These nonrandom tendencies are often called 'strategies' or 'biases' ('bias' not in a pejorative sense, but rather in a statistical sense, that is biased away from randomness). **Table 1** lists some commonly studied social learning biases, divided into categories describing 'who' is copied, 'what' is copied, 'when' individuals copy others rather than rely on personal information, and 'how' they copy (following Laland, 2004).

Experimental and ethnographic work has been devoted to identifying whether, and if so when, individuals employ such biases in the lab and in real life (Henrich and Henrich, 2010; Hewlett *et al*., 2011; McElreath *et al*., 2005; Mesoudi and Whiten, 2008). Modelling work has explored the implications of learning biases for large-scale patterns of cultural change and diversity (see section titled Cultural Macroevolution). For example, payoff or success bias seem necessary to permit cumulative cultural evolution, given that beneficial modifications need to be selectively preserved; conformity generates high between-group cultural variation and low within-group cultural variation, which may support cultural group selection (see section titled Cooperation); and a side-effect of prestige bias may be the spread of maladaptive behaviours, such as smoking or even suicide, that are associated with prestigious individuals who otherwise exhibit adaptive behaviours.

Although there are many parallels between genetic and cultural evolution, we should not ignore the differences. One key difference is that while genetic inheritance has high fidelity and does not itself generate evolutionary change, cultural inheritance may do so. Cognitive anthropologists have shown that learning from others is not a passive process of replicating what is received, but rather individuals often transform what they receive in nonrandom, systematic ways (Sperber, 1996). For example, a folk tale may be made more narratively coherent with repeated retelling. This systematic transformation resembles the so-called

Table 1 Microevolutionary cultural transmission biases studied in the cultural evolution literature

Type of bias	Bias	Description
Who	Vertical cultural transmission	Copy one's biological parents
	Oblique cultural transmission	Copy unrelated members of an older generation
	Horizontal cultural transmission	Copy unrelated members of the same generation
	Conformist bias	Copy the majority, that is the trait exhibited by the most number of group members
	Success bias	Copy the most successful individual
	Prestige bias	Copy the individual who has the highest freely conferred social status
What	Social bias	Preferentially acquire, remember and pass on information about social interactions
	Disgust bias	Preferentially acquire, remember and pass on information that elicits emotional reactions of disgust
	Negativity bias	Preferentially acquire, remember and pass on information about negative events or consequences
	Payoff bias	Preferentially acquire, remember and pass on information that confers a higher payoff, for example in terms of food, mating opportunities, offspring or wealth
When	Copy-when-uncertain	Copy others when individual learning is ineffective and existing knowledge is unreliable
	Copy-when-young	Copy others during juvenile periods when others are likely to have more experience
	Copy-in-stable-environments	Copy others when environments have cues of long-term stability, such that others will not possess out-dated information
How	Imitation	Copy others' motor actions
	Emulation	Copy the end results of others' actions
	Stimulus enhancement	Learn from indirect cues provided (intentionally or inadvertently) by others, for example about relevant parts of the environment
	Teaching	When one individual modifies their behaviour at some cost in order to maximise another individuals' chances of learning from them
	Spoken language	Verbal communication of information
	Written language	A physical, relatively permanent record of linguistic communication

'Lamarckian' inheritance of acquired modifications but is not inconsistent with Darwinian evolution (Henrich *et al*., 2008).

Cultural Macroevolution

Cultural macroevolution describes the population-level patterns of cultural change and diversity that occur over long time scales; this is Darwin's 'descent with modification'. As noted above, phylogenetic methods have been borrowed from evolutionary biology to reconstruct the history of present-day cultural diversity and test hypotheses concerning the tempo and mode of cultural macroevolution. These methods solve 'Galton's problem' which had vexed anthropologists since that field's foundation (Mace and Pagel, 1994). Galton's problem states that if two traits, say cattle keeping and patrilineal inheritance of wealth, co-occur in many present-day societies, it is difficult to know whether there is a causal relationship between these two traits (e.g. cattle-keeping causes patriliny) or whether this is a historical accident, and all these societies descend from a common ancestral society that happened to practice both cattle-keeping and patriliny. Comparative phylogenetic methods solve this statistical problem of potential nonindependence of datapoints by explicitly incorporating shared history. Cattle-keeping, incidentally, did seem to cause the switch from matriliny to patriliny, even controlling for phylogenetic history (Holden and Mace, 2003).

Other macroevolutionary analyses have revealed that cultural evolution, similar to biological evolution, sometimes evolves in punctuated bursts of change interspersed with periods of stasis (Atkinson *et al*., 2008), that geography (e.g. sea barriers) can shape cultural diversity (Bouckaert *et al*., 2012), and that the internal cooperative dynamics of societies can determine the spread and decline of empires (Turchin, 2003; Turchin *et al*., 2013).

Gene-culture Coevolution

Gene-culture coevolution describes the interaction of genetic and cultural evolution within a single species (Laland *et al*., 2010). In humans, advances in genomics such as whole genome sequencing and ancient DNA analysis have revealed numerous genetic changes in our species that followed the adoption of agriculture around 10 000 years ago. As the name suggests, agriculture is a form of cultural evolution, in which practices such as cultivation and domestication are invented, cumulatively modified and spread via social learning. For example, the cultural evolution of dairy farming led to the spread of lactose tolerance alleles in European and Middle-Eastern populations; the domestication of rice and the invention of rice fermentation in southern China led to the spread of alcohol dehydrogenase genes; and the adoption of yam farming in sub-Saharan Africa caused the spread of sickle-cell alleles that conferred resistance against the malaria brought by mosquitoes that bred in the standing water left after forests were cleared to grow yams (Laland *et al*., 2010). In all these cases, cultural evolution has caused the selection of novel genetic alleles that would not have spread otherwise. While gene-culture coevolution is typically considered a human phenomenon given our extensive culturally driven reshaping of our environments, there have been claims of gene-culture coevolution in other cultural species such as killer whales (Foote *et al*., 2016).

Common Topics

Language

Language is a mechanism of cultural microevolution (**Table 1**), allowing information to be transmitted from one individual to another with higher fidelity than nonlinguistic means of communication. Language is also a commonly studied topic in cultural macroevolution, where phylogenetic methods are used to reconstruct the long-term change and diversification of whole languages and language families (Pagel, 2009). While other species possess sophisticated communication systems, only humans possess fully grammatical language that allows us to communicate about concepts or events that are not immediately present, such as past or future events, or imaginary concepts such as 'justice'. There is a lively ongoing debate over the extent to which language relies on genetically evolved cognitive mechanisms that are dedicated to language learning, or whether linguistic structure emerges as languages culturally evolve to be maximally learnable as they pass through general-purpose cognitive mechanisms (Kirby, 2017).

Cooperation

The evolution of cooperation has received much attention within evolutionary biology since Darwin pondered the existence of nonreproductive helper castes of eusocial insects, given that helping others does not appear to be a behaviour that could evolve. Since the 1960s, cooperation in nonhuman species has been successfully explained by both indirect benefits (e.g. kin selection) and direct benefits (e.g. reciprocity) (West *et al*., 2007). However, some cultural evolution researchers have asked whether the large-scale cooperation seen in humans, which often occurs between unrelated strangers in one-shot encounters, might be tied to our capacity for cultural evolution. Boyd and Richerson (Boyd and Richerson, 1985, 2009) have proposed the theory of *cultural group selection*. Here, social learning processes such as payoff bias or conformity generate high between-group cultural variation and low within-group cultural variation. If this group-structured cultural variation is related to cooperation, such as norms to share resources, punish noncooperators or sacrifice oneself for one's fellow group members, and if there is group-level selection such as inter-group warfare, then cooperative norms might evolve via group-level cultural selection. This controversial theory requires further testing but may explain the unusual levels of cooperation seen in humans compared to other primates. Cultural group selection can be placed within a more general framework of *cultural multilevel selection*, where selection may occur at multiple levels of a social hierarchy, from the trait level, to the individual and their cultural traits, to the group level when groups are culturally homogenous. The challenge is to delineate how cultural selection at these different levels balances out, particularly for cooperative traits which experience positive selection at the group level but selected against at the individual level (Turchin *et al*., 2013).

Technology

Many species use tools, defined as objects external to the body used to achieve some goal. Tool use is often socially learned. Chimpanzees learn to crack open nuts using rocks as hammers and anvils from other individuals, resulting in tool use traditions where there is variation in tool use knowledge between groups (Whiten *et al*., 1999). Human technology seems orders of magnitude more extensive than any other species' tool use, as a result of the accumulation of knowledge over successive human generations (Boyd *et al*., 2014). As well as the microevolutionary biases described earlier (e.g. payoff bias), recent work has highlighted how technological evolution is also shaped by demography, that is the size and structure of human groups. Henrich (2004) argued that prehistoric Tasmanians lost various technological skills and knowledge after becoming isolated from the Australian mainland and a consequent reduction in effective population size. Henrich modelled this scenario, showing that when the social learning of complex skills is imperfect, then when population size is below a certain threshold, there are not enough knowledgeable teachers to ensure the preservation of technological knowledge. Subsequent work has tested this link between technological complexity and population size in various datasets (Henrich *et al*., 2016), and experimental work has probed aspects of demography beyond simply population size, such as the interconnectedness of sub-populations (Derex and Boyd, 2016).

Innovation

Historically, most cultural evolution research has focused on social learning, seeking to describe the many ways in which individuals acquire knowledge and skills from others (**Table 1**). Arguably, this has led to a neglect of individual learning, or innovation, which describe the emergence of new knowledge and skills (Fogarty *et al*., 2015). The latter is analogous to mutation in genetic evolution, although whereas genetic mutation is typically blind with respect to adaptive function, innovation in cultural evolution may be guided or directed (although not perfectly (Mesoudi, 2008)). Recent empirical work has attempted to catalogue the types of innovation seen in culturally evolving systems. Miu *et al*. (2018) recently analysed data from a computer programming competition, in which entrants submitted computer code to solve a computationally difficult problem. Most modifications were small 'tweaks' to existing code and were quite likely to generate small improvements. Rare innovative 'leaps', on the other hand, constituted big changes from what had gone before. These risky leaps had a high chance of failure, but a small chance of a major improvement. Furthermore, recombination (the combination of existing code to create new code) increased in frequency over time, a pattern also seen in the patent record (Youn *et al*., 2015). Recombination is also, of course, a source of novel genetic variation in genetic evolution.

Migration

Migration (or gene flow) is one of the fundamental drivers of biological evolution along with selection, mutation and drift. Migration also plays a key role in cultural evolution, where it can spread beneficial new technologies and practices across group boundaries, but also spread harmful or socially corrosive practices such as corruption or obesogenic diets. Archaeological and ancient DNA data has shown that migration played a key role in the spread of early agriculture, as early farmers replaced existing hunter-gatherer populations (Skoglund *et al*., 2012). A major difference between genetic and cultural evolution is that while migrants cannot change their genes, they can change their cultural traits via the process of *acculturation*, or social learning from members of the new society. Bell (2013) found different acculturation rates for different cultural traits in second-generation Tongan Americans. Some traits common in Tonga such as sibling adoption have been almost entirely lost amongst the diaspora, while others such as family lineage ranking have been maintained. Acculturation may maintain between-group cultural variation in some traits where otherwise migration would erode between-group cultural diversity (Mesoudi, 2018).

Religion

Religious beliefs are a good example of a culturally evolving trait: they are clearly cultural (there are no genes for Christianity, Islam, etc.), and while every human society possesses religious belief of some form, they are strikingly diverse and have gradually changed over time in a cumulative fashion. Simplistic notions that religious beliefs are 'selfish memes' parasitising the brain have given way to more sophisticated theories drawing on cognitive science and the evolution of cooperation (Norenzayan *et al*., 2016). Leading theories posit that religious beliefs originally emerged as by-products of genetically evolved cognitive functions, such as a tendency to seek agency in the inanimate world resulting in beliefs that supernatural agents control the weather, harvest yields and so on (Atran, 2002). Cultural evolution then selected for those religious beliefs that also facilitated large-scale cooperation, such as a belief in moralising gods that punish free-riders, given the group-level benefits of such prosocial beliefs (Norenzayan *et al*., 2016).

Conclusion: Cultural Evolution and the Biological and Social Sciences

In a sense, cultural evolution is a theory and field that links the biological and the social sciences. The biological sciences typically focus on how natural selection acts on genetic variation. For many species this is adequate, but for some, particularly humans, neglecting cultural inheritance becomes problematic. This is because the ecological success of humans, and our striking behavioural diversity, seem difficult to explain in terms of genes alone. The ecological knowledge, technological skills and social systems and institutions that allow our species to survive in virtually every environment on the planet are primarily cultural, not genetic. And as seen in the section titled Gene-culture Coevolution, much recent genetic change in humans has been driven by cultural evolution.

Conversely, the social sciences and humanities (e.g. anthropology, archaeology, sociology, psychology, history, economics, linguistics) study many of the phenomena discussed above (language, religion, agriculture, etc.) but typically proceed with few if any links to the biological or evolutionary sciences (Slingerland and Collard, 2011). There is little attempt to understand the evolutionary origins or function of human behaviour, and few comparisons with nonhuman species within a comparative framework. The social sciences and humanities, while providing rich descriptions of human lifeways, are often methodologically limited, at least compared to the biological sciences. The quantitative methods of cultural evolution, such as the mathematical modelling of learning biases, or phylogenetic analyses of historical lineages, offer powerful means of testing hypotheses that are lacking in traditional social science disciplines. Finally, just as evolutionary theory acted to synthesise the biological sciences in the early-mid twentieth century, so too can evolutionary theory synthesise the diverse social sciences and humanities, which typically proceed with little exchange of ideas between different disciplines (Mesoudi *et al*., 2006). While huge challenges remain in explaining the complex manner in which genetic and cultural evolution intertwine to allow species to adapt to, create, and sometimes harm, their environments, a synthetic approach that links genes and culture within a coherent, synthetic evolutionary framework is surely what is needed.

Glossary

Cultural evolution The theory that cultural change constitutes an evolutionary process that shares key characteristics with (but also differences with) genetic/biological evolution.

Cultural macroevolution The population-level dynamics of cultural change, such as adaptation to different environments or diversification into different lineages.

Cultural microevolution The individual-level details of who learns what, from whom, how and when.

Cultural multilevel selection The idea that cultural evolution can occur at different hierarchical levels of social organisation, for example at the level of the cultural trait, the individual who bears the cultural trait, or, in cases where entire groups share a cultural trait, the group or society.

Cultural traditions Stable, between-group variation in behaviour that results from social learning.

Culture Information capable of affecting behaviour that is acquired by individuals via social learning.

Cumulative cultural evolution The gradual improvement in a cultural trait or lineage as a result of successive modification and social learning over multiple individuals and generations.

Gene-culture coevolution The manner in which genetic evolution and cultural evolution interact.

Individual (or asocial) learning Learning on one's own, as opposed to copying others, via associative learning processes such as classical or operant conditioning, or higher-level cognitive processes such as inference or insight.

Social learning Learning that is facilitated or enabled by the observation of or interaction with others, or the products of others' behaviour.

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