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Ancient tropical extinctions at high latitudes contributed to the latitudinal diversity gradient*

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3 **(ii) Running title:** Asymmetric gradient of tropical extinction

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24
25
26 The datasets supporting the results, the commands used in the analyses and the
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28 **Abstract**

29 Global biodiversity currently peaks at the equator and decreases toward the poles.
30 Growing fossil evidence suggest this hump-shaped latitudinal diversity gradient (LDG)
31 has not been persistent through time, with similar diversity across latitudes flattening
32 out the LDG during past greenhouse periods. However, when and how diversity declined
33 at high latitudes to generate the modern LDG remains an open question. Although
34 diversity-loss scenarios have been proposed, they remain mostly undemonstrated. We
35 outline the ‘asymmetric gradient of extinction and dispersal’ framework that
36 contextualizes previous ideas behind the LDG under a time-variable scenario. Using
37 phylogenies and fossils of Testudines, Crocodylia and Lepidosauria, we find that the
38 hump-shaped LDG could be explained by (1) disproportionate extinctions of high-
39 latitude tropical-adapted clades when climate transitioned from greenhouse to
40 icehouse, and (2) equator-ward biotic dispersals tracking their climatic preferences
41 when tropical biomes became restricted to the equator. Conversely, equivalent
42 diversification rates across latitudes can account for the formation of an ancient flat
43 LDG. The inclusion of fossils in macroevolutionary studies allows revealing time-
44 dependent extinction rates hardly detectable from phylogenies only. This study
45 underscores that the prevailing evolutionary processes generating the LDG during
46 greenhouses differed from those operating during icehouses.

47

48 **Keywords:** biodiversity; climate change; extinction; fossils; Holarctic; tropics

49

50 **Introduction**

51 The current increase in species richness from the poles toward the equator, known as
52 the latitudinal diversity gradient (LDG), is one of the most conspicuous patterns in
53 ecology and evolution. This pattern has been described for microbes, insects,
54 vertebrates, and plants, and for marine, freshwater, and terrestrial ecosystems (Willig et
55 al. 2003; Hillebrand 2004; Novotny et al. 2006; Kreft and Jetz 2007; Fuhrman et al.
56 2008; Jenkins et al. 2013).

57 For decades, it has been thought that the modern steep LDG, with higher
58 diversity concentrated at the equator, persisted throughout the Phanerozoic (the last
59 540 million years), even if the gradient was sometimes shallower (Mittelbach et al.
60 2007), based on published fossil record studies (Crame 2001; Alroy et al. 2008).
61 However, the methodological limitations of fossil sampling have called this conclusion
62 into question. Analyses controlling for sampling bias have suggested that, for many
63 groups, the LDG was less marked in the past than it is today (*i.e.* with similar species
64 diversity across latitudes) or even developed a paleotemperate peak during some
65 periods (see Mannion et al. (2014) for a review). This sampling-corrected flattened LDG
66 in deep time has been demonstrated for non-avian dinosaurs (Mannion et al. 2012),
67 mammals (Rose et al. 2011; Marcot et al. 2016), birds (Saupe et al. 2019a), tetrapods
68 (Brocklehurst et al. 2017), insects (Archibald et al. 2010, 2013; Labandeira and Currano
69 2013), brachiopods (Krug and Patzkowsky 2007; Powell 2007; Powell et al. 2012),
70 bivalves (Crame 2000, 2020), coral reefs (Leprieur et al. 2016), foraminifers (Fenton et
71 al. 2016), crocodiles (Mannion et al. 2015), turtles (Nicholson et al. 2015, 2016), or
72 plants (Coiffard and Gomez 2012; Peralta-Medina and Falcon-Lang 2012; Shiono et al.
73 2018).

74 The pattern emerging from fossil studies also suggests that steep LDGs, such as
75 that currently observed, have been restricted to the relatively small number of short

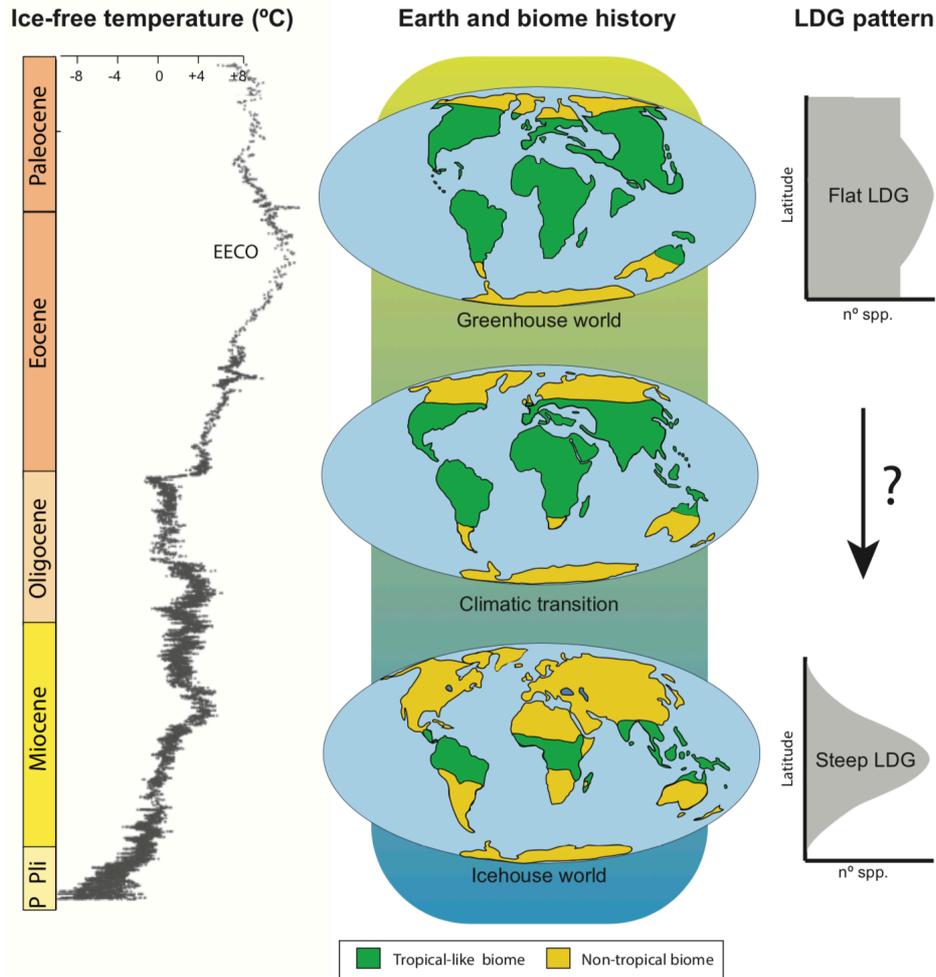
76 icehouse periods during the Earth's history: the Ordovician/Silurian, the
77 Carboniferous/Permian, and the Neogene. Most of the Phanerozoic has instead been
78 characterized by warm greenhouse climates associated with a flatter LDG (Mannion et
79 al. 2014; Marcot et al. 2016). Hence, the last change in the shape of the LDG
80 hypothetically occurred during the greenhouse to icehouse transition of the Cenozoic, in
81 the last 66 million years (**Fig. 1**).

82

83 **Figure 1.** Changes in global temperatures and extension of the tropical belt during the Cenozoic, in relation
84 with the shape of the LDG. Early Cenozoic global temperatures were higher than today and paratropical
85 conditions extended over high latitudes. From the early Eocene climatic optimum (EECO; ca. 53-51 Ma), a
86 global cooling trend intensified and culminated with the Pleistocene glaciations. Warm-equable regimes got
87 then restricted to the equator. The LDG evolved following these global changes; during greenhouse periods
88 diversity was similar across latitudes, such that the LDG flattened, while in cold periods diversity peaked at
89 the equator (a steep LDG) (Mannion et al. 2014). The question mark denotes the focus of this study, which is
90 to unveil the processes that mediated the transition between a flat and steep LDG. The relative temperature
91 curve of the Cenozoic is adapted from (Zachos et al. 2008). Maps represent the extension of the tropical belt
92 and Earth tectonic changes as derived from (Ziegler et al. 2003; Morley 2007). P=Pleistocene, Pli=Pliocene.

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Our perception on how diversity was latitudinally distributed in the past underlies LDG interpretations. Up to now, most studies have assumed the equator is the source of world diversity (Donoghue 2008; Jablonski et al. 2013) and diversity was always lower in the Holarctic (*i.e.* a steep LDG persisted in the deep time). The current shape of the LDG thus results from lower paces of diversity accumulation in the Holarctic than at the equator through time. Slower diversity accumulation in the Holarctic (hereafter ‘H’) have been explained either by greater tropical diversification and limited dispersal out of the equatorial region (hereafter ‘equator’ or ‘E’) ($r_e > r_h$; $d_{eh} > d_{he}$) (Latham and Ricklefs 1993; Wiens and Donoghue 2004; Mittelbach et al. 2007; Rolland et al. 2014), or by high rates of turnover in the Holarctic, *i.e.* similar high speciation (λ) and extinction (μ) rates ($\lambda_h \approx \mu_h$; **Table 1**). This has been widely shown throughout the tree of life: amphibians (Wiens 2007; Pyron and Wiens 2013), birds

108 (Cardillo et al. 2005; Ricklefs 2006; Weir and Schluter 2007), butterflies (Condamine et
109 al. 2012), plants (Leslie et al. 2012; Kerkhoff et al. 2014), fishes (Siqueira et al. 2016),
110 mammals (Weir and Schluter 2007; Rolland et al. 2014), or lepidosaurs (Pyron 2014).

111 Contrary to the 'slow Holarctic diversity accumulation' hypotheses, a scenario
112 assuming the Holarctic was also a source of tropical diversity that flattened the LDG in
113 the deep past could be considered. The current steep shape of the LDG would thus result
114 from diversity lost in the Holarctic through evolutionary time, referred to as the
115 'Holarctic diversity loss' hypothesis. The recent fossil investigations showing, for many
116 lineages, similar diversity levels across latitudes in the past lend support to this
117 scenario, suggesting we do not necessarily need to explain why diversity accumulated at
118 slower rates in the Holarctic through time, but the question being how and when
119 diversity was lost at high latitudes, giving rise to the current shape of the LDG (Mannion
120 et al. 2014)?

121 Diversity losses in the Holarctic have been traditionally considered to underlie
122 the LDG. They were initially attributed to Pleistocene glaciations (Martin and Klein
123 1989), but this hypothesis can be called into question since the LDG substantially
124 predates the Pleistocene (Mittelbach et al. 2007). More ancient extinctions have also
125 been considered (Latham and Ricklefs 1993; Markwick 1998; Roy and Pandolfi 2005;
126 Hawkins et al. 2006; Weir and Schluter 2007; Dunn et al. 2009; Eiserhardt et al. 2015;
127 Pulido-Santacruz and Weir 2016). For example, recent studies suggested the avian LDG
128 resulted from the differential extirpation of older warm-adapted clades from the
129 temperate regions newly formed in the Neogene (Hawkins et al. 2006; Pulido-Santacruz
130 and Weir 2016; Saupe et al. 2019a). Pyron (2014) suggested that higher temperate
131 extinction represents a dominant force for the origin of LDG in lepidosaurs. Wiens &
132 Donoghue (2004) also proposed that range contractions ($d_{eh} < d_{he}$) followed climate
133 cooling.

134 Unfortunately, using phylogenies of extant taxa alone, studies on the LDG have
135 not clearly demonstrated diversity losses in the Holarctic but instead high regional
136 turnover ($\lambda \approx \mu$) (Cardillo et al. 2005; Weir and Schluter 2007; Condamine et al. 2012;
137 Leslie et al. 2012; Pyron and Wiens 2013; Rolland et al. 2014, 2015; Rabosky et al.
138 2018). Nonetheless, high turnover in the Holarctic can only explain a slow accumulation
139 of lineages, with one fauna being replaced by another, but does not explain diversity
140 decline (*i.e.* a reduction in the net number of species) as elevated speciation rates
141 counter-balance the effect of extinction. Diversity declines occur when extinction
142 exceeds speciation ($\mu > \lambda$), resulting in negative net diversification rates ($r = \lambda - \mu$; $r < 0$).
143 Accordingly, ‘diversity loss’ hypotheses differ from ‘high turnover’ scenarios.

144 The perceived difficulty for inferring negative diversification rates from
145 phylogenetic data of extant species (Rabosky 2010; Burin et al. 2018) and the
146 assumption that diversity levels always remained lower in the Holarctic than at the
147 equator have resulted in ‘diversity loss’ hypotheses being repeatedly proposed but
148 seldom demonstrated using phylogenetic data (Pulido-Santacruz and Weir 2016).
149 Meanwhile, numerous fossil investigations have detected signatures of extinction and
150 diversity loss in the Northern Hemisphere. For instance, Archibald *et al.* (2010, 2013)
151 sampled insect diversity at an Eocene site in Canada, and in present-day temperate
152 Massachusetts (USA) and tropical sites of Costa Rica. Insect diversity was higher at the
153 Eocene paleotropical site than the modern temperate locality, and comparable to the
154 modern-day tropical locality, suggesting that post-Eocene Nearctic insects have suffered
155 great levels of extinction. This pattern is consistent with other studies on various
156 taxonomic groups, including birds (Mayr 2016), invertebrates (Wilf et al. 2005),
157 mammals (Blois and Hadly 2009; Rose et al. 2011; Marcot et al. 2016), and plants
158 (Frederiksen 1988; Smith and al. 2012; Xing et al. 2014). Fossil studies are, however,
159 generally restricted to a reduced geographic and temporal scale, which makes difficult
160 to extrapolate local inferences of extinction in the global context of the LDG.

161 Here, we use comparative methods for both phylogenies and fossils to estimate
162 the evolutionary processes behind the LDG of Testudines, Crocodylia and Lepidosauria,
163 and test the alternative predictions of two hypotheses: “slow diversity accumulation”
164 ($d_{eh} > d_{he}; \mu_h \leq \lambda_h$) vs. “diversity loss” ($d_{eh} < d_{he}; \mu_h > \lambda_h$) in the Holarctic. To this end, we
165 propose to include a temporal component to study the LDG in which prevailing
166 speciation, extinction and dispersal dynamics may change between warm- and cold-time
167 intervals. The extant Crocodylia and Lepidosauria comprise mostly tropical-adapted
168 species with a classic LDG pattern as shown by diversity peaks at equatorial latitudes
169 (Markwick 1998; Pyron 2014). We investigate the origin of the LDG in subtropical taxa
170 as well, by extending the study to Testudines, which display a hump-shaped gradient of
171 diversity centered on subtropical latitudes (10°S–30°N) (Angielczyk et al. 2015). By
172 contrast, the paleolatitudinal distribution of turtles was concentrated in the Holarctic
173 (30–60°N) during the Cretaceous (Nicholson et al. 2015, 2016). All these lineages are
174 ancient and likely experienced climatic transitions during the early Cenozoic (Markwick
175 1998; Pyron 2014; Angielczyk et al. 2015; Mannion et al. 2015; Nicholson et al. 2015).
176 They show contrasting patterns of species richness: turtles and crocodiles are species-
177 poor (350 and 25 species, respectively), while lepidosaurs include a large number of
178 species (10,000+ species), and all have a rich fossil record extending back to the Triassic
179 (Early Cretaceous for crocodiles), providing information about the variation of
180 latitudinal species richness accumulation during their evolutionary history.

181 **Methods**

182 ***Molecular phylogenies and the fossil record.*** A time-calibrated phylogeny for turtles
183 (order Testudines) was obtained from Jaffe *et al.* (2011), including 233 species. We
184 preferred this phylogeny over other more recent and slightly better sampled trees
185 (Rodrigues and Diniz-Filho 2016) because the divergence time estimates are more

186 consistent with recent estimates based on genomic datasets (Pereira et al. 2017; Shaffer
187 et al. 2017). For scaled lizards (Lepidosauria), we retrieved the most comprehensive
188 dated tree available, including 4161 species (Pyron 2014), and a complete phylogeny
189 was obtained for crocodiles (Crocodylia) (Oaks 2011).

190 Fossil occurrences were downloaded from the *Paleobiology Database*
191 (<https://paleobiodb.org/#/>, last accessed October 25th 2017). We reduced potential
192 biases in the taxonomic assignation of turtle, crocodile and lepidosaur fossils, by
193 compiling occurrence data at the genus level. We further cleaned the fossil datasets by
194 checking for synonymies between taxa and for assignment to a particular genus or
195 family on the basis of published results.

196

197 ***Estimation of origination and extinction rates with phylogenies.*** We ensured
198 comparability with previous LDG studies and investigated possible differences between
199 Holarctic and equatorial regions by combining the turtle and lepidosaur phylogenies
200 with distributional data to fit trait-dependent diversification models in BiSSE (Maddison
201 et al. 2007). We accounted for incomplete taxon sampling in the form of trait-specific
202 global sampling fraction (FitzJohn et al. 2009). We did not use the geographic-state
203 speciation and extinction model (Goldberg et al. 2011), which is appropriate for dealing
204 with widespread species, because most of the species in our datasets were endemic to
205 the Holarctic or equatorial regions (see below), and, for a character state to be
206 considered in SSE models, it must account for at least 10% of the total diversity (Davis et
207 al. 2013). We did not apply the BiSSE model to crocodiles, because simulations have
208 shown that trees containing fewer than 300 species may have too weak a phylogenetic
209 signal to generate sufficient statistical power (Davis et al. 2013).

210 We initially implemented a constant-rate BiSSE model in the R-package
211 *diversitree* 0.9-7 (FitzJohn 2012) with six parameters: two speciation rates, one
212 associated with the Holarctic ('H', λ_H) and the other with other equatorial and

213 subtropical regions ('equator' or 'E', λ_E), two extinction rates associated with the
214 Holarctic (μ_H) and the equator (μ_E), and two transition rates (dispersal), one for the
215 Holarctic to equator direction (q_{HE}), and the other for the equator to Holarctic direction
216 (q_{EH}). We categorized each species as living in the equator or the Holarctic according to
217 the threshold latitudes defining the tropics (23.4°N and 23.4°S). According to our
218 distribution data, 84% of extant species of turtles, lepidosaurs and crocodiles lives in the
219 tropics, 15% in temperate regions and 1% span both biomes. For turtles, there were 239
220 tropical species, 84 temperate and 6 spanning both biomes (7 were marine). For
221 lepidosaurs, 7955 tropical, 1337 temperate and 124 spanning both biomes. Crocodiles
222 had 23 tropical and two temperate species (Tables S1-3).

223 We then used the time-dependent BiSSE (BiSSE.td) model, in which speciation,
224 extinction, and dispersal rates are allowed to vary between regions and to change after
225 shift times. We introduced two shift times to model different diversification dynamics
226 between greenhouse, transitional, and icehouse periods. We assumed that a global
227 warm tropical-like climate dominated the world from the origin of the clades until 51
228 Ma (corresponding to the temperature peak of the Cenozoic). Thereafter, the climate
229 progressively cooled until 23 Ma (the transitional period), when the climate definitively
230 shifted to a temperate-like biome in the Holarctic (Ziegler et al. 2003; Morley 2007;
231 Zachos et al. 2008). The climatic transition in the Cenozoic may have different temporal
232 boundaries, with potential effects on the results. We thus applied the same model but
233 with different combinations of shift times (we tested 51/66 Ma and 23/34 Ma for the
234 upper and lower bounds of the climatic transition). We used a Markov Chain Monte
235 Carlo (MCMC) approach to investigate the credibility intervals of the parameter
236 estimates, with an exponential prior $1/(2r)$ and initiated the chain with the parameters
237 obtained by maximum likelihood. We ran 10,000 MCMC steps, with a burn-in of 10%.

238

239 ***Estimation of origination and extinction rates with fossils.*** We analyzed the three
240 fossil records using a Bayesian model implemented in PyRate (Silvestro et al. 2019) for
241 simultaneous inference of the temporal dynamics of origination and extinction, and of
242 preservation rates (Silvestro et al. 2014). The turtle fossil dataset contains 4084
243 occurrences for 420 genera (65 extant and 355 extinct; Table S4). The lepidosaur fossil
244 dataset comprises 4798 occurrences for 638 genera (120 extant and 518 extinct; Table
245 S5). The crocodile fossil dataset includes 1596 occurrences for 121 genera (9 extant and
246 112 extinct; Table S6). In this analysis, the preservation process is used to infer the
247 individual origination and extinction times of each taxon from all fossil occurrences and
248 an estimated preservation rate expressed as expected occurrences per taxon per million
249 years. We followed a birth-death shift approach (Silvestro et al. 2015), also known as the
250 Bayesian skyline model, and used a homogeneous Poisson process of preservation (-
251 mHPP option). We used default settings and accounted for the variation of preservation
252 rates across taxa, using a Gamma model with gamma-distributed rate heterogeneity (-
253 mG option) and four rate categories to discretize the gamma distribution.

254 Given the large number of occurrences analyzed and the vast timescale
255 considered, we dissected the birth-death process into time intervals, and estimated
256 origination and extinction rates within these intervals. In one set of analyses, we defined
257 time intervals using the geological epochs of the stratigraphic timescale (Ogg et al.
258 2004). In another set of analyses, we defined time intervals according to the major
259 climatic periods characterizing the Cenozoic: the greenhouse world, the climatic
260 transition, and the icehouse world, testing two alternatively boundaries for the climatic
261 transition in the Cenozoic (34/23 Ma). We adopted this solution as an alternative to the
262 algorithms implemented in the original PyRate software for joint estimation of the
263 number of rate shifts and the times at which origination and extinction shift (Silvestro et
264 al. 2014). The estimation of origination and extinction rates within fixed time intervals
265 improved the mixing of the MCMC and made it possible to obtain an overview of the

266 general trends in rate variation over a long timescale. Both the preservation and birth-
267 death processes were modelled in continuous time but without being based on
268 boundary crossings. One potential problem when fixing the number of rate shifts *a*
269 *priori* is over-parameterization. The Bayesian skyline model overcame this problem by
270 assuming that the rates of origination and extinction belonged to two families of
271 parameters following a common prior distribution, with parameters estimated from the
272 data with hyper-priors (Gelman 2004).

273 We ran PyRate for 10 million MCMC generations on each of the 10 randomly
274 replicated datasets. We monitored chain mixing and effective sample sizes by examining
275 the log files in Tracer 1.7 (Rambaut et al. 2018). After excluding the first 20% of the
276 samples as a burn-in, we combined the posterior estimates of the origination and
277 extinction rates across all replicates to generate plots of the change in rate over time.
278 The rates of two adjacent intervals were considered significantly different if the mean of
279 one lay outside the 95% credibility interval of the other, and vice versa.

280 In the context of the LDG, we performed additional analyses with different
281 subsets of fossils, to separate the speciation, extinction and preservation signals of
282 different geographic regions (equator or Holarctic) and ecological conditions
283 (temperate or tropical). For example, for turtles, we split the global fossil dataset into
284 four subsets: one for the fossil genera occurring at the equator (429 occurrences), one
285 for the fossils occurring in the Holarctic (3568 occurrences), one for the fossil genera
286 considered to be adapted to temperate conditions (993 occurrences), and one for the
287 fossils considered to be adapted to tropical conditions (2996 occurrences). We excluded
288 the few fossil occurrences for the southern regions of the South Hemisphere (about 180)
289 only in subset analyses, as they were poorly represented in our dataset. Note that a
290 given fossil can be present in both the 'Holarctic' and 'tropical' datasets. We encoded
291 tropical/temperate preferences by considering macro-conditions in the Holarctic to be
292 paratropical until the end of the Eocene, as previously reported (Ziegler et al. 2003;

293 Morley 2007). We also assumed that taxa inhabiting the warm Holarctic were adapted
294 to tropical-like conditions (*i.e.* a high global temperature, indicating probable adaptation
295 to tropical climates). After the late Eocene, we categorized each species as living in the
296 temperate biome as defined above. With these datasets, we reproduced the same PyRate
297 analyses as for the whole dataset.

298 Finally, we examined the apparent incongruence between paleontological and
299 phylogenetic estimates of diversification (*see Results*) using the birth-death
300 chronospecies (BDC) model in PyRate (Silvestro et al. 2018). This model allows
301 examining whether alternative speciation modes described for the fossil record, *i.e.*
302 budding, bifurcation or anagenesis (Silvestro et al. 2018), are responsible for driving
303 incongruences between fossil and phylogenetic estimates. We compared an *(i)* Equal
304 rates model where diversification parameters estimated with stratigraphic data (λ^* and
305 μ^*) are the same to those estimated with phylogenetic data (λ and μ), *i.e.* $\lambda^* = \lambda$, $\mu^* = \mu$;
306 *(ii)* a Compatible model where parameters differ, but the differences could be explained
307 by differences in speciation mode. In this model λ^* , λ , μ , μ^* are constrained such that $\lambda^* -$
308 $\lambda = \mu^* - \mu$ (*i.e.* equal net diversification rates) and $\lambda^* \geq \lambda$; *(iii)* an Incompatible model,
309 where parameters λ , λ^* , μ , μ^* are allowed to take any value and thus differences in λ and
310 λ^* , as well as μ and μ^* , cannot be explained by differences in speciation mode.

311 We estimated λ , μ , λ^* , μ^* simultaneously for the Testudines, Crocodylia and
312 Lepidosauria phylogenies pruned to the genus level, and the corresponding fossil data
313 using maximum-likelihood optimization and assuming constant diversification rates
314 through time. To assess support for the BDC model we applied a likelihood ratio test
315 (Silvestro et al. 2018), comparing which of the equal, compatible or incompatible rates
316 models are supported by our data.

317 Since the evolutionary histories of Testudines, Lepidosauria and Crocodylia is
318 long and exhibit great amount of temporal heterogeneity in both speciation and
319 extinction rates (*see results*), we also implemented a Bayesian skyline model with rate

320 shifts at the climatic epoch boundaries defined above. We ran 10 million MCMC
321 iterations to obtain joint posterior distributions of the stratigraphic and phylogenetic
322 rates. We used the joint posterior samples of λ^* , μ^* , λ , and μ obtained under the
323 incompatible rates model to verify the conditions predicted by the compatible BDC
324 model (i.e. $\lambda^* - \lambda = \mu^* - \mu$ and $\lambda^* \geq \lambda$) and assess the support for each model as suggested
325 in previous studies (Silvestro et al. 2018).

326

327 ***Inferring ancestral geographic distribution with phylogenies and fossils.*** We
328 performed biogeographic analyses with the parametric likelihood method DEC (Ree and
329 Smith 2008) using the fast C++ version (Smith 2009) ([https://github.com/rhr/lagrange-](https://github.com/rhr/lagrange-cpp)
330 [cpp](https://github.com/rhr/lagrange-cpp)). Turtle, lepidosaur, and crocodile species distributions were obtained from online
331 databases (www.iucnredlist.org and www.reptile-database.org). We also chose 23.4°N
332 and 23.4°S as the threshold latitudes defining the tropics, and categorized each species
333 as living in the Holarctic, in the southern temperate regions, or in the equatorial tropics
334 and subtropical regions. We considered that all ranges comprising three areas could be
335 considered an ancestral state ($maxareas = 3$).

336 We set up three different DEC analyses. We first ran DEC with no particular
337 constraints, using only the distribution of extant species. We then performed DEC
338 analyses including fossil information in the form of ‘fossil constraints’ at certain nodes,
339 according to the range of distribution of fossil occurrences assigned to a particular taxon
340 during the relevant time frame. For example, the crown age of Carettochelyidae
341 (Testudines) dates back to the Late Jurassic (150 Ma), and we set a geographic
342 constraint on this node reflecting the distribution of all the Late Jurassic fossils
343 attributed to Carettochelyidae. Similarly, for the origin of turtles (210 Ma), distribution
344 constraints represent the range of Late Triassic fossils assigned to turtles.

345 We followed two different approaches to include fossil distributions. First, we
346 used a soft fossil constraints (SFC) approach to incorporate fossil data into the

347 anagenetic component of the likelihood framework. The direct impact of a given fossil is
348 limited to the particular branch to which it has been assigned, although it may indirectly
349 influence other branches. The inclusion of a fossil conditions the estimated geographic-
350 transition probability matrix for that branch by imposing a spatiotemporal constraint on
351 the simulation process. Only the simulations resulting in a geographic range including
352 the area of fossil occurrence contribute to the geographic-range transition probability
353 matrix for the branch concerned; simulations not meeting this constraint are discarded
354 (Moore et al. 2008). This was achieved with existing functions in the C++ version of
355 Lagrange, using the command '*fossil*'. We consider this to be a 'soft' constraint, because
356 other areas different from that in which the fossil was found could be included in the
357 ancestral states. In some cases, the SFC model may still overlook known fossil
358 information. Second, we then implemented a hard fossil constraints (HFC) approach,
359 where the estimation of ancestral areas was fixed to the location of fossils. For HFC, we
360 used the command '*fixnode*'. By fixing nodes to the distribution area of fossils, we
361 assume fossil occurrences reflect the distribution of the ancestors. This is a strong
362 assumption, but it makes it possible to recover all fossil ranges in the ancestral
363 estimations. The real scenario probably lies somewhere between SFC and HFC
364 inferences.

365 We then compared the timing and number of range extinction and dispersal
366 events inferred with the three different biogeographic approaches through time. In DEC,
367 extinction (range contraction) and dispersal (range expansion) events are modeled as
368 stochastic processes occurring along the branches of the tree (Ree and Sanmartin 2009),
369 with the probability of any extinction/dispersal event to occur being constant along the
370 entire length of the branch. We therefore estimated the periods at which range
371 extinction and dispersal occurred by dividing the phylogeny into intervals of 25 million
372 years and calculating the number of branches for which extinction/dispersal was

373 inferred crossing a particular time interval (the same branch could cross two continuous
374 intervals).

375 **Results**

376 ***Phylogeny-based diversification analyses: are diversification rates higher at the***
377 ***equator?*** Under the time-constant BiSSE model, net diversification rates for turtles were
378 higher in the Holarctic than at the equator (Fig. S1a), but this difference was not
379 significant, and rates of dispersal '*into the equator*' were ten times higher than those '*out*
380 *of the equator*'. For lepidosaurs, a similar dispersal pattern was recovered, but net
381 diversification rates were significantly higher in the equator (Fig. S1b). The time-
382 variable BiSSE models, with shift times at 51 and 23 Ma, indicated that speciation and
383 extinction rates of turtles were similar in the Holarctic and at the equator until the
384 icehouse period, when Holarctic speciation increased. For lepidosaurs, speciation was
385 lower in the Holarctic and extinction higher until the icehouse period, when Holarctic
386 speciation increased and extinction decreased (Fig. S2). Dispersal was symmetric
387 between regions (*into the equator = out of the equator*) during greenhouse periods, and
388 asymmetric (*into the equator > out of the equator*) during the climatic transition and
389 icehouse period. The same patterns were obtained assuming different combinations of
390 shift times (51/66 Ma and 23/34 Ma; Fig. S3, S4).

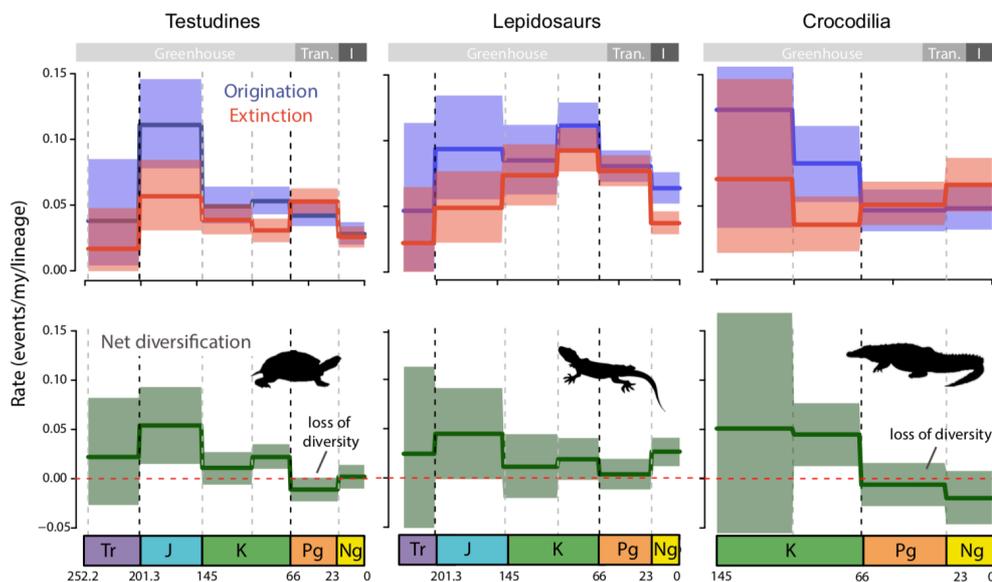
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392 ***Fossil-based diversification analyses: evidence for ancient tropical extinctions?*** We
393 first inferred global diversification dynamics by analyzing the fossil datasets as a whole.
394 For turtles, origination rates peaked during the Jurassic, subsequently decreasing until
395 the present. Extinction rates were generally low and constant during the Mesozoic, but
396 increased during the Jurassic and the Paleogene, resulting in negative net diversification
397 during the Paleogene only (**Fig. 2**). For lepidosaurs, origination rates peaked in the

398 Jurassic and Late Cretaceous, whereas extinction increased steadily until the Late
 399 Cretaceous. In the Paleogene, net diversification approached zero, suggesting a high
 400 turnover. Crocodile origination peaked in the Early Cretaceous, subsequently decreasing
 401 toward the present, and extinction rates were generally low and constant. We also
 402 identified diversity losses in the Paleogene extending to the present, suggesting that
 403 crocodiles are still in a phase of declining diversity (**Fig. 2**).

404

405 **Figure 2.** Global pattern of turtle, lepidosaur, and crocodile diversification through time based on the fossil
 406 record. Origination (blue) and extinction (red) rates were estimated using time bins as defined by epochs of
 407 the geological timescale (on the top, main climatic periods are shown as follows: Greenhouse, Tran. =
 408 climatic transition, and I. = icehouse). Solid lines indicate mean posterior rates, whereas the shaded areas
 409 show 95% credibility intervals. Net diversification rates (green) are the difference between origination and
 410 extinction. The vertical lines indicate the boundaries between geological periods. Tr=Triassic; J=Jurassic;
 411 K=Cretaceous; Pg=Paleogene, and Ng=Neogene.



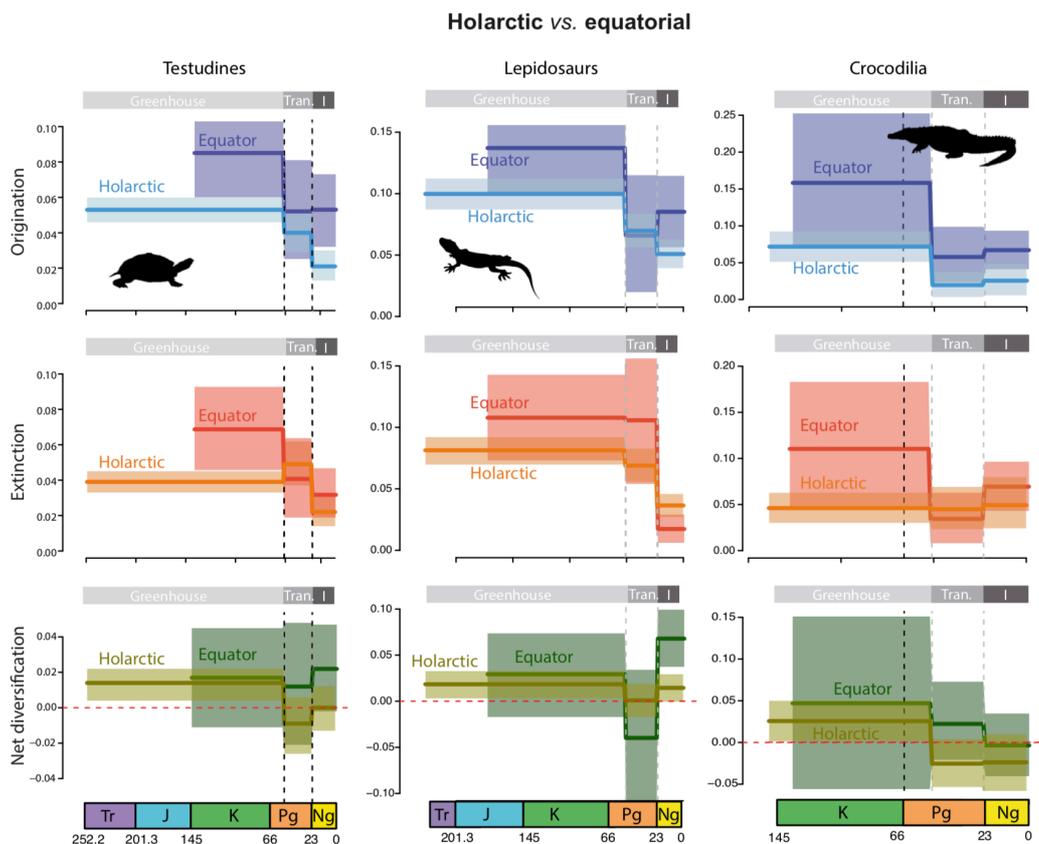
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413 Additional analyses with different subsets of the three fossil datasets separating
 414 origination and extinction signals between geographic regions (equator or Holarctic)
 415 and ecological conditions (temperate or tropical), showed that the diversity losses
 416 experienced by turtles and crocodiles during the Paleogene were mostly attributable to
 417 species living in the Holarctic and under tropical conditions (**Figs. 3, 4**). The global

418 diversity loss inferred for crocodiles during the Neogene was attributed to taxa living in
 419 both the Holarctic and equatorial regions (adapted to temperate and tropical conditions
 420 respectively), providing further support for the hypothesis that this whole group is in
 421 decline.

422

423 **Figure 3.** Global pattern of turtle, lepidosaur and crocodile diversification between Holarctic and equatorial
 424 regions, based on the fossil record. Diversification dynamics are compared between fossils distributed in
 425 Holarctic and equatorial regions. Origination (blue) and extinction (red) rates were estimated using time
 426 bins as defined by the main climatic intervals since the Mesozoic (on the top, climatic periods are shown as
 427 follows: Greenhouse, Tran. = climatic transition, and I. = icehouse). Solid lines indicate mean posterior rates,
 428 whereas the shaded areas show 95% credibility intervals. Net diversification rates (green) are the
 429 difference between origination and extinction. The vertical lines indicate the boundaries between climatic
 430 intervals. Tr=Triassic; J=Jurassic; K=Cretaceous; Pg=Paleogene, and Ng=Neogene.



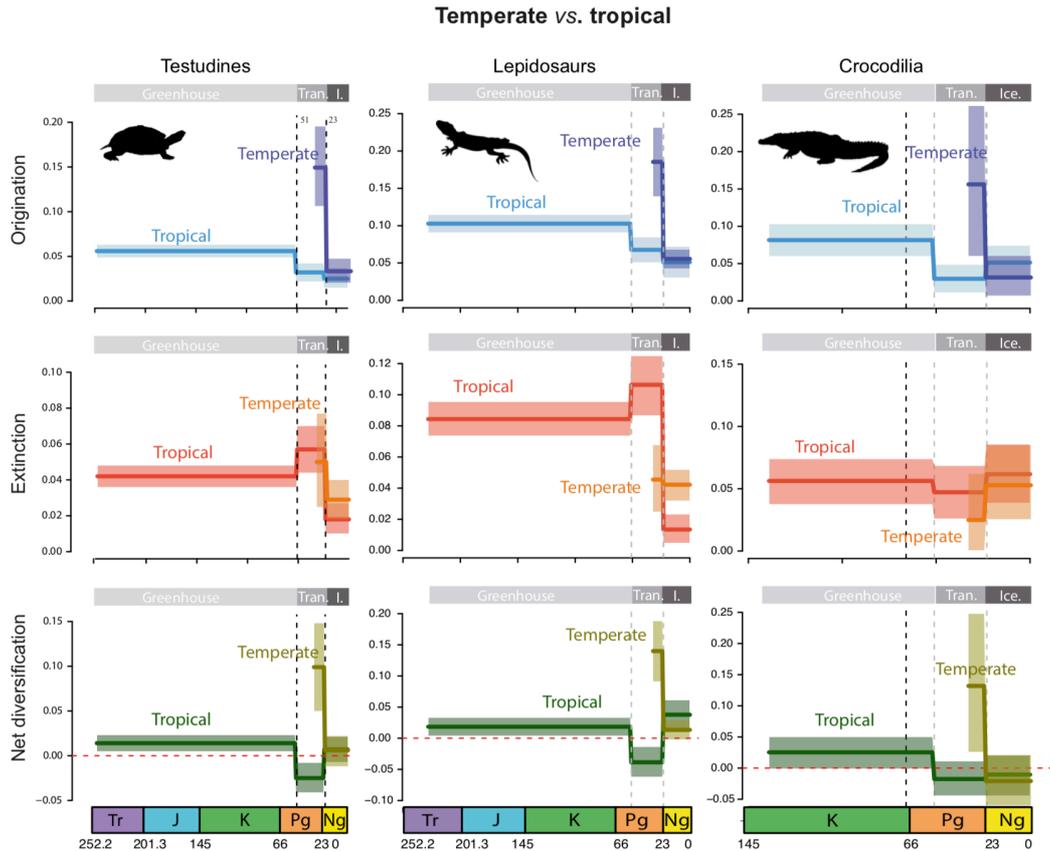
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432 For all groups, temperate taxa have been estimated to have high rates of
 433 diversification during the Oligocene, but lower rates during the Neogene. For the

434 equatorial datasets, extinction and origination rates decreased over time, resulting in
435 constant net diversification rates (except for lepidosaurs, which displayed a decrease in
436 diversification during the Paleogene, followed by an increase during the Neogene). The
437 same patterns were obtained for analyses with temporal boundaries defined according
438 to the main climatic periods of the Cenozoic (Figs. S11–S13), and assuming a different
439 combination of shift times to represent uncertainty on the temporal boundaries of the
440 largest climatic oscillations (23/34 Ma; Fig. S5-S10). PyRate analyses also estimated
441 similar preservation rates in the Holarctic and the equator for turtle and crocodile
442 fossils, while preservation rates for lepidosaurs are much higher in the Holarctic than in
443 the equator (**Table 2**).

444

445 **Figure 4.** Global pattern of turtle, lepidosaur and crocodile diversification across temperate and tropical
446 climates, based on the fossil record. Diversification dynamics are compared between fossils inhabiting
447 under temperate and tropical macroclimates, by considering macro-conditions in the Holarctic to be
448 (para)tropical until the end of the Eocene, and temperate from this period to the present (see text).
449 Origination (blue) and extinction (red) rates were estimated using time bins as defined by the main climatic
450 intervals since the Mesozoic (on the top, climatic periods are shown as follows: Greenhouse, Tran. = climatic
451 transition, and I. = icehouse). Solid lines indicate mean posterior rates, whereas shaded areas show 95%
452 credibility intervals. Net diversification rates (green) are the difference between origination and extinction.
453 Vertical lines show boundaries between climatic intervals. Tr=Triassic; J=Jurassic; K=Cretaceous;
454 Pg=Paleogene, Ng=Neogene.



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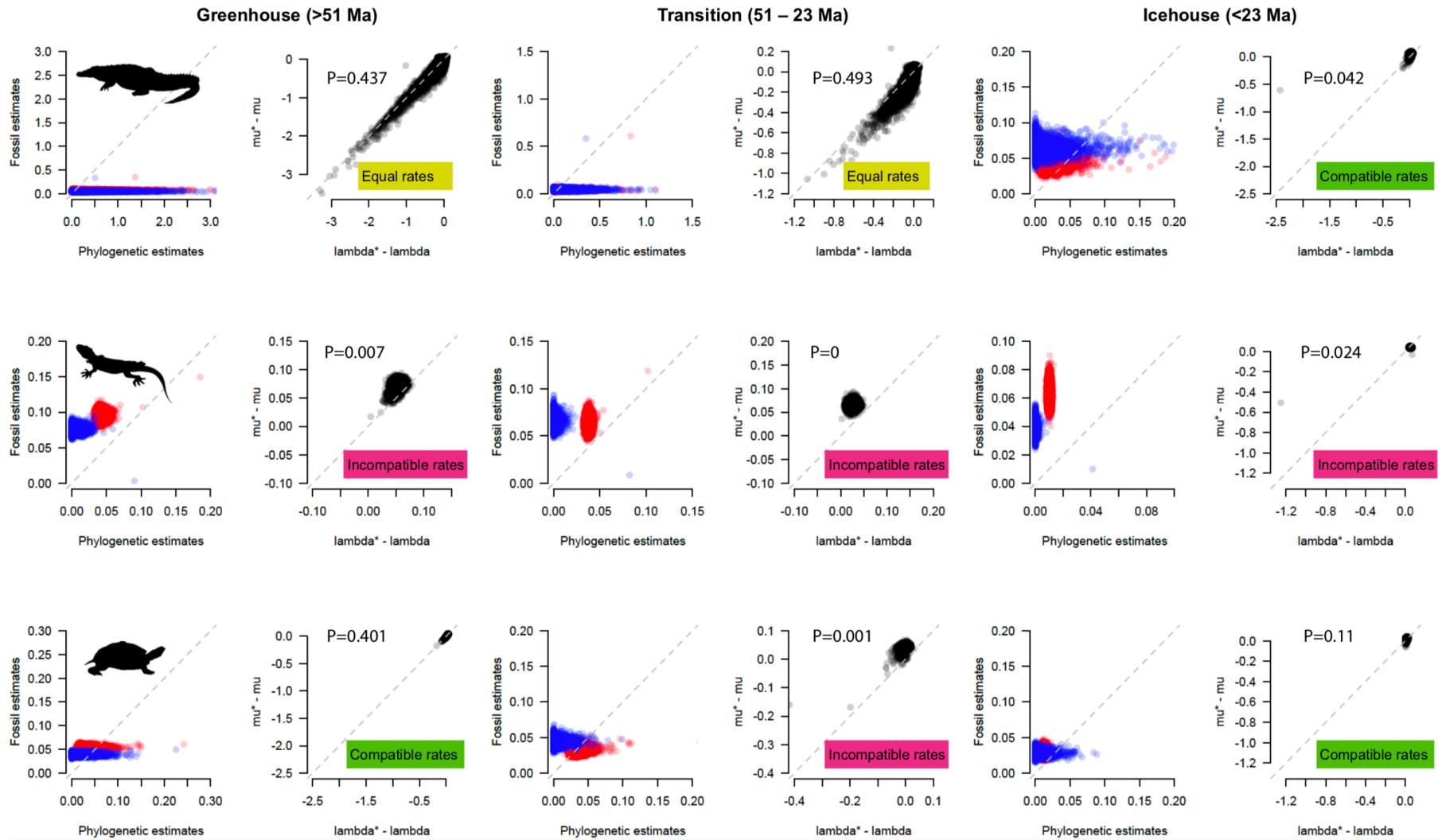
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469

Finally, we found that crocodiles conform to the expectations of the compatible rates BDC model under a constant rate assumption and likelihood threshold values of 0.95 (they conform to the equal rates model at 0.99 threshold). For Testudines and Lepidosauria, the time-constant BDC model was rejected in favor for the incompatible rates model in all cases (Table S7). Relaxing the assumption of constant rates resulted in strong support for the compatible rates BDC model in turtles ($P > 0.01$ or 0.05) and the incompatible rates model in lepidosaurs ($P < 0.01$). Phylogenetic and fossil estimates of diversification for crocodiles are not significantly different during the first two-time intervals (from the origin to 23 Ma) supporting the equal rates model (Fig. 5).

Figure 5. Results from a joint Bayesian analysis of fossil and phylogenetic data for crocodiles, lepidosaurs and turtles under the skyline BDC model. Posterior samples of speciation (blue) and extinction (red) rates are plotted against one another and calculated over three-time intervals to account for rate heterogeneity; posterior samples of the two terms $\lambda^* - \lambda$ and $\mu^* - \mu$ are shown in black. Analyses were run assuming

470 independent rates (λ , μ for phylogeny, and λ^* , μ^* for fossils), and their joint posterior samples were used to
471 assess which model (equal rates, compatible rates, or incompatible rates) best fit the data. The best model is
472 indicated by the labels in the plots, and based on whether the posterior samples conform to the properties
473 of the equal rate model ($\lambda = \lambda^*$, $\mu = \mu^*$), and the compatible rate BDC model: $\lambda < \lambda^*$, $(\lambda^* - \lambda) = (\mu^* - \mu)$. P values
474 indicate whether phylogenetic and fossil parameter estimates differ significantly. For crocodiles (also for
475 turtles), there is little phylogenetic information in speciation and extinction rates before to 23 Ma (as shown
476 by the large spread of posterior values). For Lepidosauria there is little fossil information, especially after
477 23 Ma.



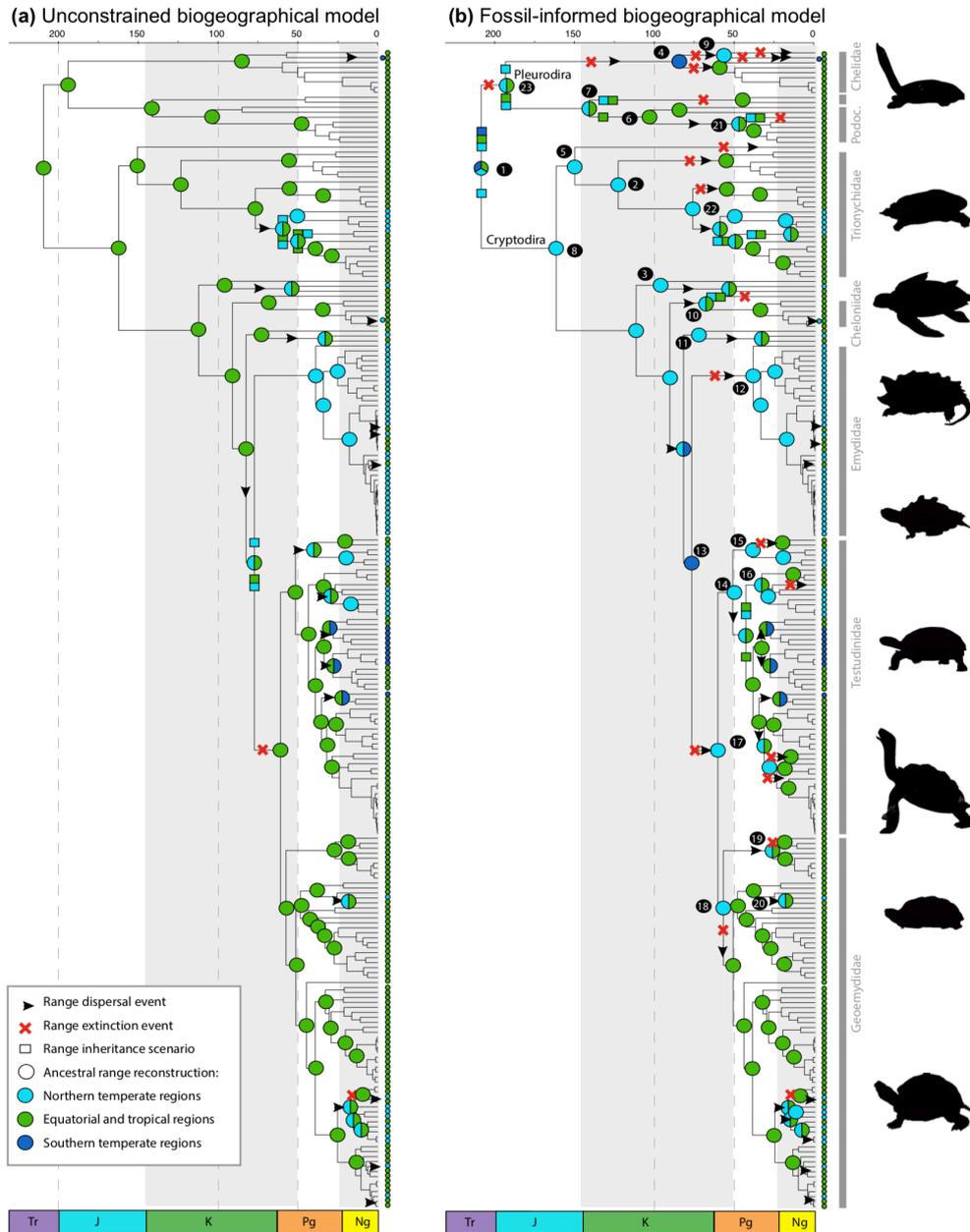
479 ***Estimations of ancestral origins: did groups preferentially originate at the equator?***

480 Based on the unconstrained DEC analysis, we inferred an equatorial distribution for the
481 deepest nodes for the turtles and lepidosaurs, whence these lineages colonized the other
482 regions (**Fig. 6a**, Fig. S14). Crocodile ancestors were found to have been widespread
483 during the Cretaceous, with an early vicariant speciation event separating *Alligator* in
484 the Holarctic from the other genera of Alligatoridae in equatorial regions (Fig. S15). In
485 contrast, our biogeographic estimates based on extant and fossil data yielded very
486 different histories for the three groups (turtles: **Fig. 6b**, Fig. S16; lepidosaurs: Figs. S17-
487 18; and crocodiles: Figs. S19-20), with Cretaceous and early Cenozoic ancestors of
488 Testudines, Crocodylia and Lepidosauria distributed in the Holarctic. We implemented
489 23 fossil constraints for turtles (Table S8), 30 fossil constraints for lepidosaurs (Table
490 S9), and 8 for crocodiles (Table S10). Under the SFC model, turtles were found to have
491 originated in the Northern Hemisphere (under the HFC model they were spread over
492 both regions), whence lineages migrated toward the equator and southern regions (Fig.
493 S16). Most dispersal therefore occurred ‘*into the equator*’ (Fig. S21, Table S11). We also
494 detected a larger number of geographic extinctions when fossil ranges were considered,
495 predominantly for turtle lineages in the Holarctic (53 and 11 lineages disappeared from
496 this region under the HFC and SFC models, respectively) and in southern temperate
497 regions (9 in the HFC model; Fig. S21, Table S12). The same pattern of Holarctic
498 extinction was observed when the number of extinction/dispersal events was divided
499 by the number of lineages currently distributed in each region (**Fig. 7**). The uncertainty
500 associated to this estimation does not affect the overall result (Table S13 and Appendix
501 1).

502

503 **Figure 6.** Biogeographic estimations of Testudines showing the effects of the incorporation of fossil
504 information into biogeographic inference. **a**, Results with DEC based on the distribution of extant taxa. **b**,
505 Results under the fossil-informed HFC (hard fossil constraint) model. Colored circles at tips and nodes
506 represent current and ancestral ranges, respectively, while squares represent range inheritance scenarios.

507 Colors correspond with the discrete areas in the legend. Black circles indicate fossil range constraints
 508 included in the analysis, with numbers corresponding with taxa in Table S8. The reconstruction under the
 509 soft fossil constraint (SFC, see text) model is presented in Fig. S16. Tr=Triassic; J=Jurassic; K=Cretaceous;
 510 Pg=Paleogene, and Ng=Neogene.



511

512 The most supported biogeographic scenarios in both SFC and HFC analyses also

513 suggest that lepidosaur ancestors were widespread (Figs. S17-18; uncertainty presented

514 in Tables S14 and Appendix 1). During the greenhouse period, dispersal 'into the

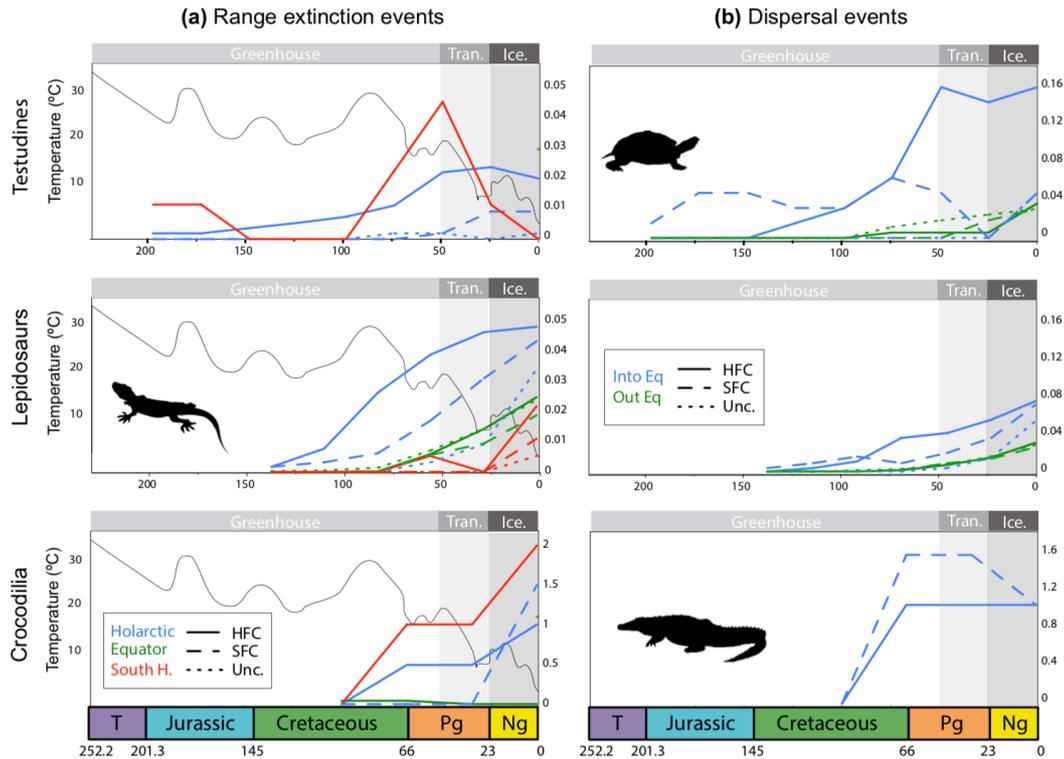
515 equator' occurred at the same rate (or at a higher rate in the HFC model) than dispersal

516 'out of the equator', and dispersal 'out of the equator' prevailed thereafter (Fig. S21,
517 Table S11). Estimates of range extinction rates were high in this group under the
518 unconstrained model, with 30 lineages extirpated from the Holarctic, two from southern
519 temperate regions and 152 from the equator (Fig. S21, Table S12). Under fossil-
520 informed models, the number of Holarctic extinctions increased (109 and 66 lineages in
521 the HFC and SFC models, respectively), whereas the number of lineages extirpated from
522 the equator was similar (144 and 109 in the HFC and SFC models, respectively; Fig. S21).
523 When the number of events was controlled for the extant number of lineages distributed
524 in each region, the number of Holarctic extinctions and dispersals 'into the equator'
525 increased dramatically, exceeding equatorial dispersal/extinctions (**Fig. 7**).

526 For crocodiles, analyses including fossil ranges showed that all deep nodes were
527 distributed in the Holarctic (Figs. S19-20), and range extinctions were detected: four
528 lineages disappeared from the Holarctic, three from southern temperate regions, and
529 two from the equator (HFC model; Fig. S21, Tables S12). Only two lineages disappeared
530 from the Holarctic in the SFC model. The same trends were observed after controlling
531 the number of events for the current number of lineages in each region (**Fig. 7**). The
532 uncertainty associated to this estimation does not affect the overall result (Table S15
533 and Appendix 1). A summary of all the results is presented in Table S17.

534

535 **Figure 7.** Estimated number of range extinction and dispersal events through time. Analyses were
536 performed for turtles, lepidosaurs and crocodiles under the unconstrained model (Unc.), based on present
537 evidence only, and the fossil-based hard (HFC) and soft fossil constraint (SFC) biogeographic models. **a**,
538 Inferred number of range extinction events through time and across regions relative to the number of
539 lineages currently distributed in each region. The black line represents the global mean temperature curve
540 as modified from (Zachos et al. 2008). **b**, Inferred number of dispersal events from the Holarctic into the
541 equator (IntoEq) and out of the equatorial zone (OutEq), relative to the current number of lineages
542 distributed in the Holarctic and equatorial zones, respectively. Tr, Triassic; J, Jurassic; K, Cretaceous; Pg,
543 Paleogene; and Ng, Neogene, Tran. = climatic transition, and Ice. = icehouse.



544

545 Discussion

546 *Time-variable evolutionary processes shaping the latitudinal diversity gradient*

547 Fossil investigations have shown that, at certain times during the Phanerozoic, the LDG
 548 has flattened, weakened or developed a paleotemperate peak, with diversity at high
 549 latitudes being greater than currently for many groups (Mannion et al. 2014; Marcot et
 550 al. 2016). This observation has multiple consequences for the study of the LDG. The
 551 evolutionary mechanisms required to explain the formation of the current steep LDG are
 552 radically different whether we consider or not that high diversity levels existed
 553 previously in the Northern Hemisphere: if the pattern transitioned from flatten to steep,
 554 as suggested by fossils, then one hypothesis can argue for diversity loss in the Northern
 555 Hemisphere to explain the current LDG, via extinction or range contractions (Hawkins et
 556 al. 2006). If diversity was never elevated at high latitudes then an alternative hypothesis
 557 can argue for slow accumulation of species in the Northern Hemisphere, due to limited

558 dispersal to the Holarctic (Latham and Ricklefs 1993; Wiens and Donoghue 2004), high
559 Holarctic turnover (Weir and Schluter 2007; Pyron 2014; Pulido-Santacruz and Weir
560 2016), or high rates of equatorial diversification (Ricklefs 2006; Wiens 2007; Jansson et
561 al. 2013; Pyron and Wiens 2013; Rolland et al. 2014). Hypotheses related to ‘slow
562 Holarctic diversity accumulation’, however, cannot alone account for the formation of a
563 flattened LDG, or for the transition from higher to lower diversity in the Holarctic.

564 Furthermore, although the processes shaping biodiversity vary over time and
565 space, this has been largely overlooked in the context of the LDG, which has been
566 generally explained in terms of time-constant uniform processes. That is, the
567 parametrization of previous evolutionary models requires only one value per parameter
568 (speciation/extinction/dispersal) and region (Holarctic and Equator) to explain the
569 persistence of a steep LDG in the deep time. Conversely, in our time-variable framework,
570 these parameters adopt different values per region and through time: one value in each
571 region during the greenhouse period, and different values during icehouses (**Table 1**).
572 Doing this, our models identify gains and losses of tropical diversity at high latitudes,
573 with prevailing speciation, extinction and dispersal dynamics changing between warm
574 and cold time intervals.

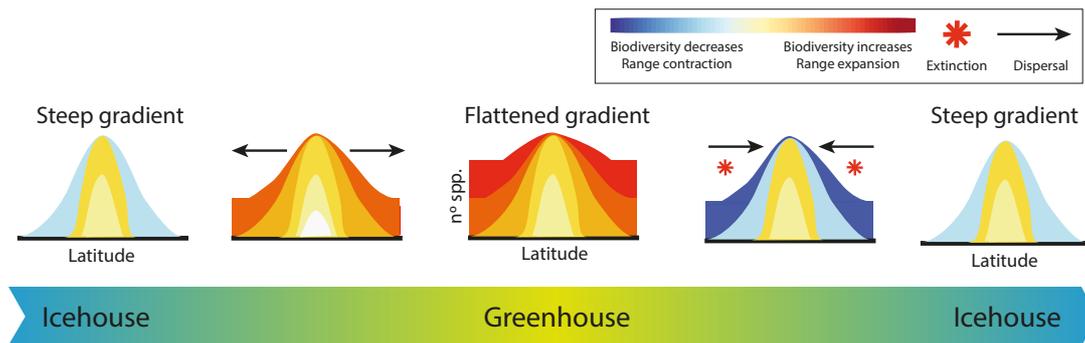
575 Our time-variable fossil-based analyses support ‘Holarctic diversity loss’
576 scenarios to explain the LDG of turtles and crocodiles. Diversification rates estimated in
577 the Holarctic and equatorial regions were similar during the equable greenhouse period
578 of the Cretaceous-early Cenozoic for all groups studied here (overlapping credibility
579 intervals; **Fig. 3**; Figs. S5–10), consistent with the idea of the existence of a flattened LDG
580 during this phase (Mannion et al. 2014; Marcot et al. 2016). We hypothesize that the
581 expansion of tropical conditions to higher latitudes during greenhouse periods might
582 have induced species diversification in the new paratropical areas (De Celis et al. 2019)
583 and facilitated movements within the broad ‘tropical belt’, such that tropical equatorial
584 clades were able to disperse ‘*out of the equator*’ (Jablonski et al. 2006, 2013) (**Fig. 8**). By

585 contrast, the contraction of the tropical biome following climate cooling provoked
586 periods of declining diversity at high latitudes (**Fig. 3**), where climate change was more
587 intensively felt, and mediated dispersal '*into the equator*' (**Figs. 7, 8**). We found that
588 diversification rates of turtles and crocodiles decreased in all regions during the
589 transition to colder climates (**Fig. 3**) – they decreased since the Cretaceous in the
590 analyses with time intervals defined by the main geological periods (Figs. S11–13). The
591 slowing of diversification was much stronger in the Holarctic than at the equator, with
592 extinction exceeding speciation in this region (*i.e.* Holarctic diversity loss). In addition,
593 using phylogenetic-based biogeographic models informed by fossils, we inferred that all
594 groups had a widespread ancestral distribution that subsequently contracted toward
595 the equator. This result is in agreement with previous fossil investigations for turtles
596 (Nicholson et al. 2015, 2016; Joyce et al. 2016) and crocodiles (Markwick 1998;
597 Mannion et al. 2015; De Celis et al. 2019). Range contraction in our study started in the
598 Cretaceous, intensifying during the late Paleogene cooling. They resulted from range
599 extirpations at higher latitudes combined with '*into the equator*' dispersals (Condamine
600 et al. 2012) (**Figs. 6, 7**). Hence, our results suggest that climate change has likely driven
601 the development of an “asymmetric gradient of extinction and dispersal” (AGED) within
602 the tropical biome, and could have mediated the formation of a steep LDG (**Fig. 8**).

603

604 **Figure 8.** Prevalent evolutionary processes behind the latitudinal diversity gradient under the AGED model.
605 It shows the hypothetical change in evolutionary dynamics between Holarctic and equatorial regions through
606 different climatic intervals: the greenhouse, icehouse and transitions. For each climatic interval, inset plots
607 represent the hypothetical distribution of species richness across latitudes (LDG shape).

608



609

610

611 The AGED hypothesis reconciles previous contending ideas on the origin of the
 612 LDG by placing them in a temporal scenario (**Table 1, Fig. 8**). For instance, there is
 613 controversial support around the tropics being '*cradle*' or '*museum of diversity*' (Stebbins
 614 1974), and dispersal prevailing '*out of*' (Jablonski et al. 2006, 2013) or '*into the tropics*'
 615 (Condamine et al. 2012; Pyron 2014; Rolland et al. 2015). The interpretation of our
 616 results alternatively invokes the '*museum of diversity*' regarding the equatorial tropics as
 617 refuge during icehouse transitions, but also the '*cradle of diversity*' during greenhouse
 618 periods. Similarly, our hypothesis invokes '*out of the equator*' dispersals during
 619 greenhouse transitions and '*into the equator*' dispersals during icehouse transitions.

620 Support for the AGED hypothesis and for a 'Holarctic diversity loss' scenario is
 621 mixed for lepidosaurs. On the one hand, we found similar diversification rates in the
 622 Holarctic and equator during the greenhouse period, and widespread ancestral
 623 distributions (**Fig. 3**). We also found a higher proportion of lepidosaur species that
 624 actually lost their ancestral Holarctic distribution and dispersed '*into the equator*'
 625 (Pyron 2014) than the other way around (**Fig. 7**), in agreement with the idea of an
 626 ancient flattened pattern shaped by extinction. On the other hand, we detected that
 627 during climate cooling, diversity losses of lepidosaurs occurred only in the equator (**Fig.**
 628 **3**). However, equatorial estimates remain uncertain: diversity dynamics for species
 629 distributed at the equator have broad credibility intervals probably due to the poverty
 630 of the equatorial dataset in terms of the number of fossil lineages and the small number

631 of records per lineage (Table S16). In the Holarctic, turnover rates were high during the
632 transitional period to cold, indicating that species did disappear from high latitudes, but
633 that a lepidosaur community got replaced by another. This result suggests the number
634 of lepidosaur species may always have been unbalanced between regions with higher
635 diversity in the equator. The high Holarctic turnover likely contributed to the
636 maintenance of this pattern, together with the inferred temporal increases in
637 diversification at the equator (**Fig. 3**), as previously hypothesized (Pyron 2014).

638

639 ***Towards an integrative phylogenetic niche conservatism framework to explain the***
640 ***LDG***

641 Accumulating fossil, ecological and molecular evidence demonstrates that global climate
642 changes over geological timescales could generate large-scale patterns of biodiversity
643 (Mannion et al. 2014; Fenton et al. 2016; Saupe et al. 2019a). In the last decade,
644 phylogenetic niche conservatism (PNC), *i.e.* tendency of species to retain their ancestral
645 niches over time, emerged as a general principle to explain the effects of climate over
646 diversity (Peterson et al. 1999). Wiens & Donoghue (2004) proposed PNC as a major
647 explanation behind the LDG. The tropical niche conservatism (TNC) hypothesis posits
648 that the difficulty of many tropical lineages to invade or persist in temperate
649 environments determined the distribution of global diversity (Wiens and Donoghue
650 2004; Donoghue 2008). However, they were less specific about the mechanisms by
651 which PNC shaped diversity. They considered time, limited dispersal, and also the
652 contraction of the tropical belt (Wiens and Donoghue 2004; Donoghue 2008). They
653 argued that tropical regions had a greater geographical extent in the past to explain why
654 most taxa have tropical adaptations, but did not consider that diversity could have once
655 reached equivalent levels across latitudes. This probably explains why extinction was
656 not part of their original predictions. For example, Wiens et al. (2010) published a
657 review on the topic where only limited dispersal explains the LDG. Moreover, diversity

658 loss (and range contractions), if ever seen as an original prediction of the TNC, have not
659 transcended in the literature as part of the TNC formulations. This is manifest in
660 subsequent studies, which interpreted the LDG in terms of limited dispersal and PNC
661 (Cardillo et al. 2005; Condamine et al. 2012; Kerkhoff et al. 2014; Rolland et al. 2014;
662 Siqueira et al. 2016). For example, Kerkhoff et al. (2014) finds that high current tropical
663 diversity results from a combination of *(i)* differential net diversification rates of
664 tropical lineages due to larger cumulative area of tropical environments, *(ii)* greater
665 time for diversification in tropical environments, and *(iii)* limited dispersal of tropical
666 lineages into the temperate environments. We therefore argue that the AGED model
667 represents an extension of the TNC hypothesis, by formalizing the mechanisms by which
668 PNC shaped diversity (extinction and range contraction during icehouses, speciation
669 and range expansion during greenhouses) in a time-variable scenario and a varying LDG
670 shape (**Fig. 8**).

671 Behind the AGED model prevails the PNC idea: when the tropical biome
672 retreated towards the equator, most of the tropical-adapted taxa at high latitudes were
673 unable to adapt and either went extinct or got their distribution restricted. The
674 ancestors of turtles, lepidosaurs and crocodiles were adapted to tropical conditions
675 during the Late Cretaceous (Markwick 1998; Waterson et al. 2016; Pie et al. 2017). Our
676 fossil-based diversification results when analyzing differences between taxa adapted to
677 different climates indicate that extinction events were not random (Eiserhardt et al.
678 2015; Reddin et al. 2019), but instead preferentially affected taxa living in tropical-like
679 climates at high latitudes (**Fig. 4**). Similar climatic-driven extirpation scenarios have
680 been proposed for other vertebrates (Hawkins et al. 2006; Saupe et al. 2019b). This
681 suggests that climate change could have imposed an asymmetric gradient of extinction
682 and dispersal within the tropical biome due to PNC.

683 Lineages possessing or having evolved the appropriate adaptations to cope with
684 cold climates diversified in the new temperate areas (Kindlmann et al. 2007; Meseguer

685 et al. 2018). After the transition to temperate climates in the late Eocene, we found that
686 diversification rates of turtles, crocodiles and lepidosaurs living in temperate climatic
687 conditions were significantly higher than those of tropical-adapted taxa living in
688 Holarctic and equatorial regions (**Fig. 4**). New Neogene temperate habitats likely
689 constituted an opportunity for diversification due to increased geographic ranges and
690 ecological niches (Wiens 2007), eventually driving an inverse LDG for some groups
691 (Kindlmann et al. 2007; Leslie et al. 2012). Several radiations following the appearance
692 of temperate biomes have been identified in other groups, such as plants (Meseguer et
693 al. 2018), mammals (Ge et al. 2013) or insects (Condamine et al. 2018). After this period,
694 we estimated similar diversification rates between tropical and temperate lineages
695 because speciation decreased dramatically in the temperate lineages of our focal groups
696 (**Fig. 4**), possibly due to the effect of the Pleistocene glaciations. Thus our study does not
697 support lower rates of diversification under cold environments, in agreement with
698 previous studies (Weir and Schluter 2007; Pyron 2014).

699 These results overall suggest that differences in species richness between
700 geographic regions (*i.e.* the Holarctic vs. the equator) may be explained by asymmetric
701 diversification and dispersal across regions and time. Differences in species richness
702 between ecological types (*i.e.* tropical- vs. temperate-adapted taxa) may be explained by
703 the longer time available for tropical-adapted clades to diversify in tropical areas
704 (Stephens and Wiens 2003). Turning up that the factors driving diversity differ between
705 geographic regions and ecological types.

706 Here, we encoded tropical/temperate preferences by considering macro-
707 conditions in the Holarctic to be paratropical until the end of the Eocene, as generally
708 recognized (Ziegler et al. 2003; Sluijs et al. 2006; Morley 2007; and references therein),
709 and temperate afterwards. However, we acknowledge that the post-Eocene Holarctic
710 could be seen as tropical-like during warming events. We also assumed that taxa
711 inhabiting the warm Holarctic were adapted to tropical-like conditions (*i.e.* a high global

712 temperature, indicating probable adaptation to tropical climates). For turtles, crocodiles
713 and lepidosaurs this assumption is supported by Cenozoic climatic niche modeling
714 (Waterson et al. 2016; Pie et al. 2017), stable isotope analyses and other climate proxies
715 (Markwick 1998; Tütken and Absolon 2015). These assumptions are, of course,
716 oversimplifications that may introduce biases in the analyses, but we consider that
717 general patterns may nevertheless emerge from such analyses (Romdal et al. 2013).

718

719 *Reconciling fossil and phylogenetic evidence*

720 Our results demonstrate that the inclusion of fossils in macroevolutionary studies
721 improves detecting ancient high-latitude extinctions and range extirpations (**Figs. 3, 7**),
722 otherwise hardly detectable with molecular phylogenies only. The results exclusively
723 based on extant species (time-constant and time-variable BiSSE models, and
724 biogeographic analyses, **Figs. 6, 7**; Figs. S1-S4, S14-S15) differed from the analyses
725 including fossils in our study; they suggest higher levels of Holarctic diversification for
726 turtles during Cenozoic cooling, together with an equatorial origin and recent invasion
727 of high-latitude regions, resulting in less time for lineages to diversify in the Holarctic
728 (**Figs. 6, 7**; Figs. S1-4). This is in agreement with the TNC hypothesis (Wiens and
729 Donoghue 2004) and recent investigations (Pereira et al. 2017; Rodrigues et al. 2017).
730 For crocodiles they support the diversification hypothesis, with higher origination rates
731 close to the equator and no effect on dispersal (**Fig. 7**, Fig. S15). For lepidosaurs, they
732 support the high temperate turnover and into the tropics hypotheses (Condamine et al.
733 2012) (**Fig. 7**; Figs. S1-S4, S14), as suggested before (Pyron 2014). This conflict between
734 extant and fossil evidence may extend beyond our study, pervading the LDG literature.

735 The observed incongruences between paleontological and neontological
736 analyses could be attributed to the geographic and/or preservation biases of the fossil
737 record (Albino and Brizuela 2014). We argue, however, that sampling artifacts on fossils
738 have not biased diversification and biogeographic results for Testudines and Crocodylia.

739 Preservation rates estimated for these lineages are similar for Holarctic and equatorial
740 regions (overlapping credibility intervals; **Table 2**). PyRate has also been shown to
741 correctly estimate the dynamics of speciation and extinction rates under low levels of
742 preservation or severely incomplete taxon sampling (Silvestro et al. 2014).
743 Nevertheless, since diversification dynamics were inferred independently for Holarctic
744 and equatorial fossils, inferences of the Holarctic are robust and based on a large
745 number of fossils (Table S16), indicating diversity loss during the climate transition.

746 In the case of lepidosaurs, preservation rates are higher in the Holarctic than at
747 the equator, and thus we have a relative oversampling of Holarctic fossils (**Table 2**).
748 Whilst this might have a lower impact on diversification estimates (as explained above),
749 we cannot discard that higher preservation rates at higher latitudes potentially biased
750 the biogeographic results for lepidosaurs towards non-equatorial origins, and artificially
751 increased the estimates of '*into the equator*' dispersals. Nonetheless, the biogeographic
752 reconstruction based on extant data only was not able to recover Holarctic distributions
753 for lepidosaur ancestors, despite extensive fossil evidence suggesting a widespread
754 (Holarctic and equatorial) distribution for these lineages (Table S16; **Fig. 7**). Meanwhile,
755 the reconstruction including fossils recovers widespread ancestors. The number of
756 Holarctic and equatorial fossil constraints for lepidosaurs was relatively low given the
757 size of the tree, but these constraints significantly increased the absolute number of
758 Holarctic range extinctions (from 30 to 109) and '*into the equator*' dispersals (from 40 to
759 124) relative to estimates without such constraints. Meanwhile, the inclusion of fossil
760 data did not alter the number of events estimated for equatorial taxa (Tables S11-12).
761 This finding suggests that there is an oversampling of equatorial species in the present
762 (possibly due to extinction of Holarctic species in the past), which may lead to spurious
763 increases of the probability of estimating dispersions '*out of the equator*', compared to
764 '*into the equator*' if fossils are not considered. A better understanding of lepidosaur

765 fossil taxonomy might facilitate the assignment of fossils on the tree, and the detection
766 of additional high-latitude range extinctions not detected here.

767 Incongruences between paleontological and neontological analyses have also
768 been attributed to the difficulty to estimate extinction rates from phylogenetic data.
769 Although demonstrated mathematically (Nee et al. 1994; Sanmartín and Meseguer
770 2016), estimations of extinction in phylogenetic analyses are often inaccurate and highly
771 underestimated (Rabosky 2010). This has been attributed to sampling biases (Pybus
772 and Harvey 2000), lack of statistical power (Davis et al. 2013), violations of model
773 assumptions (Rabosky 2010; Morlon et al. 2011) or substantial rate heterogeneity
774 (Morlon et al. 2011; Sanmartín and Meseguer 2016). We cannot exclude these artifacts
775 affected our phylogenetic-based results. In the last years, however, studies proposed
776 alternative explanations to biases in the data/methods. Conceptual differences on how
777 ages, speciation and extinction rates are estimated from paleontological data and
778 molecular phylogenies could explain some of the incongruences (Huang et al. 2015;
779 Silvestro et al. 2018). In our study, fossil and phylogenetic data for Crocodylia and
780 Testudines fit the expectations of the BDC model, suggesting that discrepancies between
781 phylogenetic and paleontological estimates are probably attributed to intrinsic
782 differences in the fossil and phylogenetic properties due to bifurcating and anagenetic
783 speciation events (Table S7, **Fig. 5**). These speciation modes are not detectable from
784 phylogenetic data, which could alter evolutionary rates and contribute to an apparent
785 incongruence between fossil and phylogenetic estimates (Silvestro et al. 2018). The BDC
786 model was rejected for Lepidosauria, suggesting that differences between fossils and
787 phylogenies may not be entirely explained by different speciation modes and are rather
788 attributable to potential biases in the data/methods.

789 In previous LDG studies, difficulties to recover diversity-loss scenarios could be
790 attributed to the use of SSE models assuming that diversification parameters remain
791 constant over time (Pyron and Wiens 2013; Pyron 2014; Rolland et al. 2015; Pulido-

792 Santacruz and Weir 2016; Siqueira et al. 2016). Time-constant models are inadequate for
793 testing complex scenarios where the processes underlying the LDG varied across
794 latitudes and time. Moreover, the power of time-constant models for detecting negative
795 diversification rates is questionable, since inferring negative diversification for the
796 entire history of lineages conflicts with the fact that these groups are still extant. Testing
797 the hypothesis of diversity declines thus requires the implementation of time-variable
798 models (Morlon et al. 2011; Freyman and Hoehna 2018). When applied to the study of
799 diversity patterns, time-variable SSE models have revealed extinction signatures in
800 tropical clades (Spriggs et al. 2015). The incorporation of time-shifts into BiSSE
801 improves but not completely reconciles paleontological and phylogenetic evidence in
802 our study. These artifacts highlight the importance of combining fossils and phylogenies
803 in macroevolutionary inferences (Fritz et al. 2013). The fossil record remains
804 incomplete, but it provides the only direct evidence of the past diversity, and thus is
805 fundamental in the study of extinction scenarios.

806 **Conclusion**

807 Speciation, extinction and dispersal shape the LDG but the contribution of these
808 processes remains a debated topic in evolutionary ecology. Our results indicate these
809 processes operated at different rates over time and space as climate changed. The
810 current LDG of turtles and crocodylians can be explained by ancient high-latitude
811 tropical diversity loss and range contractions as a consequence of the retraction of the
812 tropical biome due to climate cooling. During greenhouse periods, equivalent
813 diversification rates across latitudes prevailed, explaining the formation of a flattened
814 LDG. Changes in global diversification and dispersal dynamics imposed by large-scale
815 climatic transitions could represent a mechanism that shapes the LDG. This 'asymmetric
816 gradient of extinction and dispersal' hypothesis might account for the LDG of tropical-

817 adapted groups that were once diverse at high latitudes, but might not be fully
818 applicable to all organisms currently displaying a LDG, as shown here for lepidosaurs.

819

820 **Conflict of interests**

821 The authors of this manuscript declare that they have no financial conflict of interest
822 with the content of this article.

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- 1136

1137 **Table 1. Predictions of the most common LDG hypotheses, including the *Asymmetric gradient of extinction and dispersal (AGED)* proposed**
 1138 **here.** Main evolutionary hypotheses can be classified according to three criteria: **(1)** the mechanisms behind regional differences in species richness,
 1139 including explanations based on evolutionary time (t), on dispersal (d), and on diversification (the composite value $r = \lambda - \mu$). Explanations based
 1140 on evolutionary time assume most groups originated in the tropics and had less time to diversify in the temperate regions (Stephens and Wiens
 1141 2003). Hypotheses focusing on the role of geographic movements (d), include the Tropical niche conservatism model assuming that most groups
 1142 originated in the tropics and the LDG results from limited dispersal to the temperate regions (Farrell et al. 1992; Wiens and Donoghue 2004). The
 1143 “*Into the tropics*” model assumes instead the LDG results from dispersals towards the equator (Condamine et al. 2012). Hypotheses that emphasize
 1144 the LDG is generated by regional differences in net diversification rates, being higher in the tropics (Ricklefs 2006; Wiens 2007) assume the
 1145 outstanding tropical diversity is the outcome of higher rates of speciation in the tropics than in the extra-tropical regions ($\lambda_t > \lambda_e$) under the “*cradle*
 1146 *of diversity*”, and/or result from lower rates of extinction ($\mu_t < \mu_e$) under the “*museum of diversity*” (Stebbins 1974). The LDG could also results from
 1147 higher turnover rates (*i.e.* higher λ and μ) in the Holarctic (Weir and Schluter 2007). Diversification and dispersal hypotheses are not mutually
 1148 exclusive. In the “*out of the tropics*” model the tropics are regarded as both cradle and museum, with lineages preferentially originating in the tropics
 1149 and expanding into high latitudes (Jablonski et al. 2006; Donoghue 2008). Hypotheses could also be classified according to **(2)** the rate at which
 1150 processes acted through time; most studies assumed evolutionary processes acted constantly. In the AGED model, which extends the Tropical niche
 1151 conservatism hypothesis (Wiens and Donoghue 2004), diversification/dispersal parameters vary for each temporal interval (the transition from
 1152 icehouse to greenhouse, and *vice versa*). **(3)** Hypotheses can be classified according to the origin of tropical diversity: “*Lower Holarctic species*
 1153 *accumulation*” hypotheses assume the equator is the source of world diversity and species accumulated at slower rates on higher latitudes.
 1154 Conversely, “*Holarctic diversity loss*” hypotheses assume the Holarctic was also a source of diversity that was lost during evolutionary history.
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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)	<i>Time for speciation</i> (Stephens and Wiens 2003)	<i>Cradle of diversity</i> (Stebbins 1974)	<i>Museum of diversity</i> (Stebbins 1974)	<i>Holarctic turnover</i> (Weir and Schluter 2007)	<i>Into the tropics</i> (Condamine et al. 2012)	<i>Tropical niche conservatism</i> (Wiens and Donoghue 2004)	<i>Out of the tropics</i> (Jablonski et al. 2006; Donoghue 2008)	<i>Asymmetric gradient of extinction and dispersal</i> (this study)	
Predictions	$t_{trop} > t_{temp}$ ($\Gamma_{trop} = \Gamma_{temp}$) ($d_{trtp} = d_{tpr}$)	$r_e > r_h$ ($\lambda_e > \lambda_h$) $d_{eh} = d_{he}$	$r_e > r_h$ ($\mu_e < \mu_h$) $d_{eh} = d_{he}$	$r_h = 0$ ($\mu_h = \lambda_h$) $d_{eh} = d_{he}$	$r_e = r_h$ $d_{eh} < d_{he}$	$r_e = r_h$ $d_{eh} > d_{he}$	$r_e > r_h$ ($\lambda_e > \lambda_h$) ($\mu_e < \mu_h$) $d_{eh} > d_{he}$	Ice-greenhouse transition	$r_e = r_h$ ($\mu_h < \lambda_h$; $r_h > 0$) $d_{eh} > d_{he}$
							Green-icehouse transition	$r_e > r_h$ ($\mu_h > \lambda_h$; $r_h < 0$) $d_{eh} < d_{he}$	

1156 Abbreviations: λ = speciation, μ = extinction, d = dispersal, t = time, e = equatorial, h = Holarctic, trp = Tropical biome, $temp$ = Temperate biome.

1157 **Table 2. Posterior (median) estimates of the preservation rate and heterogeneity parameter.** Preservation rate is the expected number of
 1158 occurrences per lineage per Myr, and the heterogeneity parameter is the shape parameter of the Gamma distribution, as estimated under the
 1159 BDMCMC model. Lower and upper bounds of the 95% credibility intervals are provided in parentheses.
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Clade	Preservation rate	Heterogeneity parameter	Clade age (Ma)
All crocodiles	1.2123 (1.0392-1.3431)	0.7566 (0.5207-0.89)	144.61 (140.99-152.14)
Holarctic crocodiles	1.1763 (1.0745-1.2881)	0.4439 (0.3653-0.5979)	145.81 (140.17-160.34)
Equatorial crocodiles	0.9774 (0.8264-1.1529)	0.7474 (0.5425-0.9496)	128.36 (125.03-129.43)
All turtles	0.7953 (0.754-0.8441)	0.6243 (0.5834-0.6692)	256.54 (248.8-275.06)
Holarctic turtles	0.8601 (0.7139-0.929)	0.6407 (0.5828-0.6996)	256.78 (250.68-273.94)
Equatorial turtles	0.897 (0.6289-1.1096)	0.3941 (0.176-0.4903)	145.2 (140.22-155.92)
All lepidosaurs	1.3108 (1.0566-1.5153)	0.6561 (0.6022-0.7169)	235.08 (228.69-247.45)
Holarctic lepidosaurs	1.5333 (1.116-1.6753)	0.6498 (0.6065-0.6973)	235.79 (228.05-249.92)
Equatorial lepidosaurs	0.3132 (0.2378-0.4074)	0.6934 (0.4226-1.037)	178.46 (173.73-182.08)

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