

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

Article

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1 Classification: Biological Sciences (Evolution)

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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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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 [Δ 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; Δ 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 (Δ 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 (~ 0.07 speciation
139 events for every Myr) with an early onset of speciation slowdown from the Late
140 Triassic ~ 215 Ma to the Early Cretaceous ~ 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 (Δ 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 (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 (ΔDIC) 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

327 **References**

- 328 1. Sloan RE, Rigby JK, Jr., LM VANV, & Gabriel D (1986) Gradual dinosaur
329 extinction and simultaneous ungulate radiation in the hell creek
330 formation. *Science* 232(4750):629-633.
- 331 2. Dodson P (1990) Counting Dinosaurs - How Many Kinds Were There.
332 *Proceedings of the National Academy of Sciences of the United States of*
333 *America* 87(19):7608-7612.
- 334 3. Sarjeant WAS & Currie PJ (2001) The "Great Extinction" that never
335 happened: the demise of the dinosaurs considered. *Canadian Journal of*
336 *Earth Sciences* 38(2):239-247.
- 337 4. Fastovsky DE, *et al.* (2004) Shape of Mesozoic dinosaur richness. *Geology*
338 32(10):877-880.
- 339 5. Sullivan RM (2006) The shape of Mesozoic dinosaur richness: a
340 reassessment. *New Mexico Museum of Natural History and Science Bulletin*
341 35:403-405.
- 342 6. Wang SC & Dodson P (2006) Estimating the diversity of dinosaurs. *Proc*
343 *Natl Acad Sci U S A* 103(37):13601-13605.
- 344 7. Taylor MP (2006) Dinosaur diversity analysed by clade, age, place and
345 year of description. in *Ninth international symposium on Mesozoic*
346 *terrestrial ecosystems and biota*, eds Barrett PM & Evans SE (Cambridge
347 Publications, Manchester, UK), pp 134-138.
- 348 8. Lloyd GT, *et al.* (2008) Dinosaurs and the Cretaceous Terrestrial
349 Revolution. *Proceedings of the Royal Society B-Biological Sciences*
350 275(1650):2483-2490.
- 351 9. Barrett PM, McGowan AJ, & Page V (2009) Dinosaur diversity and the rock
352 record. *Proceedings of the Royal Society B-Biological Sciences*
353 276(1667):2667-2674.
- 354 10. Upchurch P, Mannion PD, Benson RBJ, Butler RJ, & Carrano MT (2011)
355 Geological and anthropogenic controls on the sampling of the terrestrial
356 fossil record: a case study from the Dinosauria. *Geological Society, London,*
357 *Special Publications* 358(1):209-240.
- 358 11. Archibald JD (2012) Dinosaur extinction: Past and present perceptions.
359 *The Complete Dinosaur*, ed Brett-Surman MK, Holtz, T. R., Farlow, J. O.,
360 Walter, B. (Indiana Press, Bloomington), Second Edition Ed, pp 1027-
361 1038.
- 362 12. Lloyd GT (2012) A refined modelling approach to assess the influence of
363 sampling on palaeobiodiversity curves: new support for declining
364 Cretaceous dinosaur richness. *Biology Letters* 8(1):123-126.
- 365 13. Brusatte SL, *et al.* (2015) The extinction of the dinosaurs. *Biological*
366 *Reviews* 90(2):628-642.
- 367 14. Schulte P, *et al.* (2010) The Chicxulub Asteroid Impact and Mass
368 Extinction at the Cretaceous-Paleogene Boundary. *Science*
369 327(5970):1214-1218.
- 370 15. Hadfield JD (2010) MCMC methods for multi-response Generalized Linear
371 Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*
372 33(2):1-22.
- 373 16. Benson RB, *et al.* (2014) Rates of dinosaur body mass evolution indicate
374 170 million years of sustained ecological innovation on the avian stem
375 lineage. *PLoS Biol* 12(5):e1001853.

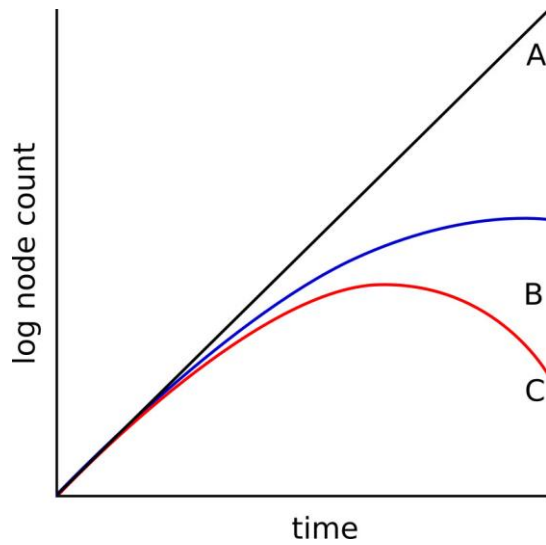
- 376 17. Venditti C, Meade A, & Pagel M (2011) Multiple routes to mammalian
377 diversity. *Nature* 479(7373):393-396.
- 378 18. Jetz W, Thomas GH, Joy JB, Hartmann K, & Mooers AO (2012) The global
379 diversity of birds in space and time. *Nature* 491(7424):444-448.
- 380 19. Rabosky DL, *et al.* (2013) Rates of speciation and morphological evolution
381 are correlated across the largest vertebrate radiation. *Nat Commun* 4.
- 382 20. Schluter D (2000) *The ecology of adaptive radiation* (Oxford University
383 Press, Oxford, UK).
- 384 21. Lee MSY, Cau A, Naish D, & Dyke GJ (2014) Sustained miniaturization and
385 anatomical innovation in the dinosaurian ancestors of birds. *Science*
386 345(6196):562-566.
- 387 22. Brusatte SL, Lloyd GT, Wang SC, & Norell MA (2014) Gradual assembly of
388 avian body plan culminated in rapid rates of evolution across the
389 dinosaur-bird transition. *Current Biology* 24(20):2386-2392.
- 390 23. Norman DB, Witmer LM, & Weishampel DB (2004) Basal Thyreophoran.
391 *The Dinosauria: second edition*, eds Weishampel DB, Dodson P, &
392 Osmolska H (University of California Press), pp 335-342.
- 393 24. Horner JR, Weishampel DB, & Forster CA (2004) Hadrosauridae. *The*
394 *Dinosauria*, eds Weishampel DB, Dodson P, & Osmolska H (University of
395 California Press, Berkeley, USA), Second Edition Ed, pp 438-463.
- 396 25. Jud NA (2015) Fossil evidence for a herbaceous diversification of early
397 eudicot angiosperms during the Early Cretaceous. *Proceedings of the*
398 *Royal Society of London B: Biological Sciences* 282(1814).
- 399 26. Brusatte SL, Butler RJ, Prieto-Marquez A, & Norell MA (2012) Dinosaur
400 morphological diversity and the end-Cretaceous extinction. *Nat Commun*
401 3.
- 402 27. Mallon JC & Anderson JS (2015) Jaw mechanics and evolutionary
403 paleoecology of the megaherbivorous dinosaurs from the Dinosaur Park
404 Formation (upper Campanian) of Alberta, Canada. *Journal of Vertebrate*
405 *Paleontology* 35(2).
- 406 28. Holtz TR, Chapman RE, & Lamanna MC (2004) Mesozoic biogeography of
407 Dinosauria. *The Dinosauria*, eds Weishampel DB, Dodson P, & Osmolska H
408 (University of California Press, Berkeley, USA), Second Edition Ed, pp 627-
409 642.
- 410 29. Horner JR, Varricchio DJ, & Goodwin MB (1992) Marine Transgressions
411 and the Evolution of Cretaceous Dinosaurs. *Nature* 358(6381):59-61.
- 412 30. Moen D & Morlon H (2014) Why does diversification slow down? *Trends*
413 *in Ecology & Evolution* 29(4):190-197.
- 414 31. Rabosky DL (2013) Diversity-dependence, ecological speciation, and the
415 role of competition in macroevolution. *Annu Rev Ecol Evol S* 44:481-502.
- 416 32. Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or*
417 *the Preservation of Favoured Races in the Struggle for Life* (London, UK)
418 First Edition Ed.
- 419 33. Mayr E (1942) *Systematics and the origin of species, from the viewpoint of*
420 *a zoologist* (Harvard University Press).
- 421 34. Haq BU, Hardenbol J, & Vail PR (1987) Chronology of fluctuating sea
422 levels since the Triassic. *Science* 235(4793):1156-1167.
- 423 35. Butler RJ, Benson RBJ, Carrano MT, Mannion PD, & Upchurch P (2011) Sea
424 level, dinosaur diversity and sampling biases: investigating the 'common

- 425 cause' hypothesis in the terrestrial realm. *Proceedings of the Royal Society*
426 *B-Biological Sciences* 278(1709):1165-1170.
- 427 36. Chenet AL, *et al.* (2009) Determination of rapid Deccan eruptions across
428 the Cretaceous-Tertiary boundary using paleomagnetic secular variation:
429 2. Constraints from analysis of eight new sections and synthesis for a
430 3500-m-thick composite section. *J Geophys Res-Sol Ea* 114.
- 431 37. Li LQ & Keller G (1998) Maastrichtian climate, productivity and faunal
432 turnovers in planktic foraminifera in south Atlantic DSDP sites 525A and
433 21. *Mar Micropaleontol* 33(1-2):55-86.
- 434 38. Li LQ & Keller G (1998) Abrupt deep-sea warming at the end of the
435 Cretaceous. *Geology* 26(11):995-998.
- 436 39. Naafs BDA, *et al.* (2016) Gradual and sustained carbon dioxide release
437 during Aptian Oceanic Anoxic Event 1a. *Nature Geosci* 9(2):135-139.
- 438 40. Miller KG, *et al.* (2005) The phanerozoic record of global sea-level change.
439 *Science* 310(5752):1293-1298.
- 440 41. Wilson GP, *et al.* (2012) Adaptive radiation of multituberculate mammals
441 before the extinction of dinosaurs. *Nature* 483(7390):457-460.
- 442 42. Sheehan PM, Fastovsky DE, Barreto C, & Hoffmann RG (2000) Dinosaur
443 abundance was not declining in a " 3 m gap " at the top of the Hell Creek
444 Formation, Montana and North Dakota. *Geology* 28(6):523-526.
- 445 43. Lyson TR, *et al.* (2011) Dinosaur extinction: closing the '3 m gap'. *Biology*
446 *Letters* 7(6):925-928.
- 447 44. Benson RBJ & Mannion PD (2012) Multi-variate models are essential for
448 understanding vertebrate diversification in deep time. *Biology Letters*
449 8(1):127-130.
- 450 45. Benson RBJ, *et al.* (2016) Near-Stasis in the Long-Term Diversification of
451 Mesozoic Tetrapods. *PLoS Biol* 14(1):e1002359.
- 452 46. Close Roger A, Friedman M, Lloyd Graeme T, & Benson Roger BJ (2015)
453 Evidence for a Mid-Jurassic Adaptive Radiation in Mammals. *Current*
454 *Biology*.
- 455 47. Brusatte SL, Benton MJ, Ruta M, & Lloyd GT (2008) Superiority,
456 competition, and opportunism in the evolutionary radiation of dinosaurs.
457 *Science* 321(5895):1485-1488.
- 458 48. Bapst DW (2012) paleotree: an R package for paleontological and
459 phylogenetic analyses of evolution. *Methods in Ecology and Evolution*
460 3(5):803-807.
- 461 49. O'Hara RB & Kotze DJ (2010) Do not log-transform count data. *Methods in*
462 *Ecology and Evolution* 1(2):118-122.
- 463 50. Alroy J (2010) Geographical, Environmental and Intrinsic Biotic Controls
464 on Phanerozoic Marine Diversification. *Palaeontology* 53:1211-1235.
- 465 51. Smith AB & McGowan AJ (2007) The shape of the phanerozoic marine
466 palaeodiversity curve: How much can be predicted from the sedimentary
467 rock record of western Europe? *Palaeontology* 50:765-774.
- 468 52. Peters SE & Foote M (2001) Biodiversity in the Phanerozoic: a
469 reinterpretation. *Paleobiology* 27(4):583-601.
- 470 53. Brocklehurst N, Upchurch P, Mannion PD, & O'Connor J (2012) The
471 Completeness of the Fossil Record of Mesozoic Birds: Implications for
472 Early Avian Evolution. *Plos One* 7(6).

- 473 54. Benton MJ (2008) How to find a dinosaur, and the role of synonymy in
474 biodiversity studies. *Paleobiology* 34(4):516-533.
- 475 55. Benton MJ, Dunhill AM, Lloyd GT, & Marx FG (2011) Assessing the quality
476 of the fossil record: insights from vertebrates. *Geol Soc Spec Publ* 358:63-
477 94.
- 478 56. Cleary TJ, Moon BC, Dunhill AM, & Benton MJ (2015) The Fossil Record of
479 Ichthyosaurs, Completeness Metrics and Sampling Biases. *Palaeontology*
480 58(3):521-536.
- 481 57. Prothero D (1999) Fossil record. *Encyclopedia of paleontology*, ed Singer R
482 (Fitzroy Dearbon Publishers, Chicago, USA).
- 483 58. Raup DM (1991) *Extinction: bad genes or bad luck?* (W. W. Norton, New
484 York).
- 485 59. Raup DM (1972) Taxonomic Diversity during the Phanerozoic. *Science*
486 177(4054):1065-1071.
- 487 60. Ren L, *et al.* (2008) The movements of limb segments and joints during
488 locomotion in African and Asian elephants (vol 211, pg 2735, 2008).
489 *Journal Of Experimental Biology* 211(18):3057--3057.
- 490 61. Benton MJ, Ruta M, Dunhill AM, & Sakamoto M (2013) The first half of
491 tetrapod evolution, sampling proxies, and fossil record quality.
492 *Palaeogeography Palaeoclimatology Palaeoecology* 372:18-41.
- 493 62. Turner AH, Pol D, Clarke JA, Erickson GM, & Norell MA (2007) A basal
494 Dromaeosaurid and size evolution preceding avian flight. *Science*
495 317(5843):1378-1381.
- 496 63. Marsicano CA, Irmis RB, Mancuso AC, Mundil R, & Chemale F (2016) The
497 precise temporal calibration of dinosaur origins. *Proceedings of the*
498 *National Academy of Sciences* 113(3):509-513.
- 499 64. Revell LJ (2012) phytools: an R package for phylogenetic comparative
500 biology (and other things). *Methods in Ecology and Evolution* 3(2):217-
501 223.
- 502 65. Stadler T (2011) Simulating Trees with a Fixed Number of Extant Species.
503 *Systematic Biology* 60(5):676-684.
- 504 66. Mooers A, Gascuel O, Stadler T, Li HY, & Steel M (2012) Branch Lengths on
505 Birth-Death Trees and the Expected Loss of Phylogenetic Diversity.
506 *Systematic Biology* 61(2):195-203.
- 507 67. Pennell MW, Sarver BAJ, & Harmon LJ (2012) Trees of Unusual Size:
508 Biased Inference of Early Bursts from Large Molecular Phylogenies. *Plos*
509 *One* 7(9).
- 510 68. Hartmann K, Wong D, & Stadler T (2010) Sampling Trees from
511 Evolutionary Models. *Systematic Biology* 59(4):465-476.
- 512 69. Mallon JC & Anderson JS (2013) Skull Ecomorphology of
513 Megaherbivorous Dinosaurs from the Dinosaur Park Formation (Upper
514 Campanian) of Alberta, Canada. *Plos One* 8(7).
- 515 70. Mallon JC & Anderson JS (2014) Implications of beak morphology for the
516 evolutionary paleoecology of the megaherbivorous dinosaurs from the
517 Dinosaur Park Formation (upper Campanian) of Alberta, Canada.
518 *Palaeogeography Palaeoclimatology Palaeoecology* 394:29-41.
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522 **Figures**

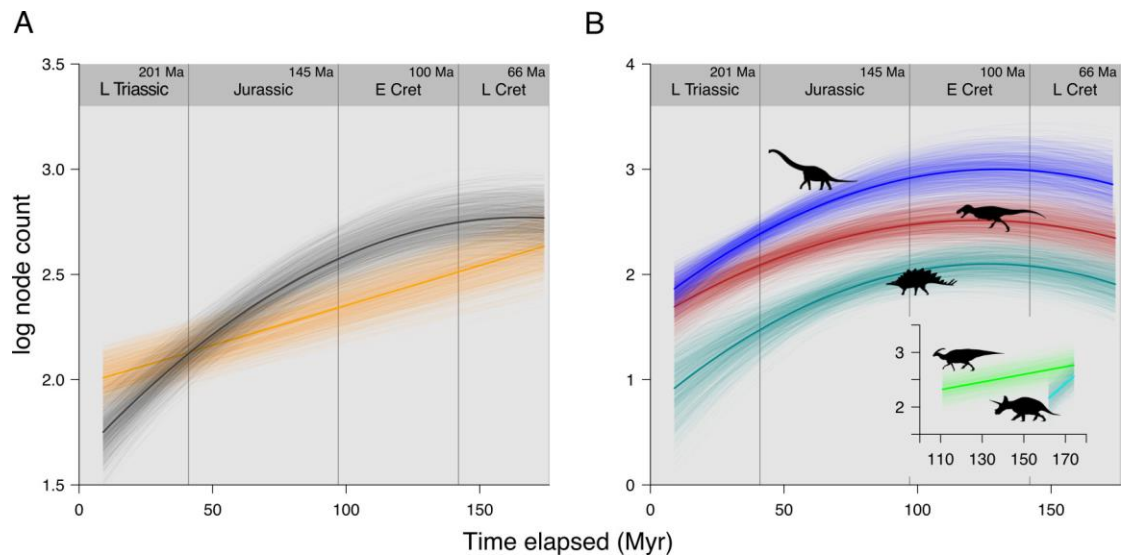


523

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

544

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

545

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

546

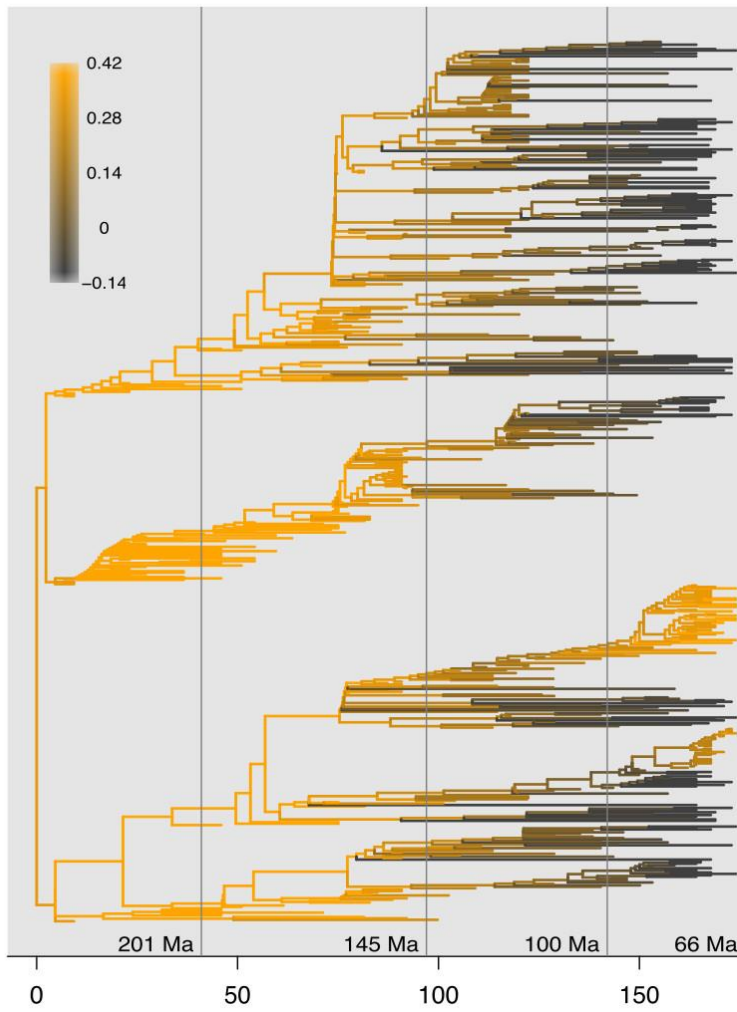
Mean posterior values are in bold. Vertical lines indicate major stratigraphic

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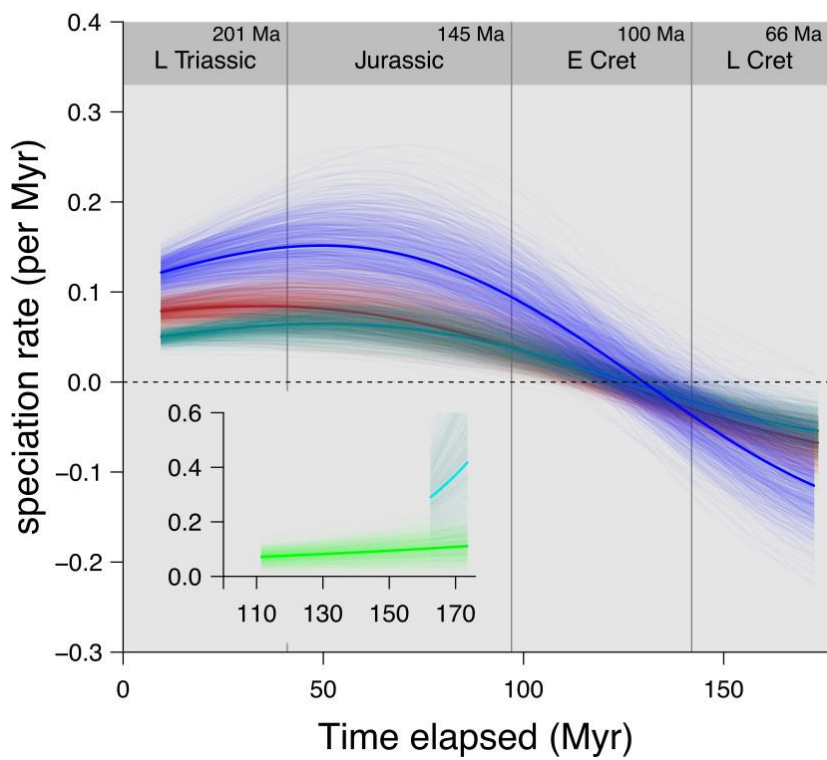
boundaries (with their ages in Ma). Silhouettes from phylopic.org.

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