

# Gene–Culture Coevolution

Intermediate article

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*Evolution in species with a dynamic, socially transmitted culture may be different from evolution in other species. Population geneticists have proposed the gene–culture coevolutionary approach to describe the way in which cultural change may drive a population’s biological evolution.*

## INTRODUCTION

Many researchers have noted analogies between the processes of biological evolution and cultural change. For instance, both genes and culture are informational entities that are differentially transmitted from one generation to the next. These similarities have led to the idea that culture evolves, and prompted the development of mathematical models of cultural evolution.

The main scientific approach to the study of how culture evolves is a branch of theoretical population genetics, known variously as ‘cultural evolution’, ‘gene–culture coevolution’, or ‘dual inheritance’ theory. This intellectual tradition has nothing in common with the nineteenth-century ‘cultural evolution’ schools, which, based on an erroneous view of evolution as progressive, set out to model stages of societal development. Rather, the population genetics approach regards culture as an evolving pool of ideas, beliefs, values, and knowledge that is learned and socially transmitted between individuals. Researchers focus on a single trait, such as a preference for drinking milk, or for sons over daughters, and employ a rigorous mathematical approach to describe how the cultural trait changes over time, sometimes coevolving with genetic variation. Where the cultural entity is a discrete package, it has much in common with Richard Dawkins’ idea of the ‘meme’, defined as a cultural analogue of the gene (Dawkins, 1976).

Stone tools appear in the archeological record approximately two and a half million years ago. If, as is widely believed, lithic technologies and

skills were transmitted from one generation to the next, these simple artifacts represent the earliest evidence for culture. In fact, comparative evidence for social learning in a variety of vertebrate species suggests that cultural transmission almost certainly preceded *Homo habilis* by a considerable length of time. However, social learning in other animals is rarely stable enough to support traditions in which information accumulates from one generation to the next. For at least 2 million years our ancestors have reliably inherited two kinds of information, one encoded by genes, the other by culture.

There is only one evolutionary approach to the study of human behavior that takes up the challenge of understanding genetic and cultural evolution simultaneously by focusing directly on their interaction. Gene–culture coevolutionary theory (or dual inheritance theory), together with evolutionary psychology and human behavioral ecology, is one of three principal evolutionary approaches that emerged in the aftermath of the human sociobiology debate (Smith, 2000).

Conceptually, gene–culture coevolution is like a hybrid between memetics and evolutionary psychology, although its methods are quite different, relying as they do on rigorous mathematical theory. Like memeticists, gene–culture coevolution enthusiasts treat culture as evolving learned knowledge. Like evolutionary psychologists, these researchers believe that the cultural knowledge individuals adopt may sometimes – although certainly not always – depend on their genetic constitution. Moreover, selection acting on the genetic system is commonly generated or modified by the spread of cultural information. For gene–culture coevolutionary theorists, the ‘leash’ that ties culture to genes tugs both ways. The advent of culture was a precipitating evolutionary milestone, generating selection that favored a reorganization of the human brain, and leaving it specialized to acquire, store, and use cultural information. It was culture,

loosely guided by genes, that allowed humans the adaptive flexibility to colonize the world.

The quantitative study of gene–culture coevolution began in 1976, when two population geneticists, Luca Cavalli-Sforza and Marc Feldman of Stanford University, published the first simple dynamic models with both genetic and cultural inheritance. The fundamental innovation that Cavalli-Sforza and Feldman instigated was that, in addition to modeling the differential transmission of genes from one generation to the next, they incorporated cultural information into the analysis, allowing the evolution of the two systems to be mutually dependent. However, one curious feature of the history of gene–culture coevolution is that both archetypal sociobiologists and some of their most severe critics almost simultaneously recognized the importance of gene–culture interactions, with each starting to develop methods to address the problem. By the late 1970s, Charles Lumsden and Edward Wilson at Harvard University were engaged in a race with Cavalli-Sforza and Feldman to produce the first book on this topic. While Lumsden's and Wilson's *Genes, Mind and Culture* was published first (Lumsden and Wilson, 1981), it was not well regarded (Maynard-Smith and Warren, 1981). In contrast, Cavalli-Sforza's and Feldman's more cautious tome *Cultural Transmission and Evolution* (Cavalli-Sforza and Feldman, 1981) was much better received.

Together with many co-workers, Cavalli-Sforza and Feldman gradually built up an impressive body of mathematical theory exploring the processes of cultural change and interaction between genes and culture. Frequently they took advantage of the parallels between the spread of a gene and the diffusion of a cultural innovation to borrow or adapt established models from population genetics. Drawn by the ongoing sociobiology debate, other mathematically minded researchers joined the fray, most notably anthropologists Rob Boyd and Peter Richerson, whose book *Culture and the Evolutionary Process* introduced a variety of novel theoretical methods and stimulating ideas (Boyd and Richerson, 1985). Gradually a consensus as to the most appropriate methods for tackling gene–culture interactions began to emerge, which today forms the basis of modern coevolutionary theory.

The technical and explicitly mathematical nature of modern gene–culture coevolution is one of several features that distinguishes this perspective from alternatives such as evolutionary psychology. A second is the incorporation into analyses of a variety of genetic and cultural processes in addition

to the natural selection of genes. Gene–culture coevolution exhibits a concern for nonadaptive and even maladaptive outcomes of the evolutionary process. This stance continues both to surprise and confuse outside observers used to characterizing all these evolutionary approaches as 'sociobiology'. However, the rigorous theoretical approach has led to little experimentation or other forms of empirical work, and this school remains the prerogative of a comparatively small band of workers.

The emerging body of theory has developed in a variety of ways. One class of models investigates the inheritance of behavioral and personality traits, extending traditional models by incorporating a transmitted cultural component into the analysis. Other models address general questions about the adaptive advantages of learning and culture. More recently, these methods have been applied to address specific cases in which there is an interaction between cultural knowledge and genetic variation that influences its prevalence. These include the evolution of language and of handedness, an analysis of changes in the genetic sex ratio in the face of sex-biased parental investment, the spread of agriculture, the coevolution of hereditary deafness and sign language, the emergence of incest taboos, and an exploration of how cultural niche construction affected human evolution (see Feldman and Laland, 1996).

As the rules of cultural transmission are usually different from those of genetic transmission, similar selective regimes may result in very different equilibria. A good example of this is provided by the hypothesis of Boyd and Richerson (1985) that group selection can act on cultural variation. The theoretical argument against group selection is based on models which assume genetic inheritance, and the criticisms may not hold for culturally transmitted traits. When individuals adopt the behavior of the majority a conformist transmission is generated (Boyd and Richerson, 1985). As a result of its frequency dependence, conformist transmission can act to amplify differences in the frequency of cultural traits in different subpopulations, but reduce variance within groups. Boyd and Richerson showed that one of the by-products of a conformist bias is an increase in the strength of the group selection of cultural variation so that it may be a strong force relative to forces acting within groups, such as natural selection. Since selection between groups may favor beliefs and attitudes that benefit the group at the expense of the individual, Boyd and Richerson's theory provides a new explanation for human cooperation.

## EVIDENCE FOR TRANSMITTED CULTURE

For most social scientists ‘culture’ is a given. The notion that much of the variation in the behavior of humans is brought about by their being exposed to divergent cultures is so widespread and intuitive that is beyond dispute. While it used to be fashionable to define culture as the interwoven complex of behavior, ideas, and artifacts that characterize a particular people (e.g. Tylor, 1871), among social scientists this view has been superseded by a more cognitive perspective that restricts culture to information stored in the brain. In contrast, biological approaches to culture (including those of most sociobiologists, human behavioral ecologists, and evolutionary psychologists) tend to regard the transmitted elements of culture as either exerting a comparatively trivial influence on human behavior, or that whatever influence they have is strictly circumscribed by genes.

For advocates of gene–culture coevolution these biological perspectives underemphasize one critical factor: socially transmitted culture. Too much culture changes too quickly to be feasibly explained by genetic variation, while the fact that different behavioral traditions can be found in similar environments would appear to render environmental explanations of behavior impotent much of the time. To give an example, Guglielmino *et al.* (1995) analyzed variation in cultural traits among 277 contemporary African societies, and found that most traits examined correlated with cultural history rather than with ecology. Such findings suggest that most human behavioral traits are maintained in populations as distinct cultural traditions, rather than evoked by the natural environment. Genes and environment undoubtedly account for some variation in human behavior, but the socially transmitted component of culture is also important.

A capacity for culture is an unusual adaptation. It allows humans to learn about their world rapidly and efficiently. We do not have to scour our environment for sources of food and water, devise our own means of communication, or reinvent technological advances from first principles. Our capacity to acquire valuable skills and information from more knowledgeable others, such as parents, teachers or friends, as well as indirectly through artifacts such as books and computers, furnishes us with a short cut to adaptive (and sometimes maladaptive) behavior. Advocates of gene–culture coevolution share with the vast majority of social scientists the view that what makes culture

different from other aspects of the environment is the knowledge passed between individuals. Culture is transmitted and inherited in an endless chain, frequently adapted and modified to produce cumulative evolutionary change. This infectious, information-based property of transmission is what allows culture to change rapidly, to propagate a novel behavior through a population, to modify the selection pressures acting on genes, and to exert such a powerful influence on our behavioral development.

Gene–culture enthusiasts point to countless studies that have found that the attitudes of parents and offspring are similar. They maintain that the most obvious explanation for this is that children learn social attitudes in the family. For instance, a study of Stanford University students revealed that the religious and political attitudes were strongly consistent between parents and offspring (Cavalli-Sforza *et al.*, 1982). The same applies to nonindustrial societies. For instance among Aka pygmies, an African group of hunter-gatherers, there was evidence for parent to child transmission of many customs (Hewlett and Cavalli-Sforza, 1986). Such correlations do not prove cultural transmission to be prevalent: for instance, there could be heritable genetic effects. However, the weight of evidence supports the notion of a transmitted culture; see Boyd and Richerson (1985) for a more extensive collation of evidence for cultural transmission.

## TYPES OF CULTURAL SELECTION

Researchers in the gene–culture coevolution tradition have described a number of processes that underpin cultural change. In order to distinguish cultural from biological evolution, Cavalli-Sforza and Feldman (1981) defined ‘cultural selection’ as a process by which particular socially learned beliefs, or pieces of knowledge, increase or decrease in frequency owing to their adoption by other individuals at different rates. In contrast, natural selection can change the frequency of a cultural preference through the differential survival of individuals expressing different types of preference. For instance, in developed countries fertility control (contraception) is at a clear disadvantage in natural selection as users typically have fewer offspring, but has spread by virtue of its advantage in cultural selection since fertility control is a popular choice. Working on these two interacting subsystems simultaneously helps us to understand how nonadaptive cultural traditions could evolve (Cavalli-Sforza and Feldman, 1981). When it has

sufficiently high cultural fitness, cultural information can increase in frequency despite decreasing genetic fitness. Cavalli-Sforza and Feldman's framework also considers cases in which cultural selection operates without affecting Darwinian fitness (e.g. a preference for a particular soft drink).

Researchers in gene–culture coevolution are also interested in how information spreads within populations. The mode of transmission is the route by which cultural knowledge spread among individuals (Cavalli-Sforza and Feldman, 1981), and different models are required for alternative modes of information transmission. Social transmission can occur vertically (that is, from parents to offspring), obliquely (from the parental to the offspring generation; for instance, learning from teachers or religious elders) or horizontally (that is, within-generation transmission such as learning from friends or siblings). Genetic inheritance is exclusively vertical, and as social transmission frequently occurs through some combination of these modes of information transmission, cultural evolution and gene–culture coevolution will exhibit quite different properties from those of biological evolution.

Boyd and Richerson (1985) extended the taxonomy of cultural processes by splitting the general concept of 'cultural selection' into subtypes. One such subtype is 'guided variation', which refers to a process by which individuals acquire information about a behavior culturally, and then modify the behavior on the basis of their personal experience. Here cultural variation is guided by individual experience which, as human behavioral ecologists envisage, allows behavioral traditions to evolve gradually towards the adaptive optimal behavior for that environment.

Another set of processes that Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) consider is known as 'biased cultural transmission'. Biased transmission occurs when, given a choice between two alternative behavior patterns, individuals are more likely to adopt one variant than another. Various types of bias exist. In direct bias, individuals choose which of two or more alternative behavior patterns to adopt. A direct bias might result from a genetic predisposition to favor certain types of information. Stanford University anthropologist Bill Durham has argued that the individual choices underpinning these cultural processes are guided, but not determined, by predispositions and prior knowledge (Durham, 1991).

In the case of frequency-dependent bias, however, the commonness or rarity of a behavior affects the probability of information transmission. When,

as frequently seems to be the case, individuals are predisposed to adopt the behavior of the majority, this frequency-dependent bias generates conformity. People may also use cues about one trait, for example, wealth, to choose which individuals to observe in order to acquire information about another trait, such as clothes fashions. Boyd and Richerson call this 'indirect bias'.

### **A Case Study: Coevolution of Dairy Farming and Genes for Processing Milk**

The evolution of the ability of adult humans to consume dairy products represents a good example of gene–culture coevolution. Unlike that of human infants, virtually all of whom can all drink milk without problems, the milk digestive physiology of adult humans varies considerably. In fact, if the entire world's population is considered, consuming dairy products makes the majority of adult humans ill. This is because the activity level of the enzyme lactase in their bodies is insufficient to break down the energy-rich sugar lactose in dairy products, and milk consumption typically leads to sickness and diarrhea. The ability of adult humans to digest lactose largely depends on whether they possess the appropriate variants of a single gene. A correlation exists between the incidence of the genes for lactose absorption and a history of dairy farming in populations, with absorbers reaching frequencies of over 90% in dairy-farming populations, but typically less than 20% in populations without dairy traditions (Durham, 1991). The correlation is extremely suggestive. Milk and milk products have been a component of the diets of some human populations for over 6000 years, roughly 300 generations. Is it conceivable that dairy farming might have created the selective regime under which the allele for absorption was favored?

Feldman and Cavalli-Sforza (1989) used gene–culture coevolutionary models to investigate the evolution of lactose absorption. They assumed that the capacity to absorb lactose was affected by alleles (variants) of a single gene, with one particular allele allowing adults to digest milk. In addition, they modeled the cultural transmission of milk usage. The analysis suggested that whether or not the allele allowing adult lactose absorption and milk digestion achieves a high frequency depends critically on the probability that the children of dairy-product users themselves become milk consumers. If this probability is high, then a significant fitness advantage to the genetic capacity for lactose absorption will generally result in the selection of

the absorption allele to high frequency within 300 generations. However, if a significant proportion of the offspring of milk users do not exploit dairy products, then unrealistically strong selection favoring absorbers would be required for the gene for absorption to spread. In other words, differences in the strength of cultural transmission between cultures may account for genetic variability in lactose absorption. The analysis is able to account for both the spread of lactose absorption, and the culturally related variability in its incidence. Moreover, there is a broad range of conditions under which the absorption allele does not spread despite a significant fitness advantage, indicating that traditional genetic models would frequently give the wrong answer. Cultural processes complicate the selection process to the extent that the outcome may differ from that expected under purely genetic transmission.

The traditional view among the scientific community was that adult lactose tolerance in humans is an adaptation to reduced exposure to the sun, as both the sun and the enzyme lactase promote calcium absorption (Durham, 1991). However, an analysis by Holden and Mace (1997) of a phylogeny of human cultural groups using sophisticated statistical techniques found no evidence for the latitudinal theory, but strong support for the dairy-farming hypothesis. Moreover, their analysis revealed that dairy farming evolved first, which then favored tolerance to lactose, and not the other way around. Holden and Mace's analysis provides compelling confirmation of the findings of this gene–culture coevolutionary analyses.

## DO GENES AND CULTURE COEVOLVE?

It is frequently suggested that genetic evolution is too slow and cultural change too fast for the latter to drive the former. In fact, selection experiments and observations of natural selection in the wild reveal that biological evolution may be extremely fast, with significant genetic and phenotypic change sometimes observed in a small number of generations. At the same time, observations of hominid stone tool technologies reveal that cultural change can be extraordinarily slow. Acheulian and Oldowan stone tools traditions remained very similar for hundreds of thousands – even millions – of years. Even cultural institutions such as labor markets can be extremely persistent, albeit on a shorter time scale. Furthermore, theoretical analyses have revealed that cultural transmission may change selection pressures to generate

unusually fast genetic responses to selection in humans (Feldman and Laland, 1996). It is thus entirely feasible that genetic and cultural evolution could operate at similar rates. In fact, the past 2 million years of human evolution may even have been dominated by gene–culture coevolution. Culture can, of course, cause rates of environmental change that really are too fast for human genetic evolution to track, and it is probably doing so increasingly. In fact, in the last 25 000–40 000 years the dominant mode of human evolution has probably been exclusively cultural.

## Gene–Culture Coevolution and Niche Construction

Organisms frequently choose, regulate, construct, and destroy important components of their environments, such as nests and burrows, in the process changing the selection pressures to which they and other organisms are exposed. These processes are known as niche construction (Odling-Smee, 1988). Niche-constructing traits are more than just adaptations, because they have the additional role of modifying natural selection pressures. Like natural selection, niche construction can be regarded as an evolutionary process potentially capable of generating a complementary match between organism and environment. Organisms may adapt to environments, and environments may be shaped by organisms. In humans, culture has greatly amplified our capacity for niche construction and our ability to modify selection pressures, and cultural niche construction may frequently instigate further biological or cultural change (Laland *et al.*, 2000).

Standard gene–culture analyses incorporate niche construction implicitly, by assuming that some human cultural activities feed back to modify some selection pressures in human environments, and thus cultural transmission may affect the fate of some selected human genes. Generally, the relevant aspect of human selective environments is defined as cultural. For example, the trait that affected human genetic evolution in the lactose tolerance case was milk usage (Durham, 1991). Here, gene–culture theory is applicable because the link between milk usage and its genetic consequences are sufficiently simple to allow it to be modeled without bringing in any intermediate variables (Feldman and Cavalli-Sforza, 1989).

However, standard gene–culture coevolutionary models are less appropriate in more complicated situations. Take, for example, the case of Kwa-speaking yam cultivators in West Africa, who increased the frequency of a gene for sickle cell

anemia in their own population as a result of the indirect effects of yam cultivation. These people traditionally cut clearings in the rainforest, creating more standing water and increasing the breeding grounds for malaria-carrying mosquitoes. This, in turn, intensified selection for the sickle cell allele, because of the protection offered by this allele against malaria in the heterozygotic condition (Durham, 1991). Here the causal chain is so long that simply plotting the cultural trait of yam cultivation against the frequency of the sickle cell allele would be insufficient to yield a clear relationship between the cultural trait and allele frequencies (Durham, 1991). The crucial variable is probably the amount of standing water in the environment caused by the yam cultivation, but standing water is an ecological variable, not a cultural variable, and it partly depends on factors (rainfall) that are beyond the control of the population. So here the simplifying assumption of a direct link between cultural and genetic inheritance distorts reality too much to allow their interaction to be modeled in the standard way. This time the two human inheritance systems can interact only via an intermediate, abiotic, ecological variable subject to niche construction, which should be included to complete the model.

This shortcoming led Laland *et al.* (2000) to propose an extended version of gene–culture coevolutionary theory, which incorporated niche construction as a general evolutionary process. Culturally modified selection pressures are regarded as a part of a more general legacy of modified natural selection pressures bequeathed by humans to their descendants. Laland *et al.* (2001) used extended gene–culture coevolutionary models to explore the evolutionary consequences of culturally generated niche construction through human evolution. The analysis revealed circumstances under which cultural transmission can overwhelm natural selection, accelerate the rate at which a favored gene spreads, initiate novel evolutionary events, and trigger hominid speciation. Because cultural processes typically operate faster than natural selection, cultural niche construction is likely to have more profound consequences than gene-based niche construction, and is likely to have played an important role in human evolution.

### Empirical Studies of Gene–Culture Coevolution

While gene–culture coevolution has a strong and rigorous theoretical foundation, it is vulnerable to the charge that it has not spawned a vigorous

empirical science. Where gene–culture analyses have been applied to specific case studies they do make a variety of testable predictions; for instance, Soltis *et al.* (1995) used data on rates of population extinction in New Guinea to test Boyd and Richerson’s group selection hypothesis. Yet no general empirical method has been established. The closest to a general approach is that advocated by anthropologist Bill Durham, who illustrates with compelling examples, each backed by considerable data, how variability in human behavior and society may be interpreted as resulting from interactions between genetic and cultural processes (Durham, 1991). Durham identifies five categories of interaction:

- genetic mediation, where genetic differences underlie cultural variation, as may be the case for the terms used by humans to describe color which reflect features of the human nervous system;
- cultural mediation, where culture drives genetic change, such as with the evolution of adult lactose absorption in populations that consume dairy products;
- enhancement, where culture reinforces genetic predispositions, as with the emergence of incest taboos that guard against the deleterious effects of inbreeding;
- neutrality, where memes are adopted independently of an individual’s genotype, as is the case for learning different languages;
- opposition, where culture leads to maladaptive traditions, for instance the cannibalism of the Fore, a New Guinea community, which spread the deadly nerve disease kuru.

### CONCLUSION

Gene–culture coevolutionary theory has rarely been subject to the same level of criticism as human sociobiology or evolutionary psychology. In fact, in the debates over human sociobiology and its progeny, it has been almost completely ignored, perhaps because of its technical nature. However, some social scientists have objected to the idea that culture can be modeled as if composed of discrete psychological or behavioral characteristics, while others have questioned the legitimacy of ‘borrowing’ population genetics processes to model culture, or criticized the analyses as promoting a false gene–culture dichotomy. However, for gene–culture researchers these assumptions do not represent ideological stances but are made purely for pragmatic reasons. Culture is difficult to analyze unless it is broken down into manageable units. Building on population genetic models is a reasonable place to start developing models of cultural evolution (providing the differences between

biological and cultural processes are accommodated). Gene–culture methods represent comparatively simple descriptions of the interactions between genetic and cultural processes. However, approaches that focus on a single process (be it exclusively cultural or exclusively genetic) have made the fundamental and sweeping assumption that the processes do not interact, or that there is only one process that matters.

Gene–culture coevolutionary analyses suggest that evolution in species with a dynamic, socially transmitted culture may be different from evolution in other species. Culture is a particularly effective means of modifying natural selection pressures and driving the population's biological evolution, as was the case for lactose absorption. Culture may generate new evolutionary processes, for instance cultural group selection. Moreover, cultural transmission may strongly affect evolutionary rates, sometimes speeding them up and sometimes slowing them down. Such findings suggest that traditional evolutionary approaches to the study of human behavior may not always be adequate.

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