Received: 9 May 2024 | Accepted: 5 August 2024
DOI: 10.1111/2041-210X.14442

Methods in Ecology and Evolution

PERSPECTIVE

Felsenstein Review

Simpson's tachytely or bradytely? The importance of quantifying rate uncertainty

Rosana Zenil-Ferguson[1] | **Lee Hsiang Liow**[2,3]

[1]Department of Biology, University of Kentucky, Lexington, Kentucky, USA
[2]Natural History Museum, University of Oslo, Oslo, Norway
[3]Department of Geosciences, Centre for Planetary Habitability, University of Oslo, Oslo, Norway

Correspondence
Rosana Zenil-Ferguson
Email: roszenil@uky.edu

Funding information
Division of Environmental Biology, Grant/Award Number: 2323170

Handling Editor: Daniele Silvestro

Abstract

1. The spectacular variation in species forms and richness across space and time can be explored using sophisticated and powerful tools recently developed by evolutionary modellers. In this contribution, we ask if the classic 'Simpsonian' view of tachytelic (fast), horotelic (standard) and bradytelic (slow) diversification rates can be distinguished with currently available tools and data. A neglected topic here is the role that the uncertainty of diversification rate estimates plays, where the lack of in-depth uncertainty measures could hinder our ability to confidently suggest differences in speciation or extinction rates in any given comparison.
2. We propose quantifying the relative uncertainty of diversification estimates, to better compare diversification tempo across phylogenies of different sizes and ages. We present three case studies, using the most popular models for diversification rate estimation, with or without fossils, to investigate claims of bradytely or tachytely. Using summary statistics and linear models, we ask if point estimates of diversification rates are comparable across clades. More specifically, we fit a linear model to understand which phylogenetic tree properties (including size and age) may affect the uncertainty of diversification estimates.
3. We found the 'Goldilocks of uncertainty': Phylogenies that are young with insufficient tips or that are old increase the uncertainty of diversification estimates. The choice of diversification modelling approach is independent of the pattern of diversification rates decaying exponentially with clade age.
4. In practice, we still cannot confidently compare diversification rates or their variation, due to uncertainties stemming from clade age, sample size and biased sampling. We emphasize the need for researchers to focus on estimating and presenting uncertainty in their estimates. Such uncertainty estimates are currently absent from many publications, limiting our ability to compare the tempo of diversifications across the tree of life. We conclude by proposing solutions and guidelines to encourage new studies for measure uncertainty.

KEYWORDS
comparative phylogenetics, evolutionary rate variation, macroevolution, phenotypic rates, uncertainty

1 | RATES FROM SIMPSON TO SEPKOSKI AND COMPARATIVE PHYLOGENETICS

Species richness and phenotypic forms vary, everywhere in the tree of life. Understanding and estimating the processes underlying variation is one of our common goals in studying macroevolution, with our varied data sources and modelling approaches in estimating diversification. Part of the variation, observed in space, time, habitat and among clades/branches, is the direct result of evolution where populations undergo phenotypic divergence, mutations, selection, immigration/emigration, extinction and habitat change. The other part of the variation is the result of key macroevolutionary dynamics, such as adaptive radiations, convergent evolution, mass extinctions and episodic diversification, modifying the diversification process. G. G. Simpson was not the first to write about evolutionary rate variation, but his emphasis on comparative rates and their distribution has been seminal in guiding our research today (Simpson, 1944). Simpson made explicit, testable statements about evolutionary rates, such as 'Each group of animals has a standard evolutionary rate distribution, here called horotelic, with a strongly prominent mode and with frequencies of rates falling off steeply on each side, more steeply on the side of fast rates'. In addition, when focusing on the extremes of the distribution of evolutionary rates, he argued that 'Tachytelic lines either become extinct or usher in new major adaptive grades in which the phyla become on the whole horotelic, but often one line or a minority of lines are bradytelic.' (Simpson, 1944). The Simpsonian terms tachytelic and bradytelic refer to 'exceptional [fast and slow, respectively] rates that fall outside the horotelic distribution of rates'. Exceptional rates in organisms ranging from tetrapods to plants have been identified via the modelling of lineage diversification rate shifts in a phylogenetic context inferred using mostly molecular data (Alfaro et al., 2009; Magallón et al., 2019), the modelling of diversification rates using only fossil data (Simões & Pierce, 2021) or a combination of both data types (Coombs et al., 2022).

Yet, in modern terms, these classes of rates, which can refer to both lineage origination/extinction rates and phenotypic rates of change, seem poorly defined due to the differences in the data examined and the modelling approaches used to calculate them. We are left then with two key questions: What are the average and range of these rates? and what biological meaning do these values have? These questions were also central to Sepkoski (1998) who proposed a canonical rate of speciation of two to six species per year, based on the palaeobiological 'law' that speciation should be approximately equal to extinction, on average (Marshall, 2017). Yet, this is very different from more recent estimates, inferred using both molecular phylogenies and fossil data, that place speciation rate at 0.1–1 species per million years (Henao Diaz et al., 2019), albeit with a broad spread of values. Meanwhile, extinction rates based on recent comparative methods are frequently estimated as close to zero (Louca & Pennell, 2021), in contrast to palaeobiological expectations where the extinction rate was expected to be only slightly lower than speciation (Sepkoski, 1998). Yet, these values reflect averages from heterogeneous sources, using different models and inferential frameworks, including temporal scaling (Harmon et al., 2021) or trait dependency (Maddison et al., 2007).

In this contribution, we focus on identifying if a cohesive framework for rate estimation exists and whether the *exceptional* rates can be defined statistically and/or biologically and discuss if these definitions have a purpose. We briefly review recent method developments in rate estimation, tackling both lineage diversification and diversification linked to phenotypic evolution. We do so with the goal of exploring the sources of uncertainty in the estimation of rates and their variation and scrutinizing whether inferred rate variation can be compared with confidence. Using three case studies, we discuss when estimated rate variation likely represents true biological variation, focusing on how their uncertainties are quantified and presented. Then, armed with these insights, we come back to questioning whether some of the Simpsonian questions in 'Tempo and Mode' (1944, Chapter 4) can currently be answered and the implications of the answers or lack thereof. We also make recommendations as to how we can make progress in the estimation of rates, a crucial quantification in many branches of evolutionary biology.

2 | ESTIMATING LINEAGE DIVERSIFICATION RATES

Speciation and extinction rates of lineages are commonly modelled using birth–death models (Nee, 2006); in these models, speciation and extinction are rates representing the instantaneous probability of lineages splitting or disappearing. Many variations of the birth–death model attempt to quantify branch or lineage-specific rates (Barido-Sottani et al., 2020), and/or net diversification rate differences among clades (Rabosky, 2014), geographic regions (Goldberg et al., 2011), traits (Maddison et al., 2007) or time intervals (Höhna, May, & Moore, 2016), and where rate differences result in varied species richness. In practice, this quantification usually involves averaging the aforementioned instantaneous rates over the factor(s) of interest (e.g. clade, region, trait, temporal interval). In addition, modelling time series of plausible forcing mechanisms that contribute to influencing speciation and extinction rates has been a recent topic of interest (MacPherson et al., 2021). However, as we will show below, much of the uncertainty and variation estimated using the fossil record or phylogenies with only extant lineages could be the result of sampling error, temporal, topological and/or model uncertainty, rather than biological variation per se (Figure 1).

The estimation of diversification rates belongs, historically, to the realm of quantitative palaeontology (e.g. Foote, 2000; Raup, 1978; Sepkoski & Miller, 1998; Stanley, 1979). One of the greater known sources of uncertainty in diversification using observations of fossils is variation in preservation. To counter the variation in preservation and sampling, diverse approaches have been developed to tackle heterogeneity in fossil recovery (Alroy et al., 2001; Foote, 1997, 2003; Nichols & Pollock, 1983; Silvestro et al., 2014). Increasingly effective molecular sequencing and phylogenetic tree inference have led to the boom of speciation and extinction rate estimation using reconstructed

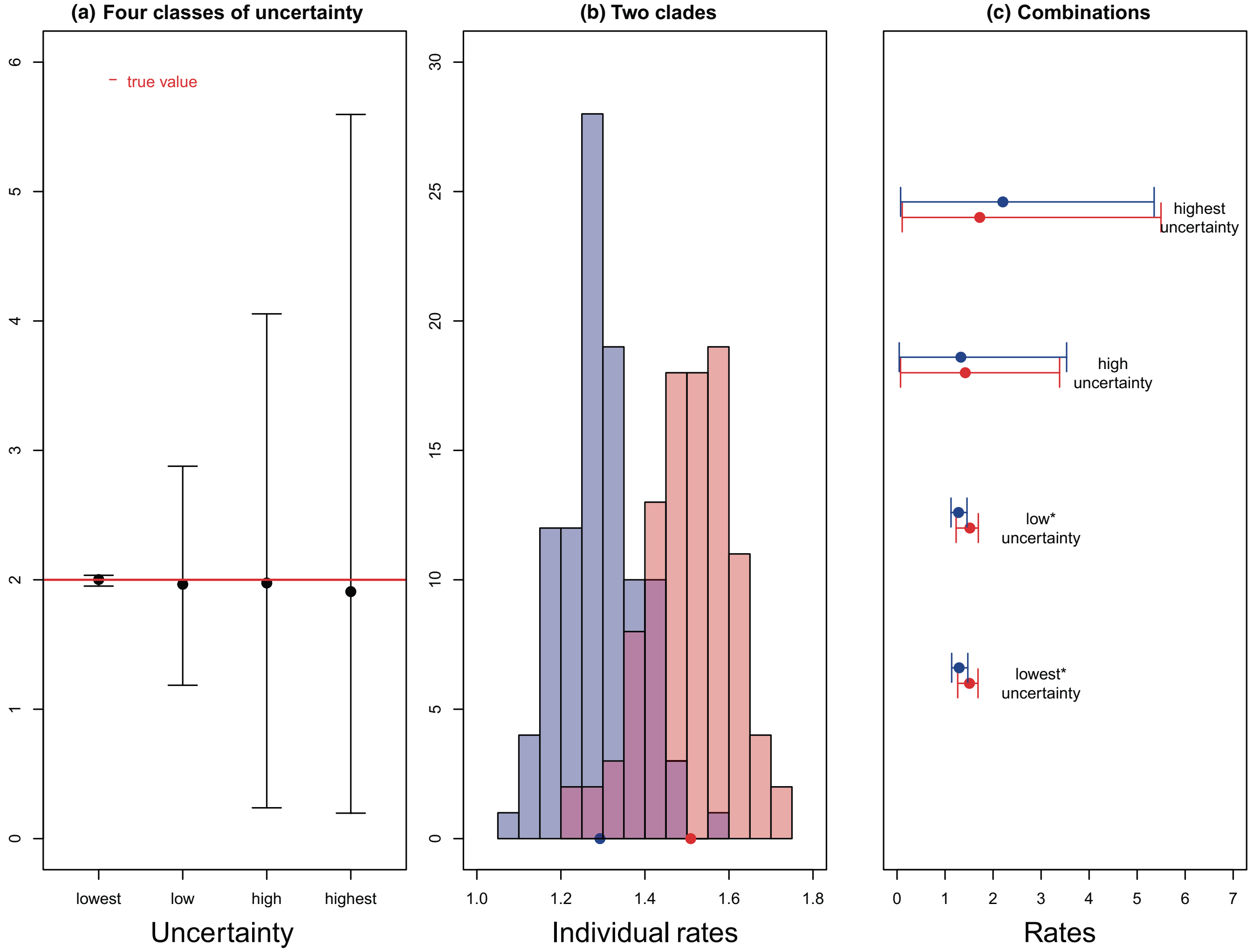

FIGURE 1 The combined effect of true rate variation and variation in uncertainty. Uncertainty, often neglected or downplayed in the presentation of rate estimations, can strongly influence downstream inference, illustrated here with simulated data. (a) Four 'classes' of uncertainties in estimation, possibly arising from, for example, the method or model applied, inherent phylogenetic topological uncertainty and/or the age uncertainty of the fossils used. In all four classes, the same, true mean value is marked with a red line. Dots show medians from 100 random draws and lines are 95% ranges. (b) Histograms of true individual rates of two clades (blue and red) which have statistically different means. Dots show medians of the clades. (c) Combinations of uncertainty from (a) and (b), where the two highest uncertainty classes do not allow us to infer that the 'blue' and 'red' clades (or geographic region, or time interval or trait grouping) are statistically significantly different in their rates as opposed to lower uncertainty classes (type II error). * indicates statistical significance at the $p = 0.05$ level, using a *t*-test. Note that it is also possible to be overly confident in detected differences (type I error), when point estimates are presented without appropriate measures of uncertainty.

phylogenetic histories (e.g. Magallón & Sanderson, 2001; Nee, 2006), with the realization that the topological structure and timing of branching of phylogenetic trees contain information on extinction and speciation probabilities and rates (Nee, 2006). The harnessing of information associated with such inferred histories using data from extant lineages is especially useful for clades that leave little in terms of a fossil record, like diverse radiations of Andean flowering plants. In practice, empirical phylogenetic trees are usually reconstructed from phenotypic data by which we mean molecular sequences, morphological or behavioural traits or other potentially phylogenetically informative data and their combinations and subsequently used to reconstitute the generating processes of speciation and extinction. Tree topology and diversification rates could potentially be jointly estimated although this is challenging due to demanding computational resources required to accomplish this task. In the past couple of decades, we have been productive in comparing empirical diversification rate differences and their consequences (commonly species richness) among clades, regions and traits and in the exploration of potential factors driving such differences (e.g. Magallón & Sanderson, 2001; Upham et al., 2019; Wiens, 2011). Parallel to empirical data analyses, the field of tree-based diversification rate estimation is seeing substantial method advancement (Barido-Sottani et al., 2020; Vasconcelos et al., 2022), accompanied by corresponding software development, such as the widely used stand-alone software BAMM (Rabosky, 2014), BEAST (Bouckaert et al., 2019), RevBayes (Höhna, Landis, et al., 2016) and R packages including ape (Paradis & Schliep, 2019) and RPanda (Morlon et al., 2016).

Surprisingly, despite modelling advances to estimate the rates of speciation and extinction, little is known about the variation of speciation and extinction rates and their interval (uncertainty) estimates. Furthermore, we do not know much about the ranges of diversification rate values such that deciding the thresholds for fast or slow macroevolutionary rates is challenging. Most of the software and statistical inference for diversification rate estimation can calculate or approximate interval estimates, given the assumptions of the models but rarely are those interval estimates presented and/or discussed. Historically, point estimates and their differences are taken as examples to claim fast and slow diversification without having a frame of reference of what is horotelic. In the following, we present three case studies to show how interval estimates of diversification rates or information about ranges of point estimates can teach us something about the expected ranges of diversification rates. Our goal is to show that the distributions of diversification rates and their sources of uncertainty are necessary to make claims of exceptional diversification rates and to further our understanding of rate variation in general.

3 | CASE STUDY 1: MEASURING UNCERTAINTY IN LARGE SYNTHESIS ANALYSES IDENTIFIES DIVERSIFICATION EXTREMES AND PROBLEMS WITH SAMPLING

Henao Diaz et al. (2019) compiled more than 100 published phylogenies of extant organisms to quantify the relationship between clade age and diversification rates. They concluded that there is a strong time scaling effect where younger clades diversify at much faster rates than older ones. Using their compiled data, we calculated the approximate 95% confidence interval (Wald interval) for tip speciation and extinction rates using the estimated average and standard error $(\hat{\mu} + 2\hat{\sigma})$, allowing us to compare estimates across the different clades. We observe that the confidence interval estimates are narrower as we go back in time (Figure 2b). This pattern of reduced variance towards the past could be produced by several non-mutually exclusive reasons:

First, the averages of the speciation and extinction rate estimates for older trees have reduced uncertainty because an older tree is likely to have more lineages, reducing the variance in the estimates of average speciation and extinction. Second, we might expect fewer lineages with more extreme rate histories (higher extinction and speciation rates) to make it to the present to allow for sampling in extant phylogenies. Third, a vast array of diversification histories may be obscured within older clades by summarizing errors of averages of speciation and extinction rates. Fourth, rate variation that might have occurred in older (larger) clades could also be obscured if the model(s) used for rate estimate do not take into consideration possible temporal variation (for which more time is available) within the clade. In any case, it is striking, and perhaps initially counter-intuitive, that we seem to more confidently estimate rates in the deeper past than in the more recent past. Therefore, it is key to emphasize that these different sources of uncertainty, which range from choosing a summary statistic to properties of the age of the phylogenetic tree, are confounded when claims of tempo of diversification are made.

In the first of the listed reasons above, observed reduction of the total standard error bars over time can make us think that older estimates mean less uncertainty; hence, having older trees is better. However, the scale of mean speciation and extinction rates is dramatically different in Figure 2 (mean speciation spans 0.01 to 1.5, i.e. an 88-fold difference over the x-axis). Hence, it is important to compare these interval estimates in relative terms. We compare them by calculating the relative range of the standard error bars as

$$y = \frac{\text{Upper limit standard error} - \text{Lower limit standard error (of speciation rate)}}{\text{Estimated average (of speciation rate)}}.$$

We fit a linear model that considers tree age, four arbitrary sampling categories for tips shown in Figure 2 (1—less than 100, 2—between 100 and 300, 3—between 300 and 500 and 4—more than 500), and the interaction between tree age and sampling category as the variables that can explain y, the relative range of standard error. In mathematical terms, we fit the linear model

$$\begin{aligned} y = \beta_0 + \beta_1 \times \text{Tree Age} + \beta_i \times \text{Number of tips (category)} \\ + \beta_j \times (\text{Tree Age} \times \text{Number of tips (category)}) \\ + \varepsilon, \text{where } i,j = 1, 2, 3, 4. \end{aligned} \tag{1}$$

In Figure 3, we plot the linear model from Equation (1) using the predicted values for the relative range $(\hat{y})$ against tree age. We find that both tree age and sampling categories are statistically significant at the 0.05 level (p-values of 0.04 and 2.4×10^{-10}, respectively) at explaining relative range of estimate error. Most interestingly, an interaction between tree size and number of tips occurs (p-value $= 0.03$): for smaller trees (less than 300 tips in our categorization), the error decreases with older trees. For larger trees (more than 300 tips), younger ones are extremely informative about speciation but not the older ones where error in speciation estimation increases. For all trees, regardless of the number of tips, as trees get old, the relative range of standard error for average speciation estimates converges around 0.6. This result shows that there is a 'Goldilocks uncertainty' in speciation estimates, the best inference comes from trees with more than 300 tips that are young, but this is almost impossible to achieve: For any phylogenetic tree, as younger trees often do not have that many species, and trees with hundreds or thousands of tips are often old. Phylogenetic trees are the result of speciation and extinction, it is extinction that makes it difficult to achieve the balance between age and number of tips and get over the Goldilocks uncertainty in diversification estimation.

While on the topic of the number of tips in trees, it is also appropriate to consider how much of the uncertainty is the result of sampling fraction. Previous studies have found that sampling fraction is essential when estimating diversification parameters (Chang et al., 2020; Mynard et al., 2023), and biases when sampling fraction is less than 50% the diversity can result not only in poor estimation but incorrect model selection (Mynard

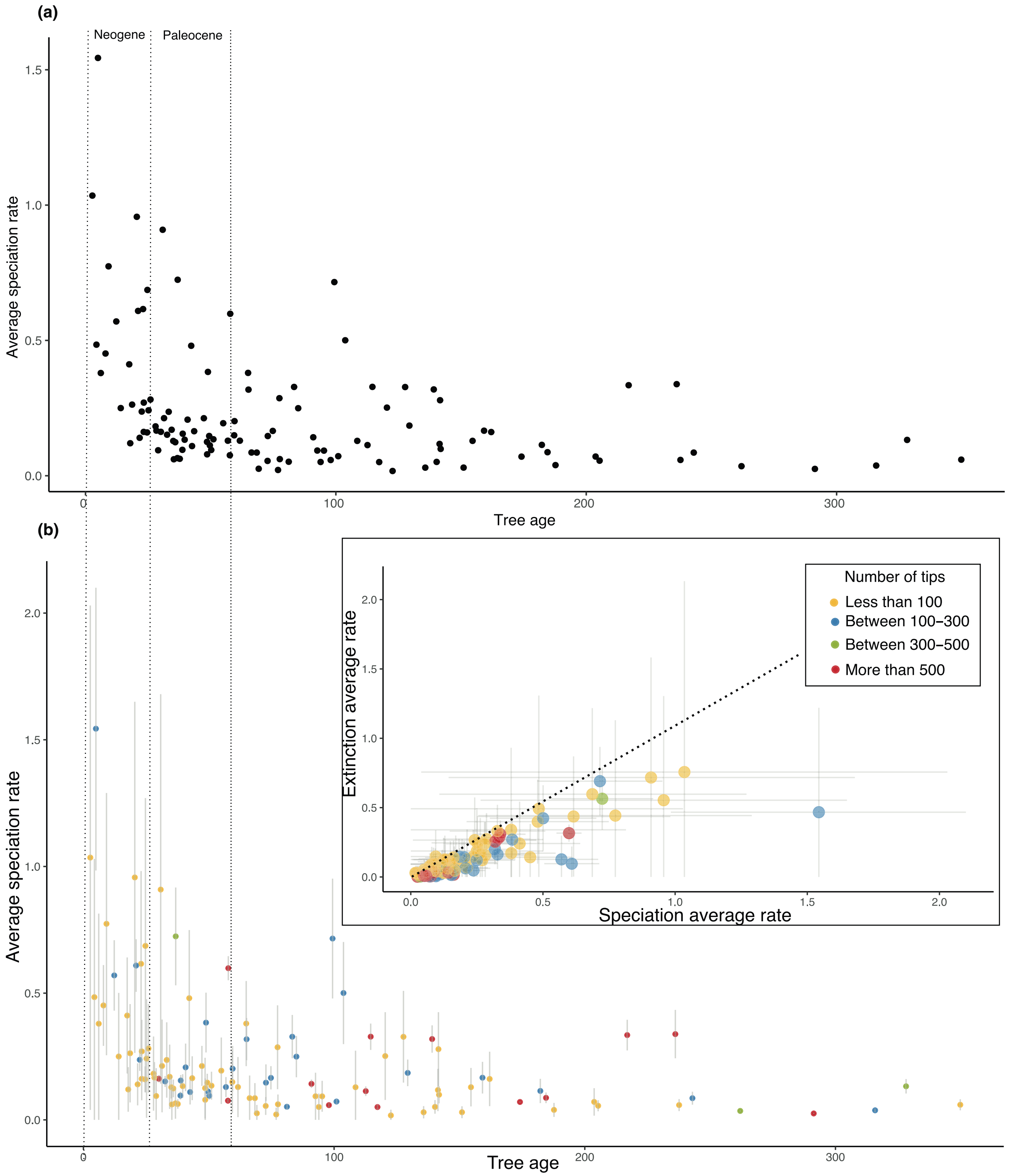

FIGURE 2 Average speciation rate and tree age. In (a), we reproduced the figure from Henao Diaz et al. (2019) who argued that the rates of diversification (speciation) are slower with tree age. In (b), we added uncertainty estimates to the estimates of average speciation (grey lines) and points where colour represents the number of tips in each of the trees presented. In general, older extant trees have more tips and more of these tips are sampled, which makes uncertainty seem smaller over time. Inset plots speciation and extinction average rates, and grey lines their standard error intervals. The dotted line shows the 1:1 relationship: Notice that estimated extinction rates decline as estimated speciation rates increase.

et al., 2023). To investigate the effect of sampling, we fit the linear model $y=\beta_0+\beta_1\rho+\varepsilon$, where ρ is the sampling fraction defined as number of tips divided by number of known taxa in the clade. We find that the slope estimate of sampling fraction (β_1) is not significant ($t=1.48$, p-value$\,=0.14$), meaning that sampling fraction does not explain the uncertainty of average speciation

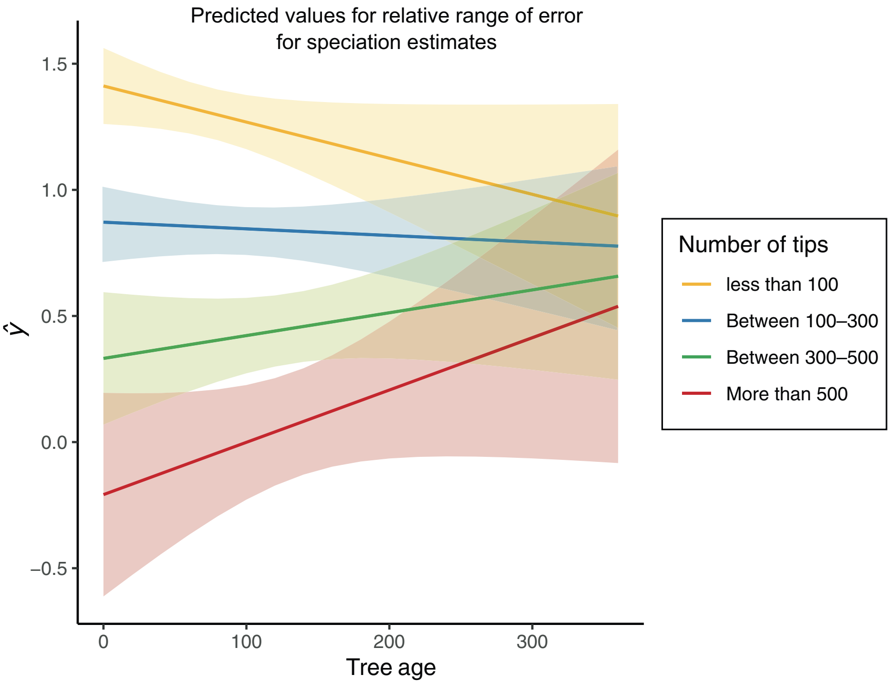

FIGURE 3 Predicted values for relative range of standard error of speciation estimates ($\hat{y}$) against tree age from linear model in Equation (1). We observed that, for trees that are small (less than 300 tips), increasing tree age decreases interval estimates of average speciation, whereas trees with more than 300 tips have less error in speciation when they are young, and as trees get old, the uncertainty in error increases. This is the 'Goldilocks uncertainty' the interplay between tree age and number of tips for speciation rate interval estimates.

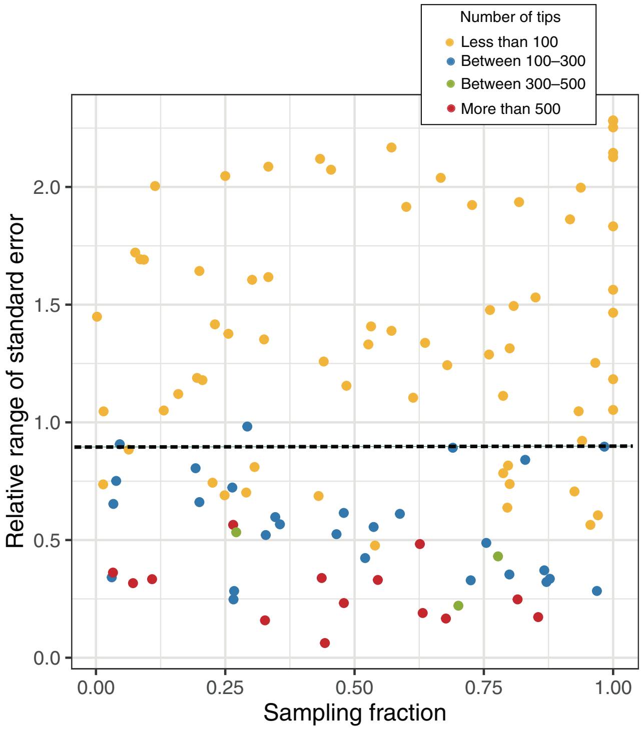

FIGURE 4 Sampling fraction (ρ) versus relative range of standard error (y). Increasing sampling fractions does not decrease the relative range of standard error of average speciation estimate. A tree with more than 100 tips would have smaller uncertainty in their estimates (blue, green and red dots). The dashed line is the average of relative range of standard error across all sampling fractions.

rates (Figure 4). When sampling fraction increases, the relative range of standard error does not decrease (Figure 4). Here, we also observe that trees with more tips have lower relative ranges of standard error, regardless of how well they are sampled (Figure 4).

When we explore the diversification rates within temporal intervals, we can partially account for variation due to clade age (Henao Diaz et al., 2019; Louca et al., 2022) and different environmental conditions across periods. In Figure 5, we show the average speciation rates as distributions of the Palaeocene (23–60 ma) versus the Neogene (0–23 ma). These two speciation distributions are radically different in shape, with the Neogene having a wider uncertainty.

Using these two distributions of the average speciation and extinction rates for a given clade within a period we can ask: what is on the extreme of the diversification rate distribution? If we assume an arbitrary statistical cut-off for identifying 'outliers', we can identify clades with extreme rate values. We calculate the 5% threshold, that is, the 2.5% and 97.5% quantiles of the tails of the densities in Figure 4. Using this 5% threshold, speciation rates above denoted by the 97.5% quantile $Q_{0.975}=1.35$ are the fastest in the Neogene, where the Centropogonid clade of Neotropical bellflowers (Lagomarsino et al., 2017) falls in the fast category. This finding might be unsurprising to researchers studying plant radiations in the Andean mountains, as the unique and recent biogeographical configurations and the mountain uplift (Pérez-Escobar et al., 2022) provided the opportunity for rapid speciation or turnover. On the slow side of diversification for the Neogene, we found a clade from the Fabaceae family (Tosso et al., 2018) with a speciation rate lower than the 2.5% quantile ($Q_{0.025}=0.12$). As far as we are aware, Tosso et al. (2018) and other Fabaceae researchers have not singled the genus *Guigourtia* as particularly slow-diversifying. Earlier estimates suggest angiosperm speciation rates (0.077–0.089) that seem to be lower than the 'low' (0.12) we have identified here (Magallón & Sanderson, 2001). We discuss if these differences are comparable in the Discussion section.

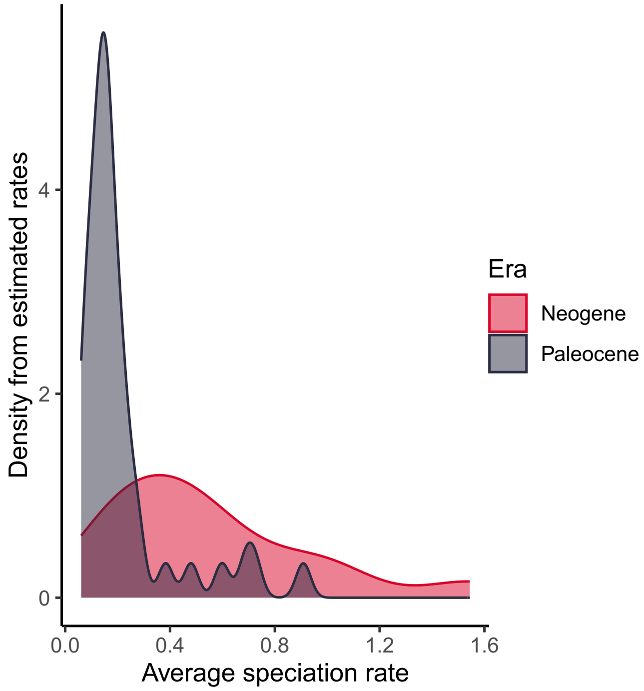

FIGURE 5 Density plots of average speciation rate by period. Density from estimated average speciation rates for trees from Figure 2 (data from Henao Diaz et al., 2019) that are 23 million years or younger are represented in the Neogene density (red), and average speciation rates for trees between 23 and 60 million years old are represented in the Palaeocene density (grey). The Neogene density has a wider distribution, and much of the sample of average speciation rates comes from trees with less than 100 tips (or all less than 300), which explains its wide uncertainty.

We found, within the Palaeocene, that dove and pigeons (Soares et al., 2016) and an Andean plant clade Rhinantheae (Uribe-Convers & Tank, 2015) have estimated rates above $Q_{0.975}=0.59$, but there were no studies presenting speciation rates below the $Q_{0.025}=0.005$. The contrast between the shape of the speciation rate distributions in the Neogene and Palaeocene suggest two important findings: First, estimated rates could be temporal context dependent. Second, a comparative approach with a substantial number of case studies is necessary for the identification of 'slow' and 'fast' estimated rates, potential artefacts of estimation must first be eliminated. We argue that declaring tachytelic or bradytelic rates of diversification depends on tree age, modelling approach and quality of the distribution of diversification rates across multiple examples.

4 | CASE STUDY 2: STATE-DEPENDENT DIVERSIFICATION: THE DIVERSIFICATION AND TRANSITION RATES LACK UNCERTAINTY ESTIMATES

We use the estimates from state-dependent speciation and extinction models (SSEs) compiled in the synthesis study of Helmstetter et al. (2023) to understand the range and spread of point estimates of net diversification (defined as speciation minus extinction) for 152 studies of plant diversifications (Figure 6). Helmstetter et al. (2023) showed using predictive models that finding a link between diversification and discrete traits is strongly dependent on age and size of the phylogenetic tree, and sampling fraction on a given study. A second recent study by Mynard et al. (2023) also found that sampling bias might contribute to finding diversification rate differences in SSEs. Just as in Case study 1, slower rates of net diversification with the overall narrower spread of point estimates are found for trees that are rooted in the Palaeocene or older (Figure 6a, most between 0.5 and −0.5). Meanwhile, phylogenetic trees rooted in the Neogene, have smaller number of tips (less than 100) and reflect a wider range of point estimates of net diversification (Figure 6a) showing rates equivalent to −2 to 3 net lineage splits per million year. This general tendency is also seen in the point estimates of the transition rates between states (Figure 6b), and interestingly the temporal trend is like that of average speciation rates discussed in Case 1 (Figure 2b), reminding us of an exponential decay. Rarely are transition rates greater than 0.5 for phylogenetic trees in the Palaeocene or older. Currently, most studies applying SSE models (also beyond those presented in Helmstetter et al. (2023)) focus on model comparison (e.g. comparing whether binary state-dependent speciation and extinction model is better than the hidden state-dependent speciation and extinction model) rather than parameter estimation per se (i.e. where the focus is on quantifying rates). Yet, SSE point estimates compiled in Helmstetter et al. (2023) are largely detached from their uncertainty estimates or the latter are simply unavailable, preventing us from doing a formal comparison of the range of these estimates and diminish the possibility to argue what is bradytelic or horotelic.

5 | CASE STUDY 3: TOPOLOGY FREE DIVERSIFICATION RATE ESTIMATION USING FOSSILS

A somewhat more direct approach to estimating diversification rates and their variation is to use observations of fossils. There was an earlier focus on estimating the consequence of speciation and extinction rates, namely the number of species (or genera and higher taxa) through time (Raup, 1972; Sepkoski et al., 1981) But increasingly, palaeontological studies have focused on the generating processes of such taxon counts, that is, origination, extinction and preservation sampling (Alroy, 2008; Foote, 2003; Liow & Nichols, 2010; Silvestro et al., 2014; Warnock et al., 2020). There is also an increasing push for incorporating fossil observations in different guises, even when phylogenetic trees can be estimated from extant organisms only (Cole et al., 2022; Heath et al., 2014). Fossil morphology and age information are usually needed for the time calibration of phylogenetic hypotheses that in turn enable us to estimate time-varying rates of diversification from the phylogenetic relationships of the living members of the

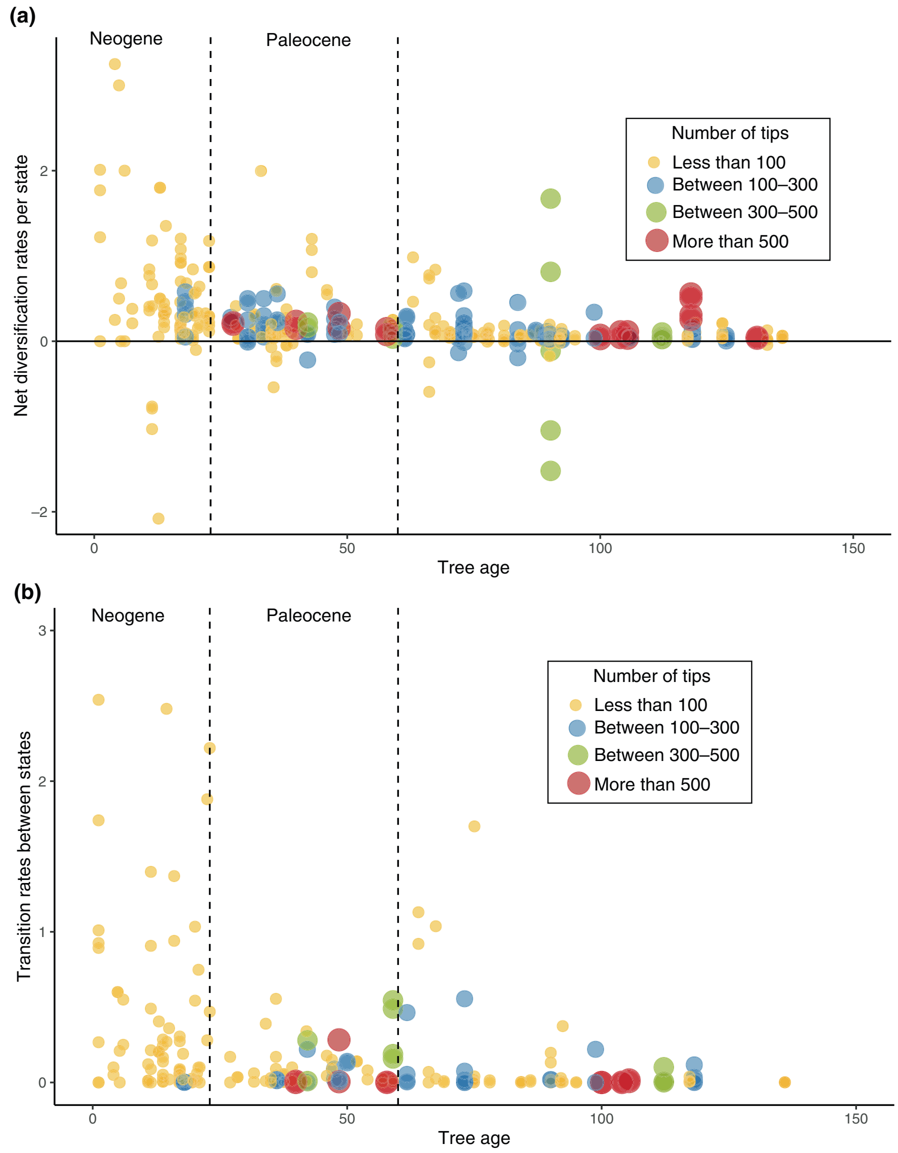

FIGURE 6 (a) Tree age (in millions of years) versus net diversification rates (speciation minus extinction) per state for analyses of state-dependent speciation and extinction models (SSEs). Older trees presented in Helmstetter et al. (2023) have more sampled tips which minimize the value of rates of net diversification. (b) Tree age versus transition rates between states for the same analyses show a decrease of range over time. In both net diversification and transition rates, trees with less than 100 tips broader ranges in point estimates, independent of age, where recent and small trees having the broadest range of net diversification values. *Notice that interval estimates are absent*.

clade in question. It is also increasingly clear that tip dating is less biased than the more traditional node dating (Luo et al., 2020), whose consequences percolates to diversification estimation. Even when phylogenetic relationships cannot be estimated, it is beneficial to consider a birth–death process while also considering a fossil sampling process, whether this is in terms of the 'traditional' first and last occurrence data (Stadler et al., 2018) or multiple observations of the same lineages. This is despite the current evidence that fossils (i.e. direct temporal information) are unlikely directly help with congruence issues (Louca et al., 2022) although fossils and other independent data can reduce both model and parameter space (Liow et al., 2023).

The palaeontological community is often interested in temporal variation in diversification rates and capturing uncertainty due to incomplete or biased temporal sampling. The reasons for non-random sampling in the fossil record are the results of complex interactions between preservation (e.g. taphonomy), geology (e.g. exposure and availability of fossil outcrops), both of which change through time in complex ways, and modern sampling (e.g. taxonomic practices, geographic biases), the latter which also applied to extant organisms. Another source of uncertainty here is the age uncertainty of fossils, which can be on the order of millions, or even tens of millions of years. The evolutionary palaeobiology research community is much smaller than the evolutionary community and this is also reflected in a lower rate of method development, also in diversification rate estimation. Some diversification rate estimation approaches include boundary-crosser approach (Foote, 2000), gap-filler and related approaches (Alroy, 2014), the Pyrate family of models (Silvestro et al., 2014, 2019), capture–recapture approaches (Liow & Nichols, 2010; Nichols & Pollock, 1983) and a class of 'topology-free' models in the RevBayes FBD framework (Liow et al., 2023), where the latter approaches provide model-based uncertainty estimates.

To explore diversification rate variation within a specific modelling context using only fossil observations as a parallel case study to Case Study 1, we choose to use empirical estimates from the Pyrate Bayesian framework as this is the most commonly used model-based method in palaeontology in the more recent literature and where it is more common to perform species-level analyses rather than genus-level analyses as is common in the paleontological literature, for comparison to case study 1. We compiled MCMC log outputs by searching for papers citing the Pyrate software (Silvestro et al., 2014) and directly contacting authors when posterior distributions were not provided with the said publications.

The compiled data set is small, consisting of 19 publications (the associated output files were not available for several of the older publications and rerunning the analyses would have been time-consuming for the authors contacted). Like in Figure 2, there is a lot of variation in the size of the credibility intervals for different data sets, even within a given period (e.g. Neogene). There is less of signal of time scaling of diversification rates estimated only from fossils, but there are still hints of higher rates towards the recent (Figure 7). Specific temporal rates measured over shorter time intervals can be high, but over time, the 'normal rates' swamp it out (and the uncertainty that is averaged almost certainly comes from occasional high and low rates). Unlike the tree-based estimates (Figure 2), the credibility intervals from this smaller data set do not show clear temporal structure, but there is some indication that rather than the age of the clade, it is the time interval over which diversification rates are averaged that may be associated with differences in credibility intervals, specifically, there is less uncertainty when averaged over a longer time interval.

The uncertainty in the Pyrate comes from the times of speciation and extinction given the shape of the temporal distribution of observed fossils within lineages, informed by empirical temporal distributions of fossil occupancy (Foote et al., 2007; Liow & Stenseth, 2007). This shape is modelled using the PERT distribution. In addition, the age uncertainty of each fossil observation is considered by using random draws of age, given an interval in which each fossil is assigned. However, the uncertainty in the number of species represented in the clade is not accounted for, as estimates of diversification are conditioned on lineages being observed at least once.

6 | 'TRUE' VERSUS 'NUISANCE' RATE VARIATION

As comparative biologists, we are interested in true biological (and/or environmental) differences in diversification and phenotypic changes. Commonly asked questions are if certain clades evolve faster than others, if certain traits promote speciation or extinction, or if certain time intervals or geographic regions are associated with more radiations or extinctions. However, in practice when comparing diversification and phenotypic rates, we need to be aware of the uncertainty in estimated parameters that can arise from other sources of uncertainty that ranging from sampling fraction biases in phylogenetic trees (Chang et al., 2020; Mynard et al., 2023), biased sampling of fossils, specific model assumptions (Zenil-Ferguson et al., 2023), geographic heterogeneity in the same clades (Benson et al., 2021), trait-coding assumptions or even taxonomic practice (Donoghue & Edwards, 2019; Faurby et al., 2016) including differences in species definitions (e.g. when comparing diversification rates of lichens vs. metazoans).

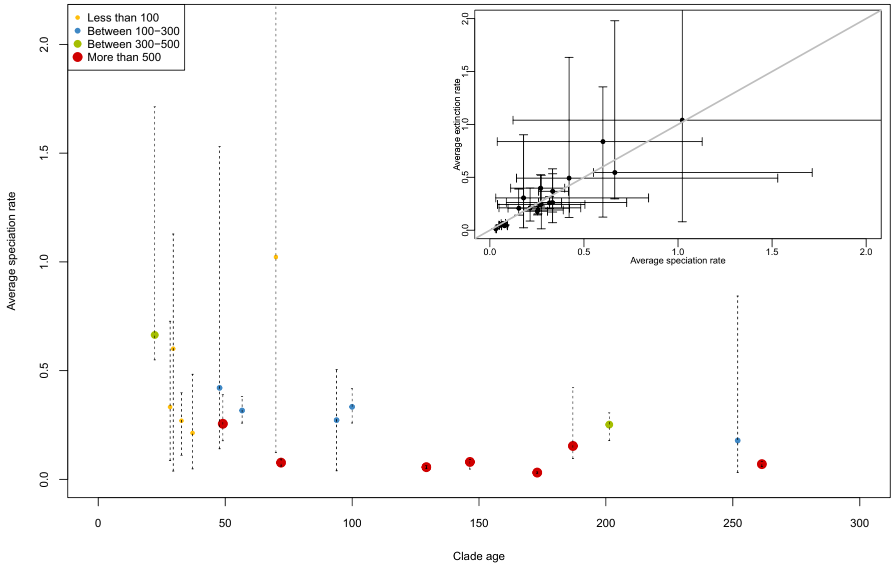

FIGURE 7 Diversification rates' variation and their interval estimates from fossil observations. Pyrate estimates of average speciation rates from 19 taxonomic diverse data sets. Clade age is taken as the oldest observation in the given data set, the grey dotted lines are the 95% credibility intervals from the PyRate MCMC outputs bubbles where colour and size represent the number of species that are presented in the data set. The inset shows average extinction rates from the same data sets plotted against their average speciation rates in the main plot, with 95% credibility intervals for both. Notice that that estimated extinction rates and estimated speciation rates fall on the 1:1 line more closely than in Figure 2, as expected due to the nature of the data (extant only in Figure 2 vs. extant and extinct here in Figure 7).

The three cases we have discussed suggest that clade size and age and perhaps in part large-scale environmental conditions experienced in common across clades (e.g. within the Paleogene vs. with the Neogene) could predictably affect rate estimates. Biases introduced by clade age seem stronger for estimates based only on extant tips than for those that include extinction (compare Figures 2 and 6). Variability in estimates due to the uncertainty in tree topology and age uncertainties of fossils used for calibrations (Barido-Sottani et al., 2020) or their placement (Mongiardino Koch et al., 2023) is important to discuss within any empirical study of rates, and we hope this becomes a best practice. Although many new diversifications rate estimation frameworks account at least partially for incomplete sampling (Chang et al., 2020; Mynard et al., 2023), systematically missing information (e.g. extinct species when using molecular phylogenies and unsampled species when using Pyrate, and ephemeral species in general that maybe common but hard to sample in any type of study) have consequences for rate estimation. As already mentioned, it is possible to constrain parameters in models to reflect more plausible extinction estimates to yield better speciation rate estimates (i.e. Zenil-Ferguson et al., 2023) and it may also be possible to use data augmentation or other techniques to account for species that are completely missing within data sets.

Despite our attempt at identifying bradytelic and tachytelic clades in Case Study 1, we feel no security in suggesting that the *Guigourtia* or Rhinantheae are exceptional examples of diversification. This is because choosing only the average speciation or extinction rates as presented in Henao Diaz et al. (2019) confounds multiple sources of uncertainty, without disentangling those factors, it is hard to claim what is in the extremes.

7 | WHEN ARE RATES HIGHER, LOWER OR 'EXTREME'? STATISTICALLY VERSUS BIOLOGICALLY?

We cannot conclude if horotely is all that exists, but assuming that there is substantial rate variation, such variation may have biological and/or environmental causes. However, the question remains as to which rates can be considered extreme (bradytelic and tachytelic, in Simpson's words) and/or if extreme rates need special explanation, after all the uncertainty due to methodological issues mentioned in the last section are accounted for. Given a distribution of rates, one might arbitrarily decide, based on a statistical 'cut-off' (e.g. our example in Case Study 1, Figure 2) for what can be considered 'exceptional' or simply the 'background' and then propose hypotheses as to why they 'outliers' exist (i.e. they need 'special explanation'). Such an approach has been taken in the literature, for example, identifying mass extinctions (Raup & Sepkoski, 1982), adaptive radiations (e.g. Lerner et al., 2011) and 'living fossil' lineages (Liow, 2004).

An important common thread across our three case studies is a reduction in rate values as the phylogenetic trees get older. This could be the effect of time as argued by Henao Diaz et al. (2019), but a second explanation is simply the choice of birth and death models as tools for estimating speciation and extinction rates. In the recent work of De Lisle and Svensson (2023), the latter authors use the probabilities of the birth and death rate parameters to argue that the negative linear relationship between rates and time is the result of recent phylogenies representing a smaller denominator in the probabilities used for the estimation of rates. However, rates represent change by time and are not constant across phylogenies, in our Case studies 1 and 2, we have shown that there is more variation associated with younger phylogenies, and that in many cases this variation is not the result of time itself, rather reduced sampling of lineages and that the interaction between clade size and tree age can inform this variation (Figure 3). Chang et al. (2020) show that when sampling fractions are used (i.e. correction is done by percentage of species sampled) instead of 'stochastic polytomy resolution' (shortened as 'TACT', implemented as corrections by estimation of branching times of unsampled taxa using a taxonomic hierarchy), the resulting likelihood of the speciation rate estimate is flatter and wider, indicating that interval estimates and uncertainty will be also wider. Incomplete sampling is an undeniable great challenge in all analyses of diversification (Cusimano & Renner, 2010; Louca et al., 2022) from fossils to recent clades, and one that requires more attention if we want to understand horotely. For example, fossil sampling has been explicitly modelled in diversification rate estimation using capture–recapture approaches (Nichols & Pollock, 1983) and it warrants more attention by both modellers and scientists gathering data to include the appropriate data structure so true absences can be modelled. In SSE models, there are still open questions about how to appropriately model missing taxa and tips with multiple states, or missing clades, currently we only know that missing a lot of taxa can result in spurious net diversification differences (Mynard et al., 2023). Our case study 1 results show that sampling fraction is not correlated with relative size of uncertainty in estimates of diversification. Our result, along with previous findings (Chang et al., 2020; Louca & Pennell, 2020; Mynard et al., 2023), suggests that sampling fractions can bias point estimates but do not worsen the uncertainty and that the uncertainty around point estimates is correlated to tree age and clade size. Therefore, to improve our estimates of diversification, it is important to obtain larger numbers of taxa where possible. A second and important key issue of birth and death models is the inability of calculating accurately extinction rates from phylogenies with only extant taxa or even in the presence of fossils (Louca & Pennell, 2021). Accurate extinction estimates will aid with the location of distributions of diversification rates allowing us to understand the spread of diversification histories. However, the lack of accurate extinction estimates should not prevent researchers from exploring, as an initial assumption, enhanced extinction histories and how those extinctions might affect their final diversification claims of the tempo of diversification. For example, Magallón and Sanderson (2001) explore an enhanced extinction of 0.9 with the simplest birth and death model, and more recently, Zenil-Ferguson et al. (2023) show that enhance extinction is possible to consider a priori for SSE models. We consider that, in the absence of good estimation methods for extinction, using empirical rates estimate from other clades to constrain extinction rates (Liow et al., 2023) and/or exploring the accuracy of diversification results under faster extinction rates is an essential step forward.

8 | BEST PRACTICES AND THE WAY FORWARD FOR TACHYTELIC, BRADYTELIC AND HOROTELIC RATES

8.1 | Present rate parameter estimates and also their associated intervals

We cannot control for all sources of uncertainty in inferences but we strongly encourage authors to present interval estimates and not only point estimates of rates of diversification, to start the good practice of quantifying uncertainty. Although it is standard practice for other fields to present error bars, or confidence intervals, in phylogenetic comparative methods, it can be more computationally challenging to calculate such uncertainty estimates. Software developers have often strived to supply computationally robust estimates of uncertainty for diversification and transition rates, for example, diversitree R package (FitzJohn, 2012) offers MCMC outputs and hence posterior distributions that can provide credible intervals, HiSSE package (Beaulieu & O'Meara, 2016) has a function that approximates confidence and bootstrap intervals from parameter estimates, and for MCMC outputs from RevBayes (Höhna, Landis, et al., 2016), credible intervals are easily calculated. For studies that use Bayesian inference, the interpretation of posterior distributions is the key to present parameter uncertainty, and new approaches including software like the R package dentist (Boyko & O'Meara, 2024) are overcoming computational challenges, making it possible to integrate parameter uncertainty studies using likelihood frameworks. It should be achievable for end users to present such interval estimates rather than only point estimates in figures, text or tables, of the key parameters. Interval estimates would also help meta-analyses like the ones presented here, since having better information on uncertainty can clarify what is comparable, and would aid in creating fairer summary statistics. It is already commonplace today to present estimates using different tree topologies and there is a drive for including stratigraphic uncertainty when using fossil observations. In addition, software developers need to be more critical about how the output of their models is presented to end users. Estimated intervals should be presented as an option in output. A reminder that intervals should be calculated and presented will help with the quality of results in the field, a task that could also be shared by peer reviewers.

8.2 | Discuss if the models implemented have accounted for major sources of known uncertainty

Different models and approaches available in the literature may not have accounted explicitly for major sources of uncertainty, which may be blatantly clear for end users who know their clades, geographic and temporal/evolutionary context. Availability of rate uncertainty can better inform meta-analyses and would make it easier to identify source of biases or justify tachytelic or bradytelic examples.

Even if there is no clear way to model or quantify these uncertainties, they should be explicitly discussed for a nuanced view of any rate variation or lack-there-of inferred. For example, adding a small discussion on how incomplete sampling was accounted for is key to determine if results across clades are comparable even under the same model. Sensitivity analyses can also be considered to explore how much sampling fraction and other sources of variation could affect empirical inferences.

8.3 | Think about statistical versus biological ‘significance’

Stochasticity and variability are implied in biology. Hence, there will always be variation due to ‘drift’ and ‘chance’. How important perceived or detected differences are may not just be a statistical question but also a biological one that must arise from natural history or/theoretical insights. For example, while using available statistical software to estimate and suggest diversification scenarios for clade(s) we are interested in, it is always essential to be sceptical about the qualitative and quantitative results, consider the estimates broadly, centre them in biology and perhaps also apply other methods or approaches to reproduce findings. Ascertainment bias is a big issue in the field of diversification (Beaulieu & O'Meara, 2018), and a combination of good biological expertise with better methods can help prevent spurious results.

8.4 | ‘All models are wrong, but some are useful’. Defining ‘useful’ is important too

It is important to question what the main goal of any given macroevolutionary inferences might be. Given these goals, are the models fit to the data adequate for the questions being asked? Birth and death models might be useful and adequate for the estimation of simple diversification histories or basic simulations, but they fail at estimation of time-dependent diversification (Louca & Pennell, 2020), accurate ancestral state reconstruction (Holland et al., 2020) or distinguishing between time-dependent versus diversity-dependent diversification (Pannetier et al., 2021). Current models also ignore longer memory accumulation in the process of diversification. Model adequacy frameworks (i.e. Schwery et al., 2023) have the potential to alleviate concerns about the usefulness of macroevolutionary models.

8.5 | Archive not just code but also intermediate output

While compiling diversification rate estimates, we have realized how often authors do not retain their MCMC runs and other 'intermediate' output files. Our argument here that it is not just good for documentation to retain and make publicly available such 'intermediate' files, but these also allow the downstream work of reconstructing uncertainties. Public databases like Zenodo (European Organization For Nuclear Research & OpenAIRE, 2013) and Dryad (Dryad Website: https://datadryad.org) can help with these goals, and many publishers have made them available for free to accompany new articles. A remarkable example of a step forward in the reproducibility are journals requiring data and code open access, for example, Methods in Ecology and Evolution requires this from default (Methods in Ecology and Evolution data guidelines, 2024) and American Naturalist recently integrated to the review process a 'data editor' who reviews code and data to recreate the article (The American Naturalist Journal data guidelines, 2022).

8.6 | Process-based estimates to allow for estimation of potentially comparable parameters regardless of data type (phylogenetic or only fossil observations)

There is a practice of using ad hoc metrics that may have directly interpretable or transferable biological meaning. General, process-based estimates like those increasingly used in birth–death models that include fossilization and sampling (Heath et al., 2014; Stadler et al., 2018; Warnock et al., 2020) which are 'transferable' regardless of data type should be encouraged. When working with, say a phylogeny of birds, where fossilization probability is close to zero, a fossilization birth–death model still can be applied for easier comparison of estimated parameters and their interval estimates to a phylogeny of mammals, where fossilization will be much more common. On the other end, even when ancestor–descendent relationships are hard to quantify (e.g. in say Palaeozoic bivalves), fossilized birth–death (FBD) models can still be applied (or modifications of capture–recapture or Pyrate models such that model parameters are comparable). Having comparable estimates will also allow us to compare them across different types of data and systems such that discrepancies and deviations can be discovered and potentially understood.

9 | SUMMARY

The Simpsonian questions within 'Tempo and Mode' (1944, Chapter 4) are important in evolutionary biology and still being actively pursued today. Our progress in documenting rate variation is substantial. Yet, our ability to compare rates both with and across groups, and even when using specific models with groups, is still hampered by the lack of explicit quantification of uncertainties. We hope empiricists will dedicate more effort to estimating and discussing uncertainties and the method developers will contribute by making it easier to extract uncertainty estimates for end users of models and software.

AUTHOR CONTRIBUTIONS

Rosana Zenil-Ferguson and Lee Hsiang Liow collected publicly available data, designed methodology and analysed the data. Both authors wrote the manuscript and contributed critically to all drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Authors thank Executive Editor Dr. Aaron Ellison, Senior Editor Natalie Cooper and two anonymous reviewers for their thoughtful comments. We also thank Francisco Henao Díaz for providing data from his study, and Fernando Blanco, Andrés Solórzano, Matheus Januário Sousa, Alexandre Siqueira, Sergio Daniel Tarquini, Juan Cantalapeidra, Nick Crouch, Fabien Condamine, Katie Jamson, David Cerny, Thomas Neubauer, for kindly providing their Pyrate outputs. Rosana Zenil-Ferguson was supported by NSF DEB 2323170.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14442.

DATA AVAILABILITY STATEMENT

Data available via Zenodo https://doi.org/10.5281/zenodo.13624001 (Zenil-Ferguson & Liow, 2024).

ORCID

Rosana Zenil-Ferguson https://orcid.org/0000-0002-9083-2972
Lee Hsiang Liow https://orcid.org/0000-0002-3732-6069

REFERENCES

Alfaro, M. E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D. L., Carnevale, G., & Harmon, L. J. (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(32), 13410–13414. https://doi.org/10.1073/pnas.0811087106

Alroy, J. (2008). Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(supplement_1), 11536–11542. https://doi.org/10.1073/pnas.0802597105

Alroy, J. (2014). Accurate and precise estimates of origination and extinction rates. *Paleobiology*, *40*(3), 374–397. https://doi.org/10.1666/13036

Alroy, J., Marshall, C. R., Bambach, R. K., Bezusko, K., Foote, M., Fürsich, F. T., Hansen, T. A., Holland, S. M., Ivany, L. C., Jablonski, D., Jacobs, D. K., Jones, D. C., Kosnik, M. A., Lidgard, S., Low, S., Miller, A. I., Novack-Gottshall, P. M., Olszewski, T. D., Patzkowsky, M. E., …

Webber, A. (2001). Effects of sampling standardization on estimates of phanerozoic marine diversification. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(11), 6261–6266. https://doi.org/10.1073/pnas.111144698

Barido-Sottani, J., Vaughan, T. G., & Stadler, T. (2020). A multitype birth–death model for Bayesian inference of lineage-specific birth and death rates. *Systematic Biology*, *69*(5), 973–986. https://doi.org/10.1093/sysbio/syaa016

Beaulieu, J. M., & O'Meara, B. C. (2016). Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Systematic Biology*, *65*(4), 583–601. https://doi.org/10.1093/sysbio/syw022

Beaulieu, J. M., & O'Meara, B. C. (2018). Can we build it? Yes we can, but should we use it? Assessing the quality and value of a very large phylogeny of campanulid angiosperms. *American Journal of Botany*, *105*(3), 417–432. https://doi.org/10.1002/ajb2.1020

Benson, R. B. J., Butler, R., Close, R. A., Saupe, E., & Rabosky, D. L. (2021). Biodiversity across space and time in the fossil record. *Current Biology*, *31*(19), R1225–R1236. https://doi.org/10.1016/j.cub.2021.07.071

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., Du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., … Drummond, A. J. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *15*(4), e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Boyko, J. D., & O'Meara, B. C. (2024). Dentist: Quantifying uncertainty by sampling points around maximum likelihood estimates. *Methods in Ecology and Evolution*, *15*(4), 628–638. https://doi.org/10.1111/2041-210X.14297

Chang, J., Rabosky, D. L., & Alfaro, M. E. (2020). Estimating diversification rates on incompletely sampled phylogenies: Theoretical concerns and practical solutions. *Systematic Biology*, *69*(3), 602–611. https://doi.org/10.1093/sysbio/syz081

Cole, T. L., Zhou, C., Fang, M., Pan, H., Ksepka, D. T., Fiddaman, S. R., Emerling, C. A., Thomas, D. B., Bi, X., Fang, Q., Ellegaard, M. R., Feng, S., Smith, A. L., Heath, T. A., Tennyson, A. J. D., Borboroglu, P. G., Wood, J. R., Hadden, P. W., Grosser, S., … Zhang, G. (2022). Genomic insights into the secondary aquatic transition of penguins. *Nature Communications*, *13*(1), 3912. https://doi.org/10.1038/s41467-022-31508-9

Coombs, E. J., Felice, R. N., Clavel, J., Park, T., Bennion, R. F., Churchill, M., Geisler, J. H., Beatty, B., & Goswami, A. (2022). The tempo of cetacean cranial evolution. *Current Biology*, *32*(10), 2233–2247.e4. https://doi.org/10.1016/j.cub.2022.04.060

Cusimano, N., & Renner, S. S. (2010). Slowdowns in diversification rates from real phylogenies May not be real. *Systematic Biology*, *59*(4), 458–464. https://doi.org/10.1093/sysbio/syq032

De Lisle, S. P., & Svensson, E. I. (2023). Evolutionary change is remarkably constant across timescales. bioRxiv.12.02.569704. https://doi.org/10.1101/2023.12.02.569704

Donoghue, M. J., & Edwards, E. J. (2019). Model clades are vital for comparative biology, and ascertainment bias is not a problem in practice: A response to Beaulieu and O'Meara (2018). *American Journal of Botany*, *106*(3), 327–330. https://doi.org/10.1002/ajb2.1255

European Organization For Nuclear Research & OpenAIRE. (2013). *Zenodo: Research. Shared*. https://doi.org/10.25495/7GXK-RD71

Faurby, S., Eiserhardt, W. L., & Svenning, J. (2016). Strong effects of variation in taxonomic opinion on diversification analyses. *Methods in Ecology and Evolution*, *7*(1), 4–13. https://doi.org/10.1111/2041-210X.12449

FitzJohn, R. G. (2012). Diversitree: Comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution*, *3*(6), 1084–1092. https://doi.org/10.1111/j.2041-210X.2012.00234.x

Foote, M. (1997). Estimating taxonomic durations and preservation probability. *Paleobiology*, *23*(3), 278–300. https://doi.org/10.1017/S0094837300019692

Foote, M. (2000). Origination and extinction components of taxonomic diversity: General problems. *Paleobiology*, *26*(S4), 74–102. https://doi.org/10.1017/S0094837300026890

Foote, M. (2003). Origination and extinction through the phanerozoic: A new approach. *The Journal of Geology*, *111*(2), 125–148. https://doi.org/10.1086/345841

Foote, M., Crampton, J. S., Beu, A. G., Marshall, B. A., Cooper, R. A., Maxwell, P. A., & Matcham, I. (2007). Rise and fall of species occupancy in cenozoic fossil mollusks. *Science*, *318*(5853), 1131–1134. https://doi.org/10.1126/science.1146303

Goldberg, E. E., Lancaster, L. T., & Ree, R. H. (2011). Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Systematic Biology*, *60*(4), 451–465. https://doi.org/10.1093/sysbio/syr046

Harmon, L. J., Pennell, M. W., Henao-Diaz, L. F., Rolland, J., Sipley, B. N., & Uyeda, J. C. (2021). Causes and consequences of apparent timescaling across all estimated evolutionary rates. *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 587–609. https://doi.org/10.1146/annurev-ecolsys-011921-023644

Heath, T. A., Huelsenbeck, J. P., & Stadler, T. (2014). The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(29), E2957–E2966. https://doi.org/10.1073/pnas.1319091111

Helmstetter, A. J., Zenil-Ferguson, R., Sauquet, H., Otto, S. P., Méndez, M., Vallejo-Marin, M., Schönenberger, J., Burgarella, C., Anderson, B., De Boer, H., Glémin, S., & Käfer, J. (2023). Trait-dependent diversification in angiosperms: Patterns, models and data. *Ecology Letters*, *26*(4), 640–657. https://doi.org/10.1111/ele.14170

Henao Diaz, L. F., Harmon, L. J., Sugawara, M. T. C., Miller, E. T., & Pennell, M. W. (2019). Macroevolutionary diversification rates show time dependency. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(15), 7403–7408. https://doi.org/10.1073/pnas.1818058116

Höhna, S., Landis, M. J., Heath, T. A., Boussau, B., Lartillot, N., Moore, B. R., Huelsenbeck, J. P., & Ronquist, F. (2016). RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology*, *65*(4), 726–736. https://doi.org/10.1093/sysbio/syw021

Höhna, S., May, M. R., & Moore, B. R. (2016). TESS: An R package for efficiently simulating phylogenetic trees and performing Bayesian inference of lineage diversification rates. *Bioinformatics*, *32*(5), 789–791. https://doi.org/10.1093/bioinformatics/btv651

Holland, B. R., Ketelaar-Jones, S., O'Mara, A. R., Woodhams, M. D., & Jordan, G. J. (2020). Accuracy of ancestral state reconstruction for non-neutral traits. *Scientific Reports*, *10*(1), 7644. https://doi.org/10.1038/s41598-020-64647-4

Lagomarsino, L. P., Forrestel, E. J., Muchhala, N., & Davis, C. C. (2017). Repeated evolution of vertebrate pollination syndromes in a recently diverged Andean plant clade. *Evolution*, *71*(8), 1970–1985. https://doi.org/10.1111/evo.13297

Lerner, H. R. L., Meyer, M., James, H. F., Hofreiter, M., & Fleischer, R. C. (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Current Biology*, *21*(21), 1838–1844. https://doi.org/10.1016/j.cub.2011.09.039

Liow, L. H. (2004). A test of Simpson's "Rule of the survival of the relatively unspecialized" using fossil crinoids. *The American Naturalist*, *164*(4), 431–443. https://doi.org/10.1086/423673

Liow, L. H., & Nichols, J. D. (2010). Estimating rates and probabilities of origination and extinction using taxonomic occurrence data: Capture-mark-recapture (CMR) approaches. *The Paleontological Society Papers*, *16*, 81–94. https://doi.org/10.1017/S1089332600001820

Liow, L. H., & Stenseth, N. C. (2007). The rise and fall of species: Implications for macroevolutionary and macroecological studies. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1626), 2745–2752. https://doi.org/10.1098/rspb.2007.1006

Liow, L. H., Uyeda, J., & Hunt, G. (2023). Cross-disciplinary information for understanding macroevolution. *Trends in Ecology & Evolution*, *38*(3), 250–260. https://doi.org/10.1016/j.tree.2022.10.013

Louca, S., Henao-Diaz, L. F., & Pennell, M. (2022). The scaling of diversification rates with age is likely explained by sampling bias. *Evolution*, *76*(7), 1625–1637. https://doi.org/10.1111/evo.14515

Louca, S., & Pennell, M. W. (2020). Extant timetrees are consistent with a myriad of diversification histories. *Nature*, *580*(7804), 502–505. https://doi.org/10.1038/s41586-020-2176-1

Louca, S., & Pennell, M. W. (2021). Why extinction estimates from extant phylogenies are so often zero. *Current Biology*, *31*(14), 3168–3173.e4. https://doi.org/10.1016/j.cub.2021.04.066

Luo, A., Duchêne, D. A., Zhang, C., Zhu, C.-D., & Ho, S. Y. W. (2020). A simulation-based evaluation of tip-dating under the fossilized birth–death process. *Systematic Biology*, *69*(2), 325–344. https://doi.org/10.1093/sysbio/syz038

MacPherson, A., Louca, S., McLaughlin, A., Joy, J. B., & Pennell, M. W. (2021). Unifying phylogenetic birth–death models in epidemiology and macroevolution. *Systematic Biology*, *71*(1), 172–189. https://doi.org/10.1093/sysbio/syab049

Maddison, W. P., Midford, P. E., & Otto, S. P. (2007). Estimating a binary Character's effect on speciation and extinction. *Systematic Biology*, *56*(5), 701–710. https://doi.org/10.1080/10635150701607033

Magallón, S., Sánchez-Reyes, L. L., & Gómez-Acevedo, S. L. (2019). Thirty clues to the exceptional diversification of flowering plants. *Annals of Botany*, *123*(3), 491–503. https://doi.org/10.1093/aob/mcy182

Magallón, S., & Sanderson, M. J. (2001). Absolute diversification rates in angiosperm clades. *Evolution*, *55*(9), 1762–1780. https://doi.org/10.1111/j.0014-3820.2001.tb00826.x

Marshall, C. R. (2017). Five palaeobiological laws needed to understand the evolution of the living biota. *Nature Ecology & Evolution*, *1*(6), 0165. https://doi.org/10.1038/s41559-017-0165

Methods in Ecology and Evolution. (2024). *Code and data review*. https://besjournals.onlinelibrary.wiley.com/hub/journal/2041210X/author-guidelines#data_for_review

Mongiardino Koch, N., Garwood, R. J., & Parry, L. A. (2023). Inaccurate fossil placement does not compromise tip-dated divergence times. *Palaeontology*, *66*(6), e12680. https://doi.org/10.1111/pala.12680

Morlon, H., Lewitus, E., Condamine, F. L., Manceau, M., Clavel, J., & Drury, J. (2016). RPANDA: An R package for macroevolutionary analyses on phylogenetic trees. *Methods in Ecology and Evolution*, *7*(5), 589–597. https://doi.org/10.1111/2041-210X.12526

Mynard, P., Algar, A. C., Lancaster, L. T., Bocedi, G., Fahri, F., Gubry-Rangin, C., Lupiyaningdyah, P., Nangoy, M., Osborne, O. G., Papadopulos, A. S. T., Sudiana, I. M., Juliandi, B., Travis, J. M. J., & Herrera-Alsina, L. (2023). Impact of phylogenetic tree completeness and mis-specification of sampling fractions on trait dependent diversification models. *Systematic Biology*, *72*(1), 106–119. https://doi.org/10.1093/sysbio/syad001

Nee, S. (2006). Birth-death models in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 1–17. https://doi.org/10.1146/annurev.ecolsys.37.091305.110035

Nichols, J. D., & Pollock, K. H. (1983). Estimating taxonomic diversity, extinction rates, and speciation rates from fossil data using capture-recapture models. *Paleobiology*, *9*(2), 150–163. https://doi.org/10.1017/S0094837300007533

Pannetier, T., Martinez, C., Bunnefeld, L., & Etienne, R. S. (2021). Branching patterns in phylogenies cannot distinguish diversity-dependent diversification from time-dependent diversification. *Evolution*, *75*(1), 25–38. https://doi.org/10.1111/evo.14124

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*(3), 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pérez-Escobar, O. A., Zizka, A., Bermúdez, M. A., Meseguer, A. S., Condamine, F. L., Hoorn, C., Hooghiemstra, H., Pu, Y., Bogarín, D., Boschman, L. M., Pennington, R. T., Antonelli, A., & Chomicki, G. (2022). The Andes through time: Evolution and distribution of Andean floras. *Trends in Plant Science*, *27*(4), 364–378. https://doi.org/10.1016/j.tplants.2021.09.010

Rabosky, D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One*, *9*(2), e89543. https://doi.org/10.1371/journal.pone.0089543

Raup, D. M. (1972). Taxonomic diversity during the phanerozoic: The increase in the number of marine species since the Paleozoic may be more apparent than real. *Science*, *177*(4054), 1065–1071. https://doi.org/10.1126/science.177.4054.1065

Raup, D. M. (1978). Cohort analysis of generic survivorship. *Paleobiology*, *4*(1), 1–15. https://doi.org/10.1017/S0094837300005649

Raup, D. M., & Sepkoski, J. J. (1982). Mass extinctions in the marine fossil record. *Science*, *215*(4539), 1501–1503. https://doi.org/10.1126/science.215.4539.1501

Schwery, O., Freyman, W., & Goldberg, E. E. (2023). adequaSSE: Model adequacy testing for trait-dependent diversification models. bioRxiv.03.06.531416. https://doi.org/10.1101/2023.03.06.531416

Sepkoski, J. J. (1998). Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1366), 315–326. https://doi.org/10.1098/rstb.1998.0212

Sepkoski, J. J., Bambach, R. K., Raup, D. M., & Valentine, J. W. (1981). Phanerozoic marine diversity and the fossil record. *Nature*, *293*(5832), 435–437. https://doi.org/10.1038/293435a0

Sepkoski, J. J., & Miller, A. I. (1998). Analysing diversification through time. *Trends in Ecology & Evolution*, *13*(4), 158–159. https://doi.org/10.1016/S0169-5347(98)01341-X

Silvestro, D., Salamin, N., Antonelli, A., & Meyer, X. (2019). Improved estimation of macroevolutionary rates from fossil data using a Bayesian framework. *Paleobiology*, *45*(4), 546–570. https://doi.org/10.1017/pab.2019.23

Silvestro, D., Schnitzler, J., Liow, L. H., Antonelli, A., & Salamin, N. (2014). Bayesian estimation of speciation and extinction from incomplete fossil occurrence data. *Systematic Biology*, *63*(3), 349–367. https://doi.org/10.1093/sysbio/syu006

Simões, T. R., & Pierce, S. E. (2021). Sustained high rates of morphological evolution during the rise of tetrapods. *Nature Ecology & Evolution*, *5*(10), 1403–1414. https://doi.org/10.1038/s41559-021-01532-x

Simpson, G. G. (1944). *Tempo and mode in evolution*. Columbia University Press.

Soares, A. E., Novak, B. J., Haile, J., Heupink, T. H., Fjeldså, J., Gilbert, M. T. P., Poinar, H., Church, G. M., & Shapiro, B. (2016). Complete mitochondrial genomes of living and extinct pigeons revise the timing of the columbiform radiation. *BMC Evolutionary Biology*, *16*, 1–9.

Stadler, T., Gavryushkina, A., Warnock, R. C. M., Drummond, A. J., & Heath, T. A. (2018). The fossilized birth-death model for the analysis of stratigraphic range data under different speciation modes. *Journal of Theoretical Biology*, *447*, 41–55. https://doi.org/10.1016/j.jtbi.2018.03.005

Stanley, S. M. (1979). *Macroevolution: Pattern and process (reprinted with new introd)*. The Johns Hopkins University Press.

The American Naturalist Journal. (2022). *American Naturalist Policy on data and code archiving*. https://www.amnat.org/announcements/data-and-code-announcement.html

The Dryad Platform. Dryad data curation website. https://datadryad.org/stash

Tosso, F., Hardy, O. J., Doucet, J.-L., Daïnou, K., Kaymak, E., & Migliore, J. (2018). Evolution in the Amphi-Atlantic tropical genus *Guibourtia* (Fabaceae, Detarioideae), combining NGS phylogeny and morphology. *Molecular Phylogenetics and Evolution*, *120*, 83–93. https://doi.org/10.1016/j.ympev.2017.11.026

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology*, *17*(12), e3000494. https://doi.org/10.1371/journal.pbio.3000494

Uribe-Convers, S., & Tank, D. C. (2015). Shifts in diversification rates linked to biogeographic movement into new areas: An example of a recent radiation in the Andes. *American Journal of Botany*, *102*(11), 1854–1869. https://doi.org/10.3732/ajb.1500229

Vasconcelos, T., O'Meara, B. C., & Beaulieu, J. M. (2022). A flexible method for estimating tip diversification rates across a range of speciation and extinction scenarios. *Evolution*, *76*(7), 1420–1433. https://doi.org/10.1111/evo.14517

Warnock, R. C. M., Heath, T. A., & Stadler, T. (2020). Assessing the impact of incomplete species sampling on estimates of speciation and extinction rates. *Paleobiology*, *46*(2), 137–157. https://doi.org/10.1017/pab.2020.12

Wiens, J. J. (2011). The causes of species richness patterns across space, time, and clades and the role of "ecological limits". *The Quarterly Review of Biology*, *86*(2), 75–96. https://doi.org/10.1086/659883

Zenil-Ferguson, R., & Liow, L. H. (2024). Code for Simpson's tachytely or bradytely? The importance of quantifying rate uncertainty. *Zenodo*, https://doi.org/10.5281/zenodo.13624001

Zenil-Ferguson, R., McEntee, J. P., Burleigh, J. G., & Duckworth, R. A. (2023). Linking ecological specialization to its macroevolutionary consequences: An example with passerine nest type. *Systematic Biology*, *72*(2), 294–306. https://doi.org/10.1093/sysbio/syac083

How to cite this article: Zenil-Ferguson, R., & Liow, L. H. (2025). Simpson's tachytely or bradytely? The importance of quantifying rate uncertainty. *Methods in Ecology and Evolution*, *16*, 4–18. https://doi.org/10.1111/2041-210X.14442