Ancestral Reconstruction: Theory & Practice

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Key Points

- Ancestral reconstruction is a popular and widely-used method that involves estimating phenotypic trait values at internal nodes of a phylogenetic tree.
- Contemporary ancestral reconstruction invariably uses explicit mathematical models of trait evolution, allowing us to make probabilistic statements about the condition of our phenotypic character at internal nodes of our phylogeny.
- The dominant model for the reconstruction of ancestral states for discretely-valued characters is a continuous-time Markov chain model called the M*k* model.
- For discrete characters, we can distinguish between marginal and joint ancestral state reconstruction. In the former case, we compute the marginal likelihood of each condition at each node, integrating over all possible conditions at all other nodes of the tree in proportion to their probability. In the latter, we identify the set of states at all nodes that jointly maximizes the probability of the observed data.
- For continuous characters, the dominant model used for ancestral reconstruction is a continuous-time stochastic diffusion model called Brownian motion.
- The Brownian model is parameterized by a starting condition (z_0) and instantaneous variance (σ^2). In ancestral state reconstruction under Brownian motion we identify z_0, σ^2, and the set of values at all nodes of the tree that make the observed data most probable: these are our Maximum Likelihood ancestral states.
- Though ancestral reconstruction is relentlessly popular, it has some important shortcomings. Key among these is that uncertainty, particularly for deep nodes of the tree, is typically quite broad. Even more perniciously, ancestral reconstruction can be very sensitive to model inadequacy, meaning that our findings from ancestral reconstruction may be highly unreliable when our model of evolution is a poor description of the genuine evolutionary process of our traits.
- Given these limitations, it is useful to be circumspect in the interpretation of results from ancestral reconstruction on a phylogenetic tree.

Glossary

Branch or Edge Connection between two different nodes in a phylogeny, the parent (ancestral) node and a daughter (descendant) node (Yang, 2006; Baum and Smith, 2012).

Brownian motion Model of stochastic diffusion based on the movement of particles in a fluid that is the predominant model for ancestral state reconstruction of continuously valued traits (Felsenstein, 1985; Revell and Harmon, 2022).

Continuous character Phenotypic attribute that can assume any of an infinite number of values on a real number scale.

Discrete character Phenotypic attribute that can only assume one of a fixed and finite set of values. Qualitative, ordinal, and meristic (countable) traits are usually treated as discrete.

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M*k* model Stochastic continuous time *k*-state Markov chain model used to study discrete character evolution on trees and to reconstruct ancestral states (Pagel, 1997; Lewis, 2001; Harmon, 2019).
Node Hypothetical ancestral taxon located at the connecting point of two edges in a phylogenetic tree (Yang, 2006; Baum and Smith, 2012).
Phylogenetic tree Acyclic directed graph used as a model to represent the relationships of entities, such as biological species, connected via a history of common descent (Felsenstein, 2004; Yang, 2014; Revell and Harmon, 2022).
Q matrix $k \times k$ matrix, for a discrete character trait with k levels, containing the transition rates between states per unit of time for each pair of trait levels (Pagel, 1997; Harmon, 2019; Revell and Harmon, 2022).
Tip or Leaf External node of a tree connected (via an edge) to a parent node, but lacking any descendant (i.e., daughters). Tips typically include a label, identifying the tip to a species or other operational taxonomic group (Yang, 2006; Baum and Smith, 2012).

Abstract

Ancestral reconstruction involves estimating the value or condition of a phenotypic trait or attribute at one or more internal nodes of a phylogenetic tree. Ancestral state reconstruction has long been among the most popular endeavors in phylogenetic comparative biology because it purports to offer researchers interested in trait evolution a window on the evolutionary past. Contemporary ancestral state reconstruction relies on explicit mathematical models for the evolutionary process of our traits. In the present section, I will outline ancestral state reconstruction for discretely-valued characters (such as qualitative or ordinal features), as well as for continuously-valued traits (such as numerical quantitative measures of morphology, behavior, or ecology). I will then proceed to briefly illustrate the application of ancestral character reconstruction to two different empirical datasets: feeding mode in centrarchid fishes; and body mass evolution in mammals. In spite of its popularity, ancestral character reconstruction includes some significant shortcomings. I will end by commenting on the general practice of ancestral state reconstruction and its limitations.

Introduction

Ancestral state reconstruction is the practice of estimating the state or set of states for a phenotypic attribute for one or more nodes of a reconstructed phylogenetic tree (Schluter et al., 1997; Yang, 2006; Nunn, 2011; Revell and Harmon, 2022). Because it purports to offer evolutionary biologists a window on the past, ancestral reconstruction is a relentlessly popular endeavor of phylogenetic comparative research (Revell and Harmon, 2022).

Modern ancestral state reconstruction requires that we specify or hypothesize a model for how our character may have evolved on the tree. We then proceed to estimate ancestral character values at internal nodes of the phylogeny while conditioning on that hypothesized model (Schluter et al., 1997; Nunn, 2011; Revell and Harmon, 2022).

Ancestral Reconstruction of Discrete Characters

The M*k* Model

The standard model for ancestral state estimation of discretely-valued phenotypic characteristics is one that is popularly known as the M*k* model and that describes a continuous-time, *k*-state Markov chain (Pagel, 1994, 1997; Lewis, 2001; Harmon, 2019). This model is fully-parameterized by a $k \times k$ matrix that gives the transition rates between all pairs of states and is referred to as the **Q** matrix (Harmon, 2019; Revell and Harmon, 2022). An example of what this matrix might look like for a two-state (i.e., $k = 2$) discrete character is given below.

$$\mathbf{Q} = \begin{bmatrix} -q_{0,1} & q_{0,1} \\ q_{1,0} & -q_{1,0} \end{bmatrix}$$

In this matrix, the instantaneous transition rates between each pair of character levels, i and j, are provided by the elements $q_{i,j}$ of the matrix, and the diagonal is equal to the negative row sum. A matrix of transition probabilities for any arbitrary elapsed time t, $\mathbf{P}$, can be obtained by calculating the matrix exponential of $\mathbf{Q} \times t$, i.e., $\mathbf{P} = \exp(\mathbf{Q}t)$, in which $\exp(\mathbf{X})$ denotes the matrix exponential of $\mathbf{X}$ (Pagel, 1997; Lewis, 2001; Harmon, 2019). To compute the total probability of a set of observed data at the tips of a tree given a pre-specified value of $\mathbf{Q}$, we must sum over all possible states at all internal nodes, which can be done efficiently using the pruning algorithm of Felsenstein (1981). If we select the value of $\mathbf{Q}$ that maximizes this probability (i.e., the probability of our data given $\mathbf{Q}$

and our tree), we have performed Maximum Likelihood estimation of **Q** under the M*k* model (Harmon, 2019; Revell and Harmon, 2022).

Marginal Ancestral State Estimation

Marginal reconstruction for a discrete character trait involves traversing the tree node by node, and at each node calculating the probability of the tip data while conditioning on each value of the discrete character at each node in turn (Yang, 2006; Revell and Harmon, 2022). At any node, the sum of these conditional probabilities is equal to the total probability of the data, i.e., the likelihood of our model. Dividing each value by this sum gives us the marginal scaled likelihoods, which are also a type of probability (called an empirical Bayes posterior probability; Yang, 2006) that each node is in each state of the character. **Fig. 1** gives an example of a ten taxon tree and binary discrete character with marginal ancestral state reconstructions given for all internal nodes.

Marginal ancestral reconstruction is the overwhelmingly predominant method for estimating ancestral character states of a discrete trait and should be used whenever we are interested in making specific statements about the relative likelihood of one condition or another at particular nodes of the tree (Yang, 2006; Revell and Harmon, 2022).

Joint Ancestral State Estimation

In contrast to marginal ancestral state reconstruction, discussed above, joint reconstruction involves identifying the single set of states at *all* internal nodes of the phylogeny that jointly maximize the probability of obtaining the data observed at the tips, once again under our assumed evolutionary model (Yang, 2006; Revell and Harmon, 2022). This can be most-easily understood by imagining a comprehensive enumeration of all possible combinations of states at all internal nodes of a tree, computing the probability of the observed data under our model conditioning on each set of states, and then choosing the set that make the observed data at the tips most probable. The sum of the probabilities across all possible internal node states is *also* equal to the total probability of the data, i.e., the likelihood of our model. In practical terms, it will usually be unfeasible, if not impossible, to enumerate all possible combinations of states at all nodes as there will be k^m such sets for k states and m internal nodes. ($k^m =$ 512 for even the very modest-sized phylogeny of **Fig. 1**.) In practice, efficient algorithms exist to find the set of states with the highest likelihood under our model (Yang, 2006). **Fig. 2** shows an example of joint ancestral state estimation for a binary character using the same phylogeny and data as in **Fig. 1**.

Joint ancestral reconstruction is much less commonly used in phylogenetic comparative biology, but might be employed if we are interested in reporting the single most probable evolutionary scenario for our trait, or in passing that scenario to another analysis, such as one that involves fitting multiple discrete character regimes to the evolution of a continuous trait (e.g., O'Meara et al., 2006). An important observation is that the Maximum Likelihood joint ancestral state reconstruction does not necessarily correspond to the set of states with the highest marginal scaled likelihoods (Yang, 2006, 2014).

Stochastic Character Mapping

In addition to marginal and joint reconstruction, an extremely popular and widely-used discrete character ancestral state reconstruction method is a procedure called stochastic character mapping (Nielsen, 2002; Huelsenbeck et al., 2003; Bollback, 2006; Revell and Harmon, 2022; Revell, 2024). According to the method of stochastic character mapping, character histories, complete with state changes along edges, are sampled from their probability distribution under a model (Huelsenbeck et al., 2003; Bollback, 2006). Stochastic character mapping is a computer-intensive method that normally involves first randomly sampling trait histories at all nodes of the phylogeny from their joint distribution in proportion to their probability, and then using simulation and rejection sampling to generate character histories along the edges of the tree that are consistent with these sampled node states. A set of twenty stochastic character maps for the tree and data of **Figs. 1** and **2** are given in **Fig. 3**. (Normally, however, we would sample 100 or 1000 stochastic maps.).

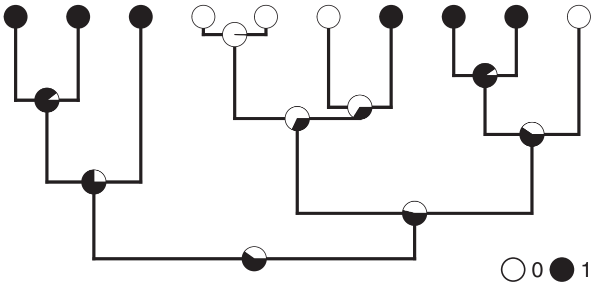

Fig. 1 A ten taxon phylogeny with a binary (0/1) trait mapped at the tips of the tree. Pie charts at internal node give the marginal ancestral states at all nodes under the Maximum Likelihood fitted model of trait evolution for the character. See main text for more details.

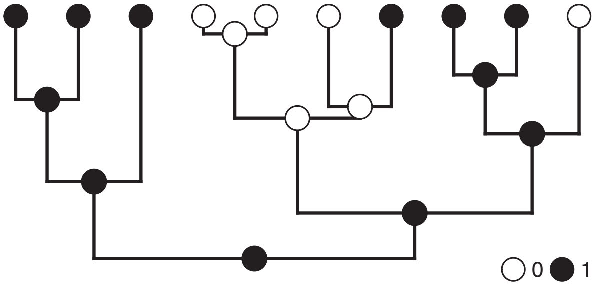

Fig. 2 A ten taxon phylogeny with a binary (0/1) trait mapped at the tips of the tree. Colors at internal node give the joint ancestral state reconstruction at all nodes under the Maximum Likelihood fitted model of trait evolution for the character. See main text for more details.

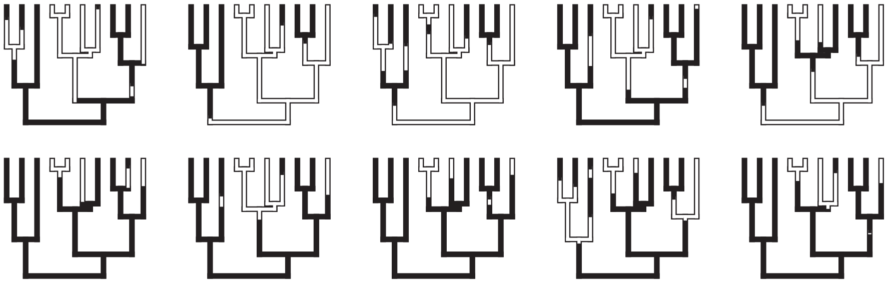

Fig. 3 A set of twenty stochastic character maps for the phylogeny and discrete character data of **Figs. 1** and **2**. Individual stochastic maps cannot be interpreted individually, but should always be analyzed in aggregate. In an empirical study that used stochastic mapping, we would normally obtain 100 or 1000 stochastic maps and integrate over our sample. See main text for more details.

Note that each of the character histories shown in **Fig. 3** are different one from the other, but compatible with the observed data at the tips as shown in **Figs. 1** and **2**. Very little can be learned from a single stochastic character history so they should invariably be considered in aggregate. One can, for instance, use a set of such maps to estimate the probability that any node is in a particular state and even to obtain a (posterior) distribution of the likely number of changes of each type in the tree (e.g., Revell and Harmon, 2022; Revell, 2024).

Ancestral Reconstruction of Continuous Characters

The Brownian Motion Model

Much as the M*k* model is the predominant model for ancestral state estimation of discrete traits, the Brownian motion model overwhelmingly dominates ancestral reconstruction of continuous characters (Felsenstein, 1973, 1985; O'Meara et al., 2006; Harmon, 2019). Brownian motion is a stochastic diffusion process in which successive evolutionary changes are independent and come from a normal distribution with variance $\sigma^2 \times t$ and mean z_0, in which σ^2 is the Brownian rate of evolution, t is elapsed time in the units of the branch lengths of our tree, and z_0 is the initial condition of the process (Harmon, 2019). **Fig. 4** shows an example of Brownian motion evolution on the phylogeny of **Figs. 1–3**.

Under this scenario of evolution on a phylogenetic tree, the pattern of similarity of related species is one in which species values are a random variable from a multivariate normal distribution where the correlation between any pair of terminal taxa is exactly proportional to their fraction of shared ancestry above the root (O'Meara et al., 2006). The distribution of tip and internal node values is also given by a multivariate normal distribution, and thus the set of parameter values of the Brownian model (σ^2 and z_0) and vector of node values ($\mathbf{z}_a$) that maximizes this probability function, given the observed species values for the trait ($\mathbf{x}$) and the tree, are Maximum Likelihood ancestral state estimates (O'Meara et al., 2006; Harmon, 2019).

$$L\left(\sigma^2, z_0, \mathbf{z}_a \middle| \mathbf{x}, \mathbf{C}\right) = \frac{\exp\left(-\frac{1}{2}([\mathbf{x}, \mathbf{z}_a] - \mathbf{1}z_0)^{'}(\sigma^2\mathbf{C})^{-1}([\mathbf{x}, \mathbf{z}_a] - \mathbf{1}x_0)\right)}{\sqrt{(2\pi)^{(N+m-1)} \times \det(\sigma^2\mathbf{C})}}$$

In the density function above, N is the number of terminal species (tips) in the tree, m is the number of internal nodes, $\mathbf{1}$ is a conformable vector of 1.0s, and $\mathbf{C}$ is an $(N+m-1) \times (N+m-1)$ matrix containing the height above the root of the common ancestor of each pair of N species and m internal nodes, except for the root itself (Revell and Harmon, 2022). The Maximum Likelihood solutions for σ^2, z_0, and $\mathbf{z}_a$ can be obtained using computationally intensive numerical optimization, but there are also

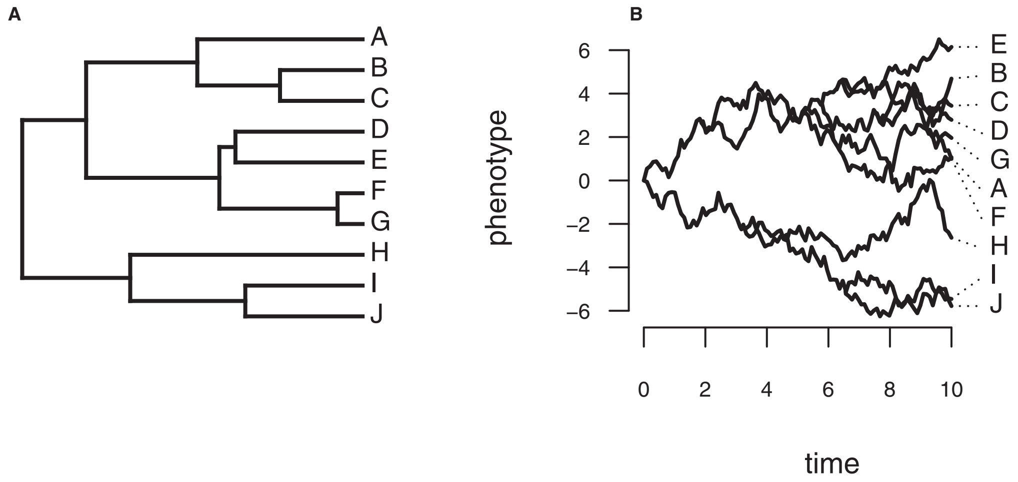

Fig. 4 Simulated Brownian motion evolution of a continuously-valued trait for the ten taxon phylogeny of **Figs. 1–3**. Note the key properties of Brownian evolution: that variance tends to accumulate with time; and that related species tend to have more similar trait values, with a degree of similarity proportional to their shared history.

a number of fast algorithms (described elsewhere) that can be used to obtain the Maximum Likelihood ancestral states under this model (e.g., Felsenstein, 1985; Rohlf, 2001).

Empirical Examples

Discrete Character Ancestral States: Feeding Mode in Centrarchidae

To illustrate ancestral state reconstruction for discrete characters, I will use a phylogeny and dataset of feeding mode (non-piscivory vs. piscivory) for a phylogeny of 28 species of Centrarchidae (the sunfish) from Near et al. (2005) and Revell and Collar (2009), respectively. To begin, I fit a two-parameter M*k* trait evolution model in which I permitted the two different transition types (from non-piscivory → piscivory, and the reverse) to assume different rates. The Maximum Likelihood estimate of the transition matrix, **Q**, between the two levels of the trait is given below.

$$\mathbf{Q} = \begin{array}{c c} & \begin{array}{cc} non. & pisc. \end{array} \\ \begin{array}{c} non. \\ pisc. \end{array} & \begin{bmatrix} -6.09 & 6.09 \\ 3.05 & -3.05 \end{bmatrix} \end{array}$$

Fig. 5 shows the marginal reconstruction (in panel 5A) and joint reconstruction (panel 5B) of non-piscivory (white) and piscivory (black) across all the nodes of the tree of centrarchid fishes, conditioning on our fitted Maximum Likelihood transition model. Interestingly, even in this relatively simple example, we can observe a number of nodes in which the condition with the highest marginal scaled likelihood *does not* correspond to the condition in the Maximum Likelihood joint reconstruction at the same node (as described in Yang, 2006). For example, the common ancestor of *Lepomis cyanellus* (the green sunfish) and *Lepomis gulosus* (the warmouth) has the highest marginal likelihood for non-piscivory in the marginal reconstruction (**Fig.** 5A) but is piscivorous in the joint reconstruction (**Fig.** 5B).

Continuous Character Ancestral States: Mammal Body Size

To illustrate ancestral state reconstruction of a continuous trait, I used log-transformed body mass and a phylogeny of 49 species of mammals from Garland et al. (1992). **Fig. 6** shows the Maximum Likelihood ancestral state reconstruction of this character projected onto the edges and nodes of the phylogeny using the visualization method of Revell (2013). Predictably, deep nodes in the phylogeny have intermediate body masses; however, we can nonetheless observe multiple instances of the evolution of large mass in different parts of the tree. The species with the smallest mass in this dataset is *Mephitis mephitis*, the striped skunk, whereas the species with the largest body mass is *Ceratotherium simum*, the white rhinoceros.

A Comment on Ancestral State Reconstruction in Phylogenetic Comparative Biology

Though it remains a remarkably popular category of analysis in phylogenetic research, ancestral state reconstruction has been subject to numerous well-justified criticisms (e.g., Cunningham et al., 1998; Cunningham, 1999; Omland, 1999; Losos, 2011;

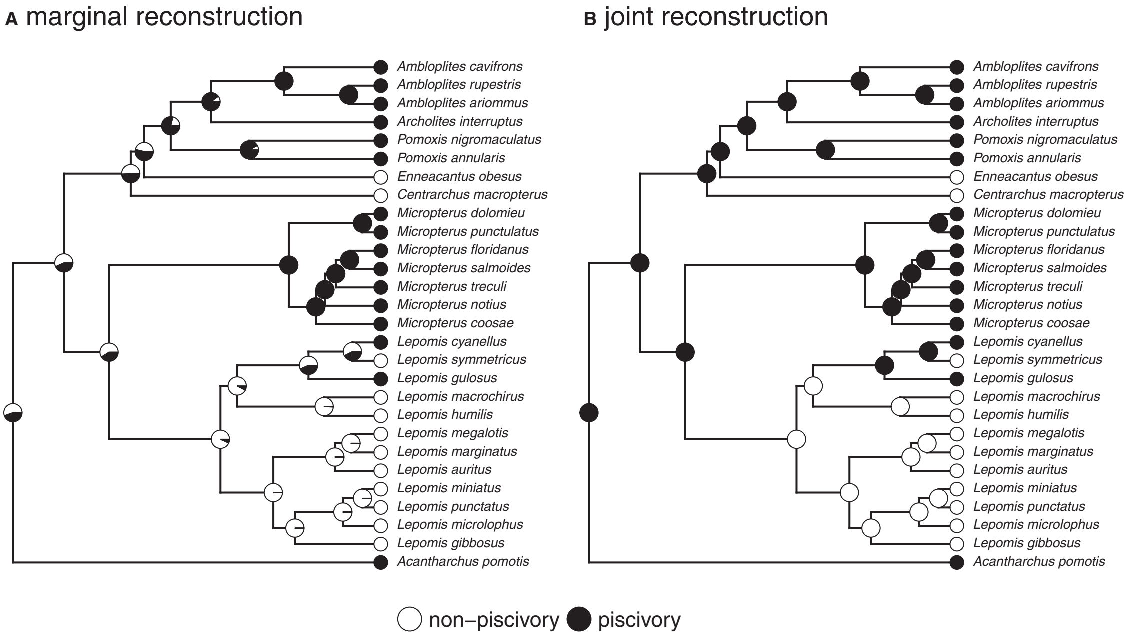

Fig. 5 Ancestral state reconstruction of feeding mode (non-piscivory vs. piscivory) on a phylogeny of centrarchid fishes from Near et al. (2005). (A) Marginal reconstruction. (B) Joint reconstruction. Both panels (A) and (B) assume the same underlying trait evolution model. See main text for more details.

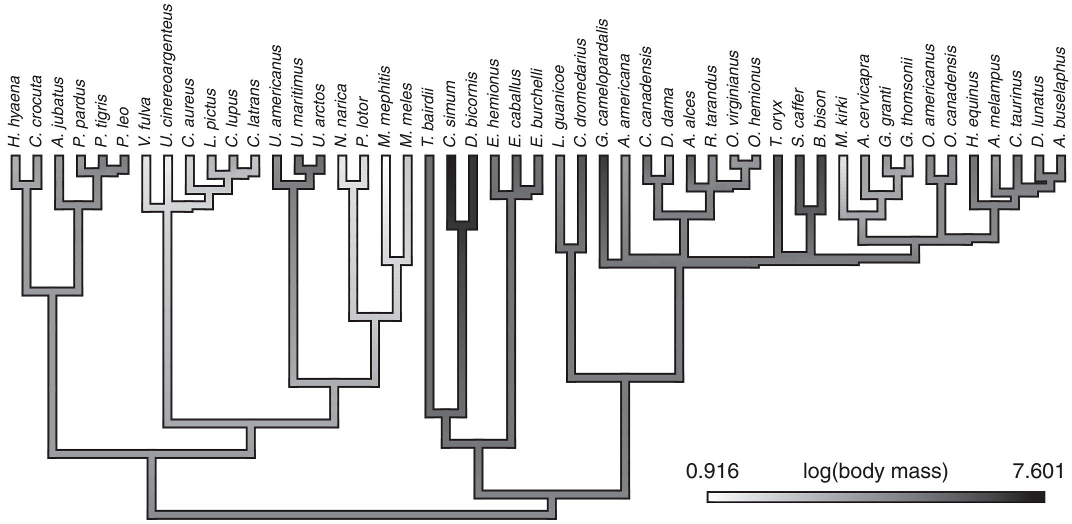

Fig. 6 Ancestral state reconstruction for log(body mass) across a phylogeny of various species of mammals. The phylogeny and trait dataset derive from Garland et al. (1992), and the projection of the reconstruction onto the tree uses a method described in Revell (2013). See main text for more details.

Gascuel and Steel, 2020). These critiques fall broadly into two categories. On the one hand, the uncertainty around ancestral estimates for phenotypic characteristics, particularly deep in the phylogenetic tree, are often *very wide* (Ané, 2008; Gascuel and Steel, 2020; Revell and Harmon, 2022). For example, in some instances ancestral reconstructions of continuous traits for deep nodes of the phylogeny may included almost all observed trait values of the character (Schluter et al., 1997; Revell and Harmon, 2022). Nonetheless, when the assumed model is correct, ancestral state reconstruction can be accurate, unbiased, and with appropriate confidence intervals (Revell and Harmon, 2022).

On the other hand, it has also been shown elsewhere (e.g., Revell and Harmon, 2022) that ancestral reconstruction can sometimes be both inaccurate and positively misleading. That is, confidence intervals may be broad but still fail to include the underlying generating (i.e., correct) ancestral states. This tends to occur when model assumptions are violated, although since neither the M*k* model nor Brownian motion is likely to be *literally* true for any genuine empirical data (remember, "all models are wrong, but some

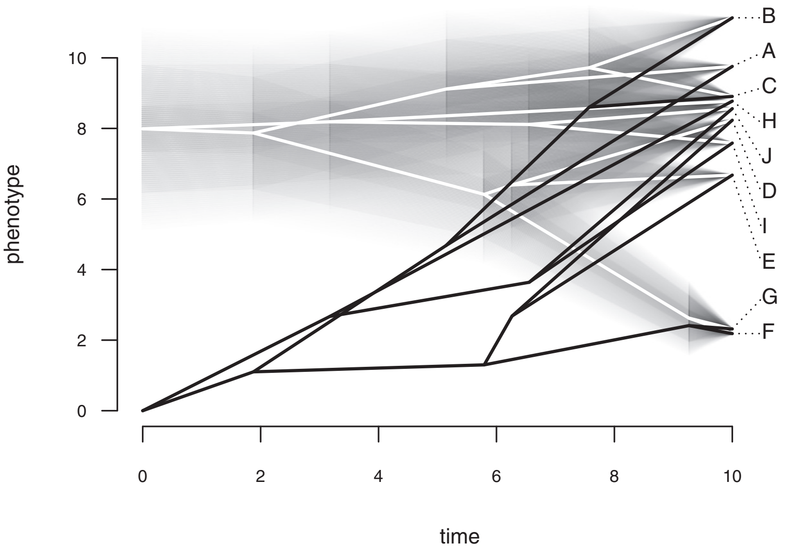

Fig. 7 Ancestral state reconstruction for data simulated under trended Brownian motion, i.e., Brownian motion evolution but with a tendency towards increasing values over time. The black lines give the known, true character history of the trait. The white lines give the Maximum Likelihood ancestral states under an assumption of Brownian motion, and the gray shading represents 95% confidence intervals around estimated states. See main text for more details.

are useful"; Box, 1976), we should be carefully attentive to precisely *how* badly our trait evolution model assumptions might be violated by our data, as well as being circumspect about the interpretation of our results. Fig. 7, for example, shows an illustration of this problem. The generating evolutionary process in this instance was Brownian motion but with a trend towards larger trait values through time and the real history of the trait is given by the solid black lines of the plot. With Maximum Likelihood estimates (white lines) and 95% confidence intervals (gray shading) overlain, it becomes plain that even as uncertainty is broad compared to the observed range of the trait, deep nodes of the tree are confidently misestimated due to the model assumption violation at play (Fig. 7).

A Short Note on Implementation

Ancestral character estimation is implemented in the R statistical computing software (R Core Team, 2024) package *phytools* (Revell, 2012, 2024). *phytools* in turn depends on the core R phylogenetics package *ape* (Paradis and Schliep, 2019). R, *phytools*, and *ape* were used to undertake the analyses and generate the figures of this section.

Conclusions

Ancestral state reconstruction is a procedure in which we estimate phenotypic trait values for internal nodes of a phylogeny based on an evolutionary model. Ancestral reconstruction has long been among the most popular phylogenetic comparative methods. It has reliable statistical properties when the model of evolutionary change for the trait accurately captures the genuine evolutionary process, but can be sensitive to violations of model assumptions. In this way, ancestral reconstruction behaves like a typical statistical inference procedure (Revell and Harmon, 2022). Nonetheless, researchers undertaking ancestral character estimation should always keep these limitations in mind and be carefully circumspect in the interpretation of their findings.

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