

# A phylogenetic approach to cultural evolution

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**There has been a rapid increase in the use of phylogenetic methods to study the evolution of languages and culture. Languages fit a tree model of evolution well, at least in their basic vocabulary, challenging the view that blending, or admixture among neighbouring groups, was predominant in cultural history. Here, we argue that we can use language trees to test hypotheses about not only cultural history and diversification, but also bio-cultural adaptation. Phylogenetic comparative methods take account of the non-independence of cultures (Galton's problem), which can cause spurious statistical associations in comparative analyses. Advances in phylogenetic methods offer new possibilities for the analysis of cultural evolution, including estimating the rate of evolution and the direction of coevolutionary change of traits on the tree. They also enable phylogenetic uncertainty to be incorporated into the analyses, so that one does not have to treat phylogenetic trees as if they were known without error.**

## Introduction

Phylogenetic approaches to linguistic and cultural evolution promise to increase our understanding of human prehistory and adaptation. Among the many recent studies applying phylogenetic methods to languages and other aspects of cultural variation, two subfields stand out in particular: (i) inferring phylogenies of language families and cultural artefacts; and (ii) testing comparative hypotheses about human bio-cultural evolution, which refers to the ways in which humans adapt, biologically and culturally, to their diverse environments. Whereas much previous work in cultural evolution was predominantly theoretical in focus [1], the newly emerging field of cultural phylogenetic analysis is strongly empirical. An unexpected result of recent phylogenetic analyses of languages is just how well their histories fit a branching tree model [2–4], at least in their basic vocabulary. This challenges the view, dominant within archaeology and anthropology throughout the second half of the 20th century, that blending processes were predominant in cultural history. Here, we argue that language trees can be used to test hypotheses about not only cultural history and diversification, but also bio-cultural adaptation, using phylogenetic comparative methods. Comparative analysis is of primary importance in scientific anthropology, partly because opportunities for

experimentation are limited, but also because humans show such a remarkable range of cross-cultural variation.

## Cultures as species

We define culture broadly, as behavioural traditions that are transmitted by social learning. At the population level, humans structure themselves into cultures or ethno-linguistic groups, which we define here as a group of people who speak the same language. Many parallels have been drawn between cultural and biological evolution, both at the level of parallels between genes and cultural traits (or variants), and at the level of species and cultures [5]. Culture evolves in the sense that occasional errors arise in cultural transmission (equivalent to mutations in biological evolution), leading to change through time [6,7].

For the purposes of phylogenetic analysis, languages and cultures are treated as being analogous to species (Table 1), although there has been a vigorous debate about how far we can treat cultures as discrete, bounded units, similar to species [8]. Empirical studies of how far individual cultural variants are transmitted within and between ethno-linguistic groups suggest that a large proportion of cultural transmission occurs within groups, from parents to children, and from mother cultures to descendant cultures [9–11]. Conformist tradition in language is important within a group of communicating individuals if they are to remain mutually intelligible, and is also likely to be important for a range of other cultural traits, such as marriage practices.

There are several theoretical reasons to believe that cultural evolution can maintain discrete cultural groups, even in the face of limited genetic admixture. For most of our evolutionary past, we lived in small hunter-gatherer bands, where ethno-linguistic groups could be as small as a few hundred individuals. Inter-group marriage would result in genetic admixture, but perhaps not significant linguistic admixture, if the immigrant spouse adopted the language of his or her new group. Relationships between hunter-gatherer groups were often hostile and analyses of the ethnographies of horticulturalist clans in Papua New Guinea over the past century suggest that between 1.3% and 31.3% of clans every generation were driven to extinction through warfare [12]. Survivors, especially reproductive-age women, might integrate themselves into the victorious cultures, thus cultural extinction does not necessarily imply genetic extinction; but such migrants would have to learn the ways of their new community if they are to survive and reproduce among

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**Table 1. Some parallels between biological and cultural evolution**

Attribute	Genetic systems	Cultural systems
<b>At the gene or cultural trait level<sup>a</sup></b>		
Discrete units	Nucleotides, codons, genes and individual phenotypes	Cultural traditions, memes, ideas, artefacts, words, grammar and syntax
Replication	Transcription and reproduction	Teaching, learning and imitation
Dominant mode(s) of inheritance	Parent–offspring (mendelian), occasionally clonal	Parent–offspring, peer groups, generational and teaching (sometimes biased e.g. prestige bias)
Horizontal transmission	Many mechanisms (e.g. hybridization, viruses, transposons and insects); rare	Borrowing or imposition; common
Mutation	Many mechanisms (e.g. slippage, point mutations and mobile DNA)	Innovation, mistakes and vowel shifts
Selection of favoured variants	Natural selection of traits that enhance survival and reproductive success	Natural and cultural selection (e.g. societal trends and conformist traditions)
Rates of evolution	Many generations; slow	Fast or slow
<b>At the species or population level</b>		
Discrete units	Species	Cultures and ethno-linguistic groups
Replication	Speciation (usually allopatric); hybridization rare	Groups split, occasionally join
Selection of favoured variants	Competition between species	Multi-level selection (groups can drive other groups extinct through warfare)
Rates of evolution	So slow it might never lead to species level adaptations	Probably slow

<sup>a</sup>Adapted from [29].

them. Several authors have argued that such population dynamics can lead to group-level selection occurring in human cultural evolution [6,13–15] and could explain a range of uniquely human behaviours, from high-level cooperation with unrelated individuals [8,14,16] to ethnic markers and psychology [17]. Such processes could maintain the identity of discrete cultural groups even when genetic distinctions are more blurred or even absent.

#### Phylogenetic trees of languages and cultural artefacts

Another debate concerns how far different cultural groups themselves are related in a tree-like way, analogous to phylogenetic trees of species. We make the case here that several theoretical arguments, as well as accumulating empirical evidence, suggest that cultures are related in such a way. The anthropological literature contains examples of cultural groups, particularly those that increased in size, that have split as a result of within-group competition for resources, including women [18]. This might have been common during Neolithic population expansions [19]. The alternative view is that merging processes were predominant [20–22]; however, the anthropological literature suggests that, in the face of conflict, one culture tends to dominate the other; merging among cultures only occurs when groups are under extreme pressure and could be depopulated, as in the case of Iroquois experiencing epidemics and armed conflicts with European colonists in 17th-century America [23]. Tribal populations have been under high extinction pressure as a result of colonial expansions over recent centuries, but if splitting is a response to growth, and merging a response to depopulation, then the extant anthropological record is likely to contain predominantly those cultures that experienced expansions and splits; thus, a phylogenetic model should fit cultural diversification well.

Phylogenetic methods advance this debate because it is possible to test how well a data set fits on a cladogram statistically. Consistency and retention indices measure, respectively, the extent of homoplasy and synapomorphy in the data. Support for individual nodes on the tree can be

tested using bootstrap analysis, or in the case of Bayesian phylogenetic inference, by estimating posterior probabilities of each node. Language groups analysed using phylogenetic methods include Indo-European [4,24], Austronesian [2] and Bantu [3]. The results of these studies indicate that linguistic data sets are as tree-like as are biological data sets of morphological or molecular characters, at least in their basic vocabulary (standard 100- or 200-word lists of conservative, cross-culturally universal meanings such as ‘woman’ and ‘moon’). This result was surprising because linguistic borrowing (the transfer of linguistic elements between languages) is often described as widespread, but the analogous biological process, gene flow, is thought to be rare. Material culture data sets, including decorative traits on Native Californian baskets [25], Turkmen carpet designs [26], a variety of artefacts from Coastal New Guinea [27] and prehistoric American arrowheads [28], have also been analysed using phylogenetic tree-building methods. The extent to which material culture traits reflect linguistic or ethno-historical relationships varies; Californian basketry designs appear to be largely horizontally transmitted, whereas vertical transmission seems to be at least as important as horizontal transmission in the other examples.

Phylogenetic methods for building trees have other advantages over the distance-based methods that were formerly used in archaeology and linguistics (known as lexicostatistical methods in linguistics). By operating directly on discrete data, phylogenetic methods avoid the loss of information that is inherent in calculating an average distance between pairs of taxa. They also distinguish between primitive and derived traits (in linguistic terms, retentions and innovations), using only innovations to define subgroups. In this respect, phylogenetic methods are similar to the linguistic ‘comparative method’, a method for inferring language trees that was developed independently in historical linguistics. In addition, phylogenetic methods use an explicit optimality criterion to choose among trees, and enable branch lengths to be calculated that are proportional to the number of changes (innovations) per branch. Some

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