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Time best explains global variation in species richness of amphibians, birds and mammals

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ABSTRACT

Aim The general pattern of higher species richness in tropical areas has been long recognized but the underlying cause is still debated. Two major hypotheses have emerged in recent years. The Rate Hypothesis attributes this pattern to a high rate of diversification, whereas the Time Hypothesis attributes it to greater lineage age. Here, we revisited these two hypotheses with global data sets of amphibians, birds and mammals.

Location Global.

Methods To test these hypotheses we evaluated the relationship between crown age and species richness, and between diversification rate and species richness within biogeographical regions. We also compared diversification rates of tropical and temperate clades, and assessed the usefulness of two phylometrics, evolutionary distinctiveness (ED) and evolutionary rate (ER), as proxies of age and diversification rate. Finally, we used those phylometrics in a grid cell approach to explore the spatial distribution of clade age and diversification rate.

Results We found species richness of these tetrapods is best described by time (age of lineages) and that diversification rates are not significantly different between tropical and temperate areas. In addition to time, we found that historical biogeography, in some cases, has an influence on species richness patterns. In turn, this suggests that the latitudinal diversity gradient is a result of the gradient in climatic stability, with younger assemblages (hence, fewer species) occupying higher latitudes.

Main conclusion Our results indicate that time, and not rate of diversification, best describes species richness patterns of amphibians, birds and mammals, and that this pattern is a 'climate effect' ultimately deriving from the latitudinal gradient in climatic stability.

Keywords
amphibians, biodiversity patterns, birds, mammals, Rate Hypothesis, species richness, Time Hypothesis

INTRODUCTION

Many factors are responsible for the current distribution of biodiversity on Earth, including evolutionary history, geography, organismal biology and function, the physical environment, and the ecological environment (e.g. interactions among species). Although it is possible to point to specific cases that illustrate the importance of each factor, their relative contributions are still not understood in a comprehensive way. The most widely studied pattern of biodiversity distribution has been the latitudinal diversity gradient (LDG), which is the increase in species richness from the poles to the tropics seen in a diversity of groups (Currie, 1991; Hillebrand, 2004). Many studies have focused on this simple pattern to better understand mechanisms that explain variation in species richness on earth (reviewed in Mittelbach *et al.*, 2007). The two leading hypotheses to explain the pattern involve *rate* versus *time*. In other words,

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either a higher diversification rate or a greater age of lineages in the tropics is responsible for the higher number of species observed there compared to the temperate zone (Stevens, 2011; Jansson *et al.*, 2013).

The Rate Hypothesis proposes that various biological and ecological factors, such as mutation rate, generation time, ambient temperature, physiology and energy, are responsible for patterns of species richness and the LDG (Rohde, 1992; Allen *et al.*, 2006). For all of these factors, the mechanism is thought to involve differential diversification rate (the balance between speciation and extinction rate) and therefore all are variants of the Rate Hypothesis (Rohde, 1992). In contrast, the Time Hypothesis suggests that time and history are responsible for the high tropical species richness because many groups originated in that region and therefore had more time to diversify (e.g. Axelrod, 1952; Cronquist, 1968; Willis, 1922; Jablonski *et al.*, 2006).

These two hypotheses have been debated, and recent studies using the largest (global) data sets have supported the Rate Hypothesis (Davies *et al.*, 2004; Cardillo *et al.*, 2005; Pyron & Wiens, 2013; Rolland *et al.*, 2014) instead of the Time Hypothesis (Jablonski *et al.*, 2006; Soria-Carrasco & Castresana, 2012). Although there has been substantial effort in testing one or the other hypotheses, a study testing both hypotheses simultaneously across a wide taxonomic and geographical scale has been lacking.

The impetus for this study was the recent discovery that most groups of organisms are undergoing a constant rate of diversification and are not saturated (Hedges *et al.*, 2015). In general, this could support the Time Hypothesis if there were no significant or biased spatial variation in rate. Therefore, we revisited the LDG using newly-developed methods and the largest and most comprehensive global data sets for amphibians, birds and mammals, which all exhibit a strong LDG (Fig. 1). For our primary analyses, we examined the individual and combined influence of time and rate on species richness within biogeographical regions (Holt *et al.*, 2013) to take into account history and geography. We also compared evolutionary rates (net diversification, extinction and speciation) in temperate versus tropical areas, controlling for time. In a second approach, we used different methodology, employing phylometric proxies for time and rate, to analyse spatial patterns in the light of known biogeographical events.

MATERIALS AND METHODS

The R language was used for the analyses (2.11.1; http://www.r-project.org), along with the following packages; APE (Paradis *et al.*, 2004), CAPER (Orme, 2013), DIVERSITREE (FitzJohn, 2012), MAPS (Becker & Wilks, 2014), MAPTOOLS (Bivand & Lewin-Koh, 2014), RASTER (Hijmans & van Etten, 2014), RGDAL (Bivand *et al.*, 2013), RGEOS (Bivand & Rundel, 2014), SP (Pebesma *et al.*, 2014), SPDEP (Bivand *et al.*, 2015) and TREESIM (Stadler, 2013). The statistical analyses were conducted at a 5% alpha risk.

Evolutionary rate estimation

To estimate evolutionary rates we used the BAMMTOOLS package (Rabosky *et al.*, 2014) on smoothed trees of amphibians, birds and mammals (Hedges *et al.*, 2015) because the program requires fully resolved timetrees with non-zero branch lengths. The rates estimated were speciation (λ), extinction (μ) and net diversification ($r_D = \lambda - \mu$). Those trees were extracted from a global timetree of life (Hedges *et al.*, 2015), obtained by averaging mean divergence times from 2274 studies. The aim of the program Bayesian analysis of macroevolutionary mixtures (BAMM) is to model speciation and extinction dynamics over time and between lineages using reversible jump Markov chain Monte Carlo.

The function 'setBAMMpriors' was used to generate a prior block that matched the 'scale' (e.g., depth of the tree) of our data. Both λ and μ were allowed to vary through time and across lineages, and 50,000,000 generations of MCMC simulation were performed. A global sampling fraction was specified by setting the 'globalSamplingFraction' parameter for each timetree (0.99, 0.99, and 0.97 for amphibians, birds and mammals respectively). A burnin of 0.5 was applied and the convergence was checked by calculating the effective sample size of the log-likelihood and of the number of shifts events present in each sample that should be over 200.

Comparisons within biogeographical regions

All clades occurring entirely within each of the 19 biogeographical regions (Holt *et al.*, 2013) were determined based on species distributional areas (all of the species belonging to the selected clades occurred in the area of interest). Crown age (the divergence time of the most recent common ancestor of all species in a clade) and evolutionary rate (r_D, λ and μ) obtained with BAMM (see above) for each clade were compared with species richness, within regions using the Bayesian information criterion (BIC). We also tested the combined effect of clade age and r_D in explaining the variation of species richness and compared the nested models by ANOVA and BIC scores. When the model with two explaining variables (clade age and r_D) had a significantly better fit to the data than the model with one explaining variable, we used multiple linear regressions with beta (or standardized) coefficients to evaluate the relative importance of each variable.

Comparisons between temperate and tropical areas

All exclusively tropical (between -23.5 and 23.5 degrees of latitude) and temperate (below -23.5 and above 23.5 degrees of latitude) clades were selected. All the species belonging to the selected clades occurred in the area of interest; species occurring in both areas were excluded. Clade evolutionary rates (obtained with BAMM) were compared within small time windows, from 0 to 30 Ma every 5 Ma.

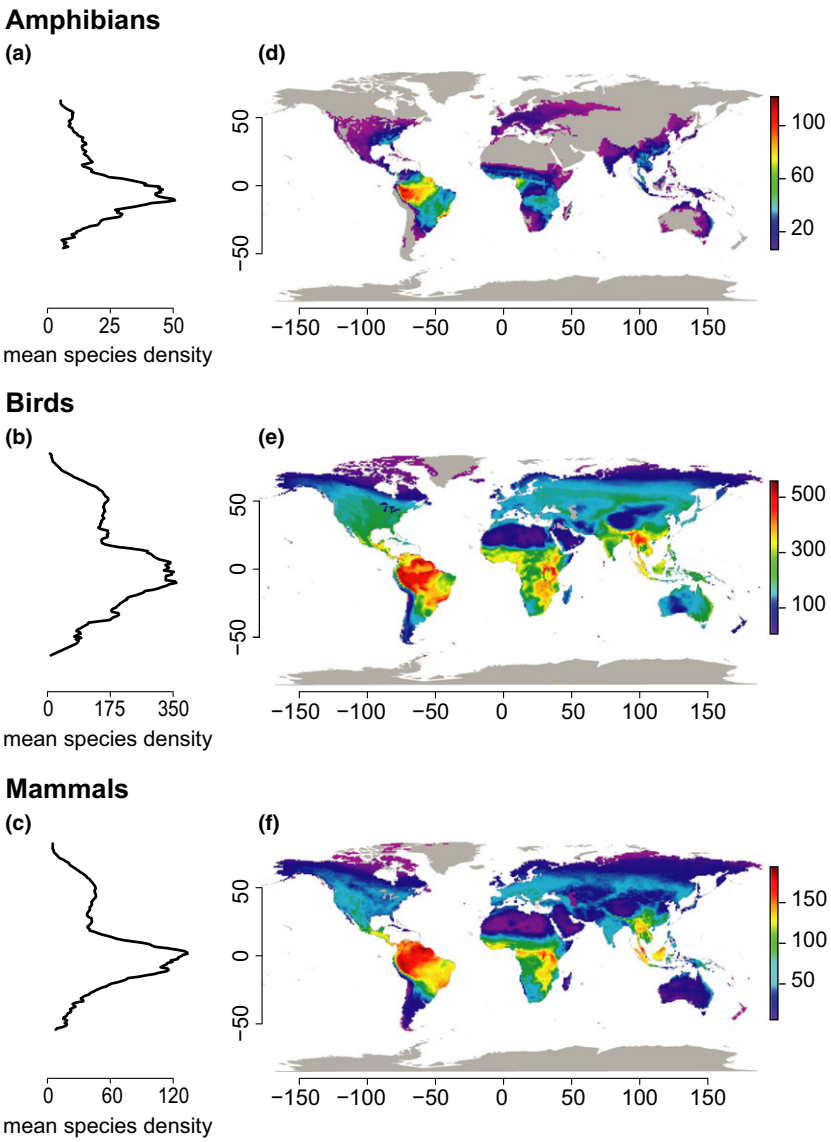

Figure 1 Mean species richness against latitude and species richness maps of amphibians (a,d), birds (b,e) and mammals (c,f) within 100 km × 100 km grid cells.

We also compared the mean branch lengths [= stem age (the next earlier split before crown age) minus crown age] of tropical versus temperate clades with un-smoothed and smoothed trees in order to evaluate un-smoothed trees and to provide an alternative method to BAMM. We used branch length as a proxy of r_D, because a higher r_D will lead to shorter branches. We checked the validity of this method using simulations: 5000 trees were generated ($t = 400$, $n = 100$), under a pure birth model with a varying λ, to obtain a range of r_D. We obtained a significant negative relationship between r_D and the mean branch length calculated for each tree (P-value $< 2.2 \times 10^{-16}$; $r = -0.77$). This method was then applied to our data set and the branch length proportions (temperate versus tropical) were tested with a t-test or a Welch t-test within small time windows, from 0 to 30 Ma every 5 Ma. In three cases, the time windows had to be enlarged to obtain sufficient sample size, resulting in an interval between 20 and 30 Ma for mammals (smoothed tree) and amphibians (un-smoothed tree) and between 10 and 30 Ma for birds (un-smoothed tree).

Phylogenetic simulations

In order to visualize the spatial variation between realms (biogeographical regions are nested within realms; Holt *et al.* (2013)) of clade ages and r_D we investigated the usefulness of two phylometrics, the evolutionary distinctiveness metric (Redding & Mooers, 2006; Isaac *et al.*, 2007; ED) as a proxy of clade age, and the diversification rate metric (Jetz *et al.*, 2012; DR) as a proxy of r_D. The latter is different from r_D that can be estimated by programs such as BAMM (Rabosky *et al.*, 2014). The evolutionary distinctiveness metric measures the 'uniqueness' of a species (a tip) within a tree and is applied as a metric to a single species or (if averaged) to a region. Each branch length is divided by the number of species subtending the branch, those numbers are then added

up from the root to each tip to obtain the ED score of a species. We checked via simulation that ED, which is based on branch lengths, was related to clade age. The phylometric DR corresponds to 1/ED, and has been used as a measure of r_D (Jetz *et al.*, 2012). Those phylometrics were applied to the three tetrapod groups (amphibians, birds and mammals) for each 1° × 1° grid cell. To describe the relationship of those phylometrics to phylogenetic tree topology, we created simulations to investigate the influence of clade age and diversification rates on ED and ER.

We used the method of Davies & Buckley (2012) for the first two simulations. First, we focused on tree crown age (t) and generated 5000 trees of 100 tips (approximately the diversity of mammals within a moderately species-rich cell of size 1° × 1°) of various crown ages (between 50 and 1000) under a pure birth model. The speciation rate was estimated as $\lambda = \ln(n/2)/t$ with n the number of extant species, r_D is then constrained. Next, we looked at r_D, and 5000 trees were generated (t = 400, n = 100), under a pure birth model with a varying λ (between 0.001 and 0.1). Finally, to evaluate the effect of species richness and the relative explanation of clade age and r_D by ED and DR we simulated 5000 timetrees with varying crown age (t between 10 and 500) and varying size (n between 6 and 600). The speciation rate of each tree was obtained as previously with $\lambda = \ln(n/2)/t$. We then sampled randomly 1–4 different trees and averaged their clade age and r_D. The randomization approach (described below) was applied to ED and DR respectively (obtaining EDr and DRr) to correct for species richness.

For the first two simulations, the relationship between each parameter (clade age and r_D) and the phylometrics (ED and DR) was evaluated by correlation analysis (Pearson coefficient). For the third simulation, the relationship between each parameter and the two phylometrics (EDr and DRr) was evaluated by a multiple linear regressions using beta (or standardized) coefficients. We confirmed that the residuals and the fitted values were not correlated.

Patterns in amphibians, birds and mammals

We used un-smoothed and smoothed trees with interpolated species (species without any genetic data) of mammals (5364 species) and birds (9879 species) (Hedges *et al.*, 2015). Interpolated species were added to the amphibian tree, which was afterwards smoothed, as described elsewhere (Hedges *et al.*, 2015). Those timetrees are part of the timetree of life (TTOL), a compilation of 2274 studies representing 50,632 species. We also checked the influence of interpolated species, species lacking molecular data that were added to their own generic clade, on ED and DR scores. The first two simulations (variation in clade age and in r_D) were performed again with 30.3% of the species removed randomly, corresponding to the percentage of interpolated species in the mammalian data set.

The distributional data were obtained from the IUCN Red list for amphibians and terrestrial mammals (IUCN 2013) and from BirdLife International for birds (BirdLife International & NatureServe 2013). Marine species were removed. The correspondence between the timetrees and the IUCN maps led to the use of a slightly lower number of mammals (5007 species), birds (9686 species), and amphibians (6044 species) (see Table S1 in Appendix S2 in Supporting Information). The appropriate spatial resolution depends on the quality of the data, and for well-known taxa like mammals the recommended resolution (cell size) is 1° × 1° (Hurlbert & Jetz, 2007). Because our final data sets (species with spatial data and present in the tree) included more than 84% of the described species (97% of the birds, 91% of the mammals, and 84% of the amphibians), all of the species were rasterized at 1° resolution, corresponding roughly to 100 km× 100 km cells. Cells with less than 5 species were removed from the analyses to avoid bias induced by outliers.

An ED score was assigned to each species (Redding & Mooers, 2006) and added up for each cell. To avoid bias induced by species richness and range size, we applied the randomization approach described in Safi *et al.* (2013). For all observed values of species richness (i in 1 to n) we sampled 1000 times i species, with replacement, from the global pool of species, using a weighted sampling scheme with the probability for each species being selected proportional to the size of its geographical range. From these 1000 samples for each grid cell we derived an empirical distributional function to investigate the dispersion of the realized ED scores (EDr). A DR score was obtained from the ED scores for each species (ER = 1/ED). We applied the same randomization procedure to correct for species richness and range size (DRr). The difference in EDr and DRr between biogeographical realms (Holt *et al.*, 2013) was established by ANOVA followed by a pairwise t-test (pairwise comparisons between group means with corrections for multiple testing.

RESULTS

Comparisons within biogeographical regions

Because biogeographical regions have both historical and geographical components, we used the group delineation of Holt *et al.* (2013) to explore relationship between species richness and time or rate within each of the 20 defined areas. Almost half (45.4%) of the species were captured by our approach (50.8%, 43.2% and 47.2% of amphibians, birds and mammals respectively). The remaining species were retrieved because they did not branch directly with another species occurring in the same biogeographical region. Over 19 biogeographical regions and 18 for amphibians (no clades were retrieved in the Polynesian group for the three tetrapod clades and in the Arctico-Siberian group for amphibians), 12, 17, and 15 showed a significant relationship between age and species richness for amphibians, birds and mammals respectively (Table 1). The relationship between r_D (estimated with BAMM) and species richness was significant in two biogeographical regions for amphibians and mammals,

Table 1 Summary table of the analyses within biogeographical regions. Clades within each biogeographical region were selected and their crown age and net diversification rate [estimated with Bayesian analysis of macroevolutionary mixtures (BAMM) (Rabosky *et al.*, 2014)] were compared to species number by correlation analyses (Pearson coefficient). The total number (no.) of species in each biogeographical region was recorded as well as the number of clades and species captured in clades. Significant values (P-value < 0.05) are in bold.

Biogeographical region	No of clades	No of species captured in clades	Total no of species	Age versus species richness		Net diversification rate versus species richness	
				P-value	r	P-value	r
Amphibians							
African	80	270	499	**2.97×10^{-4}**	0.394	**0.041**	0.229
Amazonian	259	887	1484	**4.44×10^{-16}**	0.475	0.815	−0.015
Arctico Siberian	–	–	28	–	–	–	–
Australian	27	129	182	**1.44×10^{-5}**	0.732	0.086	−0.336
Chinese	23	58	148	**0.032**	0.449	0.64	−0.103
Eurasian	26	63	136	0.601	0.107	0.674	−0.086
Guineo Congolian	75	225	431	**0.028**	0.254	0.285	0.125
Indo Malayan	56	155	358	0.208	0.171	0.35	0.127
Japanese	5	15	43	0.105	0.799	0.365	−0.523
Madagascan	37	115	199	**3.04×10^{-4}**	0.561	**0.031**	0.356
Mexican	21	51	144	0.232	0.272	0.42	−0.186
North American	47	177	252	**1.99×10^{-4}**	0.517	0.93	0.013
Novozelandic	17	47	101	0.544	0.158	0.878	0.04
Oriental	88	261	550	**0.003**	0.311	0.835	0.022
Panamanian	116	337	796	**4.69×10^{-4}**	0.32	0.384	0.081
Papua Melanesian	46	139	292	**1.57×10^{-4}**	0.529	0.89	0.021
Saharo Arabian	4	10	77	0.644	0.356	0.443	−0.557
South American	131	394	800	**3.64×10^{-7}**	0.427	0.668	0.038
Tibetan	26	79	195	**0.01**	0.494	0.619	−0.102
Birds							
African	321	1109	1835	**1.543×10^{-13}**	0.397	0.982	0.001
Amazonian	474	1626	2597	**$< 2.2 \times 10^{-16}$**	0.4	0.64	0.021
Arctico Siberian	83	220	693	**1.597×10^{-5}**	0.454	0.463	−0.082
Australian	82	271	673	**8.42×10^{-4}**	0.362	0.593	−0.06
Chinese	95	219	898	**0.039**	0.212	0.37	0.093
Eurasian	141	395	993	**0.001**	0.268	0.564	0.049
Guineo Congolian	217	630	1356	**5.51×10^{-8}**	0.359	0.855	0.012
Indo Malayan	249	677	1600	**1.89×10^{-12}**	0.427	0.211	0.08
Japanese	26	56	356	0.167	0.279	0.964	−0.009
Madagascan	37	100	485	**0.003**	0.478	0.429	0.134
Mexican	89	228	768	0.098	0.176	0.833	0.023
North American	91	233	702	**0.022**	0.239	0.665	0.046
Novozelandic	66	170	607	**0.001**	0.381	0.697	0.049
Oriental	257	704	1563	**3.67×10^{-6}**	0.284	0.659	0.028
Panamanian	338	942	2112	**1.54×10^{-9}**	0.321	0.142	0.08
Papua Melanesian	152	399	1023	**4.16×10^{-6}**	0.363	0.154	−0.116
Saharo Arabian	141	343	1157	**0.016**	0.203	0.8	0.021
South American	353	1055	2128	**7.95×10^{-10}**	0.32	0.344	−0.05
Tibetan	163	431	1176	**1.51×10^{-6}**	0.366	0.598	0.041
Mammals							
African	161	516	870	**2.37×10^{-11}**	0.495	0.323	0.078
Amazonian	136	481	763	**0.003**	0.255	0.135	0.127
Arctico Siberian	27	68	253	0.267	0.221	0.135	0.243
Australian	36	140	245	0.145	0.248	0.143	0.249
Chinese	32	68	301	0.083	0.311	0.307	0.186
Eurasian	89	281	561	**8.46×10^{-4}**	0.347	0.855	0.02
Guineo Congolian	96	286	595	**1.83×10^{-7}**	0.502	0.895	−0.014
Indo Malayan	113	303	612	**3.33×10^{-5}**	0.38	0.619	−0.047
Japanese	11	26	113	**0.017**	0.695	0.954	−0.02
Madagascan	31	103	212	**6.48×10^{-6}**	0.714	0.47	−0.135
Mexican	53	145	360	**3.54×10^{-4}**	0.472	0.778	−0.04

Table 1 Continued

Biogeographical region	No of clades	No of species captured in clades	Total no of species	Age versus species richness		Net diversification rate versus species richness	
				P-value	*r*	*P*-value	*r*
North American	63	204	364	**1.66×10^{-4}**	0.457	0.159	−0.18
Novozelandic	11	37	143	0.121	0.496	0.136	0.479
Oriental	105	273	604	**2.96×10^{-4}**	0.346	**0.015**	0.236
Panamanian	101	255	564	**1.3×10^{-4}**	0.372	0.776	0.029
Papua Melanesian	38	119	311	**0.012**	0.401	0.478	0.118
Saharo Arabian	48	118	431	**0.047**	0.288	0.948	0.01
South American	128	452	724	**0.006**	0.239	**0.021**	0.203
Tibetan	56	131	457	**0.037**	0.28	0.803	0.034

and no significant relationship was found for birds (Table 1). Similar results were obtained when comparing λ and μ with species richness (see Table S2 in Appendix S2). The model with crown age instead of r_D to explain species richness rate was preferred (BIC scores) in 17, 19 and 17 biogeographical regions for amphibians, birds and mammals respectively (see Table S3 in Appendix S2).

A model with two explaining variables (crown age and r_D) had a better fit to the data than the simplest model in two, one, and five (ANOVA) or three, one, and seven (BIC scores) biogeographical regions for amphibians, birds and mammals respectively. When a model with two explaining variables was chosen, crown age always had a higher importance in explaining species richness variation than r_D (see Table S3 in Appendix S2) with the exception of the Australian region for mammals. However, no significant relationship was retrieved between clade age or r_D with species richness in that region for mammals. Smoothed trees (no zero branch length) are required to use the program BAMM. One might assume that smoothing the trees can modify the diversification rates, however, we found comparable results when using smoothed or non-smoothed trees in the comparison between tropical and temperate areas (see below).

Comparisons between temperate and tropical areas

To evaluate the diversification rates in tropical and temperate areas, we selected 200 temperate (1275 species) and 577 tropical (3245 species) clades of mammals, 216 temperate (1469 species) and 1077 tropical (5714 species) clades of birds and 172 temperate (1051 species) and 815 tropical (4686 species) clades of amphibians. Using BAMM, no significant difference was found for mammals for either r_D, λ or μ (see Table S4 in Appendix S2). For birds and amphibians, over the 36 possible comparisons, 15 showed a significant difference. However, five of these differences were not highly significant (*P*-value > 0.01).

We also evaluated the difference between relative branch lengths (i.e. r_D) of tropical and temperate clades of amphibians, birds and mammals. For the majority of the time windows (14 out of the 17 possible comparisons) we did not find differences between tropical and temperate clades for smoothed trees (*P*-value > 0.05) (see Table S5 in Appendix S2). Also, the three significant differences were not highly significant. Very similar results were retrieved with non-smoothed trees: 11 out of the 13 possible comparisons were not significant and none of the two others was highly significant (see Table S5 in Appendix S2). Because branch length-by-time windows are related to r_D, we can conclude that amphibians, birds and mammals present an equivalent r_D in tropical and temperate assemblages.

Our results on diversification rates within small time windows globally showed a similar r_D between tropical and temperate areas. We found a few dissimilarities between the two approaches that might be due to the estimation method of the diversification rates. While BAMM evolutionary rates are estimated in the global context of the whole phylogeny, adjacent and ascendant branches of a clade influence the estimated evolutionary rate of the clade, whereas the 'branch length' method estimates r_D only from the branches present in the studied clade.

Phylogenetic simulations

Tree crown age was positively correlated with summed ED ($r = 0.95$; *P*-value $< 2.2 \times 10^{-16}$) and negatively with summed DR ($r = -0.70$; *P*-value $< 2.2 \times 10^{-16}$). The diversification rate was negatively correlated with summed ED ($r = -0.90$; *P*-value $< 2.2 \times 10^{-16}$) and positively with summed DR ($r = 0.93$; *P*-value $< 2.2 \times 10^{-16}$). In order to evaluate the influence of interpolated species we removed, randomly, 30.3% (same percentage as the interpolated species of mammals). Similar relationships were retrieved between summed ED or ED and clade age ($r = 0.95$; *P*-value $< 2.2 \times 10^{-16}$ and $r = -0.70$; *P*-value $< 2.2 \times 10^{-16}$ respectively), whereas a weak or no correlation was detected between summed ED or DR and diversification rate ($r = -0.03$; *P*-value = 0.03 and $r = 0.02$; *P*-value = 0.07), indicating the necessity of adding interpolated species in this type of study to estimate the diversification rates.

In order to disentangle the relative ability of ED and DR to explain crown age and r_D, we simulated different assemblages of clades of different sizes and corrected for species

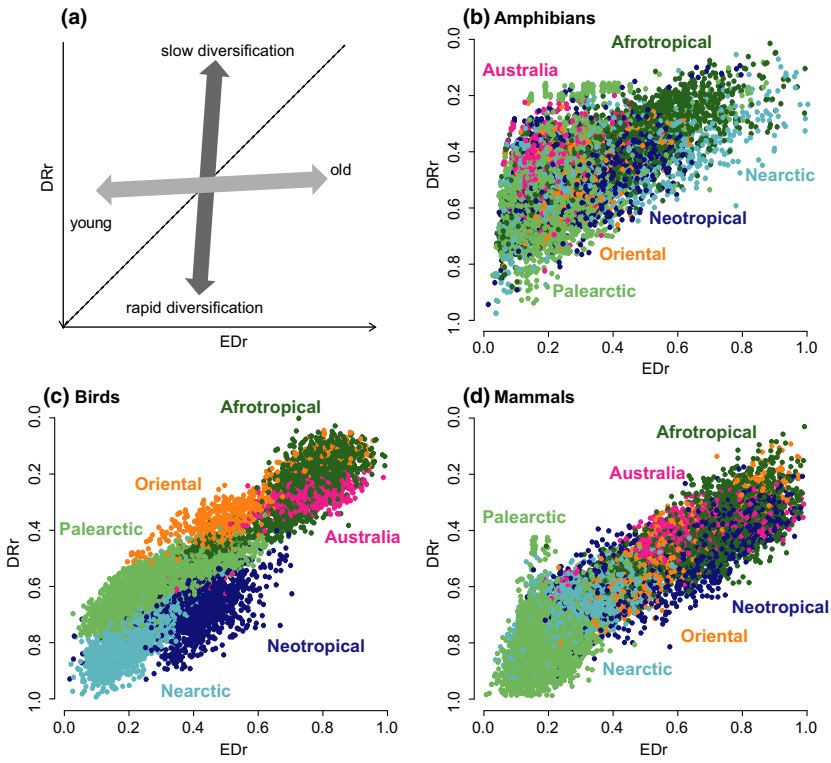

Figure 2 Dispersion of diversification rate metric (DRr) versus dispersion of evolutionary distinctiveness metric (EDr): patterns of simulated (a) and empirical data (b,c,d). (a) Summary of the relationship between diversification rate (slow to rapid) and clade age (young to old) with DRr and EDr obtained via simulations (a). The slopes of the arrows are proportional to their respective correlation coefficient *r* shown in Table 2. Patterns of DRr (proxy of diversification rate) versus EDr (proxy of clade age) in amphibians (b), birds (c) and mammals (d). They are colour coded by realm (Holt *et al.*, 2013) and only the major realms (Afrotropical, Australian, Nearctic, Neotropical, Oriental and Palearctic) are represented here.

Table 2 Results of the multiple linear regressions between the tree parameters and the phylometrics. The relative importance of the EDr (dispersion of evolutionary distinctiveness metric) and DRr (dispersion of diversification rate metric) in explaining the variation of clade age and diversification rate was assessed by multiple linear regressions, with *r* the correlation coefficient. The slopes were obtained by multiplying 90° by the proportion explained by each predictor (the estimate over the sum of the two estimates in absolute values).

Response	Predictor	*P*-value	*r*	Estimate	*t*-value	*P*-value	Slope(°)
Clade age	EDr	$< 2.2 \times 10^{-16}$	0.77	7.56×10^{-1}	56.25	$< 2.2 \times 10^{-16}$	86.83
	DRr			-2.76×10^{-2}	−2.05	0.04	3.17
Diversification rate	EDr	$< 2.2 \times 10^{-16}$	0.88	-3.39×10^{-2}	−3.32	9×10^{-4}	3.43
	DRr			8.56×10^{-1}	83.79	$< 2.2 \times 10^{-16}$	86.57

richness, obtaining EDr (dispersion of evolutionary distinctiveness metric) and DRr (dispersion of diversification rate metric). Multiple linear regressions with standardized coefficients were employed to assess the relative importance of EDr and DRr (negatively correlated but this is not a one-to-one correlation; Appendix S1) in explaining the variation of clade age (between 10 and 500 Ma) and r_D (between 0.002 and 0.95) (Fig. 2a and Table 2). All correlations tested were significant (*P*-values < 0.05). DRr was a better explanation of r_D (estimate $\beta = 8.56 \times 10^{-1}$) than EDr (estimate $\beta = -3.39 \times 10^{-2}$), whereas EDr was a better explanation of clade age (estimate $\beta = 7.56 \times 10^{-1}$) than DRr (estimate $\beta = -2.76 \times 10^{-2}$). To reflect the ages of clades present in a cell, EDr was preferred over the raw age of clades (crown age of each monophyletic group of a cell) because of the difficulty to retrieve complete (or almost complete) clades in cells. Indeed when we selected all clades in each cell for mammals (complete at least at 75%) we recovered only 11% on average of the total number of species present in each cell (results not shown), which is why EDr was used as a proxy of clade age.

Patterns of amphibians, birds and mammals

We used the realm delineation of Holt *et al.* (2013) to explore the historical biogeography of these groups with the relationship between the two phylometrics. As biogeographical regions, realms have both historical and geographical components, but represent larger areas (regions are nested within realms) and are therefore more suitable to visualize in a figure (Fig. 2). The patterns obtained differed among the three groups of tetrapods, but the difference was the most striking between the amphibians and the two other groups, birds and mammals.

For mammals (Fig. 2d), Australian, Afrotropical and Neotropical assemblages are the oldest, with the first two realms having a relatively slower r_D that the others. Temperate

patterns are different, with Nearctic and Palearctic zones characterized by younger and faster-diversifying clades.

The pattern in birds was similar to that in mammals, with some differences (Fig. 2c). The Australian and Afrotropical realms had older communities with a relatively slower r_D. On the other hand, the temperate zones (Palearctic and Nearctic realms) and the Neotropical realm, had younger communities with faster rates.

The amphibian pattern differed from that of birds and mammals (Fig. 2b) and the realm boundaries did not correspond to distinct EDr and DRr patterns compared to those other groups. The oldest assemblages of amphibians are found in the Nearctic and Afrotropical zones, whereas Neotropical, Palearctic and Australian faunas are younger.

The ANOVA analyses confirmed the presence of distinct EDr and DRr patterns (P-values $< 2 \times 10^{-16}$ for amphibians, birds and mammals). The difference in EDr and DRr between realms was further assessed by a pairwise t-test (see Tables S6 and S7 in Appendix S2) revealing very distinct patterns for birds and mammals (4 out of 180 comparisons were not significantly different for both EDr and DRr). Amphibian patterns were more similar between them (24 out of 90), with, for example, similar DRr scores between Panamanian and Sino-Japanese realms (P-value = 0.25) or between Neotropical and Palearctic realms (P-value = 0.11).

DISCUSSION

Species richness patterns of tetrapods are well documented (Jenkins *et al.*, 2013), and high species richness is typical of tropical areas, which is the basis of the LDG (Hillebrand, 2004). Throughout our analyses, we detected (broadly) a significant relationship between species richness and clade age (Time Hypothesis) but very few or no significant relationships between species richness and evolutionary rate (Rate Hypothesis). Separately, by using narrow time windows and hence controlling for age, we were able to compare diversification rates and branch lengths and therefore test the Rate Hypothesis. We found that the same average diversification rate occurred in temperate and tropical areas. All of these analyses led to the same conclusion that the persistence time of species and lineages (Time Hypothesis), and not diversification rate, best explains the LDG. Using the phylometrics EDr and DRr as proxies for clade age and diversification rate, we also detected a strong influence of history in the mammalian, avian, and amphibian faunas with distinguishable DRr versus EDr patterns among realms, consistent with previous results obtained for mammals and birds (Hawkins *et al.*, 2012). Moreover, as we found a positive and significant relationship between clade age and clade size within most of the biogeographical regions, our results are in favour of an expanding diversity and not a saturated diversity, and thus in agreement with our previous study that used different methods to reach that conclusion (Hedges *et al.*, 2015).

Historical biogeography has only modified, not obscured, the overall contribution of time on patterns of species richness. For example, the composition of the living South-American mammal fauna has been influenced most strongly by transatlantic dispersal (from Africa) and the formation of the Isthmus of Panama only 10–3 Mya (Cox, 2000; Webb, 2006). This latter connection led to uneven patterns of dispersal between continents, some rapid radiations, and extinction of old lineages, especially in South America (Webb, 2006). These historical events are consistent with our results for mammals and those obtained with other phylometrics (Davies & Buckley, 2012). The high EDr of African and South American mammals characterize the presence of old clades (on average) and the lower DRr of South American (but not African) communities reflects recent speciation in South America (Fig. 2d). Temperate clades of mammals have been subject to glacial cycles which are claimed to have been responsible for large-scale extinction events (Dynesius & Jansson, 2000) and potentially faster speciation (Weir & Schluter, 2007). High levels of extinction coupled with fast speciation should lead to young clades characterized by high diversification rate (high DRr and low EDr), which is true for Palearctic and Nearctic realms.

Following the break-up of Gondwana, diverse groups of birds were isolated in Australia before spreading around the world (Cracraft, 2001; Hedges & Kumar, 2009). These patterns are reflected in our analyses that showed old clades in Australia (Fig. 2c) and relatively faster-diversifying clades in temperate zones (Nearctic and Palearctic realms) with intermediate values for the Oriental realm (South-East Asia and Indonesia). A major part of the Amazonian bird diversity arose in the Quaternary, probably driven by sea-level rises and vegetation changes (Nores, 1999), explaining our results of substantial recent speciation in the Neotropics (Fig. 2c).

Among amphibians, the oldest clades are found in Laurasia (Feller & Hedges, 1998; Bossuyt & Roelants, 2009). For example, early-branching families of salamanders occur in Spain and south-eastern North America, leading to old communities (EDr) in those regions (Fig. 2b). The diversification of the major frog group in South America (Nobleobatrachia) appears to have occurred after the asteroid impact at the end-Cretaceous (66 Ma) (Bossuyt & Roelants, 2009), reflected by young and diversifying clades in the Neotropical realm. The higher species richness of tropical amphibians has been previously explained by higher diversification rates in the tropics and higher extinction rates in temperate regions (Pyron & Wiens, 2013). Although we acknowledge that higher diversification rates in South America (r_D estimated with BAMM: 0.074 and 0.062 in the Amazonian and in the Guineo-Congolian regions respectively) promoted a higher species richness, we nonetheless found diversification rates to be similar between tropical and temperate areas in general.

Although we found that the LDG is best explained by time within biogeographical regions (areas sharing the same history), there is nonetheless some variation in diversification rate between regions (Fig. 2) that can be likely attributed to historical biogeography and Earth history, such as the effects of asteroid impacts, continental fissions and fusions, sea-level

changes, and vegetation changes. Because we did not find any difference between tropical and temperate rates, rate variation between realms is explained best by historical events and not by temperature. Despite the influence of historical events, highlighting the role played by differential extinction and speciation processes, species have since diversified nearly constantly, as shown by the positive relationship between species richness and time. By restricting analyses to within biogeographical regions we were able to reduce these historical effects and determine that time is the best explanation for global richness patterns.

In this study, we evaluated the relative importance of time and diversification rate in explaining the species richness patterns and found time to be the best explanation: temperate assemblages of species are younger than tropical assemblages. This agrees with biogeographical evidence from selected groups of organisms that supports a tropical origin for temperate groups (Jansson, 2003; Jablonski *et al.*, 2006). In turn, this predicts a decrease in endemism with latitude (Jablonski *et al.*, 2006), which was observed for amphibians, birds and mammals among other groups (Jansson, 2003). However, the 'out of the tropics' hypothesis (Jablonski *et al.*, 2006) also states that there is a higher λ and lower μ in the tropics (referred to as 'cradle' and 'museum' respectively), which our results reject. Instead, we suggest that the LDG has an even simpler explanation: a response to the latitudinal climatic gradient. The reason why a significantly higher extinction rate is not observed in higher latitude clades, where climate change is greater, is probably because they contract towards the equator and into refugia during times of harsh climate, instead of going extinct.

In conclusion, disentangling the underlying cause of the LDG has been a challenge for biodiversity researchers over the years. Here, we approach this problem differently by using nearly-complete, time-calibrated phylogenies of major vertebrate groups to study age and diversification rate of evolutionary clades within biogeographical regions. We find that time, not diversification rate, best describes the LDG in amphibians, birds and mammals: the tropics have older species assemblages. In turn, we suggest that the ultimate cause of the LDG is climatic stability (a 'climate effect'), with younger assemblages (hence, fewer species) occupying higher latitudes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Relationship between EDr and DRr.
Appendix S2 Tables S1 to S7.

BIOSKETCHES

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