

Research

Macro-evolutionary studies of cultural diversity: a review of empirical studies of cultural transmission and cultural adaptation

Ruth Mace^{1,*} and Fiona M. Jordan²

¹*Department of Anthropology, UCL, 14 Taviton Street, London WC1H 0BW, UK*

²*Evolutionary Processes in Language and Culture, Max Planck Institute for Psycholinguistics, PB310, 6500 Nijmegen, The Netherlands*

A growing body of theoretical and empirical research has examined cultural transmission and adaptive cultural behaviour at the individual, within-group level. However, relatively few studies have tried to examine proximate transmission or test ultimate adaptive hypotheses about behavioural or cultural diversity at a between-societies macro-level. In both the history of anthropology and in present-day work, a common approach to examining adaptive behaviour at the macro-level has been through correlating various cultural traits with features of ecology. We discuss some difficulties with simple ecological associations, and then review cultural phylogenetic studies that have attempted to go beyond correlations to understand the underlying cultural evolutionary processes. We conclude with an example of a phylogenetically controlled approach to understanding proximate transmission pathways in Austronesian cultural diversity.

Keywords: cultural transmission; cultural diversity; cultural adaptation

1. ADAPTIVENESS AND MALADAPTIVENESS IN CULTURAL EVOLUTION

Humans are an extremely successful species, able to inhabit almost any environment on Earth. The way in which we do that is undoubtedly aided by a range of subsistence strategies that span from simple extraction techniques to extensive agricultural production. These diverse strategies were facilitated by our complex cognitive skills, especially our ability to observe the behaviour of others, learn from it, and then possibly improve on it, and pass that knowledge on to our descendants [1]. Cumulative cultural evolution saves us the costs of individual trial-and-error learning each generation, enables us to benefit from the discoveries of previous generations and undoubtedly has given us the edge over other non-cultural or proto-cultural species.

Given how clearly culture has been so useful for our species, it is perhaps surprising that most cultural anthropologists do not consider most cultural behaviour to be adaptive—certainly not in the Darwinian sense at any rate [2–4]. And while most evolutionary anthropologists would consider our evolutionary endowment as a cultural species and the ability to learn from others as an adaptation, probably as much attention has been focused on explaining how cultural transmission (or social learning) could generate apparently maladaptive aspects of

human behaviour as has focused on cultural transmission's benefits in helping humans adapt to their environments. Relatively few studies have tried to examine proximate transmission or test ultimate adaptive hypotheses about behavioural or cultural diversity at the macro-level. Here, we examine these ideas and suggest that phylogenetic approaches are a fruitful way in which cultural evolution at the macro-level can be explored.

Adaptations are features of organisms that are designed by natural selection to maximize inclusive fitness. Behavioural ecologists use three main approaches to test adaptive hypotheses about the evolution of behaviour: experimentation, testing the predictions of optimality models and the comparative method. When a particular adaptive model fails to explain observed phenomena, the usual *modus operandi* is to seek a better model, assuming that some vital cost or benefit has been overlooked; hence our understanding of the evolutionary basis of that behaviour is enhanced by ruling out multiple alternative explanations.

There are a number of reasons why behaviour may not be adaptive. The most important one is that a rapid change in the environment will cause temporary maladaptiveness, as evolution takes time to work. This is often referred to as a 'mismatch' argument, or an example of 'evolutionary lag'. If the proximate mechanisms for social learning or other determinants of behaviour (such as preferences) evolved in environmental conditions that are no longer current, then emergent behaviour may no longer promote fitness. Unfortunately, these mismatch arguments are difficult

* Author for correspondence (r.mace@ucl.ac.uk).

One contribution of 14 to a Theme Issue 'Evolution and human behavioural diversity'.

to test, partly owing to testing a negative, but also simply because it is difficult to establish what the costs and benefits of behaviour were in an environmental or cultural context that no longer exists. The question of how long behavioural adaptations take to evolve is not likely to have a unitary answer for all contexts. A number of recent studies have given us a window on the pace of genetic evolution in the face of cultural changes in subsistence practices. Lactose tolerance has evolved multiple times among those keeping livestock for dairy [5,6], alleles protective against prion-based neurodegenerative disease (kuru) in the Fore of New Guinea have been selected for by cannibalism [7] and the frequency of alleles associated with alcohol dehydrogenase appears to map onto the history of rice cultivation in south Asia [8]. These all provide demonstrations of recent strong selection causing rapid evolution, occurring within the past few thousand years or less, in genetic traits associated with changes in the subsistence strategy and diet. The complexities of behavioural genetics [9] and epigenetics mean that clear signatures of how specific genes influence behaviour are likely to remain elusive and poorly understood, but it would nonetheless seem unlikely that behavioural adaptation is altogether slower than digestive adaptation.

Evolutionary psychologists who assert that our behaviour is adapted to Pleistocene, or 'composite' species-wide conditions, have faced opposition [2]. Cultural evolution can be much faster than genetic evolution, so mismatch arguments for maladaptiveness in cultural traits are perhaps on even shakier ground than mismatch arguments about genetic traits. Some have argued that cultural evolution may have in fact caused genetic evolution to accelerate [10], perhaps by generating so many new niches. Alternatively niche construction could be a mechanism by which humans can avoid mismatches between their environment and their optimal living conditions [11,12].

Because generalized social learning rules may promote the spread of a cultural trait, but not necessarily the inclusive fitness of the person performing the associated behaviour(s), some evolutionary anthropologists take the position that cultural inheritance mechanisms can generate stable outcomes that result in behaviours that are not necessarily adaptive in the genetic sense [13]. Social learning enables cultural traits to move between individuals in a non-Mendelian way. Many cultural traits are copied directly from biological parents, but it is also true that learning rules might involve a range of possible 'cultural parents' chosen on grounds of frequency of contact, proximity, prestige, efficacy or any other criteria, often referred to as biased transmission [13]. Variation in the possible modes of cultural transmission can therefore influence the types and dynamics of cultural behaviours that evolve. For example, the transmission mode of conformist bias (copying the common cultural traits in your group) can cause cultural groups to resist invasion by mutant cultural types. This could allow between-group variation to be maintained long enough to be subject to cultural group selection; this might lead to the evolution of traits that favour the group [14]. However, the cultural evolution of traits that spread via their benefits to the whole group might be rather slow [15].

One example of a model of how transmission mechanisms alone can be invoked to explain maladaptive behaviour is presented in Tanaka *et al.* [16]. They explore the role of social learning mechanisms in explaining the persistence of self-prescribed medical treatments that have no efficacy: so-called 'traditional', 'alternative' and even some modern medical treatments. In this example, individuals are modelled to copy self-medication treatments in proportion to the rate at which they observe those treatments being used by other individuals suffering medical conditions similar to their conditions. This very interesting paper makes some counterintuitive predictions, including, for example, that if a user takes the treatment for a longer period of time because the illness does not get better, then the opportunity for them to become a model for other social learners increases [16]. This means that behaviour might persist because social learning is generally more effective than trial and error, but can lead to copying harmful traits in some circumstances. This is essentially a proximate explanation for why a harmful or neutral behaviour might persist. However, one might expect humans to improve their learning mechanism over time; perhaps using a more sophisticated rule about when and when not to use social learning could enhance inclusive fitness in the long run. Thus, the explanation for the persistence of the use of ineffective medical treatments becomes based either on constraints (the task at hand is simply beyond the capacity of the human mind to resolve) or a mismatch argument at the level of the mechanism, which is set to random copying. This is not to say that the model does not provide a convincing *proximate* explanation for the observed phenomena of useless self-medication. Such cultural evolutionary models have as yet rarely been parametrized by fitting to datasets from real behaviour, and are supported only by the observation that the general phenomenon described does exist. So, as yet, it is hard to know how frequent such cases of truly maladaptive behaviour, arising owing to social learning, really are.

2. TESTING HYPOTHESES ABOUT ADAPTATION IN HUMAN CULTURAL BEHAVIOUR THROUGH CROSS-CULTURAL COMPARISON

There is no theoretical reason why the study of human cultural adaptation should not be investigated in roughly the same manner as behavioural ecologists seek adaptation in the natural world, although human studies can present additional challenges. In anthropology, experimental manipulation of cultural or environmental conditions, such as the subsistence system, are rarely possible in a naturalistic setting. Sometimes, it is possible to make use of development interventions or similar to find 'natural experiments' [17]. Optimality models are very useful, and have been used to show how human behaviour can be understood as adaptive in certain environments in a number of domains, especially to foraging theory and reproductive behaviour (topics beyond this review, some of which are discussed elsewhere in this volume). These approaches use individual-level variation within populations. These individual-level

effects can also explain wider cultural differences, although cultural differences are, almost by definition, a property of the group rather than a property of the individual; and individual deviation from cultural norms can be strongly suppressed (e.g. by legal restriction or ostracism). So, when interpreting cultural differences, a cross-cultural comparative method becomes a key tool. Cross-cultural comparison was indeed the historical basis of anthropology.

(a) *Ecological correlates of human social behaviour*

An intuitively appealing method with which to understand ecological adaptation is to examine how human social traits covary with ecological variables across cultures. In a recent review of a number of such studies, most cultural traits examined were found to be correlates of parasite prevalence and/or latitude [18]. Latitude itself correlates with parasite load, as there are more species near the tropics, including parasites. Thus, the latitudinal gradient in cross-cultural human ecology is rather similar to socio-economic status within human populations: nearly everything correlates with it, and it is very hard to control for fully. For this reason (and others, below), many of the studies listed in Nettle [18] are in danger of serious misinterpretation: for example, polygynous marriage, promiscuous socio-sexuality, high fertility and a more female-biased sex ratio are all more common in the tropics where there are more parasites. Is this due to parasites? Or to alternative explanations: to different subsistence strategies related to non-parasitic aspects of ecology, to alternative cultural histories and trajectories in Africa and Europe, or due to economic development that for various reasons has occurred more in the north than the south, or other reasons [19]? As an example, Mace & Jordan found that, worldwide, female-biased sex ratio at birth correlated with high fertility and mortality rates, even after controlling for phylogenetic relationships between groups [20]. Our interpretation was that high costs of reproduction caused fewer male births, in line with sex-ratio theory. High fertility and mortality covary strongly with economic development (and the progress of the demographic transition) as well as parasite load and latitude, so an association with high fertility could underlie the geographical patterns that generate correlations with all these variables. We stress this point because the difficulty of interpreting ecological correlation is nothing new; formal cross-cultural comparisons that confuse correlation and causation through simple association metrics may have contributed to cultural anthropologists becoming so sceptical about quantitative methods that they all but abandoned them.

Modern methods of controlling for cultural and biological history are discussed below (see §2c). But that is only one dimension of the wider problem with correlational studies, which is that they are not explicit about the evolutionary processes that generate the associations observed. One of the advantages of modern phylogenetic comparative methods is that they enable us to discern between

explicitly defined alternative evolutionary models [21,22]. Second, and related to the above, most studies of ecological correlates of behaviour do not address differences in the subsistence system. Subsistence systems influence how human populations get resources from their environment, and they can have a profound influence on human social systems and behaviour.

One recent study that considers changes in subsistence formally evaluates explicit evolutionary models, and is also notable for being a cultural or a gene-cultural coevolutionary study in which models are fitted to real data; this is Itan *et al.*'s [23] simulation of the spread of agriculture and lactase persistence across Europe. It presents a gene-culture coevolutionary model of the emergence of lactose tolerance (lactase persistence into adulthood) as an adaptation to milk-drinking, in a population where individuals can switch between gathering, farming and pastoralism. Lactase persistence shows a strong latitudinal gradient in Europe, which on the face of it supports the hypothesis that it is selected for in ecological conditions with low levels of sunshine owing to vitamin D deficiency [24]. Itan *et al.* [23] fit some of their model parameters explicitly by using Bayesian inference [25] to determine which parameters of the model best predict the present-day distribution of the allele associated with lactose tolerance in Europeans (known as *-13910-T*). This exercise in statistical inference not only locates the likely starting point of this gene-cultural coevolutionary process in central Europe about 7500 years ago, but also shows that the latitudinal gradient in the T allele is not due to stronger selection at high latitudes but simply due to the demographic history of the wave of expansion generated by an increasing density of farmers taking over new territory to the north [23]. The genes for lactase persistence ride on the crest of the wave of advance of territories occupied by the new subsistence strategies, rather than work their way back into existing populations. Holden & Mace [26] also found no evidence for the vitamin D hypothesis for lactase persistence using a global cross-cultural sample and a phylogenetic comparative method. Itan *et al.* [23] show that a model based on demic expansion best explains the patterns of the allele distribution observed today (which, incidentally, they estimate has not yet reached equilibrium). Hence, both proximate models of emergence and ultimate adaptive function are addressed together in a coevolutionary model of subsistence change and human biology.

(b) *How social behaviour is adapted to subsistence strategies*

Changes in the subsistence strategy were instrumental in many of the major evolutionary transitions in human evolution; particularly important was the advent of agriculture, which can be linked with increased population densities, increases in social inequality and changes and divergence in social structure. The behavioural ecology of all these coadaptive changes in kinship, descent and marriage systems is now reasonably well understood.

Hunter-gatherers lived in bands, probably with (serially) monogamous marriage, relatively low fertility, no heritable wealth of consequence and relatively egalitarian social systems. Since the adoption of agriculture and other intensive forms of plant/animal domestication, human social systems have been largely shaped by the existence of important resources (such as fields, gardens, livestock, fishing territories, etc.) that can be controlled or owned (by individuals or by groups) and passed down to future generations. Access to such resources greatly influences the future reproductive success of descendants and generates inequalities in wealth and political power [27]. Population densities increased with the advent of agriculture: more complex political systems emerged, correlating with human ethno-linguistic groups becoming larger and more politically complex [28,29]. Systems of wealth inheritance are fundamentally linked with systems of marriage and the associated transfers of wealth at marriage, and thus marriage and descent systems are products of the socio-economic system on which societies are based. As is well known to behavioural ecologists, if males are able to monopolize access to territory that has the resources required for breeding, then that resource can be used to attract females, who will mate polygynously, if need be, to acquire that resource. Thus, resource-defence polygyny, not dissimilar to that described in birds [30], is also common in humans [31]. As in other species, such polygynous systems can only really emerge where there are sufficient resources for females to raise their children without a great deal of individual help from fathers. Resources such as livestock are particularly associated with polygynous marriage and male-biased wealth inheritance [32]. If the number of grandchildren can be enhanced more by leaving livestock to sons (enabling them to marry earlier and more often) than to daughters, which is the case under resource-based polygyny, then patrilineal wealth inheritance norms doing just that will emerge [33].

Within lineal family systems, patriliney is by far the most common pattern worldwide, but a significant minority (about 17%) of systems described in the *Ethnographic Atlas* [34], are matrilineal. Marriage bonds are often weak in matrilineal systems, with women frequently marrying several husbands over the course of their lives, as resources are passed down the female line. The ecology that is predictive of matriliney is biased towards systems where resources cannot be easily monopolized by males to attract females. In Africa, it is strongly associated with the absence of livestock [35,36]. African crop production is often not land-limited but labour-limited, so, whereas livestock offer women the promise of resources relatively easily accumulated, land of the type that is only of value after back-breaking field labour does not generally provide men with the opportunity to monopolize large areas to attract mates. Women will only remain married to men as long as they help them work the land. In other parts of the world, matriliney has been proposed to be associated with high male mortality and/or absence rates, either because of warfare, as in some matrilineal native American groups [37], or

trade networks and ocean fishing as in the Pacific ([38]; F. M. Jordan 2007, unpublished PhD thesis). Whatever the underlying ecology, women in matrilineal systems rely on mothers, daughters and sisters to support their family, as help from males is often transitory. Paternity uncertainty tends to be high in matrilineal systems, although the extent to which this is a cause or consequence of matrilineal descent systems is a matter of debate [39]. In the case of correlations between subsistence and kinship systems, understanding of how fitness is maximized at the individual level helps explain larger scale cross-cultural patterns.

(c) *Cultural phylogenetics*

Elsewhere, we have argued that phylogenetic comparative methods are an appropriate formal comparative method to use in anthropology [40], just as they are in evolutionary biology [41]. Phylogenetic comparative methods take into account the fact that cultures are not independent of each other, and, in a manner analogous to biological evolution, daughter cultures evolve from mother cultures, generating a tree-like pattern of origin, or a phylogeny. While a bifurcating phylogeny may not be a perfect model for the evolution of cultures (as indeed it sometimes is not even for the evolution of many biological species), it is generally a far better approximation than the model on which other general statistical methods rely, that is, assuming that all societies are related to each other completely equidistantly. Ignoring the ancestor-descendent relationships between cultures can generate significant errors of both types. Furthermore, a powerful set of statistical tools have been developed by evolutionary biologists for understanding diversity, and these go beyond just seeking correlation to examine a whole host of evolutionary processes and questions: rates of change, ancestral states, the tempo and mode of evolution, phylogenetic signal and reticulation [22]. In recent years, we and others have been applying this toolkit to examine cultural evolution; periodic reviews can be found in Mace & Holden [42] and Gray *et al.* [43].

Cultural phylogenetics comprises two related sets of techniques: building phylogenies and using phylogenies. The need to build trees on which to use phylogenetic comparative methods was also partly responsible for a resurgence of interest in inferring historical patterns of human migrations beyond the data afforded by genetics [44]. Cultural trees that track human population history have been mostly built using comparison elements of language, and the bulk of this work has used lexical core vocabulary (word) data (though see [45] for an approach using aspects of linguistic structure). Inferring linguistic trees of population history has been especially productive in some large language families: Bantu [46], Indo-European [47] and Austronesian [48,49], where the trees generated fit well with what linguists, archaeologists and historians believe to be realistic models of population spread [50]. Beyond these three 'great families', phylogenetic tree-building methods have also been applied to other linguistic

data, for example, the Semitic languages [51] and Chinese dialects [52], and archaeologists have also applied these techniques to aspects of material culture. In the case of the large language families, phylogenetic reconstructions have enabled us to arbitrate between different historical migration proposals in cases that genetic, archaeological and other data or methods have not enabled us to distinguish [47,49]. It is probably not a coincidence that these families have had relatively recent dispersals, largely based on technological advances, enabling them to successfully advance into new territories [53]. Language trees may have such a strong historical signal because language is a neutral trait (i.e. the forms of words themselves have no fitness implications) and strong pressures maintain these distinct but consistent forms. These pressures include conformist bias from within (or frequency dependence); you and your children have to speak the language most of those around you are speaking if you are to succeed. Those from without may include forces that act to maintain group boundaries, to signal difference from and promote mutual unintelligibility with one's neighbours. When migrants enter new groups, they may pass their genes into their new population, but they do not usually pass on their language. Gene flow from even one migrant can muddy a genetic tree, so linguistic phylogenies may be much more appropriate models of the population histories with which evolutionary anthropologists are concerned. Language is so tree-like that phylogenetic methods are also now being used to study linguistic evolution itself [54,55].

Building trees is only 'step one' for evolutionary anthropologists who want to test cultural hypotheses using phylogenetic comparative methods. These trees are then used as historical controls in further analyses, as 'step two' involves mapping the cultural traits of interest onto the branches. The first use of phylogenetic comparative methods in anthropology was to examine the coevolution of cultural traits, or cultural and biological traits. Whereas simple regressions across cultures, not accounting for phylogeny, can generate spurious correlations, phylogenetic comparative methods seek evidence for the fact that change in one character on the tree is associated with change in another character, hence providing evidence that the two traits are functionally linked. The method we and others have used most often to examine the coevolution of discrete traits on phylogenies is Discrete [56], which directly compares different models of evolution, including those in which the evolution of two discrete (i.e. taking a value of presence or absence) traits is correlated, and those in which traits are evolving independently of each other. This algorithm can be implemented in a maximum-likelihood—and more recently a Bayesian—framework [57], which is then used to determine which model is most likely to have generated the extant patterns of data observed at the tips of the tree (i.e. in the present) [58]. Because models of evolution are specifically defined in these methods, it is possible to go beyond a simple assessment of correlation to also estimate the most likely direction of causation and to evaluate alternative evolutionary models. Because estimates of (i) ancestral

state probabilities, and (ii) the rate of change between states are derived from the data, it is possible to ask whether a change in one trait drives the change in another, or vice versa. For example, while it has long been known that people living in cultures with a history of dairying are more likely to be lactose tolerant (i.e. able to digest lactose and thus drink milk as an adult), we were able to use Discrete to show that a model in which a shift to keeping cattle preceded a switch to lactose tolerance was a far better fit than a model in which the switch to lactose tolerance occurred before the adoption of dairying—thus providing strong support for the hypothesis that lactose tolerance evolves in direct response to, and as an adaptation to, milk-drinking [26].

Since that early study, we have examined the coevolution of subsistence systems and aspects of social structure such as marriage and descent rules. We have been able to show that in Bantu-speaking populations, patrilineal social systems were associated with pastoralism, whereas matrilineal systems were associated with a lack of cattle-keeping [36]; and the model of direction of change that best fits the data confirmed the hypothesis that a transition to pastoralism precedes a switch to patrilineal descent systems. In other studies, it has been shown that monogamous marriage coevolves with dowry (although in this case the arrow of causation is less clear) in Indo-Europeans [59,60].

Other than examining coevolution, cultural phylogenetic methods have also been used to infer ancestral states. Phylogenetic techniques rely on using the extant distribution of traits, and the phylogeny, to infer which evolutionary processes were most likely to have generated that distribution [58]. This involves attributing a likelihood that any particular node on the tree was at a particular state. In the case of Bayesian methods, the likelihood that that node actually existed (given the uncertainty in the phylogeny) is also taken into account [57]. Hence, implicit in the method is the inference of ancestral conditions. In evolutionary biology, this has actually become the purpose for which Discrete [56] has been most used, and we suspect a similar trend could emerge in anthropology. Social systems rarely leave any trace in the archaeological record, and although sex-specific genetic patterns are often argued to reflect aspects of past human mating systems (e.g. [61,62]), such inferences are usually post hoc discussion points [63]. Most anthropology and ethnography is confined to the present and recent history within living memory or, in exceptional cases, in written or oral histories. Cultural phylogenetic techniques potentially enable us to put pre-history back into anthropology. We have used these techniques to show that the most likely ancestral condition of Proto-Malayo-Polynesian (approx. 4500 years ago) was matrilineal and matrilocal, with patrilineal systems evolving later on in the Austronesian family [64]. Similarly, we have been able to show that dowry and monogamy were probably ancestral in Indo-European [59]. While studies of ancestral condition do not necessarily demonstrate adaptation, they are essential in arbitrating between different causal hypotheses for the origins of cultural traits. For example, if the

ancestral Indo-Europeans were monogamous, then monogamy long predates the emergence of Christianity (which is only about 2000 years old), de-bunking the common assumption that Christianity was the driving force behind monogamy in Europe. It provides support for the notion that prevailing local social systems and conventions generally determine religious rules rather than vice versa.

3. PROXIMATE MODES OF TRANSMISSION BETWEEN CULTURES

(a) *The transmission of traits from mother to daughter cultures*

A key assumption of phylogenetic methods is that the groups under consideration are hierarchically related. Phylogenetic trees to describe these relationships are best inferred from a set of neutral, or near-as-neutral traits, such as lexical data, and the ensuing phylogenies can be interpreted as reasonable models of cultural history, especially if they concur with independent lines of evidence (see §2c). Comparative methods assume that most traits are inherited vertically (along the lineages specified by the branches of trees), rather than transmitted horizontally; but because they estimate the degree to which traits are gained or lost, whether it be spontaneously or by horizontal transmission between groups, and whether this occurs with or independently of other traits, comparative methods provide us with the information we need to distinguish between different models of cultural evolutionary processes.

There is some confusion in the literature regarding horizontal transmission within and between groups, which have very different implications but are not always clearly distinguished from each other. Horizontal transmission within cultural groups (i.e. social learning from one's peers) would be expected if there are such things as a 'cultural norm'—indeed it is almost a prerequisite. It is the degree of vertical and horizontal transmission between groups in traits of interest that is relevant to the use of cultural phylogenetic models. Tree-building does require vertical conservation in the traits used to infer the main pattern of population history, although some horizontal transmission of traits (sometimes called diffusion) between closely related groups is not very problematic for tree-building [65]. When seeking evidence of correlated evolution, horizontal transmission between groups is considered just like any other example of loss or gain of a trait on the branch of the tree. Very high rates of random horizontal transmission can sometimes obscure results, but crucially do not invalidate phylogenetic comparative methods, which still function better than non-phylogenetic models applied to hierarchically related data [66]. And indeed horizontally transmitted traits, such as subsistence innovations like the keeping of livestock, can provide a useful source of cultural variation to use in order to seek evidence for the coevolution of traits [40]. A high frequency of horizontal transmission of a large number of cultural traits would suggest that trees of lexical data are not necessarily good underlying models for the historical patterns of those cultural norms. However, it is worth noting that even the use

of the words 'horizontal' and 'vertical' are predicated on an assumption of an underlying tree-like model. These would in fact be meaningless terms unless we believed a branching process did indeed underpin our population history and hence cultural diversification.

Understanding the mode of transmission for different types of cultural variants, and how those variants are exchanged between groups, is thus an important empirical question, though not explicitly a test of adaptation. Few studies have investigated proximate means of trait transmission in a large cross-cultural context. Guglielmino *et al.* [67] examined cultural variation in 277 sub-Saharan Africa societies coded in the *Ethnographic Atlas* in an attempt to disentangle modes of cultural transmission, while a follow-up by the same group of authors [68] investigated why African cultures were likely to share traits, and added measures of genetic distance to their analyses. In both studies, kinship/family traits were found to be associated with linguistic proxies for historical relatedness, while geographical diffusion explained the distribution of a miscellanea of traits with no clear theme, including, for example, house-building traits and beliefs in high gods. The majority of traits had more than one explanatory model. In both investigations, even though the studies were primarily set up to determine modes of transmission, ecological correlations were identified as a locus of 'adaptation'; in any case, the broad ecological categories employed were not related in any significant way with genetic, linguistic or cultural similarity. But, as we discussed in the previous section, such correlations are not necessarily a good test of ecological adaptation. Neither of these studies controlled for phylogenetic relatedness in a statistical way: they used broad-scale linguistic classifications across language family boundaries that were at a rather coarse level with which to address between-society transmission.

(b) *A study of cultural transmission in Austronesian groups*

To provide a comparative regional dataset to [67] and [68], we studied the transmission of cultural traits in 80 Austronesian societies of the Pacific, but took a different approach that controlled for phylogenetic relatedness. We examined individual cultural traits to see whether they were best predicted by a society's geographical (GNN) or phylogenetic nearest neighbour (PNN). If phylogeny predicts similarity, it suggests this trait is inherited from mother culture to daughter culture. If geography predicts similarity, this could be due to diffusion between neighbouring cultures, ecological constraint or due to phylogenetically related groups remaining geographically clustered. We include this exploratory analysis as an example of how phylogenetic methods can be used to study cultural transmission at the macro-level.

(i) *Data*

Data on cultural traits were from Murdock's *Ethnographic Atlas* [34], and comprised 80 Austronesian-speaking societies that could be matched to their

languages. Each variable was dichotomized, so that multi-state variables became presence–absence binary variables and semi-continuous variables were binned in two or three classes. To eliminate spurious reconstructions owing to missing data, only those traits that were displayed by at least 10 per cent of cultures were used ($n = 78$). Language data were from 80 languages in an early version of the Austronesian Basic Vocabulary Database [69]. PAUP* was used to find a single best lexical phylogeny using maximum-parsimony methods. This tree does not differ substantially from the consensus tree that summarizes later Bayesian analyses on these Austronesian data (e.g. [48]) in that PNNs are equivalent. We used ARCMAP v. 9.1 to calculate the pairwise distance in kilometres, taking the geographical latitude and longitude for each society from the *Ethnographic Atlas* [34].

(ii) *Phylogenetic and geographical nearest neighbours*

We asked the question: for each cultural trait in each society, does the GNN or PNN best predict the state of the cultural trait? We again used the binary-coded *Ethnographic Atlas* and noted the state of each cultural trait in each society, the state in that society's PNN and that society's GNN. GNNs were found using a distance matrix. PNNs were taken from the linguistic tree of 80 Austronesian societies (see figure 1 for how these values were calculated).

We examined each cultural trait separately and used a logistic regression model where the variables PNN and GNN were used as predictors of the state of the trait in each society. No interaction term was included, as we were interested in comparing geographical and phylogenetic similarity with other studies, none of which have controlled for their (undoubtedly present) collinearity between geography and phylogeny: phylogenetically related groups will be geographically clustered to some extent. Forced-entry (block) logistic regression analysis was run on each separate cultural trait using SPSS 12. Table 1 summarizes the analyses and lists the traits predicted by a GNN, PNN or both cultural transmission models, and traits not predicted by any model.

(iii) *Results and discussion*

PNN predicted the state of slightly more cultural traits than did GNN, though there was no difference between 'economic' and 'social' classes of traits with respect to PNN and GNN. Given that social and economic traits coevolve, this is perhaps not surprising. Most social stratification traits ('wealth classes', 'former slavery' and 'hereditary succession') were predicted by the PNN. It is interesting to note that those traits that involve heritable resources show by far the strongest phylogenetic effect—either material resources, such as domesticated animals, or social resources, such as the presence of slavery. It is almost as though important parent–offspring transmission of the means of subsistence at the micro-level is still of relevance when explaining mother-culture to daughter-culture macro-level cultural variation. This could be construed as a form

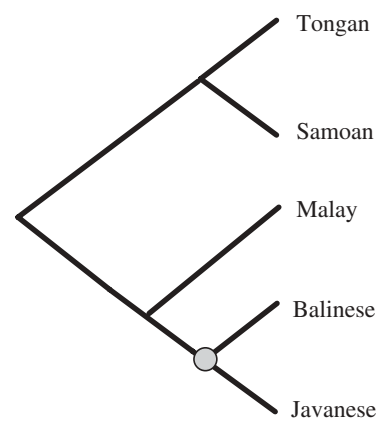


Figure 1. Estimation of phylogenetic nearest neighbours (NNs). The NN for each culture is either a tip or a node: for Samoan it is Tongan, for Javanese it is Balinese and for Malay it is the internal node indicated by the grey filled circle. The state of each tip was available from the ethnographic data, while the state of the trait at the internal node was calculated using the maximum-likelihood method of Discrete [56,57]. We obtained a probabilistic estimate that the trait was state 0 or 1, using an explicit model of evolution and the information on branch lengths contained in the phylogeny. The presence of the trait was only assumed when 100 maximum-likelihood tries provided an average likelihood over 70% that the trait was state 0 or 1. If the method was unable to provide an estimate of a society's PNN for any trait, that trait was not examined for that society. This is a conservative measure that takes into account the uncertainty in reconstructing the node on the phylogeny.

of niche construction, that is, whereby individuals modify the source of natural selection in their own environment [12]. In this case, by creating forms of heritable resources, individuals create selection pressures for subsequent generations to continue to transmit such a strategy vertically.

The Austronesian language family is one of several worldwide associated with agricultural dispersal, and over half of the economic traits predicted by the PNN are concerned with animal domesticates. These consist of the Oceanic 'package' of pig, dog and chicken, as well as the Asian water buffalo and Bali cattle that are concentrated in a restricted set of societies in Island Southeast Asia. Plant-based subsistence traits, however, are associated with geography. It may be that horticultural or crop traits diffuse more readily than domesticated animals, being less 'expensive' technologies. In addition, crop types are more likely to be constrained by the type of ecological environment to which they are suited, which may be reflected in geographical ranges. Animals, in the societies that possess them, are frequently consumers of household waste (e.g. pigs) and not so subject to ecological constraints. In addition, animals may represent heritable wealth, and as such may be more likely to be conserved vertically.

Kinship traits concerning descent and inheritance were frequently associated with phylogeny in this analysis. Descent systems structure patterns of relationship, defining who is kin and who is not, and

Table 1. Nearest neighbour model predicting state of cultural traits, highlighting those traits predicted by geographical and phylogenetic nearest neighbours ($p < 0.5$). Traits are followed by their odds ratio ($\exp(\beta)$).

trait class	geographical nearest neighbour	phylogenetic nearest neighbour	not predicted by any model
social/kinship ($n = 37$)	preference for cousin marriage (13.1), slavery (12.3), ambilineal descent (5.3), segmented communities (4.9), Iriquois kin terminology (4.8), cousin marriage not allowed (4.8), brideprice (3.6, 3.6) ^a , no marriage transactions (4.6, 3.2) ^a , first cousin marriage (0.37, 0.38) ^a	single-community patriline (12.9), former slavery (11.1), wealth distinctions (9.3), Eskimo kin terminology (8.7), matrilineal descent (4.9), unilineal descent (4.7), hereditary succession to office (2.7), cognatic descent (0.23), brideprice (3.6, 3.6) ^a , no marriage transactions (4.6, 3.2) ^a , first cousin marriage (0.37, 0.38) ^a	gift exchange for wives, monogamy OR monogamous families, polygyny OR polygynous families, post-marital residence type ($n = 4$), agamous communities, Hawaiian kin terms, bilateral descent, mixed descent, lack of classes OR elaborated classes, non-hereditary succession to office
	<i>total traits predicted by one model 19%</i>	<i>total traits predicted by one model 24%</i>	<i>total traits not predicted 43%</i>
economic/ subsistence ($n = 29$)	grain crops (49.1), low dependence on fishing (8.3), tree fruit crops (5.0), root/tuber crops (3.7), high dependence on fishing (0.1) ^b , horticulture (4.4, 4.3) ^a	high dependence on animal husbandry (148.8), metalworking (34.5), absence of domesticates (25.6), bovine domesticates (6.9), pig domesticates (5.1), males predominant in agriculture (3.7), hunting (3.7), low dependence on animal husbandry (0.5) ^b , horticulture (4.4, 4.3) ^a	gathering, agriculture, extensive agriculture, irrigated agriculture, plough (absent OR aboriginal), males predominant in fishing, equal OR female-biased labour in agriculture, house-building traits ($n = 3$), settlement types ($n = 2$)
	<i>total traits predicted by one model 17%</i>	<i>total traits predicted by one model 24%</i>	<i>total traits not predicted 48%</i>

^aTraits when predicted by both PNN and GNN. The odds ratio for the geographical model is given first.

^bFishing and animal husbandry were coded as high, medium and low.

to whom rights and wealth will be accorded. As such, it is unsurprising that they follow a vertical sort of transmission. However, ambilineal descent, where there is flexibility in the kinship system such that descent can be traced through either sex, is associated with the geographical model, and thus may covary with aspects of the environment.

Compared with previous results, which have found positive evidence of a greater relationship of social traits and a phylogenetic model, and ambiguous or low evidence for a geographical model associated with economic traits, our data do show positive evidence for the association between geographical proximity and economic trait similarity. It may be that in the Pacific, more marginal and/or proscriptive environments restrict the variation possible in subsistence systems compared with Africa, and geography thus accounts for more of the observed similarity. Geographical diffusion—trait ‘borrowing’—after the initial spread of the Austronesian language family approximately 5500–5200 years ago [48,70]—should be expected to have the effect of washing out some of the initial signature of historical relationship. It is important to note that diffusion does not imply maladaptation as earlier discussed; trait borrowing could be (and perhaps is most likely to be) for adaptive reasons. Adaptation also drives further diversification, also potentially obscuring evidence of history.

Given the coarse and uneven grain at which the cultural traits have been examined, and the very conservative test used, the persistent and significant

correlations are noteworthy, though they remain hypotheses for further testing.

4. CONCLUSIONS

Modelling proximate mechanisms of cultural change within populations is a well-developed field, although the empirical branch of the field is still small. Some models predict that generalized social learning mechanisms may cause maladaptive behaviour to emerge, but whether such cases are rare or widespread in the real world is not really known. We argue that models of cultural adaptation can be subjected to the same or similar tests that behavioural ecologists have used to seek evidence for adaptive behaviour in other species. Phylogenetic comparative methods are proving useful, for both studying coevolutionary hypotheses (be they cultural and or gene–culture coevolution) and estimating ancestral states of prehistoric societies. This form of formal cross-cultural comparison is helping to put history back into anthropology, and helping us to understand cultural evolutionary processes at a number of levels.

Empirical examinations of proximate models of cultural transmission at the macro-level are also rather few. We presented an analysis of the extent to which similarity owing to geography or ancestry predominates in a sample of Austronesian cultural traits. We find that when treated as classes, social/kinship traits are predicted by phylogenetic and geographic measures of distance in roughly equal measures. When we drill down to the individual traits, more

specific patterns emerge. Perhaps the most striking result we present here is that, from an unbiased sample of cultural traits, those that were most similar between mother and daughter culture were those related to heritable resources, with heavy reliance on animal husbandry and then metalworking showing the strongest phylogenetic similarity. These traits are lifestyles that require the expertise and wherewithal of a specialized mode of subsistence; that are passed on most probably from parents; cannot necessarily be easily acquired by neighbours; and possibly it is the skills and/or material goods needed for these lifestyles that provide the adaptive advantage. That advantage may be the reason why those cultures have diversified into more, similar daughter cultures. It may be that the processes that drive the evolution of cultural variation at the micro-level are the processes underlying the macro-evolutionary trends.

We thank the editor and two anonymous referees for comments on this paper.

REFERENCES

- 1 Tomasello, M. 2003 The human adaptation for culture. *Ann. Rev. Anthropol.* **28**, 509–529.
- 2 Laland, K. & Brown, G. 2002 *Sense and nonsense*. Oxford, UK: Oxford University Press.
- 3 Perry, G. & Mace, R. 2010 Lack of acceptance of evolutionary approaches to human behaviour. *J. Evol. Psychol.* **8**, 105–125. (doi:10.1556/JEP.8.2010.2.2)
- 4 Segerstrale, U. 2000 *Defenders of the truth: the battle for science in the sociobiology debate and beyond*. Oxford, UK: Oxford University Press.
- 5 Bersaglieri, T., Sabeti, P. C., Patterson, N., Vanderploeg, T., Schaffner, S. F., Drake, J. A., Rhodes, M., Reich, D. E. & Hirschhorn, J. N. 2004 Genetic signatures of strong recent positive selection at the lactase gene. *Am. J. Hum. Genet.* **74**, 1111–1120. (doi:10.1086/421051)
- 6 Ingram, C. J. E., Mulcare, C. A., Itan, Y., Thomas, M. G. & Swallow, D. M. 2009 Lactose digestion and the evolutionary genetics of lactase persistence. *Hum. Genet.* **124**, 579–591. (doi:10.1007/s00439-008-0593-6)
- 7 Mead, S. *et al.* 2009 A novel protective prion protein variant that colocalizes with kuru exposure. *New Engl. J. Med.* **361**, 2056–2065. (doi:10.1056/NEJMoa0809716)
- 8 Peng, Y., Shi, H., Qi, X.-B., Xiao, C.-J., Zhong, H., Ma, R.-L. & Su, B. 2010 The ADH1B Arg47His polymorphism in East Asian populations and expansion of rice domestication in history. *BMC Evol. Biol.* **10**, 15. (doi:10.1186/1471-2148-10-15)
- 9 Plomin, R., DeFries, J. C., McClearn, G. E. & McGuffin, P. 2001 *Behavioral genetics*, 4th edn. New York, NY: Worth.
- 10 Hawks, J., Wang, E. T., Cochran, G. M., Harpending, H. C. & Moyzis, R. K. 2007 Recent acceleration of human adaptive evolution. *Proc. Natl Acad. Sci. USA* **104**, 20 753–20 758. (doi:10.1073/pnas.0707650104)
- 11 Laland, K. N. & Brown, G. R. 2006 Niche construction, human behavior, and the adaptive-lag hypothesis. *Evol. Anthropol.* **15**, 95–104. (doi:10.1002/evan.20093)
- 12 Odling-Smee, J., Laland, K. & Feldman, M. W. 2003 *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.
- 13 Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- 14 Richerson, P. J. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
- 15 Soltis, J., Boyd, R. & Richerson, P. J. 1995 Can group-functional behaviors evolve by cultural-group selection—an empirical-test. *Curr. Anthropol.* **36**, 473–494. (doi:10.1086/204381)
- 16 Tanaka, M. M., Kendal, J. R. & Laland, K. 2009 From traditional medicine to witchcraft: why medical treatments are not always efficacious. *PLoS ONE* **4**, e5192.
- 17 Gibson, M. A. & Mace, R. 2006 An energy-saving development initiative increases birth rate and childhood malnutrition in rural Ethiopia. *PLoS Med.* **3**, 476–484.
- 18 Nettle, D. 2009 Ecological influences on human behavioural diversity: a review of recent findings. *Trends Ecol. Evol.* **24**, 618–624. (doi:10.1016/j.tree.2009.05.013)
- 19 Diamond, J. 1997 *Guns, germs and steel*. London, UK: Vintage.
- 20 Mace, R. & Jordan, F. M. 2005 The evolution of human sex-ratio at birth: a bio-cultural analysis. In *The evolution of cultural diversity: a phylogenetic approach* (eds R. Mace, C. Holden & S. Shennan), pp. 207–216. London, UK: Left Coast Press.
- 21 Ord, T. J. & Martins, E. P. 2010 Evolution of behaviour: phylogeny and the origin of present-day diversity. In *Evolutionary behavioural ecology* (eds D. Westneat & C. W. Fox). Oxford, UK: Oxford University Press.
- 22 Pagel, M. 1997 Inferring evolutionary processes from phylogenies. *Zool. Script.* **26**, 331–348. (doi:10.1111/j.1463-6409.1997.tb00423.x)
- 23 Itan, Y., Powell, A., Beaumont, M. A., Burger, J. & Thomas, M. G. 2009 The origins of lactase persistence in Europe. *PLoS Comput. Biol.* **5**, e1000491. (doi:10.1371/journal.pcbi.1000491)
- 24 Flatz, G. & Rotthauwe, H. 1973 Lactose nutrition and natural selection. *Lancet* **302**, 76–77. (doi:10.1016/S0140-6736(73)93267-4)
- 25 Beaumont, M. A., Zhang, W. Y. & Balding, D. J. 2002 Approximate Bayesian computation in population genetics. *Genetics* **162**, 2025–2035.
- 26 Holden, C. & Mace, R. 1997 Phylogenetic analysis of the evolution of lactose digestion in adults. *Hum. Biol.* **69**, 605–628.
- 27 Kaplan, H. S., Hooper, P. L. & Gurven, M. 2009 The evolutionary and ecological roots of human social organization. *Phil. Trans. R. Soc. B* **364**, 3289–3299. (doi:10.1098/rstb.2009.0115)
- 28 Currie, T. E. & Mace, R. 2009 Political complexity predicts the spread of ethnolinguistic groups. *Proc. Natl Acad. Sci. USA* **106**, 7339–7344. (doi:10.1073/pnas.0804698106)
- 29 Johnson, A. W. & Earle, T. 2000 *The evolution of human societies: from foraging group to agrarian state*. Stanford, CA: Stanford University Press.
- 30 Orians, G. H. 1969 On the evolution of mating systems in birds and mammals. *Am. Nat.* **103**, 589–603.
- 31 Borgerhoff Mulder, M. 1990 Kipsigis women's preference for wealthy men: evidence for female choice in mammals? *Behav. Ecol. Sociobiol.* **27**, 255–264.
- 32 Hartung, J. 1982 Polygyny and the inheritance of wealth. *Curr. Anthropol.* **23**, 1–12. (doi:10.1086/202775)
- 33 Mace, R. 1996 Biased parental investment and reproductive success in Gabbra pastoralists. *Behav. Ecol. Sociobiol.* **38**, 75–81. (doi:10.1007/s002650050219)
- 34 Murdock, G. P. 1967 *Ethnographic atlas*. Pittsburgh, PA: University of Pittsburgh Press.
- 35 Aberle, D. F. 1961 Matrilineal descent in cross-cultural perspective. In *Matrilineal kinship* (eds D. M. Schneider & K. Gough), pp. 655–727. Berkeley, CA: University of California Press.

- 36 Holden, C. J. & Mace, R. 2003 Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis. *Proc. R. Soc. Lond. B* **270**, 2425–2433. (doi:10.1098/rspb.2003.2535)
- 37 Keegan, W. F. & Maclachlan, M. D. 1989 The evolution of avunculocal chiefdoms—a reconstruction of Taino kinship and politics. *Am. Anthropol.* **91**, 613–630. (doi:10.1525/aa.1989.91.3.02a00050)
- 38 Hage, P. & Marck, J. 2003 Matrilineality and the Melanesian origin of Polynesian Y chromosomes. *Curr. Anthropol.* **44**, S121–S127. (doi:10.1086/379272)
- 39 Hartung, J. 1985 Matrilineal inheritance: new theory and analysis. *Behav. Brain Sci.* **8**, 661–668. (doi:10.1017/S0140525X00045520)
- 40 Mace, R. & Pagel, M. 1994 The comparative method in anthropology. *Curr. Anthropol.* **35**, 549–564. (doi:10.1086/204317)
- 41 Harvey, P. & Pagel, M. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
- 42 Mace, R. & Holden, C. J. 2005 A phylogenetic approach to cultural evolution. *Trends Ecol. Evol.* **20**, 116–121. (doi:10.1016/j.tree.2004.12.002)
- 43 Gray, R. D., Greenhill, S. J. & Ross, R. M. 2007 The pleasures and perils of Darwinizing culture (with phylogenies). *Biol. Theory* **2**, 360–375. (doi:10.1162/biot.2007.2.4.360)
- 44 Foster, P. & Renfrew, C. 2006 *Phylogenetic methods and the prehistory of languages*. Cambridge, UK: MacDonald Institute of Archaeological Research.
- 45 Dunn, M., Terrill, A., Reesink, G., Foley, R. A. & Levinson, S. C. 2005 Structural phylogenetics and the reconstruction of ancient language history. *Science* **309**, 2072–2075. (doi:10.1126/science.1114615)
- 46 Holden, C. J. 2002 Bantu language trees reflect the spread of farming across sub-Saharan Africa: a maximum-parsimony analysis. *Proc. R. Soc. Lond. B* **269**, 793–799. (doi:10.1098/rspb.2002.1955)
- 47 Gray, R. D. & Atkinson, Q. D. 2003 Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature* **426**, 435–439. (doi:10.1038/nature02029)
- 48 Gray, R. D., Drummond, A. J. & Greenhill, S. J. 2009 Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* **323**, 479–483. (doi:10.1126/science.1166858)
- 49 Gray, R. D. & Jordan, F. M. 2000 Language trees support the express-train sequence of Austronesian expansion. *Nature* **405**, 1052–1055. (doi:10.1038/35016575)
- 50 Mace, R., Holden, C. & Shennan, S. 2005 *The evolution of cultural diversity: a phylogenetic approach*. London, UK: Left Coast Press.
- 51 Kitchen, A., Ehret, C., Assefa, S. & Mulligan, C. J. 2009 Bayesian phylogenetic analysis of Semitic languages identifies an Early Bronze Age origin of Semitic in the Near East. *Proc. R. Soc. B* **276**, 2703–2710. (doi:10.1098/rspb.2009.0408)
- 52 Hamed, M. B. 2005 Neighbour-nets portray the Chinese dialect continuum and the linguistic legacy of China's demic history. *Proc. R. Soc. B* **272**, 1015–1022. (doi:10.1098/rspb.2004.3015)
- 53 Diamond, J. & Bellwood, P. 2003 Farmers and their languages: the first expansions. *Science* **300**, 597–603. (doi:10.1126/science.1078208)
- 54 Pagel, M. 2009 Human language as a culturally transmitted replicator. *Nat. Rev. Genet.* **10**, 405–415.
- 55 Pagel, M., Atkinson, Q. D. & Meade, A. 2007 Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature* **449**, 717–717. (doi:10.1038/nature06176)
- 56 Pagel, M. 1994 Detecting correlated evolution on phylogenies—a general-method for the comparative-analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**, 37–45. (doi:10.1098/rspb.1994.0006)
- 57 Pagel, M. & Meade, A. 2006 Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.* **167**, 808–825.
- 58 Pagel, M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
- 59 Fortunato, L., Holden, C. & Mace, R. 2006 From bride-wealth to dowry? A Bayesian estimation of ancestral states of marriage transfers in Indo-European groups. *Hum. Nat.* **17**, 355–376.
- 60 Pagel, M. & Meade, A. 2005 Bayesian estimation of correlated evolution across cultures: a case study of marriage systems and wealth transfer at marriage. In *The evolution of cultural diversity: a phylogenetic approach* (eds R. Mace, C. Holden & S. Shennan). London, UK: UCL Press and Left Coast Press.
- 61 Kayser, M., Brauer, S., Weiss, G., Schiefenhovel, W., Underhill, P., Shen, P. D., Oefner, P., Tommaseo-Ponzetta, M. & Stoneking, M. 2003 Reduced Y-chromosome, but not mitochondrial DNA, diversity in human populations from West New Guinea. *Am. J. Hum. Genet.* **72**, 281–302. (doi:10.1086/346065)
- 62 Seielstad, M. T., Minch, E. & Cavalli-Sforza, L. L. 1998 Genetic evidence for a higher female migration rate in humans. *Nat. Genet.* **20**, 278–280. (doi:10.1038/3088)
- 63 Wilkins, J. F. & Marlowe, F. W. 2006 Sex-biased migration in humans: what should we expect from genetic data? *Bioessays* **28**, 290–300. (doi:10.1002/bies.20378)
- 64 Jordan, F. M., Gray, R. D., Greenhill, S. J. & Mace, R. 2009 Matrilocal residence is ancestral in Austronesian societies. *Proc. R. Soc. B* **276**, 1957–1964. (doi:10.1098/rspb.2009.0088)
- 65 Greenhill, S. J., Currie, T. E. & Gray, R. D. 2009 Does horizontal transmission invalidate cultural phylogenies? *Proc. R. Soc. B* **276**, 2299–2306. (doi:10.1098/rspb.2008.1944)
- 66 Currie, T. E., Greenhill, S. J. & Mace, R. 2010 Is horizontal transmission really a problem for phylogenetic comparative methods? A simulation study using continuous cultural traits. *Phil. Trans. R. Soc. B* **365**, 3903–3912. (doi:10.1098/rstb.2010.0014)
- 67 Guglielmino, C. R., Viganotti, C., Hewlett, B. & Cavalli-Sforza, L. L. 1995 Cultural variation in Africa: role of mechanisms of transmission and adaptation. *Proc. Natl Acad. Sci. USA* **92**, 7585–7589. (doi:10.1073/pnas.92.16.7585)
- 68 Hewlett, B. S., de Silvestri, A. & Guglielmino, C. R. 2002 Seme and genes in Africa. *Curr. Anthropol.* **43**, 313–321. (doi:10.1086/339379)
- 69 Greenhill, S. J., Blust, R. & Gray, R. D. 2008 The Austronesian basic vocabulary database: from bioinformatics to lexomics. *Evol. Bioinform.* **4**, 271–283.
- 70 Bellwood, P. 1997 *The prehistory of the Indo-Malaysian archipelago*, 2nd edn. Honolulu, Hawai'i: University of Hawai'i Press.