



# Effects of the interaction between Linnean and Darwinian shortfalls on diversification gradients

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## Abstract

It is now widely recognized that broad-scale patterns in species richness, particularly the Latitudinal Diversity Gradients (LDGs), are driven by complex interactions among ecological, evolutionary, and historical processes. However, even if it is now possible to better evaluate evolutionary explanations for LDGs based on speciation and diversification rates estimated from phylogenies, a subtle interaction between such estimates and the geographic structure of the Linnean shortfall, forming the Latitudinal Taxonomy Gradient (LTG), was recently recognized. Here, we expand on previous simulation results and show that a relatively small geographical bias in the Linnean shortfall, adding less than 20% of new species phylogenetically correlated with previously described ones in the southern (richer) region, would be enough to change the patterns in diversification rates, based on different methods (tip rates DR and GeoSSE). Further investigations of the magnitude of LTG and new empirical modeling of problems in species delimitation are thus necessary to evaluate the robustness of the estimates of the diversification gradients to biased knowledge and taxonomic uncertainty, allowing a better understanding of the evolutionary dynamics underlying LDGs.

## Highlights

- Geographical patterns in the Linnean shortfall, creating Latitudinal Taxonomy Gradients (LTGs), may jeopardize robust estimates of diversification gradients and our understanding of processes underlying diversity patterns.
- Simulations show that a relatively small geographic bias in the Linnean shortfall, adding new undiscovered species phylogenetically close to the known ones, is

sufficient to invert patterns in diversification rates estimated by two distinct methods.

- A more comprehensive assessment of the magnitude of diversification gradients in respect to the LTGs is necessary to evaluate the robustness of our understanding of LDGs.
- Empirical modeling of species delimitation quality and simulations adding small branches in the phylogenies, mitigating simultaneously both Linnean and Darwinian shortfalls, may provide more consistent evidence for drivers of LDGs accounting for taxonomic uncertainty.

## Keywords

Darwinian shortfall, diversity gradients, diversification rates, GeoSSE, latitudinal taxonomy gradient, Linnean shortfall, macroecology

## Introduction

There is now some consensus that the broad-scale diversity patterns, in particular the Latitudinal Diversity Gradients (LDGs), are a product of complex interactions between historical patterns and ecological responses to changing environments (Saupe 2023). Although there are still many important discussions about the multiple possible causal pathways leading to these diversity patterns and how to disentangle them (Diniz-Filho et al. 2023a), it is gradually becoming clear that geographically-structured variation in diversification rates (i.e., the difference between speciation and extinction rates) is involved in the origin and maintenance of such patterns over both deep and more recent time-scales (Wiens

and Donoghue 2004; Ricklefs 2006; Mittelbach et al. 2007; Storch et al. 2018; Etienne et al. 2019; Saupé 2023).

The subtle shift from contrasting ecological and evolutionary diversification in the attempt to understand broad-scale diversity patterns has been possible because, in the last 20 years or so, there has been an increase in the available phylogenetic information that allows the application of new methods to estimate more comprehensively diversification rates. These advances are facilitated by the ease of getting and producing new molecular data, allowing the building of phylogenies for large groups of organisms, as well as using imputation procedures to fill the gaps in the available backbone phylogenies (e.g., Ricklefs 2007; Pyron and Burbrink 2013). These advances in the ability to reconstruct the phylogenetic history of organisms were quickly matched by the development of new statistical and computational methods to estimate such rates in a geographically explicit context (Goldberg et al. 2011; Jetz et al. 2012; Caetano et al. 2018; Nurk et al. 2020).

Despite these advances and the optimism in estimating diversification rates from molecular phylogenies, there are still many issues to solve, both theoretically and methodologically, including underdetermination issues (Louca and Pennell 2021, but see Morlon et al. 2022), the biases in such estimates when the fossil record is not taken into account (Quental and Marshall 2010), and the difficulty in modeling complex, non-stationarity diversification processes (Morlon 2014; Marshall and Quental 2016). Although comprehensive phylogenies are available for some large groups of organisms, especially terrestrial vertebrates, there are still many gaps in our knowledge of the phylogenetic relationships among species for most of Earth's biodiversity. This has several implications for understanding diversification patterns and trait evolution (Diniz-Filho et al. 2013; Hortal et al. 2015). Despite a lack of knowledge of detailed phylogenetic relationships for many groups of organisms, Diniz-Filho et al. (2013) proposed that using diversity metrics and conservation strategies based on phylogenetic patterns would be more robust than counting species. Thus, for practical purposes, solving or mitigating the Darwinian shortfall might be a way to "by-pass" the urgency to describe new species and better delimitate the known ones (i.e. the Linnean shortfall; see Whittaker et al. 2005; Costello et al. 2013; Hortal et al. 2015) and improve our understanding of the overall biodiversity patterns (e.g., Blackburn et al. 2019; Lum et al. 2022). However, a recent proposal by Freeman and Pennell (2021) suggests that this strategy of indirect mitigation of the Linnean shortfall by minimizing Darwinian shortfall does not apply when it is necessary to estimate diversification rates and the ecological and evolutionary processes involved in the origin and maintenance of the latitudinal diversity gradients, as recently discussed by Diniz-Filho et al. (2023b).

Freeman and Pennell (2021) recently called attention to a geographically structured pattern in which temperate species are better delimited and better studied than tropical ones, resulting in what they called the "Latitudinal Taxonomic Gradient" (LTG). Even though the large differences

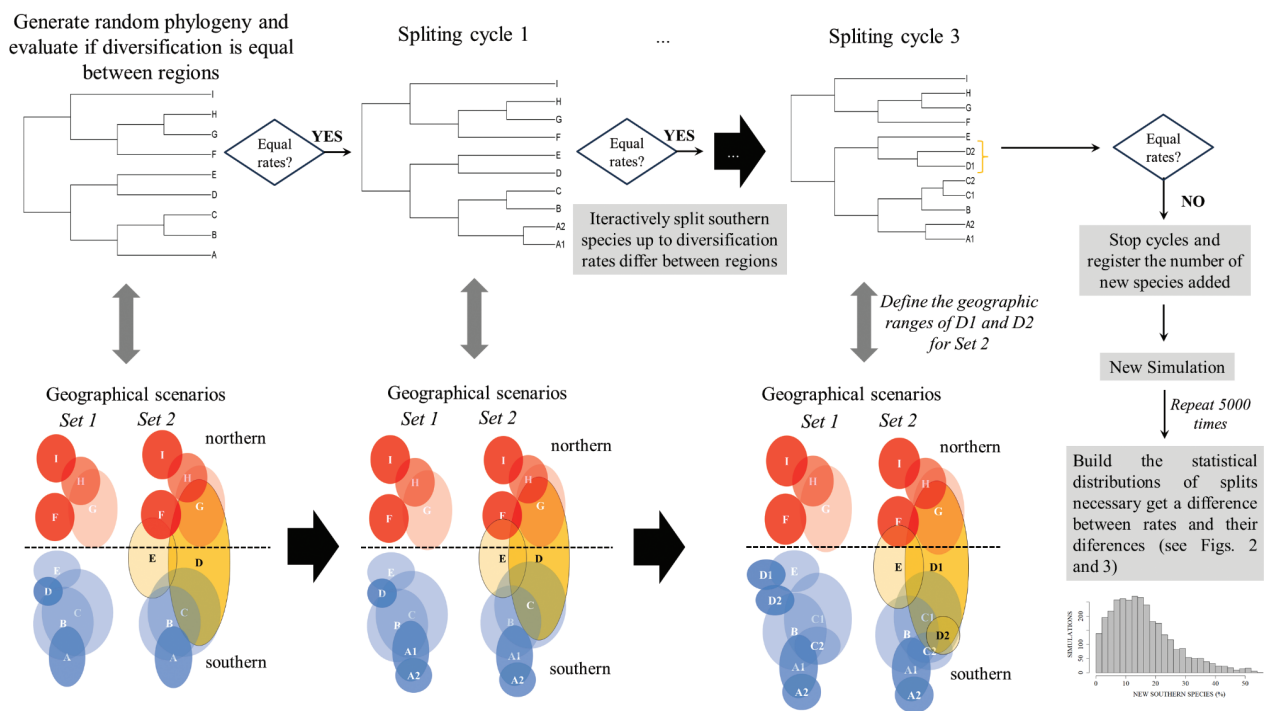
between temperate and tropical richness, as well as the potential subdivision of poorly known tropical species, are not likely to qualitatively change our understanding of the magnitude of the latitudinal gradients and their main geographical trends, they can strongly disturb the estimates of diversification rates. This is because such estimates are heavily affected by changes in the more recent branches in a phylogeny, resulting from subdividing currently known tropical species, through the raising of subspecies to full species, for instance. The LTG can thus completely disturb our understanding of the evolutionary dynamics underlying the latitudinal gradients and how speciation and extinction interact with environmental changes through time to generate the current patterns (Diniz-Filho et al. 2023b). At least in part, the LTG may be involved in the current uncertainty and discussions about geographic patterns in these rates (Jansson et al. 2013; Rolland et al. 2014; Puldido-Santacruz and Weir 2016; Schluter and Pennell 2017; Rabosky et al. 2018; Tietje et al. 2022)

Here, we expanded the discussions by Diniz-Filho et al. (2023b) and show how the LTG can affect our interpretation of the geographical patterns in diversification rates by developing a simulation approach with differential probabilities of splitting for species in northern and southern hemispheres. We started with a scenario in which these distinct regions are occupied by sister clades with equal diversification rates, but with a higher number of southern species. We assume, however, that these equal diversification rates are actually an artifact of the LTG. The approach proposed by Diniz-Filho et al. (2023b) involves sequentially subdividing poorly delimited southern species and adding small branches close to the tips of the phylogeny to evaluate how estimates of diversification rates are affected. Our main goal with these simulations is to evaluate the amount of uncertainty in tropical species delimitation that would be required to shift the diversification rates estimated using different methods.

## Methods

### Simulations of LTGs

Simulations follow the basic framework discussed by Diniz-Filho et al. (2023b), revealing the interactions between Linnean and Darwinian shortfalls when analyzing geographical patterns in diversification rates underlying the LDGs (Fig. 1). We started by generating random phylogenies with the number of species (tips) ranging between 50 and 500, assigning each species to northern or southern regions based on the first split at the root of a simulated phylogeny (i.e., the southern clade was the one with a higher number of species, mimicking the well-known LDG). Based on this approach, about 75% of the species in each randomly generated phylogeny are defined as southern species. We also generated a second set of simulations with a more complex geographical assignment in which 20% of the species would have geographic ranges encompassing



**Figure 1.** Methodological steps to evaluate the interaction between Linnean and Darwinian shortfalls under LTG driving biased estimates of diversification rates. We start with a randomly generated phylogeny and define northern and southern (richer) clades, and two geographical sets are defined. In the first geographical set, associated with tests based on mean diversification rates DR, species are assigned to northern and southern regions, and mean DR are compared using a PGLS. In the second set, 20% of the species are common to both regions (widespread species), allowing comparisons of speciation, extinction, and dispersal rates using GeoSSE. When a widespread shift, it is necessary to define the geographical distribution of the new species (the species D in the above framework). We start with a random phylogeny in which rates in northern and southern regions are equal and begin the splitting cycle in the southern species. The cycle stops when a difference between mean DR values appears in the PGLS and when a  $\Delta AIC > 3$  is obtained by comparing GeoSSE fit with a null model in which rates are equal between regions. This process is repeated 5000 times, generating a statistical distribution of the minimum number of new species added to the southern region that is sufficient to shift the diversification rates.

both northern and southern regions (widespread species), so that the GeoSSE could be applied (see below).

We then assume that there is a LTG underlying this simulated data, so that southern species are not well delimited due to a lack of more refined studies, making them more prone to subdivisions when more data become available. Thus, southern species can be subdivided into two “daughter” species (i.e., the currently known one and a newly defined one). We are thus assuming that the new species to be described are closely related to previously described ones (i.e., Isaac et al. 2004; Lum et al. 2022). This subdivision process in southern species was done sequentially, in a splitting cycle in which one species is subdivided at each step. At each step, we evaluated whether there was a significant shift in the diversification (speciation) rates estimated by the different methods (see next section) and stopped the splitting cycle when a significant shift appears.

In the first set of simulations, after each subdivision the newly described species are kept in the same (southern) region of the originally known species. In the second set, however, if the subdivision occurs for a species distributed in both northern and southern regions, it is necessary to further define the geographical scenario underlying this recent and previously unknown speciation, to give a more

realistic account of the biological interpretation of the simulations. We defined this probabilistically, considering four potential geographical scenarios. First, the pair of species after subdivision can still be found in both regions, with a probability for this scenario set for  $P = 0.1$ . Alternatively, the current geographic range can be divided between a southern and a northern species, revealing then a recent allopatric speciation, with a  $P = 0.35$ . We also assigned a  $P = 0.35$  to another scenario in which the original species can still be found in both regions, but the newly described one is restricted only to the southern region. This scenario thus assumes peripatric speciation and increase richness in the southern only, revealing an overlap between Linnean and Wallacean shortfall. Finally, it is also possible that the original species is still found in both regions, but the newly described one is restricted to the northern region and assigned to this scenario a  $P = 0.2$ .

## Analyses

We ran 5000 simulations for each of the two sets of simulations, which were associated with the two methods applied to detect shifts in diversification rates. In the first set,

we estimated the Diversification Rates (DR) following Jetz et al. (2012, see also Title and Rabosky 2019), given by the inverse of evolutionary distinctiveness of each species in the phylogeny (Reeding and Mooers 2006; Isaac et al. 2007). We then computed the mean tip rates for northern and southern regions and compared them (before starting the splitting cycles) using a Phylogenetic Generalized Least-Squares (PGLS) model accounting for the phylogeny. After that, we proceeded to the sequential splits of randomly selected species (the splitting cycles) only if the initial PGLS did not show significant differences between mean DRs in the two regions. This ensures that the difference between the two regions at the end of splitting cycles is a consequence of mitigating the lack of knowledge that leads to poor species delimitation. We stopped the splitting cycles when the PGLS gave a significant difference between the mean DR in the two regions, giving thus the smallest amount of Linnean shortfall that is necessary to change the interpretation of the diversification gradient. An additional operational stopping rule was to end the simulations if the number of splits achieves the total number of species (even with  $P > 0.05$  for the PGLS).

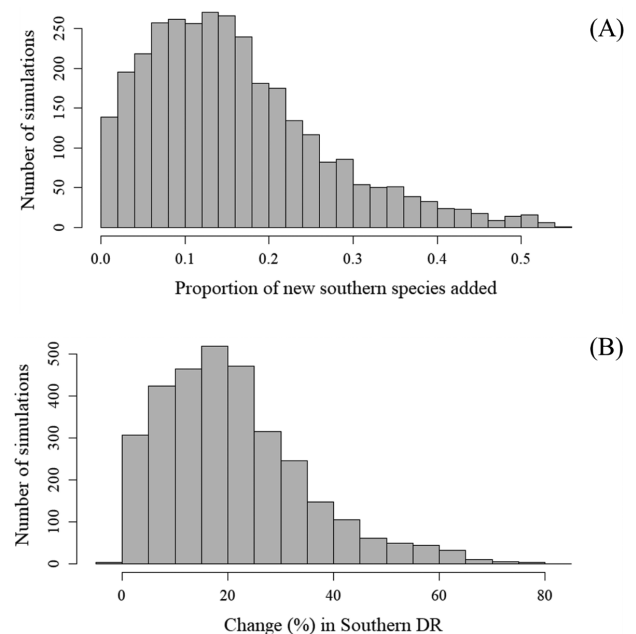
We also estimated the speciation rates for the northern and southern regions using GeoSSE (Goldberg et al. 2011; Rabosky and Goldberg 2015). The GeoSSE furnishes estimates of diversification rates for the entire region and is derived from original binary State Speciation-Extinction (BiSSE) models. These SSE models allow estimating by maximum likelihood the probabilities of different events of maintenance or transition of a binary state (i.e., 0 or 1) along each branch of a phylogeny. Goldberg et al. (2011) proposed GeoSSE as an expansion of BiSSE to analyze geographic transitions between two regions throughout a phylogeny, by calculating speciation and extinction rates for each region (as the presence/absence of the species in two regions could be viewed, in principle, as a binary trait). However, some species may be widespread and found in both regions, so that states are not a simple binary and thus a more complex model than BiSSE was necessary to analyze such data. GeoSSE also allows estimating the probability that a species, which originated in the past in the southern region and is still found there, for instance, has expanded its range into the northern region by dispersal, or vice versa. At the same time, a widespread species found in both regions can give rise to two new species in each region or become extinct in one of them due to geographic range contraction. So, there are six parameters to estimate in GeoSSE, which can be combined to generate many alternative scenarios (i.e., Alves et al. 2017; Caetano et al. 2018). Moreover, it is possible to compare the likelihood of such scenarios for a particular group of organisms or for simulated data using likelihood ratios or the Akaike Information Criterion (AIC) (e.g., Jansson et al. 2013; Roland et al. 2014; Pulido-Santacruz and Weir 2016).

For our purposes here, and following the same reasoning previously described for evaluating patterns in DR, we started GeoSSE analysis by conservatively retaining for further splitting cycles only those simulated phylogenies for which  $\Delta AIC < 3$ . This involved comparing the fitted GeoSSE with

a null model where there is no difference in speciation, extinction, and dispersal rates between northern and southern regions. A low proportion of simulations with  $\Delta AIC < 3$ , even when dealing with randomly generated phylogenies with the same diversification (but varying richness), is expected due to the relatively high “type I error” of GeoSSE (see Alves et al. 2017). We then started the subdivision cycles and, at each step, recalculated the AIC, interrupting the process when  $AIC > 3$ . This gives, again, the smallest amount of Linnean shortfall that changes the patterns in the diversification rates among regions, and we also compared the relative (%) shifts in the speciation parameter estimated for the northern and southern regions under this minimum increase of species.

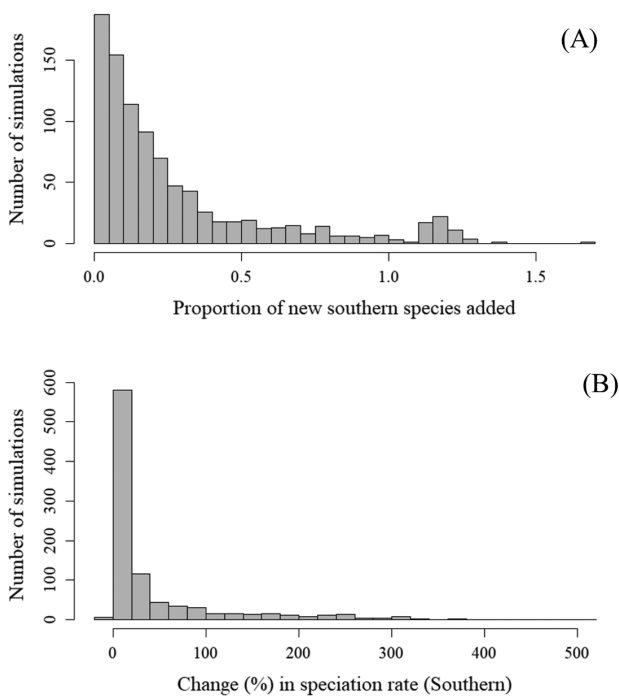
## Results

For the DR, we analyzed about 65% of the simulations in which initial diversification rates were, by chance, not significantly different between northern and southern regions. On average, the non-random geographic structure on the diversification rates, revealing a shift from non-significant to significant difference between northern and southern DRs, appears when adding about 14% of new daughter species in the southern region, with a right-skewed distribution (Fig. 2A). With this stopping rule for the simulations, the DR values increased by a median of 26% (Fig. 2B). The two distributions (i.e., shifts in DR and proportion of new species added to the southern region) are strongly correlated ( $r = 0.97$ ), and these have some correlation with the magnitude of the initial gradient between the two regions ( $r = 0.5$ ).



**Figure 2.** The statistical distribution of the minimum proportion of new species added to the southern region to create a significant ( $P < 0.05$ ) geographical gradient in the mean diversification rates (DR) using a PGLS (A), and the percentual change in mean DR between the two regions under this minimum increase in species' number (B).

Results for the GeoSSE are qualitatively similar to those obtained for DR, but with even more right-skewed distributions. Based on the 18% of simulations where  $\Delta\text{AIC} < 3$  between the fitted model and null expectation (i.e., equal speciation rates) before the splits, we found that the  $\Delta\text{AIC}$  becomes larger than 3 when about 15% of new southern species are added in the simulations. Alternatively, when considering both southern or widespread new species being incorporated, this value decreases to 11.3%. In most cases, this change in AIC results in less than doubling speciation rates in the southern region (Fig. 3B).



**Figure 3.** The statistical distribution of the minimum proportion of new species added to the southern region to generate a  $\Delta\text{AIC} > 3$  when comparing fitted GeoSSE with a null model in which speciation, extinction and dispersal rates between northern and southern regions are the same (A), and the percentual change in speciation rate in these cases with the minimum number of splitting cycles adding species to the southern region (B).

## Discussion

In this paper, we expand the original proposal by Diniz-Filho et al. (2023b) and showed, using more complex simulations and analytical methods, that relatively slight geographic structure in the quality of species delimitation biased towards the richer region is sufficient to qualitatively change the estimates of diversification or speciation rates. Consequently, this change affects the interpretation of the evolutionary dynamics underlying the latitudinal diversity gradient. For the two methods used here (i.e., Diversification Rates DR and the GeoSSE), it would be necessary to subdivide approximately 14% and 16% of poorly delimited species in the southern (richer) region to increase the diversification or speciation rates. This would create a

latitudinal gradient in these rates, starting with a random model in which the two regions have the same rates.

It is intuitive, from an evolutionary point of view, that higher diversification rates should explain the LDG in what have been called “evolutionary” models (see Ricklefs 2006; Mittelbach et al. 2007). However, it was extremely difficult to estimate such rates, and at the same time it would be hard to ignore the large differences in current environmental conditions and its stability among temperate and tropical regions, leading to what are usually termed “ecological” and “historical” (for stability and age) explanations for the LDGs (Fine 2015; Pontarp et al. 2019). Although these distinctions are still used and sometimes operationally and useful for providing more comprehensive explanations, there have been many attempts to integrate all of them (e.g., Ricklefs 2004; Wiens and Donoghue 2004; Allen et al. 2006; Storch et al. 2018; Pontarp et al. 2019; Diniz-Filho et al. 2023a). For instance, in some models, including Tropical Niche Conservatism (TNC) models (Wiens and Donoghue 2004; Wiens et al. 2010), the diversification rates are not different between tropical and temperate regions. The historical component is related to differences in age and origin of the clades coupled with lower possibility of niche shifts (see also Roy and Goldberg 2007; Goldberg et al. 2011; Romdal et al. 2012). Also, within models in which there is a carrying capacity for diversity and density-dependent diversification, estimates are much more complex and time-dependent, making empirical comparisons between regions much more difficult (i.e., Rabosky 2009; Marshall and Quental 2016; Storch et al. 2018).

However, when the possibility of estimating diversification rates and their geographic patterns became more widespread, considering the more intuitive reasoning in which richness and diversification rates are directly correlated, ambiguous and sometimes counterintuitive results were found. In some cases, weak or absence of geographical gradients in diversification or speciation rates were found, reinforcing the higher plausibility of recent ecological mechanisms driving diversity gradients or historical processes involving species’ accumulation under TNC (e.g., Hawkins et al. 2003; Wiens and Donoghue 2004; Wiens et al. 2010). In other situations, the patterns were even inverted, showing higher speciation and extinctions rates but balancing towards lower diversification rates in the temperate regions (Jansson et al. 2013; Rolland et al. 2014; Schluter and Pennell 2017; Rabosky et al. 2018; Igea and Tanentzap 2020; Tietje et al. 2022). In all these cases, even though it is always clear in macroecology that species should be considered as particles, many species are currently undescribed, especially in the richer tropical regions under the Linnean shortfall (i.e., Balakrishnan 2005). It is always thought that this would actually reinforce the currently known patterns and processes, as more species are expected to be described in the tropical region. Correlations with environmental variables would be even higher, or an increase in richness by the description of new species ecologically similar to previously known species would reinforce niche conservatism. However, even when

accounting for this geographical bias in the knowledge of richness, expressed by the Linnean shortfall, its impact on the estimation of diversification and speciation rates were most likely underestimated. The problem arises because, even when the geographical biases in richness are potentially recognized, it was not explicitly considered that a bias in the distribution of branch lengths would strongly affect the diversification rates, as pointed out by Freeman and Pennell (2021, see also Diniz-Filho et al. 2023b) and reinforced by the simulation results shown here.

As pointed out by Freeman and Pennell (2021), the LTG is most likely widespread, even though a comprehensive review is still needed. Our results reveal that even a relatively small bias in the Linnean shortfall of about 20% is sufficient to change the interpretation of underlying mechanisms related to diversification. Thus, our results open several avenues for further investigation that would allow evaluating if the lack (or inversion) of diversification gradients can be due to a geographical structure in Linnean shortfall creating an LTG, and we can highlight at least two of them.

First, by considering the simple simulation results obtained here, it would be important to assess how realistic an LTG of at least 20% would be, especially considering that the biases strongly vary among groups of organisms. Jansson et al. (2013) analyzed more than one hundred phylogenies for different groups of organisms and found complex patterns based on GeoSSE analyses, but in general supporting higher speciation and extinction rates in the temperate regions. They found for multi-clades (their S1 table, appendix 2) that temperate speciation rates were twice as high as tropical ones, thus lower than more frequently obtained here using GeoSSE (see Fig. 2B). Thus, patterns found by Pulido-Santacruz and Weir (2016), which revealed an inverted gradient for New World birds but with relatively small differences between speciation rates (i.e., smaller than 50% for all birds), may be due to problems in tropical species delimitation. Similarly, the diversification gradients in DR found by Jetz et al. (2012; e.g., their fig. 4) are small and would be inverted by adding less than 20% of new tropical or southern bird species. Conservatively, although Linnean shortfall in birds is not expected to be high, it would be sufficient to disturb these previous estimates. However, the overall situation seems to be quite different for other groups of terrestrial vertebrates, such as amphibians and reptiles (see Blackburn et al. 2019; Moura and Jetz 2021; Lum et al. 2022), and even higher biases are expected for other groups of organisms such as plants and insects, for instances (e.g., ter Steege et al. 2020; Freitas et al. 2021). Thus, a comprehensive evaluation of the magnitude of this gradient and the geographical structure of Linnean shortfall for multiple groups of organisms is required.

Although our simulations suggest that geographical structure in the Linnean shortfall and LTG may be a plausible explanation for patterns in diversification or speciation rate, it is still necessary to improve our understanding of this effect via empirical analyses, opening a second large research avenue. For instance, a first step would be to de-

velop consistent predictive models for the Linnean shortfall (i.e., based on socioeconomic and historical components of taxonomic research, e.g. Parsons et al. 2022; Guedes et al. 2023), allowing us to evaluate the intensity of LTGs for distinct groups of organisms and regions of the world. Simultaneously, it would be possible to use such models to evaluate which species are more likely to be not well delimited and empirically evaluate the robustness of estimated diversification gradients, accounting for LTGs, by simulating splits of current described species into closely phylogenetically related hypothetical new species.

Again, our analyses reinforce the importance of better accounting for LTGs proposed by Freeman and Pennell (2021) when trying to investigate mechanisms underlying broad-scale patterns, such as LDGs, and to develop strategies to incorporate this information to establish more effective approaches in conservation biogeography.

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## Author Contributions

GRGT led the study and did all the programming and analyses, based on the design that was also defined by LEFF and JAFDF. All authors contributed intellectually to the project and participated in writing the final version of this manuscript.

## Conflict of Interest

The authors declare that the present research was conducted without any commercial or financial relationship that could be construed as a potential conflict of interest.

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