

# How does dinosaur diversity through time change through time?

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Our knowledge of the number of dinosaur species is dependent on the publication record, and how this taxonomic archive varies through historical time. Recently, a number of high-profile studies have analysed patterns in dinosaur diversity that assess the raw numbers of species, also accounting for ecological changes in the shape of the species abundance curve, both of which are dependent on databases compiled from the primary published literature. However, how the shape of these 'diversity curves' is 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. In all three groups, the shape of raw global diversity through publication time remains intriguingly consistent. While theropod and sauropod diversity both increase notably throughout publication time, most apparent in the Cretaceous, these changes are fairly evenly distributed throughout the Cretaceous and do not distort the overall shape of diversity. When subsampling is applied, the relative magnitude of these global changes is greatly emphasised, highlighting a major decline in ornithischian diversity through the Early-Late Cretaceous transition, a major decline in sauropod diversity in the Campanian-Maastrichtian, and a double-dip decline in theropod diversity through the 'middle' Cretaceous, each of which become increasingly more emphasised through publication history. The continental signal reflects this global pattern too, with changes in subsampled diversity through time consistently indicating greater changes than the raw data reveal. When comparing each of these temporal diversity curves to sea level, we find that the correlation strength varies through publication time, is consistently weakly negative, but overall has decreased. Our results suggest that historical changes in database compilation, particularly in terms of the publication of additional specimens of previously identified species, affects the shape of macroevolutionary patterns for dinosaurs and our interpretations of the processes that govern them.

# 1 How does dinosaur diversity through time change through time?

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6

## 7 Abstract

8 Our knowledge of the number of dinosaur species is dependent on the publication record, and how this  
9 taxonomic archive varies through historical time. Recently, a number of high-profile studies have analysed  
10 patterns in dinosaur diversity that assess the raw numbers of species, also accounting for ecological  
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13 influenced by the history of publication remains largely unknown. Here, we investigate the influence of  
14 publication history between 1991 and 2015 on our understanding of dinosaur evolution using raw  
15 diversity estimates and Shareholder Quorum Subsampling for the three major subgroups, Ornithischia,  
16 Sauropodomorpha and Theropoda. In all three groups, the shape of raw global diversity through  
17 publication time remains intriguingly consistent. While theropod and sauropod diversity both increase  
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20 subsampling is applied, the relative magnitude of these global changes is greatly emphasised, highlighting  
21 a major decline in ornithischian diversity through the Early-Late Cretaceous transition, a major decline in  
22 sauropod diversity in the Campanian-Maastrichtian, and a double-dip decline in theropod diversity  
23 through the ‘middle’ Cretaceous, each of which become increasingly more emphasised through  
24 publication history. The continental signal reflects this global pattern too, with changes in subsampled  
25 diversity through time consistently indicating greater changes than the raw data reveal. When comparing  
26 each of these temporal diversity curves to sea level, we find that the correlation strength varies through  
27 publication time, is consistently weakly negative, but overall has decreased. Our results suggest that  
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29 of previously identified species, affects the shape of macroevolutionary patterns for dinosaurs and our  
30 interpretations of the processes that govern them.

31

## 32 **Introduction**

33 In the latter half of the 20<sup>th</sup> Century, palaeobiology underwent a renaissance by adopting a more  
34 quantitative analytical approach to understanding changes in the fossil record through time (Raup 1972;  
35 Raup 1975; Sepkoski Jr 1982; Sepkoski Jr 1992; Sepkoski Jr 1996; Sepkoski Jr et al. 1981; Sepkoski Jr et al.  
36 2002). This seminal work was largely focussed around estimating patterns of animal diversity, extinction  
37 and speciation through time, and what the external controls and processes governing these were. To this  
38 day, reconstructing the diversity of life through geological time remains one of the most crucial aspects  
39 of palaeobiology. These earlier analyses were largely based on an archive of range-through taxa of marine  
40 animals, known as the ‘Sepkoski Compendium’. More recently, analytical palaeobiology has had a second  
41 wave of innovation, in part thanks to development of large fossil occurrences databases such as the  
42 Paleobiology Database ([www.paleobiodb.org](http://www.paleobiodb.org)) and Fossilworks ([fossilworks.org](http://fossilworks.org)), and also due to  
43 development of increasingly sophisticated analytical subsampling (Alroy 2000a; Alroy 2003; Alroy 2010a;  
44 Starrfelt & Liow 2016) and modelling (Lloyd 2012; Smith & McGowan 2007) techniques. There are 1,920  
45 published records in Google Scholar with the term “Paleobiology Database” in as of 27 April 2017,  
46 highlighting its importance in research.

47 All of these studies, both older and more recent, are under-pinned by a single principle, in that they rely  
48 on counts of the number of taxa present through geological time. Despite meticulous work to ensure that  
49 these databases and compendia represent the best possible records of historical trends, there have been  
50 continuing questions as to the accuracy of the data and the existence of what is broadly termed as ‘bias’.  
51 This includes factors such as sampling intensity, different sampling availability, and variable depth of  
52 taxonomic research (Raup 1972; Raup 1976). In 1993, Sepkoski added an additional dimension to these  
53 diversity studies by assessing how database compilation history through changes in taxonomy,  
54 stratigraphic resolution, and sampling influences the shape of macroevolutionary patterns (Sepkoski Jr  
55 1993). This analysis was based on comparing two records built in 1982 and 1992, and found that in spite  
56 of numerous taxonomic changes over ten years, the overall pattern structure for marine animals remained  
57 relatively constant, with the main notable change being that overall diversity was consistently higher in  
58 the 1992 compilation. Following this example, Alroy (2000b) further showed that database age does have

59 an influence on North American mammal diversity estimates, but this apparent phenomenon has been  
60 largely ignored since then.

61 At the present, there are three main arguments regarding the historical reliability of diversity curves:  
62 firstly, that because independent datasets yield similar diversity curves, this suggests that convergence on  
63 a common signal indicates accuracy; secondly, that the addition of new data to existing compilations  
64 should yield only minor changes to resulting diversity estimates; and thirdly, that the addition of new data  
65 can potentially dramatically alter shape of diversity. Since Sepkoski's library work, surprisingly little  
66 consideration has been given to how publication or database history can influence macroevolutionary  
67 patterns (Alroy 2000b), despite an enormous reliance on their research utility. In particular, to our  
68 knowledge, no one has yet tested the potential influence using an occurrence-based dataset, such as  
69 those available from the Paleobiology Database or Fossilworks. This is important, given that a wealth of  
70 recent studies, and in particular on tetrapod groups, have been focussed on estimating diversity patterns  
71 through geological time, with many using occurrence-based subsampling protocols, and interpreting what  
72 the potential drivers of these large-scale evolutionary patterns might be (Benson et al. 2016a; Benson &  
73 Butler 2011; Benson et al. 2016b; Brocklehurst et al. 2017; Butler et al. 2009; Butler et al. 2011; Grossnickle  
74 & Newham 2016; Mannion et al. 2015; Nicholson et al. 2015; Nicholson et al. 2016; Tennant et al. 2016a;  
75 Tennant et al. 2016b). Many of these studies employ subsampling methods that are sensitive to changes  
76 in the shape of the taxonomic abundance distribution, which we would expect to change in a non-random  
77 fashion based on new discoveries through time as they are published (Benton 2015; Benton et al. 2011;  
78 Benton et al. 2013).

79 While the data used in these analyses is typically based on a 'mature' dataset, that has undergone rigorous  
80 taxonomic scrutiny and data addition or refinement, they usually neglect explicit consideration of the  
81 potential influence of temporal variations in the publication record (which these databases are explicitly  
82 based on). This has important implications for several reasons. Firstly, we expect the shape of raw diversity  
83 curves to change (either uniformly, randomly, or structurally) through time in concert with new taxonomic  
84 discoveries and as sampling increases (Alroy 2000b; Sepkoski Jr 1993). Secondly, we therefore expect that  
85 our interpretations of the relative magnitude, tempo and mode of radiations and extinctions to change as  
86 these discoveries are made. As our data are refined, capturing this influence of sampling variation  
87 becomes more important through longer periods of time. Thirdly, as the shape of estimated diversity  
88 curves change (either based on raw or 'corrected' data), we expect that results from analyses based on  
89 model-fitting or pairwise correlation analyses with extrinsic factors such as sea-level or

90 palaeotemperature (Butler et al. 2011; Mannion et al. 2015; Martin et al. 2014; Nicholson et al. 2015;  
91 Tennant et al. 2016a; Tennant et al. 2016b) will change. Recently, this was highlighted by Jouve et al.  
92 (2017), who tested the conclusions of Martin et al. (2014) and their assertion that sea-surface  
93 temperature was the primary factor driving marine crocodylomorph evolution, contra Mannion et al.  
94 (2015) and Tennant et al. (2016a). They found that the correlations reported by the first study, also non-  
95 replicable by (Mannion et al. 2015) and (Tennant et al. 2016a), were fairly unstable even based on very  
96 recent changes in taxonomy, highlighting how small changes in publication history can lead to mixed  
97 interpretations of macroevolutionary patterns.

98 In this study, we investigate the influence of how publication history can affect our reading and  
99 understanding of diversity analyses through time. This study does not discuss the following: (1) what time-  
100 binning methods are appropriate for the fossil record; (2) what analytical methods are optimal for  
101 accounting for the incompleteness of the fossil record, and (3) what the impact of secular variation in the  
102 rock record through space and time have on our understanding of diversity, and these factors are  
103 appropriately discussed in more detail elsewhere (Benson & Mannion 2011; Benson & Upchurch 2013;  
104 Benson & Butler 2011; Benson et al. 2016b; Benton 2015; Benton et al. 2013; Dunhill et al. 2014; Heim &  
105 Peters 2011; Peters & Heim 2010; Peters & Heim 2011; Tennant et al. 2016a; Tennant et al. 2016b). We  
106 want to test a simple hypothesis: How does our understanding of diversity patterns change through time  
107 as we discover more new taxa and additional fossil occurrences of those taxa in time and space. For this,  
108 we elected to use the clade Dinosauria (excluding Aves) as a study group, as more than almost any other  
109 vertebrate group they have received an intensely sampled fossil record, and have a rich history of  
110 taxonomy and macroevolutionary research.

111

## 112 **Material and Methods**

### 113 *Dinosaur occurrences dataset*

114 We used a pre-existing dataset of dinosaur body fossil occurrences drawn from the Paleobiology Database  
115 that spans the entirety of the Jurassic to Cretaceous (201–66 Ma) (Carrano et al. 2015; Tennant et al.  
116 2016b). This comprised only body fossil remains, and excluded ootaxa and ichnotaxa. This dataset was  
117 divided into the three major clades, Sauropodomorpha (SI 1), Ornithischia (SI 2), and Theropoda  
118 (excluding Aves) (SI 3), and resolution is provided at the genus level. We excluded Aves as, due the  
119 differences in the skeletons of volant taxa, they have a fossil record dominated by exceptional modes of

120 preservation (Brocklehurst et al. 2012; Dean et al. 2016). We elected to use genera, as this means that we  
121 can integrate occurrences that are resolved only to the genus level (e.g., *Allosaurus* sp.), and therefore  
122 include a substantial volume of data that would be lost at any finer resolution (Robeck et al. 2000). A  
123 potential issue with this approach is that many dinosaur genera are multispecific, but this is randomly  
124 distributed throughout our dataset and therefore should not have any substantial impact on resulting  
125 curves. It has also been repeatedly demonstrated that the shape of species and genus curves are strongly  
126 correlated in spite of differential taxonomic treatment (Alroy 2000b; Butler et al. 2011; Mannion et al.  
127 2015), and therefore a genus level compilation should be sufficient for the scope of the present study.  
128 These data were based on a comprehensive data compilation effort from multiple workers over a long  
129 period of time, and represents the state of the art in dinosaur taxonomy and palaeontology at this time.  
130 We elected to use a stage-level binning method based upon the Standard European Stages and absolute  
131 dates provided by Gradstein et al. (2012), as opposed to a more equal-length time binning approach as  
132 others have used recently (Benson et al. 2016a; Mannion et al. 2015). For our study, it is less important  
133 what time binning scheme we use relative to the consistent treatment of it across different publication  
134 intervals. Only body fossil occurrences that had their complete stratigraphic range contained within a  
135 single stage bin were included in order to avoid the over-counting of taxa or occurrences that have poorly  
136 constrained temporal durations or contained within multiple time bins. Each dinosaurian sub-group was  
137 further sub-divided into approximately contiguous palaeocontinental regions: Africa, Asia, Europe, South  
138 America, and North America (Mannion et al. 2015). Unfortunately, sampling is too poor to analyse  
139 patterns in Antarctica, Australasia, or Indo-Madagascar, although these regions remain included in the  
140 global analyses.

141

#### 142 *Calculating diversity through time*

143 To test how diversity changes through time, we reduced this primary dataset by successively deleting data  
144 from publications of occurrences recursively at 2 year intervals. Note that this is not the same as the date  
145 that the entries were made into the database, but the explicit date of publication of that occurrence  
146 record in the published version of record. We stopped at 1991, giving 12 sequential temporal datasets for  
147 each dinosaurian clade. What this represents is the maturity of the dataset with respect to its present  
148 state based on publication history. Two methods were used to assess diversity patterns. Firstly, empirical  
149 diversity based on raw in-bin counts of taxa. This method has been repeatedly shown to be a 'biased' or  
150 poor estimator of true diversity as it is influenced by heterogeneous sampling (Benson & Upchurch 2013;

151 Benson & Butler 2011; Benson et al. 2010; Butler et al. 2013; Mannion et al. 2015; Newham et al. 2014;  
152 Smith & Benson 2013; Tennant et al. 2016a; Tennant et al. 2016b). Secondly, we employed the  
153 shareholder quorum subsampling (SQS) method, which was designed to account for differences in the  
154 shape of the taxon-abundance curve (Alroy 2010a; Alroy 2010c), and implemented in Perl (SI 4, 5). This  
155 dual method is important, as not all publications name new taxa – some add to our knowledge of existing  
156 taxa by publishing on new occurrences or collections, and therefore by applying a method that accounts  
157 for changes in taxonomic abundance we can see how publication history influences diversity through  
158 subsampling methods.

159

#### 160 *Model-fitting of extrinsic parameters*

161 For our model-fitting protocol, we follow the standard procedure outlined in numerous recently analytical  
162 studies, by employing simple pairwise correlation tests to the residuals of detrended time series at the  
163 stage level (Benson & Butler 2011; Butler et al. 2013; Butler et al. 2011; Mannion et al. 2015; Tennant et  
164 al. 2016a; Tennant et al. 2016b). Residuals for each of the two environmental parameters were calculated  
165 using the arima() function, which uses maximum likelihood to fit a first-order autoregressive (AR(1)) model  
166 to each time series (Gardner et al. 1980). This method eliminates the potential influence of any long-term  
167 background trend (i.e., a directed change in the mean value of the complete time series through time)  
168 within the time series, which has the potential to artificially inflate correlation coefficients in pairwise  
169 tests (Box & Jenkins 1976), and also accounts for any potential serial autocorrelation (i.e., the correlation  
170 of a variable with itself through successive data points). This protocol has become standard practice now  
171 for palaeontological time series analysis following its recommendation by Alroy (2000b). For sea level, we  
172 used the curve of Miller et al. (2005), which has been widely applied in recent analyses of tetrapod  
173 diversification (Benson et al. 2010; Butler et al. 2011; Mannion et al. 2015; Martin et al. 2014; Tennant et  
174 al. 2016a; Tennant et al. 2016b), and for palaeotemperature we used the data from Prokoph et al. (2008).

175 We performed pairwise correlation tests between our diversity estimates and each environmental  
176 parameter using parametric (Pearson's product moment correlation coefficient [ $r$ ]) and non-parametric  
177 (Spearman's rank [ $\rho$ ]) tests. For each test, both the raw and adjusted p-values are reported, the latter  
178 calculated using the p.adjust() function, and using the 'BH' model (Benjamini & Hochberg 1995). This  
179 method accounts for the false-discovery test when performing multiple hypothesis tests with the same  
180 data set, which can inflate type-2 error (i.e., in order to avoid falsely retaining a false null hypothesis; a  
181 false negative). We avoided the more commonly used 'Bonferroni correction', due the undesirable

182 property it has of potentially increasing type 2 error to unacceptable levels (Nakagawa 2004). This  
183 adjustment was performed on ‘families’ of analyses, rather than on all correlation tests together,  
184 otherwise we potentially run the risk of setting the pass rate for statistical significance too low.

185 Differently to Tennant et al. (2016b), we excluded the first 5 Jurassic data points from our analyses instead  
186 of treating them as missing data. We performed pairwise correlations for subsampled diversity estimates  
187 at each two year iteration for each group to assess how the strength and direction of correlation changes  
188 through publication history. We do not use a maximum likelihood model fitting approach as rather than  
189 trying to distinguish between a set of candidate models, we are simply assessing how the strength of  
190 correlations changes through publication history. All analyses were carried out in R version 3.0.2 (R  
191 Development Core Team 2013).

192

## 193 **Results**

### 194 *Global patterns of raw diversity*

195 The overall shape of the raw theropod diversity curve remains consistent through publication history (Fig.  
196 1A). Similar to ornithischians, we see steadily increasing Middle to Late Jurassic diversity, fluctuating  
197 ‘middle’ Cretaceous diversity, and then a major Campanian to Maastrichtian rise, where diversity remains  
198 constant. The lowest diversity is the Coniacian, which is poorly sampled in terrestrial faunas. Notable  
199 variations due to publication history are in the Barremian to Cenomanian, where the diversity peak  
200 increases in magnitude through time, exceeding that of Late Jurassic diversity more recently.

201 Sauropodomorph empirical diversity is unique among other dinosaurian groups in that there are  
202 numerous substantial changes in raw patterns through time, and particularly in the Cretaceous (Fig. 1B).  
203 Late Jurassic patterns are consistent, documenting a steady increase from the Middle to the end of the  
204 Jurassic, before a major decline across the J/K boundary. The Barremian to Cenomanian is approximately  
205 constant in diversity, and consistently increasing through time. Diversity in the Turonian and Coniacian is  
206 as low as the Berriasian, before steadily increasing until the end of the Cretaceous. The magnitude of this  
207 Late Cretaceous increase has almost doubled in the last 20 years.

208 Raw ornithischian diversity (Fig. 1C) is remarkably constant and stable to changes in publication history,  
209 similar to that for theropods. The magnitude of longer-term trends is obscured by the relative over-  
210 sampling of the Campanian and Maastrichtian, which are almost an order of magnitude higher than any  
211 other Jurassic or Cretaceous stage interval. Indeed, the Campanian shows no sign of slowing down in

212 increasing diversity, and is the highest and most rapidly increasing of any time interval. In spite of this, the  
213 overall trends in raw diversity remain, with steadily increasing Middle to Late Jurassic diversity, a small  
214 earliest Cretaceous decline followed by a 'middle' Cretaceous peak in the Aptian, a shallow decline into  
215 the early Late Cretaceous, and a massive increase in the Campanian-Maastrichtian.

216

#### 217 *Global patterns of subsampled diversity*

218 The overall pattern, and the magnitude of disparity through publication time, are emphasised for  
219 theropod diversity (note that SQS reveals changes in relative diversity, not absolute diversity) (Fig. 2A). In  
220 the Late Jurassic, we see a switch from steadily increasing subsampled diversity to a Callovian-Oxfordian  
221 peak and subsequent diversity crash in the Kimmeridgian. The Tithonian peak and J/K boundary decline  
222 are both consistently recovered through publication time. Diversity is highest during the Aptian than at  
223 any other stage during the Jurassic/Cretaceous interval, and has doubled in the last 20 year, revealing an  
224 overall decline in diversity throughout the 'middle' Cretaceous and early Late Cretaceous. Campanian  
225 diversity is as high as the Cenomanian, and increases slightly towards the end of the Cretaceous, a pattern  
226 that remains consistent through publication time.

227 When we look at subsampled sauropodomorph diversity, this pattern changes dramatically too (Fig. 2B).  
228 The Late Jurassic shows a double dip in diversity in the Oxfordian and Tithonian that is stable through  
229 publication time. Barremian, Aptian, and Cenomanian diversity has almost doubled in the last 20 years.  
230 Campanian diversity has more than doubled, whereas Maastrichtian diversity has increased at a much  
231 slower pace, revealing an increasing magnitude of diversity decline before the end-Cretaceous.

232 Subsampled ornithischian diversity shows a distinctly different pattern from the raw curve, both in terms  
233 of overall trends, and in terms of the magnitude of the effect of publication history (Fig. 2C). The Jurassic  
234 is generally too poorly sampled to reveal a constant signal, but there is evidence of a 'double-dip' decline  
235 over the Jurassic/Cretaceous transition, which remains constant through publication time. This is followed  
236 by a Barremian peak, an Aptian decline, and then a large Albian radiation, in which ornithischian diversity  
237 is at its joint highest throughout the Cretaceous. The magnitude of this radiation has rapidly increased  
238 over publication time, the result being that originally what appeared to be stable diversity over the  
239 Early/Late Cretaceous transition now shows a major decline from the Albian to Coniacian. Santonian  
240 subsampled diversity remains unknown, but when we see a signal emerge in the Campanian, diversity is  
241 as high as the Albian, before declining by more than half into the Maastrichtian. This overall structure,

242 besides the Albian, remains consistent throughout publication time with no major perturbations to the  
243 global curve.

244

245 *The geographical structure of dinosaur diversity*

#### 246 ***Ornithischians***

247 In North America, diversity is flat and low throughout the Late Jurassic and most of the Cretaceous (Fig.  
248 3A). There is a Campanian peak, and order of magnitude higher than any prior interval, which is rapidly  
249 increasing through publication time. Diversity decreases from this into the Maastrichtian, in which  
250 diversity has remained stable through publication time. Subsampled diversity greatly reduces the  
251 magnitude of this Campanian radiation, but the major decline into the Maastrichtian remains, and is  
252 constant through publication history (Fig. 3D). Raw diversity in Europe shows increasing diversity across  
253 the J/K boundary, constant 'middle' Cretaceous diversity, and an increase from the Campanian to  
254 Maastrichtian (Fig. 3B). Subsampled diversity reveals a shift from increasing diversity across the J/K  
255 boundary to stable diversity through publication time, and gradually decreasing diversity throughout the  
256 remainder of the Early Cretaceous, punctuated by a Hauterivian trough (Fig. 3E). The increasing diversity  
257 from the Campanian to Maastrichtian remains, with Maastrichtian diversity increasing by almost a third  
258 through publication time. Raw Asian diversity is fairly constant through the Cretaceous, until a Campanian  
259 peak and Maastrichtian decline (Fig. 3C). Subsampled diversity reveals a major decline across the Early-  
260 Late Cretaceous transition, and a moderate increase from the Campanian to Maastrichtian (Fig. 3F). Both  
261 raw and subsampled African ornithischian diversity is too inconsistent to analyse any changes through  
262 geological time or publication time. Sampling in South America is also relatively poor, with the only  
263 notable change being the increasing magnitude of raw Campanian diversity and the subsequent  
264 Maastrichtian diversity crash, a pattern partially reflected in the subsampled diversity patterns, with  
265 Maastrichtian diversity becoming unknown.

266

#### 267 ***Theropods***

268 In North America, raw pre-Campanian diversity is again dwarfed by the intensive sampling of latest  
269 Cretaceous dinosaurs, and is therefore constantly relatively flat (Fig. 4A). Campanian and Maastrichtian  
270 diversity is constantly increasing at a faster rate than any other time interval, and consistently reveals a  
271 diversity decline into the end-Cretaceous. This regional pattern is completely different to the subsampled

272 diversity estimates, which reveal increasing diversity from the Kimmeridgian to Tithonian, and relatively  
273 low 'middle Cretaceous' diversity in the Aptian and Albian, which is emphasised by steadily increasing  
274 Barremian and Cenomanian diversity (Fig. 4D). There is a clear radiation from the Santonian to the  
275 Campanian, with Campanian diversity equal to that at the end of the Jurassic, and a shallow decline into  
276 the Maastrichtian, which remains consistent throughout publication history. Raw European diversity is  
277 much more constant due to a more intensive sampling history (Fig. 4B). There is a Middle Jurassic diversity  
278 peak in the Bathonian, followed by a Callovian-Oxfordian trough, a second larger Kimmeridgian peak, and  
279 then constant decline from the Tithonian to the Valanginian. Barremian diversity is increasing rapidly  
280 through publication time, and is as high as the Kimmeridgian. Aptian and Albian diversity is low.  
281 Campanian diversity is slowly increasing, but Maastrichtian diversity is increasing much faster through  
282 time, emphasising the rate of diversity change towards the end of the Cretaceous. When subsampling is  
283 applied, the only part of this pattern that remains is the large J/K boundary decline, but instead with a  
284 small bounce back in diversity during the Valanginian (Fig. 4E). In Asia, raw Late Jurassic diversity is  
285 generally lower than the Cretaceous (Fig. 4C). The Cretaceous sees three peaks in diversity during the  
286 Aptian, Turonian and Campanian-Maastrichtian, with the latter interval being considerably more diverse  
287 than any previous one. The signal becomes much patchier when subsampling is applied, with fairly  
288 constant and low diversity through the Jurassic and into the Early Late Cretaceous (Fig. 4F). The  
289 Campanian was historically less diverse than the Maastrichtian, but now this picture has changed in recent  
290 years and now there appears to be a diversity loss from the Campanian to Maastrichtian, with Campanian  
291 diversity increasing at a faster rate than that for the Maastrichtian. Raw South American diversity is very  
292 unstable, with almost every interval in which dinosaurs are available to be sampled leading to rapidly  
293 increasing diversity changes through publication time, especially in the 'middle' and Late Cretaceous. This  
294 relative instability is emphasised when SQS is applied, as only a single interval is sampled well enough to  
295 produce a signal. Here, the Cenomanian still shows a 7-fold increase in subsampled diversity over the last  
296 20 years. As with ornithischians, African theropods are generally too poorly sampled at the stage level to  
297 recognise any consistent patterns. There is a Cenomanian spike in the early Late Cretaceous, but how this  
298 compares to the rest of the Cretaceous is obscured by patchy sampling. However, what is clear when  
299 subsampling is applied is that there is a theropod radiation across the Early-Late Cretaceous boundary,  
300 with diversity almost quadrupling in Africa.

301

302 ***Sauropodomorphs***

303 The North American sauropod record is very patchy, with the latest Jurassic showing a shift from rapidly  
304 increasing raw diversity to a slight drop from the Kimmeridgian to Tithonian (Fig. 5A). Subsampling  
305 appears to corroborate this pattern, and the shift becomes more dramatic through time (Fig. 5B). In  
306 Europe, sauropods show a consistent and major decline in raw diversity from the Kimmeridgian to  
307 Berriasian (Fig. 5B). Much of the rest of the Cretaceous is too poorly sampled, but there is evidence for  
308 increasing diversity towards the end of the Cretaceous. Subsampling again reduces this signal due to an  
309 overall poor sampling of Cretaceous sauropods in Europe, although there is strong evidence for the  
310 sauropod decline beginning prior to the Jurassic/Cretaceous boundary (Fig. 5E). There is also evidence for  
311 an Aptian to Albian diversity drop, and increasing diversity from the Campanian to Maastrichtian, all of  
312 which appear to be stable patterns through publication history. In Asia, raw taxonomic diversity is  
313 generally low compared to the Maastrichtian interval, in which diversity is relatively high and still rapidly  
314 increasing (Fig. 5C). Subsampling greatly reduces the amount of signal, but we see increasing latest  
315 Jurassic and latest Cretaceous diversity with publication history (Fig. 5F). Sauropodomorph dinosaurs are  
316 generally better sampled than theropods and ornithischians in Africa, but still inconsistent enough  
317 through publication and geological time to produce consistent patterns that we can meaningfully  
318 interpret. When subsampling is applied, the few intervals in which a signal emerges reveal a fairly constant  
319 level of diversity through the Jurassic and Cretaceous, and through publication time, with the notable  
320 exception being greater diversity in the latest Jurassic. The South American sauropod record is also  
321 relatively poor, mostly confined to the Late Cretaceous. Here, we see Campanian, Cenomanian, and  
322 Maastrichtian diversity all increasing rapidly through publication time, with this consistently revealing a  
323 Campanian to Maastrichtian decline. Subsampling does not support this pattern, with instead the only  
324 notable recovered pattern being that Campanian diversity is about 1.5 times that of Cenomanian diversity,  
325 with both increasing steadily and equally through publication time. Full subsampling results are provided  
326 in Supplementary Information 6.

327

328 *Model-fitting results*

329 ***Dinosaur diversity and sea level***

330 Our results find varying strength of correlation between subsampled dinosaur diversity for each clade and  
331 sea level. Similar to Tennant et al. (2016b) who used 10 million year time bins, our results using standard  
332 pairwise correlation tests at the stage level find consistently weak and non-significant relationships  
333 between sea level and diversity for each of ornithischians, sauropodomorphs, and theropods. However,

334 the strength of this relationship varies through time. In 1991, half of the variance in sauropodomorph  
335 diversity could be explained by sea level changes. This relationship declined consistently and even became  
336 negative up until 2005, and from 2007-2015 remains a weak but positive relationship, with no more than  
337 around 20-30% of variance being accounted for by sea level. In Ornithischians, the amount of variance in  
338 diversity that sea level explains is consistently between 0.3 and 0.5 through time based on a Spearman's  
339 test. The strength of this correlation is much more variable using a Pearson's test, ranging from -0.16 to  
340 0.45 through time, but in neither of these tests do any of the correlation results approach the traditional  
341 threshold for statistical significance. The relationship between theropod diversity and sea level has  
342 progressively weakened through time, and shifted from being weakly positive in the 1990s to weakly  
343 negative or close to zero approaching modern times. If we sum all three clades together to represent total  
344 dinosaur diversity, then a striking pattern emerges. There is a consistently negative and moderate to  
345 strong correlation between summed diversity and sea level, with the strength of this correlation often  
346 exceeding 0.5. While the strength of this has decreased during publication time, in 2015 at least a third of  
347 total dinosaur diversity could be explained by sea level, but with a negative correlation.

348

#### 349 ***Dinosaur diversity and palaeotemperature***

350 Similar to our sea level results, we find little to no evidence of any strong or consistent relationship  
351 between the diversity of any dinosaur group and palaeotemperature. In sauropodomorphs, the  
352 relationship is consistently weakly negative, become slightly weaker throughout publication history. In  
353 ornithischians, the pattern is similar, but the strength of the negative correlation is much stronger,  
354 averaging around -0.4-0.5 through time. In theropods, the relationship varies between weak negative and  
355 weak positive, never exceeding around -0.3, but becoming gradually more positive with time. When all  
356 dinosaurs are looked at together, the relationship is consistently moderately strongly negative. The  
357 strength of this gradually weakens through time, and never approaches the traditional threshold for  
358 statistical significance. Full model fitting results are given in Supplementary Information 7.

359

#### 360 **Discussion**

##### 361 *The influence of geology, sampling, and publication history on dinosaur diversity*

362 The impact of dinosaur diversity changes through publication time has direct consequences for our  
363 interpretation of their evolutionary history and diversification. As research on dinosaurs continues in this

364 century and new taxa are described from existing fossiliferous formations, one implication of this is that  
365 raw diversity is expected to become less correlated with rock availability as result of increasing sampling  
366 effort (Benton 2015; Raup 1977; Wang & Dodson 2006), and represents a bibliographic form of publication  
367 bias (Alroy 2000b; Jouve et al. 2017; Sepkoski Jr 1993). In this study, we tested whether by comparing  
368 successive dinosaur diversity logistic curves we are approaching the end of the exponential phase of  
369 dinosaur diversity increase, making our diversity analyses for this clade more stable and reliable for further  
370 examination and interpretation. What we seem to be seeing is that for raw diversity estimates, we find  
371 evidence for relatively stable patterns in spite of any ‘bonanza effect’ (Benton 2015; Raup 1977). The fact  
372 that the curves remain relatively linearly consistent despite the non-random addition of new taxa also  
373 provides support for the ‘redundancy’ hypothesis, that fossils and sampling are non-independent from  
374 each other, when only raw data are considered (Benton 2015; Benton et al. 2011; Benton et al. 2013;  
375 Dunhill et al. 2014). While others are now reaching the same conclusion, at least for the Mesozoic tetrapod  
376 record, this further suggests that ‘correcting’ diversity estimates by using static proxies for sampling is not  
377 an appropriate methodology (Benton 2015; Brocklehurst 2015; Sakamoto et al. 2017).

378 However, what is the explanation for the diversity patterns we obtained so far, and what does the  
379 variation in these patterns tell us? Generally, a dinosaur bearing formation availability effect makes the  
380 Kimmeridgian, Barremian, Albian, Aptian, Campanian, and Maastrichtian the most productive stages  
381 (Barrett et al. 2009; Butler et al. 2011; Tennant et al. 2016b; Upchurch et al. 2011). By counting genus  
382 density (number of genera per million year), three stages from these stand out: Kimmeridgian, Campanian  
383 and Maastrichtian (Taylor 2006), with Asia being the most productive continent followed closely by North  
384 America, then Europe, South America, Africa, Australasia and finally Antarctica. There is a major  
385 recognised influence of the amount of rock available for palaeontologists to search for dinosaur fossils,  
386 which have consequences for our interpretations of diversity patterns. This raises questions about the  
387 extent to which many aspects of diversity curves could be artefacts caused by changes in global sea levels,  
388 tectonics, and other geological processes related to preservational or geological megabiases (Heim &  
389 Peters 2011; Peters & Foote 2001; Peters & Heim 2010; Peters & Heim 2011; Smith & Benson 2013; Smith  
390 et al. 2001; Smith et al. 2012; Smith & McGowan 2007). As a way of exploring this, Barrett et al. (2009)  
391 applied the “residuals” method (formerly designed by Smith & McGowan (2007) for marine fossil taxa)  
392 to account for these sorts of structural biases, and demonstrated that many features of dinosaur diversity  
393 curves are sampling artefacts that reflect changes in the amount of fossiliferous rocks and thus reflect  
394 geological rather than biological signals. The influence of these geological biases appears to have been  
395 largely mitigated in recent studies by considering a historically accurate account of sampling and

396 modelling variation through time (Alroy 2010a; Alroy 2010b; Alroy 2010c; Grossnickle & Newham 2016;  
397 Mannion et al. 2015; Newham et al. 2014; Nicholson et al. 2015; Tennant et al. 2016a; Tennant et al.  
398 2016b). Here, sampling heterogeneity in terms of both collection effort and rock availability can be  
399 accounted for through subsampling methods, which appear to capture and alleviate at least part of the  
400 geological signal.

401 These relative changes in the amount of rock available for sampling, the number and abundance of  
402 different taxa, and the historical sampling intensity of different rock formations have implications for the  
403 patterns of palaeobiological change that we infer from them. We find that there are three main time  
404 periods when great caution should be applied to interpreting further processes or patterns based on  
405 dinosaur diversity, especially at a global level. These are: (1) the Middle-Late Jurassic interval for  
406 theropods; (2) the Middle-Late Cretaceous interval for theropods; and (3) the Middle-Late Cretaceous  
407 interval for ornithischians. These represent the times when diversity estimates are changing most rapidly  
408 due to a combination of taxonomic revision and discovery-driven publication. While we cannot predict  
409 the future of dinosaur discovery, or the fickle nature of publication, it seems prudent to suggest that we  
410 are cautious in our interpretation of events in dinosaur macroevolution in these intervals. An interesting  
411 extension of the present study, which explores historical publication bias, would be to test how the  
412 historical context of sampling (e.g., outcrop area variation or availability through time, sampling intensity  
413 through time) corresponds to our historical estimates of diversity.

414

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

#### 416 ***Ornithischians***

417 The Jurassic/Cretaceous (J/K) boundary decline remains constant and recognisable throughout  
418 publication history, with this stability suggesting that either this is a real biological signal and not a  
419 publication artefact (Tennant et al. 2016b). However, more focussed sampling needs to occur on J/K  
420 boundary deposits to reveal the true global signal, as much of this pattern is based on fossils exclusively  
421 from historically well-sampled European localities (Tennant et al. 2016c). Ornithischian diversity  
422 decreases steadily through Early Cretaceous, with a possible radiation from the Campanian to  
423 Maastrichtian, perhaps explained by an increase of recent occurrences of latest Cretaceous dinosaurian  
424 findings mainly in Spain, Portugal, France and Romania (Csiki et al. 2010; Riera et al. 2009). However, many  
425 of these latest Cretaceous European dinosaur faunas are not particularly well-resolved stratigraphically

426 compared to the well-studied North-American sections, which makes the timing of any regional extinction  
427 here and comparison with North America and Asia difficult at the present. Despite the increasing  
428 availability of Early Cretaceous DBFs in Africa in the last 20 years (e.g., Tunisia, Niger; (Anderson et al.  
429 2007; Taquet & Russell 1999)), sampling here is still too limited to reveal any consistent patterns in  
430 ornithischian diversity (Mannion et al. 2011; Tennant et al. 2016b; Upchurch et al. 2011).

431 Ornithischian diversity in Asia has been increasing steadily through publication time in the ‘middle’  
432 Cretaceous, filling in the gap from equivalent latitude European deposits at this time, and plausibly due  
433 to the radiation of Parksosauridae and Ankylopollexia clades, two of the most dominant Late Cretaceous  
434 dinosaurian clades around this time. Together with the North American record, this manifests as a great  
435 global decline across the Early-Late Cretaceous interval, a pattern that was not recognised until more  
436 recent years thanks to the discovery of more Konzentrat-Lagerstätten in Mongolia and China around this  
437 time (Godefroit et al. 2008; Lambert et al. 2001; Upchurch et al. 2011). A perceived Late Cretaceous  
438 diversity increase for Asian taxa, particularly hadrosauroids, could be also due to anthropogenic sampling  
439 bias, following a renaissance in the discovery of Cretaceous Asian dinosaurs over the past two decades  
440 (Barrett et al. 2009; Lloyd et al. 2008; Mo et al. 2016; Upchurch et al. 2011; Zhou & Wang 2010).

441 Globally, advanced ornithischian faunas appear to have hyperdiversified in the latest Cretaceous, but this  
442 is classically explained by the oversampling of North American “Judithian” localities, including the Hell  
443 Creek Formation and Dinosaur Park Formation, and their approximate temporal equivalents. Although a  
444 small rise in diversity is recovered from the Campanian to the Maastrichtian in both Europe and Asia, this  
445 is considerably less marked than the decline in North America, where subsampling reveals that  
446 ornithischian diversity was actually declining from the Campanian to Maastrichtian (Brusatte et al. 2015).  
447 This regional distinction could be due to the tie between ecomorphological function and biological  
448 diversity, as Asian hadrosauroids increased in morphological disparity during the latest Cretaceous,  
449 whereas in North America large-bodied bulk-feeding ornithischians decreased in their disparity (Brusatte  
450 et al. 2012; Campione & Evans 2011). Furthermore, this diversity decline in ornithischians coincided with  
451 a decrease in their provinciality (i.e., beta diversity) and disruption of North American dinosaurian food  
452 webs (Mitchell et al. 2012; Vavrek & Larsson 2010). In North America, several abiotic factors, including  
453 extreme fluctuations of the Western Interior Sea, and the Laramide orogeny and proposed biogeographic  
454 provincialism, may have affected the evolution of North America dinosaurs in distinct ways from species  
455 on other continents (Arbour et al. 2016; Gates et al. 2012), meaning that the North American record is  
456 unlikely to be representative of global diversity pattern (Simpson et al, 2010).

457 ***Theropods***

458 As already shown elsewhere (Barrett et al., 2009, Brusatte et al., 2012), global theropod diversity trends  
459 are overall very similar to that of Ornithischia, with significant diversity increases during the Late Jurassic  
460 (Callovian-Oxfordian and Tithonian peaks punctuated by a Kimmeridgian crash), late Early Cretaceous  
461 (Aptian), early Late Cretaceous (Cenomanian) and latest Cretaceous with a notable decline in diversity  
462 during the Maastrichtian (with a less marked drop than that observed in the ornithischian before the K-  
463 Pg). A notable exception to this congruence is the Late Triassic, where theropods exhibit a small peak in  
464 diversity at a time when ornithischians are exceptionally rare (Butler et al. 2007; Irmis 2010; Irmis et al.  
465 2007; Nesbitt et al. 2007). Middle and Late Jurassic diversity are high with a greater Late Jurassic radiation,  
466 representing the radiation of major tetanuran and coelurosaurian clades, and a wealth of new discoveries  
467 in recent years, particularly from Asia (Benson et al. 2014; Carrano et al. 2012; Tennant et al. 2016b;  
468 Upchurch et al. 2011; Xu et al. 2011).

469 As for Ornithischia, the African theropod record is too patchy to show a consistent diversity record  
470 (Upchurch et al. 2011), with some exceptions highlighted by our subsampling approach. There is a  
471 Cenomanian boom mainly due to the multitaxic theropod dominated Kem Kem beds and other Albian-  
472 Cenomanian (“middle” Cretaceous) equivalents in Northern Africa, but this signal might have been altered  
473 by time averaging effects constraining a more timely diluted diversity in a single unit (Chiarenza & Cau  
474 2016; Evers et al. 2015; Mannion & Barrett 2013). Asian diversity peaks in the Aptian, Turonian,  
475 Campanian and Maastrichtian might be explained by a Lagerstätten ‘bonanza’ effect, especially  
476 considering the high quality preservation deposits discovered and heavily sampled in the last 20 years  
477 (e.g. Liaoning) (Godefroit et al. 2013; Lloyd et al. 2008; O’Connor & Zhou 2015; Tennant et al. 2016b;  
478 Tennant et al. 2016c; Zhou & Wang 2010).

479 European diversity is more constant than in other regions, with a Bathonian peak followed by a Callovian-  
480 Oxfordian trough, and a Kimmeridgian peak followed by a Tithonian to Valanginian drop. This can, at least  
481 in part, be explained by an abundance of well-sampled Late Jurassic formations from the UK, Central  
482 Europe (e.g. Solnhofen), Spain and Portugal (Benson et al. 2013; Tennant et al. 2016b; Tennant et al.  
483 2016c; Upchurch et al. 2011). Barremian diversity is increasing rapidly through publication history, and is  
484 now as high as calculated for the Kimmeridgian. As with the Late Jurassic, at least part of this signal  
485 represents the influence of a Lagerstätten effect (e.g., Las Hoyas, Spain) (Buscalioni et al. 2008; Sánchez-  
486 Hernández & Benton 2012; Upchurch et al. 2011), highlighting that single, well-sampled formations can  
487 have a profound historical effect on our understanding of regional diversity patterns. The European

488 Aptian-Albian record is increasing slower through time compared to the Campanian-Maastrichtian.  
489 However, this might possibly change in the future, as the ichnological record in southern Europe is quite  
490 abundant for the Aptian-Albian interval, and suggests a currently unrecognised dinosaurian diversity  
491 present there (Dalla Vecchia 2002; Meyer & Thuring 2003).

492 The North American pre-Campanian record is surely dwarfed by an oversampling of latest Cretaceous  
493 dinosaur-bearing formations (e.g. Dinosaur Provincial Park, Hell Creek Formation). An increasingly more  
494 even representation of latitudinally diverse localities from the Cenomanian-Campanian of Utah, Colorado,  
495 New Mexico and Mexico (e.g. Wahweap Formation), may increase the magnitude of the high apparent  
496 diversity drop through the Maastrichtian. Subsampling highlights a latest Jurassic peak in diversity (due to  
497 the abundance of remains from the well-sampled Morrison Formation; (Foster 2003)), matching the  
498 Campanian level of diversity. Conversely to Brusatte et al. (2015), who found no evidence for a progressive  
499 Campanian-Maastrichtian decline in North American theropod faunas using similar SQS analyses  
500 (implemented in R; see (Tennant et al. 2016a; Tennant et al. 2016b) and (Alroy 2010a; Alroy 2010c) for  
501 comparative discussions), we find a slight decline that remains constant (around 20% loss) through  
502 publication history, that likely relates to our usage of a more refined subsampling approach (Alroy 2010c).  
503 Albian-Aptian diversity dwarfs the Barremian level due to the more-sampled localities from Montana to  
504 Texas (Cifelli et al. 1999; Kirkland et al. 1997; Kirkland & Madsen 2007). Similarly to the pattern in Africa,  
505 South America theropod diversity sparkles compared to other stages, as increasingly new taxa have been  
506 discovered, often altering our knowledge of dinosaur phylogeny and biogeography from the ‘middle’  
507 Cretaceous of Patagonia and Brasil (Canale et al. 2009; Novas et al. 2013; Novas et al. 2005; Novas & Pol  
508 2005).

### 509 ***Sauropods***

510 Sauropodomorph diversity patterns share some characteristics of those for theropods and ornithischians,  
511 despite having an overall poorer fossil record due to taphonomic differences (Dean et al. 2016; Mannion  
512 & Upchurch 2010; Mannion & Upchurch 2011). This is compounded by a difficulty in assigning a large  
513 number of taxa to specific stage bins, which excludes many of them from our analyses (SI 1). These  
514 similarities include diversity peaks during the Late Jurassic, late Early Cretaceous and latest Cretaceous,  
515 with a major decline during the early Late Cretaceous. Numerous sauropodomorph taxa were present  
516 during the late Triassic to Middle Jurassic interval, while ornithischian diversity was relatively low  
517 throughout this period. This divergence in diversity patterns has classically been interpreted as being due  
518 to exclusive competition between the two main herbivorous dinosaurian subtaxa (Butler et al. 2009), with

519 an explosive radiation in ornithischians during the Early Cretaceous resulting from the apparent decline  
520 in diversity of sauropodomorphs. In fact, the J/K boundary represents a major extinction event for  
521 sauropodomorphs, reflecting the decline of non-neosauropods, diplodocoids and basal macronarians  
522 (Mannion et al. 2013; Tennant et al. 2016b). Sauropodomorph faunas have a low diversity in the earliest  
523 Cretaceous, coupled with a generally poor fossil record (Mannion & Upchurch 2010), but at a time when  
524 we otherwise see rapid increases in theropod and ornithischian diversity and a prolonged phase of faunal  
525 turnover (Tennant et al. 2016b; Upchurch & Mannion 2012). Sauropodomorph diversity levels are  
526 maintained at an almost constant level during the final latest Cretaceous radiation, and did not decline  
527 prior to the end-Cretaceous boundary. This find is somewhat contrary to that of Sakamoto et al. (2016)  
528 who found that their decline was initiated in the Early Cretaceous, and that the diversification of  
529 titanosaurs was at an insufficient rate to compensate for the overall loss of sauropodomorph lineages  
530 throughout the rest of the Cretaceous. Sauropodomorphs appear to be overrepresented with respect to  
531 what we might expect based on the number of DBFs for almost the entire duration of the Jurassic, whereas  
532 the opposite is true for the Cretaceous (Mannion et al. 2011; Tennant et al. 2016b; Upchurch et al. 2011).  
533 Sauropodomorph diversity patterns are distinct compared to theropods and ornithischians for being  
534 inconsistent with them through time, although part of this might be due to a relatively patchier fossil  
535 record. The general pattern of diversity follows a steady increase from Middle to the end of Jurassic with  
536 major decline through J/K boundary (Tennant et al. 2016b; Upchurch & Mannion 2012). The magnitude  
537 of Late Cretaceous diversity increases in the last 20 years can at least partially be explained by the constant  
538 discovery of new titanosaurian taxa especially from Gondwanan continents (Bandeira et al. 2016; de Jesus  
539 Faria et al. 2015; Poropat et al. 2016; Vieira et al. 2014), and only recently a more appreciated diversity of  
540 diplodocoids (e.g., dicraeosaurids, rebbachisaurids) from relatively poorly sampled regions such as Africa  
541 (Ibrahim et al. 2016; Mannion & Barrett 2013; Wilson & Allain 2015).

542 Large-bodied sauropod diversity in the Tithonian is certainly influenced by oversampling of the North  
543 American Morrison Formation, where there is an unusually high diversity and cranial disparity of  
544 megaherbivores within a relatively resource-poor environment (Button et al. 2014). In addition,  
545 sauropods appear to be better sampled than theropods and ornithischians in Africa, although their  
546 records remain too inconsistent and patchy record to reveal any major patterns. When subsampling is  
547 applied, Jurassic and Cretaceous levels of diversity are relatively low in all regions, with the notable  
548 exception of the Tithonian. Here, high diversity remains in spite of our accounting for large collection  
549 biases associated with Konzentrat-Lagerstätten (Alroy 2010a; Alroy 2010c), implying that the Late Jurassic  
550 was when sauropodomorphs reached their true zenith in diversity. Asian raw diversity is constantly lower

551 than both theropods and ornithischians until the Maastrichtian, where it increases substantially based on  
552 a series of recent discoveries from Pakistan and China (Junchang et al. 2013; Malkani 2010). This  
553 phenomenon could be explained by a taphonomic size bias discriminating against the preservation of  
554 larger-bodied animals in pre-Late Cretaceous Konservat-Lagerstätten, while they are more present  
555 although more rare in the dense bone assemblages from the latest Cretaceous of Mongolia, China and  
556 India (Kidwell, 2001).

557 There is a marked increase in European sauropod diversity from the Campanian to Maastrichtian due to  
558 relatively good sampling of latest Cretaceous deposits in western Europe (Csiki-Sava et al. 2015; Upchurch  
559 et al. 2011). Application of SQS reduces an already degraded European signal because of the very poor  
560 sampling through much of the Cretaceous, but there is a notable diversity decline through the J/K  
561 boundary, as with other dinosaurian groups (Tennant et al. 2016b; Upchurch & Mannion 2012), but  
562 conversely to results when other methods (e.g., TRIPS) are applied and don't find any evidence for a  
563 decline (Starrfelt & Liow 2016). Subsampling also reverses the latest Cretaceous decline, and instead this  
564 reveals a small increase in diversity in the Maastrichtian. The sauropod record in South America is poor  
565 and mostly confined to the Late Cretaceous, with the Cenomanian, Campanian and Maastrichtian as the  
566 best represented stages and with diversity increasing rapidly through publication time, and revealing a  
567 biodiversity decline in from the Campanian to Maastrichtian. However, this pattern is not supported after  
568 application of subsampling, with the Campanian being more diverse than the Cenomanian, but with both  
569 steadily increasing as new taxa get identified from emerging Patagonian and Brazilian deposits (Novas,  
570 2007, 2009).

571 Here, it is worth noting the distinction between global and regional records. On a global level, we appear  
572 to have strong evidence for a substantial sauropod diversity crash from the Campanian to Maastrichtian.  
573 However, the Campanian signal is dominated by the South American record, which, although present, is  
574 lost in the Maastrichtian due to failing to reach the SQS quorum. Instead, the 'global' signal in the  
575 Maastrichtian being comprised of a medley of Asian, European, and North American records, neither of  
576 which reveal a regional extinction. Therefore, the 'global extinction' of sauropods in the latest Cretaceous  
577 is actually due to regionally heterogeneous sampling signals that are summed into a mis-leading 'global'  
578 curve. Thus, when looking at diversity signals, interpretation of global patterns without considering  
579 structural changes on a regional level is not recommended. Furthermore, the 'filtering' of data from the  
580 fossil record should also be considered when interpreting these patterns, as there are two main stages of  
581 data loss. Firstly, taxa from geological formations that do not fit exclusively into a single time bin will be

582 excluded from data pools; this will not be in a random fashion, and will depend on the temporal longevity  
583 of formations, as well as the stratigraphic resolution to which they have been resolved. Future work  
584 should investigate the degree to which these can be carefully integrated into diversity analyses, in order  
585 to maximise the data potential and signal. Secondly, poorly sampled time intervals that fail to meet the  
586 quorum will be excluded, which becomes an issue when summing regions together to look at 'global'  
587 patterns, as above, and for performing additional statistical analysis. Therefore, a range of different  
588 sampling thresholds should always be considered in order to explore the extent to which a diversity signal  
589 can be obtained, as well as the impact this has on the magnitude of diversity changes between intervals.

590

591 *How do interpretations of the extrinsic drivers of dinosaur diversity change through time?*

592 Our model fitting results suggests one of two things. As Tennant et al. (2016b) suggest, use of pairwise  
593 correlations with such small sample sizes (n is very small for subsampled curves) and for stage level data  
594 when so many data are absent, may be inappropriate in testing for correlations, and instead a maximum  
595 likelihood approach that performs better with smaller sample sizes is preferable to detect optimal models  
596 among candidates. Alternatively, it suggests that sea level is a poor predictor of dinosaur diversity at the  
597 stage level, and that dinosaur diversity and sea level are perhaps only related on broader temporal scales  
598 (Butler et al. 2011; Haubold 1990; Tennant et al. 2016b). However, what we do see, at least for  
599 sauropodomorphs and ornithischians, is that the strength of the relationship between sea level and  
600 subsampled diversity is strongly contingent on the publication history of the group. This supports the  
601 recent analysis of Jouve et al. (2017), who also found that small changes in the taxonomic composition of  
602 a dataset can lead to divergent interpretations of the environmental regulators of diversity.

603

604 *Considering the implications for publication-based databases*

605 Often, only new species are published on as these are deemed 'more impactful' and therefore more likely  
606 to be published, whereas new findings of already identified species are less likely to be published on as  
607 they are deemed less publishable. Indeed, many palaeontologists are aware of the 'Top journals will  
608 publish anything with feathers' phenomenon over the last 20 years, where many of the most high profile  
609 papers published in our field, and certainly those with media attention, have been those that describe  
610 new dinosaur taxa. The presently unknown and unquantifiable effect of this is that such publication bias  
611 skews our interpretation of the species-abundance distribution by being more densely favoured towards

612 new species. This is especially a problem when it comes to using data sources like the Paleobiology  
613 Database (which has 283 official publications at the time of writing this;  
614 <https://paleobiodb.org/classic/publications?a=publications> – retrieved 18/05/2017), as well as  
615 automation tools like PaleoDeepDive (Peters et al. 2014), where the source data are both largely, and in  
616 some cases entirely, based on publication records. Museum collections also contain numerous  
617 unpublished specimens, and digitisation of these and their continued integration with databases based  
618 exclusively on publication records, like the Paleobiology Database, will be essential in generating more  
619 reliable datasets in the future.

620 As we have shown, the interpretation of macroevolutionary patterns in dinosaurs is highly sensitive to  
621 changes in the taxon-abundance curve, and we further distort this by relying on a biased source of data  
622 for our analyses. In the future, palaeontologists can alleviate this potential issue in several ways. When  
623 collection fossils in the field, collect all fossils, and not just those which are easiest to collect, or potentially  
624 new to science. Where this is not possible, carefully document the records that were not able to be  
625 collected. Make sure that all of this ends up in a publicly accessible institute for others to re-use, and if  
626 possible, digitise the information and integrate it into databases like the Paleobiology Database. Finally,  
627 when publishing specimens, we should always be comprehensive and consider the broader impact we  
628 have when only selecting to publish on cherry-picked specimens, and exclude data based on perceived  
629 value or ‘newsworthiness’. There is beauty in the bone bed, and we have everything to gain in terms of  
630 research quality by ensuring that our data are based on the present state of the fossil record. After all, it  
631 is already biased enough without us contributing further to it with our publication habits.

632

### 633 **Conclusions**

634 In this study, we tested diversity trends through time for three major clades of Dinosauria (Ornithischia,  
635 Sauropodomorpha and Theropoda), reducing primary dataset of body fossils occurrences by progressively  
636 removing publications at each 2 year intervals, up until 1991. By analysing both empirical and subsampled  
637 curves, we have been able to see how publication history influences different estimates of dinosaur  
638 diversity. We found that while increases in raw diversity through publication history generally do not  
639 affect the overall shape of each curve, global diversity is growing much faster in all three groups during  
640 the latest Cretaceous, late Early Cretaceous, and for theropods and sauropods during the Late Jurassic.  
641 When we apply subsampling, we see a different structure emerge, that there are major discrepancies

642 between the 1991 and 2015 curves for theropods in the Late Jurassic, and for ornithischians and  
643 theropods in the late Early Cretaceous. Sauropodomorphs, on the other hand, show almost no changes in  
644 global subsampled diversity through publication history, although at least part of this is likely due to their  
645 overall different taphonomy and fossil record quality. Almost without exception, these seemingly  
646 continuous ‘global’ diversity patterns are the product of summing together different, and invariably  
647 patchier, continental signals with vastly different trends. In ornithischians, a J/K boundary decline is based  
648 almost exclusively on European fossils, and a perceived global reduction in their diversity in the latest  
649 Cretaceous is the result of an overpowering North American signal. Similarly, ‘global’ subsampled  
650 theropod diversity is prevalently based on the European record, with Asia and North America contributing  
651 substantially more after the earliest Cretaceous. Theropod diversity in the latest Cretaceous is changing  
652 the most rapidly of any other time, and therefore we should be careful not to over-interpret patterns  
653 coming up to the end-Cretaceous mass extinction without considering the historical context. For  
654 sauropods, an apparent ‘global’ decline in the latest Cretaceous is actually the result of well-sampled  
655 Campanian deposits in North America being followed by relatively poorly sampled Maastrichtian deposits  
656 from Laurasia. Gondwanan dinosaurian faunas are still relatively poorly sampled despite intensive  
657 exploration in the last 20 years, and we expect the influence of discovery in Africa and South America to  
658 become more important in the future. The consequences this appears to have on our interpretation of  
659 the extrinsic drivers of ‘global’ dinosaur diversity are fairly minimal, although we do find that for  
660 sauropodomorphs and ornithischians, the strength of correlations is dependent on their publication  
661 history. The results of this study should be of interest to those who use occurrence-based compilations  
662 like the Paleobiology Database that rely heavily on the published literature. Both the addition of new taxa,  
663 and new occurrences of existing taxa, are clearly important in establishing stable and re-usable diversity  
664 curves for further research. By ignoring the publication history, and potential biases involved in this, we  
665 open ourselves up to mis-interpreting the patterns and processes involved in their evolution, and we  
666 should be careful to exercise more caution as a discipline in the selectivity of our publishing behaviour.

667

## 668 **Acknowledgements**

669 JPT is funded by a National Environmental Research Council PhD studentship. AAC is funded by an Imperial  
670 College London Janet Watson Departmental PhD Scholarship. We are grateful for the combined efforts of  
671 all those who have collected Jurassic–Cretaceous dinosaur data, and to those who have entered these  
672 data into the Paleobiology Database, especially J. Alroy, M. T. Carrano, R. B. J. Benson, and R. J. Butler. We

673 also thank J. Alroy for providing the Perl script used to perform SQS analyses. This is Paleobiology Database  
674 official publication number XXX. JPT would like to thank Lisa Matthias (aka 'Engelchen') for putting up  
675 with, and also feeding, him during the writing of this paper. We would both like to thank Serjoscha Evers  
676 for helping to come up with this idea in the pub during Progressive Palaeontology 2016, and for  
677 subsequent discussions, also mostly in the pub.

678

#### 679 **Author contributions**

680 Both authors contributed to the design of the study, the analyses, drafting the figures, and writing this  
681 manuscript.

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1004 **Figure captions**

1005 Figure 1: Raw global diversity for a) Theropoda, b) Sauropodomorpha, and c) Ornithischia based on our  
1006 published knowledge in 1991 and 2015.

1007 Figure 2: Subsampled global diversity for a) Theropoda, b) Sauropodomorpha, and c) Ornithischia based  
1008 on our published knowledge in 1991 and 2015.

1009 Figure 3: Raw and subsampled regional ornithischian diversity for North America (A, D), Europe (B, E), and  
1010 Asia (C, F) based on our published knowledge in 1991 and 2015.

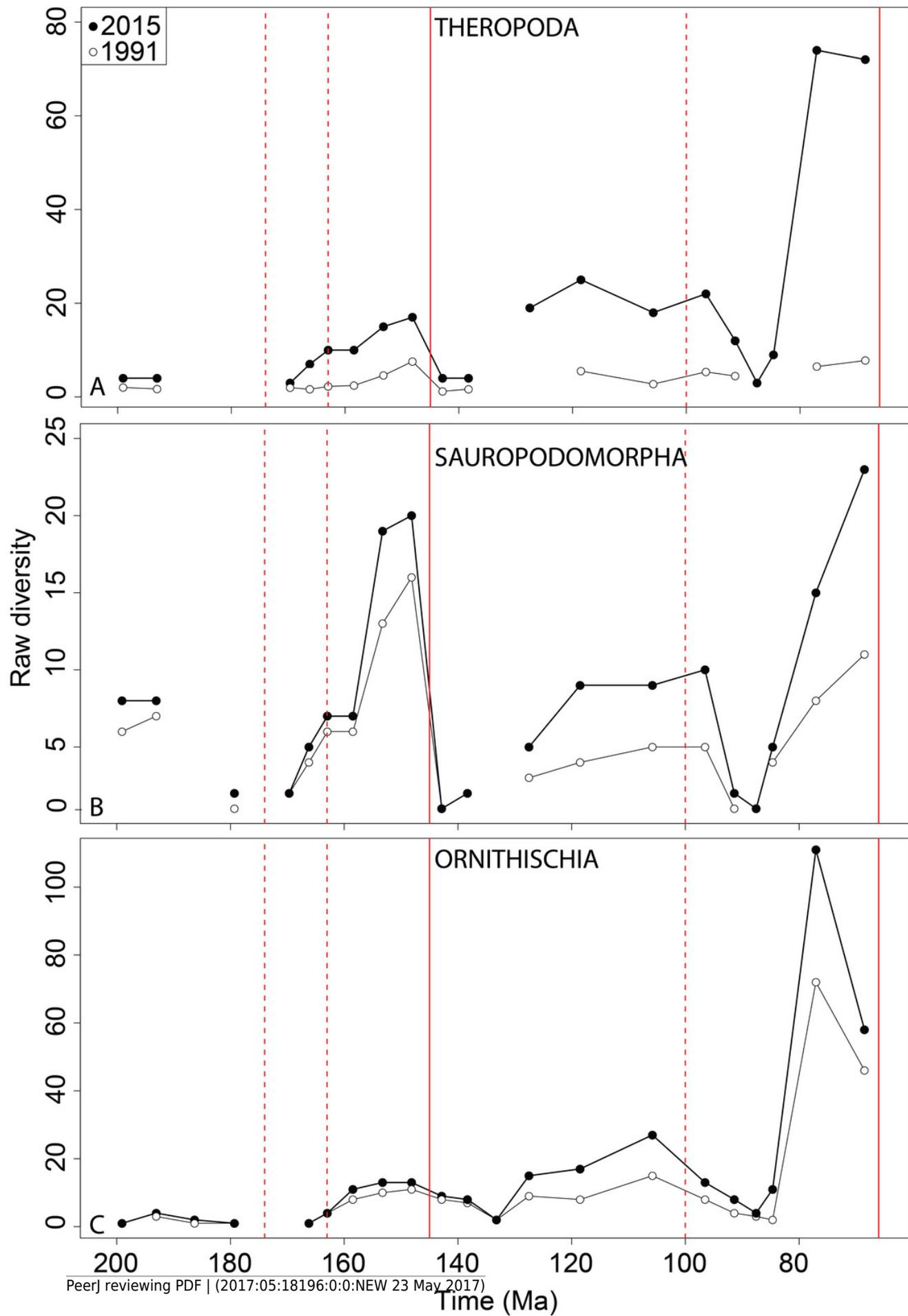
1011 Figure 4: Raw and subsampled regional theropod diversity for North America (A, D), Europe (B, E), and  
1012 Asia (C, F) based on our published knowledge in 1991 and 2015.

1013 Figure 5: Raw and subsampled regional sauropodomorph diversity for North America (A, D), Europe (B,  
1014 E), and Asia (C, F) based on our published knowledge in 1991 and 2015.

# Figure 1

Figure 1

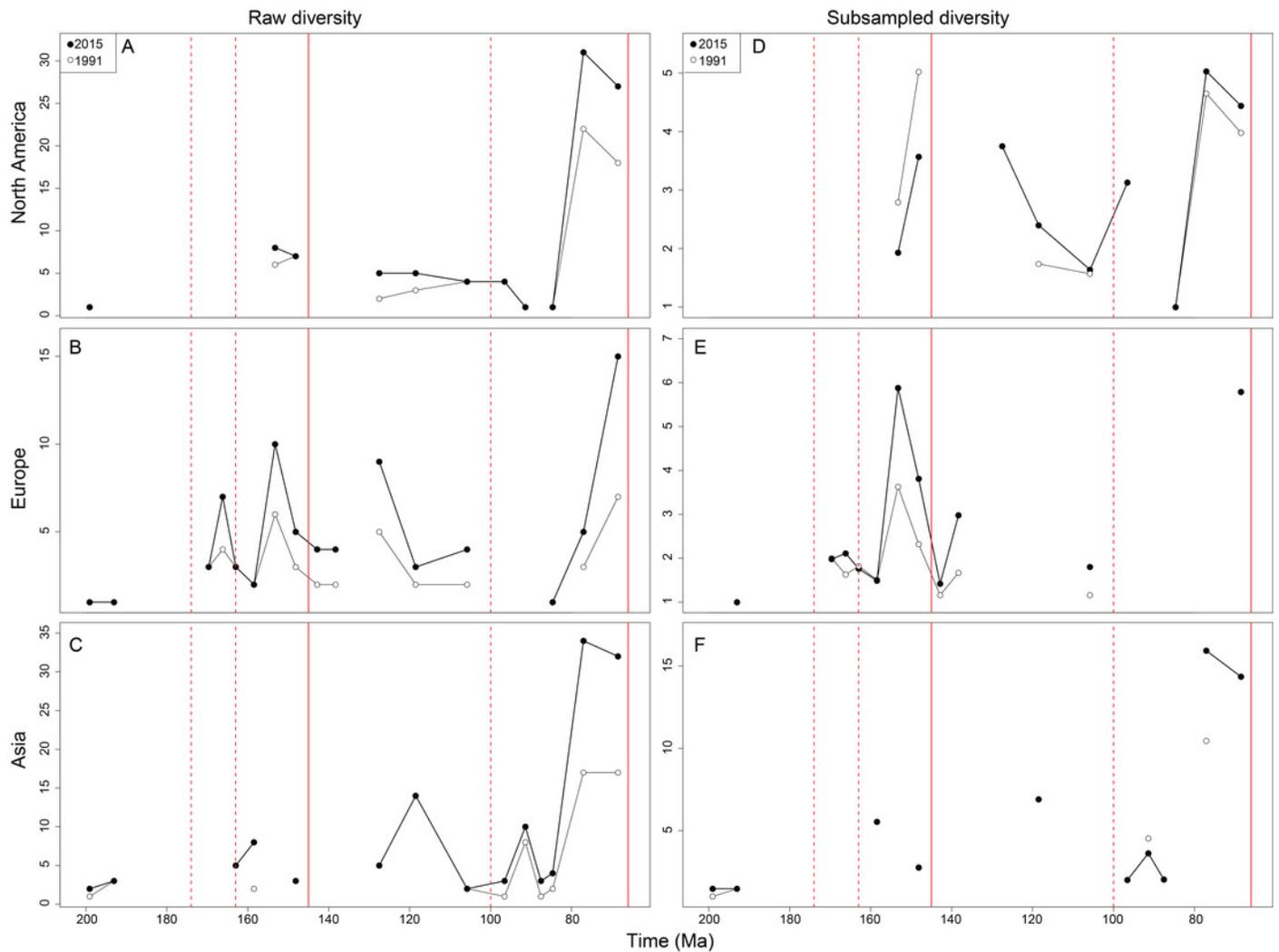
Figure 1: Raw global diversity for a) Theropoda, b) Sauropodomorpha, and c) Ornithischia based on our published knowledge in 1991 and 2015. si-l? ?i? ?



# Figure 2

## Subsampled theropod diversity

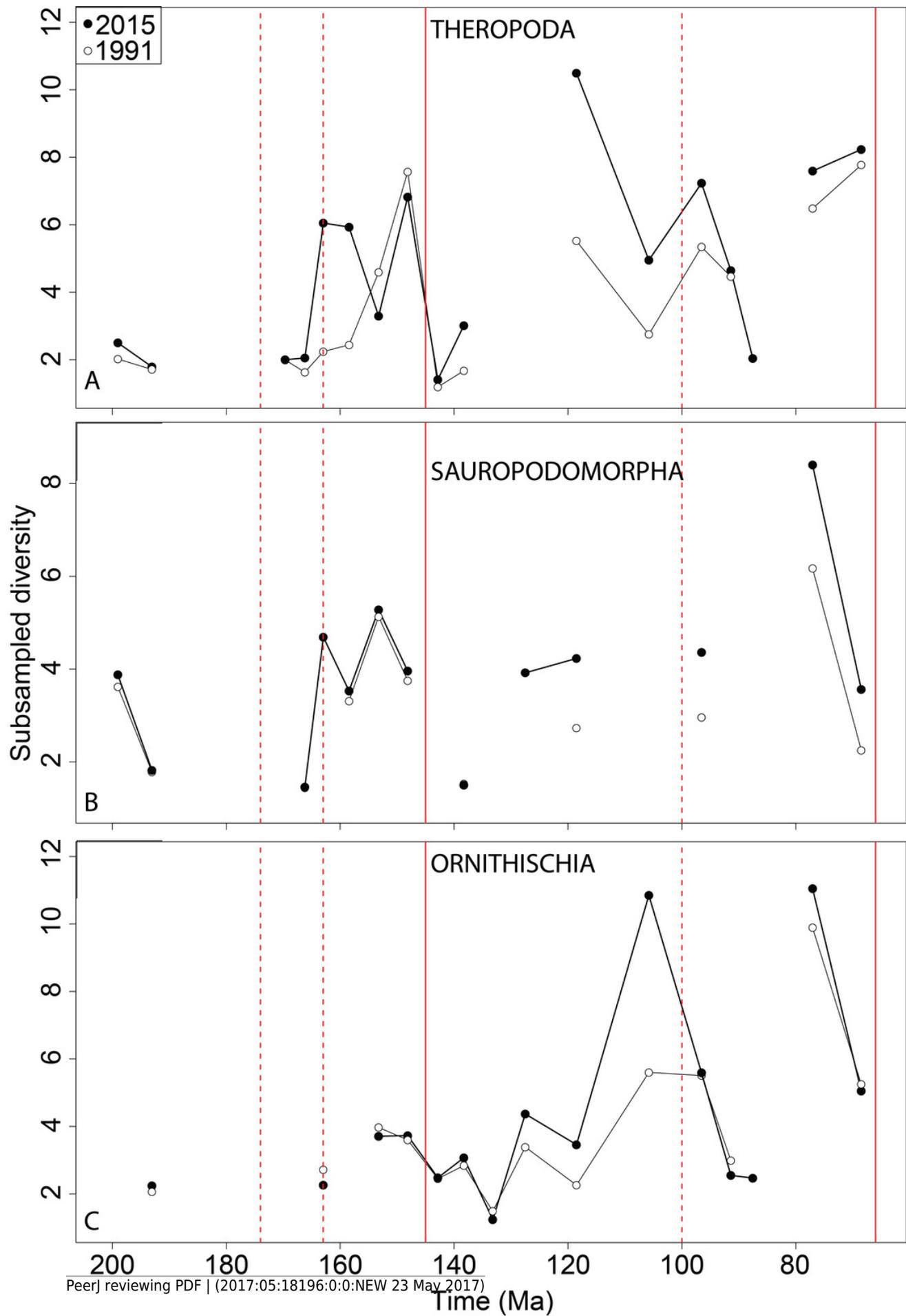
Figure 4: Raw and subsampled regional theropod diversity for North America (A, D), Europe (B, E), and Asia (C, F) based on our published knowledge in 1991 and 2015. ? 



## Figure 3

Subsampled global diversity

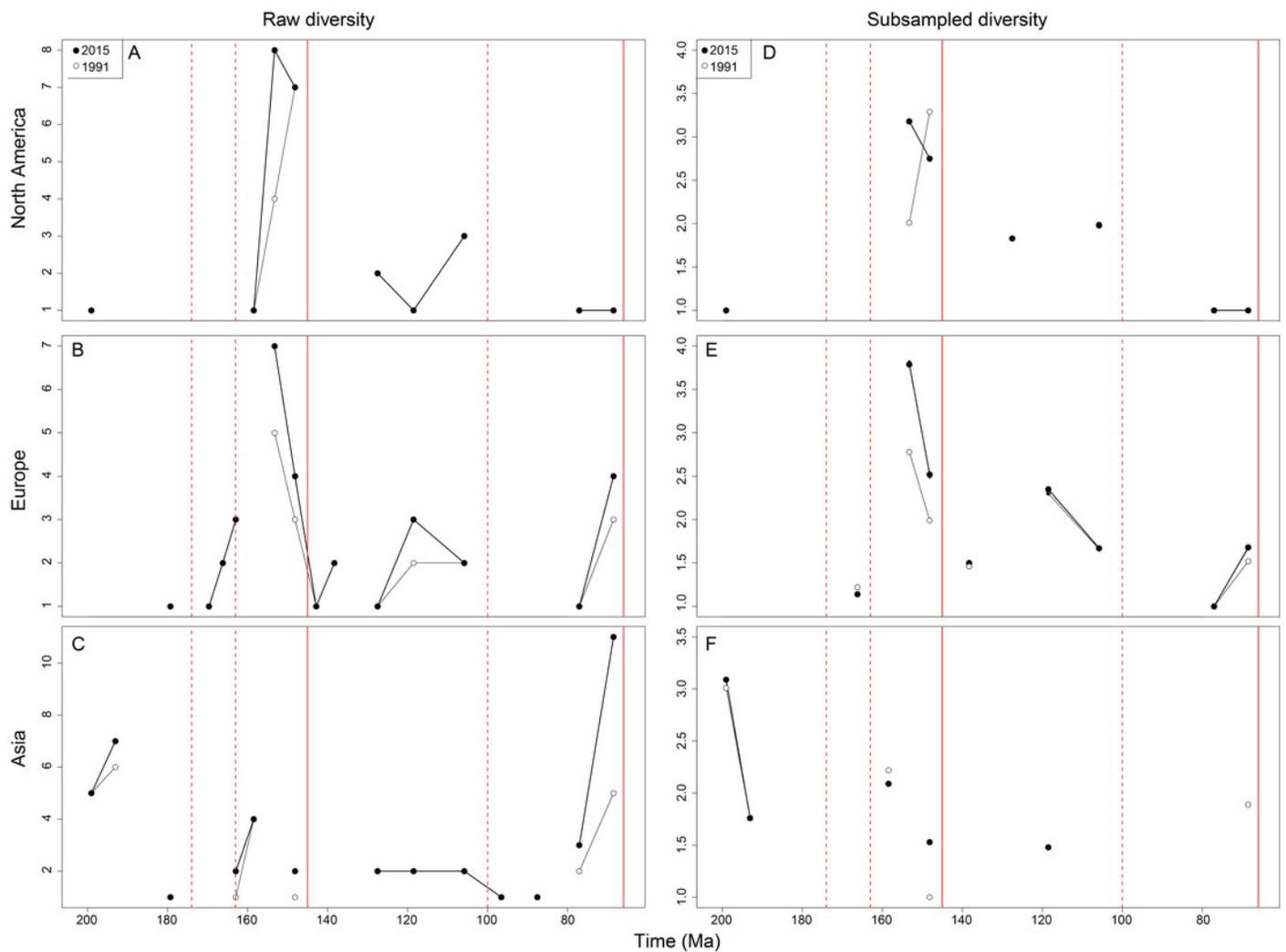
Figure 2: Subsampled global diversity for a) Theropoda, b) Sauropodomorpha, and c) Ornithischia based on our published knowledge in 1991 and 2015. body>



# Figure 4

## Regional sauropod diversity

Figure 5: Raw and subsampled regional sauropodomorph diversity for North America (A, D), Europe (B, E), and Asia (C, F) based on our published knowledge in 1991 and 2015. S



# Figure 5

## Regional ornithiscian diversity

Figure 3: Raw and subsampled regional ornithiscian diversity for North America (A, D), Europe (B, E), and Asia (C, F) based on our published knowledge in 1991 and 2015. ? S

