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Phylogenetic Insights into Diversification

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Abstract

Species diversification—the balance between speciation and extinction—is fundamental to our understanding of how species richness varies in space and time and throughout the Tree of Life. Phylogenetic approaches provide insights into species diversification by enabling support for alternative diversification scenarios to be compared and speciation and extinction rates to be estimated. Here, we review the current toolkit available for conducting such analyses. We first highlight how modeling efforts over the past decade have fostered a notable transition from overly simplistic evolutionary scenarios to a more nuanced understanding of how and why diversification rates vary through time and across lineages. Using the latitudinal diversity gradient as a case study, we then illustrate the impact that modeling choices can have on the results obtained. Finally, we review recent progress in two areas that are still lagging behind: phylogenetic insights into microbial diversification and the speciation process.

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1. INTRODUCTION

The diversity of living species on Earth results from a succession of speciation and extinction events. Starting in the 1990s with the pioneering work of Sean Nee and collaborators (Nee et al. 1992, 1994), a wealth of studies have fitted birth–death models to phylogenetic trees to study these historical events (reviewed in Pennell & Harmon 2013, Stadler 2013, Morlon 2014). At the core of these studies are the rates at which speciation and extinction events occur, as well as their difference, referred to as the net diversification rate. Over the last 30 years, the development of birth–death diversification models, and their applications to various empirical systems, has shed light on a wide range of key questions in evolutionary biology. Central questions include the importance of adaptive radiations and key innovations in generating diversity (Simpson 1953, Schluter 2000); the role of evolutionary time, speciation rates, and extinction rates in explaining diversity gradients (Wiens & Donoghue 2004, Schluter & Pennell 2017); and the relative importance of biotic versus abiotic processes in modulating diversification rates (Barnosky 2001, Benton 2009).

From the very first phylogenetic diversification models, which assumed constant diversification rates shared among all species (Nee et al. 1992, 1994), to today, models have gradually increased in realism by accounting for heterogeneity in time and across lineages. This has led to an increasingly nuanced view of how diversification proceeds. Our aim here is to review the current toolkit available to conduct phylogenetic diversification analyses and the insights into diversification facilitated by these phylogenetic approaches.

2. MODELING SPECIES DIVERSIFICATION USING A PHYLOGENETIC APPROACH

Modern phylogenetics defines a species as a separately evolving metapopulation lineage (De Queiroz 2007) and speciation as the process that leads to the formation of such lineages. In most cases, speciation happens as a continuous process of separation and divergence from one lineage into two. While speciation can take several hundred thousand years (Etienne et al. 2014) and can also occur through hybridization (Abbott et al. 2013, Hernández-Hernández et al. 2021), most birth–death models used in the phylogenetic approach consider speciation as the result of instantaneous and bifurcating events (**Figure 1a**). The phylogenetic analysis of diversification can be summarized as follows. At present, extant species are delimited using operational criteria [such as reproductive isolation (RI), morphological differences, genetic divergences, and/or monophyly], and representative molecular sequences and/or morphological characters are used to reconstruct their phylogenetic tree, which is most often assumed to be fully bifurcating. Extinct or unsampled lineages are missing in a reconstructed phylogeny, such that only speciation events that lead to extant sampled species are represented; they appear as nodes in the phylogenetic tree (**Figure 1b**). Birth–death models are used to represent alternative hypotheses about how speciation (birth) and extinction (death) events proceed. Fitting them to reconstructed phylogenetic trees, most often using likelihood-based inference, allows the testing of various hypotheses about diversification and the estimation of crucial parameters, such as speciation and extinction rates. A variety of such tools have been developed, reviewed here in **Figure 2** and **Supplemental Table 1**. The approach has some limitations, which are more or less severe depending on the taxonomic group studied (**Supplemental Appendix 1**). This phylogenetic approach is referred to as the neontological approach, as present-day data are used to infer past evolutionary history. Recent advancements have facilitated the incorporation of paleontological data (see Section 3), the consideration of reticulated evolution (see the sidebar titled Reticulated Evolution and the Birth–Death–Hybridization Process), and the representation of speciation as a gradual, continuous
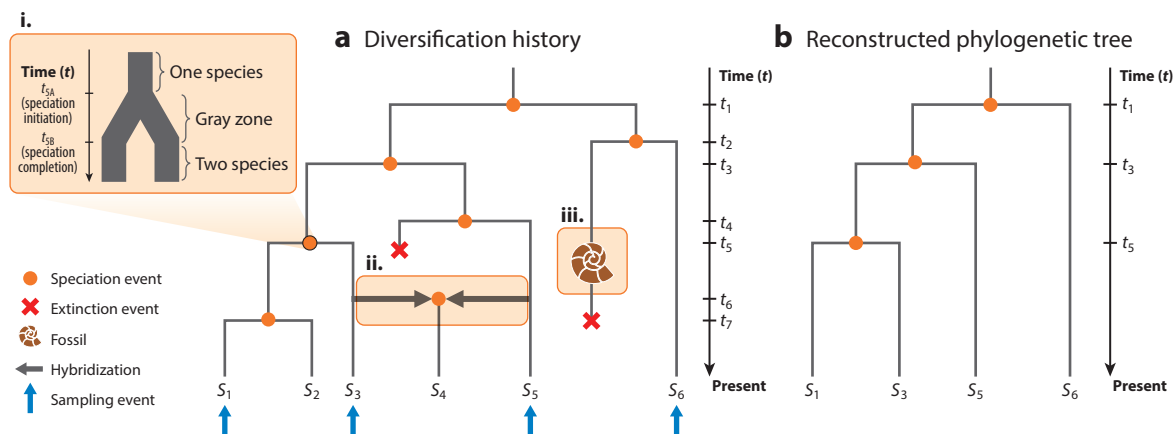
Figure 1

Birth–death models used to study species diversification. (*a*) The diversification of a clade is assumed to result from a succession of speciation and extinction events considered to be instantaneous (happening at a given time, *t*) and bifurcating. The simplest model, the constant-rate birth–death model, assumes that speciation events happen at rate λ, while extinctions happen at rate μ, with both rates being constant through time and across lineages. (*i*) In reality, speciation is a continuous process characterized by the duration between speciation initiation, when two lineages start to diverge, and speciation completion, when the two lineages evolve independently. (*ii*) In addition, hybridization events may happen and generate nonbifurcating, reticulated evolutionary relationships between species. These aspects, along with (*iii*) the incorporation of paleontological data, are the subjects of recent or ongoing model developments (*orange boxes*). (*b*) The reconstructed phylogenetic tree is obtained from the extant sampled species; some of the speciation events that happened during clade diversification are therefore not represented in this tree.

process (see Section 7). There has also been a focus on dealing with diversification scenarios that are indistinguishable with the data at hand (**Supplemental Appendix 2**) and on enhancing implementations (**Supplemental Appendices 3** and **4**).

3. JOINT PHYLOGENETIC AND PALEONTOLOGICAL INFERENCE

Most species in Earth's history have gone extinct (Jablonski 2004). As a result, diversification estimates obtained from extant phylogenies alone can provide a biased picture of their dynamics, especially as inferences reach out further into the past. In particular, whether reliable estimates of extinction rate can be obtained from purely extant clades has been questioned (Rabosky 2010). Recent methodological developments have tackled this issue by enabling the integration of information from the fossil record into phylogenetic diversification analyses (Stadler 2010, Heath et al. 2014, Wright et al. 2022).

In paleontological databases, fossil specimens are assigned to morphospecies based on morphological characters. This leads to a vertical species concept, wherein morphospecies are characterized by their stratigraphic range, delimited by their first and last occurrences in the fossil record. This concept is fundamentally different from the horizontal species concept used in modern phylogenetics, which delineates species at a given time (see Section 2). Fossil morphospecies are sensitive to morphological evolution in addition to species diversification, which results in three modes of morphospecies appearance in the fossil record (Stadler et al. 2018): (*a*) the budding mode, where the ancestral morphospecies survives and a new morphospecies arises, which corresponds to speciation and substantial morphological evolution in one of the two descending lineages; (*b*) the bifurcating mode, where the ancestral morphospecies goes extinct and two new morphospecies arise, corresponding to speciation and substantial morphological evolution in the two descending lineages; and (*c*) the anagenetic mode, where the ancestral morphospecies disappears (a so-called

Morphospecies: groups of organisms classified as part of the same species based on their similar morphological characters

Stratigraphic range: time span between the earliest and latest occurrences of a morphospecies in the fossil record
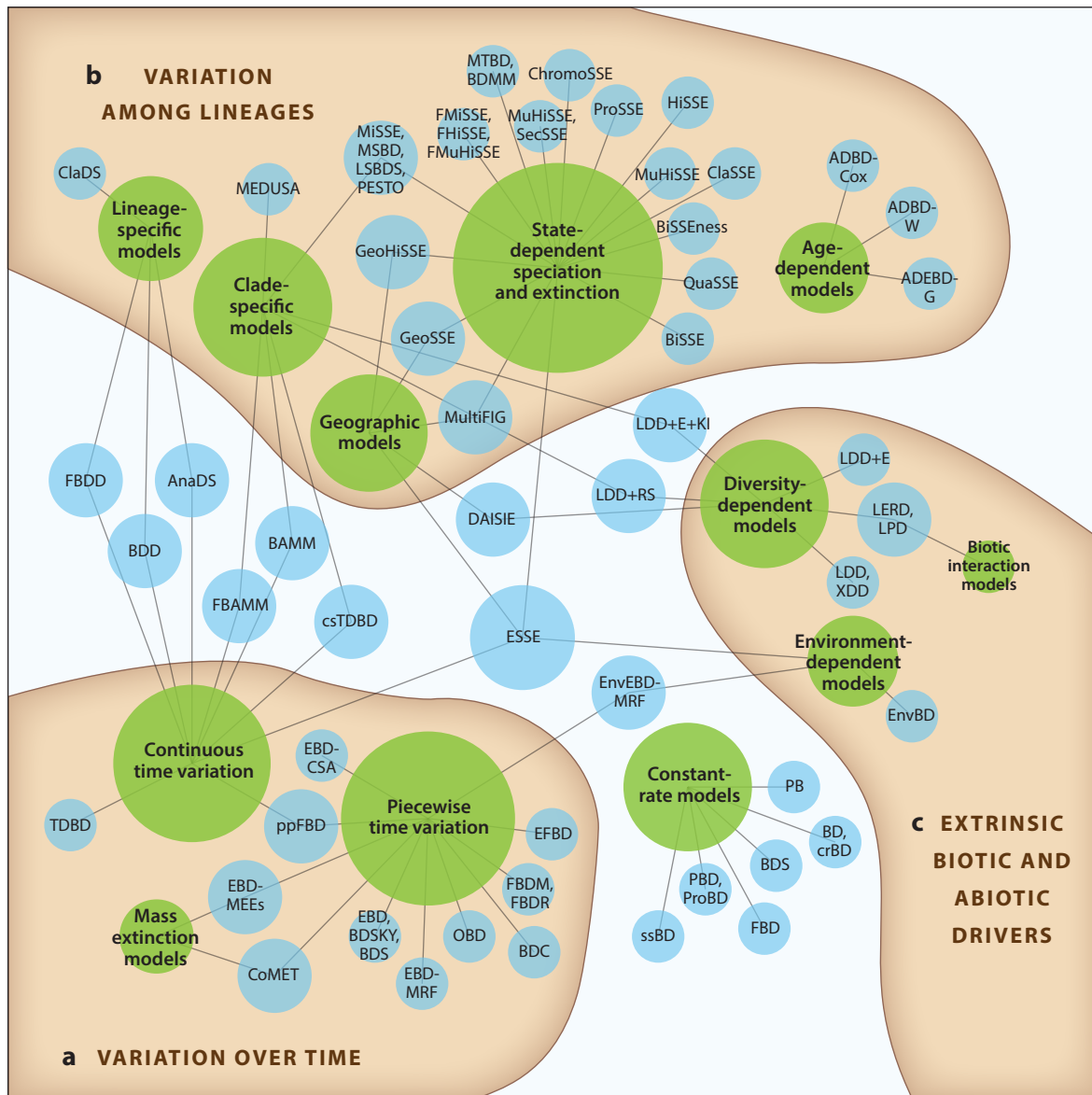
Figure 2

Overview of birth–death models available for phylogenetic diversification analyses. Each blue node represents a distinct model, character-ized by specific assumptions about speciation and extinction rates. Full model names, characteristics, and implementation(s) are available in **Supplemental Table 1**. Green nodes denote model types, which can themselves be grouped into three main categories: models de-veloped to capture (*a*) temporal diversification dynamics, (*b*) across-lineage heterogeneity, and (*c*) drivers of these variations. Each model is connected to its corresponding type(s), reflecting the underlying assumptions and evolutionary scenarios it is designed to explore.

pseudoextinction event) and is replaced by a new morphospecies, corresponding to substantial morphological evolution in the absence of speciation. The two first modes are characterized by the formation of a new lineage (i.e., a speciation event) and are represented as a bifurcating event in a phylogenetic tree, while the third mode leaves no mark in the phylogenetic tree.

RETICULATED EVOLUTION AND THE BIRTH–DEATH–HYBRIDIZATION PROCESS

There is increasing evidence of speciation events occurring by hybridization (Abbott et al. 2013, Hernández-Hernández et al. 2021). Such events are thought to be particularly frequent in microorganisms, but they also occur in plants and animals (Hernández-Hernández et al. 2021). The traditional phylogenetic approach to species diversification does not account for those reticulated speciation events and instead assumes that speciation always results from the divergence of an ancestral species into two descendants, well represented by dichotomous branching nodes in phylogenetic trees (**Figure 1**). On the other hand, there has been a growing effort to reconstruct phylogenetic networks, which represent reticulated species evolution, including hybridization and introgression (Elworth et al. 2018). Studying diversification from such phylogenetic networks, including estimating rates of hybrid speciation, requires considering the birth–death–hybridization process, which adds events of speciation by hybridization to the traditional birth–death process (**Figure 1**) (Morin & Moret 2006, Zhang et al. 2018, Justison et al. 2023). Zhang et al. (2018) implemented the birth–hybridization process as a prior for the phylogenetic network in BEAST2 (Bouckaert et al. 2019), thus allowing the species network and the (reticulated) diversification process to be inferred jointly (see **Supplemental Appendix 4**). The application of these models to large clades, however, remains constrained by computational complexity. One (suboptimal but currently unavoidable) approach to study speciation by hybridization in large clades therefore involves first reconstructing phylogenetic networks using efficient network approaches and second analyzing the network. For example, DeBaun et al. (2023) estimated rates of speciation by hybridization from the slope of the reticulation-through-time plot, an analog to the well-known lineage-through-time plot showing the accumulation of speciation by hybridization events throughout the clade's history on a semilog scale. One could also apply the birth–death–hybridization model to the reconstructed (fixed) network, which would allow accounting for the effect of extinction and provide more robust rate estimates.

The fossilized birth–death (FBD) process (Stadler 2010, Heath et al. 2014) can be used to construct phylogenies encompassing both extant and extinct species and to estimate speciation, extinction, and fossilization rates across the entire phylogeny. In the original FBD model, new morphospecies appear solely by budding, ignoring bifurcation and anagenesis. In addition, fossil specimens are sampled through a Poisson process, which implies that the number of samples for a given species correlates with the duration between its origination and extinction, while morphospecies are often represented by just their first and last appearances in the fossil record. These discrepancies have resulted in important differences between speciation or extinction rates estimated through FBD inferences and those estimated using methods based only on the fossil record (Stadler et al. 2018). The FBD morphospecies model, developed to address this issue by considering the three modes of morphospecies appearance and stratigraphic ranges, can indeed reconcile the discrepancy between fossil and phylogenetic rate estimates (Stadler et al. 2018, Silvestro et al. 2018). The FBD process can be combined as well with other methodological developments to integrate both time-dependent (see Section 3) and lineage-dependent (see Section 4) variations in diversification rates (MacPherson et al. 2021). Fossil Bayesian analysis of macroevolutionary mixtures (BAMM) (Mitchell et al. 2019), which estimates among-lineage discrete variation in diversification rates (see Section 4), incorporates fossil occurrences within stratigraphic ranges to inform a clade-wide fossilization rate, thereby matching the fossil sampling assumption of the original FBD process.

Progress is also being made on integrating occurrences not assigned to particular lineages. These occurrences cannot be placed into a phylogeny; however, their presence, age, and number can still inform estimates of the global diversity of a clade through time. The occurrence birth–death process (Manceau et al. 2021) uses occurrences in combination with a regular FBD inference

to obtain simultaneous estimates of the rates and phylogeny and then infer the total number of lineages over time, including those that did not leave any sampled descendants in the present. In particular, it has been applied to estimate the global diversity of the Cetacea clade, successfully recovering its boom and bust dynamics (Andréoletti et al. 2022).

Another approach exploits the information on extinction provided by the fossil record to inform phylogenetic diversification analyses, by first independently estimating the temporal dynamics of extinction from fossil data (Upham et al. 2021, Quintero et al. 2024). These extinction curves are then used to perform phylogenetic inference on speciation. For example, Upham et al. (2021) used an extinction curve obtained by subsampling the mammalian fossil record and the pulled speciation rate curve estimated from the mammal phylogeny (see **Supplemental Appendix 2**) to estimate temporal variations in speciation rates. Quintero et al. (2024) used clade-specific extinction curves across mammals obtained with PyRate (Silvestro et al. 2014) to constrain extinction rates in the phylogenetic birth–death diffusion (BDD) model (see Section 4). This framework uses fossil and phylogenetic data separately rather than jointly, as in the FBD process, but enables inference at large taxonomic scales, for thousands of species, while incorporating a much more accurate picture of past extinction dynamics than when using extant-only information.

4. AN INCREASINGLY NUANCED VIEW OF HOW AND WHY DIVERSIFICATION RATES VARY THROUGH TIME

It is now well established that phylogenetic trees frequently deviate from those expected under scenarios where speciation and extinction rates are constant through time. A tendency for diversification to slow down as clades diversify, coined the early-burst pattern, has been reported since the 1990s (reviewed in Moen & Morlon 2014), and this tendency has been confirmed by several recent meta-analyses (Condamine et al. 2019, Ronquist et al. 2021).

A much-discussed explanation for diversification rate slowdowns is that clade diversification becomes limited by the filling of total niche space (Rabosky 2009). Under this view, a lineage that invades a new adaptive zone, for example by acquiring a key innovation or entering a new geographical space, experiences a fast adaptive radiation until the number of niches that can be occupied reaches saturation (Simpson 1953). This hypothesis spurred the development of diversity-dependent models of diversification (Etienne et al. 2012). Empirical support for diversity-dependent dynamics has been found in iconic examples of adaptive radiations, such as the Madagascan vangas (Jønsson et al. 2012). It is, however, far from ubiquitous in broader tests, even on islands with restricted geographical space where we might expect strong constraints (Valente et al. 2020), suggesting that early-burst patterns do not necessarily reflect diversity-dependent dynamics (Moen & Morlon 2014).

Among alternative explanations, those that invoke changing environmental conditions dominate. Condamine et al. (2019) proposed that the cooling of the Earth during the Cenozoic played a significant role in slowing down diversification dynamics, as expected if diversification rates were higher during warm geological periods. Several models that specify a functional response of diversification rates to paleontological environmental data are now available to test such hypotheses (Condamine et al. 2013, Palazzesi et al. 2022, Quintero et al. 2023). Applying these models with paleoclimatic data across tetrapods, Condamine et al. (2019) found that temperature-dependent models better explain diversification in 44% of the clades, time-dependent models in 29%, and diversity-dependent models in 13% [the remaining 14% did not reject a constant rate model (see also Perez-Lamarque et al. 2022)]. This confirms the limited support for diversity-dependent diversification and suggests that temperature cooling may indeed have played a role in driving

diversification slowdowns. Instead of environmental conditions per se, periods of rapid environmental or geological change may have spurred high speciation rates at the origin of present-day clades that subsequently decreased (Moen & Morlon 2014). For example, periods of glaciation cycles or rapid mountain uplift are thought to be periods when frequent vicariance events spurred speciation (Quintero & Jetz 2018). Empirical support for this hypothesis remains scarce, however. Investigating the link between rates of environmental change and diversification, Quintero et al. (2023) discovered that environmental determinants are idiosyncratic rather than universally applicable across major tetrapod clades. In addition, diversification slowdowns may be indicative of waxing–waning dynamics, where diversity declines after an initial rising phase, rather than diversity-dependent dynamics (Quental & Marshall 2010, Moen & Morlon 2014). This can occur when species fail to keep up with a changing environment, leading to extinction becoming more frequent than speciation. More evidence for waxing–waning dynamics has been found in phylogenetic data in recent years, but what triggers them remains elusive (Mazet et al. 2023).

In addition to elucidating early burst diversification patterns, evolutionary biologists have shown a keen interest in discerning the predominant influence between Red Queen mechanisms, which are commonly employed in the field to refer to biotic processes, extending Van Valen's original coevolutionary theory (Van Valen 1973), and Court Jester mechanisms, which serve as a metaphor for the impact of abiotic fluctuations (Barnosky 2001, Benton 2009). Nevertheless, diversification models rarely incorporate biotic interactions, which are typically restricted to those considering within-clade competition through diversity-dependent diversification. Across-clade interactions are also believed to modulate diversification rates and are associated with key questions, such as the extent to which diversification in one clade is influenced by the species richness of the interacting clade or how specialization or partner shift influence diversification (Hembry & Weber 2020, Cogni et al. 2022). One approach to assess the first question involves modeling the diversification rates of a given clade as a function of the past richness of another interacting clade (e.g., estimated from the fossil record) (Condamine et al. 2020, Perez-Lamarque et al. 2022). Cophylogenetic methods can also be used to detect partner shifts and test for the presence of codiversification, where two interacting clades experience speciation events simultaneously, but these methods do not provide diversification rate estimates (Dismukes et al. 2022). There is clearly room for new developments in this area, including models that directly consider the simultaneous diversification of interacting clades and models that account for both biotic and abiotic effects in a unified framework.

5. AN INCREASINGLY NUANCED VIEW OF HOW AND WHY DIVERSIFICATION RATES VARY ACROSS LINEAGES

5.1. From Clade-Wide to More Subtle Rate Variations

Besides deviating from scenarios where diversification is constant through time, phylogenetic trees often also deviate from homogeneous diversification dynamics, where all lineages at any given time share identical diversification rates. There has been substantial interest in identifying specific nodes within a phylogeny where diversification rates undergo notable shifts from their ancestral values (Alfaro et al. 2009, Rabosky 2014, Barido-Sottani et al. 2020). Indeed, these shifts likely reflect major events, such as key innovations, the invasion of new geographical spaces, genomic rearrangements, or the transition to alternative reproduction modes. Several models were developed for this purpose [e.g., BAMM (**Figure 2** and **3a**, see also the clade-specific models in **Supplemental Table 1**). These models assume that a given clade experiences a mixture of distinct diversification regimes during its history, with episodic transitions among regimes. The different models differ by some of their assumptions, most importantly the diversification dynamics within
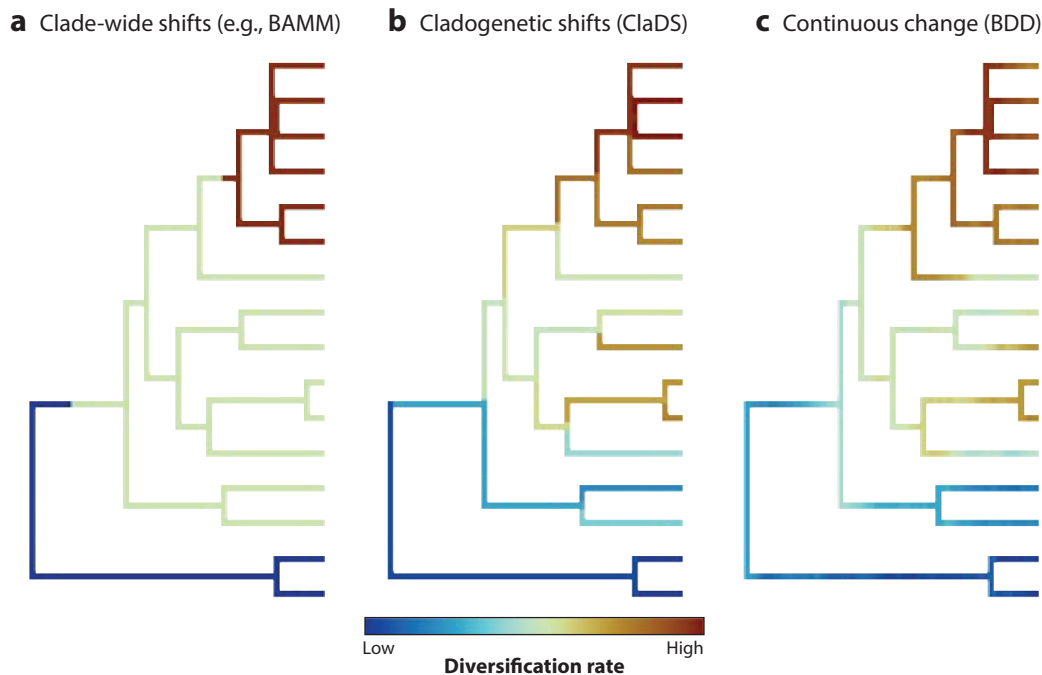
a Clade-wide shifts (e.g., BAMM)   **b** Cladogenetic shifts (ClaDS)   **c** Continuous change (BDD)

Low ▬▬▬▬▬▬▬▬ High
Diversification rate

Figure 3

Different views on the variability of diversification rates. (*a*) Clade-specific models (**Figure 2**, **Supplemental Table 1**) assume instantaneous transitions between diversification rates that are shared clade-wide by all descendants until the next rate shift. (*b,c*) Lineage-specific models assume more gradual rate variation with rate shifts occurring either (*b*) at speciation or (*c*) along phylogenetic branches. Abbreviations: BAMM, Bayesian analysis of macroevolutionary mixtures; BDD, birth–death diffusion model; ClaDS, cladogenetic diversification rate shift model.

regimes and the transition process, and by their implementations (**Supplemental Table 1**), yet they all assume instantaneous transitions between regimes that are shared clade-wide by all descendants until the next regime shift (**Figure 3a**).

Recently, models that assume gradual changes in diversification rates, rather than sudden transitions between distinct evolutionary regimes, have been developed. The cladogenetic diversification rate shift (ClaDS) model (Maliet et al. 2019, Maliet & Morlon 2022) and the BDD model (Quintero et al. 2024) characterize the evolution of diversification rates as a process in which diversification rates along phylogenetic branches are autocorrelated. ClaDS (**Figure 3b**) represents cladogenetic rate variation, where rate shifts occur at speciation, which happens if speciation is associated with profound modifications of intrinsic or extrinsic characteristics of species that affect speciation and extinction rates, such as phenotypes, range sizes, and the abiotic and biotic environment. Conversely, the BDD model represents anagenetic rate variation, where rate fluctuations are not directly tied to speciation events. Instead, speciation and extinction rates evolve as geometric Brownian processes along branches of the phylogeny, and these rates are inherited at speciation (**Figure 3c**). This type of rate variation can occur, for instance, in the context of anagenetic changes in species characteristics that govern diversification rates. Importantly, both ClaDS and BDD were implemented using Bayesian data augmentation techniques (**Supplemental Appendix 3**) (Maliet & Morlon 2022, Quintero et al. 2024). The approach provides posterior samples of complete trees, together with instantaneous lineage-specific diversification rate estimates. This allows the

estimation of paleodiversity curves, i.e., variations in species richness over time, as well as speciation rates averaged over all lineages, whether they are represented in the empirical tree or not (Maliet & Morlon 2022, Quintero et al. 2024). For example, using the fossil-informed BDD model (see Section 3) on all mammals, Quintero et al. (2024) were able to estimate the proportion of diversity loss during the Cretaceous–Paleogene boundary and the impact on average speciation rates.

Only a handful of studies have compared the statistical support for models with gradual rate variation to that for models with sudden rate shifts on empirical phylogenies. A study on bird phylogenies found significantly greater support for ClaDS than for models with sudden shifts (Ronquist et al. 2021). Quintero et al. (2024) also found, in mammals, that large increases in speciation rates occur ephemerally on isolated lineages, inconsistent with the idea of discrete diversification regimes shared clade wide. These models reflect previous theoretical departures from the key innovations/adaptive zones paradigm by characterizing diversification as a more subtle process (Donoghue & Sanderson 2015). Although more empirical studies are required before definite conclusions can be drawn, these findings suggest that gradual diversification rate fluctuations provide a more faithful representation of diversification rate variations than abrupt discrete shifts. If verified, this perspective should shift the focus from pinpointing specific instances when significant events triggered evolutionary radiations toward embracing a more nuanced view of evolution. In this view, diversification rates respond to a multifaceted interplay of intrinsic and extrinsic factors that change over evolutionary timescales.

5.2. Correlates of Rate Variation

Whether diversification rates vary punctuationally or gradually, there has been wide interest in identifying the drivers of such variation, and many phenotypical and environmental traits have been proposed. Two broad families of methods have been developed to test the association between these candidate traits and diversification rates using phylogenies and trait measurements at the tips. The first is model based and relies on so-called state-dependent speciation and extinction (SSE) models, where diversification rates depend on characteristics that themselves evolve during species diversification (Maddison et al. 2007, FitzJohn 2012). These characteristics can represent geographical attributes of the species (Goldberg et al. 2011); diversification and dispersal rates can now depend on geographic features, such as the area of regions and the distances among them, which are assumed to remain constant (Landis et al. 2022) or allowed to vary through time (Quintero et al. 2023). To avoid finding strong support for spurious correlations between traits and diversification rates (Rabosky & Goldberg 2015), these models now also incorporate one or several unobserved, hidden traits used to represent unaccounted characteristics that contribute to rate variations (Beaulieu & O'Meara 2016). When all traits are hidden, SSE models with discrete characters turn into the clade-specific models mentioned above (**Figure 3a**). In the future, another approach to account for unknown factors contributing to rate variations would be to use a birth–death process in which diversification rates have a component that responds to one or several candidate trait(s) in addition to a component that evolves gradually on the tree following, for example, the ClaDS or BDD processes (**Figure 3b,c**).

The second family of methods, known as tip-rate correlation tests, involves testing the association between (discrete or continuous) trait values across the tips of a phylogeny and tip-specific estimates of diversification rates. These estimates can be obtained using heterogeneous birth–death models; among these, models with gradual rate variation have the advantage of being truly lineage specific (**Figure 3b,c**), whereas clade-specific models with transitions between regimes bin tips into a few discrete regimes (**Figure 3a**). Tip-rate estimates can also be obtained with metrics

such as the inverse equal splits [also known as tip diversification rate (DR)], although the latter is a good estimator of speciation only in the absence of extinction (Jetz et al. 2012). The association between traits and tip speciation rates is then evaluated while accounting for the nonindependence of the tips resulting from shared evolutionary history using phylogenetic generalized least squares, or, more broadly, phylogenetic generalized linear mixed models. Importantly, by using the phylogenetic tree to account for covariances among tips, phylogenetic regressions assume a specific model of trait or diversification rate evolution across the tree. Other options include using randomizations or simulations (Rabosky & Goldberg 2017, Harvey & Rabosky 2018).

A recent study by Smyčka et al. (2023) nicely illustrates the potential pitfalls of tip-rate correlation tests. The authors set out to test the relationship between range size and diversification rates in mammals and found a negative association at the tips, suggesting that diversification rates are faster in small-ranged species. However, when they used cladogenetic SSE models where states (here, range sizes) can change at speciation events, they instead found higher speciation rates in large-ranged species. They additionally found high rates of asymmetrical speciation, where a large-ranged species produces one large- and one small-ranged daughter. Using simulations, they showed that under such a process of asymmetrical speciation, tip-rate correlation tests often output misleading results, particularly if one of the states has high extinction rates. Indeed, in the absence of any additional information at the tips, metrics or models used to obtain rate estimates cannot possibly infer different rates for sister species at the tips; in this situation, the test is therefore necessarily misleading. By explicitly modeling range size changes during speciation, and associated changes in diversification rates, SSE models recover the proper association between range size and diversification rates, while tip-rate correlation tests support the opposite (incorrect) association. These findings could have a notable impact on some of the conclusions drawn from tip-rate correlation tests, particularly those related to latitudinal gradients in diversification rates (as discussed in Section 5) and the microevolutionary factors associated with diversification rates (as discussed in Section 7).

6. LATITUDINAL GRADIENTS IN DIVERSIFICATION RATES

The present-day decrease in diversity toward the tropics, that is, the latitudinal diversity gradient (LDG), is one of the most recognized biogeographical patterns, but its underlying evolutionary processes remain a matter of much debate (Mittelbach et al. 2007, Schluter & Pennell 2017). Since geographic variation in species richness can result only from differences in the number of speciation, extinction, or dispersal events, any hypothesis attempting to explain the LDG must, ultimately, link to variation in the rates at which—or duration over which—these events occur (Fine 2015). While remarkable progress has been made in elucidating the diversification dynamics responsible for the LDG, with an emerging picture emphasizing the major role of extratropical extinctions in several clades (Pyron & Wiens 2013, Rolland et al. 2014, Meseguer & Condamine 2020, Pulido-Santacruz & Weir 2016, Quintero et al. 2023), a unanimous consensus is yet to be reached. It is becoming increasingly evident that this lack of consensus can be explained, at least in part, by the simplifying nature of the available models and the different methodological choices made in different studies.

Two main approaches have been used to investigate latitudinal gradients in diversification rates, as outlined in Section 4.2. The first has focused on estimating tip diversification (most often speciation) rates in the present, employing various methods and testing for an association of these tip rates with latitude. Some of these studies found higher speciation rates at high latitudes (Rabosky et al. 2018, Igea & Tanentzap 2020), while others found no relationship (Jetz et al. 2012, Harvey et al. 2020, Quintero et al. 2023). Aside from important differences in how tip rates were estimated

and how correlations with latitude were performed, these approaches often disregard potential latitudinal differences in extinction and dispersal, which can lead to biased inferences. If, in addition, many speciation events are associated with a latitudinal shift in at least one of the daughter lineages with strong asymmetries in speciation rates across latitudes, as could be expected under the "out of the tropics" hypothesis (Jablonski et al. 2006), this would result in a situation where tip-rate correlations lead to spurious results (as discussed in Section 4.2 for range size and diversification).

The second approach employed to investigate latitudinal gradients in diversification rates reconstructs the reciprocal effects of diversification and geographic evolution based on spatially explicit diversification models [geographic state speciation and extinction (GeoSSE)] (Goldberg et al. 2011; for examples, see Pyron & Wiens 2013, Rolland et al. 2014, Pulido-Santacruz & Weir 2016, Igea & Tanentzap 2020, Quintero et al. 2023). By considering area-specific speciation, extinction, and dispersal events in a process-based framework, these models account for the deeper history of clades and should be more robust to fleeting or spurious present-day associations. An exemplifying conflict is found in Igea & Tanentzap (2020), where tip speciation rates were found to decrease toward the tropics, but when using GeoSSE, no regional differences were found. Across tetrapods, studies have highlighted the role of extinction at high latitudes but found contrasting evidence on speciation and dispersal rates (Pyron & Wiens 2013, Rolland et al. 2014, Pulido-Santacruz & Weir 2016), which might stem from differences in the source data, the delimitation of the tropics, and the algorithm not reaching the global likelihood optimum (Cunha Crescente Alves et al. 2017, Quintero et al. 2023).

In addition, the tropics and the extratropics, and thus the shape of the LDG, have not been static through time, and there is evidence that present-day high speciation rates are associated with low species richness (Quintero & Jetz 2018, Harvey et al. 2020), which could be indicative of nonconstant diversification dynamics. This can be tested using a new geographic SSE model where region-specific diversification and dispersal rates can vary as a function of time or regional environmental variables (Quintero et al. 2023). The model can be used to test whether fluctuations of, say, temperature or area of a given region over geological time have had an effect on regional speciation and dispersal rates. Applied to tetrapods, the model suggests that the extratropics have acted as an evolutionary sink, characterized by a highly asymmetrical influx of tropical species and higher extinction rates. These results are congruent with those from the fossil record (Meseguer & Condamine 2020, Quintero et al. 2023) and pave the road toward some initial consensus on the role of extratropical extinction and asymmetrical dispersal in explaining the LDG. Progress toward unifying phylogenetic and paleontological data, including creating spatial models of diversification for trees that include fossil information and building increased model complexity that directly tests ecological mechanisms behind the LDG, holds much promise for confirming or rebutting these results and their underlying determinants.

7. RATES AND PATTERNS OF DIVERSIFICATION ACROSS THE TREE OF LIFE

The phylogenetic study of species diversification has historically focused on taxonomic groups that are easily identifiable and for which patterns of diversity are well established, such as vertebrates and plants. In comparison, the diversification dynamics of microbial groups (i.e., prokaryotes and microeukaryotes), characterized by a large and partially described diversity, have remained scarcely explored. This bias is slowly being reduced thanks to global sampling and DNA sequencing efforts that more comprehensively capture microbial diversity. Diversification studies on microorganisms have emerged, including studies on fungi (Varga et al. 2019, Perez-Lamarque et al. 2022), protists (Lewitus 2018), bacteria (Marin et al. 2016, Louca et al. 2018), and archaea

(Gubry-Rangin et al. 2015). Applying phylogenetic diversification models to microbial clades remains particularly challenging (**Supplemental Appendix 1**). One of these difficulties arises from the reticulated nature of microbial evolution, which would ideally require working with phylogenetic networks rather than bifurcating trees (see the sidebar titled Reticulated Evolution and the Birth–Death–Hybridization Process).

Horizontal gene transfer: transfer of genetic material between organisms that are not parent and offspring

As phylogenetic diversification studies on microorganisms started to emerge, a key interest has been to compare results to those typically obtained for macroorganisms (Cohan 2001, Scholl & Wiens 2016, Hernández-Hernández et al. 2021). Although the very broad classification between macro- versus microorganisms groups together taxa with very divergent evolutionary histories and distinct ecologies, this comparison is meaningful due to the consistent covariation of key biological attributes—such as population size, dispersal ability, and the frequency of horizontal gene transfer—with both body size and diversification rates. Prokaryotes in particular are thought to have extremely high population sizes, which can increase their chances of experiencing divergent ecological selection leading to speciation (Cohan 2001, Cohan & Koeppel 2008). Many microorganisms are also thought to be less dispersal limited than macroorganisms (Fenchel & Finlay 2006, Louca 2022). Whether this should foster or impede speciation is unclear, as speciation rates are believed to be highest at intermediate dispersal levels, where the combination of geographical opportunities and limited gene flow can lead to allopatric speciation. Some have argued that virtually unlimited dispersal should lead to very low speciation rates in microorganisms (Fenchel & Finlay 2006), but there is now evidence for dispersal limitation and allopatric speciation in the microbial world (Martiny et al. 2006, Singer et al. 2019). Microorganisms, in particular prokaryotes, experience horizontal gene transfers at high frequency compared to macroorganisms. Many microorganisms reproduce mostly clonally, and the rate at which they experience homologous recombination through horizontal gene transfers determines their genetic homogenization; frequent homologous recombination is expected to limit divergence and thus speciation (Fraser et al. 2007). On the other hand, nonhomologous gene transfers may foster speciation through the acquisition of ecological innovations enhancing population divergence (Cohan & Koeppel 2008). With respect to extinction rates, it has been suggested that microbial lineages may experience fewer extinctions than larger organisms, due to their large populations, high dispersal rate, and ability to withstand unfavorable environmental conditions through dormancy (Dykhuizen 1998). Diversification rates estimated from the empirical phylogenies of microbial clades remain too rare (and potentially biased) (see **Supplemental Appendix 1**) to draw general conclusions regarding these hypotheses (**Figure 4**). Several studies have reported speciation rates one order of magnitude lower in prokaryotes and some lineages of microeukaryotes than in macroorganisms (Scholl & Wiens 2016, Lewitus 2018, Louca et al. 2018, Perez-Lamarque et al. 2022). Archaea seem to diversify particularly slowly (Yang et al. 2021). However, high speciation rates have been reported for some microeukaryotes (e.g., ciliates or lichenized fungi), and some lineages of macroorganisms appear to speciate at low rates. In addition, evidence of extinction is rather substantial in at least some microbial clades (Lewitus 2018, Louca et al. 2018).

The extent to which the diversification rates of microorganisms vary through time remains debated. In prokaryotes, several phylogenetic studies suggest constant diversification rates (Marin et al. 2016, Straub & Zhaxybayeva 2017, Louca et al. 2018). This apparent constant diversification rate can be found under a model of clonal reproduction if drift dominates over selection (Straub & Zhaxybayeva 2017). However, other phylogenetic studies on microorganisms, including prokaryotes, have shown evidence for temporal variations in diversification rates (Morlon et al. 2012, Gubry-Rangin et al. 2015, Lewitus 2018, Perez-Lamarque et al. 2022). These temporal variations include the early burst pattern often observed in macroorganisms (see Section 3) (Morlon et al. 2012, Perez-Lamarque et al. 2022). Temporal variations in diversification rates
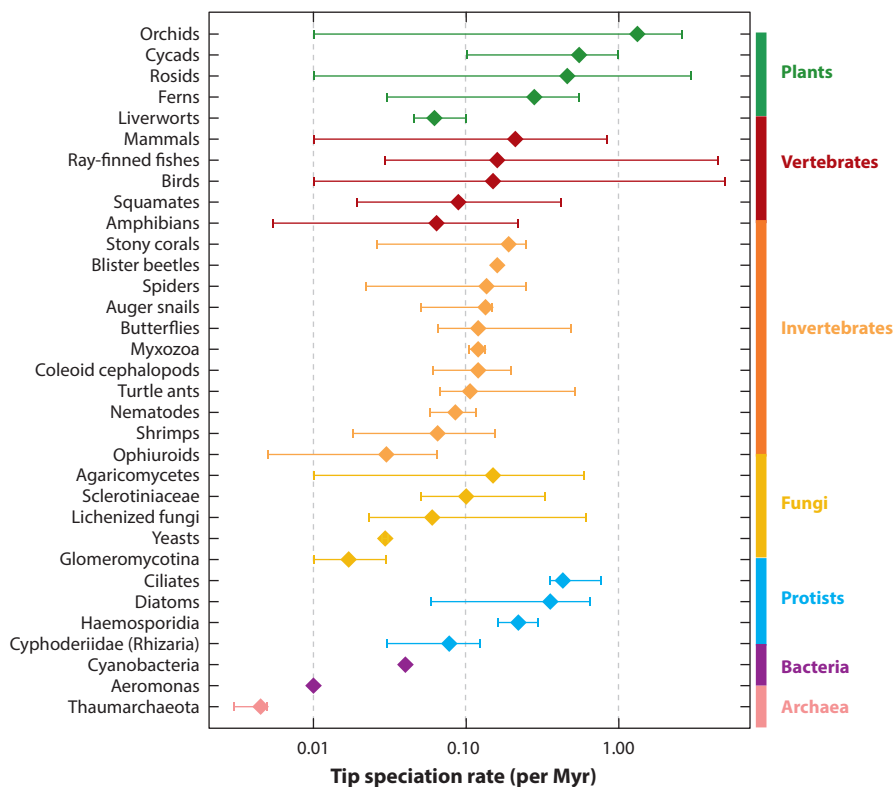
Figure 4

Speciation rates across the Tree of Life. Tip speciation rate estimates obtained using a phylogenetic approach in various clades of macro- and microorganisms are reported. When available, we favored estimates obtained using models allowing rate variation in time and across lineages. The list of references for each clade and details on the methodology are provided in **Supplemental Table 2**. For each clade, when available, the mean, minimum, and maximum tip speciation rates are represented. When only the minimum and the maximum were available (**Supplemental Table 2**), the represented mean is the average between the minimum and the maximum.

found in microorganisms have been attributed to a variety of factors. Among abiotic factors, average temperature, pH, solar radiation, and resource availability have been shown to modulate microbial diversification, depending on the taxonomic group considered (Lewitus 2018, Perez-Lamarque et al. 2022). Biotic interactions are also probably key modulators of microbial diversification, although their effect is harder to detect with currently available phylogenetic diversification models (see Section 3). In diatoms, both abiotic and biotic factors influence diversification rates, with idiosyncratic patterns across clades (Lewitus 2018). Biotic effects are expected to be particularly strong for host-associated microorganisms, such as plant-associated mycorrhizal fungi (Varga et al. 2019, Perez-Lamarque et al. 2022). In the case of vertically transmitted host-associated microorganisms, such as arthropod-associated endosymbionts (Hernández-Hernández et al. 2021) or a significant fraction of the bacterial gut microbiota of primates (Perez-Lamarque & Morlon 2019), microbial diversification could even mirror that of their hosts, a process referred to as codiversification.

How diversification rates vary across microbial lineages remains largely unexplored. Many phylogenetic diversification rate estimates for microorganisms were obtained by applying

homogeneous rate models. However, when compared across large taxonomic groups, these diversification rate estimates appear to vary by orders of magnitude (**Figure 4**), suggesting a wide heterogeneity in diversification rates at large taxonomic scales. Within more restricted taxonomic groups, prokaryotes and microeukaryotes seem to exhibit less variation in lineage-specific diversification rates than macroorganisms, although this needs to be confirmed with a broader application of heterogeneous rate models to microbial clades. For instance, tip speciation rates estimated with heterogeneous birth–death models vary from 0.01 to 5 events/Myr in birds (Maliet et al. 2019) and only from 0.01 to 0.03 in arbuscular mycorrhizal fungi (Perez-Lamarque et al. 2022) and from 0.35 to 0.77 in ciliates (Fernandes & Schrago 2019). If this general trend is confirmed, it could contribute to the formulation of hypotheses explaining why diversification rates appear to be more constrained in some species groups than others. This is not well understood, even in macroorganisms (Maliet et al. 2019).

<div style="border-left: 3px solid #6699aa; padding-left: 1em;">

Speciation initiation:
formation of an isolated or almost isolated population expected to eventually evolve to different species in allopatry

</div>

8. LINKING DIVERSIFICATION RATES TO THE SPECIATION PROCESS

Most phylogenetic diversification approaches consider speciation as an instantaneous event and estimate a macroevolutionary speciation rate, which quantifies the average number of successful speciation events per species per time unit (see Section 2). These approaches have revealed that speciation rates can vary by several orders of magnitude even within taxonomically restricted species groups, and they have been heavily used to identify intrinsic or extrinsic factors that correlate with speciation rates, as discussed above. A more mechanistic understanding of how these factors influence species formation to modulate speciation rates requires a full consideration of the speciation process (**Figure 5a**) (Rabosky 2016, Hua & Bromham 2017, Harvey et al. 2019, Rolland et al. 2023). For macroorganisms with sexual reproduction, the most common process of species formation begins when population subsets become isolated (speciation initiation or population formation); their survival in isolation must then be maintained over a period significant enough that the accumulation of differences prevents interbreeding between individuals from different populations or makes their hybrids less fit (RI or speciation completion) (**Figure 5a**) (Coyne & Orr 2004). The macroevolutionary speciation rate thus intuitively depends on the frequencies at which populations form, come back into contact again as one species, and go extinct, as well as the time it takes to achieve RI.

In the last decade, several studies have investigated the empirical relationship between macroevolutionary speciation rates, as estimated at the tips of phylogenies (see Section 4), and characteristics of species expected to reflect aspects of the speciation process. The initial and final stages of the speciation process, namely population formation and RI, have received the most attention. The rate of population formation has been measured using two proxies: the number of genetically distinguishable populations within species divided by species age (Harvey et al. 2017) and the slope of the relationship between geographic distance and the genetic divergence between populations (**Figure 5b**) (Singhal et al. 2018, 2022; Burbrink et al. 2023). While a significant positive correlation between this rate of population formation and speciation rate was found in birds (Harvey et al. 2017), it does not seem to hold in squamates (Singhal et al. 2018, 2022; Burbrink et al. 2023). The rate at which populations evolve RI has been measured as the slope of the relationship between reproductive barriers—estimated as the percentage of inviable or sterile offspring in experimental crosses—and the genetic distance between the crossed individuals (**Figure 5b**) (Rabosky & Matute 2013). In birds and *Drosophila*, some lineages evolve RI much faster than others, yet this does not seem to result in faster speciation rates (Rabosky & Matute 2013). These somewhat unexpected, and sometimes contradictory results, suggest that the persistence of populations and their spatial isolation over time, which are not captured by proxies
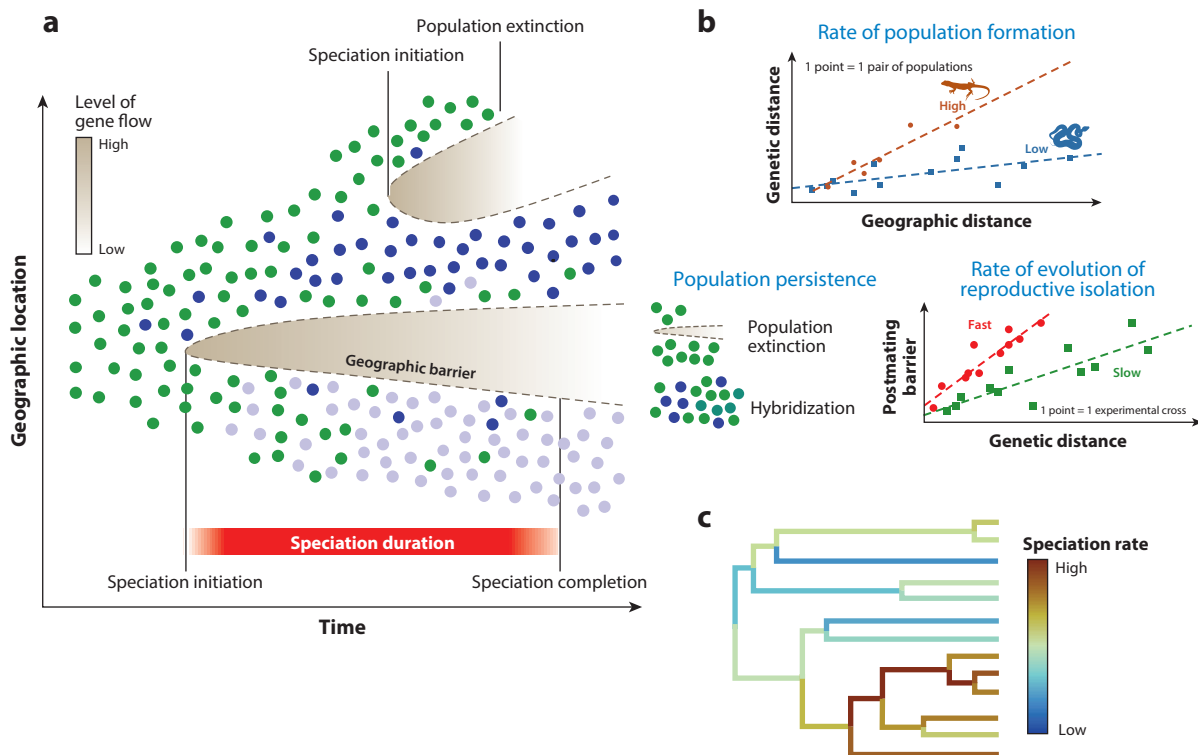
Figure 5

Various steps of the speciation process that can modulate macroevolutionary speciation rates. (*a*) Schematic representation of the different steps of the speciation process, from speciation initiation to speciation completion. Each dot represents one individual, colored by its genotype. The shaded regions correspond to geographic barriers, with color indicating the degree of gene flow within the gray zone of speciation (see **Figure 1**). (*b*) Schematic representation of how rates of key steps of the speciation process can be estimated: The slope of the relationship between geographic distance and genetic distance is indicative of the rate of population formation. Here, better dispersers (snakes) have a lower rate of population formation than poor dispersers (lizards); population persistence is estimated from the probability of extinction or hybridization; and the slope of the relationship between genetic distance and postzygotic reproductive isolation (RI) (e.g., measured as the percentage of inviable or sterile offspring in experimental crosses) is indicative of the rate of evolution of RI. (*c*) Together, rates of population formation, population persistence, and evolution of RI explain macroevolutionary speciation rates, as estimated on a phylogeny. The blue snake silhouette is adapted from Phylopic (**https://www.phylopic.org**, CC0 1.0).

of population formation and the rate at which populations evolve RI, may play a larger role than the two latter processes in modulating speciation rates (Rabosky 2016, Harvey et al. 2019).

A better understanding of these results, and ultimately of the processes that modulate macroevolutionary speciation rates as estimated from phylogenies, requires first a better theoretical and empirical understanding of how macroevolutionary speciation rates are related to the rates of speciation initiation; population extinction; and speciation duration, i.e., the time it takes to evolve RI. Theoretically, this amounts to establishing a mathematical link between the parameters of the instantaneous birth–death process used to estimate macroevolutionary speciation rates (see Section 2) and those of the protracted birth–death process, which includes rates of speciation initiation and population extinction, as well as speciation duration (Etienne & Rosindell 2012). To our knowledge, such a link has yet to be formally established. Empirically, one challenge arises from the fact that it is not possible to estimate all the parameters of the protracted

birth–death process from a species-level molecular phylogeny of extant species (Etienne et al. 2014). Nevertheless, speciation duration can be estimated from extant phylogenies (Etienne et al. 2014) or using fossil data (Benton & Pearson 2001), and it could be insightful, for example, to investigate whether this duration is inversely correlated to the macroevolutionary speciation rate and/or to the rate at which species evolve RI, as could be expected. In addition, a recent study suggests that the parameters of the protracted birth–death process can be accurately estimated from a population-level (rather than species-level) phylogeny (Hua et al. 2022). While such phylogenies remain rare, this paves the way for empirical tests of the relationship between macroevolutionary speciation rates and rates of speciation initiation, population extinction, and speciation duration.

Second, we need to better understand how each of the main stages of the speciation process is influenced by key characteristics of a species such as its population size, dispersal capacity, mutation rate, and the selection pressures it experiences in its biotic and abiotic environment. The goal here is not to improve our estimates of speciation rates but rather to better understand how species attributes modulate these rates. Particularly relevant factors are interactions with other species, such as competition, parasitism, or mutualism, or with abiotic factors, such as climatic changes, orogenesis, or habitat fragmentation. A wealth of theoretical and empirical studies from population dynamics, population genetics, and speciation theory exist to build upon (Rabosky 2016, Harvey et al. 2019). For example, how biotic and abiotic factors influence the extinction risks of populations or species has been studied at length (Wiens & Slaton 2012, Chichorro et al. 2019), and numerous studies have investigated the mechanisms by which genetic incompatibilities lead to speciation (for a review, see Satokangas et al. 2020), the effect of processes such as migration and niche partitioning on the accumulation of RI (Westram et al. 2022), and the dynamics of accumulation of RI in nature (for a review, see Kulmuni et al. 2020). However, these studies have often focused on only one stage of the speciation process, while it is becoming clear that all stages need to be considered simultaneously if we are to understand how microevolutionary processes modulate macroevolutionary speciation rates. This is key, because some characteristics of species can accelerate one step of the speciation process while decelerating another, which complexifies expectations. For example, species that disperse readily can colonize new environments, which may increase rates of speciation initiation [see for instance the "great speciator" Zosteropidae (Moyle et al. 2009)], but at the same time lead to more gene flow between populations, which may increase the time it takes to complete speciation (Claramunt et al. 2012). Similarly, species with large population sizes may be less likely to fix nearly neutral mutations that end up causing genetic incompatibilities between individuals from diverging populations, which may increase speciation duration (Gavrilets 2000, Maya-Lastra & Eaton 2021) but at the same time decrease the probability that populations go extinct before completing speciation. Quantitative predictions of the direction and magnitude of the effect of such species characteristics on speciation initiation, population survival, and RI, backed up with empirical evidence, can then be used to predict their effect on the macroevolutionary speciation rate, provided the relationship between the latter and the former has been clarified (c.f. previous paragraph). If these macroevolutionary predictions are confirmed by phylogenetic diversification models, we will have made significant progress in elucidating the main factors that modulate speciation rates.

9. CONCLUSION

Phylogenetic diversification models are becoming more biologically realistic and increasingly integrative, connecting with paleobiology, paleoclimatology, trait and molecular evolution, ecology, microbiology, and population genetics. These advancements come with the challenge of increased

computational complexity, requiring the development of innovative inference techniques. The rewarding outcome is a better understanding of the processes that shape biodiversity.

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