

Tip rates, phylogenies and diversification: What are we estimating, and how good are the estimates?

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Abstract

1. Species-specific diversification rates, or 'tip rates', can be computed quickly from phylogenies and are widely used to study diversification rate variation in relation to geography, ecology and phenotypes. These tip rates provide a number of theoretical and practical advantages, such as the relaxation of assumptions of rate homogeneity in trait-dependent diversification studies. However, there is substantial confusion in the literature regarding whether these metrics estimate speciation or net diversification rates. Additionally, no study has yet compared the relative performance and accuracy of tip rate metrics across simulated diversification scenarios.
2. We compared the statistical performance of three model-free rate metrics (inverse terminal branch lengths; node density metric; DR statistic) and a model-based approach (Bayesian analysis of macroevolutionary mixtures [BAMM]). We applied each method to a large set of simulated phylogenies that had been generated under different diversification processes. We summarized performance in relation to the type of rate variation, the magnitude of rate heterogeneity and rate regime size. We also compared the ability of the metrics to estimate both speciation and net diversification rates.
3. We show decisively that model-free tip rate metrics provide a better estimate of the rate of speciation than of net diversification. Error in net diversification rate estimates increases as a function of the relative extinction rate. In contrast, error in speciation rate estimates is low and relatively insensitive to extinction. Overall, and in particular when relative extinction was high, BAMM inferred the most accurate tip rates and exhibited lower error than non-model-based approaches. DR was highly correlated with true speciation rates but exhibited high error variance, and was the best metric for very small rate regimes.
4. We found that, of the metrics tested, DR and BAMM are the most useful metrics for studying speciation rate dynamics and trait-dependent diversification. Although BAMM was more accurate than DR overall, the two approaches have complementary strengths. Because tip rate metrics are more reliable estimators of speciation rate, we recommend that empirical studies using these metrics exercise caution when drawing biological interpretations in any situation where the distinction between speciation and net diversification is important.

KEYWORDS

Bayesian analysis of macroevolutionary mixtures, diversification, DR statistic, node density, terminal branch length, tip rates, trait-dependent diversification

1 | INTRODUCTION

Rates of speciation and extinction vary through time and among lineages (Alfaro et al., 2018; Etienne & Haegeman, 2012; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Moen & Morlon, 2014; Nee, Mooers, & Harvey, 1992; Sanderson & Donoghue, 1996), contributing to dramatic heterogeneity in species richness across the tree of life (Alfaro et al., 2009; Barker, Burns, Klicka, Lanyon, & Lovette, 2013; Jetz et al., 2012). By characterizing variation in rates of speciation and extinction, we can better understand the dynamics of biological diversity through time, across geographic and environmental gradients (Mittelbach et al., 2007; Rabosky, Title, & Huang, 2015; Ricklefs, 2006; Silvestro, Schnitzler, & Zizka, 2011; Zink, Klicka, & Barber, 2004), and in relation to traits and key innovations (Beaulieu & O'Meara, 2016; FitzJohn, Maddison, & Otto, 2009; Near et al., 2012). Consequently, there has been great interest in statistical methods for inferring rates of speciation and extinction from molecular phylogenies.

Although rates of diversification have traditionally been quantified for clades, there has been a growing interest in estimating species-specific rates of diversification, which we refer to here as 'tip rates'. Tip rates are increasingly used to describe patterns of geographic and trait-associated variation in diversification (Freckleton, Phillimore, & Pagel, 2008; Harvey & Rabosky, 2017; Jetz et al., 2012; Kennedy et al., 2016; Quintero & Jetz, 2018; Rabosky et al., 2018). It may seem strange to view evolutionary rates as a property of individual lineages, but such rates emerge naturally from the birth–death model we typically use to conceptualize the diversification process (Nee, May & Harvey 1994; Nee et al., 1992). Under the birth–death process, individuals (species) are characterized by per-lineage rates of species origination (speciation, λ) and extinction (μ). For the purposes of inference, these rates are typically assumed to be constant among contemporaneous members of a focal clade. However, tip rates can be viewed as our best estimate of the present-day rate of speciation or extinction for an individual lineage, conditional on past (usually recent) evolutionary history. As such, they provide information about the expected amount of time that will elapse before a lineage splits or becomes extinct.

A number of approaches have been used to estimate tip rates, including both model-based and non-model-based approaches (i.e. models that are parameterized with speciation and extinction rates, vs. metrics that simply rely on branch lengths and splitting events). These approaches vary in terms of how much information they derive from a focal species (i.e. a terminal branch) relative to the amount of information they incorporate from other regions of the phylogeny. On one end of the spectrum, tree-wide estimates (i.e. one rate for the entire phylogeny) of speciation and extinction rates under a constant-rate birth–death (CRBD) model provide tip rates

that are maximally auto-correlated (identical) across species in the clade; such rates for any given species are not independent of rates for any other species in the group of interest. On the other end of the spectrum, terminal branch lengths can be used to derive a censored estimate of the rate of speciation that is minimally autocorrelated with rates for other species in the focal clade. Terminal branch lengths are largely unique to each species (rates might be identical only for sister taxa), but provide a noisy measure of speciation, due to the stochasticity inherent in the diversification process (Nee, May, et al., 1994), and they have been employed as a summary statistic in assessing model adequacy (Bromham, Hua, & Cardillo, 2016; Gomes, Sorenson, & Cardoso, 2016). In contrast to single (terminal) branch estimates, tree-wide estimates should be less susceptible to stochastic noise, because they incorporate information from the entirety of the tree (e.g. multiple branches are used in the estimates). Of course, the tree-wide estimate necessarily assumes that all tips share a common underlying diversification process. Other tip rate metrics fall somewhere between these two extremes, incorporating some tree-wide information but relaxing the assumption of homogeneous rates across all lineages (node density metric: Freckleton et al., 2008; DR: Jetz et al., 2012). The estimation of tip-specific rates thus entails a trade-off between the precision of individual estimates and the stochastic error associated with those estimates.

Bayesian analysis of macroevolutionary mixtures (BAMM; Rabosky, 2014) is a model-based approach that can accommodate heterogeneity in the rate of diversification through time and among lineages. BAMM simulates a posterior distribution of macroevolutionary rate shift configurations given a phylogeny of interest; marginal rates of speciation and extinction for individual taxa can then be extracted from this distribution. In this framework, the correlation in rates between any pair of species is a function of the posterior probability that they share a common macroevolutionary rate regime (Rabosky, Donnellan, Grudler, & Lovette, 2014). If the tree-wide posterior probability of rate variation is low, the marginal rates estimates for individual species will be similar across the entire tree, as under a CRBD model. Likewise, any pair of taxa that are consistently assigned to the same macroevolutionary rate regime will necessarily have identical tip rates.

Tip rates are best suited to a host of questions and hypotheses where the diversification dynamics over the evolutionary history of a group are either less relevant, or no more relevant, than the rates of diversification closer to the present day. For example many hypotheses involving trait-dependent diversification implicitly assume a time-homogeneous, or constant through time, effect of the trait on diversification rate (Claramunt, 2010; Coyne & Orr, 2004; FitzJohn, 2010; Jablonski, 2008; Kay et al., 2006). Harvey and Rabosky (2017) found that the use of tip rates for assessing correlations between

continuous traits and diversification has good performance across a range of diversification scenarios. Furthermore, hypotheses pertaining to non-historical geographic patterns of diversity are also better addressed with recent rates of diversification. For example many hypotheses for the latitudinal diversity gradient propose time-homogeneous effects of particular environmental factors (temperature, energy, geographic area) on rates of diversification (Kennedy et al. 2014; Mittelbach et al., 2007; Rabosky et al., 2018, 2015; Schluter, 2016). Put simply, if such time-homogeneous processes have shaped the latitudinal diversity gradient (e.g. correlation between speciation and temperature: Rohde, 1992), then the effect should be manifest in the distribution of present-day evolutionary rates.

At present, there is substantial confusion in the literature over what quantity various tip rate metrics actually measure. The DR statistic (Jetz et al., 2012) was originally described as a measure of the 'species-level lineage diversification rate'. While supplemental analyses and subsequent work suggested that DR was a better measure of speciation rate than net diversification (Belmaker & Jetz, 2015; Jetz et al., 2012; Quintero & Jetz, 2018), many studies have nonetheless continued to describe DR as an estimate of the lineage-level net diversification rate (Cai et al., 2017; Marin & Hedges, 2016; Oliveira et al., 2016; and many others). The node density metric of Freckleton et al. (2008) has also been described as a measure of net diversification. Whether these metrics more accurately measure speciation or net diversification is critically important for interpreting biodiversity patterns (e.g. two regions might differ dramatically in speciation rate, but net diversification rates in each might nonetheless be zero). An objective of our study is thus to compare the ability of DR, node density and other metrics to estimate speciation and net diversification rates.

Despite the potential utility of tip rates in geographic and trait-based analyses of speciation rate heterogeneity (Belmaker & Jetz, 2015; Jetz et al., 2012; Oliveira et al., 2016; Quintero & Jetz, 2018), there has yet been no comprehensive comparative assessment of the accuracy and precision of the estimates, save for supplemental analyses in Jetz et al. (2012) and Quintero and Jetz (2018). BAMM has low power to infer small rate regimes (Meyer & Wiens, 2017; Rabosky, Mitchell, & Chang, 2017), leading to the possibility that other approaches might perform better for smaller phylogenies or when the variation in rates among clades is subtle. However, DR and related methods will always identify variation in tip rates, even when none exists, provided there is stochastic variation in branch lengths. A goal of this study is therefore to evaluate the trade-off between the stochastic noise inherent in non-model-based approaches, and the conservative but less noisy estimates from model-based metrics. We compare the performance of these metrics across a range of simulation scenarios, which include both discrete and continuous variation in rates.

2 | MATERIALS AND METHODS

2.1 | Tip rate metrics

We assessed the accuracy of four tip rate metrics in this study at quantifying rates of speciation. As we demonstrate below (see also

Supplementary figure 5 in Jetz et al., 2012; extended figure 5 in Quintero & Jetz, 2018; Belmaker & Jetz, 2015), these metrics are estimators of speciation rate and not net diversification rate, and we refer to them as such throughout. The first metric is the inverse of the equal splits measure (Redding & Mooers, 2006), also called the *DR statistic* (Jetz et al., 2012), *DivRate* (Belmaker & Jetz, 2015; Oliveira et al., 2016), *ES* (Harvey & Rabosky, 2017) or *tip DR* (Quintero & Jetz, 2018), which we denote in this study as λ_{DR} . This species-specific measure incorporates the number of splitting events and the internode distances along the root-to-tip path of a phylogeny, while giving greater weight to branches closer to the present (Jetz et al., 2012; Redding & Mooers, 2006). λ_{DR} is computed as:

$$\lambda_{DR_i} = \sum_{j=1}^{N_i} b_j \frac{1}{2^{j-1}}$$

where λ_{DR_i} is the tip rate for species i , N_i is the number of branches between species i and the root, b_j is the length of branch j , starting at the terminal branch ($j = 1$) and ending with the root. Jetz et al. (2012) demonstrated that, for trees deriving from a Yule process, and with mild extinction, the mean λ_{DR} across tips converges on the true speciation rate.

We also considered a simpler metric, node density (Freckleton et al., 2008; denoted by λ_{ND}). This is simply the number of splitting events along the path between the root and tip of a phylogeny, divided by the age of the phylogeny. While λ_{DR} down-weights the contribution of branch lengths that are closer to the root, λ_{ND} equally weights the contributions of all branches along a particular root-to-tip path, regardless of where they occur in time. Under a pure-birth model ($\mu = 0$), both λ_{DR} and λ_{ND} should yield unbiased estimates of the rate of speciation.

The third measure we considered is the inverse of the terminal branch lengths (λ_{TB}). Rapid speciation rates near the present should be associated with proportionately shorter terminal branches; smaller values of λ_{TB} should thus characterize species with faster rates of speciation. This measure has recently been used as a summary statistic to assess model adequacy in trait-dependent diversification studies (Bromham et al., 2016; Gomes et al., 2016; Harvey & Rabosky, 2017). Following Steel and Mooers (2010), we note that the terminal branch lengths can be used to derive an estimate of the speciation rate; this follows from the fact that interior and terminal branches have the same expected value under the Yule process (Steel & Mooers, 2010). The corresponding estimator for the i 'th tip, λ_{TB} is approximately $1/2b$ where b is the length of a given terminal branch (Steel & Mooers, 2010). To our knowledge, λ_{TB} has not been used to explicitly estimate tip rates as we do here, but given its utility as a summary statistic and general theoretical properties (Steel & Mooers, 2010), we see value in comparing the performance of this metric to others currently in use.

Finally, we considered a Bayesian, model-based approach to estimating tip rates. BAMM (Rabosky, 2014) assumes that phylogenies are generated by a set of discrete diversification regimes. Using MCMC, the program simulates a posterior distribution of rate shift regimes, from which marginal posterior rate distributions can be

extracted for each tip in the phylogeny. Priors for BMM analyses were set using default settings from the `setBMMpriors` function from `BMMTOOLS` (Rabosky, Grudler, et al., 2014). The prior parameterizations specified by this function ensure that the prior density on relative rate changes across the tree is invariant to the scale of the tree (e.g. multiplying branch lengths by 10^6 will not change inferences about relative rates across the tree). We denote BMM tip speciation rates (mean of the marginal posterior) as λ_{BMM} . As BMM also estimates extinction rates for each regime, we also calculated tip-specific net diversification rate as $\lambda_{\text{BMM}} - \mu_{\text{BMM}}$, denoted as r_{BMM} .

2.2 | Tip rate metrics estimate speciation, not net diversification

As suggested previously (Belmaker & Jetz, 2015; supplemental analyses in Jetz et al., 2012), DR and presumably other tip-based measurements, more accurately estimate the rate of speciation than the rate of net diversification. However, numerous studies continue to refer to DR as a measure of net diversification (Marin & Hedges, 2016; Oliveira et al., 2016; Cai et al., 2017; Quintero & Jetz, 2018; and many others). This is incorrect and it is straightforward to demonstrate that λ_{TB} , λ_{ND} and λ_{DR} are more reliable measures of speciation rates and not net diversification rates, at least when extinction is moderate to high.

To illustrate this property of the metrics, we applied all approaches to constant-rate-death phylogenies simulated across a range of extinction fractions ($\epsilon = \mu/\lambda$), including pure-birth trees ($\epsilon = 0$) as well as trees exhibiting very high turnover ($\epsilon = 1$). To evaluate accuracy of speciation estimates as a function of ϵ , we generated 1,000 phylogenies with 100 tips each, where λ and ϵ were drawn from uniform distributions (λ : [0.05, 0.3]; ϵ : [0, 1]). Importantly, when λ is sampled uniformly with respect to ϵ , the distribution of r is not uniform: the mean, range and variance in r decrease dramatically as ϵ increases. To evaluate the accuracy of r as a function of ϵ , we thus generated a second set of trees by sampling r and ϵ from uniform distributions (r : [0.05, 0.3], ϵ [0, 1]). As a result, λ has constant mean and variance with respect to ϵ in the first set of simulations, and the same is true for r in the second set of simulations (Figure S1). All phylogeny simulations were conducted with the `TREE-SIM` package in R (Stadler, 2011).

We compared tip rate metrics to true speciation rates λ_{TRUE} (with the first simulation set) and to true net diversification rates r_{TRUE} (with the second simulation set). We evaluated mean per-tip accuracy of the tip rate metrics with three measures of error:

$$\text{mean absolute error} = \frac{1}{N} \sum_{i=1}^{N_i} |\lambda_i - \lambda_{\text{TRUE}_i}|$$

$$\text{RMSE} = \sqrt{\frac{1}{N} \sum_{i=1}^{N_i} (\lambda_i - \lambda_{\text{TRUE}_i})^2}$$

$$\text{mean proportional error} = \frac{1}{N} \sum_{i=1}^{N_i} \frac{\lambda_i - \lambda_{\text{TRUE}_i}}{\lambda_{\text{TRUE}_i}}$$

where λ_i is the estimated tip rate for species i out of N total species, λ_{TRUE} is the true tip rate. Mean absolute error and root mean square error capture the magnitude in error in tip rates, and mean proportional error quantifies the bias in tip rates, as a function of the true tip rates (Rabosky, Donnellan, et al., 2014). In analyses below, all error summaries yield generally congruent results; results for mean absolute error are presented in the main text, and others in the supplement.

2.3 | Assessment of tip rate metrics

We tested the performance of the metrics by compiling publicly available datasets from a number of simulation-based studies (Table 1). By focusing on simulations from previously published work, we thus ensured that the simulation process itself was effectively blinded to the objectives of this study. We further note that our trial datasets included several studies that were critical of BMM (Meyer & Wiens, 2017; Moore, Höhna, May, Rannala, & Huelsenbeck, 2016). These simulated trees include rate heterogeneity in time and across lineages. Together, these phylogenies present a wide range of tree sizes and diversification rate shifts, providing an ideal comparative dataset for our purposes. To more easily distinguish between these tree types in the text, we refer to the BMM-type, multi-regime time-constant phylogenies simply as ‘multi-regime’, and the multi-regime diversity-dependent phylogenies simply as ‘diversity-dependent’, even though discrete rate shifts are present in both types of trees. In addition to discrete-shift scenarios (e.g. BMM-type process), we simulated phylogenies under an ‘evolving rates’ model of diversification (Rabosky, 2010; as corrected in Beaulieu & O’Meara, 2015) to explore performance of tip rate metrics when diversification rates change continuously and independently along branches, as might occur if diversification rates are correlated with an underlying continuous trait (FitzJohn, 2010). In these simulations, we allowed the logarithm of λ to evolve across the tree under a Brownian motion process, while holding ϵ constant. The magnitude of rate heterogeneity among branches is controlled by the diffusion parameter σ , where greater values lead to greater heterogeneity in speciation rates. Although published phylogenies with rate data were unavailable for this simulation scenario, we used simulation code and parameters taken directly from Beaulieu and O’Meara (2015) to generate trees with similar statistical properties to those in their study. Simulations were performed with the following parameters: $\lambda = 0.078, 0.103, 0.145, 0.249$ and $\epsilon = 0.0, 0.25, 0.50, 0.75$. We simulated 100 phylogenies for each (λ, ϵ) pair, and for three values of σ ($\sigma = 0.03, 0.06, 0.12$). We evaluated tip rate accuracy by comparing estimated to true tip rates, using the absolute and proportional error metrics described above. We also examined the correlation between true and estimated tip rates, combining tip rates from all phylogenies generated under the same class of diversification process, and visualizing these data as density scatterplots, generated with the `LSD` package in R (Schwalb et al., 2018), where colours indicate the density of points.

TABLE 1 Summary of simulated phylogenies used in this study

Simulation model	Number of trees	Tree size	Regime number	Source
Single-regime, constant-rate birth–death	100	100	1	Mitchell and Rabosky (2016)
Single- and multi-regime, constant-rate birth–death	100	51–148	1–6	Moore et al. (2016)
Single- and multi-regime, constant-rate birth–death	400	10–4,296	1–67	Rabosky et al. (2017)
Multi-regime, constant-rate birth–death	20	939–3,708	11	Meyer & Wiens (2017)
Single- and multi-regime, constant-rate birth–death	188	4–3,955	1–73	Mitchell et al. (2018)
Single-regime, constant-rate birth–death, lambda uniform	1,000	100	1	This study
Single-regime, constant-rate birth–death, net diversification uniform	1,000	100	1	This study
Pure birth root regime, 1–4 discrete shifts to diversity-dependent regimes	1,200	54–882	1–5	Rabosky (2014) and Mitchell and Rabosky (2016)
Speciation rate evolves via diffusion process	1,200	25–1,208	1	Rabosky (2010), Beaulieu and O'Meara (2015), and Rabosky (2016); and this study

Size of diversification rate regimes might be an important factor in a tip rate metric's ability to accurately estimate rates. For example BMM's statistical power in detecting a shift to a new rate regime is a function of the number of taxa in that rate regime, and tip rates for taxa from small regimes will more likely be parameterized according to the larger parent regime or the tree-wide average rate (Rabosky et al., 2017); this is the expected behaviour when BMM fails to identify a rate shift. However, non-model-based approaches such as those examined in this study might be more accurate for small regimes. To explore how rate regime size influences the accuracy of tip rate metrics, we calculated the mean tip rate for each true rate regime from all multi-regime phylogenies (simulation datasets from Meyer & Wiens, 2017; Mitchell, Etienne, & Rabosky, 2018; Moore et al., 2016; Rabosky et al., 2017). We then calculated the Pearson correlation coefficient and the slope of a linear model between true and estimated mean regime rates. We explored the performance of all metrics with respect to regime sample size, as in Rabosky et al. (2017, figure 13). For comparison, we repeated all performance summaries on tip rates estimated by applying a simple constant-rate birth–death (CRBD) process to each simulated phylogeny. This exercise is an important control, because it indicates how much error we would expect for each simulated phylogeny under the simplifying (incorrect) assumption that rates are constant among lineages and through time for each dataset.

3 | RESULTS

3.1 | Speciation or net diversification?

As expected, the tip rate metrics examined in this study are more accurate estimators of the rate of speciation (λ) and not the net rate of species diversification (r). Mean absolute error increased

exponentially with respect to the extinction fraction ϵ (Figure 1). However, mean absolute error in speciation rate was largely invariant with respect to ϵ (0.95 quantile of r -based and λ -based mean absolute error for λ_{DR} : 2.28 and 0.17 respectively). Nearly identical patterns were found with RMSE (Figure S2). Note that r and λ for these simulations were drawn from identical uniform distributions, and absolute error in the rates is thus comparable. Proportional error generally exhibited the same pattern, and in terms of λ vs. r , differences in speciation-based error varied across ϵ (Figure S3). There was a weak but significant trend towards progressively greater underestimation of speciation rates with increasing values of relative extinction (linear model slopes: -0.08 , -0.014 , -0.011 for λ_{ND} , λ_{DR} and λ_{BMM} respectively). Overall, error was highest for λ_{TB} by an order of magnitude (Figure S4), and decreased progressively with λ_{ND} and λ_{DR} , with the lowest overall error in λ_{BMM} . BMM estimates of net diversification rate were relatively accurate, except at the highest values of ϵ (Figures 1, S2 and S3).

3.2 | Tip rate accuracy across rate-variable phylogenies

Tip rates estimated with BMM were consistently more accurate than those obtained using the other methods across all diversification scenarios considered, including multi-regime, diversity-dependent and evolving rates trees (Figure 2). λ_{DR} was the second-most accurate metric, although its relationship with true rates was substantially weaker than λ_{BMM} . λ_{ND} and λ_{TB} were correlated with true rates but performed relatively poorly overall. However, λ_{TB} performed better than λ_{ND} , and just as well as λ_{DR} at estimating speciation rates for diversity-dependent trees (Figures 2 and S5). All metrics performed best for multi-regime trees, followed by evolving rates and diversity-dependent trees respectively. For

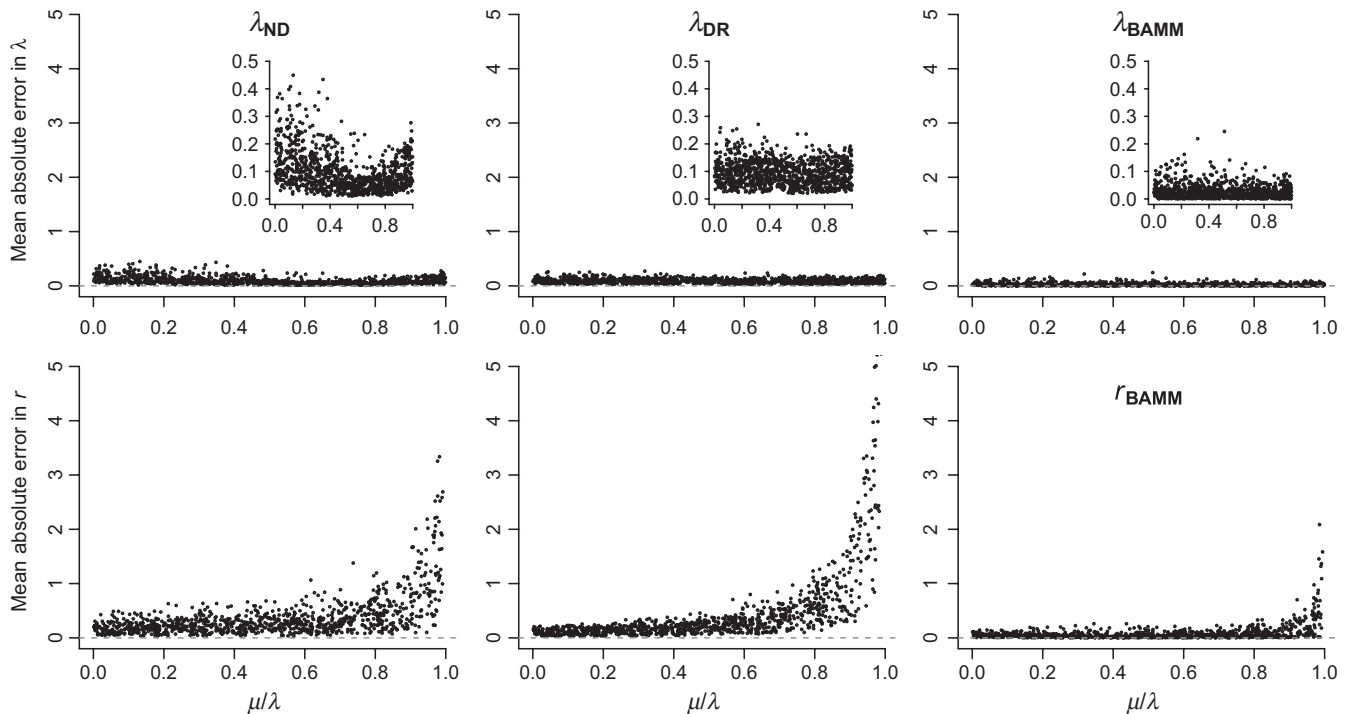


FIGURE 1 Mean absolute error in λ (top) and r (bottom) for three different tip rate metrics, across a range of relative extinction rates. For BAMM, the estimated speciation and net diversification rates are presented in the top and bottom panels respectively. Absolute error of zero implies perfect accuracy. Inset plots show error in λ with truncated y -axis scale to facilitate comparison among metrics. All tip rate metrics track λ more accurately than they track r . See Figure S4 for λ_{TB} , which performed much worse than the other metrics

diversity-dependent trees, λ_{ND} rates are effectively uncorrelated with the true rates (Figure 2). Additionally, the performance of the different tip rate metrics for multi-regime phylogenies is not sensitive to the source of the simulated phylogenies (Figure S6). We found that BAMM substantially outperformed all other metrics on datasets from studies that independently assessed BAMM's performance (Figure S6: Moore et al., 2016; Meyer & Wiens, 2017). Tip rates were also generally but more weakly correlated with true net diversification rates, with the exception of λ_{ND} , which was uncorrelated with true rates for diversity-dependent trees, presumably because this metric equally weights the full depth of the tree (Figure S7).

In terms of mean per-tip error, λ_{BAMM} consistently outperformed the other metrics for multi-regime, diversity-dependent and evolving rates trees (Figures 3 and S8). Error in λ_{BAMM} increased as a function of rate heterogeneity for evolving rate phylogenies, but was largely independent of the magnitude of rate heterogeneity for the other scenarios. λ_{DR} generally exhibited greater error than λ_{BAMM} , and this error increased as a function of the level of heterogeneity for both the evolving rates and multi-regime trees. Error in λ_{DR} was generally invariant to the number of rate regimes for the diversity-dependent scenarios. However, λ_{DR} tended to have greater error than tip estimates from a simple model that assumes no variation in rates through time or among lineages (λ_{CRBD} ; all tips assigned the tree-wide CRBD rate). λ_{ND} performed somewhat similar to λ_{DR} for constant-rate and evolving rates trees, but worse for

diversity-dependent trees. Error in λ_{TB} increased with increasing rate heterogeneity for constant-rate and evolving rates trees, but was relatively unaffected by rate heterogeneity in diversity-dependent trees (Figure S9). However, error for this metric was far greater than for all other tip metrics.

3.3 | Effects of regime size on performance

Both metrics of performance assessment – the Pearson correlation and OLS slope – generally increased with increasing regime size (Figure 4). This was found to be true for all tip rate metrics, although λ_{TB} and λ_{ND} never achieved high performance. λ_{DR} tended to perform better than other metrics when small rate regimes were included (e.g. 10 tips or fewer); however, the slope between estimated and true rates was greater than 1 across the majority of minimum regime sizes, indicating that λ_{DR} overestimates speciation rates (see also Figure S3). Similar patterns were observed for net diversification rates with λ_{DR} , but the magnitude of the overestimation was greater than for speciation (Figure S10). λ_{BAMM} , in contrast, approached a slope of 1 when estimating speciation rates and slightly underestimated net diversification rates (regimes with >30 tips: OLS slope = 0.96 for λ , 0.87 for r).

Absolute error in regime mean tip rates was lowest for λ_{DR} and λ_{BAMM} , regardless of the size of the rate regime (Figure 5). BAMM's ability to accurately estimate tip rates improved with regime size, whereas absolute error was relatively consistent across regime sizes

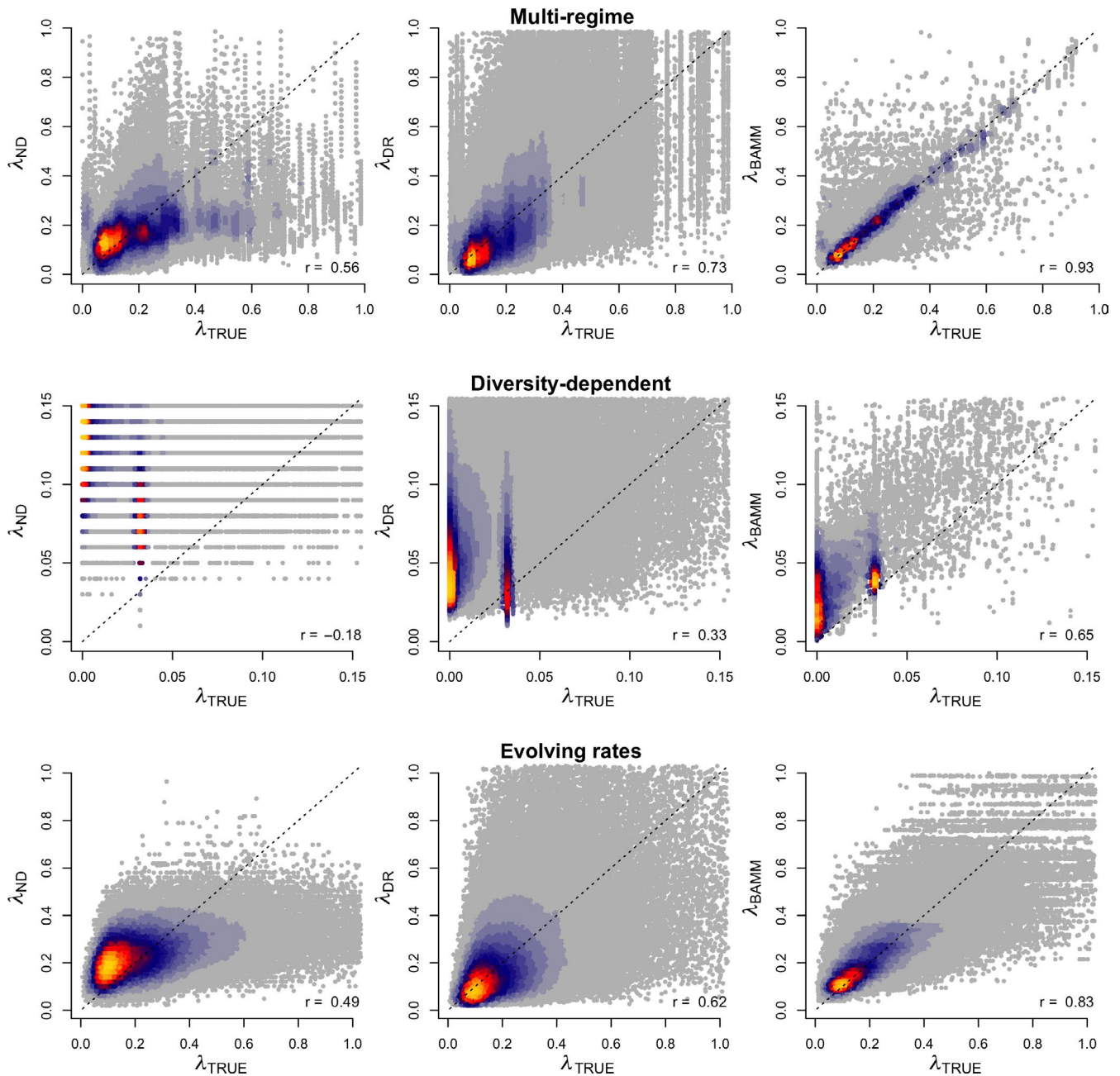


FIGURE 2 True tip rates (λ_{TRUE}) in relation to estimated tip rates. Tip rates were compared separately for different major categories of phylogeny simulations (rows) and are plotted separately by inference method (columns). Plotting region is restricted to the 99th percentile of true rates, but Spearman correlations between true and estimated rates (lower right of each figure panel) are based on the full range of the data. Colours indicate the density of points in the scatter plots. The horizontal gaps in λ_{ND} for diversity-dependent trees are an artefact of all trees having the same crown age. λ_{BAMM} exhibited the strongest correlation with true rates for all simulation categories

for λ_{DR} for regimes greater than 10 species. We also found that λ_{DR} slightly outperformed λ_{BAMM} for small rate regimes.

Note that, in Figures 4 and 5, each rate regime is treated as a single data point. Rate regimes of sizes 1,000, 100 and 1 tip are equivalent under this method of error assessment. Figure 4 assesses how well these methods estimate rates for individual regimes, regardless of the size of those regimes. In contrast, Figures 1–3 ask how well these methods perform at estimating rates for a given tip.

4 | DISCUSSION

We assessed several tip rate metrics and confirmed that these are more accurate estimators of the rate of speciation, rather than net diversification (Figures 1, 4, S7 and S10). This distinction was especially pronounced at high extinction fractions, where the rate of lineage turnover is high, and rates of speciation and net diversification have the potential to be more divergent. These results are consistent with supplemental analyses performed in Jetz et al. (2012).

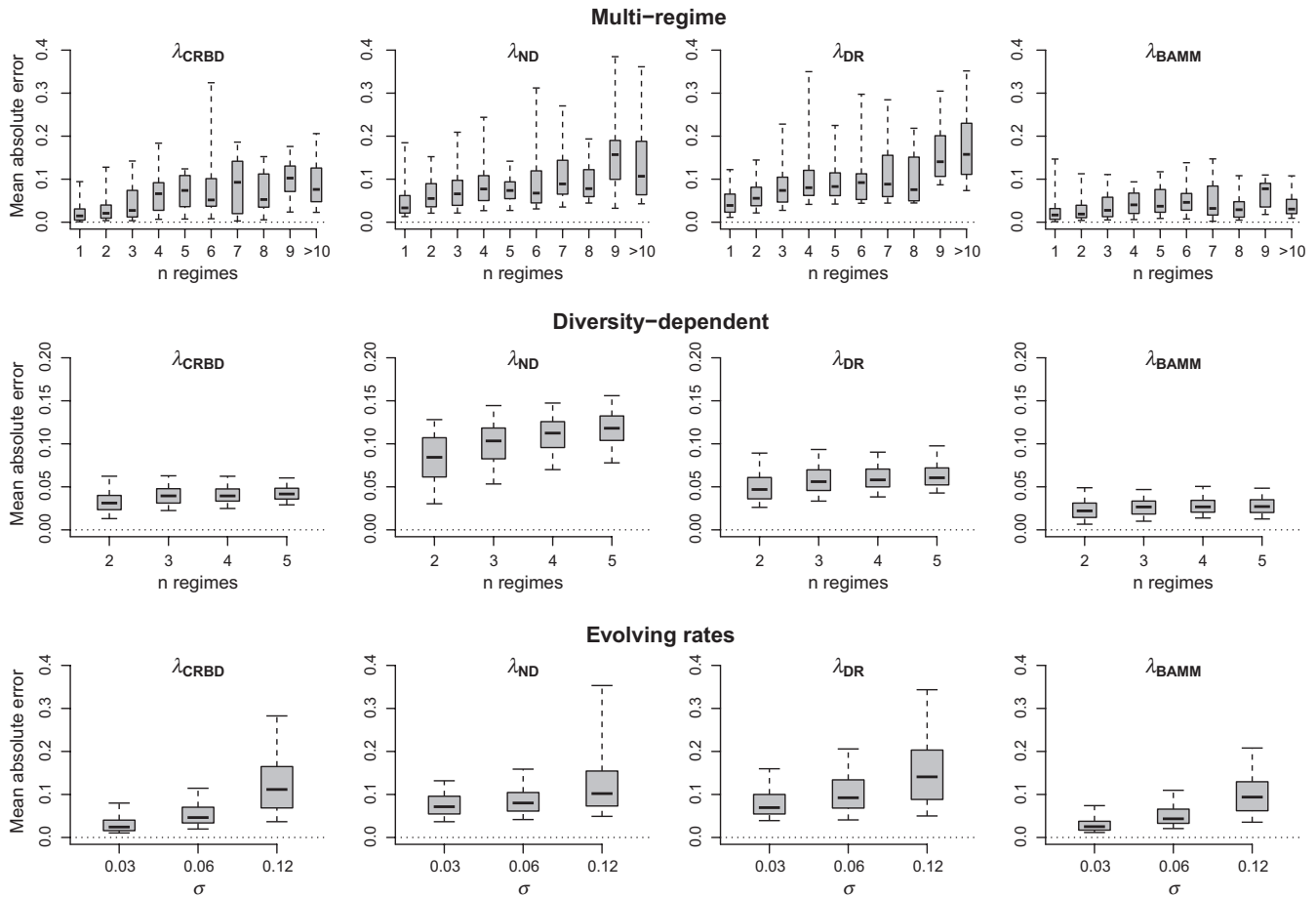


FIGURE 3 Mean per-tip absolute error in speciation rates as a function of the magnitude of rate heterogeneity in each simulated phylogeny. Results are presented separately for different categories of rate variation (Table 1); left column shows estimates from a constant-rate birth–death model for reference. The boxes and whiskers represent the 0.25–0.75, and the 0.05–0.95 quantile ranges respectively. In some cases, λ_{ND} and λ_{DR} had more error than a simple CRBD model with no variation in tip rates. λ_{BAMM} had the least amount of error across all amounts of rate heterogeneity. See Figure S9 for λ_{TB}

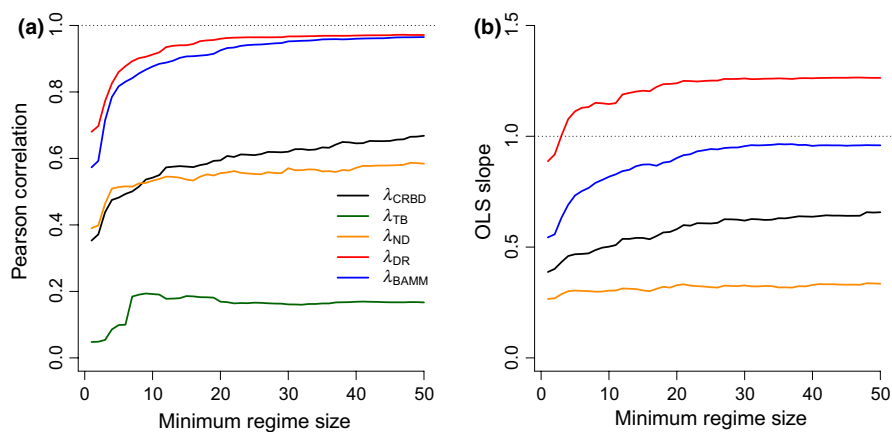


FIGURE 4 Performance of tip rate metrics as a function of regime size, including Pearson correlation (a) and OLS regression slope (b) for mean rates with respect to λ_{TRUE} : λ_{DR} and λ_{BAMM} outperform the other metrics when summarized in this fashion, although λ_{DR} tends to overestimate the rate of speciation. The x-axis denotes the minimum regime size across which performance was summarized. For example, $x = 20$ corresponds to the correlations and slopes computed for all regimes with 20 or more tips; a value of $x = 1$ is the corresponding results for all regimes. The OLS slope for λ_{TB} is not visible as it ranges between 7 and 9

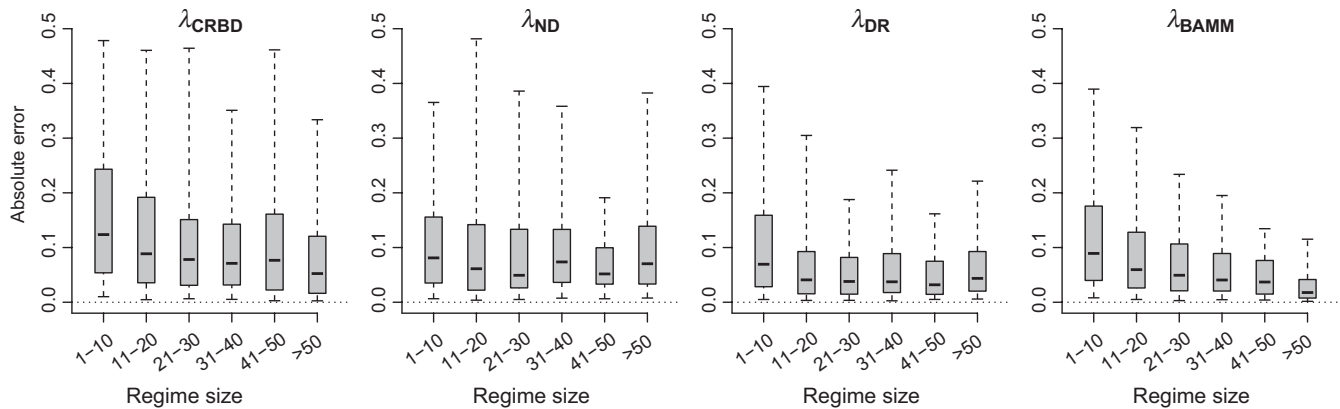


FIGURE 5 Mean per-regime absolute error in relation to true rate regime size, as binned into 10 size categories. The boxes and whiskers represent the 0.25–0.75, and the 0.05–0.95 quantile ranges respectively. Perfectly estimated rates have an error of zero. λ_{DR} and λ_{BAMM} exhibit the least error when averaged by regimes, and λ_{DR} does slightly better for small clades (10-clade median error 0.07 for λ_{DR} , and 0.08 for λ_{BAMM})

It is also important to note that recent extinction will have a much greater influence on these metrics than extinction events deeper in time (Quental & Marshall, 2011). Net diversification rate is a critical determinant of species richness, yet this quantity is potentially independent of the underlying rate of speciation. Misinterpretation of tip rate metrics could therefore lead to highly misleading perspectives on large-scale diversity dynamics. As we demonstrate (Figures 1, S2 and S3), tip rate metrics (λ_{ND} , λ_{DR}) provide relatively little information about net diversification, and high values of these metrics are fully consistent with equilibrational models of speciation where the true net diversification rate is zero. Thus, λ_{DR} and λ_{ND} should not be used to support claims about the dynamics of species richness or net diversification *per se* without independent evidence bearing on plausible levels of extinction.

In terms of accuracy, we found that BAMM performed better than non-model-based metrics across all datasets we considered: estimated tip rates were most highly correlated with true tip rates, and mean per-tip error in rates was lower across a range of rate-variable simulation scenarios. This performance is likely to be at least partially due to the inclusion of extinction in the BAMM inference model. BAMM is expected to perform well for phylogenies with discrete shifts in diversification rates as this type of rate variation is most consistent with BAMM's assumptions (Mitchell & Rabosky, 2016; Mitchell et al., 2018; Rabosky, 2014; Rabosky et al., 2017). However, BAMM performed surprisingly well for the evolving rates phylogenies, which conform poorly to the assumptions of the inference model. In these trees, the rate of speciation changes continuously under a diffusion process, and as a result, the phylogeny exhibits rate heterogeneity without discrete rate shifts.

On evolving rates phylogenies, λ_{BAMM} performed better than λ_{DR} (Figure 2; Spearman's ρ for λ_{BAMM} = 0.83, ρ for λ_{DR} = 0.62), despite the fact that λ_{DR} does not rely on the detection of distinct rate regimes to estimate tip rates (Figure 5). λ_{BAMM} also exhibited the lowest mean per-tip error across varying levels of rate heterogeneity (Figure 3).

Why do λ_{BAMM} and λ_{DR} exhibit such striking differences in performance across the simulation scenarios considered here? To illustrate the differences between inference under these metrics, we compared true tip rates to λ_{BAMM} and to λ_{DR} on a simulated birth-death tree with a single rate shift (Figure 6), as well as on one evolving rates tree simulated for this study (Figure 7). It is clear that if BAMM has the statistical power to detect true rate shifts, then it will perform well under rate shift scenarios. In contrast, λ_{DR} tracks true rate shifts but exhibits high sample variance. With an evolving rates tree (Figure 7), the simulation model is very different from the inference model in BAMM. However, it conservatively places rate shifts in order to accommodate rate heterogeneity that is spread across the phylogeny under a rather different model of rate variation. λ_{DR} also broadly tracks the overall pattern of the true rates, but the variance in the corresponding estimates is so high that performance is negatively affected. If we calculate mean (absolute) per-tip error in λ_{BAMM} and λ_{DR} , the error is relatively similar between λ_{BAMM} and λ_{DR} , but the variance in per-tip error for λ_{DR} is higher. Overall, BAMM exhibited substantially lower error than λ_{DR} under precisely this scenario (Figure 3).

Thus, although BAMM is conservative in the estimation of tip rates relative to λ_{DR} , the method exhibits lower overall error. It appears that λ_{DR} can recover more subtle rate heterogeneity relative to BAMM (see Rabosky et al., 2017 for discussion of power in BAMM), but this apparent power advantage comes at the cost of increased variance (error) in the resulting estimates. Remarkably, on a per-tip basis, we find that a simple constant-rate birth-death process (λ_{CRBD}) frequently yields tip estimates with lower median error and less error variance than those obtained with λ_{DR} (Figure 3), despite the simplifying (and incorrect) assumption that rates are identical across all tips in a given tree. For example across all multi-regime simulations (Figure 3), λ_{CRBD} point estimates were more accurate than the corresponding λ_{DR} point estimates for 84% of trees in the simulations; for λ_{BAMM} , the λ_{CRBD} estimates were more accurate for a much smaller fraction of the total (36%). Similar results were noted for diversity-dependent (λ_{CRBD} more

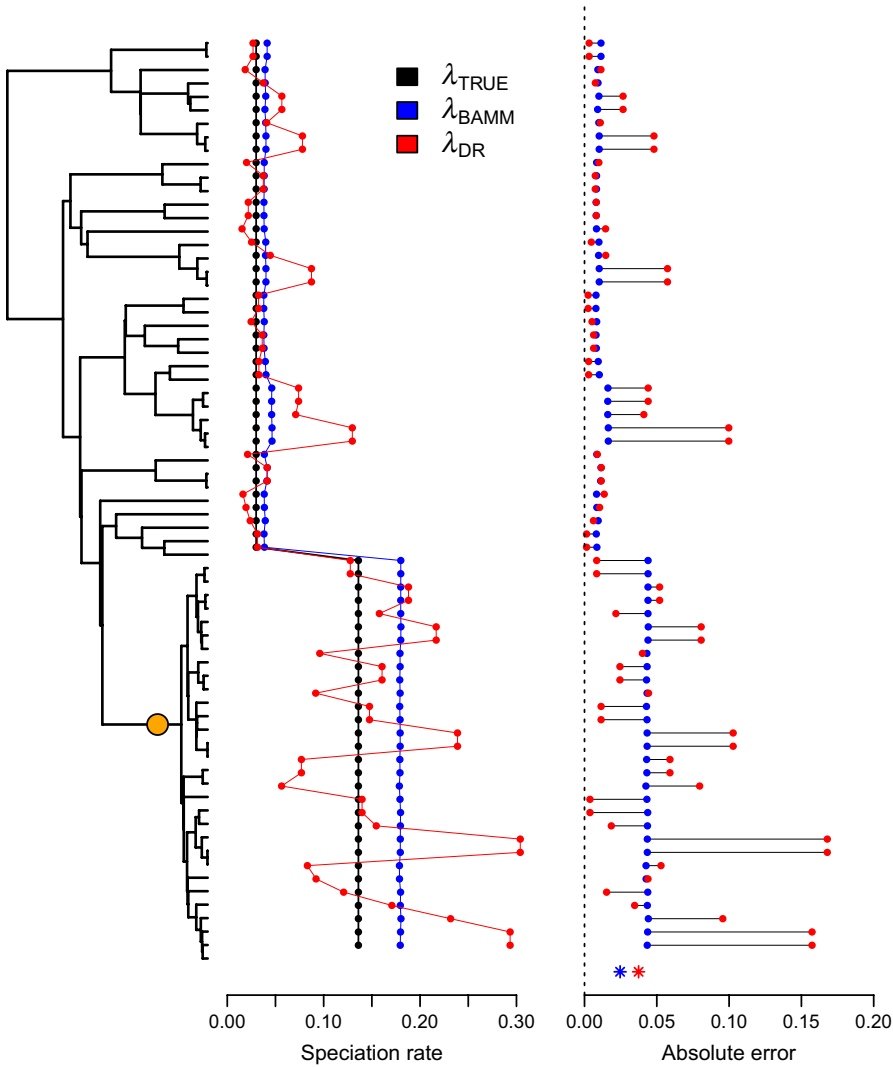


FIGURE 6 Relationship between λ_{TRUE} , λ_{BMM} , and λ_{DR} for a simulated phylogeny containing a single rate shift (orange circle). Subplots to the right of the tree illustrate true and estimated rates for each tip (left) and corresponding absolute error (right). Asterisks at the bottom denote mean per-tip error in tip rate metrics. Mean per-tip error is relatively low and similar between λ_{DR} and λ_{BMM} , but the sample variance in λ_{DR} tip rates is high. In this example, the variance in absolute per-tip error in λ_{DR} is 0.002 vs. 0.0003 for λ_{BMM} . On average, λ_{DR} tends to either overestimate or underestimate rates relative to λ_{BMM} , even if the mean per-tip error is relatively low for both metrics

accurate than 98% of λ_{DR} estimates, vs. 15% of λ_{BMM} estimates) and evolving rates trees (λ_{CRBD} more accurate than 93% of λ_{DR} estimates, vs. 36% of λ_{BMM} estimates). Given that λ_{DR} can and does track true heterogeneity in speciation rate (Figures 6 and 7), this pattern suggests that the metric is especially sensitive to the stochastic variation in branch lengths that can emerge even when all tips have the same underlying speciation rate.

Regardless of the performance summaries presented in this article, important questions remain with respect to how well tip rate metrics can estimate the true rate of speciation from empirical phylogenies. The phylogenies analysed in this study were simulated under idealized processes and neglect potential biases and sources of uncertainty that are present in real datasets. For example if the process of speciation takes time to complete, as is generally believed to be the case (i.e. the protracted speciation process; Rosindell, Cornell, Hubbell, & Etienne, 2010; Etienne & Rosindell, 2012), then the most recent speciation events may still be on-going at the present and typical species-level molecular phylogenies may fail to recognize these events. This will lead to an overestimation of terminal branch lengths, as some terminal branches potentially include incipient species. A related bias might

arise due to incomplete taxon sampling, which disproportionately affects the length of terminal (or otherwise recent) branch lengths (Pybus & Harvey, 2000). Likewise, variation in taxonomic practice across a phylogeny might lead to spurious rate variation, particularly if different species concepts are used, or if some clades in the phylogeny – but not others – have been subject to population genetic analysis or screens for cryptic species diversity. Additionally, it has been shown that BMM and other methods may fail to infer accurate speciation rate dynamics if the phylogeny is in diversity decline – that is when extinction rates increase towards the present and ultimately exceed speciation rates (Burin, Alencar, Chang, Alfaro, & Quental, 2018; Quental & Marshall, 2011). A major, if obvious, caveat in the interpretation of tip rates is that they apply to recent speciation rates and are necessarily limited with respect to inferences about historical variation in speciation rate.

The greater the importance of the terminal branches in tip rate metrics, the greater the impact these biases might have on tip rate estimates. On one end of the spectrum, metrics such as λ_{TB} will be very sensitive to such biases as they rely exclusively on terminal branch lengths. Such approaches may retain utility as summary statistics

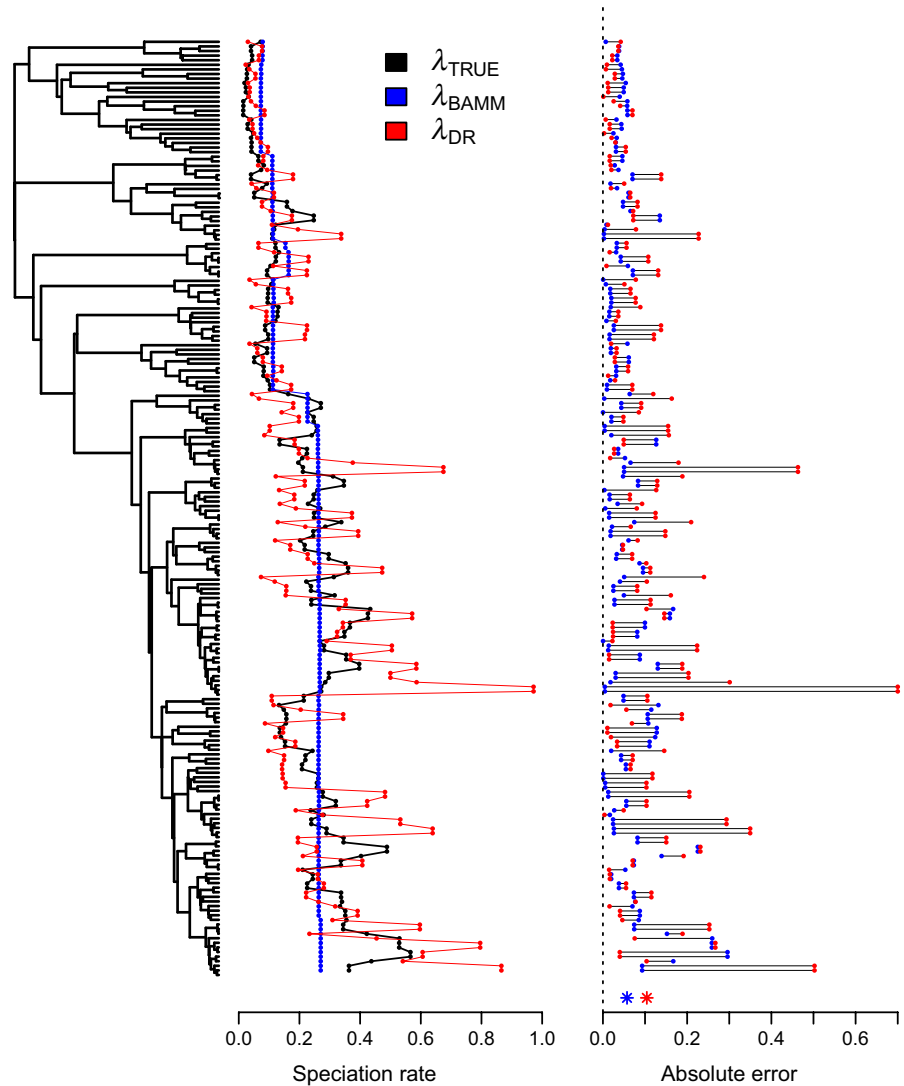


FIGURE 7 Relationship between λ_{TRUE} , λ_{BAMM} , and λ_{DR} for a phylogeny simulated under an 'evolving rates' model, such that the speciation rate itself varies under a diffusion model. See Figure 6 for additional details. Neither metric is particularly well equipped to infer the true rate variation in this case. However, λ_{BAMM} 's conservative estimates are still more accurate relative to λ_{DR} , which is negatively impacted by high variance in tip rates. Here, variance in absolute per-tip error in λ_{DR} is 0.012 vs. 0.003 for λ_{BAMM}

(e.g. Bromham et al., 2016), but we found that λ_{TB} exhibited the greatest amount of error in estimating speciation rates. On the other end of the spectrum, a metric like λ_{ND} would be minimally impacted as this metric is attempting to capture an average speciation rate over an entire root-to-tip path and does not upweight the contribution of recent branch lengths. λ_{DR} is likely somewhere in the middle of this spectrum, as it gives decreasing weight to branches towards the root. λ_{BAMM} is potentially sensitive to such issues as well, although it may be possible to analytically correct for some biases in the mechanics of the model itself (e.g. Etienne & Rosindell, 2012; Rosindell et al., 2010).

Potential empirical biases aside, tip rates present a number of practical advantages in the study of diversification rate variation. First, tip rates can be summarized and compared across non-monophyletic assemblages of species (Belmaker & Jetz, 2015; Jetz et al., 2012; Kennedy et al., 2016; Oliveira et al., 2016; Quintero & Jetz, 2018; Rabosky et al., 2018), making it possible to summarize rate characteristics of entire communities or regional assemblages of species. Second, estimation of rates at the present should be more robust to the influence of extinction, as extinction can erase the

history of lineage splitting deeper in the phylogeny (Nee, May, et al., 1994; Nee, Holmes, May, & Harvey et al., 1994; Rabosky & Lovette, 2008). Third, tip-specific rates can be paired with species-specific trait values or geographic attributes in order to test potential trait- or geography-dependent speciation rates (Freckleton et al., 2008; Harvey & Rabosky, 2017; Jetz et al., 2012; Rabosky & Goldberg, 2017). Tip rates make it possible to relax strong assumptions of rate homogeneity within character states, which are inherent to certain trait-dependent models, including BiSSE and GeoSSE (Goldberg, Lancaster, & Ree, 2011; Maddison, Midford, & Otto, 2007; Ng & Smith, 2014). Recent work has provided a conceptually rich and robust interpretive framework for SSE models that does not assume rate-constancy within character states (Beaulieu & O'Meara, 2016; Caetano, O'Meara, & Beaulieu, 2018), but tip rates nonetheless can provide an important check on results obtained with SSE models by providing a direct means of visualizing the relationship between branch lengths and character states (Bromham et al., 2016; Harvey & Rabosky, 2017; Hua & Bromham, 2016). Visual inspection of data in this fashion has the potential to reduce false positives by calling attention to potential outliers and other sources of model inadequacy

(Maddison & FitzJohn, 2014; Rabosky & Goldberg, 2015). A final advantage for non-model-based tip rates, especially λ_{DR} , is that they can profitably be applied to extremely large phylogenies: there are few computational limits to using them on phylogenies with tens of thousands of tips or more, in contrast to formal model-based approaches for which BAMM, HiSSE (Hidden State Speciation and Extinction; Beaulieu & O'Meara, 2016), and other methods are poorly suited. This computational efficiency also lends itself to more readily accounting for phylogenetic uncertainty, because tip rate metrics can rapidly be computed across posterior distributions of phylogenies and averaged (e.g. see Jetz et al., 2012; Rabosky et al., 2018).

In summary, tip rates offer a number of theoretical and practical advantages, particularly in the study of associations between traits and diversification. We found that λ_{BAMM} outperformed other metrics evaluated in this study and proved to be relatively accurate, even under diversification scenarios that depart from the BAMM inference model. λ_{DR} underperformed in comparison to λ_{BAMM} , but in many cases still did reasonably well, particularly for small rate regimes. Despite our performance results, λ_{DR} is likely to remain a useful tool in the study of trait- and geography-dependent diversification (Harvey & Rabosky, 2017; Rabosky & Goldberg, 2017).

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AUTHORS' CONTRIBUTIONS

P.O.T. and D.L.R. designed the project. P.O.T. assembled the datasets and performed all analyses. P.O.T. and D.L.R. wrote the manuscript. Both authors contributed critically to subsequent drafts and approved the final publication.

DATA ACCESSIBILITY

All trees, data and code necessary to repeat the analyses have been deposited in the Dryad repository: <https://doi.org/10.5061/dryad.5hr25nv> (Title & Rabosky, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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