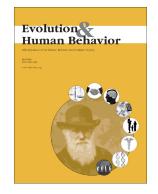
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Post-Marital Residence Patterns Show Lineage-Specific Evolution

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Abstract

Where a newly-married couple lives, termed post marital residence, varies cross-culturally and changes over time. While many factors have been proposed as drivers of this change, among them general features of human societies like warfare, migration and gendered division of subsistence labour, little is known about whether changes in residence patterns exhibit global regularities. Here, we study ethnographic observations of post-marital residence in societies from five large language families (Austronesian, Bantu, Indo-European, Pama-Nyungan and Uto-Aztecan), encompassing 371 ethnolinguistic groups ranging widely in local ecologies and lifeways, and covering over half the world's population and geographical area. We apply Bayesian comparative methods to test the hypothesis that post-marital residence patterns have evolved in similar ways across different geographical regions. By reconstructing past post-marital residence states,

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we compare transition rates and models of evolution across groups, while integrating the historical descent relationships of human societies. We find that each language family possesses its own best fitting model, demonstrating that the mode and pace of post-marital residence evolution is lineage-specific rather than global.

Keywords: Kinship; Post-marital residence; Cross-cultural comparison; Bayesian phylogenetics

1. Introduction

The decision about who will leave home after marriage and who will stay – post-marital residence – influences social structures in important ways, including inheritance of property (Leacock, 1955; Agarwal, 1988), household size (Ember, 1973; Divale, 1977), types of marriage and broader family structure (Divale & Harris, 1976). From an evolutionary perspective, investment in grand-children hinges on factors including co-residence (Sear & Mace, 2008), and differential movements of men and women on marriage even impact genetic variability in sex-specific DNA (Guillot et al., 2016; Lansing et al., 2017).

Post-marital residence states vary widely, but in ethnographically-attested societies worldwide, the most common residence pattern is *patrilocality* (Murdock, 1967), where women move to live with the family of their husband. Nonetheless, other residence practices are also common, the most frequent of which are: *matrilocality*, where women remain with their natal community, while men move; *ambilocality*, where a newly-wed couple lives with the family of either the husband or wife; and *neolocality*, where the couple establishes a new residence separate from their respective families.

Importantly, the social norms of post-marital residence that individuals and societies follow – their 'residence rules' – are not static, but change over time. Residence is heavily co-articulated with other aspects of descent, marriage and kinship, but residence itself has commonly been viewed as one of the key driving forces of broader social structure (Murdock, 1949). Consequently, explanations

for transitions in post-marital residence tend to focus mostly on external factors, and a number of theories have been proposed to explain when and why residence patterns change. These factors typically invoke major cultural disruptors; behaviours that are sufficiently common globally that they might be expected to influence residence dynamics in universal ways, such as gender-biased division of subsistence labour (Lippert & Murdock, 1931; Ember & Ember, 1971), warfare (Ember & Ember, 1971) and migration (Divale, 1974). Conversely, individual choices – of people and communities (Ly et al., 2018) – also play a role in creating these new cultural norms. Here, we set out to explore which of these views is most supported by the data.

There are multiple reasons why a community might adopt a new post-marital residence rule; for instance, ecological changes or technological developments (including transitions to agricultural, pastoral (Aberle, 1961) or wage-labour (Ember, 1967; Zhang, 2008) lifestyles) often change the gender-productivity balance (Brown, 1970), and communities may come to favour the more economically beneficial sex (Lippert & Murdock, 1931; Murdock, 1949; Ember & Ember, 1971). Modelling has suggested that these changes in residence can be evolutionarily stable (Ji et al., 2016).

Warfare can also drive post-marital residence change: war with external parties often disrupts male labour, while feuding within a community can encourage related men to cluster together for protection (Ember & Ember, 1971; Ember, 1974). Villages at war could have high death rates and thus may switch to matrilocal residence, replenishing losses by attracting men from allied villages that are not at war (Divale, 1974, 1984).

It has been suggested that matrilocal societies are more peaceful (Van Velzen & Van Wetering, 1960), with matrilocal bands perhaps acting as a frontier-advancing structure (Jones, 2011). Feuding is common in patrilocal societies (Otterbein & Otterbein, 1965; Ember & Ember, 1971; Divale, 1974, 1984), forcing them to develop explicit peacemaking mechanisms and enacting political integration to reduce infighting. This in turn leads to the linkage of patrilocal residence with the increasing political complexity of societies (Murdock, 1949;

Ember & Ember, 1971), thus presupposing a global trend towards patrilocality with the rise of polities and states. Ambilocality has been considered to be an adaptive social configuration, especially for forager or hunter-gatherer groups, who rely on a broad resource base (Marlowe, 2004) or are affected by resource instability (Kelly, 1995). While most hunter-gatherers seem to be classified as patrilocal (Ember, 1978) due to their culturally preferred residence, this might contrast with their actual social flexibility.

Finally, human behavioural ecologists have drawn attention to context-specific inclusive fitness considerations that, in aggregate, may shape community-level norms of residence (Marlowe, 2004; Wood & Marlowe, 2011; Scelza & Bliege-Bird, 2008; Kramer & Greaves, 2011). It has been proposed that paternity uncertainty influences post marital residence (Greene, 1978; Hartung, 1981), where men in situations of high uncertainty may preferentially choose to invest in their sister's children rather than their own. Disentangling inclusive fitness effects on residence from those on descent and inheritance is difficult (Holden & Mace, 2003; Mattison, 2011). Furthermore, the costs and benefits of particular residence norms may vary by the investing sex and over the course of individuals' lives (Wood & Marlowe, 2011). The extent to which such context-specific, individual-level, adaptive forces might scale up, or be generalisable, across different human groups, and thus influence macroevolutionary patterns, is still a topic of investigation.

Generic factors can affect any society. For instance, while particular instances of warfare or migration are geographically restricted, their general trends are often truly global, especially since many geographically-widespread language families have spread through demographic expansions into previously settled regions. Divale (1974, 1984) suggests that while many drivers of residence change appear essentially stochastic, they exhibit cycles of change (for instance, from patrilocal, to matrilocal, to avunculocal and back to patrilocal residence), with each residence change providing the drivers for its successor.

Regardless of the exact causes of residence change, identifying transitions in post-marital residence remains challenging, as they are often hard to ob-

serve on a human time scale and leave few direct traces in the archaeological record. While early studies of residence patterns relied on relatively underpowered association tests and correlations (Driver, 1956; Aberle, 1961; Tooker, 1968; Blalock, 1971), modern methods aim to explicitly model the evolution of post-marital residence through time. By using language trees as a proxy for historical relationships between cultures (Mace & Pagel, 1994), modern phylogenetic comparative approaches can infer ancestral post-marital residence states statistically against a background of phylogenetic divergence within language families (Currie, 2013). Past residence states, and the rates at which societies have transitioned between those different states, can therefore be reconstructed from the present distribution of post-marital residence states using a continuous-time Markov chain within a Bayesian statistical framework (Pagel et al., 2004).

However, developing methods to analyse patterns across, rather than within, language trees has proven challenging, and to date the evolution of post-marital residence has only been studied using phylogenetic comparative methods – separately – in three language families: Austronesian (Jordan et al., 2009), Bantu (Opie et al., 2014) and Indo-European (Fortunato & Jordan, 2010; Fortunato, 2011). Now, however, newly available language phylogenies and improved crosscultural analyses afford an opportunity to undertake the largest investigation of cultural evolution in post-marital residence across multiple language families.

Here, we model transitions in post-marital residence across five language phylogenies, with the aim of testing the hypothesis that a globally common set of processes has governed changes in post-marital residence states. If the processes implied by these theories of residence change operate universally, we would expect to observe similar patterns of residence evolution globally. The alternative is that individual transitions are instead driven primarily by local factors.

2. Materials and Methods

2.1. Language trees and post-marital residence data

For cross-cultural comparison of post-marital residence evolution, language families were chosen according to their size and the availability of sufficient linguistic cognate data, resulting in five language families being studied: Austronesian, Bantu, Indo-European, Pama-Nyungan, and Uto-Aztecan. Post-marital residence has previously been analysed individually for the Austronesian (Jordan et al., 2009), Bantu (Opie et al., 2014) and Indo-European (Fortunato & Jordan, 2010; Fortunato, 2011) language families, whose phylogenies and post-marital residence state encodings were obtained from the authors.

For the Uto-Aztecan and Pama-Nyungan language families, a literature search was performed to determine the primary social norm of post-marital residence for each language community (see Supplementary Material for details). The Uto-Aztecan language tree was obtained from Ross and colleagues (Ross et al., In prep.), while Pama-Nyungan language data were obtained from the Chirila database (Bowern, 2016) and re-analysed with BayesPhylogenies v 1.1 (Pagel & Meade, 2004) running for 10^7 generations using the m1p model, in which cognates are lost and gained at the same rate. Trees were pruned to contain only languages with known residence states. Due to the absence of calibration points, chronological trees were not obtainable for all language families, and tree branches were scaled by the number of cognate substitutions. A posterior tree sample (500 < n < 1000) was used for all language families, with variation dictated by the availability of posterior samples for published trees. A summary of residence states observed for each language family is given in Supplementary Table 1. Schematics of the distribution of residence states in the five trees are presented in Figure 1.

2.2. Transition rates

Some authors (Murdock, 1949; Divale, 1974, 1984) suggest that there may be strong directionality in post-marital residence transitions and thus that some

transitions may not occur at all or only at much lower frequency. Given this possibility, Reversible Jump Markov Chain Monte Carlo (RJ-MCMC) was explicitly chosen to fully explore the complex model space. This method aims to reduce the number of parameters by dynamically setting some to zero, or grouping them under a single governing parameter (e.g., setting all transitions to a single universal rate). Importantly, RJ-MCMC can explicitly test the level of evidence for different patterns and directions of post-marital residence change, which is a feature we exploit below.

BayesTraits v 2 (Pagel & Meade, 2006) was used to calculate the transition rates. Five independent trials of MCMC, each with 10^8 steps, were performed for each language family with a sampling frequency of 10^4 and an exponential prior for the frequency of residence transitions $\text{Exp}(\lambda)$. λ was distributed according to the hyperprior $\frac{1}{\lambda} \sim \text{U}(0,200)$ for all datasets except Pama-Nyungan, for which the hyperprior was defined as $\frac{1}{\lambda} \sim \text{U}(0,400)$. These values were chosen from initial maximum likelihood estimates. The convergence of the MCMC runs was explored using convergence tests implemented in the R package coda v 0.18-1 (Plummer et al., 2006), and posterior distributions were inspected and summarized using R v 3.3.2 (R Core Team, 2017).

To determine whether each language family has its own mode of evolution, we tested each tree to ascertain whether the transition matrix from any other tree was as good a fit or better to its data. To do so, we calculated the likelihoods of observed residence states for a particular language family tree given the rate matrices of each other language family. From these likelihoods, Bayes factors were calculated by comparing the fit of the original rate matrix with rate matrices estimated from all of the other datasets in pairwise fashion. These values indicate whether the likelihoods are significantly different.

2.3. Simulations

To place rates in a more easily interpretable context, we simulated the number of residence changes on each language tree as defined by its unique transition matrix. Following Huelsenbeck and colleagues (Huelsenbeck et al., 2003) and

using the R package phytools v 0.5-64 (Revell, 2012), 5000 SIMMAP simulations of residence evolution were run using the mean rate transition matrices for each tree. Step-by-step transitions between pairs of states with respect to branch lengths on the maximum clade credibility tree were inferred using the rate ma- $\operatorname{trix} Q$, as estimated by Bayes Traits. Transitions were generated by first drawing time from an exponential distribution according to the diagonal elements of the matrix, followed by choosing the type of transition with probability proportional to its rate. The probability of transitioning from residence state s_i to state s_j is defined as $\Pr(s_i \to s_j) = \frac{q_{ij}}{\sum_{k \neq i} q_{ik}}$, where q_{ij} is the rate of switching from state i to j. In other words, probabilities were normalized by the rate of change from the current state s_i to any other state. Estimates of the time to each transition were sampled from an exponential distribution parametrized by the negative of this normalization factor, and samples were drawn until the branch length was reached. To save computation time, instead of sampling from the posterior distribution of the rate matrix calculated by BayesTraits, the posterior distribution was summarized by the mean rate matrix Q, which accounts for zero values in the RJ-MCMC. The total number of simulated transitions in each language family was then normalized by the number of language substitutions (i.e., the total branch length of each tree).

2.4. Scaling dynamics

To test how post-marital residence evolves relative to language branch lengths, a scaling parameter κ (Pagel, 1999) was added to the length of tree branches, such that $t_{\rm new} = t_{\rm old}^{\kappa}$. If $\kappa \approx 1$, then the branch length reflects the evolution of post-marital residence, while $\kappa > 1$ or < 1 indicate that longer branches are scaled more than shorter branches. At the extreme, $\kappa = 0$ would suggest that there is no relationship with branch length, and thus post-marital residence would evolve independently of the branches on which changes are observed to occur (i.e., cultural change would be independent of linguistic change).

3. Results

Our analysis focuses on five language families where data are sufficient to explore the evolution of post-marital residence: the previously reported Austronesian (Island Southeast Asia and the Pacific), Bantu (Sub-Saharan Africa) and Indo-European (Eurasia), together with new data for Uto-Aztecan (West-ern USA and Mesoamerica) and Pama-Nyungan (Australia) (for a overview of residence states in these datasets, see Supplementary Table 1). Cumulatively, these languages cover over half the world's population and geographical area (see Supplementary Figure 1). Several of these language families have been associated with Neolithic farming expansions, and they include communities that currently are, or were until very recently, farmers, foragers or pastoralists, with a geographic range from the tropics to temperate regions, and from islands to continents.

We assigned ethnographically observed states of residence pattern norms to contemporary ethnolinguistic groups (Figure 1). To begin, we tested whether language trees with branches scaled by cognate changes are appropriate for analysing post-marital residence. Branch lengths reflect observed language change and are a proxy for evolutionary time. We rescaled branches using Pagel's κ (Pagel, 1999) to measure the extent to which the observed branch lengths can be rescaled without changing the variability in residence patterns. This simple metric scales all branch lengths by raising them to the same exponent, κ . A value of κ close to zero would suggest that a model with all branches the same length would fit the residence data better; a value close to one provides justification for the current model; while higher values of κ make the tree more star-like, which would mean that the branches effectively have independent random lengths. While inferred κ values (Supplementary Table 9) have large credibility intervals, they strongly centre around 1, supporting the hypothesis that language trees with branches delimited in shared cognates provide a robust basis for inferring post-marital residence change.

From the trees (Figure 1), it is clear that residence patterns vary widely,

even among groups that speak closely related languages. Even a cursory examination suggests great variation in the underlying processes; for instance, not all residence states are found in every language family. Estimated rates of transitions between residence states also indicate differences between language families (Table 1, Supplementary Table 2), with comparatively little change in Bantu in contrast to frequent change in Pama-Nyungan.

Figure 2 further suggests that patterns of residence change differ between language families. To explicitly test this, we fitted the estimated mean rate matrix for a given tree to every other tree and calculated the likelihood of the fit to the observed residence data. In each case, the tree's own rate matrix fitted significantly better than the rate matrix from any other language family (see Supplementary Table 3 and Supplementary Table 4).

The best statistical support for residence transitions in the language trees occurs from patrilocality to matrilocality, and back. The Uto-Aztecan tree is interesting because there is strong evidence against most directions of residence change (Supplementary Table 2). A benefit of RJ-MCMC, as mentioned previously, is that all directions of change are tested explicitly in our models.

SIMMAP (Huelsenbeck et al., 2003) simulations of residence transitions using the observed rate matrices provide additional insight into patterns of change (Supplementary Table 5). In all datasets except Bantu and Uto-Aztecan, several transitions are typically seen to occur along each individual branch. Bantu and Uto-Aztecan are exceptions because estimated rates of residence evolution are low and the number of languages in the tree is small, respectively.

To place these values within a more intuitive conceptual framework, we can make 'back of the envelope' estimates of how these changes map on to the approximate time depth of each language family (Supplementary Table 6). If we assume that the families studied here (or the parts of them represented in the trees) are somewhere around 4,000 to 7,000 years old, post-marital residence transitions seem to have occurred once along any given lineage every \sim 425 years in the Austronesian and Indo-European trees and every \sim 1280 years in the Bantu tree (see Supplementary Material). The similar estimates for

the Austronesian and Indo-European language families are striking, given that they differ in many key aspects, such as age, magnitude of residence rates and amount of language change. However, the less well-studied Pama-Nyungan and Uto-Aztecan language families give a wider range of values (Supplementary Table 6). More rapid changes in residence in the Pama-Nyungan family might be explained by the fast demographic spread of the language family through Australia, quickly colonizing a wide range of ecological regions (Bouckaert et al., 2018), as well as the social flexibility of indigenous Australian groups, as evidenced by the rapid spread of 'section' kinship systems (Dousset, 2005).

Across all the trees, there is a tendency for patrilocality to be the most common and persistent state, both from the perspective of simulated transition rates and the time spent in each residence state. 64% of communities are patrilocal, and unlike matrilocality, ambilocality or neolocality, patrilocality appears in all five language trees. The importance of this residence state can be measured by comparing estimated transitions to and from each residence state (Supplementary Table 7), with patrilocality acting as a culturally favoured state (Ji et al., 2016).

Patrilocal residence may stabilize a set of social-structural axes by centralizing both authority and the inheritance of property; for instance, in many matrilocal and/or matrilineal societies, women's brothers still act as heads of household over many decisions (Richards, 1950; Schneider, 1961; Schlegel, 1972; Divale & Harris, 1976). This apparent conflict between descent and decision power was termed the matrilineal puzzle by Audrey Richards (1950) (reviewed by Mattison, 2011). However, this does not mean that matrilocality is necessarily unstable or non-favoured (see review by Mattison, 2016), as it is still the second most common state in the Austronesian and Bantu trees. Transitions from matrilocality to patrilocality, and back, and the generally low frequency of ambilocality, suggest that the primary role of ambilocality is not simply as an intermediate state. While ambilocality can occur when the frequency of patrilocal and matrilocal marriages is similar (see Murdock (1949) and Goodenough (1956) for field examples), our analyses predominantly support the role

of ambilocality as a separate functional state with its own dynamics.

As with transition rates, exploring post-marital residence change through time using SIMMAP simulations (here measured in terms of language change) suggests that patrilocality is cumulatively the most common state, found almost 90% of the time in Pama-Nyungan to around half the time in Austronesian and Uto-Aztecan (Supplementary Table 8). Matrilocality is the next most common residence state, but does not occur at all in the Indo-European family. Neolocality also occurs reasonably often, but the length of time spent in this state is usually short. The exception is Indo-European, where societies are estimated to have spent 23% of their time practising neolocality, which is comparable to the time spent in ambilocal or matrilocal residence in other language families. An unusually high rate of switching is observed from patrilocality to neolocality in Indo-European (Table 1), in line with findings that suggest a special role for neolocality as an alternative residence strategy in Indo-European prehistory (Fortunato, 2011).

Other cultural dynamics unique to particular language families are observed. For instance, transition rates are inferred robustly for Bantu, but are relatively infrequent, as is clear by visual inspection of the tree (Figure 1). This suggests that there were surprisingly few switches between residence states compared to the other language families in our dataset, which is especially interesting as the Bantu tree is relatively large (here, 120 languages), and yet using SIMMAP simulations parameterized on the transition rate matrix, only 20–36 transitions between residence states were inferred, compared to 255–351 transitions in the Austronesian tree (134 languages). The Austronesian tree also shows evidence for all twelve possible transitions between the four residence states, a property it shares only with the much smaller Uto-Aztecan tree (25 languages). At the other extreme, the Pama-Nyungan tree only exhibits two residence states, patrilocality and matrilocality. However, in contrast to the Bantu tree, a very fast rate of residence change was estimated for Pama-Nyungan, even though relatively few transitions appear on visual inspection of the tree (Figure 1).

4. Discussion

The analyses presented here represent a new design for tests of evolutionary and cross-cultural hypotheses using cultural phylogenetic methods. Examining the dynamics of post-marital residence in five language families has been made possible by nearly two decades of innovation in the study of language variation via phylogenetic modelling (Gray & Jordan, 2000; Gray et al., 2009; Grollemund et al., 2015; Kolipakam et al., 2018). This approach is further enabled by recent moves to make these language trees, as well as cultural and environmental datasets that map to the relevant ethnolinguistic groups, openly available via resources such as D-PLACE (Kirby et al., 2016) and others. When hypotheses speak to the evolution of human behaviour as a whole, we urge other researchers to test their ideas across multiple language families. Phylogenetic methods circumvent old qualms about Galton's Problem (e.g., Ross & Homer, 1976; Mace & Pagel, 1994; Korotayev & Munck, 2003), and when these modern computational approaches are combined with spatial and environmental data, this approach re-enables the use of global cross-cultural data to inform our understanding of the processes that drive cultural evolution.

In the specific context of post-marital residence, transitions between residence states have been associated with many different factors, such as intense warfare (Ember & Ember, 1971; Divale, 1974, 1984), prolonged male absence (Murdock, 1949; Korotayev, 2003; Ember, 2011), sudden depopulation (Murdock, 1949; Ember, 1967, 2011), changing economic conditions (Murdock, 1949; Ember, 1967), new technological developments (Murdock, 1949; Ember, 1967), inclusive fitness considerations such as paternity certainty and kin altruism (Shenk & Mattison, 2011), post-colonial contact (Ember, 1967; Korotayev, 2003), and even the spread of new dominant cultural practices, like religions (Goody, 1983; Fortunato & Archetti, 2010). However, the most influential theories for macro-evolutionary patterns have emphasized warfare (Ember & Ember, 1971), migration (Divale, 1974) and changes in the gender-based division of subsistence labour (Lippert & Murdock, 1931; Murdock, 1949; Ember

& Ember, 1971), all of which are commonly observed globally. As with previous studies that have used phylogenetic comparative methods (Jordan et al., 2009; Fortunato & Jordan, 2010; Opie et al., 2014), we do not attempt to model these putative causal factors directly, but instead employ a probabilistic model that treats transitions in post-marital residence states as a stochastic process with many possible causes. We recognize, however, that not all transitions were necessarily independent; for example, contact with Papuan groups was likely an ongoing driver of the switch to patrilocality among Austronesian-speaking groups (Jordan et al., 2009), and Christianity changed the nature and form of family structures in Europe (Goody, 1983), crossing deep relationships in the Indo-European language tree. Both speak to contact-induced versus internally-driven change. The patterns of post-marital residence that we observe likely represent the cumulative outcome of many interlinked processes, and detailed coevolutionary testing has the potential to tease many of these factors apart in the future.

Overall, our results provide strong evidence that each language family has its own unique dynamics of post-marital residence change, providing little support for the view that common factors have driven similar processes of change in residence states globally. Instead, the evolution of societies seems to be dominated more by local causes, potentially including common factors acting within locally specific contexts. This is especially apparent from estimates of transition rates, presence/absence of residence states and different patterns of robustly inferred rates, all of which vary widely among the language families. Even groups with similar historical trajectories, such as the rapid agriculturallydriven expansions of Bantu and Austronesian speakers, show very different past and modern patterns of post-marital residence. These findings echo the lineagespecific patterns observed for linguistic structural features, such as word order (Dunn et al., 2011). Far from arguing for global commonality in the processes underlying post-marital residence change, these results lend support to the idea that a suite of causal factors, many perhaps local in origin, have driven past shifts in post-marital residence.

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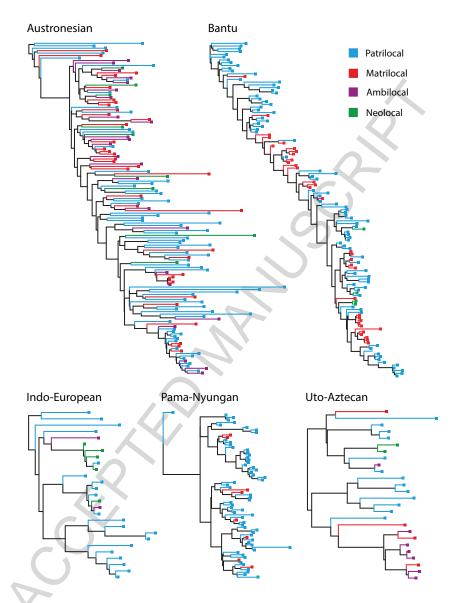


Figure 1: Ethnographic observations of post-marital residence states mapped on to five language trees: Austronesian, Bantu, Indo-European, Pama-Nyungan, and Uto-Aztecan. Terminal branches are coloured according to the main post-marital residence state recorded for each society. Branch lengths of each maximum clade credibility tree are drawn proportional to the number of observed lexical substitutions. To show the residence states clearly, trees are not drawn to the same scale.

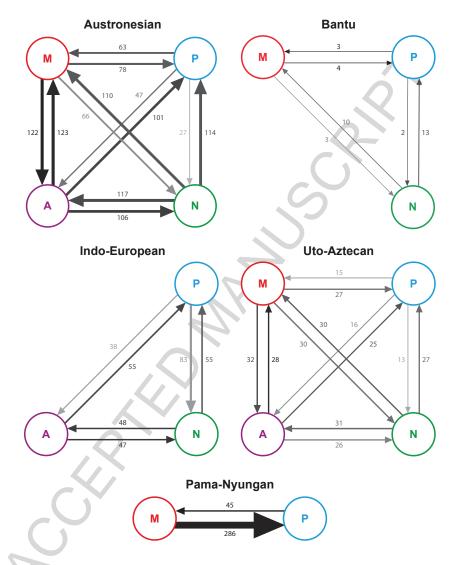


Figure 2: Graphs showing transition rates between post-marital residence states for each language family. M, matrilocality; P, patrilocality; A, ambilocality; N, neolocality. Arrow weights indicate mean transition rates inferred from the analysis (with values shown adjacent), while shading indicates how frequently the rate is inferred to be zero (lighter shades indicate less certainty). Node colours indicate post-marital residence states, as in Figure 1.

Table 1: Rates of transitions between post-marital residence states. Means and 95% credible intervals are reported (rounded to the nearest integer); dashes indicate transition states that are not observed in a given language tree. Note that zeros were removed from each distribution and are reported separately (see Supplementary Table 2).

	Aust	Austronesian	Be	Bantu	Indo-E	Juropean	Pama-	Indo-European Pama-Nyungan	Uto-A	Uto-Aztecan
	mean	95% CI	mean	mean 95% CI	mean	95% CI	mean	95% CI	mean	mean 95% CI
$ambi \to matri$	123	(10; 292)					1		28	(2;72)
$ambi \to neo$	106	(10; 267)	ì		47	(0; 185)	I		26	(2;70)
$\operatorname{ambi} \to \operatorname{patri}$	101	(8; 220)	I		55	(0; 235)	I	l	25	(2;57)
matri→ambi	122	(18; 283)	I	ı		7	I	I	32	(2;79)
matri→neo	99	(6; 218)	3	(1; 6)	I		1	l	30	(2;78)
$matri {\rightarrow} patri$	78	(8; 201)	4	(1; 12)	I		286	(1;801)	27	(2; 71)
neo \rightarrow ambi	117	(9; 292)	I	I	48	(0; 188)	5	C	31	(2;78)
neo \rightarrow matri	110	(9; 295)	10	(1; 51)	I		1		30	(2;77)
neo →patri	114	(9;291)	13	(1;76)	55	(0; 258)	I		27	(2;69)
$patri \rightarrow ambi$	47	(7; 129)	I	I	38	(0; 185)	I	1	16	(1;40)
$patri \to matri$	63	(6; 172)	33	(1; 5)	I		45	(1; 131)	15	(1; 42)
patri →neo	27	(5; 71)	2	(0; 5)	83	(0;334)	I	I	13	(1;34)
mean	88		9		54		165		25	

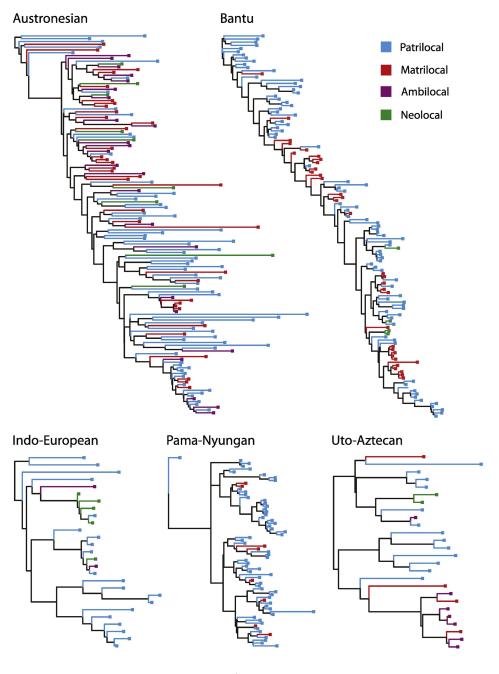


Figure 1

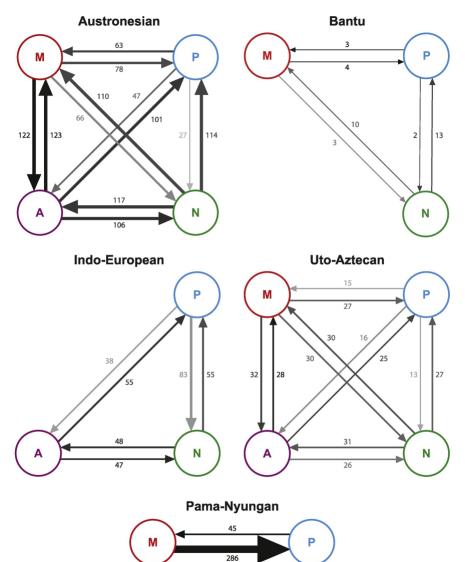


Figure 2