RESEARCH PAPER

A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning

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ABSTRACT

Aim Modern biodiversity peaks in the tropics and declines poleward, a pattern that is potentially driven by climate. Although this latitudinal biodiversity gradient (LBG) also characterizes the marine invertebrate fossil record, distributions of ancient terrestrial faunas are poorly understood. This study utilizes data on the dinosaur fossil record to examine spatial patterns in terrestrial biodiversity throughout the Mesozoic.

Location We compiled data on fossil occurrences across the globe.

Methods We compiled a comprehensive dataset of Mesozoic dinosaur genera (738), including birds. Following the utilization of sampling standardization techniques to mediate for the uneven sampling of the fossil record, we constructed latitudinal patterns of biodiversity from this dataset.

Results The dominant group of Mesozoic terrestrial vertebrates did not conform to the modern LBG. Instead, dinosaur diversity was highest at temperate palaeolatitudes throughout the 160 million year span of dinosaurian evolutionary history. Latitudinal diversity correlates strongly with the distribution of land area. Late Cretaceous sauropods and ornithischians exhibit disparate LBGs.

Main conclusions The continuity of the palaeotemperate peak in dinosaur diversity indicates a diminished role for climate on the Mesozoic LBG; instead, dinosaur diversity may have been driven by the amount of land area among latitudinal belts. There is no evidence that the tropics acted as a cradle for dinosaur diversity. Geographical partitioning among major clades of herbivorous dinosaurs in the Late Cretaceous may result from the advanced stages of continental fragmentation and/or differing responses to increasing latitudinal climatic zonation. Our results suggest that the modern-day LBG on land was only established 30 million years ago, following a significant post-Eocene recalibration, potentially related to increased seasonality.

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INTRODUCTION

Most living groups of organisms conform to a latitudinal biodiversity gradient (LBG), in which species richness decreases away from the tropics (Rosenzweig, 1995; Willig *et al.*, 2003; Hillebrand, 2004). This gradient has been documented on land as well as in the marine realm. It exists in both hemispheres and is regarded as one of the most fundamental macroecological patterns governing life on Earth (Willig *et al.*, 2003; Hillebrand, 2004). The modern-day LBG appears to be dependent on a range of biological and abiotic forces influencing the spatiotemporal distribution of species. For example, latitude is a proxy for

numerous interacting environmental gradients, such as temperature and seasonality (Willig *et al.*, 2003; Hillebrand, 2004). As a consequence of this complexity, the causes of the gradient are still strongly debated and there is little consensus (Hillebrand, 2004). Of the many hypotheses proposed to explain the LBG, only a handful cannot be readily refuted. Climate may be the prime driver, influencing biodiversity either directly or via increased productivity in the tropics (Hawkins *et al.*, 2003; Willig *et al.*, 2003; Hillebrand, 2004; Field *et al.*, 2009). Thus, during warmer intervals many organismal ranges exhibit poleward and/or elevational shifts (Parmeson & Yohe, 2003; Root *et al.*, 2003; Colwell *et al.*, 2008). However, the global distribution of area provides an alternative explanation, in which the greater areal extent in the tropics is able to support more species than other biomes (Terborgh, 1973; Rosenzweig, 1995; Willig *et al.*, 2003). These and other hypotheses are not mutually exclusive, nor are they without problems, and exceptions to the rule exist (Willig *et al.*, 2003; Hillebrand, 2004; Krug *et al.*, 2007). However, understanding the evolution of latitudinal biodiversity gradients is integral to predicting biodiversity loss driven by present-day climate change and explaining geographical variation in biodiversity.

The fossil record offers a unique deep time perspective on this issue. Although climatic variables and the global distribution of area are static at the present time, they show substantial variation over durations spanning hundreds of millions of years. Thus, ancient biodiversity gradients provide data that can help unravel the causes of today's LBG. A modern-type LBG has been recognized in the fossil records of marine invertebrates (e.g. Crame, 2002; Jablonski *et al.*, 2006; Alroy *et al.*, 2008) and terrestrial plants (Crane & Lidgard, 1989; Donoghue, 2008). However, contrarian results have been recovered in the terrestrial realm: a temperate diversity peak was reported in the Late Jurassic dinosaur (*c.* 161–145 million years ago, Ma) (Rees *et al.*, 2004) and middle Cretaceous–early Cenozoic crocodilian fossil record (*c.* 112–34 Ma) (Markwick, 1998), no gradient was recovered for middle Palaeocene mammals (*c.* 63–58 Ma) (Rose *et al.*, 2011) and an analysis of insects found no evidence for a modern-type LBG until after the Eocene (*c.* 34 Ma) (Archibald *et al.*, 2010). All four studies suggest that a modern-type LBG appeared only recently. However, these studies either did not account for potential sampling biases (Markwick, 1998; Rees *et al.*, 2004) or were geographically and temporally restricted (Archibald *et al.*, 2010; Rose *et al.*, 2011), and thus unsuited to tracking the evolution of the LBG. Otherwise, consideration of the effect of latitude on ancient terrestrial faunas has been mainly restricted to qualitative discussions in regional-scale studies (e.g. Brinkman, 2003; Fanti & Miyashita, 2009).

In order to characterize more completely the deep-time LBG of terrestrial animals, it is necessary to study a widespread, ecologically diverse and long-lived clade, using a fossil record that is adequate for the application of sampling standardization techniques. Here we analyse the fossil record of dinosaurs, a cosmopolitan and diverse component of Mesozoic terrestrial ecosystems for 160 million years (Myr), from the Late Triassic to the terminal Cretaceous (230–65.5 Ma). Most of this time interval has been neglected in studies of the LBG. Dinosaur remains are abundant and known from almost all Late Triassic–Cretaceous terrestrial ecosystems in which vertebrate fossils have been discovered (Weishampel *et al.*, 2004; Carrano, 2008). They are also well studied and therefore represent an excellent exemplar group for examining spatial and temporal patterns in ancient biodiversity (Upchurch *et al.*, 2002; Lloyd *et al.*, 2008; Barrett *et al.*, 2009; Butler *et al.*, 2011).

MATERIALS AND METHODS

Additional information on Materials and Methods is available in Appendix S1 in Supporting Information.

Taxonomic and stratigraphic data

Several authors have highlighted problems with using species as a unit for estimating palaeodiversity, including issues relating to inconsistent taxonomic treatment between different workers and the serendipity of preserving species (Robeck *et al.*, 2000; Smith, 2001; Krug *et al.*, 2009). Higher taxonomic levels, such as families, are unsuitable because their content is arbitrary, with some families comprising a single genus whereas others are diverse and have broad spatiotemporal ranges (Rhodes & Thayer, 1991; Smith, 1994). Consequently, we used genera as the taxonomic unit of analysis in this study. Although genera could also be argued to constitute arbitrary units, the vast majority of current dinosaur genera are monospecific (87%), and so there is little difference between using genera or species in our study. Furthermore, if we used species instead of genera, this would exclude occurrences such as *Diplodocus* sp., thereby reducing the size of our dataset.

Based on updates to *The Paleobiology Database* (Carrano, 2008), we compiled stratigraphic ranges and modern geographical coordinates for occurrences of Mesozoic theropods (including birds) and ornithischians (2525 occurrence records, accessed March 2010). We compiled sauropodomorph data differently, using an updated version (as of March 2010) of an individual-level (i.e. specimen-level) database (Mannion *et al.*, 2011). Only valid dinosaur genera were included, i.e. we did not attempt to incorporate 'cryptic' diversity represented by taxonomically undiagnostic fossil specimens that potentially represent distinct taxa (based on their stratigraphic or geographical separation from other fossil specimens; Mannion *et al.*, 2011), nor did we infer ghost lineages based on phylogenetic diversity estimates (e.g. Lloyd *et al.*, 2008; Barrett *et al.*, 2009). The resulting dataset consists of 738 genera (Theropoda: 325; Ornithischia: 223; Sauropodomorpha: 190) and is available in Appendix S2 in Supporting Information (modified from Butler *et al.*, 2011; Mannion *et al.*, 2011; Upchurch *et al.*, 2011).

We analysed our data in seven time slices representing epochs [Late Triassic, Early Jurassic, Middle Jurassic, Late Jurassic, 'early' Cretaceous (Berriasian–Barremian), 'middle' Cretaceous (Aptian–Cenomanian) and 'late' Cretaceous (Turonian–Maastrichtian)]; additional analyses were implemented using the entire Jurassic and Cretaceous periods as bins. We present

key results from the Late Triassic, Jurassic and Cretaceous in the text. Results from other time slices are found in Appendix S2. Analysis in time slices allows us to see whether spatial patterns have changed through the Mesozoic and avoids the problem of temporal overprinting, whereby conflicting diversity patterns during different time intervals obscure one another (Benson *et al.*, 2010; Mannion *et al.*, 2011). The unequal durations of these time slices are not expected to introduce bias into our analyses as we are not concerned with whether one time period had higher diversity than another, only whether there was a change in the latitudinal diversity gradient between intervals. However, it is possible that geographical variation in origination/extinction rates may lead to the accumulation of more diversity in some latitudinal zones over a given time interval than in other zones.

We converted modern day coordinates of dinosaur occurrences into palaeolatitudes using PointTracker, a program which transforms present-day coordinates back in time according to palaeogeographical reconstructions of continental drift (Scotese, 2004). This was implemented for seven time slices at: 220 Ma (Late Triassic), 200 Ma (Early Jurassic), 180 Ma (Middle Jurassic), 160 Ma (Late Jurassic), 140 Ma ('early' Cretaceous), 100 Ma ('middle' Cretaceous) and 70 Ma ('late' Cretaceous) time slices. For the Jurassic and Cretaceous time slices, we used the rotated data of the smaller time slices (i.e. Early Jurassic or middle Cretaceous), using the mean location when an occurrence extended across multiple time slices.

We summed diversity for each time slice for palaeolatitudinal bins spanning distances of both 10° and 30°, with the Northern and Southern Hemispheres treated separately, thereby resulting in eighteen 10° and six 30° latitudinal bins in each time slice.

Sampling data

Macrostratigraphic (i.e. uneven quantities of rock available for fossil sampling) and anthropogenic factors (i.e. uneven sampling of the available rock record by palaeontologists) might distort macroevolutionary patterns by influencing the numbers of fossils available from different spatiotemporal segments and thus bias fossil taxon counts (e.g. Peters & Foote, 2001, 2002; Smith & McGowan, 2007; Barrett *et al.*, 2009; Butler *et al.*, 2009, 2011; Benson *et al.*, 2010; Mannion *et al.*, 2011). It is possible that any palaeolatitudinal pattern recovered may merely reflect the influence of sampling biases in the fossil record (Allison & Briggs, 1993; Krug *et al.*, 2009). Despite its importance, the impact of sampling biases on the palaeolatitudinal biodiversity gradient among extinct species has been almost entirely ignored (but see Alroy *et al.*, 2008; Archibald *et al.*, 2010; Rose *et al.*, 2011). We considered two global sampling proxies: numbers of dinosaur-bearing collections (DBCs) and formations (DBFs) were compiled from *The Paleobiology Database* (accessed March 2010), based on all Mesozoic dinosaur records. These proxies help mediate macrostratigraphic and anthropogenic heterogeneity in fossil record sampling (see Appendix S1). Estimated counts of DBCs and DBFs include all formations and fossil collections from which dinosaur remains have been recovered,

regardless of the taxonomic status of the discoveries (i.e. even DBCs/DBFs yielding undiagnostic dinosaur discoveries were counted, following Upchurch & Barrett, 2005; Barrett *et al.*, 2009; Butler *et al.*, 2011; Mannion *et al.*, 2011; Upchurch *et al.*, 2011). Following the treatment of our diversity data, we summed DBCs and DBFs for both the 10° and 30° palaeolatitudinal bins in each of our time slices, with the Northern and Southern Hemispheres treated separately.

We also compiled data on non-marine surface area based on palaeogeographical reconstructions of Mesozoic coastlines (Smith *et al.*, 1994; see also Butler *et al.*, 2011). We manually divided a Mollweide projection into 648 equidimensional quadrants and used this as an overlay to sum the numbers of quadrants with land present for each latitudinal bin for each time slice. We used the following maps from Smith *et al.* (1994): map 29 (Late Triassic); map 27 (Early Jurassic); map 24 (Middle Jurassic); map 21 (Late Jurassic); map 18 ('early' Cretaceous); map 16 ('middle' Cretaceous); map 10 ('late' Cretaceous). Based on these smaller time slices, we also calculated a duration-weighted mean average value for the Jurassic (i.e. Early, Middle and Late Jurassic summed together) and Cretaceous (i.e. 'early', 'middle' and 'late' Cretaceous).

Analyses

To test for the possibility of varying palaeolatitudinal 'quality' in collections (see Allison & Briggs, 1993; Krug *et al.*, 2009), for each time slice we summed sauropodomorph abundance (i.e. the number of individuals of valid genera) for each palaeolatitudinal bin (10° and 30°) and then divided this value by the numbers of DBCs in that bin. We then compared the 'quality' of tropical, temperate and polar collections. Only sauropodomorphs were used (based on data from Mannion *et al.*, 2011), because specimen-level data permitting abundance counts are not currently available for theropods or ornithischians.

Subsampling methods mediate uneven fossil sampling by simulating an even sample across all data segments, although problems can occur when applied to datasets with highly heterogeneous taxic abundances (see Olszewski, 2004). We applied the most commonly used method in ecology (Gotelli & Colwell, 2001) and palaeobiology (e.g. Alroy, 2000; Fastovsky *et al.*, 2004; Mannion *et al.*, 2011), namely sample-based rarefaction, which simulates uniform sample size via subsampling. We also applied an alternative subsampling method: shareholder quorum subsampling (SQS), which simulates uniform 'coverage' (the sum of the frequencies of sampled species), as measured by Good's *u* (Alroy, 2010a,b). We applied both subsampling methods to the dinosaur dataset for the Late Triassic, Jurassic and Cretaceous time slices, using 30° palaeolatitudinal bins. We restricted subsampling to this coarse scale because of the need for large in-bin sample sizes for conducting meaningful subsampling analyses (Krebs, 1999). Analyses of dinosaur subclades (i.e. Theropoda, Sauropodomorpha and Ornithischia), narrower time slices, or finer latitudinal slices, were not possible because of the smaller in-bin sample sizes, which would have dramatically reduced the level of statistical support, thereby obfuscating diversity patterns

(Mannion *et al.*, 2011). All sample-based rarefaction analyses were implemented in PAST (Hammer *et al.*, 2001); SQS was carried out using the analysis tools available in *The Paleobiology Database* (see Appendix S1).

We also used multiple regression models with an underlying autoregressive model (see Benson & Mannion, 2011) in order to test the relationships between sampling, non-marine surface area (i.e. habitable land area) and taxic diversity of dinosaurs as a whole, and of the three major dinosaurian subclades (Theropoda, Sauropodomorpha and Ornithischia), in all nine time slices. Multiple regression models require larger numbers of data points (i.e. an increased number of latitudinal bins) to detect statistically significant relationships (Burnham & Anderson, 2001), so 10° latitudinal bins were used. Empty bins (bins containing zero DBCs or DBFs) were common at high latitudes and were deleted prior to analysis. We tested each multiple regression model using autoregressive models of orders zero, one and two to remove the potentially biasing effect of spatial autocorrelation (Burnham & Anderson, 2001). Data for the three dinosaurian subclades analysed separately were too sparse to yield meaningful analytical results in some time slices. Thus, they were only analysed for the 'middle' and 'late' Cretaceous. Similarly, data on Mesozoic birds (80 genera) were too few, and too patchy in spatiotemporal distribution, to analyse separately. All data were $\log_{10}$-transformed prior to analysis in R, version 2.10.1 (R Development Core Team, 2010).

Finally, we applied the modelling approach of Smith & McGowan (2007) to dinosaurian biodiversity in the 10° latitudinal bins remaining after exclusion. In this approach, a linear least squares regression model (the 'sampling model') of the expected relationship between sampling and observed taxic diversity is constructed by rank-ordering diversity and a sampling proxy. This model produces estimates (and 95% prediction confidence intervals) of the amount of taxic diversity expected in a latitudinal bin if sampling intensity is the sole predictor of observed taxic diversity. Subtraction of this 'modelled diversity estimate' from the actual observed diversity produces the 'residual' diversity not explained by sampling alone, which we interpret as a measure of actual ancient biodiversity. An additional measure of certainty is given by confidence intervals around the sampling model, calculated as ± 1.96 the residual standard error of the sampling model (Lloyd, 2011).

RESULTS

Raw dinosaur diversity (i.e. uncorrected for sampling) displays peaks in diversity at palaeotemperate latitudes (Fig. 1; see Appendix S2 in Supporting Information for results from additional time slices). In analyses testing the relationship between dinosaur latitudinal palaeodiversity and sampling, sampling proxies were included as statistically significant variables in the multiple regression models with the best (i.e. lowest) Akaike second-order corrected information criterion (AICc) scores for all three Mesozoic periods (Tables 1 & 2; see Appendix S2). This indicates that spatial heterogeneity in sampling intensity influences observed dinosaur palaeodiversity, confirming the rela-
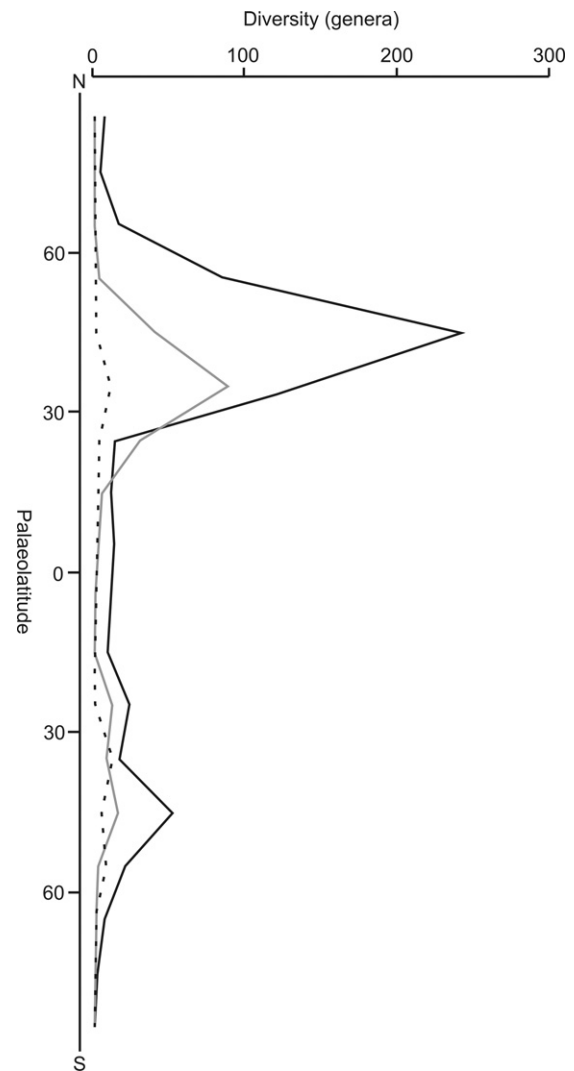

Figure 1 Raw (uncorrected) dinosaur diversity for the Late Triassic (dashed black line), Jurassic (grey solid line) and Cretaceous (black solid line).

tionship seen in temporal datasets (Barrett *et al.*, 2009; Butler *et al.*, 2011; Upchurch *et al.*, 2011). Following standardization for sample size, genus richness peaks at temperate palaeolatitudes (30–60°), contrasting with the modern-day tropical peak that characterizes the distribution patterns of most modern and extinct clades (Willig *et al.*, 2003; Hillebrand, 2004; Jablonski *et al.*, 2006). We obtained this result through both subsampling methods in the Late Triassic and Cretaceous (Fig. 2) and by the observation of 'residual diversity' resulting from the modelling approach of Smith & McGowan (2007) in all time slices (Figs 3 & 4; see Appendix S2 for results from additional time slices). In the Northern Hemisphere, Jurassic rarefied diversity shows no distinction between palaeotropical (0–30° N) and palaeotemperate (30–60° N) regions; however, SQS results reveal a palaeotropical peak. The Southern Hemisphere palaeotemperate peak is lower than that of either rarefied diversity value for the Northern Hemisphere (Fig. 2), but this asymmetry is not recovered

Table 1 Comparison of a priori generalized least squares regression models attempting to explain observed dinosaur palaeodiversity in 10° latitudinal bins during the three Mesozoic periods.

Model	R^2	P	AICc	ΔAIC	w_i	R^2	P	AICc	ΔAIC	w_i
	Late Triassic (316 occurrences)					Jurassic (1206 occurrences)				
Genus diversity ~ sampling 1 (DBF)	**0.53**	**0.02**	**15.39**	**0**	**0.28**	0.71	< 0.0001	7.51	9.3	< 0.01
Genus diversity ~ sampling 2 (DBC	**0.49**	**0.03**	**16.17**	**0.79**	**0.19**	**0.85**	**< 0.0001**	**−1.80**	**0**	**0.79**
Genus diversity ~ land area (NMA)	0.20	0.13	18.64	3.26	0.06	0.14	0.13	28.73	30.5	< 0.01
Genus diversity ~ DBF+NMA	**0.64**	**0.006**	**16.57**	**1.18**	**0.16**	0.73	< 0.0001	10.04	11.8	< 0.01
Genus diversity ~ DBC+NMA	**0.64**	**0.006**	**16.55**	**1.16**	**0.16**	**0.86**	**< 0.0001**	**0.89**	**2.7**	**0.20**
	Cretaceous (2323 occurrences)									
Genus diversity ~ DBF	0.30	0.01	14.12	10.80	< 0.01					
Genus diversity ~ DBC	0.52	0.0004	7.94	4.63	0.08					
Genus diversity ~ NMA	0.19	0.06	20.85	17.54	< 0.01					
Genus diversity ~ DBF+NMA	0.44	–	14.06	10.74	< 0.01					
Genus diversity ~ DBC+NMA	**0.70**	**< 0.0001**	**3.31**	**0**	**0.90**					

Of the two sampling proxies, dinosaur-bearing collections (DBCs) usually provided a better fit than dinosaur-bearing formations (DBFs). Land area estimates (non-marine area, NMA) were taken from Smith *et al.* (1994).

AIC, Akaike information criterion; AICc, Akaike second-order corrected information criterion; R^2, generalized R^2; w_i, Akaike weight.

Preferred models are indicated in bold. See Appendices S1 & S2 for further explanation and model fits for Mesozoic epochs and dinosaur subclades.

Table 2 Estimated best-fit model parameters for the three Mesozoic periods (see Table 1 for comparison of model fits).

	Late Triassic ($n = 10$)			Jurassic ($n = 16$)			Cretaceous ($n = 17$)		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Sampling only model (genus diversity ~ DBC)									
Intercept	−0.025	0.17	0.89	−0.33	0.12	0.017*	−0.068	0.15	0.66
Sampling (DBC)	0.50	0.14	0.006*	0.78	0.06	< 0.0001*	0.69	0.08	< 0.0001*
Sampling + NMA model (genus diversity ~ DBC+NMA]									
Intercept	−1.47	0.58	0.04*	−0.73	0.35	0.059	−0.79	0.24	0.005*
Sampling (DBC)	0.60	0.14	0.004*	0.78	0.06	< 0.0001*	0.70	0.06	< 0.0001*
Land area (NMA)	1.29	0.50	0.036*	0.38	0.32	0.25	0.72	0.21	0.0035*

See Appendix S2 for model parameters pertaining to Mesozoic epochs, dinosaur subclades, and other models (e.g. those using the DBF sampling proxy). Statistically significant values are indicated by an asterisk.

DBC, dinosaur-bearing collections; NMA, non-marine area (from Smith *et al.*, 1994); *n*, the number of time bins for each interval.

using SQS. For many intervals, including the Late Triassic and Cretaceous, we also recovered non-marine area as a significant factor in some of the best multiple regression models (Tables 1 & 2). This relationship was not observed in the Jurassic, for which the relationship between diversity and land area is weak (Table 2). This may result from the uneven sampling of Jurassic data, with no data available for several palaeolatitudinal bins (e.g. 0–20° S). However, land area explains a significant component of the latitudinal distribution of dinosaurs in the data-rich Cretaceous Period (Tables 1 & 2).

In examining temporal patterns within major dinosaurian clades (Theropoda, Sauropodomorpha and Ornithischia),

most statistical comparisons of sampling-corrected palaeo-latitudinal diversity between adjacent time slices yield a strongly significant, positive correlation. Thus, there is little change in the LBG from one time interval to the next. There is no correlation between the latitudinal distributions of ornithischian and sauropodomorph diversity in the 'middle' Cretaceous, and there is a strong negative correlation in the 'late' Cretaceous (Fig. 4). This results from high sauropodomorph diversity at low palaeotemperate latitudes (*c.* 40–50°) and high ornithischian diversity at higher palaeolatitudes (*c.* 50–70°); this pattern occurs in both hemispheres.
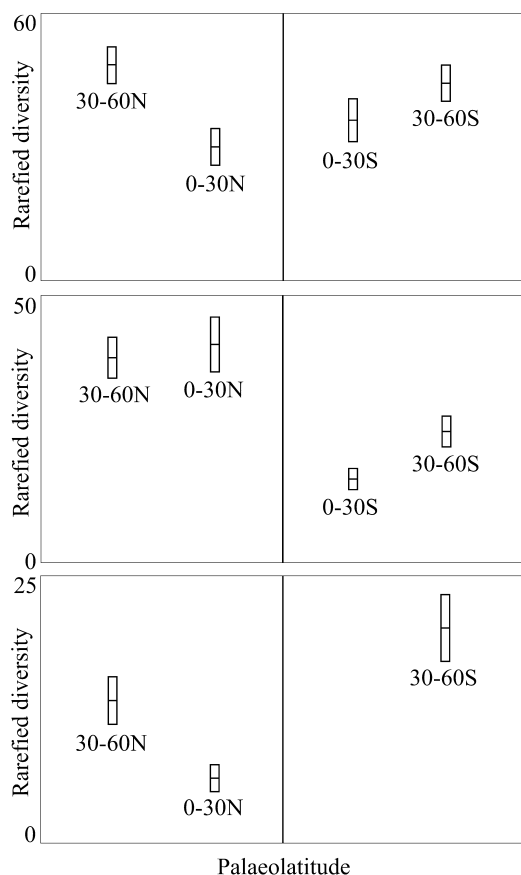
Figure 2 Rarefied dinosaur diversity for the Late Triassic (bottom figure), Jurassic (middle) and Cretaceous (top). Only latitudinal bins containing enough data points to implement rarefaction are shown. Each bar shows the subsampled diversity value for the latitudinal bin, as well as the associated 95% confidence intervals. Subsampled (rarefied) diversity values (*y*-axis) are the numbers of genera for each time bin based on the following sample sizes: Late Triassic (sample size = 31); Jurassic (sample size = 91); Cretaceous (sample size = 52). See Appendices S1 & S2 for additional information.

DISCUSSION

With the exception of one result (Jurassic subsampled diversity in the Northern Hemisphere), a palaeotemperate diversity peak occurs consistently across the entire span of dinosaurian evolutionary history (*c.* 160 Myr) and in both hemispheres, using subsampling and residuals (Figs 2 & 3). This Jurassic 'anomaly' may relate to the extremely high abundance of a small number of genera (e.g. *Allosaurus* and *Camarasaurus*), alongside a large number of singleton taxa, resulting in a highly heterogeneous distribution. The Jurassic also displays asymmetrical diversity when rarefaction is implemented, with the Southern Hemisphere palaeotemperate peak lower than that of either diversity value for the Northern Hemisphere. However, hemispherical asymmetry in terms of total diversity is common amongst modern day organisms and there are also a number of instances of asymmetrical gradients (e.g. Dunn *et al.*, 2009).

There are two possible factors that might produce an artefactual palaeotemperate peak in dinosaur diversity. First, modern geographical areas corresponding to Mesozoic temperate palaeolatitudes might have been sampled more intensively than palaeotropical regions. However, the consistency of our results over many time slices and in both hemispheres, despite cross-latitudinal continental drift, indicates that this has not occurred. This consistency also suggests that the possible bias relating to geographical variation in origination/extinction rates does not affect our results. Second, individual fossil collections from temperate palaeolatitudes might be inherently 'better' (i.e. yielding more, or better preserved, fossils, and thus more dinosaur taxa) than palaeotropical collections. However, analysis of collection 'quality' (i.e. the total number of individuals reported from each dinosaur-bearing collection) demonstrates that some time slices show 'better' collections in the palaeotropics and others in the palaeotemperate zones (see Appendix S2 in Supporting Information), also suggesting that systematic latitudinal preservation bias is absent. As a result, we consider the recovery of this palaeotemperate diversity peak to be a genuine and analytically robust pattern.

The results from our clade analyses show that Late Cretaceous sauropods were more diverse at lower palaeolatitudes than ornithischians. This suggest that the Late Cretaceous 'north–south' divide, in which sauropods dominate Gondwanan faunas and ornithischians dominate Laurasian faunas (Bonaparte & Kielan-Jaworowska, 1987), may partly result from the predominance of sampling of ornithischian-poor, low-palaeolatitude deposits in the Southern Hemisphere. Despite this, sauropods do seem to have been genuinely depauperate in the Northern Hemisphere at this time (Fig. 4). The sum of sauropod and ornithischian diversity is strongly correlated with theropod diversity in the middle–late Cretaceous, more strongly so than when either clade is compared independently. Thus, theropod diversity and the total diversity of major herbivorous clades both conformed to a general 'dinosaurian' LBG (Fig. 4), suggesting that the disparate Late Cretaceous ornithischian and sauropod LBGs resulted from geographical partitioning. Increased faunal heterogeneity in the Late Cretaceous may reflect the advanced stages of continental fragmentation (Smith *et al.*, 1994), or clade-specific responses to increasing latitudinal climatic zonation as a result of reduced seasonality (Janzen, 1967; Kozak & Wiens, 2007), combined with different environmental and/or dietary preferences for each clade (Butler & Barrett, 2008). Interestingly, Late Cretaceous crocodyliforms show a similar pattern to sauropods, exhibiting high diversity at low latitudes and low diversity, including the absence of the major clade Notosuchia, at higher latitudes (Carvalho *et al.*, 2010).

The continuity of a palaeotemperate peak in dinosaur diversity throughout the Mesozoic indicates that this pattern is not controlled by climatic fluctuations, such as the middle Cretaceous greenhouse interval (see also Allison & Briggs, 1993; Rose *et al.*, 2011). It is possible that the Mesozoic climatic gradient was much weaker than today (e.g. Hay, 2008; Littler *et al.*, 2011) and therefore exerted less control on spatial biodiversity pat-
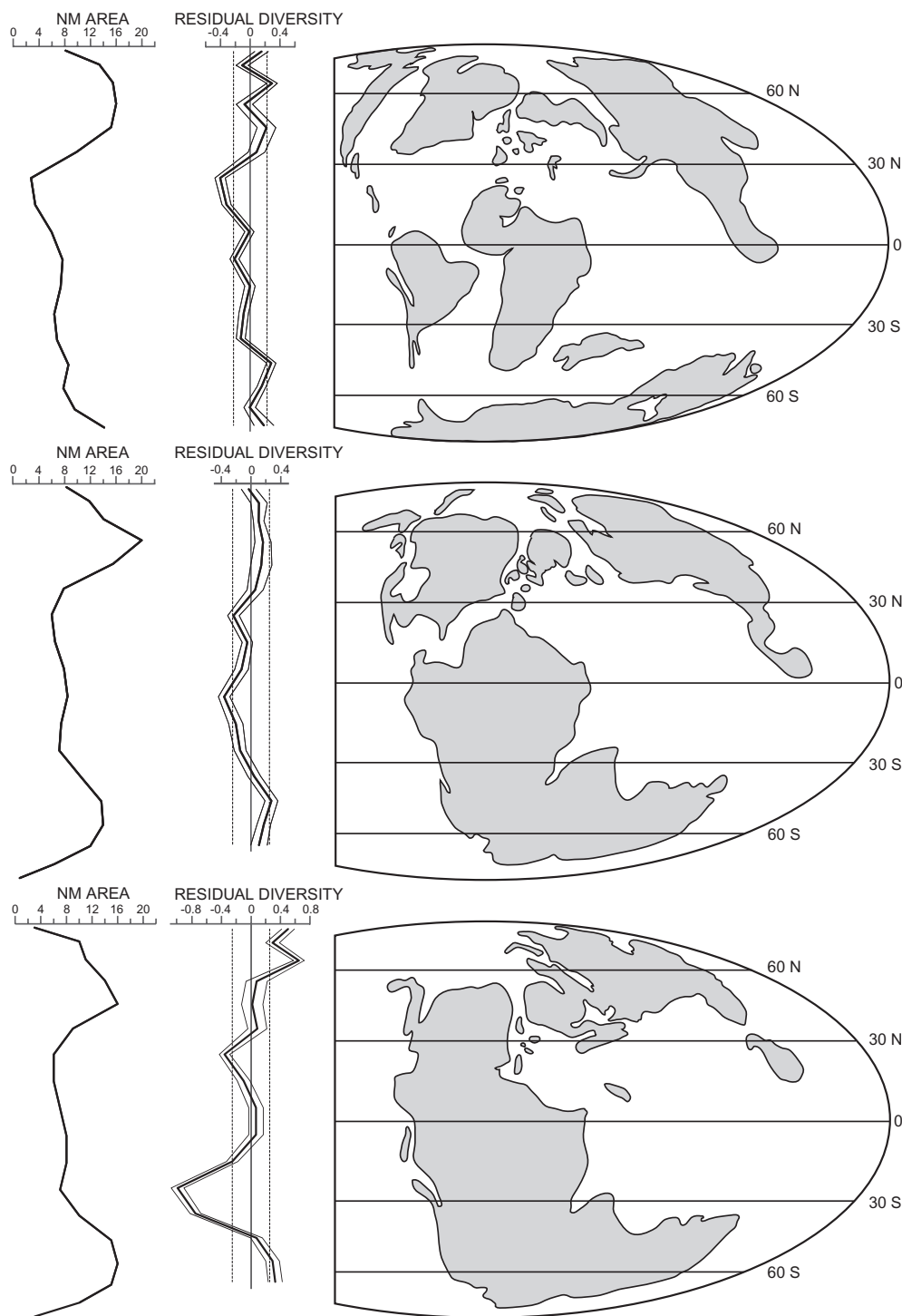
Figure 3 Residual dinosaur diversity (thick solid lines) after controlling for numbers of dinosaur-bearing collections (DBCs) and formations (DBFs), plotted against non-marine area (NM area) and palaeogeographical reconstructions (using Mollweide projections) for the Late Triassic (bottom), Jurassic (middle) and Cretaceous (top). 95% prediction confidence intervals (dashed lines) and confidence intervals around the sampling model calculated as ± 1.96 the residual standard error of the sampling model (thin solid lines) are also included in the plots. See Tables 1 & 2 for regression model results.

terns. This flattened climatic gradient thereby enabled areal extent to act as the primary control on the Mesozoic LBG.

Unlike the 'out of the tropics' diversification model proposed for several invertebrate groups (Jablonski *et al.*, 2006), there is no evidence that the palaeotropics acted as a cradle for dinosaur diversity at any point in their evolutionary history: the earliest known representatives of most clades are from temperate palae-olatitudes. As well as potentially driving the diversity peak at
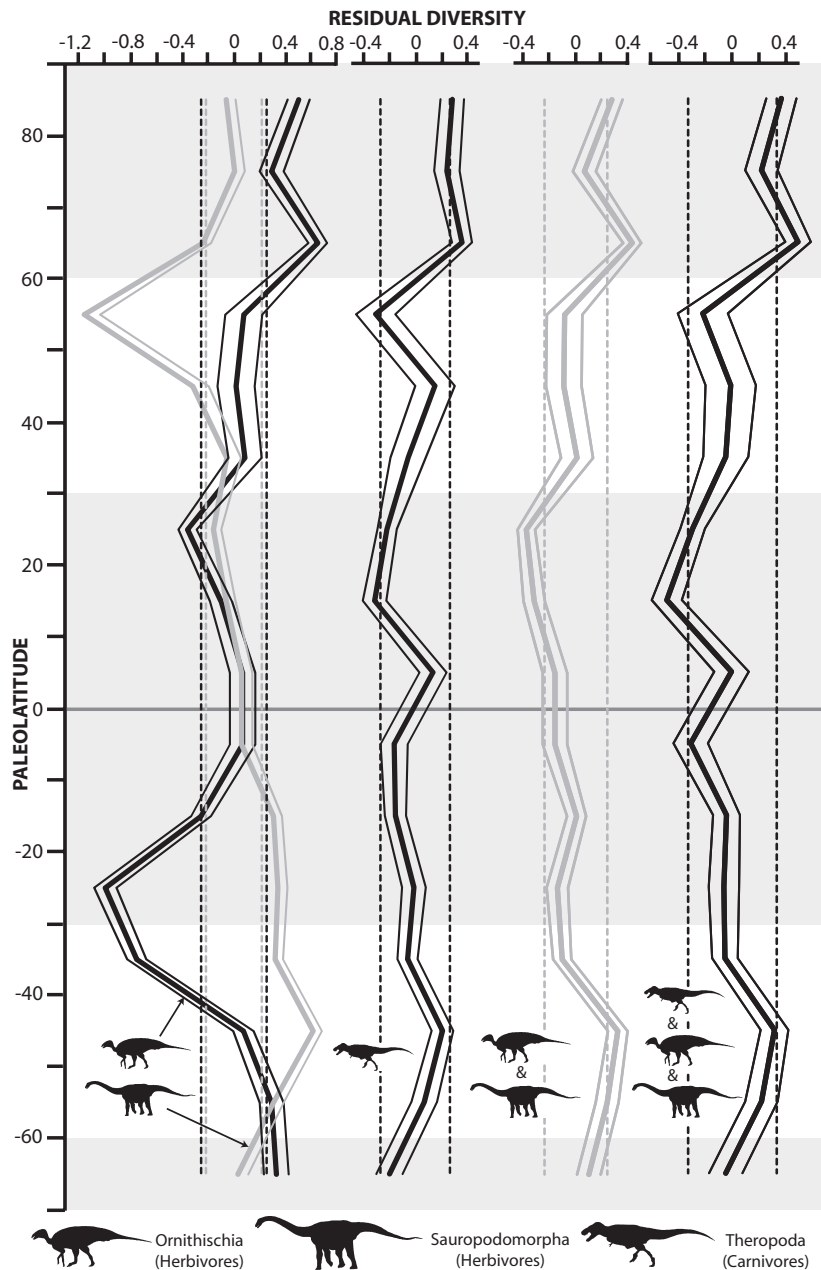
Figure 4 Late Cretaceous residual diversity for dinosaur subclades after controlling for numbers of dinosaur-bearing collections (DBCs) and formations (DBFs). The left plot shows ornithischian diversity (black solid line) plotted against sauropod diversity (grey solid line); the second plot shows theropod diversity (black solid line); the third plot shows a combined diversity curve for ornithischians plus sauropods (herbivores) (grey solid line); the far right plot shows a combined diversity curve for all three dinosaur clades (black solid line). 95% prediction confidence intervals (dashed lines) and confidence intervals around the sampling model calculated as ±1.96 the residual standard error of the sampling model (thin solid lines) are also included in the plots. See Appendix S2 for regression model results.

temperate palaeolatitudes, the preponderance of palaeotemperate land area may also have facilitated the gigantic size attained by many dinosaurs (Burness *et al.*, 2001).

The conformity of post-Eocene birds to the 'standard' LBG (Hawkins *et al.*, 2006, 2007; Weir & Schluter, 2007) contrasts dramatically with Mesozoic dinosaurs (which include birds). Unfortunately, data on Mesozoic birds are too sparse to yield meaningful results when analysed separately. However, the post-

Eocene pattern may indicate increased Cenozoic origination rates and migrations (see Louchart, 2008) into the tropics, and/or a reduction in extratropical speciation rates as a consequence of increased seasonality (Eldrett *et al.*, 2009; Archibald *et al.*, 2010) and a strengthened climatic gradient (Bijl *et al.*, 2009) across the Eocene/Oligocene boundary (*c.* 34 Ma). Terrestrial insects have also been shown to only display the 'standard' LBG after the Eocene (Archibald *et al.*, 2010).

As exemplar organisms for studying terrestrial biodiversity over extended time-scales, dinosaurs indicate that modern ecological 'rules' cannot be uncritically extrapolated into deep time. Indeed, our results extend over a 160-Myr interval, whereas evidence for the modern day LBG on land appears restricted to the last 30 Myr. These results suggest that the distribution of land area is the primary control on the terrestrial LBG during times of a weakened climatic gradient. Finally, this work provides an important new context for the geographical distribution of diversity in the modern terrestrial realm, one that suggests that a significant recalibration took place in the middle Cenozoic.

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SUPPORTING INFORMATION

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Appendix S1 Supplementary Materials and Methods.
Appendix S2 Dataset.

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BIOSKETCH

Our research group investigates macroevolutionary patterns in vertebrate biodiversity, with particular emphasis on Mesozoic ecosystems and the impact of sampling biases on observed diversity in the fossil record.

Author contributions: P.D.M., R.B.J.B., R.J.B. and M.T.C. compiled the data. P.D.M., R.B.J.B. and R.J.B. carried out the analyses. P.D.M. and R.J.B. prepared the figures. All authors discussed the results and contributed to writing the manuscript.

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