The study of culture and evolution across disciplines

Submitted to:
Cambridge Handbook of Evolutionary Perspectives on Human Behavior (eds Lance Workman, Will Reader, Jerome Barkow)

Alex Mesoudi
Human Biological and Cultural Evolution Group,
Department of Biosciences, University of Exeter, UK

Word counts:
7970 (not including references)
10,629 (with references)
No figures or tables

Abstract

A source of continued tension within the evolutionary human behavioural / social sciences, as well as between these fields and the traditional social sciences, is how to conceptualise 'culture' in its various manifestations and guises. One of the earliest criticisms of E O Wilson's sociobiology project was the focus on presumed genetically evolved behavioural universals, and lack of attention to cultural diversity and cultural (as opposed to genetic) history. As sociobiology split into different fields during the 1980s, each developed their own approaches and assumptions. Human behavioural ecologists employed the 'phenotypic gambit', assuming that culture is a proximate means by which natural selection generates currently-adaptive behavioural strategies. Evolutionary psychologists distinguished between transmitted and evoked culture, the former involving the social transmission of information, the latter involving the triggering of genetically-prespecified behaviours in response to different environmental cues (typically ancestral cues, such that behaviour may no longer be currently adaptive). Evoked culture has been the focus of most research in evolutionary psychology. Cognitive anthropologists have a similar notion of 'cultural attraction', where universal aspects of cognition evoke predictable responses due to individual learning. Finally, cultural evolution (or gene-culture coevolution) approaches stress the causal role of transmitted culture. Here, human cognition is assumed to be relatively domain-general and content-free, with genetic evolution having shaped social learning processes to allow the rapid spread of locally adaptive knowledge (although occasionally allowing the spread of maladaptive behaviour, due to the partial decoupling of genetic and cultural evolution). All the while, the traditional social sciences have remained steadfastly unwilling to accept that evolutionary approaches to human behaviour have any merit or relevance, and indeed have abandoned the scientific method in favour of more politically motivated interpretive methods. Most curiously, the social sciences have abandoned the concept of culture, as they define it. I will discuss all of these approaches in terms of (i) the extent to which they give causal weight to genetic inheritance, individual learning and social learning, and how these process interact; (ii) their assumptions about the domain-specificity of human cognition; (iii) ultimate-proximate causation; (iv) specific debates over language evolution, cooperation and the demographic transition; and (v) prospects for reconciliation and integration of these tensions across the evolutionary human sciences and the social sciences more broadly.

1. Introduction

Evolutionary scholars often appear to disagree strikingly about the value of 'culture' in explaining human behavior. John Tooby, one of the founders and figureheads of evolutionary psychology, recently responded to the Edge.org question "What scientific idea is ready for retirement?" with the answer "Learning and culture" (Tooby, 2014). At around the same time, Joseph Henrich, Professor of Human Evolutionary Biology at Harvard, published a book titled "The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter" (Henrich, 2015). How can two highly reputable scholars, both committed to understanding human behavior within an evolutionary framework, come to such apparently opposing conclusions? Should the concept of 'culture' be retired, or heralded as the secret to humanity's evolutionary success?

'Culture' is also often partly why many scholars within the traditional social sciences and humanities are reluctant to accept or adopt evolutionary approaches to human behavior at all. Evolutionary theory is often assumed (incorrectly, as we will see below) to predict species-wide universals of human behavior, and to be inconsistent with the extensive cultural diversity and historical contingency documented by anthropologists, archaeologists, historians and other social scientists. Such debates are often played out in the context of the nature-nurture dichotomy, with 'culture' and 'learning' on the 'nurture' side and 'genes' or 'evolution' on the 'nature' side. For many social scientists, nurture/culture wins this contest every time, and evolution can be safely ignored.

In this chapter I explore these issues. I begin by discussing different definitions of culture. I then review how culture has been understood and used within the main branches of the human evolutionary behavioral sciences (Laland and Brown, 2011): sociobiology, human behavioral ecology, evolutionary psychology and cultural evolution / gene-culture coevolution. Finally, I discuss why, despite the increasing focus on culture within evolutionary approaches, the mainstream social sciences remain steadfast in their rejection of evolutionary theory as a useful tool for understanding human behavior.

2. What is culture?

Scholars have proposed literally hundreds of definitions of culture (Baldwin et al., 2006; Kroeber and Kluckohn, 1952), and I will not review them all here. Instead I will pick out four common uses that have relevance to the evolutionary approaches discussed later. The first two are examples, in my view at least, of unsuitable definitions of culture. The last two are the focus of later discussion.

2.1 Definition 1: "Culture is everything that humans do (and other species don't)"

Many definitions of culture simply define it as everything that humans do, with the implicit or explicit additional assumption that it is what humans do and no other species does. For example, Cronk (1999) summarises the typical definition of culture in anthropology textbooks as something similar to "Everything that people have, think, and do as

members of a society" (p.4). These usually derive from Tylor's (1871) influential definition of culture as "that complex whole which includes knowledge, beliefs, art, law, morals, custom, and any other capabilities and habits acquired by man [sic] as a member of society" (p.1)

This kind of definition is problematic because, as Cronk (1999) points out, it is far too broad. Humans have, think and do all kinds of things, from bipedal locomotion and menopause, to forming social hierarchies and obeying marriage rules, to producing late night talk shows and sending animals into space. A concept that explains everything simultaneously explains nothing. And particularly within the evolutionary human sciences, there is vigorous debate, as we will see below, about the extent to which genetic evolution, individual learning and other processes have shaped different forms of human activity. Labelling them all 'culture' from the outset puts the cart before the horse.

Defining culture as 'whatever is unique to humans and absent in other species' is also problematic. It makes a claim that precludes *a priori* any similarities between humans and other species in anything 'cultural'. In fact, there is a thriving field of study uncovering the cultural capacities of diverse species (Galef and Laland, 2005; Whiten et al., 2016). This comparative work provides valuable insights into the evolutionary origins and function of culture, insights that would be lost if we decided beforehand that culture is uniquely human. There are also many derived human traits, such as bipedalism, that most people would probably not class as 'culture'.

2.2 Definition 2: "Culture involves higher, more civilised forms of activity"

This definition, often associated with literary critics such as Matthew Arnold (1869), is what we might colloquially call 'high culture'. This is the 'culture' of Sunday newspaper supplements: opera, art galleries, fine dining and high-brow literature written by novelists who wear unusual glasses.

This rather elitist definition (who decides what is high culture?) was understandably rejected by early social scientists who were interested in explaining *all* of human behavior, not just that which is deemed important by a certain section of society. Tylor's (1871) inclusive and broad definition of culture given in the previous section is an example of a reaction against this elitist definition.

Evolutionary scholars would agree with this rejection of the elitist definition. But it is historically noteworthy here because while Tylor eliminated the within-society elitist connotations of culture, he just moved the elitism up a level, to entire societies. Tylor advocated a theory of unilinear progressive social evolution, where entire societies can be classed as 'higher' or 'lower' along a ladder of increasing 'evolutionary' complexity, from savagery to barbarism to civilisation. Tylor and others (e.g. Morgan, 1877) placed contemporary hunter-gatherers and other small-scale societies at the bottom of this ladder, and the Western British and American societies of which they (not uncoincidentally) were members at the top.

Many social scientists still associate evolution with this unilinear, progressive, society-

level notion of social evolution espoused by these late 19th century scholars, which Boas (1940) and others later convincingly showed to be empirically untenable. It is important to note that this is very different to the idea of cultural evolution that we will come to later, which makes no claims about the inevitable progression of entire societies along ladders of complexity. This notion of ladder-like progress along stages is a very un-Darwinian idea that draws more from Herbert Spencer than Charles Darwin (Freeman, 1974).

2.3 Definition 3: "Culture as between-group variation in behavior"

This is a more useful definition, although still not without its problems. Culture in this sense describes systematic between-group variation in human (or other species') behavior. One might think of cultural variation in, say, marriage practices, means of subsistence, or religious customs, as documented by cultural anthropologists over the last century (Murdock, 1967). Cultural psychologists have similarly documented cultural variation in various psychological processes, along dimensions such as individualism-collectivism or analytic-holistic cognition (Heine, 2011). The term 'culture' here may become synonymous with the 'group' or 'society' being described, be it nation state (e.g. "Japanese culture") or an ethnic or linguistic group (e.g. "Hopi culture").

In the non-human literature, between-group differences in behavior that cannot be attributed to genes or environmental constraints are typically referred to as cultural 'traditions' (Fragaszy and Perry, 2003). Tool-use traditions in chimpanzees are a prominent example of non-human cultural traditions, with some members of some chimpanzee groups habitually practicing, say, nut-cracking, and other groups failing to ever nut-crack despite the availability of nuts and rocks (Whiten et al., 1999).

While culture is frequently used in this sense, there are reasons to be cautious about this definition. Between-group variation in behavior may result from many different processes, only some of which certain scholars are happy calling 'cultural'. Culture in this sense is really only a description, not an explanation. We must also be careful not to essentialise these group differences, which tends to happen if 'culture' is used as a group descriptor: there is much individual variation in behavior *within* Japan, and *within* Hopi communities, and much overlap with other groups (e.g. Koreans or Navajos). Really it is a shorthand for the statistical signature of 'relatively more between-group variation than within-group variation in the behavior of interest'.

2.4 Definition 4: "Culture as socially learned information"

This is perhaps the most common definition of culture used by evolutionary scholars, as well as being implicit within most social science definitions (the "acquired by man [sic]" part of Tylor's definition, for example). Richerson and Boyd (2005) provide a good example:

"Culture is information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission" (Richerson & Boyd, 2005, p. 5)

The terms ‘social transmission’, ‘social learning’, ‘cultural learning’ and ‘cultural transmission’ are used in this chapter synonymously to mean the non-genetic passing on of information from one individual to another. ‘Information’ here is a broad term referring to what we might colloquially call knowledge, beliefs, skills, attitudes or norms.

This definition is non-human-specific, leaving scope for the comparative study of non-human culture. It is also not elitist, and does not restrict culture to certain sections of societies, or some societies rather than others. And it provides a causal explanation for (at least some of) the behavioral variation that we considered in the previous definition: those traits common to people in Japan, such as speaking Japanese or using chopsticks, are common because they are socially learned from other Japanese people. Thus, cultural variation is that part of behavioral variation that is generated by the social transmission of information from person to person within a particular group. The common distinction made by sociologists between ‘culture’ and ‘society’ is useful here: ‘culture’ (our definition 4) concerns a pool of socially transmitted information - beliefs, knowledge, attitudes, norms etc. - whereas ‘society’ describes a set of social relations and social structures that characterize a particular group (our definition 3). These social relations and structures may be determined by culturally transmitted norms and values, as well as genetically inherited predispositions.

A particular kind of transmitted culture is *cumulative culture* (Dean et al., 2014). This term has arisen within comparative psychology to refer to the supposedly uniquely-human ability to preserve and build up socially-learned information over successive generations. So while other species may have transmitted culture, in the sense that they learn from one another (e.g. chimpanzees learn how to nut-crack from others), and may have cultural traditions (e.g. nut-cracking is common in some chimpanzee groups due to social learning), there is no sense in which nut-cracking technology accumulates in efficiency or complexity over time in the way that human technology does. The reasons for this are currently much debated (Dean et al., 2014; Kempe et al., 2014; Tennie et al., 2009), but probably require high fidelity social learning of the kind only seen in humans. This notion of cumulative culture will become important when we consider cultural evolution below.

3. Culture in the evolutionary human sciences

3.1 Sociobiology

The modern resurgence of evolutionary thinking in the human sciences began with the final chapter of E.O. Wilson’s *Sociobiology* (Wilson, 1975), where Wilson applied the theoretical tenets of social evolution theory (e.g. Hamilton, 1964) and ethology or behavioral ecology (e.g. Tinbergen, 1963) to our own species. Wilson argued that purportedly universal or near-universal patterns of human behavior such as aggression, territoriality, warfare, genocide, xenophobia, mating systems, homosexuality, the sexual division of labour and reciprocity all show homologues in other species, are partly-genetically-caused fitness-enhancing adaptations (or part of ‘human nature’), and can be explained in terms of sexual selection, kin selection, reciprocal altruism and other principles devised and used to explain non-human behavior.

As has been well documented (Segerstråle, 2000), this led to fierce opposition from both social scientists and other evolutionary biologists (Kitcher, 1985; Sahlins, 1976; Sociobiology Study Group of Science for the People, 1976). The criticisms were many, including some unjustified political attacks on Wilson for the imagined consequences of his arguments (e.g. eugenics, patriarchy, ruthless capitalism) that he neither intended nor advocated. And Wilson should be given credit for at least *attempting* to bridge the gulf that then existed between the natural and social sciences, rather than simply assuming, as did (and do) many social scientists, that humans are so flexible as to make our evolutionary history irrelevant.

But the critics had a valid point when they charged Wilson of ignoring or downplaying culture, both in the form of cultural variation and transmitted culture (definitions 3 and 4). Wilson stated at the outset that "human qualities will be discussed insofar as they appear to be general traits of the species" (p.548), seemingly dismissing cultural variation as irrelevant. Speculative claims were made about the genetic basis of phenomena such as socio-economic class differences ("A key question...is whether there exists a genetic predisposition to enter certain classes and to play certain roles. Circumstances can easily be conceived in which such genetic differentiation might occur", p.554) which social scientists understandably balked at.

Wilson later lamented the omission of culture from his early writings, and a few years after *Sociobiology* he attempted to make amends. His book with Charles Lumsden, "Genes, Mind and Culture", presented mathematical models aiming to show how culture (in the form of socially transmitted 'culturgens' controlled by 'epigenetic rules') can be incorporated into a gene-culture co-evolutionary framework (Lumsden and Wilson, 1981). Yet this was not positively received (Kitcher, 1985; Smith and Warren, 1982). Lumsden and Wilson's (1981) models showed that culture is kept on a tight leash by genetic evolution, and the suspicion was that the models were set up to ensure this sociobiology-like conclusion. As we will see later, other approaches to gene-culture coevolution (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981) afforded more explanatory power and independence to transmitted culture, and were consequently received more positively. Lumsden and Wilson's (1981) work received much less attention.

3.2 Human behavioral ecology

As the label "human sociobiology" became increasingly taboo, it transformed into new fields each of which attempted to address the criticisms of its forebearer (Laland and Brown, 2011). One major problem was that sociobiological theory as applied to humans was vague and loose, offering broad generalizations that were seldom tested quantitatively against empirical data (Kitcher, 1985). In contrast, the field of (non-human) behavioral ecology applied many of the same evolutionary principles to non-human behavior but using rigorous optimality models tested against carefully collected data (Krebs and Davies, 1984). Human behavioral ecologists sought to use similarly rigorous quantitative models and data to test evolutionary theories of human behavior (Borgerhoff Mulder and Schacht, 2012; Nettle et al., 2013; Winterhalder and Smith, 2000).

Of particular interest here is human behavioral ecologists' focus on cross-cultural comparisons. Human behavioral ecologists assume that human behavior is flexible enough to generate adaptive responses to diverse environmental conditions, in contrast to the sociobiological focus on behavioral universals or fixed genetically-evolved predispositions. Consequently, human behavioral ecologists showed how marriage practices may vary in a biologically adaptive manner, with polyandry emerging in harsh environments where more than one man is needed to raise offspring (Crook and Crook, 1988; Smith, 1998), and polygyny emerging when men can monopolize resources and accumulate wealth, particularly via pastoralism (Borgerhoff Mulder, 1990). Another line of research has examined cross-cultural and historical variation in fertility, seeking to explain why societies differ in their average number of children, and why this number has dropped over time as societies become richer (the 'demographic transition': Borgerhoff Mulder, 1998; Lawson et al., 2012).

Human behavioral ecology addresses sociobiology's lack of cultural variation (definition 3). Yet it does not address our definition 4, culture in the sense of socially learned information. Human behavioral ecologists, like behavioral ecologists in general (Grafen, 1984), adopt the 'phenotypic gambit'. Behavior is assumed to be biologically adaptive, but the means by which this adaptiveness is achieved are tactically ignored. Adaptive behavior (e.g. polyandry) might arise as a result of genetically-specified 'if-then' mechanisms: if in harsh conditions, then adopt polyandry. Or it might arise due to individual learning: people use a genetically-evolved but flexible intelligence to independently figure out that in their harsh environment, polyandry is the best option. Or it might arise due to social learning: people acquire polyandry norms from other members of society through observation or instruction, as the result of a historical process of cultural evolution. (Actually, these are not mutually exclusive alternatives: cultural evolution requires some kind of individual learning to provide innovation, while all forms of learning are at some level genetic adaptations.)

The point is that human behavioral ecologists intentionally choose to ignore these proximate mechanisms in favour of answering what is, to them, the more interesting ultimate question: is a particular behavior biologically adaptive? This is a perfectly reasonable, and often highly productive, scientific strategy. After all, we do not expect theories of human behavior to include interactions between atoms; there must be some limit to how far down our explanations go. Ultimate questions of evolutionary function and history can often be studied without considering proximate functions of development and mechanism (Tinbergen, 1963). Yet as we will see later, other evolutionary human scientists disagree that proximate factors such as learning and transmitted culture can be safely ignored when thinking about ultimate factors.

3.3 Evolutionary psychology

Evolutionary psychology emerged in the 1990s as a fusion of sociobiological theory and cognitive science (Barkow et al., 1992; Buss, 2009; Pinker, 1997). Evolutionary psychologists typically focus on how natural selection has shaped psychological mechanisms during our species' evolutionary past to maximize inclusive fitness. It is assumed that the resulting cognitive adaptations evolved to deal with adaptive challenges

in past environments (sometimes called the 'environment of evolutionary adaptedness'), and not necessarily current environments, in contrast to human behavioral ecologists. Key topics within evolutionary psychology have included cognitive adaptations for cheater detection that evolved for maintaining reciprocal interactions (Cosmides, 1989), sex differences in mating preferences that evolved due to differential parental investment (Buss et al., 1990) and patterns of homicide that can be predicted from kin selection (Daly and Wilson, 1988).

To some degree, early evolutionary psychologists shared human sociobiologists' preoccupation with behavioral universals rather than cultural variation (Tooby and Cosmides, 1992, pp. 88–93). Brown (1991) notably compiled a list of hundreds of 'human universals', including division of labour, aggression, ethnocentrism, gossip, reciprocity and play (interestingly, this reads much like Wilson's list above). In a prominent cross-cultural study, Buss et al. (1990) found consistent sex differences in mating preferences across 37 societies, predictable on the basis of differential parental investment. For example, men rated markers of fertility higher, such as youth, while women rated markers of offspring provisioning higher, such as wealth.

This focus on universals was an explicit reaction against what Tooby and Cosmides (1992) called the 'Standard Social Science Model', which they characterized as a denial of human nature and an extreme cultural determinism where evolution played no role in shaping human behavior. While this was a laudable aim, some have argued that evolutionary psychologists swung too far the other way. As Laland and Brown (2011) point out, in Buss et al.'s (1990) cross-cultural study of mating preferences, much more variation (around 14%) in responses was explained by the cultural background of the participants than was explained by sex (only around 2%). Yet the study is typically cited as evidence for the universality of human mating strategies. The situation has improved since these early studies, however, with evolutionary psychologists now formulating specific hypotheses about particular patterns of cultural variation, and testing them in targeted cross-cultural comparisons (Apicella and Barrett, 2016).

Tooby and Cosmides (1992) also proposed an important distinction between *transmitted culture*, which is our definition 4 above, and *evoked culture*. The latter involves a universal, evolved human psychology that responds differently to different environmental conditions. In the context of our definitions above, Tooby and Cosmides are arguing that some 'cultural' variation (definition 3) may not in fact be generated by transmitted culture (definition 4), it may be the result of genetically evolved, pre-existing responses to predictable environmental cues. Note that this is different to Wilson's (1976) earlier speculations that genetic differences might explain behavioral differences between groups of people. Tooby and Cosmides explicitly disavowed this, instead arguing that people everywhere are genetically far too similar to explain any behavioral variation directly (which concurs with modern genetic data: Feldman, 2014). Genes instead generate a set of universal responses to predictable environmental variation.

An example of evoked culture that has received much recent attention involves pathogens (Nettle, 2009; Schaller, 2006). Thornhill, Fincher and colleagues have argued that a country's current or past exposure to pathogens is a key environmental trigger that evokes different behavioral responses (Fincher et al., 2008; Fincher and Thornhill, 2012).

For example, many East Asian countries exhibit high collectivism, which entails a wariness of contact with foreigners and other outgroup members. Thornhill, Fincher and colleagues view this as an adaptive, evoked response to high levels of pathogens, which are most often transmitted from outgroups who carry novel diseases to which the ingroup has no immune defence. Positive correlations between collectivism and past and present pathogen prevalence are offered in support of this hypothesis (Fincher et al., 2008; although for critical analyses see Currie and Mace, 2012; Hruschka and Henrich, 2013).

A similar notion to evoked culture has been proposed by cognitive anthropologists such as Dan Sperber (Claidière et al., 2014; Claidière and Sperber, 2007; Sperber, 1996). Like evolutionary psychologists, Sperber downplays the role of high fidelity cultural transmission (definition 4), instead arguing that cultural diversity and stability (definition 3) emerge as people independently reconstruct representations based on pre-existing cognitive biases, or 'attractors'. In a sense, this is like evoked culture but where 'the environment' is people's cognition, rather than something external like pathogens. An example is bloodletting (Miton et al., 2015): diverse societies have seemingly independently converged on the practice of cutting the skin near the location of an ailment to release 'bad blood'. Although this has no medical efficacy, it seems to be universally cognitively attractive and so has been 're-discovered' multiple times.

In sum, an early focus within evolutionary psychology on human universals (e.g. Brown, 1991) has given way to an appreciation that cultural variation (definition 3) is not only perfectly consistent with an evolved human psychology (Barrett, 2015) but that cultural variation can be utilised to test evolutionary predictions (Apicella and Barrett, 2016). In this, evolutionary psychology has converged with human behavioral ecology. What of definition 4, transmitted culture? Evolutionary psychologists typically focus instead on evoked culture, and either downplay the role of transmitted culture, or take the human behavioral ecologists' approach that transmitted culture is simply a proximate mechanism by which human groups arrive at biologically adaptive (or ancestrally adaptive) behavioral equilibria. In this, both of these fields differ quite substantially from the field to which we turn next.

3.4. Cultural evolution / gene-culture coevolution

I noted above that E.O. Wilson's response to criticism that sociobiology failed to take culture seriously was to develop theoretical models of gene-culture coevolution (Lumsden and Wilson, 1981). These models explored how transmitted culture (definition 4) and genetic inheritance jointly produce human behavior. While a step in the right direction, Lumsden and Wilson's models were heavily criticised for merely recapitulating Wilson's earlier claims that genes 'hold culture on a leash' (Smith and Warren, 1982).

In parallel to Wilson's own attempts, a group of anthropologists and biologists were developing a body of theory that gave more explanatory power, and more independence, to transmitted culture. Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) used the mathematical techniques of population genetics to examine two questions. First, under what conditions does transmitted culture evolve? In other words, if we treat the capacity for transmitted culture as a trait that evolved just like any other, we can ask,

what is its adaptive function, relative to pure genetic adaptation and/or purely individual learning?

Boyd and Richerson (1985) developed models showing that transmitted culture is favored when environments change moderately quickly, too fast for genes to track, but not so fast that the culturally transmitted behavior is out of date (see also Aoki et al., 2005). Transmitted culture also evolves when individual learning is costly (Boyd and Richerson, 1985). Under such conditions, however, social learning evolves but does not increase the average fitness of the population. This phenomenon became known as "Rogers' paradox" after Alan Rogers, the first person to clearly point it out (Rogers, 1988). The fact that social learning does not enhance average population fitness is not inherently paradoxical, but does contradict the common claim that humans are so ecologically and demographically successful because of transmitted culture.

Rogers' paradox occurs because the success of social learning is frequency-dependent. When rare, social learners do well because they forego the costs borne by individual learners. But when common, and environments change, social learners will be copying other social learners' out-dated information. At equilibrium, social and individual learners have equal fitness, which will be equal to the fitness of a population entirely composed of individual learners (which is fixed, because their learning is not dependent on others). Thus, social learning evolves, but does not enhance fitness in a way that could be described as the 'secret to our success'.

However, transmitted culture *can* enhance the average fitness of a population when (i) individuals learn selectively, only copying others when individual learning is inaccurate or selectively copying successful individuals, and/or (ii) socially learned traits can be accumulated over successive generations such that individuals can learn socially what they could never invent alone: this is the cumulative culture noted above (Boyd and Richerson, 1995; Enquist et al., 2007; Kendal et al., 2009). There is evidence that a range of species, including humans, show selective social learning (Hoppitt and Laland, 2013; Whiten et al., 2016), while as noted above only humans appear to possess cumulative culture (Dean et al., 2014; Tennie et al., 2009).

The second question is, assuming transmitted, selective, cumulative culture *has* evolved in humans, what consequences does this have for our understanding of human behavior? Do genes keep culture on a tight leash, such that it acts as a proximate mechanism that ultimately maximizes past or present inclusive fitness, as assumed by evolutionary psychologists and human behavioral ecologists? Or does it make genes irrelevant, as assumed by most mainstream social scientists?

Cultural evolutionists' answer to this is typically "neither". In Richerson and Boyd's words, "culture is on a leash, all right, but the dog on the end is big, smart and independent. On any given walk, it is hard to tell who is leading who" (Richerson and Boyd, 2005, p.194). The key argument here is that transmitted, cumulative culture (definition 4) constitutes an evolutionary process in its own right (Campbell, 1965; Plotkin, 1995). In *The Origin of Species*, Darwin (1859) specified three requirements for the evolutionary process: variation, inheritance and selection. Applied to genetic evolution, these are genetic variation that arises through mutation and recombination, genetic inheritance via DNA

replication, and natural selection due to competition between genes or individuals for survival and reproduction. Many scholars, beginning with Darwin himself, have noted that these three requirements are also met for culture: there is cultural variation in beliefs, attitudes, skills etc.; there is cultural inheritance, i.e. the transmitted culture of our definition 4; and there are various selective forces that cause some cultural variants to be more likely to survive and reproduce than others (Mesoudi et al., 2004).

Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) modeled this process of cultural evolution given what is known about human cultural change and learning. Of particular interest were cases where the dynamics of cultural evolution appear different to those of genetic evolution. So Cavalli-Sforza and Feldman (1981) modeled horizontal cultural transmission (learning from an unrelated member of the same generation) and oblique cultural transmission (learning from an older non-parent) as well as gene-like vertical cultural transmission (learning from one's parents). Boyd and Richerson (1985) modeled processes such as conformity, where the most common cultural trait is preferentially adopted, and prestige bias, where one preferentially learns from people with high social status. 'Guided variation' they defined as the intentional modification of acquired traits, a Lamarckian-like process that has no clear parallel in genetic evolution.

Boyd and Richerson's (1985) analyses suggested that while general learning heuristics such as conformity and prestige bias are broadly adaptive, they can sometimes lead to biologically maladaptive outcomes. For example, conformity can lead to the failure to switch to a superior product or tool when an inferior one is already established (Henrich, 2001). Prestige bias can lead to cultural hitch-hiking, as people copy neutral or harmful traits from prestigious individuals because it is hard to figure out what causes social success (Henrich and Gil-White, 2001). This can be relatively trivial, such as copying the clothing style of prestigious celebrities, but also potentially drastic, such as copycat suicides that follow a highly publicized celebrity suicide (Mesoudi, 2009). Boyd and Richerson (1985) also suggest that prestige bias can account for the 'demographic transition', the systematic reduction in family size that has occurred at different times in different countries over the last several decades. If 'family size' is a culturally transmitted trait, and prestigious people have smaller families because they choose to invest more in attaining cultural prestige than having children, then family size will drop as people copy preferences for small families from prestigious others (see Colleran, 2016). Finally, Bentley and colleagues (Bentley et al., 2007, 2004) have shown that various cultural traits change in a random fashion, akin to genetic drift. Examples include first names, dog breeds and pottery decorations.

This explains cases of biologically maladaptive or adaptively neutral human behavior, answering the common criticism that evolutionary approaches are 'adaptationist' and incorrectly assume that every human behavior is biologically adaptive (Gould and Lewontin, 1979). But the key message of cultural evolutionists is that the overall package of transmitted, cumulative culture *is* adaptive, and indeed is the key to our species' extraordinary ecological and demographic success over the last 10,000 years or so (Boyd et al., 2011; Henrich, 2015). While other species rely on the slow process of genetic evolution to adapt to novel environments, they argue that we have successfully colonized virtually every terrestrial environment due to cultural adaptations such as complex tool-kits and social institutions. These cultural adaptations represent the accumulated wisdom

of multiple generations of people, as beneficial modifications are selectively preserved and culturally transmitted to subsequent generations via relatively content-neutral social learning biases. This contrasts with some evolutionary psychologists' explanation of our species' success, which credits our content-rich, domain specific cognition and the ability of single individuals to come up with solutions to adaptive problems 'on-the-fly' (Pinker, 2010). For cultural evolutionists, cultural adaptations go beyond what any single individual could create alone, moving the explanation from individual cognition to population-level cultural evolution, and from evoked culture to cumulative, transmitted culture.

Cultural evolutionists also place more emphasis on cultural history, as opposed to genetic history. A group of scholars has borrowed phylogenetic methods – originally developed in biology to reconstruct the evolutionary history of species – and applied them to cultural traits, based on the logic that these cultural traits evolve through a process of descent with modification just like species (Gray et al., 2007; Mace and Holden, 2005; O'Brien and Lyman, 2003; Pagel, 2009). Language is a good example of a socially learned trait that forms very long-lasting lineages: languages (English, French etc.) are socially learned by children with relatively high fidelity, allowing such languages to persist for thousands of years. Bouckaert et al. (2012) reconstructed the cultural evolutionary history of the Indo-European language family, finding that it originally spread along with farming practices from present-day Turkey around 8,000 years ago. Similar questions about the historical spread of empires have been addressed by Turchin and colleagues (Turchin, 2003; Turchin et al., 2013). In these cases we can see links emerging between our definitions 3 and 4: contemporary cross-cultural variation (definition 3) emerges as the result of the long term transmission of cultural traits (definition 4). Indo-European languages are transmitted from person to person, generation to generation, ultimately generating the cultural variation in languages that we see today.

Finally, note that this modern cultural evolution approach is very different to the progressive 'social evolution' theories of the late 1800s (Morgan, 1877; Tylor, 1871). The modern focus is often on traits (languages, tools) that may diffuse across social boundaries rather than the transformation of entire monolithic societies, and the evolutionary process is one of branching diversification that may or may not result in increased (cultural) adaptation, rather than linear, inevitable progress along fixed stages.

4. Comparison of approaches

While all modern evolutionary approaches to human behavior seek to explain cultural variation (definition 3), cultural evolution, much more than any other field, focuses on transmitted culture (definition 4) as an explanation for this variation. Cultural evolutionists argue that complex behavioral traits, from technology to institutions, can be explained as cultural adaptations that evolve not genetically but culturally. Genes provide the social learning apparatus that this rests on, as explored in models of the evolution of culture, but the real 'explanatory action' is at the level of selectively preserved, culturally transmitted skills, beliefs, and knowledge. Evolutionary psychology, and similar approaches such as cultural attraction, focus on biologically-evolved, content-rich, domain-specific cognitive adaptations for dealing with past ancestral challenges. Here, the explanatory action is very much with natural selection and genetic adaptation. Human behavioral ecologists

share this latter assumption, although differ in certain details from evolutionary psychology, such as focusing on behavior rather than cognition, and stressing current adaptiveness rather than ancestral adaptiveness.

These seemingly disparate approaches do not necessarily conflict if we consider them to be targeting different phenomena. Most cultural evolutionists would probably agree that learning is not entirely content-free. Indeed, one prominent strand of cultural evolution research examines 'content biases', presumed genetically evolved biases in human social learning that favor the acquisition and transmission of biologically adaptive information. Examples include biases for information about social interactions (Mesoudi et al., 2006), disgusting and potentially disease-carrying substances (Eriksson and Coultas, 2014), and dangerous animals (Barrett and Broesch, 2012). Content biases may also result from the individual transformation of information according to features of human cognition, such as the hierarchical structure of event knowledge which favors increasingly 'schematized' descriptions of events (Mesoudi and Whiten, 2004). This seems very similar to the idea of cultural attraction (Sperber, 1996).

Furthermore, cultural evolution research has demonstrated that content-neutral cultural transmission rules such as prestige bias can lead to biologically adaptive behavior, in a way perfectly consistent with the other approaches. For example, Henrich and Henrich (2010) found that food taboos in Fiji prohibiting pregnant women from eating certain fish were (i) adaptive, in the sense that these fish contained high levels of toxins that increased the chances of miscarriage, and (ii) maintained via prestige biased social learning, as women learned the taboos from prestigious 'wise women' within the community. This seems perfectly consistent with, say, human behavioral ecologists' assumption that transmitted culture will, at a proximate level, result in what is ultimately biologically adaptive behavior.

Other research questions appear to require an answer explicitly in terms of transmitted culture, with genetic evolution relegated to the background. For example, the question "why do people in England speak English, and people in France speak French?" surely must be answered in terms of the cultural evolutionary history of the Indo-European language family (Bouckaert et al., 2012), with these languages representing different tips of the branching language tree that diverged due to various cultural forces, including drift-like mutations, demographic shifts, borrowing from other languages, and ultimately the spread of ancestral languages from Anatolia with farming about 8000 years ago. Evolutionary psychologists, in contrast, would be interested in the even more ultimate question of "how did the language faculty evolve biologically?" (Pinker, 1994). There is no conflict here, just different levels of explanation (Tinbergen, 1963).

Or another example might be, "how do we explain the rise and fall of specific empires throughout history?", which Turchin and colleagues (Turchin, 2003; Turchin et al., 2013) have been addressing using cultural evolution models tested against historical data. More relevant to contemporary societies might be, "why do some modern countries function better than others?", which cultural evolution researchers are beginning to address in terms of the cultural transmission and evolution of inclusive institutions which reduce inequality (Henrich et al., 2010; Hruschka and Henrich, 2013; Matthews et al., 2016). Evolutionary psychologists, in contrast, would be more interested in the cognitive

adaptations (e.g. reciprocity) that make such institutions possible in the first place.

Yet on closer inspection, this neat division becomes less clear-cut. Take language as an example. Recently, a group of cultural evolutionists have challenged Chomsky's (1965) notion of an innate universal grammar that structures all languages within specific constraints (Pinker, 1994). They argue that systematic grammatical regularities instead arise due to the repeated transmission of languages as they are learned by each new speaker (Chater et al., 2009; Christiansen and Chater, 2008; Kirby et al., 2008, 2007). In other words, rather than the brain having genetically evolved to constrain and structure languages, languages have instead culturally evolved to become more easily learnable. There is no innate 'language acquisition device', just general cognitive constraints that are not specific to language learning. The 'explanatory action' in this cultural evolution account shifts from genetic to cultural adaptation.

Another prominent example concerns cooperation. Another group of cultural evolutionists have argued that while standard sociobiological principles of kin selection and reciprocity can certainly explain *some* aspects of human cooperation, they can't explain the large-scale, non-kin-based cooperation that characterizes human societies, from hunter-gatherer bands to historical empires to modern-day nation states, where large numbers of genetically unrelated people cooperate often with no expected return on their cooperation (Boyd and Richerson, 1985; Gintis et al., 2003; Henrich, 2004; Richerson et al., 2015; Turchin, 2015). They argue that cultural evolution is the key to this large-scale cooperation, because it allows altruism to be selected and favored at the level of the cultural group. Imagine that different cultural groups (e.g. tribes, empires or nations) vary in the extent to which their members act altruistically to one another, such as sharing food or participating in collective group defense. If those groups are reasonably cohesive, and compete with one another either directly (e.g. via warfare) or indirectly (e.g. for resources), then those groups that are more internally-cooperative and feature self-sacrificial behavior for the good of the group will do better than less internally-cooperative groups in which everyone is out for themselves. This kind of group selection does not work for genetic evolution because free-riders out-reproduce altruists and migration breaks down genetically homogenous groups (Williams, 1966). But it does work, at least in theory, for cultural groups, assuming those groups have culturally-transmitted norms for dealing with free-riders (e.g. punishment) and biases for maintaining within-group cultural homogeneity in the face of migration (e.g. conformity).

These theories of the evolution of language and of cooperation are controversial. Many evolutionary psychologists and behavioral ecologists argue that kin selection and reciprocity can, in fact, explain large-scale human cooperation (Krasnow et al., 2013; West et al., 2011), and that language regularities *do* result from a genetically evolved, universal language instinct (Pinker, 1994). These are topics of ongoing empirical tests (Kirby et al., 2008; Lamba and Mace, 2011). And as noted earlier, a broader debate concerns the basis for our species' extraordinary ecological and demographic success compared to other primates: cultural evolutionists attribute this to our ability to rapidly culturally adapt to novel environments and accumulate complex technology and institutions via content-neutral transmission biases (Boyd et al., 2011; Henrich, 2015), while evolutionary psychologists credit our genetically evolved cognitive adaptations (Barrett et al., 2007; Pinker, 2010).

In sum, while there are large areas of agreement, evolutionary scholars disagree over how much explanatory power to assign to transmitted culture. Evolutionary psychologists and human behavioral ecologists typically treat transmitted culture as a proximate mechanism that helps to explain how we arrive at genetically adaptive behavior. Much cultural evolution work is consistent with this, as in the case of genetically-evolved content biases. But many cultural evolutionists argue that transmitted culture also often changes the rules of the human evolutionary game, creating new equilibria (e.g. large-scale cooperation), spreading maladaptive behavior (e.g. copycat suicide, small family sizes) and replacing genetic evolution as a source of adaptation (e.g. resulting in complex technology and institutions, or grammatical structure).

5. Culture, evolution and the mainstream social sciences

What of the mainstream social sciences since their vehement reaction against sociobiology in the late 1970s (Sahlins, 1976; Sociobiology Study Group of Science for the People, 1976)? Has the increasing appreciation within evolutionary psychology of cultural variation (Apicella and Barrett, 2016) led to greater acceptance amongst social scientists? And what of the burgeoning field of cultural evolution (Mesoudi, 2011), which seems to speak directly to most social scientists' criticism that sociobiologists ignored transmitted culture? Has cultural evolution been welcomed as an advance over the sometimes crude genetic determinism of early sociobiology?

Sadly not. Evolutionary approaches to human behavior are still typically ignored or rejected by mainstream social scientists (Barkow, 2005; Horowitz et al., 2014). Evolutionary psychology has received many of the same criticisms that sociobiology received in the 1970s, including charges of genetic determinism, just-so storytelling and hidden political agendas (Rose and Rose, 2000). Many of these criticisms are simply misguided (Kurzban and Haselton, 2006). For example, no evolutionary psychologist has ever claimed that genes entirely determine human behavior, with no environmental influence. The case of evoked culture is a good example of a clear and explicit gene x environment interaction: genes specify possible behavioral reactions to different environmental inputs. And evolutionary psychologists and anthropologists are often just as liberal as non-evolutionary scholars in their political leanings (Lyle and Smith, 2012) – not that this should matter for questions of science.

I suspect this rejection of anything 'evolutionary' or 'biological' is a continued legacy of the divide in the early 20th century between biology and culture. In anthropology, Kroeber (1917) explicitly partitioned the 'organic', or biological, from the 'superorganic', or cultural. This split between biological and cultural anthropology persists today. Back in the 1910s, the desire on the part of the cultural side of the discipline to distance itself from the crude, inaccurate and politically distasteful race theories of the time (see Gould, 1996) was quite understandable. The progressive social evolution theories (Morgan, 1877; Tylor, 1871) were not much better, as discussed above. Yet modern evolutionary approaches to human behavior bear no resemblance to these early 'evolutionary' approaches.

One might imagine that cultural evolution would be viewed more favorably by mainstream

social scientists, given that it gives more explanatory power to transmitted culture. Yet this field is just as fiercely criticized (Fracchia and Lewontin, 1999; Ingold, 2007). Typical criticisms of cultural evolution, aside from it being confused with the aforementioned progress theories of social evolution, are that it denies individual agency, that it inappropriately reduces culture to a collection of unconnected 'traits' that cannot be divorced from their proper social context, and that it simplifies processes such as cultural transmission which are too complex and un-generalizable to fit into neat categories such as 'horizontal' or 'vertical'. Fracchia and Lewontin (1999), for example, ask

"Is culture "transmitted" at all? An alternative model, one that accords better with the actual experience of acculturation, is that culture is not "transmitted" but "acquired". Acculturation occurs through a process of constant immersion of each person in a sea of cultural phenomena, smells, tastes, postures, the appearance of buildings, the rise and fall of spoken utterances" (p.73).

This kind of criticism has its roots in the wider rejection of the scientific method within socio-cultural anthropology, sociology and other more humanities-oriented social sciences. The 'writing culture' movement of the 1980s (Clifford and Marcus, 1986) abandoned any pretense that ethnography should be a scientific methodology in favor of producing 'thick descriptions' of other societies, more akin to literature than science. The 'writing against culture' movement (Abu-Lughod, 1996) argued that the use of 'culture' to describe a group of people (a version of our definition 3) acts to essentialize between-group differences and ignore within-group diversity, much like the earlier concept of 'race'. Ironically, this has led mainstream social scientists to abandon the concept of 'culture' just as it is becoming increasingly popular within the evolutionary sciences. The recent 'ontological turn' within cultural anthropology (Viveiros de Castro, 2014) seemingly rejects any possibility of cross-cultural comparison or scientific investigation, seeking instead to understand each society entirely in its own ontological terms, and especially not with reference to, or use of, scientific concepts, which are viewed as products of Western power structures. Indeed, much of modern socio-cultural anthropology has become a form of political activism, rather than a scientific endeavor (see, for example, Allen and Jobson, 2016).

It is a real shame that these barriers persist, particularly in light of the emergence of the field of cultural evolution. As we have seen, the assumption of Kroeber and others that culture is separate to biology has been explored formally by cultural evolution modelers, as well as tested in a large body of empirical research. It is not enough to simply assert that culture is independent of biology; this is an empirical question. The models and findings reviewed above suggest that neither the genetic determinists nor the cultural determinists of the early 20th century were correct. An acultural biology does not determine human behavior, but nor does an abiological culture. The cultural evolutionists would say that culture evolved, it is broadly adaptive, but does not simply do our genes' bidding because culture itself constitutes an evolutionary process whose very function is to be partially independent of our much slower genetic evolution.

In the absence of a scientific approach to culture within the social sciences, cultural evolutionists are proceeding to address questions and topics that have been of longstanding interest to social scientists, but using more rigorous quantitative methods:

phylogenetic methods to examine the spread of language families (Bouckaert et al., 2012; Pagel, 2009), dynamical models and hypothesis testing to explore the historical rise and fall of empires (Turchin, 2003; Turchin et al., 2013), and multi-level selection theory to explain the origin and function of cooperative social institutions (Henrich, 2006, 2004; Hruschka and Henrich, 2013). The criticisms that these methods and concepts are too simplistic and reductionist (Fracchia and Lewontin, 1999; Ingold, 2007) represent a misunderstanding of the use of models, statistics and hypothesis-testing in science. Simple models do not imply that the modeler thinks that the real world really is simple. Rather, as in biology, simple models are the best way of understanding a complex reality (Servedio et al., 2014; Smaldino, 2016). One could adopt Fracchia and Lewontin's approach of embracing complexity, but then, how does one study the "immersion in a sea of the appearance of buildings"? Models of, say, vertical, horizontal and oblique transmission may be gross simplifications, but they still provide useful insights that apply across societies (McElreath and Strimling, 2008). The same goes for lab and field experiments (Henrich et al., 2010; Mesoudi and Whiten, 2008) and cross-cultural comparisons (Mace and Holden, 2005). Of course all societies are different, but they are not *so* different as to make comparisons invalid. This is not to say that such methods are perfect; witness the recent replication crisis within the behavioral sciences (Open Science Collaboration, 2015) and the growing realization that traditional statistical methods are flawed (McElreath, 2016). But this necessitates the adoption of better standards (e.g. pre-registration) and methods (e.g. Bayesian statistics), rather than the wholesale abandonment of the scientific method.

6. Conclusions

'Culture' does not appear to be a concept ready to be retired. Within the evolutionary sciences, one might even say that it is a concept entering the prime of its life. Evolutionary psychologists are increasingly paying attention to cultural variation (Apicella and Barrett, 2016) as human behavioral ecologists have been doing for many years (Nettle et al., 2013). Cultural evolutionists are applying evolutionary methods and concepts to study cultural change in a way that fills a gap left by the shift in the mainstream social sciences and humanities away from scientific methodologies (Mesoudi, 2011). There are broad areas of agreement across these different evolutionary fields: all would agree, for example, that culture itself is a biological adaptation, and that learning is often guided to make the acquisition of biologically adaptive information more likely. There are also areas of disagreement, with cultural evolutionists willing to give transmitted culture more explanatory power and independence. Ultimately these are empirical issues, as models, experiments, ethnographic observation, historical data and cross-cultural comparisons are brought to bear on key topics such as the evolution of technology, cooperation, language and sociality.

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