# A Comment on the Use of Stochastic Character Maps to Estimate Evolutionary Rate Variation in a Continuously Valued Trait

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Phylogenetic comparative biology has progressed considerably in recent years (e.g., Butler and King 2004; Rabosky 2006; Bokma 2008; Alfaro et al. 2009; Stadler 2011; Slater et al. 2012). One of the most important developments has been the application of likelihood-based methods to fit alternative models for trait evolution in a phylogenetic tree with branch lengths proportional to time (e.g., Butler and King 2004; O'Meara et al. 2006; Thomas et al. 2006; Revell and Collar 2009; Beaulieu et al. 2012). An important example of this type of method is O'Meara et al. (2006) "noncensored" test for variation in the evolutionary rate for a continuously valued character trait through time or across the branches of a phylogenetic tree (also see Thomas et al. 2006 for a closely related approach). According to this method, we first hypothesize evolutionary rate regimes on the tree (called "painting" in Butler and King 2004); and then we fit an evolutionary model, specifically the popular Brownian model (Cavalli-Sforza and Edwards 1967; Felsenstein 1973, 1985), in which the instantaneous variance of the Brownian random diffusion process has different values in different parts of the phylogeny (O'Meara et al. 2006).

In their original article, O'Meara et al. (2006) did not focus specifically on how to hypothesize evolutionary regimes on the tree. The authors did, however, suggest that to test the hypothesis that a discrete character state had influenced the rate of a continuous character, one could use the approach of (Nielsen 2002; Huelsenbeck et al. 2003; Bollback 2006) to first stochastically map the discretely valued trait, and then "test to see whether the portions of the tree with one state for the discrete character have a different rate of evolution for the continuous character than portions of the tree to which the other discrete state has been mapped" (O'Meara et al. 2006, p. 931). Indeed, this has become common practice for this and other closely related methods (e.g., Collar et al. 2009, 2010; Revell and Collar 2009; Martin and Wainwright 2011; Price et al. 2011). Normally, then, the set of evolutionary rate estimates from the stochastically mapped trees are averaged across all the trees in the sample. This is presented as a method of obtaining rate estimates that "integrate over uncertainty in…ancestral states" (Collar et al. 2010, p. 1035). Figure 1 illustrates this analysis pipeline.
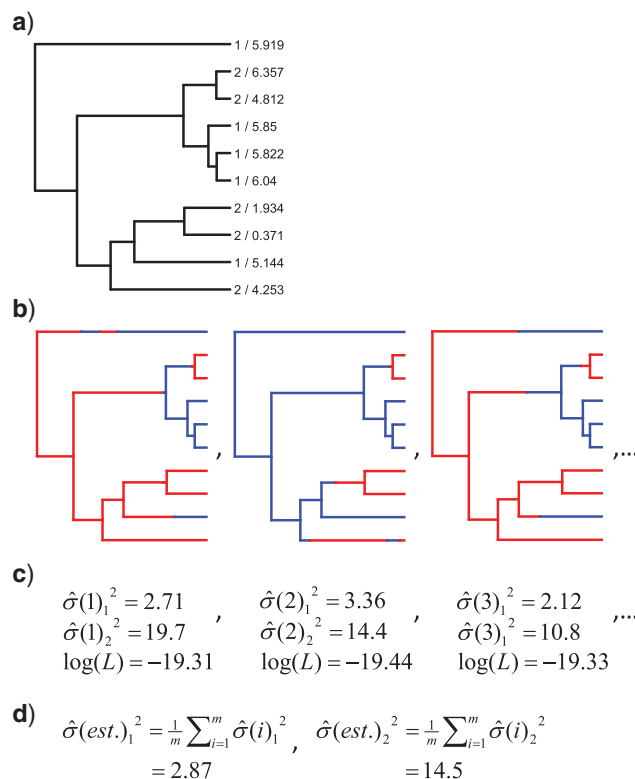


FIGURE 1. Typical pipeline for the analysis of evolutionary rates. a) Phylogeny with data for a binary state (here coded "1" and "2") and a continuously valued trait. b) Stochastically mapped character histories for the binary trait on the tree. c) ML evolutionary rates estimated for each tree and mapped character history. d) The average rates across 100 simulated histories (97 not shown).

Here, I examine this practice. In particular, I show that evolutionary rates estimated this way (i.e., by using maximum likelihood [ML] to fit a multirate model on each stochastically mapped tree; and then averaging across trees) are systematically biased to be more similar to each other than are the underlying generating parameters. My analysis also reveals that this effect is dependent on the rate of evolution for the discrete trait. Specifically, if the rate of evolution for the discrete character is low then the difference between the true history and any stochastically mapped

history is generally small. This results in evolutionary rates for the continuous trait that are estimated with little bias. Conversely, if the rate of evolution for the discrete character is very high, then the true and hypothesized character histories are often extremely dissimilar, evolutionary rate estimates are biased to be more similar to each other than their underlying generating values, and we lose power to distinguish evolutionary rates on the tree.

### SIMULATION AND ANALYSES

To test the hypothesis that the common practice of fitting a multiple-rate Brownian motion model by simulating stochastic character maps for a binary or multistate character and then fitting the model separately conditioned on each map results in estimated evolutionary rates that are biased to be more similar to each other than the generating rates, I conducted the following experiment. First, I generated 100 stochastic pure-birth phylogenetic trees and rescaled the trees to have a total length from the root to any tip of 1.0. On each tree, I simulated a single character history for a binary trait evolving on the tree with evolutionary rates $q_{12} = q_{21} = q$. This history was used as the generating history. Next, I simulated the evolution of a continuous trait with rate $\sigma_1^2 = 1.0$ on branches (and branch segments) with state "1" and $\sigma_2^2 = 10.0$ and on branches (and branch segments) with state "2."

With these data in hand, I replicated our typical data analysis procedure in two ways. First, I assumed that the generating history was known without error. This will be very rare for empirical studies. Using this true character history, I fit the two-rate continuous character model using likelihood (following O'Meara et al. 2006). Second, I assumed the more realistic scenario in which the states for the discrete and continuous characters at the tips of the tree are known; but in which the generating history is not and thus must be estimated from the data. In this case, for each generating tree and data vector, I simulated 100 stochastic character mapped trees and then fit the two-rate model to each simulated mapping (e.g., Collar et al. 2010; Price et al. 2011). To obtain the stochastic character mapped trees, I sampled character histories from their conditional posterior distribution, in which I conditioned on the rate of evolution for the binary trait being the ML estimate of the rate. (This differs from the method implemented in Bollback 2006, in which rates and histories are sampled from their joint posterior distribution. In a small sample of simulations conducted using both methods, I did not find any significant effect on the main result of this study by substituting one procedure for the other.) Note that I invariably assume that the tree and branch lengths are known without error. Although this will not typically be true of empirical studies, so doing allows us to focus on the effects of stochastic mapping on parameter estimation in isolation from other potential sources of error.

To summarize the results from these analyses, I did the following. For the data fit to the generating (i.e., true) character history, I computed the mean and variance of the parameter estimates (and the mean and variance of their ratio $\hat{\sigma}_2^2 / \hat{\sigma}_1^2$) across simulations. I also computed the standard errors of each rate parameter based on the Hessian matrix of partial second derivatives of the likelihood surface at the optimum ($\mathbf{H}$), and calculated the fraction of times that the true parameter values lay on the 95% confidence interval for the estimates. An asymptotic property of likelihood estimation is that our ML estimates will have a variance–covariance matrix, $\mathbf{V}$, that is given by $\mathbf{V} = -\mathbf{H}^{-1}$ (Lynch and Walsh 1998). To estimate the standard errors of each of the parameter in the model, then, one just takes the square root of diag($\mathbf{V}$). Based on these standard errors, I also computed the fraction of times that the 95% confidence intervals for $\sigma_1^2$ and $\sigma_2^2$ were nonoverlapping. This fraction was used as a measure of our power to detect the difference in rate that I simulated. I chose this over the more common likelihood-ratio test to compare this result with the result obtained from the stochastic character mapping analysis, described later.

For the data fit to the simulated character histories, I computed the mean and variance across simulated maps for each tree; and then the mean and variance of these means across simulations. In addition, I counted the fraction of times that the true parameter values lay on the 95% confidence interval, as before, and the fraction of times that the confidence intervals for $\sigma_1^2$ and $\sigma_2^2$ overlapped. However, in this case I computed the variance on the estimated parameters as the sum of the variance among mappings and the mean variance from the Hessian matrix (e.g., Price et al. 2011). Finally, for each simulated stochastic character map I also computed the fractional overlap between the simulated map and the known true history. This measure is on the interval $0.0 – 1.0$, where 0.0 would indicate that the 2 mapped character histories have no branch length in common, and 1.0 indicating that the character histories are identical. This fraction can also be interpreted as the probability that, for any randomly chosen position on our phylogeny, the states mapped on the true tree and the generating tree are the same; thus (for a binary character), overlap of 0.5 means that the generating and simulated character histories have no more mapped branch length in common than expected by random chance.

For each discrete character simulation, I initiated the root with state "1" or state "2" with equal probability. Then, I conducted simulations with the following values for $q_{12} = q_{21}$: 0.5, 1.0, 2.0, 4.0, and 8.0. I chose these rates not because of any inherent biological realism, but because exploratory analysis suggested that these rates span the range of performance for the data analysis pipeline of Figure 1. In addition, I also rejected (and repeated) any simulation in which "1" or "2" was represented by <10 tip species in each 100 taxon tree. This was to avoid totally confounding the rate of evolution, $q$, with the number of tips in each state— because for a sufficiently low rate of evolution the

expected number of tips in the derived state can be low. This rejection procedure only resulted in the rejection of about 4% of trees for the lowest value of $q$ (for higher values, the rejection rate was effectively zero). I conducted all the aforementioned analysis in the statistical computing environment R (R Development Core Team 2011) using the packages "geiger" (Harmon et al. 2008) and "phytools" (Revell 2012). Both of these libraries depend heavily on the core multifunctional "ape" phylogenetics package (Paradis et al. 2004; Paradis 2012). All code and simulation results are available online (doi:10.5061/dryad.8mj66m5c).

### RESULTS

When the true character history for the discrete character is known, then evolutionary rates, $\sigma_1^2$ and $\sigma_2^2$, are estimated more or less without bias (Fig. 2a,b). The estimated ratio, $\hat{\sigma}_2^2/\hat{\sigma}_1^2$, seems to be slightly upwardly biased (Fig. 2c). In contrast, the estimated parameters are biased when the stochastic character mapping method is used. The bias is upward for the low rate ($\sigma_1^2$, in this study) and downward for the high rate ($\sigma_2^2$; Fig. 2a,b), although in the latter case only for very high values of $q$. Similarly, $\hat{\sigma}_2^2/\hat{\sigma}_1^2$ is downwardly biased. This pattern, like the bias on individual parameter estimates, is minimal for low $q$; but increases to become quite substantial as $q$ grows (Fig. 2c).

I also examined the relationship between "map overlap" (i.e., the similarity between the simulated and generating character history for the discrete character) and bias in the fitted rate ratio. Figure 3a shows the mean overlap for each simulated tree and data set plotted against the value of $\hat{\sigma}_2^2/\hat{\sigma}_1^2$ for that simulation. The pattern that we see across simulations is also often (but not always) found across different stochastic maps within a single simulated data set, particularly when different maps vary widely in their degree of overlap with the generating character history. Figure 3b shows this pattern for a representative sample ($q=1.0$).

In addition, I asked if the 95% confidence intervals for the fitted model parameter values, $\hat{\sigma}_1^2$ and $\hat{\sigma}_2^2$, included the generating values, $\sigma_1^2$ and $\sigma_2^2$. Figure 4a shows a summary of these results. In general, we see that the 95% confidence intervals on the estimated evolutionary parameters encompassed the true parameter values at about the same rate for $\sigma_1^2$ and $\sigma_2^2$ when estimated from the generating tree; but at a rate that decreased for increasing $q$ on the stochastically mapped trees for $\sigma_1^2$ (but not $\sigma_2^2$ over the range of parameters simulated). Furthermore, this fraction did not consistently exceed 0.95 across all values of $q$ for either the generating or stochastically mapped trees (Fig. 4a). The fact that the confidence intervals did not include the generating parameter values 95% of the time even when the true character history was used suggests that the variances estimated from the Hessian matrix are too
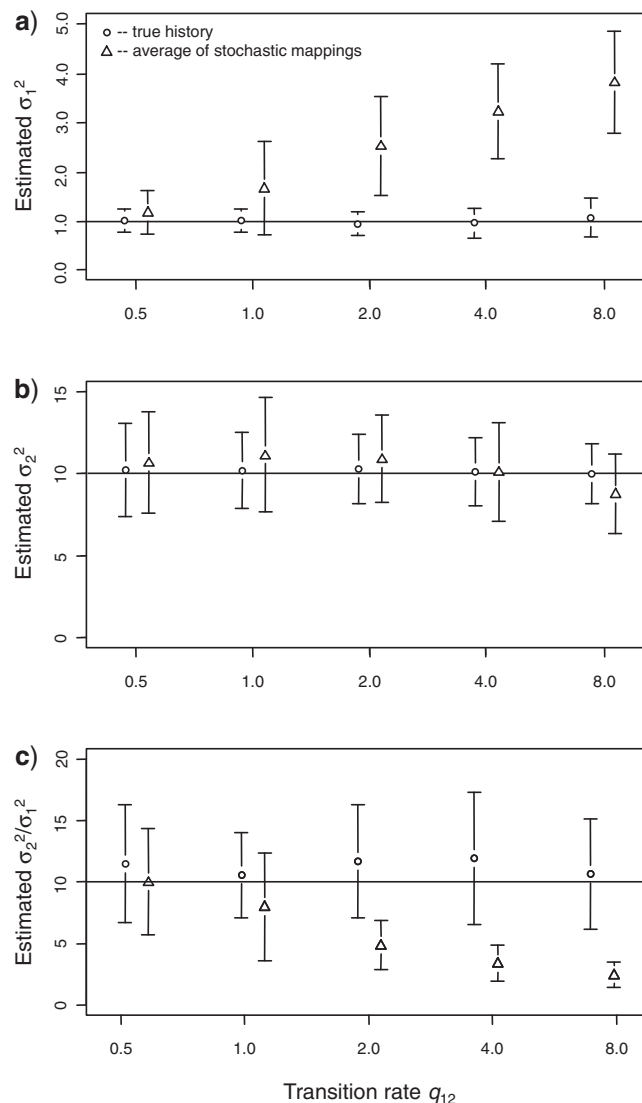


FIGURE 2.    Results from simulation analysis. a) Mean estimated $\sigma_1^2$ for each value of $q$. Open circles represent estimation from the "true" (i.e., generating) character history; whereas open triangles represent the average of 100 stochastic maps. Error bars are standard deviations across simulations. The horizontal line represents the simulated value of $\sigma_1^2$. b) Same as (a), but for $\sigma_2^2$. c) Same as (a) and (b), but for the ratio $\sigma_2^2/\sigma_1^2$.

small. Because the variance–covariance matrix for the parameters is only asymptotically approximated by the negative inverse of the Hessian matrix for large sample sizes (Lynch and Walsh 1998), this result implies that "large" data sets for comparative studies (i.e., 100 species, as in this simulation study; e.g., Mahler et al. 2010) might be insufficient to estimate confidence intervals from the likelihood surface.

Second, I asked if bias in rate estimation resulted in a decrease in power to detect true differences in evolutionary rate. Figure 4b shows the probability of detecting a difference in the estimated evolutionary rates (the power) for each value of $q$. This was assessed by identifying simulations with nonoverlapping 95%
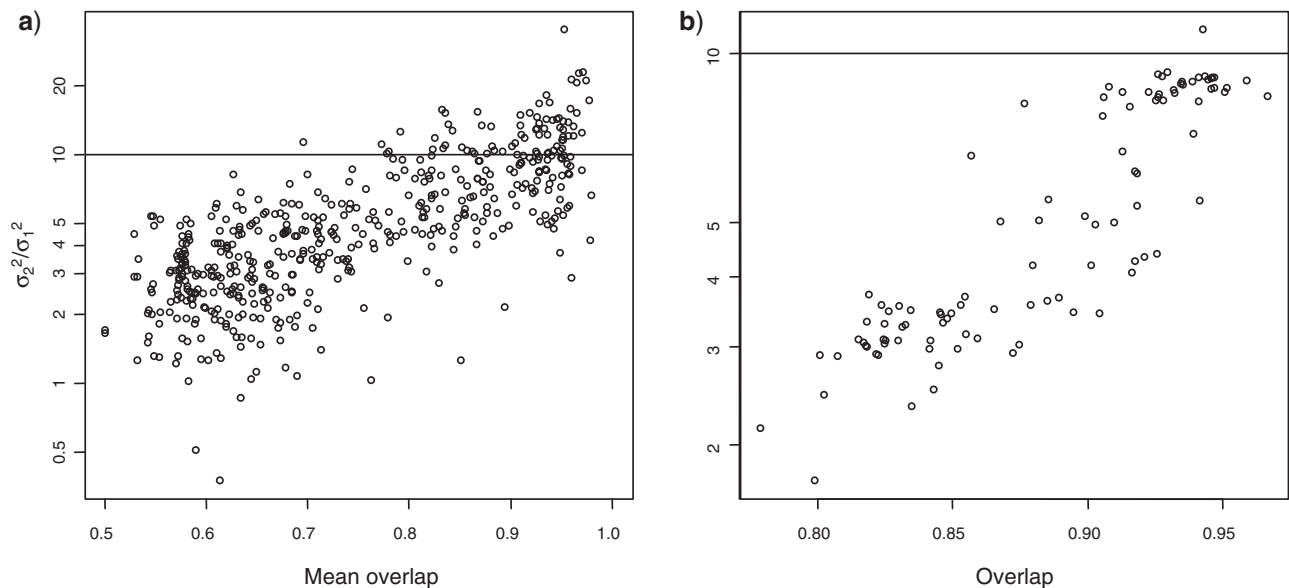
FIGURE 3.    a) Mean overlap between the stochastically simulated and true character history, plotted against $\sigma_2^2/\sigma_1^2$ for each simulation. b) The same as (a), but among maps for a single simulation ($q=1.0$). Not all simulations showed as strong a correlation as (b); however, this general pattern was common.
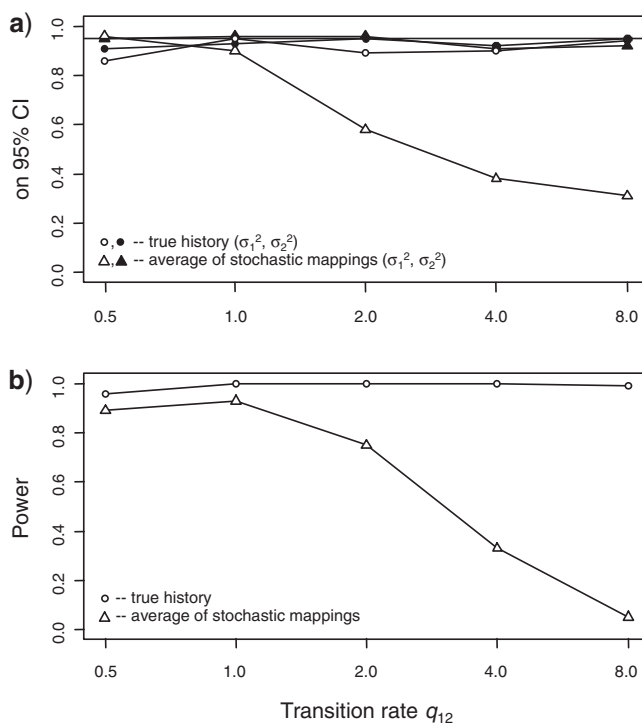


FIGURE 4.    a) Fraction of the analyses in which the 95% confidence intervals for $\sigma_1^2$ or $\sigma_2^2$ included the generating parameters. b) Power measured as the fraction of simulations in which the 95% confidence intervals for estimated $\sigma_1^2$ or $\sigma_2^2$ did not overlap.

confidence intervals on $\hat{\sigma}_1^2$ and $\hat{\sigma}_2^2$. I used this procedure rather than a likelihood-ratio test because each stochastically mapped history produces a different likelihood ratio and $P$-value; however as both procedures are based on asymptotic properties of the likelihood

surface, I expect their results to be similar. I found that power is high for both mapped and generating trees for low $q$, but decreases substantially on the mapped trees, but not on the generating trees, as $q$ is increased (Fig. 4b).

## DISCUSSION

An important step forward in the phylogenetic comparative analysis of continuously valued traits has been the development of likelihood-based methods that allow for different evolutionary parameters (e.g., rate, selective optimum) to assume differing values on different parts of a phylogeny (Butler and King 2004; O'Meara et al. 2006; Thomas et al. 2006; Revell and Collar 2009; Beaulieu et al. 2012). However, a typical requirement of these methods is that we specify regimes a priori, usually on the basis of information external to our continuous trait data (but see Eastman et al. 2011; Revell et al. 2012). With increasing regularity, researchers are using the method of stochastic character mapping (Nielsen 2002; Huelsenbeck et al. 2003) to simulate a sample of possible character histories for a discretely valued hypothesized evolutionary regime (e.g., habitat or geographic region), and then fitting the model to each tree in this sample. This analysis pipeline is illustrated in Figure 1.

In this article, I show that this method will produce evolutionary parameters (in this case, instantaneous rates for the Brownian process) that are biased to be more similar to one another than are the underlying generating values. In other words, low rates are upwardly biased; whereas estimates of high rates obtained in this manner are biased in a downward fashion, resulting in decreased power to detect rate variation on the tree. This has not

previously been noted in the literature. Rather, it seems to be typically assumed that averaging over a sample of plausible character histories will produce unbiased estimates of the underlying evolutionary rates (although this is not usually stated explicitly). In some cases, the bias can be quite severe (Fig. 2).

That said, however, the observed bias does not result in confidence intervals around the estimated parameters that are vastly smaller than if the true character history was known without error. In fact, for most of the simulation conditions of this study it was the confidence intervals around the parameter estimates from the true character history that were too small (Fig. 4a). This suggests that we should not be overly concerned about the possibility of being substantially misled by this method. The effect that bias in parameter estimation has on hypothesis testing in this case is in fact a loss of power to identify rate heterogeneity when it exists (Fig. 4b). In other words, researchers finding a significant difference in the estimated rates across a mapped discrete character can probably be fairly confident that this result reflects a real underlying rate difference; however, they should be cautious about interpreting the estimated rates which might be biased.

Although the trend is found at all values of the transition rate for our discrete trait, $q$, it only becomes severe for large values (Fig. 2). A reasonable consideration, particularly in light of the fact that $q$ scales with branch lengths for a given tree (specifically, multiplying the branch lengths of the tree by factor $k$ will scale estimated $q$ by $1/k$), is to ask what is meant by a "high" rate of transition in the discrete character.

A productive exercise here might be to calculate the expected number of changes on the tree given a fitted rate of character change. For a binary character with $q_{12} = q_{21} = q$, this quantity will just be equal to the total branch length of the tree multiplied by $q$. Thus, with a specific estimate of the phylogeny and branch lengths (in vector **v**) we can compute the expected number of changes $q \sum_{i=1}^{m} v_i$, for $m$ branches in the tree. Theory also tells us that for an unknown Yule tree (a constant-rate pure-birth phylogeny) of length $t$ and size $N$ the expected number of changes in a binary character with transition rate $q$ is given by $qt(N-1)/\log(N/2)$. This is simply derived from the number of edges in an $N$ taxon bifurcating tree: $2N-2$; the speciation rate for an $N$ species pure-birth tree of length $t$: $\lambda = \log(N/2)/t$; the mean branch length on a pure-birth phylogeny with speciation rate $\lambda$: $1/(2\lambda)$ (Mooers et al. 2012); and a small amount of algebra. Because I conducted all my analyses with pure-birth trees, we can use this equation to calculate that the expected number of changes for discrete traits simulated with rates $q = 0.5$, 1.0, 2.0, 4.0, and 8.0, will be about 13, 25, 51, 101, and 202, respectively. It is very important to note that these values for the expected number of changes are different from both the minimum number of changes (obtained, for instance, using parsimony), which will be lower; and from the realized number of changes in any given simulation, which might be higher or lower. Nonetheless, in most studies of the influence of

habitat, trophic level, mating system, or other discretely varying character on continuous trait evolution, $q = 2.0$, 4.0, or 8.0, on a pure-birth tree of unit length containing 100 species would be a very fast evolving character indeed!

Certainly part of the reason that the data analysis pipeline of Figure 1 can lead to biased evolutionary rate estimates is because no information from the continuous character is used to choose among alternative character histories for the discrete trait. Thus, the best method for incorporating data for a discrete trait might involve simultaneously maximizing the likelihood of our discrete character history along with the likelihood of our continuous trait data conditioned on that history. Unfortunately, this is not as simple as merely using the likelihood of the set of ancestral states at internal nodes implied by our maps. These likelihoods are computed by summing across all possible character histories between nodes consistent with that set of states, whereas our stochastic map represents one specific history. As an appealing alternative one could adopt a fully Bayesian framework and simultaneously sample rate regimes and evolutionary rates conditioned on both our data for the continuous trait and a discrete character hypothesized to influence its rate of evolution. These approaches are, however, beyond the scope of the present short note.

Although simultaneous estimation of the rates of continuous character estimation along with the discrete character history upon which they depend might help mitigate the bias described in this study, I feel that the problem is in many ways more fundamental. Specifically, in our generating model some periods of evolutionary change have low variance (when the discrete character is in state "1") and others have high variance (state "2"). Error in the discrete character history (an avoidable result of incomplete historical knowledge, regardless of our methodology) will inevitably result in the misattribution of some episodes of high evolutionary change to state "1"; as well as other periods of relatively low evolutionary change to state "2." Like any situation in which we mix distributions of unequal variance (but equivalent mean, as under Brownian motion), the result is a distribution with an intermediate variance—as I have found in this study. This argument is consistent with the strong relationship between the mean overlap of the stochastic maps with the generating character history and our bias in the estimated rates (Fig. 3). What gives me cause for optimism, however, is that this effect is relatively minor (essentially undetectable from the number of simulations conducted here) as long as the rate of change in the discrete character is modest; which means that most empirical data sets probably fall toward the right side of Figure 3 where overlap between a typical stochastic map and the true character history is high and bias in the estimation of evolutionary rates is relatively slight.

Finally, in addition to being applied in the data analysis pipeline described herein, the general procedure of stochastic character mapping (Nielsen 2002; Huelsenbeck et al. 2003; Bollback 2006) has

many other uses in phylogenetic biology. For instance, stochastic character mapping has also been used to generate a sampling distribution on transition rates (e.g., Anacker et al. 2011), to reconstruct ancestral character states at internal nodes (e.g., Brockington et al. 2011; Calvente et al. 2011), to obtain sampling distributions for the timing or number of changes in a discrete trait along the branches of a phylogeny (e.g., Algar and Losos 2011; van Wilgenburg et al. 2011), and to estimate the evolutionary correlations between discrete characters evolving on the tree (e.g., Brockington et al. 2011). So far as I am aware, the results of this study do not carry any implications for these other common applications of stochastic mapping in phylogenetics.

## Conclusions

Likelihood-based methods for analyzing character evolution in the context of a tree are becoming increasingly popular. Here, I examined a common data analysis pipeline in which investigators test for the relationship between the state of a discrete character and the rate of evolution in a continuous trait first by mapping the discrete trait using the technique of stochastic character mapping and then by using ML to fit a multirate evolutionary model for the continuous character. I show that this pipeline causes estimated rates to be more similar to one another than are their underlying generating values. However, I also show that although this error results in decreased power, it is less likely to lead to a type I error. Furthermore, I show that the effect is only severe when the discrete character changes frequently, resulting in a character history that is highly uncertain.

## Supplementary Material

Data files and/or other supplementary information related to this paper have been deposited on Dryad at http://datadryad.org under doi: 10.5061/dryad. 8mj66m5c.

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