




Pulled Diversification Rates, Lineages-Through-Time Plots, and Modern Macroevolutionary Modeling

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Abstract.—Estimating time-dependent rates of speciation and extinction from dated phylogenetic trees of extant species (timetrees), and determining how and why they vary, is key to understanding how ecological and evolutionary processes shape biodiversity. Due to an increasing availability of phylogenetic trees, a growing number of process-based methods relying on the birth–death model have been developed in the last decade to address a variety of questions in macroevolution. However, this methodological progress has regularly been criticized such that one may wonder how reliable the estimations of speciation and extinction rates are. In particular, using lineages-through-time (LTT) plots, a recent study has shown that there are an infinite number of equally likely diversification scenarios that can generate any timetree. This has led to questioning whether or not diversification rates should be estimated at all. Here, we summarize, clarify, and highlight technical considerations on recent findings regarding the capacity of models to disentangle diversification histories. Using simulations, we illustrate the characteristics of newly proposed “pulled rates” and their utility. We recognize that the recent findings are a step forward in understanding the behavior of macroevolutionary modeling, but they in no way suggest we should abandon diversification modeling altogether. On the contrary, the study of macroevolution using phylogenetic trees has never been more exciting and promising than today. We still face important limitations in regard to data availability and methods, but by acknowledging them we can better target our joint efforts as a scientific community. [Birth–death models; extinction; phylogenetics; speciation.]

A major goal in evolutionary biology is to understand the large-scale processes that have shaped biodiversity patterns. One important way to investigate this is by modeling species diversification using speciation and extinction, which can vary over time and among groups. It is commonplace to find regions, or clades, in phylogenetic trees that accumulate lineages faster than others. Macroevolutionary models often aim to explain this variation in diversification patterns by associating bursts of speciation or extinction with factors such as time (May et al. 2016), lineages (Rabosky et al. 2013; Rabosky 2014), character traits (Maddison et al. 2007), or the environment (Condamine et al. 2013).

The growing number of large phylogenetic trees that capture a substantial proportion of living species provide increasing power and resolution for such studies (Jetz et al. 2012; Smith and Brown 2018; Stein et al. 2018; Upham et al. 2019). Furthermore, the availability of a wide variety of methods and software (e.g., BAMM (Rabosky 2014), state-speciation and extinction (SSE) models (Maddison et al. 2007; FitzJohn 2012), RPANDA (Morlon et al. 2016), MEDUSA (Alfaro et al. 2009)) has made diversification studies increasingly popular in the

last decade. Approaches that can link diversification to a particular process or trait are among the most appealing to researchers because they enable us to test long-standing hypotheses in evolutionary biology and ecology. Examples include those related to the evolution of key innovations (Silvestro et al. 2014), the colonization of new areas (McGuire et al. 2014), the effect of elevation (Lagomarsino et al. 2016; Quintero and Jetz 2018), and the latitudinal diversity gradient (Rolland et al. 2014; Pulido-Santacruz and Weir 2016; Rabosky et al. 2018; Igea and Tanentzap 2020).

A typical workflow for diversification rate modeling using molecular phylogenetic trees starts with obtaining DNA sequence data for species in a study group, which are then used to estimate species relationships in the form of a phylogenetic tree. Usually, this phylogenetic tree contains only extant species, and it is time-calibrated using ages derived from different sources including fossils (Ho and Phillips 2009; Parham et al. 2012; Sauquet 2013). The output of this process is referred to as an extant timetree. Once a tree has been generated, a birth–death model is fitted to explain patterns of diversification in the tree. Note that fossils are generally

used for node calibration and tree shape estimation but are rarely incorporated in any subsequent estimation of diversification rates, although it is now possible to incorporate fossils as tips in phylogenetic trees (Ronquist et al. 2012; Heath et al. 2014) and in birth–death models for diversification rate estimation (Mitchell et al. 2019). Some of the most recent developments have now also allowed researchers to coestimate the phylogenetic tree and diversification model (Höhna et al. 2016; Barido-Sottani et al. 2020).

The simplest birth–death models assume that each branch of a phylogenetic tree shares the same rate of “birth” (speciation) events, as well as “death” (extinction) events (Nee et al. 1994; Nee 2006; Ricklefs 2007; Morlon et al. 2011). There are two principal parameters in the birth–death model, the speciation rate (λ)—the rate at which lineages arise, and the extinction rate (μ)—the rate at which lineages disappear. In addition, a third parameter known as sampling fraction (or ρ) is often included to account for the fact that not all extant taxa are included in the phylogenetic tree. Sampling fraction can be defined as the ratio of sampled species over the total extant species diversity for a given clade. Under the simplest framework, λ and μ are constant over time (time-independent) and the same across all clades (clade-independent). However, we can begin to relax these assumptions by allowing models to be time-dependent (Morlon et al. 2011; Louca and Pennell 2020), clade-dependent (Maddison et al. 2007; Maliet et al. 2019; Barido-Sottani et al. 2020), or both (Rabosky et al. 2013). By making use of these different parameters and assumptions, birth–death models allow us to investigate whether the net diversification rate, defined as $r = \lambda - \mu$, has varied over time or among clades and ultimately

uncover the processes that have given rise to extant biodiversity across the tree of life.

A recent study (Louca and Pennell 2020 abbreviated to LP) demonstrates, using an approach based on lineages-through-time (LTT) plots, that rates of speciation and extinction over time cannot be reliably estimated using extant timetrees (see also Kubo and Iwasa 1995). LP show how results of this approach can be misleading and provide potential solutions to the issues raised by proposing new summary statistics. This study has already provoked a response from the community (e.g., Morlon et al. 2020) and stimulated considerable discussion, with some going so far as to suggest that speciation and extinction rates cannot be estimated using phylogenetic trees (Pagel 2020). As a result, this study has called into question the meaning of diversification rate estimates generated from any analytical framework. Here, we try to render this discussion accessible to the broader audience of evolutionary biologists, who might use the available methods to study diversification but do not themselves develop macroevolutionary models. Thus, we aim to outline the major concepts discussed in LP in an accessible way, put the results and conclusions of LP into historical context, and explore how the implications of this study apply to macroevolutionary modeling today.

A SUMMARY OF THE MAIN CONCEPTS AND FINDINGS IN LOUCA AND PENNELL (2020)

An LTT plot shows how extant lineages accumulated over time, using a phylogenetic tree (Nee et al. 1992) (Fig. 1). Each point in an LTT corresponds to a change in the number of lineages from the root of a phylogenetic

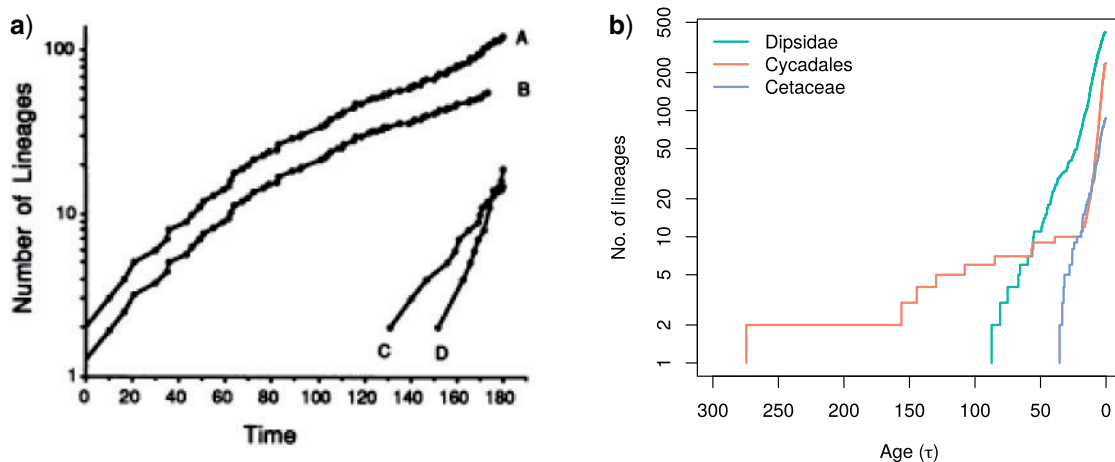


FIGURE 1. a) The first example of a lineages-through-time plot (LTT), taken from Nee et al. (1992) and based on a phylogenetic tree of birds. On the y-axis is the number of lineages (log scale) and the x-axis is time since origin (present on the right hand side of the graph). “Each point corresponds to a change in the number of lineages. Line A, the pattern of origination of all 122 lineages; line B, same as A, but without the Passeri (line C) and the Ciconiiformes (line D). Line B has been shifted downward to aid visual comparison. The diversification rate is quantified by the steepness of the slope.” In this panel, time is displayed from past to present as time since origin (t). b) Three LTTs from modern phylogenetic trees of Dipsidae (campanulids) (Beaulieu and Donoghue 2013; Beaulieu and O’Meara 2016), Cycadales (Condamine et al. 2015) and Cetacea (Slater et al. 2010). In this panel, time is shown from present to past as an age (τ).

tree at $t=0$ to the present day at $t=T$ (Fig. 1a). Alternatively, as in LP, time can be considered as an age ($\tau=T-t$), where $\tau=0$ at the present and $\tau=T$ at the origin of the clade, or the root age (Fig. 1b). For consistency with LP, we will generally consider timescale as age (τ) in the equations we use throughout this article.

Simply put, when a clade diversifies faster, the slope of the LTT becomes steeper, but when diversification slows, the slope of the LTT levels off. When only extant lineages are considered, as in LP, LTT plots will never exhibit a drop in total lineage diversity over time (Ricklefs 2007). Regardless of whether time is τ or t in the equations, the LTT is usually plotted with the present on the right, thus its slope will never be negative. However, this does not mean that extinction does not have an effect on the shape of the LTT (Nee 2006). Previous work from almost 30 years ago (Nee et al. 1992, 1994; Harvey et al. 1994) clearly demonstrated how an LTT may change when extinction is present alongside speciation (birth–death), as opposed to speciation alone (pure-birth) in the context of models where diversification rates were constant over time. If the growth of an extant timetree is represented as an LTT on a semilog scale (i.e., lineage number is logarithmic, time is not, see Fig. 1), we would expect the trend to be linear under a pure-birth process (with constant speciation and no extinction). If extinction is introduced, the LTT would deviate from this linearity. When both rates are constant and greater than 0, the curve is expected to be linear over most of its history, but as time reaches the present the rate of lineage accumulation will increase (i.e., the LTT slope will become steeper) as the effect of extinction diminishes (Nee et al. 1994; see also Fig. 4 in Nee (2006)). By examining other deviations from linearity in the LTT plot we can begin to understand how diversification rates fluctuated over the history of a clade (Ricklefs 2007) and develop evolutionary hypotheses on why these fluctuations occurred.

The Deterministic Lineages-Through-Time Plot

The birth–death model is often implemented as a continuous-time Markov chain where at any given age (τ) we can calculate the probability of speciation (birth of a lineage) or extinction (death of a lineage) happening. Because the birth–death process is stochastic, each run (i.e., realization of the process) will result in a different history of diversification, even if the probabilities for speciation and extinction are the same.

For such models, we can approximate their expected value by conducting many realizations of the stochastic model. Alternatively, we can calculate the expected values using a set of continuous equations, which is known as a deterministic model. Although the stochastic and deterministic models both rely on the same birth–death process their behavior can be different, notably when using small phylogenetic trees (see Box 1). The deterministic model produces the expected value one would get by averaging over an infinite number of simulations, thus it is

BOX 1: HOW FAST CAN SPECIATION AND EXTINCTION RATES VARY?

Although it is standard practice, it should be noted that the approach of LP involves using and solving differential equations and therefore considers speciation and extinction to be continuous processes: at any infinitesimal time interval, the species number changes infinitesimally through speciation and extinction. In the birth–death process, however, the smallest amount of change in the number of species is one, and this happens only at particular moments in time.

Even if speciation, in reality, is a complex process that takes time (Etienne and Rosindell 2012), the branching events that represent speciation in phylogenetic trees are instantaneous. This means that the number of lineages will immediately jump from n to $n+1$, rather than gradually, in a continuous process (i.e., the durations of speciation and extinction are much shorter than the time between two events). An empirical LTT plot will thus show discrete events, appearing step-wise rather than being a continuous function, as is the dLTT. To measure pulled rates, LP propose calculating the slope and curvature of the LTT plot (though other ways of doing this now exist; Louca et al. 2021). For the dLTT, where the number of lineages is a continuous function of time, these are the first and second derivative of this function. For empirical LTT plots, one has to calculate the slope and curvature using some time interval. When working with a large phylogenetic tree and many species (as in the examples discussed by LP and Louca et al. 2018), the LTT is smooth and the slope and curvature, which are necessary for the estimation of the pulled rates, can be reliably estimated. However, many studies attempt to estimate diversification rates with relatively small numbers of species (i.e., < 1000 , e.g., Hutter et al. 2017 or even < 100 , e.g., Duan et al. 2018). Thus, as the number of species diminishes, one has to be aware that overparameterization might occur, and it would be wiser to stick to simple functions of diversification (or their pulled variants) through time, the simplest being time-independent rates, and even these are associated with large uncertainty (Aldous et al. 2011). Such problems are not unique to the estimation of pulled rates, and may be found in various macroevolutionary methods that rely on small samples of discrete variables. Yet, even in large trees, rates will always be estimated using a time interval that contains a sufficient number of speciation and extinction events. The consequences of this are that rapid changes in diversification rates might be missed due to the resolution of the chosen interval, and that capturing macroevolutionary dynamics at deep timescales will require very wide intervals, at the cost of reduced temporal resolution.

deterministic because it is fully defined by the parameters—no uncertainty from stochasticity is involved. This kind of approach is widely used and is also taken by LP who model the birth–death process as a set of differential equations, which is advantageous because these equations can be solved analytically.

LP refer to an LTT obtained from such models as a deterministic LTT (dLTT), which corresponds here to the expected LTT generated by trees with given speciation and extinction rates. Empirical LTTs generated using extant timetrees can be compared to model-generated dLTTs (where λ and μ are known) to disentangle how speciation and extinction have influenced patterns of diversity over time. To do this, the probability of the data given the model, or the likelihood, is calculated. Importantly, LP showed that, when λ and μ are clade-independent across the tree, the likelihood can be fully written as a function of the observed LTT and the dLTT generated by the model, even when rates vary over time (see also Lambert and Stadler 2013). Typically, by changing the parameters in the model, its dLTT resembles the empirical LTT to a greater or lesser extent, and the model is more or less likely. The best-fitting model can then be selected, representing our best hypothesis for how and to what extent speciation and extinction rates varied over time.

Model Congruence and Congruence Classes

Consider a simple model where λ and μ are constant over time and among clades and all lineages have been sampled ($\rho = 1$). In this case, the slope of the LTT plot is $r = \lambda - \mu$, except at times close to the present, where the effect of extinction diminishes and the slope becomes λ (Nee et al. 1994). Thus, with these slopes yielding λ and r we can calculate $\mu = \lambda - r$ (in practice, all parameters can be inferred at once within a likelihood framework using equations in Nee et al. (1994)). LP develop upon this classical knowledge to show that if rates vary over time (τ) it is no longer possible to estimate $\lambda(\tau)$, as the value of $\lambda(\tau)$ at present does not yield any information about its past dynamics. In other words, it is possible to choose almost any historical scenario for $\lambda(\tau)$ and obtain a complementary scenario of $\mu(\tau)$ that produces the same dLTT. If different models produce the same dLTT then they will also share the same likelihood for any given LTT.

LP call the set of models that generate the same dLTT a “congruence class.” These congruence classes contain an infinite number of models with different parameter values that all produce the same dLTT. LP explain that when trying to select the best model we often start with a relatively small set of allowed models that we test. For example, a set of two models where speciation rate is fixed and extinction rate is allowed to vary over time, or *vice versa*. This would produce two equally likely models when trying to explain a slowdown in diversification, one indicating the case was an increase in extinction rate, the other a drop in the speciation rate—there is no way

of distinguishing between them (Rabosky and Lovette 2008; Crisp and Cook 2009; Burin et al. 2019).

LP propose, and have recently developed upon (Louca et al. 2021; Louca and Pennell 2021), the idea that instead of selecting the model closest to the true process, we are selecting the model closest to the congruence class that includes the true process (see Fig. 3 in LP). In extreme cases, the best fitting model could thus be further from the true process than a more correct model, just because the former is included in the congruence class and the latter is not. However, LP also state that because we only assess a limited set of models, it is unlikely that we encounter models belonging to the same congruence class, but it is nevertheless possible. The consequence of multiple, equally likely models with different speciation and extinction rates is that these rates cannot be determined. This is a statistical phenomenon known as unidentifiability—the likelihood is the same for multiple parameter values making it impossible to choose one over another.

Unidentifiability

In macroevolutionary modeling, we might be interested to know how both λ and μ have changed over time (Rabosky 2006; Morlon et al. 2010). The unidentifiability issue outlined above means that we would not be able to ascertain the true parameter values of the models that generate our dLTTs. Another well-known example of this in evolutionary biology is the unidentifiability of substitution rates and divergence times when estimating phylogenetic trees (Rannala 2002). The molecular character data we use as input gives us the estimate of their product, which could be explained by different combinations of rates and times. In this case, we usually try to overcome the unidentifiability issue through the use of informative priors, such as those often placed on node ages in Bayesian approaches. This problem is not unique to macroevolutionary models, and, in fact, stems from a basic mathematical issue (Rannala 2002; Ponciano et al. 2012).

Consider a simple example in which we want to determine the parameter values for x and y :

$$2x + y = 7 \quad (1)$$

$$3x + 2y = 12. \quad (2)$$

For each value of x in equation 1, we can find a y that satisfies this equation—and there are an infinite number of equally likely possibilities. It is only when we add more information (in the form of equation 2) that we can determine the unique pair of values for x and y . Put simply, a solution can be found only if you possess at least the same number of equations as unknowns. If there are fewer equations, the unidentifiability is caused by overparameterization—there is an excess of parameters such that the model cannot estimate the values of any of them.

Though the LTT is generated through the use of many different observations and elements (DNA, fossils for

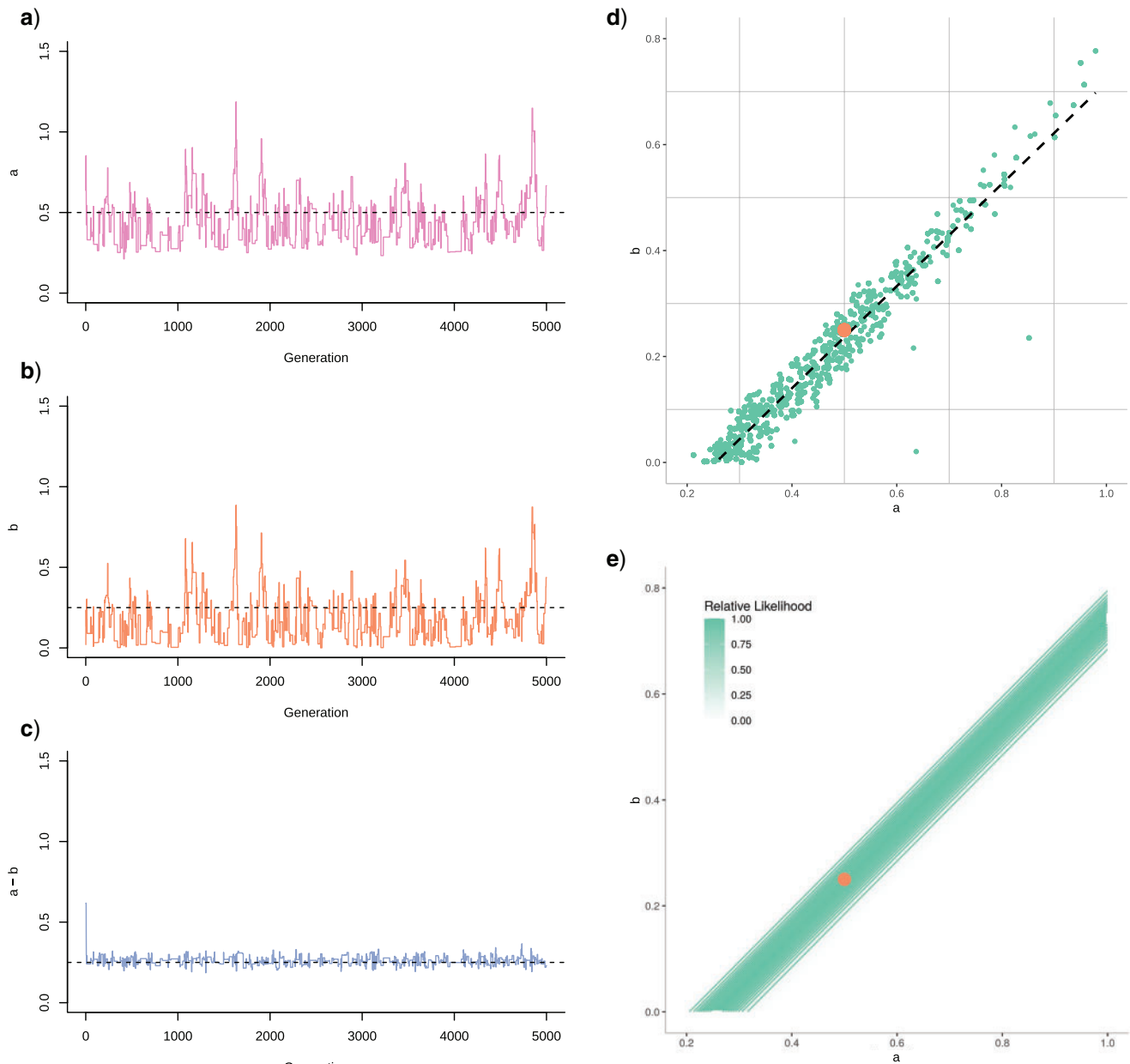


FIGURE 2. An example of unidentifiability issues encountered when trying to estimate values of two parameters (a and b) for the slope $a-b$. We used a Bayesian Monte-Carlo Markov Chain approach to try to estimate the values of a and b separately. We ran a chain for 5000 generations, sampling each generation. The traces for a) a and b) b show a great deal of uncertainty in the parameter estimates compared to the estimates for c) $a-b$. True values are shown as black dashed lines in panels (a–c) and as large circles in panels (d,e). We plotted a against b and found that the two parameters were highly correlated (d). We then calculated the relative likelihood over a range of parameters values and found a flat ridge in the likelihood where different pairs of values for a & b are equally likely—or unidentifiable (e). Further details and code showing how these analyses, and all others in this study were conducted can be found in the [Supplementary material](https://doi.org/10.5061/dryad.5tb2rbp4g) available on Dryad at <https://doi.org/10.5061/dryad.5tb2rbp4g> and in the associated rcompedium (Casajus 2021) at <https://github.com/ajhelmstetter/pulledRates>.

time-calibration, extant species sampling) it is represented by a single curve made up of one observation at any given point in time that represents the number of lineages in a clade (Fig. 1). Fitting a model to an LTT is like fitting two parameters (a and b) for a single value, the slope ($a-b$). If we try to estimate a and b separately we find it impossible (Fig. 2a,b). However, we can estimate $a-b$ (Fig. 2c) with much greater accuracy. Estimates of

a and b are fully correlated (Fig. 2d) and we find a flat surface in the likelihood where different pairs of values for a and b are equally likely (Fig. 2e), signifying unidentifiability.

This problem has been highlighted previously in a macroevolutionary context (Nee 2006; Kubo and Iwasa 1995), where $a-b$ is akin to the net diversification rate ($r = \lambda - \mu$). However, the birth–death model is more

TABLE 1. A table detailing the parameters we can estimate with the lineages-through-time plot (LTT) approach used in Louca and Pennell (2020) when rates are either constant or time-dependent. When speciation and extinction rate are constant we are able to infer all traditional (r , λ , μ) and pulled rates (r_p , λ_p , μ_p). If sampling fraction (ρ) is unknown, we lose the ability to infer λ and μ . If λ and μ vary over time only pulled rates remain identifiable.

	Speciation	Extinction	Sampling fraction	Ref	Identifiable parameters
Constant rates	$\lambda = a$	$\mu = b$	$\rho = 1$	Nee et al. (1994)	$r, \lambda, \mu, r_p, \lambda_p, \mu_p$
	$\lambda = a$	$\mu = b$	$\rho < 1$ (known)	Nee et al. (1994)	$r, \lambda, \mu, r_p, \lambda_p, \mu_p$
	$\lambda = a$	$\mu = b$	$\rho < 1$ (unknown)	Stadler (2013)	r, r_p, λ_p, μ_p
Time-dependent rates	$\lambda = f(\tau)$	$\mu = g(\tau)$	$\rho = 1$	Louca and Pennell (2020)	r_p, λ_p, μ_p
	$\lambda = f(\tau)$	$\mu = g(\tau)$	$\rho < 1$ (known)	Louca and Pennell (2020)	r_p, λ_p, μ_p
	$\lambda = f(\tau)$	$\mu = g(\tau)$	$\rho < 1$ (unknown)	Louca and Pennell (2020)	r_p, λ_p, μ_p

complex than the example illustrated in Figure 2. As explained above, speciation and extinction rates are actually identifiable when time-independent because the slope of the LTT reaches λ at the present. Our ability to reliably estimate these traditional diversification rates (λ , μ , and r) depends on the amount of information we have available, and the assumptions we make in our model. For example, if the sampling fraction (ρ) is not known (or assumed) we can no longer reliably estimate λ and μ because this third unknown parameter in the model leads to unidentifiability (Table 1). However, in this case r remains identifiable, as the system is reduced to two parameters only (r and ρ). Likewise, as LP show, if we relax the assumption of constant rates (i.e., time-independent rates) and allow λ and μ to vary over time, then all traditional parameters become unidentifiable, including $r(\tau)$, even if ρ is known or assumed (Table 1). To exemplify the problem, LP used a very large phylogenetic tree of seed plants (Smith and Brown 2018) to show that the observed LTT is congruent with two opposing (but not symmetrical) scenarios (Fig. 2 in LP): either a continuous increase or a continuous decline in both $\lambda(\tau)$ and $\mu(\tau)$ (though the resulting diversification rates ($r(\tau)$) of these two scenarios are very similar). If we want to infer something from LTTs, then traditional model-based variables are inadequate, and we must look towards other possible solutions.

Pulled Rates

The solution proposed by LP is to use the approach described in Louca et al. (2018), namely not to estimate $\lambda(\tau)$, $\mu(\tau)$, and ρ , but “pulled” rates that can be directly measured from the shape of the LTT. There are three pulled rates (λ_p , μ_p , r_p) in Louca et al. (2018). These pulled rates are based directly on the dLTT—they can be calculated using the slope at a given time (τ) and the change in the slope, or curvature of the plot. Thus, any dLTT yields a unique set of pulled rates that summarize a congruence class, thereby eliminating the unidentifiability issue. However, these rates are not the speciation and extinction rates everyone knows—so what are they and how are they different from traditional rates?

An important consequence of using extant timetrees when investigating patterns of diversification is that LTT

plots will likely underestimate the number of lineages at any given time because our trees are missing species (Ricklefs 2007; Silvestro et al. 2018). Species can be missing for two reasons: i) they went extinct or ii) they are extant but were not sampled. These two factors will have different effects on the LTT plot and our estimates of diversification rates. Extinction must have occurred in the past. Lineages that originated recently have had less time to go extinct (Nee et al. 1994; Ricklefs 2007), so the effect of extinction on our estimates using only extant species is reduced towards the present. As mentioned above, this leads to an increase in the rate of lineage accumulation towards the present, as the effect of extinction decreases, which occurs even when rates are constant (Fig. 3). Conversely, incomplete sampling of a group occurs up to the present day and more strongly affects estimates of recent history (Heath et al. 2008; Phillimore and Price 2008; Cusimano and Renner 2010), as the deeper nodes in the phylogeny can be reconstructed with only a few species. The relative importance of extinction and sampling fraction will influence whether λ_p departs from λ more in the past or in the present. To summarize, the presence of extinction will cause us to underestimate speciation rate further in the past, because the number of extinct species increases as we consider more time, while incomplete sampling will lead to underestimation of speciation rates that are more recent (Heath et al. 2008; Cusimano and Renner 2010; Brock et al. 2011).

Formally, at a given time (τ), λ_p is the estimated speciation rate multiplied by 1 minus the probability that a lineage is missing from the tree due to extinction or incomplete sampling, E . We will not go into details regarding the calculation of E here, but further information can be found in S1.1 of the supplementary material of LP. λ_p is calculated using the following equation:

$$\lambda_p(\tau) = \lambda(\tau)(1 - E(\tau)). \quad (3)$$

So, if all species are in the tree and there is no extinction (i.e., the probability of missing lineages, or E , is 0) then the λ_p is equal to the (unpulled) speciation rate, λ . Any increase in extinction rate or the number of unsampled lineages (i.e., $E > 0$) will cause λ_p to drop, or be “pulled,” below speciation rate (Fig. 3). The lower the extinction rate and the greater the sampling fraction, the closer the estimate of λ_p will be to λ .

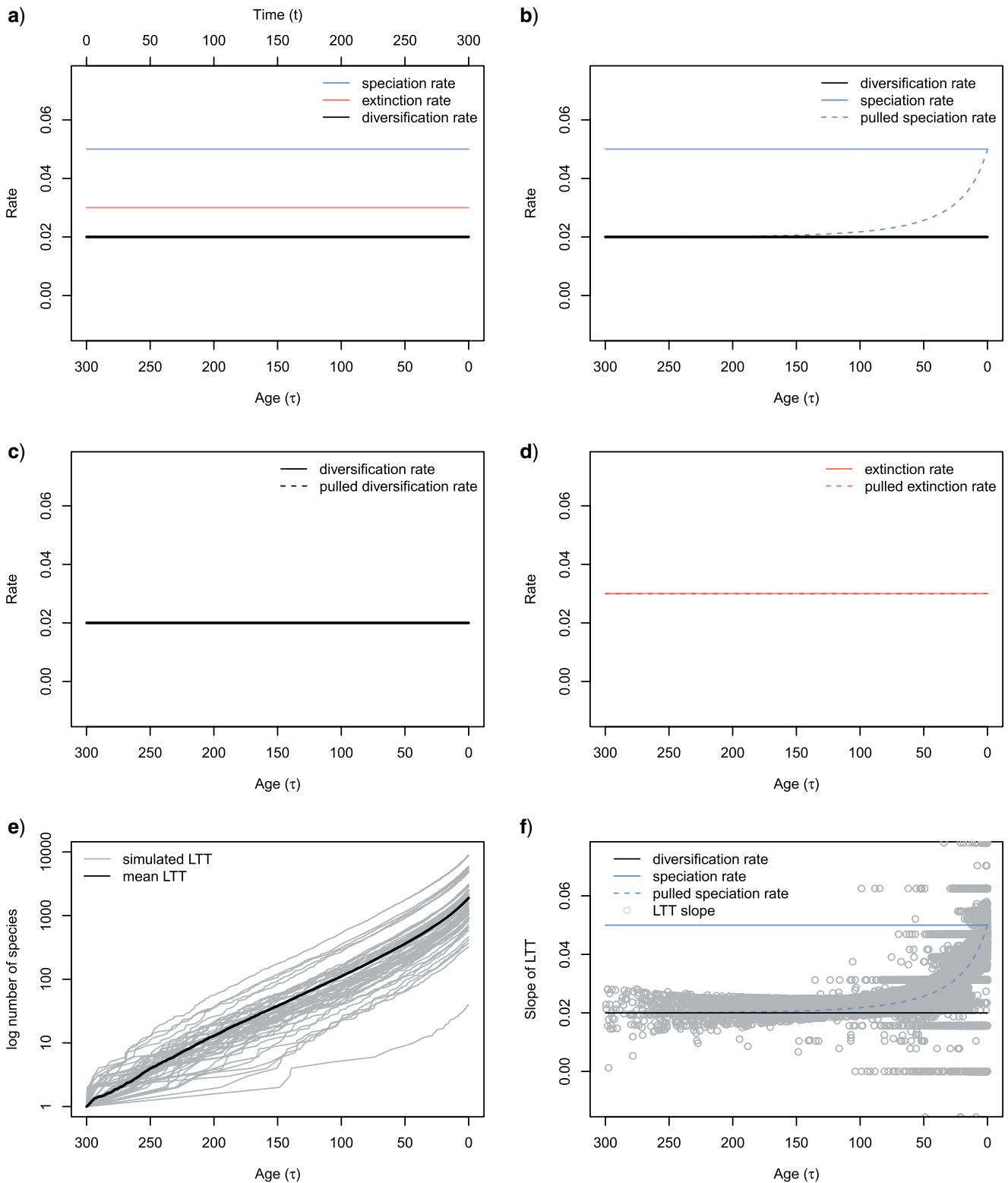


FIGURE 3. A simple example of the relationship between constant diversification rates and corresponding pulled rates. Panel a) shows values of speciation rate (λ), extinction rate (μ), and diversification rate (r) over time (τ). An additional axis, at the top of panel a) shows time since origin (t). Panel b) shows how in the past, pulled speciation rate (λ_p) is identical to the diversification rate (if sampling fraction = 100%) while closer to the present λ_p approaches speciation rate. The following two panels compare c) r and pulled diversification rate (r_p) and d) compares μ and pulled extinction rate (μ_p). In these two cases the pulled rates are identical to the traditional rates. Panel e) shows 50 LTT plots (grey lines) simulated with the parameters used in panels (a–d) and the mean LTT (black line). Panel f) shows the slopes of the LTTs in panel e) over time, matching λ_p and depicting the expected increase towards the present caused by the lack of effect of extinction—lineages do not have enough time to go extinct towards the present. Further details on how LTTs were simulated can be found in the [Supplementary material](https://ajhalmstetter.shinyapps.io/pulled_rates/) available on Dryad. An interactive version of this plot, in which parameters can be modified, can be found at https://ajhalmstetter.shinyapps.io/pulled_rates/.

LP also use pulled diversification rate (r_p), a parameter that is similar to the net diversification rate ($r = \lambda - \mu$) but is again modified by another term. This new term is the relative ($\frac{1}{\lambda}$) rate of change in speciation rate over time ($\frac{d\lambda}{d\tau}$). This causes the pulled diversification rate to lag behind the unpulled rate. The “pull” of r_p is actually a delay in the response of this parameter when compared to diversification rate. This is in contrast to the “pull” of λ_p , which refers to a reduction in the estimated value of λ_p relative to λ . Pulled diversification rate is given by the following equation:

$$r_p = \lambda - \mu + \frac{1}{\lambda} \cdot \frac{d\lambda}{d\tau}. \quad (4)$$

Consider an example where we have an increase in speciation rate at around 100 Ma in a clade (Fig. 4). When considering time as an age (using τ), speciation rate increases as τ decreases from the origin of the clade ($\tau = 300$ Ma) to the present ($\tau = 0$). This means that when speciation accelerates, $\frac{d\lambda}{d\tau}$ is negative. This leads to a “drop” in r_p (Fig. 4c) before it stabilizes at a new value of r_p that is higher than the previous value, reflecting the increase in λ . However, the change in the slope of the LTT plot (Fig. 4e,f) is very small, so this is not precisely measurable from a realistically sized phylogenetic tree (see Box 1 for additional discussion). We note that LP also defined a pulled extinction rate, (μ_p), which can be calculated from λ_p and r_p but does not add any new information, so we do not discuss it here (see LP, Louca et al. (2018) for further details).

With these new metrics we can revisit questions such as: has diversification been constant over time? Pulled rates can be estimated with many commonly used models of diversification (Louca and Pennell 2020). For example, λ_p is the speciation rate one would get by constraining extinction to be 0 and assuming complete species sampling. For r_p , this involves estimating r by making λ time-independent. In summary, λ_p provides information about how λ changes over time while taking into account past extinction and the proportion of lineages sampled. r_p provides a slightly delayed estimate of r with extreme responses to rapid changes in λ . While λ_p can be very different from the underlying speciation and extinction rates, r_p is close to the net diversification rate as long as λ does not change too rapidly. To illustrate this, we performed simulations to identify some extreme scenarios in which the pulled rates differ markedly from their nonpulled counterparts (see Supplementary material available on Dryad), but such cases correspond to specific and unrealistic scenarios of rate variation.

IMPLICATIONS FOR ANALYSES OF SPECIES DIVERSIFICATION

Pulled Rates Can Be Difficult to Interpret

LP compared the usefulness of pulled rates to effective population size (N_e) in population genetics. N_e can be broadly defined as the number of breeding individuals in an idealized population (e.g., constant size, random

mating etc.) that would be able to explain the summary statistics (e.g., amount of polymorphism, level of inbreeding) of an observed population. N_e is fairly intuitive and will react to biological phenomena in expected ways (e.g., under population structure; Whitlock and Barton 1997 or nonrandom mating; Caballero and Hill 1992). LP state that the variables they introduce are “easily interpretable.” Their terminology, however, is not completely consistent nor coherent with more traditional uses, which can cause confusion. Given that $r = \lambda - \mu$ one might intuitively think that $r_p = \lambda_p - \mu_p$, but this is not the case. Pulled rates are simply different ways of summarizing congruence classes and each one is calculated using both speciation and extinction rates. λ_p is reasonably intuitive, though given that extinction is also included it is more similar to a diversification rate than a speciation rate. Indeed, λ_p is defined as the slope of the LTT plot (Louca et al. 2018) (see Figs. 3f and 4f), which corresponds to the past diversification rate, and to the speciation rate at present in the case that all extant species are included (Nee et al. 1994).

Pulled diversification rate, however, is much more difficult to interpret, perhaps initially because the “pull” of r_p is not the same as the “pull” of λ_p (see Box 2). Whereas λ_p decreases in value relative to λ , r_p is delayed in time relative to r (Fig. 5) and could therefore better be termed as “delayed” rather than “pulled.” We simulated a variety of commonly investigated diversification scenarios, from simple to more complex (Fig. 5), and show that r_p and r are similar in most cases. However, r_p is at first sight not as intuitive as r or N_e . For example, drastic increases in r can lead to sharp decreases in r_p (Fig. 5a). The inverted pattern r_p presents in this case would make it challenging to present in a clear and concise way. Even so, compared to other pulled rates r_p could be particularly useful, not as an effective parameter like N_e , but as a reasonable approximation of the value of r . To investigate this further, we conducted an exploration of many different scenarios (see Supplementary material available on Dryad) and find that in a large majority of cases r_p is close to r and therefore can be used as a reasonable approximation of r for biological interpretation. The worst case arises when there are parallel patterns of variation in λ and μ . In this case r remains constant while r_p can fluctuate wildly (see Fig. 5d for an example). Yet, we found that if we introduce slight differences in the patterns of variation of the two rates r_p immediately begins to resemble r . But how would we know if λ is varying too rapidly to produce viable estimates? A general guideline would be to be cautious with inferences when λ_p and r_p are very different, that is, in cases where the slope of the LTT changes a lot. Conversely, when these two pulled rates are close it means that biological interpretations can reasonably be done. Attempting to biologically interpret fine-scale variations in r_p would certainly lead to spurious conclusions. However, changes in r_p at a large scale are good proxies for large scale variation in r . This is clearly illustrated in Figure 5a where the main trend of the r_p is a recent increase in diversification. Given that we are

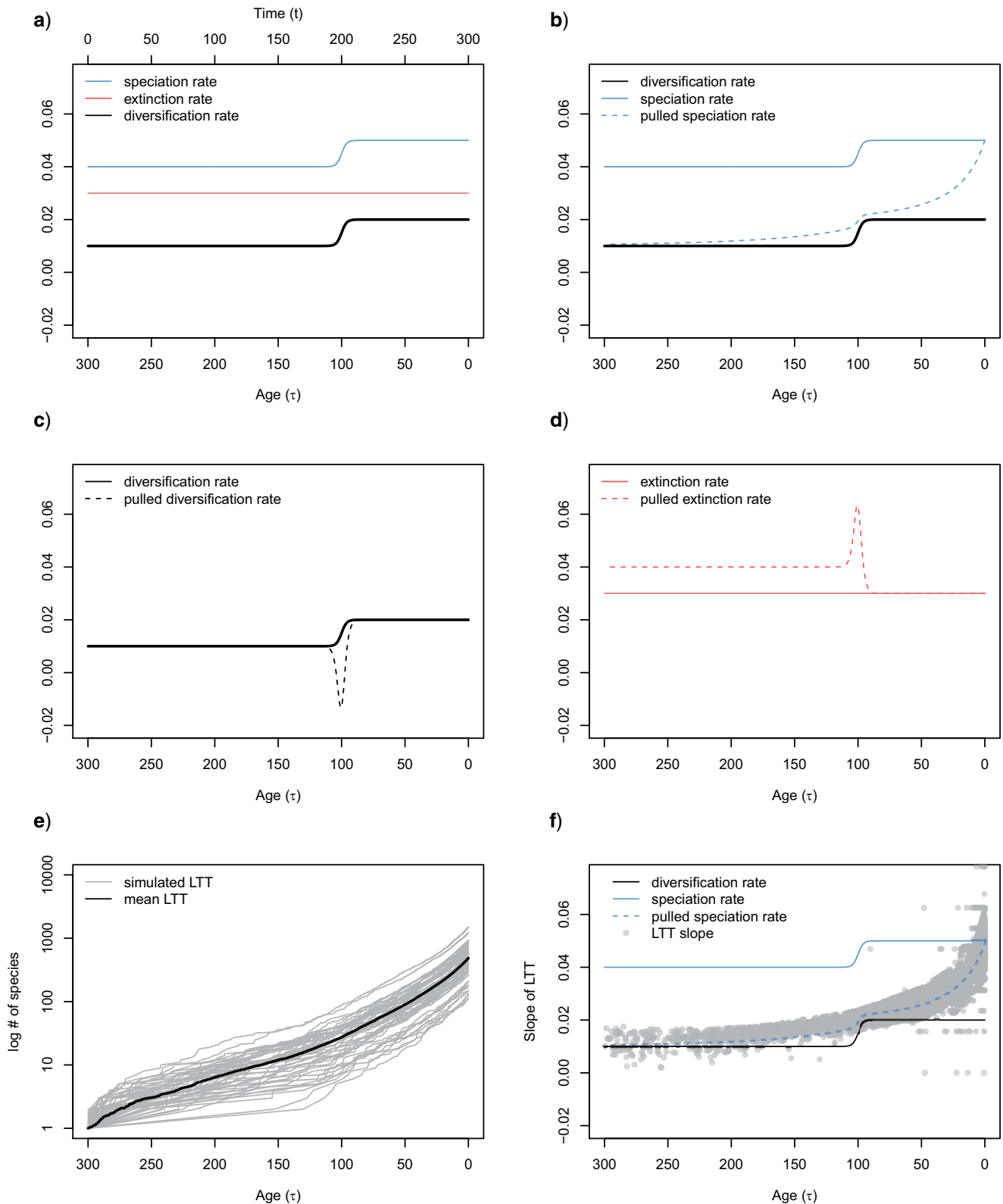


FIGURE 4. A slightly more complex example of the relationship between diversification rates and corresponding pulled rates where a single shift—an increase in speciation rate—has taken place. Panel a) shows values of speciation rate (λ), extinction rate (μ), and diversification rate (r) over time. An additional axis, at the top of panel a) shows time since origin (t). Panel b) shows the gradual change in pulled speciation rate (λ_p) during the shift in λ . Panel c) compares r and pulled diversification rate (r_p). The rapid increase in λ causes r_p to decrease suddenly before recovering to the new r . Panel d) compares μ and pulled extinction rate (μ_p) and shows an inverse pattern to panel (c). Panel e) shows 50 LTT plots (grey lines) simulated with the parameters used in panels a–d) and the mean LTT (black line). Panel f) shows the slopes of the LTTs in panel e) over time, matching λ_p and again depicting the expected increase towards the present caused by the lack of effect of extinction.

BOX 2: THE “PULL” IN r_p IS A RESULT OF THE LAG TIME BETWEEN EXTINCTION AND SPECIATION

Consider a simple case with no extinction ($\mu = 0$) so that changes in r only come from changes in λ . If so, $r = \lambda$ but r_p is not exactly λ because of temporal variations in λ (the term $\frac{1}{\lambda} \cdot \frac{d\lambda}{d\tau}$ in equation 4). LP suggest that “the pulled diversification rate can be interpreted as the effective net diversification rate if λ was time-independent.” In our example, this means replacing a scenario, where μ is constant (at 0) and λ varies with a scenario where λ is constant and μ varies, as in LP. The difficulty of using μ to explain variation is that there is a slight delay between the effect of speciation and the effect of extinction. It is necessary to wait for species to arise before they can go extinct.

As mentioned previously, lineages that originated more recently have had less time to go extinct. In a constant birth–death process, this is only visible in recent history: the slope of the LTT plot is $r = \lambda - \mu$ during most of the past but increases to λ for very recent times where the stationary behavior has not yet been reached (Fig. 3). However, this phenomenon is not unique to very recent times—it will also occur whenever there is a change in speciation rate. Ultimately, this is the cause of the difference between r_p and r .

To illustrate this, imagine a massive increase in the number of lineages caused by a burst of speciation (Fig. 4). Over a short time period many new lineages have become available for potential extinction but they have yet to go extinct because not enough time has passed since they appeared for extinction to take place. There is now a disequilibrium between speciation and extinction, manifested as a lag in the time extinction takes to affect all of the new lineages. As time continues, these numerous new lineages will begin to go extinct, meaning that frequency of species extinction will increase to “catch up” to speciation and reach a new stationary point. This effect is stronger when λ varies rapidly (i.e., high $\frac{1}{\lambda} \cdot \frac{d\lambda}{d\tau}$). Conversely, speciation cannot occur in a lineage after it has gone extinct, so there is no similar lag caused by changes in extinction rate. This is also why variation in extinction rate would not cause r_p to deviate from r (Fig. 5b).

often interested in variation in r (rather than in both λ and μ) at a large-scale we can be less pessimistic than the identifiability result of LP would suggest. LP clearly issue a warning on overinterpretation of phylogenetic data, but our exploration of pulled rates suggests that it is still possible to get modest (in term of precision) but biologically meaningful information about variation in diversification rate. Given the difficulty of the interpretation of r_p , further work should be done to better understand the behavior of this composite parameter under different scenarios.

In summary, pulled rates are advantageous because they are nonparametric estimates that do not suffer from unidentifiability issues and they can be estimated using only information contained in the LTT plot. However, they cannot be directly interpreted in biologically meaningful terms. To estimate rates that are meaningful (e.g., λ , μ , and r) we need to make further assumptions such as constant rates of speciation and extinction over time. Likewise, if we wish to test hypotheses about species diversification using pulled rates it will be important to remember that such parameters are complicated transformations of the traditional rates we are familiar with. Framing and testing hypotheses with pulled rates is currently possible but will be challenging until we get a better grasp of their nature and utility. To alleviate this issue, we call for a more thorough investigation of the relationship between traditional and pulled rates during scenarios of interest (e.g., Fig. 5) with extensive

simulations to make them more tractable and easier to interpret. Furthermore, we need studies on their inference and performance using phylogenetic trees based on empirical data.

Diversification Rates Vary among Clades

An LTT plot is a simplified way to visualize and summarize a time-calibrated phylogenetic tree, which relies on the assumption that all lineages diversify at equal rates (Morlon et al. 2011). Thus, under the assumption that λ and μ are clade-independent, LP showed that the LTT plot contains the complete information about the underlying branching process (see also Lambert and Stadler 2013). This provided the opportunity for LP to show mathematically how LTTs can lead to misinterpretation. Though the LTT plot is appropriate for a clade-independent framework, such as in LP, it lacks information that is critical for much of the macroevolutionary modeling done today. For example, useful information from extinct species such as fossils can play no role. More importantly, it does not take rate variation among lineages into account, so it is impossible to identify such variation on different parts of the tree from which the LTT was plotted.

LP show how we can test hypotheses about whether diversification rates deviate from constancy over time using pulled rates. We would be unable to pin this on changes in speciation or extinction rates, but would

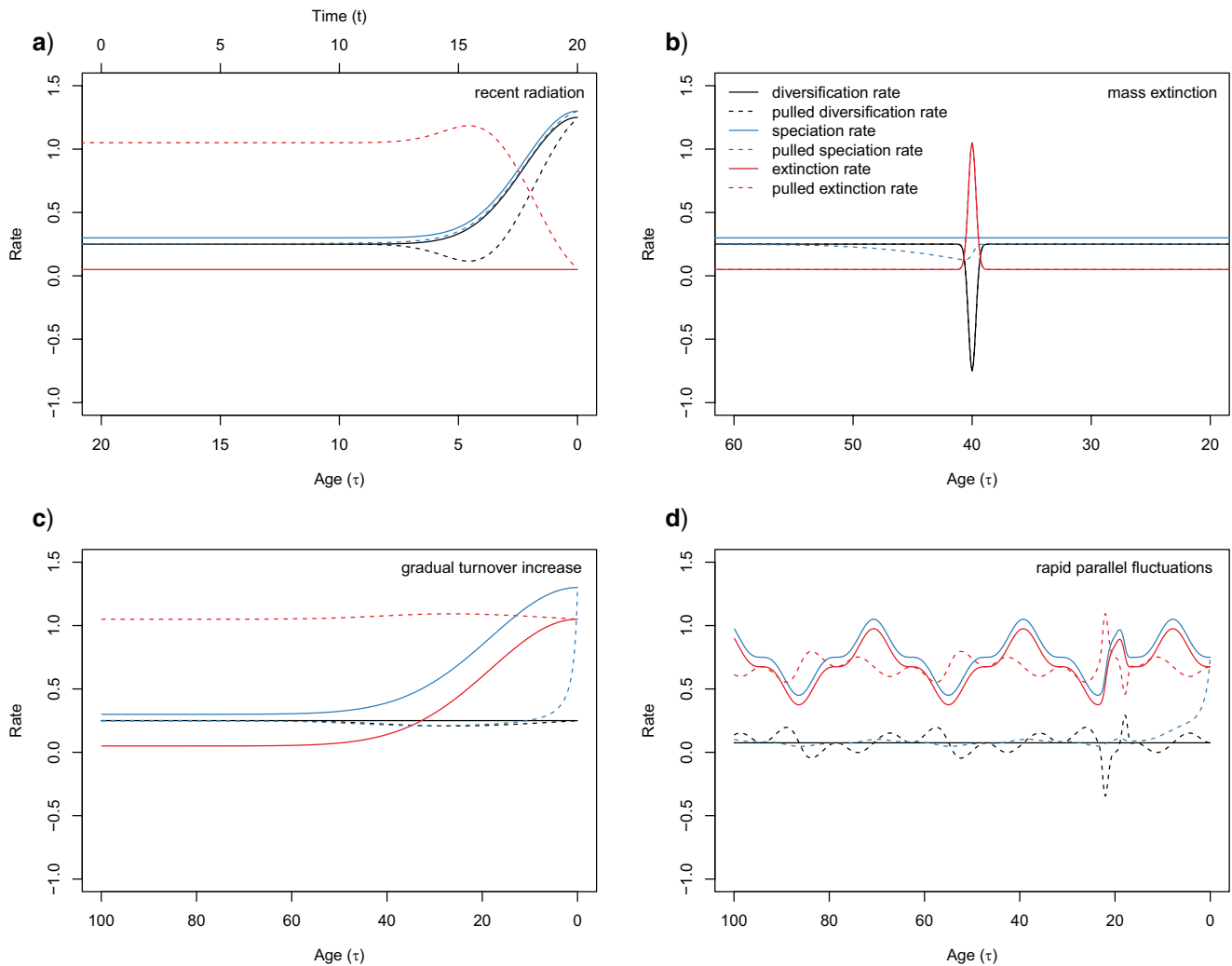


FIGURE 5. Comparison of traditional and pulled rates under five simulated diversification scenarios that are commonly investigated (a–c) and a final, more complex scenario. Panel a) shows a recent radiation where diversification rate and speciation rate sharply increase towards the present. An additional axis, at the top of panel a) shows time going forward (t). Panel b) shows a mass extinction event at 40 Ma in which extinction rate briefly but rapidly increases and then falls back to previous levels. Panel c) shows a gradual increase in species turnover rate (both speciation and extinction rate increase slowly over time). Panel d) shows a scenario where speciation and extinction rates are rapidly varying in parallel to each other. This results in a constant diversification rate (r) and a fluctuating pulled diversification rate (r_p).

get a sense of how variable diversification has been (Burin et al. 2019). This would be useful for testing whether diversification in particular clades has remained constant or been subject to large shifts in diversification (e.g., mass extinctions) but not when diversification rate has shifted in a subclade (e.g. due to the evolution of a key innovation).

The first use of pulled rates was in Louca et al. (2018), where they studied bacterial diversification, stating “Our findings suggest that, during the past 1 billion years, global bacterial speciation and extinction rates were not substantially affected during the mass extinction events seen in eukaryotic fossil records.” This might suggest that nothing particularly extraordinary happened in the macroevolutionary dynamics of bacteria in the last billion years. However, it is important to note that to be able to infer how rates vary over time, the framework used in Louca

et al. (2018) and Louca and Pennell (2020) makes the assumption that rates do not vary among clades. Louca et al. (2018) touch on this point themselves: “It is possible that diversification within individual bacterial clades may have been influenced by eukaryotic radiations and extinctions, and that these cases are overshadowed when considering all bacteria together.” The rates estimated using such clade-independent models will correspond to the average rates over time in the entire study group, therefore missing out on any variation among clades—for example any difference in diversification rates between those species that use terrestrial versus marine environments (Louca et al. 2018). Subclades are important in driving inferred diversification patterns (see Morlon et al. 2011; Maliet et al. 2019; Rabosky 2020), so ignoring this variation may mean that we miss out on influential and interesting dynamics when using pulled rates. Such an assumption

enables us to investigate patterns of diversification through time but prevents us from investigating some of the most interesting and fundamental questions in macroevolutionary biology, notably, why are some clades more diverse than others?

To demonstrate how contrasting patterns of speciation and extinction can produce the same LTT plot, LP used a large phylogenetic tree of seed plants (Smith and Brown 2018) that contained 79,874 species. These range from small ephemeral plants like *Arabidopsis thaliana* to gigantic, long-lived trees such as *Eucalyptus regnans*. A large amount of research has shown that diversification rates have varied significantly among seed plant clades (e.g., O'Meara et al. 2016; Igea et al. 2017; Vamosi et al. 2018; Onstein 2020; Soltis et al. 2019; Magallón et al. 2019; Zenil-Ferguson et al. 2019). By assuming that rates are clade-independent we can use pulled rates to get a global view of what has happened in seed plants, but this goes little way towards understanding the evolutionary processes that have shaped their diversity.

Fortunately, the assumption of clade-independent rates is not common in modern approaches. Some models assume that rates are both clade-dependent and time-dependent such as Bayesian Analysis of Macroevolutionary Mixtures (BAMM) (Rabosky et al. 2013; Rabosky 2014), relaxing the assumption that all lineages share the same evolutionary rates at a given point in time (Rabosky 2017). This is a key difference from the models used in LP because it allows lineages to differ in their rates of speciation and extinction. With BAMM, the entire phylogeny could be described using a model similar to what is used in Louca and Pennell (2020), or alternatively, it could be described using multiple processes that explain rates of diversification on different parts of the tree. Within each of these processes, λ and μ are still susceptible to the same unidentifiability issues outlined in LP because they are usually estimated from extant timetrees. However, BAMM makes use of the full topology that includes information (e.g., branch lengths) that an LTT lacks and also allows for clade-dependent rates. Often, the goal of using such approaches is to determine whether one clade is diversifying faster than another. While LP are concerned with estimating exact, identifiable estimates of diversification rate parameters this may not be important if what we are actually interested in is the difference between diversification rates in two clades e.g. are diversification rates always higher in clade A than clade B? These are two fundamentally different goals that, at the most basic level, require different models and assumptions to assess. Understanding the interaction between clade-dependent and time-dependent rates is an important avenue of future research and will make issues raised in LP more relevant to the richer, more modern modeling approaches used today.

Time-Independent, Clade-Dependent Models Are Not Implicated

Another class of models are those that allow rates to vary among clades but keep them fixed over time.

Among them is the Binary-State Speciation and Extinction (BiSSE) model (Maddison et al. 2007), part of a family of models known as the state-dependent models of diversification (SSE models; Ng and Smith 2014; Beaulieu and O'Meara 2016; O'Meara and Beaulieu 2016; Caetano et al. 2018). These models are extensions of the birth–death model that also include information about character states of extant species. SSE models jointly estimate ancestral states at each node of the phylogenetic tree, rates of transition between character states, and state-dependent diversification rates that remain constant through time. As in BAMM, BiSSE makes use of evidence not included in the LTT, such as the full tree topology (Maddison et al. 2007). It also considers character state evolution, rather than just the timing of branching events as in the LTT plot. LP suggest that it remains unclear how the dependence on character states (which, if removed, collapses equations in BiSSE to those shown in Nee et al. (1994)) affects the unidentifiability issues they highlight. They go on to state that the likelihood functions of SSE models are too complex to be addressed in their study, but suggest that the same problems they uncover probably still apply.

Here, we argue that this may not be the case. Unlike BAMM, SSE models such as BiSSE are not richer versions of the framework used in LP, they are members of a different class of models. In this case, the assumed time-independence and the clade-dependence of rates are the inverse of the assumptions at the base of LP. SSE models examine rate variation that is impossible to detect when summarizing a tree with just one LTT, so it does not follow that issues found in the single LTT-based framework in LP apply. The assumption of time-independence in SSE models is important because it allows traditional rate parameters to be identifiable. Depending on our knowledge of sampling fraction, this may be all traditional rates, or net diversification rate only (Table 1). As an example, recall that LP show that λ equals λ_p when i) sampling fraction is 100% and ii) $\mu = 0$. Complete sampling was assumed in the original BiSSE model (Maddison et al. 2007), though it has since been relaxed (FitzJohn et al. 2009) so that a given sampling fraction can be assumed instead. Extinction can be set to 0 in SSE models, as this is a constant rate, and enables the estimation of λ (e.g., Joly and Schoen 2021). Therefore, under the conditions outlined in LP, SSE models can estimate λ , and therefore μ and r as well. Similarly, r_p equals r when λ is constant, which is also an assumption in BiSSE (and any other time-independent model) and suggests that BiSSE produces an identifiable estimation of r . It is clear from these examples that using time-independent, clade-dependent approaches like BiSSE can overcome (or pre-empt) the unidentifiability issues raised in LP because they allow the congruence class to collapse to a single model. However, this does not mean that BiSSE actually estimates the different diversification rates of a clade correctly; LP's results show we should take these BiSSE estimates as proxies. Users of SSE-like models should therefore take care when interpreting values of

rate parameters that are time-independent as we know that diversification rates can vary over time. Moreover, many studies report whether diversification rates among groups are significantly different, rather than speciation and extinction rates (cf [Onstein 2020](#)), as it is generally acknowledged that it is difficult to disentangle speciation and extinction (see also [Burin et al. 2019](#); [Louca and Pennell 2021](#)). It is indeed possible to extend SSE models to estimate time-dependent speciation and extinction rates ([Rolland et al. 2014](#); [Condamine et al. 2017](#); [Meseguer and Condamine 2020](#)) but such models likely suffer from the unidentifiability issues formalized in LP. However, we stress that the likelihood of time-dependent diversification models (as in LP) is not the same as the likelihood of clade-dependent diversification models (e.g., typical SSE models), and what is unidentifiable in the former does not tell us about identifiability in the latter.

Overall, the issues raised in LP cannot yet be readily applied to commonly used macroevolutionary approaches without further work to show that criticisms related to approaches that assume rates are time-dependent and clade-independent (i.e., the LTT) are applicable to these richer or altogether different models. Yet, even if unidentifiability issues remain in such models they may not be relevant to the questions the models were built to answer, for example when the objective is to determine whether one clade has higher diversification rates than another. In cases like these, it is not the precise values of rates that are important but instead the rate difference that is, whether rates in one group of lineages are higher than another. Perhaps most importantly, this means that we should not forego building models that estimate diversification rates because one, relatively simplistic approach has long-standing problems ([Kubo and Iwasa 1995](#)) but instead continue to improve them and build upon the work done in LP. A case in point is the issue of false positives when using SSE models that was raised by [Rabosky and Goldberg \(2015\)](#). This criticism spurred on innovation that led to the development of models with hidden states ([Beaulieu and O'Meara 2016](#)), which are now present in various new incarnations of the SSE approach (e.g., [Caetano et al. 2018](#); [Herrera-Alsina et al. 2019](#)).

On the Use of Models

The discussion sparked by LP highlights an important issue: evolutionary biologists should be interested in the actual history of diversification of the clades they study but, at the same time, must keep in mind that this history is difficult to infer. The framework developed by [Louca et al. \(2018\)](#) shows how to do this using the shape of the LTT plot, without making strong assumptions about past speciation and extinction rates. Indeed, the slope and curvature of the LTT plot contain useful information about the diversification history of the clade. Much of the debate, however, focuses on the ability to recover a “true” history of diversification. The goal of a scientific

study should be to find out what really happened, but it becomes confusing if one considers a simulated birth–death process as the “true” history. This birth–death process is determined by two parameters (λ and μ) that can vary over time, and these parameters are supposed to correspond to the rate that a lineage splits into two lineages, or goes extinct. In reality, however, a species does not have a speciation and an extinction rate in the same way it has a geographic distribution and a population size. These rates only make sense when they are aggregated over a number of species and a certain amount of evolutionary time. That is, they are descriptive statistics summarizing much more complex processes that are acting at the microevolutionary level, and that would eventually lead to speciation or extinction. LP convincingly show that one cannot estimate these statistics reliably from LTT plots, and thus propose statistics that can be estimated more reliably. That these alternative statistics do not exactly correspond to the parameters of the birth–death process is not a problem; the birth–death process is only a model of diversification, and not the truth about diversification itself. The framework built by [Louca et al. \(2018\)](#) and LP allows us to use the LTT plot to test whether diversification rates were constant or not. If researchers want to understand how speciation and extinction actually changed to give rise to a diversification history, they will have to use other methods and data.

CONCLUSION

[Louca and Pennell \(2020\)](#) have pointed out key issues with how we approach macroevolutionary modeling, namely the inability to distinguish historical diversification scenarios under certain circumstances. Their formalization of the unidentifiability issues in models with time-dependent, clade-independent diversification rates is an important step forward that provides the mathematical tools to study the associated issues further. LP highlight the avenues we must consider and develop upon to ensure we do not make similar mistakes in the future. Whether variation in diversification rate is due to changes in speciation or extinction is certainly an interesting avenue of research, but LP have shown that exploring this would require much more than just fitting a model with speciation and extinction rates to an LTT plot. Indeed, more recent diversification models go beyond this by making use of additional information that is ignored by models relying only on an LTT. Awareness and consideration of potential unidentifiability issues is important for macroevolutionary biologists going forward when they employ such models of diversification. However, it is important to note that LP do not show that speciation and extinction rates cannot be estimated with evolutionary trees ([Pagel 2020](#)). Instead, they show that when using extant timetrees under the assumptions of an LTT-based approach, unidentifiability issues are encountered in the estimation of speciation and extinction rates, and that these problems can be

circumvented by making use of pulled rates, or by making other assumptions. Further work is needed to identify the extent to which the issues raised in LP apply to the more complex models of diversification used today. Comparisons should be made in empirical studies that use both traditional and pulled rates, to see if differences in results exist between these approaches in practice. In the meantime, it is important that the field continues to grow by using and building upon modern macroevolutionary methods, albeit with a critical eye.

CODE AVAILABILITY

Code associated with this manuscript is available from the following rcompendium: <https://github.com/ajhelmstetter/pulledRates>.

SUPPLEMENTARY MATERIAL

Supplementary text and data are available through the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5tb2rbp4g>.

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