

1 **Mechanistic phylodynamic models do not provide conclusive evidence that non-**
2 **avian dinosaurs were in decline before their final extinction**

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This peer-reviewed article has been accepted for publication but not yet copyedited or typeset, and so may be subject to change during the production process. The article is considered published and may be cited using its DOI.

10.1017/ext.2024.5

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16 Impact statement

17 Dinosaurs are well known for their abrupt demise at the end of the Cretaceous period,
18 coincident with the Chicxulub asteroid impact at 66 Ma. However, their diversity
19 dynamics over the course of their preceding 180 million year history are less well
20 understood. It is not known, for instance, whether dinosaurs were thriving or already in
21 decline just prior to the impact event. This is in large part due to their highly fragmentary
22 fossil record. Phylogenetic trees depicting evolutionary relationships provide additional
23 information, including capturing a portion of lineage history that is otherwise not
24 observable from fossil occurrence data. Previous analyses based on dinosaur
25 phylogenies have reached conflicting conclusions about the evolutionary trajectory of
26 dinosaurs before their final extinction. Here, we revisit this conflict using a phylodynamic
27 modelling approach, which is more explicit and transparent than previous approaches,
28 especially with respect to the assumptions made about how the dinosaur fossil record
29 has been sampled. Using two alternative models, which differ in how they use
30 information about the sampling process and how they model changes in the number of
31 species through time, we show that based on available phylogenies we cannot currently
32 reach a definitive conclusion about dinosaur diversification during the Cretaceous. More
33 densely-sampled and accurate fossil timetrees, as well as models that capture more
34 information about the quality of the dinosaur fossil record, may help to solve this debate.

35 **Abstract**

36 Phylodynamic models can be used to estimate diversification trajectories from time-
37 calibrated phylogenies. Here we apply two such models to phylogenies of non-avian
38 dinosaurs, a clade whose evolutionary history has been widely debated. While some
39 authors have suggested that the clade experienced a decline in diversity, potentially
40 starting millions of years before the end-Cretaceous mass extinction, others have
41 suggested that the group remained highly diverse right up until the Cretaceous-
42 Paleogene (K-Pg) boundary. Our results show that model assumptions, likely with
43 respect to incomplete sampling, have a large impact on whether dinosaurs appear to
44 have experienced a long-term decline or not. The results are also highly sensitive to the
45 topology and branch lengths of the phylogeny used. Developing comprehensive models
46 of sampling bias, and building larger and more accurate phylogenies, are likely to be
47 necessary steps for us to determine whether dinosaur diversity was or was not in
48 decline prior to the end-Cretaceous mass extinction.

49

50 Introduction

51 Dinosaurs were the dominant land animals of the Mesozoic, renowned for their
52 diversity, disparity, and ecological novelty, but they are now represented by a single
53 surviving subclade, birds (Brusatte et al., 2015; Benson, 2018). The extinction of non-
54 avian dinosaurs at the end of the Cretaceous period (around 66 Ma) is widely accepted
55 to be coincident with, and likely caused by, an asteroid impact (Alvarez et al., 1980;
56 Schulte et al., 2010; Chiarenza et al., 2020; Hull et al., 2020). However, the trajectory of
57 dinosaur diversity throughout the Mesozoic, especially towards the end of the
58 Cretaceous, remains controversial. A wide variety of methods have previously been
59 employed to estimate either the number of dinosaur species or their diversification
60 rates, including interpolation or extrapolation (Fastovsky et al., 2004; Wang and Dodson
61 2006; Lloyd et al., 2008; Brusatte et al., 2015; Close et al., 2018) and modelling (via
62 regression (Barrett et al., 2009; Lloyd, 2011; Sakamoto et al., 2016; Bonsor et al.,
63 2020), species-area relationships (Russell, 1995; Le Loeuff, 2012), or inferring
64 evolutionary and/or sampling rates (Starrfelt and Liow, 2016; Condamine et al., 2021;
65 Černý et al., 2022; Langer and Godoy, 2022)). Several papers have suggested that the
66 group was already in decline prior to the asteroid impact (Han et al., 2022), and had
67 been for the preceding 10 million years (Sloan et al., 1986; Archibald, 2014; Condamine
68 et al., 2021), 24 million years (Sakamoto et al., 2016), or even the whole Cretaceous
69 (Lloyd, 2011). However, others have argued that this was not the case, and that
70 dinosaurs remained highly diverse right up until the latest Cretaceous (Fastovsky et al.,
71 2004; Wang and Dodson, 2006; Brusatte et al., 2015; Starrfelt and Liow, 2016; Bonsor
72 et al., 2020). This debate sits within the context of approximately constant terrestrial

73 tetrapod species richness throughout the Mesozoic (e.g. Benson et al., 2016; Close et
74 al., 2017). Several possible drivers of a Cretaceous dinosaur decline have been put
75 forward, such as environmental change resulting from Deccan Traps volcanism or sea
76 level fluctuations, however, the poor temporal resolution of geological records at this
77 time has hindered efforts to correlate potential causes and effects (Brusatte et al., 2015;
78 Benson, 2018; Chiarenza et al., 2019, 2020). There is evidence of trophic restructuring
79 in the latest Cretaceous, which may have left Maastrichtian food webs more vulnerable
80 to perturbations (Mitchell et al., 2012; García-Girón et al., 2022).

81 Many previous studies have commented on variability in the sampling of the
82 dinosaur fossil record, across space, time and clades (Wang and Dodson, 2006; Barrett
83 et al., 2009; Benton et al., 2011; Upchurch et al., 2011; Benson, 2018; Chiarenza et al.,
84 2019; Cashmore et al., 2020; Dean et al., 2020). This hinders efforts to accurately
85 estimate species richness or diversification over geological time, as any true changes in
86 diversity are likely to be obscured by sampling bias (e.g. Starrfelt and Liow, 2016;
87 Benson et al., 2021). The various methods that have been applied to estimating
88 dinosaur diversity handle this information differently: some simply take the fossil record
89 at face value and assume that any potential sampling biases are negligible, whereas
90 others explicitly model the incompleteness of the fossil record and thereby infer what we
91 do not know from the fossils we have. An example of this latter viewpoint is Chiarenza
92 et al. (2019), who used ecological niche modelling to infer where dinosaurs could have
93 lived during the Late Cretaceous based on their environmental preferences,
94 extrapolating beyond the area represented by known fossil occurrences.

95 The diversification history of a clade can be quantified using raw fossil
96 occurrences (via approaches such as PyRate (Silvestro et al., 2014; Condamine et al.,
97 2021; Černý et al., 2022; Langer and Godoy, 2022)) and phylogenetic trees (e.g. Černý
98 et al., 2022; Langer and Godoy, 2022, Truman et al., 2024). While the fossil record
99 contains key information about the presence of taxa at a specific place and time in the
100 geological past, this information is highly patchy, whereas phylogenies have the
101 advantage of capturing a portion of evolutionary history that is not directly observable
102 (e.g. Lloyd et al., 2008; Starrfelt and Liow, 2016; Benson, 2018). Tree shape, in
103 particular the temporal distribution of node ages and branch lengths, is informative
104 about patterns of diversification, and provides insight into parts of the tree of life which
105 are not currently represented within the known fossil record (Lloyd et al., 2008).

106 A handful of studies have previously used phylogenies to test whether dinosaur
107 diversity was in decline prior to the Cretaceous-Paleogene (K-Pg) mass extinction. One
108 approach is using phylogenetic generalized linear mixed models (GLMMs), which
109 assess the line of best fit between the time elapsed from the root to the tips (the
110 predictor variable) and net speciation (the response variable). The shape and slope of
111 this line can be used to determine whether diversity has remained constant, increased
112 or decreased over time. Sakamoto et al. (2016) applied phylogenetic GLMMs to three
113 dinosaur supertrees and found evidence of a diversity decline, starting at least 24
114 million years prior to the end-Cretaceous mass extinction. However, subsequent
115 discourse (Bonsor et al., 2020; Sakamoto et al., 2021) has raised questions about the
116 "correct" way to apply this method, including how best to interpret mixed results and
117 how sensitive the method is to the shape of the phylogeny. The adequacy of model fit

118 may also be problematic (Hadfield, 2010); in part, this may occur because the method
119 fits a single smoothed curve to the entirety of the clade's evolutionary trajectory, which
120 does not allow for short-term fluctuations in rates to be recovered. Sakamoto et al.
121 (2016) also attempted to account for sampling bias by including geological and
122 sampling proxy data as covariates in their phylogenetic GLMMs, and found that this did
123 not change their overall results. However, this approach does not incorporate the
124 sampling process explicitly or formalise the relationship between diversification and
125 sampling (Bonsor et al., 2020; Warnock et al., 2020). As a result, the effect of
126 incomplete fossil sampling on phylogenetic GLMMs is difficult to assess.

127 To examine the potential impact of modelling assumptions on estimates of
128 diversification from the non-avian dinosaur fossil record, we apply Bayesian
129 phylodynamic models. While phylogenetics describes the process of inferring
130 evolutionary relationships, phylodynamics seeks to infer characteristics of the history of
131 the clade, such as diversification rates or diversity through time (Grenfell et al., 2004).
132 Here, we use two different phylodynamic models, which make different assumptions
133 about sampling and changes in the number of species through time, to infer dinosaur
134 diversification over the Mesozoic. Both models generate piecewise-constant
135 trajectories, allowing parameters to be estimated within a series of predefined time
136 intervals. The first, a coalescent model, conditions the diversification process on the
137 observed fossil ages, treating each sample as an independent event, while the second,
138 a birth-death-sampling model, instead models sampling as an explicit process which
139 generates the observed fossil record. The number of species through time changes
140 deterministically under the coalescent model, but under the birth-death model, this

141 change is stochastic. In the manner by which both sampling and species numbers are
142 treated, the coalescent model is more similar to phylogenetic GLMMs. Our results show
143 that phylodynamic models do not conclusively support the decline of dinosaur diversity
144 towards the end of the Cretaceous, and indicate that accurately modelling sampling bias
145 is likely to be key to understanding diversification dynamics in deep time.

146

147 **Methods**

148 *Phylogenies*

149 We used four dinosaur supertrees, the same three as Sakamoto et al. (2016) in addition
150 to a more recently constructed “metatree” (Lloyd et al., 2017). To create a fully
151 bifurcating topology for the metatree, we sampled 1000 phylogenies from the set of
152 most parsimonious trees and generated a maximum clade credibility tree using
153 TreeAnnotator (Rambaut and Drummond, 2021).

154 In order to infer the branch lengths of the phylogenies, age range data for all non-
155 avian dinosaur species was downloaded from the Paleobiology Database (Uhen et al.,
156 2023) in December 2022, with species names then matched to the tip names in the
157 phylogenies (modifications are described in the electronic supplement). Any informal
158 species, birds (*Archaeopteryx* and more bird-like species), and species without age
159 information were removed from the phylogenies, using the ape (Paradis and Schliep,
160 2019) and palaeoverse (Jones et al., 2023) packages in R (R Core Team, 2022).
161 Following this cleaning, the smallest phylogeny contained 391 dinosaur species (Lloyd
162 et al., 2008) (hereafter ‘Lloyd1’), the two medium-sized phylogenies comprised the
163 same 542 species but differed in their topologies (Benson et al., 2014) (hereafter

164 'Benson1' and 'Benson2'), and the largest phylogeny contained 750 species (Lloyd et
165 al., 2017) (hereafter 'Lloyd2'). As well as analysing the supertrees in full, we also
166 divided each into its three major subclades (Ornithischia, Theropoda and
167 Sauropodomorpha). We therefore conducted our analyses on a total of 16 phylogenies.

168

169 *Phylogenetic models*

170 We used two distinct Bayesian phylodynamic models to infer diversification dynamics
171 from these species trees: the birth-death skyline (BDSKY) model (Stadler, 2011; Stadler
172 et al., 2013; Gavryushkina et al., 2014; Heath et al., 2014) and a piecewise-exponential
173 population size model based on Kingman's n -coalescent process (Kingman, 1982;
174 Griffiths and Tavaré, 1994). While both models are often used in the analysis of
175 epidemiological phylogenies, they are yet to be widely applied in macroevolution.

176 The BDSKY model assumes that all of the observed species are the result of a
177 birth-death process that began with a single species at some unknown time in the past.
178 It also assumes that time is divided into one or more intervals; here, we defined 8 time
179 bins based on different geological intervals (see below). Within a single interval i ,
180 species give rise to new species at the constant rate λ_i (per co-existing species per
181 Myr), and go extinct at constant rate μ_i (per species per Myr). Additionally, fossils are
182 produced at rate ψ_i (per co-existing species per Myr). Species are not removed after
183 sampling, allowing (in principle) sampled species to be direct ancestors of one another
184 (Gavryushkina et al., 2014). As our phylogenies only include non-avian (extinct)
185 dinosaurs, we assume no extant sampling ($\rho = 0$), and condition the model on producing

186 at least one fossil. A diversification ($\lambda_i - \mu_i$) rate was calculated post-hoc for each interval
187 in each iteration.

188 The piecewise-exponential coalescent model we use assumes that the observed
189 tree is the result of a coalescent process parameterized by a time-dependent effective
190 population size function, $N(t)$. At any given time, the value of this function can be
191 interpreted as proportional to a number of extant species, and thus we also refer to it as
192 the effective species richness. We assume that this function has a continuous,
193 piecewise-exponential form, with growth rates in each interval given by the
194 diversification rate parameter, together with the effective species richness at the end of
195 the most recent interval (here, the Coniacian–Maastrichtian), N_i . A key difference
196 between this model and the BDSKY model is that the coalescent does not explicitly
197 model the sampling process; it simply assumes that the sample dates (fossil ages) are
198 independent of the number of species over time, and that the species sampled are
199 drawn randomly from all co-existing species.

200 We used the boundaries of 8 geological intervals of approximately equal length
201 (Early–Mid Triassic, prior to 237 Ma; Late Triassic, 201.4–237.0 Ma; Early Jurassic,
202 174.7–201.4 Ma; Middle Jurassic, 161.5–174.7 Ma; Late Jurassic, 145.0–161.5 Ma;
203 Berriasian–Barremian, 121.4–145.0 Ma; Aptian–Turonian, 89.8–121.4 Ma; Coniacian–
204 Maastrichtian, 66.0–89.8 Ma (Cohen et al., 2013)) as the change times for the
205 piecewise rates in all models.

206

207 *Bayesian inference of model parameters*

208 Our models constitute a specific hypothesis for how the empirical phylogenetic tree T
 209 was produced, and are evaluated using the probability of observing this tree given the
 210 model-specific parameters. We used Bayesian inference to infer these model
 211 parameters, as well as the branch lengths, from the predetermined phylogenetic
 212 relationships in the supertrees and the imposed tip constraints.

213 Specifically, conditional on a phylogenetic tree T and a particular phylodynamic
 214 model M , we seek to infer the model parameters Θ_M . In the case that M is the BDSKY
 215 model, $\Theta_{BDSKY} = \{\vec{\lambda}, \vec{\mu}, \vec{\psi}, t_{or}\}$, while when M is the coalescent model $\Theta_C = \{\vec{N}, \vec{r}\}$. In the
 216 Bayesian context, inference amounts to characterization of the posterior distribution

$$217 \quad P(\Theta_M|T, M) = \frac{P(T|M, \Theta_M)P(\Theta_M|M)}{P(T|M)},$$

218 where $P(T|M, \Theta_M)$ is the likelihood of the model parameters given the tree under the
 219 particular model M , $P(\Theta_M|M)$ is the prior probability distribution for the model
 220 parameters, and $P(T|M)$ is the marginal likelihood of the model (which is constant with
 221 respect to the model parameters). In both the BDSKY and coalescent models, we
 222 express $P(\Theta_M|M)$ as a product of priors for each of the individual model parameters,
 223 meaning that we assume no correlation between these individual parameters.

224 The prior probability distributions used for the individual parameters are listed in
 225 Table 1. The scale of the birth and death rate priors was based on estimates from a
 226 study calculating diversification rates in a large number of extant and extinct
 227 phylogenies (0.02 to 1.54 speciation/extinction events per lineage per million years)
 228 (Heno Diaz et al., 2019). In the absence of robust methods for estimating sampling
 229 completeness from the fossil record, our prior on the sampling rate favours smaller

230 values (the mean represents one sample per lineage per five million years; Table 1) but
231 does not explicitly exclude larger values.

232 The branch lengths of the phylogenies were also inferred within the BDSKY and
233 coalescent analyses. Tip constraints were placed on each species, in the form of a
234 uniform probability distribution ranging from the oldest possible age of the oldest fossil
235 to the youngest possible age of the youngest fossil. In each MCMC iteration, the age of
236 each fossil, together with internal node ages and phylodynamic parameters, was
237 sampled. Through this joint inference, we take into account uncertainty in the branch
238 lengths, with the origination and extinction times of each lineage occurring before and
239 after the sampled fossil age, respectively. In this analysis, the K-Pg boundary is treated
240 as analogous to the “present day” when analysing extant phylogenies, allowing
241 branches to reach the boundary without becoming extinct. Modelling the sampling and
242 extinction processes separately makes our approach robust to issues such as the
243 Signor-Lipps effect (Signor & Lipps, 1982).

244 Both of the models described were implemented using the phylogenetic
245 inference software BEAST 2 (Barido-Sottani et al., 2018; Bouckaert et al., 2019), using
246 its MCMC algorithm to sample the above posterior probability distributions conditional
247 on each of the trees. Each BDSKY and coalescent chain was run until the effective
248 sample size (ESS) for each model parameter was greater than 200, and therefore
249 considered to have converged. The first 10% of each chain was discarded as burn-in
250 prior to further analysis. Subsequent data processing and figure plotting was carried out
251 in R (R Core Team, 2022). All relevant BEAST 2 input files and R scripts are available
252 in the electronic supplement.

253

254 **Results**

255 The results of the coalescent analyses conducted using the 16 phylogenies are
256 summarized in Figure 1, with the corresponding numerical estimates shown in the
257 Supplementary Tables. There is clear variation in the median diversification estimates
258 obtained, and the width of the error bars, between the analyses based on different
259 clades, phylogenies and branch lengths. However, most of the exponential coalescent
260 models indicate a small but negative diversification rate in dinosaurs in the Coniacian-
261 Maastrichtian (69.8% of posterior negative for Lloyd1, 96.5% for Benson1, 96.8% for
262 Benson2, 94.1% for Lloyd2), and for some, this is also true of the preceding Aptian-
263 Turonian (99.2% of posterior negative for Lloyd1, 68.2% for Benson1, 68.9% for
264 Benson2, 100.0% for Lloyd2). Positive diversification rates are generally favoured in all
265 other time bins, with the exception of the Early Jurassic (94.4% of posterior negative for
266 Lloyd1, 98.9% for Benson1, 89.7% for Benson2, 99.7% for Lloyd2). In the full
267 phylogenies and all three subclades, diversification rate uncertainty is highest in the
268 Early-Mid Triassic and tends to decrease over the Mesozoic. There is most
269 disagreement between the phylogenies for the sauropods, with the smallest (Lloyd1)
270 phylogeny showing opposite diversification trends to the other three. However, for all of
271 the phylogenies, most of the posterior probability lies on a strong Coniacian-
272 Maastrichtian decline for the clade (100.0% of posterior negative for Lloyd1, 90.2% for
273 Benson1, 90.2% for Benson2, 100.0% for Lloyd2). For theropods, a small but negative
274 diversification rate is inferred immediately before the K-Pg boundary (99.4% of posterior
275 negative for Lloyd1, 99.9% for Benson1, 99.9% for Benson2, 97.0% for Lloyd2). For the

276 ornithischians, the two Benson and larger Lloyd trees all indicate a latest Cretaceous
277 decline (94.5% of posterior negative for Benson1, 94.6% for Benson2, 97.3% for
278 Lloyd2), while the smaller Lloyd tree suggests no substantial change in diversity during
279 this interval (49.2% of posterior negative).

280 The results of the birth-death analyses are summarized in Figures 2 and 3, which
281 show the piecewise-constant estimates of diversification and sampling rates
282 respectively from each of the phylogenies, and Supplementary Tables, which provides
283 the estimated parameter values. There is less variation in BDSKY results between the
284 different subclades, and based on the different tree topologies, than in the coalescent
285 results.

286 The most apparent pattern is that all of the models have much greater
287 uncertainty on diversification rates in the final time bin, the Coniacian-Maastrichtian
288 (Figure 2). This is coupled with an increase in the inferred sampling rates during this
289 interval (Figure 3). In the full phylogenies and all three subclades, the scale of this effect
290 decreases with increasing phylogeny size.

291 Despite this, in the BDSKY analyses, all four phylogenies place most posterior
292 probability on a positive diversification rate for dinosaurs in the latest Cretaceous
293 (90.0% of posterior positive for Lloyd1, 98.0% for Benson1, 98.1% for Benson2, 99.9%
294 for Lloyd2). In all three subclades, it is more unclear as to whether diversification was
295 positive or negative, or simply constant, prior to the K-Pg boundary. All of the models
296 appear to favour positive diversification in the Late Jurassic (99.9% of posterior positive
297 for Lloyd1, 100.0% for Benson1, 100.0% for Benson2, 100.0% for Lloyd2), and also in

298 the Aptian-Turonian (98.4% of posterior positive for Lloyd1, 98.4% for Benson1, 97.4%
299 for Benson2, 99.2% for Lloyd2).

300

301 **Discussion**

302 In this study, we characterise dinosaur diversification using two different phylodynamic
303 models: the birth-death-sampling (BDSKY) and coalescent skyline models. The
304 coalescent model recovered a downturn in diversity during the latest Cretaceous with a
305 posterior probability of 97% using the Benson phylogenies, and a posterior probability of
306 94% using the larger Lloyd phylogeny (Figure 1). The BDSKY model instead inferred an
307 increase in dinosaur diversity in the latest Cretaceous with a posterior probability of over
308 98% based on these three largest phylogenies (Figure 2). Our results therefore span
309 the range of diversification estimates obtained using other methods in previous
310 literature. The difference in results we obtained using the two phylodynamic models can
311 be linked directly to the different assumptions they make, highlighting that modelling
312 decisions, whether conscious or unconscious, can qualitatively impact estimated
313 diversification trajectories.

314 Firstly, while the number of species through time changes stochastically in the
315 birth-death model, this change is a deterministic (exponential) function of the
316 parameters in the coalescent model. This contrast should have the largest impact when
317 the number of species is very low, meaning early in the history of the clade, and just
318 prior to total extinction. As a result, we might expect to see the greatest difference
319 between the model results in the first and last time bins (so this could be considered an
320 “edge effect”). This effect may be contributing to the stark difference in our

321 diversification estimates for the Coniacian-Maastrichtian time bin between the two
322 models.

323 Secondly, the coalescent model assumes no relationship between species
324 richness dynamics and the number and times of the samples: practically, each
325 fossilisation event is treated as an independent phenomenon. The birth-death model
326 instead treats sampling as a process, parameterised in the model as a rate (which is
327 constant within each time bin). This rate is dependent upon the number of lineages, and
328 therefore species, present at that time. The Coniacian-Maastrichtian is the most heavily
329 sampled interval in our dataset (Supplementary Figure 1; Close et al., 2017; Close et
330 al., 2019), and for the coalescent analyses, this results in relatively narrow HPD
331 intervals on these diversification estimates in comparison with the other time bins
332 (Figure 1). In contrast, in all of the birth-death-sampling analyses, we see drastically
333 elevated uncertainty in estimated diversification rates for the Coniacian-Maastrichtian
334 (Figure 2), with correspondingly high uncertainty in the sampling rate (Figure 3). The
335 birth-death-sampling model cannot discern whether this increased density of fossil
336 sampling is due to a higher sampling or diversification rate, as reflected in the posterior
337 distributions. However, we also see that the width of the HPD intervals for estimated
338 diversification and sampling rates in the Coniacian-Maastrichtian decrease with
339 increasing phylogeny size (Figure 2, 3). Providing the birth-death-sampling model with
340 more data therefore seems to reduce the uncertainty in our parameter estimates;
341 increasing the size of the phylogenies used to conduct our skyline analyses may
342 therefore allow us to infer more accurate diversification estimates in future.

343 The birth and death rates estimated in our birth-death-sampling models are, in
344 some cases, fairly high in relation to previous estimates: median values for some
345 phylogenies reach over 3 events per lineage per million years (Supplementary Table 1),
346 whereas Henao Diaz et al. (2019) estimated 0.02 to 1.54 events across a variety of
347 clades, and Lloyd et al. (2017) estimated 0.94 events for dinosaurs. However, these
348 models generally estimated relatively low diversification rates (Figure 2), with birth and
349 death rates closely coupled in all time intervals, except the Coniacian-Maastrichtian, for
350 all phylogenies (Supplementary Table 1). This coupling has previously been observed in
351 other analyses of diversification in the fossil record (Alroy, 2008; Henao Diaz et al.,
352 2019; Černý et al., 2022), and suggests that while diversification can probably be
353 estimated fairly reliably, disentangling speciation and extinction rates is more difficult.

354 While the birth-death-sampling results suggest that all three dinosaur clades
355 maintained their diversity or experienced a slight positive diversification throughout the
356 Cretaceous, the coalescent results suggest that dinosaurs may have been in decline
357 from the Aptian to Maastrichtian (Figure 1 & 2). The coalescent models suggest that
358 while ornithischians and theropods may only have experienced a Coniacian-
359 Maastrichtian decline, sauropodomorphs may have had negative diversification rates
360 between the Aptian and Maastrichtian. This is consistent with other previous studies
361 which found that ornithischians may have had higher diversification rates in the
362 Cretaceous, particularly hadrosaurs and ceratopsids (Lloyd et al., 2008; Barrett et al.,
363 2009; Sakamoto et al., 2016), alongside a previously reported reduction in the number
364 of sauropodomorph fossils into the Late Cretaceous (Barrett and Upchurch, 2005;
365 Mannion et al. 2011; Starrfelt and Liow, 2016). Positive Late Jurassic diversification

366 rates in all clades suggested by the birth-death models correspond to an observed peak
367 in local dinosaur richness (Close et al. 2019).

368 Previous attempts to include sampling bias in methods that estimate
369 diversification have used proxy data, measurable variables thought to correlate with less
370 tangible factors affecting diversity in the fossil record. The number of dinosaur-bearing
371 geological formations is a commonly used example, thought to correlate with the
372 amount of terrestrial rock outcrop area for each geological stage, which is expected to
373 be a strong influence on the age distribution of collected fossils (Wang and Dodson,
374 2006; Barrett et al., 2009; Lloyd, 2011; Upchurch et al., 2011; Starrfelt and Liow, 2016).
375 Sakamoto et al. (2016) used proxy data as a covariate in their phylogenetic GLMMs,
376 and some modelling approaches have used various types of proxy data to try and
377 extract "residual" patterns of dinosaur diversity (Barrett et al., 2009; Lloyd, 2011).
378 However, simulation studies have demonstrated that residual modelling, particularly
379 using geological proxies, may degrade the biological signal in the data rather than
380 eliminating bias (Brocklehurst, 2015; Sakamoto et al., 2017; Dunhill et al., 2018). A
381 proxy-based approach also fails to acknowledge the wide variety of biases that affect
382 the fossil record (Raup, 1976), such as Lagerstätten effects (Walker et al., 2020),
383 preservation biases based on morphology (Brusatte et al., 2015; Benson, 2018), and
384 "dark data" in museums and private collections (Marshall et al., 2018). Aside from rock
385 outcrop area, the geography of fossil collection is also greatly driven by political and
386 socio-economic factors (Raja et al., 2022), and specifically for dinosaurs, the known
387 record is highly concentrated in North America (Hurlbert and Archibald, 1995; Le Loeuff,
388 2012; Brusatte et al., 2015; Chiarenza et al., 2019; Dean et al., 2020; Han et al. 2022),

389 even if the strength of this bias has reduced, and increasingly been accounted for, over
390 time (e.g. Close et al. 2019). Fossil abundance metrics have also been used, but even
391 these are an imperfect proxy for sampling bias, especially when integrating data from
392 phylogenies and fossil databases that do not contain the same taxa.

393 The approaches to sampling employed by our coalescent and birth-death-
394 sampling models are also not a perfect fit for the true nature of the fossil record, and
395 violations of both models' sampling assumptions may be biasing our results (e.g.
396 Karcher et al., 2016). However, methods for estimating diversity which attempt to
397 mechanistically model sampling in a more realistic way will likely be a necessary step in
398 unravelling how fossil record bias impacts our understanding of biodiversity in deep time
399 (Brusatte et al., 2015; Starrfelt and Liow, 2016; Černý et al., 2022). Aside from this,
400 there are additional ways in which the approach we used might be improved in future.
401 Both of our models expect that sampling is randomly distributed across co-existing
402 lineages, an assumption held by most approaches to estimating diversity in the fossil
403 record, but which is not true (Hurlbert and Archibald, 1995; Wang and Dodson, 2006;
404 Benson, 2018; Černý et al., 2022). Multi-type models may be used to allocate species to
405 categories with different sampling parameters (Kühnert et al., 2016), however more
406 thought is needed on how best to assign species to discrete categories. Piecewise-
407 constant models, as used in this paper, may be vulnerable to inaccuracies when large
408 fluctuations in rates are present within a single bin (similarly to TRiPS (Starrfelt and
409 Liow, 2016)), and more understanding of how change time choice is important for
410 achieving convergence and obtaining meaningful rate estimates is needed (e.g. Allen et
411 al. 2023). Others have also commented on the sensitivity of models to input parameters

412 and priors more broadly (Starrfelt and Liow, 2016; O'Reilly and Donoghue, 2020; Černý
413 et al., 2022), and highlighted the importance of making careful, informed decisions when
414 choosing analyses and carrying out model adequacy tests when possible. Careful prior
415 choice is also required to avoid rate non-identifiability (Smiley, 2018; Louca and Pennell,
416 2020; Černý et al., 2022), although piecewise-constant methods may be more robust to
417 this problem than those which generate continuous curves (Legried and Terhorst, 2022;
418 Truman et al. 2024).

419 Previous authors have commented on the necessity of continuing to collect new
420 fossils to improve our knowledge of dinosaur evolutionary dynamics (e.g. Benson, 2018;
421 Bonsor et al., 2020; Černý and Simonoff, 2023), to which we would add that there are
422 also many ways in which we could make better use of the fossils and data we already
423 have. With further model development, full Bayesian phylodynamic inference of the tree
424 and model parameters may become possible, allowing estimation of evolutionary rates
425 across uncertainty in the topology and branch lengths of the phylogeny. This would
426 address issues around the sensitivity of results to tree shape in currently available
427 methods (shown here but also by Bonsor et al. (2020)). Such an approach could also
428 allow for the inclusion of more data, such as the incorporation of more fossil age
429 information (Stadler et al., 2018; Warnock et al., 2020), and utilising fossils both with
430 and without character data (Andréoletti et al., 2022). Larger phylogenies may also
431 enable such a model to infer evolutionary rates at a finer temporal resolution. Between
432 the results presented here and the aforementioned potential for future improvement, it is
433 clear that phylodynamic models can provide important insights into macroevolutionary
434 processes.

435

436 **Conclusions**

437 The trajectory of non-avian dinosaur diversification prior to their demise at the K-Pg
438 boundary has been fiercely debated. Here, we apply two phylodynamic models to
439 dinosaur phylogenies, to investigate the influence of sampling assumptions on
440 estimates of evolutionary rates. Our birth-death-sampling skyline model results do not
441 support a Cretaceous downturn in dinosaur diversity, while the piecewise-exponential
442 coalescent model results do. This disparity in results indicates that fundamental
443 differences in model design, especially with respect to sampling, can have a dramatic
444 influence on estimates of diversification. It also highlights the importance of
445 understanding model assumptions more broadly, providing context for results and
446 facilitating comparison between models. Future work examining the fit of existing
447 phylodynamic models to palaeontological datasets will help to illuminate whether one
448 model should be favoured above the other and highlight areas for future model
449 development.

450

451 **Acknowledgements**

452 We thank members of the Computational Evolution group, particularly Louis du Plessis,
453 for helpful discussion, and Graeme Lloyd for assistance with using the phylogenies. We
454 thank the anonymous reviewers for their comments, which helped to improve the
455 manuscript. All BEAST 2 analyses were conducted using the ETH Zurich Euler cluster.
456 We thank those who have contributed to the Paleobiology Database data used in this
457 study. This is Paleobiology Database Official Publication No. XXX. We also thank the
458 artists who contributed the Phylopic images used in our figures: Matt Dempsey, Jaime
459 Headden, and Iain Reid.

460

461 **Author contributions**

462 RCMW, TS and TGV developed the study concept. MVVO and BJA wrote the code,
463 with help from RCMW and TGV. BJA and MVVO conducted the analyses, and BJA
464 made the figures. BJA, RCMW and TGV wrote the manuscript. All authors edited the
465 manuscript and approved its final version.

466

467 **Financial support**

468 This work was supported by the Amgen Scholars Program (MVVO) and an ETH+ grant
469 (BJA, "BECCY").

470

471 **Conflicts of Interest**

472 None

473

474 **Data availability**

475 All files and code necessary to run these analyses are available in the electronic
476 supplement. A Taming the Beast tutorial (Barido-Sottani et al. 2018) explaining how to
477 apply these methods (using these analyses as a case study) is also available at
478 <https://taming-the-beast.org/tutorials/>.

479

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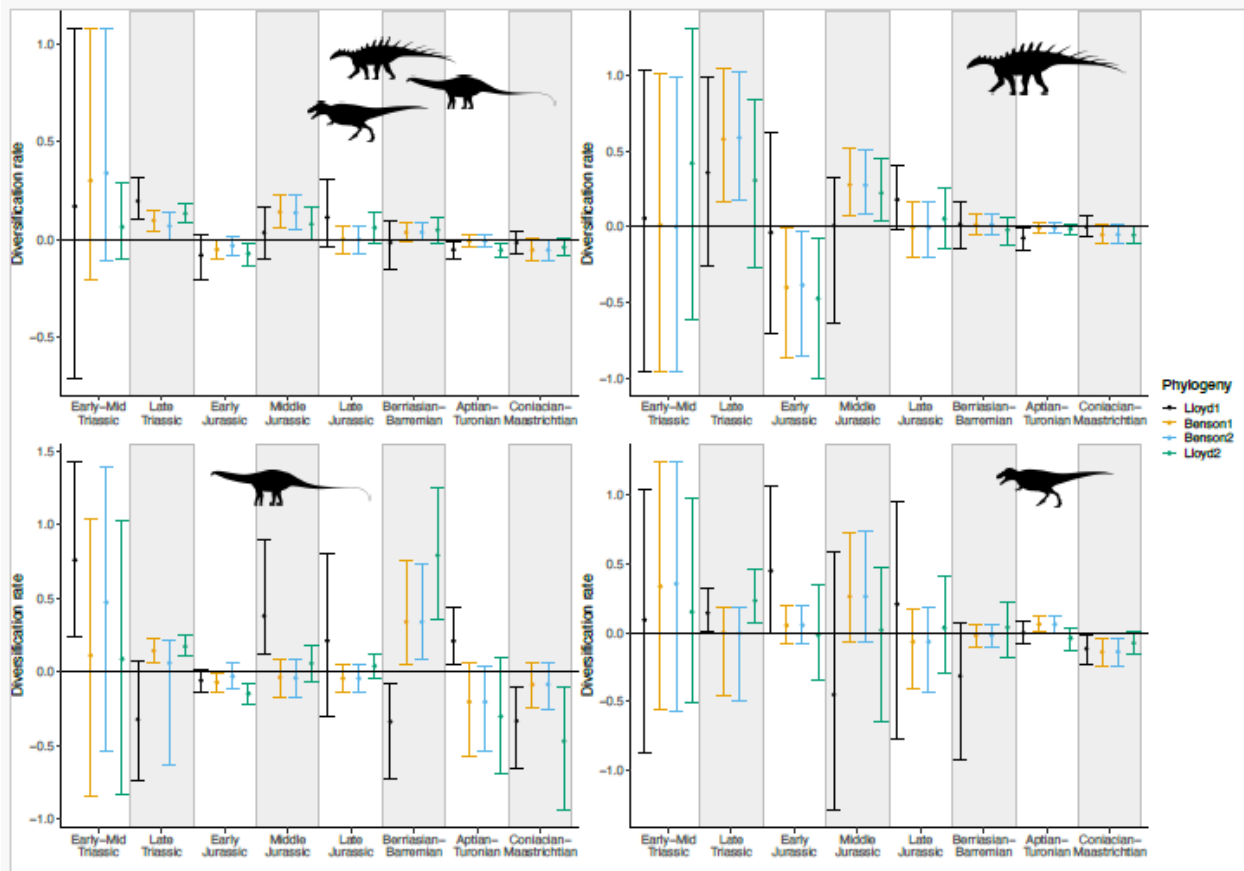
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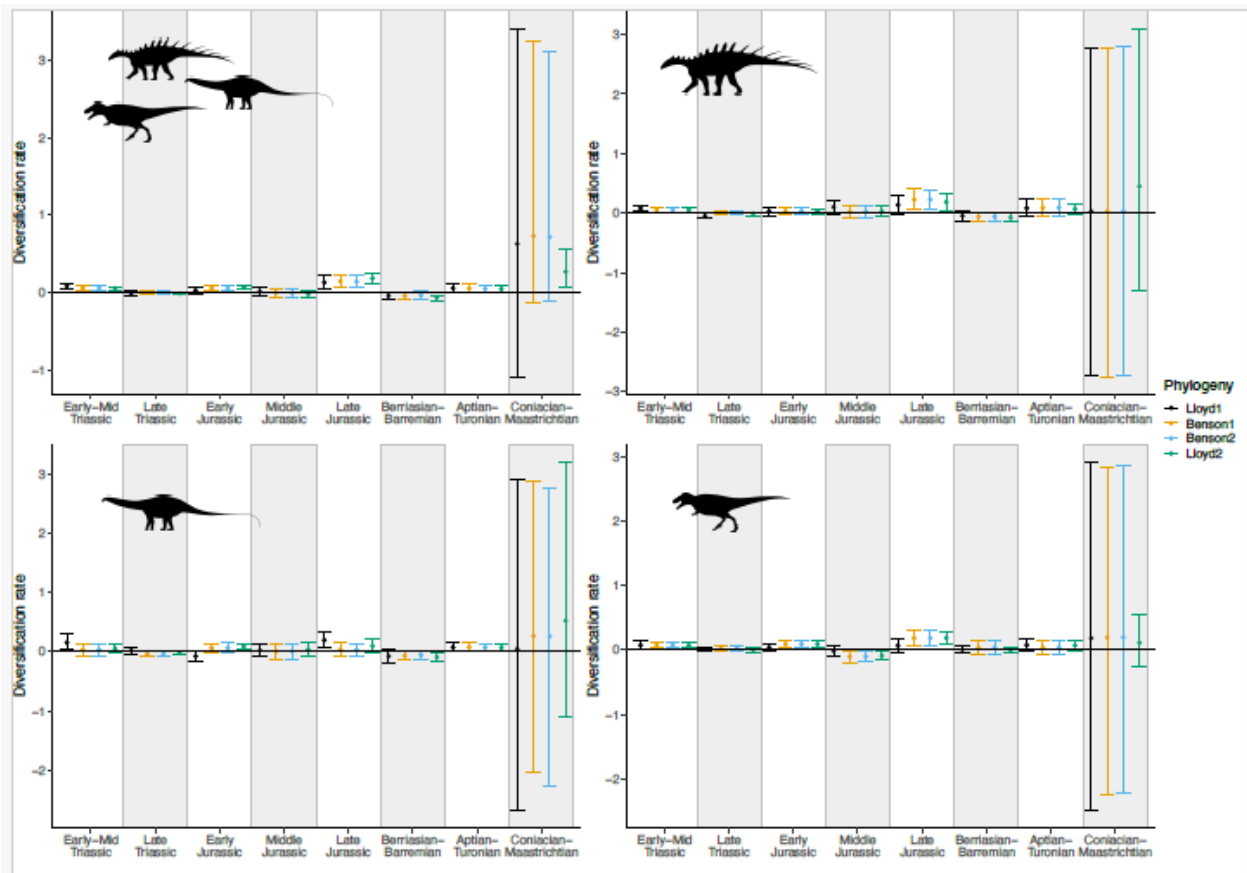
728 **Figure 1** Diversification rates estimated using the piecewise-exponential coalescent
 729 model. Time moves forwards from left to right along the x-axis, with the K-Pg boundary
 730 at the end of the Coniacian-Maastrichtian bin. Estimates are shown for each of four
 731 phylogenies, ordered from smallest to largest. Points show the median values, and error
 732 bars indicate 95% highest posterior density. Dinosaur silhouettes for Ornithischia (top
 733 right), Sauropodomorpha (bottom left) and Theropoda (bottom right) are from Phylopic.



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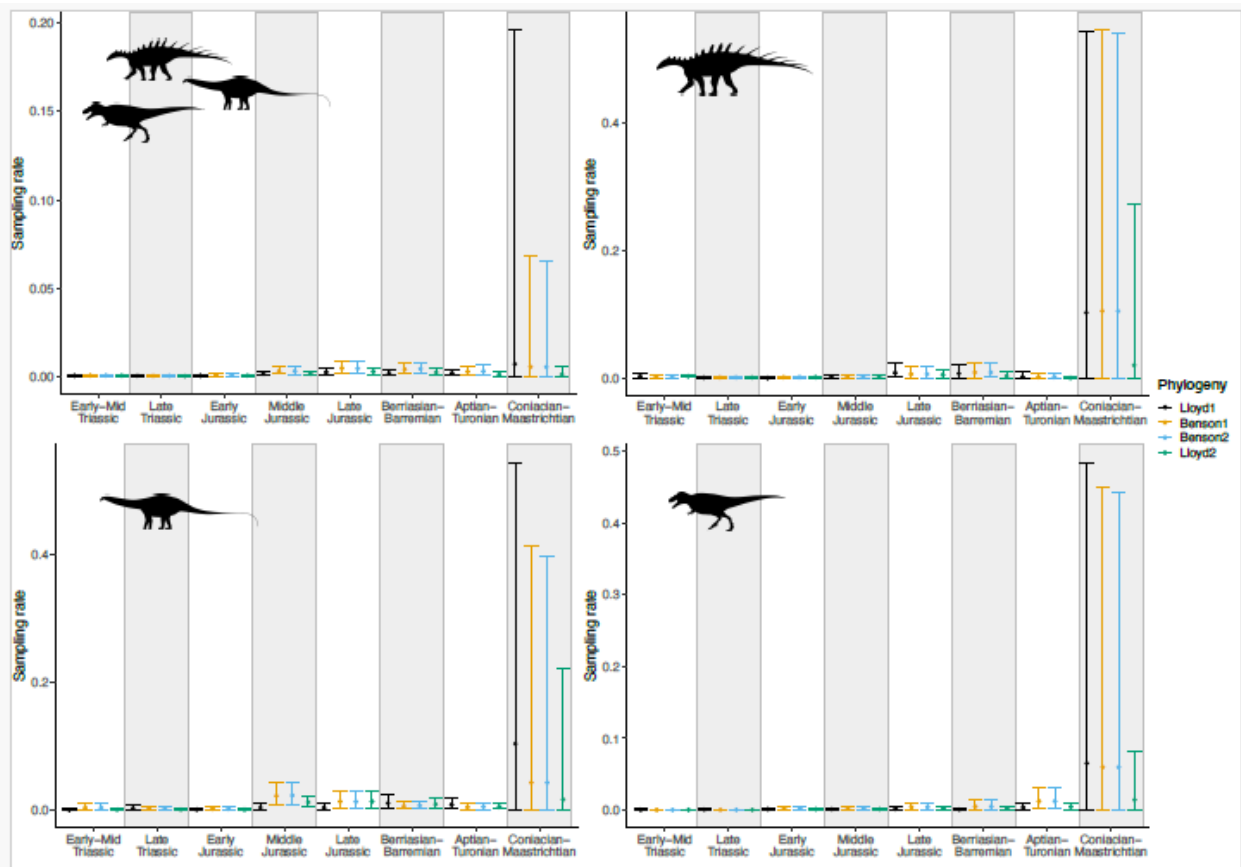
736 **Figure 2** Diversification rates estimated using the piecewise-constant fossilised birth-
 737 death skyline model. Time moves forwards from left to right along the x-axis, with the K-
 738 Pg boundary at the end of the Coniacian-Maastrichtian bin. Estimates are shown for
 739 each of four phylogenies, ordered from smallest to largest. Points show the median
 740 values, and error bars indicate 95% highest posterior density. Dinosaur silhouettes for
 741 Ornithischia (top right), Sauropodomorpha (bottom left) and Theropoda (bottom right)
 742 are from Phylopic.



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744

745 **Figure 3** Sampling rates estimated using the piecewise-constant fossilised birth-death
 746 model. Time moves forwards from left to right along the x-axis, with the K-Pg boundary
 747 at the end of the Coniacian-Maastrichtian bin. Estimates are shown for each of four
 748 phylogenies, ordered from smallest to largest. Points show the median values, and error
 749 bars indicate 95% highest posterior density. Dinosaur silhouettes for Ornithischia (top
 750 right), Sauropodomorpha (bottom left) and Theropoda (bottom right) are from Phylopic.



751

752

753 **Tables**

754

755 *Table 1*

756

757 Priors for the Bayesian phylodynamic analyses.

758

Model	Parameter	Units	Prior
BDSKY	t_{or}	Ma	Unif(66,266)
	λ_i	Ma ⁻¹	Exp(1.0)
	μ_i	Ma ⁻¹	Exp(1.0)
	ψ_i	Ma ⁻¹	Exp(0.2)
Piecewise coalescent	r_i	Ma ⁻¹	Unif($-\infty, \infty$)
	N_f	Ma	$1/N_f$

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760