

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
At the gene or cultural trait level^a		
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
At the species or population level		
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

^aAdapted 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

phylogenetic methods offer the possibility of estimating dates for ancestral nodes on the tree [29], and the tree can be calibrated using archaeological dates, as seen in a recent study supporting the agricultural origins of Indo-European in the 8th millennium BP [24].

In spite of these strengths, any tree remains a hypothesis about past relationships among taxa. Often, the data fit more than one tree equally well, with ambiguous relationships arising from parallel evolution or linguistic borrowing. Networks, unlike trees, enable us to represent more than one evolutionary pathway on a graph, by allowing branches to join as well as diverge. Networks have been used to describe relationships within Celtic [30] and Indo-European languages [31]. New Bayesian MCMC (Markov chain Monte Carlo) methods approach the problem of phylogenetic uncertainty differently, by constructing a sample of trees in which trees are represented in proportion to their likelihood [32]. The proportion of trees in the sample on which a node is found

is equivalent to its posterior probability (Figure 1). Alternative evolutionary pathways, including those arising from linguistic borrowing, are represented on different trees within the sample.

Although language and some other neutral cultural variants, such as pottery decorations [33], reflect population or cultural history, the distribution of cultural traits that confer a selective advantage, such as pastoralism, is likely to reflect both adaptive pressures within particular environments and history. Yet empirical studies show that adaptive cultural traits also often have a strong phylogenetic signature [10,11,34,35], presumably because parents who transmit such traits to their offspring will have higher reproductive success.

Although taken together these results indicate that the historical affiliations of an ethno-linguistic group can be used to predict its cultural make-up more accurately than can the cultural states of its geographical neighbours, some horizontal transmission between cultures also

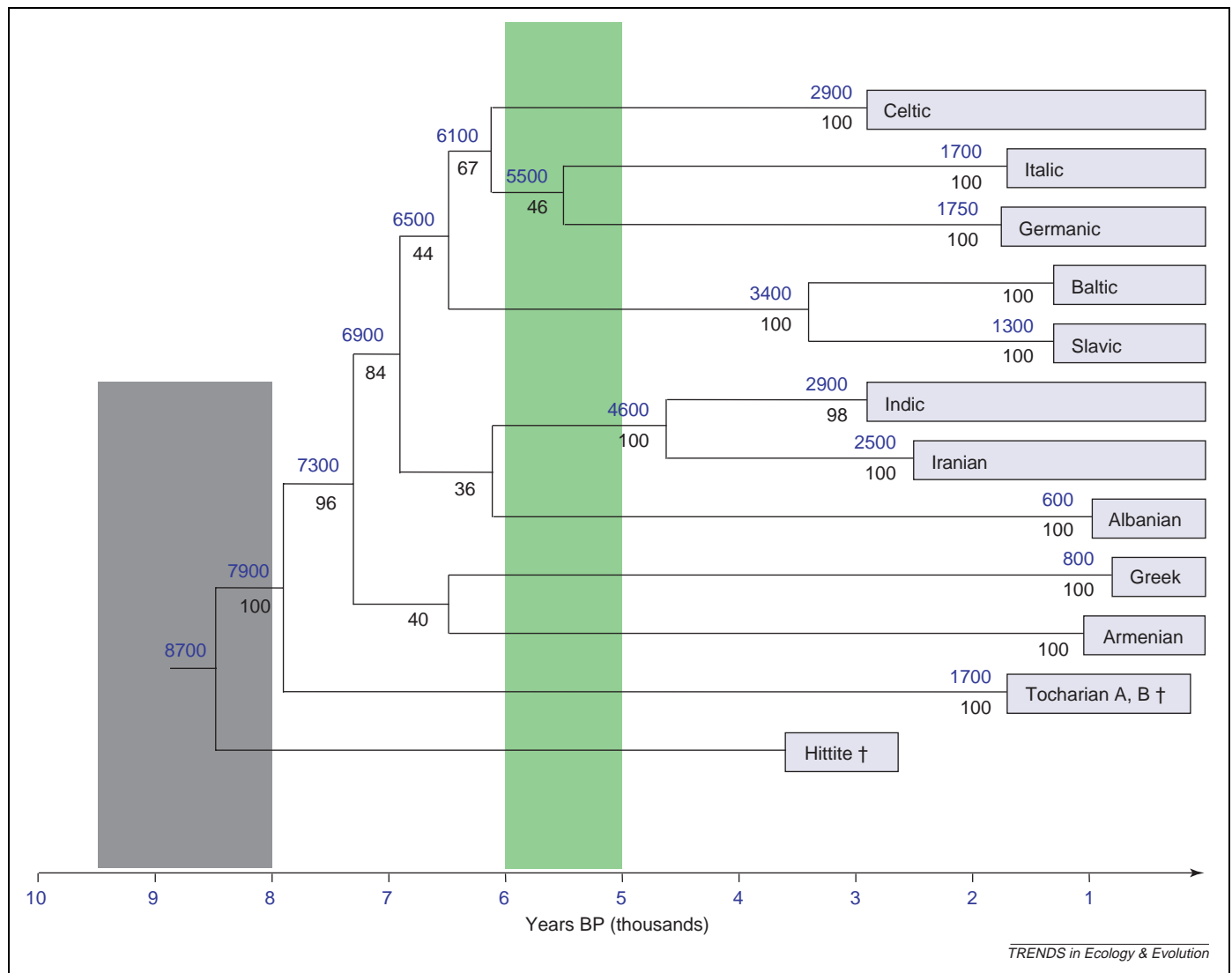


Figure 1. Dating the Indo-European language tree. The figure summarizes a majority-rule tree for a Bayesian sample of 1000 trees, constructed by Gray and Atkinson [24]. Tips show language groups. Blue labels show the estimated age for the node above (moving towards the tips of the tree) (years BP). The date of the root (8700 BP) supports the hypothesis of an agricultural origin of Indo-European (9500–8000 BP, shown by the grey bar). The alternative hypothesis, that the earliest Indo-European languages were spread during the Kurgan expansions in the 6th millennium BP (shown by green bar) was not supported. However, it is possible that the Celtic, Germanic, Italic and possibly Indo-Iranian groups originated during the Kurgan expansions. Black labels indicate the posterior probability of each node; nodes near the tips are well supported, but some lower nodes remain uncertain.

occurs. Horizontal transmission could tell us about historical contacts between groups [31], and can also provide useful data for use in phylogenetic comparative methods about the functional significance of the borrowed trait; the conditions under which new or borrowed cultural traits might appear on branches of a phylogenetic tree can tell us with what, if anything, that trait is coevolving.

Phylogenetic comparative tests of cultural adaptation

The tree-like nature of cultural diversification has important implications for testing adaptive hypotheses across cultures. As with species, we need to control for non-independence among cultures when statistically testing coevolutionary hypotheses in cultural or bio-cultural evolution [36], otherwise type 1 errors (false positive results) will be inflated, as cultures within clades containing the same traits are spuriously treated as independent evolutionary events. One simple and widely used method to avoid dependence among cultures is to sample cultures thinly across the world by using the Standard Cross-cultural Sample (SCCS) [37], which consists of 196 cultures worldwide. However, in using such a sample, one discards variance that could potentially be used to test hypotheses, leading to Type 2 errors and a loss of the ability to make detailed regional studies; moreover, one does not eliminate similarity that results from more distant historical relationships among cultures [36].

Although accepted in biology, the fact that historically related cultures share similarities as a result of their common history, as well as by parallel evolution, remains controversial in anthropology, because it is often argued that cultural traits are so labile that they show no phylogenetic signature. But mapping cultural traits onto a linguistic or genetic tree reveals that many cultural traits show a strong association with phylogeny; moreover, many also appear to be historically conservative. For example, dowry and monogamy date back to the earliest known Indo-European culture, the Hittites in the 4th millennium BP, and remained predominant until recent times among Indo-European cultures, although are rare worldwide [38]. Furthermore, one recent comparative method enables us to estimate a parameter that tells us whether the tree is influencing the correlation between traits, and simplifies to a standard regression if it is not [39]. This method has been used to demonstrate an association between marriage payments and adult sex ratio in a worldwide sample [31].

Phylogenetic comparative methods avoid Galton's problem, of the non-independence of cultures, because the units of analysis are not cultures, but instances of evolutionary change. These methods test for correlated evolution in two or more traits along the branches of a tree. Cultural states, known at the tips of the tree from ethnographic data, are mapped onto the tree statistically, and their ancestral states and probable pattern of historical change along the tree branches are inferred. For constructing the phylogenetic tree (onto which cultural traits are mapped) linguistic data are currently available for more cultures than are genetic data, and so can be more useful in this type of analysis. Whereas

earlier studies used traditional language classifications [33,40,41], more recent studies have used the phylogenetic language trees described above [38,42,43]. Several phylogenetic comparative methods have been used in cross-cultural analysis; Maddison's Concentrated changes test, which uses parsimony, has been used to investigate social organization in East Africa (Figure 2; [41]) and Felsenstein's method of comparative analysis using independent contrasts [44,45] has been used to study the coevolution of work patterns and sexual dimorphism in stature [34].

One problem with maximum parsimony reconstructions is that evolution in general, and cultural evolution in particular, is not always parsimonious. Reversals, when a trait switches and then switches back again, possibly more

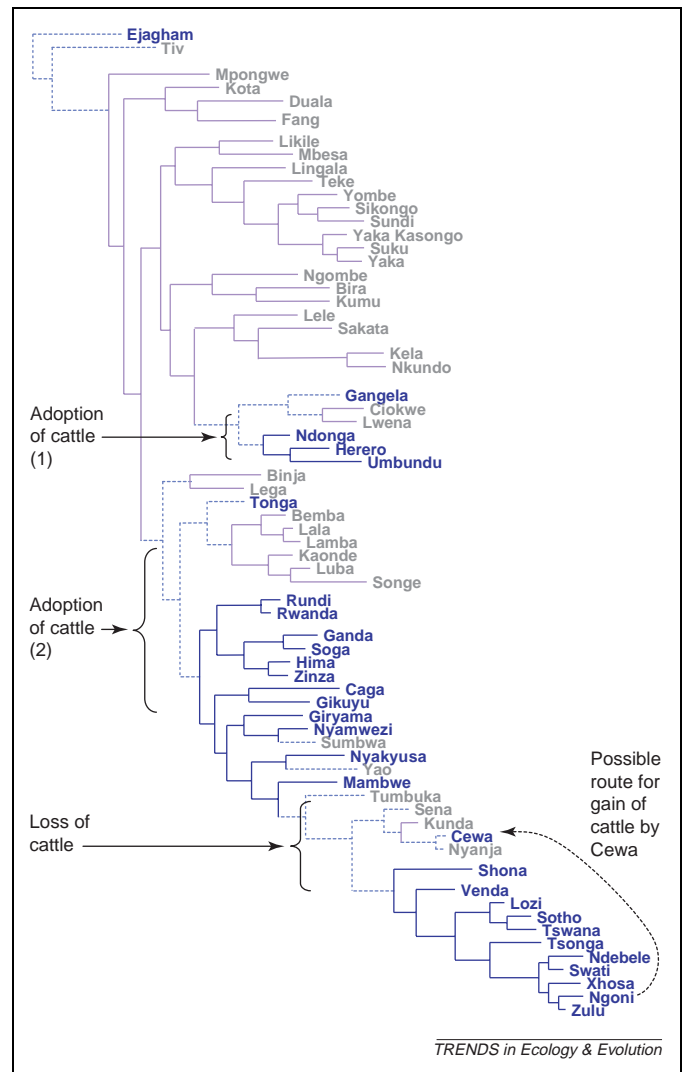


Figure 2. Inferring ancestral cultural states on a phylogeny: cattle-keeping in Bantu-speaking Africa [42,47]. The figure shows a phylogenetic tree that was constructed using maximum parsimony and basic vocabulary for 68 African populations [3]. Ancestral states were estimated by mapping ethnographic data from Murdock's Ethnographic Atlas [53] onto the tree, using the maximum likelihood method DISCRETE [46]. Blue text and solid lines indicate that cattle are kept, whereas purple text and lines indicate that they are not; dashed blue lines indicate that cattle keeping is ambiguous. Ancestral states agree with archaeological and linguistic evidence that cattle were absent in the earliest Bantu-speaking populations, but were probably acquired twice from non-Bantu-speaking populations in East Africa, perhaps during the late 3rd millennium BP, spreading independently to Southern Africa via south-eastern and south-western routes [54]. Gain and loss of cattle are quite rare; one possible later horizontal transfer, from the Ngoni to the Cewa, is shown.

than once, along a branch of the tree, might be common. In methods using maximum likelihood, evolutionary models are more explicit. Thus, the rate of evolution, either fast or slow, can be estimated independently for each transition in each trait; and it is possible to test whether one model of evolution is more likely than another to give rise to the patterns of cultural diversity observed (Figure 2; [46]).

As well as testing whether two traits are correlated, it is also possible, using Pagel's DISCRETE test [46], to estimate directional relationships (even when two traits both change on one branch). This method has been used to show how pastoralism led to the evolution of lactose tolerance [40] and patrilineal descent in Africa (Figure 3, [42]). Ancestral states can be described as probabilities rather than just one or other condition [38,39]. From the distribution of the traits in question on a tree, we can also estimate the rate of change in different traits using archaeological dates to calibrate the tree [47].

Phylogenetic comparative methods have been justly criticized for treating the tree as though it was known without error, whereas all phylogenetic trees, including language trees, have some uncertainties, including Indo-European, the best studied and most tree-like of the language phyla (Figure 1). In early studies [34,40], attempts were made to address this problem by using two or three alternative genetic and linguistic trees, thereby incorporating a range of hypotheses about past relationships among groups. It is now possible to address this problem in a more principled way, by using Bayesian MCMC techniques [48]. As we discuss above, these methods are used to construct a sample of trees in which trees are represented in proportion to their likelihood. By performing all subsequent analyses across the entire tree sample, phylogenetic uncertainty or error can then be

incorporated into our analysis. To estimate an ancestral state at a particular node, the probability of that node on the tree is weighted against the probability of it taking a particular state [49]. Phylogenetic approaches to cultural evolution have often been criticized because a single tree cannot capture relationships that involved admixture among populations, but using a range of trees enables more than one evolutionary pathway to be represented for such cultures, in a comparable way to using a network model. The new Bayesian MCMC methods have been used to demonstrate, for example, the coevolution of dowry and monogamy in Indo-European cultures [43].

Conclusion

Evolutionary ecology and comparative biology bring a useful toolkit of statistical methods to cultural evolutionary studies. There is a strong tradition of comparative studies in linguistics, archaeology and anthropology [50–52], which have informed much of our knowledge of both human migration and adaptation, but statistical methods are often viewed with suspicion. Anthropologists are fond of pointing out the complexity of cultural systems, and either using it as an excuse to not ask precise questions, or to question the validity of the assumptions of the models being used. But questions about the prevalence of horizontal transmission, or how long cultures endure, do not make sense if no phylogeny is implied. New methods are rendering many of the old debates irrelevant, as the influence of phylogeny on the data distribution can now be tested, and phylogenetic uncertainty can also be incorporated. Within the phylogenetic framework, anthropologists are now asking – and sometimes answering – such questions empirically, and with a new level of precision.

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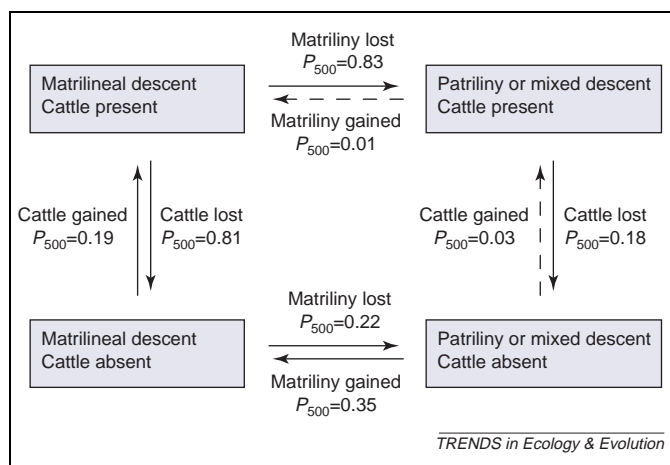


Figure 3. Correlated evolution in cattle keeping and descent system in Bantu-speaking populations [47]. DISCRETE [46] was used to estimate the rate of each evolutionary transition and hence whether the rate of change depends on the state of the other trait (or, whether the two traits are coevolving), given the tree in Figure 2. Dotted arrows indicate non-significant transitions. P_{500} represents the probability of a particular state change over 500 years, taking into account the probability of changing state more than once. For example, it is highly probable ($P_{500}=0.81$) that a matrilineal culture with cattle loses its matrilineal descent, but extremely unlikely that a cattle-keeping culture with patrilineal or mixed descent becomes matrilineal ($P_{500}=0.01$). Being matrilineal and keeping cattle is an unstable cultural state; such cultures are likely to either lose their cattle or to change their descent system. By contrast, being patrilineal and keeping cattle is a stable cultural state. These results support the hypothesis that the spread of cattle led to the loss of matrilineal descent in Bantu-speaking Africa.

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