

## The cophylogeny of populations and cultures: reconstructing the evolution of Iranian tribal craft traditions using trees and jungles

Jamshid J. Tehrani, Mark Collard and Stephen J. Shennan

*Phil. Trans. R. Soc. B* 2010 **365**, 3865-3874

doi: 10.1098/rstb.2010.0020

---

### References

[This article cites 37 articles, 8 of which can be accessed free](#)

<http://rstb.royalsocietypublishing.org/content/365/1559/3865.full.html#ref-list-1>

### Rapid response

[Respond to this article](#)

<http://rstb.royalsocietypublishing.org/letters/submit/royptb;365/1559/3865>

### Subject collections

Articles on similar topics can be found in the following collections

[behaviour](#) (1559 articles)

[taxonomy and systematics](#) (292 articles)

[evolution](#) (2136 articles)

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

---

To subscribe to *Phil. Trans. R. Soc. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

---

# The cophylogeny of populations and cultures: reconstructing the evolution of Iranian tribal craft traditions using trees and jungles

Jamshid J. Tehrani<sup>1,2,\*</sup>, Mark Collard<sup>2,3</sup> and Stephen J. Shennan<sup>2,4</sup>

<sup>1</sup>*Evolutionary Anthropology Research Group, Department of Anthropology, Science Site, South Road, Durham University, Durham DH1 3LE, UK*

<sup>2</sup>*AHRC Centre for the Evolution of Cultural Diversity, and*

<sup>3</sup>*Laboratory of Human Evolutionary Studies, Department of Archaeology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada*

<sup>4</sup>*Institute of Archaeology, University College London, London, WC1H 0PY, UK*

Phylogenetic approaches to culture have shed new light on the role played by population dispersals in the spread and diversification of cultural traditions. However, the fact that cultural inheritance is based on separate mechanisms from genetic inheritance means that socially transmitted traditions have the potential to diverge from population histories. Here, we suggest that associations between these two systems can be reconstructed using techniques developed to study cospeciation between hosts and parasites and related problems in biology. Relationships among the latter are patterned by four main processes: co-divergence, intra-host speciation (duplication), intra-host extinction (sorting) and horizontal transfers. We show that patterns of cultural inheritance are structured by analogous processes, and then demonstrate the applicability of the host–parasite model to culture using empirical data on Iranian tribal populations.

**Keywords:** cultural phylogenies; population history; coevolution; cophylogeny; cultural evolution; Iranian tribes

## 1. INTRODUCTION

The extent to which cultural traditions track the descent histories of populations has long been debated. For most of the last century, the consensus among anthropologists and archaeologists has been that any evidence relating to the historical origins of cultural assemblages would probably be swamped by the rapid rate of cultural evolution, and by the effects of trade, intermarriage and exchange among neighbouring groups (e.g. Boas 1940; Kroeber 1948; Moore 1994). However, recent applications of techniques of phylogenetic analysis borrowed from biology have succeeded in reconstructing coherent and long-lasting lineages of cultural inheritance across a number of domains (e.g. Mace *et al.* 2005; Lipo *et al.* 2006). For instance, analyses of relationships among languages suggest that resemblances among word forms can often be traced back to ancestral speech communities that existed many thousands of years ago (e.g. Gray & Jordan 2000; Gray & Atkinson 2003; Kitchen *et al.* 2009). Similarly, it would appear that many craft styles and technologies are handed down from generation to generation,

eventually giving rise to new forms that are recognizably derived from their parent tradition (e.g. Tehrani & Collard 2002, 2009a,b; O'Brien & Lyman 2003; Buchanan & Collard 2007, 2008; Lycett 2007, 2009).

The reconstruction of such lineages can provide useful evidence about the origins and dispersal of populations, especially in cases where genetic data are scarce or noisy. For example, phylogenies derived from cultural traits have been used to test competing hypotheses about the colonization of the Pacific (Gray & Jordan 2000; Gray *et al.* 2009), the Bantu expansions in Africa (Holden 2002), the origins of the Indo-Europeans (Gray & Atkinson 2003) and the peopling of the Americas (Buchanan & Collard 2007). However, while most studies indicate that cultural phylogenies and population histories are usually highly correlated (e.g. Gray & Jordan 2000; Holden 2002; Tehrani & Collard 2002, 2009a,b), the match is not always perfect. For example, Tehrani & Collard (2002) noted that some of the relationships among Turkmen and rural Iranian (Tehrani & Collard 2009a,b) weaving traditions contradict written and oral histories about the tribes' origins. Similar inconsistencies have been reported in reconstructions of indigenous Californian basketry assemblages (Jordan & Shennan 2003), Siberian material culture (Jordan & Mace 2006), Baltic stringed instruments (Temkin & Eldredge 2007) and Polynesian canoes (Rogers *et al.* 2009).

\* Author for correspondence ([jamie.tehrani@durham.ac.uk](mailto:jamie.tehrani@durham.ac.uk)).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rstb.2010.0020> or via <http://rstb.royalsocietypublishing.org>.

One contribution of 14 to a Theme Issue 'Cultural and linguistic diversity: evolutionary approaches'.

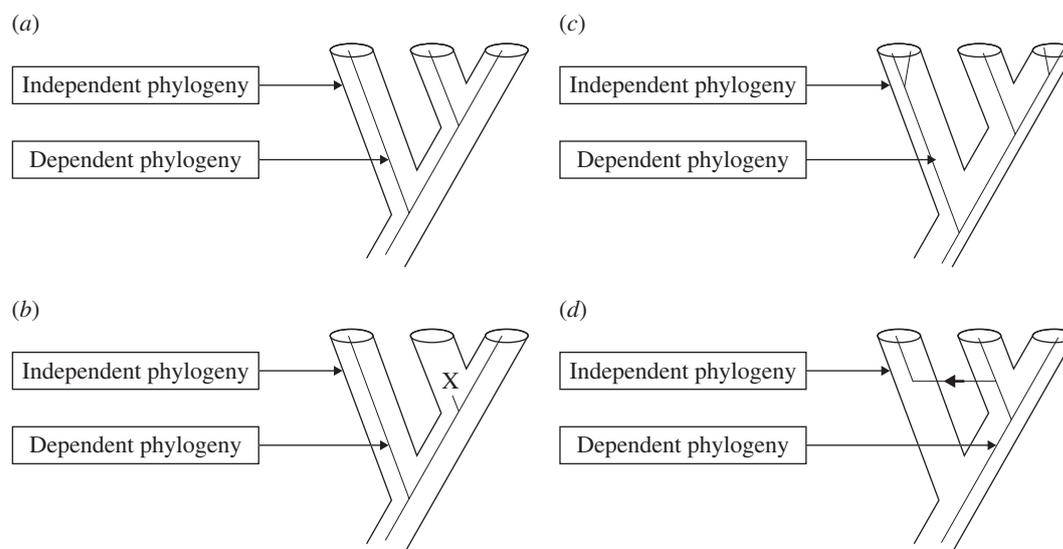


Figure 1. Terminology of historical associations between a dependent (parasite) phylogeny and independent (host) phylogeny. (a) Co-divergence, (b) sorting event, (c) duplication and (d) horizontal transfer.

To shed more light on these issues, we draw on ideas from dual-inheritance theory or gene–culture coevolutionary theory (e.g. Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Durham 1991; Richerson & Boyd 2005). Dual inheritance theory views culture and genes as separate but coevolving systems of heritable variation, each based on autonomous mechanisms of information transmission (i.e. imitation and teaching versus biological reproduction). At the individual level, this requires models that can account for the interactions between genetic traits, which can only be transmitted ‘vertically’ from parents to offspring, and learned behaviours that can be acquired vertically, ‘obliquely’ from other adults, or ‘horizontally’ among members of the same generation. Similar models are needed at the group level. These would recognize that, while cultural traditions and populations may be closely linked, the processes involved in their propagation, dispersal and extinction are ultimately independent of one another. The main aim would then be to understand what kinds of processes lead to correlations between cultural phylogenies and population histories, and what kinds of processes lead to divergences. Following the suggestions of Jordan & Mace (2006), Gray *et al.* (2008) and Riede (2009), we argue that such a model can be developed from the study of long-term co-evolutionary, or ‘cophylogenetic’, relationships in biology.

## 2. THE COPHYLOGENETIC FRAMEWORK

The study of cophylogeny spans several domains in biology, including cospeciation in host and parasite organisms, the reconciliation of species trees and gene trees, and associations between species histories and area histories in vicariance biogeography (e.g. Brooks & McLennan 1991; Page 2003). The key issue in each of these endeavours is essentially identical to the one we face here. It concerns how far the history of one group of entities (i.e. the parasites, genes, organisms or cultural traditions) is determined by the history of another group (i.e. the hosts, species,

geographical areas or populations). This is addressed by mapping a dependent phylogeny (i.e. the parasite, gene, or organism tree) onto an independent phylogeny (the host, species, or geographical tree). Historical relationships between the two systems of interest can then be described in relation to four generic processes: co-divergence, sorting, duplication and horizontal transfer (e.g. Page 2003; figure 1). Each of these processes can be readily identified in cultural evolution.

### (a) *Co-divergence*

In co-divergence, the dependent lineage splits as a result of the independent lineage splitting. In the case of hosts and parasites, co-divergence is equivalent to cospeciation, and typically occurs when the speciation of a host organism results in the speciation of associated parasites (e.g. Hafner & Nadler 1988). In molecular phylogenetics, co-divergence occurs when a genetic lineage diverges into daughter lineages coincident with a speciation event (interspecific coalescence), while in biogeography a co-divergence takes place when a new species arises in geographic isolation as a result of a geological event (vicariance) (e.g. Hafner & Page 1995; Ronquist 1998). In all these instances, co-divergence results in a direct correspondence between the dependent and independent phylogenies.

In the case of cultural evolution, co-divergence is equivalent to the division of cultural traditions resulting from population splits, which is often associated with the demographic expansion of populations. The impact of co-divergence in generating cultural patterns is exemplified by the spread of agriculture. The Neolithic expansions in Europe, Oceania and Africa not only left strong genetic signatures, but also were associated with the growth and spread of distinct language families (e.g. Gray & Jordan 2000; Holden 2002; Gray & Atkinson 2003). In each of these cases, new languages appear to have evolved primarily as a result of population dispersals.

**(b) *Sorting***

In host–parasite studies, sorting refers to the extinction of a parasite lineage within a host lineage. Sorting events can also occur as a result of a parasite ‘missing the boat’ when a descendent of the host species does not inherit all the latter’s parasites (e.g. Paterson *et al.* 1999). The extinction of a genetic lineage within a species or of a species in a habitat is also classified as a sorting event (e.g. Hafner & Page 1995; Page & Charleston 1998). Sorting can be thought of as the pruning of some branches on the dependent phylogeny, which results in mismatches with the tips of the independent phylogeny.

Sorting events are likely to be common in cultural and linguistic evolution. Globalized capitalism and the spread of modern communications systems have caused (or at least coincided with) the decline of innumerable dialects, technologies and other cultural practices associated with indigenous peoples around the world. For example, Ohangari & Berkes (1997) found that traditional bush skills are in decline among the Cree of James Bay, Canada, because their communities no longer depend on hunting and fishing for subsistence. Instances of cultural loss are also known from historical evidence. One of the most dramatic of these occurred in Tasmania. Archaeological evidence suggests that the first humans to arrive in Australia possessed a relatively sophisticated set of weapons, tools and crafts. While many of these were maintained by mainland groups, in the 10 000 years prior to the arrival of the first Europeans, native Tasmanians appear to have lost techniques required to fish, prepare furs, make bone tools, arrows and boomerangs, and even the knowledge required to make fire (Henrich 2004).

**(c) *Duplication***

In duplication, the branches of the dependent phylogeny split but the branches of the independent phylogeny do not. In other words, duplication events create mismatches between the dependent phylogeny and independent phylogeny by adding branches to the dependent phylogeny. In the host–parasite case, this equates to the intra-host speciation of a parasite species. In genetics, duplication results in an organism carrying two copies of the same gene. In the case of organism–area associations, duplication is equivalent to sympatric speciation, which occurs within an undivided geographical area or habitat range (Page & Charleston 1998).

The history of sport is replete with examples of cultural duplication. For instance, modern football and rugby are descended from ball games played in nineteenth century England, and that were not recognizably distinct from one another. It was only after the establishment of separate governing bodies who formally codified the rules that the two sports diverged. A later schism gave rise to separate codes of Rugby League and Rugby Union. Like the earlier split from football, the diversification of these sports occurred within an undivided population and can therefore be classed as a duplication. Duplication can also be seen in the diversification of religious sects and denominations. Although ideological disputes

can result in congregations dividing into separate communities of worship, this does not usually result in the formation of genetically, ethnically or linguistically distinct populations. In modern societies, members of different religious communities frequently intermarry and may even change their faith several times over their lives. These examples show how cultural lineages can diversify independently of the populations with which they are associated.

**(d) *Horizontal transfer***

Some parasite species colonize new hosts via a process known as ‘switching’. Switches are described as horizontal transfers because they involve a host acquiring a parasite from a non-ancestral species that they have come into contact with. This process can lead to major discrepancies between the phylogenies of the two groups of species (Page 2003). Horizontal transfers can be similarly problematic in other areas. In molecular evolution, horizontal transfers, or ‘reticulations’, are considered rare but are known to occur in some organisms, such as the exchange of plasmid DNA in bacteria. This can greatly complicate the reconstruction of these organisms’ phylogenies (Doolittle 1999). In biogeography, horizontal transfers are equivalent to the dispersal of a species from one region to another. In this context, the phylogeny of a group of species may not map well onto the geological histories of the territories in which they are found (e.g. Ronquist 1998).

Horizontal transfers are likely to be a significant problem in reconciling cultural traditions with population histories. There is considerable evidence that horizontal transfers can occur across a variety of domains. One such domain is technology, where useful innovations can spread far from their original point of origin through trade and contact among populations. This phenomenon has been extensively studied by anthropologists and archaeologists since the nineteenth century. For example, Balfour (1889) carried out detailed analyses of composite bows from the Pitt Rivers collection, literally dissecting them to examine their shared ‘anatomical’ characteristics. Balfour (1889) proposed a Central Asian origin for the bow, which was then adopted and successively modified by populations who adopted it as it spread north to the Arctic regions and then west into Siberia and across the Bering Strait into America, west to Persia and Europe, and south to the Indian subcontinent. Similar kinds of processes have been documented in the spread of doctrinal religions as populations are converted by other populations with whom they have contact. Buddhism is an excellent example. Buddhism emerged in India in the sixth century BCE. Within 200 years it underwent a massive expansion, spreading south to Sri Lanka, east into Indochina and northwest into Central Asia, eventually reaching China via the Silk Route (Conze 1980). While the central tenets of Buddhism remained more-or-less the same, specific doctrines and rituals were adapted by the various populations who adopted it. This gave rise to new traditions of Buddhism that are phylogenetically derived from India, even though many of their respective adherents are not.

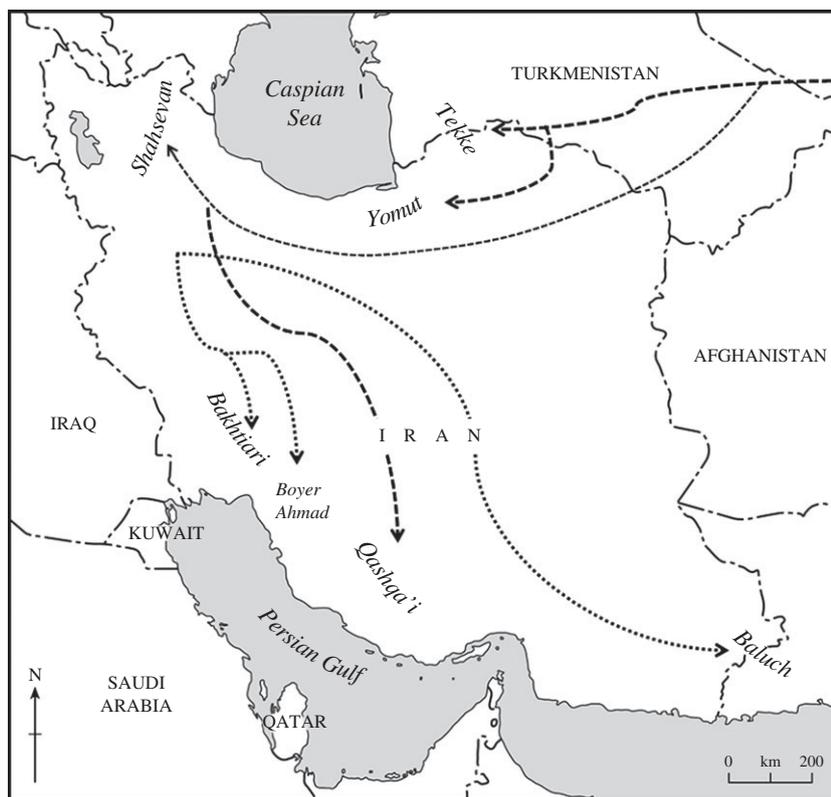


Figure 2. Map showing locations of Iranian tribal populations included in the case study and their approximate migration histories. Dashed line, Turkic migrations; dotted lines, Iranian migrations.

### 3. CASE STUDY: THE SPREAD OF WEAVING IN IRANIAN TRIBAL GROUPS

The generic nature of the processes described above means that there has been considerable cross-over in the methods used to study cophylogeny in different biological contexts. We are not the first researchers to realize the potential value of extending them to cultural evolution. For example, *Gray et al.* (2008) have suggested that techniques used to reconcile gene trees with species trees could be useful for studying the ways in which word histories are embedded in language histories. *Jordan & Mace* (2006) and *Riede* (2009) have used methods to test for cospeciation in host and parasite lineages to explore historical correlations among different components of material culture assemblages (e.g. *Jordan & Mace* 2006; *Riede* 2009). In this section, we present a case study that applies a comprehensive co-phylogenetic framework to reconstruct historical relationships between cultural traditions and populations. The study focused on weaving traditions in seven Iranian tribal populations, whose geographical distributions are shown in the map in figure 2.

Unfortunately, there are currently no genetic data on the population histories of the tribes. However, it is possible to draw inferences about their origins and relationships to one another from linguistic affiliations and oral history (e.g. *Barthold* 1962; *Oberling* 1974; *Amanolahi* 1988; *Grimes* 2002; *Windfuhr* 2007). These suggest that the populations can be divided into two main lineages. The first lineage comprises Iranian-speaking groups that are believed to have originated in western Iran (*Amanolahi* 1988). The groups

are the Baluch, the Boyer Ahmad and Bakhtiari. Members of this lineage can be further divided into the Baluch on the one side, and the Boyer Ahmad and the Bakhtiari on the other. The latter two groups speak Lori and inhabit the Zagros Mountains of western Iran. The ancestors of the Baluch are believed to have migrated from western Iran to the desert regions of southeastern Iran, western Afghanistan and northwest Pakistan some 900 years ago (*Frye* 1960; *Thompson* 2002), splitting from the ancestral population that gave rise to the Lors (*Amanolahi* 1988). The second main lineage comprises the Qashqa'i, Shahsevan, Tekke and Yomut. These populations claim descent from Oguz Turkic hordes that invaded Iran between the tenth and twelfth centuries (e.g. *Barthold* 1962; *Oberling* 1974; *Beck* 1986). All four of these groups speak Turkic languages. They can be subdivided into two sub-groups, one that speaks Turkmani, which belongs to the eastern branch of Oguz Turkic languages, and the other Azeri, which belongs to the western branch (*Grimes* 2002). The Yomut and the Tekke speak Turkmani. Both groups inhabit the northeastern region of Iran and Turkmenistan. The Shahsevan and the Qashqa'i speak Azeri. The Shahsevan are located in northwestern Iran close to the Caspian Sea. The ancestors of the Qashqa'i are believed to also have originated near the Caspian Sea, but migrated south to the Zagros Mountains about 500 years ago (*Oberling* 1974), where they are now neighbours of two of the Iranian-speaking groups, the Bakhtiari and Boyer Ahmad. The hypothesized migration histories of the tribes are shown in the map in figure 2.

There are several reasons to suspect that the history of weaving traditions is likely to be strongly correlated with population histories. The first is that textile weaving is intimately connected to the nomadic–pastoralist mode of subsistence pursued by members of these communities until recently. Unlike objects made from other materials such as wood and metal, woven rugs, bags and bands can be folded or rolled and are therefore much easier to carry on long and physically challenging migrations between seasonal camps, which in some cases covered distances of hundreds of miles across difficult, mountainous terrain. Furthermore, the raw materials and equipment for weaving were easy to obtain locally: wool can be sheared from sheep and goats, while in the past dyes were extracted from plants, insects and fruits. The second reason is that weaving skills are transmitted in a highly vertical and conservative fashion from mothers to their daughters (Tehrani & Collard 2009a). Endogamous marriage norms mean that females do not usually marry males from other tribes. This in turn implies that daughters do not generally inherit from their mothers craft traits that are foreign in origin. Lastly, even when weavers do adopt traits from non-maternal sources, they usually copy members of their immediate community. Social norms prevent women from travelling far from their father's or husband's household, with the result that they have few opportunities to interact with weavers from other tribes.

To reconstruct the history of the tribes' weaving traditions, we carried out a cladistic analysis of 150 characters in each of the seven tribes' assemblages. The weavings of the Qashqa'i, Bakhtiari and Boyer Ahmad were sampled by J.J.T. during two field surveys carried out in southwestern Iran in May 2001 and September–December 2002. Data on the weavings of the Baluch, Shahsevan, Yomut and Tekke were gathered from published catalogues (Baluch: Konieczny 1979; Yomut and Tekke: Thompson 1980; Tzavera 1984; Shahsevan: Tanavoli 1985). The characters consisted of textile traits, including techniques of preparation and fabrication (e.g. spinning, knotting, etc.), the use of different materials (e.g. wool, goat hair, dyes, etc.) and variation in decorative features (e.g. carpet designs, border patterns, etc.). We used a prehistoric archaeological textile assemblage as an outgroup for the analysis. The assemblage comprised rugs, mats and decorative felts excavated from the ice-filled tombs of nomadic people who inhabited the Pazyryk valley in the Altai Mountains of Siberia in the fourth to fifth century BCE (Rudenko 1970). These artefacts provide the best available information on the roots of weaving among Central and Western Asian nomadic pastoralists and, as such, are a useful means of inferring the likely ancestral states of the characters used in the present study. The data matrix is provided in electronic supplementary material, S1.

The analysis was carried out in the software program PAUP 4.0\* (Swofford 1998). A branch-and-bound search of the data returned a single most parsimonious cladogram, which is shown in figure 3. The relationships shown in the cladogram are compatible with those reported by Tehrani & Collard (2009b)

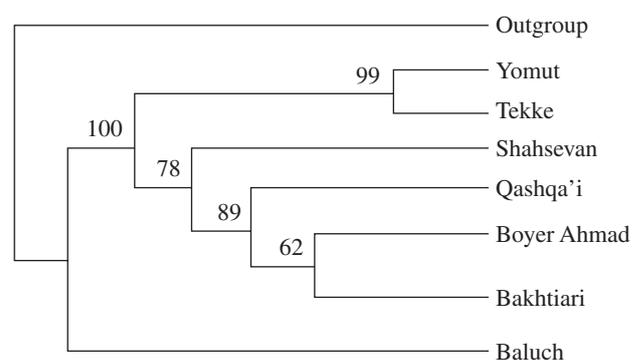


Figure 3. Cladogram for the woven assemblages, with bootstrap support percentages for individual clades shown beside each node.

in a previous analysis of these data, in which a different outgroup was used (Arab Bedouin). The fit between the cladogram and the data was measured using the Retention Index (RI) and bootstrapping. RI is a measure of the number of homoplastic changes that a cladogram requires independent of its length (Farris 1989a,b). A maximum RI of 1 indicates that the cladogram fits perfectly with the dataset, whereas the worse it fits, the closer the RI score approaches 0. The RI of this cladogram was 0.62. Simulation work (see Nunn *et al.* 2010) suggests that a RI as high as this provides strong evidence that these assemblages evolved by descent with modification from ancestral assemblages. The phylogenetic bootstrap is a technique for measuring support for individual clades (Felsenstein 1985). It involves generating cladograms by creating 'pseudo' datasets of the same size as the original by randomly re-sampling characters from the original dataset with replacement a large number of times (in this case, 10 000) and calculating the percentage of replicates that support a given clade. As can be seen in figure 3, all of the relationships were supported by a large percentage of the bootstrap replicates.

Several of the relationships indicated in the cladogram are consistent with ethnohistorical and linguistic evidence about the relationships among the populations, while several others are not. The finding that the weavings of the Yomut and Tekke are descended from an exclusive common ancestor is compatible with the fact that both populations speak the same Turkic language, Turkmani. Similarly, the finding that the assemblages of the Bakhtiari and Boyer Ahmad are more closely related to each other than they are to those of any other group is supported by the fact that they both speak closely related dialects of Lori and inhabit the same area. However, contrary to ethnohistorical and linguistic evidence, the assemblages of the two Lor groups appear to be more closely related to those of Turkic-speaking groups (the Yomut, Tekke, Qashqa'i and Shahsevan) than they are to the other Indo-Iranian-speaking group, the Baluch. Furthermore, the cladogram suggested that the Qashqa'i and Shahsevan share a more recent common ancestor with the three Lor-speaking groups than they do with the Yomut and Tekke, which again contradicts linguistic groupings. Finally, the Qashqa'i assemblage appears to be more closely

related to those of the Boyer Ahmad and Bakhtiari than it is to the Shahsevan, even though the latter speak a closely related dialect of the same language.

To assess the importance of these differences, we compared the number of changes required by each character on the most parsimonious tree with the number of changes required by a tree in which the relationships among the assemblages were forced to reflect the tribes' population histories. The difference in the character lengths was then evaluated using a one-tailed Wilcoxon sign-ranks test, as described by Templeton (1983). The analysis found that the population tree required a significant number of extra steps compared with the most parsimonious tree (total number of extra steps = 38,  $p < 0.01$ ). Thus, the strong phylogenetic signature recovered from the textile data cannot simply be accounted for purely in terms of descent with modification from common ancestral populations.

To shed more light on the relationships between the population history of the tribes and their weaving traditions, we carried out a cophylogenetic analysis in which the best estimate of tribal population history was treated as the independent phylogeny and the cladogram derived from the weaving data was treated as the dependent phylogeny. Previous efforts to apply cophylogenetic techniques to cultural evolution (e.g. Jordan & Mace 2006; Riede 2009) were limited by methods that only mapped three types of relationships: codivergences, sorting events and duplications. They were therefore unable to address the potential role played by horizontal transfers in generating mismatches between the compared trees. Here, we were able to overcome this constraint using the program TREE-MAP v. 2.0 (Page & Charleston 2002), which implements an algorithm called 'jungles' (Charleston 1998). Jungles is an advancement on previous tree reconciliation methods because it considers all four cophylogenetic processes, including horizontal transfer.

First, a jungles analysis generated all the possible solutions to the cophylogeny of the craft tree and population tree. The total cost of each solution was then estimated according to the number of events other than co-divergences that they hypothesized. Solutions with lower costs are considered preferable to those with higher costs, since the latter require a greater number of independent evolutionary events to explain how the observed patterns of association between the two sets of entities arose. This approach is known as 'event-based parsimony' (Ronquist 1996). In principle, it is possible to impose additional optimality criteria by assigning different costs to each type of event. However, for the purposes of this study, we assumed that there is an equal likelihood of horizontal transfers, duplications and sorting events and therefore assigned the same cost (1) to each of them (with a cost of 0 for co-divergences).

Figure 4 shows three different solutions to the cophylogeny of the craft tree and language tree returned by TREE-MAP. Figure 4*a* hypothesizes four co-divergences and two horizontal transfers. Thus, the total cost of the reconciliation between the two

trees is 2. Figure 4*b* also has a reconciliation cost of 2. It hypothesizes five co-divergences and one horizontal transfer and a sorting event. Figure 4*c* hypothesizes a reconstruction of events that involves no horizontal transfers. Instead, it suggests that there were three duplications early in the history of weaving that gave rise to several distinct craft lineages. All the lineages subsequently underwent extensive pruning as a result of sorting events that occurred at each juncture where ancestral populations split into new ones. In total, the jungle proposes three duplications and nine sorting events, with a total reconciliation cost of 12.

To test the validity of these various explanations, a further analysis was carried out that involved randomizing the associate tree and measuring how often the randomized trees fit, as well as the original tree. The results of this analysis suggested that the number of events hypothesized by both the first two jungles was significantly fewer ( $p < 0.05$ ) than the number of events that would be required to explain associations between the population tree and random trees. In contrast, the number of events hypothesized by the third jungle was not less than what would be expected by chance. We can therefore reject the hypothesis shown in figure 4*c*.

The analyses were unable to distinguish which of the other two reconstructions represent a better explanation for associations among the tribes' weaving traditions and population histories. Both explanations were found to be statistically significant and both had the same cost (2). Since we currently lack convincing reasons to assume that horizontal transfers are either more or less costly than sorting events, we cannot reject *a priori* an explanation that requires two horizontal transfers (figure 4*a*) in favour of one that requires only one horizontal transfer but also one sorting event (figure 4*b*) or vice versa. We can however judge the merits of each reconstruction against other existing lines of evidence.

The horizontal transfers hypothesized in figure 4*a* are compatible with geographical evidence and historical records. The hypothesis that the ancestor of the Bakhtiari and Boyer Ahmad acquired weaving from the ancestor of the neighbouring Qashqa'i is consistent with the fact that they are close neighbours. It is also compatible with ethnohistorical data suggesting that the ancestors of the Qashqa'i arrived in the region prior to the divergence of the Bakhtiari and Boyer Ahmad. As noted earlier, whereas the ancestors of the Qashqa'i are believed to have migrated to their present day territories in southwestern Iran some 500 years ago (Oberling 1974), the Bakhtiari and Boyer Ahmad did not emerge as distinct tribal entities until the eighteenth or nineteenth century (Garthwaite 1983; Amanolahi 1988). It is therefore plausible that the Bakhtiari and Boyer Ahmad inherited weaving from a common ancestor that had adopted it as a result of contact with the ancestors of the Qashqa'i.

The other horizontal transfer hypothesized in figure 4*a* occurs between the ancestor of the Shahsevan, Qashqa'i, Tekke and Yomut and the ancestor of the Baluch. As mentioned previously, the Baluch are thought to be descended from a tribe that migrated from the southern Caspian Sea to southwestern Iran

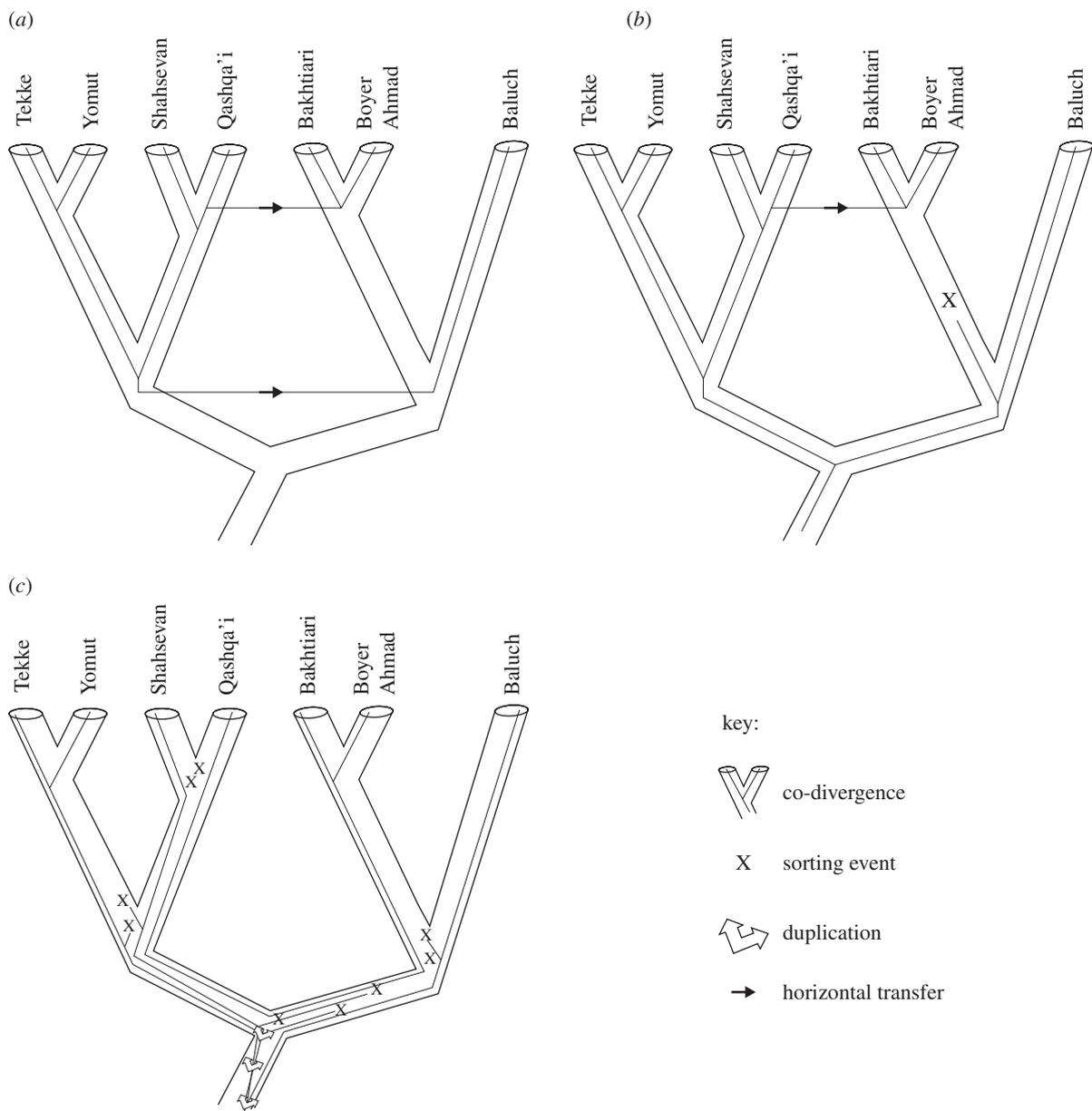


Figure 4. Three solutions to the cophylogeny of the tribes' weaving traditions and population histories, as reconstructed in TREE-MAP v. 2.0. The independent tree (hollow cladogram) represents the populations' histories, while the dependent tree (solid lines) represents the history of their craft traditions. The different events hypothesized in each reconstruction are indicated by symbols that are explained in the key.

some 900 years ago. This event is roughly contemporaneous with (and may perhaps have even been caused by) the expansion of Oguz Turks into western Iran in the eleventh and twelfth centuries (Thompson 2002), from who the Shahsevan and Qashqa'i are descended (Oberling 1974). It is certainly possible, therefore, that the Baluch split from the Boyer Ahmad and Bakhtiari before the Shahsevan and Qashqa'i split from the Tekke and Yomut, and that all five groups acquired their weaving traditions from a common Oguz Turkic source.

The explanation in figure 4b also hypothesizes a horizontal transfer from the ancestor of the Qashqa'i to the ancestor of the Bakhtiari and Boyer Ahmad. As pointed out above, this scenario is plausible in the light of the historical evidence. However, instead of assuming that the Baluch acquired weaving from the ancestor of the Tekke, Yomut, Qashqa'i and

Shahsevan, figure 4b suggests that the weavings of the Baluch are derived from an ancestral Iranian tradition that went extinct in the Boyer Ahmad–Bakhtiari lineage. It further indicates that the relationship between the weavings of the Baluch and those of the Shahsevan, Qashqa'i, Tekke and Yomut can be explained by descent from a common ancestor of both Turkic and Iranian-speaking groups. However, given that the best estimate from historical linguistics (e.g. Gray & Atkinson 2003) is that the relationship between Turkic and Iranian languages probably predates the origins of agriculture and therefore the keeping of animals for wool, this hypothesis seems unrealistic. It is more plausible that Baluchi weaving traditions, like those of the Boyer Ahmad and Bakhtiari, were originally borrowed from Turkic peoples their ancestors came into contact with. On that basis, we believe that the reconstruction of events as shown

in figure 4a represents the best explanation for the origins and spread of weaving among the populations.

#### 4. DISCUSSION AND CONCLUSIONS

Phylogenetic approaches to cultural diversity have shown that the diversification and spread of cultural traditions are often closely linked to the dispersal histories of populations (e.g. Mace *et al.* 2005; Collard *et al.* 2006; Lipo *et al.* 2006). The findings of our case study lend further weight to this evidence. Borrowing techniques from biology that are designed to study coevolutionary relationships, we found that relationships between Iranian tribal craft traditions and population histories could be largely accounted for in terms of ‘co-divergence’—the parallel cladogenesis of one lineage with another. Thus, in the two best reconstructions returned by the analyses, all of the relationships among the Turkic tribal assemblages could be explained by population phylogenesis, as could the relationship between the assemblages of two of the Iranian-speaking groups, the Boyer Ahmad and Bakhtiari.

Nevertheless, it was also clear that some of the relationships between textile assemblages were incompatible with data on the groups’ population histories. Following other researchers (e.g. Jordan & Mace 2006), we have suggested that such anomalies can be explained in relation to dual inheritance theory whereby, just as individuals can copy cultural behaviours from role models other than their parents, populations may sometimes acquire traditions from sources other than their immediate ancestors. However, as biologists have long known, horizontal transfers are not the only cause of discrepancies between co-evolving systems. In order to estimate horizontal transfers accurately, it is crucial to consider the possible roles played by sorting events and duplications, both of which have direct analogues in cultural evolution.

Using the jungles algorithm, we were able to evaluate the likely role played by each of these processes in generating the conflicts between the textile phylogeny and population tree. Two of the reconstructions returned by the analysis involved horizontal transfers, while a third did not. Since the latter required a significantly greater number of events than the other two, it was rejected. The two remaining reconstructions were equally parsimonious. One required two horizontal transfers, while the other required one horizontal transfer and one sorting event. By comparing both reconstructions with other sources of evidence, we concluded that the former was the more realistic scenario. Thus, having considered and ruled out the alternatives, we can be reasonably confident that in this case, horizontal transfers are likely to be the major source of inconsistencies between the textile phylogeny and the population phylogeny reconstructed from linguistic data and oral histories.

Of course, like weaving, both language and oral histories are socially transmitted, and as such cannot be regarded as unproblematic guides to population history. Some studies suggest that mismatches between language and genetic history are common among

pastoralist populations in the Middle East (Nettle & Harriss 2003), and that oral accounts of group origins can be ambiguous or misleading. As Barth (1961) explained in his classic study of nomads of South Persia, linguistic and ethnic identities are often based on a group’s political affiliations, rather than its actual historical origins. Barth (1961) describes several cases where groups are known to have adopted the language of politically dominant groups, initially becoming bi-lingual but ultimately switching completely to their new tongue. Thus, in the absence of genetic data, we cannot be certain that language and oral history provide an accurate reflection of group histories. Instead, they and the weaving traditions may represent different ‘packages’ of cultural inheritance (e.g. Boyd *et al.* 1997), whose descent histories differ from each other and from the ‘true’ population history of the tribes.

An even more intriguing possibility is that these traditions are all tracking population histories, but *different aspects* of population history. Thus, whereas weaving is transmitted down the female line, oral history and ethno-linguistic affiliations are usually traced via males. Studies of population genetics in other patrilineal pastoralist groups in the region suggest that there are often differences in the migration histories of males and females in these populations, which can occur as a result of some patrilineal expanding into others’ territories and then marrying with local females (e.g. Perez-Lezaun *et al.* 1999; Chaix *et al.* 2007). The complexities of human genetic and cultural histories here and elsewhere mean that in most cases there will not be a single phylogeny for either populations or their traditions. Reconciling these diverse lineages of inheritance is likely to present us with significant challenges. Fortunately, the progress that has been made in addressing similar problems in biology means that we are well-equipped to face them.

We thank Fiona Jordan, Jeremy Kendal, Kenny Smith, Robert Layton, Emma Flynn and Rachel Kendal for their input into the development of this article. We are also grateful for the feedback provided by participants at the CECD Theme B workshop on Cultural and Linguistic Diversity, where we presented this research. During the period in which most of the data were collected J.J.T. was funded by the Economic and Social Research Council, the Arts and Humanities Research Council and the Wenner-Gren Foundation for Anthropological Research. During the period in which the paper was written J.J.T. was supported by the Research Councils UK’s Academic Fellowship scheme. M.C. is supported by the Social Sciences and Humanities Research Council, the Canada Research Chairs Program, the Canada Foundation for Innovation, the British Columbia Knowledge Development Fund and Simon Fraser University.

#### REFERENCES

- Amanolahi, S. 1988 *Tribes of Iran—vol. 1: Luristan, Bakhtiari, Kuh Gilu and Mamsani*. New Haven, CT: Human Relations Area Files.
- Balfour, H. 1889 On the structure and affinities of the composite bow. *J. Anthropol. Inst. Great Britain and Ireland* **19**, 220–250. (doi:10.2307/2842074)

- Barth, F. 1961 *Nomads of south Persia*. Oslo, Norway: Oslo University Press.
- Barthold, W. 1962 *Four studies on the history of Central Asia*. Leiden, The Netherlands: E.J.Brill.
- Beck, L. 1986 *The Qashqa'i of Iran*. New Haven, CT: Yale University Press.
- Boas, F. 1940 *Race, language and culture*. Chicago, IL: Chicago University Press.
- Boyd, R. & Richerson, P. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Boyd, R., Borgerhoff Mulder, M., Durham, W. H. & Richerson, P. 1997 Are cultural phylogenies possible? In *Human by nature* (eds P. Weingart, S. D. Mitchell, P. J. Richerson & S. Maasen), pp. 355–386. Mahwah, NJ: Lawrence Erlbaum.
- Brooks, D. R. & McLennan, D. A. 1991 *Phylogeny, ecology and behavior*. Chicago, IL: University of Chicago Press.
- Buchanan, B. & Collard, M. 2007 Investigating the peopling of North America through cladistic analyses of early Paleoindian projectile points. *J. Anthropol. Archaeol.* **26**, 366–393. (doi:10.1016/j.jaa.2007.02.005)
- Buchanan, B. & Collard, M. 2008 Phenetics, cladistics and the search for the Alaskan ancestors of the Paleoindians: a reassessment of the relationships among the Clovis, Nenana and Denali archaeological complexes. *J. Archaeol. Sci.* **35**, 1683–1694. (doi:10.1016/j.jas.2007.11.009)
- Cavalli-Sforza, L. L. & Feldman, M. 1981 *Cultural transmission and evolution: a quantitative approach*. Princeton, NJ: Princeton University Press.
- Chaix, R., Quintana-Murci, L., Hegay, T., Hammer, M., Mobasher, Z., Austerlitz, F. & Heyer, E. 2007 From social to genetic structures in Central Asia. *Curr. Biol.* **17**, 43–48. (doi:10.1016/j.cub.2006.10.058)
- Charleston, M. A. 1998 Jungles: a new solution to the host/parasite phylogeny reconciliation problem. *Math. Biosci.* **149**, 191–223. (doi:10.1016/S0025-5564(97)10012-8)
- Collard, M., Shennan, S. J. & Tehrani, J. 2006 Branching, blending and the evolution of cultural similarities and differences among human populations. *Evol. Human Behav.* **27**, 169–184. (doi:10.1016/j.evolhumbehav.2005.07.003)
- Conze, E. 1980 *A short history of Buddhism*. London, UK: George Allen & Unwin.
- Doolittle, W. F. 1999 Phylogenetic classification and the universal tree. *Science* **284**, 2124–2128. (doi:10.1126/science.284.5423.2124)
- Durham, W. H. 1991 *Co-evolution: genes, culture, and human diversity*. Chicago, IL: Stanford University Press.
- Farris, J. S. 1989a The retention index and homoplasy excess. *Syst. Zool.* **38**, 406–407. (doi:10.2307/2992406)
- Farris, J. S. 1989b The retention index and the rescaled consistency index. *Cladistics* **5**, 417–419. (doi:10.1111/j.1096-0031.1989.tb00573.x)
- Felsenstein, J. 1985 Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791. (doi:10.2307/2408678)
- Frye, R. 1960 Baluchistan. A geography and history. *Encycl. Islam* **1**, 1005–1006.
- Garthwaite, G. R. 1983 *Khans and Shahs: a documentary analysis of the Bakhtiyari in Iran*. Cambridge, UK: Cambridge University Press.
- Gray, R. & Atkinson, Q. 2003 Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature* **426**, 435–439. (doi:10.1038/nature02029)
- Gray, R. F. & Jordan, F. 2000 Language trees support the express-train sequence of Austronesian expansion. *Nature* **405**, 1052–1055. (doi:10.1038/35016575)
- Gray, R. D., Greenhill, S. J. & Ross, R. M. 2008 The pleasures and perils of Darwinizing culture (with phylogenies). *Biol. Theory* **2**, 360–375. (doi:10.1162/biot.2007.2.4.360)
- 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)
- Grimes, B. F. 2002 *Ethnologue: languages of the world*, 14th edn. Dallas, TX: Summer Institute of Linguistics.
- Hafner, M. & Nadler, S. 1988 Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* **332**, 258–259. (doi:10.1038/332258a0)
- Hafner, M. & Page, R. 1995 Molecular phylogenies and host–parasite cospeciation: gophers and lice as a model system. *Phil. Trans. R. Soc. Lond. B* **349**, 77–83. (doi:10.1098/rstb.1995.0093)
- Henrich, J. 2004 Demography and cultural evolution. How adaptive cultural processes can produce maladaptive losses—the Tasmanian case. *Am. Antiquity* **69**, 197–214. (doi:10.2307/4128416)
- 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)
- Jordan, P. & Mace, T. 2006 Tracking culture-historical lineages: can ‘descent with modification’ be linked to ‘association by descent’? In *Mapping our ancestors* (eds C. Lipo, M. O’Brien, M. Collard & S. Shennan), pp. 149–168. New Brunswick, NJ: Aldine Transaction.
- Jordan, P. & Shennan, S. J. 2003 Cultural transmission, language, and basketry traditions amongst the Californian Indians. *J. Anthropol. Archaeol.* **22**, 42–74. (doi:10.1016/S0278-4165(03)00004-7)
- 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)
- Konieczny, M. G. 1979 *Textiles of Baluchistan*. London, UK: British Museum.
- Kroeber, A. 1948 *Anthropology: race, language, culture, psychology and prehistory*. New York, NY: Brace.
- Lipo, C., O’Brien, M., Collard, M. & Shennan, S. J. (eds) 2006 *Mapping our ancestors: phylogenetic approaches in anthropology and prehistory*. New Brunswick, NJ: Aldine Transaction.
- Lycett, S. 2007 Why is there a lack of Mode 3 Levallois technologies in East Asia? A phylogenetic test of the Movius–Schick hypothesis. *J. Anthropol. Archaeol.* **26**, 541–575. (doi:10.1016/j.jaa.2007.07.003)
- Lycett, S. 2009 Are Victoria West cores ‘proto-Levallois’? A phylogenetic assessment. *J. Human Evol.* **56**, 175–191. (doi:10.1016/j.jhevol.2008.10.001)
- Mace, R., Holden, C. & Shennan, S. 2005 *The evolution of cultural diversity—a phylogenetic approach*. London, UK: UCL Press.
- Moore, J. H. 1994 Putting anthropology back together again: the ethnogenetic critique of cladistic theory. *Am. Anthropol.* **96**, 925–948. (doi:10.1525/aa.1994.96.4.02a00110)
- Nettle, D. & Harriss, L. 2003 Genetic and linguistic affinities between human populations in Eurasia and West Africa. *Hum. Biol.* **75**, 331–344. (doi:10.1353/hub.2003.0048)
- Nunn, C. L., Arnold, C., Matthews, L. & Mulder, M. B. 2010 Stimulating trait evolution for cross-cultural comparison. *Phil. Trans. R. Soc. B* **365**, 3807–3819. (doi:10.1098/rstb.2010.0009)
- O’Brien, M. J. & Lyman, R. L. 2003 *Cladistics and archaeology*. Salt Lake City, UT: University of Utah Press.
- Oberling, P. 1974 *The Qashqa'i nomads of fars*. The Hague, The Netherlands: Mouton.

- Ohangari, K. & Berkes, F. 1997 Transmission of indigenous knowledge and bush skills among the western James Bay Cree women of subarctic Canada. *Human Ecol.* **25**, 197–222. (doi:10.1023/A:1021922105740)
- Page, R. (ed.) 2003 *Tangled trees: phylogeny, cospeciation and coevolution*. Chicago, IL: University of Chicago Press.
- Page, R. & Charleston, M. 1998 Trees within trees: phylogeny and historical associations. *Trends Ecol. Evol.* **13**, 356–359. (doi:10.1016/S0169-5347(98)01438-4)
- Page, R. & Charleston, M. 2002. TreeMap 2.0. Available to download at <http://taxonomy.zoology.gla.ac.uk/%7Emac/treemap/index.html>.
- Paterson, A. M., Wallis, G. P. & Gray, R. D. 1999 How frequently do avian lice miss the boat? *Syst. Biol.* **48**, 214–223. (doi:10.1080/106351599260544)
- Pérez-Lezaun, A. *et al.* 1999 Sex-specific migration patterns in Central Asian populations, revealed by analysis of Y-chromosome short tandem repeats and mtDNA. *Am. J. Human Genet.* **65**, 208–219. (doi:10.1086/302451)
- Richerson, P. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
- Riede, F. 2009 Tangled trees: modelling material culture evolution as host–associate co-speciation. In *Pattern and process in cultural evolution* (ed. S. Shennan), pp. 85–99. Berkeley, CA: University of California Press.
- Rogers, D., Feldman, M. & Ehrlich, P. 2009 Inferring population histories using cultural data. *Proc. R. Soc. B* **276**, 3835–3843. (doi:10.1098/rspb.2009.1088)
- Ronquist, F. 1996 Reconstructing the history of host–parasite associations using generalised parsimony. *Cladistics* **11**, 73–89. (doi:10.1111/j.1096-0031.1995.tb00005.x)
- Ronquist, F. 1998 Phylogenetic approaches in coevolution and biogeography. *Zool. Scripta* **26**, 313–322. (doi:10.1111/j.1463-6409.1997.tb00421.x)
- Rudenko, S. 1970 *Frozen tombs of Siberia: the Pazyryk burials of iron-age horsemen*. Berkeley, CA: University of California Press.
- Swofford, D. L. 1998 *PAUP\* 4. phylogenetic analysis using parsimony (\*and other methods)*, v. 4. Sunderland, MA: Sinauer.
- Tanavoli, P. 1985 *Shahsevan Iranian rugs and textiles*. New York, NY: Rizzoli.
- Tehrani, J. & Collard, M. 2002 Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles. *J. Anthropol. Archaeol.* **21**, 443–463. (doi:10.1016/S0278-4165(02)00002-8)
- Tehrani, J. & Collard, M. 2009a On the relationship between inter-individual cultural transmission and population-level cultural diversity: a case study of weaving in Iranian tribal populations. *Evol. Human Behav.* **30**, 286–300. (doi:10.1016/j.evolhumbehav.2009.03.002)
- Tehrani, J. & Collard, M. 2009b The evolution of cultural diversity among Iranian tribal populations. In *Pattern and process in cultural evolution* (ed. S. Shennan), pp. 99–111. Berkeley, CA: University of California Press.
- Temkin, I. & Eldredge, N. 2007 Phylogenetics and material culture evolution. *Curr. Anthropol.* **48**, 146–153. (doi:10.1086/510463)
- Templeton, A. 1983 Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* **37**, 221–224. (doi:10.2307/2408332)
- Thompson, J. 1980 Turkmen carpet weavings. In *Turkmen: tribal carpets and traditions* (eds L. Mackie & J. Thompson), pp. 60–191. Washington, DC: The Textile Museum.
- Thompson, J. 2002 The Baluch. In *The nomadic peoples of Iran* (eds R. Tapper & J. Thompson), pp. 298–304. London, UK: Thames and Hudson.
- Tzavera, E. 1984 *Rugs and carpets from Central Asia*. Leningrad, USSR: Aurora Art Publishers.
- Windfuhr, G. 2007 *Iranian languages*. London, UK: Routledge Curzon.