

Temperature dependence of evolutionary diversification: differences between two contrasting model taxa support the metabolic theory of ecology

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Abstract

Biodiversity patterns are largely determined by variation of diversification rates across clades and geographic regions. Although there are multiple reasons for this variation, it has been hypothesized that metabolic rate is the crucial driver of diversification of evolutionary lineages. According to the metabolic theory of ecology (MTE), metabolic rate – and consequently speciation – is driven mainly by body size and environmental temperature. As environmental temperature affects metabolic rate in ecto- and endotherms differently, its impact on diversification rate should also differ between the two types of organisms. Employing two independent approaches, we analysed correlates of speciation rates and, ultimately, net diversification rates for two contrasting taxa: plethodontid salamanders and carnivoran mammals. Whereas in the ectothermic plethodontids speciation rates positively correlated with environmental temperature, in the endothermic carnivorans a reverse, negative correlation was detected. These findings comply with predictions of the MTE and suggest that similar geographic patterns of biodiversity across taxa (e.g. ecto- and endotherms) might have been generated by different ecological and evolutionary processes.

Introduction

Diversification of evolutionary lineages is an essential process largely responsible for the patterns of biological diversity across space and time (Ricklefs, 2007). Net diversification rates, defined as the difference between speciation rate and extinction rate, have been thoroughly studied only recently due to availability of well-resolved phylogenies. Numerous diversification-controlling factors have been identified, but it is still unclear which of them are the most relevant to explain current biodiversity patterns (Emerson & Kolm, 2005; Adams *et al.*, 2009; Rabosky, 2009a; Kozak & Wiens, 2010; Rabosky & Glor, 2010).

It has recently been suggested that the ultimate factor affecting speciation, diversification and, consequently, biodiversity patterns is the metabolic rate (Allen *et al.*, 2006). Advocates of the ‘metabolic theory of ecology’ (MTE) argue that metabolic rate, which is dependent mainly on body size and temperature, is responsible for all biological rates including mutation and then speciation rates (Brown *et al.*, 2004; Allen *et al.*, 2006). The MTE provides quantitative predictions concerning the effects of temperature and body size on speciation rates and the resulting biodiversity patterns (Allen *et al.*, 2002, 2007). These predictions received some support (Allen *et al.*, 2002; Wang *et al.*, 2009; Cassemiro & Diniz-Filho, 2010) and are generally in agreement with the common observation that most species indeed live in warm environments (Davies *et al.*, 2007; Sanders *et al.*, 2007; Fuhrman *et al.*, 2008; Tittensor *et al.*, 2010; Belmaker & Jetz, 2011; Simova *et al.*, 2011) and are small bodied (Storch & Gaston, 2004). However, other studies

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did not detect the predicted patterns (Algar *et al.*, 2007; Hawkins *et al.*, 2007), and it has turned out that most of the MTE's predictions concerning diversity patterns are very difficult to test due to many potentially confounding factors (e.g. the effect of population size on extinction probability) (Gillooly & Allen, 2007; Storch, 2012).

Still, there is one particular prediction that can be tested in a conveniently straightforward manner: if speciation rate and, consequently, net diversification rate is driven by the rate of metabolism, it will be affected by environmental temperature differently in ecto- and endothermic animals. Thus, ectotherms are expected to diversify more rapidly in warmer environments where their metabolic rates are accelerated. This should not apply to endotherms whose metabolic rates are effectively independent of environmental temperature. Although some differences between ecto- and endotherms have indeed been revealed (Allen *et al.*, 2002), this prediction has not yet been explicitly tested. Body size, in contrast, is expected to negatively correlate with speciation rates in both ecto- and endotherms (Brown *et al.*, 2004; Allen *et al.*, 2006, 2007) as mass-controlled metabolic rate decreases with body mass.

Herein, we explore the effect of body size and environmental temperature on speciation rate in two contrasting vertebrate taxa, ectothermic plethodontid salamanders (Amphibia: Plethodontidae) and endothermic carnivorans (Mammalia: Carnivora). Both groups are monophyletic with a few hundred extant species (cca. 420 vs. 264, respectively), both have wide geographic distribution (plethodontids in Americas and Eurasia, carnivorans in Eurasia, Africa and Americas), and both experienced widespread continental-scale dispersals (even the plethodontids, now mostly restricted to Americas, probably had a worldwide range 60–100 million years ago, leaving a few relict species in the Mediterranean and East Asian regions) (Min *et al.*, 2005; Vieites *et al.*, 2007; Eizirik *et al.*, 2010; Vieites *et al.*, 2011). Paleontologically, the plethodontids are even older than the carnivorans as the initial split within plethodontids occurred in the Late Cretaceous (Vieites *et al.*, 2007). During the two global warming periods (late Cretaceous and Paleocene-Eocene), the plethodontid salamanders experienced episodes of rapid lineage diversification (Vieites *et al.*, 2007, 2011; Pyron & Wiens, 2011). The latter, Paleocene–Eocene episode coincided with the basal diversification of the Carnivora (59 Mya) and their major subclades (49 Mya for Caniformia, 45 Mya for Feliformia) (Eizirik *et al.*, 2010). Both Plethodontidae and Carnivora, moreover, include speciose clades that were derived from recent and rapid radiations (e.g. *Plethodon*, *Desmognathus*; Canidae, Mustelidae, Herpestidae, Felidae).

We note that larger phylogenies along with distributional maps have been published recently (e.g. Bininda-Emonds

et al., 2007; Hoffmann *et al.*, 2010; Pyron & Wiens, 2011). However, these data sets suffer from being rather incomplete so that it is inherently difficult to judge whether the detected patterns are legitimate or mere artefacts resulting from a particular distribution of polytomies throughout the phylogeny, varying reliability of distributional maps across taxa, etc. (Hoffmann *et al.*, 2010; Boitani *et al.*, 2011; Collen *et al.*, 2011). Therefore, we used plethodontids and carnivorans with highly resolved evolutionary relationships and well-known distributions as our model taxa, which allowed us to draw less extensive but more reliable conclusions (Kozak & Wiens, 2010; Nyakatura & Bininda-Emonds, 2012). Indeed, results for these two model groups will also help generate questions and hypotheses for future research, once more accurate data sets for higher taxa are available.

To address our questions, we adopted two conceptually distinct methodologies: ancestral reconstructions and the QuaSSE approach. While the former approach consists in reconstruction of environmental niches and body sizes for ancestral species, the latter relies on life-history data of extant species. Despite their extensive use, methods of ancestral reconstruction may suffer from certain setbacks when applied to deeper nodes of a phylogeny (Schluter *et al.*, 1997) or when the reconstructed trait itself modulates diversification (Maddison, 2006). To circumvent these pitfalls, we employed the likelihood-based QuaSSE approach (Fitz-John, 2010) which has been specifically designed to uncover the relationships between traits and diversification. In this sense, QuaSSE approach is superior to ancestral reconstructions in terms of generality and precision. Together, ancestral reconstructions and QuaSSE provide two parallel lines of evidence, which substantially enhances reliability of the obtained findings.

Our analytical framework stems from the basic predictions of the MTE: (i) speciation rates negatively correlate with body size in both ecto- and endotherms, (ii) speciation rates positively correlate with environmental temperature in ectotherms but not in endotherms. Employing distributional maps and dated phylogenetic trees for plethodontids and carnivorans, we first inferred how speciation rate is affected by environmental temperature and body size from present-day data by means of the QuaSSE modelling. Then, we calculated speciation rates for each node of our two trees and correlated it with the corresponding values of ancestral temperatures and ancestral body sizes. Herein, we derive speciation rates from net diversification rates assuming an extinction fraction of $d/b = 0.1$. However, our results apply to both speciation and net diversification equally because these two are mutually interchangeable in the studied taxa, and we discuss our findings in the context of both speciation and diversification. Results of both of these approaches (i.e. QuaSSE

and ancestral reconstructions) were compared with the MTE's predictions.

Materials and methods

Assembling dated phylogenies for plethodontid salamanders and carnivorans

Phylogeny of the plethodontid salamanders was adopted from Adams *et al.* (2009). The present plethodontid tree included 190 of the 420 recognized species (Vieites *et al.*, 2011). To avoid bias due to incomplete and possibly nonrandom sampling, only 15 well-sampled and well-supported clades with 173 species in total were selected for further analyses. This approach is justified in detail by Adams *et al.* (2009) and Kozak & Wiens (2010).

Phylogenetic tree of carnivorans was adapted from Machac *et al.* (2011) and expanded to include also marine species (= Pinnipedia, i.e. Phocidae, Otariidae, Odobenidae) (Higdon *et al.*, 2007; Fulton & Strobeck, 2010); see the original study (Machac *et al.*, 2011) for details. Thus, the complete dated tree of all extant carnivorans (264 species) was assembled.

Compiling the data on environmental temperatures and body sizes

We inferred current environmental temperature for each species from its geographic distribution, which was taken from the IUCN (www.iucnredlist.org) and/or AmphibiaWeb (www.amphibiaweb.org) databases. Once the geographic distributions were digitized in ArcView GIS (v3.2[®]; ESRI, Redlands, CA, USA), environmental temperatures were computed. Temperature rasters were obtained from the WorldClim data set (Hijmans *et al.*, 2005) and resampled to a 1.5° resolution, as recommended by Hurlbert & Jetz (2007). For each species, we calculated both mean and median of annual mean temperature, maximum temperature of the warmest month and minimum temperature of the coldest month (i.e. climate variables BIO1, BIO5 and BIO6; Hijmans *et al.*, 2005) across its geographic range. Hence, we obtained six variables characterizing environmental temperature for each carnivoran and plethodontid species. As inferred environmental temperatures for marine carnivorans (Pinnipedia) would be hardly comparable with those for terrestrial species, we only used the marine taxa for calculation of carnivoran diversification rates (see below).

Data on species' body sizes were compiled from literature (Grzimek, 1990; Kingdon, 1997; Adams *et al.*, 2009). In the case of plethodontid salamanders, we inferred body size from body volume (in cm³) calculated for each species based on its morphometric data (Adams *et al.*, 2009). In the case of carnivorans, body size was expressed as body mass (in kg). Highly skewed distributions of body sizes required a log-transformation.

Analysing the relationships: the QuaSSE approach

To infer how diversification is affected by environmental temperature and body size from present-day data, we employed QuaSSE modelling (FitzJohn, 2010), which is basically an extension of the BiSSE method (Maddison *et al.*, 2007) to quantitative traits. This method assumes that diversification of evolutionary lineages follows a birth–death process, whereby speciation and extinction rates vary as the character under study evolves. The variation of speciation and extinction rates can be modelled via different functions that are fitted to the data (i.e. dated tree and trait values) by means of likelihood optimization. Fits of different speciation and extinction scenarios can then be compared using Akaike's information criterion (AIC) and/or likelihood ratio tests (FitzJohn, 2010).

We modelled plethodontid and carnivoran speciation rates as both constant and linear functions of (i) environmental temperature and (ii) body size. Extinction was implemented as a background process of invariable rate as the metabolic rate is expected to drive speciation rather than extinction (Allen *et al.*, 2002) and inference of complex extinction functions is often unreliable (FitzJohn, 2010). The resultant QuaSSE models were then compared by AIC and likelihood ratio tests. Analyses were performed using the 'R' package diversitree (FitzJohn, 2010).

Analysing the relationships: ancestral reconstructions

We estimated speciation rates, ancestral environmental temperatures and ancestral body sizes for each node of the plethodontid and the carnivoran tree. Subsequently, we correlated speciation rates with ancestral temperature and ancestral body size across all nodes of the two trees.

To calculate speciation rates, we first inferred net diversification rates using equation no.7 from Magallon & Sanderson (2001) under the extinction fraction of $d/b = 0.1$. Once the net diversification rates were calculated, we derived speciation rates assuming the previously defined extinction fraction (i.e. speciation = net diversification + extinction; extinction = $0.1 \times$ speciation). Importantly, our results were independent of the extinction fraction used (see Fig. S2). Therefore, net diversification rates would yield the same conclusions as speciation rates, but we report only the latter for brevity. Then, we discuss our results in the context of both speciation and diversification as both of them are relevant to diversity patterns of the studied taxa.

After the speciation rates were estimated, we reconstructed ancestral environmental temperatures and ancestral body sizes for each node of our plethodontid and carnivoran tree. We used the method of least squares to fit the Brownian motion model of evolution into our data and infer ancestral states, as described in

Felsenstein (1985). Afterwards, we calculated mean ancestral state for each node from ancestral states of its descendant nodes. A more refined measure weighting the ancestral values with branch lengths could be used, but we decided to use the unweighted mean for simplicity. This procedure ensured that ancestral states along the entire interval from the node in question to its tips (i.e. not solely the state at the focal node) were considered. This is important because our estimates of speciation rates also considered the whole interval from the focal node to its tips.

We note that there are many alternative methods for speciation rate estimation and ancestral reconstruction. However, these methods are mathematically similar and usually yield consistent results. In a supplementary analysis, we verified whether this consistency applies to our carnivoran and plethodontid data as well. First, we used several alternative methods (see Table S1) to estimate speciation rates and ancestral states. Then, we compared the obtained alternative estimates with estimates described previously. Indeed, both ancestral reconstructions and the diversification rate estimation have certain limitations; for their thorough discussion, see Schluter *et al.* (1997); Cunningham *et al.* (1998); Rabosky (2009a). Analyses were performed using the 'R' package ape (Paradis *et al.*, 2004).

As the values of speciation rates and ancestral states were associated with nodes of the two phylogenies and hence, mutually phylogenetically correlated, we analysed their relationships by means of phylogenetically corrected generalized linear models (PGLM; Freckleton *et al.*, 2002). The PGLM algorithm estimates phylogenetic dependence of variables included in the model by searching for the maximum likelihood value of the parameter λ which varies between zero and one (zero value refers to phylogenetic independence, whereas $\lambda = 1$ indicates phylogenetic signal consistent with the Brownian evolutionary model). Then, while controlling for the detected dependence in data, a GLM model is fitted and its phylogenetically corrected parameter estimates are returned (Freckleton *et al.*, 2002). All the analyses throughout this paper, if not stated otherwise, were conducted in the R 2.11 environment (R Development Core Team, 2011).

Results

Results of the QuaSSE modelling are summarized in Table 1. Likelihood ratio tests and AIC comparisons consistently indicated that speciation rate positively correlated with temperature in plethodontids; in carnivorans, however, negative correlation was detected. Body size correlated positively with speciation rate in plethodontids, whereas carnivoran speciation rate appeared independent of body size (see Table 1).

The ancestral reconstructions yielded practically identical results as the QuaSSE modelling (Table 2, Fig. 1). We found positive correlation between speciation

Table 1 Results of the QuaSSE modelling. The outcomes indicate that speciation rate is positively associated with environmental temperature and body size in plethodontids. In the case of carnivorans, negative correlation between temperature and speciation rate was detected. Constant function (i.e. speciation independent of trait values) served as a null model. The results are generally supported by Akaike's information criterion (AIC) as well as likelihood ratio tests (LRT).

	Correlation		LRT <i>P</i> -value
	pos/neg	Δ AIC (linear-null)	
Plethodontids			
BIO1 mean temperature*	+	-44.0	0.001
BIO1 mean temperature†	+	-44.2	0.001
BIO5 max temperature*	+	1.4	0.433
BIO5 max temperature†	+	1.2	0.373
BIO6 min temperature*	+	-23.0	0.001
BIO6 min temperature†	+	-23.8	0.001
Body volume	+	-3.6	0.016
Carnivorans			
BIO1 mean temperature*	-	-24.0	0.001
BIO1 mean temperature†	-	-24.3	0.001
BIO5 max temperature*	-	-25.5	0.001
BIO5 max temperature†	-	-26.6	0.001
BIO6 min temperature*	-	-24.3	0.001
BIO6 min temperature†	-	-24.7	0.001
Body mass	-	2.0	0.874

*Mean throughout the geographic range.

†Median throughout the geographic range.

rate and environmental temperature in plethodontids ($r_{1,15} = 0.6$, $P = 0.01$; Table 2), whereas in carnivorans the correlation was negative ($r_{1,158} = -0.2$, $P < 0.001$; Table 2). In the case of body sizes, no correlation was detected in plethodontids ($r_{1,15} = -0.131$, $P = 0.643$; Table 2) as well as carnivorans ($r_{1,158} = 0.002$, $P = 0.981$; Table 2).

An additional PGLM model showed that environmental temperature and body size were not mutually correlated in either plethodontids ($r_{1,15} = 0.029$, $P = 0.694$) or carnivorans ($r_{1,230} = 0.028$, $P = 0.673$). Moreover, alternative methods of ancestral state and speciation rate estimation (e.g. speciation rates calculated under different levels of extinction; see Table S1) yielded estimates that were highly correlated with the estimates described previously (Figs S1 and S2). Additionally, as speciation rates calculated with different extinction fractions are mutually correlated (Fig. S2), speciation rates and net diversification rates can be considered mutually interchangeable in the context of our study.

Discussion

What drives evolutionary diversifications is one of the central questions of evolutionary ecology. Although the role of temperature in the context of diversifications has been acknowledged, it has not yet been sufficiently emphasized that its effects may substantially differ in

Table 2 PGLM models indicating the relationship between ancestral temperatures, ancestral body sizes and speciation rates. In agreement with the QuaSSE inference, speciation rate increases with temperature in plethodontids, but this correlation is negative in carnivorans. Speciation rates in both carnivorans and plethodontids appeared independent of body size.

	<i>r</i>	d.f.	<i>P</i>
Plethodontids			
BIO1 mean temperature*	0.617	15	0.014
BIO1 mean temperature†	0.630	15	0.012
BIO5 max temperature*	0.070	15	0.804
BIO5 max temperature†	0.242	15	0.385
BIO6 min temperature*	0.616	15	0.014
BIO6 min temperature†	0.617	15	0.014
Body volume	-0.131	15	0.643
Carnivorans			
BIO1 mean temperature*	-0.311	158	< 0.001
BIO1 mean temperature†	-0.304	158	< 0.001
BIO5 max temperature*	-0.289	158	< 0.001
BIO5 max temperature†	-0.288	158	< 0.001
BIO6 min temperature*	-0.291	158	< 0.001
BIO6 min temperature†	-0.290	158	< 0.001
Body mass	0.002	158	0.981

*Mean throughout the geographic range.

†Median throughout the geographic range.

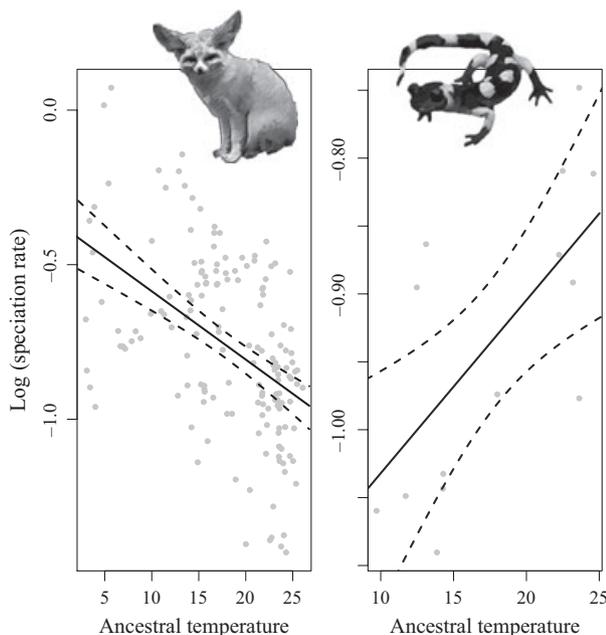


Fig. 1 Regression of speciation rate on ancestral environmental temperature. The relationship is negative in endothermic carnivorans (left) but positive in ectothermic plethodontids (right). In this figure, annual mean temperature was used to represent environmental temperature. Dashed lines indicate 95% confidence intervals.

taxa of different body temperature regulation. Herein, we employed two conceptually distinct methodologies, the QuaSSE approach and ancestral reconstructions, to test whether environmental temperature modulates speciation rates and, ultimately, net diversification rates differently in two model taxa, carnivorans and plethodontids. Our analyses consistently document that elevated environmental temperatures are coupled with accelerated speciation rate in ectothermic plethodontids but not in endothermic carnivorans, which is in agreement with the MTE's predictions. These findings suggest that the biodiversity-generating mechanisms may predictably differ between taxa with respect to the character of their metabolism.

The MTE assumes that metabolic rate is independent of environmental temperature in endotherms as their body temperature is constant. However, it has been reported that endotherms keep their metabolism at high level in colder environments, whereas their metabolic rates are much more variable in high environmental temperatures (Anderson & Jetz, 2005). Consequently, endotherms have on average higher metabolic rates in cold environment and thus may be expected to diversify more rapidly there. This corresponds with the detected negative correlation between speciation rate and environmental temperature in carnivorans. Similar effect could also explain the findings of Weir & Schluter (2007) who documented that net diversification rates in mammals increase with latitude.

In agreement with previous studies that did not detect any evident connection between body size and species richness of phylogenetic lineages in either ectotherms (Stuart-Fox & Owens, 2003) or endotherms (Orme *et al.*, 2002; Isaac *et al.*, 2005), we did not find any considerable effect of body size on diversification. This seems controversial, given that body size is associated with many important biological attributes of a species, including its metabolic rate (Brown *et al.*, 2004). However, this multitude of body size correlates may actually be the reason for the lack of any clear pattern; it is possible that some of the numerous body size correlates are mutually antagonistic with respect to evolutionary diversification. For instance, small-bodied species have higher mass-specific metabolic rates but, at the same time, larger populations that are less prone to genetic drift and speciation (Gavrilets *et al.*, 2000). Moreover, net diversification rate depends on the rate of extinction, whose relation to body size may also be complex. Therefore, body size might affect evolutionary diversifications in many mutually restraining ways, which could ultimately obscure the effect of body size.

Despite the analogies between plethodontids and carnivorans mentioned earlier, it is still possible that the differences in temperature-diversification dependence between the two taxa are underlain by factors unconnected with metabolism. For example, timing of colonization events, nonrandom extinctions or negative

diversity dependence have been demonstrated to affect diversification processes. A thorough discussion of these potentially confounding, yet often methodologically elusive effects is provided, for example, in Wiens *et al.* (2007), Rabosky & Lovette (2008), Rabosky (2009a,b), Rabosky & Glor (2010) and Wiens (2011). For example, it has been argued that diversification may be negatively diversity-dependent so that it slows down when a taxon attains high diversity, eventually reaching an equilibrium in which speciation rates are balanced by extinction rates (Rabosky & Glor, 2010). Deviance of taxa from such biodiversity equilibrium might considerably affect their diversification (Rabosky & Lovette, 2008; Rabosky, 2009a,b; Rabosky & Glor, 2010). Therefore, if carnivorans and plethodontids were unequally departed from their biodiversity equilibrium, this would (independently of metabolic differences) contribute to the dissimilarity of their diversification patterns. However, there is no reason to expect a priori that plethodontids are closer to their equilibrium in colder environments and carnivorans in warmer environments so that they do not diversify in these environments anymore.

Although ancestral state and speciation rate estimates calculated for both plethodontids and carnivorans were highly robust with respect to the means of inference (Figs S1 and S2), it should be noted that ancestral estimates are associated with some uncertainty and bias particularly when niche evolution does not follow the phylogeny (see Grandcolas *et al.*, 2011). However, recent analyses for the world's amphibians (Hof *et al.*, 2010) and New World carnivorans (Diniz-Filho *et al.*, 2010) documented phylogenetic signal in their realized climatic niches (in carnivorans only at the lower levels of phylogeny). Moreover, our conclusions were supported also by the QuaSSE modelling (Table 1) which utilizes current temperature and body size data only, thus circumventing the potential pitfalls of ancestral reconstructions (FitzJohn, 2010).

There is no doubt that net diversification rates are determined by many factors (Ricklefs, 2007; Wiens *et al.*, 2007; Rabosky & Lovette, 2008; Rabosky, 2009a,b; Rabosky & Glor, 2010; Wiens, 2011). Their detailed exploration would require broad sampling, yet sufficient data for such in depth analyses are currently lacking. However, as temperature has been identified as the main determinant of large-scale geographic diversity patterns (Fuhrman *et al.*, 2008; Tittensor *et al.*, 2010; Belmaker & Jetz, 2011; Simova *et al.*, 2011), its effect on diversification should be examined using model taxa of highly resolved phylogenies and well-known distributions. Employing such an approach, we illustrate that temperature may affect diversity patterns via its effect on speciation, and ultimately net diversification, as predicted by the MTE. Whether the differences between plethodontids and carnivorans reflect more general rules applying to all

ecto- and endotherms should be further tested on more diverse sets of taxa. Our study identifies the potentially promising research areas for such future studies (e.g. effects of metabolic rate on macroevolutionary dynamics and biodiversity gradients) and outlines productive methodological strategies (e.g. phylogenetic approach towards MTE). To analyse the link between metabolism and macroevolution more directly, we recommend that future diversification studies consider not only ecological (environmental preferences, latitude of occurrence) but also physiological parameters of the studied clades (e.g. mode of body temperature regulation). Notably, the fact that the temperature-related latitudinal diversity gradient has been reported not only for ectotherms but also for endotherms (Davies *et al.*, 2007; Belmaker & Jetz, 2011), whose speciation rates should not increase with environmental temperature, indicates that similar geographic patterns of biodiversity, including the latitudinal diversity gradient, might emerge due to rather distinct processes across different taxa.

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Supporting information

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

Figure S1 Ancestral state estimates.

Figure S2 Diversification rate estimates.

Table S1 Alternative methods of diversification rate and ancestral state estimation.

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