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

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Abstract

Biodiversity currently peaks at the equator, decreasing towards the poles. Growing fossil evidence suggest that this hump-shaped latitudinal diversity gradient (LDG) has not always existed, with periods of similar species diversity across latitudes flattening out the LDG during past "greenhouse" periods. This provides a new starting point for LDG research. Most studies test hypotheses to explain the higher accumulation of diversity in the tropics than in the temperate regions, through limited dispersal, higher equatorial diversification, and higher turnover in temperate regions, for example. However, fossil investigations suggest that we need to explain when and why diversity was lost at high latitudes to generate the LDG. Here, we outline the 'asymmetric gradient of extinction' (AGE) framework, which formalizes and expands previous ideas of extinction behind the LDG in the context of a time-variable scenario. We suggest that the current steep LDG may be explained by the extinction of clades adapted to warmer conditions from the new temperate regions formed in the Neogene, together with the equator-ward dispersal of organisms tracking their own climatic preferences, when tropical biomes became restricted to the equator. Conversely, high rates of speciation and pole-ward dispersal can account for the formation of an ancient flat LDG during the Cretaceous–Paleogene greenhouse period. Phylogenies and fossils of the Testudines, Crocodilia and Squamata showed the LDG to have varied over time, with high latitudes serving as a source of tropical diversity during periods of warm climate, whereas paramount extinctions of tropical lineages and range contractions due to equator-ward dispersals during the transition to colder climates impoverished the Holarctic, shaping the current LDG. Our results demonstrate that the inclusion of fossils in macroevolutionary studies allows detecting extinction events undetectable in analyses restricted to present-day data only.

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

Introduction

The current increase in species richness from the poles towards the equator, known 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].

For decades, the current steep LDG (with higher diversity at the equator) has been thought to date back several million years, to the respective origins of the groups of organisms concerned, and to have been maintained thereafter[7]. This hypothesis is based on published fossil record studies suggesting that the steep LDG persisted through the Phanerozoic, over the last 540 million years[8,9]. However, the methodological limitations of fossil sampling have called this conclusion into question[10,11]. Analyses controlling for sampling bias have suggested that, for many groups, the LDG was less marked in the past than it is today, and that this gradient may even have been flat (*i.e.* with similar species diversity across latitudes) during some periods in the past (see ref.[12] for a review). This has been shown to be the case for 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], and plants[25,26]. The pattern emerging from fossil studies also suggests that steep LDGs, such as that currently observed, have been restricted to the relatively small number of short "coldhouse" periods during the history of the Earth: the Ordovician/Silurian, the Carboniferous/Permian, the end of the Jurassic, and the Neogene[12,27-29]. Most of the Phanerozoic has instead been characterized by warm greenhouse climates associated with a flatter LDG[10,11,13,16] (**Fig. 1**).

Recent fossil evidence has provided a new starting point for LDG research. Most hypotheses are based on the assumption that equatorial regions are the source of world diversity[30,31], the aim being to explain the lower level of diversity accumulation in the Holarctic than at the equator through time[7,32,33]. Previous studies have explained the LDG as a

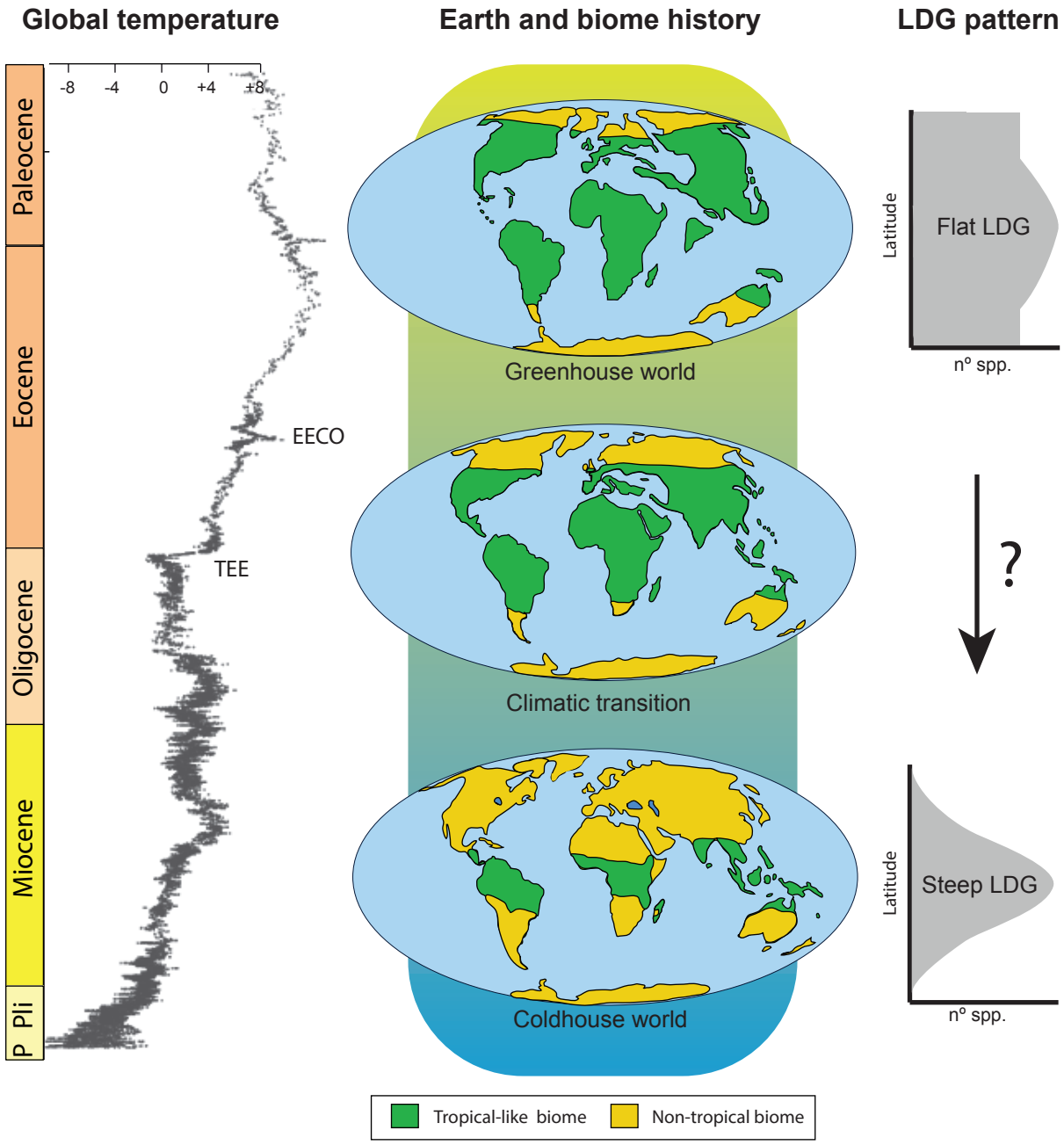

Figure 1 | Changes in global temperature and extension of the tropical belt during the Cenozoic, in relation with the shape of the LDG. Early Cenozoic global temperatures were higher than today and paratropical conditions extended over northern and southern latitudes. From the early Eocene climatic optimum (EECO; ca. 53-51 Ma), a global cooling trend intensified on Earth and culminated with the Pleistocene glaciations. Global cooling was punctuated by sharp declines of temperatures, such as the terminal Eocene Event (TEE, ca. 33.9 Ma) and periods of relative warmth. Warm-equable regimes got then restricted to the equator. The LDG evolved following these global changes[12]; during greenhouse periods diversity was uniform across latitudes, such that the LDG flattened, while in 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]. Abbrev.: P=Pleistocene, Pli=Pliocene

77 result of greater diversification and limited dispersal out of the equatorial region[7,32,34], or by
78 high rates of turnover in the Holarctic (*i.e.* similar high speciation and extinction rates),
79 keeping diversity levels in this region low over time (**Table 1**), for amphibians[35,36],
80 birds[33,37,38], butterflies[39], conifers[40], fishes[41], mammals[34,38], and squamates[42], for example.
81 Here, we group these mechanisms together under the 'low Holarctic species accumulation'
82 hypothesis, because they all assume that the LDG results from lower levels of species
83 accumulation in the Holarctic than at the equator. However, recent fossil investigations have
84 shown that, for many lineages, diversity levels in the Holarctic were once similar to those at
85 the equator. Thus, the real question is why, how and when was diversity lost at high latitudes,
86 giving rise to the current shape of the LDG?.

87 Phylogenetic investigations have suggested potential mechanisms that might explain
88 the transition from high to low Holarctic diversity. Some studies have considered high
89 latitudes as a possible source of diversity, with the high species richness observed in the
90 tropics today resulting from differential dispersal (*d*) from high to low latitudes following the
91 contraction of the tropical biome[39,42,43]. However, disproportionate high-latitude extinctions
92 — a scenario in which extinction (μ) outweighs speciation (λ), resulting in negative net
93 diversification rates ($r = \lambda - \mu; r < 0$) — could also explain this transition. Diversity losses
94 in the Holarctic are sometimes considered to underlie the LDG[38]. They were initially
95 attributed to Pleistocene glaciations[44], but this hypothesis has been called into question by the
96 finding that the LDG predates the Pleistocene[7,12]. More ancient extinctions have also been
97 considered[45-52]. For example, Hawkins *et al.*[49] suggested that the avian LDG resulted from the
98 differential extirpation of older warm-adapted clades from the temperate regions newly
99 formed in the Neogene. Unfortunately, it is difficult to demonstrate diversity losses in the
100 Holarctic beyond high regional turnover[31,38], but this phenomenon can account only for a slow
101 accumulation of lineages, not for diversity decline. The difficulty inferring extinction rates

Table 1. Predictions of the most common LDG hypotheses, including the *Asymmetric gradient of tropical extinction* (AGE) hypothesis proposed in this study. The main evolutionary hypotheses published to date can be classified according to three criteria: **(1)** the mechanisms behind regional differences in species richness[7], including explanations based on evolutionary time, on dispersal *(d),* and on diversification *(r=λ, μ)*. Explanations based on evolutionary time assume that most groups originated in the tropics and had less time to diversify in the temperate regions[127], but regional differences in evolutionary rates are not invoked. Hypotheses focussing on the role of geographic movements *(d),* include the "*tropical niche conservatism*" model, assuming that most groups originated in the tropics and the LDG results from limited dispersal to the temperate regions, as only few of tropical species succeeded to adapt to the temperate regimes[32]. The "*out of the tropics*" model synthesizes this idea that the tropics are regarded as both a cradle and a museum, with lineages preferentially originating in the tropics and expanding over time into high latitudes[28,30]. The "*Into the tropics*" model assumes instead the LDG results from dispersals towards the equator[39,43]. Hypotheses that emphasize the LDG is generated by regional differences in net diversification rates (the composite value $r = \lambda - \mu$), being higher in the tropics[33,35] assume that the outstanding tropical diversity could be the outcome of higher rates of speciation in the tropics than in the extra-tropical regions ($\lambda_t > \lambda_e$) under the "*cradle of diversity*" hypothesis, and/or could result from lower rates of extinction ($\mu_t < \mu_e$) under the "*museum of diversity*" hypothesis[128]. The LDG could also result from higher turnover rates (*i.e.* higher λ and μ) in the Holarctic[38]. Diversification and dispersal hypotheses are not mutually exclusive. In addition, evolutionary hypotheses could be classified according to **(2)** the rate at which processes acted through time; most studies assumed evolutionary processes acted constantly through time to explain the LDG. The AGE model, conversely, includes various diversification and dispersal parameters for each temporal interval (greenhouse, coldhouse, transition). **(3)** Finally, the hypotheses can be classified according to the source of tropical diversity: "*Lower Holarctic species accumulation"* hypotheses assume that the equator is the source of world diversity and species accumulated at slower rates on the higher latitudes. Conversely, "*Holarctic diversity loss"* hypothesis assumes the Holarctic was also a source of diversity but this diversity was lost at some periods of the evolutionary history (e.g. climate change from greenhouse to coldhouse).

1. mechanism	Time (*t*)	Differences in *r*			Differences in *d*		Both			
2. rate	Time-constant models							Time-variable models		
3. source	Lower Holarctic species accumulation							Holarctic diversity loss		
Hypothesis (reference)	***Time for speciation***[127]	***Cradle of diversit***[128]	***Museum of diversity***[128]	***Holarctic turnover***[38]	***Into the tropics***[39,43]	***Tropical niche conservatism***[32]	***Out of the tropics***[23,30]	***Asymmetric gradient of extinction***		
								Greenhouse	**Transition**	**Coldhouse**
Predictions	$t_{trop} = t_{temp}$ ($r_{trop} = r_{temp}$) ($d_{trtp} = d_{tptr}$)	$r_e > r_h$ ($\lambda_e > \lambda_)$ $d_{eh} = d_{he}$	$r_e > r_h$ ($\mu_e < \mu_h$) $d_{eh} = d_{he}$	$r_h = 0$ ($\mu_h = \lambda_h$) $d_{eh} = d_{he}$	$r_e = r_h$ $d_{eh} < d_{he}$	$r_e = r_h$ $d_{eh} > d_{he}$	$r_e > r_h$ ($\lambda_e > \lambda_h$) ($\mu_e < \mu_h$) $d_{eh} > d_{he}$	$r_e = r_h$ $d_{eh} = d_{he}$	$r_e > r_h$ ($\mu_h > \lambda_h$) $d_{eh} < d_{he}$	$r_e > r_h$ ($r_h = 0$) $d_{eh} = d_{he}$

Abbreviations: λ = speciation, μ = extinction, *d* = dispersal, *t* = time, e = equatorial, h = Holarctic, trop = Tropical biome, temp = Temperate biome.

from present-day data[53,54] and the assumption that diversity levels were always lower in the Holarctic than at the equator have resulted in 'diversity loss' hypotheses seldom being considered (but see refs.[42,45,52]).

This article has two goals: 1) to outline a new framework for studying the LDG, the 'asymmetric gradient of extinction' (AGE) model, which formalizes and expands previous notions about the contribution of extinctions to the LDG in the context of a time-variable pattern; 2) to test the predictions of the AGE model.

From a flat to a hump-shaped LDG: an asymmetric gradient of extinction

Over the history of the Earth, the geographic extent of the tropical biome around the equator has fluctuated, with periods of pole-ward expansion during which warm paratropical conditions appeared at high latitudes[54-57], followed by periods of equator-ward contractions[58,59] (**Fig. 1**). The last 100 million years have been a period of contraction towards the equator, due to the cooling of the Earth since the Cretaceous–early Cenozoic period (the most recent greenhouse period), culminating in the Pleistocene glaciations[60]. According to the AGE model, the expansion of tropical-like conditions to higher latitudes induced species diversification in the new paratropical areas (**Fig. 2a**) and facilitated movements within the broad '*paleotropical belt*', such that tropical equatorial clades were able to disperse *'out of the equator'* into high-latitude warm regions[28,30] (or towards the south in the case of northern origins). An equable Cretaceous-early Cenozoic greenhouse climate thus triggered the formation of a flat LDG (**Fig. 2a**). By contrast, tropical biome retractions following the cooling of the climate in the late Eocene induced periods of declining diversity at high latitudes (where climate change was more intensively felt), and initiated biotic movements '*into the equator*' (**Fig. 2b**). Extinction rates were high for tropical-adapted lineages at high latitudes, but lower for low-latitude tropical lineages. Climate change would thus have driven

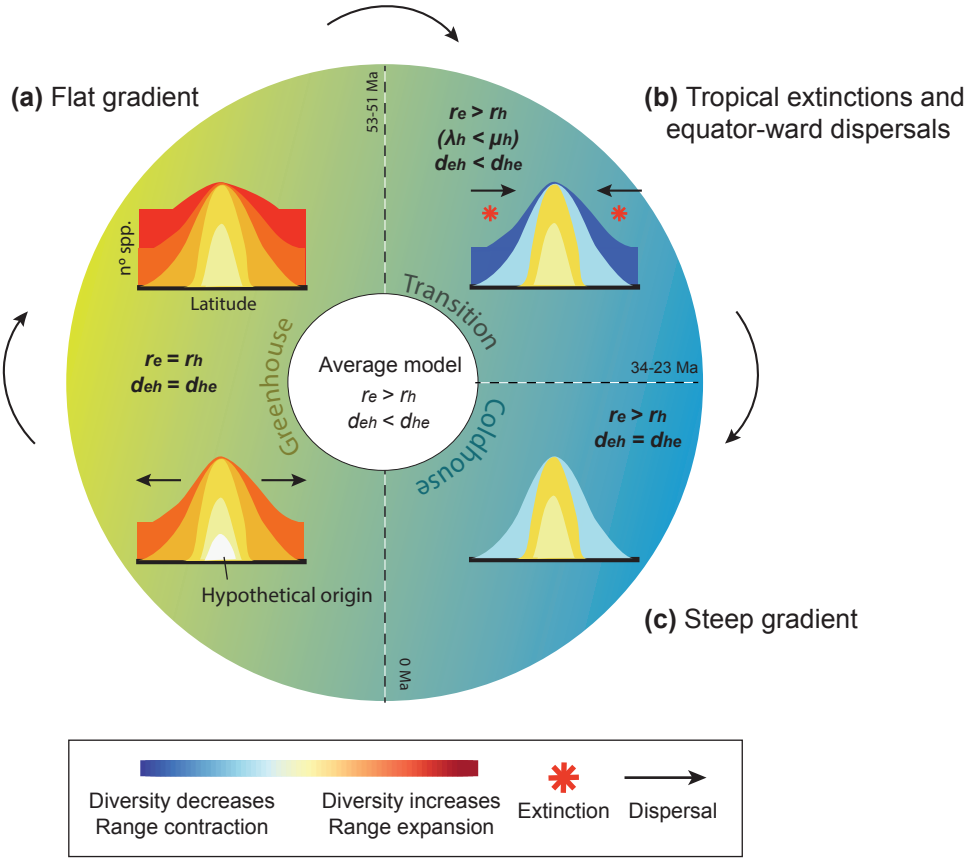

Figure 2 | Prevalent evolutionary processes behind the latitudinal diversity gradient under the AGE time-variable framework. The graphic shows the hypothetic change in evolutionary dynamics (diversification "r", speciation "λ", extinction "μ" and dispersal "d") between Holarctic and equatorial regions (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 in the AGE hypothesis under a single, constant rate, evolutionary model.

127 the development of an asymmetric gradient of extinction within the tropical biome, and
128 mediated the formation of a steep LDG (**Fig. 2c**). The AGE model imposes a temporal
129 context in the study of the LDG, in which prevailing speciation, extinction and dispersal
130 dynamics change between warm and cold intervals.

131 The predictions (P) of the AGE model could be formulated as follows (**Fig. 2; Table**
132 **1**): **P1**; similar diversification rates between Holarctic ($_H$) and equatorial ($_E$) regions during
133 greenhouse periods ($r_E = r_H$), **P2**; similar dispersal rates between Holarctic and equatorial
134 regions during greenhouse periods ($d_{HE} = d_{EH}$), **P3**; extinction rate exceeding the speciation
135 rate at high latitudes during climatic transitions towards cooler climates, *i.e.* declining
136 diversity ($r_H < 0$), with the equatorial regions remaining stable, and **P4**; rate of dispersal '*into*
137 *the equator*' greater than that '*out of the equator*' during climatic transitions ($d_{HE} > d_{EH}$).

138 The AGE model is based on the notion of niche conservatism due to physiological
139 limits[31,32]: when the tropical biome retreated towards the equator, most of the tropical-adapted
140 taxa at high latitudes were unable to adapt and either went extinct or suffered restrictions of
141 their distributions. Accordingly, the AGE model focuses on the fate of tropical-adapted clades
142 under climate cooling conditions. Nevertheless, for groups originating in or adapted to
143 temperate conditions (having evolved the appropriate adaptations to cope with climate
144 change[61]), it should be possible to extend the AGE model to the prediction that temperate
145 lineages probably diversified in Neogene habitats and contributed to an inverse LDG[62].

146 The dynamic history of the paleotropical belt and its wider ancient extension have
147 been considered before as a way of explaining different dispersal opportunities for tropical
148 lineages over time[39,43,63,64], or the large number of groups originating in the tropics, as a result
149 of the increase in area of this region[65]. However, the losses in biodiversity resulting from
150 tropical biome contractions have rarely been considered as a major mechanism underlying the

151 LDG[52]. This notion is straightforward in theory[66], but received little experimental support to
152 date.

153 We used comparative methods for both phylogeny and fossil record analyses, to test
154 the predictions of the AGE model for the Testudines, Crocodilia and Squamata. The modern-
155 day Crocodilia and Squamata comprise mostly tropical-adapted species with a classic LDG
156 pattern, with an accumulation of diversity at equatorial latitudes[42,47]. We evaluated the
157 applicability of our framework to subtropical taxa, by extending this study to Testudines, a
158 taxonomic group displaying a hump-shaped gradient of diversity centred on subtropical
159 latitudes (10°S–30ºN)[67]. By contrast, the paleolatitudinal distribution of turtles was
160 concentrated in the Holarctic (30–60ºN) during the Cretaceous[23,24]. All these lineages are
161 ancient and experienced climatic transitions during the early Cenozoic [22,23,42,47,67]. They
162 display contrasting patterns of species richness: turtles and crocodiles are species-poor (330
163 and 25 species, respectively), while squamates include a large number of species (9400+
164 species) and have a rich fossil record extending back to the Triassic (Early Cretaceous for
165 crocodiles), providing information about the variation of latitudinal species richness
166 accumulation during evolution[22,23,47].

167

168 **Results**

169 ***Phylogeny-based diversification analyses: are diversification rates higher at the equator?***

170 According to current distribution data, the species richness of turtles, squamates and
171 crocodiles peaks near the equator, with 84% of all extant species living in the tropics, only
172 15% living in temperate regions and 1% spanning both biomes. We classified each species
173 reported in the phylogeny (Supplementary Tables 1-3) as living close to the equator (the
174 modern-day tropical biome) or the Holarctic and Southern Hemisphere (the modern-day
175 temperate biome). For turtles, there were 239 tropical species, 84 temperate species and 6

species spanning both biomes (7 were marine species). For squamates, there were 7955 tropical species, 1337 temperate species and 124 spanning both biomes. The species-poor crocodile clade had only 23 tropical species and two temperate species.

We analyzed differences in diversification rates between the Holarctic and equatorial regions, with the binary state change speciation and extinction model (BiSSE[68,69], see *Methods*). We did not use the geographic state change speciation and extinction model[70], which is an appropriate model for dealing with widespread species, because most of the species in our datasets were endemic to the Holarctic or equatorial regions, and, for a character state to be considered in SSE models, it must account for at least 10% of the total diversity[71]. We did not apply the BiSSE model to crocodiles, because simulation studies have shown that trees containing fewer than 300 species may have to weak a phylogenetic signal to generate sufficient statistical power[71].

We first used the time-constant BiSSE model, which is generally used in studies of the LDG[36,41-43,52]. For turtles, net diversification rates were higher in the Holarctic than at the equator (**Table 2**, Supplementary Fig. 1a), but this difference was not significant, and rates of dispersal '*into the equator'* were ten times higher than those '*out of the equator'*. For squamates, a similar dispersal pattern was recovered, but net diversification rates were significantly higher towards the equator (Supplementary Fig. 1b). We tested the AGE hypothesis, by introducing two shift times, at 51 and 23 million years ago (Ma), to detect differences in diversification dynamics between greenhouse, transitional, and coldhouse periods. This model indicated that the net diversification of turtles was similar in the Holarctic and at the equator, whereas it was lower in the Holarctic for squamates until the coldhouse period, when Holarctic diversification increased (**Table 2**, Supplementary Fig. 2). Dispersal was considered to be symmetric between regions (*into the equator = out of the equator*) during greenhouse periods, and asymmetric (*into the equator > out of the equator*) during the

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.

	Data source	Model	Turtles			Squamates			Crocodiles		
			Greenhouse	**Transition**	**Coldhouse**	**Greenhouse**	**Transition**	**Coldhouse**	**Greenhouse**	**Transition**	**Coldhouse**
Diversification analyses	Fossil	PyRate	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e = r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e = r_h$	$\lambda_e = \lambda_h$ $\mu_e > \mu_h$ $r_e < r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e = r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e > \lambda_h$ $\mu_e > \mu_h$ $r_e > r_h$
	Present	BiSSE (time-variable)	$\lambda_e = \lambda_h$ $\mu_e = \mu_h$ $d_{he} = d_{eh}$	$\lambda_e = \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	$\lambda_e < \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $d_{he} < d_{eh}$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $d_{he} > d_{eh}$	$\lambda_e < \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	-	-	-
	Present	BiSSE (constant)	$\lambda_e < \lambda_h$ $\mu_e < \mu_h$, $r_e < r_h$, $d_{he} > d_{eh}$			$\lambda_e < \lambda_h$ $\mu_e < \mu_h$, $r_e > r_h$, $d_{he} > d_{eh}$			-		
Biogeographic analyses	Present	DEC	$R\mu_e < R\mu_h$ ($R\mu_e < R\mu_h$)* $d_{he} < d_{eh}$ ($d_{he} < d_{eh}$)*			$R\mu_e > R\mu_h$ ($R\mu_e = R\mu_h$)* $d_{he} < d_{eh}$ ($d_{he} = d_{eh}$)*			$R\mu_e = R\mu_h$ ($R\mu_e = R\mu_h$)* $d_{he} = d_{eh}$ ($d_{he} = d_{eh}$)*		
	Present + fossil	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

201 climatic transition and coldhouse period. The same patterns were obtained for inferences with
202 the same model but with different combinations of shift times (51 Ma and 34/23 Ma;
203 Supplementary Fig. 3).
204
205 ***Fossil-based diversification analyses: evidence for ancient tropical extinctions?***
206 We also analyzed differences in diversification rates between the Holarctic and equatorial
207 regions based exclusively on fossil data. The turtle fossil dataset comprised 4084 occurrences
208 for 420 genera (65 extant and 355 extinct; Supplementary Table 4). The squamate fossil
209 dataset comprised 4798 occurrences for 638 genera (120 extant and 518 extinct;
210 Supplementary Table 5). The crocodile fossil dataset comprised 1596 occurrences for 121
211 genera (9 extant and 112 extinct; Supplementary Table 6). We first inferred global
212 diversification dynamics by analyzing the fossil datasets as a whole with a Bayesian approach
213 to inferring the temporal dynamics of origination and extinction rates based on fossil
214 occurrences[71] (see *Methods*). For turtles, origination rates peaked during the Jurassic,
215 subsequently decreasing until the present day. Extinction rates were generally low and
216 constant during the Mesozoic, but increased during the coldhouse periods of the Jurassic and
217 Paleogene, resulting in negative net diversification during the Paleogene (**Fig. 3**, **Table 2**,
218 Supplementary Figs. 4, 5). For squamates, origination rates peaked in the Jurassic and Late
219 Cretaceous, whereas extinction increased steadily until the Late Cretaceous. In the Paleogene,
220 net diversification approached zero, suggesting a high rate of turnover (**Fig. 3**, Supplementary
221 Figs. 6, 7). Crocodilia origination peaked in the Early Cretaceous, subsequently decreasing
222 towards the present day, and extinction rates were generally low and constant. We also
223 identified losses of diversity in the Paleogene extending to the present, suggesting that
224 crocodiles are still in a phase of steadily declining diversity (**Fig. 3**, Supplementary Figs. 8,
225 9).

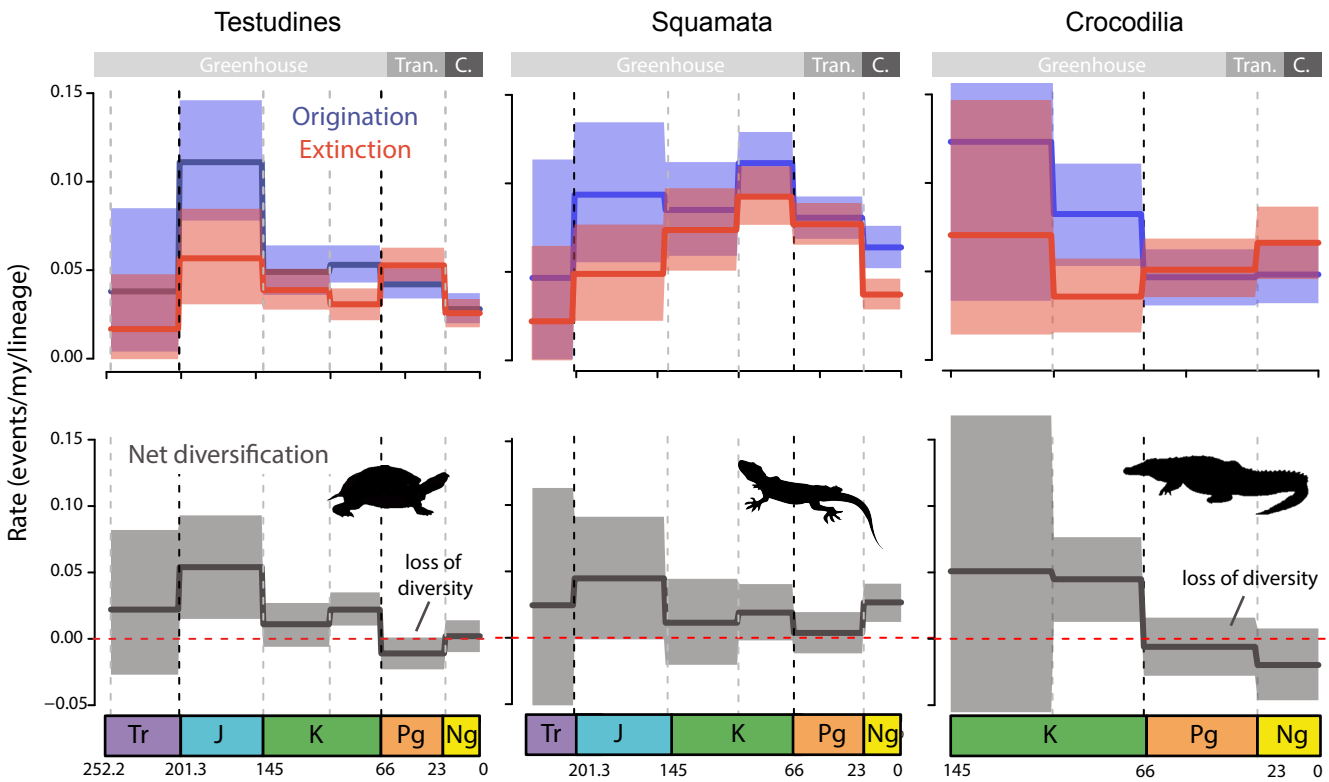

Figure 3 | Global pattern of turtles, squamates and crocodiles diversification through time based on the fossil record, and analysed with a Bayesian model. Origination (blue) and extinction (red) rates were estimated using time bins as defined by epochs of the geological timescale (on the top, main climatic 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. Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; and Ng, Neogene.

226 We performed additional analyses with different subsets of the three fossil datasets, to
227 separate the speciation and extinction signals between geographic regions (equator or
228 Holarctic) and ecological conditions (temperate or tropical, see *Methods*). These analyses
229 showed that the diversity losses experienced by turtles and crocodiles were mostly attributable
230 to species living in the Holarctic and under tropical conditions (**Figs. 4**, **5, Table 2**). The
231 global diversity loss inferred for crocodiles during the Neogene was attributed to taxa living
232 in both the Holarctic and equatorial regions, adapted to tropical and temperate conditions,
233 providing further support for the hypothesis that this whole group is in decline. For all groups,
234 temperate taxa have been estimated to have high rates of diversification during the Oligocene,
235 but lower rates during the Neogene. For the equatorial datasets, extinction and speciation rates
236 decreased over time, resulting in constant net diversification rates (except for squamates,
237 which displayed a decrease in diversification during the Paleogene, followed by an increase in
238 diversification during the Neogene).
239
240 ***Estimations of ancestral origins: did groups preferentially originate close to the equator?***
241 We tested the predictions of the AGE hypothesis further, by performing biogeographic
242 analyses with the dispersal-extinction-cladogenesis (DEC) model[73] and dated phylogenies
243 (see *Methods*). We first analyzed the data in an unconstrained DEC analysis in which all
244 ranges covering three areas could be in an ancestral state. We inferred an equatorial
245 distribution for the most basal nodes for the turtles and squamates, whence these lineages
246 colonized the other regions (**Fig. 6a**, **Table 2**, Supplementary Fig. 10). Crocodile ancestors
247 were found to have been widespread during the Cretaceous, with an early vicariant speciation
248 event separating *Alligator* in the Holarctic from the other genera in equatorial regions
249 (Supplementary Fig. 11).

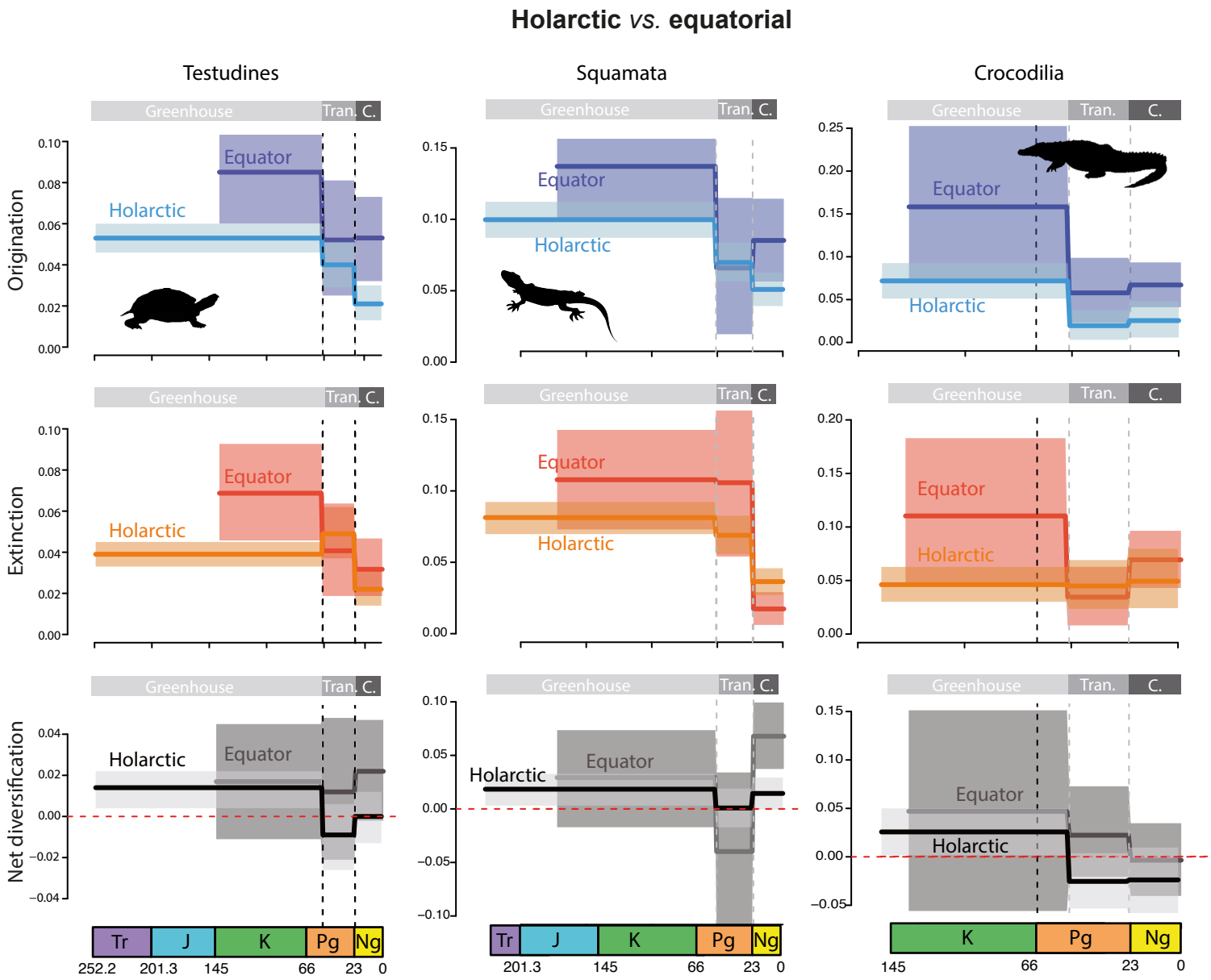

Figure 4 | Global pattern of turtle, squamate and crocodile diversification between Holarctic and equatorial regions, based on the fossil record. Diversification dynamics are compared between fossils distributed in Holarctic and equatorial regions. Origination (blue) and extinction (red) rates were estimated 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

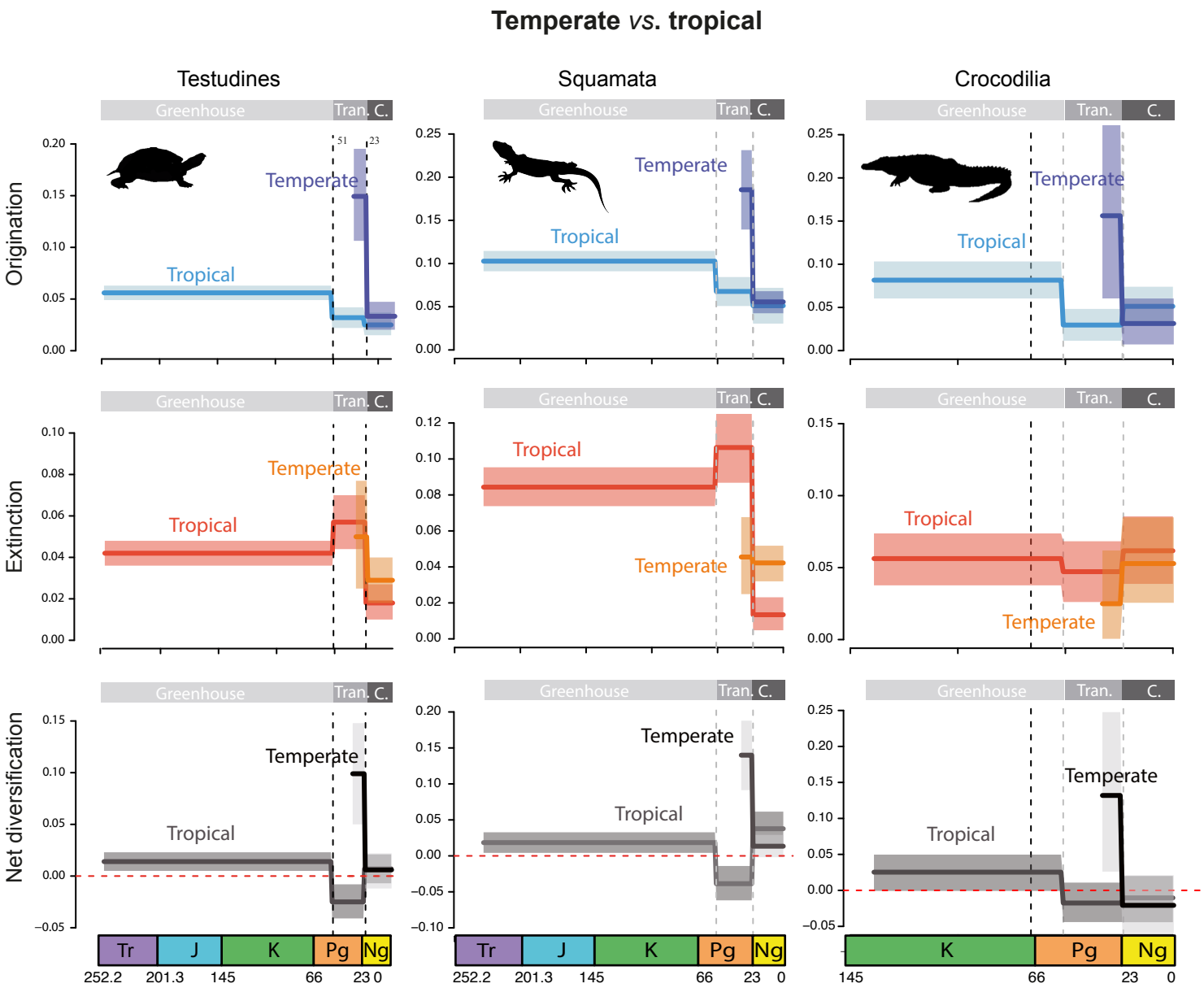

Figure 5 | Global pattern of turtle, squamate and crocodile diversification across temperate and tropical climates, based on the fossil record. Diversification dynamics are compared between fossils inhabiting under temperate and tropical macroclimates. Origination (blue) and extinction (red) rates were 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.

250 Biogeographic estimates based exclusively on extant data conflict with the fossil
251 record[22-24,74]. We overcame this bias, by introducing information about the distribution of
252 fossils into DEC, in the form of hard (HFC) and soft (SFC) geographic fossil constraints at
253 specific nodes (see *Methods*; Supplementary Tables 7–9). The inclusion of fossil information
254 yielded very different biogeographic histories for the three groups (**Table 2**; turtles: **Fig. 6**,
255 Supplementary Fig. 12; squamates: Supplementary Figs. 13, 14; and crocodiles:
256 Supplementary Figs. 15, 16). Under the SFC model, turtles were found to have originated in
257 the Northern Hemisphere (under the HFC model they were spread over both regions), whence
258 lineages migrated towards the equator and southern regions (**Fig. 6b**, Supplementary Fig. 12).
259 Most dispersal therefore occurred '*into the equator*' (Supplementary Fig. 17,
260 Supplementary Table 10). We also detected a larger number of geographic extinctions when
261 fossil ranges were considered, predominantly for turtle lineages in the Holarctic (53 and 11
262 lineages disappeared from this region under the HFC and SFC models, respectively) and in
263 southern temperate regions (9 in the HFC model; Supplementary Fig. 17, Supplementary
264 Table 11). The same trend was observed when the number of extinction/dispersal events was
265 controlled for the number of lineages currently distributed in each region (**Fig. 7**).
266 Squamates originated in both regions in both SFC and HFC analyses (Supplementary
267 Figs. 13, 14). During the greenhouse period, dispersal '*into the equator*' occurred at the same
268 rate (or at a higher rate in the HFC model) than dispersal '*out of the equator*', and dispersal
269 '*out of the equator*' prevailed thereafter (Supplementary Fig. 17, Supplementary Table 10).
270 Estimated range extinction rates were very high in this group under the unconstrained model,
271 with 30 lineages extirpated from the Holarctic, two from southern temperate regions and 152
272 from the equator (Supplementary Fig. 17, Supplementary Table 11). Under fossil-informed
273 models, the number of Holarctic extinctions was larger (109 and 66 lineages in the HFC and
274 SFC models, respectively), whereas the number of lineages extirpated from the equator was

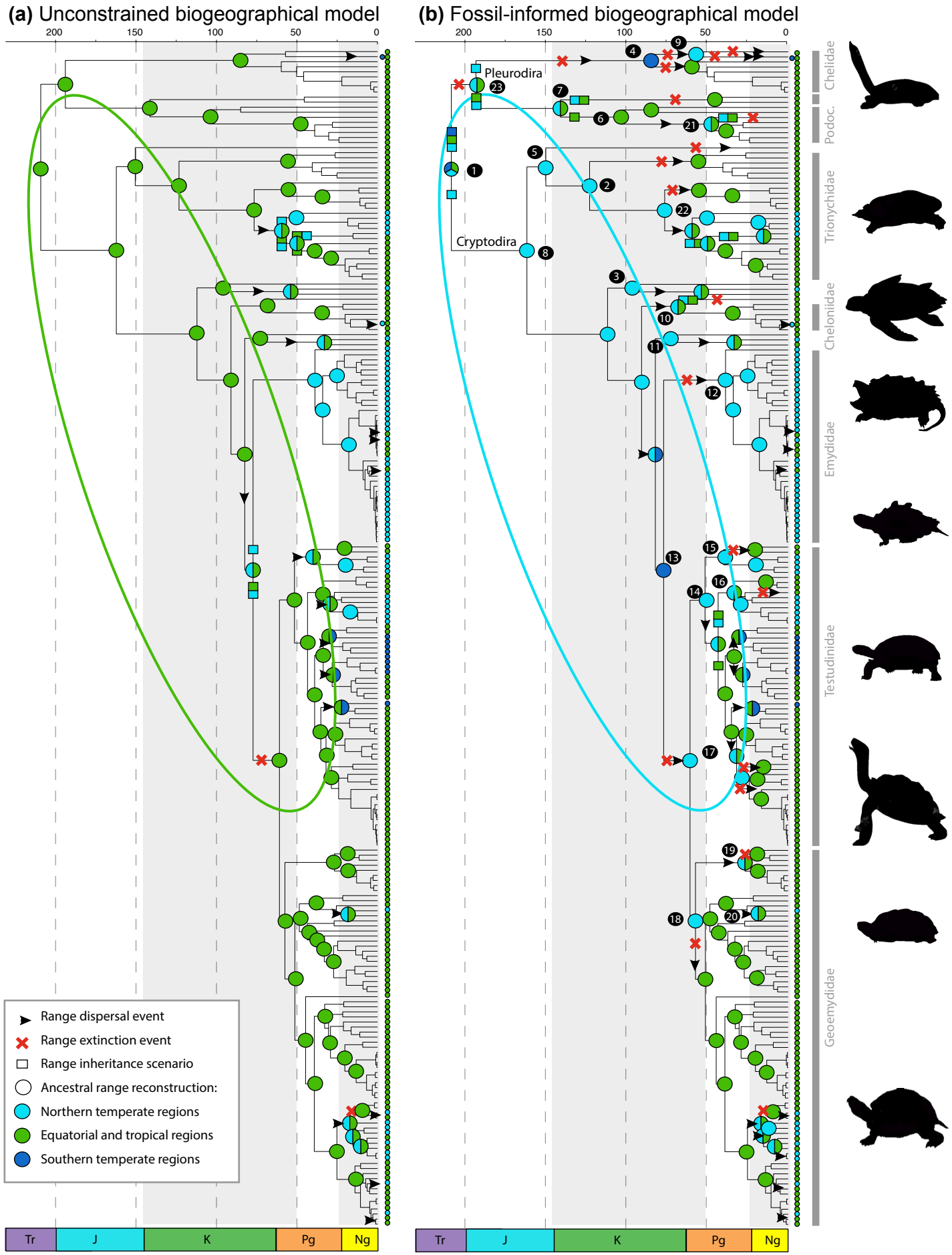

Figure 6 | Biogeographic reconstruction of Testudines showing the effects of the incorporation of fossil information into biogeographic inference. **a**, Biogeographic reconstruction inferred with DEC based on the distribution of extant taxa. **b**, Biogeographic reconstruction under the fossil-informed 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 S7. The reconstruction under the *soft fossil constraint* (SFC, see text) model is presented in Supplementary Fig. 12.

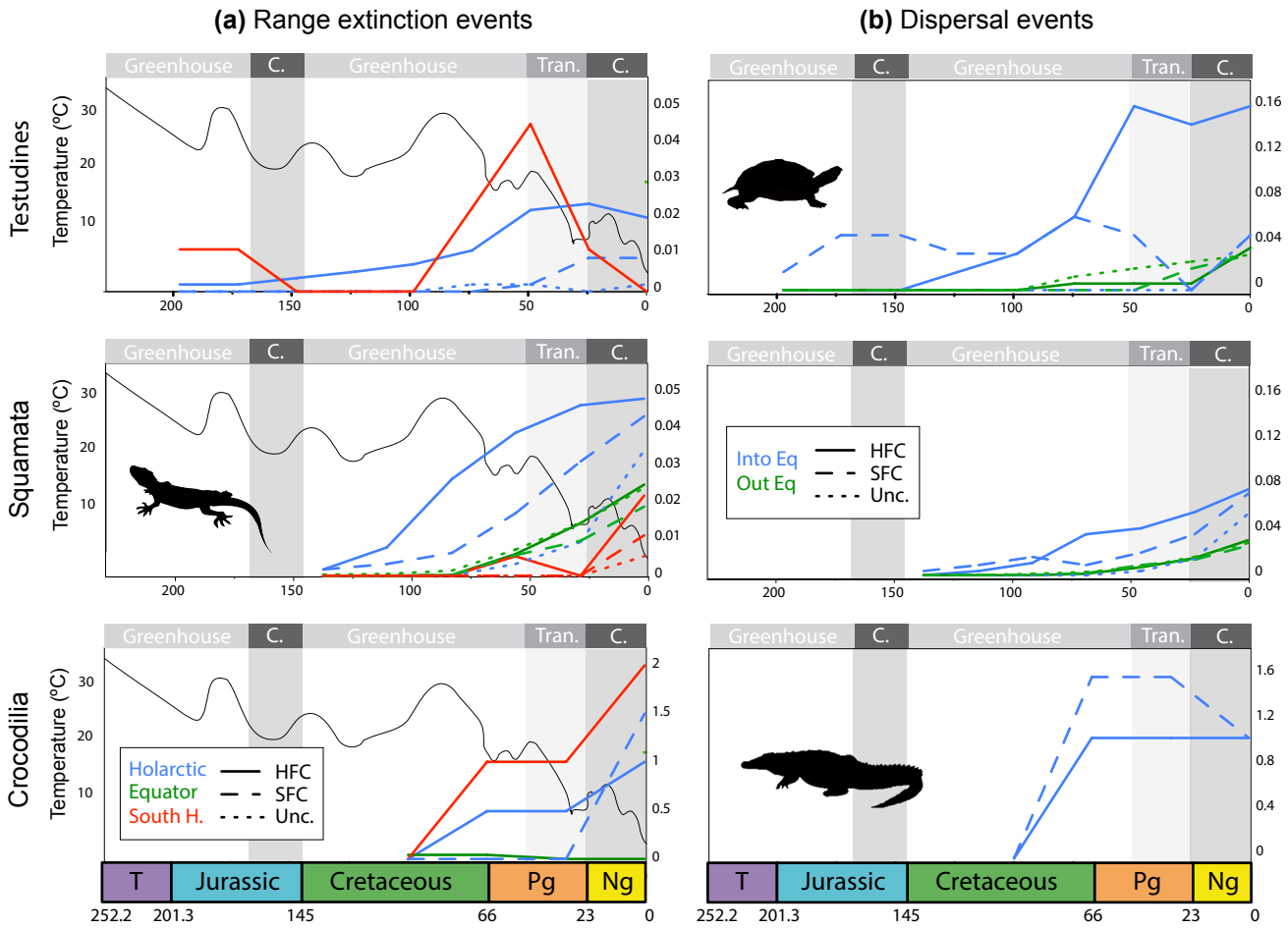

Figure 7 | Estimated number of range-extinction and dispersal events through time. Analyses were performed for Testudines, Squamata and Crocodiles under the *unconstrained model* (Unc.), based on present evidence only, and the fossil-based *hard* (HFC) and *soft fossil constraint* (SFC) biogeographic 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.

275 similar (144 and 109 in the HFC and SFC models, respectively; Supplementary Fig. 17).
276 When the number of extinctions was controlled for the actual number of lineages distributed
277 in each region, the number of Holarctic extinctions and dispersals '*into the equator*' increased
278 dramatically, exceeding equatorial dispersal/extinctions (**Fig. 7**). For crocodiles, analyses
279 including fossil ranges showed that all the early nodes were distributed in the Holarctic
280 (Supplementary Figs. 15, 16), and range extinctions were detected: four lineages disappeared
281 from the Holarctic, three from southern temperate regions, and two from the equator (HFC
282 model; Supplementary Fig. 17, Supplementary Tables 11, 12). Only two lineages disappeared
283 from the Holarctic in the SFC model. The same trends were observed after controlling the
284 number of events for the current number of lineages in each region (**Fig. 7**).
285

286 ## Discussion

287 ***Generation of the current LDG***

288 Fossil investigations showed that diversity at high latitudes was greater in some periods of the
289 past than currently, and sometimes even equivalent to diversity levels at the equator, for many
290 groups[11,12]. Hypotheses relating to 'slow Holarctic species accumulation', such as limited
291 dispersal to the Holarctic[32], high Holarctic turnover[38], or high rates of equatorial
292 diversification[33-36,42,52,75], cannot themselves account for the formation of the LDG, its
293 flattening, or the transition to lower diversity in the Holarctic observed in many groups[11,12].
294 Furthermore, although the processes shaping biodiversity vary over time and space[66], this has
295 been largely overlooked in the context of the LDG, which has been generally explained in
296 terms of the actions of time-constant process[36,42,52,75]. We account here for temporal changes
297 in the global distribution of biodiversity, by proposing a scenario involving losses of tropical
298 diversity at high latitudes, in which the AGE hypothesis captures components of previous
299 studies[12,30,32,36,43] in the context of a time-variable LDG. A comparison of the AGE model

300 with the LDG for turtles, crocodiles and squamates showed that this evolutionary scenario
301 was poorly supported by analyses based purely on data for extant species, but was supported
302 by fossil-informed investigations (**Table 1, 2**).

303 For the analyses based on extant species, biogeographic analyses of turtles support the
304 '*tropical niche conservatism*' hypothesis, with an equatorial origin and recent invasion of
305 high-latitude regions, resulting in less time for lineages to diversify[32] (**Figs. 6, 7**, **Table 1, 2**),
306 consistent with the findings of recent investigations[76,77]. Time-constant and time-variable
307 BiSSE analyses are consistent with higher levels of Holarctic diversification and the '*into the*
308 *tropics*' hypothesis (Supplementary Figs. 1a, 2a, 3a). For squamates, biogeographic analyses
309 support the '*out of the tropics*' hypothesis, whereas BiSSE supports both higher rates of
310 equatorial diversification and the '*into the tropics*' hypothesis to explain the LDG (**Fig. 7**,
311 Supplementary Figs. 1-3, 10). Biogeographic results for crocodiles support the diversification
312 hypothesis, with higher origination rates close to the equator and no effect on dispersal (**Fig.**
313 **7**, **Table 2**, Supplementary Fig. 11).

314 By contrast, results for fossil-only and fossil-informed phylogenetic-based
315 biogeographic analyses were largely consistent with the AGE hypothesis (**Table 2**). The AGE
316 hypothesis predicts that '*on average*' (*i.e.* integrated over time under a constant-rate
317 evolutionary model), the diversification of a group is lower in the Holarctic (overall extinction
318 being higher; the 'average AGE hypothesis' of **Fig. 2**), as generally accepted for the origin of
319 the LDG[33,39,78]. However, the temporal context proposed made it possible to disentangle the
320 relative contributions of speciation, extinction and dispersal for each particular period in the
321 formation of the LDG. As predicted by the AGE hypothesis (**P1**), diversification rates for
322 turtles, squamates and crocodiles were similar in the Holarctic and equatorial regions during
323 the greenhouse period (overlapping credibility intervals; **Fig. 4**; Supplementary Figs. 1-3, 4-
324 9), consistent with the flattened LDG observed during this phase[12]. We obtained mixed

325 evidence for similar rates of dispersal between the Holarctic and equatorial regions during
326 greenhouse periods (**P2**) for these groups: BiSSE showed similar rates of dispersal in both
327 directions between biomes (**Table 2**, Supplementary Figs. 1-3), whereas fossil-based
328 biogeographic analyses indicating higher rates of dispersal '*into the tropics*' (**Fig. 7**,
329 Supplementary Table 11). These findings do not necessarily conflict with the AGE
330 hypothesis, but reflect the idiosyncratic history of these groups, with many ancestors
331 distributed in the Holarctic whence they colonized southern regions.

332 Our analyses revealed that diversification rates subsequently decreased in all regions,
333 during the transition to colder climates (**Fig. 3**). Nevertheless, the slowing of diversification
334 was much stronger in the Holarctic than at the equator for turtles and crocodiles, with
335 extinction rates exceeding speciation ($r < 0$) and diversity losses (**P3**; **Fig. 4**). Our results
336 also suggest that turtles and crocodiles had a widespread ancestral distribution that
337 subsequently contracted towards the equator due to both higher levels of range extirpation at
338 higher latitudes and higher rates of '*into the equator*' dispersal during Cenozoic cooling (**P4**;
339 **Figs. 6, 7**). This result is consistent with BiSSE dispersal results (Supplementary Figs. S2,
340 S3), and with previous fossil investigations on turtles[23,24,74] and crocodiles[22,47]. Overall, our
341 results suggest that the LDG of these groups results from the combined effect of widespread
342 Mesozoic tropical origination, followed by diversity losses and range extirpations at high
343 latitudes (**Table 2**, **Figs. 4**), together with high rates of '*into the equator*' dispersal (**Fig. 7**)
344 during the transition to a colder climate.

345 Paleontological evidence shows that paratropical conditions and the associated warm-
346 adapted taxa disappeared from high latitudes between the mid-late Eocene (51-34 Ma) and the
347 Neogene (23 Ma)[54,58,59]. Our results, with extinctions at high latitudes, range contractions and
348 southward dispersals peaking at the end of the Paleogene, are consistent with these
349 observations, and indicate that Cenozoic climate cooling had a profound effect on the shape

350 of the current LDG. We cannot exclude the possibility that diversity losses occurred earlier at
351 high latitudes (as suggested by our fossil-based diversification analyses with time intervals
352 defined by the main geological periods; Supplementary Figs. 4, 6, 8), as the result of the K-Pg
353 mass extinction, because of the drop in temperatures caused by the impact-associated
354 winter[47,79,80], although crocodiles and turtles were only marginally affected by the K-Pg
355 extinction event[81,82] and even recovered pre-extinction levels of diversity[83,84]. This scenario
356 does not necessarily conflict with our interpretations, because our results consistently show
357 higher rates of extinction at high latitudes than at low latitudes, regardless of the definition
358 used for time intervals (Supplementary Figs. 4–9). Moreover, these two hypotheses are not
359 mutually exclusive; range extinctions and southward dispersals increased between the K-Pg
360 and Neogene (**Fig. 4, 7**), suggesting an additive effect of K-Pg and Neogene cooling on
361 depopulation of the Holarctic.

362 The ancestors of turtles and crocodiles adapted to tropical conditions during the Late
363 Cretaceous[47,85]. Our results indicate that extinction events were not random, instead
364 preferentially affecting taxa living in tropical-like climates at high latitudes[51] (**Figs. 4, 5**). This
365 suggests that many species adapted to warm conditions living in the Holarctic were unable to
366 adapt to the new temperate regimes and either went extinct or escaped extinction by
367 contracting their ranges in a southerly direction (**Fig. 7**).

368 Our fossil-based results for turtles and crocodiles support the AGE hypothesis, but this
369 scenario is only partially supported by the data for squamates. During Cenozoic cooling,
370 extinction rates for squamates were no higher at higher latitudes than at the equator (**Fig. 4**).
371 However, diversity dynamics for the species distributed at the equator may not be entirely
372 reliable, due to the poverty of the equatorial dataset in terms of the number of fossil lineages
373 and the small number of records per lineage (Supplementary Table 12). Uncertainties
374 therefore remain on the estimated rates, which have wide credibility intervals, probably due to

375 geographic biases in the fossil record[86]. Turnover rates were very high in the Holarctic,
376 indicating that species did disappear from high latitudes, but that they were replaced by a new
377 squamate community. The number of squamate species may always have been unbalanced
378 between regions. The high Holarctic turnover would contribute to the maintenance of this
379 pattern, together with the inferred increases in diversification at the equator over time, up to
380 the present (**Fig. 4**), as previously hypothesized[42].

381 Nevertheless, high-latitude diversity losses could not be completely ruled out. In
382 absolute terms, more species migrated into than out of the Holarctic (Supplementary Fig. 17),
383 but the number of species in the equatorial region today is four times the number of lineages
384 elsewhere. After controlling for the imbalance in species sampling in our tree, we found that
385 more squamate species lost their ancestral Holarctic distribution and emigrated towards the
386 equator than the other way around (**Fig. 7**). This is in consistent with our BiSSE results
387 indicating higher rates of dispersal '*into the equator*'[42]. The current LDG of squamates may
388 result from the Cenozoic climate cooling, through range extinctions and southward dispersals
389 of species from high latitudes (**Fig. 7**), but not necessarily through the promotion of
390 extinctions (**Fig. 4**). We reconciled the phylogeny and fossil records for Squamata, by
391 incorporating a number of fossil constraints in the biogeographic analyses, but these
392 constraints were relatively few in number given the size of the tree (30 fossils for 4161
393 nodes). Nevertheless, these constraints significantly increased the absolute number of
394 Holarctic range extinctions and '*towards the equator*' dispersal events relative to estimates
395 without such constraints (from 30 to 109 and from 40 to 124, respectively; Supplementary
396 Tables 10, 11). Meanwhile, the inclusion of fossil data did not alter the number of events
397 estimated for equatorial taxa. These findings suggest that a deeper understanding of squamate
398 fossil taxonomy might facilitate the assignment of fossils to particular position on the tree,
399 and the detection of other high-latitude extinctions.

The AGE hypothesis focuses essentially on the Northern Hemisphere, but similar processes (*i.e.* diversity losses and dispersals '*into the equator*') may have occurred in the temperate regions of the Southern Hemisphere. Indeed, we found high rates of range extinction in these regions for all the groups (red lines on **Fig. 7**). Unfortunately, we were unable to estimate speciation and extinction rates based on fossils for the southern regions of the Southern Hemisphere because very few fossils are available for this region (see *Methods*).

Reconciling fossil and phylogenetic evidence

Our results unequivocally demonstrate that the inclusion of fossils in macroevolutionary studies makes it possible to detect signals of ancient high-latitude extinctions and range extirpations (**Figs. 4-7**), otherwise undetectable in analyses based exclusively on present-day data. BiSSE models detected only '*into the equator*' dispersals but such dispersals were not identified in the unconstrained biogeographic analyses[76,77] (**Figs. 6, 7**, Supplementary Figs. 10, 11). This conflict between extant and fossil evidence may extend beyond our study, pervading the LDG literature in general.

On the one hand, high extinction rates have occasionally been inferred in tropical lineages[61,87-89]. Hypotheses relating to extinction have often focused on temperate taxa and recent time scales, such as the effects of recent Pleistocene glaciations, for example[34,36,38,42,44]. In reported cases of extinction, origination rates were found to be high in high-latitude groups (high turnover)[33-44], while diversity losses ($r < 0$) have to our knowledge never been inferred in phylogenetic studies of the LDG[7].

On the other hand, ancient tropical extinction at high latitudes is supported by fossil studies documenting the existence of similar levels of diversity across latitudes during the Paleogene greenhouse period, 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 at the modern temperate site, and similar to that at the modern-day tropical locality. Post-Eocene insects thus suffered higher rates of extinction in the Nearctic than around the equator. This pattern is consistent with results of other fossil studies on various taxonomic groups, including birds[49,90], invertebrates[50,91], mammals[11,92] and plants[93,94].

If the extinction of tropical clades at high latitudes was paramount and trait-dependent (tropical-adapted lineages having a higher risk of extinction), then entire tropical clades could have disappeared without leaving any phylogenetic footprint. This was the case for crocodiles, turtles and squamates, in which extinction preferentially occurred in warm-adapted lineages at high latitudes in a cooling climate (**Fig. 5**). Most of the evidence of an ancient Holarctic and southern temperate distribution for these groups was erased by species extinctions and range contractions (**Figs. 4, 7**). The last decade has seen many efforts to reconcile fossil and phylogenetic evidence[95,96]. Simulation and empirical studies have shown that, under such asymmetric-rate scenarios, comparative phylogenetic methods often fail to recover the real processes, simply because there is insufficient phylogenetic evidence to predict the loss of the focal character along each terminal branch[54,73,97,98]. Consequently, if the LDG was shaped by asymmetric extinction and dispersal, as hypothesized here, the current diversity patterns of many groups may be poorly representative of the historical diversification processes (**Figs. 6, 7**), and the inclusion of fossils may be crucial to overcome this problem[99]. Fossil records remain incomplete, but they nevertheless provide the only direct evidence of the diversity that existed in the past. By contrast to molecular phylogenies, the incompleteness of the fossil record has a less problematic effect on the estimation of speciation and extinction rates, because removing a random set of taxa does not affect the observed occurrences of other lineages[72]. Simulations have shown that PyRate correctly

450 estimates the dynamics of speciation and extinction rates under low levels of preservation or
451 severely incomplete taxon sampling.

452 LDG studies are often based on state-dependent speciation and extinction
453 models[33,36,41-43,52,100]. These models are designed to test differential diversification and
454 asymmetric transition scenarios, such as that suggested here, but LDG studies often assume
455 that diversification parameters remain constant over time[36,42]. If the evolutionary processes
456 shaping the LDG have varied across latitudes and time, then time-constant models are not
457 very powerful for testing more complex scenarios underlying the LDG. The testing of our
458 scenario required the implementation of time-variable models. When applied to the study of
459 diversity patterns, these models have revealed marked extinction signatures in ancestral
460 tropical plant clades, indicating that large temperate groups do not undergo monophyletic
461 radiation, but instead that polyphyletic clusters of lineages are derived from the tropics and
462 masked by extinction[101]. However, the incorporation of time-shifts into our BiSSE analyses
463 did not completely reconcile the fossil evidence with extant diversity, and time-variable
464 BiSSE analyses correctly identified the main direction of dispersal in different periods but
465 failed to detect the negative diversification rates suggested by fossils. Identifying the causes
466 of this problem and finding solutions are beyond the scope of this study, but this artifact
467 highlights the importance of fossils in macroevolutionary inferences.

468

469 ***Differences in diversification between temperate- and tropical-adapted taxa***

470 One long-standing question in ecology and evolution directly related to the formation of the
471 LDG concerns the possible differences in diversification rates between taxa living in
472 temperature and tropical climates. According to the metabolic theory of ecology, warm
473 tropical environments promote higher rates of speciation than colder climates, mostly due to
474 higher rates of molecular evolution[102], and/or greater robustness to mutation[103]. This theory

475 received early support in the literature[104], but other studies have suggested that per capita
476 speciation rates are highest in the temperate zone[42,44,105,106]. If we are to answer this question
477 from an evolutionary perspective, we need to consider today's equatorial belt as merely a
478 fraction of the wider extension of the tropics in the past, and to take into account the former
479 presence in the Holarctic of lineages with tropical-like affinities[58,59,65] (**Fig. 1**). Geographic
480 diversification results cannot therefore be directly extrapolated to assess differences in
481 diversification between ecological types, because, if high extinction rates are estimated for
482 taxa in the Holarctic, extinction may have affected lineages living under either tropical or
483 temperate conditions (depending on the time point considered). We therefore think that one
484 major problem that has been largely overlooked is that the principal hypotheses relating to the
485 LDG put forward have sought to answer two related but slightly different questions, which
486 may account for some of the discrepancies between ecological and phylogenetic perspectives.
487 We found that the diversification rates of turtles, crocodiles and squamates living in
488 temperate climatic conditions were significantly higher than those of tropical-adapted taxa
489 after the transition to temperate climates in the late Eocene (**Fig. 5**, **Table 2**). The new
490 temperate niches constituted an opportunity for diversification because they increased
491 geographic ranges and ecological niches[35], and may have driven an inverse LDG for some
492 groups[40,62]. Several radiations following the appearance of the temperate biome have been
493 identified in other groups of organisms, such as plants[40,107-109], mammals[110,111] and insects[112].
494 After this period, speciation decreased dramatically in the temperate lineages of our focal
495 groups, possibly due to the effect of the Pleistocene glaciations, and no difference in
496 diversification between tropical- and temperate lineages is currently evident (**Fig. 5**,). In
497 summary, our study suggests that differences in species richness between geographic regions
498 may be explained by differences in diversification rates and higher rates of extinction in the
499 Holarctic. Differences in species richness between ecological types may be explained by the

500 longer time available for tropical-adapted clades to diversify in tropical areas, but not by a
501 higher rate of speciation in warm tropical environments.
502
503 ***Conclusion***
504 After decades of research and the proposal of countless hypotheses, the processes shaping the
505 LDG remain among the most hotly debated topics in ecology and evolutionary biology. We
506 propose here the AGE hypothesis, which unifies some of the ideas previously put forward
507 concerning the LDG in a common framework and explains the origin of the current LDG
508 through the changes in global diversification and dispersal dynamics imposed by large-scale
509 climatic transitions. Our analyses testing the predictions of the AGE hypothesis for reptiles
510 indicated that the processes shaping the LDG have changed over time, the current form of this
511 gradient being the result of ancient high-latitude tropical extinctions and range contractions as
512 a consequence of the retraction of the tropical biome due to climate cooling. We think the
513 AGE hypothesis can account for the LDG of tropical-adapted groups that were once diverse at
514 high latitudes, but might not be applicable to all organisms currently displaying a LDG, as
515 shown here for squamates.
516
517 **Methods**
518 ***Time-calibrated phylogenies and the fossil record.*** We compared the predictions of the AGE
519 hypothesis with the LDG of three vertebrate groups: turtles (order Testudines), crocodiles
520 (order Crocodilia), and scaled reptiles (order Squamata). A time-calibrated phylogeny for
521 each group was obtained from published data. For turtles, we used the phylogeny of Jaffe *et*
522 *al.*[113], including 233 species. We preferred this phylogeny over other more recent and slightly
523 better sampled trees[114] because the divergence time estimates of Jaffe *et al.*[113] are more
524 consistent with recent estimates based on genomic datasets[76,115]. For squamates, we retrieved

525 the most comprehensive dated tree available, including 4161 species[42], and a complete
526 phylogeny was obtained for crocodiles[116].

527 Fossil occurrences were downloaded from the *Paleobiology Database*
528 (https://paleobiodb.org/#/, last accessed October 25th 2017). We reduced potential biases in
529 the taxonomic assignation of turtle, crocodile and squamate fossils, by compiling occurrence
530 data at the genus level. The fossil datasets were cleaned by checking for synonymies between
531 taxa and for assignment to a particular genus or family on the basis of published results
532 (Supplementary Table 4–6).

533

534 ***Estimation of origination and extinction rates with phylogenies.*** We investigated possible
535 differences between Holarctic and equatorial regions, by combining the turtle and squamate
536 phylogenies with distributional data (Supplementary Tables 1, 2) to fit trait-dependent
537 diversification models in BiSSE[65]. We accounted for incomplete taxon sampling as the global
538 sampling fraction of extant species with a given trait[117].

539 We ensured comparability with previous LDG studies[34,36,41-43,52], by initially using a
540 constant-rate trait-dependent diversification model. The constant-rate BiSSE model has six
541 parameters: two speciation rates (without range shift, or *in situ* speciation), one associated
542 with the Holarctic (hereafter 'H', λ_H) and the other with other equatorial and subtropical
543 regions (hereafter 'equator' or 'E', λ_E), two extinction rates associated with the Holarctic (μ_H)
544 and the equator (μ_E), and two transition rates (dispersal or range shift), one for the Holarctic to
545 equator direction (q_{H-E}), and the other for the equator to Holarctic direction (q_{E-H}).

546 We then assessed the effect of species distribution on diversification, allowing for rate
547 changes at specific time points. This approach is associated with a lower bias than the use of
548 constant rates, and makes it possible to assess the roles of extinction and climate change in
549 LDG generation. We used the time-dependent BiSSE (BiSSE.td) model, in which speciation,

550 extinction, and dispersal rates are allowed to vary between regions and to change after the
551 shift times[101]. We introduced two shift times to model different diversification dynamics
552 between greenhouse, transitional, and coldhouse periods. We assumed that a global warm
553 tropical-like climate dominated the world from the origin of the clades until 51 Ma
554 (corresponding to the temperature peak in the Cenozoic). Thereafter, the climate
555 progressively cooled until 23 Ma (the transitional period), when the climate definitively
556 shifted to a temperate-like biome in the Holarctic[58-60]. The shift times at 51 Ma and at 23 Ma
557 are initial values that are re-estimated by the model during the likelihood calculation. The
558 climatic transition in the Cenozoic may have different temporal boundaries, with potential
559 effects on the results. We thus applied the same model but with different combinations of shift
560 times (we tested 51/66 Ma and 34/23 Ma for the upper and lower bounds of the climatic
561 transition).

562 Analyses were performed with the R package *diversitree* 0.9-7[69], using the *make.bisse*
563 function to construct likelihood functions for each model from the data, and the functions
564 constrain and *find.mle* to apply different diversification scenarios. Finally, we used a Markov
565 Chain Monte Carlo (MCMC) approach to investigate the credibility intervals of the parameter
566 estimates. Following the recommendations of FitzJohn[69], we used an exponential prior 1/(2r)
567 and initiated the chain with the parameters obtained by maximum likelihood methods. We ran
568 10,000 MCMC steps, with a burn-in of 10%.

569

570 ***Estimation of origination and extinction rates with fossils.*** We also used fossil data to
571 estimate diversification rates over time. We analyzed the three fossil records, using a
572 Bayesian model for simultaneous inference of the temporal dynamics of origination and
573 extinction, and of preservation rates[72]. This approach, implemented in PyRate[118], uses fossil
574 occurrences that can be assigned to a taxon, in this case fossil genera, to model the

575 preservation and diversification processes simultaneously. The preservation process is used to
576 infer the individual origination and extinction times of each taxon from all fossil occurrences
577 and an estimated preservation rate; it is expressed as expected occurrences per taxon per
578 million years.

579 We followed the birth-death shift approach developed by Silvestro *et al.*[119], which
580 focuses on the variation of origination and extinction at a global scale and over large temporal
581 ranges. We used a homogeneous Poisson process of preservation (-mHPP option). We also
582 accounted for the variation of preservation rates across taxa, using a Gamma model with
583 gamma-distributed rate heterogeneity (-mG option). We used four rate categories to discretize
584 the gamma distribution, to allow for a greater variability of preservation rates across taxa.

585 Given the large number of occurrences analyzed and the vast timescale considered, we
586 dissected the birth–death process into time intervals, and estimated origination and extinction
587 rates within these intervals. In one set of analyses we defined the time intervals using the
588 geological epochs of the stratigraphic timescale[120] (Supplementary Figs. 4, 6, 8). In another
589 set of analyses, we defined the intervals according to the different climatic periods
590 characterizing the Cenozoic (Supplementary Figs. 5, 7, 9), as discussed in the main text. We
591 adopted this solution as an alternative to the algorithms implemented in the original PyRate
592 software for joint estimation of the number of rate shifts and the times at which origination
593 and extinction shift[72,118]. The estimation of origination and extinction rates within fixed time
594 intervals improved the mixing of the MCMC and made it possible to obtain an overview of
595 the general trends in rate variation over a long timescale[119]. Both the preservation and birth–
596 death processes were modeled in continuous time but without being based on boundary
597 crossings. Thus, the origination and extinction rates were measured as the expected number of
598 origination and extinction events per lineage per million years. One potential problem when
599 fixing the number of rate shifts *a priori* is over-parameterization. We overcame this problem

600 by assuming that the rates of origination and extinction belonged to two families of
601 parameters following a common prior distribution, with parameters estimated from the data
602 with hyper-priors[121].

603 We ran PyRate for 10 million MCMC generations on each of the 10 randomly
604 replicated datasets. We monitored chain mixing and effective sample sizes by examining the
605 log files in Tracer 1.6[122]. After excluding the first 20% of the samples as a burn-in, we
606 combined the posterior estimates of the origination and extinction rates across all replicates to
607 generate plots of the change in rate over time. The rates of two adjacent intervals were
608 considered significantly different if the mean of one lay outside the 95% credibility interval of
609 the other, and vice versa. We looked at the marginal posterior distributions of origination and
610 extinction rates through the evolutionary history of the three groups and assessed the effect of
611 very different environments, such as the greenhouse world (Cretaceous), the climatic
612 transition (Paleogene), and the coldhouse world (Neogene until the present).

613 In the context of the LDG and under a hypothesis of tropical extinction, we performed
614 additional analyses with different subsets of fossils, to separate the speciation and extinction
615 signals of different geographic regions (equator or Holarctic) and ecological conditions
616 (temperate or tropical). For example, for turtles, we split the global fossil dataset into four
617 subsets: one for the fossil genera occurring at the equator (429 occurrences), one for the
618 fossils occurring in the Holarctic (3568 occurrences), one for the fossil genera considered to
619 be adapted to temperate conditions (993 occurrences), and one for the fossils considered to be
620 adapted to tropical conditions (2996 occurrences). We excluded the few fossil occurrences for
621 the southern regions of the South Hemisphere (about 180) only in subset analyses, as they
622 were poorly represented in our dataset. Note that a given fossil can be present in both the
623 'Holarctic' and 'tropical' datasets. We encoded tropical/temperate preferences by considering
624 macroconditions in the Holarctic to be paratropical until the end of the Eocene, as previously

625 reported[58-60] (and references therein). We also assumed that taxa inhabiting the warm
626 Holarctic were adapted to tropical-like conditions (*i.e.* a high global temperature, indicating
627 probable adaptation to tropical climates). This is, of course, an oversimplification that may
628 introduce bias into the analysis, but general patterns may nevertheless emerge from such
629 analyses[123]. This assumption can also be justified by the presence of early Cenozoic
630 vegetation assemblages in the Holarctic corresponding to tropical vegetation, as demonstrated
631 by their paleofloristic composition[54,57]. For turtles, this assumption is supported by a recent
632 study modeling the climatic niche of this group during the Late Cretaceous, which found that
633 the Holarctic ancestors of turtles were adapted to tropical conditions[85]. After the late Eocene,
634 we categorized each species as living in the temperate biome or the tropical biome, according
635 to the threshold latitudes defining the tropics (23.4°N and 23.4°S) suggested in a previous
636 study.[34]. This delineation is also consistent overall with the Köppen climate classification.
637 With these datasets, we reproduced the same PyRate analyses as for the whole dataset (see
638 above). In general, the fossil datasets included mostly Holarctic fossils, with a smaller number
639 of occurrences for the equator. Caution is therefore required when drawing conclusions from
640 the equatorial datasets.
641
642 ***Inferring ancestral geographic distribution with phylogenies and fossils.*** We performed
643 biogeographic analyses with the parametric likelihood method DEC[73,] using the fast C++
644 version[124]. Turtle, squamate, and crocodile species distributions were obtained from online
645 databases (www.iucnredlist.org and www.reptile-database.org). We chose 23.4°N and 23.4°S
646 as the threshold latitudes defining the tropics, and categorized each species as living in the
647 Holarctic, in the southern temperate regions, or in the equatorial tropics and subtropical
648 regions[34]. We considered that all ranges comprising three areas could be considered an
649 ancestral state (*maxareas* =3).

650 We set up three different DEC analyses. We first ran DEC with no particular
651 constraints, using only the distribution of extant species. We then performed DEC analyses
652 including fossil information in the form of 'fossil constraints' at certain nodes, according to
653 the range of distribution of fossil occurrences assigned to a particular taxon during the
654 relevant time frame. For example the crown age of Carettochelyidae (Testudines) dates back
655 to the Late Jurassic (150 Ma, *node 5*, **Fig. 3**; Supplementary Table 7), and we set a constraint
656 on this node reflecting the distribution of all the Late Jurassic fossils attributed to this clade.
657 Similarly, for the origin of turtles (210 Ma, *node 1*), distribution constraints represent the
658 range of Late Triassic fossils assigned to turtles. For the crown of Trionychidae, in the Early
659 Cretaceous (123 Ma, *node 2*), the early fossils assigned to the clade were used to constrain the
660 geographic origin of Trionychidae. In total, we implemented 23 fossil constraints for turtles
661 (Supplementary Table 7), 30 fossil constraints for squamates (Supplementary Table 8), and 8
662 for crocodiles (Supplementary Table 9).

663 We included the fossil distribution in two different approaches: *(i)* a soft (SFC), and
664 *(ii)* hard fossil constraints (HFC). For the SFC approach, fossil data were incorporated into the
665 anagenetic component of the likelihood framework. The direct impact of a given fossil is
666 limited to the particular branch to which it has been assigned, although it may indirectly
667 influence other branches. The inclusion of a fossil conditions the estimated geographic-
668 transition probability matrix for that branch by imposing a spatiotemporal constraint on the
669 simulation process. Only the simulations resulting in a geographic range including the area of
670 fossil occurrence contribute to the geographic-range transition probability matrix for the
671 branch concerned; simulations not meeting this constraint are discarded[125]. For SFC, we used
672 the command '*fossil*' in DEC. We consider this to be a 'soft' constraint, because other areas
673 different from that in which the fossil was found could be included in the ancestral states. In
674 some cases, in which today's diversity is not very representative of past diversity (*e.g.* due to

675 extreme levels of extinction), the SFC model may still overlook known fossil information. We
676 therefore also implemented an HFC model in which the estimation of ancestral areas was
677 fixed to the location of fossils. This was achieved with existing functions in the C++ version
678 of Lagrange[124] (https://github.com/rhr/lagrange-cpp), using the command '*fixnode*'. By fixing
679 nodes to the distribution area of fossils, we assume fossil occurrences reflect the distribution
680 of the ancestors, *i.e.* that the fossil record is complete. This is a strong assumption, but it
681 makes it possible to recover all fossil ranges in the ancestral estimations. The real scenario
682 probably lies somewhere between the SFC and HFC inferences.

683 We then compared the timing and number of range extinction and dispersal events
684 inferred with the three different biogeographic analyses. In DEC, range-subdivision
685 (inheritance) scenarios (vicariance, duplication and peripatric isolation) occur at cladogenetic
686 events, whereas extinction (range contraction) and dispersal (range expansion) are modeled as
687 stochastic processes occurring along the branches of the tree[54,126]. As the probability of any
688 extinction/dispersal event is constant along the entire length of the branch [73,126], we can
689 estimate the periods at which range extinction and dispersal occurred, by dividing the
690 phylogeny into intervals of 25 million years and calculating the number of branches for which
691 extinction/dispersal was inferred crossing a particular time interval (the same branch could
692 cross two continuous intervals).

693

694 **References**

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Author contributions

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

Competing interests

The authors have no competing financial interests to declare.