

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.

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Abstract

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.

Introduction

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

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

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

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

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

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

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

Material and Methods

Dinosaur occurrences dataset

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

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

Calculating diversity through time

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

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

Model-fitting of extrinsic parameters

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

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

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

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

Results

Global patterns of raw diversity

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

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

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

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

Global patterns of subsampled diversity

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

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

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

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

The geographical structure of dinosaur diversity

Ornithischians

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

Theropods

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

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

Sauropodomorphs

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

Model-fitting results

Dinosaur diversity and sea level

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

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

Dinosaur diversity and palaeotemperature

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

Discussion

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

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

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

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

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

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

Discovery influences regional patterns of dinosaur diversity through time

Ornithischians

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

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

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

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

Theropods

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

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

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

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

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

Sauropods

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

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

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

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

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

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

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

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

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

Considering the implications for publication-based databases

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

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

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

Conclusions

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

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

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Author contributions

Both authors contributed to the design of the study, the analyses, drafting the figures, and writing this 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? ?

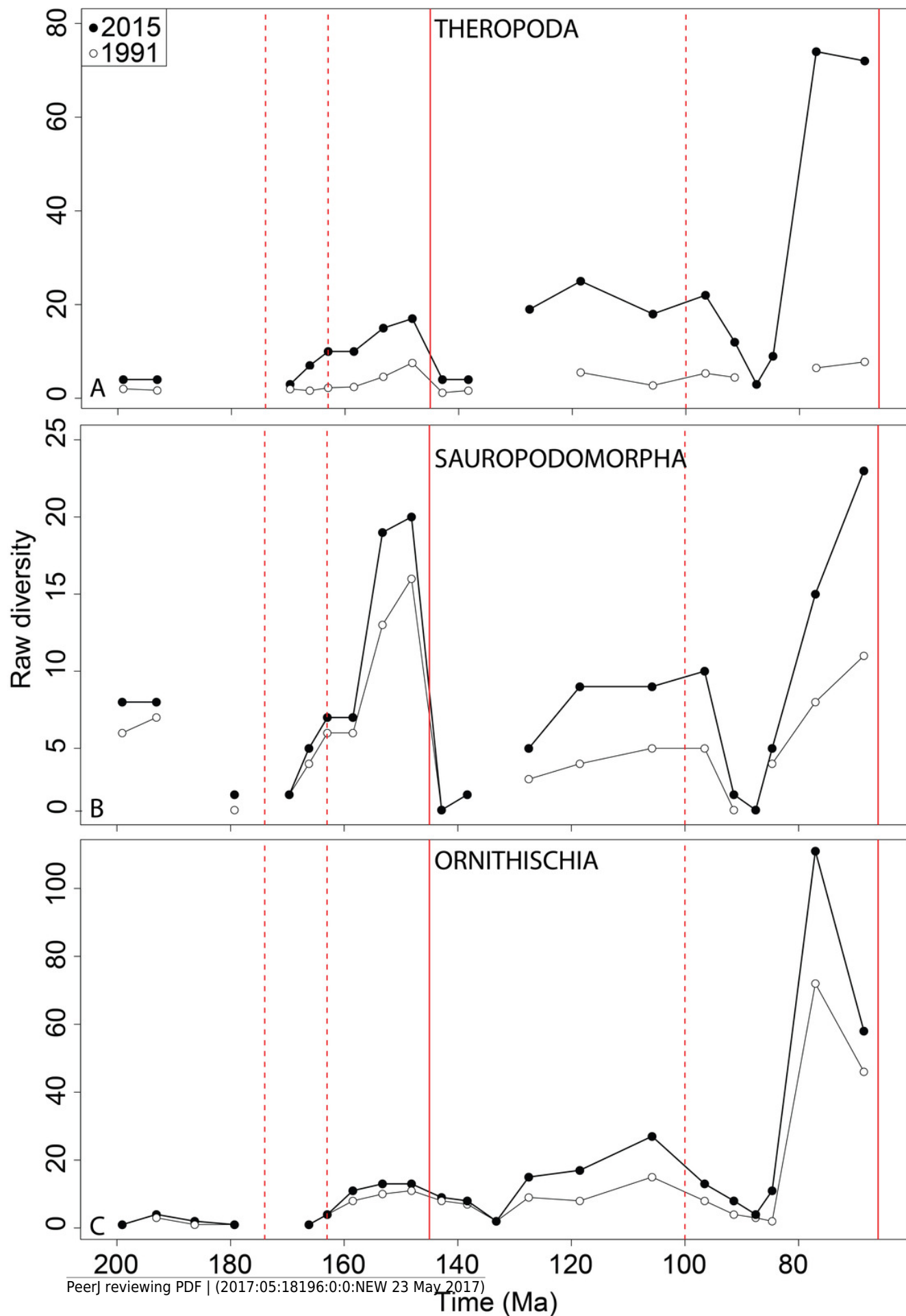



Figure 2

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. ? 

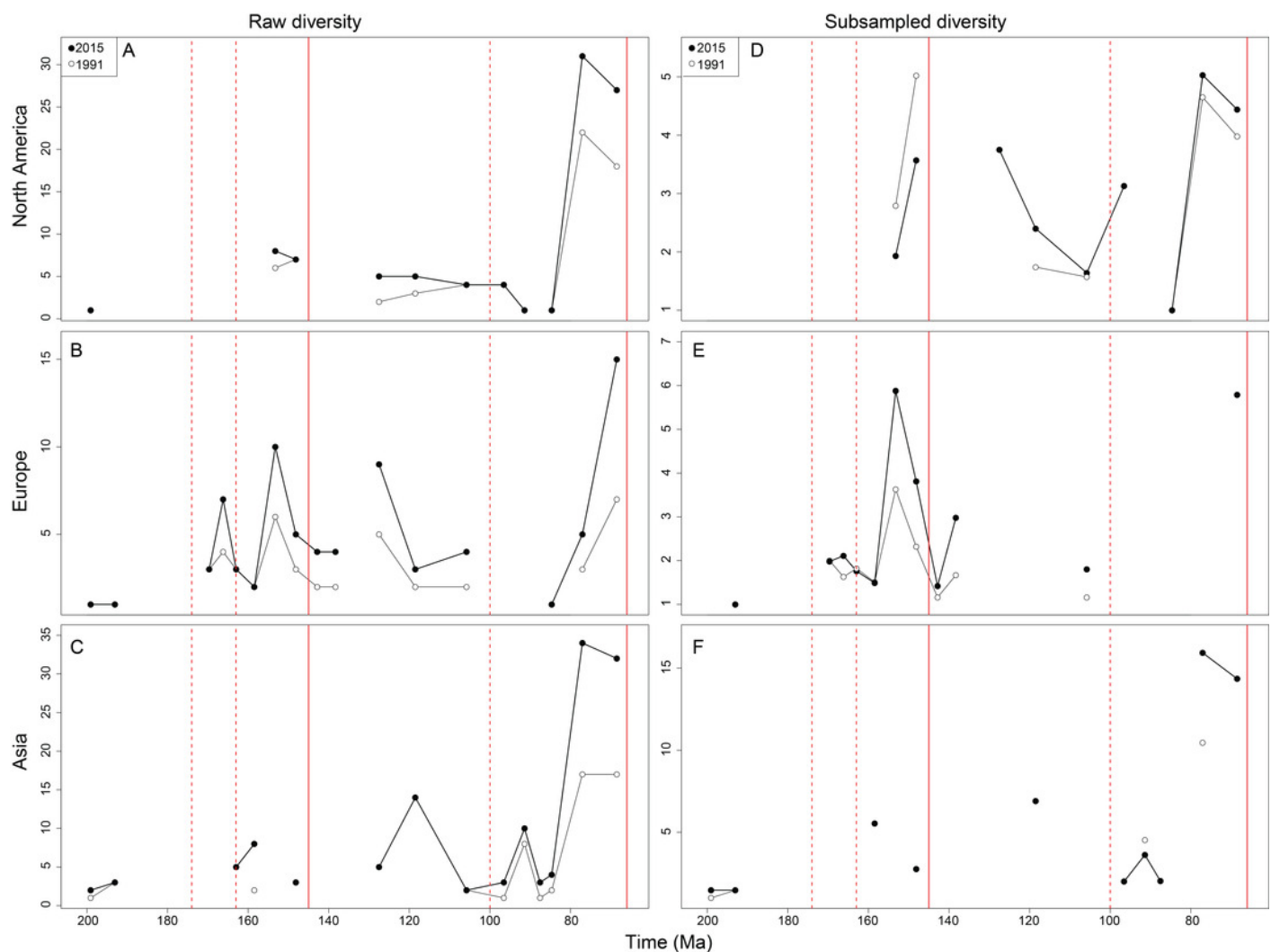


Figure 3

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>

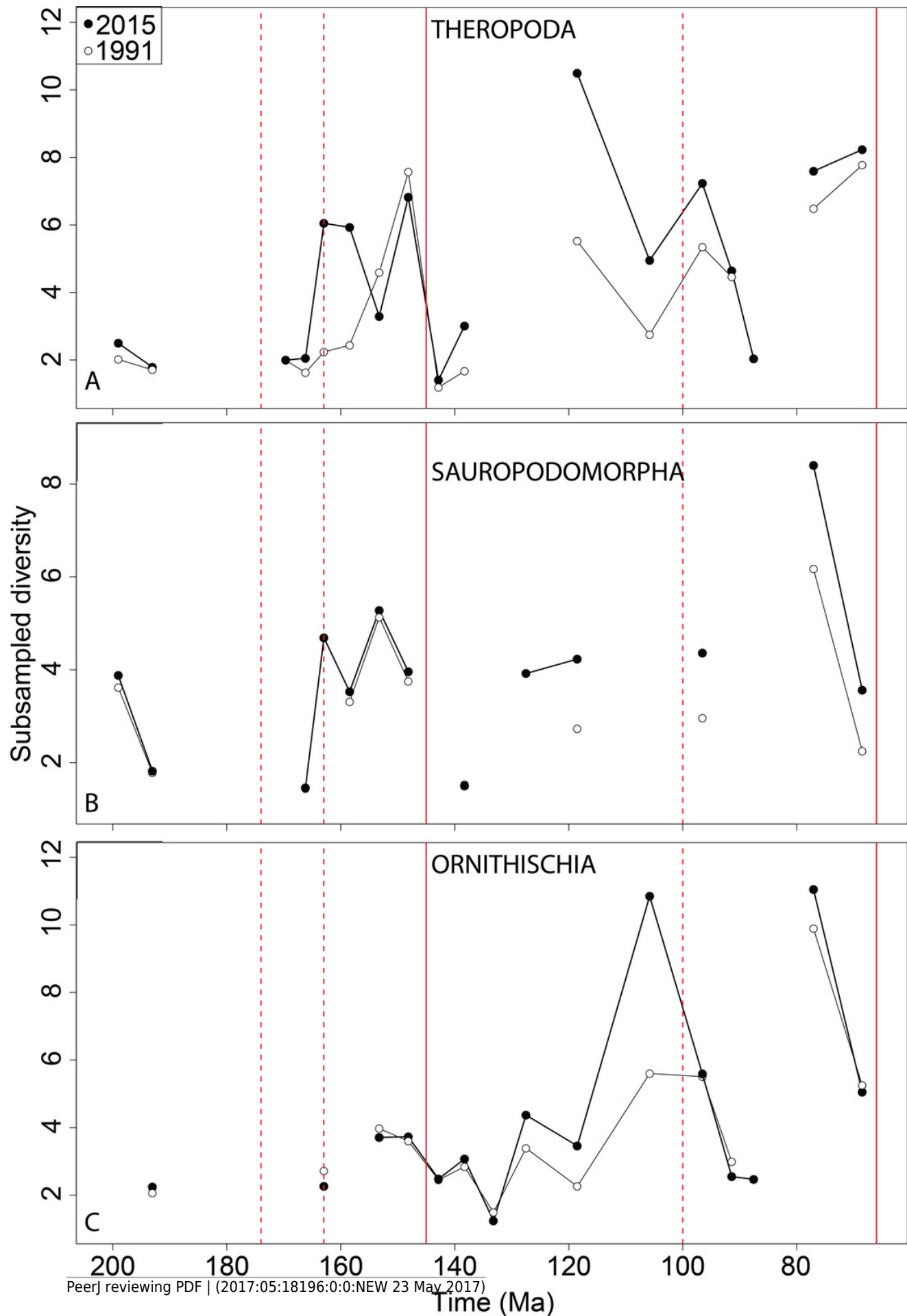


Figure 4

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

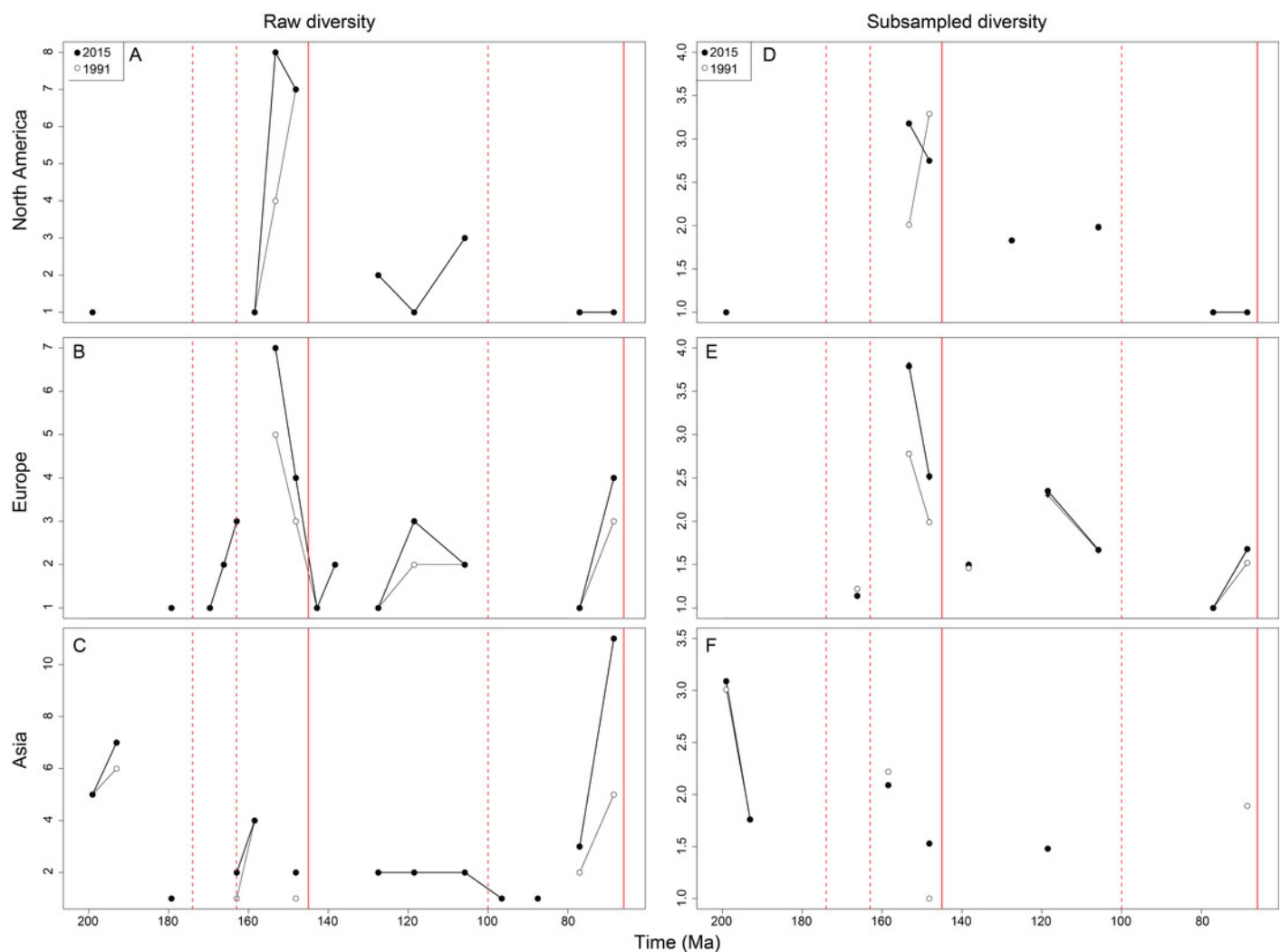


Figure 5

Regional ornithischian diversity

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

