

The spatiotemporal distribution of Mesozoic dinosaur diversity

Philip D. Mannion

Department of Earth Sciences, University College London, London, WC1E 6BT, UK

Author for correspondence (Email: philipdmannion@gmail.com)

Abstract

Much of our view on Mesozoic dinosaur diversity is obscured by biases in the fossil record. In particular, spatiotemporal sampling heterogeneity affects identification of the timing and geographical location of radiations, the recognition of the latitudinal diversity gradient, as well as interpretation of purported extinctions, faunal turnovers, and their drivers, including the Early Jurassic Jenkyns Event and across the Jurassic/Cretaceous boundary. The current distribution of sampling means it is impossible to robustly determine whether these ‘events’ were globally synchronous and geologically instantaneous, or spatiotemporally staggered. Accounting for sampling heterogeneity is also paramount to reconciling notable differences in results based on sampling-standardised dinosaur species richness versus reconstructions of diversification rates, particularly with regards to the lead-up to the Cretaceous/Paleogene mass extinction. Incorporation of a greater proportion of stratigraphically well-resolved dinosaurs into analyses is also imperative and must include the substantial Mesozoic radiation of birds. Given the relative rarity of temporally successive, well-sampled spatial windows, it remains possible that dinosaur species richness and diversification rate showed little change after the clade’s initial radiation until the Cretaceous/Paleogene boundary. However, better understanding of underlying sampling, combined with a holistic approach to reconstructing dinosaur diversity and diversification, is an important step in testing this hypothesis.

Keywords: Common cause hypothesis, Dinosauria, Diversity, Extinction, Latitudinal diversity gradient, Mesozoic

1. Introduction

Dinosaurs first appear in the fossil record in the Middle or Late Triassic (Brusatte et al. 2010; Langer et al. 2010, 2018; Nesbitt et al. 2013), approximately 230 million years ago (Ma). They diversified and dispersed to become a cosmopolitan radiation, dominating Mesozoic terrestrial ecosystems (e.g. Benson 2018; Benton 2024) (Fig. 1A–C). Dinosaurs also survived two mass extinction events (Brusatte et al. 2010, 2015; Langer et al. 2010), and today represent one of the most speciose clades of terrestrial vertebrates (Jetz et al. 2012). Understanding how, when, and why dinosaurs diversified remains a central macroevolutionary question, as does the nature of the extinction of all non-neornithine lineages at the end of the Mesozoic, 66 Ma (Brusatte et al. 2015; Benson 2018; Benton 2024).

A key component of addressing this centres on understanding how dinosaur diversity fluctuated through the Mesozoic. Diversity can be defined in numerous ways, but this contribution focuses on taxonomic rather than ecomorphological diversity, i.e. species richness. Many dinosaur studies focus on genus, rather than species diversity; however, given that ~99% of dinosaur genera are monospecific (Barrett et al. 2009), the unit of species is used

herein for consistency throughout, even when the original study estimated diversity at the genus level. Globally, the number of species at any time is dependent on diversification rate, i.e. the net balance of origination and extinction, with dispersal also an important factor at regional scales. As such, diversification rate is an additional important measure when discussing dinosaur species richness.

Several authors have attempted to quantitatively estimate how many dinosaur species were alive during the Mesozoic, using a range of methods, including coverage and richness extrapolators. These estimates range from 900 to 3400 species in total during this 160 million year time interval (Dodson 1990; Russell 1995; Wang and Dodson 2006; Starrfelt and Liow 2016). By contrast, based on a species–area relationship, Le Loeuff (2012) estimated that 628–1078 non-avian dinosaur species were alive solely in the late Maastrichtian, which, if extrapolated, would imply an order of magnitude higher count for Mesozoic diversity compared to other estimates (Benson 2018). Based on data in *The Paleobiology Database* (<https://paleobiodb.org/>), approximately 1550 dinosaur species are currently recognised as valid for the entirety of the Mesozoic (Fig. 1D), of which ~225 species are birds. Using the more conservative estimate range, this would mean that between 45% and 100% of Mesozoic dinosaur species have already been discovered (with potentially a large number of currently recognised species representing *nomina dubia*), whereas extrapolations based on the Le Loeuff (2012) estimate suggest that less than 10% of species have been discovered. This dichotomy in estimates provides a useful platform for considering how Mesozoic dinosaur diversity, and our sampling of it, varies through time and space.

2. Reconstructing patterns in dinosaur diversity and diversification

In addition to trying to calculate how many species of dinosaurs were alive during the Mesozoic, a number of studies have sought to determine how the group's diversity varied through time. The earliest analyses reconstructed this by counting the number of species in each time interval (Sloan et al. 1986; Dodson 1990; Haubold 1990; Hunt et al. 1994). However, reading the fossil record at face value had long been recognised as problematic, with apparent peaks and troughs in diversity through time potentially merely artefacts of heterogeneous sampling (Raup 1972; see below).

2.1. The impact of sampling

Unsurprisingly, the discovery and description of new species has an effect on reconstructions of dinosaur diversity and diversification (Tarver et al. 2011; Tennant et al. 2018; Benton 2024). This includes the extension of clades backwards and forwards in time, as well as in geographic spread (e.g. Pol and Rauhut 2012; Xu et al. 2018; Longrich et al. 2021), but increases in sampling more broadly have a notable impact on overall patterns, particularly for spatiotemporal windows that have been historically under-sampled (Benton 2008; Tennant et al. 2018; Cashmore et al. 2020; Raja et al. 2022).

A suite of underlying sampling biases influences the available fossil record (Nanglu and Cullen 2023) (Fig. 2). Of these, perhaps the most obvious and pervasive pertains to the spatial distribution of sampling, both in terms of the availability and accessibility of suitable sedimentary outcrop (Wang and Dodson 2006; Barrett et al. 2009), but also with regards to collection effort (Upchurch et al. 2011) (Figs 1, 2A), which shows a clear socioeconomic bias towards high and upper-middle-income countries (Raja et al. 2022). The spatial coverage of

the sampling window within any time interval species will therefore dictate the diversity that can be observed (Fig. 2A). Consequently, studies of dinosaur diversity through time that have typically relied on global estimates are problematic, given that the 'global' sample in each time interval varies substantially in terms of spatial extent (Close et al. 2017; Benson et al. 2021). These problems also encompass issues pertaining to data absence, i.e. whether a species was genuinely absent from a spatiotemporal window, or if it is merely not sampled (=sampling failure), which affects estimates of species richness, origination, and extinction (Chiarenza et al. 2019).

A number of studies have demonstrated statistically significant correlations between dinosaur subclades and the type of depositional environment from which specimens are most frequently recovered (Butler and Barrett 2008; Mannion and Upchurch 2010a, 2011; Lyson and Longrich 2011; Arbour et al. 2016; Sales et al. 2016). As such, if our spatiotemporal sampling is not environmentally homogeneous, then reconstructions of diversity and diversification patterns might also be affected by this, with some clades unsampled (Fig. 2B). As an additional complication, the environment of deposition also has a taphonomic effect, with certain settings more suitable for preservation, and these are not necessarily consistent across clades, especially given substantial disparity in body size and skeletal fragility (Brocklehurst et al. 2012; Gardner et al. 2016; Cashmore and Butler 2019; Woolley et al. 2024).

The completeness of skeletons also affects our interpretation of dinosaur diversity and diversification patterns (Fountaine et al. 2005; Mannion and Upchurch 2010b; Brocklehurst et al. 2012). Body size plays a role with regards to completeness (Fig. 2B), with a bias against the preservation of smaller-sized taxa (approximately <70 kg), except those discovered within Lagerstätten deposits (Brocklehurst et al. 2012; Brown et al. 2013, 2022; Benson 2018; Cashmore and Butler 2019). Among larger-bodied dinosaurs, there is less of a clear correlation between size and completeness (Cashmore et al. 2020; Leach et al. 2021). Low levels of completeness can result in unrecognized diversity because of an inability to identify new species (Fig. 2B). Conversely, it can also lead to an inflation in diversity through the erection of synonymous species based on non-overlapping elements (Mannion and Upchurch 2010b; Cashmore et al. 2021). Furthermore, species known from highly incomplete specimens are less likely to be incorporated in phylogenetic analyses (Fig. 2B) and their placement is often highly labile when they are included. As such, they are often excluded from phylogeny-based diversification analyses.

The choice of time bin duration appears to have little effect when evaluating large-scale diversity dynamics throughout the Mesozoic (e.g. Butler et al. 2011), but its impact is more apparent at finer temporal scales (Dean et al. 2020; Maidment 2023), such as when attempting to decipher patterns in the lead-up to the end-Cretaceous extinction (see below). One particular problem is that non-contemporaneous stratigraphic units (and by extension the species within them) are often lumped together, giving misleading time-averaged notions of species richness that can also have notable effects on reconstructions of spatial diversity patterns, including identification of endemism (Vavrek and Larsson 2010; Fowler 2017; Chiarenza et al. 2019; Maidment et al. 2021). Cashmore et al. (2020) re-evaluated temporal patterns in fossil record completeness of sauropodomorph dinosaurs, testing for the effect of ten years of new data on the results of an earlier study (Mannion and Upchurch 2010b). They demonstrated that the most substantial change resulted from the revision of stratigraphic ages of fossil occurrences, which potentially has important ramifications for diversity analyses

given that equivalent corrections have yet to be made for datasets utilized for theropods and ornithischians.

2.2. Analytical solutions to sampling heterogeneity?

Although a small number of authors have continued to take a literal reading of the dinosaur fossil record (Sullivan 2006; Archibald 2014; Han et al. 2022), most subsequent studies have attempted to address the critical issue of sampling heterogeneity. This includes the incorporation of phylogenetic relationships to capture unsampled ghost lineages (Sereno 1997, 1999; Weishampel and Jianu 2000; Upchurch and Barrett 2005; Lloyd et al. 2008; Barrett et al. 2009; Mannion et al. 2011; Langer and Godoy 2022), the calculation of residuals from a modelled relationship between diversity and a proxy for sampling (Barrett et al. 2009; Butler et al. 2011; Mannion et al. 2011; Upchurch et al. 2011; Benson and Mannion 2012; Brocklehurst et al. 2012; Lloyd 2012), and application of a richness extrapolator (Starrfelt and Liow 2016). However, all of these approaches are problematic in that they do not appear to resolve underlying sampling issues, especially those pertaining to spatial and temporal heterogeneity (Lane et al. 2005; Benton 2015; Brocklehurst 2015; Sakamoto et al. 2017; Close et al. 2018; Dunhill et al. 2018).

This has left two primary approaches that authors have used to reconstruct dinosaur diversity: sampling standardisation and estimates of diversification rates. Fastovsky et al. (2004) were the first to apply sampling standardisation to estimate dinosaur species richness, demonstrating that some of the face-value patterns described by earlier authors were sampling artefacts. Sampling-standardisation approaches have since become a mainstay of attempts to reconstruct dinosaur diversity (Mannion et al. 2011, 2012; Vieira et al. 2014; Brusatte et al. 2015; Benson et al. 2016; Tennant et al. 2016, 2018; Close et al. 2017, 2020; Dean et al. 2020), with most analyses using some form of shareholder quorum subsampling (SQS), also known as coverage-based rarefaction (Alroy 2010; Chao and Jost 2012). However, estimating species richness through time in this way does not allow us to determine whether fluctuations are a result of changes in origination or extinction rate, or both. A second subset of analyses has therefore focused on reconstructing diversification rates, either based on fossil occurrences, using SQS (Tennant et al. 2016) or PyRate (Condamine et al. 2021; Langer and Godoy 2022), which incorporates a measure of sampling rate, or via analyses of phylogenetic trees (Lloyd et al. 2008; Sakamoto et al. 2016, 2021; Bonsor et al. 2020; Yu et al. 2021; Černý et al. 2022; Langer and Godoy 2022; Allen et al. 2024).

As outlined in the preceding section, there is a substantial problem with estimating 'global' diversity. This issue was identified in earlier studies of the marine realm (Jackson and Johnson 2001; Vermeij and Leighton 2003), but was not explicitly considered in initial analyses of dinosaur diversity. Whereas some studies attempted to ameliorate this issue through the reconstruction of regional (=continental) diversity curves (Upchurch et al. 2011; Benson et al. 2013, 2016; Brusatte et al. 2015; Tennant et al. 2016, 2018), subsequent analyses have incorporated a spatial component to the subsampling approach (Close et al. 2017, 2020). Neither of these considerations has yet to be fully factored into reconstructions of dinosaur diversification rates (Bonsor et al. 2020; Condamine et al. 2021; Černý et al. 2022; Allen et al. 2024).

A remaining problem that neither type of analysis can ameliorate is the issue of genuine versus pseudo-absence. This has been recently addressed through the application of ecological niche modelling, in which dinosaur habitat suitability is projected into space,

shedding light on whether unsampled regions could have hosted dinosaur species (Chiarenza et al. 2019, 2020, 2022). However, although this can aid in determining whether an apparent diversity trough represents a genuinely depauperate spatiotemporal window, it cannot necessarily be used as a proxy for species richness (Benton 2024).

3. Mesozoic dinosaur diversity and diversification

Whereas debate often centres on whether or not extinction events are genuine, one often neglected impact of spatiotemporal sampling heterogeneity is the possible misidentification of radiations. Well-sampled spatiotemporal intervals with high taxonomic diversity of a particular clade are often regarded as capturing genuine radiations, with such an interpretation regularly supported quantitatively by biogeographical analysis. Below, several purported radiations and extinctions during the Mesozoic are discussed in this light. Given the issues raised above, including the relative rarity of temporally successive, well-sampled spatial windows (Fig. 1D), it remains possible that Mesozoic dinosaur diversity and diversification rate showed little in the way of change after the clade's initial radiation (see also Benson et al. 2016; Close et al. 2017, 2020; Benson 2018).

3.1. Did dinosaurs originate in the early Late Triassic of southern Gondwana?

The stratigraphically earliest known unequivocal dinosaurs come from the upper Carnian (lower Upper Triassic) Ischigualasto and Santa Maria formations of Argentina and Brazil, respectively (Langer et al. 2018; Desojo et al. 2020), as well as the Carnian Pebbly Arkose Formation of Zimbabwe (Griffin et al. 2022) (Fig. 3A). As a result of the high taxonomic and morphological diversity of dinosaurs in these formations, alongside their absence from Laurasia until the Norian, nearly all studies regard southern Gondwana as the likely centre of origin for the clade (Marsola et al. 2019). However, this does not consider the possibility that unsampled contemporaneous regions (Fig. 1) might also have harboured dinosaurs. Perhaps more importantly, it does not take into account that dinosaurs presumably evolved prior to the late Carnian, as evidenced by putative earlier members (e.g. Nesbitt et al. 2013), alternative phylogenetic topological arrangements (e.g. Baron et al. 2017; Fonseca et al. 2024), and divergence time estimates (Lloyd et al. 2016), and thus potentially originated elsewhere. These considerations also potentially complicate interpretations of the Carnian Pluvial Event as a driver of early dinosaur diversification (Bernardi et al. 2018; Mancuso et al. 2020).

3.2. The Triassic/Jurassic boundary

Although recognised as the one of the 'Big 5' Phanerozoic mass extinctions, dinosaurs appear to have passed through the Triassic/Jurassic (T/J) boundary relatively unscathed. There is little evidence for substantial losses in dinosaur diversity or a reduction in diversification rate across the boundary, with some studies indicating that the extinction event paved the way for the clade's subsequent radiation (Brusatte et al. 2010; Langer et al. 2010). Nevertheless, most analyses have been based on a 'global' appraisal of the T/J transition (e.g. Barrett et al. 2009; Sakamoto et al. 2016; Langer and Godoy 2022). Sampling within the time intervals either side of the boundary is spatially disparate (e.g. Upchurch et al. 2011; Benson et al. 2016; Tennant et al. 2018) (Figs. 1D, 3B), meaning that it is essentially

impossible to confidently determine dinosaur diversity dynamics across the T/J boundary. Nevertheless, the survival of most dinosaur lineages across the T/J boundary suggests that the clade was less affected by the extinction event than other taxonomic groups, which in itself remains an important unanswered conundrum.

3.3. The Jenkyns Event and Middle Jurassic dinosaur radiation

A number of studies have discussed dinosaur diversity patterns during the late Early to Middle Jurassic. These contributions have highlighted a faunal turnover tied to heightened activity of the Karoo-Ferrar Large Igneous Province in the early Toarcian (the Jenkyns Event), followed by the subsequent radiation of multiple lineages (Rauhut et al. 2016; Pol et al. 2020; Reolid et al. 2022). However, although there is a clear difference in taxonomic composition between late Early Jurassic and Middle Jurassic dinosaurs (e.g. from ‘basal’ sauropodomorph- to eusauropod-dominated faunas), there are also substantial spatiotemporal sampling gaps during this transition (Figs. 1D, 3C), and very few dinosaur-bearing deposits can be unequivocally dated to the early Middle Jurassic (Mannion et al. 2011; Upchurch et al. 2011; Starrfelt and Liow 2016). As such, it is possible that the apparent faunal turnover was neither globally synchronous, nor geologically rapid, and that the rise of ‘derived’ dinosaur lineages that went on to dominate ecosystems in the Middle–Late Jurassic onwards was spatiotemporally staggered.

3.4. Is diversity in the Late Jurassic unusually high?

The Late Jurassic is often highlighted as the heyday of sauropod dinosaur diversity (e.g. Upchurch and Barrett 2005). Much of this derives from the high species richness recorded in the Upper Jurassic Morrison Formation of the USA (Figs. 1D, 3D), particularly with regards to diplodocids, and which is frequently cited as evidence for a North American origin of this clade (e.g. Whitlock and Wilson Mantilla 2020). However, this formation is essentially a form of Lagerstätte, with a long history of dinosaur fossil collection stemming back to the late 19th Century. Interpreting its high diversity at face value is similar to regarding the rich avialan fossil record preserved in the late Early Cretaceous Jehol Biota (e.g. Zhou 2014) as capturing the actual diversification of birds. In both cases, these represent exceptional windows into diversity within a particular spatiotemporal interval; however, there is no *a priori* reason to assume that species richness was not comparable in other spatiotemporal windows and thus that these radiations could not have happened earlier and/or elsewhere. This reasoning is borne out by analysis of alpha diversity, which shows broadly consistent upper levels of local richness for dinosaurs throughout much of the Mesozoic (Close et al. 2019).

Furthermore, new species are still being discovered in the Morrison Formation (e.g. van der Linden et al. 2024), as well as from other stratigraphic units and localities generally regarded as well-sampled for dinosaurs, such as the latest Cretaceous Dinosaur Park and Hell Creek formations of North America and the contemporaneous Nemegt Formation of Mongolia (e.g. Brown et al. 2013; Funston et al. 2018). Small-bodied dinosaur species, including avialans, are also typically exceedingly rare in many formations otherwise thought to be well sampled, meaning that substantial subsets of these ecosystems are missing (e.g. Brown et al. 2013, 2022; Benson 2018). When even collector curves from stratigraphic units with historically long fieldwork programmes and extensive fossil records are yet to approach

an asymptote (e.g. Funston et al. 2018), this indicates that the diversity of other formations is likely to be heavily undersampled.

3.5. Was there a mass extinction at the Jurassic/Cretaceous boundary?

Originally regarded as a mass extinction event, dinosaur diversity patterns across the Jurassic/Cretaceous (J/K) boundary remain uncertain (Tennant et al. 2016, 2017; Benton 2024). This interval perhaps best exemplifies many of the issues surrounding sampling bias and heterogeneity outlined above, as well as how our ideas of dinosaur diversity can change.

As an example of the problems associated with deciphering this interval, diplodocids were initially thought to have gone extinct at the J/K boundary (Upchurch & Barrett, 2005), following their apparent Late Jurassic boom. The discovery of Cretaceous Gondwanan representatives showed that this was incorrect (Gallina et al. 2014), but their continued absence from the Cretaceous Laurasian record suggests that they might have become extirpated at the J/K boundary in the Northern Hemisphere. Until recently, the dearth of pre-Barremian terrestrial deposits in North America meant that it was impossible to determine whether the Morrison Formation diplodocids died out at the J/K boundary or at some point in the subsequent 20 million years. However, the revised chronostratigraphic framework for the unconformably overlying Yellow Cat Member of the Cedar Mountain Formation in Utah (Fig. 3D) dates this stratigraphic unit to the upper Berriasian–Valanginian, substantially closing this temporal gap (Kirkland et al. 2024). Given the preservation of other sauropod clades in the Yellow Cat Member, this suggests that the absence of diplodocids is genuine, and provides some support that the demise of North American representatives of the clade occurred at or close to the J/K boundary (Kirkland et al. 2024).

As demonstrated in this one example, new discoveries, revised stratigraphy, and consideration of regional rather than ‘global’ diversity, can all contribute to our interpretation of this one time interval. Currently, our understanding of dinosaur diversity across the J/K interval hinges primarily on the European record (Figs. 1D, 3D), which provides evidence for a prolonged period of turnover, rather than a discrete extinction event (Tennant et al. 2016). It remains to be seen whether changes in dinosaur diversity were global and/or synchronous, which also makes it difficult to hypothesize which of the contemporaneous environmental perturbations might have been responsible (Tennant et al. 2017).

3.6. Turnover and diversification in the Late Cretaceous

Evidence for a faunal turnover in dinosaur communities during the Cenomanian–Turonian (early Late Cretaceous) interval (Fig. 1D) has been presented by several authors (e.g. Coria and Salgado 2005), tied to environmental perturbations resulting from Oceanic Anoxic Event 2 and the Cretaceous Thermal Maximum (see Benson et al. 2013), and potentially linked to the angiosperm radiation (see Barrett 2014; Benton 2024). Our understanding of this interval is affected by similar problems as the Early–Middle Jurassic interval (see above), including poor chronostratigraphic constraint in some regions. This is exacerbated by a proportional decrease in terrestrial sedimentary outcrop as a result of the Turonian sea-level highstand, with limited global sampling until the Campanian (Mannion et al. 2011; Benson et al. 2013). Taking sampling heterogeneity into consideration, there is currently no evidence for a globally synchronous or geologically instantaneous faunal turnover during the Cenomanian–Turonian interval (Eaton et al. 1997; Butler et al. 2011; Upchurch et al. 2011; Benson et al. 2013), with

little change in reconstructed diversification rates at this time either (Sakamoto et al. 2016; Condamine et al. 2021). Increasing chronostratigraphic resolution of relevant successions (Krause et al. 2020; Tucker et al. 2023; Kirkland et al. 2024) should allow this to be more robustly tested in the future.

Gates et al. (2012) suggested that orogenic events led to dinosaur diversification in the Late Cretaceous of North America, and mountain-building tectonic events have been proposed as an important mechanism in driving mammalian diversity dynamics in both the Mesozoic and Cenozoic (e.g. Weaver et al. 2024). Although basin- and larger-scale tectonics almost certainly would have impacted dinosaur diversity, e.g. through stimulating allopatric speciation and generating habitat heterogeneity (Gates et al. 2012; Vavrek 2016; Weaver et al. 2024), it has a dual role on sampling, whereby increased sedimentation and run-off would have led to heightened fossil preservation potential and thus greater observed diversity (Chiarenza et al. 2019; Maidment et al. 2021) (Fig. 2C). This 'common cause' scenario has been well-studied with regards to the effects of sea level (Fig. 2C), including for Mesozoic dinosaurs (Butler et al. 2011; Tennant et al. 2016), but is yet to be evaluated at a comparable level for tectonism.

3.7. Sudden versus gradual extinction in the latest Cretaceous?

Despite a 160 million year record, much of the published literature on dinosaur diversity has focused on the last ten million years of the Mesozoic. This has centred on whether or not dinosaurs were in long-term decline prior to the demise of all non-neornithine members of the group, as well as the cause(s) of their extinction (see reviews in Sarjeant and Currie 2001; Archibald 2014; Brusatte et al. 2015; Chiarenza and Brusatte 2023; Benton 2024). Studies that have taken the fossil record at face value have typically supported a gradual extinction (Sloan et al. 1986; Dodson 1990; Sarjeant and Currie 2001; Sullivan 2006; Han et al. 2022) (Fig. 1D), whereas most sampling-standardised approaches indicate little evidence for diversity decline prior to K/Pg boundary, implying that the extinction was geologically instantaneous (Fastovsky et al. 2004; Brusatte et al. 2015). By contrast, reconstructions of dinosaur diversification rate typically support longer-term decline (Sakamoto et al. 2016, 2021; Condamine et al. 2021; though see Bonsor et al. 2020; Černý et al. 2022; Allen et al. 2024).

This discussion has been dominated by studies of the well-sampled North American record, for which detailed work on local sections has shaped our views on dinosaur diversity dynamics in the lead-up to the end-Cretaceous extinction (e.g. Sheehan et al. 2000; Pearson et al. 2002; Mallon et al. 2012; Eberth et al. 2013). These rich study systems provide a template for how a detailed understanding of regional diversity, based on high-quality, well-constrained datasets, can be scaled to infer global dynamics. Data from other regions can potentially be brought to bear on this topic, with increased sampling and stratigraphic resolution in the last decade, particularly for Asia, Europe, and South America (e.g. Jesus Faria et al. 2015; Vila et al. 2016; Han et al. 2022), which will enable us to eventually test whether the North American pattern represents a global signal. However, analyses of these regions also need to account for spatiotemporal sampling heterogeneity.

Uncertainty in the temporal nature of the extinction has also led to a long-standing debate with regard to the kill mechanism. Whereas the bolide impact that struck the Earth at the K/Pg boundary is coincident with the demise of the non-neornithine dinosaurs and explains their sudden extinction (e.g. Chiarenza et al. 2020), a more gradual decline has typically been explained via the impact of Deccan volcanism and other environmental perturbations (e.g.

Condamine et al. 2021). A clearer understanding of dinosaur diversity dynamics outside of North America might shed light on this issue.

One problem with nearly all of these studies is that they typically evaluate a paraphyletic Dinosauria that excludes birds. Yet, ~15% of currently recognised Mesozoic dinosaur species are birds and we know that avialan dinosaurs represent a substantial Mesozoic radiation that is almost certainly undersampled as a result of taphonomic filters (see above). This includes an increase in diversification rate during the Late Cretaceous that corresponds to the initial radiation of crown birds (Yu et al. 2021), the first appearance of neornithine birds in the latest Cretaceous fossil record (Clarke et al. 2005; Field et al. 2020), and a diverse latest Cretaceous avifauna (Longrich et al. 2011). The exclusion of birds from dinosaur diversity analyses is equivalent to omitting ornithomorphs or titanosauriforms, groups that are each similarly speciose to Mesozoic birds, and which would artificially result in lowered reconstructed diversity in Cretaceous ornithomorphs and the apparent extinction of sauropods in the early Late Cretaceous, respectively. Although the different preservation potential of bird skeletons compared to most other dinosaurs is a potential reason to evaluate avialan diversity separately (e.g. Brocklehurst et al. 2012; Gardner et al. 2016), many non-avialan paravian theropod dinosaurs have similarly delicate bones, yet are evaluated alongside their larger-bodied dinosaurian relatives.

An important consideration is that measures of diversity and diversification rate are not interchangeable: it is possible that species richness remained high whilst diversification rate showed overall decline (Sakamoto et al. 2021). Finally, if there was a decline in dinosaur diversity or diversification rate in the latest Cretaceous, this does not necessarily mean that the group was headed for extinction (Brusatte et al. 2015). Previous time intervals also show evidence for comparable stage-to-stage diversity declines (Barrett et al. 2009; Upchurch et al. 2011; Starrfelt and Liow 2016); yet, dinosaurs not only did not go extinct at these times, but experienced subsequent diversifications.

4. The latitudinal diversity gradient of Mesozoic dinosaurs

Whereas most studies to consider dinosaur diversity have evaluated temporal patterns, how the distribution of this species richness varied spatially is also important. This is arguably of paramount importance given that our understanding of diversity dynamics through time is dependent on spatial sampling heterogeneity. Biodiversity through time is entwined with biodiversity through space and the two must be considered together (Benson et al. 2021). This is perhaps best exemplified by the latitudinal diversity gradient (LDG).

In the present day, species richness is greatest in the tropics and declines towards the poles, representing a first-order macroecological pattern; yet, attempts to understand the LDG are precluded by covariation with latitude of the various proposed drivers (Pontarp et al. 2019). By contrast, many of these variables were decoupled in the Mesozoic (Brodie and Mannion 2023). The few studies to quantitatively evaluate how the distribution of dinosaur diversity varied with latitude have all recovered evidence for a flattened LDG, with a peak in diversity at temperate palaeolatitudes (Mannion et al. 2012; Dunne et al. 2021; Chiarenza et al. 2022; Maidment 2023). Although these studies accounted for latitudinal sampling heterogeneity within temporal windows, there are still problems pertaining to local versus 'global' sampling coverage (Close et al. 2017), with no attempt to factor in longitudinal sampling heterogeneity. Nevertheless, alternative approaches to evaluating the dinosaur LDG, utilising climate data and ecological niche modelling (Dunne et al. 2021, 2023; Chiarenza et al. 2022), reinforce the

view that the distribution of dinosaur diversity did not conform to the present-day unimodal LDG, which likely formed only during the late Cenozoic (Brodie and Mannion 2023). Collectively, these studies also suggest that the diversity of sauropodomorphs was more latitudinally restricted than that of ornithischians and theropods (Mannion et al. 2012; Dunne et al. 2021, 2023; Chiarenza et al. 2022), with these latter clades extending into polar regions (e.g. Druckenmiller et al. 2021).

5. Future directions

Returning to the question of how many dinosaurs were alive during the entirety of the Mesozoic, extrapolations based on Le Loeuff (2012) appear to be more realistic than other published estimates given the high number of observed species despite pervasive spatiotemporal sampling failure. Although this contribution might seem overly pessimistic about our current understanding of Mesozoic dinosaur diversity, an increased awareness of the problems pertaining to sampling heterogeneity and recognition of the incomplete nature of the underlying data are important first steps. The last couple of decades have witnessed great strides in our approaches to addressing questions pertaining to dinosaur diversity and diversification, including increasingly refined and sophisticated methods.

Although the underlying datasets are richer and more readily available than ever, the quality and quantity of these data require refinement. Both occurrence-based and phylogenetic methods require stratigraphic information on species, and yet few analyses utilize updated stratigraphic data on dinosaurs (Cashmore et al. 2020; Dean et al. 2020). Occurrence-based methods essentially include all Mesozoic dinosaur species, but most phylogeny-based methods sample only approximately a third of this diversity (though see Sakamoto et al. 2021), and most studies exclude birds regardless of approach. Improved chronostratigraphic resolution and incorporation of a greater proportion of dinosaur diversity, including birds, is a necessary step to elucidating diversity dynamics in this clade, as well as for enabling inter-model comparisons.

All studies of dinosaur diversity and diversification must consider both temporal and spatial sampling heterogeneity. Global reconstructions of diversity dynamics are problematic at best and this affects both sampling standardisation and diversification rate approaches. The development of sampling-standardized regional diversification rate estimates will be an important next step, allowing a fairer and more meaningful comparison with results emanating from sampling standardisation-based analyses. Such approaches have recently been developed and applied to estimations of diversification rates in the marine fossil record (Flannery-Sutherland et al. 2022; Allen et al. 2023), providing a starting point for their incorporation into analyses of dinosaur diversification. Similar spatiotemporal sampling problems also pervade 'global' reconstructions of time series of environmental variables (Jones and Eichenseer 2022), which are often used to test for correlations with dinosaur diversity dynamics. As such, it is also important to consider spatially appropriate environmental variables to provide meaningful tests of drivers of dinosaur diversity and diversification, whilst also taking into account the possibility of common cause effects (Fig. 2C).

Approaches such as ecological niche modelling (e.g. Chiarenza et al. 2019) and occupancy modelling (e.g. Lawing et al. 2021) can also be utilized to better understand whether absences of species from particular spatiotemporal windows are genuine or artefactual. Studies addressing diversity patterns within a time interval need to consider sampling heterogeneity

latitudinally, but also longitudinally. Biogeographical analyses need to factor in sampling heterogeneity too, and future studies should consider whether a sampling standardization approach is required both for occurrence-based and phylogenetic biogeographic methods.

Finally, there is no reason not to consider a more holistic approach to evaluating dinosaur diversity dynamics. Both species richness and diversification rate are important measures. Each of the approaches discussed herein have their problems, which might be overcome by bringing a range of methods to bear on this topic.

Data accessibility. This article has no additional data.

Declaration of AI use. I have not used AI-assisted technologies in creating this article.

Authors' contributions. P.D.M.: conceptualization, writing.

Conflict of interest declaration. I declare I have no competing interests.

Funding. The Royal Society (UF160216, URF\R\221010).

Acknowledgements. Collaborations and discussions with numerous colleagues over the last 15 years have helped to shape the views and ideas presented in this contribution, with particular thanks to Paul Barrett, Roger Benson, Richard Butler, Matthew Carrano, Alessandro Chiarenza, Roger Close, Natalie Cooper, Christopher Dean, Emma Dunne, Joel Heath, Lewis Jones, Susannah Maidment, Jonathan Tennant, and Paul Upchurch. Christopher Dean is additionally thanked for providing comments on an earlier draft of this contribution and I am also grateful to reviewer comments from Gregory Funston, Flávio Pretto, and one anonymous referee. Finally, I thank Paul Barrett and Susannah Maidment for organising this special issue and for inviting me to contribute this article. This is *Paleobiology Database* official publication number 506.

References

- Allen BJ, Clapham ME, Saupe EE, Wignall PB, Hill DJ, Dunhill AM. 2023. Estimating spatial variation in origination and extinction in deep time: a case study using the Permian–Triassic marine invertebrate fossil record. *Paleobiology* 49, 509–526.
- Allen BJ, Volkova Oliveira MV, Stadler T, Vaughan TG, Warnock RCM. 2024. Mechanistic phylodynamic models do not provide conclusive evidence that non-avian dinosaurs were in decline before their final extinction. *Cambridge Prisms: Extinction 2*, e6.
- Alroy J. 2010. The shifting balance of diversity among major marine animal groups. *Science* 329, 1191–1194.
- Arbour VM, Zanno LE, Gates T. 2016. Ankylosaurian dinosaur palaeoenvironmental associations were influenced by extirpation, sea-level fluctuation, and geodispersal. *Palaeogeography, Palaeoclimatology, Palaeoecology* 449, 289–299.
- Archibald JD. 2014. What the dinosaur record says about extinction scenarios. *Geological Society of America Special Papers* 505, 213–224.
- Baron MG, Norman DB, Barrett PM. 2017. A new hypothesis of dinosaur relationships and early dinosaur evolution. *Nature* 543, 501–506.

- Barrett PM. 2014. Paleobiology of Herbivorous Dinosaurs. *Annual Review of Earth and Planetary Sciences* 42, 207–230.
- Barrett PM, McGowan AJ, Page V. 2009. Dinosaur diversity and the rock record. *Proceedings of the Royal Society B* 276, 2667–2674.
- Benson RBJ. 2018. Dinosaur Macroevolution and Macroecology. *Annual Review of Ecology, Evolution, and Systematics* 49, 379–408.
- Benson RBJ, Butler RJ, Alroy J, Mannion PD, Carrano MT, Lloyd GT. 2016. Near-stasis in the long-term diversification of Mesozoic tetrapods. *PLoS Biology* 14, e1002359.
- Benson RBJ, Butler RJ, Close RA, Saupe E, Rabosky DL. 2021. Biodiversity across time and space in the fossil record. *Current Biology* 31, R1225–R1236.
- Benson RBJ, Mannion PD. 2012. Multi-variate models are essential for understanding vertebrate diversification in deep time. *Biology Letters* 8, 127–130.
- Benson RBJ, Mannion PD, Butler RJ, Upchurch P, Goswami A, Evans SE. 2013. Cretaceous tetrapod fossil record sampling and faunal turnover: implications for biogeography and the rise of modern clades. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372, 88–107.
- Benton MJ. 2008. Fossil quality and naming dinosaurs. *Biology Letters* 4, 729–732.
- Benton MJ. 2015. Palaeodiversity and formation counts: redundancy or bias? *Palaeontology* 58, 1003–1029.
- Benton MJ. 2024. The dinosaur boom in the Cretaceous. *Geological Society, London, Special Publications* 544 (doi: 10.1144/SP544-2023-70).
- Bernardi M, Gianolla P, Petti FM, Mietto P, Benton MJ. 2018. Dinosaur diversification linked with the Carnian Pluvial Episode. *Nature Communications* 9, 1499.
- Bonsor JA, Barrett PM, Raven TJ, Cooper N. 2020. Dinosaur diversification rates were not in decline prior to the K-Pg boundary. *Royal Society Open Science* 7, 201195.
- Brocklehurst N. 2015. A simulation-based examination of residual diversity estimates as a method of correcting for sampling bias. *Palaeontologia Electronica* 18.3.7T, 1–15.
- Brocklehurst N, Upchurch P, Mannion PD, O'Connor JK. 2012. The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. *PLoS ONE* 7, e39056.
- Brodie JF, Mannion PD. 2023. The hierarchy of factors predicting the latitudinal diversity gradient. *TRENDS in Ecology and Evolution* 38, 15–23.
- Brown CM, Evans DC, Campione NE, O'Brien LJ, Eberth DA. 2013. Evidence for taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial alluvial-paralic system. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372, 108–122.
- Brown CM, Campione NE, Wilson Mantilla GP, Evans DC. 2022. Size-driven preservational and macroecological biases in the latest Maastrichtian terrestrial vertebrate assemblages of North America. *Paleobiology* 48, 210–238.
- Brusatte SL, Butler RJ, Barrett PM, Carrano MT, Evans DC, Lloyd GT, Mannion PD, Norell MA, Peppe DJ, Upchurch P, Williamson TE. 2015. The extinction of the dinosaurs. *Biological Reviews* 90, 628–642.
- Brusatte SL, Nesbitt SJ, Irmis RB, Butler RJ, Benton MJ, Norell MA. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews* 101, 68–100.
- Butler RJ, Benson RBJ, Carrano MT, Mannion PD, Upchurch P. 2011. Sea-level, dinosaur diversity, and sampling biases: investigating the 'common cause' hypothesis in the terrestrial realm. *Proceedings of the Royal Society B* 278, 1165–1170.
- Cashmore DD, Butler RJ. 2019. Skeletal completeness of the non-avian theropod dinosaur fossil record. *Palaeontology* 62, 951–981.

- Cashmore DD, Butler RJ, Maidment SCR. 2021. Taxonomic identification bias does not drive patterns of abundance and diversity in theropod dinosaurs. *Biology Letters* 17, 20210168.
- Cashmore DD, Mannion PD, Upchurch P, Butler RJ. 2020. Ten more years of discovery: revisiting the quality of the sauropodomorph dinosaur fossil record. *Palaeontology* 63, 951–978.
- Černý D, Madzia D, Slater GJ. 2022. Empirical and Methodological Challenges to the Model-Based Inference of Diversification Rates in Extinct Clades. *Systematic Biology* 71, 153–171.
- Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93, 2533–2547.
- Chiarenza AA, Brusatte SL. 2023. Dinosaurs, Extinction theories for. In: Encyclopedia of Biodiversity, 3rd Edition (Scheiner SM, ed.), Academic Press, 298–309.
- Chiarenza AA, Farnsworth A, Mannion PD, Lunt DJ, Valdes P, Morgan JV, Allison PA. 2020. Asteroid impact, not volcanism, caused the end-Cretaceous dinosaur extinction. *Proceedings of the National Academy of Sciences, USA* 117, 17084–17093.
- Chiarenza AA, Mannion PD, Farnsworth A, Varela S, Carrano MT. 2022. Climatic constraints on the biogeographic history of Mesozoic dinosaurs. *Current Biology* 32, 570–585.
- Chiarenza AA, Mannion PD, Lunt DJ, Farnsworth A, Jones LA, Kelland S-J, Allison PA. 2019. Ecological niche modelling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. *Nature Communications* 10, 1091.
- Clarke JA, Tambussi CP, Noriega JI, Erickson GM, Ketchum RA. 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature* 433, 305–308.
- Close RA, Benson RBJ, Alroy J, Behrensmeyer AK, Benito J, Carrano MT, Cleary TJ, Dunne EM, Mannion PD, Uhen MD, Butler RJ. 2019. Diversity dynamics of Phanerozoic terrestrial tetrapods at the local-community scale. *Nature Ecology and Evolution* 3, 590–597.
- Close RA, Benson RBJ, Alroy J, Carrano MT, Cleary TJ, Dunne EM, Mannion PD, Uhen MD, Butler RJ. 2020. The apparent exponential radiation of Phanerozoic land vertebrates is an artefact of spatial sampling biases. *Proceedings of the Royal Society B* 287, 20200372.
- Close RA, Benson RBJ, Upchurch P, Butler RJ. 2017. Controlling for the species-area effect supports long-term Mesozoic terrestrial vertebrate diversification. *Nature Communications* 8, 15381.
- Close RA, Evers SW, Alroy J and Butler RJ. 2018. How should we estimate diversity in the fossil record? Testing richness estimators using sampling-standardised discovery curves. *Methods in Ecology and Evolution* 9, 1386–1400.
- Condamine FL, Guinot G, Benton, MJ, Currie PJ. 2021. Dinosaur biodiversity declined well before the asteroid impact, influenced by ecological and environmental pressures. *Nature Communications* 12, 3833.
- Coria RA, Salgado L. 2005. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. *Geological Society, London, Special Publications* 252, 317–327.
- Dean CD, Chiarenza AA, Maidment SCR. 2020. Formation binning: a new method for increased temporal resolution in regional studies, applied to the Late Cretaceous dinosaur fossil record of North America. *Palaeontology* 63, 881–901.
- Desojo JB, Fiorelli LE, Ezcurra MD, Martinelli AG, Ramezani J, Da Rosa ÁAS, von Baczko MB, Trotteyn MJ, Montefeltro FC, Ezpeleta M, Langer MC. 2020. The Late Triassic Ischigualasto Formation at Cerro Las Lajas (La Rioja, Argentina): fossil tetrapods, high-resolution chronostratigraphy, and faunal correlations. *Scientific Reports* 10, 12782.

- Dodson P. 1990. Counting dinosaurs: how many kinds were there? *Proceedings of the National Academy of Sciences, USA* 87, 7608–7612.
- Druckenmiller PS, Erickson GM, Brinkman D, Brown CM, Eberle JJ. 2021 Nesting at extreme polar latitudes by non-avian dinosaurs. *Current Biology* 31, 3469–3478.
- Dunhill AM, Hannisdal B, Brocklehurst N, Benton MJ. 2018. On formation-based sampling proxies and why they should not be used to correct the fossil record. *Palaeontology* 61, 119–132.
- Dunne EM, Farnsworth A, Benson RBJ, Godoy PL, Greene SE, Valdes PJ, Lunt DJ, Butler RJ. 2023. Climatic controls on the ecological ascendancy of dinosaurs. *Current Biology* 33, 206–214
- Dunne EM, Farnsworth A, Greene SE, Lunt DJ, Butler RJ. 2021. Climatic drivers of latitudinal variation in Late Triassic tetrapod diversity. *Palaeontology* 64, 101–117.
- Eaton JG, Kirkland JI, Hutchison JH, Denton R, O'Neill RC, Parrish JM. 1997. Nonmarine extinction across the Cenomanian–Turonian boundary, southwestern Utah, with a comparison to the Cretaceous–Tertiary extinction event. *GSA Bulletin* 109, 560–567.
- Eberth DA, Evans DC, Brinkman DB, Therrien F, Tanke DH, Russell LS. 2013. Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climate influence. *Canadian Journal of Earth Sciences* 50, 701–726.
- Fastovsky DE, Huang Y, Hsu J, Martin-McNaughton J, Sheehan PM, Weishampel DB. 2004. Shape of Mesozoic dinosaur richness. *Geology* 32, 877–880.
- Field DJ, Benito J, Chen A, Jagt JWM, Ksepka DT. 2020. Late Cretaceous neornithine from Europe illuminates the origins of crown birds. *Nature* 579, 397–401.
- Flannery-Sutherland JT, Silvestro D, Benton MJ. 2022. Global diversity dynamics in the fossil record are regionally heterogeneous. *Nature Communications* 13, 2751.
- Fonseca AO, Reid IJ, Venner A, Duncan RJ, Garcia MS, Müller RT. 2024. A comprehensive phylogenetic analysis on early ornithischian evolution. *Journal of Systematic Palaeontology*, 22, 2346577.
- Fontaine TM, Benton MJ, Dyke GJ, Nudds RL. 2005. The quality of the fossil record of Mesozoic birds. *Proceedings of the Royal Society B* 272, 289–294.
- Fowler DW. 2017. Revised geochronology, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America. *PLoS ONE* 12, e0188426.
- Funston GF, Mendonca SE, Currie PJ, Barsbold R. 2018. Oviraptorosaur anatomy, diversity and ecology in the Nemegt Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 494, 101–120.
- Gallina PA, Apesteguía S, Haluza A, Canale JI. 2014. A diplodocid sauropod survivor from the Early Cretaceous of South America. *PLoS ONE* 9, e97128.
- Gardner EE, Walker SE, Gardner LI. 2016. Palaeoclimate, environmental factors, and bird body size: a multivariable analysis of avian fossil preservation. *Earth-Science Reviews* 162, 177–197.
- Gates TA, Prieto-Márquez A, Zanno LE. 2012. Mountain building triggered Late Cretaceous North American megaherbivore dinosaur radiation. *PLoS ONE* 7, e42135.
- Griffin CT, Wynd BM, Munyikwa D, Broderick TJ, Zondo M, Tolan S, Langer MC, Nesbitt SJ, Taruvunga HR. 2022. Africa's oldest dinosaurs reveal early suppression of dinosaur distribution. *Nature* 609, 313–319.
- Han F, Wang Q, Wang H, Zhu X, Zhou X, Wang Z, Fang K, Stidham TA, Wang W, Wang X, Li X, Qin H, Fan L, Wen C, Luo J, Pan Y, Deng C. 2022. Low dinosaur biodiversity in central China 2

- million years prior to the end-Cretaceous mass extinction. *Proceedings of the National Academy of Sciences, USA* 119, e2211234119.
- Haubold H. 1990. Dinosaurs and fluctuating sea levels during the Mesozoic. *Historical Biology* 4, 75–106.
- Hunt AP, Lockley MG, Lucas SG, Meyer CA. 1994. The global sauropod fossil record. *GAIA* 10, 261–279.
- Jackson JBC, Johnson KG. 2001. Measuring past biodiversity. *Science* 293, 2401–2404.
- Jesus Faria CC, González Riga B, Candeiro CRA, Marinho TS, Ortiz David L, Simbras FM, Castanho RB, Muniz FP, Costa Pereira PVLG. 2015. Cretaceous sauropod diversity and taxonomic succession in South America. *Journal of South American Earth Sciences* 61, 154–163.
- Jetz W, Thomas G, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* 491, 444–448.
- Jones LA, Eichenseer K. 2022. Uneven spatial sampling distorts reconstructions of Phanerozoic seawater temperature. *Geology* 50, 238–242.
- Kirkland JJ, Sertich JJW, Titus AL. 2024. Dinosaur biostratigraphy of the non-marine Cretaceous of Utah. *Geological Society, London, Special Publications* 545 (doi: 10.1144/SP545-2023-211).
- Krause JM, Ramezani J, Umazano AM, Pol D, Carballido JL, Sterli J, Puerta P, Cúneo NR, Bellosi ES. 2020. High-resolution chronostratigraphy of the Cerro Barcino Formation (Patagonia): Paleobiologic implications for the mid-Cretaceous dinosaur-rich fauna of South America. *Gondwana Research* 80, 33–49.
- Lane A, Janis CM, Sepkoski Jr JJ. 2005. Estimating paleodiversities: a test of the taxic and phylogenetic methods. *Paleobiology* 31, 21–34.
- Langer MC, Ezcurra MD, Bittencourt JS, Novas FE. 2010. The Origin and Early Evolution of Dinosaurs. *Biological Reviews* 85, 55–110.
- Langer MC, Godoy PL. 2022. So Volcanoes Created the Dinosaurs? A Quantitative Characterization of the Early Evolution of Terrestrial Pan-Aves. *Frontiers in Earth Science* 10, 899562.
- Langer MC, Ramezani J, Da Rosa ÁAS. 2018. U-Pb age constraints on dinosaur rise from south Brazil. *Gondwana Research* 57, 133–140.
- Lawing AM, Blois JL, Maguire KC, Goring SJ, Wang Y, McGuire JL. 2021. Occupancy models reveal regional differences in detectability and improve relative abundance estimations in fossil pollen assemblages. *Quaternary Science Reviews* 253, 106747.
- Leach CT, Hoffman E, Dodson P. 2021. The promise of taphonomy as a nomothetic discipline: taphonomic bias in two dinosaur-bearing faunas in North America. *Canadian Journal of Earth Sciences* 58, 852–869.
- Le Loeuff J. 2012. Paleobiogeography and biodiversity of Late Maastrichtian dinosaurs: How many dinosaur species went extinct at the Cretaceous-Tertiary boundary? *Bulletin de la Société Géologique de France* 183, 547–559.
- Lloyd GT. 2012. A refined modelling approach to assess the influence of sampling on palaeobiodiversity curves: new support for declining Cretaceous dinosaur richness. *Biology Letters* 8, 123–126.
- Lloyd GT, Bapst DW, Friedman M, Davis KE. 2016. Probabilistic divergence time estimation without branch lengths: dating the origins of dinosaurs, avian flight and crown birds. *Biology Letters* 12, 20160609.

- Lloyd GT, Davis KE, Pisani D, Tarver JE, Ruta M, Sakamoto M, Hone DWE, Jennings R, Benton MJ. 2008. Dinosaurs and the Cretaceous terrestrial revolution. *Proceedings of the Royal Society of London B* 275: 2483–2490.
- Longrich NR, Pereda Suberbiola X, Pyron RA, Jalil N-E. 2021. The first duckbill dinosaur (Hadrosauridae: Lambeosaurinae) from Africa and the role of oceanic dispersal in dinosaur biogeography. *Cretaceous Research* 120, 104678.
- Longrich NR, Tokaryk T, Field DJ. 2011. Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary. *Proceedings of the National Academy of Sciences, USA* 108, 15253–15257.
- Lyson TR, Longrich NR. 2011. Spatial niche partitioning in dinosaurs from the latest Cretaceous (Maastrichtian) of North America. *Proceedings of the Royal Society B* 278, 1158–1164.
- Maidment SCR. 2023. Diversity through time and space in the Upper Jurassic Morrison Formation, western U.S.A. *Journal of Vertebrate Paleontology* 43, e2326027.
- Maidment SCR, Dean CD, Mansergh RI, Butler RJ. 2021. Deep-time biodiversity patterns and the dinosaurian fossil record of the Western Interior, North America. *Proceedings of the Royal Society B* 288, 20210692.
- Mallon JC, Evans DC, Ryan MJ, Anderson JS. 2012. Megaherbivorous dinosaur turnover in the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 350–352, 124–138.
- Mancuso AC, Benavente CA, Irmis RB, Mundil R. 2020. Evidence for the Carnian Pluvial Episode in Gondwana: New multiproxy climate records and their bearing on early dinosaur diversification. *Gondwana Research* 86, 104–125.
- Mannion PD, Benson RJB, Upchurch P, Butler RJ, Carrano MT, Barrett PM. 2012. A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Global Ecology and Biogeography* 21, 898–908.
- Mannion PD, Upchurch P. 2010a. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology* 36, 253–282.
- Mannion PD, Upchurch P. 2010b. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology* 36, 283–302.
- Mannion PD, Upchurch P. 2011. A re-evaluation of the ‘mid-Cretaceous sauropod hiatus’ and the impact of uneven sampling of the fossil record on patterns of regional dinosaur extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299, 529–540.
- Mannion PD, Upchurch P, Carrano MT, Barrett PM. 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* 86, 157–181.
- Marsola JCA, Ferreira GS, Langer MC, Button DJ, Butler RJ. 2019. Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs. *Palaeontology* 62, 473–482.
- Nanglu K, Cullen TM. 2023. Across space and time: A review of sampling, preservational, analytical, and anthropogenic biases in fossil data across macroecological scales. *Earth-Science Reviews* 244, 104537.
- Nesbitt SJ, Barrett PM, Werning S, Sidor CA, Charig AJ. 2013. The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. *Biology Letters* 9, 1–5.
- Pearson DA, Schaefer T, Johnson KR, Nichols DJ, Hunter JP. 2002. Vertebrate biostratigraphy of the Hell Creek formation in southwestern North Dakota and northwestern South Dakota. *Geological Society of America Special Paper* 361, 145–167.

- Pol D, Ramezani J, Gomez K, Carballido JL, Paulina Carabajal A, Rauhut OWM, Escapa IH, Cúneo NR. 2020. Extinction of herbivorous dinosaurs linked to Early Jurassic global warming event. *Proceedings of the Royal Society B* 287, 20202310.
- Pol D, Rauhut O. W. M. 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B* 279, 3170–3175.
- Pontarp M, Bunnefeld L, Cabral JS, Etienne RS, Fritz SA, Gillespie R, Graham CH, Hagen O, Hartig F, Huang S, Jansson R, Maliet O, Münkemüller T, Pellissier L, Rangel TF, Storch D, Wiegand T, Hurlbert AH. 2019. The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models. *TRENDS in Ecology and Evolution* 34, 211–223.
- Raja NB, Dunne EM, Matiwane A, Khan TM, Nätscher PS, Ghilardi AM, Chattopadhyay D. 2022. Colonial history and global economics distort our understanding of deep-time biodiversity. *Nature Ecology & Evolution* 6, 145–154.
- Rauhut OWM, Hübner TR, Lanser KP. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovia) of north-western Germany: Implications for theropod evolution and faunal turnover in the Jurassic. *Palaeontologia Electronica* 19, 26A.
- Raup DM. 1972. Taxonomic diversity during the Phanerozoic. *Science* 177, 1065–1071.
- Reolid M, Ruebsam W, Benton MJ. 2022. Impact of the Jenkyns Event (early Toarcian) on dinosaurs: Comparison with the Triassic/Jurassic transition. *Earth-Science Reviews* 234, 104196.
- Russell DA. 1995. China and the lost worlds of the dinosaurian era. *Historical Biology* 10, 3–12.
- Sakamoto M, Benton MJ, Venditti C. 2016. Dinosaurs in decline tens of millions of years before their final extinction. *Proceedings of the National Academy of Sciences, USA* 113, 5036–5040.
- Sakamoto M, Benton MJ, Venditti C. 2021. Strong support for a heterogeneous speciation decline model in Dinosauria: a response to claims made by Bonsor et al. (2020). *Royal Society Open Science* 8, 202143.
- Sakamoto M, Venditti C, Benton MJ. 2017. ‘Residual diversity estimates’ do not correct for sampling bias in palaeodiversity data. *Methods in Ecology & Evolution* 8, 453–459.
- Sales MAF, Lacerda MB, Horn BLD, Oliveira IAP, Schultz CL. 2016. The “ χ ” of the Matter: testing the relationship between paleoenvironments and three theropod clades. *PLoS ONE* 11, e0147031.
- Sarjeant WAS, Currie PJ. 2001. The Great Extinction that never happened: the demise of the dinosaurs considered. *Canadian Journal of Earth Sciences* 38, 239–247.
- Sereno PC. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* 25, 435–489.
- Sereno PC. 1999. The evolution of dinosaurs. *Science* 284, 2137–2147.
- Sheehan PM, Fastovsky DE, Barreto C, Hoffmann RG. 2000. Dinosaur abundance was not declining in a ‘3 m gap’ at the top of the Hell Creek Formation, Montana and North Dakota. *Geology* 28, 523–526.
- Sloan RE, Rigby Jr JK, Van Valen LM, Gabriel DL. 1986. Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation. *Science* 234, 1173–1175.
- Starrfelt J, Liow LH. 2016. How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model. *Philosophical Transactions of the Royal Society of London B* 371, 20150219.
- Sullivan RM. 2006. The shape of Mesozoic dinosaur richness: a reassessment. *New Mexico Museum of Natural History and Science Bulletin* 35, 403–405.

- Tarver JE, Donoghue PCJ, Benton MJ. 2011. Is evolutionary history repeatedly rewritten in light of new fossil discoveries? *Proceedings of the Royal Society B* 278, 599–604.
- Tennant JP, Chiarenza AA, Baron M. 2018. How has our knowledge of dinosaur diversity through geologic time changed through research history? *PeerJ* 6, e4417.
- Tennant JP, Mannion PD, Upchurch P. 2016. Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. *Nature Communications* 7, 12737.
- Tennant JP, Mannion PD, Upchurch P, Sutton MD, Price GD. 2017. Biotic and environmental dynamics across the Late Jurassic–Early Cretaceous transition: evidence for a protracted period of faunal and ecological turnover. *Biological Reviews* 92, 776–814.
- Tucker RT, Crowley JL, Mohr MT, Renaut RK, Makovicky PJ, Zanno LE. 2023. Exceptional age constraint on a fossiliferous sedimentary succession preceding the Cretaceous Thermal Maximum. *Geology* 51, 962–967.
- Upchurch P, Barrett PM. 2005. A phylogenetic perspective on sauropod diversity. In: *The Sauropods: evolution and paleobiology* (Curry Rogers KA, Wilson JA, eds.), pp. 104–124. University of California Press, Berkeley.
- Upchurch P, Mannion PD, Butler RJ, Benson RBJ, Carrano MT. 2011. Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. *Geological Society, London, Special Publications* 358, 209–240.
- van der Linden T, Tschopp E, Sookias R, Wallaard J, Holwerda F, Schulp A. 2024. A new diplodocine sauropod from the Morrison Formation, Wyoming, USA. *Palaeontologia Electronica* 27, a48.
- Vavrek MJ. 2016. The fragmentation of Pangaea and Mesozoic terrestrial vertebrate biodiversity. *Biology Letters* 12, 20160528.
- Vavrek MJ, Larsson HC. 2010. Low beta diversity of Maastrichtian dinosaurs of North America. *Proceedings of the National Academy of Sciences, USA* 107, 8265–8268.
- Vermeij GJ, Leighton LR. 2003. Does global diversity mean anything? *Paleobiology* 29, 3–7.
- Vieira WLS, Vieira KS, Nóbrega RP, Montenegro PFGP, Pereira Filho GA, Santana GG, Nóbrega Alves RR, Almeida WO, Vasconcellos A. 2014. Species Richness and Evidence of Random Patterns in Assemblages of South American Titanosauria during the Late Cretaceous (Campanian–Maastrichtian). *PLoS ONE* 9, e108307.
- Vila B, Sellés AG, Brusatte SL. 2016. Diversity and faunal changes in the latest Cretaceous dinosaur communities of southwestern Europe. *Cretaceous Research* 57, 552–564.
- Wang SC, Dodson P. 2006. Estimating the diversity of dinosaurs. *Proceedings of the National Academy of Sciences, USA* 103, 13601–13605.
- Weaver LN, Kelson JR, Holder RM, Niemi NA, Badgley C. 2024. On the role of tectonics in stimulating the Cretaceous diversification of mammals. *Earth-Science Reviews* 248, 104630.
- Weishampel DB, Jianu C-M. 2000. Planteaters and ghost lineages: dinosaurian herbivory revisited. In: *The Evolution of Herbivory in Terrestrial Vertebrates. Perspectives from the Fossil Record* (Sues H-D, ed.), pp. 123–143. Cambridge University Press, Cambridge.
- Whitlock JA, Wilson Mantilla JA. 2020. The Late Jurassic sauropod dinosaur ‘*Morosaurus*’ *agilis* Marsh, 1889 reexamined and reinterpreted as a dicraeosaurid. *Journal of Vertebrate Paleontology* 40, e1780600.
- Woolley CH, Bottjer DJ, Corsetti FA, Smith ND. 2024. Quantifying the effects of exceptional fossil preservation on the global availability of phylogenetic data in deep time. *PLoS ONE* 19, e0297637.

Xu X, Upchurch P, Mannion PD, Barrett PM, Regalado-Fernandez OR, Mo J, Ma J, Liu H. 2018. A new Middle Jurassic diplodocoid suggests an earlier dispersal and diversification of sauropod dinosaurs. *Nature Communications* 9, 2700.

Yu Y, Zhang C, Xu X. 2021. Deep time diversity and the early radiations of birds. *Proceedings of the National Academy of Sciences, USA* 118, e2019865118.

Zhou Z. 2014. The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: New discoveries and implications. *National Science Review* 1, 543–559.

Figure captions

Figure 1. The spatiotemporal distribution of Mesozoic dinosaurs, including birds: (A) Spatial distribution of Late Triassic occurrences. (B) Spatial distribution of Jurassic occurrences. (C) Spatial distribution of Cretaceous occurrences. (D) Observed dinosaur species richness through the Mesozoic, showing contributions from each palaeocontinental region. Data in parts A–C plotted on a present-day Mollweide map projection using *The Paleobiology Database* navigator (<https://paleobiodb.org/navigator/>). Data in part D plotted at the midpoint of each stratigraphic stage based on data in *The Paleobiology Database* as of the 31st July 2024.

Figure 2. Impact of sampling on dinosaur diversity: (A) Schematic of the spatial sampling filter that affects consistency of sampling effort, with differing sampling coverage (i.e. size, location, environment) dictating observed diversity; (B) Taphonomic filter that affects preservation and recognition of species and their inclusion in analyses of dinosaur diversity (C) Terrestrial common cause scenarios that affect both genuine and observed species richness.

Figure 3. Palaeogeographic reconstructions of Mesozoic intervals showing spatial distribution of well-sampled dinosaur body fossil-bearing deposits: (A) Carnian (purple circles) (plate reconstruction = 232 Ma); (B) latest Triassic (purple circles) to earliest Jurassic (dark blue circles) (plate reconstruction = 200 Ma); (C) Toarcian (dark blue circles) to early Middle Jurassic (light blue circles) (plate reconstruction = 179 Ma); (D) Kimmeridgian–Tithonian (light blue circles) to earliest Cretaceous (green circles) (plate reconstruction = 147 Ma).