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Authors

Borgerhoff Mulder, Monique

Nunn, C L

Towner, M. C.

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CULTURAL MACROEVOLUTION AND THE TRANSMISSION OF TRAITS

Monique Borgerhoff Mulder

University of California

Department of Anthropology

Davis, CA 95616 USA

email: mborgerhoffmulder@ucdavis.edu

Charles L. Nunn

University of California

Department of Integrative Biology

Berkeley, CA 94720-3140 USA

Max Planck Institute for Evolutionary Anthropology

Leipzig, Germany

email: nunn@eva.mpg.de

Mary C. Towner

University of California

Department of Anthropology

Davis, CA 95616 USA

email: mctowner@ucdavis.edu

Monique Borgerhoff Mulder is at the Department of Anthropology (UC Davis) and also a member of the Center for Population Biology and the Graduate Group in Ecology. Charles Nunn is a scientist at the Max Planck Institute for Evolutionary Anthropology and in the Department of Integrative Biology at UC Berkeley. Mary Towner is a post doctoral fellow in the Department of Anthropology at UC Davis

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Cultural traits are distributed across human societies in a patterned way. Study of the mechanisms whereby cultural traits persist and change over time is key to understanding human cultural diversity. For over a century a central question has engaged anthropologists interested in the study of cultural trait variation. What is the source of cultural variation? More precisely, are cultural traits transmitted primarily from ancestral to descendant populations (vertical transmission), between contemporary, typically neighboring, populations (horizontal transmission), or do they emerge as independent innovations? While debates among unilineal evolutionists and diffusionists have long since faded, there is still much uncertainty over how traits are transmitted at this macroevolutionary level, and over the implications of these transmission patterns for testing hypotheses for the adaptive function of particular cultural traits across human populations.

In recent years an analogy between cultural and biological evolution has gained prominence, especially among those interested in the processes responsible for producing cultural similarities and differences within and between societies.¹⁻⁷ Theorists have for some time recognized that cultural evolution has key Darwinian properties.^{8,9} Defining culture as acquired information, strong arguments can be made for the three principal tenets of Darwinism:⁶ cultural traits are variable both within and between populations; cultural variants are in competition with one another; and cultural traits are heritable, with the more favorable variants accumulating over time. Though there is tremendous power in this metaphor, everyone recognizes that cultural traits are not constrained to being transmitted from parents to offspring, but also diffuse among unrelated individuals through learning, imitation, teaching and other processes. Cavalli-Sforza and Feldman⁸ borrow from epidemiology the terms vertical transmission and horizontal transmission to describe, respectively, the transmission of cultural traits from biological parents to their offspring, and the transmission of traits within a single biological generation. Their framework has inspired empirical studies of inter-individual trait transmission that show both strong vertical patterns^{10, 11} and clear horizontal signature,¹² as well as investigations into the extent to which trait distributions can be explained by random drift.¹³

Despite major conceptual developments in studying the transmission of cultural traits *within* populations,^{8, 9, 14} the dynamics of cultural macroevolution (the patterning of similarity and dissimilarity in cultural traits across a set of populations) are still not well understood. Cultural variability across human societies is self-evident, but researchers disagree about the dominant forces responsible for this variation and its continuity over space and time. Is the pattern of variation due primarily to the budding off of daughter cultures (vertical transmission), as seen with core cultural traditions that persist across generations and within daughter populations in Polynesia and Central Africa?^{15, 16} Is it the result of the diffusion of cultural traits between historically unrelated groups (horizontal transmission), as with the expansion of Islam across West Africa¹⁷, the diffusion of cultural practices within the early Christian church¹⁸, and the spread of technical innovations?¹⁹ Or does cultural variation reflect independent innovations, as with the practice of agriculture which appeared prehistorically in at least three different parts of the world?²⁰ To understand more clearly these dynamics, evolutionary anthropologists and others are capitalizing on new genetic, linguistic and archaeological data to explore the spread of populations, languages and technologies among human populations^{5, 20-23} and incorporating analyses of cultural traits.²⁴⁻²⁸ As yet, however, there is no consensus on the predominant factors that drive cultural trait transmission, with some overviews emphasizing that cultures “inherit” the cultural traits of their parent populations,^{7, 29} others maintaining that both vertical and horizontal transmission are significant processes,^{30, 31} and yet others adhering to a model wherein traits diffuse across populations largely irrespective of ancestry.³

Recent reviews^{7, 29, 32, 33} focus on the positive evidence for vertical transmission and the importance of phylogenetic analysis for the comparative method. Here we argue this view may be premature. After a brief historical introduction, we discuss an array of exciting new methods for detecting vertical and horizontal trait transmission, and the implications of recent findings for the study of cultural trait adaptation. We include a glossary (Box 1) of the more technical terms, keyed with underlined text.

(Box 1 here)

HISTORICAL ROOTS IN ANTHROPOLOGY

Even before Darwin there were evolutionary undercurrents to the study of cultural variation, especially in the area of language diversity. As early as 1786 Sir William Jones observed that similarities among Sanskrit, Greek, Celtic, Persian, Gothic and Latin might suggest a common linguistic source, and by 1836 an evolutionary tree of the Indo-European family had appeared.³⁴ In *The Origin of Species*, Darwin noted the “genealogical” relationships fundamental to classifications of both species and languages, and since his time it has been widely recognized that just as biological lineages split and diverge into family trees, so do language lineages. Indeed, the fundamental processes in biological evolution, such as cladogenesis, selection, drift, extinction and mutation, have clear linguistic analogues.³⁵ These early comparisons of language already hinted at two major transmission modes for cultural traits – what we identify today as vertical transmission of traits between parent and daughter societies or populations, and horizontal transmission between populations.

The significance of these transmission modes lay at the heart of 19th and early-20th century anthropological investigations of cultural trait origins, with two notorious paradigms dominating the field: unilinear evolution and diffusionism. Foundering on racism and ethnocentrism, unilinear evolution became synonymous with the notion of progress from savagery to civilization, as in the work of Sir Henry Maine and E. B. Tylor. In contrast, diffusionism, as put forth by Freidrich Ratzel and Leo Frobenius, emphasized instead the spread of ideas and tangible objects between different societies. It too stalled, lost in speculation over how western European culture could be traced back to one or more early centers of civilization – a theme of the Kulturkreise school.³⁶ With the passing of time evolution was eventually purged of its unilinear assumptions (and subsequent damaging social Darwinian – or rather Spencerian – taints), and diffusionism stripped of its connotation that peoples untouched by early centers of civilization are somehow degenerate, leaving intact the two underlying cultural transmission modes—one based on vertical connections between societies, the other horizontal.

Franz Boas was the first modern anthropologist to revisit these issues. From his investigations into the distribution of mythical elements across the Americas, he recognized that some elements probably survived from very early cultural forms, some were the product of extended borrowing (sometimes back and forth), and yet others were true innovations. Boas

puzzled lengthily over whether the possession of similar traditions by two geographically separate populations is due to borrowing, or whether “there are other causes at work,”³⁷ page 144 independent inventions which for Boas lay in the workings of the human mind. These ideas helped stimulate classic cultural ecology and the modern field of human evolutionary ecology.

In recent years archaeologists have reinvigorated the debate over cultural trait transmission, adopting the terms phylogenesis for intra-lineage change (or branching), and ethnogenesis for change from outside sources (or blending).^{30, 31, 38} As captured in a now famous illustration (FIGURE 1) published by Boas’ student Alfred Kroeber, the model of phylogenesis suggests that cultural evolution takes the form of descent with modification through a successive subdivision of cultural assemblages, producing a constantly diverging tree, or phylogeny.^{1, 7, 15, 21, 22} In contrast, the ethnogenesis model proposes that cultural evolution occurs through the borrowing and blending of ideas and practices, and the trade and exchange of objects, among contemporary populations, leading to a reticulated tree.^{3, 39, 40}

The relative importance of phylogenesis and ethnogenesis, and by implication the underlying mechanisms of vertical and horizontal transmission, is still subject to debate. Ethnographic overviews typically suggest that phylogenesis (or descent) plays a central role in the distribution of cultural traits across the world. For example, Hallpike’s⁴¹ comparison of pastoralism in East Africa and the Indo-Iranian region shows distinct differences in social organization and religion, with East African societies organized by age-based principles and espousing monotheism, and Indo-Iranian societies showing no age organization and worshipping multiple gods. Given similar ecologies and means of subsistence, Hallpike concludes that historical relationships are key to understanding cultural diversity. Sahlins⁴² and Vansina¹⁶ have made similar arguments for Melanesia-Polynesia and Central Africa, respectively. There is however the possibility that these historical cases were studied precisely *because of* the clear signal they evince, and others have claimed adamantly to demonstrate regional patterns that are not simply the result of ancestral tradition.^{39, 40}

Studies of cultural macroevolution are becoming increasingly sophisticated, both in theory and methods.⁴³ Theoretical arguments have been made for analyzing the correlated

evolution of cultural traits with phylogenetic procedures.⁴⁴ Furthermore, in terms of methods, recent years have seen tremendous advances in molecular genetic techniques and huge increases in computational power, allowing for easier managing of large data bases and increasingly sophisticated statistical approaches in relevant fields (e.g., language comparisons, spatial statistics, and tree building). Anthropologists now recognize that macroevolutionary patterns of cultural trait distributions allow inference regarding histories of human populations and culture (though they maintain, along with Boas, that commonalities among genes, language and culture reveal nothing about genetic determination). To draw such historical inferences, researchers have turned to a variety of methods, some better suited than others to detecting cultural transmission mechanisms, and it is to these that we now turn.

METHODS FOR DETECTING TRANSMISSION MODES

Do Cultural Traits Show Evidence of Vertical Transmission?

We start by considering two tree-based approaches to determining whether a cultural trait has been transmitted vertically among a group of societies. The first approach assesses the “tree-likeness” of a cultural trait, considering the extent to which the similarities and differences in the trait across societies can be represented as a bifurcating tree, in other words, the phylogenetic signal of a trait. As mentioned above, this approach has historically been used most prominently with language, a cultural trait for which variants are expected to be largely selectively neutral. Employing phylogenetic methods developed within biology, modern linguists are reconstructing language and, by inference, population histories, such as the expansion of Austronesian languages across the Pacific,²¹ Bantu in Africa,²² and Indo-European across Europe.⁵ By incorporating maximum likelihood⁴⁵ and Bayesian inference,⁴⁶ modern linguists overcome many of the uncertainties in determining tree topology and branch lengths that plagued earlier methods, primarily because they can evaluate likelihoods associated with a sample of all possible trees as well as estimate confidence intervals around different branches.^{34, 47} Furthermore, by using only basic vocabulary that appears in Swadesh word or meaning lists,⁴⁷ linguists exclude words likely to have been borrowed between unrelated languages, words that would introduce inaccurate

signals to the tree building algorithm; (such procedures exaggerate phylogenetic signature, an issue we return to later).

Efforts are now afoot to determine the tree-likeness of cultural traits other than language. Evolutionary archaeologists have been at the forefront of this work, studying artifact frequencies as extended phenotypes (*sensu* Dawkins⁴⁸), subject to natural selection, drift and other evolutionary forces.⁴⁹ Using assemblages such as pottery,³⁰ textiles,⁵⁰ and basketry,⁵¹ evolutionary archaeologists construct clades of related cultural taxa using derived characters. In a remarkably synthetic overview of the tree-likeness of cultural trait phylogenies produced by archaeologists as well as sociocultural anthropologists, Collard et al.³¹ contrast 9 cultural data sets with 21 biological data sets, using a tree building program to evaluate how well the most parsimonious phylogeny explains the distribution of similarities and differences within each data set. Looking at the Retention Index (RI), a goodness-of-fit measure, they find that cultural and biological traits show very similar values: for biological traits, the mean RI was 0.60 (range 0.35 to 0.94), and for cultural traits it was 0.60 (range 0.17 to, 0.93). Because this runs counter to the expectation that RIs would be lower in cultural than biological data sets (cultural traits diffuse across population boundaries more easily than genetic traits across species boundaries), the authors concluded that cultural traits are largely vertically transmitted. The key assumption here is that data sets with high RIs indicate vertical transmission and population branching, whereas data sets with low RIs result from horizontal transition or independent innovation.^{21, 31}

Critics of phylogenetic tree building for linguistic,⁵² archaeological,⁵³ and cultural traits^{3, 39} point out that the tree-building approach in itself cannot reveal “non-tree likeness”. Tree-building, of course, starts from the assumption that a tree (and by inference vertical transmission) is responsible for a trait’s current distribution. But other mechanisms could also produce a high RI, even in the face of horizontal transmission, especially for traits that are highly correlated. For example, the high RI indices in Collard et al.’s study could simply reflect a tendency for suites of correlated traits to be borrowed among closely related neighboring societies as a packet; it might also reflect a pattern of daughter populations settling close to their parent populations, or in habitats ecologically similar to those they left (phylogenetic niche conservatism, or habitat selection⁵⁴). Fortunately new statistical techniques of maximum likelihood and Bayesian

inference can, to some extent, remedy this situation, in that they allow the probability of different trees based on different evolutionary assumptions, or the confidence levels surrounding the length of different branches, to be estimated. With creative application these methods can reveal signs of “non-tree likeness”. Thus, McMahon and McMahon⁴⁷ use bootstrapping techniques, effectively resampling with replacement the words in a word list, to determine the robustness of the Indo-European language tree. They found that the Slavic languages are particularly prone to changing places, suggestive (to the authors) of possible extensive horizontal borrowing between languages in this subfamily. Our view is that **tree building is a powerful method and provides considerable insight, particularly when based on maximum likelihood and Bayesian inference procedures. However, without principled methods designed to uncover horizontal transmission, there is a danger of biasing findings towards vertical transmission if we only use tree-building methods.**

One way of getting around the potential problem of circularity with tree-building programs, or of putting too much faith in the assumption that tree-likeness indicates a history of vertical transmission and population fissioning, is to examine the fit between the distribution of cultural traits and an *independently* derived tree, based on linguistic, morphological or genetic patterns. This is the second approach we promised to the identification of vertical transmission. Path-breaking work by Cavalli-Sforza and others examined parallels between genetic trees and linguistic variation,⁵⁵⁻⁵⁸ and newer studies look at how traits like family and kinship,²⁷ sexual dimorphism,⁵⁹ and farming^{20, 22, 60} map onto genetic or linguistic trees. In our view, research that uses independently-derived trees offers stronger support for vertical transmission than trees built on the traits of interest. For three reasons, however, we still need to scrutinize the conclusions of such studies. First, phylogenetic trees constructed for humans are not entirely equivalent to those constructed for biological species, in so far as human populations are not reproductively isolated in a biological sense, with gene flow more or less a constant possibility. Second, linguistic or genetic distances between populations are often confounded with geographic distances; in fact, because of the phylogenetic niche conservatism mentioned above,⁵⁴ sister populations are often neighbors and share ecological characteristics. This we illustrate with an example of how the distribution of polygyny across East Africa fits very nicely with the linguistic tree but is also

strongly geographically patterned (Box 2); often the methods for untangling these interrelations are inadequate (a topic we explore more below).

(Box 2 here)

Finally, we cannot assume that all (or even the majority of) cultural traits will show a close correlation with linguistic or genetic trees. For data on 35 East African societies,⁶¹ Moylan et al.⁶² studied the fit of 55 cultural traits (in domains such as “kinship and family” and “rituals, beliefs, and attitudes”) to an independently derived linguistic phylogeny. Using a test developed by Abouheif,⁶³ only 33% of cultural traits showed clear evidence of vertical transmission, at least in so far as vertical transmission is inferred from a close fit between the linguistic and culture trait trees. Moreover, when the same data were analyzed using Maddison and Slatkin’s steps test⁶⁴ and Bonferroni corrections for the number of variables analyzed, only four of these associations were statistically significant. This was true even for kinship and family traits (such as residence and marriage patterns), a result at odds with the longstanding belief among anthropologists that this is a particularly conservative cultural domain.²⁴ The results are consistent with the hypothesis that other mechanisms, such as horizontal transmission or independent innovation, may account for variation in cultural traits at some scale and/or in some parts of the world (see below).

Do Cultural Traits Show Evidence of Horizontal Transmission?

Both tree-based approaches discussed above are stimulating highly interdisciplinary investigations into cross-cultural variation, but provide no insights into the importance of cultural transmission forces other than vertical transmission. This could change, however, with recent methodological advances such as split decomposition⁶⁵ that can evaluate borrowing within a tree, and perfect phylogenetic networks.⁶⁶ Split decomposition methods do not force the data to fit a tree, but rather check for non-treelike signals in the data.⁶⁷ In studying the evolution of Austronesian languages in the Pacific, Hurler et al.²³ use split decomposition to show that horizontal language transmission occurs at periods when there was a pause, archaeologically-speaking, in the expansion of the Lapita people, and presumably when there was a chance for more genetic and cultural exchange among the indigenous and the newly-arrived dispersing populations. A variety of other innovative alternatives are also being developed for determining

non-phylogenetic histories of different traits,^{47, 68-70} approaches that are especially well-suited to situations where we cannot be entirely confident of a pure tree solution.

Spurning trees altogether, some have argued that horizontally transmitted traits are better represented by maximally connected networks or reticulated graphs⁷¹. Others have employed spatial methods that focus on the geographic clustering of traits. If traits are transmitted horizontally between societies through such diverse behaviors as copying, trade or intermarriage, the similarities and dissimilarities among cultures might best be represented by the frequency and intensity of contact among populations, the potential for which is likely associated with geographic distance between societies. Following this reasoning, Guglielmino et al.²⁷ developed a clustering index that expressed the degree to which geographically close societies share traits (also see ref. 25). Such methods provide useful insights into the interconnections between societies, but tend to obscure vertical transmission, just as tree-based approaches obscure horizontal transmission. Consequently, major breakthroughs in attempts to unravel horizontal and vertical transmission lie in tackling both patterns simultaneously.

Studies that look at the correlations between genetic and cultural (usually linguistic) variation while controlling for spatial distance are particularly useful. Nettle and Harriss⁵⁷ review evidence showing how the worldwide association between linguistic and genetic classifications⁵⁵ is in fact quite variable across regions. Following Sokal's⁵⁶ lead, they investigate the residual relationship of genetic and linguistic affiliations once geographic distance is controlled. They find that in Europe, and to some extent in East and Central Asia, linguistic and genetic distances are correlated even when geographic distance is controlled; in South East Asia and West Asia language relatedness declines with increasing geographic distance, but is not associated with genetic distance, and in West Africa language is associated neither with geography nor genes. One lesson from this analysis is that non-correlation of genetic and linguistic diversity can be as informative about past population processes as their correlation, suggestive of an absence of large-scale demic diffusions and more prominent areal diffusion.⁵⁷

Rather than treating geographic distance (and hence the potential for horizontal transmission) as a control variable, a more sophisticated approach is to weigh the relative

evidence for different transmission mechanisms. In one of the first empirical studies to attempt such an analysis, Guglielmino et al.²⁷ used data from Murdock's Ethnographic Atlas to examine the fit of cultural traits to three different models of trait evolution: demic diffusion (vertical transmission), cultural diffusion (horizontal transmission), and ecological adaptation (independent evolution). The authors use contingency tables to examine associations of a trait with language (a measure of historical relationships) and ecological setting (a measure of independent adaptation to environments), comparing the results to the trait's clustering index (described above). From such comparisons, they attempt to draw broad conclusions, for instance that a model of vertical transmission is supported for "family and kinship" traits, with horizontal transmission supported for other traits, such as "labor division by sex". **Given the frequency with which this innovative study is cited for supporting vertical transmission, it is worth pointing out that the authors' approach to model evaluation and statistical inference is not entirely sound.** It rests heavily on two unsound practices⁷² – interpreting p-value levels as indicative of the strength of evidence for a particular pattern (focusing only on results with $p < 0.005$), and asserting the null hypothesis for non-significant findings (even findings meeting traditional standards of significance). For example, when one considers their oft-cited result that "family and kinship" traits support a model of vertical transmission, eight of the twelve traits considered also correlate significantly ($p < 0.05$) with their ecological measure, and for over half of the traits the geographic clustering index falls within the range observed for their "labor division by sex" category, which they argue shows a high degree of clustering (taken as evidence of horizontal transmission). So although we see their effort to compare alternative models as progressive, a more rigorous approach to model comparison⁷³ should be undertaken before any general conclusions (e.g., ref. 7) regarding the relative importance of vertical and horizontal transmission are warranted.

A final and more satisfactory approach to investigating cultural trait transmission is to represent expected distributions of trait values under particular types of transmission mode. The statistical fit of the observed versus expected distribution of cultural traits can then be compared.⁷⁴⁻⁷⁶ One approach uses partial Mantel tests to study the association between genes, trait values and geography. Thus Pocklington⁷⁴ examines associations between cultural traits and geographical and genetic distance matrices, partialing out the effects of shared history (vertical

transmission) and geographic proximity (horizontal transmission). For a sample of 32 of Guglielmino et al.'s societies, he finds that some traits, such as religious practices, are correlated with geography, while other traits show stronger correlations with genes or language groups (e.g., characteristics of the social hierarchy and familial organization). Moreover family traits fall into two broad clusters – one apparently quite labile and the other showing strong vertical transmission. In a similar vein Holden and Mace⁵⁹ use multiple regression to examine how sexual dimorphism, women's work, agriculture, hunting and polygyny are associated with linguistic and geographical distances. They find that four of the five traits (and marginally women's work) are significantly correlated with linguistic similarity among populations, and that two of the traits (women's work and agriculture, and marginally sexual dimorphism) are correlated with geographic similarity. This approach seems reasonable – casting the question of what influences trait diversity into a multivariate framework – and notably shows more complex patterns.

Remaining Challenges in Untangling Transmission Patterns

We have so far seen that anthropologists have an exciting set of tools—both borrowed from other disciplines and inherited from our intellectual ancestors—to study the extent of horizontal and vertical trait transmission. We have also seen that to understand cultural macroevolution, we need to put the historical *and* geographic context of trait variation onto a level playing ground in which neither vertical nor horizontal transmission is methodologically privileged.

Given our limited knowledge of horizontal and vertical transmission in real-world datasets we can, like biologists,⁷⁷ use simulation to evaluate the consequences of different transmission modes for broad patterns of cultural evolution. Computer simulation provides insights to cultural evolution by generating comparative datasets with known degrees of horizontal and vertical transmission, along with information on the historical and geographical relationships among different societies, while forcing the investigator to produce explicit models of trait evolution. We used such a simulated dataset to test whether partial Mantel tests can discriminate vertical from horizontal transmission under different conditions (Box 3). Our results

show, as expected, that under conditions of low horizontal transmission phylogenetic distance was a better predictor of trait distance than geographic distance, and that the opposite was true in conditions of greater horizontal transmission. However the key finding was that the Mantel test's ability to detect different models of trait transmission is relatively crude and imprecise, at least as implemented in this model.

(Box 3 here)

This worrying finding in part reflects the fact that the geographic and phylogenetic distance matrices produced by the model were significantly correlated in most of the simulations. Unfortunately, this is also likely to be true in the real world: as we have noted above, cultures that are closely related in historical terms (as measured by genetic or linguistic differences) are also likely to be geographically clustered. Consequently, history and geography (and also ecology) often covary, as evidenced in practically every study that looks at geography and history together.^{27, 28, 59, 61, 74} This generates huge problems of collinearity, that in turn produce unstable statistical models. Furthermore, variables that are more quantitatively coded may provide higher statistical power to detect true effects of geography or phylogeny, potentially making it difficult to compare different traits. **This does not mean that horizontal and vertical transmission cannot be untangled, only that we need to be aware of the pitfalls in assuming that one mechanism dominates when the other has not been carefully considered.**

There is also plenty of evidence to suggest that transmission modes vary in different world regions, and across different scales, and that they are not necessarily trait-specific. First, consider world regions. There are four regions where vertical transmission seems predominant, at least as regards language. Demic expansions appear to account for linguistic patterns in the Pacific,²¹ in Europe (the Indo-European language expansion),⁵ in East and Central Asia, with the spread of Sino-Tibetan and Altaic speaking peoples,⁵⁸ and in the Bantu areas of Sub-Saharan Africa.²² Horizontal transmission dominates more clearly in other regions. For example, the languages of western North American Indians diffused widely, and "linguistic features spilled across dozens of languages, creating the linguistic counterparts to culture areas".^{78, page 79} In an analysis of this variability Nettle and Harriss⁵⁸ show how the famously tight correlations between language and genetic differences⁵⁵ occur only under specific conditions, such as where there have been large scale demic diffusions in the past few thousand years followed by sedentism⁷⁹;

in areas that have been settled for a long time language-gene associations tend to break down. Second, patterns of transmission are likely to reflect the geographic scale of analysis, specifically the distance between sampled populations. In Hewlett et al.'s²⁸ study of transmission mechanisms in Africa the *average* pairwise distance is 3000 kms, whereas in Jordan and Shennan's⁵¹ study of Californian basketry the two *furthest* samples are roughly 1500 km apart. It seems plausible that horizontal transmission would more likely occur at local scales (as was indeed the case in the basketry study), rather than at more broadly-defined regional or global scales. Scale also enters into consideration in relation to how cultural traits are defined. We suggest that traits such as matriliney or patriliney are less likely to diffuse horizontally than are traits that are measured simply in terms of their prevalence, as with our polygyny example. As discussed in Box 2, the prevalence of polygyny may be driven by characteristics of neighboring groups – are they cattle (or wife) raiders, what is their population density, do they have a shortage of agricultural land?⁸⁰ Conversely, neighboring populations are perhaps less likely to adopt an entire inheritance system, shifting from patriliney to matriliney, as a result of the behavior of their neighbors.⁸¹ Finally it is quite possible that a specific trait may show vertical transmission in one context and horizontal transmission in another. Polygyny, for example, is often considered to be part of a core of conservative cultural family traditions,^{24, 27} evidenced (at least superficially) by the kind of phylogenetic distribution that we presented for East Africa in Box 2. In Western North America, by comparison, there is little evidence of vertical transmission (Box 4).

(Box 4 here)

Given these arguments, generalizations about the transmission pattern of a particular trait at different spatial scales, and between different world regions, will often be misleading. Similarly generalizations across traits, or even the same trait coded in different ways, might be problematic. **We conclude that most traits will exhibit a combination of horizontal and vertical transmission, with horizontal transmission dominating at some times and vertical transmission at others, and that assumptions cannot substitute for better empirical investigation.** But whatever the mode of transmission we are still left with the question, why? Studies of cultural evolution must address not only the source of cultural traits (vertical, horizontal, or independent innovation), but also the reasons why certain traits are adopted.

IMPLICATIONS FOR THE STUDY OF ADAPTATION

As noted at the outset, anthropologists commonly attribute cultural differences to three factors – vertical transmission, horizontal transmission or independent innovation. Almost universally only the latter is cast as the adaptationist hypothesis. For example Hewlett et al.²⁸ examined whether the distribution of an array of cultural traits supported hypotheses for demic transition, cultural diffusion or ecological adaptation. The authors find rather few correlations with ecological differences and conclude that the role of ecological adaptation in explaining cultural similarities and differences is minor (despite elsewhere recognizing the need to separate explanatory models from mechanisms of transmission). **In our view these studies do not provide an adequate test for adaptive function. Vertical and horizontal transmission are not alternatives to adaptation. Traits that diffuse across cultural boundaries are not necessarily functionally neutral.** If high marriage payments spread to a neighboring population with low divorce rates, and not one with high divorce rates, is it accurate to portray this as a case of cultural diffusion rather than as one of adaptation? It seems to us that neither vertical nor horizontal transmission provide evidence against adaptation, and that adaptation can be involved in both the transmission of traits from parent to daughter populations and in the borrowing of traits from neighboring populations.^{53, 82}

Tests of adaptation are based on hypotheses for correlated evolution, for example that polygyny will evolve in the presence of patrilineal inheritance and bridewealth⁸³ or monopolizable resources.⁸⁴ Anthropologists have recently adopted biology's phylogenetic comparative method^{44, 85, 86} an approach that uses phylogenetic reconstruction to identify independent instances of trait changes as opposed to simply counting trait co-occurrences across tree tips. These methods have drawn attention insofar as anthropologists' previously favored solution, using a sample (e.g., the SCCS) designed to maximize independence,⁸⁷ provides inadequate correction.⁸⁸ Although phylogenetic methods have drawn criticism for failing to recognize that for highly functional facultative traits the influence of history (vertical transmission) may be washed out by adaptation to current conditions,^{32, 89-91} and for eliding questions regarding the origins versus the maintenance of traits,^{92, 93} we focus here only on the question of how sensitive they are to the predominant mode of trait transmission, sticking to our

theme of cultural trait transmission. Since the generality of vertical transmission mechanisms is by no means well established (as discussed earlier), and this assumption is rarely evaluated quantitatively before application of phylogeny-based methods, this is an important question.

Again, computer simulation is illuminating. Using the program introduced in Box 3 we investigated the extent to which tests for correlated evolution using phylogenetically independent contrasts⁸⁵ are sensitive to the horizontal transmission events that are possible with cultural data.⁹⁴ Specifically, we investigated whether an increasing probability of horizontal transmission reduces the statistical performance of independent contrasts, focusing on Type I errors (incorrectly rejecting true null hypotheses of no association between traits). When considering traits that were entirely uncorrelated, we found, as anticipated, that Type I error rates increased with increasing probability of horizontal transmission (FIGURE 2); notably too, analyses that were not corrected for phylogenetic distance also showed increased Type 1 error rates as horizontal transmission increased.

More broadly, our simulations show that results can be misleading when borrowed innovations are treated as traits that are transmitted vertically, or in other words when we overlook the possibility that each cultural trait has its own tree.⁶⁸ **We do not argue that horizontal transmission is a non-adaptive process, rather that when horizontal transmission is ignored, a phylogenetic approach to understanding cultural variation misrepresents the history of trait evolution, including the statistical evidence for correlated evolution of traits.** The effect of this error on studies of cultural trait evolution is unknown, although our simulations suggest that it could be quite substantial. In a similar vein, recent empirical work in biology on rapidly evolving traits such as bird song suggests that trying to correct for phylogeny when unnecessary can introduce serious error.⁹⁵

CONCLUSIONS

The analogy between cultural and biological evolution is by no means perfect. Current understanding of the relative importance of horizontal and vertical transmission is shaky, to say

the least, and recent reviews focusing only on positive evidence for vertical transmission do a disservice both to empirical evidence and to the suite of new approaches now available.

We are not claiming that phylogenetic methods are useless, only that their results be interpreted with caution. Just as evolutionary biologists and biological anthropologists are careful to check the assumptions of independent contrasts, anthropologists should develop assumption checks appropriate for the questions that interest them.^{86, 96} In our view the relative importance of vertical and horizontal is still an empirical question and will remain so until methods are implemented that avoid prioritizing one or another transmission mechanism. Luckily new methods are increasingly available: in addition to the approaches discussed here, further methodological breakthroughs are on the horizon, as evolutionary biologists grope with horizontal transmission⁷⁰ in their analyses of the reticulate origins of life among Bacteria, Eukarya and Archaea.⁹⁷

Finally we must be more creative in our use of data. To date only geographical proximity is used as a measure of the potential for horizontal transmission. If we are to uncover past opportunities for cultural diffusion we will need other sources of evidence for historical interconnectedness among societies,⁹⁸ such as trade, loan words,⁴⁷ and trees modified to show inter-group contact histories⁶⁷.

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BOX 1. GLOSSARY

Comparative method: Comparison of the values of a set of variables for multiple species or populations, with the goal of understanding relationships or trends among these characters and how they have influenced patterns of evolution. Such correlations are often used to test adaptive hypotheses.

Culture: acquired information, such as knowledge, beliefs and values that is inherited through social learning and expressed in behavior and artifacts

Cultural evolution: culture changes according to a set of processes similar to those by which species change, for example selective retention of favorable cultural traits, as well as other nonselective processes such as drift.

Cultural traits: behavioral characteristics of human societies that are potentially transmitted by non-genetic means. Not all human behavioral variation is culturally transmitted; some traits have a genetic component, while others reflect direct adaptation to the environment potentially through trial and error learning (Boyd and Richerson's notion of "guided variation" ⁹).

Ethnogenesis: cultural evolution occurs through the borrowing and blending of ideas and practices, and the trade and exchange of objects, among contemporary populations; the source of change is external.

Horizontal transmission: Occurs when traits are borrowed or copied from other extant societies, often neighbors, or imposed through conquest or other forms of forcible influence. Horizontal transmission is also called lateral (or in some cases oblique) transmission.

Independent contrasts: A method to deal with the non-independence of species values in comparative tests of biological hypotheses. Briefly, the method calculates differences between two taxa (species or higher nodes) since they last shared a common ancestor.^{85, 96} After controlling for time since divergence, these contrasts are used in statistical tests of hypotheses or to generate new hypotheses.

Macroevolution (cultural): the evolution of cultural traits that characterize societies or populations, not individuals.

Perfect phylogenetic networks: a phylogenetic method that identifies borrowing "contact edges" within a tree structure.

Phylogenetic comparative methods: comparisons that test hypotheses that a specific *derived* cultural trait arose in response to selection pressures in a new ecological or social context.

Phylogenesis: cultural evolution takes the form of descent with modification through a successive subdivision of cultural assemblages, with the source of change being internally generated.

Phylogenetic signal: the extent to which the historical relationships among cultural traits can be plotted as a branching tree structure.

Phylogeny: Defined in biology as the evolutionary history of a group of organisms; referring in this paper to the historical relationships among societies or traits that are plotted as a branching tree structure. Phylogenies may be based on genes, language or other cultural characters.

Retention index (RI): Measures the number of steps a tree requires independent of its length. RI varies between 0 and 1, with a RI of 1 indicating that a tree has the minimum number of changes possible for that character (i.e., no homoplasy).

Reticulate evolution: A tree that exhibits non-bifurcating structure due to matings that occur among lineages (e.g., hybridization in biological systems).

Society: Here denotes an ethnographically described distinct unit, identified (in many studies) on linguistic as well as ethnographic grounds. Often used interchangeably with the term “cultural group” or “population”. Complete boundedness of the unit is not assumed, yet contemporary societies are thought to be related to ancestral societies through descent with modification.

Split decomposition: a phylogenetic method that does not assume a pure tree model and therefore can be used to investigate conflicting signals in empirical data, and portray them both as parsimony trees and as “splits graphs”.

Vertical transmission: Occurs when daughter populations inherit cultural traits from parent populations through the cumulative effects of individual-level teaching, learning and imitation during the production of the next generation. More diffuse processes of cultural/institutional persistence or inertia are often termed tradition.

BOX 2. VERTICAL AND HORIZONTAL TRANSMISSION OF TRAITS

As with phylogenetic patterns across species, a cultural trait may arise multiple times. When direct historical information is lacking on the diffusion of traits across societies, however, reconstruction of ancestral states can be misleading. The figure below (Figure A) represents the evolution of polygyny in a subset of the societies used by Borgerhoff Mulder et al.⁶¹ under two extreme scenarios. On the phylogeny at left, polygyny (coded as greater than 20% of men in a society are polygynous) evolves one time in the common ancestor of the Karamojong-Kipsikiis clade, with subsequent vertical transmission to descendent societies and one loss of the trait in one society (Karamojong). On the phylogeny to the right, however, polygyny arises on a terminal branch (Datooga) and shortly thereafter spreads to neighboring societies. (Note that although polygyny is usually thought to be ancestral in humans, on this smaller clade it appears as a derived trait.)

(Figure A here)

Given only information on the distribution of characters states at the terminal tips, a strictly phylogenetic approach would reconstruct the situation in which the trait is transmitted vertically (left panel). With the additional geographic information presented in the map (Figure B in Box 2) the case for the tree in the right panel can be made. Since most of the societies in the Karamojong-Kipsikiis clade lie in closer vicinity to each other than to the societies with rare polygyny (Murle, Acholi, and others), it is quite plausible that polygyny is transmitted between neighbors, particularly in contexts in which fraternal interest groups raid cattle from surrounding ethnic groups in order to acquire the bridewealth for multiple marriages, or to settle new territory.⁸⁰ In reality the truth probably lies somewhere in between, with rates of polygyny varying both in response to socioecological conditions⁹⁹ and reflecting an ancestral tradition.⁶¹ It is worth adding a point to which we will return, that horizontal transmission is much more likely to occur (and to be detected) in fine grain regional studies such as this, where the mean and maximum distances between populations are about 300 and 1100 kms, respectively, than in, for example, a pan African study where the equivalent figures are approximately 3000 and 8000 kms.²⁸

(Figure B here)

BOX 3 SIMULATING CULTURAL EVOLUTION

To test the ability of statistical methods in discriminating vertical from horizontal transmission under different conditions, Nunn et al.⁹⁴ have written a computer program that simulates cultural evolution in a spatially explicit framework and allows for horizontal transmission of trait values, evolution of discrete and continuous traits, and extinction and diversification of existing populations. The goal is to simulate different transmission processes under varying probabilities for model parameters, rather than to conduct phylogenetic analyses. The simulation begins with a single population that inhabits one cell in a matrix. Populations can expand to one or more adjacent cells if they are empty, or populations can go extinct, with user-set probabilities of expansion or extinction. Populations that diversify to new cells are treated as distinct societies in the next round of simulation. Through a Brownian motion model,⁸⁵ continuous traits evolve over time, while evolution of discrete traits is based on user-defined probabilities of changing states in each generation. Vertical transmission occurs through the inheritance of trait values from one generation to the next, as well as through diversification of populations into empty niches. Horizontal transmission occurs stochastically, with the user defining the probability that a population borrows a trait from a neighbor.

(Figure A here)

Example output is provided for a continuous trait (Figure A), with each cell of the lattice representing the spatial location of each society in relation to the others. These data were simulated under the same parameters (number of generations=100, probability of a population expanding to open cells=0.9, probability of extinction=0.07, probability of horizontal transmission=0.05, variance of trait change=0.005). The table reveals that societies that are in close spatial contact tend to share trait values. Based on a Mantel test using 5000 permutations of simulated output, this pattern is significant for continuous data ($P=0.0002$), for which the standard Mantel test is most appropriate. Three sets of continuous variables are identical in spatially close societies (shaded cells in Figure A), representing horizontal transmission or diversification of a population into an open cell in the final generation of the simulation.

We used this program to examine the performance of Mantel tests in assessing vertical versus horizontal transmission, with the expectation that geographic distance provides a better estimate of cultural trait variation as the rate of horizontal transmission increases;⁹⁴ conversely, phylogenetic distance should give a better estimate as horizontal transmission declines. We found general support for our prediction (Figure B). Increasing horizontal transmission rendered geographic distance a better predictor of trait distance and phylogenetic distance a poorer predictor of trait distance. However although our prediction was supported, the majority of tests detected significant correlations between distance matrices. Even at the highest levels of horizontal trait transmission ($P_{\text{horizontal}}=0.15$), the phylogenetic distance matrix was significantly associated with trait distance in 51.2% of the simulations. At the opposite extreme, with $P_{\text{horizontal}}=0$, the geographic distance matrix was significantly correlated with the trait matrix in 19.8% of the simulations. Furthermore the actual amount of variation explained by horizontal and vertical transmission depended significantly on other parameters, such as rates of societal extinction, rates of trait evolution, and the configuration of societies.

(Figure B here)

BOX 4 POLYGYNY PREVALENCE IN WESTERN NORTH AMERICA

We showed in Box 2 how the results of mapping polygyny onto an independent linguistic phylogeny can appear, at least superficially, to indicate vertical transmission. Here we show how the transmission mechanism for the same cultural trait might differ in different parts of the world, or in different language families. We present a contrast to the East African marriage patterns by looking at data from the Western North American Indian Data Set (WNAI).⁷⁸ In each of the 172 societies in the WNAI, monogamy is reportedly the dominant form of marriage (accounting for “about 60 percent or more of all marriages”^{100, pages 235-236}). That said, polygyny is also present in the vast majority of societies – in only 16% (n=28) is polygyny reported to be rare or absent.

In a recent analysis of polygyny in the WNAI, Sellen and Hruschka⁸⁴ analyze a subset of 118 societies according to whether polygyny prevalence is “low” (0-10%, n=84) or “high” (11-25%, n=34). Although cultural transmission mechanisms are not the main focus of the study, Sellen and Hruschka recognize the possible implications of lack of independence between societies and categorize their sample according to “Major Amerind Language Phylum” (n=5 phyla). There does appear to be some large-scale relationship between polygyny incidence and language, with two phyla (the Central Aztec-Tanoan and Hokan Northern) including only a single society with a high prevalence of polygyny. In contrast, the distribution of polygyny within the other three phyla (Penutian Northern, Na-Dene, and Almosan-Keresiouian Northern) suggests no simple phylogenetic history (Figure B). In fact, Sellen and Hruschka report that they do “not use certain prevailing methods of phylogenetically based comparative methods” because of the high “volatility” of polygyny prevalence “over the linguistic phylogeny” (p. 712, see also CA+sidebar H). Even the most parsimonious mappings of polygyny onto the linguistic phylogeny indicate a minimum of 15 independent gains of high polygyny prevalence and 4 losses.

So, in contrast to the East African sample, why would polygyny prevalence show such “volatility” in this set of societies? Possibly it reflects the acute ecological sensitivity of this highly facultative trait, in conjunction with relatively greater ecological variation in production

systems in western North America than East Africa. Indeed the authors' hypothesis that polygyny prevalence correlates with male control over extracted-food resources is strongly supported by the data, most notably for terrestrial and aquatic game resources. Where such tight ecological relationships are found, the influence of history (vertical transmission) may quickly be washed out by adaptation to current conditions.⁸⁹⁻⁹¹ For highly facultative traits it is therefore possible that phylogenetic analyses will not only prove intractable but could also be misleading.

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Figure 1. Kroeber's depiction of organic and cultural evolution.

The branches on the left constantly diverge whereas those in the tree on the right branch and then join, creating a reticulated tree structure (taken from ref. 36).

Figure 2. Type I error rates and horizontal transmission.

Plot shows how the probability of horizontal transmission impacts Type I error rates ($\alpha=0.05$) for independent contrasts (+) and non-phylogenetic tests (circles). Plotted values reflect the proportion of results in the simulation run ($n=1000$) in which a significant association was found between the two (uncorrelated) traits. Since the traits used in the simulations were uncorrelated, the proportion of results in the simulation producing significant associations should not exceed 0.05. (From ref. 94, Figure 5, in a 6x6 matrix with probability of extinction equal to 0.02).

Box 2 Figure A
 Two scenarios for the evolution of polygyny in East Africa

Box 2 Figure B

Map of East Africa showing populations in polygyny analysis

A circle denotes polygyny rare (<20%) and a star denotes polygyny extensive (>20%)

Box 3 Figure A

A lattice of 40 societies showing trait values after final simulation run

Similar grids can be produced for discrete data. “Rows” and “Columns” indicate different societies in their spatial orientation in this lattice structure.

-0.735	-0.514	-0.476	-0.249	-0.152	-0.119	-0.131	0.858
-0.571	-0.615	0.001	0.587	0.587	-0.230	-0.081	0.842
-0.247	0.028	-0.041	0.458	0.005	0.624	1.273	1.273
-0.041	0.557	0.307	0.689	0.314	0.401	-0.473	1.273
0.363	0.256	0.735	1.017	0.741	0.401	1.163	1.263

Box 3 Figure B

Detecting trait correlations with phylogenetic and geographic distance matrices

Plot shows the probability of detecting a significant association between the trait matrix and the phylogenetic distance matrix (open circle) or geographic distance matrix (closed circle) in a 6x6 matrix with probability of extinction equal to 0.02. (From ref. #94, Figure 7).

Box 4 Figure A

Polygyny in the Na-Dene language phylum

One section (the Na-Dene language phylum) of the phylogenetic tree Sellen and Hruschka (ref #84) use in their mapping of polygyny prevalence on a linguistic phylogeny for their NWAf sample. The root is reconstructed as low polygyny based on evidence from the whole tree not just the NA-dene phylum. (Unpublished tree data kindly provided by Sellen and Hruschka).