How has our knowledge of dinosaur diversity through geologic time changed through research history?

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Assessments of dinosaur macroevolution at any given time can be biased by the historical publication record. Recent studies have analysed patterns in dinosaur diversity that are based on secular variations in the numbers of published taxa. Many of these have employed a range of approaches that account for changes in the shape of the taxonomic abundance curve, which are largely dependent on databases compiled from the primary published literature. However, how these 'corrected' diversity patterns are influenced by the history of publication remains largely unknown. Here, we investigate the influence of publication history between 1991 and 2015 on our understanding of dinosaur evolution using raw diversity estimates and Shareholder Quorum Subsampling for the three major subgroups: Ornithischia, Sauropodomorpha and Theropoda. We find that, while sampling is generally improving through time, there remain periods and regions in dinosaur evolutionary history where diversity estimates are highly volatile (e.g., the latest Jurassic of Europe, the mid-Cretaceous of North America, and the Late Cretaceous of South America). Our results show that historical changes in database compilation can often substantially influence our interpretations of dinosaur diversity. 'Global' estimates of diversity based on the fossil record are often also based on incomplete, and distinct regional signals, each subject to their own sampling histories. Changes in the taxon abundance distribution, either through discovery of new taxa or addition of existing taxa to improve sampling evenness, are important in improving the reliability of our interpretations of dinosaur diversity. Furthermore, as the number of occurrences and newly identified dinosaurs is still rapidly increasing through time, suggesting that it is entirely possible for much of what we know about dinosaurs at the present to change within the next 20 years.

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9   **Abstract**

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11 record. Recent studies have analysed patterns in dinosaur diversity that are based on secular variations

12 in the numbers of published taxa. Many of these have employed a range of approaches that account for

13 changes in the shape of the taxonomic abundance curve, which are largely dependent on databases

14 compiled from the primary published literature. However, how these 'corrected' diversity patterns are

15 influenced by the history of publication remains largely unknown. Here, we investigate the influence of

16 publication history between 1991 and 2015 on our understanding of dinosaur evolution using raw

17 diversity estimates and Shareholder Quorum Subsampling for the three major subgroups: Ornithischia,

18 Sauropodomorpha and Theropoda. We find that, while sampling is generally improving through time,

19 there remain periods and regions in dinosaur evolutionary history where diversity estimates are highly

20 volatile (e.g., the latest Jurassic of Europe, the mid-Cretaceous of North America, and the Late

21 Cretaceous of South America). Our results show that historical changes in database compilation can

22 often substantially influence our interpretations of dinosaur diversity. 'Global' estimates of diversity

23 based on the fossil record are often also based on incomplete, and distinct regional signals, each subject

24 to their own sampling histories. Changes in the taxon abundance distribution, either through discovery

25 of new taxa or addition of existing taxa to improve sampling evenness, are important in improving the

26 reliability of our interpretations of dinosaur diversity. Furthermore, as the number of occurrences and

27 newly identified dinosaurs is still rapidly increasing through time, suggesting that it is entirely possible

28 for much of what we know about dinosaurs at the present to change within the next 20 years.

Introduction

31 In the latter half of the 20th Century, palaeobiology underwent a renaissance by adopting a more

32 quantitative analytical approach to understanding changes in the fossil record through time (Valentine &

33 Moores 1970; Raup 1972; Gould & Eldredge 1977; Sepkoski et al. 1981; Van Valen 1984; Sepkoski Jr

34 1996). This seminal work was largely focussed around estimating patterns of animal diversity, extinction

35 and speciation through time, and what the external processes governing these were. To this day,

36 reconstructing the diversity of life through geological time remains one of the most crucial aspects of

37 palaeobiology, as it allows us to ask broader questions about the evolution of life and what the

38 mechanisms of extinction and recovery are. These pioneering analyses were largely based on an archive

39 of range-through taxa of marine animals, known as the 'Sepkoski Compendium'. More recently,

40 analytical palaeobiology has had a second wave of innovation, in part due to development of large fossil

41 occurrence databases such as the Paleobiology Database (www.paleobiodb.org), and also due to

42 development of increasingly sophisticated analytical subsampling (Alroy 2000a; Alroy 2003; Alroy 2010a;

43 Starrfelt & Liow 2016) and modelling (Smith & McGowan 2007; Lloyd 2012) techniques. These are

44 helping us to provide new insight into the evolutionary patterns and processes that we can infer from

45 the fossil record.

46 All of these studies, both older and more recent, are under-pinned by a single principle, in that they rely

47 on the recorded number of identifiable fossiliferous occurrences present through geological time.

48 Despite meticulous work to ensure that these databases and compendia represent the best possible

49 records of historical trends, there have been continuing questions as to the accuracy of the data and the

50 existence of what is broadly termed as 'bias', which can confound our estimates of palaeodiversity. This

51 includes factors such as heterogeneous sampling intensity, fossiliferous rock availability, and variable

52 depth of taxonomic research (Raup 1972; Raup 1976; Uhen & Pyenson 2007; Benton 2008a; Benton

53 2008b; Marx & Uhen 2010; Tarver et al. 2011; Smith et al. 2012; Smith & Benson 2013).

54 In 1993, Sepkoski added an additional dimension to these studies by assessing how database

55 compilation history through changes in taxonomy, stratigraphic resolution, and sampling influences the

56 shape of macroevolutionary patterns (Sepkoski Jr 1993). This was based on comparing two compendia

57 built in 1982 and 1992, and found that in spite of numerous taxonomic changes over ten years, the

58 overall patterns of diversity for marine animals remained relatively constant, with the main notable

59 change being that overall diversity was consistently higher in the 1992 compilation. Following this, Alroy
60 (2000b) similarly showed that database age does appear to have an influence on North American
61 mammal diversity estimates, and Alroy (2010c) further demonstrated that diversity estimates based on
62 data from the Paleobiology Database were proportionally similar to either the genus- or family-level
63 results based on Sepkoski's original compendium. At the present, there are three main arguments
64 regarding the historical reliability of diversity curves (e.g., (Sepkoski et al. 1981); Sepkoski Jr (1993);
65 Alroy (2000b): firstly, that because independent datasets produce similar diversity curves, this suggests
66 that convergence on a common signal reflecting either a real evolutionary, fossil record structure, or
67 taxonomic phenomenon; secondly, that the addition of new data to existing compilations should yield
68 only minor changes to resulting diversity estimates; and thirdly, that the addition of new data can
69 potentially dramatically alter shape of diversity (counter to the first and second arguments). At the
70 present, the first argument appears to be the best supported by analytical evidence.

71 However, besides Sepkoski and Alroy's work, relatively little consideration has been given to how
72 publication or database history can influence macroevolutionary patterns, despite an enormous reliance
73 on their research utility (although see Benton (2008a); Benton (2008b); Tarver et al. (2011) for examples
74 using vertebrates). In particular, to our knowledge, no one has yet tested this potential influence using
75 an occurrence-based tetrapod dataset, such as those available from the Paleobiology Database. This is
76 important, given that a wealth of recent studies, and in particular on tetrapod groups, have focussed on
77 estimating diversity patterns through geological time and interpreting what the potential drivers of
78 these large-scale evolutionary patterns might be (Butler et al. 2009; Benson & Butler 2011; Butler et al.
79 2011; Mannion et al. 2015; Nicholson et al. 2015; Benson et al. 2016; Grossnickle & Newham 2016;
80 Nicholson et al. 2016; Tennant et al. 2016a; Brocklehurst et al. 2017). Many of these studies have
81 employed subsampling methods that are sensitive to changes in the shape of the taxonomic abundance
82 distribution, which we would expect to change in a non-random fashion based on new fossil discoveries
83 through time as they are published (Benton et al. 2011; Benton et al. 2013a; Benton 2015) (e.g., due to
84 the opening up of new discovery regions for geopolitical reasons, or the historical and
85 macrostratigraphic availability of fossil-bearing rock formations). Furthermore as sampling increases
86 through time we might also expect the relative proportion of singleton occurrences to decrease,
87 improving the evenness of the underlying sampling pool (Alroy 2010a; Chao & Jost 2012), and therefore
88 influencing calculated diversity estimates (see Methods below). Assessing this influence in a historical
89 context is therefore important for understanding how stable our interpretations of evolutionary
90 patterns are.

91   While the data used in these analyses are typically based on a 'mature' dataset that has undergone

92   rigorous taxonomic scrutiny and data addition or refinement, they often tend to neglect explicit

93   consideration of the potential influence of temporal variations in the publication record (which these

94   databases are explicitly based on). This has important implications for several reasons. Firstly, we might

95   expect the shape of both raw and subsampled diversity curves to change through time in concert with

96   new discoveries and as sampling increases (Sepkoski Jr 1993; Alroy 2000b). Secondly, this could

97   therefore impact our interpretations of the relative magnitude, tempo and mode of apparent radiations

98   and extinctions, or we might find that subsampled diversity estimates stabilise at some point. Thirdly, if

99   the shape of estimated diversity curves change (either based on raw or 'corrected' data), we could see

100   that the strength of results from comparisons of diversity with extrinsic factors such as sea-level or

101   palaeotemperature (Benson et al. 2010; Benson & Butler 2011; Butler et al. 2011; Peters & Heim 2011b;

102   Mayhew et al. 2012; Martin et al. 2014; Mannion et al. 2015; Nicholson et al. 2015; Tennant et al. 2016a;

103   Tennant et al. 2016b) will change.

104   As our data become more refined, capturing this influence of sampling variation becomes more

105   important through longer periods of time. We might expect sampling error to be highest earlier on in

106   sampling history, and to reduce through time, therefore improving the reliability of our correlation

107   estimates. However, if our subsampled diversity estimates remain stable through historical time, then

108   we can be more confident in these interpretations, as well as the effectiveness of subsampling methods

109   in reliably estimating diversity. Recently, this was potential issue highlighted by Jouve et al. (2017) in a

110   small study of Jurassic and Cretaceous thalattosuchian crocodylomorphs. These authors tested the

111   conclusions of Martin et al. (2014) and their assertion that sea-surface temperature was the primary

112   factor driving marine crocodylomorph evolution, contra Mannion et al. (2015) and Tennant et al.

113   (2016a). They found that the strength of the relationships reported by the first study, also different to

114   those reported by (Mannion et al. 2015) and (Tennant et al. 2016a), were fairly unstable even based on

115   very recent changes in taxonomy. This taxonomically constrained example provides an interesting case

116   of how small changes in publication history can lead to potentially mixed interpretations of

117   macroevolutionary patterns.

118   In this study, we investigate the influence of publication history on our reading and understanding of

119   diversity patterns through time. For this, we use the clade Dinosauria (excluding Aves) as a study group,

120   as they have an intensely sampled fossil record and a rich history of taxonomic and macroevolutionary

121   research. We note that this is just one of a whole suite of potential biases in paleodiversity studies (e.g.,

122   appropriate time-binning methods, optimal analytical protocols, or the impact of variation in the rock

123   record through space and time), and these factors are appropriately discussed in more detail elsewhere

124   (Peters & Heim 2010; Benson & Butler 2011; Heim & Peters 2011; Peters & Heim 2011b; Benson &

125   Upchurch 2013; Benton et al. 2013b; Dunhill et al. 2014; Benton 2015; Benson et al. 2016; Tennant et al.

126   2016b).

127

128   **Material and Methods**

129   *Dinosaur occurrences dataset*

130   We used a primary dataset of dinosaur body fossil occurrences drawn from the Paleobiology Database

131   (November, 2017; note a new download was performed subsequent to peer review) that spans the

132   entirety of the Late Triassic to end- Cretaceous (66-235 Ma) (SI 1). This comprised only body fossil

133   remains, and excluded ootaxa and ichnotaxa. This dataset was divided into the three major clades,

134   Sauropodomorpha, Ornithischia, and Theropoda. We excluded Aves as they have a fossil record

135   dominated by different and often exceptional modes of preservation. Having limited occurrences of

136   exceptionally preserved fossils will bias our results, particularly in time periods characterised by the

137   presence of avian-bearing Konservat-Lagerstätten (Brocklehurst et al. 2012; Dean et al. 2016). We

138   elected to use genera, as these are more readily identified and diagnosed, which means that we can

139   integrate occurrences that are resolved only to the genus level (e.g., *Allosaurus* sp.), and therefore

140   include a substantial volume of data that would be lost at any finer resolution (Robeck et al. 2000). A

141   potential issue with this genus-level approach is that analysing palaeodiversity at different taxonomic

142   levels can potentially lead to different interpretations about what the external factors mediating it are

143   (Wiese et al. 2016). Despite the fact that some dinosaur genera are multispecific, it has been shown

144   previously that both genus- and species-level dinosaur diversity curves are very similar (Barrett et al.

145   2009), and that there is more error in species level dinosaur taxonomy than for genera (Benton 2008b).

146   It has also been repeatedly demonstrated that the shape of species and genus curves are strongly

147   correlated in spite of differential taxonomic treatment (Alroy 2000b; Butler et al. 2011; Mannion et al.

148   2015), and therefore a genus level compilation should be sufficient for the scope of the present study.

149   These databases are based on a comprehensive data compilation effort from multiple workers, and

150   represent updated information on dinosaur taxonomy and palaeontology at this time. We elected to use

151   a stage-level binning method based upon the Standard European Stages and absolute dates provided by

152   Gradstein et al. (2012). Others have used an equal-length time binning approach (Mannion et al. 2015;

153   Benson et al. 2016), but this has limitations in that it reduces the number of data points for statistical

154   analyses, and can artificially group fossil occurrences from different stages that never temporally co-

155   existed, which would confound our analyses. Only body fossil occurrences that could be unambiguously

156   assigned to a single stage bin were included, and those in which assignment to a single stage bin was

157   either ambiguous or not possible were excluded. This procedure was in order to avoid the over-counting

158   of taxa or occurrences that have poorly constrained temporal durations or contained within multiple

159   time bins. Each dinosaurian sub-group was further sub-divided into approximately contiguous

160   palaeocontinental regions: Africa, Asia, Europe, South America, and North America (Mannion et al.

161   2015). Unfortunately, sampling is too poor to analyse patterns in Antarctica, Australasia, or Indo-

162   Madagascar, although these regions remain included in the global analyses. We also provide data on the

163   number of newly identified occurrences (SI 2) and newly named genera (SI 3) based on publication date.

164

165   *Calculating diversity through time*

166   To test how diversity changes through time, we reduced this primary dataset by successively deleting

167   data from publications of each individual occurrence recursively at two year intervals. Note that this is

168   not the same as the date that the entries were made into the database, but the explicit date of

169   publication of that occurrence record in the published version of record. We stopped at 1991, giving 12

170   sequential temporal datasets for each dinosaurian clade. What this represents is the maturity of the

171   dataset with respect to its present state based on publication history. Two methods were used to assess

172   diversity patterns. Firstly, empirical diversity based on raw in-bin counts of taxa. This method has been

173   strongly suggested to be a 'biased' or poor estimator of true diversity as it is influenced by

174   heterogeneous sampling (Benson et al. 2010; Benson & Butler 2011; Benson & Upchurch 2013; Butler et

175   al. 2013; Smith & Benson 2013; Newham et al. 2014; Mannion et al. 2015; Tennant et al. 2016b).

176   Secondly, we employed the shareholder quorum subsampling (SQS) method, which was designed to

177   account for differences in the shape of the taxon-abundance curve (Alroy 2010c; Alroy 2010a), and

178   implemented in Perl (SI 4, 5).

179   SQS standardizes taxonomic occurrence lists based on an estimate of coverage to determine the relative

180   magnitude of taxonomic biodiversity trends (Alroy 2010c; Alroy 2010a). In this method, each taxon

181   within a sample pool (time bin) is treated as a 'shareholder', whose 'share' is its relative occurrence

182   frequency. Taxa are randomly drawn from compiled in-bin occurrence lists, and when a summed

183   proportion of these 'shares' reaches a certain 'quorum', subsampling stops and the number of sampled

184   taxa is summed. Coverage, as a measure of sampling quality, is defined as the proportion of the

185   frequency distribution of taxa within a sample. It is estimated by using randomized subsampling to

186   calculate the mean value of Good's u, which is defined as 1 minus the number of singleton occurrences,

187   divided by the total number of occurrences (Good 1953). A coverage value of zero indicates that all taxa

188   are singleton occurrences (i.e., that all occurrences of a taxon are restricted to a single collection within

189   a time bin). Higher coverage values indicate more even sampling of taxa, and therefore provides a

190   measure of sample completeness that is independent of the overall sample pool size. For each time bin,

191   u is then divided into the quorum level (Alroy 2010a), thereby providing an estimate of the coverage of

192   the total occurrence pool. In all subsampling replicates, singletons were excluded to calculate diversity

193   (but included to calculate Good's u), as they can distort estimates of diversity. Dominant taxa (those

194   with the highest frequency of occurrences per bin) were included, and where these taxa are drawn, 1 is

195   added to the subsampled diversity estimate for that bin (Alroy 2010c). Finally, single large collections

196   that can create the artificial appearance of poor coverage were accounted for by counting occurrences

197   of taxa that only occur in single publications, as opposed to those which occur in single collections, and

198   excluding taxa that are only ever found in the most diverse collection. 1000 subsampling trials were run

199   for each dataset (Theropoda, Ornithischia, and Sauropodomorpha, for each region and 2 year time

200   interval), and the mean diversity reported for each publication time interval. For each sequential

201   subsampling iteration, whenever a collection from a new publication was drawn from the occurrence list,

202   subsequent collections were sampled until exactly three collections from that publication had been

203   selected (Alroy 2010a). We set a baseline quorum of 0.4, as this has been demonstrated to be sufficient

204   in accurately assessing changes in diversity, and widely used (Alroy 2010c; Alroy 2010a; Mannion et al.

205   2015; Nicholson et al. 2015; Tennant et al. 2016a). Diversity is not reported for any analyses in which

206   this quorum could not be attained, and given an NA value. This dual method is important, as not all

207   publications name new taxa – some add to our knowledge of existing taxa by publishing on new

208   occurrences in different collections (or sites), and therefore by applying a method that accounts for

209   changes in taxonomic abundance across collections we can see how publication history influences

210   diversity through subsampling methods.

211

212   *Correlation between diversity extrinsic parameters*

213   For our model-fitting protocol, we follow the procedure outlined in numerous recent analytical studies,

214   by employing simple pairwise correlation tests to the residuals of detrended time series at the stage

215 level (Benson & Butler 2011; Butler et al. 2011; Butler et al. 2013; Mannion et al. 2015; Tennant et al.

216 2016a). Residuals for each of the two environmental parameters were calculated using the arima()

217 function, which uses maximum likelihood to fit a first-order autoregressive model to each time series

218 (Gardner et al. 1980). This method detects the potential influence of any long-term background trend

219 (i.e., a directed change in the mean value of the complete time series through time) within the time

220 series, which has the potential to artificially inflate correlation coefficients in pairwise tests (Box &

221 Jenkins 1976), and also accounts for any potential serial autocorrelation (i.e., the correlation of a

222 variable with itself through successive data points). This protocol has become standard practice now for

223 palaeontological time series analysis following its recommendation by Alroy (2000b). For sea level, we

224 used the curve of Miller et al. (2005), which has been widely applied in recent analyses of tetrapod

225 diversification (Benson et al. 2010; Butler et al. 2011; Martin et al. 2014; Mannion et al. 2015; Tennant

226 et al. 2016a), and for palaeotemperature we used the data from Prokoph et al. (2008), available as Stage

227 level data from Hannisdal & Peters (2011) (SI 6).

228 We performed an assessment of normality for each time series prior to any correlation analyses, using

229 the Shapiro-Wilk test (shapiro.test() function in R). From the output, if the p-values are greater than the

230 pre-defined alpha level (traditionally, 0.05, and used here) this implies that the distribution of the data

231 are not significantly different from a normal distribution, and therefore we can assume normality and

232 use Pearson's test (Pearson's product moment correlation coefficient [r]). If $p > 0.05$, we performed a

233 non-parametric Spearmans rank correlation (ρ). For each test, both the raw and adjusted p-values are

234 reported, the latter calculated using the p.adjust() function, and using the 'BH' model (Benjamini &

235 Hochberg 1995). This method accounts for the false-discovery test when performing multiple hypothesis

236 tests with the same data set, which can inflate type-1 error (i.e., in order to avoid falsely rejecting a true

237 null hypothesis; a false positive). We avoided the more commonly used 'Bonferroni correction', due the

238 undesirable property it has of potentially increasing type 2 error to unacceptable levels (Nakagawa

239 2004). This adjustment was performed on 'families' of analyses (i.e., non-independent tests), rather than

240 on all correlation tests together, otherwise we potentially run the risk of setting the pass rate for

241 statistical significance too low.

242 We performed pairwise correlations for the detrended subsampled diversity estimates at each two year

243 iteration for each group to assess how the strength and direction of correlation changes through

244 publication history. We do not use a maximum likelihood model fitting approach because rather than

245 trying to distinguish between a set of candidate models, we are simply assessing how the strength of

246   correlations changes through publication history. All analyses were carried out in R version 3.0.2 (R

247   Development Core Team 2013) using the functions available in the default *stats* package..

248

249   **Results**

250   *Occurrences and genera through time*

251   From the first dinosaur discoveries until around 1950, the number of dinosaur occurrences published

252   remained mostly consistent and steadily increasing through time (Fig. 1). From the mid-to the end of

253   20th century, the number of published occurrences has increased substantially. This is mostly due to the

254   publication of theropod and ornithischian occurrences, which reached a peak around the turn of the

255   millennium, with occurrences of all three groups remaining high but declining in rate of publication after

256   this. A very similar pattern is observed for genera, with the publication of newly named genera

257   increasing exponentially since around 1990, and at an equal rate for all three groups (Fig. 2). The

258   cumulative frequency of newly named genera shows that, although the rate of growth remains

259   approximately comparable and increasing for all three groups, there are times when the relative overall

260   number of genera between groups changes through publication history. For example, while

261   sauropodomorphs had more named genera than theropods until around 1935, this changed at around

262   1960 when new theropod genera became more frequently published than sauropodomorphs. The

263   recent rate of growth of newly named theropod genera in the last 15 years means that they are now

264   named as frequently as newly named ornithischian genera.

265   [Figure 1 – Occurrences through time]

266   [Figure 2 – Genera through time]

267   *'Global' patterns of total dinosaur diversity*

268   Apparent 'global' empirical dinosaur diversity steadily rises until the end of the Jurassic (Fig. 3A).

269   Diversity is low across the J/K interval until the Hauterivian, before recovering in the late Early

270   Cretaceous. There is a second decline through the late Early to early Late Cretaceous interval, before

271   diversity increases to its zenith in the latest Cretaceous. This general pattern remains constant

272   throughout publication history, although diversity in the 'middle' Cretaceous and latest Cretaceous

273   intervals shows the greatest increases. Subsampled global dinosaur diversity retains this overall pattern

274   (Fig. 3B). The J/K interval decline is still visible, but the late Early Cretaceous apparent diversity increase

275   supersedes Late Jurassic levels. The early Late Cretaceous decline is also still present, but the magnitude

276   of the latest Cretaceous diversity increase is much lower than that recovered for the empirical data. The

277   reason for this distinction between subsampled and raw diversity is that SQS estimates diversity by

278   standardising coverage of the taxon-abundance distribution, and thereby reduces the impact of

279   intensely sampled time intervals such as the latest Cretaceous.

280   [Figure 3 – Dinosaur global diversity]

281

282   *Patterns of raw and subsampled diversity by group*

283   ***Ornithischians***

284   Raw 'global' ornithischian diversity (Fig. 4A) is constant and stable throughout publication history. The

285   apparent magnitude of longer-term trends is obscured by the relative over-sampling of the Campanian

286   and Maastrichtian, which are almost an order of magnitude higher than any other Jurassic or Cretaceous

287   stage interval. Indeed, the Campanian shows no sign of slowing down in increasing diversity, and is the

288   highest and most rapidly increasing of any time interval. In spite of this, the overall trends in raw

289   diversity remain, with steadily increasing Middle to Late Jurassic diversity, a small earliest Cretaceous

290   decline followed by a 'middle' Cretaceous peak in the Aptian, a shallow decline into the early Late

291   Cretaceous, and an increase in the Campanian.

292   Raw diversity in Europe shows increasing diversity across the J/K transition before an earliest Cretaceous

293   decline (Valanginian to Hauterivian), constant 'middle' Cretaceous diversity, and an increase from the

294   Campanian to Maastrichtian (Fig. 4B). Raw African ornithischian diversity is too inconsistent to analyse

295   any changes through geological time or publication time (Fig. 4C). Raw Asian diversity is fairly constant

296   through the Cretaceous, until an apparent major Campanian peak and Maastrichtian decline (Fig. 4D). In

297   North America, empirical diversity is flat and low throughout the Late Jurassic and most of the

298   Cretaceous (Fig. 4E). There is a Campanian peak, and order of magnitude higher than any prior interval,

299   which is rapidly increasing through publication time. Diversity decreases from this into the Maastrichtian,

300   in which diversity has remained relatively stable through publication time. Sampling in South America is

301   also relatively poor, with apparent diversity remaining low and flat where a signal is obtained (Fig. 4F).

302   [Figure 4 – Ornithischians, raw]

303 Subsampled 'global' ornithischian diversity shows a distinctly different pattern from the raw curve, both

304 in terms of overall trends, and in terms of the magnitude of the effect of publication history (Fig. 5A).

305 The Jurassic is generally too poorly sampled to reveal a constant signal, but there is evidence of a decline

306 through the Jurassic/Cretaceous transition, which remains constant through publication time. This is

307 followed by a middle-Cretaceous increase, in which ornithischian diversity is at its second highest level

308 throughout their history. The magnitude of this Albian radiation has rapidly increased over publication

309 time, the result being that originally what appeared to be increasing subsampled diversity over the

310 Early/Late Cretaceous transition now shows a major decline from the Albian to Coniacian. Santonian

311 subsampled diversity remains unknown, but when we see a signal emerge in the Campanian, diversity is

312 higher than the Albian, reaching its highest level before declining by more than half into the

313 Maastrichtian. This overall structure, besides the Albian, remains consistent throughout publication time

314 with no major perturbations to the apparent 'global' curve.

315 [Figure 5 – Ornithischians, SQS]

316 Subsampled European diversity reveals increasing diversity across the Tithonian/Berriasian transition,

317 followed by overall gradually decreasing diversity throughout the remainder of the Early Cretaceous (Fig.

318 5B). In Africa, the signal is too poor to reveal anything besides a Kimmeridgian/Tithonian subsampled

319 diversity drop (Fig. 5C), and in Asia, there is evidence of a decline in subsampled diversity across the

320 Albian/Cenomanian transition (Fig. 5D). In North America, subsampled diversity reveals a decline across

321 the Early-Late Cretaceous transition, and a major decline from the Campanian to Maastrichtian, a

322 pattern that remains stable through publication history (Fig. 5E). In South America, the subsampled

323 signal is too poor to say anything about ornithischian diversity (Fig. 5F).

324 If we look at how coverage has changed through publication history (based on Good's u), we should

325 expect that subsampled diversity patterns are reflective of this. At a global level, coverage in the

326 Cretaceous is much better than the Jurassic (Fig. 6A). Much of this, however, is based on patchy regional

327 record. In Europe, we find that coverage increases across the J/K interval (Fig. 6B), and is the only place

328 where a consistently reliable record here can be obtained. In Africa, coverage is generally poor, besides

329 in the latest Jurassic (Fig. 6C). In Asia, coverage is poor up until the late Early Cretaceous (Fig. 6D). In

330 North America, coverage is good in the latest Jurassic and 'middle' to Late Cretaceous, but non-existent

331 in Early to Middle Jurassic and earliest Cretaceous (Fig. 6E). Coverage is generally poor for the entire

332 South American ornithischian record (Fig. 6F), explaining why obtaining a subsampled diversity signal

333 here is difficult.

334   [Figure 6 – Ornithischia, u]

335

336   ***Theropods***

337   The overall shape of the raw 'global' theropod diversity curve remains consistent through publication

338   history for the Jurassic (Fig. 7A), similar to ornithischians, where we see steadily increasing Middle to

339   Late Jurassic diversity. 'Middle' Cretaceous raw diversity fluctuated, followed by a major Campanian to

340   Maastrichtian rise. The lowest apparent diversity is in the Coniacian, reaching earliest Cretaceous levels.

341   Notable variations due to publication history are in the Barremian to Cenomanian, where diversity

342   increases in magnitude through time, gradually exceeding that for Late Jurassic diversity. Raw European

343   diversity is fairly constant through publication history (Fig. 7B), with a Middle Jurassic diversity peak in

344   the Bathonian, followed by a Callovian-Oxfordian trough, a second larger Kimmeridgian peak, and then

345   constant decline from the Tithonian to the Valanginian. Barremian diversity is increasing through

346   publication time, and is as high as Kimmeridgian levels. Aptian and Albian diversity is relatively low

347   through publication history. Campanian and Maastrichtian diversity levels are slowly increasing through

348   publication history. As with ornithischians, African theropods are generally too poorly sampled at the

349   stage level to recognise any consistent empirical patterns (Fig. 7C). There is a Cenomanian raw diversity

350   spike, but how this compares with much of the rest of the Cretaceous is obscured by patchy sampling. In

351   Asia, raw Late Jurassic diversity is generally lower than for the Cretaceous (Fig. 7D). The Cretaceous sees

352   three peaks in apparent diversity during the Aptian, Turonian and Campanian-Maastrichtian, with the

353   latter being considerably higher than any previous one, and growing rapidly through publication history.

354   In North America, raw diversity levels are dwarfed by the intensive sampling of latest Cretaceous

355   theropods, with major gaps in the Middle to Late Jurassic and earliest Cretaceous records (Fig. 7E).

356   Campanian and Maastrichtian raw diversity is constantly increasing at a faster rate than any other time

357   interval, and consistently reveals a slight apparent diversity decline into the end-Cretaceous. Raw South

358   American diversity estimates are changing rapidly through publication history, with almost every

359   interval in which dinosaurs are available to be sampled doubling or tripling since 1991 (Fig. 7F). Of note

360   is a recently emerging Late Jurassic theropod fossil record in South America, which at the present

361   reveals an apparent low diversity.

362   [Figure 7 – Theropoda, raw]

363   When subsampling is applied, in the Late Jurassic we see a switch from steadily increasing subsampled

364   diversity to a major Oxfordian peak and subsequent decline in diversity through the J/K transition

365   decline, a pattern that is consistently recovered through publication time (Fig. 8A). Subsampled diversity

366   is at its highest level during the Aptian than at any other stage during theropod history, and has doubled

367   in the last 20 years of publication history. Campanian and Maastrichtian diversity are as high as the

368   Cenomanian, a pattern that remains consistent through publication time. We see the 'global' J/K

369   transition decline reflected in Europe (Fig. 8B), and a strong Barremian peak, which is not captured on a

370   'global' scale. Latest Triassic subsampled diversity is higher than at any other point in the Jurassic in

371   Europe. Maastrichtian subsampled diversity remains high, reaching the same level as that for the

372   Kimmeridgian. In Africa, as with ornithischians the signal is very patchy after subsampling is applied (Fig.

373   8C), but captures an Albian-Cenomanian diversity increase, which remains constant throughout

374   publication history, and flat diversity in the latest Cretaceous. The subsampled theropod diversity signal

375   is also patchy in Asia, but does reveal a very high latest Cretaceous diversity level, which is not otherwise

376   seen throughout theropod evolutionary history (Fig. 8D). In North America, the subsampled record is as

377   patchy as that for ornithischians, but remains stable through publication history (Fig. 8E). Here, we see

378   slightly increasing subsampled diversity in the latest Jurassic, a large decline from the Aptian to Albian,

379   and a major diversification from the Santonian to Campanian. In South America a subsampled diversity

380   signal is almost entirely absent, although we do see a reduction in almost half from the Norian to

381   Rhaetian, which remains stable through publication history.

382   [Figure 8 – Theropoda, SQS]

383   Theropod coverage levels are quite patchy at the 'global' level, remaining constant in the Late Triassic,

384   fluctuating in the Middle Jurassic to earliest Cretaceous, but remaining fairly stable in the 'middle' and

385   latest Cretaceous through publication history (Fig. 9A). On a regional level, this apparent 'global' signal

386   across the Jurassic/Cretaceous transition is again emphasised in Europe, but in the Valanginian and

387   Albian, coverage is getting notably worse through publication history (Fig. 9B). Coverage in Africa (Fig.

388   9C) and Asia (Fig. 9D) is very patchy, and does not appear to have changed in the last 20 years overall,

389   besides the origin of moderate coverage levels in the Oxfordian and Aptian of Asia. In North America,

390   coverage levels are moderately high in the latest Jurassic, Aptian and Albian, and latest Cretaceous, only

391   improving in the latest Jurassic through publication history (Fig. 9E). In South America, coverage is

392   generally poor throughout the Jurassic and Cretaceous, but appears to be declining in the Norian and

393   Rhaetian theropod records (Fig. 9F).

394   [Figure 9 – Theropoda, u]

395   ***Sauropodomorphs***

396   Sauropodomorph empirical diversity emphasises some more changes in raw patterns through

397   publication time, particularly in the 'middle' and Late Cretaceous (Fig. 10A). Late Jurassic patterns are

398   fairly consistent, with a rising Kimmeridgian and Tithonian raw diversity emphasising an apparent major

399   decline across the J/K interval. In Europe, sauropods show a consistent and major decline in raw

400   diversity from the Kimmeridgian to the Berriasian (Fig. 10B). Much of the rest of the Cretaceous is too

401   poorly sampled, but raw sauropod diversity never attains Kimmeridgian levels in Europe for the rest of

402   their evolutionary history. Sauropodomorph dinosaurs are generally better sampled than theropods and

403   ornithischians in Africa, showing an apparent decline through the Triassic/Jurassic transition, a latest

404   Jurassic raw diversity peak, and low levels through the 'middle' to Late Cretaceous transition (Fig. 10C).

405   In Asia, raw taxonomic diversity is generally low compared to the Maastrichtian, in which diversity is

406   relatively high and still rapidly increasing through publication history (Fig. 8C). The North American

407   sauropod record is very patchy, with the latest Jurassic showing a shift from rapidly increasing raw

408   diversity from the Oxfordian to a slight drop from the Kimmeridgian to Tithonian (Fig. 10E). The South

409   American Jurassic sauropod record is patchy, but raw diversity is increasing throughout the 'middle' to

410   Late Cretaceous through publication history.

411   [Figure 10 – Sauropodomorpha, raw]

412   At a 'global' level, Jurassic sauropodomorph subsampled diversity remains consistent through

413   publication history (Fig. 11A). Here, we see steadily increase diversity levels through the Middle and Late

414   Cretaceous, before a decline through the Jurassic/Cretaceous transition, which might have been

415   initiated before the J/K boundary itself. The greatest change in subsampled diversity is in the Albian,

416   which has almost doubled in the last 20 years, with implication for the 'mid-Cretaceous sauropod hiatus'

417   (Mannion & Upchurch 2011). Subsampling reduces the European diversity signal due to poor sampling

418   of sauropods, although there is evidence for the sauropod decline beginning prior to the J/K transition

419   (Fig. 11B). In Africa, when subsampling is applied, the few intervals in which a signal emerges reveal a

420   fairly constant level of diversity through the Jurassic and Cretaceous, and through publication time, with

421   the notable exception being an increase in subsampled diversity in the latest Jurassic (Fig. 11C). In Asia,

422   the signal is also fairly poor after subsampling is applied (Fig. 11D). Here, we see an increase in

423   subsampled diversity across the Triassic/Jurassic transition, and the highest diversity level is in the

424   Maastrichtian, where subsampled estimates have increased by more than double in the last 20 years. In

425   North America, the subsampled signal is highly degraded, although of note is a near doubling of Albian

426   diversity levels in the last 20 years (Fig. 11E). In South America, the signal is very inconsistent, but

427   improving through publication history, with a patchy Late Cretaceous signal beginning to emerge (Fig.

428   11F). Full subsampling results are provided in Supplementary Information 7 and 8.

429

430   *Correlation results*

431   Our results find varying strength of correlation between subsampled 'global' dinosaur diversity for each

432   clade and both palaeotemperature and sea level, although the correlations are consistently weak (SI 9).

433   This lack of statistical strength occurs for subsampled diversity estimates at the two year intervals for

434   each of ornithischians (Table 1), sauropodomorphs (Table 2), theropods (Table 3), and dinosaurs overall

435   (Table 4), meaning that we cannot interpret anything from these results with any high level of

436   confidence. The only time the results come close to alpha (0.05) is for the correlation between

437   Ornithischia and sea level during 2007-2013 (p = 0.062-0.084, ρ = 0.481-0.516), but our correction

438   methods reduce the strength of all our statistical results. This hints that it is possible for changes in

439   subsampled diversity estimates based on publication history to be potentially somewhat influential.

440   [Tables 1- 4]

441

442   **Discussion**

443   *The influence of sampling and publication history on dinosaur diversity estimates*

444   The impact of publication history on estimates of both raw and subsampled dinosaur diversity has direct

445   consequences for our interpretation of their evolutionary history and diversification (Benton 2008a;

446   Tarver et al. 2011). What we have found using a small window of historical discovery, is that dinosaur

447   diversity remains highly volatile in specific geographical regions and geological time, typically where

448   sampling levels remain very uneven or the overall sampling pool is very small (Sepkoski 1993; Alroy

449   2000c). In poorly sampled areas, it is clear that even small changes to the data can yield substantial

450   changes, as we are often dealing with very small total sample sizes. This is reflected much less on an

451   apparent 'global' scale, and much more so when we look at regional signals after subsampling is applied.

452 As the rate of dinosaur discovery is increasing (both taxonomically and for occurrences) (Figs. 1, 2), we

453 expect this volatility to remain in the future.

454 As research on dinosaurs continues and new taxa are described and published from existing fossiliferous

455 formations, one implication of this is that raw diversity is expected to become more correlated with rock

456 availability as result of increasing sampling effort (Raup 1977; Wang & Dodson 2006; Benton 2015), and

457 represents a form of publication bias (Sepkoski 1993; Alroy 2000c; Jouve et al. 2017). Further research

458 has shown that new dinosaur discoveries, and changes in their taxonomy and phylogenetic relationships,

459 can strongly influence our understanding and interpretation of their fossil record and diversification

460 patterns (Weishampel 1996; Tarver et al. 2011). In this study, we examined the historical trajectory of

461 different dinosaur diversity estimates to observe whether sampling curves are beginning to stabilise or

462 not. What we seem to be observing is that for raw diversity estimates, we find evidence for relatively

463 stable patterns in spite of any 'bonanza effect' (i.e., fossil discoveries driving formation counts,

464 especially prevalent in Lagerstätten) (Raup 1977; Benton 2015). The fact that the curves remain

465 relatively consistent, despite the variable addition of new taxa, suggests we are seeing some form of the

466 'redundancy' hypothesis at play, in that fossils and sampling are non-independent from each other,

467 when only raw data are considered (Benton et al. 2011; Benton et al. 2013a; Dunhill et al. 2014; Benton

468 2015). Conversely, a more appropriate interpretation might be that we are generally sampling fairly, or

469 consistently, from an underlying occurrence pool through historical time, or that our application of

470 subsampling based on a standardised estimate of coverage is sufficient to eliminate any such sampling

471 biases.

472 However, what is the explanation for the diversity patterns we obtained so far, and what does the

473 variation in these patterns tell us? Generally, a dinosaur bearing formation availability effect makes the

474 Kimmeridgian, Barremian, Albian, Aptian, Campanian, and Maastrichtian the most productive stages

475 (Barrett et al. 2009; Butler et al. 2011; Upchurch et al. 2011; Tennant et al. 2016b). By counting genus

476 density (number of genera per million year), three stages from these stand out: Kimmeridgian,

477 Campanian and Maastrichtian (Taylor 2006), with Asia being the most productive continent followed

478 closely by North America, then Europe, South America, Africa, Australasia and finally Antarctica.

479 However, what is clear from our analyses is that this is not historically consistent, and prone to changing

480 as new regions are opened up for exploration and discovery.

481 There is a well-recognised relationship between the amount of rock available for palaeontologists to

482 search for dinosaur fossils, and how this influences our interpretations of their diversity patterns

483   (Barrett et al. 2009; Butler et al. 2011; Mannion et al. 2011; Upchurch et al. 2011). This raises questions

484   about the extent to which many aspects of diversity curves could be artefacts caused by changes in

485   global sea levels, tectonics, and other geological processes related to preservational or geological

486   megabiases (Peters & Foote 2001; Smith et al. 2001; Smith & McGowan 2007; Peters & Heim 2010;

487   Heim & Peters 2011; Peters & Heim 2011a; Smith et al. 2012; Smith & Benson 2013). As a way of

488   exploring this, Barrett et al. (2009) applied the "residuals" method (formerly designed by Smith &

489   McGowan (2007) for marine fossil taxa) to account for these sorts of geological biases, and

490   demonstrated that many features of dinosaur diversity curves are sampling artefacts that reflect

491   changes in the amount of fossiliferous rocks and thus reflect geological rather than biological signals.

492   The influence of these geological biases appears to have been largely mitigated in recent studies by

493   considering a historically accurate account of sampling and modelling variation through time (Alroy

494   2010c; Alroy 2010a; Alroy 2010b; Newham et al. 2014; Mannion et al. 2015; Nicholson et al. 2015;

495   Grossnickle & Newham 2016; Tennant et al. 2016b). Here, sampling heterogeneity in terms of both

496   collection effort and rock availability can be accounted for through subsampling methods, which appear

497   to capture and alleviate at least part of the geological signal. These relative changes in the amount of

498   rock available for sampling, the number and abundance of different taxa, and the historical sampling

499   intensity of different rock formations have implications for the patterns of palaeobiological change that

500   we infer from them. An interesting extension of the present study, which explores historical publication

501   bias, would be to test how the historical context of sampling (e.g., outcrop area variation or availability

502   through time, sampling intensity through time) corresponds to our historical estimates of diversity.

503   We find that there are four main time periods when great caution should be applied to interpreting

504   further processes or patterns based on dinosaur diversity, based on volatility in subsampled diversity

505   estimates and coverage levels. These are: (1) the Late Jurassic interval for theropods in Europe, North

506   America, and Asia (Figs. 8, 9); (2) the Middle-Late Cretaceous interval for theropods in South America

507   and Asia (Figs. 8, 9); and (3) the mid-Late Cretaceous interval for ornithischians in North and South

508   America and Asia (Figs. 5, 6); (4) the mid-Late Cretaceous for sauropodomorphs in Africa, Asia, and

509   South America (i.e., Gondwana) (Figs. 11, 12). As well as this, the Late Triassic dinosaurian record is in a

510   state of flux at the present (Baron et al. 2017), and should be interpreted carefully (Figs. 5, 8, 11). These

511   represent the times when diversity estimates are changing most rapidly due to a combination of

512   taxonomic revision and discovery-driven publication. While we cannot predict the future of dinosaur

513   discovery, or the selective nature of publication, it seems prudent to suggest that we are cautious in our

514   interpretation of events in dinosaur macroevolution in these intervals, similar to the conclusions

515   reached by Tarver et al. (2011).

516

517   *Discovery influences regional patterns of dinosaur diversity through time*

518   ***Ornithischians***

519   The Jurassic/Cretaceous (J/K) interval decline in subsampled diversity remains constant and recognisable

520   throughout publication history, with this stability suggesting that either this is a real biological signal and

521   not a publication artefact (Tennant et al. 2016b). However, more focussed sampling needs to occur on

522   J/K interval deposits to reveal the true global signal, as much of this pattern is based on fossils

523   exclusively from historically well-sampled European localities (Tennant et al. 2016c) (Figs. 5, 9, 11).

524   Ornithischian subsampled diversity decreases steadily through the Early Cretaceous in Europe, with a

525   possible radiation in the Campanian to Maastrichtian, perhaps explained by an increase of recent

526   occurrences of latest Cretaceous dinosaurian findings mainly in Spain, Portugal, France and Romania

527   (Riera et al. 2009; Csiki et al. 2010). However, many of these latest Cretaceous European dinosaur

528   faunas are not particularly well-resolved stratigraphically compared to the well-studied North-American

529   sections, which makes the timing of any regional extinction here and comparison with North America

530   and Asia difficult at the present. Advanced ornithischian faunas, including ceratopsians and hadrosaurids,

531   appear to have diversified extremely rapidly in the latest Cretaceous, but this is classically explained by

532   the oversampling of North American Late Campanian localities, like Dinosaur Park Formation and its

533   approximate temporal equivalents. Although a small rise in subsampled diversity is recovered from the

534   Campanian to the Maastrichtian in Europe, this is considerably less marked than the decline in North

535   America, where subsampling reveals that ornithischian diversity was actually declining from the

536   Campanian to Maastrichtian (Brusatte et al. 2015).

537   Ornithischian subsampled diversity in Asia has been increasing steadily through publication time in the

538   'middle' Cretaceous, filling in the gap from equivalent latitude European deposits at this time. This is

539   plausibly due to the radiation of Parksosauridae and Ankylopollexia clades, two of the most dominant

540   Late Cretaceous dinosaurian taxa around this time. Together with the North American record, this

541   manifests as a great global decline across the Early-Late Cretaceous interval, a pattern that was not

542   recognised until more recent years due to the discovery of more Konzentrat-Lagerstätten in Mongolia

543   and China around this time, such as the Jehol Biota (Lambert et al. 2001; Godefroit et al. 2008; Upchurch

544 et al. 2011). A perceived Late Cretaceous subsampled diversity increase for Asian taxa, particularly

545 hadrosauroids, could be due to a renaissance in the discovery of Cretaceous Asian dinosaurs over the

546 past two decades (Lloyd et al. 2008; Barrett et al. 2009; Zhou & Wang 2010; Upchurch et al. 2011; Mo et

547 al. 2016). Despite the increasing availability of Early Cretaceous dinosaur-bearing formations (DBFs) in

548 Africa in the last 20 years (e.g., Tunisia, Niger; (Taquet & Russell 1999; Anderson et al. 2007)), sampling

549 here is still too limited to reveal any consistent patterns in ornithischian subsampled diversity (Mannion

550 et al. 2011; Upchurch et al. 2011; Tennant et al. 2016b) (Figs. 5, 6).

551 This regional distinction could be due to the tie between ecomorphologlogical function and biological

552 diversity, as Asian hadrosauroids increased in morphological disparity during the latest Cretaceous,

553 whereas in North America large-bodied bulk-feeding ornithischians decreased in their disparity

554 (Campione & Evans 2011; Brusatte et al. 2012). (Vavrek & Larsson 2010; Mitchell et al. 2012). In North

555 America, several abiotic factors, including extreme fluctuations of the Western Interior Sea, and the

556 Laramide orogeny and proposed biogeographic provincialism, may have affected the evolution of North

557 America dinosaurs in distinct ways from species on other continents (Gates et al. 2012; Arbour et al.

558 2016), meaning that the North American record is unlikely to be representative of global diversity

559 pattern (Sampson et al. 2010; Brusatte et al. 2012).

560 ***Theropods***

561 As already shown elsewhere (Barrett et al., 2009, Brusatte et al., 2012), 'global' theropod diversity

562 trends are overall very similar to that of Ornithischia, with subsampled diversity increases during the

563 Late Jurassic (Oxfordian and Tithonian peaks punctuated by a Kimmeridgian decline), late Early

564 Cretaceous (Aptian), early Late Cretaceous (Cenomanian) and latest Cretaceous. Moderately high

565 Middle and Late Jurassic diversity subsampled levels represent the radiation of major avetheropodan

566 clades, and a wealth of new discoveries in recent years, particularly from Asia (Upchurch et al. 2011; Xu

567 et al. 2011; Carrano et al. 2012; Benson et al. 2014; Tennant et al. 2016b).

568 European subsampled theropod diversity is more constant than in other regions, with a Bajocian peak

569 followed by a Bathonian-Oxfordian trough, and a Kimmeridgian peak followed by a Tithonian to

570 Valanginian drop. This can, at least in part, be explained by an abundance of well-sampled Late Jurassic

571 formations from the across Western Europe (Upchurch et al. 2011; Benson et al. 2013; Tennant et al.

572 2016c). Barremian diversity is increasing rapidly through publication history, and is now as high as

573 calculated for the Kimmeridgian. As with the Late Jurassic, at least part of this signal represents the

574   influence of a Lagerstätten effect (e.g., Las Hoyas, Spain) (Buscalioni et al. 2008; Upchurch et al. 2011;

575   Sánchez-Hernández & Benton 2012), highlighting that single, well-sampled formations can have a

576   profound historical effect on our understanding of regional diversity patterns, even when subsampling

577   methods are applied. The European Aptian-Albian record is increasing slower through time compared to

578   the Campanian-Maastrichtian. However, this might possibly change in the future, as the ichnological

579   record in southern Europe is quite abundant for the Aptian-Albian interval, and suggests a currently

580   unrecognised dinosaurian diversity present there (Dalla Vecchia 2002; Meyer & Thuring 2003).

581   The North American theropod record is dwarfed by an oversampling of latest Cretaceous dinosaur-

582   bearing formations (e.g. Dinosaur Provincial Park, Hell Creek Formation). An increasingly even

583   representation of latitudinally diverse localities from the Cenomanian-Campanian of Utah, Colorado,

584   New Mexico and Mexico (e.g. Wahweap Formation), may increase the magnitude of the small

585   subsampled diversity drop through the Maastrichtian. Subsampling highlights a latest Jurassic peak in

586   diversity (due to the abundance of remains from the well-sampled Morrison Formation; (Foster 2003)),

587   although Jurassic subsampled diversity never attains that of the Cretaceous highs during the Aptian and

588   Campanian. Conversely to Brusatte et al. (2015), who found no evidence for a progressive Campanian-

589   Maastrichtian decline in North American theropod faunas using similar SQS analyses (implemented in R;

590   see (Tennant et al. 2016a; Tennant et al. 2016b) and (Alroy 2010c; Alroy 2010a) for comparative

591   discussions), we find a very slight decline that remains constant through publication history, that likely

592   relates to our usage of a slightly different subsampling approach. Aptian subsampled diversity is

593   relatively high due to the more heavily sampled localities from Montana to Texas (Kirkland et al. 1997;

594   Cifelli et al. 1999; Kirkland & Madsen 2007).

595   In Africa, there is a Cenomanian radiation (Fig. 8C) mainly due to the multitaxic theropod dominated

596   Kem Kem beds and other Albian-Cenomanian ("middle" Cretaceous) equivalents in Northern Africa, but

597   this signal might have been altered by time averaging effects constraining a more temporally diluted

598   diversity in a single unit (Mannion & Barrett 2013; Evers et al. 2015; Chiarenza & Cau 2016). Asian

599   subsampled diversity peaks in the Aptian, Campanian and Maastrichtian might be explained by a

600   Lagerstätten 'bonanza' effect, especially considering the high quality preservation deposits discovered

601   and heavily sampled in the last 20 years (e.g. Liaoning) (Lloyd et al. 2008; Zhou & Wang 2010; Godefroit

602   et al. 2013; O'Connor & Zhou 2015; Tennant et al. 2016c), although coverage remains only moderate

603   (around 0.5) in each of these intervals (Fig. 9). Similarly to the pattern in Africa and Asia, South American

604   theropod subsampled diversity stands out compared to other North America and Europe, remaining

605 relatively signal deficient. Despite an increasing rate of discovery of new taxa, which often alter our

606 knowledge of dinosaur phylogeny and biogeography from the 'middle' Cretaceous of Patagonia and

607 Brazil (Novas et al. 2005; Novas & Pol 2005; Canale et al. 2009; Novas et al. 2013), coverage remains

608 poor at the stage level, emphasising the need for greater stratigraphic resolution of the theropod-

609 bearing formations here.

610 ***Sauropodomorphs***

611 Subsampled diversity patterns of sauropodomorphs share some characteristics of those of theropods

612 and ornithischians, despite having a different fossil record due to taphonomic differences (i.e., larger,

613 more robust skeletons being preferentially preserved in different environmental settings) (Mannion &

614 Upchurch 2010; Mannion & Upchurch 2011; Dean et al. 2016). This is compounded by a difficulty in

615 assigning a large number of taxa to specific stage bins, which unfortunately excludes many of them from

616 our analyses (SI 1). Differences in diversity patterns between sauropodomorphs and ornithischians have

617 classically been interpreted as being due to exclusive competition between the two main herbivorous

618 dinosaurian subtaxa (Butler et al. 2009), with an explosive radiation in ornithischians during the Early

619 Cretaceous resulting from the apparent decline in diversity of sauropodomorphs. In fact, the J/K

620 transition represents a major extinction 'event' for sauropodomorphs, reflecting the decline of non-

621 neosauropods, diplodocoids and basal macronarians (Mannion et al. 2013; Tennant et al. 2016b).

622 Sauropodomorph faunas have a low subsampled diversity in the earliest Cretaceous, coupled with a

623 generally poor fossil record (Mannion & Upchurch 2010), but at a time when we otherwise see rapid

624 increases in theropod and ornithischian diversity and a prolonged phase of faunal turnover (Upchurch &

625 Mannion 2012; Tennant et al. 2016b). Sauropodomorph subsampled diversity levels fluctuate from the

626 'middle' Cretaceous until the final latest Cretaceous radiation, with a possible small decline in the

627 Maastrichtian. This find is somewhat contrary to that of Sakamoto et al. (2016) who found that their

628 decline was initiated in the Early Cretaceous, and that the diversification of titanosaurs was at an

629 insufficient rate to compensate for the overall loss of sauropodomorph lineages throughout the rest of

630 the Cretaceous. However, we find that sauropodomorphs are at their most diverse during the Albian (Fig.

631 11). Sauropodomorphs appear to be overrepresented with respect to what we might expect for almost

632 the entire duration of the Jurassic, whereas the opposite is true for the Cretaceous (Mannion et al. 2011;

633 Upchurch et al. 2011; Tennant et al. 2016b). The general patterns of 'global' subsampled diversity shows

634 a steady increase from Middle to the end of Jurassic with a decline through J/K transition (Upchurch &

635 Mannion 2012; Tennant et al. 2016b). The relatively high Late Cretaceous subsampled diversity levels

636 can at least be partially explained by the constant discovery of new titanosaurian taxa, especially from

637 Gondwanan continents (Vieira et al. 2014; de Jesus Faria et al. 2015; Bandeira et al. 2016; Poropat et al.

638 2016), and only recently a more appreciated diversity of diplodocoids (e.g., dicraeosaurids,

639 rebbachisaurids) from relatively poorly sampled regions such as Africa (Mannion & Barrett 2013; Wilson

640 & Allain 2015; Ibrahim et al. 2016).

641 Large-bodied sauropodomorph diversity in the Tithonian is certainly influenced by the intense sampling

642 history of the North American Morrison Formation, where there is an unusually high diversity and

643 cranial disparity of megaherbivores within a relatively resource-poor environment (Button et al. 2014).

644 Here, high diversity remains in spite of our accounting for large collection biases associated with

645 Konzentrat-Lagerstätten (Alroy 2010c; Alroy 2010a), implying that sauropodomorphs reached their

646 zenith in diversity during the Late Jurassic. Sauropodomorphs appear to be better sampled than

647 theropods and ornithischians in Africa (Fig. 12C), although their records remain largely too inconsistent

648 and patchy record to reveal any major patterns. Asian subsampled diversity is constantly low until the

649 Maastrichtian, where it increases moderately due to a series of recent discoveries from Pakistan and

650 China (Malkani 2010; Junchang et al. 2013). However, the Asian Cretaceous sauropodomorph record is

651 otherwise very poorly sampled, especially compared to ornithischians and theropods. This phenomenon

652 could be explained by a taphonomic size bias discriminating against the preservation of larger-bodied

653 animals in pre-Late Cretaceous Konservat-Lagerstätten, while they are more present although more rare

654 in the dense bone assemblages from the latest Cretaceous of Mongolia, China and India (Kidwell, 2001).

655 There is a notable subsampled diversity decline in European sauropodomorphs through the J/K

656 transition, as with other dinosaurian groups (Upchurch & Mannion 2012; Tennant et al. 2016b). This is

657 distinct from results obtained with other methods (e.g., TRiPS) which do not find any evidence for such a

658 decline (Starrfelt & Liow 2016). Subsampling also reveals that sauropodomorph diversity in the latest

659 Cretaceous of Europe was relatively flat. The sauropodomorph record in South America is poor and

660 mostly confined to the Late Cretaceous, with diversity levels rising and resolution improving through

661 publication time as coverage increases and as new taxa get identified from emerging Patagonian and

662 Brazilian deposits (Novas, 2007, 2009).

663 Here, it is worth noting the distinction between global and regional sauropodomorph records. On a

664 global level, we appear to have strong evidence for a substantial sauropod subsampled diversity decline

665 from the Campanian to Maastrichtian. However, this decline is not represented in any of the regional

666 sauropodomorph diversity signals. Instead, the 'global' signal in the Maastrichtian is comprised of a

667   medley of regional records, which are only continuous with the Campanian record in Europe and North

668   America. Therefore, the 'global extinction' of sauropods in the latest Cretaceous is actually due to

669   regionally heterogeneous sampling signals that are summed into a misleading 'global' curve. A similar

670   case can be made for the apparently 'global' radiation in the Albian, which is primarily a reflection of a

671   well-sampled North American Albian sauropodomorph record (Fig. 11). Thus, when looking at diversity

672   signals, interpretation of global patterns without considering structural changes on a regional level is not

673   recommended.

674

675   *Limitations of the present study*

676   As we have shown, the interpretation of subsampled diversity estimates in dinosaurs is often highly

677   sensitive to changes in the taxon-abundance curve, and we can further distort this by relying on a

678   historically biased source of data for our analyses. Our overwhelmingly weak correlation results mean

679   that in no cases could we confidently reject any null hypotheses. As such, it is difficult to say exactly how

680   the correlations have potentially changed through time. Some of the reasons for this might be that the

681   tests are inadequate for picking apart temporal trends over such a long time period, a small n (often

682   with a lot of missing data). Alternatively, it suggests that sea level is a poor predictor of dinosaur

683   diversity at the stage level, and that dinosaur diversity and sea level are perhaps only related on broader

684   temporal scales (Haubold 1990; Butler et al. 2011; Tennant et al. 2016b). We also only elected to use a

685   single autocorrelation model, and it would be interesting in the future to explore the modelling a wider

686   range of serial correlation structures on palaeontological data in the future, and the impact this might

687   have on correlation analyses. Alternatively, our choice of using genus-level data might have been

688   influential (see Benton (2008a); Benson et al. (2016)), despite previous assertions that the species and

689   genus level diversity curves for dinosaurs are quite similar (Barrett et al. 2009). Future research could

690   investigate the influence that taxonomic resolution has on our interpretation of dinosaur evolution. In

691   addition, as mentioned above, it might simply be inappropriate to analyse 'global' correlations between

692   diversity and extrinsic parameters, due to the regionally heterogeneous nature of diversity data.

693   However, what we do see is that the strength of the relationship between sea level and subsampled

694   diversity, despite being consistently weakly statistically supported, is contingent on the publication

695   history of the group. This lends some support the recent analysis of Jouve et al. (2017), who also found

696   that small changes in the taxonomic composition of a dataset can lead to divergent interpretations of

697   the environmental regulators of diversity, although this phenomenon requires further investigation.

698   The accuracy of the results from the Gondwanan continents should be treated with caution, as it is clear

699   that the fossil record is substantially patchier than the Laurasian record, reflected in the publication

700   histories of specimens from these regions. High-magnitude changes in even moderately well-sampled

701   intervals through publication history suggests we should acknowledge the limitations of any biological

702   interpretations of the dinosaur record in Africa and South America until more reliable data is obtained

703   (Barrett et al. 2009; Mannion et al. 2011; Upchurch et al. 2011; Tennant et al. 2016b).

704   We did not test for how changes in the stratigraphy of dinosaur-bearing formations through time (e.g.,

705   as chronological dates are found or refined) influences the structure of sampling pools in each time bin,

706   a factor which is quite under-studied in paleodiversity reconstructions (Gibert & Escarguel 2017).

707   Furthermore, by explicitly excluding occurrences that did not fit within a single stage-level time bin, we

708   influence what data are not included in our analyses by rejecting specific formation pools from bins. This

709   will have a particularly stronger effect in formations that span multiple time bins, as well as in

710   formations that have less well-studied chronostratigraphy or less accurate dates. Furthermore, we used

711   stage-level bins that are inherently of uneven duration, as opposed to other commonly used methods

712   such as 2/9/10/million year approximately equal duration bins (Wang & Dodson 2006; Barrett et al.

713   2009; Butler et al. 2011; Upchurch et al. 2011; Brusatte et al. 2012; Lloyd 2012; Mannion et al. 2012);

714   there is currently little consensus on which time binning methods are most appropriate for the fossil

715   record, but we do know that different bins can influence resulting diversity estimates (Tennant et al.

716   2016a).

717   The impact that all of these factors can have on diversity estimates is an ongoing discussion in research

718   about palaeodiversity, and exploring them all is beyond the scope of the present study. What is more

719   important for us in terms of study design was a single, appropriate methodology that could be

720   compared through publication history, which is what we performed. That is not to say that each of these

721   factors do not also variably influence diversity estimates through time, and investigating how these

722   potential stratigraphic biases influences diversity estimates would be a useful future research avenue.

723

724   **Conclusions**

725   In this study, we investigated diversity trends through time for three major clades of Dinosauria

726   (Ornithischia, Sauropodomorpha and Theropoda), by reducing a primary dataset of body fossil

727   occurrences by progressively removing publications at each 2 year intervals, up until 1991. By analysing

728 both empirical and subsampled curves, we have been able to see how publication history influences
729 different estimates of dinosaur diversity.

730 Subsampling reveals that there are major discrepancies between the 1991 and 2015 curves for
731 theropods in the Oxfordian, Aptian, and Cenomanian, for ornithischians in the late Early Cretaceous, and
732 for sauropods in the Albian and latest Cretaceous. However, almost without exception, these seemingly
733 continuous 'global' diversity patterns are the product of summing together different, and invariably
734 patchier, continental signals with vastly different trends, reflective of distinct geographic sampling
735 histories. In ornithischians, a J/K transition decline is based almost exclusively on European fossils, and a
736 perceived global reduction in their diversity in the latest Cretaceous is the result of an overpowering
737 North American signal. Similarly, 'global' subsampled theropod diversity is prevalently based on the
738 European record, with Asia and North America contributing substantially more after the earliest
739 Cretaceous hiatus. Theropod diversity in the latest Cretaceous is changing the most rapidly compared to
740 any other time interval. In these places where see the most volatility in both subsampled diversity and
741 coverage, we should be careful not to over-interpret patterns, especially in the context of apparent
742 radiations and extinctions. Gondwanan dinosaurian faunas are still relatively poorly sampled despite
743 intensive exploration in the last 20 years, and we expect the influence of discovery in Africa and South
744 America to become more important in the future. Based on this, we urge caution in any evolutionary
745 interpretations relying on Gondwanan dinosaur diversity until sampling improves.

746 The consequence that this appears to have on our interpretation of the potential extrinsic controls of
747 'global' dinosaur diversity are fairly minimal. However, the results of this study should be of interest to
748 those who use occurrence-based compilations like the Paleobiology Database that rely heavily on the
749 published literature, especially when ongoing research can potentially dramatically alter our
750 understanding of the evolutionary history of dinosaurs (Baron et al. 2017). Both the addition of new taxa,
751 and new occurrences of existing taxa, are clearly important in establishing stable and re-usable diversity
752 curves for further research, and the maturity and growth of taxonomic datasets must be assessed prior
753 to further macroevolutionary study (Tarver et al. 2011). By neglecting the publication history, and
754 potential biases involved in this, we open ourselves up to potentially misinterpreting the patterns and
755 processes involved in dinosaur evolution. In light of this, it is possible that many previous dinosaur
756 diversity studies are likely now incorrect due to the large number of new discoveries being made every
757 year (Figs. 1, 2). Furthermore, it is also likely that the analyses presented in this paper will be

758   demonstrated to be wrong in several years' time, and it remains to be seen whether we will be ever able

759   to faithfully reconstruct an accurate diversity curve for Dinosauria.

760   Future research could investigate the changes in taxonomy, systematics, and validity of dinosaur taxa

761   through publication history (Benton 2008a; Benton 2008b), and the influence that changes in the

762   historical quality and stratigraphic resolution of the fossil record has on this. Furthermore, given the

763   importance of sampling biases on our interpretations of the dinosaur fossil record (Barrett et al. 2009;

764   Butler et al. 2011; Mannion & Upchurch 2011; Upchurch et al. 2011; Benton 2015; Tennant et al. 2016b),

765   research could look at how the relationships between sampling proxies and dinosaur diversity change

766   through time.

767

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777

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1112   **Figure and table captions**

1113   Figure 1: Frequency (A) and cumulative frequency (B) of newly published dinosaur occurrences through

1114   publication time. Please note that all raw figure files (PDF) and the R code for generating these are

1115   available in SI 10.

1116   Figure 2: Frequency (A) and cumulative frequency (B) of newly published dinosaur genera through

1117   publication time.

1118   Figure 3: Total dinosaur 'global' diversity patterns for a) raw and b) subsampled data. The vertical red

1119   lines represent major interval boundaries. Time stage abbreviations (in chronological order) N= Norian;

1120   R= Rhaetian, He= Hettangian; S= Sinemurian; P= Pliensbachian; T= Toarcian; A= Aalenian; Bj= Bajocian;

1121   B= Bathonian; C= Callovian; O= Oxfordian; K= Kimmeridgian; Ti= Tithonian; Be= Berriasian; V=

1122   Valanginian; Ha= Hauterivian; Ba= Barremian; Ap= Aptian; Al= Albian; Ce= Cenomanian; Tu= Turonian;

1123   Co= Coniacian; Sa= Santonian; Cam= Campanian; M= Maastrichtian. Vertical dashed red lines indicate

1124   boundaries between different periods (Triassic/Jurassic, Jurassic/Cretaceous and Cretaceous/Paleogene).

1125   Figure 4: Raw ornithischian diversity at a) global and b-f) regional levels (Europe, Africa, Asia, North

1126   America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1127   Abbreviations as Figure 3.

1128   Figure 5: Subsampled ornithischian diversity at a) global and b-f) regional levels (Europe, Africa, Asia,

1129   North America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1130   Abbreviations as Figure 3.

1131   Figure 6: Good's u estimates for ornithischians at A) global and B-F) regional levels (Europe, Africa, Asia,

1132   North America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1133   Abbreviations as Figure 3.

1134   Figure 7: Raw theropod diversity at A) global and B-F) regional levels (Europe, Africa, Asia, North

1135   America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1136   Abbreviations as Figure 3.

1137   Figure 8: Subsampled theropod diversity at A) global and B-F) regional levels (Europe, Africa, Asia, North

1138   America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1139   Abbreviations as Figure 3.

1140   Figure 9: Good's u estimates for theropods at A) global and B-F) regional levels (Europe, Africa, Asia,

1141   North America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1142   Abbreviations as Figure 3.

1143   Figure 10: Raw sauropodomorph diversity at A) global and B-F) regional levels (Europe, Africa, Asia,

1144   North America, and South America, respectively) based on our published knowledge in 1991 and 2015.

1145   Abbreviations as Figure 3.

1146   Figure 11: Subsampled sauropodomorph diversity at A) global and B-F) regional levels (Europe, Africa,

1147   Asia, North America, and South America, respectively) based on our published knowledge in 1991 and

1148   2015. Abbreviations as Figure 3.

1149   Figure 12: Good's u estimates for sauropodomorphs at a A) global and B-F) regional levels (Europe,

1150   Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991

1151   and 2015. Abbreviations as Figure 3.

1152

1153   Table 1. Ornithischian correlation test results.

1154   Table 2. Sauropodomorph correlation test results.

1155   Table 3. Theropod correlation tests results.

1156   Table 4. Total dinosaur correlation tests results.

Figure 1

Frequency (A) and cumulative frequency (B) of newly published dinosaur occurrences through publication time.

Please note that all raw figure files (PDF) and the R code for generating these are available in SI 10.

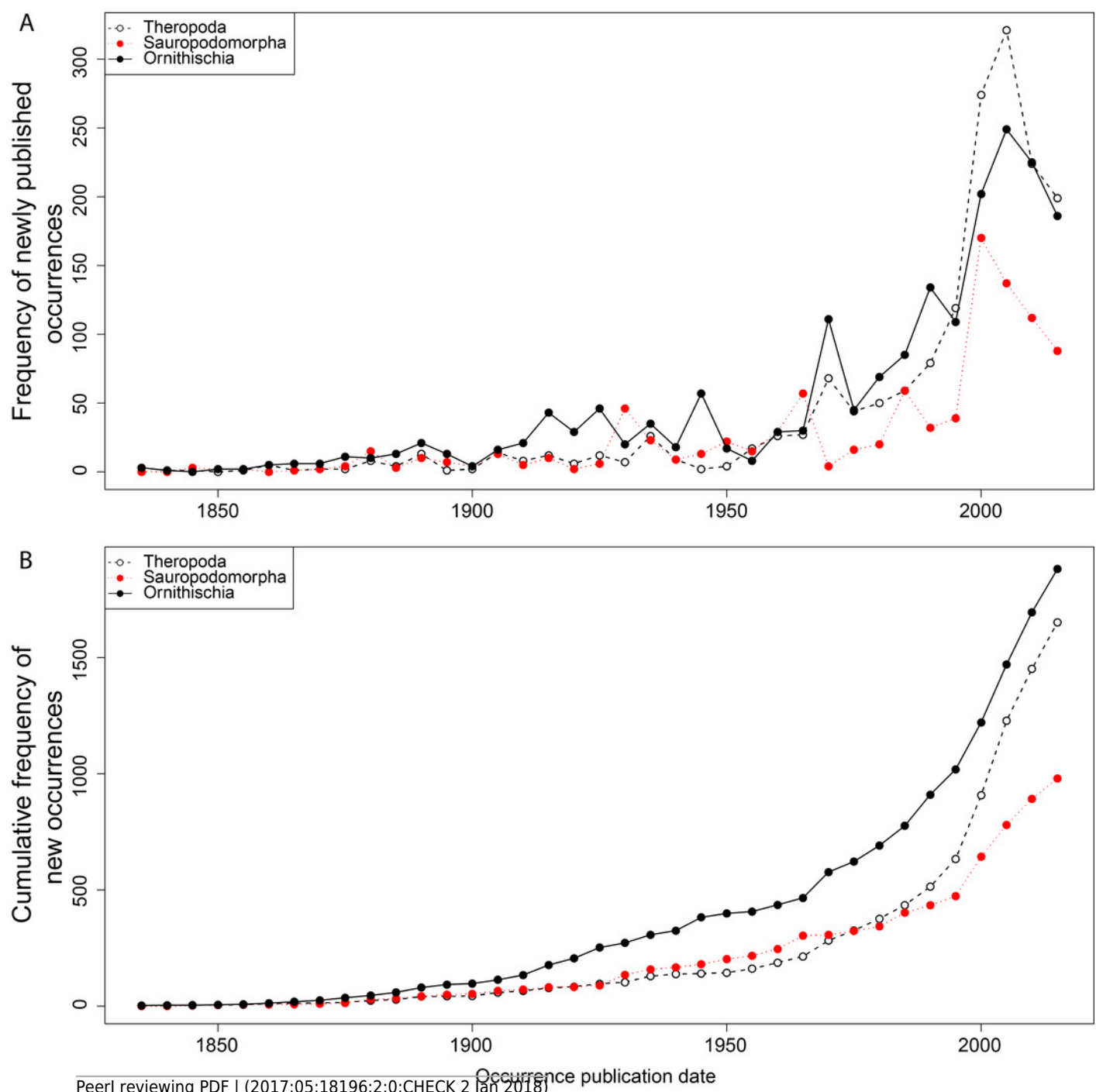



Figure 2

Frequency (A) and cumulative frequency (B) of newly published dinosaur genera through publication time.

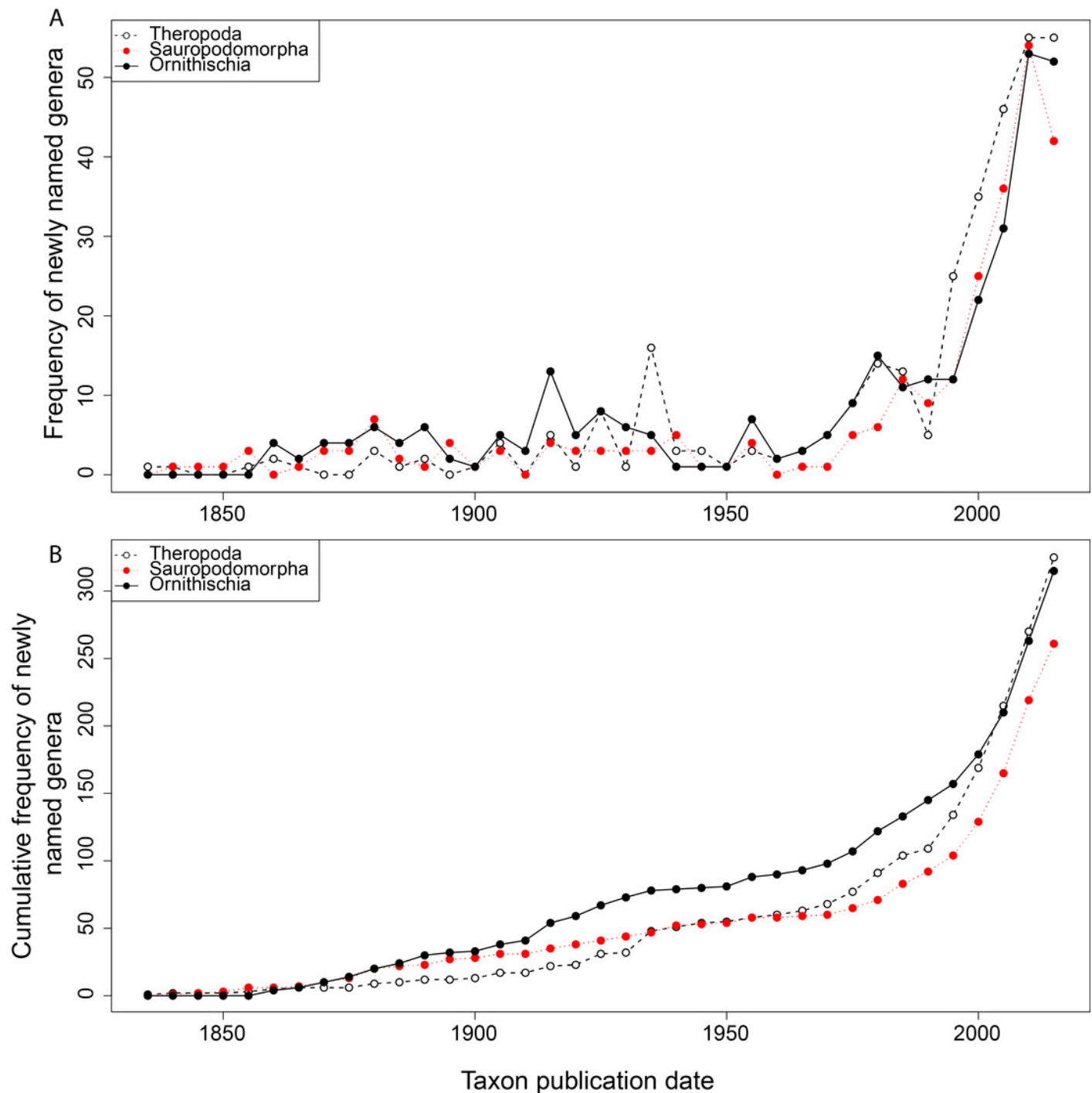



Figure 3

Total dinosaur diversity patterns for a) raw and b) subsampled data. The vertical red lines represent major interval boundaries.

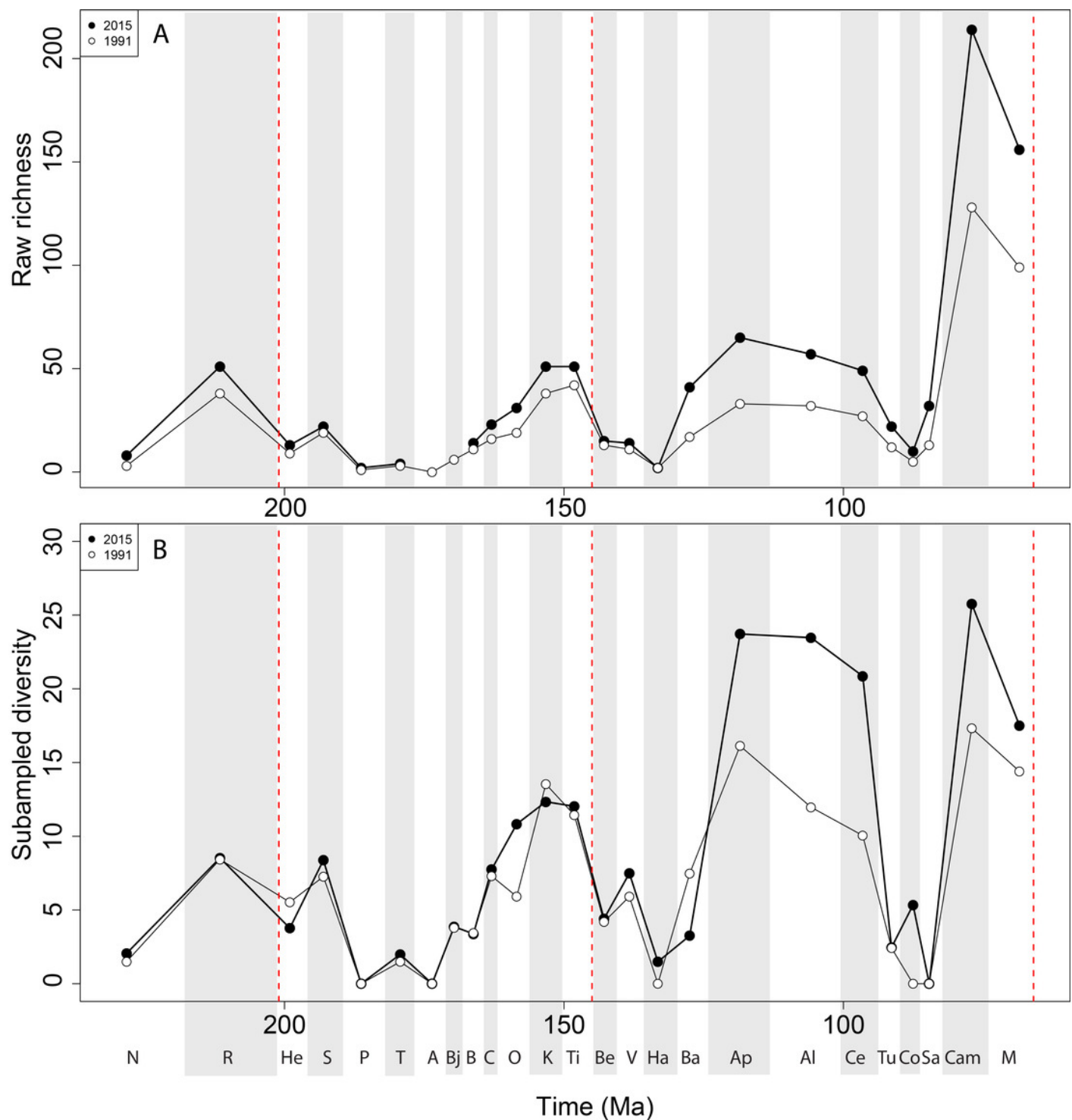



Figure 4

Raw ornithischian diversity at a) global and b-f) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

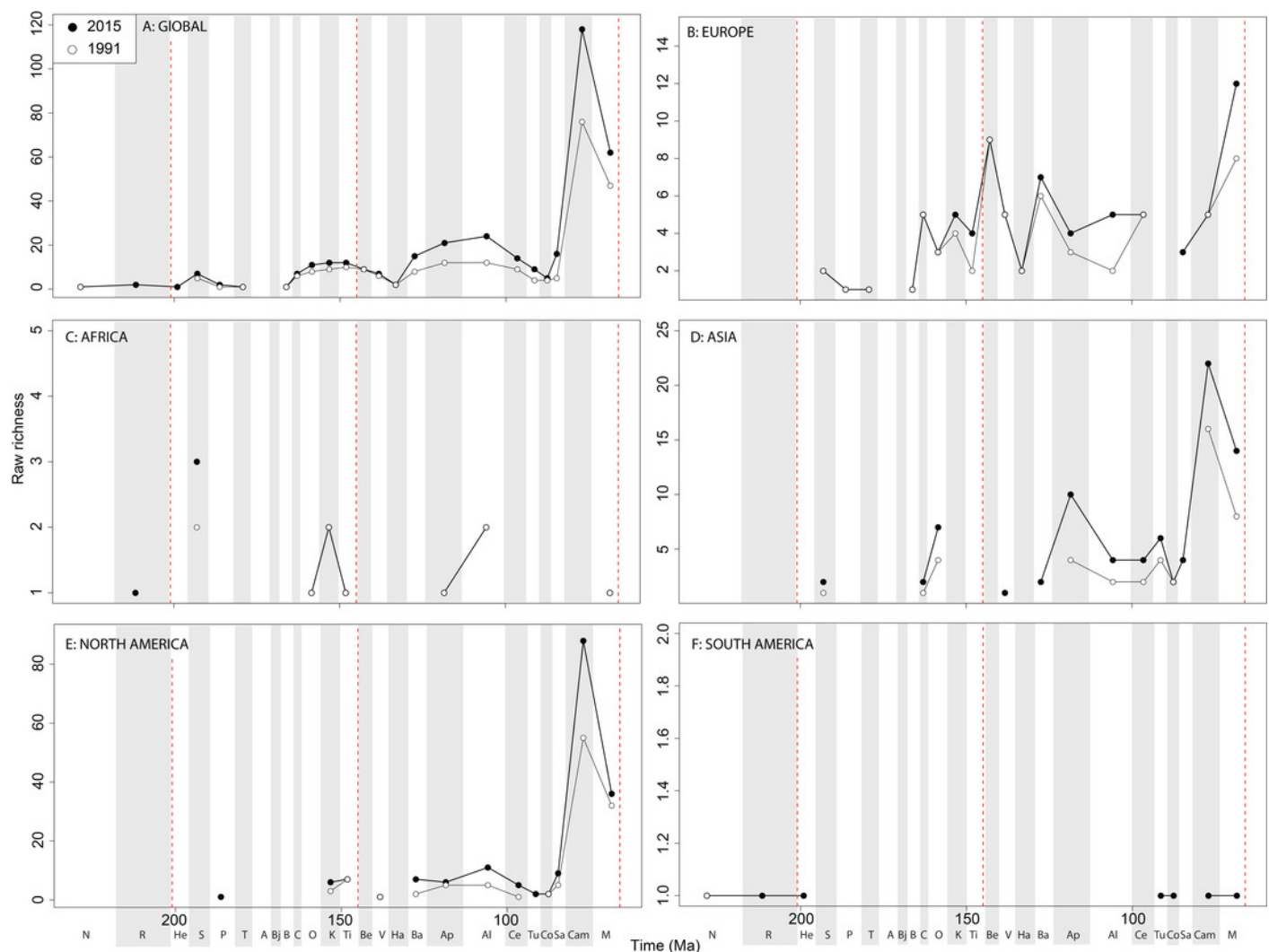



Figure 5

Subsampled ornithischian diversity at a) global and b-f) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015.

Abbreviations as Figure 3.

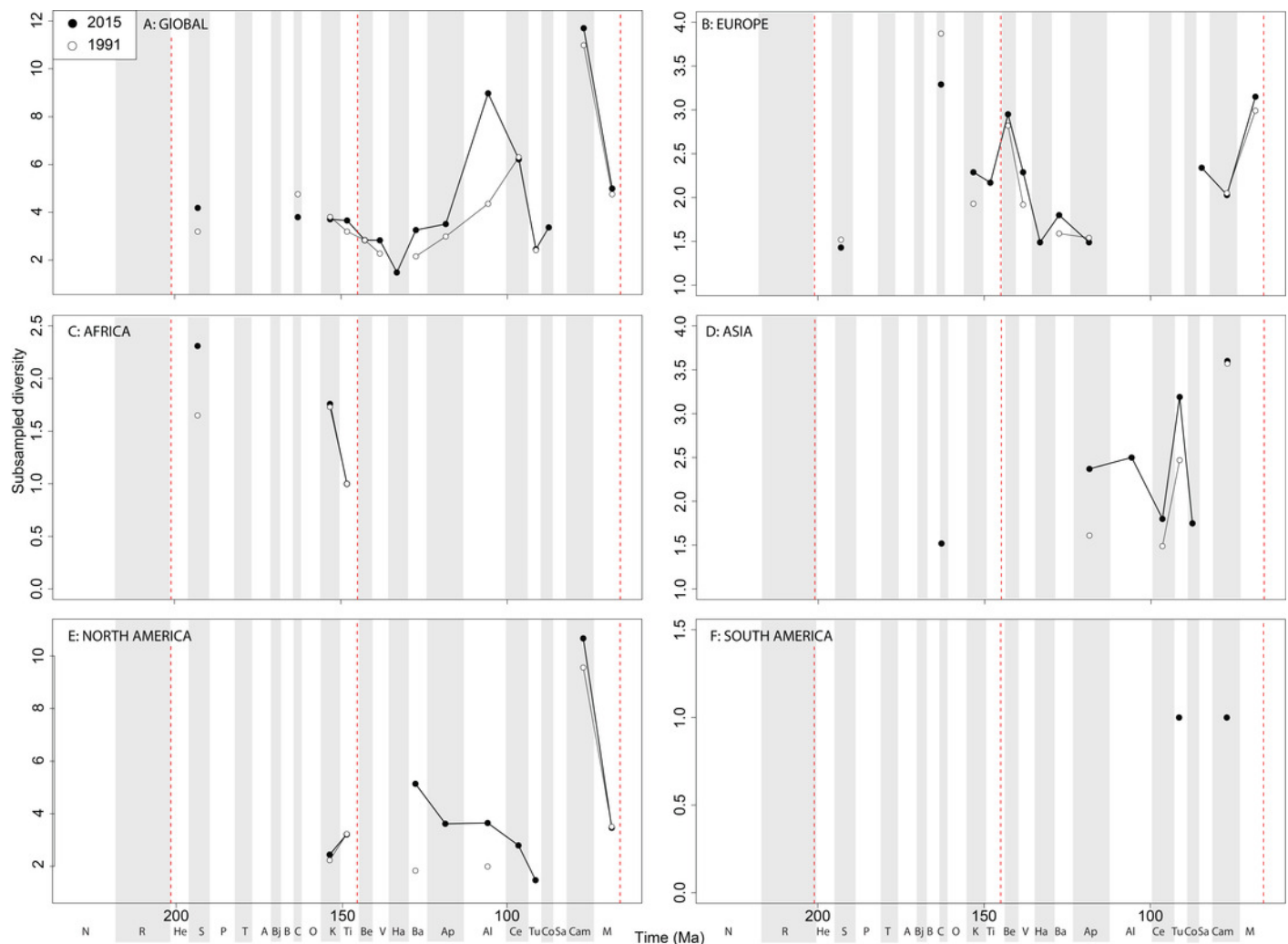



Figure 6

Good's *u* estimates for ornithischians at A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

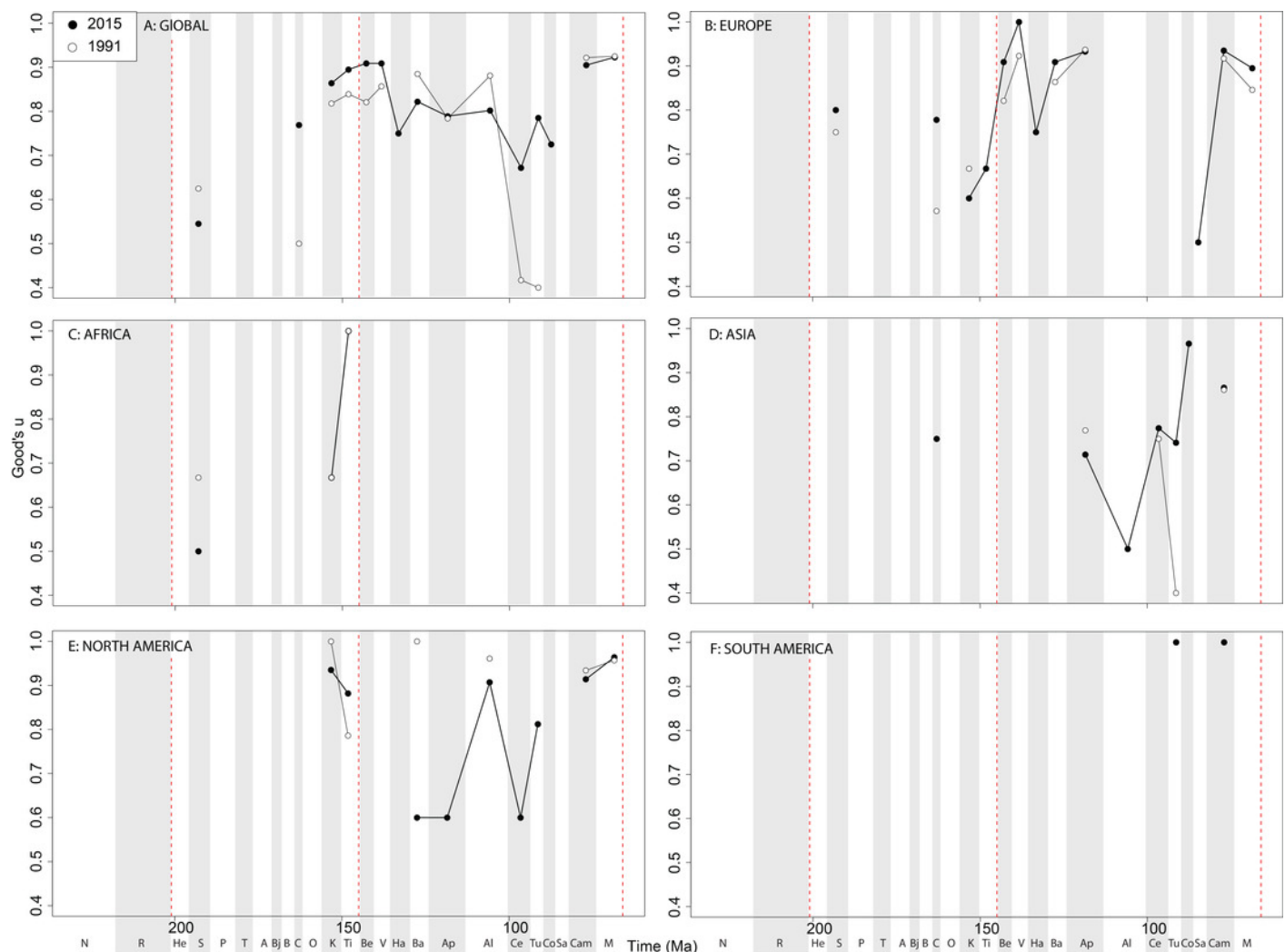



Figure 7

Raw theropod diversity at A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

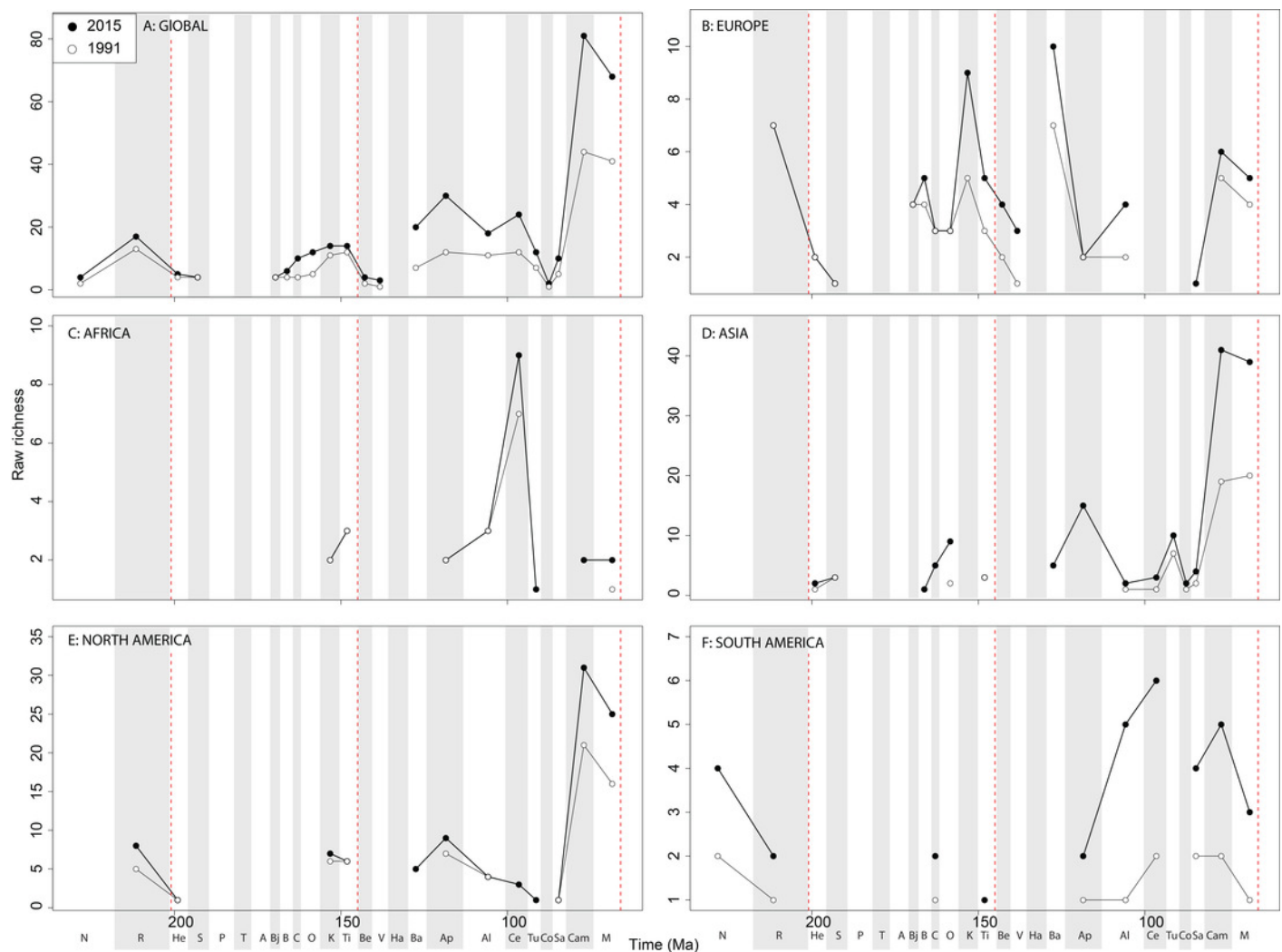



Figure 8

Subsampled theropod diversity at A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

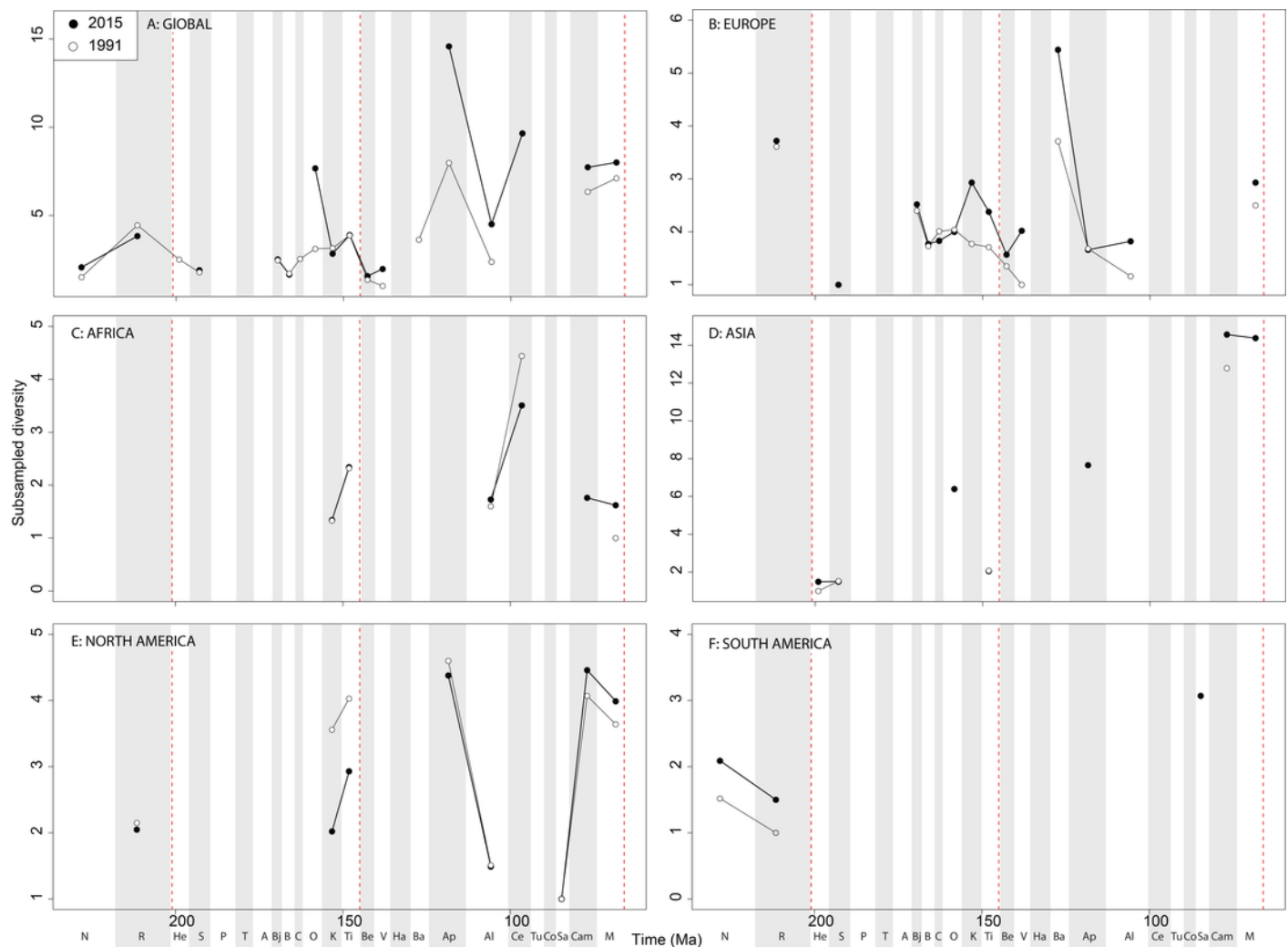



Figure 9

Good's *u* estimates for theropods at A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

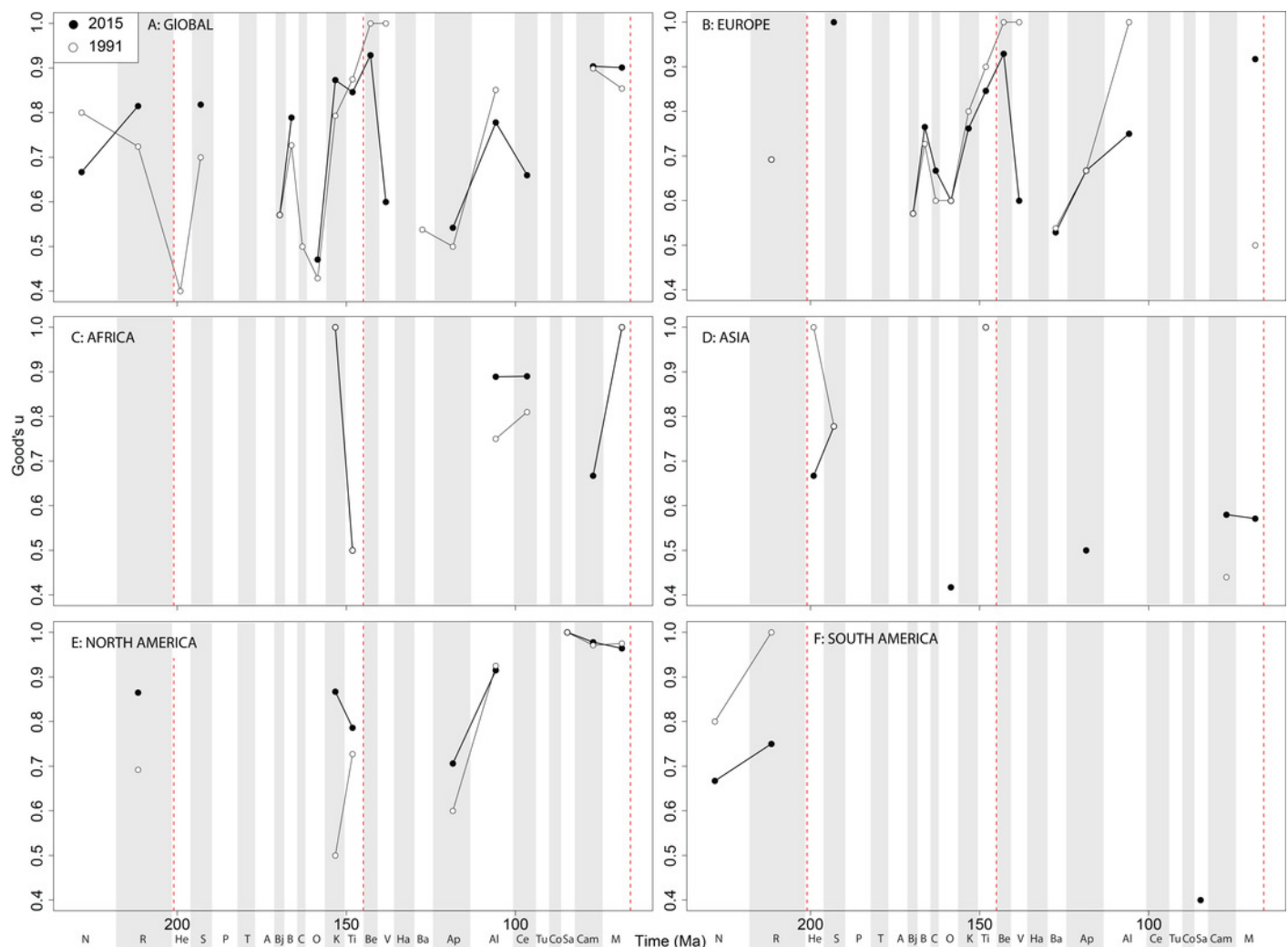



Figure 10

Raw sauropodomorph diversity at A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

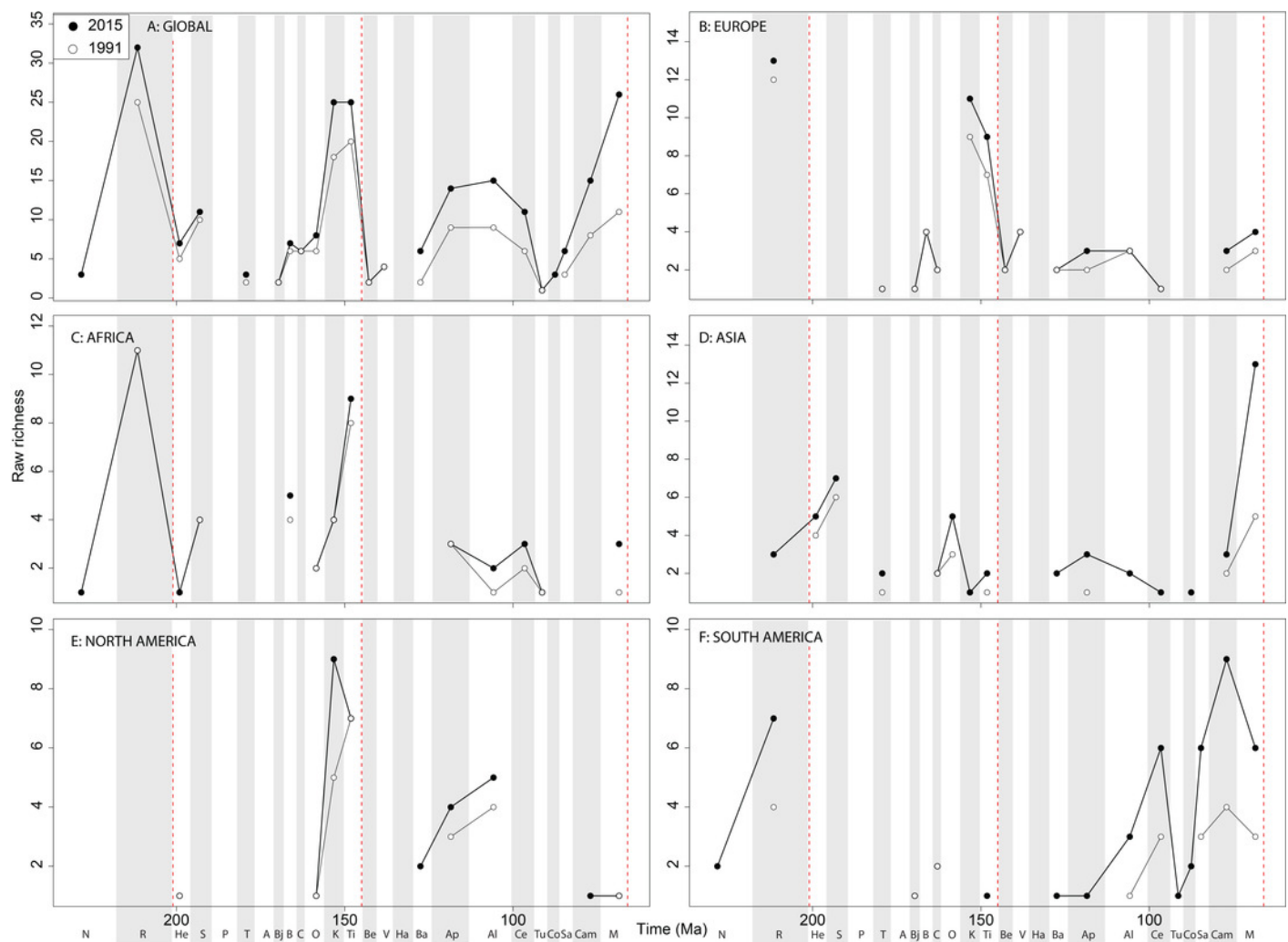
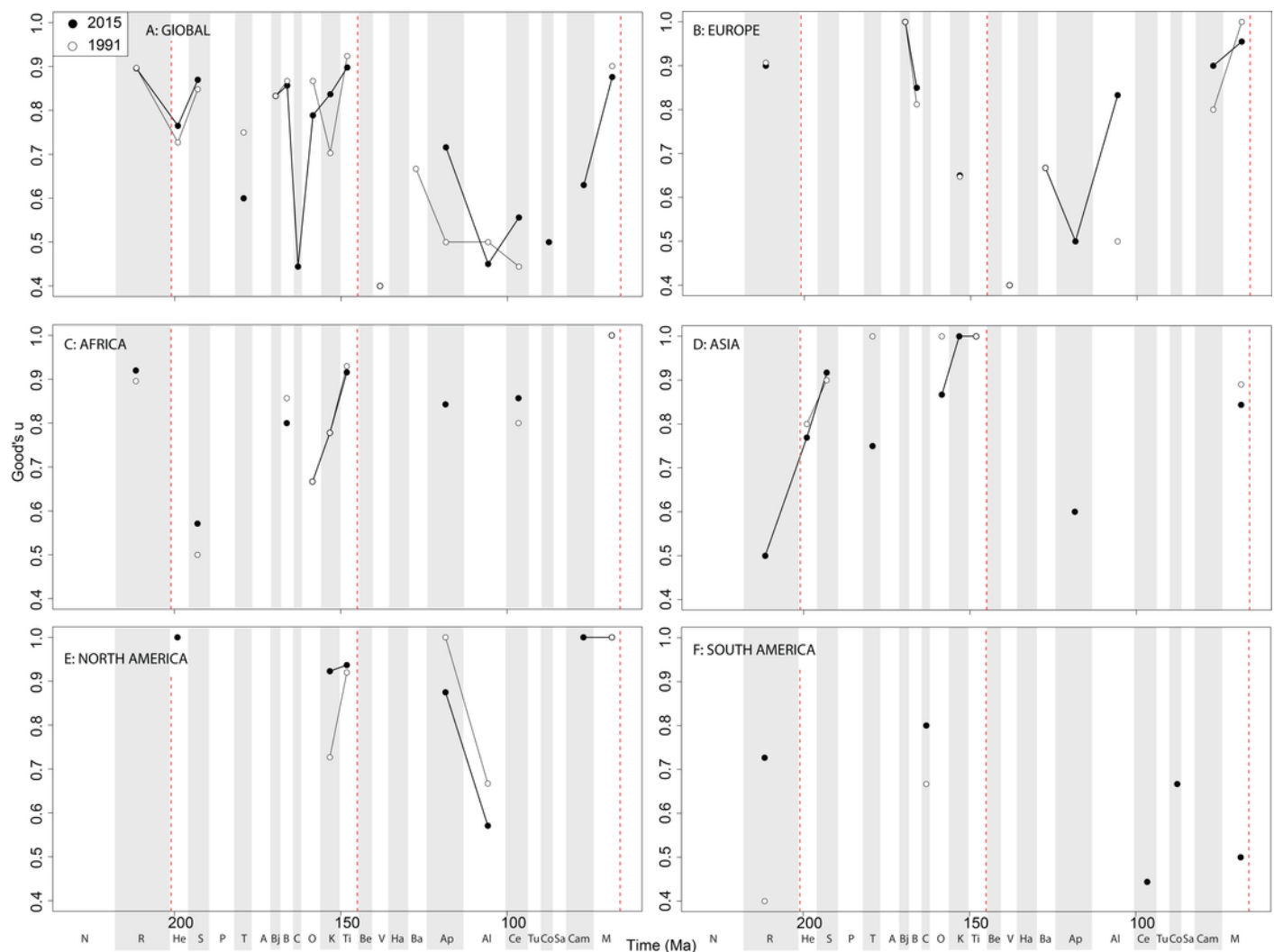



Figure 11

Subsampled sauropodomorph diversity at A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

Figure 12

Good's *u* estimates for sauropodomorphs at a A) global and B-F) regional levels (Europe, Africa, Asia, North America, and South America, respectively) based on our published knowledge in 1991 and 2015. Abbreviations as Figure 3.

Ornithischian correlation test results.

Ornithischians			Sea level			Palaeotemperature		
	Shapiro-Wilk (p)	Correlation test	cor	p	adjusted p	cor	p	adjusted p
2015	0.003	Spearman	0.42	0.137	0.322	-0.432	0.109	0.235
2013	0.002	Spearman	0.481	0.084	0.273	-0.396	0.145	0.235
2011	0.002	Spearman	0.481	0.084	0.273	-0.396	0.145	0.235
2009	0.002	Spearman	0.516	0.062	0.273	-0.429	0.113	0.235
2007	0.001	Spearman	0.503	0.069	0.273	-0.471	0.078	0.235
2005	<0.001	Spearman	0.358	0.209	0.273	-0.346	0.206	0.237
2003	0.002	Spearman	0.314	0.274	0.322	-0.325	0.237	0.237
2001	0.001	Spearman	0.332	0.246	0.322	-0.329	0.232	0.237
1999	0.002	Spearman	0.327	0.253	0.322	-0.432	0.109	0.235
1997	0.001	Spearman	0.341	0.233	0.322	-0.429	0.113	0.235
1995	<0.001	Spearman	0.258	0.394	0.394	-0.367	0.197	0.237
1993	0.001	Spearman	0.413	0.185	0.322	-0.495	0.089	0.235
1991	0.002	Spearman	0.329	0.297	0.322	-412	0.163	0.235

Sauropodomorph correlation test results.

Sauropodomorphs			Sea level			Palaeotemperature		
	Shapiro-Wilk (p)	Correlation test	cor	p	adjusted p	cor	p	adjusted p
2015	0.036	Spearman	-0.114	0.711	0.795	-0.171	0.527	0.609
2013	0.045	Spearman	-0.08	0.795	0.795	-0.138	0.609	0.609
2011	0.274	Pearson	0.399	0.201	0.877	0.095	0.736	0.81
2009	0.192	Pearson	0.399	0.201	0.877	0.067	0.813	0.813
2007	0.052	Pearson	0.161	0.619	0.877	-0.197	0.482	0.81
2005	0.477	Pearson	0.115	0.71	0.877	-0.221	0.41	0.81
2003	0.19	Pearson	0.168	0.614	0.877	-0.235	0.4	0.81
2001	0.385	Pearson	0.007	0.991	0.991	-0.199	0.477	0.81
1999	0.124	Pearson	0.105	0.75	0.877	-0.174	0.522	0.81
1997	0.887	Pearson	-0.145	0.673	0.877	-0.116	0.692	0.81
1995	0.485	Pearson	-0.091	0.797	0.877	-0.147	0.615	0.81
1993	0.763	Pearson	-0.155	0.654	0.877	-0.147	0.617	0.81
1991	0.295	Pearson	-0.145	0.673	0.877	-0.147	0.615	0.81

Theropod correlation tests results.

Theropods			Sea level			Palaeotemperature		
	Shapiro-Wilk (p)	Correlation test	cor	p	adjusted p	cor	p	adjusted p
2015	0.036	Spearman	0.175	0.588	0.672	0.115	0.71	0.868
2013	0.098	Pearson	0.234	0.464	0.464	0.334	0.264	0.362
2011	0.027	Spearman	0.099	0.751	0.751	0.059	0.844	0.868
2009	0.032	Spearman	0.17	0.579	0.672	0.055	0.856	0.868
2007	0.029	Spearman	0.17	0.579	0.672	0.055	0.856	0.868
2005	0.072	Pearson	0.289	0.316	0.464	0.363	0.184	0.362
2003	0.027	Spearman	0.407	0.151	0.659	-0.061	0.832	0.868
2001	0.006	Spearman	0.346	0.247	0.659	-0.086	0.773	0.868
1999	0.028	Spearman	0.379	0.202	0.659	-0.051	0.868	0.868
1997	0.193	Pearson	0.476	0.1	0.25	0.254	0.362	0.362
1995	0.107	Pearson	0.511	0.074	0.25	0.257	0.355	0.362
1993	0.101	Pearson	0.251	0.409	0.464	0.264	0.342	0.362
1991	0.013	Spearman	0.209	0.494	0.672	-0.071	0.803	0.868

Total dinosaur correlation tests results.

All dinosaurs			Sea level			Palaeotemperature		
	Shapiro-Wilk (p)	Correlation test	cor	p	adjusted p	cor	p	adjusted p
2015	0.327	Pearson	0.189	0.467	0.467	-0.051	0.832	0.984
2013	0.233	Pearson	0.226	0.385	0.467	-0.099	0.678	0.984
2011	0.059	Pearson	0.324	0.204	0.467	0.108	0.652	0.984
2009	0.021	Spearman	0.284	0.268	0.367	-0.072	0.763	0.876
2007	0.489	Pearson	0.233	0.367	0.467	0.01	0.966	0.984
2005	0.045	Spearman	0.207	0.407	0.367	-0.095	0.682	0.876
2003	0.053	Pearson	0.305	0.218	0.467	0.025	0.914	0.984
2001	0.043	Spearman	0.232	0.367	0.367	-0.089	0.71	0.876
1999	0.066	Pearson	0.342	0.179	0.467	0.005	0.984	0.984
1997	0.27	Pearson	0.358	0.159	0.467	-0.048	0.84	0.984
1995	0.13	Pearson	0.275	0.303	0.467	0.021	0.931	0.984
1993	0.119	Pearson	0.221	0.429	0.467	0.046	0.856	0.984
1991	0.049	Spearman	0.261	0.347	0.367	-0.04	0.876	0.876