

# The Evolution of Cultural Diversity

## A Phylogenetic Approach

Edited by  
Ruth Mace,  
Clare J Holden &  
Stephen Shennan



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# **THE EVOLUTION OF CULTURAL DIVERSITY**

## PREFACE

This book arose proximally out of a session at the Human Behaviour and Evolution Society annual meeting that was held at University College London in 2001. Present at that session were a number of us that were interested in applying phylogenetic methods to understanding cultural diversification, be it in languages, material artefacts or behavioural and bio-cultural traits. For all of us, our interest had arisen some time earlier. In my case, I trained as an evolutionary ecologist working in zoology, then moved into human behavioural ecology; I first wrote about applying phylogenetic comparative methods to cultural evolution soon after I had joined the Department of Anthropology at University College London, when I co-authored a paper with Mark Pagel in 1994 (who at that time was at the Department of Anthropology at Harvard). Clare Holden joined me as a PhD student not long after that and has worked on phylogenetic approaches to linguistic and cultural evolution at UCL ever since. Meanwhile, Stephen Shennan, at the Institute of Archaeology at UCL, had a longstanding interest in evolutionary archaeology, and in 1999 began working on formal phylogenetic approaches to material culture with Mark Collard (in Anthropology at UCL). Archaeology and Anthropology at UCL and Archaeology at Southampton jointly put forward a successful bid to set up the AHRB Centre for the Evolutionary Analysis of Cultural Behaviour, which was up and running by 2000. Most of the contributors to this book have been members of or visitors to the CEACB at some time. We thank all the members of the Centre for their discussions of many of these papers at seminars. And we are grateful to the UK Arts and Humanities Research Board, the Wellcome Trust and the Leverhulme Trust for the funding which has made much of this work possible. This book covers our range of interests in cultural phylogenies and comparative methods to date, and includes much of the pioneering work in this field. But the field is moving forward and growing all the time – hopefully an indication of the value of this approach to understanding the evolution of human cultural diversity.

*Ruth Mace*  
*London, UK*  
2005

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# INTRODUCTION: A PHYLOGENETIC APPROACH TO THE EVOLUTION OF CULTURAL DIVERSITY

*Ruth Mace*

Humans are a young species, showing surprisingly little genetic variation; we are capable of interbreeding across our entire range. Attempts to divide humanity into discrete groups on the basis of our genes are not very successful; some genetic elements may be more common in some regions of the world than others, but different genes follow different geographical patterns. For example, contours of similarity in blood protein polymorphisms tend to lie north-south, whereas contours of similarity in skin colour lie east-west, parallel to the equator (Boyd and Silk 2003).

Yet cultural diversity in humans is very great. Maps of language or ethnicity largely divide the world into discrete ethno-linguistic groups. As a broad generalisation, cultural diversity within these groups is much less than between them, not just in language but across a range of cultural traits. On the basis of relatively few pieces of key information on language, dialect and customs, you could probably identify the origins of most human beings to within a few hundred miles. Cultural diversity, at least until recently, appears to have been rather more strongly spatially structured than its genetic counterpart.

Much of this cultural diversity is useful. Humans colonised almost every habitat on earth, because they were using a wide range of foraging systems and technologies to survive. Individuals from one part of the world would have great difficulty surviving in a foreign land, with a different ecology. The genetic make-up of an immigrant may not, for example, offer enough protection from the sun, or from local diseases. But if this new immigrant did not have helpers with local knowledge to support him, it is highly likely that he would meet his death either from starvation or from intraspecific violence long before his genetic shortcomings became significant. Human adaptation is about culture as much as it is about genes. And it is the evolution of cultural diversity that is the secret of our species' success.

This book is about the study of cultural diversity from an evolutionary perspective. Our focus is specifically to explore the phylogenetic approach to cultural evolution. Phylogenies (or trees) typically describe the descendent relationships between species; yet here we use them to describe variation – in this case cultural variation – within one species. In this introductory chapter, I shall describe why cultural diversity and genetic diversity have some similarities but also some differences, and why it is that models originally devised to explore diversity across species might actually work well when applied to evolutionary studies of human cultural diversity.

## NEUTRAL AND ADAPTIVE CHANGE IN HUMAN CULTURES

Evolution in biological systems means descent with modification. It is genes that are inherited, and mutations that generate the diversity within species which can ultimately lead to speciation. The longer two populations have been separated, the greater the genetic differences between them. Drift, selection or both underpin most of this genetic divergence.

Similar gene sequences found in nearby populations are typically taken as evidence of shared ancestry. The amount of genetic code that is shared can inform us as to whether two populations were recently or only very distantly in contact with each other, or were historically one population. Human populations are no different from animal populations in this respect. As the science of gene sequencing has advanced over the last two decades, new genetic studies of human population history have mushroomed. Such studies like to focus on genetic elements that are unlikely to be subject to strong selection. It is in neutral traits, which drift, that change is more strongly related to the length of time that two populations have been separated, and thus these traits are the most informative about the historical relationships between populations. Genetic code that is not subject to strong selection may be carried along in migrating groups – thus our DNA leaves traces of our evolutionary history and past migrations. Genetic elements that don't mix with other elements through recombination are particularly informative; hence the emphasis on Y chromosomes and mitochondrial DNA in genetic studies of human population history.

But an understanding of the origins of any particular human population is not usually gained from genes alone (Cavalli-Sforza *et al* 1994). Long before genetic data were even available, archaeologists and linguists used data on cultural similarities and differences to examine the historical relationships between human groups. The comparison of languages has underpinned the classification of human cultures. The parallels between genetic and linguistic evolution are clear. Languages pass from one generation to the next with only slight modification. As populations separate in space and time, their languages diverge. Linguists search for cognate (or related) words in different languages to infer their common origin. When dealing with diversity in other cultural traits, such as material artefacts, the parallels with genetics are not as clear as they are in language; but cultural traits can also be inherited, and archaeologists frequently use artefacts such as pottery to infer historical relationships between groups. Much of this cultural diversification is in neutral traits, that is, traits that do not confer any particular advantage. For example, one linguistic term may be as good as any other at conveying meaning. This is why language is turning out to be so useful for studying human population history.

But many cultural traits do confer specific fitness advantages and these will be subject to selection. Evolution by natural selection refers to the differential survival of certain forms due to their ability to out-live or out-reproduce others. Some of the similarities between populations are attributable not to common ancestry, but to evolution by natural selection. Similar phenotypes may emerge in unrelated populations because individuals in those populations are experiencing

similar selective pressures. This could be true whether the phenotype was genetic or cultural (Boyd and Richerson 1985). Selection on useful cultural variants will lead to cultural adaptation.

Cultural innovations can contribute greatly to the success, or otherwise, not only of individuals but also of the populations in which they arose. The ideas that underpin such innovations, or indeed any cultural behaviour, have been variously referred to in the literature as memes (Dawkins 1976), culturgens (Lumsden and Wilson 1981) and semes (Hewlett *et al* 2002), and these terms can refer to very individual beliefs or culture-wide norms. The notion that culture can evolve in a Darwinian way has been somewhat hampered by long debates about what culture is (Are there faithfully replicating cultural units? How can they be defined?). But, as Mesoudi *et al* (2004) point out, Darwin did not know the answer to any of these questions when he put forward his theory of evolution by natural selection, because genes were unknown at that time. These questions of definition are not essential to making the case for an evolutionary process of cultural adaptation.

Whether or not cultural traits can be easily defined, the evidence that human culture can evolve through the differential adoption of cultural variants in a Darwinian manner is everywhere. Sometimes cultural technological advances fuelled the dispersal of whole cultural groups over continents. It can be difficult to distinguish whether an idea spread through the minds of indigenous populations who adopted the innovation, or whether the source population simply gained so much from the innovation that it out-reproduced indigenous groups and replaced them, although both scenarios represent an essentially Darwinian process leading to cultural adaptation. The latter scenario was proposed by Ammerman and Cavalli-Sforza (1984) to explain the Neolithic spread of farming from the Near East across Europe, in the form of a 'wave of advance' of expanding population taking Indo-European languages with them. Some studies of European Y chromosome diversity estimate that only about 20% of the patriline in Europe originate from the Near Eastern farmers, lending support to the theory that farming, and the Indo-European languages spoken by the earliest farmers, were adopted by the local populations (Semino *et al* 2000). However, such estimates of the relationship between the present-day genetic composition of the population of a region and the relative sizes of immigrant and indigenous populations several thousand years ago that they imply rely on the statistical model used. Other models that allow for admixture with local populations actually come to the very different conclusion that the majority of European Y chromosomes arrived due to the population expansion of the Near Eastern farmers (Chikhi *et al* 2002), supporting something much closer to Ammerman and Cavalli-Sforza's original hypothesis. A further complication is that studies of Y chromosome haplotypes actually only tell us about the origin of males, and female migration patterns could have been rather different (Seielstad *et al* 1998). But whichever view is correct, few would doubt that farming fuelled the expansion of a population of ultimately Near Eastern origin into Europe; or, in another example, led the West African Bantu to dominate most of the African continent south of the Sahara. The success of these populations depended on a cultural innovation that opened up a new niche and fuelled the reproductive success of individuals and ethnic groups alike.

WHAT CAN CULTURE DO THAT GENES CANNOT?

Our capacity for culture, which we define here simply as socially transmitted information, clearly separates us from other species. Some obvious examples of things that only humans do well are language, the creation of cultural artefacts and the creation of complex political structures. Some species can do one of these tricks, usually in a simple way, but only humans do all of them, do them all the time, and do them with increasing levels of sophistication through our evolutionary history. We assume that our high levels of intelligence and self-awareness underlie all these phenomena, and many more.

I have discussed some of the similarities between genetic and cultural evolution above: genes and cultural traits replicate; they both evolve by descent with modification; and both are subject to selective forces and to drift, which cause genetic and/or cultural change and adaptation (Pagel and Mace 2004; Mesoudi *et al* 2004). But there are also differences: culture is not inherited in a Mendelian way (we can have numerous cultural parents), we can change our cultural phenotype during our lives, and thus cultural evolution can be very fast (Table 1.1). Social anthropologists and evolutionary anthropologists frequently disagree about the relevance of cultural versus evolutionary processes in shaping human social behaviour. This is something of a false dichotomy, as culture is also clearly subject to evolution, as I have just described. There is no need to choose between genes and culture as opposing forces in the formation of human societies – both matter. Genes and culture have influenced each other’s evolution so profoundly in human evolution that cultural diversity in our species has to be understood as the product of both genetic and cultural evolutionary processes. But it is nonetheless worth considering which behaviours could evolve simply through selection acting on genes and which might be the result of some form of gene-culture co-evolutionary process.

Table 1.1 Differences between genes and memes (*sensu* Dawkins 1976).

Unit of replication	Gene	Meme
Method of replication	Reproduction	Teach an idea to another individual
Direction of inheritance	Parent to offspring	Parent to offspring or vertical/horizontal transmission to related/unrelated individuals
Pattern of inheritance	Mendelian	Biased (preferential adoption from certain individuals)

Kin selection and reciprocal altruism are the two main evolutionary explanations of social behaviour, be it in animals or humans. A huge body of literature attests to

how these evolutionary forces explain so much of what we do, particularly in areas of reproductive and parental behaviour (Hrdy 2000). But even in this domain, some of the things humans do, like limit our fertility even when we are wealthy, present something of a challenge to the adaptationist view. It is particularly in the area of communal, social behaviour that the well-understood evolutionary forces of kin selection and reciprocal altruism may not be enough to explain all that we do (Richerson and Boyd 1999). A particular puzzle is the apparent altruism, or at least high level co-operation, that humans sometimes exhibit towards those beyond the bounds of their immediate family. Some actions may be at a cost to their own reproductive success. Due to the asymmetries between genetic and cultural transmission and inheritance, cultural evolution may be able to generate some forms of behaviour that natural selection on genes alone would never produce.

Humans like to do things in groups. They organise their domestic daily lives in small family groups, but also consider themselves to be part of a much wider group, possibly including hundreds, thousands or even more other individuals. In pre-state or tribal societies, affinity is sometimes organised around lineages, where an individual's group identity is traced through either their mother (matrilineal identity) or their father (patrilineal identity). Anthropologists have noted that individuals will often identify themselves more closely with a member of their lineage than with an equally genetically related individual in another lineage. For example, a cousin who is your mother's brother's son could be equally or more closely related to you than a cousin who is your father's brother's son, but one is ingroup and the other is outgroup, and could possibly be considered a competitor or enemy. These larger groupings, be they a lineage or clan or even the entire ethno-linguistic group, usually share a moral or behavioural code; indeed the group may be defined by such shared norms. Frequently they inhabit the same ecological niche and occasionally call on individuals to act as a group – particularly fighting in wars against other such groups.

Economists have recently become interested in observations of unexpected altruistic acts amongst players in economic games (Fehr and Gächter 2002). Players seem ready to share payoffs with other players in the group, even if their identity is not revealed so that it is impossible to gain status from such acts. They are willing to punish players who refuse to contribute to some wider group scheme, even if that punishment is itself costly and does not generate any immediate return. This is suggestive of some innate sense of fairness, and a desire to enforce social norms of behaviour, sometimes also referred to as 'strong reciprocity' (Gintis 2000; Fehr *et al* 2002). Economic games have also been played amongst pre-industrial populations, where high levels of apparently 'irrational' altruism are sometimes found, although it is notable that the levels of altruism observed in the games vary according to the level and sometimes the nature of co-operative activity that is generally observed in that particular culture (Henrich *et al* 2001). The altruism does have an ecological context.

Such observations pose interesting challenges to our understanding of evolutionary processes. Evolutionary biologists have been clear since the 1960s

that selection basically operates at the level of the individual or gene – not the group (Williams 1966; Dawkins 1976). Migration of individuals between groups destroys the integrity of groups; genes replicate so much faster than groups that selective pressures favouring the individual or the gene will always out-compete the forces of group selection. Genetic group selection is so slow that it never gets off the ground. Thus individually costly behaviour that is beneficial to the group is hard to explain by natural selection on genes.

As groups grow in size, the forces of kin selection and reciprocal altruism are quickly diluted. The maintenance of co-operation in large groups requires more. Many authors are now arguing that forms of group selection may be operating at a cultural level (Wilson and Sober 1994; Gintis 2000; Fehr and Fischbacher 2003; Boyd *et al* 2003). Group selection may be something that culture can do that genes cannot. The kinds of cultural group selection being proposed bear little relation to the old genetic group selection, to the extent that it may not be helpful to use the term, but a variety of models have been developed in which human co-operation can emerge in ways that may confer an advantage to the group as a whole.

If group level behaviour is more efficient in one cultural group than in another, one group may out-reproduce the other (Wilson and Sober 1994; Richerson and Boyd 1999). In the domain of warfare, clearly the more efficient group could exterminate the other, as in the well-known case of the Nuer, whose patrilineal, hierarchical social structure is thought to have facilitated their ability to call large numbers of warriors into a co-ordinated army that defeated the Dinka (Kelly 1985). When a group is defeated it may cease to exist, although surviving individuals from within it may hastily integrate themselves into the winning culture. In New Guinea, ethnographies suggest that clan extinction might be occurring with a median of 10% of clans becoming extinct every 25 years (Soltis *et al* 1995). Women or other prisoners are frequently taken as trophies of war, or are even the main object of warfare in the first place. If they marry into the victorious culture, again, the cultural integrity of the winning group can be maintained even when their genes are mixing with those of other groups.

Conformist traditions might help to maintain differences between groups. If individuals migrate into a new group, they will often have to change their cultural behaviour in order to survive. This is again something that is very important when considering cultural diversity, but not necessarily so when considering genetic diversity – genes probably do not show much ‘conformist tradition’ (with the possible exception of genes for physical appearance, Diamond 1991). Language is an obvious example of something that requires conformity – neither you nor your children are likely to succeed if you continue to speak your native language after migration into a new ethno-linguistic group. Maintaining independent procedures, be they marriage practices, food sharing rules, religious rituals or almost anything else, is likely to be a risky strategy. Integration into a new culture may cause your genes to cross into a new group, but your cultural traditions may have to be left behind. We may also have evolved behavioural mechanisms for ensuring that groups remain somewhat distinct. Theoretical models have been developed in which ethnic psychology, and ethnic markers, can evolve by gene-culture co-evolution (McElreath *et al* 2003). If interactions with

those sharing your social norms are more efficient than interactions with people with different norms, then interacting with a group member becomes a matter not of altruism but of mutual benefit, which is much more evolutionarily stable in groups. McElreath *et al* argue that ethnic markers and ethnic psychology facilitate this, and will be favoured by selection, especially at the boundaries of groups where costly interactions with those with different norms are more likely to occur.

Punishment appears to be a powerful force for maintaining group-level codes and rules, that can lead to the evolution of efficient social systems (Boyd and Richerson 1992; Boyd *et al* 2003). Boyd *et al* (2003) argue that altruistic punishment (the enforcement of rules even at some small cost to the enforcer) can lead to the evolution of co-operation in groups of up to around 600 individuals; this is as large as the typical ethno-linguistic groups that dominated the landscape prior to the great population expansions that accompanied the adoption of agriculture. These models assume some level of cultural group selection. They are less sensitive to migration between groups than genetic models would be, but nonetheless, levels of inter-group mixing do still have to be low for group-level co-operation to evolve.

Whatever the most important mechanisms are, it seems that our capacity for culture has contributed to our need to divide ourselves up into ethno-linguistic groups. How fluid or long-lasting such cultural groups were in the past is a matter of debate. Some archaeologists and anthropologists go so far as to resist the notion that pattern and structure can be found underlying the mass of cultural diversity we see around us. But we will argue that these groups are fundamental to our analyses of cultural diversity. We present in this book evidence from both linguistic and other cultural data that these groups evolve by descent with modification – always changing but leaving a record of their history that can be empirically examined. When cultural groups are evolving in a hierarchical fashion, then it is appropriate to apply a phylogenetic perspective to understand the cultural evolutionary process.

## A PHYLOGENETIC PERSPECTIVE ON CULTURAL EVOLUTION

The diversification of cultures has several parallels with speciation. Speciation occurs due to either physical barriers to gene flow or natural selection against hybrids between individual inhabiting different niches. It is very likely that processes similar to both of these scenarios also drive linguistic and cultural diversification (Pagel and Mace 2004).

Environmental features which typically promote speciation by impeding gene flow (like mountain ranges) also act as barriers to linguistic communication (Barbujani and Sokal 1991). Similarly, language difference can itself reduce gene flow, so once groups begin to diverge, the process of ethnic differentiation is enhanced by language barriers (Sokal *et al* 1988; Sokal *et al* 1993). At this point, the emergence of ethnic psychology, discussed above, could come into play.

There is plenty of evidence that the diversification of ethno-linguistic groups has an ecological component. There is a striking correspondence between



biological and cultural diversity (Mace and Pagel 1995; Maffi 2001; Moore *et al* 2002). For example, species often show a latitudinal gradient with diversity declining from the equator to the poles, as do language groups in North America (Mace and Pagel 1995) and Africa (Moore *et al* 2002). This suggests that the productivity of the land, which influences the range size over which a group needs to forage, influences not only population density but also linguistic density. Smith (2001) finds, albeit on a small sample, that Native American cultural groups are more diverse where the natural resources on which they depend are more dense and localised.

Correspondence between biodiversity and ethno-linguistic diversity may emerge, due not only to similarities in the processes that generate diversity but also to similarities in the processes that destroy it. Linguistic diversity was probably highest over 10,000 years ago when humanity was characterised by small, tribal groupings of foragers. If such groups face competition from groups with more advanced technologies, such as farmers, then not only group extinction but also linguistic and cultural shifts in favour of the cultures based on the new technology will occur. Whilst the hybridising of cultures is theoretically possible, elite dominance (the extinction of the cultural characteristics of the less successful group in favour of those associated with the more powerful group) is probably much more common (Renfrew 1987). Batibo (2001) describes the process as it is occurring in modern day Botswana, although not dissimilar forces probably operated even in the Neolithic. Surviving individuals from minority cultures are keen to associate themselves with the new technologies, educating themselves and their children in the languages of the economically more successful groups, and, when intermarriage occurs across cultures, children speak the language of the dominant culture. The same processes that fuel economic success deplete natural resources on which the minority cultures were based, and the knowledge of how to survive on or even describe the ecological resources which those groups used to depend on is lost.

Estimates of the total number of languages that have ever existed throughout our species' existence start at around 100,000 but could be many more (Pagel 2000b). This compares with about 6,000 languages that we know about today. The remainder are most likely to have been trampled into the mud of ethnic conflict and competition throughout our evolutionary past. As a small number of cultural groups have achieved economic and political domination in the modern era, the extinction of species, languages and cultures proceeds at an unprecedented pace.

As culture evolves by descent with modification, cultural groups give rise to daughter cultures. Cultures are hierarchically related, in a way that is similar to hierarchy in species. There are many cases where phylogenies based on language similarity support what we know about the history of the peoples of that region: in particular, phylogenetic trees of language groups from the Pacific (Gray and Jordan 2002a), the Bantu in sub-Saharan Africa (Holden 2002) and the Indo-Europeans (Gray and Atkinson 2003). The culturally neutral trait of language appears to be a very good tool for estimating historical relationships between groups. These population expansions were recent in evolutionary terms, which may be why the phylogenetic signals are so clear in these groups. However, there



are likely to have been hundreds or even hundreds of thousands of such trees hidden in human history. As migration overlays migration, and cultures go extinct, we may find it impossible to place some of the extant ethno-linguistic groups and prehistoric cultures that we observe within a particular family of closely related cultures. But it might well have been possible to do so had we had enough data on extinct cultures and their prehistoric migrations.

Language is not the only cultural trait to show evidence of vertical descent. Guglielmino *et al* (1995) find that traits associated with kinship and subsistence are very likely to be transmitted vertically down the populations, as do Holden and Mace (1999). Clearly, having used culture to adapt and reproduce successfully, this information, possibly along with the necessary physical resources (like cattle or land), is passed on to descendants.

This is not to say that individual cultural traits do not move between cultures through copying or some other means. Further, the existence of trees isn't necessarily incompatible with borrowing. If you imagine an innovation, or linked package of innovations, spreading from a centre and being adopted locally, then it may well undergo localised innovation at various points as it spreads, thus generating a tree-like structure for those particular traits.

## **The contents of this book**

In this book, we take a phylogenetic perspective on cultural evolution – in Part I we test the assumption of the phylogenetic model for cultural diversification, and in Part II we then apply this phylogenetic model to the study of cultural adaptation.

Papers in the first Part of the volume address the question of the extent to which different traits are related across different cultures by vertical descent or by borrowing. If vertical descent is important, then phylogenetic signals will emerge from the data. Whilst both processes are clearly occurring, various authors find strong phylogenetic signals across a range of cultural data, including languages and archaeological artefacts. The theory underpinning the search for phylogenetic signal, and a summary of the results obtained in the case studies in this book, are reviewed by Holden and Shennan in the Introduction to Part I.

If we assume that cultural diversification is tree-like, rather like speciation, then we need to take that into account when trying to work out which traits are co-evolving with others. If a cultural trait is adopted many times in the branches of the phylogenetic tree, and this happens repeatedly in the presence of some particular feature of the environment, or some other particular cultural trait, then the evidence that these two traits are co-evolving can be evaluated. The chapters in Part II of the book address this issue, using phylogenetic comparative methods originally developed to explore adaptive, co-evolutionary hypothesis in biology. Spurious correlations between traits can emerge simply due to shared ancestry (Harvey and Pagel 1991). But phylogenetic methods allow us to untangle these effects, and test precise, adaptive hypotheses about cultural or bio-cultural evolution (Mace and Pagel 1994). The rationale for these methods, a reply to many