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

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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. Recent studies have analysed patterns in dinosaur diversity that are based on variations in the numbers of taxa. These have employed a range of approaches that account for ecological changes in the shape of the taxonomic abundance curve, which are largely dependent on databases complied 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 relative magnitude 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. Recent studies have analysed patterns in dinosaur diversity that are based on variations in the numbers of taxa. These have employed a range of approaches that account for ecological changes in the shape of the taxonomic abundance curve, which are largely dependent on databases complied 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 relative magnitude 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 1982; Sepkoski 1992; Sepkoski 1996; Sepkoski et al. 1981; Sepkoski 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 due to development of large fossil occurrences databases such as the Paleobiology Database (www.paleobiodb.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 (Benton 2008a; Benton 2008b; Raup 1972; Raup 1976; Tarver et al. 2011). 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 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 (e.g., Alroy (2000b); Sepkoski (1993)): 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 (counter to the second argument). Since Sepkoski's 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 & 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 are 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 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. We want to test a simple question: 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 they have an intensely sampled fossil record and a rich history of taxonomy and macroevolutionary research. In this study we do 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 temporal 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 & 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).

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). 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 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 these are more readily identified and diagnosed, which 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 analysing palaeodiversity at different taxonomic levels can potentially lead to different interpretations about what the external factors mediating it are (Wiese et al. 2016). Despite the fact that some dinosaur genera are multispecific, it has been shown previously that both genus- and species-level dinosaur diversity curves are very similar (Barrett et al. 2009), and that there is more error in species level dinosaur taxonomy than for genera (Benton 2008b). 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 are based on a comprehensive data compilation effort from multiple workers, and represent updated information on 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 strongly suggested 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).

SQS standardizes taxonomic occurrence lists based on an estimate of coverage to determine the relative magnitude of taxonomic biodiversity trends (Alroy 2010a; Alroy 2010c). In this method, each taxon within a sample pool (time bin) is treated as a 'shareholder', whose 'share' is its relative occurrence frequency. Taxa are randomly drawn from compiled in-bin occurrence lists, and when a summed proportion of these 'shares' reaches a certain 'quorum', subsampling stops and the number of sampled taxa is summed. Coverage, as a measure of sampling quality, is defined as the proportion of the frequency distribution of taxa within a sample. It is estimated by using randomized subsampling to calculate the mean value of Good's *u*, which is defined as 1 minus the number of singleton occurrences over the total number of occurrences (Good 1953). A coverage value of zero indicates that either all taxa are singleton occurrences, or that there are simply no taxa to sample. The advantage of SQS here, then, is that it returns estimates of diversity even at very low sampling levels. Higher coverage values indicate more even sampling of taxa, and therefore provides a measure of sample completeness that is independent of the overall sample pool size. For each time bin, *u* is divided into the quorum level (Alroy 2010a), thereby providing an estimate of standardised diversity in a manner that is flexible in response to changes in the shape of the taxon occurrence distribution. In all subsampling replicates, singletons were excluded to calculate diversity (but included to calculate Good's *u*), as they tell us little about the underlying taxon distribution (i.e., a linear relationship of 1:1), and can distort estimates of diversity. Dominant taxa (those with the highest frequency of occurrences per bin) were included, and where these taxa are drawn, instead of their share contributing towards the quorum, 1 is added to the subsampled diversity estimate for that bin (Alroy 2010c). Finally, single large collections that can create the artificial appearance of poor coverage were accounted for by counting occurrences of taxa that only occur in single publications, as opposed to those which occur in single collections, and excluding taxa that are only ever found in the most diverse collection. 1000 subsampling trials were run for each dataset (Theropoda, Ornithischia, and Sauropodomorpha), and the mean diversity reported for each publication time interval. For each sequential subsampling iteration, whenever a collection from a new publication was drawn from the occurrence list, subsequent collections were sampled until exactly three collections from that publication had been selected (Alroy 2010a). We set a baseline quorum of 0.4, as this has been demonstrated to be sufficient in accurately assessing changes in diversity (Alroy 2010a; Alroy 2010c; Mannion et al. 2015; Nicholson et al. 2015; Tennant et al. 2016a).

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 recent 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 arima() 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-1 error (i.e., in order to avoid falsely rejecting a true null hypothesis; a false positive). 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 (i.e., non-independent tests), 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 because 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

Occurrences and genera through time

From the first dinosaur discoveries until around 1950, the number of dinosaur occurrences published remained mostly linear and steadily increasing through time (Fig. 1). Since the mid-20th century, the number of published occurrences has increased exponentially, and shows no sign of slowing down. This is mostly due to the publication of theropod and ornithischian occurrences, which reached a peak around the turn of the millennium, with occurrences of all three groups remaining high but declining in rate of publication after this. A very similar pattern is observed for genera, with the publication of newly named genera increasing exponentially since around 1990, and at an equal rate for all three groups (Fig. 2). The cumulative frequency of newly named genera shows that, although the rate of growth remains approximately similar and exponential for all three groups, there are times when the relative overall number of genera between groups changes through publication history. For example, while sauropodomorphs had more named genera until around 1935 than theropods, this changed around 1960 when new theropod genera became more frequently published than sauropodomorphs. The recent rate of growth of newly named theropod genera in the last 15 years means that they are now named as frequently as newly named ornithischian genera.

Global patterns of total dinosaur diversity

Empirical summed dinosaur diversity steadily rises until the end of the Jurassic (Fig. 3A). Diversity is low across the J/K boundary until the Hauterivian, before recovering in the late Early Cretaceous. There is a second decline across the Early to Late Cretaceous boundary, before diversity increases to its zenith in the Campanian and Maastrichtian. This general pattern remains constant throughout publication history, although diversity in the 'middle' Cretaceous and latest Cretaceous intervals shows the greatest increases. Subsampled global dinosaur diversity retains this overall pattern, but the magnitude of relative changes varies (Fig. 3B). The J/K boundary decline is still apparent, but the late Early Cretaceous increase supersedes Late Jurassic levels. The early Late Cretaceous decline is also still apparent, but the magnitude of the latest Cretaceous diversity increase is much lower than that recovered for the empirical data.

Total dinosaur subsampled diversity shows a starkly different pattern to that revealed by the empirical data. The steady Jurassic rise remains, but with a diversity dip in the Oxfordian. The Jurassic/Cretaceous decline also remains, however there is a slight recovery in the Valanginian, unseen in the raw data. The most major distinction is during the latest Cretaceous, where the magnitude of the Campanian radiation reduces from almost 400% in the raw results to around 20% when subsampling is applied, compared to late Early Cretaceous diversity levels. The reason for this distinction between SQS and raw diversity is that subsampling is sensitive to changes in the species abundance pool, and thereby reduces the impact of intensely sampled time intervals such as the latest Cretaceous.

Global patterns of raw diversity by group

Raw ornithischian diversity (Fig. 4A) is remarkably constant and stable to changes in publication history. 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 an increase in the Campanian.

The overall shape of the raw theropod diversity curve remains consistent through publication history for the Jurassic (Fig. 4B), similar to ornithischians, where we see steadily increasing Middle to Late Jurassic diversity. 'Middle' Cretaceous diversity fluctuated, followed by 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 diversity increases in magnitude through time, gradually exceeding that for Late Jurassic diversity.

Sauropodomorph empirical diversity is unique among other dinosaurian groups because there are relatively more changes in raw patterns through time, and particularly in the Cretaceous (Fig. 4C). 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 to become more decoupled in magnitude. Diversity in the Turonian and Coniacian is as low as the Berriasian, before rapidly increasing until the end of the Cretaceous. The magnitude of this Late Cretaceous increase has almost doubled in the last 20 years.

Global patterns of subsampled diversity by group

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. 5A). The Jurassic is generally too poorly sampled to reveal a constant signal, but there is evidence of a two-phase decline through the Jurassic/Cretaceous transition, which remains constant through publication time. This is followed by a Barremian rise, 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 Albian 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 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. 5B). 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 subsequent 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 years, 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.

Subsampled sauropodomorph diversity also varies through publication time (Fig. 5C). The Late Jurassic shows a double decline in diversity in the Oxfordian and Tithonian, a pattern that is stable through publication time. However, Aptian, and Cenomanian diversity has almost doubled in the last 20 years. Campanian diversity has also increased, whereas Maastrichtian diversity has grown at a slower pace, revealing a slightly increasing magnitude of diversity decline before the end-Cretaceous.

The geographical structure of dinosaur diversity

Ornithischians

In North America, empirical diversity is flat and low throughout the Late Jurassic and most of the Cretaceous (Fig. 6A). 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 relatively stable through publication time. Subsampled diversity greatly reduces the relative magnitude of this Campanian radiation, but the major decline into the Maastrichtian remains, and is constant through publication history (Fig. 6D). Raw diversity in Europe shows increasing diversity across the J/K boundary before an earliest Cretaceous decline (Valanginian to Hauterivian), constant 'middle' Cretaceous diversity, and an increase from the Campanian to Maastrichtian (Fig. 6B). Subsampled European diversity reveals similarly increasing diversity across the J/K boundary, and overall gradually decreasing diversity throughout the remainder of the Early Cretaceous, punctuated by a Hauterivian trough (Fig. 6E). 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 with just relatively small changes, until a major Campanian peak and Maastrichtian decline (Fig. 6C). Subsampled diversity reveals a major decline across the Early-Late Cretaceous transition, and a moderate increase in the Campanian (Fig. 6F). Both raw and subsampled African ornithischian diversity are 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 theropods, and is therefore constantly relatively flat (Fig. 7A). Campanian and Maastrichtian diversity is constantly increasing at a faster rate than any other time interval, and consistently reveals a slight 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 (Fig. 7D). 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 (Fig. 7B), with a Middle Jurassic diversity peak in the Bathonian, followed by a Callovian-Oxfordian trough, a second Kimmeridgian peak, and then constant decline from the Tithonian to the Valanginian. Barremian diversity is increasing through publication time, and is as high as Kimmeridgian levels. Aptian and Albian diversity is relatively low, similar to that for the Berriasian and Valanginian. Campanian diversity is slowly increasing through publication history, but Maastrichtian diversity is increasing relatively 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 diversity recovery during the Valanginian (Fig. 7E) Maastrichtian diversity remains high, reaching the same level as that for the Kimmeridgian. In Asia, raw Late Jurassic diversity is generally lower than for the Cretaceous (Fig. 7C). 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. 7F). A small diversity decline from the Campanian to Maastrichtian is now also recovered based on more recent discoveries. 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 (SI 6).

Sauropodomorphs

The North American sauropod record is very patchy, with the latest Jurassic showing a shift from rapidly increasing raw diversity from the Oxfordian to a slight drop from the Kimmeridgian to Tithonian (Fig. 8A). Subsampling appears to corroborate this pattern, and the shift becomes more pronounced through time (Fig. 8B). In Europe, sauropods show a consistent and major decline in raw diversity from the Kimmeridgian to the Berriasian (Fig. 8B). Much of the rest of the Cretaceous is too poorly sampled, but there is evidence for an Aptian to Albian decline, and 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 evidence for the sauropod decline beginning prior to the J/K boundary (Fig. 8E). Evidence for an Aptian to Albian diversity drop remains, as does a pattern of 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, in which diversity is relatively high and still rapidly increasing through publication history (Fig. 8C). Subsampling greatly reduces the signal, but we see increasing latest Jurassic diversity with publication history (Fig. 8F). 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 (SI 7). 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, the correlation between sauropodomorph diversity and sea level had a strength of 0.5. This relationship declined consistently and even became negative up until 2007, and from 2009-2015 remains a weak but positive relationship, with a correlation strength of no more than 0.217 with sea level. In Ornithischians, the strength of the relationship between diversity and sea level 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 (i.e., $p < 0.05$). 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 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 to -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 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 sampling and publication history on dinosaur diversity

The impact of publication history on estimates of dinosaur diversity has direct consequences for our interpretation of their evolutionary history and diversification (Benton 2008a). 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 1993). Further research has shown that new dinosaur discoveries strongly influence our understanding of their fossil record and diversification patterns in a phylogenetic context (Tarver et al. 2011; Weishampel 1996). In this study, we examined the historical trajectory of dinosaur diversity to observe whether curves are beginning to stabilise or not. 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' (i.e., fossil discoveries driving formation counts, especially prevalent in Lagerstätten) (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 well-recognised relationship between the amount of rock available for palaeontologists to search for dinosaur fossils, and our interpretations of their 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 geological 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 selective nature of publication, it seems prudent to suggest that we are cautious in our interpretation of events in dinosaur macroevolution in these intervals, similar to the conclusions reached by Tarver et al. (2011). 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) interval 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 interval 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 dinosaur-bearing formations (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 taxa 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 due to the discovery of more Konzentrat-Lagerstätten in Mongolia and China around this time, such as the Jehol Biota (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 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, including ceratopsians and hadrosaurids, appear to have diversified extremely rapidly 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 ecomorphologlogical 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 (Brusatte et al. 2012; Sampson 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 diversity increases during the Late Jurassic (Callovian-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). 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 radiation 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 temporally 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 dwarfed by an oversampling of latest Cretaceous dinosaur-bearing formations (e.g. Dinosaur Provincial Park, Hell Creek Formation). An increasingly 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 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 slightly different subsampling approach (Alroy 2010c) (see Methods section). 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 stands out 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).

Sauropodomorphs

Diversity patterns of sauropodomorphs share some characteristics of those of theropods and ornithischians, despite having a different fossil record due to taphonomic differences (i.e., larger, more robust skeletons being preferentially preserved in different environmental settings) (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. Differences in diversity patterns between sauropodomorphs and ornithischians have 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 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, although part of this might be due to a relatively patchier fossil record. The general patterns of diversity shows 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 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 the sampling history 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 sauropodomorphs reached their zenith in diversity during the Late Jurassic. 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. However, there is a notable diversity decline through the J/K boundary, as with other dinosaurian groups (Tennant et al. 2016b; Upchurch & Mannion 2012).This is distinct from results obtained with other methods (e.g., TRiPS) which do not find any evidence for such 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 Brasilian 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 decline 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 (0.4). 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 such as correlation tests. 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 varies but is generally very small for subsampled curves) and for stage level data when so many data are absent, may be inappropriate in testing for correlations. This is especially the case when the data used for correlations changes each year, with some time bins that are initially missing data becoming filled out through time. 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

New species are often only 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. The presently unknown and unquantifiable potential effect of this is that such publication bias can skew 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. This issue is also emphasised by the seemingly exponential current growth in the publication of new dinosaur genera and occurrences (Figs. 1, 2), but where the rate of new occurrences published in the last 15 years is declining relative to the publication of new genera. 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 collecting 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.

Conclusions

In this study, we tested diversity trends through time for three major clades of Dinosauria (Ornithischia, Sauropodomorpha and Theropoda), by reducing a 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 compared to any other time interval. Therefore, we should be careful not to over-interpret patterns coming up to the end-Cretaceous mass extinction without considering the historical context of theropod discovery. 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 potential extrinsic controls 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, especially when ongoing research can potentially dramatically alter our understanding of the evolutionary history of dinosaurs (Baron et al. 2017). 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, and the maturity and growth of taxonomic datasets must be assessed prior to further macroevolutionary study (Tarver et al. 2011). By ignoring the publication history, and potential biases involved in this, we open ourselves up to potentially mis-interpreting the patterns and processes involved in dinosaur evolution.

Future research could investigate the changes in taxonomy, systematics, and validity of dinosaur taxa through publication history (Benton 2008a; Benton 2008b), and the influence that changes in the historical quality of the fossil record has on this. Furthermore, given the importance of sampling biases on our interpretations of the dinosaur fossil record (Barrett et al. 2009; Benton 2015; Butler et al. 2011; Mannion & Upchurch 2011; Tennant et al. 2016b; Upchurch et al. 2011), research could look at how the relationships between sampling proxies and dinosaur diversity change through time.

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Figure captions

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

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

Figure 3: Total dinosaur diversity patterns for a) raw and b) subsampled data. The vertical red lines represent major interval boundaries.

Figure 4: Raw global diversity for a) Ornithischia, b) Theropoda, and c) Sauropodomorpha based on our published knowledge in 1991 and 2015.

Figure 5: Subsampled global diversity for a) Ornithischia, b) Theropoda, and c) Sauropodomorpha based on our published knowledge in 1991 and 2015.

Figure 6: 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.

Figure 7: 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 8: 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.

Figure 1

Frequency and cumulative frequency of newly published dinosaur occurrences through publication time.

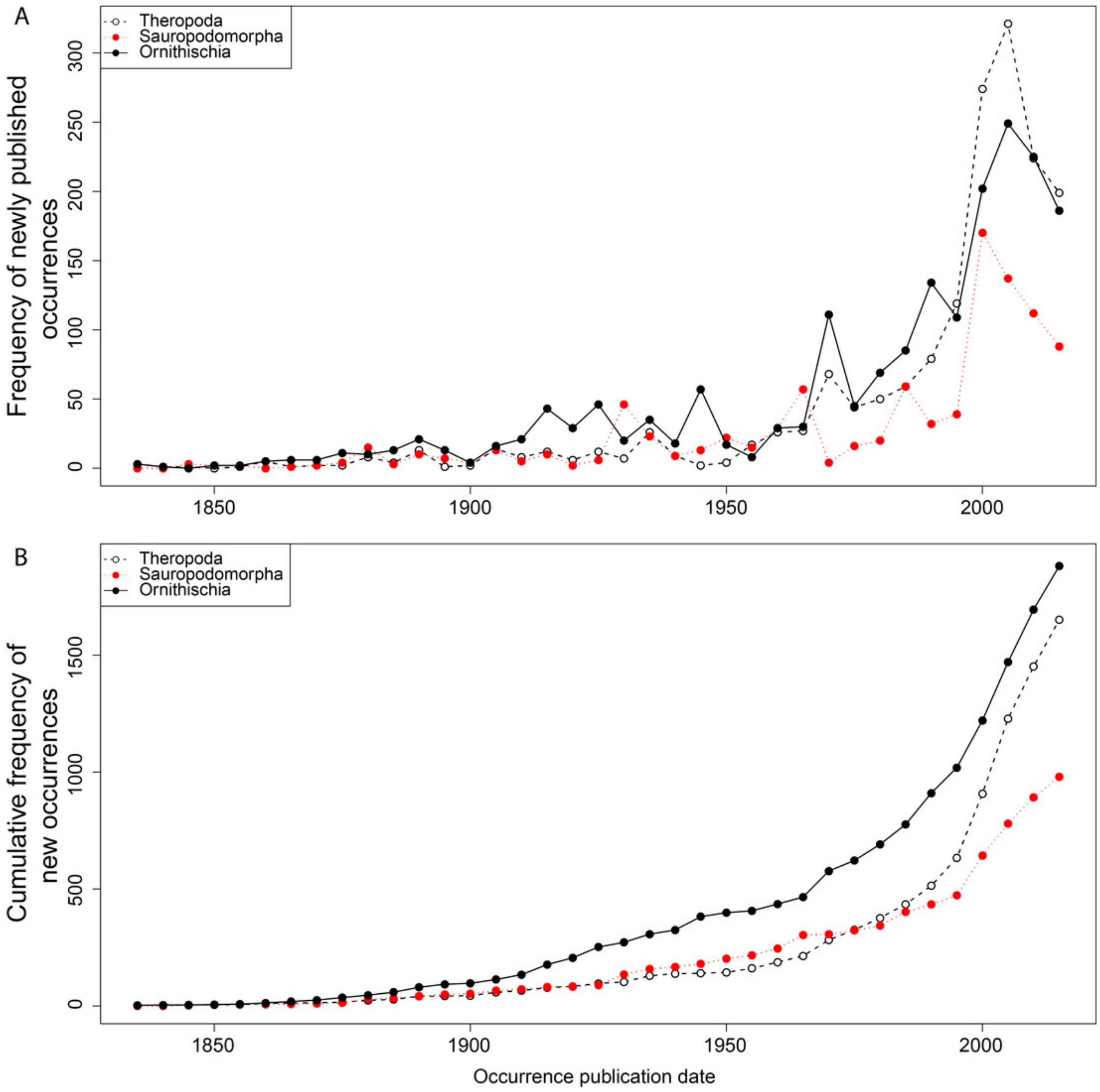


Figure 2

Frequency and cumulative frequency of newly published dinosaur genera through publication time.

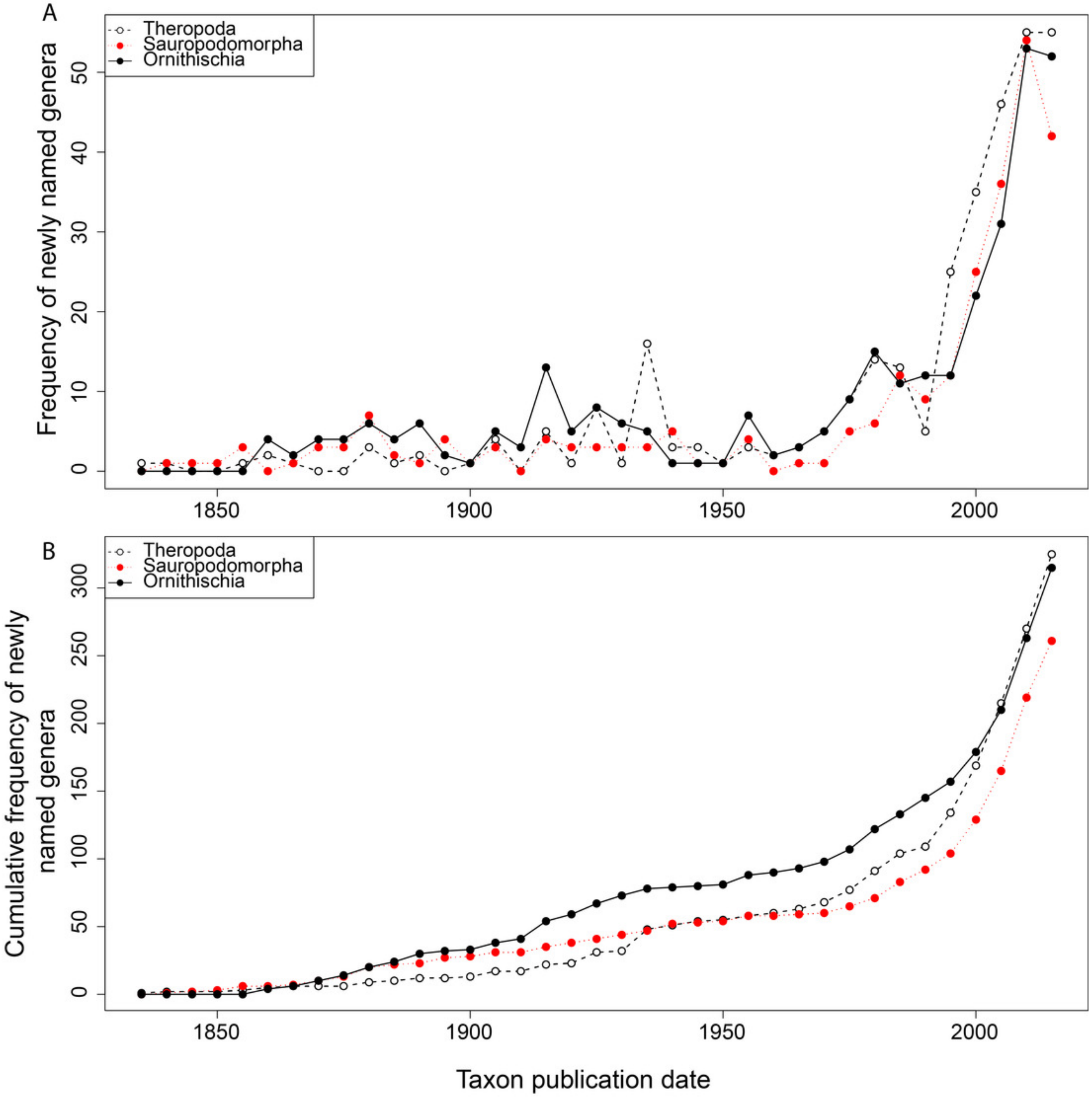


Figure 3

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

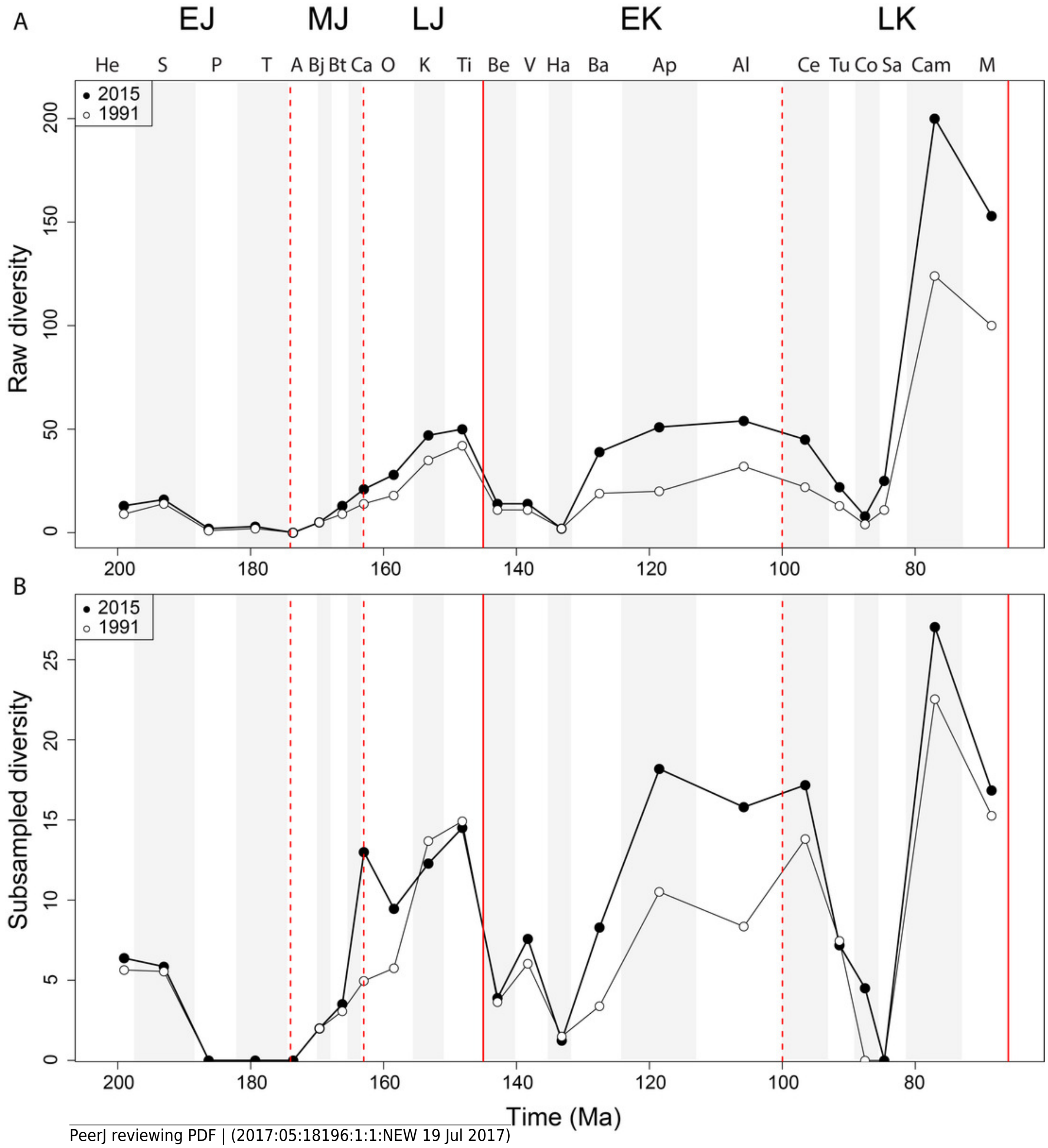
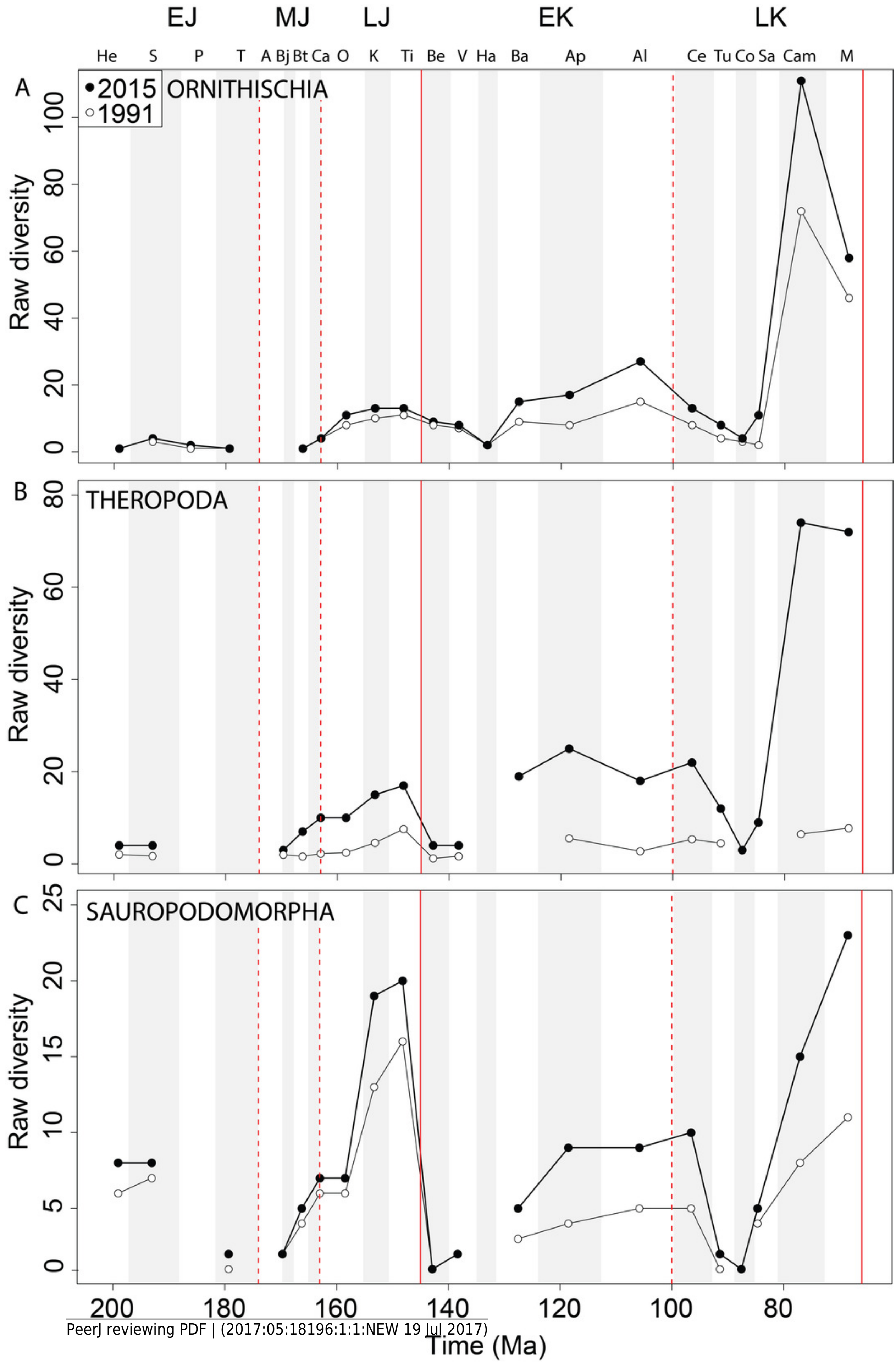


Figure 4

Raw global diversity for a) Ornithischia, b) Theropoda, and c) Sauropodomorpha based on our published knowledge in 1991 and 2015.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Ce
Tu
Co
Sa
Cam
M
A
● 2015
○ 1991
ORNITHISCHIA
Raw diversity
0
20
40
60
80
100
B
THEROPODA
Raw diversity
0
20
40
60
80
C
SAUROPODOMORPHA
Raw diversity
0
5
10
15
20
25
200
180
160
140
120
100
80
Time (Ma)

Figure 5

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

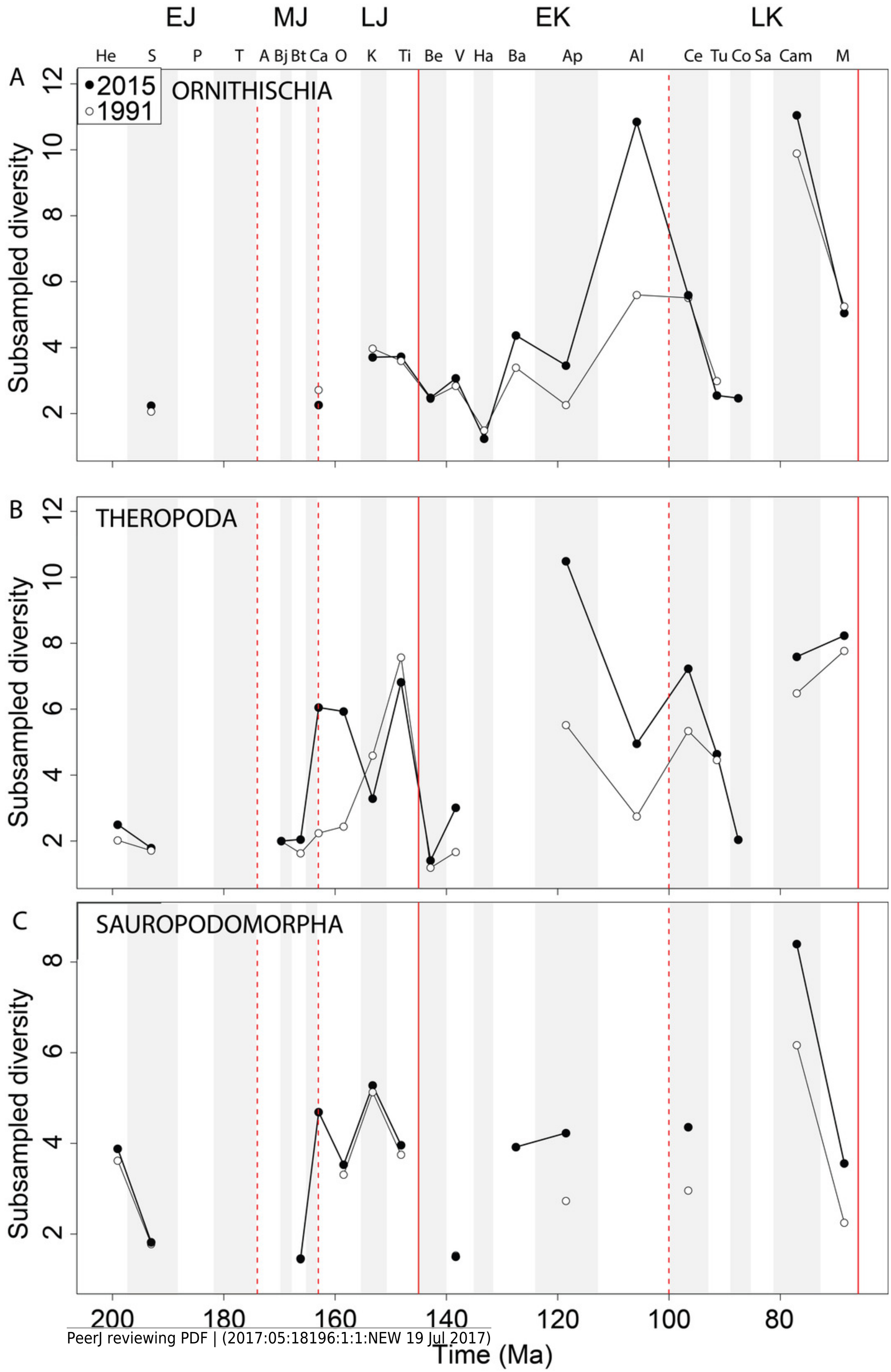
EJ
MJ
LJ
EK
LK
He
S
P
T
A
Bj
Bt
Ca
O
K
Ti
Be
V
Ha
Ba
Ap
Al
Ce
Tu
Co
Sa
Cam
M
A
●2015
○1991
ORNITHISCHIA
B
THEROPODA
C
SAUROPODOMORPHA
Subsampled diversity
2
4
6
8
10
12
200
180
160
140
120
100
80
Time (Ma)

Figure 6

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.

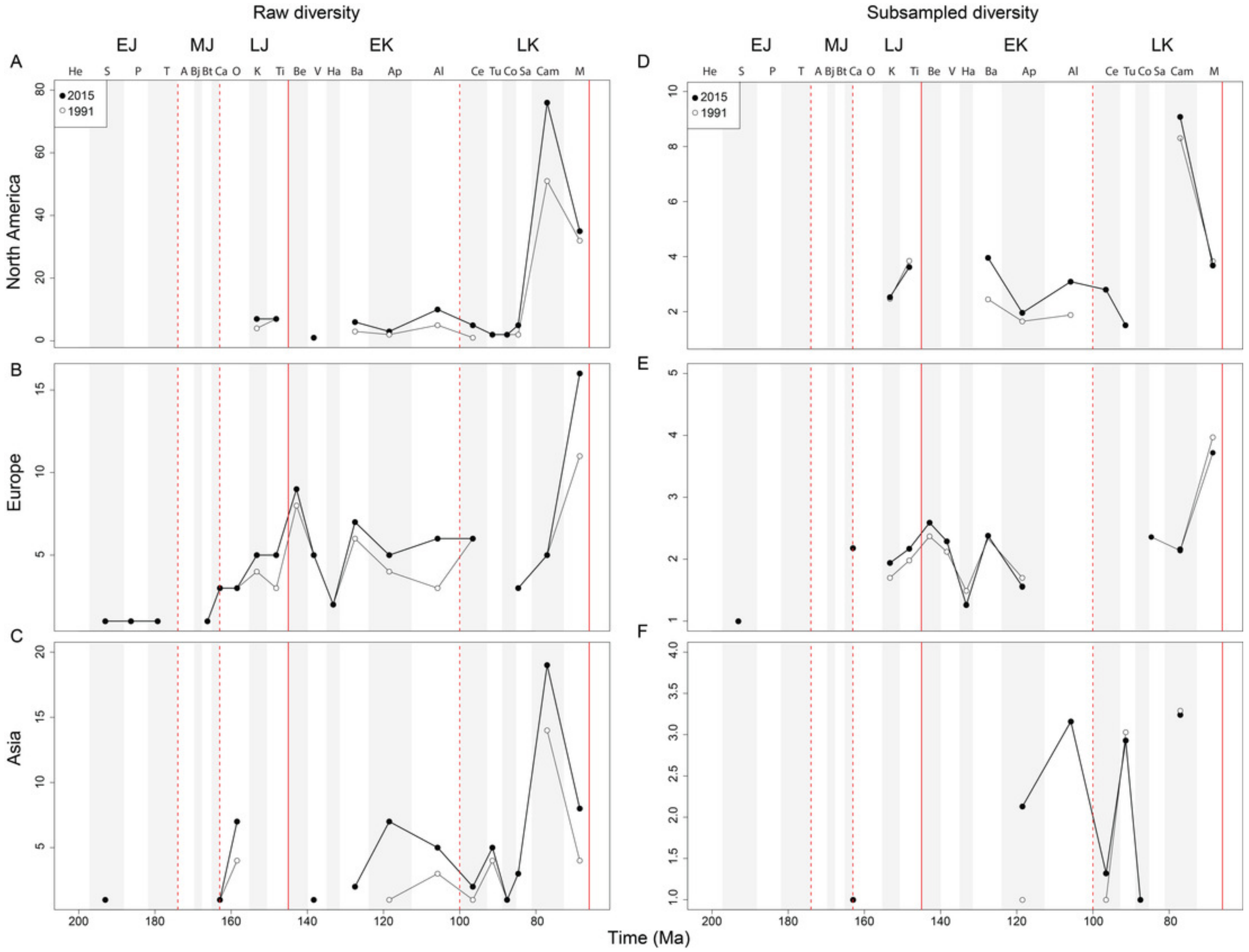

Figure 7

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.

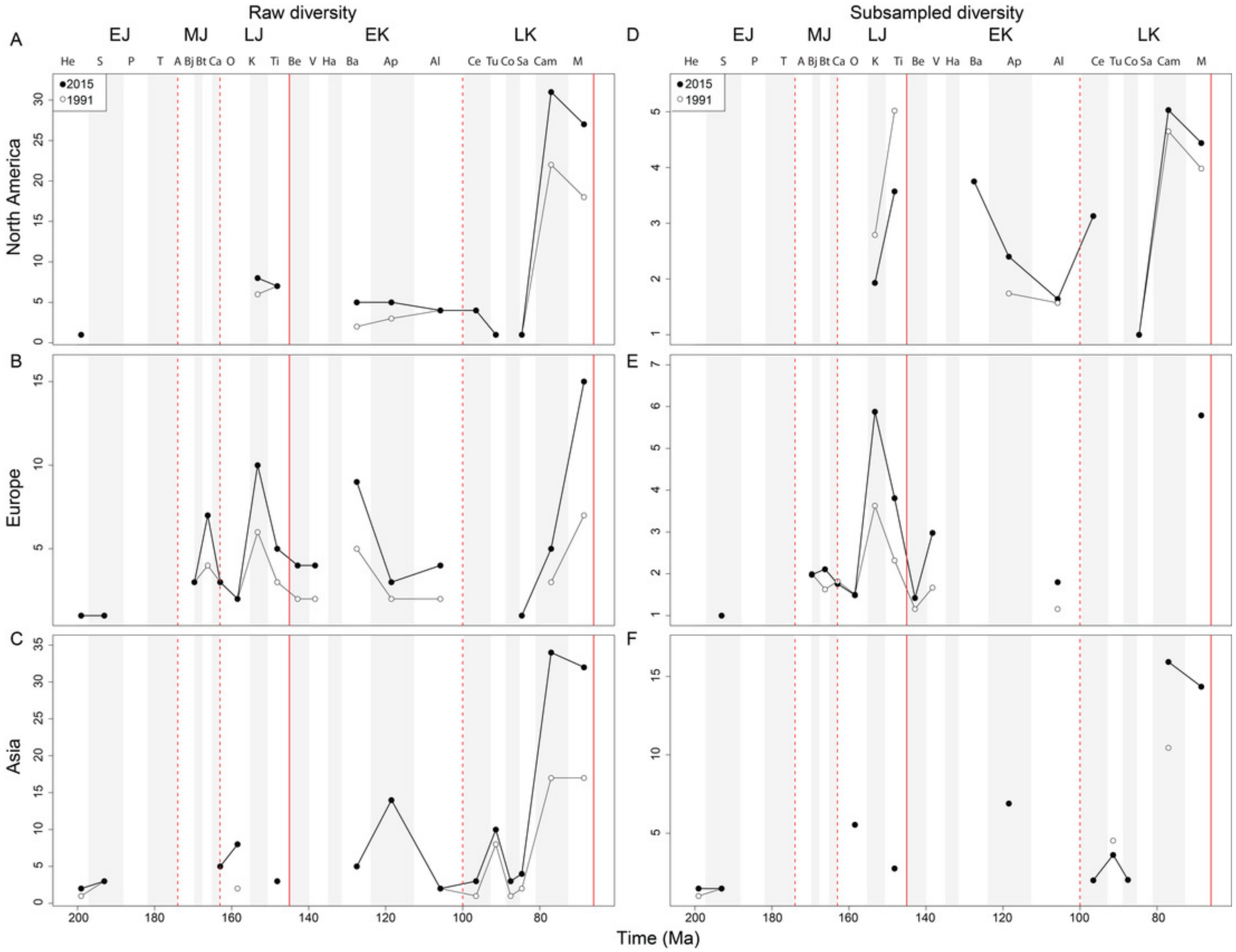

Figure 8

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.