GENE-CULTURE COEVOLUTION

Coevolution refers to a process where two or more different inherited traits affect selection on one another. Some of the most famous cases relate to coevolution between predators and prey, or between host defense mechanisms and parasite virulence. In these examples, both traits are typically expressed as a result of genetic inheritance. By contrast, a prerequisite for gene-culture coevolution is that there are two different tracks of inheritance; one for genetically transmitted information and the other for culturally transmitted information. Gene-culture coevolutionary theory examines interactions between traits that are derived from these two inheritance systems.

How Genetic and Cultural Inheritance Systems Interact

Many animals can learn from one other. However, learned behavior that is socially transmitted across many generations can in some cases constitute a consistent environment that affects genetic selection. Gene-culture coevolution ensues if there is a statistical association between the differential fitness of genetically inherited variants and culturally inherited variants. For these occasions, either a purely genetic or purely cultural model underspecifies the evolution of phenotypic variation. Thus, the most parsimonious unit of selection is the combination of each genetic variant and cultural variant, sometimes referred to as the *phenogenotype.*

Necessarily, gene-culture coevolution describes systems where the phenotypic variation under investigation is highly unlikely to be explained only by genetic variation. For instance, while the genetic makeup of humans may contribute to their intelligence, it would be ridiculous to suggest that variation in particular types of farming methods can be explained by genetic variation across human farming populations. Yet, different farming technologies can be stably transmitted across generations, and thus modeled as an evolutionary process that is subject to descent with modification.

A gene-culture coevolutionary model is developed by explicitly accounting for (1) the transmission of genetic and cultural variants between generations, accounting for phenogenotype mating probabilities and biases in the pathways of cultural transmission, and (2) the differential fitness of the phenogenotypes per generation. For diploid organisms, genetic information is commonly transmitted vertically, from parents to offspring. Cultural information, however, is often recognized to be transmitted vertically, obliquely (between generations but not from parents to offspring), horizontally (within a generation), or some combination thereof. Gene-culture coevolution requires the stable transmission of cultural variants across generations and thus typically is assumed to rely on vertical transmission, oblique transmission, or a mechanism whereby individuals conform to commonly held views or beliefs.

By accounting for both patterns of transmission and fitness, the relative frequency of phenogenotypes can be traced across generations. Initially, gene-culture coevolutionary models were developed by modifying population genetic theory to account for culturally specific forms of inheritance. For instance, the two-locus model can be modified to consider the coevolution of a genetic trait and a cultural trait, in place of two genetic traits at separate loci.

These relatively simple systems were tractable for mathematical analysis, and yet yielded a rich set of dynamics that provided predictions distinct from those of equivalent genetic models. This is because the cultural trait dynamics often behave differently from genetic trait dynamics. Cultural variants can spread much faster than genetic variants and can alter the rate of genetic evolution. For instance, the effect of farming on available diet is likely to have increased the rate of genetic evolution affecting physiology and disease resistance. Alternatively, the swift cultural evolution of health interventions can potentially buffer or shield otherwise deleterious genetic variants from selection. Furthermore, patterns of cultural transmission can be biased in ways that are distinct from genetic transmission, altering evolutionary trajectories by modulating the statistical association between the cultural and genetic variants.

Comparisons with Other Approaches

Gene-culture coevolutionary theory has been contrasted with a number of other approaches to explain the evolution of human behavior. The school of human behavioral ecology typically assumes that behaviour is adaptive and evolves to maximize lifetime reproductive success, while evolutionary psychologists often assume that psychological predispositions are adaptations to past environments during human evolution. By contrast, gene-culture coevolutionary models are typically minimalist in this regard, as they do not require either assumption to hold.

A second difference from the approaches of these other schools is the explicit distinction between genetic and cultural transmission systems. While many human behavioral ecologists and evolutionary psychologists would not deny that cultural transmission occurs, gene-culture coevolutionary theorists emphasize that some patterns of behavior and psychology are affected by interactions between genes and culture over evolutionary time.

Cultural Niche Construction and Rapid Genetic Selection of Traits

Since the sequencing of the human genome, a substantial number of genes have been identified as having been subject to rapid and recent selection. Many of these genes have putative functions whose fitness may have been affected by a culturally modified environment, sometimes referred to as *cultural niche construction*, and thus are prime candidates for gene-culture coevolution. The functional domains for these genes include the capacity for learning, forms of intelligence, and the facility for language (e.g. FOXP2). It is easy to envisage that a selective advantage for the capacity for innovation and social learning of adaptive information could coevolve with cumulative adaptive knowledge.

The cultural evolution of some innovations is likely to have affected the recent and rapid genetic evolution of anatomical, physiological and immune-related traits. For instance, the cultural transmission of cooking techniques and the production of new diets may have affected selection of genes relating to reduced jaw musculature and metabolism, respectively. Furthermore, it is highly plausible that farming practices and domestication in the Neolithic provoked strong selection in disease-susceptibility genes through exposure to infectious and nutritional disease.

Other genes that appear to have been subject to recent, rapid selection contribute to external physical characteristics such as hair, eye and skin colour. These traits may have been subject to selection induced by cultural influences on patterns of human migration, affecting survival in particular physical environments, such as the effect of low-UVR outside the tropics on selection for skin depigmentation to enhance vitamin D biosynthesis. Also, external features can be subject to sexual selection, coevolving with culturally transmitted mating preferences.

The most well known case of gene-culture coevolution is perhaps that of dairy farming and lactase persistence. Following weaning, most mammals, including most humans, cannot digest the sugar, lactose, found in unprocessed milk as they cease production of the enzyme, lactase, to break down the sugar. However, a small number of independently evolved genetic variants originating in European, African and Middle Eastern populations allow the persistence of lactose absorption after weaning through continued high production of lactase. For instance, most Europeans are lactose tolerant as a result of a single nucleotide base substitution in a region of the genome that promotes lactase gene activity.

It is now well established that the European genetic variant for lactase persistence spread as a consequence of dairy farming in the Neolithic, approximately 7,500 years ago. Gene-culture coevolutionary models showed that for lactase persistence to spread, it was important that there was a high probability of cultural transmission for using dairy products between generations, which would facilitate a statistical association between dairy farming and the genetic variant over evolutionary time. The coevolutionary explanation was supported further by evidence that dairy farming originated prior to the evolution of lactase persistent alleles, and thus provided the selective environment for the genetic evolution of lactase persistence, and not the other way around. Among dairy farmers, those individuals who exhibit the lactase persistent variant would be at a selective advantage, benefiting from the consumption of milk; a regular, nutrient-rich and high calorific dietary supplement. Thus, the genetic trait and the cultural practice coevolved.

An interesting example of gene-culture coevolution relating farming and disease resistance is found in West African, Kwa-speaking populations of yam cultivators, who cut clearings in forests to grow crops, with a cascade of consequences. The clearings increase the amount of standing water, which provide better breeding grounds for mosquitoes and increase the prevalence of malaria. One consequence of the culturally transmitted farming practice was to provoke genetic selection for malarial resistance in these yam cultivating populations.

In most human populations, the sickle-cell allele, HbS is rare as it results in sickle-cell anemia in its recessive homozygous form (i.e. expressed when both gene copies are of type

HbS). However, in the heterozygous form (i.e. where only one copy is of type HbS) the sickle-cell allele confers protection against malaria, with only mild sickling of the red blood cells. This heterozygous form is more prevalent in the West African yam cultivating populations than neighboring non-yam cultivating populations, indicating that the cultural practice has coevolved with malarial resistance. Interestingly, the relatively high frequency of sickle cell may actually encourage further yam cultivation, as these crops appear to have medicinal properties circumventing the sickling effects.

The gene-culture coevolutionary system can also apply across species. A classic case is the coevolution of human antibiotic use and bacterial antibiotic-resistant strains. This is effectively a special case of a host-parasite coevolutionary system, where the host behavior, antibiotic use, is culturally derived. Cultural transmission of antibiotic use favors selection of resistant bacterial strains, which in turn can result in cultural selection for the avoidance of antibiotic use. Thus culturally transmitted host behavior can maintain bacterial strain polymorphism where it would not otherwise be expected.

Possible Derivation of Prosocial Behaviors

Aspects of prosocial behavior, characteristically exhibited in humans more than in other primates, may have been derived through gene-culture coevolution. This argument has been made to explain a number of prosocial features including a propensity for conformity to norm adherence; strong reciprocity, where the cooperative activity of others is rewarded while norm-violators are punished at a cost to the punisher; and parochial altruism, where altruism is only directed within a culturally defined group. The suggestion is that cultural group selection, that is, cultural selection between culturally distinct groups, may have favoured the spread of social norms for cooperative behaviour through enhanced economic and demographic success, success in between-group conflict, and through prestige bias where norms are preferentially copied from the most successful groups. The adaptive normative practices will then favour genetic selection for predispositions relating to prosociality including the desire to punish norm violators, character virtues such as honesty and trust, norm internalization and conformity. The mutual reinforcement between genetic selection of such predispositions and cultural selection of normative practice may have contributed to the evolution of prosociality.

Sex Ratios and Gene-Culture Coevolution

A final example of gene-culture coevolution pertains to the genetic evolution of sex-ratio distorter genes and the cultural evolution of preference for sons, manifest for example through neglect of female offspring, sex-selective abortion or direct infanticide. Sex-ratio distorter genes can affect the sex at conception, for instance by altering the proportion or viability of sperm carrying an X or Y chromosome. The primary sex ratio, that is the fraction of male offspring from a mating prior to any sex-specific mortality, can differ from the adult sex ratio, measured at reproductive age. Gene-culture coevolutionary models have shown that a female-biased primary sex ratio can evolve if parents always increase their proportion of sons by a fixed amount, compensating for loss of daughters by having more children. In this case, the mating success of an excess of sons is less than that of daughters, resulting in an increase in frequency of female-bias distorter genes. Eventually, the strength of parental bias for sons over daughters matches the female-biased primary sex ratio, resulting in an unbiased adult sex ratio (recovering a standard result in sex-ratio theory). In contrast, if parents attempt to bring their offspring sex ratio closer to their ideal preference but without compensating for offspring loss, models predict that the primary sex ratio can become biased until it matches the male-biased preference exhibited in the adult sex ratio. Thereafter, there would be no further sex ratio adjustment by parents as the primary sex ratio matches their ideal preference.

The Future

The future of gene-culture coevolutionary studies lies in examining possible interactions between culturally transmitted practices and specific genes that have undergone rapid and recent selection. This is a complex, interdisciplinary task, often requiring geneticists, psychologists, archaeologists, anthropologists, demographers, mathematicians and computer scientists. Cross-population studies are required to identify signatures of genetic selection, and often, complex gene functions need to be established. Meanwhile archaeological and anthropological data are needed to infer rates of cultural change based on particular patterns of cultural transmission, cognitive biases and demographic change. Mathematical models and computer simulation studies can then re-derive the most likely patterns of genetic and cultural evolution, testing for interactions that suggest gene-culture coevolution.

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See also Human Behavioral Ecology, Sociobiology

FURTHER READINGS

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