Impact of Evolutionary Relatedness on Species Diversification: A New Birth-Death Model

Evolutionary relatedness shaping species diversification

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Conflict of interest

The authors declare no conflict of interest

Data availability

The code implementation underlying this article is available

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Abstract

Slowdowns in lineage accumulation are often observed in phylogenies of extant species. One explanation for this is the presence of ecological limits to diversity and hence to diversification. Previous research has examined whether and how species richness (SR) impacts diversification rates, but rarely considered the evolutionary relatedness (ER) between species, even though phylogenetic distance can play a role in the degree of competition between species, which likely sets these ecological limits. To understand the influence of ecological limits represented by ER on species diversification, and to investigate the interplay between SR and ER effects on diversification, we present a new phylogenetic birth-death model in which the speciation rate depends on the ER between species. We use different metrics of ER that operate at different scales, from lineage-specific to clade-wide. We find that the different scales of ER effect yield distinct patterns in speciation rates and various tree statistics. When ER operates across the whole tree, we observe smaller and more balanced phylogenetic trees, with internal nodes concentrated more closely to the root and speciation rates distributed more evenly across the tips than in scenarios with lineage-specific ER effects. Importantly, we find that the presence of negative SR dependence can reduce the influence of ER on some of the tree statistics. This suggests that these tree statistics should not be used to detect an effect of evolutionary relatedness on clade diversification.

Keywords: Phylogeny, Tree topology, Simulation, Biodiversity, Niche space, Filtering, Over-dispersion, Extinction

Introduction

The change in species richness (SR) through time has traditionally been studied using the paleo-record. Early research found that the stochastic constant-rates birth-death model of diversification can generate similar phyletic patterns as those observed in paleontological data (Raup et al., 1973; Nee, 2006), although many species leave no trace in the fossil record (Stanley, 1998; Rabosky, 2013). Over the last two

decades, the increasing availability of DNA sequence data and tools to reconstruct phylogenetic trees from these data has led to the development of many models and methods that use molecular phylogenies as a source of information to study diversification dynamics (Nee et al., 1992; Purvis, 2008; Quental and Marshall, 2010; Etienne et al., 2012). Lineage-through-time (LTT) plots, semi-logarithmic plots that track the number of lineages that have descendants at the present through time, are a powerful way of summarizing diversification dynamics. If per-lineage rates of speciation and extinction have been constant through time, the accumulation of lineages increases through time exponentially, with an even stronger increase close to the present, a phenomenon called the pull-of-the-present (Nee et al., 1994; Kubo and Iwasa, 1995). However, empirical phylogenies often show recent deceleration (Purvis, 2008; Phillimore and Price, 2008; Moen and Morlon, 2014; Aguile et al., 2018), which tends to lead to estimates of zero extinction rate, in contrast to the fossil record (Etienne et al., 2012; Louca and Pennell, 2021).

Several hypotheses have been put forward to explain the observed slowdowns in phylogenies of extant species (Moen and Morlon, 2014), such as time-dependent speciation rate (Moen and Morlon, 2014), protracted speciation (Etienne and Rosindell, 2012) and negative diversity-dependent diversification (Valentine, 1973; Sepkoski, 1978; Etienne et al., 2012). In negative diversity-dependent diversification models, the speciation rate declines with increasing diversity.

Current models of diversity-dependent diversification assume that speciation rate depends on global SR, regardless of evolutionary relationships of the species. The general underlying idea is that species diversification results in the occupation of available niche spaces, leaving limited opportunities for subsequent species to use those niches (Figure 1), because evolving clades compete for finite ecological resources (Wiens, 2011). In these models, SR acts as a proxy for more mechanistic factors such as functional traits, niches and ecological interactions, which ultimately may influence ecological limits (Srivastava et al., 2012; Kondratyeva et al., 2019). While past ecological interactions between species are difficult to infer, a useful proxy for them is evolutionary relatedness (ER), a measure of phylogenetic distance between species. ER can represent the ecological roles of the species well (Helmus et al., 2007; Pigot et al., 2016), as closely related species are more likely to share trait states and ecological functions than distantly related species (Srivastava et al., 2012), and evolutionary distance may be related to fitness and niche differences (Cadotte et al., 2012), which in turn can affect speciation and extinction. Here, we may learn from insights from phylogenetic community ecology (Webb et al., 2002; Mayfield and Levine, 2010; HilleRisLambers et al., 2012) and invasion biology. For example, alien species that are evolutionarily distant from those in the local community may have a

greater chance of establishing (Zheng et al., 2018), so using ER as a proxy to quantify open niche spaces may explain the success of plant invaders (Henn et al., 2019; Qin et al., 2020).

The potentially powerful phylogenetic proxies for ecological interactions, however, have been the subject of intense debate because the underlying assumptions are often not robustly supported (Gerhold et al., 2015; Pigot et al., 2016). Indeed, there is mixed evidence regarding the effectiveness of these proxies. On the one hand, Tucker et al. (2018) concluded that phylogenetic diversity is a useful proxy for functional diversity, because phylogenetic diversity correlates more strongly with functional diversity when trait dimension increases (multidimensional trait space), although that correlation is weakened when trait evolution models become increasingly complex. On the other hand, Mazel et al. (2018) found that in many cases phylogenetic diversity only poorly captures functional diversity, even less so than random selection. Furthermore, Venail et al. (2015) found that trait and functional variation among species is largely explained by SR but not phylogenetic relatedness (a concept similar to ER). Recently, Pie et al. (2023) found that sympatry with closely-related species does not lead to decreasing speciation rates in a variety of vertebrate clades, implying that the underlying mechanisms of diversity-dependent diversification remain unconfirmed.

While these concerns indicate that support for a role of ER on diversification is not clear, this may be because we do not know what signal ER would leave in phylogenetic trees and extant communities (Rabosky, 2009b; Ricklefs, 2010; Wiens, 2011). Most studies have only considered diversity-dependence within clades of phylogenetically closely related species (Rabosky and Glor, 2010; Etienne et al., 2012; Foote et al., 2018), whereas only a few have considered diversity-dependence between clades of phylogenetically disparate species (Pires et al., 2017). Etienne et al. (2023). A recent study (Etienne et al., 2023) using empirical data on island frogs found that a model with diversity-dependence between closely related species was preferred over one with diversity-dependence also occurring with more distantly related species, indicating that interactions of species with close relatives, but not with distant relatives, negatively affect colonization and diversification. This suggests an important role of ER in species diversification and the need for distinguishing between different levels of ER and scales at which it may have an effect on diversification. However, none of the above-mentioned studies has investigated whether ER directly impacts macro-evolutionary dynamics (Rillo and Etienne, 2022).

Assuming ER affects diversification rates, what signatures does this effect leave in phylogenetic trees of communities? What emergent phylogenetic patterns are expected if species facilitate or compete more strongly with their close relatives? Can

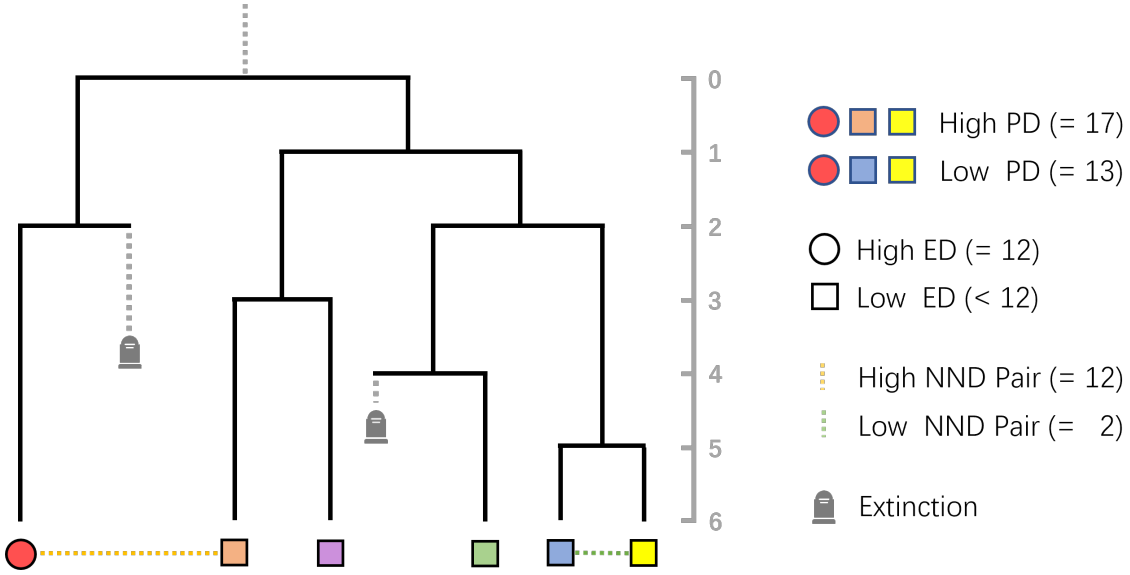

Figure 1: Illustration of how evolutionary relatedness (ER) is computed within clades and species in a phylogeny, as measured by three metrics: PD (phylogenetic diversity), ED (evolutionary distinctiveness), and NND (nearest neighbor distance). The tree on the left represents a phylogeny with extant and extinct (marked by tombstone icons) species. The numbered axis in the middle marks the branch lengths in evolutionary time (million-years). The colored circle and squares at the tips of the phylogeny represents corresponding species. On the right of the plot, the species denoted by a grey circle, an orange square and a yellow square form a combination of high PD (17), while the species denoted by the grey circle, the blue square and the yellow square form a combination of low PD (13). The species with the highest ED value (12) is represented by a circle, and those with lower ED values (less than 12) are represented by a square. The yellow and green dashed-lines between species illustrate two pairs of species, one with a low NND value (2) and one with a high NND value (12).

phylogenetic limits imposed by ER be differentiated from those imposed by SR? And how do ER effects operating at the whole clade versus more lineage-specific scales affect phylogenies? To address these questions, here we present a new phylogenetic birth-death model that incorporates both SR and ER. The model allows for positive, neutral, or negative effects of both SR and ER on diversification rates. We measure ER using three different mechanisms of how ER can affect diversification (see Methods) each considering a different scale of the effect of ER. We use the new model to simulate communities under a stochastic branching process where speciation rate can vary according to SR and ER, and analyze whether ER leaves a signature on the diversification dynamics by looking at various tree summary statistics.

Methods

Model

We employed a phylogenetic stochastic model that simulates the processes of species birth and death over time (Nee et al., 1994). The model is a mechanistic process-based model that is parameterized by speciation and extinction rates along with the effect sizes of SR and ER. It allows us to explore different evolutionary trajectories from phylogenetic trees given specific parameter settings at the start of the simulation. We assumed that all species on the same tree belong to the same clade, thus our study focuses on species diversification patterns within a clade, and the phylogenies simulated include all the extant species in the clade. We investigated different types of effects of ER on species diversification by considering three measures of ER: phylogenetic diversity (PD), evolutionary distinctiveness (ED), and nearest neighbor distance (NND).

PD measures the amount of evolutionary history represented by a group of species and is commonly used to determine how species occupy different niches (Tucker et al., 2018). We calculated PD using Faiths index (Faith, 1992), which represents the total branch length of a phylogenetic tree reconstructed from all species in a clade. ED quantifies the uniqueness of a species relative to other species and is a valuable tool in conservation efforts (Cadotte and Jonathan, 2010). ED is defined as the sum of the pairwise distances between each lineage and all other lineages, divided by the number of lineages minus one. NND also quantifies the uniqueness of a species, but only on a very local phylogenetic scale, as it is defined as the phylogenetic distance (branching length of the path) between a lineage and its nearest neighbor. NND measures the degree to which species are locally clustered within specific clades, and is less sensitive to higher-level phylogenetic structures than ED (Webb, 2000). Unlike PD, which is a clade-level metric and assigns a single value for all species in the clade, ED and NND are lineage-specific metrics, with each lineage assigned its own value.

When using PD as an ER metric, we assume that the speciation rate of all lineages λ_{PD} can be written as

$$\lambda_{\mathrm{PD}} = \max\left(\lambda_0 + \beta_N N + \beta_\Phi \Phi,\ 0\right) \tag{1}$$

where λ_0 is the intrinsic speciation rate of all the lineages, N is the total species richness, Φ is the value of ED, β_N is a coefficient to adjust the size of the effect of species richness on the speciation rate and β_Φ is a coefficient to adjust the size of the effect of ER on the speciation rate. β_N and β_Φ can be positive, zero, or negative.

To account for the strong correlation between phylogenetic diversity and time, we included an offset method in our model to compensate for the inflation of branch

lengths in the phylogenetic tree. The method subtracts the tree age t from Φ_t which is the phylogenetic diversity at time t. The adjusted Φ'_t is then given by

$$\Phi'_t = \Phi_t - t. \tag{2}$$

Unlike PD, both ED and NND are calculated for every lineage: λ_i, the speciation rate of a specific lineage i, is given by

$$\lambda_i = \max\left(\lambda_0 + \beta_N N + \beta_\Phi \Phi_i,\ 0\right) \tag{3}$$

where λ_0 is the intrinsic speciation rate of all the lineages, N is the species richness (across all lineages), Φ_i is the per-lineage ER (either ED or NND) of the lineage i, β_N is a coefficient to adjust the effect size of species richness on the speciation rate and β_Φ is a coefficient to adjust the effect size of ER on the speciation rate. β_N and β_Φ can be positive, zero, or negative.

We assumed that the extinction rate μ is fixed to the intrinsic rate of extinction which is constant through time and across lineages:

$$\mu = \mu_0. \tag{4}$$

Simulations

We ran a series of simulations of the model under different scenarios in order to investigate the effect and signature of ER on various phylogenetic summary statistics. We started the simulations with two ancestral lineages, setting the values of ER of both lineages to zero. We used the Gillespie algorithm (Gillespie, 1976), in which the waiting time between two evolutionary events is sampled from an exponential distribution with a mean equal to the inverse of the sum of the rates of all possible events. The probability of each event is proportional to its own rate relative to the sum of the rates of all possible events.

Two types of events can occur: speciation and extinction. When a speciation event happens, a lineage at the tip of the tree bifurcates into two lineages. When an extinction event happens, a species is marked as extinct. The simulation lasts for a predetermined time, which equals the crown age of the final phylogeny. A successful simulation is conditional on survival of both crown lineages; the simulation will start over if one of the crown lineages goes extinct entirely (see Figure 2 for the illustration of the simulation). Our R package "eve" (Qin, 2023) contains the implementation of our model and simulation code.

We simulated phylogenies using a variety of parameter combinations (see Table 1). We assumed a crown age of 6 time units, which can be interpreted as 6 million years.

Parameter	Value
Intrinsic speciation rate	0.4, 0.5, 0.6
Intrinsic extinction rate	0, 0.1, 0.2
Crown age	6
Coefficient species richness N (β_N)	-0.04, -0.02, 0
Coefficient evolutionary relatedness (β_Φ)	-0.04, -0.02, 0, 0.001, 0.002
Evolutionary relatedness metric	PD, ED, NND

Table 1: Parameters used in the simulations

All combinations of parameters in Table 1 were used, to a total of 135 combinations, and each was repeated for the three different ER scenarios: PD, ED and NND. Thus, we had a total of 405 parameter sets. For each set we simulated 100 phylogenetic trees using the Peregrine high performance computing cluster of the University of Groningen. The parameter sets were chosen such that the simulation can be finished within the time and resource limits of the cluster. For this reason, the positive β_Φ values are kept relatively small to avoid large memory cost taken up by very large phylogenies.

Data analysis

Raw output from the simulations was processed using the "eve" package into data compatible with statistics functions in other R packages. For each parameter set, the "treestats" (Janzen, 2023b) and "eve" packages were used to calculate summary statistics for all extant trees, excluding those with only two extant lineages. The statistics chosen were the following: the J One balance index (Lemant et al., 2022), the Gamma statistic (Pybus and Harvey, 2000), mean branch length (MBL), mean pairwise distance (MPD) (Webb et al., 2002) and the Rogers J index of imbalance (Rogers hereafter) (Rogers, 1996), see glossary for their definitions.

The effects of SR and ER were measured by the values of β_N and β_Φ, respectively. The effects of the scale at which the effect operates, from whole-clade, to species-specific were determined by the ER mechanism (one of the three ER measures: PD (whole-clade), ED (intermediate) and NND (species-specific).

Speciation rate evenness

In the ED and NND scenarios, speciation rates are expected to vary between tree tips. We measured how these rates are distributed in phylogenies by adopting a concept similar to measuring species evenness in a community, but instead quantifying

the evenness of speciation rates across lineages weighted by their phylogenetic distances. Each phylogeny of n lineages was given by a correlation matrix $\boldsymbol{C}$ with each lineage i's speciation rate represented by λ_i $(i = 1, 2, 3, \ldots, n)$. The phylogenetic evenness index E is then defined as

$$E = \frac{\lambda \operatorname{diag}(\boldsymbol{C})^\top \boldsymbol{M} - \boldsymbol{M}^\top \boldsymbol{C} \boldsymbol{M}}{\lambda^2 - \bar{\lambda}_i \lambda} \tag{5}$$

which was originally proposed by Helmus et al. (2007). In the equation, λ denotes $\operatorname{sum}(\lambda_1, \lambda_2, \lambda_3, \ldots, \lambda_n)$ and $\bar{\lambda}_i$ denotes $\operatorname{mean}(\lambda_1, \lambda_2, \lambda_3, \ldots, \lambda_n)$, $\operatorname{diag}(\boldsymbol{C})$ denotes the diagonal elements of the correlation matrix $\boldsymbol{C}$ (see below), $\boldsymbol{M}$ denotes an $n \times 1$ column vector containing values of λ_i. The value of E ranges between 0 and 1. The maximum value (i.e., 1) of E only occurs when speciation rates among lineages are equal and the tree is completely balanced (star-like). Values of E less than 1 represent increasing unevenness of speciation rates among the lineages. E is sensitive to tree topology such that trees with uniform speciation rates can have different values of evenness.

The correlation matrix $\boldsymbol{C}$ is the standardized pairwise distance matrix computed as

$$\boldsymbol{C} = \frac{2t - \boldsymbol{R}}{2t} \tag{6}$$

where $\boldsymbol{R}$ is the pairwise distance matrix of all the lineages of the phylogeny of n lineages, with r_{ij} $(i = 1, 2, 3, \ldots, n; j = 1, 2, 3, \ldots, n)$ represents the pairwise phylogenetic distance between lineage i and j:

$$\boldsymbol{R} = \begin{bmatrix} 0 & r_{12} & r_{13} & \ldots & r_{1n} \\ r_{21} & 0 & r_{23} & \ldots & r_{2n} \\ r_{31} & r_{32} & 0 & \ldots & r_{3n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ r_{n1} & r_{n2} & r_{n3} & \ldots & 0 \end{bmatrix}. \tag{7}$$

Data visualization

For visualization purposes, we selected one representative tree for each tree set of 100 trees representing a single parameter set. This tree was chosen among the complete trees based on its index vector, which has the smallest mean Mahalanobis distance (De Maesschalck et al., 2000) to the other trees in the same tree set. In order to calculate the Mahalanobis distance for each tree, we first defined the index

vector for the i-th tree in a set of trees resulted from k-th parameter set, where k denotes one of the parameter sets in the 405 combinations in our simulation, as

$$\boldsymbol{v}_{i,k} = \left(v_{\mathrm{J}}^{i,k},\quad v_{\mathrm{G}}^{i,k},\quad v_{\mathrm{P}}^{i,k},\quad v_{\mathrm{M}}^{i,k},\quad v_{\mathrm{R}}^{i,k}\right)^{\top} \tag{8}$$

where each element of $\boldsymbol{v}_{i,k}$ represents a summary statistic of the i-th tree in the k-th set. $v_{\mathrm{J}}^{i,k}$ denotes J One, $v_{\mathrm{G}}^{i,k}$ denotes Gamma, $v_{\mathrm{P}}^{i,k}$ denotes PD, $v_{\mathrm{M}}^{i,k}$ denotes MPD, $v_{\mathrm{R}}^{i,k}$ denotes Rogers and $\top$ denotes the transpose of vector. These five statistics were selected based on a clustering dendrogram of various summary statistics, where they were found to be less correlated and more evenly spaced than other statistics (see Appendix B).

The Mahalanobis distance of $\boldsymbol{v}_{i,k}$ is given as

$$d_{\mathrm{M}}(\boldsymbol{v}_{i,k}) = \sqrt{(\boldsymbol{v}_{i,k} - \bar{\boldsymbol{v}}_k)^{\top}\boldsymbol{S}^{-1}(\boldsymbol{v}_{i,k} - \bar{\boldsymbol{v}}_k)} \tag{9}$$

where $\boldsymbol{v}_{i,k}$ is the index vector for the i-th tree of the k-th set. $\bar{\boldsymbol{v}}_k$ comprises five mean values of each element respectively in the index vectors in the k-th set, $\top$ denotes the vector transpose, $\boldsymbol{S}$ is the covariance matrix of these vectors and $\boldsymbol{S}^{-1}$ denotes the inverse of $\boldsymbol{S}$.

For each representative tree (i.e. the tree with the smallest Mahalanobis distance to the other trees), we mapped the historical speciation rates onto the tree using the "eve" package. The variation of speciation rates along tree lineages is represented by a continuous color scale. The actual rate values corresponding to colors were calculated as mean speciation rates (mean value of speciation rates at the beginning and at the end) of the time frames between evolutionary events in a simulation.

LTT plots were generated using the "eve" package for each tree set by summarizing all the trees in the set and then displaying the mean LTT curve along with shading representing the confidence interval of the set. The LTT plots were based on extant species only.

Results

Simulation performance

All simulation jobs were completed within seven hours on the computing cluster, with most of the parameter sets finishing within one hour.

In most of the parameter sets and ER scenarios, the simulation reached an equilibrium state or at least the lineage accumulation is decelerating, as can be concluded

from the decreasing slopes of the curves on the LTT plots (see the animations in Appendix C). In the cases where extinction rates are 0 and no species richness effect is present, a deceleration in lineage accumulation is observed in the PD scenario, but only when β_Φ is negative (see Figure 3).

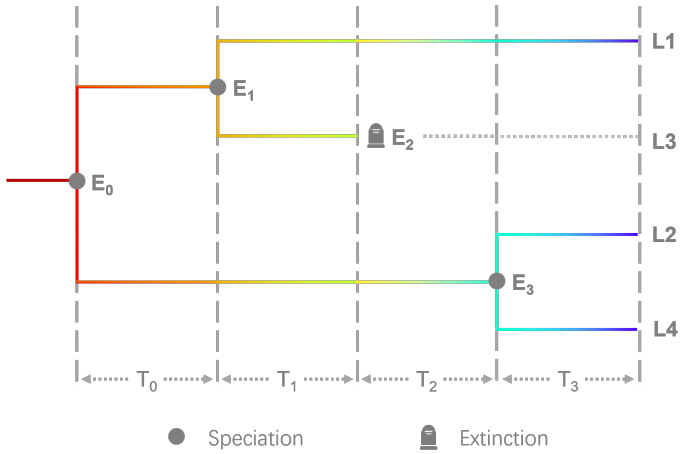

Figure 2: Illustration representing a stochastic simulation under the assumptions of positive speciation and extinction rates alongside a negative coefficient of evolutionary relatedness, exemplified through a scenario where phylogenetic diversity (PD) acts as a clade-wide constraint. Two event types are depicted: speciation (solid grey circles) and extinction (tombstone symbols). During a speciation event, a lineage at a tree tip bifurcates into two lineages (e.g., E_0, E_1 and E_3). An extinction event marks a species as extinct (e.g., E_2). The branch color transition from red to blue signifies the variation in the speciation rate of lineages along PD. The simulation unfolds as follows: it initiates from E_0 with two ancestral lineages $L1$ and $L2$, setting the initial PD value to 0. Speciation rates for all extant lineages (initially $L1$ and $L2$) are derived from PD. The first time interval, T_0, extends the branch lengths of $L1$ and $L2$. Prior to sampling event E_1, PD is recalculated based on extant lineages, and speciation rates are updated. Event E_1 illustrates $L1$ bifurcating into $L1$ and $L3$. The subsequent time interval T_1 further extends the branch lengths of $L1$, $L2$, and $L3$. Before sampling each event, PD and speciation rates are updated. Event E_2 marks the extinction of $L3$, halting its branch growth while $L1$ and $L2$ continue to extend through time interval T_2. Event E_3 illustrates the speciation of $L2$ into $L2$ and $L4$. The final time interval, T_3, stops the simulation because the cumulative time $(T_0+T_1+T_2+T_3)$ surpasses a pre-determined time threshold, T. T_3 is then set to $T-(T_0+T_1+T_2)$. The branch lengths of $L1$, $L2$, and $L4$ extend by T_3, marking the simulation endpoint.

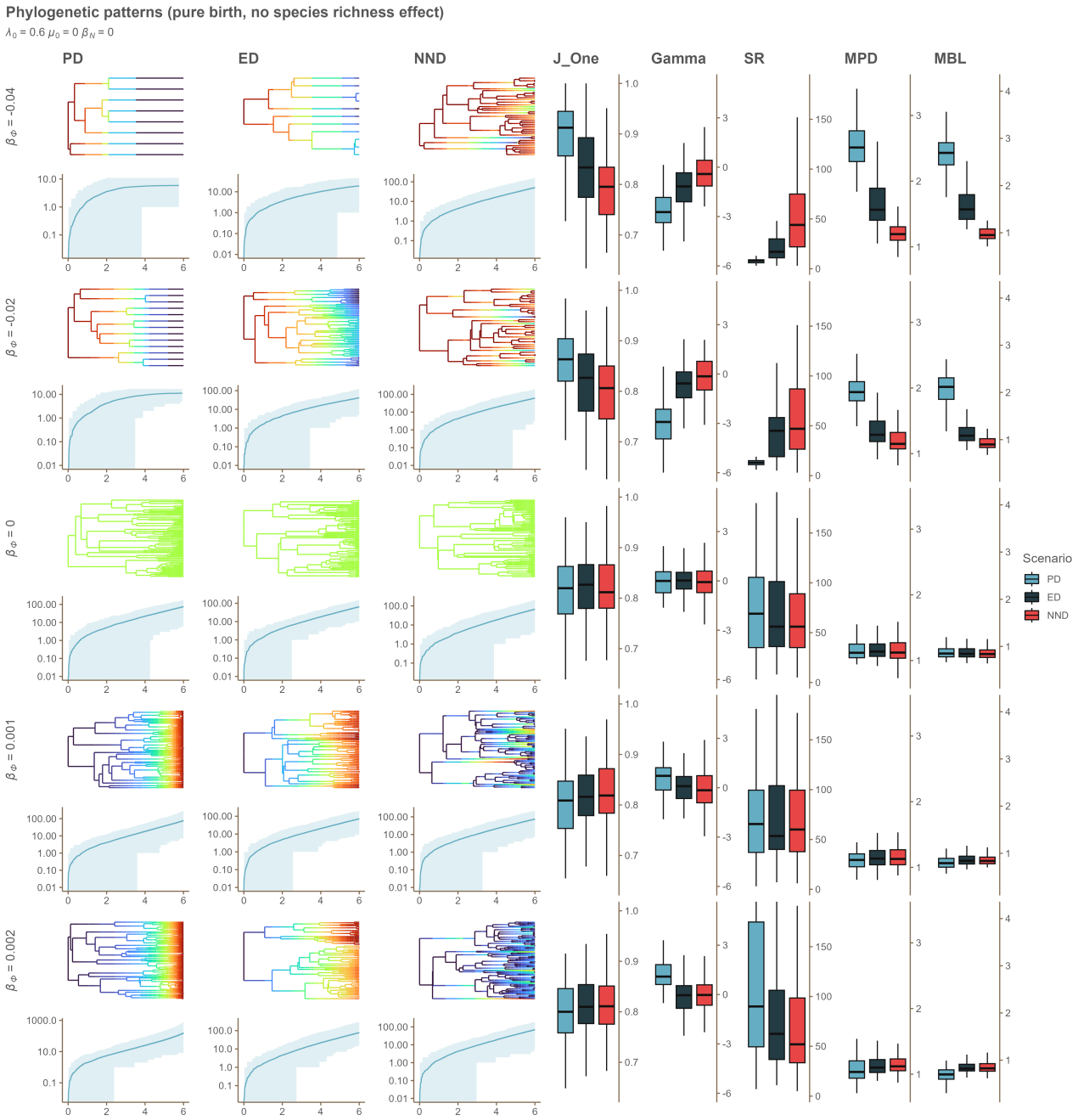

Figure 3: Overview of results of simulations of a pure birth process (no extinction, see Appendix C for other speciation and extinction rate combinations), with dependence of speciation on evolutionary relatedness. For all parameters sets shown in the figure, the intrinsic speciation rate at the start of the simulation (λ_0) is 0.6, the intrinsic extinction rate (μ_0) is 0, and the coefficient of the species richness effect (β_N) is 0. The results are grouped by rows according to varying levels of β_Φ (the coefficient of the evolutionary relatedness effect). On the left, representative simulated phylogenies and associated lineage-through time (LTT) plots are shown for dependence of speciation rates on three metrics of ER (left - phylogenetic diversity (PD), middle - evolutionary distinctiveness (ED), and right - nearest neighbor distance (NND) scenario). The colors mapped onto the trees represent the values of the speciation rate for each of the lineages during simulation time. The rates increase from blue to red. The trees coloured in green are cases where the speciation rate remains unchanged throughout the simulation. Blue line in the LTT plots represents lineage accumulation through time and the shaded area is the 95% confidence interval. On the right of each row, boxplots for the corresponding summary statistics are shown: J One - J One balance index; Gamma - Gamma statistic; SR - total number of extant lineages; MPD - mean pairwise distance; MBL - the mean branch length.

Effects of evolutionary relatedness on phylogenetic patterns

We observed a hierarchical structuring in tree topology patterns, from PD to ED to NND. Under the PD scenario, trees exhibit a higher degree of balance (interpreted from the J One balance index) than in the ED scenario, which in turn exhibits more balanced trees than the NND scenario. This pattern is more prominent when β_Φ decreases from zero towards more negative values, that is, when evolutionary relatedness imposes a stronger reduction of the speciation rate of the communities. As β_Φ increases from negative to positive values, the differences in tree balance between PD, ED and NND scenarios are diminished, and the trees exhibit generally lower degree of balance (see the animations in Appendix A ending with J_One).

As β_Φ increases from -0.04 to 0, a general decrease in the mean pairwise distances (MPDs) of the trees is observed. However, no substantial change occurs when β_Φ shifts from 0 to positive values. When β_Φ is negative, the trees under the PD scenario exhibit larger MPD than those in the ED scenario and the trees under the ED scenario exhibit larger MPD than those in the NND scenario. As β_Φ increases from -0.04 to 0, the disparities in MPDs among PD, ED, and NND scenarios decrease (see the animations in Appendix A ending with MPD and MBL). The patterns of MBL across β_Φ settings are similar to those of MPD.

The distribution of internal nodes, or the concentration of speciation events, were interpreted using the Gamma statistic. When β_Φ is negative, the speciation events in the PD scenario are located more closely to the root than in the ED scenario, and the events in the ED scenario are closer to the root than those in the NND scenario. These differences are reduced as β_Φ increases from negative values towards zero. This pattern changes as β_Φ shifts from zero towards positive values, particularly when β_N is 0. As β_Φ increases from -0.04 to 0.002, the distributions of speciation events in all three scenarios change from being closer to the root to being more evenly distributed throughout the temporal range of the phylogeny (see the animations in Appendix A ending with Gamma).

The trees become notably larger (more species) as β_Φ increases from -0.04 to 0. This increase is minimized when β_Φ increases from 0 to 0.002. When β_Φ is negative, the tree sizes are generally largest in the NND scenario, second largest in the ED scenario and smallest in the PD scenario. This pattern does not persist when β_Φ is zero or positive. The pattern is reversed when β_Φ is positive, in which case the PD scenario generally has the largest tree sizes and the NND scenario the smallest (see the animations in Appendix A ending with SR).

Of all model parameters, β_Φ has the strongest effect on the evenness of the speciation rates across lineages. In all parameter combinations, the disparities of Speciation rate evenness between PD, ED and NND scenarios decline with increasing β_Φ (see

Figure 4B and the animations in Appendix A ending with ERE).

Interaction between the effects of evolutionary relatedness and species richness

The effects of β_Φ (for instance the degree of disparities of the statistics between PD, ED and NND scenarios, and the changes of the statistics along with varying β_Φ) appear more prominent when β_N imposes a less pronounced (i.e. less negative) effect on the communities, with the strongest effects observed at $\beta_N = 0$. From another point of view, the influence of β_N on the tree summary statistics is more prominent when β_Φ shifts towards more negative values (see Figure 4A).

When the negative effect of SR on speciation rate becomes weaker (β_N increases from -0.04 to 0), the trees become larger and less balanced, mean branch lengths (MBLs) and mean pairwise distances (MPDs) of the trees become smaller, the distribution of speciation events changes from being closer to the root to being more evenly distributed, and the degrees of disparities of speciation rate evenness among PD, ED and NND increase (see Figure 4A for details and see all the animations in Appendix A starting with beta_n for animated comparisons). Generally, stronger negative SR effect reduces the differences of tree statistics among PD, ED and NND scenarios, it also reduces the differences of the statistics between different β_Φ settings. This is particularly true for the Gamma statistic and J One balance index.

The above described patterns, however, do not apply to speciation rate evenness. When the negative effect of SR on speciation rate becomes stronger (β_N decreases from 0 to -0.04), the disparities of speciation rate evenness among PD, ED and NND scenarios appear more prominent when β_Φ value becomes more negative.

Effects of intrinsic speciation and extinction rates

Higher intrinsic speciation rates (λ_0) lead to less balanced phylogenetic trees and more disparities among the scenarios. Higher intrinsic extinction rates (μ_0), however, lead to more balanced trees and less disparities. The effects of λ_0 and μ_0 are intertwined with both β_Φ and β_N. The effects are described in detail in Appendix E. Besides Figure 4, we also produced a set of animated plots (Appendix A), showing how tree summary statistics we measured change along with β_Φ, β_N, λ_0 and μ_0, to help interpret the patterns resulting from different levels of evolutionary relatedness effects (as determined by β_Φ) and between the three different versions of ER dependence.

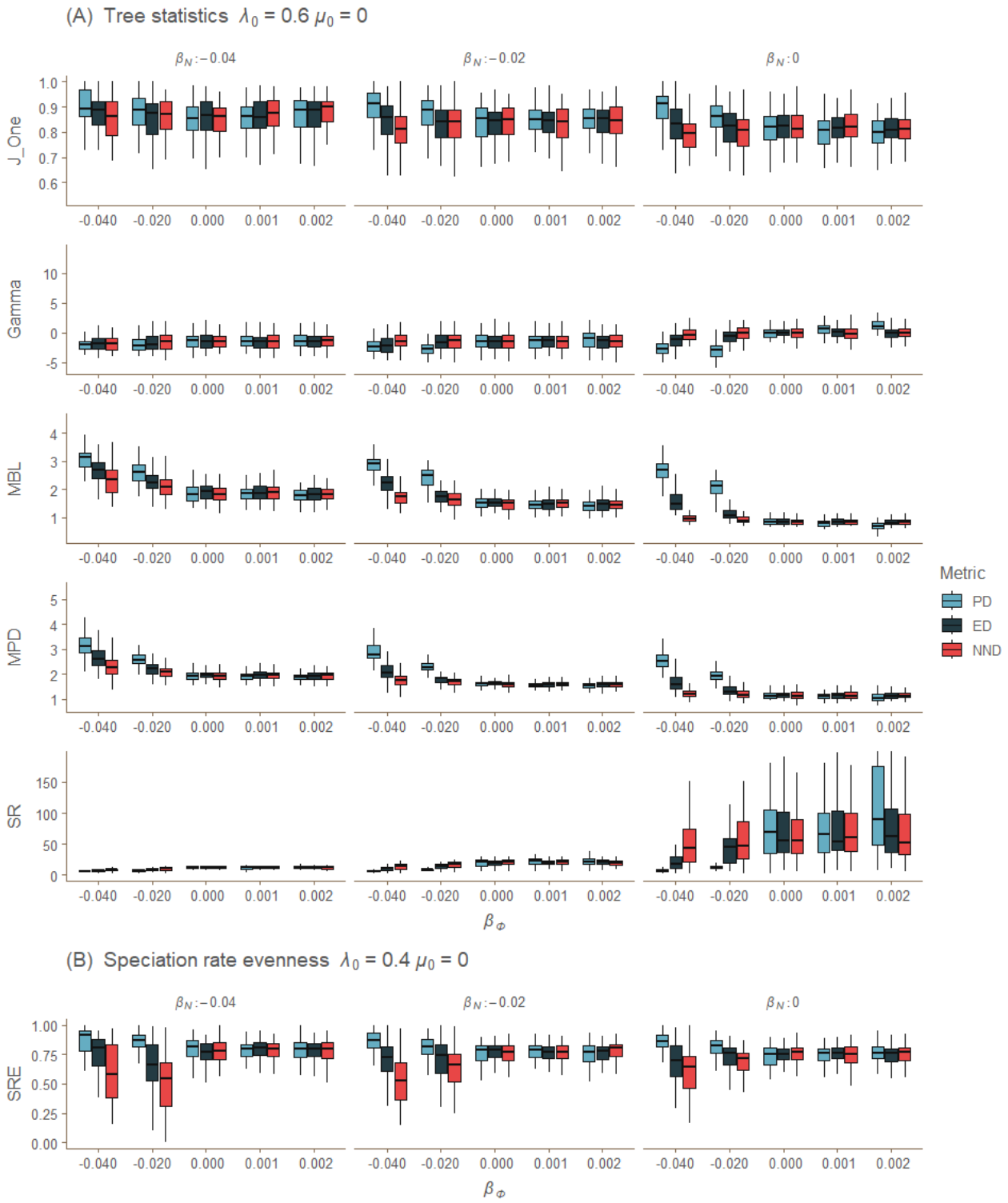

Figure 4: Tree summary statistics for the three scenarios of dependence of speciation rates (dependence on phylogenetic diversity (PD), evolutionary distinctiveness (ED) and nearest neighbor distance dependence (NND)), for various levels of the evolutionary relatedness effect (β_Φ) and the species richness effect (β_N). λ_0 - initial speciation rate; μ_0 - fixed extinction rate; x-axis: strength of ER effects; y-axis: value of the statistics. The following statistics are shown in panel A: J One - J One balance index; Gamma - Gamma statistic; MBL - the mean branch length; MPD - mean pairwise distance; SR - total number of extant lineages. The folloing statistic is shown in panel B: SRE - speciation rate evenness. SRE is shown in a separated panel because it has different patterns and is in a different parameter setting. We pick SRE from this parameter setting to better present the disparities among different scenarios and across different levels of the ER effect.

Discussion

From clade-wide to lineage-specific: ecological limits shape evolutionary trajectories

Evidence for ecological limits on diversity has been found or suggested in many studies (Rabosky, 2009a; Mittelbach et al., 2007), and ecological limits may exert influence on diversification by directly impacting rates of speciation (Wiens, 2011). Our simulations further suggested that, from clade-wide to lineage-specific, different extents of ecological limits result in unique phylogenetic tree properties, when using ER as a proxy.

Within the PD scenario, a negative ER effect (or β_Φ, the corresponding parameter in our simulations) can be interpreted as a niche space limitation on clade expansion as phylogenetic diversity increases, which applies equally to all species in the clade. Under this model, an increase in phylogenetic diversity within a clade leads to saturation of niches. Conversely, a positive ER effect provides the clade with the potential to exploit additional resources as phylogenetic diversity increases, potentially resulting in a rapid accumulation of species as the potential for biotic interactions increases.

By relating clade-wide speciation rate to ER, the PD scenario exhibits similarities to models with diversity carrying capacity (e.g. DDD model), with negative β_Φ imposing an upper limit on phylogenetic diversity carrying capacity. Both negative β_N and β_Φ markedly reduce average tree sizes, given a constant simulation time.

In the ED and NND scenarios, a negative ER effect indicates a scenario where more distantly related species are less likely to speciate, which may reflect sympatric speciation (Bolnick and Fitzpatrick, 2007), which can be an outcome of competition for resources, or may reflect environmental filtering (Thakur and Wright, 2017), where closely related species are more likely to speciate. In contrast, a positive ER effect indicates that these more distantly related species are more likely to produce descendants, for example, allopatric speciation (Kozak and Wiens, 2006) due to species adapting to different environmental conditions.

By relating lineage-specific speciation rates to ER, the ED and NND scenarios can account for evolutionary trajectories in which niches are either conserved (more similar than expected), constrained (diverging within a restricted range of available niches), or divergent (less similar than expected), based on different settings of ER effects (see the illustration of niche conservatism by Pyron et al. (2015)). Negative β_Φ also trims the average tree sizes in the ED scenario, but this effect seems diminished or even absent in the NND scenario. The negative effects of β_Φ decrease from PD to ED to NND; along this "gradient" of metrics, ecological limits exert increasingly smaller influence on overall species richness of the communities, due to their impacts

being more concentrated to close relatives (see also the speciation rate transitioning in Figure 3).

The unevenness of speciation rates among the tips increases from PD to ER and NND (note that although in PD scenario all tips of a tree have the same speciation rate, PD trees from the same parameter setting could still have different unevenness due to different tree topology). When β_Φ is negative, the more distinct lineages are less likely to spawn new lineages, leading to a "clustering" where closer lineages have closer speciation rates. As the effect of ER goes from PD to ER to NND, large "clusters" break apart into small and separate clades on the tree, thereby increasing unevenness. When we shift β_Φ to positive, more distinct lineages are more prone to speciate, which may cause an "overdispersion" of the rates rather than a "clustering" (Figure 4B). In the ED and NND scenarios, the speciation rates among the tips are directly determined by their distances to the clade (ED) or their immediate neighbors (NND), so the observed unevenness could also be interpreted as an unevenness of ER.

In general, we observed hierarchical patterns in various summary statistics (e.g. J One, Gamma and speciation rate evenness) from clade-wide to lineage-specific ecological limits when β_Φ is negative. These patterns fade as β_Φ increases to 0. However, we also observed prominent difference of tree sizes between scenarios, with PD trees being the smallest, ED trees being noticeably larger and NND trees being the largest on average. Tree size often shows strong correlation with phylogenetic tree statistics, even after applying size correction methods, regardless of the underlying model (Janzen, 2023a). This may explain why β_Φ impacts the balance and MPD of PD trees, even though speciation rates across lineages are consistently uniform. To verify if tree size confounds our interpretation, we compared all the statistics from our results with the tree size correlation curves by Janzen (2023a). We found that the correlations between statistics and tree size in our results are opposite to patterns observed by Janzen (2023a) as tree size increases from 10 to 100. This implies that our findings are unlikely to be due to an effect of tree size. Rather, if the effect of tree size would be corrected for, we would expect our patterns to be even more pronounced.

Species richness effect reduces evolutionary relatedness signature

Debates in ecology persist regarding the efficacy of phylogenetic metrics serving as proxies for species richness or functional diversity (Mazel et al., 2018; Owen et al., 2019). Our model introduces a more flexible scenario wherein species richness and phylogenetic (or evolutionary) relatedness operate concurrently. We observed a stronger impact of ER effect size as SR exerts a less negative effect on speciation rate

in communities, with the most pronounced ER impact occurring at $\beta_N = 0$, where SR has no influence on species diversification. Furthermore, we noted that as SR imposes a more negative effect, the disparities in various tree statistics (e.g., J One, MBL, MPD, and Gamma) among PD, ED, and NND scenarios become less evident or even disappear. Based on these patterns, we suggest that the presence of an SR effect can conceal the signature of evolutionary relatedness. However, ER can still elucidate biodiversity if the effect of SR is minor and the effect of ER is substantial, as the sizes of these effects may vary among natural communities globally.

Conclusion

We have introduced a novel perspective on the influence of ecological limits, represented by the effects of evolutionary relatedness on species diversification patterns, which lead to a variety of macro-evolutionary trajectories. Our results show that the effects of ecological limits associated with phylogenetic distance between species are highly dependent on the scale at which these limits operate, as well as whether the effects of evolutionary relatedness on speciation rates are positive or negative.

We have also presented evidence of the complex interplay between the effects of species richness and evolutionary relatedness on diversification, suggesting that strong species richness effects can reduce the influence of evolutionary relatedness on species diversification, thereby complicating interpretations of diversity slowdowns in macroevolutionary studies. This finding suggests a re-evaluation of how these factors operate concurrently to shape biodiversity patterns is needed.

Glossary

ED Evolutionary distinctiveness, a measure of how unique or distinct a species is in terms of its evolutionary history. ED is computed by summing the pairwise distances between each lineage and all other lineages, divided by the number of lineages minus one. A species with high ED has fewer close relatives and represents a larger amount of independent evolutionary history than a species with low ED (Cadotte and Jonathan, 2010)..

ER Evolutionary relatedness, a measure of evolutionary relationships between species. In our study, ER can be measured as PD, ED or NND (see definitions below)..

Gamma Gamma statistic, a measure of internal node distribution. The value of gamma is calculated based on the distribution of node heights. A negative gamma value suggests a decrease in diversification rate over time, while a positive gamma value indicates an increase in diversification rate (Pybus and Harvey, 2000)..

J One J One balance index, a measure of the degree of balance of a phylogeny. It is defined for trees with any degree distribution, and enables meaningful comparison of trees with different numbers of tips (Lemant et al., 2022)..

MBL Mean branch length, a measure of average evolutionary change or divergence represented in a phylogenetic tree. It is calculated by summing the lengths of all the branches in a phylogenetic tree and dividing by the total number of branches (Webb et al., 2002)..

MPD Mean pairwise distance, a measure of the average pairwise phylogenetic distance between species in a clade. It calculates the average of all pairwise distances between species in a phylogenetic tree, providing a measure of the overall phylogenetic spread (Webb et al., 2002)..

NND Nearest neighbor distance, a measure of how distinct a species is in terms of its evolutionary history with respect to the most closely related species. NND is computed by taking the branch length distance on a phylogenetic tree from one species to its nearest neighbor on the tree. While ED measures distinctiveness on a global phylogenetic level, NND measures it on a local phylogenetic level (Webb, 2000)..

PD Phylogenetic diversity, a measure of biodiversity that takes into account the evolutionary relationships between species. Specifically, PD is the minimum total length of all the phylogenetic branches required to span a given set of taxa on the phylogenetic tree. It provides insight into the evolutionary history represented by a group of species (Faith, 1992)..

Rogers Rogers balance index, a measure of "patristic distance", which represents the sum of branch lengths between two taxa in a phylogenetic tree which reflects the total amount of change along the evolutionary path between two taxa (Rogers, 1996)..

Speciation rate evenness a measure of how evenly the speciation rates are distributed on the tips of a phylogeny, using an approach originally proposed by Helmus et al. (2007), which is similar in concept to Pielo's evenness index in community ecology. Its value is between 0 and 1. Values less than 1 represent increasing unevenness of speciation rates. It is also sensitive to tree topology: if the tips of a tree have the same speciation rates, the evenness value will be 1 (maximum) only when the tree is star-like..

SR Species richness, a measure of the number of different species present in a particular area or ecological community. It is a simple count of species..

Appendix A. Animation of main simulation

Animated plots were generated to aid the explanation of model behaviors and phylogenetic patterns of the main simulation. The plots were named in a format of "parameter_statistic.gif" where parameter refers to the changing parameter in the animation and statistic refers to the summary statistic the plot shows. For example, "beta_n_Gamma.gif" is an animation showing the Gamma statistics among different parameter settings and transitioning in β_N.

Appendix B. Heatmaps

Heatmaps were plotted to visualize the correlation matrix of a number of tree statistics under different ER scenarios. A representative tree was selected based on the heatmaps, using the statistics that are less correlated and more evenly spaced on the heatmap. There are three heatmaps, each presenting one scenario.

Appendix C. Tree statistics and LTT plots with representative trees

Tree statistics and LTT plots with representative trees were plotted for all the parameter settings of the main simulation. The plots were named in a format of "λ_0_μ_0_β_N.png". For example, "0.6_0_0.png" presents the results under the parameter setting $\lambda_0 = 0.6$, $\mu_0 = 0$ and $\beta_N = 0$.

Appendix D. Trees statistics at different sizes

Tree statistics were also plotted in animation to examine the patterns without tree size effect and how they change through increasing tree size (number of tips). The plots were named such that the file names refer to the tree statistic the plot presents. Besides those animations there are also two static plots with file names containing more than one statistic name.

Appendix E. Effects of intrinsic speciation and extinction rates

We found that the intrinsic speciation rate (λ_0) also showed a substantial impact on tree statistics. The effects of this parameter are intertwined with both β_Φ and β_N (see animations in Appendix A starting with lambda and mu).

As λ_0 increases, the differences in tree balance across scenarios increase, particularly when β_Φ has smaller positive effect or the effect is more negative. The trees become generally less balanced as λ_0 increases. The effects of λ_0 are stronger when

β_Φ is more negative and β_N is closer to zero, with the most profound case being $\beta_\Phi = -0.04$ and $\beta_N = 0$ where increasing λ_0 results in most evident increase of disparities of balance between PD, ED and NND scenarios (see the animations in Appendix A starting with lambda and ending with J_One).

In contrast to λ_0, an increase in the intrinsic extinction rate (μ_0) results in more balanced trees and less disparities of balance among the PD, ED and NND scenarios. The reduction of disparities is more prominent when β_Φ becomes more negative. The most prominent case is when $\beta_\Phi = -0.04$ and $\beta_N = 0$ where increasing μ_0 results in most evident reduction of disparities of balance between PD, ED and NND scenarios (see the animations in Appendix A ending with J_One) (see the animations in Appendix A starting with mu and ending with J_One).

An increase in λ_0 from 0.4 to 0.6 generally leads to a reduction in MBL and MPD, while an increase in μ_0 from 0 to 0.2 generally leads to an increase in these statistics (see the animations in Appendix A staring with lambda and mu, ending with MPD and MBL).

The disparities of speciation events distributed across the phylogeny among PD, ED and NND scenarios, as measured by the gamma statistic, become more prominent as λ_0 increases and less prominent as μ_0 increases. The distribution of speciation events changes from being closer to the root to being more evenly distributed as μ_0 increases (see the animations in Appendix A staring with lambda and mu, ending with Gamma).

When β_Φ effect is negative, increasing λ_0 has the largest effect of increasing the tree sizes in the NND scenario. This effect is smaller in the ED scenario and even smaller in the PD scenario. Increasing μ_0 has the largest effect of reducing the tree sizes in the NND scenario; this effect is smaller in the ED scenario and even smaller in the PD scenario. When β_Φ effect is zero or positive, these trends are diminished (see the animations in Appendix A staring with lambda and mu, ending with SR).

Increasing λ_0 only has the effect of reducing the disparities of speciation rate evenness among PD, ED and NND when β_Φ is negative and β_N is 0. μ_0 has no obvious effect on the evenness of the speciation rates (see Figure 4B and the animations in Appendix A staring with lambda and mu, ending with ERE).

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