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## Contributions of Bayesian Phylogenetics to Exploring Patterns of Macroevolution in Archaeological Data

Gjesfjeld, Erik; Jordan, Peter

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# Chapter 9

## Contributions of Bayesian Phylogenetics to Exploring Patterns of Macroevolution in Archaeological Data



Erik Gjesfjeld and Peter Jordan

### Introduction

Charles Darwin, in his “B” notebook on the transmutation of species, now famously wrote “I think” directly above a sketch that visualizes evolutionary relationships as a network of interconnected branches or tree (Barrett 2009). This simple tree sketch, drawn nearly 20 years before *On the Origin of Species* (Darwin 1859) was published, has now become a powerful metaphor in understanding the evolutionary history of organisms. Since Darwin, the methods for constructing trees have changed dramatically, but the overall goal of phylogenetic methods remains the same, to represent evolutionary relationships between taxa.

The application of phylogenetic methods in archaeology relies on the perspective that material culture participates in a system of inheritance and transformation (sensu Boyd and Richerson 1985) and that material culture diversity results from historical processes of cultural change. Broadly, phylogenetic inference provides a methodological framework to reconstruct the dynamics of cultural macroevolution, which emphasizes cultural change over longer time scales and between cultural traditions and artifact *lineages* (see Chapter 6, this volume). Phylogenetic methods are often most helpful as a basis for classification, to reconstruct historical relationships in the absence of complete data and/or to examine traits shared between entities due to their common ancestry (Boyd et al. 1997). We stress that phylogenetic inference emphasizes a macroevolutionary perspective which is a related but alternative perspective to microevolutionary models of social learning and cultural transmission. This is not to suggest that cultural transmission processes are not an important part of shaping the archaeological record but rather an acknowledgement that cultural phylogenies are often better suited to examine broader historical changes between and across artifact *lineages* (see Box 9.1 Glossary for definition). This includes variability in the tempo of artifact change, temporal periods of divergence between artifact *lineages*, and the dynamic relationship between the emergence and loss of artifact traditions.

We argue here that recent advancements in phylogenetic methods provide substantial added value to archaeological research by permitting the exploration of unique macroevolutionary phenomena.

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E. Gjesfjeld (✉)  
Department of Archaeology, University of Cambridge, Cambridge, UK  
e-mail: [eg540@cam.ac.uk](mailto:eg540@cam.ac.uk)

P. Jordan  
Faculty of the Arts, Arctic and Antarctic Studies, University of Groningen, Groningen, The Netherlands  
e-mail: [p.d.jordan@rug.nl](mailto:p.d.jordan@rug.nl)

We demonstrate the potential of model-based inference by providing a worked case study that applies Bayesian phylogenetics to the archaeological record of the Great Plains. Through this example we guide the reader through key components of the analysis including data acquisition, model selection, and archaeological interpretation. Our goal is to demonstrate how a Bayesian approach can help to illuminate poorly understood patterns of material culture diversity and aid in refining interpretations of the archaeological record and the complexities of material culture evolution.

### **Box 9.1: Glossary for Definition**

**Bayes Factor:** The ratio between marginal likelihoods from different models. These are commonly used to evaluate whether there is evidence to favor one model over another (Drummond and Bouckaert 2015).

**Bayesian Skyline Coalescent Prior:** Prior distribution on tree shape that links the divergence times of artifact lineages from the same population. The process broadly works by merging characters through time from most recent to least recent by estimating population sizes at each coalescent interval. For additional details, consult Drummond et al. (2005).

**Burn-in:** Initial part of the Markov chain Monte Carlo when it is approaching the sampling distribution from its starting point (BEASTdoc Glossary 2018).

**Clock Model:** A model setting based on the assumptions of a molecular clock. A strict clock model assumes constant but stochastic change across branches of the phylogeny. A relaxed clock allows the rate of change to vary across lineages, or among different parts of the phylogeny (BEASTdoc Glossary 2018).

**Characters/Character States:** Characters are a set of mutually exclusive attributes that can be used to categorize the variation of an artifact assemblage (O'Brien and Lyman 2003). The choice of characters in a phylogenetic analysis is often based on which traits of the artifact are expected to change most over time as a result of vertical transmission (O'Brien et al. 2002). Each character can take a range of values which are known as character states so that every artifact is defined by at least one character state in each class of characters.

**Gamma Rate Categories:** Number of discrete divisions that are used to approximate the gamma distribution of rates with the mean of each category used to represent all the rates falling in the category (Yang 1994).

**Homoplasy:** Character states that cannot be shown to be homologous or shared by a set of artifacts that is present in their common ancestor (O'Brien and Lyman 2003).

**Lineage:** A sequence of artifacts that are thought to have direct descent from a particular ancestor or ancestral group (O'Brien and Lyman 2003).

**Marginal Likelihood:** Also referred to as model evidence, this is the likelihood of the data integrated over all parameter configurations.

**Markov Chain Monte Carlo:** Stochastic algorithm for drawing samples from a posterior distribution. Often used to search the space of possible trees in order to identify trees with the highest likelihoods, which go on to form the posterior distribution (BEASTdoc Glossary 2018).

**Maximum Likelihood:** The highest probability of the observed data given the model of evolution (i.e., the tree, the rate of change, the gamma shape, etc.) (BEASTdoc Glossary 2018).

**Mk Model:** A model of character state change developed by Lewis (2001) and Pagel (1994) that assumes the transition among characters states follows a random Markov process where the probability of change from one state to another depends only on the current state (Harmon 2018). The model also assumes that every state is equally likely to change to any other states and is therefore similar to the Jukes-Cantor model for sequence evolution (Harmon 2018).

(continued)

**Box 9.1** (continued)

**Monophyletic:** A complete set of taxa that is descended from a common ancestor (O'Brien and Lyman 2003).

**Parameters:** Numerical characteristics that specify the properties of a mathematical model or distribution (Everitt and Skronidal 2010). In phylogenetics, parameter values often aim to describe the rate of change or substitution in character states.

**Parsimony:** The scientific principle of choosing from among competing hypotheses the one that explains the data most simply (O'Brien and Lyman 2003).

**Path Sampling:** Path sampling (via the stepping stone algorithm Baele et al. (2012)) is a technique to estimate the marginal likelihood by running MCMC chains at different “temperatures” (Drummond and Bouckaert 2015). Bayes factors can be calculated from these techniques in order to compare different models.

**Prior:** The prior probability distribution, which represents your prior assumptions about the different model parameter values before analyzing the data. The prior combined with the likelihood yields the posterior (BEASTdoc Glossary 2018).

**Posterior:** The posterior probability distribution, which represents the probability distribution over the parameter state space given the data under the chosen model of evolution (BEASTdoc Glossary 2018).

**Rate Heterogeneity:** Variability in the rates of change among character states among lineages. Constant rate models assume no rate heterogeneity across character states, whereas variable rate models often use a gamma distribution to model differences in rates between lineages (Skinner 2010).

**Tip Dates:** Temporal date specified for each individual unit of analysis (i.e., house style).

**Topology:** The arrangement of taxa (such as artifact classes or house styles) on a phylogenetic tree (O'Brien and Lyman 2003).

**Yule Tree Prior:** A prior parameter that describes the net rate of origination and assumes a constant rate of lineage emergence for each branch in the tree (Bouckaert et al. 2014).

## Model-Based Approaches to Phylogenetic Inference

Over the last 25 years, computational biology has witnessed remarkable advancements in the statistical methods used to infer phylogenies. The initial and continuing driving force behind many of these new approaches is the rapid accumulation of large-scale genetic data. The emergence of new “molecular” approaches has perpetuated a misconception that model-based phylogenetic inference is only applicable to genetic data, even though these approaches can be equally applied to sequence data, morphological data, or cultural data.

The most significant difference of “molecular” phylogenetic methods is the use of an explicit mathematical model of how biological or cultural traits change over time. Previously, the reconstruction of evolutionary relationships primarily relied on cladistic methods (Hennig and Davis 1999; O'Brien and Lyman 2003). These methods were often advertised as “model-free” (Harmon et al. 2006) as the principle of *parsimony* is used to infer how traits change over time. *Parsimony* advocates that nature favors simplicity and that trees with the fewest number of changes are the trees that best represent the evolutionary relationships between taxa (Straffon 2016). When presented with a range of phylogenetic hypotheses, *parsimony* acts as the optimality criterion for selecting among the different trees (García Rivero 2016). The reality is that minimizing the changes in *character states* (i.e., *parsimony*) may not technically be a model of character change, but it is still a very strong assumption about how *character states* evolve through time (Swofford et al. 1996).

Starting in the 1990s, Bayesian phylogenetic methods were introduced into evolutionary biology and since their introduction have become an influential tool for inferring the evolutionary history of genomic sequences (Yang and Rannala 1997; Huelsenbeck et al. 2001). The popularity of Bayesian methods can be attributed to two factors: the development of powerful models of data analysis and the availability of user-friendly computer programs to apply these models (Nascimento et al. 2017). Broadly, Bayesian phylogenetic inference builds from *maximum likelihood* estimation where the data is treated as a fixed observation and the analysis aims to find values of model *parameters* that best explain the data (see Greenhill and Gray 2009 for an extended discussion of likelihood calculations).

Current models of how *character states* change vary from simple to increasing complex depending on the number or model *parameters*. One of the simplest DNA models of change is the Jukes-Cantor model (Harmon 2018), which assumes equal rates of change across *character states* and therefore has only one *parameter*. More complex DNA models, such as the generalized time-reversible (GTR) model, has up to 12 *parameters* which specify different frequencies and rates of change across DNA sites. In a traditional statistical sense, model-based approaches can be viewed as parametric models of character evolution, where we assume that we have a general understanding of the distribution of *character states* (Lukhtanov 2010).

One of the most commonly leveled criticisms against a model-based approach is that models of character evolution developed in the biological sciences are inappropriate for understanding change in artifacts, cultural traits, or languages. As highlighted by Greenhill and Gray (2009, p. 6), this criticism represents a misunderstanding of model-based inference. The application of a seemingly simple model of change does not invalidate the methodology of model-based inference, but rather emphasizes the balance between finding a model with *parameters* that capture the process of change. For example, Greenhill and Gray (2009, p. 6) highlight a biological model that assumes symmetrical change, where the rate of a trait arising is the same as the rate of a trait being lost. However, the symmetrical change assumption may not be appropriate for linguistic data as once a cognate word has arisen, it is much more likely for it to be lost than for that same cognate word to arise in another language. In this situation, model *parameters* can be modified based on our expectations such as adding a second *parameter* so that there is one rate for the origination of a new cognate and one rate for the loss of a cognate. We may even want a more flexible model where each *character* (or artifact trait) is given an inherent rate of change so that some traits may arise or be lost more rapidly, whereas other traits may be more resistant to change (Greenhill and Gray 2009).

Drawing on the success of Bayesian approaches in biology and linguistic anthropology, we argue here that these methods can provide three contributions to improving our understanding of macroevolutionary patterns in archaeological data.

- *Mosaic evolution*: Mosaic evolution can be defined as the process of independent changes in different portions of the phenotype (Stanley 1979). The concept highlights that different organism traits can evolve at different rates as opposed to the assumption that organism traits evolve as an integrated whole (Prentiss et al. 2016). Characterizing mosaic evolution requires the ability to quantify and visualize variability in the rates that artifact *lineages* (or *characters*) are evolving. As highlighted above, a model-based approach allows us to relax the assumption that change occurs at a constant rate or that the fewest number of changes is the correct model of change. Instead, we are able to investigate how rates of change may vary (or not vary) across artifact *lineages* and traits. This quantification of *rate heterogeneity* is a valuable step toward disentangling patterns of “mosaic evolution” that are likely prevalent within many cultural contexts (Prentiss et al. 2016).
- *Divergence times*: Model-based approaches also allow for the integration of temporal information in order to time calibrate our trees. In contrast to linguistic and anthropological data, archaeologists often have fairly robust knowledge of when particular changes occurred in the archaeological record. Model-based methods allow us to integrate this valuable information into our analysis by

either assigning *tip dates* to artifact *lineages* or constraining specific nodes in the tree to make sure divergence events occurred during specific time frames.

- *Rates of diversification*: Recent advancements in quantitative paleontology provide a set of Bayesian model-based tools to explore changing rates of diversification through time. These approaches provide new insights into old archaeological questions about how variability in rates of origination and extinction influence patterns of artifact diversity (Lyman and O'Brien 2000). We argue here that by inferring rates of artifact diversification over time, we can shift our expectations beyond tracing the diversity of artifact *lineages* through time and closer toward a more comprehensive understanding of the unique macroevolutionary patterns found in cultural data.

## Application of Bayesian Phylogenetic Methods to Archaeological Evidence

Despite the potential of Bayesian phylogenetic methods, their application to archaeological data can seem daunting. Our goal is to provide a worked example of a Bayesian approach that will help facilitate the application of these methods to additional archaeological datasets. We will demonstrate the implementation and interpretation of our framework by working through key stages in the research process: (1) defining research questions, (2) data acquisition and classification, (3) model selection, (4) tree-building, (5) modeling macroevolutionary patterns, and (6) archaeological interpretation.

All of the phylogenetic analysis performed in this chapter uses the freely available BEAST2 program (Bouckaert et al. 2014) with additional help from packages available in the R statistical environment (R Core Team 2017). The data and code used here are available for download at GitHub and Zenodo (Gjesfjeld 2018). The files in the repositories contain all the necessary files in order to replicate this analysis along with a help file that provides supplementary details on performing the phylogenetic analysis.

### Defining Research Questions

The Great Plains of North America is a geographic area consisting of roughly 25% of the United States and represents the largest cultural area of American Indians. Early archaeological and ethnographic research in the Great Plains often emphasized the shared characteristics between cultural groups such as the importance of large game hunting (Lowie 1954). The features of Great Plains groups served as a basis for the stereotypical image of American Indians as heavily reliant on the horse, living in skin tipis, wearing feather headdresses, and hunting bison (Wood 1998). One obvious exception to this is the Plains Village period, which is broadly defined as groups that engaged in a small-village, semi-horticultural way of life beginning around 900 AD and ending after European contact. The emergence and continuity of traditions during this period are of primary interest to this project as we broadly aim to address the question of whether the similarities between Plains Village cultural groups developed due to recent shared ancestry or through independent convergence.

Our decision to focus on the archaeology of the Plains Village period does not stem from any previous affiliation or strong knowledge about the archaeology of the region but rather an interest into defining and resolving questions about cultural continuity, blending, and divergence. We believe that the questions faced by Great Plains archaeologists are common to many archaeological contexts, and we therefore aim to demonstrate how a phylogenetic approach can provide insights into disentangling the historical relationships between archaeological traditions.

**Table 9.1** Major periods and cultural traditions in three Plains subareas (redrawn from original in Lehmer 1971, p. 30)

Major Periods	Subareas		
	Northwestern Plains	Central Plains	Middle Missouri
Equestrian	Disorganized Coalescent		
Plains Village	Horse Tribes	Coalescent Tradition	
Plains Woodland		Central Plains Tradition	Middle Missouri Tradition
Foraging	Plains Woodland Complexes		
Paleo-Indian	Foraging Complexes		
	Early Hunting Complexes		

The Plains Village period is viewed as a geographical and cultural intermediate between the nomadic groups present in the Northwestern Plains and the fixed settlement populations of the Eastern Woodlands. The emergence of this lifestyle appears in various geographic subareas including the Central Plains (southeastern Nebraska and Eastern Kansas) (Wedel 2001) and the Middle Missouri (southeastern South Dakota and west-central North Dakota) (Wood 2001). The origins of the Central Plains and Middle Missouri cultural traditions are largely considered unknown and subject to debate (Wood 2001, p. 190; Wedel 2001, p. 183) but are often viewed as independent from each other with similar horticultural practices arising through connections with neighboring populations to the south and east.

The later tradition of the Plains Village period is referred to as the Coalescent, beginning around 1400 AD and centering around the Missouri River in central South Dakota. As highlighted by Krause (2001), the origins of the Coalescent are considered a product of immigration from the Central Plains geographic subarea, which brought their cultural practices north to the Middle Missouri geographic subarea. Here, Central Plains populations are believed to have resettled abandoned or at least sparsely settled areas that were previously associated with the Middle Missouri tradition. Post-European contact variants of the Coalescent tradition are identified as an amalgamation of Central Plains and Middle Missouri traditions (Table 9.1).

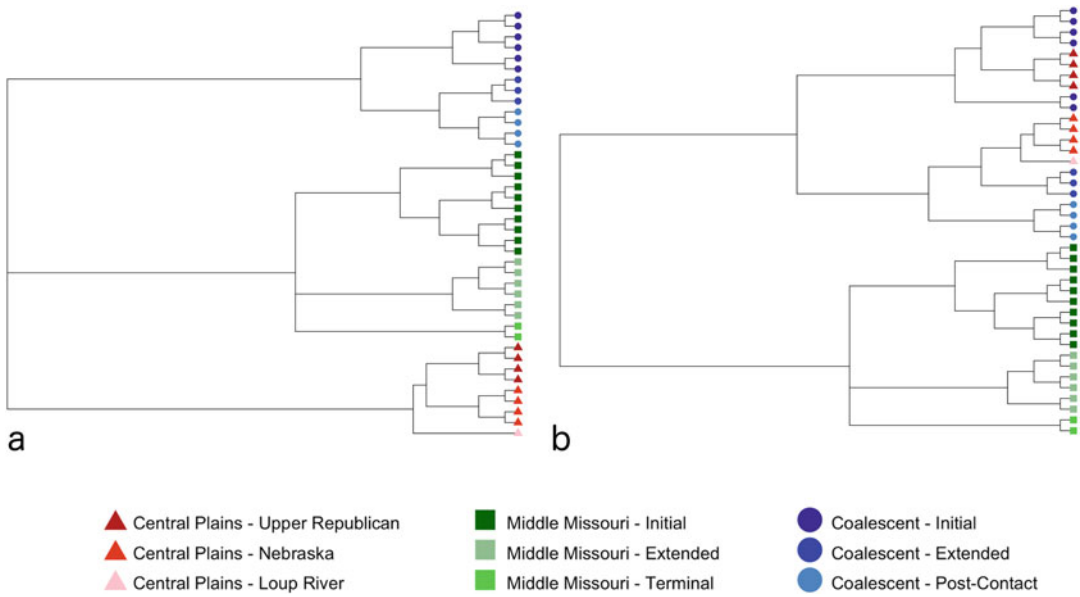
Based on this archaeological background, we can develop a set of initial expectations for what we would expect from our phylogenetic analysis.

**Expectation 1:** No shared ancestry between the Central Plains tradition and the Middle Missouri tradition as current archaeological evidence suggests that these are traditions with independent origins from each other. The phylogenetic expectation is that distinct or *monophyletic* clades for each tradition will be apparent in the tree *topology* (Fig. 9.1).

**Expectation 2:** Partial shared ancestry between the Central Plains tradition and the Coalescent tradition as the origins of the Coalescent are viewed as a product of immigration from the Central Plains region. The phylogenetic expectation is that artifact traditions associated with sites from the Central Plains will group within clades that also contain artifact traditions from Coalescent sites (Fig. 9.1).

Our expectations are intentionally presented as broad hypotheses about the historical relationships between Plains Village cultural traditions. We want to emphasize that tree *topologies* from either cladistics or model-based frameworks should not be used as confirmatory tests of cultural transmission but rather as exploratory hypotheses of the heritable continuity between our units of analysis. If our tree *topology* mirrors our simple archaeological expectations, we could argue that our phylogenetic model is a potentially useful proxy for the culture history of the Plains Village period. If it becomes





**Fig. 9.1** Hypothetical tree topologies for expectations of shared ancestry between Plains Village traditions. Tree on left is suggestive of the first expectation of no shared ancestry between traditions indicated by deep branch lengths between monophyletic clades that are associated with each cultural tradition. The tree topology on the right suggests partial shared ancestry between the Central Plains and the Coalescent traditions as the clades contain sites that are associated with both traditions

apparent that our phylogenetic model clearly does not fit with our previous archaeological knowledge, we should critically evaluate whether our phylogenetic assumptions and/or our archaeological data are appropriate to evaluate questions about the cultural continuity between Plains Village traditions.

**Data Acquisition and Classification**

One of the most significant challenges in applying phylogenetic analysis to archaeological data is the construction of taxa (O’Brien et al. 2002). In biology, the most common forms of taxa construction use the species concept, despite many debates surrounding the definition of a species. In archaeology, defining artifact *lineages* based on the species concept is problematic at best, so we use our own paradigmatic classification scheme which defines each artifact or feature on a series of unordered and unweighted *character states* (O’Brien et al. 2002; Prentiss et al. 2014). We used house feature data from 30 archaeological sites associated with specific Plains Village traditions. Seven *characters* with between three and eight *character states* were used to categorize each house style (see Table 9.2). Each house style was recorded as a series of binary variables based on the presence or absence of each *character state*. The raw data can be accessed in the online data repository associated with this volume (Gjesfeld 2018). The choice of *characters* to be included is based on expectations as to which parts of house would change most over time and thus would create the strongest phylogenetic signal (see O’Brien et al. 2002 for an extended discussion about choosing *characters* for analysis).

It is important to note that the characters used in this analysis are assumed to be independent. This assumption of character independence is a necessary but often incorrect assumption when



**Table 9.2** *Characters and character states used to classify house features*

<i>Character</i>	
<i>Character state</i>	
I. Interior posthole pattern	V. Entrance direction
1. Circular	1. North
2. Square/rectangular	2. Northeast
3. Linear	3. East
4. Double linear	4. Southeast
	5. South
II. Number of central postholes	6. Southwest
1. Two	7. West
2. Four	8. Northwest
3. More than five	
	VI. Number of hearths
III. Exterior posthole pattern	1. 0
1. Circular	2. 1
2. Square	3. 2 or more
3. Rectangular	
	VII. Estimated size of house (sq. ft.)
IV. Number of exterior postholes	1. 0–250
1. Less than ten	2. 251–500
2. 11–20	3. 501–750
3. 21–30	4. 751–1000
4. 31–40	5. 1001–1250
5. 41–50	6. 1251–1500
6. 51–60	7. 1501–1750
7. 61–70	8. 1751–2000
8. 71–80	
9. 81–90	
10. Over 91	

evaluating morphological (or technological) characters as these traits often strongly interact with each other (Harmon 2018). If traits are thought to be non-independent, it can no longer be assumed that the phylogeny is a direct measure of phylogenetic signal and may in fact represent functional relationships between *characters*. This does not undermine the construction of the tree topology but may alter the inference of shared ancestry between taxa. The statistical determination of character independence is a topic outside of the scope of this chapter but has been widely discussed and should be considered in any phylogenetic analysis. Depending on the structure of the data used, helpful methods include testing for the correlated evolution of different characters (Dunn et al. 2011) or assessing the nonrandom association of character states across various characters (i.e., linkage disequilibrium).

The taxa (i.e., house styles) used in this analysis (Table 9.3) were chosen to represent a range of time periods, cultural phases, and geographic regions (similar to Prentiss et al. 2014). The house styles used in this analysis by no means represent a comprehensive list of house styles associated with Plains Village traditions and variants. In this respect, we view this study as a preliminary demonstration of how to apply Bayesian phylogenetic inference with future studies needing to consult with specialists in Great Plains archaeology to identify additional sites and samples for analysis.

**Table 9.3** List of archaeological sites where house styles were chosen from along with literature reference

Central Plains tradition		Middle Missouri tradition	
<i>Upper Republican phase</i>		<i>Initial Middle Missouri variant</i>	
Red willow	Grange (1980)	Dodd	Lehmer (1954)
Owens	Wedel (1933)	Breeden	Brown (1974)
Holdredge	Wedel (1934)	Swanson	Hurt (1951)
Mowry bluff	Wood (1969)	Langdeau	Caldwell and Jensen (1969)
<i>Nebraska phase</i>		Pretty head	Caldwell and Jensen (1969)
Theodore Davis	Gradwohl (1969)	Jiggs Thompson	Caldwell and Jensen (1969)
Patterson	Bozell and Ludwickson (1994)	Mitchell	Alex (1973)
Little Pawnee Creek	Bozell and Ludwickson (1994)	<i>Extended Middle Missouri variant</i>	
<i>Loup River phase</i>		Thomas Riggs	Hurt (1953)
Sweetwater	Champe (1936)	Cannonball	Griffin (1984)
Coalescent tradition		Bendish	Theissen (1976)
<i>Initial variant</i>		Fire Heart Creek	Lehmer (1966)
Black Partizan	Caldwell (1966)	<i>Terminal variant</i>	
Arzberger	Spaulding (1956)	Huff	Howard (1962)
Crow Creek	Kivett and Jensen (1976)	Shermer	Sperry and Bass (1968)
Talking crow	Smith (1977)		
<i>Extended variant</i>			
Demery	Woolworth and Wood (1964)		
Over's La Roche	Hoffman (1968)		
Molstad	Hoffman (1967)		
<i>Post-contact</i>			
Big village	O'Shea and Ludwickson (1992)		
Like a fishhook	Smith (1972)		

## Model Selection

All scientific models aim to find the balance between being too simple and too complex. One of the advantages of a model-based phylogenetic framework is the ability to evaluate a range of different models and select the model that best fits our data. This explicit testing between models of change is perhaps one of the most significant differences from cladistics where it is assumed that the best-fitting model is the one with the fewest changes.

## Choosing the Model Family

The archaeological data used in this case study is structured as a set of binary *character states* (see Table 9.2) that summarize the morphology of each house feature. Based on literature from biological systematics, we implemented the *Mk model* (Lewis 2001) in our analysis of Plains Village house features for a number of reasons. First, in the estimation of phylogeny from discrete morphological data, the *Mk model* assumes that no *character state* is predetermined as ancestral or dependent, which is in contrast to a *parsimony* framework that encourages the user to select an ancestral form or outgroup. Second, the *Mk model* allows *characters* to change freely back and forth between two states, and this probability of change is symmetrical (Lewis 2001, p. 916; Harmon et al. 2006, p. 217). Third, a *character* can change state at any instance in time, which is a valid assumption for any scenario where change at the day-to-day or even year-to-year scale is unknown (Harmon et al. 2006). Finally, the *Mk model* does not favor any broad trend of evolutionary change and therefore provides

equal weight to either gradual or punctuated change. The *Mk model*, like most phylogenetic models, is not an exact specification of how characteristics change but rather a broader set of assumptions given what we know about our data. In some instances, such as DNA nucleotide substitutions, model assumptions may be highly specified given our existing knowledge. In cultural contexts, where we know less about *character state* changes, it may be beneficial to implement a broad model of change so that we can explore a wide range of *parameter* values. The *Mk model* is implemented in BEAST2 by installing the additional morph-model (MM) package.

The *Mk model* has also demonstrated greater accuracy in tree reconstruction than *parsimony* methods (O'Reilly et al. 2016; Wright and Hillis 2014). In two independent studies, phylogenies produced using likelihood models were considered more accurate in recovering a tree *topology* from simulated morphological data. Model-based approaches also demonstrated less error in analyses that used fewer *characters* and realistic values of *homoplasy*. However, O'Reilly et al. (2016) do suggest that while *parsimony* methods were less accurate than likelihood methods, they did achieve higher levels or precision (i.e., higher consistency in the number of nodes reconstructed across a range of tree *topologies*).

### Specifying Model Settings

A model-based framework also strongly encourages the researcher to specify model settings in order to improve the fit of our model to the data. The first setting to adjust is the number of *gamma rate categories*. The number of *gamma rate categories* aims to encompass the amount of variation in the rates of change between different *characters*. For example, a gamma category count of one would suggest there is no variability in rates of change between *characters* (i.e., all house style traits change at approximately the same rate), whereas a value of four would indicate higher variability in rates. Broadly, you can imagine that with four rate categories, we are suggesting that each house style *character* is able to change at one of four different speeds such as very slow, slow, medium, and fast (Greenhill and Gray 2009).

We can also investigate how the branches of the tree (not just the traits) vary in their rates of change, referred to as the *clock model*. A strict clock assumes that there is no variation in rates of change across branches. A relaxed clock assumes variation across branches is autocorrelated, so that neighboring branches are more similar in their rates of change than branches that are further apart from each other.

Finally, as this is a Bayesian framework, we can also consider different *priors* on the underlying process that generates the tree (Drummond and Bouckaert 2015). Here, we consider two *priors*. The first is a pure-birth *Yule process* which starts with one lineage and then splits into two *lineages* after some amount of time, similar to a traditional bifurcating tree. The second is a *Coalescent Bayesian Skyline prior* (Drummond et al. 2005) which moves backward in time merging *characters* together according to a random process that assumes each *character state* is equally likely to have been passed from one generation to the next.

Adjusting model settings is most easily accomplished in BEAST2 by loading the morphological data (as a nexus file) into the BEAUTi interface. The user is then able to select the *Mk model* under the Site Model tab and adjust the clock model settings, Bayesian prior settings, tip dates, and MCMC settings. After the necessary settings are chosen, BEAUTi will create an XML control file, which will be imported in BEAST, with the preferred configuration of model settings. The nexus and XML control files associated with this analysis can be found in the repositories highlighted above.

**Table 9.4** Results of model selection presenting the top six models (out of 16) including their *parameter* settings, *marginal likelihoods*, and *Bayes factors*

$\gamma$ rate categories	Clock	Prior	Marginal likelihood	Bayes factor
4	Strict	Coalescent Bayes skyline	−582	–
2	Strict	Coalescent Bayes skyline	−583	2
3	Relax	Coalescent Bayes skyline	−583	2
4	Relax	Coalescent Bayes skyline	−583	2
2	Relax	Coalescent Bayes skyline	−585	6
3	Relax	Yule	−586	8

### Choosing the Best-Fitting Model

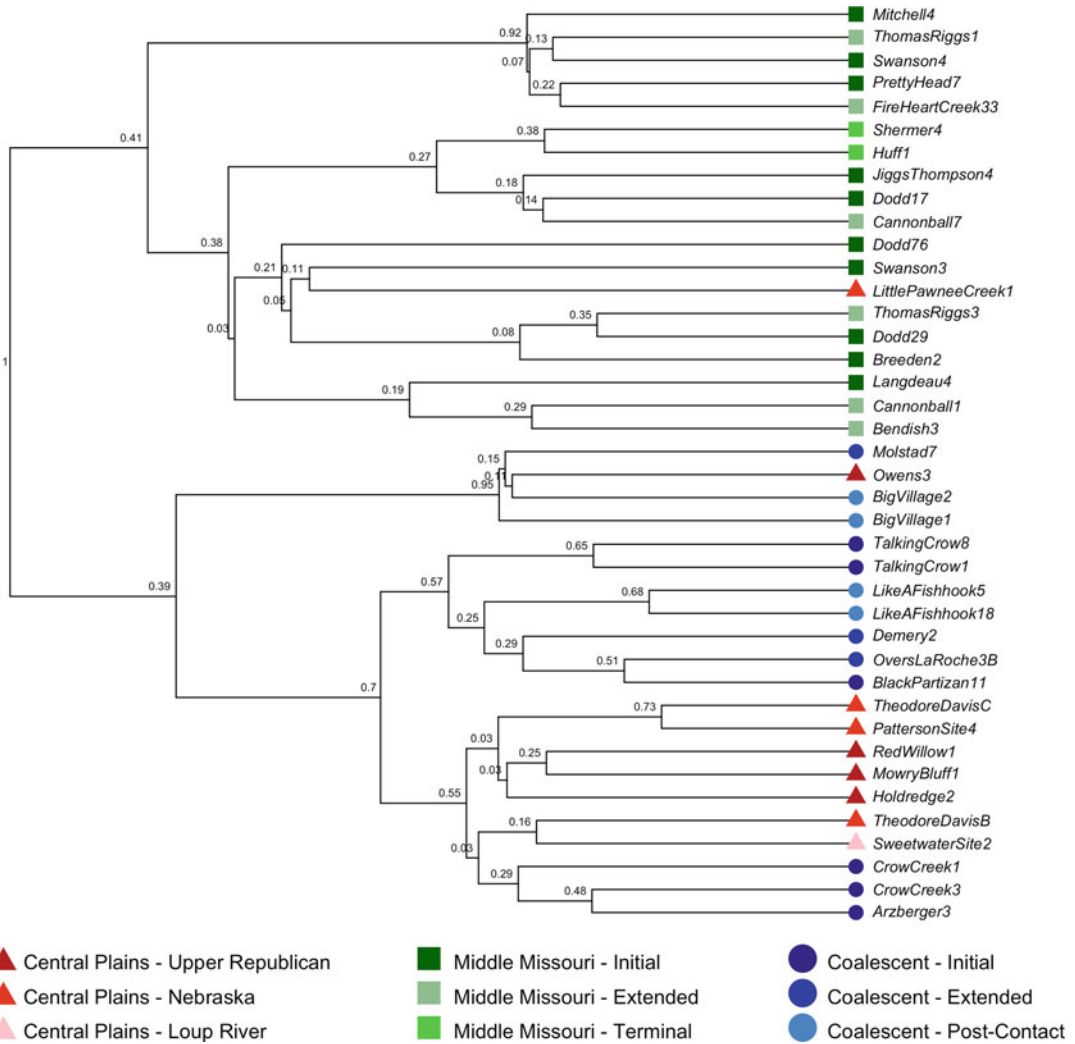
We created 16 different models based on our three different settings. This included proposing between one and four different *gamma rate categories* (1, 2, 3, 4), two different *clock models* (strict, relaxed), and two different tree *priors* (*Yule* and *Coalescent Bayesian Skyline*). To choose the best-fitting model, we implemented a *path sampling* procedure in BEAST2 (Suchard et al. 2001), which can be implemented through the additional BEAST2 path sampling app (see Bouckaert 2014 for additional details). Broadly, path sampling calculates the *marginal likelihood* of each model by comparing *posterior* likelihoods across a range of “temperatures.” The highest *marginal likelihood* value indicates the best-fitting model given our data. Results of the model selection procedure reveal that the best-fitting model of character evolution for Plains Village houses is a strict clock with four *gamma rate categories* and a *Coalescent Bayesian Skyline prior*. However, it is important to note that three other models demonstrate nearly the same strength of evidence based on *Bayes factor* (Kass and Raftery 1995) comparisons (see Table 9.4).

### Tree-Building

Perhaps the most significant difference of a Bayesian phylogenetic approach to other approaches is that there is no attempt to maximize or minimize some aspect of the tree, such as finding the tree(s) with the highest likelihood or the tree(s) with the minimum number of changes. Bayesian approaches sample the entire space of all possible trees. In this regard, the workhorse of many Bayesian analyses relies on the implementation of a *Markov chain Monte Carlo (MCMC)* (Nascimento et al. 2017). The goal of the *MCMC* is to search through the range of possible trees and identify which trees best fit our data given the model and our *priors*.

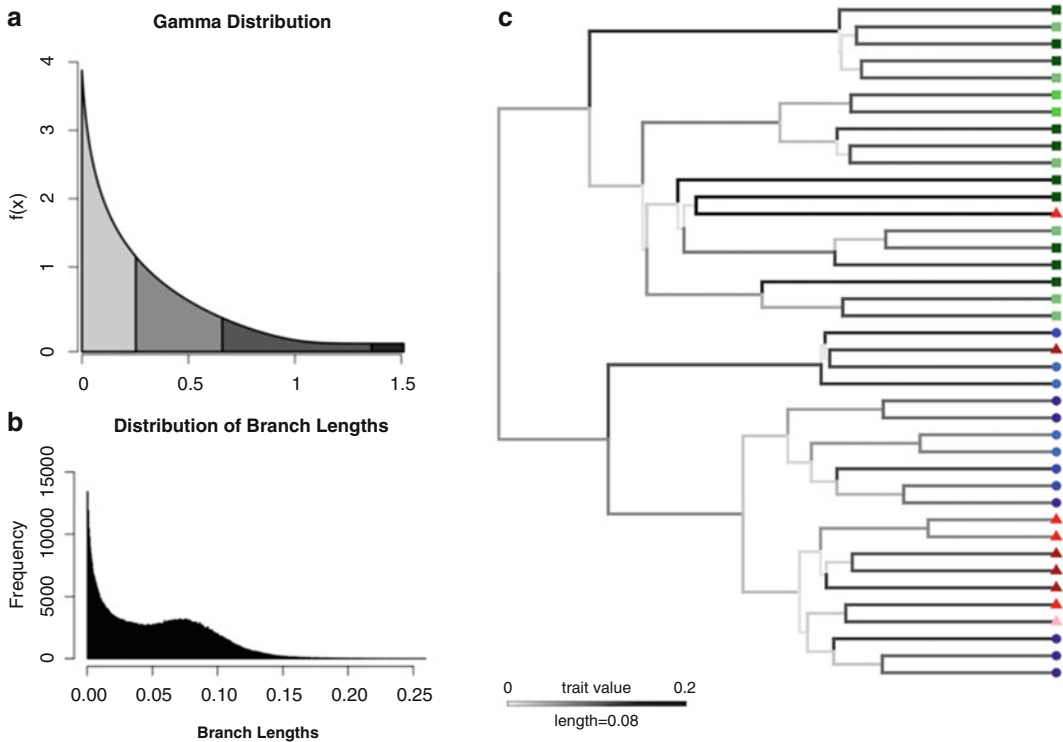
The search process starts with an initial tree and random values for the number of *parameters* in the model. After initialization, a neighboring tree (one that has a similar likelihood score) is proposed, and if the newly proposed tree has a higher *posterior* probability than the initial or current tree, the *MCMC* algorithm will accept the new tree (Yang and Rannala 2012, p. 310). The *MCMC* search will proceed to explore the space of all possible trees and if run long enough will provide a representative sample of the most probable trees. The general expectation is that trees with higher *posterior* probabilities, meaning a better fit of the data to the model, will be visited more often by the *MCMC* algorithm. By simply counting the frequency by which each tree is visited, we can get an estimate of the *posterior* probabilities for the trees (Yang and Rannala 2012, p. 310).

Based on the results of our model selection procedure, we can build our tree based on the best-fitting model specifications. In our case, these are four *gamma rate categories*, a strict clock, and a *Coalescent Bayesian Skyline prior*. Using BEAST2, we sample the entire space of possible trees using the *MCMC* chains to identify which trees best fit our data given our model and our *priors*. We



**Fig. 9.2** Maximum clade credibility tree with *posterior* probabilities as the node labels and branch lengths that are proportional to the amount of change in each branch. Tip labels correspond to Plains Village tradition and variant/phase categories

summarize post-burn *in* trees sampled by the *MCMC* algorithm into a single tree *topology*, known as the maximum clade credibility tree (Fig. 9.2). The maximum clade credibility tree can be created by reading the full sample of trees into the TreeAnnotator program associated with the BEAST2 package. Once the maximum clade credibility tree is produced, this file can be read into the R statistical environment (R Core Team 2017) using the phyloch package (Heibl 2008). The plotting and visualization of trees, including those provided here, can be done with R packages such as ape (Paradis et al. 2004), phytools (Revell 2012), and phangorn (Schliep et al. 2017). Additional packages in R can also perform a wide range of tasks including diversification analysis, tree simulations, trait evolution, and ancestral state reconstruction to name only a few.



**Fig. 9.3** Examples of three different methods to examine the variation of rates across our tree including (a) the distribution of *gamma rate categories* for a gamma shape of 0.95 following Yang (1994), (b) a histogram of branch lengths across all trees in the *posterior* distribution, and (c) a rate of substitution for each branch lengths plotted across the tree with darker branches indicating a branch with a higher rate of character state changes (i.e., substitutions) and lighter branches indicating a slower rate of character changes

## Modeling Macroevolutionary Patterns

In addition to more accurate tree-building, Bayesian methods provide additional benefits to modeling patterns of cultural macroevolution. Here we focus on three features that provide insights into the variability of rates, divergence times, and patterns of diversification.

### Mosaic Evolution

One of the most significant advantages of a model-based approach is being able to more fully understand variation in rates of change across the tree (*rate heterogeneity*). This is particularly important for interpreting material culture phylogenies where the units of analysis (such as artifact traditions) are known to be an assemblage of many units or *characters*. Furthermore, change across these different units is not likely to be constant with some traits changing more or less quickly than others, often referred to as mosaic evolution (Prentiss et al. 2016). Model-based approaches allow researchers to relax assumptions of constant change by using rate variation to their benefit. Broadly, *characters* that change quickly are used to resolve more recently derived *lineages* and more slowly evolving *characters* to resolve deeper divergences in the tree (Wright and Hillis 2014).

Here, we demonstrate three ways to explore rate differences between taxa (i.e., house styles). The first is to identify the variability of rates, which is achieved by examining the shape of the gamma

distribution that is estimated from our Bayesian analysis. The mean gamma shape estimate from our analysis of house styles is 0.95, which produces a skewed, long-tailed distribution, which suggests our data consists of a majority of slow rates but also a few more quickly evolving artifact *lineages* (see Fig. 9.3a). Our model selection results reinforce this notion by indicating that best-fitting division of our gamma distribution is into four rate categories, so that most of our *lineages* are evolving slowly, but a few are evolving much more quickly. We can also plot all the branch lengths from the trees that were sampled by the *MCMC* and view the distribution of substitution rates. We can see in Fig. 9.3b that a majority of our branch lengths have fairly small amounts of change, but we do have some branches that demonstrate longer branch lengths and therefore greater rates of change. Finally, we can map substitution rates from our Bayesian analysis onto each branch of our maximum clade credibility tree to visually examine which branches of the tree may be changing fast or slow in relation to other branches (see Fig. 9.3c). Plotting trait values onto tree topologies is most easily accomplished using the functions associated with phytools (Revell 2012).

### Divergence Time Estimates (Time Calibration)

One of the most potentially informative aspects of model-based phylogenetic inference is its ability to estimate times of divergence. Early applications of divergence time estimation typically used a strict clock where change was assumed to be constant. In more recent approaches, where we fully expect *rate heterogeneity* across the tree, calculating divergence time estimates requires supplemental dating information. In general, the branch lengths of a tree created from a model-based framework are proportional to the amount of change in that branch, typically expressed as the rate of substitution (Greenhill and Gray 2009). In order to time calibrate our phylogeny, we need to add calibration points. In other words, we need to place age ranges on certain nodes of the tree, which in turn allows certain branches of the tree to either change faster or slower than others depending on the date estimate. When chronological information of artifact *lineages* is known precisely, then divergence time estimates may not provide increased resolution. However, in cases where little chronological information is available, as is common with languages or cultural traits, divergence time estimates can provide intriguing insights into the evolutionary histories of populations (Gray and Atkinson 2003; Gray and Jordan 2000).

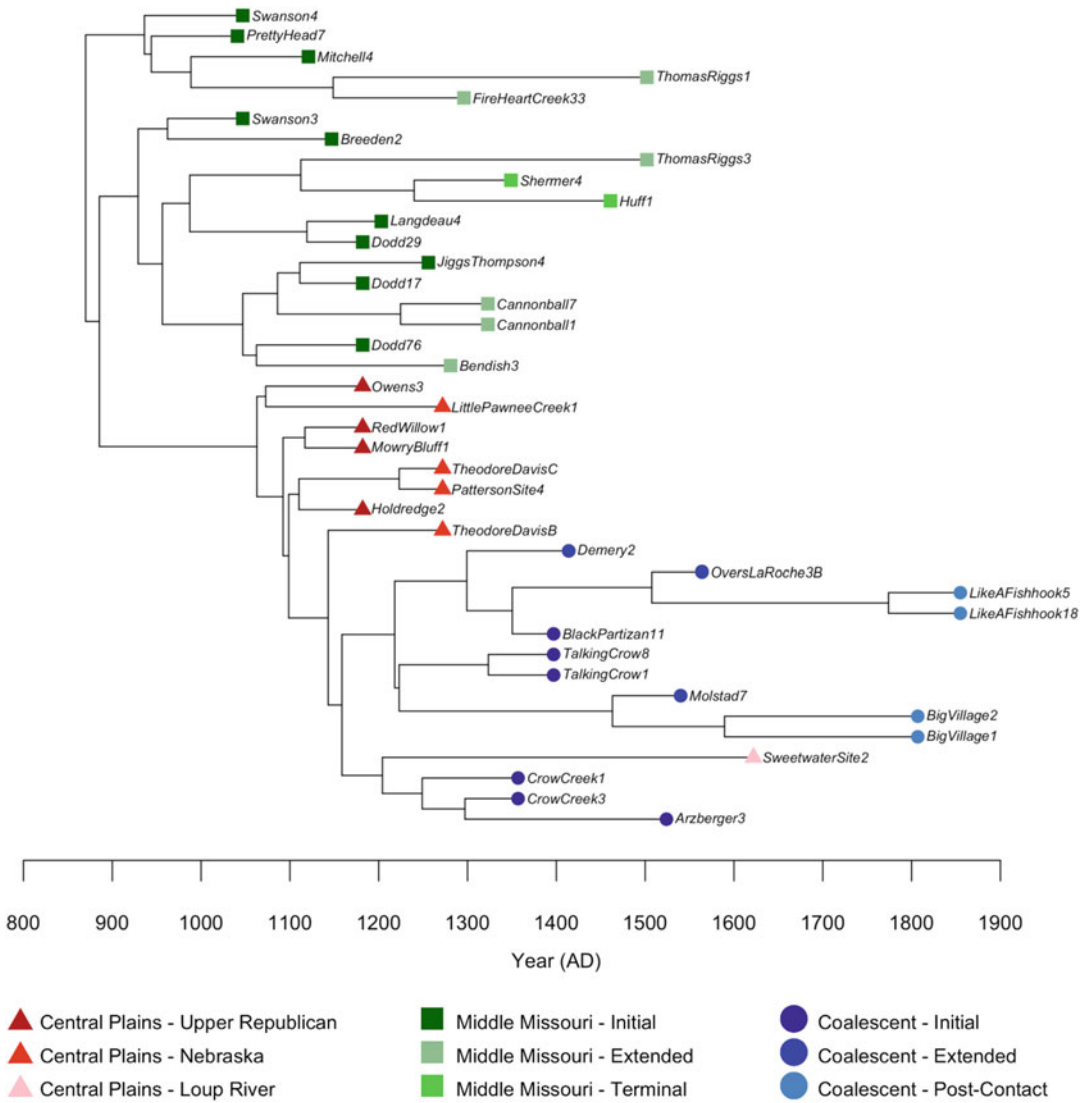
In this example, we used a combination of existing radiocarbon dates and generally accepted Plains Village age ranges to time calibrate our maximum clade credibility tree. We constrained divergence points for house features associated with the Central Plains to 1050–1250 AD, Middle Missouri to 1000–1300 AD, and Coalescent to 1300–1600 AD. Each house feature used in the analysis was also given a mean date of occupation based on chronological data from Johnson (2007), O’Shea and Ludwickson (1992), Smith (1972), and Wedel (2001). The resulting time-calibrated tree can be seen in Fig. 9.4. This tree was also produced using BEAST2 (Bouckaert et al. 2014) with tip dates added to the dataset through the tip dates option in BEAUTi. The range of ages associated with each monophyletic clade was incorporated into the analysis by adjusting the shape of the log normal distribution in the prior section of the BEAUTi.

### Diversification Rates (Origination and Extinction)

The goals of cultural macroevolution find strong parallels with research themes in evolutionary paleobiology such as measures of taxonomic diversity, rates of taxonomic change, the quality of preservation, and stratigraphy (Foote 2000). The parallels are undoubtedly influenced by similar limitations of the fossil and archaeological records, such as sampling and preservation biases.

One of the more significant advancements in paleontology is the ability to estimate diversification rates from occurrence data, which at a minimum is a set of two dates for the first and last appearance

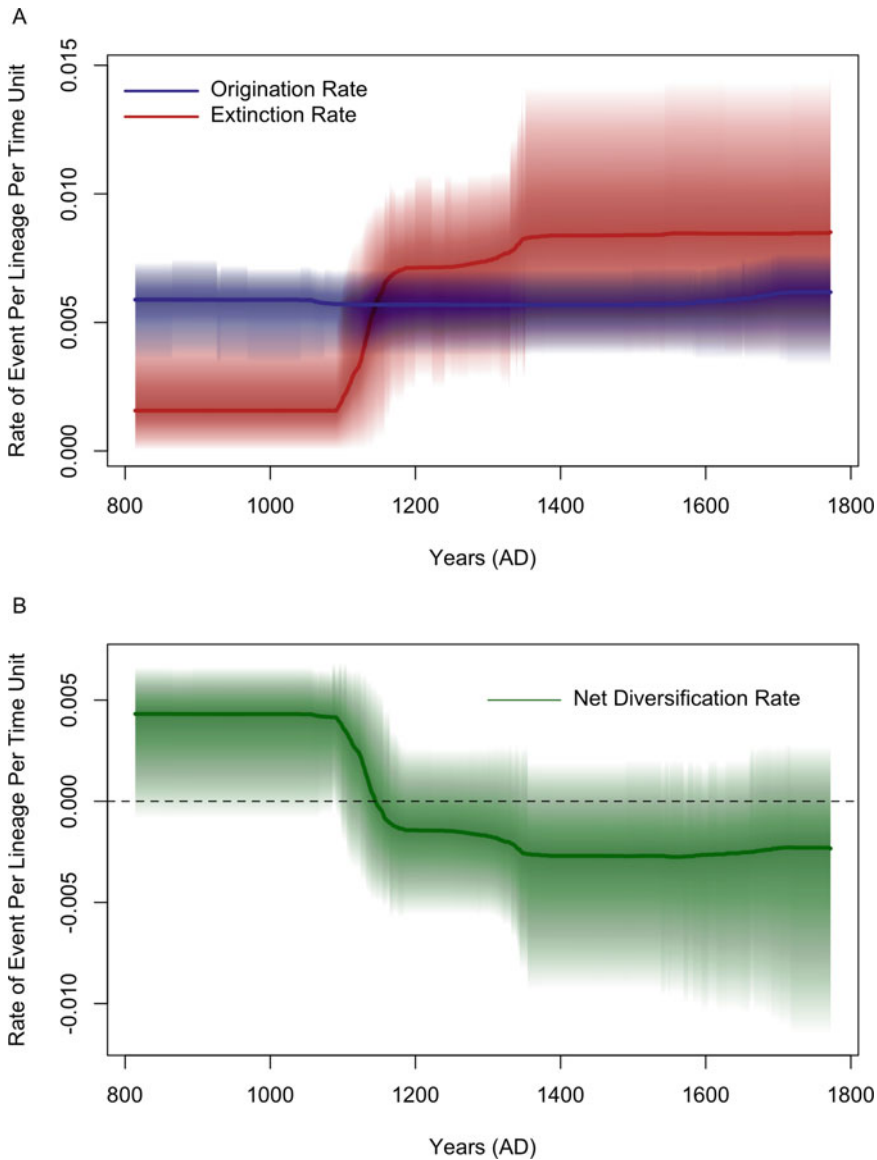




**Fig. 9.4** Time-calibrated maximum clade credibility tree

of a *lineage* (or only one date if a *lineage* is extant). Given that the times of first and last appearance in the fossil record are unlikely to reflect true origination or extinction events, refinements have been made to estimate rates of diversification from incomplete data (Foote 2001; Foote and Raup 1996). Recently, paleontological methods have implemented Bayesian inference to model the dynamics of origination and extinction from incomplete occurrence data (Silvestro et al. 2014). We argue here that these methods provide an intriguing set of tools for archaeologists as they minimize phylogenetic assumptions such as the contemporaneity of taxa and a constant rate of extinction over evolutionary history. For an example of these emerging paleontological methods applied to modern technological data, see Gjesfeld et al. (2016).

Here, we applied a Bayesian approach to estimating diversification rates (Fig. 9.5) from occurrence data as outlined by Silvestro et al. (2014). This approach uses the program PyRate, which is implemented in python with code and tutorials freely available (Silvestro 2018). Once again, temporal



**Fig. 9.5** Origination and extinction rates (a) of house styles across all three Plains Village traditions (Central Plains, Middle Missouri, and Coalescent). Net diversification rate (b) is calculated by subtracting the extinction rate from the origination rate with the dotted line indicating a net diversification of zero. If the net diversification rate is above this line, then diversity is increasing, whereas values below this line suggest diversity in house styles is decreasing. Shaded areas represent the 95% highest *posterior* density

data was derived from a combination of radiocarbon dates and established cultural chronologies so that each house style could be assigned an estimated date of first and last appearance (or age range). If radiocarbon dates could be tied to a specific house structure, then these dates were used; otherwise dates were aggregated for each cultural variant. It should be noted that many of the radiocarbon dates used in this work were compiled and calibrated by the Plains Village Dating project with the results published as an excellent monograph by Johnson (2007).

## Archaeological Interpretations

The Bayesian frameworks highlighted above provide various pieces of evidence with which to evaluate our archaeological expectations and build archaeological interpretations. Evidence produced includes (1) a maximum clade credibility tree that hypothesizes the evolutionary relationships between house styles, (2) *posterior* probabilities that can indicate support for the *topology* of the tree, (3) insights into how fast or slow each house style is changing in relation to other house styles in the analysis, (4) estimates for the time in which each house style (or cultural tradition) last shared a common ancestor, and (5) the overall rate of house style diversification based on occurrence data. We believe that the additional pieces of evidence that result from our Bayesian approaches help to not only evaluate our existing expectations but also build hypotheses about patterns of cultural macroevolution.

Our first expectation posited limited shared ancestry between the Central Plains tradition and the Middle Missouri tradition. With the possible exception of the house style associated with Little Pawnee Creek, house styles associated with the Middle Missouri tradition demonstrate a nearly complete *monophyletic clade* and a clear divergence from house styles associated with the Central Plains and Coalescent traditions. This lends support to theories that view the ancestral history of Middle Missouri populations as strongly different from their neighbors to the north and south (Wood 2001). This phylogenetic result is an encouraging “proof of method” as significant differences in Middle Missouri house shape and size have been well-chronicled in Great Plains archaeology (Lehmer 1971).

We can draw from our additional pieces of evidence to suggest that the lack of shared ancestry between Middle Missouri and Central Plains traditions is not due to a more recent, rapid evolution of house styles in either tradition. Overall, we see rates of *character state* change (or substitution rate) remain low across the tree (Fig. 9.2b, c) with only a few sites demonstrating higher rates of change (Dodd, Swanson, Little Pawnee Creek). These observed rates of change are on average slightly slower than rates of linguistic evolution (Greenhill et al. 2010) but still firmly within the range of variability. This suggests that the differences in house style morphology are more likely due to longer independent origins rather than more recent origins with rapid independent adaptation to different social and environmental circumstances.

The second expectation highlighted in this work is the potential for shared ancestry between the Central Plains tradition and the Coalescent tradition. The MCCT tree that results from our Bayesian analysis suggests that house styles from the Central Plains are more closely related to house styles from the Coalescent than they are to the Middle Missouri. However, two distinct clades in the bottom half of the tree generally divide house styles associated with the Coalescent tradition and house styles associated with the Central Plains tradition. Perhaps the most intriguing is that the three Coalescent house styles (Crow Creek House 1, Crow Creek House 3, Arzberger House 3) that are most closely related to Central Plains house styles all are associated with the Initial Coalescent variant. This would suggest that fairly substantial differences exist between house styles associated with the Initial Coalescent and those associated with later Extended and Post-Contact house styles like those from Big Village and Like-A-Fishhook village. It is important to note that good archaeological data for the diversity of house styles during the Post-Contact variant is hard to come by as some villages were extremely large, but most were likely much smaller and scattered around the landscape (Lehmer 2001).

The broader macroevolutionary pattern that can be extracted from our suite of Bayesian analyses is that changes in Plains Village house styles are generally regular over time, but some time periods and house styles show higher rates of change. Our estimation of diversification rates (Fig. 9.5) based on occurrence data demonstrates a strong rise in the extinction rate between 1100 and 1250 AD, which suggests a decrease in house style diversity over this time period. This can also be identified in the time-calibrated tree which highlights numerous divergence events during this time frame and a clear expectation of Central Plains and Coalescent divergence.

Undoubtedly, the quality and resolution of house style dates plays a significant role in creating this pattern, but the results do demonstrate that the rate of house style loss is not constant through time.

These results suggest that the strongest influence on the diversity of house styles is not the innovation of new house styles but rather the disappearance of previous house styles. This may indicate that the cultural evolution of Plains Village traditions is not indicative of gradual change but rather a complex series of punctuated events (such as village abandonments).

In summary, through the application of our Bayesian framework, we are able to collaborate existing archaeological perspectives that the Middle Missouri and Central Plains traditions do not appear to share a recent common ancestor and any similarities are more likely due to independent convergence. In addition, the emergence of the Coalescent tradition appears to be more heavily influenced by the Central Plains tradition than the Middle Missouri tradition. Potential new insights that are gained through our approach include the acknowledgment of a fairly stable origination of new house styles through time but a period of increased divergence and loss of house style *lineages* between 1150 and 1300 AD.

## The Future of Model-Based Phylogenetics in Archaeology

Phylogenetic inference is an undeniably powerful set of tools with which infer macroevolutionary patterns, but it does not come without challenges. Some concerns are conceptual in nature, in that artifact lineages are impacted by many different cultural transmission processes that can obscure our attempts to reconstruct evolutionary relationships. Other concerns are methodological, such as inherent assumptions about the non-independence of characters or a branching pattern of evolutionary change. Here, we suggest that for the effective use of model-based phylogenetics using archaeological data, we must continue to not only refine our models of evolutionary change but also our expectations for the archaeological questions we are able to answer.

For example, previous applications of phylogenetic inference using archaeological data often sought to infer microevolutionary processes from macroevolutionary patterns. One of the most common, and perhaps incorrect, expectations was that tree topologies could provide insights into cultural transmission processes such as the degree of vertical transmission or horizontal transmission. Broadly, the degree of transmission was evaluated by interpreting the consistency or retention index (RI) provided in a cladistic analysis. The RI examines the relationship between the fraction of possible *homoplasy* in the tree divided by the maximum possible value of *homoplasy* with values closest to zero indicating complete *homoplasy* and values closer to one indicating no *homoplasy* (Tripp 2016). The predominant view is that higher RI values indicate a stronger fit of the data to bifurcating tree model with a related assumption of greater vertical transmission, whereas lower RI values indicated higher amounts of horizontal transmission. Based on research from Crema et al. (2014) and Nunn et al. (2010), we view high RI values as potentially indicative of vertical transmission but also view interpretations of horizontal transmission from low RI values with skepticism due to numerous confounding effects. Future application of either cladistic or model-based phylogenetic inference needs to rely on not a single tree metric but rather responsible use of a range of various tests and metrics to evaluate the relationship between data and tree topology (Marwick 2012).

Given what we know about the dynamics of cultural evolution, we have reason to believe that our models of technological change are overly simplistic. However, we view an explicit modeling approach that requires exposing our assumptions about evolutionary change as an opportunity to continually refine and test models of macroevolution. One of the distinct advantages of a model-based approach is to select and adjust model *parameters* to better fit our data. The process of finding the best-fitting model not only improves confidence in our phylogenetic inference but also allows us to explore the variability of our data. For simplicity, we chose to compare the fit between models within the same general family (the *Mk model*) with various combinations of initial model settings. However, there is nothing to limit us from exploring a wider range of model families that may align more closely to assumptions we have about our data. If we look at the Bayesian approach as applied in linguistics, we see the comparison of numerous models of *character* change including the continuous-

time Markov chain (CTMC) model, the covarion model, and the stochastic Dollo model. The Dollo model, for example, is based on a model of *character* evolution where once a feature is lost, it can never be regained. Depending on the data, the Dollo model may at times perform poorly, whereas the covarion or CTMC model may perform better (Bouckaert and Robbeets 2017).

In evolutionary biology, the ability to infer macroevolutionary patterns has been greatly facilitated in recent years by emerging computer programs such as PyRate (Silvestro et al. 2014), which was used above to estimate diversification rates from occurrence data. This program has a similar goal of estimating rates of diversification but does so based on occurrence data and not on a tree *topology* produced from a paradigmatic classification of artifact traits. Furthermore, PyRate removes any strict assumptions about the underlying model of evolutionary change or the “tree-likeness” of the data. We view these new Bayesian tools as holding incredible potential for modeling emergent macroevolutionary patterns without imposing potentially difficult and unwarranted assumptions about material culture change.

## Conclusions

We have demonstrated a working example of how Bayesian phylogenetics can be used to study macroevolutionary patterns in archaeological data. Through this case study, we emphasized that Bayesian approaches can facilitate new questions and understandings about the tempo of change in artifacts, time periods of cultural divergences, and the unique macroevolutionary dynamics of material culture. Our Bayesian approach was applied to a dataset of 40 house styles that were associated with the Central Plains, Middle Missouri, and Coalescent traditions of the Great Plains Village period. We highlight that our phylogenetic analysis broadly agreed with our archaeological expectations for the relationship between these traditions but also provided new insights into the variability of changes between house styles and the importance of village abandonment between 1100 and 1250 AD in shaping the diversity of house styles in the archaeological record. We believe that this is one of the first examples of a thoroughly Bayesian approach to an explicitly archaeological data set, and we hope that by sharing this worked example, other researchers will be encouraged to follow a similar approach.

Despite the limited use of model-based phylogenetics in archaeology to date, we believe that the methodological approach taken here can provide a new generation of insights into the dynamic patterns of macroevolution. We see that model-based approaches to phylogenetic inference as important in operationalizing our interests in macroevolutionary patterns as they provide a robust framework for testing different models of *character* change and estimating rates of diversification from our tree *topologies*. As we continue to develop more informed models of cultural change, we are optimistic that model-based phylogenetics may help to illuminate novel evolutionary patterns that we are not yet aware of. Ultimately, we aim to more fully integrate phylogenetic analyses with the wealth of archaeological and ethnohistorical data that we already have to achieve a fuller and more holistic understanding of how macroevolutionary processes have contributed to cultural diversity and change.

**Data Sharing Statement** The data and help files supporting the results of the book chapter are available in repositories at Zenodo (DOI: <https://doi.org/10.5281/zenodo.1443276>) and GitHub ([https://github.com/erikgjes/Bayes\\_Phylogenies](https://github.com/erikgjes/Bayes_Phylogenies)).

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