

CULTURAL EVOLUTION

One of the most significant facts about us may finally be that we all begin with the natural equipment to live a thousand kinds of life but end in the end having lived only one.

--- Clifford Geertz (1973)

The student of anthropology knows that it is the range of human experiences that represents “one of the most significant facts about us” (Geertz 1973). While human universals exist (Brown 1991), including subsistence, marriage, and politics, there is no single, species-typical way in which humans live out their lives. Each human universal conceals a constellation of cross-cultural variation. While other animals have cultural traditions (Box 1), human variation is something altogether different. There are over 6,000 languages spoken across the globe, and there were many, many more before the ages of empire and colonialism. Human nature—if we choose to speak of such a thing—consists not of a characteristic way of life, but a set of cognitive and developmental mechanisms including our cultural capacity, “the natural equipment to live a thousand kinds of life” (Geertz 1973). It is the peculiarities of our cultures interacting with these mechanisms that shapes the specific kind of life each one of us ends up living.

Since the dawn of our genus, culture has been our faithful handmaiden, transforming a Plio-Pleistocene primate at the mercy of Nature, first into a Holocene human that colonized every corner of the globe, diversifying into a thousand kinds of life, each exploring and elaborating their own particular lifeway comprising unique material cultures, social institutions, and artistic traditions; and eventually into an Anthropocene annihilator bending that same Nature to its will and in the process wreaking havoc across the biosphere. These transformations raise many questions. Why did our cultural capacity evolve during the Plio-Pleistocene? How did our species diversify into thousands of distinct ethnolinguistic groups during the Holocene? And how did the accumulation of cultural innovations in technology and social organization birth the agricultural, industrial, and scientific revolutions; launch us to the moon, to the edge of the solar system, and into the far reaches of the cosmos?

The discipline of *cultural evolution* provides a framework for studying these kinds of questions (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985; see also Durham 1991, Sperber 1996; for reviews, see Richerson and Boyd 2005, Mesoudi 2011, Henrich 2015, Laland 2017). With its roots going back to the 1970s and 1980s, cultural evolution developed in the wake of sociobiology and alongside evolutionary psychology and human behavioral ecology (Laland and Brown 2011). Whereas human behavioral ecology emerged from cultural anthropology as a theoretically

inspired but ethnographically based enterprise, cultural evolution emerged from population genetics as an ethnographically inspired but theoretically based enterprise. This chapter reviews both the theory of cultural evolution and recent empirical studies showcasing how it has been applied to the study of human behavior and evolution.

1. THE THEORY OF CULTURAL EVOLUTION

This section organizes cultural evolutionary theory into three parts. The first aligns with *evolutionary psychology* (Barkow et al. 1992, Pinker 2003, Gaulin and McBurney 2003, Buss 2014, Barrett 2015, **EVOLUTIONARY PSYCHOLOGY CHAPTER**), studying how natural selection, acting on genes, favored a psychological capacity for cultural transmission. The second studies adaptation to the ecology. Whereas *human behavioral ecology* (Borgerhoff Mulder 1991, Cronk 1991, Smith and Winterhalder 1992a, Winterhalder and Smith 2000) focuses on adaptive outcomes, cultural evolution focuses on adaptive processes by modeling evolutionary forces and their interactions. And the third addresses the co-evolution of genes and culture, an example of *niche construction* (Odling-Smee et al. 1996, Laland et al. 2000, Odling-Smee et al. 2003), in which biological evolution gives rise to a cultural system of inheritance only to have the resulting cultural environments impose selection pressures back on the genes.

1.1 THE EVOLUTION OF THE CULTURAL CAPACITY

Why did natural selection favor a capacity for culture in our ancestors? What role did culture play in the spectacular success and spread of our species? Why did culture evolve during the Pleistocene and not earlier? Why did other species, especially our closest relatives, not evolve a similar adaptation? These are but a few of the many questions we might ask about the evolved psychology underlying our cultural capacity. This section addresses the first two and Box 1 the next two.

Perhaps natural selection favored our cultural capacity so that social learners could avoid the hard work of discovering adaptive behavior on their own. Perhaps the innovation of some allows others to imitate, an intuition captured by the idiom warning against reinventing the wheel. This hypothesis might also suggest an answer to the second question. Perhaps culture creates a profitable division of labor as in the economics argument for specialization and trade. Perhaps the innovation of some allows others to pursue other activities—and everyone ends up better off. How might we test these hypotheses? Without access to a time machine, paleontologists and archaeologists turn to the next best thing, the fossil and material records. Building mathematical models provides another kind of test (Maynard Smith 1982, Gintis 2000, McElreath and Boyd 2007, Kokko 2007, Otto and Day 2007, Epstein 2008, Smaldino 2017). Rather than test hypotheses against data, models allow us to evaluate an argument's logical coherence, a good first step

as there's no use in pursuing logically inconsistent hypotheses.

Rogers (1988) developed an evolutionary model of culture to test whether social learning evolves and whether everyone ends up better off for it. In the model, the environment is characterized by one of two states (e.g. wet or dry), periodically switching from one to the other. Each environmental state is associated with an adaptive behavior (e.g. farming or herding).¹ Individuals engage in one of two genetically heritable strategies: *individual learners* pay a cost (e.g. trial and error learning) and correctly select the adaptive behavior, whereas *social learners* avoid this cost by randomly copying someone else but only acquire the adaptive behavior if that person behaves adaptively.²

To analyze the model, we start with an ancestral state in which everyone individually learns and then introduce a mutant social learner. With everyone else learning on their own—and therefore making the correct choice, the lone social learner is sure to acquire the adaptive behavior. And without having to pay for it, the social learner has higher fitness than individual learners—and so leaves behind more offspring. But the social learner's advantage is short lived. As the frequency of social learning increases, the average fitness of the social learning strategy decreases. Remember, the environment periodically shifts. When it does, prior knowledge becomes obsolete; only individual learning increases the frequency of adaptive behavior in the population. The more social learners there are, the more likely it is that any one of them copies another social learner. In the aftermath of an environmental switch, copying a social learner guarantees maladaptive behavior.

The Rogers model seems to answer our first question. Natural selection can favor social learning as a form of information scrounging. However, the social learning strategy does not go to fixation and drive individual learning to extinction. Instead, the two strategies settle down to a stable equilibrium in which each strategy has the same average fitness (Figure 1a). In many behavioral domains, especially culture, cooperation, and conflict, the payoff to pursuing a particular strategy depends on the behavior of others and fitness is often *frequency dependent* (Maynard Smith 1982, Gintis 2000, McElreath and Boyd 2007, Kokko 2007, **COOPERATION CHAPTER**). Social learners do best when rare, as they are sure to acquire the adaptive behavior by copying from an individual learner without having to pay the cost. Individual learners also do best when rare, but for a different reason. Social learners slavishly copy others and never pay attention to

¹ Framing this as a choice between discrete behavioral options highlights the analogy with discrete alleles in a biological system. In doing so, this framing also assumes away the problem of discovering these alternatives and all the incremental steps that go into each variant. This kind of modeling assumption is meant to aid in scientific reasoning, not represent a commitment about reality. Box 1 explores the cumulative evolution of cultural adaptations.

² This assumption means that individual learning in this model is not about discovery and innovation, but instead about identifying the correct behavior among two previously discovered alternatives. Section 1.2 explores innovation in the context of guided variation.

the real world. A population comprised only of social learners becomes an echo chamber, prisoners in a cave of their own construction with no correspondence between environment and adaptive behavior. Individual learners ignore and instead observe the real world and acquire adaptive behavior. When rare, each strategy can increase relative to the other. In this model, individual learning pumps adaptive behavior into the population, social learners scrounge it from them, and the population settles down to a stable mix of the two strategies.

What about our second question? Is everyone better off when some learn individually and the rest learn socially? Does the evolution of cultural transmission as information scrounging, in part, explain the spectacular success of our species? No, it does not. At least according to the Rogers model. The average fitness of a mix of individual and social learners is the same as the average fitness of a population comprised only of individual learners (Figure 1a). To understand why, let's focus on individual learners. Regardless of what others do, individual learners pay a cost to acquire the adaptive behavior. Unlike social learners, the fitness of individual learning does not depend on the frequencies of each strategy. Instead, the fitness of individual learning is a constant. If the fitness of individual learners is the same as the fitness of social learners at the evolutionary equilibrium, and if the fitness of individual learning is a constant, then the average fitness at the equilibrium must be identical to the fitness of a population of only individual learning. Barring some other process, such as group selection (Box 2, **COOPERATION CHAPTER**), if social learning is only about information scrounging, it readily evolves but no one is better off for it.

This result may seem counterintuitive but the logic is sound. Does this mean that culture played no role in the success of our species? Not necessarily. Models do not automatically resolve scientific mysteries. Like maps, models are nothing more than representations of reality, each reflecting their creator's assumptions. Being mere representations means that all models are necessarily wrong. But like maps, some models are nevertheless useful (Box 1976). Rogers assumed that individual and social learning were distinct and independent strategies. As a result, the fitness of individual learning is frequency independent, and so the evolution of social learning cannot explain an increase in average fitness.

Boyd and Richerson (1995; see also Perreault et al. 2012) instead assumed that everyone pursues the same strategy, one which combines individual and social learning. Individuals first engage in individual learning, trying out both behavioral alternatives and comparing results. In some instances, experiments yield decisive results. In others, experiments prove inconclusive and individuals copy from someone else. Individuals vary in their reliance on social learning. Some rely heavily on social learning, turning to personal experience only when results are decisive; others rely mostly on individual learning, accepting even the weakest evidence from their own experiments.

The Boyd and Richerson model allows us to ask how natural selection strikes a balance between personal experience and social learning. At the evolutionary equilibrium of this model, the average fitness of the population is higher than the average fitness of a population comprised only of individual learners (Figure 1b). Why the difference with the Rogers model? In the Boyd and Richerson model, individuals are selective social learners, relying on personal experience only when it is decisive and otherwise turning to social learning. Selectively combining individual and social learning in this way is a game changer, increasing the effectiveness of individual learning and spreading that increased effectiveness through social learning. And, as a by-product, everyone is better off. Just to be clear, this is no appeal to group selection. Individuals pursue the strategy that maximizes individual fitness and as a by-product everyone is better off.

BOX 1: THE PSYCHOLOGY AND PHYLOGENY OF CUMULATIVE CULTURE

“If I have seen further, it is by standing on the shoulders of Giants.” Newton’s quip captures a key feature of human culture, the cumulative evolution of complex adaptations.³ While social learning and cultural traditions are common among nonhuman animals (Galef 1996, Huffman 1996, Hunt and Gray 2003, Perry et al. 2003, Rendell and Whitehead 2001, van Schaik et al. 2003, Whiten et al. 1999), only humans seem capable of harnessing social learning to evolve complex cultural adaptations (Tomasello et al. 1993, Boyd and Richerson 1996, Hill et al. 2009, Dean et al. 2014; but see Whiten 2019). As with biological evolution, the recipe involves beneficial modification, selective retention, and high-fidelity transmission. Repeat this process over and over and you get the countless technological and social innovations that contributed to our species’ remarkable success. If this process is so simple, why is it that no other species—especially chimpanzees—has anything like it, perhaps not even one cultural tradition so complex that it could not have been invented from scratch by a single individual?

Let’s start with *mechanism* (Tinbergen 1963, Bateson and Laland 2013), comparing social learning in adult chimps and human children. An early hypothesis held that chimps *emulate* the outcomes of conspecifics’ actions whereas humans *imitate* the behavioral sequences themselves (Tomasello 1996, Tennie et al. 2006).⁴ Emulating outcomes imposes a ceiling on the complexity of transmitted behavior as learners must re-invent entire behavioral sequences. By directly imitating behavioral sequences rather than inferring them from outcomes, learners have greater opportunity to experiment with modifications. As is often the case, subsequent studies sullied this simple story. Children and chimps each possess a portfolio of social learning mechanisms, including imitation and emulation, though they deploy

³ Newton’s quip itself seems to be a product of cultural evolution, not entirely his own creation. While Newton gets credit, the idea goes back hundreds of years (Merton 1993).

⁴ Here, and elsewhere, italicized words and phrases often have meanings specific to the scientific context, meanings which may or may not correspond with common usage.

these mechanisms differently (Whiten et al. 2009). While chimps can imitate, they do not do so with skill or ease. Chimps are also conservative when it comes to social learning, only adopting new tactics if they do not already have something that works (Tennie et al. 2009). Contrast this with children who often and automatically copy everything an experienced individual does, including actions which seem causally irrelevant, a process dubbed *overimitation* (Lyons et al. 2007, Nielsen and Tomaselli 2010, Nielsen et al. 2014; but see Berl and Hewlett 2015). So, the outline of the simple story still stands: Social learning in humans relies heavily on imitation, resulting in high fidelity social transmission and allowing the cumulative evolution of complex cultural adaptations. Without this faculty, social learning in nonhuman animals—mutating Newton’s quip—allows them only to glimpse what the tallest amongst them can already see. Nevertheless, this kind of social learning, common in non-human animals, facilitates the spread of adaptive behavior and generates cultural traditions (Whiten et al. 2009, McElreath et al. 2018).

Next, let’s turn to *evolution* (Tinbergen 1963, Bateson and Laland 2013), asking why humans ended up with cumulative culture while other apes did not. Assuming the common ancestor of humans and chimps possessed capacities for emulation and imitation suggests that humans added higher fidelity imitation since the split some 6–7 million years ago (Whiten et al. 2009). The Pleistocene (roughly 2.5 million to 12,000 years ago), an epoch characterized by markedly increased environmental variability, may have played a key role in this transition (Richerson and Boyd 2000, 2013). Genetically evolved adaptations are sufficient when environments are stable generation after generation. When environments are highly unpredictable from one generation to the next, it is better to turn to individual learning. Cultural evolution excels in between, when the rate of environmental change is too fast for biological evolution to track but too slow to ignore the wisdom of elders (e.g. Schniter 2014).

While this hypothesis may explain when cumulative culture evolved, it does not explain why humans alone made this transition. We know that brain sizes increased across a range of species during the Pleistocene (Jerison 1973; see also Muthukrishna et al. 2018). However, as with other aspects of human uniqueness, it is hard to know with certainty why a trait evolved when it only did so in one lineage. Perhaps free forelimbs resulting from bipedalism provided a crucial pre-adaptation for technological evolution when combined with a big-brained and social ape (Washburn 1959, Neco and Richerson 2014). Perhaps complex culture co-evolved along with other traits, including an extended juvenile period, language, and cooperation (Richerson and Boyd 2020). Regardless, the same cultural capacity that allowed our ancestors to keep pace with the constantly shifting Pleistocene, when paired with the stability of the Holocene, resulted in explosions in population size and ethno-linguistic diversity, and a series of technological and social transformations including the agricultural revolution, the rise of cities and states, and the industrial revolution (Richerson et al. 2001).

1.2 THE FORCES OF CULTURAL EVOLUTION

As anyone knows, if you throw a ball into the air, it falls back down. Few, however, can predict the precise location where it lands. In fact, no one could until Newton discovered the laws of motion. Armed with Newton's second law, an undergraduate can now build a mathematical model that accounts for the various physical forces acting on the ball and predict the precise path of a projectile from launch to landing. Since Newton, physicists have used mathematics to make sense of all manner of matter and motion. Inspired by the "unreasonable effectiveness of mathematics in the natural sciences" (Wigner 1960), biologists too built models to understand how the various forces acting on a population—mutation, migration, drift, and natural selection—result in evolution, the change in genetic composition from one generation to the next. These efforts, in turn, led cultural evolutionists to build models to understand how the cultural composition of a population changes as a result of the various forces acting upon it, including forces analogous to those in biological evolution—mutation, migration, drift, and natural selection—as well as decision-making forces novel to cultural evolution—guided variation and various social learning biases (Figure 2; the taxonomy presented here follows Richerson and Boyd 2005; see also Henrich and McElreath 2003, Mesoudi 2011).

NATURAL SELECTION ON CULTURAL VARIATION

As any student of biology knows, natural selection acting on genetic variation favors traits that help their bearers to survive and reproduce. In cultural evolution, *natural selection acting on cultural variation* (Figure 2) favors traits that are better able to thrive and replicate, regardless the effect these traits have on their bearer's biological survival and reproduction (Boyd and Richerson 1985: chapter 6). In this chapter, *biological natural selection* or simply *natural selection* refers to natural selection acting on genetic variation, whereas *cultural natural selection* refers to natural selection acting on cultural variation. Biological natural selection and cultural natural selection are analogous but not identical evolutionary forces. Because they operate on different transmission mechanisms—genes and culture, they can have different evolutionary properties. For example, when parents socialize their children (*vertical transmission*), cultural natural selection favors cultural traits that also maximize reproductive success. In this case, cultural and biological natural selection act in concert. All else equal, if some people prefer to have children while others do not, cultural natural selection on cultural variation will eliminate childlessness as there will be no biological parents to pass along this preference. By contrast, when children are influenced by peers (*horizontal transmission*) or non-parental influences, including aunts and uncles, teachers, and the prestigious (*oblique transmission*), cultural natural selection on cultural variation can, in some cases, favor the spread of genetically neutral or even maladaptive behaviors.

When it comes to culture, many evolutionary social scientists still subscribe to

Wilson's (1978) metaphor of biology as the master holding its dog, culture, on a tight leash. In this view, culture is nothing more than a proximate means by which the interests of our genes are ultimately met (Figure 3a). To explain and predict behavior, one need only consider the logic of fitness maximization. While metaphors are indispensable tools for making sense of the unknown, we must never forget that metaphors are just that, tools. If we're not careful, we can become prisoners of our metaphors, trapped into particular ways of perceiving the world. As Rosenblueth and Weiner warned, "The price of metaphor is eternal vigilance" (Lewontin 2001). Traits that are favored by cultural evolution need not promote the biological reproductive success of their bearers. For example, if young people imitate the rich and famous and forgoing children increases the likelihood of becoming rich and famous, a preference for childlessness can spread—even if those holding this preference have no biological children of their own. The demographic transition (**HUMAN EVOLUTIONARY DEMOGRAPHY CHAPTER**) may be an example of just such a process, in which a cultural preference for lower fertility was favored, in part, as a result of novel socialization patterns and economic opportunities, a point to which we will return in Section 2.1.

GUIDED VARIATION

As with group selection (Box 2), most students of biology were taught that *Lamarckism* was not just wrong and antithetical to *Darwinism*, but also silly and perhaps even dangerous (Riskin 2016).⁵ Lamarck, like many of his contemporaries, believed that organisms could develop useful characteristics during their lifetimes and transmit these acquired characteristics to their offspring. The textbook example is the giraffe's long neck. Ever stretching to reach the highest leaves, ancient giraffe ancestors were thought to have elongated their necks, and then transmitted these longer necks to their offspring. The repetition of this process generation after generation resulted in modern giraffes. But since the *Modern Synthesis*, students of biology have been taught that development and evolution are separate and distinct processes. Any changes to organisms during their lifetimes cannot be transmitted to offspring—and thus development processes cannot contribute to evolutionary outcomes. Instead, evolution results from various forces that change gene frequencies from one generation to the next. Adaptation results from natural selection whittling away at novel variation generated by random genetic mutations. While this model may be a decent approximation of biological reality, the line between evolution and development is blurry. So much so that some biologists and philosophers advocate for an *Extended Evolutionary Synthesis*, one that incorporates Lamarckian processes including epigenetic transmission as well as 'plasticity first' adaptation in which development becomes a source of variation on which natural selection can act (Oyama et al. 2001, Pigliucci and Miller 2010, Jablonka and Lamb 2014, Laland et al. 2015; see also Peterson 2017).

⁵ Of course, the dirty secrets many of us were not taught was that Darwin himself subscribed to both group selection and Lamarckism!

In contrast to biological evolution, cultural evolution is fundamentally Lamarckian. Culture represents a pool of adaptive information from which people can learn. They can then transform what they have learned socially through various individual learning mechanisms. In many cases, these transformations will not be random, but will instead be biased toward adaptive outcomes. In biology, this would be like having a genetic system in which mutations were not random, but instead fitness-enhancing. The opportunity for social learning then means that the next generation can pick up where the previous one left off. Instead of re-inventing the wheel, they can improve on its design. This process of linking innovations from individual learning to transmission through social learning results in the force of *guided variation* (Figure 2; Boyd and Richerson 1985: chapter 4) and contributes to the cumulative evolution of complex adaptations (Box 1).

SOCIAL LEARNING BIASES

When it comes to genetics, inheritance is destiny. We are our parents' children.⁶ Not so with culture. Through the force of guided variation, individuals can intentionally modify what they have learned and transmit these modifications to others. In addition, there are various *social learning biases* (Figure 2) that influence whom or what learners choose to imitate. Unlike guided variation, which is a creative process that introduces novel variation, these social learning biases, like biological and cultural natural selection, are culling processes that selectively favor certain cultural variants over others.

A *content bias* refers to the preferential adoption of certain cultural variants over others based on the characteristics of the variants rather than the individuals bearing them (Figure 2; also called a *direct bias*; Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985: chapter 5, Durham 1991). A content bias might result from individuals comparing alternatives and choosing based on perceived benefits and costs. The rate of cultural evolution will be fast when comparison is easy, such as choosing metal tools over stone tools. When difficult, beneficial innovations may spread slowly or not at all. For example, convincing people to boil water is difficult because waterborne diseases are not the only reason people get sick, because fuel is expensive, and because the idea of microscopic bacteria may not resonate with folk medical beliefs (Rogers 1995). Content biases can also result from features of cognition that make some variants more appealing than others. Boyer (1994) and Atran (2002) argue that a content bias favoring “minimally counterintuitive” stories, in which some of our folk intuitions are violated while others are not, helps explain the prevalence of supernatural beliefs. Ghosts, for example, violate our understanding of physics by crossing through solid objects, but otherwise behave in ways consistent with our expectations of human behavior.

⁶ Not entirely, of course. Environmental factors influence genetic expression. And, whether a blessing or a curse, genetic engineering is no longer science fiction (Cyranoski 2018).

When the comparison of material consequence or psychological appeal proves difficult, individuals can ignore the variants and focus instead on the individuals bearing them. In *conformist biased* learning, individuals disproportionately adopt the most common cultural variant (Figure 2; Boyd and Richerson 1985: chapter 7, Henrich and Boyd 1998). Suppose, for example, that you pursue a career in academic research, despite the protestations of your loved ones. After landing that coveted tenure track professorship, you notice that six of your ten department colleagues don a blazer while teaching. With a strict *frequency bias*, you too would wear a blazer with 60% probability. With a conformist bias, the probability would be higher still. How much higher depends on the degree of conformity. With a weak bias, the adoption probability will be close to the frequency of blazers among your colleagues. As the conformist bias strength increases, the probability of adopting the more common variant approaches 100%. Disproportionately adopting common cultural variants can be adaptive when other forces of cultural evolution, including cultural natural selection, guided variation, and content bias, result in adaptive variants becoming common but not going to fixation. In this way, a conformist bias amplifies other adaptive processes by allowing individuals to leverage the “wisdom of crowds” (Surowiecki 2004). This process results in the loss of uncommon variants, homogenizing social groups and maintaining differences among them, potentially fueling *cultural group selection* (Box 2).

A *prestige bias* refers to the preferential imitation of high status people (Figure 2; Boyd and Richerson 1985: chapter 8; Henrich and Gil-White 2001). Returning to our academic example, if your colleagues vary in status, you might want to adopt the wardrobe of the Nobel Prize winner rather than the most common outfit. Such a bias would have been adaptive to our ancestors in situations in which it was easier to infer successful individuals than to infer the secret of their success. A prestige bias can result in naive individuals imitating a wide range of traits, including traits that may be correlated with but not causally contributing to success, similar to overimitation (Box 1).

WHY CULTURE AND MODELING CULTURE MATTER

Critics of the cultural evolutionary approach often complain that culture is not an adequate causal explanation and that modeling cultural evolutionary processes is unnecessary in predicting behavioral outcomes. Let’s address these criticisms in turn. The criticism that culture is not an explanation amounts to a claim that human behavior can be sufficiently explained in terms of evolved psychology and local ecology. Once these factors are accounted for, there is nothing left for ‘culture’ to explain. This criticism would be accurate if the strength of social learning biases dwarfed the power of cultural natural selection (Figure 2). If this were the case, the study of cultural evolution would reduce to an environmental and behavioral science, one in which proximate explanations of why people adopt the beliefs and

behaviors they do focus on behavioral ecology and ultimate explanations focus on evolutionary psychology. If, instead, cultural natural selection is an important force, then cultural history matters, too, and the study of culture requires the social sciences in addition to ecology and psychology. Salamon's (1995; reviewed in Richerson and Boyd 2005) ethnographic study of Illinois farming communities provides an example. Salamon identified two distinct farming strategies that have persisted across multiple generations even though everyone farms the same land. These approaches to farming reflect cultural historical differences, not ecological differences. Farmers with English ancestry treat farming as a business and land as a commodity, whereas those with German ancestry see farming as a way of life and land as a sacred family possession.

The second criticism, that modeling cultural evolution is unnecessary, invokes the *phenotypic gambit* (Grafen 1984), that culture is just a proximate means by which the interests of our genes are ultimately met (Wilson 1978). Smith and Winterhalder (1992b), for example, argue that "selection will favour traits with high fitness...irrespective of the particulars of inheritance". This approach works for simple adaptive topographies. In the limiting case, the details of genetics, culture, or learning are irrelevant in predicting outcomes; every adaptive process will discover the same fitness optimum. But adaptive topographies are not always simple. There may be multiple adaptive peaks that shift over time. In these more complex cases, the details of the inheritance system matter. To understand why particular cultural variants spread while others perish in these cases, we need to predict the net effect of all these forces of cultural evolution (Figure 2). This is often difficult if not impossible using intuition and verbal reasoning alone. Sometimes it is better to set aside the metaphor and build a model.

BOX 2: CULTURAL GROUP SELECTION AND THE EVOLUTION OF COOPERATION

Until the 1960s, biologists often invoked *biological group selection* to explain the mystery of altruism (Wynne-Edwards 1962). Natural selection favors groups with more altruists willing to sacrifice their own reproductive success for the good of the group, or so the logic went. Williams (1966) identified the fatal flaw in this argument. For there to be selection, there must be variation (Lewontin 1970). The problem with biological group selection is that migration across group boundaries erodes genetic variation between groups faster than mutation can pump it back in (Figure 4a). No between-group variation means no group selection (McElreath and Boyd 2007, Okasha 2009).

It was Hamilton's (1964) *inclusive fitness theory* which finally resolved the mystery of altruism. Natural selection favors genes that sacrifice the reproductive success of their host organism (*direct fitness*) so long as this cost is more than offset by a commensurate gain in the reproductive success of closely related organisms housing identical genes due to common descent (*indirect fitness*). While organisms may appear

altruistic, it is only in service of their “selfish” genetic masters (Dawkins 1976). The 1960s saw the rise of sociobiology and demise of group selection, representing a revolution in evolutionary thought and, as part of a broader shift to methodological individualism across the social and behavioral sciences, resulted in an obsessive focus on individual behavior and selection (Williams 1996, Segerstrale 2000). Since the revolution, group selection has become a failed paradigm, a dirty word, and inextricably linked to the problem of cooperation.

This legacy contributes to the deep confusion over *cultural group selection* (Henrich 2004a, Richerson and Boyd 2005, McElreath and Boyd 2007, Panchanathan 2011, **COOPERATION CHAPTER**). Cultural group selection is not the same as old-school biological group selection—nor is it typically invoked as a direct solution to the problem of cooperation. Cultural group selection builds on the theory of *multi-level selection* (Price 1970, Hamilton 1975, Okasha 2009), and is comprised of two parts. Cultural group selection first argues that the nature of cultural transmission, unlike genetic transmission, gives rise to multiple stable equilibria. When people conform to norms or imitate prestigious individuals, they do so for purely self-interested reasons, to acquire adaptive behavior. As a byproduct, groups become homogeneous and variation between groups can be maintained despite migration (Figure 4b). This effect is amplified by other social processes including behavioral assortment using ethnic markers (Barth 1998, Boyd and Richerson 1987, McElreath et al. 2003) and social sanctions (Boyd and Richerson 1992, Boyd et al. 2003, Panchanathan and Boyd 2004). Recent research offers empirical support, finding that substantial cultural variation resides between rather than within social groups (Bell et al. 2009, Handley and Mathew 2020).

The second part of cultural group selection theory focuses on the problem of equilibrium selection. If different groups end up at different social equilibria, which equilibria spread and why? While studying individual behavior may explain why people conform to norms, it offers limited guidance in predicting which norms spread and which norms perish. Norms, like social institutions, are group-level traits (Smaldino 2014), emergent social phenomena that cannot be reduced to the individual level. To explain the cultural evolution of group-level traits, we need a theory of cultural group selection. Cultural group selection mechanisms include conflict and conquest among groups (Soltis et al. 1995, Boyd et al. 2003), imitation across group boundaries (Hirschman 1970, Boyd and Richerson 2002), and selective migration between groups (Hirschman 1970, Boyd and Richerson 2009). And all else equal, these mechanisms favor the spread of cooperative, group-beneficial norms.

Sociobiology has provided us with two ways of understanding the evolution of social behavior. The *selfish gene* perspective (Hamilton 1964, Dawkins 1976) focuses on individuals and their social interactions, whereas the *multi-level* perspective (Price 1970, Hamilton 1975, Okasha 2009), which includes cultural group selection, focuses on groups and the social interactions within and between them. Too often,

discussions of social evolution turn into debates about which approach is correct and which approach is incorrect. This is a mistake. These two approaches are formally equivalent perspectives on the same underlying process, neither correct nor incorrect (Hamilton 1975; McElreath and Boyd 2007). When it comes to studying the evolution of social institutions like marriage, kinship, and political organization, evolutionary social scientists need not choose between these perspectives. In fact, they might do better by adopting and internalizing both, a “gestalt-switching pluralism” (Kerr and Godfrey Smith 2002) that can reveal more than either perspective does by itself.

1.3 GENE-CULTURE CO-EVOLUTION

Consider yourself privileged if you can take milk with your coffee.⁷ Most adults around the world are lactose intolerant due to a steep decline in lactase production during adolescence. This pattern is the norm across mammals. *Lactase persistence* is restricted to a small subset of human populations. For most human societies and all other mammalian species, milk is baby food. Since the only function of lactase is to digest the milk sugar lactose, natural selection favored the cessation of lactase production around the time of weaning. This adaptive logic held for our Pleistocene ancestors. With the advent of herding, however, humans had ready access to milk as adults. Natural selection then favored lactase persistence resulting in the pattern we see today: high rates of lactase persistence among those with ancestry from northern Europe and some regions of Africa; intermediate rates among those with ancestry from the Mediterranean, the Middle East, and central and south Asia, populations that often ferment milk into cheese or yogurt; and low rates for Native Americans, many sub-Saharan Africans, and everyone else. Lactase persistence is a population-specific rather than a species-typical adaptation, evolving independently in populations with long histories of pastoralism and milk consumption (Simoons 1970, Durham 1991, Holden and Mace 2009, Itan et al. 2009, Séguirel and Bon 2017).⁸

Lactase persistence is an example of *gene-culture co-evolution* (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Richerson and Boyd 2005; for a recent review, see Laland 2017). The cultural evolution of pastoralism created an environment which favored the biological evolution of lactase persistence. Gene-culture co-evolution represents an example of *niche construction* (Odling-Smee et al. 1996, Laland et al. 2000, Odling-Smee et al. 2003). When we speak of “selection pressures” we often treat natural selection as an external force acting on populations. In the niche construction perspective, organisms modify their environments and these modified environments in turn impose new selection

⁷ But mistaken. Black is better.

⁸ This commonly-told story of why some are lactose tolerant while others are not may be an oversimplification. It seems that most people can become at least somewhat lactose tolerant regardless of their genetic makeup (Byers and Savaiano 2005).

pressures on organisms. Naked mole rats provide an example. As the ancestors of naked mole rats burrowed deeper underground, natural selection favored a gradual loss of hair and vision. In this way, the environment is transformed from an exogenous variable to an endogenous one, requiring the researcher to keep track of the co-evolutionary dynamics between organism and environment. Gene-culture co-evolutionary dynamics in humans may be a particularly powerful form of niche construction (Richerson and Boyd 2005, Laland 2017).

Once you adopt the gene-culture co-evolution perspective, it becomes difficult not to see its effects everywhere. Take language. Compared to us, our ancestors had rudimentary communicative skills. Any selection on improved communication would have resulted in a more complex linguistic environment. This human-induced environment would then have selected for improved communicative ability. In this way, the capacity for language and the complexity of the linguistic environment co-evolved (Pinker and Bloom 1990, Pinker 1994, Richerson and Boyd 2010). The human capacity for large scale cooperation may represent another example of gene-culture co-evolution (Richerson and Boyd 2005, Bowles and Gintis 2011). Our pre-cultural ancestors inherited a set of behavioral predispositions shared with other primates, arising from kin selection and reciprocity, and enabling cooperation among family, friends, and local group members. The advent of our cultural capacity unleashed a process of cultural group selection and favored the cultural evolution of large-scale cooperation (Box 2). This novel cultural environment of cooperation then favored the biological evolution of a new set of behavioral predispositions unique to humans, including prosocial preferences, a moral psychology willing to adopt social norms and punish violators, and in-group favoritism spanning large, symbolically marked tribes. As a result, human societies resemble eusocial insect colonies in many ways, except for a reproductive division of labor. Neither ape nor ant are we, but something in between, a “crude superorganism” characterized by conflict and cooperation (Richerson and Boyd 1999).

The evolution of language and cooperation through gene-culture co-evolution represent examples of species-typical adaptations that arose during the Pleistocene. The evolution of lactase persistence, by contrast, is an example of a population-specific adaptation that arose during the Holocene. The prevalence of sickle-cell anemia among those of African descent may represent another example (Durham 1991, Laland et al. 2010). West African agriculturalists cleared forests to grow yams, resulting in pools of stagnant water after the rains, a perfect breeding ground for mosquitos. As mosquitos spread malaria, natural selection favored the sickle-cell allele, which conferred malarial resistance. And as we learn more from genomics, we will likely discover many more cases of population-specific adaptations arising from gene-culture co-evolution (Laland et al. 2010, Richerson et al. 2010, Laland 2017).

In Wilson's (1978) metaphor of dog and master, culture was but one form of *adaptive plasticity* controlled by the genes, helping to tailor phenotypic development to the local ecology (Figure 3a). Heeding Rosenblueth and Weiner's warning, "eternal vigilance" (Lewontin 2002) helps us know when to discard old metaphors for new ones. As part of a larger call for an extended evolutionary synthesis (Oyama et al. 2003, Pigliucci and Miller 2010, Jablonka and Lamb 2014, Laland et al. 2015), perhaps we might re-imagine gene-culture co-evolution as an intricate ballet in which genes and culture take turns leading and following (Figure 3b). And, despite giving birth to culture, as social and technological complexity increase, it may be our genes that spend less time leading and more time following.

2. THE EMPIRICS OF CULTURAL EVOLUTION

In reviewing the "three styles" of evolutionary social science, Smith (2000) characterized cultural evolution as "theoretically rich and sophisticated, but empirically impoverished" when compared to human behavioral ecology and evolutionary psychology. While cultural evolution was never a purely theoretical research paradigm (e.g. Hewlett and Cavalli-Sforza 1986, Soltis et al. 1995), the discipline was historically dominated by theoretical investigation. But this characterization is no longer accurate. The past two decades has seen rapid growth in the empirical study of cultural evolution (Mesoudi 2011, 2017). This section reviews recent examples, categorizing them into three methods: (1) fieldwork, (2) laboratory experiment, and (3) phylogenetics and history.

2.1 CULTURAL EVOLUTION IN THE FIELD

Just as each culture follows customary rituals, each scientific discipline practices customary methods. Economists construct models. Psychologists crank out experiments. And anthropologists conduct fieldwork.⁹ While models sharpen reason and experiments allow control, only observational fieldwork studies humans on their terms and in their natural habitats.

Fertility in rural Poland

Fertility rates have plummeted since the industrial revolution, beginning in Europe and later spreading to the rest of the world. Though the *demographic transition* has been well documented, explaining why it began and later spread has been a "central

⁹ These characterizations are clearly caricatures. We should never essentialize "cultures" or "scientific disciplines" as discrete, bounded, and homogenous groups (Gupta and Ferguson 1992). Economists also conduct behavioral experiments and analyze historical data; psychologists also build computational models and conduct cross-cultural research; and anthropologists also build evolutionary models and conduct experiments in the field. As with everything else in nature, "cultures" and "scientific disciplines" are characterized by variation. Nevertheless, caricatured constructs can capture meaningful variation between groups. All models are wrong after all, but some are nevertheless useful (Box 1976).

theoretical problem of human sociobiology” (Vining 1986; see also Borgerhoff Mulder 1998, Colleran 2016, **HUMAN EVOLUTIONARY DEMOGRAPHY CHAPTER**). One point of contention centers on whether the fundamental cause is ‘economic’ or ‘cultural’. One version of the economic hypothesis argues that the transition to market economies favored investment in *embodied capital* resulting in fewer offspring with higher levels of parental investment (Kaplan 1996, Kaplan et al. 2002, Shenk et al. 2013, Colleran 2016). One version of the cultural hypothesis argues that higher rates of non-parental social transmission (horizontal or oblique rather than vertical) coupled together with new avenues of social status competition favored the spread of low fertility norms. Some anthropologists argue that separating ‘cultural’ and ‘economic’ in this way makes no sense as economic systems and preferences are inseparable from other aspects of culture (e.g. Chibnik 2011, Sahlins and Graeber 2017). Even if they don’t go this far, most researchers agree that complex phenomena like the demographic transition are unlikely to result from a single cause. Nevertheless, most research focuses either on the economic hypothesis using individual-level data or the cultural hypothesis using population-level data (but see Shenk et al. 2013).

Colleran et al. (2014) compared these two explanations of fertility decline by studying the relationship between education and fertility both within and between communities in rural Poland. Women’s education is a key predictor of fertility decline, but it is not clear whether this supports the economic or the cultural hypothesis. According to the economic hypothesis, fertility declines as individual women’s education increases. According to the cultural hypothesis, the aggregate level of education should also matter. In more educated communities, all women, even those without an education, will be more heavily exposed to and influenced by low fertility norms. Colleran et al.’s results indicate that aggregate education is a better predictor of fertility decline than individual education. For example, regardless of their own characteristics, women in the most educated community had half as many children as women in the least educated community. The lesson here is not that individual attributes are irrelevant or that the economic hypothesis is incorrect. In fact, some of Colleran et al.’s findings were consistent with the economic hypothesis. Instead, the results highlight the ways in which cultural norms may shape fitness-relevant domains of behavior, including reproduction, alongside ecological factors—and that, in some cases, the two may reinforce each other.

Cattle raiding in Turkana

Like the capacity for complex and cumulative culture (Box 1), large-scale cooperation among unrelated individuals represents a uniquely human adaptation (Box 2, **COOPERATION CHAPTER**). And like the demographic transition, cooperation represents another “central problem of sociobiology” (Wilson 1975). The challenge of cooperation lies in solving the *free rider problem*. If everyone enjoys the benefits of

cooperation regardless of their own contribution, self-interested individuals will, of course, choose not to contribute. Models (Boyd and Richerson 1992, Boyd et al. 2003) and experiments (Yamagishi 1986, Ostrom et al. 1992, Fehr and Gächter 2002) show how the voluntary sanctioning of free riders can sustain cooperation. But punishment just begs another question: If administering punishment is costly, what motivates self-interested individuals to punish free riders? There are various solutions to this *second-order free rider problem*. In complex, state-level societies, governments police crime and administer punishment. But formal institutions like police forces and court systems were not the norm across human history. Another class of solutions, including costly signaling (Gintis et al. 2001) and social exclusion (Panchanathan and Boyd 2004), makes sanctioning individually beneficial, transforming a public good into a private one, thereby eliminating the second-order free rider problem. But these mechanisms become increasingly unworkable as group size increases. A third class of solutions focuses on unique properties of cultural transmission compared to genetic transmission, such as conformist transmission (Henrich and Boyd 2001, Guzmán et al. 2007), and how they fuel cultural group selection (Box 2; Boyd et al. 2003, Richerson et al. 2016).

Mathew and colleagues (Mathew and Boyd 2011, Mathew and Boyd 2014, Handley and Mathew 2020) studied cattle raiding among Turkana pastoralists to test aspects of the cultural group selection hypothesis. The Turkana, an East African ethnolinguistic group numbering roughly a million people, practice a form of nomadic pastoralism that includes a perpetual struggle for existence with other ethnolinguistic groups, raiding their neighbors' cattle and protecting their own. This kind of 'informal warfare,' perhaps counterintuitively, represents a stark example of large-scale cooperation. Warriors incur substantial private costs in the form of injury and death, costs which are not obviously offset by the gains of private goods in the form of captured cattle. In addition, warfare provides a public good to everyone in the form of territorial defense and expansion. Raiding parties comprise hundreds of unrelated men drawn from subsections across Turkana society, providing individuals with strong temptations to desert in the lead up to a raid and take off with more cattle than socially prescribed in the aftermath—and as many as half do. Turkana cattle raiding would collapse if not for collectively administered punishment in the form of insults, fines, and beatings. While foragers and horticulturalists routinely engage in cooperation comprising dozens of related and face-to-face interactants (Gurven 2004, Hill et al. 2009), cooperatives are sufficiently small to be explained by a combination of kin selection, reciprocity, and reputation. For centralized states, cooperation among millions or more can be sustained through formal punishment institutions. The Turkana represent something in between, cooperating and sanctioning free riders at the scale of an ethno-linguistic group to support inter-group warfare without recourse to a centralized political structure, a pattern of social organization and behavior that may have been common during much of human prehistory (Bowles and Gintis 2011). The maintenance of these cooperation and sanctioning norms at the scale of

ethno-linguistic units is consistent with cultural group selection and hard to explain with mechanisms like kin selection, reciprocity, and reputation.

2.2 CULTURAL EVOLUTION IN THE LAB

While observational fieldwork has the benefit of ecological validity, it comes with a cost. How confident can we be about causal inferences when we cannot manipulate target variables? The real world is messy. Everything interacts with everything else. By isolating and manipulating theoretically relevant variables and controlling others, the experimenter, whether in the field or in the lab, can draw stronger causal inferences than can the observer.

The evolution of sanctioning institutions

The Turkana case study (Section 2.2) demonstrates how punishment sustains collective action in an ecologically valid setting. But demonstrating how a social institution functions is one thing. Demonstrating how it spreads is quite another. Gürer et al. (2006) designed a cultural evolution experiment to do exactly this. Each period of the experiment comprised four stages. First, participants independently and simultaneously chose between living in a society that permitted punishment and a society that did not. Second, participants in each society chose how much of their endowment to contribute to the public good. Each dollar not contributed to the public good is a dollar the participant kept. Each dollar contributed to the public good was multiplied by a certain amount and then distributed equally to everyone in that society. Third, and only in the society that permitted punishment, participants had the option to sanction others at a personal cost. Fourth, individuals were provided anonymized data about the earnings of participants in both societies. Only one in three participants initially chose the society permitting punishment—two in three preferred a world without punishment. By the end of the experiment, however, most of the participants chose the society with punishment, having learned that punishment deters free riding. In the punishment-free society, free riders earned more than contributors. Not so in the society with punishment. These results suggest that people only reluctantly adopt punishment institutions. Many initially imagine all the people living life in peace. But as reality strikes back, more and more participants “vote with their feet” (Hirschman 1970, Boyd and Richerson 2009) and migrate to the society with punishment, a form of cultural group selection that favors the spread of group-beneficial norms (Box 2).

Demography and technological complexity

The first people to set foot on Tasmania did so around 35,000 years ago, when it was

still a peninsula of Australia. Some 6,000 years ago, rising sea levels separated these first people from their Australian counterparts. And until the late 18th century, Tasmanians remained in a state of not-so-splendid isolation (Diamond 1978, Henrich 2004b). At the time of European contact, the differences in technological complexity between Tasmanians and Australians were striking, resulting in stark differences in well-being. Whereas the Australians across the Bass Strait had hundreds of tools, Tasmanians had only a few dozen. And Australian tools were comparatively more complex than Tasmanian tools. Why these dramatic differences despite similar ecologies? Theoretical models point to the importance of demography in the evolution of cumulative culture (Henrich 2004b, Powell et al. 2009). In these models, individuals vary in their skill level (e.g. some make more complex and/or more efficient spears than others). Naïve individuals imitate the most skilled members of their group. Imitation is assumed to be noisy and biased towards relative simplicity, with most imitators ending up with a lower skill level than those they imitate and only a few making improvements. In small populations, the downward force of imperfect imitation dominates, and the population ends up with a low overall level of technological complexity. In large populations, the occasional innovative leap is sufficient to overcome this entropic force, sustaining and even further developing technological complexity, a process analogous to the “ratchet” of innovation and imitation discussed in Box 1. Field tests of this hypothesis remain mixed (Collard et al. 2005, Kline and Boyd 2010), and so we turn to an experimental approach.

Derech et al. (2013) used a laboratory experiment to test the hypothesis that population size is a key variable in the evolution of cumulative culture. The experiment lasted 15 time periods. In each period, participants chose to build either an arrowhead or a fishing net. Each task required multiple steps. Participants were rewarded based on how closely their efforts matched the optimal design. An optimally designed fishing net yielded a higher reward than an optimally designed arrowhead. However, the optimal fishing net required discovering both the appropriate shape and the order in which to build it, whereas the optimal arrowhead required only discovering the appropriate shape. Designing an efficient arrowhead was far easier than designing an efficient fishing net. Participants interacted in groups of two to sixteen people. After each period, participants could see everyone’s score. They could then observe the procedure used by one of their group members. The results were consistent with several predictions arising from the hypothesis that population size affects the evolution of cumulative culture. First, across all group sizes, the complex technology was more likely to be lost than the simple technology—no one chose to build a fishing net in later periods. Second, the complex technology persisted longer in larger groups. Third, performance on the complex technology deteriorated in smaller groups, but remained stable in larger groups. These results underscore the importance of social dynamics in the cultural evolutionary process. When it comes to cultural adaptation, it is not enough to study how individuals adapt. We must also study how they interact.

2.3 CULTURAL PHYLOGENETICS AND HISTORY

In biological evolution, the effects of various evolutionary forces result in *descent with modification*. Micro-evolutionary processes give rise to macro-evolutionary patterns. Biologists use various methods to reconstruct these *phylogenetic trees*. Over the last few decades, anthropologists have borrowed these methods, using patterns of culture to infer the processes shaping cultural evolution (Mace and Pagel 1994, Gray et al. 2007, Currie 2013). *Phylogenetic comparative methods* allow the analyst to make inferences about the sequence and timing of cultural trait evolution and co-evolution. The researcher first constructs a phylogenetic tree that is supposed to reflect the historical relationships between the groups being studied. Most studies have used linguistic features like basic vocabularies. Armed with this linguistically based phylogenetic tree, the analyst can reconstruct a possible history for the cultural trait of interest, such as residence or marriage system, and even test distinct hypotheses for the processes that may have led to the current distribution of traits (e.g. Ross et al. 2016). As with any other statistical technique, care must be taken when interpreting these results in causal terms (Uyeda et al. 2018). In addition, some researchers remain skeptical about the applicability of phylogenetic methods in the domain of cultural evolution given the differences between cultural and genetic transmission (Borgerhoff Mulder et al. 2006, Nunn et al. 2006, Foster and Evans 2019, Lukas et al. 2021, Evans et al. 2021).

The evolution of political complexity

Anthropology has a long and controversial history of categorizing and sometimes ranking societies based on political complexity (Currie and Mace 2011, **POLITICAL ORGANIZATION AND INEQUALITY CHAPTER**). Theorists in the 19th century argued for *unilineal theories of social evolution*, such as Morgan's (1877) sequence of savagery, barbarism, and civilization, which often ascribed notions of "progress" to the evolutionary process. Subsequent theories, including Service's (1962) classic model of bands, tribes, chiefdoms, and states remained evolutionary while abandoning both a unilineal sequence and any notion of progress. But questions remained. Does political evolution proceed in a gradual sequence of incremental increases in complexity or can political evolution happen in jumps—e.g. Can a tribe-level society transition directly to a state without first passing through a chiefdom stage? Is social evolution a one-way ratchet resulting in ever-greater levels of political complexity or can cultures collapse to lower levels of complexity—e.g. Can a chiefdom revert to a tribe? Currie et al. (2010) used phylogenetic comparative methods to study the evolution of political complexity among a sample of 84 Austronesian societies, first constructing a phylogeny based on language and then testing different models about how changes in political organization occurred. Their results support a model of social evolution in which changes in political complexity can go in either direction (e.g. tribes can transform into chiefdoms, and

chiefdoms can revert to tribes). While transitions in political complexity are bi-directional, the magnitude of these transitions are not equivalent. Increases seem to be incremental, while decreases can be extreme. When it comes to the evolution of political organization, sometimes it's one step forward, two steps back.

The co-evolution of kinship and subsistence

Anthropologists long ago noticed that cultural traits in different domains are not independent but instead co-vary in predictable ways. For example, societies with *matrilineal kinship* (tracing descent through females) tend to practice *horticulture* (small-scale, low-intensity farming without the use of the plow or draft animals), whereas societies that make their living through *pastoralism* (herding large animals) tend to be *patrilineal* (tracing descent through males). Correlations like these suggest that certain bundles of cultural traits may be adaptive. But simple correlations fall victim to *Galton's problem*: Cultures cannot be treated as independent data points as they may share cultural traits because of either convergent evolution (analogy) or common ancestry and proximity (homology). When testing functional hypotheses, we need to isolate analogous traits. For kinship and subsistence, we cannot distinguish between adaptive co-evolution and shared ancestry when observing cultural complexes like matrilineal horticulturalists or patrilineal pastoralists. To deal with this problem, Holden and Mace (2003; but see Surowiec et al. 2019) conducted a phylogenetic analysis of 68 Bantu-speaking societies. They used linguistic data to construct a phylogeny among the sample. Their analysis suggests that the earliest Bantu-speaking populations practiced horticulture. It is not clear whether these populations were predominantly matrilineal or patrilineal. Later, a small fraction of these horticultural societies adopted pastoralism. It seems the cultural complex of matriliney and pastoralism is highly unstable. Matrilineal societies that adopted pastoralism either revert to horticulture (matrilineal horticulturalists) or also adopt patriliney (patrilineal pastoralists). By contrast, the cultural complex of patriliney and pastoralism seems to be highly stable.

CONCLUSION

This chapter reviewed the theory of cultural evolution and recent empirical studies inspired by this body of theory. The cultural evolution approach argues that humans evolved a dual inheritance system, in which genes and culture both contribute to human adaptation, often working in concert but sometimes in conflict with each other. The field of cultural evolution arose in the wake of sociobiology and developed alongside evolutionary psychology and human behavioral ecology. Like evolutionary psychology, cultural evolution investigates the biological evolution of the psychological capacities underlying culture (Section 1.1). And like human behavioral ecology, cultural evolution studies the factors underlying cultural diversity (Section 1.2). Cultural evolution also studies the ways in which genes and

culture influence the evolutionary dynamics of each other, an example of niche construction (Section 1.3).

While the empirical studies reviewed in this chapter focus on traditional problems in the study of human behavior and evolution, including marriage, reproduction, and cooperation, the reach of the cultural evolutionary framework extends much further, offering an integrative framework to help organize cognitive, behavioral, and social science research. Geneticists have begun to catalogue the many ways in which cultural environments shaped genetic evolution (reviewed in Laland et al. 2010, Richerson et al. 2010, Laland 2017). Psychologists have drawn from cultural evolutionary theory in the study of child development and social learning (Wertz and Wynn 2014, Legare and Nielsen 2015). Economists have been inspired by and contributed to cultural group selection and gene-culture co-evolution (Bowles and Gintis 2011). Historians have used cultural evolutionary approaches to study the rise and fall of empires (Turchin 2003, 2008). Some have argued that social systems and structures constitute a third system of inheritance in addition to genes and culture (Runciman 2009, Koditschek 2019). Philosophers have begun to incorporate cultural evolution into their political theorizing (Gaus 2021, Sterelny 2021). Cultural evolution has also been applied to epistemology and metascience, offering insights into how we can understand and improve the scientific method (McElreath and Smaldino 2015, Smaldino and McElreath 2016), and sustainability, exploring how multi-level selection might inform socio-ecological interventions (Waring et al. 2015).

The subject of this edited volume is human behavioral ecology. How can cultural evolution further contribute to and be informed by human behavioral ecology? Despite shared interests, human behavioral ecology and cultural evolution emerged from different disciplinary backgrounds and employed different methodologies—and so approached research problems in different ways. Emerging from cultural anthropology, human behavioral ecologists tried to make sense of the myriad ways in which populations adapt to their local socioecological conditions. The focus was on testing locally contextualized predictions using ethnographic fieldwork. Emerging from population genetics, cultural evolutionists tried to understand how culture evolves and in what ways is it adaptive. The focus was on building general theory using mathematical models. While these early cultural evolution models were built up from empirical studies of psychology and cultural ecology, they were rarely designed with the purpose of being empirically tested—and so were often of little use to field researchers.

But this is all in the past. The lines between cultural evolution and human behavioral ecology—and also evolutionary psychology—are blurring as the disciplines borrow from one another. We are witnessing the birth of an integrated and integrative evolutionary social science. Field researchers have contributed to this integration by studying the ways in which local conditions structure social

learning (e.g. Berl and Hewlett 2015, Boyette 2016, Cristia et al. 2019, Garfield et al. 2016, Kline 2015, Lew-Levy et al. 2017, Lew-Levy et al. 2018, Nielsen and Tomaselli 2010). Advances in statistical methods will become increasingly important in bridging the gap between observational field research and theoretical model building (McElreath 2018). Kandler and Powell (2018), for example, draw from recent advances in population genetics and develop tools to infer the relative magnitudes of different social learning mechanisms using population-level observational data.

Theoreticians can also contribute to this integration by developing new models. Early models were intentionally simple and abstract—so that they could address general questions about the cultural evolutionary process. New models should be more complex and tailored to local conditions—so that they might be of more use to field researchers. In addition, cultural evolutionists might reconsider some of their foundational assumptions, especially if they want to bring non-evolutionary social scientists into the fold. Critics of the cultural evolution approach (e.g. Durham 1991, Fracchia and Lewontin 1991; but see Boyd and Richerson 1985: Chapter 8) have complained that culture is not just socially transmitted information affecting behavior, but also a system of values and meanings; that individuals cannot easily be categorized into discrete and non-overlapping groups, but instead are embedded in many different and partially overlapping social networks; that individuals do not have unfettered agency and cannot freely choose whom to imitate or how to behave, but are often influenced, pressured, and coerced through power and ideology. None of these criticisms are damning, but neither are they wrong. Early models of cultural evolution were not built to address these kinds of concerns. As the field has matured, these earlier models have done their jobs, and some may have outlived their usefulness (Levins 1966). As scientific knowledge accumulates, we should set aside old models and build new ones.

ACKNOWLEDGMENTS

I would like to thank Jeremy Koster, Brooke Scelza, and Mary Shenk for inviting me to write this chapter and for providing valuable feedback during the writing process. I would also like to thank the official reviewers for greatly improving the book chapter: Monique Borgerhoff Mulder, Cristina Moya, and the anonymous Reviewer 3. Finally, I would like to thank the many unofficial reviewers who read and commented on previous drafts: Ritwik Agrawal, André Ariew, Clark Barrett, Heidi Colleran, Tom Currie, Martin Daly, Maxime Derex, Charles Efferson, Willem Frankenhuis, Kotrina Kajokaite, Michelle Kline, Ted Koditschek, Kathryn Lauria, Lee Lyman, Ruth Mace, Sarah Mathew, Richard McElreath and the Max Planck Institute for [Evolutionary Anthropology](#), Alex Mesoudi, Daniel Nettle, Charles Perrault, Sean Prall, Pete Richerson, Paul Smaldino, and Leonid Tiokhin.

REFERENCES.

- Atran, S. *In Gods We Trust: The Evolutionary Landscape of Religion*. Oxford University Press, 2002.
- Barkow, Jerome H., Leda Cosmides, and John Tooby, eds. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford University Press, 1992.
- Barrett, H.C. *The Shape of Thought*. Oxford University Press, 2015.
- Barth, Frederik. *Ethnic Groups and Boundaries: The Social Organization of Culture Difference*. Waveland Press, 1998.
- Bateson, Patrick, and Kevin N. Laland. “Tinbergen’s four questions: an appreciation and an update.” *Trends in Ecology & Evolution* 28 (2013): 712–718.
- Bell, Adrian V., Peter J. Richerson, and Richard McElreath. “Culture rather than genes provides greater scope for the evolution of large-scale human prosociality.” *Proceedings of the National Academy of Sciences* 106 (2009): 17671–17674.
- Berl, Richard EW, and Barry S. Hewlett. “Cultural variation in the use of overimitation by the Aka and Ngandu of the Congo Basin.” *PloS one* 10.3 (2015): e0120180.
- Borgerhoff Mulder, M. “Human behavioural ecology.” *In Behavioural Ecology: An Evolutionary Approach*, edited by J. R. Krebs and N. B. Davies. Blackwell, 1991: 69–98.
- Borgerhoff Mulder, M. “The demographic transition: are we any closer to an evolutionary explanation?” *Trends in Ecology & Evolution* 13 (1998): 266–270.
- Borgerhoff Mulder, Monique, Richard McElreath, and Kari Britt Schroeder. “Analogies are powerful and dangerous things.” *Behavioral and Brain Sciences* 29.4 (2006): 350–351.
- Bowles, Samuel, and Herbert Gintis. *A Cooperative Species*. Princeton University Press, 2011.
- Box, G.E.P. “Science and statistics.” *Journal of the American Statistical Association* 71 (1976): 791–799.

- Boyd, Robert, et al. "The evolution of altruistic punishment." *Proceedings of the National Academy of Sciences* 100 (2003): 3531–3535.
- Boyd, Robert, and Peter J. Richerson. *Culture and the Evolutionary Process*. University of Chicago Press, 1985.
- Boyd, Robert, and Peter J. Richerson. "The evolution of ethnic markers." *Cultural Anthropology* 2 (1987): 65-79.
- Boyd, Robert, and Peter J. Richerson. "Punishment allows the evolution of cooperation (or anything else) in sizable groups." *Ethology and Sociobiology* 13 (1992): 171–195.
- Boyd, Robert, and Peter J. Richerson. "Why does culture increase human adaptability?" *Ethology and Sociobiology* 16 (1995): 125–143.
- Boyd, Robert, and Peter J. Richerson. "Why culture is common, but cultural evolution is rare." *Proceedings-British Academy*. Vol. 88. Oxford University Press, 1996.
- Boyd, Robert, and Peter J. Richerson. "Group beneficial norms can spread rapidly in a structured population." *Journal of Theoretical Biology* 215 (2002): 287–296.
- Boyd, Robert, and Peter J. Richerson. "Voting with your feet: Payoff biased migration and the evolution of group beneficial behavior." *Journal of Theoretical Biology* 257 (2009): 331–339.
- Boyer, Pascal. *The Naturalness of Religious Ideas: A Cognitive Theory of Religion*. University of California Press, 1994.
- Boyette, Adam H. "Children's play and culture learning in an egalitarian foraging society." *Child Development* 87.3 (2016): 759–769.
- Brown, Donald E. *Human Universals*. McGraw-Hill, 1991.
- Buss, David M. *Evolutionary Psychology: The New Science of the Mind*. Psychology Press, 2014.
- Byers, Katherine G., and Dennis A. Savaiano. "The myth of increased lactose intolerance in African-Americans." *Journal of the American College of Nutrition* 24 (2005): 569–573.
- Cavalli-Sforza, Luigi Luca, and Marcus W. Feldman. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press, 1981.
- Chibnik, Michael. *Anthropology, Economics, and Choice*. University of Texas Press, 2011.
- Collard, M., Kemery, M. & Banks, S. "Causes of toolkit variation among hunter-gatherers: a test of four competing hypotheses." *Canadian Journal of Archaeology* 29 (2005): 1–19.
- Colleran, H. "The cultural evolution of fertility decline." *Philosophical Transactions of the Royal Society B* 371 (2016): 1–12.
- Colleran, H., G. Jasienska, I. Nenko, A. Galbarczyk, and R. Mace "Community-level education

- accelerates the cultural evolution of fertility decline.” *Proceedings of the Royal Society of London B: Biological Sciences* 281 (2014): 1–7.
- Cristia, Alejandrina, et al. “Child-directed speech is infrequent in a forager-farmer population: A time allocation study.” *Child Development* 90.3 (2019): 759–773
- Cronk, Lee. “Human behavioral ecology.” *Annual Review of Anthropology* 20 (1991): 25–53.
- Currie, Thomas E. “Cultural Evolution Branches Out: The Phylogenetic Approach in Cross-Cultural Research.” *Cross-Cultural Research* 47 (2013): 102–30.
- Currie, Thomas E., et al. “Rise and fall of political complexity in island South-East Asia and the Pacific.” *Nature* 467 (2010): 801–804.
- Currie, Thomas E., and Ruth Mace. “Mode and Tempo in the Evolution of Socio-Political Organization: Reconciling ‘Darwinian’ and ‘Spencerian’ Evolutionary Approaches in Anthropology.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (2011): 1108–17.
- Cyranoski, David. “CRISPR-baby scientist fails to satisfy critics.” *Nature* 564.7734 (2018): 13–15.
- Dawkins, Richard. *The Selfish Gene*. Oxford University Press, 1976.
- Dean, Lewis G., et al. “Human cumulative culture: a comparative perspective.” *Biological Reviews* 89 (2014): 284–301.
- Derex, Maxime, et al. “Experimental evidence for the influence of group size on cultural complexity.” *Nature* 503 (2013): 389–391.
- Diamond, J. “The Tasmanians—the longest isolation, the simplest technology.” *Nature* 273 (1978) 185–186.
- Durham, William H. *Coevolution: Genes, Culture, and Human Diversity*. Stanford University Press, 1991.
- Epstein, Joshua M. “Why model?” *Journal of Artificial Societies and Social Simulation* 11.4 (2008): 12.
- Evans, Cara L., et al. “The uses and abuses of tree thinking in cultural evolution.” *Philosophical Transactions of the Royal Society B* 376.1828 (2021): 20200056.
- Fehr, Ernst, and Simon Gächter. “Altruistic punishment in humans.” *Nature* 415 (2002): 137–140.
- Foster, Jacob G., and James A. Evans. “Promiscuous inventions.” *Beyond the Meme: Development and Structure in Cultural Evolution* 22 (2019).
- Fracchia, Joseph, and Richard C. Lewontin. “Does culture evolve?” *History and Theory* 38.4 (1999): 52–78.
- Galef, B.G. “Social enhancement of food preferences in Norway rats: a brief review.” In *Social*

- Learning in Animals: The Roots of Culture* (eds C.M. Heyes & B.G. Galef). Academic Press, Inc., 1996. 49–64.
- Garfield, Zachary H., Melissa J. Garfield, and Barry S. Hewlett. “A cross-cultural analysis of hunter-gatherer social learning.” In *Social learning and innovation in contemporary hunter-gatherers*. Springer, Tokyo, 2016. 19–34.
- Gaulin, S.J.C. and D.H. McBurney. *Evolutionary Psychology*. Pearson, 2003.
- Gaus, Gerald. *The Open Society and Its Complexities*. Oxford University Press, 2021.
- Geertz, Clifford. *The Interpretation of Cultures*. Basic Books, 1973.
- Gintis, Herbert. *Game Theory Evolving: A Problem-Centered Introduction to Modeling Strategic Behavior*. Princeton University Press, 2000.
- Gintis, Herbert, Eric Alden Smith, and Samuel Bowles. “Costly signaling and cooperation.” *Journal of Theoretical Biology* 213 (2001): 103–119.
- Grafen, A. “Natural selection, kin selection and group selection.” In *Behavioural Ecology: An Evolutionary Approach* (2nd Edition), edited by J.R. Krebs and N.B. Davies. Sinauer Associates, 1984. 62–84.
- Gray, Russell D., Simon J. Greenhill, and Robert M. Ross. “The pleasures and perils of Darwinizing culture (with phylogenies).” *Biological Theory* 2.4 (2007): 360–375.
- Gupta, Akhil, and James Ferguson. “‘Beyond culture’: Space, identity, and the politics of difference.” *Cultural Anthropology* 7 (1992): 6–23.
- Gürerk, Özgür, Bernd Irlenbusch, and Bettina Rockenbach. “The competitive advantage of sanctioning institutions.” *Science* 312 (2006): 108–111.
- Gurven, Michael. “To give and to give not: the behavioral ecology of human food transfers.” *Behavioral and Brain Sciences* 27 (2004): 543–559.
- Guzmán, Ricardo Andrés, Carlos Rodríguez-Sickert, and Robert Rowthorn. “When in Rome, do as the Romans do: the coevolution of altruistic punishment, conformist learning, and cooperation.” *Evolution and Human Behavior* 28 (2007): 112–117.
- Hamilton, William D. “The Genetical Evolution of Social Behaviour I and II”. *Journal of Theoretical Biology* 7 (1964): 1–52.
- Hamilton, William D. “Innate Social Aptitudes of Man: An Approach From Evolutionary Genetics.” In *Biosocial Anthropology* (Ed. Robin Fox). Malaby Press, 1975. 133–53.
- Handley, Carla, and Sarah Mathew. “Human large-scale cooperation as a product of competition between cultural groups.” *Nature Communications* 11 (2020): 1–9.
- Henrich, J. “Cultural group selection, coevolutionary processes and large-scale cooperation.” *Journal*

of Economic Behavior & Organization 53.1 (2004a): 3–35.

Henrich, J. “Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case.” *American Antiquity* 69 (2004b): 197–214.

Henrich, Joseph. *The Secret of our Success: How Culture is Driving Human Evolution, Domesticating our Species, and Making us Smarter*. Princeton University Press, 2015.

Henrich, Joe, and Robert Boyd. “The evolution of conformist transmission and the emergence of between-group differences.” *Evolution and Human Behavior* 19 (1998): 215–241.

Henrich, Joseph, and Robert Boyd. “Why people punish defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas.” *Journal of Theoretical Biology* 208.1 (2001): 79–89.

Henrich, Joseph, and Francisco J. Gil-White. “The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission.” *Evolution and Human Behavior* 22 (2001): 165–196.

Henrich, Joseph, and Richard McElreath. “The evolution of cultural evolution.” *Evolutionary Anthropology: Issues, News, and Reviews* 12 (2003): 123–135.

Hewlett B.S. and Cavalli Sforza L.L. “Cultural transmission among Aka pygmies.” *American Anthropologist* 88 (1986): 922–934.

Hill, K., M. Barton, and A.M. Hurtado. “The emergence of human uniqueness: Characters underlying behavioral modernity.” *Evolutionary Anthropology: Issues, News, and Reviews* 18 (2009): 187–200.

Hirschman, Albert O. *Exit, Voice, and Loyalty: Responses to Decline in Firms, Organizations, and States*. Harvard University Press, 1970.

Holden, C.J., and R. Mace. “Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis.” *Proceedings of the Royal Society of London B: Biological Sciences* 270 (2003): 2425–2433.

Holden, C., and R. Mace. “Phylogenetic analysis of the evolution of lactose digestion in adults.” *Human Biology* 81 (2009): 597–619.

Huffman, M.A. “Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques.” In *Social Learning in Animals: The Roots of Culture* (eds C.M. Heyes & B.G. Galef). Academic Press, Inc., 1996. 267–289.

Hunt, Gavin R., and Russell D. Gray. “Diversification and cumulative evolution in New Caledonian crow tool manufacture.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270 (2003): 867–874.

Itan, Y., Powell, A., Beaumont, M. A., Burger, J., & Thomas, M. G. “The origins of lactase persistence in Europe.” *PLoS Computational Biology* 5 (2009): e1000491.

- Jablonka, Eva, and Marion J. Lamb. *Evolution in Four Dimensions, Revised Edition: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*. MIT press, 2014.
- Jerison, H.J. “Evolution of the Brain and Intelligence.” *Current Anthropology* 16 (1973): 403–426.
- Kandler, Anne, and Adam Powell. “Generative inference for cultural evolution.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 373.1743 (2018): 20170056.
- Kaplan, H. “A theory of fertility and parental investment in traditional and modern societies”. *Yearbook of Physical Anthropology* 39 (1996): 91–135.
- Kaplan, H., J.B. Lancaster, W.T. Tucker, and K.G. Anderson. “Evolutionary approach to below replacement fertility”. *American Journal of Human Biology* 14 (2002): 233–256.
- Kerr, Benjamin, and Peter Godfrey-Smith. “Individualist and multi-level perspectives on selection in structured populations.” *Biology and Philosophy* 17 (2002): 477–517.
- Kline, Michelle Ann. “How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals.” *Behavioral and Brain sciences* 38 (2015): 1–71.
- Kline, Michelle A., and Robert Boyd. “Population size predicts technological complexity in Oceania.” *Proceedings of the Royal Society B: Biological Sciences* 277 (2010): 2559–2564.
- Koditschek, Theodore. “An evolutionary approach to complex hierarchical societies.” *Behavioural Processes* 161 (2019): 117–128
- Kokko, Hannah. *Modelling for Field Biologists and Other Interesting People*. Cambridge University Press, 2007.
- Laland, Kevin N. *Darwin's Unfinished Symphony: How Culture Made the Human Mind*. Princeton University Press, 2017.
- Laland, Kevin, and Gillian Brown. *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour*. Oxford University Press, 2011.
- Laland et al. “Niche construction, biological evolution, and cultural change. *Behavioral and Brain sciences* 23 (2000): 131–146.
- Laland, Kevin N., John Odling-Smee, and Sean Myles. “How culture shaped the human genome: bringing genetics and the human sciences together.” *Nature Reviews Genetics* 11 (2010): 137–148.
- Laland, Kevin N., et al. “The extended evolutionary synthesis: its structure, assumptions and predictions.” *Proceedings of the Royal Society B: Biological Sciences* 282.1813 (2015): 20151019.
- Legare, Cristine H., and Mark Nielsen. “Imitation and innovation: The dual engines of cultural learning.” *Trends in Cognitive Sciences* 19 (2015): 688–699.
- Lew-Levy, Sheina, et al. “How do hunter-gatherer children learn subsistence skills?.” *Human Nature*

28.4 (2017): 367–394.

Lew-Levy, Sheina, et al. “How do hunter-gatherer children learn social and gender norms? A meta-ethnographic review.” *Cross-Cultural Research* 52.2 (2018): 213–255.

Lewontin, Richard C. “The units of selection.” *Annual Review of Ecology and Systematics* (1970): 1–18.

Lewontin, Richard C. *The Triple Helix: Gene, Organism, and Environment*. Harvard University Press, 2001.

Lukas, Dieter, Mary Towner, and Monique Borgerhoff Mulder. “The potential to infer the historical pattern of cultural macroevolution.” *Philosophical Transactions of the Royal Society B* 376.1828 (2021): 20200057.

Lyons, Derek E., Andrew G. Young, and Frank C. Keil. “The hidden structure of overimitation.” *Proceedings of the National Academy of Sciences* 104.50 (2007): 19751–19756.

Mace, Ruth, and M. Pagel. “The comparative method in anthropology.” *Current Anthropology* 35 (1994): 549–564.

Mathew, Sarah, and Robert Boyd. “Punishment sustains large-scale cooperation in prestate warfare.” *Proceedings of the National Academy of Sciences* 108 (2011): 11375–11380.

Mathew, Sarah, and Robert Boyd. “The cost of cowardice: punitive sentiments towards free riders in Turkana raids.” *Evolution and Human Behavior* 35 (2014): 58–64.

McElreath, Mary Brooke, et al. “Complex dynamics from simple cognition: The primary ratchet effect in animal culture.” *Evolutionary Behavioral Sciences* 12 (2018): 191.

McElreath, Richard. *Statistical rethinking: A Bayesian course with examples in R and Stan*. Chapman and Hall/CRC, 2018.

McElreath, Richard, and Robert Boyd. *Mathematical Models of Social Evolution: A Guide for the Perplexed*. University Of Chicago Press, 2007.

McElreath, R., R. Boyd, and P.J. Richerson. “Shared norms and the evolution of ethnic markers.” *Current Anthropology* 44 (2003): 122–130.

McElreath, Richard, and Paul E. Smaldino. “Replication, communication, and the population dynamics of scientific discovery.” *PLoS One* 10 (2015): e0136088.

Merton, R.K. *On the Shoulders of Giants: A Shandean Postscript*. University of Chicago Press, 1993.

Mesoudi, Alex. *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences*. University of Chicago Press, 2011.

Mesoudi, Alex. “Pursuing Darwin’s curious parallel: Prospects for a science of cultural evolution.” *Proceedings of the National Academy of Sciences* 114 (2017): 7853–7860.

Morgan, L.H. *Ancient society*. H. Holt, 1877.

Muthukrishna, Michael, et al. “Beyond Western, Educated, Industrial, Rich, and Democratic (WEIRD) psychology: Measuring and mapping scales of cultural and psychological distance.” *Psychological Science* 31 (2020): 678–701.

Muthukrishna, M., Doebeli, M., Chudek, M., & Henrich, J. “The Cultural Brain Hypothesis: How culture drives brain expansion, sociality, and life history.” *PLoS Computational Biology*, 14 (2018): e1006504.

Neco, Lucia C., and Peter J. Richerson. “Was human evolution driven by Pleistocene climate change?” *Ciência and Ambiente* (2014): 107–118.

Nielsen, Mark, and Keyan Tomaselli. “Overimitation in Kalahari Bushman children and the origins of human cultural cognition.” *Psychological Science* 21 (2010): 729–736.

Nielsen, M., Mushin, I., Tomaselli, K., & Whiten, A. “Where culture takes hold: ‘Overimitation’ and its flexible deployment in Western, Aboriginal, and Bushmen children.” *Child Development* 85 (2014): 2169–2184.

Nunn, Charles L., Monique Borgerhoff Mulder, and Sasha Langley. “Comparative methods for studying cultural trait evolution: A simulation study.” *Cross-Cultural Research* 40 (2006): 177–209.

Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman. “Niche construction.” *The American Naturalist* 147 (1996): 641–648.

Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman. *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, 2003.

Okasha, Samir. *Evolution and the Levels of Selection*. Oxford University Press, 2009.

Ostrom, Elinor, James Walker, and Roy Gardner. “Covenants with and without a sword: Self-governance is possible.” *American Political Science Review* 86 (1992): 404–417.

Otto, Sarah P., and Troy Day. *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University Press, 2007.

Oyama, Susan, Paul E. Griffiths, and Russell D. Gray, eds. *Cycles of Contingency: Developmental Systems and Evolution*. MIT Press, 2001.

Panchanathan, Karthik. “George Price, the Price equation, and cultural group selection.” *Evolution and Human Behavior* 32 (2011): 368–371.

Panchanathan, Karthik, and Robert Boyd. “Indirect reciprocity can stabilize cooperation without the second-order free rider problem.” *Nature* 432 (2004): 499–502.

Perreault, Charles, Cristina Moya, and Robert Boyd. “A Bayesian Approach to the Evolution of Social Learning.” *Evolution and Human Behavior* 33 (2012): 449–59.

- Perry, Susan, et al. "Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a neotropical primate." *Current Anthropology* 44 (2003): 241–268.
- Peterson, Erik L. *The Life Organic: The Theoretical Biology Club and the Roots of Epigenetics*. University of Pittsburgh Press, 2017.
- Pigliucci & Muller. *Evolution, The Extended Synthesis*. MIT Press, 2010.
- Pinker, S. *The Blank Slate: The Modern Denial of Human Nature*. Penguin Books, 2003.
- Pinker, Steven. *The Language Instinct*. William Morrow & Co., 1994.
- Pinker, Steven, and Paul Bloom. "Natural selection and natural language." *Behavioral and Brain Sciences* 13 (1990): 707–784.
- Powell, Adam, Stephen Shennan, and Mark G. Thomas. "Late Pleistocene demography and the appearance of modern human behavior." *Science* 324 (2009): 1298–1301.
- Price, George R. "Selection and covariance." *Nature* 227 (1970): 520–521.
- Rendell, Luke, and Hal Whitehead. "Culture in whales and dolphins." *Behavioral and Brain Sciences* 24 (2001): 309–324.
- Richerson, Peter J., et al. "Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence." *Behavioral and Brain Sciences* 39 (2016).
- Richerson, Peter J., and Robert Boyd. "Complex societies." *Human Nature* 10 (1999): 253–289.
- Richerson, Peter J., and Robert Boyd. "Climate, culture and the evolution of cognition." *The evolution of cognition* (2000): 329–45.
- Richerson, Peter J., and Robert Boyd. *Not by Genes Alone*. W.W. Norton & Company, 2005.
- Richerson, Peter J., and Robert Boyd. "Why possibly language evolved." *Biolinguistics* 4 (2010): 289–306.
- Richerson, Peter J., and Robert Boyd. "Rethinking paleoanthropology: A world queerer than we supposed." In *Evolution of Mind, Brain, and Culture* (Eds. G. Hatfield & H. Pittman). University of Pennsylvania Museum of Archaeology and Anthropology, 2013. 263–302.
- Richerson, Peter J., and Robert Boyd. "The human life history is adapted to exploit the adaptive advantages of culture." *Philosophical Transactions of the Royal Society B* 375.1803 (2020): 20190498.
- Richerson, Peter J., Robert Boyd, and Robert L. Bettinger. "Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis." *American Antiquity* 66.3 (2001): 387–411.

- Richerson, Peter J., Robert Boyd, and Joseph Henrich. "Gene-culture coevolution in the age of genomics." *Proceedings of the National Academy of Sciences* 107 (2010): 8985–8992.
- Riskin, Jessica. *The Restless Clock: A History of the Centuries-Long Argument over What Makes Living Things Tick*. University of Chicago Press, 2016.
- Rogers, Alan R. "Does biology constrain culture?" *American Anthropologist* 90 (1988): 819–831.
- Rogers, E.M. *The Diffusion of Innovations*. Free Press, 1995.
- Ross, Cody T., et al. "The origins and maintenance of female genital modification across Africa." *Human Nature* 27.2 (2016): 173–200.
- Runciman, W.G. *The Theory of Cultural and Social Selection*. Cambridge University Press, 2009.
- Sahlins, Marshall, and David Graeber. *Stone Age Economics*. Routledge, 2017.
- Salamon, Sonya. *Prairie Patrimony: Family, Farming, and Community in the Midwest*. UNC Press Books, 1995.
- Schniter, Eric. "Older adults' contributions to the Tsimane forager-farmer economy." *Anthropology and Aging* 35 (2014): 56–58
- Seegerstrale, Ullica. *Defenders of the Truth: The Battle for Science in the Sociobiology Debate and Beyond*. Oxford University Press, 2000.
- Ségurel, Laure, and Céline Bon. "On the Evolution of Lactase Persistence in Humans." *Annual Review of Genomics and Human Genetics* 18 (2017): 297–319.
- Service, E.R. *Primitive Social Organization: An Evolutionary Perspective*. 1962.
- Shenk, Mary K., et al. "A model comparison approach shows stronger support for economic models of fertility decline." *Proceedings of the National Academy of Sciences* 110.20 (2013): 8045–8050.
- Simoons, Frederick J. "Primary adult lactose intolerance and the milking habit: a problem in biologic and cultural interrelations." *The American Journal of Digestive Diseases* 15 (1970): 695–710.
- Smaldino, Paul. "The cultural evolution of emergent group-level traits." *Behavioral and Brain Sciences* 37 (2014): 243–295.
- Smaldino, Paul E. "Models are stupid, and we need more of them." *Computational Social Psychology*. Routledge, 2017. 311–331.
- Smaldino, Paul E., and Richard McElreath. "The natural selection of bad science." *Proceedings of the Royal Society Biological Sciences* 3 (2016): 160384.
- Smith, Eric Alden. "Three styles in the evolutionary analysis of human behavior." *Adaptation and Human Behavior: An Anthropological Perspective* (2000): 27–46.

- Smith, Eric A., and Bruce Winterhalder, editors. *Evolutionary Ecology and Human Behavior*. Routledge, 1992a.
- Smith, E.A., and B. Winterhalder. “Natural Selection and Decision-Making: Some Fundamental Principles.” In *Evolutionary Ecology and Human Behavior* (Eds. Eric Alden Smith & Bruce Winterhalder) Routledge, 1992b. 26–60.
- Smith, John Maynard. *Evolution and the Theory of Games*. Cambridge University Press, 1982.
- Soltis, Joseph, Robert Boyd, and Peter J. Richerson. “Can group-functional behaviors evolve by cultural group selection? An empirical test.” *Current Anthropology* 36 (1995): 473–494.
- Sperber, Dan. *Explaining Culture: A Naturalistic Approach*. Blackwell, 1996.
- Sterelny, Kim. *The Pleistocene Social Contract*. Oxford University Press, 2021.
- Surowiec, Alexandra, Kate T. Snyder, and Nicole Creanza. “A worldwide view of matriliney: using cross-cultural analyses to shed light on human kinship systems.” *Philosophical Transactions of the Royal Society B* 374.1780 (2019): 20180077.
- Surowiecki, J. *The Wisdom of Crowds*. Anchor, 2005.
- Tennie, Claudio, Josep Call, and Michael Tomasello. “Push or pull: Imitation vs. emulation in great apes and human children.” *Ethology* 112 (2006): 1159–1169.
- Tennie, Claudio, Josep Call, and Michael Tomasello. “Ratcheting up the ratchet: on the evolution of cumulative culture.” *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364.1528 (2009): 2405–2415.
- Tinbergen, Niko. “On aims and methods of ethology.” *Zeitschrift für tierpsychologie* 20 (1963): 410–433.
- Tomasello, M. “Do apes ape?” In *Social Learning in Animals: The Roots of Culture* (eds C. M. Heyes & B. G. Galef). Academic Press, Inc., 1996. 319–346.
- Tomasello, Michael, Ann Cale Kruger, and Hilary Horn Ratner. “Cultural learning.” *Behavioral and Brain Sciences* 16.3 (1993): 495–511.
- Turchin, P. *Historical Dynamics: Why States Rise and Fall*. Princeton University Press, 2003.
- Turchin, Peter. “Arise ‘cliodynamics’.” *Nature* 454 (2008): 34–35.
- Uyeda, Josef C., Rosana Zenil-Ferguson, and Matthew W. Pennell. “Rethinking phylogenetic comparative methods.” *Systematic Biology* 67 (2018): 1091–1109.
- van Schaik, Carel P., et al. “Orangutan cultures and the evolution of material culture.” *Science* 299 (2003): 102–105.

- Vining, Daniel R. "Social versus reproductive success: The central theoretical problem of human sociobiology." *Behavioral and Brain Sciences* 9.1 (1986): 167–187.
- Waring, Timothy M., et al. "A multilevel evolutionary framework for sustainability analysis." *Ecology and Society* 20.2 (2015).
- Washburn, Sherwood L. "Speculations on the interrelations of the history of tools and biological evolution." *Human Biology* 31 (1959): 21–31.
- Wertz, Annie E., and Karen Wynn. "Selective social learning of plant edibility in 6- and 18-month-old infants." *Psychological Science* 25 (2014): 874–882.
- Whiten, Andrew, et al. "Cultures in chimpanzees." *Nature* 399 (1999): 682–685.
- Whiten, Andrew. "Cultural evolution in animals." *Annual Review of Ecology, Evolution, and Systematics* 50 (2019): 27–48.
- Whiten, Andrew, et al. "Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee." *Philosophical Transactions of the Royal Society B: Biological Sciences* 364.1528 (2009): 2417–2428.
- Wigner, E. "The unreasonable effectiveness of mathematics in the natural sciences." *Communications in Pure and Applied Mathematics* 13 (1960): 1–14.
- Williams, George C. *Adaptation and natural selection. A Critique of Some Current Evolutionary Thought*. Princeton University Press, 1966.
- Wilson, Edward O. "Some Central Problems of Sociobiology." *Social Sciences Information, Biology and Social Life* 14 (1975): 5–18.
- Wilson, Edward O. *On Human Nature*. Harvard University Press, 1978.
- Winterhalder, Bruce, and Eric Alden Smith. "Analyzing adaptive strategies: Human behavioral ecology at twenty-five." *Evolutionary Anthropology: Issues, News, and Reviews* 9 (2000): 51–72.
- Wynne-Edwards, V. *Animal Dispersion in Relation to Social Behaviour*. Hafner Publishing Company, 1962.
- Yamagishi, Toshio. "The provision of a sanctioning system as a public good." *Journal of Personality and Social Psychology* 51 (1986): 110–116.