Systematic Biology
75th Anniversary

Syst. Biol. 75(3):391–405, 2026
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https://doi.org/10.1093/sysbio/syaf086
Advance Access publication December 5, 2025

An Evolving View of Lineage Diversification

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Received 21 July 2025; reviews returned 20 November 2025; accepted 25 November 2025
Associate Editor: Michael Landis

Abstract.—Systematists have long been fascinated by the astounding variation in species diversity across the various branches of the tree of life, a net result of the uneven rates at which lineages undergo speciation and extinction over time. The past 30 years have seen the development and widespread application of tools that allow diversification to be quantified and characterized in empirical data sets. These advances have, in turn, enabled the statistical evaluation of hypotheses about the causes behind the uneven distribution of species richness among lineages, leading to a more nuanced understanding of diversification rate variation, as reflected in an ever-expanding literature. Here, we provide a brief review of the current understanding of these models, the types of questions they address, and some of their collective limitations, with a focus on tree-based analyses of reconstructed phylogenies. Based on this overview, we outline future considerations in the lineage diversification research program, including the potential for machine learning to revolutionize the field by making model selection and parameter estimation more efficient in highly complex models. We interpret the recent slowdown in publication pace as a sign of a maturing field, where systematists are taking a step back after becoming better equipped to understand the technicalities and current limitations of these methods, leading to more careful applications and a greater embrace of uncertainty. [Birth–death process; diversification; extinction; macroevolutionary rates; speciation.]

The Central Role of Lineage Diversification in Systematic Biology

Determining the factors responsible for the rich diversity of life forms around us inspires much of the work of systematic biologists. Often, this diversity is quantified as the number of different species that exist at any point in time or space. Evidence from the fossil record and geographical distributions shows that species longevity is variable and that the number of species alive is constantly changing through time as new species are formed while others go extinct. The tree of life is full of examples of imbalanced clade richness, such as highly species-rich groups that are sister to—sometimes dramatically—more depauperate clades (i.e., placental mammals and marsupials, Upham et al. 2019; squamate reptiles and the tuatara, Miller et al. 2009; *Amborella* and all extant angiosperms, Sauquet et al. 2017; Fig. 1). Such imbalance indicates that closely related lineages can diversify under dramatically different diversification regimes throughout their evolutionary history, motivating further exploration of rate heterogeneity within and across these groups.

Fascinated by these observations, systematists have long sought to characterize and identify mechanisms leading to the unevenness in the numbers of lineages and species among clades. The focus of lineage diversification research stems from our interest in understanding how rates of speciation and extinction vary through time, among clades, across geographic scales, and in relation to traits. In this Evolving View, we present an overview of the history of lineage diversification research with an explicit focus on tools and models that rely on reconstructed phylogenies—that is, phylogenies composed only of sampled, typically extant species—which is the primary source of data for much of the modern studies on lineage diversification (but see Silvestro, Salamin, et al. 2014). It has been increasingly recognized that analyses relying solely on reconstructed phylogenies from extant taxa pose challenges to the robust inference of diversification history (see Marshall 2017), a point we acknowledge and address in various sections throughout this perspective. First, we discuss a few important historical studies that introduced formal quantitative approaches to the study of diversification. Then, we highlight newer methods that attempt to bring diversification analyses closer to biological realism by incorporating heterogeneity in terms of both "tempo" (heterogeneity as large shifts or as a continuous process) and

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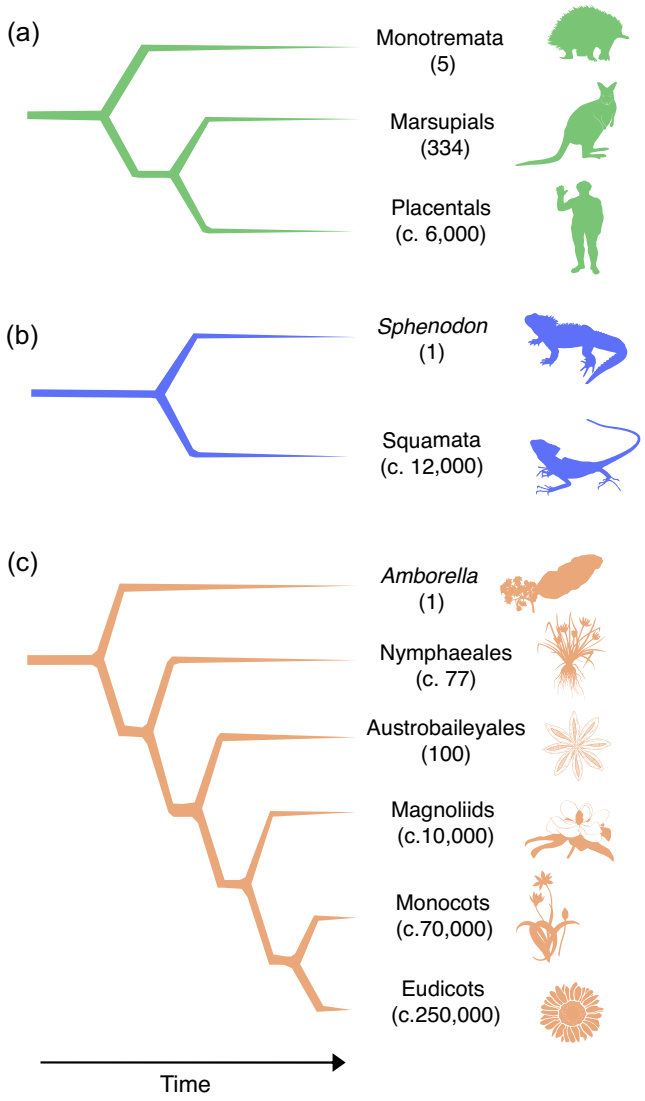


Figure 1. Examples of unbalanced diversity across the tree of life. Numbers between parentheses indicate the number of described extant species in each group: (a) mammals; (b) Lepidosauria; and (c) angiosperms (simplified). Examples are primarily intended to showcase disparities in species richness among sister clades and branch lengths do not reflect real units of time. Silhouettes from phylopic.org.

"mode" (e.g., time-dependence, diversity-dependence, clade-dependence, trait-dependence of rate variation). Finally, we discuss some of the major criticisms and overall emerging directions in the field of diversification modeling. Importantly, this review is not intended to provide an exhaustive list of the methods available to the community, as such a list was recently reviewed in Morlon et al. (2024). As an Evolving View, we present an extended discussion from our different perspectives, aiming to offer a concise historical overview of this evolving field, highlight its major milestones, and indicate potential future directions. We focus exclusively on tree-based diversification models, and do not include the rich paleontological literature on occurrence-based approaches for studying diversification (e.g., Sepkoski et al. 1981; Foote 2003; Alroy et al. 2008).

Modeling Diversification as a Simple Birth–Death Process

Speciation and extinction events of most lineages cannot be directly observed as they are historical events that often unfold over long evolutionary timescales. This has led systematists to adapt probabilistic models and computational tools to infer the scale at which these processes have unfolded over time. Generally, this is achieved by modeling scenarios that optimize the likelihood function or posterior distribution of observing a phylogenetic tree for particular speciation and extinction rate values. To that end, most tools used to model diversification descend from the stochastic birth–death model first mathematically characterized by William Feller (1939). Feller's advance merged ecological ideas through models of population growth with extinction of individuals in the population, while assuming that populations were infinitely large to leverage new developments in measure (probability) theory (Kolmogoroff 1931). The stochastic birth–death model is often attributed first to Kendall (1948) because he generalized the birth and death rates to be functions of time and not constant as assumed by Feller (1939), and perhaps because Kendall's work was available in English, unlike Feller's German publication. Kendall's birth–death model has historically been cited next to Yule's 1925 contribution of the birth deterministic model (Yule 1925). However, Kendall was only aware of Feller's ideas on population ecology and stochastic models (acknowledged in the first paragraph of Kendall 1948) but not Yule's contributions at the time he formalized the birth–death process (Pennell and MacPherson 2025). Yule's birth model addressed the birth of new species given the age of a clade (making a clade equivalent to a genus) to show that a clade's age does not necessarily determine its geographic range (Pennell and MacPherson 2025). In systematic biology, birth–death processes started making their way in discussions at the historical Woods Hole Group in the 1970s where a group of paleontologists became interested in creating falsifiable hypotheses of tree shape through quantitative approaches (Mooers and Heard 1997). In particular, the resulting work of Raup et al. (1973), stemming from two Woods Hole Marine Laboratory meetings, and Yule's work about the complex relationship between a clade's age and its geographical distribution, explained phylogenetic diversity through a series of simulations that assumed three key processes: all lineages have a common ancestor, new lineages branch from a preexisting lineage, and lineages can be terminated at any point in their history. Raup et al. (1973)'s simulations provided specific time intervals where three events, extinction, persistence, or branching, could occur based on random numbers. Although

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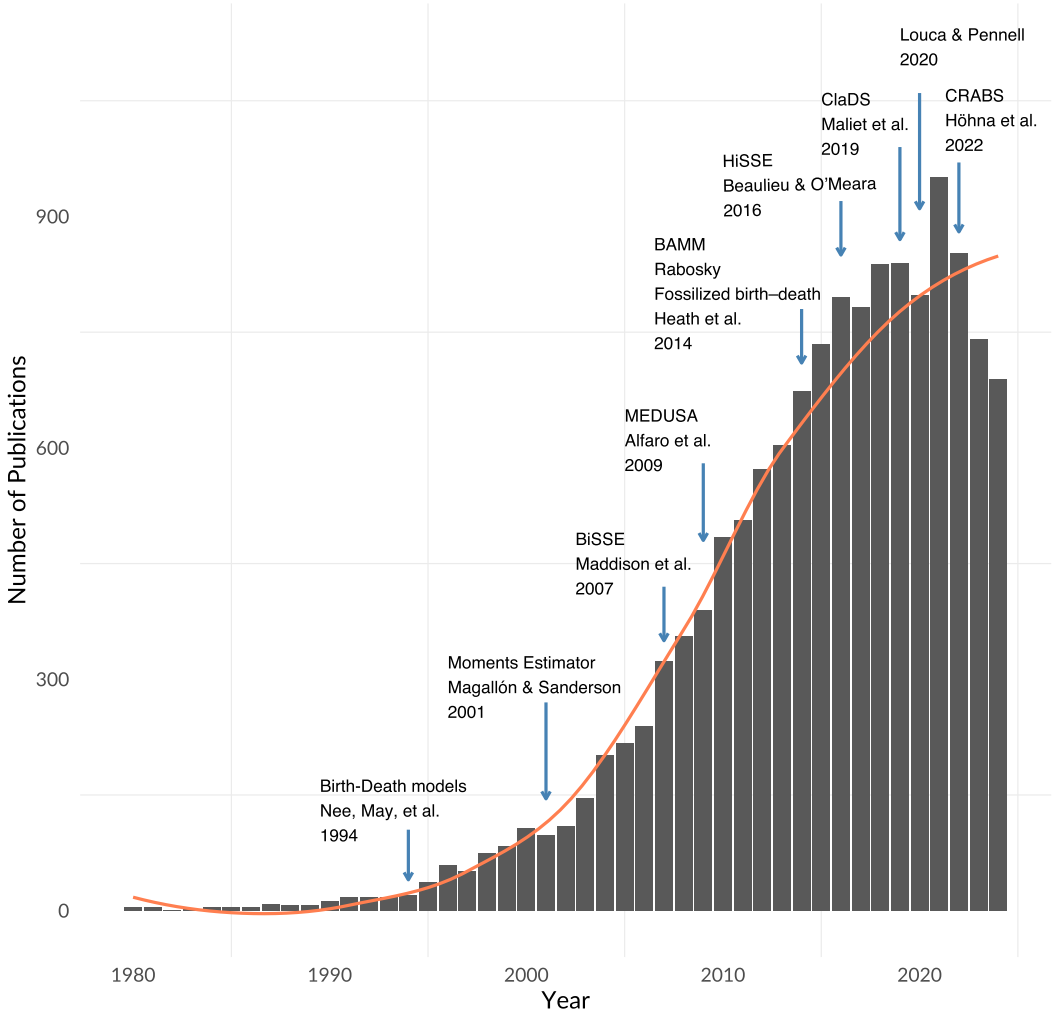


FIGURE 2. Number of publications containing the search term "diversification rates" from the Web of Knowledge (Clarivate) in the last 45 years (smooth function as bold line). We have highlighted a subset of foundational peer-reviewed articles in the field of diversification that have shifted the way we approach inferences of speciation and extinction rates.

this approach is not a stochastic birth–death model simulation (because waiting times for an event are fixed in the simulation rather than being drawn as random variables), this simulation opened the door to statistical inferential approaches to understand phylogenetic tree shape as a birth and death process.

The earliest empirical studies applying birth–death models to explore lineage diversification emerged in the 1990s and early 2000s, laying the groundwork for the field over the following three decades. These approaches were significant because they permitted the estimation of phylogeny-wide diversification rates under the assumption of constant rates (Nee et al. 1992) and using only species richness and clade age (Magallón and Sanderson 2001). Notably, the apparent simplicity in the first sentence from Nee et al. (1992) "*Have rates of cladogenesis changed through time, and if so, why?*", inadvertently sparked a new field in systematic biology (Fig. 2).

Using one of the earliest avian phylogenies (Sibley and Ahlquist 1990), Nee et al. (1992) assumed that molecular phylogenies contained information about the "effective rate of cladogenesis"—a parameter that was interpreted as the rate at which extant lineages gave rise to new extant lineages. In their implementation, the effective—and instantaneous—rate of cladogenesis is defined as the difference between the birth and death rate parameters of a birth–death model, known as the net diversification rate. Shortly thereafter, the "reconstructed evolutionary process" was introduced as the framework for the constant-rate birth–death model (Nee, May, et al. 1994). This work not only derived the likelihood function for estimating speciation and extinction rates but, in concert with Nee, Holmes, et al. (1994), also offered insights into a well-known pattern observed in reconstructed phylogenies. These studies suggested that when a lineage-through-time plot is generated—that is,

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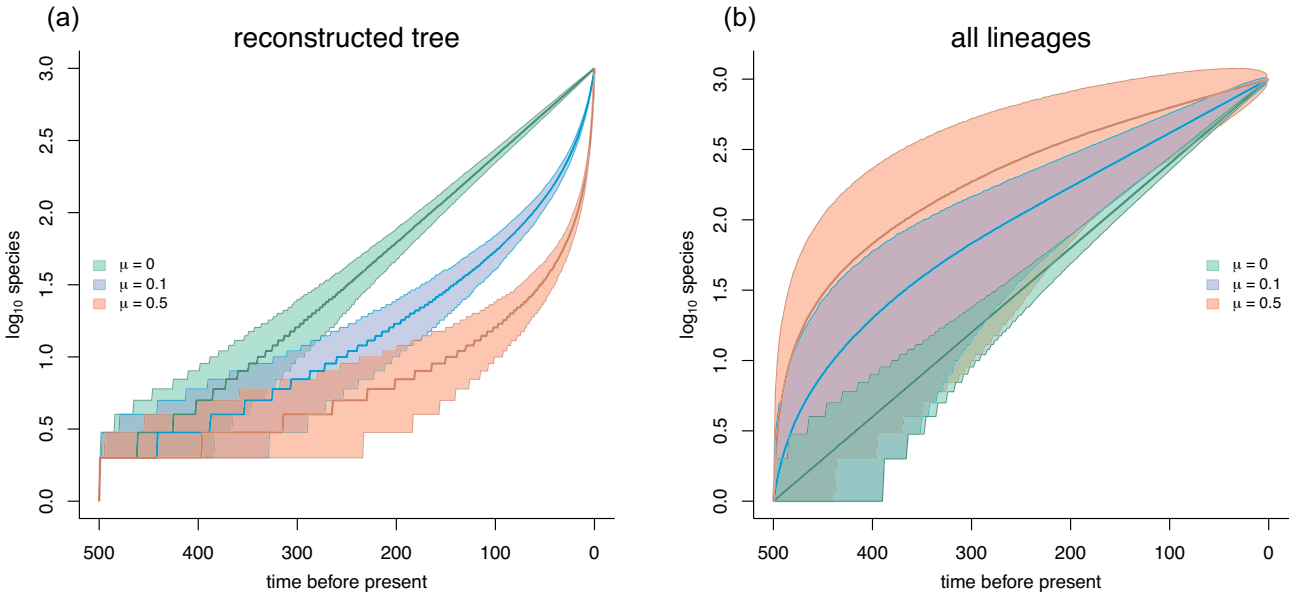


FIGURE 3. Lineage-through-time (LTT) distributions under three different extinction rates, for 1000 simulated trees. In panel (a), the "pull of the present" becomes increasingly clear as the rate of extinction (μ) increases. Unlike in panel (a) where the number of lineages through time pertains to the reconstructed phylogeny, in panel (b) LTT trajectories track all species present at a given time (including extinct lineages), showcasing an increasing signature of the "push of the past" as extinction rate increases. Speciation rates were set to the maximum likelihood value under the given extinction rate, 500 time-steps, and a target extant richness of 1000 species. Envelopes represent 95% confidence intervals. Parameter values were replicated from Budd and Mann (2018).

a cumulative count of lineages through time—a rapid accumulation of lineages toward the present is typically observed. This pattern, known as the "pull of the present" (Fig. 3a), occurs because recent lineages have experienced less overall extinction, driving up the rate of cladogenesis (Nee et al. 1992; Nee, Holmes, et al. 1994). Conversely, a related concept, the "push of the past", describes a survivorship bias resulting from focusing on clades that survived long enough—either to fossilize or persist to the present—due to an elevated number of early speciation events (Budd and Mann 2018) (Fig. 3, Nee, Holmes, et al. 1994). Further, Nee, Holmes, et al. (1994) also proposed that extinction ("death") rates can in principle be estimated from empirical reconstructed trees, although the reliability of such estimates is a focus of considerable debate as we discuss in a later section of this overview. Building on these foundational insights, several current models for estimating the pace of evolution descend from these ideas of the effective rate of cladogenesis, reconstructed process, and lineages-through-time, including methods that explore how clades, time, or traits might modify the pace of this rate (Nee 2006; Morlon 2014; Fig. 2).

Another foundational study was conducted by Magallón and Sanderson (2001), who were some of the first systematic biologists to apply quantitative approaches to measure diversification rates in one of the richest clades in the tree of life: the angiosperms. In this work, the authors leveraged known probabilities and summary statistics from the stochastic birth–death model to calculate diversification rates. In the absence of explicit information about clade diversity over time, Magallón and Sanderson (2001) proposed a method-of-moments to estimate the difference between birth and death rates (net diversification) for a crown group, which is the logarithm of the total of species minus two divided by the age of the phylogeny. This simple metric gained popularity in the systematists' toolkit as it offered a straightforward way to quantify net diversification rates from readily available data, and it remains relevant in certain scenarios even today (see prior distributions in Zenil-Ferguson et al. 2023).

Toward Biological Realism: Modeling Heterogeneity in the Diversification Process

The foundational study by Nee et al. (1992) demonstrated that speciation and extinction rates could be estimated from extant trees using equal rates birth–death models, and after that the estimation of diversification rates became an active pursuit of many systematists. However, these early approaches assumed that all lineages within a clade share a single, constant rate of diversification, which is unlikely to be biologically realistic (Ricklefs 2007; Alfaro et al. 2009). The same is true for the method-of-moments estimator of Magallón and Sanderson (2001): the metric is useful under the assumption of zero-valued or known constant extinction fractions, but these assumptions also rarely characterize empirical data where rates are likely to vary, often sharply,

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through time (Morlon 2014). For instance, the Chicxulub impact nearly 66 Ma triggered the K-Pg mass extinction of three-quarters of living taxa, including all non-avian dinosaurs (Morgan et al. 2022), followed by a rapid pulse in speciation rates in other clades (Klein et al. 2021; Foley et al. 2023; Berv et al. 2024; Quintero et al. 2024). Plate tectonics, mountain building and erosion, as well as climatic fluctuations, have all led to changes of varying magnitude in the accessibility and connectivity of regions and landmasses (Hoorn et al. 2010; Mazel et al. 2017; Antonelli, Kissling, et al. 2018). Furthermore, fragmented or unstable landscapes can lead populations within a species to continuous cycles of geographic isolation and gene flow interruption. This process often results in the formation of short-lived metapopulations, which increases the chances of both speciation (through isolation) and extinction (due to small population sizes) (Gittenberger et al. 1991; Vasconcelos et al. 2022). This shifting biogeographic landscape and the ensuing reorganization of species' distributions are all likely to lead to major changes in rates of both speciation and extinction through time (as observed with both fossil and phylogenetic evidence—Antonelli, Zizka, et al. 2018; Quintero and Jetz 2018; García-Rodríguez et al. 2021; Hagen et al. 2021; Hoorn et al. 2023).

Beyond biogeographic factors, key innovations have played a critical role in the general conceptualization of adaptive radiations, where a single ancestral species diversifies rapidly to occupy diverse new niches, thanks to a novel trait or ability (Schluter 2000). Empirical and theoretical developments have both explored this topic in the context of how the emergence of such a trait or ability could lead a clade to undergo a major ecological shift (Weber and Agrawal 2014; Miller et al. 2023), enabling it to enter new adaptive zones (Simpson 1953; Schluter 2000). Such fundamental changes in how species interact with their environment and resources also have the potential to impact net diversification rates (Hunter 1998), leading to shifts into a new diversification regime and decoupling speciation and/or extinction dynamics of a clade from the broader phylogenetic context within which the clade is embedded (although such impacts on diversification in and of themselves are not required to define a key innovation; Givnish 2015; Rabosky 2017). In either case, recurrent evidence from both extant and extinct groups suggests that clade-specific and time-variable diversification are common and necessary to obtain biologically realistic estimates (Alfaro et al. 2009; Foley et al. 2023; Berv et al. 2024; Quintero et al. 2024).

In other words, the simplifying assumption of rate homogeneity of those initial approaches, albeit employed through null models, often departs from biological reality: diversification is rarely uniform, and variation in speciation and extinction rates across lineages or through time is to be expected, particularly across greater phylogenetic breadth (Alfaro et al. 2009). Advances in statistical phylogenetic and comparative methods have also encouraged the field to infer whether differences in clade richness have arisen because of a fundamental change in the diversification process, or if such differences might simply be the result of a stochastic process that does not require any changes to the diversification process at play (Raup et al. 1973). These approaches have shown that clades that we consider depauperate or speciose may simply be the stochastic outcome of a birth–death model of diversification.

Starting in the late 1990s, diversification researchers rapidly developed models that account for factors potentially correlated with shifts in diversification dynamics. In general, three categories of models emerged to explain changes in the mode of diversification: (1) models that assign rate variation to clades or diversity, (2) models that assign rate variation to phenotypic change or biogeographical change, and (3) models that assign rate variation to time. In the following sections, we provide a brief overview of the conceptual background for each model category.

Clade Dependence

Clade-dependent diversification rates can arise through multiple mechanisms, such as when higher speciation rates are observed in clades with greater phenotypic lability (Rabosky et al. 2013; Jablonski 2022; Peoples et al. 2025) or particular genomic structural attributes (e.g., smaller genome size; Kraaijeveld 2010). Several models account for clade-dependent diversification by identifying discrete break points that imply instantaneous shifts in diversification from homogeneous trends (Alfaro et al. 2009; Stadler 2011a; Rabosky 2014; Laudanno et al. 2021; Barido-Sottani et al. 2020; Magee et al. 2020; Kopperud and Höhna 2025). These approaches identify inferred shift locations on the tree that signal periods in the evolutionary history of a clade that appear sufficiently distinct from the background dynamics to warrant further attention or to form the basis for subsequent hypothesis testing. Systematists quickly embraced these approaches because they created the opportunity to estimate shifts in the pace of diversification and their location on a given phylogeny. Many of the models also provided the field with usable software that enabled applications to empirical systems and visualizations of stochastic maps (Alfaro et al. 2009; Rabosky 2014). From these applications of clade-dependent diversification models emerged the need to correlate these shifts in the tempo of diversification with biotic and abiotic factors. For example, in a study of *Nitrososphaeria* (*Thaumarchaeota*, Archaea), Gubry-Rangin et al. (2015) estimated diversification rates across the phylogeny and found three key shifts in diversification. The estimated diversification rates were then correlated with archaeal environmental factors, revealing that the pH adaptation rate followed the same pattern as the diversification rate changes. This is just one example of an increasingly common approach, where correlations between diversification rates and abiotic or biotic factors

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can be explored, although there is a clear need for other process-based and hypothesis-driven diversification models.

Interestingly, before the development of clade-dependent diversification, a proposal to understand shifts in the timing of diversification attributed to ecological competition was already available via diversity-dependent diversification models (Rabosky 2006a). We describe the origin of diversity-dependent models in its own section below. However, the diversity-dependent diversification ideas that catalyzed growth in fitting explicit diversification models to phylogenies became less popular as attention shifted toward the clade-dependent diversification methods and in light of statistical issues inherent to diversity-dependent parameter estimation (Etienne et al. 2016).

Trait-Dependent Diversification Models

Diversification dynamics are often hypothesized to be influenced by the evolution of specific traits or the colonization of particular biogeographical areas, as these can modify gene flow (e.g., reproductive isolation), species interactions, or survival chances (e.g., extinction risk, Donoghue and Sanderson 2015; Givnish 2015). Characterizing phenotypic traits and the geographical distribution of species in a clade of interest is often already part of a systematist's work, so unsurprisingly the models that integrate diversification, phenotypes, and biogeography—the state-dependent speciation and extinction (SSE) family of models—have become some of the most popular diversification tools currently available (Fig. 2). As the name implies, SSE models were first developed to test the effects of observed character states on speciation and extinction dynamics. The first proposed model, BiSSE (Binary State Speciation and Extinction model, Maddison et al. 2007), was created to address the limitations of sister clade comparisons, a nonparametric tool popular in the 1990s and early 2000s (e.g., Farrell et al. 1991; Barraclough et al. 1998; Vamosi and Vamosi 2005; Paradis 2011). Sister-group comparisons consider sister lineages that differ in the states of a discrete character and ask if they also consistently differ in their species richness. However, this approach has several downsides. First, it can only determine that the net diversification rate of clades in one trait state is higher than clades in the other but cannot distinguish whether this is due to more speciation or to less extinction or to both. Second, because the focal character state needs to be present in the entire clade of interest, labile characters where states differ between closely related species cannot be tested, limiting the scope of questions these methods can address. Third, sister clade comparisons cannot differentiate whether the observed pattern is due to accelerated diversification rates associated with a character state or high transition rates to that character state (Maddison 2006; Käfer and Mousset 2014).

SSE models address these limitations by estimating parameters that simultaneously account for the processes of speciation, extinction, and character evolution. At the time BiSSE was developed, likelihood calculations were already independently available for transition rates between the states of a binary character (Pagel 1994) and for speciation and extinction rates based on extant phylogenies (Nee, May, et al. 1994). The BiSSE model proposed a likelihood calculation that combined both; this was later extended to address questions about the evolution of characters with multiple states (MuSSE, FitzJohn 2012), states that undergo cladogenetic change, including biogeographical ones (ClaSSE and GeoSSE, Goldberg et al. 2011; Goldberg and Igić 2012; Magnuson-Ford and Otto 2012; Caetano et al. 2018; Landis et al. 2022), and continuous characters (QuaSSE, FitzJohn 2010). However, Rabosky and Goldberg (2015, 2017) found that diversification rate heterogeneity could be spuriously linked to a trait under study—regardless of its relationship with that rate heterogeneity—resulting in model inadequacy and high false positive rate. This led to the development of subsequent extensions of "hidden state" models that can better accommodate diversification rate heterogeneity, for example, with the use of latent variables (Beaulieu and O'Meara 2016; Caetano et al. 2018), although further caution is warranted in general (see Mynard et al. 2023).

Time and Diversity Dependence

The majority of the models we have discussed so far treat diversification rates as time-constant (Alfaro et al. 2009; Höhna et al. 2019; Maliet et al. 2019; Vasconcelos et al. 2022; Kopperud and Höhna 2025; SSE models—see references in the section above). However, diversification rates can change over time, for example, if there is diversity-dependent diversification (Rabosky 2006a). Assuming a constant rate of both speciation and extinction is useful mathematically, but typically not biologically realistic, as diversification rates can accelerate or slow down due to factors such as the inability of lineages to survive changing environments and niche saturation due to competition (Moen and Morlon, 2014; Cutter and Gray 2016; Crampton et al. 2018; Anderson et al. 2023). In particular, diversity-dependent models (Rabosky 2009, 2017) draw inspiration from adaptive radiations (Schluter 2000) where ecological opportunity is considered the primary driver of diversification (but see Germain et al. 2021). For instance, Phillimore and Price (2008) showed that avian phylogenies exhibit declining diversification rates over time due to ecological niche saturation. Cautious interpretation of diversity-dependent models is warranted; however, as Etienne et al. (2016) showed that parameter estimation (carrying capacity) can be biased when diversity-dependent diversification models are conditioned on survival given the crown age. Furthermore, Pannetier et al. (2021) have shown that diversity-dependent

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models are very difficult to distinguish statistically from more mechanism-agnostic time-dependent models, which do not account for any ecological processes, but simply allow diversification rates to vary with time.

Rapid diversification followed by a slowdown in rates toward the present is a common feature across the tree of life (Moen and Morlon 2014; Morlon 2014), observed in the fossil record (Stanley 1973; Sepkoski 1998) as well as in molecular phylogenies (Weir 2006; Phillimore and Price 2008; Etienne and Rosindell 2012). This presented a need for flexible tools allowing for both diversification rate shifts in clades and time-varying rates. Two key tools addressed these requirements: LASER (Rabosky 2006b) and BAMM (Rabosky 2014). Initially, LASER offered a straightforward way to contrast alternative scenarios of temporal rate heterogeneity through alternate rate-variable models of diversification (e.g., diversity-dependent and multi-rate birth–death models). Subsequently, the flexibility and usability of BAMM for the detection of independent diversification regimes across a phylogeny, along with the estimation of speciation and extinction rates that can vary both among clades and through time, led to its widespread adoption for systematic studies (Fig. 2). With these developments, the detection and characterization of time- and clade-dependent diversification were possible in large trees (e.g., Jetz et al. 2012; Alencar et al. 2016; Condamine et al. 2016; Testo and Sundue 2016; Economo et al. 2018; Rabosky et al. 2018). Further technical advances like Morlon et al. (2011), extended by Mazet et al. (2023), introduced a multi-rate shift model that explicitly allows for declining diversification through time, but requires *a priori* specification of potential shifts at nodes, where AIC-based (Akaike Information Criterion) model selection is used to find the optimal combination of shifts.

Diversification Heterogeneity: Rare Big Shifts or Continuous Small Shifts

Although clade-, trait-, and time/diversity-dependent approaches have long been recognized, their integration has been somewhat limited. As systematists dive deeper into the biology of their focal groups, there has been a natural interest in models that take a more flexible view of diversification. These nuances are especially relevant, given empirical observations that rate changes may be correlated with a confluence of factors instead of single causes (Donoghue and Sanderson 2015; Nürk et al. 2020). For instance, consider a species whose populations occupy different habitats. Local adaptation to these distinct environments initially drives divergence in traits related to life in each habitat, which may lead to assortative mating, reduced gene flow, and eventually speciation (Coyne and Orr 2004). As these recently diverged species continue to evolve in their respective habitats, they may encounter varying ecological opportunities or carve out new niches causing the probabilities of speciation or extinction to fluctuate continuously over time. When viewed across long timescales, these population-level dynamics can produce diversification patterns that are far more complex than those captured by models based solely on traits, geography, or clade-level factors. In such contexts, the cumulative effects of population-level processes on diversification rates can blur the distinctions between these categories of diversification rate heterogeneity.

In this way, beyond the "mode" of diversification, systematists have also been interested in understanding its heterogeneity in "tempo", that is, whether changes in diversification across clades and/or over time occur via infrequent punctual discrete shifts, or as a smoother, continuous process. On one hand, entire research programs have been centered on locating and framing diversification shifts in the context of Earth's history—continental drift and climatic changes, the rise and fall of other clades—as well as the inferred appearance of putative innovations and traits of interest (Alfaro et al. 2009; Etienne and Haegeman 2012; Rabosky 2014; Silvestro, Zizka, et al. 2014; Höhna et al. 2019; Mitchell et al. 2019; Laudanno et al. 2021). Whether or not to estimate rate shifts across the phylogeny is of both conceptual and practical importance, as inferring such shifts implies an emphasis on major events of considerable impact in the diversification history of a group.

On the other hand, many approaches dispense with the inference of discrete rate shifts and are predicated on a view that changes in diversification are not just the product of major rare events, but that a myriad of factors might also lead to large and small changes to the diversification process (Maliet et al. 2019; Maliet and Morlon 2022; Vasconcelos et al. 2022; Quintero et al. 2024). In these models, speciation and extinction rates are estimated by averaging over multiple hidden state combinations (Vasconcelos et al. 2022), per branch (Maliet et al. 2019; Maliet and Morlon 2022), or even per discretized branch segment following a diffusion process (Quintero et al. 2024). One such model that has gained popularity (ClaDS, Maliet et al. 2019) proposes that one should not only consider infrequent rate shifts of large effect, but also more frequent, functionally continuous changes in rates of diversification across the phylogeny. Practically, this model estimates per-branch rates of speciation and extinction, but does not model branch- or node-specific shifts in the diversification process.

Even though these two analytical approaches fundamentally differ in how they model diversification, they may nonetheless produce qualitatively similar results—if a major event leads to significant localized changes in diversification rates, a modeling approach that quantifies per-branch diversification rates without discrete rate shifts will likely return localized rate changes across successive branches. Likewise, if a number of smaller events influence diversification rates, then a modeling approach that employs discrete rate shifts will accommo-

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date those rate changes, especially if time-variable rates can be inferred. However, this distinction—between episodic bursts of innovation or opportunity and a more continuous background of biological evolution and environmental fluctuation—becomes crucial in situations where the goal is to localize diversification rate shifts with precision. In such cases, mischaracterizing the underlying mode of change may obscure the biological signal of interest or lead to false conclusions about the drivers of diversification, with important implications also for attempts to link microevolutionary process to macroevolutionary pattern.

Tip Rates: Diversification Rate as a Property of Taxa

New developments proposed to infer a more nuanced and continuous view of the tempo of diversification allow for the calculation of lineage-specific rates of diversification at the tips of the phylogeny. These tip-specific diversification rates, referred to as tip rates, can be extracted from many parametric models, as well as nonparametric approaches (e.g., the DR statistic, Jetz et al. 2012; Title and Rabosky 2019). The rationale behind tip rates is that, if diversification probabilities change continuously through time and across clades, then each extant species in the tree should have inherited a lineage-specific probability of speciation or extinction, which can be estimated from the recent diversification history of the species in question. Tip rates therefore provide an opportunity to reframe questions, where diversification rates are now a species-level attribute, rather than strictly a property of an entire clade. This allows diversification rates to essentially be considered as a continuous trait evolving on the tree, and thus they can be used in conjunction with common comparative methods to assess which factors predict rate variation (Vasconcelos et al. 2022; e.g., Dellinger et al. 2024) and to test predictions from above or below the species level, such as the influence of range size or population structure on diversification rates (Singhal et al. 2022; Burbrink et al. 2023; Smyčka et al. 2023).

Unreliable Extinction Estimates and Lack of Identifiability: Two Major Criticisms of Birth–Death Models on Reconstructed Phylogenies

Despite specific criticism toward some of the models we have described, two overarching issues persist across all methods based on reconstructed phylogenies: unreliable extinction estimates and lack of model and parameter identifiability. The flip side of speciation—extinction—is obviously an important process in diversification as it is both a disruptor and a creative force (Raup 1994; Lehman and Miikkulainen 2015; Seeholzer and Brumfield 2023). Yet it remains among the most elusive patterns to quantify in diversification studies. The main issue is that models fit to extant-only trees often lack the information required to confidently disentangle speciation and extinction rates, resulting in extinction being frequently estimated as zero (e.g., Rabosky 2010; Beaulieu and O'Meara, 2015, 2023; Louca and Pennell 2021). Therefore, these estimates are at odds with empirical and paleontological evidence strongly suggesting that extinction has played a major role in shaping biodiversity and it can be as large as speciation (Raup and Sepkoski 1984; Liow and Nichols 2010; Zenil-Ferguson and Liow 2025).

Extinction not only plays a role in the pull-of-the-present but also the push-of-the-past (Fig. 3b; Nee, Holmes, et al. 1994). Apparent rate slowdowns in fossil and phylogenetic analyses might arise from studying clades whose persistence is mainly due to rapid early speciation that later returns toward the mean (Harvey et al. 1994; Budd and Mann 2018). In this case, our interpretation of a clade's diversity through time is altered, as survivorship is highly dependent on the magnitude of extinction early on in a group's history. If extinction estimates are inaccurate, inference may be compromised, especially in situations where extinction exceeds speciation, as would be the case for clades in decline (Burin et al. 2019; Louca et al. 2022).

The inconsistent selectivity in extinction events (Foster et al. 2023) leaves ambiguous signatures in reconstructed phylogenies posing additional challenges in formalizing such events in tractable models (Crisp and Cook 2009). For example, a "canonical" extinction is the complete disappearance of a taxon, whereas a pseudo-extinction is the disappearance of a species from the fossil record as it evolves into a new entity (i.e., extinction by anagenesis, Archibald 1993; Newman and Palmer 2003; Silvestro et al. 2018). In contrast, mass extinctions are events of sudden loss of lineages throughout the tree of life, usually exceeding background extinction rates by orders of magnitude (Benton 1995; Barnosky et al. 2011; Plotnick et al. 2016).

Although foundational studies that employed birth–death models generally assumed extinction rates could be extracted from reconstructed trees (Nee, Holmes, et al. 1994), the difficulty in accurately estimating extinction evidenced the need for strong assumptions or fossil data to do so reliably (Quental and Marshall 2010; Rabosky 2010). However, even with fossils, extinction acts as an "information remover," leaving a faint imprint on the phylogeny. Integrated models, such as the fossilized birth–death process (e.g., Heath et al. 2014; Mitchell et al. 2019), have improved estimation, particularly when including mass extinction events (Stadler 2011b; Höhna et al. 2016), but debates persist over whether adding fossils helps or is detrimental to these estimates (e.g., Beaulieu and O'Meara 2023; Do Rosario Petrucci et al. 2025). Meanwhile, newer ideas emerged, such as protracted and age-dependent extinction (Alexander et al. 2016; Hagen et al. 2018; Saulsbury et al. 2023). These point to richer and more biologi-

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cally grounded models that may capture alternative effects of extinction in extant phylogenies (Magallon and Sanderson 2001; Zenil-Ferguson et al. 2023).

The second issue, model identifiability, relates to the effects of implicit sampling bias and information incompleteness in reconstructed phylogenies, and affects virtually all diversification methods that rely on birth–death models. Bringing back a key discussion by Kubo and Iwasa (1995), Louca and Pennell (2020) elegantly demonstrated that in time-calibrated molecular phylogenies from extant taxa there is not enough information to distinguish between time-dependent diversification rate histories. This inability stems from models belonging to a congruence class with disparate time-dependent functions of speciation and extinction but the same likelihood values. Thus, we cannot choose the best diversification history within a congruence class even if we can confidently select among congruence classes.

This striking result has encouraged modelers to understand the implications and potential solutions of this ubiquitous property of reconstructed phylogenies for diversification modeling, leading to recent in-depth investigations into how to identify congruence classes (Höhna et al. 2022) or whether it is possible to choose representatives of congruence classes to gain insights into the diversification of a clade. Furthermore, some authors have argued that lack of identifiability is not a concern for certain approaches (O'Meara and Beaulieu 2021), whereas others have demonstrated that it might also extend beyond time-dependent diversification (Rabosky and Benson 2021; Tarasov and Uyeda 2024). Importantly, this debate has prompted the field to emphasize the limits of statistical inference and the importance of hypothesis-driven analyses (Morlon et al. 2022).

Some potential solutions for continuing to estimate diversification rates using birth–death approaches have been recently proposed and can generally be categorized into two types. The first approach is reductionist and aims to break down the heterogeneity within a clade into manageable and identifiable pieces, characterized by constant diversification rates (Legried and Terhorst 2022; Rannala and Yang 2025). The second alternative is analytical and aims to select and characterize the "most-probable" model groups, hoping to find commonalities that inform a lineage's diversification history (Höhna et al. 2022; Kopperud and Höhna 2025). Alternatively, building on temporal sampling models (Stadler 2010), recent work has shown that time-dependent fossilized birth–death models are identifiable (Truman et al. 2025), and that sampling models can be efficiently employed to explore identifiability features on simulated trees (Celentano et al. 2025). Together, these strategies offer a path forward: either accept reduced complexity in exchange for increased interpretability or embrace uncertainty while seeking robust and generalizable patterns.

A New Era: the Potential for Machine Learning in Diversification

Most methods implemented until recently required the calculation of the likelihood function of each of the models. This calculation requires detailed mathematical formulae whose computational cost scales poorly with phylogenetic tree size or model complexity, while failing to distinguish between intricate evolutionary histories (Rabosky and Goldberg 2017). Therefore, potentially intractable likelihood expressions need to be generated for each proposed model. Advances in likelihood construction for diversification models (MacPherson et al. 2021) or in numerical approximations (Janzen et al. 2015) exist in our field. However, as models evolve to integrate detailed macroevolutionary histories, these approaches are becoming more computationally expensive, unstable, or inaccurate (Qin et al. 2024). Solutions to these challenges with diversification model estimation will be brought by unsupervised or partially supervised machine learning approaches.

Machine learning approaches can circumvent the calculation of difficult or intractable likelihood functions by approximating the likelihood (e.g., variational inference in Bayesian statistics, Blei et al. 2017), or by bypassing the functions entirely (e.g., generative models, Jebara 2004). Some current applications of machine learning algorithms offer the opportunity for accurate and efficient model selection (through classification) and parameter estimation (through regression) in diversification dynamics (Greener et al. 2022; Mo et al. 2024). Although machine learning is still in its early development for diversification models (but see Bokma 2006 for an early implementation), several likelihood-free and simulation-based studies have combined deep learning with a large set of tree summary statistics or a compact representation of trees. For example, deep learning, which leverages neural networks to learn patterns from simulated data, is being implemented in *phyddle*, with an emphasis on phylogenetic comparative methods (Landis and Thompson 2025). This platform could be easily extended to diversification models, and we can imagine creating models that combine unique hypotheses of diversification.

In most cases, these techniques have been at least as effective as, or superior to, the standard methods, while also requiring shorter computational time after training. Another example from Voznica et al. (2022) showed that a Convolutional Neural Network and a feed-forward neural network could distinguish between phylodynamic scenarios while inferring accurate model parameters. Computing efficiency is achieved because this approach is an extension of a regression-based Approximate Bayes Computation (ABC) that abbreviates the rejection step (i.e., rejecting and sampling from the posterior). Additionally, diversification model inference and parameter estimations have been achieved through a regression approximation on trained deep neural net-

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works, which relate simulations to their parameter values (Lambert et al. 2023). These networks efficiently and accurately recovered results similar to the constant birth–death and BiSSE models (i.e., speciation and turnover rates). Alternatively, machine learning algorithms can be used to determine complex functional forms between rates and covariables to feed into birth–death likelihood models (e.g., Hauffe et al. 2024). Further, these advances have motivated the development of new methods to represent or encode phylogenetic trees and trait data as inputs into the machine algorithms, with minimal or no data loss. Some approaches include vector and matrix representations for exclusively binary trees (Penn et al. 2025), and specifically for ultrametric (Lambert et al. 2023) and non-ultrametric (Voznica et al. 2022) phylogenies.

New machine learning implementations also offer a promising avenue to overcome several challenges. Vectorized phylogenies exhibit several advantageous properties enabling substantially greater efficiency in tree sampling or comparison (Chauve et al. 2025; Penn et al. 2025; Penn et al. 2025). Potentially, future encoding formats can include traits, fossil data, stratigraphic ranges, and acyclic edges (i.e., phylogenetic networks). Further, a deep neural network could be trained to identify, enumerate, and construct the best candidate SSE models or to uncover non-intuitive functional diversification trends. The integration of machine learning into the field will require and create a cultural and methodological shift likely facilitated by method benchmarking, the implementation of guard rails to maintain biological realism and avoid unnecessary complexity, and pedagogical exposition. However, Thompson et al. (2024) showed that, despite the gains in efficiency, deep learning approaches were prone to the same biases as their maximum likelihood counterparts. Time will tell whether these new machine learning approaches live up to the cautious excitement being attributed to them.

Discussion

The popularity of statistical methods estimating tempo and mode of lineage diversification in systematic biology is undeniable, and the development of tools to describe diversification processes from reconstructed trees is still an area of active research. However, as a new field of systematic biology born in 1992 (Nee et al. 1992), diversification has had its fair share of growing pains over the past 30 years. With so many analytical possibilities and biological processes to factor into analyses of diversification, and given the limited information contained in a reconstructed phylogeny, it is not surprising that many (if not all) of the most popular tools we have described have faced severe challenges in one way or another after their publication. For instance, clade-dependent methods, such as MEDUSA, that use stepwise AIC optimization, might miss rate shift configurations that require a rearrangement of shift nodes, as only one shift location is optimized at a time (May and Moore 2016). The BAMM software has been questioned for not properly accounting for the probability of diversification rate shifts on extinct lineages (Moore et al. 2016), although this issue may have a relatively minor impact on empirical analyses (Rabosky 2017; Barido-Sottani et al. 2020; Laudanno et al. 2021). Trait-dependent methods, such as SSE models, have also been criticized for exhibiting high rates of type 1 error, detecting a signal that a focal character influences diversification even when that character was simulated to have no effect (Rabosky and Goldberg 2015). Such frequent critical evaluation has led to a rapid turnover of models in the field and the continuous development of tools that attempt to address limitations of previous approaches. This has led to the current practice of applying a battery of diversification models to an empirical system, rather than a more thoughtful approach of selecting and applying the most appropriate model available to address the biological question at hand.

More recently, as systematists are reminded of the importance of understanding the technical basis of diversification models (Louca and Pennell 2020), it seems that the field has been forced to take a step back, and the recent slowdown in the pace of publications using diversification tools, following an initially prolific period (Fig. 2), may reflect a growing appetite for nuance as the field "matures," although this pattern will need to be confirmed in a few years, given the recency of this apparent effect. This apparent setback has resulted in an opportunity for reflection, and thoughtful responses and proposed approaches have begun to emerge (Helmstetter et al. 2022; Höhna et al. 2022; Legried and Terhorst 2022; Morlon et al. 2022; Andréoletti and Morlon 2023; Kopperud et al. 2023). Although some descriptive metrics continue to be relevant today (e.g., tree shape and topology statistics), the field appears to be shifting to a new era of: (1) embracing uncertainty, instead of focusing on point estimates (Boyko and O'Meara 2024; Zenil-Ferguson and Liow 2025), and (2) more careful framing of explicit, testable hypotheses (Morlon et al. 2022).

The first represents a welcome and commendable approach, as we often forget that diversification is a historical science in which uncertainty should be seen as an inevitable feature. In that way, uncertainty will likely always be inherent to the study of diversification. However, model-based uncertainty in existing methods is underutilized, perhaps because it is challenging to interpret in a biological context. Although uncertainty in the locations of rate shifts on phylogenies is often explored and presented (e.g., competing rate shift configurations with BAMM), posterior distributions of diversification rates (and especially tip rates) are typically reduced to representative means, and the variance in those rates is often not incorporated into analyses. There is a missed opportunity to incorporate this uncertainty and indicate the robustness of downstream results and conclusions (Beaulieu and O'Meara 2025). Beyond uncertainty in pa-

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rameter estimates, non-identifiability in the form of variability within congruence classes will also need to be incorporated (Louca and Pennell 2020; Höhna et al. 2022; Tarasov and Uyeda 2022).

In hypothesis-driven frameworks, diversification models and approaches that consider natural history and incorporate other sources of evidence (e.g., biogeography, fossil records, ecology) have the potential to disentangle some of the complicated dynamics of diversification change. However, independent of how good our hypothesis-driven approaches can be, modelers have shown us that some key questions remain challenging, for example: "What causes diversification to happen?". Current models and tools cannot indicate causation, and experimental approaches to reveal causation for macroevolution are not easily developed in most systems, but phylodynamics (Dellicour et al. 2021) and newer phylogenetic comparative models that use causal statistics (i.e., Hardenberg and Gonzalez-Voyer 2013; Von Hardenberg and Gonzalez-Voyer 2025) or that simulate complex biodiversity and evolutionary dynamics under mechanistic models (Rangel et al. 2018; Hagen et al. 2021) can be the opening frontier for diversification modeling by observing extinction directly or by proposing models that can estimate a causal relationship (see for instance Alencar et al. 2024). The importance of demonstrating causation has been argued for other phylogenetic comparative approaches (Uyeda et al. 2018; Thorson and Van Der Bijl 2023), and will be valuable in diversification studies as well.

As diversification models are developed to be broadly applicable to most biological systems, systematists applying these models are faced with difficult choices about implementation while being thoughtful about the biological context of their study system. Emphasizing the incorporation of biological evidence into complex models will enhance our understanding of the tempo and mode of diversification across the tree of life.

Acknowledgments

We would like to thank the Society of Systematic Biologists Legacy Committee for providing us the opportunity to write this article and share our perspectives. We also thank Michael Landis, Brian O'Meara, Matt Pennell, and two anonymous reviewers for feedback that substantially improved this manuscript.

Funding

This work was supported by National Science Foundation DEB 2323170 (R.Z.-F.). L.F.H.-D. was supported by the Chicago Fellows Program and National Science Foundation DEB 2325837.

Data Availability

As this is a perspective article, no new data were generated.

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Syst. Biol. 75(3):391–405, 2026
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https://doi.org/10.1093/sysbio/syaf086
Advance Access publication December 5, 2025