Title

Ancient tropical extinctions contributed to the latitudinal diversity gradient

Authors

Andrea S. Meseguer[1,2]†* and Fabien L. Condamine[2]†*

Affiliations

[1]INRA, UMR 1062 CBGP (INRA, IRD, CIRAD, Montpellier SupAgro), 755 Avenue du Campus Agropolis, 34988 Montferrier-sur-Lez, France.

[2]CNRS, UMR 5554 Institut des Sciences de l'Evolution (Université de Montpellier), Place Eugène Bataillon, 34095 Montpellier, France.

†These authors contributed equally.

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.

Corresponding authors (*)

Andrea S. Meseguer (asanchezmeseguer@gmail.com), Fabien L. Condamine (fabien.condamine@gmail.com)

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

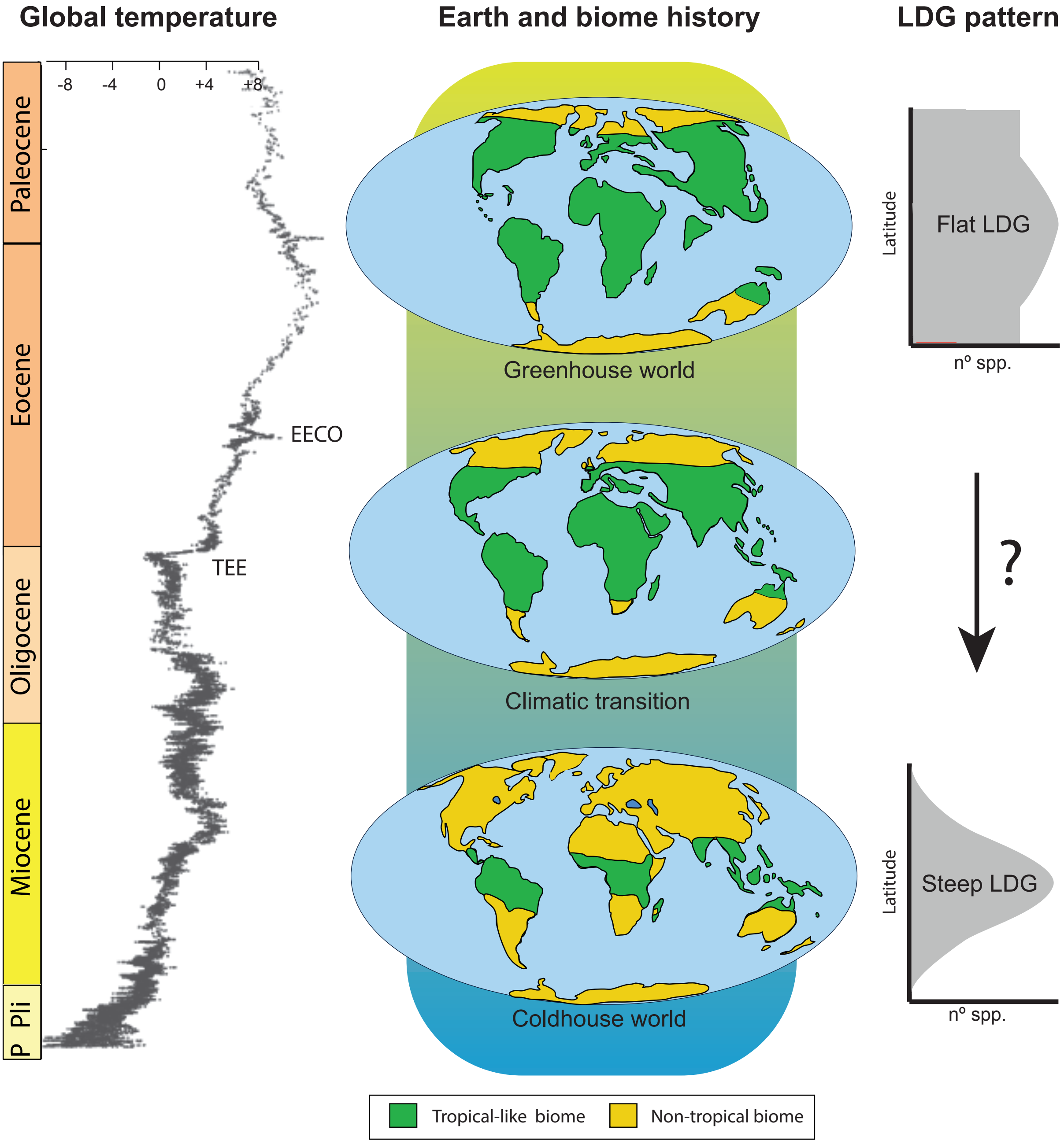

Figure 1 | Changes in global temperature and extension of the tropical belt during the Cenozoic, in relation with the shape of the LDG. Early Cenozoic global temperatures were higher than today and paratropical conditions extended over northern and southern latitudes. From the early Eocene climatic optimum (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 result of greater diversification and limited dispersal out of the equatorial region[7,32,34], or by high rates of turnover in the Holarctic (*i.e.* similar high speciation and extinction rates), keeping diversity levels in this region low over time (**Table 1**), for amphibians[35,36], birds[33,37,38], butterflies[39], conifers[40], fishes[41], mammals[34,38], and squamates[42], for example. Here, we group these mechanisms together under the ‘low Holarctic species accumulation’ hypothesis, because they all assume that the LDG results from lower levels of species accumulation in the Holarctic than at the equator. However, recent fossil investigations have shown that, for many lineages, diversity levels in the Holarctic were once similar to those at the equator. Thus, the real question is why, how and when was diversity lost at high latitudes, giving rise to the current shape of the LDG?.

Phylogenetic investigations have suggested potential mechanisms that might explain the transition from high to low Holarctic diversity. Some studies have considered high latitudes as a possible source of diversity, with the high species richness observed in the tropics today resulting from differential dispersal (*d*) from high to low latitudes following the contraction of the tropical biome[39,42,43]. However, disproportionate high-latitude extinctions — a scenario in which extinction (μ) outweighs speciation (λ), resulting in negative net diversification rates ($r = \lambda - \mu; r < 0$) — could also explain this transition. Diversity losses in the Holarctic are sometimes considered to underlie the LDG[38]. They were initially attributed to Pleistocene glaciations[44], but this hypothesis has been called into question by the finding that the LDG predates the Pleistocene[7,12]. More ancient extinctions have also been considered[45-52]. For example, Hawkins *et al.*[49] suggested that the avian LDG resulted from the differential extirpation of older warm-adapted clades from the temperate regions newly formed in the Neogene. Unfortunately, it is difficult to demonstrate diversity losses in the Holarctic beyond high regional turnover[31,38], but this phenomenon can account only for a slow 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

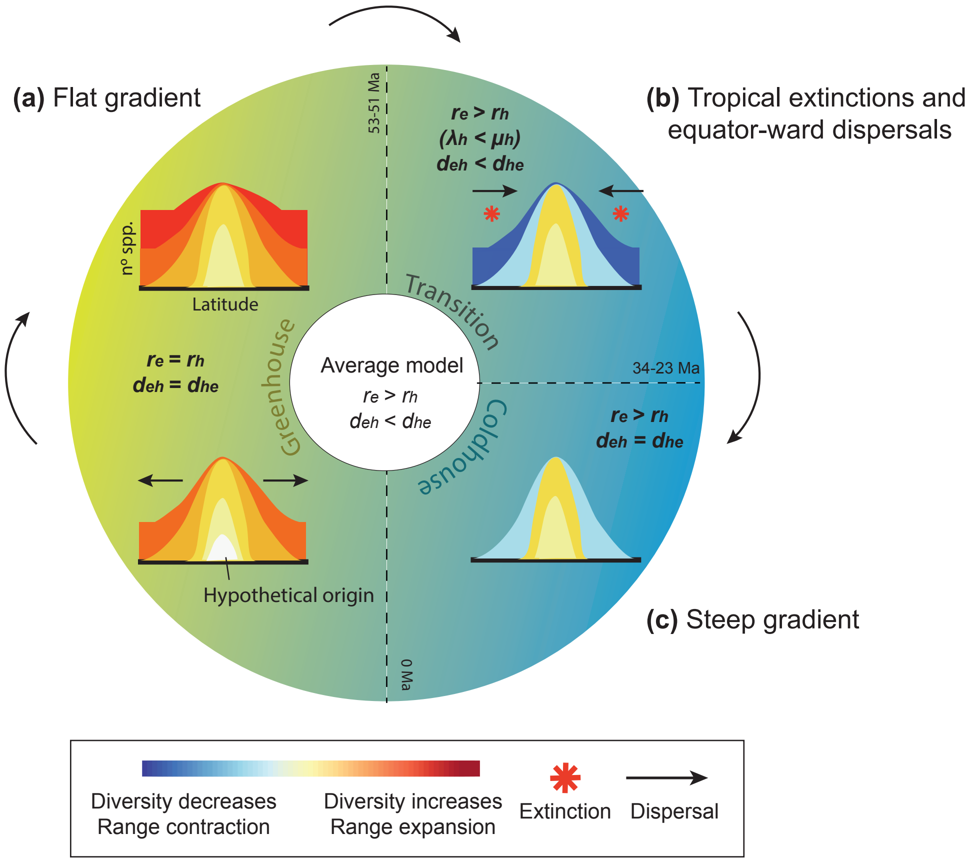

Figure 2 | Prevalent evolutionary processes behind the latitudinal diversity gradient under the AGE time-variable framework. The graphic shows the hypothetic change in evolutionary dynamics (diversification “r”, speciation “λ”, extinction “μ” and dispersal “d”) between Holarctic and equatorial regions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

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

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

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

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

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

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

Results

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

According to current distribution data, the species richness of turtles, squamates 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 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

climatic transition and coldhouse period. The same patterns were obtained for inferences with the same model but with different combinations of shift times (51 Ma and 34/23 Ma; Supplementary Fig. 3).

Fossil-based diversification analyses: evidence for ancient tropical extinctions?

We also analyzed differences in diversification rates between the Holarctic and equatorial regions based exclusively on fossil data. The turtle fossil dataset comprised 4084 occurrences for 420 genera (65 extant and 355 extinct; Supplementary Table 4). The squamate fossil dataset comprised 4798 occurrences for 638 genera (120 extant and 518 extinct; Supplementary Table 5). The crocodile fossil dataset comprised 1596 occurrences for 121 genera (9 extant and 112 extinct; Supplementary Table 6). We first inferred global diversification dynamics by analyzing the fossil datasets as a whole with a Bayesian approach to inferring the temporal dynamics of origination and extinction rates based on fossil occurrences[71] (see *Methods*). For turtles, origination rates peaked during the Jurassic, subsequently decreasing until the present day. Extinction rates were generally low and constant during the Mesozoic, but increased during the coldhouse periods of the Jurassic and Paleogene, resulting in negative net diversification during the Paleogene (**Fig. 3**, **Table 2**, Supplementary Figs. 4, 5). For squamates, origination rates peaked in the Jurassic and Late Cretaceous, whereas extinction increased steadily until the Late Cretaceous. In the Paleogene, net diversification approached zero, suggesting a high rate of turnover (**Fig. 3**, Supplementary Figs. 6, 7). Crocodilia origination peaked in the Early Cretaceous, subsequently decreasing towards the present day, and extinction rates were generally low and constant. We also identified losses of diversity in the Paleogene extending to the present, suggesting that crocodiles are still in a phase of steadily declining diversity (**Fig. 3**, Supplementary Figs. 8, 9).

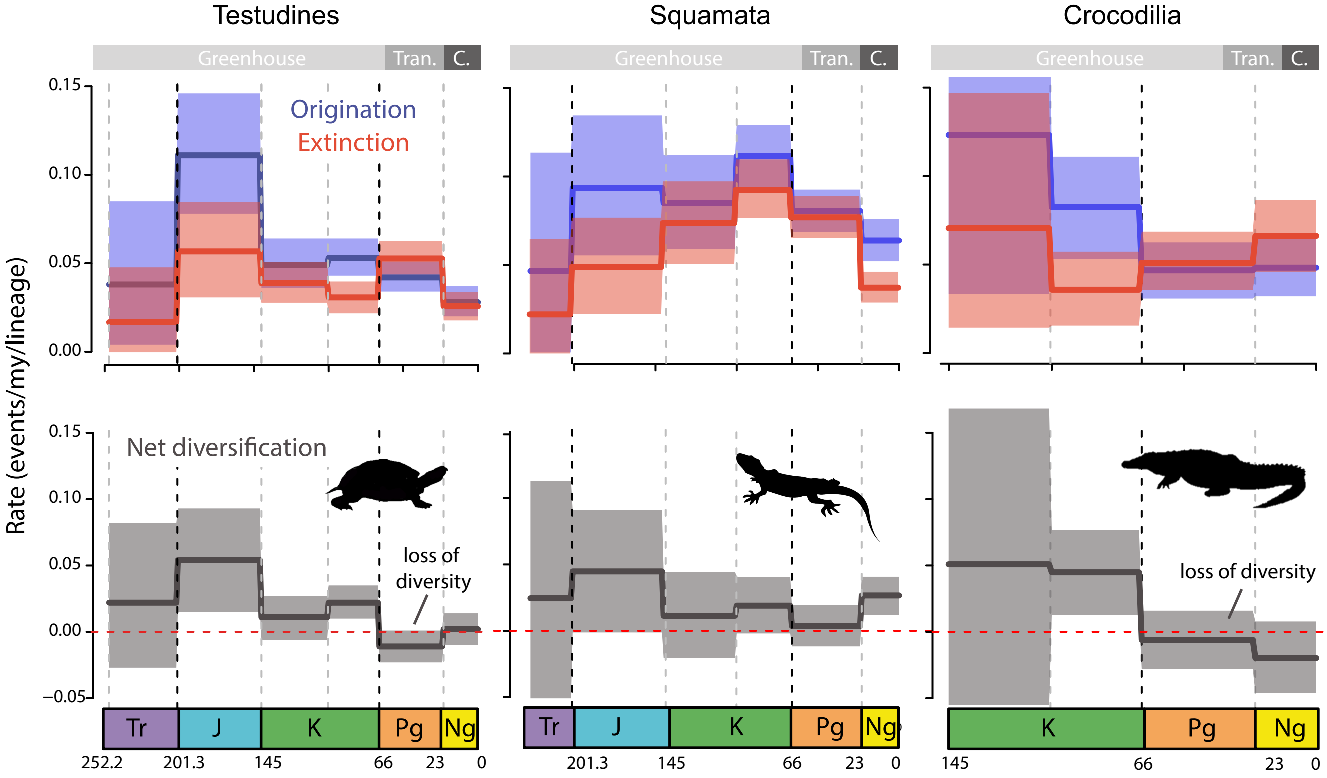

Figure 3 | Global pattern of turtles, squamates and crocodiles diversification through time based on the fossil record, and analysed with a Bayesian model. Origination (blue) and extinction (red) rates were estimated using time bins as defined by epochs of the geological timescale (on the top, main climatic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

We performed additional analyses with different subsets of the three fossil datasets, to separate the speciation and extinction signals between geographic regions (equator or Holarctic) and ecological conditions (temperate or tropical, see *Methods*). These analyses showed that the diversity losses experienced by turtles and crocodiles were mostly attributable to species living in the Holarctic and under tropical conditions (**Figs. 4**, **5, Table 2**). The global diversity loss inferred for crocodiles during the Neogene was attributed to taxa living in both the Holarctic and equatorial regions, adapted to tropical and temperate conditions, providing further support for the hypothesis that this whole group is in decline. For all groups, temperate taxa have been estimated to have high rates of diversification during the Oligocene, but lower rates during the Neogene. For the equatorial datasets, extinction and speciation rates decreased over time, resulting in constant net diversification rates (except for squamates, which displayed a decrease in diversification during the Paleogene, followed by an increase in diversification during the 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[73] 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 most basal nodes for the turtles and squamates, 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 genera in equatorial regions (Supplementary Fig. 11).

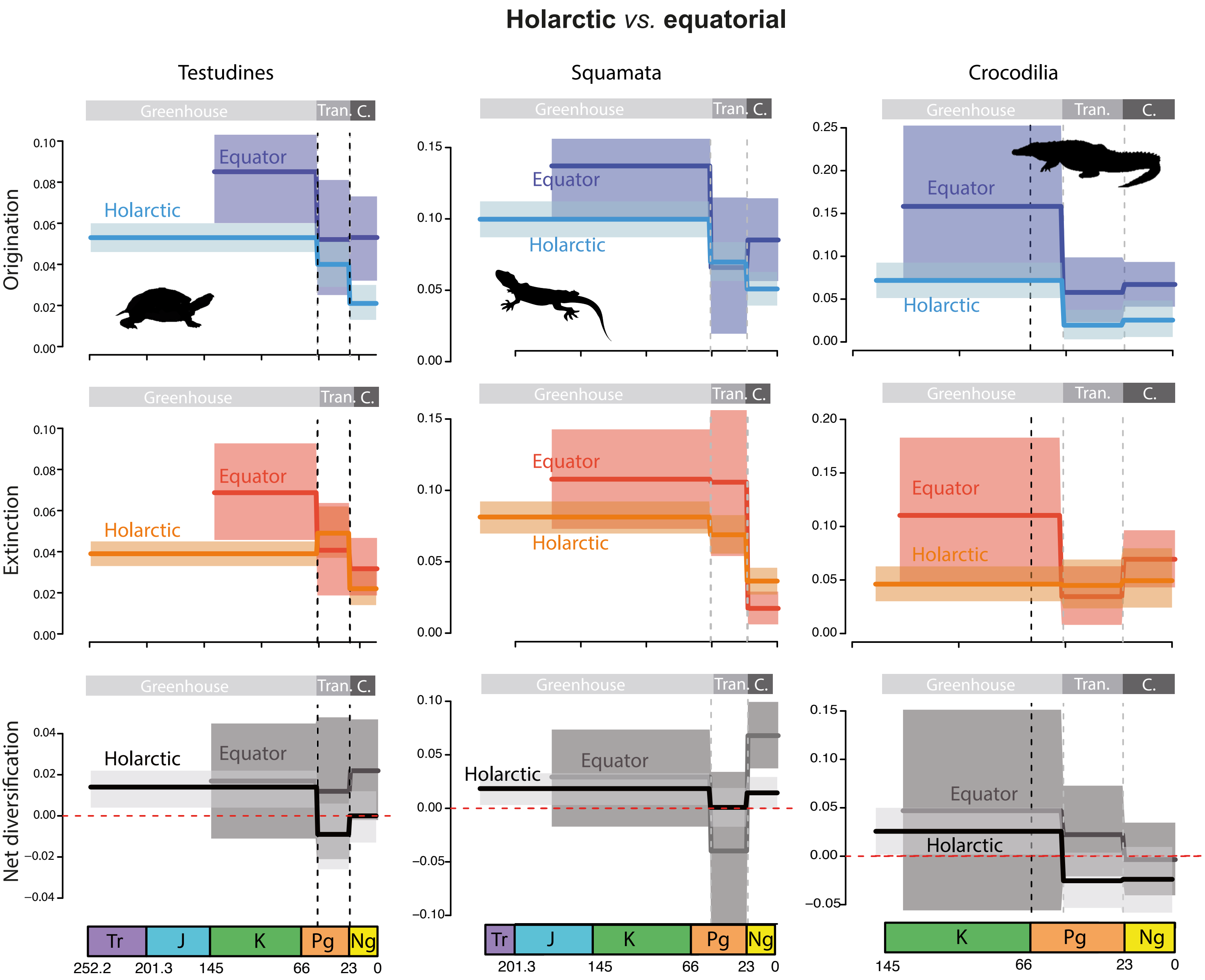

Figure 4 | Global pattern of turtle, squamate and crocodile diversification between Holarctic and equatorial regions, based on the fossil record. Diversification dynamics are compared between fossils distributed in Holarctic and equatorial regions. Origination (blue) and extinction (red) rates were estimated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

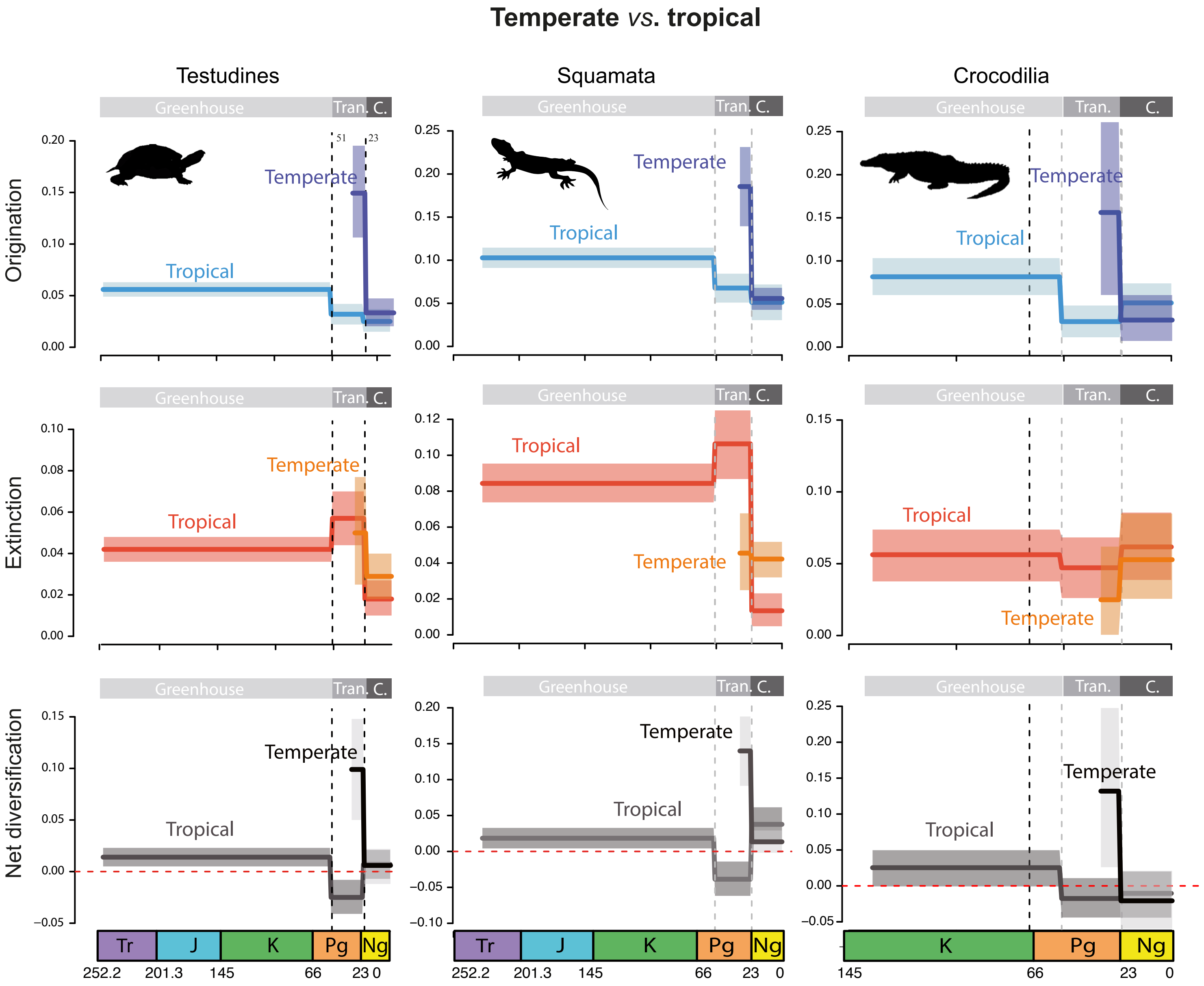

Figure 5 | Global pattern of turtle, squamate and crocodile diversification across temperate and tropical climates, based on the fossil record. Diversification dynamics are compared between fossils inhabiting under temperate and tropical macroclimates. Origination (blue) and extinction (red) rates were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

Biogeographic estimates based exclusively on extant data conflict with the fossil record[22-24,74]. 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. 6**, Supplementary Fig. 12; squamates: 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 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**).

Squamates 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 very 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 larger (109 and 66 lineages in the HFC and SFC models, respectively), whereas the number of lineages extirpated from the equator was

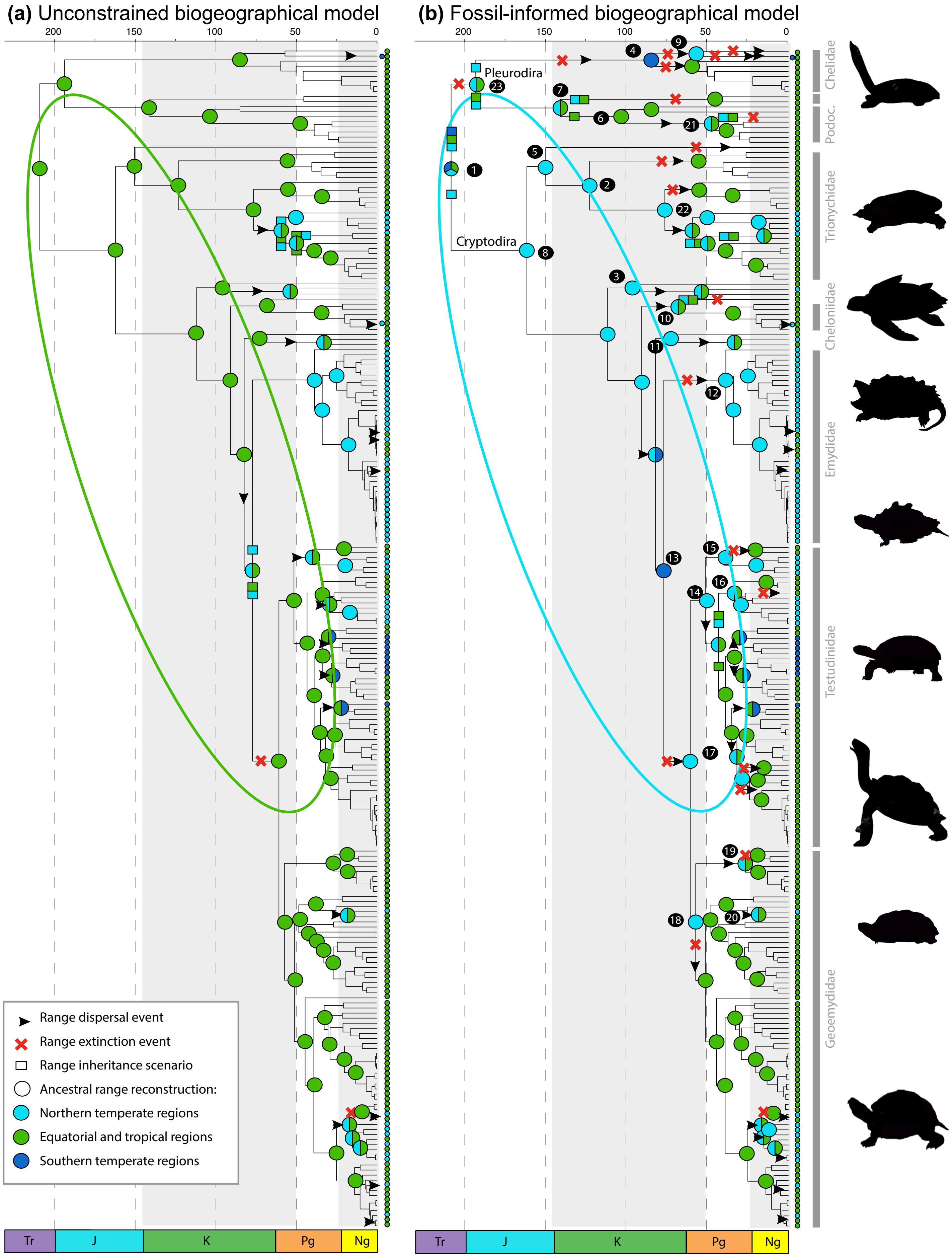

Figure 6 | Biographic reconstruction of Testudines showing the effects of the incorporation of fossil information into biogeographic inference. **a**, Biogeographic reconstruction inferred with DEC based on the distribution of extant taxa. **b**, Biogeographic reconstruction under the fossil-informed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

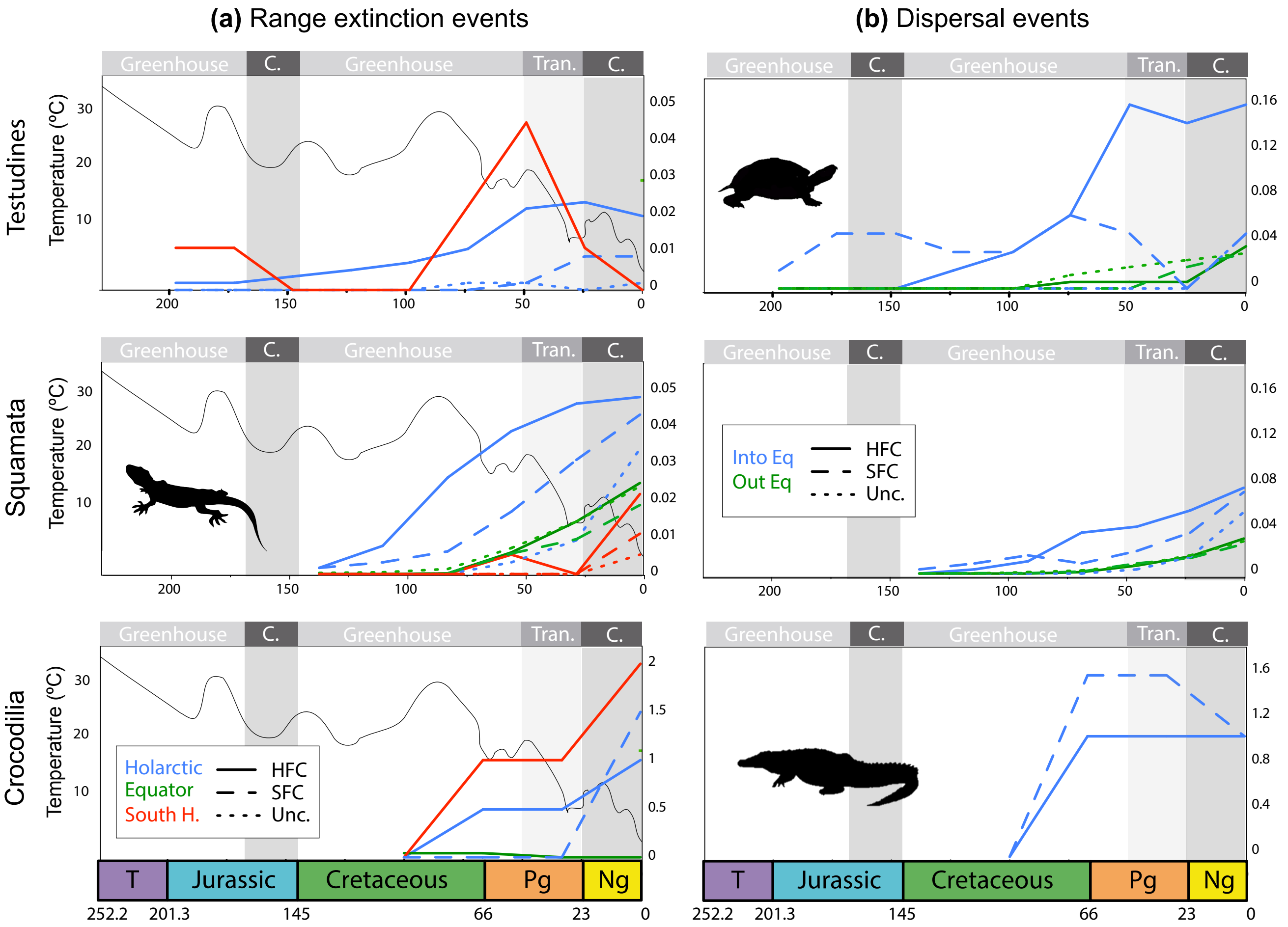

Figure 7 | Estimated number of range-extinction and dispersal events through time. Analyses were performed for Testudines, Squamata and Crocodiles under the *unconstrained model* (Unc.), based on present evidence only, and the fossil-based *hard* (HFC) and *soft fossil constraint* (SFC) biogeographic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

similar (144 and 109 in the HFC and SFC models, respectively; Supplementary Fig. 17). When the number of extinctions 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

Fossil investigations showed that diversity at high latitudes was greater in some periods of the past than currently, and sometimes even equivalent to diversity levels at the equator, for many groups[11,12]. Hypotheses relating to 'slow Holarctic species accumulation', such as limited dispersal to the Holarctic[32], high Holarctic turnover[38], or high rates of equatorial diversification[33-36,42,52,75], cannot themselves account for the formation of the LDG, its flattening, or the transition to lower diversity in the Holarctic observed in many groups[11,12]. Furthermore, although the processes shaping biodiversity vary over time and space[66], this has been largely overlooked in the context of the LDG, which has been generally explained in terms of the actions of time-constant process[36,42,52,75]. We account here for temporal changes in the global distribution of biodiversity, by proposing a scenario involving losses of tropical diversity at high latitudes, in which the AGE hypothesis captures components of previous studies[12,30,32,36,43] in the context of a time-variable LDG. A comparison of the AGE model with the LDG for turtles, crocodiles and squamates showed that this evolutionary scenario was poorly supported by analyses based purely on data for extant species, but was supported by fossil-informed investigations (**Table 1, 2**).

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

By contrast, results for fossil-only and fossil-informed phylogenetic-based biogeographic analyses were largely consistent with the AGE hypothesis (**Table 2**). The AGE hypothesis predicts that '*on average*' (*i.e.* integrated over time under a constant-rate evolutionary model), the diversification of a group is lower in the Holarctic (overall extinction being higher; the 'average AGE hypothesis' of **Fig. 2**), as generally accepted for the origin of the LDG[33,39,78]. However, the temporal context proposed made it possible to disentangle the relative contributions of speciation, extinction and dispersal for each particular period in the formation of the LDG. As predicted by the AGE hypothesis (**P1**), diversification rates for turtles, squamates and crocodiles were similar in the Holarctic and equatorial regions during the greenhouse period (overlapping credibility intervals; **Fig. 4**; Supplementary Figs. 1-3, 4-9), consistent with the flattened LDG observed during this phase[12]. We obtained mixed evidence for similar rates of dispersal between the Holarctic and equatorial regions during greenhouse periods (**P2**) for these groups: BiSSE showed similar rates of dispersal in both directions between biomes (**Table 2**, Supplementary Figs. 1-3), whereas fossil-based biogeographic analyses indicating higher rates of dispersal '*into the tropics*' (**Fig. 7**, Supplementary Table 11). These findings do not necessarily conflict with the AGE hypothesis, but reflect the idiosyncratic history of these groups, with many ancestors distributed in the Holarctic whence they colonized southern regions.

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

Paleontological evidence shows that paratropical conditions and the associated warm-adapted taxa disappeared from high latitudes between the mid-late Eocene (51-34 Ma) and the Neogene (23 Ma)[54,58,59]. Our results, with extinctions at high latitudes, range contractions and southward dispersals peaking at the end of the Paleogene, are consistent with these observations, and indicate that Cenozoic climate cooling had a profound effect on the shape of the current LDG. We cannot exclude the possibility that diversity losses occurred earlier at high latitudes (as suggested by our fossil-based diversification analyses with time intervals defined by the main geological periods; Supplementary Figs. 4, 6, 8), as the result of the K-Pg mass extinction, because of the drop in temperatures caused by the impact-associated winter[47,79,80], although crocodiles and turtles were only marginally affected by the K-Pg extinction event[81,82] and even recovered pre-extinction levels of diversity[83,84]. This scenario does not necessarily conflict with our interpretations, because our results consistently show higher rates of extinction at high latitudes than at low latitudes, regardless of the definition used for time intervals (Supplementary Figs. 4–9). Moreover, these two hypotheses are not mutually exclusive; 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 and crocodiles adapted to tropical conditions during the Late Cretaceous[47,85]. Our results indicate that extinction events were not random, instead preferentially affecting taxa living in tropical-like climates at high latitudes[51] (**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**).

Our fossil-based results for turtles and crocodiles support the AGE hypothesis, but this scenario is only partially supported by the data for squamates. During Cenozoic cooling, extinction rates for squamates were no higher at higher latitudes than at the equator (**Fig. 4**). However, diversity dynamics for the species distributed at the equator 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 the estimated rates, which have wide credibility intervals, probably due to geographic biases in the fossil record[86]. Turnover rates were very high in the Holarctic, indicating that species did disappear from high latitudes, but that they were replaced by a new squamate community. The number of squamate species may always have been unbalanced between regions. The high Holarctic turnover would contribute to the maintenance of this pattern, together with the inferred increases in diversification at the equator over time, up to the present (**Fig. 4**), as previously hypothesized[42].

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

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

Differences in diversification between temperate- and tropical-adapted taxa

One long-standing question in ecology and evolution directly related to the formation of the LDG concerns the possible differences in diversification rates between taxa living in temperature and tropical climates. According to the metabolic theory of ecology, warm tropical environments promote higher rates of speciation than colder climates, mostly due to higher rates of molecular evolution[102], and/or greater robustness to mutation[103]. This theory received early support in the literature[104], but other studies have suggested that per capita speciation rates are highest in the temperate zone[42,44,105,106]. If we are to answer this question from an evolutionary perspective, we need to consider today's equatorial belt as merely a fraction of the wider extension of the tropics in the past, and to take into account the former presence in the Holarctic of lineages with tropical-like affinities[58,59,65] (**Fig. 1**). Geographic diversification results cannot therefore be directly extrapolated to assess differences in diversification between ecological types, because, if high extinction rates are estimated for taxa in the Holarctic, extinction may have affected lineages living under either tropical or temperate conditions (depending on the time point considered). We therefore think that one major problem that has been largely overlooked is that the principal hypotheses relating to the LDG put forward have sought to answer two related but slightly different questions, which may account for some of the discrepancies between ecological and phylogenetic perspectives.

We found that the diversification rates of turtles, crocodiles and squamates living in temperate climatic conditions were significantly higher than those of tropical-adapted taxa after the transition to temperate climates in the late Eocene (**Fig. 5**, **Table 2**). The new temperate niches constituted an opportunity for diversification because they increased geographic ranges and ecological niches[35], and may have driven an inverse LDG for some groups[40,62]. Several radiations following the appearance of the temperate biome have been identified in other groups of organisms, such as plants[40,107-109], mammals[110,111] and insects[112]. After this period, speciation decreased dramatically in the temperate lineages of our focal groups, possibly due to the effect of the Pleistocene glaciations, and no difference in diversification between tropical- and temperate lineages is currently evident (**Fig. 5**,). In summary, our study suggests that differences in species richness between geographic regions may be explained by differences in diversification rates and higher rates of extinction in the Holarctic. Differences in species richness between ecological types may be explained by the longer time available for tropical-adapted clades to diversify in tropical areas, but not by a higher rate of speciation in warm tropical environments.

Conclusion

After decades of research and the proposal of countless hypotheses, the processes shaping the LDG remain among the most hotly debated topics in ecology and evolutionary biology. We propose here the AGE hypothesis, which unifies some of the ideas previously put forward concerning the LDG in a common framework and explains the origin of the current LDG through the changes in global diversification and dispersal dynamics imposed by large-scale climatic transitions. Our analyses testing the predictions of the AGE hypothesis for reptiles indicated that the processes shaping the LDG have changed over time, the current form of this gradient being the result of ancient high-latitude tropical extinctions and range contractions as a consequence of the retraction of the tropical biome due to climate cooling. We think the AGE hypothesis can account for the LDG of tropical-adapted groups that were once diverse at high latitudes, but might not be applicable to all organisms currently displaying a LDG, as shown here for squamates.

Methods

Time-calibrated phylogenies and the fossil record. We compared the predictions of the AGE hypothesis with the LDG of three vertebrate groups: turtles (order Testudines), crocodiles (order Crocodilia), and scaled reptiles (order Squamata). A time-calibrated phylogeny for each group was obtained from published data. For turtles, we used the phylogeny of Jaffe *et al.*[113], including 233 species. We preferred this phylogeny over other more recent and slightly better sampled trees[114] because the divergence time estimates of Jaffe *et al.*[113] are more consistent with recent estimates based on genomic datasets[76,115]. For squamates, we retrieved the most comprehensive dated tree available, including 4161 species[42], and a complete phylogeny was obtained for crocodiles[116].

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

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

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

We then assessed the effect of species distribution on diversification, allowing for rate changes at specific time points. This approach is associated with a lower bias than the use of constant rates, and makes it possible to assess the roles of extinction and climate change in LDG generation. We used the time-dependent BiSSE (BiSSE.td) model, in which speciation, extinction, and dispersal rates are allowed to vary between regions and to change after the shift times[101]. We introduced two shift times to model different diversification dynamics between greenhouse, transitional, and coldhouse periods. We assumed that a global warm tropical-like climate dominated the world from the origin of the clades until 51 Ma (corresponding to the temperature peak in the Cenozoic). Thereafter, the climate progressively cooled until 23 Ma (the transitional period), when the climate definitively shifted to a temperate-like biome in the Holarctic[58-60]. The shift times at 51 Ma and at 23 Ma are initial values that are re-estimated by the model during the likelihood calculation. The climatic transition in the Cenozoic may have different temporal boundaries, with potential effects on the results. We thus applied the same model but with different combinations of shift times (we tested 51/66 Ma and 34/23 Ma for the upper and lower bounds of the climatic transition).

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

Estimation of origination and extinction rates with fossils. We also used fossil data to estimate diversification rates over time. We analyzed the three fossil records, using a Bayesian model for simultaneous inference of the temporal dynamics of origination and extinction, and of preservation rates[72]. This approach, implemented in PyRate[118], uses fossil occurrences that can be assigned to a taxon, in this case fossil genera, to model the preservation and diversification processes simultaneously. The preservation process is used to infer the individual origination and extinction times of each taxon from all fossil occurrences and an estimated preservation rate; it is expressed as expected occurrences per taxon per million years.

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

Given the large number of occurrences analyzed and the vast timescale considered, we dissected the birth–death process into time intervals, and estimated origination and extinction rates within these intervals. In one set of analyses we defined the time intervals using the geological epochs of the stratigraphic timescale[120] (Supplementary Figs. 4, 6, 8). In another set of analyses, we defined the intervals according to the different climatic periods characterizing the Cenozoic (Supplementary Figs. 5, 7, 9), as discussed in the main text. We adopted this solution as an alternative to the algorithms implemented in the original PyRate software for joint estimation of the number of rate shifts and the times at which origination and extinction shift[72,118]. The estimation of origination and extinction rates within fixed time intervals improved the mixing of the MCMC and made it possible to obtain an overview of the general trends in rate variation over a long timescale[119]. Both the preservation and birth–death processes were modeled in continuous time but without being based on boundary crossings. Thus, the origination and extinction rates were measured as the expected number of origination and extinction events per lineage per million years. One potential problem when fixing the number of rate shifts *a priori* is over-parameterization. We overcame this problem by assuming that the rates of origination and extinction belonged to two families of parameters following a common prior distribution, with parameters estimated from the data with hyper-priors[121].

We ran PyRate for 10 million MCMC generations on each of the 10 randomly replicated datasets. We monitored chain mixing and effective sample sizes by examining the log files in Tracer 1.6[122]. 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 very different environments, such as the greenhouse world (Cretaceous), the climatic transition (Paleogene), and the coldhouse world (Neogene until the present).

In the context of the LDG and under a hypothesis of tropical extinction, 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[58-60] (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[123]. This assumption can also be justified by the presence of early Cenozoic vegetation assemblages in the Holarctic corresponding to tropical vegetation, as demonstrated by their paleofloristic composition[54,57]. 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 tropical conditions[85]. After the late Eocene, we categorized each species as living in the temperate biome or the tropical biome, according to the threshold latitudes defining the tropics (23.4°N and 23.4°S) suggested in a previous study.[34]. This delineation is also consistent overall with the Köppen climate classification. With these datasets, we reproduced the same PyRate analyses as for the whole dataset (see above). In general, the fossil datasets included mostly Holarctic fossils, with a smaller number of occurrences for the equator. Caution is therefore required when drawing conclusions from the equatorial datasets.

Inferring ancestral geographic distribution with phylogenies and fossils. We performed biogeographic analyses with the parametric likelihood method DEC[73,] using the fast C++ version[124]. Turtle, squamate, and crocodile species distributions were obtained from online databases (www.iucnredlist.org and www.reptile-database.org). We chose 23.4°N and 23.4°S as the threshold latitudes defining the tropics, and categorized each species as living in the Holarctic, in the southern temperate regions, or in the equatorial tropics and subtropical regions[34]. We considered that all ranges comprising three areas could be considered an ancestral state (*maxareas* =3).

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

We included the fossil distribution in two different approaches: *(i)* a soft (SFC), and *(ii)* hard fossil constraints (HFC). For the SFC approach, fossil data were incorporated into the anagenetic component of the likelihood framework. The direct impact of a given fossil is limited to the particular branch to which it has been assigned, although it may indirectly influence other branches. The inclusion of a fossil conditions the estimated geographic-transition probability matrix for that branch by imposing a spatiotemporal constraint on the simulation process. Only the simulations resulting in a geographic range including the area of fossil occurrence contribute to the geographic-range transition probability matrix for the branch concerned; simulations not meeting this constraint are discarded[125]. For SFC, we used the command '*fossil*' in DEC. We consider this to be a 'soft' constraint, because other areas different from that in which the fossil was found could be included in the ancestral states. In some cases, in which today's diversity is not very representative of past diversity (*e.g.* due to extreme levels of extinction), the SFC model may still overlook known fossil information. We therefore also implemented an HFC model in which the estimation of ancestral areas was fixed to the location of fossils. This was achieved with existing functions in the C++ version of Lagrange[124] (https://github.com/rhr/lagrange-cpp), using the command '*fixnode*'. By fixing nodes to the distribution area of fossils, we assume fossil occurrences reflect the distribution of the ancestors, *i.e.* that the fossil record is complete. This is a strong assumption, but it makes it possible to recover all fossil ranges in the ancestral estimations. The real scenario probably lies somewhere between the SFC and 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[54,126]. As the probability of any extinction/dispersal event is constant along the entire length of the branch [73,126], we can 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).

References

1. Hillebrand, H. On the generality of the latitudinal diversity gradient. *Am. Nat.* **163**, 192-211 (2004).

2. Fuhrman, J. A. *et al.* A latitudinal diversity gradient in planktonic marine bacteria. *Proc. Natl Acad. Sci. USA* **105**, 7774-7778 (2008).

3. Novotny, V. *et al.* Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**, 1115-1118 (2006).

4. Jenkins, C. N., Pimm, S. L. & Joppa, L. N. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl Acad. Sci. USA* **110**, E2602-E2610 (2013).

5. Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *Proc. Natl Acad. Sci. USA* **104**, 5925-5930 (2007).

6. Willig, M. R. *et al.* Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273-309 (2003).

7. Mittelbach, G. G. *et al.* Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10**, 315-331 (2007).

8. Crame, J. A. Taxonomic diversity gradients through geological time. *Divers. Distrib.* **7**, 175–189 (2001).

9. Alroy, J. *et al.* Phanerozoic trends in the global diversity of marine invertebrates. *Science* **321**, 97-100 (2008).

10. Mannion, P. D. *et al.* A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Glob. Ecol. Biogeogr.* **21**, 898-908 (2012).

11. Marcot, J. D., Fox, D. L. & Niebuhr, S. R. Late Cenozoic onset of the latitudinal diversity gradient of North American mammals. *Proc. Natl Acad. Sci. USA* **113**, 7189-7194 (2016).

12. Mannion, P. D. *et al.* The latitudinal biodiversity gradient through deep time. *Trends Ecol. Evol.* **29**, 42-50 (2014).

13. Rose, P. J., Fox, D. L., Marcot, J. & Badgley, C. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology* **39**, 163-166 (2011).

14. Brocklehurst, N., Day, M. O., Rubidge, B. S. & Fröbisch, J. Olson's Extinction and the latitudinal biodiversity gradient of tetrapods in the Permian. *Proc. R. Soc. Biol. Sci.* **284**, 20170231 (2017).

15. Archibald, S. B. *et al.* Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* **36**, 374-398 (2010).

16. Archibald, S. B. *et al.* Seasonality, montane beta diversity, and Eocene insects: Testing Janzen's dispersal hypothesis in an equable world. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **371**, 1-8 (2013).

17. Labandeira, C. C. & Currano, E. D. The fossil record of plant-insect dynamics. *Annu. Rev. Earth Planet. Sci.* **41**, 287-311 (2013).

18. Krug, A. Z. & Patzkowsky, M. E. Geographic variation in turnover and recovery from the Late Ordovician mass extinction. *Paleobiology* **33**, 435–454 (2007).

19. Powell, M. G. Latitudinal diversity gradients for brachiopod genera during late Palaeozoic time: links between climate, biogeography and evolutionary rates. *Glob. Ecol. Biogeogr.* **16**, 519-528 (2007).

20. Crame, J. A. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. *Paleobiology* , 26, 188–214 (2000).

21. Leprieur, F. *et al.* Plate tectonics drive tropical reef biodiversity dynamics. *Nature Commun.* **7**, 11461 (2016).

22. Mannion, P. D. *et al.* Climate constrains the evolutionary history and biodiversity of crocodylians. *Nature Commun.* **6**, 8438 (2015).

23. Nicholson, D. B., Holroyd, P. A., Benson, R. B. & Barrett, P. M. Climate-mediated diversification of turtles in the Cretaceous. *Nature Commun.* **6**, 7848 (2015).

24. Nicholson, D. B., Holroyd, P. A., Valdes, P. & Barrett, P. M. Latitudinal diversity gradients in Mesozoic non-marine turtles. *R. Soc. Open Sci.* **3**, 160581 (2016).

25. Coiffard, C. & Gomez, B. Influence of latitude and climate on spread, radiation and rise to dominance of early angiosperms during the Cretaceous in the Northern Hemisphere. *Geol. Acta* **10**, 181–188 (2012).

26. Peralta-Medina, E. & Falcon-Lang, H. J. Cretaceous forest composition and productivity inferred from a global fossil wood database. *Geology* **40**, 219–222 (2012).

27. Benson, R. B. J. & Upchurch, P. Diversity trends in the establishment of terrestrial vertebrate eco-systems: interactions between spatial and temporal sampling biases. *Geology* **41**, 43–46 (2013).

28. Jablonski, D. *et al.* Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl Acad. Sci. USA* **110**, 10487-10494 (2013).

29. Montañez, I. P. *et al.* Climate, pCO_2 and terrestrial carbon cycle linkages during late Palaeozoic glacial-interglacial cycles. *Nature Geosci.* **9**, 824-828 (2016).

30. Jablonski, D. *et al.* Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**, 102-106 (2006).

31. Donoghue, M. J. A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl Acad. Sci. USA* **105**, 11549-11555 (2008).

32. Wiens, J. J. & Donoghue, M. J. Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* **19**, 639-644 (2004).

33. Ricklefs, R. E. Global variation in the diversification rate of passerine birds. *Ecology* **87**, 2468-2478 (2006).

34. Rolland, J., Condamine, F. L., Jiguet, F. & Morlon, H. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.* **12**, e1001775 (2014).

35. Wiens, J. J. Global patterns of diversification and species richness in amphibians. *Am. Nat.* **70**, S86-S106 (2007).

36. Pyron, R. A. & Wiens, J. J. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proc. R. Soc. Biol. Sci.* **280**, 20131622 (2013).

37. Cardillo, M., Orme, C. D. L. & Owens, I. P. F. Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* **86**, 2278–2287 (2005).

38. Weir, J. T. & Schluter, D. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574-1576 (2007).

39. Condamine, F. L., Sperling F. A. H., Whalberg, N., Rasplus, J.-Y. & Kergoat, G. J. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecol. Lett.* **15**, 267-277 (2012).

40. Leslie, A. B. *et al.* Hemisphere-scale differences in conifer evolutionary dynamics. *Proc. Natl Acad. Sci. USA* **109**, 16217-16221 (2012).

41. Siqueira, A. C., Oliveira-Santos, L. G. R., Cowman, P. F. & Floeter, S. R. Evolutionary processes underlying latitudinal differences in reef fish biodiversity. *Global Ecol. Biogeogr.* **25**, 1466-1476 (2016).

42. Pyron, R. A. Temperate extinction in squamate reptiles and the roots of latitudinal diversity gradients. *Glob. Ecol. Biogeogr.* **23**, 1126-1134 (2014).

43. Rolland, J., Condamine, F. L., Beeravolu, C. R., Jiguet, F. & Morlon, H. Dispersal is a major driver of the latitudinal diversity gradient of Carnivora. *Glob. Ecol. Biogeogr.* **24**, 1059-1071 (2015).

44. Martin, P. S. & Klein, R. G. (Eds.) Quaternary extinctions: a prehistoric revolution. University of Arizona Press (1989).

45. Latham, R. E. & Ricklefs, R. E. Continental comparisons of temperate-zone tree species diversity. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R. E. & Schluter, D.) 294-314 (University of Chicago Press, 1993).

46. Wing, S. L. Global warming and plant species richness: a case study of the Paleocene/Eocene boundary. In *Biodiversity II: Understanding and Protecting our Biological Resources* (eds Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O.) 163-185 (Joseph Henry Press, Washington, D.C., 1997).

47. Markwick, P. J. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data for global change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **137**, 205-271 (1998).

48. Roy, K. & Pandolfi, J. M. Responses of marine species and ecosystems to past climate change. In: *Climate Change and Biodiversity* (1 edn.) (eds Lovejoy, T.E & Hannah, E.L.). 160-175 (Yale University Press, 2005).

49. Hawkins, B. A. *et al.* Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J. Biogeogr.* **33**, 770-780 (2006).

50. Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerdá, X. et al. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol. Lett.*, **12**, 324-333 (2009).

51. Eiserhardt, W. L., Borchsenius, F., Plum, C. M., Ordonez, A. & Svenning, J.-C. Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecol. Lett.* **18**, 263–272 (2015).

52. Pulido-Santacruz, P. & Weir, J. T. Extinction as a driver of avian latitudinal diversity gradients. *Evolution*, **70**, 860-872 (2016).

53. Rabosky, D. L. Extinction rates should not be estimated from molecular phylogenies. *Evolution* **64**, 1816-1824 (2010).

54. Sanmartín, I. & Meseguer, A. S. Extinction in phylogenetics and biogeography: From lineages to the assembly of regional biotas. *Front. Genet.*, **7**, 35 (2016).

54. Greenwood, D. R. & Wing, S. L. Eocene continental climates and latitudinal temperature gradients. *Geology* **23**, 1044-1048 (1995).

55. Johnson, K. R. & Ellis, B. A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary. *Science* **296**, 2379-2383 (2002).

56. Sluijs, A. *et al.* Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature* **441**, 610-613 (2006).

57. Suan, G. *et al.* Subtropical climate conditions and mangrove growth in Arctic Siberia during the early Eocene. *Geology* **45**, 539-542 (2017).

58. Ziegler, A. *et al.* Tracing the tropics across land and sea: Permian to present. *Lethaia* **36**, 227-254 (2003).

59. Morley, R. J. Cretaceous and Tertiary climate change and the past distribution of megathermal rainforests. In: *Tropical Rainforest Responses to Climatic Changes* (eds Bush, M. B. & Flenley, J.). 1-31 (Praxis Publishing, Chichester, 2007).

60. Zachos, J. C., Dickens, G. R. & Zeebe, R. E. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279-283 (2008).

61. Meseguer, A. S., Lobo, J. M., Cornuault, J., Beerling, D., Ruhfel, B. R., Davis, C. C. et al. Reconstructing deep-time palaeoclimate legacies in the clusioid Malpighiales unveils their role in the evolution and extinction of the boreotropical flora. *Global Ecol. Biogeogr.* doi.org/10.1111/geb.12724 (2018).

62. Kindlmann, P., Schödelbauerová, I. & Dixon, A. F. Inverse latitudinal gradients in species diversity. In: *Scaling Biodiversity* (eds Storch, D., Marquet, P. A. & Brown, J. H.). 246–257 (Cambridge University Press, Cambridge, 2007).

63. Couvreur, T. L., Forest, F. & Baker, W. J. Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biol.* **9**, 44 (2011).

64. Christenhusz, M. J. & Chase, M. W. Biogeographical patterns of plants in the Neotropics – dispersal rather than plate tectonics is most explanatory. *Bot. J. Linn. Soc.* **171**, 277-286 (2013).

65. Fine, P. V. A. & Ree, R. H. Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *Am. Nat.* **186**, 796–804 (2006).

66. Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge University Press, 1995).

67. Angielczyk, K. D., Burroughs, R. W. & Feldman, C. R. Do turtles follow the rules? Latitudinal gradients in species richness, body size, and geographic range area of the world's turtles. *J. Experimental Zool. B* **324**, 270-294 (2015).

68. Maddison, W. P., Midford, P. E. & Otto, S. P. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* **56**, 701-710 (2007).

69. FitzJohn, R. G. Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.* **3**, 1084-1092 (2012).

70. Goldberg, E. E., Lancaster, L. T. & Ree, R. H. Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* **60**, 451-465 (2011).

71. Davis, M. P., Midford, P. E. & Maddison, W. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evol. Biol.* **13**, 38 (2013).

72. Silvestro, D., Schnitzler, J., Liow, L. H., Antonelli, A. & Salamin, N. Bayesian estimation of speciation and extinction from incomplete fossil occurrence data. *Syst. Biol.* **63**, 349–367 (2014).

73. Ree, R. H. & Smith, S. A. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**, 4-14 (2008).

74. Joyce, W. G., Rabi, M., Clark, J. M. & Xu, X. A toothed turtle from the Late Jurassic of China and the global biogeographic history of turtles. *BMC Evol. Biol.* **16**, 236 (2016).

75. Jansson, R., Rodríguez-Castañeda, G. & Harding, L. E. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of tropics, and diversification rate hypotheses. *Evolution* **67**, 1741-1755 (2013).

76. Pereira, A. G., Sterli, J., Moreira, F. R. & Schrago, C. G. Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Mol. Phylogenet. Evol.* **113**, 59-66 (2017).

77. Rodrigues, J. F. M., Olalla-Tárraga, M. Á., Iverson, J. B., Akre, T. S. & Diniz-Filho, J. A. F. Time and environment explain the current richness distribution of non-marine turtles worldwide. *Ecography* **40**, 1402–1411 (2017).

78. Jansson, R. & Davies, T. J. Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecol. Lett.* **11**, 173-183 (2008).

79. Vellekoop, J. *et al.* Rapid short-term cooling following the Chicxulub impact at the Cretaceous–Paleogene boundary. *Proc. Natl Acad. Sci. USA* **111**, 7537-7541 (2014).

80. Kaiho, K. *et al.* Global climate change driven by soot at the K-Pg boundary as the cause of the mass extinction. *Sci. Rep.* **6**, 28427 (2016).

81. Lyson, T. R. Joyce, W. G. Knauss, G. E. & Pearson, D. A. *Boremys* (Testudines, Baenidae) from the latest Cretaceous and early Paleocene of North Dakota: an 11-

million-year range extension and an additional K/T survivor. *J. Vertebrate Paleontol.* **31**, 729-737 (2011).

82. Holroyd, P. A., Wilson, G. P. & Hutchison, J. H. Temporal changes within the latest Cretaceous and early Paleogene turtle faunas of northeastern Montana. *Geol. Soc. Am. Spec. Pap.* **503**, 299–312 (2014).

83. Longrich, N. R., Bhullar, B. A. S. & Gauthier, J. A. Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. *Proc. Natl Acad. Sci. USA* **109**, 21396-21401 (2012).

84. D'Hondt, S., Donaghay, P., Zachos, J. C., Luttenberg, D. & Lindinger, M. Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction. *Science* **282**, 276-279 (1998).

85. Waterson, A. M. *et al.* Modelling the climatic niche of turtles: a deep-time perspective. *Proc. R. Soc. B Biol. Sci.* **283**, 20161408 (2016).

86. Albino, A. M. & Brizuela, S. An overview of the South American fossil squamates. *Anat. Rec.* **297**, 349-368 (2014).

87. Antonelli, A. & Sanmartín, I. Mass extinction, gradual cooling, or rapid radiation? Reconstructing the spatiotemporal evolution of the ancient angiosperm genus *Hedyosmum* (Chloranthaceae) using empirical and simulated approaches. *Syst. Biol.* **60**, 596-615 (2011).

88. Sun, Y. *et al.* Lethally hot temperatures during the Early Triassic greenhouse. *Science* **338**, 366-370 (2012).

89. Crisp, M. D. & Cook, L. G. How was the Australian flora assembled over the last 65 million years? A molecular phylogenetic perspective. *Annu. Rev. Ecol. Evol. Syst.* **44**, 303-324 (2013).

90. Mayr, G. The early Eocene birds of the Messel fossil site: a 48 million-year-old bird community adds a temporal perspective to the evolution of tropical avifaunas. *Biol. Rev.* **92**, 1174-1188 (2017).

91. Wilf, P., Labandeira, C. C., Johnson, K. R. & Cúneo, N. R. Richness of plant–insect associations in Eocene Patagonia: a legacy for South American biodiversity. *Proc. Natl Acad. Sci. USA* **102**, 8944-8948 (2005).

92. Blois, J. L. & Hadly, E. A. Mammalian response to Cenozoic climatic change. *Annu. Rev. Earth Planet. Sci.* **37**, 181–208 (2009).

93. Smith, R. Y., Basinger, J. F. & Greenwood, D. R. Early Eocene plant diversity and dynamics in the Falkland flora, Okanagan Highlands, British Columbia, Canada. *Palaeobio. Palaeoenv.* **92**, 309-328 (2012).

94. Xing, Y., Onstein, R. E., Carter, R. J., Stadler, T. & Linder, H. P. Fossils and a large molecular phylogeny show that the evolution of species richness, generic diversity, and turnover rates are disconnected. *Evolution* **68**, 2821-2832 (2014).

95. Morlon, H., Parsons, T. L. & Plotkin, J. B. Reconciling molecular phylogenies with the fossil record. *Proc. Natl Acad. Sci. USA* **108**, 16327-16332 (2011).

96. May, M. R., Höhna, S. & Moore, B. R. A Bayesian approach for detecting the impact of mass-extinction events on molecular phylogenies when rates of lineage diversification may vary. *Methods Ecol. Evol.* **7**, 947-959 (2016).

97. Betancur-R, R., Ortí, G. & Pyron, R. A. Fossil-based comparative analyses reveal ancient marine ancestry erased by extinction in ray-finned fishes. *Ecol. Lett.* **18**, 441-450 (2015).

98. Meseguer, A. S., Lobo, J. M., Ree, R., Beerling, D. J. & Sanmartín, I. Integrating fossils, phylogenies, and niche models into biogeography to reveal ancient evolutionary history: the case of *Hypericum* (Hypericaceae). *Syst. Biol.* **64**, 215-232 (2015).

99. Fritz, S. A. *et al.* Diversity in time and space: wanted dead and alive. *Trends Ecol. Evol.* **28**, 509-516 (2013).

100. Ng, J. & Smith, S. D. How traits shape trees: new approaches for detecting character state-dependent lineage diversification. *J. Evol. Biol.* **27**, 2035-2045 (2014).

101. Spriggs, E. L. *et al.* Temperate radiations and dying embers of a tropical past: the diversification of *Viburnum*. *New Phytol.* **207**, 340-354 (2015).

102. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Towards a metabolic theory of ecology. *Ecology* **85**, 1771-1789 (2004).

103. Puurtinen, M. *et al.* Temperature-dependent mutational robustness can explain faster molecular evolution at warm temperatures, affecting speciation rate and global patterns of species diversity. *Ecography* **39**, 1025-1033 (2016).

104. Allen, A. P., Gillooly, J. F., Savage, V. M. & Brown, J. H. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl Acad. Sci. USA* **103**, 9130–9135 (2006).

105. Bromham, L. & Cardillo, M. Testing the link between the latitudinal gradient in species richness and rates of molecular evolution. *J. Evol. Biol.* **16**, 200-207 (2003).

106. Schluter, D. Speciation, ecological opportunity, and latitude. *Am. Nat.* **187**, 1-18 (2016).

107. Spriggs, E. L., Christin, P. A. & Edwards, E. J. C_4 photosynthesis promoted species diversification during the Miocene grassland expansion. *PLoS One* **9**, e97722 (2014).

108. Spalink, D. *et al.* Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants. *J. Biogeogr.* **43**, 1893-1904 (2016).

109. Favre, A. *et al.* Out-of-Tibet: the spatio-temporal evolution of *Gentiana* (Gentianaceae). *J. Biogeogr.* **43**, 1967-1978 (2016).

110. Ge, D. *et al.* Evolutionary history of lagomorphs in response to global environmental change. *PLoS One* **8**, e59668 (2013).

111. Pisano, J. *et al.* Out of Himalaya: the impact of past Asian environmental changes on the evolutionary and biogeographical history of Dipodoidea (Rodentia). *J. Biogeogr.* **42**, 856-870 (2015).

112. Condamine, F. L., Rolland, J., Höhna, S., Sperling, F. A. H. & Sanmartín, I. Testing the role of the Red Queen and Court Jester as drivers of the macroevolution of Apollo butterflies. *Syst. Biol.* doi.org/10.1093/sysbio/syy009 (2018).113. Jaffe, A. L., Slater, G. J. & Alfaro, M. E. The evolution of island gigantism and body size variation in tortoises and turtles. *Biol. Lett.* **7**, 558–561 (2011).

114. Rodrigues, J. F. M. & Diniz-Filho, J. A. F. Ecological opportunities, habitat, and past climatic fluctuations influenced the diversification of modern turtles. *Mol. Phylogenet. Evol.* **101**, 352-358 (2016).

115. Shaffer, H. B., McCartney-Melstad, E., Near, T. J., Mount, G. G. & Spinks, P. Q. Phylogenomic analyses of 539 highly informative loci dates a fully resolved time tree for the major clades of living turtles (Testudines). *Mol. Phylogenet. Evol.* **115**, 7-15 (2017).

116. Oaks, J. R. A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution* **65**, 3285-3297 (2011).

117. FitzJohn, R. G., Maddison, W. P. & Otto, S. P. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst. Biol.* **58**, 595-611 (2009).

118. Silvestro, D., Salamin, N. & Schnitzler, J. PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. *Methods Ecol. Evol.* **5**, 1126-1131 (2014).

119. Silvestro, D., Cascales-Miñana, B., Bacon, C. D. & Antonelli, A. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol.* **207**, 425-436 (2015).

120. Gradstein, F. M., Ogg, J. G., Schmitz, M. & Ogg, G. (Eds.). *The Geologic Time Scale 2012*. Elsevier (2012).

121. Gelman, A. Parameterization and Bayesian modeling. *J. Am. Stat. Assoc.* **99**, 537-545 (2004).

122. Rambaut, A., Suchard, M. A., Xie, D. & Drummond, A. J. Tracer v1.6. Available at: http://tree.bio.ed.ac.uk/software/tracer/ (2017).

123. Romdal, T. S., Araújo, M. B. & Rahbek, C. Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecol. Biogeogr.* **22**, 344-350 (2013).

124. Smith, S. A. Taking into account phylogenetic and divergence-time uncertainty in a parametric biogeographical analysis of the Northern Hemisphere plant clade Caprifolieae. *J. Biogeogr.* **36**, 2324-2337 (2009).

125. Moore, B. R., Smith, S. A., Ree, R. H. & Donoghue, M. J. Incorporating fossil data in biogeographic inference: A likelihood approach. *Proc. 52nd Annu. Syst. Symposium* Available at: http://www.phylo.org/pdf_docs/2006_MoBot_biogeo.pdf (2006).

126. Ree, R. H. & Sanmartín, I. Prospects and challenges for parametric models in historical biogeographical inference. *J. Biogeogr.* **36**, 1211-1220 (2009).

Acknowledgements

The authors are very grateful to Arne Mooers, Joaquin Hortal, Juan Arroyo, and anonymous reviewers for comments and suggestions that greatly improved the study. Previous versions of the manuscript benefited from the comments of Gary Mittlebach, Emmanuelle Jousselin and Jonathan Rolland. Financial support was provided by a Marie-Curie FP7–COFUND (AgreenSkills fellowship–26719) grant to A.S.M. and a Marie Curie FP7-IOF (project 627684 BIOMME) grant to F.L.C. This work benefited from an "Investissements d'Avenir" grant managed by the "Agence Nationale de la Recherche" (CEBA, ref. ANR-10-LABX-25-01).

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.