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How many dinosaur species were there?

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True richness estimated using a Poisson sampling model (TRiPS)

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13

14 **Abstract**

15 The fossil record is a rich source of information about biological diversity in the past. However, the fossil
16 record is not only incomplete but has inherent biases due to geological, physical, chemical and biological
17 factors such that not all individuals or species are equally likely to be discovered at any point in time or
18 space. In order to use the fossil record to reconstruct temporal dynamics of diversity, biased sampling
19 must be explicitly taken into account. Here, we introduce an approach that utilizes the variation in the
20 number of times each species is observed in the fossil record to estimate both sampling bias and true
21 richness. We term our technique TRiPS (Trueness Richness estimated using a Poisson Sampling model) and
22 explore its robustness to violation of its assumptions via simulations before applying it to an empirical
23 dataset. We then venture to estimate sampling bias and absolute species richness of dinosaurs in the
24 geological stages of the Mesozoic. Using TRiPS, we present new estimates of species richness trajectories
25 of the three major dinosaur clades; the sauropods, ornithischians and theropods, casting doubt on the
26 Jurassic-Cretaceous extinction event and demonstrating that all dinosaur groups are subject to
27 considerable sampling bias throughout the Mesozoic.

28 Keywords: Dinosauria, Poisson, taxonomic richness, fossil record, sampling bias, Ornithischia,
29 Sauropodomorpha, Theropoda, diversity curve.

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33 **Introduction**

34 One of the main goals of paleobiology is to reconstruct diversity using information from the fossil record.
35 While the patterns of diversity in space and through time are interesting in themselves, understanding the
36 dynamics of taxon richness is also the first step in elucidating the biotic and abiotic forces that shape the
37 spatial and temporal variation in taxon diversity. In other words, we need an accurate picture of patterns
38 of past diversity to understand processes that operate on long time scales. As in all study systems where
39 data samples in themselves cannot be assumed a complete picture of the underlying population, richness
40 studies based on the fossil record must consider the incompleteness of the fossil record.

41 Not all organisms enter the fossil record or have the same potential of doing so. Once created, a fossil
42 record (a physical record of the existence of organisms that were alive in the past) is subject to eternal
43 loss through erosion, subduction and other physical processes. Whether or not a fossilized organism can
44 be found is also affected by variability in outcrop accessibility. Last but not least, sampling intensity
45 encompassing factors including academic/commercial interest, geographic location and sampling design
46 also influence information from the fossil record we have access to. While some of these factors
47 contribute to noise in our inference of historical patterns and processes, and thus only cloud biological
48 signals, some may cause systematic bias so as to yield misleading results if the data are interpreted at face
49 value or with inappropriate methods.

50 Several classes of approaches for estimating richness using an incomplete fossil record have been
51 developed. These might be loosely grouped into subsampling approaches, phylogenetic corrections and
52 residual approaches. It is not our purpose to give a full overview of the approaches available, which have
53 variously been reviewed elsewhere (see e.g. 1,2), but we briefly describe these in order to clarify why we
54 have developed a new approach here. Subsampling approaches, including rarefaction (reviewed in 1) and
55 SQS (3,4), attempt to standardize temporal (or spatial) samples so as to achieve comparable relative
56 richness across samples. Phylogenetic approaches use phylogenetic hypotheses of the clade in question to
57 infer ghost lineages that are not observed in the fossil record but did exist as implied by the given
58 phylogenetic hypothesis (5). These ghost lineages are thus assumed to give a minimum estimate of the
59 lineages we have failed to observe in the fossil record. The residual approach (see also many chapters in
60 McGowan & Smith 2,6,7) assumes that a given proxy for sampling (e.g. outcrop area or number of fossil
61 bearing collections) captures the biases that might influence our observations and uses that to model how
62 a completely sampling-driven signal would appear. Deviations from such a model are thought to reveal
63 the real troughs and peaks in richness. In all of these three approaches, we can only hope to estimate

64 relative richness through time and not true richness. Additionally, none of these approaches attempts to
65 estimate the bias itself, i.e. the differential sampling across time, space or taxa. Without an estimate of
66 sampling bias that is separate from richness estimates, it is not possible to use these approaches to shed
67 light on the Common Cause Hypothesis; where a common factor affects both biological dynamics and
68 sampling (8,9).

69 Here, we introduce an approach that explicitly models the sampling process while estimating richness,
70 using multiple observations of fossils belonging to an organismal group. We named it TRiPS (TTrue
71 Richness estimated using a Poisson Sampling model). While we and others have used the simultaneous
72 estimation of extinction, speciation and sampling processes to study diversification processes (10–13),
73 there has not been a direct attempt to use multiple observations of fossil species to estimate true richness,
74 rather than relative richness, while simultaneously and explicitly estimating sampling, as far as we are
75 aware. Specifically, TRiPS assumes that a particular species, if observed multiple times in a given time
76 interval, has a relatively high probability of fossilization and modern day discovery. We use this type of
77 information across related species that are likely to have similar fossilization potential and modern day
78 discovery rates to estimate the number of species we might be missing and hence the true number of
79 species that might have existed.

80 Dinosaurs are used as an example to illustrate our approach, not least because there is a lot of interest in
81 estimating the both the absolute (14–16) and relative temporal richness (17–21) of dinosaur taxa. As
82 earlier analyses suggests that the three major dinosaur groups Sauropodomorpha, Ornithischia and
83 Theropoda exhibit both different diversity dynamics and differential impact of sampling bias (e.g. 7,22),
84 we estimate sampling rates and true richness for all dinosaurs as well as these groups independently. We
85 present stage-specific dinosaur sampling rates (i.e. bias) and dinosaur species richness through the
86 Mesozoic as estimated from TRiPS, compare our estimates with those discussed in the literature and
87 present simulations that explore the power of our approach and the sensitivity of TRiPS to violations of
88 key assumptions.

89 **Methods and data.**

90 **Data**

91 We downloaded records of Dinosauria, Ornithischia, Sauropodomorpha and Theropoda separately from
92 the Paleobiology Database (PaleoDB, <https://paleobiodb.org/#/>, download August 13th 2015) using the R
93 toolbox paleobioDB (23). Each row of data downloaded from the PaleoDB is associated with an observed
94 taxon, its location and age range, and their metadata. Only data where identifications were made to the

95 species level and where reported age ranges were specified to stage level were in used in our subsequent
96 analyses. Note that while most of the Dinosauria records were assigned to Ornithischia,
97 Sauropodomorpha or Theropoda, 179 occurrences representing 67 species are not associated with any of
98 these groupings. We summarize the data in Table 1 but also supply the raw data we downloaded as
99 supporting information. For each species we tallied the number of observations in each stage in the
100 Mesozoic, generating an observation count matrix. The reported age range of a given record can span
101 several geological stages. In such cases, we assigned a stage within its age range with a probability that is
102 proportional to the duration of those stages. Because of this random assignment of records to stages
103 within the given age range, we performed TRiPS analyses (described below) on 100 replicated occurrence
104 count matrices and used the median estimated sampling rate for species richness estimation. We also
105 analyzed genus level data but because both richness and sampling dynamics are similar to species level
106 dynamics, we refer readers to the SI for genus level estimates.

107 **Model: Fossil sampling as a Poisson process**

108 Here, we treat the process of fossil sampling, which we will estimate from records from the Paleodb (see
109 previous section) as the combined processes of fossilization and detection. We assume that sampling can
110 be viewed as a homogenous Poisson process inside a particular time interval. For our data, the Poisson
111 intensity or rate at which species are sampled is assumed constant for the duration of a geological stage.
112 Formally, let the Poisson intensity λ_t be the parameter controlling the sampling process in a given time
113 interval t . The number of observations $O_{i,t}$ for a species i in that time interval t with duration d_t has a
114 Poisson distribution with mean $\lambda_t d_t$. The likelihood of the sampling rate λ_t given $O_{i,t}$ occurrences in that
115 interval is then

$$L(\lambda_t | O_{i,t}, d_t) = \frac{(\lambda_t d_t)^{O_{i,t}}}{O_{i,t}!} e^{-\lambda_t d_t} \quad (1)$$

116

117 Here we explicitly assume that a species detected in a time interval is extant during that whole time
118 interval. Because any species that is represented in the database must have left at least one detected fossil
119 we must condition the likelihood of λ_t on $O_{i,t} > 0$. The likelihood of λ_t is then

$$L(\lambda_t | O_{i,t}, d_t) = \frac{(\lambda_t d_t)^{O_{i,t}}}{O_{i,t}!} e^{-\lambda_t d_t} \quad (2)$$

120 The maximum likelihood estimate for the sampling rate of a group of species in a given interval is found
121 by maximizing the product of eq (2) over all the observed species (n_t) belonging to that group;

$$\hat{\lambda}_t = \max_{\lambda_t} \prod_{i=1}^{n_t} \frac{(\lambda_t d_t)^{O_{i,t}} e^{-\lambda_t d_t}}{O_{i,t}! (1 - e^{-\lambda_t d_t})} \quad (3)$$

122 If our data consist of only single records (i.e. $O_{i,t} = 1$, for all i), estimating λ_t using maximum likelihood
 123 will yield an estimate of 0. Hence, the minimum data requirement for estimating the fossilization rate is a
 124 dataset where at least one of the species has more than one observation.

125 We assume that sampling rates estimated are constant for all species within a clade in the same time
 126 interval (i.e. the sampling rates estimated are time-specific but not species-specific). We can then
 127 estimate the probability of detecting a species from this group as $1 - \text{Pois}(0, \hat{\lambda}_t * dt)$, i.e. 1 minus the
 128 probability of not detecting a species if it was actually extant, according to the Poisson process. We
 129 further use this binomial probability in deriving the most likely true richness. The binomial probability of
 130 a species sampled during an interval d_t is

$$p_{binom,t} = 1 - \text{Pois}(0, \hat{\lambda}_t d_t) = 1 - e^{-\hat{\lambda}_t d_t} \quad (4)$$

131

132 where $\text{Pois}(0, \hat{\lambda}_t d_t)$ is the probability of 0 sampling events in one lineage with a rate $\hat{\lambda}_t$ in a bin of
 133 duration d_t . The last step in estimating the true richness in a given time interval is to find the true species
 134 richness (n_{true}) that maximizes the binomial likelihood

$$L(n_{true} | p_{binom,t}, n_t) = \binom{n_{true}}{n_t} p_{binom,t}^{n_t} (1 - p_{binom,t})^{(n_{true} - n_t)} \quad (5)$$

135

136 where $p_{binom,t}$ is the binomial probability calculated from the estimated sampling intensity (eq 4) using
 137 maximum likelihood (eq 3) and n_t is the observed number of species in the time interval. Thus the value
 138 n_{true} that maximizes eq 5 is the maximum likelihood estimate of the true richness where n_t species were
 139 observed.

140 To quantify the uncertainty surrounding the estimate of the sampling rate and the true species richness we
 141 utilize the relationship between the χ^2 distribution and log likelihood profiles (see e.g. 24). For the
 142 confidence bounds on the maximum likelihood estimate $\hat{\lambda}_t$ we find the range of values for λ that satisfy
 143 the inequality

$$2 \left(\log \left(L(\hat{\lambda}_t | O_{i,t}, d_t) \right) - \log \left(L(\lambda | O_{i,t}, d_t) \right) \right) < \chi_1^2(\alpha) \quad (6)$$

144

145 where $\chi_1^2(\alpha)$ is the upper quantile function of the χ^2 distribution with 1 degree of freedom. Similarly the
146 upper and lower confidence bounds for the estimated true richness n_{true} is found using the lower and
147 upper confidence bounds on the sampling probability ($p_{binom,t}$) summarizing the uncertainty surrounding
148 both sampling and richness estimates.

149 TRiPS thus yields maximum likelihood estimates and confidence intervals of true species richness for a
150 given time interval by estimating a sampling rate (detected fossils per species per million year). This
151 sampling rate can be transformed into a time interval specific sampling probability (probability of fossil
152 detection per species) and thereby appropriately take the duration of time interval into account. In other
153 words, we do not need to conform the data to equal durations as commonly done (18,e.g. 25). The
154 sampling rates estimated from TRiPS are thus directly comparable across unequal geological intervals.
155 Note that while we have described TRiPS using species observations it can also be directly applied to
156 genera or lineages defined in other ways. In fact, groupings believed to exhibit similar sampling rates
157 might be combined, whether or not they actually are taxonomic clades.

158 We estimate the sampling rates and richness for all dinosaurs and Ornithischia, Sauropodomorpha and
159 Theropoda in each geological stage in the Mesozoic, data permitting.

160 **Simulations using a birth-death-fossilization process**

161 To evaluate our method's applicability and power we performed a large number of continuous time birth-
162 death (BD) simulations, coupled with a fossilization scheme, which we interpret as sampling. In a classic
163 BD process a lineage either gives rise to a new species or goes extinct at a certain rate; our fossilization
164 scheme adds a third potential event: that of a lineage leaving a fossil. We are thus simulating a 'fossil
165 record' given a set of parameters controlling the dynamics and sampling of the simulated clade, and then
166 using TRiPS to estimate the true number of species in these simulations. Our birth-death-fossilize model
167 has 6 parameters which we all will vary; speciation and extinction rate (in per species per time unit),
168 sampling rate (fossils per species per time unit), number of species at the start of the simulation and
169 number of time units (in continuous time) to run the simulation. The final parameter scales the variability
170 of sampling rates between individual species; where the sampling rate is a clade mean and each species
171 has a sampling rate drawn from a normal distribution with a given coefficient of variation. For our
172 simulations these 6 parameters were either set to zero or drawn from a given distribution.

173 In case of no biological dynamics and identical sampling rates for all lineages TRiPS will consistently
174 recover true richness. In two rounds of simulations, we explicitly investigate the robustness of our
175 approach to violations of TRiPS's two main assumptions, 1) equal sampling rates for all species in the

176 clade in question and 2) and negligible species turnover within a time interval. We then use the results of
177 our simulations to aid interpretation of our estimates based on dinosaur records.

178 In the first round of simulations speciation and extinction rates were set to 0 (i.e. no changes in species
179 richness), durations of time simulated ranged from 1 to 20 time units (uniform distribution), the number
180 of species between 10 and 500 (uniform distribution), mean sampling rates from 0.002 to 1.5 fossils per
181 species per time unit (log uniform distribution), coefficient of variation of sampling rate across species
182 from 0 to 0.1 (uniform distribution). Each species thus has its own unique sampling rate drawn from a
183 normal distribution with means and variance differing across simulations. We ran 1000 simulations in this
184 set.

185 The second round of simulations we simulated BD process with speciation and extinction rates > 0 which
186 leads to species turnover. Speciation and extinction rates were drawn from log-uniform distributions
187 spanning 0.005 to 0.158 per species per time unit and interval durations ranging from 2 to 20 time units
188 (uniform distribution). The number of initial species was also varied in the range 10 through 250 (uniform
189 distribution). Mean sampling rates of all species were allowed to vary from 0.01 to 0.5 fossils per species
190 per time unit (log uniform). As in the first round, we also varied the variability in sampling across species
191 within a simulation (coefficient of variation in the range 0 to 0.1, uniform distribution). We ran 100,000
192 simulations in which the parameter values were sampled using a latin-square hypercube to best span all
193 combinations of parameters. We tracked the records of observations of species through time, and then
194 analyzed these data with TRiPS. These simulations allowed us to explore the effects of violating TRiPS's
195 assumption that a species, if found in a given time interval, is extant during the entire time interval. We
196 evaluated TRiPS's ability to infer sampling rates and true species richness by 1) tabulating the number of
197 simulations in which the true species richness was inside the predicted confidence interval and 2)
198 estimating the bias in the maximum likelihood prediction of species richness
199 $(N_{predicted} - N_{actual})/N_{actual}$. Details and code for the simulations are presented in the supporting
200 information, and also available on the websites of the authors.

201 **Implementation**

202 All aspects of the data analysis was performed in *R* (R Core Team 26). Code necessary for the analysis,
203 combined with scripts to directly download relevant (and thus updated) data from Paleobiology Database
204 will be made available on the authors' website (or other appropriate repository). The birth-death-fossilize
205 model was implemented and analyzed in MatLab (27) and code and simulation data are also available.

206 **RESULTS AND DISCUSSION**

207 Why (and when to) use TRiPS to estimate richness: simulations and comparisons

208 Estimating taxon richness using data collected from the fossil record and compiled into databases, such as
209 the PaleoDB, is not a trivial exercise as fossilization, outcrop exposure and modern day sampling and data
210 compilation are heterogeneous processes. The approach we have developed capitalize on the readily
211 availability of fossil observation data in the PaleoDB. Unlike commonly used approaches, including
212 subsampling (1,25,28) and bias-corrected residual analysis (7,29), that also use such data, our approach,
213 TRiPS, estimates true rather than relative richness by utilizing information on sampling which is inherent
214 in PaleoDB. In addition, unlike the residual approach, we do not make presuppositions that an external
215 time series can be used to correct for sampling. This is important because such external time series (e.g.
216 amount of outcrop, sea level) may constitute a factor driving both richness and sampling as postulated by
217 the Common Cause Hypothesis (8,9) or be an effect of such a third factor. Also, in some cases, assumed
218 proxy time series can be dubious; for instance using formation counts as a sampling proxy there will
219 always be a correlation between proxy and richness, regardless of the degree of sampling (30,31)

220 In TRiPS, we tackle bias in the fossil record directly by estimating rates of sampling. This also allows us
221 to disentangle sampling and richness dynamics such that tests of links between potential drivers can be
222 done on sampling and richness independently (see also 32). An advantage of TRiPS is that our treatment
223 of sampling allows sampling probabilities to be directly comparable between intervals of unequal
224 duration. One assumption we do explicitly make which cannot be true most of the time, is that a species
225 detected in a given time interval is extant during that whole time interval. This is because most species are
226 unlikely to become extinct exactly at the late boundary of a time interval or originate exactly at the early
227 boundary of a time interval. While other methods for estimating richness also assume that turnover is
228 clumped at interval boundaries (see e.g. 28, p. 74), we do need to examine the robustness of our estimates
229 to the violation of this crucial assumption.

230 Our first round simulations show that when speciation and extinction rates are 0 (and hence where there
231 are no changes in species richness through time) but species in the group are allowed to vary in their
232 sampling rates, TRiPS still work remarkably well with more than 98% of our 1000 simulations yielding
233 confidence intervals of richness that included the true richness value, with no clustering of the ‘failures’
234 in any part of parameter space. Hence, even if species vary in their potential for fossilization and
235 detection, TRiPS still yields adequate results.

236 In the second round, where speciation and extinction rates are not zero, most simulated species do not
237 span the whole interval in which they were sampled. Across the whole parameter space simulated (see
238 previous section) TRiPS analysis yielded confidence intervals including the true richness in 71% of

239 simulations and true sampling rates were inside the confidence interval in 67% of simulations (see SI for
240 effect of all parameter ranges on the success). In other words, TRiPS has reasonable success at capturing
241 true species richness despite large deviations from the assumption that species are extant throughout the
242 time interval they were sampled in, i.e. even with turnover within a time interval. At moderate levels of
243 sampling and shorter durations (of time intervals) TRiPS works very well (Fig 1).

244 While richness dynamics within time intervals reduce the probability of correct inferences of both
245 sampling rates and true richness according to TRiPS, cases in which true values fall outside of estimated
246 confidence intervals are not unreasonable: across such “failure” cases, the correlations between estimated
247 and true sampling and richness are 0.91 and 0.93 respectively, and the mean bias in the estimated richness
248 is smaller than across all that are deemed ‘successful’. Many cases of ‘failure’ seem to be due to an
249 unwarranted narrowness of confidence intervals rather than a complete breakdown of approach.

250 We note two caveats to the estimates from TRiPS. First, although the ability to estimate proper bounds on
251 richness is relatively robust to deviations from our assumptions under our simulations, TRiPS does give
252 biased maximum likelihood estimates of richness when there are within-bin dynamics such that estimates
253 are usually lower than the true richness (see Fig SI 3). The estimated richness is thus best treated as
254 possibly minimum richness estimate, particularly for intervals in which there is reason to believe that the
255 changes in true richness have been substantial, such as in long geological stages. Second, with longer
256 simulations (which gives more time for in-bin dynamics) and higher sampling, rates TRiPS fails more
257 often (Fig. 1). On the other hand, one of the benefits of our explicit approach is that it is straightforward
258 to simulate a birth-death-fossilization process and check whether or not the empirical estimates of
259 sampling rates and richness can be thought to be robust to violation of the assumption of negligible
260 turnover within an interval (see below). It is also worth highlighting that other approaches for
261 reconstructing past richness also fall victim to deviations from constant richness (see e.g. 28), even
262 though such violations have not been explicitly examined by published simulations as far as we know.

263

264 Varying sampling estimates among clades and through time

265 The sampling estimates from TRiPS (Fig. 2 and Table 1) clearly show that sampling rates and
266 probabilities for dinosaurs do not monotonically increase through the Mesozoic, but exhibit a
267 combination of high and low sampling regimes. This observation runs counter to the common held belief
268 that younger geological strata exhibit a higher level of fossil sampling (e.g. 17,19). Sampling probabilities
269 are particularly high during the first two stages of Jurassic (Hettangian (201.3 – 199.3 Myr) and
270 Sinemurian (199.3-190.8 Myr)), the Tithonian (152.1-145 Myr), the Albian (113-100.5 Myr) and the

271 Maastrichtian (72.1-66 Myr) but these high sampling intervals are interspersed with lower ones. Note that
272 sampling rates (λ) and sampling probabilities ($p_{binom,t}$) while sharing some commonalities, are not the
273 same. For instance, the Norian (Nor) has relatively low sampling rates (λ_i), i.e. sampling events per
274 lineage per million years, but the probability of a species being sampled, given that it was extant in the
275 Norian is quite high (>0.74 for all groups, see Table 1). In general, the relative changes in sampling
276 dynamics are similar for our genus level analyses although sampling rates and probabilities are naturally
277 higher for genera (SI Fig 6 & 7).

278 Our sampling estimates are often quite different across boundaries for which high taxon turnovers have
279 been noticed previously. For instance, sampling estimates are low in the Rhaetian (208.5-201.3 Myr) but
280 high in the Hettangian (201.3-199.3 Myr), indicating that differential sampling processes were occurring
281 across the Triassic-Jurassic boundary. The Jurassic-Cretaceous boundary (Tithonian-Berriasian) also
282 shows a significant drop in sampling, indicating that the previously noted diversity loss (17) may, at least
283 in part, be a sampling signal. While our estimates corroborate that the last two stages of the late
284 Cretaceous have high sampling rates (7,18,33), the Santonian has extremely low sampling rates, at odds
285 with a previous analysis of sampling bias (22). The Hettangian exhibits very high sampling rates, which
286 leads to binomial sampling probabilities at the same level as the following Sinemurian stage, despite the
287 Sinemurian lasting almost five times as long.

288 The three clades have notably different sampling estimates from stage to stage and also when compared
289 with one another, with binomial sampling probabilities spanning from about 0.1 to almost 1. Theropods
290 show higher sampling rates relative to ornithischians and sauropods in Triassic but much lower rates in
291 the early stages of the Cretaceous. This runs counter to earlier conclusions that richness trajectories of
292 Theropoda and Ornithischia seems to largely be driven by sampling bias, whereas sauropodomorphs are
293 less affected by bias in the fossil record (21,22).

294 Comparing our empirical sampling rate estimates with the second set of simulations that violated key
295 assumptions of TRiPS (Fig. 1), we find most of our empirical estimates fall within parameter ranges in
296 which we are able to retrieve true richness estimates reliably. This is with the caveat that the simulated
297 speciation and extinction rates are realistic for dinosaurs.

298 Our estimates of differential sampling across stages give a very different picture of bias than what the
299 residual approach would. To reiterate, the residual approach assumes that a chosen external time series
300 fully captures the sampling bias, and uses a model of fixed diversity to predict how richness would look *if*
301 *only* biased sampling drove the detected signal. In many cases, at least for dinosaurs, the number of fossil
302 collections from different intervals that contains at least one dinosaur (DBC) are often used as a proxy

303 for sampling (19,22,34). DBC should capture some of the sampling bias inherent in the dinosaur fossil
304 record, but a valid question is how much sampling bias it captures. To explore this, we compare our
305 proxy-free sampling estimates to DBCs. We performed correlation tests of the binomial sampling
306 probabilities estimated and the linearly detrended log₁₀ number of collections for all downloaded
307 dinosaur occurrences. Pearson product-moment correlations for the four taxonomic groups were: 0.55
308 ($p < 0.003$), 0.51 ($p < 0.019$), 0.69 ($p < 0.001$) and 0.68 ($p < 0.001$), for Dinosauria, Ornithischia,
309 Sauropodomorpha and Theropoda sampling probabilities, respectively, indicating that there is a common
310 signal in DBCs and our estimated sampling probabilities. However, not only is there remaining sampling
311 bias not captured by DBC introducing noise (since correlations are < 1), but possibly also adding bias if
312 used in richness estimation of dinosaurs.

313 **Dinosaur richness during the Mesozoic**

314 The species richness estimates from TRiPS shares dynamics with those painted by both the raw counts of
315 species and range-through species richness using the same dataset (Fig 3A). However, only in about half
316 the stages are the range-through estimates within the confidence interval of TRiPS estimates. Genus
317 richness dynamics are similar to species dynamics (SI figure) and indicate that for at least this dataset
318 using these analyses, genus level estimates can be a proxy for species estimates, corroborating Jablonski
319 and Finarell (35)'s findings. While genus richness estimates are lower, they are similar to species
320 estimates, unsurprisingly given there are few dinosaur species per genera (1.38 identified species per
321 genera in our data). Earlier attempts to estimate true taxon richness using ecological richness estimators
322 (e.g. 14), species-area curves (16,36) and using estimated durations of genera in a diversification
323 framework (15), they do not explicitly estimate sampling bias. Dodson (1990) estimated the total number
324 of dinosaur genera to be 900-1200 for the whole Mesozoic, with about 100 genera at any one geological
325 stage. Our estimates are more in line with Wang and Dodson's (14) estimates of genus richness based on
326 the Abundance Coverage Estimator, a metric frequently used in ecology, which inferred that the final
327 stages of the Cretaceous saw 200-300 genera of dinosaurs roaming our planet (our estimates are 279 and
328 305 genera for Campanian and Maastrichtian respectively (see Fig SI 7)). Wang and Dodson's (2006)
329 mixture of epoch and stage level (late Cretaceous only) genus richness estimates are difficult to compare
330 directly with our stage level only analysis. They estimated that, across the Mesozoic, genus richness of
331 dinosaurs was 1844, with only 527 genera actually having been observed. In our downloaded data there
332 are 1272 genera for dinosaurs, showing an immense increase in dinosaur occurrences compiled from the
333 literature since 2006. Calculating a mean binomial sampling probability for genera across the Mesozoic
334 using our stage specific sampling probabilities (weighted by estimated richness per stage) yields an
335 overall binomial probability of 0.80 (0.74 – 0.86), and estimates of true number of genera for the whole

336 Mesozoic is 1580 (CI: 1448-1761), slightly below Wang & Dodson's 1844. A Mesozoic mean sampling
337 probability at the species level (again, weighted by estimated richness from each stage) yield estimates of
338 total dinosaur species richness at 2983 (CI: 2462 – 3660).

339 The literature on dynamics of dinosaur species richness is vast, varied and sometime contradictory. Rather
340 than exhaustively comparing our estimates to those from all of the recent literature, we extract salient
341 points from Brusatte's (17) review for our discussion. According to Brusatte (2012, pg. 247), it is
342 currently accepted that dinosaurs did not rapidly diversify when they appeared around the start of the Late
343 Triassic. Rather, sauropodomorphs diversified during the final part of the Triassic, while ornithischians
344 and theropods increased in richness in the early Jurassic (17,33). While this pattern is in part corroborated
345 by our analysis for sauropods, sampling rates for ornithischians cannot be estimated with confidence for
346 any interval in the Triassic. In contrast to the received view (17,33), our estimates show that theropods
347 underwent diversification already in the Triassic, with estimated species richness being higher in Rhaetian
348 than the Hettangian, albeit with rather weak confidence (figure 2, Table 1). Sauropodomorphs, on the
349 other hand, exhibit rather high levels of both observed and estimated species richness already in the
350 Norian, and our estimate of sauropodomorph species richness during the Rhaetian is so high that it not
351 even surpassed by the diversity in the final stages of the Cretaceous, nor the supposed diversity peak in
352 the mid-Jurassic (37). In other words, our results indicate that a sauropodomorphs peak is reached in the
353 Rhaetian, and not in the Norian as earlier studies (22), due to the estimated low sampling for this clade in
354 this final stage of the Triassic.

355 The Jurassic-Cretaceous boundary (~145 Myr) is believed to have experienced clear diversity loss
356 (17,21,22), which Brusatte (2012) claims is particularly pronounced for Sauropodomorphs. Though the
357 observed species counts partially corroborates this, the sampling rates for the early part of the Cretaceous
358 are estimated to be much lower than late Jurassic (Fig 2), yielding only very small negative changes in
359 absolute species richness in the Jurassic-Cretaceous boundary (compare Tithonian and Berriasian in Table
360 1) for Sauropodomorpha and no clear signal of richness loss for the other groups. Genus level analyses
361 (see Fig SI 7) estimate that the number of Sauropodomorph genera in Berriasian is in fact ~10% higher
362 than in the Tithonian. It is also worth emphasizing that the confidence intervals for the estimated species
363 diversity are much wider in Berriasian compared to Tithonian, implying that an actual increase in the true
364 richness across this boundary cannot be excluded. The fact that the lower sampling rates during the
365 Berriasian is clear in all subgroups as well as for all dinosaurs (for both species and genus level analysis)
366 suggest that this "clear diversity loss", might be an artefact of sampling bias and that the 'major extinction'
367 of dinosaurs across the Jurassic-Cretaceous boundary (21,22,37–39) might be less severe than previously
368 thought.

369 In his review of the dinosaur literature, Brusatte (2012) also states that the dynamics of species richness
370 for the whole Mesozoic did not show a continual increase, but rather a collection of troughs and peaks.
371 This general statement is corroborated by our estimates. In particular, there is general agreement that not
372 only is there no decline in richness prior to the end-Cretaceous extinction, there is in fact a sharp increase
373 in diversity in the late Cretaceous (Brusatte 2012).

374 This Cretaceous increase in dinosaur diversity has been put in the context of the Cretaceous explosion of
375 terrestrial life (termed the Cretaceous Terrestrial Revolution (KTR)) (18,20,40) which saw the rapid rise
376 of flowering plants, insects and mammals. It has thus been hypothesized that the radiation of angiosperms
377 preceded the late Cretaceous increase in dinosaur diversity (18). Brusatte (2012) and Lloyd et al. (7,18)
378 attributes this increase in dinosaur richness in the two final stages of the Cretaceous to a sampling artifact
379 since these intervals show a high volume of fossiliferous rocks, thus arguing against the dinosaurs being a
380 part of the KTR. Our analysis corroborates Brusatte and Lloyd's claims that the final two stages both have
381 high sampling rates compared to earlier stages in the Late Cretaceous (Fig 2), indicating that, at least for
382 theropods and sauropodomorphs, there is little evidence of high diversification during the Late Cretaceous.
383 Nevertheless, ornithischians seem to reach an all-time diversity high in the final 20 million years of the
384 Cretaceous (Fig 2 and Table 1), increasing from a mere 11 species in the Coniacian to around 177 in the
385 Campanian. It is also worth noting that our reconstructed richness trajectory for sauropods shows a
386 relatively steady (but shallow) increase in richness the last 60 million years before the end of the
387 Cretaceous. Our estimated sampling rates for the Santonian (86.3-83.6 Ma) are remarkably low for all
388 groups (also in the preceding stage for sauropodomorphs), which indicates that the high level of diversity
389 of ornithischians and theropods was reached earlier (Santonian) than the consensus view that only the two
390 last stages of the Cretaceous show elevated richness (17).

391 This late Cretaceous increase in dinosaur diversity has also been framed as a debate on whether or not
392 dinosaurs showed a decline in species richness prior to the Cretaceous-Paleogene extinction event
393 (7,14,17,20,21,41). Brusatte et al. (2015) argues that, while there was no global long-term decline prior to
394 the end-Cretaceous extinction, there is evidence for ceratopsids and hadrosaurids (members of
395 Ornithischia) exhibiting declines in both species richness and morphological disparity in the final 15 Ma
396 of the Cretaceous (41). On the other hand, Lloyd (2012) claims sauropods and ornithischians both show
397 long-term declines throughout most of the Cretaceous while Barrett et al. (21) highlight a negative trend
398 in taxic diversity for theropods and ornithischians in the last two stages of the Cretaceous, but suggests a
399 'radiation' of sauropods in Late Cretaceous (see also 37). Our analysis indicates that ornithischians
400 decreased in richness (about 10 % reduction) in the last stage of the late Cretaceous (Fig 3, Table 1), but
401 shows no negative longer-term trend for any of the groups. The apparent trough in richness in the

402 Santonian and Coniacian for Sauropodomorphs and Theropods seem to be the result of poor sampling,
403 and not a true biological signal (Fig 2, Table 1), and sauropods show a marginal, but steady increase in
404 richness across most of the Cretaceous in contrast to their claimed radiation (21,37).

405 It is largely accepted that the Oxfordian (163.5-157.3 million years ago) exhibits remarkably low diversity,
406 perhaps even the most depauperate stage throughout the Age of the Dinosaurs (7,e.g. 17), and particularly
407 so for sauropodomorphs (22). Our approach, in contrast, estimates the sampling probability in this
408 particular stage to be the culprit of this trough and especially so for sauropodomorphs (see Fig 3 & Table
409 1). Instead of inferring low species richness in this stage, our estimates indicate the sauropodomorph
410 richness has quadrupled from the previous stage (Calloviaian), and a great richness increase is also evident
411 in ornithischians and the dinosaurs as a whole. More intense sampling efforts, both in the field and in
412 museum collections, and detailed analysis on the observations from the Oxfordian are clearly needed.

413 Conclusions and future directions

414 To properly paint the picture of past species richness, including the identification of periods of high
415 diversification rates and major extinction events, the bias inherent the fossil record that may mislead and
416 confound our inferences needs to be taken into account. Here we have detailed TRiPS, a new approach
417 for estimating both temporally varying sampling and species richness. The application of TRiPS to a
418 global dataset of dinosaur records indicates that several of the commonly held beliefs about the species
419 richness trajectory of dinosaurs might be effects of either sampling bias or the use of methods that might
420 have introduced new biases to richness estimates through their assumptions.

421 As a tool that estimates both sampling rates directly *and* true richness, TRiPS is pregnant with
422 possibilities and have applicability to a range of other paleontological questions. Richness and sampling
423 estimates from TRiPS allow us to test the Common Cause Hypothesis in a straightforward manner if
424 potential common drivers can be measured in the geological record. Estimates of sampling can be used in
425 predicting true ranges of a given species, if we can make the assumption that species have the same
426 temporally varying sampling rates. The two forms of sampling estimates may help paleontologists focus
427 their sampling and taxonomic efforts in time intervals (or geographic regions) which require most effort
428 given the specific questions we wish to answer as a community. While the application of TRiPS we
429 demonstrated here attempts to estimate global richness of dinosaurs and its major subclades, TRiPS can
430 be applied to any collection of lineages that are assumed or shown to have similar sampling rates, and
431 could also be used to estimate taxonomic richness on local to continental contexts.

432 **Data accessibility statement.**

433 All data were downloaded from Paleobiology Database (<https://paleobiodb.org/#/>). A copy of the
434 download will be made available on the authors' website together with the necessary code for
435 reproducing the results.

436 **Competing interests statement.**

437 The authors declare no competing interests.

438 **Authors' contributions**

439 JS conceived the study, performed the analysis and wrote the manuscript with substantial contributions to writing
440 and interpretation by LHL. Both authors gave final approval for publication.

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447 Publication XXX.

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451 **Supporting Information**

452 Online Supporting information contains details of the simulations, results regarding these simulations,
453 estimated sampling rates with confidence intervals, results from estimating sampling from all 100
454 replicated datasets detailed in the main text as well as estimated sampling rates and true richness counts
455 for dinosaur genera.

456

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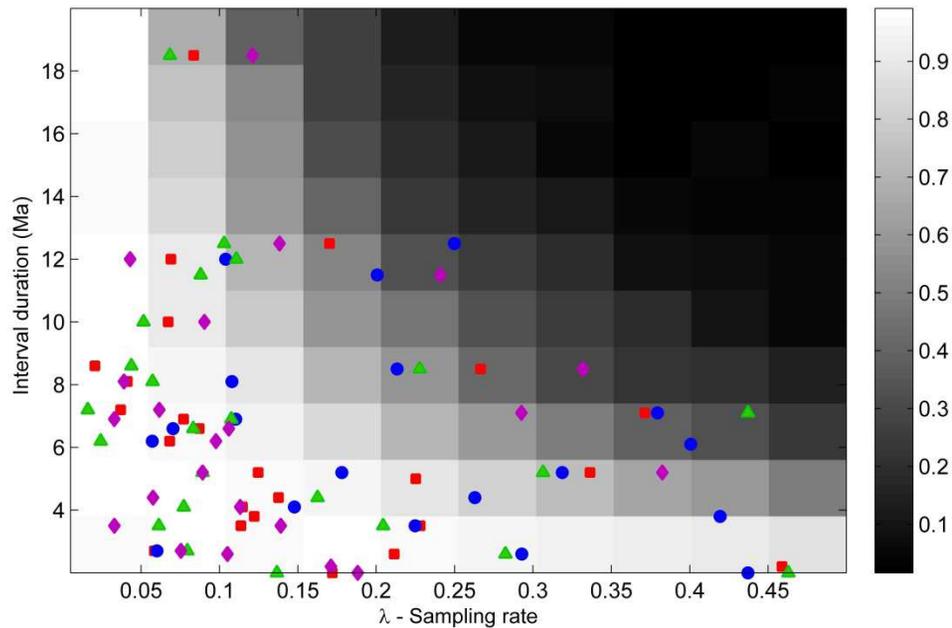
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550 Figures and table with captions



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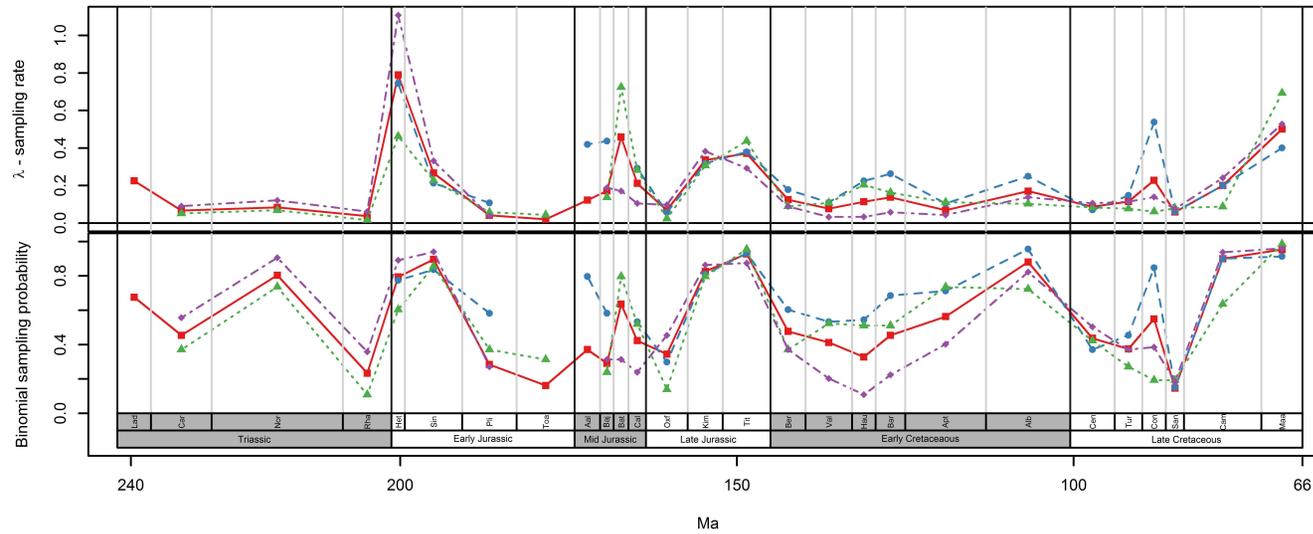
552 Figure 1

553 Simulation and estimation results. The grayscale indicates how often TRiPS is successful (the proportion of simulations inside a square that had a
554 95 % confidence interval that include the true richness) across mean sampling rates and time interval durations. All simulations presented here
555 violate both the assumption of constant richness within time interval dynamics and identical sampling rates for species, but TRiPS still manages to
556 capture the true richness in a large part of parameter space. Speciation and extinction rates are log uniformly distributed between 0.005 and 0.158.
557 Sampling rates for all dinosaurs (red squares), ornithischians (blue circles), sauropodomorphs (green triangles), theropods (purple diamonds) are
558 plotted against their corresponding stage durations (see Table 1 for 8 rates that had sampling rates higher than 0.5 not plotted here).

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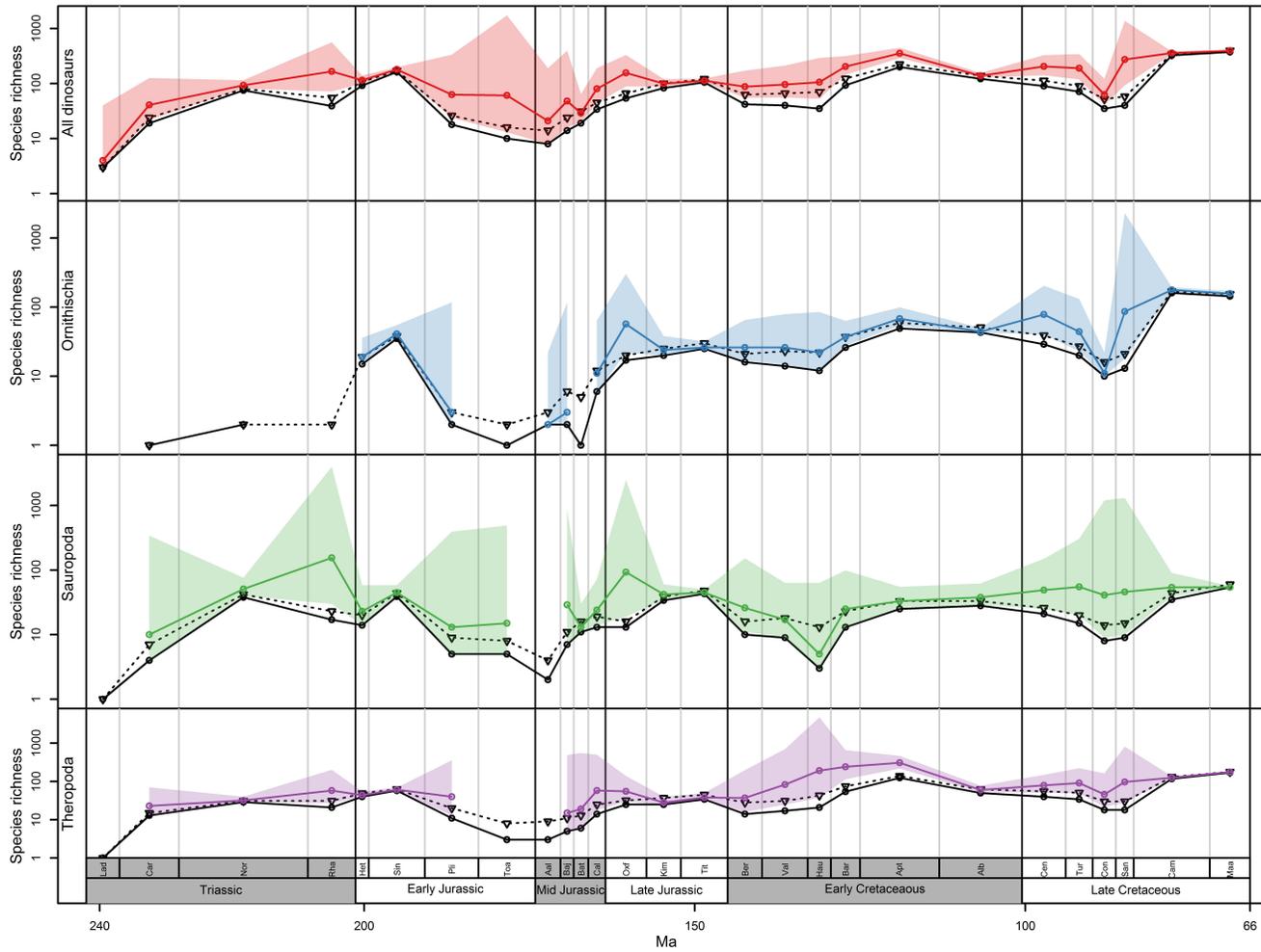
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564 Figure 2. Sampling estimates from TRiPS for all dinosaurs, ornithischian, sauropodomorph and theropod species considered separately. A.

565 Estimated sampling rates (λ) in sampling events per species per million years. B. Estimated binomial sampling probabilities ($p_{binom,t}$) of species
 566 within the plotted time interval. In both panels, estimates are in red (squares and full line) for all dinosaurs, blue for Ornithischia (circle and dashed
 567 line), green for Sauropodomorpha (triangles with dotted line) and purple for Theropoda (diamonds with dash-dotted line). Confidence intervals on
 568 all rates and probabilities and estimates from 100 replicated occurrence counts (see main text) are reported in the SI. For abbreviations of stage
 569 names see Table 1.

570



571

572 Figure 3. Species richness estimates from TRiPS. A. Dinosauria. B. Ornithischia. C. Sauropodomorpha. D. Theropoda. Black circles connected by
 573 full line indicates observed species counts, triangles connected by dotted line indicate range-through species counts while colored line and shading
 574 indicate maximum likelihood estimate and 95% confidence intervals for the true species richness estimated using TRiPS. Corresponding sampling
 575 estimates can be seen in Fig 2.

Stage (Abbr)	Interval details (Ma)			Dinosauria			Ornithischia			Sauropodomorpha species richness			Theropoda species richness			
	Start	End	Duration	1751 species with 4694 occurrences			521 species with 1485 occurrences			391 species with 979 occurrences			772 species with 2051 occurrences			
				Species richness	Sampling probability		Species richness	Sampling probability		Species richness	Sampling probability		Species richness	Sampling probability		
				N _{obs} (RT)	N _{me} (CI)		N _{obs} (RT)	N _{me} (CI)		N _{obs} (RT)	N _{me} (CI)		N _{obs} (RT)	N _{me} (CI)		
Late	Maastrichtian (Maa)	72.1	66	6.1	375 (397)	393 (383 - 407)	0.95 (0.94 - 0.96)	144 (154)	157 (148 - 171)	0.91 (0.89 - 0.93)	54 (60)	54 (54 - 57)	0.99 (0.98 - 0.99)	170 (178)	177 (171 - 185)	0.96 (0.95 - 0.97)
	Campanian (Cam)	83.6	72.1	11.5	324 (341)	359 (343 - 381)	0.9 (0.88 - 0.92)	160 (169)	177 (167 - 193)	0.9 (0.87 - 0.92)	35 (44)	54 (39 - 90)	0.64 (0.49 - 0.76)	118 (131)	125 (120 - 136)	0.94 (0.91 - 0.96)
	Santonian (San)	86.3	83.6	2.7	40 (58)	273 (93 - 1373)	0.15 (0.04 - 0.33)	13 (21)	86 (18 - 2288)	0.15 (0.01 - 0.5)	9 (15)	46 (10 - 1307)	0.19 (0.01 - 0.59)	18 (30)	97 (28 - 813)	0.18 (0.03 - 0.46)
	Coniacian (Con)	89.8	86.3	3.5	35 (52)	63 (41 - 122)	0.55 (0.37 - 0.71)	10 (16)	11 (10 - 22)	0.85 (0.64 - 0.95)	8 (14)	41 (9 - 1200)	0.19 (0.01 - 0.59)	18 (30)	46 (22 - 163)	0.39 (0.16 - 0.63)
	Turonian (Tur)	93.9	89.8	4.1	71 (90)	189 (119 - 343)	0.38 (0.25 - 0.51)	20 (27)	44 (23 - 131)	0.45 (0.22 - 0.69)	15 (20)	55 (20 - 305)	0.27 (0.08 - 0.55)	34 (51)	91 (49 - 222)	0.37 (0.2 - 0.56)
	Cenomanian (Cen)	100.5	93.9	6.6	90 (113)	205 (142 - 327)	0.44 (0.32 - 0.55)	29 (39)	78 (40 - 203)	0.37 (0.19 - 0.57)	21 (26)	49 (25 - 150)	0.42 (0.2 - 0.66)	40 (55)	79 (51 - 148)	0.5 (0.34 - 0.66)
Early	Albian (Alb)	113	100, 5	12.5	122 (138)	138 (128 - 155)	0.88 (0.84 - 0.91)	43 (51)	44 (43 - 50)	0.96 (0.93 - 0.98)	28 (33)	38 (29 - 62)	0.72 (0.57 - 0.84)	50 (62)	60 (52 - 78)	0.82 (0.74 - 0.89)
	Aptian (Apt)	125	113	12	199 (224)	353 (291 - 444)	0.56 (0.49 - 0.63)	49 (59)	68 (54 - 99)	0.71 (0.59 - 0.81)	25 (33)	33 (26 - 55)	0.74 (0.58 - 0.85)	124 (139)	307 (218 - 465)	0.4 (0.31 - 0.5)
	Barremian (Bar)	129.4	125	4.4	93 (123)	204 (145 - 315)	0.45 (0.35 - 0.56)	26 (37)	37 (28 - 63)	0.69 (0.53 - 0.81)	13 (23)	25 (13 - 99)	0.51 (0.21 - 0.79)	54 (75)	241 (114 - 659)	0.22 (0.1 - 0.38)
	Hauterivian (Hau)	132.9	129, 4	3.5	35 (70)	106 (53 - 292)	0.33 (0.16 - 0.53)	12 (22)	22 (12 - 85)	0.54 (0.22 - 0.82)	3 (13)	5 (3 - 63)	0.51 (0.12 - 0.87)	21 (43)	192 (38 - 4721)	0.11 (0.01 - 0.39)
	Valanginian (Val)	139.8	132, 9	6.9	40 (66)	96 (56 - 211)	0.41 (0.25 - 0.59)	14 (23)	26 (15 - 79)	0.53 (0.27 - 0.77)	9 (18)	17 (9 - 63)	0.52 (0.24 - 0.78)	17 (31)	83 (25 - 698)	0.2 (0.04 - 0.49)
Berriasian (Ber)	145	139, 8	5.2	42 (63)	88 (55 - 171)	0.48 (0.31 - 0.64)	16 (21)	26 (17 - 65)	0.6 (0.35 - 0.81)	10 (16)	26 (11 - 152)	0.37 (0.11 - 0.68)	14 (28)	37 (16 - 197)	0.37 (0.11 - 0.68)	
Late	Tithonian (Tit)	152.1	145	7.1	105 (121)	113 (107 - 123)	0.93 (0.9 - 0.95)	25 (30)	26 (25 - 32)	0.93 (0.87 - 0.97)	43 (48)	45 (43 - 50)	0.96 (0.92 - 0.97)	34 (45)	38 (34 - 50)	0.87 (0.79 - 0.93)
	Kimmeridgian (Kim)	157.3	152, 1	5.2	83 (100)	100 (88 - 120)	0.83 (0.76 - 0.88)	20 (25)	24 (20 - 38)	0.81 (0.66 - 0.91)	34 (39)	42 (35 - 60)	0.8 (0.68 - 0.88)	25 (37)	28 (25 - 40)	0.86 (0.75 - 0.93)

Cretaceous

Jurassic

	Oxfordian (Oxf)	163,5	157,3	6,2	54 (66)	156 (89 - 330)	0,34 (0,21 - 0,5)	17 (20)	57 (22 - 301)	0,3 (0,09 - 0,59)	13 (16)	93 (19 - 2476)	0,14 (0,01 - 0,47)	25 (32)	55 (30 - 139)	0,45 (0,25 - 0,66)
Mid	Callovian (Cal)	166,1	163,5	2,6	34 (45)	80 (45 - 190)	0,42 (0,24 - 0,62)	6 (12)	11 (6 - 64)	0,53 (0,18 - 0,84)	13 (19)	24 (14 - 72)	0,52 (0,28 - 0,74)	14 (25)	58 (18 - 496)	0,24 (0,05 - 0,56)
	Bathonian (Bat)	168,3	166,1	2,2	19 (31)	29 (20 - 64)	0,64 (0,41 - 0,82)	1 (5)	NA	NA	11 (16)	13 (11 - 30)	0,8 (0,53 - 0,94)	6 (13)	19 (6 - 553)	0,31 (0,02 - 0,78)
	Bajacian (Baj)	170,3	168,3	2	14 (24)	48 (16 - 394)	0,29 (0,06 - 0,64)	2 (6)	3 (2 - 117)	0,58 (0,05 - 0,96)	7 (11)	29 (7 - 853)	0,24 (0,02 - 0,68)	5 (11)	15 (5 - 488)	0,31 (0,02 - 0,78)
	Aalenian (Aal)	174,1	170,3	3,8	8 (14)	21 (8 - 190)	0,37 (0,08 - 0,74)	2 (3)	2 (2 - 22)	0,8 (0,25 - 0,99)	2 (4)	NA	NA	3 (9)	NA	NA
Early	Toarcian (Toa)	182,7	174,1	8,6	10 (16)	61 (13 - 1721)	0,16 (0,01 - 0,52)	1 (2)	NA	NA	5 (8)	15 (5 - 488)	0,31 (0,02 - 0,78)	3 (8)	NA	NA
	Pliensbachian (Pli)	190,8	182,7	8,1	18 (26)	63 (24 - 334)	0,28 (0,08 - 0,57)	2 (3)	3 (2 - 117)	0,58 (0,05 - 0,96)	5 (9)	13 (5 - 394)	0,37 (0,03 - 0,84)	11 (20)	40 (13 - 355)	0,27 (0,05 - 0,61)
	Sinemurian (Sin)	199,3	190,8	8,5	162 (171)	180 (169 - 197)	0,9 (0,87 - 0,92)	35 (38)	41 (36 - 55)	0,84 (0,74 - 0,9)	39 (44)	45 (40 - 58)	0,86 (0,78 - 0,91)	58 (63)	61 (58 - 69)	0,94 (0,91 - 0,96)
	Hettangian (Het)	201,3	199,3	2	92 (107)	115 (101 - 140)	0,79 (0,73 - 0,85)	15 (19)	19 (15 - 36)	0,77 (0,56 - 0,91)	14 (20)	23 (14 - 58)	0,6 (0,35 - 0,81)	40 (49)	44 (40 - 55)	0,89 (0,83 - 0,94)
Late	Rhaetian (Rha)	208,5	201,3	7,2	39 (55)	166 (72 - 562)	0,23 (0,09 - 0,43)	0 (2)	NA	NA	17 (23)	155 (30 - 3982)	0,11 (0,01 - 0,39)	21 (31)	58 (27 - 202)	0,36 (0,15 - 0,6)
	Norian (Nor)	227	208,5	18,5	75 (80)	93 (81 - 115)	0,8 (0,73 - 0,86)	2 (2)	NA	NA	38 (42)	51 (40 - 76)	0,74 (0,61 - 0,84)	29 (31)	32 (29 - 40)	0,91 (0,83 - 0,95)
	Carnian (Car)	237	227	10	19 (24)	41 (22 - 126)	0,45 (0,22 - 0,69)	1 (1)	NA	NA	4 (7)	10 (4 - 340)	0,37 (0,03 - 0,84)	13 (15)	23 (13 - 70)	0,56 (0,28 - 0,79)
	Ladinian (Lad)	242	237	5	3 (3)	4 (3 - 40)	0,68 (0,18 - 0,96)	0 (0)	NA	NA	1 (1)	NA	NA	1 (1)	NA	NA

577

578 Table 1. Sampling and richness observations and estimates for all dinosaurs, ornithischians, sauropodomorphs and theropods. Details of the start,
 579 end and duration of all intervals used (as downloaded from PaleobioDB) are shown in the first 3 columns. Observed species richness N_{obs} (range
 580 through in parenthesis), the maximum likelihood estimated true richness N_{true} (confidence intervals in parenthesis) and the maximum likelihood
 581 estimated sampling probability (confidence intervals) are then given for each group in each stage. NA indicates combinations of intervals and
 582 groups in which there was not enough data to estimate sampling rates, and thus no estimated true richness. Sampling probabilities in bold indicate
 583 estimates outside the range of Fig 1.

584