



Cultural evolutionary theory: How culture evolves and why it matters

Nicole Creanza^{a,1}, Oren Kolodny^{b,1,2}, and Marcus W. Feldman^b

^aDepartment of Biological Sciences, Vanderbilt University, Nashville, TN 37235; and ^bDepartment of Biology, Stanford University, Stanford, CA 94305

Edited by Kevin N. Laland, University of St. Andrews, St. Andrews, United Kingdom, and accepted by Editorial Board Member Andrew G. Clark April 29, 2017 (received for review January 16, 2017)

Human cultural traits—behaviors, ideas, and technologies that can be learned from other individuals—can exhibit complex patterns of transmission and evolution, and researchers have developed theoretical models, both verbal and mathematical, to facilitate our understanding of these patterns. Many of the first quantitative models of cultural evolution were modified from existing concepts in theoretical population genetics because cultural evolution has many parallels with, as well as clear differences from, genetic evolution. Furthermore, cultural and genetic evolution can interact with one another and influence both transmission and selection. This interaction requires theoretical treatments of gene–culture coevolution and dual inheritance, in addition to purely cultural evolution. In addition, cultural evolutionary theory is a natural component of studies in demography, human ecology, and many other disciplines. Here, we review the core concepts in cultural evolutionary theory as they pertain to the extension of biology through culture, focusing on cultural evolutionary applications in population genetics, ecology, and demography. For each of these disciplines, we review the theoretical literature and highlight relevant empirical studies. We also discuss the societal implications of the study of cultural evolution and of the interactions of humans with one another and with their environment.

cultural evolution | mathematical models | gene–culture coevolution | niche construction | demography

Human culture encompasses ideas, behaviors, and artifacts that can be learned and transmitted between individuals and can change over time (1). This process of transmission and change is reminiscent of Darwin’s principle of descent with modification through natural selection, and Darwin himself drew this explicit link in the case of languages: “The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel” (2, 3). Theory underpins most scientific endeavors, and, in the 1970s, researchers began to lay the groundwork for cultural evolutionary theory, building on the neo-Darwinian synthesis of genetics and evolution by using verbal, diagrammatic, and mathematical models (4–8). These models are, by necessity, approximations of reality (9), but because they require researchers to specify their assumptions and extract the most important features from complex processes, they have proven exceedingly useful in advancing the study of cultural evolution (10). Here, we review the field of cultural evolutionary theory as it pertains to the extension of biology through culture. We focus on human culture because the bulk of cultural evolutionary models are human-centric and certain processes such as cumulative culture seem to be unique to humans. However, numerous nonhuman species also exhibit cultural transmission, and we consider the areas of overlap between models of human and animal culture in *Discussion*.

The study of cultural evolution is important beyond its academic value. Cultural evolution is a fundamentally interdisciplinary field, bridging gaps between academic disciplines and facilitating connections between disparate approaches. For example, the advent of technologies for revealing genomic variation has led to a plethora of studies that measure association

between DNA variants and traits that have major cultural components, such as years of schooling, marriage choices, IQ test results, and poverty. Perhaps because of the perceived greater precision of the genomic data, these culturally transmitted components have been relegated to the deep background, creating a misleading public portrayal of the traits as being predetermined by genetics (see, e.g., ref. 11). Models of the dynamics of interaction among culture, demography, and genetics, which uncover the complexities in the determination of these behaviors and traits, are crucial to remedy this potentially dangerous misinterpretation.

Here, we explore the ways in which cultural evolutionary theory and its applications enhance our understanding of human history and human biology, focusing on the links between cultural evolutionary theory and population genetics, human behavioral ecology, and demography. Throughout, we give examples of efforts to apply theory to data, linking models of cultural evolution to empirical studies of genetics, language, archaeology, and anthropology. For example, studies of cultural factors, including language and customs, help biologists interpret patterns of genetic evolution that might be misinterpreted if the cultural context were not taken into account. Finally, we outline several societal implications of cultural evolutionary theory.

Population Genetics and Cultural Evolution

Many of the first models of cultural evolution drew explicit parallels between culture and genes by modifying concepts from theoretical population genetics and applying them to culture. Cultural patterns of transmission, innovation, random fluctuations, and selection are conceptually analogous to genetic processes of transmission, mutation, drift, and selection, and many of the mathematical techniques used to study genetics can be useful in the study of culture (1, 12). However, these mathematical approaches had to be modified to account for the differences between genetic and cultural transmission. For example, we do not expect cultural transmission to follow the rules of genetic transmission strictly. Indeed, cultural traits are likely to deviate from all three laws of Mendelian inheritance: segregation, independent assortment, and dominance (13).

The simple observation that cultural traits need not conform to Mendelian inheritance is sufficient to produce complex evolutionary dynamics: If children are likely to reject a cultural trait that both of their parents possess, the frequency of that trait in the population may oscillate between generations (4). In addition, if two biological parents have different forms of a cultural trait, their child is not necessarily equally likely to acquire the

This paper results from the Arthur M. Sackler Colloquium of the National Academy of Sciences, “The Extension of Biology Through Culture,” held November 16–17, 2016, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. The complete program and video recordings of most presentations are available on the NAS website at www.nasonline.org/Extension_of_Biology_Through_Culture.

Author contributions: N.C., O.K., and M.W.F. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. K.N.L. is a guest editor invited by the Editorial Board.

¹N.C. and O.K. contributed equally to this work.

²To whom correspondence should be addressed. Email: okolodny@stanford.edu.

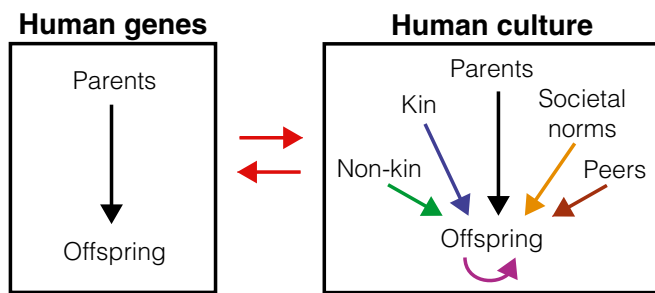


Fig. 1. Cultural transmission is more complex than genetic transmission and may occur on short timescales, even within a single generation.

mother's or father's form of that trait (14). Further, a child can acquire cultural traits not only from its parents (vertical transmission) but also from nonparental adults (oblique) and peers (horizontal) (1, 12); thus, the frequency of a cultural trait in the population is relevant beyond just the probability that an individual's parents had that trait (Fig. 1). In most cases, the more common a cultural trait is in the population, the more likely it is for an individual to have the opportunity to acquire it through social learning (15). However, the size of the population may also influence the continuing transmission, and thus survival, of a cultural trait (16). The relative importance of a population's size, and its environmental context, for the retention and perhaps expansion of the cultural repertoire constitutes an ongoing debate (16–20).

The Roles of Transmission and Innovation in Cultural Evolution. Thus far, we have made the analogy between alleles of a gene and forms of a cultural trait, implying that the cultural trait in question can be represented in a binary or discrete manner. Although this approximation is appropriate for some culturally transmitted traits, such as knowing or not knowing how to use a certain tool, or smoking or not smoking, some cultural traits are more naturally regarded as continuous or quantitative traits. For example, cultural norms and preferences, such as degree of risk tolerance, have been modeled as continuous traits (e.g., ref. 21), and knowledge of a tool or technique has usefully been represented in terms of a quantitative “skill level” (e.g., refs. 16, 22, and 23).

Like genes, cultural traits can be more or less adaptive depending on the environment and spread accordingly. An interesting question is the following: If a certain behavior may be either innate (i.e., genetically determined) or culturally acquired (and thus potentially responsive to the environment), which environmental patterns would favor the genetic transmission? Models predict that spatially varying environments will favor cultural transmission, whereas only highly stable environments would favor the genetic determination of the behavior (24–26). Cavalli-Sforza and Feldman note an important reason that genes, cultural traits, and environments should all be considered together: “Given the existence of individual plasticity in response to the environment, correlations between biological relatives are expected even if there is no genetic variation whatsoever” (14).

Unlike in genetics, where mutations are the source of new traits, cultural innovations can occur via multiple processes and at multiple scales (1, 27–29). Most of the models described above include the cultural transmission of existing traits without providing a mechanism for novel traits to be introduced to the population. In many models of social learning, new information enters a population via trial-and-error learning or individual interactions with the environment, and this information can then be culturally transmitted (30, 31). New cultural traits can also originate when existing traits are combined in novel ways, which can lead to exponential rates of cultural accumulation (32). Recent models represent innovation as the result of multiple interacting processes (27–29), and cultural traits can accumulate in punctuated bursts when these processes of innovation are interdependent: A truly groundbreaking innovation can pave the

way for many related innovations and novel combinations (28). Such dynamics may explain some of the punctuated bursts that are observed in the archaeological record of stone tools, like the dramatic increases in complexity near the transitions from the Middle to the Upper Paleolithic and from the Paleolithic to the Neolithic (33–35), and may provide an account of the dynamics of technological development in historical times (36–39). In many models of cultural evolution, the frequency of one or more cultural traits is tracked over time, and the equilibrium properties are sought. However, recent research highlights the dynamics of cultural accumulation that occur in the transient phase before the system approaches an equilibrium (28). For example, if innovation processes are interdependent, as described above, the cultural repertoire can fluctuate dramatically before approaching an equilibrium because the loss or gain of a groundbreaking innovation can lead to the loss or gain of its related innovations as well (28). In addition, these models demonstrate how innovation processes can change the parameters, and therefore the dynamics, of cultural evolution, possibly altering the cultural equilibrium, if there is one (29). For example, a game-changing innovation, such as the transition from foraging to agriculture, could allow a population to feed many more people; thus, a cultural innovation can alter the size of the population, which is generally set as a fixed parameter in cultural evolutionary models (29). Such nonequilibrium dynamics arise, for example, in a recent comparison between modeling predictions and the archaeological record that showed that the frequencies of Neolithic pottery features over time are not consistent with a cultural system at equilibrium (40).

Linking Genetic and Cultural Evolution. As mentioned above, theoretical treatments of cultural transmission and evolution can usefully draw on concepts from theoretical population genetics, extending them to accommodate cultural processes. However, cultural and genetic evolutionary processes can also interact with one another and with the environment (Fig. 2), and elucidating the relative contributions of genes, culture, and environment to a phenotype can be very difficult (41). Extensive theoretical work has been devoted to characterizing these interactions, termed gene–culture coevolution (1, 42), culture–gene coevolution (43), dual inheritance theory (12, 44), or cultural niche construction (45, 46). When cultural and genetic evolution interact, the dynamics of both genetic and cultural traits are likely to be very different from those characteristic of only one mode of transmission (47, 48). Further, cultural traits can alter the selection pressures on genetic traits and vice versa: For example, genetic traits that are adaptive in one cultural background might not be adaptive in another (49, 50). The classic example of these interactions between cultural and genetic evolution is lactase persistence in adulthood: For much of human history, there was little reason to digest milk after weaning, and adults did not typically produce the enzyme that digests lactose. However, with the cultural

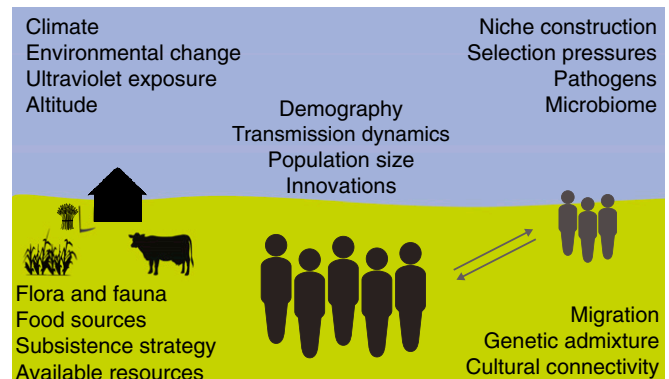


Fig. 2. Cultural, genetic, and environmental factors influencing evolution.

practice of cattle domestication and dairying, a genetic mutation that enabled the production of the lactase enzyme in adulthood was strongly favored by selection (51, 52).

Theoretical analyses show that gene–culture coevolution can be dynamically complex and surprisingly unpredictable. For example, a well-known finding in population genetics is that a fitness advantage to heterozygote genotypes maintains genetic variation in a population. However, it is not sufficient to maintain genetic variation for heterozygote offspring to be superior to homozygotes in their ability to acquire an advantageous cultural trait that is transmitted culturally by a parent (12). In fact, the fitness advantage to the culturally transmitted trait has to be sufficiently large that it overcomes imperfection in vertical cultural transmission. In a similar vein, Aoki et al. (26, 53) modeled the evolution of a genetic trait that increased the efficiency of teaching, defined as vertical transmission of a cultural trait. Genetic variation at this teaching locus could not be maintained with asexual haploid genetics and uniparental cultural transmission, but sexual haploid genetics and biparental cultural transmission could preserve both genetic polymorphism of the teaching locus and polymorphism of the cultural trait. These examples illustrate the theoretical complexity that emerges when standard population genetic theory is extended to include the interactions between genetic and cultural traits; the result is a highly nonlinear theory with complications not seen in purely biological theory.

The theoretical literature on gene–culture interactions has become increasingly relevant in the genomic era. Genome-wide association studies (GWAS) have shown many genomic associations with a wide array of complex phenotypes and have allowed detection of signals of genetic adaptation (54). However, GWA studies of behavioral phenotypes such as IQ, educational attainment, and life history should be interpreted with care (55–58). As the authors of one such study state: “Studies of genetic analyses of behavioural phenotypes have been prone to misinterpretation, such as characterizing identified associated variants as ‘genes for education.’ Such characterization is not correct for many reasons: Educational attainment is primarily determined by environmental factors” (55). Statistical relationships between genetic variants and behaviors need not be causal because assortative mating, spatial autocorrelation, and a shared environment can influence such relationships (55, 59–61). Twin studies of tobacco smoking point to interacting roles of genetics, environment, and assortative mating in the initiation and continuance of smoking (62). In large-scale studies of human health, environmental and cultural factors should also be considered because these could conflate the effects of genetics and ancestry with those of poverty, stress, racism, or socioeconomic status (63–65). For example, data from the large-scale Health and Retirement Study showed an association between African ancestry and hypertension: The prevalence of hypertension was eight percentage points higher in respondents with the highest quartile of African ancestry compared with those with the lowest quartile (63). However, controlling for a subset of factors related to socioeconomic status (childhood disadvantage, education, income, and wealth) explained ~38% of this disparity, reducing it to a five-percentage-point difference (63).

Nonrandom Assortment and Biased Transmission

Many theoretical population genetic studies make the assumption that mating is random within a population. However, in real human populations, this assumption is often violated, as individuals tend to prefer mates with similar phenotypes, such as eye color (66), height, IQ (67), education level (61), and smoking status (68). Cultural evolutionary theory has led to significant advances in our understanding of the effects of nonrandom mating, revealing that the transmission and dynamics of cultural traits can be sensitive to both phenotypic and environmental assorting (41). Assortative mating, leading to an increased correlation between mates for genetic or cultural traits, can increase both genotypic and phenotypic variance in a population (69, 70). In addition, assortative mating (and other forms of homophily) acting

on one cultural trait can influence the evolutionary dynamics of other cultural traits, facilitating the spread of rare cultural or genetic variants (71, 72). More generally, assorting can affect not just mate choice but many types of cultural interactions, termed “assortative meeting” (73). Empirical work supports this theoretical finding; for example, beneficial health behaviors spread more readily through a social network when individuals’ social contacts were more similar to themselves (74, 75). Culturally mediated assortment can also lead to biological differences: Partners that are more similar tend to have more offspring (76), thus increasing fitness, and assortative mating within highly homophilic groups affects the average length of homozygous DNA segments (59, 77), leading to the appearance of higher levels of inbreeding than might actually exist. Humans can also assort by language; however, studies of the interactions between language and genetic population structure show that the resulting dynamics can differ by population. For example, in some geographic regions, language boundaries do not seem to act as barriers to gene flow (78–80) whereas, in other places, assorting with respect to language seems to have had a large effect, and genetic similarity is more closely associated with language than with geographic distance (80–83). Assortative mating has had a measurable effect on human genomic architecture, and genetic and phenotypic correlations between partners are substantial (84).

In addition to choosing their mates nonrandomly, individuals can also choose their cultural role models; these cultural transmission biases affect the relationship between a trait’s frequency in the population and its likelihood of transmission (Fig. 3). For example, conformity bias is an exaggerated preference for the cultural variant practiced by the majority of the population, which can lead to an increasingly large majority over time (85, 86). Alternatively, individuals might preferentially seek out novel cultural traits, termed rarity bias or novelty bias (30). These frequency-dependent biases can lead to patterns of cultural diffusion in which the prevalence of a cultural trait can change dramatically over short timescales, producing logistic growth (“S-shaped” curves) of trait frequency over time (87, 88). Examples of cultural traits that are likely to exhibit frequency-dependent transmission are fashion trends (89), career choices (12), and baby names (90). Conformist transmission is likely to dominate when the environment is relatively stable and common cultural traits are well adapted to that environment (86, 91).

Other types of transmission biases reflect not how common a trait is in a population, but the characteristics of the people who have the trait. In the case of prestige bias, individuals attempt to acquire cultural traits that are perceived to be high quality by selectively learning from those individuals with high social rank (92). For example, in an experimental test, children were much more likely to choose an adult cultural role model if they had observed bystanders attending to the potential model rather than ignoring him or her (93); thus, even at a very early age, humans can assess such characteristics as prestige or social standing. Individuals can also use observations of success associated with a cultural trait, such as a fruitful hunt with a certain tool, to develop a preference for cultural role models that are

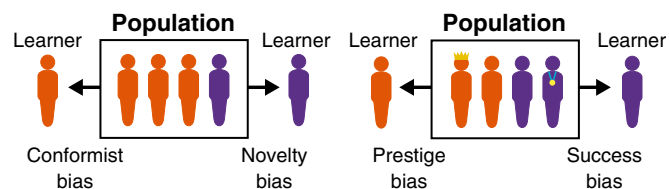


Fig. 3. Biased cultural transmission mechanisms, where orange and purple represent two forms of an arbitrary cultural trait. Conformity bias predicts that learners will copy the most common trait, and novelty bias predicts they will copy the most rare. Prestige bias predicts learners will copy an individual of high social status (indicated by a crown) whereas success bias predicts they will copy a successful individual (indicated by a gold medal).

demonstrably successful (30). This bias has been demonstrated experimentally (94, 95); for example, when individuals participated in simulated hunting with virtual arrowheads and then modified their arrowheads either by trial and error or imitation, copying successful individuals gave significantly better results than trial and error (94).

Models of Culture and Human Ecology

For thousands of generations humans have been carving their existence in the world with cultural tools that have become integral to their livelihoods, thereby shaping their environment at all scales, both intentionally and unintentionally. Attempting to answer the question of what are the extensions of human biology through culture leads to a striking conclusion: There are few aspects of human biology that have not been shaped by our culture. Human culture has also affected the biology, even the survival, of nonhuman species (96). In this section, we review a number of cases for which incorporating culture into models of ecoevolutionary dynamics has proven valuable for the interpretation, prediction, and, in some cases, direction of human ecology and of human impact on the ecosystem.

Human Niche Construction. Niche construction is a process in which organisms modify their environment in a way that alters the selective pressures that these organisms experience, thus affecting evolution (97). A special case of niche construction is cultural niche construction: the alteration of the environment through cultural practices, which may themselves evolve. Cultural niche construction involves complex dynamics in which selective pressures act on the culture itself, interacting with genetic evolution and the environment to influence the spread of both genetic and cultural traits (71). Because cultural change has the potential to occur faster than genetic adaptation, dynamics of niche construction that are driven by cultural traits play a prominent role in human evolution; yet, only in recent decades has cultural evolution begun to be explicitly incorporated into human evolutionary ecology (98). Studies that pioneered this approach showed how it can provide insight into the dynamics of the demographic transition in postindustrialized societies (e.g., refs. 1 and 99). For example, the reduction in birth rate during the demographic transition is often characterized as a paradox because, from a Darwinian fitness perspective, individuals should prefer to have more offspring, not fewer (100). However, if a cultural norm favoring small family size spreads, the fertility rate can drop as well, resulting in a culturally induced demographic transition (99, 101), which is a case where natural selection and cultural transmission seem to be in opposition.

The niche-construction approach has been productive in many other studies, such as those that describe culturally driven change at the ecosystem level: for example, the extinction of megafauna after the arrival of humans (102), the change of broad-scale landscapes as a result of cultivation in early and recent times (103–105), and the traditional use of fire as a means to manipulate the environmental dynamics in a way beneficial for humans (106, 107). Niche construction is also important in understanding the evolutionary dynamics driven by changes in the immediate environment that humans experience, such as via construction of shelters and production of clothing that enabled the expansion of humans into otherwise uninhabitable regions (108), and the use of fire for food handling, which allowed dramatic changes in subsistence and may even have led to significant change to the anatomy of the human jaw (109).

Major Cultural Shifts. A key aspect of human evolution is the change over time in human subsistence strategies. Several models consider the interaction of hunter-gatherers with the populations of organisms that they consume and how these interact over time. They propose that predation pressure can decrease a prey species' population and exert selective pressures in favor of early reproduction at a smaller body size, potentially leaving a telltale pattern in the archaeological record. The result may be the

prey species' extinction, which forces humans to shift their diet in response. Such models as the Diet Breadth Model, the Broad Spectrum Revolution, and Nutritional Ecology (110–113) capture some of these processes, and, although they differ in many important dimensions, such as in the role they assign to plants in the diet, they share the realization that cultural dynamics, genetic evolution, and ecological processes must be considered jointly to understand human evolution. Studies in this tradition have also proposed how gradually changing cultural practices may have created the conditions that culminated in the Neolithic revolution, with the domestication of multiple plant and animal species and the subsequent changes in almost every aspect of human existence (114–116). An interesting niche-construction perspective of these topics is proposed by Smith and Zeder (117).

Models in Human Behavioral Ecology. Human behavioral ecology applies approaches that were developed with a focus on nonhuman species to the interpretation of human behavior (118). One of these approaches is based on optimality in behavior, and studies frequently devise models that capture human behavioral constraints and alternatives, as well as their associated payoffs, which are then considered jointly in predicting behavior or explaining the evolutionary underpinnings of observed behaviors, often under the assumption that humans behave in a way that maximizes their fitness. A broad range of empirical and theoretical studies of culturally determined behaviors bear directly on human fitness, past and present. Human ecological traits, such as life history profiles, subsistence strategies, mating preferences, economic decision making, and social structures (119–122), have been analyzed to predict individual behavior and to support potential intervention that might alter human behaviors at the societal level.

Interestingly, few studies in human ecology consider the dynamics of cultural evolution on which the studied behaviors depend; thus, for example, it is frequently assumed that alternative possible behaviors are available to the human group of interest when they might not be, such as different subsistence strategies. Similarly, with some notable exceptions (e.g., refs. 123–128), human behavioral ecology models often do not consider ecological and evolutionary dynamics that may depend on the studied behavior and that play out on intermediate and long timescales: For example, how would prey populations evolve over long periods of time in response to a certain human foraging strategy, and how would that feed back onto human strategy choice? We suggest that these aspects are promising avenues for further exploration.

Interspecies and Intergroup Dynamics. One of the hotly debated topics in human prehistory is the replacement of Neanderthals by modern humans ~40,000 y ago. A recent study (129) proposed an ecocultural model that incorporated cultural differences between two competing species into Lotka–Volterra competition dynamics and showed that a difference in culture between moderns and Neanderthals could have driven the latter's extinction. This model explicitly includes cultural evolutionary dynamics and shows that a difference in population sizes between moderns in Africa and Neanderthals in Eurasia could have led to a difference in the cultural complexity between the two populations, allowing the small groups of moderns that migrated out of Africa to gradually outcompete the larger population of Neanderthals that they encountered.

This pattern—with one group replacing another as a result of a culturally derived advantage—is likely to have taken place repeatedly throughout human history. Thus, for example, genetic evidence largely supports a scenario in which the Neolithic revolution spread throughout the world not by diffusion of farming practices among groups but by replacement of hunter-gatherer groups by farmers (130) (see also refs. 34, 131, and 132). A second revolution occurred 6,000 to 4,000 y ago, when the early Neolithic farmers were overwhelmed by Yamnaya invaders from the Russian Steppe, who had the cultural advantage of

transportation by horses (133, 134). Such dynamics, in which cultural adaptation to temporally variable conditions may play an important role, are also pervasive more recently: For example, competition between pastoralists and agriculturalists and replacement of one by the other are documented from biblical times to the present (135, 136).

Culture and Microbes. Models are also important in analyzing humans' cultural and genetic coevolution with pathogens, the realm in which many of our species' harshest evolutionary challenges have occurred. Some of the clearest signals of natural selection in the human genome are found near genes that are directly related to coping with diseases such as malaria (137, 138), Kuru (139), and others (140–142), and the understanding of their evolutionary dynamics is greatly enhanced when we are able to couple such genetic evidence with cultural dynamics that influenced them. Durham (143), for example, argues that yam farming practices in West Africa significantly increased standing water, thus increasing breeding sites for malaria-carrying mosquitoes, which led to high exposure to malaria and exerted selective pressure in favor of genetic variants that increase resistance to malaria. In the New Guinea highlands, cannibalism practices that were widespread until the 1940s drove the Kuru epidemic among the people of this region (144). A model of culture–pathogen interactions demonstrated that different behavioral regimes could shape dynamics of pathogenic bacteria, leading to nonintuitive outcomes (145). For example, antibiotic-resistant strains will spread throughout the population in the presence of ubiquitous antibiotic use whereas the WT bacteria have a fitness advantage if antibiotics are not used; however, if people modify their behavior by decreasing use of antibiotics when they become less effective, both WT and resistant pathogens can coexist (145).

A fast-growing body of research focuses on the host-associated microbiome: the communities of organisms, mostly bacteria, that live in and on eukaryotes. The dynamics of the microbiome can interact with those of its host, including genetic variation, cultural practices, and environmental context, further complicating the study of evolutionary processes. Thus, for example, the interaction between dairy farming and selection on the lactase persistence gene has become the poster child of gene–culture coevolution; however, lactose-using bacteria in humans' digestive tracts are very likely to have played a prominent role in the emergence of dairy farming (146). Moreover, these bacteria continue to affect individuals who do not carry a genetic mutation that allows them to efficiently digest dairy in adulthood. Understanding how cultural practices influence human–microbe interactions may provide us not only with insight into the Neolithic farming revolution or early cattle domestication and related human evolution since then, but also with the necessary tools to make informed nutritional choices, such as those related to dairy utilization in our present lives. Thus, worldwide dietary recommendations stand to benefit significantly from an improved understanding of microbe–human interactions (147).

Demography and Cultural Evolution

The growth and age structure of human populations are both affected by norms and beliefs of their members. A predominantly agricultural lifestyle produced higher population growth than the hunting-gathering lifestyle it replaced (148, 149). This increased growth was most likely due to the spread of a complex of cultural traits (150) whose adoption may have created conditions that favored the accumulation of subsequent culturally transmitted behaviors (151, 152). Beginning in the late 19th century, parts of Europe, Asia, the United States, Australia, and New Zealand began to undergo a second demographic transition, which involved a change from a high birth rate, high mortality regime to a lower birth rate, low mortality regime. These changes were due to the spread of fertility-reducing and survival-increasing behaviors that became part of the developed countries' cultures.

Standard quantitative models of demographic change do not include within-population variation in behaviors that affect fecundity or mortality. Projections usually use fixed values for birth and death rates; however, religious preferences, marriage customs, dietary choices, population subdivision, and mortality profiles may affect fecundity but are usually not part of demographic models. Further, aspects of cultural transmission, such as prestige bias and the choice of nonparental cultural role models, can facilitate the spread of fertility-reducing behaviors (12, 153). Thus, cultural evolutionary approaches should be integrated into demography, especially the processes that have led to fertility decline (154).

Many models for life history analysis of humans divide the lifespan into an ordered series of age classes. These models first define the fertility rates of each age class and the survival rates from one age class to the next. Then, they iterate the number in each age class produced by these parameters to determine the dynamics of the population, including whether the number in each age class approaches a stable equilibrium, termed the stationary age distribution, or whether the population will grow or go extinct and at what rate (155).

Carotenuto et al. proposed a demo-cultural framework for such an age-structured population, in which each individual carried one variant of a dichotomous trait, say H or h , where H represents the presence of a socially learned behavior (for example, fertility control) and h is its absence (156). An individual of type H might also be more likely to survive into the next age class. This integration of demography and culture yields complex dynamics; for example, the trait H can persist in the populations even if it lowers fertility, as long as the cultural transmission of H is reliable enough, or if H also sufficiently increases the chance of survival. Additional learning steps can also be added to age-structured models, such that vertical and horizontal transmission can occur at different rates for different age classes (101). In this case, horizontal learning accelerated the trait's spread and led to faster population growth than vertical transmission alone.

An important outgrowth of demo-cultural modeling has been its application to the sex-ratio problem. In many places, the sex ratio at birth is strongly biased in favor of males and, in China and parts of India, has resulted in up to 120 male births for every 100 female births (157). This cultural preference for sons can be manifested in sex-selective abortion or withholding of resources from daughters. This bias has both economic and socio-cultural antecedent, as well as important ethical and demographic consequences (158).

Data on cultural transmission of son preference can be incorporated into formal demographic analysis (159), linking these data to real-world policy applications (160). Theoretical models can also aid in predicting the effects of policies: For example, one such model tracked the cultural transmission of the perceived present value of a son relative to a daughter, the sex ratio at birth, and their effects on demographic change (161). The results of this model suggest that interventions focused on peer-to-peer cultural transmission of a perceived higher value of daughters might complement existing economic incentives to support and educate daughters, with the goal of mitigating the effects of son preference. The literature on the interaction between cultural transmission and formal demography is quite sparse. Given the large variety of customs that relate to birth and death rates in different human societies, population projections for the future needs of diverse populations should incorporate more cultural dynamics than is currently standard practice.

Discussion

With the extensive body of theoretical and empirical literature on cultural evolution, researchers in this field are now combining information from multiple disciplines and integrating disparate approaches. Part of this new frontier involves more fully bridging the divide between theory and data, as well as developing mathematical models than can aid in the interpretation of anthropological and archaeological information. In addition to

aiding our understanding of human history, the study of cultural transmission and evolution is extremely relevant in the modern era. Insights from cultural evolution and the diffusion of innovations have been coopted in advertising and social media to quantify the viral spread of information (e.g., ref. 162). How can these cultural evolutionary insights be better used for positive action and public health? In addition, how can we better use knowledge about cultural evolution to more fully understand patterns of human genetic variation and population structure? As we continue to understand more about the human genome, it becomes increasingly important to consider environmental and cultural contexts as well as genetic variation; however, in the study of gene-culture interactions, faulty logic or racial biases about “causes” of human differences may be used and must be cautiously guarded against (reviewed in ref. 163).

In this paper, we have reviewed aspects of human cultural evolutionary theory, focusing on those that are most closely linked to the extension of biology through culture. With this focus, we could not do adequate justice to many important domains of cultural evolutionary theory. In brief, many models of cultural evolution focus primarily on the transmission of cultural traits and not on their interactions with genes or fitness. These models include, but are not limited to, models of social learning (e.g., refs. 164–167), models of language evolution (e.g., refs. 168–171), empirically driven verbal models of human evolution based on patterns in material culture (e.g., refs. 172–174), and models of cultural dynamics within and between groups (e.g., refs. 86 and 175–178). In addition, we focused on human studies, although cultural processes are present in many other species. For example, social learning has been extensively studied in non-human animals, in which behavioral strategies, such as producer and scrounger, and cultural trajectories can be more clearly defined than in humans (166, 179). Cultural transmission also has large-scale evolutionary implications for some nonhuman animals: For example, theoretical studies suggest that nonrandom

mating in birds based on culturally transmitted songs could accelerate speciation (180, 181) and that sexual selection on learned songs could influence evolution of the neural underpinnings of learning (182). Recently, studies in a range of animal species have shown that cultural practices can emerge, spread, and change over time, potentially influencing individuals’ fitness (183–187). Tool use among chimpanzees and capuchins (188–190) is one such example, which also provides insight regarding the possible origins of the early phases of our own species’ adaptation to the “cultural niche” (191, 192).

In recent years, models that are used for decision making in various fields, such as economics and public health, have begun to take cultural evolution into account, and a growing number also incorporate the modeling—verbal or mathematical—of the human ecosystem’s expected coevolution with the spread of cultural practices. These models play a prominent role in planned strategies related to climate change and reduction of carbon emissions (193), in predicting global food shortages and requirements (194), and in assessing the distribution of new practices and technologies in agriculture (195, 196). In addition, models in epidemiology have begun to integrate cultural transmission of health practices and pathogen ecological dynamics with regard to drug distribution and combating epidemics (e.g., ref. 197).

Deeper analysis of how human culture, human ecology, and the human environment coevolve is necessary for understanding historical and present dynamics, and for predicting future trends. These analyses will provide much-needed tools for the planning and direction of such dynamics. Humans’ worldwide well-being and that of the ecosystem we live in depend on our ability to make such predictions and act accordingly.

ACKNOWLEDGMENTS. We thank the John Templeton Foundation and Stanford Center for Computational, Evolutionary, and Human Genomics for funding.

- Cavalli-Sforza LL, Feldman MW (1981) *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton Univ Press, Princeton).
- Darwin C (1859) *On the Origin of Species by Means of Natural Selection* (Murray, London).
- Darwin C (1888) *The Descent of Man, and Selection in Relation to Sex* (Murray, London).
- Feldman MW, Cavalli-Sforza LL (1976) Cultural and biological evolutionary processes, selection for a trait under complex transmission. *Theor Popul Biol* 9:238–259.
- Feldman MW, Cavalli-Sforza LL (1975) Models for cultural inheritance: A general linear model. *Ann Hum Biol* 2:215–226.
- Blum HF (1978) Uncertainty in interplay of biological and cultural evolution: Man’s view of himself. *Q Rev Biol* 53:29–40.
- Cavalli-Sforza L, Feldman MW (1973) Models for cultural inheritance. I. Group mean and within group variation. *Theor Popul Biol* 4:42–55.
- Alland A, Jr (1972) Cultural evolution: The Darwinian model. *Soc Biol* 19:227–239.
- Burnham KP, Anderson DR (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach* (Springer, New York).
- Haldane JBS (1964) A defense of beanbag genetics. *Perspect Biol Med* 7:343–359.
- Guedes JD, et al. (2013) Is poverty in our genes? *Curr Anthropol* 54:71–79.
- Boyd R, Richerson PJ (1985) *Culture and the Evolutionary Process* (Chicago Univ Press, Chicago).
- Mesoudi A (2017) Pursuing Darwin’s curious parallel: Prospects for a science of cultural evolution. *Proc Natl Acad Sci USA* 114:7853–7860.
- Cavalli-Sforza LL, Feldman MW (1973) Cultural versus biological inheritance: Phenotypic transmission from parents to children. (A theory of the effect of parental phenotypes on children’s phenotypes). *Am J Hum Genet* 25:618–637.
- Giraldeau L-A (1994) Social foraging: Individual learning and cultural transmission of innovations. *Behav Ecol* 5:35–43.
- Henrich J (2004) Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses—The Tasmanian case. *Am Antiq* 69:197–214.
- Henrich J, et al. (2016) Understanding cumulative cultural evolution. *Proc Natl Acad Sci USA* 113:E6724–E6725.
- Vaesen K, Collard M, Cosgrove R, Roebroeks W (2016) Population size does not explain past changes in cultural complexity. *Proc Natl Acad Sci USA* 113:E2241–E2247.
- Collard M, Ruttle A, Buchanan B, O’Brien MJ (2013) Population size and cultural evolution in nonindustrial food-producing societies. *PLoS One* 8:e72628.
- Collard M, Buchanan B, Morin J, Costopoulos A (2011) What drives the evolution of hunter-gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. *Philos Trans R Soc Lond B Biol Sci* 366:1129–1138.
- Bisin A, Verdier T (2010) The economics of cultural transmission and the dynamics of preferences. *Handb Soc Econ* 319:339–416.
- Kobayashi Y, Aoki K (2012) Innovativeness, population size and cumulative cultural evolution. *Theor Popul Biol* 82:38–47.
- Baldini R (2015) Revisiting the effect of population size on cumulative cultural evolution. *J Cogn Cult* 15:320–336.
- Boyd R, Richerson PJ (1983) The cultural transmission of acquired variation: Effects on genetic fitness. *J Theor Biol* 100:567–596.
- Aoki K, Feldman MW (2014) Evolution of learning strategies in temporally and spatially variable environments: A review of theory. *Theor Popul Biol* 91:3–19.
- Aoki K, Wakano J, Feldman M (2005) The emergence of social learning in a temporally changing environment: A theoretical model. *Curr Anthropol* 46:334–340.
- Fogarty L, Creanza N, Feldman MW (2015) Cultural evolutionary perspectives on creativity and human innovation. *Trends Ecol Evol* 30:736–754.
- Kolodny O, Creanza N, Feldman MW (2015) Evolution in leaps: The punctuated accumulation and loss of cultural innovations. *Proc Natl Acad Sci USA* 112:E6762–E6769.
- Kolodny O, Creanza N, Feldman MW (2016) Game-changing innovations: How culture can change the parameters of its own evolution and induce abrupt cultural shifts. *PLOS Comput Biol* 12:e1005302.
- Henrich J, McElreath R (2003) The evolution of cultural evolution. *Evol Anthropol* 12: 123–135.
- Rendell L, et al. (2010) Why copy others? Insights from the social learning strategies tournament. *Science* 328:208–213.
- Enquist M, Ghirlanda S, Jarrick A, Wachtmeister C-A (2008) Why does human culture increase exponentially? *Theor Popul Biol* 74:46–55.
- Klein RG, Edgar B (2002) *The Dawn of Human Culture* (Wiley, New York).
- Bar-Yosef O (1998) On the nature of transitions: The Middle to Upper Palaeolithic and the Neolithic revolution. *Camb Archaeol J* 8:141–163.
- Roebroeks W (2008) Time for the Middle to Upper Paleolithic transition in Europe. *J Hum Evol* 55:918–926.
- Darmstaedter L, Du Bois-Reymond R (1904) *4000 Jahre Pionier-Arbeit in den Exakten Wissenschaften* (JA Stargardt, Berlin).
- Aiyar S, Dalgaard C-J, Moav O (2008) Technological progress and regress in pre-industrial times. *J Econ Growth* 13:125–144.
- Kuhn SL (2012) *Emergent Patterns of Creativity and Innovation in Early Technologies: Origins of Human Innovation and Creativity* (Elsevier, Oxford), pp 69–88.
- Lehman HC (1947) The exponential increase of man’s cultural output. *Soc Forces* 25: 281–290.
- Crema ER, Kandler A, Shennan S (2016) Revealing patterns of cultural transmission from frequency data: Equilibrium and non-equilibrium assumptions. *Sci Rep* 6:39122.
- Feldman MW, Cavalli-Sforza LL (1979) Aspects of variance and covariance analysis with cultural inheritance. *Theor Popul Biol* 15:276–307.

42. Feldman MW, Laland KN (1996) Gene-culture coevolutionary theory. *Trends Ecol Evol* 11:453–457.
43. Chudek M, Henrich J (2011) Culture-gene coevolution, norm-psychology and the emergence of human prosociality. *Trends Cogn Sci* 15:218–226.
44. Richerson PJ, Boyd R (1978) A dual inheritance model of the human evolutionary process. I. Basic postulates and a simple model. *J Soc Biol Struct* 1:127–154.
45. Laland KN, Odling-Smee J, Feldman MW (2000) Niche construction, biological evolution, and cultural change. *Behav Brain Sci* 23:131–146. discussion 146–175.
46. Odling-Smee J, Laland KN, Feldman MW (2003) *Niche Construction: The Neglected Process in Evolution* (Princeton Univ Press, Princeton).
47. Laland KN, Kumm J, Van Horn JD, Feldman MW (1995) A gene-culture model of human handedness. *Behav Genet* 25:433–445.
48. Mesoudi A, Whiten A, Laland KN (2006) Towards a unified science of cultural evolution. *Behav Brain Sci* 29:329–347, discussion 347–383.
49. Rendell L, Fogarty L, Laland KN (2011) Runaway cultural niche construction. *Philos Trans R Soc Lond B Biol Sci* 366:823–835.
50. Laland KN, O'Brien MJ (2012) Cultural niche construction: An introduction. *Biol Theory* 6:191–202.
51. Feldman MW, Cavalli-Sforza LL (1989) On the theory of evolution under genetic and cultural transmission with application to the lactose absorption. *Mathematical Evolutionary Theory*, ed Feldman MW (Princeton Univ Press, Princeton), pp 145–173.
52. Ingram CJ, Liebert A, Swallow DM (2012) Population genetics of lactase persistence and lactose intolerance. *eLS*, 10.1002/9780470015902.a0020855.pub2.
53. Aoki K, Wakano J, Feldman M (2016) Gene-culture models for the evolution of altruistic teaching. *On Human Nature: Biology, Psychology, Ethics, Policy, and Religion*, eds Tibayrenc M, Ayala F (Academic, Amsterdam), pp 279–296.
54. Berg JJ, Coop G (2014) A population genetic signal of polygenic adaptation. *PLoS Genet* 10:e1004412.
55. Okbay A, et al.; Lifelines Cohort Study (2016) Genome-wide association study identifies 74 loci associated with educational attainment. *Nature* 533:539–542.
56. Benyamin B, et al.; Wellcome Trust Case Control Consortium 2 (WTCCC2) (2014) Childhood intelligence is heritable, highly polygenic and associated with FNBP1L. *Mol Psychiatry* 19:253–258.
57. Davies G, et al. (2011) Genome-wide association studies establish that human intelligence is highly heritable and polygenic. *Mol Psychiatry* 16:996–1005.
58. Minkov M, Bond MH (2015) Genetic polymorphisms predict national differences in life history strategy and time orientation. *Pers Individ Dif* 76:204–215.
59. Abdellaoui A, et al. (2015) Educational attainment influences levels of homozygosity through migration and assortative mating. *PLoS One* 10:e0118935.
60. Piffer D (2015) A review of intelligence GWAS hits: Their relationship to country IQ and the issue of spatial autocorrelation. *Intelligence* 53:43–50.
61. Domingue BW, Fletcher J, Conley D, Boardman JD (2014) Genetic and educational assortative mating among US adults. *Proc Natl Acad Sci USA* 111:7996–8000.
62. Maes HH, et al. (2006) Genetic and cultural transmission of smoking initiation: An extended twin kinship model. *Behav Genet* 36:795–808.
63. Marden JR, Walter S, Kaufman JS, Glymour MM (2016) African ancestry, social factors, and hypertension among non-Hispanic Blacks in the Health and Retirement Study. *Biodemogr Soc Biol* 62:19–35.
64. Paradies Y, et al. (2015) Racism as a determinant of health: A systematic review and meta-analysis. *PLoS One* 10:e0138511.
65. Nugent NR, Tyrka AR, Carpenter LL, Price LH (2011) Gene-environment interactions: Early life stress and risk for depressive and anxiety disorders. *Psychopharmacology (Berl)* 214:175–196.
66. Laeng B, Mathisen R, Johnsen JA (2007) Why do blue-eyed men prefer women with the same eye color? *Behav Ecol Sociobiol* 61:371–384.
67. Keller MC, et al. (2013) The genetic correlation between height and IQ: Shared genes or assortative mating? *PLoS Genet* 9:e1003451.
68. Treur JL, Vink JM, Boomsma DI, Middeldorp CM (2015) Spousal resemblance for smoking: Underlying mechanisms and effects of cohort and age. *Drug Alcohol Depend* 153:221–228.
69. Feldman MW, Cavalli-Sforza LL (1977) The evolution of continuous variation. II. Complex transmission and assortative mating. *Theor Popul Biol* 11:161–181.
70. Rice J, Cloninger CR, Reich T (1978) Multifactorial inheritance with cultural transmission and assortative mating. I. Description and basic properties of the unitary models. *Am J Hum Genet* 30:618–643.
71. Creanza N, Fogarty L, Feldman MW (2012) Models of cultural niche construction with selection and assortative mating. *PLoS One* 7:e42744.
72. Creanza N, Feldman MW (2014) Complexity in models of cultural niche construction with selection and homophily. *Proc Natl Acad Sci USA* 111(Suppl 3):10830–10837.
73. Eshel I, Cavalli-Sforza LL (1982) Assortment of encounters and evolution of cooperativeness. *Proc Natl Acad Sci USA* 79:1331–1335.
74. Centola D (2010) The spread of behavior in an online social network experiment. *Science* 329:1194–1197.
75. Centola D (2011) An experimental study of homophily in the adoption of health behavior. *Science* 334:1269–1272.
76. Thiessen D, Gregg B (1980) Human assortative mating and genetic equilibrium: An evolutionary perspective. *Ethol Sociobiol* 1:111–140.
77. Abdellaoui A, et al. (2013) Association between autozygosity and major depression: Stratification due to religious assortment. *Behav Genet* 43:455–467.
78. Hunley K, et al. (2008) Genetic and linguistic coevolution in Northern Island Melanesia. *PLoS Genet* 4:e1000239.
79. Hunley K, Long JC (2005) Gene flow across linguistic boundaries in Native North American populations. *Proc Natl Acad Sci USA* 102:1312–1317.
80. Srithawong S, et al. (2015) Genetic and linguistic correlation of the Kra–Dai-speaking groups in Thailand. *J Hum Genet* 60:1–10.
81. Barbujani G, Sokal RR (1990) Zones of sharp genetic change in Europe are also linguistic boundaries. *Proc Natl Acad Sci USA* 87:1816–1819.
82. Karafet TM, et al. (2016) Coevolution of genes and languages and high levels of population structure among the highland populations of Daghestan. *J Hum Genet* 61:181–191.
83. de Filippo C, et al. (2011) Y-chromosomal variation in sub-Saharan Africa: Insights into the history of Niger-Congo groups. *Mol Biol Evol* 28:1255–1269.
84. Robinson MR, et al. (2017) Genetic evidence of assortative mating in humans. *Nat Hum Behav* 1:0016.
85. Efferson C, Lalive R, Richerson PJ, McElreath R, Lubell M (2008) Conformists and mavericks: The empirics of frequency-dependent cultural transmission. *Evol Hum Behav* 29:56–64.
86. Henrich J, Boyd R (1998) The evolution of conformist transmission and the emergence of between-group differences. *Evol Hum Behav* 19:215–241.
87. Rogers EM (2010) *Diffusion of Innovations* (Simon and Schuster, New York).
88. Henrich J (2001) Cultural transmission and the diffusion of innovations: Adoption dynamics indicate that biased cultural transmission is the predominate force in behavioural change. *Am Anthropol* 103:992–1013.
89. Acerbi A, Ghirlanda S, Enquist M (2012) The logic of fashion cycles. *PLoS One* 7:e32541.
90. Acerbi A, Alexander Bentley R (2014) Biases in cultural transmission shape the turnover of popular traits. *Evol Hum Behav* 35:228–236.
91. Kendal J, Giraldeau LA, Laland K (2009) The evolution of social learning rules: Payoff-biased and frequency-dependent biased transmission. *J Theor Biol* 260:210–219.
92. Henrich J, Gil-White FJ (2001) The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol Hum Behav* 22:165–196.
93. Chudek M, Heller S, Birch S, Henrich J (2012) Prestige-biased cultural learning: By-stander's differential attention to potential models influences children's learning. *Evol Hum Behav* 33:46–56.
94. Mesoudi A, O'Brien MJ (2008) The cultural transmission of Great Basin projectile-point technology II: An agent-based computer simulation. *Am Antiq* 73:627–644.
95. Mesoudi A (2011) An experimental comparison of human social learning strategies: Payoff-biased social learning is adaptive but underused. *Evol Hum Behav* 32:334–342.
96. Alberti M, et al. (2017) Global urban signatures of phenotypic change in animal and plant populations. *Proc Natl Acad Sci USA*, 10.1073/pnas.1606034114.
97. Laland KN, Brown GR (2006) Niche construction, human behavior, and the adaptive-lag hypothesis. *Evol Anthropol* 15:95–104.
98. Laland KN, Odling-Smee J, Feldman MW (2001) Cultural niche construction and human evolution. *J Evol Biol* 14:22–33.
99. Ihara Y, Feldman MW (2004) Cultural niche construction and the evolution of small family size. *Theor Popul Biol* 65:105–111.
100. Borgerhoff Mulder M (1998) The demographic transition: Are we any closer to an evolutionary explanation? *Trends Ecol Evol* 13:266–270.
101. Fogarty L, Creanza N, Feldman MW (2013) The role of cultural transmission in human demographic change: An age-structured model. *Theor Popul Biol* 88:68–77.
102. Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306:70–75.
103. Lansing JS, Cox MP, Downey SS, Janssen MA, Schoenfelder JW (2009) A robust budding model of Balinese water temple networks. *World Archaeol* 41:112–133.
104. Erickson CL (1992) Prehistoric landscape management in the Andean highlands: Raised field agriculture and its environmental impact. *Popul Environ* 13:285–300.
105. Delcourt P, Delcourt HR (2004) *Prehistoric Native Americans and Ecological Change: Human Ecosystems in Eastern North America Since the Pleistocene* (Cambridge Univ Press, Cambridge, UK).
106. Boyd R (1999) *Indians, Fire, and the Land in the Pacific Northwest* (Oregon State Univ Press, Corvallis, OR).
107. Bliege Bird R, Bird DW, Codding BF, Parker CH, Jones JH (2008) The “fire stick farming” hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proc Natl Acad Sci USA* 105:14796–14801.
108. Roebroeks W, et al. (1992) Dense forests, cold steppes, and the palaeolithic settlement of Northern Europe. *Curr Anthropol* 33:551–586.
109. Wrangham RW (2009) *Catching Fire: How Cooking Made Us Human* (Basic Books, New York).
110. Stiner MC (2001) Thirty years on the “broad spectrum revolution” and paleolithic demography. *Proc Natl Acad Sci USA* 98:6993–6996.
111. Davis S, Rabinovich R, Goren-Inbar N (1988) Quaternary extinctions and population increase in western Asia: The animal remains from Biq'at Quneitra. *Paéorient* 14: 95–105.
112. Hockett B, Haws JA (2005) Nutritional ecology and the human demography of Neanderthal extinction. *Quat Int* 137:21–34.
113. Hardy BL (2010) Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. *Quat Sci Rev* 29:662–679.
114. Flannery KV (1969) Origins and ecological effects of early domestication in Iran and the Near East. *The Domestication and Exploitation of Plants and Animals*, eds Ucko PJ, Dimbleby GW (Gerald Duckworth, London), pp 73–100.
115. Valla FR, Bar-Yosef O, eds (1991) *The Natufian Culture in the Levant* (International Monographs in Prehistory, Ann Arbor, MI).
116. Rowley-Conwy P, Layton R (2011) Foraging and farming as niche construction: Stable and unstable adaptations. *Philos Trans R Soc Lond B Biol Sci* 366:849–862.
117. Smith BD, Zeder MA (2013) The onset of the Anthropocene. *Anthropocene* 4:8–13.
118. Winterhalder B, Smith EA (2000) Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evol Anthropol Issues News Rev* 9:51–72.

119. Henrich J, et al. (2001) In search of homo economicus: Behavioral experiments in 15 small-scale societies. *Am Econ Rev* 91:73–78.
120. Kaplan H, Hill K, Lancaster J, Hurtado AM (2000) A theory of human life history evolution: Diet, intelligence, and longevity. *Evol Anthropol Issues News Rev* 9: 156–185.
121. Winterhalder B, Lu F, Tucker B (1999) Risk-sensitive adaptive tactics: Models and evidence from subsistence studies in biology and anthropology. *J Archaeol Res* 7: 301–348.
122. Voland E (1998) Evolutionary ecology of human reproduction. *Annu Rev Anthropol* 27:347–374.
123. Belovsky GE (1988) An optimal foraging-based model of hunter-gatherer population dynamics. *J Anthropol Archaeol* 7:329–372.
124. Winterhalder B, Baillargeon W, Cappelletto F, Daniel IR, Prescott C (1988) The population ecology of hunter-gatherers and their prey. *J Anthropol Archaeol* 7: 289–328.
125. Broughton JM (1997) Widening diet breadth, declining foraging efficiency, and prehistoric harvest pressure: Ichthyofaunal evidence from the Emeryville Shell-mound, California. *Antiquity* 71:845–862.
126. Low BS, Heinen JT (1993) Population, resources, and environment: Implications of human behavioral ecology for conservation. *Popul Environ* 15:7–41.
127. Stiner MC, Munro ND, Surovell TA, Tchernov E, Bar-Yosef O (1999) Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283:190–194.
128. Stiner MC, Munro ND, Surovell TA (2000) The tortoise and the hare. *Curr Anthropol* 41:39–79.
129. Gilpin W, Feldman MW, Aoki K (2016) An ecocultural model predicts Neanderthal extinction through competition with modern humans. *Proc Natl Acad Sci USA* 113: 2134–2139.
130. Skoglund P, et al. (2012) Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. *Science* 336:466–469.
131. Aoki K, Shida M, Shigesada N (1996) Travelling wave solutions for the spread of farmers into a region occupied by hunter-gatherers. *Theor Popul Biol* 50:1–17.
132. Patterson MA, Sarson GR, Sarson HC, Shukurov A (2010) Modelling the Neolithic transition in a heterogeneous environment. *J Archaeol Sci* 37:2929–2937.
133. Allentoft ME, et al. (2015) Population genomics of bronze age Eurasia. *Nature* 522: 167–172.
134. Goldberg A, Günther T, Rosenberg NA, Jakobsson M (2017) Ancient X chromosomes reveal contrasting sex bias in Neolithic and Bronze Age Eurasian migrations. *Proc Natl Acad Sci USA* 114:2657–2662.
135. Wossink A (2009) *Challenging Climate Change: Competition and Cooperation Among Pastoralists and Agriculturalists in Northern Mesopotamia (c. 3000-1600 BC)* (Sidestone, Leiden, The Netherlands).
136. Spielmann KA, Eder JF (1994) Hunters and farmers: Then and now. *Annu Rev Anthropol* 23:303–323.
137. Kwiatkowski DP (2005) How malaria has affected the human genome and what human genetics can teach us about malaria. *Am J Hum Genet* 77:171–192.
138. Tishkoff SA, et al. (2001) Haplotype diversity and linkage disequilibrium at human G6PD: Recent origin of alleles that confer malarial resistance. *Science* 293:455–462.
139. Mead S, et al. (2003) Balancing selection at the prion protein gene consistent with prehistoric kurulike epidemics. *Science* 300:640–643.
140. Bustamante CD, et al. (2005) Natural selection on protein-coding genes in the human genome. *Nature* 437:1153–1157.
141. Sabeti PC, et al.; International HapMap Consortium (2007) Genome-wide detection and characterization of positive selection in human populations. *Nature* 449: 913–918.
142. Enard D, Cai L, Gwennap C, Petrov DA (2016) Viruses are a dominant driver of protein adaptation in mammals. *eLife* 5:e21469.
143. Durham WH (1991) *Coevolution: Genes, Culture, and Human Diversity* (Stanford Univ Press, Stanford, CA).
144. Lindenbaum S (2015) *Kuru Sorcery: Disease and Danger in the New Guinea Highlands* (Routledge, Abingdon, UK).
145. Boni MF, Feldman MW (2005) Evolution of antibiotic resistance by human and bacterial niche construction. *Evolution* 59:477–491.
146. Walter J, Ley R (2011) The human gut microbiome: Ecology and recent evolutionary changes. *Annu Rev Microbiol* 65:411–429.
147. Szilagy A, Galitsatos P, Xue X (2016) Systematic review and meta-analysis of lactose digestion, its impact on intolerance and nutritional effects of dairy food restriction in inflammatory bowel diseases. *Nutr J* 15:67.
148. Bocquet-Appel J (2002) Paleoanthropological traces of a Neolithic demographic transition. *Curr Anthropol* 43:637–650.
149. Gage TBB, DeWitte S (2009) What do we know about the agricultural demographic transition? *Curr Anthropol* 50:649–655.
150. Ammerman AJ, Cavalli-Sforza LL (1984) *The Neolithic Transition and the Genetics of Populations in Europe* (Princeton Univ Press, Princeton).
151. Henn BM, Cavalli-Sforza LL, Feldman MW (2012) The great human expansion. *Proc Natl Acad Sci USA* 109:17758–17764.
152. Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324:1298–1301.
153. Richerson PJ, Boyd R (1984) Natural selection and culture. *Bioscience* 34:430–434.
154. Collier H (2016) The cultural evolution of fertility decline. *Philos Trans R Soc Lond B Biol Sci* 371:20150152.
155. Leslie PH (1948) Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213–245.
156. Carotenuto L, Feldman MW, Cavalli-Sforza L (1989) Age structure in models of cultural transmission. Working paper (Morrison Institute for Population and Resource Studies, Stanford, CA), No 16.
157. Banister J (2004) Shortage of girls in China today. *J Popul Res* 21:19–45.
158. Tuljapurkar S, Li N, Feldman MW (1995) High sex ratios in China's future. *Science* 267:874–876.
159. Li N, Feldman MW, Li S (2000) Cultural transmission in a demographic study of sex ratio at birth in China's future. *Theor Popul Biol* 58:161–172.
160. Bhattacharjya D, Sudarshan A, Tuljapurkar S, Shachter R, Feldman M (2008) How can economic schemes curtail the increasing sex ratio at birth in China? *Demogr Res* 19: 1831–1850.
161. Fogarty L, Feldman MW (2011) The cultural and demographic evolution of son preference and marriage type in contemporary China. *Biol Theory* 6:272–282.
162. Barkow JH, O'Gorman R, Rendell L (2012) Are the new mass media subverting cultural transmission? *Rev Gen Psychol* 16:121–133.
163. Creanza N, Feldman MW (2016) Worldwide genetic and cultural change in human evolution. *Curr Opin Genet Dev* 41:85–92.
164. Enquist M, Ghirlanda S (2007) Evolution of social learning does not explain the origin of human cumulative culture. *J Theor Biol* 246:129–135.
165. Rendell L, Fogarty L, Laland KN (2010) Rogers' paradox recast and resolved: Population structure and the evolution of social learning strategies. *Evolution* 64: 534–548.
166. Arbilly M, Weissman DB, Feldman MW, Grodzinski U (2014) An arms race between producers and scroungers can drive the evolution of social cognition. *Behav Ecol* 25: 487–495.
167. Rendell L, et al. (2011) Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends Cogn Sci* 15:68–76.
168. Hruschka DJ, et al. (2009) Building social cognitive models of language change. *Trends Cogn Sci* 13:464–469.
169. Nowak MA, Krakauer DC (1999) The evolution of language. *Proc Natl Acad Sci USA* 96:8028–8033.
170. Gray RD, Greenhill SJ, Ross R (2007) The pleasures and perils of Darwinizing culture (with phylogenies). *Biol Theory* 2:1–26.
171. Kolodny O, Lotem A, Edelman S (2015) Learning a generative probabilistic grammar of experience: A process-level model of language acquisition. *Cogn Sci* 39:227–267.
172. Hovers E (2012) Invention, reinvention and innovation: The makings of Oldowan lithic technology. *Origins of Human Innovation and Creativity*, ed Elias S (Elsevier, Oxford).
173. Bar-Yosef O (2002) The Upper Paleolithic revolution. *Annu Rev Anthropol* 31:363–393.
174. Klein RG (2008) Out of Africa and the evolution of human behavior. *Evol Anthropol* 17:267–281.
175. Boyd R, Richerson PJ (2009) Voting with your feet: Payoff biased migration and the evolution of group beneficial behavior. *J Theor Biol* 257:331–339.
176. Wiens JJ, Hollingsworth BD (2000) War of the Iguanas: Conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. *Syst Biol* 49:143–159.
177. Borgerhoff Mulder M, et al. (2009) Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* 326:682–688.
178. Fogarty L, Strimling P, Laland KN (2011) The evolution of teaching. *Evolution* 65: 2760–2770.
179. Feher O, Wang H, Saar S, Mitra PP, Tchernichovski O (2009) De novo establishment of wild-type song culture in the zebra finch. *Nature* 459:564–568.
180. Verzijden MN, et al. (2012) The impact of learning on sexual selection and speciation. *Trends Ecol Evol* 27:511–519.
181. Lachlan RF, Servedio MR (2004) Song learning accelerates allopatric speciation. *Evolution* 58:2049–2063.
182. Creanza N, Fogarty L, Feldman MW (2016) Cultural niche construction of repertoire size and learning strategies in songbirds. *Evol Ecol* 30:285–305.
183. Aplin LM, et al. (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518:538–541.
184. Rendell L, Whitehead H (2001) Culture in whales and dolphins. *Behav Brain Sci* 24: 309–324, discussion 324–382.
185. Whiten A, et al. (1999) Cultures in chimpanzees. *Nature* 399:682–685.
186. Whitehead H (2017) Gene-culture coevolution in whales and dolphins. *Proc Natl Acad Sci USA* 114:7814–7821.
187. Perry SE, Barrett BJ, Godoy I (2017) Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proc Natl Acad Sci USA* 114:7806–7813.
188. Fragasz D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG (2004) Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am J Primatol* 64:359–366.
189. Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:737–740.
190. Ottoni EB, Izar P (2008) Capuchin monkey tool use: Overview and implications. *Evol Anthropol* 17:171–178.
191. Whiten A (2011) The scope of culture in chimpanzees, humans and ancestral apes. *Philos Trans R Soc Lond B Biol Sci* 366:997–1007.
192. Whiten A (2017) Culture extends the scope of evolutionary biology in the great apes. *Proc Natl Acad Sci USA* 114:7790–7797.
193. Seneviratne SI, Donat MG, Pitman AJ, Knutti R, Wilby RL (2016) Allowable CO₂ emissions based on regional and impact-related climate targets. *Nature* 529:477–483.
194. Fischer RA, Byerlee D, Edmeades G (2014) *Crop Yields and Global Food Security* (ACIAR, Canberra, Australia).
195. Garibaldi LA, et al. (2017) Farming approaches for greater biodiversity, livelihoods, and food security. *Trends Ecol Evol* 32:68–80.
196. Kassam A, Friedrich T, Shaxson F, Pretty J (2009) The spread of conservation agriculture: Justification, sustainability and uptake. *Int J Agric Sustain* 7:292–320.
197. Rhines AS (2013) The role of sex differences in the prevalence and transmission of tuberculosis. *Tuberculosis (Edinb)* 93:104–107.