A COMPARATIVE PHYLOGENETIC APPROACH

TO

AUSTRONESIAN CULTURAL EVOLUTION

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ABSTRACT

Phylogenetic comparative methods were used to test hypotheses about cultural evolution in ethnolinguistic groups from the Austronesian language family of the Pacific. The case for quantitative statistical approaches to the empirical evolution of linguistic and cultural features was presented. Phylogenetic trees of 67 Austronesian languages were constructed using maximum parsimony and Bayesian Markov Chain Monte Carlo likelihood algorithms on a database of lexical items.

The predominant transmission mode of 76 cultural traits was examined at the macroevolutionary level with (i) partial Mantel matrix tests and (ii) multiple regression on phylogenetic and geographic nearest neighbours. Mantel tests showed that both geographic and phylogenetic transmission was correlated with cultural diversity. Geographic distance had a greater overall partial correlation with cultural distance than did phylogenetic distance, but only phylogenetic correlations were found with kinship/social traits. Multiple regression on individual traits found that phylogenetic nearest neighbours predicted more cultural traits, especially those involving the inheritance of resources.

Ancestral states of kinship traits were reconstructed using a Bayesian comparative method on a sample of 1000 phylogenies. The root of the tree was reconstructed as having matrilocal post-marital residence and a bilateral, flexible descent system. Proto Oceanic was reconstructed as unilocal and unilineal, and an hypothesis of matriliny and matrilocality could not be rejected. Murdock's main-sequence theory of the co-evolution of post-marital residence and descent systems was tested. The most likely model of the evolutionary pathway demonstrated that residence changed before descent. Rates of change in residence and descent traits were estimated. A co-evolutionary hypothesis of matriliny and male absence was tested. Contrary to anthropological theory, a high

dependence on fishing showed no clear pattern of co-evolution with matrilineal social organisation.

Population size of the language community was hypothesized to be a factor influencing lexical change. Conventional statistics showed a significant strong inverse correlation, indicating a relationship between small populations and accelerated lexical change. This correlation disappeared when comparative methods were used to control for phylogeny. Population size appeared to be evolving according to a drift model, while lexical change did not fit a neutral model of evolution.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ABV	Austronesian Basic Vocabulary
ACD	Austronesian Comparative Dictionary
AN	Austronesian
BP	years before the present
CMP	Central Malayo-Polynesian
EA	Ethnographic Atlas
EMP	Eastern Malayo-Polynesian
HRAF	Human Relations Area Files
MCMC	Markov-chain Monte Carlo
ML	maximum likelihood
MP	Malayo-Polynesian
MP	maximum parsimony
OC	Oceanic
PCE	Proto Central-Eastern
PPD	posterior probability distribution
SCCS	Standard Cross-Cultural Sample
SH–WNG	South Halmahera—West New Guinea
SIL	Summer Institute of Linguistics
WMP	Western Malayo-Polynesian

Note: The addition of “P” before language subgroups denotes “Proto” (e.g. POC = Proto Oceanic).

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The thousands of societies that exist today, or once existed on the surface of the earth, constitute so many experiments, the only ones we can make use of to formulate and test our hypotheses, since we can't very well construct them or repeat them in the laboratory ... These experiments, represented by societies unlike our own, described and analyzed by anthropologists, provide one of the surest ways to understand what happens in the human mind and how it operates. That's what anthropology is good for in the most general way and what we can expect from it in the long run.

(Levi-Strauss 1972:41)

Why, for example, is it a nonpossibility for a terminological system to recognize not two, but three or four sexes; for new marriages to take place after each pregnancy, the first monogamous, the second polyandrous, the third polygynous; or why not descent which is patrilineal in the morning, matrilineal in the afternoon, bilateral in the evening, and double on Sundays? Shall we not ask, in other words, why elephants do not have two heads, why cabbages do not grow on clouds, and why the moon is not made of Swiss cheese? The limited possibilities of nature are none other than the forms which evolution has produced. The task of science is to explain why they were produced.

(Harris 2001:626)

CHAPTER ONE

THE PHYLOGENETIC APPROACH TO CULTURAL EVOLUTION

1.1 Summary

The last 25 years have seen the establishment of a strong Darwinian programme with multiple subfields in the social sciences (Barkow, Cosmides, and Tooby 1992; Cronk, Chagnon, and Irons 2000; Barrett, Dunbar, and Lycett 2001). Within this programme is the emerging field of cultural evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985, 1996; Durham 1991, 1992; Mesoudi, Whiten, and Laland 2004; Richerson and Boyd 2005), which may be broadly defined as the application of models and methods from evolutionary biology to investigate cultural processes and patterns. The scope of this endeavour includes among other questions, the study of (i) diversity: the patterns of culture traits in space and time; (ii) change: cultural transmission and innovation; and (iii) adaptation: which aspects of culture co-evolve? Evolutionary biologists adopt a phylogenetic approach to these questions, that is, they take historical relationships between species into account by using evolutionary tree diagrams (Harvey and Pagel 1991). Anthropologists are now beginning to study cultural evolution, and the questions above, with a similar set of tools (e.g. Holden and Mace 1997, 1999; Sellen and Mace 1997, 1999; Mace and Holden 1999, 2004; Collard and Shennan 2000; Gray and Jordan 2000; Borgerhoff Mulder 2001; Borgerhoff Mulder, George-Cramer, Eshleman, and Ortolani 2001; O'Brien, Darwent, and Lyman 2001; Holden 2002; Shennan 2002; Tehrani and Collard 2002; Gray and Atkinson 2003; Jordan and Shennan 2003; Mace, Jordan, and Holden 2003; Fortunato, Holden, and Mace 2006; also see volumes edited by Lipo, O'Brien, Shennan, and Collard 2005; Mace, Holden, and Shennan 2005; Forster and Renfrew 2006).

In this chapter, I briefly review the history of cultural evolutionary studies, including the relevant current approaches. I then outline the analogy between biological and cultural systems, and address the implications of differences between these evolutionary systems. "Galton's Problem"—the non-independence of cultures—is introduced as a prelude to the phylogenetic approach. I review current work in "cultural phylogenetics" that has used both tree-building methods and comparative (co-evolutionary) tests on linguistic, cultural, and archaeological data. Finally, I introduce the ethnographic context of this thesis, the Austronesian-speaking societies of the Pacific, and outline the hypotheses to be tested in the subsequent chapters.

1.2 Culture and evolution: History and current approaches

1.2.1 History

In *The Descent of Man*, Darwin recognised that the evolutionary processes he described could be seen in aspects of human culture as well as in the biological world. Of language, he noted "striking homologies due to community of descent" (1871:60). However, anthropological applications of Darwin's theories by the early "cultural evolutionists" in the 19th century (Tylor 1871 [1973]; Morgan 1877 [1964]) took a naïve unilinear view of evolution, positing that cultures could be placed along scales of progress or development towards some "civilised" ideal. Discredited as racist, these ideas were roundly rejected by relativist social anthropologists such as Boas (1948) and Malinowski (1944 [1970]), who sought to contextualise cultures on their own terms. Beginning in the early 20th century, the large-scale collection of ethnographic information by field anthropologists allowed researchers to test hypotheses about cultural diversity by the method of cross-cultural comparison. The Human Relations Area Files (HRAF) (Murdock 1954), *Standard Cross-Cultural Sample* (SCCS) (Murdock and White 1969), and Murdock's (1967) *Ethnographic Atlas* (EA) all acted as systematic repositories of comparative cultural information, useful for testing correlations in cultural traits. Researchers have used these resources to uncover worldwide correlates in cultural traits such as polygyny (Whiting 1964; White and Burton 1988), warfare (Otterbein and Otterbein 1965) and inheritance (Murdock 1949). While sometimes using evolutionary terminology, these cross-cultural analyses did not however comprise a formal approach to cultural evolution.

1.2.1.1 Cultural ecology

Mid-20th century, cultural ecologists used evolutionary concepts such as adaptation and radiation to examine and interpret human-environment interactions (White 1949; Steward 1955; Sahlins and Service 1960; Vayda 1969). In particular, these workers were interested to what degree local environments constrained and influenced core aspects of culture, and whether in this respect human societies followed any general rules. Investigations of this type, however, did not occur within an explicitly Darwinian framework.

1.2.1.2 Sociobiology

The emergence of behavioural ecology and sociobiology in the 1970s (Wilson 1975; Dawkins 1976; Krebs and Davies 1997) led some workers to examine culture through a new kind of evolutionary lens, using the theoretical and methodological tools of evolutionary biology and behavioural ecology (Alexander 1979; Chagnon and Irons 1979; Lumsden and Wilson 1981). The fragmentation of the sociobiological movement (Segerstrale 2001) resulted in a number of current subfields that derive from this evolutionary-informed perspective. While sharing a central Darwinian worldview about human behaviour, there are three broad schools of thought that differ in their methodologies, the kinds of questions they ask, and their approaches to concepts such as fitness and adaptation (Laland and Brown 2002). These three are discussed below, along with approaches to population history, as an introduction to cultural phylogenetics.

1.2.2 Current approaches

1.2.2.1 Evolutionary psychology

Evolutionary psychology (Barkow et al. 1992), one of these three subfields, aims to identify the selection pressures in the past that shaped the design of our cognitive mechanisms. On this view, these psychological mechanisms respond to environmental input to produce our behaviours, including "evoked" cultural behaviours (Tooby and Cosmides 1989). Evolutionary psychologists are more interested in behaviour thought to be universally human rather than in explaining cultural diversity, for example, cross-cultural patterns in mate-choice (Buss 1989) or mechanisms for the detection of cheaters in social contracts (Cosmides and Tooby 1989). For evolutionary psychologists, it is the brain architecture producing cultural traits that evolves, and thus the selection pressures on that brain organisation that are of interest.

1.2.2.2 Human behavioural ecology

A second subfield has its roots in animal behaviour. The central tenet of behavioural ecology is that organisms act in ways that maximise their reproductive success; the field examines individual behaviour in the context of fitness-maximisation or optimality models (Krebs and Davies 1997). In human behavioural ecology (HBE), adaptive hypotheses are tested in specific ecological contexts, under the assumption that humans flexibly alter their behaviour to meet Darwinian goals in a changing environment (Mace 2000). For example, where men control wealth, the polygyny threshold model predicts that women will choose to enter a polygynous marriage if this will provide more resources than a monogamous union (Borgerhoff Mulder 1990). The HBE field uses empirical data to test hypotheses about cultural diversity (e.g. Smith and Winterhalder 1992; Cronk et al. 2000), and with this perspective, cultural behaviour—the capacity for which is itself an evolved adaptation—is viewed as another adaptive phenotypic response to, or part of, the environment. Cultural behaviours that promote individual reproductive success are assumed more adaptive, and hence more likely to be adopted or maintained. The spread of some cultural traits, however, cannot be explained in terms of differential reproductive success, as changes take place in less than a generation. Therefore, supplementary models are needed (Boone and Smith 1998).

1.2.2.3 Dual-inheritance theories

A third current evolutionary approach to culture is frequently mathematical in focus and is variously termed gene-culture co-evolutionary theory, evolutionary culture theory or dual-inheritance theory (Richerson and Boyd 1978; Durham 1990; Laland and Brown 2002). The dynamics of cultural transmission are modeled using the techniques of population genetics, exploring how cultural traits can not only co-evolve with and influence biological evolution, but how they can evolve independently via a separate inheritance system (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985, 1992; Durham 1991; Laland, Kumm, and Feldman 1995; Boyd et al. 1997; Richerson and Boyd 2005). Social learning from conspecifics alters the dynamics of behaviour in a group, as each individual does not have to learn through individual trial-and-error.

Dual inheritance models stress the importance of social learning opportunities as a factor in the transmission of cultural traits and demonstrate how cultural change can arise because of transmission biases (Boyd and Richerson 1985, 2005). Direct bias, where a trait is chosen because of some intrinsic property of its own, is a form of cultural selection. Indirect bias is found where traits are chosen due to some aspect of the model and includes biases such as conformist transmission, where traits are more likely to be adopted because they are common or the norm, and prestige bias, where the association of a trait with a prestigious individual makes it more likely to be adopted (Henrich and Gil-White 2001). These social learning dynamics can also be useful in exploring how so-called maladaptive cultural traits may evolve, such as smoking (Feldman and Laland 1996), and how adaptive traits may be lost, as with the pre-contact Tasmanian toolkit that Henrich (2004) suggests was caused by depopulation, thus leading to a critical lack of expert teachers.

1.2.2.4 Population history

Gene-culture co-evolution examines how individual cultural traits could be co-evolving together with aspects of human biology. For example, in the Kwa-speaking populations in West Africa, sickle-cell anaemia appears to be an adaptive response to the malarial conditions created by slash-and-burn agriculture (Durham 1991). Similarly, the evolution of lactose tolerance genes in some populations appears to be associated with cattle farming and milk-drinking (Feldman and Cavalli-Sforza 1989; Durham 1991; Mace and Holden 1997). Other approaches to cultural evolution have looked at the degree to which genes and culture evolve together through space and time; that is, if ethnolinguistic groups are enduring entities with a population history. Cavalli-Sforza and colleagues (Cavalli-Sforza, Piazza, Menozzi, and Mountain 1988; Cavalli-Sforza, Minch, and Mountain 1992; Cavalli-Sforza, Menozzi, and Piazza 1994) made an attempt to demonstrate a high correspondence, indicative of parallel dispersal/migration processes, between worldwide linguistic and genetic groups. Genes and languages are both attributes of human populations, so when a population splits, then the linguistic and genetic characteristics of the groups will also tend to show divergence over time. At the broad scale, their results appeared generally robust given that the strength of correlations will depend on how information is transmitted; to the extent that languages transmit horizontally, we should expect imperfect correlations (Penny, Watson, and Steel 1993).

Other researchers (Chen, Sokal, and Ruhlen 1995) and those working at finer regional scales (e.g. Lum 1998 for Oceania) have also claimed consistent correspondences between phylogenies derived from genetic and language data. However, there can be high levels of exchange between humans groups (Bateman et al. 1990; Moore 1994) and we find evidence that genes and culture do not always evolve together; for example, Lapp populations in Finland genetically resemble other Indo-

European populations, but speak an unrelated Uralic language (Cavalli-Sforza et al. 1994).

These studies embody the issues of a larger debate concerning to what degree genes, languages, and culture are related in human prehistory (Renfrew 1987; Bateman et al. 1990; Moore 1994, 2001; Dewar 1995; Bellwood 1996b; Kirch and Green 1997; Sims-Williams 1998; Terrell, Hunt, and Gosden 1997; Terrell, Kelly, and Rainbird 2001). Phylogenetic processes, emphasising the dispersal and migration of groups, and reticulate or "rhizotic" processes, emphasising network-like interaction between groups, operate jointly, as human history is neither entirely bifurcating nor hopelessly reticulate. The truth lies in between and cannot be determined *a priori*. However, for many human groups, especially those language families associated with Neolithic dispersals (Diamond and Bellwood 2003), a branching tree model may be an appropriate characterisation of population history.

1.2.3 Cultural phylogenetics

Most recently, the phylogenetic tree-building and comparative methods commonly employed in evolutionary biology have been applied to questions of cultural evolution (e.g. Cowlishaw and Mace 1996; Sellen and Mace 1997; Holden and Mace 1997, 1999, 2003; Gray and Jordan 2000; Borgerhoff Mulder et al. 2001; Tehrani and Collard 2002; Gray and Atkinson 2003; Jordan and Shennan 2003; Mace et al. 2003; Greenhill and Gray 2005; Shennan and Collard 2005; Fortunato et al. 2006; Nunn, Borgerhoff Mulder and Langley 2006). This body of work may be loosely called *cultural phylogenetics*. It does not affiliate simply with the approaches described above, but rather draws on their theoretical and empirical findings as the basis for a new way to examine human cultural diversity. A review of current theoretical and empirical literature is found in §1.4. Here the approach is described in brief.

In the phylogenetic approach, researchers use genetic, linguistic or cultural data about societies (or their artefacts) to infer phylogenies, or, family trees. These trees may be of human populations or their cultural traits. These trees are of interest in themselves for what they can reveal about the processes (such as drift, selection, population bottlenecks, or contact) through by which the observed diversity in cultural traits was produced. Futhermore, cultural traits can be mapped onto these phylogenies to provide a control for the effects of shared ancestry and population history. This addresses "Galton's Problem"—that merely tallying cultures in which the trait of interest appears does not provide a count of independent instances of culture change, as some cultures will be closely related and share common ancestors. Correlated evolution, rates of evolutionary change, and the reconstruction of ancestral states can all then be examined with rigorous statistical methods that possess a number of advantages over other approaches to cultural evolution, as detailed below in §1.4.2 and in Chapters Two and Three. I take a primarily phylogenetic approach in this thesis, but draw on other current evolutionary approaches where appropriate.

In the next section I outline the general case for cultural evolution as a process, by examining the analogy between biological and cultural systems.

1.3 Culture has Darwinian properties

Recent years have seen the establishment of a body of theoretical and empirical work cataloguing the strong similarities between biological and cultural evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Durham 1991; Mesoudi et al. 2004, 2006). Darwin (1871:60–61) himself recognised that languages evolve in a manner similar to the branching process of speciation. Ethnolinguistic populations can split and diversify in space and time, very much like biological populations of organisms. At an individual level, cultural traits appear to follow similar patterns and processes to those of biological units of inheritance, such as genes. In principle, cultural traits display Darwin's (1859) properties necessary for evolutionary processes to take place: variation, heritability, and selection.

Variation between cultures and cultural traits is extensive. The *Ethnologue* lists some 6900+ languages worldwide (Gordon 2005). As well, individual ethnolinguistic groups will contain heterogeneous forms of cultural traits. For example, there were over 170 religions recorded in the 2001 UK Census (Office for National Statistics 2001). That some of the individual variation in cultural behaviour is heritable has been shown in traditional societies such as the Aka (Hewlett and Cavalli-Sforza 1986), in the political and religious attitudes of the United States (Cavalli-Sforza, Feldman, Chen, and Dornbusch 1982), and by studies of children's social learning (Whiten et al. 1996), including craft traditions (Shennan and Steele 1999). Moreover, there is evidence from cross-cultural studies showing that some types of social organisation and kinship traits are similar between closely related cultural groups, i.e. that differences are heritable at a group level (e.g. Guglielmino, Viganotti, Hewlett, and Cavalli-Sforza 1995; Hewlett, Silvestri, and Guglielmino 2002).

Selection of cultural traits can be natural (i.e. with effects on survival and reproduction) or purposeful because of human agency. It is an empirical issue whether undirected or "blind" selection is necessary for the evolutionary model to be appropriate, as some critics argue (e.g. Pinker 1997). At the individual level, cognitive constraints ensure that some cultural variants will be more successful than others, as humans have limited attention. Using seriation, O'Brien and Lyman (2000) have shown that there may be selective processes at work in lineages of artefacts such as arrowheads, as forms oscillate in (possibly competitive) frequency through time. Social selection may occur when cultural traits are coupled with the status of a bearer—a prestige bias (Henrich and Gil-White 2001). Cultural group selection may also occur if differences among groups that affect the persistence of the group are transmitted through time (Richerson and Boyd 1999), which Soltis, Boyd, and Richerson (1994) have argued is the case in their study of group extinction and formation rates in traditional societies of New Guinea.

1.3.1 Similarities between biological and cultural evolution

To render the analogy more concrete, Table 1.1 lists some key correspondences between biological and cultural systems. Some authors restrict their analysis of these parallels to genetic aspects of biology, but genes are not the only things that are inherited in a biological context. Modern evolutionary biology does not restrict the concept of inheritance to the DNA, as other features, for example cytoplasmic organelles or *Wolbachia* bacteria, are inherited by offspring from their parents (Gray 1992; Griffiths and Gray 2001; Mameli 2004). Moreover, the nature-nurture dichotomy implicit in such a table is not intended to be representative of evolutionary processes, where interactive co-evolutionary forces must account for a significant part of an organism's development (Jablonka and Lamb 2005). The biology-culture comparison is presented only to validate the use of evolutionary methods in the cultural domain, not to encourage further dissociation.

1.3.1.1 Language evolution

It is instructive to view the similarities in Table 1.1 and discuss them with reference to language, which provides good examples of these correspondences. Many others exist in the burgeoning literature on cultural evolution (e.g. Durham 1991; Aunger 2000; Mesoudi et al. 2004, 2006; Richerson and Boyd 2005). The transmission of language is intergenerational and predominantly vertical—children learn firstly from their parents, but also in later life from peers and other adults. Change in languages is brought about through innovations and mistakes in both performance and transmission (Lindblom 1995; Lass 1997) that can be thought of as akin to genetic mutation. The frequency of those innovations is calibrated through the forces of drift (Trask 1996; Blust 1981a) and selection. For example, sociolinguistic change can occur as a result of differential status between model and learner (social selection) or functional selection can be due to aspects of the language forms themselves (Labov 1972; Pawley and Syder 1983; Chambers 2003; Kochetov 2006).

Table 1.1. Parallels between biological and cultural systems.

	Biological	**Cultural**
Trait-level		
Units	DNA: genes, nucleotides, codons Phenotypic traits: e.g. cell structures	Cultural traits: traditions, ideas, artefacts, words, "memes"
Replication	Transcription, development, and reproduction	Teaching, learning, imitation
Mode(s) of inheritance	Vertical > clonal, horizontal	Vertical (parent-offspring) Oblique (teacher to pupil) Horizontal (peer group)
Horizontal transmission	Viral transfer, hybridisation, insects; may be rare	Peers, borrowing, imposition, teaching; may be common
Change	Mutation, drift	Mistakes, innovations, drift
Selection	Natural selection acts on fitness differences between traits that enhance survival and reproductive success	Fitness differences as for natural selection; conformism, social norms, and trends
Rates	Tied to generation time, can be slow	Can be rapid
Population-level		
Units	Species or demes	Cultures, lineages, ethnolinguistic groups
Replication	Speciation, hybrids rare ("phylogenesis")	Splitting, joining occasional ("ethnogenesis")
Selection	Competition between populations	Multi-level selection
Extinction	Trait or species loss	Loss/replacement of populations or traits
Fossils	Archaeological remains	Historical artifacts, "dead" languages

Adapted from Jordan (1999), Pagel (2001), and Mace and Holden (2005).

Language change may lead to divergent dialects and languages when populations speaking different variants separate through geographical barriers or cultural isolating mechanisms such as warfare. Finally, historical linguists use components of language such as words, phonemes, or grammar to reconstruct tree diagrams of relatedness (Trask 1996), similar to biologists' use of genes or specific morphological features to reconstruct species phylogenies. Mesoudi et al. (2004) have examined the analogy further by revisiting the arguments that Darwin made in the *Origin of Species* and presenting the evidence for cultural evolution. From their synthesis, we may add to the list above the functional evidence for adaptation as demonstrated by human behavioural ecologists (e.g. Smith and Winterhalder 1992), the gradual accumulation of modifications exemplified by technological developments such as the electric motor, and the evidence for functional change as demonstrated by vestigial cultural traits such as the QWERTY keyboard (Mesoudi et al. 2004).

Mesoudi et al. (2006) have examined the structural similarities between biological and cultural systems by comparing sub-disciplines within evolutionary biology to their putative opposite numbers in the social sciences. For example, they see the macroevolutionary subfields of systematics, paleontology and biogeography as having direct correspondence with evolutionary work in comparative (phylogenetic) anthropology, evolutionary archaeology, and cross-cultural anthropology respectively. Mapping subfields across disciplines in this way will, they argue, facilitate the integration of evolutionary cultural sciences into a coherent research programme and highlight fertile areas for further research. As well, such a framework may identify areas where the adoption of evolutionary methodologies may not be appropriate, as the dynamics of cultural evolution may bear some differences that have no observable biological parallel, such as certain forms of transmission biases (Richerson and Boyd 2005).

1.3.2 Differences between biological and cultural evolution

The analogies discussed above do not constitute a complete one-to-one mapping, and certain key differences exist between biological and cultural evolution. Differing viewpoints regarding the implications of these disanalogies for phylogenetic approaches have unfortunately polarised many of the debates in the literature (Bateman et al. 1990; Moore 1994; Boyd et al. 1997; Terrell et al. 2001; for an overview see Bellwood 1996b). Below I discuss some of these evolutionary disanalogies and show that many, if not most, are not unresolvable differences in kind.

1.3.2.1 Many cultural parents

First, cultural traits (or individuals, or groups) may have many cultural parents: for example we learn our "own" version of the story of Little Red Riding Hood from many sources, including teachers, parents, and books (Sperber 1996; Mace 2005). This is in contrast to most genetic inheritance, where gene copies come from either one or two parents, although some mobile genetic elements can blur this distinction (Miller and Capy 2006). While an individual may have many models from which to learn a cultural trait, some types of trait are likely to be more restricted or conservative in the mode of transmission than others, for example, certain political and religious values appear to be conservatively inherited from parent to child (Cavalli-Sforza et al. 1982). At the macroevolutionary level, a society may contain immigrants or influences from other groups. In the course of human evolution, it is likely that many newcomers were women, who would find it more advantageous to learn the local language and customs in order to pass these on to their offspring (Mace and Holden 2004). True "merging" between cultural groups appears to be rare and most likely only happens when groups are depopulated. The multiplicity of cultural parents is a matter for further study and not one than can be generalized to all types of traits or cultures *a priori*.

1.3.2.2 Cultural evolution can be rapid

Next, high rates of innovation can operate, fostering rapid cultural evolutionary change in comparison to the rate of biological evolution. Human genetic evolution is necessary constrained by a generation time of approximately 25 years, but cultural change can operate on much quicker timescales. While of importance when considering co-evolutionary or adaptive links between genetic and cultural traits, the mere fact of rapid change is not problematic for modern phylogenetic methods such as maximum likelihood (Pagel 1999a, 1999b; methods are discussed in Chapters Two and Three). Viruses, bacteria and other organisms can all evolve at extremely high rates. For example, bacterial antibiotic resistance can render drugs ineffective within a decade (Anderson 1999).

1.3.2.3 Multiple lineages and multiple phenotypes

Lamarckian processes—the evolution of acquired characteristics or the conscious choice of favourable cultural variants—may be an important driving force in cultural evolution as well as strictly undirected selection (Jablonka, Lamb, and Avital 1998; Jablonka and Lamb 2005). Relatedly, individuals may express the capacity for more than one cultural phenotype during their lifetime, such as the acquisition of a second language that is then taught to one's offspring. The relevance of acquired characteristics for phylogenetic methods is not well understood due to lack of empirical tests. Until such time, we may look to the well-studied literature on phenotypic plasticity—the capacity of organisms to express contingent behaviours or responses to changing ecological demands—and see that evolutionary and phylogenetic methods are routinely used in such investigations (Via, Gomulkiewicz, De Jong, Scheiner, Schlichting, and Van Tienderen 1995; Pigliucci 2001). Within-species, there are often no unique branching patterns of individuals or groups that correspond with the branching patterns of cultural traits (Borgerhoff Mulder 2001). These issues, however, are all present in evolutionary biology, especially in the literature concerning gene trees versus species trees (Page and Charleston 1998; Pamilo and Nei 1988) and the co-evolution of hosts and parasites (Klaasen 1992). Suitable phylogenetic methodologies have been developed to identify, quantify, and deal with these issues (Page and Holmes 1999; Page 2003; Atkinson and Gray 2005).

1.3.3 Units of culture

Some aspects of culture display clear parallels with units of biological evolution, for example, discrete word-forms in languages may be thought of as akin to genes. For other culture traits, such as beliefs, rituals, subsistence methods, or kinship systems, the case is not so clear. Indeed, many anthropologists find the idea that "units of culture" exist, let alone evolve, as somewhat inflammatory (Bateman et al. 1990; Moore 1994). Dawkins (1976) coined the term "meme" to describe a unit of culture that might evolve in a fashion similar to genes. Debates over "memes", "semes", "ideational units", and other putative units of culture are rife in the literature (e.g. Blackmore 1999; Aunger 2000; Boyd and Richerson 2000; Jeffreys 2000; Sperber 2001; Hewlett et al. 2002; Sterelny 2006) and, while philosophically interesting, they do not as yet offer much for an empirical evolutionary science of culture (Laland and Brown 2002). In fact, the debates that exist over the partible nature of cultural units are eerily similar to those concerning the atomisation of biological traits (Gould and Lewontin 1979) and even genes (Neumann-Held 2001). Accordingly, this thesis will not address in detail issues concerning units of culture. For analytical purposes we may however expand on Mace and Holden (2005) and usefully define a "cultural trait" as a reliably reproduced, normative behaviour tradition exhibited by members of a society and transmitted through social learning.

1.3.3.1 Core and periphery

Some authors have made the distinction between core and peripheral cultural traits (Boyd et al. 1997). Core traits "constitute the basic conceptual and interpretive framework" (1997:371) of a society and should maintain coherence through time as a related bundle of traditions. Peripheral components are those that may freely and easily become detached from the core and diffuse along independent trajectories, not necessarily vertically. Peripheral elements can be functional without reference to any other aspect of culture, i.e. they are self-contained. For example, the "age-set" social organisation in some Bantu groups of East and Central Africa appears to diffuse between unrelated groups easily, being an internally coherent small unit of transmission. Whilst these distinctions make intuitive sense, the identification of a trait (as defined) as core or periphery can only be made with reference to a phylogenetic pattern. Thus, if "core components exhibit a remarkable resilience in the course of cultural history" (Boyd et al. 1997:371), we must know the cultural history to establish the descent of the trait, else core and periphery notions will remain post-hoc labels.

1.3.3.2 Cultures as species

A phylogenetic approach proceeds by viewing cultures as analogous to species (Mace and Pagel 1994; Mace and Holden 2004; Pagel and Mace 2004) and by following similar sorts of branching patterns through isolation and descent by modification. Debate exists as to how far we can assume that cultures are bounded units for functional analysis, but it should be noted that the definition and boundedness of species is also far from clear in evolutionary biology. Numerous species concepts exist: the phylogenetic or evolutionary species concept, which defines a species as a lineage with its own historical fate (Simpson 1953; Cracraft 1983) and the reproductive species concept, which stresses actual or potential interbreeding (Mayr 1982), are just two examples.

Some anthropologists argue that cultural boundaries between societies are fuzzy and permeable, and dissuade any attempts to impose a continuity of genes, language or cultural traits through time (Welsch, Terrell, and Nadolski 1992). However, borders between societies do exist, and cultural and genetic discontinuities can sometimes be quite pronounced (Barbujani 1997; Barbujani, Bertorelle, and

Chikhi 1998). Transmission isolating mechanisms (Durham 1990) are cultural features akin to reproductive isolating mechanisms in species and thus mitigate against fuzzy boundaries to encourage a coherent, enduring cultural tradition. Examples may be language differences and the need to maintain intra-group comprehension (Nowak and Komarova 2001), warfare (Soltis et al. 1997), ethnocentrism (Gil-White 2001), and behaviours that discourage cooperation (Nettle 1999a). In this thesis, I use the terms culture, society and population interchangeably to refer to an ethnographically-attested group of people speaking the same language. Whilst it is recognized that such entities are not closed or static systems, treating cultures akin to species is a necessary abstraction for phylogenetic analysis.

1.3.3.3 Horizontal transmission

One general issue that cultural evolutionary studies must confront is to determine the frequency of horizontal transmission: the transfer of information between individuals or cultures that are not related in a parent-offspring fashion, such as diffusion, imposition, copying, or borrowing. That horizontal transmission occurs in cultural evolution is without doubt. Lexical and typological features are easily exchanged between languages (Lynch 1998). At a population level, cultures can adopt multi-faceted features from their unrelated neighbours, as in the case of the spread of major religions such as Christianity and Islam. The degree to which horizontal transmission is important is, however, an open, empirical question (Wiener 1987; Bateman et al. 1990; Mace and Holden 2004) and is discussed further in the sections below. It is noted here that horizontal transmission occurs also in biology, most notably in viruses and plants but also in animals (Li and Graur 1991), yet McDade (1992) found that frequent hybridisation between plant species was unlikely to cause significant problems in the reconstruction of phylogenies. The existence of horizontal transmission is not an *a priori* reason to dismiss evolutionary and/or phylogenetic approaches.

Relatedly, biology and culture are profoundly intertwined in human evolution and it is not necessary to set them up as opposing choices in explaining cultural diversity (Durham 1991; Oyama, Griffiths, and Gray 2001; Mace 2005). As a rule, the objections to applying evolutionary models to culture can usually be addressed by examining how evolutionary biologists are actually using their models and methods. Culture is complex and messy, but biology is not magically simpler. It is perhaps reluctance on the part of social scientists to use simplifying models that sustains many of their objections (Bloch 2000).

1.4 The phylogenetic approach to cultural evolution

1.4.1 Summary

The previous sections have set out the history of evolutionary approaches to culture and described the Darwinian features of culture that make the use of evolutionary methods viable. Here the phylogenetic approach to cultural evolution is described in detail. I introduce "Galton's Problem" and how it is addressed with phylogenetic methods. Then, I review recent work in cultural evolution in two areas: (i) building phylogenies with cultural data and (ii) the use of phylogenetic comparative methods to address questions of adaptive cultural evolution. The potential pitfalls in applying the phylogenetic method to cultural data are discussed with reference to how this corpus of work has been relevant to the broader debate of "phylogenesis" and "ethnogenesis" in cultural evolution.

1.4.2 Cross-cultural comparison and Galton's Problem

Many questions about cultural evolution, especially adaptive hypotheses, can be framed as hypotheses of cross-cultural co-evolution. Systematic ethnographic information is available for a large number of world cultures in Murdock's

Ethnographic Atlas (1967), the HRAF, and similar collections. To test cross-cultural hypotheses, most workers have used these data in correlation analyses, and positive associations are then interpreted as adaptive or co-evolutionary (Ember and Levinson 1991). However, these kinds of correlations suffer from what has come to be known in anthropology as “Galton’s Problem”, from Galton’s (1889) recognition that societies could not be treated as independent from one another due to their shared ancestry.

Tallying cross-cultural instances of associations between traits may include a number of non-independent (i.e. historically related) data points, over-inflating any correlations we might find and leading to Type I errors (false positives). An evolutionary hypothesis of relationships such as a phylogenetic tree provides us with a model of historical relatedness to address any non-independence (Figure 1.1).

Methods to build phylogenetic trees and to use them to test co-evolutionary hypotheses have revolutionized evolutionary biology in the last 20 years (Ridley 1983; Harvey and Pagel 1991; Page and Holmes 2000; Felsenstein 2003). Only by knowing the descent relationships of a set of taxa are we able to make proper inferences about the process of evolutionary change. In some circumstances one needs to be able to distinguish what biologists term homology (structures that are similar due to descent from a common ancestor) and homoplasy (convergent or independently evolved structures). By mapping traits onto trees we can distinguish these two processes (Figure 1.2).

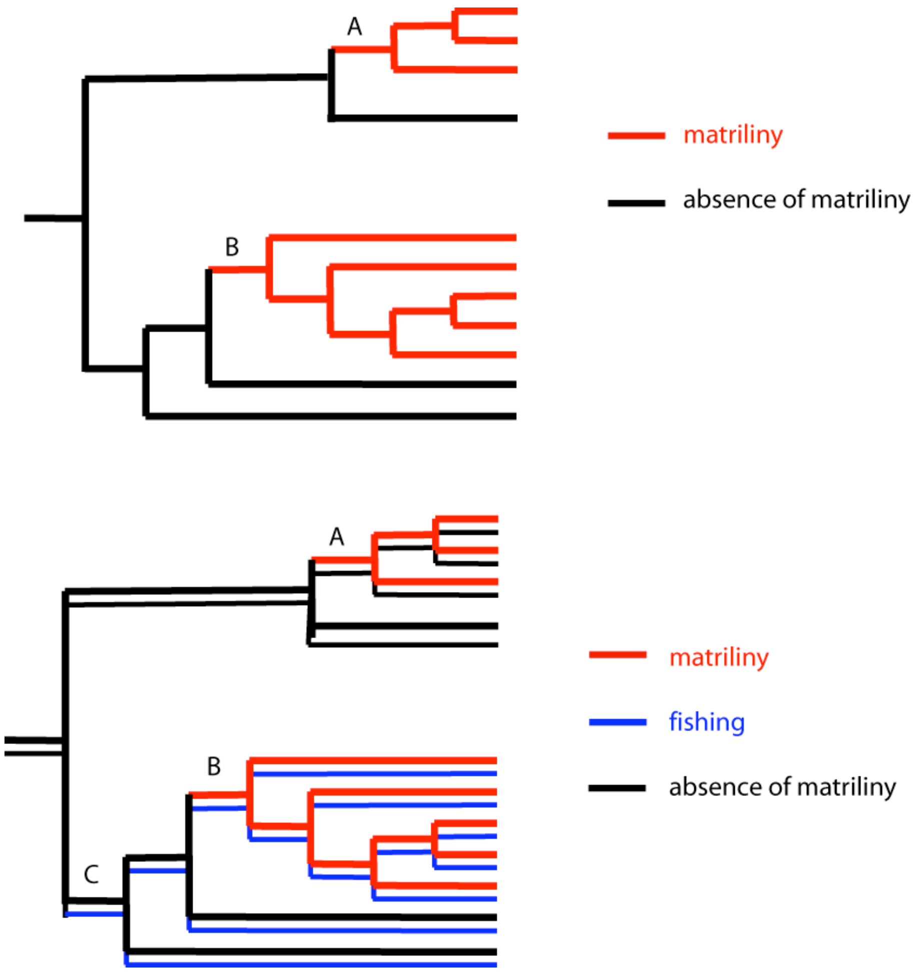

Figure 1.1. A demonstration of Galton’s Problem. Counting single instances of traits across related populations can lead to over-estimating the number of instances of independent evolutionary change. The phylogenies (trees) show the hierarchical branching relationships of a group of cultures. Time proceeds from left to right. **Top.** Eight cultures have evolved (in red) a trait of interest, such as matriliny. These are not eight independent instances of a culture acquiring matriliny; a better explanation is that matriliny evolved twice, at node A and B. **Bottom.** The same principles as applied to co-evolution. Here we overlay the evolution of fishing (blue) on the first tree. If we suspect that matriliny is correlated with subsistence fishing (red and blue together), a simple count will show five of eight co-occurrences. However, fishing appears to have evolved only once, at C. The evidence for correlated evolution is thus not as numerically strong as initially estimated by a simple counting of tips.

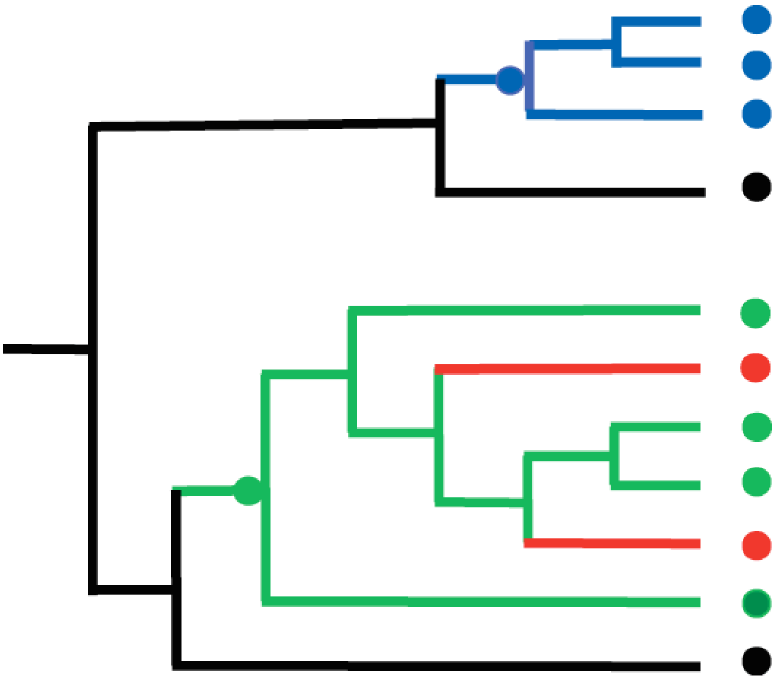

Figure 1.2. Tree terminology, using the phylogeny from the previous figure. Three characters (red, blue, and green) have been mapped onto the branches, using their distribution across the taxa at the tips of the tree. Blue characters are *homologous*, as the three blue taxa are exclusively descended from the common ancestor at the internal node (blue circle). They thus comprise a *monophyletic* group. Blue is a *shared derived* character, as opposed to green, which is a *shared retention* because not all taxa that are descendants of the green node have the green character. Red has evolved twice independently and these taxa are thus *homoplasious* for this character.

We may also wish to distinguish (i) shared derived traits (also called shared innovations) that define a group of cultures as the daughter populations of some exclusive parent, and (ii) shared ancestral traits. Shared ancestral traits are not usefully informative for hierarchical levels of descent as they can be shared by all or some daughter populations, as well as by taxa outside the group of interest. With respect to anthropology, these concerns have also been acknowledged:

> A serious weakness of comparative ethnology as an instrument for doing prehistory is that it has no very reliable way of distinguishing between shared resemblances among a set of contemporary cultures that are due to (a) retention from a common ancestral tradition, (b) convergent development, or (c) diffusion. (Green and Pawley 1999:34)

Thus, “counting cultures” overestimates the number of true innovations of a trait, as cultures may share traits simply due to being derived from a common ancestral tradition. Given these problems, what methods have been developed to avoid Galton’s Problem?

1.4.3 Methods to address Galton’s Problem

1.4.3.1 Sampling methods

Sampling methods, where closely related cultures are excluded from the sample, are commonly used by anthropologists and are the basis for the *Standard Cross-Cultural Sample* (SCCS) of 186 world cultures (Murdock and White 1969) upon which a great deal of cross-cultural correlation work has been focused (e.g. Ember and Levinson 1991). Historical relatedness is still not controlled for by this method but is merely pushed back a step, as more distant relationships may account for similarities between cultural clusters. For example, the SCCS contains three Micronesian cultures (Truk, Kiribati, and Marshallese) that share many aspects of their common heritage, such as the presence of matrilineal clans. Thus, sampling methods can return overestimates of the true number of independent instances of trait evolution, in this case matriliny. Moreover, this approach results in the loss of information about closely related cultures, the study of which is invaluable for controlled comparison (Mace and Pagel 1994), and leads to Type II errors (false negatives).

1.4.3.2 Controlled comparison

Eggan's (1954) method examines cultural variation in a small group of closely related cultures, taking advantage of their shared geographic and ecological background, and the ability to examine variations within a given type of social structure (e.g. moiety kinship systems). At this regional level, cross-cultural comparisons are more likely to focus on appropriately comparable elements (White 1988; Peoples 1993). While some researchers have proposed that this fine-grained level of analysis may create a new level of independence among cultures (Borgerhoff Mulder 2001), the problem of association due to shared inheritance still remains.

1.4.3.3 Autocorrelation

Autocorrelation methods (Dow, Burton, White, and Reitz 1984; Dow 1991) attempt to remove variation due to spatial proximity and use the residual variance to conduct cross-cultural analyses. For example, White, Burton, and Dow (1981) used these methods to examine the causes and consequences of the sexual division of labour in Africa, finding that 50 percent of the variation in female contribution to subsistence was explained by the Bantu language family. While these methods may remove some of the shared variation caused by phylogenetic history, they do not do so with reference to any explicit evolutionary model (Purvis, Gittleman, and Luh 1994).

1.4.3.4 Phylogenetically controlled comparison

Evolutionary biology avoids the exactly parallel "counting species" problem by observing phylogenetic history. Over the last 20 years, sophisticated computational methods have been developed for dealing with the hierarchical relatedness of species and populations (Felsenstein 2003). These phylogenetic comparative methods are of two sorts. Tree-building methods, implemented in computer software, construct a phylogeny from a set of data according to some optimality criterion such as maximum parsimony or likelihood (e.g. Swofford 1999). Comparative methods test for adaptation and co-evolution whilst taking evolutionary history into account, by mapping traits of interest onto the branches of a phylogenetic tree (Harvey and Pagel 1991). The details of these methods and the software used to implement them are described in more detail in Chapters Two and Three.

Using phylogenetic and comparative methods in anthropology has been advocated for some time (Ruvolo 1987; Mace and Pagel 1994; O'Hara 1996) but only in the last few years has a body of work begun to emerge that utilise these methods fully (e.g. see papers in volumes edited by Lipo et al. 2005; Mace et al. 2005; Forster and Renfrew 2006). As in evolutionary biology, work has focussed in two areas—applying phylogenetic tree-building methods to cultural data, and testing adaptive hypotheses using comparative methods. If cultural diversification proceeds by descent with modification, it follows that tree methods can be used to explore the underlying evolutionary processes. Synchronic cultural data on current or archaeological populations is used to reconstruct hierarchical past relationships by grouping populations in a nested set of relationships known as a phylogeny or tree. The fit of a tree model to various data sets can help us understand the relative importance of phylogenetic (vertical, descent) and ethnogenetic (horizontal, blending) processes in cultural evolution. Then, by using the phylogeny to control for non-independence and mapping on our characters of interest, we can make accurate inferences about correlated evolution. In the next section I describe the first type of phylogenetic approach: constructing trees (or networks) of evolutionary relatedness from languages and material culture.

1.4.4 Language phylogenies

In building a phylogeny using language data, aspects of the language system—most often lexical (word) items but occasionally typological or grammatical features—are coded and quantitatively analysed in the same way that biologists use molecular or morphological features to build trees of species relatedness. The uses and implementation of these methods are described in more detail in Chapter Two. To date, a number of major language families have been investigated using computational methods: the Austronesian language family of the Pacific (Gray and Jordan 2000; Greenhill and Gray 2005), the Bantu languages of sub-Saharan Africa (Holden 2002; Rexova, Bastin, and Frynta 2006), and the Indo-European language family (Ringe, Warnow, and Taylor 2002; Gray and Atkinson 2003; Nakhleh, Ringe, and Warnow 2005; Rexova, Frynta, and Zrzavy 2003). Other language families are beginning to be studied with these methods, including Andean (McMahon, Heggarty, McMahon, and Slaska 2005), Chinese dialects (Ben-Hamed 2005; Ben-Hamed and Wang 2006), Papuan languages (Dunn, Terrill, Reesink, Foley, and Levinson 2005), Mayan (Atkinson 2006), and Uto-Aztecan (Ross in preparation).

One measure of the success of these methods in recovering linguistic phylogenies is demonstrated by the degree to which they agree with established classifications of historical linguists[1] and concur with population dispersal processes reflected in the archaeological record. For example, Gray and Jordan (2000) statistically tested an archaeological model of Austronesian colonisation, the "express-train" sequence, against a maximum-parsimony tree of 77 Austronesian languages. They showed that the language phylogeny fit the archaeological model far better than would be expected by chance, and that a competing hypothesis did not. Further analyses using newer likelihood methods confirmed these findings (Greenhill and Gray 2005). In a similar vein, Holden (2002; Holden et al. 2005) found evidence that a parsimony tree of Bantu languages corresponded with archaeological models of the spread of farming across sub-Saharan Africa during the Neolithic and Early Iron Age. More importantly, the data in these studies has been shown to be as "tree-like" as

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[1] It should be noted that neither agreement *or* disagreement with previous linguistic classifications should be taken as necessary and sufficient evidence for the robustness of any particular phylogeny. Different parts of language can display different patterns of cultural transmission (for example, core vocabulary may be more resistant to borrowing than other vocabulary, or syntax). As such, our expectations of close matches between phylogenies derived from different datasets may be variable. I thank A. McMahon for bringing this point to my attention.

morphological or molecular data sets of similar sizes by using statistics such as the consistency index (CI) that determine how well the data fits a tree model (Sanderson and Donoghue 1989). This indicates that for linguistic vocabulary at least, vertical inheritance seems to be the predominant mode of transmission.

A common criticism of applying these methods to languages is that languages, like other aspects of culture, contain some certain amount of horizontally transmitted items. Words may be borrowed between closely related cultures and between even cultures in vastly different language families—for example, the English word "taboo" comes from the widespread (Proto-) Polynesian form **tapu*[2]. In addition, a single phylogeny may not adequately capture the complex histories of a group of words that may have evolved along different trajectories, for example, by borrowing. Newer network methods such as *NeighbourNet* (Bryant and Moulton 2004; Huson and Bryant 2006) have been applied to languages and these methods relax the bifurcating restriction of a branching phylogeny by allowing taxa to connect to more than one other group, identifying the degree and nature of reticulation and homoplasy in the data set. For example, Ben-Hamed (2005) represented Chinese dialect patterns with these methods, McMahon et al. (2005) used networks to suggest that contact explained similarities in Quechua and Aymara basic vocabulary, and Bryant et al. (2005) demonstrated how network methods could be used to investigate the degree of tree-like evolution in Indo-European languages.

1.4.5 Material culture phylogenies

Phylogenetic methods have also been applied to both present-day and archaeological material culture items (Collard and Shennan 2000; O'Brien, Darwent, and Lyman 2001; Shennan and Collard 2005). In these studies, variation in artefacts is used to construct a tree of the artefacts themselves or of the populations that constructed

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[2] An asterisk (*) before a word denotes a linguistic reconstruction for a proto-language.

them. For example, O'Brien et al. (2001) reconstructed a phylogeny of Paleoindian projectile points from the southwestern USA. Some artefacts, such as Turkmen carpet designs (Tehrani and Collard 2002) show a signal of vertical transmission over horizontal diffusion; phylogenetic relationships accounted for ~70 percent of the resemblance between woven assemblages of different Turkmen groups. In contrast, variation in Native Californian basketry motifs (Jordan and Shennan 2003) are apparently accounted for by a mainly horizontal transmission model as opposed to the vertical descent relationships of ethnolinguistic groups. Collard and Shennan (2000) stress that any a priori assumption of ethnogenesis (emphasising horizontal transmission processes) needs to be replaced by a case-by-case assessment of the importance of phylogenetic processes in cultural evolution, as they did for Merzbach pottery assemblages (2000) and for material culture variation on the north coast of New Guinea in their 2005 reanalysis of Welsch et al. (1992).

1.4.6 Comparative tests of cultural hypotheses

Comparative methods proceed by mapping traits of interest onto a phylogeny to test for significant associations while controlling for history. Type I errors of non-independence (Galton's Problem, above) are thus avoided as we count only independent instances of change across the phylogeny (Figure 1.1). Before language phylogenies using computational methods became available, workers employed the available classificatory trees of languages (Ruhlen 1987) or worldwide genetic trees from Cavalli-Sforza et al. (1994) as simple phylogenies of human cultural groups, and used these to test adaptive hypotheses about gene-culture co-evolution. For example, Mace and co-workers found that polygyny is associated with male-biased inheritance (Cowlishaw and Mace 1996) and that increased dependence on agriculture is associated with higher fertility (Sellen and Mace 1997). Holden and Mace showed that the evolution of lactose tolerance followed the keeping of livestock (1997), and that human sexual dimorphism is reduced in populations with greater female contribution to subsistence (Holden and Mace 1999). Other studies have examined correlates of kinship and marriage variables in East African societies (Borgerhoff Mulder et al. 2001; Moylan, Borgerhoff Mulder, Graham, Nunn, and Håkansson et al. 2006).

Most early studies used parsimony-based comparative methods such as the concentrated changes test (Maddison 1990) and the method of independent contrasts (Felsenstein 1985; Purvis and Rambaut 1995) to test hypotheses. Comparative methods have become more sophisticated in the last few years and now there are Bayesian (statistical) likelihood methods that allow uncertainty about both the tree topology and the model of evolution to be incorporated into these analyses (Pagel 1999a). Most recently, tests of adaptive hypotheses have utilised the statistically-derived language phylogenies (or statistical samples of phylogenies) described above in combination with modern likelihood-based phylogenetic comparative methods. Examples follow.

1.4.6.1 Matriliny and cattle in the Bantu

In an evolutionary context, sex-biased inheritance occurs when parents invest preferentially in one sex over another through the allocation of resources. Holden and Mace (2003, 2005) investigated patriliny (male-biased inheritance) and matriliny (female-biased inheritance) in Bantu societies using comparative methods. Using a phylogenetic tree of 68 Bantu languages as a model of population history (Holden 2002), they tested the hypothesis that patriliny co-evolves with pastoralism, and that matriliny is lost when cultures adopt pastoralist subsistence. Using the likelihood-based method of *Discrete* (Pagel 1994), they constructed an evolutionary flow-diagram, showing the most probable pathway was that non-cattle-keeping populations acquired cattle and then switched to patriliny, while cattle-keeping populations were very unlikely to become matrilineal. In Africa, cattle represent significant movable and defendable wealth, and as male reproductive variance is higher than female, investment in sons through the transfer of movable wealth is likely to increase reproductive success (Holden, Sear, and Mace 2003).

1.4.6.2 Worldwide sex ratio and marriage costs

Sex ratio at birth varies worldwide, and may reflect the different costs and benefits of producing male versus female babies in different environments (Trivers and Willard 1973). Mace, Jordan, and Holden (2003; Mace and Jordan 2005) investigated the global variation in sex ratio at birth (SRB), testing the hypothesis that SRB correlated with other demographic variables such as fertility and mortality. We used a genetic phylogeny based on Cavalli-Sforza et al. (1994) for Old World countries containing a major ethnic group represented on the tree. The program *Continuous* (Pagel 1997) was used to detect correlated evolution in continuous demographic traits. Additionally, the scaling parameter lambda was used to assess if the traits were evolving in a phylogenetic manner. With phylogenetic correction for the non-independence of societies, Mace et al. found that in countries where SRB was skewed towards girls, fertility and mortality were higher. As the costs of producing and raising boys may be higher than girls (Wells 2000), in countries where fertility is high the cost-benefit differentials may be greater and may thus be affecting a small skew in the SRB towards female babies.

A further comparative analysis examined the correlation of SRB and the costs of sex-specific marriage transfers (Mace and Jordan 2005). Bridewealth means that sons will be more costly, while dowry means that daughters will cost more, adding another variable to the cost-benefit trade-off. Although a standard correlation across cultures would have shown that marriage payments and SRB were evolving together, a phylogenetic correlation did not return a significant association between the two traits. Sex ratio in adulthood (male-biased) was associated with the presence of bridewealth, indicating that men are competing for brides and thus need to pay for them, but this is a demographic interaction rather than an example of gene-culture coevolution. In all the tests, the lambda parameter was shown to be greater than zero, indicating a need for phylogenetic control in the analyses.

1.4.6.3 Marriage transfers in Indo-European societies

Fortunato et al. (2006) investigated variation in marriage transfers (bridewealth and dowry) in 51 Indo-European societies. Using lexical data, they constructed a Bayesian sample of language phylogenies. This set of 1000 trees contained differing tree topologies in proportion to their likelihood, which meant that uncertainties about the "true tree" were addressed. They used the maximum-likelihood method of Pagel (1994) in a Bayesian context (Pagel et al. 2004) to estimate the ancestral state of marriage transfers in Indo-European societies. By reconstructing the ancestral state of each trait at a given node as a posterior probability, rather than the present/absent/equivocal states reconstructed in parsimony methods, their methodology identified which trait reconstructions could be regarded as stable inferences. Results indicated that dowry, while rarer in present-day societies, was likely to have been the ancestral state, with bridewealth evolving at least four separate times in the Indo-European family. Further work on this sample using co-evolutionary tests in the same Bayesian context has demonstrated that polygyny and bridewealth, and monogamy and dowry, appear to be evolving together (Fortunato and Mace, in press).

1.4.7 Objections to phylogenetic and comparative methods

What are the dangers of forcing the phylogenetic model onto cultural data? Some of the objections to studies of cultural evolution in general (§1.3.2) are argued to apply especially to the phylogenetic approach. Some critics have argued that rapid evolutionary change, reticulation (borrowing), and cultural recombination all violate the assumptions of a unique branching pattern characterising a group of cultures (Bateman et al. 1990; Terrell et al. 1997; Borgerhoff Mulder 2001). However, these are not so much barriers to the use of phylogenetic models as they are empirical questions to be tested with different data sets. For example, phylogenetic methods allow us to assess the appropriateness and fit of a tree model to our data with tools such as consistency indices and bootstrapping methods.

Moreover, a unique branching pattern does not have to characterise all cultural traits in order for us to investigate cultural evolution; different patterns may exist for "core" and "periphery" traits (Boyd et al. 1997), and may be compared in the same way that biologists compare "gene trees" and "species trees" (Pamilo and Nei 1988; Page 1998). Some authors have suggested that we should be tracing the unique phylogenetic histories of different traits rather than constructing population histories using languages or material culture as a proxy for ethnolinguistic populations (Pocklington, McElreath, and O'Brien 2005). Studies of this type, employing "iterated" (McElreath 1997) or "perfect" (Nahkleh et al. 2005; Ringe et al. 2002) parsimony, attempt to remove homoplasious traits from the data and retain only those with clear branching lineages. However, there is substantial loss of information inherent in such approaches, and if we are interested in questions about (for example) rates of evolution or adaptation, we proceed most profitably by plotting traits of interest on a background of evolutionary relationships, even if that phylogeny is only an imperfect model of history.

Relatedly, while discriminating vertical from horizontal transmission can be crucial in determining some processes of cultural diversification, in the context of testing for adaptation, a borrowed trait counts as an instance of adaptation just as much as if the trait was invented along a lineage. As long as a trait is adopted by "choice", not imposed by force (Durham 1991) or acquired as a side-effect of some other complex of traits, the acquisition through borrowing or contact should be another independent instance of adaptive cultural change (Mace and Pagel 1994). To disregard borrowings in adaptive tests is unreasonably conservative.

Borgerhoff Mulder (2001) argues that the need for phylogenetically controlled comparison is still an open question, and that while broad global patterns of trait distribution (such as modes of marriage) may retain an historical signal, at a more fine-grained local level natural or cultural selection pressures may act on traits to produce a new level of independence among related populations. Cashdan and Rogers

(1997) have also argued that comparative methods lack statistical power by decreasing the number of data points available for analysis. This is however a misconception of the concept of power, as the number of significant correlations found in non-phylogenetic analyses will contain some amount—unknown until phylogeny is controlled for—of Type I error (Mace 2005). Borgerhoff Mulder et al. (2001) examined the need for phylogenetic control in a study of local variation in East African kinship and marriage. They compared phylogenetically controlled analyses to standard correlations for each of their 36 hypotheses. Of these, 21/36 were non-significant under both types of methods, 5/36 were significant under both types, 8/36 were significant under conventional correlations but not when phylogenetically controlled, and 2/36 were significant when phylogenetically controlled but not under conventional tests (2001:1072). It is notable that nearly two-thirds of conventionally significant trait associations disappeared with phylogenetic control, indicating a definite need for this kind of analysis where possible.

In their discussion and elsewhere, Borgerhoff Mulder and colleagues argue that comparative methods are conservative tests and these results, like other phylogenetic tests, are not showing two types of important adaptive processes. Firstly, comparative methods focus on the origins of adaptive trait associations to the exclusion of evolutionary forces maintaining an association between traits (stabilizing selection). Secondly, comparative methods mask the effect of habitat selection, where closely related groups move into similar environments (Borgerhoff Mulder 2001). However, both points, sometimes under the rubric of "phylogenetic inertia", are recognized in comparative biology (Orzack and Sober 2001); likelihood methods that allow the direction and order of evolutionary change to be determined can address origin/maintenance questions (e.g. Pagel 1994), and the points above do not constitute grounds for not using an historical method when one is available.

On the issue of phylogenetic inertia, stability *or* lability in cultural traits cannot be assumed at the outset. If a trait is shared by many closely related cultures, it does not necessarily imply that evolution is weak, as there may be a good adaptive reason to retain the trait. By mapping traits onto a phylogeny we can show that many aspects of culture show a remarkable time-depth, for example, the practice of dowry can be reconstructed for the root of the Indo-European tree, a time depth of approximately 6,000 years (Fortunato et al. 2006). Even traits without clear adaptive function may demonstrate considerable variation in lability. Marck (1996) compared the names and functions of the first-order anthropomorphic Polynesian gods against the background of phylogeny provided by Polynesian languages. While some types of gods could be traced to their Proto Nuclear Polynesian ancestor e.g. **Tuu*, god of war (1996:247), suggesting a cultural stability of over 2800 years, others had gone through changes in function, in name, and in importance even in closely related cultures. For example, the sea god Tangaroa is a first order deity in Mangarevan society, but in the closely related Marquesas, thought to have diverged less than 800 years ago (Kirch and Green 2001), Tangaroa was reduced to a 39th-generation offspring of the gods and accorded no great importance.

1.4.8 Simulations

By far the most common objection to the application of the phylogenetic model to cultural data is the (unquantified) presence of horizontal transmission between societies. Some workers have used simulation studies to address the impact that differing levels of horizontal transmission have on (i) recovering phylogenies, and (ii) accurately testing for correlated evolution. Atkinson, Nicholls, Welch, and Gray (2005) modelled the effects of increasing levels of horizontal transmission in a linguistic data set on the ability of tree-building methods to estimate the divergence date (time depth) of a phylogeny. As well as modeling random horizontal transmission, they used a spatially realistic model of evolution where borrowing was much more likely between closely related as well as spatially close languages. They found that borrowing levels of 20 percent—a significant amount of vocabulary—only altered estimates of divergence time by, at most, 500 years from an 8500 year time depth.

Nunn et al. (2006) simulated the co-evolution of two traits in a spatial grid and calculated Type I error rates under conventional correlations and the phylogenetic method of independent contrasts. Under differing conditions of extinction and spatial configuration, they found that phylogenetic methods always outperformed conventional correlations. By varying the level of horizontal transmission in the simulation they were able to show that small amounts of horizontal transmission increased the Type I error rates of phylogenetic method; however, in all analyses the phylogenetic method outperformed conventional correlations (2006:193). It is important to note that this study used a parsimony-based comparative method. These methods have been shown to perform poorly when multiple changes may take place along a lineage and when rates of evolutionary change are high (Felsenstein 2003). Likelihood-based or Bayesian methods that use the information contained in branch lengths, and incorporate a more explicit model of evolution may not be as affected by horizontal transmission.

Both simulation studies investigated the impact of increasing levels of horizontal transmission on the two broad types of phylogenetic approaches to cultural evolution, tree building and comparative tests. In a survey of work published to date, Collard, Shennan, and Tehrani (2005) took an empirical approach to determine the relative importance of vertical and horizontal processes. They reviewed nine studies that had used phylogenetic methods on cultural data (language, and archaeological and material culture artefacts) and compared the tree-statistics derived from these analyses with 21 biological analyses of molecular, morphological, and behavioural data. By comparing the retention index (RI), which is a measure of the fit of the data to a tree model where 1 indicates a perfect fit, Collard et al. tested the expectation that cultural data sets would show more evidence of horizontal transmission and so be less tree-like, thus having a lower RI, than the comparable biological data sets. Their results showed that the cultural data sets actually had the same mean RI (0.60) as the biological data sets, although the range of RI was wider for the cultural analyses. Although it is true that tree-building programs will produce a tree regardless of the degree of vertical signal in the data, statistics such as these indicate that for the small amount of empirical work published, vertical transmission of cultural traits is apparently important. As well, horizontal transmission is not so endlessly reticulate as to render phylogenetic methods unusable, as has been suggested by some critics (Moore 1994; Terrell et al. 2001). More importantly, most workers have now realized that the production of a tree from a set of data is only the first step (Borgerhoff Mulder et al. 2006); a phylogeny is a hypothesis about evolutionary relationships—a model of population history—and can be used in conjunction with independent data sets to examine the pattern of cultural evolution.

1.4.9 Different lines of evidence

The use of different types of data to investigate questions of human prehistory is an approach that Kirch and Green (2001) have termed “triangulation”. Their methodology involves the use of historical linguistics, comparative ethnography, and archaeological data to make inferences about the past, drawing on all available information to paint a complete picture of cultural evolution and diversity. Prehistoric human migrations associated with a Neolithic agricultural dispersal (Bellwood 1996a, 1996b; Bellwood and Renfrew 2002; Diamond and Bellwood 2003) appear to have resulted in cultural groups with a meaningful degree of biological and cultural continuity through time and space. Although this continuity is not a necessary requirement for the use of phylogenetic approaches, it facilitates the use of different lines of evidence (e.g. biological, linguistic, ethnological, archaeological) to address the same questions, as they are geographically and historically framed together. We cannot assume that agricultural peoples *always* expand and migrate because of their technological innovations and/or population pressure: sometimes agriculture has allowed people to “stay at home” (Campbell 2002) and consolidate their presence in already-occupied territories, such as may be the case for Mixe-Zoquean (Olmec) languages (Hill 2001). However, general consensus holds that the Austronesian language family of the Pacific region is clearly one such example of a agriculturally-motivated Neolithic dispersal (Diamond and Bellwood 2003), and as such, provides an excellent case study for these combined approaches.

Additionally, regional rather than worldwide studies are preferred in comparative anthropology (Eggan 1954). Firstly, the focus is on a lesser time depth, allowing us to use language relationships to build a model of population history. Secondly, we are likely to being comparing “like with like” in regional studies; that is, making appropriate comparisons and inferences about the types of cultural traits under study. Thirdly, the problem of isolates (both linguistic and genetic), and the uncertain relationships of human populations at the base of any worldwide tree render a phylogenetic model in the global context more problematic. In the next section I present the ethnographic context for the specific regional case that was studied in this thesis.

1.5 The ethnographic context: Austronesian cultures of the Pacific

1.5.1 Summary

This section describes the regional focus for the thesis, the Austronesian cultures of the Pacific. The prehistoric colonisation of the Pacific and current models of Austronesian dispersal are reviewed. Molecular anthropological findings from mtDNA and Y-chromosomal markers show differing pictures, possibly due to sex-specific migration patterns. Although the “island laboratory” model is now considered inadequate, previous work in the region has used evolutionary concepts such as adaptation. Variation in descent rules and post-marital residence patterns may reflect adaptive evolution in kinship systems. Austronesian societies vary in their kinship organisation but the evolution of these traits is not well understood, thus, the thesis will test co-evolutionary hypotheses on the evolution of matriliny and reconstruct ancestral states of descent and residence patterns. The chapters are described in brief.

1.5.2 Pacific colonisation

Prehistoric human expansion into the Pacific took place over the last 60,000 years (Kirch 2000). Pleistocene hunter-gatherer populations from Southeast Asia crossed open water to colonise Sunda—Australia and New Guinea, connected by lowered sea-levels (Spriggs 2000)—by around 56,000 BP (Roberts et al. 2001), reaching the Bismarck Archipelago by 39,500 BP (Leavesley et al. 2002) and Buka in the Solomon Islands by 29,000 BP (Wickler and Spriggs 1988). Further migrations may have followed, as the area from Island Southeast Asia through to the Solomons—Near Oceania (Green 1991)—constituted what Irwin (1992) has termed a voyaging nursery, with calm weather and undemanding sailing conditions. The descendants of these people are dispersed throughout New Guinea and parts of Island Melanesia (Figure 1.3); they speak a diverse range of languages—“Papuan” or Non-Austronesian (NAN)—whose heterogeneity indicates a long time depth in the region (Foley 2000). Here they are referred to as “indigenous Melanesians”, following Hurles et al. (2002). By 9000 BP there is evidence for tree-crop cultivation in highland New Guinea (Golson 1991), but not intensive agriculture or high population density in the region.

The environs of southern China have been identified as a center of early agriculture (Diamond and Bellwood 2003), and many Asian language families such as Tai-Kadai and Hmong-Mien have their deepest roots in this region (Benedict 1975; Bellwood 1996a). The Austronesian (AN) language family also derives from this region, with its highest diversity—nine of ten first-order subgroups—centred on Taiwan (Blust 1984-5; Pawley and Ross 1993; Blust 1999). An agricultural dispersal model involves the movement of Neolithic peoples out of Taiwan around 4500–6000 BP, carrying with them newly developed agricultural technology and domesticates, and speaking

Austronesian (AN) languages (Bellwood 1985, 1997, 1991; Blust 1985, 1995, 1996; Pawley and Ross 1993; Bellwood, Fox, and Tryon 1995; Pawley 1997; Spriggs 1997, 2000). From Island Southeast Asia, AN speakers moved through the Pacific, overreaching the extent of the existing populations to colonise the uninhabited regions of Remote Oceania, the islands of Micronesia and Polynesia (Figure 1.3). The AN family numbers some 1200 languages and its speakers are dispersed over half the circumference of the Earth, from Madagascar to Easter Island (Tryon 1995) (Figure 1.4).

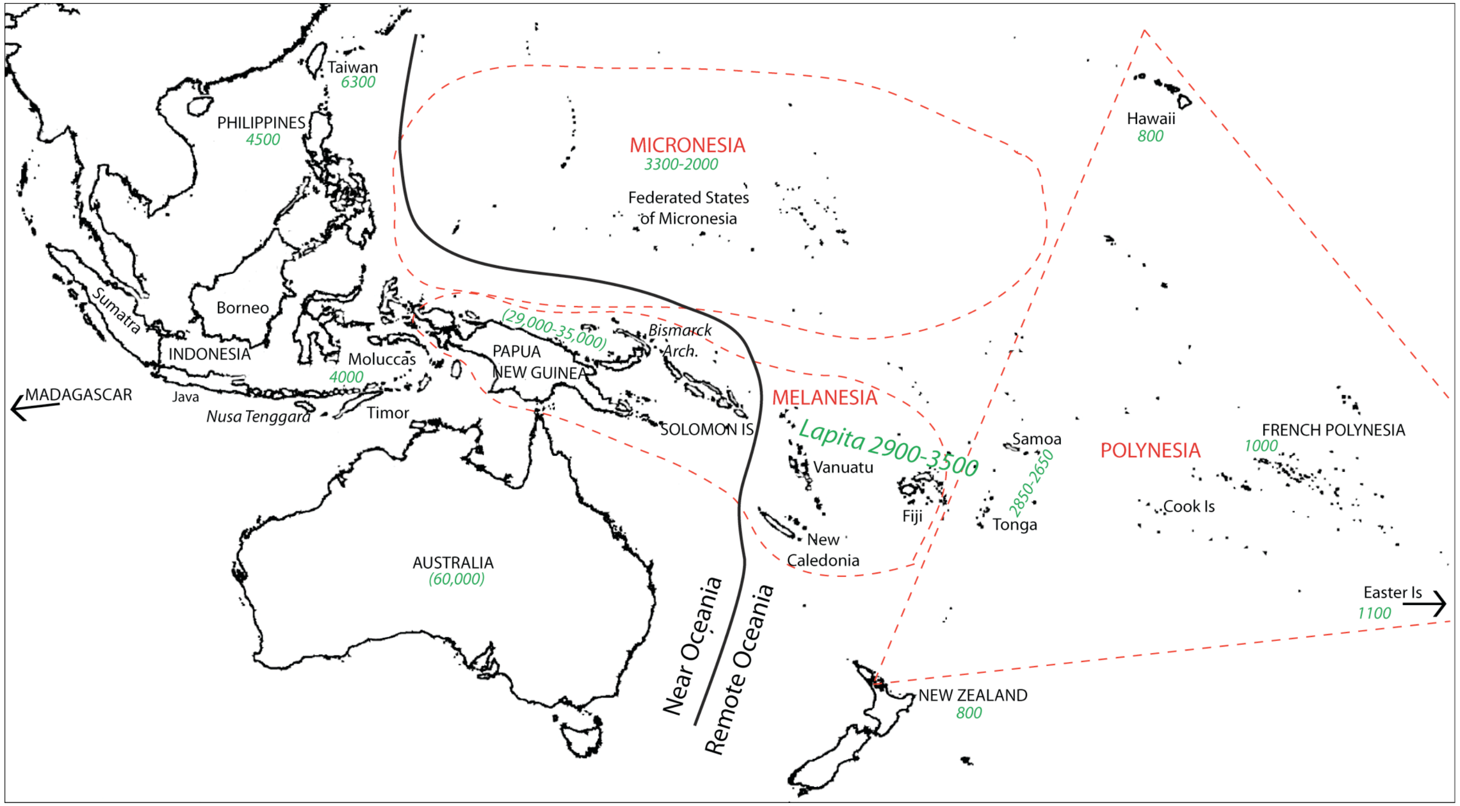

Figure 1.3. Map of the Pacific showing geographic and culture areas. Conservative dates (years BP) of AN archaeological settlement in key areas are shown in green, from Hurles et al. (2002) and Kirch (2000). The traditional classification of Melanesia, Micronesia, and Polynesia are used primarily as geographic designations; in preference we use Near and Remote Oceania (Green 1991). Near Oceania denotes areas settled before the Lapita horizon c. 3300 BP, where islands are for the most part intervisible. Remote Oceania denotes areas uninhabited by humans before Lapita, predominately far-flung islands.

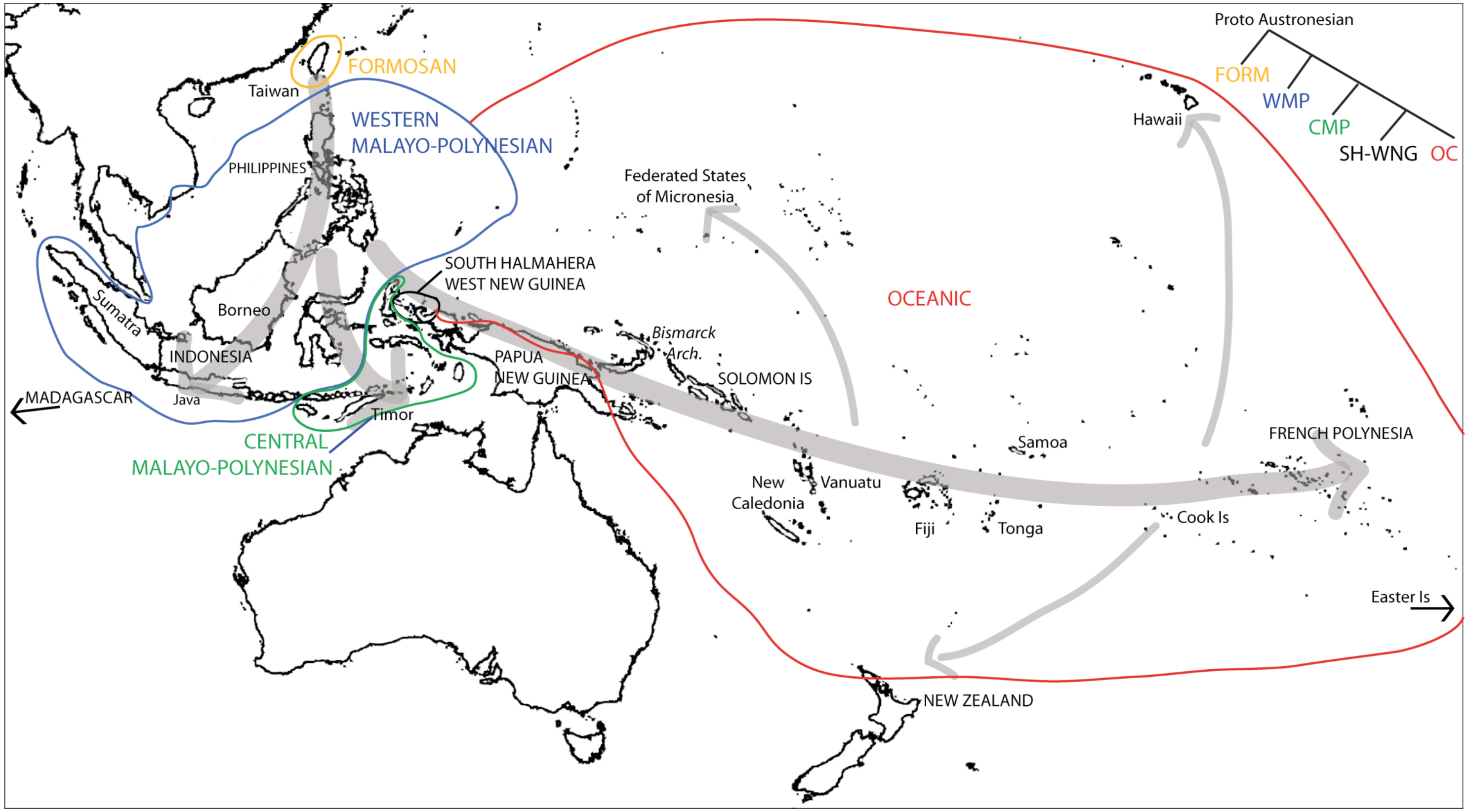

Figure 1.4. Map of the Pacific showing the extent of the Austronesian language family. The boundaries of high-order AN subgroups are indicated and their branching patterns are shown in the top right-hand corner. Non-Austronesian (NAN) languages are spoken in most of New Guinea and on some off-shore islands. Different language families are present in Australia and Mainland Southeast Asia. The grey arrow-paths trace the approximate direction of the Austronesian expansion.

1.5.3 Austronesian languages

Early European travellers in the Pacific such as Captain Cook observed word similarities between far-flung languages like Tahitian and Malay. Early work by Dempwolff (1934–1938) characterised the rough outline of the AN language tree, grouping closely related languages together and tracing them back to a putative "mother-tongue", Proto Austronesian. Historical linguistics proceeds by a "comparative method" comparing cognate terms (words assumed to have a common origin) across languages and working out regular sound correspondences (Trask 1996; Crowley 1997). These correspondences are then used to establish the directionality of change in language and to reconstruct proto-vocabulary. The method is recursive in that each new cognate examined refines the subgrouping hypotheses, confirming (or not) the placement of a language in the family hierarchy. Careful comparative reconstruction is an ongoing endeavour by Pacific scholars, and on the basis of this work Blust (n.d.) and Tryon (1995) have collated large comparative dictionaries of AN languages.

1.5.3.1 Austronesian subgrouping

Blust (1998, 1999, in preparation), synthesizing work across the discipline as well as his own, and others (Pawley 1997; Tryon 1995), have described the internal subgrouping of Austronesian. The high-order subgroups of AN are primarily Formosan (9/10 are found on Taiwan), with one branch forming the rest of the family, Malayo-Polynesian (MP). MP then splits into Western (WMP) and a Central-Eastern branch (CEMP). The WMP languages, which include those on the Philippines, Borneo, Sumatra, Java, Sulawesi, and parts of Indonesia, are not considered a true (exclusive) innovation-defined group, but rather are a catch-all for non-CEMP languages (Ross 1997). CEMP splits into Central (languages on the islands of Timor, the Lesser Sundas, and Maluku), which is also considered innovation-*linked* rather than defined (Blust 1993b) and an Eastern branch (Blust 1978). This Eastern branch splits into South

Halmahera-West New Guinea, comprising languages around the Bird's Head of Irian Jaya and Halmahera (SHWNG), and the large Oceanic (OC) group. The Oceanic subgroup is well defined as a whole but is possessed of a "rake-like" high-order subgrouping rather than a bifurcating family tree structure.

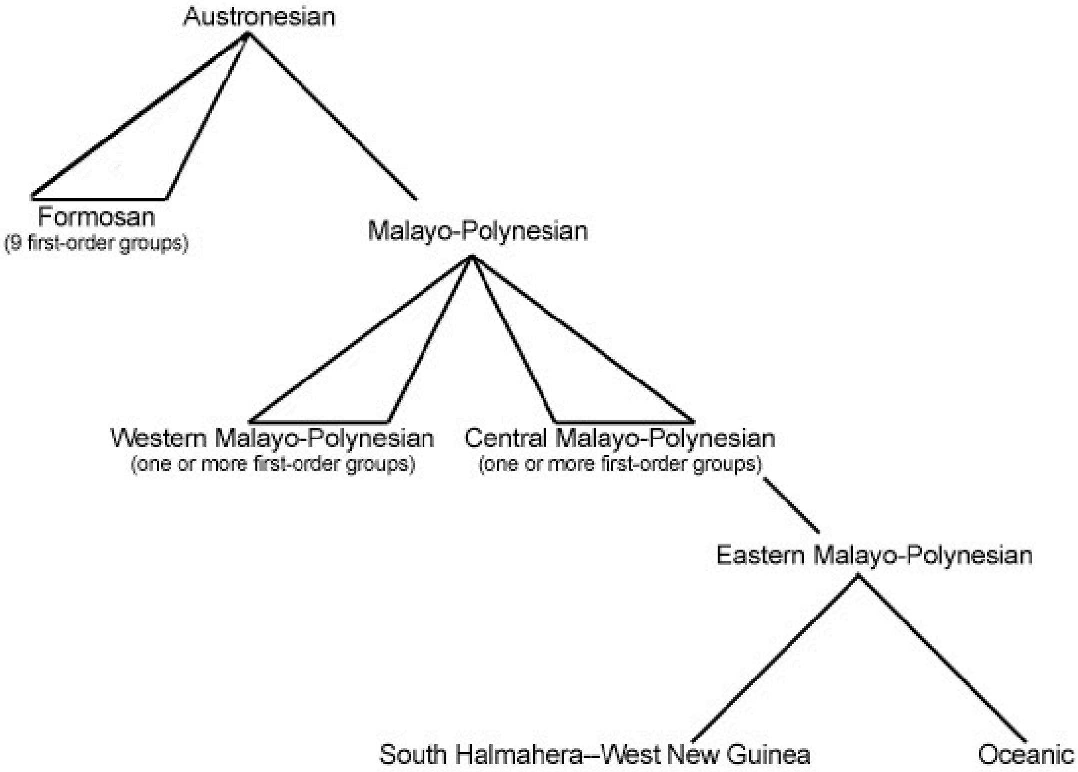

Figure 1.5. Subgrouping of the Austronesian language family. Taken from Tryon (1995), Pawley (1999), and Blust (in preparation). Formosan languages are spoken on Taiwan. The WMP and CMP subgroups are not clearly innovation-defined, that is, they are a residual collection defined by their exclusion from another branch (Proto Central-Eastern and Proto Eastern Malayo-Polynesian, respectively).

Dialect networks, or chains, form when language communities maintain overlapping ties with each other for an extended period of time before (if ever) diverging completely (Ross 1997). In a phylogenetic context, words will not have unique branching histories, and trees will appear to have low resolving power at nodes representing parts of a dialect chain. Dialect diffusion may in fact be ubiquitous through the whole of the higher-level subgrouping of AN languages reflecting (i) the speed of the AN expansion through Island Melanesia and/or (ii) the maintenance of dialect networks over the voyaging-corridor area (Pawley 1997; Green 1999).

1.5.4 The Austronesian dispersal

Linguistic, archaeological and biological evidence gathered by Pacific scholars over the last fifty years has been used to argue a number of different scenarios for the Austronesian colonisation of the Pacific. Historical linguistics in particular has been important in establishing the internal relationships of Austronesian-speaking populations, and through cross-talk with archaeologists, linguists have been able to correlate language sub-families with particular archaeological horizons (e.g. Shutler and Marck 1975; Pawley and Green 1984; for Proto Oceanic and the Lapita horizon in the Bismarck Archipelago). In addition, by reconstructing proto-vocabulary for a putative prehistoric period, linguists can corroborate the archaeological record (e.g. the POC term for a particular fish lure, **bayan*) and can supply information where none might be archaeologically available, as in the case of the Proto Polynesian lunar calendar (Kirch and Green 2001).

All modern workers agree that Pacific peoples had their ultimate roots in Asia, but disagree as to the timing, speed, and degree of intermixing between populations. A mainstream archaeological consensus (Bellwood 1997; Kirch 2000; Green 2003) for the geographic spread of speakers of AN languages might proceed roughly as follows. People from Taiwan moved into Island Southeast Asia through the Philippines at approximately 4200 BP with early “red-slip” pottery, taro and yam horticulture, chickens, and outrigger canoes, penetrating south and easterly into Wallacea. From the Philippines, people moved through Borneo to Nusa Tenggara, later spreading to Madagascar and the Malaysian peninsula. Others migrated south-easterly through North Sulawesi, the Moluccan Strait and Banda Sea. In Island Southeast Asia, it appears that AN languages replaced those of the indigenous cultures (Adelaar 1995). It is unclear to what degree these new populations initially practiced intensive agriculture (Spriggs 1997). After a pause, from this Wallacean region AN speakers spread quickly through Halmahera and around Cenderawasih Bay (Irian Jaya), along the north coast of New Guinea to the Bismarck Archipelago. These people carried their AN languages as part of the "Lapita Cultural Complex" as far as the Solomon Islands, Vanuatu, and New Caledonia by 3300 BP (Specht and Gosden 1997).

Lapita, named after a decorated pottery style, appears as an archaeologically distinct package consisting of animal and horticultural domesticates, over-water stilt houses, characteristic fishing technologies, outrigger canoes, personal adornments, and other items of material culture (Kirch 1997; Spriggs 1997; Green 2003). Lapita sites first appear in the Bismarck Archipelago around 3300 BP and quickly spread to Fiji, Tonga, and Samoa (Western Polynesia) by 2950 BP (Anderson 2002; Spriggs 2000). Some Lapita pottery features show continuity with earlier AN Neolithic sites, such as the Ta-p'en-k'eng and then Yuan-shan pottery assemblages in Taiwan, thus supporting a descent relationship from Asian traditions (Chang and Goodenough 1996; Bellwood 1997). Other features of the Lapita complex, such as tree crops, suggest these items come from integration with indigenous Melanesian societies (Denham 2004).

Expansion further into Remote Oceania may be linked with atoll emergence through sea-level drops around 2000 BP (Nunn 1994). Lapita descendants expanded northerly up to Central and Eastern Micronesia around 2000 BP, possibly from the Vanuatu region (Intoh 1997). In Western Polynesia, an archaeological "pause" of ~1000 years is evident before the attested dates of 1700–1200 BP in the Marquesas

(Central/Eastern Polynesia), with the far corners of the Polynesian triangle—Hawai'i, Rapa Nui (Easter Island), and Aotearoa (New Zealand)—being settled around 800–1000 BP (Spriggs and Anderson 1993; Bellwood 1997; Kirch 1997; Green 1999; Burley and Dickinson 2001; Kirch and Green 2001; Anderson 2002).

1.5.5 Models of colonisation

1.5.5.1 Express train/Out of Asia

According to the "express train to Polynesia" model (Diamond 1997; Diamond 1988), the AN expansion from the Taiwanese homeland was a swift and relatively encapsulated event. Following other Neolithic farming expansion models (Renfrew 1987), on this model the Austronesians were propelled by a successful package of technological inventions—rice cultivation from China and then horticultural and sailing technologies from Island Southeast Asia. On leaving Taiwan around approximately 4500 BP, Austronesian speakers took only 1500 years to reach the edges of Western Polynesia—a distance of 10,000 kilometres (Bellwood 1978). Under this hypothesis, genetic mixing with indigenous Melanesians was minimal, although it has occurred since. Green (2003:5) notes that the "metaphor of a train journey…" should by now be "rendered suspect", but that its persistence in the literature is largely due to molecular biologists wishing to test simple predictive models.

1.5.5.2 Entangled bank

In contrast, a minority group of workers dispute the adequacy of the agricultural dispersal model at all for explaining the distribution of AN-speaking Lapita people throughout Oceania (Terrell et al. 1997, 2001). In the past this perspective has been associated with an indigenous Melanesian origin of the Polynesians (Clark and Terrell 1978; Allen and White 1989). Often vague with respect to testable assertions, these workers have offered no viable alternative model beyond 45,000 years of ongoing interaction in Near Oceania (Terrell 2001:107). Both this position and the strong claims for speed and isolation made by the "express train" model represent extreme ends of a continuum embodying ethnogenesis and phylogenesis in population history (Jordan and Gray 2001). Intermediate scenarios exist and are more likely to capture the complex population history of the area. These scenarios have been stimulated in part by new genetic data.

1.5.6 Molecular anthropology in the Pacific

The last 15 years have seen heated debate concerning the origins, timing, and degree of AN–NAN interaction, stimulated in part by new genetic evidence from molecular anthropology. Most of these studies have used uniparental loci: mitochondrial DNA (mtDNA) inherited through the maternal line, and the non-recombining portion of the Y-chromosome inherited through males. Both these loci are non-recombining and have small effective population sizes, increasing the likelihood of drift and population differentiation over short periods of time. They can thus be more suitable than nuclear loci for tracing population histories in a regional context.

1.5.6.1 Mitochondrial DNA

High frequencies of a nine base-pair (bp) mtDNA deletion in the COII/tRNA^{Lys} region, and characteristic motifs in the mitochondrial control region, are present in Polynesian populations (Melton et al. 1995; Redd, Takekazi, Sherry, McGarvey, Sofro, and Stoneking 1995; Sykes, Leiboff, Low-Beer, Tetzner, and Richards 1995). The precursors of this "Polynesian motif" can be traced back to Island Southeast Asian populations including Taiwan, but these lineages are virtually absent from NAN-speaking populations in New Guinea and Island Melanesia (Lum and Cann 1998; Merriwether, Friedlaender, Mediavilla, Mgone, Gentz, and Ferrell 1999). Lack of indigenous Melanesian mitochondrial lineages in Polynesia also implies little female genetic admixture. The 9bp deletion is also found in mainland East Asian populations, confirming the "Out of Asia" scenario for the ultimate origins of the Austronesians. By estimating the time to the most recent common ancestor (MRCA) of the Polynesian motif, Oppenheimer and Richards (2001a, 2001b) postulate the AN expansion to have derived from Eastern Indonesia during the Pleistocene (~17,000 BP) rather than Taiwan. However, this interpretation—the "Slow Boat"—remains contentious, due to wide confidence intervals on the coalescent time (5500–34,500 BP) and the direct conflict of these conclusions with the significant body of linguistic evidence. Moreover, further work shows that Indonesian mtDNA sequences are consistent with a MRCA during the Holocene (Cox 2005).

1.5.6.2 Y-chromosome lineages

A more complex picture has emerged from studies of Y-chromosome haplotype diversity. A pre-Holocene, indigenous origin for a majority of Oceanic and Southeast Asian Y-chromosome lineages was argued by Capelli et al. (2001) on the basis of the distribution of haplogroup C, coalescing at >12,000 BP across the region. Other studies have similarly found that while all Pacific-region Y haplotypes appeared to ultimately originate in Asia, the proximate origins of Polynesian Y-chromosomes are predominantly indigenous Melanesian (Kayser et al. 2000; Hurles et al. 2002). The Y-chromosome genetic patterns of Oceanic populations may concur with the general sequence of the "express train" model (Hurles et al. 2002), but show evidence for much more interaction with indigenous populations in Eastern Indonesia and Melanesia along the way than is suggested by that earlier model. A lack of both Taiwanese- and Melanesian-specific Y-chromosome lineages in a Cook Island (Polynesian) population (Su et al. 2000) shows how founder effects and drift may complicate analyses and highlights the need for widescale sampling.

1.5.6.3 Autosomal markers

Some nuclear loci, usually short tandem repeats (STRs), have been used in Pacific molecular anthropology. Lum and Cann (2000) used neutral autosomal loci as well as mtDNA to evaluate genetic distances between Pacific Island and Asian populations.

mtDNA distances suggested that Micronesians and Polynesians originated in Island Southeast Asia, but autosomal distance markers suggested substantial, ongoing male gene flow of Remote Oceanic populations with indigeous Melanesians in Near Oceania. Correlating autosomal genetic distances with geographic and linguistic distances showed a similar pattern (Lum et al. 2002).

1.5.6.4 Sex-specific patterns of dispersal

Y-chromosome and mtDNA patterns tell the histories of male and female movements. Approximately 70 percent of societies practice patrilocal residence, that is, women move to their husband's kin group on marriage (Murdock 1949:38). In comparison, matrilocal residence involves the movement of men to their wives' kin group, and is much less common worldwide. An eight-fold higher migration rate for females worldwide was claimed on the basis of mtDNA versus Y-chromosome diversity (Sielstad et al. 1998), although this may only hold regionally (Wilder et al. 2004). Oota, Settheetham-Ishida, Tiwawech, Ishida, and Stoneking (2001) compared mtDNA and Y diversity in matrilocal and patrilocal Thai hill-tribe villages. They found that mtDNA diversity was restricted and Y-chromosome diversity greater in the matrilocal villages, while the reverse pattern was obtained in the patrilocal societies. Kayser et al. (2003) found much higher levels of diversity in mtDNA as opposed to Y-chromosomes in Irian Jaya, attributing this to extreme patrilocality and/or male-biased parental investment in the region. Hage and Marck (2003) argue that the discordant molecular findings in the Pacific are best accounted for in a model where Proto Oceanic society was matrilocal and/or matrilineal, that is, where migrating AN speakers incorporated diverse males (and their genes) into social groups whilst retaining a restricted, ancestral set of female-specific genetic markers. These claims are addressed in Chapters Five and Six.

1.5.7 An integrated model

Molecular work, especially the conflicting results from sex-specific markers, can be integrated into a messier but ultimately more realistic model of Pacific prehistory. The intermediate "Triple I" (Intrusion, Innovation, Interaction) model (Green 1991, 2003; Kirch 2000) allows for ongoing interaction—genetically, linguistically and culturally—between both NAN and AN cultures in a "voyaging corridor" stretching from Eastern Indonesia through to the Bismarck Archipelago during the middle part of the AN expansion. The geographical sequence of AN dispersal remains broadly as described, but a number of "pulse, pause, and step" sequences are proposed. At each step, specific cultural or technological developments are surmised to have taken place, such as the appearance of *Conus* shell ornaments in Proto Oceanic society, or the integration of crop domesticates from Island Southeast Asia (Green 2003:5).

1.5.8 Later developments in Austronesian history

Monsoon sailing across the Bay of Bengal to Island Southeast Asia led to Indian trading and subsequent Hindu and Buddhist influence in Indonesia, especially Java and Bali, from approximately 1700–1500BP, although it took some centuries for this influence to become established in religious and political institutions (Geertz 1980; Bellwood 1997). Indianisation appears to have only affected elite institutions and had little impact on established cultural traditions of the peasantry. Islam, brought to Island Southeast Asia in early medieval times, spread through an association with favourable trading and power alliances with native rulers, as well as through conversion (Kumar 1979, cited in Bellwood 1997). By 500 BP Islamic and Portuguese influence meant that the Indo-Malaysian Archipelago was part of the greater Asian world, with emergent Malay sultanates and coastal mini-empires in southern Sulawesi, such as the Bugis and Makassarese (LeBar 1975).

East of Island Southeast Asia, Indian and Islamic impact was not evident. Societies in both Remote and Near Oceania west of Irian Jaya retained contact and trade networks, some over large distances—for example, the *kula* ring in the Massim Archipelago of Papua New Guinea (Malinowski 1922) and the *sawei* tribute network in the Caroline Islands of Micronesia (Lessa 1950)—but were not significantly involved in the larger Asian world system. European contact and Christianisation, beginning in the 18th century, affected all Remote Oceanic societies to some degree, although most retained largely traditional lifeways until the Second World War (Denoon 1997).

1.6 Cultural evolution in the Pacific

1.6.1 Islands as laboratories

Goodenough, observing the linguistic and anthropological patterns in the Pacific, suggested that the advantage of studying cultural evolution in Oceania (i.e. the remote Pacific Islands) was the limited contact that those societies had with unrelated traditions. As such, all changes could be seen as elaborations of the parent culture, and systematic comparisons between populations could reveal important characteristics of ancestral “proto-cultures” (1957:153). Sahlins famously observed the Pacific islands to be a sort of cultural laboratory: an “extended series of experiments in cultural adaptation and evolutionary development … where culture so experiments, anthropology finds its laboratories—makes its comparisons” (1963:285). Indeed, the isolation provided by distance in previously uninhabited Oceanic islands might seem the perfect setting for studies of adaptive radiation (Simpson 1953), without the complications imposed by frequent contact, borrowing, or warfare. Similarly, Kirch stated that we might view islands as excellent “theatres” (1980:39) for the study of human-environment co-evolution. In the Polynesian case at least, a diversity of human cultural adaptations is derived from a common source population.

However, the idealised notion of closed, non-interacting populations on Oceanic islands has been dispelled by work in the last 25 years. The archaeology of trade items and raw materials (Weisler 1998), voyaging simulation (Irwin 1992), studies of borrowing in language and cultural traits (Tent and Geraghty 2004), and more sophisticated models of genetic interaction (Hurles et al. 2002; Lum et al. 2002) have shifted thinking away from the island laboratory model. Pacific peoples saw the ocean as a pathway, rather than a barrier, to interaction (Peoples 1993), although long-distance voyaging declined in Remote Oceania in the last 600 years (Rolett 2002). In addition, for Austronesian societies in Island Southeast Asia the island laboratory model has never been suggested; it is thus not appropriate to apply such a metaphor to the family as a whole.

1.6.2 Evolutionary approaches

A range of ecological environments is present in the Pacific: semi-continental landmasses, continentally derived islands, volcanic ("high") islands, and coral atolls (Thomas 1963). Across this range of environments, Austronesian-speaking peoples display significant variation in cultural diversity. For a number of years, evolutionary concepts have been used to describe this diversity (Goodenough 1957; Goldman 1970; Alkire 1974; Kirch 1984). Drift and founder effects have been used to describe the attenuation of linguistic forms from West to East across the Pacific (Elbert 1953; Blust 1981a). Frequently, aspects of social life have been described as adaptations to aspects of the environment. Sahlins (1958) examined levels of social stratification in Polynesia as adaptive responses to spatial and ecological features of atolls versus high islands. Extending this, Kirch (1980) modelled increases in social stratification as the outcome of population pressure and shifting cultivation. In the Caroline Islands, matrilocal residence and dispersed family settlements were related by Alkire (1974) to a pattern of multiple-crop subsistence; when economies were concentrated on a single crop other forms of social organisation emerged.

These authors and others (Hainline 1965; Goldman 1970; Kirch and Green 1997) viewed Oceanic and Polynesian societies as especially suited for comparative analysis because they represented closely related elaborations of a common ancestral tradition. Kirch and Green's reconstruction of Ancestral Polynesian Society is an exceptional application of the "triangulation" method (2001:42) in historical anthropology. They control for shared history with language phylogeny, and examine archaeological and ethno-historical data as well as proto-vocabulary to reconstruct aspects of ancestral Polynesian social structure, material culture, subsistence, ritual and ecology. However, theirs is a non-computational phylogenetic approach, without quantitative hypothesis testing.

Other projects attempt to relate the vocabulary of proto-languages to archaeological and ethno-historical evidence, for example, the Oceanic Lexicon Project (Ross et al. 1998, 2003; http://rspas.anu.edu.au/linguistics/projects/oceanic), which has used the linguistic comparative method to reconstruct aspects of Proto Oceanic material culture (such as sailing and fishing technology) and the physical world (such as concepts of time). Unlike material culture, many aspects of past lifeways—especially social structure—leave no direct evidence in the archaeological record. While some authors have extrapolated the post-marital residence patterns of past societies from floor plans of Chaco settlements (Peregrine 2001) such associations are highly inferential (Schillaci and Stojanowski 2003).

Linguistic reconstructions by analogy with ethnographic examples have been the primary means with which we can infer the social behaviours of ancestral Austronesian cultures. For example, Blust (1980) has inferred the existence of descent groups in the extra-Formosan AN languages. Similarly, Hage (1998) has used linguistic reconstruction to show how Proto Oceanic society was likely to have had senior and junior lines of chiefly authority. Building on this base, by using phylogenetic methods we can now statistically infer the ancestral states of Austronesian social systems, and test co-evolutionary hypotheses about the distribution of cultural diversity.

1.7 Austronesian kinship

1.7.1 Descent

Descent systems delineate which relatives an individual affiliates with most closely (Murdock 1949). Inheritance, rights and obligations, the regulation of marriage, and social and material assistance are all affected to some degree by kinship rules that stipulate who is and is not regarded as part of one's descent group. Virtually all types of descent organisation can be found amongst the Austronesian-speaking cultures of the Pacific (Table 1.2). Even on Taiwan, the consensus homeland of Austronesian expansion, there exists a diversity of descent systems spanning the range of cross-cultural variation (Mabuchi 1960). This diversity broadly reflects that seen worldwide (Murdock 1949) and thus Austronesian societies are a useful regional case with which to test hypotheses about the evolution of descent. Descent systems fall into two broad categories (Fox 1967; Holy 1996). *Unilineal* descent means that an individual is a member of one, non-overlapping kin group, traced through either their father's male ancestors (patriliny) or their mother's female ancestors (matriliny). *Non-unilineal* descent (also called cognatic) occurs when individuals trace kin relationships in overlapping kin groups, and can be through ancestors of either sex. Bilateral and ambilineal systems fall under this heading.

Table 1.2. Variation in descent systems for 101 Austronesian societies described in the *Ethnographic Atlas*. Data are taken from variable 43, "major type of descent".

Descent type	Description	Frequency
Patrilineal	Affiliation with kin of both sexes through men only	.22
Matrilineal	Affiliation with kin of both sexes through women only	.23
Duolateral	Affiliation with mother's matrilineal and father's patrilineal kin	.08
Ambilineal	Affiliation with kin through either men or women; some kinds of relations may exist on both sides, e.g. land rights vs. succession to office; individuals may "choose" their affiliation	.25
Bilateral	Affiliation with both mother's and father's kin	.23

1.7.2 Residence

Individuals are generally affiliated with some descent group at birth, but newlywed couples face the choice of determining with whom to live, and consequently to which group their children will belong. Thus, post-marital residence rules are related to a society's descent system. Patrilineal descent usually occurs with patrilocal residence, where the wife lives with the husband's kin; this pattern is the most common worldwide (Murdock 1949:38). Similarly, matrilineal descent usually occurs with matri- or avunculocality (residence with the maternal uncle of the husband). However, while descent and residence rules often co-vary together, they do not do so systematically.

1.7.2.1 Parental investment

Descent and residence rules stipulate where parents may allocate their resources, such as rights to land or the labour of their offspring. Accordingly, the principles of parental investment theory (Trivers 1972; Clutton-Brock 1991) may be productive for examining descent and residence variations, especially if these systems are adaptive responses to other aspects of the social or ecological environment. For example, Holden et al. (2003) used comparative methods and demographic data as evidence that the evolution of matriliny among Bantu cultures was an example of daughter-biased parental investment. While the focus of this thesis is on group-level norms rather than on individual behaviour, where it is appropriate to do so the results are cast in terms of parental investment theory.

1.7.3 Previous work

Previous studies have attempted to account for variation in Austronesian descent and residence by conjecture about the ancestral state of descent systems. Murdock (1949: 349) concluded based on kin terminologies that early Austronesian societies were bilateral and lacked clear lineages. In the 1950s, debate focused on the preponderance of cognatic or bilateral descent systems in Pacific societies and the difficulty of applying the strict lineal models that had been developed with success in Africa to the Oceanic case (Davenport 1959; Firth 1957; Leach 1962). Ethnolinguistic work since that time has suggested that ancestral Austronesian societies may have had unilineal descent groups with respect to land tenure (Goodenough 1955; Blust 1980; Pawley 1982), and ancestral Oceanic societies may have had a “matricentric orientation” (Burton, Moore, Whiting, and Romney 1996; Hage 1998, 1999; Hage and Marck 2001, 2003). Despite a great degree of descriptive work on the matrilineal societies in the Austronesian family (e.g. Malinoskwi 1929 and Weiner 1976, 1988 on the Trobrianders; Goodenough 1951 on Chuuk; Chowning 1958 on the Lakalai; Petersen 1982 on Ponape; Kahn 1980 and Sanday 2002 on the Minangkabau), no tests of evolutionary hypotheses have been published. While Pacific cultures were included in the worldwide analyses of matriliny by Aberle (1961), there are no systematic cross-cultural studies of the determinants of descent and residence in Austronesian cultures. This thesis aims to begin addressing these questions, with particular reference to the evolution of matriliny.

1.8 Structure of the thesis

Chapter One has introduced the theoretical foundations for the phylogenetic approach to cultural evolution, and covered some of the main debates that background this type of research. The ethnographic context of the Austronesian language family of the Pacific has been described with especial references to debates about prehistory and colonisation, as the analyses to come in later chapters speak to these issues of origins and migrations. As a whole, the thesis has three main themes: cultural diversity, cultural transmission, and cultural adaptation, and these are explored in the following chapters.

Chapters Two and Three are methodological in focus. Phylogenetic tree-building methods have been successfully applied to data from a number of language families, and provide us with a model of population history with which to test hypotheses. In Chapter Two, I describe the language tree-building process in general, and elaborate on new Bayesian likelihood methods for estimating phylogenies. This chapter contains empirical results as well. Specifically, I describe the Austronesian language data set, describe the construction of both parsimony and Bayesian likelihood trees, and present the results of these phylogenetic analyses in the context of Austronesian linguistic and archaeological hypotheses.

The phylogenetic comparative method is the focus of Chapter Three. Here I elaborate on the need to control for historical relationships in comparative analyses, and compare parsimony- and likelihood-based methods. Bayesian likelihood methods have a number of advantages over other approaches and this brief chapter covers these points. Bayesian comparative methods do not just test for adaptive correlated evolution between two traits, but can reconstruct ancestral states, estimate the best model of the evolutionary pathway and determine the order of change in the traits, and allow us to estimate the rates of change over different time periods. All of these features work while allowing us to estimate the degree of uncertainty in our models.

Chapter Four examines cultural transmission between societies on a large scale. Here, I take a number of approaches to examine if certain types of cultural traits preferentially follow either a phylogenetic or geographic mode of transmission. Using data on 74 cultural traits from Murdock's (1967) *Ethnographic Atlas* across 80 Austronesian societies, I use partial Mantel matrix tests to correlate matrices of cultural, linguistic, and geographic distances. Using logistic regression models, I test if geographical or phylogenetic "nearest neighbours" (estimated using a comparative method) have more of an effect in producing patterns of cultural similarity. Both sets of analyses show that phylogenetic and geographic transmission are associated with broadly different classes of cultural traits, but that individual traits may be best predicted by specific models of transmission.

The next two chapters turn to individual cultural traits, specifically, the evolution of kinship patterns. In Chapter Five I use a Bayesian comparative method to reconstruct the ancestral states of descent systems and post-marital residence patterns in 67 Austronesian societies. Descent and residence are coded a number of ways in order to tease apart how these forms of social organisation have evolved and infer what type of kinship system is ancestral to this group of cultures. The hypothesis that Proto Oceanic, and possibly Proto Austronesian society, was matrilineal/matrilocal is tested. Bilateral kinship characterises the earliest parts of the tree, with lineal systems developing later. Matrilineal organisation for Proto Oceanic is supported by the data. Results show that descent and residence are labile cultural traits with many changes apparent over the phylogeny. For these Austronesian societies, flexibility in residence is an ancestral trait.

Chapter Six tests two models of correlated evolution. The first, Murdock's (1949) "main sequence theory", states that changes in residence precede changes in descent. Using a comparative method that allows us to test for the direction of evolutionary change, I found strong evidence for the main sequence model. Additionally, by relating the results to archaeological time, I obtained estimates of the rate of cultural change in these kinship traits. The second model was an hypothesis that matriliny is an adaptive response to conditions of male absence, specifically, high dependence on male fishing. There was no evidence for correlated evolution between the two traits, although there was evidence that transitions to matriliny in the presence of high fishing dependence occurred quicker than other evolutionary changes. Additionally, by using a phylogenetic comparative method to control for the non-independence of related cultures, the results in this chapter ran counter to the results obtained by conventional tests of association, underlining the importance of taking a phylogenetic approach in cross-cultural studies.

Chapter Seven investigated the relationship between population size and the amount of language change, drawing on theory from population genetics. Estimating the amount of linguistic change since the break-up of Proto Austronesian directly from the phylogeny of 67 languages, I correlated this with estimates of the number of speakers (population size) of each language. Conventional correlation analyses returned a strong association that suggested that as population size decreased, linguistic innovation increased. However, with a comparative method to control for evolutionary relationships, the correlation disappeared. Scaling parameters in the comparative method revealed intriguing differences in the evolutionary trajectories of the two traits; population size was following a punctuational, random drift model of evolution, while lexical change had a directional aspect and could be described by an adaptive radiation model. Applications of "power law" models further showed that population size conformed closely to a neutral model of change, while language change diverged from the power law.

Each chapter has a stand-alone discussion and conclusion section, but in Chapter Eight I present brief remarks that draw together some of the themes emerging from the thesis. Together, the results demonstrate and validate the use of phylogenetic comparative methods on cultural data and questions. That validation, in particular, comprises the substantive contribution of this thesis to anthropological knowledge.

CHAPTER TWO

PHYLOGENETIC METHODS AND AUSTRONESIAN LANGUAGE TREES

2.1 Summary

Phylogenetic tree-building methods for cultural evolution are introduced. Phylogenies of human populations can use molecular data or traditional classifications from historical linguistics. Language data is also appropriate for computational phylogenetic analysis, as evidenced by a number of recent studies. Methods of tree-building include parsimony, likelihood, and Bayesian methods: all are described with an emphasis on Bayesian methods. The results of two phylogenetic analyses are presented: (i) a parsimony tree of 80 Austronesian (AN) languages and (ii) a consensus tree from a 1000-tree sample using Bayesian likelihood methods on 67 AN languages. Both phylogenies recover standard subgroups of the AN family, although the Bayesian analyses outperform parsimony. The tree topologies are discussed in relation to other work and linguistic hypotheses.

2.2 Introduction

2.2.1 Phylogenetic methods

Phylogenetic methods in evolutionary biology fall into two broad categories. First, there are *tree-building methods* used to create models of the descent relationships between taxa (e.g. species or organisms; in cultural evolution taxa refer to cultures, languages, or archaeological/material culture assemblages). A phylogeny is an hierarchical branching diagram—an evolutionary tree. Second, there are *comparative methods* that use these trees to control for the effects of shared descent, and allow us to ask comparative, co-evolutionary questions. Tree-building thus precedes the use of a comparative method. In this chapter I discuss phylogenetic methods and how they are applied to linguistic and cultural data; the next chapter covers comparative methods.

2.2.2 Phylogenetic trees of human populations

All tree-building methods use the information about variety in distributions of organisms in order to infer their evolutionary past. Biologists use genetic, morphological, and behavioural data to construct species phylogenies. Within-species, genetic markers that change rapidly (e.g. non-coding or non-recombining parts of the genome such as microsatellites or the non-recombining portion of the Y-chromosome) need to be chosen to resolve population-level branching patterns. Phylogenies of human populations using genetic markers or sequences have provided useful information on population history (Cavalli-Sforza et al. 1994) and have demonstrated that genetic and cultural histories may follow similar trajectories on a worldwide scale (Cavalli-Sforza et al. 1988; Penny et al. 1993). At a regional scale, mitochondrial and Y-chromosomal data—both non-recombining loci with the advantage of smaller effective population sizes and thus a greater chance for population differentiation—have provided the basis for the majority of genetic studies of human population dispersals and movements in prehistory. For example, Hurles et al. (2003) review studies in Oceanic molecular anthropology that cover broad-scale population movements across the Pacific, the sex-specific patterns of male and female markers, and the identification of European mitochondrial lineages in Polynesian populations. However, molecular studies of human populations are intraspecific, that is, they concern taxa which are not reproductively isolated, and even small amounts of gene flow can disrupt the assumptions of a phylogenetic method.

2.2.3 Language phylogenies

Languages can also be used to infer phylogenies of human populations. It appears legitimate and in many cases preferable to investigate cultural evolution with a linguistic phylogeny for a number of reasons. Linguistic change operates on the appropriate time scale to examine cultural evolution, and provides resolution at a greater society-level scale than does genetic data. Even fast-evolving sequences such as the control region of mtDNA only change at a rate of ~1% per generation (Parsons et al. 1997). “Leakage” of genes between populations entails minimal transfer of cultural information. While recessive alleles can invade and be maintained in a population at low levels through a single instance of gene flow, language traits such as words or sound changes require usage to transmit them throughout the population and/or into the next generation. Thus, language change generally involves deeper cultural exchange, as sociolinguistic mechanisms such as conformist transmission may tend to keep a cultural group and their language much more in tandem through time and space. Linguistic data is cultural by nature and can reveal historical information through reconstruction of proto-terminology (Kirch and Green 2001). Finally, unlike genetic data, linguistic information is available for virtually all societies, and coarse level classifications are easy to obtain from sources such as the *Ethnologue* (Gordon

2005). Even these non-quantitative classifications can provide a minimum but desirable level of phylogenetic control in cross-cultural studies.

2.2.4 Historical linguistics

The field of historical linguistics has traditionally used its own "Comparative Method" (not to be confused with the method of the same name in biology) to establish linguistic family relationships (Trask 1996). Shared innovations, such as regular but unusual sound changes, features of morphology and phonology, grammar, and lexical items, are clustered into sets of nested relationships and used to subgroup languages and reconstruct proto-terminology. Words or other structures that are presumed to derive from the same source are termed *cognate*. Whilst the linguistic comparative method is a careful technique, it is arduous and recursive, and lacks any explicit optimality criteria to judge from among equally possible family trees. The field of *lexicostatistics* was an attempt to quantify aspects of historical reconstruction by using the percentages of core vocabulary terms shared between pairs of languages to construct distance matrices, and from these produce tree diagrams (Swadesh 1972; Dyen 1975). Lexicostatistics resembles the phenetic approach in biological systematics, where overall similarities in groups of organisms are used to construct first a distance matrix, and then from this matrix a phylogeny (Wiener 1987). Like the phenetic approach, lexicostatistics suffers from a number of flaws, most notably the use of overall linguistic similarity rather than shared innovations (Bergsland and Vogt 1962). Blust (2001) offers an up-to-date critique of lexicostatistics and glottochronology, a related method that attempted to date language splits by applying a decay function to linguistic distances. Slowly evolving languages may be erroneously grouped together if they retain many features of the ancestral proto-language. Most crucially, measures of divergence must concentrate on shared derived characters (new innovations) rather than shared retentions. A famous case of how the lexicostatistical approach deals unsuccessfully with language classification through precisely these failings comes from the Pacific. Dyen's (1963) application of lexicostatistics to the Austronesian family indicated that languages spoken around Island Melanesia were the most divergent. From this, Murdock (1964) extrapolated a complicated readjustment of Pacific culture history, postulating that the early Malayo-Polynesians voyaged towards the fringes of Southeast Asia from Island Melanesia, borrowed root and tree crops and other aspects of agriculture from those inhabitants, and then turned back eastwards across the Pacific towards Polynesia, distributing their new food technologies as they progressed. Even at the time, this scenario conflicted with theories that derived the Austronesian people and their cultural complex from Southeast Asia.

2.2.5 Computational methods for language phylogenies

Considering the above limitations in historical linguistics, numerous authors have advocated the application of phylogenetic tree-building methods to linguistic data (Ruvolo 1987; Wiener 1987; Mace and Pagel 1994; O'Hara 1996; Atkinson and Gray 2005). Constructing an evolutionary tree is a combinatorial problem of great difficulty: how should the nested hierarchies of relatedness be organised to best account for the data? For a given number of taxa the number of rooted bifurcating trees increases rapidly: at only 10 languages there are 34 million trees to consider (Felsenstein 1978). Above about 20 taxa enumerating all possibilities is computationally impossible, so we must use heuristic computer methods. Various algorithms for building evolutionary trees from comparative data on morphological or, more commonly, molecular data exist (Felsenstein 2003). Modern computational methods in evolutionary biology are typically implemented in computer programs such as *PAUP** (Swofford 1999) *Phylip* (Felsenstein 2005) and *MrBayes* (Huelsenbeck and Ronquist 2001).

2.2.6 Survey of studies

Recently, these methods have been applied to linguistic data from diverse families: Gray and Jordan (2000) on Austronesian, Dunn et al. (2005) on New Guinea languages, Atkinson (2006) on Mayan, Holden (2002) on Bantu, and Ringe et al. (2002), Rexova, Frynta, and Zyzavy (2003), and Gray and Atkinson (2003) on Indo-European. In addition to recovering phylogenies that agree with traditional linguistic classifications, Holden (2002) and Gray and colleagues have shown that their linguistic phylogenies fit well with archaeological data concerning farming and agriculture-related population dispersals. This is not merely impressionistic scenario-matching but rather statistical testing of dispersal hypotheses, enabling different models to be weighed against the evidence. Table 2.1 is a survey of published studies that have used different phylogenetic methods on linguistic data.

Table 2.1. Survey of published linguistic phylogenies that have used computational phylogenetic methods.

	Language family	**Data (taxa)**	**Conclusions**
Parsimony methods			
Gray and Jordan 2000	Austronesian	Lexical (77)	Concordance with linguistics and archaeology
Holden 2002[1]	Bantu	Lexical (65)	Concordance with linguistics and archaeology
Rexova et al. 2003[1]	Indo-European	Lexical (84)	IE is tree-like, concordance with linguistics
Ringe et al. 2002[1] Nakleh et al. 2005[1]	Indo-European	Lexical, morphological, phonological (24)	Demonstration of “perfect phylogenetic network” methods
Dunn et al. 2005	Austronesian, Papuan	Typology (31)	Typological features could recover deep relationships
Likelihood/Bayesian methods			
Gray and Atkinson 2003[1]	Indo-European	Lexical (87)	Estimates of time depth
Gray and Greenhill 2005	Austronesian	Lexical (77)	Likelihood methods an improvement over parsimony methods
Rexova et al. 2005[1,3]	Bantu	Lexical, grammar (87)	Unorthodox scenario for Bantu expansion
Atkinson 2006[1,2]	Mayan	Lexical (35)	Highland origin for the Mayan Proper clade
Network methods			
Forster and Toth 2003	Indo-European	Lexical (13)	Early split of single Celtic branch
McMahon et al. 2005[1]	Andean languages	Lexical (19)	Quechua and Aymara similarities due to contact rather than descent
Bryant et al. 2005[1]	Indo-European	Lexical (84)	Borrowing in Germanic, IE is treelike
Ben-Hamed 2005 Ben-Hamed and Wang 2006	Chinese dialects	Lexical (24)	Parsimony outperforms lexicostatistics, dialects are not tree-like
Holden and Gray in press[1,4]	Bantu	Lexical (95)	Extensive borrowing amongst East African languages

1. Swadesh 100 or 200-word list.
2. Unpublished data.
3. Parsimony methods also used.
4. Likelihood/Bayesian methods also used.

2.2.7 Algorithms for inferring evolutionary trees

These studies have demonstrated the validity of phylogenetic tree-building using lexical data with both of the most popular optimality algorithms, *maximum parsimony* (MP) and *maximum likelihood* (ML). Parsimony methods find the shortest tree: the phylogeny that requires the smallest number of evolutionary changes to account for the data. In contrast, likelihood methods calculate the likelihood of observing a particular set of data, given a tree and some explicit model of evolution (Felsenstein 1981, 2003; Page and Holmes 1999). Parsimony methods have been used more extensively in the past due to their intuitiveness and ease of implementation, but ML methods have gained increasing popularity in recent years as computing power, Bayesian estimation, and more explicit models of evolution have become available (Pagel 1999b; Huelsenbeck, Ronquist, Neilson, and Bollback 2001). In particular, likelihood methods outperform parsimony when characters have unequal rates of evolutionary change (Kuhner and Felsenstein 1994), which is very likely to be the case in linguistic evolution (Blust 2001). Computer programs implementing phylogenetic methods allow linguistic phylogenies to be assessed statistically with a variety of measures: the goodness-of-fit of the data, the amount of support for branches and/or nodes, comparisons with other trees, and estimates of uncertainty in reconstruction.

	Head	waves	thunder	eye	three
Tongan	'ulu	*peau*	*mana*	mata	tolu
Samoan	ulu	galu	faititili	mata	tolu
Maori	*matenga*	ngaru	whaitiri	mata	toru

Character →	1	2	3	4	5
Tongan	0	0	0	1	1
Samoan	0	1	1	1	1
Maori	1	1	1	1	1

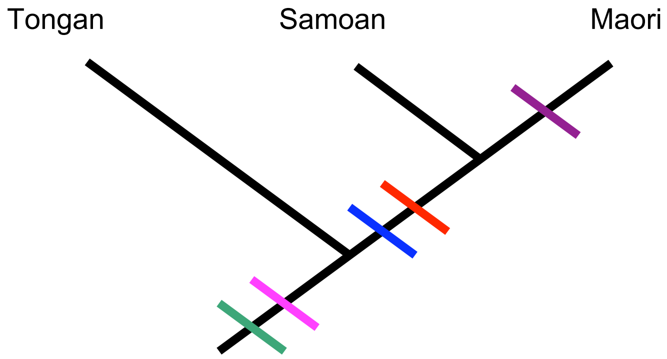

Figure 2.1. Basic principles of computational linguistic phylogenetics, showing how a tree diagram can be inferred from a set of words with the same meaning across different languages. **Top**. A wordlist for three languages. Terms that have been determined to share a common ancestor (by virtue of rare but recurrent sound changes, for example) are termed *cognate*. Non-cognate terms are italicised. Data can also be typological or grammatical as well as lexical. **Middle**. Cognate terms converted into a binary matrix. **Bottom**. Tree diagram found by parsimony (i.e. by minimising the number of evolutionary changes) with changes shown on branches. The linguistic Comparative Method will derive a tree without an explicit statistical optimality criterion such as parsimony. Lexicostatistics will construct a “percentage shared” distance matrix of the characters without discriminating between shared innovations (characters 1–3) and shared retentions (characters 4 and 5).

2.2.8 Non-tree methods

Other programs such as *NeighborNet* (Bryant and Moulton 2004) and *SplitsTree* (Dress, Huson, and Moulton 1996) that do not require the data to be represented as a strict tree can explore and reveal reticulation (borrowing) in linguistic data (Jordan 1999; Ben Hamed 2005; Bryant, Filimon, and Gray 2005; Holden and Gray, in press). Thus, the common criticism that language (and cultural features in general) do not evolve in a strictly tree-like fashion can be explored with network models. For example, in a study of Micronesian and Polynesian languages, the SplitsTree method revealed borrowing between Ponape (a Micronesian language) and Kapingamarangi (a Polynesian “Outlier” atoll geographically located in Micronesia) to be responsible for homoplasy in the language data (Jordan 1999). While network methods can be useful tools for examining assumptions about the tree-ness of the data and can help identify sources of reticulation and homoplasy, statistical tests of significance regarding tree-ness are still being developed. Present comparative methods, however, require a strictly branching phylogeny to proceed.

2.3 Bayesian methods

2.3.1 Bayesian inference of phylogeny

Comparisons of ML and MP approaches suggest that under many conditions both methods perform similarly and return concordant topologies, although ML is coming to be preferred (reviewed in Archibald, Mort, and Crawford 2003; Steel and Penny 2000). Likelihood frameworks have many advantages over parsimony: they use more information in the data (e.g. branch lengths) and they can incorporate more explicit and complex models of evolution such as rate heterogeneity (Pagel 1999b). However, ML methods are hampered by computational inefficiency when dealing with taxa numbering over about 20. Recently, Bayesian methods have been proposed as a new approach (Rannala and Yang 1996; Larget and Simon 1999; Huelsenbeck et al. 2001). Bayesian inference is a statistical approach where the model of evolution and the model parameters are treated as random variables, and the data treated as fixed observations (Ronquist 2004). In a Bayesian analysis, we update a prior belief regarding the model and its parameters to a posterior belief once the model and parameters have been applied to the data (Pagel and Meade 2005).

Applied to the phylogenetic context, these methods simulate a "universe of trees" which can be sampled to obtain phylogenies in proportion to their likelihood, and crucially, incorporate the Markov Chain Monte Carlo algorithm, which allows likelihood methods to be computationally tractable on large data sets (Archibald et al. 2003). These methods differ from other approaches in that they incorporate uncertainty about the phylogeny by approximating a probability distribution of trees rather than returning a single, optimal tree. This is especially important in comparative analyses, where any investigation of correlated evolution may depend on the particular phylogeny being used, for rarely do we know the true phylogeny without error (Felsenstein 1988). For example, Ronquist and Liljeblad (2001) investigated the evolution of gall wasps and their host-plant associations by mapping characters onto a large sample of trees from a parsimony bootstrap analysis, finding that their results contradicted many previous hypotheses about the ecological relationships of these insects.

Phylogenetic uncertainty as a source of error can be addressed using more than one tree in an analysis, but ad-hoc sets of most-parsimonious trees or random samples do not provide a statistically principled way to address the problem. *Bootstrapping* techniques are resampling-with-replacement methods, and can assess the uncertainty of an estimate of the phylogeny (Felsenstein 1985, 2003), but they can be computationally arduous in a likelihood framework. Bayesian methods offer a workable solution.

2.3.2 Markov chain Monte Carlo

Bayesian tree-building methods employ a Markov chain Monte Carlo (MCMC) algorithm to take a “random walk” through a parameter space (“treespace”) that approximates a probability distribution. Markov models use a rate matrix *Q*, which describes the transition between states of the data (in binary coded language models, the change from 0 →1 and 1→0) in an infinitely small period of time. To gain the transition rates for a given data set, the rate matrix is integrated over time as *P(t)*, and this matrix is used to estimate the transition rates for the observable data (Pagel 1994; Rohnquist 2004). Each step in the walk, or chain, involves a random modification of a parameter(s) such as topology or branch length. Periodically, we sample these values and for each step the posterior probability is calculated. If this is larger than the prior probability (a value specified by our model), the step is taken. If smaller, then the action depends on the ratio of the new to the current posteriors. The Markov chain thus only jumps to a new state as a function of the current state (Pagel and Meade 2005) and does not, like parsimony, hill-climb along a gradient imposed by previous states. The chain thus visits areas of treespace in proportion to their posterior probability. Another way to think of the posterior probability of a tree is that it is that tree’s portion of the overall probability weighted by the prior beliefs (Pagel and Meade 2005). At length, the chain reaches an equilibrium distribution where it is not seeking an optimally best tree but is sampling better and worse trees into a sample used to approximate the posterior distribution of all trees.

2.3.3 Support for nodes: Posterior probability distributions

The posterior probabilities (for each node on each possible tree) are a good measure of nodal support and can be interpreted in a similar manner to the bootstrap in a parsimony analysis. For example, if 100,000 trees are visited and a group comes out as monophyletic 78,956 times, then that node has a posterior probability of 0.78956

(Lewis 2001). The tree sample can then be summarised to a single phylogeny by some consensus method that displays the prior probability for particular clades (roughly, their measure of support), or the tree sample used in further analyses. In a comparison of MP versus Bayesian likelihood methods on an Austronesian language data set, Greenhill and Gray (2005) found that Bayesian methods outperformed parsimony in reconstructing known linguistic subgroups, and concurred more closely with archaeological models of population dispersal.

2.4 Phylogenetic trees of Austronesian languages

2.4.1 Aims

In this section I describe the language data and tree-building methods used in this thesis. The results of the phylogenetic reconstructions are described with reference to previous findings and the linguistic literature.

2.4.2 Austronesian Comparative Dictionary

In previous work with Russell Gray at the University of Auckland, we obtained a database of Austronesian (AN) languages from Robert Blust at the University of Hawaii, the *Austronesian Comparative Dictionary* (ACD) (Blust n.d.). Blust estimated this to be approximately 25 percent complete. The ACD consisted of 5185 lexical items across 191 Austronesian languages and was organised so that separate entries consist of sets of cognate terms (cognacy judgements made by Blust) with the languages in which they appear. For the purposes of analyses, the presence of a language in a cognate set was coded as “1” in a languages x words matrix. If a language was not in a particular cognate set, that language was coded as “0”. Thus the ensuing data matrix represented presence/absence coding, with cognate words sharing the character state “1”.

Using 77 of these languages, we conducted a number of investigations investigating the feasibility of applying phylogenetic parsimony methods to linguistic data (Jordan 1999; Gray and Jordan 2000). Figure 2.2 shows a representative language phylogeny obtained in these analyses. This language data set was an unrestricted set of the lexicon, contrasting with the basic vocabulary of 100- or 200-word lists (Swadesh 1951) used by authors of other published linguistic phylogenies.

2.4.3 Austronesian Basic Vocabulary Database

More recently, Gray and colleagues have assembled a larger database of 467 languages, using the core vocabulary terms of the Swadesh 200 word list to produce a more representative and even sampling of both AN subgroups and cognate terms (Blust, Gray, and Greenhill, 2003–2005). This *Austronesian Basic Vocabulary* (ABV) is available online at http://language.psy.auckland.ac.nz/austronesian and, as at January 2007, comprises 98,887 entries. Coding methods remain as for the ACD, with binary cognate sets comprising character data. Other analyses have used multi-state "semantic slots" (Holden 2002; Ringe et al. 2002) where there may be many states across all languages for one term. However, it is easier to develop workable likelihood models of evolution for binary data (Pagel 1999, 2001), and binary-coded cognate terms represent discrete "low-level" evolutionary units without requiring further classification into more subjective hierarchical categories (Greenhill and Gray 2005).

Data entry and cognate classification in the ABV are ongoing collaborative projects with Pacific language scholars. The data used in this thesis was obtained from the database at four time points (1) June 2001 (the original ACD data set) (2) March 2005 (n=34) (3) January 2006 (n=80) (4) March 2006 (n=67). A number of analyses were run on more than one of these data sets. The final set of languages represented higher-quality coverage of all lexical items (R. Gray, personal communication), thus an improvement in data quality at the expense of a smaller sample size was made.

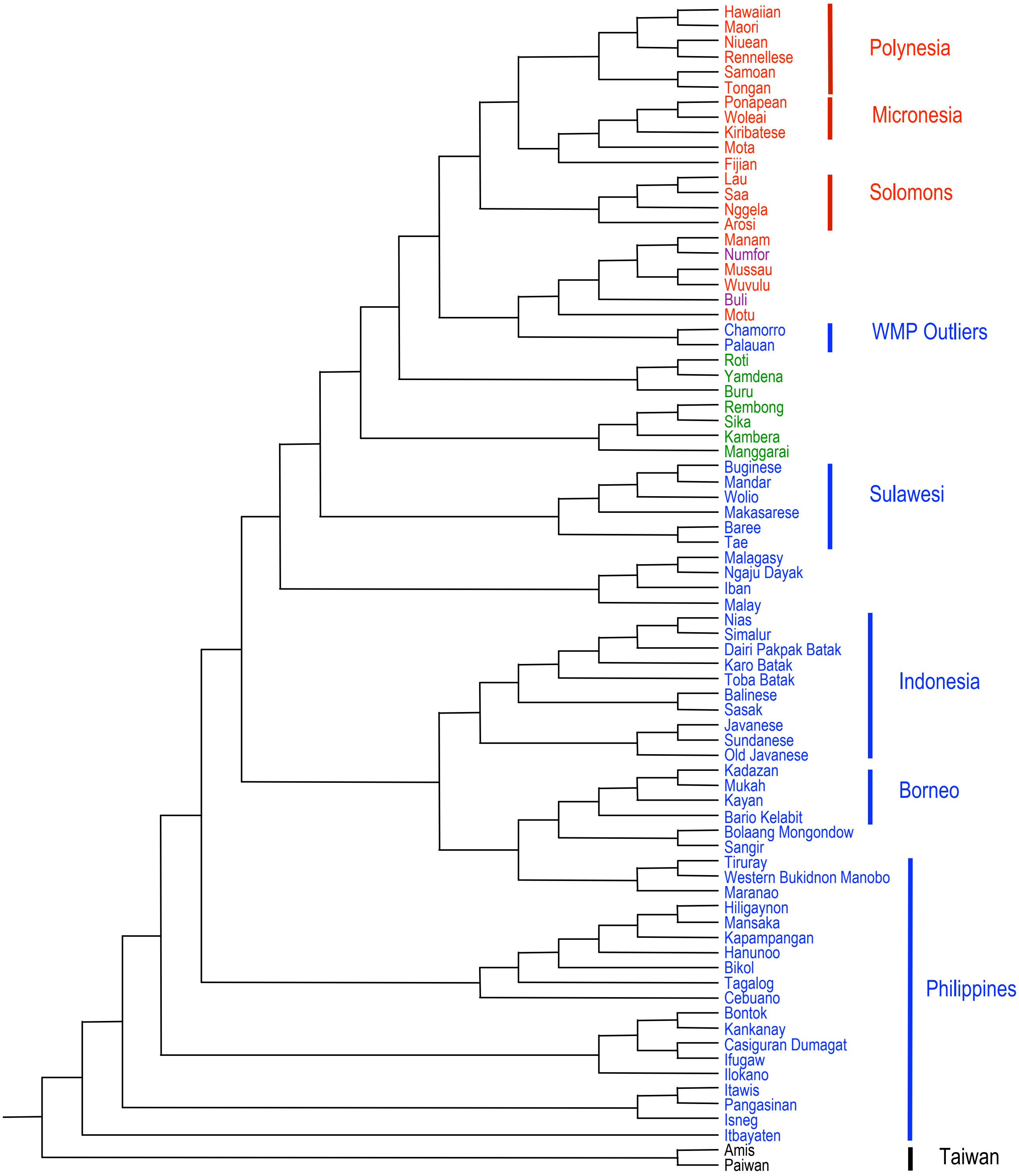

Figure 2.2. Shortest tree of 77 Austronesian languages found by parsimony analysis, from Jordan (1999) and Gray and Jordan (2000). High order subgroups are coloured as follows: **Formosan**, **Western Malayo-Polynesian**, **Central Malayo-Polynesian**, **South Halmahera-West New Guinea**, **Oceanic**.

2.4.4 Data used in this thesis

From the January 2006 set of 357 languages I extracted 80 languages that could be matched to cultures in the *Ethnographic Atlas*. This set of languages was used in the analyses in Chapter Four. There were 4435 cognates, of which 2307 were constant and 1163 were parsimony uninformative, leaving 965 parsimony informative cognates. From the final March 2006 data set I extracted 67 languages that could be matched to cultures in the EA and other ethnographic sources. There were 4289 cognates, and as this set of languages was used in Bayesian analyses, *all* characters are informative. This demonstrates how likelihood frameworks make greater use of the data than do parsimony approaches. The large number of languages compared favourably with other phylogenetic analyses in Table 2.1. Appendix A lists the languages and their matching cultures.

2.5 Tree searches using parsimony

2.5.1 Tree searches using parsimony: The 80-language data set

Linguistic trees were constructed with *PAUP* 4.0d81* (Swofford 1999) using heuristic search algorithms. Eighty taxa were added to the trees using 1000 random addition sequences, with TBR branch swapping used to bisect and rejoin subtrees in order to maximise the chance of finding the optimal trees (Kitching 1992). The Goloboff fit criterion, which weights characters according to their homoplasy (Goloboff 1993), was employed (kappa = 2). This method compares trees during the tree-search and gives more weight to characters that display less homoplasy. With the AN languages, such a weighting is preferred as the higher-order topology of the tree is very “rake-like” (Pawley 1997), with short internal branches (Gray and Jordan 2000) implying a rapid differentiation of the major language subgroups. There is thus bound to be some degree of homoplasy due to the asymmetric breaking of dialect chains (rather than the neat bifurcation of parent populations), and the Goloboff criterion helps us to reconstruct a tree that gives greater weight to non-homoplastic characters. Trees were rooted using the Formosan languages as an outgroup based on standard AN linguistic subgrouping hypotheses (Pawley and Ross 1995; Blust 1999).

2.5.1.1 Bootstrap analysis

Bootstrap analysis was performed on the language data using 100 bootstrap replicates and the search criteria above. The bootstrap is a resampling-with-replacement technique that indicates a conservative level of support in the data set for particular branches (Felsenstein 1985). The data is sampled randomly with replacement until it is the same size as the original data set, and then a tree is built from this new data set. A bootstrap value for a node can be interpreted as the percentage of sampling replicates in which a group of languages come together to the exclusion of all others. It can be compared to the node posterior probability under Bayesian tree sampling (see §2.6).

2.5.2 Results

A single best tree of tree length 4918 was found (Figure 2.3), and goodness-of-fit measures were calculated. The *consistency index* (*CI*) is a measure of homoplasy (characters that evolve on the phylogeny more than once), and is calculated by dividing the minimum possible number of steps by the observed number. A value of one represents no homoplasy. However, the *CI* is affected the number of taxa and characters, and is not independent of tree length (Farris 1989). The *retention index* (*RI*) is not so affected, and is derived by using a ratio that includes the minimum amount of change required by any conceivable phylogeny. For this phylogeny, the *CI* = 0.43 and the *RI* = 0.57. These values are within the range found by phylogenetic analyses of 21 cultural data sets (Collard et al. 2006), and are an improvement on the corresponding values (0.27 and 0.24 respectively) from earlier analyses on the ACD (Gray and Jordan 2000).

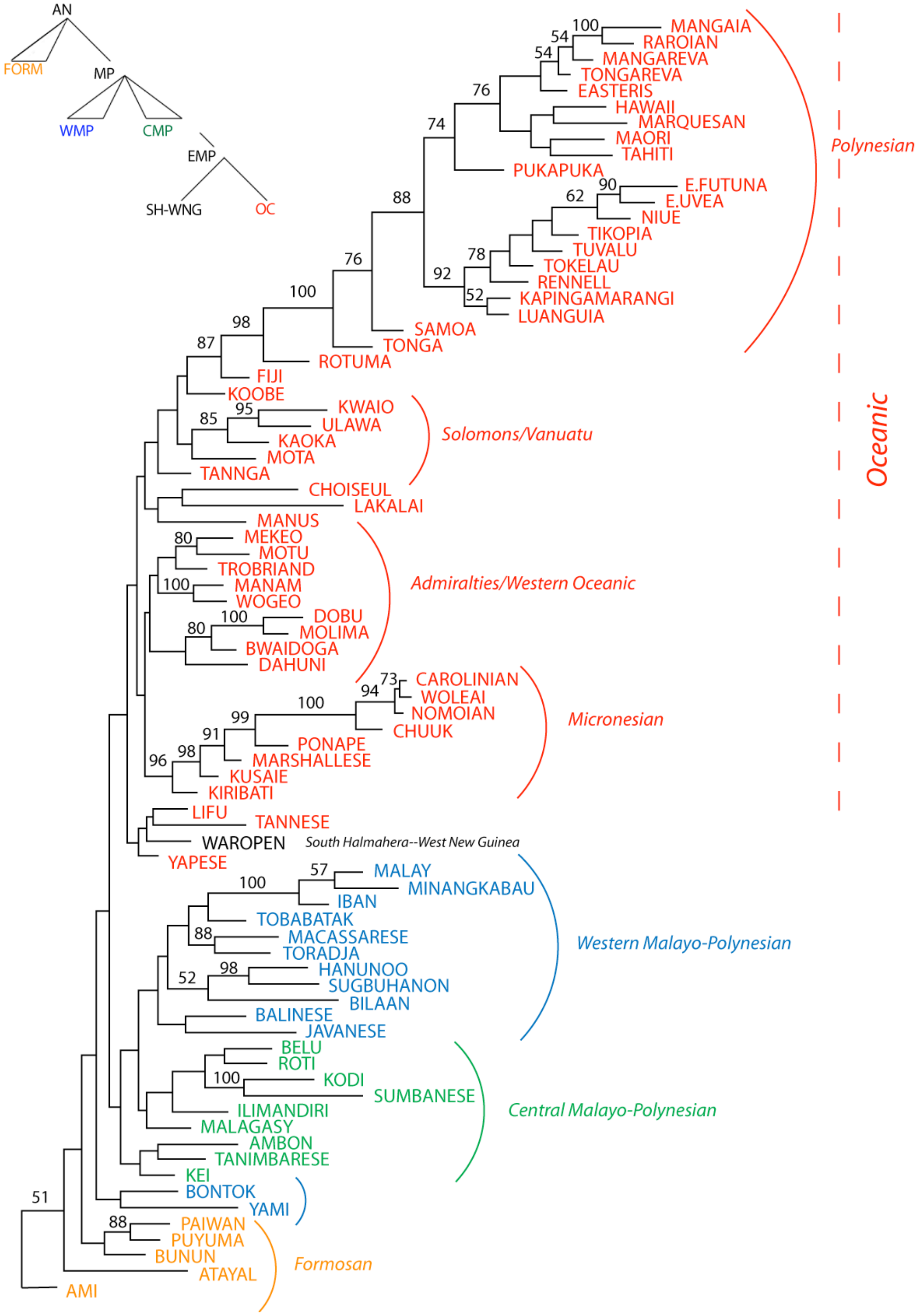

Figure 2.3. Maximum parsimony tree of 80 Austronesian languages. Numbers above branches are bootstrap values, indicating the percentage of times that a node was recovered in the 100 bootstrap replicates; these are only reported for values > 50. Language subgroups are colour-coded to reflect standard AN subgroups (top-left).

2.5.3 Tree topology

The tree corresponds to many of the major subgroups of the Austronesian language family (see top-left Figure 2.3 for traditional linguistic classification of AN). The Formosan languages are at the base of the tree. Neither the WMP or CMP languages fall out as an exclusive clade derived from a single common ancestor, that is, they do not display *monophyly*. This may reflect current thought that there is no strong evidence for either WMP or CMP as exclusive subgroups; they should be thought of as linkages (Blust in press) or as several primary branches of Malayo-Polynesian (Gordon 2005). The Sundic languages fall inside a group with languages from Sulawesi. This group also contains the Philippine languages, except *Bontok,* which groups more basally with *Yami* (spoken on Botel Tobago between the Philippines and Taiwan). The CMP languages constitute two separate branches whose members correspond to low-level subgrouping hypotheses (Tryon 1995). This is true of most of these WMP/CMP languages, except *Malagasy*, which should fall in with *Iban*.

An anomalous grouping of *Yapese*, a Micronesian language of contentious placement, the lone SH-WNG representative *Waropen*, and *Tannese* and *Lifu* is most likely a result of "missing cognacy" for these languages (S. Greenhill, personal communication). Thus, parsimony is able to group them within the Oceanic group but relegates them to the base, as the program will assume that their lack of cognacy with other languages indicates early branching.

Within the Oceanic languages several subgroups are recovered. The Micronesian languages form a monophyletic group, as do Central Pacific and Polynesian. The Polynesian languages contain an Eastern Polynesian clade (Marck 1999). The Southeast Solomon languages, along with *Mota* (Vanuatu) form a group. The remaining Western Oceanic and Admiralties languages are variably resolved, in accordance with the well-known "rake-like" structure of those parts of the Oceanic language family. In this situation, the bifurcating tree model appears least applicable due to a rapidly dispersing and unevenly-breaking dialect network (Ross 1997; Pawley

1997), and accordingly, the hierarchical arrangement of these languages is poorly supported by the bootstrap values. Overall, this tree contains many attested subgroups of Austronesian, recovers relationships of sister-taxa well, and is comparable to standard hypotheses in its outline. This phylogeny was used in Chapter Four as a model of population history.

A single phylogeny, however, cannot capture the degree of uncertainty that must necessarily be present in the historical relationships of human groups. The following section described and presents the results of Bayesian phylogenetic analyses that address this problem.

2.6 Tree searches using Bayesian methods

2.6.1 Bayesian estimation of phylogeny

A variety of computer programs for ML and/or Bayesian estimation of phylogeny have become available recently such as *MrBayes* (Huelsenbeck and Ronquist 2001) and *BAMBE* (Simon and Larget 2000). I used *BayesPhylogenies* (Pagel and Meade 2004; UNIX binary available at http://www.evolution.rdg.ac.uk/BayesPhy.html) to obtain a posterior probability distribution of trees under this method because the outputs were directly related to the comparative methods *BayesMultiState* (Pagel, Meade, and Barker 2005) and *Discrete* (Pagel 1994) that I used in later chapters. In addition, *BayesPhylogenies* contains models of evolution that have been developed for use on language data (M. Pagel, personal communication).

I used the Bayesian MCMC method in *BayesPhylogenies* to estimate a posterior probability distribution of trees. This is not a set of optimally likely trees, but rather a set of trees where topologies are represented in proportion to their likelihood—that is, they contain some low, some high, and some intermediate values of likelihood and the set is thus a distribution with likelihood on the x axis and frequency on the y.

2.6.2 Analyses

2.6.2.1 Initial Bayesian analyses

The 80 language data set was initially used to build language trees under various combinations of model parameters and outgroup designations (not shown). The great majority of the trees in the outcome of these analyses contained subgroups of languages in non-standard placements, such as the Polynesian languages at the base of the tree. In addition, single languages would “float” about the tree, showing no stability of placement. The improvement in data quality in the 67 language data set was demonstrated in greater stability of the major subgroups. This led to the decision to use the smaller sample size of 67 languages.

2.6.2.2 Models of word evolution and the choice of priors

The MCMC method can implement one of two different statistical models of word evolution for discrete binary characters (*BayesPhylogenies* software, http://www.evolution.rdg.ac.uk). These are based on those models used in papers describing the software (Pagel et al. 2004). M1P is a one-parameter model in which the rates of gain and loss of words are presumed to be equal. M2P is a two-parameter model where rates of gain and loss can be unequal, but can be computationally time-consuming with large data sets; therefore, M1P models were used preferentially. Word meanings were allowed to evolve at different rates drawn from a gamma distribution with four rate categories (Yang 1994). Base frequencies of the character states were estimated from the data.

The prior. In a Bayesian analysis, we calculate the posterior probability of the data given a tree and a model of evolution, but we require a prior belief about the probability of the tree and model parameters in advance. The choice of prior is a controversial aspect of Bayesian phylogenetic analysis as it can be regarded as subjective (Alfaro and Holder 2006). By using a *uniform* prior, all parameters and topologies are considered equally likely, introducing no further assumptions about the model of word evolution. The program routine is thus free to propose any combination of (for example) branch lengths and topologies on each step. Alternatively, we can specify a more informative prior if we have background information (Ronquist 2004), or we can use a non-uniform prior such as a probability distribution with a specified mean. Uniform priors were used in the generation of Bayesian tree samples[1], as they are effective when the phylogenetic signal in the data is strong (Pagel et al 2004).

2.6.2.3 Outgroup rooting

Old Chinese (a non-Austronesian language included in the ABV for comparative purposes) was initially used to root the tree, although this language could not be tied to a particular ethnographic source (Sagart 1993). Preliminary tree searches revealed that this choice of outgroup found trees in which the Formosan (Taiwanese) languages fell out basally, in accordance with standard Austronesian linguistic theory (Pawley and Ross 1993; Blust 1999). In two out of three tree searches the Formosan languages formed a monophyletic group and in the other *Atayal* and *Bunun* formed the first, post-*Old Chinese* branch. Sagart (2004) has recently suggested that *Atayal* may be the earliest branching of the Formosan languages in this data set, based on an hypothesis that early AN expansion took place counter-clockwise in a circle around Taiwan, starting from the north-east (2004:437). Tree searches where *Atayal* was used as a single language to root the tree produced phylogenies with peculiar arrangements of the Polynesian and WMP languages. As the analyses with *Old Chinese* had demonstrated their placement at the base of the tree, I used the five Formosan languages in the sample (*Atayal, Ami, Bunun, Paiwan,* and *Puyuma*) as outgroup taxa in all subsequent analyses.

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[1] In comparative analyses (Chapter Three) where signal is weaker due to fewer data points, an exponentially distributed prior was used on the assumption that very high rates of cultural change were not as likely as lower or moderate rates. This was a conservative assumption and did not affect the ancestral state reconstructions except to reduce uncertainty by small (<.10) amounts.

2.6.3 Results

2.6.3.1 MCMC sample

The Markov chain, the states of which are different phylogenies, started from a random tree and was sampled every 1000 trees. Four separate chains were run to ensure that the analyses converged to the same region of the space of possible trees. Chains were run for between 1 x 10^6 and 10 x 10^6 iterations. Each run included a "burn-in" period before the log-likelihood values converged on a fluctuating value (stationarity). Trees from the burn-in period were discarded from the sample, and the final posterior probability distribution (PPD) consisted of 1000 trees sampled every 2000 iterations from one of the post-convergence chains. The PPD is a distribution containing not only topologies of trees and their likelihoods, but is also a distribution of branch lengths and the other parameters, such as transition rates, estimated by the model of word evolution (Pagel and Meade 2005).

2.6.3.2 Autocorrelation

The degree of autocorrelation between successive trees in the probability sample was calculated in order to test for independence. When the chain is still in the convergence period, successive topologies should be increasing overall in their likelihood. Post-convergence trees and their likelihoods should wander about the likelihood surface without apparent pattern, and autocorrelation should thus be very close to zero. By plotting likelihoods against their iteration, autocorrelation can be calculated. Here, $r = 0.00037$. Figure 2.4 shows the convergence of the Markov chain from the random starting point towards equilibrium. The inset shows how the Markov chain wanders around the equilibrium point after convergence. The posterior probability distribution of the log-likelihoods that were sampled post-convergence is shown in Figure 2.5. The distribution is approximately normal with a mean of -51859.5 ± 23.82.

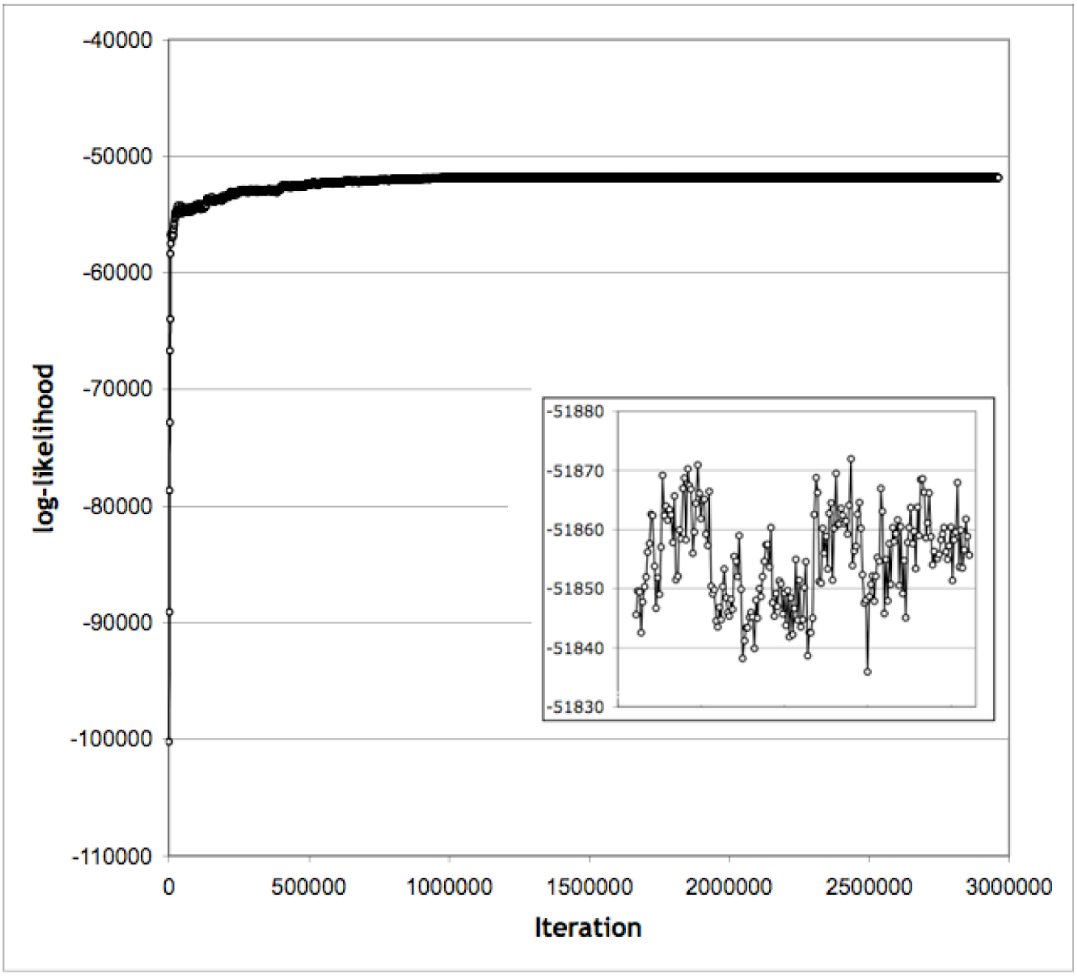


Figure 2.4. Convergence of the Markov chain through 3,000,000 iterations. The chain takes some time to reach stationarity, with the likelihood gradually increasing through the first million iterations. The inset shows a portion of the chain around 2.5 million iterations, demonstrating how the likelihood wanders up and down around a central tendency but does not show a directional trend.

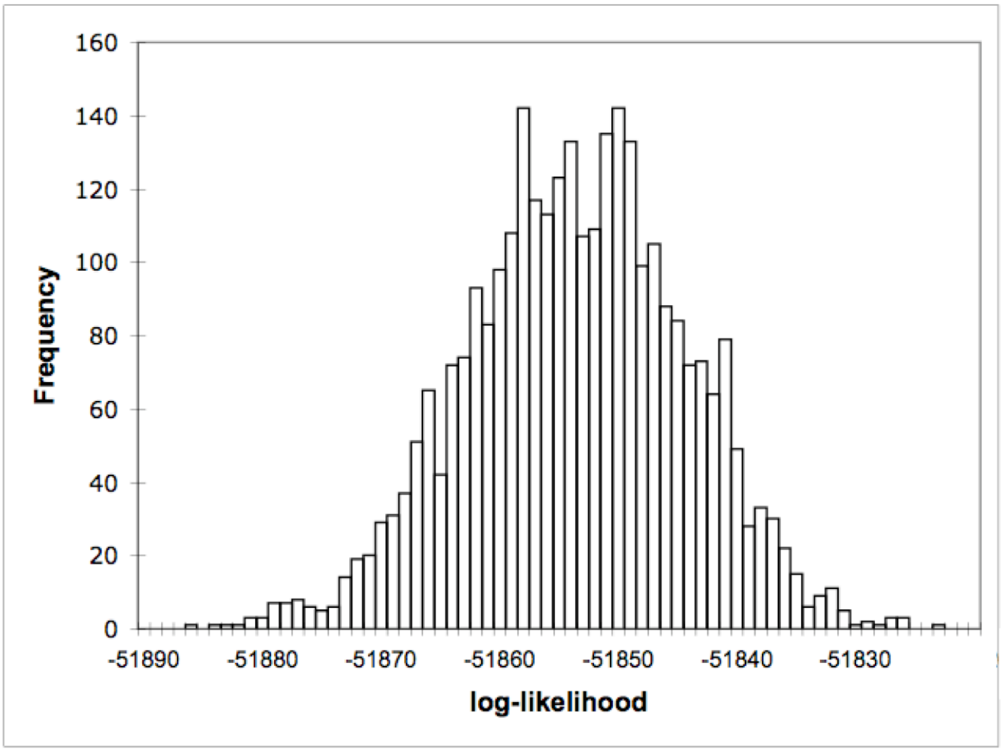


Figure 2.5. Posterior probability distribution of log-likelihoods in the 1000 phylogenetic trees sampled from the converged Markov chain. The distribution is effectively normal (kurtosis = -1.2, skewness = 0.000), with a mean of -51859.5 ± 5.52. The majority of the sample features trees of intermediate likelihood, with only a few very good or very poor likelihoods.

2.6.4 Bayesian phylogeny

The consensus linguistic phylogeny of 67 AN languages is shown in Figure 2.6. Consensus trees are not the “best” tree or even necessarily an actual tree present in the sample but rather display a summary of the nodes frequently found in the sample. Figure 2.7 shows six phylogenies drawn at random from the sample, to illustrate the range of variation within and to stress that the sample is a distribution. In Figure 2.6 each node is labelled with the posterior probability of that node—the probability that the node is true, given the model of evolution—and reflects the number of times a node appears in the sample. The node’s posterior probability is a measure of stability within the sample, not of confidence in general (Pagel and Meade 2005). That some of the nodes have a low posterior probability reflect the importance of using statistical approaches that take uncertainty about the phylogeny into account.

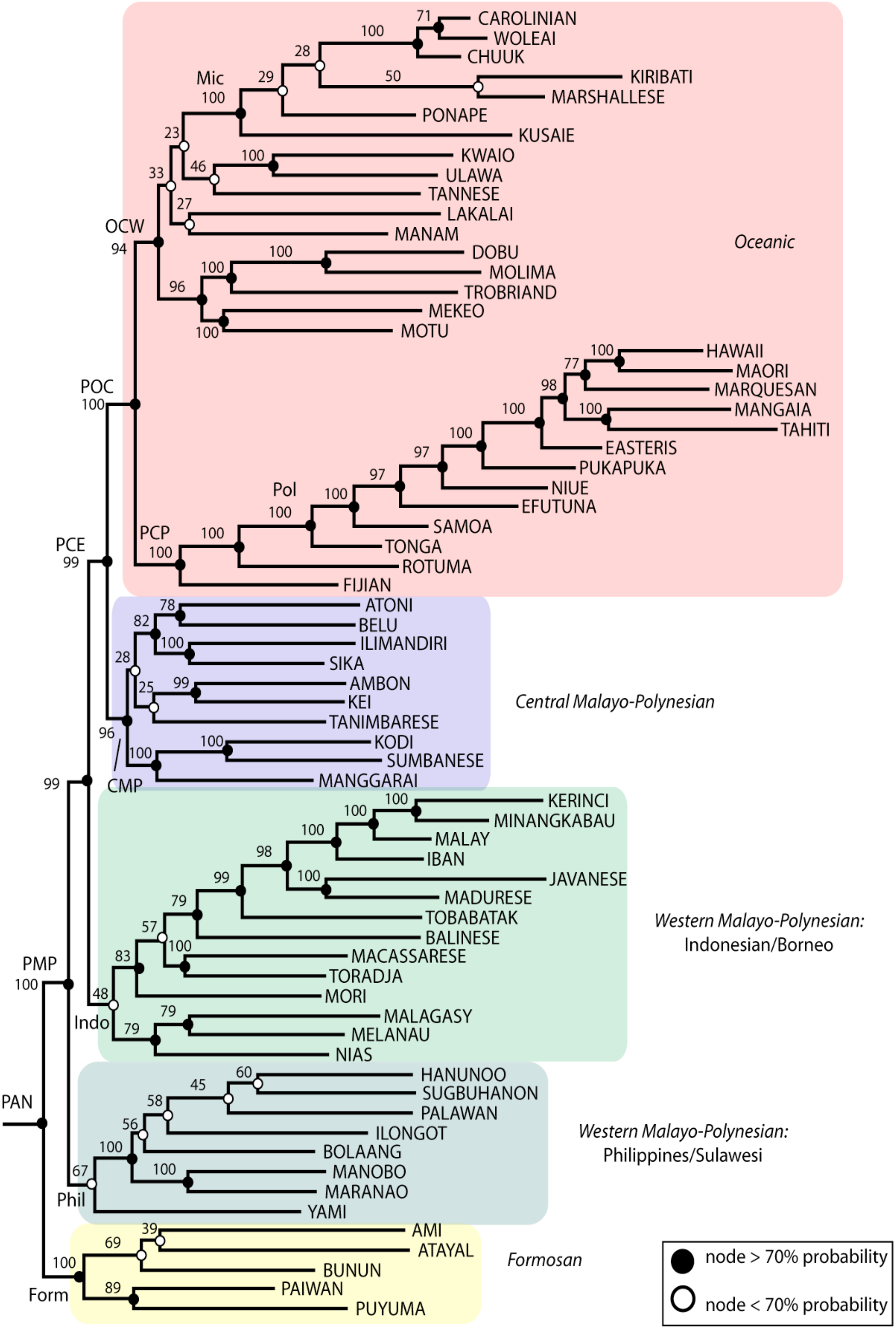


Figure 2.6. Consensus linguistic tree of the Bayesian 1000-tree sample. Full description follows on the next page.

Figure 2.6. (on the previous page). Consensus linguistic tree of the 1,000-tree sample, showing clades present in over 50% of the sample as well as those that do not conflict with the majority. Figures over branches correspond to the posterior probabilities of the nodes. A value of 100 indicates that a node appeared in every tree in the sample. Black circles indicate those nodes with a posterior probability distribution >0.70, a threshold for confidence in the existence of that node (Pagel 1999b), while white circles indicate a *PPD* <0.70. Nodes denoting language subgroups/proto-language stages are as follows: *PAN* Proto Austronesian, *PMP* Proto Malayo-Polynesian, *PCE* Proto Central-Eastern Malayo-Polynesian, *POC* Proto Oceanic, *PCP* Proto Central Pacific, *CMP*, Central Malayo-Polynesian, *Mic* Micronesian, *Pol* Polynesian, *Form* Formosan. Other nodes are labelled as: *Phil* Philippines/Sulawesi, *Indo* Indonesia *OCW* Oceanic-West.

Figure 2.7. (on the following page). Six trees drawn at random from the Bayesian sample of 1,000 trees in order to give an indication of the variation contained therein. Arrows indicate differences from the consensus tree in Figure 2.6, described for each tree as follows: (1) the clade of Ambon, Kei, and Tanimbarese is basal to the CMP group; (2) Micronesian and Polynesian are sister-clades; (3) the clade of Nias, Malagasy, and Melanau falls outside the Indonesian group; (4) Nias is basal to the Indonesian grouping; (5) Ponape groups with the western Micronesian languages (6) three different most-recent sister-taxa for Lakalai, Marquesan, and Hanunoo.

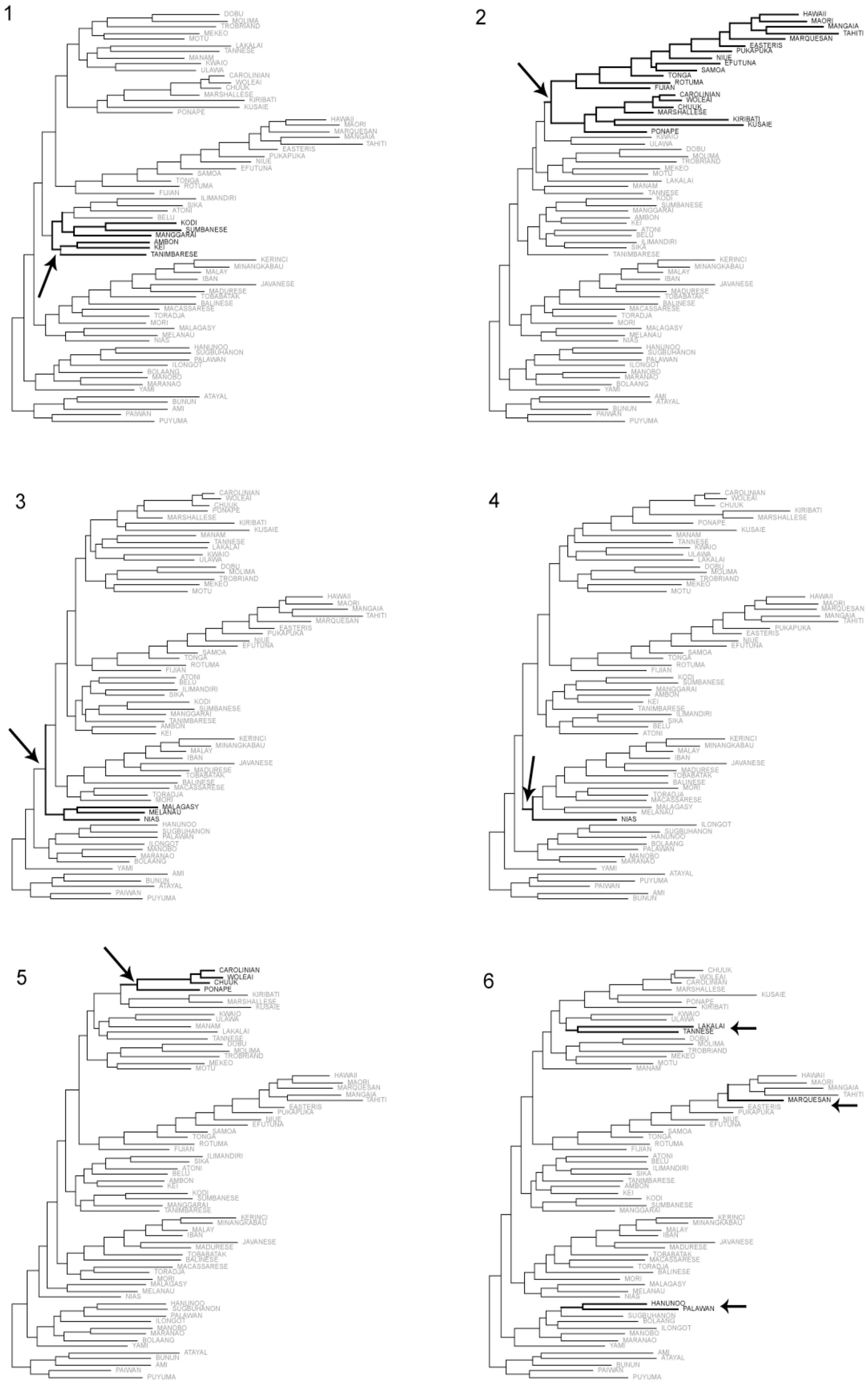


Figure 2.7. Six random trees from the Bayesian sample. Full description on previous page.

2.6.5 Topology

The consensus tree recovers all the major subgroups of the Austronesian language family (highlighted in coloured groups). The Formosan languages consistently divide into two groups that do not reflect any standard linguistic hypothesis, as Atayal groups with Ami and Bunun, rather than forming a basal branch (Blust 1999; Sagart 2004). This may, however, be an artefact of the artificial monophyly imposed by the outgroup method.

As in the parsimony analysis, the WMP languages do not fall out as a monophyletic group. Rather, they group into a well-supported clade (mean *PPD* = 67) of Philippine languages and a less well-supported group (mean *PPD* = 47) of Indonesian languages from Sumatra, Borneo, and Java. The Philippine languages (including *Yami*) fall out as monophyletic, a hypothesis supported by the majority of Austronesian linguists (Zorc 1986; Blust 1991) Within the second group, the Sundic languages including *Malay* fall out as an exclusive clade (mean *PPD* = 79), and the Sulawesi languages (*Macassarese, Toradja*) also come together consistently. The placement of *Malagasy* next to *Melanau,* spoken on Borneo, makes good sense, as Proto Malagasy is thought to have originated in Borneo c. 1200 BP (Dahl 1991). *Nias,* off the southeast coast of Sumatra, may have been excluded from the "linguistic levelling" that took place in many WMP languages through the last millennium (Nothofer 1990, 1991). This homogenisation may have been due to widespread trading networks and the influence of Indian, then Islamic influences (Bellwood 1997), as well as the growth of Malay and Javanese as a lingua franca. Thus, populations that were outside the central Indonesian sphere of interaction may group together simply due to shared retentions of earlier linguistic forms rather than reflect the budding off of daughter populations.

A Central-Eastern Malayo-Polynesian node is strong (mean *PPD* = 99), splitting into equally strong CMP (there are no SH-WNG languages in this sample) and Oceanic groups. Internal resolution in this group is fair at more recent levels, but only the Bima-Sumbanese clade (*Kodi*, *Sumbanese*, *Manggarai*) has good support. This is interesting, as evidence for the Bima-Sumba group has been called elusive by Blust (1993b).

The Oceanic group divides into two branches, one representing the Central Pacific group (Geraghty 1983) of *Fiji*, *Rotuma*, and the Polynesian languages and the other consisting of a strong clade of Western Oceanic (excluding *Lakalai*), Micronesian (whose internal relationships are not well resolved, though the clade itself has strong support) and uncertain arrangements of the other languages from Vanuatu, the Solomons, and the Admiralties. While the Eastern Polynesian subgroup appears as a clade, the internal structure of the Polynesian languages is counter to current hypotheses (Pawley 1996) that group Tongic languages (*Tonga* and *Niue*) exclusive of and basal to the rest, but supports the paraphyly of the other Nuclear (but not Eastern) Polynesian languages as Marck (1999) suggested. It may be that despite the long-standing cliché of the "island laboratory" model of cultural evolution in Polynesia, implying a bifurcating tree model and isolated populations, there is considerable evidence for language reticulation and contact amongst these populations. Preliminary analyses using network models show this to be true of both Polynesia and Micronesia (Jordan 1999; S. Greenhill, personal communication).

Overall the tree has short internal branch lengths, especially at the base of the tree, and longer terminal branches. This could imply that (i) much of the language evolution has taken place in terminal taxa, and relatedly (ii) that the language data contains many unique characters, (iii) that homoplasy and reticulation through, for example, the breaking of dialect chains, has led to conflicting signals in the data, or (iv) that dispersion of the languages was rapid enough for cumulative change along the deeper branches to be fairly minor. Most likely a combination of these factors will account for this topology. Factors (i) and (ii) are certainly an influence, as terminal branches are long, and approximately 10 percent of the characters are unique to a single language, while the presence of dialect-chain breaking in Oceanic languages is well-attested (e.g. Geraghty 1983; Ross 1997). Recent Bayesian analyses with the entire ABV data set (350+ languages) support the notion that rapid dispersion is a strong feature of these languages (R. Gray, personal communication).

2.6.6 Comparison with other results

Compared to the parsimony tree of 80 AN languages (§2.5), the consensus phylogeny of the 1000 tree sample is superior in two respects. Firstly, this Bayesian tree is more resolved, especially at deeper nodes, allowing us to have more confidence in the historical relationships indicated by the tree. The bootstrap and posterior probabilities of nodes are superficially comparable as measures of support, although they are not mathematically equivalent (Felsenstein 2003). Where comparable across trees, Bayesian posterior probabilities are virtually always higher than the corresponding bootstrap, although bootstraps are known to be conservative (Alfaro et al. 2003; Doaudy et al. 2003). For example, the parsimony analysis returned a bootstrap value of 76 for the Eastern Polynesian languages, while support was at 100 percent for the Bayesian posterior probabilities. Secondly, the phylogeny produced by this Bayesian analysis conforms more to standard linguistic hypotheses than does the parsimony tree.

Although the sample of languages differs significantly, the Bayesian analysis of the 77 ACD languages by Greenhill and Gray (2005) included most of the main subgroups of AN included here. Like here, they found high posterior probabilities for a Philippine subgroup, but no evidence for a monophyletic WMP group. They also recovered a well-supported Sundic group and probabilities approaching 100 on the Micronesian and Polynesian subgroups. With respect to topologies, Greenhill and Gray's trees show a similar pattern of some very short internodes and some longer ones, with intriguing hints that this may correspond to expansions and pauses in population dispersals (Greenhill 2004).

2.7 Conclusions

Both parsimony and Bayesian likelihood methods returned phylogenies that provide useful models of population history. They conform to standard subgrouping hypotheses of Austronesian languages, and display statistical properties indicating they are robust phylogenies. These trees are used in the following chapters. The parsimony tree provides phylogenetic distances and phylogenetic nearest neighbours for the analyses in Chapter Four. The Bayesian sample of 1000 trees has been used in all comparative analyses of residence and descent that use *BayesMultiState* (Chapters Five and Six), and the consensus phylogeny of the Bayesian sample has been used in Chapter Seven with the program *Continuous* to investigate the relationship between language change and population size.

CHAPTER THREE

THE COMPARATIVE METHOD IN ANTHROPOLOGY

3.1 Summary

Comparative methods for phylogenetic tests are introduced. Parsimony and likelihood methods are contrasted. Likelihood models allow uncertainty to be incorporated into comparative analyses. A likelihood ratio test can choose between an independent and dependent (co-evolutionary) model for discrete traits evolving on a phylogeny. The Bayesian approach to comparative analysis using the Bayes Factor as a test statistic is described in detail. Reverse-jump MCMC, a new method for estimating the appropriate model of trait evolution, is described. Bayesian frameworks are powerful tools for the investigation of cultural trait evolution, and are exploited in subsequent chapters.

3.2 Introduction

3.2.1 The comparative method

Lions and tigers and bears are separate species, but they do not provide us with three separate instances of the evolution of meat-eating. They are all members of the mammalian order *Carnivora*, and, because the branching process of evolution means that species share common ancestors, we cannot therefore treat them as independent outcomes in statistical analyses. If we incorporate the phylogenetic pattern of descent amongst a group of species into an analysis, we will count only those *branches* (rather than species) on which evolution has taken place. Methods that control for historical relationships are called phylogenetic comparative methods. Comparative methods test for regular associations between variables across a number of hierarchically related taxa (e.g. species, populations, cultures), and such correlations are generally interpreted as the best evidence for co-evolution or adaptation (Clutton-Brock and Harvey 1977; Ridley 1983; Harvey and Pagel 1991). While tests vary, comparative methods generally proceed by plotting character states (for example, colouration and environment) on the branches of a phylogeny. Some optimality criterion, often parsimony or likelihood, is then used to reconstruct ancestral states, identify independent instances of evolutionary change, and from these, evaluate the statistical evidence for co-evolution of the characters.

Chapter One outlined Galton’s Problem in anthropology, that is, the analogous need to control for the historical non-independence of cultures when conducting cross-cultural tests. Comparative methods from evolutionary biology address this need. With respect to cultural evolution, by using a linguistic phylogeny as a proxy for population history we are able to place known character states of the “ethnographic present” on the phylogeny and reconstruct cultural traits for putative parent populations. Thus, if we have a hypothesis of the historical relationships between a group of cultures (a tree phylogeny), and information about the variation in cultural traits amongst them, then we are able to make quantitative inferences about the possible states of these cultural traits in the past.

Data for use in comparative analyses can be discrete or continuous. Discrete data can be binary, indicating the presence or absence of a variable. For example, Holden and Mace (2003) coded cattle-keeping and matriliny as present or absent in their co-evolutionary analysis of descent and pastoralism in Bantu cultures. Discrete data may also be multi-state, that is, exist in more than two categories but not have an ordinal relationship. For example, human marriage systems might be classified as polygynous, monogamous, and polyandrous. Continuous data are often used in evolutionary biology and are some measurable trait of an organism such as body mass or population sex ratio. In cross-cultural tests, continuous variables include traits such as dependence on horticulture for subsistence (expressed as a percentage) or the sexual division of labour (Murdock 1967). The type of data may affect what comparative method the investigator uses. Below I discuss different types of comparative methods and their advantages and disadvantages.

3.3 Parsimony-based methods

3.3.1 Characteristics of parsimony-based comparative methods

Parsimony methods of ancestral state reconstruction minimize the number of evolutionary changes on the phylogeny required to explain the observed character distribution at the tips. For instance, if two sister taxa share a trait, then the ancestor of those two is assumed to have the trait, rather than positing two separate instances of character evolution. Comparative methods employing parsimony differ according to whether variables are discrete or continuous. For discrete data, parsimony methods test whether changes in a binary character are randomly distributed over the branches of the phylogeny (Ridley 1983; Maddison 1990). *MacClade* (Maddison and Maddison 1992) and *Mesquite* (Maddison and Maddison 2006) implement versions of these concentrated-changes tests. For continuous data, or a combination, Felsenstein's (1985) method of independent contrasts is widely used, and is commonly implemented in the program *CAIC* (Purvis and Rambaut 1995). By virtue of sharing a common ancestor, the differences in traits between sister-taxa are independent of the differences between other sister-taxa pairs on a phylogeny; the same logic holds true for all adjacent nodes across the tree. These phylogenetically controlled independent contrasts can then be used in standard correlations. Other methods exist, including autocorrelation and generalised least-squares (GLS) (Cheverud, Dow, and Leutenegger 1985; Martins 1995; reviewed in Rohlf 2001).

3.3.1.1 Shortcomings of parsimony

While intuitively easy to understand, there are some problems with parsimony-based comparative methods. Most do not use branch length information and thus if traits evolve at different rates over the tree they may under- or overestimate the number of evolutionary changes. As well, some of these methods do not perform well under conditions of rapid evolutionary change (Cunningham 1998). All assume a neutral/drift model of trait evolution (Steel and Penny 2000), and none are able to detect the order of character changes (i.e. the direction of causality in adaptive change). Likelihood-based and Bayesian comparative methods offer a useful alternative, the key points of which are summarised in Table 3.1.

Table 3.1 Comparison of parsimony and likelihood-based comparative methods.

	Parsimony Approaches	**Likelihood/Bayesian Approaches**
Ancestral state reconstruction	Single value assigned to each character at internal nodes	Probability distribution of character states at internal nodes
Phylogenetic uncertainty	Most treat phylogeny as known without error	Some methods incorporate uncertainty by using a tree sample
Character-mapping uncertainty	Ancestral states treated as known	Ancestral states treated as probabilistic states
	May underestimate amounts of change	Useful when trait evolution may be rapid
Branch length	Information generally not incorporated into model	Information incorporated; used to calculate rates of character transition
Models of evolution	Neutral drift (“Brownian motion”)	Stochastic; Bayesian methods allow for the specification of a prior model
Gains and losses, rates of evolution	All types of change treated as equally likely	Transition-rate parameters calculated for each type of change, rates of evolution can be calculated
Order of changes	Difficult to detect	Possible to detect
Incorporation of prior information	None	Defining characteristic of Bayesian methods
Computational abilities	Fast	Can be slow, Bayesian estimates improve speed

3.4 Likelihood comparative methods

3.4.1 Characteristics of likelihood-based comparative methods

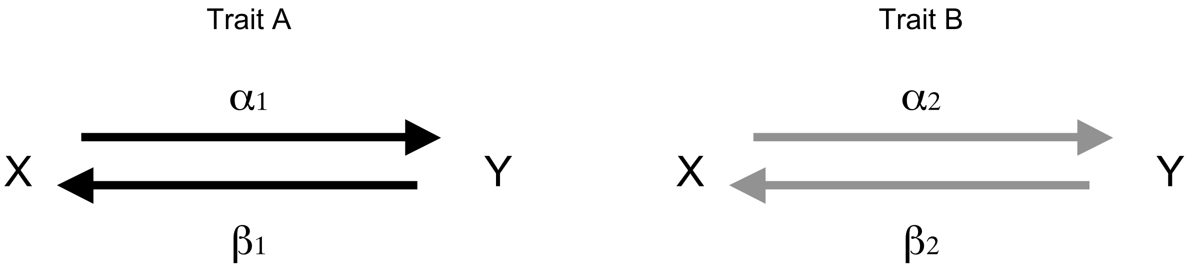
Maximum-likelihood phylogenetic methods ask about the probability of the observed data, given a phylogeny and some specified model of evolution. These methods offer several advantages over parsimony methods (Table 3.1), most notably that they incorporate uncertainty about ancestral character states and rates of evolution by estimating a model of probability distributions and rate parameters. Few comparative methods use likelihood frameworks, but those that do include certain modules in *Mesquite* (Maddison and Maddison 2006), *SIMMAP* (Bollback 2006) and the methods by Pagel and colleagues (Pagel 1994, 1997, 1999a, 1999b; Pagel et al. 2004).

3.4.1.1 Pagel's method

Pagel (1994) described a likelihood ratio test (implemented in the program *Discrete* and in a Bayesian framework in *BayesMultiState*) that allows testing for correlated evolution by comparing two models; the *independent model*, where two characters evolve independently, and the *dependent model*, where characters evolve together (Pagel 1994; Pagel 1999b). In the course of this analysis, the programs also reconstruct the probability of ancestral states at each node in the tree. Transition-rate parameters (the probability of change from 0→1 and 1→0) are estimated for each model, using a continuous time-varying Markov model (Figure 3.1). The likelihood of the data given the tree is calculated using the logic that if the two variables change independently, the joint probability of change equals the product of the separate probabilities of change. The likelihood of assigning the state of a variable to the terminal branches of the tree (the "tips"—our taxa of interest) is given by the product over all of the branches of the tree. Simply put, this method searches for the transition-rate parameters in two models—independent and dependent—that make the observed data most likely, and compares the obtained likelihoods.

Independent (Null) Model.

Traits may take two states, X and Y. On this model, Trait A evolves independently of the state of Trait B on each branch of the tree. Four transition-rate parameters ($\alpha 1$, $\alpha 2$, $\beta 1$, $\beta 2$) are estimated that account for the evolutionary change in the data, given the phylogenetic model.



Dependent (Correlated) Model.

Traits may take two states, X and Y. On this model, the state of Trait A is dependent on the state of Trait B in each branch of the tree, effectively creating four 'states'. Note that because change is dependent, moving from XX (state 1) to YY (state 4) requires two steps. Eight parameters ($q12$, $q21$, $q13$, $q31$, $q24$, $q42$, $q43$, $q34$) must be estimated by the model to account for the data.

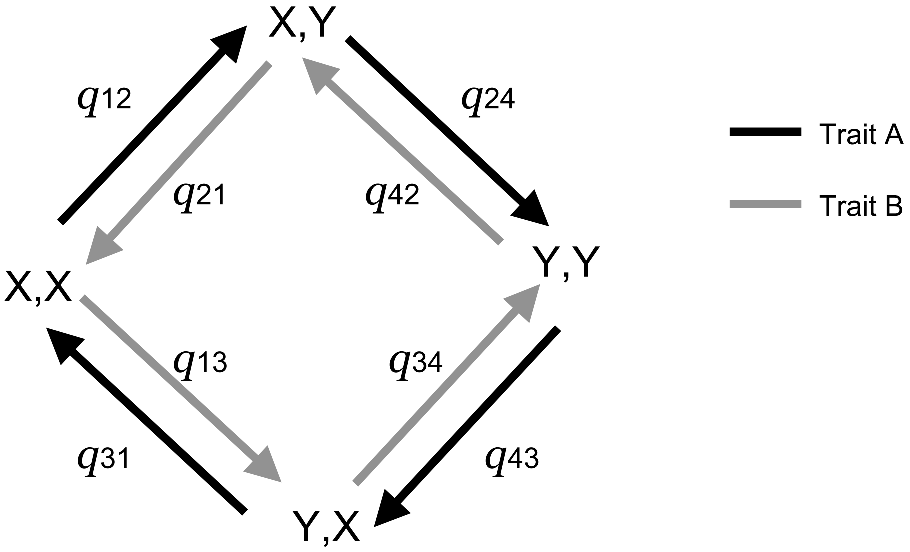


Figure 3.1. The two models estimated in Pagel's likelihood/Bayesian methods (1994, 1999, 2004), and their transition-rate parameters.

Once we obtain the likelihood scores for the two models we can compare the likelihood of each model. This assesses the goodness of fit by calculating the likelihood ratio:

$$LR = -2 \log_e [lh(\mathrm{I})/lh(\mathrm{D})] \qquad \text{[Eq. 1]}$$

Where *lh*(I) is the likelihood of the independent model and *lh*(D) is the likelihood of the dependent model. By simulating a null distribution of LR scores, we can use the chi-square distribution (with degrees of freedom equivalent to the difference in model parameters) to compare if our obtained LR for the independent and dependent model is significant. If it is, and the dependent model fits significantly better, this method provides us with evidence for correlated evolution.

Phylogenies impose a correlation on characters, even if they evolve independently (Lewis 2001). The model implemented by Pagel's methods test if the correlation is above the one that is imposed phylogenetically. The null model of independent evolution is a constrained version of the general model, as the correlation is constrained to zero, thus, the dependent model will fit better than the independent if the true correlation between the characters is not equal to zero.

3.4.2 Bayesian comparative methods

Bayesian comparative methods incorporate the likelihood-based estimation of ancestral states and correlated evolution (i.e. by estimating rate parameters that explain the observed data) with a Bayesian-derived tree sample to represent phylogenetic uncertainty. Many methods deal with this uncertainty by using the "best" tree by some optimality criterion, or a consensus tree derived from a set of "best" trees, yet neither can be presumed to be the true tree. Bayesian approaches to estimating uncertainty about the phylogeny were described in Chapter Two. Similarly, many comparative methods work by assigning a single value of a character state to each node, producing a source of error called *mapping uncertainty* (Frumhoff and Reeve

1994; Ronquist 2004). Bayesian comparative methods address both these source of uncertainty by implementing a Markov model that estimates rate transitions of character states in a similar fashion to the rate matrices described for word evolution in §2.6.2.1, then integrates these rates, and other parameters in the model, over a posterior probability distribution of trees. The probability of a particular character state at a particular node, or a combination of states when testing for co-evolution, is thus weighted by the likelihood of that node appearing in the data set.

3.4.2.1 BayesMultiState

Lutzoni, Pagel, and Reeb (2001) used *Discrete* to investigate the ancestral states of lichen-forming *Ascomyta* fungi, estimating character states at each node over a Bayesian sample of trees and generating likelihood plots of character-state likelihood x node likelihood. These plots were then used in conjunction with the consensus phylogeny to interpret the symbiotic evolution of lichen and fungi. More recently, Pagel et al. (2004) described an integrated procedure for the Bayesian estimation of ancestral states at internal nodes, released as the program *BayesMultiState*. Using the posterior probability distribution of trees rather than a single phylogeny, ancestral states are estimated over the entire tree sample. Here, the likelihood of a state at a particular node is further moderated by the likelihood of that node existing in the tree sample, taking a statistically principled approach to uncertainty about both phylogeny and mapping (character-state) reconstruction.

An example describes this approach. We may wish to calculate the ancestral state of marriage patterns, for example the presence of polygyny, in Eastern Polynesian and Philippine cultures. We have a Bayesian sample of language phylogenies, as described in Chapter Two. In this sample, the posterior probability distributions are 0.98 for the Eastern Polynesian node and 0.67 for the Philippine node. This represents our phylogenetic uncertainty. The comparative method (described below) estimates the PPD for polygyny in the two groups of cultures, and returns 0.75 for Eastern Polynesia, and 0.99 for the Philippine group. This represents our mapping uncertainty.

We then multiply the uncertainties together to ask the question: “What is the likelihood of the ancestral state being polygyny, given uncertainty about character-state reconstruction *and* uncertainty about the phylogeny?” In this example, although the character-state estimation for the Philippine cultures is very certain, the Philippine node only exists on two-thirds of the trees in the sample, reducing the ancestral state estimation to 0.66. However, the Eastern Polynesian group is very robust, so the ancestral state estimation remains high, at 0.74. By identifying the sources of uncertainty in this way, we can make more realistic inferences about evolutionary processes.

Correlated evolution can be tested, as the *BayesMultiState* program implements a Bayesian version of the *Discrete* test of independent and dependent models as described above (Pagel and Meade 2006), and also implements the *Continuous* algorithm for continuous data (Pagel 1997) into the software. In this thesis, all comparative analyses of ancestral state reconstruction, evolutionary rates, and co-evolutionary hypotheses were tested, where appropriate, using this software.

3.4.3 Model testing using reversible-jump MCMC

In the absence of specific knowledge, biologists will generally choose a model that makes the least assumptions about the evolutionary process. Although one of the strengths of a Bayesian approach is that prior knowledge can be incorporated into the analysis, in practice we do not often know many relevant details about the parameters in our models. The choice of the best-fitting model of trait evolution can thus be the outcome of trial-and-error experimentation. A further refinement of the *BayesMultiState* program is the addition of a reversible-jump (RJ) MCMC approach (Pagel and Meade 2006). The likelihoods of the models themselves are estimated alongside testing hypotheses of correlated evolution. The RJ method constructs a Markov chain that visits these models in proportion to their posterior probabilities, just as in a tree-building Markov chain individual trees are visited in proportion to their probability. The description that follows is based on Pagel and Meade (2006) and personal communications from the authors.

3.4.3.1 Reverse-jump MCMC

In a two-character, two state test there are thousands of different possible models of evolution. The independent model (no correlated evolution) says that the transition rates for trait A between states are not dependent on the state of trait B. Thus, we can group the transition rates into pairs that, under the independent model, should be equal. When equivalent pairs of transition rates (e.g. q_{12}, q_{34}) do not share the same rate class, the dependent model is implied. The four pairs of transition parameters give us eight rates that can be estimated and classed together (or not). By using Stirling numbers for combinatorial permutations, we can estimate the number of ways to arrange a set of objects into classes, and for these eight rates there are 21,146 different models of evolution to be explored. The program gives an output that displays models with their likelihoods, and they can be ranked accordingly. As not all of the ~21,000 models will be visited, nor all in equal amount, the program provides a guide to which of the models is most appropriate to the characterisation of the data.

3.4.3.2 Bayes factor.

The Bayesian implementation of the comparative method uses a different statistic to the likelihood ratio to assess which model fits best: the Bayes factor (Raftery 1996). Rather than comparing two likelihoods, we compare two posterior probability distributions, derived by sampling the parameters through an MCMC method. As in the likelihood tests we compare the models after accounting for the fact that the independent model, having extra parameters, will always fit the data better. Thus, a penalty for these extra parameters must be imposed. The Bayes factor (*BF*) is the ratio of marginal likelihoods, these likelihoods being the probability of the data given the model but scaled by the posterior probability of the parameters. In the context of the *BayesMultiState* output, the ratio of marginal likelihoods is found by obtaining the harmonic mean of the likelihoods (Pagel and Meade 2006). The Bayes factor test thus compares the models and returns which one accounts for the greater proportion of the probability of the data. A log *BF* of 3-5 constitutes positive evidence for the dependent model, log *BF* >5 is strong evidence for the dependent model, whilst log *BF* <0 is evidence for the independent model (no correlated evolution).

3.5 Conclusions

Chapter Two showed how powerful Bayesian methods can be in reconstructing language phylogenies, by incorporating more realistic models of evolution and out-performing parsimony analyses in recovering linguistic subgroups. Additionally, the Bayesian methods described in this chapter are potentially powerful tools, and are ideally suited to the investigation of cultural trait evolution on linguistic trees. Cultural traits may evolve quickly and language phylogenies may lack resolution at some nodes, leading to considerable uncertainty in standard parsimony reconstructions. With the Bayesian approach, this uncertainty becomes explicit. The common criticism of the phylogenetic approach to cultural evolution—that a single tree model cannot hope to capture complex, often reticulate histories of human interaction—is addressed by methods that take multiple population histories, and the uncertainty about their reconstruction, into account. In subsequent chapters, I use these new Bayesian frameworks to reconstruct ancestral states of cultural traits, to construct models of the order of change in cultural traits, and to test for correlated evolution.

CHAPTER FOUR

DO CULTURES RESEMBLE THEIR NEIGHBOURS OR THEIR COUSINS?

A TEST OF PHYLOGENETIC AND GEOGRAPHIC DISTANCE

4.1 Summary

Societies may share cultural traits for a number of reasons, including phylogenetic history and geographic proximity. This chapter investigates between-group transmission processes on a regional, cross-cultural scale in 80 Austronesian societies. Taking data on 74 cultural traits from Murdock's (1967) Ethnographic Atlas, I used partial Mantel matrix tests to correlate matrices of cultural, linguistic, and geographic distances. "Social" and "economic" classes of cultural traits vary equally with phylogenetic distance matrices, but only economic traits vary with geographic distance. In a logistic regression model, I test if geographical or phylogenetic "nearest neighbours" (estimated using a comparative method on a linguistic phylogeny) have more of an effect in producing patterns of cultural similarity. Unlike the findings of previous authors, social and economic classes of traits were not predicted by a predominant transmission model. Rather, cultural traits concerning heritable resources—either material or social—were associated with phylogenetic nearest neighbours. I discuss the results in the context of the Austronesian expansion.

4.2 Introduction

4.2.1 Cultural transmission between groups

Disentangling competing explanations for why cultures share traits is one of the main challenges for an effective program of cultural evolution. Just as biologists attempt to explain diversity and design using evolutionary concepts such as adaptation, admixture, and inheritance, evolutionarily-minded cultural anthropologists invoke these processes to account for cultural variation. Hewlett and Cavalli-Sforza defined cultural transmission as “a process of social reproduction in which the culture’s technological knowledge, behaviour patterns, cosmological beliefs, etc., are communicated and acquired” (1986:922). The predominant mode of transmission for different types of cultural variants, and how those variants are exchanged both between individuals and between groups is an important empirical question.

Using theory from population genetics, a substantial amount of work has considered the dynamics of cultural trait transmission between individuals (e.g. Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985, 2005a). These are, in effect, microevolutionary processes. More recently, these transmission models have been extended to the consideration of how cultural traits might be population-level phenomena arising from these individual cost-benefit interactions, for example, Henrich (2004b) discusses how our social learning capabilities can produce multiple behavioural equilibria, some of which are group-beneficial. Here we are interested in the macroevolutionary or between-group transmission of cultural traits. It is expected that the individual-level processes that operate within groups (such as, for example, prestige bias) bear some relation to the types of processes that act on between-group transmission: entire societies will not interact with other entire societies, but rather, successive individuals or sub-populations belonging to different societies will come into contact. We consider here two generalised types of processes that speak to important debates about human prehistory—the degree to which societies share cultural traits because of shared history or inheritance from a parent population (phylogenetic processes), and the degree to which societies share traits because of geographic proximity and classical cultural diffusion.

4.2.2 Macroevolutionary studies of between-group cultural transmission

Guglielmino et al. (1995) examined cultural variation in 277 Sub-Saharan Africa societies coded in the *Ethnographic Atlas* (Murdock 1967) in an attempt to disentangle three modes of cultural transmission (see Figure 4.1). Demic diffusion refers to inheritance from a common ancestor; in this thesis I use the term *phylogenetic transmission* as akin to demic diffusion. Ecological adaptation is a change in cultural traits in response to the environment; here it is referred to as simply *adaptation,* in recognition of the fact that adaptations may be responses to the social as well as the physical environment. Cultural diffusion is the classic phenomena of a cultural trait spreading through neighbouring groups, referred to here as *geographic transmission* or horizontal transmission.

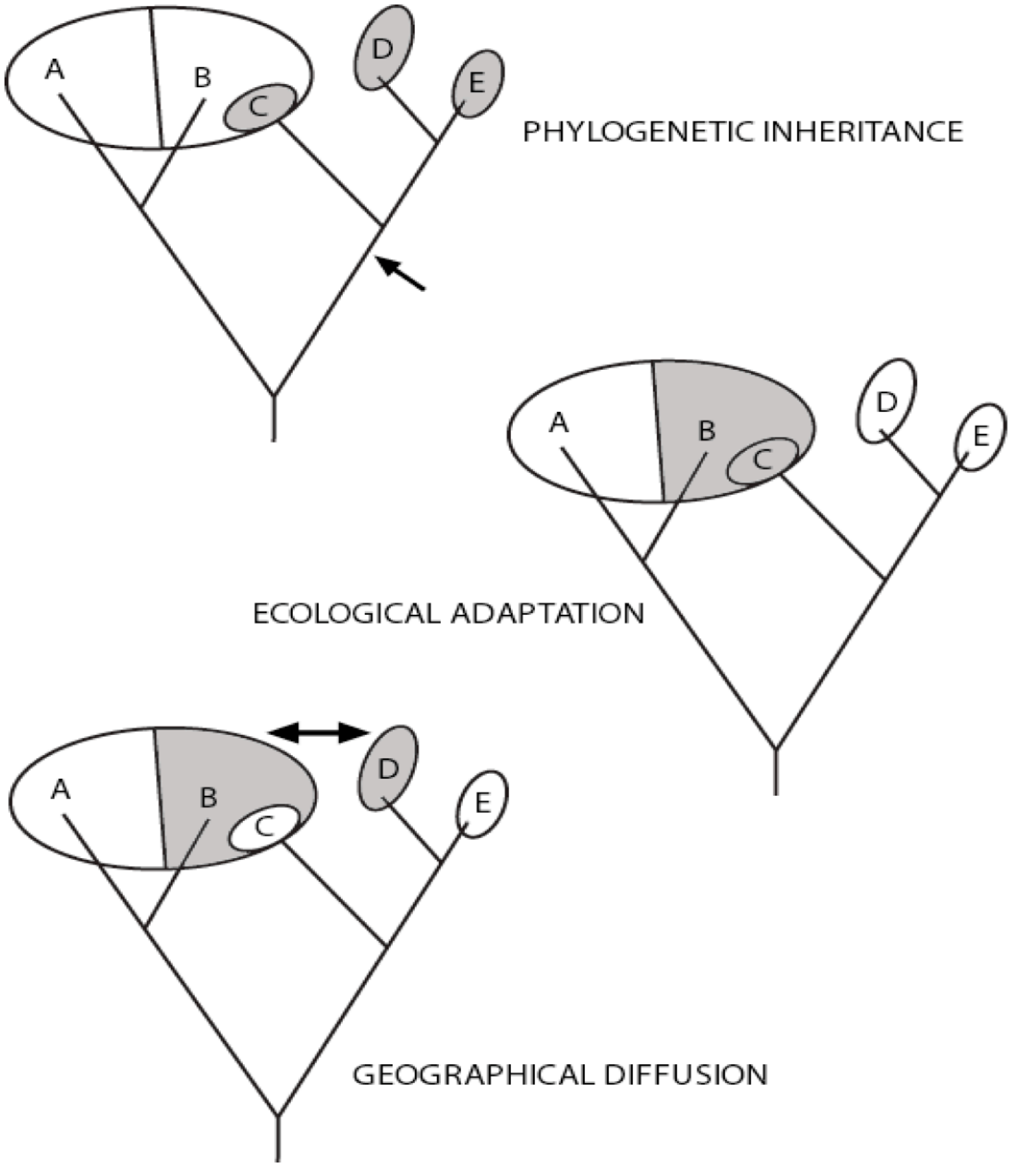


Figure 4.1. Populations may share cultural traits for a number of reasons. Consider societies A–E on three islands, whose languages are related by the branching relationships shown in the tree diagram. Areas in grey represent shared cultural traits. **Top**. Phylogenetic inheritance is where societies are similar because they share recent common ancestry. In the case of C–E, the shared trait may have evolved at the point indicated by the arrow. **Middle**. Ecological adaptation occurs when societies face some similar environmental “problem” and converge on the same “solution”, as demonstrated by the trait shared by B and C in an overlapping environment. **Bottom**. Geographical diffusion is the classic diffusion of traits between neighbouring/ interacting societies, demonstrated by B and D who perhaps share trade links. In addition, societies may share traits by chance, a type of convergent evolution.

Using a contingency table approach with the G_2 statistic, Guglielmino et al. divided their 47 cultural traits into six groups: (i) family and kinship, (ii) economy, (iii) social stratification, (iv) sexual division of labour, (v) house, and (vi) "other". They examined pairwise contingency tables for each class of cultural trait, finding more than 60 percent internal correlations within the first four groups of traits. They then looked at the correlations of each trait within language family (for phylogenetic transmission) and vegetation class (a proxy for ecology, to assess adaptation). Language family affiliation was correlated with more cultural traits than ecological affiliation, especially family and kinship traits, demonstrating that these traits are transmitted more likely to be phylogenetically. That family/kinship traits are associated with a vertical (phylogenetic) mode of transmission is not surprising as the authors observe that these traits are likely to be learnt in the family and at a young age, encouraging their conservation. Adaptation to the ecological environment was not strongly associated with any class of traits in particular. To assess the degree of geographic clustering, the authors created a clustering index that expresses the geographical closeness of neighbours sharing a trait. Sexual division of labour, house traits, and "other" traits (such as a belief in gods, or post-partum sex taboos) all had higher clustering indices relative to social and economic traits, indicating geographic diffusion as an important mode of transmission.

Further work by the same group of authors (Hewlett et al. 2002) investigated why cultures were likely to share traits or "semes" (specifically transmitted cultural units). Here they used genetic distances from the Stanford genetic database, cultural data from the *Ethnographic Atlas*, linguistic data from Ruhlen's (1987) world classification, and the geographic clustering index described above to create distances between each pair of 36 African cultures. Using z-scores, they then evaluated which model(s)—phylogenetic, geographic, adaptation—best fit each of 109 cultural traits. Of these, 45 had a primary model of explanation, with demic diffusion again associated with many kinship traits. Geographical diffusion explained a number of "house" and "other" traits. The majority of traits had more than one explanatory model, and ecological variation was not related in any significant way with genetic, linguistic or cultural similarity.

While this work has been useful in establishing clear theoretical models of trait transmission, there exist a number of problems. Firstly, there is no clear control for phylogenetic relatedness between cultures, even though phylogeny is being used as an explanatory model. The reported correlations may spuriously over-count the number of independent trait associations. Secondly, Guglielmino et al. used as a proxy for phylogeny a broad language-family membership (of six groups only) that is probably too coarse to address transmission at a between-cultures level. Hewlett et al. used a language distance measure based on sharing levels of Ruhlen's classification scheme, which has the unfortunate effect of inflating distances when language groups are well studied (and thus have more classification levels). The use of more principled linguistic distance measures is desirable if language is to be an effective indicator of phylogeny. Thirdly, by using vegetation as a proxy for the ecological environment the authors only take into account one portion of environmental variability—one that in Africa at least is heavily correlated with latitude/longitude and thus confounded with geographical distance. Lastly, the African societies in these studies belong to more than one large-scale language group, and as such we should expect to find a reasonable signal of phylogenetic transmission. Examining cultural transmission modes within a *single* language family may shed more light on to what degree traits are conserved by vertical inheritance at a regional level.

4.2.3 Adaptation and ecology

The consistent correlation of behavioural or cultural traits with aspects of the ecological environment is one of the lines of evidence used by behavioural ecologists to determine adaptation (Cronk et al. 2000). However, no clear evidence for adaptation to local ecology was found in the studies above. Guglielmino et al. found that more cultural traits shared a correlation with linguistic affiliation than with ecology, even under different grouping schemes; moreover, this African analysis comprised societies from major language phyla and very broad scale ecological classifications. We know that a diversity of cultural and subsistence systems can co-exist within a particular type of ecosystem, and each may be a specialized strategy, so detecting adaptation is clearly not always as simple as correlation with one aspect of ecology. Especially in large-scale analyses, ecological variation is also confounded with spatial proximity. Also, people may move to areas resembling the local ecology with which they are familiar, so ecology may have a degree of historical autocorrelation as well. While it makes intuitive sense to correlate ecological and cultural variation and is thus tempting to suggest an adaptive relationship, adaptation is a special concept that should not be invoked without careful exclusion of competing hypotheses (Williams 1966). Further chapters will use the phylogenetic comparative method to test specific adaptive hypotheses, but in this multi-trait, multi-society analysis the rationale for assigning adaptation to any correlation of ecology and cultural traits is very weak.

4.2.4 Cultural transmission in Austronesian societies

The Pacific arena, and in particular the Austronesian language family, presented an ideal situation in which to address these shortcomings and provided a comparative regional approach to the African findings described above.

4.2.4.1 Replication

To investigate if there were different outcomes when using methods that control for evolutionary history, a straight replication of the contingency table approach outlined in Guglielmino et al. (1995) was initially attempted. Ecological classifications given in the EA were too coarse to provide resolution at this regional scale. Sources used to classify the predominant ecology of each culture were Barkley (1968), *The Times Atlas* *of the World* (1990), and Oviedo, Maffi, and Larsen (2000). However, the sample size of Pacific societies (80 versus 277 African societies) was too small to obtain sensible results with the G_2 statistic, as many cells in the contingency table analysis violated the assumptions of the statistical method. Collapsing categories was only possible in the few cases of ordinal variables and not appropriate for the vast majority of categorical cultural traits. This analysis was abandoned.

4.2.4.2 Alternative approaches

Here are presented two alternative approaches to the study of cross-cultural transmission that control for historical relationships in a more principled way than previous attempts. First, I use Mantel matrix tests to correlate pairwise distances between societies based on linguistic, geographic and cultural measures. Linguistic distances provide a degree of control for autocorrelation due to phylogeny. Second, I examine individual cultural traits to see if they are best predicted by a society's geographic or phylogenetic nearest neighbour, deriving phylogenetic information from a linguistic tree and estimating states of internal nodes with maximum-likelihood comparative method.

4.3 Mantel tests of cultural, geographic, and linguistic distances

4.3.1 Aim

To investigate if there are significant correlations between geographic, phylogenetic (language) and cultural distances between pairs of societies.

4.3.2 Distance matrices for tests of diversity

A distance matrix is a way of describing the patterned variation between pairwise comparisons of ethnolinguistic groups. By correlating distance matrices, we can see if the patterns described by different metrics (for example, genetic systems, languages, geographic isolation) bear any relationship to one another. Using these methods on anthropological data is not without precedent, although most work to date has focussed on comparing genetic distances with geography and/or language (e.g. Lum et al. 2002). For example, Eller (1999) examined the effect of geographic distance and shared population history (as represented by language distance) on worldwide genetic distance data, finding that when holding language affiliation and population size constant, there was a 76 percent correlation between genetic and geographic distances, indicating significant population substructure. Chen et al. (1995) examined the correspondence between language and blood-group alleles in 130 worldwide populations. Holding geographic distances constant in a partial correlation analysis, they found moderate but significant associations between language affiliation and nine out of 11 of the gene systems under study. The pooled allelic distances gave an overall correlation with language distance of $r = .22$, indicating some degree of spatial autocorrelation between genes and languages on a global scale. However, in these studies, as with most others (e.g. Fagundes 2002 for South America) linguistic distances were rough subjective estimates taken from classification hierarchies and did not follow any formal statistical criteria.

Though infrequent, Mantel methods have been used with cultural data other than language. Shennan and Collard (2005), reanalysing data from Welsch et al. (1992), looked at the effects of language and geography on material culture from the north coast of New Guinea. Linguistic and geographic distances were highly correlated, but taken together only accounted for 12 percent of the variation in the cultural data, in roughly equal amounts. In this case, the test did not discriminate a dominant mode of cultural transmission. Jordan and Shennan (2005) examined variation in indigenous Californian basketry techniques, and found that while regional variation precluded any universal patterns, linguistic affinity had lower partial correlations with basketry variation than did geographic factors, indicating a greater role for diffusion processes. Hage, Harary, and Krackhardt (1998) used Mantel tests as a way of testing significant similarities between networks of cultural and voyaging distance. For a small number of Polynesian societies, they found a significant correlation (r = .496) between a distributional analysis of cultural traits (Burrows 1938) and Irwin's (1992) mutual accessibility matrices of voyaging distances. They concluded that island voyaging may have continued post-settlement to produce the patterns of geographic similarity of culture traits.

4.3.3 Hypotheses

The question in this section is whether we can determine a predominant transmission mode for different types of cultural traits. Using the Mantel test approach to control for the confounding effects of geographic proximity and phylogenetic relationship (as represented by linguistic distance), we can look at matrices derived from different sorts of cultural traits and see with which model—"vertical" or "horizontal"—the variation contained therein correlates best with. Following previous work (Guglielmino et al. 1995), we hypothesise that social and kinship traits will show more correlation with a matrix of language distances than do economic and political traits. Economic and political traits, mainly describing cultural variation to do with subsistence patterns, are hypothesised to correlate more closely with geographical distances.

4.3.4 Data

4.3.4.1 Cultural data

Data on cultural traits were taken from the updated version of Murdock's *Ethnographic Atlas* (1967) made available through the *World Cultures* editors (Gray 1999), and comprised 80 Austronesian-speaking societies that could be matched to languages in the Austronesian Basic Vocabulary (ABV). Appendix A lists the cultures and their matching languages. The *Ethnographic Atlas* (EA) was dichotomized so that each multi-state cultural variable became a presence-absence binary variable. For example, "descent", a variable with six categories, became six different variables of presence-absence: patrilineal versus non-patrilineal, bilateral versus non-bilateral, and so forth. Variables concerning dependence on modes of subsistence are categorised in the EA in a semi-continuous fashion in ten classes of "percent dependence". For these analyses those variables were categorised into discrete bins of two or three classes, e.g. high, moderate, and low dependence on fishing. Only those traits that were displayed by at least 10 percent of cultures were used.

4.3.4.2 Language data

Language was used as a proxy for the phylogenetic history of these cultures. Societies in the EA were matched up with their language using a number of sources: the *Encyclopaedia of World Cultures* (Levinson 1993), *Ethnologue*, 15th ed. (Gordon 2005), and others (Wurm and Hattori 1981; Ruhlen 1987; Price 1990) and cross-checked across these sources where available. Language data for phylogenetic analysis comes from the ABV as described in Chapter Two.

4.3.4.3 Geographic data

The geographic location of each society was found using the latitude/longitude data in the *Ethnographic Atlas*. Using the Summer Institute of Linguistics (SIL) codes from the online *Ethnologue*, these were then cross-checked against the society's designated "language area" described in the World Language Mapping System GIS shapefiles (GMI International 2005). Figure 4.2 shows the geographical distribution of the 80 ethnolinguistic groups.

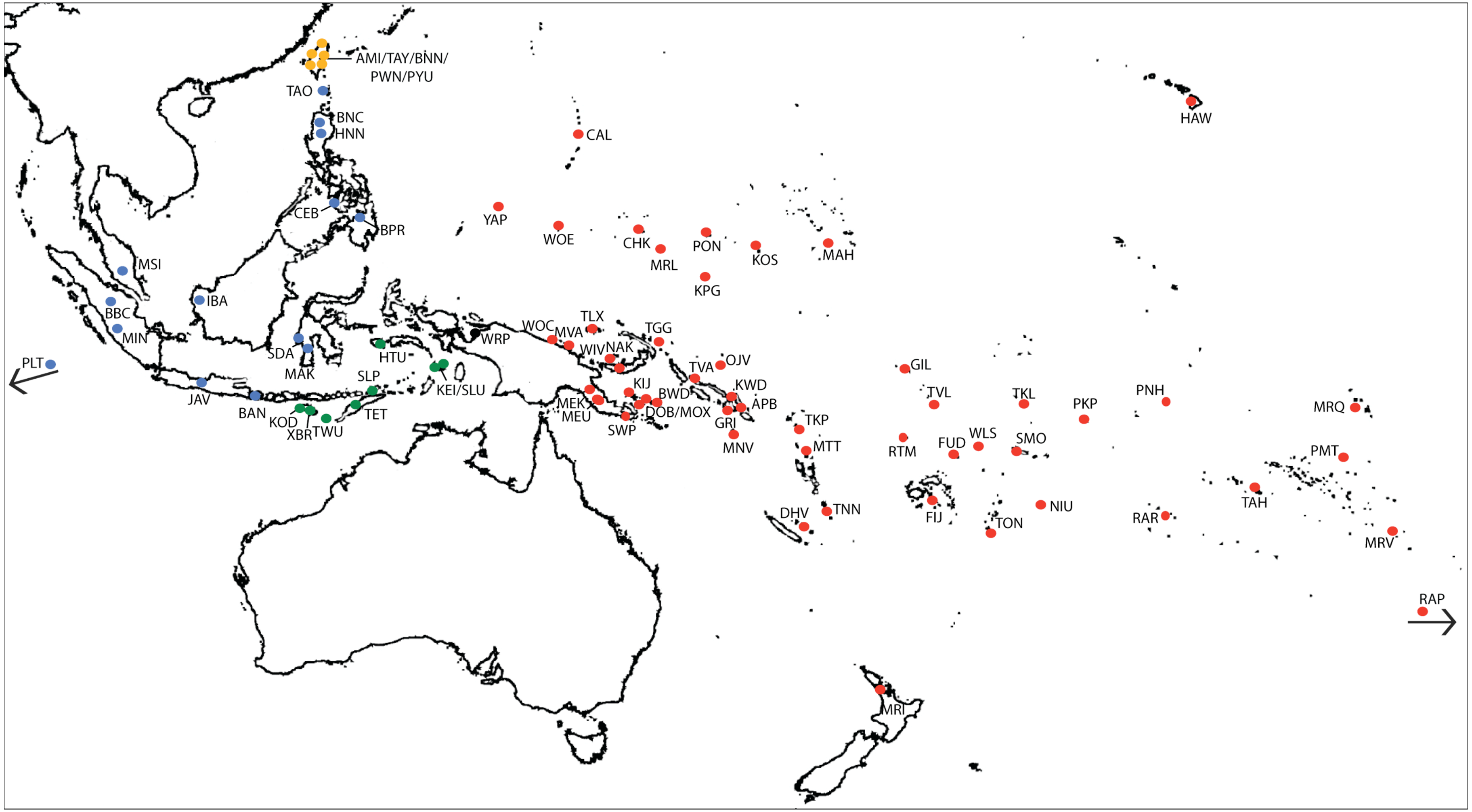


Figure 4.2. Geographical location of the 80 Austronesian societies used in these analyses. Societies are labelled with their *Ethnologue* "SIL code" (Gordon 2005) listed in Appendix A. Colours represent subgroups: Formosan, WMP, CMP, SH-WNG, Oceanic.

4.3.5 Mantel matrix tests

The Mantel test (Mantel 1967) tests if distance matrices are correlated, allowing us to evaluate the relationships among distance measures. This is useful for cases when we cannot use a simple correlation coefficient or ANOVA because cases are not independent, as when cultures are phylogenetically related. The Mantel test is robust against unknown amounts of non-independence because it uses a permutation method which preserves the autocorrelation (Hage et al. 1998). A correlation coefficient (R_o) is calculated for the relationship between the matrices M_1 and M_2. We then permute the rows and columns within M_1 a number of times (e.g. 10,000) and calculate R each time. If M_1 and M_2 are correlated, the permutations will decrease the new R_p. If M_1 and M_2 are uncorrelated, the permutations may increase R_p. The permutations act as the null distribution and provide a p-value, such that if we have 1000 permutations and only one exceeds the original R_o, $p = .001$. Thus,

$$p = n(R_p) > n(R_o) / n \text{ permutations} \qquad \text{[Eq. 2]}$$

where R_o is the original correlation coefficient and R_p is the correlation of the permuted coefficients.

This method allows the analysis of continuous and categorical variables in same model, is applicable to all kinds of distance measures and can also be used to test partial correlations of more than two variables (Oberrath and Bohning-Gaese 2001), making it ideal for examining linguistic, cultural, and geographic data together. We can then ask how much of the variation in sets of cultural traits can be explained by geographical distance and how much by phylogeny—two of the models of cultural transmission—whilst at the same time controlling for their interaction and phylogenetic effects. Simulation studies have demonstrated that simple pairwise Mantel tests may fail to resolve the mode of cultural transmission when there is some degree of horizontal transmission (Nunn et al. 2006); thus, we use the partial correlation method in preference.

4.3.5.1 Program

The program *zt* (Bonnet and Van de Peer 2002) was used to calculate simple and partial correlations between the linguistic, geographic, and cultural matrices. In all cases, the matrices were permuted 100,000 times to give a null distribution of the correlations (R_p), which were then compared to the original obtained R_o.

4.3.6 Distance matrices

4.3.6.1 Cultural distances

SPSS 11 for Mac was used to derive dissimilarity (distance) matrices from the 78 binary-coded EA cultural traits. Jaccard distances for binary scores were calculated between pairs of societies and transformed to a score between zero and one, with zero representing no distance. Three cultural distance matrices were constructed: one containing all traits (CUL, n = 78), one containing only social/kinship traits (SOC, n = 36), and one containing only economic/political traits (ECO, n = 42). Traits were assigned to these categories *a priori* following the sorting in Guglielmino et al. (1995) and Hewlett et al. (2002) for comparison. Further subdivision of the data set into cultural trait categories was not attempted, as it was likely to decrease the power of the method, however, these two classes are sufficient to allow us to address the question of whether social and economic traits follow different patterns of cultural transmission.

4.3.6.2 Linguistic distances

A linguistic distance matrix (LND) was extracted from the raw binary data using the Upholt criterion in *PAUP** (Swofford 1999). Phylogenetic distance methods are less preferable to those like patristic calculations that incorporate character information (Felsenstein 2003); however, as the cultural distance matrices are based on overall comparisons a distance matrix is appropriate. A single most-parsimonious tree of the 80 languages was found using *PAUP**(see Chapter Two for details on tree-building and the particulars of the phylogeny). From this tree *PAUP** was then used to calculate patristic distances, that is, the pairwise distances between each language, taking into account the number of changes along each branch back to the node that joins the two taxa (LNP). This matrix was tested against geographic distance and the LND matrix.

4.3.6.3 Geographic distances

Using each society's geographic position, *ArcMap* v.9.1 (ESRI International 1992-2005) calculated a pairwise distance matrix with arbitrary units. These units were calibrated to kilometres using a scaling factor from the same program. The Haversine formula (Sinnott 1984) for great-circle distances was then used to spot-check a number of these distances. In cases where the matrix returned a culture with two neighbours of equal distance, the linguistic maps described above, and those in Wurm and Hattori (1981), were used to estimate which pair of cultures were geographically closer. I estimated which society shared a greater or more accessible border with the target society, or, in those cases where the information was known, estimated the distance from where the target site of ethnographic description fell within the language area. Distance was then entered for this pair as half the amount given by *ArcMap* to complete the matrix (GEO). Hage et al. (1998) suggest that the inverse of geographical distance be used in pairwise comparison of multiple societies, as beyond some particular range any increase in distance will not have an effect. A similar effect can be obtained by log-transforming the matrix. Analyses were run using both raw distances and their natural logarithms (GEL).

4.3.6.4 Population size

Following a suggestion in Eller (1999) concerning the effects of drift in small populations, I constructed a matrix that represented differences in population size. Population size data came from the *Ethnologue* and was originally collected for the analyses in Chapter Seven. The harmonic means of the pairwise comparisons (n_{ij}) were derived $(1/n_i + 1/n_j)^1$ in order to accentuate the effect of small population sizes (POP).

4.3.7 Matrix correlations

There was a positive correlation between the matrices representing linguistic and geographic distance (LND.GEO, $r = .166$, $p = .01375$; LNP.GEO, $r = .179$, $p = .00005$). This indicates the need to control for the independent effects of history and geography through a partial correlation technique. The overall distance and patristic distance matrices were not correlated significantly with each other, suggesting they are capturing different aspects of phylogenetic relationship. Because terminal branch lengths on this tree are long compared to the internal branches (see Chapter Two), it is likely that the variation in the LNP matrix is insufficient to return significant correlations with the cultural matrices. LND was used for all further comparisons.

4.3.7.1 Geographic distance

Transforming the geographic distances to their natural logarithms had no effect on the matrix comparisons. All analyses proceeded with simple geographic distances (GEO).

4.3.7.2 Population size

In simple comparisons, none of the matrices were correlated in any significant way with the population size matrix. This implies that population size differences do not account for the patterns of variation in the other variables, and so this matrix was not included in any subsequent analyses.

4.3.7.3 Cultural distance

Social and Economic matrices were correlated with each other only moderately (SOC.ECO, $r = .12$, $p < .001$). When the overall cultural distance matrix is held constant, the partial correlation is extremely strong and negative

(SOC.ECO(CUL), $r = -.93$, $p < .000$) indicating that the SOC and ECO do capture different, probably orthogonal, dimensions of cultural variability. Table 4.1 shows the results of both the simple and partial Mantel tests on the cultural distance matrices. Partial correlations hold one of the matrices constant and allow us to assess the independent effect of the second "predictor" variable; they are thus the more useful of the tests.

Table 4.1. Simple and partial correlations between geographic, linguistic and cultural distance matrices using Mantel's test. *P*-values are from 100,000 random matrix permutations. Values in brackets are non-significant (*p* < .05). Partial correlations show geographic distance controlling for language (phylogenetic) distance, then language distance controlling for genetic distance.

	Correlations				**Partial Correlations**			
Matrix[1]	**GEO**	***p***[2]	**LND**	***P***	**GEO(LND)**	***p***	**LND(GEO)**	***p***
CULT	.37	.00	.25	.00	.34	.00	.21	.00
SOC	.09	.01	.18	.00	(.07)	(.08)	.17	.00
ECO	.43	.00	.20	.00	.41	.00	.14	.00
LND	.17	.00	-	-	-	-	-	-

1. CULT, matrix of all cultural trait distances; SOC, matrix of all social/kinship trait distances; ECO, matrix of economic/political trait distances; LND, matrix of language distances; GEO, matrix of geographic distance.

The matrix of all cultural traits co-varies significantly with both geographic and phylogenetic distance ($p < .001$). The same pattern obtains under both simple and partial correlations: geographic distances have a higher correlation ($r = .34$) with cultural distance than do phylogenetic distances ($r = .21$). This indicates that patterns of cultural trait distribution across the cultures in the sample reflect geographic similarity to a greater degree than historical association, although it is not possible to state if these differences are significant. Cultural difference is possibly a cruder scale.

4.3.7.4 Language and geography

The combined (CUL) and separate (SOC, ECO) cultural trait matrices all vary significantly with language distance at approximately the same moderate level of partial correlation (*r* = .21—.14) when geographic distance is held constant. In the converse situation, correlating geography and holding language distance constant, we still obtain a significant correlation of all cultural traits with geographic distance, but when parcelled out, we find that only economic traits maintain the correlation and social traits do not appear to co-vary with geographic distance.

4.3.8 Mantel tests: Discussion

Correlating distance matrices is one way to determine what processes of cultural transmission may account for patterns of variation in cultural traits. The first hypothesis was that social organisation/kinship traits (for example, “polygyny” or “patrilocal residence”) would follow a more conservative (vertical) mode of transmission, as these traits are learned within the context of the family environment (Guglielmino et al. 1995). We thus expect that verticality should be recovered by examining correlations with linguistic distances, as language relationships should reflect some degree of human population history. Social traits do correlate significantly with language, but at no greater extent than economic/political traits. More interestingly, we find that social traits do not correlate with geographical distance; thus, while the phylogenetic co-variation with the social trait matrix is moderate, it is the predominant signal. Thus, like other authors (Hewlett and Cavalli-Sforza 1986; Guglielmino et al. 1995) we find that a vertical mode of cultural transmission plays a role in the patterning of social and kinship traits, and that in this domain, history matters. The second hypothesis proposed that economic/political traits should follow a more geographical pattern. In this case economic traits have significant partial correlations with both language and geography, but the geographical correlation is stronger, and is the highest partial correlation in the analysis. Subsistence traits such as (for instance) “dependence on fishing” and “types of crops” comprise approximately half of the economic/political traits used to derive the matrix: as these sorts of cultural features depend heavily on the type of environment the society is situated within, it is unsurprising that we find a strong geographic signal.

4.3.8.1 Alternative models

None of the matrices were highly correlated (above r =.5) with any particular model, indicating that explanations other than historical or geographical relationship may account for the patterns in the data. Adaptation and innovation may account for some of the remaining variation, although it is likely that random factors and high rates of cultural change may have erased the phylogenetic and geographic signals of the original spread of these peoples across the Pacific. In Polynesia, post-settlement voyaging continued in some areas up until 1450 BP (Rolett 2002), further clouding the picture. Indeed one would expect the strongest phylogenetic signals in traits that are neutral, and, other than language, many cultural traits may well not be. Nonetheless, given the coarse and uneven grain at which the cultural traits have been examined, the persistent and significant correlations are noteworthy.

4.4 Nearest neighbour analysis

4.4.1 Aim

To examine the transmission mode of individual cultural traits. A “nearest neighbour” approach was taken following Holden (1999). This asks the question: For each trait in each society, does the geographic or phylogenetic nearest neighbour best predict the state of the cultural trait?

4.4.2 Phylogenetic and geographic nearest neighbours

Holden and Mace (1999) defined 76 worldwide societies’ phylogenetic and geographic nearest neighbours and used them as predictor variables in a multiple regression on five bio-cultural variables associated with sexual dimorphism. They found a significant phylogenetic relationship with sexual dimorphism in four of the traits and a significant geographic relationship with two. Though this analysis provided a useful method for examining the horizontal and vertical transmission of individual bio-cultural traits, it has not been applied to other sorts of cultural data. Here I use a modified form of their method on all individual traits in the EA across the 80 Austronesian cultures on a linguistic phylogeny.

4.4.3 Estimating nearest neighbours

The dichotomised *Ethnographic Atlas* was used (see §4.3.6.1). For each cultural trait I found the state in each society, the state in that society’s phylogenetic nearest neighbour, and that society’s geographic nearest neighbour. Appendix B lists the traits investigated and how they were categorised. Geographic nearest neighbours (GNN) were found in the distance matrix prepared for the Mantel tests (§4.3.6.3). Phylogenetic nearest neighbours (PNN) were found on a linguistic phylogeny of 80 societies with full data in the *Ethnographic Atlas*. This was a single shortest tree found under parsimony using *PAUP**, described in Chapter Two.

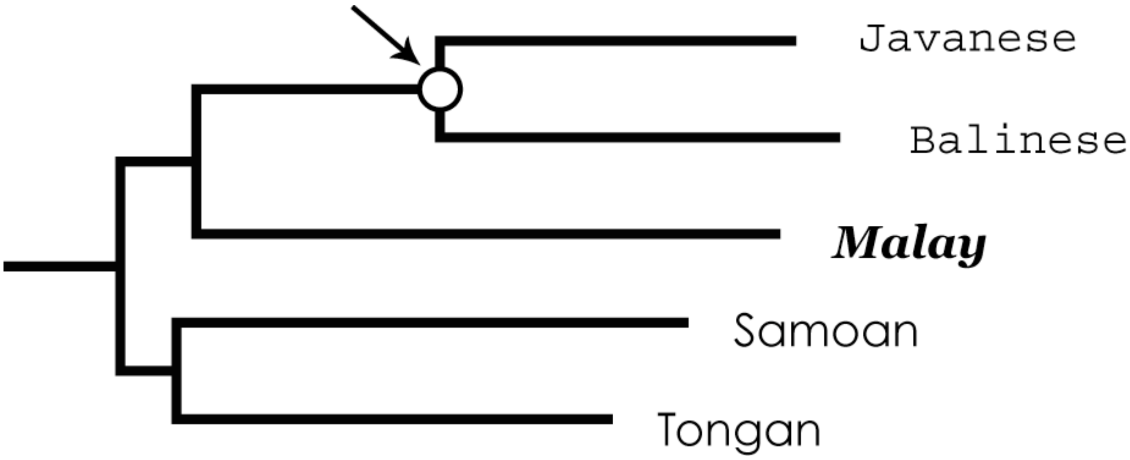


Figure 4.3. Estimation of phylogenetic nearest neighbours. The nearest neighbour for Javanese is Balinese (they are *sister-taxa*, indicated by the same font). Similarly, the nearest neighbour for Samoan is Tongan. However, the nearest neighbour for Malay is the internal node indicated by the arrow. A simple method to determine state at an internal node is to average the trait value over the concordant clade. For example, if Javanese was “2” and Balinese was “4” on some continuous variable, Malay’s phylogenetic nearest neighbour might have a value of “3”. More principled likelihood methods of probabilistic reconstruction take into account how the trait is evolving over the whole phylogeny, for example, by assessing how common values of “4” really are. Likelihood methods can also calculate node values for discrete characters.

The PNN for each culture is either a tip or a node (Figure 4.3). While the state of each tip is readily available, we must calculate the likely state of the trait at the internal node. The maximum-likelihood method of Discrete (Pagel 1994) was used to estimate the state of the PNN when this was a node. *BayesMultiState* (Pagel and Meade 2005) provides a probabilistic estimate (between 0 and 1) that the trait is state 0 or 1, using an explicit model of evolution and the information on branch lengths contained in the phylogeny. This method is described in full in Chapter Three. The presence of the trait was only assumed when 100 maximum-likelihood tries provided an average likelihood over 70 percent that the trait was state 0 or 1. If the method was unable to provide an estimate of a society's PNN for any trait, that trait was not examined for that society. This is a conservative measure that takes into account the uncertainty in reconstructing the node on the phylogeny. As such, spurious phylogenetic relationships are very unlikely to occur.

4.4.4 Logistic regression analysis

All traits tested by Holden and Mace (1999) were continuous and allowed a standard linear regression to be used. For these data, logistic regression was the most appropriate form of analysis as it deals with multiple binary predictor variables and a binary dependent variable. Logistic regression applies maximum likelihood estimation after transforming the dependent into a logit variable (the natural log of the odds of the dependent occurring or not) (Hosmer and Lemeshow 2000). In this case, we examine each cultural trait separately and use a model where the variables PNN and GNN predict the state of the trait in each society. No interaction term was included, as we are interested in comparing geographic and phylogenetic similarity with other studies, none of which have controlled for their (undoubtedly present) collinearity between geography and phylogeny. Regressions including an interaction term (not reported) returned a significant interaction in less than one-quarter of the tests.

Forced entry (block) logistic regression analysis was run on each separate cultural trait using *SPSS 12* for Mac. Results are summarised in Table 4.2 and reported in full in Table 4.3, along with their model of cultural transmission.

Table 4.2. Summary results of nearest neighbour analysis.

	Model		
Trait class	**Geography**	**Phylogeny**	**Both**
Economic/subsistence	5/29 (.17)	7/29 (.24)	1/29 (.03)
Social/kinship	7/37 (.19)	9/37 (.24)	2/37 (.05)
All	12/66 (.18)	16/66 (.24)	3/66 (.04)

4.4.5 Results of nearest neighbour tests

Due to the small number of data points in many comparisons, approximately half the results were not associated with any model—a problem also found by previous researchers (Guglielmino et al. 1995). While the logistic method of regression is the only appropriate method for these data, it may not be powerful enough to detect correlations between two binary variables with a small sample size. The summary table shows that the state of the PNN predicted slightly more traits (16/66) than the state of the GNN (12/66). Three traits were associated with both models. There are no differences between economic/subsistence and social/kinship traits with respect to the models they are associated with. Of the nine economic/subsistence traits predicted by their PNN, it is notable that five are to do with animal husbandry and domestication. All economic/subsistence traits predicted by GNN concern crop-type and mode of subsistence. Of the social/kinship traits predicted by PNN, 5/11 are concerned with descent and inheritance, although "ambilineal descent" is predicted by GNN. Five of the ten social/kinship traits predicted by GNN are concerned with marriage transaction rules and cousin marriage prescriptions.

Table 4.3. Binary logistic regression on geographic and phylogenetic nearest neighbours to predict the presence of a cultural trait in a society.
Model: *G,* geographical nearest neighbour, *P*, phylogenetic nearest neighbour. Significance values are asterisked: * *p* < .05, ** *p* < .01, *** *p* < .001

	Model	**β**	**S.E.**	**Wald**	**Sig.**	**Exp(β)**
Economic and subsistence traits						
Gathering	G	.563	.734	.588	.443	1.756
	P	.589	.666	.781	.377	1.802
Hunting	G	.150	.617	.059	.808	1.162
	P*	1.298	.600	4.671	.031	3.661
Fishing (low)	G**	2.116	.757	7.823	.005	8.301
	P	.986	.759	1.687	.194	2.680
Fishing (high)	G**	-2.027	.723	.7867	.005	.133
	P	-1.267	.727	3.036	.081	.282
Animal Husbandry (low)	G	-.799	.739	1.169	.280	.450
	P***	1.584	.593	7.126	.008	4.872
Animal Husbandry (high)	G	1.538	1.501	1.049	.306	4.654
	P***	5.003	1.515	10.909	.001	148.797
Agriculture (low)	G	1.099	.843	1.700	.192	3.000
	P	1.099	.773	2.020	.155	3.000
Agriculture (high)	G	.291	.843	.119	.730	1.338
	P	.628	.767	.670	.413	1.873
Extensive/shifting agriculture	G	1.083	.894	1.469	.225	2.954
	P	.172	.809	.045	.831	1.188
Horticulture	G*	1.491	.713	4.371	.037	4.442
	P*	1.478	.703	4.419	.036	4.386
Intensive irrigated agriculture	G	.864	1.081	.639	.424	2.373
	P	.987	1.019	.940	.332	2.684
Crops: tree fruits	G*	1.606	.714	5.060	.024	4.985
	P	-.076	.758	.010	.920	.927

Table 4.3. *Continued.*

	Model	**β**	**S.E.**	**Wald**	**Sig.**	**Exp(β)**
Crops: roots/tubers	G*	1.302	.554	5.528	.019	3.677
	P	.256	.551	.216	.642	1.292
Crops: grain	G***	3.894	.770	25.595	.000	49.089
	P	-.450	.758	.352	.553	.638
Plow absent	G	1.230	.767	2.574	.109	3.421
	P	.452	.761	.353	.552	1.572
Plow aboriginal	G	-.516	1.481	.121	.728	.597
	P	2.619	1.425	3.378	.066	13.716
Domesticates: absent	G	-.364	1.084	.113	.737	.695
	P***	3.240	.823	15.489	.000	25.543
Domesticates: pigs only	G	.327	.538	.370	.543	1.387
	P**	1.637	.534	9.405	.002	5.137
Domesticates: bovine	G	1.488	.928	2.570	.109	4.426
	P*	1.926	.902	4.562	.033	6.859
Metalworking	G	.963	1.000	.928	.335	2.620
	P***	3.540	1.003	12.447	.000	34.470
Fishing: males predominant	G	-.427	.505	.716	.398	.652
	P	.504	.495	1.037	.309	1.656
Agriculture: males predominant	G	.775	.629	1.514	.218	2.170
	P*	1.319	.610	4.680	.031	3.740
Agriculture: labour division equal	G	-.591	.508	1.353	.245	.554
	P	-.118	.505	.055	.815	.888
Agriculture: females predominant	G	-.969	1.196	.656	.418	.379
	P	1.655	1.025	2.608	.106	5.234
House: ground floor	G	.448	.488	.843	.359	1.566
	P	.572	.496	1.330	.249	1.771
House: platform floor	G	1.420	.735	3.729	.053	4.136
	P	.702	.769	.835	.361	2.019

Table 4.3. *Continued.*

	Model	β	S.E.	Wald	Sig.	Exp(β)
House: raised floor	G	9.166	39.946	.053	.819	9563.61
	P	-7.740	39.948	.038	.846	.000
Hamlets	G	-.360	.841	.183	.669	.698
	P	.972	.816	1.417	.234	2.642
Compact settlements	G	-.763	.903	.713	.398	.466
	P	1.307	.906	2.079	.149	3.693
Social and kinship traits						
Brideprice	G*	1.289	.591	4.749	.029	3.629
	P*	1.289	.591	4.749	.029	3.629
Gift exchange for wives	G	1.135	.950	1.425	.233	3.110
	P	-.197	1.076	.034	.855	.821
No marriage transactions	G**	1.532	.573	7.146	.008	4.626
	P*	1.188	.554	4.597	.032	3.280
Monogamous nuclear family	G	-7.530	29.870	.064	.801	.001
	P	.580	.888	.427	.514	1.786
Polygynous families	G	-.022	.591	.001	.970	.978
	P	.531	.545	.949	.330	1.701
Extended families	G	-.418	.503	.693	.405	.658
	P	.607	.502	1.461	.227	1.835
Monogamy	G	.733	.642	1.304	.254	2.081
	P	.733	.642	1.304	.254	2.081
Polygyny	G	-.169	.585	.083	.773	.845
	P	.956	.577	2.746	.097	2.602
Patrilocality	G	.209	.489	.184	.668	1.233
	P	.445	.496	.804	.370	1.560
Ambi/neolocality	G	9.807	51.464	.036	.849	18155
	P	-17.67	69.814	.064	.800	.000

Table 4.3. *Continued.*

	Model	**β**	**S.E.**	**Wald**	**Sig.**	**Exp(β)**
Matrilocality	G	-1.109	1.017	1.189	.276	.330
	P	1.451	.985	2.172	.141	4.268
Alternate form of residence	G	.007	.492	.000	.988	1.007
	P	-.483	.485	.993	.319	.617
Agamous communities	G	.862	.585	2.171	.141	2.369
	P	-.117	.583	.040	.841	.889
Segmented communities	G**	1.523	.564	7.283	.007	4.584
	P	-.538	.573	.883	.347	.584
Single community patrilineages	G	1.951	1.012	3.721	.054	7.037
	P**	2.554	.900	8.050	.005	12.855
Multiple-community patrilineages	G*	1.533	.685	5.010	.025	4.631
	P	-.242	.773	.098	.754	.785
Matrilineages	G	.537	.560	.919	.338	1.711
	P	.712	.600	1.407	.235	2.037
Cognatic descent	G	-.792	.533	2.207	.137	.453
	P**	-1.464	.540	7.342	.007	.231
Unilineal descent	G	.898	.540	2.773	.096	2.456
	P**	1.540	.544	8.010	.005	4.665
Marriage: first and/or second cousins	G*	-1.004	.508	3.9110	.048	.366
	P*	-1.029	.522	3.882	.049	.357
Marriage: no cousins	G**	1.562	.601	6.761	.009	4.768
	P	.360	.594	.366	.545	1.433
Preference for type of cousins	G**	2.569	.972	6.982	.008	13.059
	P	-2.145	1.119	3.672	.055	.117
Eskimo	G	.556	1.118	.247	.619	1.744
	P*	2.162	.963	5.039	.025	8.689

Table 4.3. *Continued.*

	Model	**β**	**S.E.**	**Wald**	**Sig.**	**Exp(β)**
Hawaiian	G	-.297	.518	.329	.566	.743
	P	.888	.524	2.870	.090	2.431
Iriquois	G*	1.576	.725	4.726	.030	4.836
	P	-.131	.787	.028	.867	.877
Descent: patrilineal	G	.841	.780	1.164	.281	2.319
	P	.524	.807	.422	.516	1.689
Descent: matrilineal	G	.268	.764	.123	.726	1.308
	P*	1.596	.697	5.248	.022	4.932
Descent: ambilineal	G**	1.666	.614	7.367	.007	5.290
	P	1.027	.609	2.845	.092	2.794
Descent: bilateral	G	1.827	1.070	2.914	.088	6.217
	P	1.017	.944	1.159	.282	2.764
Descent: mixed	G	1.504	1.484	1.027	.311	4.500
	P	-8.731	36.454	.057	.811	.000
No classes	G	.703	.848	.689	.407	2.021
	P	.703	.848	.689	.407	2.021
Wealth distinction	G	-.384	1.126	.117	.733	.681
	P*	2.230	1.055	4.468	.035	9.298
Elaborated class distinctions	G	.243	.543	.200	.654	1.275
	P	.665	.559	1.414	.234	1.944
Slavery	G*	2.509	1.004	6.245	.012	12.288
	P	.920	.908	1.028	.311	2.510
Former presence of slavery	G	1.955	1.101	3.154	.076	7.065
	P*	2.406	.929	6.710	.010	11.090
Hereditary succession to office	G	.059	.521	.013	.909	1.061
	P*	.981	.519	3.569	.049	2.668
Non-hereditary succession	G	-.475	.510	.869	.351	.622
	P	1.566	.840	3.479	.062	4.788

4.4.6 Nearest neighbour tests: Discussion

Using a nearest-neighbour regression method I found that phylogenetic nearest neighbour predicted the state of slightly more cultural traits than did geographic nearest neighbour. There was no difference between “economic” and “social” classes of traits with respect to PNN and GNN. Compared with these results, Guglielmino et al. (1995) found that economic traits (their “Economy” and “Social stratification”) were explained well by all three modes of transmission, and in their later paper (Hewlett et al. 2002) these authors found phylogeny to explain many social stratification traits. Similarly in the present analysis, three of the four significant social stratification traits (“wealth classes”, “former slavery”, and “hereditary succession”) were predicted by the PNN. It is interesting to note that those traits that involve heritable resources—either material resources, such as domesticated animals, or social resources, such as the presence of slavery—seem to be those that show strong phylogenetic signal. It is almost as though important parent-offspring transmission of the means of subsistence at the micro-level is still of relevance when explaining macro-level cultural variation. This could be construed as a form of niche construction (Laland, Odling-Smee, and Feldman 2000), that is, whereby individuals modify the source of natural selection in their own environment. In this case, by creating forms of heritable resources, individuals create selection pressures for subsequent generations to continue to transmit such a strategy vertically.

The Austronesian language family is one of several worldwide associated with an agricultural dispersal (Diamond and Bellwood 2003). Over half of the economic traits predicted by the PNN are concerned with animal domesticates. Archaeological evidence from Lapita sites throughout Oceania reveal a consistent “package” of pig, dog and chicken transported as domesticated animals (Lynch 1991; Kirch 1997; Spriggs 1997), while the presence of bovine animals such as the Asian water buffalo and Bali cattle appear to be concentrated in a restricted set of societies in Island

Southeast Asia (Lau et al. 1998). Plant-based subsistence traits, however, are associated with geography. It may be that horticultural or crop traits diffuse more readily than domesticated animals, being less “expensive” technologies. In addition, crop types are more likely to be constrained by type of ecological environment they are suited to, which may be reflected in geographical ranges. Animals, in the societies that possess them, are frequently consumers of household waste (e.g. pigs) and not subject to such ecological constraints. In addition, animals may represent heritable wealth, and as such may be more likely to be conserved vertically.

Kinship traits concerning descent and inheritance were frequently associated with phylogeny in this analysis. Descent systems (e.g. cognatic or unilineal descent) structure patterns of relationship, defining who is kin and who is not, and to whom rights and wealth will be accorded. As such, it is unsurprising that they follow a vertical sort of transmission. Descent systems, especially matriliny, are the subject of later comparative analyses (Chapters Five and Six); the results of the present analyses demonstrate that a phylogenetic method is necessary to control for non-independence (Galton’s Problem). However, ambilineal descent, where there is flexibility in the kinship system such that descent can be traced through either sex, is associated with the geographic model, and thus may co-vary adaptively with aspects of the environment.

4.5 Cultural transmission: Discussion

4.5.1 Comparison with previous work

Using Mantel matrix tests and a nearest neighbour approach, the analyses demonstrated that cultural trait variation was moderately but significantly correlated with both geographic proximity and phylogenetic relationship. Both historical and diffusion processes account for the patterns of cultural similarity in this group of Austronesian societies. We cannot compare the Mantel correlations and nearest-neighbour regression results directly, but we can compare the patterns in the findings. Mantel tests are probably closer to the previous analyses of Guglielmino et al. and Hewlett et al. in that they do not contain a strict, character-based control for phylogeny, but work on overall similarities. Mantel matrix analyses here showed a greater overall partial correlation of geographic versus phylogenetic distances with all cultural traits; however, it appeared that economic traits were responsible for this result. There was no association between social trait distances and geographic distances. Compared to previous results, which have found positive evidence of a greater relationship of social traits and a phylogenetic model, and ambiguous or low evidence for a geographic model associated with economic traits, we found the opposite: positive evidence for the association between geographic proximity and economic trait similarity. It may be that in the Pacific, more marginal and/or proscriptive environments such as atolls, where limited topsoil restricts crops to species such as *Colocasia* taro and coconuts (Barrau 1961) restrict the variation possible in subsistence systems compared to Africa, and geography thus accounts for more of the observed similarity.

The work of previous authors did not directly compute correlations with geographical distance but constructed a clustering index. This index indicated a similar degree (~.30) of geographic clustering for both social and economic traits, which the nearest-neighbour regression in the present study also found. The regression analysis showed an equal influence of phylogenetic and geographic effects across both types of cultural traits. Here a slightly higher effect of phylogeny was found overall, but it is not remarkable. In neither analysis was there positive evidence for phylogenetic transmission being of more than marginally *greater* importance than geographic transmission in respect to social traits overall. However, many kinship traits were predicted by a phylogenetic model.

A common criticism of the use of phylogenetic methods on cultural variation is that human societies borrow, impose, and generally diffuse aspects of their culture on other societies, potentially obscuring any historical signal. Geographic diffusion—trait "borrowing"—after the initial spread of the Austronesian language family approximately 5500 years ago (Bellwood 1997) should be expected to have the effect of washing out the initial signature of phylogenetic relationship. Although diffusion and adaptation are not mutually exclusive, and any trait borrowing could be for adaptive reasons, it is unlikely that this historical signal would be renewed through any subsequent (and exactly complementary) movements of people. Thus, any macroevolutionary cultural analysis should expect to find at least some evidence of geographic diffusion. We know that even in the case of the remote Polynesian islands there was post-colonisation trade and voyaging for a least some period of time, evidenced by the archaeological remains of volcanic glass and basalt adzes between far-flung islands in the Marquesas and Pitcairn groups (Weisler 1998; Rolett 2002). Given some certain degree of diffusion, it is unsurprising that the correlations with geographical distance should equal or be greater than those with linguistic distance, and in instances where they do not exist, in the case of social/kinship traits under the Mantel test, can be taken as strong evidence for historical signal.

4.5.2 Consideration of the methodologies

The nearest neighbour method was a conservative test, requiring a reliable estimate of the PNN to proceed. As such, for a number of the traits examined, the effective sample sizes were small (~40), and we may have lost statistical power to determine effects. The significant associations of GNN and PNN with individual cultural traits should therefore be seen as positive evidence under a stringent test and within a regional context. As well, they confirm the approach taken by Holden and Mace (1999) as a useful one, as it allows us to identify those traits that require a phylogenetic method in order to control for historical relationships.

Separate regression analyses (not shown) included an interaction term to assess the degree of collinearity in the data. Interaction terms were significant in less than one quarter of the traits, and did not consistently appear with significant GNN/PNN predictors. Thus, there is some degree of collinearity between phylogeny and geography, but not in every trait, and not always when another significant predictor was found. The Mantel tests, by computing partial correlations, allowed us to hold these interaction effects constant.

Simple linear distance measures represent the opportunities for geographic diffusion in these analyses. Prevailing winds and currents may determine the frequency of interaction of ocean-voyaging societies more than does simple proximity. In addition, we cannot be certain if a unit of geographic distances across land presents an equal conduit or barrier for interaction than the corresponding unit of distance across the ocean. With such a widely spread language family as Austronesian, we might assume that past a certain point all distances are equally far (and thus equally unlikely). However, using log-transformed distances did not indicate such an effect. It may be that societies form chains of interaction spheres, so that even though individuals from one place do not visit or encounter individuals from a far-distance place, cultural traits do diffuse along overlapping sets of pairwise societies. For further resolution it would be desirable to draw from models of ocean voyaging such as Irwin (1992) to weight sets of neighbours as more or less likely according to variables such as currents or target island size.

4.5.3 Conclusion

Phylogenetic and geographic transmission are associated with different traits, indicating that the *type* of cultural trait under study may be subject to differing evolutionary forces. When modelling cultural transmission, we cannot assume a "one-mode-fits-all" model. Importantly, the results of the second analysis suggest that a phylogenetic model that controls for the effects of shared ancestry is relevant when examining descent-related cultural traits, and suggests that even in vastly different environmental and cultural contexts (Africa versus the Pacific), similar patterns of cultural transmission may account for cultural diversity in descent traits. These issues are explored further in the comparative analyses in Chapters Five and Six.

CHAPTER FIVE

ANCESTRAL STATES OF DESCENT AND RESIDENCE

> Systematic comparison of Oceanic cultures should enable us to reconstruct in large measure the shape of the parent culture.
> (Goodenough 1957:154)

5.1 Summary

Descent groups and post-marital residence patterns are important facets of social organisation, as they determine where and how individuals associate with kin and invest their resources. Descent and residence in Austronesian societies is variable and hypotheses about the ancestral states of these traits abound in the literature, although none have been formally tested. Here I use a Bayesian MCMC comparative method to estimate the ancestral states of (i) descent and (ii) residence at each node in a sample of 1000 language trees. The cultural traits are examined with both binary and multi-state coding to tease apart the evolution of social organisation. Measures of certainty in the ancestral states are estimated and combined with measures of phylogenetic uncertainty. Model likelihoods vary systematically over the tree sample, indicating that phylogenetic control is necessary. Early Austronesian social organisation is reconstructed to have bilateral descent groups and inheritance, with matrilocal residence. Lineal systems are later developments in the tree; patrilineality characterises Near Oceania and Polynesia, matrilineality characterises Micronesia. The hypothesis of matricentric kinship in Proto Oceanic society is supported by the data. Residential flexibility is an ancient Austronesian feature. Results are interpreted in the light of the theoretical models of Austronesian kinship and the ethnographic literature.

5.2 Introduction

Robin Fox began *Kinship and Marriage* (1967:27) with the observation that his subjects were about “the basic facts of life”. While anthropology’s approach to what was once its core concern has changed drastically since then (Holy 1996), becoming particularist to the point where cross-cultural notions of kinship are regarded as merely a product of Western bias (Schneider 1984), evolutionarily-minded social scientists still treat kinship as fundamentally important in understanding general principles of human social behaviour. Two aspects of kinship that can determine with whom an individual associates are (i) descent and (ii) residence, and their rules may influence one another. Descent systems are ways in which societies stipulate who is and who is not kin, while residence rules state where individuals live.

5.2.1 Descent

Individuals may be genealogically related to many other people, but in most societies, there are descent groups that circumscribe only a portion of those relatives (and perhaps include other non-relatives) to be recognised as kin. Thus, descent systems track the group membership of relatives one considers close kin, sometimes in a quite different way from what simple quotients of biological relatedness would suggest (Sanderson 2001). Inheritance, rights and obligations, the regulation of marriage, and social and material assistance are all affected to some degree by kinship rules that stipulate who is and is not regarded as part of one’s descent group. From an evolutionary point of view, descent rules determine where individual invests her time and resources, and these rules may be seen as expressing forms of parental or kin investment (Trivers 1972; Clutton-Brook 1991). Cross-cultural variation in descent rules thus presents an intriguing set of questions for evolutionary theory to address.

Descent systems fall into two broad categories (Fox 1967; Holy 1996). *Unilineal* descent means that an individual is a member of one, non-overlapping kin group, traced through either one's father's male ancestors (patriliny) or one's mother's female ancestors (matriliny). More rarely, some societies have double descent, meaning that both patrilineal and matrilineal groups are present; Austronesian examples include Pukapuka in Polynesia and the Caroline Islands in Micronesia (Damas 1979). Ambilineal descent is a special case of lineal descent where individuals choose to affiliate with mother's or father's descent line without set rules (Firth 1957). This choice may be an active consideration by an individual or their parents, or it may be the result of gradual fulfilment of various rights and obligations that lead to adult membership in one group at the expense of another. Ambilineal descent is found frequently in Austronesian societies, such as Kiribati in Micronesia, where individuals may belong to many ancestors' descent groups, but main affiliation is determined by the parents' place of residence and the ongoing participation in lineage-specific activities (Lambert 1966).

In contrast, *non-unilineal* descent occurs when individuals trace kin relationships in often overlapping kin groups; these can be through ancestors of either or both sexes. Bilateral and cognatic systems fall under this heading. Modern English family organisation follows a bilateral principle; an individual's network of relatives "on either side" is unique and does not form a permanent, enduring lineage, persisting only through her lifetime. Fox (1967:169) makes this distinction:

> [W]hat matters is not so much the division into unilineal and cognatic, as the difference between the *ego-focus* on the one hand with its personal 'groups', and the *ancestor-focus* on the other with its descent groups.

Partly as reaction to the proliferative taxonomy of descent nomenclature, in the middle of the 20th century anthropologists suffered some anxiety over whether ancestor-oriented yet non-unilineal societies had "descent groups" in the sense that Africanist anthropologists had come to use the concept (Goodenough 1955; Davenport 1959; Leach 1962). These "cognatic" forms of social organisation were especially common in Southeast Asian and insular Pacific societies, such as the Maori (Firth 1957; Scheffler 1964). Kirch and Green (2001) use Levi-Strauss' (1982) "House society" concept in their reconstruction of kinship in Ancestral Polynesian Society, as does Fox (1993, 1995) for societies in Island Southeast Asia. Irrespective of notions of "ascent" (Fox 1995) versus descent, and other debates about lineage models (Howard and Kirkpatrick 1989), a House society is a social unit that is time-enduring, holds fixed property (both land and houses), and acts as an organising principle for the transmission of resources, be they material or social (Kirch and Green 2001). From an evolutionary perspective, the continuity of a kin group through time, and its association with the transmission of resources is sufficient cause to regard such societies as having descent groups that set them aside from bilateral kin systems.

While rules of descent may determine who is kin, the rules may differ according to the type of behaviour or purpose being specified. For instance, rules for the inheritance of land may differ from those that determine inheritance of titles or movable property, or obligations for assistance, or access to marriage partners. The Lakalai of New Britain, as described by Chowning (1966), have mostly-exogamous matrilineal units to which people belong by birth; these "sibs" share resources such as land and a water supply, transmit certain food taboos and offer solidarity in times of feuding. However, a person is also bound by ties of obligation to a bilateral hamlet, and men transmit some private property such as pigs to their sons. The Lakalai consider their matrilineal sibs to be permanent and enduring aspects of their kinship (1966:499). Thus, although there are most certainly nuances of human social behaviour that cannot be encapsulated with simple classification schemes, the kinship categories described above capture a significant dimension of the cross-cultural variation in how people organise their kin relationships. Like the simplifying assumptions made in all forms of biological comparison, basic kinship categories are a useful starting point for an eventual understanding of the evolutionary dynamics of social organisation. Figure 5.1 shows traditional kinship diagrams representing the common categories.

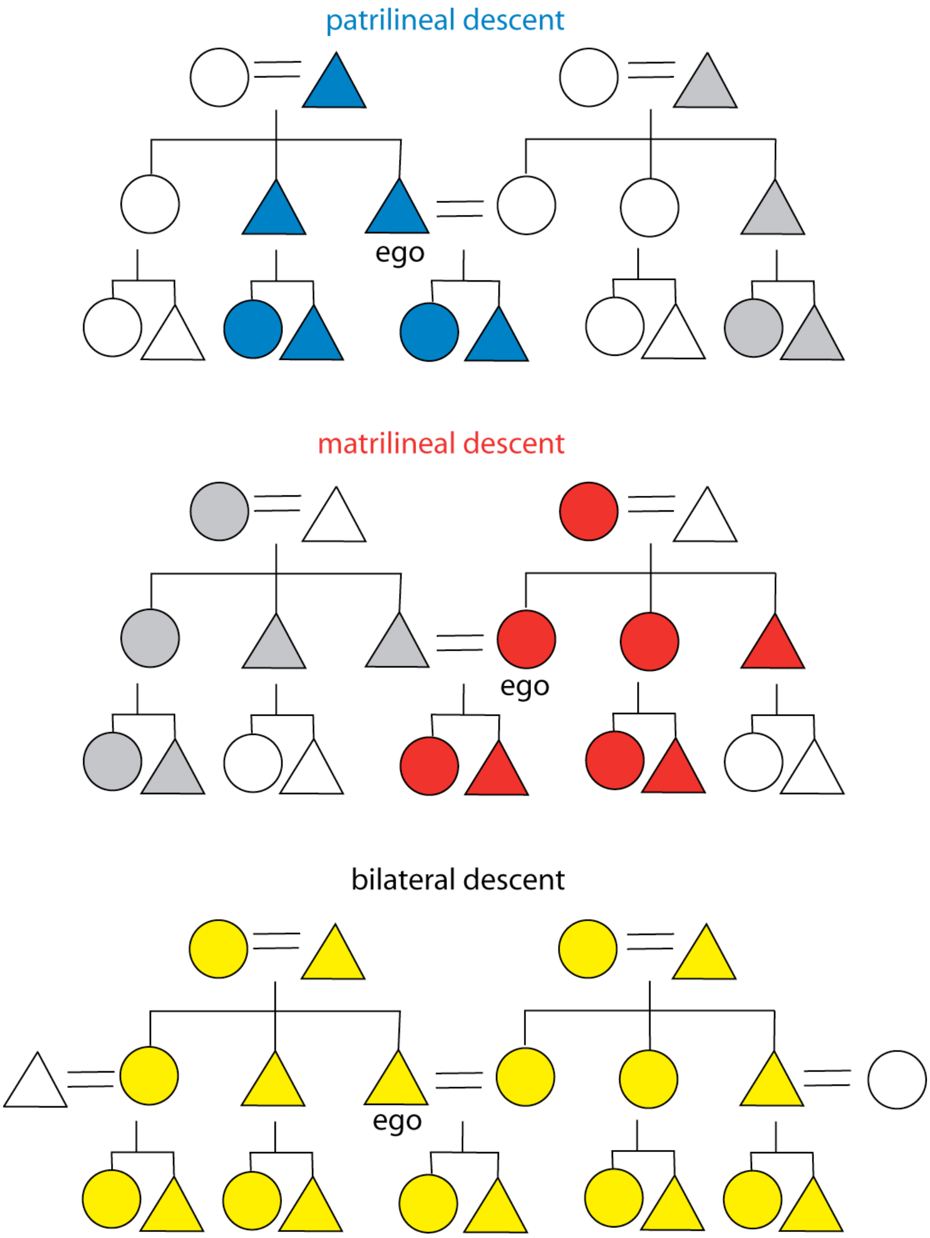


Figure 5.1. Traditional kinship diagrams. Circles represent females, triangles represent males. Marriage relationships are denoted by = (double horizontal lines), descent relationships by | (vertical lines) **Top**. Patrilineal descent, showing Ego's patriline in blue. Members of another patriline are shown in grey. **Middle**. Matrilineal descent, showing Ego's matriline in red. Members of another matriline are shown in grey. **Bottom**. Bilateral descent, showing Ego's kindred in yellow. In bilateral descent, the degree of relationship fades the further up and out from Ego one progresses.

5.2.2 Residence

Individuals are generally affiliated with some descent group(s) at birth, but newlywed couples face the choice of determining with whom to live, and consequently to which group their children will belong. Thus, post-marital residence rules are related to a society's descent system. Patrilineal descent usually occurs with patrilocal residence, where the wife lives with the husband's kin. This pattern is the most common worldwide (Murdock 1949:38), occurring in about 70 percent of societies (Levinson and Malone 1980:101). Similarly, matrilineal descent usually occurs with matri- or avunculocality (residence with the maternal uncle of the husband). Cognatic, bilateral, and ambilineal descent may often co-occur with ambilocality, where newlyweds choose with which set of parents or kin they will reside. However, while descent and residence rules often co-vary together in a systematic fashion (Levinson and Malone 1980:102), they do not do so exclusively (Murdock 1949:59, Table 9). This co-variation is the subject of Chapter Six. Here, I concentrate on the separate dynamics of descent and residence.

5.2.3 Austronesian descent and residence

The Austronesian-speaking cultures of the Pacific represent a close approximation of the range of worldwide cross-cultural variation in descent and residence (Lane 1961). Parts of the Austronesian world may be characterised as having predominately one type of descent system, such as the "matrilineal sea" of Micronesia (Weckler 1953), but the distribution of variation is not entirely regular. The diversity of descent and residence systems in the 67-society data set is shown in Figures 5.2, 5.3, and Table 5.1. This diversity means that Austronesian societies are a useful regional case with which to test hypotheses about the evolution of kinship organisation.

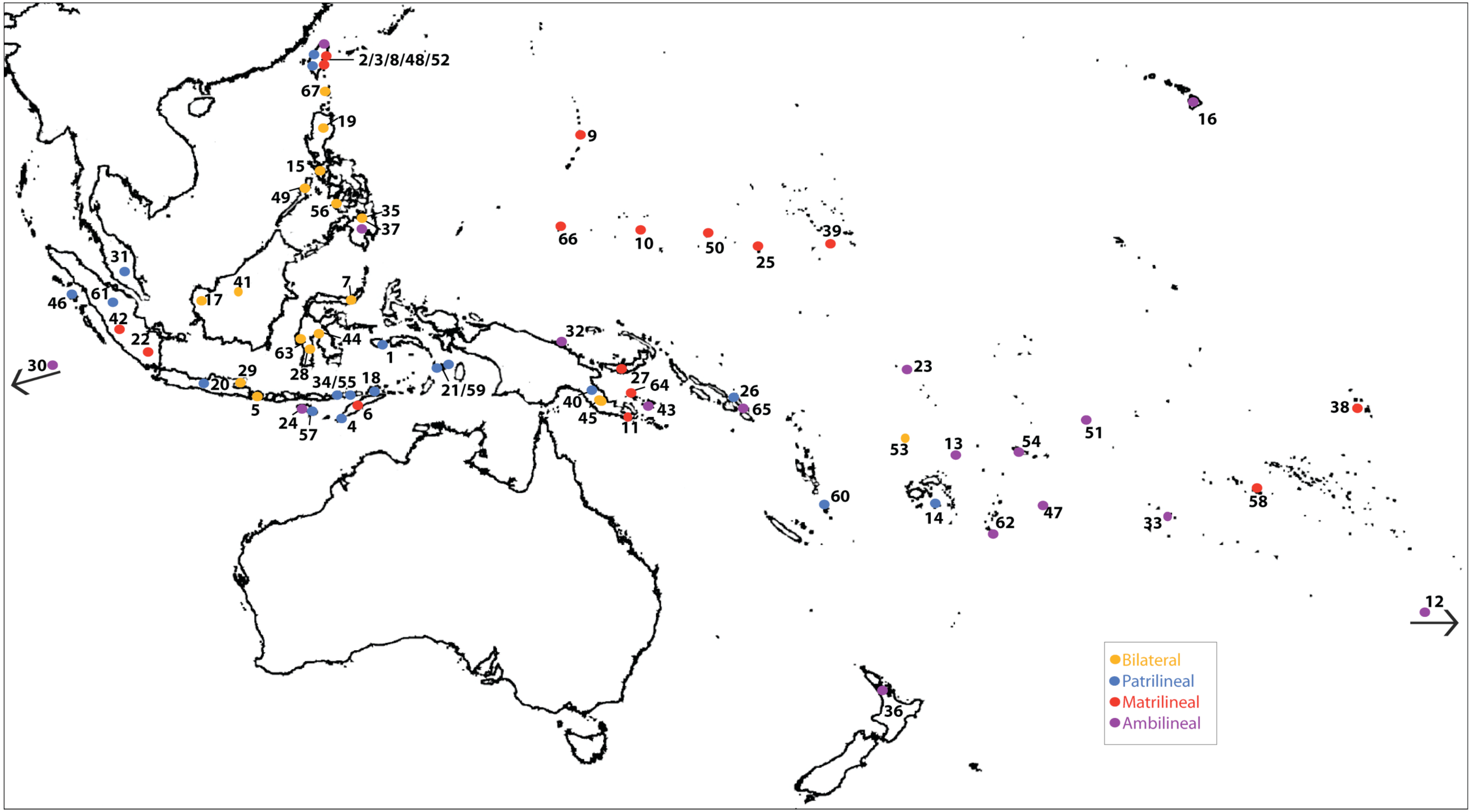


Figure 5.2. Geographical distribution and form of descent in 67 Austronesian societies. Numbers correspond to Table 5.2

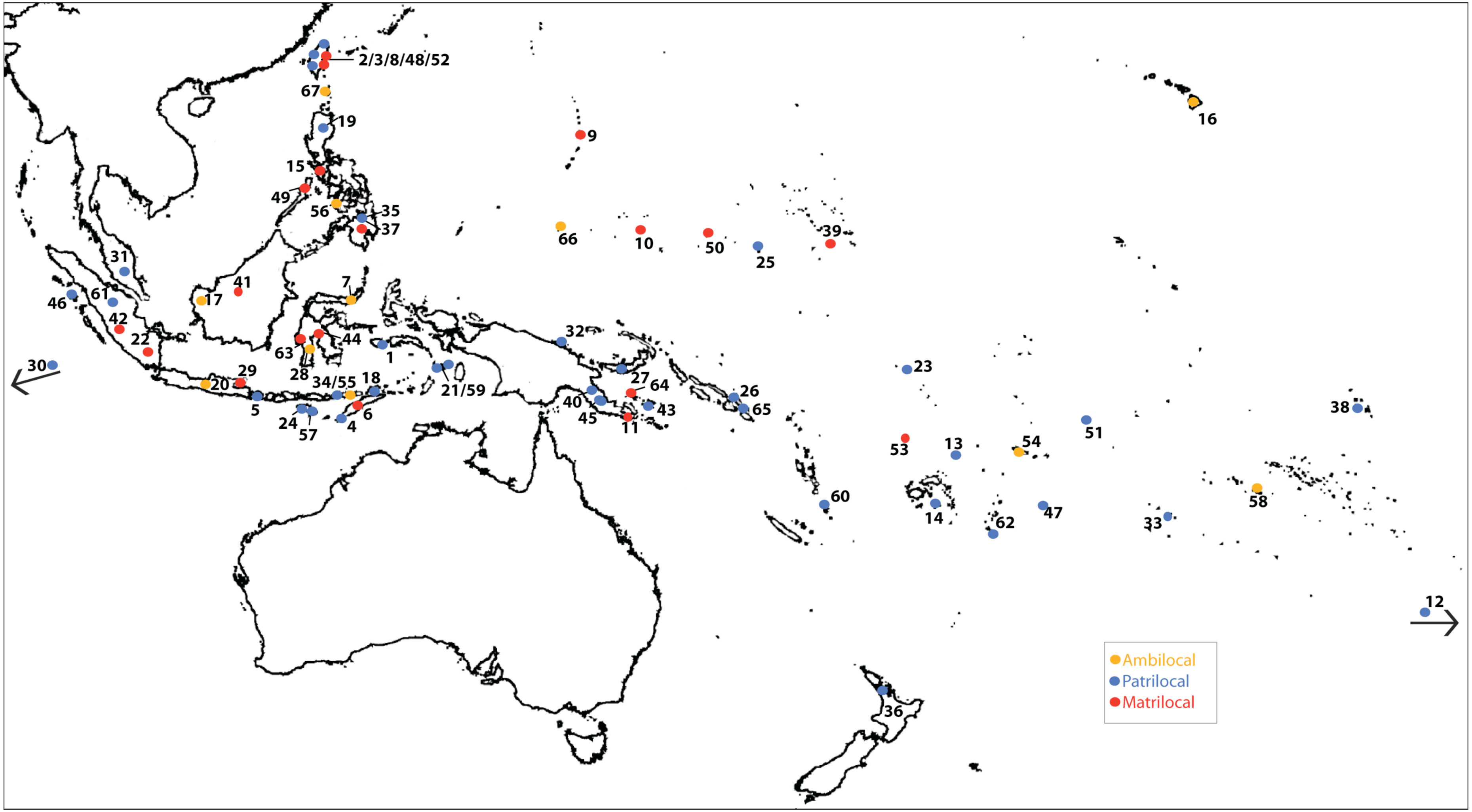


Figure 5.3. Geographical distribution and form of residence in 67 Austronesian societies. Numbers correspond to Table 5.2

Table 5.1 Types of descent and residence, and their frequencies worldwide and in the 67-society Austronesian sample.

	Description	Frequency	
		Worldwide	**Austronesian**
Descent			
Patrilineal	Affiliation with kin of both sexes through father's male line only	.40	.21
Matrilineal	Affiliation with kin of both sexes through mother's female line only	.16	.18
Ambilineal	Affiliation with kin through either mother or father dependent on context; may be regulated through residence and obligation	.03	.22
Duolateral	Affiliation with both mother's line and father's line but for separate contexts	.06	.16
Bilateral	Affiliation with both mother's and father's kin irrespective of sex	.35	.22
Residence			
Patrilocal/Virilocal	Residence with husband's kin	.70	.53
Matrilocal/Uxorilocal	Residence with wife's kin	.11	.24
Avunculocal	Residence with maternal uncle of husband	.06	.06
Bilocal/Ambilocal/ Duolocal	Residence is established optionally with kin of either spouse	.08	.13
Neolocal	Residence apart from kin of both spouses	.05	.03

1. Descent: Worldwide frequencies from Standard Cross-Cultural Sample (Murdock and White 1969)
2. Residence: Worldwide frequencies from Levinson and Malone (1979:101) based on *Ethnographic Atlas* data.

Table 5.1 lists definitions and frequencies for the types of descent and residence found in the 67-society Austronesian sample. Comparing these figures with frequencies found worldwide, the Austronesian region has higher numbers of ambilineal and duolateral societies, as well as less patriliny. As well, there are more matrilocal and "multilocal" residence patterns found in Austronesian cultures, and comparatively less patrilocal residence. However, the general patterns are fairly representative of worldwide diversity, compared with other regions such as Europe, with a predominance of bilateral kinship, and Africa, with mostly lineal systems (Murdock 1949, Goody 1976).

5.3 Ancestral states

Cultural behaviours do not fossilise, nor do they leave clear traces in the archaeological record, so the nature of ancestral Austronesian kinship systems remains an open question. In order to ultimately explain the causative processes of cultural change that have led to the observed distribution of cultural diversity, we need to estimate the probable ancestral states of descent and residence.

Conjecture about the ancestral state of kinship systems in Austronesian prehistory has concentrated on two stages: the early Proto Austronesian and Proto Malayo-Polynesian stage (PAN, PMP, c. 6-4500 BP), and the development of Proto Oceanic (POC) society, c. 3500 BP. Here, I borrow the linguistic convention of naming a hypothetical ancestral language "Proto X" where X is a language subgroup, and denote a hypothetical ancestral society as "Proto X" in a similar fashion. This is not to imply that any "Proto Society" was necessarily a single homogenous entity at a defined point in time, but, to the degree we can reconstruct ancestral forms for a group of ethnographically attested societies, this serves as a convenient shorthand. This approach is similar to that taken by Kirch and Green (2001) for "Ancestral Polynesian Society". At the very least, there is some evidence that the Proto Oceanic stage may coincide with the archaeological horizon of the Lapita tradition, and thus may refer to real populations with a degree of cultural, geographical, and biological overlap (Kirch 2000).

5.3.1 Debates in the literature: Bilateral or lineal?

One frequent point of contention is whether ancestral Austronesian societies had bilateral or lineal descent, and, if lineal, what form of lineality. Murdock (1949:228–31, 349–350), extrapolating from his theoretical model of descent-group development (since termed “main sequence theory” e.g. Levinson and Malone (1980)) concluded on the basis of kinship terminologies—that is, comparative terms for family members—that PMP and POC society lacked exogamous unilinear kin groups. He proposed that these ancestral societies were bilateral, lacked strict lineages, and had an Hawaiian form of social organisation, meaning that the only distinctions in kin terminologies were on the basis of age and sex. According to Murdock, any unilineal forms of social organisation in Austronesian societies were the product of later developments. On culture-distributional evidence he reconstructed the ancestral Malayo-Polynesian social system as having a bilocal extended family organisation; in effect, residence was a choice between the husband or wife’s kin. Kroeber (1919) had also examined kin terminology for Philippine groups and come to a similar conclusion that their common ancestor was bilateral, without descent groups.

Goodenough (1955) reconsidered Murdock’s claims by positing that land-owning lineages were necessarily present in PMP society because in a number of widespread Austronesian societies, individual rights to land were associated with kin group membership (1955:78). These groups, however, were determined by residence and co-existed within a bilateral kin organisation structure (e.g. the Kiribati *kainga,* the Ifugao *ooi*, and the Ulawan *komu*). By comparing Oceanic and Philippine societies, Goodenough also concluded that early AN residence may have been ambilocal. He noted that where residence became unilocal so as to clarify rights to land, it had a direct effect on the descent system: “where residence became patrilocal or matrilocal, these groups tended automatically to be transformed into patrilineal or matrilineal sibs and lineages" (1955:80).

In contrast, Lane (1961), following suggestions by Rivers (1914) and Burrows (1938), claimed that the bilateral descent systems present in Polynesia and other Oceanic societies represented a breakdown of earlier unilineal organisation. He recorded kinship patterns from Vanuatu, noting that societies previously attested as matrilineal had residence patterns and kin terminologies that suggested a shift to bilateral/ambilocal organisation. This shift he attributed to demographic factors, specifically depopulation, and he saw bilateral organisation as a flexible social response to the pressures of marginal Oceanic environments.

Linguistic work by Pawley (1979) reconstructed the POC term **kainanga* to mean "landholding descent group", where the cognate terms for this word in other Oceanic languages can denote the full range of descent group forms—patrilineal, matrilineal, and cognatic (Kirch and Green 2001). The inference here is that POC society had some form of lineal descent group associated with land tenure. Furthermore, comparative ethnolinguistic work by Blust (1980, 1993) revisited Murdock's evolutionary algorithm, pointing out that on Murdock's model PMP society could not only be reconstructed as bilateral and Hawaiian in kin terminology, but could equally have had ancestor-oriented (unilineal) kin groups, and a matrilateral organisation of marriage rules. Later examination of AN sibling terms by Blust (1993a) reiterated this argument and used comparative linguistic evidence to establish that Van Wouden's (1935) reconstruction of Eastern Indonesian kinship, which posited the exchange of marriage partners between matrilaterally related groups as central to social organisation, was indeed likely.

Comparative ethnography was the basis for Fox (1985) to conclude, like Murdock, that early Austronesian groups in Island Southeast Asian were originally bilateral, and that lineal systems grew out of earlier non-lineal ones. He surmised that the Southern Philippines was the origin for lineal organisation, which became more elaborate in eastern Indonesia. Burton et al. (1996), analysing social structure traits in world ethnographic "regions" via a statistical method using principal components analysis, concluded that Oceanic societies had a "matricentric orientation" even when they were classified as predominately cognatic or patrilineal. Bellwood (1997) attempted to summarise the comparative ethnographic work in this area, but could only conclude that early AN residence and descent could be equally reconstructed as unilinear/-local or cognatic/ambilocal. Clearly, there is as yet no consensus.

5.3.2 Were early Austronesian societies matrilineal?

In a more multi-disciplinary approach, Hage and colleagues (Hage 1998, 1999; Hage and Marck 2001, 2003) have re-examined Murdock's reconstructions for POC society. They revisited the reconstruction of Oceanic kin terminologies, especially those associated with matrilineal/matrilocal organisation, such as a distinct term for the mother's brother, and have argued from comparative ethnographic, distributional, and historical linguistic evidence that POC was very likely to be unilineal, specifically, matrilineal. In addition, Hage and Marck (2003) have used this concept of matrilineal social organisation in POC society to address questions in Pacific molecular anthropology. Recent genetic work highlights the differences in male- and female-specific inherited molecules, suggesting sex-specific differences in population interactions (Hurles et al. 2001, 2002). Molecular anthropologists have been interested in the colonisation of the Pacific for a number of years (Sykes et al. 1995; Melton et al. 1998; Lum and Cann 2000; Su et al. 2000), with the aim of "triangulating" (Kirch and Green 2001) evidence from genetics with linguistic, archaeology, and ethnography. Maternally transmitted mtDNA has for the most part concurred with the received view (Bellwood 1991; Bellwood 1997; Green 2003) of AN dispersal, but recent work on the paternally-transmitted Y-chromosome has suggested that more admixture took place than previously thought, with Y-chromosome diversity being much greater, much older, and more spread throughout Near Oceania (Kayser et al. 2000; Capelli et al. 2001).

Hage and Marck (2003) argue that these molecular findings are best accounted for in a model where POC society was matrilineal, that is, where migrating AN speakers incorporated diverse males (and their genes) into social groups whilst retaining a restricted, ancestral set of female-specific genetic markers. Disentangling the different molecular signatures left by males and females will only make sense in light of whichever kinship systems are presumed to be operating. Thus, reconstructing descent and residence rules may shed light on the interpretation of these genetic findings.

5.3.3 Evolutionary interpretations of kinship structure

Just as molecular anthropologists are now beginning to realise that knowledge of kinship structure is critical for interpreting their genetic findings (Oota et al. 2001; Wilkins and Marlowe 2006), the study of kinship itself has benefitted from evolutionary and ecological interpretations of the adaptive nature of social organisation. Traditional explanations for patriliny that have stressed male authority and social control over women gain an evolutionary interpretation where women are seen as the “ultimate scarce resource for men” (van den Berghe 1979:100). If a wealth surplus is possible, as in a traditional agricultural or pastoralist society, men should attempt to prioritise the use of wealth to increase their inclusive fitness by investing in their sons, on whose reproductive success resources will have a greater effect (Trivers and Willard 1973). They can do this by buying high quality wives (through brideprice) and/or more than one wife (through polygyny) (Goody 1976).

Matriliny, on the other hand, is much rarer than patriliny, but is still recurrent worldwide. Matriliny has been associated with horticulture and fishing (Aberle 1961), and with increased levels of paternity uncertainty (Gaulin and Schelgel 1980; Flinn 1981; Hartung 1981, 1985). Modelling wealth transmission in horticultural African groups, Holden, Mace, and Sear (2003) suggested that matriliny could represent a form of daughter-biased parental investment in societies where land is abundant but too unproductive to benefit sons more than daughters, as the degree of relationship to daughter's children will always be higher.

Bilateral systems, with their concentration on the nuclear family and flexibility, are hypothesised to be prevalent in small-scale societies without large amounts of (heritable) material wealth, such as foraging bands, and/or large-scale industrialised societies where kinship ties are secondary to reciprocal collectives, such as government states (Aberle 1961; ven den Berghe 1979).

5.3.4 Inferring ancestral states

At present, the ancestral states of descent and residence across the AN family remain open questions. A new way to approach these questions is to use comparative methods from evolutionary biology to reconstruct ancestral states. Biologists use information about the states of characters in present-day organisms to infer the ancestral states of those characters in the past. For example, Pfenniger et al. (2005) investigated the evolution of the curious "shell hairs" in *Trochulus* snails by constructing a phylogeny from genetic information, and plotting shell morphology and habitat features of each species onto the tree using a comparative method. They determined that having the shell hairs was the ancestral state for the clade, that the character had been lost three times in the genus, and that the hairs were an adaptation to moist environments.

Bayesian estimates of ancestral states allow us to estimate the probability of a particular trait at any node on a phylogeny, whilst also taking into account the uncertainty of the tree topology. Here we use a Bayesian MCMC approach on the sample of Austronesian language trees, employing a statistical method to reconstruct ancestral states and test hypotheses about the evolution of descent and residence.

5.3.5 Questions

In this chapter I address the following questions:

1. Under different coding schemes, what are the ancestral states of (i) descent and (ii) residence at each node of the phylogeny?
2. How certain can we be in those estimates?
3. Did Proto Austronesian, Proto Malayo-Polynesian and Proto Oceanic have bilateral or lineal descent?
4. Was Proto Oceanic matrilineal and/or matrilocal?
5. In determining ancestral states, how important is it to control for the effects of phylogenetic uncertainty?

5.4 Methods

5.4.1 Linguistic data

Linguistic data for phylogenetic analysis were as described in Chapter Two for the 67-language data set.

5.4.2 Cultural data

Data on descent and residence for the 67 societies were obtained from (i) Murdock's (1967) *Ethnographic Atlas*, in updated form as an SPSS database as collated by Gray (1999), (ii) the *Encyclopaedia of World Cultures* (EWC, Levinson 1993), and (iii) *Ethnic Groups of Island South-East Asia* (EGI, LeBar 1975), and supplemented by the ethnographic literature where necessary. Descent and residence were coded in a number of different ways according to specific hypotheses and in order to unpack the various aspects of these cultural traits. *BayesMultiState*, the comparative program used in these analyses, can accept either discrete binary or multi-state coding. Both forms were used. Tables 5.2, 5.3, and 5.4 present the data from the *EA*, Levinson (1993) and LeBar (1975) used to make coding judgments for aspects of descent and residence.

Table 5.2. Information on descent for 67 Austronesian societies.

		ETHNOGRAPHIC ATLAS VARIABLES				OTHER SOURCES[1]	CODING[2]		
No.	**Society Name**	**Descent[3,4]**	**Cognatic kin groups**	**Patrilineal kin groups**	**Matrilineal kin groups**	**Descent information**	**Descent**	**Lineal**	**Matrilineal aspect**
1	Ambon	Mixed	Kindreds (recent)	Single-community lineages	None	Patrilineal clans	P	L	O
2	Ami	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
3	Atayal	Mixed	Ramages: ancestor oriented	Single-community lineages	None	Patrilineal	P	L	O
4	Atoni	*Patrilineal*	-	-	-	Occasional ambilineal recruitment	P	L	O
5	Balinese	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	Patrilineal	P	L	O
6	Belu	Matrilineal	Unilineal descent groups	None	Single-community lineages	Matrilineal	M	L	M
7	Bolaang	*Bilateral*	-	-	-	Bilateral	B	B	O
8	Bunun	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	Patrilineal	P	L	O
9	Carolinian	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	-	M	L	M
10	Chuuk	Mixed	Kindreds	None	Multiple-community lineages	Matrilineal	M	L	M
11	Dobu	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
12	Easter Is.	Ambilineal	Ramages: ancestor oriented	None	None	Lineal clans controlled territories	MP	L	M
13	E. Futuna	Ambilineal	Ramages: ancestor oriented	None	None	Ambilineal	MP	L	M
14	Fijiian	Patrilineal	Unilineal descent groups	Single-community lineages	None	Patrilineal clans	P	L	O
15	Hanunoo	Bilateral	Kindreds	None	None	Bilateral	B	B	O

Table 5.2 (Continued). Information on descent for 67 Austronesian societies.

		ETHNOGRAPHIC ATLAS VARIABLES				OTHER SOURCES[1]	CODING[2]		
No.	**Society Name**	**Descent[3,4]**	**Cognatic kin groups**	**Patrilineal kin groups**	**Matrilineal kin groups**	**Descent information**	**Descent**	**Lineal**	**Matrilineal aspect**
16	Hawaii	Bilateral	Ramages: ancestor oriented	None	None	Bilateral for commoners	B	B	O
17	Iban	Bilateral	Kindreds	None	None	Bilateral	B	B	O
18	Ili Mandiri	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	Patrilineal	P	L	O
19	Ilongot	*Bilateral*	-	-	-	Bilateral with some “claimed memberships”	B	B	O
20	Javanese	Bilateral	Bilateral descent	None	None	Bilateral, some matri-inheritance	B	B	M
21	Kei	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	-	P	L	O
22	Kerinci	*Matrilineal*	-	-	-	Matrilineal	M	L	M
23	Kiribati	Ambilineal	Ramages: ancestor oriented	None	None	Ambilineal	MP	L	M
24	Kodi	Duolateral	Unilineal descent groups	Multiple-community lineages	Single-community lineages	-	MP	L	M
25	Kusaie	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
26	Kwaio	Mixed	Kindreds	Multiple-community lineages	None	Patrilineal	P	L	O
27	Lakalai	Mixed	Kindreds	None	Multiple-community lineages	Matrilineal	M	L	M
28	Macassarese	Ambilineal	Ramages: ancestor oriented	None	None	Bilateral	B	B	O
29	Madurese	*Bilateral*	-	-	-	Bilateral	B	B	O
30	Malagasy	Duolateral	Unilineal descent groups	Multiple-community lineages	Matrilineal exogamy	-	MP	L	M
31	Malay	Bilateral	Kindreds	None	None	Bilateral	B	B	O

Table 5.2 (Continued). Information on descent for 67 Austronesian societies.

ETHNOGRAPHIC ATLAS VARIABLES						OTHER SOURCES[1]	CODING[2]		
No.	**Society Name**	**Descent[3,4]**	**Cognatic kin groups**	**Patrilineal kin groups**	**Matrilineal kin groups**	**Descent information**	**Descent**	**Lineal**	**Matrilineal aspect**
32	Manam	Patrilineal	Unilineal descent groups	Single-community lineages	None	Ambilineal (patri- more important)	MP	L	M
33	Mangaia	Ambilineal	Ramages: exogamous	None	None	Ambilineal	MP	L	M
34	Manggarai	*Patrilineal*	-	-	-	Patrilineal			
35	Manobo	*Bilateral*	-	-	-	Bilateral	B	B	O
36	Maori	Ambilineal	Ramages: ancestor oriented	None	None	Bilateral	MP	L	M
37	Maranao	*Ambilineal*	-	-	-	Ambilineal claim to rights	MP	L	M
38	Marquesan	Bilateral	Bilateral descent	None	None	Bilateral	B	B	O
39	Marshallese	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
40	Mekeo	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	Patrilineal	P	L	O
41	Melanau	*Bilateral*	-	-	-	Bilateral; patriliny important in rank	B	B	O
42	Minangkabau	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
43	Molima	Ambilineal	Ramages: ancestor oriented	None	None	-	MP	L	M
44	Mori	*Bilateral*	-	-	-	Bilateral	B	B	O
45	Motu	Mixed	Kindreds	Single-community lineages	None	Cognatic	B	B	O
46	Nias	*Patrilineal*	-	-	-	Patrilineal	P	L	O

Table 5.2 (Continued). Information on descent for 67 Austronesian societies.

		ETHNOGRAPHIC ATLAS VARIABLES				OTHER SOURCES[1]	CODING[2]		
No.	**Society Name**	**Descent[3,4]**	**Cognatic kin groups**	**Patrilineal kin groups**	**Matrilineal kin groups**	**Descent information**	**Descent**	**Lineal**	**Matrilineal aspect**
47	Niue	Ambilineal	Ramages: ancestor oriented	None	None	Ambilineal	MP	L	M
48	Paiwan	Ambilineal	Ramages: ancestor oriented	None	None	Ambilineal	MP	L	M
49	Palawan	*Bilateral*	-	-	-	Bilateral	B	B	O
50	Ponape	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
51	Pukapuka	Mixed	Kindreds	Multiple-community lineages	Multiple-community lineages	Double descent	MP	L	M
52	Puyuma	Matrilineal	Ramages: ancestor oriented	None	None	Matrilineal	M	L	M
53	Rotuma	Mixed	Kindreds	None	Single-community lineages	Bilateral	B	B	M
54	Samoan	Ambilineal	Exogamous ramages	None	None	Cognatic	MP	L	M
55	Sika	*Patrilineal*	-	-	-	Patrilineal	P	L	O
56	Sugbuhanon	Bilateral	Bilateral descent	None	None	-	B	B	O
57	Sumbanese	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	-	P	L	O
58	Tahiti	Ambilineal	Ramages: ancestor oriented	None	None	Bilateral; ambiliny at chiefly levels	B	B	O
59	Tanimbarese	Patrilineal	Unilineal descent groups	Single-community lineages	None	-	P	L	O
60	Tannese	Patrilineal	Unilineal descent groups	Single-community lineages	None	Patrilineal	P	L	O
61	Toba Batak	Patrilineal	Unilineal descent groups	Multiple-community lineages	None	Patrilineal	P	L	O

Table 5.2 (Continued). Information on descent for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES					OTHER SOURCES[1]	CODING[2]		
No.	**Society Name**	**Descent[3,4]**	**Cognatic kin groups**	**Patrilineal kin groups**	**Matrilineal kin groups**	**Descent information**	**Descent**	**Lineal**	**Matrilineal aspect**
62	Tonga	Ambilineal	Ramages: ancestor oriented	None	None	Patriliny; matriliny at chiefly levels	MP	L	M
63	Toradja	Bilateral	Bilateral descent	None	None	Bilateral	B	B	O
64	Trobriand	Matrilineal	Unilineal descent groups	None	Multiple-community lineages	Matrilineal	M	L	M
65	Ulawa	Ambilineal	Ramages: ancestor oriented	None	None	-	MP	L	M
66	Woleai	Mixed	Kindreds	None	Multiple-community lineages	Matrilineal	M	L	M
67	Yami	Bilateral	Kindreds	None	None	-	B	B	O

1. **Other Sources**: Information from entries in the *Encyclopaedia of World Cultures* (Levinson 1980) and *Ethnic Groups of Island Southeast Asia* (LeBar 1975).
2. **Coding**. *Descent*: M = matrilineal P = patrilineal, MP = ambilineal/double descent/duolateral, B = bilateral/cognatic. *Lineal*: L = lineal, B = bilateral. *Matrilineal aspect:* M = matrilineal aspect, O = no matrilineal aspect.
3. **Descent**: From variable "Descent" in the *Ethnographic Atlas*. Entries in italics are not present in the EA; these denote societies whose main form of descent was inferred from the other sources.
4. **"Mixed descent"**: society has matrilineal and/or patrilineal groups present but they are not strictly unilineal.

Table 5.3. Information on inheritance for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES			**OTHER SOURCES[1]**	**CODING[2]**
Society Name	**Succession to Headman**	**Inheritance of, or access to land**	**Movables**	**Inheritance**	**Inheritance**
Ambon	Patrilineal heir	Patrilineal (sons)	Patrilineal	Corporate patrilineal ownership/ inheritance of houses/land	P
Ami	Formal consensus	Matrilineal (sister's sons)	Matrilineal	Matrilineal	M
Atayal	Formal consensus	Patrilineal (sons)	Patrilineal	Patrilineal	
Atoni	-	-	-	Land/heirloom property patrilineal, marriage property (money) to spouse/children	P
Balinese	Formal consensus	Patrilineal (sons)	Patrilineal	Patrilineal	P
Belu	Matrilineal heir	No individual property rights	-	-	-
Bolaang	-	-	-	Equally amongst children, land usufruct is village owned	-
Bunun	Patrilineal heir	Patrilineal (sons)	Patrilineal	Property inherited according to domestic contribution	P
Carolinian	-	-	-	-	-
Chuuk	Matrilineal heir	Patrilineal (sons)	Patrilineal	Land controlled by both corporate matrilines and by individuals	MP
Dobu	No such office	Matrilineal (sister's sons)	Matrilineal	Land and movables inherited matrilineally	M

Table 5.3 (Continued). Information on inheritance for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]	CODING[2]
Society Name	**Succession to Headman**	**Inheritance of, or access to land**	**Movables**	**Inheritance**	**Inheritance**
Easter Is.	Patrilineal heir	-	-	Both sexes could inherit/leave property	MP
E. Futuna	Formal consensus	-	-	Land/property in male line, tapa and mats (movables) in female line	MP
Fijiian	Patrilineal heir	-	Patrilineal	Land to sons	P
Hanunoo	No such office	No individual property rights	Equal to M/F children	Bilateral	B
Hawaii	Patrilineal heir	Equal to M/F children	Equal to M/F children	Men more likely to inherit land rights than women	P
Iban	Informal consensus	Equal to M/F children	Equal to M/F children	Male and female inherit equally	B
Ili Mandiri	-	Patrilineal (sons)	Patrilineal	Patrilineal clan lands	P
Ilongot	-	-	-	Land belongs to those who clear it, inheritance is rare	B
Javanese	Formal consensus	Equal to M/F children	Equal to M/F children	Equal, although gardens and dwellings inherited by daughters	M
Kei	Patrilineal heir	Patrilineal (sons)	Patrilineal	-	P
Kerinci	-	-	-	Status/rank matrilineal rank through mother's brother, land to daughters	M

Table 5.3 (Continued). Information on inheritance for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]	CODING[2]
Society Name	**Succession to Headman**	**Inheritance of, or access to land**	**Movables**	**Inheritance**	**Inheritance**
Kiribati	Formal consensus	Children, with daughters receiving less	Equal to M/F children	Ambilineal land rights, associated with residence	B
Kodi	-	-	-	-	-
Kusaie	-	-	-	Modern land rights held individually	-
Kwaio	-	-	-	Patrilineal	P
Lakalai	Informal consensus	-	Equal to M/F children	Matrilineal clan lands, but wealth held by men is used for son's bridewealth	MP
Macassarese	Patrilineal heir	-	-	Equal to M/F children	B
Madurese	-	-	-	Equal to M/F children	B
Malagasy	Appointment	Equal to M/F children	Equal to M/F children	Equal to M/F children	B
Malay	-	Patrilineal (sons)	Equal to M/F children	Bilateral	P
Manam	Patrilineal heir	Patrilineal (sons)	-	Bilateral, more to sons	P
Mangaia	Patrilineal heir	-	-	Land through male line	P
Manggarai	-	-	-	Land via the patrilineage	P
Manobo	-	-	-	Equal to surviving kin	B

Table 5.3 (Continued). Information on inheritance for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]	CODING[2]
Society Name	**Succession to Headman**	**Inheritance of, or access to land**	**Movables**	**Inheritance**	**Inheritance**
Maori	Patrilineal heir	Patrilineal (sons)	Patrilineal	Corporate land rights, movables to same-sex offspring	P
Maranao	-	-	-	Equal division to children, land individually owned, usually transferred to sons	P
Marquesan	Patrilineal heir	Children, with daughters receiving less	Children, with daughters receiving less	Emphasis on primogeniture	B
Marshallese	Patrilineal heir	Matrilineal heirs	No individual property rights or rules	Ambilineal; matri-clans control land tenure	M
Mekeo	Patrilineal heir	Patrilineal (sons)	-	Patrilineal rights to clan lands; matrilineal transfer of some movables	P
Melanau	-	-	-	Equal to M/F children	B
Minangkabau	Matrilineal heir	No individual property rights	Other matrilineal	Cultivated land strictly matrilineal, some movables transferred from father to son	M
Molima	-	-	-	-	-

Table 5.3 (Continued). Information on inheritance for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]	CODING[2]
Society Name	**Succession to Headman**	**Inheritance of, or access to land**	**Movables**	**Inheritance**	**Inheritance**
Mori	-	-	-	Property equally to M/F children	B
Motu	Patrilineal heir	Children, with daughters recieving less	Children, with daughters receiving less	Houses and movables to sons	P
Nias	-	-	-	Patrilineal	P
Niue	-	-	Patrilineal	-	P
Paiwan	Patrilineal heir	Equal to M/F children	Equal to M/F children	Primogeniture without respect to sex; land belongs to chiefly lineages	MP
Palawan	-	-	-	Equally to remaining kin	B
Ponape	Matrilineal heir	Other matrilineal heirs	Other matrilineal	Traditionally matrilineal control of land	M
Pukapuka	Patrilineal heir	-	-	Lands through mother, gardens through father	MP
Puyuma	Informal consensus	-	-	Land owned by heads of aristocracy, rented to commoners	-
Rotuma	Patrilineal heir	-	-	Senior male as steward of land, bilateral inheritance	B
Samoan	Patrilineal heir	-	-	Corporate rights to land	MP
Sika	-	-	-	Patrilineal, land to sons	P

Table 5.3 (Continued). Information on inheritance for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]	CODING[2]
Society Name	**Succession to Headman**	**Inheritance of, or access to land**	**Movables**	**Inheritance**	**Inheritance**
Sugbuhanon	Formal consensus	Equal to M/F children	Equal to M/F children	-	B
				-	P
Sumbanese	Patrilineal heir	Patrilineal (sons)	Patrilineal		
Tahiti	Patrilineal heir	-	-	Male succession for lands and title	P
Tanimbarese	Patrilineal heir	Patrilineal (sons)	Patrilineal	-	P
Tannese	Patrilineal heir	Patrilineal (sons)	Patrilineal	Patrlineal to sons	P
Tobabatak	Patrilineal heir	Patrilineal (sons)	Patrilineal	Patrilineal for land and houses	P
Tonga	Patrilineal heir	Other patrilineal heirs	-	Patrilineal; traditionally land was held corporately	P
Toradja	Formal consensus	Equal to M/F children	Equal to M/F children	Bilateral rights to property	B
Trobriand	Matrilineal heir	Matrilineal (sister's sons)	Matrilineal	Land inherited matrilineally	M
Ulawa	Patrilineal heir	Equal to M/F children	Equal to M/F children	-	MP
Woleai	Matrilineal heir	-	-	Matrilineal corporate land	M
Yami	No such office	Patrilineal (sons)	Patrilineal	-	P

1. **Other Sources**: As for Table 5.2.
2. **Coding**. M = matrilineal P = patrilineal, MP = ambilineal i.e. significant transfers through separate lineages, B = bilateral/cognatic.

5.4.2.1 Coding: Descent

Multi-state coding. Three states were used (M = matrilineal, P = patrilineal, B = bilateral/cognatic). A culture was assigned as matrilineal (*n* = 14) or patrilineal (*n* = 17) if it were coded as such in variable 43 of the *EA* ("Descent: Major Type", a code not in the original *EA* but derived from variables 17, 19, and 21) or described primarily as such in the other sources. Cultures described as ambilineal or duolateral (i.e. having both matri- and patrilineal kin groups) were coded as MP, as the *BayesMultiStates* program allows for the assignment of dual states to taxa (*n* = 16). Cultures described as bilateral in v43 and having ego-oriented kindreds in v21 ("Cognatic kin groups"), or described in the other sources as bilateral or cognatic, were coded as bilateral (*n* = 20). In all coding situations, any ambiguities were resolved by cross-checking across the three main sources or referring to the primary literature. When ambiguities were not resolvable the society was coded as "missing" for that variable.

Inheritance of resources. Information was taken from variables concerning inheritance in the EA ("Inheritance Rule for Real Property" "Movable Property", "Succession to Headman") and other sources as described above. Three states were used (M = matrilineal, P = patrilineal, B = equal). MP was used for societies where some resources were transmitted patrilineally (e.g. property rights) and other resources transmitted matrilineally (e.g. movables). Where a culture had an absence of individual property rights, it was coded as missing (*n* = 7).

Lineality. Cultures were coded by the presence of lineal descent groups (L, *n* = 48) or their absence (B, *n* = 19). Unilineal comprised all those cultures with a matrilineal or patrilineal system of inheritance, as well as ambilineal systems, as these imply the presence of lineal kin groups. Ambilineality, a flexible system of kinship and inheritance rules that has been linked with changing needs in a fluctuating environment (Fox 1967), describes a large number of Austronesian societies. Non-unilineal comprised all societies with bilateral descent or cognatic kindreds without lineal kin groups.

Matrilineality. Cultures were coded as having a matrilineal aspect (M) if they possessed some type of matrilineal descent group (variable 19 in the *EA*) or some degree of matrilineal inheritance (variables “Real Property”, “Movable Property”, “Succession to Headman”), or similar as described in the other sources. This variable was intended to distinguish those cultures with some aspect of matrilineal organisation (n = 31) from strictly bilateral or patrilineal systems (n = 36).

5.4.2.2 Coding: Post-marital residence

For those cultures in the *EA*, I used the variable “Marital residence with kin: after first years” as the primary indicator of residence patterns, because 48/54 cultures in the *EA* were not different from earlier years. A number of coding systems were used. Table 5.4 presents residence information used to make the following coding judgements.

Primary mode of residence. Cultures were coded according to the primary indicator in the *EA* or whichever was designated most common in the other sources. Three states were used: patrilocal including virilocal, as both involve the residence with the groom's patrilineal kin (P, n = 38), matrilocal including uxorilocal and avunculocal (M, n = 19), or ambilocal (A, n = 10). Two neolocal cultures were coded as ambilocal.

Scale. I constructed a five-point scale of residence from strong matrilocal through to strong patrilocal residence. On this scale, “1” = primary residence as matrilocal with no alternatives, strict matrilocality (n = 9); “2” = matrilocal with alternatives, mainly matrilocal (n = 10); “3” = ambilocality or neolocality (n=12); “4” = patrilocal with alternatives, mainly patrilocal (n=28); “5” = patrilocal with no alternative, strictly patrilocal (n = 8).

Matrilocal option. According to Murdock's theory of kinship change (1949), residence changes first of all aspects of social structure. Identifying those cultures with some matrilocal aspect to their organisation provides an indicator of which cultures may be on some transition pathway in this putative sequence. This investigation was preparatory to the hypotheses tested in Chapter Six. A culture was coded as having a matrilocal option if, in the *EA*, it were coded on the primary indicator as ambilocal, matrilocal, uxorilocal, or avunculocal, or if it had an alternate or earlier form in any of those states (*n* = 43). For other sources the same obtained for cultures with a description of some matrilocal option (*n* = 13). In effect, this coding distinguishes strictly patrilocal/virilocal systems (*n* = 11) from all others.

Flexibility. For cultures in the *EA*, a culture was coded flexible if it was ambilocal in the primary indicator, possessed an alternate form of residence under the variable "Transfer of residence at marriage: alternate form", or had a different mode of residence in early years (*n* = 39). Cultures in other sources were coded as flexible if recorded as ambilocal or if their description featured an alternative along the lines above (*n* = 11). All others were coded as non-flexible (*n* = 17).

In summary, eight sets of analyses were conducted under the different coding schemes: four for descent and four for residence.

Table 5.4. Information on post-marital residence for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES		OTHER SOURCES[1]	CODING[2]			
	Main Residence[3]	**First years/Alternate form[4]**	**Residence information**	**Primary**	**Scale**	**Flexibility**	**Matrilocal option**
Ambon	Patrilocal	None/Neolocal	Patrilocal	P	4	F	O
Ami	Matrilocal	None/None	Matrilocal	M	1	N	M
Atayal	Patrilocal	None/Matrilocal	-	P	4	F	M
Atoni	*Patrilocal*	*-/Matrilocal*	Virilocal with temporary uxorilocality	P	4	F	M
Balinese	Patrilocal	None/Matrilocal	Patrilocal	P	4	F	M
Belu	Matrilocal	None/None	Matrilocal	M	1	N	M
Bolaang	*Ambilocal*	-/-	Ambilocal	A	3	F	M
Bunun	Patrilocal	None/None	Patrilocal	P	4	F	M
Carolinian	Matrilocal	None/None	-	M	1	N	M
Chuuk	Matrilocal	None/Patrilocal	Matrilocal	M	2	F	M
Dobu	Matrilocal	None/None	Ambilocal (matri- or avunculocal)	M	3	F	M
Easter Is	Patrilocal	None/Matrilocal	-	P	4	F	M
E. Futuna	Patrilocal	Ambilocal/Matrilocal	Ambilocal	P	3	F	M
Fijiian	Patrilocal	None/None	Patrilocal	P	4	F	M
Hanunoo	Matrilocal	None/Patrilocal	Matrilocal	M	2	F	M
Hawaii	Ambilocal	None/None	Ambilocal	A	3	F	M
Iban	Ambilocal	None/None	Ambilocal	A	3	F	M

Table 5.4 (Continued). Information on post-marital residence for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES		OTHER SOURCES[1]	CODING[2]			
	Main Residence[3]	**First years/Alternate form[4]**	**Residence information**	**Primary**	**Scale**	**Flexibility**	**Matrilocal option**
Ilimandiri	Patrilocal	None/Matrilocal	Ambilocal	P	4	F	M
Ilongot	*Matrilocal*	*-/Patrilocal*	Matrilocal, can be patrilocal when bridewealth paid	P	2	F	M
Javanese	Neolocal	Matrilocal/None	Ambilocal/neolocal, but uxorilocal common	A	3	F	M
Kei	Patrilocal	None/Matrilocal	-	P	4	F	M
Kerinci	*Matrilocal*	-	Matrilocal	M	1	N	M
Kiribati	Patrilocal	None/Matrilocal	Patrilocal	P	4	F	M
Kodi	Patrilocal	None/Matrilocal	-	P	4	F	M
Kusaie	Patrilocal	None/Neolocal	Ambilocal	P	4	F	M
Kwaio	Patrilocal	None/Matrilocal	Patrilocal with flexibility	P	4	F	M
Lakalai	Optionally patrilocal	Patrilocal/Neolocal	Patrilocal	P	4	F	M
Macassarese	Ambilocal	None/Neolocal	No dominant pattern	A	3	F	M
Madurese	*Matrilocal*	-/-	Ideally neolocal, usually matrilocal	M	2	F	M
Malagasy	Patrilocal	None/None		P	5	N	O
Malay	Patrilocal	Matrilocal/Neolocal	Neolocal	P	4	F	M
Manam	Patrilocal	None/Neolocal	Patrilocal	P	4	F	O
Mangaia	Patrilocal	None/Matrilocal	Ambilocal then neolocal	P	4	F	M

Table 5.4 (Continued). Information on post-marital residence for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES		OTHER SOURCES[1]	CODING[2]			
	Main Residence[3]	**First years/Alternate form[4]**	**Residence information**	**Primary**	**Scale**	**Flexibility**	**Matrilocal option**
Manggarai	*Patrilocal*	*Matrilocal/-*	Matrilocal, patrilocal once bridewealth paid	P	4	F	M
Manobo	*Patrilocal*	*Matrilocal/Matrilocal*	Brideservice then ambilocal but usually patrilocal	P	4	F	M
Maori	Patrilocal	None/None	Patrilocal, only occasional chiefly ambilocality	P	5	N	O
Maranao	*Matrilocal*	*-/Ambilocal*	Matrilocal, bridewealth payment leads to choice	M	2	F	M
Marquesan	Patrilocal	Matrilocal/Neolocal	Patrilocal	P	4	F	M
Marshallese	Matrilocal	None/None	Ambilocal	M	1	N	M
Mekeo	Patrilocal	None/None	Patrilocal	P	5	N	O
Melanau	*Matrilocal*	-	Uxorilocal	M	1	N	M
Minangkabau	Matrilocal	None/Matrilocal	Couples do not establish initial common residence	M	1	N	M
Molima	Patrilocal	None/Avunculocal	-	P	4	F	M
Mori	*Matrilocal*	*-/Neolocal*	Initially matrilocal, then can be neolocal	M	2	F	M
Motu	Patrilocal	None/Matrilocal	Patrilocal	P	4	F	M
Nias	*Patrilocal*	*None/Matrilocal*	Patrilocal with matrilocal alternatives	P	4	F	M
Niue	Patrilocal	None/Matrilocal	-	P	4	F	M
Paiwan	Patrilocal	None/Matrilocal	Ambilocal	P	4	F	M

Table 5.4 (Continued). Information on post-marital residence for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES		OTHER SOURCES[1]	CODING[2]			
	Main Residence[3]	**First years/Alternate form[4]**	**Residence information**	**Primary**	**Scale**	**Flexibility**	**Matrilocal option**
Palawan	*Matrilocal*	-/-	Uxorilocal	M	2	F	M
Ponape	Matrilocal	None/Avunculocal	Ambilocal	M	2	F	M
Pukapuka	Patrilocal	None/None	Patrilocal bias	P	5	N	O
Puyuma	Matrilocal	None/Patrilocal	Matrilocal	M	2	F	M
Rotuma	Matrilocal	None/Avunculocal	Matrilocal preference	M	1	N	M
Samoan	Ambilocal	None/None	Mainly patrilocal, initially matrilocal	A	3	F	M
Sika	Ambilocal	-/-	Ambilocal	A	3	F	M
Sugbuhanon	Neolocal	None/None	-	A	3	F	O
Sumbanese	Patrilocal	None/None	-	P	5	N	O
Tahiti	Ambilocal	None/None	Ambilocal	A	3	F	M
Tanimbarese	Patrilocal	Matrilocal/None	-	P	4	F	M
Tannese	Patrilocal	None/None	Virilocal	P	5	N	O
Toba Batak	Patrilocal	None/Matrilocal	Viriocal then neolocal is desirable	P	4	F	M
Tonga	Patrilocal	None/Avunculocal	Patrilocal	P	4	F	M
Toradja	Matrilocal	None/None	Ambilocal/neolocal also	M	1	N	M
Trobriand	Matrilocal	None/Patrilocal	Virilocal and avunculocal	M	2	F	M

Table 5.4 (Continued). Information on post-marital residence for 67 Austronesian societies.

	ETHNOGRAPHIC ATLAS VARIABLES		OTHER SOURCES[1]	CODING[2]			
	Main Residence[3]	**First years/Alternate form[4]**	**Residence information**	**Primary**	**Scale**	**Flexibility**	**Matrilocal option**
Ulawa	Patrilocal	None/None	-	P	5	N	O
Woleai	Ambilocal	None/None	Matrilocal option	A	3	F	M
Yami	Patrilocal	None/None	-	P	5	N	O

1. Other sources: As for Table 5.2
2. Coding. *Primary*: M = matrilocal, P = patrilocal, A = ambilocal. *Scale*: 1 – 5 such that 1 = strictly matrilocal, 3 = ambilocal, 5 = strictly patrilocal. *Flexibility*: F = flexibility in residence, N = not flexible. *Matrilocal option*: M = matrilocal option, O = no matrilocal option.
3. Residence terms have been simplified such that uxorilocal/avunculocal = matrilocal, and virilocal = patrilocal. Entries in italics are not in the EA but are inferred from information given in the “Other Sources” column.
4. Combined information from the variables “Residence: First years” and “Residence: Alternate form”.

5.4.3 Phylogeny estimation

BayesPhylogenies (Pagel and Meade 2004) was used to produce a 1000-tree sample by Bayesian MCMC analysis as described in Chapter Two. All trees shown in this chapter use the consensus tree of this sample, but the analyses themselves were conducted on all 1000 trees.

5.4.4 Estimation of ancestral states

A continuous-time Markov model of trait evolution, implemented in the program *BayesMultiState* (Pagel et al. 2004; Pagel and Meade 2005) was used to estimate the ancestral states of descent and residence across the sample of 1000 trees. The program takes into account uncertainty about the evolutionary scenario of cultural trait evolution as well as the model of history proposed by the phylogeny, and was described in detail in Chapter Three. The instantaneous rate of change between two binary traits, for example, matrilocal option (M) and no matrilocal option (O), is measured by transition-rate parameters qMO and qOM. These transition rates are then used to define the probability of changes between these two states along the branches of the tree. In the Bayesian context, a Markov chain that samples the values periodically across the tree-sample creates a posterior probability distribution (PPD) of values of the rate parameters (Pagel 1999). Most importantly, the ancestral state at each node can be characterised by a PPD of each trait (e.g. M or O) whose mean and confidence interval we can define.

As these methods estimate not only the state of the ancestral trait but account for uncertainty in the phylogeny by summing over the tree sample, the estimated posterior probabilities are derived by combining the probability of a state at each node with the probability the node exists. Continuing the above example with the matrilocal option versus no option, we may say that (i) $P(n)$ is the probability that a node exists in the tree sample, (ii) $P(M|n)$ is the estimated posterior probability of a matrilocal option given that the node is present, and (iii) *P(M)* is the probability that the node is matrilocal taking into account the proportion of trees in which the node actually exists, and is obtained by multiplying as follows: $P(M) = P(M|n) \times P(n)$. Conversely, we obtain the probability of no matrilocal option, $P(O)$, through $P(O) = P(O|n) \times P(n)$. $P(n)$ effectively places an upper limit on our confidence in reconstructing ancestral states.

The comparative analysis for reconstruction of ancestral states was performed over the sample of 1000 trees on descent and residence data for 67 Austronesian societies. In general, rates of trait switching (the transition rate parameters) were estimated from the data rather than set to prior values. The proposal mechanism, which the Markov chain uses as a criterion for accepting a change in the parameters, was initially set at 50 for the binary coding and 30 for the multi-state coding. Preliminary analyses were run to find values of the proposal mechanism that fell between .20 and .50, meaning that between 20 and 50 percent of changes were accepted between sampling events (M. Pagel, personal communication 2005). Preliminary runs indicated that for some codings the data could be described well by a wide range of parameters, thus, in order to improve the likelihoods an exponential prior was used in some analyses to constrain the values (beta distribution with a mean of 10; A. Meade, personal communication). For all analyses, the MCMC simulation started from a random tree, ran for 10 million iterations, and the parameters were sampled from the chain every 1000–10,000 iterations. This ensured that each tree was repeatedly visited and different combinations of rate parameters were proposed. A period of burn-in (at least 10,000) was allowed for the chain to reach convergence, and PPD samples of the parameters, likelihoods and estimates of ancestral states at each internal node were taken from at least 1000 iterations post-convergence.

PPD graphs for each internal node were assembled and analysed in Microsoft Excel. The arbitrary value of .70 for combined probabilities (e.g. $p(M)$, $p(O)$) was taken as the threshold value of certainty for an ancestral state at a node, following Pagel et al. (2004).

5.5 Results

5.5.1 Phylogeny

Figure 5.4 shows the consensus phylogeny of 1000 trees found by Bayesian MCMC analysis, as reported in Chapter Two. Nodes are marked as to their posterior probability (threshold of certainty = 70%). Certain nodes are labelled with well-known proto-language stages, or other groupings that are particularly interesting in the reconstruction of these cultural traits. These are referred to throughout the results and discussion.

5.5.2 Ancestral state reconstructions

For each analysis I present (i) a colour-coded phylogeny and (ii) a set of "posterior density" distribution panels. The phylogeny is shown annotated with reconstructed ancestral states that have a combined probability that equals or is greater than .70. Four or more nodes of interest are also shown as a distribution panel. These panels plot, for those nodes, the probability of the ancestral state (from zero to one) on the *x*-axis, and the number of iterations in the Markov chain with that probability on the *y*-axis. They are thus the estimated posterior probability distributions of the reconstructed state at these nodes. The distributions are derived from those trees in which the node exists, and beneath each panel is the combined probability obtained by multiplying the PPD of the trait by the PPD of the node, as described above in §5.4.4. The panels are informative in the shape of their distribution, for example, panels where the values are tightly clustered about a value indicate a great deal of robustness in the reconstruction of the ancestral state, whereas a flattened curve spread out over many values means a less certain reconstruction.

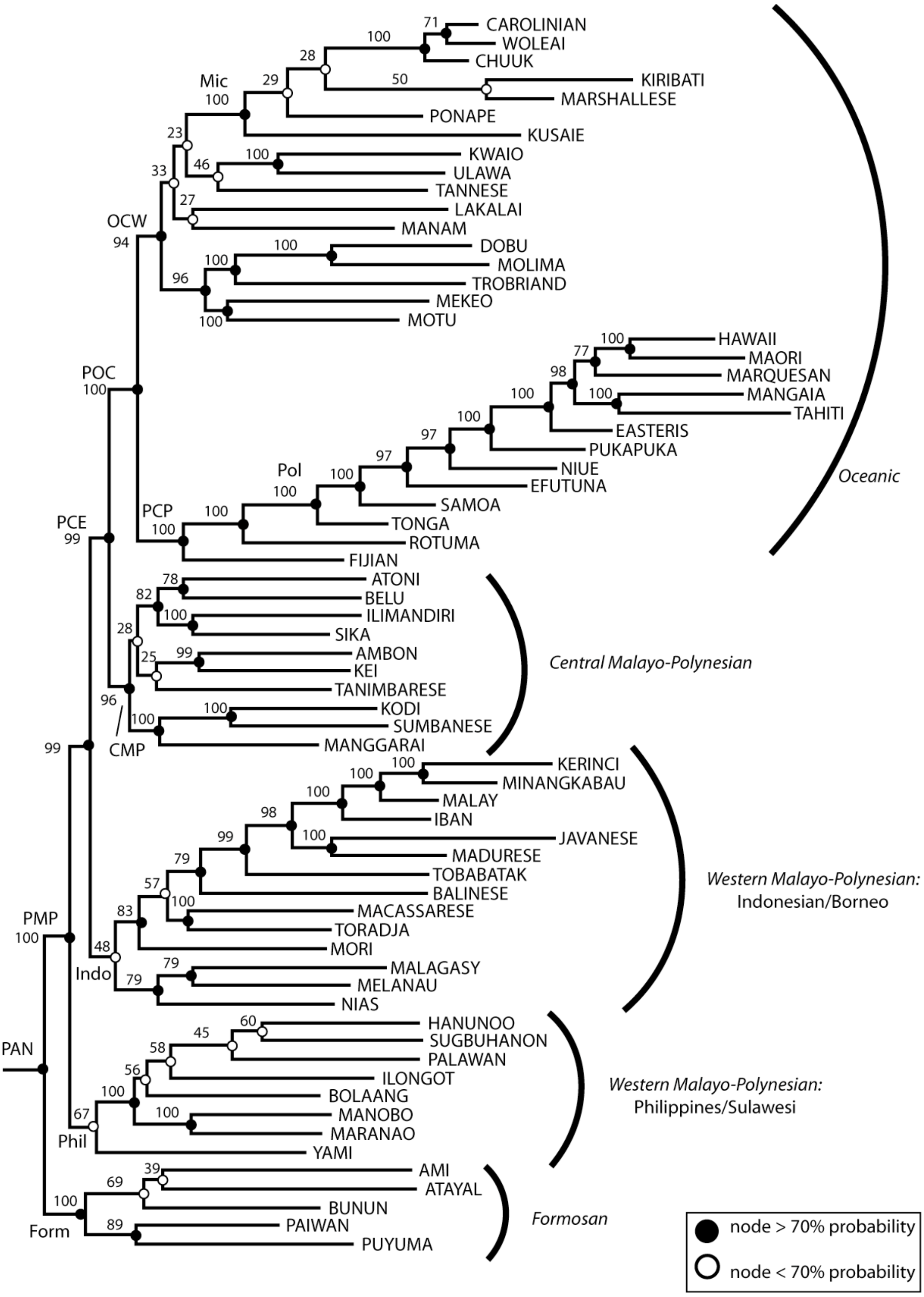


Figure 5.4. Consensus phylogeny of 1000 Bayesian trees for 67 Austronesian languages. Nodes are labelled as followed: PAN, Proto Austronesian; PMP, Proto Malayo-Polynesian; PCE, Proto Central-Eastern Malayo-Polynesian, POC, Proto Oceanic, Form, Formosan, Phil, Philippine and Sulawesi, Indo, Western Indonesian; CMP Central Malayo-Polynesian; Poly, Polynesian, OCW, Oceanic (Western); Mic, Micronesian. A filled circle at the node indicates that its posterior probability is equal to or greater than .70; it is thus a node we may have some certainty of existing in more than 70% of trees in the sample. Open circles indicate a posterior probability of less than .70; these nodes are phylogenetically uncertain.

5.5.3 Descent: Multi-state coding

5.5.3.1 Ancestral states

The ancestral state reconstruction used an exponential prior with a mean of ten, and had a mean marginal likelihood $lh_{harmonic}$ = -55.63. Using multi-state coding, only 25 of the 66 internal nodes show a combined probability greater than .70 (Figure 5.4). It may be difficult to use multi-state coding on these data and obtain high combined probabilities, or it may be that descent rules are actually evolving quickly on the phylogeny, leading to uncertainty in the reconstructions. As well, a large number of ambilineal societies, which were coded as "MP" to indicate the presence of both matrilineal and patrilineal descent groups, may have contributed to the high uncertainty in this particular analysis. At the root (PAN) the method reconstructs bilateral descent as most likely ($P(B)$ = .66), although this is not over the .70 threshold, and the probabilities form a flattened posterior probability distribution in Figure 5.6 (top-left panel), indicating that a range of reconstructions are likely. This is further suggested by the individual probabilities for the root, which range from .00001 to .999 for bilateral, from .00001 to .89 for matrilineal, and from .00001 to .99 for patrilineal.

The Malayo-Polynesian node (PMP) is bilateral ($P(B)$ = .88), with the PPD strongly skewed to high probabilities (Figure 5.6, top-right panel). WMP societies in the Philippines and Sulawesi (node "Phil") and Indonesia (node "Indo") groups are strongly bilateral, but we have less than .70 phylogenetic certainty in their ancestral nodes. Matriliny evolves once in the Indonesian clade. As the tree branches further, the Proto Central-Eastern (PCE) and Proto Oceanic (POC) nodes switch to patriliny. Only at PCE is this with certainty, however, and one third of the POC reconstructions return matriliny (Figure 5.6, middle-right panel). Polynesia (node "Poly") continues a patrilineal trend while containing substantial matriliny, most likely because these societies are heavily ambilineal. Matriliny also appears in some of the other Oceanic-Western ("OCW") societies, especially in Micronesia where the Proto Micronesian node ("Mic") reaches a probability $P(M)$ =. 98 for matriliny.

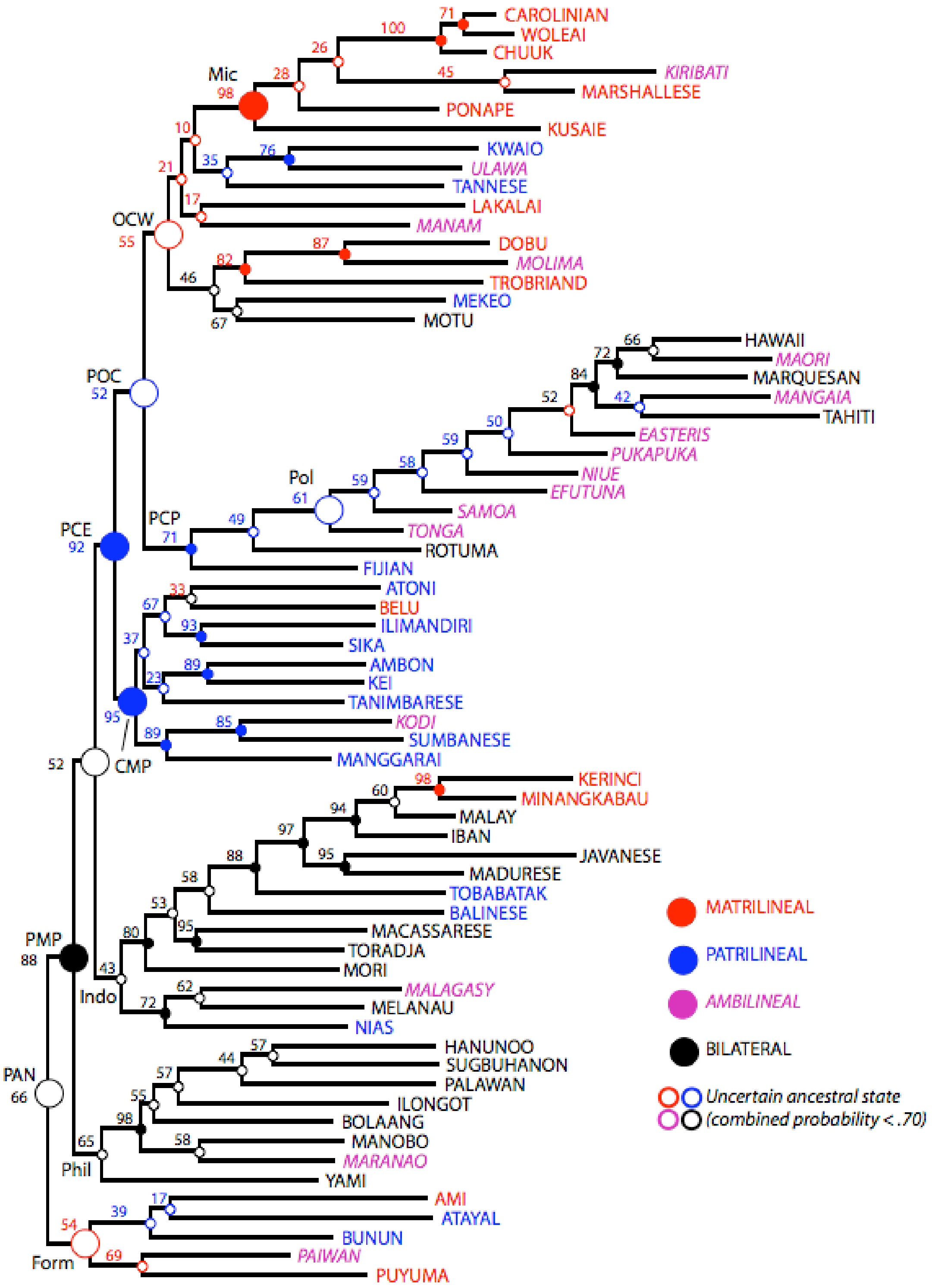
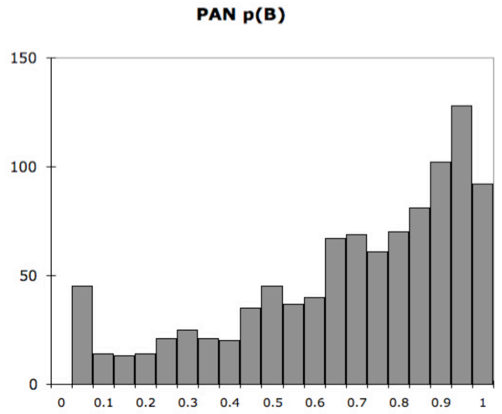
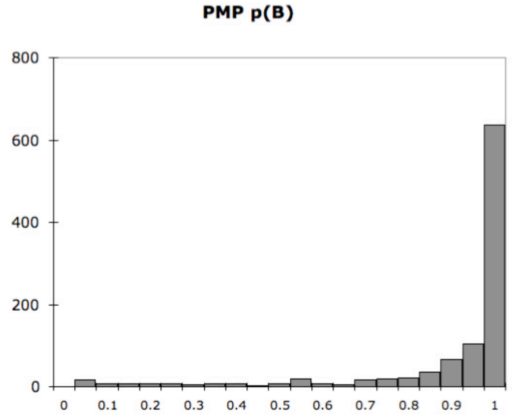


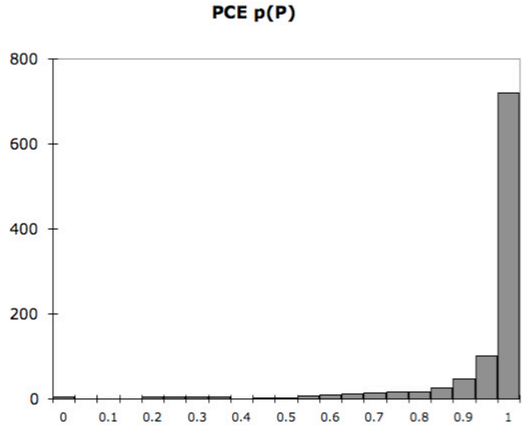
Figure 5.5. Ancestral state reconstruction of descent (multi-state coding) in 67 Austronesian societies. Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability.



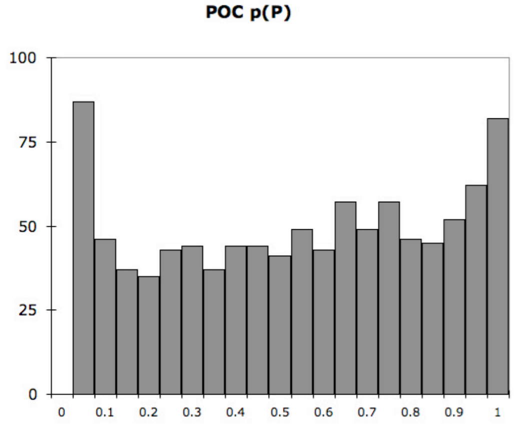
P(B|n) = 0.66±0.02
P(B) = 0.66*1, P(P) = 0.23*1, P(M) = 0.11*1



P(B|n) = 0.88±0.01
P(B) = 0.88*1, P(P) = 0.11*1, P(M) = 0.01*1



P(P|n) = 0.93±0.01
P(B) = 0.02*0.99, P(P) = 0.93*0.99, P(M) = 0.05*0.99



P(P|n) = 0.52±0.02
P(B) = 0.13*1, P(P) = 0.52*1, P(M) = 0.35*1

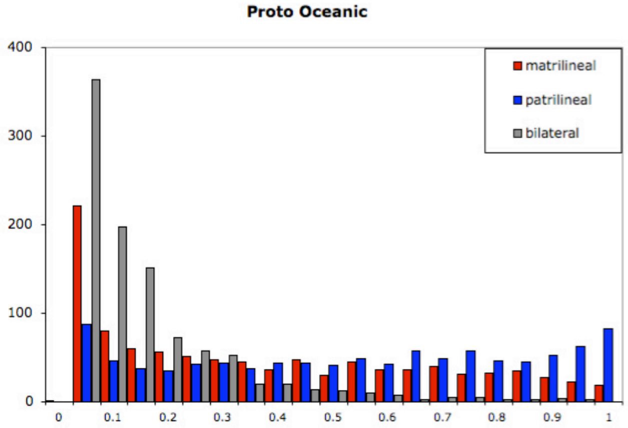


Figure 5.6. Panels showing the estimated posterior probability distribution (PPD) of **descent** with multi-state characters (bilateral, B; matrilineal, M; patrilineal, P) at four selected nodes from the phylogeny in Figure 5.4. Below each panel is the estimated PPD and 95% confidence intervals for the character state with the highest average probability (first line), and the probabilities for all three states taking into account uncertainty about the nodes (second line). There is a switch from bilateral organisation at the base of the tree (PAN and PMP nodes) to patriliny (PCE, POC); only PMP and PCE reach the threshold of certainty. The final panel shows the PPD for all three character states at the Proto Oceanic node to demonstrate the relative estimates of these ancestral states. There is a good deal of uncertainty about POC descent.

5.5.3.2 Rates of trait switching

For this analysis there were six transition rate parameters, estimated as follows: q_{MP}= 9.86, q_{MB}= 8.16, q_{PM}= 11.75, q_{PB}= 12.39, q_{BM}= 14.39, q_{BP}= 21.37. All were roughly equivalent, as setting rates to be equal did not affect the marginal (harmonic) mean of the likelihood as measured by the log-Bayes factor test (described in Chapter Three, section §3.4.3.2). Here the Bayes factor (*BF*) is computed as –2*(-55.63 – -55.81) = .36. A Bayes factor greater than 5 is evidence in support of the model being tested, so we conclude that there is no evidence for a difference between the estimated rate parameters and a model where they are set to be equal. If we assume the PAN root to be bilateral, it appears more likely that societies will evolve patriliny (q_{BP}= 21.37) rather than matriliny (q_{BM}= 14.39), but, as explained, the difference in the rate parameters is not statistically significant in this case.

5.5.4 Inheritance: Multi-state coding

5.5.4.1 Ancestral states

Like descent rules, the reconstruction of multistate-coded inheritance returned less than half the nodes (n = 25) as having a combined probability for any state greater than .70. The ancestral state reconstruction used an exponential prior with a mean of ten, and had a mean marginal likelihood $lh_{harmonic}$ = -54.97. PMP inheritance reconstructs as bilateral *P(B)* = .70, but the root is uncertain (*P(B)* = .56), possibly due to patrilineal inheritance in the Formosan societies Atayal, Bunun, and Paiwan. The uncertainty about PAN is demonstrated by the flat distribution of the PPD for bilateral inheritance, top-left panel in Figure 5.8. Bilateral inheritance with occasional matriliny appears through the Philippines, Sulawesi, and Western Indonesia, but there is a switch to patrilineal inheritance in Eastern Indonesia and beyond (PCE at *P(P)* = .92 and CMP *P(P)* =.90). Proto Oceanic has a patrilineal trend (*P(P)* = .69), again with an underlying set of matrilineal principles (*P(M)* = .19) but is not certain. Patrilineal inheritance strengthens in the Polynesian societies (Poly at *P(P)* = .98), but the sister group of western Oceanic societies has a mixture of inheritance rules with uncertain reconstructions. Micronesia once again reconstructs as strongly matrilineal (*P(M)* = .92) in inheritance.

5.5.4.2 Rates of trait switching

The transition rate parameters (q_{MP}= 10.67, q_{MB}= 10.34, q_{PM}= 7.04, q_{PB}= 17.94, q_{BM}= 11.93, q_{BP}= 33.99) indicate that the least likely change is from patrilineal to matrilineal inheritance. Setting the transition q_{PM} to zero and comparing with the unrestricted model returns a *BF* of –2.94, indicating that there is no statistical difference between the unrestricted estimate of q_{PM} and zero. The high rate from bilateral to patrilineal inheritance (q_{BP}= 33.99) can be tested if a model in which all rates are set to be equal is compared to one where q_{BP} is allowed to take its maximum likelihood estimate. Here the *BF* = 4.32, which is evidence in favour of the high rate (Raftery 1996). Therefore, a switch from patrilineal to matrilineal inheritance is statistically unlikely for these societies, and bilateral inheritance is more likely to evolve into a patrilineal rather than matrilineal system.

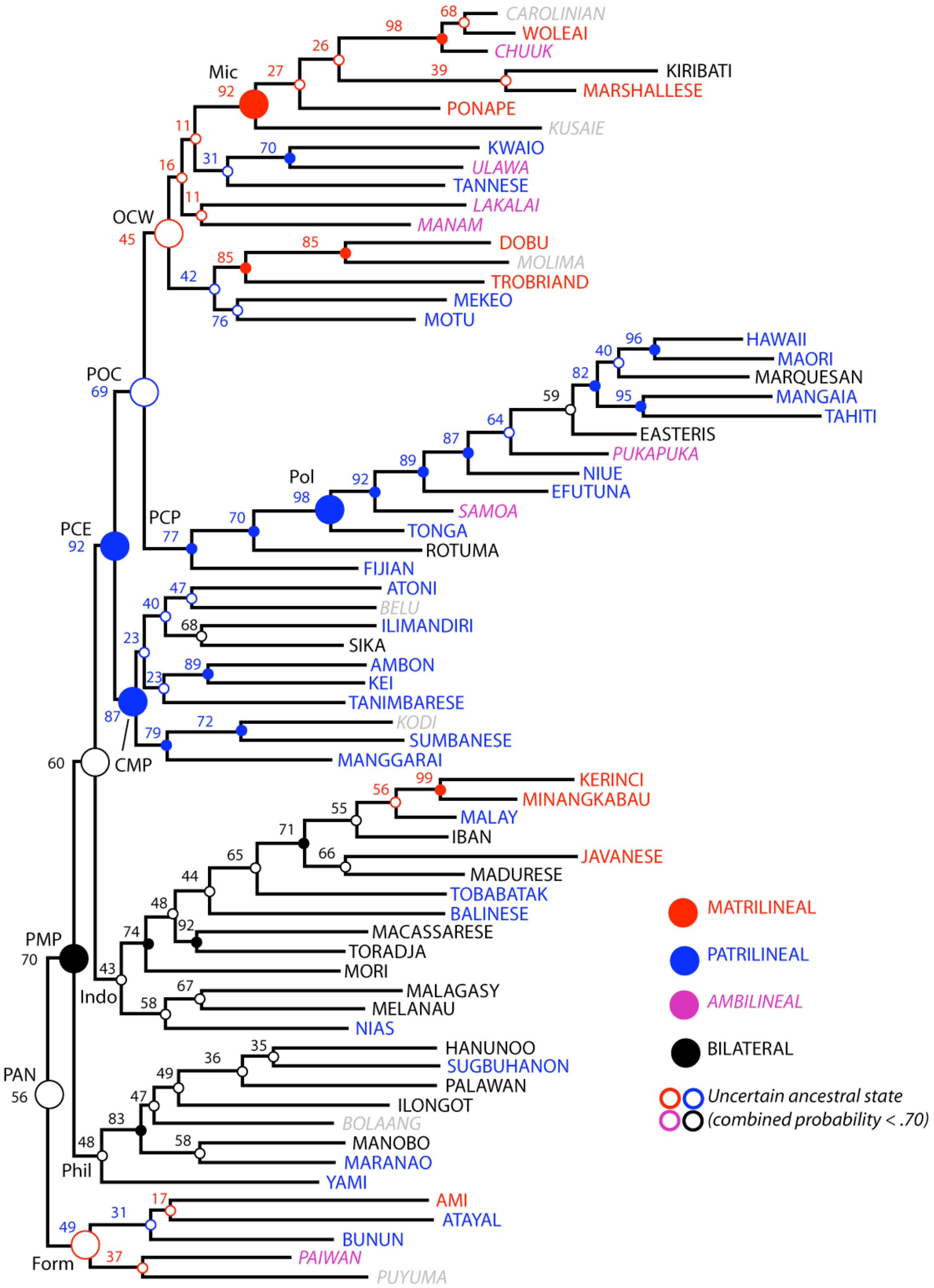
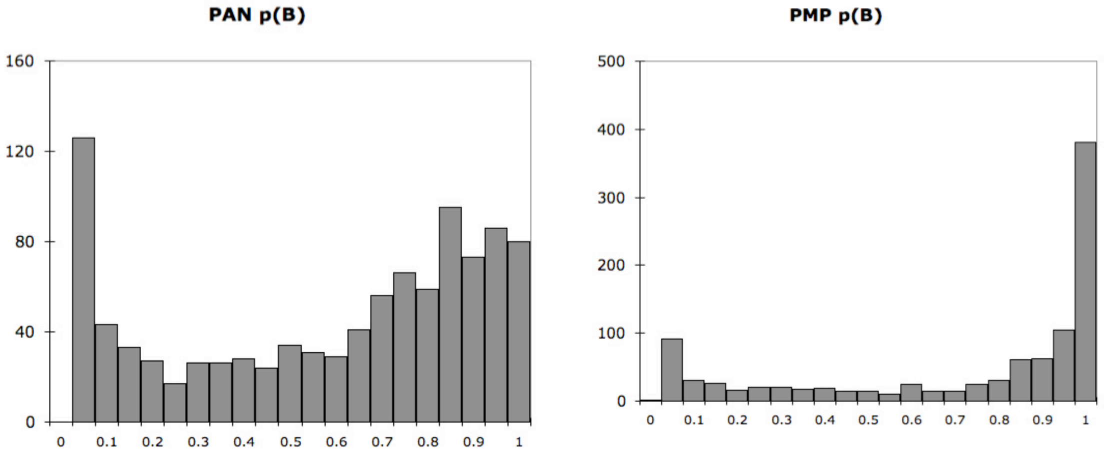


Figure 5.7. Ancestral state reconstruction of inheritance (multi-state coding) in 67 Austronesian societies. Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability. Societies in grey have missing data.

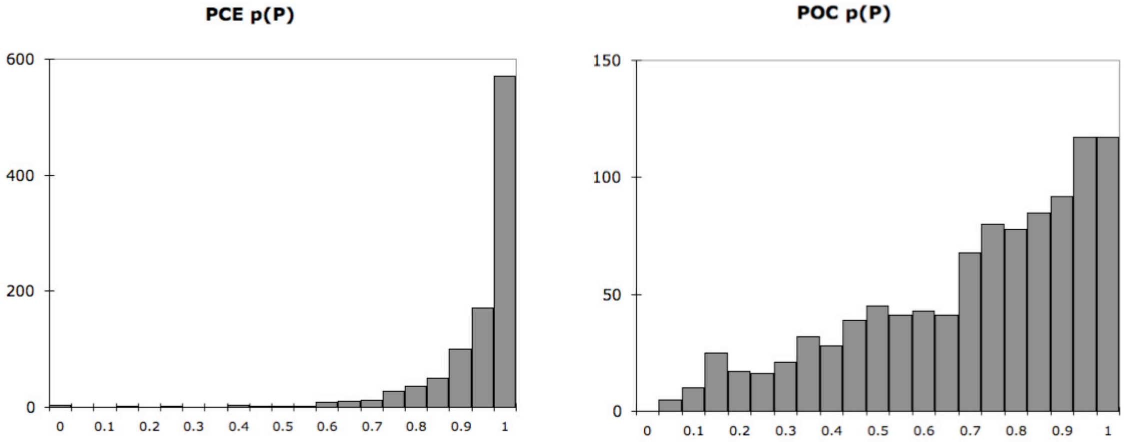


P(B|n) = 0.56±0.02

P(B) = 0.56*1, P(P) = 0.39*1, P(M) = 0.05*1

P(B|n) = 0.70±0.02

P(B) = 0.70*1, P(P) = 0.29*1, P(M) = 0.01*1



P(P|n) = 0.92±0.01

P(B) = 0.06*0.99, P(P) = 0.92*0.99, P(M) = 0.01*0.99

P(P|n) = 0.69±0.01

P(B) = 0.12*1, P(P) = 0.69*1, P(M) = 0.19*1

Figure 5.8 PPD of inheritance with multi-state characters (bilateral, B; matrilineal, M; patrilineal, P) at four selected nodes from the phylogeny in Figure 5.7. This figure can be read as complimentary to Figure 5.6 (multi-state descent). As in Figure 5.6, there is a switch from bilateral inheritance to patrilineal inheritance from earlier to later nodes, but only PMP and PCE are statistically certain.

5.5.5 Descent: Lineality

5.5.5.1 Ancestral states

Binary coding, as opposed to multi-state, allowed for much more certainty in the reconstruction of ancestral states. For this analysis, the ancestral state reconstruction used an exponential prior with a mean of ten, and had a mean marginal likelihood $lh_{harmonic}$ = -51.72. While the Formosan societies reconstruct with a lineal form of descent group in their ancestor (node "Form", *P(L)* = .94), the PAN root comes out as bilateral (*P(B)* = .78), as does PMP (*P(B)* = .98) and the Philippine and Indonesian societies, though the latter two are not nodes with strong phylogenetic certainty. Thus, although the Formosan societies are basal and are all coded as lineal, the program reconstructs the root as bilateral, possibly due to the large number of bilateral societies in the two subsequent branches. At PCE, descent switches to lineality (*P(L)* = .99): the CMP node is lineal, and all the nodes of interest in the Oceanic clade, including POC, are lineal. The PPD panels for lineal descent in Figure 5.10 show the switch from a low probability of lineal descent to a high probability as one progresses across the tree.

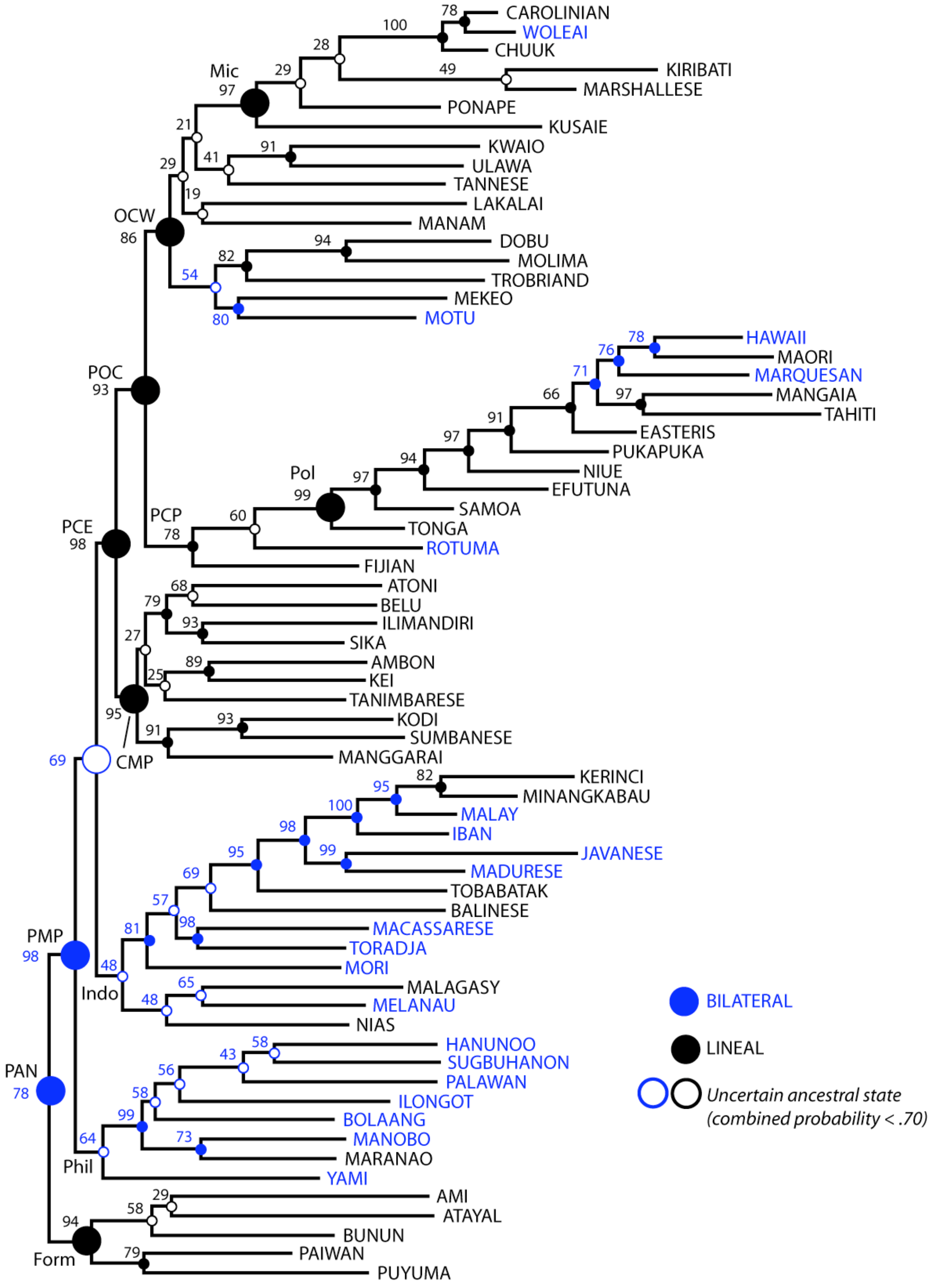
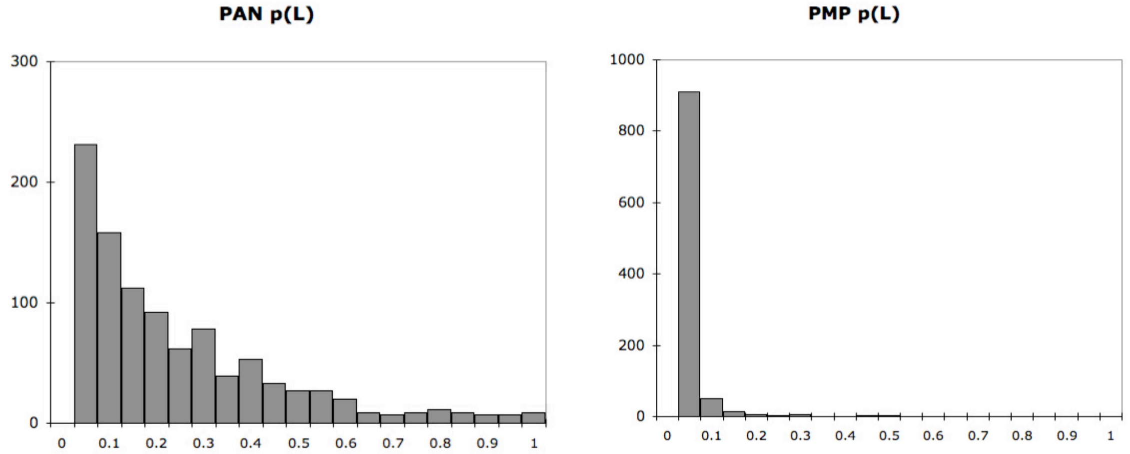


Figure 5.9. Ancestral state reconstruction of bilateral versus lineal descent. Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability.

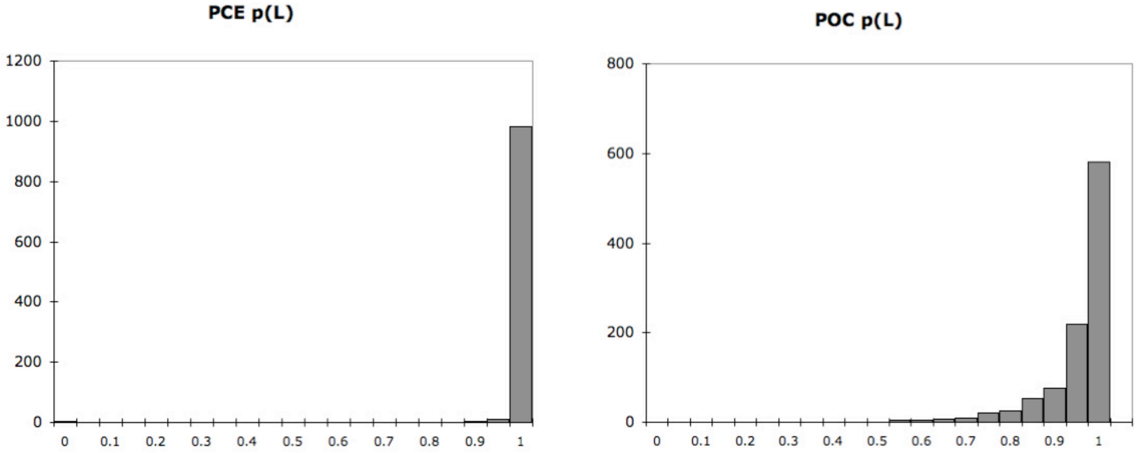


P(L|n) = 0.22±0.01

P(L) = 0.22*1, P(B) = 0.78*1

P(L|n) = 0.02±0.00

P(L) = 0.02*1, P(B) = 0.98*1



P(L|n) = 0.99±0.00

P(L) = 0.99*0.99, P(B) = 0.01*0.99

P(L|n) = 0.93±0.01

P(L) = 0.93*1, P(B) = 0.07*1

Figure 5.10. PPD of bilateral (B) versus lineal (L) descent at four selected nodes from the phylogeny in Figure 5.9. All panels show the PPD of ancestral states for lineality. The early nodes are bilateral (PAN, PMP), but there is a switch to lineality between the Indonesian societies (not shown) and PCE/POC, which reconstruct as lineal. At the root of the tree (PAN) there is more uncertainty in the reconstruction, possibly because the Formosan societies' ancestor (Figure 5.9) is reconstructed as lineal.

5.5.5.2 Rates of trait switching

The switch from bilateral to lineal is more frequent than the reverse switch if we compare the transition rate parameters $q_{\mathrm{BL}} = 26.96$ and $q_{\mathrm{LB}} = 8.09$. Setting the rates to be equal, a Bayes factor test shows that there is statistical evidence for the difference ($q_{\mathrm{LB}} = q_{\mathrm{BL}}$, $BF = 27.92$). Setting $q_{\mathrm{BL}} = 0$, thus forcing the root to be lineal, returns a *BF* of –11.6. A *BF* of less than zero provides evidence for the unrestricted model (in this case, where the parameters take their maximum likelihood estimates and are not equivalent), indicating that there is no evidence that the root is lineal, even accounting for phylogenetic uncertainty. Gaining a lineal system from a bilateral one appears to be the probable evolutionary pathway in these societies.

5.5.6 Descent: Matrilineal aspect

5.5.6.1 Ancestral states

The ancestral state reconstruction used an exponential prior with a mean of ten, and had a mean marginal likelihood $lh_{harmonic} = -57.13$. From the root (PAN, $P(O) = .86$) through PMP ($P(O) = .86$), to PCE ($P(O) = .89$) and the CMP node ($P(O) = .95$), the nodes are reconstructed as having “no matrilineal aspect” in descent. This is reflect in the first three PPD panels of Figure 5.12. The Formosan node reconstructs with the matrilineal aspect ($P(M) = .71$), as does POC ($P(M) = .78$) and other labelled nodes in the Oceanic societies, e.g. Micronesian ($P(M) = .98$). The matrilineal aspect evolves more than once in the Austronesian family, possibly at least seven separate times, but most notably at Proto Oceanic, where it is retained by most societies and lost approximately four times.

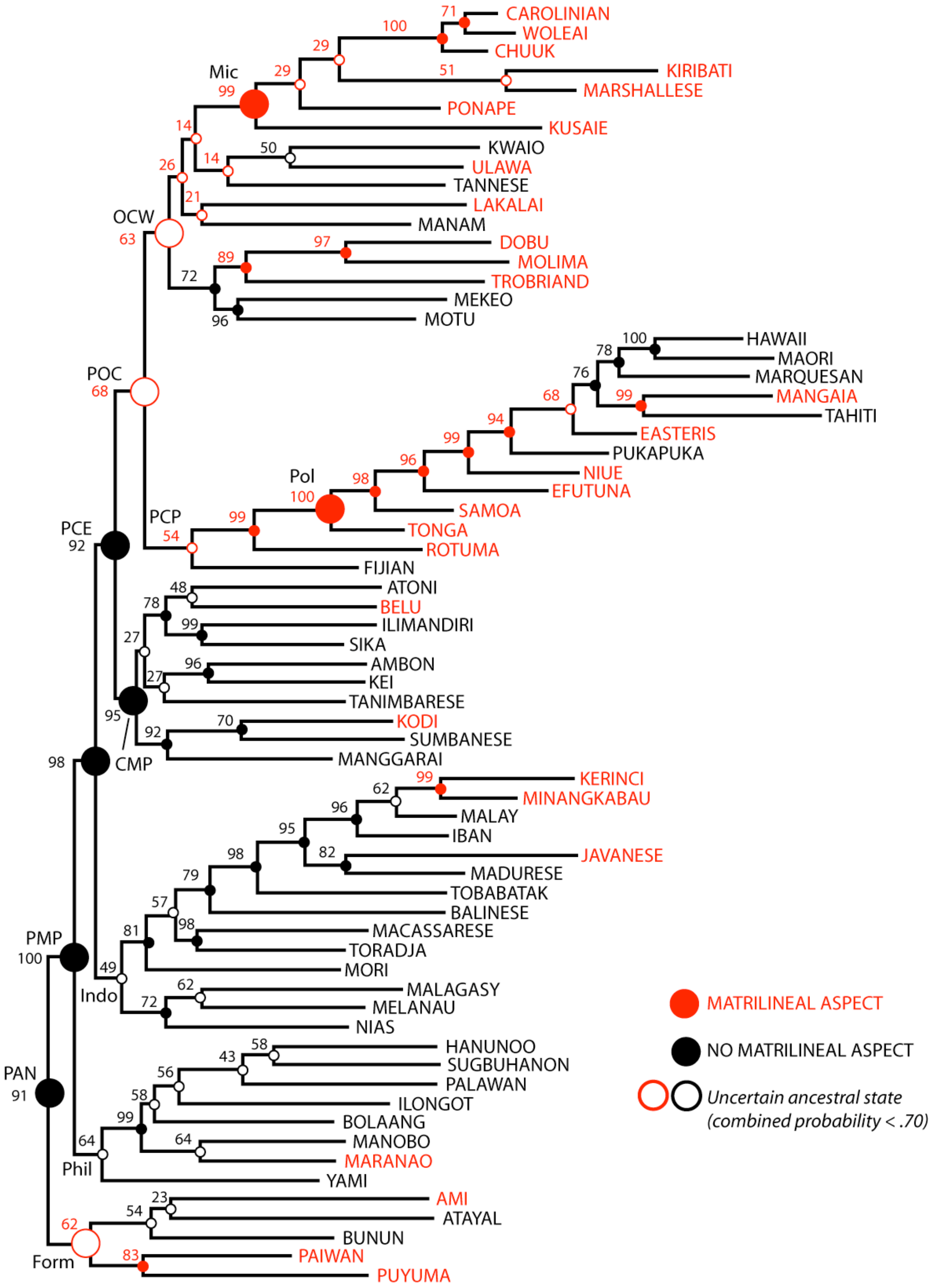
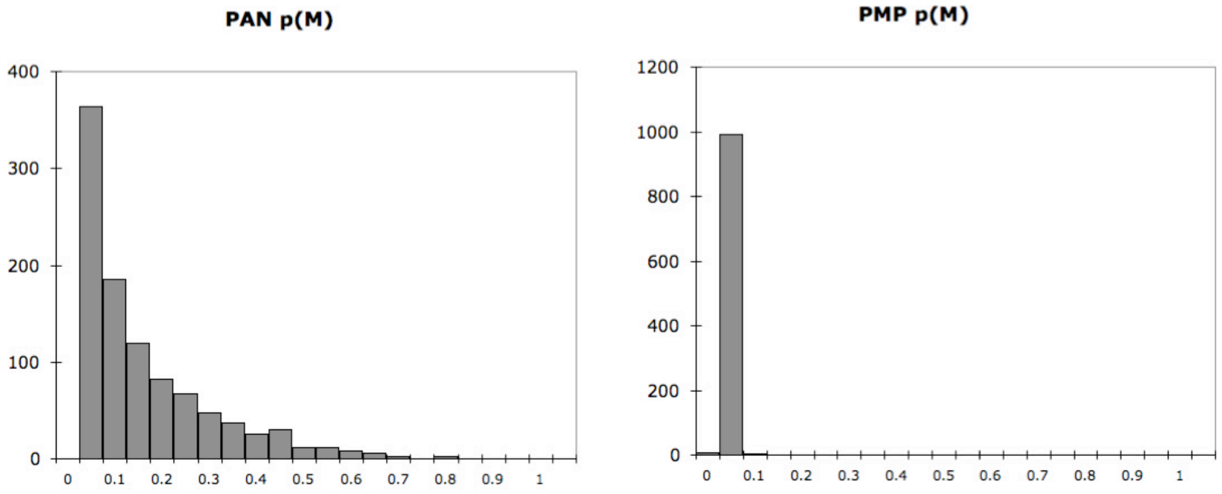
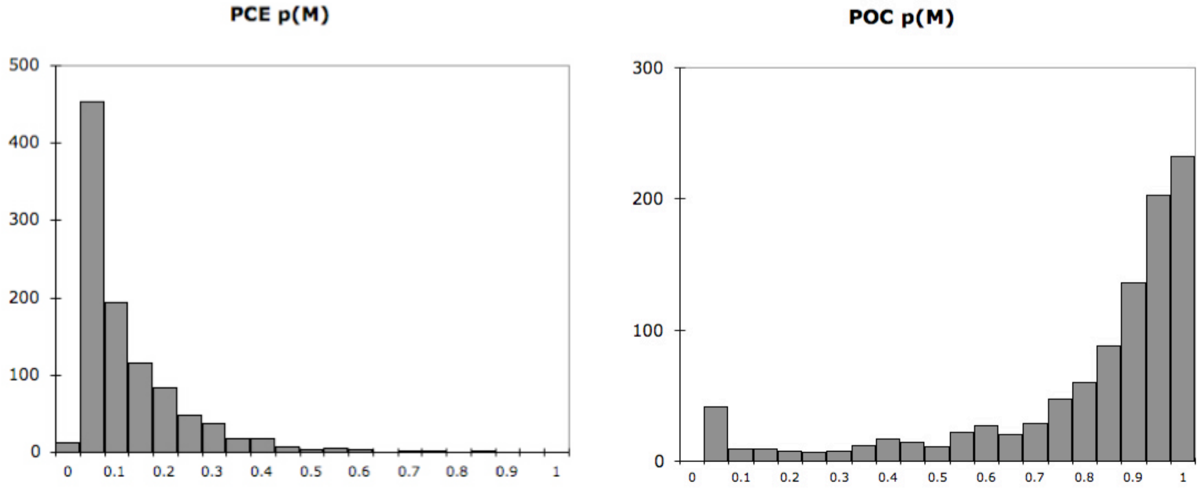


Figure 5.11. Ancestral state reconstruction of a matrilineal aspect in descent versus no matrilineal aspect. Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability. The matrilineal aspect appears to evolve a number of times in western Pacific societies, then once at the POC node and be lost sporadically thereafter.



P(M|n) = 0.14±0.01
P(M) = 0.14*1, P(O) = 0.86*1

P(M|n) = 0.14±0.00
P(M) = 0.14*1, P(O) = 0.86*1



P(M|n) = 0.11±0.01
P(M) = 0.11*0.99, P(O) = 0.89*0.99

P(M|n) = 0.78±0.02
P(M) = 0.78*1, P(O) = 0.22*1

Figure 5.12 PPD of descent contrasting systems with a matrilineal aspect (M) and those without (O) at four selected nodes from the phylogeny in Figure 5.11. Although the ancestor of the Formosan societies reconstructs as having a matrilineal aspect (0.71, not shown), the three early nodes all have an ancestral state with no matrilineal aspect. The matrilineal aspect appears to evolve in the POC node.

5.5.6.2 Rates of trait switching

The transition rates between the states of having and not having a matrilineal aspect are similar (q_{MO}= 14.08, q_{OM}= 19.46) and setting them to be equal makes no difference to the likelihoods, as the Bayes factor is only 1.2. Setting q_{OM} to zero, which forces the root to have the matrilineal aspect, returns a *BF* of –12.94 in favour of the model without the restriction. This means that the estimate of the root as having no matrilineal aspect is strongly supported by the data, but that the trait is free to vary across the phylogeny in both directions.

5.5.7 Residence: Scale

5.5.7.1 Ancestral states

In this analysis residence was coded on a five point scale, with "1" the matrilocal end, "5" the patrilocal end, and "3" representing ambilocality. When ancestral states were estimated, only six of the nodes had a posterior probability over the .70 threshold of certainty, so the tree and PPD panels are not shown. Results are however reported in the summary in Table 5.5. Two nodes in the Polynesian clade reconstructed as mainly patrilocal ("4") at combined probabilities of $P(4)$ = .85 and $P(4)$ = .87, as did PCE ($P(4)$ = .82) and CMP ($P(4)$ = .77). The parent node of Kerinci and Minangkabau reconstructed as strictly matrilocal at $P(1)$ = .96, and the Philippine/Sulawesi node (excluding Yami) reconstructed as mainly matrilocal at $P(2)$ = .74. With five character states, 20 rate parameters needed to be simultaneously estimated. It is likely that the analysis did not reach equilibrium as even after 50 x 10^6 iterations the likelihoods fluctuated widely (mean marginal likelihood $lh_{harmonic}$ = -105.96), even when constrained with an exponential prior.

5.5.8 Residence: Primary mode

5.5.8.1 Ancestral states

Three states were used: ambilocality (A), patrilocality (P) and matrilocality (M). The analysis used an exponential prior with a mean of ten, and had a mean marginal likelihood $lh_{harmonic}$ = -55.63. Residence is very variable across the phylogeny. Both the PAN (*P(M)* = .73) and PMP (*P(M)* = .75) nodes reconstruct as having matrilocal residence. The Formosan, Philippine/Sulawesi, and Indonesian nodes are not certain in their phylogenetic reconstructions, although matrilocality is the state with the highest probability in all three. At PCE residence becomes patrilocal (*P(P)* = .75), continued in the CMP group (*P(P)* = .77), and although predominant, patrilocality is uncertain in POC (*P(P)* = .57). The bottom PPD panel in Figure 5.14 shows the relative estimates of the ancestral state of POC; ambilocality has low probability across the tree sample, while matri- and patrilocality are found at a range of probabilities depending on the phylogeny. The Polynesian ancestral node is patrilocal (*P(P)* = .87), while in the more western Oceanic societies residence is variable; matrilocality predominates in Micronesia and the ancestral node reconstructs as matrilocal with a probability of *P(M)* = .89.

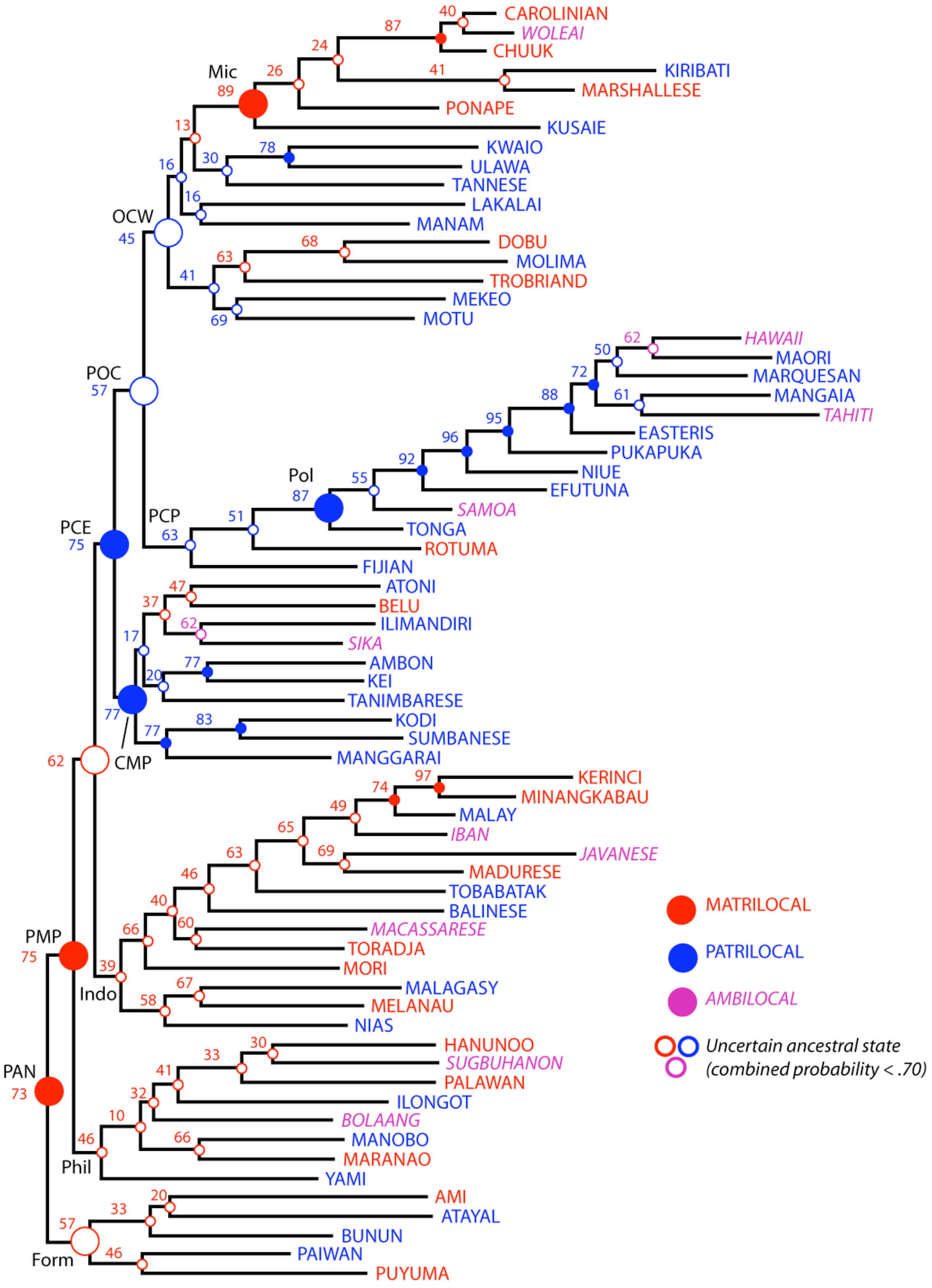
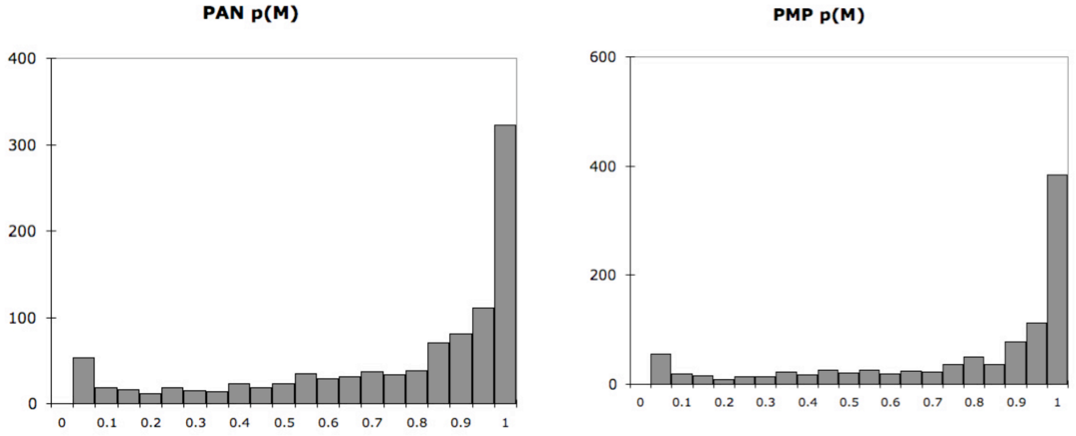
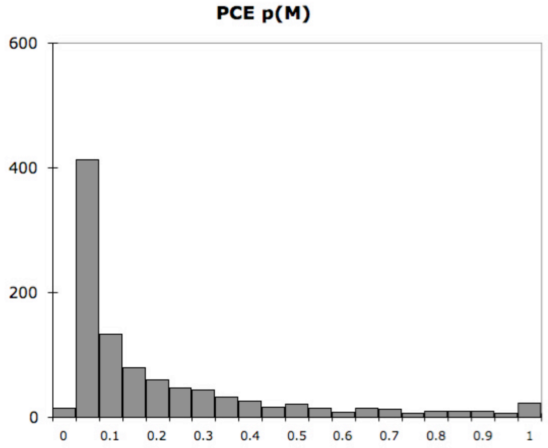


Figure 5.13. Ancestral state reconstruction of the primary mode of residence (multi-state coding). Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability.

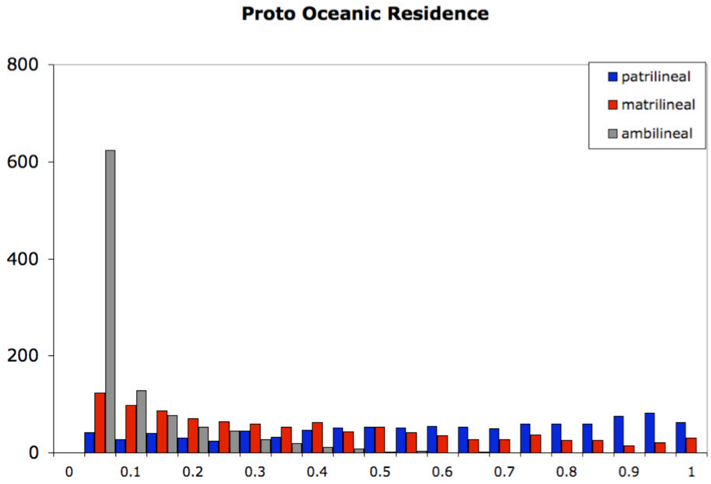


P(M|n) = 0.73±0.01
P(A) = 0.09*1, P(P) = 0.18*1, P(M) = 0.73*1

P(M|n) = 0.75±0.01
P(A) = 0.09*1, P(P) = 0.16*1, P(M) = 0.75*1



P(M|n) = 0.18±0.01
P(A) = 0.05*0.99, P(P) = 0.75*0.99, P(M) = 0.18*0.99



P(M|n) = 0.36±0.04
P(A) = 0.07*1, P(P) = 0.57*1, P(M) = 0.36*1

Figure 5.14 PPD of the **primary mode of residence** with multi-state characters (ambilocal, A; matrilocal, M; patrilocal, P) at three selected nodes from the phylogeny in Figure 5.13. Nodes are contrasted on their reconstruction of matrilocality. Matrilocality appears to be ancestral to the Austronesian family with increasing amounts of patrilocality appearing in the later nodes. The final panel shows the PPD for all three character states of residence at the Proto Oceanic node to demonstrate the relative estimates of these ancestral states.

5.5.8.2 Rates of trait switching

Six transition rate parameters were estimated for the three states as follows: (q_{MP} = 35.67, q_{MA} = 18.13, q_{PM} = 11.12, q_{PA} = 10.83, q_{AM} = 20.71, q_{AP} = 26.94). The highest rate is from matrilocal to patrilocal, and the two lowest rates are those leading away from patrilocality. Patrilocality may thus be some sort of "attractor" state that is easy to get into but hard to change, which makes sense given the ubiquitous appearance of patrilocality in all groups on the tree. This was tested by setting $q_{PM} = q_{PA} = 0$ and comparing this model with the model where parameters take their maximum likelihood estimates. If the two models are equivalent (*BF* <5) we have evidence that the rate of change away from patrilocality is effectively zero. The *BF* was 2.16, supporting this hypothesis. Additionally, I tested a model where $q_{MP} = q_{MA} = 0$, which forced the root to be a state other than matrilocal. Here, the *BF* was –16.62, indicating that there was much more support for the unrestricted model where the root was matrilocal.

5.5.9 Residence: Matrilocal aspect

5.5.9.1 Ancestral states

No prior was used in this analysis as the range of values explored in preliminary runs was acceptably constrained. The mean marginal likelihood was $lh_{harmonic}$ = -39.72. Many more societies had a matrilocal option than did not (56 versus 11) and this state reconstructed with high probabilities throughout much of the tree. As with the multi-state primary mode of residence analysis, the root had the matrilocal aspect (*P(M)* = .78). Examining the PPD panels shows that PAN was more variable in the range of probabilities than PMP, where the reconstruction was constrained to a narrower range of probabilities with a mean of *P(M)* = .81. PCE and POC are not certain in their reconstructions, though they show a trend towards the matrilocal option. We can compare this with the multi-state analysis where PCE was patrilocal and POC uncertain, trending towards patrilocality. Micronesian and Polynesian are matrilocal at *P(M)* = .82 and *P(M)* = .93 respectively. Even the strongly patri-biased CMP group shows a trend towards the matrilocal option in the parent node (*P(M)* = .65). However, it should be noted that this coding captured any aspect of matrilocality in residence, not just the predominant mode for the society.

5.5.9.2 Rates of trait switching

Gaining the matrilocal option has a higher transition rate than losing it: $q_{\mathrm{OM}} = 70.12$ compared with $q_{\mathrm{MO}} = 21.66$. Setting the rates to be equal, a Bayes factor test shows that there is statistical evidence for the difference (*BF* = 7.6, favouring the unrestricted model); thus, gaining a matrilocal option in residence will be likely when the parent node does not have the matrilocal option. Setting $q_{\mathrm{OM}} = 0$ and so forcing the root to have *no* matrilocal option returns a *BF* of 18.38 in favour of the unrestricted model, indicating that there is strong statistical evidence that PAN did indeed have the matrilocal option.

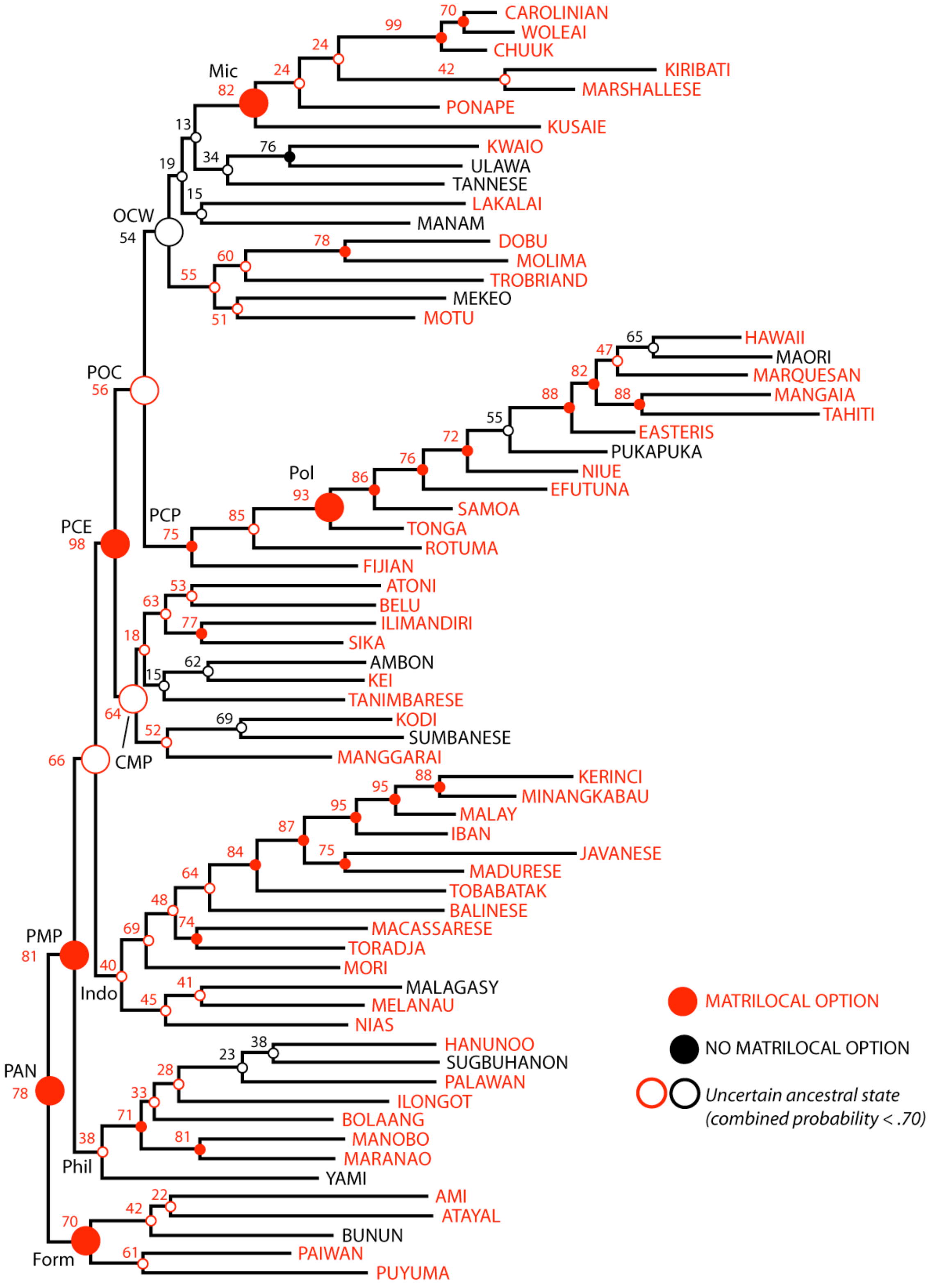
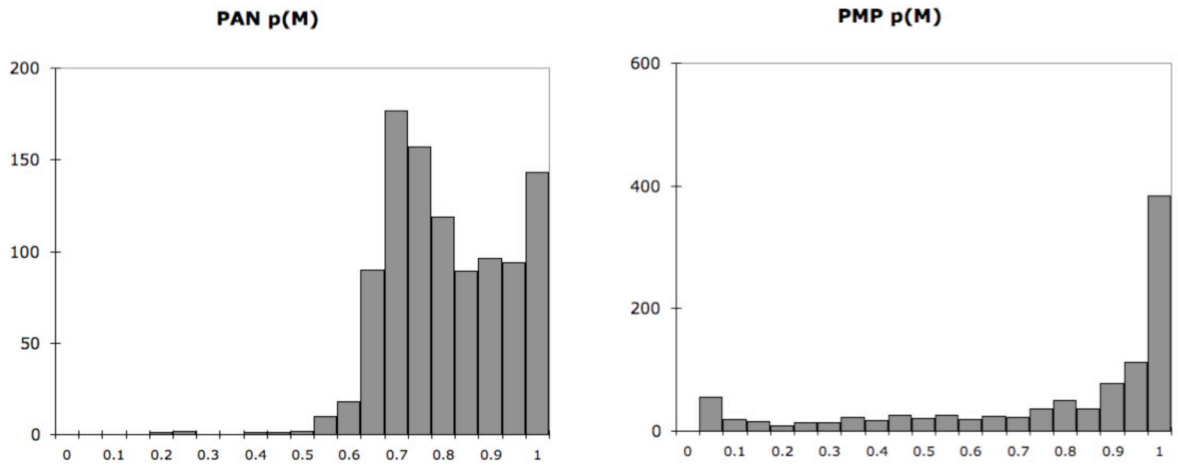


Figure 5.15. Ancestral state reconstruction of a matrilocal residence option versus no matrilocal option. Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability.

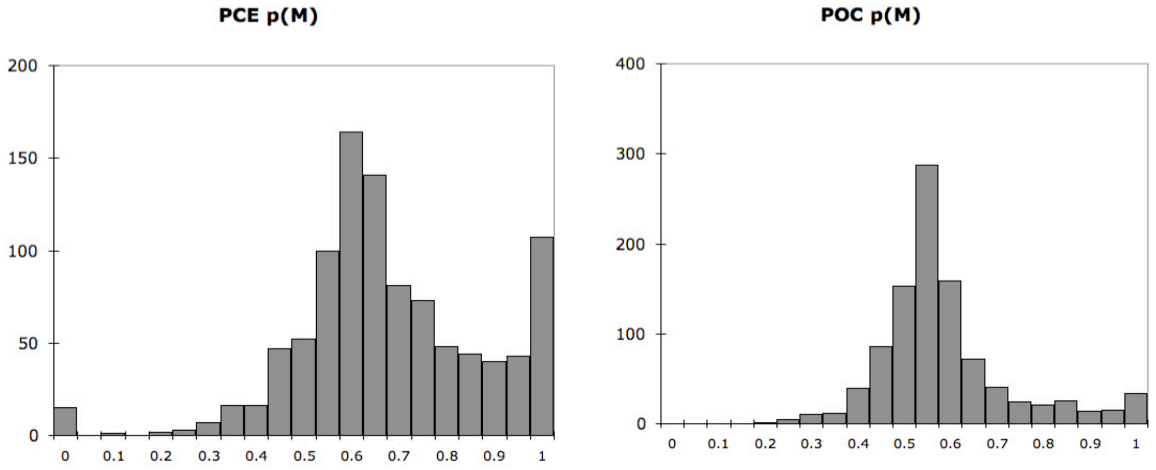


P(M|n) = 0.78±0.02

P(M) = 0.78*1, P(O) = 0.22*1

P(M|n) = 0.81±0.01

P(M) = 0.81*1, P(O) = 0.19*1



P(M|n) = 0.66±0.04

P(M) = 0.66*0.99, P(O) = 0.34*0.99

P(M|n) = 0.56±0.02

P(M) = 0.56*1, P(O) = 0.44*1

Figure 5.16. PPD of residence contrasting societies with a matrilocal option (M) and those without (O) at four selected nodes from the phylogeny in Figure 5.14. The matrilocal option appears quite variable across the phylogeny as demonstrated by the spread in the four PPD panels; however, all four nodes show that some phylogenies in the sample support the reconstruction of the matrilocal option. States at the base of the tree (PAN and PMP) are more certain than the more recent nodes (PCE and POC).

5.5.10 Residence: Flexibility

5.5.10.1 Ancestral states

The analysis used an exponential prior with a mean of ten and had a mean marginal likelihood $lh_{harmonic}$ = -44.14. Many societies (50/67) had a flexible system of residence, and flexibility was reconstructed as the ancestral state with high probabilities over much of the tree. All four of the main nodes in the PPD panels show a narrow range of high probabilities in favour of flexible residence.

5.5.10.2 Rates of trait switching

Gaining flexibility in residence has a higher transition rate than losing it, although the difference is slight: $q_{\mathrm{NF}} = 24.15$ compared with $q_{\mathrm{FN}} = 19.24$. Setting the rates to be equal, a Bayes factor test shows that these rates are functionally equivalent as there is no statistical evidence for the difference ($BF = .74$). Setting $q_{\mathrm{NF}} = 0$, thus forcing the root to be a strictly proscriptive residence system without flexibility, returns a BF of –21.52 in favour of the unrestricted model, indicating that there is strong statistical evidence that PAN had flexible residence.

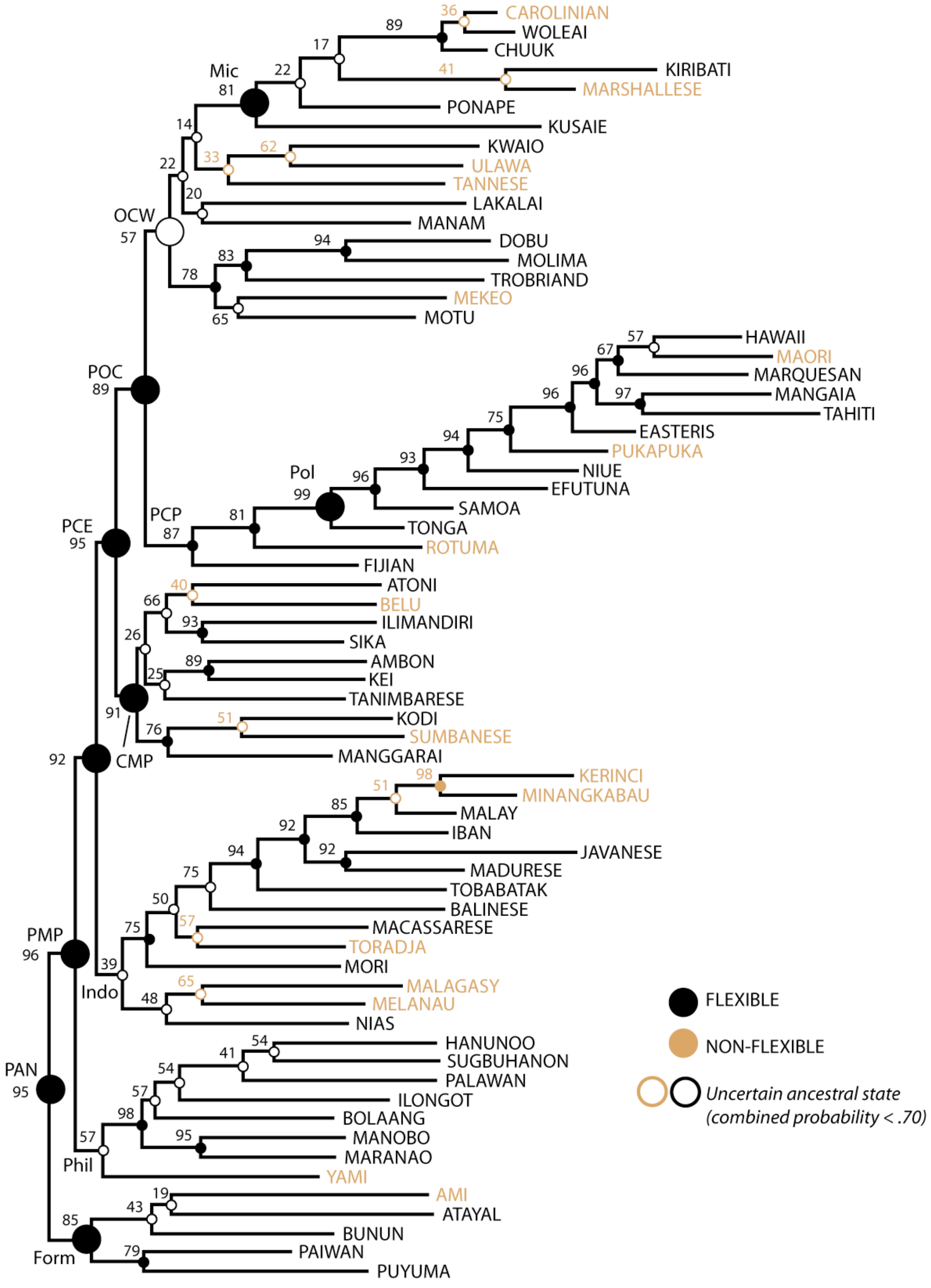
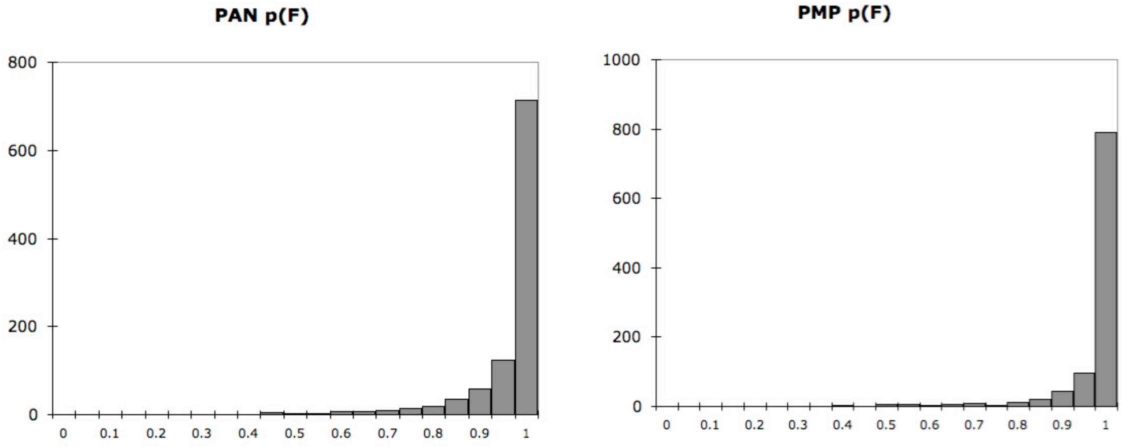


Figure 5.17. Ancestral state reconstruction of flexible versus non-flexible systems of residence. Filled nodes indicate a node reconstruction with probability >.70. Coloured nodes indicate a state reconstruction with probability >.70 according to the legend. Numbers above nodes indicate the state probability.

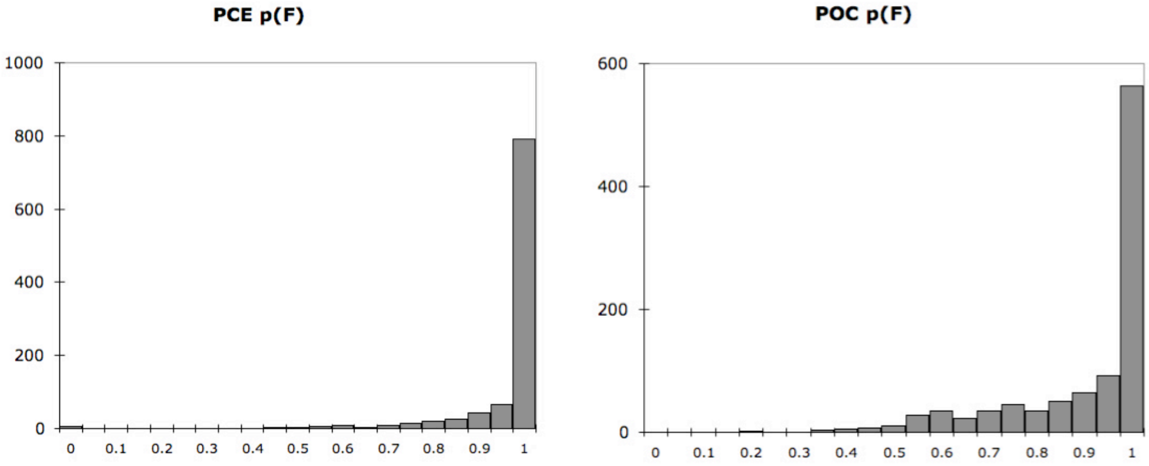


P(F|n) = 0.95±0.00

P(F) = 0.95*1, P(O) = 0.05*1

P(F|n) = 0.96±0.00

P(F) = 0.96*1, P(O) = 0.04*1



P(F|n) = 0.96±0.00

P(F) = 0.96*0.99, P(O) = 0.04*0.99

P(F|n) = 0.89±0.01

P(F) = 0.89*1, P(O) = 0.11*1

Figure 5.18 PPD of flexible (F) versus non-flexible (O) systems of residence at four selected nodes from the phylogeny in Figure 5.17. Flexibility in residence appears to be a trait ancestral to all Austronesian societies.

Table 5.5 Summary table of ancestral state reconstructions at four deep nodes: Proto Austronesian (PAN), Proto Malayo-Polynesian (PMP), Proto Central-Eastern Malayo-Polynesian (PCE), and Proto Oceanic. Values are the combined posterior probabilities of each node, i.e., the probability of the state multiplied by the probability of the node. Values in bold are those over the threshold of certainty (.70), whereas values in italics do not reach .70 but are the highest value reconstructed for that node. Definitions of each state class are described in the methods.

		PAN	**PMP**	**PCE**	**POC**
Descent groups	Bilateral	*.66*	**.88**	.02	.13
	Matrilineal	.11	.01	.05	.35
	Patrilineal	.23	.11	**.93**	*.52*
Inheritance	Bilateral	*.56*	**.70**	.06	.12
	Matrilineal	.05	.01	.01	.20
	Patrilineal	.39	.29	**.93**	*.68*
Lineality	Bilateral	**.78**	**.98**	.01	.07
	Lineal	.22	.02	**.98**	**.93**
Matrilineal aspect	Present	.14	.14	.10	**.78**
	Not present	**.86**	**.86**	**.89**	.22
Residence	Patrilocal	.18	.16	**.75**	*.57*
	Matrilocal	**.73**	**.75**	.18	.36
	Ambilocal	.09	.09	.05	.07
Residence scale	Strictly matrilocal	.26	.26	.07	.15
	Mainly matrilocal	.19	.21	.01	.06
	Ambilocal	.15	.17	.07	.13
	Mainly patrilocal	*.38*	*.32*	**.82**	*.57*
	Strictly patrilocal	.03	.04	.02	.09
Flexibility in residence	Flexibility	**.95**	**.96**	**.96**	**.89**
	No flexibility	.05	.04	.03	.11
Matrilocal aspect	Present	**.78**	**.81**	*.67*	*.56*
	Not present	.22	.19	.33	.44

5.5.11 Summary of ancestral states results

A number of consistent patterns can be drawn out from these analyses. First, early Austronesian descent and inheritance appear to be bilateral. Both the PAN root and the PMP node reconstruct as bilateral as opposed to lineal, and under multi-state analysis PMP has a high probability of being bilateral. Second, lineal descent appears to characterise PCE and POC, so that any lineal systems in the western Pacific (Indonesia, the Philippines, and Sulawesi) may be of later development. Third, matrilocality seems to be present in early Austronesian society, with patrilocal systems coming to predominate in the CMP groups of Eastern Indonesia, and in Polynesia. However, and fourthly, residential flexibility is an ancestral and predominant characteristic of Austronesian societies.

5.5.12 Was Proto Oceanic matrilineal and/or matrilocal?

Only three states are statistically certain for Proto Oceanic (i) a lineal descent system, (ii) a matrilineal aspect to descent, and (iii) flexibility in residence (Table 5.5). However, besides reconstructing the Proto Oceanic node directly, *BayesMultiStates* allows us to test the hypothesis that POC was matrilineal and/or matrilocal by using a "fossil" command (*BayesMultiStates* manual, http://www.evolution.rdg.ac.uk). This elegant test compares two models: an unrestricted model where parameters take their maximum likelihood estimates, and a model where the POC node is fixed, or fossilised, to a selected character state, in this case matriliny or matrilocality. Using the Bayes factor, we then compare the mean marginal likelihoods of the two models to determine if fossilisation makes the likelihood worse than in the unrestricted model. If the likelihood is not worsened by fossilisation, then we cannot rule out matri-centric descent and residence in POC, even when the ancestral state estimates have returned uncertain probabilities. The results of the fossilisation tests are presented in Table 5.6.

Table 5.6. Fossilisation analyses to test the hypotheses that Proto Oceanic was matrilineal and/or matrilocal. A significant Bayes factor (*BF* > 5) indicates the fossilisation worsened the likelihood of the model and that the data support the node estimates for the unrestricted model. *BF* < 5 indicates that fossilising the node does not significantly worsen the likelihood and the fossilised state is statistically likely.

Measure	Lh(unrestricted)	Lh(POC fossilised)	*BF*
Descent: multi-state	-55.65	-55.50	.30
Descent: matrilineal aspect	-40.51	-41.11	-1.20
Residence: multi-state	-70.2	-72.01	-4.0
Residence: matrilocal option	-30.92	-33.56	-5.28

Fossilising POC to matrilineal descent and matrilocal residence under both multi-state and binary coding (Table 5.6) does not cause the likelihood to differ significantly from the unrestricted model. Thus, we cannot reject the hypothesis that POC society may have been matrilineal and matrilocal, as suggested by Hage (1998) and Hage and Marck (2003).

5.5.13 Contribution of phylogenetic uncertainty

The Markov chain visits each tree in the sample multiple times in the analysis. We can determine how important phylogenetic uncertainty is to the reconstruction of ancestral state by a one-way analysis of variance (ANOVA) where each bin represents the variance in one of the trees in the sample (Pagel et al. 2004:681). Ten trees which had been visited a minimum of fifty times by the Markov chain were chosen at random from the sample of 1,000 (trees 2, 141, 353, 470, 511, 700, 755, 881, 955, and 999). By computing an ANOVA of the log-likelihoods we can determine if the model of trait evolution fits some trees better than others. If this is true, then accounting for phylogenetic uncertainty is particularly important. We can also compute an ANOVA for the transition-rate parameters to see how the shape of the phylogeny affects the estimation of these parameters.

Table 5.7. Estimates of the between- and within-tree components of variance in ancestral state reconstruction of descent (multi-state coding), given for the log-likelihood and a transition-rate parameter (qBM). Ten randomly chosen trees which were visited 50 times each by the Markov chain were used for each ANOVA.

Measure	**Mean square between trees**	**Mean square within trees**	***F* (MSB/MSW)**	***p*-value**
Log-likelihood	6.29 (*df*=9)	1.41 (*df*=480)	4.46	>.0001
qBM	239.5 (*df*=9)	61.62 (*df*=480)	3.89	>.0001

Table 5.7 shows how the log-likelihood and a rate parameter are affected by the tree used to estimate them; the ANOVA is highly significant, indicating that controlling for phylogenetic uncertainty is very important.

5.6 Discussion

A decade ago, reconstructing the social organisation of ancestral populations was considered a fanciful and “unreal” enterprise for Pacific prehistorians (Sutton 1996), even though careful extrapolation from archaeology, ethnography, and historical linguistics—the “triangulation” approach (Kirch and Green 2001)—has allowed anthropologists to make rich inferences about past societies (e.g. Blust 1986/87; Hage 1998, 1999; Pawley and Green 1984). However, none of this work has used an explicitly phylogenetic approach to control for Galton’s Problem. Now, new Bayesian comparative methods from evolutionary biology have allowed us to reconstruct the probable ancestral states of post-marital residence and descent in Austronesian societies. Crucially, the comparative method has allowed us to quantify the uncertainty in these reconstructions, and to statistically test hypotheses in a scientific framework.

Proto Austronesian and Proto Malayo-Polynesian society was found to be bilateral, without a matrilineal aspect to descent, but with (flexibly) matrilocal residence. In the context of the literature, these results walk a middle line. Murdock (1949), Fox (1993), and Goodenough (1955) all argued for bilaterality in PMP society. However, beginning with Goodenough (1955), many anthropologists and linguists have argued that some sort of lineal descent group, possibly matrilineal but definitely a land-owning corporate, may have also been present in PMP society (Lane 1961; Blust 1980, 1993b; Hage 1998). The results here strongly suggest that matrilocality is ancestral to the AN family, but not matriliny. Linguistic reconstruction using kin terminology, which preserves relict aspects of older kinship systems, is the main evidence for PAN/PMP matriliny; future comparative work using kin terms (e.g. Marck 2006) should provide a more precise "fossil set" for phylogenetic reconstruction. Moreover, the ABV language now contains more Formosan languages with updated cognate judgements (R. Gray, personal communication); as they function as the outgroup, the cultural-trait coding of these societies is crucial in determining the state of residence and descent in PAN and PMP.

5.6.1 Austronesian matriliny

Lineal descent groups are reconstructed for both Proto Central-Eastern Malayo-Polynesian and Proto Oceanic; strongly patricentric in descent, inheritance, and residence for PCE, but uncertain for POC. However, a matrilineal aspect to descent is strongly supported for POC, though not matrilocality. Fossilising the POC node to matrilineal and matrilocal did not worsen the likelihood of the evolutionary model in all cases; this study then adds to those (Lane 1961; Burton et al. 1996; Hage 1998; Hage and Marck 2003) that have adduced matrilineality and/or matrilocality in POC society. This is an attractive hypothesis for two reasons.

First, matrilineal social organisation in POC/Lapita peoples (Shutler and Marck 1975; Pawley and Green 1994; Kirch 1997) would result in relatively restricted female genetic diversity, and increased male diversity due to in-marrying men, thus providing a framework in which to interpret the divergent mtDNA and Y-chromosome findings in Pacific molecular anthropology (Hage and Marck 2003). Taking kinship structure into account is crucial (Wilkins and Marlow 2006), as human genetic diversity in the Pacific is thoroughly scrutinised, being regarded as pivotal in contributing to debates over human population prehistory (Hurles et al. 2002; Hurles et al. 2003). Secondly, a matricentric social organisation may be adaptive for voyaging or colonising populations, as well as those with high rates of male absence through warfare, trade, raiding, or fishing. The putative POC, and possibly PCE/PMP, populations may correspond to points in archaeological time when significant Austronesian expansion into new territories took place (Anderson 2002; Green 2003). If matrilocality is an “emergency response” to male absence or mortality, and becomes institutionalised if the emergency (such as warfare or protracted migration) persists, then the adoption of matricentric kinship make sense (Harris 1979). Keegan and Maclachan (1989) have argued a similar model for prehistoric Taino societies in the Bahamas: that matricentric kinship developed in response to ongoing pathfinding and migration throughout the West Indies that left women at home. The “male absence” theory is investigated further in the next chapter.

5.6.2 Flexible kinship systems

While residence and descent patterns were clustered, they also showed flexibility, switching back and forth a number of times on the phylogenies. For example, a matrilineal aspect in descent evolved at least four times, then to be lost in daughter societies. Flexibility in residence is apparently an ancestral Austronesian feature, with few societies having strictly proscriptive forms of residence. The cultural ecologists Vayda and Rappaport (1962) wrote that cultural traits in an island context were all about “getting people to resources and resources to people” (1962:137); if kin ties are traced flexibly, individuals and families have more options in times of uncertainty. For example, in New Britain, the Lakalai live in region of tectonic instability and volcanic activity that can render farmland unproductive. Disease epidemics can also depopulate villages (Goodenough 1962). While the Lakalai have matrilineal clans, they also have bilateral groups and flexible residence, which Goodenough proposed were “adjustments to a series of catastrophes in fairly recent times … [this] common adjustment may be those attending environmental instability and recurring disaster" (1962:10). Malleable social structures, such as bilateral or ambilineal descent, or flexibility in residence, might be adaptive responses to depopulation (Lane 1961) or to marginal environments such as isolated or small atolls where there is a land shortage, as Campbell (1985) proposed was the case in Tongareva. Where we see flexible systems in Oceanic societies there may be some functional link, a possible hypothesis for further research. Additionally, the results of Chapter Four suggest that a different evolutionary dynamic may be determining ambilineal descent, which was best predicted by geographical nearest neighbour, in contrast to matrilineal, patrilineal, and unilineal descent, which were all best predicted by phylogenetic nearest neighbour. Flexible kinship in Island Southeast Asia may require different explanations. Bilateral descent, for example in the Hanunoo and Subanun, is possibly favoured in conditions of low population density and shifting cultivation—that is, where permanent field agriculture is or was not present (Frake 1956), and when "land and labour are not in short supply" (Bellwood 1997:145).

5.6.3 Comparative methodologies

Where multi-state codings (three and five states) were used to reconstruct ancestral states, it was difficult to obtain high probabilities of any one state. Unless our data are very "clean", and evolutionary patterns very regular, multi-state analyses may be plagued with more uncertainty than binary-coded traits. This is unfortunate, as cultural traits do not often come in regular dichotomous pairs. Based on these results, I would recommend the use of multiple coding schemes as standard, in order to pick apart the evolutionary dynamics of a complex cultural domain.

In these analyses, the ANOVA of between- and within- tree variance indicated that fitting a model of cultural trait evolution on different tree topologies gave varying likelihoods. This indicates that it is absolutely necessary to control for the historical relationships of societies when estimating how traits evolve, just as it is necessary to control for the genealogical relationships of organisms (Pagel et al. 2004). Ignoring phylogeny is an unprincipled way to investigate cultural evolution.

5.7 Conclusion

To anthropologists interested in the dynamics of cultural evolution, the ability to infer aspects of social organisation in past societies should be extremely exciting. Bayesian methods for estimating ancestral states not only allow us to project the present onto the past in a rigorously statistical manner, but let us do so in a way that frees our inferences from relying on any one hypothesis about population history.

CHAPTER SIX

CAUSE AND EFFECT IN SOCIAL ORGANISATION:

CORRELATED EVOLUTION OF DESCENT AND RESIDENCE

6.1 Summary

Cross-cultural hypotheses concerning descent and post-marital residence abound in the anthropological literature, yet almost none have been tested rigorously with statistical methods that control for historical relatedness. Causal models of Austronesian kinship structure have never been tested with a phylogenetic comparative method. Here I used the Austronesian 67-language tree sample, and ethnographic data on kinship and subsistence, to test two propositions. First, I tested whether residence and descent co-evolve according to Murdock's "main sequence" theory, which posits that changes in residence precede other changes in social organisation. Using a Bayesian method that explores models of evolution while testing for correlated evolution, results showed that residence and descent were co-evolving, and residence appeared to change first. The probability of evolutionary change was found to be higher for residence than descent over a 1000-year period. Second, I tested the hypothesis that matriliny was an adaptive response to male absence, as exemplified by high rates of dependence on male fishing. The model of correlated evolution was not supported for these data, although there was evidence that matriliny and high fishing represented an evolutionary stable strategy. Conclusions examined the findings in the context of Austronesian ethnography and remarked on the utility of Bayesian methods of analysis for testing cultural evolutionary hypotheses.

6.2 Introduction

The estimation of ancestral states of social organisation (Chapter Five) may be intellectually satisfying, but for an evolutionarily-minded anthropologist these findings are only a first step. Behavioural ecology provokes us to ask deeper questions. How are descent and residence related—do they co-evolve together? If so, which changes first? What factors favour matriliny? In this chapter, I use comparative methods to address some of the “cause-and-effect” questions raised by earlier analyses.

For evolutionary biologists testing cause and effect means asking “why”. Such questions can take different forms at different levels of analysis (Tinbergen 1963). One form of question asks if the trait is in some way an adaptation, that is, does it co-evolve with some aspect of the biological or ecological environment? The comparative method, which allows us to test the hypothesis of a regular association between variables while taking aspects of evolutionary history into account, is one of the ways in which behavioural ecologists test adaptation (Ridley 1983; Harvey and Pagel 1991; Reeve and Sherman 1993; Krebs and Davies 1997), other ways are approaches such as optimality modelling and direct experiments.

Human behavioural ecologists have used predictions from life-history theory to test adaptation, most often in traditional societies (Hill and Kaplan 1999; Winterhalder and Smith 2000). For example, Silk (1980) examined the high rate of adoption in Oceanic societies in a Darwinian framework that revealed the inclusive fitness benefits of close-kin adoption. However, as described in earlier chapters, most anthropologists have not typically availed themselves of comparative methods in cross-cultural studies. Mostly they have restricted their analyses to non-phylogenetic statistics, such as chi-square tabulations that do not control for Galton’s Problem, in order to infer co-evolution. In a recent example, Korotayev (2003) reanalysed the worldwide SCCS data on post-marital residence and the sexual division of labour in an elaborate series of contingency-table analyses without historical control. This is unfortunate, as the comparative method is a sophisticated question-asking machine. Not only can we test for adaptation and co-evolution, but we can estimate rates of change, create detailed models of evolutionary pathways, and test hypotheses while controlling for historical uncertainty.

Having established the ancestral states of descent and residence in Austronesian societies, we are now in a position to ask anthropologically meaty questions about the processes, adaptive or otherwise, behind the patterns shown in Chapter Five.

6.2.1 Questions

This chapter is divided into two sections, each addressing a separate set of questions about kinship organisation in these 67 Austronesian societies. First, I ask if there are regularities in the way that descent and residence patterns change. Specifically, I test Murdock's "main sequence" hypothesis of social organisation (1949), which states that changes in post-marital residence cause changes in descent, using a model of correlated evolution that allows the directionality of change to be specified. Second, I investigate the evolution of matriliny by testing if matriliny/matrilocality co-evolve with factors that promote male absence, specifically, a dependence on fishing. Each set of hypotheses is introduced and discussed separately, but the chapter contains a general conclusion that attempts to link the findings together.

6.3 Testing the “main sequence”

6.3.1 Introduction

Murdock (1949:221-222) claimed that changes in residence patterns preceded all other types of changes in social organisation, such as descent and kin terminology, by altering the physical distribution of related individuals.

> Rules of residence reflect general economic, social and cultural conditions. When underlying conditions change, rules of residence tend to be modified accordingly. The local alignment of kinsmen is thereby altered, with the result that a series of adaptive change is initiated which may ultimately produce a reorganization of the entire social structure. (Murdock 1949:17)

In its general form, this has become known as “main sequence kinship theory” (Fox 1967; Naroll 1970; Divale 1974). Thus, different patterns of post-marital residence produce different arrangements of kin: patrilocality groups fathers and brothers—termed “fraternal interest groups” by Divale (1974)—together with unrelated women, while matrilocality groups related women together with their brothers as well as their respective husbands. Whilst residence rules show some patterns of correspondence with descent rules—for example, patrilocal residence is almost always found with patrilineal descent (Coult and Habenstein 1965; Levinson and Malone 1980)—the relationship is not altogether straightforward. Many matrilineal societies have patrilocal or ambilocal forms of residence (van den Berghe 1979), such as the famously bilocal Dobu of the D’Entrecasteaux Islands (Young 1993). When residence does not match with descent or kin terms, a society may be seen (on Murdock’s model) to be in transition from one state to another. Driver (1956; 1969) found support for the main sequence model amongst North American societies, and identified that the sexual division of labour between the sexes was a major factor in determining residence, and thus descent. Similarly, other studies have proposed various catalysts for a change in post-marital residence, including the presence of internal versus external warfare (Ember and Ember 1971), recent migration (Divale 1974), or the sexual division of labour regarding subsistence (White et al. 1981; Korotayev 2003). However, Oceanic societies have usually been found to have no association between sexual division of labour and residence, as Alkire (1974) demonstrated for Micronesia. From a Darwinian point of view, matriliny and matrilocality may be seen as daughter-biased parental investment, allowing maternal kin (especially grandmothers) to assist with child-rearing, which has been shown to have positive effects on child survival and thus inclusive fitness (Sear, Mace, and McGregor 2000; Holden, Sear, and Mace 2003; Mace and Sear 2004). Ember, Ember, and Pasternak (1974) asked if unilocal and unilineal descent regularly co-occurred in a worldwide sample of 42 societies. They found unilocal residence to be a "necessary but not sufficient" cause of unilineal descent, as not all unilocal societies were unilineal (1974:92), only becoming so as responses to warfare.

Thus, while main sequence theory has largely been examined with emphasis on factors which adjust residence, the sequence itself remains a largely untested proposition. This has set up an unwarranted division between those cross-cultural anthropologists who believe in a sequential alteration of kinship organisation and who concentrate on the factors affecting residence, and those who ascribe changes in kinship traits to other causes and may be working from a more evolutionary or ecological perspective. For example, alternatives to a main sequence theory seek to explain patterns of descent and residence by means of ecological factors such as horticultural subsistence and the predominant type of physical environment (Aberle 1961:668; Gough 1961:551; Service 1962:120). Given that so much of the literature on descent and residence has taken a position on the main sequence theory, or has derived hypotheses from causal models related to it, such as the Embers' "warfare" theory (Ember and Ember 1971; Ember 1974), it seems prudent to test the sequential model in its most general form before testing any of the multiple models derived from it.

Testing the general model is especially important when we consider that many of the specific models, for example, Divale's (1974) explanation of matrilineal and matrilocal societies as "recently migrated", hinge on an *a priori* assumption of ancestral states as patrilineal and patrilocal (Divale 1974:77; Levinson and Malone 1980), a position frequently found in the literature (e.g. Ember 1975; Service 1967; Rodseth et al. 1991; Foley 1996). In contrast, others have suggested (Murdock 1949; Eggan 1968; van den Berghe 1979) that foraging populations were likely to have multilocal, flexible residence patterns, while Ember and Ember (1972:397) argue that "multilocality and associated features of social organization are probably recent consequences of European contact". More recently, Marlowe (2004) has re-examined foraging societies residence patterns and shown that they tend to be much more fluid and multilocal than non-foragers, with individual decisions resting on considerations of childcare and care of elderly parents. Clearly, any "ancestral" form of kinship organisation is elusive, and should rather be treated as an empirical fact to be established, whether in regional studies or in the global context. Testing the main sequence assumption properly should be part of this project.

To date, the main sequence theory has not been tested by a formal phylogenetic model. Comparative methods such as *Discrete* allow us to estimate the probable direction of evolutionary change by examining the likelihood of transitions between different character states, providing a way to test Murdock's model in the Austronesian context whilst controlling for phylogenetic relationships. Determining the likelihood of ancestral states of residence and descent was the first step in testing this model.

6.3.1.1 Hypotheses

I tested two hypotheses related to the "main sequence" theory. First, I tested whether descent and residence were co-evolving together under two coding schemes, unilineality and patrilineality. These coding schemes relate to two common sets of divisions in the cross-cultural literature on kinship, those to do with the evolution of unilocal and unilinear (as opposed to multilocal and bilateral) forms of descent and residence (e.g. Goodenough 1957; Lowie 1961; Ember et al. 1974; Goody 1976), and the evolution of patrilineal organisation, as opposed to other forms of descent (Ember and Ember 1971; Hartung 1976). Second, I tested if post-marital residence changed first and/or changed at a higher rate when traits were evolving on a phylogeny, as would be predicted by the sequential theory.

6.3.2 Methods

6.3.2.1 Phylogeny estimation

The 67-language data set and the corresponding 1000-tree Bayesian sample, as described in Chapter Two, were used for these analyses. Character-state data for the traits under investigation was mapped onto the consensus phylogeny as in previous chapters (Figures 6.2 and 6.3).

6.3.2.2 Cultural data and coding schemes

The ethnographic data on descent and residence compiled for Chapter Five were used in these analyses (see Chapter Five). Two different coding schemes were used. First, societies were coded “U_D” as unilineal if they were primarily patrilineal or matrilineal, and “U_R” as unilocal if primarily patrilocal/avunculocal or matrilocal. Non-unilineal (“N_D”) and non-unilocal (“N_R”) societies comprised all others, including ambilineal and ambilocal societies. This was to test a general model of lineal and non-lineal social organisation. Second, societies were coded as patrilineal/patrilocal or with an absence of patri-traits. A society was coded “P_D” for the presence of patriliny if it were primarily patrilineal, ambilineal or had double descent. All others were “O_D”. A society was coded “P_R” for the presence of patrilocality if it were patrilocal or ambilocal. All others were “O_D”. This coding was to test a more specific model of the evolutionary sequence, that is, that patri-centric shifts in residence co-evolved with patri-centric descent. Patriliny was chosen as the focus simply because it was the most common form of social organisation in the sample. Table 6.1 shows the distribution of societies under each coding scheme in a contingency table. Chi-squared tests were conducted on the data to see what the results of a "traditional" cross-cultural test of association would show.

Table 6.1. Contingency table for unilineal descent and unilocal residence showing the number of societies classified in each trait class. Each of the cells corresponds to one of the four states in the evolutionary "flow diagrams".

	Unilineal (U_D)	**Non-unilineal (N_D)**
Unilocal (U_R)	44	12
Non-unilocal (N_R)	6	5
	Patrilineal (P_D)	**Other (O_D)**
Patrilocal (P_R)	32	16
Other (O_R)	1	18

6.3.2.3 Testing correlated evolution

The framework of *Discrete* (Pagel 1994), implemented in the Bayesian context in *BayesMultiState* (Pagel and Meade 2006; now released as *BayesTraits* at http://www.evolution.rdg.ac.uk/SoftwareMain.html) was used to test for correlated evolution. *Discrete*, described in full in Chapter Three, tests for co-evolutionary change between two binary-coded characters by estimating the likelihood (*Lh*) of two models. The *Lh* is a numerical estimate of the likelihood of obtaining the data, given the tree(s) and a specific model of evolution. In Pagel's comparative method, the model is specified by a set of transition-rate parameters that indicate the probability of change from one character state to the other (see Figure 6.1). An independent model (I), where the two characters are free to evolve separately, is compared to a dependent model (D), where the two characters are co-evolving together. Because more parameters are required to describe the dependent model, if the independent model is true, then it will have a higher likelihood. This is because it requires fewer parameters to describe the data, as some of them will be equal. If the likelihood ratio (*LR*) of the independent and dependent model is significant, we can then reject the null hypothesis of no co-evolution.

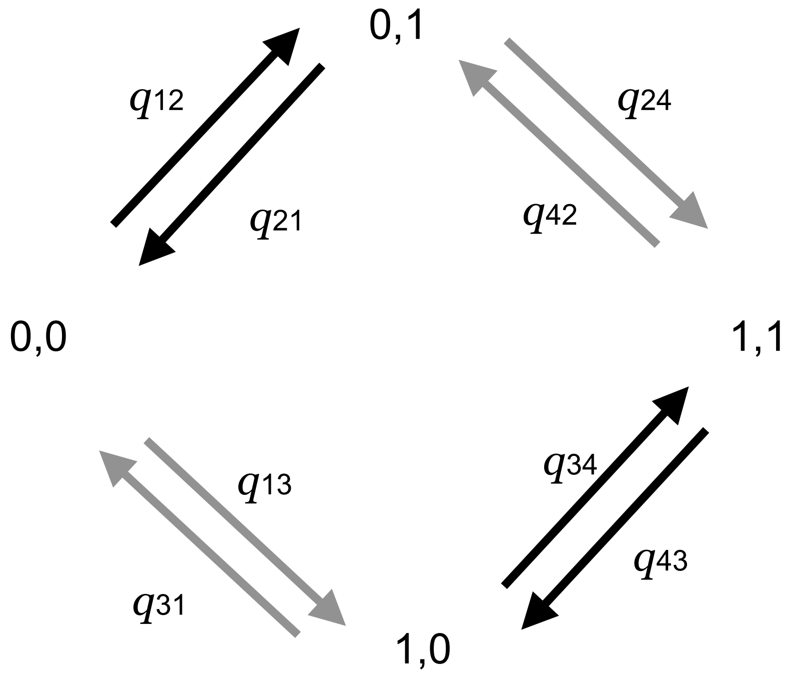


Figure 6.1. Transitions among four combinations of states with two binary variables in the dependent model of evolution. Transition-rates are denoted by q_{12}, q_{24} etc., and are estimated as the parameters of the model of evolution. High rates of (for example) q_{13} and q_{24} compared to all others indicates that the first trait is changing from 0 → 1 more often or quicker than other changes.

Chapter Two described the Bayesian implementation of *Discrete*; it is recapped here for context. Briefly, instead of conducting a comparative test for co-evolution on a single tree, the method uses a Bayesian sample of trees, so that inferences about the character co-evolution are not wedded to any particular phylogenetic hypothesis. As well as removing the effects of phylogenetic uncertainty, the method accounts for mapping (character) uncertainty by computing probability *distributions* of the four character-state combinations at each node, rather than assigning single probability values, or just single values, to each node. We can then plot the posterior probability distributions of the transition-rates between these character states, as was shown for the ancestral state estimations in Chapter Five, to investigate the degree of certainty we may have in the results.

In the Bayesian context, we do not compare two single likelihoods to test the independent versus dependent models, but rather we compare the two posterior probability distributions of the likelihoods, in which there will be variation according to the phylogenetic and trait uncertainty. We then ask a slightly different question: which model, the dependent or the independent, accounts for a higher proportion of the probability of the data? To do this we use the harmonic (marginal) means of the likelihoods, derived at the convergence of the Markov chain run. We compute the Bayes factor as $BF = -2*(I-D)$, where a BF of 3–5 indicates positive evidence for the dependent model, and greater than five indicates strong evidence (Pagel and Meade 2006). Harmonic means are sensitive to outliers and as such the analyses were run for as long as possible to ensure that harmonic means were stable.

Markov chain. To run a co-evolutionary analysis, the program took two files, (i) the tree-sample of 1000 phylogenies, and (ii) for each culture, information about the state of the two traits presumed to be co-evolving. The independent and dependent model parameters were estimated from a Markov chain that ran for 100×10^6 iterations, repeatedly visiting each tree in the sample of 1000. After convergence of the chain, outcomes were sampled every 1000 iterations to avoid autocorrelation. This provided 100,000 samples with which to estimate the marginal likelihoods, posterior distributions and transition-rate parameters of the dependent and dependent models.

6.3.2.4 Using RJ MCMC to find the best models of evolutionary change

The transition rate parameters in Figure 6.1 give us a relative measure of which transitions occur more often. *BayesMultiState* outputs these parameters, which we then use to estimate the probable direction of evolution, that is, which trait changes first in a possible evolutionary pathway. We are also able to determine the significance of these changes using statistical tests. Previously, in the non-Bayesian (ML) version of *Discrete*, the investigator proceeded by (arduously) setting each transition to zero, or setting sets of transitions as equal, to see if this decreased the likelihood of the model significantly; if it did, then that parameter was retained “as is” in the model of evolution. If it did not alter the likelihood, then that switch was regarded as unimportant in the co-evolutionary pathway. By reducing the number of transitions in this manner, it was possible to compare the rate parameters and clarify which trait was driving any co-evolutionary change, as Holden and Mace (2003) did in their analysis of matriliny and cattle-keeping in Bantu-speaking societies.

The reversible-jump (RJ) MCMC procedure circumvents some of these aspects of model-construction by using the Markov-chain device to explore the universe of possible models, visiting them in proportion to their probability (Pagel and Meade 2006:809). In this context, a "model" is described as the set of eight transition-rate parameters between the four states of character evolution, where transition-rates are sorted into classes that are functionally equivalent. For example, the model "1100000Z" denotes a situation where the transition rates of q_{12} and q_{13} are equivalent, but different to all other rates in the flow diagram, except q_{43}, which is indistinguishable from zero. In the implementation of the RJ procedure, the program reports the number of visits to each model in the sample. There are 21,147 possible dependent models. Some number of these models will be equivalent to the independent model (e.g. 00000000 or 11010100) because pairs of transitions will have been assigned to the same rate class. The ratio of independent to dependent models in the sample give an indication of whether correlated evolution is occurring. From Stirling numbers (Pagel and Meade 2006) we expect a ratio of 413, that is, the dependent model should be 413 times more prevalent in the sample than the independent, i.e., the independent model should only account for 0.24% of those present. If the chain visits independent models less than this, we have evidence for correlated evolution. Ideally, only a small number of models will account for the majority of the sample, indicating that other visited models are "noise" that may be disregarded. Unlikely models may be visited a few times, but we are interested in those that are repeatedly visited.

6.3.2.5 Hypothesis testing

In order to understand the most probable evolutionary pathways in the flow diagram, we can (i) investigate the most commonly-visited model and (ii) select those models which fit our hypothesis and compare their likelihoods (using the Bayes factor) against those which do not. Comparing the dependent and independent models is the most general form of this approach. For a more particular example, we might obtain transition-rate parameters that indicate that the transition q_{13} is 100, compared to q_{12} which is 10. We wish to test if $q_{13} > q_{12}$ is statistically significant, that is, whether q_{13} is a "faster" rate and thus more likely to change first. To do this, we isolate those models in which q_{13} is greater than q_{12}, and note the harmonic mean of their marginal likelihoods. These are then compared to the sample harmonic mean of marginal likelihoods of the rest of our sample in the standard Bayes factor equation and the significance of the test is thus judged from the outcome. Because harmonic means are sensitive to extreme values, we compare only equal-size samples.

6.3.2.6 Using kappa to estimate the mode of character evolution

Kappa is a parameter that tests for punctuational versus gradual evolution by altering the length of individual branches. $\kappa = 0$ indicates a star phylogeny when applied to tree-building, or a punctuational mode of evolution when considering the evolution of characters on a phylogeny (Freckleton et al. 2002). Kappa > 1.0 indicates that there is more evolution on long branches (i.e., it stretches these more than short ones), while values of $\kappa < 1.0$ indicate more evolution on shorter branches and thus compresses longer ones. As well as being informative in its own right, κ can be estimated from the data and then added to the model to improve the fit. I report κ values for all analyses.

6.3.3 Results

6.3.3.1 Phylogeny

The standard consensus phylogeny labelled with trait data is presented for the unilineal/unilocal coding in Figure 6.2, and for the patrilineal/patrilocal coding in Figure 6.3, overleaf. Both phylogenies show that more societies have the unilocal form of residence than the unilineal form of descent. Figure 6.2 also has the ancestral states of unilineal/unilocal traits mapped onto the early nodes of the trees. For this coding, the program estimated the root to be unilocal ($P(U_R) = .71$) and non-unilineal ($P(N_D) = .77$) under the independent model, and similarly ($P(U_{R,} N_D) = .44$) under the dependent model. For the patri-coding, the estimates were less certain, with the root equivocally patrilocal ($P(P_R) = .50$) and non-patrilineal ($P(O_D) = .60$) under the independent model, and the same ($P(P_{R,} O_D) = .57$) under the dependent model.

6.3.3.2 Chi-square tests

A chi-square test (2 x 2 with 1 *d.f.*) for the unilineal coding was not significant (χ^2= 2.80, p ≤ .10). For the patri- coding there was a significant association as χ^2= 20.53, p ≤ .001.

6.3.3.3 Kappa

For the unilineal-coded analyses, kappa was estimated and found to have a mean of .52 ±.15, with estimates ranging from .00 to 1.06. As this was a departure from the default, implying a moderately punctuational mode of evolution, this parameter was incorporated into subsequent co-evolutionary analyses. For the patri-coded analyses, kappa was estimated using the independent model and found to have a mean of 1.06 ±.22. As this was hardly different from the program default ($\kappa = 1$), it was left unchanged in further analyses. However, estimates of kappa ranged from .00 to 1.62 (Figure 6.4), indicating that this parameter varied with different topologies and/or models of evolution.

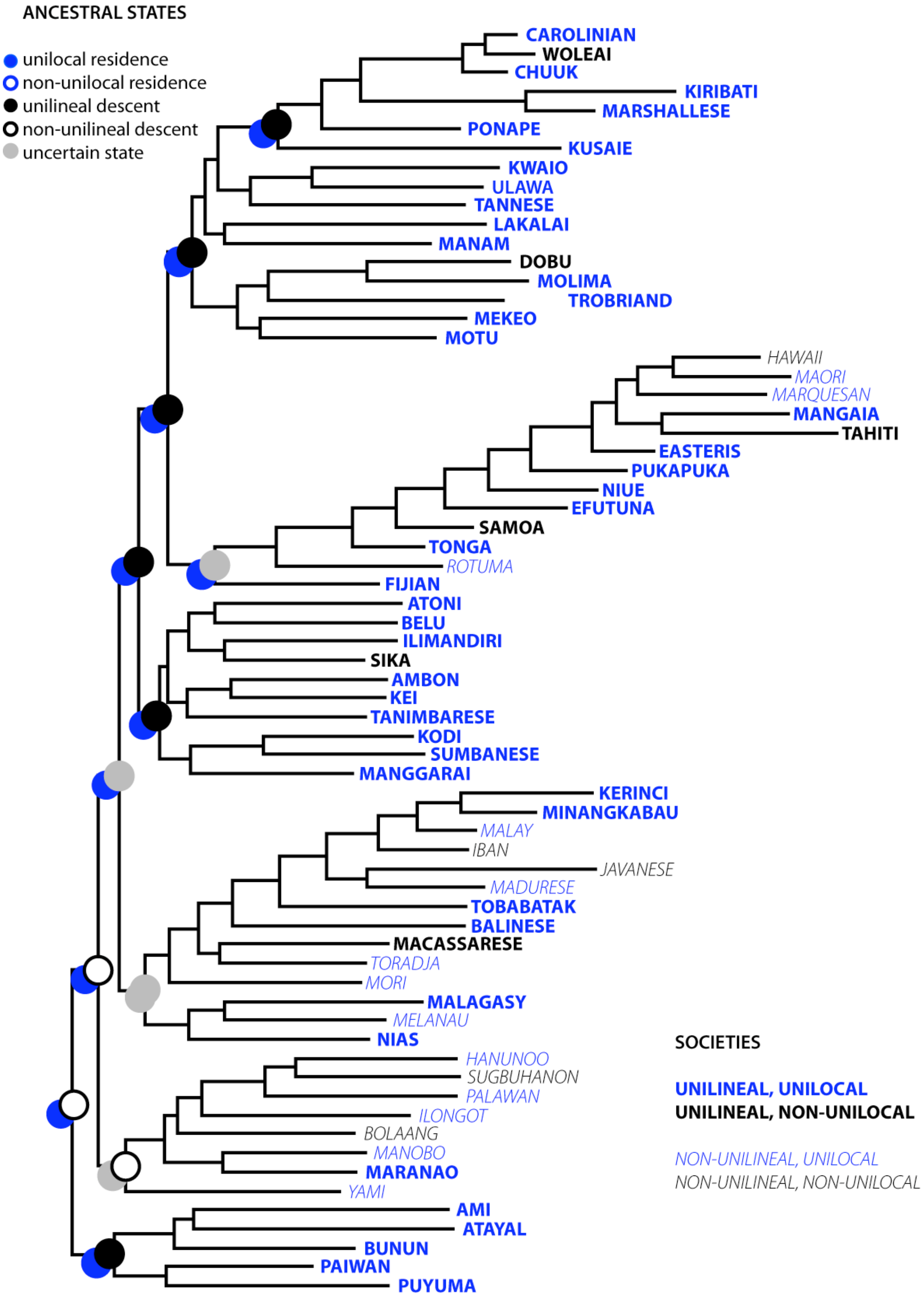


Figure 6.2. Consensus phylogeny of 67 Austronesian societies showing the evolution of unilineal descent and unilocal residence. Descent is denoted by font: unilineal societies appear in bold, non-unilineal societies in italics. Residence is denoted by colour: unilocal societies are in blue, non-unilocal societies are in black. Ancestral states are indicated by the coloured dots at early nodes and show that unilocal residence is more ancestral that unilineal descent.

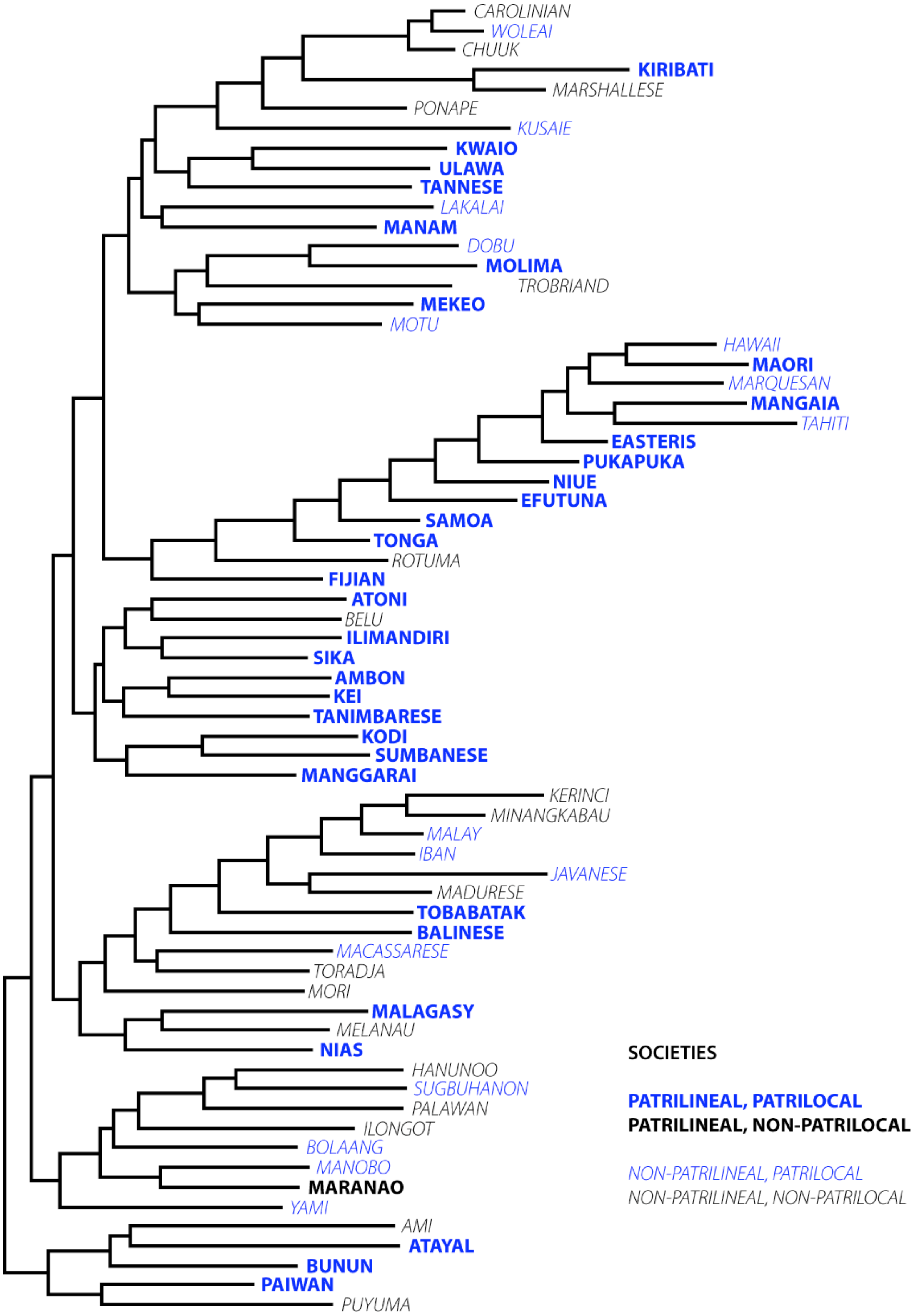


Figure 6.3. Phylogeny showing the evolution of patrilineal descent and patrilocal residence. Descent is denoted by font: patrilineal societies appear in bold, non-patrilineal societies in italics. Residence is denoted by colour: patrilocal societies are in blue, non-patrilocal societies are in black.

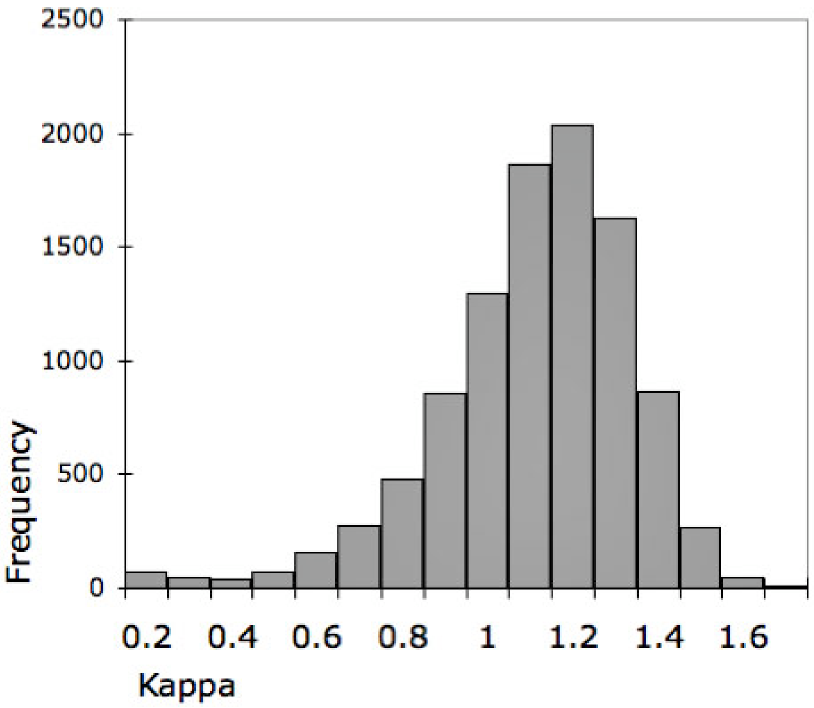


Figure 6.4. Distribution of estimated kappa values for patri-coding. Low kappa values indicate a punctuational mode of evolution, values around one indicate a gradualist mode with change proportionate to branch length, while kappa values larger than one indicate more change on longer branches. As the majority of values (87%) exceed .90, we may conclude that these traits are evolving according to the phylogeny, i.e. they are not following a punctuational mode.

6.3.3.4 Tests for co-evolution

For the unilineal coding, the mean marginal likelihood of the independent model, using the harmonic mean, was –71.68, while that of the dependent model was –68.22. Using the Bayes factor calculation, –2*(I–D), *BF* = 6.91, indicating that the hypothesis of correlated evolution between descent and residence was positively supported. Similarly, for the patri-coded data, there was strong positive evidence for the co-evolution of the two traits (*BF* = 21.44).

The RJ MCMC procedure can also test if the hypothesis of correlated evolution is supported by the data without using the Bayes factor. For each of the 100,000 samples, the program tells us if the model string found corresponds to an independent or dependent model. Recall that the dependent model should be present 413 times more than the independent for correlated evolution, i.e., the independent model should represent 0.24% or less of the sample. For the unilineal coding, the independent model accounted for (exactly) 0.24% of samples, and for the patri-coding, the independent model only accounted for 0.002%. This is extra confirmation that the co-evolutionary, dependent model fits these data better than the independent model.

We can probe further into the probable evolutionary pathway by examining the transition-rate parameters. Descriptions of these evolutionary transitions are given in Table 6.2. Flow diagrams (Pagel 1997) of evolutionary change are shown in Figures 6.5 and 6.6. For testing the hypothesis of co-evolution between descent and residence, we are interested in the rates of q_{13}, q_{31}, q_{24}, and q_{42}, where a change in residence occurs before a change in descent, and especially q_{13} and q_{24}, where the transition occurs towards lineality in social organisation.

Table 6.2. Description of the rate coefficients as applied to residence/descent data. These descriptions can apply equally to the patri- coded data (Figure 6.5). The two transitions in italics denote pathways towards lineal descent and residence where residence changes first.

Coefficent	**Evolutionary transition**
Gains	
q_{12}	Gain of unilinear descent system in the presence of non-unilocal residence
q_{13}	*Gain of unilocal residence in the presence of non-unilinear descent system*
q_{24}	*Gain of unilocal residence in the presence of unilinear descent system*
q_{34}	Gain of unilinear descent system in the presence of unilocal residence
Losses	
q_{21}	Loss of unilinear descent system in the presence of non-unilocal residence
q_{31}	Loss of unilocal residence in the presence of non-unilinear descent system
q_{42}	Loss of unilocal residence in the presence of unilinear descent system
q_{43}	Loss of unilinear descent system in the presence of unilocal residence

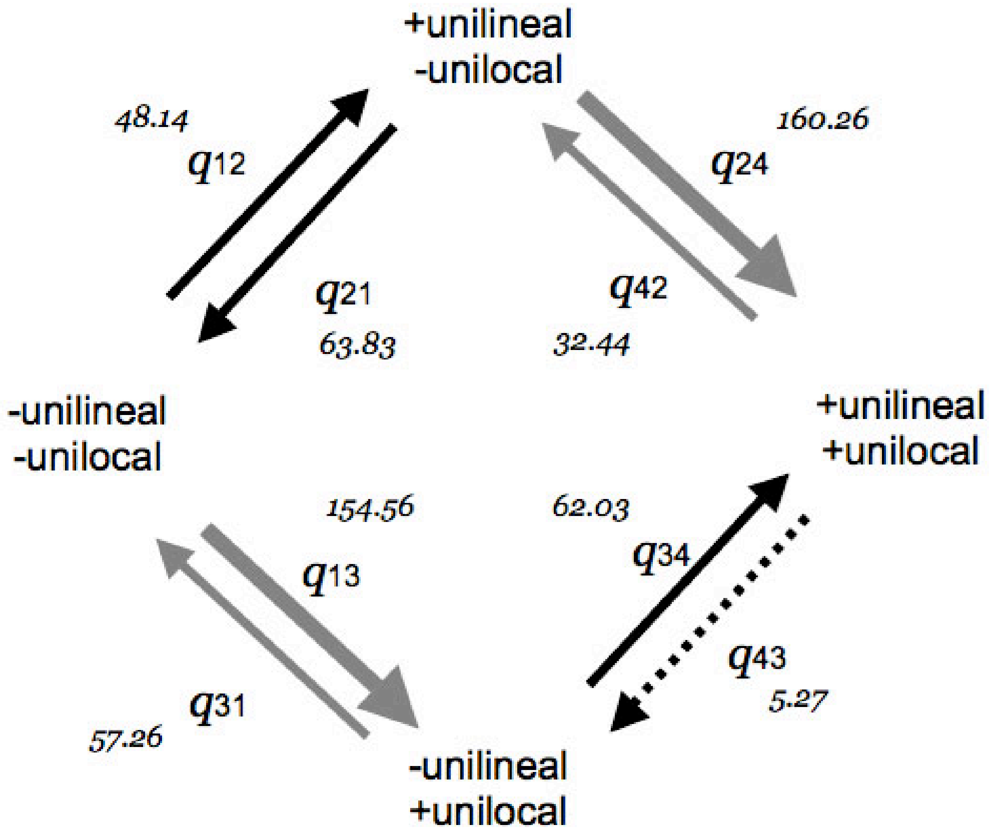


Figure 6.5. Evolutionary flow diagram between the four possible state of descent and residence (unilineal coding). The labels "–unilineal" and "–unilocal" refer to non-unilineal and non-unilocal respectively. Arrows show the direction of the evolutionary transition; these are annotated with the mean value of the posterior distribution for that transition rate. The larger the rate, the more probable that particular pathway of evolution. Dotted pathways are effectively zero, while large arrows indicate rates that are significantly higher. Regular arrows have equivalent rates. The pathway is taken from the most probable model under the RJ MCMC procedure (below). Changes toward unilocal residence are highly likely, no matter what the state of descent, but the loss of unilinear descent is rare if residence is unilocal.

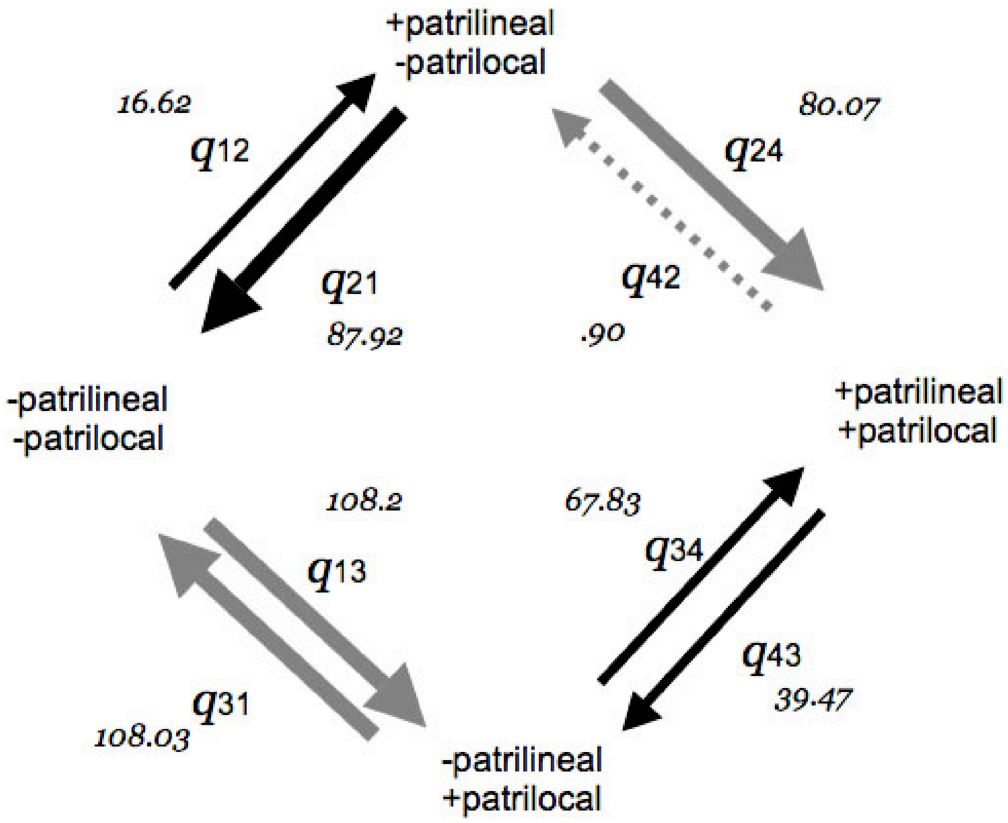


Figure 6.6. Evolutionary flow diagram between the four possible state of descent and residence (patri- coding). The labels "–patrilineal" and "–patrilocal" refer to non-patrilineal and non-patrilocal respectively. Arrows show the direction of the evolutionary transition; these are annotated with the mean value of the posterior distribution for that transition rate. The larger the rate, the more probable that particular pathway of evolution. Dotted pathways are effectively zero, while large arrows indicate rates that are significantly higher. Regular arrows have equivalent rates. The pathway is taken from the most probable model under the RJ MCMC procedure (below). Changes in residence are all likely, especially before descent, and when a society is not patrilineal. However, once a society is both patrilineal and patrilocal residence is unlikely to change.

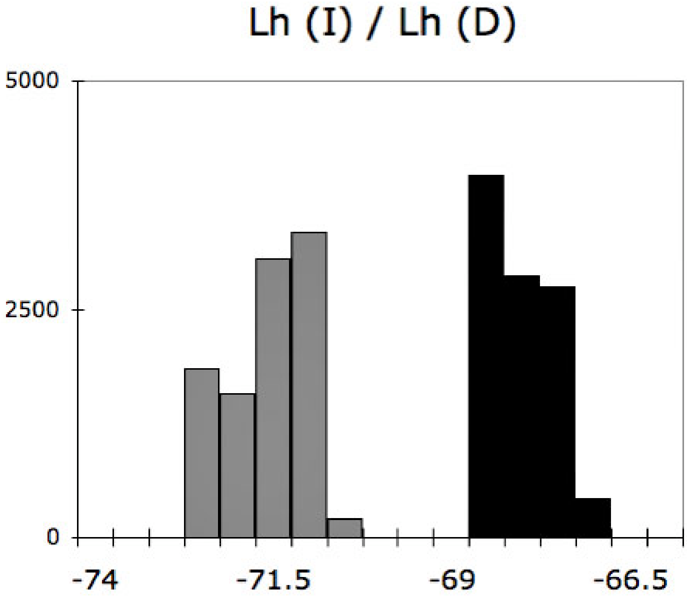


Figure 6.7. Posterior distribution of the log-likelihoods of the independent and dependent model for unilineal coding. Although they are only a few log-units apart the distributions are clearly separated, indicating that the independent and dependent models are occupying very different areas of parameter-space.

Testing the directionality of change. Figure 6.8 shows the posterior distributions of the rate parameters under the dependent model for unilineal coding. We know that the data support a hypothesis of correlated evolution, but we wish to determine the model that describes the direction of evolutionary change. Examining the plots in Figure 6.8, we see that the transitions where residence changes first have less of their samples in the "zero bin". Comparing q_{13} (residence first) and q_{12} (descent first), we note that q_{13} has a wide distribution of rates, virtually all greater than zero and with a mean of 160, while q_{12} has a majority of rate coefficients in the zero bin. The same pattern holds for q_{42} (residence first) and q_{43} (descent first).

The output of the RJ MCMC procedure gives us "model strings" which sort the transition-rates into classes, some of which may be the zero bin. Tables 6.3 and 6.4 show the most frequent models for both the unilineal and patri- coding.

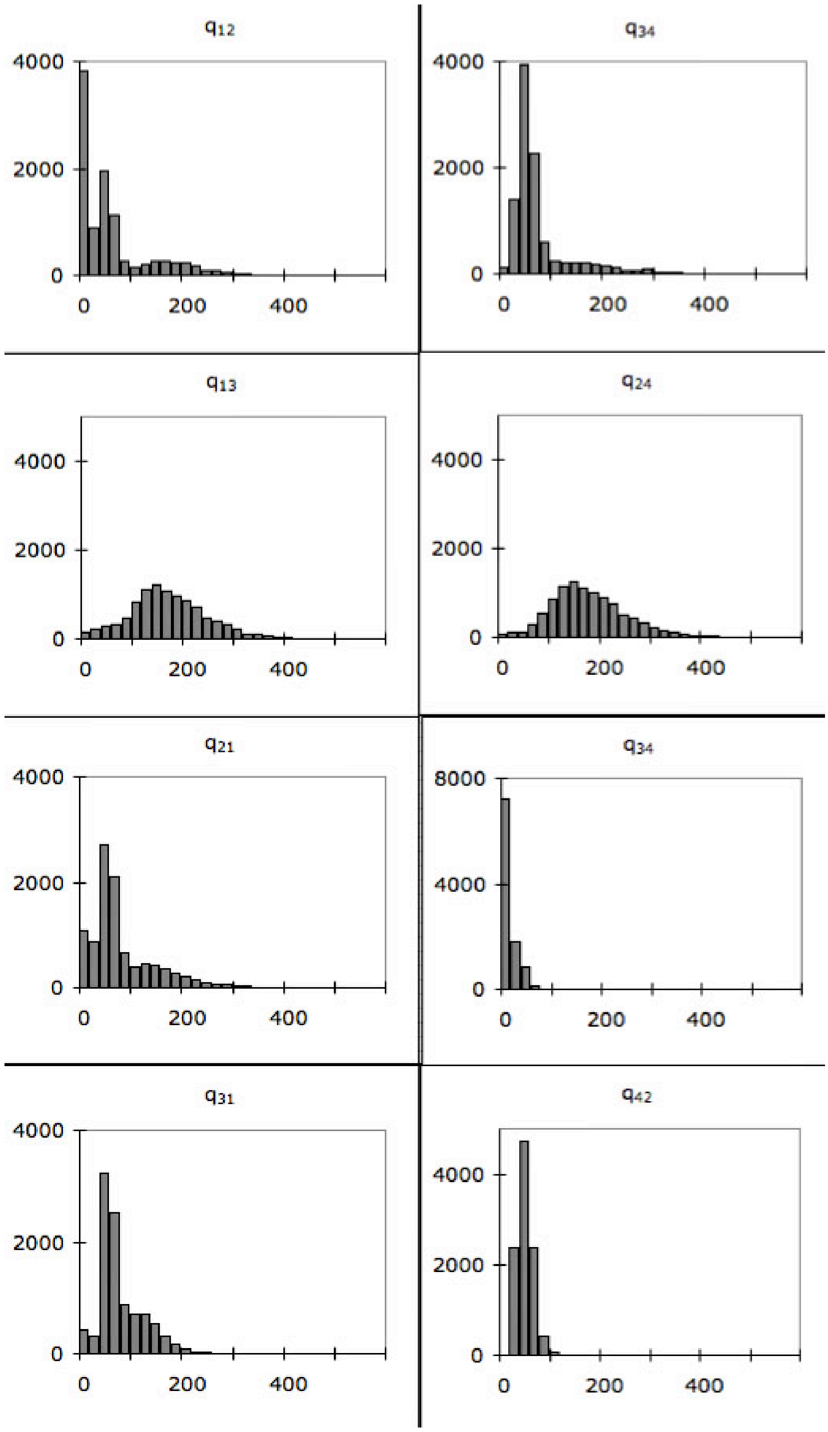


Figure 6.8. Posterior distributions of the rate coefficients for unilineal descent and unilocal residence under the dependent model of evolution. Plots are arranged so that each row contains a pairs of rates that must be equal for the independent model to be true (e.g. q_{12}, q_{34}), that is, the rates refer to the same evolutionary change in one trait irrespective of the state in the other trait. There are differences between the first, third, and fourth pairs in both the shape of the distribution and the number of time the rate is at zero.

Table 6.3. Unilineal/unilocal data showing the seven most frequent models found by RJ MCMC model-search, accounting for 55% of all the 10,000 samples. All models have two parameters, meaning they are versions of the dependent model. The flow diagram in Figure 6.5 is presented according to the most-frequent model.

Model string	Frequency	Cumulative frequency	No. of parameters
0101000Z	1651	0.17	2
Z010111Z	1504	0.32	2
0000111Z	651	0.38	2
0101100Z	348	0.42	2
Z000101Z	339	0.45	2
Z0Z01011	331	0.48	2
0010111Z	323	0.51	2

The first two models, which account for nearly one-third of the sample, are equivalent except for one difference, that of the transition q_{12} (gaining unilineal descent before unilocal residence) being in the zero bin as well as q_{43}. A large number of models have the parameter q_{43} set to zero, indicating this transition (retaining unilocal residence while losing unilineal descent) to be very unlikely. Taken together, these two transitions being frequently set to zero is strong evidence that residence is changing first for these data.

Table 6.4. Patrilineal/patrilocal data showing the eight most frequent models found by RJ MCMC model-search, accounting for 48% of all samples. Only the third most-frequent model has one parameter, equivalent to the independent model. All others are a version of the dependent model. The flow diagram is presented according the most-frequent model.

Model string	Frequency	Cumulative frequency	No. of parameters
011110Z0	9384	0.093841	2
Z00100Z1	7483	0.168672	2
Z00000Z0	5982	0.228492	1
Z00Z00Z1	5960	0.288093	2
Z00000Z1	5762	0.345713	2
010110Z0	5609	0.401804	2
011111Z0	5285	0.454655	2
01Z110Z0	2958	0.484235	2

For the patri-coding, the q_{42} parameter (representing the loss of patriliny while retaining patrilocality) is always in the zero bin, meaning that this transition is effectively zero. The q_{12} parameter, where patriliny is gained before patrilocality, is also frequently in the zero bin or in a lower rate class than other transitions. Models where the parameters indicate that residence changes first or at a higher rate dominate the sample.

We calculate if the models presented in the flow diagram are significant by comparing the marginal means of those likelihoods to the likelihoods of an equal-sized sample of all other models. For the unilineal coding, the flow-diagram model is significant, as the likelihood was –62.38, compared to all other models whose mean likelihood was –65.30, giving $BF = 5.84$. This is positive evidence in support of the flow-diagram model. For the patri- coding, the flow diagram model likelihood was –68.73 and that of all other models was –70.53, giving a $BF = 3.6$, which is moderate evidence for the flow-diagram model. Thus, for both sets of coding, models in which residence is likely to change first and/or changes in descent are less likely were statistically supported by the data.

Calculating the posterior to prior odds. One final way of interrogating the data to determine if a transition rate is significant is by calculating the posterior to prior odds (M. Pagel, personal communication). To do this we use the full range of the output and here test the proposition that $q_{13} > q_{12}$, that is, that unilocal residence is gained before unilineal descent. We can calculate the prior odds by examining the list of all possible models ($n = 21{,}147$). First we remove those models in which $q_{13} = q_{12}$ (leaving 17,000), and then isolate those models in which $q_{13} > q_{12}$ ($n = 7{,}000$). Thus, we expect .4 of the models (7,000/17,000) to support the hypothesis *a priori*. Then, we use the Bayesian theorem to calculate the following (21,147 - 0.6*21,147) / (0.6*21,147) where .6 is the proportion of models that *cannot* support the hypothesis (Lewis 2001). The prior odds are thus (1 – 0.6)/0.6 = 0.666.

We then compare these prior (expected) odds to the observed data. We find that the proportion of the observed sample that supports our hypothesis is .79, and the proportion that does not support the hypothesis is .21. Using the Bayesian theorem, the posterior odds are 10,000*(1 – .21)/.21*10,000 where 10,000 is the sample size, giving 3.76. The Bayes factor is then 3.76/.66, $BF = 5.65$, supporting the hypothesis that $q_{13} > q_{12}$.

6.3.3.5 Rates of change over time

Finally, we can examine the rate of cultural evolution in descent and residence by using the time scale of the Austronesian language tree to estimate the probability of a change happening over a certain number of years. To do this we first derive an approximate date for the root of the AN tree. The combination of archaeology and linguistic evidence for the Austronesian expansion suggests that pottery-making and/or agriculturalist peoples had moved from Taiwan to the Northern Philippines by at least 5500 BP and to parts of Borneo by 4500 BP (Blust 1995; Bellwood 1998). Evidence for an earlier start to the spread of Austronesian-speaking peoples has not been forthcoming, so we may date Proto Austronesian to c.6000 BP, i.e. the tree “length” from root to tips is 6000 years.

Taking the simplifying assumption that language change is proportionate to time, we derive the length of the root-to-tip distances for each of the 67 societies and average these to gain a measure of language change per year. *TipToRoot*, a program to find these distances, was written for this purpose by A. Meade (personal communication). The average tip-to-root distance was .04, meaning there was a 4% change that the character state would change over the branch. As there were 17474 lexical characters, this meant that on average 698 characters changed from the root to the tip. We use the following equation (Pagel and Meade 2005) to approximate the probability of change from 0→1 on a branch of length *t*:

$$P(0\rightarrow 1)_t = (\alpha/(\alpha + \beta))^*(1 - e^{-(\alpha+\beta)t}) \qquad \text{[Eq. 3]}$$

where α and β are the transition-rate parameters between two states. Plugging the transition rates for the dependent model of unilineal/unilocal evolution into Equation 3, we obtain the probability of change over different time periods (branch lengths), shown in Table 6.5 and Figure 6.9.

Table 6.5. Probability of change in descent (top four parameters) and residence (bottom four parameters) over three time periods. Parameters are taken from the dependent model of evolution, as residence and descent show correlated evolution.

Evolutionary transition	**Probability of change over *x* years**		
	100	**1000**	**6000**
q_{12} Gain unilineal descent without unilocal residence	.03	.23	.43
q_{21} Lose unilineal descent without unilocal residence	.04	.30	.56
q_{34} Gain unilineal descent with unilocal residence	.04	.33	.86
q_{43} Lose unilineal descent with unilocal residence	.00	.03	.07
q_{13} Gain unilocal residence without unilineal descent	.09	.55	.73
q_{31} Gain unilocal residence without unilineal descent	.04	.20	.27
q_{24} Gain unilocal residence with unilineal descent	.10	.59	.79
q_{42} Lose unilocal residence with unilineal descent	.03	.15	.21

Plotting the rates for residence and descent (Figure 6.9) shows that while there are only small probabilities of change in both traits over 100 years, over the 1000-year period the traits diverge. Residence is more labile, with a 15–59% chance of change over 1000 years, compared to descent at 3–33%. Gains of unilocality have the highest probability in a 1000-year period. Over the whole Austronesian tree, with a time period of roughly 6000 years, the highest probability of all is the gain of unilineal descent against a background of unilocal residence, indicating this is a stable state.

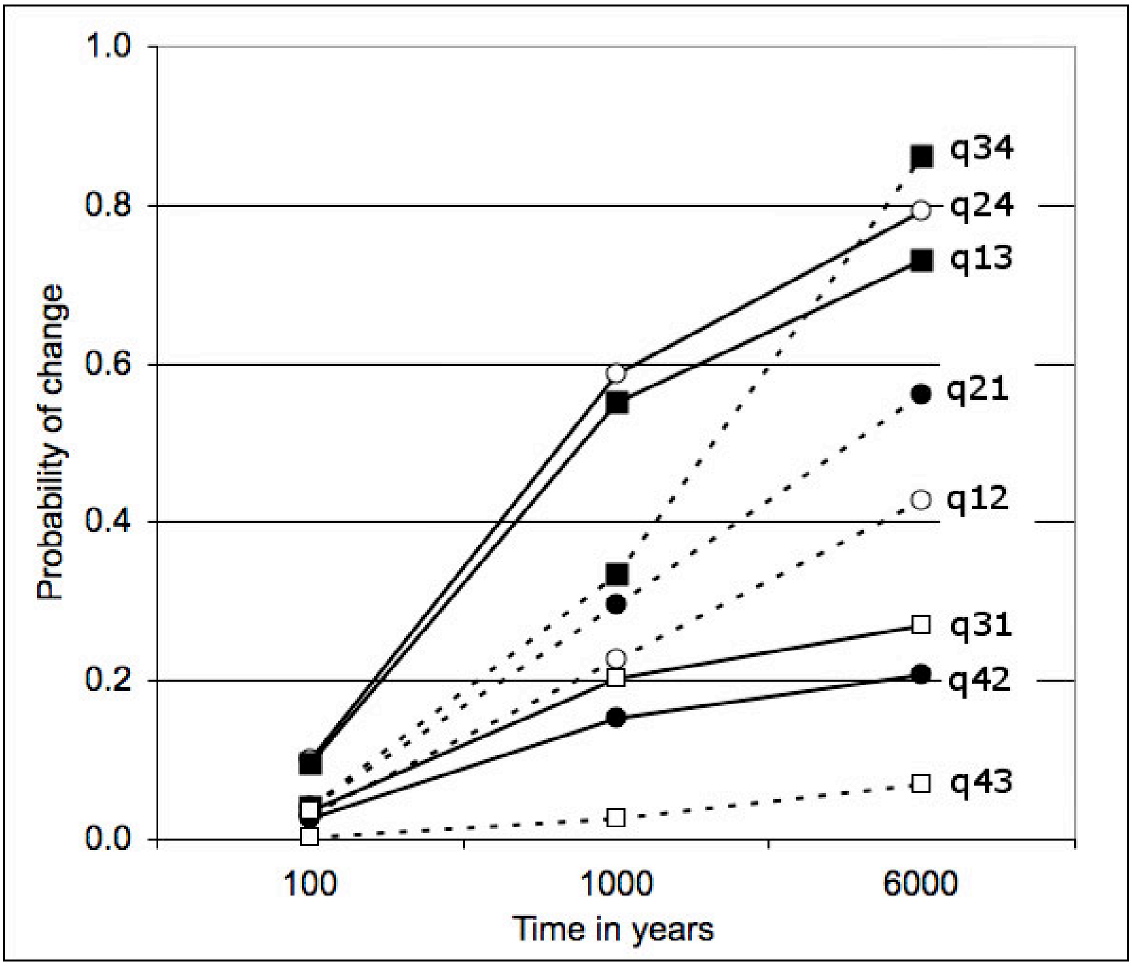


Figure 6.9. Probability of change over time in each of eight transitions according to the dependent model. Dotted lines indicate changes in descent, solid lines indicate changes in residence. There is a ~10% chance of change in both types of traits in the 100-year period. Changes to unilineal and –local forms are most probable over 1000 years, especially in residence, where there is a one in two chance of change. By 6000 years the traits have reached an equilibrium (i.e. probabilities add to one).

6.3.4 Discussion

Using a Bayesian MCMC procedure that controlled for phylogenetic uncertainty, I found that changes in post-marital residence preceded changes in descent in 67 Austronesian societies, supporting the "main sequence" theory of kinship. This relationship held true when the data was coded to reflect unilineal/-local versus non-unilineal/-local kinship, and when coded to separate patrilineal/-local kinship from other forms. Relating the changes to archaeological time, both traits had a low probability of change over 100 years, but in a 1000-year period, residence had a 50% likelihood of changing form.

6.3.4.1 Scenarios for the evolution of Austronesian unilocal and unilineal forms

Ancestral states for the AN tree, estimated in Chapter Five, give us the "start point" for the evolutionary pathways that are presented in the flow diagrams. The most-likely scenario for the evolution of unilineal descent and unilocal residence reconstructs the root as non-unilineal (bilateral) but unilocal (possibly matrilocal, from Table 5.5). The most common transition from this state is gaining unilineal descent, as in, for example, the Formosan and Central Malayo-Polynesian societies. However, many WMP societies in the Philippines and Indonesia "lose" unilocal residence, and are bilateral and multilocal (e.g. Hanunoo, Balinese). One likely scenario for this transition is that brideprice moderates residence in the poorer strata of many Island Southeast Asian societies, for example, the Atoni of Timor (Cunningham 1967). Instead of paying a brideprice, or as well as, the husband will live with the bride's family for some period of brideservice, creating a non-unilocal residence system. Considerations of brideprice may also affect affiliation to one lineage or another in ambilineal cultures (Bellwood 1997). Indian and Islamic influences throughout Island Southeast Asia, from around 1000 BP (LeBar 1975; Denoon 1992) may also be a factor in the number of non-unilineal systems in this area, although their effects on peasant classes (until recently for Islam) are not well known (Alkire 1972). As well, many societies traditionally practised shifting cultivation and had no shortage of land, a condition likely to favour bilateral kinship e.g. the Iban of Borneo (Freeman 1981).

Unilineal descent evolves in the Proto Central-Eastern/Proto Oceanic part of the tree, and once gained in the Oceanic group, only a few Polynesian societies revert to a wholly non-unilineal form of descent, such as Hawai'i with bilateral descent groups (Kirch 1984). Many Oceanic societies are ambilineal or have double descent, so that both matri- and patri-lineal kin groups are present. By coding ambilineal societies as unilineal, we capture the presence of lineal descent groups—the "unbroken line" (Holy 1996)—in a society's kinship structure, but we lose the aspect of flexibility in social organisation that ambilineal societies share with cognatic and bilateral systems. This flexibility may be important in explaining the predominance of ambilineal and multilocal societies in Remote Oceania (Firth 1957; Fox 1967).

Non-unilineal systems. By allowing the individual some degree of choice in their alignment with specific groups of kin, or permitting membership in multiple types of kin groups, the apparent popularity of non-unilinear kin groups on small islands may be a response to population pressure on a small area of land (Fox 1967). Goodenough (1955) suggests that a number of social devices for the redistribution of under-abundant land exist in Austronesian societies, chief amongst these being non-unilinear kinship groups. When land was in abundance or the ecological environment was predictable, tendencies towards unilinear descent could develop (1955:147). Eggan (1966), examining North American societies, argued that buffalo-hunting societies demonstrated a flexible social organisation that included multilocality and cognatic descent, in response to the seasonal and precarious nature of their subsistence.

Is non-unilineal descent (and multilocal residence) adaptive for societies that face environmental risk? It may be the case that cognatic/ambilineal descent reflects an adjustment to fluctuating or marginal environments. The dangers of long distance voyaging and depopulation during migration have also been suggested as possible factors encouraging the development of non-unilineal descent in Oceania (Lane 1961).

Some authors (Forde 1947; Lee 1972) have noted that residential flexibility is adaptive when resources are unpredictable. If, as the results presented here suggest, Murdock's theory of kinship change is correct, then further studies should assess if there is a consistent correlation between environmental risk factors and non-unilineal social organisation in Austronesian societies.

6.3.4.2 Patrilineal organisation in Austronesian societies

The ancestral states analyses in Chapter Five indicated that the root of the AN tree was probably neither patrilineal nor patrilocal. Thus, the most likely evolutionary scenario for these cultures is that patrilocality is rapidly gained and lost against the background of a non-patrilocal descent system. Lessa (1950) describes the matrilineal descent and patrilocal residence of Ulithi Atoll in Micronesia, remarking that bride-service sometimes requires residence with the bride's family. It is easy to see that in conditions like these, residence patterns, as "cultural traits", are more likely to be decisions for the individual, and are likely to have high rates of change. According to the flow diagram model, however, once patrilocality is gained, some further "push" may be required to shift the kinship structure towards patriliny. In Austronesian societies this push may be entwined with aspects of ranking, primogeniture, and status (Bellwood 1996c; Kirch and Green 2001). So for instance, while the Kwaio of the Solomon Islands have a bilateral/cognatic form of descent, patrilineally-affiliated members have higher status (Keesing 1970), and conversely, in the cognatic *hapu* systems of the New Zealand Maori, affiliation was traditionally preferentially to the fathers' line, except when the line of the mother had higher status (Scheffler 1964).

Once a society is both patrilineal and patrilocal it is unlikely to shift away from this state. If it does, it will most certainly not shift to a different residence system first. The only society in our sample that has patrilineal descent groups and non-patrilocal residence is the Maranao of the Southern Philippines, who are matrilocal and neolocal. However, their descent system is complex: "all persons inherit at least two descent lines, some claim as many as fifteen" (Mednick 1975). Thus, Murdock's assertion that "although unilocal residence does not necessarily lead to unilinear descent … unilinear descent can arise in no other way than through unilocal residence" (1949:209) applies, at least to patriliny.

Service (1962) observed that patrilocality occurs in so many different ecological and cultural contexts that no clear patterns can emerge to explain its global predominance. However, as evidenced by its prevalence worldwide (~70%, Levinson and Malone 1980), patriliny may "stick" in many cases as it conforms to some basics of evolutionary biology (Hartung 1976; Alexander 1979). That is, the greater reproductive variance of males as opposed to females means that if resources are available to be transferred, it makes more sense to invest them in males: "a daughter's reproductive success is less affected by poverty than a son's" (van den Berghe 1979:96). On this model, in those Austronesian societies where individuals may acquire heritable wealth, patriliny may become common, as is the case in Bantu-speaking populations in Africa (Mace 1996; Holden and Mace 2003). This may be the situation for the Manggarai of Flores, in the "patrilineal" CMP clade, who keep buffalo and horses for prestige and for brideprice payments. In this respect, however, they are unlike many Austronesian societies (especially those in the Remote Pacific) who do not have large domestic livestock or similar forms of transferable wealth.

Bellwood (1997) has tentatively suggested that contact with non-Austronesian populations in eastern Indonesia and Melanesia may have provoked a shift towards unilineal organisation. These NAN societies are predominantly unilineal, especially patrilineal in the case of Papuan-speaking New Guinea societies (Brown 1978), and may have influenced the Austronesian populations that travelled through and/or settled in those areas (i.e. CMP and Oceanic groups) towards unilineal descent, while those societies in western Island Southeast Asia remained, or developed non-unilineal kinship. This suggestion, though speculative, does not conflict with the findings presented here.

6.3.4.4 Rates of cultural evolution

By calibrating the language tree with archaeological estimates of the age of the Austronesian language family, we were able to estimate rates of cultural evolution. Two points are of note. First, different dynamics of change are at work over different time periods. The probability of change to unilocal post-marital residence over a 1000-year period was much more than the probability over 100 years, but was less than a linear relationship with time would suggest. This indicates that there may be limits on the rate of cultural change, or, that some form of equilibrium where societies can switch their residence pattern back and forth is reached. Second, rates of cultural change are not homogenous for all traits. For these societies, change to unilocal residence had a much higher probability (and more variation) of change over the 1000-year period than did descent, indicating that of the two it may indeed be the more labile trait. Goodenough (1956) found that residence patterns in Chuuk, as recorded in census data, could fluctuate throughout a decade. We would expect this to follow from the main sequence hypothesis, if it is the underlying conditions causing residence change, rather than descent, which act first. In addition, Divale (1974) estimated that some societies had unilocal residence for up to a thousand years without developing a unilineal form of descent, so whatever benefits are to be gained by unilocal residence, they do not necessarily cause an immediate transition to unilineality. From an evolutionary perspective, localising one type of kin (male or female) may have benefits that are not to do with inheritance of resources/material wealth, but concern aspects of kin investment through childcare and time allocation.

6.3.4.5 Desirability of multi-state models

A more complex model of the transitions between descent and residence in Austronesian societies remains to be constructed and tested. The primary drawback is that we are effectively limited to a two-state test using binary coding, when ideally a multi-state coding is preferred. Chapter Five revealed the difficulties in applying a multi-state model to a data set of this size and "messy" cultural nature; it is difficult to gain statistical significance when the variance must be partitioned in a combinatorial arrangement of three states for two characters. Unfortunately, in the Austronesian world there are real-world functional differences between bilateral, ambilineal, and patri- or matri-lineal descent groups. Ambilineal societies occupy an uneasy space between bilateral/cognatic and pure lineal systems, but the fact that they are prevalent and pervasive in the Pacific is indication that they are a distinct form of kinship organisation deserving of independent explanation. For example, Murdock (1949:205) attributes the predominance of ambilocal systems in Polynesia to the importance of senior-junior ranking and primogeniture, as opposed to differentiation by sex, because the higher-status (first-born) spouse will often remain with the natal family regardless of sex. In another vein, Service (1962) had suggested that depopulation events should trigger a shift from unilocal to ambilocal residence as groups sought to re-establish control of resources by a flexible attitude towards social organisation. In addition, C. Ember (1974) found that hunter-gatherer ambilocalism was predicted by a depopulation event (at least a 25 percent decrease) in the 30 years prior to the ethnographic present. In the Pacific context, a migration event could be seen as equivalent to depopulation, and thus may account for the large number of ambilocal societies seen in the Pacific.

Understanding the relationships between bilateral, ambi-, matri-, and patrilineal descent, and different forms of residence, will require careful tests that unpack functional and/or causal relationships. Testing the main sequence was the very beginning of this process, but clearly demonstrated the necessity of a phylogenetic comparative approach to testing these anthropological "truisms".

6.4 Is matriliny co-evolving with male absence?

6.4.1 Introduction

Burton et al. (1996), analyzing worldwide trends in social structure through correspondence analysis, characterised the Southeast Asia and the insular Pacific as a "matricentric" region, one that organised "kinship groups around women through matrilocal or uxorilocal residence or through matrilineal kinship groups" (1996:93). Matrilineal descent and matrilocal residence are found at a higher frequency in the Austronesian societies of the *Ethnographic Atlas* than the overall worldwide average (see Table 5.1). In matrilineal societies, inheritance of property and political title are usually passed from mother's brother to sister's son (Gaulin and Schlegel 1980), as in the Trobriand Islanders (Weiner 1978), or from mother to daughter, as in the Minangkabau (Kahn 1980; Sanday 2002). Matriliny presents a "puzzle" (Richards 1950) because kinship is organised around women, yet men remain politically and socially dominant. Pursuing the solution to the matrilineal puzzle has provoked anthropologists into proposing a number of explanatory hypotheses.

Cross-culturally, matriliny has been associated with a horticultural mode of production (Murdock 1949; Aberle 1961). In the African Bantu language family, Holden and Mace (2003) used phylogenetic comparative methods to demonstrate that the adoption of domestic livestock as a subsistence practice led to the loss of matriliny. Cultures that possessed cattle were more likely to be patrilineal or have double descent. In an evolutionary context, the acquisition of cattle is the acquisition of heritable/defendable wealth, which can then be passed (patrilineally) on to sons to improve their chances of reproductive success. However, the majority of Austronesian cultures do not have large herds of domestic livestock, and so this explanation is not appropriate to the Pacific context. The general form, that heritable and transferable wealth encourages patrilineal forms of social organisation, is also hard to apply in the Austronesian context. Houses, land, and gardens are just as likely to be collectively owned by a lineage or some other form of corporate descent group as by individuals;

membership in descent groups regulates access to resources, not ownership (Crocombe 1974; Ward 1997).

High paternity uncertainty has long been associated with the matrilineal transmission of wealth to sisters' sons (Morgan 1877), as maternity certainty ensures a man of his relationship to his sister and her offspring. Hartung (1981, 1985) proposed a model in which only small amounts of paternity uncertainty are necessary for matrilineal inheritance to be adaptive over a few generations, and reviewed cross-cultural evidence to suggest that matrilineal societies were often those with moderate to low certainty of paternity. The causal arrow could, however, go both ways, and factors which may promote paternity uncertainty are of interest in this instance.

Using data from Otterbein and Otterbein (1965), Ember and Ember (1972) proposed a model in which the nature of warfare experienced by societies moderated the effect of the sexual division of labour (SDL) on residence. Simply, the presence of internal warfare (i.e. fighting between intermarrying communities) favours patrilocal residence, as matrilocal residence causes a conflict of interest for men between their natal and their wives' community. Ember and Ember found that a significant association between SDL and residence only holds when only external warfare is present, remarking that "if the males have to be away often on long trading trips (as in parts of Micronesia and Melanesia in the recent past) … and work has to be done while they are away, the women might end up doing at least as much as the men in subsistence activities, even though warfare is no longer present" (1972:581).

Harris (1985) made the general argument that matrilineality is favoured under conditions when there is prolonged male absence—and by extension, high male mortality. In Harris's view, the lineage interests of absent brothers (due to warfare, trade, voyaging, or resource exploitation) are best managed by their sisters, who have a familial interest, rather than by unrelated wives. Matri-dominant social organisation in the Caribbean and West Indies was seen, in a similar vein, to be a response compelled by absent (warfaring or seafaring) husbands (Keegan and Maclachan 1989). Levi-

Strauss (1984) observed that in Micronesia, a matrilineal form of social organisation meant that males were easily assimilated, a probable necessity for a seafaring population where male mortality might be high (Keegan 1989). We may re-cast these arguments in terms of resource allocation and inclusive fitness by considering how maternal grandparents might wish to invest their resources in their grandchildren, as Hartung (1985:684) wondered:

> "In the face of high rates of mortality for males in their reproductive prime, matrilineality may have been a more fundamental form of social security than has since been invented."

Hage and Marck (2003) also associate the continuation of regular long-distance voyaging in Micronesia with that area's matrilineal kin groups. Moreover, Aberle (1961) found that although horticultural production was the predominant mode of susbistence associated with matriliny (though not in Oceania), there was an unexplained tendency for matriliny to be associated with fishing. He noted that:

> "The logical possibility exists that the connection between matrilineality and horticulture is accidental, and that the crucial issue is the amount of fishing or the kind of fishing done." (Aberle 1961:703)

Thus, the "absence of males" or high male mortality in the Austronesian context might be due to dependence on fishing, warfare, or voyaging/trade. Each of these provides a comparative hypothesis for testing in a phylogenetic framework. In addition, the absence of males may be a reason for low paternity certainty, if we can invoke Hartung's hypothesis. Here I concentrate on the association of matriliny and fishing. Although the relationship has been noted in the literature, it has not been tested in a quantitative manner by either traditional cross-cultural association tests or phylogenetic methods, affording a novel opportunity to statistically assess an untested anthropological proposition.

6.4.1.1 Hypotheses

Here I test the hypothesis of correlated evolution between matrilineal social organisation and an aspect of “male absence”, namely a high degree of dependence on male fishing for subsistence. In the Austronesian/Pacific context, this may be the most appropriate single measure to quantify “male absence”, due to the large number of oceanic/island societies. As well, quantitative data on the dependence of fishing, as well as information on the sexual division of labour, are available for many of these societies in the *EA* (Murdock 1967). Secondly, I test whether matriliny and high fishing dependence (and/or the absence of both) represent “evolutionary stable strategies” (Maynard Smith 1992) or stable states by testing if transitions towards those states have higher likelihoods than other transitions.

6.4.2 Methods

6.4.2.1 Phylogeny estimation

The 67-language data set and the corresponding 1000-tree Bayesian sample, as described in Chapter Two, were used for these analyses.

6.4.2.2 Cultural data and coding schemes

The ethnographic data on descent and residence compiled for Chapter Five were used in these analyses (see Tables 5.2 and 5.4). Two tests were conducted, one using matrilineal descent, the other using matrilocal residence. Societies were coded “M_D” as matrilineal in descent if they were matrilineal, ambilineal, or had double descent. All others were non-matrilineal (“O_D”). This corresponded to the “matrilineal aspect” coding in Chapter Five. Societies were coded for matrilocality in residence (“M_R”) if they were matrilocal, avunculocal or ambilocal. All others were coded as non-matrilocal (“O_R”).

Data for dependence on fishing came from the three ethnographic sources used in Chapter Five: the *Ethnographic Atlas*, plus the *Ethnic Groups of Island South-east Asia*, and the *Encyclopaedia of World Cultures*. I used the *EA* codes for "dependence on fishing" and "sexual division of labour for fishing", supplementing this with additional ethnographic descriptions in the other sources, to construct a binary coding scheme for dependence on (male) fishing (Table 6.5). A society was coded "F" it had "dependence on fishing" greater than 25 percent (or a high dependence was noted in other sources), *and* an indication that men did appreciably more fishing than women *and* at least some fishing was offshore (n = 30). Where information was available that sea-voyaging trade was important, that society was also coded "F". Societies not meeting these criteria were coded "N" (n = 34). Three societies were coded as having missing data due to insufficient information. Table 6.7 shows the contingency table for the coded traits. Chi-square tests are reported in the results.

Table 6.6. Contingency table for matriliny and fishing showing the number of societies classified in each trait class. Each of the cells corresponds to one of the four states in the evolutionary "flow diagrams".

	Matrilineal (M_D)	**Non-matrilineal (O_D)**
***High dependence on male fishing* (F)**	44	12
***Low dependence on male fishing* (N)**	6	5

Table 6.7. Information on fishing for 67 Austronesian societies.

ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]		
Society Name	**Dependence[2]**	**Sex differences: fishing[3]**	**EWC**	**EGI**	**Code[4]**
Ambon	26–35%	Missing data	Men fish, fishing important	–	F
Ami	6–15%	Males only	Fishing not remarked	–	N
Atayal	6–15%	Males only	Highland group, fishing by poison	–	N
Atoni	–	–	Fishing not remarked	Inland communities, fishing not remarked	N
Balinese	0–5%	Absent/unimportant	Fishing not remarked	–	N
Belu	0–5%	Missing data	Fishing insignificant	–	N
Bolaang	–	–	–	Fishing present; coastal village; supplemental	N
Bunun	0–5%	Absent/unimportant	Highland settlements	Inland (riverine)	N
Carolinian	46–55%	Males only	–	–	F
Chuuk	46–55%	Differentiated but equal	Men fish offshore, women fish on reef, trade with other islands	–	F
Dobu	26–35%	Males appreciably more	Men offshore on *kula* expeditions	–	F
Easter Is.	6–15%	Males appreciably more	Men fished, but not a major activity	–	N
E. Futuna	26–35%	Females appreciably more	Men fish coastally (offshore dangerous), women reef	–	F
Fijiian	46–55%	Males appreciably more	Men offshore, women reef, wide trading networks by canoe	–	F
Hanunoo	6–15%	Males appreciably more	Fishing important, mainly trapping–	–	N

Table 6.7 (Continued). Information on fishing for 67 Austronesian societies.

ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES[1]		
Society Name	**Dependence[2]**	**Sex differences: fishing[3]**	**EWC**	**EGI**	**Code[4]**
Hawaii	36–45%	Males appreciably more	Men offshore, women reef, occasional trading/voyaging	–	F
Iban	16–25%	Males appreciably more	Riverine fishing, traditional raiding	–	N
Ili Mandiri	26–35%	Missing data	Men fish; whaling in Lamaholot	–	F
Ilongot	–	–	Fish trapping	Highland village, stream fishing	N
Javanese	0–5%	Absent/unimportant	Fishing insignificant	–	N
Kei	16–25%	Missing data	Fishing important	–	-
Kerinci	–	–	–	Lake fishing, men fish	F
Kiribati	46–55%	Males appreciably more	Men do most of the fishing, sea voyaging/trading	–	F
Kodi	0–5%	Missing data	–	–	N
Kusaie	36–45%	Differentiated but equal	Men use canoes	–	F
Kwaio	26–35%	Missing data	Men fish, tradition of elaborate canoe building	–	F
Lakalai	16–25%	Differentiated but equal	Men offshore, women stream	–	N
Macassarese	16–25%	Males only	Men fish in coastal villages	–	N
Madurese	–	–	Men fish by outrigger canoe and net	Important for subsistence, offshore fishing	F
Malagasy	6–15%	Females appreciably more	–	–	N
Malay	16–25%	Males only	Important depending on village	–	N

Table 6.7 (Continued). Information on fishing for 67 Austronesian societies.

ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES		
Society Name	**Dependence**[2]	**Sex differences: fishing**[3]	**EWC**	**EGI**	**Code**[4]
Manam	26–35%	Males appreciably more	Men fish, canoe trading with mainland	–	F
Mangaia	36–45%	Males appreciably more	Men offshore	–	F
Manggarai	–	–	Insignificant	Not remarked	N
Manobo	–	–	Fishing not remarked	Highlands, stream trapping mostly by women (Cole 1956)	N
Maori	16–25%	Males appreciably more	Men offshore occasionally	–	N
Maranao	–	–	Fishing important	Fishing in Lake Lanao important	F
Marquesan	36–45%	Males appreciably more	Men fish, local trade between islands	–	F
Marshallese	46–55%	Males appreciably more	Men fish, inter-atoll trade	–	F
Mekeo	6–15%	Equal participation	Not important	–	N
Melanau	–	–	Males more, but reliant on sago	Coastal and riverine fishing important	-
Minangkabau	6–15%	Males only	Men fish if fishing available	–	N
Molima	26–35%	Missing data	–	–	F
Mori	–	–	Canoes built	–	-
Motu	36–45%	Males appreciably more	Men fish, some coastal canoe trading	–	F
Nias	–	–	Men fish with canoes, fish supplemental	Fishing of secondary importance	N

Table 6.7 (Continued). Information on fishing for 67 Austronesian societies.

ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES		
Society Name	**Dependence[2]**	**Sex differences: fishing[3]**	**EWC**	**EGI**	**Code[4]**
Niue	46–55%	Differentiated but equal	Men fish (coastal, offshore difficult)	–	F
Paiwan	6–15%	Males only	Fishing present	–	N
Palawan	–	–	–	Fishing insignificant	N
Ponape	26–35%	Males appreciably more	Men fish, night fishing important	–	F
Pukapuka	36–45%	Differentiated but equal	Men offshore, women reef	–	F
Puyuma	6–15%	Males only	Fishing present	–	N
Rotuma	16–25%	Differentiated but equal	Infrequent offshore by men, historical sea-voyaging	–	N
Samoan	26–35%	Differentiated but equal	Men offshore, women reef		F
Sika	–	–	–	Limited offshore fishing, mainly in coastal villages	N
Sugbuhanon	16–25%	Males appreciably more	–	–	N
Sumbanese	0–5%	Missing data	–	–	N
Tahiti	36–45%	Males appreciably more	Men fish more and offshore, regular inter-island trading	–	F
Tanimbarese	16–25%	Males only	Fishing important	–	N
Tannese	16–25%	Missing data	Men offshore but unimportant	–	N
Toba Batak	6–15%	Missing data	Fishing on Lake Toba not remarked	–	N

Table 6.7 (Continued). Information on fishing for 67 Austronesian societies.

ETHNOGRAPHIC ATLAS VARIABLES			OTHER SOURCES		
Society Name	**Dependence[2]**	**Sex differences: fishing[3]**	**EWC**	**EGI**	**Code[4]**
Tonga	26–35%	Males appreciably more	Men offshore, women reef, extensive voyaging and trade	–	F
Toradja	0–5%	Missing data	Inland villages, both sexes fish	–	N
Trobriand	26–35%	Males appreciably more	Men fish, part of *kula* ring expeditions	–	F
Ulawa	26–35%	Males appreciably more	–	–	F
Woleai	36–45%	Males appreciably more	Men offshore, women reef, only men use canoes, trading networks	–	F
Yami	36–45%	Males appreciably more	–	Flying-fish catch very important for subsistence and community life	F

1. **Other Sources**: EWC, information from entries in the *Encyclopaedia of World Cultures* (Levinson 1993); EGI, information from entries in *Ethnic Groups of Island Southeast Asia* (LeBar 1975).
2. **Dependence on fishing**: From variable “dependence on fishing” in the *EA*.
3. **Sex differences: fishing**: From variable on sexual division of labour (fishing) in the *EA*.
4. **Coding**. *Male fishing important* (F) when a society has “dependence on fishing” > 26% (or stated high dependence in other sources), plus there is an indication that men do appreciably more fishing and/or fishing is offshore. Where information was available that sea-voyaging trade was important, that society also scored F. *Male fishing unimportant* (N) for all others. A dash (-) indicates there was not enough information for a judgement so the society was coded as having missing data.

6.4.2.3 Testing for correlated evolution

BayesMultiState was used in *Discrete* mode as described previously. The independent and dependent model parameters were estimated from a Markov chain that ran for 500 x 10^6 iterations, repeatedly visiting each tree in the sample of 1000. After convergence of the chain, outcomes were sampled every 10,000 iterations to avoid autocorrelation. This provided 50,000 samples with which to estimate the marginal likelihoods, posterior distributions and transition-rate parameters of the dependent and dependent models. The proposal mechanism for the Markov chain was set to 20, resulting in ~35% of proposed models being accepted as the next step in the chain. An exponential distribution with a mean of 50 was used to constrain the values from which the chain drew its prior probabilities, effectively constraining the wide parameter space to be explored more thoroughly. Bayes factor tests using the marginal means of the likelihoods were used to test hypotheses of (i) co-evolution and (ii) identify which trait was changing first.

6.4.3 Results

6.4.3.1 Phylogenetic analysis

The phylogeny is shown in Figure 6.10 with cultural data on fishing and matrilineal descent plotted for each society. The most probable ancestral states at the root of the tree under the independent model are non-matrilineal descent, $P(O_D) = .98$, and with low dependence on male fishing, $P(N) = .78$. This finding concurs with the estimation of the root as having non-matrilineal descent in Chapter Five. Under the dependent model the highest estimate for the root is the same as for the independent $P(O_D,N) = .62$, followed by $P(M_D,N) = .27$. This means that a quarter of the reconstructions show a root that was already matrilineal.

The ancestral state at the root was equivocally matrilocal, $P(M_R) = .55$. This difference from estimates in Chapter Five may stem from the more strict definition of matrilocality used in the present analysis. Results presented here will refer mainly to the co-evolution of matrilineal descent and fishing, as there was considerable overlap in the coding of societies as matrilineal and matrilocal.

6.4.3.2 Kappa and chi-square tests

Kappa was estimated to be .86 (± .10), ranging from .23–1.25. As this was a small departure from the default value of 1.0, kappa = .86 was incorporated into subsequent analyses. A chi-square test (2 x 2 with 1 *d.f.*) showed a significant association between matriliny and fishing ($\chi^2 = 8.88$, $p \leq .01$). Thus, in a traditional non-phylogenetic test, the two traits would be positively correlated.

Descriptions of the evolutionary transitions are given in Table 6.8. In terms of testing the hypothesis of correlated evolution, we are especially interested in q_{34}, where matriliny is gained against a background of high fishing dependence, and q_{21}, where matriliny is lost against a background of low fishing dependence.

Table 6.8. Description of the rate coefficients as applied to matri-traits and fishing.

Coefficent	Evolutionary transition
Gains	
q_{12}	Gain of matriliny in the presence of low fishing dependence
q_{13}	Gain of high fishing dependence without matriliny
q_{24}	Gain of high fishing dependence in the presence of matriliny
q_{34}	Gain of matriliny in the presence of high fishing dependence
Losses	
q_{21}	Loss of matriliny in the presence of low fishing dependence
q_{31}	Loss of high fishing dependence without matriliny
q_{42}	Loss of high fishing dependence in the presence of matriliny
q_{43}	Loss of matriliny in the presence of high fishing dependence

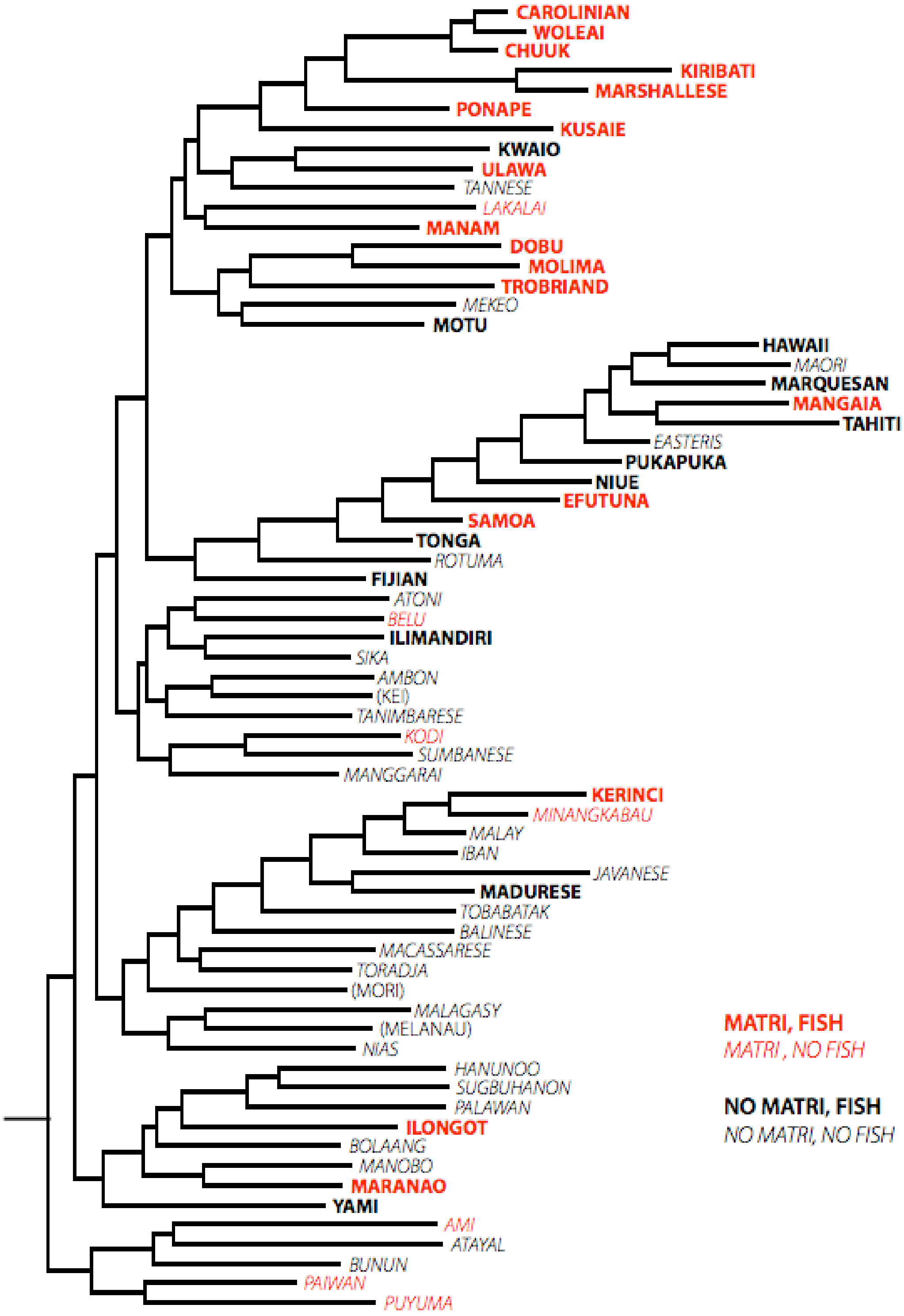


Figure 6.10. Phylogeny showing the evolution of matrilineal descent and high dependence on male fishing. Descent is denoted by colour: matrilineal societies appear in red, non-matrilineal societies in black. Fishing is denoted by font: high dependence societies are in bold, low dependence in italics. Those in brackets have missing data. Fishing is concentrated in Oceanic societies, as is matriliny, although matriliny appears sporadically throughout the tree both with and without fishing.

6.4.3.3 Test for correlated evolution

For the matrilineal coding, the marginal likelihood of the independent model, using the harmonic mean, was –79.22, while that of the dependent model was –80.82. Using the Bayes factor test, *BF* = –3.2, indicating that the hypothesis of correlated evolution between matriliny and fishing is not supported for these data. For the matrilocal coding, *BF* = –4.1, additionally confirming that the co-evolutionary model is not supported. Using the RJ MCMC procedure to test the hypothesis of correlated evolution we compare the number of times that versions of the dependent model are visited compared to versions of the independent model. For the co-evolutionary hypothesis to be supported the independent model should represent 0.24% or less of the sample. For the matrilineal coding, the independent model accounted for 5175/50,000 (10.35%) of samples, and for the matrilocal coding 17.8%.

6.4.3.4 Identifying models of evolutionary change

Figure 6.11 shows the flow diagram of evolutionary change. Even though matriliny and fishing do not appear to be correlated, we can examine the transition-rate parameters from the dependent model to see if there are any patterns in terms of the direction of evolutionary change. Figure 6.11 shows probability distribution plots of the rate parameters and the likelihoods.

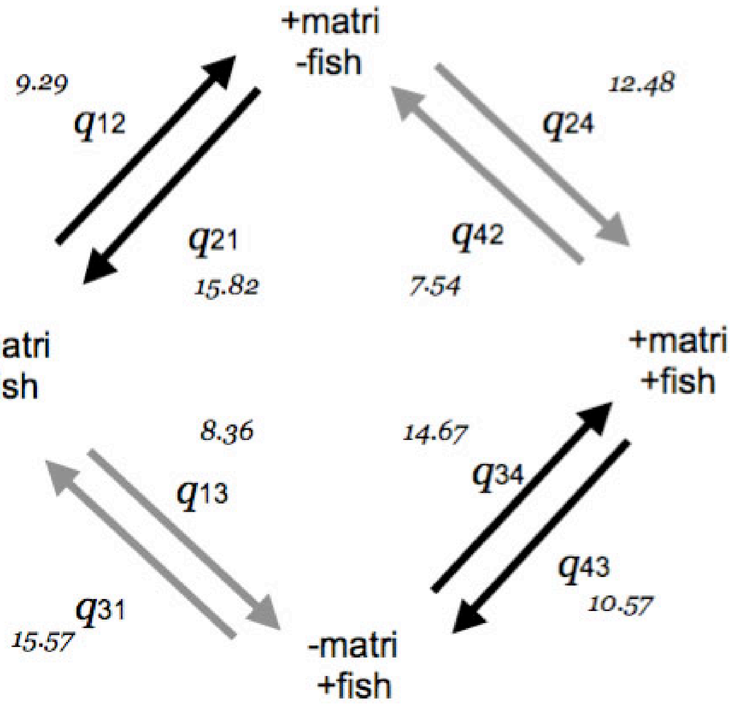


Figure 6.11. “Flow diagram” showing all transition rates between the four possible combinations of states for matriliny and fishing. The values of the rate coefficients are the means of the posterior probability distributions for each rate parameter, derived from the dependent model of evolution. The larger the rate, the more probable that particular pathway of evolution. Two of the smallest rates (q_{42} and q_{12}) both describe evolutionary pathways towards matriliny and low fishing dependence; this may be an uncommon or unstable state. The two highest rates (q_{21} and q_{34}) describe pathways towards what our hypothesis predicts to be the two evolutionary stable states: matriliny and high fishing dependence, and their absence. However, the most probable model under the RJ MCMC procedure is the independent model, where all transitions occupy the same “rate class”.

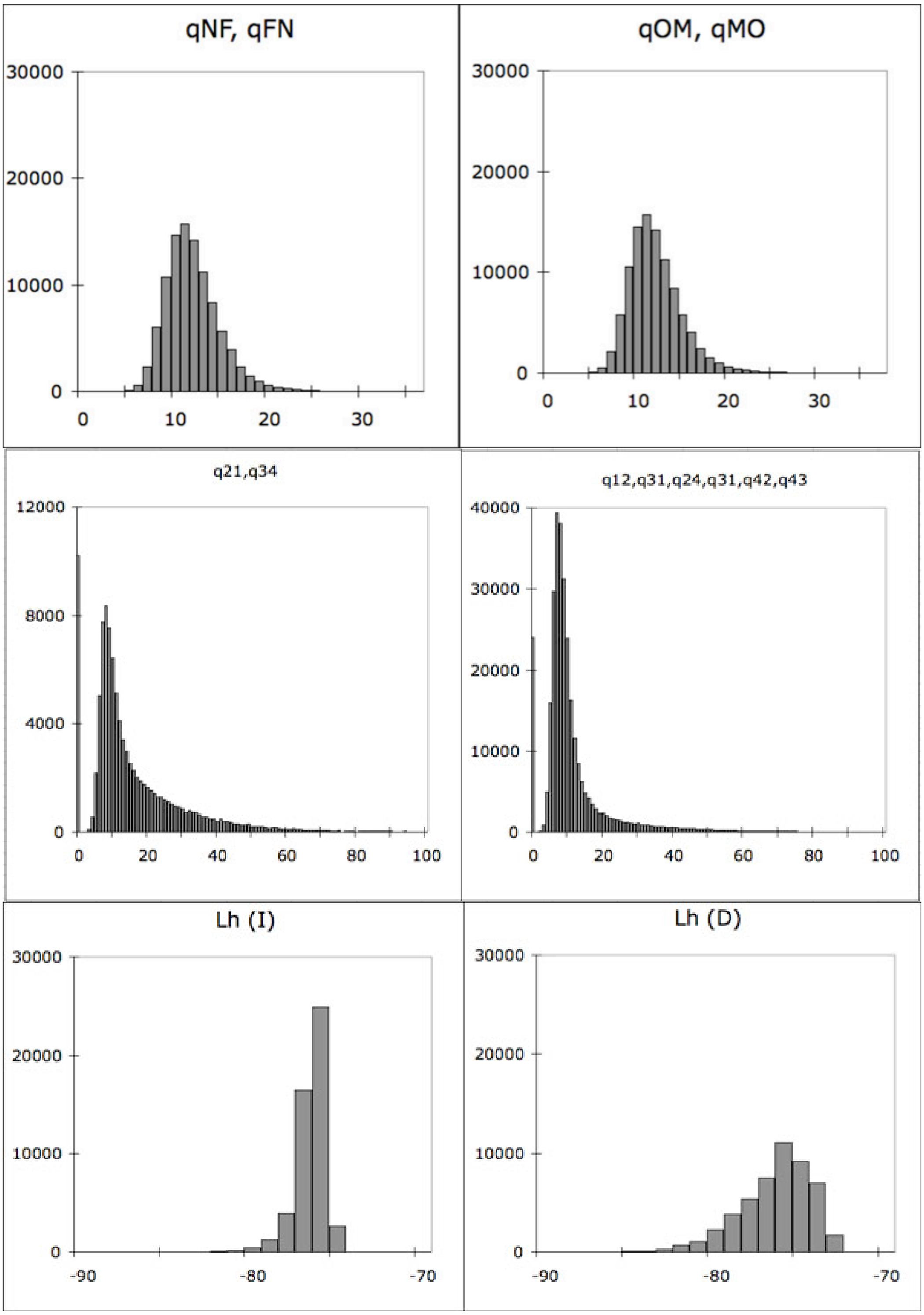


Figure 6.12. Posterior distribution panels for matriliny and fishing. **Top.** PPDs of the rate coefficients for the independent model. **Middle.** PPDs of the rate coefficients for the dependent model of evolution, divided into two classes. *q*21 and *q*34 have a slightly fatter right-hand tail which contributes to their higher likelihoods.
Bottom. PPDs of the likelihoods for the independent and dependent models.

In Figure 6.12 the bottom two panels showing the distribution of the likelihoods for the dependent and independent models demonstrate why the evidence for correlated evolution is not strong. The two distributions overlap around the same mean, but the likelihoods for the independent model are tightly clustered compared to the dependent model. Thus, under the dependent model of evolution there may be some combinations of tree-topologies and rate parameters that do improve the likelihood, and, in a single test, would provide evidence of correlated evolution. However, in this Bayesian context, where we are attempting to control for uncertainty in our estimates, the probabilistic model demonstrates that we cannot reject the hypothesis that the two traits are evolving independently.

The top two panels show that under the independent model, both matriliny and fishing are changing at rates higher than zero, which practically identical distributions. Based on this, we can infer that both traits are evolutionarily labile, that is, they have changed back and forth across the phylogeny a number of times. The transition rates for matriliny have a "longer tail", that is, there are some higher transition rates than for fishing, but this is not obvious at the scale of the PPD plots.

The RJ MCMC procedure indicates that the second most likely model (below; Table 6.7) is one that assigns different (higher) rates to the parameters q_{21} and q_{34} compared to all others. We can see in the distribution plots of these parameters (middle left panel) that there are more instances of higher rates, i.e., the right tail is fatter. This finding is notable because, although we did not find evidence for correlated evolution, the rates q_{21} and q_{34} are the parts of the evolutionary pathway that would drive an association between matriliny and fishing, as described in Table 6.8.

Table 6.9. Matriliny and fishing data showing the most frequent models found by RJ MCMC model-search, accounting for 24% of all samples. The most-frequent model, accounting for 10% of all models, has only one parameter, making it equivalent to the independent model. A total of 1703 unique models were visited, indicating a wide variety of ways to describe the data. The flow diagram is presented according to the most-frequent model.

Model string	Frequency	Cumulative frequency	No. of parameters
00000000	4822	0.10	1
00100100	1778	0.13	2
001Z0100	1644	0.16	2
00011Z00	1430	0.19	2
00Z11Z00	1298	0.22	2
001ZZ100	1191	0.24	2

Are there stable states of matriliny and fishing? Together, the second, third, and sixth most-frequent models account for 4613/50,000, almost as many as the top (independent) model. These model strings all describe dependent models where there is a change away from what our hypothesis would predict is an "unstable state", that is, the loss of matriliny when fishing dependence is low, and the gain of matriliny when fishing dependence is high. Here, I test if those models in the sample where q_{21} and q_{34} are higher than other rates (the "matri-fish" models) have higher mean marginal likelihoods than an equal-sized sample of all "other" models. Using the procedure described above in 6.3.3.4, the likelihood of "matri-fish" models was –74.77, and the likelihood of "other" models was –77.04, giving a $BF = 4.54$. Thus, although there is no evidence for correlated evolution, the data support a hypothesis that non-matrilineality and low fishing dependence, and matriliny and high fishing dependence, are stable or attractor states compared to other combinations.

6.4.3.5 Results of an earlier analysis

For comparison, I present here the results of a previous analysis (2002) using the maximum likelihood version of *Discrete* (Pagel 1994). This was used to fit the independent and dependent model of trait evolution on a phylogeny of 34 AN languages derived via parsimony methods (Jordan 1999). The obtained likelihood ratio (*LR*) for the model was then compared to a null distribution of likelihood ratios in order to test for evidence of correlated evolution. A chi-square analysis, the "traditional" method of testing for a cross-cultural association, was non-significant ($\chi_2 = 3.33$, $df = 1$, n.s.). However, using the comparative method of *Discrete*, a statistically significant association between matriliny and dependence on fishing was found ($LR = 2.06$, $p < 0.02$), indicating that the two characters were evolving together on the phylogeny. Fixing each rate parameter to zero in a stepwise fashion, and fixing q_{21} equal to q_{34} in order to test for the directionality of this association, revealed no significant trends. This indicates that the model was assessing ancestral states as equally probable, and thus for these societies, it may be that matriliny evolved rapidly and could switch back and forth in the presence or absence of fishing.

6.4.4 Discussion

Using a Bayesian comparative method on ethnographic data from 67 Austronesian societies, I tested the hypothesis that matriliny co-evolved with a high dependence on male fishing. Compared to the results of an earlier analysis, and a chi-square test, the model of correlated evolution was not supported by the data. However, estimates of the transition-rates to the "stable" states of (i) matriliny and fishing, and (ii) the lack thereof, revealed that paths leading to the stable states had significantly higher likelihoods than transitions between all other states.

There are two explanations why positive evidence for co-evolution was not found. Firstly, there may be an association, but the data and/or the test are insufficient to reveal it. Secondly, we may require an alternative explanation for the evolution of matriliny in these cultures.

Using a Bayesian, likelihood-based comparative method meant that the analysis made use of all the information in the cultural data and the phylogenetic sample (Lewis 2001). The RJ MCMC procedure revealed that dependent co-evolutionary models were visited frequently, showing that co-evolution is a possible interpretation of these data. However, no one set of dependent models exceeded the visits to the independent model, and because of that uncertainty, we cannot accept a hypothesis of co-evolution. The nature of cross-cultural analyses using sources such as the *Ethnographic Atlas* is such that we may be quick to blame our data: it may be incomplete or inaccurate, we may be comparing apples and oranges, or the pre-existing coding schemes may be insufficient for the hypothesis. It is unlikely that either the kinship or the fishing data is biased, as all sources examined were neutral on the hypothesis.

Using historical linguistics to inform anthropology, Blust (1990), Hage (1998) have inferred the former presence of matriliny in Austronesian society by cataloguing or reconstructing kinship terms that are associated with matrilineal organisation, such as unique terms for the mother's brother, or matrilateral cross-cousins. Marck (in preparation) used these kin terms as positive indicators of former matriliny in order to infer the evolution of Oceanic kinship. In an attempt to use all available information, in the present test I coded societies that were ambilineal or ambilocal as matrilineal, making a similar inference that a matrilineal option existed for that society.

What may be lacking is an adequate measure of "male absence". High dependence on male fishing may be a sufficient but not necessary cause of matrilineal social organisation, and may explain why the initial test in the 34-society sample produced a positive correlation, and why evolutionary transitions towards some states are more likely. The measure of fishing dependence could be refined with information on the average fishing range, duration of absence, and risks involved in the method of fishing, some of which may be extracted from the literature of Pacific fishing (e.g. Kirch and Dye 1979; Bryan 1984). Male mortality while fishing at sea is recorded historically as a significant cause of death in Micronesia (Lessa and Myers 1965). As well, the analyses in Chapter Four indicated that dependence on fishing was associated with geographic nearest neighbours, suggesting that while matriliny may be vertically transmitted, ecology and/or diffusion may act to "break up" the association with fishing. Similarly, estimates of male absence may need to incorporate historical and ethnographic information on the types of trade, voyaging and warfare practised by each society. Adequate data on warfare exist for those societies in the SCCS, but this number includes only 11 Austronesian societies (Murdock and White 1969). Pilot investigations on the feasibility of coding warfare data revealed this to be a comprehensive task beyond the scope of the present investigation, as scholars of warfare have attested (Otterbein and Otterbein 1968; Vayda 1978). The task of creating a comprehensive code for "male absence" is daunting, but may reveal much about Austronesian social organisation.

Darwinian theory leads us to believe that the "male absence" hypothesis may be a factor in explaining Austronesian matriliny and matrilocality, even though the present analysis only offered it as an intriguing possibility. Male absence may be highly correlated with increased paternity uncertainty, and, as Hartung (1981) and Holden et al. (2003) have shown, only small levels of paternity uncertainty are required for female-biased investment (of whatever sort) to be adaptive, for both males and females. From this, Holden and Mace (2003) argued that matriliny and/or matrilocality might be a "default" arrangement in the absence of heritable resources because of a greater relatedness to the matriline, and because matrilineal kin appear to do more to promote child survival (Mace and Sear 2004). Interestingly, Mace and Sear point out that it is patrilineal kin who may enhance female fertility. In the Austronesian context, societies that retain matricentric organisation may be those more concerned with child survival, while those with patricentric organisation may have a strategy to increase fertility. These may be the two "stable states" we are seeing in the flow diagram. This hypothesis offers a fruitful direction for further analysis, combining information on ecology, environment, and demography.

6.4.4.1 Alternative explanations for matriliny

The present study tested only one hypothesis for the evolution of Austronesian matriliny and matrilocality. Several others in the anthropological literature may be relevant to the Austronesian situation.

First, Murdock (1949) suggested that matrilocal societies change to become either patrilocal or avunculocal in the presence of internal warfare, as these patterns keep unilineal alliances of related males together. However, if there is very high male mortality (which may be the case in voyaging, trading, or fishing societies as well as those with high internal warfare), avunculocality, which localises matrilineally-related men, may be more practical to scattered patrilocality. Second, and related to the fishing hypothesis, it may be that the sex doing the greatest amount of subsistence-related work is the one whose kin are localised together (Driver 1956). This predicts that when males do most of the subsistence work, patrilocal and avunculocal rules will emerge. When women do more, matrilocal patterns will emerge, and when both sexes contribute equally, then bi-, neo-, and ambilocal rules will apply. In the Pacific, the gathering of littoral and reef resources is chiefly women's work (Kirch and Dye 1979; Firth 1984; Chapman 1987); this kind of "dependence on fishing" may be a factor in matriliny, *contra* the original hypothesis. However, Ember and Ember found no significant correlations between subsistence contribution and residence rules on a worldwide data set of 455 societies (1971, 1972), and an opposite association in Oceania. A number of studies have tested this proposition (Levinson and Malone 1980): it may hold regionally, such as in North America (Driver 1956) or be moderated by other considerations such as warfare, but the hypothesis remains to be tested phylogenetically.

Third, recent migration may have some relationship with matricentric social organisation. Divale (1974) argued that migration (within the last 500 years of the ethnographic present) into new, but inhabited, areas was likely to be ultimately responsible for matrilocality. Matrilocality, on this hypothesis, assisted in keeping warfare at bay by dispersing related males in a new territory. There is the intriguing possibility that Proto Oceanic matrilocality (Hage 1999; Hage and Marck 2003; Chapter Five) may result from the “incursion” of Lapita-era populations into the inhabited areas of Island Melanesia.

Lastly, Peregrine (1994) has proposed that incorporation into the world system produces changes in social organisation through competition and the division of labour. He argues that societies are “transformed through the introduction of new trade relations, for the introduction of trade may put pressure on populations to transform descent and residence toward matrilineal forms” (1994:100). This is a modern extension of the earlier work by the Embers on warfare: Peregrine argues that the world system places the same kinds of pressures on a population as does external warfare. For example, employment in cash industries requires a group of co-ordinated labour with a single loyalty. Also, female kin can be concentrated in one place in the face of extended male absences seeking or undertaking work in cities. Using 87 societies from the SCCS, Peregrine examined the introduction of trade into the subsistence economy of each culture. Using spatial autocorrelation corrections and linguistic relationships to attempt to control for Galton’s Problem, he found a significant relationship between (i) trade and matri-focused descent, and (ii) trade and matrilocality. Peregrine argues that matrilineal groups are “pre-adapted” for world-system trade, and are also less able to resist trade than other groups. He notes that long-term extensive incorporation into the world system is likely to break down unilineal descent systems to bilateral groups or nuclear families, echoing Murdock (1949), Fox (1967), and others. Careful examination of the ethnographic literature would be required to operationalise trade and the extent of trading in Austronesian societies, and crucially, choose appropriate time periods for comparison. Nonetheless, the hypothesis is relevant, as it can directly speak to whether the processes of change in kinship organisation are uniformitarian, that is, whether current social change resembles past processes.

6.4.4.2 Does isolation break down matriliny?

Matriliny in Austronesian societies may of course have more than one motivating factor. If we assume the Proto Austronesian ancestral state to have at least one aspect of matrilineal organisation (matrilocal residence, Table 5.5), then a complete explanation will pinpoint factors that have led to the *loss* of matriliny. Schneider and Gough (1961) reckoned matriliny to be an unstable type of social organisation, one that was easily broken down into other forms. In an investigation of kin terminologies in Oceania, Marck (2006) has suggested that matriliny has undergone a patchwork pattern of loss. Hage and Marck (2002) have suggested that the cessation of regular inter-island voyaging (for trading or raiding) may be a factor in those Micronesian societies that have adopted different forms of residence and descent. Double descent in the eastern Carolines, where matriliny served only to regulate marriage rules, may have been such a case: the "relative isolation of the atolls ... appears to have promoted conditions which served to weaken matrilineality" (Damas 1979:192). Isolation, on their model, means that patriliny or cognatic descent can develop, as the men are no longer absent. Intriguingly, it appears that the so-called "AD 1300 event", where climate cooling led to sea-level falls, a reduction of marine resource availability, and a shift to inland production rather than coastal exploitation for many Oceanic societies (Nunn 2003) may have coincided with increased levels of warfare or conflict in (for example) Tikopia (Kirch 1984) and Tonga (Burley 1998), and after this time, there may have been a reduction in long-distance voyaging (Rolett 2002). Further work to identify if and when male absence through voyaging declined, leaving men "at home", as well as estimates of the degree of physical and/or social isolation of each society, may reveal if this explanation can be extended to the Austronesian family as a whole.

6.5 Conclusion

Using cutting-edge Bayesian comparative methods, I tested two simple but influential anthropological models of kinship. One, the “main sequence” theory, was confirmed. The other, the matriliny and fishing association, was not supported by the data. Obtaining a positive *and* a null result on the same data set is encouraging, because it gives us confidence that our method is not overly generous nor overly stringent.

Because the same tree sample and methodology was used for both sets of tests, it is possible to remark on the rate of cultural change. Although we did not estimate the rates of cultural evolution for all traits, we can compare the transition rates of the matriliny-fishing analysis with that of the main sequence tests. The matriliny-fishing rates are lower overall that the residence-descent rates, indicating that not only may individual traits change at different rates, but co-evolutionary rates will vary as well. It is thus vital that the evolutionary dynamics of each cultural trait are examined separately, as was seen in Chapter Four.

Pagel and Meade’s (2006) reverse-jump MCMC procedure is extremely useful. As an heuristic device, the method works by allowing the data to reveal what models are supported, independent of the hypothesis under consideration. In contrast, previous implementations of the *Discrete* algorithm required the investigator to select which transition were to be made equivalent or set to zero. Not only is this laborious, but there are ~21,000 different models possible, not all of which are able to be tested. Cultural traits may evolve quickly or unpredictably, and the RJ procedure lets the data talk to us directly, indicating the most fruitful avenues for model testing.

The Bayesian framework removes the dependence on any single phylogenetic hypothesis, and the comparative test becomes "tree-free". Integrating transition-rates over a tree sample, examining their probability distributions, and seeing, for example, how often they are in the “zero bin” allows insight into the variability in our evolutionary scenarios. In this way we make explicit the uncertainty about culture change that so worries many skeptics of the phylogenetic approach.

Both investigations highlighted how crucial a phylogenetic comparative method is when testing cross-cultural hypotheses, because the conventional chi-square test of association returned results counter to the phylogenetic analyses. In the main sequence test, the comparative method provided evidence for co-evolution in both the coding systems, but the chi-square only showed a significant association for patriliny. In the matriliny and fishing tests, the chi-square returned a significant association, but the comparative method found no significant co-evolution. Researchers relying on non-phylogenetic statistics must control for Galton's Problem, not simply because their conventional tests may find an association when the data do not support one, but because they may also fail to detect a real association in the data. Even if we are skeptical of a phylogenetic comparative approach (e.g. Boyd et al. 1997; Borgerhoff Mulder 2001; Nunn et al. 2006), the non-phylogenetic alternatives are extremely unsatisfactory. In contrast, a Bayesian approach allows us to account for uncertainty about population history, estimate the uncertainty in adaptive hypotheses, and develop illuminating models of evolutionary relationships.

CHAPTER SEVEN

EVOLUTIONARY ANALYSES OF LEXICAL CHANGE AND POPULATION SIZE

7.1 Summary

Aspects of language vary in their rates of evolution and subsequently different languages may accumulate different amounts of lexical (word) change once they split from a common ancestor. These differences may be produced by a number of factors; here I tested for an association between lexical change and a demographic variable, population size, in the Austronesian languages. Conventional correlation analyses revealed a significant inverse relationship, suggesting that as population size increased, lexical change decreased. However, phylogenetic comparative methods found no evidence for correlated evolution, demonstrating the need to control for shared descent in cross-cultural analyses. Scaling parameters in the phylogenetic method showed how the two traits were evolving under different evolutionary models. Population size could be characterised by a punctuational and/or random drift model, whereas lexical change had a directional aspect and showed evidence for adaptive radiation. Plotting the two traits according to the power law distribution supported these conclusions. Alternative explanations for lexical change in Austronesian languages are considered.

7.2 Introduction

7.2.1 Language change

Factors affecting language change tend to be well-described for individual languages, yet general cross-cultural principles, especially those concerning the rate of change, are not well known. A constant rate of linguistic change (in basic vocabulary) was assumed in early lexicostatistical work (Swadesh 1951), and Nicholls (1992) assumed linear rates of change in estimating patterns of worldwide linguistic diversity. Nettle (1998) questioned the rate-constancy assumption, arguing that linguistic change declined over time following radiation of ethnolinguistic groups into new areas. However, there have been no quantitative evolutionary tests of the factors causing differential rates of change. Linguistic change can be seen as an expression of the larger dynamics of cultural change, and so we may approach questions of language change with the theory and methods of cultural evolution.

The sources of variation in language change can come from imperfect learning (i.e. mistakes in the transmission of variants from parent to offspring), from deliberate change (either individual or group consensus) and from one-off performance variants (Lindblom 1995). Factors that may affect language change include the method of language transmission to children, the degree and type of contact with other communities and/or their languages (including the degree of bilingualism), and other social factors such as name or word taboos (Crowley 1997). Demographic factors and population dynamics may have an effect at the intra-group level by affecting how quickly language changes are passed on to the next generation, and at the inter-group level by contributing to the levels of diversity in daughter languages. Nettle (1999b) argues from Nichols (1992) data that language diversity—as expressed in languages per stock—is greater in the New World and Australia/Pacific due to smaller overall population sizes. Here we are mainly concerned with population size effects at the between-language level: how might population size affect the rate of evolutionary change?

7.2.2 Founder effects

In biology, the founder effect (Mayr 1963) is a sampling effect that refers to the establishment of a new population by a small group of founders who carry some reduced amount of the genetic variation of the original population. Stochastic effects (genetic drift) on small samples can mean the variation in the new population is very different to the original. Founder effects can be caused by migration, by population subdivision without migration, or by population bottlenecks (fluctuation in size due to some retardation on population growth). As well, the effects of random variation on small populations are greater due to the lack of demographic buffer. Founder effects and genetic, cultural, and linguistic drift are all features of Austronesian population history. Polynesian populations represent the end-point of consecutive voyages by small populations from Island Southeast Asia, and as such, some genetic markers such as the substitution motifs accompanying the 9bp deletion are at high fixation rates compared to source populations (Melton et al. 1995). Blust (1981a) notes that consonants decrease in number in languages as one travels eastwards across the Pacific, leaving only eight in Hawaiian, and similarly, many items of material culture such as metalworking, loom weaving, and pottery decline in the same direction (Blust 1995). Population crashes on small and/or ecologically vulnerable islands also exacerbate the stochastic nature of drift. For example, Typhoon Lengkiekie devastated the atoll Pingelap (Micronesia) in 1775, reducing the population drastically. A ~30% prevalence of autosomally-recessive achromatopsia (colour-blindness) in the present-day population has been linked to this event (Sacks 1997; Sundin et al. 2000).

7.2.3 Punctuated equilibrium

Dixon (1997) borrowed the concept of punctuated equilibrium (Eldredge and Gould 1972) from evolutionary biology and applied this to language change. On this model, the majority of change is slow and gradual, with most linguistic innovations languishing un-transmitted in a single generation. Demographic or ecological factors cause disruption to the social system in some fashion, often through migration or technological innovation, and this causes a cascade of rapid and significant change in language. Thus, repeated punctuation events give rise to the hierarchical branching tree model of language evolution, as subdivided populations become linguistically isolated from one another. The punctuation model may be of especial significance in the Austronesian family, where not only is the family expansion as a whole thought to be driven by the engine of agricultural technology (Diamond and Bellwood 2003), but where a series of repeated migrations to island environments characterised the Oceanic phase of expansion. These migration events are essentially demographic changes, and as such, an examination of the effect of population size on language change is warranted.

7.2.4 Demography and the rate of change in biosocial variables

Demographic variables such as fertility rates, sex ratios, and population size are often included in cross-cultural comparisons either as determinants of some biosocial variable or as the dependent variable itself. For example, Mace and Jordan (2005) found that a female-biased sex ratio at birth in African countries might be associated with the greater physiological costs of producing male babies, but was not associated with the presence of bridewealth. However, no studies to date have examined the effect of population size on the rate of evolutionary change in some human biosocial variable. This is remarkable considering that the effects of population size on diversity and rates of evolution have been discussed in the theoretical and experimental population genetics literature since Wright (1931), and mathematical treatments of cultural evolution have also included population size in their equations (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985).

The paucity of research may be because it is difficult to obtain data on population size for cross-cultural analysis. While census information at a country level is usually freely available e.g. The CIA World Factbook, (https://www.cia.gov/cia/publications/factbook), and the Demographic and Health Survey project (http://www.measuredhs.com) provides village or town level population numbers, the investigator is often left with large gaps in the analysis. Many studies have thus resorted to using country-level statistics, which by their aggregate nature are unsatisfactory when dealing with ethnolinguistic groups that may be spread over two or more countries, or who may be only one of many groups in a country. Other information sources such as the *Ethnographic Atlas* or the *Standard Cross-Cultural Sample* contain limited population information, often only expressed in 3–5 classes, and in the case of the former, much of this is missing for Pacific cultures.

One source that contains population figures for individual languages is the *Ethnologue* (Gordon 2005). Here, numbers refer not to the demographic population but rather the number of language speakers at a recent point in time. As such, this figure can be thought of as equivalent to the effective population size (N_e) or “breeding population” (Wright 1931), as it represents the number of individuals able to transmit the language to the next generation. This is thus a more suitable variable than standard population numbers. It will of course be an approximate estimate, but the figures are available for all 67 languages in the Austronesian sample, allowing hypotheses about the rate of change to be tested.

7.2.5 Modelling the rate of word evolution

Lexical items (words) constitute one aspect of the linguistic system that can be examined as an evolving cultural trait. Other features might be aspects of typology, such as word order, or phonology (sound change). The method of glottochronology (Swadesh 1955) was an attempt to understand the rate of lexical replacement in languages as similar to a radioactive decay function. Glottochronology was an approach to estimating the time-depth of a lexicostatistical tree and used a formula specifying the relationship between shared cognate percentages, a universal retention rate, and time depth in millennia. Numerous flaws with lexicostatistical and glottochronological methods mean these approaches are largely discredited (Bergsland and Vogt 1962; Blust 1999; Campbell 2004). The most trenchant criticism, that these methods did not distinguish shared innovations from shared retentions, is addressed by the use of phylogenetic methods that use only synapomorphies (shared evolutionary innovations) to build trees. Newer methods to estimate the rate of word evolution have employed phylogenetic statistical models to assess the rate of evolutionary change in lexical items and test hypotheses about language dating in the Indo-European language family (Gray and Atkinson 2003). These Bayesian methods look to be the most productive avenue for research aimed at dating ancestral languages/cultures or assessing the rate of change in cultural traits.

Other workers have used computer simulations to investigate the dynamics of lexical change. Nettle (1999a) simulated language change by modelling social and functional (adaptive) selection on the uptake of new words in a population. He found that influential individuals who adopt a new word were a major factor in the dynamics of language change, and related these findings to the “threshold problem”. Unlike the genetic situation where a mutation has a high probability of being passed on to the next generation, linguistic mutations are less likely to be passed on due to (i) a higher number of cultural parents, and (ii) conformity bias, the tendency to copy the most common variant (Boyd and Richerson 1985). Further work by Nettle (1999b) simulated population size effects on the rate of language change, because as population size increases, the threshold problem is magnified: “As community size increases, then, the probability of some individual adopting a rare variant *q* becomes smaller, and the number of such adoptions which are required for *q* to become the community norm increases.” (1999b:123). Nettle’s simulation found that the rate of change declined with increasing community size. What could be the proximate mechanisms of this relationship? The rate of change in languages of large population size may be affected by institutions that act to maintain linguistic homogeneity, such as schooling norms or a body of written literature. In smaller populations, it may be that language norms are more likely to be vertically transmitted only, and thus more prone to copying errors.

The attempts to model the evolutionary dynamics of lexical change have shown that a phylogenetic perspective is required, and that population size may be a factor in the rate of change. Other approaches consider a null model of neutral change.

7.2.6 Models of neutral or random change

Demographic estimates are important components in modelling the patterns of diversity and/or coalescent (times to most recent common ancestor) of gene markers. For example, genetic studies have calculated that the human species is relatively young in terms of genetic diversity, undergoing a bottleneck c.100,000 years ago in Africa, where the population was limited to only about 1000–10,000 individuals (Harpending et al. 1997; Underhill et al. 2001). In population genetics, the neutral model (Kimura 1968) describes how the vast majority of evolutionary change is due to the random fixation of selectively neutral alleles. As a consequent, neutral theory states that in the absence of other evolutionary forces (e.g. selection, migration, mutation) the probability of fixation of a new allele in a population is inversely related to population size, as proposed by Wright (1931). In the genetic situation, this relationship is moderated by a corresponding increase in the overall mutation rate producing similar variants. In the linguistic situation there may not be the same eliminating selection on these variants, and so the balance created by an increase mutation rate may not hold for language change (Nettle 1999b), thus allowing population size to affect the rate of change. By identifying departures from a constant-variance or neutral model of evolution, we can infer the presence of additional evolutionary forces.

Power laws have been invoked to explain the distribution properties of many real-world systems such as language. For example, word frequencies in usage are inversely proportional to their rank (Zipf 1949). Power laws describe a decay curve that plots as a straight line on a log-log scale; as they are supposedly a feature of self-organising systems (Bak 1996) they can thus seen as a null or random change model, akin to neutral drift in population genetics (Hahn and Bentley 2003). Recently, Bentley et al. (2004) have demonstrated that aspects of culture such as popularity in baby names, dog breeds, and patent citations conform to this law through a random copying process. Departures from the power law may indicate processes other than random change at work in a system, for example, in their study of dog breed popularity through time, Hertzog, Bentley, and Hahn (2004) found that Dalmatians did not conform to the power law, probably due to films that popularised the breed. With respect to language, Wichmann (2005) ranked world language families by the number of languages they contained and found that they conformed to the power law distribution, but the number of speakers in each language did not demonstrate this relationship. Similarly, we can rank languages in a single family according to their amount of lexical change or their population size to see if they conform to the power law distribution.

7.2.7 Aims of the study

Here I examine the evolutionary processes affecting (i) language population size and (ii) the amount of lexical change using empirical data from the Austronesian language family. Some authors (Borgerhoff Mulder 2001) have questioned whether phylogenetic controls are necessary in cross-cultural tests; here, a number of conventional and phylogenetic comparative methods are employed, as it is not possible to determine the need for historical control *a priori*. This serves as a demonstration case for the phylogenetic approach. The purpose is to characterise the tempo and mode of evolution of population size and lexical change by seeing if they evolve according to a constant-variance model of change, and to test for any co-evolutionary relationship between the two traits. If founder effects cause greater differentiation in daughter populations through the "fixation" of random effects, we should expect that small populations are more different to the source population than are large populations. Thus, we might predict an inverse relationship between population size and the amount of lexical change.

7.3 Data

7.3.1 Demographic data

Data on population size were obtained from the online version of the *Ethnologue* (Gordon 2005). These data are approximate numbers, indicating the number of current speakers rather than being a demographic indicator of population. There will be inconsistencies between the dates when the language *population* data were recorded and the dates when each language itself was recorded. In some cases, the population sizes may be underestimates of the ethno-linguistic population due to language or population decline. In other cases they may be large overestimates; some languages such as Malay and Javanese have speakers in the millions in the highly populous islands of Indonesia, and many of these speakers may be bi- or tri-lingual in other languages. However, we should not expect the population size estimates to be systematically biased with respect to the hypotheses. Population estimates were log-transformed and were found to approximate a normal distribution.

7.3.2 Language data

Lexical data were obtained from the ABV project at the University of Auckland. I used the sample of 67 languages for which cultural and demographic data were also available, as described in detail in Chapter Two.

7.3.3 Geographic data

ArcMap 9.1 was used to find the size of the language "territory" using the corresponding entry in the Word Language Mapping System GIS shapefiles (Global Mapping International 2001). Island size was found in the Island Directory of the United Nations Environment Program website at http://islands.unep.ch/isldir.htm (Dahl 2005).

7.4 Analysis and Results

7.4.1 Phylogenetic trees

BayesPhylogenies (Pagel and Meade 2004) was used to build a sample of language trees under a Bayesian MCMC methodology. Tree-building methodologies were as described in Chapter Two. A common argument against the use of phylogenies in cultural analyses is that we may not be certain that we have the true tree. Where possible for these analyses, a sample of 500 post-convergence trees was used in order to incorporate uncertainty about the phylogenetic relationships and the amount of change in each language group over time. Figure 7.1 shows the consensus phylogeny.

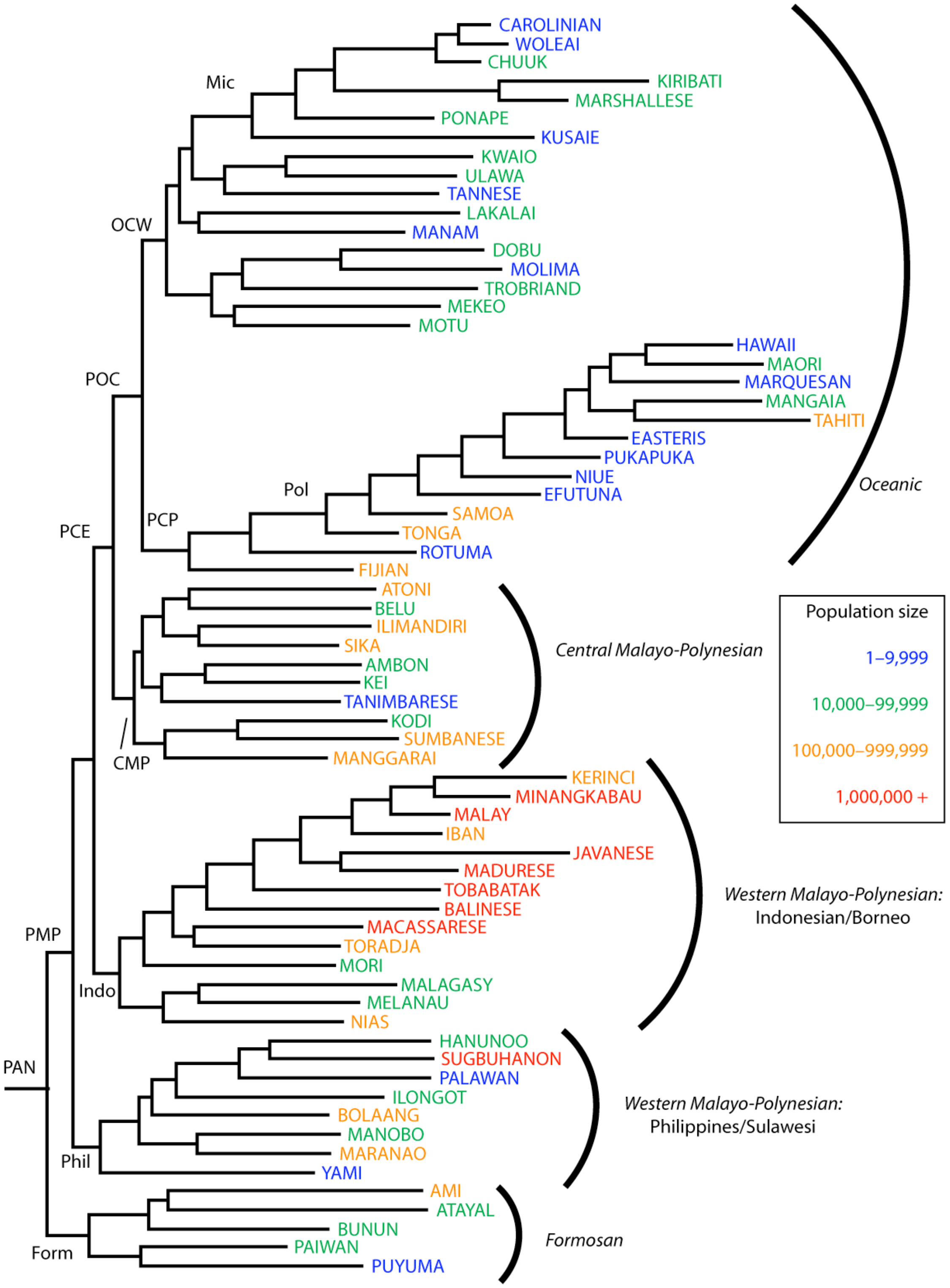


Figure 7.1. Consensus phylogeny of a 500-tree sample obtained by Bayesian MCMC analysis. Languages are colour-coded to indicate population size according to the key.

7.4.2 Calculating language change

Tip-to-root distances were calculated for each language as an estimate of the amount of language change (lexical replacement). These distances were calculated by summing the total path lengths along the path from the root using a UNIX program written for this purpose (*TipToRoot*, A. Meade, personal communication). The figures obtained by this program were not units of lexical change per se, but were rather the posterior probabilities of change along the branch. Thus the total path length for each language was multiplied by the overall number of characters to give an index, Total Lexical Change (TLC) that was used as the measure of lexical change in the subsequent analyses. TLC values were calculated for all languages over all 500 trees. From these, I calculated the mean TLC for each language, shown in Table 7.1. Figure 7.2 shows a representative distribution of the TLC for two languages, Ambon and Yami.

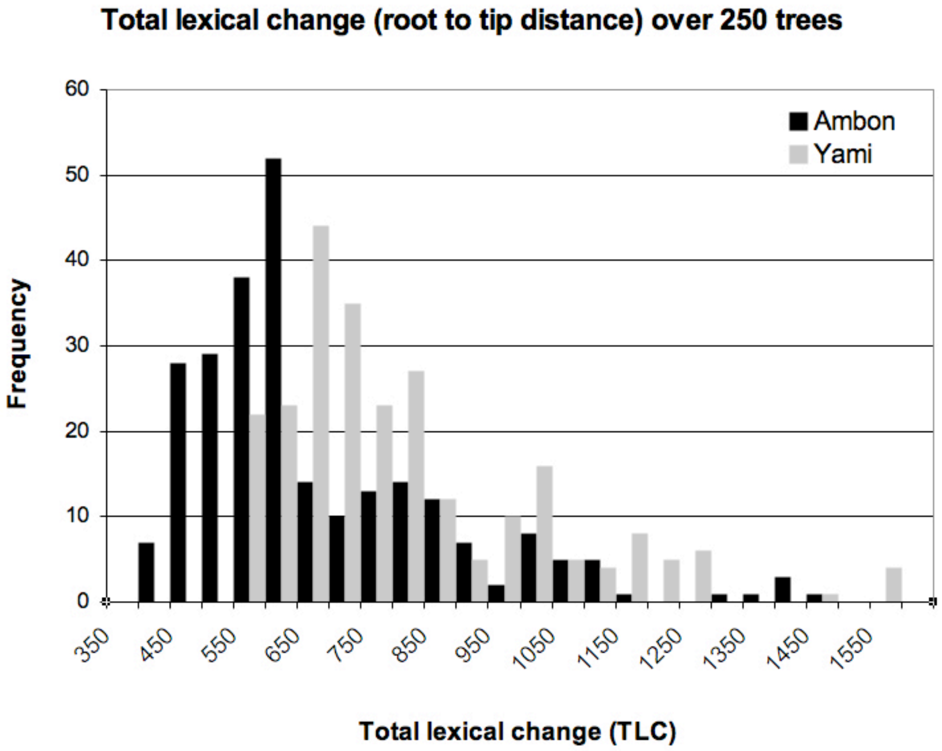


Figure 7.2. The root-to-tip distance or total lexical change (TLC), for two languages, Ambon and Yami, across a sample of 250 trees. All languages followed this slightly left-skewed distribution, showing a large number of TLC values about the mean and a few, more extreme values at the right tail of the distribution.

Table 7.1. Language groups used in the analyses. The table shows the number of speakers, the mean total lexical change of each language derived from a sample of 500 trees, mean terminal branch length (TBL) demonstrating language-specific amounts of change, and the ranking of each language in terms of amount of change (1 = highest).

Language	Number of speakers (POP)	Mean total lexical change (TLC)	Mean terminal branch length (TBL)	POP Rank	TLC Rank
Ambon[d]	15965	594.92	68	43	54
Ami	130000	697.98	129.12	22	39
Atayal	63000	996.04	129.56	27	9
Atoni	586000	661.75	69.80	11	44
Balinese	3800000	717.23	110.92	6	35
Belu	50000	597.01	69.80	32	53
Bolaang	900000	653.96	122.04	9	46
Bunun[a]	34000	711.93	129.68	36	37
Carolinian[d]	3000	827.97	77.04	60	23
Chuuk[d]	38341	844.96	77.56	35	19
Dobu[c]	10000	1038.93	85.36	50	7
Easter Is.[b,d]	2450	869.75	96.88	61	16
East Futuna[b,d]	3600	843.48	99.88	56	20
Fijian	330441	742.39	103.88	16	31
Hanunoo	11000	559.57	122.16	48	59
Hawaii[b]	1000	960.13	92.88	66	12
Iban	400000	536.13	110	15	65
Ilimandiri	150000	670.40	70.48	21	42
Ilongot	50786	810.85	121.96	31	25
Javanese[a]	75200000	806.22	111.04	1	26
Kei[d]	86000	587.99	68	26	57
Kerinci	300000	633.30	108	17	47
Kiribati[d]	58320	1138.21	79.60	29	3
Kodi	40000	720.03	72.52	34	34
Kusaie[d]	6900	1158.12	80.64	55	2
Kwaio[c]	16700	918.08	85.96	42	14
Lakalai[c]	13000	985.17	89.88	46	10
Macassarese[a]	1600000	654.57	110.56	8	45
Madurese[a]	13000000	594.27	111.04	3	55
Malagasy	88000	736.79	117.60	25	33
Malay[a]	10000000	531.18	109	4	66
Manam[c]	7000	840.30	87.44	54	21
Mangaia[b,d]	16800	896.40	94.88	41	15

Table 7.1 (Continued). Language groups used in the analyses.

Language	Number of speakers	Mean total lexical change	Mean terminal branch length	POP Rank	TLC Rank
Manggarai	500000	589.98	73.52	13	56
Manobo	12500	542.30	124.28	47	63
Maori[b]	60000	984.00	92.88	28	11
Maranao	776169	529.33	124.28	10	67
Marquesan[b,d]	3400	942.68	93.88	57	13
Marshallese[d]	43900	803.19	79.28	33	27
Mekeo[c]	25120	1002.26	87.36	40	8
Melanau	19000	540.00	117.64	38	64
Minangkabau[a]	6500000	601.56	108	5	51
Molima[c]	3186	1078.60	85.36	58	5
Mori	15000	632.73	115.44	44	48
Motu[c]	14000	790.49	87.36	45	28
Nias	480000	620.60	118.40	14	50
Niue[b,d]	2240	781.86	98.88	62	29
Paiwan	53000	543.46	130.72	30	62
Palawan	2041	597.15	123.20	63	52
Ponape[d]	27700	862.17	80.56	37	17
Pukapuka[b,d]	840	846.31	97.88	67	18
Puyuma	7225	625.65	130.76	53	49
Rotuma[d]	9000	816.70	102.88	51	24
Samoa[b]	199377	744.70	100.88	19	30
Sika	175000	571.34	70.48	20	58
Sugbuhanon[a]	14713220	558.32	122.48	2	60
Sumbanese	234000	683.66	72.52	18	41
Tahiti[b]	117000	1054.16	94.88	23	6
Tanimbarese	8000	713.04	73.32	52	36
Tannese[c,d]	2000	1158.98	86.16	64	1
Toba Batak[a]	2000000	668.34	112.92	7	43
Tonga[b,d]	103200	690.91	101.84	24	40
Toradja	500000	548.05	110.52	12	61
Trobriand[c,d]	22000	1102.31	86.36	39	4
Ulawa[c,d]	10700	740.01	85.96	49	32
Woleai[d]	1631	830.58	77.40	65	22
Yami	3000	711.36	126.12	59	38

1. Number of speakers obtained from the *Ethnologue*.
2. Total lexical change obtained by multiplying the posterior probability of change by the number of cognate changes in the data set (17464).

a: “Super-language”: population size over one million. b: Polynesian language. c: Territory/ island size less than 1000 sq km. d: “Contact” language: a language geographically situated near Non-Austronesian languages, around the coast of New Guinea.

7.4.3 Statistical tests

SPSS v.12 for Mac was used to perform statistical analyses on the language and population data. Permutation was used to assess whether these data could have given rise to the correlations merely by chance. The TLC values were randomly permuted without replacement (reshuffled) across the language taxa on 100 trees in order to gain a null distribution of correlations. A formula written in *Excel X* for Mac was used for permutation:

`SHUFFLE=INDEX(A$2:A$68,ROWS(A$2:A$68)*RAND()+1,COLUMNS(A$2:A$68)*RAND()+1)`

where data was contained in A2:A68. Correlations were then redone on these permuted data to obtain a null distribution of *R*, which could then be compared with the obtained distribution of *R* in the unpermuted data.

There was a significant negative correlation ($r = -.450$) between population size (POP) and the mean total lexical change (TLC) for each language (Figure 7.3). Thus, languages with smaller population sizes had more lexical replacement than languages with large population sizes. One outlier (Javanese) was identified and removed from subsequent analyses.

Permutation analysis created a null distribution with which to contrast the correlations of POP x TLC obtained over the 500-tree sample. In this way, differences in the TLC that are due to uncertainty in the phylogenetic reconstruction can be addressed. The permuted correlations are spread in a shallow distribution centred on zero (mean = -.01, range = -.27 – .37), none of which were significant at $p > .05$. The obtained (real) correlations cluster tightly about a mean of -.47 (range = -.39 – -.55), and all were significant at $p > .001$. There was no overlap between the two distributions (Figure 7.4). We can thus be confident that the obtained correlations are reflecting a real trend in the data and are not an artefact of using a single phylogeny.

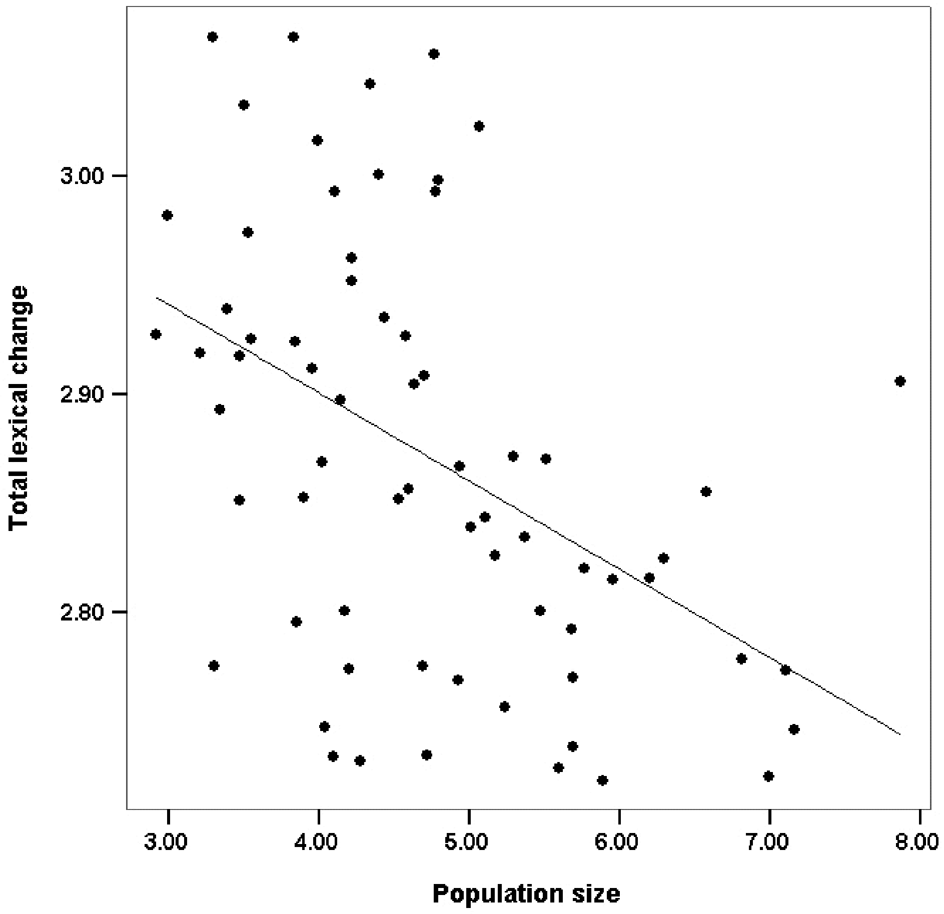


Figure 7.3. Scatterplot showing the relationship (*r* = .45, R^2 = .21) between the logarithms of mean total lexical change and language population size for all languages. TLC is the value averaged across 500 trees.

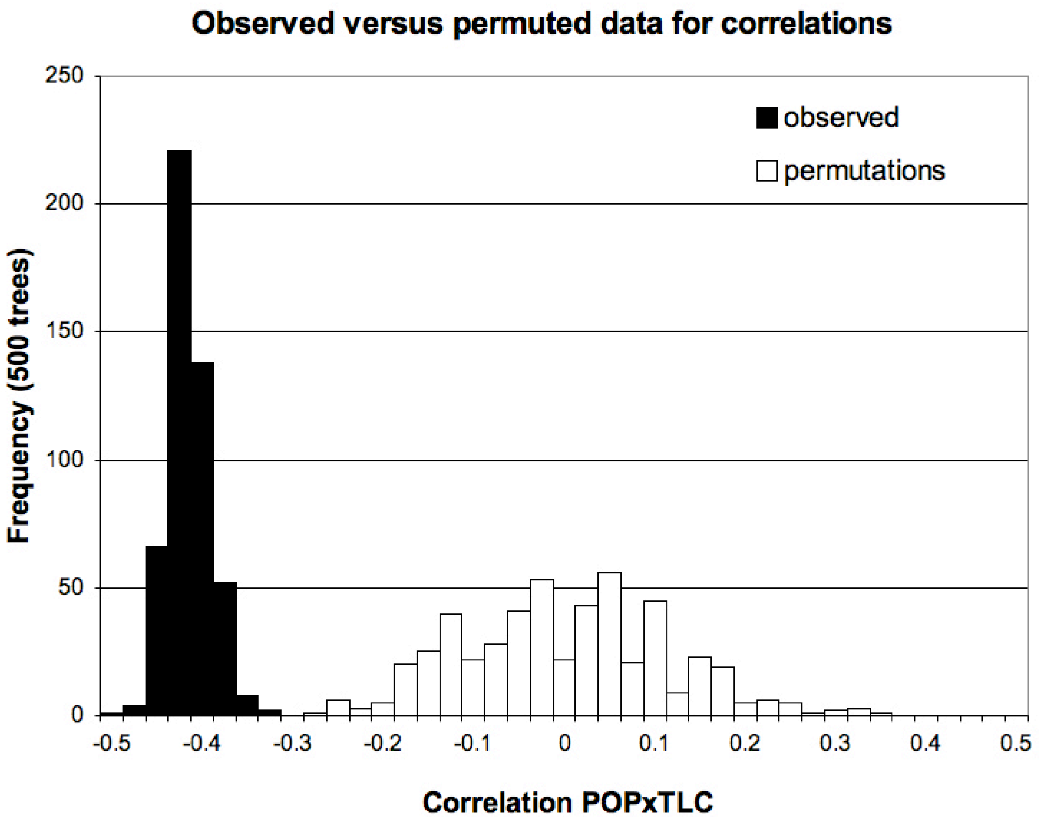


Figure 7.4. Distributions of (i) permuted data and (ii) obtained correlations between language population size (POP) and amount of lexical replacement (TLC) for each of 500 trees in the sample. All languages except the outlier Javanese were included.

Examining the plot in Figure 7.3 revealed possible sources of bias, as certain languages clustered together. On the consensus phylogeny, the Polynesian clade of languages appears to have an accelerated rate of evolution (i.e. branch lengths are longer), so it was important to examine if these languages accounted for some of the observed correlation. A further concern was that very large language population sizes might be skewing the results: subsequently, "super-languages" in Island Southeast Asia that had speakers numbering in excess of one million were excluded. Finally, those languages whose territory or island size was small were excluded. Plotting language territory size revealed a natural break at approximately 1000 sq km, so this was chosen as an arbitrary size for a "small" territory.

Table 7.2. Correlations of language population size (POP) and amount of lexical replacement (TLC). Four subsets of languages were excluded in order to test if the relationship was robust.

Languages examined[1]	**N**	**Correlation**[2] (range)	***p*-value** (range)
All languages	67	-.450	.000
		(-.549 – -.397)	(.000 – .001)
Excluding Polynesian	57	-.438	.000
		(-.543 – -.392)	(.000 – .003)
Excluding “super-languages”	58	-.422	.001
		(-.459 – -.353)	(.001 – .006)
Excluding “contact” languages	56	-.369	.006
		(-.455 – -.245)	(.001 – .066)
Excluding small territories	41	-.357	.020
		(-.453 – -.292)	(.003 – .075)

1. See text for details.
2. Correlation obtained using mean TLC followed by the range of correlations obtained over each of 500 trees.

The rank of languages in order of their TLC (Table 7.1) indicated possible alternative reasons for differential rates of language change. Ten languages were identified as being in a New Guinea contact zone of Non-Austronesian (NAN) languages; contact with languages from very different families has been suggested as a possible causal factor in accelerating lexical change in AN (Blust 1999).

Overall, correlations remained significant (Table 7.2), showing that smaller population sizes are associated with greater rates of lexical replacement. However, excluding (i) small territory languages and (ii) “contact” languages decreased the observed correlations across the range of the tree sample, with a few (<10) failing to reach significance. This implies that these languages are responsible for a noticeable part of the observed relationship.

7.4.3.1 Language-specific change

The total path length expressed by the TLC variable contains some phylogenetic structure, as any two languages may share a certain amount of that total path length. Thus, the terminal branch length (TBL) was used as a metric to quantify the amount of language-specific change, i.e. the amount of change since splitting from its final sister taxa. The branch-length table output in *PAUP** was used to find the TBL for each taxa, for 30 randomly selected trees from the Bayesian sample. The mean value of TBL for each language is listed in Table 7.2. TBL was correlated with POP and with mean TLC over a random sample of 30 phylogenies as shown in Table 7.3.

Table 7.3. Terminal branch lengths (TBL) correlated with population size (POP) and overall path length (TLC).

	Correlation (range)	**p-value (range)**
TBL x POP	.238 (.226 – .253)	.053 (.039 – .066)
TBL x TLC	**-.278** (-.287 – -.266)	**.023** (.019 – .030)

The correlation between population size and terminal branch length is moderate and reaches the .05 level of significance on slightly less than half of the trees. When it does, the relationship is positive, in the opposite direction of the correlation of population size with TLC, implying that larger populations have more lexical change. However, there is a great deal of uncertainty in this association, as it appears to be contingent on the particular phylogeny. There is an inverse and significant relationship between total path length and terminal branch length, which suggests that high overall divergence is associated with less language-specific change and/or that low levels of overall change have a greater proportion of change in terminal branches. From this, an adaptive radiation process could be inferred, with greater probabilities of change in early branches on the tree.

7.4.5 Phylogenetically controlled analyses

Conventional statistical tests have shown a correlation between population size and the overall amount of lexical change. It could be argued that population size is reduced and created anew as each language group fissions, and as such, it is a variable without a phylogenetic history. The preceding tests attempted to reduce possible confounds by excluding languages that appeared to cluster in the correlation, but we cannot be certain that this is sufficient historical control. Here, a comparative method is used to investigate any effects of phylogeny on population and language change, both separately and by testing for co-evolution.

Pagel's *Continuous* (1997) uses a generalised least squares (GLS) comparative method that investigates how continuously varying traits evolve on a phylogeny. This method is appropriate for tests of language rate and population size, as both characters vary continuously. Characters may accumulate evolutionary change with constant variance, that is, by Brownian motion, such that the number of changes is proportional to the time or distance along the branches of the tree. In assessing whether the assumption of constant variance is true for each character, *Continuous* estimates a number of parameters that reveal information about the nature of the evolutionary process. These parameters set the method aside from other comparative tests such as Felsenstein's (1985) independent contrasts (Pagel 1997). *Continuous* also allows us to test for co-evolution.

Across all taxa, each trait value can be described by a regression equation. This equation relates the total path length from root to tip of each language and the value of the trait (Pagel 1997). The beta coefficient is the "slope", and, if taxa are independent, can be estimated by a standard regression. Phylogenetic structure means that two taxa will share at least some of their total path length. If taxa share much of their total path length, they will have similar values of the trait. Therefore, the beta value must be adjusted for a specified level of non-independence. To do this, a shared variance-covariance matrix is derived from the shared path lengths over the whole phylogeny and for all pairs of species. In effect, this provides a null model of the expected proportion of covariance we expect due to phylogeny.

Continuous v.1 was used with the 67-language data set. The Nexus file of the consensus phylogeny of 1000 trees was converted to "*.pag" file format and annotated with two columns of comparative data: (i) the root-to-tip lexical changes and (ii) population size. Both variables were log-transformed in the program. Except where noted, all tests involved comparing a null (H_0) and alternative model (H_1) in a nested log-likelihood ratio (LR) test. A nested test is one where the alternative model has an extra parameter compared to the null i.e. the null is a simpler case. This test compares the goodness of fit of these models to the data. The LR statistic is calculated as $-2 \log_e (H_0/H_1)$ and is distributed as approximately χ^2 with degrees of freedom equivalent to the difference in the numbers of parameters between the two models.

7.4.6 Drift versus directional models of evolution

In this test we compare two models. The random-walk model estimates the standard constant-variance model of evolution, which is equivalent to drift. The directional model estimates an extra directional parameter that indicates if there is any trend in the value of the trait(s) from root to tips. Applied to these data, the directional model would suggest that lexical change is accumulating faster (or slower), and that population size is getting bigger or smaller.

The directional model fits the language change trait better than the constant model ($LR = 75.37$, $p = .000$, $d.f. = 1$). Thus, lexical change is not accumulating at some metronomic rate through time, but rather, it is affected by other evolutionary processes that are causing change to speed up or slow down. Population size, however, fits the simpler drift model and does not show any trend across the tree ($LR = .12$, $p = .624$, $d.f. = 1$). Large populations are not giving rise to larger ones or vice versa. When the two traits are allowed to co-vary, we can estimate the best-fit model simultaneously. Again, the simple drift model applies to the combined traits ($LR = .19$, $p = .535$, $d.f. = 1$).

7.4.7 Mode and tempo of evolution

Three informative scaling parameters can be estimated from the data. The following descriptions come from the software manual for Continuous, available at http://www.evolution.rdg.ac.uk/SoftwareMain.html.

Kappa (κ) is a parameter that scales branch lengths and can be used to infer a punctuational or gradual mode of evolution (Pagel 1997). A value of κ between zero and one implies a model where short branches have many changes, with $\kappa=0$ indicating punctuational evolution and $\kappa=1$ indicating a default gradualism, that is, change proportional to branch length. Values of κ greater than 1 mean that there is more change on long branches.

Lambda (λ) assesses the contribution of phylogeny to the model and promises to be a useful diagnostic tool for deciding which comparative method to choose (Freckleton et al. 2002). It takes a value between zero and one, where $\lambda=0$ indicates that the phylogenetic correction is not necessary for the trait (the phylogeny is effectively a star), and where $\lambda=1$ means that the trait is evolving according to the default phylogeny. Intermediate values indicate the degree to which phylogenetic history will affect how the model of evolution is estimated.

Delta (δ) detects differential rates of evolution over the course of time in the phylogeny by scaling the root-to-tip distances. A value of $\delta=1$ indicates default gradualism, while $\delta<1$ suggests that change occurred early in the tree—evidence for adaptive radiation. Values of δ greater than one thus suggest taxa-specific adaptation, that is, change occurring in the latter, possibly terminal branches of the tree.

The scaling parameters were estimated for both traits separately and then simultaneously by allowing the two to co-vary. Then, the fit of a model where they were allowed to take their maximum-likelihood estimate was compared to one where they were set to the default gradualism value of one.

Table 7.4. Maximum-likelihood estimates of three scaling parameters showing how three traits evolve on a phylogeny: population size, amount of overall lexical change, and amount of language-specific change. Significant departures (in bold) from the default gradualism model are determined by likelihood ratio tests. Parameters were estimated under the drift or directional model determined to best fit the data.

	Kappa (κ)		**Lambda (λ)**		**Delta (δ)**	
	Punctual v. gradual		Contribution of phylogeny		Early v. late change	
	ML estimate (95% C.I.)	LR test	ML estimate (95% C.I.)	LR test	ML estimate (95% C.I.)	LR test
Population size[§]	**.34** **(.00-.77)**	*LR* = 4.41 *p* = .00	**.69** **(.35-.95)**	*LR* = 3.67 *p* = .01	1.29 (.59-2.10)	*LR* = .31 *p* = .43
Total lexical change[§§]	.98 (.93-1.04)	*LR* = .08 *p* = .69	1.00 (.89->1.00)	*LR* = 0 *p* = 1	**.24** **(.00-.57)**	*LR* = 8.37 *p* = .00
POP x TLC coevolving	.98 (.92-1.04)	*LR* = .30 *p* = .44	.91 (.68->1.00)	*LR* = .93 *p* = .17	**.40** **(.15-.72)**	*LR* = 4.68 *p* = .00
Terminal branch length[§]	**.00** **(.00-.06)**	*LR* = 8.97 *p* = .00	1.00 (.98->1.00)	*LR* = 0 *p* = 1	**.05** **(.00-.22)**	*LR* = 7.03 *p* = .00

[§] Estimated under the constant-variance (drift) model. [§§] Estimated under the directional model.

Abbreviations: lang. = language, Pop. = population, LR = likelihood ratio test statistic, CI = confidence interval. All tests have d.f. = 1.

The kappa value for population size is less than one and indicates that short branches contain proportionately more changes than long branches. Thus, a punctuational model of change in population size is appropriate and makes intuitive sense. Lambda values for population are also below one, suggesting that phylogeny has a reduced effect on this trait. There is a trend towards temporally later change, shown by the delta value greater than one, but the LR test does not distinguish this trend as significantly different from the gradual assumption.

The opposite pattern is obtained for the overall language change variable. Here, the gradualism model applies to both kappa and lambda because their ML estimates are not a significantly better fit than the default value of one, indicating that phylogenetic control is important. The delta parameter suggests that most change occurs in the early branches of the phylogeny, and an adaptive radiation model is appropriate. This pattern also applies to the parameters when the traits are allowed to co-evolve together.

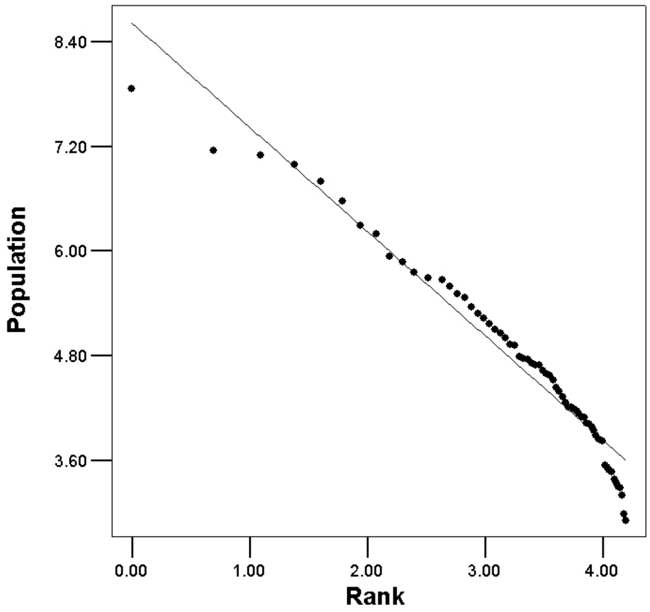
Language-specific change appears to be evolving under a punctuational model according to the kappa value of zero; the delta parameter (also zero) indicates that this change may have taken place early in the phylogeny. The lambda value suggests there is phylogenetic structure to the data, so, although most of the phylogenetic splitting may have been compressed to a short punctuational burst, closely related languages continue to evolve lexical change at the same rate in their terminal branches.

7.4.8 Phylogenetic tests of correlated evolution

We may test the hypothesis that the two traits are evolving together on the tree by comparing a model where the traits are allowed to take their ML estimates to one where their co-variances are set to zero. This is a phylogenetically controlled version of the conventional correlation in §7.4.3, removing the proportion of covariance between taxa that is due to shared path lengths on the tree. The correlation reduces from $r = -.49$ in the conventional test to $r = -.09$ with phylogenetic control. The LR test finds that this is not significantly different from a co-variance of zero (*LR* = .26, *p* = .473). The lambda estimate of population size by itself indicated that this trait does not seem to be influenced much by phylogeny and all observations could possibly be treated as independent. However, the disappearance of the significant correlation with the comparative test suggests that any concerted change in the two traits was likely caused by similarity due to descent. Correlations using the language subsets in Table 7.2 were also not significantly different from zero in all case. Similarly, there was no correlation between language-specific change (TBL) and population size (*LR* = .025, *p* = .825).

7.4.9 The power law: A null model of change

The final investigation of total lexical change and population size looked at whether these variables are distributed according to the power law. A power law equation is of the form $y = bx^a$ where b is the constant of proportionality and a is the exponent of the power law; the equation transforms to the straight line $y = ax + b$ when logged both sides. Here, both variables were ranked in order of the value of each trait. Then, the rankings and the trait values were log-transformed and plotted against each other (Figure 7.5) to find the R^2 value.



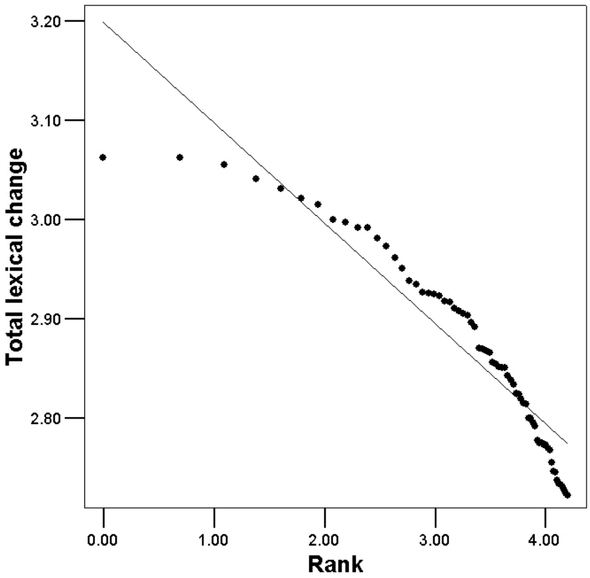


Figure 7.5. Log-log scatterplots of (top) lexical change and (bottom) population size, versus their ranks. The line represents the power law distribution. The *x*-axis plots the logged rank of the language, and the *y*-axis is the logged value.

Population size conforms most closely to the power law distribution (R^2 = .95), and holds over three orders of magnitude, although the two largest and nine smallest languages deviate noticeably under the straight line. This tells us that the largest populations are not as sizable as they "should" be, and the smallest populations are even smaller than expected. While it does not conform as closely (R^2 = .89), the same pattern holds for lexical change (TLC): the three highest ranked languages are not as innovative as the power law predicts. This may imply an upper bound on how quickly language can change. The nine least-changing languages also have lower rates of innovation than the power law predicts. In contrast, the remaining majority of languages have higher amounts of change than would be predicted. While the power law might describe the majority of the population size data, it does not appear to apply as well to the lexical change data. These results are then in accordance with the preceding analyses, which found a constant-variance model to apply to population size, but a directional and phylogenetically-dependent model to apply to total lexical change.

7.5 Discussion

> If there is some selection against language change, then language in a large community might be expected to evolve more slowly than in a smaller one. By contrast, under a neutral model of language evolution, the rate would be independent of population size. (Hurles et al. 2003: 539)

7.5.1 Findings of the present study

Conventional and phylogenetic methods were used to test for an association between the amount of lexical change in a language and its population size. Standard correlations showed a significant and robust inverse relationship, suggesting that change was accelerated in small populations. However, this demographic drift effect did not stand up to phylogenetic analysis. Using a comparative method to control for shared history, the correlation was not significantly different from zero. Accordingly, this analysis demonstrates the importance of using a phylogenetic approach in cross-cultural tests.

It is surprising that such a strong correlation disappeared. Why might this be so? Phylogenetic scaling parameters, estimated for each trait separately, indicated that there might be different sorts of evolutionary processes affecting the two traits. The lambda parameter demonstrated that the correction for phylogeny was not as critical for population as it was for total lexical change. Population size also showed no directional trend over the phylogeny, and it conformed more closely to the neutral model of random change as expressed by the power law. While it cannot be said that population size is completely independent of phylogeny, it appears to evolve here in a fairly stochastic manner. Multiple occurrences of population founder effects, such as might occur in fissioning populations and especially in the case of repeated voyaging migrations across the ocean, could be expected to produce these stochastic drift effects.

In contrast, the total amount of lexical change was strongly influenced by phylogeny. Lexical change did not tightly fit the power law neutral model, and also exhibited a directional trend in evolutionary change. We have evidence that this trend is a decline in the amount of lexical change from root to tip. The delta values for TLC and TBL show that evolutionary change is accelerated in the temporally early part of the tree, and lexical change can thus be seen under a model of adaptive radiation. This concurs with what historical linguists have called the “network-breaking” or dialect-chain model for the high-order subgrouping of Austronesian languages (Pawley 1997; Ross 1997), creating a rake-like effect in the deep structure of the phylogeny. The spread of Lapita in the archaeological record also suggests a rapid initial spread of ethnolinguistic populations into new territories, followed by a period of ongoing contact (Green 1999). In addition, if lexical change was accelerating, we should see an inverse correlation between total lexical change and terminal branch length, which is not obtained with a phylogenetic method. From this, we can infer that language innovation slows down across the tree.

If there is a dominant trend to lexical change, closely related languages will have similar values of this measure. Without phylogenetic correction, Type I errors increase, as the trend reduces the number of independent data points available for the correlation. Population size appears to have less of a phylogenetic signature, and thus, when the number of data points is reduced by a comparative test, a correlation is no longer apparent between the traits. Even if a correlation remained, it might be argued that once a population size is over a (fairly small) threshold it ceases to be an important factor in determining the rate of language evolution. Thus, while there may be more models from which a learner can sample, an individual is constrained by the size of their social network, which may maximally be in the hundreds (Dunbar 1992), and which does not grow in size proportionate to the overall population.

7.5.2 Power law distributions

The power law distribution is not a perfect representation of either lexical change or population size, although population size fits more closely. In contrast, Wichmann (2005) found that population size of languages (worldwide) deviated from the power law ($R^2 = .78$). In further work, Holman et al. (submitted) have suggested that there is disequilibrium between the process of language death in the many languages with very few speakers, and those few “mega-languages” with millions of speakers. They hypothesise that after the imminent period of language extinction for endangered languages (Nettle and Romaine 2000), there might be a reversion to a power law distribution in number of speakers. It may be that this sample of 67 AN languages differs from worldwide patterns, possibly because there are few moribund languages in the original ABV data set. The “super-languages” in the sample are a relatively recent phenomenon and have such large population sizes mainly through historical accident: their use as trade languages or lingua franca is a relatively recent phenomena. The language population sizes of Malay, Javanese, and Balinese, for example, have grown by orders of magnitude in the last 100 years (Gordon 2005).

7.5.3 Alternative explanations

If population size is excluded, and a neutral model is not applicable, other factors might moderate the rate of lexical change, such as selection, culture contact, or ecological variables.

7.5.3.1 Selection

Sociolinguistic selection mechanisms were demonstrated by Nettle's (1999a) simulation model, showing that influential, prestigious or high-status individuals can accelerate the spread of innovations throughout a population. There is variation throughout the AN world with respect to political organisation and the degree of social stratification. Historically, anthropologists have distinguished between the more egalitarian "big-man" societies of Melanesia and the presence of elaborate chiefdoms, some intricate and complex, in Polynesia (Sahlins 1958; Pawley 1982; Kirch 1984). Other stratified entities have existed in Island Southeast Asia, for example, the Makassarese and Bugis "empires" of Nusa Tenggara (LeBar 1975). Further analyses will need to tease out the relationship between social stratification and language change.

7.5.3.2 Contact

Culture contact may be an important engine of linguistic change, as suggested by recent work on pidgins and creoles—"mixed" languages that appear when two or more language communities are in close contact (Thomason and Kaufman 1988; Crowley 1997; Mufwene 2004). Previous work on AN basic vocabulary has shown that there are differences between languages in their retention of reconstructed Proto Malayo-Polynesian (PMP) forms (Blust 1981b, 2001). Western Malayo-Polynesian (WMP) languages are more conservative than the Oceanic (OC) subgroup, for example, Malay (a WMP language) retains 58 percent of basic vocabulary from PMP, while Dehu (OC) retains only 9.8 percent. As POC and PMP reconstructed basic vocabulary do not differ greatly, Blust (2001) has suggested that the more innovative OC languages have lower retention rates due to contact with Non-Austronesian (NAN) languages in the areas around New Guinea. This study found that languages that have been in contact with NAN do have higher mean TLCs, and their exclusion reduced the range and mean of the non-phylogenetic correlations. However, these languages group together in a single clade on 94 percent of the phylogenies in the sample, and excluding them made no difference to the phylogenetically controlled correlation. We require more detailed linguistic phylogenies of the region to test the hypothesis rigorously; unfortunately, language subgroups such as Papuan Tip are undersampled in the ABV database (S. Greenhill, personal communication).

As well, there are many highly innovative, or “aberrant” (Grace 1992) languages, such as Yap in Micronesia, that have *not* had significant contact with other families. Although population size was not found to be significantly associated with language change, it may be that an examination of the demographic and ecological *history* of “aberrant” languages is useful. Some areas of the Pacific have recurrent typhoons that can cause population crashes, for example, the outer islands of the Philippines and many parts of Micronesia. Other areas have recurrent volcanic activity, such as Tanna in Vanuatu, while endemic diseases such as malaria in parts of New Guinea may cause occasional but recurrent population fluctuations (Clark and Kelly 1993).

7.5.3.3 Ecology

Biocultural diversity studies have examined aspects of ecology such as land area, resource availability, and climate variables as determinants of cultural and linguistic diversity (Nettle 1998; Smith 1999; Collard and Foley 2002; Maffi 2005). Here, language population size was hypothesised to represent an “outcome” variable or “principal component” of ecological factors, following other workers who have found a relationship between environmental factors and population size (Birdsell 1953; Hainline 1965). Future work could examine ecological variables that influence culture contact, such as terrain accessibility and proximity to other islands, as these may co-evolve in some fashion with linguistic change.

7.5.4 Limitations

The data are approximate and there are discrepancies between the dates of each language population size estimate and the (possibly multiple) times of gathering the lexical data. It is likely that the population estimates are more recent than the lexical data in most cases, but probably by no more than 50–100 years (Gordon 2005)—a short space of time for any considerable change to occur. Moreover, for the date-discrepancy to have produced the non-phylogenetic correlation results, languages with high divergence ought to have preferentially decreased in population in the intervening time, while less divergent languages ought to have had a population increase. Excluding the “super-languages” controlled for the latter possibility, but it is hard to imagine a causal mechanism that might have accomplished both ends simultaneously.

Implicit in this analysis is the assumption that each language corresponds to a single population of speakers, that is, the dynamics of change in one language are not affected by the population size of that language’s geographically and phylogenetically close relatives. Marck (1985) noted that in Micronesia, a geographic distance of 100 km or less (the “overnight voyage”) was enough to maintain the mutual intelligibility of dialects. Thus, in the case of languages that are part of dialect chains or are otherwise mutually intelligible with their neighbours, the population size estimates given may be underestimates. For example, the population figure for Ponape was taken from that language’s Ethnologue entry, but as Ponape is part of a dialect network with both Mokil and Pingelap (Rehg 1984), number of speakers for those languages might also be added to that of Ponape. However, determining which languages required such attention was beyond the scope of the study, and there is no reason to believe any subsequent error would have affected the data systematically.

7.5.5 Conclusions

This study presented the first phylogenetic analysis of the effect of a demographic variable on culture change. Theoretical models of genetic and cultural evolution often find that population size has an effect on the evolutionary dynamics of a trait. Standard correlations showed an intuitively satisfying inverse relationship between the amount of lexical change in a language and population size. However, phylogenetic comparative methods reveal no co-evolutionary relationship and reduce the correlation to zero, demonstrating how important it is for cross-cultural researchers to control for shared descent in their tests.

CHAPTER EIGHT

CONCLUDING REMARKS

> [The historical sciences] all endeavour to ascend to a past state, by considering what is the present state of things, and what are the causes of change. (Whewell 1847:638)

The type of anthropology presented in this thesis is at once bleeding-edge and innovative, yet staggeringly old-fashioned. Using modern phylogenetic comparative methods from evolutionary biology to test cultural evolutionary hypotheses is a new approach to a very old problem. That problem—how to explain cross-cultural patterns of behaviour—has sadly fallen out of favour in its "home field". Yet questions of human origins and cultural diversity are inherently fascinating, and endure changes in academic fashion. Here I briefly address some of the overarching issues and themes that arise from the previous chapters.

8.1 Is a "comparative phylogenetic approach" necessary?

Should we use tree models to represent population history? Is a comparative method necessary? Justifications of the phylogenetic approach were outlined in the introductory chapters, following a critical mass of debate in the literature. In Chapter Two, we saw that it was possible to use phylogenetic methods on appropriately-coded language data and obtain results that concur closely with linguistic and archaeological hypotheses. We also saw that by using a Bayesian likelihood approach, one can estimate the uncertainty associated with any particular subgrouping hypothesis with the posterior probabilities of each internal node. As well, by using a large sample of trees that are represented in proportion to their likelihood, we remove dependence on any one particular phylogenetic hypothesis.

Chapter Four showed that different cultural traits follow different patterns of transmission on a phylogeny, with some, such as social classes, following a descent relationship with phylogenetic nearest neighbours, while others, such as crop types, follow patterns with geographic distance. We cannot make an *a priori* judgement that all cultural traits have a phylogenetic history, but we also cannot assume the inverse that they do not. As well, while broad classes of cultural traits may have a predominant model of transmission, there will be exceptions. For example, "economic" traits may be predicted by a geographic proximity model more than a phylogenetic one, but some types of subsistence practice may be phylogenetically conserved, such as the keeping of bovine domesticates.

The Bayesian methodologies introduced in Chapters Two and Three and implemented in Five, Six, and Seven show that although phylogenies are abstract models that do not capture all complex reticulate history between societies, this can be overcome by using probability samples of trees that represent different hypotheses about population history. By testing models of cultural trait evolution on these large samples, we account for phylogenetic uncertainty and allow for multiple cultural contacts. Chapter Six demonstrated that to test cross-cultural hypotheses we must control for Galton's Problem, as conventional chi-square tests returned quite different results to the phylogenetic test. For example, a conventional test would have found a positive association between matriliny and fishing, which the phylogenetic test did not support. Even if our phylogenetic model is not completely accurate, it is a better assumption than that of equal relationships or rampant reticulation. As well, the Bayesian methods make our model-testing "tree-free" by allowing us to integrate the models of cultural trait evolution over a set of trees. Chapter Seven demonstrated again that correlations, such as between language change and population size, which appear robust with conventional statistics, can disappear entirely with phylogenetic control.

8.2 Are we “butterfly-collecting”?

To say that one is “using Murdock”, that is, employing the *Ethnographic Atlas* or similar in a cross-cultural study, is an admission fraught with resigned defensiveness, sure to end with “... but it’s the best we have.” Contemporary anthropologists have developed a knee-jerk response to codified data, as exemplified by Fox, referring to attempts to establish general patterns of Austronesian descent (1995:29):

> The issue is not simply the extraordinary curiousness of these characterisations, but rather the inherent dubiousness of typologyzing in the effort of comparison ... one can describe such efforts as the equivalent of butterfly collecting and, in the case of Murdock's Malayo-Polynesian typologies, as a classification using only wing-tip colour as a critical defining feature.

Such criticisms of anthropological “typology” have existed since the *Human Relations Area Files*, *Ethnographic Atlas*, and *Standard Cross-Cultural Sample* were set up (e.g. Kobbens 1952). These bring to mind the similarly dismissive remark, commonly attributed to Ernest Rutherford, that science is only physics: all else is stamp collecting. Though the *Ethnographic Atlas* in its current form contains basic cultural data on well over 1200 societies, is coded by independent researchers without heed to any particular research question, has been corrected and updated (Gray 1999) and is clearly traceable back to the original ethnographic sources, its use often invites derision or complaint (Hartung 1983). For what reasons?

> Does one object to the isolation, codification, and cross-cultural comparison of traits in general, or is it that one objects to the *mistakes* which are made in the name of this procedure? (Harris 2001:617)

It is easy to be entirely sympathetic to arguments against cross-cultural terminologies, especially if the first lesson of undergraduate anthropology is that cultures are to be understood holistically, on their own internally relevant terms, not by comparing them one to another (Haviland et al. 2004). One must decide if descent-group concepts, classifications of the main type of marriage, or a quantitative measure of subsistence type bear any relation to the complex reality of life described by the ethnographer. My own opinion is that such terminologies, however constrained, capture some real and functional dimension of social life *more than they do not*. In this respect anthropological typologies are very much like biological categories such as “insectivores” or “tree-dwellers”; both are useful abstractions with which to build simple models. I address the appropriateness of simple models below.

Moreover, the utility of cross-cultural databases is not simply their comprehensiveness and accessibility, but is because they have been independently coded. This means that any errors—substantive or minor—in classification should appear as random noise in our analyses. While annoying, error should not bias our results in any particular way. Using primary ethnographic sources to create new variables or flesh out existing ones emphasises the need to maintain strict distance from the hypotheses to be tested. Where necessary, I referred to information on fishing practice in the literature for the analyses in Chapter Six. The depth of information can be revealing, and can also suggest alternative hypotheses for future research. Despite the lack of independent coding, supplementing databases with reference to primary ethnographic material can be very useful.

8.3 Should we use language trees?

Some criticisms of the comparative method have suggested that using language phylogenies to investigate cultural evolution may not be appropriate, because data on language and data on cultural traits might have come from different sources, or refer to different sub-populations of the same society (Boyd et al. 1997; Cashdan and Rogers 1997). While it is true that investigators should be vigilant in matching up languages with the most appropriate ethnographic description possible, the onus is on critics to provide evidence that within-society variation is so heterogeneous as to systematically bias any analyses. Like with coding error, any mismatches between language population and ethnographic population will most likely contribute random noise to an analysis, not lead to finding associations where there are none.

It may be that language trees are insufficient controls for history due to borrowing between closely-related societies (Borgerhoff Mulder 2001). Thus, their utility at a regional level may be questionable. Borrowed words can be detected using the (linguistic) comparative method, and assumptions of borrowing can be investigated in language evolution with network methods, making this an empirical hypothesis. As well, reticulation or "borrowing" is a concept that only makes sense against the background of a phylogenetic model, which acts as a null model. There must be *some* control for history; if language, or some other set of cultural traits, is not sufficient to characterise population history due to rampant borrowing, then genetic phylogenies will hardly improve the situation given how a single instance of mating can diffuse genes across populations. Even at a regional level, language is likely to be a neutral trait that is transmitted vertically more than horizontally, acting as an ethnic marker (McElreath et al. 2003), whereas other cultural traits may have adaptive benefits or transmission biases that make them more likely to be borrowed.

The Austronesian Basic Vocabulary, from which the specific language data used in this thesis is derived, is an excellent resource for comparative phylogenetic work and should be a model system for future databases. It has been collated and coded with phylogenetic *analyses* in mind, yet without heed to any specific *hypotheses* of language subgrouping or evolution. Recently, Blust, Greenhill, and Gray (2003–2007) have enlisted the help of expert Pacific linguists in adding word lists and improving cognate judgements. Particular improvements have been made to Near Oceanic and Formosan languages (R. Gray, personal communication), which will resolve the relationships and node posterior probabilities in these areas.

8.4 Are simple models justified?

Bloch (2000) notes that contemporary social anthropology has become lost in its own particularities and penchant for theorising. Thus, whilst the data used in this thesis derive from the field and theoretical work of social anthropologists, and the topic of kinship once occupied centre stage in anthropology, most social anthropologists would not recognise this work as "of their own". Most probably this is because I take an evolutionarily-informed approach, one that continues the biological tradition of using simple models and assumptions (Mesoudi et al. 2006) in an attempt to gradually build up a more complex picture of kinship and social organisation.

Many anthropologists will argue that the immense complexities and contradictions in human social life, and the dynamic nature of culture, preclude the use of any simplifying models or assumptions (e.g. Schneider 1984). Reading ethnography is especially unsettling for the comparativist's peace of mind, as the exceptions and contradictions of social life are what make for interesting anthropology—but not for simple science. However, the biological world is also of immense complexity, and this has not stopped fields such as community ecology, cellular biology, and protein synthesis from proceeding apace. They do this by being prepared to test simple hypotheses in pursuit of a more complex global picture.

One of the simple abstractions used here is treating ethnolinguistic populations—what I have generally termed "societies"—as cultural units analogous to species (Mace and Holden 2004). The "culture" as a unit of culture is a contentious issue in the broader field of anthropology (Bashkow 2004). Contemporary anthropologists would wish to emphasise the internal variability and porous (if any) boundaries of a cultural group, yet vast amounts of scholarship have been undertaken using the concept of a cultural group as a recognisable social community with some continuity in space and time.

The features used to identify such a cultural group have varied with the history of anthropology as a discipline. We now recognise that the degree of genetic variation within a group far exceeds that between groups (Lewontin 1972; Barbujani 1997), and thus no significant genetic discontinuities can be employed to define “races”. Languages avail us of a more appropriate means with which to identify cultural groups, with the caveat that (for example) a speaker of Malay is not necessarily a member of the Malay cultural group, for within Island Southeast Asia many distinct cultural groups speak Malay as a lingua franca or second language. Patterns of material culture or norms of behaviour, such as kinship reckoning may be another form by which we might recognise a cultural group (Burton et al. 1996), and it is these sorts of traits that have been the domain of systematic ethnographic comparison. Moreover, the definition of operational “groups” is not restricted to anthropology. Biologists have also had to confront the difficulties inherent in defining their operational groups, especially species (Ridley 1983). Reproductive potential (Mayr 1942), morphological differentiation, and phylogenetic relationship (Futuyma 1986) have all been used as ways to assign organisms to different species. Often the choice of species concept or operational taxonomic unit depends on the question under investigation.

8.5 The central role of kinship

Plotkin (2003:248) lamented what he called “the great cultural anthropological fallacy”: that social science should take as its program the understanding of diversity, and, because there is great diversity in human culture, there can be no commonalities. One of the commonalities that has lost out in such a program is the study of kinship. Aspects of kinship are extremely variable across cultures, yet do not even begin to approach the range of cultural variability that is possible (Murdock 1949; Fox 1967; van den Berghe 1979). Harris (2001), in the quote that prefaces this thesis, recognises that such restricted diversity demands scientific explanation. Human behavioural ecologists, working on the brass-tacks facts of “birth, copulation, and death” (Eliot

1926), have gradually built a corpus of work that provides such evolutionary explanations for some of the basics of kinship, such as polygyny (e.g. Strassman 1997) and wealth inheritance (e.g. Mace 1998). Within the framework of Darwinian analysis, such rich behavioural analyses dovetail neatly with the comparative phylogenetic approach, providing a sound experimental and/or demographic basis to any proposed adaptive hypothesis.

As a topic, the analysis of matriliny lost favour through the latter part of the 20th century, like most of the classic concerns of kinship. While matrilineal social organisation was addressed in feminist anthropology and in regional studies, the mid-century debates about lineages and kinship theory intimidated many researchers (Peters 1997). However, the evolution of matriliny can be revitalised by behavioural ecology approaches that ask questions about female-biased parental investment (Holden et al. 2003) and by the phylogenetic comparative method that lets us take a principled cross-cultural approach. In such a combined framework, the “puzzles” (Richards 1950) of matriliny are thus not about what may constitutes a lineage, nor are they as a result of male-bias towards gender issues (Schlegel 1972), but they become interesting and tractable questions about the different strategies that men and women use to maximise inclusive fitness.

8.6 Cultural evolution in the Austronesian world

The cultural phylogenetic perspective on Austronesian prehistory has allowed us to, in Whewell’s (1847) phrasing, “ascend to past states”. From the results presented here, we can sketch what early Austronesian societies may have looked like in terms of social organisation. Proto Austronesian and Proto Malayo-Polynesian societies appear to have had bilateral descent groups, only evolving lineal systems later in time and/or further from the Austronesian homeland. This conclusion sides with ethnologists such as Murdock and Kroeber, is in contrast to the predominantly “paleolinguistic” approach of Blust and Pawley, and is not in conflict with the Y chromosome and mtDNA data discussed throughout the thesis.

Ecological and internal social factors could provide possible catalysts for these changes in kinship patterns; additionally, external contact with Non-Austronesian societies, especially in the Island Melanesia regions of Near Oceania, and cultural traditions such as Islam and Hinduism in the Indonesian archipelago are equally possible as causal agents of change. Great scope exists for more detailed path analysis of the processes and conditions (including residence, as demonstrated in Chapter Six) that lead bilateral systems to change into lineal ones and vice versa. Post-marital residence was and is flexible throughout most of the Austronesian world, and even though there are many patrilocal societies, matrilocal residence appears to be an ancient and persistent feature of the family overall. Further work is required to understand the matrilineal/-local trends apparent in the region: if the best model is an adaptationist hypothesis, as explored in this thesis, or whether culture contact, phylogenetic inertia and lineage loss can also explain the distribution of matri-centric kinship systems in the Austronesian past and present.

Scholars of Pacific prehistory, most notably Kirch and Green (2001), have touted the Austronesian situation as the best-case scenario for an integrative approach combining information from archaeology, ethnography and linguistics, especially in Remote Oceania, where human populations recently settled on previously uninhabited islands and had less opportunities for casual interaction with other societies. These conditions may make Austronesian cultural diversity more suited to phylogenetic analysis than other language families or culture areas, and, in the absence of written records, may be seen as a "benchmark" for how fruitful an interdisciplinary phylogenetic approach might be. This is especially important in light of the increasing popularity of molecular anthropology as a tool for understanding prehistory, migration and diversity. Accurate inference of social and kinship structure may be necessary to reconcile discordant genetic patterns, or just as importantly, bring them into focus.

The beauty of the phylogenetic comparative approach lies not just in its elegant control for Galton's Problem, or the ability to interface with other evolutionarily-informed fields of social science, but also in the fact that the methodologies can be applied to a wide range of data and questions. Such an approach will allow for greater integration between ethnography, historical linguistics, archaeology, and genetics, enabling us to paint richer pictures of the evolution of human diversity.

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Appendix A. Data on the Austronesian societies and their corresponding languages.

Culture	Source	EA Code[1]	Geographical location[2]	Area[2]	Lat.	Lon.	SIL code[3]	ABV language[4]	Data set[5]
Ambon	EA	Ic11	Ambon Is.	Maluku	-4	128	HTU	Hitu Ambon	67/80
Ami	EA	Ia9	S.E. Taiwan	Taiwan	22	121	AMI	Central Amis	67/80
Atayal	EA	Ia1	C. Taiwan	Taiwan	24	121	TAY	Ciuli Atayal	67/80
Atoni	EGI/EWC	-	Timor	Nusa Tenggara	-10	124	AOZ	Atoni	67
Balinese	EA	Ib3	Bali	Nusa Tenggara	-8	115	BAN	Balinese	67/80
Belu	EA	Ic3	Timor	Nusa Tenggara	-9	126	TET	Tetum	67/80
Bilaan	EA	Ia17	Mindanao	Philippines	7.5	125	BPR	Koronadal Blaan	80
Bolaang	EGI/EWC	-	N. Sulawesi	Sulawesi	0	124	MOG	Bolaang Mongondow	67
Bontok	EA	Ia8	Luzon	Philippines	16	122	BNC	Bontok Guinaang	80
Bunun	EA	Ia10	C. Taiwan	Taiwan	24	121	BNN	Bunun	67/80
Bwaidoga	EA	Ig16	D'Entrecasteaux Is.	S.E. PNG	-9.5	150	BWD	Bwaidoga	80
Carolinian	EA	If15	Saipan	Micronesia	15	146	CAL	Carolinian	67/80
Choiseul	EA	Ig12	Choiseul Is.	Solomon Is.	-7.1	156	TVA	Vaghua Choiseul	80
Chuuk	EA	If2	Romonum Is.	Micronesia	7	152	CHK	Chuukese	67/80
Dahuni	EA	Ig14	Milne Bay	S.E. PNG	10	150	SWP	Suau	80
Dobu	EA	Ig5	Goulvain Is.	Massim Arch.	-10	151	DOB	Dobuan	67/80
E. Futuna	EA	Ii8	E. Futuna	Polynesia [PO]	-14	-178	FUD	Futuna	67/80
E. Uvea	EA	Ii13	East Uvea	Polynesia [PO]	-13	-176	WLS	East Uvea	80
Easter Is.	EA	Ij9	Easter Is.	Polynesia	-27	-190	RAP	Easter Is.	67/80
Fijiian	EA	Ih14	Viti Levu	Polynesia	-18	179	FIJ	Bau Fijian	67/80
Hanunoo	EA	Ia5	Mindoro	Philippines	13	121	HNN	Hanunoo	67/80

Culture	Source	EA Code[1]	Geographical location[2]	Area[2]	Lat.	Lon.	SIL code[3]	ABV language[4]	Data set[5]
Hawaii	EA	Ij6	Hawaii	Polynesia	20	-156	HAW	Hawaiian	67/80
Iban	EA	Ib1	Sarawak	Borneo	2	112	IBA	Iban	67/80
Ilimandiri	EA	Ic7	E. Flores	Nusa Tenggara	-8	123	SLP	Lamaholot	67/80
Ilongot	EGI/EWC	-	Luzon	Philippines	16	121	ILK	Ilongot	67
Javanese	EA	Ib2	Java	Java	-7	110	JAV	Javanese	67/80
Kaoka	EA	Ig20	Guadalcanal	Solomon Is.	-10	160	GRI	Ghari Guadalcanal	80
Kapingamarangi	EA	Ii7	Kapingamarangi	Micronesia [PO]	1	155	KPG	Kapingimarangi	80
Kei	EA	Ic8	Kei Is.	Maluku	-6	133	KEI	Elat Kei Besar	67/80
Kerinci	EGI/EWC	-	Sumatra	Sumatra	-2	101	KVR	Kerinci	67
Kiribati	EA	If7	Onotoa Is.	Micronesia	-2	174	GIL	Kiribati	67/80
Kodi	EA	Ic13	Sumba Is.	Nusa Tenggara	-10	119	KOD	Kodi	67/80
Koobe	EA	Ig17	New Britain	Bismarck Arch.	-6	151	WIV	Vitu	80
Kusaie	EA	If11	Kosrae Is.	Micronesia	5	163	KOS	Kusaie	67/80
Kwaio	EA	Ig18	Malaita	Solomon Is.	-9	161	KWD	Kwaio	67/80
Lakalai	EA	Ig7	New Britain	Bismarck Arch.	-5	151	NAK	Lakalai	67/80
Lifu	EA	Ih7	Loyalty Is.	New Caledonia	-21	167	DHV	Dehu	80
Luanguia	EA	Ii5	Ontong Java	Solomon Is. [PO]	-5	160	OJV	Luangiua	80
Macassarese	EA	Ic1	S. Sulawesi	Sulawesi	-5	119	MAK	Makasarese	67/80
Madurese	EGI/EWC	-	Madura	Java	-7	113	MAD	Madurese	67
Malagasy	EA	Eh2	Madagascar	Madagascar	-19	46	PLT	Merina Malagasy	67/80
Malay	EA	Ej8	Terengganu	Malaysia Pen.	5	103	MSI	Malay Bahasa	67/80
Manam	EA	Ie29	Manam Is.	N. PNG	-4	145	MVA	Manam	67/80

Culture	Source	EA Code[1]	Geographical location[2]	Area[2]	Lat.	Lon.	SIL code[3]	ABV language[4]	Data set[5]
Mangaia	EA	Ij1	Cook Gr.	Polynesia	-22	-158	RAR	Rarotongan	67/80
Mangareva	EA	Ij7	Fr. Poly. Gr.	Polynesia	-23	-135	MRV	Mangareva	80
Manggarai	EGI/EWC	-	Flores	Nusa Tenggara	-9	120	MQY	Manggarai	67
Manobo	EGI/EWC	-	Mindanao	Philippines	9	125	MBB	W. Bukidnon	67
Manus	EA	Ig9	Manus Is.	Bismarck Arch.	-2	147	TLX	Levei	80
Maori	EA	Ij2	N. New Zealand	Polynesia	-35	175	MRI	Maori	67/80
Maranao	EGI/EWC	-	Mindanao	Philippines	8	124	MRW	Maranao	67
Marquesan	EA	Ij3	Fr. Poly. Gr.	Polynesia	-9	-140	MRQ	Marquesan	67/80
Marshallese	EA	If17	Kili Is.	Micronesia	6	169	MAH	Marshallese	67/80
Mekeo	EA	Ie22	C. Province	S. PNG	-9	147	MEK	Mekeo	67/80
Melanau	EGI/EWC	-	Sarawak	Borneo	2	112	MEL	Melanau	67
Minangkabau	EA	Ib6	W. Sumatra	Sumatra	-1	101	MIN	Minangkabau	67/80
Molima	EA	Ig19	D'Entrecasteaux Is.	Massim Arch.	-10	151	MOX	Molima	67/80
Mori	EGI/EWC	-	C. Sulawesi	Sulawesi	-2	121	XMZ	Mori	67
Mota	EA	Ih1	Mota	Vanuatu	-14	168	MTT	Mota	80
Motu	EA	Ie10	Port Moresby	S. PNG	-9	147	MEU	Motu	67/80
Nias	EGI/EWC	-	Nias	Sumatra	1	98	NIA	Nias	67
Niue	EA	Ii9	Niue	Polynesia	-19	-169	NIU	Niue	67/80
Nomoian	EA	If10	Mortlock Gr.	Micronesia	5	154	MRL	Mortlockese	80
Paiwan	EA	Ia6	E. Taiwan	Taiwan	22	121	PWN	Paiwan	67/80
Palawan	EGI/EWC	-	Palawan Is.	Philippines	10	118	PLW	Palawan Batak	67
Ponape	EA	If5	Pohnpei	Micronesia	7	158	PON	Ponapean	67/80

Culture	Source	EA Code[1]	Geographical location[2]	Area[2]	Lat.	Lon.	SIL code[3]	ABV language[4]	Data set[5]
Pukapuka	EA	Ii3	Cook Gr.	Polynesia	-11	-166	PKP	Pukapuka	67/80
Puyuma	EA	Ia11	E. Taiwan	Taiwan	23	121	PYU	Puyuma	67/80
Raroian	EA	Ij5	Tuamotu Gr.	Polynesia	-16	-142	PMT	Tuamotu	80
Rennell	EA	Ii10	Rennell Is.	Solomon Is. [PO]	-12	160	MNV	Rennellese	80
Roti	EA	Ic4	Roti	Nusa Tenggara	-11	123	TWU	Roti Termanu	80
Rotuma	EA	Ih6	Rotuma	Polynesia	-13	177	RTM	Rotuman	67/80
Samoan	EA	Ii1	Manua Is.	Polynesia	-14	-170	SMO	Samoan	67/80
Sika	EGI/EWC	-	Flores	Nusa Tenggara	-9	122	SKI	Sika	67
Sugbuhanon	EA	Ia12	Cebu	Philippines	10	124	CEB	Cebuano	67/80
Sumbanese	EA	Ic9	Sumba Is.	Nusa Tenggara	-10	120	XBR	E. Sumbanese Kambera	67/80
Tahiti	EA	Ij8	Tahiti	Polynesia	-18	-150	TAH	Tahitian	67/80
Tanimbarese	EA	Ic6	Selaru Is.	Nusa Tenggara	-8	131	SLU	Kei Tanimbar	67/80
Tannese	EA	Ih10	Tanna Is.	Vanuatu	-20	168	TNN	S.W. Tanna	67/80
Tannga	EA	Ig21	Tanga (NI)	Bismarck Arch.	-3	153	TGG	Tanga	80
Tikopia	EA	Ii2	Tikopia	Solomon Is. [PO]	-12	168	TKP	Tikopia	80
Toba Batak	EA	Ib4	N. Sumatra	Sumatra	2	99	BBC	Toba Batak	67/80
Tokelau	EA	Ii6	Tokelau	Polynesia [PO]	-9	-172	TKL	Tokelau	80
Tonga	EA	Ii12	Tongatapu	Polynesia	-20	-174	TON	Tonga	67/80
Tongareva	EA	Ij10	Cook Gr.	Polynesia	-9	-158	PNH	Penrhyn	80
Toradja	EA	Ic5	S. Sulawesi	Sulawesi	-2	121	SDA	Tae Toraja	67/80
Trobriand	EA	Ig2	Trobriand Is.	Massim Arch.	-8	151	KIJ	Kilivila	67/80
Tuvalu	EA	Ii4	Tuvalu Gr.	Polynesia [PO]	-7	179	TVL	Tuvalu	80

Culture	Source	EA Code[1]	Geographical location[2]	Area[2]	Lat.	Lon.	SIL code[3]	ABV language[4]	Data set[5]
Ulawa	EA	Ig6	Ulawa Is.	Solomon Is.	-10	161	APB	Sa'a	67/80
Wogeo	EA	Ie4	Wogeo Is.	N. PNG	-3	144	WOC	Wogeo	80
Woleai	EA	If4	Woleai Is.	Micronesia	7	147	WOE	Woleai	67/80
Yami	EA	Ia14	Orchid Is.	Taiwan	22	122	TAO	Yami	67/80
Yapese	EA	If6	Caroline Gr.	Micronesia	10	138	YAP	Yapese	80

1. Source: EA, Ethnographic Atlas (Murdock 1967); EGI, Ethnic Groups of Island Southeast Asia (LeBar 1975); EWC, Encyclopaedia of World Cultures (Levinson 1991).
2. Key to geographical areas: Arch., Archipelago; Is. Island; PNG, Papua New Guinea; NG, New Guinea; S., South; E., East; W., West; N., North; C., Central; PO, Polynesian Outlier; Nusa Tenggara, Lesser Sunda Is.
3. SIL Code: Summer Institute of Linguistics code for the Ethnologue (http://www.ethnologue.com/).
4. ABV language: Language name in the Austronesian Basic Vocabulary (http://language.psy.auckland.ac.nz/austronesian/)
5. Data set: 67, present in the 67-language data set; 80, present in the 80-language data set; 67/80, language appears in both.

Appendix B. *Ethnographic Atlas* (Murdock 1967) variables recoded into dichotomous categories.

Ethnographic Atlas variable	**Recoded as:**	**Code**	**Values**
Subsistence/ecology variables			
Gathering	Gathering	S1	1 = >6% dependence 0 = 0-5% dependence
Hunting	Hunting	S2	1 = >6% dependence 0 = 0-5% dependence
Fishing	Low dependence on Fishing	S3	1 = 0-15% dependence 0 = all others
	Moderate dependence on Fishing	S4	1 = 16-35% dependence 0 = all others
	High dependence on Fishing	S5	1 = >36% dependence 0 = all others
Animal Husbandry	Low Husbandry	S6	1 = 0-5% dependence 0 = all others
	Significant Husbandry	S7	1 = >16% dependence 0 = all others
Agriculture	Low Agriculture	S8	1 = 0=45% dependence 0 = all others
	Primarily Agriculture	S9	1 = >66% dependence 0 = all others

Appendix B. (continued)

Ethnographic Atlas variable	**Recoded as:**	**Code**	**Values**
Intensity of Agriculture	Extensive or Shifting Agriculture	S10	1 = extensive or shifting agriculture 0 = all others
	Horticulture	S11	1 = horticulture 0 = all others
	Intensive Irrigated Agriculture	S12	1 = intensive irrigated agriculture 0 = all others
Major Crop Type	Tree Fruits	S13	1 = tree fruits 0 = all others
	Roots/Tubers	S14	1 = roots/tubers 0 = all others
	Grain	S15	1 = cereals grains 0 = all others
Plow	Plow absent	S16	1 = plow absent 0 = all others
	Plow aboriginal	S17	1 = plow aboriginal prior to contact 0 = all others
Type of Animal Husbandry	Absence of domestics	S18	1 = absence or near absence of large domestic animals 0 = all others
	Pigs only	S19	1 = pigs the only large animals 0 = all others

Appendix B. (continued).

Ethnographic Atlas variable	Recoded as:	Code	Values
Type of Animal Husbandry	Bovine	S20	1 = bovine animals 0 = all others
Sexual division of labour (SD): Metalworking	Metalworking present	S21	1 = males only 0 = all others
SD: Fishing	Fishing: males predominant	S22	1 = males only, appreciably more 0 = all others
SD: Agriculture	Agriculture: males predominant	S23	1 = males only, appreciably more 0 = all others
	Agriculture: labour equal	S24	1 = differentiated but equal, equal participation 0 = all others
	Agriculture: females predominant	S25	1 = females only, appreciably more 0 = all others
Dwelling: floor plan	Ground floor	S26	1 = floor formed by ground 0 = all others
	Platform floor	S27	1 = elevated platform 0 = all others
	Raised floor	S28	1 = substantially raised floor 0 = all others
Settlement Patterns	Hamlets	S29	1 = dispersed homesteads, separated hamlets 0 = all others

Appendix B. (continued).

Ethnographic Atlas variable	**Recoded as:**	**Code**	**Values**
Settlement Patterns	Compact	S30	1 = compact relatively permanent, complex settlements 0 = all others
Kinship variables			
Primary mode of marriage	Brideprice	K1	1 = brideprice, -wealth, -service, token brideprice 0 = all others
	Gift exchange	K2	1 = reciprocal gift exchange 0 = all others
	No consideration of marriage transactions	K3	1 = absence of consideration 0 = all others
Domestic organisation	Monogamous nuclear family	K4	1 = independent monogamous nuclear family 0 = all others
	Polygyny	K5	1 = all polygynous forms 0 = all others
	Extended families	K6	1 = minimal, small & large extended families 0 = all others
Monogamy and Polygamy	Monogamy	K7	1 = monogamous 0 = all others
	Polygamy	K8	1 = all polygamous forms 0 = all others

Appendix B. (continued).

Ethnographic Atlas variable	**Recoded as:**	**Code**	**Values**
Transfer of Residence: after first years	Patrilocality	K9	1 = wife to husband's group 0 = all others
	Ambi/Neolocality	K10	1 = Couple to either group or neolocal 0 = all others
	Matrilocality	K11	1 = husband to wife's group 0 = all others
Residence: alternate form	Alternate form of residence	K12	1 = some alternative form 0 = all others
Community marriage organisation	Agamous communities	K13	1 = agamous communities 0 = all others
	Segmented but not exogamous	K14	1 = Segmented communities without local exogamy 0 = all others
Largest Patrilineal kin group	Single-community patrilineages	K15	1 = patrilineages in single community 0 = all others
	Multiple-community patrilineages	K16	1 = sibs or phratries 0 = all others
Largest Matrilineal kin group	Matrilineages	K17	1 = all types of groups 0 = all others
Cognatic kin groups	Bilateral descent	K18	1 = bilateral descent 0 = all others

Appendix B. (continued).

Ethnographic Atlas variable	**Recoded as:**	**Code**	**Values**
Cognatic kin groups	Kindreds	K19	1 = kindreds 0 = all others
	Ramages	K20	1 = ramages: ancestor-oriented and exogamous 0 = all others
	Unilineal descent	K21	1 = unilineal descent groups 0 = all others
Subtypes of cousin marriage	First cousins	K22	1 = one to four of first cousin subtypes permitted 0 = all others
	Second cousins	K23	1 = no first cousins but all second cousins permitted 0 = all others
	No first, second unknown	K24	1 = no first cousins permitted, second unknown 0 = all others
	No first or second	K25	1 = no first or second cousins permitted 0 = all others
Preferred subtype of cousin marriage	Preferred subtype of cousin marriage	K26	1 = all preferences 0 = no preferred cousin marriages
Kin terms for cousins	Eskimo	K27	1 = Eskimo 0 = all others
	Hawaiian	K28	1 = Hawaiian 0 = all others

Appendix B. (continued).

Ethnographic Atlas variable	**Recoded as:**	**Code**	**Values**
Kin terms for cousins	Iroquois	K29	1 = Iroquois 0 = all others
Descent	Patrilineal	K30	1 = patrilineal 0 = all others
	Matrilineal	K31	1 = matrilineal 0 = all others
	Ambilineal	K32	1 = ambilineal 0 = all others
	Bilateral	K33	1 = bilateral 0 = all others
	Mixed	K34	1 = mixed, duolateral 0 = all others
Political			
Community hierarchy	Three levels of community hierarchy	P1	1 = three levels of community hierarchy 0 = all others
	Four levels of community hierarchy	P2	1 = four levels of community hierarchy 0 = all others
Beyond-community hierarchy	None	P3	1 = no levels beyond community 0 = all others

Appendix B. (continued).

Ethnographic Atlas variable	Recoded as:	Code	Values
Beyond-community hierarchy	One	P4	1 = one level beyond community 0 = all others
	Two or more	P5	1 = two or more levels beyond community 0 = all others
Class stratification	No classes	P6	1 = absence among freemen 0 = all others
	Wealth distinctions	P7	1 = wealth distinctions 0 = all others
	Elaborated class distinction	P8	1 = elite, dual, complex classes 0 = all others
Type of slavery	Slavery	P9	1 = any type present 0 = all others
Former presence of slavery	Former slavery	P10	1 = formerly present but not current 0 = all others
Succession to office of headman	Hereditary succession	P11	1 = patrilineal, matrilineal heir 0 = all others
	Non-hereditary succession	P12	1 = appointment, seniority, consensus, influence 0 = all others