Author for correspondence:
Julie Marin
e-mail: juliemarin46@gmail.com

THE ROYAL SOCIETY
PUBLISHING

Evolutionary time drives global tetrapod diversity

Julie Marin[1,2], Giovanni Rapacciuolo[3,4], Gabriel C. Costa[5],
Catherine H. Graham[6], Thomas M. Brooks[7,8,9], Bruce E. Young[4],
Volker C. Radeloff[10], Jocelyn E. Behm[1,11], Matthew R. Helmus[1]
and S. Blair Hedges[1]

[1]Center for Biodiversity, Temple University, 502 SERC Building, 1925 N. 12th Street, Philadelphia, PA 19122, USA
[2]Institut de Systématique, Evolution, Biodiversité UMR 7205, Département Systématique et Evolution,
Muséum national d'Histoire naturelle, Sorbonne-Universités, 75231 Paris Cedex 05, France
[3]Life and Environmental Sciences, University of California Merced, 5200 N Lake Road, Merced, CA 95340, USA
[4]NatureServe, 4600 N. Fairfax Drive, 7th Floor, Arlington, VA 22203, USA
[5]Department of Biology, Auburn University at Montgomery, Montgomery, AL 36124, USA
[6]Swiss Federal Institute for Forest Snow and Landscape, Birmensdorf, Switzerland
[7]International Union for Conservation of Nature, Gland, Switzerland
[8]World Agroforestry Center (ICRAF), University of the Philippines Los Baños, Laguna 4031, Philippines
[9]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia
[10]SILVIS Lab, Department of Forestry and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA
[11]Department of Animal Ecology, VU University Amsterdam, 1081 HV Amsterdam, The Netherlands

JM, 0000-0002-7160-9302; GR, 0000-0003-1494-9017; TMB, 0000-0001-8159-3116

Global variation in species richness is widely recognized, but the explanation for what drives it continues to be debated. Previous efforts have focused on a subset of potential drivers, including evolutionary rate, evolutionary time (maximum clade age of species restricted to a region), dispersal (migration from one region to another), ecological factors and climatic stability. However, no study has evaluated these competing hypotheses simultaneously at a broad spatial scale. Here, we examine their relative contribution in determining the richness of the most comprehensive dataset of tetrapods to our knowledge (84% of the described species), distinguishing between the direct influences of evolutionary rate, evolutionary time and dispersal, and the indirect influences of ecological factors and climatic stability through their effect on direct factors. We found that evolutionary time exerted a primary influence on species richness, with evolutionary rate being of secondary importance. By contrast, dispersal did not significantly affect richness patterns. Ecological and climatic stability factors influenced species richness indirectly by modifying evolutionary time (i.e. persistence time) and rate. Overall, our findings suggest that global heterogeneity in tetrapod richness is explained primarily by the length of time species have had to diversify.

1. Introduction

Species diversity is distributed unevenly across the planet. The clearest manifestation of this variation is an increase in the number of species towards the tropics—a pattern known as the latitudinal diversity gradient. With a few exceptions (e.g. mosses [1]), this pattern has been observed for diverse taxonomic groups (e.g. terrestrial vertebrates, fishes, insects and plants) on continents as well as in the ocean [2]. It has been recognized for more than 150 years [3], and can be said to have stimulated the development of community ecology [2]. However, the underlying cause for the latitudinal biodiversity gradient remains the subject of much debate. Accordingly, many hypotheses focusing on evolutionary, ecological and climatic factors have been proposed to explain it [4,5]. The hypothesized processes are not independent but organized hierarchically, and act concomitantly to shape biodiversity patterns. For example, evolutionary factors, which include evolutionary time, evolutionary rates (speciation, extinction and
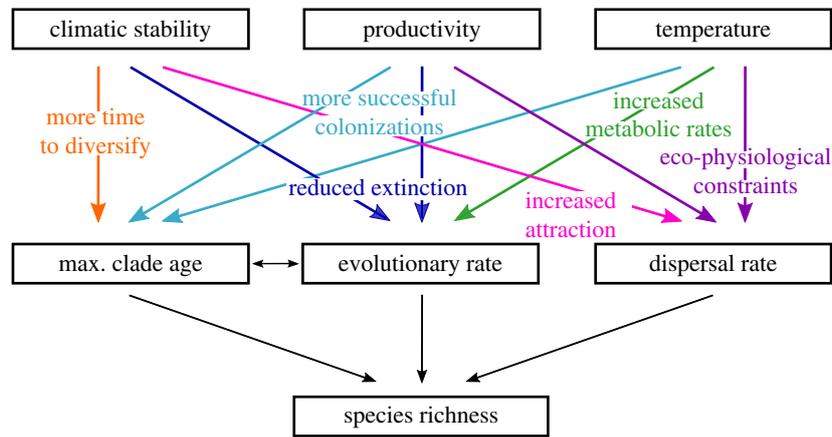
Figure 1. Theoretical framework depicting the relationships, and the underlying hypotheses, between evolutionary, ecological, climatic stability and richness variables. max., maximum.

hence diversification rates) and dispersal, drive species richness patterns directly, whereas ecological and stability factors influence species richness indirectly through their effect on evolutionary factors (figure 1). However, the vast majority of studies to date have focused on either evolutionary, ecological or climatic stability hypotheses separately, or have not acknowledged the hierarchical structure of these effects on species richness [6–13]. For example, in two recent papers, the 'rate hypothesis' was evaluated through ecological variables and climatic stability [14,15], but the influence of clade age [13] was not tested. Here, we use structural equation models to evaluate the influence of direct (evolutionary time, rate and dispersal) and indirect (productivity, temperature and climatic stability) factors in shaping global tetrapod species richness patterns.

Direct factors are hypothesized to drive higher diversity in the tropics [16,17] via either a higher diversification rate (speciation minus extinction), a higher migration towards tropical areas (i.e. colonization from higher latitudes) or a longer evolutionary time (i.e. greater age of lineages). The 'rate hypothesis' suggests that evolutionary rates (speciation, extinction and hence diversification rates) are affected by various biological and ecological factors such as geographic area, mutation rate, generation time, ambient temperature, physiology and energy [5,18,19]. The 'time hypothesis' proposes that species richness is linked to the ages of clades. After a lineage or a species first colonizes an area, species accumulate at a nearly constant rate (constant diversification rate), producing a positive relationship between time and species richness [20]. Because many groups originated in the tropics, this hypothesis has been used to explain why tropical regions have higher species richness (e.g. [9,21,22]). In addition to 'rate' and 'time', species richness patterns can be directly influenced by dispersal [23], through range expansion, contraction and dispersal constraints [19,24–26]. The latitudinal diversity gradient could be either reinforced by the limited dispersal of tropical species into temperate regions because of dispersal constraints (i.e. niche conservatism) [24] or be mitigated by range expansion [26].

The main ecological hypothesis to explain global species richness is the 'energy richness hypothesis', which states that lower extinction rates occur in areas of higher productivity because these areas can support a higher number of individuals, and thus a higher number of species [27–29]. The effect of productivity on species richness is therefore indirect, through its effect on evolutionary rate (figure 1). This hypothesis is

appealing because net primary productivity, which is largely dependent on solar radiation and water availability, increases markedly from the poles to the tropics [30]. Alternatively, species diversity may be indirectly influenced by temperature, with higher temperatures hypothesized to increase metabolic rates and, thus evolutionary rates [31] (figure 1). Moreover, temperature and productivity could also modulate species distributions through eco-physiological constraints on dispersal by limiting or promoting dispersal depending on the tolerance range of species [14,32,33] (figure 1). We can also assume older lineages to be predominant in more productive and warmer areas because, according to the energy richness hypothesis, areas of higher productivity are less prone to extinction [27–29].

Climate stability has also been hypothesized to drive biodiversity patterns through its effect on either or both evolutionary rate and evolutionary time (figure 1). Under the 'climatic stability hypothesis', species persist longer and/or diversify more in regions that are climatically stable over geological time [9]. The constancy in resources resulting from climatic stability may enable finer specialization and adaptation possibilities (i.e. smaller niches) [34]. As a consequence, climatic stability could affect species richness via its effect on evolutionary rates if species in the more climatically stable tropics are able to persist when rare, while rare species in more climatically unstable temperate areas are driven to extinction (rate hypothesis). Alternatively, climatic stability could affect species richness via its effect on evolutionary time by providing lineages more time to diversify (time hypothesis) within a stable environment [9] (figure 1).

In this study, we examine all primary hypothesized drivers of global species richness simultaneously, using the most complete dataset of tetrapod vertebrates to date (approx. 27 000 species). Specifically, we tested for the direct influence of evolutionary factors (rate, time and dispersal) and the indirect influence of ecological (productivity and temperature) and climatic stability factors, on tetrapod species richness (figure 1 and table 1; see also electronic supplementary material, figure S2). Furthermore, we evaluate the relative importance of direct evolutionary effects in explaining tetrapod richness patterns. We provide a comprehensive picture of the main direct and indirect drivers of tetrapod species richness, and find conclusive evidence for the overarching importance of evolutionary time.

Table 1. Recapitulation table of the variables used in these study to test the direct and indirect species richness predictors.

species richness predictors	variables used in the analyses and description
direct factors	
dispersal	*dispersal rate*: dispersal rate from any bioregion to the focal bioregion
evolutionary rate	*speciation* (or *diversification*) *rate*: average rate of the clades[a] of the focal bioregion
evolutionary time	*maximum clade age*: age of the oldest clade[a] of the focal bioregion
indirect factors	
climatic stability	*area through time*: integration of the focal bioregion area over the past 55 Myr
productivity	*productivity*: total productivity of the focal bioregion
temperature	*temperature*: mean temperature of the focal bioregion

[a]We only considered the clades in which all component species are found in the focal bioregion. See also the electronic supplementary material, figure S2.

2. Material and methods

We conducted global-scale analyses among 32 bioregion units, defined as the biomes nested within the world's main biogeographic realms, distributed as described by Olson *et al*. [35] (electronic supplementary material, figure S1). Species distribution data were used to obtain species lists for each of these bioregions (see the electronic supplementary material, methods for details). We performed structural equation modelling and variance partitioning analyses using richness, phylogenetic (*dispersal rate*, *maximum clade age* and *speciation rate*), ecological (*productivity* and *temperature*) and palaeoclimatic (*area through time*) data to evaluate evolutionary, ecological and climatic stability hypotheses for tetrapods overall, and individually for each of the four major groups of tetrapods (amphibians, birds, mammals and squamate reptiles) (table 1; electronic supplementary material, figure S2). For any given bioregion, the variable *dispersal rate* was the dispersal rate from any bioregion to the focal bioregion (calculated with the program GeoSSE [36]); *maximum clade age* was the age of the oldest clade in the focal bioregion (with all component species found in the focal bioregion), and represented the time during which species have successfully evolved and diversified; *speciation rate* was the average speciation rate of the clades belonging to the focal bioregion (calculated with the program BAMM [37]); *productivity* was the total productivity of the focal bioregion; *temperature* was the mean temperature of the focal bioregion; and *area through time* was the integration of the focal bioregion area over the past 55 Myr (see the electronic supplementary methods for details).

(a) Analyses

We evaluated the relationship between species richness and direct (*maximum clade age*, *speciation rate* and *dispersal rate*) and indirect (*productivity, temperature* and *area through time*) predictors for all tetrapods combined and for amphibians, birds, mammals and squamate reptiles. We did not use spatial models for bioregion analyses because of the strong independence of sampling in terms of response (low species overlap, 5, 12, 7 and 4% on average for amphibians, birds, mammals and squamates, respectively) and

predictor variables (each bioregion is distinct) [15]. We first checked whether any variables were collinear by calculating variance inflation factors (VIFs) [38]. We found a low collinearity between our variables, with VIF scores between 1.56 and 3.34, and did not discard any variable. We also evaluated the relationship between each pair of variables by correlation analyses (Pearson coefficient) (electronic supplementary material, table S1).

(b) Structural equation modelling

We modelled the direct effects of evolutionary predictors (*dispersal rate*, *maximum clade age* and *speciation rate*) and the indirect effects of ecological (*productivity* and *temperature*) and climatic stability (*area through time*) predictors, through evolutionary predictors, on *species richness* using structural equation modelling with the package 'lavaan' [39] and 10 000 bootstrap iterations. Structural equations characterize the relationship between a set of variables through ordered networks of statistical dependence. The degree of relationship (i.e. the numerical effect of one variable upon another) is estimated by regression methods.

Because *dispersal rate* was not available for all bioregions, we evaluated two models, the full model (model 1) with all variables and model 2 without the variable *dispersal rate*. For model 1, we conducted the analysis among 25, 22, 28, 27 and 30 bioregions for amphibians, birds, mammals, squamates and tetrapods, respectively. For model 2, we conducted the analysis among 29, 32, 32, 29 and 32 bioregions for amphibians, birds, mammals, squamates and tetrapods, respectively. To test the effect of different combinations of variables, we used a model selection approach. We evaluated the four models and compared their AIC scores. The full model (model 1) and three alternative models, with all of the indirect but only two of the direct variables, were used to test if one variable could hide the influence of others on *richness*: *maximum clade age* and *speciation rate* (model 1a), *maximum clade age* and *dispersal rate* (model 1b), and *speciation rate* and *dispersal rate* (model 1c).

(c) Variance partitioning

To further evaluate the relative contribution to species richness of the two main direct hypotheses (age and rate), we used variance partitioning based on redundancy analysis ordination [40] as implemented in the R package 'vegan' [41]. The third direct variable, *dispersal rate*, was never associated with richness for any group, and removing this variable allowed us to increase the number of bioregions considered. We estimated the independent contribution to species richness variation for each predictor (individual fraction) as well as the shared contribution of each combination of covariate sets (shared fraction) using r^2 values adjusted for sample size, given the different number of predictors in each set. The sum of the individual and the shared fraction of each predictor set represented the predictor fraction. The total fraction was the variation explained by the complete model. Negative values can be generated in variance partitioning analyses; these should be interpreted as zeros as they correspond to cases where the explanatory variable explained less variation than would random variables [42].

The significance (i.e. whether the fraction explained a significant part of the variation) of each model and of the individual partitions was assessed by permutation (1000 permutations) [43]. For each of the predictors, we randomized the richness across regions and obtained the individual fractions (variance partitioning analysis) 1000 times to build a null distribution. We compared the observed individual fractions to the corresponding null distribution (one-tailed test, $\alpha = 0.05$).

The individual fractions were compared by bootstrapping (1000 replications) [43]. We compared the evolutionary and ecological sets, the variables *maximum clade age* and *speciation rate*, and the variables *productivity* and *temperature*. The variables
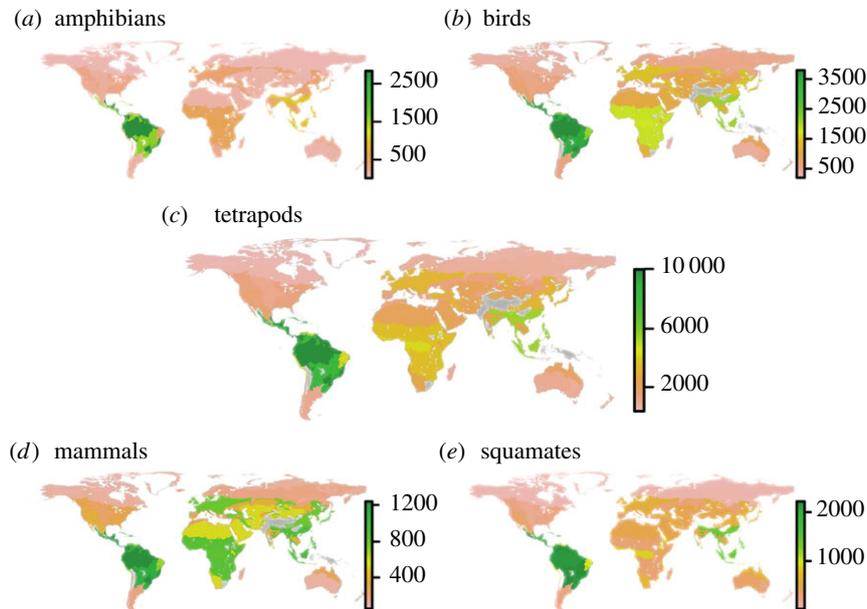
Figure 2. Global species richness maps. Species richness was computed by bioregion for (*a*) amphibians, (*b*) birds, (*c*) tetrapods, (*d*) mammals and (*e*) squamate reptiles.

(response variable and the corresponding values of the explicative variables) were sampled with replacement to obtain a sample of the same size as the observed data and we calculated the individual fractions (variance partitioning analysis) 1000 times. We compared the distributions of each pair of individual fractions (one-tailed test, $\alpha = 0.05$).

3. Results

Newly available distributional data for reptiles along with existing amphibian, mammal and bird data highlight the uneven distribution of tetrapod species richness across the globe (figure 2). The different tetrapod groups all show a broad latitudinal gradient but different spatial patterns of species richness.

We used structural equation models to examine the direct effects of evolutionary factors (*dispersal rate*, *maximum clade age* and *speciation rate*) and indirect effects of ecological factors (*productivity* and *temperature*) and climatic stability (*area through time*) on species richness for tetrapods combined and for each of the four major tetrapod clades: amphibians, birds, mammals and squamates. We quantified the relationships between variables using standardized regression coefficients (β), which enable assessing the relative contribution of each effect. When considering the full model including all above effects (model 1; electronic supplementary material, figure S3), tetrapod species richness displayed a strong and significant association with *maximum clade age* ($\beta = 0.55$) and a non-significant association with *speciation rate* (electronic supplementary material, figure S3). *Temperature* had a significant indirect effect on species richness through both *maximum clade age* ($\beta = 0.37$) and *speciation rate* ($\beta = -0.54$), though the direction of these indirect effects was opposite. Tetrapod species richness was also indirectly influenced by *area through time*, our measure of climatic stability, through its effects on *maximum clade age* ($\beta = 0.48$). Among the subgroups of tetrapods, birds and squamates showed slightly different direct effects compared with tetrapods as a whole, with *maximum clade age* ($\beta = 0.48$ and 0.46, respectively) and *speciation rate*

($\beta = 0.37$ and $\beta = 0.62$, respectively) both significantly positively associated with species richness. However, only the variable *temperature* was significantly associated with *speciation rate* and *dispersal rate* for birds ($\beta = -0.41$ and $\beta = -0.39$ respectively) and with *maximum clade age* for squamates ($\beta = 0.47$). *Maximum clade age* was the only direct variable significantly associated with mammal richness ($\beta = 0.88$). *Productivity* was associated with *maximum clade age* ($\beta = 0.35$) and *temperature* was associated with *maximum clade age* ($\beta = 0.50$) and *speciation rate* ($\beta = -0.51$). No variable was significantly associated with amphibian richness, even after the removal of Alytidae, a small outlier clade of 12 species. We identified outlier clades for amphibians, birds, mammals and squamate reptiles by comparing the mean and the maximum clade age for each bioregion. We found the largest difference (119 million years, Myr) in the Eurasian Mediterranean bioregion for amphibians (95 species), driven by that small clade of tree frogs (Alytidae). Smaller differences were found for birds (49 Myr), mammals (48 Myr) and squamate reptiles (78 Myr). *Dispersal rate* was never associated with richness for any group tested and removing this variable allowed us to include more bioregions; moreover, the model without *dispersal rate* had the lowest AIC (model 1a; electronic supplementary material, table S2). Therefore, we considered a model without *dispersal rate* and with more bioregions as an alternative model of richness (model 2).

After removing *dispersal rate*, *maximum clade age* had the strongest direct effect on species richness in all subgroups of tetrapods except squamates (figure 3). In squamates, *maximum clade age* and *speciation rate* were both strongly associated with richness ($\beta = 0.56$ and $\beta = 0.57$, respectively). When considering indirect effects, the significant associations were similar to model 1 except for *area through time*, which was significantly associated with *maximum clade age* in amphibians ($\beta = 0.43$; 0.64 after the removal of the small outlier clade) and *temperature*, which was significantly associated with *maximum clade age* in birds ($\beta = 0.48$).

In order to further discriminate the relative importance of the two evolutionary variables in explaining species richness
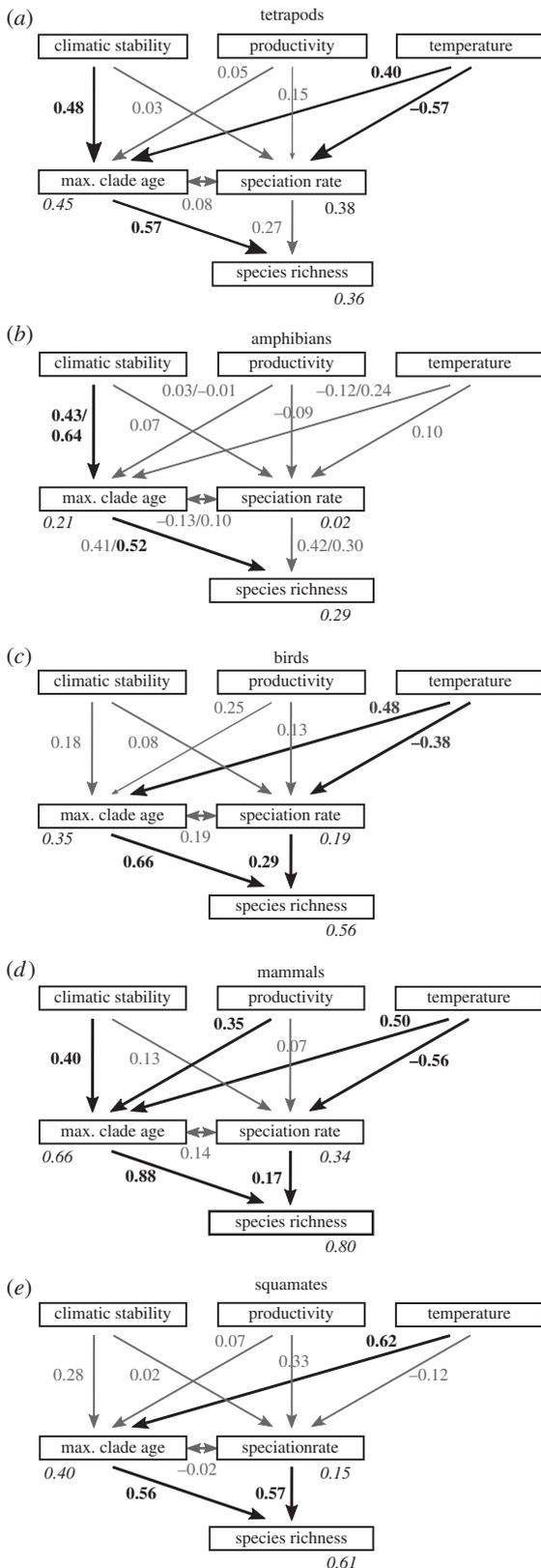
Figure 3. Structural equation models depicting the associations of direct and indirect variables with species richness (without *dispersal rate*, model 2). *Maximum clade age* and *speciation rate* are the direct variables and *area through time*, *productivity* and *temperature* the indirect variables, for (*a*) tetrapods, (*b*) amphibians, (*c*) birds, (*d*) mammals and (*e*) squamates. Bold path arrows represent significant (at $p < 0.05$) associations. Numbers adjacent to arrows represent β-standardized regression coefficients. r^2-values associated with each exogenous variable are in italics. For amphibians, we also indicated β-standardized regression coefficients and r^2-values after the removal of the outlier clade of Mediterranean Alytidae (12 species) if the result changed (value in second position). max., maximum.

Table 2. Results from partitioning the variance of maximum clade age and speciation rate variables in explaining patterns of species richness (model 3). The reported values are adjusted r^2 statistics representing the total (complete model without residuals), individual and shared (explained by both factors) proportion of richness variation explained by maximum clade age and speciation rate. In bold are the fractions explaining a significant portion of the richness variation ($\alpha < 0.05$; electronic supplementary material, table S6). Negative values can be generated in variance partitioning analyses; these should be interpreted as zeros as they correspond to cases where the explanatory variable explained less variation than would random variables [42]. max., maximum.

	total fraction	max. clade age	speciation rate	shared fraction
tetrapods	**0.606**	**0.595**	**0.113**	−0.101
amphibians	**0.231**	**0.131**	**0.142**	−0.042
amphibians[a]	**0.334**	**0.234**	0.063	0.038
birds	**0.533**	**0.438**	0.074	0.021
mammals	**0.787**	**0.784**	0.024	−0.022
squamates	**0.399**	**0.152**	0.083	0.164

[a]Amphibians without an outlier clade of Mediterranean Alytidae (12 species).

Table 3. Bootstrapped *p*-values for comparisons of maximum clade age and speciation rate variables in explaining global tetrapod species richness. The significant results are in bold ($\alpha < 0.05$). max., maximum; spe., speciation.

	max. clade age > spe. rate	spe. rate > max. clade age
tetrapods	**0.003**	0.998
amphibians	0.280	0.721
amphibians[a]	**0.027**	0.974
birds	**0.007**	0.994
mammals	**9.99×10^{-4}**	1
squamates	0.453	0.547

[a]Amphibians without an outlier clade of Mediterranean Alytidae (12 species).

patterns, we performed a variance partitioning analysis. This analysis revealed that maximum clade age explained a significant portion of the richness variation for all tetrapods combined and in the separate subgroups: amphibians (with or without the small outlier clade), birds, mammals and squamates (table 2). *Speciation rate* explained a significant portion of the richness at the tetrapod level and for amphibians, although not for the other groups or amphibians after the removal of the small outlier clade of Alytidae. Removing the outlier clades for the other groups (birds, mammals and squamate reptiles) did not change the results (electronic supplementary material, tables S3–S4). Maximum *clade age* explained a higher proportion of richness variation for tetrapods overall, and specifically for amphibians after the removal of the small outlier clade, birds and mammals specifically (table 3). *Speciation rate* never explained a higher proportion of the response variable than *maximum clade age*. In the case of squamate reptiles, the two factors explained an equal fraction of the richness (table 3), although only *maximum clade age* explained a significant fraction of the richness (table 2).

Our findings were robust to a series of sources of uncertainty. We obtained similar results by replacing *mean speciation rate* with *mean diversification rate*, *median speciation rate* or *median diversification rate* for structural equation modelling (electronic supplementary material, figures S4 and S5, and table S2) and with *diversification rate* for variance partitioning analyses (electronic supplementary material, table S5). In addition, we also performed these analyses on New World squamates only, because most of the Old World squamate richness data were based on older IUCN Red List assessments (see Material and methods). We found largely comparable results except for a significantly higher influence of *maximum clade age* ($\beta = 0.73$) over *speciation rate* ($\beta = 0.27$) on species richness. Finally, we also obtained similar results by substituting *maximum clade age* with lower and upper bounds of the 95% confidence interval (*age lower bound*, *age upper bound*, *random lower/upper age*), or *cumulative clade age* (models 3a, 3b, 3c and 3d; electronic supplementary material, table S2).

4. Discussion

Relationships between the potential drivers of species richness patterns are complex and difficult to disentangle. In addition, a focus on some but not all major hypotheses in past analyses has prevented the evaluation of the relative and the structured contributions of evolution, ecology and climatic stability to species richness patterns. For example, one of the most inclusive studies conducted on birds and mammals [14], sharing similar results with our study (see below), omitted time and dispersal as potential predictors. This study concluded that historical and evolutionary processes explain species richness in birds and mammals, but could not discriminate among age, dispersal or climatic stability. Here, with a nearly complete global tetrapod dataset, we evaluated these hypotheses simultaneously in a structured framework (figure 1), using variables capturing the main components of each hypothesis. Despite mass extinctions and range reductions induced by anthropogenic factors from the Pleistocene to the present [44], we found that clade age is the most important factor explaining the distribution of species richness in tetrapods. Evolutionary rate emerged as a secondary factor and dispersal did not significantly affect richness patterns. We also detected indirect effects of ecological and climatic stability variables on species richness through their influence on clade age and evolutionary rates.

(a) Direct effects

Based on structural equation models, our analyses showed that clade age is the major predictor of species richness patterns in tetrapods. Clade age was strongly associated with richness and explained a significant portion of its variation in each group tested individually (figure 3 and table 2). Moreover, clade age explained a significantly higher fraction of richness variation than diversification rate at the tetrapod level and for amphibians (after the removal of the small outlier clade), birds and mammals (table 2). For squamates, despite a comparable association strength between squamate richness and clade age or evolutionary rate (figure 3), only clade age explained a significant fraction of their richness variation (table 2). These results are in line with several previous studies indicating that time, and not rate of diversification, best describes species richness patterns [9,13,20,45], with the richest areas being strongly associated with older lineages. Therefore, our results also largely corroborate studies supporting an expanding diversity [46], stating that species richness is correlated to time and not density-dependent.

By contrast, the 'rate hypothesis', often invoked to explain species richness patterns [6,7,11,12,47,48], was only weakly supported by our results, as was also the case in a recent global analysis [14]. The discrepancy between our results and previous studies supporting the 'rate hypothesis' over the 'time hypothesis' might be explained by methodological differences. For example, Scholl & Wiens [48] used stem age instead of crown age, even though the former has been shown to add noise to the age–richness relationship because the stem branch is statistically unrelated to crown age [46]. Scholl & Wiens [48] also used the same sampling fraction correction across their tree, despite the fact that the tree contained clades with different levels of uncertainty around their estimated richness. We are unable to compare our results with other studies that did not consider clade age in their analyses [11,12,47]. However, due to the difficulty in estimating extinction, we acknowledge that even in the absence of a strong association between *diversification rate* and richness, lower maximum crown ages in less diverse regions might be explained by higher extinction [49].

Finally, we did not find evidence of a significant role of dispersal in shaping tetrapod species distribution. However, our findings do not rule out the role of dispersal in shaping richness locally, and finer scale analyses would be helpful to better understand its role. Our results rather suggest that dispersal has a limited importance at global scale. The highest association between dispersal and richness was detected in birds ($\beta = -0.24$; electronic supplementary material, figure S3). Even if not significant, this trend probably reflects their higher dispersal ability, relative to other tetrapod groups, with species migrating preferentially towards the less inhabited areas (negative association). This result corroborates previous studies, showing a mitigating effect of dispersal on the latitudinal richness gradient by homogenizing richness across latitude [26].

(b) Indirect effects

Productivity has been postulated to increase regional richness by allowing more niches or larger population sizes, and thus by reducing extinction rates [31,50,51]. Temperature has also been predicted to shape distributional patterns by increasing individual metabolic rates and, in turn, reducing extinction rate [31,52,53]. Our results did not corroborate these hypotheses, as we did not detect a significant relationship between speciation (or diversification) rate and productivity, and found a negative association between speciation (or diversification) rate and mean annual temperature in tetrapods overall, and separately in birds and mammals. Indeed, for birds and mammals, most of the bioregions characterized by low speciation (and diversification) rate are hot regions, including deserts and tropical dry forests. A negative association between temperature and diversification rate has also been reported recently in mammals (e.g. [54]). The addition of more variables would help to understand why some (but not all) hot regions are characterized by low evolutionary rates for birds and mammals. Our results also showed a positive association between temperature and clade age for each group except amphibians (figure 3). This pattern might reflect better conditions for successful dispersal to warmer areas for birds, mammals and squamates. The biogeographic history of these groups, already

invoked to explain time and rate patterns between biogeographic regions [13], could also explain this association, because most birds and mammals originated in Gondwana [55,56], whereas the oldest clades of amphibians are found in Laurasia, which was colder [57,58]. The origins of squamates and their major subclades are not yet established [59].

Given our finding that clade age largely predicts species richness patterns, a strong indirect association between species richness and climatic stability might be expected. This is because climatic stability reflects the amount of time a lineage could persist under unaltered climatic conditions. Our results corroborated this hypothesis for tetrapods, as well as for amphibians and mammals, as has previously been found [14]. Our finding that speciation or diversification rate is of lesser importance than clade age, and that climatic stability was never associated with evolutionary rates, suggests that climatic stability may be acting through exclusion, by altering species distributions, rather than causing species to go extinct. Under this model, lineages inhabiting unstable areas migrate towards more suitable areas or refuges when their climate becomes unsuitable, and later re-colonize the original area, when former climatic conditions are re-established. This process implies a re-set of clade age because some species (newly formed or older) might not return to the focal area, as a consequence, the clades for which all the species inhabit the area will be younger. However, conclusions based on this result are subject to uncertainty, as extinction rate estimates derived from phylogenies may not always be reliable [60,61].

New environments might also be colonized by already diversifying clades as long as the new conditions are suitable for them. This model is supported by our results for birds and squamates, with lineages (*maximum clade age*) being older than the occupied area. For example, tundra and boreal forests originated about 10 million years ago (Ma) and temperate grasslands 25 Ma [15], yet clades with ages of 20 and 40 Myr, respectively, inhabit these regions. This could explain why we did not detect an association between climatic stability and clade age in birds or squamates.

5. Conclusion

Our global analyses of more than 27 000 tetrapod species highlight the major importance of evolution in shaping geographic patterns of species richness. Of all potential drivers, clade age is of primary importance and is consistent with the notion of a speciation clock [46]. Nonetheless, temperature, productivity and climatic stability have also influenced tetrapod species richness indirectly via their influence on clade age and speciation rate.

References

1. Geffert JL, Frahm JP, Barthlott W, Mutke J. 2013 Global moss diversity: spatial and taxonomic patterns of species richness. *J. Bryol.* **35**, 1–11. (doi:10.1179/1743282012Y.0000000038)

2. Willig MR, Kaufman DM, Stevens RD. 2003 Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. System.* **34**, 273–309. (doi:10.1146/annurev. ecolsys.34.012103.144032)

3. Wallace AR. 1878 *Tropical nature and other essays*. London, UK: Macmillan and Company.

4. Pianka ER. 1966 Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* **100**, 33–46. (doi:10.1086/282398)

5. Rohde K. 1992 Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527. (doi:10.2307/3545569)

6. Davies TJ, Savolainen V, Chase MW, Moat J, Barraclough TG. 2004 Environmental energy and evolutionary rates in flowering plants. *Proc. R. Soc. Lond. B* **271**, 2195–2200. (doi:10.1098/rspb.2004.2849)

7. Cardillo M, Orme CDL, Owens IPF. 2005 Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* **86**, 2278–2287. (doi:10.1890/05-0112)

8. Graham CH, Moritz C, Williams SE. 2006 Habitat history improves prediction of biodiversity in rainforest fauna. *Proc. Natl Acad. Sci. USA* **103**, 632–636. (doi:10.1073/pnas.050 5754103)

9. Jablonski D, Roy K, Valentine JW. 2006 Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**, 102–106. (doi:10. 1126/science.1130880)

10. Werneck FP, Nogueira C, Colli GR, Sites JW, Costa GC. 2012 Climatic stability in the Brazilian Cerrado: implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *J. Biogeogr.* **39**, 1695–1706. (doi:10.1111/j.1365-2699.2012. 02715.x)

11. Pyron RA, Wiens JJ. 2013 Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proc. R. Soc. B* **280**, 20131622. (doi:10.1098/rspb.2013.1622)

12. Rolland J, Condamine FL, Jiguet F, Morlon H. 2014 Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.* **12**, e1001775. (doi:10. 1371/journal.pbio.1001775)

13. Marin J, Hedges SB. 2016 Time best explains global variation in species richness of amphibians, birds and mammals. *J. Biogeogr.* **43**, 1069–1079. (doi:10.1111/jbi.12709)

14. Belmaker J, Jetz W. 2015 Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecol. Lett.* **18**, 563–571. (doi:10.1111/ele.12438)

15. Jetz W, Fine PVA. 2012 Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biol.* **10**, e1001292. (doi:10. 1371/journal.pbio.1001292)

16. Stevens RD. 2011 Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proc. R. Soc. B* **278**, 2528–2536. (doi:10.1098/rspb. 2010.2341)

17. Jansson R, Rodríguez-Castañeda G, Harding LE. 2013 What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution* **67**, 1741–1755. (doi:10.1111/evo.12089)

18. Losos JB, Schluter D. 2000 Analysis of an evolutionary species–area relationship. *Nature* **408**, 847–850. (doi:10.1038/35048558)

19. Allen AP, Gillooly JF. 2006 Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.* **9**, 947–954. (doi:10.1111/j. 1461-0248.2006.00946.x)

20. McPeek MA, Brown JM. 2007 Clade age and not diversification rate explains species richness among animal taxa. *Am. Nat.* **169**, E97–E106. (doi:10.1086/512135)

21. Willis JC. 1922 *Age and area*. Cambridge, UK: Cambridge University Press.

22. Cronquist A. 1988 *The evolution and classification of flowering plants*. New York, NY: New York Botanical Garden.

23. Ricklefs RE. 2004 A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* **7**, 1–15. (doi:10.1046/j.1461-0248.2003.00554.x)

24. Svenning JC, Skov F. 2007 Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecol. Lett.* **10**, 453–460. (doi:10.1111/j.1461-0248.2007.01038.x)

25. Fløjgaard C, Normand S, Skov F, Svenning J-C. 2011 Deconstructing the mammal species richness pattern in Europe—towards an understanding of the relative importance of climate, biogeographic history, habitat heterogeneity and humans. *Glob. Ecol. Biogeogr.* **20**, 218–230. (doi:10.1111/j.1466-8238.2010.00604.x)

26. Baselga A, Lobo JM, Svenning JC, Aragón P, Araújo MB. 2012 Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Glob. Ecol. Biogeogr.* **21**, 1106–1113. (doi:10.1111/j.1466-8238.2011.00753.x)

27. Hutchinson GE. 1959 Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159. (doi:10.1086/282070)

28. Brown JH. 1981 Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Am. Zool.* **21**, 877–888. (doi:10.1093/icb/21.4.877)

29. Wright DH. 1983 Species–energy theory: an extension of species–area theory. *Oikos* **41**, 496–506. (doi:10.2307/3544109)

30. Brown JH. 2014 Why are there so many species in the tropics? *J. Biogeogr.* **41**, 8–22. (doi:10.1111/jbi.12228)

31. Allen AP, Gillooly JF, Brown JH. 2007 Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. In *Scaling biodiversity* (eds D Storch, PA Marquet, JH Brown), pp. 283–299. Cambridge, UK: Cambridge University Press.

32. Wiens JJ et al. 2010 Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)

33. Šímová I, Storch D, Keil P, Boyle B, Phillips OL, Enquist BJ. 2011 Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Glob. Ecol. Biogeogr.* **20**, 842–856. (doi:10.1111/j.1466-8238.2011.00650.x)

34. Klopfer PH. 1959 Environmental determinants of faunal diversity. *Am. Nat.* **93**, 337–342. (doi:10.1086/282092)

35. Olson DM et al. 2001 Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* **51**: 933–938. (doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)

36. Goldberg EE, Lancaster LT, Ree RH. 2011 Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* **60**, 451–465. (doi:10.1093/sysbio/syr046)

37. Rabosky DL, Grundler M, Anderson C, Shi JJ, Brown JW, Huang H, Larson JG. 2014 BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods Ecol. Evol.* **5**, 701–707. (doi:10.1111/2041-210X.12199)

38. Fox J. 2002 *An R and S-plus companion to applied regression*. Thousand Oaks, CA: Sage.

39. Rosseel Y. 2016 *Lavaan: latent variable analysis*. R package version 0.5-23. Vienna, Austria: Comprehensive R Archive Network.

40. Borcard D, Legendre P, Drapeau P. 1992 Partialling out the spatial component of ecological variation. *Ecology* **73**, 1045–1055. (doi:10.2307/1940179)

41. Oksanen J et al. 2013 *Vegan: community ecology package*. R package version 2.0-10. Vienna, Austria: Comprehensive R Archive Network.

42. Legendre P. 2008 Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.* **1**, 3–8. (doi:10.1093/jpe/rtm001)

43. Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006 Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* **87**, 2614–2625. (doi:10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2)

44. Faurby S, Svenning JC. 2015 Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Divers. Distrib.* **21**, 1155–1166. (doi:10.1111/ddi.12369)

45. Soria-Carrasco V, Castresana J. 2012 Diversification rates and the latitudinal gradient of diversity in mammals. *Proc. R. Soc. B* **279**, 4148–4155. (doi:10.1098/rspb.2012.1393)

46. Hedges SB, Marin J, Suleski M, Paymer M, Kumar S. 2015 Tree of life reveals clock-like speciation and diversification. *Mol. Biol. Evol.* **32**, 835–845. (doi:10.1093/molbev/msv037)

47. Pyron RA. 2014 Temperate extinction in squamate reptiles and the roots of latitudinal diversity gradients. *Glob. Ecol. Biogeogr.* **23**, 1126–1134. (doi:10.1111/geb.12196)

48. Scholl JP, Wiens JJ. 2016 Diversification rates and species richness across the Tree of Life. *Proc. R. Soc. B* **283**, 20161334. (doi:10.1098/rspb.2016.1334)

49. Schluter D, Pennell MW. 2017 Speciation gradients and the distribution of biodiversity. *Nature* **546**, 48–55. (doi:10.1038/nature22897)

50. Evans KL, Warren PH, Gaston KJ. 2005 Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* **80**, 1–25. (doi:10.1017/S1464793104006517)

51. Hurlbert AH, Jetz W. 2010 More than 'more individuals': the nonequivalence of area and energy in the scaling of species richness. *Am. Nat.* **176**, E50–E65. (doi:10.1086/650723)

52. Allen AP, Brown JH, Gillooly JF. 2002 Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**, 1545–1548. (doi:10.1126/science.1072380)

53. Currie DJ et al. 2004 Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.* **7**, 1121–1134. (doi:10.1111/j.1461-0248.2004.00671.x)

54. Oliveira BF, Machac A, Costa GC, Brooks TM, Davidson AD, Rondinini C, Graham CH. 2016 Species and functional diversity accumulate differently in mammals. *Glob. Ecol. Biogeogr.* **25**, 1119–1130. (doi:10.1111/geb.12471)

55. Cracraft J. 2001 Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event. *Proc. R. Soc. Lond. B* **268**, 459–469. (doi:10.1098/rspb.2000.1368)

56. Kemp TS. 2005 *The origin and evolution of mammals*. Oxford, UK: Oxford University Press on Demand.

57. Feller AE, Hedges SB. 1998 Molecular evidence for the early history of living amphibians. *Mol. Phylogenet. Evol.* **9**, 509–516. (doi:10.1006/mpev.1998.0500)

58. Bossuyt F, Roelants K. 2009 Frogs and toads (Anura). In *The timetree of life* (eds SB Hedges, S Kumar), pp. 357–364. New York, NY: Oxford University Press.

59. McDowell SB. 1987 Systematics. In *Snakes: ecology and evolutionary biology* (eds RA Siegel, JT Collins, SS Novak), pp. 3–50. New York, NY: Macmillan Publishing Company.

60. Rabosky DL. 2010 Extinction rates should not be estimated from molecular phylogenies. *Evolution* **64**, 1816–1824. (doi:10.1111/j.1558-5646.2009.00926.x)

61. Rabosky DL. 2016 Challenges in the estimation of extinction from molecular phylogenies: a response to Beaulieu and O'Meara. *Evolution* **70**, 218–228. (doi:10.1111/evo.12820)