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Comparative Phylogenetic Methods and the Study of Pattern and Process in Kinship

Fiona Jordan

*If we ask how it is that a society has the social institutions that it does have
at a particular time the answer can only be supplied by history.*

(Radcliffe-Brown 1950:1)

*Phylogenies can be used to infer the historical evolutionary processes that
must have existed in the past, given the patterns of diversity seen in the present.*

(Pagel 1997:331)

Anthropology began by comparing aspects of kinship across cultures, while linguists interested in semantic domains such as kinship necessarily compare across languages. In this chapter I show how phylogenetic comparative methods from evolutionary biology can be used to study evolutionary processes relating to kinship and kinship terminologies across language and culture. To properly study cultural evolution across populations, we need to account for the effect that shared ancestry may have in creating relationships and patterns in the traits we examine, a problem recognized in anthropology since Galton (Tylor 1889). To combat what is essentially the same difficulty—the hierarchical relatedness of species—evolutionary biologists employ phylogenies (family trees) of species as population histories and use a set of statistical techniques called comparative methods to control for evolutionary history in trait evolution (Felsenstein 1985; Harvey and Pagel 1991). Anthropologists, like biologists, are most often interested in evolutionary processes beyond reconstructing “the tree,” so phylogenies and comparative methods are not meant as a replacement for existing approaches but are simply another tool for the scientific tool kit.

Kinship terminologies constituted the raw material for the earliest scientific (i.e., comparative) anthropology (Morgan 1871). While the postmodern turn in anthropol-

ogy saw the abandonment of the scientific approach in many aspects (D’Andrade 2000), anthropological scholarship has turned toward deeply contextual descriptions of social life (Geertz 1973), including kinship (Colleran and Mace in press). Ethnology—the comparative study of culture—could be poised to have a renaissance because scientific comparison is now tractable and it can shed light on history. Pattern is an outcome of process, and one can be used to understand the other, as both Radcliffe-Brown and Pagel note above.

Unlike material aspects of culture, social behavior does not fossilize, so in order to gain an understanding of the historical processes that produced current cultural diversity in kinship we have to make inferences on the basis of scarce and sometimes problematic data. These include material culture correlates of social structure and demographic estimates from archaeology, historical records for societies with written traditions, and more recently, genetic narratives that interpret patterns of sex-specific markers as indicative of past marriage and dispersal behavior (Wilkins and Marlowe 2006). Taken together, these data help us triangulate our inferences about the past, but none make much use of the primary data at hand, that is, the comparative ethnographic record. Linguistic approaches to kinship in contrast *do* have a long tradition of diachronic inference. The linguistic comparative

method has the capability of reconstructing protoforms for the vocabulary of ancestral speech communities. In this way, linguistics has provided a substantial contribution to our understanding of society in prehistory (e.g., Mallory and Adams 2006; Pawley et al. 2003). However, such “linguistic paleontology” has its limits—words can be reconstructed, but their meanings may be extremely fuzzy, and reconstruction in itself is not a guarantee that the meaning (be it an item or a concept) was present in the ancestral speech community (McMahon and McMahon 2005).

Some of the long-standing questions in anthropology are to do with the evolution of kinship systems over the time scale of human history (Allen et al. 2008; Chapais 2008). What, if anything, can we say about hominid family structure? Once modern humans had language, how did we start to refer to kin? And how, over tens of thousands of years and the dispersal of humans to vastly different ecological environments around the globe, did our kin terminologies diversify into the variation we see today—albeit a restricted diversity that is remarkable for its boundedness and logical structure (Nerlove and Romney 1967)? Why do different language families contain instances of the same structural patterns in terminology, albeit with different linguistic forms? Are there rules that govern the transformation of one sort of terminological system into another? Can we derive those processes simply from an analysis of the synchronic data we have available through the ethnographic record? In the introduction to their important volume, Godelier et al. (1998) echo Morgan in stressing three of these questions: the correlated evolution of terminologies and aspects of social structure, the restricted diversity of systems worldwide, and the dynamics that govern the transformation of kin term systems; and these still remain some of the most intriguing and important questions in the study of human cultural diversity.

In the past 25 years evolutionary biologists have developed a suite of tools to investigate diversity, correlated evolution, and character transformation across species while controlling for historical relatedness (Felsenstein 1985; Ord and Martins 2010). These tools have been adopted by a small number of anthropologists and linguists interested in the same sorts of questions as above, and a burgeoning literature on their application exists (Forster and Renfrew 2006; Gray et al. 2007; Lipo et al. 2006; Mace 2005; Mace and Pagel 1994; Mace et al. 2005; Shennan 2009). Much of this work has focused on phylogenetic

tree-building, but in what follows I provide a nontechnical introduction to phylogenetic comparative approaches, discuss the components of an analysis, and detail how these methods have been applied to cultural phenomena. I then discuss in some detail two kinship case studies, one concerned with reconstructing ancestral states of post-marital residence and the other aimed at elucidating the dynamics of change in sibling terminologies. The chapter concludes with remarks for the future study of kinship terminologies with these evolutionary methods.

PHYLOGENETIC COMPARATIVE METHODS

Phylogenetic comparative methods (PCMs) are a class of statistical procedures developed in evolutionary biology to analyze the historical processes that have shaped diversity among species—or, more broadly defined, taxa of some sort. These methods work by statistically reconstructing the evolutionary pathways that are likely to have produced the observed distribution of a trait across a group of related taxa. PCMs comprise a diachronic aspect, in that they recognize the descent relationships of taxa through time, for example, the diversification of the class Mammalia in the last 100,000,000 years. They also comprise a synchronic aspect, in that they are concerned with the expression of some type of feature across a number of contemporaneous taxa—for example, different mammalian adaptations for locomotion such as forelimbs or flippers. Both are crucial, because the synchronic variation cannot be properly understood without the control for evolutionary relatedness that is provided by the ancestor–descendant relationships of the diachronic phylogenetic tree. Put simply, we cannot count lions and tigers and bears as three independent data points in a study of carnivores. We should rather count their carnivorous common ancestor as a single data point. In biology, PCMs were initially developed to overcome the problem of hierarchical relatedness in order to answer comparative questions about adaptation and coevolution (Harvey and Pagel 1991; Pagel 1999a): Are changes in one feature of an organism (or its environment) correlated with changes in other features? Besides coevolution, four other main types of evolutionary questions can be approached with PCMs: (1) assessing the amount of historical signal in the data, (2) characterizing the ancestral states of features, (3) determining the timing of evolutionary events, and (4) investigating the mode of evolutionary change (Ord and Martins 2010; Pagel 1999b)—see Figure 3.1 for more detail.

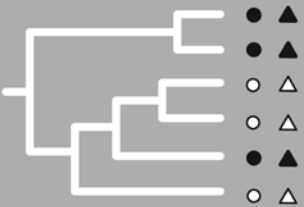
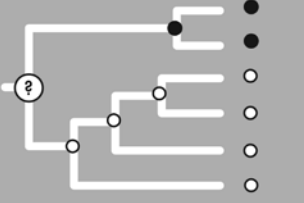
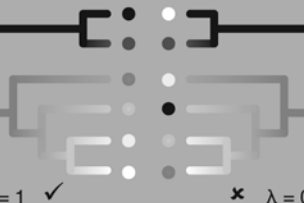
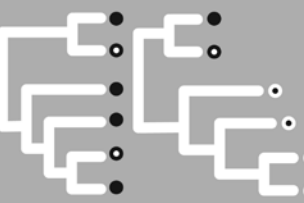
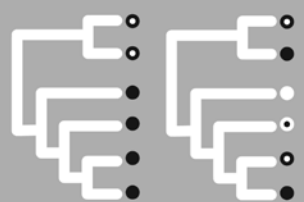
| RESEARCH QUESTION | COMPONENTS | EXAMPLE |
|--|---|--|
| <p>Correlated evolution Are two traits changing together?</p>  | <p>Data Two discrete presence/absence traits or Two continuously varying traits</p> <p>Tree Any fully-bifurcating phylogeny(s)</p> <p>Outcomes Can build up pathways of correlated changes; combined with ancestral states can infer direction of change</p> | <p>Cattle lead to loss of matriliney in Bantu-speaking societies</p> <p>Lexical tree of 68 Bantu languages</p> <p>Data: descent and pastoralism</p> <p>Dependent model of coevolution more likely than one where traits evolved independently</p> <p>Pastoralism changed before matriliney Holden & Mace 2003</p> |
| <p>Ancestral states What was the earlier form of a trait?</p>  | <p>Data A trait with 2+ categorical states or A continuously varying trait</p> <p>Tree Any fully-bifurcating phylogeny(s)</p> <p>Outcomes Can test models of sequential change; Can "fossilise" ancestral nodes if known; Can test competing hypotheses about ancestral states</p> | <p>Matrilocal residence is ancestral in Austronesian</p> <p>Lexical trees of 135 AN languages</p> <p>Data: postmarital residence</p> <p>Matrilocal residence inferred for PAN and PMP</p> <p>Switches to matrilocal residence less likely than to other forms of residence</p> <p>Jordan et al 2009</p> |
| <p>Phylogenetic signal Does a trait track history?</p>  | <p>Data Any continuously varying trait</p> <p>Tree Any fully-bifurcating phylogeny(s)</p> <p>Outcomes Can estimate degree of phylogenetic signal; Can test if signal is significant and therefore must be controlled for</p> | <p>Population size and the rate of lexical evolution</p> <p>Lexical tree of 351 AN languages</p> <p>Data: population size, amount of lexical change</p> <p>Population size and density have lambda (λ) values close to one, indicating strong historical signal</p> <p>Jordan & Currie submitted</p> |
| <p>Mode of change Is change gradual or punctual?</p>  | <p>Data Measures of branch (path) lengths or Any continuous varying trait</p> <p>Tree Any fully-bifurcating phylogeny(s) with meaningful branch lengths</p> <p>Outcomes Can use kappa statistic to quantify degree of punctual/gradual evolution in any one character</p> | <p>Languages evolve in punctuational bursts</p> <p>Lexical trees of AN, Bantu & IE</p> <p>Data: path lengths, number of nodes</p> <p>Relationship between path length and nodes suggests splitting events cause more lexical evolution</p> <p>Atkinson et al 2008</p> |
| <p>Rate of change How fast do traits change?</p>  | <p>Data Any discrete presence/absence traits</p> <p>Tree Any fully-bifurcating phylogeny(s) with meaningful branch lengths</p> <p>Outcomes Can determine rate of change of a trait; Combined with known time-depth of phylogeny can infer dates</p> | <p>Similar rates of evolution for lexical & typological features</p> <p>Lexical trees of AN & IE languages</p> <p>Data: typological features</p> <p>Estimate of evolutionary rates was equivalent across both language families and both types of features</p> <p>Greenhill et al 2010</p> |

FIGURE 3.1. Overview of five types of evolutionary questions that can be answered using phylogenetic comparative methods. The left box for each question is presented with a schematic diagram representing the approach. The middle box details the practical components (type of data, type of phylogeny, and outcomes of the procedures), and the right box describes a recent empirical example. AN = Austronesian; IE = Indo-European; PAN = Proto-Austronesian; PMP = Proto-Malayo-Polynesian.

These types of statistical explorations require three components in common: (1) a phylogenetic tree or trees representing hypotheses about the historical relationships among the taxa, (2) observations for each taxa on some trait of interest, and (3) a model of how the traits have evolved through time (Felsenstein 1985; Harvey and Pagel 1991). From there, the details of software and algorithms vary, but the principles remain the same. In a cross-cultural or cross-linguistic framework, phylogenetic trees of human populations are derived from linguistic or genetic data; comparative ethnographic or linguistic data are mapped onto the phylogeny, and a model of trait evolution is statistically inferred (Mace and Pagel 1994). Below I describe each of these steps; interested readers are referred to further literature for more technical details (see Felsenstein 2004; Lemey et al. 2009; Ord and Martins 2010; Ronquist 2004).

COMPONENTS OF A PHYLOGENETIC COMPARATIVE ANALYSIS

Phylogenetic Trees

It is important to stress at the outset that PCMs are *not* tree-building methods, though they rely on having some sort of evolutionary tree (phylogeny) as input to proceed. In this way they differ from the linguistic comparative method, which is essentially a tree-building method. In theory, PCMs can be used with any type of hypothesis about hierarchical relatedness and could take input as varied as a traditional historical linguistics tree, a tree of human populations based on features such as skull morphology or blood groups, or a set of equally likely phylogenies derived by analysis of DNA sequence data from different populations. What is important is that any phylogeny is simply a hypothesis about the descent relationships between different taxa, and in questions about human culture, a phylogeny is normally some representation of population history. Thus, because any particular tree is most likely *not* the “true tree” (especially with respect to human populations—where one “true tree” does not exist), we prefer methods that address uncertainty about the model of population history. This can be done by incorporating probability estimates of particular subgroups (clades) and by summarizing multiple and often conflicting lineages with a representative sample of trees. In recent years, a class of approaches known as Bayesian likelihood approaches has come to be the preferred method of phylogenetic inference because they do a good job of quantifying uncertainty in precisely these desired

ways. They also provide phylogenies that have meaningful estimates of evolutionary divergence, that is, branch lengths that quantify the change in a set of features since some shared common ancestor (Huelsenbeck et al. 2001; Yang and Rannala 1997).

Biologists wishing to infer the phylogenetic relationships of a set of species (to “draw a tree”) usually proceed by obtaining some set of DNA sequences, aligning those sequences to compare like with like, and then employing a phylogenetic software package to build evolutionary trees according to some optimization criterion such as parsimony or maximum likelihood. For a linguist using these methods, cognate-coded lexical items on standardized word lists are the usual input to software packages, though any codable set of characters with a structured evolutionary history may be used. Space does not permit a detailed description of the computational phylogenetic tree-inference procedures common in evolutionary biology and now being employed in evolutionary anthropology and linguistics (Dunn 2009; Gray et al. 2007). In-depth introductions to phylogeny construction are contained in Felsenstein 2004 and Lemey et al. 2009. For the remainder of this chapter, I take the existence of phylogenies as a given, but in the case studies more details will be given on the particular phylogenies used in each analysis.

Observations: Comparative Data

PCMs derive their name from the comparative data about which we wish to infer some evolutionary process. In biological analyses these data can be morphological (e.g., body size), behavioral (e.g., territorial defense strategies), physiological, or chemical—in fact, any feature of organisms that varies between populations. Likewise in cultural evolution, comparative data can be the biological characteristics of populations, such as the proportion of lactose-tolerant individuals (Holden and Mace 1997) or the sex ratio at birth (Mace and Jordan 2005). Ethnographic data are common; for example, researchers have investigated the coevolution of marriage systems and payments (Fortunato and Mace 2009), subsistence and inheritance systems (Holden and Mace 2003), or a combination of ethnographic and ecological information, for example, latitude and political complexity. Comparative linguistic data can also be analyzed with these methods: dependencies in the structural features of language (Dunn et al. 2011), the frequency of word use and rates of evolution (Pagel et al. 2007), and the relationship between popu-

lation size and the rate of lexical evolution (Jordan and Currie n.d.) have all been studied.

While the sorts of analyses undertaken will depend on the research question, there exists a small number of restrictions on the form of the comparative data. First, the data must be codable in some meaningful form, so categorical data must be expressed in a small number of meaningful classes, either as binary presence/absence or as “multistate” characters. Continuous data are frequent in biological analyses (e.g., body size) but are less common in cultural features; continuous variables may be more appropriately clustered as ordinal features, for example, percentage dependence on some type of subsistence as high/medium/low. Second, the comparative data must not be the same as those used to construct the phylogeny. Independence is important, so, for example, an analysis of grammatical features should preferably use a phylogeny built from lexical data. Third, there must be sufficient variation in the data to answer the research question, and relatedly, there must be sufficient data for the statistical models to work. A rule of thumb is that an order of magnitude more taxa are needed than characters, so for a binary feature, 20 is a desirable number of taxa for any analysis, and for two binary features we should have ~40 taxa.

Coding comparative cultural and linguistic data is a task fraught with the difficult reduction decisions familiar to all scientifically minded anthropologists. It should be noted, however, that biologists face similar decisions in their attempts to understand biological diversity: The structure of a complex ecological community in a rain forest, with mutualistic and context-dependent interactions among plants, fungi, microorganisms, insects, and vertebrates, is not a simple thing to untangle, yet biologists get on and do what they can. The use of PCMs forces us to be explicit about what hypothesis we are testing and to justify how we distill the (for example) complex behaviors of a speech community to manageable variation.

Models of Evolution

Thus far, the combination of “comparative data + population history” should be familiar and somewhat obvious to historical linguists and comparative anthropologists—for an example, see Kirch and Green’s (2001) reconstruction of ancestral Polynesian society. PCMs depart from the familiar with the introduction of a (1) quantitatively expressed and (2) statistically inferred model of change. These two features require a computational approach for the simple fact that keeping track of, and comparing and

assessing all permutations of, Trees + Data + Models is beyond the capability of a single human brain for any data sets beyond the most trivially small.

A word should be said about the definition of *model*. In the terminology of computational phylogenetics, a model specifies the assumptions we have about the process of evolutionary change, and it does so by imposing some sort of criterion on the data. A simple example is that of parsimony: we should prefer explanations for the data that minimize the amount of evolutionary change that takes place. Another model may specify that rates of change are equally likely in both directions: a trait may be gained or lost with the same probability. Models are contentious, as we only have some ideas about the proper expectations for evolutionary change. For example, in molecular evolution, elucidation of the chemical structure of DNA molecules means biologists know that certain types of mutational changes (transitions, between two purine or two pyrimidine bases) are more likely than others (transversions, between a purine and a pyrimidine) and so can weight models accordingly (Li and Graur 1991). But we have very little analogous knowledge with respect to cultural and linguistic change, and our models need to be built from the ground up with as few assumptions as possible (cf. the problem of inferring the direction of change between “Dravidian” and other kin types, as discussed in McConvell, chapter 1, this volume; and Hornborg, this volume).

The sorts of evolutionary models implemented in PCMs for organismal change, particularly behavioral change, tend to be simple maximization algorithms that either (1) maximize parsimony by preferring the least number of historical changes to explain the current data or (2) maximize the likelihood of the current data, given the phylogeny and some specifications about how to judge the likelihood of change in the character. This specification will state something like “A change from 0 to 1 is x times as likely as a change from 1 to 0,” and the algorithm will explore a number of possible values of x , returning a likelihood score for each and summing over all characters. More complex models will introduce specifications like “Allow different characters to vary their likelihood of change” or “Allow different taxa to vary their rate of evolution,” drawing values for these variable quantities from probability distributions specified by the researcher. A burgeoning literature exists on maximum likelihood, models, and their Bayesian implementation (e.g., Lewis 2001; Pagel 1999a; Ronquist 2004; Schmidt and von

Haeseler 2009). It is fairly easy to see that calculating likelihoods is not a trivial task and that computational power is necessary. Thus, for example, the “inclusion criteria” proposed by Dyen and Aberle (1974; discussed in McConvell, chapter 1, this volume) actually resemble a type of likelihood-based inference, but in their case this is based on an a priori belief that optimization will correctly characterize the process of lexico-semantic evolution. More desirable is the statistical comparison of the proposed solution to other alternatives across the data set as a whole, something implemented as routine in phylogenetic comparative inference.

Much cultural phylogenetic work has taken advantage of the probabilistic approach afforded by what are known as Bayesian Markov-chain Monte Carlo (MCMC) methods and has employed PCM software that implements this framework (Pagel and Meade 2006; Pagel et al. 2004). Say we are interested in estimating the ancestral state (presence/absence) of matrilineal cross-cousin marriage in a particular group of related societies. While some PCMs will return a simple yes/no/equivocal value that is dependent on the particular phylogeny being used, Bayesian methods will estimate something called a *posterior probability distribution* for the presence of cross-cousin marriage in the common ancestor. The methods will also return a probability distribution of the rates of change in the marriage character, that is, how frequently the character changes through time. The posterior probability of a parameter value is a quantity proportional to its likelihood of having produced the observed data and represents the probability of the parameter value given the data and model of trait evolution (Huelsenbeck et al. 2001; Lewis 2001). Because posterior probabilities cannot feasibly be computed analytically, posterior probability distributions are inferred instead using an MCMC sampling algorithm. This distributional approach provides information about the degree of statistical uncertainty in the cultural trait reconstructions. Relatedly, this approach makes it possible to account for the effect of uncertainty in the phylogenetic tree model representing population history, a nontrivial consideration in the study of cultural traits, as a single branching tree is unlikely to accurately represent human population history (Boyd et al. 1997): the estimation of parameters over a probability sample of trees yields estimates that are not dependent on any specific phylogenetic hypothesis. Finally, parameters can be estimated over different models of trait evolution, and this

yields estimates that are not dependent on any specific model of how the cultural traits have evolved.

All PCMs, Bayesian or not, offer the ability to quantify and test theoretical predictions with empirical data by using hypothesis tests or model comparisons. The boxes in Figure 3.1 describe five types of evolutionary questions that PCMs can be used for, giving a cultural/linguistic example of each and demonstrating an appropriate hypothesis test. Gray, Greenhill, and Ross (2007) give some further examples of how phylogenetic methods can answer questions about cultural evolution, in particular, how phylogenies can be built and dated using independent calibration of known events (for an Indo-European example, see Gray and Atkinson 2003) and how reticulate signal in the data, such as the borrowing of elements of languages (such as words) or dialect continua, can be explored and represented with network models (for an example using Chinese dialects, see Ben Hamed 2005). Here I elaborate on two case studies where PCMs have been used to study kinship: the reconstruction of ancestral states of postmarital residence in Indo-European and Austronesian and the comparison of sequential models of change in sibling terminologies in Austronesian and Bantu.

CASE STUDIES

Case Study 1: Postmarital Residence in Proto-Austronesian and Proto-Indo-European

Marital residence norms are an important part of human social organization. Accurately inferring past patterns of postmarital residence is a challenge to our understanding of population history (Wilkins and Marlowe 2006) because these norms shape the patterns of genetic variation within and between populations by regulating the movement of people. Indo-European and Austronesian are two large-scale language families that are thought to represent Neolithic expansions associated with new domestication technologies; their population histories have been inferred through a combination of archaeology, linguistics, genetics, and comparative anthropology (e.g., Bellwood and Renfrew 2002; Clackson 2007; Diamond and Bellwood 2003; Forster and Renfrew 2006; Hurles et al. 2003; Renfrew 1992; Zerjal et al. 2001). However, ancestral kinship patterns in these two families have mostly been inferred through reconstructions of kin terminologies in ancestral protolanguages using the linguistic comparative method and/or through geographic or distributional

arguments based on patterns of kin terms and ethnographic observations. These approaches have produced detailed and valuable hypotheses about kinship prehistory, but in Fortunato and Jordan 2010 we argue that in many respects the processes through which conclusions have been drawn from the data fail to provide explicit criteria for systematic testing of alternative hypotheses. To address this, we used PCMs on Indo-European (IE) and Austronesian (AN) lexical trees, and ethnographic data on postmarital residence, to infer the likely states of residence in the ancestors of these language families.

Analysis

We used the following posterior probability samples of language trees: (1) 27 IE ethnolinguistic groups, 750 trees published in Pagel et al. 2007; and (2) 135 AN groups, 1,000 trees published in Jordan et al. 2009. For hypothetical ancestral speech communities or groups of languages, we abbreviated Proto-Indo-Hittite (PIH; IE languages and their Hittite sister group), Proto-Indo-European (PIE), Proto-Austronesian (PAN), and Proto-Malayo-Polynesian (PMP; the hypothetical ancestor of all non-Formosan AN languages). We matched each language to ethnographic data on marital residence from a variety of sources including Murdock's *Ethnographic Atlas* (1967; for details, see Fortunato and Jordan 2010; Jordan et al. 2009). We coded societies according to both prevailing and alternative modes of residence as practicing neolocality (i.e., residence apart from the kin of either spouse as neolocal; state N), uxorilocality (i.e., residence with or near the wife's kin; state U), or virilocality (i.e., residence with or near the husband's kin; state V). Ambilocal societies, where married couples take residence optionally with (or near) the kin of either spouse, and with approximately equal frequency, were assigned the dual state UV.

We used the PCM BayesMultistate, available as part of the BayesTraits package (Pagel and Meade 2006; Pagel et al. 2004). Given the comparative data and tree sample, BayesMultistate uses a continuous-time Markov model to describe the evolution of the trait of interest along the branches of a phylogeny. Under this model, the trait "residence" can switch repeatedly among its three states, N, U, and V, in any of the branches of a tree. Three states require six rate parameters quantifying the possible transitions (switches)—in this case, q_{NU} , q_{NV} , q_{UN} , q_{UV} , q_{VN} , and q_{VU} . Rate parameters are used to define (1) the probabilities of these changes, (2) the character states at internal

nodes on a tree, and (3) the likelihood of the data (Pagel 1994, 1999b). The Bayesian MCMC implementation of Multistate estimates the posterior probability distributions of these three quantities (Pagel et al. 2004). The MCMC chain explores "parameter space" widely, randomly modifying the parameters and trying them out on the sample of trees over consecutive iterations. While the chain attempts to maximize the likelihood, it also accepts less likely combinations of parameters at a frequency proportional to their likelihood into the posterior probability distributions. This distribution then contains combinations of parameters such that those with higher support are sampled to a greater extent. A "reversible-jump" procedure that reduces the complexities of the underlying model of evolution to tractable dimensions was employed (Pagel and Meade 2006; see Fortunato and Jordan 2010).

The means of the posterior probability distribution of character states at ancestral nodes, for example, $p(V)$, $p(U)$, and $p(N)$, are combined with the posterior probability of each node existing in the tree, which represents the probability that the node exists (Lewis 2001). For PIH, PIE, PAN, and PMP this probability was 1, but when there is phylogenetic uncertainty (i.e., the node probability is less than 1), this information is combined with the estimate of the character state to give a conservative "combined probability." Once we estimated the ancestral state reconstructions for the four basal nodes, we then tested how much support we had for alternative reconstructions by fixing, or "fossilizing," each node to be one of the three possible states (N, V, U), in turn. We determined which fossilized state had relatively higher support at a given node by comparing the likelihoods using a measure called the Bayes factor (Raftery 1996).

Results for Indo-European showed that PCMs could reconstruct virilocality for PIH at $p(V) = .64 \pm .14$ and for PIE at $p(V) = .90 \pm .12$ (see Figure 3.2a). Virilocality reconstructed with high posterior probabilities within the Indo-Iranian (node F) and Balto-Slavic (node E) clades, but for the Italic, Germanic, and Celtic clade (node D) $p(V)$ dropped to .40, with the probability of neolocality inferred as equally likely. Using the fossilization test, we showed that there was strong or positive evidence for virilocality for PIE over the alternatives, but for PIH, the evidence was weaker, and none of the residence patterns had positive support. The reconstruction of early IE virilocality is in line with a popular scenario derived from the linguistic evidence, including kinship terminology

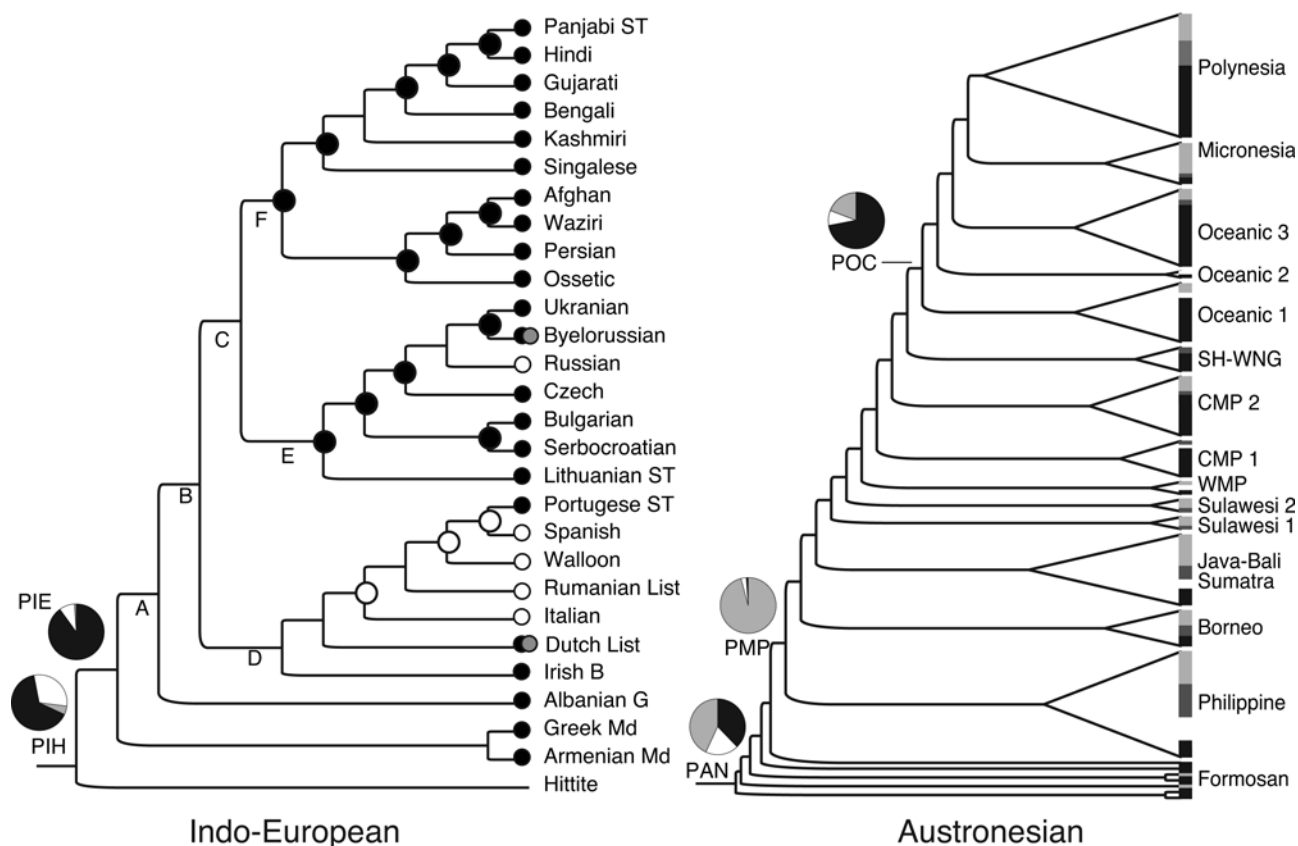


FIGURE 3.2. Trees (50 percent majority rule consensus) summarizing the sample of 1,000 phylogenies for (a) Indo-European and (b) Austronesian languages, including compatible groupings. Residence data are plotted by color: white = neolocality; light gray = uxoriolocality; black = virilocality; dark gray = ambilocality. Reconstructed nodes are shown colored according to the ancestral state reconstruction. In (a) node labels are discussed in the text: PIE = Proto-Indo-European; PIH = Proto-Indo-Hittite. In (b) collapsed groups are proportional in size to number of languages and terminate in a bar shaded proportional to residence patterns within that group: PAN = Proto-Austronesian; PMP = Proto-Malayo-Polynesian; POC = Proto-Oceanic.

(Delbruck 1889; Friedrich 1966; Mallory and Adams 2006), though Goody (1959) was critical of this scenario and its faulty interpretation of ethnological data. More strongly, we noted that Clackson (2007) has described several equally plausible alternatives for early IE peoples. Uncertainty for PIH attests to this, and these methods can progress the debate by providing rigorous quantitative tests of the evidence in integrative studies of prehistory.

In Austronesian, uxoriolocality was robustly reconstructed for PMP at $p(U) = .96 \pm .06$ (Figure 3.2b). PAN was not reconstructed to any state with certainty, in comparison to results from Jordan et al. (2009) that reconstructed uxoriolocality with $p(U) = .70$. However, that earlier work does not consider alternative modes of residence. When testing using the fossilization procedure, there was positive evidence in favor of PAN uxoriolocality over viri- and neolocality and very strong evidence

for PMP uxoriolocality over the alternatives. This is in line with some interpretations of PAN and PMP kinship terminologies (Blust 1980), although not all scholars agree (e.g., Chowning 1981). As with Indo-European, here we provide an independent confirmation from cross-cultural data. More recent work attempting to reconcile the different patterns of uniparental genetic markers seen in the Pacific (mtDNA and Y chromosome data) has suggested that uxoriolocality was a later development in Austronesian, that is, Proto-Oceanic, cultures (Hage and Marck 2003; Harvey and Pagel 1991; Kayser et al. 2008).

We also used the transition-rate parameters to characterize the dynamics of change and compare these between the two language families. Results suggested that in both Indo-European and Austronesian the loss of virilocality is a rare event, indicated by low relative values of the rate parameters capturing these transitions (q_{VU} and q_{VN}). Fur-

ther, changes from uxori- toward virilocality (q_{UV}) occur at a higher rate than the reverse transition (q_{VU}): q_{UV} is over 30 times more likely than q_{VU} in IE and one and a half times more likely in AN. This may reflect the instability of “matricentric” systems (e.g., systems involving matrilineal descent) as observed by Richards (1950) for African societies (Holden and Mace 2005; Holden et al. 2003). We further suggest that explanations for variation in residence could plausibly be linked to variation in subsistence and ecological niche in both Indo-European and Austronesian.

Implications

In Fortunato and Jordan 2010, we not only show that it is possible to reconstruct the states of kinship norms in hypothetical ancestral speech communities that existed more than 6,000 years ago but also demonstrate that it is possible to statistically test those inferences by comparing them against the alternatives. We suggest avenues for quantifying the dynamics of change in societal norms of residence, finding commonalities between the two families that support the idea that human social life is not infinitely varied but, rather, is constrained by local environments. Moreover, we propose that by asking the same questions in different ethnographic regions we can start to infer the general mechanisms of cultural evolutionary change, that is, the identification of lineage-specific processes within global domains (cf. Dunn et al. 2011; Evans and Levinson 2009). In relation to kinship terminology, our analyses demonstrate that PCMs can both confirm previous historical linguistic work (as demonstrated for Indo-European) and disagree with it. These conflicts are important, as they demand a reexamination of both our data and our theoretical framework and suggest avenues for further investigation. In the Austronesian analysis, we found (as do Jordan et al. [2009]) that Proto-Oceanic was either ambiguous or patrilocal. This is in contrast to Hage and Marck (2003), who suggest that Proto-Oceanic was matrilineal and uxorilocal, basing these inferences on both reconstructed and synchronic kinship terminologies. PCMs may be unable to reconstruct uxorilocal residence for Proto-Oceanic because many daughter societies have, while retaining an uxorilocal option, since switched to virilocality as the prevailing mode—perhaps due to cultural contact with nearby non-Austronesian societies (Jordan et al. 2009). However, aspects of the theoretical framework employed by Hage and colleagues demand reanalysis, as they rely on mid-20th-century statistical asso-

ciations between types of kinship terminology and types of social structure that themselves do not control for historical relatedness. I return to this point in the conclusion.

Case Study 2: The Evolution of Sibling Terminologies in Austronesian and Bantu

In this case study I describe some recent cross-linguistic analyses of evolutionary processes in kin terminologies. These results come from a wider project aimed at addressing the extensional semantics of complete sets of individual kin terms (see also Jordan 2011). Sibling terminologies are a useful partial set of all possible kin with which to strategically investigate evolutionary processes, and their general suitability as kin term test cases has long been established (Kronenfeld 1974; Nerlove and Romney 1967). Sibling terms are limited to a single generation, that of ego’s own; they have a limited set of parameters (such as sex or age) on which they can be distinguished; and they concern immediate lineal kin, and thus, unlike cousin terminologies, they are not heavily impacted by considerations of marriageability.

Context

The sibling terminologies analyzed here are drawn from data on the Austronesian and Bantu language families collected together by Dzielbe (2009). Both Austronesian and Bantu societies vary in ways representative of worldwide diversity in kinship (Fox 1994; Murdock 1968), and this diversity, combined with available models of population history provided by lexical phylogenies, provides two useful regional cases to test hypotheses about the nature of change in kinship terms. In Austronesian, sibling terms in particular have received attention from a number of scholars (Blust 1980, 1994; Epling et al. 1973; Firth 1936; Fox 1995; Marshall 1983, 1984). Like Austronesian, Bantu is thought to be the result of a recent dispersal (ca. 5,000–2,000 kya) of peoples and farming technologies throughout sub-Saharan Africa, although this is a matter of some debate (Huffman 1982; Phillipson 1993; Vansina 1990). The kinship terminologies of the Bantu languages have received comparatively less attention (for some recent work on East Bantu, see Marck and Bostoen 2010; Marck et al. 2010). As with cousins and other subsets of kin terms, many studies have used typological schemes to classify patterns of sibling terms (Epling et al. 1973; Kronenfeld 1974; Marshall 1984; Murdock 1968; Nerlove and Romney 1967), sometimes regardless of historical relationship, often raising the ire of historical linguists (e.g., see replies

by Blust and Chowning to Marshall 1984). Sequential, or stepwise, change processes in these structural patterns are often seen as explaining the current diversity across languages, such that appropriate models are those in which binary distinctions in meaning (e.g., male|female) were added or removed to a pattern (e.g., older sibling|younger sibling) to create the next pattern in the sequence (e.g., older brother|older sister|younger sibling). That is, these models are based on parsimony, and stepwise transformations are applied to the patterns themselves rather than the distinctions separately. However, by using statistical inference techniques to reconstruct the evolution of the semantic distinctions themselves, we need not rely on any particular typology of schemes to understand these processes. I note here also that the analyses concentrated on the distinctions in meaning: the investigation of *coevolution* in linguistic forms and meanings (the traditional purvey of historical linguistics) is a future study.

Here I show how Bayesian PCMs can specifically test the idea of sequential models of change in kin terms. A fuller account of the Austronesian study is in Jordan 2011: this case study examines the elaboration and reduction of the “same-sex|opposite-sex” distinction in Austronesian compared with Bantu. To do this, I derive evolutionary models of the transitions (gains and losses) between different meaning distinctions. Single-step changes are implicit or explicit in most lattice models (Epling et al. 1973; Hage 2001; Marshall 1984; see also Danziger, this volume). Thus the prediction is that an opposite-sex distinction (i.e., having one term for opposite-sex siblings and another for same-sex siblings) could evolve from a situation where the distinction was absent. Further, the opposite-sex term could then be elaborated by the sex of speaker, that is, it could be split into a term for “woman’s brother” and “man’s sister.” However, how often languages then collapse this elaboration back into the single term, or skip straight from absence of the distinction to a two-term system, is unknown. Read (this volume) has qualms with a research framework that investigates the addition or removal of distinctions to terms or meanings in isolation; I view these qualms as a distinction between pattern and process and return to the point in the discussion. With respect to the case at hand, we can use PCMs to address this question quantitatively.

Sibling term data from Dzielbe (2009) were coded for Austronesian and Bantu languages according to the meaning distinctions that were expressed in each language’s terminology. I matched these languages to 208 Austro-

nesian languages in the Gray et al. (2009) 400-language phylogenies and to 73 Bantu languages from the Atkinson et al. (2008) 96-language phylogenies. Languages were coded under the multistate scheme: 0 = language has no same/opposite distinction; 1 = language has a single term for opposite-sex sibling, used by both sexes; 2 = language has separate terms denoting the opposite-sex sibling for each sex (e.g., woman’s brother, man’s sister). Languages with intermediate distinctions (e.g., a term for “woman’s brother” only) were not used in this analysis because models with four or five states failed to converge on consistent likelihood estimates; these will be explored in the future. The final set of taxa with appropriate data thus comprised 180 Austronesian and 68 Bantu languages.

To analyze the evolution of the opposite-sex distinctions I used the PCM Multistate implemented in the BayesTraits package (Pagel 1999b; Pagel et al. 2004). The approach is the same as in Case Study 1: given the comparative data and a set of trees, we model the evolution of the trait of interest among its three states (0, 1, 2) along the branches of a phylogeny. Rate parameters specifying the six possible transitions (q_{01} , q_{10} , q_{12} , q_{21} , q_{02} , and q_{20}) measure the instantaneous rates of change from one state to another and are used to define the probabilities of these changes, the character states at internal nodes on a tree, and the likelihood of the data (Pagel 1994, 1999b). Again, I used a “reversible-jump” procedure to reduce the complexities of the underlying model of evolution to tractable dimensions. To give directionality for the models, an estimation of ancestral states for relative-age and relative-sex distinctions in Austronesian was obtained from earlier analyses (Jordan 2011). There, a relative-age distinction was robustly inferred for PAN and PMP, but the relative-sex distinction was not. In Bantu, the three character states directly pertaining to the opposite-sex distinction were directly inferred and found to be ambiguous at the root: $p(0) = .36$, $p(1) = .32$, $p(2) = .32$. However, these suggest that Proto-Bantu was more likely to have some form of opposite-sex distinction than none, because $p(1,2) = .64$.

Models of Change in the Elaboration of Opposite-Sex Sibling Terms

The flow diagrams in Figure 3.3 show the summaries of the most popular models found by reversible-jump Bayesian MCMC for (a) Austronesian and (b) Bantu. These diagrams compare the relative transition rates of the top three models, which account for 70 percent of all models

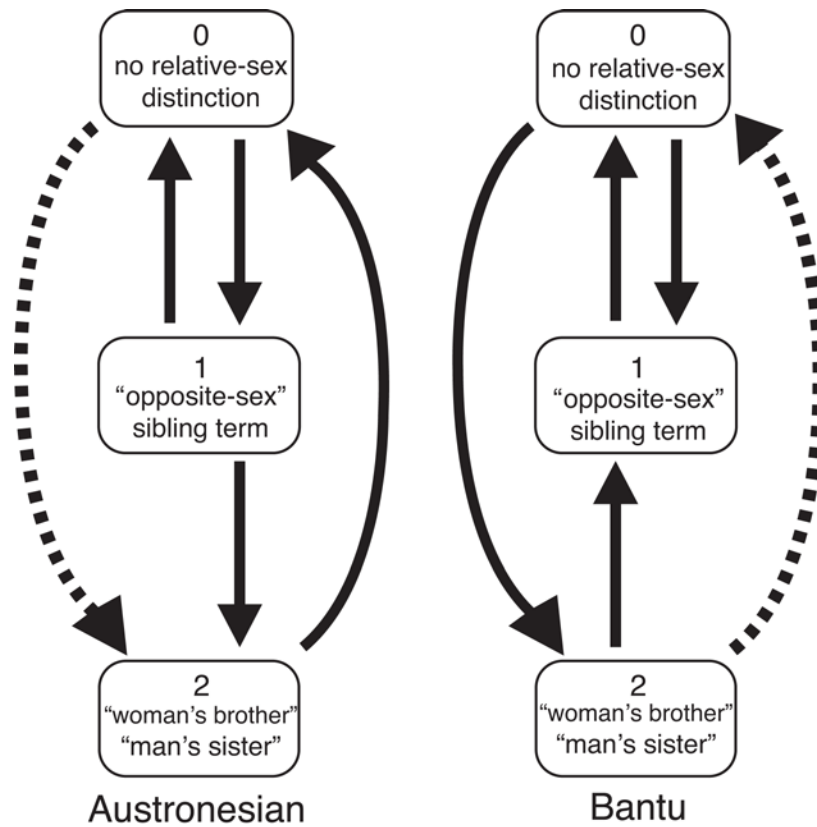


FIGURE 3.3. Models of evolution describing the elaboration of the “opposite-sex sibling” term in (a) Austronesian and (b) Bantu. Flow diagrams summarize transitions that accounted for over 70 percent of all models visited by the reversible-jump procedure. The absence of an arrow means that transition is set to 0. Dotted arrows mean that the transition includes zero values. Solid arrows are equivalent rates, i.e., those transitions happen with equal frequency.

found in both language families. The reversible-jump procedure integrates out the specific numerical parameters of the transition rates, giving models in terms of relative rate classes: rates are either zero (no arrow), infrequent (dotted arrows), or otherwise equivalent (solid arrows). This technique allows us to succinctly summarize a diverse and complex set of parameter estimates.

Figure 3.3a suggests that the most likely evolutionary pathway in Austronesian (starting at state 0: no opposite-sex distinction) was a gain of the single-term “opposite-sex sibling”; this was then elaborated into two terms—“woman’s brother”/“man’s sister”—in a number of linguistic subgroups. Jumps from the absence of the distinction to the two-term situation (q_{02}) were rare and often zero; collapses of “woman’s brother”/“man’s sister” back to the single “opposite-sex sibling” term (q_{21}) were all zero. The loss of the distinction overall occurred at a high rate (i.e., q_{20} and q_{10}). When all models are consid-

ered, those where q_{21} is in the zero bin have a higher likelihood than those where it has a nonzero rate, providing support for the hypothesis that collapses of an elaborated term are rare.

A different dynamic exists in the Bantu languages. Again, the analysis shows that some transitions are set at zero, that some are infrequent, and that all others may be set equivalent. In common with Austronesian, the gains and losses of a single-term “opposite-sex sibling” from the state without the distinction are equivalent and frequent ($q_{01} = q_{10}$). However, the dynamics governing the gain and loss of the two-term “woman’s brother”/“man’s sister” state are exactly opposite to those found in Austronesian. Here, once the two-term state is gained it rarely collapses to a complete absence (i.e., q_{20} is infrequent), but it seems to be gained from the no-distinction state frequently, and languages do not switch from a single term to a two-term system (i.e., $q_{12} = 0$). Given that the ancestral

state reconstruction suggests that early Bantu speech communities had some form of opposite-sex distinction in place already, it may be that pressures external to the sibling terminologies (perhaps considerations of marking lineal group membership, for example) act to drive these dynamics (Marck et al. 2010).

These findings are preliminary, but for the purposes of this chapter the point is, I hope, conveyed that PCMs are useful methods with which to test ideas about evolutionary transformations in kinship terminologies. Further work will combine this approach with the rich theoretical and empirical resources of historical linguistics. Because convergence (independent innovation) of the same meanings with the same linguistic forms in unrelated (or in contact) languages is vastly improbable, we shall be able to use linguistic reconstructions to “fossilize” known forms in ancestral nodes. This will give directionality to language change, and we will be able to identify when independent gains of a distinction in different languages should be invoked as explanation or when there is a shift in meaning in some daughter languages but not others. One of the most promising applications will be in testing the implicational hierarchies of change in kin terms formulated by Hage (1998), including incorporating information on markedness to test that aspect of Hage’s work. Meaning–meaning coevolution can be tested as well. For example, these analyses only trace the presence of a relative-age distinction in the sibling terminology as a whole, whereas a more fine-grained analysis will test the coevolution of an age distinction with sex of referent versus sex of speaker, as occurs in Austronesian. When combined with their evolving lexical forms, these coupled meaning–meaning changes will fully characterize the system, and from that point, testing how processes ramify through the entire terminological system will be possible (cf. Read, this volume). But even with these simple examples, it is possible to see how commonalities and divergences in kin term evolution across different language families can be discovered.

CONCLUSIONS

In this chapter, I have attempted to give an overview of phylogenetic comparative methods and their potential applications in cultural evolutionary work generally and, with the presentation of the two case studies, in the study of kinship more specifically. PCMs are tools for asking questions about evolutionary change, and many of the outstanding questions in the study of kinship and kinship terminology are, at basis, questions of evolution:

Why are human kinship systems the way they are, that is, variable yet restricted? Do historical explanations suffice, or are there regularities of the human mind, and/or of the human niche, that make some forms of kinship-directed norms more adaptive? What regularities, if any, can be found in the transformations of kinship systems cross-culturally? Such questions are the everyday investigations of comparative biologists, and to the extent to which we can accept the linguistic relatedness of cultural groups as a model of their population history, anthropologists and linguists can co-opt PCMs to answer the above questions in a statistical framework that allows for quantitative testing of hypotheses.

Objections exist. By necessity, these approaches require complex cultural and linguistic features to be assigned to a small number of abstract categories. It is not my purpose here to deal with the broader issue of opposition to scientific hypothesis testing and cultural categorizing/reification in anthropology (Colleran and Mace in press). The field of cultural phylogenetics has been relentlessly reviewed and subject to critique throughout its short history: both the tree-building enterprises and the use of PCMs have attracted skepticism. Some critiques have been methodological, or misunderstandings thereof, but in many respects these misgivings have been ameliorated by the adoption of (1) the newer, probabilistic Bayesian methods as used here; (2) simulation techniques to determine the conditions under which phylogenetic methods are inappropriate for cultural data, such as widespread borrowing and high rates of change (Atkinson et al. 2005; Greenhill et al. 2008); and (3) a plurality of techniques that do not require a branching tree structure and instead can represent noncongruent data, such as those produced by cultural contact, in a network (Gray et al. 2007). There remain two issues that force a serious critical engagement, and these are (1) the effects of cultural contact and “horizontal transmission” and (2) the multiplicity of trait lineages with different evolutionary histories within any one ethnolinguistic population (but see Mathews et al. 2011). Scholars using phylogenetic techniques are motivated to acknowledge, control for, and incorporate these concerns into their analyses, but to some extents we are simply limited by a lack of appropriate techniques: in evolutionary biology the analogous concerns are that of horizontal gene transfer at the root of the tree of life and the incongruence of individual gene trees with both each other and so-called species trees. These two topics constitute cutting-edge research in biology, attracting the serious attention of hundreds of scholars worldwide, but they

are hard problems. It may be some time before we can deal with similar, and perhaps more complex, issues in human culture.

There are some ways in which we can progress our theoretical and methodological tool kit without waiting for the biologists: here I suggest a few. First and foremost, anthropologists and linguists need to engage in digital data-sharing. The genomic revolution only took off once a critical amount of genetic information was made easily available to all: New analytic methods were developed, and geneticists are beginning to use these data for a new theoretical understanding of biological inheritance. A similar revolution, both technical and theoretical, could happen for our understanding of human social structure if databases and repositories could collate and make accessible the ephemeral but vast “ethnographic record.” Second, we need to revisit the mid-20th-century efforts of Murdock and associates, who began the task of searching for statistical regularities and associations in the ethnographic and comparative linguistic record. Many of these so-called regularities are used by scholars to draw inferences from reconstructed kin term systems to hypothetical ancestral social norms (Ehret 2008; Hage 1998, 2001). The area-sampling approach offered by (for instance) the Standard Cross-Cultural Sample acknowledged Galton’s Problem, but the implementations were rudimentary, and new approaches offer more sophisticated control for historical relatedness (Mace and Pagel 1994).

Third, and more positively, there exists a grand opportunity for the separate phylogenetic and linguistic comparative methods to be brought together in the study of kinship terminology. PCMs offer a wide range of algorithms designed to explicitly test and infer correlated evolution, where two traits change together through time in a coupled fashion. The linguistic comparative method in historical linguistics deals with the implicit coupling of form (of cognate lexical items, for example) and meaning (the semantic fields over which those forms are distributed). How form drifts over meaning and vice versa are major questions in cognitive semantics that are beginning to be considered in an evolutionary framework (Jones 2010; Jordan and Dunn 2010). As well, the relatively restricted set of referents given by kin terms (as compared with, for example, the continuous spectra of colors), as well as the empirically rich and cross-linguistically comparable data that exist, make this a tractable place to start, and efforts toward this end are obvious in other chapters in this volume (McConvell, chapter 1, this volume; Read, this volume). Read’s chapter in particular shows how the

identification of a small number of kin concepts, and the ways that human societies have of combining those together, can produce the apparent diversity of terminologies seen cross-culturally. His case study of Polynesian kin terms shows that contextualizing terminology change against the background of linguistic phylogeny is an important part of the analytic process. Read is, however, skeptical that examining term or meaning changes in isolation hides “a culturally unidentified process” (this volume), because a change in a subset of terms will of necessity have knock-on effects through the full terminological system. On this point I agree, but I think that we are coming from different angles with (I hope) complementary approaches. The phylogenetic approach takes the pattern of current diversity and infers the evolutionary process that happened in the past to produce that diversity, given some knowledge of history and a model of change. What Read is doing is specifying different (and highly specific) versions of the model of change itself—something often underspecified in a phylogenetic comparative analysis due to lack of cultural information. An exciting next step would thus be the combination of Read’s models for change with the apparatus of the comparative phylogenetic approach, across different language families and their kinship terminologies. There is a potential then to arbitrate various macrolevel hypotheses about kinship terminologies, as in Allen et al. 2008.

Finally, to return to evolution once more. The variation in how we classify kin by using language is non-random worldwide: not all combinations and distinctions exist. Our terms for kin do a specific job of work: They tell us who is kin and who is not, and they make equivalences and differentiations across a small number of consistent social and biological distinctions, such as age and sex, generation, lineage or descent group, and marriageability. Linguistically, kin terms can be understood from a perspective of semantic variation, but in contrast to other domains such as color and space, they are unique because of the onerous and vital tasks they mediate: communicating and coordinating kin-directed behaviors such as altruism, parental care and investment, grandparental care, sibling competition, marriage, and alliance. Jones (2003) postulates that the constrained set of considerations implicit in any kinship terms include group membership (e.g., male|female, in-group|out-group), genealogical distance (e.g., older|younger, levels of generation), and social rank—all candidates for a species-typical, flexibly generative psychology of kinship. Though these ideas are largely untested, theoretically they derive

from evolutionarily relevant considerations such as kin selection, the likelihood of altruistic behavior, and aspects of our primate heritage. Kinship terms are thus the

most directly Darwinian of all lexemes, and the study of how and why they evolve across languages can contribute much to our understanding of human social behavior.

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