

Introduction



Cite this article: Kolodny O, Feldman MW, Creanza N. 2018 Integrative studies of cultural evolution: crossing disciplinary boundaries to produce new insights. *Phil. Trans. R. Soc. B* **373**: 20170048.
<http://dx.doi.org/10.1098/rstb.2017.0048>

Accepted: 11 December 2017

One contribution of 16 to a theme issue 'Bridging cultural gaps: interdisciplinary studies in human cultural evolution'.

Subject Areas:

cognition, evolution, genetics, theoretical biology

Keywords:

cultural evolution, interdisciplinary research, cognition, genetics, ecology, animal behaviour

Authors for correspondence:

Oren Kolodny
e-mail: okolodny@stanford.edu
Marcus W. Feldman
e-mail: mfeldman@stanford.edu
Nicole Creanza
e-mail: nicole.creanza@vanderbilt.edu

Integrative studies of cultural evolution: crossing disciplinary boundaries to produce new insights

Oren Kolodny¹, Marcus W. Feldman¹ and Nicole Creanza²

¹Department of Biology, Stanford University, Stanford, CA, USA

²Department of Biological Sciences, Vanderbilt University, Nashville, TN 37212, USA

OK, 0000-0002-0095-693X; MWF, 0000-0002-0664-3803; NC, 0000-0001-8821-7383

Culture evolves according to dynamics on multiple temporal scales, from individuals' minute-by-minute behaviour to millennia of cultural accumulation that give rise to population-level differences. These dynamics act on a range of entities—including behavioural sequences, ideas and artefacts as well as individuals, populations and whole species—and involve mechanisms at multiple levels, from neurons in brains to inter-population interactions. Studying such complex phenomena requires an integration of perspectives from a diverse array of fields, as well as bridging gaps between traditionally disparate areas of study. In this article, which also serves as an introduction to the current special issue, we highlight some specific respects in which the study of cultural evolution has benefited and should continue to benefit from an integrative approach. We showcase a number of pioneering studies of cultural evolution that bring together numerous disciplines. These studies illustrate the value of perspectives from different fields for understanding cultural evolution, such as cognitive science and neuroanatomy, behavioural ecology, population dynamics, and evolutionary genetics. They also underscore the importance of understanding cultural processes when interpreting research about human genetics, neuroscience, behaviour and evolution.

This article is part of the theme issue 'Bridging cultural gaps: interdisciplinary studies in human cultural evolution'.

1. Introduction

In this theme issue we aim to demonstrate synergies between cultural evolution and many other fields, including anthropology, biology, psychology, archaeology, ecology, genetics and economics. An important aspect of our integrative approach is that it brings ideas and methods from historically disparate fields to bear on cultural evolution, enabling researchers to use insights from a range of fundamentally different perspectives. However, it also presents the challenge that different schools of thought differ in paradigms that are sometimes hard to synthesize, such as the kinds of empirical and theoretical analyses and the terminology used to describe them.

Some studies focus on cultural evolution from the perspective of the individual, and important insights about the individual-level processes underlying culture have stemmed from research in numerous fields: cognitive science, including the study of creativity and learning [1–3]; animal behaviour, including the trial-and-error versus culturally transmitted components of foraging [4]; and social learning, including learning strategies and transmission biases [5–9]. Other research has focused on the population level: individuals each undertake trial-and-error and social learning on their own, but how do these aggregate when these individuals come together? Studies at this level take theoretical and empirical approaches to population-level cultural dynamics, including patterns of the accumulation and loss of cultural traits in a population and the interaction between populations [10–19]. Yet other studies take an even higher-level approach, focusing on species: for example, evolutionary questions surrounding differences in social learning

mechanisms, cultural niche construction, gene–culture coevolution, and the capacity for language in humans and vocal learning in birds [3,20–37].

In addition to differing by their focus on individuals, populations or species, studies can also consider different units of selection. In Darwinian theory, the reproductive success of the individual determines whether its genetic and/or cultural traits are passed on to the next generation [38]. An alternative view of selection, popularized in *The selfish gene* [39], posits that genes themselves are units of selection, with different genes promoting their own survival and reproduction without regard for the individual or population in which they occur. This perspective has been applied to culture, since cultural traits (called memes in *The selfish gene*) can also act as units of selection, spreading through a population within a generation even if they decrease individual survival or reproductive success [10,17,39,40]. In most circumstances, evolutionary theory predicts that individuals do not act for the benefit of the group, and the evolution of most behaviours that appear to be altruistic can be explained by their benefit to closely related individuals (kin selection) [41–43]. However, recently there has been a lively debate about whether aspects of human behaviour, such as cooperation, can be explained by cultural group selection [44–51].

Studies may also differ between fields and between researchers with regard to their economic assumptions about human behaviour. In psychology and behavioural economics, most research is conducted in populations that might not generalize to all humans; some researchers have coined the term WEIRD (Western, Educated, Industrialized, Rich and Democratic) to underscore the fact that these are a small proportion of all human populations, but are disproportionately represented in experimental research [52–54]. Studies of small-scale societies typically make different assumptions, and often come to different conclusions, from research in industrialized populations: norms of cooperation, sharing, punishment and market forces are quite variable among human populations [52]. This realization is important to many studies of human behaviour that have been approached from both a cultural evolutionary and an economic perspective: assumptions and generalizations about human behaviour require great care and should be made explicit in studies involving economic forces, game theory, balance of power, division of labour, subsistence strategy and transmission biases (see, for example, the different perspectives reflected in [5,8,9,35,49,55–59]).

We suggest that explicitly highlighting these different perspectives may help find commonalities that may bridge the gaps between them and produce insights from multiple perspectives within the same study. To benefit from different perspectives, even within the same study, does not necessarily require a dogma as to which is the most appropriate perspective. In the following, we highlight four areas of research in which the synthesis of cultural evolution with another discipline has led to insights that would have been unlikely to emerge in each field alone.

2. The animal continuum: linking human culture to animal behavioural ecology

The shared essence of many definitions of culture is that it involves behaviours that are socially learned and transmitted and that are maintained stably over some period of time

[60–63]. Humans are quite clearly the most advanced practitioners of culture, but a plethora of studies have clarified that culture is not unique to humans (e.g. [62–66]). This is not surprising, given humans' shared evolutionary origins with all other animals; if anything, it is surprising that to demonstrate the existence of culture in a particular species or context often turns out to be quite challenging, leading to the intuition that human culture is sharply different from animal cultures. The study of animal cultures helps us to be explicit and precise in our characterization of culture, encourages us to define culture in specific, quantifiable terms, and pushes us to explore the dynamics that give rise to culture through the study of proximate mechanisms. A promising approach involves the search for the precursors of human culture among different organisms, with whom we share ancestors, and which can be used to research the evolution of the cognitive and behavioural traits that give rise to culture, as well as to search for regularities in the conditions and context in which culture evolves.

The literature on animal cultures is extensive, and we do not aim to review it all here. We demonstrate its value to the study of cultural evolution by highlighting three comparative evolutionary analyses by Whiten [60,61,67], which integrate experimental and observational data regarding apes and humans. These analyses synthesize studies from the laboratory and the field in order to better understand the cognitive mechanisms that underlie culture. In the following subsections, we summarize some of the insights from these three papers.

(a) Local traditions

Apes in the wild exhibit socially learned behaviours that vary from one group to another. Such learned behaviours famously include fishing for termites, a skill that requires prolonged observation, as well as interaction with socially acquired tools and much trial and error. This is elegantly demonstrated by variation in the style of termite fishing between chimpanzee groups, and the observation that juvenile females, who spend more of their time observing their mothers fishing for termites compared with the time spent by young males (which are busy with things like play-fighting), master this skill, on average, a year earlier than the males [61,68]. Many such cultural traditions exist, including some that seem not to have any immediate utility, such as a behaviour that emerged and spread among the chimpanzees in one of the groups in a chimpanzee sanctuary in northern Zambia: individuals would lodge a tuft of grass into one of their ears and leave it there while engaging in other activities [69].

(b) Near-absence of cumulative culture

Review of the approximately 40 examples of cultural traditions that have been documented in chimpanzees [64] helps to highlight an important commonality: the vast majority of traditions are simple enough to arise on short timescales, on the order of much less than a single generation. Examples like the spontaneous emergence of the grass-in-ear behaviour also demonstrate how such dynamics may take place; although potentially more transient than fitness-related activities such as using stick tools to acquire food or leaf sponges to collect drinking water [70], it seems that a major difference between chimpanzee cultures and those of humans is that the former are not cumulative in nature. A few possible exceptions have been documented; for example, a specific technique of termite fishing from deep underground nests that might have been

developed over multiple generations (e.g. [61,71]). Thus, as Whiten notes, this characterization of humans as the sole species with true cumulative culture seems quite robust and helps to focus research on the detailed dynamics of cultural inventions and their transmission [60,61,67]. Can the difference between complex human and simple chimpanzee cultures be explained by a putative inability of the latter to combine learned behaviours into increasingly complex traditions?

(c) The mechanisms of cultural behaviour

Drawing upon approaches developed in developmental psychology and the study of animal behaviour, a broad range of experiments have addressed details of social learning in chimpanzees and humans, particularly among children. These highlight commonalities as well as differences, and support a general trend in which the precursors of almost every aspect of human social learning are found in apes, whereas humans differ quantitatively in a number of respects. Whiten highlights an important one: the relative roles of copying another individual's behaviour ('imitation') and copying the context of the behaviour and its results ('emulation'). Both are found in both species, but emulation is much more prominent in apes than in human children. An exaggerated form of copying a behaviour ('overimitation'), including features of the behaviour that are irrelevant to the goal of the physical task, is common among humans (including adults), and seems rare in apes. Interpretation of these findings is debated, and the role of the experimental context in affecting these trends is the focus of many current studies (e.g. it is now clear that in children, the framing of the task strongly influences the extent to which emulation, imitation and over-imitation take place [72]). These findings are partially accountable for the relatively low fidelity of cultural transmission among apes as compared with humans, which suggests some possible grounds for the near-absence of cumulative culture among apes.

The same approach allows Whiten to draw inference about other factors, such as conformity, choices about whom to copy, conscious copying of behaviour, teaching, and causal inference regarding observed behaviours. Nearly all of these are found to some extent in apes as well as in humans, demonstrating that the underlying prerequisites for culture are graded between species rather than dichotomous. Studying these prerequisites provides a fertile ground for hypothesizing about the role of different factors in giving rise to human culture, both regarding culture's development on short timescales and in the inference of its dynamics on evolutionary timescales, including the coevolutionary feedback between culture and the genetic predispositions that support culture-related behaviours [60,61,73,74].

Rendell *et al.* [7] demonstrate the utility for the study of cultural evolution of integrating approaches from animal behaviour with those in other fields. These authors used approaches from artificial intelligence studies, economic game theory and evolutionary biology to organize a social learning tournament in which participants submitted a computer-coded behavioural strategy that aims to optimize payoffs in a computer simulation of a changing environment in which foraging for food takes place in a social context. Each agent in the simulation, in each round, could choose to exploit its own previous knowledge or to attempt to learn where to forage by individual trial and error or by copying other agents' behaviour. The framework was that of an evolutionary simulation, with new agents replacing those that die out, and with the probability of producing offspring proportional to the gained payoffs.

In this tournament, successful strategies focused almost solely on social learning and rarely favoured individual trial and error, despite the potential copying error that was involved in observing others. The value of social learning stemmed from a simple insight: individuals exploiting their previously learned knowledge tend to perform their most successful behaviour (in this case: showing which foraging locality yields high rewards), and by doing so they provide—not necessarily intentionally—public information. Another observation was that successful strategies were sensitive to changes in the environment such that exploitation of one's own existing knowledge was halted in favour of (social) learning only when it was likely to be more valuable. This study helped to introduce new concepts into the field of cultural evolution and allowed cultural evolution to borrow from other fields a valuable algorithmic frame of thought regarding behavioural strategies.

3. Population dynamics and cultural evolution: change on ecological timescales

Population dynamics play a fundamental role in ecology and evolutionary biology, and they have also played a prominent role in theoretical studies of cultural evolution. Interestingly, there are a number of levels at which the process of cultural evolution can be seen as influencing, or interacting with, population dynamics. On one hand, since the bearers of culture are individuals in a population, that population's dynamics may be influenced by the culture. For example, individuals may have increased fitness when they have a certain cultural phenotype, such as knowing how to produce or use a certain tool and passing that knowledge from parent to offspring, and the culture may be influenced by the dynamics that result from these fitness differences. On the other hand, one can think of members of a population merely as the bearers of cultural traits, and focus on the instances of cultural knowledge themselves as the entities whose dynamics are studied. When ideas or cultural traits are treated as individual entities and tracked, the population dynamics are those of the 'population of ideas' ([75,76], but see [77] for warnings about possible misconceptions inherent in this approach).

The conceptualization of cultural evolution as a spread of ideas across a network was combined with meticulous field observations of chimpanzee behaviour in a study by Hobaiter *et al.* ([70]; see also [78]). These authors tracked the emergence and spread of two novel behavioural variants related to drinking water in a group of chimpanzees in Budongo Forest, Uganda: the use of moss-sponges to soak up water from a waterhole and then drink it, and the reuse of leaf-sponges for the same purpose (use of leaf-sponges was known in the group previously, but not reuse of discarded leaf-sponges). The animals had discovered a new waterhole, and following its discovery the researchers were able to record all the behaviour near the waterhole for the duration of six consecutive days, thus documenting the first appearance of the novel behaviour, and noting which individuals saw other individuals performing each behaviour.

The cultural dynamics were represented as a spread of ideas among nodes in a network that takes into account the order of events and whose edges describe the number of times that the behaviour was observed, thus giving rise to a dynamic network in time. For the first time in the wild, these observations demonstrated the emergence and spread of a cultural variant through

social transmission; this is notoriously hard, because it is challenging to rule out alternative explanations that do not rely on social transmission. Although the occurrence of a certain behaviour in one group of chimpanzees and not in others is suggestive of local cultural traditions, it might also be explained by convergence of individually learned behaviours towards the same practice owing to environmental pressures, or the behaviour could be innate and simply not observed in other groups because of the different environmental conditions or because of geographical variation in the genetic composition of chimpanzee populations [79].

This analysis explicitly demonstrates an important feature of cultural evolution: it may occur on ecological timescales, even extremely short ones, providing a means of adaptation to novel situations. Although this is quite evident in modern human cultures, which are relatively easy to track, it is only now becoming clear that it also holds true for some animal cultures (see also [80]), and may help to identify the role and dynamics of cultural evolution among earlier hominins as well.

Population dynamics may also interact with cultural evolution through competition between subpopulations of the same species or species complex. Through population replacement, which may be driven by cultural differences, or a combination of cultural exchange, competition and partial replacement, culturally driven population dynamics may lead to extremely rapid changes, on timescales that are on the order of a few generations, much faster than most biological changes of similar scope (see [44] and commentaries therein). A study that explores such dynamics in a modelling framework [81] addresses the relatively fast replacement of Neanderthals by modern humans, as reflected in the archaeological record. This study builds on models that link population size to the level of cultural complexity at steady state (e.g. [82,83]), and suggests that a large population of modern humans that existed in Africa could have had a cultural advantage over Neanderthals (in terms, for example, of efficiency of utilization of food resources) owing to differences in population size. The authors show that this advantage would have allowed even small propagules of migrating moderns to proliferate and eventually replace the Neanderthals in Eurasia. Similar dynamics are proposed to have also taken place in later large-scale human migrations, particularly in the spread of Neolithic farmers across Europe [84–87] and in the spread of the Yamnaya people in the Bronze period [88].

4. Cultural evolution and cognition

Cultural evolution depends on the transmission of ideas, and to understand cultural transmission, we need to also understand the processes of learning that are centred in the brain. Conversely, to fully understand learning, we need to understand not only how individuals acquire and transmit information but also how these processes scale up to a societal level. Thus, cultural evolution and cognitive science are interconnected, and integrative analyses between the two fields have clear mutual benefits.

Models of cultural evolution can benefit from inclusion of insights from cognitive science and related fields. For example, 70 years ago, psychological studies noted that learning can be a process that is biased by cultural factors such as the individual's perception of the prestige of the cultural

model (e.g. [89]). More recently, such transmission biases have been integrated into the study of cultural evolution, in particular their effects on the accumulation of culture in populations [5,8,58,90]. In addition, processes of innovation and creativity were well studied in the cognitive sciences but only sporadically included in cultural evolutionary frameworks, even though innovation is an essential source of new cultural traits [91]. By modifying models of cultural evolution to incorporate insights from cognitive science about the process of human innovation, researchers could recreate dynamics of cultural accumulation in human populations, including exponential growth, punctuated bursts, and spontaneous loss of trait complexes [16,17,91,92].

A recent paper exemplified the utility of this interdisciplinary approach, using a foundation of cognitive science to propose that innovation and imitation work hand-in-hand as drivers of cultural evolution [72]. This study addressed how and when humans innovate versus imitate, particularly focusing on children, who are excellent at imitating how to use tools and how to follow social conventions. However, innovation skills, particularly for tool innovation, develop relatively slowly in human children, perhaps improving the fidelity of cultural transmission by biasing early cultural learning toward imitation [72].

Another set of studies merged cultural evolution, cognitive science and archaeology to understand the evolution of stone tool-making [93]. By recording brain activity as subjects made decisions about how to make stone tools, the authors found that making tools from the Oldowan (approx. 2.6–1.4 Ma) required relatively simple skills, but making tools from the Acheulean tradition (1.6–0.25 Ma) required predicting and evaluating the outcome of each stone-flaking action, which elicited activity in the prefrontal cortex, a region of the brain implicated in planning, decision-making and innovation [93]. Further, it was shown to be difficult for subjects to convey tool-making skills to others without the use of language, suggesting that the increasingly complex cultural artefacts in the archaeological record might be linked to the evolution of the capacity for language in ancient populations [94,95]. These lines of research suggest specific neural underpinnings for the capacities that make us human, such as the capacities to imitate, to learn socially and to plan and evaluate our actions [93,94,96,97].

5. Genetic and cultural change

The evolutionary dynamics of genes and culture have some similarities, particularly for cultural traits that are likely to be passed vertically from parent to offspring, such as language. Indeed, although he did not know about genes, Darwin himself drew a comparison between biological variation and cultural variation, noting that '[t]he formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel' [98]. However, cultural traits can easily violate the assumptions of genetic transmission: they can be transmitted within a generation, can be learned from parents but also from anyone in the population, can be invented or forgotten, and can sometimes spread quickly even when they are maladaptive [40,99–101]. Many studies in cultural evolutionary theory have used models based in theoretical genetics to explore the ramifications of modifying genetic assumptions to accommodate cultural transmission [30,40,102–106].

In the 1970s, researchers began to acknowledge, as Durham stated, that ‘the full explanation of human diversity requires attention to both biological and cultural processes’ [107]. The realization that it was important to study biological and cultural variation in tandem stemmed from two different sources. First, archaeological research had made it clear that genetic and cultural processes had been intertwined in the evolution of humans—not only for the few thousand years of recorded history, but for hundreds of thousands if not millions of years of tool use and cultural accumulation in our hominin ancestors [91,107–109]. Second, advances in genetic sequencing technology turned the joint analysis of genetic and cultural variation from a lofty goal into a reality [110–112]. In their earliest incarnations, analyses of genetic and cultural variation affirmed Darwin’s suspicions from a hundred years prior: there were some clear parallels between genetic phylogenies and language trees [112–114].

The integrative studies of genetic and cultural information that followed have deepened our understanding of human history, leading to insights that would have not been possible with either data type alone. For example, the pattern of ‘isolation by distance’, originating in population genetics, predicts that humans on average have relatively limited dispersal and are thus most likely to find a mate nearby. Over time, this pattern of dispersal will lead to a geographical gradient of genetic similarity, with any given population expected to be more genetically similar to nearby populations than to populations further away [115]. Indeed, several studies have observed a significant relationship between human genetic variation and the geographical locations of the sampled individuals [116–118]. An early study of genetic variation in Europe, however, did not find a smooth gradient of genetic similarity as isolation by distance might have predicted; instead, researchers observed zones of sharp genetic change that primarily corresponded to linguistic boundaries [119], which implies that humans might choose their mates not only based on proximity but also based on language, thus restricting gene flow between linguistic groups. Another insight from combining the study of genetics and culture arises from consideration of two studies that analysed the phylogenetic relations between Austronesian languages and the phylogenetic relations between strains of a human gut bacterium, *Helicobacter pylori*, collected in Pacific islander populations [120,121]. Convergence of the findings from these two very different modalities sheds light on the history of human populations in the Pacific [122].

References

1. Abraham A, Pieritz K, Thybusch K, Rutter B, Kröger S, Schweckendiek J, Stark R, Windmann S, Hermann C. 2012 Creativity and the brain: uncovering the neural signature of conceptual expansion. *Neuropsychologia* **50**, 1906–1917. (doi:10.1016/j.neuropsychologia.2012.04.015)
2. Aziz-Zadeh L, Liew S-L, Dandekar F. 2013 Exploring the neural correlates of visual creativity. *Soc. Cogn. Affect. Neurosci.* **8**, 475–480. (doi:10.1093/scan/nss021)
3. Moya C, Henrich J. 2016 Culture–gene coevolutionary psychology: cultural learning, language, and ethnic psychology. *Curr. Opin. Psychol.* **8**, 112–118. (doi:10.1016/j.copsyc.2015.10.001)
4. Arbilly M, Weissman DB, Feldman MW, Grodzinski U. 2014 An arms race between producers and scroungers can drive the evolution of social cognition. *Behav. Ecol.* **25**, 487–495. (doi:10.1093/beheco/aru002)
5. Mesoudi A. 2008 An experimental simulation of the ‘copy-successful-individuals’ cultural learning strategy: adaptive landscapes, producer–scrounger dynamics, and informational access costs. *Evol. Hum. Behav.* **29**, 350–363. (doi:10.1016/j.evolhumbehav.2008.04.005)
6. Laland KN. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14. (doi:10.3758/BF03196002)
7. Rendell L *et al.* 2010 Why copy others? Insights from the social learning strategies tournament. *Science* **328**, 208–213. (doi:10.1126/science.1184719)
8. Chudek M, Heller S, Birch S, Henrich J. 2012 Prestige-biased cultural learning: bystander’s differential attention to potential models influences children’s learning. *Evol. Hum. Behav.* **33**, 46–56. (doi:10.1016/j.evolhumbehav.2011.05.005)
9. Henrich J, Boyd R. 1998 The evolution of conformist transmission and the emergence of between-group differences. *Evol. Hum. Behav.* **19**, 215–241. (doi:10.1016/S1090-5138(98)00018-X)
10. Henrich J. 2004 Demography and cultural evolution: how adaptive cultural processes can produce

More recent studies that included not only higher resolution genetic data but also more detailed linguistic analyses revealed even more complex patterns [21]. In some groups, such as the Kra–Dai-speaking groups in Thailand and subpopulations in England, language is a better predictor of genetic similarity than geographical proximity; thus, in these populations, language appears to act as a barrier to gene flow [123,124]. In contrast, detailed analysis of several regions, such as North America and Melanesia, showed an opposite phenomenon: in some cases, language boundaries are preserved between populations, but these language barriers do not appear to restrict gene flow between the populations [125,126]. Thus, culturally inherited traits such as language can create stable boundaries between populations even when these boundaries do not restrict gene flow, maintaining a cultural population structure that masks an underlying genetically mixed population. Quantifying these differences helps deepen our understanding of human evolutionary history, and the patterns could not be uncovered without a truly integrative analysis of cultural evolution and genetic variation.

6. Summary

In light of the role of culture in human ecology and evolution [101], we suggest that it would not be an overstatement to paraphrase Dobzhansky [127] in saying that *nothing about humans makes sense except in the light of cultural evolution*. However, cultural evolution occurs on multiple timescales and is driven by dynamics at different levels: individuals, populations of behaving individuals, technological entities and cultural ideas. Analyses at these different levels generate interesting and complementary hypotheses and lines of investigation. We suggest that the integrative approach advocated in this special issue has been, and will continue to be, highly productive. We hope that the studies in this issue will inspire further interdisciplinary research and cross-disciplinary collaborations.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

Funding. This study was funded by the Morrison Institute for Population and Resource Studies at Stanford, the Stanford Center for Computational, Evolutionary, and Human Genetics, the Templeton Foundation, Vanderbilt University and the Ruth Landes Memorial Research Fund.

- maladaptive losses: the Tasmanian case. *Am. Antiq.* **69**, 197–214. (doi:10.2307/4128416)
11. Read D. 2012 *Population size does not predict artifact complexity: analysis of data from Tasmania, arctic hunter-gatherers, and Oceania fishing groups*. Los Angeles, CA: UCLA Center for Human Complex Systems. <https://escholarship.org/uc/item/61n4303q> (accessed 5 January 2018).
 12. Kline MA, Boyd R. 2010 Population size predicts technological complexity in Oceania. *Proc. R. Soc. B* **277**, 2559–2564. (doi:10.1098/rspb.2010.0452)
 13. Collard M, Kemery M, Banks S. 2005 Causes of toolkit variation among hunter-gatherers: a test of four competing hypotheses. *Can. J. Archaeol.* **29**, 1–19.
 14. Collard M, Ruttle A, Buchanan B, O'Brien MJ. 2013 Population size and cultural evolution in nonindustrial food-producing societies. *PLoS ONE* **8**, e72628. (doi:10.1371/journal.pone.0072628)
 15. Collard M, Buchanan B, Morin J, Costopoulos A. 2011 What drives the evolution of hunter–gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. *Phil. Trans. R. Soc. B* **366**, 1129–1138. (doi:10.1098/rstb.2010.0366)
 16. Kolodny O, Creanza N, Feldman MW. 2015 Evolution in leaps: the punctuated accumulation and loss of cultural innovations. *Proc. Natl Acad. Sci. USA* **112**, E6762–E6769. (doi:10.1073/pnas.1520492112)
 17. Kolodny O, Creanza N, Feldman MW. 2016 Game-changing innovations: how culture can change the parameters of its own evolution and induce abrupt cultural shifts. *PLoS Comput. Biol.* **12**, e1005302. (doi:10.1371/journal.pcbi.1005302)
 18. Powell A, Shennan S, Thomas MG. 2009 Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 1298–1301. (doi:10.1126/science.1170165)
 19. Creanza N, Kolodny O, Feldman MW. 2017 Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. *J. R. Soc. Interface* **14**, 20170171. (doi:10.1098/rsif.2017.0171)
 20. Fitch WT, Huber L, Bugnyar T. 2010 Social cognition and the evolution of language: constructing cognitive phylogenies. *Neuron* **65**, 795–814. (doi:10.1016/j.neuron.2010.03.011)
 21. Creanza N, Ruhlen M, Pemberton TJ, Rosenberg NA, Feldman MW, Ramachandran S. 2015 A comparison of worldwide phonemic and genetic variation in human populations. *Proc. Natl Acad. Sci. USA* **112**, 1265–1272. (doi:10.1073/pnas.1424033112)
 22. Kolodny O, Lotem A, Edelman S. 2015 Learning a generative probabilistic grammar of experience: a process-level model of language acquisition. *Cogn. Sci.* **39**, 227–267. (doi:10.1111/cogs.12140)
 23. Kolodny O, Edelman S. 2018 The evolution of the capacity for language: the ecological context and adaptive value of a process of cognitive hijacking. *Phil. Trans. R. Soc. B* **373**, 20170052. (doi:10.1098/rstb.2017.0052)
 24. Woolley SMN, Moore JM. 2011 Coevolution in communication senders and receivers: vocal behavior and auditory processing in multiple songbird species. *Ann. NY Acad. Sci.* **1225**, 155–165. (doi:10.1111/j.1749-6632.2011.05989.x)
 25. Marler P. 1997 Three models of song learning: evidence from behavior. *J. Neurobiol.* **33**, 501–516. (doi:10.1002/(SICI)1097-4695(19971105)33:5<501::AID-NEUJ2>3.0.CO;2-8)
 26. Marler P, Tamura M. 1964 Culturally transmitted patterns of vocal behavior in sparrows. *Science* **146**, 1483–1486. (doi:10.1126/science.146.3650.1483)
 27. Rowell JT, Servedio MR. 2012 Vocal communications and the maintenance of population specific songs in a contact zone. *PLoS ONE* **7**, e0035257. (doi:10.1371/journal.pone.0035257)
 28. Slabbekoorn H, Smith TB. 2002 Bird song, ecology and speciation. *Phil. Trans. R. Soc. Lond. B* **357**, 493–503. (doi:10.1098/rstb.2001.1056)
 29. Verzijden MN, ten Cate C, Servedio MR, Kozak GM, Boughman JW, Svensson EI. 2012 The impact of learning on sexual selection and speciation. *Trends Ecol. Evol.* **27**, 511–519. (doi:10.1016/j.tree.2012.05.007)
 30. Creanza N, Feldman MW. 2014 Complexity in models of cultural niche construction with selection and homophily. *Proc. Natl Acad. Sci. USA* **111**, 10 830–10 837. (doi:10.1073/pnas.1400824111)
 31. Laland KN, O'Brien MJ. 2012 Cultural niche construction: an introduction. *Biol. Theory* **6**, 191–202. (doi:10.1007/s13752-012-0026-6)
 32. Creanza N, Fogarty L, Feldman MW. 2016 Cultural niche construction of repertoire size and learning strategies in songbirds. *Evol. Ecol.* **30**, 285–305. (doi:10.1007/s10682-015-9796-1)
 33. Laland KN, Odling-Smee J, Feldman MW. 2000 Niche construction, biological evolution, and cultural change. *Behav. Brain Sci.* **23**, 131–146. (doi:10.1017/S0140525X00002417)
 34. Feldman MW, Laland KN. 1996 Gene-culture coevolutionary theory. *Trends Ecol. Evol.* **11**, 453–457. (doi:10.1016/0169-5347(96)10052-5)
 35. Lachlan RF, Slater PJB. 1999 The maintenance of vocal learning by gene–culture interaction: the cultural trap hypothesis. *Proc. R. Soc. Lond. B* **266**, 701–706. (doi:10.1098/rspb.1999.0692)
 36. Whiten A. 2017 Culture extends the scope of evolutionary biology in the great apes. *Proc. Natl Acad. Sci. USA* **114**, 7790–7797. (doi:10.1073/pnas.1620733114)
 37. Whiten A. 2017 A second inheritance system: the extension of biology through culture. *Interface Focus* **7**, 20160142. (doi:10.1098/rsfs.2016.0142)
 38. Lewontin RC. 1970 The units of selection. *Annu. Rev. Ecol. Syst.* **1**, 1–18. (doi:10.1146/annurev.es.01.110170.000245)
 39. Dawkins R. 1976 *The selfish gene*. Oxford, UK: Oxford University Press.
 40. Cavalli-Sforza LL, Feldman MW. 1981 *Cultural transmission and evolution: a quantitative approach*. Princeton, NJ: Princeton University Press.
 41. Smith JM. 1964 Group selection and kin selection. *Nature* **201**, 1145–1147. (doi:10.1038/2011145a0)
 42. Abbot P *et al.* 2011 Inclusive fitness theory and eusociality. *Nature* **471**, E1–E4. (doi:10.1038/nature09831)
 43. Eberhard MJW. 1975 The evolution of social behavior by kin selection. *Q. Rev. Biol.* **50**, 1–33, 227–267. (doi:10.1086/408298)
 44. Richerson P *et al.* 2016 Cultural group selection plays an essential role in explaining human cooperation: a sketch of the evidence. *Behav. Brain Sci.* **39**, e30. (doi:10.1017/S0140525X1400106X)
 45. Soltis J, Boyd R, Richerson PJ. 1995 Can group-functional behaviors evolve by cultural group selection?: an empirical test. *Curr. Anthropol.* **36**, 473. (doi:10.1086/204381)
 46. Mace R, Silva AS. 2016 The role of cultural group selection in explaining human cooperation is a hard case to prove. *Behav. Brain Sci.* **39**, e45. (doi:10.1017/S0140525X15000187)
 47. Lamba S. 2016 The empirical evidence that does not support cultural group selection models for the evolution of human cooperation. *Behav. Brain Sci.* **39**, e44. (doi:10.1017/S0140525X15000175)
 48. Amir D, Jordan MR, Rand DG. 2016 Cultural evolution need not imply group selection. *Behav. Brain Sci.* **39**, e32. (doi:10.1017/S0140525X 15000059)
 49. Boyd R, Richerson PJ. 2002 Group beneficial norms can spread rapidly in a structured population. *J. Theor. Biol.* **215**, 287–296. (doi:10.1006/jtbi.2001.2515)
 50. Boyd R, Richerson PJ. 2010 Transmission coupling mechanisms: cultural group selection. *Phil. Trans. R. Soc. B* **365**, 3787–3795. (doi:10.1098/rstb.2010.0046)
 51. Henrich J. 2004 Cultural group selection, coevolutionary processes and large-scale cooperation. *J. Econ. Behav. Organ.* **53**, 3–35. (doi:10.1016/S0167-2681(03)00094-5)
 52. Henrich J, Boyd R, Bowles S, Camerer C, Fehr E, Gintis H, McElreath R. 2001 In search of Homo economicus: behavioral experiments in 15 small scale societies. *Am. Econ. Rev.* **91**, 73–78. (doi:10.1257/aer.91.2.73)
 53. Henrich J, Heine SJ, Norenzayan A. 2010 Most people are not WEIRD. *Nature* **466**, 29. (doi:10.1038/466029a)
 54. Henrich J, Heine SJ, Norenzayan A. 2010 The weirdest people in the world? *Behav. Brain Sci.* **33**, 61–83. (doi:10.1017/S0140525X0999152X)
 55. Krakauer DC, Page KM, Erwin DH. 2009 Diversity, dilemmas, and monopolies of niche construction. *Am. Nat.* **173**, 26–40. (doi:10.1086/593707)
 56. Nowak MA, Tarnita CE, Wilson EO. 2010 The evolution of eusociality. *Nature* **466**, 1057–1062. (doi:10.1038/nature09205)
 57. Nowak M, Krakauer D. 1999 The evolution of language. *Proc. Natl Acad. Sci. USA* **96**, 8028–8033. (doi:10.1073/pnas.96.14.8028)
 58. Henrich J, Gil-White FJ. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196. (doi:10.1016/S1090-5138(00)00071-4)
 59. Aoki K, Lehmann L, Feldman MW. 2011 Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. *Theor. Popul. Biol.* **79**, 192–202. (doi:10.1016/j.tpb.2011.02.001)

60. Whiten A. 2011 The scope of culture in chimpanzees, humans and ancestral apes. *Phil. Trans. R. Soc. B* **366**, 997–1007. (doi:10.1098/rstb.2010.0334)
61. Whiten A. 2017 A comparative and evolutionary analysis of the cultural cognition of humans and other apes. *Span. J. Psychol.* **19**, E98. (doi:10.1017/sjp.2016.99)
62. Van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M. 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105. (doi:10.1126/science.1078004)
63. Laland KN, Galef BG. 2009 *The question of animal culture*. Cambridge, MA: Harvard University Press.
64. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 2001 Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516. (doi:10.1163/156853901317367717)
65. Rendell L, Whitehead H. 2001 Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–324. (doi:10.1017/S0140525X0100396X)
66. Whitehead H, Rendell L. 2014 *The cultural lives of whales and dolphins*. Chicago, IL: University of Chicago Press.
67. Whiten A. 2017 Social learning and culture in child and chimpanzee. *Annu. Rev. Psychol.* **68**, 129–154. (doi:10.1146/annurev-psych-010416-044108)
68. Lonsdorf EV, Eberly LE, Pusey AE. 2004 Sex differences in learning in chimpanzees. *Nature* **428**, 715–716. (doi:10.1038/428715a)
69. Van Leeuwen EJC, Cronin KA, Haun DB. M. 2014 A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*). *Anim. Cogn.* **17**, 1421–1425. (doi:10.1007/s10071-014-0766-8)
70. Hobaiter C, Poisot T, Zuberbühler K, Hoppitt W, Gruber T. 2014 Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biol.* **12**, e1001960. (doi:10.1371/journal.pbio.1001960)
71. Sanz C, Call J, Morgan D. 2009 Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* **5**, 293–296. (doi:10.1098/rsbl.2008.0786)
72. Legare CH, Nielsen M. 2015 Imitation and innovation: the dual engines of cultural learning. *Trends Cogn. Sci.* **19**, 688–699. (doi:10.1016/j.tics.2015.08.005)
73. Tennie C, Call J, Tomasello M. 2009 Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* **364**, 2405–2415. (doi:10.1098/rstb.2009.0052)
74. Byrne RW. 2007 Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Phil. Trans. R. Soc. B* **362**, 577–585. (doi:10.1098/rstb.2006.1996)
75. Lynch A. 2008 *Thought contagion. How belief spreads through society. The new science of memes*. New York, NY: Basic Books.
76. Dawkins R. 1976 Memes: the new replicators. *The selfish gene*, chapter 11, pp. 203–215. Oxford, UK: Oxford University Press.
77. Henrich J, Boyd R, Richerson PJ. 2008 Five misunderstandings about cultural evolution. *Hum. Nat.* **19**, 119–137. (doi:10.1007/s12110-008-9037-1)
78. Hoppitt W, Laland KN. 2011 Detecting social learning using networks: a users guide. *Am. J. Primatol.* **73**, 834–844. (doi:10.1002/ajp.20920)
79. Langergraber KE *et al.* 2010 Genetic and ‘cultural’ similarity in wild chimpanzees. *Proc. R. Soc. B* **278**, 408–416. (doi:10.1098/rspb.2010.1112)
80. Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541. (doi:10.1038/nature13998)
81. Gilpin W, Feldman MW, Aoki K. 2016 An ecocultural model predicts Neanderthal extinction through competition with modern humans. *Proc. Natl Acad. Sci. USA* **113**, 2134–2139. (doi:10.1073/pnas.1524861113)
82. Ghirlanda S, Enquist M. 2007 Cumulative culture and explosive demographic transitions. *Qual. Quant.* **41**, 591–600. (doi:10.1007/s11135-007-9070-x)
83. Aoki K. 2015 Modeling abrupt cultural regime shifts during the Palaeolithic and Stone Age. *Theor. Popul. Biol.* **100**, 6–12. (doi:10.1016/j.tpb.2014.11.006)
84. Skoglund P, Malmström H, Raghavan M, Storå J, Hall P, Willerslev E, Gilbert MTP, Götherström A, Jakobsson M. 2012 Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. *Science* **336**, 466–469. (doi:10.1126/science.1216304)
85. Malmström H *et al.* 2009 Ancient DNA reveals lack of continuity between Neolithic hunter-gatherers and contemporary Scandinavians. *Curr. Biol.* **19**, 1758–1762. (doi:10.1016/j.cub.2009.09.017)
86. Bar-Yosef O. 1998 On the nature of transitions: the Middle to Upper Palaeolithic and the Neolithic Revolution. *Cambridge Archaeol. J.* **8**, 141–163. (doi:10.1017/S0959774300001815)
87. Hofmanová Z *et al.* 2016 Early farmers from across Europe directly descended from Neolithic Aegeans. *Proc. Natl Acad. Sci. USA* **113**, 6886–6891. (doi:10.1073/pnas.1523951113)
88. Goldberg A, Günther T, Rosenberg NA, Jakobsson M. 2017 Ancient X chromosomes reveal contrasting sex bias in Neolithic and Bronze Age Eurasian migrations. *Proc. Natl Acad. Sci. USA* **114**, 2657–2662. (doi:10.1073/pnas.1616392114)
89. Asch SE. 1948 The doctrine of suggestion, prestige and imitation in social psychology. *Psychol. Rev.* **55**, 250. (doi:10.1037/h0057270)
90. Reyes-García V, Molina JL, Broesch J, Calvet L, Huanca T, Saus J, Tanner S, Leonard WR, McDade TW. 2008 Do the aged and knowledgeable men enjoy more prestige? A test of predictions from the prestige-bias model of cultural transmission. *Evol. Hum. Behav.* **29**, 275–281. (doi:10.1016/j.evolhumbehav.2008.02.002)
91. Fogarty L, Creanza N, Feldman MW. 2015 Cultural evolutionary perspectives on creativity and human innovation. *Trends Ecol. Evol.* **30**, 736–754. (doi:10.1016/j.tree.2015.10.004)
92. Enquist M, Ghirlanda S, Jarrick A, Wachtmeister C-A. 2008 Why does human culture increase exponentially? *Theor. Popul. Biol.* **74**, 46–55. (doi:10.1016/j.tpb.2008.04.007)
93. Stout D, Hecht E, Khreisheh N, Bradley B, Chaminade T. 2015 Cognitive demands of Lower Paleolithic toolmaking. *PLoS ONE* **10**, e0128256. (doi:10.1371/journal.pone.0121804)
94. Morgan TJH *et al.* 2015 Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nat. Commun.* **6**, 6029. (doi:10.1038/ncomms7029)
95. Stout D, Hecht EE. 2017 The evolutionary neuroscience of cumulative culture. *Proc. Natl Acad. Sci. USA* **114**, 7861–7866. (doi:10.1073/pnas.1620738114)
96. Stout D. 2011 Stone toolmaking and the evolution of human culture and cognition. *Phil. Trans. R. Soc. B* **366**, 1050–1059. (doi:10.1098/rstb.2010.0369)
97. Putt SS, Wijekumar S, Franciscus RG, Spencer JP. 2017 The functional brain networks that underlie Early Stone Age tool manufacture. *Nat. Hum. Behav.* **1**, 0102. (doi:10.1038/s41562-017-0102)
98. Darwin C. 1888 *The descent of man, and selection in relation to sex*. Glasgow, UK: Murray.
99. Boyd R, Richerson PJ. 1985 *Culture and the evolutionary process*. Chicago, IL: Chicago University Press.
100. Creanza N, Feldman MW. 2016 Worldwide genetic and cultural change in human evolution. *Curr. Opin. Genet. Dev.* **41**, 85–92. (doi:10.1016/j.gde.2016.08.006)
101. Creanza N, Kolodny O, Feldman MW. 2017 Cultural evolutionary theory: how culture evolves and why it matters. *Proc. Natl Acad. Sci. USA* **114**, 7782–7789. (doi:10.1073/pnas.1620732114)
102. Feldman MW, Cavalli-Sforza LL. 1975 Models for cultural inheritance: a general linear model. *Ann. Hum. Biol.* **2**, 215–226. (doi:10.1080/03014467500000791)
103. Cavalli-Sforza LL, Feldman MW. 1973 Cultural versus biological inheritance: phenotypic transmission from parents to children. *Am. J. Hum. Genet.* **25**, 618.
104. Richerson PJ, Boyd R. 1978 A dual inheritance model of the human evolutionary process I: basic postulates and a simple model. *J. Soc. Biol. Struct.* **1**, 127–154. (doi:10.1016/S0140-1750(78)80002-5)
105. Laland KN, Kumm J, Horn JD, Feldman MW. 1995 A gene-culture model of human handedness. *Behav. Genet.* **25**, 433–445. (doi:10.1007/BF02253372)
106. Gray RD, Greenhill SJ, Ross R. 2007 The pleasures and perils of Darwinizing culture (with phylogenies). *Biol. Theory* **2**, 1–26. (doi:10.1162/biot.2007.2.4.360)
107. Durham WH. 1982 Interactions of genetic and cultural-evolution—models and examples. *Hum. Ecol.* **10**, 289–323. (doi:10.1007/BF01531188)
108. Klein RG. 1995 Anatomy, behavior, and modern human origins. *J. World Prehistory* **9**, 167–198. (doi:10.1007/BF02221838)
109. Klein RG. 2002 *The dawn of human culture*. Hoboken, NJ: John Wiley & Sons.
110. Cavalli-Sforza LL. 2005 The human genome diversity project: past, present and future. *Nat. Rev. Genet.* **6**, 333–340. (doi:10.1038/nrg1579)
111. Ammerman AJ, Cavalli-Sforza LL. 1984 *The Neolithic transition and the genetics of populations in Europe*. Princeton, NJ: Princeton University Press.

112. Cavalli-Sforza LL, Piazza A, Menozzi P, Mountain J. 1988 Reconstruction of human evolution: bringing together genetic, archaeological, and linguistic data. *Proc. Natl Acad. Sci. USA* **85**, 6002–6006. (doi:10.1073/pnas.85.16.6002)
113. Cavalli-Sforza LL. 1997 Genes, peoples, and languages. *Proc. Natl Acad. Sci. USA* **94**, 7719–7724. (doi:10.1073/pnas.94.15.7719)
114. Cavalli-Sforza LL, Minch E, Mountain JL. 1992 Coevolution of genes and languages revisited. *Proc. Natl Acad. Sci. USA* **89**, 5620–5624. (doi:10.1073/pnas.89.12.5620)
115. Wright S. 1943 Isolation by distance. *Genetics* **28**, 114.
116. Novembre J *et al.* 2008 Genes mirror geography within Europe. *Nature* **456**, 98–101. (doi:10.1038/nature07331)
117. Lao O *et al.* 2008 Correlation between genetic and geographic structure in Europe. *Curr. Biol.* **18**, 1241–1248. (doi:10.1016/j.cub.2008.07.049)
118. Wang C, Szpiech ZA, Degnan JH, Jakobsson M, Pemberton TJ, Hardy JA, Singleton AB, Rosenberg NA. 2010 Comparing spatial maps of human population-genetic variation using Procrustes analysis. *Stat. Appl. Genet. Mol. Biol.* **9**, 1–20. (doi:10.2202/1544-6115.1493)
119. Barbujani G, Sokal RR. 1990 Zones of sharp genetic change in Europe are also linguistic boundaries. *Proc. Natl Acad. Sci. USA* **87**, 1816–1819. (doi:10.1073/pnas.87.5.1816)
120. Gray RD, Drummond AJ, Greenhill SJ. 2009 Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* **323**, 479–483. (doi:10.1126/science.1166858)
121. Moodley Y *et al.* 2009 The peopling of the Pacific from a bacterial perspective. *Science* **323**, 527–530. (doi:10.1126/science.1166083)
122. Renfrew C. 2009 Where bacteria and languages concur. *Science* **323**, 467–468. (doi:10.1126/science.1168953)
123. Longobardi G, Ghirotto S, Guardiano C, Tassi F, Benazzo A, Ceolin A, Barbujani G. 2015 Across language families: genome diversity mirrors linguistic variation within Europe. *Am. J. Phys. Anthropol.* **157**, 630–640. (doi:10.1002/ajpa.22758)
124. Srithawong S, Srikumool M, Pittayaporn P, Ghirotto S, Chantawannakul P, Sun J, Eisenberg A, Chakraborty R, Kutanan W. 2015 Genetic and linguistic correlation of the Kra–Dai-speaking groups in Thailand. *J. Hum. Genet.* **60**, 1–10. (doi:10.1038/jhg.2015.32)
125. Hunley K, Long JC. 2005 Gene flow across linguistic boundaries in Native North American populations. *Proc. Natl Acad. Sci. USA* **102**, 1312–1317. (doi:10.1073/pnas.0409301102)
126. Hunley K, Dunn M, Lindström E, Reesink G, Terrill A, Healy ME, Koki G, Friedlaender FR, Friedlaender JS. 2008 Genetic and linguistic coevolution in Northern Island Melanesia. *PLoS Genet.* **4**, e1000239. (doi:10.1371/journal.pgen.1000239)
127. Dobzhansky T. 1973 Nothing in biology makes sense except in the light of evolution. *Am. Biol. Teach.* **35**, 125–129. (doi:10.2307/4444260)