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New frontiers in the study of human cultural and genetic evolution

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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.

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Cultural and genetic evolution: a dual inheritance system

In the 1930s and 1940s, the modern evolutionary synthesis formally integrated genetics and Darwinian evolution (selection, mutation, drift, migration, and recombination) into a unified paradigm describing biological change [1–4]. 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 to 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 (e.g. general language processing, without fixed representations [15]), increase selection pressures on specific genetic variants at a given locus (e.g. lighter skin pigmentation in high latitudes [16]), or reduce selection pressures on variants at a given locus (e.g. 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 the GCC framework from mathematical formalism into empirically grounded science, with several case studies linking cultural practices with selection on genes [8].

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 [29–31], 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 of 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•], increased genetic diversity [37,38], and other genetic signatures [33••,34••]. Exomics may provide even more useful tools for identifying selection on genes underlying specific protein sequences [39].

Human cultural practices as key drivers of human genetic evolution

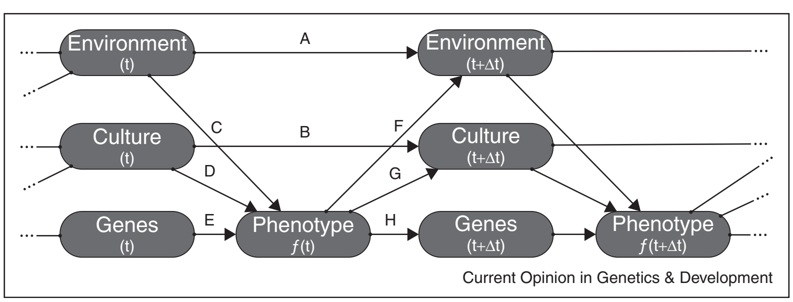
Agriculture, disease, and genes

Many human genes found to be under 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) [40,41], to malarial resistance [33••,37,42–44], and to resistance to other infectious diseases (plague, smallpox) [45]. The rise of these diseases is intricately interwoven with culturally evolved adaptations concerning agriculture, animal domestication, and city-level social organization [45–47].

Animal husbandry, pastoralism, and genes

Observations of strong, recent selection on a lactase regulatory gene [48,49] provide 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

Figure 1



A simplified graphical sketch of one complete generation of a coevolving environment-gene-culture system. **(A)** The tendency of environment to persist and vary outside of human phenotypic control. **(B)** The tendency of culture to persist (e.g. in durable form like text, artistic productions, and tools) and even vary (e.g. algorithmically controlled stock trading [18,19]) outside of direct human phenotypic control. **(C)** The effects of environment on phenotype (e.g. natural selection on genes [3], phenotypically embodied culture [6], and epigenetic modifications [20]). **(D)** The effects of culture on phenotype (e.g. enculturation [6], as biased by genetic, environmental and earlier acquired cultural factors). **(E)** Genetic [21] and epigenetic [20,22] transmission, and their influence on ontogeny. **(F)** Durable effects of humans on their environments (sometimes refereed to as niche construction [23,24]). **(G)** The formation of cultural variants (e.g. 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)** 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*($t + \Delta t$). Δt 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.