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 been persistent through time, with similar species diversity across latitudes flattening out the LDG during past "greenhouse" periods. This provides a new starting point for LDG research. Most studies assume the processes shaping the LDG have acted constantly through time and seek to understand why diversity accumulated in the Holarctic at lower levels than at the equator, *e.g.* as the result of limited dispersal, or higher turnover in Holarctic regions. However, fossil investigations suggest that we need to explain when and why diversity was lost at high latitudes to generate the LDG. Unfortunately, diversity lost scenarios in the Holarctic have been repeatedly proposed but not yet clearly demonstrated. Here, we outline the 'asymmetric gradient of extinction' (AGE) framework, which contextualize previous ideas behind the LDG in the frame of a time-variable scenario. We suggest 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 Lepidosauria support the AGE scenario and showed the LDG to have varied over time, with high latitudes serving as a source of tropical diversity but suffering disproportionate extinction during transitional periods to cold climate. Our results demonstrate that the inclusion of fossils in macroevolutionary studies allows detecting extinction events less detectable 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. This pattern has been described for microbes, insects, vertebrates, and plants, and for marine, freshwater, and terrestrial ecosystems[1–6].

For decades, it has been thought that the modern-type steep LDG (with higher diversity at the equator) persisted throughout the Phanerozoic (the last 540 million years), even if the gradient was sometimes shallower[7], based on published fossil record studies[8,9]. However, the methodological limitations of fossil sampling have called this conclusion into question. Analyses controlling for sampling bias have suggested that, for many groups, the LDG was less marked in the past than it is today, flat (*i.e.* with similar species diversity across latitudes) or even developed a paleotemperate peak during some periods in the past (see Mannion *et al.*, (2014) for a review). This sampling-corrected flatter LDG in deep time has been demonstrated for non-avian dinosaurs[11], mammals[12,13], tetrapods[14], insects[15–17], brachiopods[18–20], bivalves[21], coral reefs[22], crocodiles[23], turtles[24,25], and plants[26–28]. 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. Most of the Phanerozoic has instead been characterized by warm greenhouse climates associated with a flatter LDG1 (**Fig. 1**).

This recent fossil evidence now provides a new starting point for LDG research. Most hypotheses on the origin of the LDG are based on the assumptions that *(i)* the processes shaping the LDG have acted constantly through time and *(ii)* equatorial regions are the source of world diversity[29,30], with the LDG resulting from lower levels of diversity accumulation in the Holarctic than at the equator through time[7,31,32]. Previous studies have explained the LDG

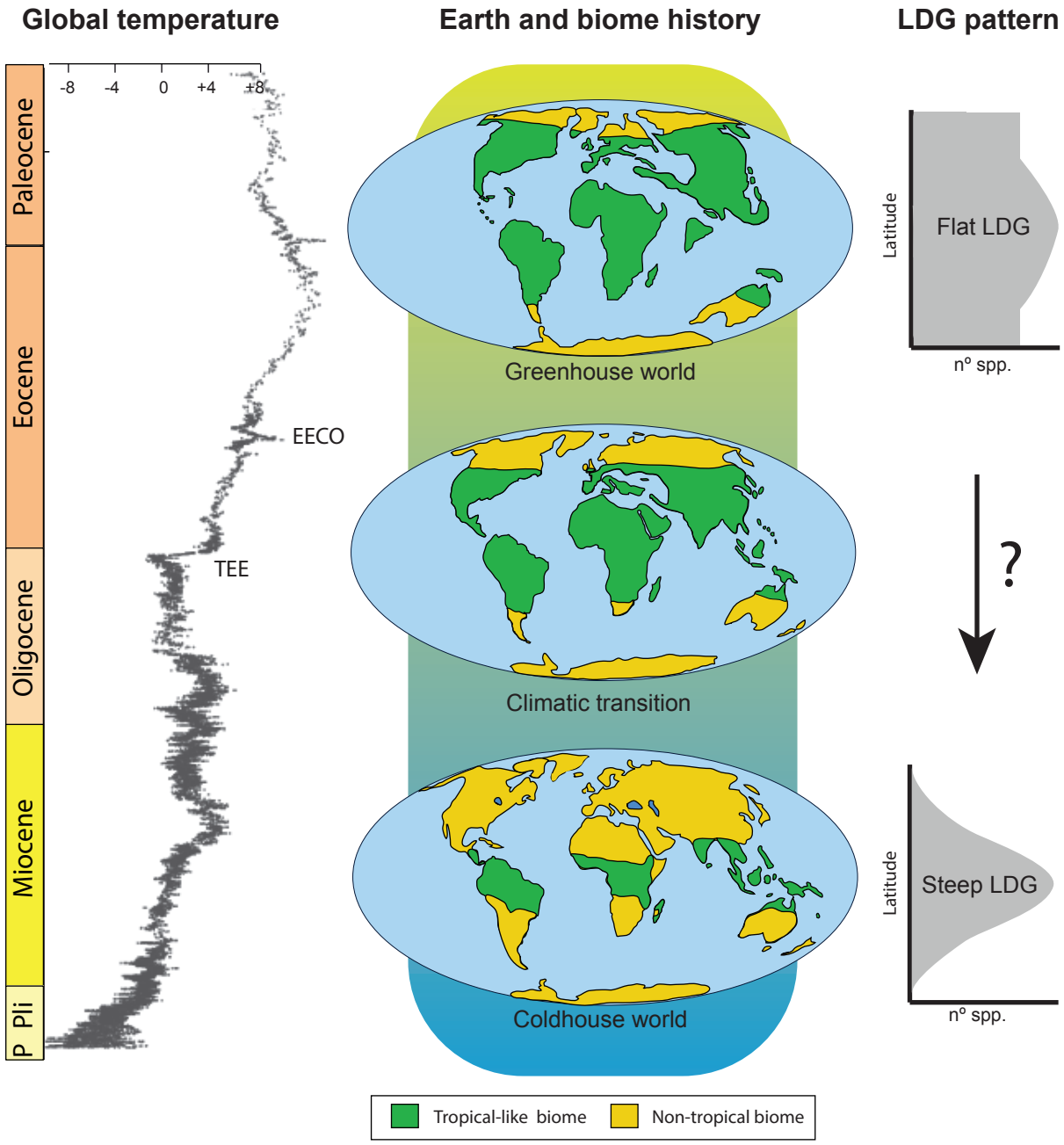

Figure 1 | Changes in global temperature and extension of the tropical belt during the Cenozoic, in relation with the shape of the LDG. Early Cenozoic global temperatures were higher than today and paratropical conditions extended over northern and southern latitudes. From the early Eocene climatic optimum (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; 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) (Mannion et al., 2014). 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 Zachos et al., (2008). Maps represent the extension of the tropical belt and Earth tectonic changes as derived from Ziegler et al., (2003) and Morley (2007). Abbrev.: P=Pleistocene, Pli=Pliocene

as a result of greater tropical diversification and limited dispersal out of the equatorial region[7,31,33], or by high rates of turnover in the Holarctic (*i.e.* similar high speciation (λ) and extinction (μ) rates; $\lambda \approx \mu$), all keeping diversity levels in this region low over time (**Table 1**), for amphibians[34,35], birds[32,36,37], butterflies[38], conifers[39], fishes[40], mammals[33,37], and lepidosaurs[41], for example. However, the recent fossil investigations showing, for many lineages, similar high diversity levels in the Holarctic and at the equator in the past suggest we do not necessarily need to explain why diversity accumulated at slower rates in the Holarctic through time, but the question being how and when diversity was lost at high latitudes, giving rise to the current shape of the LDG[10]?

Diversity losses in the Holarctic have been traditionally considered to underlie the LDG[37]. They were initially attributed to Pleistocene glaciations[42], but this hypothesis has been called into question by the finding that the LDG substantially predates the Pleistocene[7]. More ancient extinctions have also been considered[43–49]. For example, Hawkins *et al.* (2006)[46] suggested that the avian LDG resulted from the differential extirpation of older warm-adapted clades from the temperate regions newly formed in the Neogene. Pyron (2014)[41] suggested that higher temperate extinction represents a dominant force for the origin and maintenance of latitudinal gradients. More recently, Pulido-Santacruz & Weir (2016)[49] proposed the terrestrial LDG is largely the effect of a post-Eocene increase in extinction rates at high latitudes resulting from the cooling Cenozoic trend. Unfortunately, using phylogenies alone, these and other studies on the LDG have not clearly demonstrated diversity losses in the Holarctic but instead high regional turnover[33,35–39,50]. Nonetheless, high turnover can only explain a slow accumulation of lineages, with one fauna being replaced by another, but does not explain diversity decline (*i.e.* a reduction in the net number of species). Diversity declines occur when extinction exceeds speciation, resulting in negative net diversification rates ($r = \lambda - \mu; r < 0$). Accordingly, 'diversity loss' hypotheses need to be differentiated in the

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[90], 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[30]. The "*Into the tropics*" model assumes instead the LDG results from dispersals towards the equator[38,50]. 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[32,34] 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[66]. The LDG could also result from higher turnover rates (*i.e.* higher λ and μ) in the Holarctic[37]. Diversification and dispersal hypotheses are not mutually exclusive. 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[29,65]. 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 (the transition from coldhouse to greenhouse, and *viceversa*). **(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***[90]	***Cradle of diversity***[66]	***Museum of diversity***[66]	***Holarctic turnover***[37]	***Into the tropics***[38,50]	***Tropical niche conservatism***[32]	***Out of the tropics***[29,65]	***Asymmetric gradient of extinction***	
								Coldhouse to greenhouse transition	**Greenhouse to coldhouse transition**
Predictions	$t_{trop} > t_{temp}$ ($r_{trop} = r_{temp}$) ($d_{trtp} = d_{tptr}$)	$r_e > r_h$ ($\lambda_e > \lambda_)$ $d_{eh} = d_{he}$	$r_e > r_h$ ($\mu_e < \mu_h$) $d_{eh} = d_{he}$	$r_h = 0$ ($\mu_h = \lambda_h$) $d_{eh} = d_{he}$	$r_e = r_h$ $d_{eh} < d_{he}$	$r_e = r_h$ $d_{eh} > d_{he}$	$r_e > r_h$ ($\lambda_e > \lambda_h$) ($\mu_e < \mu_h$) $d_{eh} > d_{he}$	$r_e < r_h$ ($\mu_h < \lambda_h$; $r_h > 0$) $d_{eh} > d_{he}$	$r_e > r_h$ ($\mu_h > \lambda_h$; $r_h < 0$) $d_{eh} < d_{he}$

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

103 literature from 'high turnover' scenarios. The perceived difficulty for inferring negative
104 diversification rates from present-day phylogenetic data[51,52] and the assumption that diversity
105 levels were always lower in the Holarctic than at the equator have resulted in 'diversity loss'
106 hypotheses being repeatedly proposed but seldom demonstrated. Meanwhile, numerous fossil
107 investigations have detected signatures of extinction and diversity loss in the Northern
108 Hemisphere. For instance, Archibald *et al.*[15,16] sampled insect diversity at an Eocene site in
109 Canada, and in present-day temperate Massachusetts (USA) and tropical sites of Costa Rica.
110 Insect diversity was higher at the Eocene paleotropical site than the modern temperate
111 locality, and comparable to the modern-day tropical locality, suggesting that post-Eocene
112 insects have thus suffered greater levels of extinction in the Nearctic regions than around the
113 equator. This pattern is consistent with results of other studies on various taxonomic groups,
114 including birds[53], invertebrates[15,16,54], mammals[12,13,55] and plants [56–58]. However, fossil studies
115 are generally restricted to a geographic and temporal scale, which makes difficult to
116 extrapolate local inferences of extinction in the context of the LDG.

117 Here we capitalize on the current knowledge and we aim at: *(1)* outlining a new
118 framework for studying the LDG, the 'asymmetric gradient of extinction' (AGE) hypothesis,
119 which formalizes and expands previous hypotheses about the contribution of extinctions to
120 the LDG in the context of a time-variable pattern; and *(2)* testing the predictions of the AGE
121 hypothesis with three tetrapod groups.

122

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

124 Over the Earth's history, the geographic extent of the tropical biome around the equator has
125 fluctuated, with periods of pole-ward expansion during which warm paratropical conditions
126 appeared at high latitudes, followed by periods of equator-ward contractions[59–63] (**Fig. 1**). To
127 account for these biodiversity changes, we propose to include a temporal component to study

the LDG in which prevailing speciation, extinction and dispersal dynamics change between warm and cold intervals. The AGE hypothesis makes the following main postulates (P) during climatic transitions towards cooler climates (**Fig. 2; Table 1**): (**P1**) extinction rate exceeds the speciation rate at high latitudes (H), *i.e.* declining diversity ($r_H < 0$), while the equatorial (E) regions remain stable, and (**P2**) the rate of dispersal '*into the equator*' is greater than that '*out of the equator*' ($d_{HE} > d_{EH}$), thus triggering the formation of a steep LDG. Conversely, during the transition to greenhouse periods, different processes drove the formation of a flat gradient, and AGE postulates: (**P3**) diversification rates increase in the new paratropical regions ($r_E < r_H$), and (**P4**) '*out of the tropical*' dispersals increase over '*into the equator'* migrations ($d_{HE} < d_{EH}$).

For instance, the last 100 million have witnessed the contraction of tropical conditions towards the equator, due to the global cooling since the latest Cretaceous–early Cenozoic period (the most recent greenhouse period), culminating in the Pleistocene glaciations[64]. According to the AGE hypothesis, 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 'tropical belt', such that tropical equatorial clades were able to disperse '*out of the equator'* into high-latitude warm regions[29,65]. An equable Cretaceous-early Cenozoic greenhouse climate thus triggered the formation of a flat LDG (**Fig. 2a**). By contrast, tropical biome retractions following the climate cooling 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 the development of an asymmetric gradient of extinction (AGE) and dispersal within the tropical biome, and mediated the formation of a steep LDG (**Fig. 2c**).

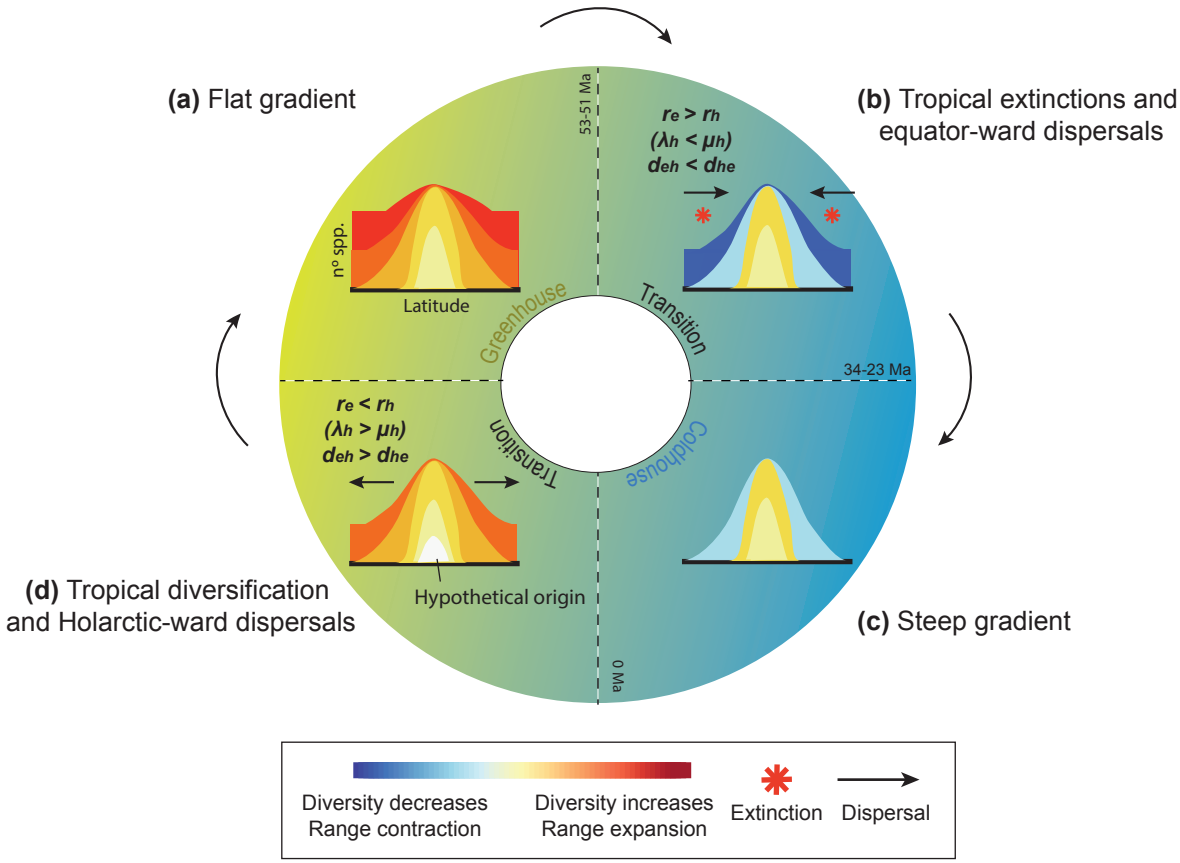

Figure 2 | Prevalent evolutionary processes behind the latitudinal diversity gradient under the AGE time-variable framework. The graphic shows the hypothetic change in evolutionary dynamics (diversification "r", speciation "λ", extinction "μ" and dispersal "d") between Holarctic and equatorial regions (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. **d**, the past and future transition to greenhouse climates. 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.

152 The AGE hypothesis attempts to reconcile previous contending hypotheses on the
153 origin of the LDG by placing them in a temporal scenario (**Table 1**). For instance, there is
154 controversial support around the tropics being '*cradle*' or '*museum of diversity*' [66], and
155 dispersal prevailing '*out of*' [29,65] or '*into the tropics*'[38,41,50]. The AGE hypothesis alternatively
156 invokes the '*museum of diversity*' regarding the equatorial tropics as refuge during coldhouse
157 transitions, but also the '*cradle of diversity*' during greenhouse periods. Similarly, the
158 hypothesis invokes '*out of the equator*' dispersals during greenhouse transitions and '*into the*
159 *equator*' dispersals during coldhouse transitions. The AGE hypothesis also assumes tropical
160 niche conservatism due to physiological limits[30,31] as we postulate that most of the tropical-
161 adapted taxa at high latitudes were unable to adapt and either went extinct or suffered
162 restrictions of their distributions when the tropical biome retreated towards the equator.
163 Accordingly, the AGE hypothesis focuses on the fate of tropical-adapted clades under
164 variable climate conditions but does not apply for groups having evolved the appropriate
165 adaptations to cope with climate change, e.g.[67,68].

166 Here, we used comparative methods for both phylogeny-based and fossil-based
167 datasets to test the predictions of the AGE hypothesis for the Testudines, Crocodilia and
168 Lepidosauria. The modern-day Crocodilia and Lepidosauria comprise mostly tropical-adapted
169 species with a classic LDG pattern as shown by an accumulation of diversity at equatorial
170 latitudes[41,44]. We evaluated the applicability of our framework to subtropical taxa as well, by
171 extending the study to Testudines, a group displaying a hump-shaped gradient of diversity
172 today centred on subtropical latitudes (10°S–30ºN)[69]. By contrast, the paleolatitudinal
173 distribution of turtles was concentrated in the Holarctic (30–60ºN) during the Cretaceous[24,25].
174 All these lineages are ancient and likely experienced climatic transitions during the early
175 Cenozoic[23,25,41,44,69]. They display contrasting patterns of species richness: turtles and
176 crocodiles are species-poor (330 and 25 species, respectively), while lepidosaurs include a

large number of species (9500+ species) and have a rich fossil record extending back to the Triassic (Early Cretaceous for crocodiles), providing information about the variation of latitudinal species richness accumulation during their evolutionary history.

Results

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

According to current distribution data, the species richness of turtles, lepidosaurs and crocodiles peaks near the equator, with 84% of all extant species living in the tropics, only 15% living in temperate regions and 1% spanning both biomes. We classified each species reported in the phylogeny (Supplementary Tables 1-3) as living close to the equator (the modern-day tropical biome) or the Holarctic and Southern Hemisphere (the modern-day temperate biome). For turtles, there were 239 tropical species, 84 temperate and 6 spanning both biomes (7 were marine species). For lepidosaurs, there were 7955 tropical species, 1337 temperate and 124 spanning both biomes. The species-poor crocodile clade had only 23 tropical 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'[70,71], see *Methods*. We did not use the geographic state change speciation and extinction model[72], which is appropriate 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[73]. 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[73].

201 We first used the time-constant BiSSE model, which is generally used in studies of the
202 LDG. For turtles, net diversification rates were higher in the Holarctic than at the equator
203 (**Table 2**, Supplementary Fig. 1a), but this difference was not significant, and rates of
204 dispersal '*into the equator'* were ten times higher than those '*out of the equator'*. For
205 lepidosaurs, a similar dispersal pattern was recovered, but net diversification rates were
206 significantly higher towards the equator (Supplementary Fig. 1b). We tested the AGE
207 hypothesis by introducing two shift times, at 51 and 23 million years ago (Ma), to detect
208 differences in diversification dynamics between greenhouse, transitional, and coldhouse
209 periods. This model indicated that the net diversification of turtles was similar in the Holarctic
210 and at the equator, whereas it was lower in the Holarctic for lepidosaurs until the coldhouse
211 period, when Holarctic diversification increased (**Table 2**, Supplementary Fig. 2). Dispersal
212 was considered to be symmetric between regions (*into the equator = out of the equator*)
213 during greenhouse periods, and asymmetric (*into the equator > out of the equator*) during the
214 climatic transition and coldhouse period. The same patterns were obtained for analyses with
215 the same model but with different combinations of shift times (51/66 Ma and 34/23 Ma;
216 Supplementary Fig. 3).
217
218 ***Fossil-based diversification analyses: evidence for ancient tropical extinctions?***
219 We also analyzed differences in diversification rates between the Holarctic and equatorial
220 regions based exclusively on fossil data. The turtle fossil dataset comprised 4084 occurrences
221 for 420 genera (65 extant and 355 extinct; Supplementary Table 4). The lepidosaur fossil
222 dataset comprised 4798 occurrences for 638 genera (120 extant and 518 extinct;
223 Supplementary Table 5). The crocodile fossil dataset comprised 1596 occurrences for 121
224 genera (9 extant and 112 extinct; Supplementary Table 6). We first inferred global
225 diversification dynamics by analyzing the fossil datasets as a whole with a Bayesian approach

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

	Data source	Model	Turtles	Squamates	Crocodiles
			Green- to coldhouse transition	**Green- to coldhouse transition**	**Green- to coldhouse transition**
Diversification analyses	Fossil	PyRate	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$	$\lambda_e = \lambda_h$ $\mu_e > \mu_h$ $r_e < r_h$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $r_e > r_h$
	Present	BiSSE (time-variable)	$\lambda_e = \lambda_h$ $\mu_e = \mu_h$ $d_{he} > d_{eh}$	$\lambda_e > \lambda_h$ $\mu_e < \mu_h$ $d_{he} > d_{eh}$	-
	Present	BiSSE (constant)	$\lambda_e < \lambda_h$ $\mu_e = \mu_h$, $d_{he} > d_{eh}$	$\lambda_e < \lambda_h$ $\mu_e < \mu_h$, $d_{he} > d_{eh}$	-
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

226 to inferring the temporal dynamics of origination and extinction rates based on fossil
227 occurrences[74] (see *Methods*). For turtles, origination rates peaked during the Jurassic,
228 subsequently decreasing until the present day. Extinction rates were generally low and
229 constant during the Mesozoic, but increased during the coldhouse periods of the Jurassic and
230 Paleogene, resulting in negative net diversification during the Paleogene (**Fig. 3**, **Table 2**,
231 Supplementary Figs. 4, 5). For lepidosaurs, origination rates peaked in the Jurassic and Late
232 Cretaceous, whereas extinction increased steadily until the Late Cretaceous. In the Paleogene,
233 net diversification approached zero, suggesting a high rate of turnover (**Fig. 3**, Supplementary
234 Figs. 6, 7). Crocodile origination peaked in the Early Cretaceous, subsequently decreasing
235 towards the present day, and extinction rates were generally low and constant. We also
236 identified diversity losses in the Paleogene extending to the present, suggesting that
237 crocodiles are still in a phase of declining diversity (**Fig. 3**, Supplementary Figs. 8, 9).

238 We performed additional analyses with different subsets of the three fossil datasets, to
239 separate the speciation and extinction signals between geographic regions (equator or
240 Holarctic) and ecological conditions (temperate or tropical, see *Methods*). These analyses
241 showed that the diversity losses experienced by turtles and crocodiles during the Paleogene
242 were mostly attributable to species living in the Holarctic and under tropical conditions (**Figs.**
243 **4**, **5, Table 2**). The global diversity loss inferred for crocodiles during the Neogene was
244 attributed to taxa living in both the Holarctic and equatorial regions (adapted to temperate and
245 tropical conditions respectively), providing further support for the hypothesis that this whole
246 group is in decline. For all groups, temperate taxa have been estimated to have high rates of
247 diversification during the Oligocene, but lower rates during the Neogene. For the equatorial
248 datasets, extinction and speciation rates decreased over time, resulting in constant net
249 diversification rates (except for lepidosaurs, which displayed a decrease in diversification
250 during the Paleogene, followed by an increase in diversification during the Neogene).

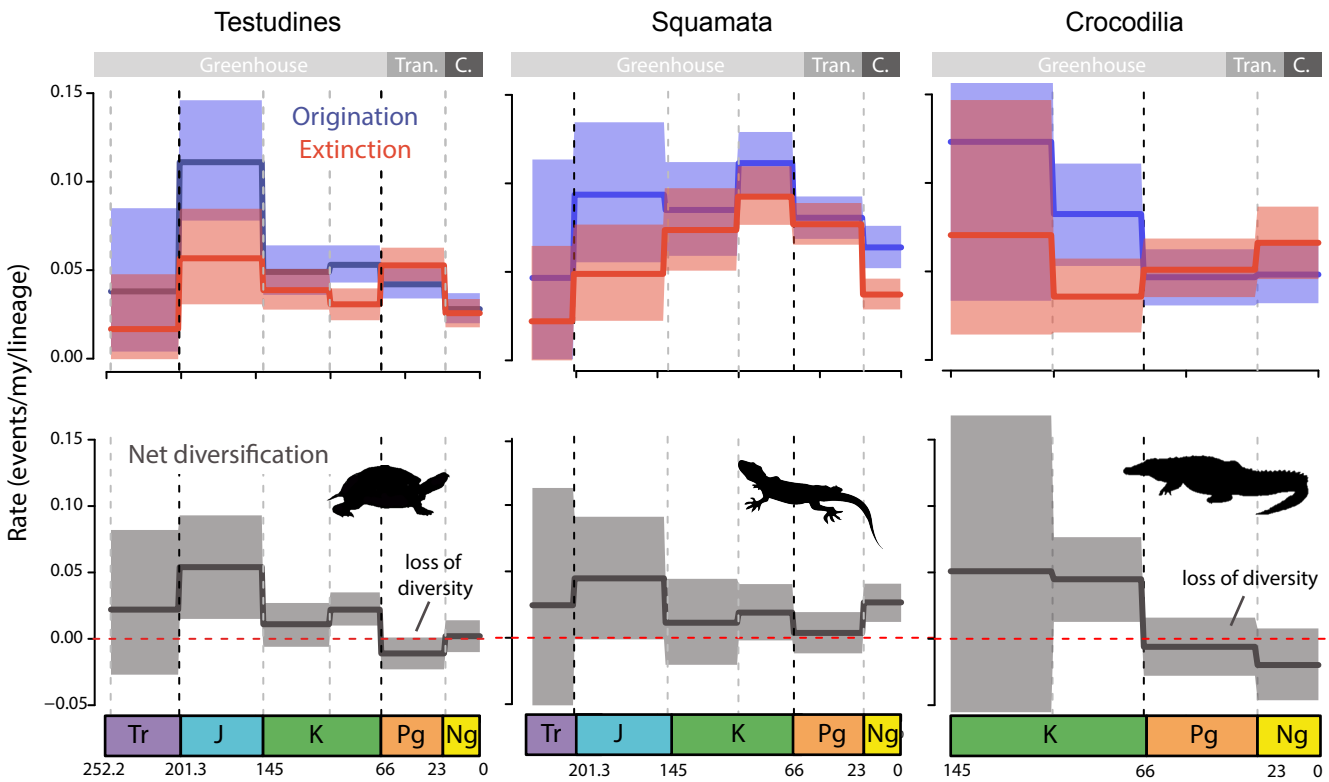

Figure 3 | Global pattern of turtles, squamates and crocodiles diversification through time based on the fossil record, and analysed with a Bayesian model. Origination (blue) and extinction (red) rates were estimated using time bins as defined by epochs of the geological timescale (on the top, main climatic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

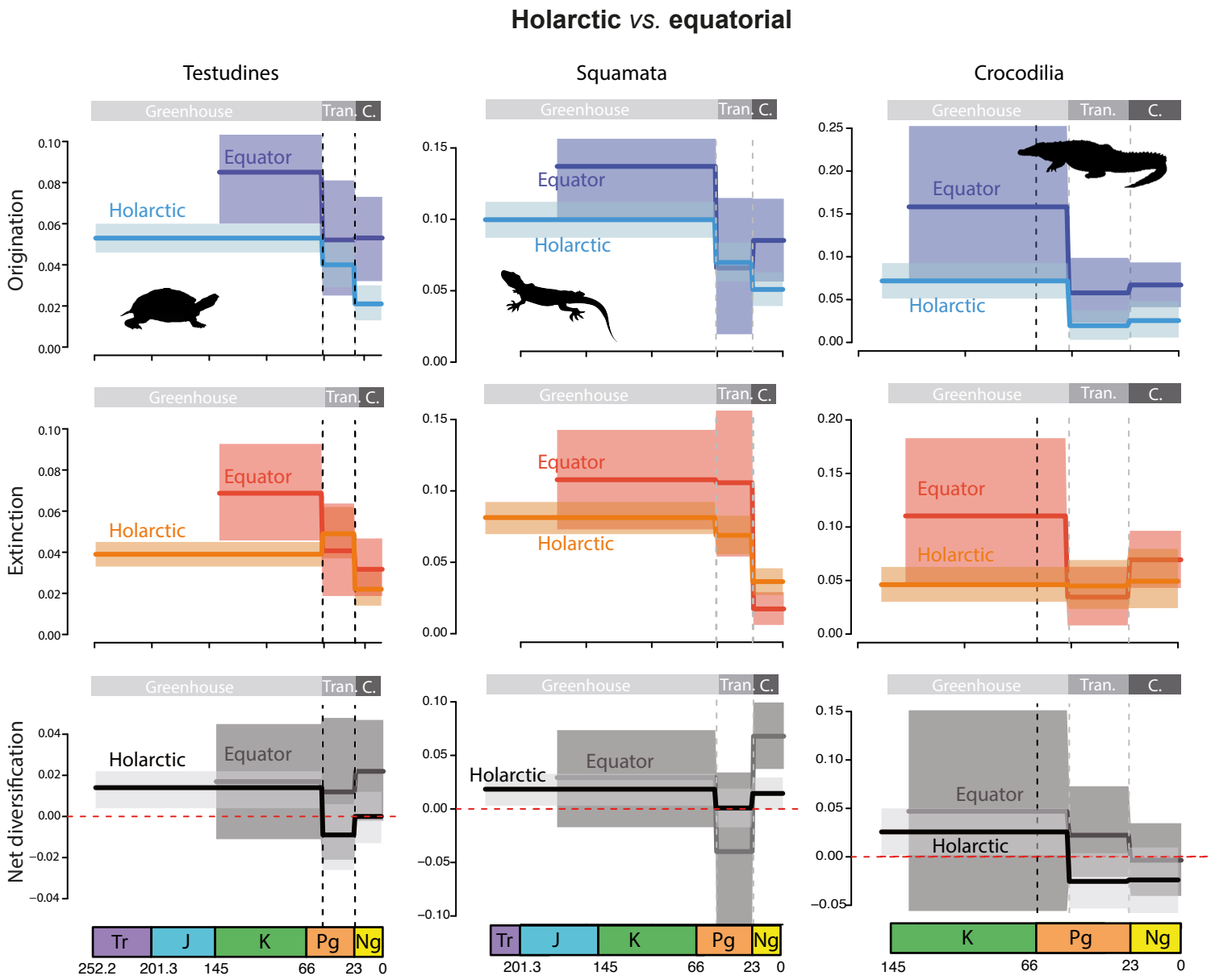

Figure 4 | Global pattern of turtle, squamate and crocodile diversification between Holarctic and equatorial regions, based on the fossil record. Diversification dynamics are compared between fossils distributed in Holarctic and equatorial regions. Origination (blue) and extinction (red) rates were estimated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

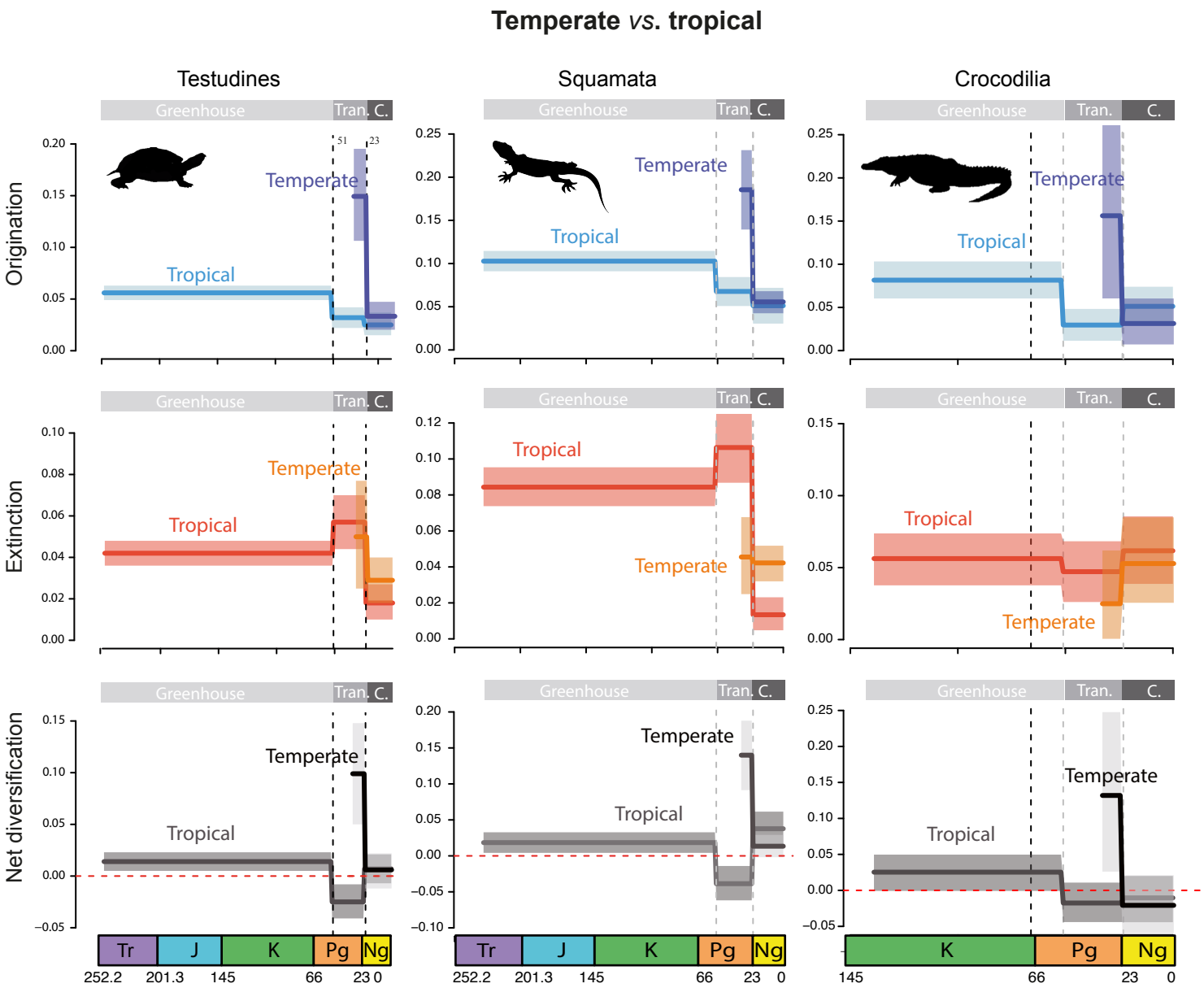

Figure 5 | Global pattern of turtle, squamate and crocodile diversification across temperate and tropical climates, based on the fossil record. Diversification dynamics are compared between fossils inhabiting under temperate and tropical macroclimates. Origination (blue) and extinction (red) rates were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

Estimations of ancestral origins: did groups preferentially originate close to the equator?

We tested the predictions of the AGE hypothesis further, by performing biogeographic analyses with the dispersal-extinction-cladogenesis (DEC) model[75] and dated phylogenies (see *Methods*). We first analyzed the data in an unconstrained DEC analysis in which all ranges covering three areas could be in an ancestral state. We inferred an equatorial distribution for the deepest nodes for the turtles and lepidosaurs, whence these lineages colonized the other regions (**Fig. 6a**, **Table 2**, Supplementary Fig. 10). Crocodile ancestors were found to have been widespread during the Cretaceous, with an early vicariant speciation event separating *Alligator* in the Holarctic from the other Alligatoridae genera in equatorial regions (Supplementary Fig. 11).

Our biogeographic estimates based exclusively on extant data conflict with the fossil record[23,24,76]. We overcame this bias by introducing information about the distribution of fossils into DEC, in the form of hard (HFC) and soft (SFC) geographic fossil constraints at specific nodes (see *Methods*; Supplementary Tables 7–9). The inclusion of fossil information yielded very different biogeographic histories for the three groups (**Table 2**; turtles: **Fig. 6b**, Supplementary Fig. 12; lepidosaurs: Supplementary Figs. 13, 14; and crocodiles: Supplementary Figs. 15, 16). Under the SFC model, turtles were found to have originated in the Northern Hemisphere (under the HFC model they were spread over both regions), whence lineages migrated towards the equator and southern regions (**Fig. 6b**, Supplementary Fig. 12). Most dispersal therefore occurred '*into the equator*' (Supplementary Fig. 17, Supplementary Table 10). We also detected a larger number of geographic extinctions when fossil ranges were considered, predominantly for turtle lineages in the Holarctic (53 and 11 lineages disappeared from this region under the HFC and SFC models, respectively) and in southern temperate regions (9 in the HFC model; Supplementary Fig. 17, Supplementary

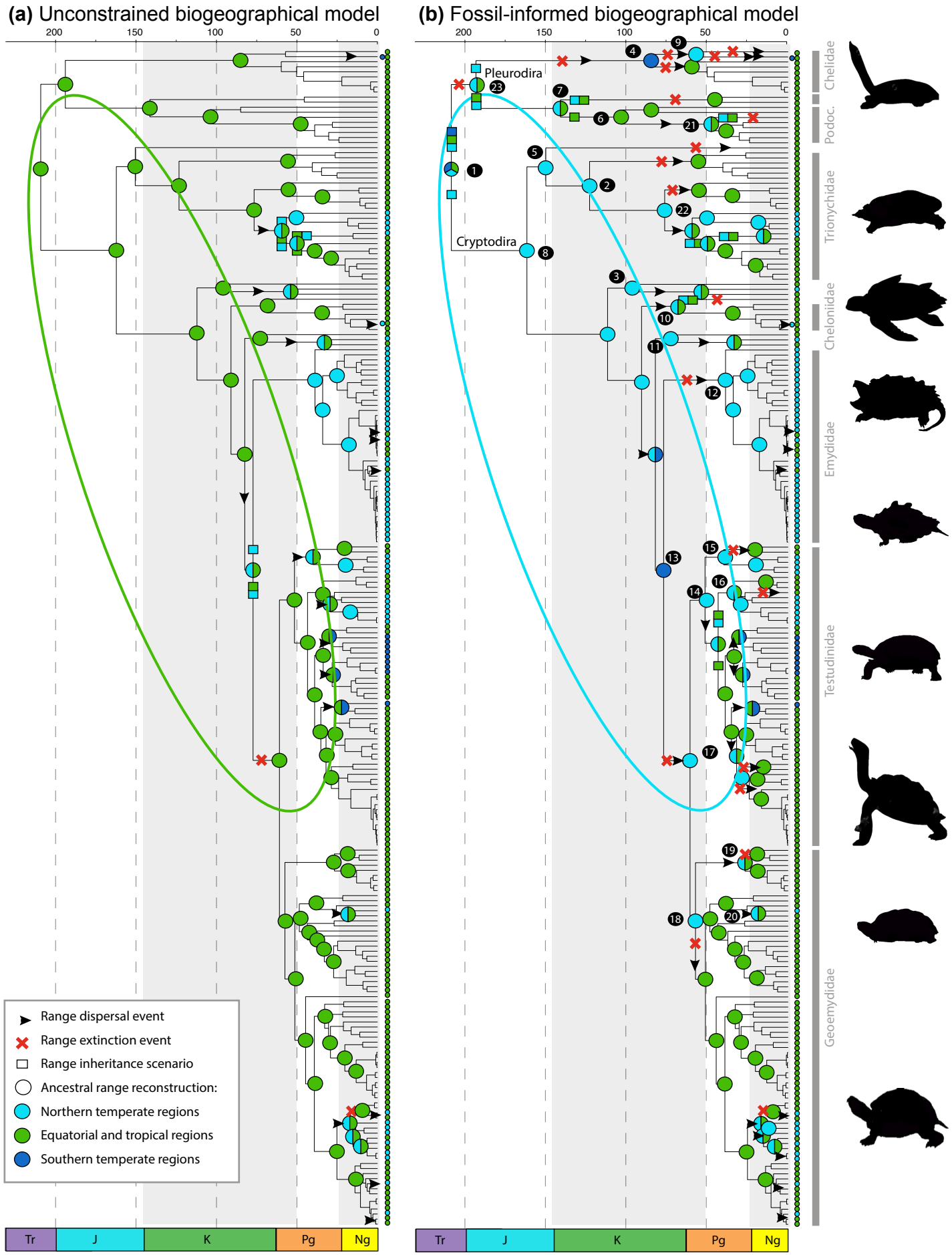

Figure 6 | Biogeographic reconstruction of Testudines showing the effects of the incorporation of fossil information into biogeographic inference. **a**, Biogeographic reconstruction inferred with DEC based on the distribution of extant taxa. **b**, Biogeographic reconstruction under the fossil-informed 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.

Table 11). The same trend was observed when the number of extinction/dispersal events was controlled for the number of lineages currently distributed in each region (**Fig. 7**).

Lepidosaurs originated in both regions in both SFC and HFC analyses (Supplementary Figs. 13, 14). During the greenhouse period, dispersal '*into the equator*' occurred at the same rate (or at a higher rate in the HFC model) than dispersal '*out of the equator*', and dispersal '*out of the equator*' prevailed thereafter (Supplementary Fig. 17, Supplementary Table 10). Estimated range extinction rates were high in this group under the unconstrained model, with 30 lineages extirpated from the Holarctic, two from southern temperate regions and 152 from the equator (Supplementary Fig. 17, Supplementary Table 11). Under fossil-informed models, the number of Holarctic extinctions was higher (109 and 66 lineages in the HFC and SFC models, respectively), whereas the number of lineages extirpated from the equator was similar (144 and 109 in the HFC and SFC models, respectively; Supplementary Fig. 17). When the number of events was controlled for the actual number of lineages distributed in each region, the number of Holarctic extinctions and dispersals '*into the equator*' increased dramatically, exceeding equatorial dispersal/extinctions (**Fig. 7**). For crocodiles, analyses including fossil ranges showed that all the early nodes were distributed in the Holarctic (Supplementary Figs. 15, 16), and range extinctions were detected: four lineages disappeared from the Holarctic, three from southern temperate regions, and two from the equator (HFC model; Supplementary Fig. 17, Supplementary Tables 11, 12). Only two lineages disappeared from the Holarctic in the SFC model. The same trends were observed after controlling the number of events for the current number of lineages in each region (**Fig. 7**).

Discussion

Generation of the current LDG

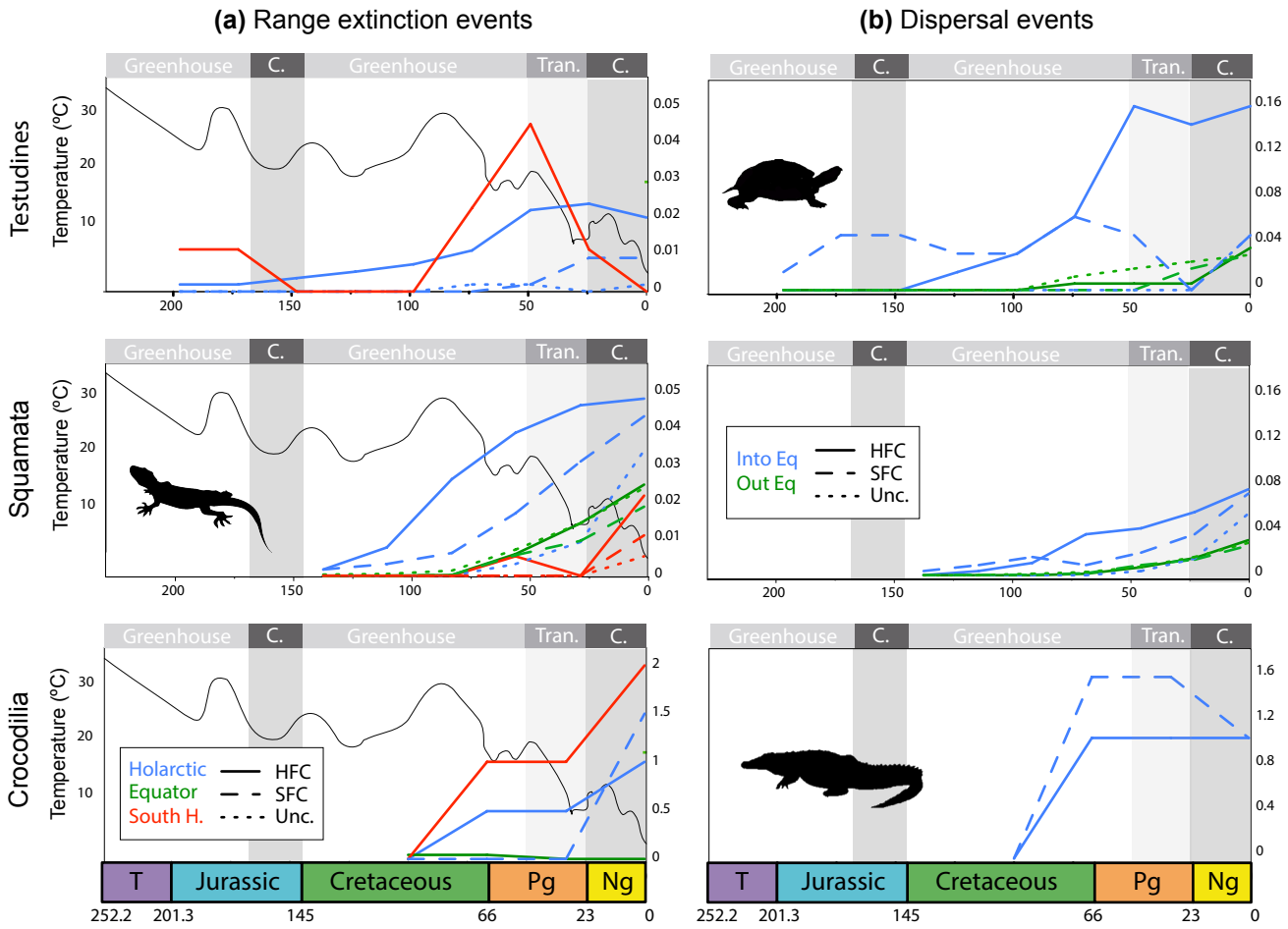

Figure 7 | Estimated number of range-extinction and dispersal events through time. Analyses were performed for Testudines, Squamata and Crocodiles under the *unconstrained model* (Unc.), based on present evidence only, and the fossil-based *hard* (HFC) and *soft fossil constraint* (SFC) biogeographic 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 Zachos et al., (2008). **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.

300 Fossil investigations have shown that at certain times during the Phanerozoic, the LDG has
301 weakened, flattened, or developed a palaeotemperate peak, with diversity at high latitudes
302 being greater in some periods of the past than currently for many groups[10,13]. Hypotheses
303 relating to 'slow Holarctic diversity accumulation', such as limited dispersal to the
304 Holarctic[31], high Holarctic turnover[37,41,49], or high rates of equatorial diversification[32–35,77],
305 cannot themselves account for the formation of a flatten LDG, or the transition from higher to
306 lower diversity in the Holarctic observed in many groups. Furthermore, although the
307 processes shaping biodiversity vary over time and space, this has been largely overlooked in
308 the context of the LDG, which has been generally explained in terms of the actions of time-
309 constant process.

310 We account for temporal changes in the global distribution of biodiversity by
311 proposing a scenario involving losses/gains of tropical diversity at high latitudes during
312 transitional periods from warm to cool conditions. The AGE hypothesis captures components
313 of previous studies[10,31,35,50,65] in the context of a time-variable LDG to disentangle the relative
314 contributions of speciation, extinction and dispersal for each particular geological period in
315 the formation of the LDG. Below, we evaluate the support of our analyses to the postulates of
316 the time-variable AGE hypothesis (**Fig. 2; Table 1**):

317 **P1: Extinction exceeds speciation at high latitudes during cool transitions, *i.e.***
318 **declining diversity ($r_H < 0$)**. Our diversification analyses based on extant species (time-
319 constant and time-variable BiSSE analyses) do not support this postulate, suggesting instead
320 higher levels of Holarctic diversification for turtles, and of equatorial diversification for
321 lepidosaurs. By contrast, results for fossil-only (PyRate) diversification analyses were
322 consistent with this prediction for turtles and crocodiles. We found that diversification rates of
323 turtles and crocodiles decreased in all regions during the transition to colder climates, but the
324 slowing of diversification was much stronger in the Holarctic than at the equator, with

extinction exceeding speciation in this region (**Fig. 3, 4**). This suggests that Holarctic diversity loss ($r < 0$) during the Paleogene could explain the formation of a steep LDG for these groups. For lepidosaurs, **P1** is not supported by fossil data; diversity losses occurred during Cenozoic cooling in the equator but not at higher latitudes (**Fig. 4**). Diversity dynamics for the species distributed at the equator, however, may not be entirely reliable, due to the poverty of the equatorial dataset in terms of the number of fossil lineages and the small number of records per lineage (Supplementary Table 12). Uncertainties therefore remain on these estimates, which have wide credibility intervals, probably due to geographic biases in the fossil record[78]. Turnover rates were very high in the Holarctic during the transitional period, indicating that species did disappear from high latitudes, but that a new lepidosaur community replaced them. This result suggests the number of lepidosaur species may always have been unbalanced between regions. The high Holarctic turnover would contribute to the maintenance of this pattern, together with the inferred temporal increases in diversification at the equator (**Fig. 4**), as previously hypothesized [41].

P2: Higher '*into the equator*' dispersal than '*out of the equator*' dispersal ($d_{HE} > d_{EH}$) during cool transitions. The DEC biogeographic analyses based on extant species do not support this postulate but instead the '*tropical niche conservatism*' hypothesis for turtles, with an equatorial origin and recent invasion of high-latitude regions, resulting in less time for lineages to diversify[31] (**Figs. 6, 7**, **Table 1, 2**). This result is consistent with the findings of recent investigations[79,80]. For lepidosaurs, they support the '*out of the tropics*' (**Fig. 7**, Supplementary Figs. 1-3, 10), and for crocodiles the diversification hypothesis, with higher origination rates close to the equator and no effect on dispersal (**Fig. 7**, **Table 2**, Supplementary Fig. 11). In contrast, time-constant and time-variable BiSSE analyses are consistent with **P2** and the '*into the equator*' hypothesis to explain the LDG (Supplementary Figs. 1a, 2a, 3a), as so they are the results for fossil-informed DEC biogeographic analyses;

350 all groups are inferred to have had a widespread ancestral distribution that subsequently
351 contracted towards the equator due to both higher levels of range extirpations at higher
352 latitudes and '*into the equator*' dispersals during Cenozoic cooling (**Figs. 6, 7**). This result is
353 also in agreement with previous fossil investigations on turtles[24,25,76] and crocodiles[23,44]. For
354 lepidosaurs, in absolute terms, more species migrated "*out of*" than "*into the equator*"
355 (Supplementary Fig. 17), but the number of species in the equatorial region today is four
356 times the number of lineages elsewhere. After controlling for the imbalance in species
357 sampling in our tree, we found that a higher proportion of lepidosaur species lost their
358 ancestral Holarctic distribution and emigrated '*into the equator*' [41] than the other way around
359 (**Fig. 7**). Although the number of fossil constraints in the biogeographic analysis of
360 lepidosaurs was relatively low given the size of the tree (30 Holarctic and equatorial fossils
361 for 4161 nodes), these constraints significantly increased the absolute number of Holarctic
362 range extinctions (from 30 to 109) and '*into the equator*' dispersals (from 40 to 124) relative
363 to estimates without such constraints (Supplementary Tables 10, 11). Meanwhile, the
364 inclusion of fossil data did not alter the number of events estimated for equatorial taxa. This
365 finding suggests that a deeper understanding of lepidosaur fossil taxonomy might facilitate the
366 assignment of fossils on the tree, and the detection of additional high-latitude extinctions not
367 detected here.

368 Unfortunately, the age of the taxa evaluated here prevents us for testing the predictions
369 associated with the transition from coldhouse to greenhouse conditions (**P3-4**). Nonetheless,
370 our fossil-based analyses show similar diversification rates in the Holarctic and equatorial
371 regions during the greenhouse period of the Cretaceous-early Cenozoic for all groups
372 (overlapping credibility intervals; **Fig. 4**; Supplementary Figs. 1-3, 4-9), consistent with the
373 idea of the existence of a flattened LDG during this phase [10]. Similarly, the AGE hypothesis
374 focuses essentially on the Northern Hemisphere, but diversity losses and dispersals '*into the*

375 *equator*' may have also occurred in the temperate regions of the Southern Hemisphere.
376 Indeed, we found high rates of range extinctions in this region for all groups (**P2**; red lines on
377 **Fig. 7**). Unfortunately, the scarce fossil record prevents any diversification estimates for this
378 region (see *Methods*).

379 Overall, the general pattern that could be extracted from our study is that the AGE
380 hypothesis was supported for crocodiles and turtles using fossil and fossil-informed
381 phylogenetic investigations (**Table 1, 2**; **P1–P2** of AGE). However, if we rely only on
382 analyses based on data for extant species using biogeographic and constant and time-variable
383 BiSSE diversification models, this evolutionary scenario was poorly supported (although
384 BiSSE analyses support **P2** of AGE**)**. Support for the AGE hypothesis is mixed in
385 lepidosaurs; on the one hand the detected Holarctic range contractions are in agreement with
386 "higher Holarctic diversity loss" scenarios (**P2** of AGE), on the other hand, the evidence for
387 high Holarctic turnover are more in line with previous "slower Holarctic diversity
388 accumulation" hypotheses.

389

390 ***The timing and effect of the last greenhouse to coldhouse climatic transition***

391 Recent fossil investigations suggest that changes in the shape of the LDG have been
392 associated with major climatic oscillations[10,13]. Accordingly, we hypothesized the
393 impoverishment of the Holarctic resulted from the contraction of the tropical biome during
394 the last greenhouse to coldhouse transition. But when this coldhouse transition took place?
395 The transitional period to cold was here defined between 51 and 23 Ma, after the early Eocene
396 Climatic Optimum (EECO), based on paleontological evidence showing that paratropical
397 conditions and the associated warm-adapted taxa disappeared from high latitudes between the
398 mid-late Eocene and the Neogene[59,61,62]. Our diversification results with time intervals defined
399 by the main climatic periods are consistent with these observations, and detect Holarctic

diversity loss during the late Paleogene. We cannot exclude, however, that diversity losses at high latitudes occurred since the Cretaceous, as suggested by our fossil-based diversification analyses with time intervals defined by the main geological periods (Supplementary Figs. 4, 6, 8) and by our fossil-based biogeographic analyses suggesting the prevalence of '*into the equator'* dispersals since the Cretaceous (**Fig. 7**, Supplementary Table 11). These findings could suggest that other processes different to climate change mediated the extinction and range contraction of Holarctic lineages in the Cretaceous, or alternatively, that a transition phase to cold started before the relatively short interval considered here. Some studies consider the EECO only represented a transient temperature peak within an otherwise cooling trend that started in the Cretaceous[64,81]. This trend was intensified by the Cretaceous-Paleogene (K-Pg) mass extinction, and the drop in temperatures caused by the impact-associated winter[82,83]. In our study, lineage extinctions, range extinctions and southward dispersals increased between the K-Pg and Neogene (**Fig. 4, 7**), suggesting an additive effect of K-Pg and Neogene cooling on depopulation of the Holarctic.

The ancestors of turtles, lepidosaurs and crocodiles were adapted to tropical conditions during the Late Cretaceous[44,84]. Our results indicate that extinction events were not random, instead preferentially affecting taxa living in tropical-like climates at high latitudes[48] (**Figs. 4, 5**). This suggests that many species adapted to warm conditions living in the Holarctic were unable to adapt to the new temperate regimes and either went extinct or escaped extinction by contracting their ranges in a southerly direction (**Fig. 7**). Meanwhile, we found that the diversification rates of turtles, crocodiles and lepidosaurs living in temperate climatic conditions were significantly higher than those of tropical-adapted taxa living in Holarctic and equatorial regions after the transition to temperate climates in the late Eocene (**Fig. 5**, **Table 2**). The new temperate habitats could have constituted an opportunity for diversification because they increased geographic ranges and ecological niches[34], and may have driven an

425 inverse LDG for some groups[39,68]. Several radiations following the appearance of the
426 temperate biome have been identified in other groups of organisms, such as plants [85,86],
427 mammals[87,88] or insects[89]. After this period, speciation decreased dramatically in the
428 temperate lineages of our focal groups, possibly due to the effect of the Pleistocene
429 glaciations, and no difference in diversification between tropical and temperate lineages is
430 currently evident (**Fig. 5**). In summary, our study suggests that differences in species richness
431 between geographic regions may be explained by differences in diversification and dispersal
432 rates. Differences in species richness between ecological types may be explained by the
433 longer time available for tropical-adapted clades to diversify in tropical areas[90] rather than
434 higher rate of speciation under warm tropical environments, as previously postulated [91].
435
436 ***Reconciling fossil and phylogenetic evidence***
437 Our results unequivocally demonstrate that the inclusion of fossils in macroevolutionary
438 studies makes it possible to detect signals of ancient high-latitude extinctions and range
439 extirpations (**Figs. 4-7**), otherwise hardly detectable with analyses based exclusively on
440 present-day data. This conflict between extant and fossil evidence may extend beyond our
441 study, pervading the LDG literature. High extinction rates have occasionally been inferred in
442 tropical lineages[67,92–94], with hypotheses relating to extinction focused on temperate taxa and
443 recent time scales, such as the effects of recent Pleistocene glaciations, for example[33,37,41,42].
444 In reported cases of extinction, origination rates were also found to be elevated in high-
445 latitude groups (high turnover)[33,37–39,41,50], while diversity losses ($r < 0$) have to our
446 knowledge never been inferred in phylogenetic studies of the LDG (with the exception of the
447 recent Pulido-Santacruz & Weir (2016) study using time constant BiSSE models, but see
448 below). On the other hand, ancient tropical extinction at high latitudes is supported by fossil
449 studies on various taxonomic groups[15,16,28,53–56].

450 The last decade has seen many efforts to reconcile fossil and phylogenetic evidence.
451 Birth-death diversification models have been developed to detect negative diversification
452 rates on reconstructed phylogenies, or total-evidence trees[95–97]. Still, their use in the literature
453 is limited and these models are difficult to implement in a trait evolution context, such as in
454 the study of the LDG. LDG studies are often based on state-dependent speciation and
455 extinction models[35,38,40,41,49,50]. These models are designed to test differential diversification
456 and asymmetric transition scenarios, such as that suggested here, but LDG studies often
457 assume that diversification parameters remain constant over time. If the evolutionary
458 processes shaping the LDG have varied across latitudes and time, then time-constant models
459 are not appropriate for testing more complex scenarios underlying the LDG. Moreover, the
460 potential of time-constant models for detecting negative diversification rates is questionable,
461 since inferring negative diversification for the entire history of lineages conflicts with the fact
462 that these groups are still extant. Testing our hypothesis thus requires the implementation of
463 time-variable models. When applied to the study of diversity patterns, these models have
464 revealed marked extinction signatures in ancestral tropical plant clades[98]. The incorporation of
465 time-shifts into our BiSSE analyses improves but not completely reconciles the fossil
466 evidence with extant diversity. Identifying the causes of this problem and finding solutions
467 are beyond the scope of this study, but this artifact highlights the importance of fossils in
468 macroevolutionary inferences[99]. Fossil records remain incomplete, but they nevertheless
469 provide the only direct evidence of the diversity that existed in the past. By contrast to
470 molecular phylogenies, the incompleteness of the fossil record has a less problematic effect
471 on the estimation of speciation and extinction rates, because removing a random set of taxa
472 does not affect the observed occurrences of other lineages[74]. Indeed, simulations have shown
473 that PyRate correctly estimates the dynamics of speciation and extinction rates under low
474 levels of preservation or severely incomplete taxon sampling.

475

476 ***Conclusion***

477 After decades of research, the processes shaping the LDG remain among the most hotly
478 debated topics in ecology and evolutionary biology. We propose here the AGE hypothesis,
479 which explains the origin of the current LDG through the changes in global diversification
480 and dispersal dynamics imposed by large-scale climatic transitions. Our analyses for turtles
481 and crocodilians indicated that the processes shaping the LDG have changed over time, the
482 current form of this gradient being the result of ancient high-latitude tropical diversity loss
483 and range contractions as a consequence of the retraction of the tropical biome and due to
484 climate cooling. The AGE hypothesis might account for the LDG of tropical-adapted groups
485 that were once diverse at high latitudes, but might not be fully applicable to all organisms
486 currently displaying a LDG, as shown here for lepidosaurs.

487

488 **Methods**

489 ***Time-calibrated phylogenies and the fossil record.*** We compared the predictions of the AGE
490 hypothesis with the LDG of three vertebrate groups: turtles (order Testudines), crocodiles
491 (order Crocodilia), and scaled lizards (order Lepidosauria). A time-calibrated phylogeny for
492 each group was obtained from published data. For turtles, we used the phylogeny of Jaffe *et*
493 *al.* (2011), including 233 species. We preferred this phylogeny over other more recent and
494 slightly better sampled trees[101] because the divergence time estimates of Jaffe *et al.* (2011) are
495 more consistent with recent estimates based on genomic datasets[79,102]. For lepidosaurs, we
496 retrieved the most comprehensive dated tree available, including 4161 species[41], and a
497 complete phylogeny was obtained for crocodiles[103].

498 Fossil occurrences were downloaded from the *Paleobiology Database*
499 (https://paleobiodb.org/#/, last accessed October 25th 2017). We reduced potential biases in

500 the taxonomic assignation of turtle, crocodile and lepidosaur fossils, by compiling occurrence
501 data at the genus level. The fossil datasets were cleaned by checking for synonymies between
502 taxa and for assignment to a particular genus or family on the basis of published results
503 (Supplementary Table 4–6).
504
505 ***Estimation of origination and extinction rates with phylogenies.*** We investigated possible
506 differences between Holarctic and equatorial regions, by combining the turtle and lepidosaur
507 phylogenies with distributional data (Supplementary Tables 1, 2) to fit trait-dependent
508 diversification models in BiSSE[70]. We accounted for incomplete taxon sampling in the form
509 of trait-specific global sampling fraction of extant species[104].
510 We ensured comparability with previous LDG studies, by initially using a constant-
511 rate trait-dependent diversification model. The constant-rate BiSSE model has six parameters:
512 two speciation rates (without range shift, or *in situ* speciation), one associated with the
513 Holarctic (hereafter 'H', λ_H) and the other with other equatorial and subtropical regions
514 (hereafter 'equator' or 'E', λ_E), two extinction rates associated with the Holarctic (μ_H) and the
515 equator (μ_E), and two transition rates (dispersal or range shift), one for the Holarctic to
516 equator direction ($q_{H\text{-}E}$), and the other for the equator to Holarctic direction ($q_{E\text{-}H}$).
517 We then assessed the effect of species distribution on diversification, allowing for rate
518 changes at specific time points. This approach is associated with a lower bias than the use of
519 constant rates. We used the time-dependent BiSSE (BiSSE.td) model, in which speciation,
520 extinction, and dispersal rates are allowed to vary between regions and to change after the
521 shift times. We introduced two shift times to model different diversification dynamics
522 between greenhouse, transitional, and coldhouse periods. We assumed that a global warm
523 tropical-like climate dominated the world from the origin of the clades until 51 Ma
524 (corresponding to the temperature peak in the Cenozoic). Thereafter, the climate

525 progressively cooled until 23 Ma (the transitional period), when the climate definitively
526 shifted to a temperate-like biome in the Holarctic[61,62,64]. The shift times at 51 Ma and at 23
527 Ma are initial values that are re-estimated by the model during the likelihood calculation. The
528 climatic transition in the Cenozoic may have different temporal boundaries, with potential
529 effects on the results. We thus applied the same model but with different combinations of shift
530 times (we tested 51/66 Ma and 34/23 Ma for the upper and lower bounds of the climatic
531 transition).

532 Analyses were performed with the R package *diversitree* 0.9-7[71], using the *make.bisse*
533 function to construct likelihood functions for each model from the data, and the functions
534 constrain and *find.mle* to apply different diversification scenarios. Finally, we used a Markov
535 Chain Monte Carlo (MCMC) approach to investigate the credibility intervals of the parameter
536 estimates. Following previous recommendations[71], we used an exponential prior 1/(2r) and
537 initiated the chain with the parameters obtained by maximum likelihood methods. We ran
538 10,000 MCMC steps, with a burn-in of 10%.

539

540 ***Estimation of origination and extinction rates with fossils.*** We also used fossil data to
541 estimate diversification rates over time. We analyzed the three fossil records, using a
542 Bayesian model for simultaneous inference of the temporal dynamics of origination and
543 extinction, and of preservation rates[74]. This approach, implemented in PyRate[105], uses fossil
544 occurrences that can be assigned to a taxon, in this case fossil genera. The preservation
545 process is used to infer the individual origination and extinction times of each taxon from all
546 fossil occurrences and an estimated preservation rate; it is expressed as expected occurrences
547 per taxon per million years.

548 We followed a birth-death shift approach[106], which focuses on the variation of
549 origination and extinction at a global scale and over large temporal ranges. We used a

550 homogeneous Poisson process of preservation (-mHPP option). We also accounted for the
551 variation of preservation rates across taxa, using a Gamma model with gamma-distributed rate
552 heterogeneity (-mG option). We used four rate categories to discretize the gamma
553 distribution, to allow for a greater variability of preservation rates across taxa.

554 Given the large number of occurrences analyzed and the vast timescale considered, we
555 dissected the birth–death process into time intervals, and estimated origination and extinction
556 rates within these intervals. In one set of analyses we defined the time intervals using the
557 geological epochs of the stratigraphic timescale[107] (Supplementary Figs. 4, 6, 8). In another
558 set of analyses, we defined the intervals according to the different climatic periods
559 characterizing the Cenozoic (Supplementary Figs. 5, 7, 9), as discussed above: the greenhouse
560 world (Cretaceous), the climatic transition (Paleogene), and the coldhouse world (Neogene
561 until the present). We adopted this solution as an alternative to the algorithms implemented in
562 the original PyRate software for joint estimation of the number of rate shifts and the times at
563 which origination and extinction shift[74]. The estimation of origination and extinction rates
564 within fixed time intervals improved the mixing of the MCMC and made it possible to obtain
565 an overview of the general trends in rate variation over a long timescale [106]. Both the
566 preservation and birth–death processes were modeled in continuous time but without being
567 based on boundary crossings. Thus, the origination and extinction rates were measured as the
568 expected number of origination and extinction events per lineage per million years. One
569 potential problem when fixing the number of rate shifts *a priori* is over-parameterization. We
570 overcame this problem by assuming that the rates of origination and extinction belonged to
571 two families of parameters following a common prior distribution, with parameters estimated
572 from the data with hyper-priors[108].

573 We ran PyRate for 10 million MCMC generations on each of the 10 randomly
574 replicated datasets. We monitored chain mixing and effective sample sizes by examining the

log files in Tracer 1.6[109]. After excluding the first 20% of the samples as a burn-in, we combined the posterior estimates of the origination and extinction rates across all replicates to generate plots of the change in rate over time. The rates of two adjacent intervals were considered significantly different if the mean of one lay outside the 95% credibility interval of the other, and vice versa. We looked at the marginal posterior distributions of origination and extinction rates through the evolutionary history of the three groups and assessed the effect of different environments.

In the context of the LDG, we performed additional analyses with different subsets of fossils, to separate the speciation and extinction signals of different geographic regions (equator or Holarctic) and ecological conditions (temperate or tropical). For example, for turtles, we split the global fossil dataset into four subsets: one for the fossil genera occurring at the equator (429 occurrences), one for the fossils occurring in the Holarctic (3568 occurrences), one for the fossil genera considered to be adapted to temperate conditions (993 occurrences), and one for the fossils considered to be adapted to tropical conditions (2996 occurrences). We excluded the few fossil occurrences for the southern regions of the South Hemisphere (about 180) only in subset analyses, as they were poorly represented in our dataset. Note that a given fossil can be present in both the 'Holarctic' and 'tropical' datasets. We encoded tropical/temperate preferences by considering macroconditions in the Holarctic to be paratropical until the end of the Eocene, as previously reported [61,62] (and references therein). We also assumed that taxa inhabiting the warm Holarctic were adapted to tropical-like conditions (*i.e.* a high global temperature, indicating probable adaptation to tropical climates). This is, of course, an oversimplification that may introduce bias into the analysis, but general patterns may nevertheless emerge from such analyses[110]. For turtles, this assumption is supported by a recent study modeling the climatic niche of this group during the Late Cretaceous, which found that the Holarctic ancestors of turtles were adapted to

600 tropical conditions[84]. After the late Eocene, we categorized each species as living in the
601 temperate biome or the tropical biome, according to the threshold latitudes defining the
602 tropics (23.4°N and 23.4°S) suggested in a previous study[33]. This delineation is also
603 consistent overall with the Köppen climate classification. With these datasets, we reproduced
604 the same PyRate analyses as for the whole dataset (see above). In general, the fossil datasets
605 included mostly Holarctic fossils, with a smaller number of occurrences for the equator.
606 Caution is therefore required when drawing conclusions from the equatorial datasets.
607
608 ***Inferring ancestral geographic distribution with phylogenies and fossils.*** We performed
609 biogeographic analyses with the parametric likelihood method DEC[75] using the fast C++
610 version[111] (https://github.com/rhr/lagrange-cpp). Turtle, lepidosaur, and crocodile species
611 distributions were obtained from online databases (www.iucnredlist.org and www.reptile-
612 database.org). We chose 23.4°N and 23.4°S as the threshold latitudes defining the tropics, and
613 categorized each species as living in the Holarctic, in the southern temperate regions, or in the
614 equatorial tropics and subtropical regions. We considered that all ranges comprising three
615 areas could be considered an ancestral state (*maxareas* =3).
616 We set up three different DEC analyses. We first ran DEC with no particular
617 constraints, using only the distribution of extant species. We then performed DEC analyses
618 including fossil information in the form of 'fossil constraints' at certain nodes, according to
619 the range of distribution of fossil occurrences assigned to a particular taxon during the
620 relevant time frame. For example the crown age of Carettochelyidae (Testudines) dates back
621 to the Late Jurassic (150 Ma, *node 5*, **Fig. 3**; Supplementary Table 7), and we set a constraint
622 on this node reflecting the distribution of all the Late Jurassic fossils attributed to
623 Carettochelyidae. Similarly, for the origin of turtles (210 Ma, *node 1*), distribution constraints
624 represent the range of Late Triassic fossils assigned to turtles. For the crown of Trionychidae,

625 in the Early Cretaceous (123 Ma, *node 2*), the early fossils assigned to the clade were used to
626 constrain the geographic origin of Trionychidae. In total, we implemented 23 fossil
627 constraints for turtles (Supplementary Table 7), 30 fossil constraints for lepidosaurs
628 (Supplementary Table 8), and 8 for crocodiles (Supplementary Table 9).

629 We included the fossil distribution in two different approaches: *(i)* a soft (SFC), and
630 *(ii)* hard fossil constraints (HFC). For the SFC approach, fossil data were incorporated into the
631 anagenetic component of the likelihood framework. The direct impact of a given fossil is
632 limited to the particular branch to which it has been assigned, although it may indirectly
633 influence other branches. The inclusion of a fossil conditions the estimated geographic-
634 transition probability matrix for that branch by imposing a spatiotemporal constraint on the
635 simulation process. Only the simulations resulting in a geographic range including the area of
636 fossil occurrence contribute to the geographic-range transition probability matrix for the
637 branch concerned; simulations not meeting this constraint are discarded[112]. For SFC, we used
638 the command '*fossil*' in DEC. We consider this to be a 'soft' constraint, because other areas
639 different from that in which the fossil was found could be included in the ancestral states. In
640 some cases, in which today's diversity is not representative of past diversity (*e.g.* due to
641 extreme levels of extinction), the SFC model may still overlook known fossil information. We
642 therefore also implemented an HFC model in which the estimation of ancestral areas was
643 fixed to the location of fossils. This was achieved with existing functions in the C++ version
644 of Lagrange, using the command '*fixnode*'. By fixing nodes to the distribution area of fossils,
645 we assume fossil occurrences reflect the distribution of the ancestors, *i.e.* that the fossil record
646 is complete. This is a strong assumption, but it makes it possible to recover all fossil ranges in
647 the ancestral estimations. The real scenario probably lies somewhere between the SFC and
648 HFC inferences.

We then compared the timing and number of range extinction and dispersal events inferred with the three different biogeographic analyses. In DEC, range-subdivision (inheritance) scenarios (vicariance, duplication and peripatric isolation) occur at cladogenetic events, whereas extinction (range contraction) and dispersal (range expansion) are modeled as stochastic processes occurring along the branches of the tree[113]. As the probability of any extinction/dispersal event is constant along the entire length of the branch, we estimate the periods at which range extinction and dispersal occurred by dividing the phylogeny into intervals of 25 million years and calculating the number of branches for which extinction/dispersal was inferred crossing a particular time interval (the same branch could cross two continuous intervals).

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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.

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