# New Frontiers in the Study of Human Cultural and Genetic Evolution

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**Abstract**

In this review, we discuss the dynamic linkages between culture and the genetic evolution of the human species. We begin by briefly describing the framework of gene-culture coevolutionary (or dual-inheritance) models for human evolutionary change. Until recently, the literature on gene-culture coevolution was composed primarily of mathematical models and formalized theory describing the complex dynamics underlying human behavior, adaptation, and technological evolution, but had little empirical support concerning genetics. The rapid progress in the fields of molecular genetics and genomics, however, is now providing the kinds of data needed to produce rich empirical support for gene-culture coevolutionary models. We briefly outline how theoretical and methodological progress in genome sciences has provided ways for the strength of selection on genes to be evaluated, and then outline how evidence of selection on several key genes can be directly linked to human cultural practices. We then describe some exciting new directions in the empirical study of gene-culture coevolution, and conclude with a discussion of the role of gene-culture evolutionary models in the future integration of medical, biological, and social sciences.

*Keywords:* Gene-Culture Coevolution, Dual-inheritance, Selection on Genes, Human Evolution

## 1. Cultural and Genetic Evolution: A Dual Inheritance System

In the 1930s and 1940s, the modern evolutionary synthesis formally integrated genetics and Darwinian evolution (mutation, drift, migration, linkage

and recombination, etc.) into a unified paradigm describing biological change [1, 2, 3, 4]. While the modern evolutionary synthesis remains the paradigm across fields in non-human biology, it was recognized by the early 1980s that the modern evolutionary synthesis could only provide a partial account of human evolution [5]. Mathematically formalized theories linking cultural and genetic inheritance systems were developed in the 1970s and 1980s [6], and these bodies of work serve as the grounding for dual-inheritance, or gene-culture coevolutionary (GCC) models of human social, behavioral, and biological evolution.

Culture has many definitions, but for the purposes of GCC models, we consider culture to be all of the information that individuals acquire from others by a variety of social learning processes including teaching and imitation [6]. The fidelity of cultural transmission is often sufficiently high for culture to act as an inheritance system [7]; however, cultural traditions also change with time, making culture a system of descent with modification.

As in the genetic inheritance system, there are several important forces that can lead to cultural evolution, such as random errors in teaching or acquiring items of culture (akin to mutation), statistical effects in small populations (akin to drift), and the effect of using different cultural variants on an individual's survival and reproduction (akin to natural selection) [8]. Several other forces driving cultural evolution are fairly distinctive from the forces of genetic evolution, and derive from the fact that culture can be transmitted through social networks [9, 10] in ways that are much more complex than gene transmission (either vertical or horizontal) in genetic systems.

Cultural agents can often evaluate and choose from a wide array of cultural variants present in their social networks. The choice between variants may be random, or may be non-random; non-random choice of cultural variants may be driven by the relative performance of the cultural variants (direct bias), the frequency in which the cultural variants are used (frequency bias), the status of the individuals using the cultural variants (prestige bias), or other biasing forces [11]. Humans also generate new cultural variants by other non-random processes such as individual learning, and recombination of existing ideas or techniques. Field evidence on evolutionary rates shows that they can be much faster for cultural evolution compared with genetic evolution, due the fact that biases and non-random innovation can create strong directional forces in cultural evolution in addition to natural selection; also, new ideas and techniques can spread rapidly through social networks, often making the cultural analog of the generation very short [10, 12, 13, 14].

Culture evolution can lead to the creation of novel culturally-constructed environments which exert selective pressures on genes; these changes may select for phenotypic plasticity (eg. general language processing, without fixed representations [15]), increase selection pressures on specific genetic variants at a given locus (eg. lighter skin pigmentation in high latitudes [16]), or reduce selection pressures on variants at a given locus (eg. a reduced importance of functional bitter taste receptor genes in humans with cultural knowledge of plant toxicity [17]). The cultural and genetic systems are linked; culture places selective pressures on genes, via natural and social selection in culturally influenced environments, and genes place selective pressures on culture, via the genetic components of bias forces and individual learning mechanisms. Figure 1 displays a graphical representation of the linkages between the cultural inheritance system, the genetic inheritance system, and the environment.

Below, we outline how progress in molecular genetics and genomics is beginning to provide the empirical data needed to move GCC from mathematical formalism into empirically grounded science, with several case studies linking cultural practices with selection on genes [8].

## 2. Quantitative Evidence for Selection on Genes

Recent advances in large-scale and whole-genome sequencing of modern humans [26], extinct archaic hominins [27, 28], and non-human primates [29, 30, 31], have provided researchers with the data needed to investigate which genes were evolving under various kinds of selection regimes, in various time periods of human evolutionary history [32, 33, 34]. Evidence of selection includes synonymous to non-synonymous mutation ratios [32], reduction in genetic diversity [32], a high-frequency derived alleles [32], cross population differences in allele frequencies [32] and cross population extended haplotype homozogysity [35], long haplotypes [32], direct estimation from subfossil DNA [36], and other genetic signatures [33, 34]. Exomics may provide even more useful tools for identifying selection on genes underlying specific protein sequences [37].

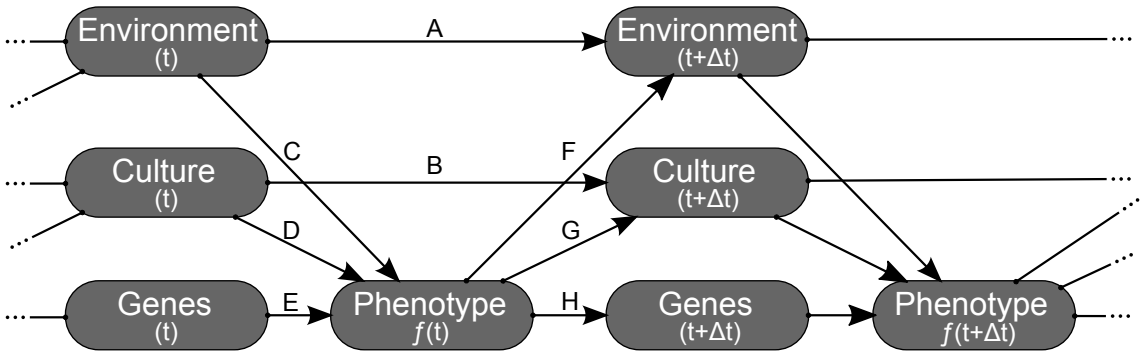


Figure 1: A simplified graphical sketch of one complete generation of a coevolving environment-gene-culture system. A) indicates the tendency of environment to persist and vary outside of human phenotypic control. B) indicates the tendency of culture to persist (eg. in durable form like text, artistic productions, and tools) and even vary (eg. algorithmically controlled stock trading [18, 19]) outside of direct human phenotypic control. C) indicates the effects of environment on phenotype (eg. natural selection on genes [3], phenotypically embodied culture [6], and epigenetic modifications [20]). D) indicates the effects of culture on phenotype (eg. enculturation [6], as biased by genetic, environmental and earlier acquired cultural factors). E) indicates genetic [21] and epigenetic [20, 22] transmission, and their influence on ontogeny. F) indicates durable effects of humans on their environments (sometimes refereed to as niche construction [23, 24]). G) indicates the formation of cultural variants (eg. older individuals may teach younger individuals traditions that were previously taught to them, as well as new traditions created through their own individual learning and invention [25]). This process is affected by experience and by natural selection on cultural variation. H) indicates the genetic transmission of naturally and culturally selected genotypes and modified epigenetic variants. *Note: Phenotype at time $f(t)$ is constrained to fall after Genes $(t)$ and before Genes $(t+\Delta t)$. $\Delta t$ is often taken to be the biological generation of an individual for modeling and notational convenience; in reality, evolutionary processes are continuous in time. Culture and environment, especially, can change appreciably in less than one biological generation.*

## 3. Human Cultural Practices as Key Drivers of Human Genetic Evolution

### *3.1. Agriculture, Disease, and Genes*

Many human genes found to be under positive selection are immune system related [32]. Of particular importance to GCC models of human evolution is evidence of selection in genes related to auto-immune disease (for instance, type-1 diabetes, Celiac, ulcerative colitis, and Crohn's disease) [38, 39], to malarial resistance [33, 40, 41, 42, 43], and to resistance to other infectious diseases (plague, smallpox) [44]. The rise of these diseases is intricately interwoven with culturally evolved adaptations concerning agriculture, animal domestication, and city-level social organization [45, 46, 44].

### *3.2. Animal Husbandry, Pastoralism, and Genes*

Observations of strong, recent selection on a lactase regulatory gene [47, 48] provides some of the first population-genetics–based evidence that a selective advantage based on additional nutrition from dairy explains lactase persistence in Europeans. This finding is extended with computational modeling linking spatially resolved genetic and cultural data to infer the history of the coevolution of lactase and dairying in Europe [49].

Other studies have found evidence of selection for lactase persistence in African populations [50, 51]; however, lactase persistence appears to have evolved through independent mutations in European and African populations [52], due to convergent socio-ecological circumstances and culturally evolved practices concerning animal husbandry.

### *3.3. Clothing, Fire, Migration, and Genes*

Culturally evolved adaptions to temperate and polar climates—such as clothing, shelter, and fire—allowed humans to occupy high latitudes. Consequently, the new ecology placed strong selection pressure on human genes, such as the genes responsible for pigmentation [53, 54], presumably due to the importance of photo-catalyzed vitamin D synthesis [55, 56], or folate regulation [16], although the exact mechanisms through which ecological pressures drove section on pigmentation-linked genes is still an area of active debate [16, 36].

These same cultural innovations allowed humans to thrive in high altitude environments, that in turn placed strong selection pressures on hypoxia-related genetic variants [57, 58]. In an interesting parallel to the convergent

evolution of lactase persistence, Tibetan and Andean populations evolved largely unique suites of genetic variants to solve the same ecological problem concerning hypoxia [59], although in the high altitude case the functional convergence is not nearly so similar as in adult lactase persistence.

## 4. New Frontiers in the Study of Human Cultural and Genetic Evolution

Exciting new areas of research in gene-cultural coevolutionary systems will investigate the roles that long-standing cultural practices *themselves* have on the evolution of important genetic variants. Below, we give two examples of emerging topics linking cultural practices and genetic evolution.

### *4.0.1. Cannibalism, Kuru, and Genes*

Prion diseases—such as Creutzfeldt-Jakob disease, bovine spongiform encephalopathy, and kuru—are invariably fatal, transmissible, neurodegenerative conditions, driven by a self-propagating conformational isomer of a normal neuronal glycoprotein (PrP), which refolds existing PrP into a non-functional variant [60].

Kuru became known to the Western scientific community in the 1950s when indigenous areas of the Eastern Highlands of Papua New Guinea came under Australian control [60, 61]. It was a common cultural practice in some New Guinea communities (especially in the Fore) for adult women and children to consume the brains of deceased relatives at mortuary feasts [60]. Local oral histories collected at the time Kuru was first discovered suggested that the practice of endocanibalism was not ancient among the Fore, but rather began only in the late 1800s [62, 60, 63]. The Kuru epidemic imposed severe morbidity and mortality on the Fore, and some villages were almost devoid of young adult women [60].

A coding polymophism in PrP has a substantial effect on survival times and disease progression of kuru-infected individual, where homozygotes of either allele have onset times of approximately 19 years, while the onset time in heterozygotes is normally over 30 years [60, 64]. If infection with kuru occurs as a child, then the reproductive window for infected homozygotes may be almost non-existent, while infected heterozygotes have more than a decade of asymptomatic reproductive life.

Differential mortality driven by cannibalistically transmitted protein created strong enough selection pressures for signatures of genetic adaptation

to be recorded less than 100 years after the origins of the cultural practice of mortuary feasts [60, 61]. Notably, out of 30 Fore women over the age of 50 who participated in mortuary rituals, 23 were heterozygotes, while the unexposed Fore population appears to be in Hardy-Weinberg equilibrium [60]. Thus, kuru in the Fore imposed exceptionally strong balancing selection on PrP variants.

#### *4.0.2. Distance Running, Pain Tolerance, Sexual Selection, and Genes*

At the 1968 summer Olympics, Kipchoge Keino won gold in the 1500 meter race, despite competing with a gull bladder infection. Since Keino's rise to fame, a small group of Kenyans—the Kalenjin (0.0005 percent of the world's population)—has produced an outstanding number of long-distance runners that have dominated world-class distance running, winning over 40 percent of international competitions [65, 66]. The dominance of one small ethnic group in world-class running has led many researchers to search for explanations based on demographic characteristics [67], food, vitamin, and macro-nutrient availability [68, 69], bioenergetics [70], local cultural history (local importance of long distance running, and a cultural history of cattle raiding) [71], hope for material and social capital [72], local ecology [73], and genetic differences [74].

It is possible that genetic differences related to bioenergetic pathways are responsible for differences in running performance, and that these adaptions are influenced by local ecology and cultural history. However, several studies of candidate genes related to bioenergetic pathways failed to find distinctions between Keyans in term of running ability [74, 75].

The lack of any definitive biological explanations led researchers to delve more deeply into cultural factors that might be responsible for distance running performance. Notably, the Kalenjin undergo circumcision as a coming of age ritual [65]. These circumcisions are performed without anesthetics, and the participants are required to show no outwards signs of weakness or pain (no grimaces, no cries), or face being branded as cowards for life and being outcasted from the marriageable population [65]. Such cultural practices have the potential to place intense selection pressure on genes for pain tolerance. It has been suggested that one reason the Kalenjin dominate in distance running is not due to genetic (bioenergetic) dispositions for increased running ability *per se*, but rather an increased genetic disposition for pain tolerance, which allows Kalenjins to push through the pain associated with high-levels of continuous physical exertion.

To our knowledge, no studies have thoroughly investigated if there are structured genetic differences related to pain tolerance between circumcising Kalenjins and non-circumcising populations in Kenya. However, one study on ethnicity-based differences in response to propofol-fentanyl anesthesia has shown that the time from discontinuation of anesthesia infusion to eye opening was $18.8 \pm 7.1$ min in Kenyans vs. $11.6 \pm 4.5$ min in Caucasians ($P < 0.01$), and time to response to verbal commands was $16.8 \pm 8$ min in Kenyans vs. $9.9 \pm 4.5$ min in Caucasians ($P < 0.01$) [76]. Other studies have shown that time to eye opening after fentanyl-based analgesia is related to genetic variants in the $\mu$-Opioid Receptor Gene, with AA variants at OPRM1 118 (SNP rs1799971) taking longer to awaken [77]. AA variants also show higher pain tolerance in experimental settings [78, 77]. In sum, these data point to the strong possibility that there may be structured genetic differences relating to pain tolerance between Kenyans and Caucasians.

More carefully directed studies may be able to test if there are structured differences in genes related to pain tolerance between Kalenjins and non-circumcising populations in Kenya. If such studies find evidence of structured differences between Kenyan subpopulations, they will provide testament to the importance of sexual selection and cultural practices in producing selection pressures on the human genome.

## 5. Looking Back, Looking Forward on The Integration of the Biological and Social Sciences

### *5.1. The Dark Clouds of History*

Despite the many attempts of the discipline of genetics as a whole to explain that the relatively slight genetic differences between human populations provide no basis for invidious discrimination among peoples, a small number of biologists and evolutionists have produced work that might give aid and comfort to racists [for examples, *see* 79, 80]. In the shadows of such actions, great caution and precision is needed in communicating scientific knowledge in such a way as to minimize misunderstandings that might insight racism or discrimination [81]. In response to scientific publications that were either directly racist, or served maintain a racist social structure, there was an enormous push-back among socio-cultural anthropologists to reject any essentializing genetic explanations for inter-group differences, as if describing genetic differences between populations automatically justified the evils of discrimination, racism, and eugenics.

We argue that this sensitivity to genetic explanation, though understandable given its historical and cultural context, was fueled in large part by logical fallacies [is-ought, appeal to nature, etc.] on the part of social scientists. A more useful and more ethical critique might have been waged against the assertion that 'genetic differences justify differential treatment,' rather than the assertion that 'genetic differences exist.' Furthermore, we note that the essentialist ideas that frequently underpin vicious ethnocentric ideologies are as likely to be based on cultural differences as genetic difference. Thus, rejection of genetic difference is not necessarily a rejection of the belief structures actually underpin racism, ethnocentrism, and discrimination.

We are, however, in agreement with much of the socio-cultural anthropological critique of excessively gene and environment centered accounts of human evolution. Like many socio-cultural anthropologists, we argue that human behavior is heavily influenced by culture in the short run; to this, we add that culture plays a large role in our genetic evolution in the long run.

### *5.2. Gene-culture Coevolutionary Theory as Integrative Bridge Linking Social Theory and Genetic Science*

Gene-culture coevolutionary models of human evolution provide a more holistic and nuanced understanding of the ways in which culture and biology interact. GCC models honor some of the most important critiques of excessively gene-centered accounts of human evolution from socio-cultural anthropology—namely that culture itself is a unique inheritance system, and one that radically alters human biological evolution to such an extent that the human genome itself can be partly viewed as cultural creation. However, GCC models avoid the unrealistic denial of genetic factors that is present in some early socio-cultural critiques of human evolutionary biology, which served to stigmatize medical and scientific research to the detriment of human health and knowledge.

GCC theory is a rapidly growing interdisciplinary field—one that is drawing an increasing amount of empirical support [82]. It is our hope that GCC models can serve as bridges linking socio-cultural theory and genetic sciences in a way that unites the strengths and partial truths that each perspective offers. In doing so, GCC theory may provide frameworks for knowledge that avoid naïve biological and ecological essentialism, while advancing scientific and medical knowledge related to human genetics.

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