Title

Ancient tropical extinctions contributed to the latitudinal diversity gradient

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Running title

Asymmetric gradient of tropical extinction

Data accessibility statement

All data used in this manuscript are presented in the manuscript and its supplementary material or have been previously published or archived elsewhere.

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Abstract

Biodiversity currently peaks at the equator and decreases towards the poles. Accumulating fossil evidence reveals that this hump-shaped latitudinal diversity gradient (LDG) has not been persistent through time, but there was comparable species diversity across latitudes such that the LDG flattened during greenhouse periods. Rather than seeing the LDG as the result of limited dispersal, higher equatorial diversification and turnover in Holarctic regions, we propose the modern-steep LDG be explained by climate-driven extinctions of warm-adapted clades from the Holarctic during coldhouse periods, coupled with equator-ward dispersals of organisms that tracked their climatic preferences when tropical biomes got restricted to the equator. Elevated rates of speciation and pole-ward dispersals, conversely, could explain the formation of a flat LDG during greenhouse periods. We studied the LDG of Testudines, Crocodilia and Squamata and found the high latitudes have been a source of tropical diversity for these groups. During greenhouse periods, diversification rates were equivalent between latitudes. During the transition to cold climates, we detected important levels of extinction for ancient tropical lineages distributed at high latitudes, coupled with high levels of range contractions and equator-ward dispersals. Our results further demonstrate the inclusion of fossils in macroevolutionary studies allows detecting the signal of ancient high-latitude tropical extinctions, otherwise vanish from analyses based on present-day data. Our results challenge the current consensus, which considers the evolutionary processes behind the LDG have acted constantly over time and suggest the LDG should be regarded as a time-varying biodiversity pattern.

Keywords: climate change; fossils; biodiversity; extinction; speciation; dispersal; tropics; Holarctic; phylogeny; niche.

Introduction

The current increase of species richness occurring from the poles towards the equator, referred to as the latitudinal diversity gradient (LDG), is one of the most conspicuous patterns in ecology and evolution[1]. This pattern has been described for microbes[2], insects[3], vertebrates[4], and plants[5], and for marine, freshwater, and terrestrial ecosystems[1,6,7].

During decades, it has been considered that the current steep shape of the LDG (with higher diversity at the equator) rooted back several million years ago to the respective origin of the groups, and has been maintained through time[7]. This idea was grounded on previous studies of the fossil record suggesting that the steep LDG has persisted through the Phanerozoic, the last 540 Myrs[8,9]. However, methodological limitations on fossil sampling cast doubts on this conclusion[10,11]. Analyses controlling for sampling biases suggest that the LDG of many groups was less pronounced than the one observed today or was even flat during some periods in the past, *i.e.* there was comparable species diversity across latitudes (see ref.[12] for a review). This is the case for groups like non-avian dinosaurs[10], mammals[11,13], tetrapods[14], insects[15-17], brachiopods[18,19], bivalves[20], coral reefs[21], crocodiles[22], turtles[23,24], or plants[25,26].

The emerging pattern from fossil studies suggests the steep modern LDG was restricted to the relatively few and short coldhouse intervals of the Earth history: the Ordovician/Silurian, the Carboniferous/Permian, the end of the Jurassic, and the Neogene[12,27-29]. Most of the Phanerozoic was characterized by warm greenhouse climates accompanied by a less pronounced (more flatten) LDG[10,11,13,16] (**Fig. 1**), such that the LDG shape fluctuates following climatic transitions. The new fossil evidence set a starting point on LDG research. Most evolutionary hypotheses published to date seek to understand why diversity did not accumulate in the Holarctic at the same levels than in the equator[7,30,31], while recent fossil

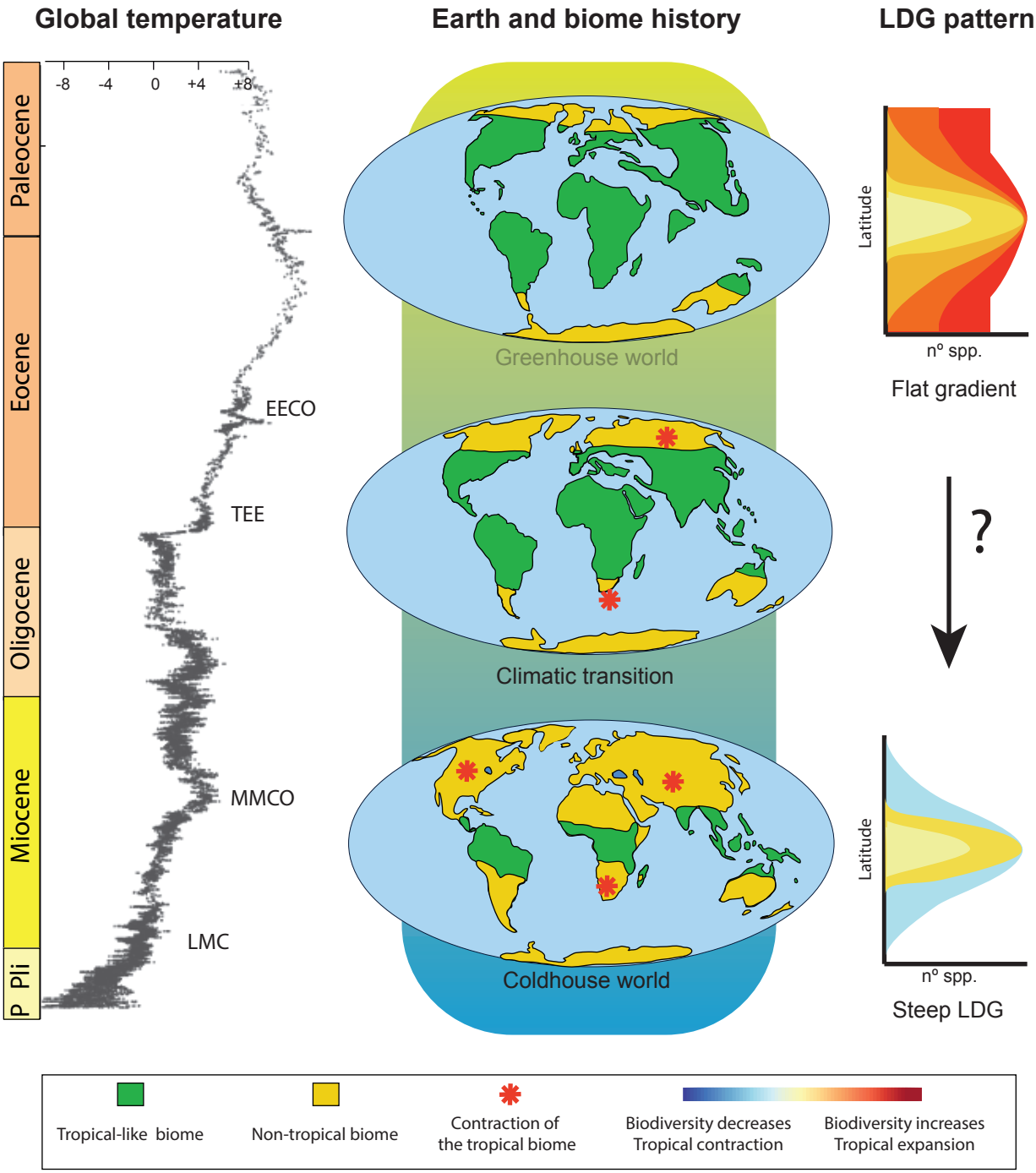

Figure 1 | Changes in global temperature and extension of the tropical belt during the Cenozoic, in relation with the shape of the LDG. During the early Cenozoic, global temperatures were higher than the present and warm paratropical conditions extended over northern and southern latitudes. From the early Eocene climatic optimum (EECO; ca. 53-51 Ma), a global cooling trend was intensified on Earth, punctuated by sharp declines of temperatures, such as the dramatic drop of the terminal Eocene Event (TEE, ca. 33.9 Ma). Warm-equable regimes got then restricted to the equator. The Neogene is characterized by a continuous decrease of temperatures, punctuated with periods of relative warmth, such as the middle Miocene climatic optimum, but also by sharp declines during the late Miocene cooling events. Neogene climate cooling culminated with major ice-sheet expansions during Pleistocene glaciations. The LDG of many groups evolved following these global changes[12]; during the greenhouse period diversity was uniform across latitudes, such that the LDG flattened, while during cold periods diversity peaked at the equator (a steep LDG). The question mark denotes the focus of this study, which is to unveil the processes that mediated the transition between a flat and steep LDG. The relative temperature curve of the Cenozoic is adapted from ref.[59]. Maps represent the extension of the tropical belt and Earth tectonic changes as derived from refs.[57,58].

investigations show that, for many lineages, we rather need to explain why, how and when diversity was lost at high latitudes to shape the current LDG.

Phylogenetic investigations proposed potential mechanisms to explain the transition from high to low Holarctic diversity. Recent studies consider the high latitudes as a possible source of diversity, and suggest the elevated species richness in the tropics today could be due to differential dispersal (*d*) from high to low latitudes, following the contraction of the tropical biome[32-35]. Disproportionate high-latitude extinctions – a scenario in which extinction (μ) overcomes speciation (λ), resulting in negative net diversification rates ($r = \lambda - \mu; r < 0$) – could also explain this transition. Often considered behind the LDG[36], diversity losses in the Holarctic have been suggested early in the literature and attributed to Pleistocene glaciations[37], but this hypothesis was strongly challenged given that the LDG has more ancient origins than the Pleistocene[7,12]. More ancient extinctions were also considered[38-42]. For example, Hawkins *et al.*[41] proposed the avian LDG resulted from the differential extirpation of older warm-adapted clades from the temperate regions newly formed in the Neogene. Unfortunately, the difficulty to infer extinction rates from present-day data[43,44] and the assumption that diversity in the Holarctic was always low in comparison with equatorial diversity have made this hypothesis seldom considered (but see ref.[45]). On the contrary, widely accepted views of equatorial regions as the source of world diversity[46,47] and the long-term persistence of the steep LDG, permeate the current consensus explaining the LDG as the result of higher diversification and limited dispersal out of the equator[7,30,48] (**Table 1**). Meanwhile, elevated turnover rates (comparable speciation and extinction rates) have been proposed to maintain the low diversity in the Holarctic through time: *e.g.* amphibians[49], birds[31,36,50], butterflies[32], conifers[51], fishes[52], mammals[48], and squamates[34].

From a flat to hump-shaped LDG

Table 1. Predictions of the most common LDG hypotheses, including the *Asymmetric gradient of tropical extinction* (AGE) hypothesis proposed in this study. The AGE model includes various diversification and dispersal parameters for each temporal interval (greenhouse, coldhouse, transition). Abbreviations: λ = speciation, μ = extinction, d = dispersal, t = time, e = equatorial, h = Holarctic, Trop = Tropical biome, Temp = Temperate biome.

	Cradle of diversity (Stebbins 1974)	***Museum of diversity*** (Stebbins 1974)	***Time for speciation*** (Stephens & Wiens 2003)[1]	***Tropical niche conservatism*** (Wiens & Donoghue 2004)	***Out of the tropics*** (Jablonsky *et al.* 2006)	***Into the tropics*** (Rolland *et al.* 2015)	***Holarctic turnover*** (Weir & Schluter, 2007)	***Asymmetric gradient of extinction***		
								Greenhouse	Transition	Coldhouse
Predictions	$r_e > r_h$ ($\lambda_e > \lambda$) $d_{eh} = d_{he}$	$r_e > r_h$ ($\mu_e < \mu_h$) $d_{eh} = d_{he}$	$t_{trop} = t_{temp}$ ($r_{trop} = r_{temp}$) ($d_{trtp} = d_{tptr}$)	$r_e = r_h$ $d_{eh} > d_{he}$	$r_e > r_h$ ($\lambda_e > \lambda_h$) ($\mu_e < \mu_h$) $d_{eh} > d_{he}$	$r_e = r_h$ $d_{eh} < d_{he}$	$r_h = 0$ ($\mu_h = \lambda_h$) $d_{eh} = d_{he}$	$r_e = r_h$ $d_{eh} = d_{he}$	$r_e > r_h$ ($\mu_h > \lambda_h$) $d_{eh} < d_{he}$	$r_e > r_h$ ($r_h = 0$) $d_{eh} = d_{he}$

[1] No specific predictions on diversification differences across regions are provided in this hypothesis but across taxa adapted to particular climates, as it assumes that tropical-adapted clades originated before temperate clades, and thus had more time to diversify than temperate clades.

Across Earth history, the extension of the tropical biome has fluctuated geographically around the equator, with periods of pole-ward expansions when warm paratropical conditions and tropical-adapted taxa appeared at high latitudes[53-56], followed by periods of equatorial-ward contractions[57,58] (**Fig. 1**). The last 100 Myrs have witnessed the last transition, with a global cooling trend set on Earth since the Cretaceous–early Cenozoic period that culminated with the Pleistocene glaciations[59].

The expansion of tropical-like conditions to the higher latitudes induced species diversification in the new paratropical areas (**Fig. 2a**) and facilitated movements within the broad "*paleotropical belt*", such that equatorial clades were able to disperse *"out of the equator"* into high-latitude warm regions[28,46] – or towards the south in the case of northern origins. A greenhouse equable climate thus would have triggered the formation of a flat LDG (**Fig. 2a**). On the contrary, tropical biome retractions following climate cooling (**Fig. 2b**) induced periods of declining diversity at high latitudes (where climate change was more intensively felt), and biotic movements "*into the equator*" prevailed over northern migrations. Higher extinction rates impacted tropical lineages at high latitudes, whereas low-latitude tropical lineages experienced lower extinction. Climate change would have thus driven an asymmetric extinction pattern within the tropical biome, and mediated the formation of a steep LDG shape (**Fig. 2c**). Biodiversity dynamics may shift between these two patterns during climatic transitions. This framework imposes a time-variable vision of the LDG in which prevailing speciation, extinction and dispersal dynamics switch during warm and cool intervals. Therefore we propose the hypothesis that the current hump-shaped LDG results from a combination of ancient tropical extinctions in high latitudes and equator-ward dispersals, both due to the global cooling of the Cenozoic. It would have led to diversity loss in the Holarctic and southern temperate regions, and contribute to the transition from a flat LDG to a steep LDG with lower diversity towards the south and north.

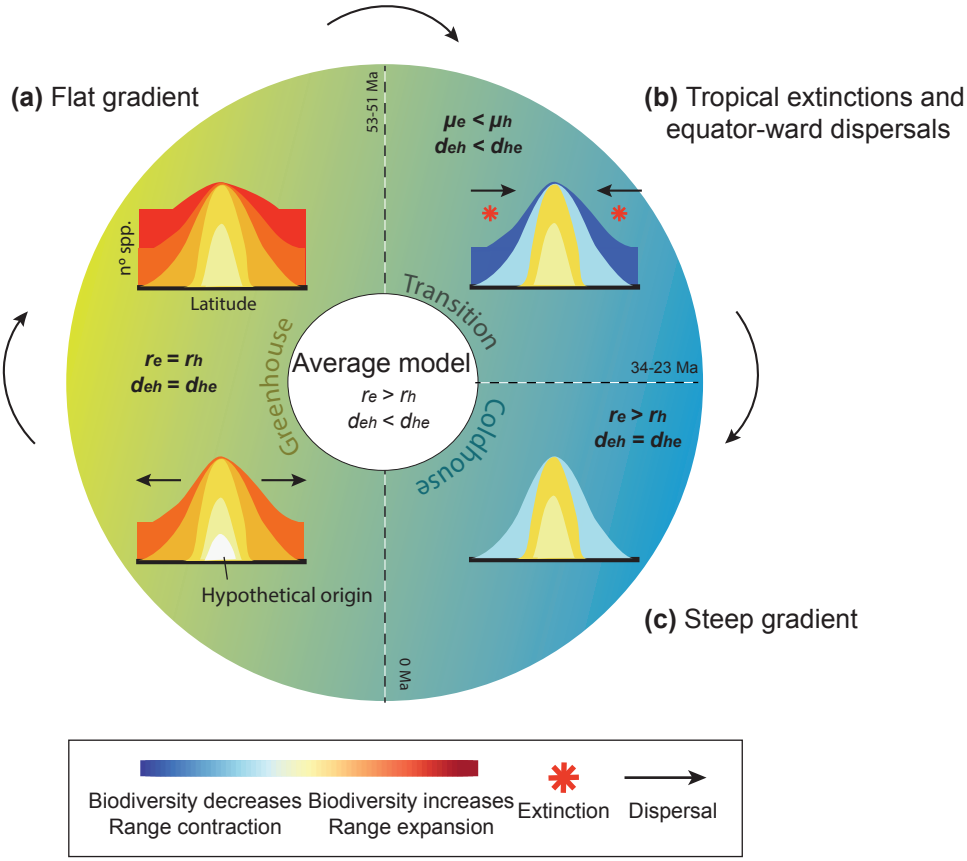

Figure 2 | Prevalent evolutionary processes behind the latitudinal diversity gradient under the AGE time-variable framework. The graphic shows the hypothetic change in evolutionary dynamics (diversification "r", speciation "λ", extinction "μ" and dispersal "d") between Holarctic and equatorial regions (denoted with "h" and "e" subscripts, respectively) and across main climatic intervals: **a**, the greenhouse late Cretaceous-early Cenozoic period. **b**, the late Eocene-Oligocene climatic transition. **c**, the Neogene coldhouse interval. For each period, inset Figs. represent the distribution of species richness across latitudes (the LDG shape) and the hypothetical change in global evolutionary dynamics under the AGE hypothesis. In the centre, the average model represents the prevalent evolutionary dynamics expected under the AGE hypothesis under a single, constant rate, evolutionary model.

We refer this hypothesis to the "Asymmetric Gradient of Extinction" (AGE). The predictions (P) of the AGE model could be formulated as follows (**Fig. 2; Table 1**): **P1**; similar diversification rates between Holarctic (H) and equatorial (E) regions during greenhouse periods ($r_E = r_H$), **P2**; similar dispersal rates between Holarctic and equatorial regions during greenhouse periods ($d_{HE} = d_{EH}$), **P3**; extinction increases relative to speciation at high latitudes during climatic transitions towards cooler climates, *i.e.* declining diversity ($r_H < 0$), while equatorial regions remain stable, and **P4**; dispersal "*into the equator*" being more important than "*out of the equator*" during climatic transitions ($d_{HE} > d_{EH}$).

The AGE hypothesis builds up from previous ideas but here framed in the context of a time-variable scenario. As noted earlier, the idea of tropical lineages occurring at higher latitudes going extinct during climatic transitions has been suggested before[38,39,41,42]. Similarly, behind this hypothesis prevails the idea of niche conservatism[30,47]: when the tropical biome retreated towards the equator, most of the tropical-adapted taxa at high latitudes were unable to adapt and either went extinct or got their distribution restricted. The dynamic history of the tropical belt has been considered before to explain different dispersal opportunities for tropical lineages through time[32,35,60,61], as well as the wider extension of the paleotropical belt to explain the large number of groups originated in the tropics, as the product of increased area size[62]. To our knowledge, however, diversity losses mediated by tropical biome contractions have seldom been considered a major mechanism behind the LDG. This idea might seem quite straightforward, but its direct formulation and corroboration has been lacking. In addition, although it is widely accepted that the processes shaping biodiversity varied over time and space[63], this has been overlooked in the context of the LDG, generally explained by the action of time-constant process[33,34,45,64]. Here, we studied the LDG

148 of Testudines, Crocodilia and Squamata using comparative methods for both the phylogeny
149 and fossil record, and we confronted the AGE hypotheses to classical LDG hypotheses.
150

151 ## Results

152 ***Phylogeny-based diversification analyses: are diversification rates higher in the equator?***
153 According to current distribution data, species richness of turtles, squamates and crocodiles
154 peaks near the equator, with 84% of all extant species living in the tropics, whereas only 15%
155 live in temperate regions and 1% span both biomes. We categorized each species reported in
156 the phylogeny (Supplementary Tables 1-3) as living in the equator (tropical biome) or the
157 Holarctic and Southern Hemisphere (temperate biome). In turtles, we found that there are 239
158 tropical species, 84 temperate species and 6 widespread species (7 are marine); while in
159 squamates, there are 7955 tropical species, 1337 temperate species and 124 widespread. For
160 the species-poor crocodile clade, there are 23 tropical species and 2 temperate species.
161 We analyzed differences in diversification rates between Holarctic and equatorial
162 regions for turtles, squamates and crocodiles using the Binary State change Speciation and
163 Extinction model (BiSSE[65,66], see *Methods*). We did not use the Geographic State change
164 Speciation and Extinction model[67], which is appropriate when dealing with widespread
165 species, because most species in our datasets are endemic to a region and to consider a
166 character state in SSE models, it must represent at least 10% of the total diversity[68]. We did
167 not apply the BiSSE model on crocodiles because simulation studies have shown that trees
168 containing fewer than 300 species may lack sufficient phylogenetic signal to produce enough
169 statistical power[68].
170 First, we used the time-constant BiSSE model as is generally applied to studies of the
171 LDG[33,34,35,45,48]. For turtles, net diversification rates were found higher in the Holarctic than in
172 the equator (**Table 2**, Supplementary Fig. 1a), although differences were not significant, and

Table 2. Results of the diversification and biogeographic analyses performed in this study. Abbreviations: λ = speciation, μ = extinction, d = dispersal, $R\mu$ = range extirpations, e = equatorial, h = Holarctic.

	Turtles			**Squamates**			**Crocodiles**		
	Greenhouse	**Transition**	**Coldhouse**	**Greenhouse**	**Transition**	**Coldhouse**	**Greenhouse**	**Transition**	**Coldhouse**
PyRate	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e = r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e = r_h$	$\lambda_e = \lambda_h$ $\mu_e > \mu_h$ $r_e < r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e = r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e > r_h$
BiSSE (time-variable)	$\lambda_e = \lambda_h$ $\mu_e = \mu_h$ $d_{he} = d_{eh}$	$\lambda_e = \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	$\lambda_e < \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $d_{he} < d_{eh}$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $d_{he} > d_{eh}$	$\lambda_e < \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	-	-	-
BiSSE (constant)	$\lambda_e < \lambda_h$ $\mu_e < \mu_h$, $r_e < r_h$, $d_{he} > d_{eh}$			$\lambda_e < \lambda_h$ $\mu_e < \mu_h$, $r_e > r_h$, $d_{he} > d_{eh}$			-		
DEC	$R\mu_e < R\mu_h$ ($R\mu_e < R\mu_h$)* $d_{he} < d_{eh}$ ($d_{he} < d_{eh}$)*			$R\mu_e > R\mu_h$ ($R\mu_e = R\mu_h$)* $d_{he} < d_{eh}$ ($d_{he} = d_{eh}$)*			$R\mu_e = R\mu_h$ ($R\mu_e = R\mu_h$)* $d_{he} = d_{eh}$ ($d_{he} = d_{eh}$)*		
DEC fossil	$R\mu_e < R\mu_h$ ($R\mu_e < R\mu_h$)* $d_{he} > d_{eh}$ ($d_{he} > d_{eh}$)*			$R\mu_e > R\mu_h$ ($R\mu_e < R\mu_h$)* $d_{he} < d_{eh}$ ($d_{he} > d_{eh}$)*			$R\mu_e < R\mu_h$ ($R\mu_e < R\mu_h$)* $d_{he} > d_{eh}$ ($d_{he} > d_{eh}$)*		

* Prevalent dynamics when the number of events is calculated relative to the number of taxa currently distributed in each region

173 dispersal '*into the equator'* was 10-fold higher than '*out of the equator'*. For squamates, the
174 same dispersal pattern is recovered but net diversification rates are significantly higher in the
175 equator (Supplementary Fig. 1b). To test the AGE hypothesis, we introduced two shift times
176 at 51 and 23 Ma to detect different diversification dynamics between greenhouse, transitional,
177 and coldhouse periods. This model indicates that net diversification of turtles was equivalent
178 between the Holarctic and equator, while it was lower in the Holarctic for squamates (**Table**
179 **2**, Supplementary Fig. 2) until the coldhouse period, when Holarctic diversification increased.
180 Dispersal was estimated symmetrical between regions (*into the equator = out of the equator*)
181 during greenhouses, and asymmetrical (*into the tropics > out of the tropics*) during the
182 climatic transition and coldhouse period. We inferred the same patterns by applying the same
183 model but with different combination of shift times (51 Ma and 34/23 Ma; Supplementary
184 Fig. 3).
185
186 ***Estimations of ancestral origins: did groups originate preferentially in the equator?***
187 To further test the predictions of the AGE hypothesis, we performed biogeographic analyses
188 using the Dispersal-Extinction-Cladogenesis (DEC) model[69] (see *Methods*). We first analyzed
189 the data using an unconstrained DEC analysis in which all ranges comprised of three areas
190 can be an ancestral state. We inferred an equatorial distribution for most basal nodes of turtles
191 and squamates, from where lineages colonized the other regions (**Fig. 3a**, **Table 2**,
192 Supplementary Fig. 4). Crocodile ancestors were reconstructed widespread during the
193 Cretaceous, but an early vicariant event separated *Alligator* in the Holarctic from the other
194 genera in equatorial regions (Supplementary Fig. 5).
195 The biogeographic estimates based on extant data only conflict with the fossil record
196 of turtles, squamates, and crocodiles[22-24,70]. To overcome this bias, we introduced information
197 about the distribution of fossils in DEC, in the form of hard (HFC) and soft (SFC) geographic

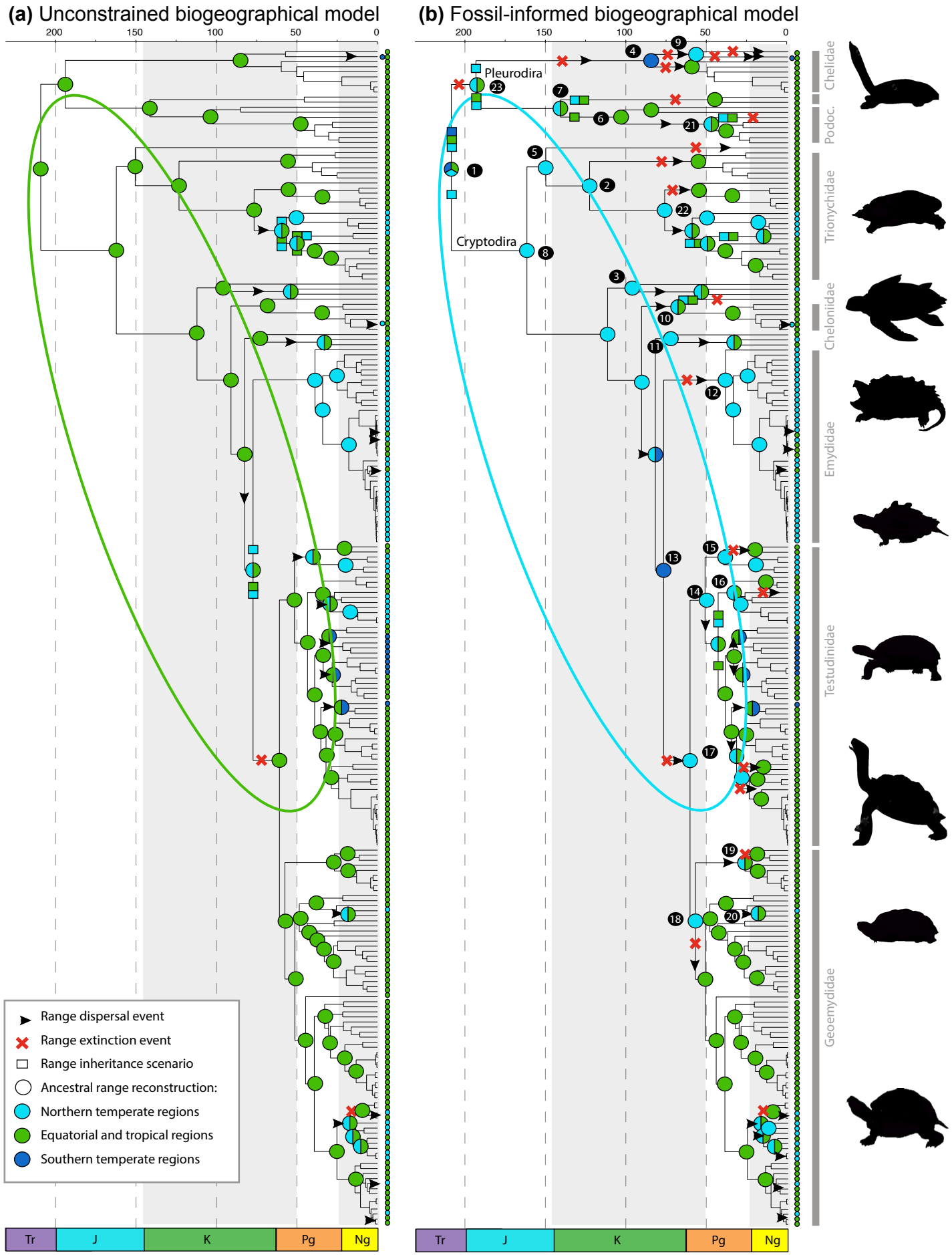

Figure 3 | Biogeographic reconstruction of Testudines showing the effects of the incorporation of fossil information into biogeographic inference. **a**, Biogeographic reconstruction inferred with DEC based on the distribution of extant taxa. **b**, Biogeographic reconstruction under the fossil-informed HFC (*hard fossil constraint*) model. Coloured circles at tips and nodes represent current and ancestral ranges, respectively, while squares represent range inheritance scenarios. Colours correspond with the discrete areas in the legend. Black circles indicate fossil range constraints included in the analysis, with numbers corresponding with taxa in Table Supplementary S4. The reconstruction under the *soft fossil constraint* (SFC, see text) model is presented in Supplementary Fig. 7.

198 fossil constraints placed at specific nodes (see *Methods*; Supplementary Tables 4-6). By
199 including fossil information, we recovered very different biogeographic histories for the three
200 groups (**Table 2**;turtles: **Fig. 3**, Supplementary Fig. 7; squamates: Supplementary Figs. 8, 9;
201 and crocodiles: Supplementary Figs. 10, 11). We found that turtles originated in the Northern
202 Hemisphere under the SFC model (they are widespread in the HFC model), from where
203 lineages migrated into the equator and southern regions (**Fig. 3b**, Supplementary Fig. 7). Most
204 dispersal is thus '*into the equator*' (Supplementary Fig. 6, Supplementary Table 7). We also
205 detected a higher number of geographic extinctions when fossil ranges were considered,
206 affecting predominantly turtle lineages in the Holarctic (53 and 11 lineages disappeared from
207 the region under the HFC and SFC model, respectively) and in southern temperate regions (9
208 in the HFC model; Supplementary Fig. 6, Supplementary Table 8). The same trend is
209 observed when the number of extinction/dispersal events is controlled by the number of
210 lineages currently distributed in each region (**Fig. 4**).

211 Squamates are recovered widespread at their origin in both SFC and HFC analyses
212 (Supplementary Figs. 8, 9). During the greenhouse period, dispersal '*into the equator*' equals
213 (or overcomes, in the HFC model) dispersal '*out of the equator*', and afterwards dispersals
214 '*out of the equator*' prevail (Supplementary Fig. 6, Supplementary Table 7). Range extinction
215 is estimated very high in this group under the unconstrained model with 30 lineages extirpated
216 from the Holarctic, 2 from southern temperate regions and 152 from the equator
217 (Supplementary Fig. 6, Supplementary Table 8). Under the fossil-informed models, the
218 number of Holarctic extinctions increases (to 109 and 66 lineages in the HFC and SFC
219 models, respectively), while the lineages extirpated from the equator remains relatively stable
220 (144 and 109 from the equator in HFC and SFC models; Supplementary Fig. 6). When the
221 number of extinction is controlled by the actual number of lineages distributed in each region,
222 the number of Holarctic extinctions and dispersal '*into the equator*' increases dramatically

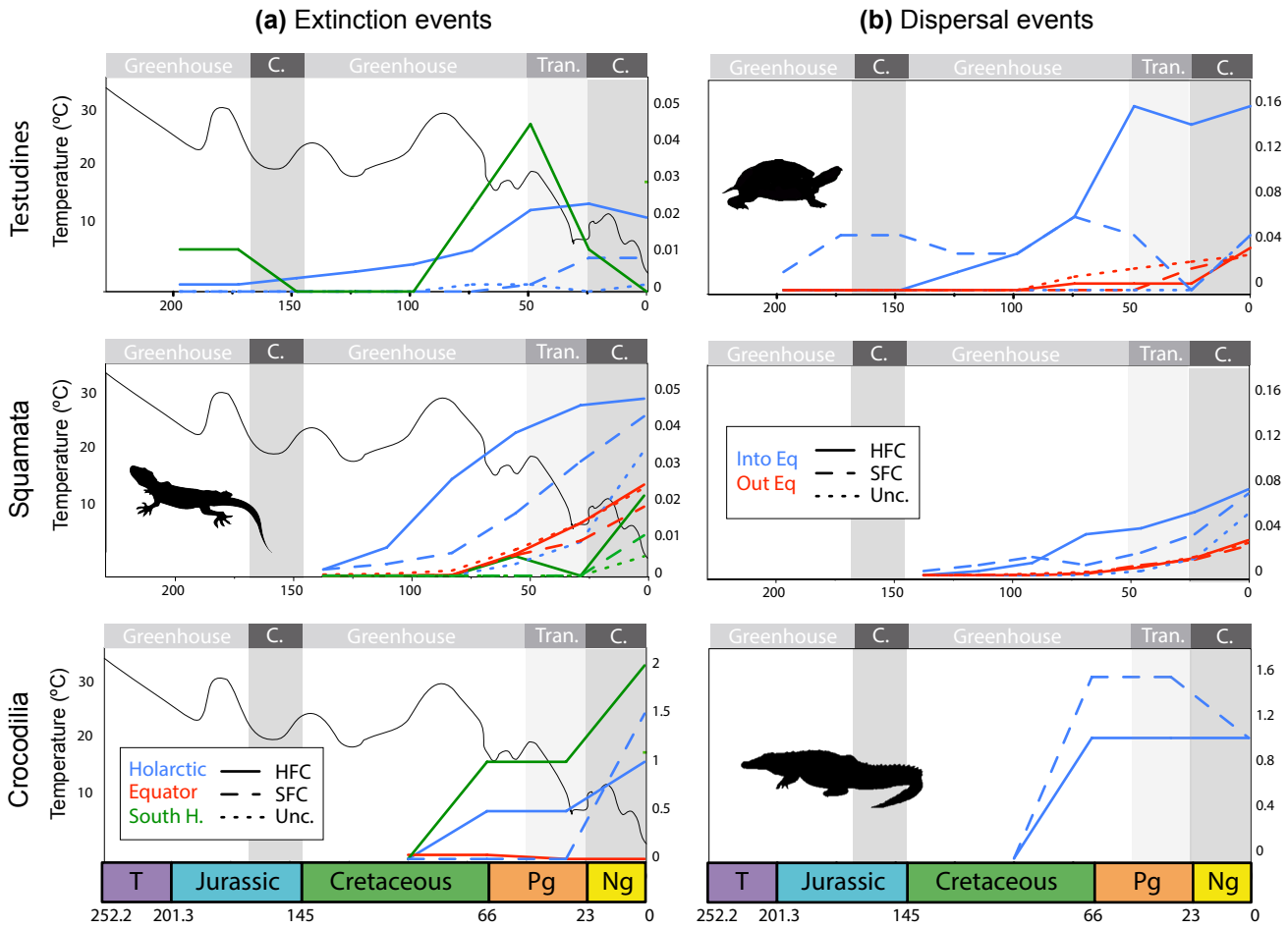

Figure 4 | Estimated number of range-extinction and dispersal events through time. Analyses were performed for Testudines, Squamata and Crocodiles under the *unconstrained model* (Unc.), based on present evidence only, and the fossil-based *hard* (HFC) and *soft fossil constraint* (SFC) biogeographic models. **a**, Inferred number of range extinction events through time and across regions relative to the number of lineages currently distributed in each region. The global mean temperature curve is modified from ref.[59]. **b**, Inferred number of dispersal events from the Holarctic into the equator (IntoEq) and out of the equatorial zone (OutEq), relative to the current number of lineages distributed in the Holarctic and equatorial zones, respectively. Abbreviations: Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; and Ng, Neogene, Trans. = climatic transition, and C. = coldhouse.

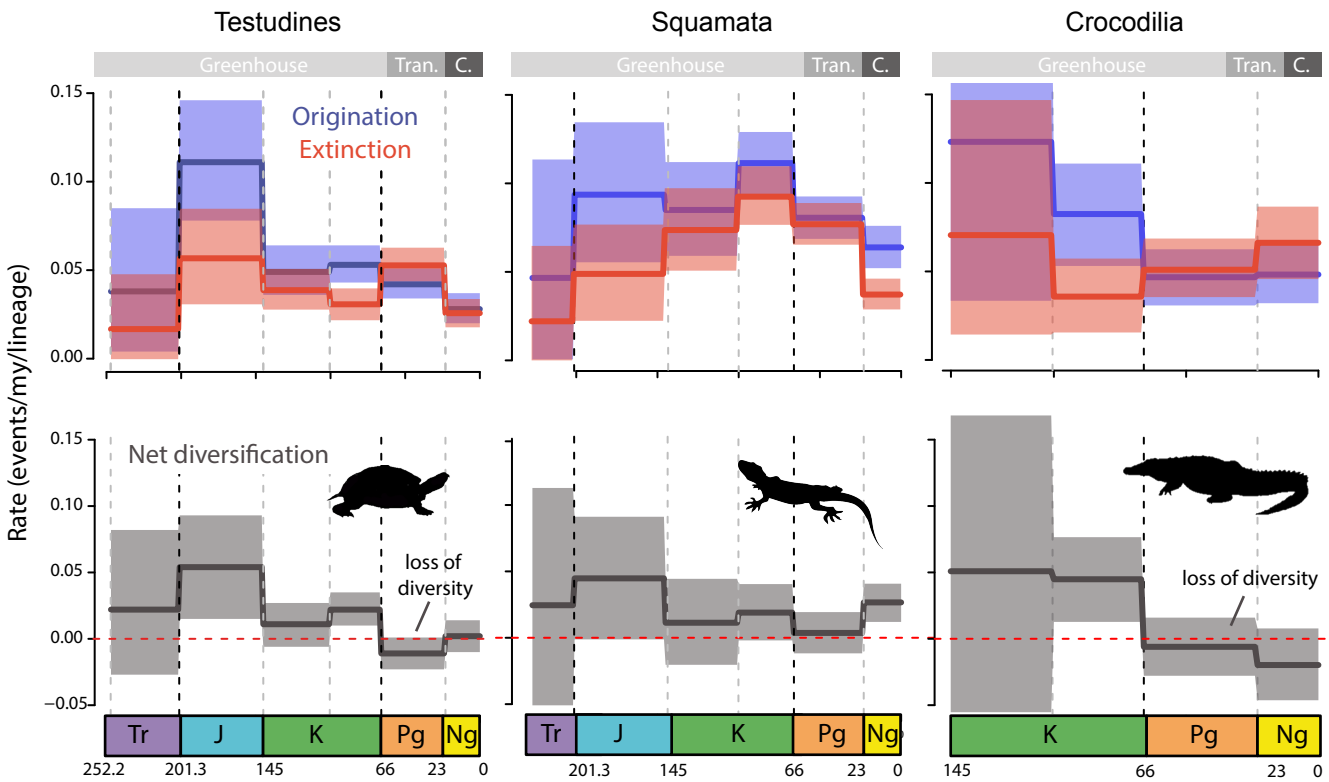

Figure 5 | Global pattern of turtles, squamates and crocodiles diversification through time based on the fossil record, and analysed with a Bayesian model. Origination (blue) and extinction (red) rates were estimated using time bins as defined by epochs of the geological timescale (on the top, main climatic periods are shown as follows: Greenhouse, Tran. = climatic transition, and C. = coldhouse). Solid lines indicate mean posterior rates, whereas the shaded areas show 95% credibility intervals. Net diversification rates (black) are the difference between origination and extinction. The vertical lines indicate the boundaries between geological periods and major mass extinction events. Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; and Ng, Neogene.

223 and overpass equatorial dispersal/extinctions (**Fig. 4**). For crocodiles, including fossil ranges,
224 we recovered that all the early nodes are distributed in the Holarctic (Supplementary Figs. 10,
225 11), and we detected range extinctions; four lineages disappeared from the Holarctic, three
226 from southern temperate regions, and two from the equator (HFC model; Supplementary Fig.
227 6, Supplementary Tables 7, 8). Only two lineages disappeared from the Holarctic in the SFC
228 model. The same tendencies are observed when the number of events is controlled by the
229 current number of lineages distributed in each region (**Fig. 4**).
230
231 ***Fossil-based diversification analyses: evidence for ancient tropical extinctions?***
232 The turtle fossil dataset comprised 4084 occurrences for 420 genera (65 extant and 355
233 extinct) (Supplementary Table 9). The squamate fossil dataset comprised 4798 occurrences
234 for 638 genera (120 extant and 518 extinct) (Supplementary Table 10). The crocodile fossil
235 dataset comprised 1596 occurrences for 121 genera (9 extant and 112 extinct) (Supplementary
236 Table 11). To infer the global diversification dynamics, we first analysed the fossil datasets as
237 a whole using a Bayesian approach that infers the temporal dynamics of origination and
238 extinction rates based on fossil occurrences[71] (see *Methods*). The results of the turtles show
239 that origination rates peaked during the Jurassic and decreased since then until the present.
240 Extinction was generally low and constant during the Mesozoic but increased during the
241 coldhouse intervals of the Jurassic and Paleogene resulting in negative net diversification
242 during the Paleogene (**Fig. 5**, **Table 2**, Supplementary Figs. 12, 13). For squamates,
243 origination rates peaked in the Jurassic and the Late Cretaceous, while extinction increased
244 steadily until the Late Cretaceous. In the Paleogene, net diversification approaches zero,
245 suggesting a high turnover (**Fig. 5**, Supplementary Figs. 14, 15). Crocodilia origination
246 peaked in the Early Cretaceous and decreased towards the present, and extinction was
247 generally low and constant. We also found diversity losses in the Paleogene that extend the

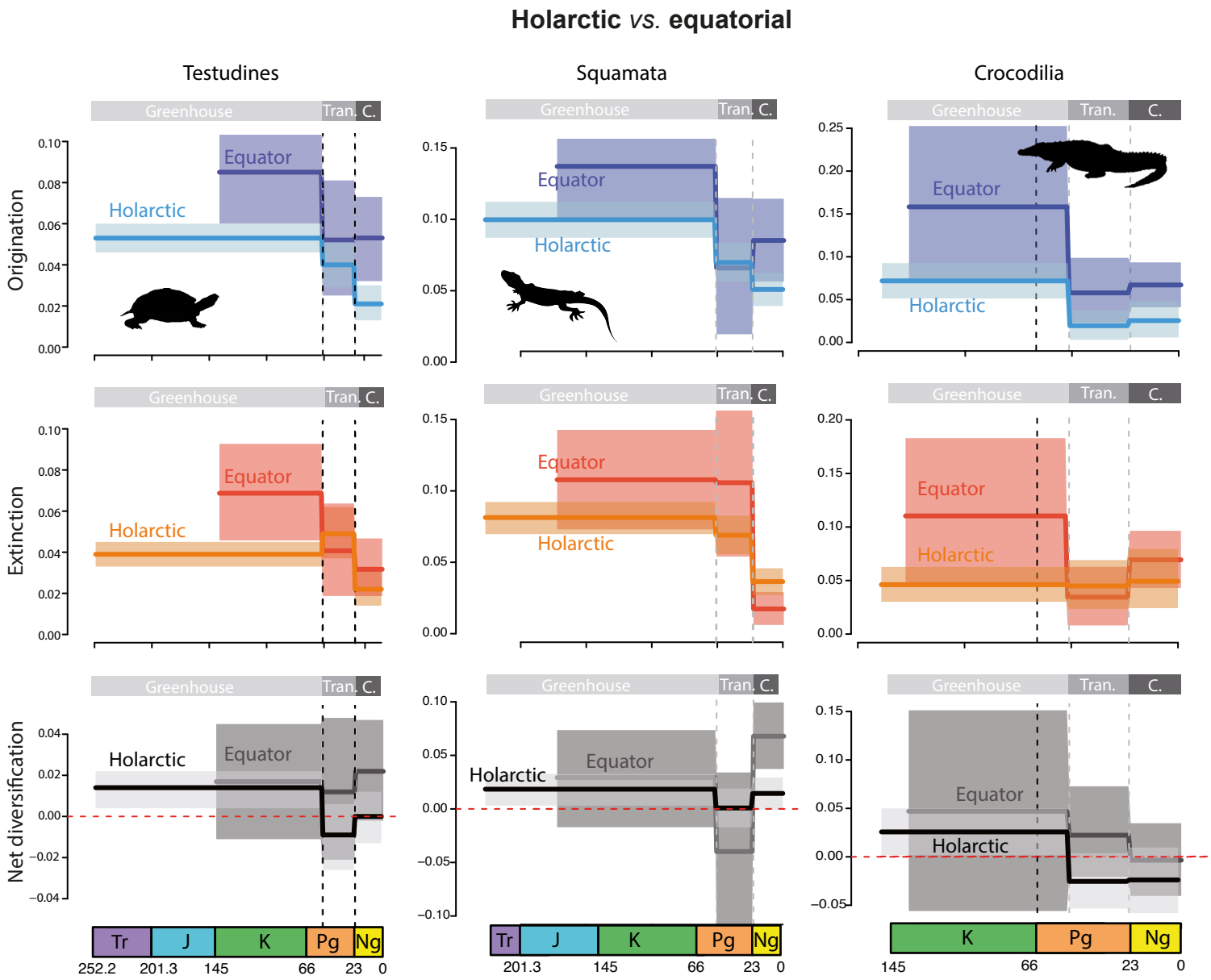

Figure 6 | Global pattern of turtle, squamate and crocodile diversification between Holarctic and equatorial regions, based on the fossil record. Diversification dynamics are compared between fossils distributed in Holarctic and equatorial regions. Origination (blue) and extinction (red) rates were estimated using time bins as defined by the main climatic intervals since the Mesozoic (on the top, climatic periods are shown as follows: Greenhouse, Tran. = climatic transition, and C. = coldhouse). Solid lines indicate mean posterior rates, whereas the shaded areas show 95% credibility intervals. Net diversification rates (black) are the difference between origination and extinction. The vertical lines indicate the boundaries between climatic intervals. Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; and Ng, Neogene

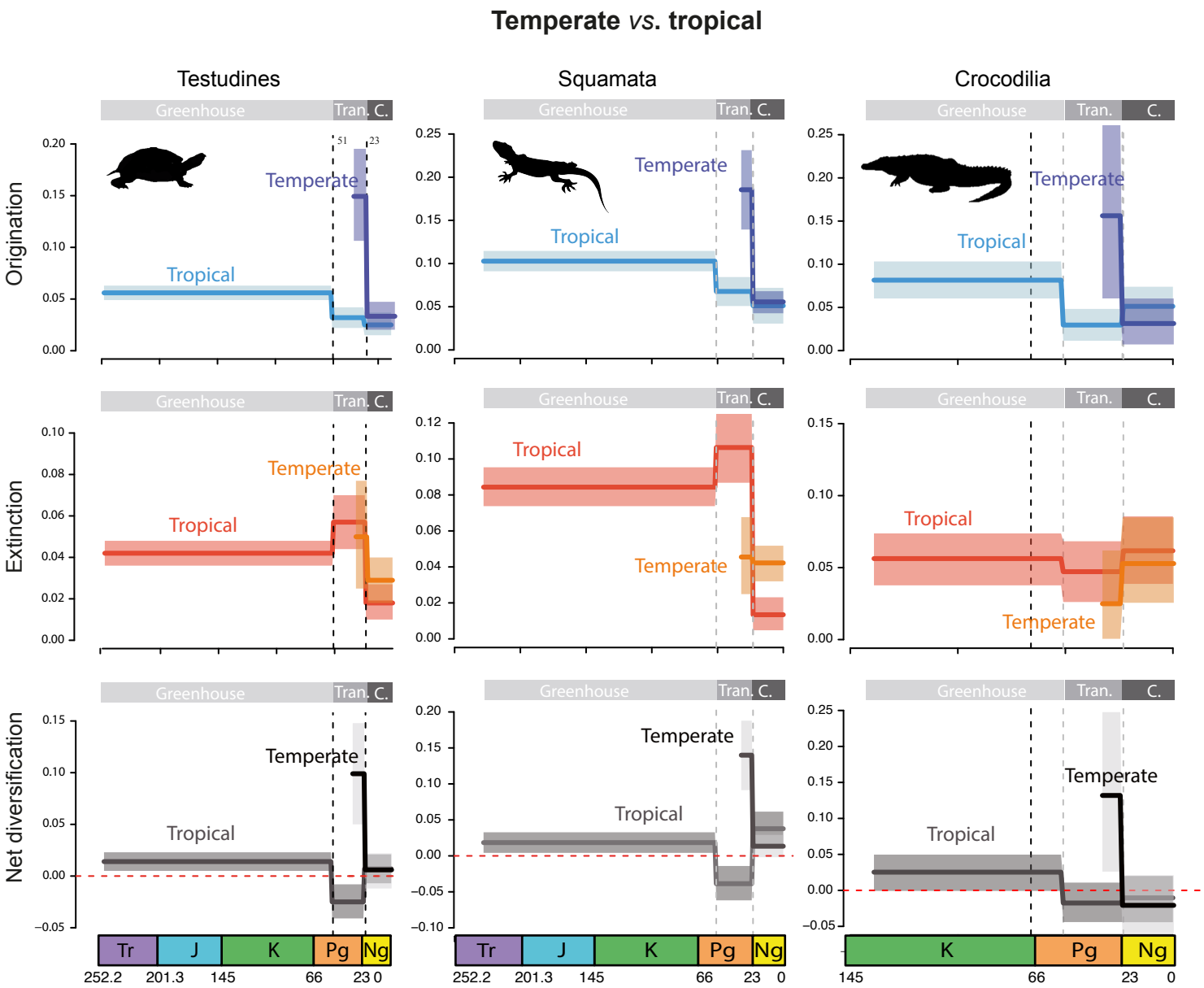

Figure 7 | Global pattern of turtle, squamate and crocodile diversification across temperate and tropical climates, based on the fossil record. Diversification dynamics are compared between fossils inhabiting under temperate and tropical macroclimates. Origination (blue) and extinction (red) rates were estimated using time bins as defined by the main climatic intervals since the Mesozoic (on the top, climatic periods are shown as follows: Greenhouse, Trans. = climatic transition, and C. = coldhouse). Solid lines indicate mean posterior rates, whereas the shaded areas show 95% credibility intervals. Net diversification rates (black) are the difference between origination and extinction. The vertical lines indicate the boundaries between climatic intervals. Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; and Ng, Neogene.

present, suggesting the crocodiles are declining in diversity since then (**Fig. 5**, Supplementary Figs. 16, 17).

We performed additional analyses with different subsets of the three fossil datasets to tease apart the signal of speciation and extinction between geographic regions (equator or Holarctic) and ecological conditions (temperate or tropical, see *Methods*). These analyses evidenced that Paleogene diversity losses in turtles and crocodiles are mostly attributed to species living in the Holarctic and under tropical conditions (**Figs. 6**, **7, Table 2**). The global diversity loss inferred for crocodiles during the Neogene is attributed to both taxa living in Holarctic and equatorial regions, and adapted to tropical and temperate conditions, reinforcing the hypothesis that the group as a whole is in decline. Diversification rates of temperate taxa are estimated high in all groups during the Oligocene but decrease during the Neogene. For the equator dataset, we found a decrease in extinction and speciation rates through time, and more or less constant net diversification (except for squamates, which show a decrease in diversification during the Paleogene, followed by a diversification increase in the Neogene).

Discussion

The genesis of the current LDG

Recent fossil investigations show that, for many groups, diversity levels at high latitudes were more elevated than in the present, or even equivalent to diversity levels in the equator, during some periods of the past[11,12]. This suggests that the LDG should be regarded as a biodiversity pattern that has changed through time, while the previous studies have generally assumed the processes shaping the LDG have acted constantly. Limited dispersal to the Holarctic[30], high Holarctic turnover[34], or high equatorial diversification[31,33,34,45,48,49,64] cannot explain the formation of a flatten LDG, nor the transition to lower diversity in the Holarctic observed in many groups[11,12].

273 To account for temporal changes in the global distribution of biodiversity, we propose
274 the AGE hypothesis that captures components of previous studies[12,30,33,35,46] in the context of a
275 new time-variable framework. When confronting the AGE hypothesis with the LDG of
276 turtles, crocodiles and squamates, this evolutionary scenario receives little support from
277 analyses based on extant species only (**Table 2**). Biogeographic analyses of turtles support the
278 '*tropical niche conservatism*' hypothesis, with an equatorial origin and recent invasion of
279 high latitude regions; thereby lineages had less time to diversify[30] (**Figs. 3**, **4**, **Table 2**), in
280 agreement with recent investigations[72,73]. Time-constant and time-variable BiSSE analyses
281 support a higher Holarctic diversification and the '*into the tropics*' hypothesis for the turtle
282 LDG (Supplementary Figs. 1a, 2a, 3a). For squamates, biogeographic analyses support the
283 '*out of the tropics*' hypothesis, while BiSSE supports both a higher equatorial diversification
284 and the '*into the tropics*' hypothesis to explain their LDG (**Fig. 4**, Supplementary Figs. 1-4).
285 Crocodile biogeographic results support the diversification hypothesis, with higher origination
286 rates in equator and no effect of dispersal (**Fig. 4**, **Table 2**, Supplementary Fig. 5). In contrast,
287 results from the fossil-based analyses are overall in agreement with the AGE hypothesis
288 (**Table 2**).

289 The AGE hypothesis predicts that "*on average*" (i.e. integrated over time under a
290 constant-rate evolutionary model), the diversification of a group was lower in the Holarctic
291 (overall extinction being higher; the "average AGE hypothesis" of **Fig. 2**), as generally
292 accepted for the origin of the LDG[31,32,50,74]. However, the time-variable scenario proposed
293 here allows disentangling the relative contribution of speciation, extinction and dispersal in
294 particular periods for the formation of the LDG. As predicted in the AGE hypothesis (**P1**), we
295 found equivalent diversification rates for turtles, squamates and crocodiles between Holarctic
296 and equatorial regions during the greenhouse period (rates overlap in their credibility
297 intervals; **Fig. 6**; Supplementary Figs. 1-3, 12-17), in agreement with the existence of a flatten

298 LDG during this phase[12]. We found mixed evidence for equivalent dispersals between
299 Holarctic and equatorial regions during greenhouse periods (**P2**) for these groups, with BiSSE
300 showing equal dispersal rates between biomes (**Table 2**, Supplementary Figs. 1-3), but fossil
301 biogeographic analyses indicating higher dispersal rates '*into the tropics*' (**Fig. 4**,
302 Supplementary Table 7). This might not necessarily conflict with the AGE hypothesis, but it
303 rather reflects the idiosyncratic history of these groups with many ancestors distributed in the
304 Holarctic from where they colonized southern regions.

305 Subsequently, our analyses reveal that diversification rates decreased in all regions
306 during the transition to cold climates (**Fig. 5**). Nonetheless, for turtles and crocodiles,
307 diversification slowdowns were more dramatic in the Holarctic than in the equator, where
308 extinction exceeded speciation ($r < 0$) and diversity losses occurred (**P3**; **Fig. 6**).
309 Additionally, our results suggest that turtles and crocodiles had a widespread distribution at
310 their origins that subsequently contracted to the equator due to elevated levels (both in
311 absolute and relative terms) of range extirpations at higher latitudes and "*into the equator*"
312 dispersals[35] during Cenozoic cooling (**P4**; **Figs. 3**, **4**). This result is in agreement with BiSSE
313 results (Supplementary Figs. S2, S3), and with previous fossil investigations on turtles[23,24,70]
314 and crocodiles[22,39]. Hence our results suggest the combined effect of widespread Mesozoic
315 tropical origins, followed by diversity losses and range extirpations at high-latitudes (**Table 2**,
316 **Figs. 6, 7**), and elevated dispersal rates "*into the equator*" (**Fig. 4**) during the climatic
317 transition to cold could have shaped the current steep LDG of turtles and crocodiles.

318 Paleontological evidence attests that paratropical conditions and associated warm-
319 adapted taxa disappeared from high latitudes at some point between the mid-late Eocene (51-
320 34 Ma) to the Neogene (23 Ma)[53,57,58]. Our results with high-latitude extinctions, range-
321 contractions and southward dispersals peaking by the end of the Paleogene, concur with these
322 observations, and indicate that the Cenozoic climate cooling had a profound effect on shaping

323 the current LDG. We cannot discard that diversity losses at high latitudes occurred earlier (as
324 suggested by our fossil-based diversification analyses with time intervals defined by the main
325 geological periods; Supplementary Figs. 12, 14, 16), as the result of the K-Pg mass extinction,
326 because of low temperature excursion brought by the impact winter[75,76]. This scenario,
327 however, might not conflict with our interpretations because our results are consistent
328 showing extinction in the high latitudes to have been superior than in the low latitudes,
329 independently on how time intervals were defined (Supplementary Figs. 12–17). Moreover,
330 both hypotheses are not mutually exclusive; the number of range extinctions and southward
331 dispersals increases from the K-Pg to the Neogene (**Fig. 4**), suggesting an additive effect of
332 K-Pg and Neogene cooling on the depopulation of the Holarctic. Nonetheless, we favour the
333 former hypothesis because *(i)* Eusuchia and Testudines are thought to be marginally affected
334 by the K-Pg boundary events[39,77,78]; and *(ii)* evidence for other organisms point towards
335 diversity recoveries to Cretaceous levels in the high latitudes by the Eocene warming[79,80].
336 Ancestors of turtles and crocodiles were adapted to tropical conditions since the Late
337 Cretaceous[39,81]. Our results show that extinction has not been random, but preferably affected
338 taxa living under a tropical-like climate at high latitudes (**Figs. 6, 7**), which suggest that many
339 of the Holarctic warm-adapted species were unable to adapt to the new temperate regimes and
340 went extinct or escaped extinction contracting their ranges to the south (**Fig. 4**).

341 While our fossil-based results for turtles and crocodiles support the AGE hypothesis,
342 this scenario is only partially supported for squamates. During Cenozoic cooling, squamates
343 in the higher latitudes did not go extinct more than in the equator but the opposite, with
344 diversity losses inferred in the equator (**Fig. 6**). Diversity dynamics for species distributed in
345 the equator, however, are difficult to trust because the equatorial dataset is the poorest of our
346 study due to the small number of fossil lineages and the small number of records per lineage
347 (Supplementary Table 12). As a result, there are uncertainties on the estimated rates with wide

348 credibility intervals probably due to geographic biases in the fossil record[82]. In the Holarctic,
349 turnover was very elevated, indicating that species did disappear from high latitudes but were
350 replaced by a new squamate community. It is possible the number of Squamata species was
351 always imbalanced between regions. The high Holarctic turnover thus contributing to
352 maintain this pattern, together with the increases in diversification inferred in the equator
353 towards the present (**Fig. 6**), as previously hypothesized[34].

354 Nonetheless, high-latitude diversity losses could not be completely ruled out.
355 Although in absolute terms the Holarctic received more immigrant species than species
356 emigrated from the region (Supplementary Fig. 6), the number of species in the equator today
357 is 4-fold the number of lineages in other areas. When controlled for this imbalance sampling
358 of species in our tree, a relatively higher number of species lost their ancestral Holarctic
359 distribution and emigrated towards the equator than the opposite way around (**Fig. 4**). This is
360 in agreement with our BiSSE results and those of Pyron[34] pointing towards a higher rate of
361 dispersal '*into the equator*'. Altogether, the current LDG of squamates could results from the
362 Cenozoic climate cooling through range extinctions and southward dispersals on species
363 distributed in the Northern Hemisphere (**Fig. 4**), and not necessarily by promoting lineage
364 extinctions (**Fig. 6**). In the aim to reconcile the phylogeny and fossil record, we used a
365 number of fossil constrains in our biogeographic analyses of Squamata, but these constraints
366 were relatively low in comparison with the size of the tree (30 fossils for 4161 nodes). The
367 few nodes constrained with fossils increased the absolute number of Holarctic range-
368 extinction and dispersal events '*into the equator*' in comparison with the estimations when
369 fossils were not considered (from 30 to 109 and from 40 to 124, respectively; Supplementary
370 Tables 7, 8). Nevertheless, the inclusion of fossils did not significantly alter the number of
371 events estimated for equatorial taxa. This suggests that a more profound understanding of the

taxonomy of squamate fossils could help to assign more fossils in the tree and detect other high-latitude range extinctions probably missed in this study.

Reconciling fossil and phylogenetic evidence

Our results unequivocally evidence the inclusion of fossils in macroevolutionary studies allows detecting the signal of ancient high-latitude extinctions and range extirpations (**Figs. 4-6**), otherwise hidden from the analyses based on present-day data. Only '*into the equator*' dispersals were detected with BiSSE models, but not with unconstrained biogeographic analyses[72,73] (**Figs. 3**, **4**, Supplementary Figs. 4, 5).

This conflict between extant and fossil evidence might not only pervade our study but also the LDG literature. On the one hand, high extinction rates have seldom been inferred among tropical lineages (but see ref.[83-85]). Hypotheses on extinction have often focused on temperate taxa and on recent times, notably on the effects of recent Pleistocene glaciations[33,34,36,37,48]. When extinction was reported, it was accompanied by elevated origination rates (high turnover) in high latitude groups[31-34,36,48-51]. Importantly, to our knowledge, diversity losses ($r < 0$) have never been inferred in phylogenetic studies of the LDG (note that the negative diversification rates, inferred for the entire history of temperate bird groups[45], are likely an error of the time-constant BiSSE model, because this result conflicts with the fact that these group are still extant).

On the other hand, ancient tropical extinction in high latitudes is supported by fossil studies documenting comparable diversity levels across latitudes during the greenhouse Paleogene, followed by diversity losses at higher latitudes during the climatic transition. For instance, Archibald *et al.*[15,16] sampled insect diversity at an Eocene site in Canada, and in present-day temperate Massachusetts (USA) and tropical sites of Costa Rica. Insect diversity was higher at the Eocene paleotropical site than the modern temperate locality, and

397 comparable to the modern-day tropical locality. Post-Eocene insects have thus suffered
398 greater levels of extinction in the Nearctic than around the equator. This pattern is consistent
399 with results of other studies on various groups like birds[41,86], invertebrates[42,87], mammals[11,88]
400 or plants[89,90].

401 If extinction of tropical clades in the high latitudes was paramount and trait dependent
402 (tropical-adapted lineages having higher risk of extinction), entire tropical clades could have
403 disappeared without leaving any phylogenetic footprint. This might be the case for crocodiles,
404 turtles and squamates, in which extinction preferably affected warm-adapted lineages at high
405 latitudes during a cooling climate (**Fig. 7**), and in which most evidence of an ancient Holarctic
406 and southern temperate distributions were erased by species extinctions and range
407 contractions (**Figs. 4, 6**). Although the recent decade has witnessed many efforts to reconcile
408 fossil and phylogenetic evidence[91,92], simulation and empirical studies have shown that under
409 such asymmetric-rate scenarios, phylogenetic comparative methods tend to fail to recover the
410 correct processes, simply because there is not enough information in the phylogeny to predict
411 the loss of the focal character along each terminal branch[44,69,93-95]. Consequently, if the LDG
412 was shaped by asymmetric extinction and dispersal, as we hypothesized here, the diversity
413 patterns we observe today for many groups might be a poor representation of the historical
414 diversification processes (**Figs. 3**, **4**), and the inclusion of fossils might be crucial to the study
415 of the LDG[96]. Although we acknowledge the fossil records are not complete: fossils still
416 represent the unique evidence of the diversity that existed in the past. In contrast to molecular
417 phylogenies, the incompleteness of the fossil record have a less problematic effect on the
418 estimation of speciation and extinction rates because removing a random set of taxa does not
419 affect the observed occurrences of other lineages[71]. Simulations have shown that PyRate
420 estimates correctly the dynamics of speciation and extinction rates under low levels of
421 preservation or severely incomplete taxon sampling.

422 Studies on the LDG are often based on state-dependent speciation and extinction
423 models[33,34,35,45,48,97]. Though these models are conceived to test scenarios of differential
424 diversification and asymmetric transitions as the one suggested here, studies on the LDG
425 often assumed that diversification parameters remain constant through time[33,34]. If the
426 evolutionary processes shaping the LDG have varied across latitudes and time, using time-
427 constant models has little power to test more complex scenarios behind the LDG. Testing our
428 scenario requires the implementation of time-variable models. When applied to the study of
429 diversity patterns, these models have revealed notable signatures of extinction among
430 ancestral tropical plant clades, showing that large temperate groups do not form monophyletic
431 radiations, but rather polyphyletic clusters of lineages derived from the tropics and masked by
432 extinction[98]. Incorporating time-shifts in our BiSSE analyses, however, has not completely
433 reconciled fossil and extant evidence, although the time-variable BiSSE analyses correctly
434 identified the main direction of dispersal in different periods. While providing the causes and
435 solutions to this issue goes beyond the purpose of this study, this potential artefact highlights
436 the importance of fossils in macroevolutionary inferences.
437
438 ***Diversification differences between temperate- and tropical-adapted taxa***
439 A long-standing question in ecology and evolution, directly related to the formation of the
440 LDG, is whether diversification rates differ between taxa living under temperate or tropical
441 climates. The metabolic theory of ecology predicts that warm tropical environments prompt
442 higher speciation rates than colder climates, mainly due to increased rates of molecular
443 evolution[99], and/or to higher mutational robustness[100]. This theory received support in the
444 literature[101], but other studies later suggested per capita speciation rates are highest in the
445 temperate zone[34,36,102,103]. Answering this question requires to consider that the today's
446 equatorial belt merely represents a fraction of the wider extension that the tropics had in

447 deeper times and the Holarctic once housed lineages with tropical-like affinities[57,58,62] (**Fig.**
448 **1**). Hence, geographic-based diversification results cannot be directly extrapolated to assess
449 diversification differences between ecological preferences, because if high extinction rates are
450 estimated for taxa in the Holarctic, extinction could have affected lineages living under both
451 tropical and temperate conditions (depending on the time interval). In this sense, we think it
452 has been overlooked that the main hypotheses on the LDG have sought to answer two related
453 but slightly different questions, which could explain some of the discrepancies found between
454 ecological and phylogenetic perspectives.

455 Here, we found that diversification rates of turtles, crocodiles and squamates living
456 under temperate climatic conditions were significantly higher than rates of tropical-adapted
457 taxa right after the late Eocene settlement of temperate climates (**Fig. 7**, **Table 2**). The new
458 temperate niches could have constituted an opportunity for diversification because of
459 increased geographic ranges and ecological opportunities[49]. Several radiations have been
460 identified in other temperate groups following the apparition of the temperate biome such as
461 plants[51,104-106], mammals[107,108] or insects[32]. After this period, speciation dramatically
462 decreased for temperate lineages, maybe due to the effect of the Pleistocene glaciations, and
463 no difference in diversification between tropical- and temperate adapted lineages could be
464 currently observed (**Fig. 7**, Supplementary Figs. 1-3).

465

466 ***Conclusion***

467 The foundations of a plausible explanation to understand large-scale diversity patterns in
468 terms of ecology and evolution are progressively assembling as we develop analytical
469 tools[95,109,110], accumulate data from several fields, and combine them into a single
470 framework[96]. We propose a framework explaining the origin of the today's LDG, where its
471 shape is mostly determined by changes in the global diversification and dispersal dynamics

472 imposed by large-scale climatic transitions. Our analyses suggest that the LDG is probably the
473 product of ancient tropical extinctions and Holarctic range contractions as the consequence of
474 the retraction of the tropical biome. We acknowledge the AGE hypothesis might not be
475 applicable to all organisms. As exemplified here, tropical extinction is not the most influential
476 cause behind the LDG of squamates. But the AGE hypothesis will be useful to explain the
477 LDG of groups that once were diverse at high latitudes. We acknowledge as well we consider
478 large geographical areas and long-time intervals that likely encompass high variability in
479 habitats and climates. The AGE hypothesis represents an effort to increase the complexity of
480 evolutionary models behind the LDG.
481

482 **Methods**

483 ***Time-calibrated phylogenies and fossil record.*** We confront the predictions of the AGE
484 hypothesis with the LDG of three vertebrate groups: turtles (order Testudines), crocodiles
485 (order Crocodilia), and the scaled reptiles (order Squamata), which are ancient clades that
486 experienced early Cenozoic climatic transitions[22,23,34,111]. They display contrasting patterns of
487 species richness: turtles and crocodiles are species-poor (330 and 25 species, respectively),
488 while squamates are species-rich (9400+ species). They all have a rich fossil record going
489 back to the Triassic for turtles and squamates (Early Cretaceous for crocodiles), which can
490 inform on how the latitudinal accumulation of species richness has varied through its
491 evolution[22,23,39]. Turtles are also remarkable because they show today a hump-shaped
492 diversity gradient centred around subtropical latitudes (10°S–30ºN)[111], while the
493 paleolatitudinal distribution of turtles was concentrated in the Holarctic, between 30–60ºN
494 during the Cretaceous[23,24].

495 Time-calibrated phylogeny for each group was obtained from published studies. For
496 turtles, we used the time-calibrated phylogeny of Jaffe *et al.*[112] including 233 species. We

497 preferred this phylogeny over other more recent and slightly better sampled trees[113] because
498 the divergence times estimates in Jaffe *et al.*[112] are more congruent with recent estimates
499 based on genomic datasets[72,114]. For squamates, we retrieved the most comprehensive dated
500 tree to date including 4161 species[34], and for crocodiles we obtained a complete phylogeny[115].
501 Fossil occurrences were downloaded from the *Paleobiology Database*
502 (https://paleobiodb.org/#/, last accessed October 25th 2017). To reduce potential biases in the
503 taxonomic assignation of turtle, crocodiles and squamates fossils, we compiled occurrence
504 data at the genus level. The fossil datasets were cleaned by checking for synonymies among
505 all taxa and for assignment to particular genus or family based on the literature
506 (Supplementary Table 9–11).
507
508 ***Estimation of origination and extinction rates with the phylogenies.*** To address whether
509 diversification differs between Holarctic and equatorial regions, we used the turtle and the
510 squamate phylogeny combined with distributional data (Supplementary Tables 1, 2) to fit
511 trait-dependent diversification models in BiSSE[65]. We also accounted for incomplete taxon
512 sampling, which is informed as a global sampling fraction of species at present having a given
513 trait[116].
514 To make our approach comparable with previous LDG studies[33-35,45,48], we first relied
515 on a constant-rate trait-dependent diversification model. The constant-rate BiSSE model has
516 six distinct parameters: two speciation rates (without range shift, or *in situ* speciation)
517 associated with Holarctic (hereafter "H", λ_H), and species occurring in other equatorial and
518 subtropical regions (hereafter "equator" or "E", λ_E), two extinction rates associated with
519 Holarctic (μ_H) and equator (μ_E), and two transition rates (dispersal or range shift) with one out
520 of Holarctic to equator (q_{H-E}), and from equator to Holarctic (q_{E-H}).

521 We also assessed the effect of species distribution on diversification, while allowing
522 for rates to change at specific points of time, which reduces the bias of using constant rates,
523 and allow testing the role of extinction and climate change on the generation of the LDG. We
524 used the time-dependent BiSSE (BiSSE.td) model, in which speciation, extinction, and
525 dispersal rates are allowed to vary between regions and to change after the shift times[98]. We
526 introduced two shift times to model different diversification dynamics between greenhouse,
527 transitional, and coldhouse periods; we assumed that a global warm tropical-like climate
528 dominated the world from the clades' origin to 51 Ma (the peak of temperature in the
529 Cenozoic), which then progressively cooled until 23 Ma (the transitional period), when
530 climate definitely shifted to a temperate-like biome in the Holarctic[59]. The shift times at 51
531 Ma and at 23 Ma are initial values that are re-estimated by the model during the likelihood
532 calculation. The climatic transition in the Cenozoic can have different temporal boundaries,
533 which might influence the results. We thus applied the same model but with different
534 combination of shift times (we tested 51/66 Ma and 34/23 Ma for the upper and lower bounds
535 of the climatic transition).

536 Analyses were performed using the R-package *diversitree* 0.9-7[66] using the functions
537 *make.bisse* to construct the likelihood functions for each model based on the data, and the
538 functions constrain and *find.mle* to apply different diversification scenarios. Finally, we used
539 a Markov Chain Monte Carlo (MCMC) approach to examine the credibility intervals of the
540 parameter estimates. Following the recommendations from FitzJohn[66], we used an
541 exponential prior 1/(2r) and started the chain with the parameters obtained by maximum
542 likelihood. We ran 10,000 steps of MCMC and applied a burn-in of 10%.

543

544 ***Inferring ancestral geographic distribution with and without fossils.*** We performed
545 biogeographic analyses with the parametric likelihood method DEC[69] using the fast C++

546 version[117]. Turtle, squamate, and crocodile species distributions were obtained from online
547 databases (www.iucnredlist.org and www.reptile-database.org). We chose 23.4°N and 23.4°S
548 as the threshold latitudes defining the tropics and categorized each species as living in the
549 Holarctic, in the southern temperate regions, or in the equatorial tropics and subtropical
550 regions[48]. We considered that all ranges comprised of three areas could be an ancestral state
551 (*maxareas* =3).

552 We set up three different DEC analyses: first, we run DEC without particular
553 constraints using only the distribution of extant species. Then, we performed DEC analyses
554 including fossil information in the form of 'fossil constraints' placed on certain nodes,
555 according to the range of distribution of fossil occurrences assigned to a particular taxon
556 during the relevant time frame. For example the crown age of Carettochelyidae (Testudines)
557 dates back to the Late Jurassic (150 Ma, *node 5*, **Fig. 3**; Supplementary Table 4), and we set a
558 constraint on this node reflecting the distribution of all the Late Jurassic fossils attributed to
559 this clade. Similarly, for the origin of turtles (210 Ma, *node 1*), distribution constraints
560 represent the range of Late Triassic fossils assigned to turtles. For the crown of Trionychidae,
561 which is Early Cretaceous age (123 Ma, *node 2*), the early fossils assigned to the clade were
562 used to constraint the geographic origin of Trionychidae (Supplementary Table 4). In total,
563 we implemented 23 fossil constraints for turtles (Supplementary Table 4), 30 fossil
564 constraints for squamates (Supplementary Table 5), and 8 for crocodiles (Supplementary
565 Table 6).

566 We included the fossil distribution following two different approaches: *(i)* a hard
567 (HFC), and *(ii)* a soft fossil constraints (SFC). With HFC, estimation of ancestral areas was
568 fixed to the fossil occurrence location. This was done using existing functions in the C++
569 version of Lagrange[117] (https://github.com/rhr/lagrange-cpp), with the command "*fixnode*".
570 By fixing nodes to the area of distribution of fossils, we assume fossil occurrences reflect the

571 distribution of the ancestors, *i.e.* the fossil record is complete. For SFC approach, fossil data
572 are incorporated into the anagenetic component of the likelihood framework. The direct
573 impact of a given fossil is limited to the particular branch to which it has been assigned,
574 although it may indirectly influence other branches. The inclusion of a fossil conditions the
575 estimated geographic-transition probability matrix for that branch by imposing a spatio-
576 temporal constraint on the simulation process. Only those simulations that realize a
577 geographic range that includes the area of fossil occurrence will contribute to the geographic-
578 range transition probability matrix of that branch; simulations that fail this constraint will be
579 discarded[118]. For SFC, we used the command "*fossil*" on DEC. We consider this as a "soft"
580 constraint because other areas different to that of the fossil could be included in the ancestral
581 states.

582 We then compared the timing and number of range extinction and dispersal events
583 inferred with the three different biogeographic analyses. In DEC, range-subdivision
584 (inheritance) scenarios (vicariance, duplication and peripatric isolation) occur at cladogenetic
585 events, while extinction (range contraction) and dispersal (range expansion) are modelled as
586 stochastic processes that occur along the branches of the tree[44,119]. Since the probability of any
587 extinction/dispersal event to occur is equal across all the branch length[69], to estimate the
588 periods at which range extinction and dispersal occurred, we divided the phylogeny in
589 intervals of 25 Ma and calculated the number of branches in which extinction/dispersal was
590 inferred that cross a particular time interval (the same branch could cross two continuous
591 intervals).

592

593 ***Estimation of origination and extinction rates with fossils.*** We analysed the three fossil
594 records using a Bayesian model to simultaneously infer the temporal dynamics of origination
595 and extinction, as well as the preservation rates[71]. This approach, implemented in PyRate[120],

596 uses fossil occurrences that can be assigned to a taxon, in this case fossil genera, and it jointly
597 models the preservation and diversification processes. The preservation process infers the
598 individual origination and extinction times of each taxon based on all fossil occurrences and
599 on an estimated preservation rate, and expressed as expected occurrences per taxon per Myr.

600 We followed the birth-death shift approach developed by Silvestro *et al.*[121], which is
601 focused on variation in origination and extinction at global scale and large temporal ranges.
602 We used a homogeneous Poisson process of preservation (-mHPP option). We also accounted
603 for varying preservation rates across taxa using the Gamma model with gamma-distributed
604 rate heterogeneity (-mG option). We used four rate categories to discretize the gamma
605 distribution, to accommodate the potential for more variability of preservation rates across
606 taxa.

607 Because of the number of occurrences analysed and of the vast timescale considered,
608 we dissected the birth–death process into time intervals, and estimated origination and
609 extinction rates within these intervals. In one set of analyses we defined the time intervals
610 using the geological epochs of the stratigraphic timescale[122] (Supplementary Figs. 12, 14, 16).
611 In another set of analyses, we defined the intervals with the different climatic periods that
612 characterized the Cenozoic (Supplementary Figs. 13, 15, 17), as discussed in the main text.
613 We adopted this solution as an alternative to the algorithms implemented in the original
614 PyRate that jointly estimate the number of rate shifts and the times at which origination and
615 extinction undergo a shift[71,120]. The estimation of origination and extinction rates within fixed
616 time intervals improved the mixing of the MCMC and allowed us to obtain an overview of the
617 general trends of rate variation throughout a long timescale[121]. Both the preservation and the
618 birth–death processes are still modelled in continuous time and are not based on boundary
619 crossings. Thus, the origination and extinction rates are measured as the expected number of
620 origination and extinction events per lineage per Myr. One potential problem in fixing *a*

621 *priori* the number of rate shifts is over-parameterization. We overcame this issue by assuming
622 that the rates of origination and extinction are part of two families of parameters following a
623 common prior distribution, with parameters estimated from the data using hyper-priors[123].
624 We ran PyRate for 10 million of MCMC generations on each of the 10 randomly
625 replicated datasets. We monitored chain mixing and effective sample sizes by examining the
626 log files in Tracer 1.6[124]. After excluding the first 20% of the samples as burn-in period, we
627 combined the posterior estimates of the origination and extinction rates across all replicates to
628 generate rates-through-time plots. Rates of two adjacent intervals were considered
629 significantly different when the mean of one lay outside of the 95% credibility interval of the
630 other, and conversely. We looked at the marginal posterior distributions of origination and
631 extinction rates through the evolutionary history of the three groups and looked at the effect
632 of the major environmental changes like the greenhouse world (Cretaceous), the climatic
633 transition (Paleogene), and the icehouse world (Neogene until the present).
634 In the context of the LDG and the hypothesis of tropical extinction, we performed
635 additional analyses with different subsets of fossils to tease apart the signal of speciation and
636 extinction between geographic regions (equator or Holarctic) and ecological conditions
637 (temperate or tropical). For example, for turtles, we split the global fossil dataset into four
638 subsets: one for the fossil genera occurring in the equator (429 occurrences), one for the
639 fossils occurring in the Holarctic (3558 occurrences), one for the fossil genera considered as
640 being adapted to temperate conditions (993 occurrences), and one for the fossils considered
641 being tropically adapted (2996 occurrences). We excluded the few fossil occurrences for the
642 southern regions of the South Hemisphere (about 180) for the different subset analyses, as
643 they are poorly represented in our dataset. Note that a given fossil can be present both in the
644 'Holarctic' and in the 'tropical' datasets. To encode tropical/temperate preferences, we
645 considered that conditions in the Holarctic were paratropical until the end of the Eocene

646 following[57-59] (and references therein), and assumed that taxa inhabiting the warm Holarctic
647 were adapted to tropical-like conditions (*i.e.* a high global temperature would indicate
648 probable adaptations to tropical climates). This is, of course, a simplifying assumption that
649 may cause bias in the analysis, but general patterns might still emerge from it[125]. Further, this
650 assumption could be justified by the presence of early Cenozoic vegetation assemblages in the
651 Holarctic that represent tropical vegetation, as evidenced by paleofloristic composition[53,56].
652 For turtles, this assumption is supported by a recent study that modelled their climatic niche
653 during the Late Cretaceous and found that Holarctic ancestors of turtles were adapted to
654 tropical conditions[81]. After the late Eocene, we categorized each species as living in the
655 temperate biome or the tropical biome following the threshold latitudes defining the tropics
656 (23.4°N and 23.4°S) following ref.[48]. This delineation is also overall congruent with the
657 Köppen climate classification. With these datasets, we reproduced the exact same PyRate
658 analyses than for the whole datasets (see above). In general, the fossil datasets include mostly
659 Holarctic fossils, with a more limited number of occurrences for the equator. Therefore we
660 remain cautious with the conclusions derived from the equatorial datasets.
661

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Author contributions

Both authors designed the study, analysed the data and wrote the manuscript.

Competing interests

The authors declare no competing financial interests.