

Ecological controls of mammalian diversification vary with phylogenetic scale

Antonin Machac^{1,2,3,4}  | Catherine H. Graham^{4,5}  | David Storch^{2,3} 

¹Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

²Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic

³Center for Theoretical Study, Charles University, Prague, Czech Republic

⁴Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York

⁵Swiss Federal Research Institute (WSL), Birmensdorf, Switzerland

Correspondence

Antonin Machac, Center for Theoretical Study, Jilská 1, 11000 Prague 1, Czech Republic.

Email: a.machac@email.cz

Funding information

National Grid Infrastructure MetaCentrum, Grant/Award Number: CESNET LM2015042; National Science Foundation, Grant/Award Number: DEB-1136586; the Czech Science Foundation, Grant/Award Number: 16-26369S; Danish National Research Foundation

Editor: Jonathan Davies

Abstract

Aim: Diversity dynamics remain controversial. Here, we examine these dynamics, together with the ecological factors governing them, across mammalian clades of different ages and sizes, representing different phylogenetic scales. Specifically, we investigate whether the dynamics are bounded or unbounded, biotically or abiotically regulated, stochastic or ecologically deterministic.

Location: Worldwide.

Time period: 150 Myr.

Major taxa studied: Mammals.

Methods: Integrating the newest phylogenetic and distributional data by means of several distinct methods, we study the ecology of mammalian diversification within a predictive framework, inspired by classic theory. Specifically, we evaluate the effects of several classes of factors, including climate, topography, geographical area, rates of climatic-niche evolution, and regional coexistence between related and unrelated species. Next, we determine whether the relative effects of these factors change systematically across clades representing different phylogenetic scales.

Results: We find that young clades diversify at approximately constant rates, medium-sized clades show diversification slowdowns, and large clades are mostly saturated, suggesting that diversification dynamics change as clades grow and accumulate species. We further find that diversification slowdowns intensify with the degree of regional coexistence between related species, presumably because increased competition for regional resources suppresses the diversification process. The richness at which clades eventually saturate depends on climate; clades residing in tropical climates saturate at low richness, implying that niches become progressively densely packed towards the tropics.

Main conclusions: The diversification process is influenced by a variety of ecological factors, whose relative effects change across phylogenetic scales, producing scale-dependent dynamics. Different segments of the same phylogeny might therefore support seemingly conflicting results (bounded or unbounded, biotically or abiotically regulated, stochastic or ecologically deterministic diversification), which might have contributed to several outstanding controversies in the field. These conflicts can be reconciled, however, when accounting for phylogenetic scale, which might, in turn, produce a more integrated understanding of global diversity dynamics.

KEYWORDS

biogeography, competition, macroevolution, niche, phylogeny

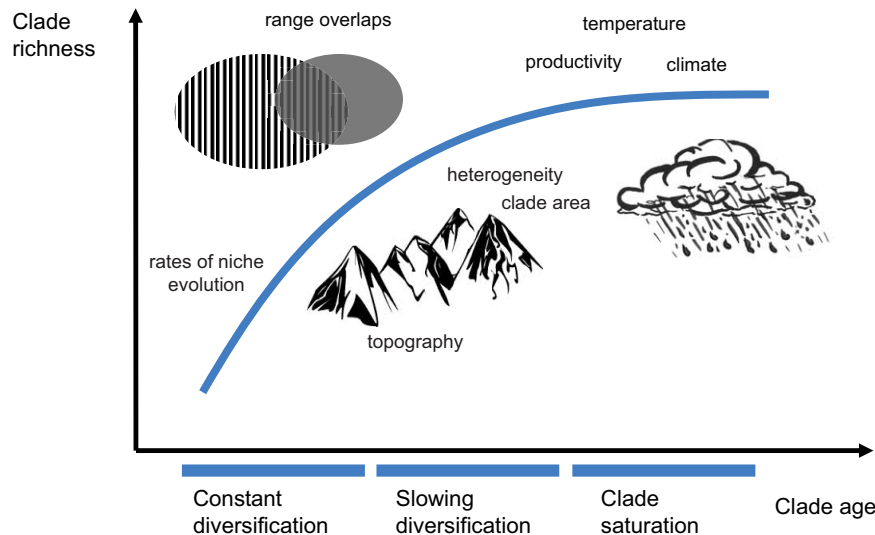


FIGURE 1 The predictive framework. We predict that clades expand at constant and slowing rates before they saturate. We further hypothesize that diversification rates are coupled with the rates of climatic-niche evolution during the initial expansion of a clade. But the following slowdowns presumably depend on environmental heterogeneity, topography and the degree of regional coexistence between mutually related species. Clade richness at saturation depends on environmental conditions, including temperature, precipitation and environmental productivity

1 | INTRODUCTION

The diversity of life was produced by the process of evolutionary diversification (Darwin, 1859; Gould, 2002; Schluter, 2000; Stanley, 1979). Yet, the dynamics and the ecological controls of this process remain controversial. Mutually conflicting sources of evidence suggest that diversification may be bounded or unbounded (Cornell, 2013; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015; Simpson, 1953; Stephens & Wiens, 2003; Van Valen, 1985), biotically or abiotically regulated (Benton, 2009; Pianka, 1966; Rabosky & Hurlbert, 2015; Van Valen, 1973, 1985), stochastic or ecologically deterministic (Benton & Emerson, 2007; Harmon & Harrison, 2015; Walker & Valentine, 1984). Here, we examine hundreds of mammalian clades of different ages and sizes to evaluate the possibility that diversification dynamics vary systematically across the phylogeny (Graham, Storch, & Machac, in press; Jablonski, 2000, 2007). We submit that much of the seemingly conflicting evidence may be reconciled when the diversification process is studied across phylogenetic scales.

Different diversification dynamics have indeed been reported for clades of different ages and sizes (Heard & Cox, 2015; Kozak & Wiens, 2012; McPeck & Brown, 2007; Morlon, Potts, & Plotkin, 2010; Purvis, Fritz, Rodríguez, Harvey, & Grenyer, 2011; Rabosky, Slater, & Alfaro, 2012; Stephens & Wiens, 2003). Young and small clades often diversify at constant rates and seemingly without bounds, especially within a newly colonized region (Kozak & Wiens, 2012; Smith, Nieto Montes de Oca, Reeder, & Wiens, 2007; Stephens & Wiens, 2003), whereas medium-sized phylogenies with hundreds of species show diversification slowdowns (McPeck, 2008; Morlon et al., 2010; Phillimore & Price, 2008), and higher taxa are often saturated in terms of their species richness (Rabosky, 2009b; Rabosky et al., 2012). Much literature has been dedicated to the question of how many clades expand at a

constant rate, at a slowing rate, and how many stay saturated (Cornell, 2013; Harmon & Harrison, 2015; McPeck, 2008; Morlon et al., 2010; Rabosky, 2009a,b). However, it seems likely that the three modes of diversification (constant, slowing and saturated) are not mutually exclusive and might represent different phases of the same diversification process. Surprisingly, this idea remains largely untested although it conforms to the well-established observation that island radiations tend to decelerate over time (Gavrillets & Losos, 2009; Glor, 2010; Rabosky & Glor, 2010) and that post-extinction rebounds of the fossil diversity tend towards a plateau over time (Alroy et al., 2008; Raup & Sepkoski, 1982; Sepkoski, 1998). Here, we test the hypothesis that old and large clades are mostly saturated because they have had sufficient opportunity to reach their equilibrium richness. Young and small clades, in contrast, should expand at constant or slowing rates (see Figure 1).

Ecological factors that govern the diversification process remain similarly elusive. Diversification might be ecologically deterministic, governed by several factors of large effect (Rabosky, 2013; Sepkoski, 1998; Simpson, 1953; Walker & Valentine, 1984). But it might also depend on countless factors whose complex interplay makes diversification dynamics effectively stochastic (Benton, 2009; Gould & Lewontin, 1979; Van Valen, 1973, 1985). Building on the classic model of ecospace filling (Simpson, 1953) and further relevant literature in the field (Hutchinson, 1959; Kozak & Wiens, 2010; Pianka, 1966; Qian & Ricklefs, 2000; Rabosky & Glor, 2010; Whittaker, 1972), we identify prominent ecological factors, widely believed to govern the diversification process, and study their relative effects (Figure 1).

Simpson's model (1953) postulates that different factors influence the diversification of a clade as the clade gradually fills its ecospace (Gavrillets & Vose, 2005; McPeck, 2008; Schluter, 2000; Van Valen, 1985; Walker & Valentine, 1984), which is defined as a multidimensional volume, whose axes represent various biotic and abiotic

conditions (Pianka, 1966; Simpson, 1953; Walker & Valentine, 1984). The model was supported by fossil and phylogenetic evidence (Gavrillets & Losos, 2009; Raup & Sepkoski, 1982) and provides the rationale to formulate testable hypotheses (Gavrillets & Losos, 2009; Rabosky, 2013; Simpson, 1953; Van Valen, 1985; Walker & Valentine, 1984); these hypotheses are admittedly not exhaustive, and we acknowledge that other models might produce further predictions (e.g., Harmon & Harrison, 2015; Price, 2007; Stephens & Wiens, 2003).

Based on the model proposed by Simpson (1953), we hypothesize that clades rapidly diversify and rapidly diverge ecologically during the initial phases of their diversification (Gavrillets & Vose, 2005; Kozak & Wiens, 2010; Rabosky, 2013; Simpson, 1953). We also hypothesize that diversification rates are increased in heterogeneous and montane regions, which provide ample opportunity for ecological divergence and speciation (Qian & Ricklefs, 2000; Schluter, 2000). Diversification should be further increased in wide-ranging clades whose extensive geographical distributions make these clades prone to speciation and resistant to extinction (Losos & Schluter, 2000; Figure 1).

Moreover, the model predicts that diversification slows down as clades gradually fill their ecospace (Simpson, 1953), and their constituent species begin to compete for regional resources (Gavrillets & Vose, 2005; Walker & Valentine, 1984), which suppresses further speciation and elevates their extinction (Gavrillets & Vose, 2005; Rabosky, 2013; Schluter, 2000; Walker & Valentine, 1984). Even though diversification slowdowns are common in molecular phylogenies (McPeck, 2008; Morlon et al., 2010; Pennell, Sarver, & Harmon, 2012; Phillimore & Price, 2008), they do not yield particularly compelling evidence for the hypothesized effects of competition. For example, the phylogenies often span geographically non-overlapping species that cannot possibly compete with each other (Harmon & Harrison, 2015; Moen & Morlon, 2014; Wiens, 2011), such that the observed slowdowns may have been produced by other factors (e.g., statistical artefacts; Pennell et al., 2012; Phillimore & Price, 2008). For more compelling evidence, phylogenies must be studied together with the geographical information on species coexistence (Harmon & Harrison, 2015; Machac et al., 2013; Wiens, 2011). Developing Simpson's (1953) rationale further, we hypothesize that slowdowns are weak in heterogeneous and montane regions, where species can readily diverge spatially and ecologically to evade competition.

Eventually, clades are expected to fill the ecospace completely (Simpson, 1953), such that their speciation and extinction equilibrate and their richness stays largely unchanged over time (Rabosky, 2013; Simpson, 1953; Van Valen, 1985; Walker & Valentine, 1984). We hypothesize that clade richness at this stage depends on environmental factors. Highly productive, warm and humid environments (especially in the tropics) presumably generate an extensive ecospace that can sustain more species than the temperate ecospace (MacArthur, 1964; Simpson, 1953; Van Valen, 1985).

Mammals afford an excellent opportunity to test our hypotheses and study the ecology of diversification, given the remarkable variety of their life histories, evolutionary trajectories and geographical distributions (e.g., echidna, aardvark, rodents, bats, large carnivores and herbivores; Buckley et al., 2010; Fortelius et al., 2014; Rolland,

Condamine, Jiguet, & Morlon, 2014; Soria-Carrasco & Castresana, 2012; Weir & Schluter, 2007). Using the newest phylogeny for mammals (Hedges, Marin, Suleski, Paymer, & Kumar, 2015), we test the prediction that diversification dynamics change over time, such that clades transition from an unbounded expansion to slowdowns and saturation. We further test the effects of relevant ecological factors (climate, geography, topography, niche evolution, regional coexistence, etc.; Figure 1; Hutchinson, 1959; Kozak & Wiens, 2010; MacArthur, 1964; Pianka, 1966; Qian & Ricklefs, 2000; Rabosky & Glor, 2010; Whittaker, 1972). We find that the effects of these factors vary systematically across phylogenetic scales and conclude that the concept of scale-dependent diversification may inform, and possibly resolve, some of the longstanding controversies in the field.

2 | MATERIALS AND METHODS

To test our hypotheses, we divided mammalian clades into three categories, depending on their mode of diversification (constant, slowing or saturated; Morlon et al., 2010) and used different diversification measures to characterize the clades within each category (Magallon & Sanderson, 2001; Pybus & Harvey, 2000; Rabosky, 2009a). Clades expanding at a constant rate were characterized by their diversification rate (Magallon & Sanderson, 2001; Raup, 1985), slowing clades by the gamma statistic (Pybus & Harvey, 2000), and saturated clades by their \log_e richness (Rabosky, 2009a). Each of these three diversification measures (diversification rate, gamma statistic and clade richness at saturation) was then regressed against a set of ecological predictors, including climate, topography and different measures of regional coexistence (based on the geographical overlaps between species distributions). The results identified the factors that influence diversification rates, diversification slowdowns and clade richness at saturation.

To avoid the problems notoriously associated with clade selection (Moen & Morlon, 2014; Pennell et al., 2012; Phillimore & Price, 2008), we used all clades of mammals for our analyses, estimating diversification modes and measures for every clade (= every node) of the phylogeny (Machac & Graham, 2017; Machac, Zrzavy, Smrckova, & Storch, 2012; Machac et al., 2013). To account for the resultant phylogenetic correlation and nestedness among our data points, we used standard phylogenetic corrections (Freckleton, Harvey, & Pagel, 2002) and repeated our analyses for exclusively non-nested clades (Machac & Graham, 2017; Machac et al., 2012, 2013). Even though non-nested analyses should generally be preferred, they often have their own pitfalls (Graham et al., in press; Machac & Graham, 2017; Machac et al., 2012, 2013). For example, the selection of non-nested clades is inherently non-random because each selection of a clade constrains the selection of subsequent clades (especially if the previously selected clades were large). For this reason, we used the two-level approach whereby nested analyses identified the most prevalent patterns in the data, which were further confirmed across non-nested analyses. The two-level approach consequently circumvented the pitfalls of either of the two separate approaches (nested and non-nested) and ensured that our results spanned a range of phylogenetic scales, that they were

comprehensive, inclusive, robust, independent of clade size, clade nestedness and clade selection (Graham et al., in press; Machac & Graham, 2017; Machac et al., 2012, 2013). We further confirmed our results using BMM (Bayesian Analysis of Macroevolutionary Mixtures) and MEDUSA (Modeling Evolutionary Diversification using Stepwise AIC) (Alfaro et al., 2009; Rabosky, 2014). Finally, we controlled for various sources of possible errors, including errors in the assignment of diversification modes and errors associated with the evaluation of small-sized clades (with < 10 and < 20 species). Further details are given below and in Supporting Methods, Results and Randomizations.

2.1 | Phylogeny and geographical distributions

We used the newest, nearly complete (4,990 species) and highly resolved (nodes-to-tips ratio: 75%) phylogeny of mammals (Hedges et al., 2015). The phylogeny updates previous mammalian trees (Bininda-Emonds et al., 2007; Meredith et al., 2011), taking advantage of both molecular and morphological data, using multiple fossil calibration points. Species without molecular sequences were grafted onto the tree, based on taxonomy, and statistically accounted for in further analyses (Hedges et al., 2015; Rabosky, 2015; see Supporting Methods). We recognize that the mammalian phylogeny might be further revised in the future as more sequences become available, new species become discovered, etc., but the present tree provides sufficient detail for the purpose of our large-scale analyses (see e.g., Hedges et al., 2015; Oliveira et al., 2016). Moreover, we repeated our analyses across mammals and their six core taxa (Carnivora, Artiodactyla, Chiroptera, Eulipotyphla, Primates and Rodentia). If similar results emerge across multiple well-resolved taxa (Carnivora, Artiodactyla and Primates), they are likely to warrant strong conclusions. If these conclusions are supported also across the less-resolved taxa (Rodentia and Chiroptera), they are likely robust, indicating that similar processes operate across mammals taxon-wide, despite their disparate life histories, evolutionary trajectories and geographical distributions. The geographical distributions of mammals were taken from the database of the International Union for Conservation of Nature (IUCN) (<http://www.iucn.org>) and converted into distributional grids with a $1^\circ \times 1^\circ$ resolution, in line with the common practice to limit false presences in the distributional data (Hurlbert & Jetz, 2007).

2.2 | Diversification modes

To identify the diversification mode for each clade (constant, slowing or saturated), we used the coalescent approach of Morlon et al. (2010). This approach uses likelihood optimization to fit nine diversification models to the phylogeny, including time-constant and time-varying rates of speciation and extinction, time-constant and time-varying diversity, and their various combinations (defined in Supporting Table S1). Following the procedure described by Morlon et al. (2010), we fitted all nine models for each mammalian clade, divided the models into three categories representing the three different modes (constant, slowing and saturated) and assessed the support for each mode using Akaike's weights (Morlon et al., 2010).

The coalescent results were further confirmed using BMM and MEDUSA (Alfaro et al., 2009; Rabosky, 2014). These methods are not suitable for some of our hypotheses (e.g., MEDUSA does not capture slowdowns, whereas BMM does not capture saturation; see also Moore, Höhna, May, Rannala, & Huelsenbeck, 2016), but they explicitly capture diversification heterogeneity across clades, within clades and over time and circumvent the issues of clade selection and nestedness (Alfaro et al., 2009; Rabosky, 2014), which makes them suitable to validate some of our key results, as detailed in the Supporting Methods.

We also controlled for the effects of other diversification modes. Clades with accelerating diversification were too rare to allow for meaningful statistical analysis and therefore removed from the dataset (Supporting Figure S5; Morlon et al., 2010). Declining clades, whose speciation rates exceed extinction rates, cannot be inferred within a likelihood framework (Morlon, Parsons, & Plotkin, 2011) compatible with the coalescent inference (Morlon et al., 2010, 2011) and therefore could not be included directly in our analyses (Morlon et al., 2010, 2011). Therefore, we identified the potentially declining clades (Supporting Figure S12), removed them from the dataset and confirmed that our conclusions remained practically unchanged (Supporting Figures S13 and S14), as detailed in the Supporting Methods and Results.

Finally, we controlled for possible errors in the assignment of diversification modes (constant, slowing or saturated) and for errors associated with the evaluation of small-sized clades (with < 10 and < 20 species; see Section 2.6 and the Supporting Methods); we also confirmed our results across clades whose diversification mode was supported with high confidence (Akaike's weight > 0.7). Together, these measures ensured that our results on the different modes of diversification (constant, slowing and saturated; Harmon & Harrison, 2015; McPeck, 2008; Morlon et al., 2010; Rabosky & Hurlbert, 2015) were robust and largely independent of the methodology used (large or small clades, clades with high or low support, BMM or MEDUSA).

2.3 | Diversification measures

Several measures have been designed to capture diversification (Magallon & Sanderson, 2001; Pybus & Harvey, 2000; Rabosky, 2009a; Raup, 1985), but each of them fits only the clades whose diversification conforms to the measure's specific assumptions. For example, diversification rates are estimated accurately only when a clade expands at a constant rate (Magallon & Sanderson, 2001; Raup, 1985), whereas diversification slowdowns and saturation are better captured by the gamma statistic (Pybus & Harvey, 2000) and the natural logarithm (\log_e) of clade richness, respectively (Rabosky, 2009a). Still, it is common practice to apply the same measure to all clades, regardless of their diversification mode, which may result in erroneous estimates (Magallon & Sanderson, 2001; Rabosky, 2009a). Here, we used the previously inferred diversification modes (constant, slowing and saturated) to identify the most suitable measure for each clade individually, thus increasing the accuracy of the estimate and the statistical strength of subsequent analyses (see Supporting Randomizations).

To characterize constant diversification, we used \log_e clade richness divided by clade age (Magallon & Sanderson, 2001; Raup, 1985).

Diversification slowdowns were captured by the gamma statistic (Pybus & Harvey, 2000), which reflects the distribution of branching times across the phylogeny and becomes increasingly negative under pronounced slowdowns (Pybus & Harvey, 2000). Saturated clades were characterized by the natural logarithm of their (equilibrium) richness (Rabosky, 2009a).

2.4 | Ecological predictors of diversification

After we characterized the diversification dynamics, we examined the ecological factors that potentially influence these dynamics: climate, environmental productivity, clade area, rates of climatic-niche evolution, topography, landscape heterogeneity and regional coexistence (captured by the geographical overlaps between species distributions). These variables are explained in the following paragraphs and over-viewed in Supporting Table S2.

Climatic data were taken from the WorldClim database of Hijmans, Cameron, Parra, Jones, and Jarvis (2005) and resampled to the resolution of our distributional maps ($1^\circ \times 1^\circ$), using bilinear interpolation. We selected mean annual temperature (BIO1) and annual precipitation (BIO12) for our analyses because they seem most relevant to mammalian macroecology and macroevolution (e.g., Buckley et al., 2010; Oliveira et al., 2016). In addition, we combined all climatic variables (BIO1–BIO19) into a single composite variable (PC1) using principal component analysis (PCA). PC1 captured the general climate, blending temperature, precipitation and seasonality, while explaining 52.7% of the variance in the climatic data (factor loadings: BIO1 = 0.929, BIO6 = 0.959 and BIO3 = 0.914). More detailed results, including all factor loadings and eigenvalues, are given in Supporting Table S4.

Environmental productivity was approximated by the actual evapotranspiration (AET) and net primary production (NPP). AET and NPP data were taken from the MODIS Global Evapotranspiration Project (MOD16; Mu, Zhao, & Running, 2011) and MODIS GPP/NPP Project (MOD17; Zhao, Heinsch, Nemani, & Running, 2005), respectively, and resampled to the $1^\circ \times 1^\circ$ resolution (Hurlbert & Jetz, 2007).

To calculate clade area, we overlaid the distributional maps of all species within each clade. As species-rich clades tend to be distributed over larger geographical areas than species-poor clades, the effects of clade area might be confounded by clade richness. To control for this issue, we regressed clade area against clade richness and used the residuals from this regression in our further analyses to examine whether clade area affected diversification independently of clade richness.

To infer the rates of climatic-niche evolution (Kozak & Wiens, 2010), we used the previously calculated climatic variables (BIO1, BIO12 and PC1) and fitted the Brownian motion model (BM) and the Ornstein–Uhlenbeck model (OU) to each of these variables across all clades. We identified the better fitting model for each clade specifically (BM or OU), using the corrected Akaike's information criterion (AICc), and extracted the corresponding rate estimates (BIO1 rate, BIO12 rate and PC1 rate; Butler & King, 2004; Felsenstein, 1985). These were defined as σ^2 under the BM model and $\sigma^2/2\alpha$ under the OU model. OU models might be favoured over BM models when the examined traits are measured with error (Silvestro, Kostikova, Litsios, Pearman, &

Salamin, 2015). Given that measurement errors are unknown for most traits and species of mammals, our results on niche evolution should be interpreted cautiously.

To capture environmental heterogeneity, we calculated the number of land cover types within clade area. We distinguished 12 different land covers (listed in Supporting Table S3), following the AVHRR (Advanced Very High Resolution Radiometer) Global Land Cover Classification (woodlands, grasslands, deciduous broadleaf forests, etc.; De Fries, Hansen, Townshend, & Sohlberg, 1998).

To capture the topography within clade area, we calculated three broadly used indices of topographic structure: terrain ruggedness index (TRI), topographic position index (TPI) and roughness (RGH; all defined in Supporting Table S2; Wilson, O'Connell, Brown, Guinan, & Grehan, 2007). We also calculated the surface of clade area and divided it by the projected clade area. This ratio equals one in plains and increases with the number, steepness and the height of the mountains within clade area. Topographic data ($1 \text{ km} \times 1 \text{ km}$ resolution) were taken from the WorldClim database (Hijmans et al., 2005).

Finally, we calculated multiple measures of regional coexistence. These measures were based on the geographical overlaps between species distributions, capturing the degree of resource sharing and partitioning across the species that coexist within a region (Machac et al., 2013; Oliveira et al., 2016; Rabosky, 2013; Rabosky & Hurlbert, 2015). Specifically, we calculated geographical overlaps between the distributions of mutually related species (i.e., all species within a given clade) but also distributional overlaps with unrelated species (species outside the clade) and with all mammals (species both within and outside the clade). Extensive overlaps between the distributions of mutually related species, presumed to be ecologically similar and thus competing for similar resources, have been hypothesized to suppress diversification and produce slowdowns across molecular phylogenies (Machac et al., 2013; Rabosky, 2013; Rabosky & Glor, 2010; Wiens, 2011). In contrast, distributional overlaps with species outside the clade and with all mammals should have limited or no effect on slowdowns.

To calculate distributional overlaps between related species (within a clade), we took all species within a given a clade, summed the geographical areas of their distributions, and divided the sum by clade area. The resultant index equals one in clades whose species are completely allopatric and increases with the extent to which species distributions overlap. To calculate distributional overlaps with unrelated species (species outside the clade) and with all species (both within and outside the clade), we summed the geographical areas of species distributions (or their parts) within clade area and divided the sum by clade area. Importantly, distributional overlaps were calculated with respect to clade area and therefore in relative (rather than absolute) terms. This ensured that the overlaps were largely independent of clade size and did not correlate with the gamma statistic for purely statistical reasons (Machac et al., 2013; McPeck, 2008; Pennell et al., 2012; Pybus & Harvey, 2000).

2.5 | Evaluating the effects of ecological predictors

To identify the factors that influence diversification, we fitted a series of regressions where the three diversification measures (diversification

rate, gamma statistic and clade richness at saturation) were predicted by the following variables: climate (BIO1, BIO12 and PC1), environmental productivity (AET and NPP), rates of climatic-niche evolution (BIO1 rate, BIO12 rate and PC1 rate), clade area, environmental heterogeneity (land covers, TRI, TPI and RGH) and distributional overlaps (within a clade, with unrelated species and with all species). The regressions were fitted across all clades within mammals and, separately, across all clades within their six core taxa (Eulipotyphla, Artiodactyla, Chiroptera, Carnivora, Primates and Rodentia), using phylogenetic generalized least squares (PGLS; Freckleton et al., 2002). To confirm the results, we fitted PGLS models for multiple subsets of mutually non-nested clades. The non-nested clades were randomly and repeatedly selected from the collection of all clades, and using BAMM (see Section 2.6 and the Supporting Methods). Phylogenetic correlations between the analysed clades were captured by covariance matrices, derived from the phylogenetic distances between the nested and non-nested clades (see Supporting Figure S1; Machac & Graham, 2017; Machac et al., 2012, 2013). All statistical analyses were performed in the 'R' environment (R Core Team, 2016), and their technical details can be found in the Supporting Methods.

2.6 | Supplementary analyses

To test whether errors in the assignment of diversification modes (constant, slowing or saturated) might have influenced our results, we randomly reshuffled the modes across clades. This ensured that the number of clades with the three respective modes, and thus the sample size of the analysis, remained unchanged. The modes were reshuffled in a completely random manner and with respect to the estimated Akaike's weights (see the Supporting Randomizations). If the same results are supported for clades selected based on their diversification mode (constant, slowing or saturated) and for randomly selected clades (modes reshuffled randomly and with respect to the Akaike's weights), the results are largely independent of the clade selection procedure and would be supported even under conventional analyses that ignore the diversification mode of the clade. However, the distinction between the clades with different modes should yield more accurate estimates of diversification measures and therefore stronger results. Detailed explanation of the randomization procedure and the rationale behind it is given in the Supporting Randomizations.

Contrary to our expectation (Figure 1; Evans, Warren, & Gaston, 2005; MacArthur, 1964; Simpson, 1953), we found negative correlations between environmental temperature, precipitation, productivity and clade richness at saturation (Supporting Table S10). This suggests that saturated clades attain low richness in the tropics, but high richness in the temperate region (Figures 3 and 4; Supporting Table S10). To illuminate these unexpected results, and their biological explanation, we conducted several post hoc analyses. One possible explanation follows from the fact that species-poor clades often consist exclusively of tropical species with small ranges, whereas species-rich clades tend also to include extra-tropical large-ranged species (Brown, Stevens, & Kaufman, 1996); the geographical configuration of species ranges, in itself, can therefore produce the observed negative correlation (Figures

3 and 4; Supporting Table S10). However, the negative correlation might also arise because ecological niches are narrow and the ecospace densely packed in the tropics (Janzen, 1967; Pianka, 1966), such that tropical clades can accumulate only limited richness before they saturate (Pianka, 1966; Quintero & Wiens, 2013; Rohde, 1992; Van Valen, 1985). To distinguish between these two explanations, we again used the randomization procedure detailed in the previous paragraph. The randomization preserves the geographical configuration of species ranges, but reshuffles the estimated diversification dynamics, thus revealing the correlation expected under the range-configuration hypothesis (Brown et al., 1996). Under the niche-packing hypothesis (Pianka, 1966; Rohde, 1992; Van Valen, 1985), tropical clades should saturate at lower richness than expected under the range configuration alone (Pianka, 1966; Rohde, 1992; Van Valen, 1985), thus producing a significantly more pronounced negative correlation than the one generated by the randomization procedure (for further details, see the Supporting Randomizations).

Moreover, we confirmed our results across non-nested clades. To this end, we compiled 1,000 clade sets, each consisting of 100 randomly selected, but mutually non-nested clades. The PGLS analyses (see above) were then repeated across all clade sets (Freckleton et al., 2002). Additionally, we identified mutually non-nested clades with distinctly slowing diversification, using BAMM, to confirm our results on diversification slowdowns (see the Supporting Methods).

Finally, we confirmed that our results were robust to possible errors across small-sized clades whose diversification can be difficult to evaluate (Morlon et al., 2010, 2011; Pybus & Harvey, 2000). In particular, we excluded clades with < 10 and < 20 species from our analyses and confirmed that the core results remained supported. Further information on the statistical analysis is given in the Supporting Methods and Randomizations.

3 | RESULTS

The three modes of diversification were represented unevenly (constant, 22.10%; slowing, 55.90%; and saturated, 22.00% out of the analyzed clades) and non-randomly across the phylogeny (Table 1). Constant diversification was prevalent across small clades, slowdowns across medium-sized clades, and large clades were mostly saturated (Figure 2; PGLS $R^2 = 23\%$, $p = .001$), suggesting that clades transition from one diversification mode to another as they grow and accumulate species.

BAMM and MEDUSA confirmed the coalescent results. BAMM's most credible set of shift configurations (95%) suggested c. 50 shifts in diversification rates across the phylogeny under the conservative priors (Supporting Table S31), but no significant shifts under the relaxed priors (Supporting Methods and Results). Both sets of priors, however, indicated a decline in diversification rates with clade age and clade size (Figure 2; Supporting Figures S8 and S10). MEDUSA identified 22 shifts on the phylogeny (Supporting Table S30). Much like BAMM, MEDUSA suggested low rates of diversification across large/old clades, whereas

TABLE 1 Diversification modes across mammalian clades

Taxon	Taxon richness	Species sampling (%)	No. of clades analysed	Proportion of clades (%)		
				Constant	Slowing	Saturated
Mammalia	4,990	75.4	1,060	22.10	55.90	22.00
Carnivora	275	90.9	66	54.30	38.20	7.50
Artiodactyla	309	93.5	90	32.00	50.00	18.00
Chiroptera	1,052	74.6	231	23.20	50.00	26.80
Eulipotyphla	401	63.3	65	23.00	61.50	15.50
Primates	350	87.1	62	32.90	56.10	11.00
Rodentia	2,066	68.6	403	14.30	61.20	24.50

Note. Particularly small clades (with fewer than five species) were not included because their diversification cannot be evaluated under the coalescent inference (Morlon et al., 2010).

small/young clades showed fast diversification (Figure 2; Supporting Figure S6).

Diversification rates depended on many different factors across the six examined taxa (Carnivora, Artiodactyla, Chiroptera, Eulipotyphla, Primates and Rodentia; Figure 3a). Increased diversification was coupled with high topographic and environmental heterogeneity in Carnivora (Supporting Table S11), but Artiodactyla showed the opposite pattern (Supporting Table S14), whereas Chiroptera (Supporting Table S17), Eulipotyphla (Supporting Table S20) and Primates (Supporting Table S23) showed no pattern at all (e.g., Supporting Table S8). Low diversification rates were associated with high precipitation in Chiroptera (Supporting Table S17), but the opposite held for Carnivora (Supporting Table S11). Similarly variable were the effects of climate (e.g., Supporting Tables S8, S11 and S14), productivity (e.g., Supporting

Tables S8, S17 and S20), clade area (e.g., Supporting Tables S8, S23 and S26) and the rates of niche evolution (e.g., Supporting Tables S8, S17 and S23). These results imply that diversification dynamics are highly taxon-specific during the initial expansion of a clade.

In contrast, diversification slowdowns were governed by similar factors across each of the six taxa (Figure 3b). Pronounced slowdowns (as indicated by negative gamma) occurred in clades whose species had extensively overlapping geographical distributions (within-clade overlap; Figures 3b and 4). These effects were detected in mammals (Supporting Table S9) and in every one of the examined taxa (Carnivora, Artiodactyla, Chiroptera, Eulipotyphla, Primates and Rodentia; Supporting Tables S12, S15, S18, S21, S24 and S27) and explained nearly half of the variation in diversification slowdowns, as measured by the gamma statistic (PGLS $R^2 = 0.43 \pm 0.18$ across taxa, $p < .05$). These

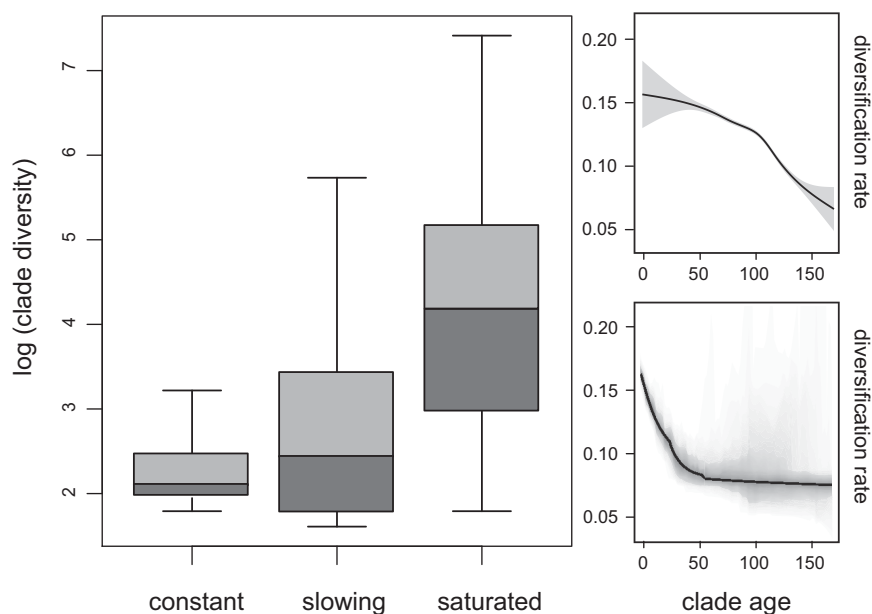


FIGURE 2 Diversification modes change with clade size (phylogenetic generalized least squares $R^2 = 23\%$, $p < .001$), as indicated by the coalescent inference (left panel). MEDUSA (upper right panel) and BAMM (lower right panel) confirm that diversification declines with clade age as well. These results together support the hypothesis that clades transition from an unbounded expansion to slowdowns and saturation, as they grow and accumulate species

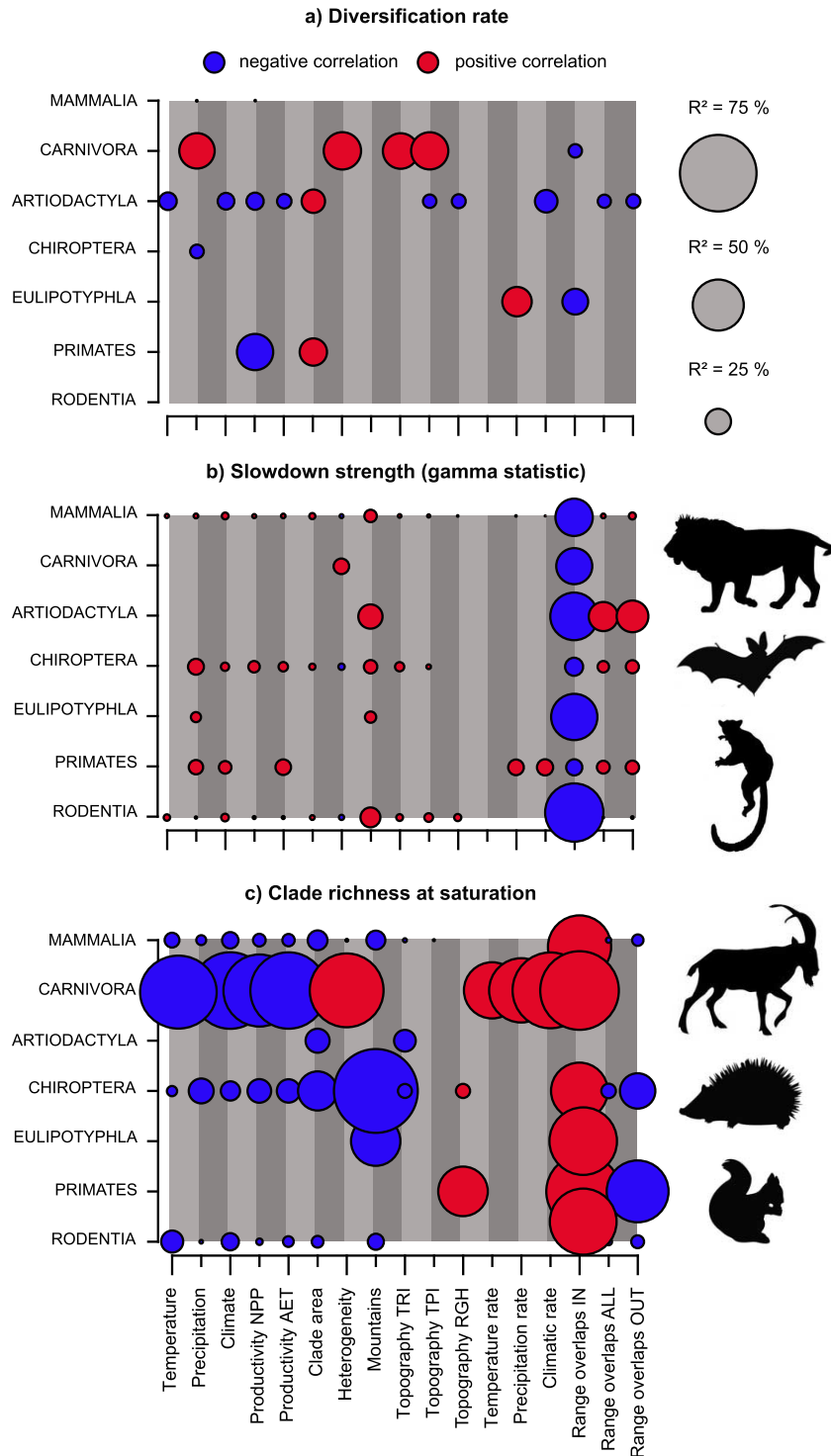


FIGURE 3 Ecological predictors of (a) diversification rate, (b) slowdown strength and (c) clade richness at saturation, identified by the PGLS. Diversification rates show mixed results across taxa. Diversification slowdowns are typically pronounced in clades whose species have extensively overlapping geographical distributions. Clades saturate at low richness in the warm, humid and highly productive climates of the tropics. The figure shows only the significant results. Complete results are given in Supporting Tables S8–S28 and explained further in the Results. The ecological predictors are overviewed in Supporting Table S2

effects cannot be explained by the influence of clade size because within-clade overlaps were defined relative to clade area (thus correcting for clade size) and because their effect on gamma remained highly significant even when clade size was added to the PGLS model (PGLS

$\beta = -1.344 \pm 0.202$, $p < .001$). Moreover, distributional overlaps with unrelated species (species outside the clade) had no detectable effect on slowdowns (Figure 3b; e.g., Supporting Tables S12, S15 and S21). The slowdowns were also significantly weaker in montane and

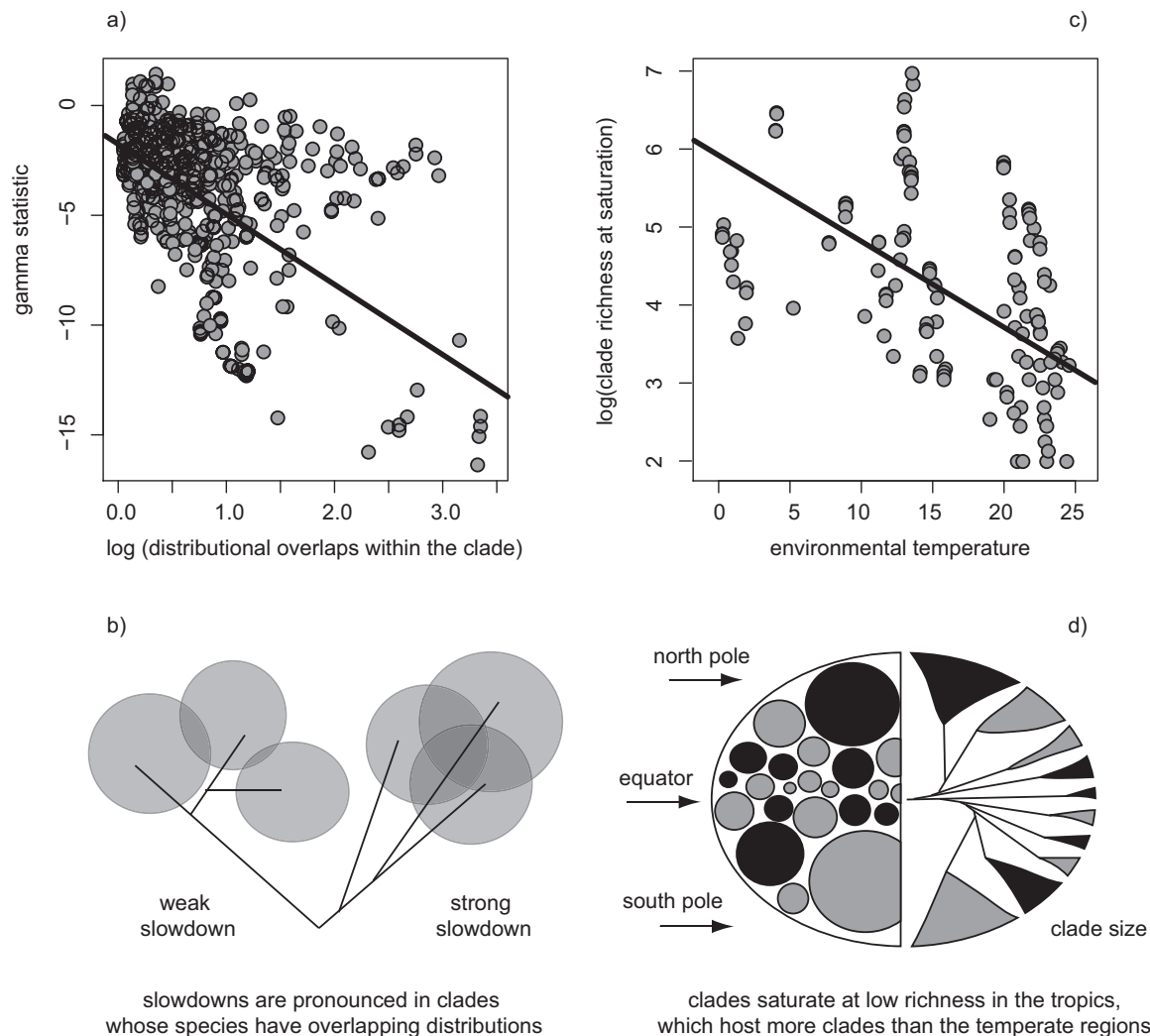


FIGURE 4 The most relevant predictors of diversification dynamics. (a) Gamma declines with the degree of distributional overlap within a clade, indicating that (b) diversification slowdowns are particularly pronounced in clades whose species have extensively overlapping geographical distributions. (c) Clade saturation depends on environmental conditions. (d) There are more clades in the tropics than in the temperate regions, but individual tropical clades saturate at lower richness than temperate clades, such that species and clades become progressively more densely packed towards the tropics

heterogeneous regions where clades had the opportunity to diverge spatially and ecologically (e.g., Supporting Tables S9, S15 and S18). These results, which were confirmed across mutually non-nested clades (Supporting Table S6 and Figure S11), are consistent with the prediction of Simpson's (1953) model that competition between related and regionally coexisting species suppresses the diversification process.

Clade richness at saturation depended mostly on climate and environmental productivity (AET and NPP). Clades of warm, humid and highly productive climates of the tropics saturated at low richness (Figure 3c; Supporting Table S10), whereas clades of cold, unproductive, temperate climates saturated at high richness (Figure 3c; Supporting Table S10). This result held for mammals (Figure 4; Supporting Table S10) and for Carnivora, Chiroptera and Rodentia (Figure 3; Supporting Tables S13, S19 and S28). Randomizations confirmed that the negative correlation between clade richness and temperature was significantly more pronounced than expected based on the geographical

configuration of species ranges (Supporting Figure S19), which suggests that the correlation was probably reinforced by the differences in clade packing across latitudes (Pianka, 1966; Rohde, 1992; Van Valen, 1985). These results again held for non-nested clades as well (Supporting Table S7). In addition, we found that saturated clades often showed extensive within-clade overlaps (Figure 3c), in line with the results previously found for slowdowns (Figure 3b).

These results were confirmed across a variety of supplementary analyses. They were confirmed across nested (Figures 3 and 4) and exclusively non-nested clades (Supporting Tables S5–S7) and across clades whose diversification mode was established with high confidence (Akaike's weight > 0.7; Supporting Figures S2–S4). They were supported when we controlled for possible errors in the assignment of diversification modes (Supporting Figures S15–S18) and when we reshuffled diversification modes across the phylogeny in a completely random manner (Supporting Figures S15 and S16) and with respect to

the estimated Akaike's weights (Supporting Figures S17 and S18). The results were further supported when we removed small-sized clades (with < 10 and < 20 species; Supporting Table S29) and clades whose diversity presumably declines (Figures S12–S24) from the analysis. We found that out of the 605 declining clades (Supporting Figure S12) 28.6% showed constant diversification (under the coalescent inference), 39.5% showed slowdowns, and 31.9% showed saturation. These percentages, however, need to be interpreted cautiously because individual clades do not represent independent observations. We also note that some of our results varied markedly across the examined taxa and methodological setups (e.g., Supporting Figures S2–S4 and Tables S5–S10), so we focus our discussion and interpretation only on the most robust results, consistently corroborated across different taxa and methods, likely to warrant biologically meaningful conclusions.

4 | DISCUSSION

We found that diversification transitions from an unbounded expansion to slowdowns and saturation, at least in mammals, and each of these three diversification phases is governed by different ecological factors. The unbounded expansion is highly taxon specific. But the slowdowns are typically pronounced in clades whose species coexist regionally, in line with the hypothesis that competition for regional resources suppresses the diversification process (Gavrilets & Losos, 2009; Gavrilets & Vose, 2005; Schluter, 2000; Simpson, 1953). Environmental conditions determine the richness at which clades eventually saturate. These results suggest that the diversification process might be governed by systematically different factors, as clades grow and accumulate species (Figures 2–4; Pontarp & Wiens, 2016; Schluter, 2000; Simpson, 1953; Van Valen, 1985). Many of the previously reported and seemingly conflicting results (e.g., Harmon & Harrison, 2015; Rabosky, 2009a; Rabosky & Hurlbert, 2015; Wiens, 2011) might therefore be reconciled under one diversification process, whose dynamics and ecological controls vary systematically across phylogenetic scales.

Diversification dynamics have been much debated in the literature (Davies, Allen, Borda-de-Água, Regetz, & Melián, 2011; Harmon & Harrison, 2015; Heard & Cox, 2015; Purvis et al., 2011; Rabosky, 2013; Rabosky & Hurlbert, 2015; Sepkoski, 1998; Van Valen, 1985; Wiens, 2011). Some studies found that diversification is unbounded, such that clade richness increases constantly (McPeck & Brown, 2007; Morlon et al., 2010; Stephens & Wiens, 2003; Wiens, Pyron, & Moen, 2011), whereas others reported that diversification decelerates over time, such that most clades eventually reach their equilibrium richness (Alroy et al., 2008; Rabosky, 2013; Rabosky & Glor, 2010; Raup & Sepkoski, 1982). We find that these results are not mutually exclusive and can be detected across different segments of the same phylogeny, presumably because they represent different phases of the same diversification process (Graham et al., in press; Machac et al., 2013; Phillimore & Price, 2008; Pontarp & Wiens, 2016). Instead of investigating whether diversification tends towards an equilibrium or not, we should perhaps identify the clades that might have reached an equilibrium and those that

keep expanding, and investigate how these clades differ from each other in terms of their ecology.

Taking this approach, we found that the early expansion of a clade is seemingly unbounded and contingent on many taxon-specific factors. For example, carnivorans diversify rapidly in the mountains, whereas artiodactyls diversify in the lowlands, and most mammals show no pattern with elevation (Figure 3). The effects of climate, climatic-niche evolution, and those of the other examined factors were similarly diverse across the six taxa (Figure 3; Supporting Table S8). This diversity of results supports the view that no single factor can guarantee the success of a new clade among the already established clades (Benton, 2009; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Van Valen, 1973); instead, new clades need to pursue new ecological strategies to become established themselves (Benton, 2009; Schemske et al., 2009; Van Valen, 1973). This conclusion reaffirms the results of previous research that identified very different correlates of diversification rates, even for closely related taxa (Buckley et al., 2010; Rolland et al., 2014; Soria-Carrasco & Castresana, 2012; Weir & Schluter, 2007).

In contrast, diversification slowdowns were governed by similar factors across each of the six taxa examined (Carnivora, Chiroptera, Eulipotyphla, Artiodactyla, Primates and Rodentia). Pronounced slowdowns occurred in clades consisting of regionally coexisting species that can compete with each other for regional resources (Figures 3b and 4). These resources can be shared by the regionally coexisting species, but the species can also partition them (through niche differentiation, specialization locally, etc.) in order to avoid immediate competition. In either case, the more species coexist within a region, the fewer resources are available for each of them (Currie et al., 2004; Evans et al., 2005; Oliveira et al., 2016; Wright, 1983), which depresses the population sizes of the regionally coexisting species, elevates their extinction risk and, consequently, suppresses their diversification (Machac et al., 2013; Mittelbach et al., 2007; Rabosky, 2013; Schluter, 2000; Simpson, 1953; Wright, 1983). Within-clade competition can also suppress speciation (Pires, Silvestro, & Quental, 2017), probably by decreasing the chances of establishment of new species because of the lack of resources. Importantly, we found that regional coexistence with unrelated mammals (species outside the clade) had no detectable effect on slowdowns, presumably because unrelated mammals are less likely to compete with the species within any given clade. The effects of competition were further implicated by the fact that slowdowns were generally weak in montane (Rodentia, Chiroptera, Eulipotyphla and Artiodactyla) and heterogeneous regions (Carnivora, Chiroptera) where species can diverge both spatially and ecologically to evade competition (Gavrilets & Losos, 2009; Qian & Ricklefs, 2000; Schluter, 2000). Even though we recognize that these effects are notoriously hard to demonstrate, different facets of our results consistently suggest that diversification slowdowns might be ecologically regulated, presumably through competition among mutually related and regionally coexisting species. These effects have been previously hypothesized and modelled (Gavrilets & Losos, 2009; Gavrilets & Vose, 2005; Schluter, 2000; Simpson, 1953), but our study is presumably the first to support them empirically across multiple taxa at a global scale.

Related species are often assumed to be ecologically similar and possibly competing with each other. This conjecture dates back to Darwin (1859) and has a long history in biology (Elton, 1946; Gause, 1934; Webb, Ackerly, McPeck, & Donoghue, 2002). However, relatedness might not necessarily translate into ecological similarity (Losos, 2008; Revell et al., 2008), and ecological similarity between regionally coexisting species might not lead to strong competition (Chesson, 2000; Godoy, Kraft, & Levine, 2014; Mayfield & Levine, 2010). Naturally, there are many examples of limited competition among close relatives (Hylidae and Asteraceae; Chesson, 2000; Mayfield & Levine, 2010; Wiens et al., 2011), as well as instances of strong competition among unrelated species (Borophaginae; Silvestro, Antonelli, Salamin, & Quental, 2015). In the case of our results on diversification slowdowns, however, it seems hard to propose an alternative parsimonious explanation for the detected effects of mountains, heterogeneity and distributional overlaps with related and unrelated species, without invoking competition. Indeed, our findings need to be further tested and refined, potentially using functional traits (Losos, 2008; Marshall & Quental, 2016; Oliveira et al., 2016), but the issues previously raised in the literature (especially the lack of connection between relatedness, similarity and competition; Chesson, 2000; Godoy et al., 2014; Mayfield & Levine, 2010) seem to act against detecting (rather than allowing us to detect) the hypothesized effects of regional coexistence on diversification slowdowns.

Environmental conditions set the richness at which clades eventually saturate (Figure 4). Contrary to the prediction (Simpson, 1953; Van Valen, 1985), we found that clades saturate at low richness in the climatically favourable tropics, whereas temperate clades saturate at high richness (Figures 3c and 4; Evans et al., 2005; Fischer, 1960), in line with the hypothesis that the tropical ecospace is enormously species rich but finely partitioned and densely packed with species and clades (Elton, 1946; Fischer, 1960; Pianka, 1966). It is possible that the favourable climates of the tropics are easily invaded by many different clades (Wiens & Donoghue, 2004; Wiens & Graham, 2005), each of which is consequently left with limited opportunity for expansion and saturates at low richness. Conversely, temperate climates are harsh and difficult to invade, but the few clades that successfully invaded the temperate region could accumulate high richness (Elton, 1946; Fischer, 1960; Pianka, 1966; Wiens & Donoghue, 2004; Wiens & Graham, 2005). This interpretation assumes competition with mammals outside the clade (but see Figures 3 and 4), and it is possible that competition increases as clades grow and accumulate species, such that both related and unrelated species influence the diversification process during saturation. In line with some recent work (Machac & Graham, 2017), our results imply that species relatedness has different effects on diversification dynamics across phylogenetic scales, and further research might be needed to illuminate the mechanisms behind this scale dependence (see Machac & Graham, 2017). Whatever the underlying mechanisms, however, there seem to be striking differences in the packing of species, clades and, possibly, ecological niches across latitudes that are interesting in their own right and cannot be explained simply by the geographical

configuration of species ranges (Figures 3c and 4; Supporting Figure S19; Brown et al., 1996).

Diversity declines represent the final, if not inevitable, terminal phase of the diversification process that has proved rather difficult to infer from phylogenetic data (Gould, Raup, Sepkoski, Schopf & Simberloff, 1977; Raup & Sepkoski, 1982; Van Valen, 1985). Mammals provide many examples of extinct (Mesotheriidae, Toxodontidae and Borophaginae) and potentially declining clades (Marsupialia, Xenarthra, Perissodactyla and Cetacea), and new methods have been developed to identify these clades using molecular phylogenies (Beaulieu & O'Meara, 2015; Morlon et al., 2011; Purvis, 2008; Quental & Marshall, 2010). These methods have their limitations, however (e.g., assumptions about diversification heterogeneity), and there is currently no clear consensus as to how reliably, and under what circumstances, they can estimate extinction (Beaulieu & O'Meara, 2015; Moore et al., 2016; Morlon et al., 2011; Rabosky, 2016), especially when extinction is high and exceeds speciation (Moore et al., 2016; Quental & Marshall, 2010; Rabosky, 2016). Using the simulation-backed approach of Morlon et al. (2011), we found that declining clades do not mask any particular diversification mode (slowdowns, etc.) and occur across a range of phylogenetic scales. This corresponds with the classic Van Valen's (1973) law of extinction that inspired the Red Queen hypothesis (i.e. clades of different ages have comparable likelihood of going extinct). However, it seems likely that the decline might be steeper among the small and young clades of mammals, which would balance out the expansion that otherwise prevails among these clades (Figure 2) and explain the saturation generally detected in large clades (Figure 2). Evaluating the relative magnitude of diversity declines across phylogenetic scales is beyond the scope of the present study, and might require validation against the fossil data. But our results provide the motivation for such research and reaffirm its importance for understanding the evolution of mammal diversity, including the longstanding question of what drives clades to a decline and, eventually, extinction (Gould et al., 1977; Morlon et al., 2011; Raup & Sepkoski, 1982; Van Valen, 1973, 1985).

The fossil record largely corroborates our key findings (Figures 2–4; Alroy, 1996; Liow & Finarelli, 2014; Raup & Sepkoski, 1982; Sepkoski, 1998; Silvestro, Antonelli et al., 2015; Van Valen, 1985). Directional changes from an unbounded expansion to slowdowns and saturation are common in marine invertebrates (Raup & Sepkoski, 1982; Sepkoski, 1998), but Eocene mammals and Neogene carnivores show similar dynamics (Alroy, 1996; Liow & Finarelli, 2014). The effects of competition on diversification slowdowns have also been reported for Eocene canids, whose increasing competition may have suppressed the diversification process and, occasionally, driven entire clades to extinction (e.g., Hesperocyoninae, Borophaginae; Silvestro et al., 2015). Moreover, the tropics of Eurasia have been typified by a dense packing of habitat and dietary niches in Neogene mammals (Fortelius et al., 2014). These observations are consistent with our key findings (Figure 4) that, in turn, complement and corroborate results previously reported from the fossil record.

Our Discussion has centred on the main trends detected in mammals (Figures 2–4), but we do not dispute that many mammalian clades might defy these trends and follow their own diversification trajectories (see Figure 3; Supporting Figures S2–S4). In principle, clades might diversify at slowing rates without ever reaching an equilibrium (e.g., increasing selection pressure on evolutionary innovation might raise the equilibrium richness of a clade before it is reached; Erwin, 2008; Marshall & Quental, 2016; Schemske et al., 2009; Van Valen, 1973). Saturated clades might break away from their presumed ecological constraints (e.g., through key adaptations, such as herbivory, hypsodonty or flight) and further expand (Glor, 2010; Losos, 2010; Schluter, 2000), and not all higher taxa need to be saturated (e.g., saturation within mammals does not preclude the expansion of vertebrates as a whole; Hedges et al., 2015; Jezkova & Wiens, 2017). Nonetheless, our study presents a promising attempt to unify the growing body of diversification results. It reveals that most clades of mammals follow similar diversification trends, governed by different classes of ecological factors over time. The most prominent factors, namely competition between regionally coexisting species, niche packing and partitioning, have been identified (Gould, 2002; Pianka, 1966; Schluter, 2000; Simpson, 1953; Van Valen, 1985), and we propose promising strategies for their further investigation (especially research across phylogenetic scales; Graham et al., in press; Machac & Graham, 2017).

We acknowledge that our results may have been influenced by several sources of error, including errors in the assignment of diversification modes (Morlon et al., 2010) and errors associated with the evaluation of small-sized clades (Morlon et al., 2010, 2011). The results may also have been influenced by clade nestedness and by the uneven resolution of the mammalian phylogeny (Hedges et al., 2015). Still, none of these errors seems likely to overturn our core conclusions, which were supported across multiple diversification methods (BAMM and MEDUSA; Figure 2; Supporting Figures S6, S8 and S10), when we randomly reshuffled diversification modes across clades, thus controlling for the possible errors in mode assignment (Supporting Figures S15–S18), when we repeated our analyses for clades whose diversification mode was assessed with high confidence (Supporting Figures S2–S4) and when we removed small-sized clades (with < 10 and < 20 species) from the analysis (Supporting Table S29). The conclusions were supported across mammals but also across multiple taxa within mammals, including the well-resolved taxa (Carnivora, Artiodactyla and Primates), but also Rodentia and Chiroptera (Figures 3 and 4). They were further supported across nested and exclusively non-nested clades (Supporting Tables S5–S7 and Figure S11) and when controlling for clades with declining diversity (Figures S12–S14). Still, we note that diversification analyses approximate only the most important trends across the phylogeny (Alfaro et al., 2009; Morlon et al., 2010, 2011; Rabosky, 2014) and rarely capture the underlying dynamics entirely (Morlon, 2014; Morlon et al., 2010, 2011; Ricklefs, 2007), especially in taxa that are extremely diversified internally (i.e., Rodentia and Chiroptera). Even though we used the model devised by Simpson (1953) and further relevant literature (Hutchinson, 1959; Kozak & Wiens, 2010; Pianka, 1966; Qian & Ricklefs, 2000; Rabosky & Glor, 2010; Whittaker, 1972) to guide our analyses, our results are not contingent on the

choice of this model and stand on their own merit. Indeed, some of the original predictions of the model were not supported (e.g., clades do not saturate at high richness in the tropics), and our results identify the elements of Simpson's (1953) model that might need to be revised in the future.

5 | CONCLUSIONS

We found that evolutionary diversification may vary across the phylogeny, with different dynamics and ecological factors prevailing across different phylogenetic scales. Here, we defined phylogenetic scale in terms of clade age and clade size. But the concept of phylogenetic scale needs to be further developed, formalized and, possibly, compared with spatial and temporal scales (which ignore phylogenetic hierarchy; Graham et al., in press; Jablonski, 2000, 2007; Purvis et al., 2011), and our work sets the stage and provides the motivation for such a research programme (Graham et al., in press). It has been debated whether diversification is unbounded or ecologically constrained, stochastic or ecologically deterministic, biotically or abiotically regulated. Our study attempts to break these dichotomies, illustrating that each of these alternatives might apply during different phases of the same diversification process. Many of the seemingly conflicting results in the literature consequently seem to complement, rather than contradict, each other (Benton, 2009; Cornell, 2013; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015), especially in the phylogenetic context that covers a range of clades of different ages and sizes. Future cross-scale analyses might therefore produce a more complete and integrated understanding of the processes that generate species diversity.

ACKNOWLEDGMENTS

We are grateful to Blair Hedges and Julie Marin for sharing their mammalian phylogeny. Adam Algar, Gabriel Costa, Bruno Oliveira, Marisa Lim, Caterina Penone, Anusha Shankar, Daniele Silvestro and Ben Weinstein provided insightful suggestions and comments on the manuscript. Computational power was lent by the NGI (National Grid Infrastructure) MetaCentrum Cluster (CESNET LM2015042). Our work was supported by the NSF (National Science Foundation) programme Dimensions of Biodiversity (DEB-1136586), the Czech Science Foundation (16–26369S) and the Danish National Research Foundation.

DATA ACCESSIBILITY

All data used in the study are freely available from the cited and publicly accessible databases.

ORCID

Antonin Machac  <http://orcid.org/0000-0001-6754-5038>

Catherine H. Graham  <http://orcid.org/0000-0001-9267-7948>

David Storch  <http://orcid.org/0000-0001-5967-1544>

REFERENCES

- Alfaro, M. E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D. L., ... Harmon, L. J. (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences USA*, 106, 13410–13414.
- Alroy, J. (1996). Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127, 285–311.
- Alroy, J., Aberhan, M., Bottjer, D. J., Foote, M., Fuersich, F. T., Harries, P. J., ... Visaggi, C. C. (2008). Phanerozoic trends in the global diversity of marine invertebrates. *Science*, 321, 97–100.
- Beaulieu, J. M., & O'Meara, B. C. (2015). Extinction can be estimated from moderately sized molecular phylogenies. *Evolution*, 69, 1036–1043.
- Benton, M. J. (2009). The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science*, 323, 728–732.
- Benton, M. J., & Emerson, B. C. (2007). How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics. *Palaeontology*, 50, 23–40.
- Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., ... Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, 446, 507–512.
- Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 1, 597–623.
- Buckley, L. B., Davies, T. J., Ackerly, D. D., Kraft, N. J. B., Harrison, S. P., Anacker, B. L., ... Wiens, J. J. (2010). Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2131–2138.
- Butler, M. A., & King, A. A. (2004). Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *The American Naturalist*, 164, 683–695.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Cornell, H. V. (2013). Is regional species diversity bounded or unbounded? *Biological Reviews*, 88, 140–165.
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J.-F., Hawkins, B. A., ... Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134.
- Darwin, C. (1859). *The origin of species*. New York, NY: Signet Press.
- Davies, T. J., Allen, A. P., Borda-de-Água, L., Regetz, J., & Melián, C. J. (2011). Neutral biodiversity theory can explain the imbalance of phylogenetic trees but not the tempo of their diversification: Neutral theory and phylogeny. *Evolution*, 65, 1841–1850.
- De Fries, R. S., Hansen, M., Townshend, J. R. G., & Sohlberg, R. (1998). Global land cover classifications at 8 km spatial resolution: The use of training data derived from Landsat imagery in decision tree classifiers. *International Journal of Remote Sensing*, 19, 3141–3168.
- Elton, C. (1946). Competition and the structure of ecological communities. *Journal of Animal Ecology*, 15, 54–68.
- Erwin, D. H. (2008). Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology and Evolution*, 23, 304–310.
- Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species–energy relationships at the macroecological scale: A review of the mechanisms. *Biological Reviews*, 80, 1–25.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125, 1–15.
- Fischer, A. G. (1960). Latitudinal variations in organic diversity. *Evolution*, 14, 64–81.
- Fortelius, M., Eronen, J. T., Kaya, F., Tang, H., Raia, P., & Puolamäki, K. (2014). Evolution of Neogene mammals in Eurasia: Environmental forcing and biotic interactions. *Annual Review of Earth and Planetary Sciences*, 42, 579–604.
- Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *The American Naturalist*, 160, 712–726.
- Gause, G. F. (1934). *The struggle for existence*. Baltimore, MD: Williams & Wilkins.
- Gavrilets, S., & Losos, J. B. (2009). Adaptive radiation: Contrasting theory with data. *Science*, 323, 732–737.
- Gavrilets, S., & Vose, A. (2005). Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences USA*, 102, 18040–18045.
- Glor, R. E. (2010). Phylogenetic insights on adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics*, 41, 251–270.
- Godoy, O., Kraft, N. J. B., & Levine, J. M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17, 836–844.
- Gould, S. J. (2002). *The structure of evolutionary theory*. Cambridge, MA: Belknap Press.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 205, 581–598.
- Gould, S. J., Raup, D. M., Sepkoski, J. J., Schopf, T. J. M., & Simberloff, D. S. (1977). The shape of evolution: A comparison of real and random clades. *Paleobiology*, 3, 23–40.
- Graham, C. H., Storch, D., & Machac, A. (in press). Phylogenetic scale in ecology and evolution. *Global Ecology and Biogeography*.
- Harmon, L. J., & Harrison, S. (2015). Species diversity is dynamic and unbounded at local and continental scales. *The American Naturalist*, 185, 584–593.
- Heard, S., & Cox, G. (2015). The shapes of phylogenetic trees of clades, faunas, and local assemblages: Exploring spatial pattern in differential diversification. *The American Naturalist*, 169, 107–118.
- Hedges, S. B., Marin, J., Suleski, M., Paymer, M., & Kumar, S. (2015). Tree of life reveals clock-like speciation and diversification. *Molecular Biology and Evolution*, 4, 835–845.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, 104, 13384–13389.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist*, 93, 145–159.
- Jablonski, D. (2000). Micro- and macroevolution: Scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology*, 26, 15–52.
- Jablonski, D. (2007). Scale and hierarchy in macroevolution. *Palaeontology*, 50, 87–109.
- Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, 101, 233–249.
- Jezkova, T., & Wiens, J. J. (2017). What explains patterns of diversification and richness among animal phyla? *The American Naturalist*, 189, 201–212.

- Kozak, K. H., & Wiens, J. J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, *13*, 1378–1389.
- Kozak, K. H., & Wiens, J. J. (2012). Phylogeny, ecology, and the origins of climate–richness relationships. *Ecology*, *93*, 167–181.
- Liow, L. H., & Finarelli, J. A. (2014). A dynamic global equilibrium in carnivoran diversification over 20 million years. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132312.
- Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003.
- Losos, J. B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist*, *175*, 623–639.
- Losos, J. B., & Schluter, D. (2000). Analysis of an evolutionary species–area relationship. *Nature*, *408*, 847–850.
- MacArthur, R. H. (1964). Environmental factors affecting bird species diversity. *The American Naturalist*, *98*, 387–397.
- Machac, A., & Graham, C. H. (2017). Regional diversity and diversification in mammals. *The American Naturalist*, *189*, 1–13.
- Machac, A., Storch, D., & Wiens, J. J. (2013). Ecological causes of decelerating diversification in carnivoran mammals. *Evolution*, *8*, 2423–2433.
- Machac, A., Zrzavy, J., Smrckova, J., & Storch, D. (2012). Temperature dependence of evolutionary diversification: Differences between two contrasting model taxa support the metabolic theory of ecology. *Journal of Evolutionary Biology*, *25*, 2449–2456.
- Magallon, S., & Sanderson, M. J. (2001). Absolute diversification rates in angiosperm clades. *Evolution*, *55*, 1762–1780.
- Marshall, C. R., & Quental, T. B. (2016). The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150217.
- Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities: Phylogeny and coexistence. *Ecology Letters*, *13*, 1085–1093.
- McPeck, M. A. (2008). The ecological dynamics of clade diversification and community assembly. *The American Naturalist*, *172*, 270–284.
- McPeck, M. A., & Brown, J. M. (2007). Clade age and not diversification rate explains species richness among animal taxa. *The American Naturalist*, *169*, 97–106.
- Meredith, R. W., Janecka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., ... Murphy, W. J. (2011). Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, *334*, 521–524.
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., ... Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, *10*, 315–331.
- Moen, D., & Morlon, H. (2014). Why does diversification slow down? *Trends in Ecology and Evolution*, *29*, 190–197.
- Moore, B. R., Höhna, S., May, M. R., Rannala, B., & Huelsenbeck, J. P. (2016). Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy of Sciences USA*, *113*, 9569–9574.
- Morlon, H. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters*, *17*, 508–525.
- Morlon, H., Parsons, T. L., & Plotkin, J. B. (2011). Reconciling molecular phylogenies with the fossil record. *Proceedings of the National Academy of Sciences USA*, *108*, 16327–16332.
- Morlon, H., Potts, M. D., & Plotkin, J. B. (2010). Inferring the dynamics of diversification: A coalescent approach. *PLoS Biology*, *8*, e1000493.
- Mu, Q., Zhao, M., & Running, S. W. (2011). Improvements to a MODIS global terrestrial evapotranspiration algorithm. *Remote Sensing of Environment*, *115*, 1781–1800.
- Oliveira, B. F., Machac, A., Costa, G. C., Brooks, T. M., Davidson, A. D., Rondinini, C., & Graham, C. H. (2016). Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, *25*, 1119–1130.
- Pennell, M. W., Sarver, B. A. J., & Harmon, L. J. (2012). Trees of unusual size: Biased inference of early bursts from large molecular phylogenies. *PLoS One*, *7*, e43348.
- Phillimore, A. B., & Price, T. D. (2008). Density-dependent cladogenesis in birds. *PLoS Biology*, *6*, 483–489.
- Pianka, E. (1966). Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist*, *100*, 33–46.
- Pires, M. M., Silvestro, D., & Quental, T. B. (2017). Interactions within and between clades shaped the diversification of terrestrial carnivores. *Evolution*, *71*, 1855–1864.
- Pontarp, M., & Wiens, J. J. (2016). The origin of species richness patterns along environmental gradients: Uniting explanations based on time, diversification rate and carrying capacity. *Journal of Biogeography*, *44*, 722–735.
- Price, T. (2007). *Speciation in birds*. Greenwood Village, CO: Freeman Press.
- Purvis, A. (2008). Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 301–319.
- Purvis, A., Fritz, S. A., Rodríguez, J., Harvey, P. H., & Grenyer, R. (2011). The shape of mammalian phylogeny: Patterns, processes and scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2462.
- Pybus, O. G., & Harvey, P. H. (2000). Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 2267–2272.
- Qian, H., & Ricklefs, R. E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, *407*, 180–182.
- Quental, T. B., & Marshall, C. R. (2010). Diversity dynamics: Molecular phylogenies need the fossil record. *Trends in Ecology and Evolution*, *25*, 434–441.
- Quintero, I., & Wiens, J. J. (2013). What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. *Global Ecology and Biogeography*, *22*, 422–432.
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabosky, D. L. (2009a). Ecological limits and diversification rate: Alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, *12*, 735–743.
- Rabosky, D. L. (2009b). Ecological limits on clade diversification in higher taxa. *The American Naturalist*, *173*, 662–674.
- Rabosky, D. L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 481–502.
- Rabosky, D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One*, *9*, e89543.
- Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth–death polytomy resolvers for downstream comparative analyses. *Evolution*, *69*, 3207–3216.
- Rabosky, D. L. (2016). Challenges in the estimation of extinction from molecular phylogenies: A response to Beaulieu and O'Meara. *Evolution*, *70*, 218–228.

- Rabosky, D. L., & Glor, R. E. (2010). Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proceedings of the National Academy of Sciences USA*, 107, 22178–22183.
- Rabosky, D. L., & Hurlbert, A. H. (2015). Species richness at continental scales is dominated by ecological limits. *The American Naturalist*, 185, 572–583.
- Rabosky, D. L., Slater, G. J., & Alfaro, M. E. (2012). Clade age and species richness are decoupled across the Eukaryotic tree of life. *PLoS Biology*, 10, e1001381.
- Raup, D. M. (1985). Mathematical models of cladogenesis. *Paleobiology*, 11, 42–52.
- Raup, D. M., & Sepkoski, J. J. (1982). Mass extinctions in the marine fossil record. *Science*, 215, 1501–1503.
- Revell, L. J., Harmon, L. J., & Collar, D. C. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, 57, 591–601.
- Ricklefs, R. E. (2007). Estimating diversification rates from phylogenetic information. *Trends in Ecology and Evolution*, 22, 601–610.
- Rohde, K. (1992). Latitudinal gradients in species-diversity: The search for the primary cause. *Oikos*, 65, 514–527.
- Rolland, J., Condamine, F. L., Jiguet, F., & Mornon, H. (2014). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology*, 12, e1001775.
- Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, 40, 245–269.
- Schluter, D. (2000). *The ecology of adaptive radiation*. New York, NY: Oxford University Press.
- Sepkoski, J. J. (1998). Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 353, 315–326.
- Silvestro, D., Antonelli, A., Salamin, N., & Quental, T. B. (2015). The role of clade competition in the diversification of North American canids. *Proceedings of the National Academy of Sciences USA*, 112, 8684–8689.
- Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. B., & Salamin, N. (2015). Measurement errors should always be incorporated in phylogenetic comparative analysis. *Methods in Ecology and Evolution*, 6, 340–346.
- Simpson, G. G. (1953). *The major features of evolution*. New York, NY: Columbia University Press.
- Smith, S. A., Nieto Montes de Oca, A., Reeder, T. W., & Wiens, J. J. (2007). A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: Why so few species in lowland tropical rainforests? *Evolution*, 61, 1188–1207.
- Soria-Carrasco, V., & Castresana, J. (2012). Diversification rates and the latitudinal gradient of diversity in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4148–4155.
- Stanley, S. M. (1979). *Macroevolution: Pattern and Process*. Baltimore, MD: The Johns Hopkins University Press.
- Stephens, P. R., & Wiens, J. J. (2003). Explaining species richness from continents to communities: The time-for-speciation effect in emydid turtles. *The American Naturalist*, 161, 112–128.
- Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory*, 1, 1–8.
- Van Valen, L. (1985). A theory of origination and extinction. *Evolutionary Theory*, 7, 133–142.
- Walker, T., & Valentine, J. (1984). Equilibrium-models of evolutionary species-diversity and the number of empty niches. *The American Naturalist*, 124, 887–899.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.
- Weir, J. T., & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, 315, 1574–1576.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213.
- Wiens, J. J. (2011). The causes of species richness patterns across space, time, and clades and the role of ecological limits. *Quarterly Review of Biology*, 86, 75–96.
- Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, 19, 639–644.
- Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, 36, 519–539.
- Wiens, J. J., Pyron, R. A., & Moen, D. S. (2011). Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecology Letters*, 14, 643–652.
- Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy*, 30, 3–35.
- Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, 41, 496–506.
- Zhao, M. S., Heinsch, F. A., Nemani, R. R., & Running, S. W. (2005). Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment*, 95, 164–176.

BIOSKETCHES

ANTONIN MACHAC studies the ecology of diversification. His research integrates phylogenies, maps and species traits.

CATHERINE GRAHAM is interested in macroecology and community ecology, particularly integrating theories and tools from different disciplines to evaluate the mechanisms that generate and maintain diversity.

DAVID STORCH is interested in macroecology and ecological theory, with particular focus on spatial diversity patterns, geometry of species distributions and diversity dynamics.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Machac A, Graham CH, Storch D. Ecological controls of mammalian diversification vary with phylogenetic scale. *Global Ecol Biogeogr*. 2018;27:32–46. <https://doi.org/10.1111/geb.12642>