The Evolution of Cultural Diversity

A Phylogenetic Approach

edited by
RUTH MACE, CLARE J. HOLDEN & STEPHEN SHENNAN

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Ruth Mace, Clare J Holden and Stephen Shennan

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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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CHAPTER 1

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 patrilines 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 Gachter 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

of the most common misunderstandings, and a summary of the findings from the three case studies can be found in the Introduction to Part II.

The study of cultural evolution tends to be dominated by theoretical models, many of which are hard to test empirically. In this book, all the studies included here contain data on cultural diversity. We include case studies from most continents, examining diversity in languages, material artefacts and other cultural and bio-cultural traits. We find that the vertical transmission of aspects of culture between hierarchically related groups abounds, and we should not be surprised. Just because culture can pass horizontally between neighbours, that is no reason to imply that that is all it can do. If we believe in cultural adaptation, then surely parents will pass on this important cultural information to their offspring. As offspring look to their parents as their primary source of information for learning how to live, then vertical transmission will prevail, for useful and neutral traits alike.

If the phylogenetic model is a good model for cultural diversification, then we can apply many of the powerful, statistical methods developed in evolutionary biology to investigate the cultural evolutionary process. A phylogenetic perspective allows us to ask a whole range of sophisticated questions: what are the ancestral states, how fast do traits evolve, and are they co-evolving with each other? We do not need to merely speculate how quickly one culture evolves into another, or how much of their cultural traditions were passed down from mother cultures or borrowed from other groups – we can attempt to estimate all these things empirically. If vertical transmission is common, then horizontal transmission becomes interesting; we can examine the conditions under which people in one culture decide to borrow the cultural inventions of another, which can sometimes provide strong evidence for the adaptive value of that particular cultural trait. That is all good news. The bad news is that we may need to rethink some of our previous analyses of cultural evolution, just as evolutionary biologists then had to, and revise them in the light of more sophisticated, phylogenetic analyses. But complexity cannot be used as an excuse for failing to come to any conclusions, as it so often is in anthropology. It is now time to take the powerful tool kit of evolutionary ecology to examine the evolution of human cultural diversity.

PART I

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CHAPTER 2

INTRODUCTION TO PART I
HOW TREE-LIKE IS CULTURAL EVOLUTION?

Clare J Holden and Stephen Shennan

In recent years, much debate has focused on the extent to which group-level cultural entities such as languages, ethno-linguistic groups and archaeological traditions, evolve by a process of branching and divergence, analogous to the evolution of species. A related question is how far individual cultural traits are transmitted from older to younger generations within a population, and how far they are transmitted by diffusion between neighbouring populations. Insofar as cultural and genetic transmission are similar processes, we can use phylogenetic methods, a powerful set of analytical techniques from evolutionary biology, to test hypotheses about cultural evolution (Gray and Jordan 2000a; Holden 2002; Holden and Mace 2003). However, phylogenetic models of population or culture history have been criticised, as neighbouring groups exchange cultural elements, leading to convergence or even fusion among them (Bateman *et al* 1990; Moore 1994b). Phylogenetic trees cannot represent such complex interrelationships among groups. Networks could provide an alternative model, allowing us to represent inter-group exchanges by reticulations (fusion) among branches (Bryant *et al* Chapter 5, this book; Forster and Toth 2003). Or perhaps cultural traits are not transmitted within populations at all. Instead, perhaps, geography rather than population history explains the patterns of cultural variation that we observe across the world. If an individual cultural trait has spread by diffusion, it may still have evolved by a branching process, but the phylogeny of that cultural trait will not reflect the history of the populations within which it is found.

In the first Part of this book we present a range of case studies, aiming to address these questions empirically, using a variety of cultural datasets from Europe, Asia, the Pacific, Africa and Native America. Results show that group-level cultural entities including languages are related in a largely tree-like way, and that individual cultural traits are mainly inherited within ethno-linguistic groups, although some cultural exchange between neighbouring groups is also found. Predominantly inherited cultural traits include languages belonging to the Indo-European, Austronesian and Bantu groups (Bryant *et al* Chapter 5; Greenhill and Gray Chapter 3; Holden *et al* Chapter 4), and one material culture tradition, Turkmen carpet designs (Collard and Tehrani Chapter 7). Artefacts from coastal Papua New Guinea show a mixture of inherited and diffused transmission (Shennan and Collard Chapter 8). Native Californian basketry designs appear to show a different pattern, being transmitted predominantly by diffusion between, rather than inheritance within, populations (Jordan and Shennan Chapter 9).

UNITS OF CULTURAL TRANSMISSION

The case studies in this book investigate cultural evolutionary processes at two different levels: first, at the level of individual cultural traits, for example word forms, decorative motifs, and aspects of social organisation such as a particular descent rule; and second, at the level of cultural groups or populations. In Part I, at the level of cultural groups we address the broad shape of cultural history, namely how such groups are related. At the trait level, we investigate the central question of how far individual cultural traits are transmitted within cultural groups, and how far they are transmitted independently of, or between, such groups.

Cultural traits

Attributes or elements of culture (eg, a cultural behaviour, practice or belief) that we are willing to define for some analytical purpose will be referred to here simply as cultural traits. Definition generally involves some kind of categorisation process, whether of descent rules, pottery decoration motifs or anything else. These categorisation processes operate at two levels: the definition of the trait or attribute itself, for example 'descent rule' or 'basketry manufacture technique', and that of the various possible states or values that the trait can take: for example, descent could be 'matrilineal' or 'patrilineal', or basketry designs could be 'twined' as opposed to 'coiled'. The definition of a cultural trait is similar to the definition of a trait or character in biology; while the values that a particular cultural trait can take are analogous to character states in biology. Character states may show discrete or continuous variation. Most case studies in this book deal with discrete character states (eg, 'twined' versus 'coiled' basketry designs), but Mace and Jordan (Chapter 11) analyse cross-cultural variation in sex ratios, a continuous variable. At both levels there may be scope for argument about definitions. At the trait level, for example, we may debate the definition of 'pastoralist', for instance where we draw the line between pastoralism and agro-pastoralism. However, we can usually arrive at a useful definition of a trait for analytical purposes; Holden and Mace (Chapter 12), for instance, use the presence or absence of cattle to define pastoralism. At the trait or attribute state level there may be discussion about how to define, for example, the differences between different pottery decoration motifs. However, these definitional issues have in no way stopped anthropologists or archaeologists over the last 150 years from identifying traits and their values and attempting to explain their distributions in time and space. If a particular trait state is found in a number of places within a specific region over a certain time period, this is either because it has been independently invented a number of times here, or more likely because, after the initial invention, the information required to reproduce it has been passed on from one person to another through some form of cultural transmission. If a cultural trait occurs repeatedly in a particular type of environment, whether it has been independently invented or adopted by imitation, this may be evidence for cultural adaptation. For example, pastoralism is found across the world in

environments that are too arid or cold for agriculture. Cultural adaptation is discussed further in Part II of this book.

Cultural traits can be transmitted vertically (from parent to child or from the older to the younger generation within one population) or horizontally (between unrelated individuals, or between neighbouring populations) (Cavalli-Sforza and Feldman 1981). Vertical transmission of cultural traits has many similarities to the transmission of genetic traits in biological reproduction. Horizontal transmission is analogous to lateral gene transfer, whose importance in biology is increasingly recognised (Boucher *et al* 2003; Woese 1998). As well as being transmitted from a parent to a child, cultural traits can also be transferred from one person to many, for example from a teacher to pupils, or from many people to one, for example from the elders of a group to an initiate. This has consequences for the conservativeness of the cultural trait. Whereas one-to-many transmission introduces the possibility of rapid cultural change, many-to-one transmission can lead to extreme cultural conservatism (Cavalli-Sforza and Feldman 1981).

Larger scale cultural entities

Human populations are also structured into larger scale cultural entities of various types, such as ethnic groups, speech communities (groups of individuals speaking the same language) and villages. Mace (Chapter 1) discusses possible underlying causes of such groupings in more detail. Archaeologists can often identify distinct traditions in material culture too, although the relationship between archaeological traditions and other types of cultural entity such as ethno-linguistic groups may not be known. To identify ethnic groups, self-identification and language are probably the cultural markers most widely used by anthropologists. The term 'ethno-linguistic group' (Jordan and Shennan Chapter 9) reflects this. (We may note in passing that many geneticists also use language to define cultural or ethnic groups when investigating human population history, eg, Cavalli-Sforza *et al* 1994.) For all these types of cultural entities (cultures, languages, archaeological traditions, etc) a significant proportion of variation occurs between groups, and there is significant within-group similarity.

Phylogenetic methods were developed to analyse relationships among biological taxa, such as species, that are reproductively isolated and hierarchically related. To apply phylogenetic models to languages, ethno-linguistic groups and archaeological traditions, such groups must also be distinct, at least partially bounded entities, which are related primarily by descent. The extent to which cultural groups are discrete entities, and how far they are related by branching alone (without merging between neighbouring groups), is highly controversial. Cultural boundaries are considered to be much more permeable than species boundaries. By definition, species are reproductively isolated, gene flow and hybridisation being treated as exceptional (Mayr 1963). In contrast, individuals and cultural traits frequently transfer between cultural groups. If there is a high level of exchange among cultural groups, this might be better represented by a network that includes fusion (reticulation) among populations (branches), rather than simply fission, as on a tree (Bateman *et al* 1990; Moore 1994b). These questions

need to be addressed empirically, as the case studies in this book do, asking how bounded cultural groups are, and how much exchange between groups occurs. Another related question is how far different cultural lineages coincide – for example, are material culture traditions transmitted along with languages, so that the histories of different cultural traits overlap?

A number of the authors in this volume make use of the distinctions made by Boyd *et al* (1997) regarding this issue. They proposed four possible structures for the organisation of culture, and for the transmission of cultural traits. (a) One extreme possibility is that cultures are tightly bounded and hermetically sealed from one another. Boyd *et al* dismissed this model, as there is consistent evidence for the diffusion of information between cultural groups. (b) The second possibility is that cultures have core elements that are transmitted intact, but peripheral elements are diffused between cultures. Cultural cores may remain intact because they are particularly meaningful, or because they relate to behaviour that forms an evolutionarily stable strategy (ESS) that is not easily invaded. Another reason why cultural cores may persist, not discussed by Boyd *et al*, is that they comprise cultural traits that are transmitted in a conservative way, for example, learnt during infancy and subject to conformist pressures. (c) The third possibility is that cultural traits are transmitted in 'packages' that are relatively independent of one another, thus different packages may have different histories. (d) At the opposite extreme from the first, a fourth possibility is that there is no coherence among the cultural traits and that individual traits are too short-lived for it to be to possible to trace phylogenies through time, either because elements recombine very frequently or because rates of change in response to adaptively new situations are very fast so that cultural traditions of any kind are largely non-existent. This also seems unlikely in view of the persistence of languages and of cultural traditions seen in the archaeological record. In summary, there are two plausible models for the structure of cultural groups and cultural transmission: cultural cores and cultural packages. Most authors in this book would probably accept one or both of these positions as working hypotheses.

The structure and transmission of languages has been far better studied than other types of cultural entities such as archaeological traditions. Languages seem to conform to the cultural core model, the core consisting of basic vocabulary and other linguistic elements that are transmitted very conservatively, but with higher levels of borrowing in other areas of the language (Bryant *et al* Chapter 5; McMahon and McMahon 2003; Ringe *et al* 2002). Basic vocabulary includes culturally neutral meanings that are present in all languages, including the lower order numerals ('one' and 'two'), body parts ('tongue') and other ubiquitous items such as 'ashes', 'louse', 'man' and 'woman'. We should note that linguistic cores are conserved as a result of transmission mechanisms for those parts of language (for example, being learnt during infancy), rather than any adaptive advantage of particular word forms. A level of homogeneity within speech communities is probably maintained by the pressure to remain mutually intelligible (Jean 1971).

The origin of a language is detectable in the more conservative aspects of language, which are normally inherited within speech communities (presumably passed down mainly from parents to children). The more heritable aspects of language include grammatical features and the basic vocabulary. When a speech community divides, the language spoken in the resulting two communities diverges over time. Languages thus diversify by a branching process, leading to hierarchical relationships among related languages. Historical linguists often represent linguistic relationships using a tree model. However, linguistic divergence is only part of the story. Neighbouring languages can also converge over time as words and other linguistic elements are borrowed. Linguistic borrowing is analogous to gene flow among biological populations (see Table 13.1). In an extreme case, this may lead in time to the development of a linguistic area or *Sprachbund* in which languages share structural features as a result of convergence rather than common origin. This is seen in the Balkans among Greek, Albanian, Bulgarian, Macedonian and Romanian (and possibly also Romani and Turkish), and on the Indian sub-continent among unrelated languages from the Dravidian, Munda, Tibeto-Burman and Indo-Iranian language groups (Campbell 1998a: 299–310). But we should not forget that within a linguistic area, the origin of languages is visible in the more heritable aspects of those languages, including the basic vocabulary and grammar. Therefore, despite the existence of linguistic borrowing, a tree can summarise descent relationships among languages in respect to their core vocabulary and grammar.

Language trees also reflect broader population history insofar as when speech communities divide, the two new populations diverge linguistically. Linguistic and genetic trees are often similar, both reflecting the same underlying population history (Barbujani 1991; Cavalli-Sforza *et al* 1988; Cavalli-Sforza *et al* 1992; Penny *et al* 1993). Language trees have often therefore been used as models of population history (Guglielmino *et al* 1995; Holden and Mace 1997; Holden and Mace 1999; Holden and Mace Chapter 12; Holden and Mace 2003; Jordan and Shennan Chapter 9). Although not every ethnic group speaks a unique language – many individuals may be bilingual, and some languages are very widespread due to elite dominance – most societies do speak their own language. Moreover, many ethnic groups use the same name to refer to their group and their language, making it relatively easy to match anthropological and linguistic records.

An important question is whether material culture lineages follow the same transmission pathways as language, producing a broad cultural and linguistic core arguably reflecting population history. If material culture lineages are closely correlated with linguistic transmission, this suggests that that aspect of material culture is predominantly transmitted within cultures. Authors in this volume have approached this question by constructing trees of artefacts and comparing them to linguistic trees (Jordan and Shennan Chapter 9; Shennan and Collard Chapter 8). In the terms of Boyd *et al* (1997) these studies investigate whether we are dealing with cores or multiple packages. Jordan and Shennan (Chapter 9) group their Californian basketry attributes according to the ethno-linguistic group of their owners, using language to define these groups. Shennan and Collard (Chapter 8) also group their data by language group (Austronesian versus non-Austronesian) as well as village. In the study of Turkmen carpets by Collard

and Tehrani (Chapter 7), one language is spoken by all groups in the sample. These authors group carpets by tribal group, and compare the carpet tree to a tree based on ethno-history.

Obviously this cannot be done for prehistoric artefacts because we do not know what languages those populations spoke. When working with prehistoric material, one option is to take the assemblages from specific archaeological sites as the entities for analysis and build trees on the basis of the variation between these assemblages. This was done by Collard and Shennan (2000) in their study of the early Neolithic pottery assemblages from a series of sites in the Merzbach valley in Germany. It is essentially identical in procedure to the trees built by Jordan and Shennan (Chapter 9; 2003) using basketry attributes, which take ethno-linguistic groups as the entities. Even if there are no language trees available for comparison in the prehistoric situation, information on spatial distance between sites is always available and can be used as a comparative basis. O'Brien and colleagues, on the other hand, use a different approach, which involves defining classes of artefacts as the first stage. Thus, in their study of Paleoindian projectile points from the south eastern USA (O'Brien *et al* 2001; O'Brien and Lyman 2002a), their first step was to define a series of characters or traits, eight in all, each trait characterised by a series of different states or values; base shape, for example, was divided into arc-shaped, normal curve, triangular and folsomoid. On the basis of the values of the points for these attributes, classes of points were defined. Class 1, for example, was defined as having state 2 for attribute I; 1 for attribute II; 2 for attribute III; 2 for attribute 4; and so on. The resultant classes were then taken as the objects for phylogenetic analysis. However, there is no suggestion that the resulting point traditions correspond to a population history, or indeed that they form a 'package' with any other cultural attributes (evidence for which, in any event, is largely lacking for the Paleoindian period).

All this returns us again to the distinction between cores and packages, the history of larger scale human cultural entities, the histories of individual cultural traits, and their relation to populations. Just as the ancestry of an individual gene may be incompatible with the species tree due to processes such as lateral gene transfer, the ancestry of individual cultural traits may differ from the main shape of population history. Useful inventions such as iron metallurgy are known to have diffused widely among divergent cultures. However, many other aspects of culture may be mainly transmitted within cultures, as we have already suggested (Guglielmino *et al* 1995; Hewlett *et al* 2002).

PHYLOGENETIC TREES

A phylogenetic tree is a hypothesis about past relationships within a group of taxa, such as species, cultures, languages or artefact types, which are thought to be hierarchically related by descent. Recent years have seen the application of phylogenetic methods from evolutionary biology to archaeology, linguistics and anthropology, both to infer cultural lineages (see Part I of this book), and to study the evolution of traits on trees (see Part II). Using trees to model cultural history is not new; historical linguists have been using trees independently of biologists for

over 100 years. However, the new phylogenetic tree-building methods are significantly more powerful than previous methods, and hold further promise for future research.

Terminology applied to phylogenetic trees is summarised in Figure 2.1. The tips of the tree represent real taxa (labelled T_1, T_2 etc). Branches (sometimes called 'edges') represent taxa through time. Internal nodes represent hypothetical ancestors (labelled N_1, N_2 etc). We refer to evolutionary change in a trait occurring on a branch. An ancestral population and its descendants are referred to as 'parent' and 'child', or 'mother' and 'daughter' populations (the latter is probably preferable since branching on a tree is like asexual reproduction). Trees can be

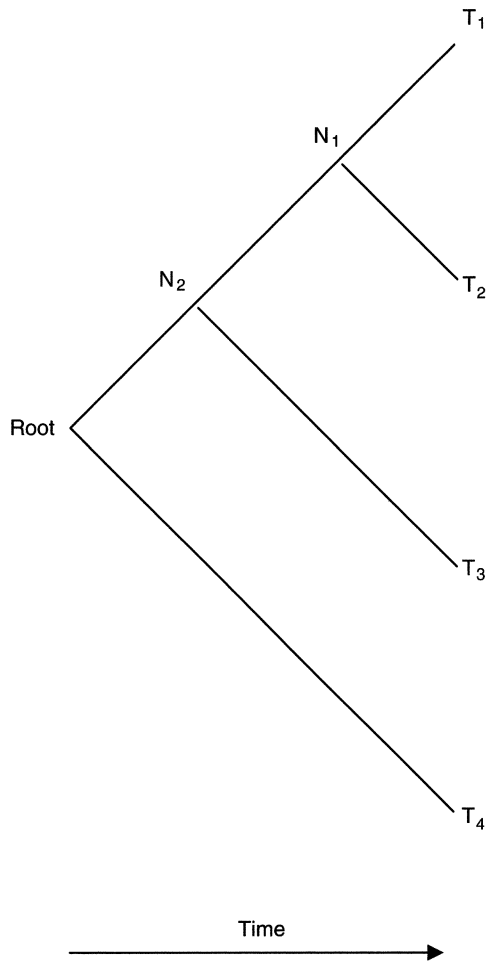

Figure 2.1 Phylogenetic tree with 4 terminal taxa (T_1, T_2 etc). Internal nodes are labelled N_1 and N_2. The root is ancestral to all other internal nodes and taxa, while internal nodes are ancestral to their descendant taxa, for example T_1 and T_2 are descendants or daughters of N_1.

rooted or unrooted (most trees in this book are rooted). Rooting a tree situates it in evolutionary time. On rooted trees, one taxon is designated as the outgroup, meaning that it diverged earliest relative to other taxa on the tree. The outgroup is usually defined using *a priori* criteria, external to the tree, for example, being geographically peripheral to other groups, or associated with older archaeological remains, suggesting that it diverged first. The root represents the (hypothetical) most recent common ancestor of all the taxa on the tree. On a phylogenetic tree there is an implied axis of time from the root (the most distant past) to the tips. O'Brien and Lyman (Chapter 6) discuss other aspects of phylogenetic trees in more detail.

Trees may or may not be fully resolved (bifurcating). On a bifurcating tree every internal node splits to form two descendants. Unresolved trees contain nodes that give rise to more than two descendants, known as polytomies. There are two types of polytomy: soft and hard. Soft polytomies arise when there is not enough data to resolve the tree. In this case, even if we believe that the real tree structure is bifurcating, we do not know the detailed relationships among taxa. Hard polytomies arise more rarely, when a taxon really did simultaneously split into several groups. Hard polytomies are likely to arise if there was rapid radiation among cultural lineages so that there was not enough time after each split for many changes to accumulate before those taxa split again. This is seen, for example, in the rake-like structure of the Oceanic language tree, which results from the rapid spread of Proto-Oceanic speakers over the Pacific (Bellwood 1996b).

We should note that not all tree diagrams represent phylogenies. Phenetic trees seek to represent similarities among taxa in the dataset, but without implying that that similarity arose by common descent; internal nodes on a phenetic tree do not represent hypothetical ancestors. Phenetic trees are constructed by grouping taxa together on the basis of similarity (or shared characters), without distinguishing between the causes of the observed similarities. In contrast, to build phylogenetic trees, we try to exclude similarities that arise from admixture, parallel evolution and chance, instead using only similarities that arise from common descent (homologies). Moreover, phylogenetic tree-building methods also make a distinction between two types of homology, which biologists call primitive (or plesiomorphic) and derived (or apomorphic) characters (Hennig 1965, 1966). Only shared derived traits provide information about relationships among taxa on our tree. Primitive traits arose earlier than the taxonomic level currently being investigated. For example, primates (together with other mammals and reptiles) have five digits. Although this is a homologous trait, it is not useful for telling us about sub-groups within the primates. In contrast, derived traits arose during the evolution of the taxonomic levels currently being investigated. For example, loss of the tail is a derived trait that characterises the great apes as opposed to monkeys. In historical linguistics, the importance of distinguishing between primitive and derived traits has been recognised for over a century. The linguistic equivalent of a derived trait is known as a linguistic innovation. Historical linguists using the linguistic comparative method (see below) define subgroups exclusively by innovations. However, despite the important theoretical distinction between phylogenetic and phenetic trees, in practice, phenetic trees (for example distance-based trees, see below) are often used as estimates of phylogeny (Felsenstein 2004).