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Species Richness Gradients Vary Across Phylogenetic Scales

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Keywords: biodiversity | diversity patterns | null model | phylogenetic scale | species richness

ABSTRACT

Aim: To determine how species richness gradients—commonly considered universal—vary across the phylogenetic hierarchy of birds and mammals, and to uncover how clade age and size predetermine the gradients.

Location: Global.

Time Period: Last 120 million years.

Taxa Studied: Birds and mammals (~15,000 species).

Methods: We used large-scale phylogenies of birds and mammals and captured the species richness gradient for each of their monophyletic clades. Gradient strength was quantified with respect to latitude, environmental productivity and temperature using multiple measures (raw slopes, log transformation, log–log transformation, and correlations). To distinguish statistical from biological effects, we compared the observed gradients to those generated by null models that randomly reassigned species to clades while preserving the phylogeny and species distributions.

Results: Species richness gradients show considerable variation. Small and young clades exhibited inconsistent gradients—including reverse or flat gradients—while older and larger clades converged on steep, consistent gradients. Even moderately large

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clades (~500 species) commonly displayed reverse gradients. Null models replicated this trend but only partially, implying that biological effects also drive gradient variation. These phylogenetic trends were sensitive to the choice of gradient measure: raw slopes frequently inflated the strength of this trend and the apparent differences among clades, while log and log–log transformations revealed only moderate trends.

Main Conclusions: Species richness gradients are not universal, nor are they phylogenetic scale-invariant. Instead, they follow systematic trends across the phylogenetic hierarchy. Young, small clades often bear signatures of their region of origin and historical dispersal, whereas older, larger clades converge on similar gradients. Recognising the variation and the phylogenetic trends within it elucidates the formation of biodiversity patterns. We offer guidelines for choosing gradient measures, arguing that multiple metrics, combined with careful use of null models, are necessary for a nuanced understanding of how, and why, global biodiversity patterns diverge from the presumed universal gradients.

1 | Introduction

The latitudinal gradient in species richness is a widespread pattern in biology, whereby the number of species decreases from the tropics toward the poles (von Humboldt and Bonpland 1807; Wallace 1878; Fisher 1961; Pianka 1966). This gradient holds for many higher taxa, such as flowering plants, molluscs, insects, or vertebrates (Fisher 1961; Rohde 1992; Hillebrand 2004; Mittelbach et al. 2007). However, lower taxa show a wide variety of gradients, including reverse gradients (e.g., Anseriformes, Timaliidae, Lagomorpha) (Figure 1) (Kindlman et al. 2007; Graham et al. 2018; Cerezer et al. 2022). This variation in species richness gradients with latitude, but also with environmental temperature and productivity, has been recognised in the literature (Hillebrand 2004; Buckley et al. 2010; Romdal et al. 2013). Yet, it has rarely been systematically investigated across the phylogenetic hierarchy using multiple well-resolved, large-scale phylogenies. The traditional focus on higher taxa (e.g., Aves, Mammalia) without examining their many smaller component clades might have produced potentially incomplete, or perhaps even biased, knowledge of the shape and form of the gradients in general.

Variation in species richness gradients is typically explained biologically. One explanation is that lower taxa show a variety of gradients due to the historical contingencies of their origin, limited time for dispersal and geographic range expansion (Hawkins et al. 2006, 2007; Smith et al. 2012; Romdal et al. 2013; Li and Wiens 2019; Bohdalková et al. 2021). Over time, taxa converge toward strong gradients consistent with the classic latitudinal diversity gradient (LDG) (Fisher 1961; Pianka 1966; Pontarp et al. 2019), presumably because regional differences in diversification rates and environmental conditions gradually overwrite the signatures of a taxon's history (Hawkins et al. 2012; Rabosky and Hurlbert 2015; Storch and Okie 2019; Cerezer et al. 2022). This implies that the processes governing the different phases of gradient formation produce a phylogenetic trend where the strength and the consistency of species richness gradients increase with clade age and size (Hutter et al. 2017; Graham et al. 2018; Li and Wiens 2019; Machac 2020). Alternatively, the gradients might vary irrespective of clade age and size, assuming that similar processes govern the gradients in both small and large clades (Hawkins et al. 2006, 2007; Hurlbert and Stegen 2014; Graham et al. 2018; Storch and Okie 2019). Under this scenario, the gradients can show variation, but there is no compelling reason to expect any clear phylogenetic trends within it (Buckley et al. 2010; Hurlbert and Stegen 2014; Graham et al. 2018). The support for the alternative scenarios, predicting the presence or absence of phylogenetic trends, has yet to be comprehensively evaluated, ideally within the same methodological framework.

Statistical effects associated with clade size might also produce phylogenetic trends (Graham et al. 2018). It has been proposed, for example, that the phylogenetic trend toward strong and consistent gradients might arise simply from the fact that higher taxa follow a concrete gradient, such as LDG, while their subclades follow heterogeneous subsets of this gradient (Bohdalková et al. 2021). Similarly, small clades cannot produce steep changes in species richness along the gradient, given that they contain only a small number of species in total (Evans et al. 2005; Graham et al. 2018; Bohdalková et al. 2021). These statistical effects can be quantified using null models, which generate artificial taxa of increasing sizes by randomly subsetting species from a given higher taxon. Comparing empirical gradients and null models, we can then tease apart the statistical and the biological effects and identify those phylogenetic trends that hold even for random subsets of species.

The method of gradient measurement might also predetermine, at least to some extent, gradient variation and the trends within it (Table 1). Traditionally, gradients have been quantified in terms of changes in the raw number of species with latitude, temperature, and productivity, which can be captured by the slope of linear regression (Fisher 1961; Pianka 1966; Hillebrand 2004). Since the slopes depend on the absolute values of species richness, however, they tend to be steeper in species-rich taxa. They also depend on measurement units, making the results, for example, for latitude and temperature incomparable; in addition, the slopes from linear regression will be misleading when applied to non-linear relationships. These issues have motivated various standardisations (Table 1) (Brown et al. 2004; Hillebrand 2004; Evans et al. 2005; Gillooly and Allen 2007; Bohdalková et al. 2021). To capture the relative instead of the absolute differences in the number of species along the gradient, species richness is often log-transformed. Moreover, the log–log transformation, which standardises both species richness and its predictor, produces regression slopes that are comparable regardless of the measurement units (Hillebrand 2004; Bohdalková et al. 2021). Correlation coefficients have similar advantages, as they capture the relative changes in species richness standardised to the length of the gradient. They can be defined in a parametric (e.g., Pearson's correlation) and, to account for non-linearity, also in a non-parametric manner (e.g., Spearman's correlation). At least for temperature, the non-linearity has also been addressed by mathematically transforming the temperature into a variable more linearly related to metabolic rates (using $1/kT$, where

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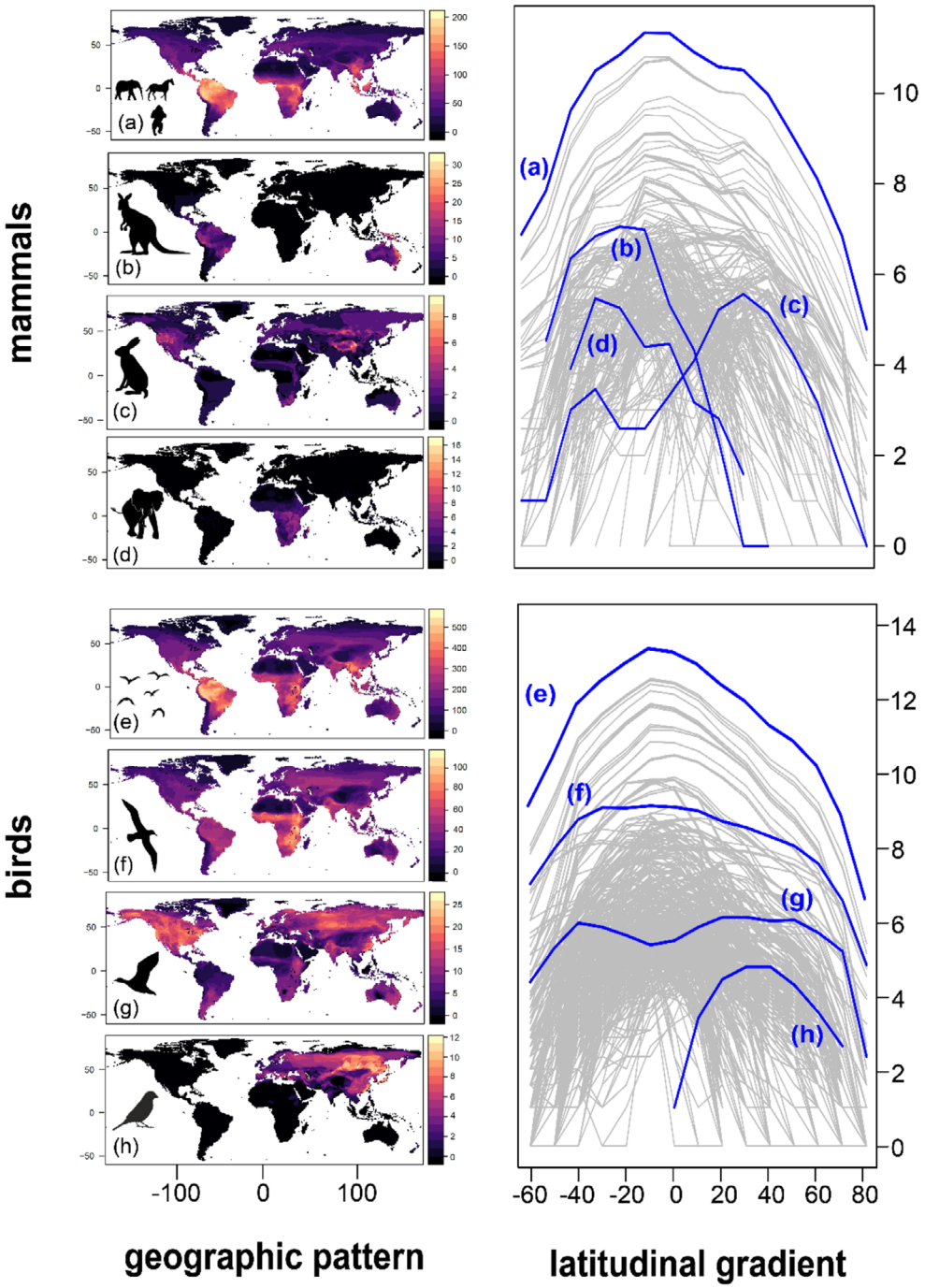

FIGURE 1 | Species richness gradients vary across the phylogeny. While many of the large and old clades within birds and mammals reach their peak richness in the tropics (a: Mammalia, e: Aves), small and young clades show heterogeneous gradients that often peak outside the tropics (b: Marsupialia, c: Lagomorpha, d: Afrotheria, h: Timaliidae) or tend to be flat (f: Procellariiformes, g: Anseriformes). Cross-continental differences in species richness emerge both in large (a, e) and small clades (b, d, f, h). Maps show the geographic patterns of species richness for select clades. The line plots show the corresponding changes (blue lines) in log-transformed species richness (vertical axis) across latitudes (horizontal axis), together with the same changes (grey lines) reconstructed for all subclades within birds and mammals, whereby the logarithm base is 2 (e.g., $2^{10} = 1024$ species).

k is the Boltzmann constant, 1.38×10^{-23}, and T is temperature in kelvins) (Brown et al. 2004; Gillooly and Allen 2007). Another way to capture the relative differences in species richness is to divide either the gradient slope or the regional richness by clade size (i.e., by the total number of species within the clade or taxon). Each of these standardisations has been widely used (Hawkins et al. 2003; Brown et al. 2004; Hillebrand 2004; Evans et al. 2005; Gillooly and Allen 2007; Storch et al. 2018; Bohdalková et al. 2021). Yet, they have rarely been examined together in a way that allows for the comparison of their behaviour, ideally across both empirical and simulated gradients. Much of the gradient variation might stem from the use of different gradient measures and standardisations, but systematic comparisons and a consensus about the most appropriate approach are still largely lacking.

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TABLE 1 | Measuring species richness gradients.

Variables	**Raw species richness**—species richness expressed in absolute values, whereby the number of species changes with latitude, temperature, and environmental productivity. Models: S~Lat; S~Temp; S~NPP
	Log-transformation—species richness expressed in multiplicative (e.g., an equal increment is always twice as many species in the given region) rather than additive terms (e.g., an equal increment is always 20 more species). This makes the gradients better comparable even across clades of different sizes. Models: log(S)~Lat; log(S)~Temp; log(S)~NPP
	Log–log transformation—captures the relative differences in species richness, given the relative differences in its predictor. This accounts for the effects of gradient length and measurement units. Models: log(S)~log(Lat); log(S)~log(Temp); log(S)~log(NPP)
	$1/kT$ temperature—aims to linearize the effects of environmental temperature on species richness by transforming it into a variable that captures kinetic energy, which more directly affects biological rates. Based on theory, the linearization holds only when using log-transformed species richness. Model: log(S)~exp($1/kT$)
Models	**Regression slope**—the slopes capture how the predicted variable (y) changes as the predictor variable (x) changes. It measures quantitative changes in the former with the latter
	Pearson's correlation coefficient—standardises by the length of the gradient, along both x (latitude, temperature, productivity) and y axes (species richness), while assuming a linear relationship
	Spearman's rank correlation coefficient—standardises by the length of the gradient, along both x and y axes, while allowing for non-linearity through the ranking of the observations
	Regional richness divided by clade size—the number of species in every region (1×1 degree grid cell) is divided by the total number of species within the examined clade. This captures the relative changes in regional richness, which are then comparable across clades of different sizes
	Regression slope divided by clade size—the regression slope is divided by the total number of species within the examined clade to account for the fact that species-rich clades produce inherently steeper gradients (e.g., 10, 20, 30 species) than species-poor clades (e.g., 1, 2, 3 species)
	Null model, given clade size—generates gradients for artificial clades that are randomly assembled from a given number of real species, thus revealing the expected variation and phylogenetic trends in gradient strength for the clade of a given size

Note: We examined the gradients in species richness (S) with respect to latitude (Lat), temperature (Temp) and environmental productivity (NPP). To capture gradient strength, steepness and directionality, we used regression slopes and correlation coefficients applied to raw species richness, log-transformed species richness, log–log transformation of both species richness and its predictor. We also investigated standardisations that account for gradient length, measurement units, and clade size (i.e., the total number of species within the clade or taxon under study).

Here, we investigate variation in species richness gradients across extant phylogenies of birds and mammals. For all monophyletic clades within their respective phylogenies, we map out species richness worldwide and examine how the uncovered gradients vary with respect to clade age and size. We do not aim to identify the causes of the individual gradients. Instead, we uncover gradient variation across the phylogeny and investigate how the variation depends on the choice of the gradient measure, statistical effects, and what it can tell us about the general mechanisms of gradient formation. We conclude with guidelines on how to efficiently measure and compare species richness gradients.

2 | Methods

To measure gradient strength, we used regression slopes and correlation coefficients, which capture the steepness and the direction of the species richness gradient (i.e., classic, reverse, or flat gradients). For each of the clades (= nodes) within the phylogenies of extant birds and mammals, we mapped out the number of species across the geographic grid cells covering the world (Figure 1). The uncovered geographic differences in species richness were examined with respect to several predictors (latitude, temperature, productivity) under multiple standardisations (e.g., log-transformation, log–log transformation, $1/kT$) (see Table 1 for the full list). The strength of the resultant gradients was studied as a function of the age and the size of the clade for which the gradient was constructed. We also searched for the hypothesised phylogenetic trends; for example, the steepness and consistency of the gradients should increase with clade age and size (Storch and Šizling 2008; Graham et al. 2018; Bohdalková et al. 2021). We confirmed our results with and without phylogenetic corrections (Rolland et al. 2020) and compared them to null models, which were designed to evaluate the pure effect of clade size, allowing us to tease apart the statistical and the biological component of the observed variation in gradient strength.

2.1 | Model System

We chose birds and mammals, as they both represent meaningfully comparable higher taxa, endothermic vertebrates. We avoided working with other higher taxa (e.g., amphibians, reptiles, angiosperms), given that their phylogenetic relationships

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are much less resolved (Jetz et al. 2012; Hedges et al. 2015). Moreover, in other higher taxa, the geographic distributions tend to be resolved more unevenly, potentially introducing further biases into our results. To avoid the notorious issues associated with clade selection (e.g., named taxa systematically differ from un-named taxa due to the possible biases of taxonomists) (Pennell et al. 2012), we analysed all monophyletic clades such that we could fully capture gradient variation across the entire bird and mammal phylogenies. Clades with less than 10 species were excluded; however, as species richness patterns in very small taxa tend to be driven by purely stochastic effects following from the law of small numbers (Storch and Šizling 2008). We did not use fossil data, given that our goal was to uncover how taxon delimitation influences the gradients observed for extant species, not for extinct species or for historical gradients.

2.2 | Phylogenetic, Geographic and Environmental Data

Bird and mammal phylogenies were taken from VertLife (Jetz et al. 2012; Upham et al. 2019). In terms of time calibration and phylogenetic relationships between the major taxa, these phylogenies are sufficiently consistent for the purposes of our analyses with the phylogenetic trees from other sources (e.g., Hedges et al. 2015). Geographic distributions were taken from IUCN (www.iucn.org). In line with the standard practice in the field, species richness was studied within geographic grid cells at the 1×1 degree resolution, which reduces the potential for false presences in the distributional data (Hurlbert and Jetz 2007) and makes our results comparable to previous work (Buckley et al. 2010; Hawkins et al. 2012; Belmaker and Jetz 2015). Species richness across the geographic grid cells worldwide was compiled for birds, mammals, and separately, for each of their monophyletic clades (Figure 1).

Latitude, temperature and environmental productivity (Zhao et al. 2005; Karger et al. 2017) are the variables most widely used when studying species richness gradients. Although they are often correlated, these variables might be linked to different mechanisms producing the gradients. Temperature, for example, might accelerate biological processes, including molecular divergence and speciation (Rohde 1992; Brown et al. 2004; Gillooly and Allen 2007), while productivity might capture the amount of environmental resources available for species coexistence within a given geographic grid cell (Currie 1991; Bohdalková et al. 2021). Nonetheless, we caution that the mere correlations of these variables (temperature or productivity) with species richness cannot prove that the gradients were actually generated by the hypothesised mechanisms. Instead, the correlations might emerge as a side effect, for example, of the gradual spread of species from the ancestral tropics toward the colder latitudes (Wiens and Donoghue 2004), producing a correlation of temperature with species richness even in the absence of its hypothesised effects on biological rates. Still, temperature and productivity are instrumental for capturing species richness gradients, their strength, direction and form, more comprehensively and arguably more meaningfully than when relying on latitude alone.

2.3 | Gradient Variation, Gradient Strength and Phylogenetic Trends

We explored two ways to quantify the strength of the gradients in species richness: linear regressions and correlations. Nonlinear gradients were accounted for by the log-transformation and the log–log transformation, which capture exponential and power-law relationships, respectively. Regression slopes and correlation coefficients were then studied as a function of clade age and clade size. Their age dependence and size dependence were interpreted as phylogenetic trends. The goal of our study is to report the full variation of the gradients across the phylogeny, given species relatedness. Removing the nestedness and the relatedness of the analysed clades makes our results less interpretable. Still, we confirmed that the phylogenetic trends, which we uncovered, held even after using phylogenetic corrections (PGLS) (Rolland et al. 2020). Similarly, we primarily report the results for clade size, unless stated otherwise, because they were similar to those for clade age. Complete results (phylogenetically corrected, for both clade age and clade size) are, nonetheless, provided in Data S1.

We used multiple ways to account for the effects of clade size. Given that regression slopes depend on the absolute values of species richness (e.g., sequence 1, 2, 3, 4 has a lower slope than sequence 10, 20, 30, 40 even though both represent perfectly linear gradients), larger clades will have generally steeper regression slopes. Thus, raw slopes naturally increase with clade size, producing an apparent phylogenetic trend. To address the issue, we used two approaches. First, we divided species richness within the geographic grid cells by the total number of species within the analysed clade, such that we could study the gradients in relative richness. This approach is, however, mathematically related to measures of beta diversity (i.e., the ratio of total and local diversity corresponds to the Whittaker's beta diversity index) and therefore might diverge from the other standardisations described above. Second, we divided the regression slopes by clade size. We compared the two approaches to each other and using simulated gradients (see Data S1). Specifically, we simulated linear gradients for clades that differed in their size. These gradients were then analysed, using (1) raw regression slopes, (2) log-transformation of regional richness, (3) log–log transformation, (4) regional richness division by clade size and (5) slope division by clade size (see detailed description in Table 1). The purpose of the simulations was not to explore a comprehensive set of scenarios but to evaluate and compare the results returned by the different standardisations when applied to known baseline gradients.

2.4 | Null Models

To further evaluate the statistical effects of clade size, we used null models. Specifically, we randomly reshuffled species identity across the phylogeny while holding species' geographic distributions and the phylogeny constant. This approach produces artificial clades of increasing sizes whose species richness gradients we analysed, using the same array of standardisations as above (Table 1). The procedure was repeated 100 times; we checked that increasing the repetitions did not change our results. Finally, we assessed how many of the empirical gradients

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were (1) consistent with the expectations of the null model, (2) stronger or (3) weaker than expected. The null models allowed us to separate the sampling effects from other, potentially biological, effects while still maintaining some degree of biological realism (i.e., the structure of the phylogeny and the geographic distributions was held unchanged within the null model). The null models further revealed the expected magnitude of the variation in species richness gradients, following simply from the statistical effects of clade size.

3 | Results

We found that species richness gradients vary non-randomly across the phylogeny (Figure 2). Gradient strength, measured in terms of regression slopes and correlation coefficients, varied markedly in small and young clades, which showed the classic but often also the reverse gradients (Figures 2–4). Clades containing more than 500 species converged toward strong gradients, consistent with the classic LDG (Figure 2). We further

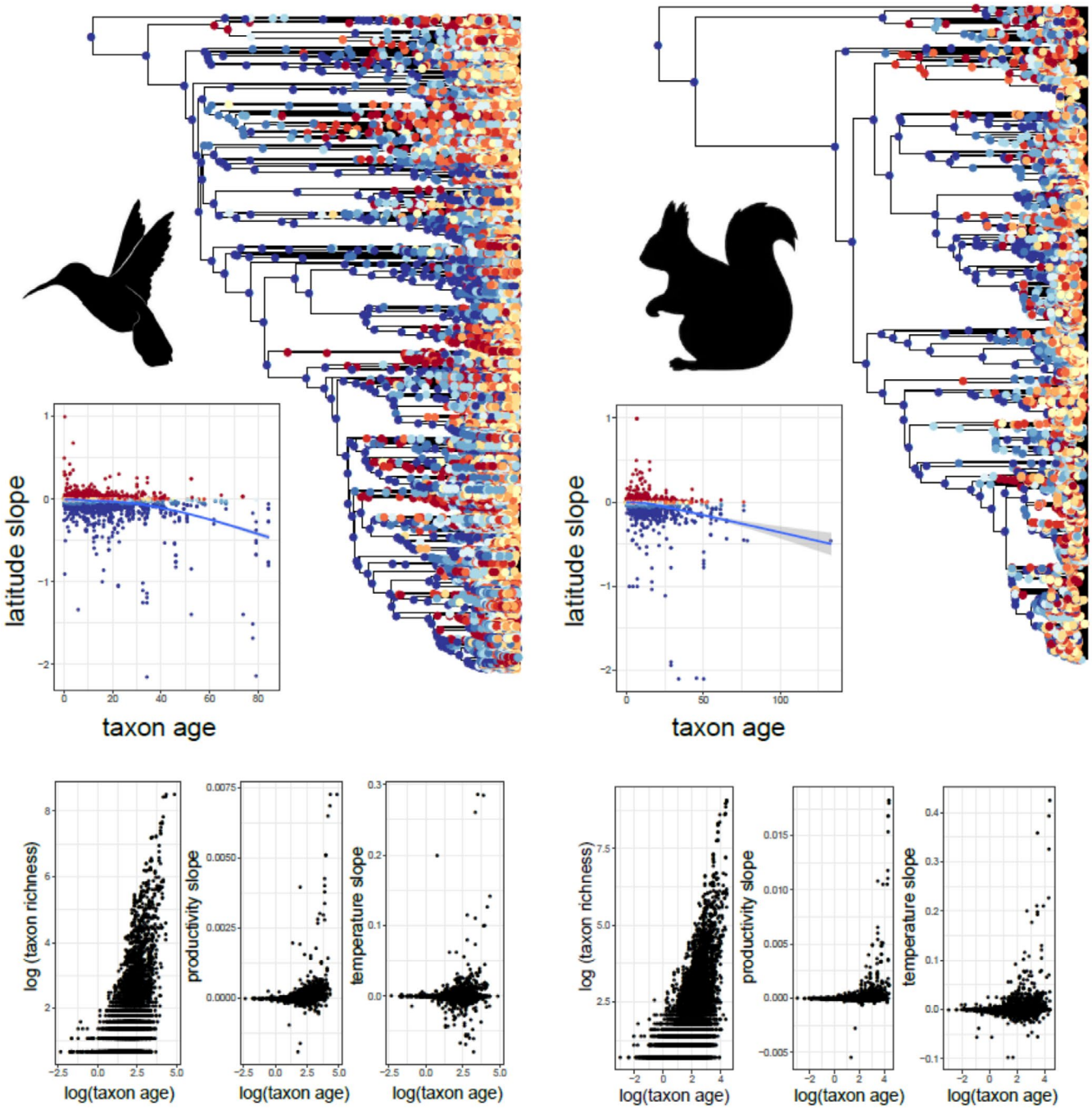

FIGURE 2 | Gradient variation with taxon age. The phylogenies show the raw slope of the relationship between species richness and latitude for all monophyletic clades (= all taxa) within birds (left) and mammals (right). The colour-coding of the nodes within the phylogeny corresponds with the associated colour-coded scatterplots, with blue indicating negative slopes and red indicating positive slopes. The black-and-white scatterplots underneath show phylogenetic trends with environmental temperature and productivity, instead of latitude. The correlation between taxon age (in millions of years) and taxon richness (total number of species within the taxon) is also depicted. Note that raw slopes need to be corrected for statistical artefacts (as done in Figure 3), given that raw slopes are naturally steeper for larger clades.

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found a phylogenetic trend (Figures 3 and 4) whereby gradient strength systematically increased with clade age (Spearman's $\rho \approx 0.2$, $p < 0.001$) and clade size (Spearman's $\rho \approx 0.3$, $p < 0.001$) in birds and mammals (Figures 3 and 4, Tables S5–S8). The trend held consistently for latitudinal (Spearman's $\rho \approx -0.25$, $p < 0.001$), temperature (Spearman's $\rho \approx 0.15$, $p < 0.001$) and productivity gradients (Spearman's $\rho \approx 0.35$, $p < 0.001$), but its magnitude was contingent on the gradient measure (raw slope, log-transformation, log–log transformation, correlation) (Figures 3 and 4). The strongest trend was observed when using raw regression slopes for species richness (Tables S5–S8), while the standardisations of species richness, its predictors, or both, produced weaker, albeit qualitatively similar, trends (Figures 3 and 4, Tables S5–S8). Null models partially reproduced these results but did not account for them fully (Figures 3 and 4).

Moreover, we found dramatic variation in the species richness gradients, which markedly exceeded the null model expectations (Figures 3 and 4). Gradients significantly stronger than expected emerged in clades with more than 500 species ($\approx 2^9$ species in Figure 2), and this threshold applied for both birds and mammals, even though birds comprise twice as many species as mammals (Figure 2). Reverse gradients emerged in 37% of clades within mammals (out of the total of 4724 clades analysed) and in 36% of clades within birds (out of 8575 clades). These numbers indicate the chance that a randomly chosen clade follows a gradient that runs counter to the gradient followed by birds and mammals as a whole. Examples of clades with reverse gradients include Anseriformes, Procellariiformes, or Lagomorpha (Figure 1).

We further found that 55% of the bird gradients and 43% of the mammal gradients fell outside the null model expectations, but only 20% of the analysed clades showed stronger than expected gradients (Figures 3 and 4). Most notable departures from the null model manifested as chains of datapoints representing progressively nested subclades of a larger clade, whose gradients defied the general trend (Figures 3 and 4). Phyllostomidae (leaf-nosed bats) and Tyrannidae (tyrant flycatchers), for example, showed steeper than expected gradients, while Muridae (murid rodents) showed shallower gradients. Both the variation and the phylogenetic trends outside of the expectations of the null model call for a biological explanation that extends beyond the statistical effects associated purely with clade size.

The phylogenetic trend in gradient strength with clade age and size held under a variety of standardisations (Figures 3 and 4, Tables S1–S8). The trend was supported also when we used phylogenetic corrections (Tables S1 and S2). Similar phylogenetic trends emerged for clade age and clade size (Figure 2). Still, the trends were generally stronger for clade size (Figures 2–4, Tables S3 and S4), suggesting that, rather than the historical effects (i.e., the time of the clade's historical origin), the size of the clade by itself (i.e., the sampling effects) contributes to the phylogenetic scaling of species richness gradients. Nonetheless, clade age and size were correlated (mammals: Spearman's $\rho = 0.559$, $p < 0.001$; birds: Spearman's $\rho = 0.641$, $p < 0.001$) (Figure 2), and, when simultaneously included in the model, they both remained statistically significant (Tables S3 and S4). Similarly, the examined standardisations (Table 1) produced mutually correlated results (Figure 2, Figure S2). The log–log transformation results were the least correlated with the others. The strongest correlation was between the two measures that involved the division of gradient slopes and the division of regional richness by clade size (Figure S2). Simulations revealed that these measures performed better than the log-transformation and the log–log transformation when applied to linear gradients (Figure S1), but not in the case of non-linear gradients. Full results are detailed in Data S1.

4 | Discussion

Clades within birds and mammals displayed a wide variety of gradients, including reverse gradients, even as they comprised up to ≈500 species. Moreover, the gradients became stronger with clade age and size, especially when using some gradient measures (esp. raw slopes) (Figures 2–4, Tables S1–S8). This held for gradients with latitude, environmental temperature, and productivity. Previous studies hypothesised that phylogenetic trends in gradient strength would emerge if different processes dominated different phases of gradient formation (Rahbek and Graves 2001; Pontarp and Wiens 2016; Machac 2020). Our results support this hypothesis, but only partially, since our null model explained approximately half of the variation in gradient strength and produced a weaker, but qualitatively similar trend (Figures 3 and 4). Together, our findings underscore that the delimitation of the studied taxon, especially its age and size, predetermines, for both biological and statistical reasons, the strength and the direction of the taxon's species richness gradient. Knowledge of the expected gradient variation across different parts of the phylogenetic hierarchy might, consequently, reconcile some of the striking differences between the gradients previously reported across studies and taxa (Graham et al. 2018; Cerezer et al. 2022).

While the gradients in species richness have been studied extensively (Willis 1922; Fisher 1961; Pianka 1966; Mittelbach et al. 2007), most research focused on the classic gradients, such as the latitudinal diversity gradient (LDG), defined by the decline of species richness with latitude. Other gradients, including those that run counter to the LDG, have received much less attention and have sometimes been dismissed as idiosyncratic (Ricklefs and Schluter 1994; Kindlman et al. 2007; Li and Wiens 2019). We find that these presumed exceptions are arguably more common than generally thought (36% of the clades within birds and mammals) and emerge even in relatively large clades (≈500 species). To address what governs species richness gradients in general, it seems imperative to study the full range of gradients emerging across clades of different ages and sizes, instead of concentrating on the classic gradients (such as LDG) that dominate only over very large phylogenetic scales.

While nearly half of the clades within birds and mammals fell within the expectations of the null model, some showed significantly steeper (e.g., leaf-nosed bats, Phyllostomidae; tyrant flycatchers, Tyrannidae) or shallower gradients (e.g., murid rodents, Muridae) (Figures 3 and 4). Steep gradients might result, for example, when different parts of the gradient are associated with dramatically different diversification rates (e.g., leaf-nosed bats diversified rapidly in the warm and productive climates of Amazonia) (Lomolino et al. 2009; Peixoto et al. 2018). The

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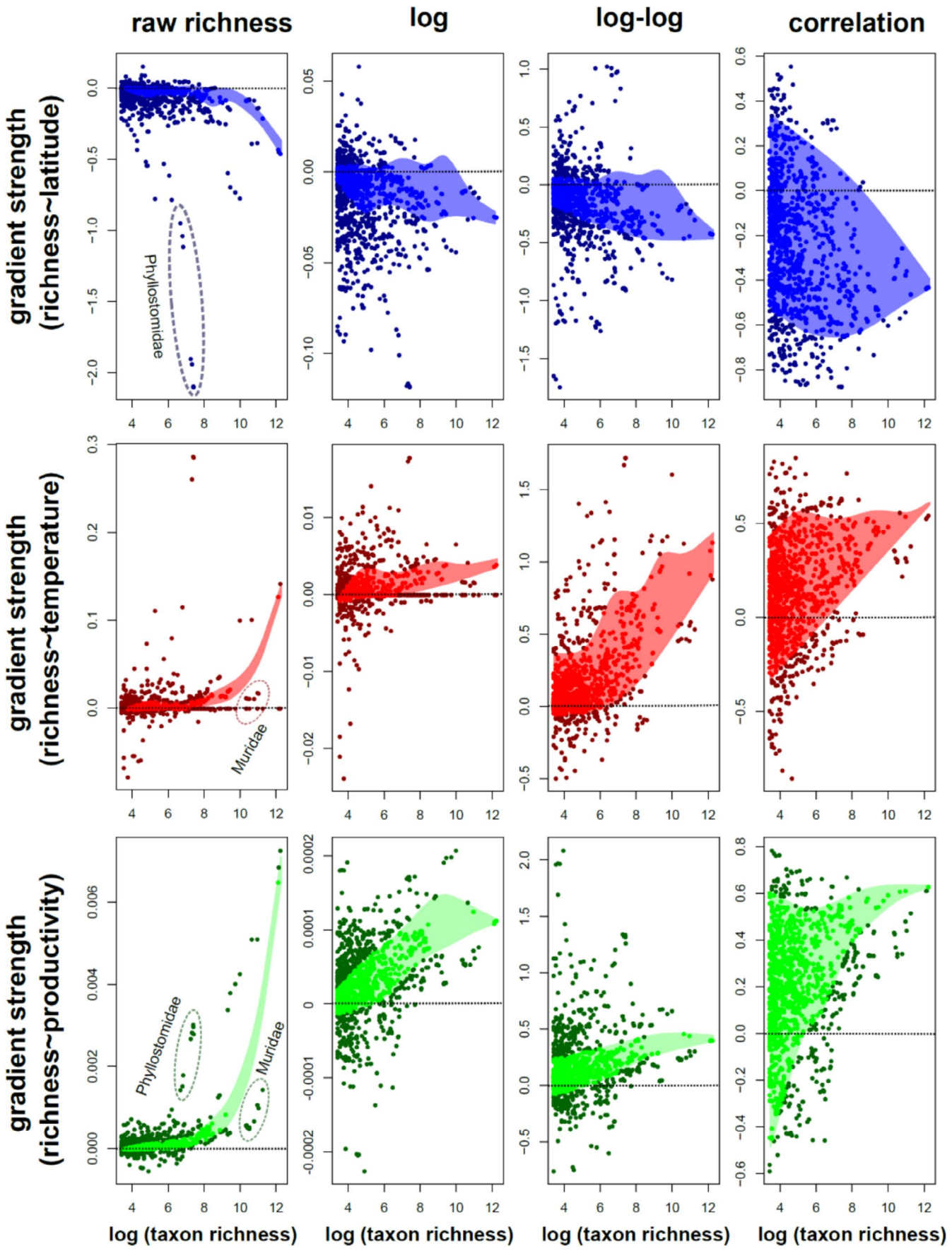

FIGURE 3 | Legend on next page.

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FIGURE 3 | Gradient strength increases with phylogenetic scale in mammals. Species richness gradients are evaluated under four standardizations (regression slopes for raw species richness, log-transformed species richness, log–log transformation, Pearson's correlation coefficients). Spearman's correlation coefficients and the division by clade size returned similar results and are given in Data S1. Null models are indicated by the light-shade envelopes (blue, red, green), which show the expected gradient strength (0.025–0.975 percentile) for a given number of species (= given taxon richness). Some of the taxa whose gradients stand out are highlighted (leaf-nosed bats: Phyllostomidae, murid rodents: Muridae). Horizontal axes show log-transformed taxon richness, which refers to the total number of species within the taxon (= clade within the mammal phylogeny) for which the gradient was constructed, and the base of the logarithm is 2 (e.g., taxon richness of $2^{10} = 1024$ species). Temperature was expressed as $-1/kT$ (see main text).

opposite might hold for taxa with shallow gradients (e.g., Muridae). Taxa with reverse gradients (e.g., Anseriformes, Procellariiformes, Lagomorpha), in contrast, often seem to have originated outside the tropics, where they have had more time to accumulate species (Rolland et al. 2014; Li and Wiens 2019; Cerezer et al. 2022). We admittedly cannot resolve why some taxa deviate from the null expectations. But our results provide a relevant benchmark to identify outliers that might merit closer examination. This might open up new lines of research into the classic, idiosyncratic, and reverse gradients, concerned with the full variation of the gradients, aiming to identify the factors that separate the typical taxa from those that stand out.

Phylogenetic trends in gradient variation (Figures 2–4) are often explained biologically (Pontarp and Wiens 2016; Graham et al. 2018; Bohdalková et al. 2021). But our results demonstrate that the statistical effects of clade size alone can produce trends, especially when using raw species richness. Basically, large taxa show steeper gradients, given that their species numbers can change more markedly along the gradient (e.g., 10, 20, 30, 40), compared to small taxa (e.g., 1, 2, 3, 4). This might motivate a reinterpretation of some previous work that relied on the raw gradient slopes (e.g., Hillebrand 2004; Buckley et al. 2010). In particular, it seems necessary to account for the sampling effects and clade size effects, using the relative measures of species richness (e.g., log-transformed species richness, correlation coefficients) or using null models, before drawing biological conclusions.

Biological explanations for the phylogenetic trends, similar to the ones that we found (Figures 2–4), stem from verbal arguments (Buckley et al. 2010) and simulations (Hurlbert and Stegen 2014; Etienne et al. 2019). These explanations have been threefold. (1) The trends can emerge because clades spread from their regions of origin, typically in the tropics, toward extratropical latitudes. Consequently, basal clades show strong and consistent gradients, while derived clades show weak, varied, or even inverse gradients (Hawkins et al. 2006, 2007; Smith et al. 2012; Romdal et al. 2013). In this case, climate-richness relationships emerge as a side effect of clade dispersal worldwide (Wiens and Donoghue 2004). While parsimonious, this explanation does not clarify why climate typically correlates more closely with species richness than the time for species accumulation (Machac 2020) and why different evolutionary histories converge on similar species richness gradients (Hawkins et al. 2012). (2) The trends are consistent with equilibrial or zero-sum dynamics. These dynamics presume that, in higher taxa, regional energy constrains species richness along the different parts of the gradient, while lower taxa show idiosyncratic gradients (Hurlbert and Stegen 2014; Storch and Okie 2019). Nonetheless, these equilibrial explanations do not clarify how the idiosyncrasies in the lower taxa emerge. (3) We advocate for the third class of explanations, which integrate the previous two and postulate that the processes that generate the gradients change as clades grow and accumulate species (Benton 2009; Pontarp and Wiens 2016; Machac et al. 2018). Deterministic differences in regional diversification and energy availability eventually produce strong, consistent, classic gradients, while lower taxa show gradients contingent on the taxon's historical region of origin (Benton 2009; Buckley et al. 2010; Pontarp and Wiens 2016; Graham et al. 2018; Machac et al. 2018; Etienne et al. 2019). Importantly, none of the three explanations, supported by our results, is compatible with the often implicit assumption that the geographic patterns of species richness are similar regardless of the phylogenetic delimitation of the studied taxon (Hawkins et al. 2003; Brown et al. 2004; Wiens and Donoghue 2004; Evans et al. 2005; Wiens and Graham 2005; Buckley et al. 2010). Instead, it seems plausible that the processes generating the classic gradients predominate only across large ensembles of species (500+ species) and differ from those shaping the gradients in smaller taxa, which might, however, still comprise hundreds of species.

The existence of phylogenetic trends in species richness gradients, including their potential biological and non-biological causes, has been indicated by some previous work (Hillebrand 2004; Storch and Šizling 2008; Buckley et al. 2010; Graham et al. 2018; Bohdalková et al. 2021; Machac 2023). Buckley et al. (2010) showed that old and large clades within mammals have typically originated in the tropics, where their current richness also peaks, while those clades that originated post-Eocene, coinciding with the expansion of temperate biomes, tend to have shallow or reverse gradients. Basal clades within birds have been reported to show steeper gradients than the derived, mostly temperate, clades (Hawkins et al. 2006, 2007), and gradient strength seems to depend on the historical climate within which the clade originated, which has been shown across a variety of taxa (Romdal et al. 2013; Smith et al. 2012). Even more broadly, Marquet et al. (2004) argued that the deconstruction of macroecological patterns can provide insights into their formation and showed that the main drivers of species richness gradients shift with the phylogenetic depth of the analysis. Building on this deconstruction method, Storch and Šizling (2008) demonstrated that phylogenetic trends might arise for purely statistical reasons. Specifically, species richness gradients in large taxa are mathematically related to the gradients in small taxa, such that phylogeny-wide trends might emerge, at least within some phylogenetic architectures, from taxon nestedness. Integrating these results with our own, it seems that phylogenetic trends result from largely biological reasons (Buckley et al. 2010; Hurlbert

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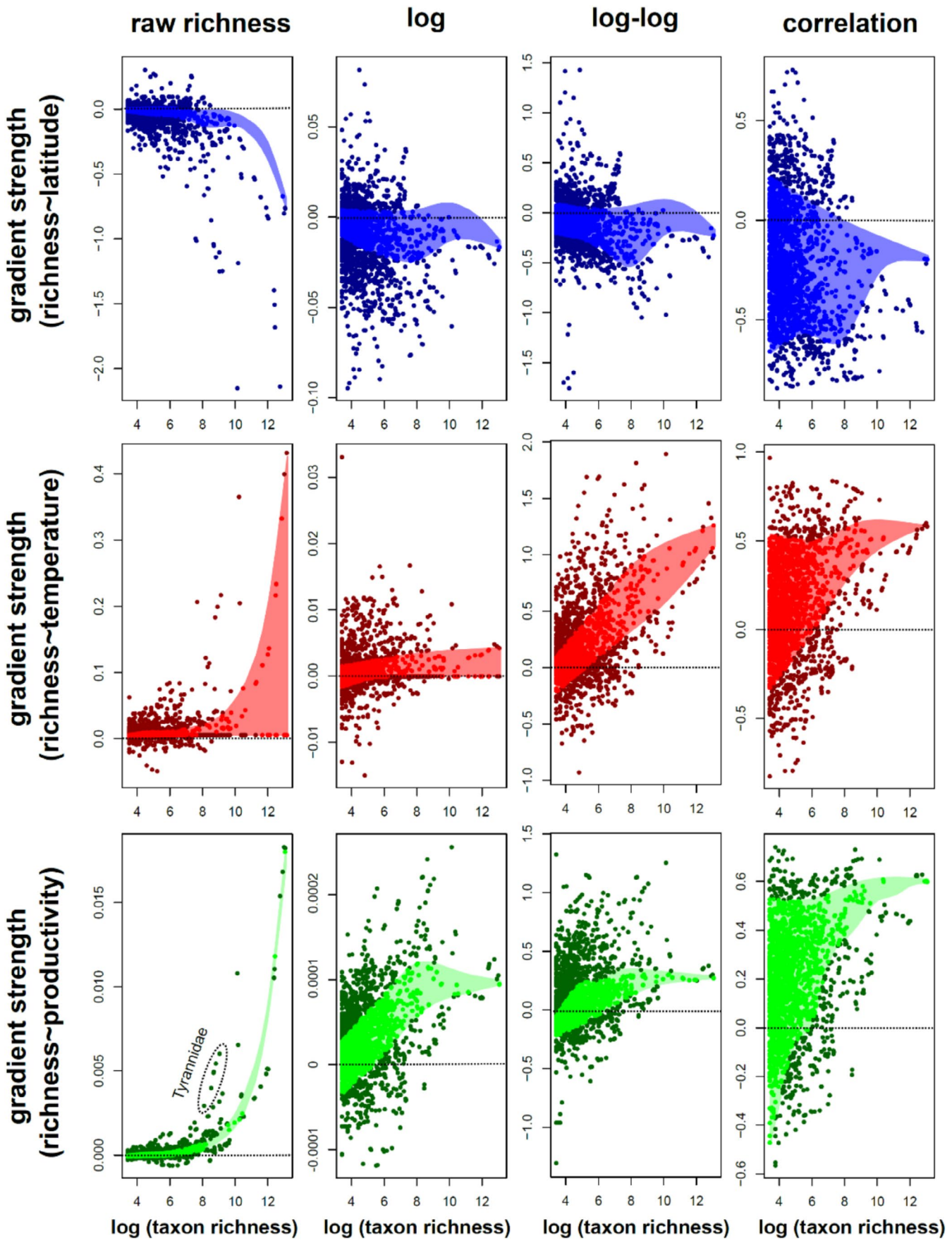

FIGURE 4 | Legend on next page.

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FIGURE 4 | Gradient strength increases with phylogenetic scale in birds. Species richness gradients are evaluated under four standardizations (regression slopes for raw species richness, log-transformed species richness, log–log transformation, Pearson's correlation coefficients). Spearman's correlation coefficients and the division by clade size returned similar results and are given in Data S1. Null models are indicated by the light-shade envelopes (blue, red, green), which show the expected gradient strength (0.025–0.975 percentile) for a given number of species (= given taxon richness). Some of the taxa whose gradients stand out are highlighted (tyrant flycatchers: Tyrannidae). Horizontal axes show log-transformed taxon richness, which is the total number of species within the taxon (= clade within the bird phylogeny) for which the species richness gradient was constructed, using the logarithm base of 2 (e.g., $2^{10} = 1024$ species). Temperature was expressed as $-1/kT$ (see main text).

and Stegen 2014; Graham et al. 2018; Machac et al. 2018). However, these trends might be further reinforced by statistical effects resulting from taxon size and taxon nestedness (Storch and Šizling 2008; Bohdalková et al. 2021).

Phylogenetic scale-dependence of diversity gradients occurs regardless of the way the gradients were measured, but the particular gradients depend on the exact measure used. Yet, despite decades of research, we still lack widely accepted guidelines for measuring species richness gradients. The chosen measure should, ideally, match the theory that is being tested. Well-developed theory exists, for example, for an exponential relationship between log-transformed species richness and temperature, expressed as $1/kT$ (Brown et al. 2004; Gillooly and Allen 2007), and this relationship has been well-supported empirically in ectotherms (Brown et al. 2004). While rigorous theory might be lacking for some of the other predictors, empirical knowledge indicates that, for example, the increase in species richness with environmental productivity is saturating, namely downward decelerating (Rosenzweig 1995; Hillebrand 2004; Šímová et al. 2011; Storch et al. 2018). Therefore, it can be linearised using power-law functions with coefficients lower than 1, implemented as the log–log transformation. The relationship with latitude is less clear, and there is still no broad consensus, theoretical or empirical, whether it tends to be linear or non-linear (Fisher 1961; Pianka 1966; Hillebrand 2004; Mittelbach et al. 2007).

When both theory and empirical knowledge are limited, using multiple measures might be preferable to any single one. The downside of this approach is that the true relationship will be distorted under some of the standardisations (e.g., linear relationships will be distorted under the log-transformation and exponential relationships under linear regression). The upside is that multiple measures capture different facets of the gradient. For example, correlation coefficients capture the association of the studied variables but fail to provide quantitative insights (e.g., how steeply species richness increases with latitude), which could be provided by the regression slopes. When calculating regression slopes, raw species richness is problematic but can be appropriately transformed, depending on the predictor (e.g., log-transformation for $1/kT$, log–log for productivity). Here, we used multiple standardisations (1) to stay agnostic about the true relationships, (2) to compare the performance of widely used metrics, and (3) to identify conclusions that hold regardless of the methodology used. While instrumental for our purposes, this approach would be suboptimal when testing a particular predictor, relationship, or theory, which could guide the approach to most appropriately capture the gradient. While these considerations are not completely new (Fisher 1961; Pianka 1966; Hillebrand 2004; Storch et al. 2018; Bohdalková et al. 2021), they are seldom explicitly taken into account in empirical research, presumably because they have rarely been overviewed within one study.

We acknowledge that our results are subject to some limitations. First, we studied species richness gradients in birds and mammals. While these represent only two distinct organismal classes, they together span over 15,000 species and thousands of clades with a variety of gradients. Second, the gradients of the analysed clades are not statistically independent of one another. Because we aimed to study the gradients comprehensively across the phylogeny, we worked across the entire phylogenetic hierarchy to describe general trends. We confirmed that our results held also when using phylogenetic corrections (Tables S1 and S2) and, importantly, they held independently across both birds and mammals, which differ markedly in their life history, macroevolution and historical biogeography. Still, further research that would extend this taxonomic scope would be valuable. Third, we modelled the gradients using linear regression. Yet, we used a variety of transformations, which together capture monotonic non-linear (accelerating or decelerating) relationships. Admittedly, they fail to capture hump-shaped or U-shaped relationships (i.e., most species occur at high/low latitudes, but few at mid-latitudes), but empirical research suggests that such relationships tend to be rare. Finally, our results pertain to widely studied predictors (latitude, temperature, and environmental productivity) that have been hypothesised to relate to species richness (Rosenzweig 1995; Rahbek and Graves 2001; Hawkins et al. 2003, 2012; Evans et al. 2005; Belmaker and Jetz 2015). While other predictors may also be relevant (e.g., temperature seasonality, environmental stability, geographic area, age of biomes), latitude, temperature, and productivity tend to be correlated with many of them (e.g., low latitudes are associated with low seasonality) (Pianka 1966; Rosenzweig 1995; Mittelbach et al. 2007; Toszogyova and Storch 2019). We also caution that, despite being widely used, these predictors, by themselves, do not necessarily explain the gradients in the biological sense. While they often correlate with species richness, the causality behind the correlation is notoriously hard to disentangle. For example, very different gradients might have the same cause (e.g., time for speciation) (García-Andrade et al. 2023) and vice versa (Cerezer et al. 2022). Regardless of the causality, however, the predictors are instrumental in capturing the shape, the form and the direction of species richness gradients. These caveats notwithstanding, our findings might arguably lay the groundwork for more meaningful cross-study and cross-taxa comparisons.

5 | Conclusions

We found that species richness gradients vary markedly across the phylogeny and follow a phylogenetic trend whereby gradient

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strength increases with the age and the size of the studied clade or taxon. The trend warrants a biological explanation since it cannot be fully explained by the null models. For example, lower taxa show highly variable gradients, which presumably reflect the historical contingencies of the taxa's origin and dispersal, while regional energy shapes the gradients in higher taxa (Hurlbert and Stegen 2014; Pontarp and Wiens 2016; Graham et al. 2018; Storch and Okie 2019; Machac 2023). While its causes require further research, the existence of the trend itself refutes that species richness gradients are phylogenetic scale-invariant and result from some universal mechanism that acts uniformly across phylogenetic scales. Instead, the confluence of multiple processes, whose relative effects vary over time as clades grow and accumulate species, could explain not only the marked gradient variation (illustrated by the contrasting examples of Muridae, Phyllostomidae, Anseriformes, and Lagomorpha), but also the existence of phylogenetic trends within the variation (Graham et al. 2018; Machac et al. 2018; Cerezer et al. 2022).

We have proposed practical guidelines for measuring the gradients based on the tested theory, the hypothesised shape of the gradient (linear, exponential, power-law), and the predictor of interest (latitude, temperature, productivity). Our results revealed that some current measures, e.g., those based on gradient slopes and raw species richness, might be misleading, especially when comparing taxa that span disparate phylogenetic scales. Altogether, we hope that these results will motivate more comprehensive biodiversity research that covers the entire phylogenetic hierarchy, including taxa with classic, idiosyncratic but also reverse gradients, while using measures that permit more meaningful cross-study and cross-taxa comparisons. Such research might expand beyond the focus on the well-known latitudinal diversity gradients and, thus, yield a more general understanding of the strikingly uneven distribution of biodiversity on Earth.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data used in the article has been obtained from the cited public databases. Processed data used for the analyses can also be accessed from Dryad (link below). The R code used for analysis is included as part of the Data S1. https://datadryad.org/stash/share/TgUw3kwwynnjITwcZbPFfLJFX9g_KVS2-vv0-CqnLNU.

References

Belmaker, J., and W. Jetz. 2015. "Relative Roles of Ecological and Energetic Constraints, Diversification Rates and Region History on Global Species Richness Gradients." *Ecology Letters* 18: 563–571.

Benton, M. J. 2009. "The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time." *Science* 323: 728–732.

Bohdalková, E., A. Toszogyova, I. Šímová, and D. Storch. 2021. "Universality in Biodiversity Patterns: Variation in Species–Temperature and Species–Productivity Relationships Reveals a Prominent Role of Productivity in Diversity Gradients." *Ecography* 44: 1366–1378.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–1789.

Buckley, L. B., T. J. Davies, D. D. Ackerly, et al. 2010. "Phylogeny, Niche Conservatism and the Latitudinal Diversity Gradient in Mammals." *Proceedings of the Royal Society B: Biological Sciences* 277: 2131–2138.

Cerezer, F. O., A. Machac, T. F. Rangel, and C. S. Dambros. 2022. "Exceptions to the Rule: Relative Roles of Time, Diversification Rates and Regional Energy in Shaping the Inverse Latitudinal Diversity Gradient." *Global Ecology and Biogeography* 31: 1794–1809.

Currie, D. J. 1991. "Energy and Large-Scale Patterns of Animal- and Plant-Species Richness." *American Naturalist* 137: 27–49.

Etienne, R. S., J. S. Cabral, O. Hagen, et al. 2019. "A Minimal Model for the Latitudinal Diversity Gradient Suggests a Dominant Role for Ecological Limits." *American Naturalist* 194: E122–E133.

Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. "Species-Energy Relationships at the Macroecological Scale: A Review of the Mechanisms." *Biological Reviews* 80: 1–25.

Fisher, A. G. 1961. "Latitudinal Variation in Organic Diversity." *American Scientist* 49: 50–74.

García-Andrade, A. B., P. A. Tedesco, J. D. Carvajal-Quintero, A. Arango, and F. Villalobos. 2023. "Same Process, Different Patterns: Pervasive Effect of Evolutionary Time on Species Richness in Freshwater Fishes." *Proceedings of the Royal Society B: Biological Sciences* 290: 20231066.

Gillooly, J. F., and A. P. Allen. 2007. "Linking Global Patterns in Biodiversity to Evolutionary Dynamics Using Metabolic Theory." *Ecology* 88: 1890–1894.

Graham, C. H., D. Storch, and A. Machac. 2018. "Phylogenetic Scale in Ecology and Evolution." *Global Ecology and Biogeography* 27: 175–187.

Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2006. "Post-Eocene Climate Change, Niche Conservatism, and the Latitudinal Diversity Gradient of New World Birds." *Journal of Biogeography* 33: 770–780.

Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2007. "Climate, Niche Conservatism, and the Global Bird Diversity Gradient." *American Naturalist* 170: S16–S27.

Hawkins, B. A., R. Field, H. V. Cornell, et al. 2003. "Energy, Water, and Broad-Scale Geographic Patterns of Species Richness." *Ecology* 84: 3105–3117.

Hawkins, B. A., C. M. McCain, T. J. Davies, et al. 2012. "Different Evolutionary Histories Underlie Congruent Species Richness Gradients of Birds and Mammals." *Journal of Biogeography* 39: 825–841.

Hedges, S. B., J. Marin, M. Suleski, M. Paymer, and S. Kumar. 2015. "Tree of Life Reveals Clock-Like Speciation and Diversification." *Molecular Biology and Evolution* 4: 835–845.

Hillebrand, H. 2004. "On the Generality of the Latitudinal Diversity Gradient." *American Naturalist* 163: 192–211.

Hurlbert, A. H., and W. Jetz. 2007. "Species Richness, Hotspots, and the Scale Dependence of Range Maps in Ecology and Conservation." *Proceedings of the National Academy of Sciences of the United States of America* 104: 13384–13389.

Hurlbert, A. H., and J. C. Stegen. 2014. "When Should Species Richness Be Energy Limited, and How Would We Know?" *Ecology Letters* 17: 401–413.

Hutter, C. R., S. M. Lambert, and J. J. Wiens. 2017. "Rapid Diversification and Time Explain Amphibian Richness at Different Scales in the

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Tropical Andes, Earth's Most Biodiverse Hotspot." *American Naturalist* 6: 828–843.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. "The Global Diversity of Birds in Space and Time." *Nature* 491: 444–448.

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the Earth's Land Surface Areas." *Scientific Data* 4: 170122.

Kindlman, P., E. Schodelbauerova, and J. Dixon. 2007. "Inverse Latitudinal Gradients in Species Diversity." In *Scaling Biodiversity*. Cambridge University Press.

Li, H., and J. J. Wiens. 2019. "Time Explains Regional Richness Patterns Within Clades More Often Than Diversification Rates or Area." *American Naturalist* 193: 514–529.

Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2009. *Biogeography*. Sinauer Associates.

Machac, A. 2020. "The Dynamics of Bird Diversity in the New World." *Systematic Biology* 69: 1180–1199.

Machac, A. 2023. "The Geography of Climate Governs Biodiversity." *Nature* 622: 463–464.

Machac, A., C. H. Graham, and D. Storch. 2018. "Ecological Controls of Mammalian Diversification Vary With Phylogenetic Scale." *Global Ecology and Biogeography* 27: 32–46.

Marquet, P. A., M. Fernández, S. A. Navarrete, and C. Valdovinos. 2004. "Diversity Emerging: Towards a Deconstruction of Biodiversity Patterns." In *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sinauer Associates.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, et al. 2007. "Evolution and the Latitudinal Diversity Gradient: Speciation, Extinction and Biogeography." *Ecology Letters* 10: 315–331.

Peixoto, F. P., P. H. P. Braga, and P. Mendes. 2018. "A Synthesis of Ecological and Evolutionary Determinants of Bat Diversity Across Spatial Scales." *BMC Ecology* 18: 18.

Pennell, M. W., B. A. J. Sarver, and L. J. Harmon. 2012. "Trees of Unusual Size: Biased Inference of Early Bursts From Large Molecular Phylogenies." *PLoS One* 7: e43348.

Pianka, E. 1966. "Latitudinal Gradients in Species Diversity: A Review of Concepts." *American Naturalist* 100: 33–46.

Pontarp, M., L. Bunnefeld, J. S. Cabral, et al. 2019. "The Latitudinal Diversity Gradient: Novel Understanding Through Mechanistic Eco-Evolutionary Models." *Trends in Ecology & Evolution* 34: 211–223.

Pontarp, M., and J. J. Wiens. 2016. "The Origin of Species Richness Patterns Along Environmental Gradients: Uniting Explanations Based on Time, Diversification Rate and Carrying Capacity." *Journal of Biogeography* 44: 722–735.

Rabosky, D. L., and A. H. Hurlbert. 2015. "Species Richness at Continental Scales Is Dominated by Ecological Limits." *American Naturalist* 185: 572–583.

Rahbek, C., and G. R. Graves. 2001. "Multiscale Assessment of Patterns of Avian Species Richness." *Proceedings of the National Academy of Sciences of the United States of America* 98: 4534–4539.

Ricklefs, R. E., and D. Schluter. 1994. *Species Diversity in Ecological Communities*. University of Chicago Press.

Rohde, K. 1992. "Latitudinal Gradients in Species Diversity: The Search for the Primary Cause." *Oikos* 65: 514–527.

Rolland, J., F. L. Condamine, F. Jiguet, and H. Morlon. 2014. "Faster Speciation and Reduced Extinction in the Tropics Contribute to the Mammalian Latitudinal Diversity Gradient." *PLoS Biology* 12: e1001775.

Rolland, J., D. Schluter, and J. Romiguier. 2020. "Vulnerability to Fishing and Life History Traits Correlate With the Load of Deleterious Mutations in Teleosts." *Molecular Biology and Evolution* 37: 2192–2196.

Romdal, T. S., M. B. Araújo, and C. Rahbek. 2013. "Life on a Tropical Planet: Niche Conservatism and the Global Diversity Gradient." *Global Ecology and Biogeography* 22: 344–350.

Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press.

Šímová, I., D. Storch, P. Keil, B. Boyle, O. L. Phillips, and B. J. Enquist. 2011. "Global Species–Energy Relationship in Forest Plots: Role of Abundance, Temperature and Species Climatic Tolerances." *Global Ecology and Biogeography* 20: 842–856.

Smith, B. T., R. W. Bryson Jr., D. D. Houston, and J. Klicka. 2012. "An Asymmetry in Niche Conservatism Contributes to the Latitudinal Species Diversity Gradient in New World Vertebrates." *Ecology Letters* 15: 1318–1325.

Storch, D., E. Bohdalková, and J. Okie. 2018. "The More-Individuals Hypothesis Revisited: The Role of Community Abundance in Species Richness Regulation and the Productivity–Diversity Relationship." *Ecology Letters* 21: 920–937.

Storch, D., and J. G. Okie. 2019. "The Carrying Capacity for Species Richness." *Global Ecology and Biogeography* 28: 1519–1532.

Storch, D., and A. L. Šizling. 2008. "The Concept of Taxon Invariance in Ecology: Do Diversity Patterns Vary With Changes in Taxonomic Resolution?" *Folia Geobotanica* 43: 329–344.

Toszogyova, A., and D. Storch. 2019. "Global Diversity Patterns Are Modulated by Temporal Fluctuations in Primary Productivity." *Global Ecology and Biogeography* 28: 1827–1838.

Upham, N. S., J. A. Esselstyn, and W. Jetz. 2019. "Inferring the Mammal Tree: Species-Level Sets of Phylogenies for Questions in Ecology, Evolution, and Conservation." *PLoS Biology* 17: e3000494.

von Humboldt, A., and A. Bonpland. 1807. *Essay on the Geography of Plants. Reprint Edition*. University of Chicago Press.

Wallace, A. R. 1878. *Tropical Nature and Other Essays*. Macmillan & Co.

Wiens, J. J., and M. J. Donoghue. 2004. "Historical Biogeography, Ecology and Species Richness." *Trends in Ecology & Evolution* 19: 639–644.

Wiens, J. J., and C. H. Graham. 2005. "Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology." *Annual Review of Ecology, Evolution, and Systematics* 36: 519–539.

Willis, J. C. 1922. *Age and Area: A Study in Geographical Distribution and Origin of Species*. Cambridge University Press.

Zhao, M. S., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. "Improvements of the MODIS Terrestrial Gross and Net Primary Production Global Data Set." *Remote Sensing of Environment* 95: 164–176.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1.**

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