

Cultural Evolution: A Review of Theory, Findings and Controversies

Alex Mesoudi^{1,2}

Received: 30 January 2015 / Accepted: 3 April 2015
© Springer Science+Business Media New York 2015

Abstract The last two decades have seen an explosion in research analysing cultural change as a Darwinian evolutionary process. Here I provide an overview of the theory of cultural evolution, including its intellectual history, major theoretical tenets and methods, key findings, and prominent criticisms and controversies. ‘Culture’ is defined as socially transmitted information. Cultural evolution is the theory that this socially transmitted information evolves in the manner laid out by Darwin in *The Origin of Species*, i.e. it comprises a system of variation, differential fitness and inheritance. Cultural evolution is not, however, neo-Darwinian, in that many of the details of genetic evolution may not apply, such as particulate inheritance and random mutation. Following a brief history of this idea, I review theoretical and empirical studies of cultural microevolution, which entails both selection-like processes wherein some cultural variants are more likely to be acquired and transmitted than others, plus transformative processes that alter cultural information during transmission. I also review how phylogenetic methods have been used to reconstruct cultural macroevolution, including the evolution of languages, technology and social organisation. Finally, I discuss recent controversies and debates, including the extent to which culture is proximate or ultimate, the relative role of selective and transformative processes in cultural evolution, the basis of cumulative cultural evolution, the

evolution of large-scale human cooperation, and whether social learning is learned or innate. I conclude by highlighting the value of using evolutionary methods to study culture for both the social and biological sciences.

Keywords Cultural evolution · Cultural transmission · Cumulative culture · Demography · Human evolution · Social learning

Introduction

Cultural evolution is the theory that cultural change in humans and other species can be described as a Darwinian evolutionary process, and consequently that many of the concepts, tools and methods used by biologists to study biological evolution can be equally profitably applied to study cultural change (Mesoudi 2011a; Richerson and Boyd 2005; Richerson and Christiansen 2013). ‘Culture’ here entails any socially (rather than genetically) transmitted information, such as beliefs, knowledge, skills or practices. Just as biologists seek to explain the diversity and complexity of life and living organisms, cultural evolution researchers seek to explain the diversity and complexity of culture and cultural phenomena.

Evolutionary biologists to whom I speak are sometimes surprised by the depth and diversity of modern cultural evolution research. Just three decades ago cultural evolution research was the almost-secret passion of a handful of scholars, and limited in method to rather technical mathematical models (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). The last two decades, however, have seen an explosion in cultural evolution research. The use of mathematical models continues to occupy the core of the field (Aoki and Feldman 2014; Enquist et al. 2011; Kempe

✉ Alex Mesoudi
a.mesoudi@exeter.ac.uk

¹ Department of Anthropology, Durham University, South Road, Durham DH1 3LE, UK

² Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, UK

et al. 2014; Lehmann et al. 2011; Lewis and Laland 2012; McElreath and Henrich 2006), but has been supplemented with laboratory experiments testing the assumptions and predictions of those models (Derex et al. 2013; Kempe et al. 2012; Kirby et al. 2008; McElreath et al. 2008; Mesoudi and Whiten 2008; Morgan et al. 2011); field studies doing the same in real-life settings (Aunger 2000; Henrich and Henrich 2010; Hewlett et al. 2011; Reyes-Garcia et al. 2009); phylogenetic studies that reconstruct the evolutionary relationships between languages (Bouckaert et al. 2012; Dunn et al. 2011; Pagel 2009), artefacts (Lipo et al. 2006; Lycett 2009; O'Brien et al. 2014; Tehrani and Collard 2002) and texts (Barbrook et al. 1998; Ross et al. 2013; Tehrani 2013); the study of historical dynamics using ecological models (Turchin 2008; Turchin et al. 2013); and the comparative study of non-human culture using many of the same methods as applied to humans (Dean et al. 2014; Laland and Galef 2009; Lycett et al. 2007; Whiten 2005).

The aim of this article is to review the theoretical foundations of this burgeoning work, provide some examples of how evolutionary concepts and methods have illuminated cultural phenomena, and explore recent controversies and outstanding research questions in the field.

A Brief History of Cultural Evolution

Long before Darwin published *The Origin of Species* in 1859, historical linguists were constructing trees of historical descent for languages, based on the principle that more similar contemporary languages most likely shared a more recent common ancestor (van Wyhe 2005). In other words, that languages—which are socially transmitted, given that there are no genes for specific languages such as English or Hindi—gradually evolve over time and thus show the same descent with modification that Darwin was later to apply to species. It is unclear whether these linguistic trees directly influenced Darwin (although intriguingly, one of the major proponents of historical linguistics in England was Hensleigh Wedgwood, Darwin's cousin and future brother-in-law: van Wyhe 2005). It is clear, however, that Darwin very quickly saw clear parallels between how species and languages change over time:

The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel...We find in distinct languages striking homologies due to community of descent. The frequent presence of rudiments, both in languages and in species, is still more remarkable. Dominant languages and dialects spread widely, and lead to the gradual

extinction of other tongues. A language, like a species, when once extinct, never reappears. We see variability in every tongue, and new words are continually cropping up; but as there is a limit to the powers of the memory, single words, like whole languages, gradually become extinct. The survival or preservation of certain favoured words in the struggle for existence is natural selection (Darwin 1871, p. 90).

Here, Darwin went further than merely applying the notion of common descent to languages, as the linguists had done. He also applied his mechanism of natural selection to language change. Similar parallels were drawn between biological evolution and technological evolution by Augustus Pitt-Rivers around the same time (Pitt-Rivers 1875), whose museum in Oxford was, and still is, innovative in displaying archaeological and ethnographic items according to their presumed evolutionary relationships, rather than their age or collector.

In an alternative universe, these strands of evolutionary thinking in the social sciences would have matured into a quantitative and rigorous science of cultural evolution, in the same way that evolutionary theory became established in the biological sciences via population genetics models in the early 1900s and then the evolutionary synthesis in the 1940s (Mayr 1982). Sadly, cultural evolution instead took an unfortunate wrong turn. In the late 1800s several anthropologists and sociologists devised schemes of cultural evolution based not on Darwin's theory of descent-based trees and natural selection, but rather on Herbert Spencer's progressive, ladder-like, unilinear theory of evolution (Freeman 1974). These schemes, such as those of Morgan (1877) and Tylor (1871), saw cultural evolution as the inevitable progress of entire societies along a sequence of fixed stages of increasing advancement, starting at savagery and barbarism, and ending at civilisation. 'Civilisation' typically resembled the Victorian English or American societies of the schemes' authors.

The racist tones of these theories is obvious today but not unusual in that time of cultural imperialism, and these Spencerian schemes were often used to justify the subjugation of supposedly 'less evolved' societies by 'more evolved' ones, frequently mixed in with ideas of eugenics. A later wave of anthropologists such as Boas (1940) see Lewis (2001) quite correctly rejected these progressive Spencerian theories not just because of their political motivation but also, perhaps more importantly, because they have little empirical basis. Entire societies simply do not fit into neat stages of increasing complexity. For many socio-cultural anthropologists today, however, this association between evolution and stage-like progression remains. It is worth emphasising that these progressive Spencerian

theories are not what is meant by ‘cultural evolution’ today, which draws on Darwin’s theory of evolution rather than Spencer’s, the latter of which resembles the development of an individual rather than the evolution of a population.

During the mid-twentieth century a few isolated scholars maintained that a properly Darwinian theory of cultural evolution was viable, such as the psychologist Campbell (1965). Richard Dawkins provoked interest but little actual empirical research with his notion of the ‘meme’ in the final chapter of *The Selfish Gene* (Dawkins 1976), intended to illustrate the substrate-neutrality of his replicator-based theory of evolution. However, just as evolutionary theory in the biological sciences only really became useful once it had been formalised mathematically by population geneticists such as Fisher, Haldane and Wright in the early 1900s, cultural evolution only really took off once two pairs of scholars devised quantitative mathematical models of cultural evolution in two books in the 1980s: one by Cavalli-Sforza and Feldman (1981) and the other by Boyd and Richerson (1985). These books were also notable in taking seriously the differences between biological and cultural evolution, rather than simply importing biological analogies to the cultural case, as perhaps both Campbell and Dawkins were guilty of doing. The following section outlines the theoretical basis of cultural evolution as presented in these books, and which has inspired much subsequent research.

The Theory of Cultural Evolution

Many textbook definitions of evolution talk of changes in gene frequencies or require Mendelian rules of genetic inheritance. While this is reasonable when one’s focus is exclusively on biological (i.e. genetic) evolution, Darwin’s theory can quite easily be formulated in a general, mechanism-neutral manner. After all, Darwin himself knew nothing about genes or Mendelian inheritance when he wrote *The Origin*. Lewontin (1970) expressed this generality by defining evolution as comprising three principles, each of which were clearly specified in *The Origin*:

1. Different entities in a population vary in their characteristics (principle of variation).
2. These entities have different rates of survival and reproduction (principle of differential fitness, or what Darwin called a ‘struggle for existence’).
3. There is a correlation between parent and offspring entities in those characteristics that contribute to differential fitness (principle of inheritance).

Lewontin (1970) goes on to state that:

It is important to note a certain generality in the principles. No particular mechanism of inheritance is specified, but only a correlation in fitness between parent and offspring. The population would evolve whether the correlation between parent and offspring arose from Mendelian, cytoplasmic, or cultural inheritance (Lewontin 1970, p. 1).

The theory of cultural evolution holds that cultural change can be described by these three general principles (Mesoudi et al. 2004), as Lewontin (1970) alludes to when he talks of cultural inheritance.¹ Thus, cultural traits (words, ideas, artefacts etc.) exhibit variation; these variants have different rates of survival and reproduction; and they are transmitted from person to person via social learning mechanisms such as imitation or speech.

To give a concrete example, Lieberman et al. (2007) used vast quantitative databases of English verb usage over the past 1200 years to show that, at any single point in time, verbs have often varied in their past tense form, including regular (e.g. chided) and irregular (e.g. chid, chode) forms (principle of variation), and that regular forms have steadily displaced irregular forms particularly for those verbs that are infrequently used (principle of differential fitness). Given that verb form is learned from others just like other aspects of one’s language (Harris 1995; Labov 1972), the principle of inheritance is also observed. So this provides quantitative support for Darwin’s informal suggestion in the quote above that words vary, they compete for expression, and they are transmitted from person to person. Thus, they evolve. Similar observations can be made for technology, such as the replacement of traditional seed corn with hybrid seed corn in Iowa during the 1940s (Henrich 2001; Ryan and Gross 1943), or any number of other well-documented examples of the diffusion of innovations (Rogers 1995) and changing frequencies of archaeological artefacts such as pottery types (Shennan 2002).

Beyond these three general principles derived from *The Origin*, no further assumptions are made about the mechanisms by which the principles operate. We do not need to—and often should not—impose mechanisms that are specific to biological evolution onto cultural evolution. These might include the mechanisms of genetic inheritance, such as the acquisition of information in equal contribution from two parents or the existence of discrete units that are inherited in a particulate fashion, or the

¹ Confusingly, the terms ‘social learning’, ‘social transmission’, ‘cultural transmission’, ‘cultural inheritance’ and variants thereof are used interchangeably within the field, to denote the passing of information non-genetically from one individual to another. Here I stick to the term ‘social learning’, although this may differ from cited sources.

randomness of genetic mutation with respect to fitness. In Mesoudi (2011a), I expressed this as follows: cultural evolution is *Darwinian*, in that it comprises the three general principles of variation, differential fitness and inheritance as laid out by Darwin in *The Origin*, but it is not *neo-Darwinian*, in that it may not necessarily exhibit the specific mechanisms of genetic inheritance, random mutation etc. that biologists subsequent to Darwin discovered and that were integrated into evolutionary theory during the evolutionary synthesis.

Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) constructed quantitative mathematical models of cultural evolution using the tools of population genetics, and which clearly made this distinction. Cavalli-Sforza and Feldman (1981) constructed models that explored the transmission of cultural traits not only from one's biological parents (vertical social learning) but also from peers (horizontal social learning) and from older unrelated members of the parental generation (oblique social learning). They constructed models of cultural mutation, analogous to genetic mutation, where novel cultural traits appear at random; cultural selection, analogous to natural selection, where certain cultural traits are more likely to be learned and transmitted than others; and cultural drift, an analogue of genetic drift, where cultural traits change in frequency due to chance. They explored the consequences of migration and other demographic processes for cultural diversity. They also modelled the evolution of continuous cultural traits, abandoning the assumption of discrete replicators and particulate inheritance. Contrary to Dawkins (1976), these models demonstrated that discrete replicators are not necessary for evolution, all that is required is some form of variation, be it discrete or continuous, and some form of inheritance, be it particulate or blending (Henrich and Boyd 2002).

Boyd and Richerson (1985) constructed models adding psychological realism to the notion of cultural selection, modelling cases where people preferentially copy the traits of successful or prestigious individuals (indirect or prestige bias), copy traits on the basis of their popularity (frequency-dependent bias, with positive frequency-dependence called conformity, and negative frequency-dependence called anti-conformity), or copy traits based on their intrinsic characteristics (e.g. their memorability or usefulness, known as direct or content bias). They also constructed models whereby individuals transform cultural traits in particular, non-random directions ('guided variation', in contrast to random genetic mutation). Finally, they explored the interaction between genetic and cultural evolution, examining the conditions under which social learning might genetically evolve, which led to analyses of specific cases of gene-culture coevolution (Feldman and Laland 1996; Laland et al. 2010).

These models concern the equivalent of what biologists would call microevolution. The following years saw the introduction of phylogenetic methods to reconstruct cultural macroevolution, within anthropology (Mace and Pagel 1994), linguistics (Gray and Atkinson 2003; Gray and Jordan 2000; Pagel 2009), and archaeology (O'Brien et al. 2001; O'Brien and Lyman 2003). These focus less on the within-population mechanisms of cultural microevolution, and more on reconstructing evolutionary relationships between languages, artefacts and customs, given the insight that these traits are related by evolutionary descent (Gray et al. 2007; Lipo et al. 2006; Pagel 2009). Just as in biology, this concerns constructing the most likely evolutionary tree given the data, distinguishing between homoplasies and homologies, and using trees to test hypotheses using the comparative method controlling for the non-independence of data points due to common descent (here, cultural rather than genetic descent). Also as in biology, initial use of maximum parsimony has given way to more sophisticated Bayesian Markov Chain Monte Carlo (MCMC) methods (Matthews et al. 2011; Pagel 2009).

In summary, cultural evolution theory rests on the principle that cultural change is Darwinian, in that it exhibits variation, differential fitness and inheritance (Mesoudi et al. 2004). It does not, however, require that these processes follow neo-Darwinian principles, such as particulate inheritance or random mutation (Mesoudi 2011a). Population-genetic-like mathematical models have formalised the processes that are thought to drive cultural microevolution, including psychological decision-making processes such as conformity or memory biases, and demographic processes such as migration or drift. Phylogenetic methods have been used to reconstruct cultural macroevolution based on the principle of inheritance. Much subsequent work has been devoted to using lab experiments, field studies of real-life populations, and historical/archaeological data to test the assumptions and predictions of these theoretical models. The following section highlights some key findings that have emerged from this theoretical foundation.

Key Findings in the Field

The following comprises a subjective selection of what I consider to be the major advances in cultural evolution research in the last decade or so, although there is much that I have not included due to space constraints. I have tried to select examples that have been addressed using multiple methods (models, experiments, field studies, historical analyses) and replicated by multiple independent labs. There is a tendency to focus on humans, again because of space constraints, but many of the same findings

equally apply to non-human species. I start with key findings related to cultural microevolution, and gradually move to cultural macroevolution.

Social Learning is Payoff-Biased and Conformist

Evolutionary models predict that social learners should be selective in when and who they copy (Boyd and Richerson 1995; Enquist et al. 2007; Laland 2004), otherwise social learning confers no adaptive benefits compared to asocial learning (Rogers 1988). Two key social learning biases, first introduced and modelled by Boyd and Richerson (1985), concern who one learns from. *Payoff bias* (also labelled *indirect bias*, *success bias*, or *copy-successful-individuals*) involves copying individuals who demonstrate some degree of success in terms of high or higher payoffs. Various forms of payoff bias have been modelled, including copying the individual with the highest absolute payoff, copying another individual if that other individual's payoff is higher than one's own, or copying in proportion to the difference between own and other's payoffs (Schlag 1998), but they all have in common some assessment of payoffs to behaviour. 'Payoff' may be defined biologically (e.g. feeding or reproductive success) or culturally (e.g. wealth, social power), which may or may not coincide.

An alternative is *conformist bias* (also labelled *positive frequency-dependent bias* or *copy-the-majority*), which involves being disproportionately more likely to copy the most common behaviour in the population irrespective of its payoff (Henrich and Boyd 1998). For example, if 6 out of 10 peers exhibit behaviour A rather than B, a conformist learner would have a >0.6 chance of adopting behaviour A (copying A with exactly 0.6 probability would describe an unbiased social learner, while copying A with <0.6 probability would be anti-conformist).

Subsequent experiments have shown that people employ both of these social learning strategies, as predicted, but that payoff bias is typically preferred to conformity. McElreath et al. (2008) found this using a simple two-option task of planting wheat or potatoes where one gave higher yields, Morgan et al. (2011) using various tasks including mental rotation and perceptual judgements, and Mesoudi (2011b) using a more complex artifact-design task. In each of these, participants could employ trial-and-error asocial learning, or use some form of social learning. A notable recent study by Molleman et al. (2014) found that participants were more likely to employ payoff bias in a two-option task where one option always has a higher payoff, but more likely to use conformity in social dilemma, coordination and evasion games where payoffs depend on other participants' behaviour.

Less research has examined these biases outside the lab, in natural settings, but findings generally reflect the

experimental results. Henrich and Henrich (2010) showed that pregnant women in Fijian fishing villages preferentially acquire adaptive food taboos from locally prestigious unrelated older women, consistent with payoff bias. Beheim et al. (2014) analysed records of opening moves of professional players of the popular East Asian board game Go, showing the preferential copying of the moves of successful players. These findings fit with data from sociology on the diffusion of innovations (Rogers 1995) showing that innovations often spread via successful or high status 'change agents', and sociolinguistics (Labov 1972) showing that dialect change spreads via the imitation of successful or prestigious individuals. Perhaps mirroring the experimental results, conformity in the sense modelled by Boyd and Richerson (1985) has received less clear non-experimental support. Henrich (2001) argued that long-tailed S-shaped diffusion curves of technological innovations are indicative of conformity, but such curves may also be consistent with other underlying learning biases (Kandler and Steele 2009).

The predictions derived from evolutionary models are not specific to humans. Indeed, recent experiments show just as good evidence for payoff bias and conformity in fish, birds and mammals. Pike et al. (2010) showed that nine-spined sticklebacks abandoned a food patch they had previously learned was optimal when they observed a demonstrator feeding at a higher-payoff patch. Conformity has been demonstrated in stickleback (Pike and Laland 2010) and great tits (Aplin et al. 2014), with an individual fish or bird disproportionately more likely to feed at a location where a majority of other individuals had fed. These studies with phylogenetically diverse species show that adaptive social learning rules likely evolved independently in response to particular ecological conditions rather than exclusively in our own species' recent ancestors. Indeed, chimpanzees are surprisingly reluctant to switch to higher-payoff behaviours (Marshall-Pescini and Whiten 2008; although see Yamamoto et al. 2013) and while they do exhibit social learning, and this is sometimes labelled 'conformity' (e.g. Whiten et al. 2005), conformity has not been demonstrated in chimpanzees in the specific sense of being disproportionately more likely to copy the majority (van Leeuwen and Haun 2013).

Why are these social learning strategies important? A key advantage of Darwinian population thinking is that we can extrapolate from small-scale individual-level decisions to large-scale population-level patterns. It has been argued (Boyd and Richerson 1995; Enquist and Ghirlanda 2007; Henrich 2004; Mesoudi 2011c) that payoff-biased social learning is a crucial component of *cumulative cultural evolution*, whereby beneficial traits are selectively preserved and built upon over successive generations (Tomasello 1999). It is not difficult to see why: only payoff bias will drive populations to selectively preserve and build

upon beneficial traits. It has also been argued that some forms of payoff-bias, particularly ones that use more indirect measures of success like prestige, can generate prestige hierarchies as people pay costs in terms of deference or material goods in exchange for access to skilled people's knowledge (Henrich and Gil-White 2001). While broadly adaptive, this may misfire when the sources of prestige are disconnected from the sources of success (Atkisson et al. 2011), and may lead to runaway selection for excessive indicators of success (Boyd and Richerson 1985). Conformity, meanwhile, has been suggested as a means to maintain between-group cultural variation, given that it forces migrants to adopt the majority behaviour of their new group (Henrich and Boyd 1998). Some have suggested that selection may then act on these homogenous cultural groups, favouring the emergence of group-level adaptations (Henrich and Boyd 2001).

Cognitive Biases can Drive Cultural Evolution Towards Cultural Attractors

A general principle of biological evolution is that inheritance alone does not cause evolutionary change, except in rare cases such as meiotic drive. This is formalised in the Hardy–Weinberg principle, as well as the Price equation (Price 1970), where for biological systems the component that specifies evolutionary change due to transmission is typically set to zero.

In cultural evolution, however, transmission is not necessarily unbiased in this manner. People typically transform cultural information they receive from others in non-random directions due to the structure and function of cognition. This was formalised by Boyd and Richerson (1985) in their models of 'guided variation', where an individual acquires a cultural trait from another individual, then modifies that trait in some non-random manner, before passing it on to another individual. The same process has been modelled using a Bayesian framework, where cognitive (or 'inductive') biases form the priors that people use when making inferences about culturally acquired information (Griffiths et al. 2008; Kirby et al. 2007). A group of cognitive anthropologists led by Dan Sperber (Boyer 1998; Claidière and Sperber 2007; Sperber 1996) have also emphasised the importance of this individual transformation due to cognitive biases, with Sperber coining the term 'cultural attractor' to describe a representation that is particularly likely to result from this individual transformation.²

Closely related, but formally distinct, are content biases (Henrich and McElreath 2003). These occur not via the transformation of information by individuals, but when individuals preferentially select certain cognitively appealing traits, without any modification or transformation. Content biases are therefore selection-like, because they change trait frequencies rather than the traits themselves. Both content biases and guided variation are likely to involve the same cognitive operations, but as Boyd and Richerson (1985) showed, they have different evolutionary dynamics: the strength of selection-like content biases, like selection in general, depends on the amount of variation in the population, while the strength of guided variation depends only on individual features of cognition rather than populational characteristics.

A wealth of experimental studies demonstrate the existence of these cognitive biases (incorporating guided variation and content biases). Several studies have used the 'transmission chain' method (Bartlett 1932; Mesoudi and Whiten 2008) which experimentally simulates the transmission of cultural information along a chain of individuals, much like the children's game Telephone. In the case of written material, for example, each person reads and recalls from memory what the previous person recalled, the new recall is given to the next person to remember, and so on along the chain.

Transmission chain studies have shown that certain kinds of information are preferentially transmitted. A result replicated by several independent labs is that information about social relationships is transmitted with higher fidelity than equivalent non-social information (McGuigan and Cubillo 2013; Mesoudi et al. 2006; Reysen et al. 2011; Stubbersfield et al. 2014), as predicted by social brain theories of the biological evolution of primate cognition (Dunbar 2003). There is also experimental support for a bias for emotionally salient disgust-inducing information (Eriksson and Coultas 2014; Heath et al. 2001). Xu et al. (2013), meanwhile, found that initially random colour terms transmitted along chains of people gradually converged on those colour terms commonly seen across actual societies, arguing that the innate features of our perceptual system makes certain colours more salient and thus more likely to emerge through repeated transmission. These would all be examples of biases in cultural evolution that have roots in biologically-evolved features of individual human cognition and perception, resulting from naturally selected adaptations for living in complex groups (social bias), protecting against disease (disgust bias), and innate features of our perceptual systems (colour perception).

Other transmission chain studies have shown how the structure of cognition shapes culturally transmitted information as a result of repeated transmission. Mesoudi and Whiten (2004) showed that detailed descriptions of events

² Some of this latter school (e.g. Claidière et al. 2014) have argued that the existence of these transformative processes requires a major revision of the standard approach to cultural evolution presented in this article; I deal with this critique separately in a later section.

become systematically ‘schematized’ during transmission, i.e. low-level details such as names and dates are lost as material is transformed into more generic higher-level knowledge. Similar effects have been found for gender and racial stereotypes (Kashima 2000; Martin et al. 2014), with stereotype-inconsistent information gradually transformed into simpler, stereotype-consistent information. Kirby et al. (2008) showed how a similar process can shape grammatical features of languages, by demonstrating that artificial languages transmitted along chains of people gradually become more learnable, and in so doing come to possess features of actual languages, such as compositionality, that are typically thought of as innate.

Transmission chain experiments have also been performed with non-human species (Whiten and Mesoudi 2008). Interestingly, similar inductive biases to those observed by Kirby et al. (2008) have been shown in songbirds, where repeated learning constraints generate structure in songs in the same way that repeated learning constraints generate structure in languages (Feher et al. 2009).

As noted previously, Darwinian population thinking allows us to link individual-level biases to population-level patterns. The cognitive biases discussed in this section are consistent with certain patterns of cultural diversity observed in ethnographic and historical records (Sperber and Hirschfeld 2004). An individual-level disgust bias may therefore explain the prevalence of disgusting information in real-life urban legends (Heath et al. 2001), while near-universal aspects of grammar and colour terminology can be explained in terms of repeated transmission constraints (Kirby et al. 2008; Xu et al. 2013). A key finding of many of these studies is that weak individual biases can be easily magnified at the population level, in a way that could not be anticipated by focusing on individual cognition alone.

Demography can Influence the Evolution of Cultural Complexity

Cavalli-Sforza and Feldman (1981) explored how demographic factors such as population size and migration can influence cultural evolution just as they can influence biological evolution. In the last decade this has been pursued further, primarily in the historical/archaeological study of past cultural change, where the influence of changing demography can be observed over long time periods.

Henrich (2004) presented Tasmania as an example of the influence of demography on cultural evolution. When Tasmanian settlers became cut off from the Australian mainland around 10,000 years ago, they lost many complex tools and skills including winter clothing, fishing spears and boomerangs. Henrich (2004) argued that this loss of complex culturally-transmitted traits was due to the reduced effective population size that occurred following

isolation from the mainland population. In smaller populations, there are fewer skilled individuals from whom to learn, and fewer individuals to make rare beneficial modifications.

To formalise this, Henrich (2004) introduced an influential model linking population size to cultural complexity. The latter he defined in abstract terms designed to represent a quantitative measure of skill in some task, such as basket-weaving ability or stone tool production accuracy. In the model, each new generation acquires the skill of the most-skilful member of the previous generation (i.e. they exhibit payoff biased social learning) with some error. This error has two components, one that determines the loss of skill due to imperfect copying, and one that represents attempts to improve the skill. Complexity increases with population size because the more individuals there are, the more likely someone is to make an improvement without significant transmission error (see also Kobayashi and Aoki 2012; Mesoudi 2011c; Vaesen 2012).

Shennan (2001) and Powell et al. (2009) applied similar models directly to archaeological data regarding Palaeolithic Europe, showing that the appearance and disappearance of complex technological and social traits such as abstract art, the bow and musical instruments all coincide with changes in population density. Other studies have used repeated founder effect models to explain declining diversity in Acheulean handaxes with distance from an East African origin (Lycett and von Cramon-Taubadel 2008), shown that island population size predicts the size and complexity of fishing technology in the Pacific (Kline and Boyd 2010), and found that across Polynesian languages new words are more likely to be gained by larger populations and existing words are more likely to be lost in smaller populations (Bromham et al. 2015). Not all studies have found a link between population size and cultural complexity, however: Collard et al. (2013), for example, did not find a link in populations of North American hunter gatherers. More mobile hunter-gatherers may experience fewer cultural benefits from large population sizes than sedentary agriculturalists.

Recently, the link between population size and cultural complexity has been explored experimentally. Henrich’s (2004) original model contained certain assumptions concerning the micro-level link between demography and complexity (e.g. payoff-biased social learning), but large-scale archaeological studies such as Powell et al. (2009) can only test the outcome of this model, not the validity of the mechanisms. Derex et al. (2013), Muthukrishna et al. (2014) and Kempe and Mesoudi (2014) all found that, as predicted, larger groups containing more individuals from whom to learn supported higher levels of cultural complexity in various tasks, including designing computerised fishing nets, knot-tying, and completing jigsaw puzzles.

While Derex et al. (2013) and Muthukrishna et al. (2014) showed that Henrich's (2004) payoff-biased mechanism works, Kempe and Mesoudi (2014) showed that the effect can also be seen when people integrate the solutions of other people into a single solution (a kind of 'blending inheritance'). Further work is needed to delineate the precise micro-evolutionary mechanisms that support the macroevolutionary link between population size and cultural complexity.

Phylogenetic Methods can Reconstruct Language Macroevolution

As noted previously, another major strand of cultural evolution research has applied phylogenetic methods to reconstruct the evolutionary relationships between culturally-transmitted traits, based on the principle of inheritance. Much of this work has focused on reconstructing language evolution (Pagel 2009). While historical linguists before Darwin were constructing language family trees based on the assumption of common descent, this endeavour continued largely separately from evolutionary science throughout the twentieth century, resulting in trees based on the subjective judgement of linguists as to what languages were most similar, and what changes were most likely (McMahon and McMahon 2003).

In the last decade, sophisticated phylogenetic methods developed in evolutionary biology have been applied to the many language datasets already assembled by linguists, in many cases resulting in significant advances in our understanding of language evolution. A good example is the origin of the Indo-European language family, described as "the most intensively studied, yet still the most recalcitrant, problem of historical linguistics" (Diamond and Bellwood 2003, p. 601). Two major hypotheses proposed by linguists are the "steppe hypothesis", that Indo-European languages originated in the Pontic-Caspian steppe region (modern Kazakhstan) with the expansion into Europe of seminomadic Kurgan horsemen around 5000–6000 years ago, and the "Anatolian hypothesis", which posits an older origin around 8000–9500 years ago in Anatolia (modern Turkey) and a spread associated with farming. Both hypotheses are consistent with the archaeological record, and are fiercely argued over amongst historical linguists (Diamond and Bellwood 2003).

Building on an earlier phylogenetic analysis (Gray and Atkinson 2003), Bouckaert et al. (2012) used spatially-explicit Bayesian phylogenetic (i.e. phylogeographic) methods to test these hypotheses. Cognates (homologous words) from 103 extinct and extant Indo-European languages were used to infer the most likely phylogeny given known past and present geographic ranges, with language range modelled as evolving over time along the branches of

the phylogeny. Bouckaert et al. (2012) found strong support for the Anatolian hypothesis: the estimated posterior distribution of the root of the Indo-European phylogeny was located in Anatolia and dated to 7000–10,500 years ago. This conclusion was robust to several different assumptions about the spread of the languages, such as the likelihood of migration across water bodies (although see Chang et al. 2015 for an alternative conclusion).

Similar phylogenetic analyses have been applied to the spread of Austronesian languages across the Pacific (Gray et al. 2009; Gray and Jordan 2000). These suggest an origin around 5500 years ago in Taiwan with a subsequent series of rapid expansion pulses interspersed by settlement pauses (the "pulse-pause" hypothesis), rather than an alternative "slow-boat" hypothesis that posits an earlier origin in Wallacea (modern-day Sulawesi) around 13,000–17,000 years ago. Moreover, internal branch lengths were used to identify the specific pulses and pauses in the Austronesian expansion, which were then linked to the emergence of specific technologies such as outrigger canoes that allowed migration from Taiwan to the Philippines (Gray et al. 2009).

The Comparative Method can Test Functional Hypotheses About Cultural Evolution

Biologists typically use phylogenies not simply to reconstruct the past, but also to test functional hypotheses about evolution by comparing traits across different species. This comparative method (Felsenstein 1985; Harvey and Pagel 1991) uses phylogenies to correct for the non-independence of data due to shared descent when comparing across species. The comparative method can also be used in cultural evolution, comparing traits across different societies and using language phylogenies to control for non-independence due to descent (Mace and Pagel 1994). Although anthropologists have long been aware of this problem of non-independence (known as 'Galton's Problem', after Francis Galton pointed it out in 1889), during the twentieth century socio-cultural anthropologists abandoned the practice of comparing across societies in order to test functional hypotheses, preferring to describe individual societies within interpretivist or post-modern frameworks.

Galton's problem was therefore left for biologists to solve, but since Mace and Pagel (1994) the comparative method as developed in biology has also been applied to cultural datasets. For example, Holden and Mace (2003) showed that, in 68 Bantu-speaking sub-Saharan African societies, the introduction of cattle-keeping in formerly horticulturalist societies led to a shift from matrilineal to patrilineal wealth inheritance. This shift makes functional sense because, in these societies, cows are more useful to sons than daughters, and therefore lead to more male-biased parental investment. Cows are more useful to sons

because grooms must pay bridewealth to the bride's family in order to marry. Once cows are being kept, then wealth can be accumulated in the form of herd size, and families with larger herds can offer a larger bridewealth.

A similar comparative phylogenetic analysis was conducted by Currie et al. (2010) for changes in political complexity in Austronesian-speaking societies in the Pacific over the last 5500 years, given the newly available Austronesian language phylogenies discussed above (Gray et al. 2009). Ethnographic data was used to classify societies based on the number of hierarchical decision-making levels, from one (an egalitarian society with no leaders), to more than two levels (what ethnographers define as 'states'). Currie et al. showed that the best-fitting model of political evolution is one where complexity increases incrementally by one level at a time (precluding leaps from, say, one level to three), but with the possibility of sudden collapses from any level down to one.³

Controversies, Criticisms and Challenges

Despite the growth in cultural evolution research, the theory has also been much criticised by both social and evolutionary scientists. In this section I explore these criticisms, beginning with what I consider to be relatively minor issues of misunderstanding that have been addressed in the literature, then moving on to more substantive challenges and ongoing debates.

Misunderstandings and Clarifications

The following criticisms, in my view at least, have been addressed earlier in the article or elsewhere in the literature, but it is worth highlighting them again as they represent continued sources of misunderstanding.

- *Cultural evolution is not progressive* As noted above, many social scientists still identify cultural evolution with progressive Spencerian theories, and reject modern cultural evolution by rejecting the notion of inevitable progress (e.g. Fracchia and Lewontin 1999). As noted, this represents a misunderstanding

³ Earlier I discussed nineteenth century progressive Spencerian theories of cultural evolution. Currie et al.'s (2010) analysis presents an interesting empirical test of a version of those claims that societies increase in complexity, although it should be noted that (1) Currie et al.'s analysis is an empirical test, whereas Tylor and Morgan offered little empirical support for their progressive schemes; (2) Currie et al. precisely defined 'complexity' in terms of political hierarchy, whereas Tylor and Morgan were vague and conflated social organisation, technology and many other traits into a single scheme; and (3) Currie et al. showed that cultural evolution is not *inevitably* progressive, in that societies often lost social hierarchical levels.

of modern cultural evolution theory, which is not Spencerian or progressive.

- *Culture is too complex for simple models* Modern cultural evolution research is often criticised on the grounds that the population-genetic-style models at the core of the field are inappropriate for capturing the complexity of cultural phenomena (Fracchia and Lewontin 1999). Largely this represents a misunderstanding of the use of formal models. Just as in biology (Servedio et al. 2014), models are not intended to simulate all aspects of reality, nor are they arguments that the real world really is simple; they are used to formalise the logic of verbal arguments about a complex world (Richerson and Boyd 1987).
- *Culture cannot be divided into memes* It is common for cultural evolution to be rejected on the grounds that culture cannot be divided into discrete units of inheritance (e.g. Bloch 2000). As noted above, this again rests on a misunderstanding: Darwinian evolution does not require discrete replicators, and many cultural evolution models assume the blending inheritance of continuously varying cultural traits (Henrich and Boyd 2002).
- *Biological evolution branches, cultural evolution blends* A critique of cultural phylogenetics is that while biological macroevolution is a process of population fissioning into distinct lineages, cultural macroevolution frequently involves cross-lineage exchange via migration or trade, thus invalidating phylogenetic methods (Moore 1994). This distinction is unfounded: biological systems also feature cross-lineage exchange in the form of horizontal gene transfer (Syvanen 2012), and empirical tests demonstrate that many cultural datasets show just as strong phylogenetic signal as biological datasets (Collard et al. 2006). Moreover, Bayesian-MCMC methods can explicitly detect and handle cross-lineage borrowing (Matthews et al. 2011).

Is Culture Proximate or Ultimate?

Cultural evolution researchers are sometimes accused of making overblown claims about the causal role of culture in explaining human behaviour (Dickins and Rahman 2012; El Mouden et al. 2014; Scott-Phillips et al. 2011). This is typically placed within the context of the proximate-ultimate distinction (Mayr 1961; Tinbergen 1963). Proximate (or "how") causes of biological phenomena are immediate mechanisms and triggering stimuli, while ultimate (or "why") causes concern the evolutionary history and function of a trait. For example, proximate causes of birdsong might include the anatomical features that allow birds to sing, or the presence of a rival bird. Ultimate causes of birdsong might include descent from an ancestral

lineage in which birdsong was present, and the selection pressures that gave rise to and maintain birdsong. Biological phenomena can be simultaneously explained at both proximate and ultimate levels.

How does culture fit into this scheme? Researchers coming from sociobiology and evolutionary psychology have typically argued that culture is proximate: a mechanism set up by genes to maximise inclusive fitness (Dickins and Rahman 2012; El Mouden et al. 2014; Scott-Phillips et al. 2011). There is merit in this argument: after all, the capacity for culture evolved genetically because it increased inclusive fitness, as explored by numerous gene-culture coevolution analyses (Boyd and Richerson 1985, 1995). Moreover, many of the cognitive biases discussed above have putative inclusive fitness benefits, such as keeping track of social relationships (Mesoudi et al. 2006) and learning about disease-carrying substances (Eriksson and Coultas 2014).

Others (myself included) have argued that non-genetic forms of inheritance such as cultural evolution can additionally constitute ultimate causes of behaviour and thus require a rethinking of the original proximate-ultimate scheme (Danchin et al. 2011; Laland et al. 2011; Mesoudi et al. 2013). For a non-cultural species, the original scheme is fairly straightforward: ultimate historical causes involve genetic lineages connected via genetic descent, and ultimate selective causes involve the natural selection of genetic variation. For a cultural species such as ours, however, ultimate historical causes may also involve cultural lineages connected via cultural descent, and ultimate selective causes may also involve the cultural selection of cultural variation.

For example, the question “why does a person living in England speak English, and a person living in France speak French?” cannot satisfactorily be answered in terms of genetic differences or natural selection; it must be answered in terms of cultural descent (being descended from a cultural lineage of English or French-speakers on the tips of the Indo-European language phylogeny), and in terms of cultural selection (the microevolutionary processes that caused the languages to change and diversify over time, which might include both selection-like social learning biases and cultural drift). In cases of gene-culture coevolution, culturally transmitted traits such as dairy farming have caused the spread of genes such as lactose tolerance (Laland et al. 2010), again blurring a simple framework in which natural selection of genes is the ultimate cause of evolutionary change.

While to some extent these issues are merely semantic (i.e. how different researchers define ‘proximate’ and ‘ultimate’), definitional and theoretical frameworks are important because they guide the research questions that are asked. At the heart of this debate is the extent to which culture is

under genetic control: if culture is proximate then it should be under tight genetic control, always (or almost always) resulting in behaviour that maximises inclusive genetic fitness. If cultural evolution can also play an ultimate role, then it may drive behaviour to novel equilibrium that are not necessarily genetically optimal, or predictable from evolutionary models containing purely genetic inheritance.

The Relative Influence of Transformative and Selective Processes

Earlier I noted that cultural evolution differs from biological evolution in that whereas genetic inheritance does not in itself generate evolutionary change (except in unusual cases such as meiotic drive or imprinting), cultural inheritance (i.e. social learning) itself may do so, through the individual transformation of information. This difference has inspired some researchers to suggest an alternative framework for modelling and understanding cultural change, one based on ‘cultural attraction’ (Claidière et al. 2014; Claidière and Sperber 2007; Sperber 1996).

Two definitions of ‘cultural attraction’ exist in the writings of Sperber and colleagues (Acerbi and Mesoudi in press). In some publications (e.g. Claidière and Sperber 2007), cultural attraction equates to individual transformation, and seems equivalent to guided variation as modelled by Boyd and Richerson (1985). Claidière and Sperber (2007), for example, present a model in which a cultural trait—cigarette smoking—is influenced by both cultural attraction, where people are individually more likely to decide to either smoke zero or 25 cigarettes a day due to the initial unpleasantness and addictiveness of smoking, and cultural selection, which takes the form of a model-based bias wherein people are more likely to copy 10-cigarette-a-day smokers. As one might expect, the final distribution of cigarette smoking depends on the relative strength of cultural attraction (guided variation) and cultural selection (model-based bias).

As noted, this sense of cultural attraction seems synonymous with Boyd and Richerson’s (1985) guided variation, and transformative processes have been much studied in the field using transmission chain methods. There does not seem to be any major disagreement here, and indeed Sperber and colleagues have made a valuable contribution in highlighting the importance of transformative processes. One might argue about the relative strength of transformative and selective processes in cultural evolution, and this is an empirical question that cannot be addressed through modelling alone. Experimental studies are beginning to examine this (Eriksson and Coultas 2014), but more field and historical studies are needed. It is likely that for certain domains where there are strong cognitive constraints or biases, then individual transformation will

dominate, such as the case of colour terminology studied by Xu et al. (2013). In other domains, particularly those involving complex, novel or rapidly changing cultural traits, there are unlikely to be any innate cognitive or perceptual biases operating, and cultural traits may be so ‘cognitively opaque’ (Csibra and Gergely 2009)—i.e. cannot be easily reconstructed or understood—that individual transformation would be unlikely to result in beneficial modification any more than chance (Boyd et al. 2011). This likely includes complex technologies that have accumulated over multiple generations and that were shown above to appear and disappear with demography, such as fishing hooks, bows, and modern technology such as computers and spacecraft. Here, selection-like processes such as payoff-biased social learning, plus random cultural mutation, are likely to be more important than individual transformation.

Elsewhere (e.g. Claidière et al. 2014), cultural attraction appears to become synonymous with the broad process of cultural evolution. Claidière et al. (2014), for example, argue that “cultural evolution is best described in terms of a process called cultural attraction..., which is populational and evolutionary, but only selectional under certain circumstances.” (Claidière et al. 2014, p. 2). Here, cultural selection is described as a “special case” of cultural attraction, which subsumes both transformative and selective processes. This broader sense of cultural attraction seems to be redundant, and confusingly redefines the notion of cultural attraction (Acerbi and Mesoudi in press). Claidière et al. (2014) present evolutionary causal matrices, a modelling scheme which they argue better represents cultural change compared to existing ‘selectional’ models, but it is unclear how useful these are compared to the already established models of Cavalli-Sforza and Feldman (1981), Boyd and Richerson (1985) and many others, which as we have seen are not, in fact, exclusively selectional and also include transformative processes.

What Underlies Cumulative Cultural Evolution?

Many species possess social learning, defined as the transmission of information non-genetically from one individual to another (Galef and Laland 2005). Many species also exhibit cultural traditions, defined as group differences generated by social learning (Lycett et al. 2007; Whiten et al. 1999). Only humans, however, appear to possess *cumulative* cultural evolution, defined as the accumulation of beneficial modifications over successive generations (Dean et al. 2014). Different groups of chimpanzees may differ in their nut-cracking behaviour (Whiten et al. 1999), but there is no sense in which nut-cracking has accumulated over successive generations such that it is beyond the inventive capacity of a single chimp. Aspects of human

culture, such as spacecraft, quantum physics, and financial markets, are the cumulative product of countless individuals over many generations.

There is ongoing comparative, experimental and modelling work trying to explain this difference between humans and other species. An initial suggestion that non-human species lack high-fidelity imitation, i.e. the copying of motor actions (Tomasello et al. 1993), failed to find support when chimpanzees were shown able to faithfully transmit behaviours through captive groups (Horner et al. 2006). Recent work has instead implicated multiple factors as being jointly necessary. A recent experimental study pointed to a suite of socio-cognitive abilities, including imitation, verbal instruction and cooperation, that permitted human children to solve cumulative tasks that chimpanzees and capuchins failed (Dean et al. 2012). Theoretical models linked to comparative data suggest that transmission fidelity and population size are jointly necessary for cumulative cultural evolution (Kempe et al. 2014). Certainly, if the confluence of multiple social, cognitive and demographic factors was necessary for the evolution of cumulative cultural evolution, then this may well explain its rarity in nature. Future comparative work will provide a better understanding of these factors.

The Evolution of Large-Scale Human Cooperation

A fiercely debated question across the biological sciences concerns the evolutionary basis of cooperation (Abbot et al. 2011; Nowak et al. 2010). Human large-scale cooperation between unrelated individuals has come under particularly intense scrutiny. Boyd and Richerson (1985), alongside their general models of cultural evolution, also presented a theory of cultural group selection to explain human cooperation. In their original formulation, social learning biases such as conformity generate within-group cultural homogeneity and between-group cultural variation. If this group-level cultural variation persists in the face of migration, if groups vary in altruistic cultural traits which benefit the group but are costly to the individual, and if selection acts at the level of the group such as via their differential extinction, then this process of cultural group selection may favour altruistic cultural norms (Boyd and Richerson 2009). Empirical support for the cultural group selection hypothesis includes behavioural economic games which show cooperation in one-shot, anonymous interactions with no possibility of reciprocity, and between-group cultural variation in the extent of this cooperative behaviour (Henrich et al. 2005).

Cultural group selection has been criticised along with other theories of group (or multilevel) selection (e.g. Wilson and Wilson 2007) by proponents of kin selection (West et al. 2007, 2011). The latter argue that all human cooperation, like non-human cooperation, ultimately has selfish

benefits to the individual, even if these benefits also occur to those individuals' groups. Cooperation in one-shot anonymous games is argued to be an artifact of the unfamiliarity of such situations (West et al. 2007).

Cultural group selection is an elegant theory that fits with many findings from across the social and behavioral sciences (Richerson et al. 2015). Of the few empirical studies that have aimed to directly test its underlying assumptions, some have found support (Bell et al. 2009) while others have not (Lamba 2014; Lamba and Mace 2011). It is also worth noting that prominent cultural evolution researchers remain sceptical of the specific theory of cultural group selection (Lehmann et al. 2008). No doubt future empirical tests will further clarify the nature of human cooperation.

Are Social Learning Biases Learned or Innate?

Many gene-culture coevolutionary models have looked at the evolution of social learning, and of different social learning biases such as payoff or conformist biases. These models typically assume that such capacities are genetically-specified, and examine when each would be favoured by natural selection. To pick one example of many, Enquist et al. (2007) assume in a model of the evolution of social learning that "Which [learning] strategy is used is genetically determined for each individual" (p. 6).

It is possible, however, that the degree of social learning employed by an individual is itself learned, either individually or socially. To an extent, models such as those of Enquist et al. (2007) do not require social learning to be genetically-specified in order for the insights of their models to be valid: social learning could equally be acquired from others culturally, without perhaps altering the results of the model. On the other hand, given the known differences between the dynamics of genetic and cultural inheritance, this may not necessarily be the case. In subsequent models, Enquist and colleagues explored this further (Acerbi et al. 2009; Ghirlanda et al. 2006), showing that when the tendency to engage in social learning can itself be socially learned, this gradually reduces individuals' reliance on social information. This is because while social learners may learn from non-social learners to become non-social learners, the reverse is less likely: non-social learners do not learn from social learners because, by definition, they do not learn socially. While this specific result may or may not be broadly applicable, it highlights the possibility that cultural dynamics may be significantly altered when one assumes that social learning can itself be socially learned.

Empirically, Mesoudi et al. (2015) showed that the tendency to engage in social learning in an experimental artifact-design task varies cross-culturally, with participants from

mainland China more likely to use social information than participants from the UK and Hong Kong, as well as Chinese immigrants living in the UK. Although further studies are needed to explore the precise determinants of human social information use, these results suggest that social learning tendencies are themselves learned from others; the Western-style learning of Chinese immigrants and Hong Kong residents in particular count against any genetic basis for learning style.

In the non-human literature, it has been argued that social learning can be explained in terms of simple associative learning mechanisms, rather than dedicated genetically-specified, domain-specific mechanisms (Heyes 2012; Heyes and Pearce 2015; Leadbeater 2015). Recent studies have shown that social learning in rats can be influenced by early developmental cues such as maternal care (Lindeyer et al. 2013), and in bees by past learning histories (Dawson et al. 2013). However, while similar processes may well operate in humans (Heyes 2012), it is difficult to explain the species differences in cumulative cultural evolution described above without positing some kind of genetic adaptation in the human lineage, perhaps involving the extent of imitation during childhood (Lyons et al. 2007) or theory of mind (Tomasello et al. 2005).

Conclusions

In this paper I have provided an overview of contemporary cultural evolution research. The details of cultural micro-evolution are becoming increasingly better understood through a combination of theoretical models, lab experiments and field studies. These focus on pathways and biases in social learning, examining who people learn from, what they learn, and how learning transforms transmitted information. Macro-evolutionary studies are also proliferating, with sophisticated analyses of the evolution of languages, technology and social organisation giving valuable insights into broad patterns of cultural change through human history and prehistory.

Major progress is likely to occur through the linking of cultural micro and macroevolution, just as occurred in biology during the evolutionary synthesis. This is greatly facilitated by the quantitative models of cultural evolution that lie at the heart of the field, as the large-scale, population-level consequences of individual-level learning processes can be explored in a manner that verbal models do not allow. Thus we have seen links made from payoff bias and demography to patterns of cumulative cultural evolution, from transformative cognitive biases to cross-cultural universals such as colour terminologies and grammatical structure, and from conformist bias to large-scale cooperation.

Much of the work presented here is consistent with existing findings in the non-evolutionary social sciences: language phylogenies are broadly consistent with informal trees constructed by linguists, for example, while social learning biases such as conformity have precedent in the work of social psychologists. The added value of viewing cultural change as an evolutionary process lies in (1) the application to cultural datasets of quantitative methods already developed by biologists, such as phylogenetic methods in linguistics, where previously inferences were subjective; (2) the grounding of human behaviour within a broader evolutionary framework, such as the use of formal models to explore the adaptiveness of different social learning biases; and (3) the linking of micro- and macro-levels of explanation, which is inherent in Darwinian population thinking but represents a perennial problem in the social sciences due to the lack of quantitative methods for making this link, and the lack of communication between disciplines that focus on the micro (e.g. psychology) and those that focus on the macro (e.g. history or archaeology).

For evolutionary biologists, cultural evolution is significant for several reasons. First, the existence of a second major evolutionary process that resembles genetic evolution but differs from it in important ways may well provide valuable insights into the processes of genetic evolution. Phylogenetic methods, for example, are now being developed in parallel for both cultural and genetic data (Pagel 2009), and phenomena common to cultural datasets such as cross-lineage borrowing is just as much a challenge for biologists facing phenomena such as horizontal gene transfer. Second, social learning is now recognised to be common across multiple taxa, not just humans. The existence of a second inheritance system—and potentially a third, if one also includes transgenerational epigenetic inheritance—means that standard explanations for phenotypic variation in terms purely of the natural selection of genetically-inherited variation will not be sufficient (Danchin et al. 2011). Finally, when considering explanations for human behaviour, biologists sometimes consider ‘culture’ to be a vague and imprecise notion, instead defaulting to explaining patterns of human behaviour in terms of genes and natural selection even where this is inappropriate. The work reviewed here should hopefully put rest to that feeling, by presenting a coherent evolutionary science of culture that is just as rigorous as evolutionary biology.

References

- Abbot, P., Abe, J., Alcock, J., Alizon, S., Alpedrinha, J. A. C., Andersson, M., et al. (2011). Inclusive fitness theory and eusociality. *Nature*, 471(7339), E1–E4.
- Acerbi, A., Enquist, M., & Ghirlanda, S. (2009). Cultural evolution and individual development of openness and conservatism. *Proceedings of the National Academy of Sciences*, 106(45), 18931–18935.
- Acerbi, A., & Mesoudi, A. (in press). If we are all cultural Darwinians what’s the fuss about? Clarifying recent disagreements in the field of cultural evolution. *Biology and Philosophy*.
- Aoki, K., & Feldman, M. W. (2014). Evolution of learning strategies in temporally and spatially variable environments: A review of theory. *Theoretical Population Biology*, 91, 3–19. doi:10.1016/j.tpb.2013.10.004.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2014). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*. doi:10.1038/nature13998.
- Atkisson, C., O’Brien, M. J., & Mesoudi, A. (2011). Adult learners in a novel environment use prestige-biased social learning. *Evolutionary Psychology*, 10(3), 519–537.
- Aunger, R. (2000). The life history of culture learning in a face-to-face society. *Ethos*, 28, 1–38.
- Barbrook, A. C., Howe, C. J., Blake, N., & Robinson, P. (1998). The phylogeny of the canterbury tales. *Nature*, 394(6696), 839.
- Bartlett, F. C. (1932). *Remembering*. Oxford: Macmillan.
- Beheim, B. A., Thigpen, C., & McElreath, R. (2014). Strategic social learning and the population dynamics of human behavior: The game of Go. *Evolution and Human Behavior*, 35(5), 351–357. doi:10.1016/j.evolhumbehav.2014.04.001.
- Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences*, 106(42), 17671–17674.
- Bloch, M. (2000). A well-disposed social anthropologist’s problems with memes. In R. Aunger (Ed.), *Darwinizing culture* (pp. 189–204). Oxford: Oxford University Press.
- Boas, F. (1940). *Race, language and culture*. New York: Macmillan.
- Bouckaert, R., Lemey, P., Dunn, M., Greenhill, S. J., Alekseyenko, A. V., Drummond, A. J., et al. (2012). Mapping the origins and expansion of the Indo-European language family. *Science*, 337(6097), 957–960.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Boyd, R., & Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology*, 16(2), 125–143. doi:10.1016/0162-3095(94)00073-G.
- Boyd, R., & Richerson, P. J. (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B*, 364(1533), 3281.
- Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences*, 108, 10918–10925.
- Boyer, P. (1998). Cognitive tracks of cultural inheritance: How evolved intuitive ontology governs cultural transmission. *American Anthropologist*, 100(4), 876–889.
- Bromham, L., Hua, X., Fitzpatrick, T. G., & Greenhill, S. J. (2015). Rate of language evolution is affected by population size. *Proceedings of the National Academy of Sciences*, 112(7), 2097–2102. doi:10.1073/pnas.1419704112.
- Campbell, D. T. (1965). Variation and selective retention in socio-cultural evolution. In H. R. Barringer, G. I. Blanksten, & R. W. Mack (Eds.), *Social change in developing areas* (pp. 19–49). Cambridge, MA: Schenkman.
- Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural transmission and evolution*. Princeton: Princeton University Press.
- Chang, W., Cathcart, C., Hall, D., & Garrett, A. (2015). Ancestry-constrained phylogenetic analysis supports the Indo-European

- steppe hypothesis. *Language*, 91(1), 194–244. doi:[10.1353/lan.2015.0005](https://doi.org/10.1353/lan.2015.0005).
- Claidière, N., Scott-Phillips, T. C., & Sperber, D. (2014). How Darwinian is cultural evolution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1642), 20130368. doi:[10.1098/rstb.2013.0368](https://doi.org/10.1098/rstb.2013.0368).
- Claidière, N., & Sperber, D. (2007). The role of attraction in cultural evolution. *Journal of Cognition and Culture*, 7(2), 89–111.
- Collard, M., Buchanan, Briggs, & O'Brien, M. J. (2013). Population size as an explanation for patterns in the Paleolithic archaeological record: More caution is needed. *Current Anthropology*, 54(S8), S388–S396. doi:[10.1086/673881](https://doi.org/10.1086/673881).
- Collard, M., Shennan, S., & Tehrani, J. J. (2006). Branching, blending, and the evolution of cultural similarities and differences among human populations. *Evolution and Human Behavior*, 27, 169–184.
- Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, 13(4), 148–153.
- Currie, T. E., Greenhill, S. J., Gray, R. D., Hasegawa, T., & Mace, R. (2010). Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature*, 467(7317), 801–804. doi:[10.1038/nature09461](https://doi.org/10.1038/nature09461).
- Danchin, E., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., & Blanchet, S. (2011). Beyond DNA: Integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, 12, 475–486.
- Darwin, C. (1871). *The descent of man*. London: Gibson Square.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dawson, E. H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. (2013). Learning by observation emerges from simple associations in an insect model. *Current Biology*, 23(8), 727–730. doi:[10.1016/j.cub.2013.03.035](https://doi.org/10.1016/j.cub.2013.03.035).
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, 335(6072), 1114–1118.
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews*, 89(2), 284–301.
- Derex, M., Beugin, M.-P., Godelle, B., & Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. *Nature*, 503(7476), 389–391.
- Diamond, J., & Bellwood, P. (2003). Farmers and their languages: The first expansions. *Science*, 300(5619), 597–603.
- Dickins, T. E., & Rahman, Q. (2012). The extended evolutionary synthesis and the role of soft inheritance in evolution. *Proceedings of the Royal Society B*. doi:[10.1098/rspb.2012.0273](https://doi.org/10.1098/rspb.2012.0273).
- Dunbar, R. I. M. (2003). The social brain. *Annual Review of Anthropology*, 32, 163–181.
- Dunn, M., Greenhill, S. J., Levinson, S. C., & Gray, R. D. (2011). Evolved structure of language shows lineage-specific trends in word-order universals. *Nature*, 473(7345), 79–82.
- El Mouden, C., André, J.-B., Morin, O., & Nettle, D. (2014). Cultural transmission and the evolution of human behaviour: A general approach based on the Price equation. *Journal of Evolutionary Biology*, 27(2), 231–241. doi:[10.1111/jeb.12296](https://doi.org/10.1111/jeb.12296).
- Enquist, M., Eriksson, K., & Ghirlanda, S. (2007). Critical social learning: A solution to Rogers' paradox of nonadaptive culture. *American Anthropologist*, 109(4), 727–734.
- Enquist, M., & Ghirlanda, S. (2007). Evolution of social learning does not explain the origin of human cumulative culture. *Journal of Theoretical Biology*, 246(1), 129–135. doi:[10.1016/j.jtbi.2006.12.022](https://doi.org/10.1016/j.jtbi.2006.12.022).
- Enquist, M., Ghirlanda, S., & Eriksson, K. (2011). Modelling the evolution and diversity of cumulative culture. *Philosophical Transactions of the Royal Society B*, 366, 412–423.
- Eriksson, K., & Coultas, J. C. (2014). Corpses, maggots, poodles and rats: Emotional selection operating in three phases of cultural transmission of urban legends. *Journal of Cognition and Culture*, 14(1–2), 1–26. doi:[10.1163/15685373-12342107](https://doi.org/10.1163/15685373-12342107).
- Feher, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. *Nature*, 459(7246), 564–568.
- Feldman, M. W., & Laland, K. N. (1996). Gene-culture coevolutionary theory. *Trends in Ecology & Evolution*, 11(11), 453–457.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist*, 125, 1–15.
- Fracchia, J., & Lewontin, R. C. (1999). Does culture evolve? *History and Theory*, 38(4), 52–78.
- Freeman, D. (1974). The evolutionary theories of Charles Darwin and Herbert Spencer. *Current Anthropology*, 15(3), 211–237.
- Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience*, 55(6), 489–499.
- Ghirlanda, S., Enquist, M., & Nakamaru, M. (2006). Cultural evolution develops its own rules: The rise of conservatism and persuasion. *Current Anthropology*, 47(6), 1027–1034.
- Gray, R. D., & Atkinson, Q. D. (2003). Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature*, 426(6965), 435–439.
- Gray, R. D., Drummond, A. J., & Greenhill, S. J. (2009). Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science*, 323(5913), 479–483. doi:[10.1126/science.1166858](https://doi.org/10.1126/science.1166858).
- Gray, R. D., & Jordan, F. M. (2000). Language trees support the express-train sequence of Austronesian expansion. *Nature*, 405, 1052–1055.
- Griffiths, T. L., Kalish, M. L., & Lewandowsky, S. (2008). Theoretical and empirical evidence for the impact of inductive biases on cultural evolution. *Philosophical Transactions of the Royal Society B*, 363, 3503–3514.
- Harris, J. R. (1995). Where is the child's environment? A group socialization theory of development. *Psychological Review*, 102, 458–489.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Heath, C., Bell, C., & Sternberg, E. (2001). Emotional selection in memes: The case of urban legends. *Journal of Personality and Social Psychology*, 81(6), 1028–1041. doi:[10.1037/0022-3514.81.6.1028](https://doi.org/10.1037/0022-3514.81.6.1028).
- Henrich, J. (2001). Cultural transmission and the diffusion of innovations. *American Anthropologist*, 103(4), 992–1013.
- Henrich, J. (2004). Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses—The Tasmanian case. *American Antiquity*, 69(2), 197–214.
- Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, 19(4), 215–241.
- Henrich, J., & Boyd, R. (2001). Why people punish defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology*, 208(1), 79–89.
- Henrich, J., & Boyd, R. (2002). On modeling cognition and culture: Why cultural evolution does not require replication of representations. *Journal of Cognition and Culture*, 2(2), 87–112.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., et al. (2005). “Economic man” in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, 28(06), 795–815. doi:[10.1017/S0140525X05000142](https://doi.org/10.1017/S0140525X05000142).
- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the

- benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165–196. doi:10.1016/S1090-5138(00)00071-4.
- Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B*, 277, 3715–3724.
- Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, 12(3), 123–135. doi:10.1002/evan.10110.
- Hewlett, B. S., Fouts, H. N., Boyette, A. H., & Hewlett, B. L. (2011). Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366(1567), 1168–1178. doi:10.1098/rstb.2010.0373.
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, 126(2), 193–202. doi:10.1037/a0025180.
- Heyes, C., & Pearce, J. M. (2015). Not-so-social learning strategies. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1802), 20141709. doi:10.1098/rspb.2014.1709.
- Holden, C. J., & Mace, R. (2003). Spread of cattle led to the loss of matrilineal descent in Africa: A coevolutionary analysis. *Proceedings of the Royal Society B*, 270(1532), 2425–2433.
- Horner, V., Whiten, A., Flynn, E., & de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences*, 103(37), 13878.
- Kandler, A., & Steele, J. (2009). Social learning, economic inequality and innovation diffusion. In M. O'Brien & S. J. Shennan (Eds.), *Innovation and evolution*. Cambridge, MA: MIT Press.
- Kashima, Y. (2000). Maintaining cultural stereotypes in the serial reproduction of narratives. *Personality and Social Psychology Bulletin*, 26(5), 594–604.
- Kempe, M., Lycett, S., & Mesoudi, A. (2012). An experimental test of the accumulated copying error model of cultural mutation for Acheulean handaxe size. *PLoS One*, 7(11), e48333.
- Kempe, M., Lycett, S. J., & Mesoudi, A. (2014). From cultural traditions to cumulative culture: Parameterizing the differences between human and nonhuman culture. *Journal of Theoretical Biology*, 359, 29–36. doi:10.1016/j.jtbi.2014.05.046.
- Kempe, M., & Mesoudi, A. (2014). An experimental demonstration of the effect of group size on cultural accumulation. *Evolution and Human Behavior*, 35, 285–290.
- Kirby, S., Cornish, H., & Smith, K. (2008). Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences*, 105(31), 10681–10686.
- Kirby, S., Dowman, M., & Griffiths, T. L. (2007). Innateness and culture in the evolution of language. *Proceedings of the National Academy of Sciences*, 104(12), 5241–5245.
- Kline, M. A., & Boyd, R. (2010). Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B: Biological Sciences*, 277(1693), 2559–2564.
- Kobayashi, Y., & Aoki, K. (2012). Innovativeness, population size and cumulative cultural evolution. *Theoretical Population Biology*, 82(1), 38–47. doi:10.1016/j.tpb.2012.04.001.
- Labov, W. (1972). *Sociolinguistic patterns*. Oxford: University of Pennsylvania Press.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning and Behavior*, 32(1), 4–14. doi:10.3758/BF03196002.
- Laland, K. N., & Galef, B. G. (2009). *The question of animal culture*. Cambridge: Harvard University Press.
- Laland, K. N., Odling-Smee, J., & Myles, S. (2010). How culture shaped the human genome: Bringing genetics and the human sciences together. *Nature Reviews Genetics*, 11(2), 137–148.
- Laland, K. N., Sterelny, K., Odling-Smee, J., Hoppitt, W., & Uller, T. (2011). Cause and effect in biology revisited: Is Mayr's proximate-ultimate dichotomy still useful? *Science*, 334(6062), 1512–1516.
- Lamba, S. (2014). Social learning in cooperative dilemmas. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1787), 20140417. doi:10.1098/rspb.2014.0417.
- Lamba, S., & Mace, R. (2011). Demography and ecology drive variation in cooperation across human populations. *Proceedings of the National Academy of Sciences*, 108(35), 14426–14430.
- Leadbeater, E. (2015). What evolves in the evolution of social learning? *Journal of Zoology*, 295(1), 4–11. doi:10.1111/jzo.12197.
- Lehmann, L., Aoki, K., & Feldman, M. W. (2011). On the number of independent cultural traits carried by individuals and populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563), 424–435.
- Lehmann, L., Feldman, M. W., & Foster, K. R. (2008). Cultural transmission can inhibit the evolution of altruistic helping. *The American Naturalist*, 172(1), 12–24. doi:10.1086/587851.
- Lewis, H. S. (2001). Boas, Darwin, science, and anthropology. *Current Anthropology*, 42(3), 381–406. doi:10.1086/320474.
- Lewis, H. M., & Laland, K. N. (2012). Transmission fidelity is the key to the build-up of cumulative culture. *Philosophical Transactions of the Royal Society B*, 367, 2171–2180.
- Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.
- Lieberman, E., Michel, J. B., Jackson, J., Tang, T., & Nowak, M. A. (2007). Quantifying the evolutionary dynamics of language. *Nature*, 449(7163), 713–716.
- Lindeyer, C. M., Meaney, M. J., & Reader, S. M. (2013). Early maternal care predicts reliance on social learning about food in adult rats. *Developmental Psychobiology*, 55(2), 168–175. doi:10.1002/dev.21009.
- Lipo, C. P., O'Brien, M. J., Collard, M., & Shennan, S. J. (Eds.). (2006). *Mapping our ancestors: Phylogenetic approaches in anthropology and prehistory*. New York: Aldine.
- Lycett, S. J. (2009). Understanding ancient hominin dispersals using artefactual data: A phylogeographic analysis of Acheulean handaxes. *PLoS One*, 4(10), 1–6.
- Lycett, S. J., Collard, M., & McGrew, W. C. (2007). Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. *Proceedings of the National Academy of Sciences*, 104(45), 17588.
- Lycett, S. J., & von Cramon-Taubadel, N. (2008). Acheulean variability and hominin dispersals: A model-bound approach. *Journal of Archaeological Science*, 35(3), 553–562.
- Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, 104(50), 19751–19756.
- Mace, R., & Pagel, M. D. (1994). The comparative method in anthropology. *Current Anthropology*, 35(5), 549–564.
- Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (Pan troglodytes) and the question of cumulative culture: An experimental approach. *Animal Cognition*, 11(3), 449–456.
- Martin, D., Hutchison, J., Slessor, G., Urquhart, J., Cunningham, S. J., & Smith, K. (2014). The spontaneous formation of stereotypes via cumulative cultural evolution. *Psychological Science*, 25(9), 1777–1786. doi:10.1177/0956797614541129.
- Matthews, L. J., Tehrani, J. J., Jordan, F. M., Collard, M., & Nunn, C. L. (2011). Testing for divergent transmission histories among cultural characters: A study using Bayesian phylogenetic methods and Iranian tribal textile data. *PLoS One*, 6(4), e14810. doi:10.1371/journal.pone.0014810.
- Mayr, E. (1961). Cause and effect in biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist. *Science*, 134(3489), 1501–1506. doi:10.1126/science.134.3489.1501.

- Mayr, E. (1982). *The growth of biological thought*. Cambridge, MA: Harvard University Press.
- McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J., & Waring, T. (2008). Beyond existence and aiming outside the laboratory: Estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1509), 3515–3528. doi:10.1098/rstb.2008.0131.
- McElreath, R., & Henrich, J. (2006). Modeling cultural evolution. In R. I. M. Dunbar & L. Barrett (Eds.), *Oxford handbook of evolutionary psychology*. Oxford: Oxford University Press.
- McGuigan, N., & Cubillo, M. (2013). Cultural transmission in young children: When social information is more important than non-social information. *The Journal of Genetic Psychology*, *174*(6), 605–619.
- McMahon, A., & McMahon, R. (2003). Finding families: Quantitative methods in language classification. *Transactions of the Philological Society*, *101*, 7–55.
- Mesoudi, A. (2011a). *Cultural evolution*. Chicago, IL: University Chicago Press.
- Mesoudi, A. (2011b). An experimental comparison of human social learning strategies: Payoff-biased social learning is adaptive but underused. *Evolution and Human Behavior*, *32*(5), 334–342. doi:10.1016/j.evolhumbehav.2010.12.001.
- Mesoudi, A. (2011c). Variable cultural acquisition costs constrain cumulative cultural evolution. *PLoS One*, *6*(3), e18239.
- Mesoudi, A., Blanchet, S., Charmantier, A., Danchin, E., Fogarty, L., Jablonka, E., et al. (2013). Is non-genetic inheritance just a proximate mechanism? A corroboration of the extended evolutionary synthesis. *Biological Theory*, *7*(3), 189–195.
- Mesoudi, A., Chang, L., Murray, K., & Lu, H. (2015). Higher frequency of social learning in China than in the West shows cultural variation in the dynamics of cultural evolution. *Proceedings of the Royal Society B*, *282*, 20142209.
- Mesoudi, A., & Whiten, A. (2004). The hierarchical transformation of event knowledge in human cultural transmission. *Journal of Cognition and Culture*, *4*(1), 1–24.
- Mesoudi, A., & Whiten, A. (2008). The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philosophical Transactions of the Royal Society B*, *363*, 3489–3501.
- Mesoudi, A., Whiten, A., & Dunbar, R. (2006). A bias for social information in human cultural transmission. *British Journal of Psychology*, *97*(3), 405–423. doi:10.1348/000712605X85871.
- Mesoudi, A., Whiten, A., & Laland, K. N. (2004). Is human cultural evolution Darwinian? Evidence reviewed from the perspective of The Origin of Species. *Evolution*, *58*(1), 1–11. Accessed 27 May 2014.
- Molleman, L., van den Berg, P., & Weissing, F. J. (2014). Consistent individual differences in human social learning strategies. *Nature Communications*, doi:10.1038/ncomms4570.
- Moore, J. H. (1994). Putting anthropology back together again: The ethnogenetic critique of cladistic theory. *American Anthropologist*, *96*, 925–948.
- Morgan, L. H. (1877). *Ancient society*. New York: Henry Holt.
- Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W., & Laland, K. N. (2011). The evolutionary basis of human social learning. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 653–662. doi:10.1098/rspb.2011.1172.
- Muthukrishna, M., Shulman, B. W., Vasilescu, V., & Henrich, J. (2014). Sociality influences cultural complexity. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 20132511.
- Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010). The evolution of eusociality. *Nature*, *466*(7310), 1057–1062.
- O'Brien, M. J., Boulanger, M. T., Buchanan, B., Collard, M., Lee Lyman, R., & Darwent, J. (2014). Innovation and cultural transmission in the American Paleolithic: Phylogenetic analysis of eastern Paleoindian projectile-point classes. *Journal of Anthropological Archaeology*, *34*, 100–119.
- O'Brien, M. J., Darwent, J., & Lyman, R. L. (2001). Cladistics is useful for reconstructing archaeological phylogenies: Palaeoindian points from the Southeastern United States. *Journal of Archaeological Science*, *28*(10), 1115–1136.
- O'Brien, M. J., & Lyman, R. L. (2003). *Cladistics and archaeology*. Salt Lake City: University of Utah Press.
- Pagel, M. (2009). Human language as a culturally transmitted replicator. *Nature Reviews Genetics*, *10*(6), 405–415.
- Pike, T. W., Kendal, J. R., Rendell, L. E., & Laland, K. N. (2010). Learning by proportional observation in a species of fish. *Behavioral Ecology*, *21*(3), 570–575. doi:10.1093/beheco/arq025.
- Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, doi:10.1098/rsbl.2009.1014.
- Pitt-Rivers, A. L. (1875). On the evolution of culture. *Journal of the Anthropological Institute*, *4*, 293–308.
- Powell, A., Shennan, S. J., & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science*, *324*(5932), 1298–1301.
- Price, G. R. (1970). Selection and covariance. *Nature*, *227*(5257), 520–521.
- Reyes-Garcia, V., Broesch, J., Calvet-Mir, L., Fuentes-Pel-ez, N., McDade, T. W., Parsa, S., et al. (2009). Cultural transmission of ethnobotanical knowledge and skills: An empirical analysis from an Amerindian society. *Evolution and Human Behavior*, *30*(4), 274–285.
- Reysen, M. B., Talbert, N. G., Dominko, M., Jones, A. N., & Kelley, M. R. (2011). The effects of collaboration on recall of social information. *British Journal of Psychology*, *102*(3), 646–661. doi:10.1111/j.2044-8295.2011.02035.x.
- Richerson, P. J., Baldini, R., Bell, A., Demps, K., Frost, K., Hillis, V., et al. (2015). Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence. *Behavioral and Brain Sciences*, doi:10.1017/S0140525X1400106X.
- Richerson, P. J., & Boyd, R. (1987). Simple models of complex phenomena: The case of cultural evolution. In J. Dupre (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 27–52). Cambridge, MA: MIT Press.
- Richerson, P. J., & Boyd, R. (2005). *Not by genes alone*. Chicago: University of Chicago Press.
- Richerson, P. J., & Christiansen, M. H. (2013). *Cultural evolution: Society, technology, language, and religion*. Cambridge, MA: MIT Press.
- Rogers, A. R. (1988). Does biology constrain culture? *American Anthropologist*, *90*(4), 819–831.
- Rogers, E. (1995). *The diffusion of innovations*. New York: Free Press.
- Ross, R. M., Greenhill, S. J., & Atkinson, Q. D. (2013). Population structure and cultural geography of a folktale in Europe. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1756), 20123065. doi:10.1098/rspb.2012.3065.
- Ryan, B., & Gross, N. (1943). The diffusion of hybrid seed corn in two Iowa communities. *Rural Sociology*, *8*, 15–24.
- Schlag, K. H. (1998). Why imitate, and if so, how? A boundedly rational approach to multi-armed bandits. *Journal of Economic Theory*, *78*(1), 130–156.
- Scott-Phillips, T. C., Dickins, T. E., & West, S. A. (2011). Evolutionary theory and the ultimate–proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, *6*(1), 38–47.
- Servedio, M. R., Brandvain, Y., Dhole, S., Fitzpatrick, C. L., Goldberg, E. E., Stern, C. A., et al. (2014). Not just a theory—The utility of mathematical models in evolutionary biology.

- PLoS Biology*, 12(12), e1002017. doi:10.1371/journal.pbio.1002017.
- Shennan, S. J. (2001). Demography and cultural innovation: A model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal*, 11(01), 5–16.
- Shennan, S. J. (2002). *Genes, memes and human history*. London: Thames and Hudson.
- Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Oxford: Oxford University Press.
- Sperber, D., & Hirschfeld, L. A. (2004). The cognitive foundations of cultural stability and diversity. *Trends in Cognitive Sciences*, 8(1), 40–46. doi:10.1016/j.tics.2003.11.002.
- Stubbersfield, J. M., Tehrani, J. J., & Flynn, E. G. (2014). Serial killers, spiders and cybersex: Social and survival information bias in the transmission of urban legends. *British Journal of Psychology*,. doi:10.1111/bjop.12073.
- Syvänen, M. (2012). Evolutionary implications of horizontal gene transfer. *Annual Review of Genetics*, 46(1), 341–358. doi:10.1146/annurev-genet-110711-155529.
- Tehrani, J. J. (2013). The phylogeny of little red riding hood. *PLoS One*, 8(11), e78871. doi:10.1371/journal.pone.0078871.
- Tehrani, J. J., & Collard, M. (2002). Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles. *Journal of Anthropological Archaeology*, 21, 443–463.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift fuer Tierpsychologie*, 20, 410–433.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28(5), 675–691.
- Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, 16(3), 495–552.
- Turchin, P. (2008). Arise “cliodynamics”. *Nature*, 454, 34–35.
- Turchin, P., Currie, T. E., Turner, E. A. L., & Gavrillets, S. (2013). War, space, and the evolution of Old World complex societies. *Proceedings of the National Academy of Sciences*, 110(41), 16384–16389. doi:10.1073/pnas.1308825110.
- Tylor, E. B. (1871). *Primitive culture*. London: John Murray.
- Vaesen, K. (2012). Cumulative cultural evolution and demography. *PLoS One*, 7(7), e40989. doi:10.1371/journal.pone.0040989.
- Van Leeuwen, E. J. C., & Haun, D. (2013). Conformity in nonhuman primates: Fad or fact? *Evolution and Human Behavior*, 34(1), 1–7.
- Van Wyhe, J. (2005). The descent of words: Evolutionary thinking 1780–1880. *Endeavour*, 29(3), 94–100.
- West, S. A., El Mouden, C., & Gardner, A. (2011). Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior*, 32, 231–262. doi:10.1016/j.evolhumbehav.2010.08.001.
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20(2), 415–432.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, 437, 52–55.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682–685.
- Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437, 737–740.
- Whiten, A., & Mesoudi, A. (2008). An experimental science of culture: Animal social diffusion experiments. *Philosophical Transactions of the Royal Society B*, 363, 3477–3488.
- Wilson, D. S., & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *The Quarterly Review of Biology*, 82(4), 327–348. doi:10.1086/522809.
- Xu, J., Dowman, M., & Griffiths, T. L. (2013). Cultural transmission results in convergence towards colour term universals. *Proceedings of the Royal Society B: Biological Sciences*, 280(1758). doi:10.1098/rspb.2012.3073.
- Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: Social learning of a more efficient tool-use technique. *PLoS One*, 8(1), e55768.