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A Phylogenetic Approach to Comparative Linguistics: a Test Study using the Languages of Borneo

Abstract

The conceptual parallels between linguistic and biological evolution are striking; languages, like genes are subject to mutation, replication, inheritance and selection. In this study, we explore the possibility of applying phylogenetic techniques established in biology to linguistic data. Three common phylogenetic reconstruction methods are tested: (1) distance-based network reconstruction, (2) maximum parsimony and (3) Bayesian inference. We use network analysis as a preliminary test to inspect degree of horizontal transmission prior to the use of the other methods. We test each method for applicability and accuracy, and compare their results with those from traditional classification. We find that the maximum parsimony and Bayesian inference methods are both very powerful and accurate in their phylogeny reconstruction. The maximum parsimony method recovered 8 out of a possible 13 clades identically, while the Bayesian inference recovered 7 out of 13. This match improved when we considered only fully resolved clades for the traditional classification, with maximum parsimony scoring 8 out of 9 possible matches, and Bayesian 7 out of 9 matches.

Introduction

“The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel… We find in distinct languages striking homologies due to community of descent, and analogies due to a similar process of formation… We see variability in every tongue, and new words are continually cropping up; but as there is a limit to the powers of the memory, single words, like whole languages, gradually become extinct … To these more important causes of the survival of certain words, mere novelty and fashion may be added; for there is in the mind of man a strong love for slight changes in all things. The survival or preservation of certain favoured words in the struggle for existence is natural selection” (Darwin, 1871). The conceptual parallels between biological evolution and linguistic evolution have been noticed since the advent of modern (Darwinian) evolutionary theory itself, nearly a century and a half ago. Languages, like species, are a product of change and evolution. They chronicle their evolutionary history in a similar way to how genes record our own evolutionary past. Just as genes are replicated and inherited, so too are the sounds, grammar and lexicon of a language learnt and passed on. Just as mutations and natural selection lead to variable populations and species, so too do shifts, innovation and societal trends lead to different dialects and languages. And just as phylogenetic inference may be muddied by horizontal transmission, so too may borrowing and imposition cloud true linguistic relations. These fundamental similarities in biological and language evolution are obvious, but do they imply that tools and methods developed in one field are truly transferable to the other? Or are they merely clever and coincidental analogies paraded by those attempting to Darwinize language and culture?

Recently, there has been a flux of studies applying phylogenetic methods to non-biological entities, particularly languages (see Gray & Jordan 2000; Holden 2002; Rexová et al 2002, 2006; Forster & Troth 2003; Gray & Atkinson 2003; Nakhleh et al 2005; Holden & Gray 2006; Atkinson et al 2008; Gray et al 2009; Kitchen et al 2009). This employment of computational statistics to infer evolutionary relatedness is standard in its home field of biology, but relatively new to historical linguistics. Somewhat surprising, given that similarities in their two respective processes of evolutionary change have been noted as far back as Darwin; but the conservativeness in applying such (phylogenetic) approaches to linguistic data is justifiable. According to critics (Gould 1987, 1991; Bateman et al 1990; Moore 1994; Belwood 1996; Borgerhoff Mulder 2001; Holden & Shennan 2005; Temkin & Eldredge 2007), phylogenetic methods based on tree-building algorithms may not be truly applicable to linguistic data. In particular, it is frequently argued that horizontal transmission of traits is relatively common in language evolution and that this violates the assumptions of traditional (tree-building) phylogenetic methods (Gould 1987; Terrell 1998; Moore 1994; Terrell et al 2001). Instead of a tree model of languages, a network model or wave model may be more appropriate. This is a valid argument and has to be addressed before any further advance on cross method application can be made.

(1) **Conceptually**, a general theory of evolutionary change, one that encompasses biological evolution, language evolution, cultural evolution and any other phenomena indicative of evolutionary change, is needed (Croft 2008). Several models attempting to do so have been developed, most notably those by Dawkins (1989, 1982), and Hull (1988, 2001). The key features to these generalized theories of evolution are that they generalize and incorporate the three most fundamental processes; that of (a) cumulative and iterative replication (leading to inheritance), (b) the generation of variation during replication, and (c) the selection of variants via some selective mechanism. The encompassing quality of such a model serves to clarify and standardize the analogies present in the constituent fields, allowing for a clearer framework for comparison and interdisciplinary method application.

(2) **Analytically**, the degree of horizontal transfer should be determined using network visualisation tools, such as SplitsTree (Huson & Byrant 2006), which do not assume a tree-like model of evolution. Only on the condition of no significant reticulation should further phylogenetic methods (based on tree-building) be considered.

Following these two criteria should support in determining both the applicability and validity of using phylogenetic methods on linguistic data. In this study, we will be testing such an approach on a subset of languages from Borneo. Given that no significant reticulation is seen, we will be testing the applicability and accuracy of three common phylogenetic methods on our linguistic data set: 1) Split Decomposition and Neighbor Net distance-based network algorithms, 2) weighted and unweighted Maximum Parsimony and 3) Bayesian Inference. The accuracy of the methods will be tested by comparing their results with those established from traditional methods.

There do of course exist some other differences between biological and linguistic evolution; for example, languages change much faster than genes and selection of favoured variants is determined by societal trends rather than fitness difference among alleles; however none of these differences are fundamental to a general theory of evolutionary change (e.g. of Dawkins 1982, 1989; Hull 1988, 2001). For instance, the former merely entails a restriction of (phylogenetic) inferences to more recent timeframes, while the latter, a superficial difference function-wise.

Table 1. Biological versus language evolution

	Biological evolution	**Linguistic evolution**
Discrete (homologous) characters	Nucleotides, genes, codons, morphological characters	Semantic categories (word cognates), grammar*, phonology*
Replication	Transcription, replication	Learning, imitation
Mutation	Sequence mutations via mutagens, transposons, radiation, viruses, faulty replication, etc	Innovations, phonological shifts, vowel shifts, mistakes
Selection mechanism	Ecological selection, sexual selection, fitness differences among alleles	Social trends/pressures
Horizontal transmission	Horizontal gene transfer via transduction (viruses), conjugation (bacterial), transformations, transposons. Hybridisation	Borrowing, contact, imposition. Pidgin/Creole languages

**referring to the discrete structural/typological aspects of these feature classes*

Traditional Methods

In the traditional comparative method, languages are classified under a system not too unlike that of cladistics; the chief feature being that languages are grouped according to exclusively shared linguistic innovations (synapomorphies) (Hoenigswald 1960). Additional key aspects to this approach are the reconstruction of a proto-language (ancestor) and a restriction on homoplasies (both back mutations and parallel innovations). This method is extremely powerful and well supported (the procedural norm in comparative linguistics), but qualitative (e.g. no explicit optimality criterion) and time consuming. An alternative and more quantitative method appeared in the 1950s, coined lexicostatistics. It employs an approach more closely related to that of phenetics in biology, in that languages are correlated based on the percentage of their sample lexicon subset being cognate - a distance measure. This technique is relatively much quicker to perform but comes with its fair share of critics; its major weakness, as with phenetics, is that it relies upon derived (pair-wise distances) rather than real (character) data, which inevitably results in a loss of information. Additionally, many (e.g. Hoijer 1956; Gudchinsky 1956) have shown that it is often difficult to consistently find equivalents to the semantic items across varying sets of languages, confounding the validity of a universal lexicostatistic list (such as the Swadesh list).

Methods & Materials

In this study, we attempt to merge the fundamental concepts of the traditional comparative method with the quantitative character (but not procedure) of lexicostatistics, primarily via the methods of maximum parsimony and Bayesian inference (which are character-based and quantitative). We seek to find out how applicable and accurate such methods can be when applied to an example linguistic data set.

1. Characters

Our study uses lexical characters to characterise linguistic information. Lexical characters here are represented by word *cognates* (literally blood relatives –Latin). These are words that demonstrably, via systematic sound correspondences, historical records and the Comparative Method derive from a common ancestor, and thus represent homologous characters akin to those in biology. The use of lexical characters has been well supported and established in comparative linguistics, and given that we adhere firmly to the criterion of using only basic vocabulary, is well suited in determining relationships that are genetic rather than due to chance or contact and borrowing. As they are relatively fast changing (Greenhill et al 2010), they also represent the most suitable unit of linguistic change for our dataset; which is one of fairly close relation (Western Malayo-Polynesian subfamily). Two other types of characters, phonological and morphological (grammatical) were also considered, but later discarded due to lack of data[1] for our set of languages. Ideally they should be included; they represent different and additional aspects of language change and can thus provide additional resolution and information at different time depths than can lexical characters, but the lack of available data and time precluded this measure.

2. Cognate Judgment

As cognates represent the characters of our data set, their correct judgement is fundamental to acquiring good results. The process of cognate judgment is thus not a trivial one. Judgement can be subjective and dependent on good historical records; for cognates do not necessarily look similar[2]. Consequently, cognate judgement was left to the linguists – we opted to source data only from language databases with present and good cognate judgements.

3. Data Set & Source

For our study, we selected a subset of 26 languages from Borneo[3]. Approximately 150 languages are currently spoken in Borneo (Lewis 2009)[4]; but the lack of research and sufficient data in many (the remaining number) prohibited (their) inclusion into our analysis. Additionally, a language outgroup from the Formosan language family was included to facilitate tree/network rooting where applicable. A Formosan (Taiwanese) ancestry for Austronesian languages has been firmly established through linguistic evidence (Blust 1999), archaeological evidence (Belwood 1997) and genetic evidence (Trejaut et al 2005).

All language data was sourced from the Austronesian Basic Vocabulary Database (ABVD) (Greenhill et al 2008). This was selected as it is currently the most complete and comprehensive database for Austronesian languages, and includes the lexical and cognate data for 667 languages. For each language, the database lists 210 word items of basic vocabulary (see Wordlist in **Appendix A2**), along with their cognate judgements. We advise you to refer to their paper (Greenhill et al 2008, *The Austronesian Basic Vocabulary Database: From Bioinformatics to Lexomics*) for any inquires into data sources, collection methodology, cognate identification procedures, database content and structure.

4. Word list

The original 210 basic word list sourced from the ABVD was reduced to 64 words after careful consideration. After examining each language wordlist side by side, we found that a fair number of the words, for our collection of languages, were not fulfilling some fundamental and requisite criteria. We have listed these criteria below:

1. Words have to be items of basic vocabulary and thus ones least prone to replacement with loan words. E.g. body parts, close kinship terms, numbers and basic verbs.
2. Words should have a firm, distinct meaning. Plasticity and homonymy, given lack of consideration, may lead to false cognate judgements.
3. Words should have all synonym forms considered and present in database. Having only one representative word per semantic category (or less than in reality) may lead to false cognate judgements.
4. Words should be transferrable. In other words, its meaning should be conceptually present across all subject languages/cultures. For example, having 'snow' as a basic semantic item across localities/languages that lack such an entity is incorrect.
5. Words should occupy conceptually basic semantic categories, and not culturally/scientifically derived categories (similar to 1). For example, a local culture

[1] *The World Atlas of Language Structures (WALS), the most comprehensive database for structural characters, unfortunately had incomplete data for many of our subject languages and feature classes.*

[2] *For example the English 'wheel' and Hindi 'cakra' are cognates even though they appear entirely different; they are only identifiable as such due to good historical records.*

[3] *See Appendix A1 for selected language list*

[4] *See Appendix for full language list and map*

may not necessarily recognize the scientifically derived distinctions between midges, flies and mosquitoes, and only have one term for all three, "small biting flying thing", so having three separate semantic categories (words) for each of them would be misleading.

6. The word should belong to a distinct and absolute semantic category, rather than one situated on a relative and continuous scale (such as temperature, colour, size etc). This is because different cultures may perceive categories differently, and divide continuous scales at different resolutions. For example, blue and green are shades of the same colour in some Chinese cultures/languages (青, *qīng* – Mandarin) while perceived as different colours/words under the English language.

These criteria were put together in order to filter out words that may lead to false cognate judgements and consequently false historical inferences. It is true that reducing the number of words (characters) potentially reduces the accuracy and support of inferred topologies (Hillis 1998; Page & Holmes 1998; Scotland et al 2003; Scotland & Wortley 2006), but this is so only if the characters removed are good and representative of evolutionary history.

Quite a few of the words removed from the original 210 were those that failed criteria 2 and 3; i.e. words whose various forms and meanings were deemed inadequately researched/considered at the time of data sourcing[5], and thus likely prone to false cognate judgements. This was a necessary step as the ABVD is still a relatively new and thus incomplete database, with entries still constantly being updated.

5. Coding

We code our lexical data similar to how we code any character data in biology; by allocating a unique number or symbol to each unique form present. An example of this process is shown below.

Table 2. Encoding methodology

	'hand'	Cognacy (ABVD)	Cognacy (renumbered)
Iranun	*lima*	1	1
Melayu	*tangan*	18	2
Singhi	*toŋan*	18	2
Bintulu	*agem*	20	4

This data representation is typically lossless with discrete and fixed character states (as with molecular data) but potentially lossy with continuous and variable ones; like morphological data and here, lexical data. For example, a lexical unit may change in a variety of ways:

- replacement with a loan;
- replacement with a novel morpheme;
- loss with no replacement;
- semantic change or addition;
- morphological change (e.g. suffixed, derived, reanalysed);
- deconstruction into two or more separate derivatives;
- unlinked changes (e.g. phonological change occurring with no simultaneous morphological or semantic change)
- creation of homophones

Of the above, only absolute loss and gain/replacement events are typically represented encoded. The more partial and nuance changes are less easily captured by discrete character encoding, yet they *are* evolutionary informative. Consequently, their exclusion through coding does lead to loss of some valuable information.

It would be interesting to see how much of an effect this lossy encoding process has on our results, but at present, it is outside the scope of our study. We can only assume, like in many other lexicostatistic and morphological (biology) studies, that their affects are relatively minor compared to the stronger loss/gain events, and that their exclusion only has minimum bearing on the topology of inferred phylogenies.

Note: *Ideally, we would want a coding system that manages to accommodate both the absolute loss/gain events with the more subtle, partial changes described above – but we found this too impractical and prohibitive to realize.*[6]

6. Multistate vs. Binary

In our study, we code lexical character data in two ways: (1) Multistate and (2) Binary.

For (1), the character states are the various cognate forms; for (2) the character states indicate the presence or absence

[5] *Word synonyms, homonyms and various forms/meanings were cross referenced with local dictionaries and speakers, for a measure of term completeness.*

[6] **It is theoretically possible to construct a hierarchical and characterstate-numerous multistate matrix to accommodate each and every different mechanism and degree of change. However, this was found to prohibitively complicated, impractical and resource intensive. For instance, you would likely end up with more than 64 character states per character (semantic category) to accommodate every different cognate form, morphology, change mechanism, etc – which is above the bit manipulation capacity of most (e.g. 32-bit, 64-bit) programmes and computers – and each character state transition would also have to be modelled (potentially) differently.*

of a cognate form. Binary characters here are merely deconstructions of the more inclusive multistate characters (see **Figure 1** for example).

There are several important differences between the two coding methods that need to be taken note off prior to analysis.

1. The parsimony-informativeness of a character is dependent on the method of coding. Take for instance, the following example. In our dataset, the word 'tongue' can be represented by 4 different cognate forms. Let us label them **1**, **2**, **3** and **4** respectively. Coded, they look like:

Figure 1. Multistate versus binary coding

For Multistate;

	Mouth	Tongue	Teeth
Language$_1$	...	**1/2/3/4**	...
Language$_2$	...	**1/2/3/4**	...
Language$_n$	...	**1/2/3/4**	...

For Binary;

	Mouth	Tongue				Teeth
	...	**1**	**2**	**3**	**4**	...
L$_1$	...	0/1	0/1	0/1	0/1	...
L$_2$	...	0/1	0/1	0/1	0/1	...
L$_n$	...	0/1	0/1	0/1	0/1	...

For our set of languages, form **1** is exhibited by 23 of the languages, whilst forms **2**, **3** and **4** are only exhibited by one of the languages each, thus they are autapomorphs. Under parsimony, a (unordered) character is informative only if at least two character states each occur in more than one taxon; otherwise, the singleton (autapomorphic) states can always be explained as single changes on terminal branches, regardless of tree topology (Swofford & Begle 1993). Thus, for our multistate example, which exhibits only one character state (**1**) with multiple occurrences and three autapomorphic states, the character 'tongue' is parsimony uninformative. However under the binary example, character **1** has both character states (0 and 1) as multiple-occurring (since the character state '0' in this case encompasses all non-**1** character states, i.e. states **2**, **3** and **4**), and is thus parsimony informative; while characters **2**, **3** and **4** remain parsimony uninformative.

This exposes a crucial difference in the coding methods; a character that is parsimony uninformative in multistate may be (partly) informative in binary. For our set of languages, we discovered 17 words that were uninformative under multistate encoding but informative under binary encoding.

2. The number and weighting of characters is dependent on coding method. As binary characters are constructed via the breakdown of multistate characters, there will inevitably be more of them. Additionally, if we assume default equal weighting for all characters, a disparity arises in the weighting of same words across coding methods. Take the following example: the word 'bone' in our dataset is represented by two cognate forms while the word 'blood' by four. Under multistate coding and the assumptions of unordered characters (as is appropriate for our data) and default weighting, each character, and thus both words "blood" and "bone", would have an equal weight of 1. Once split into multiple binary characters however, the word 'bone' would have a weight of 2 and 'blood' a weight of 4; as the number of binary characters representing a word is directly proportional to the number of cognate forms exhibited by the word (see **Figure 1**), and default equal weighting is applied on the characters (not the words).

This issue however, may be easily corrected; one only has to rescale the weights of the component (binary) characters by the reciprocal of the number of cognate forms per each respective word.[7]

3. There is a difference in the conceptual treatment of 'characters' in multistate coding versus binary coding. Specifically, the fundamental units of linguistic change in multistate coding are the semantic categories, while they are the cognate forms in binary coding. It has been argued that the latter representation is not an appropriate one for linguistic change (Evans et al 2006); though Atkinson & Gray (2006) have countered saying that since cognate sets do themselves constitute discrete, relatively unambiguous heritable units with a birth and death, there is no reason to suppose they are any more or less fundamental to language evolution than semantic categories.

For our dataset, we end up with a 26x64 multistate data matrix and a 26x155 binary data matrix (See **A3** and **A4** in **Appendix**). Hereon, choice of matrix format in our analyses will be dependent on phylogenetic technique used, as one coding method may be more appropriate to one phylogenetic approach than the other.

Analyses

We test three general statistical methods for phylogeny reconstruction: (1) distance-based network analysis, (2) maximum parsimony and (3) Bayesian inference.

Network Analysis

The main reason for running network analyses here is to establish the amount of reticulation present in our dataset

[7] *Note: this rescaling procedure is not operating on the assumption that all characters (words) should be equally weighted; rather it is purely a standardizing procedure to correct the bias of character-state (cognate) richness on weighting.*

preliminary to further tree-based phylogenetic approaches. Only on condition of little or insignificant reticulation will these latter techniques be considered. A secondary reason is for the reconstructed phylogeny.

For network visualization, we employ two separate distance-based algorithms: (1) Neighbor-Net and (2) Split Decomposition. Both algorithms were run under SplitsTree4 V4.11.3 (Huson & Byrant 2006).

The Split Decomposition method canonically decomposes a distance matrix into simple components based on weighted splits (bipartitions of the taxa set), subsequently representing these splits in a splits graph. Neighbor-Net is similar in that it also constructs and visually represents weighted splits, but differs in producing circular (rather than weakly compatible) splits and in using an agglomeration method based on the Neighbour-Joining (NJ) algorithm.

We use our data encoded in the multistate format for the network analyses. We do so in light of (a) there is no difference in informativeness between coding methods as described in (**6.1**) above, as these distance-based phenetic approaches operate outside the premise of cladistics. More specifically, autapomorphic characters here *are* informative as they are capable of defining splits; (b) for distance-based approaches, the multistate format is a more accurate representation of the data. This reason (b) is justified through the observation that binary encoding of data introduces an error whereby the absence of a character is treated as character identity (zero-distance), which skews distance measures. To highlight this problem, we observe the following example:

We have a character X, with character states **1**, **2** and **3**. Coded, it looks like:

Multistate			Binary		
				X	
	X		**1**	**2**	**3**
L_1	**1**	L_1	1	0	0
L_2	**1**	L_2	1	0	0
L_3	**2**	L_3	0	1	0
L_4	**3**	L_4	0	0	1

A transformation of the multistate character matrix to a distance one gives (assuming equal transition probabilities and unordered characters):

	L_1	L_2	L_3	L_4
L_1	0	0	1	1
L_2	0	0	1	1
L_3	1	1	0	1
L_4	1	1	1	0

While a transformation from the binary character matrix to a distance one gives[8] (with same assumptions):

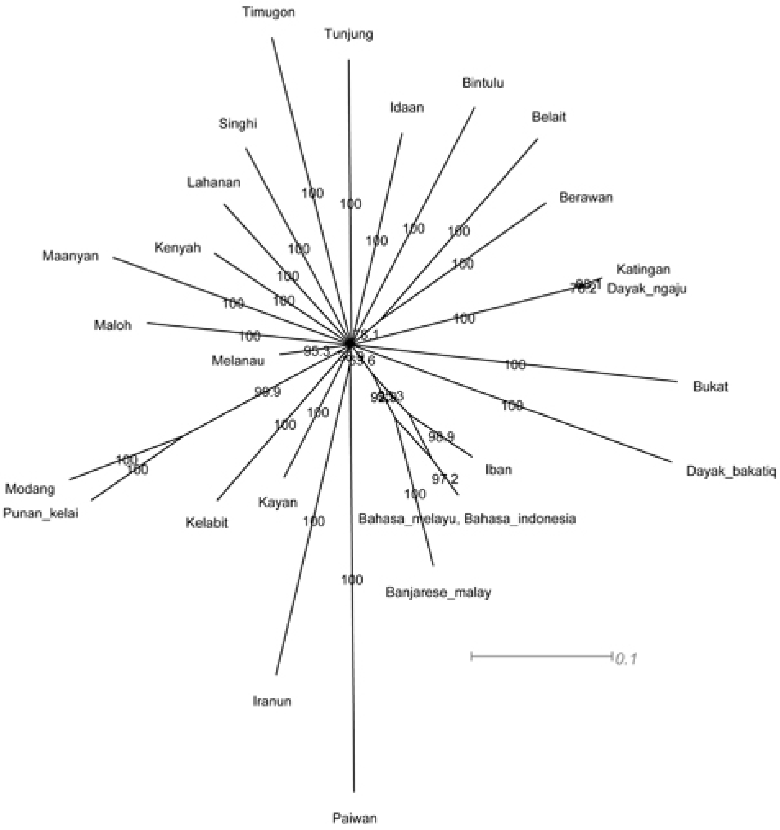
	L_1	L_2	L_3	L_4
L_1	0	0	2	2
L_2	0	0	2	2
L_3	2	2	0	3
L_4	2	2	3	0

We see here how the treatment of absence as identity skews the distance matrix under binary coding, thus giving us justified preference for the use of the multistate format.

Programme settings used for the network analyses are as follows: distance: *UncorrectedP*; draw: *EqualAngle*; network: *NeighborNet/SplitDecomposition.* A bootstrap analysis of 10,000 runs followed the network constructions to estimate support of the splits.

Results

Figure 2. Split Decomposition Network



[8] *taking the cumulative value for pair-wise distances across all three characters.*

Figure 3. NeighborNet Network

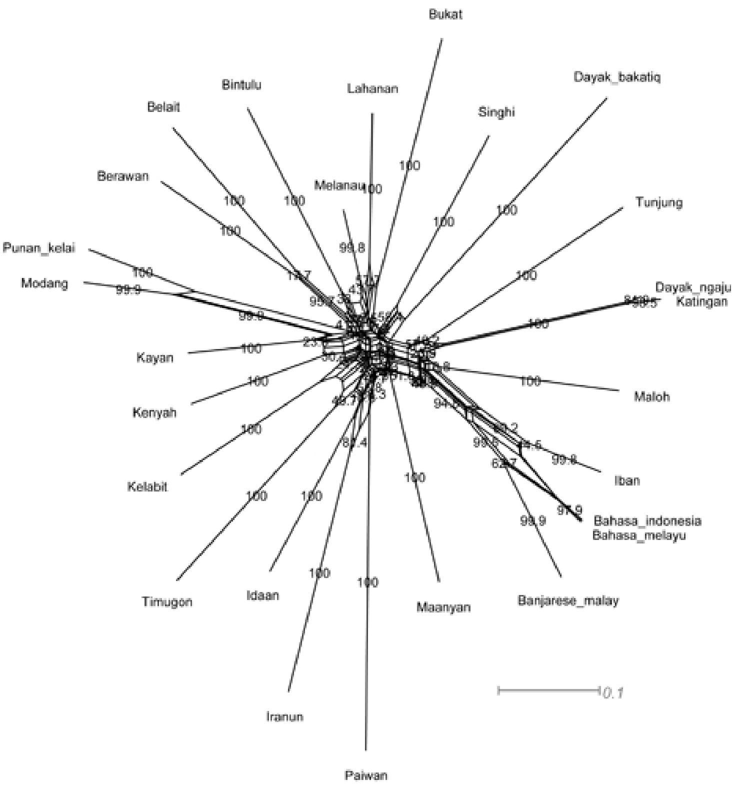
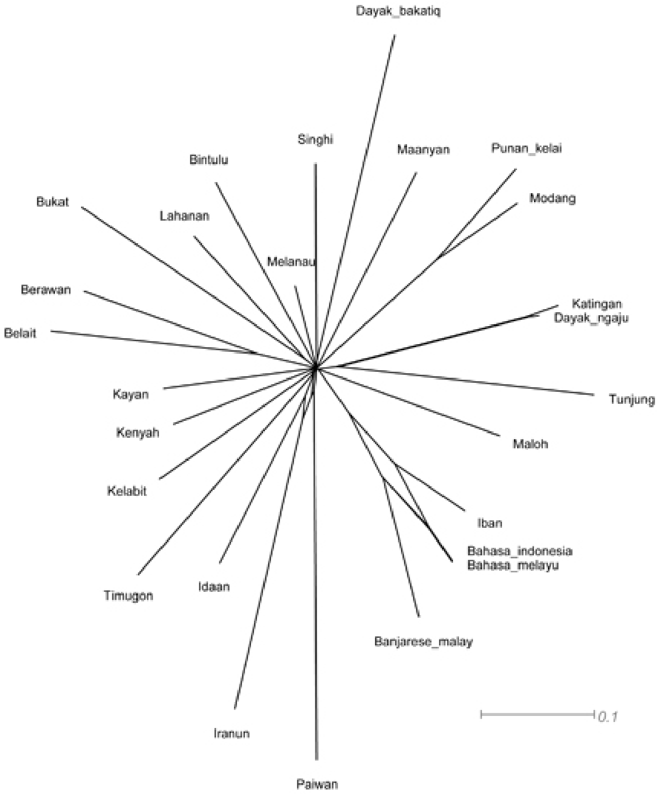


Figure 4. 50% Confidence NeighborNet Network



Interpretation

Both the Split Decomposition (SD) and the NeighborNet (NN) representations show clean, relatively unreticulated networks. The NN network is more resolved than the SD network, which is as expected from the algorithm used (Byrant & Moulton 2004), but it is also more reticulated. It is important to note that these split graphs are not explicit representations of evolutionary scenario; and that webbing does not exclusively nor necessarily imply contact (borrowing). Rather, they are the representations of all compatible and incompatible splits, and represent a combination of tree-like signal and the noise in the data. This noise (webbing), may represent contact events, but also homoplasy and/or deviation due to insufficient/misrepresentative characters. For our data, the webbing (reticulation) is minimal in SD and moderate in NN. The only occurrence of (strongly supported) webbing in SD is between *Malay (Bahasa Melayu) and Bahasa Indonesia,* which is unsurprising as the latter language is in fact a standardized variety (*Riau* dialect) of *Malay*. All splits are strongly supported in the SD network (all but one are >90% supported). For NN however, the picture is a little less clear. Removing all splits below 50% of the bootstrap replicates helps remove the weakly supported splits and clarify interpretation.

Here, we have the 50% confidence network for the NN bootstrap analyses. We see that much of the reticulation is removed after applying a 50% confidence threshold. This means that much of the incompatible splits (reticulations) are only weakly supported. The only instances of webbing that remain are the ones connecting *(a) Bahasa Melayu with Bahasa Indonesia* and *(b) Iranun with Ida'an*. A stricter confidence network (95% confidence) was also carried out, to visualize the most strongly supported splits. This resulted in an almost identical confidence network to the 50% one; indicating that the remaining reticulations (*a* and *b*) are very strongly supported, and likely real signals indicative of some contact or common/parallel evolutionary path.

As a whole, the instances of reticulation as suggested by SD and NN are minor; most are either very weakly supported or expected and few. This result consequently opens the door to further tree-building phylogenetic analyses.

Groups

The inferred phylogeny of both SD and NN reconstructions are fairly unresolved. The only groups evidently present are the {*Modang, Punan Kelai*}; {*Katingan, Dayak Ngaju*}; {*Belait, Berawan*} and {*Banjarese Malay, Bahasa Melayu, Bahasa Indonesia, Iban*} groups. All other languages remain unresolved. Note however that we have used the network analyses here primarily for reticulation inspection and not for phylogeny reconstruction. The methods mentioned hereafter are much more preferable and powerful in that regards.

Parsimony Analysis

Parsimony is a non-parametric statistical method that operates within the premise of cladistics and according to the explicit optimality criterion of simplest (least amount of) evolutionary change. It differs from the former method in its use of character data (rather than distance data), and its principle to form trees (rather than networks); and from the later Bayesian method by being non-parametric and of the optimality criterion of simplest (rather than most likely) evolutionary change.

Here we test maximum parsimony with our binary coded dataset under the programme Paup* V4.0b10 (Swofford 2002). We chose binary rather than multistate as this format provided more parsimony-informative characters (see **6.1**). Additionally, characters (cognate forms) were grouped into character sets (semantic categories) and had their weights rescaled; to standardize weights across words rather than cognate forms (see **6.2**). Differential a posteriori character weighting will be considered later, following preliminary analyses.

Parsimony searches were conducted using the heuristic search with addition sequence selected as random (10,000 repetitions) and branch swapping algorithm selected as tree bisection-reconnection (TBR). All other search settings were kept as the default. Heuristic search was selected over the branch and bound and exhaustive methods as these two methods were found to prohibitively slow and impractical; as the amount of possible topologies for our dataset of 26 languages was approximately 1.19×10^{30}. The random addition sequence and TBR swapping algorithm were selected as they were empirically found to produce the shortest and best fitting trees.

Character type was defined as either unordered (Fitch) or Dollo. An unordered approach assumes the simplest model of language change, where gain and loss of a cognate class are equally likely (see **Figure 7**); while a Dollo one assumes that every cognate class be uniquely derived (Farris 1977) and that all homoplasy takes the form of reversal to a more ancestral condition (rather than through parallel gain) (Swofford & Begle 1993). A Dollo or Dollo-like (easy loss) model of language change has been proposed (Nicholls & Gray 2006) as a more realistic representation of lexical change, as it satisfies the standard assumption that cognate classes are born only once (but may be lost multiple times). However, the standard assumptions of language evolution (see Warnow et al 2004) place a restriction not only on parallel gains, but also back mutations, i.e. all homoplasies. Of course, an absence of homoplasies would require a perfect phylogeny (where all characters are compatible on the tree); an idealistic and improbable expectation for real data. Since such a prospect is unlikely and unworkable, we settle here on the simplest (unordered) and next best workable (Dollo) models. A bootstrap support analysis (of 10,000 replicates) followed the parsimony searches to approximate support of clades in the resulting trees.

Subsequent to these searches, successive character weighting (SCW) was considered and applied. It is incorrect to assume that all characters (or words) should deserve equal weighting[9] (Farris 1983); so we consider the weighting scheme most appropriate for our data. SCW based on the rescaled consistency index (RC) successively approximates and rescales the weight of a character according to its overall fit on a tree. This index, RC, is a product of the consistency index (CI) and retention index (RI); and thus represents a good indication of both the measure of homoplasy and synapomorphy in a character. SCW thus reduces the affect of homoplastic characters (possible borrowing, homoplasies) while strengthening the affect of the synapomorphic (compatible) ones.

Results

Both Dollo and unordered optimised searches produced one most parsimonious (shortest) tree (MPC) each. The topologies of the two trees can be seen below (**Figures 5** and **6**). Support values measured from the bootstrap analyses are indicated above the clade branches. Topologies for the reweighted analyses were found to be identical to those of the original, and have their bootstrap values superimposed on the same cladograms (in brackets, **Figures 5** and **6**). The scores and ensemble indices for the trees can be seen below in **Table 2**.

Table 2. Maximum parsimony tree score and indices

	Unordered	Dollo	Unordered Reweighted	Dollo Reweighted
# of MPCs	1	1	1	1
Score of MPC	173	231	80.75	110.66
CI	0.357	0.269	0.674	0.563
HI	0.643	0.731	0.326	0.437
RI	0.508	0.786	0.779	0.960
RC	0.182	0.211	0.525	0.540

We find that the Dollo optimised runs typically exhibit a higher fraction of synapomorphy (RI), but also homoplasy (CI, HI), in their characters. The RC indices are more comparable between the two; though with a slight edge towards the Dollo optimised run. We prefer and use RC as the measure of overall character fit here as it does not suffer from some of the drawbacks of CI and RI[10], and as it combines both measures of synapomorphy and homoplasy.

[9] *Our a priori weighting of the characters done initially was not operating on the assumption that all characters (words) should be weighted equally; rather it was purely a standardizing procedure to correct the bias of character-state (cognate) richness on weighting.*

[10] *For example, CI is dependent (inversely proportional) on number of taxa, inflates with uninformative characters and does not scale down to 0. Additionally, CI only measures homoplasy while RI only synapomorphy.*

Figure 5. Maximum parsimony phylogenetic tree (Fitch optimization), with bootstrap support values (reweighted bootstraps in brackets)

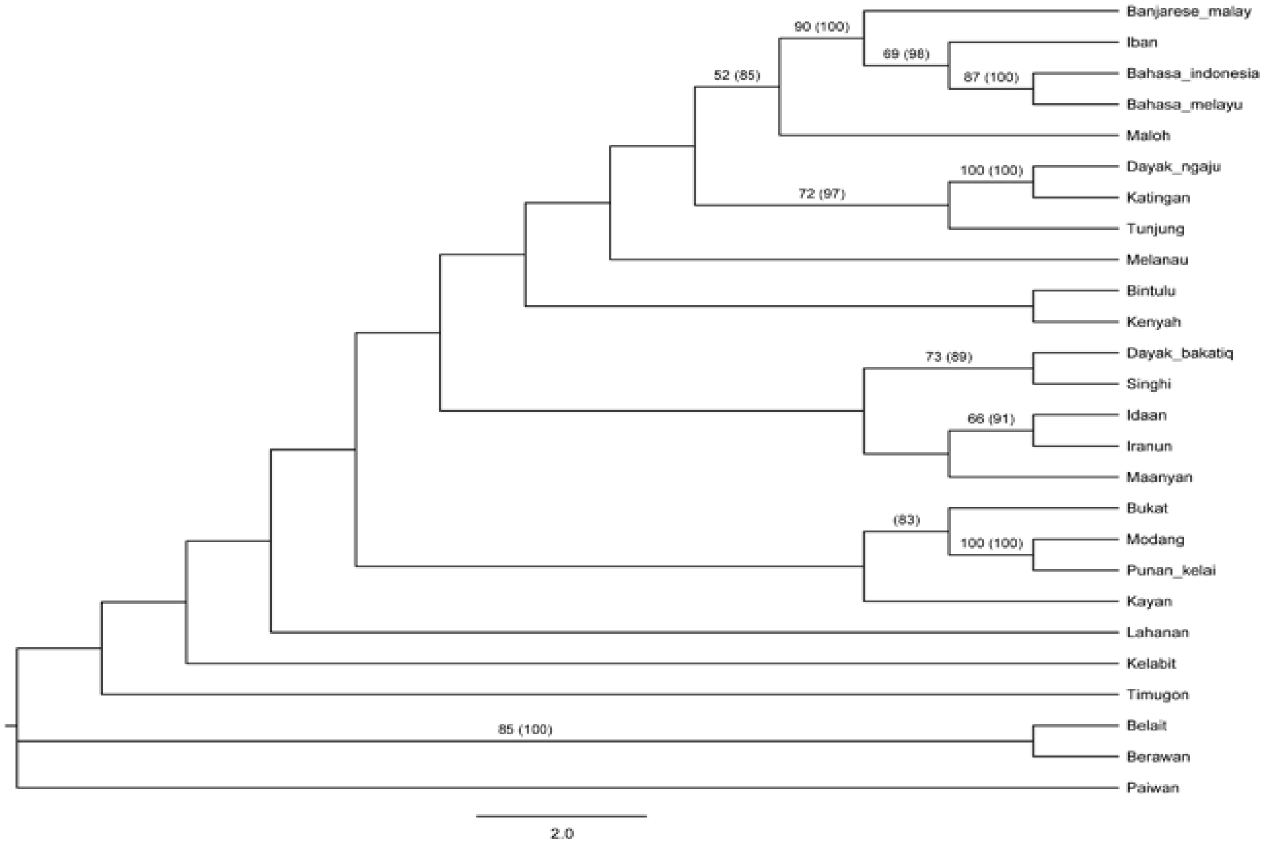
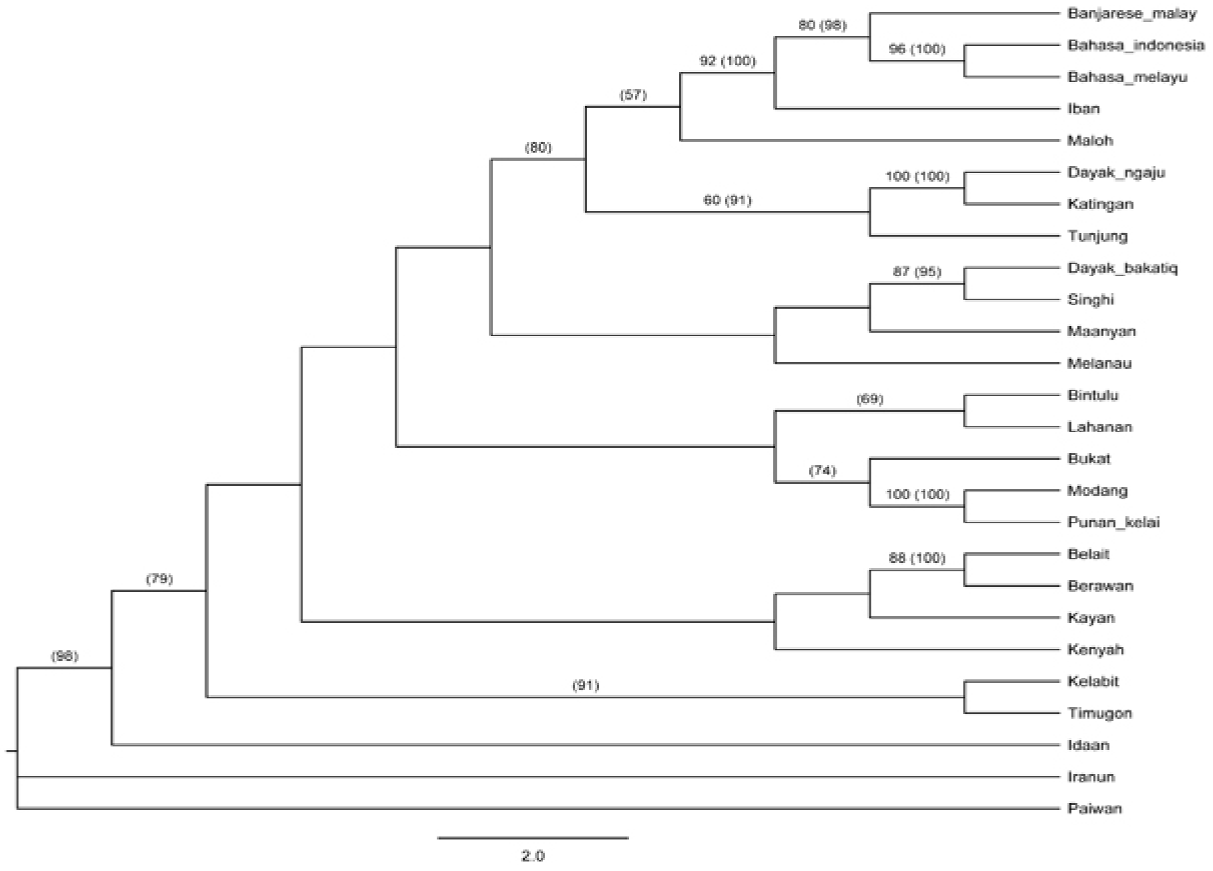


Figure 6. Maximum parsimony phylogenetic tree (Dollo optimization), with bootstrap support values (reweighted bootstraps in brackets)



We find that posterior weighting dramatically improves the indices of fit across both searches, which is as expected from a character fit based weighting approach. While overall fit (RC) is fairly similar between the unordered and Dollo optimised approaches, tree score is not; Dollo consistently exhibited higher tree scores. However, tree scores are not comparable between the unordered and Dollo methods as they operate (in Paup* 4.0) under differently weighted (transition) stepmatrices (see below, **Figure 7**).[11]

Figure 7. Unordered versus Dollo transition matrices

		Unordered (Fitch)				Dollo			
	to	0	1	2	3	0	1	2	3
f	0	-	1	1	1	-	M	2M	3M
r	1	1	-	1	1	1	-	M	2M
o	2	1	1	-	1	2	1	-	M
m	3	1	1	1	-	3	2	1	-

Where M>1

Similarly, tree scores between the original and reweighted searches are also incomparable as they are directly dependent on the weights that are in place.

Groups

We find that 10 (11)[12] of the inferred 24 clades are strongly supported (i.e. present in more than 50% of the bootstrap replicates) under the unordered optimised search; while 8 (15) of 24 clades are strongly supported under the Dollo optimised search. The groups that are strongly supported by both weighting approaches are:

for unordered,

- the clade of *Maloh, Banjarese Malay, Iban, Bahasa Melayu* and *Bahasa Indonesia*; and all its subclades.
- the clade of *Tunjung, Dayak Ngaju* and *Katingan*; and all its subclades.
- the clade of *Modang* and *Punan Kelai*
- the clade of *Dayak Bakatiq-Sara* and *Singhi.*
- the clade of *Iranun* and *Ida'an.*
- the clade of *Belait* and *Berawan*

for Dollo,

- the clade of *Maloh, Iban, Banjarese Malay, Bahasa Melayu* and *Bahasa Indonesia*; and all its subclades.
- the clade of *Tunjung, Dayak Ngaju* and *Katingan*; and all its subclades.
- the clade of *Modang* and *Punan Kelai*
- the clade of *Belait* and *Berawan*

These collections of clades are identical between the two optimisations with exceptions of the presence of the {*Iranun, Ida'an*} clade in the unordered run and the switch in position between *Iban* and *Banjarese Malay*.

Additionally, the following clades were inferred as strongly supported in at least one of the employed weighting schemes (typically the reweighted):

for Fitch,

- the clade of *Bukat, Modang* and *Punan Kelai.*

and for Dollo,

- the clade of *Bukat, Modang* and *Punan Kelai.*
- the clade of *Maloh, Iban, Banjarese Malay, Bahasa Indonesia, Bahasa Melayu, Tunjung, Dayak Ngaju* and *Katingan.*
- the clade of *Bintulu* and *Lahanan*.
- the clade of *Kelabit* and *Timugon*.
- the basal clade comprising all languages outside *Paiwan* and *Iranun*.
- the basal clade comprising all languages outside *Paiwan, Iranun* and *Ida'an*.

We find that the reweighted searches (especially the Dollo model) typically recover a higher number of clades than the unweighted searches.

We will examine the classifications inferred here with that of traditional methods later in the **Discussion** section, along with the results from the two other methods (network reconstruction and Bayesian inference). Note however that many of the groupings inferred here do match that of traditional classification (see **Discussion** section below).

Bayesian Inference

Bayesian inference is a parametric, statistical inference method that calculates the probability of the model (tree) given the data. This probability, known as the posterior probability, is related to the likelihood, prior probability and data probability through Bayes' theorem:

$$\mathrm{Pr}(\theta|\mathrm{D})=\frac{\mathrm{Pr}(\theta)\mathrm{Pr}(\mathrm{D}|\theta)}{\mathrm{Pr}(\mathrm{D})}$$

where $\mathrm{Pr}(\theta|D)$=posterior probability; $\mathrm{Pr}(\theta)$=prior probability (of the parameters); $\mathrm{Pr}(D)$= probability of the data; and $\mathrm{Pr}(D|\theta)$=likelihood value.

The requirement to define the prior probabilities beforehand allows us to explicitly define a specific model of evolution. This explicit modelling allows Bayesian inference to be much more powerful and accurate than parsimony or network analyses, on condition that the referred model of

[11] *All things being equal, a higher tree score is expected for the Dollo optimized approach as its gain transition (see Figure 7) is weighted higher than that of the unordered approach, while their loss transitions are equal.*

[12] *The number to the left (no brackets) indicates the originally weighted approach; the number on the right (in brackets) indicates the reweighted approach.*

evolution is known with confidence to reflect that of reality (for the set of characters). If not, the whole inference process will be misleading due to being based on unsound assumptions. This ability to vary the model parameters allows many different models to be compared easily (Page and Holmes 1998; Pagel 2000).

Additionally, the resulting inference in Bayesian analysis is much more explicit and representative than parsimony analysis, as it draws a probability distribution of trees rather than discrete 'optimal trees'. Specifically, uncertainties in topology and branch lengths, which will always be present in single 'optimal' trees, are explicit and present in the Bayesian inference results; whereas would require additional support analysis (e.g. bootstrapping, jackknifing, Bremer support) in parsimony analysis.

A direct analysis of this function however was found to be too impractical and time-consuming to run, especially with more than 20 languages, so we use an approach based on random sampling instead. We use a Markov Chain Monte Carlo (MCMC) approach (via the Metropolis Hasting algorithm - Metropolis et al 1953) to generate a sample of trees, whereby the frequency distribution of the sample is an approximation of the posterior probability distribution of the trees (Huelsenbeck et al 2001). Scouting and selection of trees in the MCMC is done by moving via random walks through model tree space, converging to some stationary distribution (of highest likelihood) after a certain (long enough) time. When this happens, the maximum posterior probability tree produced will be implied to be the correct or 'true' tree.

To run the MCMC analysis, we use the programme MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001). We start however by selecting a model of evolution most appropriate for our data.

Models

The simplest model of language evolution, as described in the parsimony section above, is one where the rate of cognate loss and cognate gain are equal. In other words, the rate matrix is symmetrical and the model is defined by a single parameter. This model is obviously simplistic, and likely not very realistic. A more reasonable model would consider differential rates of cognate loss and gain; through defining a second parameter. This asymmetric rate model would be able to accommodate the observation that cognate classes, once arisen, are much more likely to be lost than for another language to independently derive it. Additionally a third parameter, to allow for among site rate variation (ASRV), should be considered. One of the early criticisms of lexicostatistics, and glottochronology in particular, was that they assumed a fixed rate of cognate evolution. This assumption was subsequently found to be overly simplistic and many times false, and opened the need for a heterogeneous distribution of among site rates. A method, frequently used in molecular phylogenetics, is to model the rates of change via a gamma distribution (Yang 1994). This gamma parameter gives *each* character an inherent rate of change, so that some cognates can evolve rapidly while others can be more resistant to change.

This three-parameter model (unequal rates+ASRV), along with the simple one-parameter model (single rate) were tested in our Bayesian analyses. The two-parameter model (unequal rates) was excluded from our study as it had been found in a previous study (Luqman 2010, unpublished) to fit consistently worse than the more flexible three-parameter model for our set of languages. The models were run with our binary encoded dataset, as MrBayes (and other current phylogenetic Bayesian inference programmes[13]) did not allow MCMC algorithms to be run with multistate matrices of more than 10 character states (under the standard or morphological datatype). This also allows us to directly compare our results with those obtained from the parsimony analyses (which used the same binary encoded dataset).

Settings

We ran the MCMC analysis for 10 million generations[14], sampling every 1000 generations. We independently and simultaneously ran two separate MCMC runs, starting from different random trees, as a secondary measure of convergence (the first measure being the plateauing of the log likelihood values indicated by the average standard deviation of the split frequencies approaching zero). We Metropolis-coupled the MCMC runs (MCMCMC) by running 4 separate chains; one cold and three heated, to better sample the target distribution. Post analyses, we discarded the first 2.5 million generation as burn-in, after inspection of the log likelihood plots.

Results

Inspection of the convergence diagnostic revealed that our MCMC runs were sufficiently convergent after 10 million generations. This was confirmed by the potential scale reduction factor (PSRF) approaching 1.000 and the average standard deviation of split frequencies dropping below 0.01 towards the end of the runs. The two-rate model with gamma distribution fit the data better than the single-rate, fixed distribution model, as indicated by the Bayes Factor (Bayes Factor = 41.8) (See **Appendix A5** for details). This value for the Bayes Factor indicates very strong support for the former model (interpretation after Jeffreys 1961; Kass & Raftery 1995). This result supports our prediction that the variable rate (3-parameter) model reflects true evolutionary scenario much better than the fixed rate (one parameter) model.

[13] *E.g. BayesPhylogenies (Pagel and Meade, 2004) and BEAST (Drummond and Rambaut, 2007) were also considered.*

[14] *to allow for sufficient convergence.*

Figure 8. Bayesian inference 50% majority rule consensus tree (equal rates + no ASRV model), with posterior probabilities

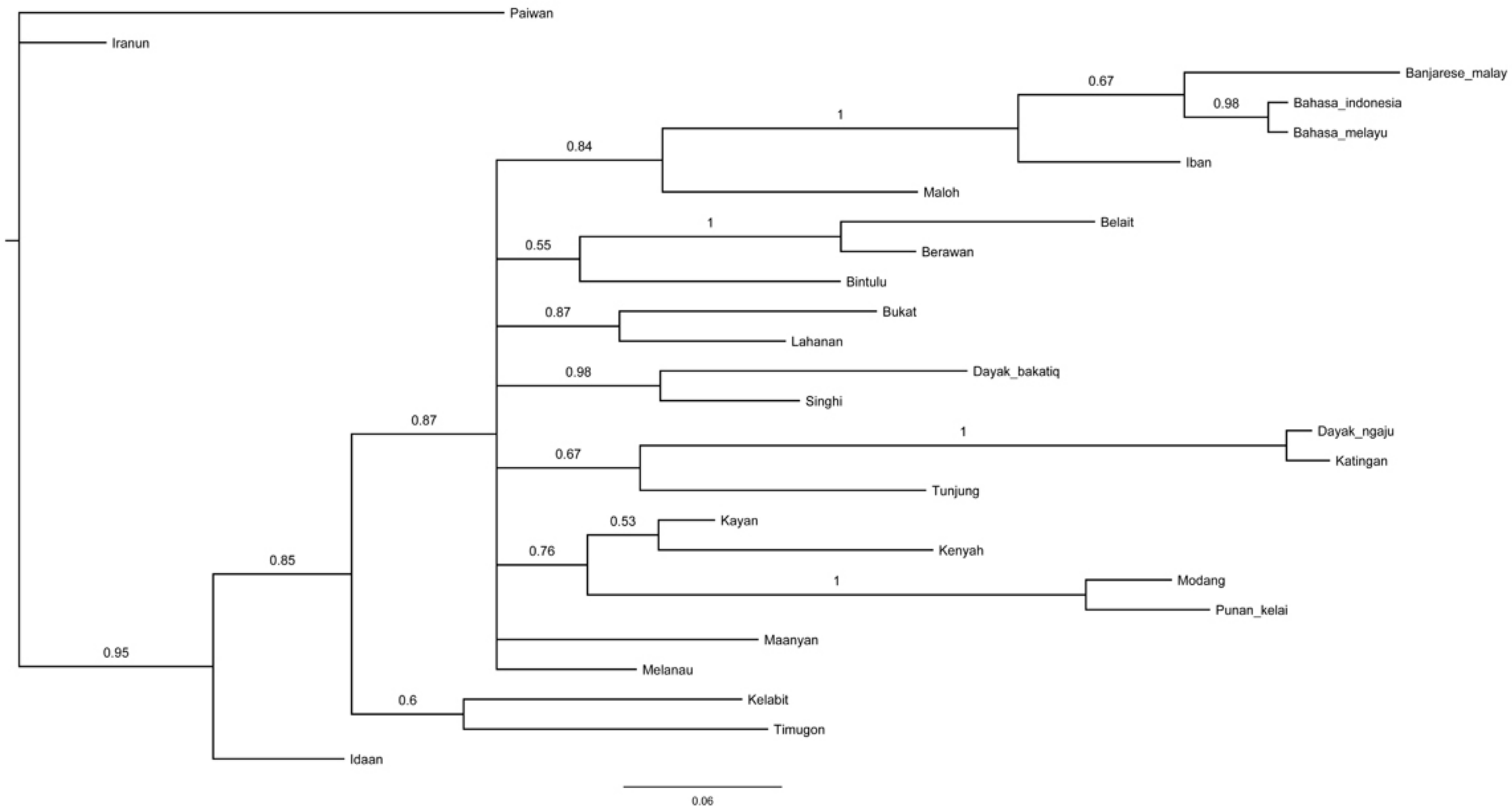
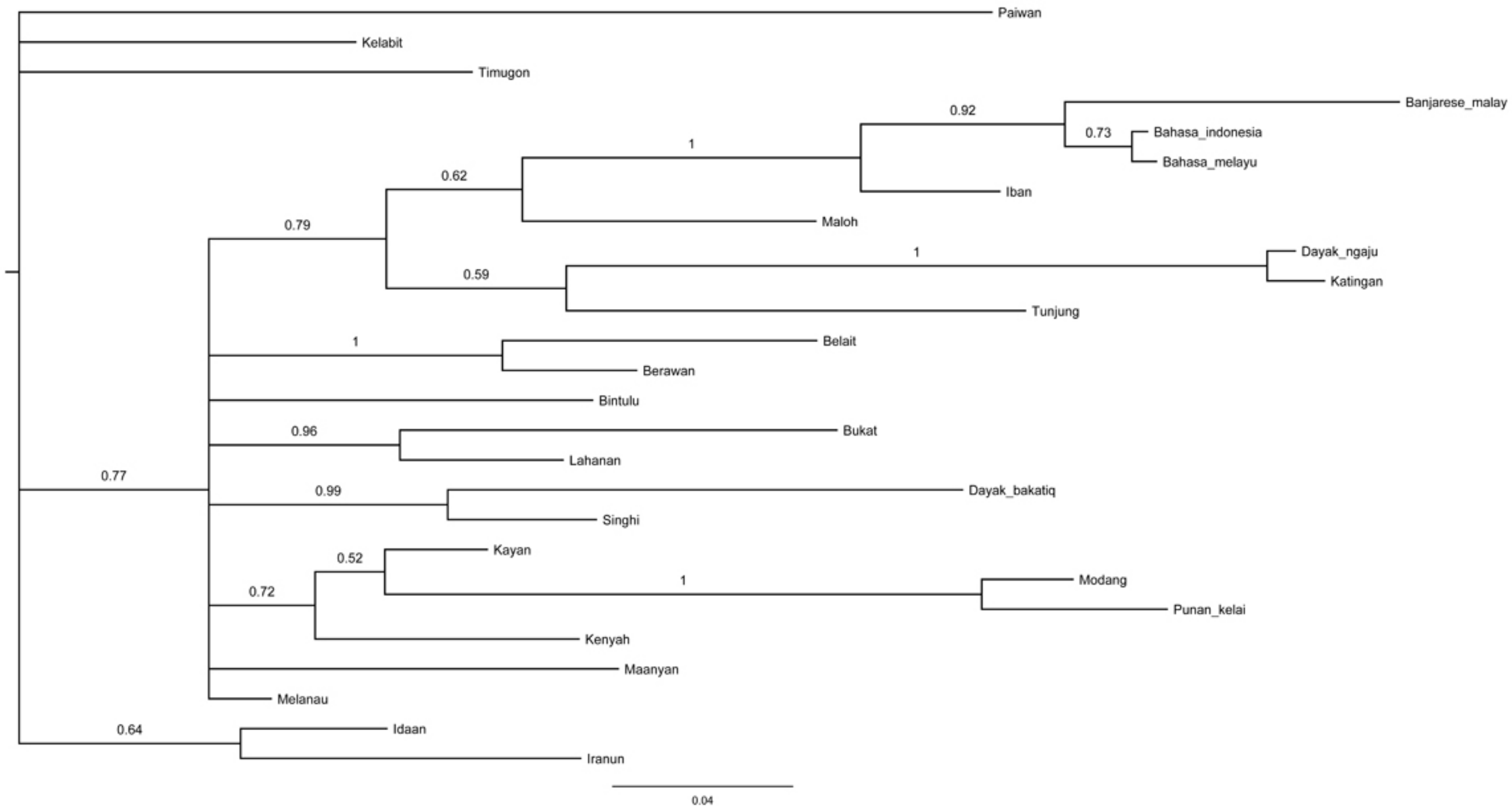


Figure 9. Bayesian inference 50% majority rule consensus tree (unequal rates + ASRV model), with posterior probabilities



Above (**Figures 8** and **9**), we show the two Bayesian inferred trees drawn with their posterior probability values. We see a fair difference at the base and mid-section of the tree topologies, but also a fair number of similarities between the terminal groups of the two models.

Groups

Clades that are common to both models (trees) are the:

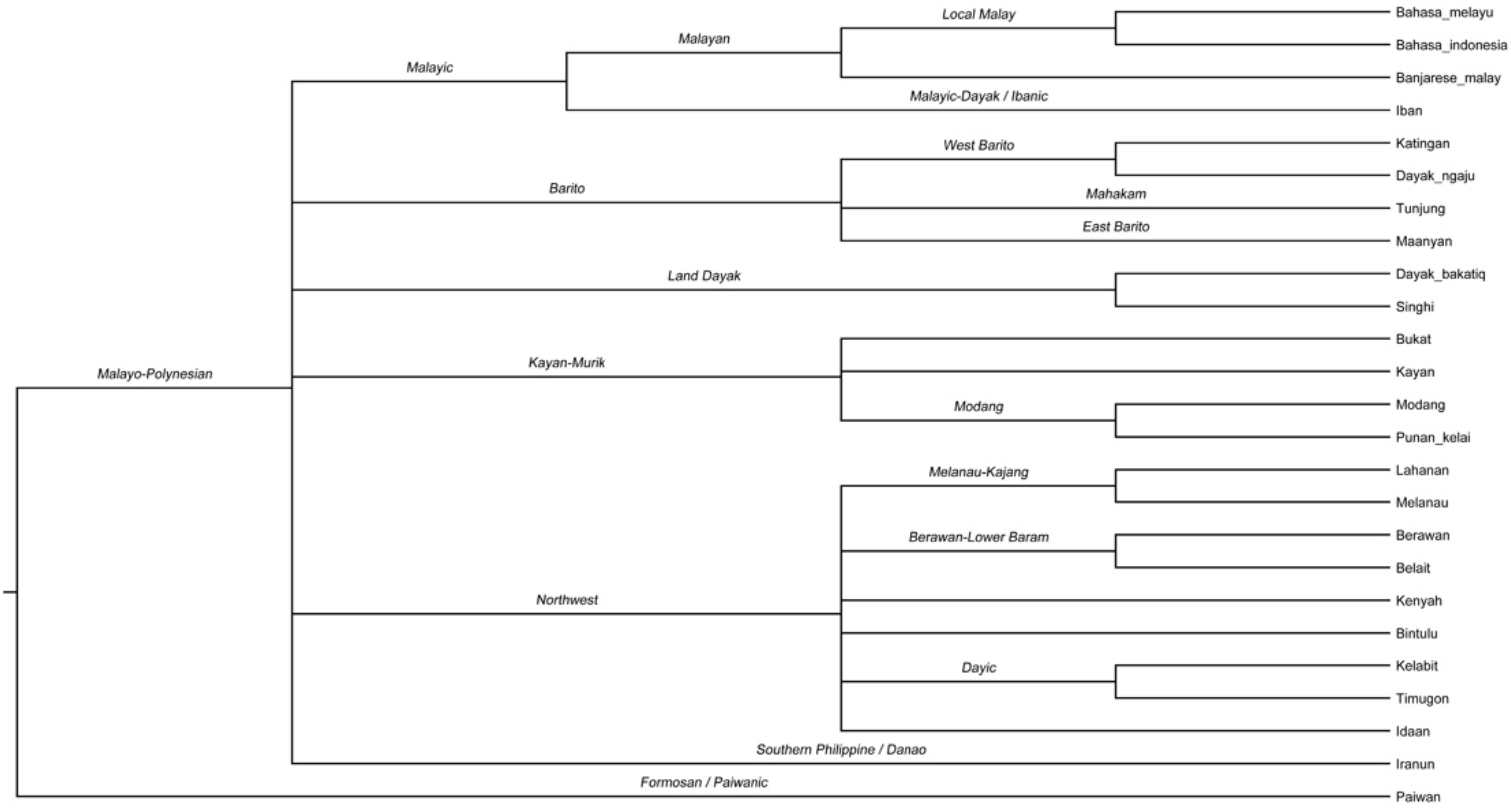
- *Maloh, Iban, Banjarese Malay, Bahasa Indonesia* and *Bahasa Melayu* clade and subclades ;
- *Tunjung, Dayak Ngaju* and *Katingan* clade and subclades;
- *Belait* and *Berawan* clade;
- *Bukat* and *Lahanan* clade;
- *Dayak Bakatiq-Sara* and *Singhi* clade;
- *Kayan, Modang* and *Punan Kelai* clade.

These clades represent most of the non-basal terminal clades. The topologies at the basal section, represented by *Paiwan, Ida'an, Iranun, Kelabit* and *Timugon*, are somewhat conflicting, as are the positions of *Ma'anyan* and *Melanau.* We will compare the results obtained here, along with the results from the other tested methods, with the traditional classification in detail in the **Discussion** section below.

Discussion

We compared the results obtained from the network reconstruction, maximum parsimony and Bayesian analyses with those established from traditional comparative methods. Specifically, we took the NeighborNet method to represent the network reconstruction method (as it is more resolved than the Split Decomposition method), the Dollo optimised parsimony run to represent the maximum parsimony method (as it has better fit than the Fitch optimised run, as indicated by the RC indices) and the two-rates plus ASRV model to represent the Bayesian results (as this had a higher likelihood, as indicated by the Bayes Factor). We use the standard classification from the *Ethnologue* (Gordon 2005) to represent the traditional comparative method, as this currently represents the most comprehensive and authoritative source for standard language classification data[15]. Below (**Figure 10**), we have constructed a cladogram for our language data set, based off the classifications from the *Ethnologue*.

Figure 10. Cladogram of Bornean languages* – Classification from traditional comparative methods (from Gordon 2005)



[15] *Note: Some have expressed concern over the fact that the Ethnologue, and its parent company Summer Institute of Linguistics (SIL), are not purely academic organisations; they are in fact Christian linguistic service organisations. Despite this, the Ethnologue remains an excellent linguistic resource, and is still used by many (e.g. Gray et al 2009; Greenhill et al 2010; etc) for comparative academic work.*

**Note: Maloh is not represented in the above cladogram, as it was absent(due to lack of data) from the Ethnologue.*

Of the 13 clades defined in the cladogram above, we find that the Dollo parsimony method correctly recovers 8, while the three-parameter Bayesian model 7. It is difficult to directly compare the NN network diagram to the tree diagram above, for obvious topographical reasons. However, at least 5 traditional clades ({*Punan Kelai* and *Modang*}, {*Dayak Ngaju* and *Katingan*}, {*Belait* and *Berawan*} and the {*Iban, Banjarese Malay*, {*Bahasa Melayu* and *Bahasa Indonesia*}} complex) are evidently present in the NN network diagram. Additionally, we find that all three methods tested correctly recover:

1. the Malayic group and sub-groups; composed of *Iban, Banjarese Malay, Bahasa Melayu* and *Bahasa Indonesia*.
2. the Barito sub-group of West Barito and Mahakam; represented by *Tunjung, Dayak Ngaju* and *Katingan*.
3. the Land Dayak group; composed of *Dayak Bakatiq-Sara* and *Singhi.*
4. the Modang subgroup; of *Modang* and *Punan Kelai.*
5. the Berawan-Lower Baram subgroup; of *Belait* and *Berawan.*

Both maximum parsimony bootstrap values and Bayesian posterior probability values strongly support the above five groups and subgroups.

The groups that are most ambiguous are the Northwest and Kayan-Murik groups, as well as the position of the *Ma'anyan* language. We have constant rearrangement in their positions and compositions across the tree topologies, though the languages *Kelabit, Timugon, Ida'an* and *Iranun* are consistently recovered as basal. It is difficult to assess and compare the more basal clades across topologies as the standard classification has many of them as unresolved (under the Malayo-Polynesian node). If we remove all unresolved clades (i.e. clades that multi-furcate into more than two braches), we find that the maximum parsimony method correctly recovers 8 out of 9 possible clades, while Bayesian inference method, 7 out of 9.

This is a remarkably good match for both tested methods. It may be tempting to conclude that the maximum parsimony approach is the more accurate of the two methods, as it matched the traditional classification better, but this would be a hasty and unsound judgement. It is difficult to compare and justifyingly select tree topologies between the parsimony and Bayesian approaches, as their trees are described under different indices of fit (RC values for the former, likelihood values for the latter). One possible way to approach this is to measure the topological distance between the traditional tree and the test tree (via e.g. the Robinson-Foulds distance (Robinson & Foulds 1981)) and select the tree with least topological distance. However, this is potentially misrepresentative with non-fully resolved trees (such as our traditional classification tree), and operates under the heavy assumption that the traditional tree is in fact the true tree, so cannot be considered further here.

There are of course some non-trivial differences between the topologies of the tested methods and the traditional method (specifically, the remaining unrecovered clades). Whether these differences reflect a disparity in method, models, characters, wordlists or prior assumptions is unclear. Any or all of these aspects could have distanced our tree from the true one. For example, our character number and selection was far from ideal. We did not include phonological or grammatical characters, and reduced our lexical characters to only 64 units. With a revised and updated wordlist, along with inclusion of phonological and grammatical characters, it may be possible to gain up to 300 representative characters for our set of languages. More and varying types of characters have been shown (Hillis 1998; Page & Holmes 1998; Scotland et al 2003; Wortley & Scotland 2006) to improve both phylogenetic accuracy and support.

Additionally, some (e.g. Poser 2003) have expressed scepticism on any purely lexical-based approach, with reason that lexical change is much more subject to cultural influence than other aspects of language change. Nakhleh et al 2005 for example, have shown that including these other aspects of linguistic change typically result in different and improved phylogenetic inferences.

Nevertheless, it is remarkable and supportive to find that the two phylogenetic methods tested (maximum parsimony and Bayesian inference), which operate under such different methodologies, can match traditional classification so well. The close approximation between the classifications inferred from these two methods with that established from the traditional comparative method is suggestive that such phylogenetic approaches can be used to infer language evolutionary history[16]. Such quantitative and computational methods are advantageous over traditional ones in that they can be run much more quickly and objectively, and are explicit in their confidence. The model plasticity of the Bayesian method in particular, holds a wealth of untapped potential. Different linguistic evolutionary scenarios can be tested and compared, and the site rate heterogeneity allows us to model time-calibrated evolution. This among site rate heterogeneity is key as it has been shown (e.g. Pagel et al 2007; Greenhill et al 2010) that word evolution rate is not fixed, rather it is variable. Gray & Atkinson (2003) and Gray et al (2009) have led the way in this approach by using a gamma distribution to model site rate variation and consequently infer evolutionary time; though how accurate this method is is still uncertain. Nonetheless, the potential is there, and such inference power opens the door to many possibilities. Questions regarding the time of divergence events, age of languages, rates of cultural and linguistic change, age and homeland (geographical origin) of

[16] *On condition of little or insignificant horizontal transmission.*

language families, and even human expansion, migration and settlement scenarios can all be addressed by such time calibrated models. These are questions not only interesting to linguists and biologists, but to all of humanity.

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References

- Atkinson, Q.D. & Gray, R.D. (2006) How old is the Indo-European language family? Progress or more moths to the flame? In: *Phylogenetic Methods and the Prehistory of Languages*. Cambridge: The McDonald Institute for Archaeological Research, 91-109.
- Atkinson, Q.D., Meade, A., Venditti, C., Greenhill, S.J., & Pagel, M. (2008) Languages evolve in punctuational bursts. *Science* **319**, 588.
- Bateman, R., Goddard, I., O'Grady, R., Funk, V. A., Mooi, R., Kress, W. J. & Cannell, P. (1990) Speaking of forked tongues: the feasibility of reconciling human phylogeny and the history of language. *Current Anthropology* **31**, 1–24.
- Bellwood, P. (1996) Phylogeny vs. reticulation in prehistory. *Antiquity* **70**, 881–890.
- Bellwood, Peter (1997) *Prehistory of the Indo-Malaysian archipelago*. Honolulu: University of Hawai'i Press.
- Blust, R. (1999)"Subgrouping, circularity and extinction: some issues in Austronesian comparative linguistics" in E. Zeitoun & P.J.K Li (Ed.) Selected papers from the Eighth International Conference on Austronesian Linguistics (pp. 31-94). Taipei: Academia Sinica.
- Borgerhoff Mulder, M. (2001) Using phylogenetically base comparative methods in anthropology: more questions than answers. *Evolutionary Anthropology* **10**, 99–111.
- Bryant, D. & Moulton, V. (2004) NeighborNet: An agglomerative method for the construction of phylogenetic networks. *Molecular Biology and Evolution*, **21**:255-265.
- Darwin, Charles (1871). *The descent of man*. Murray, London.
- Dawkins R. (1982) *The Extended Phenotype*. Oxford, UK: Freeman
- Dawkins R. (1989) *The Selfish Gene*. New York: Oxford University Press. 2nd edition.
- Drummond A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7**:214.
- Evans, S.N., D. Ringe, and T. Warnow, (2006) 'Inference of divergence times as a statistical inverse problem.' Book chapter in "*Phylogenetic Methods and the Prehistory of Languages*," pp. 119-129. Edited by Peter Forster and Colin Renfrew. Edited for the Institute by Chris Scarre (Series Editor) and Dora A. Kemp (Production Editor). Publisher: McDonald Institute for Archaeological Research/University of Cambridge, 2006.
- Farris, J. S. (1977) Phylogenetic analysis under Dollo's Law. *Systematic Zoology* **26**, 77–88.
- Farris,]. S. (1983) The logical basis of phylogenetic analysis. In: N. Platnick and V. Funk (eds), *Advances in Cladistics*. Proceedings of the second meeting of the Willi Hennig Society. Vol. 2: Columbia Univ. Press, New York: 7-36.
- Gordon, R.G. (2005) *Ethnologue: Languages of the World*, 15th edition. Dallas, Tex.: SIL International.
- Gould, S. J. (1987) *An urchin in the storm*. New York, NY: Norton.
- Gould, S. J. (1991) *Bully for brontosaurus*. New York, NY: Norton.
- Gray, R.D. & F.M. Jordan. (2000) Language trees support the express-train sequence of Austronesian expansion. *Nature* **405**, 1052-1055.
- Gray, R.D., Drummond, A.J., & Greenhill, S.J. (2009) Language Phylogenies Reveal Expansion Pulses and Pauses in Pacific Settlement. *Science* **323**: 479-483.
- Gray, RD, Greenhill, SJ, & Ross, RM (2007) The Pleasures and Perils of Darwinizing Culture (with phylogenies). *Biological Theory*, **2(4)**.
- Gray, Russell D. & Quentin D. Atkinson (2003) Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature* **426**: 435-439.
- Greenhill SJ, Atkinson QD, Meade A, & Gray RD. (2010) The shape and tempo of language evolution. *Proceedings of the Royal Society, B.*
- Greenhill, S.J., Blust. R, & Gray, R.D. (2008). The Austronesian Basic Vocabulary Database: From Bioinformatics to Lexomics. *Evolutionary Bioinformatics*, **4**:271-283.
- Gudschinsky, Sarah C. (1956) The ABC's of lexicostatistics (glottochronology). *Word* **12**: 175-210.
- Hillis, D. M. (1998) Taxonomic sampling, phylogenetic accuracy, and investigator bias. *Systematic Biology* **47**:3-8.

- Hoenigswald, H. M. (1960) *Language Change and Linguistic Reconstruction*. University of Chicago Press, Chicago.
- Hoijer H (1956) Lexicostatistics: a critique. *Language* **32**:49–60.
- Holden, C. J. & Shennan, S. (2005) *How tree-like is cultural evolution? In The evolution of cultural diversity: phylogenetic approaches* (eds R. Mace, C. J. Holden & S. Shennan), pp. 13–29. London, UK: UCL Press.
- Holden, C.J. & Gray, R.D. (2006) Exploring Bantu linguistic relationships using trees and networks. In: *Phylogenetic Methods and the Prehistory of Languages*. Forster, P & Renfrew, C. (eds). Cambridge: The McDonald Institute for Archaeological Research, pp. 19-31.
- Holden, Clare Janaki (2002) Bantu language trees reflect the spread of farming across sub-Saharan Africa: a maximum-parsimony analysis. *Proceedings of the Royal Society B: Biological Sciences* **269**(1493): 793-799.
- Huelsenbeck, J. P., and F. Ronquist (2001) MrBayes: Bayesian inference of phylogeny. *Bioinformatics* **17**:754–755.
- Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and J. P. Bollback (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* **294**:2310.
- Hull D. L. (1988) *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. Chicago, IL: University of Chicago Press.
- Hull D. L. (2001) *Science and Selection: Essays on Biological Evolution and the Philosophy of Science*. Cambridge, UK: Cambridge University Press.
- Huson, Daniel H. & Byrant, David (2006) Application of Phylogenetic Networks in Evolutionary Studies. *Molecular Biology and Evolution* **23(2)**:254-267.
- Jeffreys, H. (1961*) The Theory of Probability* (3e), Oxford; p. 432
- Kass, R.E. & Raftery, A.E. (1995) Bayes Factors. *Journal of the American Statistical Association* **430**:773-795.
- Kitchen, Andrew, Christopher Ehret, Shiferaw Assefa & Connie J. Mulligan (2009) Bayesian phylogenetic analysis of Semitic languages identifies an Early Bronze Age origin of Semitic in the Near East. *Proceedings of the Royal Society B* **276**:2703-2710.
- Lewis, M. Paul (2009) *Ethnologue: Languages of the World*, Sixteenth edition. Dallas, Tex.: SIL International.
- Metropolis, N.; Rosenbluth, A.W.; Rosenbluth, M.N.; Teller, A.H.; Teller, E. (1953) Equations of State Calculations by Fast Computing Machines. *Journal of Chemical Physics* **21 (6)**: 1087–1092.
- Moore, J. H. (1994) Putting anthropology back together again: the ethnogenetic critique of cladistic theory. *American Anthropologist* **96**, 925–948.
- Nakhleh, Luay, Tandy Warnow, Don Ringe & Steven N. Evans (2005a) A comparison of phylogenetic reconstruction methods on an Indo-European dataset. *Transactions of the Philological Society* **103(2)**: 171-192.
- Nicholls, G.K. & Gray, R.D. (2006) Quantifying uncertainty in a stochastic Dollo model of vocabulary evolution. In: *Phylogenetic Methods and the Prehistory of Languages*. Cambridge: The McDonald Institute for Archaeological Research, 161-172.
- Page, R. D. M., and E. C. Holmes (1998) *Molecular evolution: Phylogenetic approach*. University Press, Cambridge.
- Pagel, M. & Meade, A. (2004) A phylogenetic mixture model for detecting pattern heterogeneity in gene sequence or character-state data. *Systematic Biology* **53**: 571-581.
- Pagel, Mark (2000) Maximum-likelihood models for glottochronology and for reconstructing linguistic phylogenies. In: Colin Renfrew, April McMahon, & Larry Trask (eds.) *Time depth in historical linguistics*. Cambridge: McDonald Institute for Archaeological Research, 189-207.
- Pagel, Mark, Quentin D. Atkinson & Andrew Meade (2007) Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature* **449**(7163): 717-720.
- Poser, B. (2003) Dating Indo-European. Language Log.
- Rexová, Kateřina, Daniel Frynta & Jan Zrzavy´ (2002) Cladistic analysis of languages: Indo-European classification based on lexicostatistical data. *Cladistics* **19**: 120-127.
- Rexová, Kateřina, Yvonne Bastin & Daniel Frynta (2006) Cladistic analysis of Bantu languages: a new tree based on combined lexical and grammatical data. *Naturwissenschaften* **93(4)**: 189-194.
- Robinson, D.R & Foulds, L.R. (1981) Comparison of phylogenetic trees. *Mathematical Biosciences* **53**, p. 131-147.
- Scotland, R. W, R. G. Olmstead, and J. R. Bennett. (2003b) Phylogeny reconstruction: The role of morphology. *Systematic Biology* **52**:539-548.
- Scotland, Robert W. and Wortley, Alexandra H. (2006) The Effect Combing Molecular and Morphological Data in Published Phylogenetic Analyses. *Systematic Biology* **55(4)**:677-685.
- Swadesh, Morris (1952) Lexico-Statistic Dating of Prehistoric Ethnic Contacts: With Special Reference to North American Indians and Eskimos. *Proceedings of the American Philosophical Society* **96(4)**: 452-463.

- Swofford, D.L. (2000) PAUP, Version 4.0b4a. Sinauer, Sunderland, MA.
- Swofford, David L. And Begle, Douglas P (2003) Phylogenetic Analysis Using Parsimony (PAUP) Version 3.1 User's Manual. Laboratory of Molecular Systematics. Smithsonian Institution.
- Temkin, I. & Eldredge, N. (2007) Phylogenetics and material cultural evolution. *Current Anthropology* **48**, 146–153.
- Terrell, J. E. (1988) History as a family tree, history as an entangled bank: constructing images and interpretations of prehistory in the South Pacific. *Antiquity* **62**, 642–657.
- Terrell, J. E., Kelly, K. M. & Rainbird, R. (2001) Foregone conclusions? In search of 'Papuans' and 'Austronesians'. *Current Anthropology* **42**, 97–124.
- Trejaut J. A., Kivisild T., Loo J.H., Lee C.L., He C.L., Hsu, C.J., Li, Z.Y. and Lin, M. (2005) Traces of archaic mitochondrial lineages persist in Austronesian-speaking Formosan populations. *PLoS Biology* **3(8)**: e247.
- Warnow, T., Evans, S. N., Ringe, D., & Nakhleh, L., (2004) A Stochastic model of language evolution that incorporates homoplasy and borrowing. In Peter Forster, Colin Renfrew and James Clackson (eds.) *Phylogenetic Methods and the Prehistory of Languages*. Cambridge: McDonald Institute for Archaeological Research.
- Wortley, A.H. & R.W. Scotland. 2006. The effect of combining molecular and morphological data in published phylogenetic analyses. *Systematic Biology* **55(4)**: 677-685.
- Yang, Z. (1994) Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: Approximate methods. *Journal of Molecular Evolution* **39**:306–314.

Appendix

A1. Language List

1. Banjarese Malay
2. Belait
3. Berawan (Long Terawan)
4. Bintulu
5. Bukat
6. Dayak Bakatiq-Sara/Riok
7. Dayak Ngaju
8. Iban
9. Ida'an
10. Iranun
11. Katingan
12. Kayan (Uma Juman)
13. Kelabit (Bario)
14. Kenyah (Long Anap)
15. Lahanan
16. Ma'anyan
17. Bahasa Indonesia
18. Maloh
19. Melanau (Mukah)
20. Bahasa Melayu
21. Modang
22. Punan Kelai
23. Singhi
24. Timugon (Murut)
25. Tunjung
26. Paiwan (Outgroup)

A2. Austronesian Basic Vocabulary Database Wordlist (filtered)

1.	**hand**	36.	to spit	71.	to stab, pierce	106.	**snake**	141.	**wet**	176.	below
2.	**left**	37.	**to eat**	72.	to hit	107.	worm	142.	**heavy**	177.	this
3.	**right**	38.	to chew	73.	to steal	108.	louse	143.	**fire**	178.	that
4.	leg/foot	39.	to cook	74.	**to kill**	109.	mosquito	144.	to burn	179.	near
5.	to walk	40.	**to drink**	75.	**to die, be dead**	110.	spider	145.	smoke	180.	far
6.	**road/path**	41.	to bite	76.	to live, be alive	111.	**fish**	146.	ash	181.	**where?**
7.	to come	42.	to suck	77.	to scratch	112.	rotten	147.	black	182.	I
8.	to turn	43.	**Ear**	78.	to cut, hack	113.	branch	148.	white	183.	thou
9.	to swim	44.	**to hear**	79.	stick/wood	114.	**leaf**	149.	red	184.	he/she
10.	Dirty	45.	**Eye**	80.	to split	115.	**root**	150.	yellow	185.	we
11.	dust	46.	to see	81.	sharp	116.	**flower**	151.	green	186.	you
12.	**skin**	47.	to yawn	82.	dull, blunt	117.	**fruit**	152.	small	187.	they
13.	back	48.	**to sleep**	83.	to work	118.	**grass**	153.	big	188.	**what?**
14.	belly	49.	to lie down	84.	to plant	119.	earth/soil	154.	short	189.	**who?**
15.	**bone**	50.	**to dream**	85.	to choose	120.	**stone**	155.	long	190.	other
16.	intestines	51.	to sit	86.	to grow	121.	**sand**	156.	thin	191.	all
17.	liver	52.	to stand	87.	to swell	122.	**water**	157.	thick	192.	and
18.	breast	53.	person/human being	88.	to squeeze	123.	to flow	158.	narrow	193.	if
19.	**shoulder**	54.	man/male	89.	to hold	124.	sea	159.	wide	194.	how?
20.	to know	55.	woman/female	90.	to dig	125.	salt	160.	painful, sick	195.	no, not
21.	to think	56.	**child**	91.	to buy	126.	lake	161.	shy, ashamed	196.	to count
22.	**to fear**	57.	husband	92.	to open, uncover	127.	woods/forest	162.	old	197.	**One**
23.	**blood**	58.	wife	93.	to pound, beat	128.	**sky**	163.	new	198.	**Two**
24.	head	59.	**mother**	94.	to throw	129.	**moon**	164.	good	199.	**Three**
25.	**neck**	60.	**father**	95.	to fall	130.	**star**	165.	bad, evil	200.	**Four**
26.	**hair**	61.	**house**	96.	**dog**	131.	**cloud**	166.	correct, true	201.	**Five**
27.	**nose**	62.	thatch/roof	97.	**bird**	132.	fog	167.	**night**	202.	Six
28.	to breathe	63.	name	98.	**egg**	133.	**rain**	168.	day	203.	Seven
29.	to sniff, smell	64.	to say	99.	feather	134.	thunder	169.	year	204.	Eight
30.	**mouth**	65.	rope	100.	wing	135.	**lightning**	170.	**when?**	205.	Nine
31.	**tooth**	66.	to tie up, fasten	101.	to fly	136.	wind	171.	to hide	206.	Ten
32.	tongue	67.	to sew	102.	**rat**	137.	to blow	172.	to climb	207.	Twenty
33.	**to laugh**	68.	needle	103.	meat/flesh	138.	warm	173.	at	208.	Fifty
34.	**to cry**	69.	to hunt	104.	fat/grease	139.	cold	174.	in, inside	209.	One Hundred
35.	**to vomit**	70.	to shoot	105.	**tail**	140.	dry	175.	above	210.	One Thousand

Words used in study are indicated in **bold**. For word selection criteria, refer to **Section 4** under **Methods & Materials**.

A3. Multistate Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Banjarese Malay	2	5	1	1	1	1	2	1	1	6	3	1	5	3	2	1	1	2	1	1	1	1	1	2	1	1	4	2	1	1	1	4
Belait	2	4	2	1	1	1	1	1	2	3	1	1	3	1	1	4	1	1	1	3	1	3	1	3	1	1	1	1	3	3	1	1
Berawan	6	2	2	1	1	1	1	3	2	3	1	1	3	1	1	1	1	1	1	4	3	4	1	1	1	1	1	1	3	4	3	1
Bintulu	4	2	2	3	1	1	5	4	1	3	1	1	6	1	1	1	1	1	3	5	1	5	1	4	1	1	1	1	1	5	4	1
Bukat	7	2	2	4	2	1	4	1	1	7	?	1	1	5	1	5	1	1	1	6	4	1	1	1	?	1	1	1	2	6	5	1
Dayak Bakatiq	8	1	2	2	1	1	1	5	1	8	1	3	1	6	3	6	2	3	1	7	5	1	1	5	2	1	5	1	3	7	6	1
Dayak Ngaju	3	3	2	2	3	1	2	2	1	4	2	1	2	2	1	1	1	1	1	2	2	2	1	1	1	1	6	3	1	3	1	1
Iban	2	6	1	1	1	1	2	1	1	9	1	1	?	7	1	1	3	1	1	2	2	1	1	1	1	1	2	2	1	1	1	1
Ida'an	9	4	1	1	1	1	6	6	1	1	1	1	7	1	1	7	4	1	1	1	1	1	1	1	1	1	1	1	4	1	1	1
Iranun	1	4	1	1	5	1	1	7	3	1	1	2	8	1	1	8	5	1	1	1	1	6	1	1	3	2	1	1	4	1	1	1
Katingan	3	3	2	2	3	1	2	2	1	4	2	1	2	2	1	1	1	1	1	2	2	2	1	1	1	1	2	3	1	3	1	1
Kayan	10	2	2	1	2	1	3	1	1	10	1	1	1	1	1	9	1	1	1	8	6	7	1	1	1	1	1	1	1	2	1	1
Kelabit	6	4	4	1	2	1	7	1	1	1	1	1	9	1	1	10	1	1	1	2	7	1	1	6	1	1	1	1	1	8	1	2
Kenyah	11	4	2	1	2	1	3	1	1	3	1	1	1	1	1	1	1	1	1	3	1	8	1	7	1	1	7	1	1	2	1	1
Lahanan	12	2	2	3	6	1	4	1	1	2	1	1	1	1	1	2	1	1	1	9	8	1	1	8	?	1	1	1	2	3	7	1
Ma'anyan	2	1	1	1	1	1	1	8	1	11	4	1	1	1	1	11	6	1	1	10	9	1	1	9	1	3	1	1	2	1	1	1
B. Indonesia	2	1	1	1	1	1	2	1	1	1	3	1	4	3	1	1	1	1	1	1	1	1	1	1	1	1	3	2	1	1	1	3
Maloh	2	7	2	1	1	1	4	1	1	5	1	4	1	8	1	1	1	1	1	1	1	1	1	1	4	1	2	1	5	1	1	1
Melanau	4	2	2	1	1	1	1	9	1	2	1	1	1	1	1	1	1	1	1	11	1	1	1	1	1	1	1	1	2	1	1	1
B. Melayu	2	1	1	1	1	1	2	1	1	1	3	1	4	3	1	1	1	1	1	1	1	1	1	1	1	1	3	2	1	1	1	3
Modang	5	2	3	1	4	1	3	1	1	12	1	1	1	4	1	3	1	1	2	12	1	2	1	1	1	1	1	1	3	2	2	5
Punan Kelai	5	8	3	1	4	1	3	1	1	13	1	1	5	4	1	3	1	1	2	13	10	2	1	1	1	1	1	1	3	9	2	1
Singhi	2	9	2	1	1	1	8	10	1	2	1	1	1	1	1	1	7	1	1	1	11	1	2	10	5	1	1	1	?	10	8	6
Timugon	3	10	5	1	7	1	1	11	1	1	1	1	10	1	1	12	1	4	1	1	1	1	1	11	1	1	1	1	4	3	1	2
Tunjung	2	2	2	1	1	2	?	12	1	5	2	1	11	2	1	1	1	1	1	14	12	9	3	1	?	4	8	1	?	3	1	7
Paiwan	1	1	1	1	2	1	1	1	4	1	5	2	12	9	4	2	1	1	1	15	1	10	1	12	1	1	1	1	1	2	1	1

Continued..	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Banjarese Malay	2	1	2	2	2	6	1	2	2	1	1	5	?	1	1	1	1	1	1	1	1	1	2	3	3	1	2	1	1	1	1	1
Belait	1	1	1	3	1	4	1	3	4	2	1	6	5	1	1	2	?	2	2	2	1	2	2	4	5	5	1	1	1	1	1	1
Berawan	1	1	1	1	1	4	1	3	4	3	1	7	6	2	1	3	1	1	3	3	1	1	2	1	6	2	1	1	1	1	1	1
Bintulu	1	1	3	1	1	7	1	?	1	4	1	?	4	1	1	1	3	1	1	1	1	3	2	5	5	2	1	3	1	1	1	?
Bukat	4	1	4	1	3	8	1	2	3	1	1	2	1	3	?	4	1	3	?	4	1	1	2	2	7	2	1	4	1	1	1	?
Dayak Bakatiq	1	2	5	1	4	1	1	?	1	1	1	1	7	1	1	1	4	1	1	1	1	1	4	1	8	6	4	1	1	1	1	1
Dayak Ngaju	2	1	1	1	1	2	1	1	2	1	1	?	1	1	1	1	2	1	1	1	1	1	2	6	4	3	3	1	1	1	1	1
Iban	2	1	2	1	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	2	7	9	?	2	2	1	2	1	1
Ida'an	5	3	6	1	2	5	1	2	5	1	1	2	8	1	1	1	5	1	4	1	1	1	3	1	5	2	5	1	1	1	1	1
Iranun	6	4	7	1	5	9	1	4	6	5	1	8	9	1	1	1	1	1	1	1	2	1	3	8	10	7	6	1	1	1	1	1
Katingan	2	5	1	1	1	2	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	2	9	4	3	3	1	1	1	1	1
Kayan	1	1	1	1	1	10	1	2	?	1	1	9	10	1	1	5	6	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1
Kelabit	1	1	1	1	6	11	1	?	4	1	1	10	4	1	1	1	7	1	1	1	1	1	1	1	11	2	1	5	1	1	1	1
Kenyah	3	1	1	1	2	3	?	2	?	1	1	11	11	1	1	1	1	1	1	1	1	4	2	1	5	2	1	1	1	1	1	1
Lahanan	1	1	1	1	1	1	1	3	3	1	1	12	1	1	?	1	8	1	?	1	1	1	2	10	12	2	?	1	1	1	1	?
Ma'anyan	2	1	8	1	1	12	1	2	1	1	1	4	1	1	1	6	1	1	?	5	1	1	2	11	13	2	1	1	1	1	1	1
B. Indonesia	2	1	2	1	2	1	1	?	1	1	1	1	2	1	1	1	1	1	1	1	1	1	2	3	3	1	2	2	1	2	1	1
Maloh	2	1	1	1	2	2	1	1	1	1	1	4	1	4	1	1	9	1	1	?	1	1	2	12	14	1	7	1	1	1	1	?
Melanau	1	1	1	1	1	1	1	?	1	1	1	13	1	1	1	1	?	1	1	1	1	1	2	13	15	2	1	?	1	1	1	1
B. Melayu	2	1	2	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	2	3	3	1	2	2	1	2	1	1
Modang	1	1	9	1	1	3	2	2	7	1	1	3	3	1	1	7	1	1	5	1	1	1	2	2	2	2	1	1	2	1	1	?
Punan Kelai	1	1	10	1	1	3	2	1	1	1	1	3	3	1	1	8	1	1	1	1	1	1	2	2	2	2	8	1	3	1	1	?
Singhi	1	1	11	1	1	1	1	?	?	1	1	1	12	1	1	1	1	1	1	1	1	1	4	14	16	2	1	1	1	1	1	?
Timugon	3	1	2	1	7	5	1	2	4	6	1	14	13	5	1	1	1	4	6	1	1	1	1	1	17	8	1	1	1	1	1	?
Tunjung	7	1	?	1	1	13	1	2	1	1	1	1	1	1	?	1	1	1	?	1	1	1	2	1	18	4	9	1	2	1	1	1
Paiwan	8	1	1	1	8	14	3	5	8	7	2	15	1	6	2	1	10	1	7	6	3	1	5	1	1	4	10	1	1	1	1	1

	Character	Key	
1	Hand	55	Night
2	Left	56	When
3	Right	57	Where
4	Road	58	What
5	Skin	59	Who
6	Bone	60	One
7	Shoulder	61	Two
8	Fear	62	Three
9	Blood	63	Four
10	Neck	64	Five
11	Hair		
12	Nose		
13	Mouth		
14	Tooth		
15	Tongue		
16	Laugh		
17	Cry		
18	Vomit		
19	Eat		
20	Drink		
21	Ear		
22	Hear		
23	Eye		
24	Sleep		
25	Dream		
26	Child		
28	Father		
29	House		
30	Kill		
31	Die		
32	Dog		
33	Bird		
34	Egg		
35	Rat		
36	Tail		
37	Snake		
38	Fish		
39	Leaf		
40	Root		
41	Flower		
42	Fruit		
43	Stone		
44	Sand		
45	Water		
46	Sky		
47	Moon		
48	Star		
49	Cloud		
50	Rain		
51	Lightning		
52	Wet		
53	Heavy		
54	Fire		

A4. Binary Matrix

Note: Autapomorphic characters are not shown here

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Banjarese Malay	010000	0000	100	100	1000	1	0100	10	10	00000	001	10	00001	0010	0	100	1	0	10	100	10	10	1	0	1	1	000	010	1000	100	10	000
Belait	010000	0001	010	100	1000	1	1000	10	01	00100	100	10	00100	1000	1	000	1	1	10	001	10	00	1	0	1	1	100	100	0010	001	10	100
Berawan	000001	0100	010	100	1000	1	1000	00	01	00100	100	10	00100	1000	1	100	1	1	10	000	00	00	1	1	1	1	100	100	0010	000	00	100
Bintulu	000100	0100	010	001	1000	1	0000	00	10	00100	100	10	00000	1000	1	100	1	1	00	000	10	00	1	0	1	1	100	100	1000	000	00	100
Bukat	000000	0100	010	000	0100	1	0001	10	10	00000	???	10	10000	0000	1	000	1	1	10	000	00	10	1	1	?	1	100	100	0100	000	00	100
Dayak Bakatiq	000000	1000	010	010	1000	1	1000	00	10	00000	100	00	10000	0000	0	000	0	0	10	000	00	10	1	0	0	1	000	100	0010	000	00	100
Dayak Ngaju	001000	0010	010	010	0010	1	0100	01	10	00010	010	10	01000	0100	1	100	1	1	10	010	01	01	1	1	1	1	000	001	1000	001	10	100
Iban	010000	0000	100	100	1000	1	0100	10	10	00000	100	10	10010	0000	1	100	0	1	10	010	01	10	1	1	1	1	010	010	1000	100	10	100
Ida'an	000000	0001	100	100	1000	1	0000	00	10	10000	100	10	00000	1000	1	000	0	1	10	100	10	10	1	1	1	1	100	100	0001	100	10	100
Iranun	100000	0001	100	100	0000	1	1000	00	00	10000	100	01	00000	1000	1	000	0	1	10	100	10	00	1	1	0	0	100	100	0001	100	10	100
Katingan	001000	0010	010	010	0010	1	0100	01	10	00010	010	10	01000	0100	1	100	1	1	10	010	01	01	1	1	1	1	010	001	1000	001	10	100
Kayan	000000	0100	010	100	0100	1	0010	10	10	00000	100	10	10000	1000	1	000	1	1	10	000	00	00	1	1	1	1	100	100	1000	010	10	100
Kelabit	000001	0001	000	100	0100	1	0000	10	10	10000	100	10	00000	1000	1	000	1	1	10	010	00	10	1	0	1	1	100	100	1000	000	10	010
Kenyah	000000	0001	010	100	0100	1	0010	10	10	00100	100	10	10000	1000	1	100	1	1	10	001	10	00	1	0	1	1	000	100	1000	010	10	100
Lahanan	000000	0100	010	001	0000	1	0001	10	10	01000	100	10	10000	1000	1	010	1	1	10	000	00	10	1	0	?	1	100	100	0100	001	00	100
Ma'anyan	010000	1000	100	100	1000	1	1000	00	10	00000	000	10	10000	1000	1	000	0	1	10	000	00	10	1	0	1	0	100	100	0100	100	10	100
B. Indonesia	010000	1000	100	100	1000	1	0100	10	10	10000	001	10	00010	0010	1	100	1	1	10	100	10	10	1	1	1	1	001	010	1000	100	10	001
Maloh	010000	0000	010	100	1000	1	0001	10	10	00001	100	00	10000	0000	1	100	1	1	10	100	10	10	1	1	0	1	010	100	0000	100	10	100
Melanau	000100	0100	010	100	1000	1	1000	00	10	01000	100	10	10000	1000	1	100	1	1	10	000	10	10	1	1	1	1	100	100	0100	100	10	100
B. Melayu	010000	1000	100	100	1000	1	0100	10	10	10000	001	10	00010	0010	1	100	1	1	10	100	10	10	1	1	1	1	001	010	1000	100	10	001
Modang	000010	0100	001	100	0001	1	0010	10	10	00000	100	10	10000	0001	1	001	1	1	01	000	10	01	1	1	1	1	100	100	0010	010	01	000
Punan Kelai	000010	0000	001	100	0001	1	0010	10	10	00000	100	10	00001	0001	1	001	1	1	01	000	00	01	1	1	1	1	100	100	0010	000	01	100
Singhi	010000	0000	010	100	1000	1	0000	00	10	01000	100	10	10000	1000	1	100	0	1	10	100	00	10	0	0	0	1	100	100	##	000	00	000
Timugon	001000	0000	000	100	0000	1	1000	00	10	10000	100	10	00000	1000	1	000	1	0	10	100	10	10	1	0	1	1	100	100	0001	001	10	010
Tunjung	010000	0100	010	100	1000	0	????	00	10	00001	010	10	00000	0100	1	100	1	1	10	000	00	00	0	1	?	0	000	100	????	001	10	000
Paiwan	100000	1000	100	100	0100	1	1000	10	00	10000	000	01	00000	0000	0	010	1	1	10	000	10	00	1	0	1	1	100	100	1000	010	10	100

Continued..	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Banjarese Malay	010	1	01	0	01	00000	10	010	0100	1	1	0000	????	1	1	1	10	1	1	1	1	1	0100	001	00100	1000	010	10	10	10	1	1
Belait	100	1	10	0	10	00010	10	001	0001	0	1	0000	0000	1	1	0	??	0	0	0	1	0	0100	000	00001	0000	100	10	10	10	1	1
Berawan	100	1	10	1	10	00010	10	001	0001	0	1	0000	0000	0	1	0	10	1	0	0	1	1	0100	100	00000	0100	100	10	10	10	1	1
Bintulu	100	1	00	1	10	00000	10	011	1000	0	1	????	0001	1	1	1	00	1	1	1	1	0	0100	000	00001	0100	100	00	10	10	1	?
Bukat	000	1	00	1	00	00000	10	010	0010	1	1	0100	1000	0	?	0	10	0	?	0	1	1	0100	010	00000	0100	100	00	10	10	1	?
Dayak Bakatiq	100	0	00	1	00	10000	10	???	1000	1	1	1000	0000	1	1	1	00	1	1	1	1	1	0001	100	00000	0000	000	10	10	10	1	1
Dayak Ngaju	010	1	10	1	10	01000	10	100	0100	1	1	1100	1000	1	1	1	01	1	1	1	1	1	0100	000	00010	0010	001	10	10	10	1	1
Iban	010	1	01	1	01	10000	10	100	1000	1	1	1000	0100	1	1	1	10	1	1	1	1	1	0100	000	00000	##	010	01	10	01	1	1
Ida'an	000	0	00	1	01	00001	10	010	0000	1	1	0100	0000	1	1	1	00	1	0	1	1	1	0010	100	00001	0100	000	10	10	10	1	1
Iranun	000	0	00	1	00	00000	10	000	0000	0	1	0000	0000	1	1	1	10	1	1	1	0	1	0010	000	00000	0000	000	10	10	10	1	1
Katingan	010	0	10	1	10	01000	10	100	0100	1	1	0100	1000	1	1	1	01	1	1	1	1	1	0100	000	00010	0010	001	10	10	10	1	1
Kayan	100	1	10	1	10	00000	10	010	????	1	1	0000	0000	1	1	0	00	1	1	1	1	1	0100	100	10000	0100	100	10	10	10	1	1
Kelabit	100	1	10	1	00	00000	10	101	0001	1	1	0000	0001	1	1	1	00	1	1	1	1	1	1000	100	00000	0100	100	00	10	10	1	1
Kenyah	001	1	10	1	01	00100	??	010	????	1	1	0000	0000	1	1	1	10	1	1	1	1	0	0100	100	00001	0100	100	10	10	10	1	1
Lahanan	100	1	10	1	10	10000	10	001	0010	1	1	0000	1000	1	?	1	00	1	?	1	1	1	0100	000	00000	0100	???	10	10	10	1	?
Ma'anyan	010	1	00	1	10	00000	10	010	1000	1	1	0001	1000	1	1	0	10	1	?	0	1	1	0100	000	00000	0100	100	10	10	10	1	1
B. Indonesia	010	1	01	1	01	10000	10	110	1000	1	1	1000	0100	1	1	1	10	1	1	1	1	1	0100	001	00100	1000	010	01	10	01	1	1
Maloh	010	1	10	1	01	01000	10	100	1000	1	1	0001	1000	0	1	1	00	1	1	?	1	1	0100	000	00000	1000	000	10	10	10	1	?
Melanau	100	1	10	1	10	10000	10	011	1000	1	1	0000	1000	1	1	1	??	1	1	1	1	1	0100	000	00000	0100	100	11	10	10	1	1
B. Melayu	010	1	01	1	01	10000	10	010	1000	1	1	1000	0100	1	1	1	10	1	1	1	1	1	0100	001	00100	1000	010	01	10	01	1	1
Modang	100	1	00	1	10	00100	01	010	0000	1	1	0010	0010	1	1	0	10	1	0	1	1	1	0100	010	01000	0100	100	10	01	10	1	?
Punan Kelai	100	1	00	1	10	00100	01	100	1000	1	1	0010	0010	1	1	0	10	1	1	1	1	1	0100	010	01000	0100	000	10	00	10	1	?
Singhi	100	1	00	1	10	10000	10	110	????	1	1	1000	0000	1	1	1	10	1	1	1	1	1	0001	000	00000	0100	100	10	10	10	1	?
Timugon	001	1	01	1	00	00001	10	010	0001	0	1	0000	0000	0	1	1	10	0	0	1	1	1	1000	100	00000	0000	100	10	10	10	1	?
Tunjung	000	1	??	1	10	00000	10	010	1000	1	1	1000	1000	1	?	1	10	1	?	1	1	1	0100	100	00000	0001	000	10	01	10	1	1
Paiwan	000	1	10	1	00	00000	00	000	0000	0	0	0000	1000	0	0	1	00	1	0	0	0	1	0000	100	10000	0001	000	10	10	10	1	1

A5. Bayesian Inference results and the Bayes Factor

Below, we have the marginal log likelihoods for the Bayesian MCMC runs:

Estimated marginal log likelihoods for the single rate (1-parameter) model MCMC run:

Run	Arithmetic mean	Harmonic mean
1	-1498.13	-1522.53
2	-1498.28	-1526.63
Total	-1498.20	-1525.96

Estimated marginal log likelihoods for the dual rate + ASRV (3-parameter) model MCMC run:

Run	Arithmetic mean	Harmonic mean
1	-1446.75	-1484.85
2	-1448.04	-1476.78
Total	-1447.20	-1484.16

Bayes Factor

Bayes factor interpretation table (after Kass & Raftery 1995; based on Jeffreys 1961)

2 loge(B_{10})	loge(B_{10})	Evidence against H_0
0 to 2	0 to 1	Not worth more than a bare mention
2 to 6	1 to 3	Positive
6 to 10	3 to 5	Strong
>10	>5	Very strong

Where B_{10} = Bayes factor = $\frac{\text{marginal likelihood } H1}{\text{marginal likelihood } H0}$;

$\log_e(B_{10})$ = marginal likelihood H_1 – marginal likelihood H_0

Languages of Borneo Map Key

Case languages in **bold**

Location coordinates from the Ethnologue (Lewis 2009)

1. Abai Sungai
2. Ampanang
3. Aoheng
4. Bahau
5. Bah-Biau Penan
6. Bakati'
7. Bakumpai
8. Balangingi
9. Balau
10. **Banjar**
11. Baram Kayan
12. Basap
13. Bau Bidayuh
14. **Belait**
15. Benyadu'
16. Berau Malay
17. Berusu
18. Biatah Bidayuh
19. **Bintulu**
20. Bolongan
21. Bonggi
22. Bookan
23. Brunei
24. Brunei Bisaya
25. Bukar-Sadong Bidayuh
26. **Bukat**
27. Bukit Malay
28. Bukitan
29. Busang Kayan
30. Central Berawan
31. Central Dusun
32. Central Melanau
33. Coastal Kadazan
34. Cocos Islands Malay
35. Daro-Matu Melanau
36. Dumpas
37. Dusun Deyah
38. Dusun Malang
39. Dusun Witu
40. East Berawan
41. Eastern Penan
42. Embaloh
43. Gana
44. Hovongan
45. **Iban**
46. **Ida'an**
47. **Iranun**
48. Jangkang
49. Kajaman
50. Kalabakan
51. Kanowit-Tanjong Melanau
52. Kayan Mahakam
53. Kayan River Kayan
54. **Kelabit**
55. Kembayan
56. Kendayan
57. Keningau Murut
58. Keninjal
59. Kereho
60. Kimaragang
61. Kiput
62. Klias River Kadazan
63. Kohin
64. Kota Bangun Kutai Malay
65. Kota Maruda Talantang
66. Kota Maruda Tinagas
67. Kuijau
68. Labuk-Kinabatangan Kadazan
69. **Lahanan**
70. Lanas Lobu
71. Lawangan
72. Lengilu
73. Long Wat
74. Lotud
75. Lun Bawang (Lundayeh)
76. **Ma'anyan**
77. Mainstream Kenyah
78. **Malay**
79. Malayic Dayak
80. Mapun
81. Mendalam Kayan
82. Minokok
83. **Modang**
84. Molbog
85. Mualang
86. Murik
87. Narom
88. **Ngaju**
89. Okolod
90. Ot Danum
91. Paku
92. Paluan
93. Papar
94. Punan Aput
95. Punan Batu
96. Punan Merah
97. Punan Merap
98. Punan Tubu
99. Putoh
100. Rara Bakati'
101. Rejang Kayan
102. Remun
103. Ribun
104. Rungus
105. Sabah Bisaya
106. Sa'ban
107. Sajau Basap
108. Salako
109. Sanggau
110. **Sara Bakati'**
111. Seberuang
112. Sebop
113. Sebuyau
114. Segai
115. Sekapan
116. Selungai Murut
117. Semandang
118. Sembakung Murut
119. Serudung Murut
120. Sian
121. Siang
122. Sibu Melaunau
123. Southern Sama
124. Sugut Dusun
125. Tagal Murut
126. Taman
127. Tambunan Dusun
128. Tampias Lobu
129. Tatana
130. Tausug
131. Tawoyan
132. Tempasuk Dusun
133. Tenggarong Kutai Malay
134. Tidong
135. **Timugon Murut**
136. Tobilung
137. Tombonuo
138. Tring
139. Tringgus-Sembaan Bidayuh
140. **Tunjung**
141. Tutong
142. Ukit
143. Uma' Lasan
144. Uma' Lung
145. Upper Kinabatangan
146. Wahau Kayan
147. Wahau Kenyah
148. West Berawan
149. West Coast Bajau
150. Western Penan

Location coordinates from the ABVD (Greenhill et al 2008)

151. **Berawan (Long Terawan)**
152. **Katingan**
153. **Kayan (Uma Juman)**
154. **Kenyah (Long Anap)**
155. **Maloh**
156. **Melanau (Mukah)**
157. **Punan Kelai**
158. **Singhi**

• Language Map and coordinates taken with permission from the Ethnologue: Languages of the World, Sixteenth edition (Lewis, 2009) and the Austronesian Basic Vocabulary Database (Greenhill et al, 2008) •