

Exceptions to the rule: Relative roles of time, diversification rates and regional energy in shaping the inverse latitudinal diversity gradient

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Abstract

Aim: Inverse latitudinal diversity gradients (i-LDGs), whereby regional richness peaks outside the tropics, have rarely been investigated, and their causes remain unclear. Here, we investigate three prominent explanations, postulating that species-rich regions have had: (1) longer time to accumulate species; (2) faster diversification; and (3) more energy to support species-rich communities. These mechanisms have been shown to explain the tropical megadiversity, and we examine whether they can also explain i-LDG.

Location: Global.

Time period: Contemporary.

Major taxa studied: Amphibians, birds and mammals.

Methods: We estimated the time for species accumulation, regional diversification rates and regional energy for six tetrapod taxa (c. 800 species). We quantified the relative effects and interactions among these three classes of variables, using variance partitioning, and confirmed the results across alternative metrics for time (community phylometrics and BioGeoBEARS), diversification rates (BAMM and DR) and regional energy (past and current temperature, and productivity).

Results: Although regional richness across each of the six taxa peaked in the temperate region, it varied markedly across hemispheres and continents. The effects of time, diversification rates and regional energy varied greatly from one taxon to another, but high diversification rates generally emerged as the best predictor of high regional richness. The effects of time and regional energy were limited, with the exception of salamanders and cetaceans.

Main conclusions: Together, our results indicate that the causes of i-LDG are highly taxon specific. Consequently, large-scale richness gradients might not have a universal explanation, and different causal pathways might converge on similar gradients. Moreover, regional diversification rates might vary dramatically between similar environments and, depending on the taxon, regional richness might or might not depend

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on the time for species accumulation. Collectively, these results underscore the complexity behind the formation of richness gradients, which might involve a symphony of variations on the interplay of time, diversification rates and regional energy.

KEYWORDS

macroecology, macroevolution, marine diversity, species richness, temperate, terrestrial diversity, tetrapods, tropics

1 | INTRODUCTION

Ever since Humboldt (Humboldt & Bonpland, 1807), Darwin (1859) and Wallace (1889), biologists have been fascinated by the enormous species richness of the tropics. In contrast, taxa whose richness peaks outside the tropics, producing an inverse latitudinal diversity gradient (i-LDG), have received limited attention. Consequently, we know little about the causes of i-LDGs. Here, we evaluate three non-exclusive explanations, which have been powerful in the case of regular latitudinal diversity gradients (LDGs), postulating that species-rich regions tend to have: (1) longer time for species accumulation; (2) higher rates of regional diversification; and (3) more energy and resources for species coexistence within the region (Brown, 2014; Mittelbach et al., 2007; Pontarp et al., 2019). We investigate the underlying mechanisms behind these three explanations, their relative effects and interactions, using six well-known taxa within amphibians, birds and mammals (c. 800 species) whose richness peaks outside the tropics. Our results identify generalities across i-LDG taxa and inspire interesting comparisons with LDGs, for which the effects of time, diversification rates and regional energy have been extensively investigated.

Differences in regional richness might stem from differences in the timing of colonization (Stephens & Wiens, 2003; Willis, 1922). Regions that were colonized by a given taxon early on should harbour high richness because they have had an extensive time for the steady accumulation of species (Jablonski et al., 2006). Alternatively, regions might accumulate species at different rates because they differ in their intrinsic properties (e.g., topography, temperature, seasonality) that inherently promote speciation within the region, suppress regional extinction, or both (Mittelbach et al., 2007; Rohde, 1992; Whittaker et al., 2001). Finally, regions might differ in the total amount of regional energy, niches and resources, which determines the number of individuals, populations and species that can coexist stably in the region (Evans et al., 2005; Hawkins et al., 2003; Storch & Okie, 2019). Importantly, the three explanations are not necessarily exclusive, and the long-colonized regions might also accumulate species faster than the newly colonized regions (Mittelbach et al., 2007; Pontarp et al., 2019). The underlying mechanisms of the three explanations might, therefore, plausibly reinforce but also negate each other's effects; however, these interactions have not yet been resolved (Machac, 2020).

Each of the explanations has been supported but also challenged by empirical evidence. Studies for amphibians (Marin et al., 2018;

Pyron & Wiens, 2013), birds (Cardillo et al., 2005; Ricklefs, 2006) and mammals (Marin et al., 2018; Rolland et al., 2014) have reported that these taxa diversify faster in the species-rich tropics. However, other studies have found little indication for faster tropical diversification (Economato et al., 2018; Jetz et al., 2012) and sometimes even reported the opposite pattern, whereby diversification accelerated towards the species-poor temperate latitudes (Harvey et al., 2020; Igea & Tanentzap, 2020; Rabosky et al., 2018). Likewise, empirical evidence for the effects of time (Economato et al., 2018; Marin et al., 2018; Wiens, 2017) and regional energy (Cornell, 2013) are mixed. Time explains richness in some regions and taxa (Economato et al., 2018; Marin et al., 2018; Miller & Román-Palacios, 2021), but not others (Rabosky et al., 2012; Scholl & Wiens, 2016) and, although regional richness is often correlated with proxies for regional energy (Hawkins et al., 2003), empirical evidence for an energy limit on the number of regionally coexisting species is scarce (Cornell, 2013). These conflicts between previous studies result, in part, because the three explanations are rarely studied together and are regionally conflated (e.g., tropics are long colonized but also resource rich) (Buckley et al., 2010; Machac, 2020; Pontarp & Wiens, 2016). As a result, evidence for any one explanation tends to be confounded implicitly by the other two, such that definitive conclusions have been hard to draw (Pontarp et al., 2019). Moreover, the three explanations have rarely been tested across gradients that deviate from the regular LDG. Consequently, it is unclear whether the explanations hold outside the LDG for which they were originally formulated.

Although they are widely invoked to explain the tropical mega-diversity (Mittelbach et al., 2007; Pontarp et al., 2019), the three explanations are formulated in a sufficiently universal fashion to explain any richness gradient, including the i-LDG (Morales-Castilla et al., 2019; Pyron & Burbrink, 2009; Rivadeneira et al., 2011). Taxa with i-LDG are known as "exceptions to the rule", commonly cited in classic literature (Pianka, 1966; Ricklefs & O'Rourke, 1975) and, yet, surprisingly few studies have examined their richness gradients systematically. Weak LDGs or i-LDGs are thought to typify taxa with a distinct natural history, such as marine mammals (Tittensor et al., 2010), marine birds (Dalby et al., 2014), some snakes (Pyron & Burbrink, 2009), freshwater arthropods (Morinière et al., 2016), marine crustaceans (Rivadeneira et al., 2011) and some plants (Mateo et al., 2016). Although there is little consensus about the drivers of i-LDGs (Kindlmann, 2007), previous studies suggested effects of phylogenetic niche conservatism (Morales-Castilla et al., 2019; Morinière et al., 2016; Pyron & Burbrink, 2009), ecological regulation

TABLE 1 Six examined taxa with inverse latitudinal diversity gradients

Taxa	Described richness	Sampled richness	Richness peak	Taxon age (Myr)		Best explanation
				Mean	Range	
Anseriformes	178	151	Nearctic	70.88	66.45–87.49	Diversification rates
Procellariiformes	147	126	Southern cold ocean	61.34	50.08–70.60	Diversification rates
Cetacea	93	84	Western-eastern Atlantic and Western Indian oceans	22.70	12.71–37.94	Regional energy
Pinnipedia	34	32	Northern cold ocean	11.86	7.55–16.31	Diversification rates + time + regional energy
Lagomorpha	108	79	Palaeartic	41.46	29.33–54.80	Diversification rates
Caudata	762	334	Nearctic	197.68	165.01–229.88	Time

Notes: For each taxon, we indicate its described richness, the number of species included in this study, the region where its richness peaks, its mean age and its age range, and the explanation that we found to be the best supported one. The ages (in millions of years) were calculated using a set of 100 phylogenies for each taxon. Names of the terrestrial and marine realms follow Holt et al. (2013) and Miller et al. (2018), respectively. The described richness for Anseriformes and Procellariiformes were obtained from the International Ornithological Committee (IOC World Bird List, v.10.2; <https://www.worldbirdnames.org/new/>), the Mammal Diversity Database of the American Society of Mammalogists (<https://www.mammaldiversity.org/>) for Cetacea, Pinnipedia and Lagomorpha, and Amphibian Species of the World (v.6.0; <https://amphibiansoftheworld.amnh.org/>) for Caudata.

(Rivadeneira et al., 2011) and physiological adaptations to drought or frost (Mateo et al., 2016). At the same time, taxa with i-LDGs offer a unique opportunity to validate the processes originally defined for the regular gradients (Kindlmann et al., 2007). Given that nothing about the mechanisms hypothesized under the three explanations would limit their relevance to tropical regions, the explanations should, at least in principle, account for any richness gradients, including both the regular and the contrarian gradients (Pyron & Burbrink, 2009). Although the mechanisms generating the gradients might be similar, it is also clear that the gradients might differ principally in some respects. For example, i-LDG clades are known often to be nested within LDG clades (Wiens & Donoghue, 2004), which means that i-LDG clades tend to be younger than their LDG counterparts. These points of similarity and divergence motivate a more systematic comparison across taxa that vary in their richness gradients.

Here, we investigate the relative importance of time, regional diversification rates and regional energy to explain inverse gradients in species richness. We used six well-defined higher taxa with i-LDGs (Anseriformes, Procellariiformes, Cetacea, Pinnipedia, Lagomorpha and Caudata; c. 800 species), which vary markedly in their age and richness (Table 1). Given that i-LDGs are often viewed as idiosyncratic, we search for generalities across the six examined taxa and compare the results with those previously reported for regular LDGs. Our comparisons span marine and terrestrial systems, but also taxa with dramatically different physiologies, dispersal histories and geographical distributions. Consequently, the cross-taxa comparisons permit us to tease apart the mechanisms that would otherwise be hard to disentangle for any one taxon, region or richness gradient. Our results shed new light on some of the longstanding hypotheses and confirm that the three explanations might not be mutually exclusive. Therefore, we argue that by studying the exceptions to the rule, we might achieve more integrated knowledge of the mechanisms that together shape richness gradients, including i-LDG and LDG, which might be the most pervasive patterns of life on Earth.

2 | METHODS

2.1 | Inverse richness gradients

We focused on tetrapods because their geographical distributions and phylogenies are reasonably well known and well resolved. Moreover, tetrapods present a biologically well-defined unit for analysis, within which meaningful comparisons are possible (for more details, see Supporting Information Section 1). Specifically, we chose six major clades of similar rank that exhibit i-LDGs, including Anseriformes (ducks and geese), Procellariiformes (petrels and albatrosses), Cetacea (dolphins and whales), Pinnipedia (seals and sea lions), Lagomorpha (rabbits) and Caudata (salamanders). The selection of clades was inspired by the classic examples used in the literature when referring to i-LDGs (Davies et al., 2010; Dalby et al., 2014; Kindlmann et al., 2007; Rolland et al., 2014; Tittensor

et al., 2010). We disregarded i-LDG taxa whose richness was too low (Sphenisciformes, 18 species; and Gaviiformes, 5 species), for the purposes of reliable statistical inference (Title & Rabosky, 2019).

For each of the six taxa, we obtained geographical distributions from the International Union for Conservation Nature (<https://www.iucnredlist.org/>) and BirdLife International (<http://www.birdlife.org/>). We checked for concordance in names between species for which we had obtained distribution data and tips of the phylogenetic trees (Supporting Information Table S1). Therefore, we used 151 geese, 126 albatross, 84 cetacean, 32 pinniped, 79 rabbit and 334 salamander species in downstream analyses. We disregarded polygons with the presence category “possibly extant” and “presence uncertain” and polygons with origin category “introduced” and “vagrant”. We also disregard polygons of all extinct or non-native ranges. Thus, we restricted our analyses to species that fell into the presence category of “extant”, the origin categories “native” or “reintroduced”, and the seasonality categories “resident”, “breeding” or “non-breeding”. Using these range maps, we determined the presence or absence of each species in $2^{\circ} \times 2^{\circ}$ grid cells, then generated species lists for each grid cell. This resolution is considered appropriate for most vertebrates in order to reduce the number of false presences in the gridded data (Hurlbert & Jetz, 2007). The total species richness within each $2^{\circ} \times 2^{\circ}$ grid cell was defined by the number of species ranges that intersected the grid cell. To avoid bias associated with the low number of species, we disregarded grid cells with only one species.

2.2 | Phylogenies

Phylogenetic relationships for the six taxa were extracted from recently published trees (Jetz et al., 2012; Jetz & Pyron, 2018; Upham et al., 2019). For the three mammalian taxa, we used the species-level trees of extant Mammalia of Upham et al. (2019) (100 trees from “Mammals birth-death tip-dated DNA-only” distribution). For the two bird taxa, we extracted phylogenetic trees from the work of Jetz et al. (2012) (100 trees from “Hackett All Species” distribution). Lastly, for Caudata, we used the amphibian tree of life obtained from work of Jetz and Pyron (2018) (100 trees from “Amphibians Posterior All Species” distribution). All these phylogenetic proposals include the posterior distribution of species-level phylogenies considering the underlying reconstruction uncertainty (Supporting Information Section 1). To take into account the uncertainty in phylogenetic placements and node ages, we consider a sample of 100 phylogenies for each taxa. Although the phylogenies used differ in their calibration time and construction methods, they represent the current standard in the field and provide a good basis for comparisons across taxa in the search for general trends.

2.3 | Time for species accumulation

We used multiple measures to capture the time for species accumulation within a region, which included mean pairwise distance (MPD),

maximum branch length (MBL), species tip age, ancestral area reconstructions and model-based reconstructions of past dispersals (BioGeoBEARS). In comparison to other phylometrics that mix the effects of diversification rates and evolutionary time (Cavender-Bares et al., 2009), simulations have demonstrated MPD to be rather accurate in representing the age of the regional fauna (Economato et al., 2018; Oliveira et al., 2016). MBL indicates the age of the oldest species in the assemblage while assuming no extinction process, which can be used as a proxy to represent the available time of origin or colonization (García-Andrade et al., 2021; García-Rodríguez et al., 2021). The species tip age is defined by the age of its closest internal tree node (Sun et al., 2020). To account for the phylogenetic uncertainty, we averaged MPD, MBL and species tip age estimates for a set of 100 trees and projected these estimates within each grid-cell assemblage (Supporting Information Figures S1-S12). Overall, the comparisons confirmed that MPD, MBL and species tip age metrics were qualitatively consistent and predicted species richness in a similar fashion (Supporting Information Figures S13-S16). Therefore, we focus on the MPD results because these take into account the average phylogenetic distance connecting all species in a community and treat MBL and species tip age estimates as supplementary.

To cross-validate the results based on grid-cell phylometrics, we also used ancestral range reconstructions to assess where the origin of the i-LDG taxa is more likely to have occurred. First, we used species distribution maps to calculate the percentage of the species distribution within the tropics (between the Tropics of Cancer and Capricorn; index of geographical tropicality). Ancestral reconstructions were also implemented on climatic preferences, whereby average values of temperature were extracted across the distribution range of each species. To test whether geographical or climatic preferences are phylogenetically conserved across species, we evaluated phylogenetic signal using Blomberg's *K* (Blomberg et al., 2003). Second, we quantified the ancestral range probabilities using a dispersal-extinction-cladogenesis (DEC) model (Ree & Smith, 2008) as implemented by the BioGeoBEARS R package (Matzke, 2013). We coded the presence/absence of each species within two discrete areas: A = temperate area (outside the Tropics of Cancer and Capricorn) and B = tropical area (inside the Tropics of Cancer and Capricorn). Species with a widespread distribution (spanning both the temperate and the tropical areas) were coded as present in both states A and B (Supporting Information Section 2). Unlike the phylometrics or ancestral reconstructions, BioGeoBEARS explicitly models the dispersal of clades between the temperate and the tropics, such that it provides a more direct measure of the time for species accumulation.

2.4 | Diversification rates

We used two essentially different methods to estimate regional diversification rates: DR and BAMM (Jetz et al., 2012; Rabosky, 2014). DR is a species-level metric of diversification, defined as the inverse of the evolutionary distinctiveness (Jetz et al., 2012). As such, DR

measures the degree of species isolation on phylogeny and makes minimal assumptions about the diversification process. In contrast, BAMM explicitly models the diversification process along the branches of the phylogeny, while allowing for diversification heterogeneity across lineages and over time (Rabosky, 2014). BAMM was implemented under four Markov chain Monte Carlo (MCMC) chains that were run for 5×10^6 generations, with the first 25% of each run discarded as burn-in. The appropriate prior parameters for speciation rate, rate shift and extinction rate were estimated using the “setBAMMpriors” function from the BAMMTOOLS package (Rabosky et al., 2014). Using the BAMMTOOLS package, we computed the mean of the marginal posterior distribution of diversification rates for each tip in a phylogenetic tree (i.e., present-day diversification rates; Rabosky et al., 2014).

To account for the phylogenetic uncertainty associated with diversification estimates, we repeated the DR and BAMM analyses for each sample tree and averaged the 100 iterations. To obtain the estimates of present-day regional diversification, we rasterized the evolutionary variables by averaging the diversification rates of species that occurred within the grid cell (i.e., assemblage-based approach; Villalobos et al., 2020). We confirmed that the set-ups using BAMM and DR produced mutually consistent geographical results (Supporting Information Figures S29–S43) and were highly correlated (Supporting Information Figure S43). Given that the net diversification rates (speciation minus extinction) estimated for the six taxa were highly correlated with the speciation rates (Supporting Information Figure S42), we used only BAMM speciation estimates. Estimates of extinction rates have been shown to be unrealistic biologically (Mitchell et al., 2019; Rabosky, 2010), and some previous studies have suggested using only speciation estimates (Igea & Tanentzap, 2020; Rabosky, 2018; Title & Rabosky, 2019). Moreover, we compared the tip rates estimated from sub-trees (match-data tree) to those extracted from a near-complete phylogeny (e.g., 9,993 species of birds from the study by Jetz et al., 2012). We repeated this procedure under BAMM and DR and confirmed that the tip rates were mutually consistent (Supporting Information Figures S44 and S45), suggesting that the sample size for a given sub-tree did not bias the analyses. We present the tip speciation rates from BAMM in the main text and treat DR estimates as supplementary (Supporting Information Section 3).

BAMM and DR have been supported by mathematical arguments and simulations (Mitchell et al., 2019; Rabosky et al., 2017; Title & Rabosky, 2019). Although some assumptions of the diversification methods have recently been questioned (Louca & Pennell, 2020), present-day diversification estimates are generally robust because they are derived from the recent splits within the phylogeny and, importantly, we did not make any assumptions about the diversification trajectory that led to the present-day rates (see Siqueira et al., 2020; Title & Rabosky, 2019). Our analyses aimed to test for broad-scale differences in regional diversification, using a set of predictions (e.g., diversification is fast in the species-rich regions) and we did not interpret the estimates obtained beyond assessing our predictions (e.g., to estimate historical diversification in a region)

(Louca & Pennell, 2020). Finally, we combined two methods (BAMM and DR) that differ principally in their assumptions and therefore are unlikely to converge on mutually consistent present-day rate estimates, unless these rate estimates are firmly grounded in the data.

2.5 | Regional energy

The total amount of regional energy, niches and resources is hard to measure directly, but can be captured by a variety of proxies (Hawkins et al., 2003): the so-called “solar energy measures”, which capture the input of solar energy (e.g., temperature, radiation); and “productive energy measures”, which capture the energy available to convert into biomass (e.g., actual evapotranspiration, net primary productivity) (Evans et al., 2005). For each of the six examined taxa, we extracted multiple proxies for the input of solar energy and primary production across grid cells (Supporting Information Section 4).

The proxy variables were obtained from the WorldClim database (Hijmans et al., 2005), Atlas of the Biosphere (<https://nelson.wisc.edu/sage/data-and-models/atlas/index.php>) and BioOracle (Assis et al., 2018; Tyberghein et al., 2012). Given that present-day richness often reflects the historical environment (Rangel et al., 2018), we also obtained palaeoclimate from the CHELSA database (Karger et al., 2017). Palaeoclimate was represented by the temperature from the Last Glacial Maximum (c. 21 ka; Karger et al., 2017, 2021) and the Pliocene (c. 3.3 Ma; Dolan et al., 2015).

Given that multiple current and historical proxies were correlated with species richness comparably well (Supporting Information Figures S47–S48), we used for our main analyses the annual mean temperature for terrestrial taxa (BIO1) and mean sea surface temperature for marine taxa (SST) to represent regional energy. These two measures directly reflect the solar energy input and were consistently more correlated with species richness than the other climatic variables in both the terrestrial and the marine environments (Supporting Information Figures S47–S48). Therefore, the proxy variables not included in the main analyses were treated as supplementary.

2.6 | Time, diversification rates and regional energy as predictors of regional richness

To quantify the relative importance of the three explanations and to tease apart their overlaps, we performed variance partitioning based on multiple linear regression (Peres-Neto et al., 2006), as implemented in the “varpart” function in the vegan R package (Oksanen et al., 2020). This approach uses the adjusted R^2 values to evaluate the contributions of the considered explanatory variables while limiting the possible biases of sample size (Peres-Neto et al., 2006). Therefore, variance partitioning estimated the individual contributions of evolutionary time for species accumulation (MPD), regional diversification rates (BAMM speciation estimates) and regional

energy (temperature) to regional species richness, in addition to the shared contributions for each combination of the three classes of explanations. The sum of adjusted R^2 values for the individual and the shared fraction of each predictor indicates the total predictor fraction.

To examine non-linear changes in species richness with the three explanations, we also fitted multiple generalized additive models (GAMs) with a Poisson error distribution and a cubic smoothing spline method. Given that spatial autocorrelation can affect the parameter estimates and errors of underlying regression models (Diniz-Filho et al., 2003), we also implemented the analyses with spatial correction. Specifically, each GAM was refitted with a spherical spatial correlation structure (Supporting Information Section 5). All statistical procedures used in the paper were performed in the R environment (Cerezer et al., 2022; R Core Team, 2020). Additional R packages not mentioned in the main text are provided in the Supporting Information Sections 2-5.

2.7 | Sensitivity analyses

To verify the robustness of the uncovered results and confirm that our conclusions are independent of the choice of the method used, we performed a range of sensitivity analyses. Specifically, we accounted for phylogenetic uncertainty when calculating the estimates of time and diversification rates (i.e., averaging estimates for a set of 100 trees for each taxa). For estimates of diversification rates, we used two essentially different methods (BAMM and DR) and compared their outputs. For evolutionary time estimates, we used three phylometrics (MPD, MBL and species tip age) along with ancestral reconstructions (geographical/climatic reconstruction and DEC model). We considered a multitude of current predictors associated with temperature and productivity to represent regional energy, but we also verified the extent to which palaeoclimate explains present-day differences in regional richness. Additionally, we evaluated the sensitivity of our findings to spatial variation in species richness, for which we repeated analyses while removing grid cells with fewer than three, five and seven species. Lastly, we repeated the variance partitioning and GAMs while removing estimates of time, diversification and regional energy that were deemed high or low outliers (Supporting Information Section 6).

3 | RESULTS

3.1 | Effects of time, diversification rates and regional energy

In contrast to richness patterns known for many other taxa of similar taxonomic rank, the six examined taxa showed extra-tropical peaks in regional richness (Figures 1 and 2). Despite this similarity, their richness varied markedly across hemispheres and continents,

even at the same latitudes. The richness of the terrestrial taxa (geese, salamanders and rabbits) peaked in the Nearctic and Palearctic regions (e.g., North American temperate forests and grassland, Tibetan plateau and Siberia), but showed only limited richness throughout the Southern Hemisphere (e.g., tropical and subtropical moist broadleaf forests, South American grasslands) (Figure 1; Table 1). Marine taxa (albatrosses, cetaceans and pinnipeds) showed richness peaks in parts of the western-eastern Atlantic, the western Indian, the northern and the southern cold oceans (Figure 1; Table 1).

Variance partitioning revealed that the explanatory power of the evolutionary time for species accumulation, regional diversification rates and regional energy differed across the six studied taxa (Figure 3). Present-day diversification rates explained most of the variation in species richness in three of the six taxa (geese: $R^2 = 0.33$, $p < .001$; albatrosses: $R^2 = 0.48$; $p < .001$; rabbits: $R^2 = 0.15$, $p < .001$; Figure 3) and were also significantly associated with the richness gradients in the remaining groups (cetaceans: $R^2 = 0.31$, $p < .001$; pinnipeds: $R^2 = 0.27$, $p < .001$; salamanders: $R^2 = 0.09$, $p < .001$; Figure 3). For geese, albatrosses, cetaceans and rabbits, diversification rates were positively associated with species richness, whereby species-rich temperate regions had the highest diversification rates (Figure 4; Supporting Information Figures S36-S40). We found the opposite pattern for pinnipeds and salamanders, in which diversification rate peaks in species-poor regions (Figure 4; Supporting Information Figures S39 and S41).

The evolutionary time for species accumulation was not a strong determinant of species richness (maximum explanatory contribution ranged from $R^2 = 0.01$ to $R^2 = 0.19$; Figure 3). For albatrosses and cetaceans, we have not found strong evidence for the dependency of species richness and evolutionary time (Figure 3; Supporting Information Figures S13-S16). As expected given their high mobility, these two taxa showed low phylogenetic signal in both geographical [Blomberg's K for cetaceans = 0.125 [95% confidence interval (CI) of 0.117 to 0.133]; Blomberg's K for albatrosses = 0.154 (95% CI of 0.143 to 0.165); Supporting Information Figure S19] and climatic preferences [Blomberg's K for cetaceans = 0.178 (95% CI of 0.168 to 0.188); Blomberg's K for albatrosses = 0.177 (95% CI of 0.166 to 0.189); Supporting Information Figure S22]. Nonetheless, ancestral reconstructions indicated a widespread origin for albatrosses and cetaceans (Figure 4; Supporting Information Figures S17-S22, S24 and S25). When analysing the individual contributions of the three factors, we found that salamander species richness is driven primarily by the timing of the first regional colonization (Figure 3), whereby species-rich temperate regions are older (Figure 4; Supporting Information Figures S15-S16 and S28). Indeed, salamanders exhibit a high phylogenetic signal associated with geographical preferences [$K = 1.201$ (95% CI of 1.150 to 1.252); Supporting Information Figure S19], and the effects of time on species richness were even more evident when considering the MBL measure (Supporting Information Figure S13). Collectively, the results from ancestral reconstructions were mostly congruent and revealed that pinnipeds, rabbits and

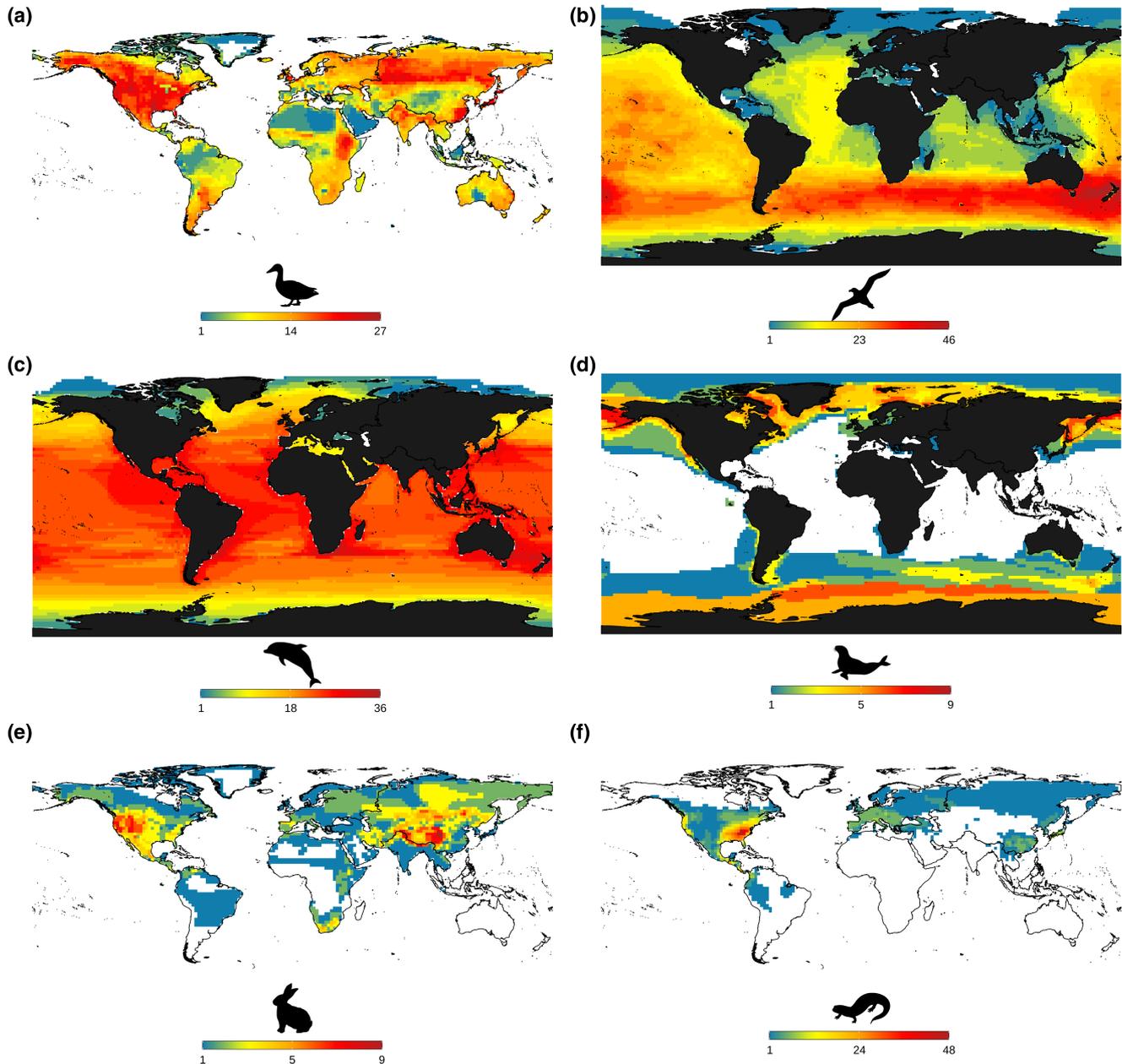


FIGURE 1 Global species richness map for (a) Anseriformes (ducks and geese); (b) Procellariiformes (petrels and albatrosses); (c) Cetacea (dolphins and whales); (d) Pinnipedia (seals and sea lions); (e) Lagomorpha (rabbits); and (f) Caudata (salamanders). Grid cells ($2^\circ \times 2^\circ$) with dark red colours indicate higher species richness. Grid cells with one species were not used in the main analyses and are represented only to illustrate the distribution range of each clade.

salamanders are more likely to have originated in temperate, colder climates (Supporting Information Figures S26–S28), whereas it was not possible to identify the region of origin for geese unambiguously (Figure 4; Supporting Information Figure S23). Finally, with the exception of marine mammals (cetaceans: $R^2 = 0.61$, $p < .001$; pinnipeds: $R^2 = 0.26$, $p < .001$), the effects of regional energy on species richness were weaker than the effects of diversification and time (R^2 ranged from 0.01 to 0.10; Figures 3 and 4).

We also found some important overlaps between the three classes of explanations. The largest fraction of the pinniped regional richness was explained by the overlapping effects of time,

diversification rates and regional energy (i.e., it was not possible to disentangle; Figure 3). Likewise, a sizeable fraction of the variation in regional richness in cetaceans and salamanders was explained by a combination of regional energy and diversification rates (Figure 3). Regarding the results of GAMs, we found that the effects of time, diversification rates and regional energy on species richness were qualitatively similar to the variance partitioning (R^2 ranged from 0.64 to 0.80), again revealing idiosyncratic behaviours of the three explanation classes (Supporting Information Tables S2 and S3). For the sake of simplicity, we treat the results of GAMs as supplementary (Supporting Information Section 5).

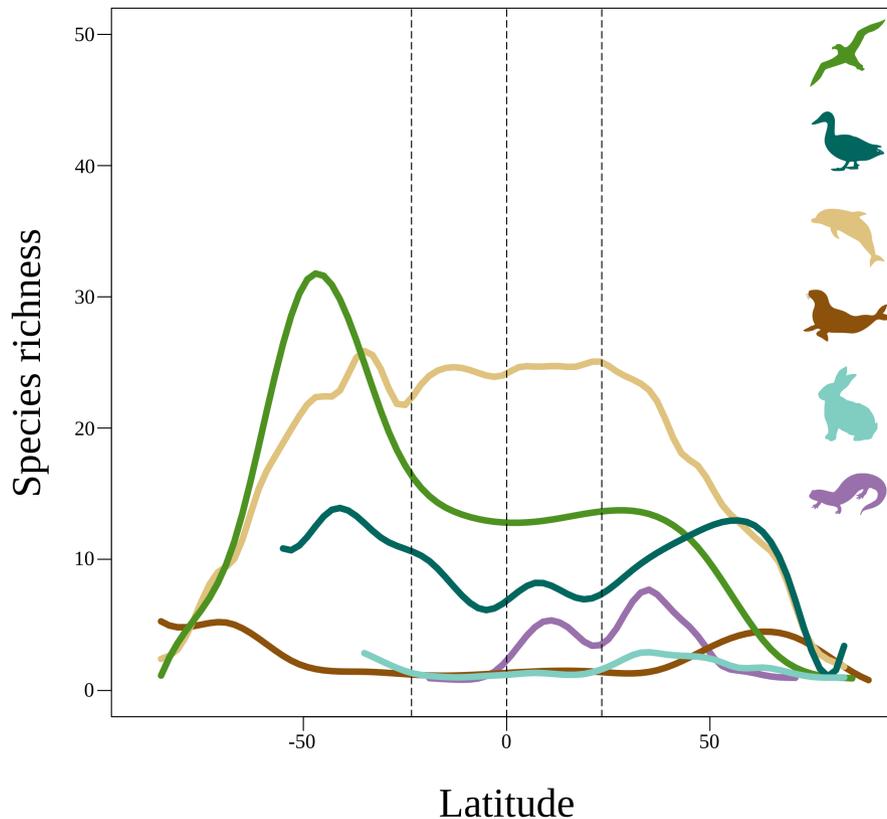


FIGURE 2 Inverse latitudinal patterns of species richness. Coloured lines with cubic polynomial fitting indicate the variation in richness across latitude for each of the six taxa: Anseriformes (ducks and geese), Procellariiformes (petrels and albatrosses), Cetacea (dolphins and whales), Pinnipedia (seals and sea lions), Lagomorpha (rabbits) and Caudata (salamanders). Vertical dashed lines delimit the tropical region. Note that the six taxa exhibit extra-tropical peaks in species richness.

3.2 | Robustness and sensitivity of the results

Our results were robust against various sources of errors, including uncertainty in the phylogenies, in the estimates of time, diversification rates and regional energy. Namely, we found that different estimates of regional diversification rates (based on BAMM and DR) were highly correlated (Spearman's rank correlation coefficients ranged from 0.506 to 0.883; Supporting Information Figure S43). Similarly robust were the estimates of evolutionary time derived from grid cell-based phylometrics, ancestral reconstructions and model-based reconstructions of past dispersal (DEC model in BioGEOBEARS), which consistently identified similar regions (temperate, tropical and, in some cases, widespread) that have had the most time for the accumulation of richness (Supporting Information Section 2). Finally, we used multiple proxies for current and past regional climate, energy and resources (Supporting Information Section 4) and found that both the current and the past climate (covering the Last Glacial Maximum, c. 21 ka, and Pliocene, c. 3.3 Ma) supported similar conclusions about the effects of regional energy.

We also confirmed our findings under other potential sources of errors, including sensitivity to variation in species richness, spatial autocorrelation and outliers (Supporting Information Sections 5 and 6). Specifically, we confirmed that the effects of the three explanations on species richness did not change while controlling

for the spatial autocorrelation (R^2 ranged from 0.080 to 0.612; Supporting Information Table S3) or when removing grid cells with fewer than three, five and seven species in both variance partitioning (Supporting Information Figures S55–S57) and GAMs (R^2 ranged from 0.059 to 0.809; Supporting Information Tables S4–S6). This suggests that the uncovered trends are unlikely to be biased by outlier regions with limited richness. We also found that the general findings obtained from variance partitioning (Supporting Information Figures S58 and S59) and GAMs (R^2 ranged from 0.604 to 0.806; Supporting Information Tables S7 and S8) were not influenced by outliers (extreme values of time, diversification rates and energy ranged from 0 to 37%). Importantly, all these changes in the source data and methodological set-ups did not overturn our main conclusions.

4 | DISCUSSION

Our findings indicate that many pathways can lead to an i-LDG, whereby the time for species accumulation, regional diversification rates and regional energy simultaneously contribute to the formation of the gradient, but in varied and taxon-specific ways (Figures 3 and 4). We found appreciable differences between terrestrial and marine taxa and between ecto- and endotherms. Yet, the following

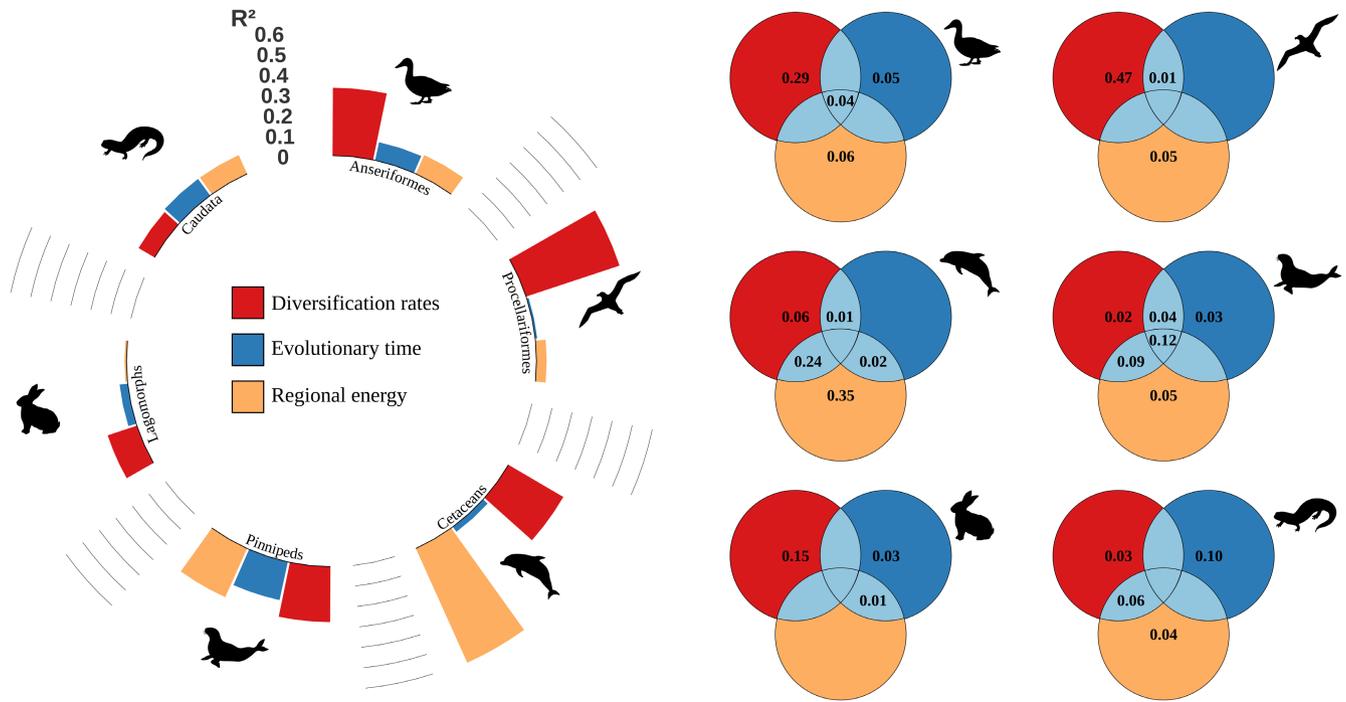


FIGURE 3 Comparing the effects of the three explanations. The figure shows variance partitioning for the effects of evolutionary time for species accumulation (MPD, blue), regional diversification rates (BAMM estimates, red) and regional energy (temperature, orange). It compares the total effects of the three explanations (left panel), their unique effects and the effects of their overlaps, depicted using the Venn diagrams (right panel). Venn diagrams show the results of variance partitioning based on multiple regression models and provide additional detail on how variance is shared by the three explanations. The values within the Venn diagrams show adjusted R^2 values, and empty fields correspond to $R^2 = 0$.

common tendencies emerged: (1) species-rich regions tend to have fast present-day diversification; (2) time constrains the accumulation of species even in the face of available resources and fast diversification, and (3) regional energy seems to shape richness gradients in the marine taxa with good dispersal. Richness gradients diverging from the famous LDG remain surprisingly understudied. Our results shed new light on the mechanisms generating the inverse but also, potentially, the regular latitudinal diversity gradients, for which the effects of time, diversification rates and regional energy on species richness have been notoriously hard to tease apart.

To summarize the comparisons across the six taxa, we found that regional richness increased with regional diversification rates, but only in geese, albatrosses, cetaceans and rabbits (Figure 4). These four taxa also most probably originated in the temperate regions, where their richness currently peaks, which indicates possible synergy between fast diversification and the evolutionary time for species accumulation (Jablonski et al., 2006; Mittelbach et al., 2007; Ricklefs, 2007). In contrast, regional richness in pinnipeds and salamanders is currently decoupled from their rates of diversification (Figure 4). Richness gradients in these two taxa might, therefore, flatten or even reverse in the future, given that both pinnipeds and salamanders rapidly diversify in the currently species-poor tropics (Figure 4). The three explanations were aligned only in the case of marine mammals, whose i-LDG probably resulted from the confluence of time, diversification rates and regional energy (Figure 3). Together, these findings illustrate how dramatically the effects of

the individual explanations vary across taxa and how they might be contingent on one another, rather than being mutually independent. Consequently, the consistency of richness gradients does not necessarily imply the consistency of their underlying causes (Hawkins et al., 2012). Instead, various combinations of the three explanations, each acting in roughly the same direction, seem to generate similar richness gradients across different taxa.

4.1 | The effects of time, diversification rates and regional energy

We found that time for species accumulation played some role in shaping richness gradients across the examined taxa. Although all taxa showed richness peaks in the temperate regions, each showed significant differences in richness across continents and hemispheres, even at the same latitudes (Figure 1). Some taxa reached exceptionally high richness in North America (e.g., salamanders) and Central Asia (e.g., geese), whereas others showed low richness in Europe (e.g., geese) and in the Alps (e.g., rabbits). These differences were especially pronounced in pinnipeds, rabbits and salamanders (Figures 1 and 4). In salamanders, their historical origin had such a pronounced effect that it counterbalanced the effects of regional diversification rates. Most salamander species were concentrated in the early colonized temperate regions of North America, although salamander diversification accelerated dramatically towards the tropics, where their richness is

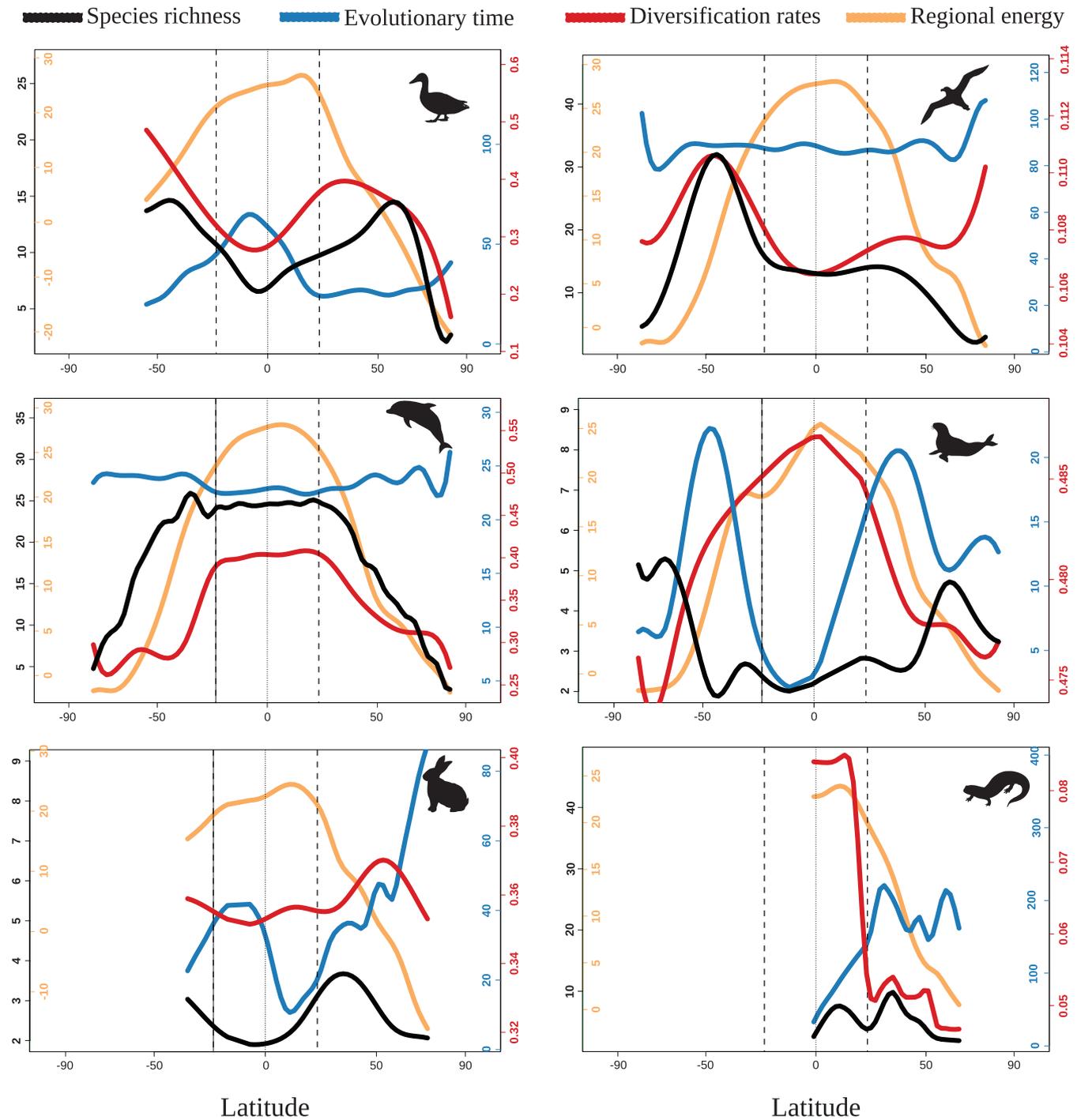


FIGURE 4 Latitudinal trends in species richness, evolutionary time (MPD), diversification rates (BAMM estimates) and regional energy (temperature) for Anseriformes (ducks and geese), Procellariiformes (petrels and albatrosses), Cetacea (dolphins and whales), Pinnipedia (seals and sea lions), Lagomorpha (rabbits) and Caudata (salamanders). Coloured lines with cubic polynomial fitting indicate the variation of species richness (black line), evolutionary time (blue line), diversification rates (red line) and regional energy (orange line) across latitudes. Dashed lines delimit the tropical regions.

currently low (Figures 3 and 4). These results are consistent with other studies, which reported that the tropics have been colonized only in recent times and that salamanders show accelerated diversification in the tropics (Kozak & Wiens, 2010; Wiens, 2007).

Regional energy seems to have contributed significantly to the broad-scale richness patterns in cetaceans and pinnipeds (Figures 3

and 4). Cetacean richness closely followed the sea surface temperature (Figure 3). Some previous studies have suggested that temperature might constrain the distribution of marine mammals (Whitehead et al., 2008), presumably owing to physiological constraints (Grady et al., 2019; Tittensor et al., 2010). Aside from cetaceans and pinnipeds, however, we found little evidence for the energy effects

(Figure 3). Their limited support is not surprising, given that we studied taxa whose richness peaks outside the resource-rich tropics. Yet, we found that regional energy failed to explain differences in richness even across continents. For example, geese and rabbits are species-rich in North America and Asia but not at the comparably resource-rich latitudes in Europe (Figure 1), although Europe and Asia are connected by contiguous landmass with suitable corridor habitats (Binney et al., 2017). Likewise, salamander richness peaks in the temperate broadleaf and mixed forests of North America, but is virtually absent from the same biomes elsewhere in the world (Figure 1). These differences might result from limited time for cross-continental dispersal (Mittelbach et al., 2007). But the lack of support for energy effects, even at the continental scale across taxa with >100 Myr history (such as salamanders), challenges the universality of regional energy as an explanation for richness gradients (Graham et al., 2018). It has been argued before that the correlations between regional richness and the proxies for regional climate, energy and resources result, at least in some cases, as a side effect of the historical spread of species from the tropics towards the temperate regions, the high rates of tropical diversification, or both (Buckley et al., 2010; Kozak & Wiens, 2010; Rabosky, 2009). For future work, it could be useful to explicitly delimit the geographical and phylogenetic scales at which regional energy might be expected to outweigh the other effects (e.g., time, diversification rates) that can generate similar richness patterns (Graham et al., 2018; Machac et al., 2018).

Although the effects of time and regional energy were highly taxon specific, those of regional diversification rates were consistent across taxa (Figure 3). We found that species-rich regions tended to show high rates of regional diversification, which held for geese, albatrosses, cetaceans and rabbits (Figure 4), although some exceptions emerged (pinnipeds and salamanders; Figure 4). The relationship between regional richness and the rates of present-day diversification within the region has been one of the focal topics in recent literature (Harvey et al., 2020; Machac, 2020; Miller et al., 2018; Rabosky et al., 2018) and therefore deserves closer attention.

4.2 | Relationship between regional richness and regional diversification rates

Whether species-rich regions show faster or slower diversification has been of much interest lately (Harvey et al., 2020; Machac, 2020; Miller & Román-Palacios, 2021; Morlon, 2020). Traditionally, species-rich regions, especially the tropics (Mittelbach et al., 2007), have been presented as the “cradles” of diversity, where species originate rapidly, and/or as diversity “museums”, with reduced extinction (Jablonski et al., 2006; Rangel et al., 2018). Contrary to this traditional view, recent evidence from a range of clades has revealed the opposite pattern (e.g., plants, fishes, birds), whereby present-day diversification tends to be faster in the species-poor regions (Harvey et al., 2020; Igea, 2020; Machac, 2020; Rabosky, 2018).

This new pattern inspired several explanations (Harvey et al., 2020; Miller & Román-Palacios, 2021; Morlon, 2020). For

example, diversification might slow down as the species gradually accumulated within a region start to compete for the finite amount of regional resources, which produces a negative diversity dependence of regional diversification rates (Machac et al., 2018; Rabosky & Hurlbert, 2015; Simpson, 1953; Storch & Okie, 2019). In addition, fast recent diversification in the temperate regions might be caused by recent extinctions owing to the Pleistocene glaciations (Miller et al., 2018; Schluter & Pennell, 2017; Weir & Schluter, 2007). In this scenario, new species have been originating rapidly in the temperate regions only recently, in order to replace the extinct diversity, meaning that fast temperate speciation is a side effect of high species turnover (Weir & Schluter, 2007). Taxa with i-LDGs do not support these two explanations entirely. If diversification rates were negatively diversity dependent, we would find fast diversification in the species-poor regions, but we found the opposite in geese, albatrosses, cetaceans and rabbits. Likewise, the Pleistocene glaciations seem to have had only limited effects, given that two of the i-LDG taxa showed slower diversification rates in the temperate regions (pinnipeds and salamanders; Figure 4). These results pertain to i-LDG clades, which are nested within some of the higher taxa for which the opposite results have recently been reported (e.g., birds) (Miller et al., 2018; Morlon, 2020; Schluter & Pennell, 2017; Weir & Schluter, 2007). Consequently, our results do not overturn the previous results, but complement them by revealing that many of the clades nested within the higher taxa conform with the traditional view, whereby fast diversification takes place across the species-rich regions (Jablonski et al., 2006; Mittelbach et al., 2007).

4.3 | The effects of scale

How the three explanations hold across the continuum of temporal, phylogenetic and geographical scales has also been debated (Graham et al., 2018; Price, 2015; Schluter, 2015; Wiens, 2017). We studied clades that rarely have a global distribution but span a variety of ages (c. 10–200 Myr; Table 1) and geological epochs (from Miocene to Palaeocene and Jurassic). It has been suggested that the effects of time and diversification rates generate diversity anomalies (e.g., biodiversity hotspots, such as those in the mountains) (Rahbek & Graves, 2001), whereas regional energy shapes broad-scale richness patterns (Graham et al., 2018; Pontarp & Wiens, 2016; Wiens, 2017). But the opposite has also been hypothesized, whereby the spread of clades from the tropics and the time for species accumulation generated the global latitudinal diversity gradient (Li & Wiens, 2019; Ricklefs, 2008; Wiens & Donoghue, 2004).

We found that the i-LDGs of some taxa result from historical effects and typically reach the highest richness in the region of the taxa's inferred origin (e.g., in salamanders). Nonetheless, within the range of their respective geographical distributions, time for species accumulation makes a small contribution to regional richness (Figure 3). It is possible that a generally lower contribution of evolutionary time results from the fact that we analysed i-LDG taxa, which tend to be relatively young. Young clades show limited age variation

across their constituent subclades, and if the subclades colonized different regions at times that were not sufficiently spread apart to produce marked variation in regional richness, time effects might be hard to detect. However, it has also been argued that time effects should be pronounced, rather than limited, in young clades (such as those with i-LDGs). As clades become older, regional differences in their diversification rates might erase the effects of time spent within the region (Li & Wiens, 2019), and regional richness might become increasingly constrained by regional energy (Cornell, 2013; Storch & Okie, 2019). Our results showed the strongest effects of time in salamanders, the oldest of the analysed clades (c. 200 Myr). This would suggest that time effects do not necessarily become suppressed as clade age increases, and the limited support for time effects, which we found, might be caused by our focus on i-LDG clades, which tend to be relatively young.

The time effects might also depend on the dispersal of the taxon. Although dispersal is hard to measure directly, it can be gauged from the phylogenetic signal in the climatic preferences of the taxon (Wiens & Graham, 2005). Taxa with conserved climatic niches do not easily colonize regions with different climates, such that their richness gradients might be shaped primarily by the timing at which they colonized the different regions and latitudes (Wiens & Donoghue, 2004). In line with this reasoning, we found pronounced time effects in salamanders, which show conserved climatic niches, are poor dispersers, and their richness gradient seems to track their gradual spread from the presumed region of their origin in North America (Vieites et al., 2007). Conversely, marine cetaceans are good dispersers, have colonized most of the oceans of the world (Tittensor et al., 2010; Whitehead et al., 2008) and show little to no conservatism in their climatic niches. These results together suggest a possible generalization whereby taxa with poor dispersal and conserved climatic niches have richness gradients shaped by colonization history and time for species accumulation. The effects of historical dispersal tend to be erased in clades that disperse well, show barely any phylogenetic signal in their climatic niches and, consequently, their richness gradients more closely follow the differences in regional diversification rates and energy (Mittelbach et al., 2007; Pontarp & Wiens, 2016). In this sense, our results support the possibility that richness gradients are shaped by different mechanisms at different scales, whereby time effects dominate in taxa with limited dispersal and geographical ranges (e.g., salamanders), whereas diversification rates and regional energy shape richness gradients in widespread taxa with global distributions (e.g., marine mammals).

4.4 | Explaining i-LDG and LDG

In comparison to the i-LDG, the LDG has received dramatically more attention, often being presented as a universal pattern (Brown, 2014; Pontarp et al., 2019; Rohde, 1992), which holds across a variety of organisms (e.g., tunicates, plants, vertebrates), geographical domains (e.g., New World, Old World) and historical eras (e.g., multiple icehouse eras) (Brown, 2014; Marcot et al., 2016; Meseguer

& Condamine, 2020; Song et al., 2020). As such, it has inspired a range of explanations (Mittelbach et al., 2007; Pontarp et al., 2019; Rohde, 1992). These explanations are often defined in a universal fashion and therefore should apply to any richness gradient at any scale, at least in principle. For example, regional differences in richness have been hypothesized to result from the differences in the time for species accumulation (Mittelbach et al., 2007; Stephens & Wiens, 2003), and this mechanism should apply regardless of whether the richness of a given taxon peaks in the temperate zone (i-LDG) or in the tropics (LDG).

Nonetheless, we found that none of the three classes of explanations (time, diversification rates and energy) holds across all the examined taxa or applies uniformly to gradients that diverge from the regular LDG (Figures 1 and 2). The findings for i-LDG motivate more rigorous formulation of the three explanations, in order to clarify the circumstances in which they can reasonably be expected to apply (Graham et al., 2018; Machac et al., 2018). Finally, the taxa we examined might be seen as exceptions, but there are other examples of groups with i-LDGs to which our results might extend, although we currently lack the necessary data for their rigorous analysis (e.g., aphids, ichneumonids, shallow-water molluscs) (Kindlmann et al., 2007; Morales-Castilla et al., 2019). Moreover, our results might extend to taxa that had inverse gradients in the past, during historical periods of global warming and cooling (Marcot et al., 2016; Meseguer & Condamine, 2020).

4.5 | Caveats and potential limitations

We recognize several sources of potential errors, associated with the estimates of evolutionary time, diversification rates and regional energy and with taxon sampling. However, we conducted a series of supplementary analyses to ensure that none of these issues would overturn our main conclusions. First, we used multiple measures of time (MPD, MBL, species tip age and BioGeoBEARS) that either modelled explicitly the historical origin and the dispersal events across tropical and temperate regions or captured the age of the regional fauna. Although we did not use methods that estimate the time effects across grid cells (Miller et al., 2018; Miller & Román-Palacios, 2021; Stephens & Wiens, 2003), our results were sufficiently robust and consistent to draw relevant conclusions (Supporting Information Section 2). Second, we used two disparate measures of present-day diversification rates (BAMM and DR) that converged on consistent estimates (Supporting Information Section 3). Although these estimates are robust, they do not reflect past variations in diversification rates, and we limit our conclusions to present-day diversification (Morlon, 2020). Third, we approximated regional energy and resources, using environmental temperature, net primary productivity, actual evapotranspiration and palaeoclimate (Last Glacial Maximum and Pliocene), such that we could capture not only current environmental conditions but also the conditions in the recent past, and all estimates returned similar results (Supporting Information Section 4). Finally, we acknowledge

that taxa with i-LDGs do not represent a random sample of all clades (e.g., they tend to be younger than taxa with LDGs). Despite this issue, our sampling spanned taxa that differed markedly in their age (c. 10–200 Myr) and size (c. 30–750 species) (Table 1). Nonetheless, further research to compare a larger number of taxa with i-LDGs, LDGs and taxa with other shapes of richness gradients, while systematically covering a range of regions, historical eras and phylogenetic scales, would clearly be valuable to zoom in on the interplay of the mechanisms generating richness gradients.

5 | CONCLUSION

We found that similar richness gradients might have different explanations. None of the classical explanations (time, diversification rates and regional energy) seems sufficient in and of itself, and the mechanisms invoked by the individual explanations tend to interact with each other. For example, diversification rates are often positively correlated with regional richness (e.g., geese, albatrosses, cetaceans and rabbits), but this pattern can be weakened or even reversed if the region with fast diversification was colonized only recently (e.g., salamanders). Likewise, regional richness might be shaped by regional energy, but few clades seem close to the presumed energy limits (e.g., they show continued diversification even across the most species-rich regions). Even among regions with similar environmental conditions, the legacy of historical dispersal seems to generate large cross-continental differences in regional richness (e.g., within rabbits and pinnipeds).

Although we studied taxa that can be seen as the “exceptions to the rule”, it is possible that other richness gradients are also created by a variety of interactions between time, diversification rates and regional energy (Machac, 2020; Miller & Román-Palacios, 2021; Mittelbach et al., 2007; Pontarp et al., 2019). Instead of searching for the Holy Grail whereby a single mechanism explains the striking richness differences, it might prove more useful to investigate the variety of mechanisms whose interactions unfold over time to produce both regular and inverse richness gradients.

AUTHOR CONTRIBUTIONS

All authors contributed to design of the study. F.O.C. and C.S.D. conducted the statistical analyses. F.O.C. wrote the first draft, with important input from A.M., T.F.R. and C.S.D. All authors contributed substantially to the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R scripts required to replicate the analyses are deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.z08kprrd4>; Cerezer et al., 2022).

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BIOSKETCH

Our group investigates how ecological and evolutionary processes determine the patterns of species diversity in space and time. Our approach focuses on questions of broad taxonomic scope using mechanistic and correlative models.

SUPPORTING INFORMATION

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