Dinosaur diversity and the rock record

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Palaeobiodiversity analysis underpins macroevolutionary investigations, allowing identification of mass extinctions and adaptive radiations. However, recent large-scale studies on marine invertebrates indicate that geological factors play a central role in moulding the shape of diversity curves and imply that many features of such curves represent sampling artefacts, rather than genuine evolutionary events. In order to test whether similar biases affect diversity estimates for terrestrial taxa, we compiled genus-richness estimates for three Mesozoic dinosaur clades (Ornithischia, Sauropodomorpha and Theropoda). Linear models of expected genus richness were constructed for each clade, using the number of dinosaur-bearing formations available through time as a proxy for the amount of fossiliferous rock outcrop. Modelled diversity estimates were then compared with observed patterns. Strong statistically robust correlations demonstrate that almost all aspects of ornithischian and theropod diversity curves can be explained by geological megabiases, whereas the sauropodomorph record diverges from modelled predictions and may be a stronger contender for identifying evolutionary signals. In contrast to other recent studies, we identify a marked decline in dinosaur genus richness during the closing stages of the Cretaceous Period, indicating that the clade decreased in diversity for several million years prior to the final extinction of non-avian dinosaurs at the Cretaceous–Palaeocene boundary.

Keywords: dinosaurs; Mesozoic; rock record; extinction; macroevolution; sampling bias

1. INTRODUCTION

A central goal of palaeobiology is to establish the trajectory of biodiversity through time (Valentine 1985; Rosenzweig 1995). Knowledge of this pattern, at various hierarchical levels, can identify important macroevolutionary signals, including mass extinctions and episodes of competitive displacement, as well as revealing the tempo and mode of adaptive radiations (e.g. Jablonski *et al.* 1996; Sepkoski 1997; Schluter 2000; Stanley 2007). To date, the majority of palaeobiodiversity investigations have focused on the marine realm, whereas trends in terrestrial biodiversity through time have received less attention (e.g. Valentine 1985; Fara & Benton 2000; Benton 2001).

Diversity curves for Mesozoic dinosaurs have been proposed by several authors, based mostly on raw counts of genera (e.g. Weishampel & Norman 1989; Dodson 1990; Barrett & Willis 2001; Taylor 2006) or phylogenetically corrected genus-richness estimates (e.g. Weishampel & Jianu 2000; Upchurch & Barrett 2005): the majority of these studies dealt with individual dinosaur clades rather than dinosaur diversity as a whole. Fastovsky *et al.* (2004) and Wang & Dodson (2006) used more sophisticated statistical approaches, including rarefaction and the abundance-based coverage estimator, to estimate total dinosaur diversity, but provided only coarse temporal sampling that may have obscured or conflated important

features of the curve. Lloyd *et al.* (2008) presented the most comprehensive account of dinosaur diversification to date: these authors used a variety of metrics and attempted to correct for possible sampling biases in their diversity estimates by using a form of rarefaction and controlling for differences in the number of known dinosaur localities between time intervals.

Recent investigations into marine invertebrate palaeobiodiversity indicate that the quality and amount of rock available for palaeontologists to search for fossils (e.g. the areal extent of fossiliferous rock outcrop per unit time) have a major influence on interpretations of diversity patterns, and also demonstrate that many features of diversity curves could be artefacts caused by changes in global sea-level, tectonics and other geological processes affecting fossil preservation (e.g. Peters & Foote 2001; Smith 2001, 2007; Peters 2005; Smith & McGowan 2007; McGowan & Smith 2008). Most previous studies on dinosaur diversity have ignored or downplayed these geological megabiases. Upchurch & Barrett (2005) found limited correspondence between sauropod dinosaur genus-richness and the number of dinosaur-bearing formations (DBF, a measure used as a proxy for the amount of available rock outcrop); by contrast, Wang & Dodson (2006) concluded that rock availability had a strong influence on the observed pattern of North American dinosaur diversity.

Here, we document the palaeobiodiversity of Mesozoic dinosaurs (inclusive of birds) through time and investigate the relationship between clade diversity and the rock record. We construct models of expected dinosaur genus richness based on the number of dinosaur-bearing rock units and compare these models with observed diversity

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patterns. It is demonstrated that many features of dinosaur diversity curves are sampling artefacts that reflect changes in the amount of available fossiliferous rock and thus reflect geological, rather than biological, events. However, some of the reconstructed diversity curves exhibit deviations from the palaeobiodiversity patterns predicted by the geological model, suggesting that several of the observed fluctuations in dinosaur diversity reflect genuine macroevolutionary signals. This study represents the first attempt to apply the modelling approach of Smith & McGowan (2007; McGowan & Smith 2008) to a terrestrial group of organisms, and thus has broader implications for assessing diversity patterns in other terrestrial clades.

2. MATERIAL AND METHODS

(a) *Diversity estimation*

Temporal ranges of 662 valid dinosaur taxa, ranging in age from Ladinian (Middle Triassic: 237.0 Myr ago) to the end of the Maastrichtian (end Cretaceous: 65.6 Myr ago), were extracted from a recent global compendium of dinosaur distribution and taxonomy (Weishampel *et al.* 2004). Dinosauria was treated as a monophyletic clade, with Mesozoic birds included (other recent studies excluded birds and were therefore confined to examining a paraphyletic array of non-avian dinosaur taxa: Wang & Dodson 2006; Lloyd *et al.* 2008). These temporal ranges were used to construct taxic diversity estimates (TDE) by summing the number of dinosaur genera present during each Mesozoic timeslice. Genus richness was selected as the taxonomic rank of choice, as the analyses of Robeck *et al.* (2000) demonstrated that data collected at lower taxonomic ranks are more reliable than those obtained for higher ranks (families and orders). Genus richness is preferred over species richness as most dinosaur genera are easily diagnosed and monospecific (Weishampel *et al.* 2004), with the effect that genus- and species-level curves are exceptionally similar (P. M. Barrett 2007, unpublished data). By contrast, dinosaur species determinations (in multi-specific genera) are often problematic and many individual specimens can only be identified accurately at the generic level (see also Benton 2008).

Unfortunately, many geological formations that have yielded dinosaur material cannot be dated precisely: as a result, the timeslices used herein are based on subdivisions of standard international stages, thereby reflecting the relative coarseness of the dataset. Conversion of this information to absolute ages (in millions of years) was rejected, as it would introduce false precision. Use of stage subdivisions allows the identification of many short-term fluctuations in the diversity curves and provides a larger number of data points for statistical analyses, contrasting with other studies that used more inclusive time bins composed of several sequential stages spanning tens of millions of years (e.g. Fastovsky *et al.* 2004; Wang & Dodson 2006; Lloyd *et al.* 2008). Nevertheless, finer splitting of the time scale can lead to several problems (Sepkoski & Koch 1996). The most significant of these occurs if taxa are assigned to the wrong interval, as is more likely with smaller bin sizes. Some studies, notably those of Alroy *et al.* (2001, 2008), generated a series of time bins of equal duration, following the methodology suggested by Sepkoski & Koch (1996). However, we did not adopt this approach as it would obscure the finer-scale patterns that can be resolved. As this study focused on diversity rather than extinction or origination, it is also likely that shifts in assignment of taxa to intervals would tend to negate each other. For each taxon that moved out of a bin, another would probably be reassigned to that bin. Such assumptions have dominated the construction of large-scale biodiversity curves (see Hallam & Wignall (1997) for discussion).

Phylogenetic diversity estimates (PDE) were generated on the basis of published cladograms for each dinosaur group, which were obtained from Weishampel *et al.* (2004: see the electronic online supplementary material). The more recent cladogram of Butler *et al.* (2008) was used to provide a broader framework for exploring ornithischian diversity. Evolutionary trees for each clade were constructed by plotting dinosaur cladograms against time, allowing the inference of ghost lineages. The latter results from discrepancies between the proposed time of taxon origination (based on the age of the oldest-known sister group) and the first appearance of the taxon in the fossil record (Norell & Novacek 1992). The temporal ranges of these ghost lineages were then summed with the known temporal ranges of the taxa included within the cladogram to produce a phylogenetically corrected diversity estimate for each timeslice.

(b) *Modelling rock availability and its relationship to diversity*

Relationships between rock record quality, TDE and PDE were investigated using the number of dinosaur-bearing geological formations as a proxy for the total amount of rock with the potential to yield dinosaur fossils. Similar approaches have been employed in several previous studies (Fara & Benton 2000; Wang & Dodson 2006; Lloyd *et al.* 2008), and it has been demonstrated that the number of formations correlates well with other measures of rock record quality, including estimates of total rock volume and numbers of sedimentary rock sections (Peters 2005). Peters & Foote (2001) argued that formations are an appropriate proxy as they record variability in the range of habitats (both ecological and geological) preserved through time. By contrast, outcrop area is more problematic, as a single, areally extensive formation could be devoid of fossils. As DBF contain the taxa of interest, this is a more credible subset of formations to use than the total number of formations available (similarly, modern ecological surveys do not expend significant search effort in habitats unfrequented by the target group of organisms), and the use of DBF provides some taphonomic control. Moreover, it has been demonstrated that relationships between the rock record and diversity are not strongly affected if unfossiliferous formations are also taken into account (Smith & McGowan 2008). Information on the number of DBF in each timeslice (1033 units in total) was obtained from Weishampel *et al.* (2004). The resulting curve of DBF distributions through time (figure 1*a*) was compared with the TDE and PDE obtained for each dinosaur clade (figure 1*b–d*) using three statistical measures (Pearson's product-moment correlation [ρ], Spearman's rank correlation [r_s] and Kendall's τ coefficient) to elucidate the degree of fit between the two time-series.

The method of Smith & McGowan (2007) was used to develop a sequence of models in which rock availability (represented by the number of DBF) was assumed to be a perfect predictor of the TDE for each dinosaur clade. This procedure involves sorting the rock and diversity time series independently, ordering each of the timeslices in a sequence from the lowest to the highest, and then fitting linear
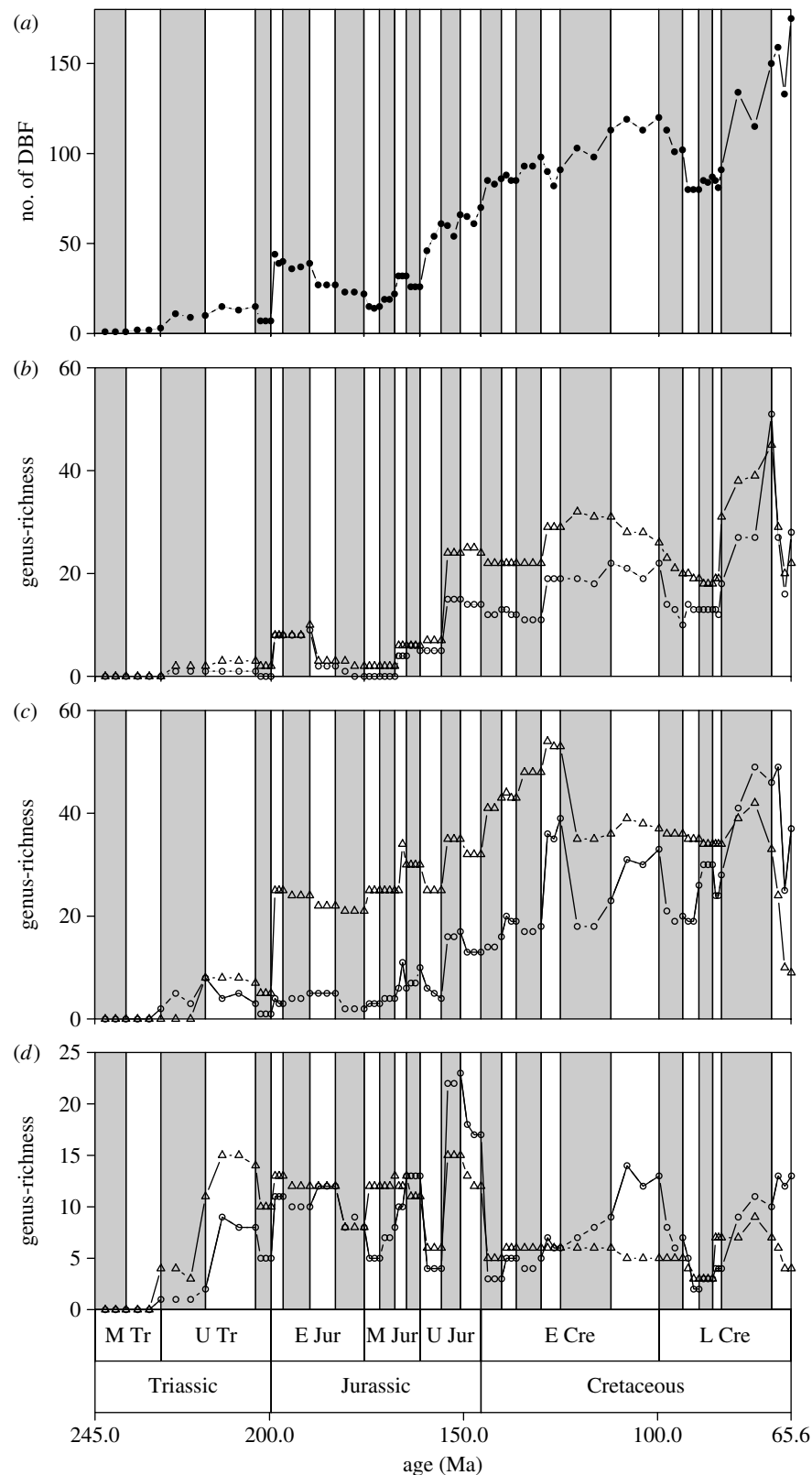
Figure 1. Time-series plots of rock-record quality and diversity for each of the three major dinosaur clades. Alternating grey/white bins mark durations of standard international stages (see Gradstein *et al.* 2004) starting with the Anisian stage of the Middle Triassic. Individual substage data points are marked on the curve. (*a*) Number of DBF. (*b*) Ornithischia TDE (unfilled circles) and PDE (unfilled triangles). (*c*) Theropoda TDE (unfilled circles) and PDE (unfilled triangles). (*d*) Sauropodomorpha TDE (unfilled circles) and PDE (unfilled triangles). The *y*-axis in figure 1*a* represents the number of DBF; in figure 1*b*–*d*, it represents the number of valid dinosaur genera (inclusive of Mesozoic birds).

least-squares regression models of the general form $y = mx + c$ to the ordered datasets (where x is equal to the number of DBF; y is the predicted number of dinosaur taxa present; m is the gradient of the line; and c is a constant). These equations were then applied to the DBF time series in its original order allowing derivation of modelled diversity estimates (MDE). Using R scripts (R Development Core Team 2008), the MDE and TDE were compared using Pearson's

product-moment correlations, in order to assess their similarity to each other. Finally, MDE were subtracted from TDE to obtain residual values representing diversity signals that could not be accounted for by variation in the rock record alone. The last step was repeated, with PDE replacing TDE, to obtain residuals of PDE from MDE. All relevant data files are provided in the electronic online supplementary material.

3. RESULTS

(a) *Dinosaur diversity through time*

Ornithischian TDE and PDE present almost identical diversity profiles (see the electronic online supplementary material for statistical comparisons between TDE and PDE for all three dinosaur clades). Ornithischian diversity is low from the Late Triassic to the end of the Middle Jurassic (figure 1*b*), although a small earliest Jurassic peak represents the radiation of heterodontosaurids and other basal ornithischian taxa. Ornithischian diversity shows a marked increase during the Late Jurassic and plateaus in the earliest Cretaceous before reaching another higher peak in the late Early Cretaceous (Barremian–Albian). A severe drop in diversity followed in the early Late Cretaceous, but from the late Santonian onward, ornithischian diversity climbed rapidly to attain its highest peak in the late Campanian, with over 50 genera worldwide. However, diversity declines to Late Jurassic levels in the latest Cretaceous (Maastrichtian) with a drop in taxonomic richness of 45 per cent (PDE) or 67 per cent (TDE) between the late Campanian and the Cretaceous–Palaeocene (K–P) boundary, although a small rebound occurs in the latest Maastrichtian.

The theropod TDE (figure 1*c*) is very similar to that obtained for Ornithischia, with significant diversity increases during the Late Jurassic, late Early Cretaceous and latest Cretaceous and a notable decline in diversity during the Maastrichtian; however, the latter is less marked than that observed in the ornithischian record (25% decrease in taxonomic richness). A notable deviation between the theropod and ornithischian curves occurs in the Late Triassic, which exhibits a small peak in theropod diversity at a time when ornithischians are exceptionally rare (Butler *et al.* 2007; Irmis *et al.* 2007). There are several discrepancies between the theropod TDE and PDE: (i) the PDE show a prominent diversity increase over the Triassic–Jurassic boundary that is not present in the TDE; (ii) the heights of the Middle and Late Jurassic diversity peaks are approximately equal in the PDE, whereas, in the TDE, the Late Jurassic diversification is greater in magnitude; (iii) a significant diversity trough is present in the PDE between the Aptian and late Santonian, while a more complex pattern of peaks and troughs occurs in the TDE; and (iv) the PDE indicates that theropod decline during the Late Cretaceous began in the Campanian (not the Maastrichtian as in the TDE) and was more severe than predicted by the TDE (79% decrease in taxonomic richness between the Campanian peak and the K–P boundary).

Sauropodomorph diversity patterns share some similarities with those of theropods and ornithischians, including peaks during the Late Jurassic, late Early Cretaceous and latest Cretaceous and a major decline in diversity during the early Late Cretaceous (figure 1*d*). However, the sauropodomorph TDE and PDE both diverge significantly from the general pattern of increasing diversity observed in the other clades: (i) peak sauropodomorph diversity occurs in the Late Jurassic, in contrast to the other clades whose diversity peaks during the Campanian (Late Cretaceous); (ii) numerous sauropodomorph taxa were present during the Late Triassic to Middle Jurassic interval, while ornithischian diversity was low throughout this period; (iii) the Jurassic–Cretaceous boundary represents a major extinction event for sauropodomorphs (loss of 82 and 58% of taxonomic diversity for the TDE and PDE, respectively), whereas this event had little impact on other dinosaur clades (compare with figure 1*b*–*c*); (iv) the earliest Cretaceous has low-diversity sauropodomorph faunas, but witnessed rapid increases in theropod and ornithischian taxonomic richness; and (v) sauropodomorph diversity levels are maintained at an almost constant level during the final latest Cretaceous radiation of this clade (seen in the TDE only) and did not decline prior to the K–P boundary. In general, the sauropodomorph TDE and PDE are exceptionally similar, but the curves diverge in two respects: (i) the PDE record higher diversity in the early Middle Jurassic, and (ii) taxic diversity peaks present in the late Early Cretaceous and latest Cretaceous are not detected in the PDE (figure 1*d*).

(b) *Influence of the rock record in dinosaur diversity*

As a first approximation, the number of DBF rises through time. However, there are notable dips in the DBF curve during the Early–Middle Jurassic and the early Late Cretaceous (figure 1*a*). The TDE and PDE for Ornithischia and Theropoda are strongly positively correlated with the DBF curve ($p < 0.01$ in all cases; table 1). Kendall's τ tests measure the synchronicity of increases and decreases in rock availability and TDE or PDE values: Ornithischia has the strongest positive correlation with DBF, followed by Theropoda (table 1). By contrast, the sauropodomorph TDE has a lower positive correlation with the DBF curve ($p < 0.01$) and a much weaker positive correlation is obtained for the PDE. The r_s test for the sauropodomorph PDE shows a weak, negative correlation with DBF ($p = 0.02$; table 1), and the Kendall's τ comparison is also weak and negative. Theropod and ornithischian diversities exhibit a general (though not smooth) increase through time, with each clade experiencing a notable reduction in diversity prior to the end of the Maastrichtian, in spite of a peak in DBF numbers at this time.

Models relating diversity to rock availability were developed using TDE (see the electronic online supplementary material, table S3). The MDE are strongly correlated with TDE in both ornithischians and theropods and explain a large amount of the variance in the TDE ($\rho = 0.808$ and 0.840, respectively), whereas the amount of variance explained in the TDE of sauropods is exceptionally low ($\rho = 0.071$). Correlations between MDE and PDE are slightly different: values for ornithischians ($\rho = 0.826$) and sauropodomorphs ($\rho = 0.077$) are similar to those obtained from comparisons between the MDE and TDE, whereas those obtained for theropods are weaker than that for the TDE ($\rho = 0.704$). Although ornithischian and theropod diversity trajectories are similar (figure 1*b*–*c*), analysis of covariance demonstrates that the slope and

Table 1. Correlations between number of DBF, TDE and PDE for each of the three dinosaur clades. (All of these results are statistically significant (see text), but the low amount of variance explained for Sauropodomorpha (as measured by adjusted ρ) contrasts strongly with the values for the other two clades.)

	Pearson's (ρ)	adjusted ρ	Spearman's (r_s)	Kendall's (τ)
Ornithischia TDE	0.900	0.808	0.910	0.750
Ornithischia PDE	0.953	0.907	0.909	0.766
Theropoda TDE	0.841	0.840	0.902	0.742
Theropoda PDE	0.841	0.704	0.769	0.632
Sauropodomorpha TDE	0.554	0.298	0.261	0.232
Sauropodomorpha PDE	0.298	0.077	−0.257	−0.174

intercept of the rock models for each clade are all highly significantly different ($p < 0.01$), indicating that genuine differences exist, based on current data.

The modelling approach assumes that diversity within a clade has been constant and varies only as a function of DBF numbers per time interval. Consequently, ornithischian and (to a lesser extent) theropod diversities appear to be closely related to the number of available DBF, whereas the latter measure is an exceptionally poor predictor of sauropodomorph diversity. Residuals obtained after removing MDE from the relevant TDE reveal that in the case of ornithischians, most of the diversity signals can plausibly be explained by variations in rock availability: the only major exceptions to this pattern are in the Early and Middle Jurassic, when ornithischians are significantly less diverse than would be expected on the basis of DBF numbers (figure 2a). Similar comments apply to theropod diversity: a few residuals lie below the expected range during the earliest and early Late Jurassic, and two significant positive residuals occur in the Late Triassic (figure 2b). Considerable differences between the sauropodomorph TDE and MDE result in the generation of high residual values in almost every timeslice (figure 2c). Sauropodomorphs appear to be over-represented in relationship to the number of DBF for almost the entire duration of the Jurassic, whereas the converse situation prevails throughout the Cretaceous. Notable peaks occur during the earliest Cretaceous and the Turonian–Coniacian. However, the wide confidence limits mean that these results are not statistically significant. Nevertheless, the weaker, sometimes negative, correlations between the sauropodomorph TDE/PDE and DBF (table 1 and the electronic online supplementary material) suggest that this pattern may be informative, and that the trajectory of sauropodomorph diversity did deviate substantially from that predicted by the rock record. The lack of statistical significance of the residuals from the MDE is due to the wide confidence limits for Sauropodomorpha relative to the other two clades (compare figure 2a,b with 2c), which results from a combination of factors: (i) sample sizes for sauropodomorphs in each time bin are generally lower than those for ornithischians and theropods, and (ii) sauropodomorphs exhibit high diversity in the Late Triassic to Late Jurassic at a time when DBF numbers are generally low, in direct contradiction to the assumption in the MDE: consequently, the MDE is poor at explaining variance in the sauropodomorph dataset. Residuals obtained by subtracting PDEs from MDEs show similar patterns to those described for TDEs (see the electronic online supplementary material).

4. DISCUSSION

Consideration of possible geological megabiases indicates that many of the peaks and troughs apparent in dinosaur diversity curves may not represent genuine biological events, but should probably be regarded as artefacts caused by variations in the amount of fossil-bearing rock preserved through time. Caution is therefore necessary when attempting to infer macroevolutionary patterns and processes from direct reading of the fossil record (see also Peters 2005; Smith & McGowan 2007; McGowan & Smith 2008). Nevertheless, when such biases are accounted for, several genuine diversity signals do appear to be present. Perhaps the most intriguing of these is the diminution of ornithischian and theropod dinosaur lineages several million years prior to the K–P extinction event: both clades underwent a drastic decline in both absolute terms (as shown in TDE and PDE) and relative to their predicted diversities (as shown by comparisons between TDE/PDE and MDE, although this decline is only statistically significant in the case of theropods; figure 2a,b and the electronic online supplementary material). This result contrasts strongly with other recent analyses that either found no evidence for a reduction in dinosaur diversification prior to the K–P boundary (Wang & Dodson 2006; Lloyd *et al.* 2008), or that explained the drop in diversity from the Campanian to the Maastrichtian as a consequence of sampling issues (Fastovsky *et al.* 2004, 2005): this difference that may be due to the fact that the diversity estimates presented herein are not based on methods that extensively resample the raw diversity/collections data (such as rarefaction). This observation supports the suggestion that factors other than the end-Cretaceous bolide impact were responsible for instigating a downward trend in taxonomic richness that preceded the unquestionably abrupt disappearance of many dinosaur taxa at the boundary itself (see also Archibald 1996; Archibald & MacLeod 2008). It is particularly notable that this diversity decline comes at a point in the Earth's history when the opportunities for collecting dinosaur fossils are at their peak: DBF numbers reach their acme during the Maastrichtian, suggesting that this diversity signal cannot be accounted for by geological biases. However, our results agree with those of previous authors in identifying a pulse of diversification in the Campanian (e.g. Fastovsky *et al.* 2004; Wang & Dodson 2006).

In contrast to the theropod and ornithischian diversity curves, sauropodomorph genus richness deviates strongly from that predicted by rock availability models. The reasons for this difference are unclear, however, as sauropodomorphs are often found in the same geological
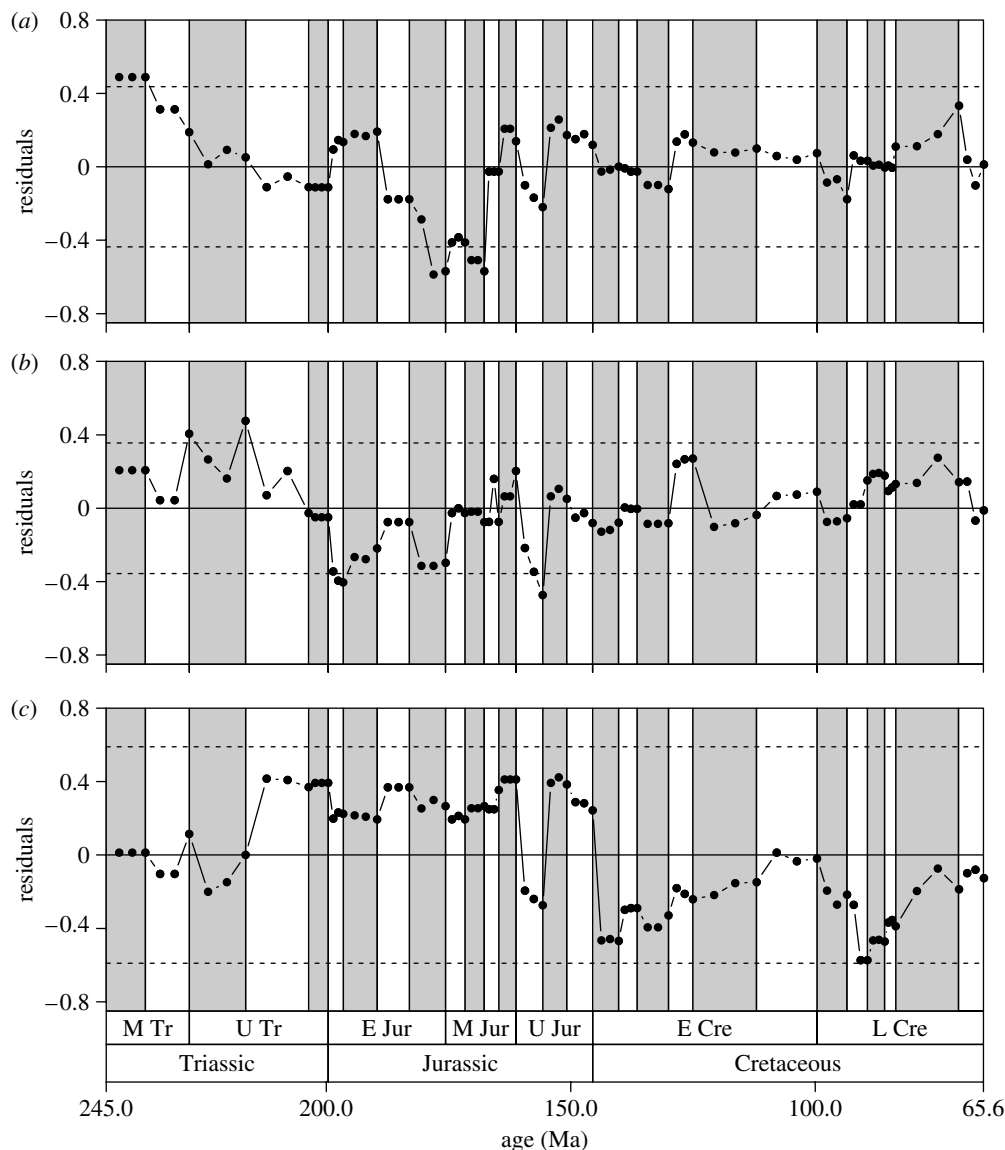
Figure 2. Time series of residuals of observed TDE from predicted MDE based on power-law models. Time-scale divisions as in figure 1. Dashed lines mark 95% confidence limits. (*a*) Ornithischia, (*b*) Theropoda and (*c*) Sauropodomorpha. See text for further details.

formations as the other clades (see Weishampel *et al.* 2004). It is possible that taphonomic factors may have played as part, as there is some evidence for habitat separation of sauropodomorphs and various ornithischian clades during the Cretaceous (Butler & Barrett 2008), but this observation requires further investigation. Nevertheless, our results suggest that geological megabiases had less influence on the sauropodomorph fossil record than expected. Changes in diversity recorded for this clade, such as their explosive radiation in the Late Triassic, the major extinction at the Jurassic/Cretaceous boundary and the radiation of Late Cretaceous sauropods, might either be attributable to other environmental factors or represent genuine macroevolutionary signals (Upchurch & Barrett 2005).

Lloyd *et al.* (2008) expressed concern that consideration of geological megabiases might seriously compromise our ability to recover genuine biological signals. However, although we have presented strong evidence for the role of rock record quality in explaining dinosaur diversity changes, we have also provided evidence of independent diversification trajectories for each of the three clades investigated and figure 2 illustrates some intervals where diversity is significantly higher or lower than predicted by the MDE (see the electronic online supplementary material). Lloyd *et al.*'s (2008) call for more refined models to investigate the relationship between the number of DBF and diversity should be addressed as it would clarify the factors that are the most significant in changing our estimates of diversity. However, it is striking that the amount of variance explained by the MDE is so high for theropods and ornithischians, especially in comparison with results obtained for marine taxa (Peters 2005; Smith & McGowan 2007; McGowan & Smith 2008).

Studies are now taking advantage of the availability of large, stable phylogenies that can be used to compensate for some of the shortcomings of the geological record. However, these serve to provide alternative models that are dependent on the strength of the phylogenies involved: just as the fossil record can be imperfect, so can phylogenies. Combining geological and phylogenetic data has a major role to play in constraining diversification

trajectories: simultaneous consideration of multiple independent clades may prove critical in developing better models to correct for the influence of geological megabiases and to reveal the genuine biological signals sought by all evolutionary biologists.

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