Chapter 6

Tangled Trees:
Modeling Material Culture Evolution as Host-Associate Co-Speciation

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Introduction

Evolutionary biologists have long been aware that species are connected in complex and reciprocal ecological as well as evolutionary relationships with one another. In evolutionary time, such linked relationships produce linked phylogenies that, at least to some degree, reflect the evolutionary history of all organisms involved (Page 2003a). The study of long-term co-evolution is part of the wider project of understanding the history of life through the construction of phylogenies and a battery of different methods is now available (e.g. Brooks and McLennan 1991; Page 2003b), many of which have been implemented in popular – and often free – software packages (see, for example, http://taxonomy.zoology.gla.ac.uk/rod/rod.html).

The development of such quantitative approaches to long-term co-evolution had its origin in molecular evolutionary studies (Goodman et al. 1979), but soon after they were also used to explore biogeographic issues (Humphries and Parenti 1986; Page 1988; Nelson and Platnick 1981) as well as host-parasite co-evolution (Hafner and Page 1995; Page 1990b, 1993, 1994a, b, 2000; Page and Charleston 1997a, b, 1998; Page and Cotton 2002; Fig.1). In fact, Page and Charleston (1998:356) have argued that the general approach and the computational procedures underlying it are applicable to a whole range of "historical associations". In anthropology and archaeology historical associations are ubiquitous too and by employing phylogenetic methods, archaeologists and anthropologists have made considerable headway in quantitatively understanding past societies and their evolution (e.g. Collard et al. 2006a, b; Mace et al. 2005; O'Brien and Lyman 2000a; O'Brien et al. 2003). Yet it remains unclear to what extent ‘descent with modification’ (within one lineage) can be linked with ‘association by descent’ (across two or more lineages; Jordan and Mace 2006).

Fig 1 about here

In this paper, I would thus like to explore in somewhat greater depth the salient points of contact between ‘historical associations’ in biological and cultural evolution. The argument presented rests on three premises, one conceptual and two methodological:

1. The relation of humans as biological entities and culture can be understood as one of host and associate (e.g. Brodie 1996; Cullen 1993a, b, 1995, 1996a, b; Dawkins 1976 Dennett 1995; Sperber 1996).
2. Useful Darwinian models of short-to-medium-term cultural evolution can be derived from quantitative epidemiology (e.g. Boyd and Richerson 1985; Durham 1991; Kendel and Laland 2000; Lumsden and Wilson 1981).
3. Long-term cultural evolution as seen in the archaeological record can be modelled using phylogenetic approaches (e.g. Lipo et al. 2006; Mace et al. 2005; O'Brien et al. 2003).

If these three premises can be shown to be robust, an application of *co-speciation* (or *co-phylogeny*) models rather than *co-evolution* models to archaeological questions is warranted because “cospeciation is coevolution that occurs in macroevolutionary time” (Page 2003a:2; see also Brooks and McLennan 1991). Microevolutionary models are at the heart of gene-culture co-evolution approaches (Boyd and Richerson 1992), but it has been argued that for archaeological problems macro-evolutionary models are analytically more appropriate (Lyman and O'Brien 2001). It is important to remember too that the degree to which a lineage displays cladogenetic patterns depends on both the evolutionary processes and forces at work (e.g. the amount of variation, the strength of selection, the degree of isolation, etc.) and also on how the units of analysis (i.e. the taxa) are defined. While the importance of particular evolutionary forces will usually emerge only *after* an analysis has been conducted, the taxonomic units must, at least initially, be defined *prior* to analysis. Biologists (e.g. Ereshefsky 1992; Hull 1965, 1978, 1987; Lewontin 1970) have grappled long since with issues of unit definition and recent efforts in archaeology have also made some headway

(Dunnell 1995; Ramenofsky and Steffen 1998). However, general discussions of unit definitions for evolutionary archaeological analyses are lacking.

This paper is divided into two parts. In part one, a brief discussion of archaeological taxonomic units and their definition sets the stage for an exploration of the conceptual premise of linked cultural evolutionary dynamics. Although some archaeologists have argued that human culture can be conceptualized as parasitic to its carriers (especially: Cullen 1993a, b, 1995, 1996a, b), it is argued here that any demonstrable historical association between the sets of artefacts studied suffices to warrant an attempt at applying co-phylogenetic methods. There is in fact no need to resort to "bizarre" (Ingold 1993:195) theories of cultural viruses: *If* two or more artefact lineages display cladogenetic evolutionary patterns and *if* the processes of social information transmission that underlie these artefact lineages are somehow linked – through, for instance, the context of their transmission, their use context or as part of multi-component artefact systems – then co-phylogenetic patterns should emerge. In line with the discussion of Page and Charleston (1998), co-speciation models and their attendant methods are *in principle* applicable in any case where sets of phylogenies are linked in their evolutionary dynamics, no matter whether these phylogenies are based on morphological, genetic or artefact data. The degree to which given lineages do show co-phylogenetic patterns then becomes an empirical question. The second part of the paper presents the rationale of co-speciation analysis and a brief case study using the co-evolution of European table knives and forks from the 16th to the 20th century (Brown 2002a; Himsworth 1953; Lassen 1960; Moore 1999; Singleton 1973). This case study serves to illustrate one possible approach that implements a co-phylogenetic approach to material culture change based on historical descent. The potential benefits are clear: Studying only one aspect of a given social group's material culture repertoire, such as knives or projectile points will inevitably yield a very limited view of the 'total' history of this group, even if this particular artefact type is in some sense historically important. Co-speciation models thus offer the possibility of exploring the historical dynamics of different artefacts, such as knives *and* forks or projectile points *and* ceramics within one archaeological culture without relinquishing quantitative and phylogenetic rigour.

Part 1: Archaeological Taxonomic Units and Historical Association

In his discussion of how fossil hominins and Palaeolithic stone tools relate to one another, Foley (1987) suggested the use of archaeological taxonomic units (ATUs) defined at the appropriate level of (technological and geographic) resolution. More recently, Gamble et al. (2005) similarly attempted to relate archaeological techno-complexes to population genetic units in the context of the Late Palaeolithic re-colonization of Europe. These ATUs are intended to be the "cultural counterpart to the operational taxonomic unit (OTU) of biology and evolutionary science" (Gamble et al. 2005:195) and their purpose is to circumvent the pitfalls of using traditional typologically defined archaeological units for Darwinian archaeological analysis (Lyman and O'Brien 2003; O'Brien and Lyman 2004; O'Brien et al. 2002). Despite their use of evidently evolutionary units, Gamble et al. (2005) stop short of employing evolutionary methods to analyse their archaeological dataset. Unless they are underwritten by some kind of evolutionary rationale, taxonomies remain inert classification exercises (Fig.2). Instead, within a cladistic approach to archaeology, taxonomic units can be defined through their character trait composition, following O'Brien and Lyman (2000a; O'Brien et al. 2002). It should then be possible to track higher-order ATUs up the cladogram: each monophyletic clade could be defined as one ATU. Traditional typological divisions of the same material may or may not map onto such cladistic unit definitions.

Fig 2 about here

Socially transmitted information is complex and extremely rich in semantic content and any given culture will harbour a plethora of "learning lineages" (Harmon et al. 2006:209), some of which will be expressed through material culture. Within a social group, information will be transmitted differentially, according to gender, age, rank, occupation and such like (e.g. Shennan 1996). In addition, the use-lives and hence 'generation lengths' of craft items varies and with this the potential for evolutionary change (i.e. how much diversity can be introduced into a lineage and how fast change can occur) will differ from lineage to lineage. Architecture, for instance often outlasts even biological generations, whilst items such as pots or arrowheads go through many 'generations' of production and reproduction within the lifetime of their maker. These differences in evolutionary potential for change between different facets of craft production within the same cultural group may give rise to a "dissonance" (Fletcher 1996:61) between the phylogenetic signals of each lineage. We should not, for example, expect ceramic and flint technology to evolve at the same rate or follow the same pattern, because each lineage will be responsive to differences in the transmission and use context. Exploring these differences as reflected in each lineage's phylogeny may then reveal interesting insights into the kinds of forces that shape cultural evolution *within* a given group.

The use of co-phylogenetic models and methods may therefore take artefact phylogenies beyond the investigation of single lineages and towards a better understanding of the bio-cultural evolutionary forces at work within past groups. An important step towards successfully addressing questions of long-term co-evolution between human biology and culture or between different aspects of human culture (material or linguistic) is selecting the appropriate ATUs for the task at hand. Page and Charleston (1998) have provided the overarching rationale for a phylogenetic approach to such co-evolution. They argue that a variety of co-evolutionary scenarios can be treated as largely identical from a methodological point of view and that phylogenetics offers a useful tool for formally exploring co-evolution scenarios. The phylogenies used can variously be based on morphological, molecular, linguistic, material culture or behavioural data and the degree to which they exhibit congruence and the reasons for why they do or do not tell the same stories, must be evaluated on a case-by case basis. Here, an approach to long-term cultural co-evolution is presented using the tree reconciliation methods from within an approach known as 'component analysis'.

Part 2: Historical Associations in Culture and the Evolution of European Cutlery

Component analysis is one of the techniques often employed in the study of long-term co-evolution between biological systems (Nelson and Platnick 1981; Page 1990a). On the basis of it a variety of co-evolutionary issues can be addressed. In the biological world these include biogeography, gene-species relations as well as host-parasite co-evolution. Component analysis is a method of analysing cladograms by dividing them into parts of analytical interest. Components refer to such usually monophyletic parts of a cladogram and "each component may be conceived of as representing a group of kinds" (Nelson and Platnick 1981:65). A small number of previous studies have tentatively explored the usefulness of tree-comparisons, comparing trees generated using biological and cultural data (Robson Brown 1995) as well as sets of trees generated on the basis of different aspects of cultural information (Jordan and Mace 2006). In the latter study, Jordan and Mace restricted themselves to comparing the topologies (shape) of their trees to randomly generated sets of trees. This kind of analysis can yield interesting insights about the coherence of cultural ‘cores’, but relies on using the same (or at least the same number of) taxonomic units for the initial or fundamental tree building.

In contrast, the approach followed here departs from this constraint – equal numbers of terminal taxonomic units are not a requirement for component analysis – whilst accepting another: for reconciling phylogenetic trees they must be fully resolved. Fully bifurcating resolution is rarely achieved in biological or cultural phylogenetic studies. Polytomies are caused by insufficient data resolution or real events – neither biological nor cultural evolution need proceed in a strictly bifurcating manner (Lewis et al. 2005; Maddison 1989; Walsh et al. 1999). European table cutlery was chosen as an example here for a variety of reasons. Data are readily available in collectors’ catalogues and individual specimens are often conveniently dated to their year of manufacture, allowing for very high chronological resolution. Table cutlery was deemed to be well suited because the technological and social environment of cutlery manufacture and use are well known (Bailey 1927; Marquardt 1997; Singleton 1973; Wolfman and Gold 1994; Brown 2002a; Moore 1999). In addition, from the 17th century onwards knives, forks and to a lesser degree spoons were sold in sets and this coupling of particular specimens (here taken as representative of the population) within a given set is indicative of ‘historical association’. This paper is intended to be primarily a methodological exploration and the main reason for the selection of this particular data set is its illustrative nature with regard to the co-phylogenetic approach. However, a larger and rather more conceptual issue is also at stake. The term ‘evolution’ is often used in literature about cutlery design and manufacture, yet the art historical or art appreciative framework in which cutlery is usually considered is steeped in a typological view of the material (Ziman 2000; Ziman et al. 2002). It has already been suggested that evolutionary archaeological approaches are applicable to historical archaeology (O'Brien and Lyman 2000b) and perhaps phylogenetic analyses of design articles will put hypotheses of recent material culture evolution on a more quantitative basis.

Tables 1 and 2 and fig 3 about here

Following the method of O'Brien et al. (2002), 15 knife taxa and 13 fork taxa were constructed. The characters and character states used are given in Fig.3 and Tables 1 and 2. Following taxon construction, cladograms were built using PAUP*4.0b (Swofford 1998). Because the technologies employed in the manufacture of cutlery are complex, the Dollo parsimony setting was used (Gould 1970). Dollo parsimony stipulates that complex characters can be lost within a lineage but not re-evolve in identical form. Although commonly referred to as ‘Dollo’s Law’, according to Gould (2002:902) it “only restates the general principles of mathematical probability for the specific case of temporal changes based on large numbers of relatively independent components”. While the general applicability of Dollo’s irreversibility law to biological systems is contested (e.g. Marshall et al. 1994; Wagner 1982), losses of *cultural* complexity may not be as rare as is often assumed (Diamond 2005; Henrich 2004; Rivers 1926) and even intentional revivals of old technologies or fashions rarely if ever lead to identical objects. While superficially similar cultural constellations certainly did evolve repeatedly, these are not true homoplasies (parallel evolution of identical character states) nor are they true reversals if they occur in the same lineage. For instance, the large tanged points of the middle Upper Palaeolithic Gravettian, the so-called Font-Robert points, appear very similar to later tanged points of almost identical dimensions, such as Bromme points, which occur primarily along the Northern European periphery during the Late Upper Palaeolithic. However, although they do both come from the ATU termed the European Upper Palaeolithic, the two point types are most certainly not historically related in any meaningful sense and they can be distinguished on technological grounds, if the identifying characters are correctly chosen.

Table 3 about here

Both the knife- and the fork-dataset exhibit a very strong phylogenetic signal and a randomization test shows that tree length is significantly shorter than expected (Table 3). The analysis yields one and two equally parsimonious fully resolved trees for knives and forks respectively. Unfortunately, not enough data were available for spoons. Bootstrapping gave branch support levels of generally between 60% and 99%. Given that all specimens come from cutlery makers associated with the Sheffield tradition (Singleton 1973) such a strong phylogenetic signal is not unexpected. All trees (Fig.4) were rooted using the oldest specimen (dated 1580) taken to represent an ‘ancestral’ form.

Fig 4 about here

In turn, these trees were reconciled using the TREEMAP and GENETREE software packages (Page 1994a; Page 1998). Two taxa were taken to be associated when they had been sold in a set. The basic output consists of a so-called tanglegram (Fig.5), which juxtaposes the two cladograms and plots the associations between terminal taxa. It is a useful tool for visually assessing the differences in branching pattern between the trees. Further, the reconciled tree incorporates information from both original trees and provides a measure of the extent to which the two lineages have diverged: Using a model of possible processes that underlie the incongruence between trees allows a quantification of optimality criteria for tree reconciliation (Table 4): Reconciliation will minimize the costs of mapping associated components onto one another and the costs of these reconciliation actions can be varied from analysis to analysis. In the default setting (the one used here), duplications and losses will be minimized, whereas it is also possible to optimize only for duplications, assigning a zero cost and thereby effectively ignoring losses. Each reconciled pair will be associated with a particular score, the sum of the events needed to fit the associate into the host tree. This goodness-of-fit can be further assessed through a randomization test, where a set of trees is randomly generated using the same number of taxa as the original host tree. The total reconciliation cost of these random trees can then be compared with the reconciliation cost of the actual host tree. A heuristic search algorithm will retrieve from within the set of associate trees those with the lowest cost and these trees will be maximally parsimonious in the sense of minimizing the total number of events required to explain the evolutionary history of the associate. For instance, if two lineages share an identical evolutionary history, reconciliation cost will be zero.

Table 4 and fig 5 about here

Because tree reconciliation aims to preserve all the historical information contained in the input tree, the reconciled tree or trees are likely to be complicated, depending primarily on the degree to which the analyzed lineages have diverged, the number of equally parsimonious trees for each lineage and the extent to which associations are shared across taxa. It is desirable to constrain the input as much as possible as the number of equal-cost reconciliations rises sharply with the number of input tree combinations. In addition, the utility of this approach is at present constrained by the need for fully resolved input trees and the inability of taking account of horizontal associations (i.e. gene transfer ~ contact). However, as Page and Charleston (1997b:63) note “the mapping and construction of reconciled trees is consistent for polytomous trees” and can potentially be incorporated into future releases of the appropriate software (see http://evolve.zoo.ox.ac.uk/software/TreeMap). With regards to horizontal associations, experimental versions of TREEMAP (Page and Charleston 2002) are able to accommodate them, producing ‘jungles’ instead of trees (Charleston 1998; Charleston and Perkins 2003).

Conclusion

It is suggested here that component analysis could be a useful further avenue for evolutionary archaeologists to explore if the phylogenetic study of culture is to be taken beyond single cladograms. Hafner and Page (1995:79) suggest that “component analysis is sufficiently general to be applied to any historical association”. Many historical processes, be it in biology (Mirkin et al. 1997), at the interface between biology and culture (Foley 1987, 2002; Robson Brown 1995) or between different facets of culture (Jordan and Mace 2006) are made up of multiple lineages of information transmission and these lineages may be linked through historical association, However, the constituent trees respond to different evolutionary pressures and dynamics and therefore exhibit different branching patterns. Although rather complex in implementation and interpretation, the co-phylogenetic approach presented here offers one possible means of operationalizing Gamble et al.’s (2005) archaeological taxonomic units. Micro-evolutionary everyday processes of tool-making, situated within their rich social context, give rise to archaeologically observable lineages of tool-making (Riede 2006). These lineages can be analyzed using cladistic methods and higher-order ATUs such as regional facies or cultures can be defined cladistically as monophyletic clades. When two or more artefact cladograms from the same cultural context are available, component analysis serves to visualize the relationship between them. Historical association of archaeological material culture lineages could, for instance, be defined through their co-occurrence in undisturbed contexts and the reconciled tree scores the extent to which the two lineages have diverged.

At present, the inability of the available software packages to deal with trees that are not fully resolved still militates against a more productive application of tree reconciliation approaches to cultural data A further exploration of this approach is equally hampered by a lack of cultural phylogenies that are historically associated (see Collard et al. 2006a and b for an overview of currently available cultural phylogenies). This paper has taken some tentative steps towards outlining the theoretical foundation for an extension of the co-speciation approach to cultural data and draws attention to the ready availability of the appropriate, albeit still limited, software. In exploring the quantitative study of historical association, it is important to keep in mind that the analogy between the different kinds of historical associations is merely a heuristic tool. The argument is not that the processes are closely analogous, but that the *patterns* produced by these very different processes are in fact very similar and can therefore be studied using similar techniques (see Page and Charleston 1998). Future work can build on this foundation by exploring case studies of historically associated kinds of material culture and thereby further refine the approach.

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