

## LETTER

# Assessing the causes of diversification slowdowns: temperature-dependent and diversity-dependent models receive equivalent support

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### Abstract

Diversification rates vary over time, yet the factors driving these variations remain unclear. Temporal declines in speciation rates have often been interpreted as the effect of ecological limits, competition, and diversity dependence, emphasising the role of biotic factors. Abiotic factors, such as climate change, are also supposed to have affected diversification rates over geological time scales, yet direct tests of these presumed effects have mainly been limited to few clades well represented in the fossil record. If warmer climatic periods have sustained faster speciation, this could explain slowdowns in speciation during the Cenozoic climate cooling. Here, we apply state-of-the-art diversity-dependent and temperature-dependent phylogenetic models of diversification to 218 tetrapod families, along with constant rate and time-dependent models. We confirm the prevalence of diversification slowdowns, and find as much support for temperature-dependent than diversity-dependent models. These results call for a better integration of these two processes in studies of diversification dynamics.

### Keywords

Birth-death models, climate change, ecological limits, macroevolution, metabolic theory of biodiversity, paleoclimate, speciation, tetrapods.

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## INTRODUCTION

Understanding how and why speciation and extinction rates vary during the evolutionary history of clades is fundamental for deciphering the temporal dynamics of biodiversity. The development of models for estimating how diversification (speciation and extinction) unfolds using phylogenies of extant taxa has considerably expanded in the last decade (Stadler 2013; Morlon 2014; Herrera-Alsina *et al.* 2019; Maliet *et al.* 2019), and several multi-phylogeny analyses have attempted to identify general principles of diversification using these models (McPeck 2008; Morlon *et al.* 2010; Hedges *et al.* 2015; Lewitus & Morlon 2016). One of the most pervasive principles is the tendency for diversification to slow down as evolution proceeds (McPeck 2008; Phillimore & Price 2008; Morlon *et al.* 2010; Moen & Morlon 2014). Such diversification slowdowns have often been interpreted as the effect of competition for resources or niche availability (McPeck 2008; Phillimore & Price 2008; Glor 2010; Moen & Morlon 2014), spurring the development of models accounting for biotic effects, such as diversity-dependent models (Rabosky & Lovette 2008; Etienne *et al.* 2012a).

In comparison, phylogenetic models of diversification directly accounting for environmental changes have been

developed only recently (Condamine *et al.* 2013; Cantalapiedra *et al.* 2014), and they have only been applied to few empirical studies (Condamine *et al.* 2015a; Kergoat *et al.* 2018; Lewitus *et al.* 2018). Most studies have only done so relying on visual inspections of phylogenies in parallel to paleoenvironmental curves or with simple birth–death models (Winkler *et al.* 2009; Condamine *et al.* 2012). As a result, we still know little about the role of abiotic factors in driving macroevolutionary dynamics, in particular for groups lacking a comprehensive fossil record (Benton 2009; Ezard *et al.* 2011, 2016). This is a major gap, given that paleontological studies have suggested a prominent effect of environmental changes on diversification, for example, by generating bursts of speciation (Jaramillo *et al.* 2006; Peters 2008; Erwin 2009; Hannisdal & Peters 2011; Mayhew *et al.* 2012). This important role of environmental changes tends to be confirmed by the few phylogenetic studies that have explicitly tested for such an effect: significant support has been found for various types of environmental effects like variations in sea level,  $\delta^{13}\text{C}$  and  $\text{CO}_2$ , or temperature (Condamine *et al.* 2015a; Kergoat *et al.* 2018; Lewitus *et al.* 2018).

Among the various abiotic variables that may have influenced diversification, temperature is one of the most likely. Global temperatures have substantially varied during Earth's

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history (Zachos *et al.* 2001; Prokoph *et al.* 2008), and these past climatic changes are thought to have played a major role in determining the fate of clades (Jaramillo *et al.* 2006; Erwin 2009; Ezard *et al.* 2011; Hannisdal & Peters 2011; Condamine *et al.* 2012; Mayhew *et al.* 2012). For example, during the climatic fluctuations of the Carboniferous, cooling events have provoked the fragmentation of large rainforest ecosystems into small refuges, decimating amphibian clades, and spurring the evolution of 'reptiles' (Sahney *et al.* 2010). Similarly, Cenozoic climatic changes had a strong influence on Neotropical plant diversity (Jaramillo *et al.* 2006) and macroperforate planktonic foraminifera (Ezard *et al.* 2011). Present-day biodiversity patterns also suggest an important effect of temperature on diversification rates: species richness is typically higher in warm areas such as the tropics than in cold areas such as the Northern Hemisphere (Gaston 2000), which, provided present-day richness reflects past diversification events rather than current ecological constraints, suggests that diversification rates are higher under warm climates. Phylogenetic analyses have indeed found higher speciation rates in the tropics (Condamine *et al.* 2012; Pyron & Wiens 2013; Rolland *et al.* 2014), although there are exceptions (Weir & Schluter 2007; Schluter & Pennell 2017).

There are four main (non-exclusive and intertwined) processes by which temperature can influence diversification rates. The first is linked to the idea that diversification rates are influenced by resource availability (ecological niche filling) and that resource availability is increased under warm and productive environments (Clarke & Gaston 2006). This 'productivity' effect predicts a relationship with temperature that is positive for speciation, and negative for extinction rates. The second is linked to the idea that diversification rates are influenced by temporal and geographic climatic heterogeneities, which are typically higher during cold geological periods (Pound & Salzmann 2017; Li *et al.* 2018; Rangel *et al.* 2018). Both types of climatic heterogeneity can spur speciation through climatic niche divergent selection (Lawson & Weir 2014), however temporal heterogeneity can instead limit niche partitioning and speciation (Dynesius & Jansson 2000). Climatic heterogeneity may also increase extinction rates (Sandel *et al.* 2011). This 'heterogeneity' effect thus predicts a relationship with temperature that is either negative or positive for speciation, and positive for extinction rates. The third process is related to Bergman's rule: endotherms evolve smaller body sizes under warm climates, as they do not need to maintain a low surface to volume ratio in order to reduce energetic loss (Smith *et al.* 2010). As small organisms generally have fast generation times and large population sizes (Gillooly *et al.* 2001), which spurs speciation and prevents extinction (Etienne *et al.* 2012b), this 'body-size' effect predicts a relationship with temperature that is positive for speciation, and negative for extinction rates, and that applies to only endotherms. Finally, ectotherms have higher mass-specific metabolic rates under warm climates following Kleiber's law (Makarieva *et al.* 2008), which can increase mutation rates (free radicals produced as a by-product of metabolism generate genetic damage, Gillooly *et al.* 2005) and, according to the Metabolic Theory of Biodiversity (MTB, Brown *et al.* 2004), ultimately affect diversification (Allen *et al.* 2006). This 'metabolic' effect

predicts a positive relationship between temperature and speciation, and applies to only ectotherms. If speciation rates are positively affected by increased temperature, as predicted by three of the aforementioned processes, this would lead to a decline in speciation rates during the Cenozoic climate cooling.

Here, we test whether and how past climatic variations have influenced the diversification of tetrapods, including endotherms and ectotherms. We compile a data set of 218 well-sampled species-level phylogenies covering more than half of tetrapod diversity and assess the relative support of a series of 26 models reflecting different hypotheses about diversification. These models assume either that speciation and/or extinction rates remain constant, that they vary through time, that they vary according to diversity-dependent processes with limits that are temperature-independent, or that they vary according to past temperature variations.

## MATERIAL AND METHODS

### Time-calibrated phylogenies

We compiled a data set of species-level time-calibrated tetrapod phylogenies from the literature, including family-level phylogenies that had at least 10 species and were at least 80% complete; for the less well-sampled squamates and amphibians, we included phylogenies that were at least 60% complete. For birds, we built a maximum clade credibility tree with 9993 species from the distributions of trees constructed on the Hackett backbone from Jetz *et al.* (2012). For mammals, we used the maximum clade credibility tree from Rolland *et al.* (2014), which was constructed from the most complete molecular mammalian tree to date, which comprises 5020 species (Bininda-Emonds *et al.* 2007; Kuhn *et al.* 2011). In addition, we used a phylogeny of 3309 amphibian species (Pyron & Wiens 2013) and one of 4161 squamate species (Pyron & Burbrink 2014), both of which were constructed with a supermatrix analysis of molecular data. Finally, we used a phylogeny of 233 species of turtles (Jaffe *et al.* 2011) and a completely sampled phylogeny of crocodiles (Oaks 2011). We did not divide these two phylogenies into family-level trees as this would have resulted in too small phylogenies. We removed the suborder Pleurodira from the turtle phylogeny as it was poorly sampled (sampling fraction = 0.25); we analysed the rest of the phylogeny (Cryptodira), which contained 213 species out of 248 (sampling fraction = 0.86). The phylogenies were constructed with various phylogenetic reconstruction techniques, described in each associated paper. These included Bayesian approaches with a pure-birth tree prior (for the birds, turtles and crocodiles), a supertree approach (mammals), and maximum-likelihood approaches (amphibians and squamates). In total, our data set comprised 218 species-level phylogenies covering half of tetrapod diversity (16 623 species out of *c.* 33 000 species); these phylogenies represented tetrapod families including birds (129 phylogenies covering a total of 9605 species, mean sampling fraction = 0.94), mammals (66, 4736 spp., 1), amphibians (10, 823 spp., 0.72), squamates (11, 1221 spp., 0.74), turtles (1, 213 spp., 0.86) and crocodiles (1, 25 spp., 1).

### Global temperature variations through time

In order to capture major trends in global climate change through time, we merged  $\Delta^{18}\text{O}$  data measured from benthic foraminifer shells preserved in oceanic sediments from Prokoph *et al.* (2008), Zachos *et al.* (2001, 2008), and Cramer *et al.* (2011). This allowed covering the last 500 Myrs, spanning the full time-range over which extant families have diversified. We converted the  $\Delta^{18}\text{O}$  data into temperature estimates using the traditional conversion  $T = 16.5 - 4.3\Delta^{18}\text{O} + 0.14(\Delta^{18}\text{O})^2$  (Epstein *et al.* 1953). We then interpolated these data into a continuous estimate of temperature through time (details below). While each individual data point is subject to certain biases (e.g. some of them don't account for sea-level fluctuations which are important during periods of large-scale glaciations, Cramer *et al.* 2011), the interpolated curve smoothens such biases, as well as geographical variations, providing a reliable estimate of global temperature trends (Veizer & Prokoph 2015). The resulting temperature curves reflect planetary-scale climatic trends that can be expected to have led to temporally coordinated diversification changes in several clades rather than local or seasonal fluctuations (Erwin 2009; Hannisdal & Peters 2011; Mayhew *et al.* 2012).

### Diversification models in a maximum-likelihood framework

We fitted 26 diversification models to each of the 218 phylogenies (Table 1). These models are birth–death models of

cladogenesis, representing speciation and extinction events, which can be fitted to reconstructed phylogenies using maximum likelihood (Stadler 2013; Morlon 2014). We considered models with diversification rates that are constant (2 models), time-varying (8 models), diversity-dependent (4 models), and temperature-dependent (12 models). These models were fitted by maximum likelihood using the *dd\_ML* function from the R-package DDD 3.7 (Etienne *et al.* 2012a), and the *fit\_bd* (for the time-constant and time-varying models) and *fit\_env* functions (for the temperature-dependent models) from the R-package RPANDA 1.1 (Morlon *et al.* 2016). We accounted for missing species by specifying the total number of known species (for diversity-dependent models) or the sampling fraction (for the other models) corresponding to each phylogeny. We used the ‘crown’ condition, which conditions the likelihood on a speciation event at the crown age and survival of the two daughter lineages.

In the time-dependent models, speciation rates  $\lambda$ , extinction rates  $\mu$ , or both varied as a continuous function of time  $t$  (Table 1, Morlon *et al.* 2011), where  $t$  is written from the present to the past. We took this function to be either linear ( $\lambda(t) = \lambda_0 + \alpha t$  and/or  $\mu(t) = \mu_0 + \beta t$ ) or exponential ( $\lambda(t) = \lambda_0 \times e^{\alpha t}$  and/or  $\mu(t) = \mu_0 \times e^{\beta t}$ ) where  $\lambda_0$  ( $\mu_0$ ) is the speciation (extinction) rate at present and  $\alpha$  ( $\beta$ ) measures the sign and rapidity of the time variation. A positive  $\alpha$  ( $\beta$ ) reflects a slowdown of speciation (extinction) towards the present, while a negative  $\alpha$  ( $\beta$ ) reflects a speed-up of speciation (extinction) towards the present.

**Table 1** Fit of all the diversification models applied to the 218 tetrapod phylogenies. The number of phylogenies best explained by each model is reported based on AICc values. MTB: form of temperature-dependency expected from the Metabolic Theory of Biodiversity. Results for diversity-dependent models (DDD) are shown only for the phylogenies for which the models converged (see numbers in parenthesis)

Type of model	Model description	Form of dependency	Model acronym	No. of phylogenies	% of the dataset
Constant-rate models	Constant speciation and constant extinction	–	BCST	60	28%
		–	BCSTDCST	1	
Time-dependent models	Speciation variable and no extinction	Linear	BTimeVar_LIN	12	18%
		Exponential	BTimeVar_EXPO	3	
	Speciation variable and constant extinction	Linear	BTimeVarDCST_LIN	1	
		Exponential	BTimeVarDCST_EXPO	0	
	Constant speciation and extinction variable	Linear	BCSTDTimeVar_LIN	3	
		Exponential	BCSTDTimeVar_EXPO	5	
Temperature-dependent models	Both speciation and extinction variable	Linear	BTimeVarDTimeVar_LIN	14	35%
		Exponential	BTimeVarDTimeVar_EXPO	2	
	Temperature-dependent speciation and no extinction	Linear	BTempVar_LIN	10	
		Exponential	BTempVar_EXPO	8	
		M.T.B.	BTempVar_MTB	32	
	Temperature-dependent speciation and constant extinction	Linear	BTempVarDCST_LIN	0	
		Exponential	BTempVarDCST_EXPO	0	
		M.T.B.	BTempVarDCST_MTB	2	
	Temperature-dependent extinction and constant speciation	Linear	BCSTDTempVar_LIN	3	
		Exponential	BCSTDTempVar_EXPO	1	
M.T.B.		BCSTDTempVar_MTB	0		
Temperature-dependent speciation and extinction	Linear	Linear	BTempVarDTempVar_LIN	9	
		Exponential	BTempVarDTempVar_EXPO	3	
	M.T.B.	Linear	BTempVarDTempVar_MTB	8	
		Exponential	BTempVarDTempVar_EXPO	3	
Diversity-dependent models	Diversity-dependent speciation and constant extinction	Linear (on 216 clades)	DDL + E	35	19%
		Exponential (on 217 clades)	DDX + E	2	
	Diversity-dependent extinction and constant speciation	Linear (on 175 clades)	DD + EL	1	
		Exponential (on 209 clades)	DD + EX	3	
				218	

In the diversity-dependent models, speciation rates or extinction rates vary as a function of the number of lineages in the clade (Etienne *et al.* 2012a). We took this function to be either linear or exponential, as explained in Etienne *et al.* (2012a). The diversity-dependent models are parameterised by  $\lambda_0$  ( $\mu_0$ ), the speciation (extinction) rate in the absence of competing lineage, and  $K$  that is referred to as the ‘carrying capacity’, and represents asymptotic clade size.

The temperature-dependent analyses are a direct application of the environment-dependent diversification models developed in Condamine *et al.* (2013, see Box 1 for a description) and thoroughly tested in Lewitus & Morlon (2018). These models extend time-dependent diversification models to account for potential dependencies between speciation and/or extinction rates and (one or several) measured environmental variable(s). The environmental data is first transformed into a continuous function of time by spline interpolation before being plugged into parametric functions describing how speciation and extinction rates vary with the environment. Here, we used temperature data as the measured environmental variable and the default ‘NULL’ option for the degree of freedom (d.f.) to be used in the spline interpolation, which resulted in a d.f. of 66. In our temperature-dependent models, speciation rates, extinction rates, or both varied as a continuous function of temperature  $T$  (Table 1). We considered the same linear and exponential dependencies as above, but with  $t$  replaced by  $T$ . In this case,  $\lambda_0$  ( $\mu_0$ ) is the expected speciation (extinction) rate under a temperature of 0 °C and  $\alpha$  ( $\beta$ ) measures the sign and strength of the temperature dependence. A positive  $\alpha$  ( $\beta$ ) indicates that speciation (extinction) rates are higher under warm climatic periods, while a negative  $\alpha$  ( $\beta$ ) indicates that speciation (extinction) rates are higher under cold climatic periods. In addition, we considered a dependence of the form  $\lambda(T) = \lambda_0 \times e^{\alpha T}$  and/or  $\mu(T) = \mu_0 \times e^{\beta T}$  inspired from predictions from the MTB (Allen *et al.* 2006), where  $\lambda_0$  ( $\mu_0$ ) is the expected speciation (extinction) rate under an arbitrarily high temperature and a positive  $\alpha$  ( $\beta$ ) indicates that speciation (extinction) rates are higher under warm climatic periods, while a negative  $\alpha$  ( $\beta$ ) indicates that speciation (extinction) rates are higher under cold climatic periods.

We fitted each of the 26 models to each phylogeny by maximum likelihood, starting from the simplest (constant rate) models and progressively increasing in complexity. The maximum-likelihood algorithm optimises parameter values (of  $\lambda_0$ ,  $\mu_0$ ,  $\alpha$  and/or  $\beta$ , or  $K$ ) that maximise the probability of the observed data (the phylogenetic tree) under a given model. Because these optimisation algorithms can be sensitive to the choice of initial parameter values (they can converge to local optima in the vicinity of the initial parameter values), we informed the initial parameter values of more complex models by those previously estimated on simpler models. There were few cases when one or several diversity-dependent models did not converge; in this case, we excluded the model(s) from the analyses (see details in Table 1 and Table S3).

We used the corrected Akaike Information Criterion (AICc), the  $\Delta$ AIC and the Akaike weight (AIC $\omega$ ) to compare the likelihood support of the different models. Because the  $\Delta$ AIC threshold used to assess confidence in model selection (typically 2) is arbitrary, we also carried a simulation

procedure inspired from Etienne *et al.* (2016): for each phylogeny, we simulated 120 trees under the second best model (with parameters estimated from the fit to the empirical phylogeny), fitted the first and second best models to these trees, and compared the empirical  $\Delta$ AIC to the distribution of  $\Delta$ AICs obtained on the simulated data.

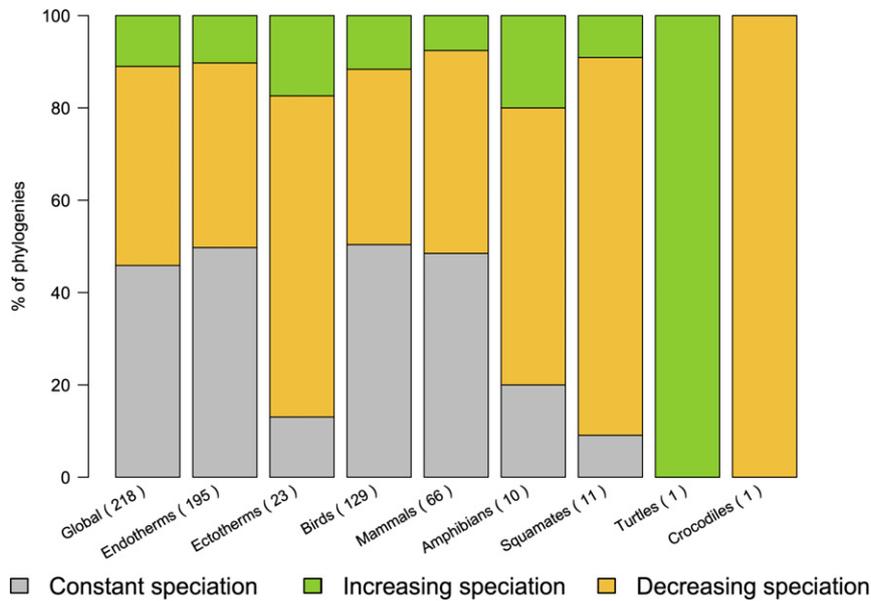
### Analysing tetrapod diversification

We first analysed the temporal trend in diversification rates by considering only models with constant or time-varying diversification rates. We identified (based on AICc values) phylogenies that supported constant, increasing, and decreasing speciation rates through time (and also carried out the same analyses for extinction rates). Next, we analysed how much temperature variations and diversity-dependence explain these temporal trends by considering all models and identifying phylogenies that supported constant, time-dependent, diversity-dependent or temperature-dependent speciation rates (respectively extinction rates). The number of models in each model category (i.e. constant, time-dependent, diversity-dependent and temperature-dependent) is not the same, which can bias support towards categories represented by more models. In order to limit this potential issue, we followed the approach used in Morlon *et al.* (2010) and first selected the best supported model in each of the four categories and computed their relative AIC $\omega$ . We also computed the  $\Delta$ AIC between the best and second best of these four models, and assessed its significance using the simulation procedure described above. For phylogenies supporting a temperature-dependent model, we tested whether specificities of the environmental curve matter for statistical support. Following Clavel & Morlon (2017), we smoothed the temperature curve using a d.f. of 3 in the spline interpolation, which kept the overall declining trend while removing finer features of the curve. We then compared AIC values obtained when the temperature curve is smoothed to the original values; we also assessed if the temperature model was still supported when smoothing the curve.

## RESULTS

### Testing if and how diversification rates vary through time

Of the 218 tetrapod phylogenies, 119 (55%) supported models with a speciation rate that varies through time (Fig. 1, Table S1); this number increased to 71% when we considered only phylogenies with more than 50 species (Fig. S1, Table S2). Of these, 80% (89% of the phylogenies with more than 50 species) supported decreasing speciation towards the present (Fig. 1, Fig. S1). 27% (44%) of the phylogenies supported models with an extinction rate that varies through time, of which 62% (70%) supported increasing extinction towards the present (Fig. S2, Table S1). The trend was consistent across endotherms versus ectotherms, and across tetrapod groups. When time-dependence was supported in speciation rates, extinction rates, or both, 71% (78%) of the phylogenies had a linear trend of speciation, and 21% (13%) had an exponential trend of speciation, while 46% (45%) of the



**Figure 1** Time-dependency of speciation rates across tetrapods. The histograms report, for all groups together (Global) and for specific sub-groups, the percentage of phylogenies best supported by a model with speciation rates that are constant (in grey, 45% of the phylogenies, i.e. 99 clades) or vary through time (in yellow and green, 55% of the phylogenies, i.e. 119 clades). Among those that support time dependency (119), speciation rates are decreasing towards the present in 80% of the phylogenies (in yellow, i.e. 95 clades) and increasing in 20% of the phylogenies (in green, i.e. 24 clades). Numbers in parentheses indicate the number of phylogenies in each group.

phylogenies had a linear trend of extinction, and 9% (10%) had an exponential trend of extinction (Fig. S2, Tables S1 and S2).

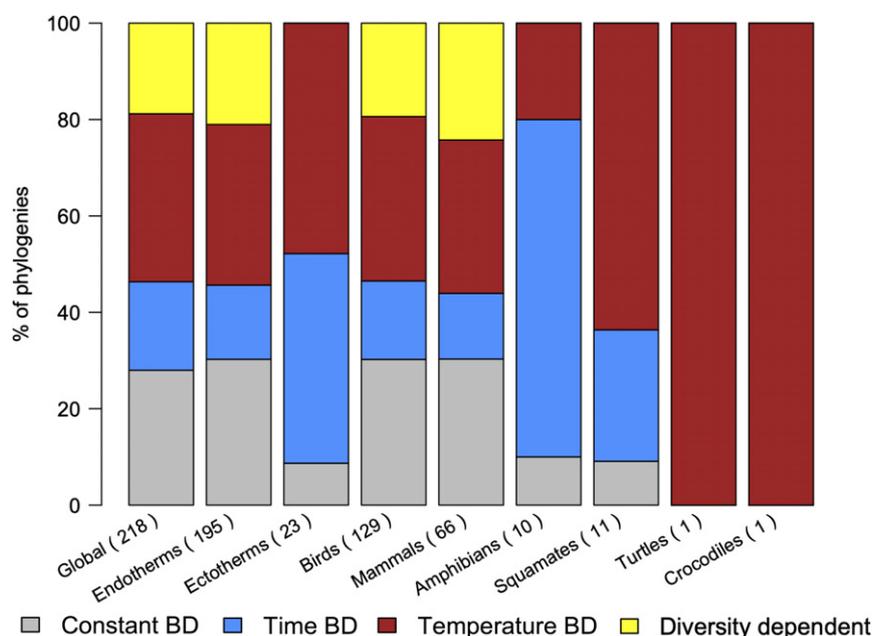
#### Testing support for temperature-dependent and diversity-dependent models

Next, we compared the fit of all 26 diversification models (constant-rate, time-dependent, diversity-dependent and temperature-dependent models) to determine which model better explains the diversification of each phylogeny (Table S4). We found that models including variation in the diversification rates (either time-dependent, temperature-dependent or diversity-dependent models) outperformed models with constant-rate diversification in 72% of the phylogenies (157 of 218, Fig. 2, Table 1); this number increased to 86% when considering only phylogenies with more than 50 species (Fig. S3, Table S3). Temperature-dependent models better explained diversification in 35% of the phylogenies (44% of the phylogenies with more than 50 species), time-dependent models in 18% (29%), and diversity-dependent models in 19% (13%). When we excluded models with no extinction from the model selection procedure, we still found a significant proportion of phylogenies that supported temperature-dependence (Table S5). We found that temperature-dependence was supported in all tetrapod groups: the best-fit model was a temperature-dependent model in 34% of the families for birds, 32% for mammals, 20% for amphibians and 64% for squamates, and it was a temperature-dependent model for the crocodiles and the turtles. When a given model was selected among the 26, its strength of support was very variable (AIC $\omega$  ranging from 0.09 to 1, with

a mean of 0.28; Table S4), but always above the 0.038 weight (1/26) that would be expected if all models were equally likely. When a type of model was selected among the four main types (constant, time-dependent, diversity-dependent, or temperature-dependent), its strength of support was reasonably high (mean AIC $\omega$  of 0.48 for constant-rate models, 0.52 for time-dependent models, 0.59 for diversity-dependent models, and 0.56 for temperature-dependent models), in general above the 0.25 (1/4) weight that would be expected if constant, time-dependent, diversity-dependent and temperature-dependent rate models were equally likely (Fig. 3; Fig. S4). Still, the  $\Delta$ AIC between the best and second best model was often below the threshold of 2 that is typically chosen to distinguish models with certainty (Fig. 3; Fig. S5), and our simulations analyses confirmed that it was not enough to distinguish the best and second best model with confidence (Fig. S6).

#### Temperature-dependent diversification

When a temperature-dependent diversification model was selected (which was the case in 76 of the 218 phylogenies), temperature-dependence affected only speciation in 68%, only extinction in 5%, and both speciation and extinction in 26% of the clades. Of the 72 families where speciation was inferred to vary with temperature, most (68) had speciation rates that depended positively on temperature (Fig. 4; Figs S7 and S8), and of the 24 families where extinction was inferred to vary with temperature, around two-third (16) had extinction rates that depended positively on temperature (Figs S9 and S10). This trend of faster speciation and extinction during warm geological periods was



**Figure 2** Temperature-dependency of speciation rates across tetrapods. The histograms report, for all groups together (Global) and for specific sub-groups, the percentage of phylogenies best supported by a model with speciation rates that are constant (in grey, 28% of the phylogenies), time-dependent (in blue, 18% of the phylogenies), diversity-dependent (in yellow, 19% of the phylogenies), or temperature-dependent (in red, 35% of the phylogenies). 30 of the 99 phylogenies that were better supported by time-constant than time-variable speciation models in Fig. 1 are even better supported either by temperature-dependent speciation models (20 of the phylogenies), or diversity-dependent speciation models (10 of the phylogenies). 87 of the 119 phylogenies that were better supported by time-variable than rate-constant models in Fig. 1 are even better supported either by temperature-dependent speciation models (56 of the phylogenies), or diversity-dependent speciation models (31 of the phylogenies). Numbers in parentheses indicate the number of phylogenies in each group.

consistent across endotherms versus ectotherms, and across tetrapod groups (Fig. 4; Fig. S7). Of the 76 phylogenies where temperature-dependence was supported (43 phylogenies with more than 50 species), 55% (44%) supported a variation of the MTB form, 29% (42%) of the linear form and the remaining 16% (14%) of the exponential form (Figs S11 and S12). Smoothing the temperature curve strongly decreased the support for temperature-dependent models (Fig. S13a) to the point where it was lost (Fig. S13b), showing that the support for temperature-dependent models was not simply due to a temporal trend in diversification rates potentially unlinked to temperature.

A positive dependence of speciation to past temperatures indicates that speciation rates tend to be higher under warm climates. If this dependency operates consistently throughout the history of clades, the warm Cretaceous, early Eocene, late Oligocene and middle Miocene are expected to be periods of frequent speciation in comparison with the cool latest Cretaceous-Paleocene, late Eocene-early Oligocene, early Miocene, and the last 12 Myrs (late Miocene until the present) (Fig. 5). The overall trend for global climatic cooling during the Cenozoic leads to a slowdown in speciation towards the present.

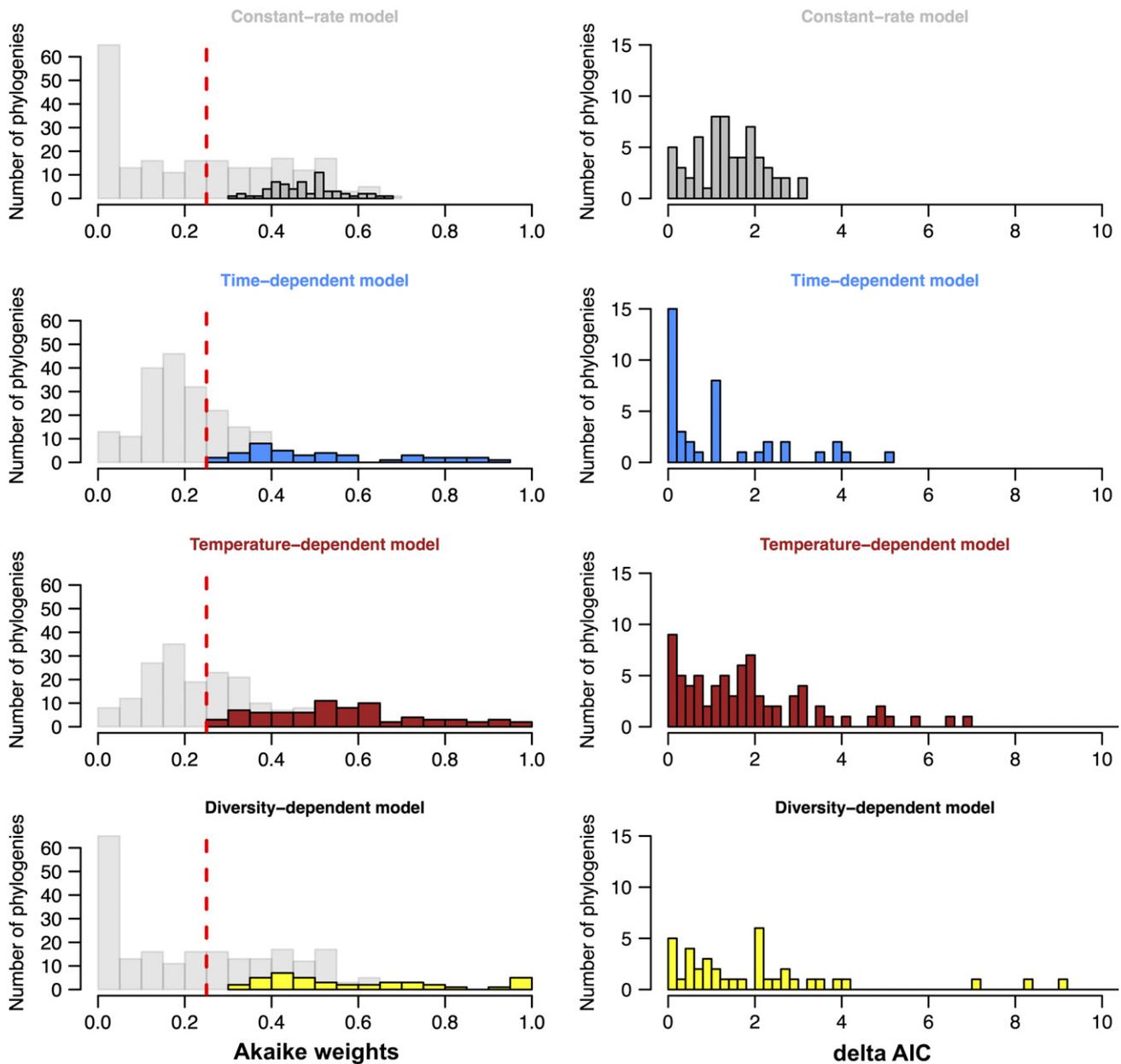
## DISCUSSION

Our multi-phylogeny analysis of tetrapods, combined with birth-death diversification models, confirms that diversification rates declined through the Cenozoic. Our analysis further reveals a potentially important role of past climates in driving

these slowdowns, although it also illustrates the difficulty of conclusively supporting either temperature-dependent or diversity-dependent models. These results have important consequences for our understanding of the processes that have shaped the macroevolutionary dynamics of clades and current diversity patterns, as well as for discussing the future of biodiversity in the context of current environmental changes.

### Diversification slowdowns and global cooling

Consistent with previous studies, we found a general trend for a slowdown in speciation rate through time across clades (McPeck 2008; Phillimore & Price 2008; Morlon *et al.* 2010). Models with a decrease of speciation rate through time have often been used as an approximation to diversity-dependent models, and interpreted as evidence of ‘niche-filling’ processes, including competition for limited resources (Pigot & Tobias 2013), adaptive radiations (Glor 2010) and potential ecological limits on the number of species within a clade (Phillimore & Price 2008; Rabosky 2013). If we had made this approximation, without considering more mechanistic truly diversity-dependent or temperature-dependent models, we would have concluded that 43% of the phylogenies support diversity-dependence. However only 18% truly support diversity-dependent models when compared to time- and temperature-dependent ones. Therefore, our results caution against comparing constant-rate models with only time-dependent models and interpreting speciation slowdowns as niche filling processes (Moen & Morlon 2014; Aristide & Morlon 2019). A

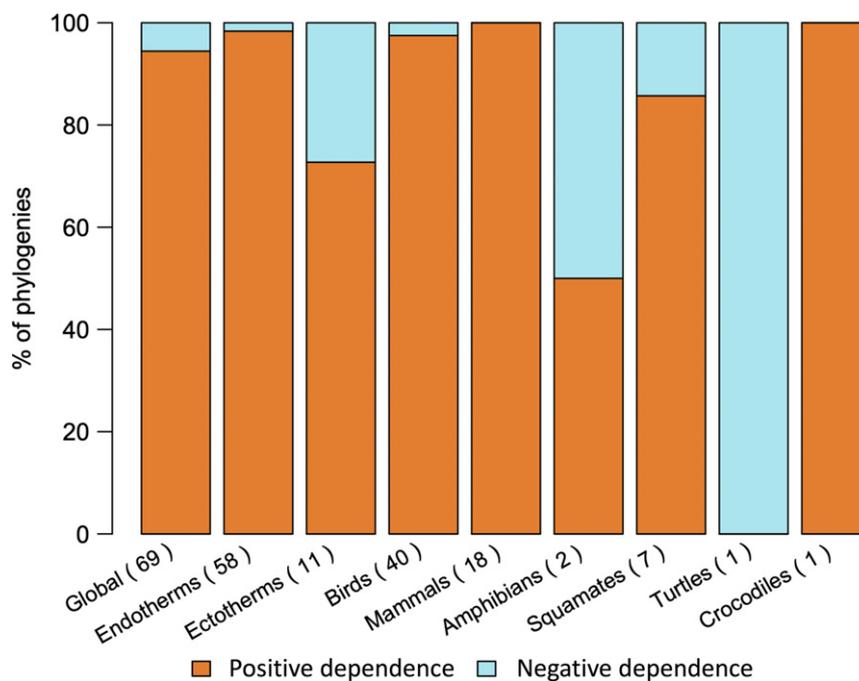


**Figure 3** Strength of support for constant, time-dependent, temperature-dependent and diversity-dependent models when they are selected. Distribution of AIC weights (left) and  $\Delta$ AIC (right) for phylogenies best supported by a constant rate (top row, dark grey), time-dependent (blue), temperature-dependent (red), and diversity-dependent model (yellow). These were computed by comparing only the best model in each of the four model categories. On the left, in light grey, distributions of AICw for the corresponding model and all the phylogenies (i.e. not just those best supported by the model) are given for comparison. The red dotted line corresponds to the expected AICw if the four models were equally likely (AICw = 0.25). Few phylogenies support a given model decisively (for example with  $\Delta$ AIC > 2 and high AICw), yet the strength of support is higher than if all the models were equally likely (AICw > 0.25).

little less than a quarter (23%) of phylogenies supporting a speciation slowdown were indeed explained by diversity-dependence, but more than half (52%) were in fact better supported by models with a positive dependence of speciation rate on temperature, while the rest were explained by neither one nor the other.

Although it is difficult to discriminate the different models with confidence, temperature-dependence finds at least as much support as diversity-dependence. Most phylogenies (89%) supporting temperature-dependent speciation suggest

that speciation rates have been higher during warm geological periods, consistent with temporal trends observed in the fossil record (Jaramillo *et al.* 2006; Erwin 2009; Mayhew *et al.* 2012; Huang *et al.* 2014) and latitudinal trend in speciation rates (Condamine *et al.* 2012; Pyron & Wiens 2013; Rolland *et al.* 2014, but see Weir & Schluter 2007; Schluter & Pennell 2017). If speciation rates are positively correlated with temperature, then the global climatic cooling of the Cenozoic would result in coordinated slowdowns in speciation rates across clades. Thus, at least part of the diversification-rate



**Figure 4** Speciation rates are positively associated with temperature across tetrapods. The histograms report, for all groups together (Global) and for specific sub-groups, the percentage of phylogenies, among those that support temperature dependency, where the dependency is positive (in orange) versus negative (in blue). Most of the phylogenies (89%) support a positive relationship between temperature and speciation. Numbers in parentheses indicate the number of phylogenies in each group. The number of phylogenies supporting a temperature-dependent model on speciation rate are displayed for each group.

slowdowns widely described in the literature may be linked to global climatic cooling.

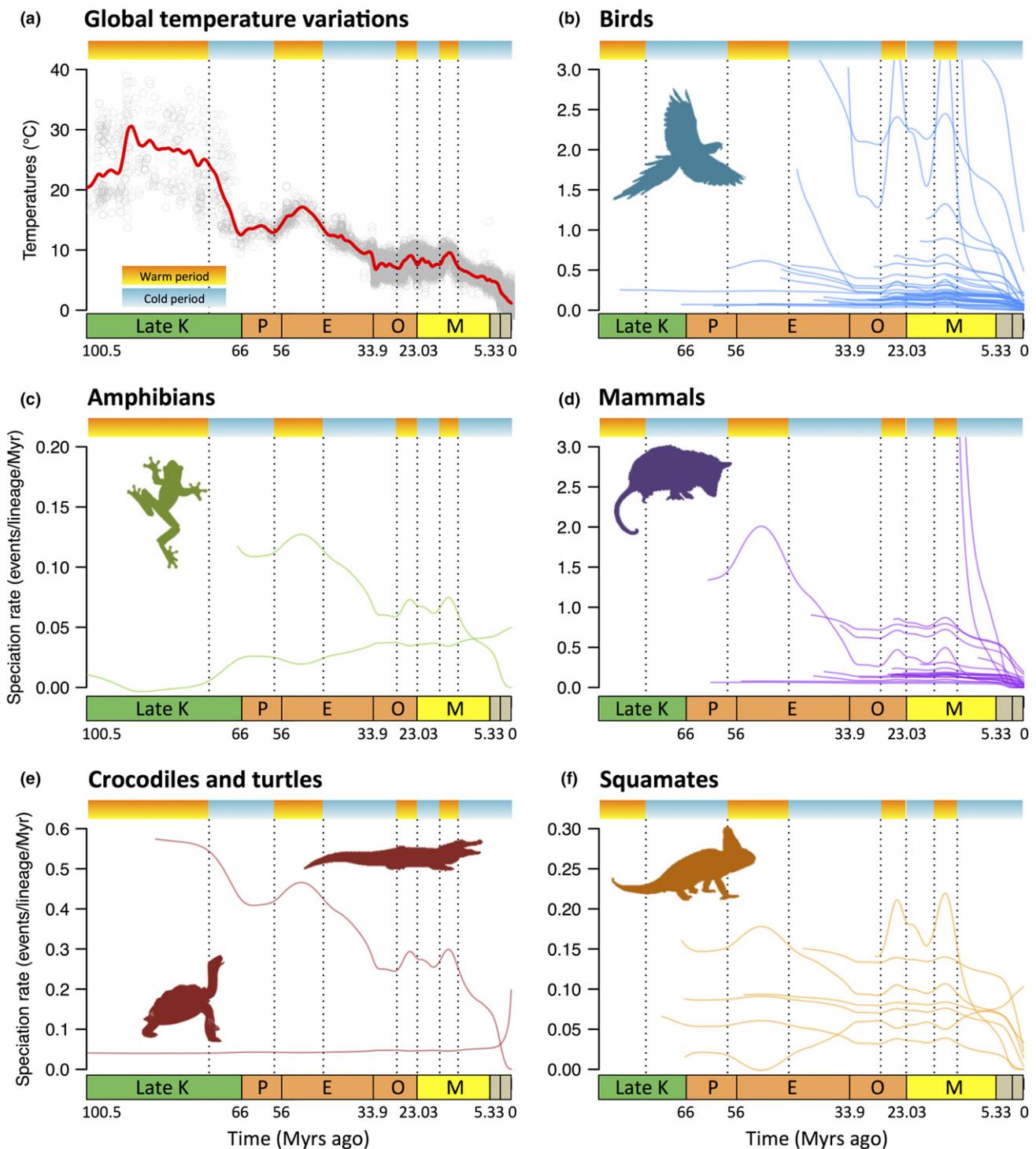
#### Explanatory hypotheses

Temperature may influence speciation rates through niche-filling processes, following the ‘productivity’ hypothesis. Warm geological periods are typically also periods of high global productivity, potentially able to sustain a greater number of ecological niches (Bains *et al.* 2000; Mayhew *et al.* 2012). Temperature could thus influence speciation rates through its effect on carrying capacity. Temperature could also positively affect speciation rates through the effect of temporal climatic stability on niche partitioning (Dynesius & Jansson 2000). The two other main hypotheses coherent with a positive relationship between temperature and speciation rates are the ‘body-size’ and the ‘metabolic’ hypotheses. The ‘body-size’ hypothesis (organisms evolve smaller body sizes under warm climates) should affect only endotherms, while the ‘metabolic’ hypothesis (organisms have faster metabolic rates under warm climates) should affect only ectotherms (Gillooly *et al.* 2001, 2005). We found similar trends for endothermic and ectothermic clades suggesting either that the body size and metabolic hypotheses do not apply and that other processes independent of thermoregulation are at play, or that the two processes operate in concert but on different clades. The fact that more than half (55%) of the phylogenies best fitted by a temperature-dependent model supports the form of temperature-dependence inspired from the MTB indicates that metabolic effects may play a role, although

such supports occurred in both ectotherms and endotherms. Refined tests of these hypotheses could be envisioned in the future, for example by examining whether endothermic clades supporting a positive association between temperature and speciation rates indeed evolved smaller body sizes under warm climates. More generally, in order to disentangle the effects of temperature mediated by niche-filling processes from other effects (linked to climatic heterogeneity, body size, and/or metabolism), we could envision developing diversity-dependent models with either the carrying capacity  $K$ , the parameter controlling the magnitude of the rate change as a function of the number of lineages, or both, varying as a function of past climates.

We do not discuss at length our results on extinction, as temperature-dependent extinction is difficult to estimate (Lewitus & Morlon 2018). With this warning in mind, in families supporting an effect of temperature on extinction, we found higher extinction rates under warm climates, which is in line with some paleontological evidence (Sun *et al.* 2012). None of the productivity, heterogeneity, body size and metabolic hypotheses (as formulated above) predict such a positive relationship between temperature and extinction rates. There is a possibility that higher mutation rates under warm climates lead to the accumulation of deleterious mutations favouring extinction, and/or that newly arising lineages – given more frequent speciation – impose a stronger competitive pressure on co-occurring species.

When temperature-dependent models were supported, we generally found a positive association between temperature and speciation. Previous studies have found a negative



**Figure 5** Speciation rates of tetrapods tend to decline towards the present as a result of climatic cooling. The curves represent the speciation rate of each of the 76 tetrapod families supporting a temperature-dependent speciation model, as estimated by the best-fit temperature-dependent model. Results are similar across endotherms and ectotherms. A colour pattern at the top of each panel indicates the succession of past warm and cool periods previously identified (e.g. Zachos *et al.* 2001, 2008; Veizer & Prokoph 2015), based on a sustained increase or decrease in Earth's average temperature relative to the preceding and succeeding periods. A geological time scale at the bottom indicates the geological periods. Abbreviations: K: Cretaceous, P: Paleocene, E: Eocene, O: Oligocene, M: Miocene (the two last periods, Pliocene and Pleistocene, are shown but not labelled), and Myrs ago: million years ago.

association between temperature and rates of phenotypic evolution (Clavel & Morlon 2017). This is counterintuitive, because several verbal evolutionary theories implicitly assume a coupling between rates of speciation and phenotypic

evolution, such as in the theories of adaptive radiation (Schluter 2000) and punctuated equilibrium (Gould & Eldredge 1977). However, there is increasing empirical (Adams *et al.* 2009; Cantalapiedra *et al.* 2017) and theoretical (Aristide &

Morlon 2019) evidence that this coupling might not be so straightforward. Developing a model where both diversification and phenotypic evolution are influenced by competition for limited resources, Aristide & Morlon (2019) found that niche packing limits speciation and increases extinctions rates, but does not reduce trait evolutionary rates, as frequent extinctions free up ecological space that is rapidly reoccupied. If such a model applies in nature, with increased availability of resources under warm climates, we expect that speciation rates will be lower during low productivity, cool geological periods, but that this will not impact trait evolutionary rates. Rather, trait evolutionary rates will be increased given higher competitive pressure and more opportunities for divergent climatic niche evolution. These expectations could be tested in the future by explicitly incorporating temperature variations in such a model.

### Limitations

Our results suggest that phylogenetic data alone might be insufficient to distinguish with confidence even simple models such as the diversity-dependent and temperature-dependent models. The power to distinguish temperature-dependency from time-dependency increases with tree size (Lewitus & Morlon 2018), and we can expect the same for diversity-dependent models. Ultimately however, the best would be to integrate temperature- and diversity-dependencies in current approaches that combine phylogenetic and fossil data (Heath *et al.* 2014; Silvestro *et al.* 2018).

There are other potential limitations to our analyses, but we do not expect that they would induce a systematic bias towards artificially supporting temperature or diversity dependence. For example, when Bayesian techniques are used for phylogenetic construction (here in birds, turtles and crocodiles), the choice of branching process prior can have important effects on the reconstructed trees and downstream diversification analyses (Condamine *et al.* 2015b; Janzen & Etienne 2017). However, our tree compilation covered a variety of techniques, not only Bayesian ones. Bayesian trees built with a pure-birth prior would tend to favour constant-rate models with no extinction, and not time-dependent, temperature-dependent, or diversity-dependent models. Also, in order to account for missing extant species in the phylogenies, we used diversification models that assume species represented in each phylogeny are uniformly drawn (i.e. randomly drawn with equal probability) in the entire clade, which can bias diversification analyses (Cusimano & Renner 2010; Höhna *et al.* 2011). There is, however, no reason to believe that this would favour a given model versus others.

Finally, the sampling scheme currently implemented in diversity-dependent models assumes that exactly  $n$  species are sampled ( $n$ -sampling), while the other models assume that each species is sampled with a fixed probability ( $\rho$ -sampling), and likelihoods associated to these two sampling schemes are not directly comparable (Stadler 2009; Lambert 2017). While we do not exclude that this might introduce biases, we expect these biases to be small because our phylogenies are overall well sampled. Recent derivations of likelihoods for diversity-dependent models with  $\rho$ -sampling

(Laudanno *et al.* 2019) should allow more consistent comparisons of diversity-dependent *versus* other models in future empirical analyses.

### Past vs. current climatic changes

Current human-driven environmental changes are different from environmental changes that happened in the past (Barnosky *et al.* 2011; Zeebe *et al.* 2016), and therefore could have different consequences on diversification. In particular, the positive association between past speciation rates and temperature suggested here may not hold today. In addition, there could be an effect of the rate of change in temperature along with temperature itself, and this rate is faster today than in the past. We can nevertheless discuss how current environmental changes may affect biodiversity in the future in light of how they affected biodiversity in the past (Barnosky *et al.* 2011; Harnik *et al.* 2012; Condamine *et al.* 2013). If the rate at which new species arise is indeed positively correlated with temperature, we may expect that current global warming will accelerate the generation of new species. This potential effect of climate might be enhanced by other human-driven factors, such as the creation of new environments, selection pressures, and opportunities of hybrid and artificial speciation, or instead counterbalanced by a reduction of the natural habitat that would affect demographic processes impacting speciation (Schluter & Pennell 2017). In addition, if the rate at which species go extinct is indeed positively correlated with temperature, we may expect that current global warming will accelerate the pace of species extinction. Climate-related local extinctions, a prelude to species extinctions, have already occurred in a wide range of species surveyed in various climatic zones, habitats, and groups of organisms (Wiens 2016). Clearly much more work is needed before we can predict how human-driven climate change will affect speciation and extinction.

### Conclusions

Temperature influences biological processes through its effects on productivity, climatic niche divergence, body size and metabolic rates. Our study suggests that the effect of temperature extends to the macroevolutionary scale by modulating the pace of speciation. In a large proportion of tetrapods, warm climates were favourable to speciation, suggesting that the slowdown in speciation widely documented across diverse clades and often interpreted as the signal of adaptive radiations may, in some cases at least, be related to global climate cooling in the Cenozoic. The mechanisms by which temperature modulates the pace of diversification remain unclear. We hope that our study will foster research in this direction, as well as a more systematic account of past environmental changes in diversification analyses.

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#### AUTHORSHIP

F.L.C. and H.M. conceived this study, F.L.C. and J.R. generated the phylogenetic data, F.L.C. and J.R. analysed the data, F.L.C., J.R. and H.M. wrote the paper. All authors discussed the results and provided input on the manuscript.

#### DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: <https://doi.org/10.6084/m9.figshare.9555842>.

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#### **SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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