

Pursuing Darwin's curious parallel: Prospects for a science of cultural evolution

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In the past few decades, scholars from several disciplines have pursued the curious parallel noted by Darwin between the genetic evolution of species and the cultural evolution of beliefs, skills, knowledge, languages, institutions, and other forms of socially transmitted information. Here, I review current progress in the pursuit of an evolutionary science of culture that is grounded in both biological and evolutionary theory, but also treats culture as more than a proximate mechanism that is directly controlled by genes. Both genetic and cultural evolution can be described as systems of inherited variation that change over time in response to processes such as selection, migration, and drift. Appropriate differences between genetic and cultural change are taken seriously, such as the possibility in the latter of nonrandomly guided variation or transformation, blending inheritance, and one-to-many transmission. The foundation of cultural evolution was laid in the late 20th century with population-genetic style models of cultural microevolution, and the use of phylogenetic methods to reconstruct cultural macroevolution. Since then, there have been major efforts to understand the sociocognitive mechanisms underlying cumulative cultural evolution, the consequences of demography on cultural evolution, the empirical validity of assumed social learning biases, the relative role of transformative and selective processes, and the use of quantitative phylogenetic and multilevel selection models to understand past and present dynamics of society-level change. I conclude by highlighting the interdisciplinary challenges of studying cultural evolution, including its relation to the traditional social sciences and humanities.

cultural evolution | cumulative culture | gene–culture coevolution | human evolution | social learning

The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel. . .

Charles Darwin, *The Descent of Man*, p 90

This quote from Charles Darwin (1) draws a parallel between, on the one hand, the genetic evolution of species, and on the other, cultural change (i.e., changes in socially learned information, such as beliefs, knowledge, tools, technology, attitudes, norms, and, as Darwin mentions, languages). This idea is the basic premise of cultural evolution: Cultural change constitutes a Darwinian evolutionary process that shares key characteristics with the genetic evolution of species. The emergence of this second evolutionary process saw an unprecedented extension of genetic evolution by allowing organisms to adapt more rapidly to, and more powerfully create and shape, their environments.

Since the 1980s, this parallel between genetic and cultural evolution has been pursued by scholars from a range of disciplines across the social, behavioral, and biological sciences. In this article, I review the current state of this interdisciplinary effort, focusing on topics of major recent research interest. No new theories or findings are presented, but in presenting disparate strands of work alongside each other, I hope to identify links between strands and foster a synthetic evolutionary science of culture (2, 3) paralleling the interdisciplinary synthesis of the biological sciences in the early 20th century.

Historical Context

Darwin's comment above was inspired by historical linguists of his time, who, even before publication of *On the Origin of Species* (4), were constructing tree-like schemas of extant languages explicitly based on the assumption of common descent (5). Although “evolutionary” ideas became popular ways of describing cultural change in the late 1800s, such ideas were confused. Many scholars erroneously saw evolution as inevitable progress along fixed stages of increasing complexity (e.g., from savagery to barbarism to civilization), drawing more from Herbert Spencer than from Darwin (6). There was also much confusion, in the absence of a clear understanding of genetics, about genetic and cultural inheritance. Theories were often literally Lamarckian, with ideas, artifacts, and words somehow thought to become part of the germ line through repeated use (7). Due to this confusion, as well as the misuse of pseudoevolutionary racial theories for distasteful political ends, early 20th century social scientists declared culture to be separate from “the organic” (8); the biological and social sciences went separate ways; and the notion of cultural evolution, or indeed any evolutionary basis for human behavior, fell from favor.

Cultural Microevolution

It was not until the 1970s and 1980s that a properly Darwinian theory of cultural change was formulated, first by Cavalli-Sforza and Feldman (9, 10) and then by Boyd and Richerson (11). This theory comprised quantitative models of cultural microevolution, describing the mechanisms by which cultural variation is transmitted from person to person, and the processes that change this variation over time within populations (Table 1), thus embodying the “population thinking” that characterizes Darwin's approach. Here, “culture” is defined as “information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission” (12). “Social transmission,” “social learning,” and “cultural transmission” are used interchangeably to denote the nongenetic transfer of learned information from one individual to another. “Cultural trait,” “cultural variant,” and sometimes “meme” are used to refer to the information (e.g., ideas, attitudes, skills) that is transmitted. All of these terms hide huge complexity and caveats. Such simplification is typical of a modeling approach. This approach follows population genetics, which makes simplifying assumptions (e.g., infinitely large populations) to understand similarly complex genetic evolutionary processes. The simplification in both cases is tactical, aiming to understand complex processes in a piecemeal fashion and to formalize verbal arguments (13).

Some of the processes in Table 1 have parallels in genetic evolution. Selection-like “content” or “direct” biases favor the acquisition and transmission of some cultural variants over others due to their memorability or effectiveness (14, 15), just as some

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Table 1. Comparison of genetic and cultural evolution as originally modeled by Cavalli-Sforza and Feldman (10) and Boyd and Richerson (11), with citations to recent empirical tests or examples

Process	Genetic evolution	Cultural evolution
Variation	Genetic mutation Recombination	Undirected cultural mutation/invention (16) Recombination (133)
Inheritance	—	Guided variation or transformation (109, 112)
	Particulate	Particulate or “meme-like” (134)
	—	Blending of continuous cultural variation (60)
Selection	Vertical (parent to offspring)	Vertical cultural transmission (75)
	Horizontal gene transfer	Horizontal/oblique cultural transmission (76, 77)
	Natural selection	Cultural selection or direct/content biases (14, 15)
Migration	—	Frequency-dependent biases (e.g., conformity) (88, 89)
	Gene flow	Indirect (e.g., success, prestige) biases (92, 99)
	—	Demic diffusion (movement of people with their cultural traits) (17)
Drift	Genetic drift	Cultural diffusion (movement of traits without people) (135)
		Cultural drift (18)

alleles have higher fitness than others. Random cultural “mutation” occurs where new variation arises randomly, such as via perceptual error (16), akin to random genetic mutation. Migration allows individuals to introduce novel variants to a population as they move (17), just as gene flow spreads alleles. Some cultural traits, such as first names, fit the expectations of neutral drift (18), just like some alleles.

However, this enterprise is not simply the unthinking transfer of models from genetic to cultural evolution. In many cases, cultural variation is generated, inherited, and changed in very different ways from genetic variation, and models have addressed these differences (10, 11). Examples include the blending of continuous, nonparticulate cultural variation; the systematic, nonrandom generation of cultural variation, or “guided variation”; frequency-dependent biases, such as conformity, where variants are adopted based on their commonness in the population; and indirect biases, where traits are adopted based on the characteristics of their bearers, such as success or prestige. Where possible, evidence from psychology, anthropology, sociology, and other fields was used to justify these processes (10, 11). However, the use of quantitative models went beyond typical theory in the social and behavioral sciences by (i) precisely and explicitly defining these processes rather than relying on imprecise verbal descriptions of phenomena (e.g., “conformity”) and (ii) exploring the population-level consequences of such processes, such as the consequences of frequency-dependent biases for between- and within-group cultural variation (19).

Cultural Macroevolution

In the 1990s, the study of cultural microevolution was supplemented by the study of cultural macroevolution, defined as long-term cultural change at or above the level of the society. Mace and Pagel (20) introduced the phylogenetic comparative method as a means to (i) reconstruct the cultural evolutionary history of a particular trait or set of traits and (ii) test functional hypotheses concerning the spread or distribution of cultural variation across societies while controlling for evolutionary history. The latter had been a problem within anthropology for over a century. In 1889, Francis Galton (21) pointed out that even if two traits (e.g., cattle-keeping and patriliney) often co-occur across many societies, this co-occurrence does not necessarily provide evidence that they are functionally associated (e.g., cattle-keeping causes patriliney), because all these societies may have culturally inherited this combination from a common ancestral society. Societies are not necessarily statistically independent data points, due to shared history. This problem is the same one facing biologists when comparing across species, and, in the meantime, biologists had developed methods for controlling for nonindependence due to common descent (22). Mace, Pagel, and others imported these methods to test functional evolutionary hypotheses in the same way, showing, for example, that cattle-keeping did likely cause a

switch from matriliney to patriliney even after controlling for descent (23).

Concurrently, archaeologists began using phylogenetic methods to reconstruct the history of artifacts, such as projectile points (24), and, following Darwin’s original insight, others began reconstructing the history of language families (25). Like for microevolution, the advantage here was in the use of quantitative methods borrowed from biology that were explicit in their assumptions about how to reconstruct historical relationships (e.g., maximum parsimony, maximum likelihood), repeatable and extendable by others, and easily scaled up to large datasets (26), in contrast to the informal, idiosyncratic, and subjective schemas of historical linguistics or archaeology.

Is It Evolution?

A common question is whether culture really evolves. This question comes from both social scientists skeptical of any kind of parallel with evolution, and biologists insistent that Darwin’s theory applies only to genetic evolution (27). Importantly, no one argues that genetic evolution and cultural evolution operate identically. From the outset, microevolutionary modelers incorporated processes unique to cultural change, such as one-to-many transmission (10) or nonrandomly guided variation (11). However, an examination of Table 1 indicates that the parallels are numerous enough to warrant an evolutionary theory of culture, as long as these differences are taken seriously. At its heart, cultural change is a process of inherited variation that changes due to selection, drift, migration, and other processes, which, in their details, may operate similar to or different from the genetic case.

Similarly, at the macroevolutionary level, it is sometimes argued that human culture is so riven with cross-lineage diffusion that it is not tree-like, and thus not amenable to phylogenetic methods (26). Although this argument may be true for some cultural domains, many, such as languages or some artifacts, have been shown to be tree-like due to strong intergenerational cultural descent (28). Moreover, cross-lineage blending is a common feature of genetic evolution when we look beyond our own kingdom to, say, prokaryotes, where horizontal gene transfer is rife (29). Indeed, network-based methods exist for dealing with non-tree-like data (30).

One indirect, but perhaps most important, test of the parallel between genetic and cultural change is whether methods borrowed from evolutionary biology, suitably modified, actually prove useful in explaining cultural change in a manner that adds to the findings of nonevolutionary methods. Table 2 lists such methods, which are further discussed throughout this article.

Evolution of Cultural Evolution

In parallel to the study of cultural change itself, that is, changes in the contents of culture, modelers have also examined when and why the capacity for cultural evolution evolved. Models

suggest social learning evolves when environments change at intermediate rates: too quickly for genes to track directly, but not so fast that socially learned information is outdated (11, 31). An influential model by Rogers (32) showed that whereas social learning readily evolves in such conditions, it does not increase mean population fitness, contrary to claims that culture is responsible for our species' evolutionary success. Further models showed that social learning does enhance population fitness when it is cumulative; that is, individuals can learn via social learning what they could not possibly learn alone (33). This finding has led to extensive study of the factors that permit cumulative culture (discussed below). Finally, gene–culture coevolution models and data have examined how cultural evolution interacts with and affects genetic evolution (34). There is extensive evidence for culture-driven genetic change in humans, including agriculture-induced genetic adaptations for digesting starch, dairy products, and alcohol (34, 35). Overall, this research shows the extent to which culture extends genetic evolution by independently tracking environmental change that is too rapid for genes to track, by generating diverse cultural adaptations to those environmental challenges, and by driving genetic evolution.

Recent Research Trends

Cumulative Culture. Just 20 y ago, little was known about social learning and culture in nonhuman species. Many definitions of culture stated that it was unique to humans, making the notion of “nonhuman culture” nonsensical. Now, it is established that a range of species from diverse taxa exhibit social learning (36), as well as cultural traditions, where social learning generates long-lasting behavioral differences between groups (37).

However, there is still a gulf between the cultural achievements of humans and other species. Recent work has focused on cumulative culture, where knowledge is built up over successive generations to exceed anything that a single individual could invent alone (38, 39). This ability appears to be unique to humans: Although chimpanzees' nut-cracking (36) or dolphins' use of protective nose-sponges (40) does not seem to exceed what a lone chimpanzee or dolphin could invent alone, it is surely impossible for a single human to have discovered quantum mechanics, invented smartphones, visited the moon, or achieved any of the other feats that require standing on the shoulders of previous generations. As noted above, models of the evolution of culture show that cumulative culture is particularly effective at increasing mean population fitness beyond the population fitness of noncumulative cultural species (33). A major research question is therefore “What allows human culture to be uniquely cumulative?”

There has been much focus on high-fidelity social learning, which is needed to preserve modifications over successive generations such that they can accumulate (41, 42). It was initially suggested that imitation (i.e., the copying of bodily actions rather than products) was key to this high fidelity (43). This claim seems doubtful, given that chimpanzees can imitate tool use techniques with high enough fidelity for alternate techniques to stabilize in different groups (44). Rather than an “imitation vs. no-imitation” dichotomy, perhaps humans are more effective, spontaneous, or compulsive imitators (45). Other comparative work has suggested roles for prosociality and language-mediated teaching (46). As well as individual cognitive abilities, cumulative culture

may also require favorable demography, such as larger populations (42, 47) or populations partially connected via migration (48, 49), as is typical of human societies (50). Currently, there is no consensus on which of these factors is key to explaining uniquely human cumulative culture. A combination of more than one factor is probably necessary, perhaps explaining why cumulative culture is confined to just one extant species.

Is “cumulative culture” synonymous with “cultural evolution”? In principle, evolutionary change can be noncumulative, involving changes in trait frequencies over time such as occurs with genetic drift or local adaptive changes in gene frequencies. In this sense, nonhuman, noncumulative cultural change can justifiably be called cultural evolution. However, genetic evolution is clearly also cumulative, involving the gradual accumulation of beneficial genetic modifications over time to produce complex adaptations, such as eyes or wings. Human cumulative cultural evolution bears a clear parallel with this form of cumulative genetic evolution. Indeed, the gradual accumulation of cultural innovations results in complex cultural adaptations, such as telescopes or airplanes, that resemble and rival complex genetic adaptations (12).

Ideas regarding the origin of cumulative culture can inform thinking about factors that might affect recent and ongoing cumulative cultural evolution. The invention of writing, followed by digital media, surely greatly increased the fidelity of social learning and, potentially, the speed of cumulative culture (51). Demographically, the threefold increase in the world population and increased global mobility in the past century should also have accelerated cumulative culture. However, there are also constraints. For example, as the amount of knowledge that is accumulated increases (which, by definition, it must), it should take longer for each new individual to acquire that knowledge. This increased acquisition cost may result in extended educational periods, and the eventual slowing down of cumulative culture as innovation becomes harder (52).

Demography. Biologists have long recognized that demographic factors, such as population size, structure, and interconnectedness, are crucial for understanding trajectories of evolutionary change (53). Although the effect of demography on cultural evolution was modeled in the 1980s (10), the past decade has seen a major focus, mostly in archaeology, on the way in which population structure affects patterns of cultural variation and the gain and loss of cultural complexity. Shennan (54) and Henrich (47) argued that population size has been a major determinant of cultural complexity in hunter-gatherers, often measured as the number of tools in a toolkit or the number of components per tool. Henrich (47) argued that the loss of toolkit complexity in Tasmania following isolation from Australia 12 kya was due to reduced effective population size, because the isolated population was too small to maintain complexity, given imperfect social learning. In his model of this process, each member of each new generation acquires the skill of the most skillful member of the previous generation with systematic loss due to copying error and some chance of improvement. Larger populations make the loss of skills due to imperfect copying less likely and improvements more likely. Shennan and coworkers (48, 54) argued that increasing population densities in Upper Paleolithic Europe around 45 kya caused the major increase

Table 2. Methods and concepts that have been adapted from evolutionary biology to study cultural change

Evolutionary biology	Cultural evolution
Population genetic models	Cultural evolution (or gene–culture coevolution) models (10, 11)
Gene-based phylogenetics	Cultural phylogenetics (24, 26)
Comparative (cross-species) method	Comparative (cross-cultural) method (20)
Population dynamic models	Historical dynamic models (120)
Multilevel selection	Multilevel cultural selection (122, 123)
Genetic drift	Cultural drift (15, 18)
Multigeneration breeding experiments	Multigeneration transmission chain experiments (111, 136)

in symbolic and technological complexity seen in the archaeological record, rather than a genetic mutation that enhanced cognitive ability.

Subsequent tests of the link between demography and cultural complexity have been mixed. Analyses of tools (55) and languages (56) on islands in the Pacific Ocean are supportive, with toolkit complexity and word gain rate increasing with island size. Others have found environmental risk, not population size, to predict toolkit complexity (57). These findings remain to be reconciled. A recent critique arguing that “population size does not explain past changes in cultural complexity” (58) is surely too strong (59). Although not even the strongest advocates of demography would argue that population size should always predict cultural complexity, the notion that demography has no effect at all is surely also incorrect in light of the positive evidence cited above. Recent models integrating population density and mobility (not simply population size) as proxies of cultural transmission (49) offer promise for more robust tests of demographic hypotheses.

Experiments have also examined how population size affects cultural complexity (60–63). Experiments cannot prove whether demography affects cultural evolution in the real world, but they can test the validity of behavioral assumptions of demographic models and manipulate factors in a way we cannot in real life. For example, the one study not to find a link between group size and cultural complexity used a simple task that is unlikely to benefit from a large pool of demonstrators (61), highlighting the importance of task difficulty. Another showed that blending inheritance, where learners combine information from multiple demonstrators, also leads to a group size effect (60), providing an alternative mechanism to the assumption that people solely copy the most skilled group member (47).

Cultural Phylogenetics. The use of phylogenetic methods to reconstruct human history has been greatly extended in both methodology and subject matter. Methodologically, maximum parsimony has been superseded by Bayesian Markov chain Monte Carlo (MCMC) techniques that allow the testing of explicit evolutionary hypotheses such as whether artifacts exhibit core packages of traits that are inherited together (64); network-based methods to handle non-tree-like reticulation (30); and/or phylogeographic methods that explicitly model the spread of cultural traits in space, making assumptions about geographical constraints [e.g., water bodies as potential barriers to language diffusion (65)].

Such methods have been used to test hypotheses about human history with more rigor than traditional nonquantitative, non-evolutionary methods, shedding light on, for example, the origin of the Indo-European language family (55), whether similarities between hand-axe assemblages are caused by shared descent or convergence (66), the historical links between folktales from different regions (30), and even the recent evolution of computer programming languages (67). These analyses do not ignore existing work in traditional historical disciplines. They often test existing hypotheses, but using larger samples and more powerful statistical techniques. For example, Currie et al. (68) found support in South-East Asia and the Pacific for the hypothesis that political complexity increases in a unilinear sequence (69), moving from acephalous to simple chiefdoms, to complex chiefdoms, to states, without skipping stages, but with possible collapses down to any earlier stage (note that this latter point is evidence against the aforementioned Spencerian “progress” theories of social evolution, which posited that progress toward increasing complexity is an inevitable law). Similarly, Haynie and Bower (70) used phylogenetic comparative analyses of Australian languages to test Berlin and Kay’s sequence model of color term acquisition (71), where languages first acquire terms for black/white, then red, then green/yellow, then blue, then brown. This model was generally supported, albeit with many exceptions to the sequence.

Empirical Tests of Social Learning Biases. Cultural evolution models contain assumptions about how people learn from one another. Some posit biases such as conformity, where people are disproportionately more likely to copy common cultural traits, or success or prestige biases, where people preferentially copy traits of successful or prestigious individuals (11). Others explore the consequences of learning from parents (vertical transmission), elders (oblique transmission), and peers (horizontal transmission) (10). Where possible, these assumptions are made using evidence from the social and behavioral sciences, such as the social learning literature in psychology (72) or the diffusion of innovations literature in sociology (73). However, such evidence was not collected with these models in mind, and is often unsuitable. For example, classic psychology studies of conformity confound social influence and personal judgment in a way that cannot reveal whether conformity in the sense modeled in the cultural evolution literature is present (74). Such differences may seem trivial, but they have significant population-level implications: Only conformity in the sense of disproportionately copying the majority can lead to within-group homogeneity (11). Consequently, the past decade has seen the use of field studies and laboratory experiments that test the assumptions and predictions of cultural microevolution models.

Field studies, typically conducted in small-scale societies where paths of social transmission are easier to trace, have examined whether and when people use vertical, oblique, or horizontal transmission to acquire key skills, beliefs, or knowledge. This research shows a cumulative refinement of findings. An initial study on the Aka, relying solely on retrospective self-report (asking people from whom they learned X), found substantial vertical transmission for most traits, including hunting skills, food gathering/preparation techniques, infant care methods, and sharing norms, with dancing and singing the only domains with substantial nonparental influence (75).

However, retrospective self-report is vulnerable to recall bias. Later studies used nonretrospective methods (e.g., asking to whom people would go to learn X) or non-self-report regressions to assess pairwise similarity across respondents, on the assumption that higher similarity indicates transmission between those individuals. These studies support a two-stage model of skill acquisition (76–79): People initially learn from their parents, and then update this knowledge by learning from older adults or peers later in life. Moreover, the updating stage typically targets highly skilled or knowledgeable individuals (76). Interestingly, this pattern resembles evidence regarding childhood learning in Western societies, where peers are more important than parents for the acquisition of key skills and knowledge (80). Such findings are also consistent with models of age-based learning schedules, which find that cumulative cultural evolution is facilitated when learning becomes increasingly oblique and horizontal with age (81). Nevertheless, these generalizations betray many exceptions, and effects may vary with domain (82).

Laboratory experiments have explored similar questions regarding from whom people learn. Experiments offer more control than field studies, albeit with reduced external validity. Participants face an unfamiliar task designed to resemble a real-life task faced by people past or present. They can solve this task through asocial learning and/or various forms of social learning (e.g., conformity, success bias). Such studies paint a consistent pattern despite using different tasks and protocols (74, 83–87). At least some people behave adaptively as predicted by models, by learning socially when appropriate (e.g., when asocial learning is costly) and in an appropriate manner (e.g., using success bias rather than copying at random). Moreover, some people exhibit adaptive flexibility, such as using payoff bias in a task to determine which of two choices yields higher payoffs, but frequency-based biases in a coordination task where it pays to match others’ choices (85).

However, across these experiments, there are unexplained individual differences in social learning use and often an underutilization of social information (74, 83–87). There is some

evidence linking this individual variation to other individual differences, such as personality (87) or intelligence (88, 89), but these correlations are weak and exploratory. There is also evidence of cross-cultural variation in social learning, specifically higher social learning in collectivistic East Asian societies than in individualistic Western societies (90, 91). Similar individual and cultural variation in nonexperimental data suggests that this finding is not just a laboratory artifact (92).

The causes and consequences of this individual and cultural variation are unclear. Individual variation in social learning is found in many species. It can be viewed on a continuum of phenotypic plasticity, from genetically polymorphic and developmentally fixed individual differences, to developmentally determined facultative responses to external environments or physiological state, to the associative learning of learning strategies (93). Whether individual variation in human social learning is nonadaptive noise, reflects frequency-dependent equilibria between information producers and scroungers with no group-level benefit (32), or is adaptive at the group level by maintaining a mix of innovation and tradition is unknown.

Cultural variation in human social learning suggests that we acquire norms via social learning that, in turn, affect our degree of social learning (93). This process may generate cultural dynamics entailing the “social learning of social learning” (94), rather than the typical modeling assumption that learning strategies are genetically inherited. The origin of this cultural variation is unknown, but it might be an historical and societal response to different rates of environmental change (95). Another line of work has identified intentional, institution-based mechanisms for generating innovation (96), suggesting similar flexibility in social learning. There is great scope to use the methods of cultural macroevolution outlined above to test these hypotheses and explain how cultural macroevolution, as well as genetic evolution, has shaped the behavioral responses measured in experiments, rather than assuming that participants are coming into the laboratory as “blank slates.”

Development. The brief mentions above of work with children belie rapid growth in the study of the developmental basis of cultural evolution (97). Such studies are crucial for understanding how people developmentally acquire the learning biases noted above to be individually and culturally variable, and how these learning biases interact with developing abilities, such as language and theory of mind. Experiments have shown that children are sophisticated social learners and exhibit biases predicted by models to be adaptive, such as preferentially learning from accurate over inaccurate individuals (98) and prestigious over nonprestigious individuals (99). There is work combining biases, finding that children copy groups over individuals when both are equally successful but copy successful individuals over unsuccessful groups, thus adaptively switching between frequency and success information (100). Other work has addressed the motivation for copying, with children more likely to imitate indiscriminately when tasks are presented as conventional rather than instrumental, such that the motivation is to affiliate with one’s group rather than acquire effective skills (101).

There are exceptions to these impressive skills, however. One study found that children copy adults over peers even when peers are more knowledgeable (102). In addition, there is similar individual (103) and cultural (90) variation as seen in adults, which has yet to be explained. Further work is needed to link the study of social learning in childhood and adulthood, ideally using models to link developmentally changing learning schedules to macroevolutionary patterns of cumulative culture (81).

Cultural Attraction. An ongoing debate has been over the relative role of preservative, selection-like processes and nonselective, transformative processes in explaining cultural change (104–107). Many of the cultural evolution models described earlier assume high-fidelity transmission plus random copying error or

mutation, with selection-like processes, such as content or conformist biases, altering the frequency of cultural traits over time. Sperber and coworkers (105, 106) have argued that many instances of cultural change do not take this form. Instead, they argue, cultural transmission is transformative: People reconstruct what they learn from others according to their preexisting knowledge, cognitive or perceptual biases, or other factors. This process of transformation is known as cultural attraction, and the points at which representations converge are called cultural attractors (105, 106) [although ambiguities in these definitions are discussed elsewhere (108)].

For example, recall the phylogenetic analysis showing that Australian languages typically acquire color terms in the specific Berlin–Kay sequence, explaining cross-cultural regularities in color terminology (70). Cultural attraction offers a plausible microevolutionary explanation for this finding: People share perceptual systems that lead them to invent and transform color terms independently in the same way. This explanation is supported by experiments in which initially random artificial color terms were passed along chains of people (109). Each participant learned unfamiliar terms for each color, with these labels, including errors, passed to the next person as his or her learning set. In each of 30 independent chains, the artificial terminology converged on the predicted Berlin–Kay scheme, as each person transformed the labels in a systematic manner. Similar experiments have shown convergence toward universal patterns of grammatical structure (110), category learning (111) and bloodletting as a medical practice (112).

The cultural attraction approach moves the explanatory focus from the population to the individual level. Rather than explaining patterns of cultural diversity, stability, and change in terms of the differential selection of certain cultural variants (e.g., content biases) or differential copying of certain individuals (e.g., success bias, prestige bias), cultural attraction focuses on how individuals systematically transform representations. The latter is similar [but not identical (107)] to evolutionary psychologists’ notion of “evoked culture” (113), where genetically evolved cognitive biases cause the independent recurrence of genetically adaptive behavior, and the process of iterated learning, where repeated learning and transmission cause convergence on inductive biases or priors (111).

Although cultural attraction is sometimes presented as an alternative to cultural evolution, the two approaches are compatible (104). Many “standard” cultural evolution models, in fact, do not model transmission as high fidelity, and allow for transformation (47, 114). The notion of guided variation (11) is similar to the individual, nonrandom transformation described as cultural attraction, and can operate in parallel to the more selection-like transmission biases in Table 1. However, cultural attraction proponents have a valid point that, in practice, such transformative processes have not received adequate attention. The relative influence of each likely varies with domain (104). Where there are clear inductive biases favoring certain representations, such as bloodletting or color terms, then explanations in terms of transformation/attraction will be useful. Where there are no clear intuitions or inductive biases, selection-like processes will be more important. Bloodletting, for example, has been replaced in many societies with surgical techniques that are the product of a long refinement and accumulation of unintuitive knowledge and skills. Many medical, scientific, and technological practices are the product of accidental invention followed by payoff-biased selection in the face of resistance due to conformity to prior practices or transformation back to intuitive attractors (115). Examples include glassmaking (116); musical instruments (12); and the theory of evolution, an unintuitive idea that needs conscious effort to understand (118).

Even where there is clear evidence for inductive biases, as in the case of color terms (109), the prediction of cross-cultural universals is only partially upheld in real-world data, as shown by the many exceptions to the Berlin–Kay scheme identified by phylogenetic analyses (70). Further work might show these

exceptions to be determined by processes like migration or prestige bias. A Bayesian framework can be useful here, having been used to model both attraction-like inductive biases (111) and selection-like biases (119). This integration of selective and transformative processes, and use of both microevolutionary evidence regarding cognitive biases and macroevolutionary analyses of actual cultural diversity and change, holds great promise.

Historical and Contemporary Social Dynamics. As well as cultural phylogenetics, another approach to understanding historical change uses population dynamic models of the kind used within ecology to model changes in population size over time in response to births, deaths, predation, or migration (120). This approach is more useful when detailed temporal data are available, such as on the rise and fall of empires. Again, models and theories are not unthinkingly imported from ecology and applied to human societies. They are adapted to take into account the unique aspects of human culture, often drawing on traditional theories from history and sociology. However, the advantages of this approach are that (i) theories can be precisely quantified in a way that generates clear predictions, unlike verbal arguments, and (ii) these predictions can be empirically tested often across multiple societies, regions, and time periods, in a way that historians seldom do (120).

For example, Turchin (120) used population dynamic models to test competing theories for the rise and fall of empires in Europe during the period from AD 0–1900. One idea, proposed by Ibn Khaldun in the 14th century, can be interpreted as a theory of multilevel selection. Here, societies grow by solving collective action problems, such as building irrigation systems or organizing collective defense against enemies. Societies that more effectively solve such problems grow in size and defeat other less internally cooperative societies, eventually becoming empires. When societies are very large, however, there is overproduction of elites who fight among themselves for power, as well as a disconnect between the majority and the squabbling elites. This internal conflict allows another society to invade, typically one in a border region with higher internal cooperation due to its smaller size and common enemy (the larger empire). This new empire grows larger, internal cooperation breaks down, the new empire is itself eventually invaded, and the cycle continues.

Turchin (120) converted this verbal theory into a quantitative model, incorporating within-group cooperation as well as factors traditionally considered important, such as access to resources and geographical overreach (121). This model provided a better fit to historical data on the rise and fall of actual empires than models without cooperation. This work shows not only the value of quantitative cultural evolution models and empirical tests as applied to history but also support for the idea of multilevel cultural selection, where societies grow as a result of superior within-group cooperation that provides an advantage in between-group competition (11, 122). Subsequent work has found further support for this theory in a spatially explicit model tested with data beyond Europe (123).

More recently, Turchin (124) has applied these ideas to current societies, particularly the United States, extending structural-demographic theories from political science (125). Worryingly, elite overproduction, interelite conflict, and social inequality, which were key markers of low within-group cooperation and impending empire collapse in the past, have been increasing in the United States in recent decades. Examples of interelite conflict include decreased Republican-Democrat cooperation in government and the Tea Party challenge within the Republican Party. The success of self-styled antiestablishment figures, such as Donald Trump, is arguably due to rising social inequality and a disconnect between the majority of voters and the increasingly conflict-ridden political elites.

Predicting the future can never be done with complete certainty, for either genetic or cultural evolution. However, the work of Turchin (124) and others makes events like the unexpected election

of Donald Trump more understandable, and provides early warning signs of societal collapse based on the long view of cultural evolution that we ignore at our peril. Continual progress toward more stable forms of political organization is far from inevitable (68), and institutions are fragile balancing acts between individual and group interests (122). Better understanding of this balance, within the long view of cultural evolution, is surely crucial for creating and maintaining sustainable societies.

Conclusions

Science itself is a cumulative cultural evolutionary process (126). Is the science of cultural evolution accumulating an increasingly reliable body of knowledge concerning human culture? I hope I have shown that it is. Initial claims derived from self-reports that cultural transmission is largely vertical have been replaced with a two-stage model in which parental knowledge is updated via horizontal or oblique transmission, often targeted in age- or skill-appropriate ways (76, 77). The common modeling assumption that social learning is under fixed genetic control is incompatible with experimental evidence of substantial individual and cultural variation, and is being revised (93). The “demographic turn” within archaeology, itself an improvement on unrealistic “single genetic mutation” explanations for increases in past cultural complexity, has been refined to focus on population density and migration rather than just population size (49). Long-standing hypotheses regarding the acquisition of color terms, origin of Indo-European languages, and trajectory of sociopolitical complexity have been tested using phylogenetic methods that are more powerful than informal comparisons using cherry-picked examples (26).

However, major questions remain, which is also the normal course of science. Ongoing work seeks to explain why only humans exhibit cumulative cultural evolution, the origins of individual and cultural variation in social learning and innovation, the relative influence of selection and attraction across domains, and the balance between individual and group interests that shape societal cohesion and stability. A welcome trend is to apply cultural evolution theory to real-world problems, including environmental sustainability (122), the social effects of new digital media (51) and society-level cooperation (124). The work reviewed here is, moreover, a small selection of cultural evolution research. There is no space to cover, say, economics (127), neuroscience (128), literature (129), or religion (130).

As well as the use of quantitative methods, often borrowed from biology (Table 2), a major strength of cultural evolution work is its interdisciplinarity. Findings from, say, experimental psychology can be applied to problems in archaeology (16). Conversely, a consideration of the population-level consequences of psychological constructs, such as conformity, highlights their limitations (74). This interdisciplinarity should be pushed further, especially by integrating microevolution and macroevolution. For example, phylogenetic analyses of actual color terminologies (70) reveal broad support but key exceptions to the universality predicted by experiments (109). Are these exceptions also predictable from individual cognition, or are other factors needed? More broadly, interdisciplinarity is facilitated by open science. Although data and analytical techniques have traditionally been kept within disciplines as protected knowledge, the public release of data and use of reproducible analyses (e.g., R scripts) encourage scholars from other disciplines to explore that data and familiarize themselves first-hand with key findings.

However, there is still an epistemological gulf between the scientific, evolutionary approach outlined here and much of the social sciences and humanities, which, after all, study the same cultural phenomena (131, 132). Most cultural anthropologists, sociologists, historians, and the like are reluctant to use the simplifying assumptions and reductionism inherent in quantitative models and methods, instead highlighting complexity and contradictions. There is also a reluctance to generalize across societies, regions, or time periods and, instead, a focus on specificity and uniqueness. There is also a reluctance to consider continuities

between human behavior and the behavior of other species, with the latter often perceived to be “instinctive” or genetically determined in a way that human behavior is not [an overview of these issues from both sides is provided elsewhere (131)].

This reluctance is, I think, misguided. The methods and approaches described here add to, rather than detract from, traditional methods and knowledge. Phylogenetic analyses typically use existing linguistic or ethnographic data to reconstruct historical relationships and test causal historical hypotheses, but with greater rigor than is possible by considering single case studies or ignoring Galton’s problem (20). Quantitative models are simply verbal arguments expressed more precisely and unambiguously, and in a way that affords easier empirical testing. Those verbal arguments often come from the social sciences and humanities (120, 121, 124, 125). There are also excellent examples of traditional ethnography providing important corrections to cultural evolution theory, such as Wilf’s (96) demonstration that cultural innovation can be institutionally driven. Furthermore, cultural evolution offers a link to the wider evolutionary

sciences without inappropriate genetic determinism. Unlike sociobiology and evolutionary psychology approaches that downplay transmitted culture (113), the work outlined here assumes that cultural evolution is semiautonomous from genetic evolution, allowing rapid cultural adaptation to novel physical and social environments without genetic change. Although some aspects of cultural diversity may reflect genetically evolved, content-rich cognitive biases, many others reflect the accumulation of modifications via content-independent learning rules such as success bias, leading to diverse, historically contingent pathways of culturally inherited knowledge. The theory of cultural evolution offers a means of taking culture seriously within a scientific, evolutionary framework.

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