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Title:

How many dinosaur species were there?

True richness estimated using a Poisson sampling model (TRiPS)

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Abstract

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

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

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Introduction

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

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

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

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

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

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

Methods and data.

Data

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

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

Model: Fossil sampling as a Poisson process

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

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

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

$$L(\lambda_t | O_{i,t}, d_t) = \frac{\frac{(\lambda_t d_t)^{O_{i,t}}}{O_{i,t}!} e^{-\lambda_t d_t}}{1 - e^{-\lambda_t d_t}} \tag{2}$$

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

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$$\widehat{\lambda_t} = \max_{\lambda_t} \prod_{i=1}^{n_t} \frac{\frac{(\lambda_t d_t)^{O_{i,t}}}{O_{i,t}!} e^{-\lambda_t d_t}}{1 - e^{-\lambda_t d_t}} \tag{3}$$

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

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

$$p_{binom,t} = 1 - Poiss\left(0, \widehat{\lambda_t} d_t\right) = 1 - e^{-\widehat{\lambda_t} d_t} \tag{4}$$

where $Poiss(0, \widehat{\lambda_t} d_t)$ is the probability of 0 sampling events in one lineage with a rate $\widehat{\lambda_t}$ in a bin of duration d_t. The last step in estimating the true richness in a given time interval is to find the true species richness (n_{true}) that maximizes the binomial likelihood

$$L\left(n_{true} \mid p_{binom,t}, n_t\right) = \binom{n_{true}}{n_t} {p_{binom,t}}^{n_t} \left(1 - p_{binom,t}\right)^{(n_{true} - n_t)} \tag{5}$$

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

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

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

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

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

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

Simulations using a birth-death-fossilization process

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

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

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

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

The second round of simulations we simulated BD process with speciation and extinction rates > 0 which leads to species turnover. Speciation and extinction rates were drawn from log-uniform distributions spanning 0.005 to 0.158 per species per time unit and interval durations ranging from 2 to 20 time units (uniform distribution). The number of initial species was also varied in the range 10 through 250 (uniform distribution). Mean sampling rates of all species were allowed to vary from 0.01 to 0.5 fossils per species per time unit (log uniform). As in the first round, we also varied the variability in sampling across species within a simulation (coefficient of variation in the range 0 to 0.1, uniform distribution). We ran 100.000 simulations in which the parameter values were sampled using a latin-square hypercube to best span all combinations of parameters. We tracked the records of observations of species through time, and then analyzed these data with TRiPS. These simulations allowed us to explore the effects of violating TRiPS's assumption that a species, if found in a given time interval, is extant during the entire time interval. We evaluated TRiPS's ability to infer sampling rates and true species richness by 1) tabulating the number of simulations in which the true species richness was inside the predicted confidence interval and 2) estimating the bias in the maximum likelihood prediction of species richness $(N_{predicted} - N_{actual})/N_{actual}$. Details and code for the simulations are presented in the supporting information, and also available on the websites of the authors.

Implementation

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

RESULTS AND DISCUSSION

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

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

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

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

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

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

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

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

Varying sampling estimates among clades and through time

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

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

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

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

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

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

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

Dinosaur richness during the Mesozoic

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

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

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

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

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

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

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

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

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

Conclusions and future directions

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

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

Data accessibility statement.

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

Competing interests statement.

The authors declare no competing interests.

Authors' contributions

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

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Supporting Information

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

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Figures and table with captions

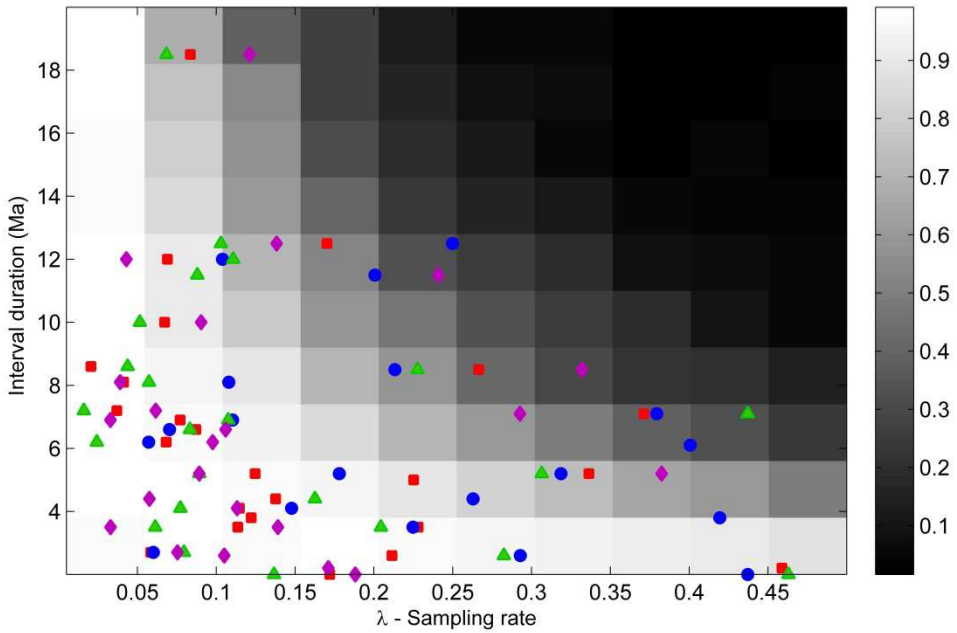

Figure 1

Simulation and estimation results. The grayscale indicates how often TRiPS is successful (the proportion of simulations inside a square that had a 95 % confidence interval that include the true richness) across mean sampling rates and time interval durations. All simulations presented here violate both the assumption of constant richness within time interval dynamics and identical sampling rates for species, but TRiPS still manages to 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. Sampling rates for all dinosaurs (red squares), ornithischians (blue circles), sauropodomorphs (green triangles), theropods (purple diamonds) are 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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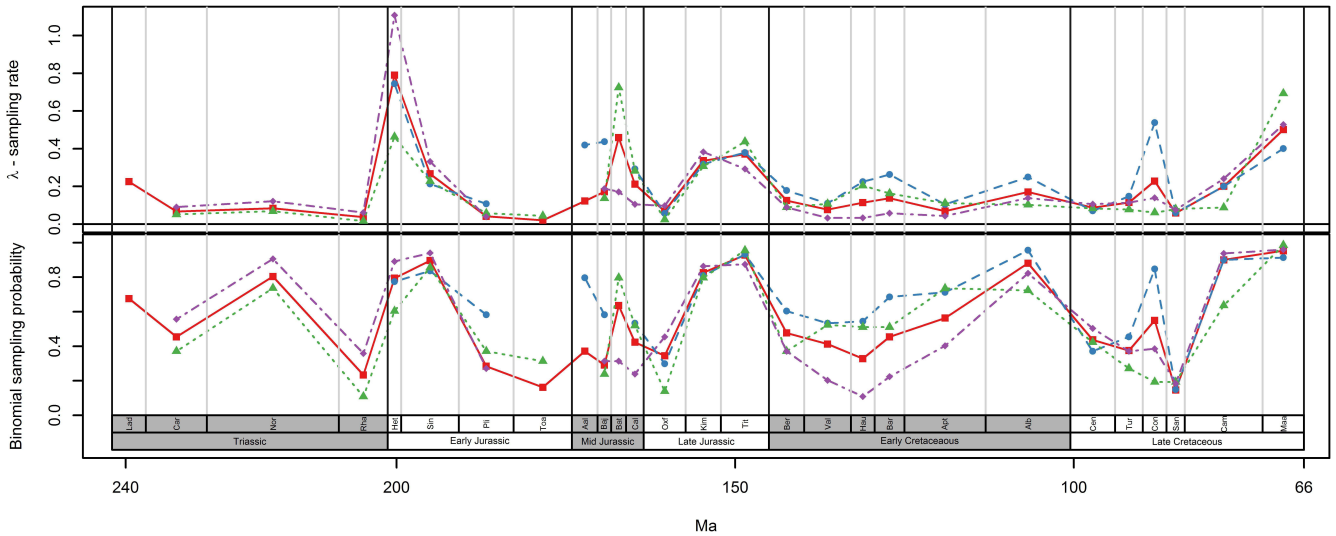

Figure 2. Sampling estimates from TRiPS for all dinosaurs, ornithischian, sauropodomorph and theropod species considered separately. A. Estimated sampling rates (λ) in sampling events per species per million years. B. Estimated binomial sampling probabilities ($p_{binom,t}$) of species within the plotted time interval. In both panels, estimates are in red (squares and full line) for all dinosaurs, blue for Ornithischia (circle and dashed line), green for Sauropodomorpha (triangles with dotted line) and purple for Theropoda (diamonds with dash-dotted line). Confidence intervals on all rates and probabilities and estimates from 100 replicated occurrence counts (see main text) are reported in the SI. For abbreviations of stage names see Table 1.

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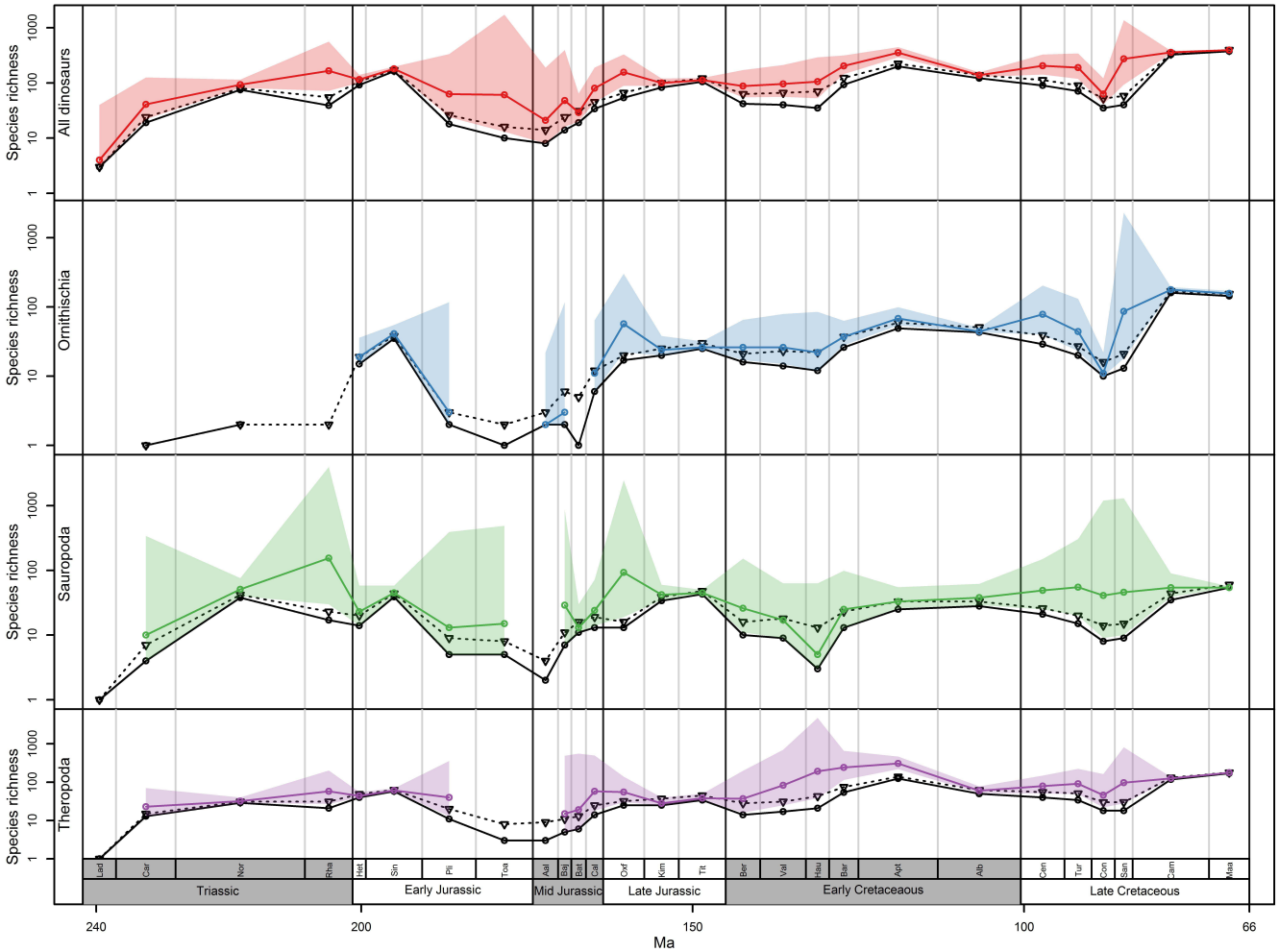

Figure 3. Species richness estimates from TRiPS. A. Dinosauria. B. Ornithischia. C. Sauropodomorpha. D. Theropoda. Black circles connected by full line indicates observed species counts, triangles connected by dotted line indicate range-through species counts while colored line and shading indicate maximum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

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		Interval details (Ma)			Dinosauria			Ornithischia			Sauropodomorpha species richness			Theropoda species richness		
					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
	Stage (Abbr)	Start	End	Duration	N_{obs} (RT)	N_{true} (CI)		N_{obs} (RT)	N_{true} (CI)		N_{obs} (RT)	N_{true} (CI)		N_{obs} (RT)	N_{true} (CI)	
Cretaceous, 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)**
Cretaceous, Late	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)
Cretaceous, Late	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)
Cretaceous, Late	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)
Cretaceous, Late	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)
Cretaceous, Late	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)
Cretaceous, 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)
Cretaceous, Early	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)
Cretaceous, Early	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)
Cretaceous, Early	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)
Cretaceous, Early	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)
Cretaceous, Early	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)
Jurassic, 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)
Jurassic, Late	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)

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		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)**
Triassic	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

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

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