

# *Dinosaurs in decline tens of millions of years before their final extinction*

Article

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6 **Dinosaurs in decline tens of millions of years**  
7 **before their final extinction**

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9 Short title: Long-term decline of dinosaurs

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20

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22 methods

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31 **Abstract**

32 **Whether dinosaurs were in a long-term decline, or whether they were**  
33 **reigning strong right up to their final disappearance at the Cretaceous-**  
34 **Paleogene (K-Pg) mass extinction event 66 million years ago (Ma), has**  
35 **been debated for decades with no clear resolution. The dispute has**  
36 **continued unresolved because of a lack of statistical rigor and appropriate**  
37 **evolutionary framework. Here, for the first time, we apply a Bayesian**  
38 **phylogenetic approach to model the evolutionary dynamics of speciation**  
39 **and extinction through time in Mesozoic dinosaurs, properly taking**  
40 **account of previously ignored statistical violations. We find overwhelming**  
41 **support for a long-term decline across all dinosaurs and within all three**  
42 **dinosaurian subclades, Ornithischia, Sauropodomorpha and Theropoda,**  
43 **where speciation rate slowed down through time and was ultimately**  
44 **exceeded by extinction rate tens of millions of years before the K-Pg**  
45 **boundary. The only exceptions to this general pattern are the**  
46 **morphologically specialized herbivores, the Hadrosauriformes and**  
47 **Ceratopsidae, which show rapid proliferations throughout the Late**  
48 **Cretaceous instead. Our results highlight that, despite some heterogeneity**  
49 **in speciation dynamics, dinosaurs showed a marked reduction in their**  
50 **ability to replace extinct species with new ones, making them vulnerable to**  
51 **extinction and unable to respond quickly to, and recover from, the final**  
52 **catastrophic event.**

53

54 **Significance Statement**

55 Whether dinosaurs were in decline or not before their final extinction 66 million  
56 years ago has been debated for decades with no clear resolution. This dispute  
57 has not been resolved because of inappropriate data and methods. Here, for the  
58 first time, we apply a statistical approach that models changes in speciation and  
59 extinction through time. We find overwhelming support for a long-term decline  
60 across all dinosaurs and within all three major dinosaur groups. Our results  
61 highlight that dinosaurs showed a marked reduction in their ability to replace  
62 extinct species with new ones, making them vulnerable to extinction and unable  
63 to respond quickly to, and recover from, the final catastrophic event, 66 Myr ago.

64 \body

## 65 **Introduction**

66 Non-avian dinosaurs met their demise suddenly, coincident with the Chicxulub  
67 impact in Mexico around 66 Ma (14). However, whether or not there was any  
68 long-term trend towards declining diversity leading to the K-Pg boundary has  
69 been controversial and debated for decades (1-13). This longstanding dispute  
70 has been prolonged partly because of differences in fossil datasets from different  
71 parts of the world and difficulties in rock dating, but most importantly from  
72 methodological weaknesses – previous attempts have been non-phylogenetic  
73 and analyses were conducted on simple time-binned tabulated data resulting in a  
74 lack of statistical rigor (phylogenetic and temporal non-independence have not  
75 been considered) and did not truly investigate evolutionary dynamics such as  
76 speciation and extinction rates. In fact, patterns of speciation and extinction in  
77 dinosaurs have gone largely unstudied (but see (8)). Here, we study speciation  
78 dynamics (relationship between speciation and extinction rates) using an  
79 exclusively phylogenetic approach in a Bayesian framework.

80 If speciation and extinction rate were constant (but speciation higher), we  
81 would expect to see a linear increase through time in the logarithm of the  
82 number of speciation events along each path of a phylogenetic tree (linear; Fig.  
83 1A; see Methods). If speciation rate decreased through time, but remained above  
84 extinction rate, then we would expect a curvilinear relationship (Fig. 1B, C). Such  
85 a relationship would reach an asymptote (speciation = extinction; Fig. 1B) and  
86 eventually turn down as extinction rate surpasses speciation during the  
87 evolutionary history of the clade (Fig. 1C). The latter would correspond to a long-  
88 term pre-K-Pg demise in the case of dinosaurs. The distinction between such  
89 evolutionary dynamics can only be made using phylogenies with taxa sampled  
90 through time.

91

## 92 **Results and discussion**

93 Using a phylogenetic generalized linear mixed model in a Bayesian framework  
94 (15) and three recent large comprehensive dinosaur phylogenies comprising  
95 respectively 420 taxa (8) and 614 taxa (two trees (16)), we found that the data  
96 are significantly better explained by a model in which extinction rate exceeds

97 speciation rate from ~24 million years before the K-Pg boundary than the  
98 simpler alternative model (Fig. 2A; difference in DIC [ $\Delta$ DIC] between linear and  
99 quadratic models > 11; Table S1). Our findings are qualitatively identical across  
100 all three trees and we report on results from one of the 614-taxon trees (16).

101         Since non-homogeneity in evolutionary rates is widespread and common  
102 in nature (17-19) and dinosaurs are diverse – from the bipedal, carnivorous  
103 theropods to the quadrupedal, megaherbivorous sauropods – we might expect to  
104 find different speciation dynamics in the different dinosaurian subclades. When,  
105 model parameters were estimated separately for each of the three main  
106 subclades, Ornithischia, Sauropodomorpha and Theropoda, the same general  
107 pattern as in the total Dinosauria model was recovered, but with extinction rates  
108 exceeding speciation rates earlier at 48-53 Myr before the K-Pg boundary (Fig.  
109 2B;  $\Delta$ DIC > 12; Table S1). Ornithischia here refers to non-hadrosauriform, non-  
110 ceratopsid ornithischians, as the two Cretaceous subclades, Hadrosauriformes  
111 and Ceratopsidae, show speciation patterns distinct from other ornithischians;  
112 Lloyd et al. (8) also identified significant diversification shifts at the base of these  
113 and comparable clades, i.e., Euhadrosauria (here Hadrosauriformes, SI) and  
114 Ceratopsidae. In line with this, these two subclades show no signs of speciation  
115 slowdowns or downturns ( $\Delta$ DIC between linear and quadratic models > 5 in  
116 favour of the linear model; Table S1) (inset Figs 2B, 3). Thus the difference in the  
117 timing of the switch from slowdown to downturn in the Dinosauria model and  
118 for the three major clades is due to the non-homogeneity in speciation processes  
119 across dinosaurian groups. However, these two subclades combined only  
120 represent 14% of dinosaur species, and over time, dinosaurs overwhelmingly  
121 experienced a reduction in their capacity to replace extinct species with new  
122 ones – net speciation per Myr at the time dinosaurs went extinct (66 Ma) were  
123 significantly below zero (speciation rate < extinction rate; Fig. 3B) in the three  
124 major clades (Table S12) – and Hadrosauriformes and Ceratopsidae are the  
125 exceptions.

126         The most prominent downturn is seen in the sauropodomorphs, where  
127 speciation increases rapidly through the Triassic and Early Jurassic (an average  
128 of 0.137 speciation events for every Myr) till ~195 Ma when speciation rate  
129 starts to slow down, and extinction rate surpasses speciation rate at ~114 Ma

130 (Figs 2B, 3). Early sauropodomorph lineages are numerous but not long-lasting,  
131 and taxa that originated earlier in geological time are successively replaced by  
132 younger ones. The near extinction of the diplodocoids at the end of the Jurassic,  
133 145 Ma, did not affect high speciation rates (Fig 3), and sauropodomorphs only  
134 begin their decline approximately 30 Myr into the Early Cretaceous (Fig 3). The  
135 subsequent originations of titanosaurian taxa were not nearly enough to  
136 compensate for the continuous loss of sauropods throughout the remainder of  
137 the Cretaceous.

138         Speciation in theropods follows a slower increase ( $\sim 0.07$  speciation  
139 events for every Myr) with an early onset of speciation slowdown from the Late  
140 Triassic  $\sim 215$  Ma to the Early Cretaceous  $\sim 120$  Ma when extinction rate exceeds  
141 speciation rate (Figs 2B, 3). Although Theropoda contains one of the most  
142 morphologically diverse dinosaurian clades, the coelurosaurs, which includes the  
143 giant carnivorous tyrannosaurs, parrot-like oviraptorosaurs, large pot-bellied  
144 therizinosaurs, ostrich-like ornithomimosaur, small sickle-clawed  
145 dromaeosaurs, and birds, most of which are Cretaceous in age, they originated in  
146 the Early to Middle Jurassic (Fig. 3), much earlier than expected from apparent  
147 fossil occurrences (8). Clades appearing even earlier, e.g. ceratosaurs,  
148 megalosauroids and allosauroids, also persist into the Late Cretaceous, all of  
149 which might suggest that the theropod speciation pattern would be a classic  
150 'early burst' or adaptive radiation type speciation (20) with long protracted  
151 branches (8), which corresponds to a speciation slowdown model. While our  
152 results do show an initial burst of speciation events and a gradual and prolonged  
153 slowdown, consistent with an early burst model, the fact that extinction rate  
154 surpasses speciation rate highlights a more complex process in theropods (Figs  
155 2B, 3).

156         Since birds underwent a radiation in the Early Cretaceous after their  
157 appearance in the Middle to Late Jurassic, one might expect that their pattern of  
158 speciation would be distinct from that of non-avian theropods. However, when  
159 we allow separate coefficients (intercept, slope and quadratic terms) in our  
160 model to be estimated for birds and non-avian theropods, the resulting  
161 regression parameters were not significant: in other words, the speciation  
162 dynamics in Mesozoic birds are not distinct from those of non-avian theropods

163 (Tables S1-S10). This is in line with recent findings of a high, sustained rate of  
164 change, from the Late Triassic to Early Cretaceous in the entire theropod lineage  
165 leading to *Archaeopteryx*, and among the earliest birds (21, 22).

166 Ornithischians show a similar increase to theropods (~0.06 speciation  
167 events for every Myr) to ~192 Ma, followed by a slowdown to ~114 Ma at which  
168 point extinction rate exceeds speciation rate (Figs 2B, 3). Key morpho-functional  
169 features in oral food processing distinguish hadrosauriforms and ceratopsids  
170 from other ornithischians, permitting them to exploit major new food sources  
171 (23, 24). Whether these herbivores were exploiting the new, small fast-growing  
172 herbaceous angiosperms that became common and widespread as early as the  
173 Aptian-Albian (125-109 Ma) of the Early Cretaceous (25) is much debated. The  
174 powerful jaws and massive dental batteries of these herbivores might have been  
175 adapted to other, tougher non-angiosperm plant food, and they benefited from a  
176 new adaptive complex in food processing.

177 Our results showing high levels of speciation in hadrosauriforms and  
178 ceratopsids, while consistent with previous findings (8), seem to contradict more  
179 recent work that suggests these groups underwent a decline in morphological  
180 diversity during the last two stages of the Cretaceous of North America (13, 26).  
181 These dinosaur species are morphologically and ecologically (at least at the  
182 family level) conserved (27), with most of the derived characteristics  
183 concentrated in their crania (24). Speciation can be high in these groups in spite  
184 of the potentially low morphological diversity, because Cretaceous dinosaurs  
185 exhibited increased provincialism (28) (speciation arising from geographic  
186 isolation rather than sympatric niche partitioning), increased alpha diversity  
187 (many more species with subtly varying skulls, but identical postcrania, sharing  
188 the herbivorous ecospace in single localities), and changing taxonomic  
189 composition of stable ecological community structures (ecological niches remain  
190 constant but taxa filling those niches changed through time (27, 29)).

191 An ecological limit on speciation, or the filling of available niches (30, 31)  
192 is commonly invoked to explain speciation slowdowns. Members of the same  
193 clade are more likely to compete for similar if not the same ecological niche or  
194 portions of ecospace (32, 33), and the more numerous the number of  
195 contemporary lineages, the fewer the number of available niches. We tested such



196 an effect by including a measure of intra-clade niche competition – cladewise  
197 lineage diversity, or the number of contemporary branches (including internal  
198 branches) for each taxon - in the model (SI). However, we find that cladewise  
199 lineage diversity is not significantly associated with speciation, nor does it  
200 explain the observed downturn; physical restrictions such as geography or range  
201 sizes could be more important.

202 We can indirectly assess the influence of geography, such as segregation  
203 by geographic barriers (30), using Mesozoic eustatic sea level reconstructions  
204 (34) as an additional covariate in our models. Although various hypotheses have  
205 been proposed regarding the influence of sea level on biodiversity in dinosaurs  
206 (see (35)), the most compelling suggests that increasing sea level results in  
207 fragmentation of large landmasses and can alter geographical distributions of  
208 habitats. In turn, this can lead to geographical segregation, reproductive isolation  
209 and ultimately speciation (30). Our results, for the first time, support this  
210 hypothesis – we find a significant positive effect of sea level on speciation ( $\Delta$ DIC  
211 [5-Group quadratic – 5-Group + sea level models] > 16; pMCMC < 0.001; Tables  
212 S1-10) – though the effect is small; for every meter increase in sea level,  
213 speciation events increased by 0.2-0.25%. Horner et al. (29) observed that the  
214 emergence of transitional morphotypes coincides with marine transgressions in  
215 Late Cretaceous rocks of western North America, consistent with our finding that  
216 rising sea levels induce speciation. Importantly, the inclusion of sea level in any  
217 of our models does not diminish the temporal decline in species proliferation,  
218 despite the substantial rise of sea levels worldwide by some 150-200 m  
219 throughout the Cretaceous (Tables S2-10).

220 While we cannot positively identify a causal mechanism for the speciation  
221 downturn in dinosaurs, there are a multitude of possible global phenomena that  
222 occurred during the Cretaceous Period – e.g., the continued breakup of the  
223 supercontinents Laurasia and Gondwana (limiting free movement and eventual  
224 para- or peripatric speciation), intense prolonged volcanism (36), climate change  
225 (37-39), fluctuations in sea levels (34, 40), and ecological interaction with  
226 rapidly expanding clades (41). In order to accurately identify causal mechanisms  
227 of Mesozoic dinosaurian demise, we recommend that future studies focus on a  
228 longer time period than just the last 10-20 Myr of the Cretaceous (4, 13, 42, 43).

229 In addition, our results highlight the importance of considering the expected  
230 increase in species number as clades expand and accounting for shared ancestry  
231 using phylogenetic approaches.

232 Our study represents the first explicitly phylogenetic statistical treatment  
233 of speciation dynamics in dinosaurs. Unlike previous non-phylogenetic attempts  
234 to study changes in dinosaur taxic diversity across geological time bins (8-10, 13,  
235 35, 44, 45), our method is robust to sampling and other potentially confounding  
236 factors (Tables S1-10; SI), and can statistically detect decreases in net speciation,  
237 which is difficult if not impossible to establish using conventional methods.  
238 Further, by accounting for the effects of shared ancestry, we provide a more  
239 accurate picture of dinosaurian speciation dynamics than the simple summing of  
240 species records through time.

241 Our results demonstrate that dinosaurs were in decline for a much longer  
242 period of time than previously thought - extinction rate surpassed speciation  
243 rate at least 40 Myr before their final extinction. This prolonged demise leaves  
244 plenty of time for other animal groups to radiate and flourish as more and more  
245 ecological niches open up, most prominently the pre-K-Pg expansion of crown  
246 mammals (46). While Mesozoic dinosaurs undoubtedly dominated the terrestrial  
247 megafauna till the end of the Cretaceous, they did see a reduction in their  
248 capacity to replace extinct species with new ones, making them more susceptible  
249 to sudden and catastrophic environmental changes like those associated with the  
250 asteroid impact.

251

252

## 253 **Materials and Methods**

254 **Phylogeny.** We used three recent large comprehensive dinosaur phylogenies  
255 comprising respectively 420 taxa (8) and 614 taxa (two trees (16)). Trees were  
256 scaled according to the midpoint time of each terminal stratigraphic range (16)  
257 using the 'equal' scaling method (47) implemented in the paleotree R package  
258 (48). Additionally we scaled the trees using two alternative sets of terminal  
259 dates, the first appearance dates (FAD) and last appearance dates (LAD) to  
260 assess the effects of tree scaling on model results.

261

262 **Generalized linear mixed models.** We fitted generalized linear mixed models  
263 (GLMM) in a Bayesian framework through Markov-chain Monte Carlo (MCMC)  
264 using the MCMCglmm R package (15). The total number of speciation events  
265 (node count) along the phylogenetic path for each taxon was modeled as the  
266 response variable, with the corresponding path length (time elapsed from root to  
267 tip) as the main effects predictor variable - this model formulation forms the null  
268 linear model (Fig. 1A). We also fitted a speciation slowdown model, with the  
269 addition of a quadratic term ( $\text{time}^2$ ) to the main effect. Incidentally, a quadratic  
270 model can also explain the opposite case, where speciation rate increases while  
271 extinction rate remains constant. We include phylogeny as a random effect in  
272 order to account for shared ancestry.

273         Separate intercepts, slopes and quadratic terms were estimated for the  
274 three major dinosaurian clades (Sauropodomorpha, Theropoda, Ornithischia) (3-  
275 Group model). Lloyd et al. (8) previously identified two significant diversification  
276 shifts in the Cretaceous ornithischians, at the base of the clades Euhadrosauria  
277 (here Hadrosauriformes) and Ceratopsidae, so we estimated separate model  
278 coefficients (intercepts and slopes) for these groups from other ornithischians  
279 (5-Group model).

280         Chains were run for  $10^6$  iterations, sampling at every 1000th iteration.  
281 We fitted a GLMM with a Poisson link to appropriately account for error  
282 structure in count data – although we discuss predicted curve shapes in log  
283 space, we did not log-transform node count for model fitting (49). MCMCglmm  
284 automatically accounts for overdispersion in the count data distribution. We  
285 used default priors ( $\mu=0$ ,  $V=I \times 10^{10}$  where  $I$  is an identity matrix) for the fixed  
286 effects and parameter expanded priors ( $V=1$ ,  $\nu=1$ ,  $\alpha.\mu=0$ ,  $\alpha.V=25^2$ ) for  
287 the phylogenetic random effects (15).

288         Model fit was assessed using Deviance Information Criterion (DIC) and  
289 inspection of model parameter significance (using p-MCMC: twice the proportion  
290 of the MCMC estimates that crosses zero). We determined the best fit model as  
291 the model with the lowest DIC score, and where the difference in DIC score  
292 compared with that of a base model ( $\Delta\text{DIC}$ ) is greater than 4. In the case where  
293 multiple models had non-significant differences in model fit (i.e.,  $\Delta\text{DIC} < 4$ ), we

294 inspected the significance of model parameters and selected the model with  
295 significant covariates (i.e., non-significant covariates were removed).

296

297 **Extrinsic factors.** As the fossil record has long been known to be incomplete  
298 (50, 51) – it is possible that the observed slowdown and downturn are by-  
299 products of undersampling. This would imply that there is a systematic  
300 downwards bias in the phylogeny towards recent times, which would be counter  
301 to the usual expectation for poor sampling (50, 51). Here, in order to test the  
302 effect of such biases, we fitted additional models with appropriate covariates,  
303 including stage-level formation counts (because formation count is widely  
304 reported to be associated with sampling bias) (9, 10, 12, 35, 44, 52, 53), taxon-  
305 specific formation counts (the number of formations in which a taxon is found),  
306 taxon-specific collection count (the number of fossil collections in which a taxon  
307 is represented), cladewise valid taxa counts (the known under-representation in  
308 the phylogeny) (54), fossil quality scores (state of preservation) (55) and body  
309 size (smaller taxa are less likely to be preserved) (56).

310 As an indirect measure of the influence of geography on speciation  
311 dynamics, such as segregation by geographic barriers (30), we used Mesozoic  
312 eustatic sea level reconstructions (34) as an additional covariate in our models  
313 (mean sea level value along each terminal branch). We also tested the ecological  
314 limit on clade diversification, or the possible effects of niche saturation, by  
315 adding a measure of intra-clade diversity taken as the number of contemporary  
316 branches (including internal branches) for each taxon (the number of tips in  
317 time-sliced trees (48)).

318

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326

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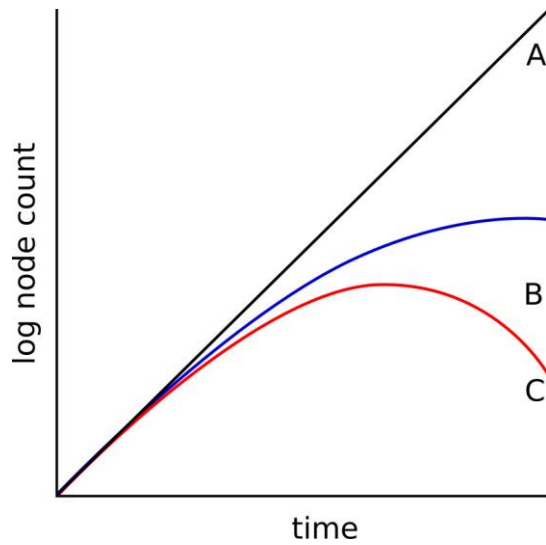
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522 **Figures**

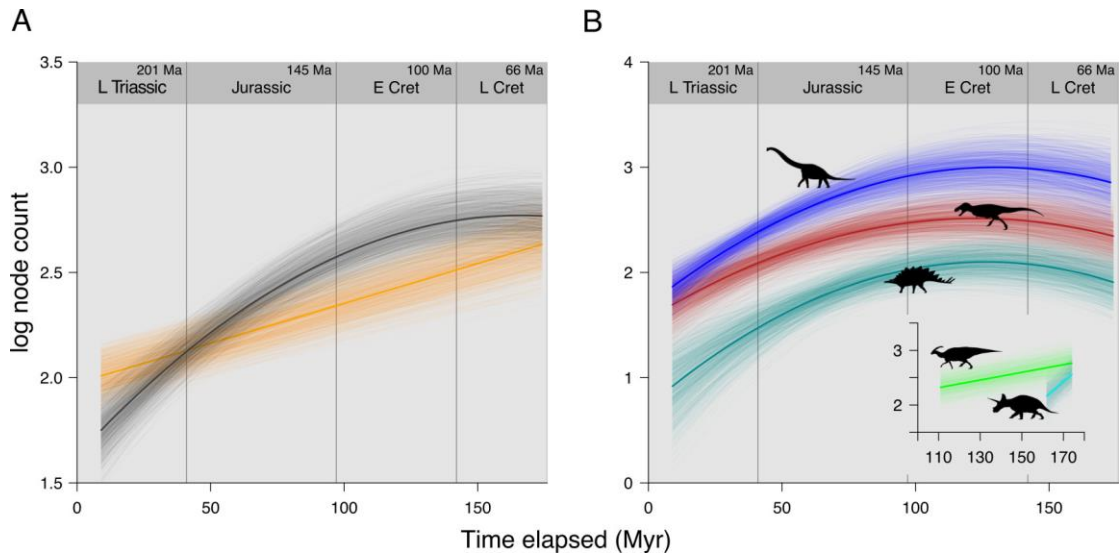


523

524 **Fig. 1. Theoretical models of speciation through time**

525 If speciation and extinction rate were constant through time (but speciation  
526 higher) in dinosaurian history, we would expect to see a linear increase through  
527 time in the logarithm of the number of speciation events along each path of a  
528 phylogenetic tree (A). If speciation rate decreased through time, but remained  
529 above extinction rate, then we would expect a curvilinear relationship (B, C).  
530 Such a relationship would reach an asymptote (speciation = extinction; B) and  
531 eventually turn down as extinction rate surpassed speciation during the  
532 evolutionary history of the clade (C). The latter would correspond to a long-term  
533 pre-K-Pg demise in the case of dinosaurs.

534



535

536

**Fig. 2. Model predictions of speciation through time in Mesozoic dinosaurs**

537

Compared with the linear model (orange), the quadratic model displaying a

538

speciation slowdown substantially improves model fit ( $\Delta \text{DIC} > 4$ ) (A). This

539

pattern holds true in the three major clades, Ornithischia (green),

540

Sauropodomorpha (blue) and Theropoda (red), and further improves model fit

541

(B). Model fit significantly improves when separate model parameters are

542

estimated for the ornithischian subclades Hadrosauriformes (light green) and

543

Ceratopsidae (light blue) from other ornithischians (inset B), but the slowdown

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and downturn are not observed for the two Cretaceous ornithischian subclades.

545

Posterior predictions (transparent lines) show the uncertainties in the model.

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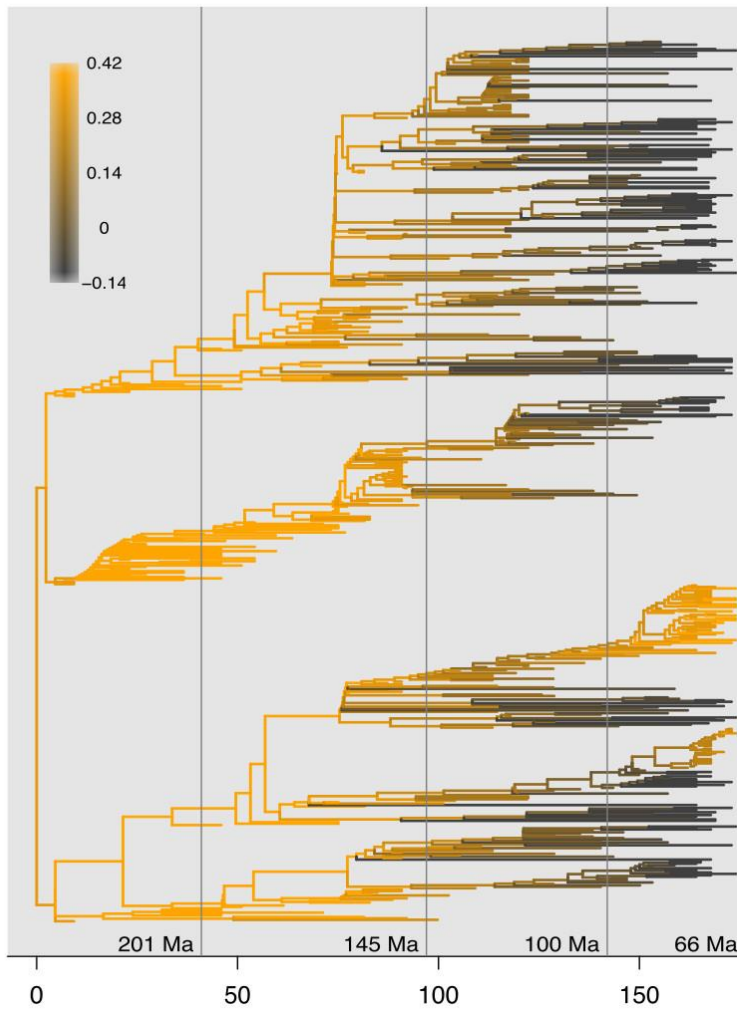
Mean posterior values are in bold. Vertical lines indicate major stratigraphic

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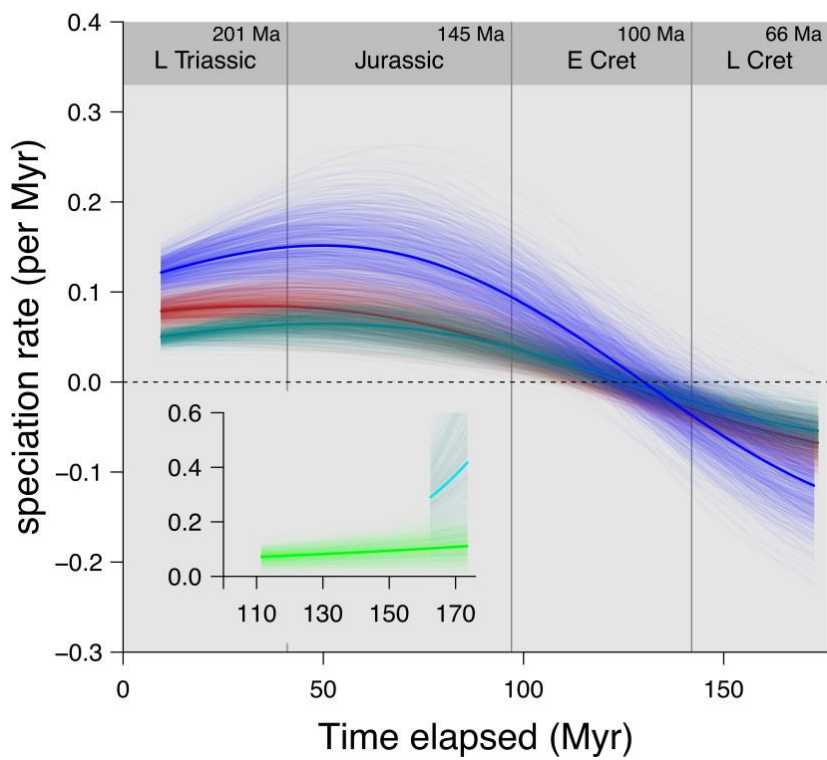
boundaries (with their ages in Ma). Silhouettes from phylopic.org.

548

A



B



550 **speciation per Myr through time in Mesozoic dinosaurs**

551 Net speciation per Myr can be calculated from model predictions (Fig. 2B) as  
552 differences between intervals, here per 1 Myr. Each branch of a dinosaurian  
553 phylogeny was assigned a net speciation per Myr value based on its temporal  
554 location and group membership, and plotted on a colour gradient (A). Earlier  
555 branches have higher net speciation per Myr (orange) while later branches have  
556 lower net speciation per Myr (dark grey), except in Hadrosauriformes and  
557 Ceratopsidae, in which net speciation per Myr increase with time. The three  
558 major dinosaur groups, Sauropodomorpha (blue), Theropods (red), and non-  
559 hadrosauriform, non-ceratopsid Ornithischia (green), show an early onset of  
560 speciation slowdown (B), until the middle of the Early Cretaceous, when  
561 speciation rates are exceeded by extinction rate (net speciation per Myr fall  
562 below zero [dashed horizontal line]). Values above zero indicate increases in  
563 species counts, while those below zero indicate decreases in species counts.  
564 Hadrosauriforms (inset, light green) show a slow increase in net speciation per  
565 Myr through time, while ceratopsians (inset, light blue) show a highly variable,  
566 but on average, a rapid increase towards the end of the Cretaceous. Posterior  
567 predictions (transparent lines) show the uncertainties in the model. Mean  
568 posterior values are in bold. Vertical lines indicate major stratigraphic  
569 boundaries (with their ages in Ma) as in Fig. 2. Silhouettes from phylopic.org.  
570