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Climatic constraints on the biogeographic history of Mesozoic dinosaurs

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SUMMARY

Dinosaurs dominated Mesozoic terrestrial ecosystems globally. However, whereas a pole-to-pole geographic distribution characterized ornithischians and theropods, sauropods were restricted to lower latitudes. Here, we evaluate the role of climate in shaping these biogeographic patterns through the Jurassic–Cretaceous (201–66 million years ago), combining dinosaur fossil occurrences, past climate data from Earth System models, and habitat suitability modelling. Results show that uniquely among dinosaurs, sauropods occupied climatic niches characterised by high temperatures and strongly bounded by minimum cold temperatures. This constrained the distribution and dispersal pathways of sauropods to tropical areas, excluding them from latitudinal extremes, especially in the Northern Hemisphere. The greater availability of suitable habitat in the southern continents, particularly in the Late Cretaceous, might be key to explaining the high diversity of sauropods there, relative to northern landmasses. Given that ornithischians and theropods show a flattened or bimodal latitudinal biodiversity gradient, with peaks at higher latitudes, the closer correspondence of sauropods to a subtropical concentration could hint at fundamental thermophysiological differences to the other two clades.

Introduction

Dinosaurs were diverse and abundant during most of the Mesozoic (from ~230–66 million years ago [Ma]), with a cosmopolitan distribution[1–4] (Figure 1). They radiated into a wide range of ecotypes, dietary habits, and body sizes, the latter including the largest land animals of all time[5–10]. Recent evidence indicates that dinosaurs evolved distinctive patterns of growth, reproduction, food assimilation, and lung ventilation[6,11–16], in some cases without clear modern analogues. These traits are directly related to the underlying biology of dinosaurs[17–20], including their thermophysiology[9,11,12,21], and might therefore be key to understanding their body-size evolution, the selective extinction of non-avian dinosaurs at the Cretaceous/Paleogene boundary, 66 Ma[22,23], as well as enigmatic aspects of Mesozoic dinosaur communities (e.g. trophic structure, migratory habits[24–26]). Given these important biological distinctions, it is likely that climate, among all the biotic and abiotic factors[9] impacting geologically long-term aspects of dinosaur macroecology and evolution, was a major constraint on the group's geographic distribution and diversification[25,27–29].

The geographic distributions of extant species largely reflect their environmental tolerance[30–34]. Today, birds and mammals have a near-global distribution, extending into high, polar latitudes[35]. By contrast, the diversity of non-avian reptiles (including lizards, snakes, turtles, and crocodylians) and amphibians is primarily restricted to lower latitudes[36–38]. Although all these tetrapod groups have their greatest concentration of species richness in the tropics, non-avian reptiles and amphibians are characterized by steeper latitudinal biodiversity gradients than birds and mammals[39–41].

In stark contrast, previous work on Mesozoic dinosaurs has suggested a peak in diversity at higher latitudes, outside of the palaeo-tropics[29,42]. Mannion et al.[42] also recovered evidence for distinctive patterns among the three main dinosaurian subclades by the Late Cretaceous (100–66 Ma), with sauropods more latitudinally restricted than ornithischians and theropods. In particular, sauropod dinosaurs apparently peaked in diversity at southern palaeolatitudes of ~40–50°[42], with their remains entirely unknown from palaeolatitudes greater than ~66° in either hemisphere[43,44]. By contrast, the apparent peak in ornithischian diversity corresponds to higher palaeolatitudes (~50–70°) in both hemispheres. If correct, this might indicate broad biological differences between sauropods and other dinosaurs. However, this previous work did not examine dinosaur distributions in the context of palaeoclimate, and therefore could not address underlying questions of dinosaur physiological diversity. In addition, although Mannion et al.[42] accounted for sampling bias in their reconstructions of dinosaur diversity, it is possible that these problems are more pervasive when assessing spatial patterns (e.g.[45–48]), and some authors have suggested that the high-latitude peak is an artefact[49,50].

Here, we re-evaluate the distribution of Mesozoic dinosaur diversity, as well as its underlying drivers, combining a near-comprehensive global dataset of dinosaur occurrences with past climate data from the HadCM3L Earth System Model. We test the competing effects of sampling biases (using a coverage-based subsampling

approach) and environmental drivers (e.g. past temperature and precipitation) on dinosaur distribution. Using habitat suitability modelling, we quantitatively define dinosaur climatic niche occupation, explicitly testing climatic constraints on the latitudinal distribution and interclade geographical partitioning of Ornithischia, Theropoda, and Sauropoda.

Results

Palaeolatitudinal sampling coverage

The distribution of dinosaur occurrences is restricted to a latitudinal band spanning approximately 50º either side of the palaeoequator in the Early Jurassic (201–174 Ma) (Figure 2). The southern extent of this distribution expands to approximately 70º in the Middle Jurassic (174–164 Ma), and there is essentially a pole-to-pole distribution in the Late Jurassic (164–145 Ma; Figure 2). This latitudinal band is broadly retained in the Early Cretaceous (145–100 Ma) in the Southern Hemisphere, whereas the northernmost occurrences are restricted to palaeolatitudes of ~70º. This distributional pattern is largely unchanged during the Late Cretaceous (100–66 Ma), with a further poleward expansion in the Northern Hemisphere during the last two intervals of this epoch (Campanian–Maastrichtian, 83–66 Ma; Figure 2). With the exception of their Southern Hemisphere distribution during the last interval of the Early Cretaceous (Albian, 113–100 Ma) and the first interval of the Late Cretaceous (Cenomanian, 100–93 Ma), sauropods do not contribute to these high latitude records. This is particularly marked in the Northern Hemisphere from the late Early Cretaceous onwards, with sauropods restricted to palaeolatitudes no higher than ~50º, despite rich records of other dinosaurs from 50–90º N (Figure 2).

Palaeolatitudinal sampling and biodiversity patterns

Palaeolatitudinal genus richness for each of the three main dinosaurian clades was reconstructed from coverage-based sampling standardization, and it is considered alongside a measure of sampling intensity (Figure 3; see STAR★Methods). Poor sampling between palaeolatitudes of 0–30° S in the Jurassic (Figures 3A–3F) corresponds with land area that is today partially covered by the Sahara Desert in Africa and the Amazon Rainforest in South America. A similar lack of equatorial coverage also characterizes the Late Triassic[29], but is less pronounced in the Cretaceous (Figures 3G–3L).

In the Early–Middle Jurassic (Figures 3A–3C), sampling is higher in the Southern Hemisphere for both ornithischians (~45º S) and sauropods (~30–45º S). By contrast, sampling of theropods is nearly bimodal, with the highest number of occurrences at ~15–30º N and ~30–40º S. Ornithischian diversity peaks at ~40º S, declining towards both the palaeoequator and the southern pole. Despite poor sampling in the Northern Hemisphere, sauropod diversity peaks at ~30º N and ~40º S, with a tropical trough. A broadly similar pattern characterizes theropods, although diversity declines at palaeolatitudes above 30º in the Northern Hemisphere.

In the Late Jurassic (Figures 3D–F), ornithischians are abundantly sampled in the Northern Hemisphere (especially at ~20–40º and ~65º). In the Southern Hemisphere, ornithischian sampling peaks at ~40º. Most of the theropod record is concentrated in the Northern Hemisphere (at ~20º) and declining towards the northern pole and palaeoequator. A small Southern Hemisphere peak in theropod sampling occurs at ~40º. The record of sauropods is also richest in the Northern Hemisphere, with a peak at 30º that declines towards both the northern pole and palaeoequator. A similar latitudinal pattern characterizes the record of sauropods in the Southern Hemisphere. Ornithischian diversity peaks at 40–70º N and declines towards the palaeoequator, flattening out across the tropics, and declining from ~40º to 70º S. Theropod diversity is broadly consistent between 0–40º S, with comparable genus richness at 40º N; however, theropod diversity is low at palaeoequatorial latitudes in the Northern Hemisphere, declining between 0–20º. Sauropod diversity shows a bimodal distribution, with peaks at ~40º N and ~65º S, and a flattened gradient between ~10º N to 40º S. In the Northern Hemisphere, sauropod diversity declines at palaeolatitudes above 40º.

The Berriasian–Barremian ('earliest' Cretaceous) ornithischian record is most abundant in the Northern Hemisphere, peaking at 30º; sampling of the clade is poor in the Southern Hemisphere, with most remains from ~60º (Figure 3G). In both hemispheres, sampling declines polewards and equatorwards from these peaks. Theropods have a rich record between the palaeoequator and 45º in the Northern Hemisphere, with a minor peak in sampling in the Southern Hemisphere at 45° (Figure 3H). Sauropod occurrences are bracketed between 45° in the Northern Hemisphere and 60° in the Southern Hemisphere, with the highest number of occurrences at the palaeoequator (Figure 3L). Ornithischian diversity is highest at ~30º in the Northern Hemisphere, with a lower diversity peak at ~45º in the Southern Hemisphere (Figure 3G). Theropod diversity is concentrated at ~45º N and declines towards the northern pole and palaeoequator, reaching a minimum in the low palaeolatitudes of the Southern Hemisphere (Figure 3H). Sauropods peak in diversity at ~40° N, with genus richness low across the palaeoequator and declining at higher palaeolatitudes in the Southern Hemisphere.

The Aptian–Coniacian ('middle' Cretaceous) ornithischian record is richest in the Northern Hemisphere, with high levels of coverage from ~60º N to the palaeoequator (Figure 3J). In the Southern Hemisphere, sampling is highest at ~45° and between ~75–90°. Theropods have a rich and almost ubiquitous record from ~75° N down to the southern pole (Figure 3K). Sauropod occurrences peak around the palaeoequator (0–15° N), with additional peaks at 45° N and 30° S. Sampling declines polewards from these latter two peaks (Figure 3L). Ornithischian diversity (Figure 3J) is highest at ~40° N, with smaller peaks at 0–15° N and at ~60° S. Theropod diversity is highest at 45° N, with a second peak at 40° S; genus richness declines equatorwards and polewards from these two peaks (Figure 3K). Sauropods peak in diversity at ~40° in both hemispheres, with the Southern Hemisphere peak representing their acme (Figure 3L). Their genus richness declines equatorwards and polewards from these two peaks.

The Santonian–Maastrichtian ('latest' Cretaceous) interval has the most densely sampled and latitudinally continuous record of Mesozoic dinosaurs. Ornithischian sampling is concentrated between 30–90º N, with the peak at ~50–60º (Figure 3M). Sampling is low across most of the palaeoequatorial region and the Southern Hemisphere, with a minor peak in sampling at ~45º. Theropods are well-sampled in both hemispheres, especially the Northern Hemisphere (~30–90º), with peaks at ~45º N and ~30º S (Figure 3N). Sampling of theropods is low to absent at the palaeoequator and at polar latitudes (>60º) in the Southern Hemisphere. The record of sauropods is richest at 30º N, with a Southern Hemisphere peak in sampling between ~20–40º (Figure 3O). Sampling declines equatorwards and towards the poles from these two peaks. Ornithischians peak in diversity at ~40–70° in the Northern Hemisphere, with a steep decline towards the palaeoequator, followed by a slight rise towards 40° S (Figure 3M). Theropods have a bimodal gradient, with peaks at ~20–40º N and 20º S, declining equatorwards and from these peaks. Latitudinal patterns in sauropod diversity could not be reconstructed for the Santonian–Maastrichtian via SQS, which is probably symptomatic of how strongly dominated the Late Cretaceous sauropod record is by Cenomanian–Coniacian occurrences (i.e. compare Figure 3L and 3O). As such, we reconstructed their diversity for the Late Cretaceous epoch (i.e. Cenomanian–Maastrichtian). The diversity of sauropods is greatest in the Southern Hemisphere, concentrated between ~20–65º, and peaking at 40º. In the Northern Hemisphere, there is a low peak in sauropod diversity at ~20–30º, with a clear decline polewards. Sauropod diversity is low around the palaeoequator.

The North American and East Asian records are unusually densely sampled, with the former largely devoid of sauropods even at intermediate latitudes. To evaluate the effect of these regions in generating global patterns, we repeated analyses for each time bin after removing their fossil occurrences. The main differences between these patterns and those presented for the global dataset (Figure 3) are reported here and illustrated in the Supplemental Information (Figures S1 and S3). Whereas general patterns for ornithischians and sauropods are broadly maintained (Figures S2 and S3), there is a steeper gradient in the northern latitudinal extremes when the North American and East Asian records are removed. Theropod diversity patterns are more strongly affected (Figure S1), particularly in the Cretaceous, with a more prominent Southern Hemisphere peak in the Aptian–Coniacian (Figure S4D) and Santonian–Maastrichtian (Figure S5E). Sauropod diversity is broadly consistent in the Early–Middle Jurassic and Late Cretaceous (Figure 3L and S2), although their Northern Hemisphere gradient terminates at lower palaeolatitudes with the exclusion of the North American and East Asian records. Beyond the specific patterns recovered with the exclusion of these densely sampled records, a Southern Hemisphere peak is still recovered for sauropods, which is particularly marked in the Cretaceous.

Evaluating the effect of spatiotemporal biases on the distribution of Mesozoic dinosaur diversity highlights the importance of considering the structure of the geological record when reconstructing macroevolutionary and macroecological patterns. This includes sampling heterogeneity between hemispheres, as well as latitudinally and longitudinally. Although methods such as coverage-based sampling standardization can reduce the impact of such factors, they cannot distinguish genuine

absences from sampling artefacts. As such, below we combine this approach with habitat suitability modelling to further elucidate the geographic distribution of Mesozoic dinosaurs.

Quantifying climatic niche occupation and suitable palaeogeographic area

Reconstructions of palaeoclimatic niche occupation throughout the Jurassic–Cretaceous interval (see Quantification and statistical tests section in the STAR★Methods) show a strikingly different climatic range for sauropods compared to other dinosaurs (Figure 4), providing additional support that they were characterized by a distinct geographic distribution (Figure 3). There is a statistically significant distinction in the temperature of the coldest and warmest months, with sauropods consistently occupying a range of higher temperatures than other dinosaurs (Table 1). When considering precipitation of the driest and wettest months, sauropods occupy significantly lower precipitation values than other dinosaurs (Table 1). Ornithischians and theropods occupy comparably wider ranges of higher precipitation values, although differ significantly from one another in their specific ranges (Table 1). All these results are robust when tested for the effect of sample size, with a small magnitude effect (Table 1).

Climatic suitability using the DOMAIN algorithm[51] is presented for several representative stages of the Jurassic–Cretaceous interval with robust model outputs (Figure 5). The complete range of stage-based outputs is documented in the SI. Models for the Early–Middle Jurassic performed poorly because of the low amount of training data points and so are not discussed here. The Tithonian (152–145 Ma, Late Jurassic, Figures 5A–C) shows a latitudinally restricted distribution for all dinosaurs, with an equivalent tropical distribution in both hemispheres, with palaeoequatorial South America and northeast Africa notable exceptions. Sauropods and ornithischians are excluded from high polar regions, with this especially marked in the latter clade, with much of East Asia also unsuitable.

In the Albian (113–100 Ma, late Early Cretaceous; Figure 5D–F), predicted climatically suitable areas for ornithischians and theropods cover much of the globe. They extend from northernmost Alaska to southern Australia and the northern Antarctic coastline. Only palaeoequatorial South America and central Africa, as well as the Antarctic and northern Asian interiors, are reconstructed as largely unsuitable (Figure 5D and 5E). By contrast, latitudinally extreme areas are unsuitable for sauropods (e.g. the Arctic, Antarctica, and Australia, except for its northwestern area; Figure 5F), with a sharper climatic barrier at ~50–60° in both hemispheres.

By the early Late Cretaceous (Cenomanian, 100–93 Ma), Antarctica is reconstructed with heightened suitability for ornithischians. This continent is slightly less suitable during this interval for theropods than it was in the Albian, but there is an emergence of a suitable corridor for sauropods along its northern coastline. There is a subtle decrease in suitability in Australia for theropods compared to the Albian, whereas more of this continent is now suitable for sauropods. There is also a reduction in suitability at mid-latitudes in South America for ornithischians. Habitability at high

northern latitudes shows an increase in ornithischians, with only the polar extremes remaining as low suitability areas.

The last stage of the Mesozoic, the Maastrichtian (72–66 Ma), shows an almost cosmopolitan distribution of habitat suitability for theropods and ornithischians (Figure 5J and 5K), ranging from northern Alaska to the Antarctic interiors, with only a spatially limited extent of unsuitable area (including parts of northern Europe and western Australia). In stark contrast, sauropods are characterised by a sharp climatic barrier at around 60°. Whereas the southern continents, other than Antarctica and parts of Australia, are almost entirely suitable, only palaeolatitudes below ~50–60° on the northern landmasses are characterised by habitats suitable for sauropods (Figure 5L).

These climatic suitability maps demonstrate the presence of temperature-related barriers for sauropods in multiple Mesozoic stages. This is particularly marked in the cold seasons, with temperature ranges for sauropods skewed towards higher temperatures than in theropods and ornithischians (Figures 4 and S4). As such, this is the climatic variable that most strongly affects the spatial distribution of sauropods (Figures 4 and S4). For this reason, we reclassified palaeogeographic maps for each of the three dinosaur clades based on the 1st and 3rd quartiles of the thermal range occupation during the cold season (Figures 4 and S4), as well as the broader absolute maximum and minimum temperature values (Figure 6). These clipped models show that areas in the most extreme palaeolatitudes are outside the fitted thermal range for sauropods, whereas these regions remain suitable for ornithischians and theropods, particularly in the Northern Hemisphere (Figure 6). Areas maintaining high suitability across the entire time interval under study are present on most Gondwanan landmasses, particularly South America, Africa, and India. These results demonstrate that minimum cold temperatures are a stronger biogeographic constraint for sauropods than for either theropods or ornithischians, even in warmer time intervals (e.g. Figures 6A and 6G).

Our analyses related to habitat suitability modelling are dependent on the General Circulation Model outputs used herein (see STAR★Methods), hence the exclusion of sauropod suitable habitats at extreme latitudes modelled in this study may be dependent on climate model choice and their intrinsic assumptions (e.g. CO_2 concentration settings), potentially affecting our conclusions (though see Chiarenza et al.[23] for sensitivity analyses). Furthermore, estimating a suitable climatic niche for fossil clades may be subject to incomplete sampling of their distributional range, an effect especially relevant in the fossil record[52,53]. This is particularly important at the edges of clade ranges, which in some cases are bounded by an absence of collections entirely, rather than localities in which some clades are absent. Despite these concerns, the global nature of this dataset, and the consistent results across broad regions and time scales, offers confidence in our results.

Discussion

Geographic partitioning in Mesozoic dinosaurs and climatic exclusion of sauropods from high latitudes

Although these suitability maps do not consider other geographic or biological constraints (e.g. dispersal capabilities, phylogenetic history, biotic interactions), they provide a novel framework for how, where, and when climatic barriers and filters might have affected the biogeographic history of dinosaurs. Colder, latitudinally extreme polar regions are predicted to have offered especially low suitability for sauropods (Figures 5F, 5I and 5L). Spatiotemporal sampling often demonstrates high levels of coverage in these areas for ornithischians and theropods (Figure 3), indicating that sauropods were at least genuinely rare at high palaeolatitudes, if not entirely absent. Whereas ornithischian and theropod dinosaurs were present at polar palaeolatitudes throughout much of the Mesozoic[23,54–56], sauropods have yet to be reported from palaeolatitudes higher than ~65°[42–44]. High diversity levels at palaeolatitudes of ~40–50° are consistently recovered for theropods and ornithischians, particularly in the Northern Hemisphere. Although sauropod diversity is often high at such palaeolatitudes in the Southern Hemisphere, their Northern Hemisphere peak tends to occur at lower latitudes (~30°) (Figures 3L and S2). These distinctive patterns of latitudinal distribution and diversity are robust to alternative binning approaches, and they remain after excluding the densely sampled records of North America and East Asia. This potentially indicates that the more climatically equable Gondwanan landmasses (particularly Africa and South America) might have housed ideal habitats for sauropods for prolonged time intervals. By contrast, even in warmhouse or hothouse climate states (e.g. Figures 1C and 1D), the conditions at the poles were always colder than sauropods could tolerate. As such, the latitudinally restricted geographic distribution of sauropods might have resulted from climatically-driven habitat suitability[57,58] that thereby constrained their palaeobiogeographic history.

Palaeolatitudinal maxima for sauropods (latitude ~65°) were reached during the Kimmeridgian–Barremian[44], and Cenomanian–Turonian[44] intervals (Figure 4). In the Late Jurassic, dinosaur-dominated ecosystems occurred in a prevalently seasonal to tropical biome for a latitudinally broad band[59]. The richest sauropod localities seem to have coincided with habitats characterised by semi-arid environments. The Cenomanian–Turonian Thermal Maximum (94–91 Ma) was one of the warmest intervals of the Phanerozoic[60]. High temperatures seem to have supported a diverse inland flora, while transient warming and cooling events during this interval might have boosted the spread of savanna-type, angiosperm-rich floras, at the expense of conifer-dominated forest ecosystems[60]. Similar to Late Jurassic conditions[59], a biome characterised by a warmer climate, high-productivity, and widespread savanna-like environments might have allowed the proliferation of large-sized primary consumers in the early Late Cretaceous[8]. While high-latitude sampling in the Jurassic is limited, precluding a robust assessment of latitudinal maxima, Late Cretaceous dinosaur bearing localities at high northern latitudes are well-sampled both in terms of body fossils and ichnofossils[26,55,61,62]. These Late Cretaceous high-latitude sites (e.g. in the Maastrichtian Prince Creek Formation in Alaska[55]) provide a rich record of ornithischian and theropod dinosaurs, but no evidence of sauropods. In the Southern

Hemisphere, an extensive record of ornithischian and theropod dinosaurs has been documented from densely sampled Early Cretaceous deposits in Victoria, southeastern Australia, without a single recognised sauropod occurrence[44,55]. Given the intensity of sampling and high-recovered diversity of other dinosaurs in macro-, micro-, and/or ichnosites in these and other high-latitude faunas, at least isolated elements of sauropods, such as teeth or footprints, would be expected if these taxa were genuinely present. Quantitative assessment of geologically/taphonomically-dependant biases in the sauropod record support this interpretation of their genuine absence from high latitudes[58,63,64].

The existence of dinosaur 'bioprovinces', characterised by different faunal compositions, have long been proposed, particularly between northern and southern landmasses. Bonaparte[65] proposed a biogeographic partitioning between the main clades of Mesozoic dinosaurs, which reached a heightened phase in the Cretaceous. A 'Eurogondwanan fauna', characterised by the presence of titanosaurian and rebbachisaurid sauropods, plus abelisaurid and spinosaurid theropods[66], was proposed to differentiate Gondwana and southern Europe from the remainder of the Northern Hemisphere. Although many of the original 'endemic' Gondwanan groups have now been recognised in Laurasia (e.g.[67–71]), Gondwana still records the highest overall richness in sauropod dinosaurs, particularly of Cretaceous titanosaurs[72]. Given the available data, a predominance of sauropods in southern landmasses and in equatorial areas appears to be a genuine characteristic of dinosaur biogeography (e.g.[57,65]). Africa and South America, in particular, are characterised by a high number of sauropod-rich fossil-bearing assemblages (Figures 1 and 3). In South America, sauropods accounted for more than 50% of dinosaurian faunal assemblages for at least 90 million years (Kimmeridgian–Maastrichtian; Figures 1B–F and 3). The limited nature of the Late Cretaceous African dinosaur record (e.g.[73]) obscures our understanding of patterns on this continent, and only future discoveries will elucidate whether this 'sauropod-rich' trend characterised Africa until the non-avian dinosaur extinction[74]. Comparably high proportions of sauropods as a component of a fossil assemblage are only reached elsewhere during warmer intervals (Figure 1), especially during the Late Jurassic in North America, Europe, and Asia, and the middle Cretaceous in Australasia[43] (Figure 5).

Given the warmer, latitudinally more equable climate of the Mesozoic, an intrinsic explanation for a climatic regulation of sauropod palaeolatitudinal range seems most likely, but its instantiation remains to be determined. The most direct explanation would be that high-latitude regions were thermally hostile to the maintenance of viable sauropod populations, and that these dinosaurs were simply unable to thrive in such settings. More indirect influences are also possible, but are difficult to test in the fossil record. Perhaps sauropods were physiologically capable of living in high-latitude environments, but were just much poorer at doing so than their dinosaurian cousins. Although these animals would have been harvesting and processing food in very different ways and had markedly different energetic requirements[7], sauropods might have been outcompeted on a grand scale by ornithopods and ceratopsians in the Northern Hemisphere, resulting in their total absence from high-latitude faunas in which resources might have been scarcer.

Ornithischians might have been merely more efficient at exploiting these resources[7,75,76]. By contrast, the near-absence of ceratopsians in the Southern Hemisphere[77], and the fact that late diverging ornithopods (i.e. Hadrosauridae[78]) were latecomers to these landmasses, might have allowed sauropods to retain a presence in far-southern latitudes where they could not do so in the north[79]. Finer-scale investigations of sauropod-rich and sauropod-depauperate dinosaur communities, along with their specific palaeoenvironments, would help to address such questions.

A climatic role in regulating the geographic distribution of sauropod diversity has been previously suggested[57,58,80], including their exclusion from cool climatic zones, particularly during time intervals characterized by a steep latitudinal temperature gradient[43]. These previous observations, combined with the results presented herein (Figures 5 and 6), support a window of high-latitude dispersal for sauropods from South America to Australasia via Antarctica in the mid-Cretaceous[43,81]. This was triggered by the development of a suitable corridor along the northern coast of Antarctica, coupled with increased climatic suitability in Australia, with this route most favourable in the Cenomanian. This high-latitude potential dispersal corridor for sauropods remained present in the middle Cretaceous even in the lowermost range of their cold climate niche (e.g. Figures 6F and I). The rich record of sauropods from the Cenomanian of Queensland, northeastern Australia[82], might result from such a climatically mediated dispersal event. In the Northern Hemisphere, the presence of *Alamosaurus* in the Maastrichtian of southwestern USA, the only known post-Cenomanian sauropod in North America[83,84], has been explained as an immigrant lineage from either a South America or East Asia[85–87]. The latter route is based on the recovery of a sister taxon relationship between *Alamosaurus* and the contemporaneous Mongolian *Opisthocoelicaudia* in some phylogenetic analyses (e.g.[86,88]), but would necessitate a high latitude dispersal via Beringia while leaving no relict populations in Canada or the northern US. The climatic unsuitability of the high latitude Beringia land bridge for sauropods in the Late Cretaceous suggests that an East Asian origin for *Alamosaurus* might not have been possible (Figure 5F and I). By contrast, other analyses recover *Alamosaurus* as a member of an otherwise South American clade (e.g.[89–91]). Climatically, our results indicate that South America is the only viable origin for the *Alamosaurus* lineage, with high suitability in the northern part of South America in the Cretaceous, and an ephemeral land bridge or filter barrier between the Americas present at least at some point during the late Campanian–Maastrichtian (e.g.[79,90,92,93]).

We suggest that the shallow latitudinal temperature gradient in the Mesozoic enabled the pole-to-pole distribution of ornithischian and theropod dinosaurs, resulting in flattened or bimodal latitudinal biodiversity gradients in these two clades. By contrast, sauropods were more tightly constrained by temperature, such that the distribution of their diversity was closer to the unimodal latitudinal biodiversity gradient that characterizes most taxonomic groups today. We propose that this difference results from a distinct biology and/or physiology in sauropods relative to other dinosaurs.

Mosaic biological traits indicating multifaceted thermal sensitivities in non-avian dinosaurs

The temperature-dependent distribution of sauropods has potential relevance to hypotheses of their biology and physiology, although precise implications cannot be constrained without additional data, such as histological or geochemical correlates of their thermophysiology. Nevertheless, the pattern of higher sauropod diversity at lower palaeolatitudes[42] (Figure 3), and their absence from high latitude dinosaur assemblages, particularly during cooler intervals (e.g.[43,44,54,94]) and in the Northern Hemisphere, raises the question of whether sauropod physiology was most efficient in warmer environments. The palaeolatitudinal distribution of sauropod diversity is broadly similar to that of crocodylomorphs[42], with temperature being a primary driver in shaping the latter group's latitudinal extent throughout their evolutionary history[95–99]. Given that extant crocodylomorphs (i.e. crocodylians) are ectothermic[100] and that the thermophysiology of at least some extinct members appears to be comparable[101], this could indicate that sauropods had a similar thermoregulatory strategy. Furthermore, given that crocodylomorph body size appears to have a positive correlation with temperature[102] (though see Godoy et al.[103] for a contrasting result), this might explain the occurrence of the largest known sauropods (>50 tonnes) in the latest Albian–Cenomanian hothouse[8,104], as well as some of the smallest known sauropod species (<10 tonnes) in the late Campanian–Maastrichtian[105], coinciding with one of the coolest intervals of their evolutionary history[106]. Additionally, other observations, summarised below, raise the possibility of genuinely distinct and biologically-induced distributional ranges between different dinosaur clades.

A mix of traits might have conferred on sauropods a higher adaptation for heat dissipation (compared to modern mammalian analogues), including an avian-like respiratory system[107], long necks and tails shaping their overall morphology into a higher proportional body surface area[108,109], and unusual adaptations in their neurovasculatory networks[110]. By comparison, many non-avian and all avian theropods were characterised by the presence of insulating integument, which has been suggested as an anatomical correlate of endothermy[111]. Similarly proposed homologous structures have been also found in early diverging ornithischians[112,113]. No similar integumentary structure has yet been found in sauropods (or the more inclusive clade Sauropodomorpha), with evidence of scaly integument with osteoderm-like structures even in embryonic specimens[114,115], making inferences of feather-like integument in sauropods even less likely[116].

Our biogeographic findings, suggesting the presence of thermoconformity in the largest dinosaurs (Sauropoda), could imply a 'meso-thermic' thermophysiology, which is consistent with an elevated metabolic rate, but lacking a thermal 'set point'[12]. Thus, sauropods would have exhibited an apomorphic physiology, emphasising poikilothermy rather than endothermic homeothermy. These traits might have released thermal constraints on the evolution of their body size, bounding them to more equable climate zones. Another possibility hinges on different models proposed for the phylogenetic topology at the base of Dinosauria (e.g.[117,118]). A sister group relationship between theropods and ornithischians (Ornithoscelida[119]), to the exclusion of sauropodomorphs, such as proposed by Baron et al.[117], might imply an

endothermic thermophysiology as synaptomorphic for ornithoschelidans (sensu Huxley[119] after Baron et al.[117]), while sauropodomorph dinosaurs might have retained the plesiomorphic ectothermic condition (although see Seymour et al.[120] for a different view on physiological polarity in archosaurs). The dominant, traditional hypothesis for phylogenetic relationships in Dinosauria[118,121,122] would, on the other hand, imply either the independent acquisition of endothermy in both ornithischians and theropods, or the secondary loss of such thermophysiology in sauropods. Additionally, the possibility of feathers (or their analogue/homologue structures) in the closely related pterosaurs[122] might imply an even earlier synaptomorphic acquisition of a tachymetabolic condition, eventually lost in later diverging clades like Sauropoda. The reason for such secondary loss is unknown, but could possibly be due to trophic constraints (e.g. unrealistic foraging habitat range requirements for a purported endothermic sauropod population[123–126]), observations that can be tested by future discoveries and further study. Regardless of the thermophysiological implications, our study suggests that no or exceedingly few sauropod occurrences will ever be found in polar palaeolatitudes outside of warm-house or hot-house intervals.

Prolonged climatic fluctuations during the Late Cretaceous have previously been invoked as the cause of a long-term decline in dinosaur diversity that began well before their extinction at the Cretaceous/Paleogene boundary[118,127,128]. Although climate might have acted as a primary driver for constraining distributional patterns of dinosaurs throughout the Mesozoic, dramatic climatic changes that occurred prior to the Late Cretaceous[106] (Figures 1 and 5H–I) appear to have had no large-scale or prolonged negative effects on the group's diversity. Empirical evidence[26] and modelling approaches[29,46], including the results reported in this study, underscore the high evolutionary adaptability of dinosaurs to long-term, climatically-driven, macroecological changes, which was probably only eroded by a geologically instantaneous episode, such as that caused by the end-Cretaceous Chicxulub impact event[23,129,130].

The methodology presented herein offers a new predictive tool to further constrain biogeographic hypotheses, which have been so far only supported by phylogenetic reconstructions and inferred land connections from palaeogeographic and tectonic reconstructions. Combining climatic suitability and phylogeographic models could potentially cast new light on long-standing debates on dinosaur biogeography (for example why tyrannosauroids did not disperse into South America), as well as for constraining the likely timing 'window' of dispersals events in general. This holistic approach, which can combine fossil occurrences, Earth System and phylogeographic models, has the potential to provide a new framework for testing hypotheses pertaining to habitat and dispersal dynamics on an evolving Earth.

Author contributions

AAC and PDM conceived and designed the research; AAC, PDM, AF and MC produced and collected data; AAC and SV analysed the data; AAC produced the figures; AAC, PDM, SV, MC wrote the manuscript. All authors provided critical comments on the manuscript.

Declaration of interests

The authors declare no competing interests.

Main-text figure/table legends
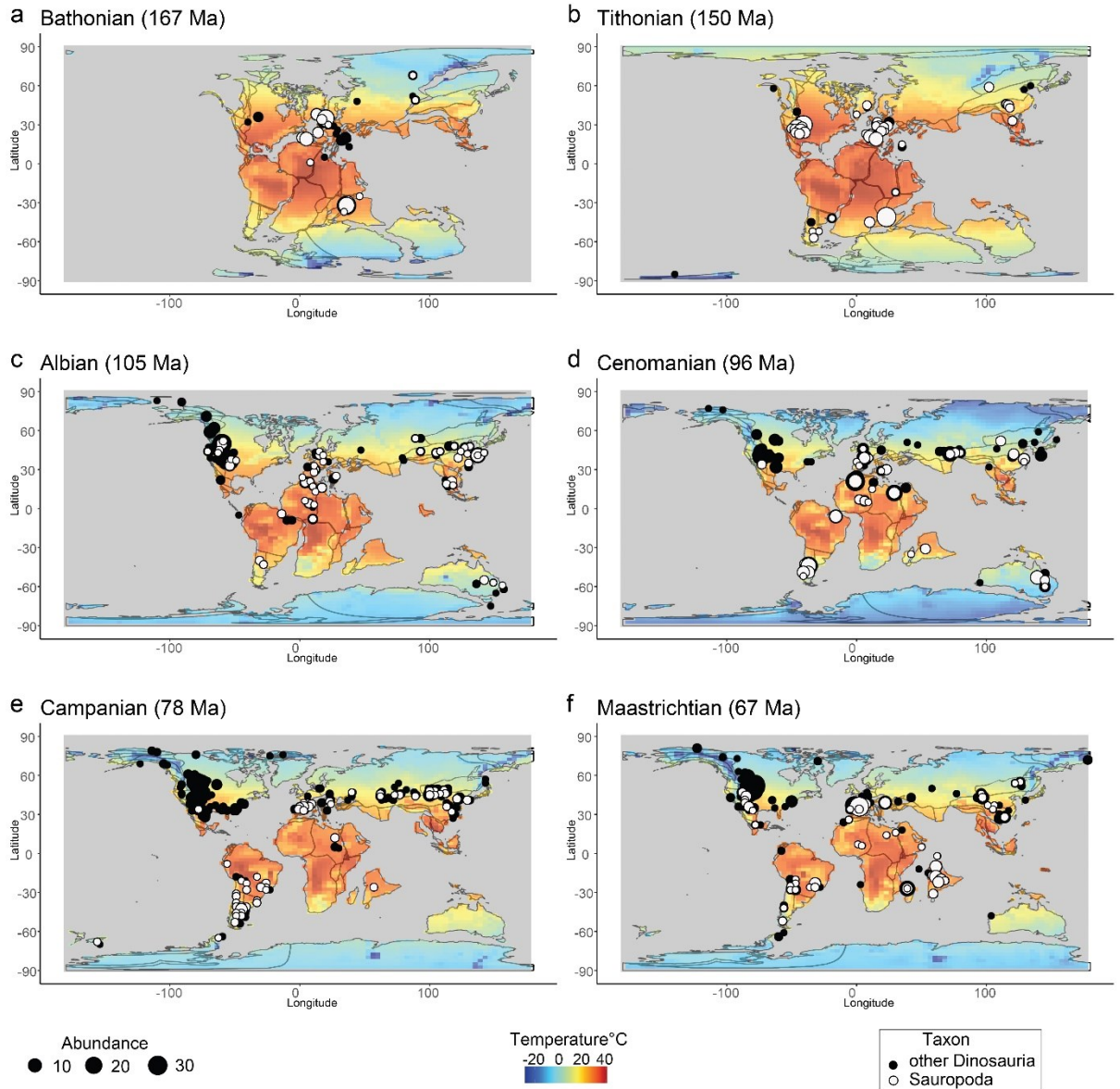
Figure 1. Palaeobiogeographic distribution of relative abundance between dinosaur groups mapping temperature during the Jurassic–Cretaceous interval. Palaeogeography, abundance and mean annual temperature based on General Circulation Modelling (GCM; STAR★Methods); A, Bathonian; B, Tithonian; C, Albian; D, Cenomanian; E, Campanian; F, Maastrichtian. **Related to Data S1.**

Figure 2. Palaeolatitudinal distribution of sauropod occurrences from Jurassic–Cretaceous. Green circles represent sauropod, while black circles indicate other non-sauropod dinosaur occurrences. Yellow, shaded area represents the tropics. **Related to Data S1.**

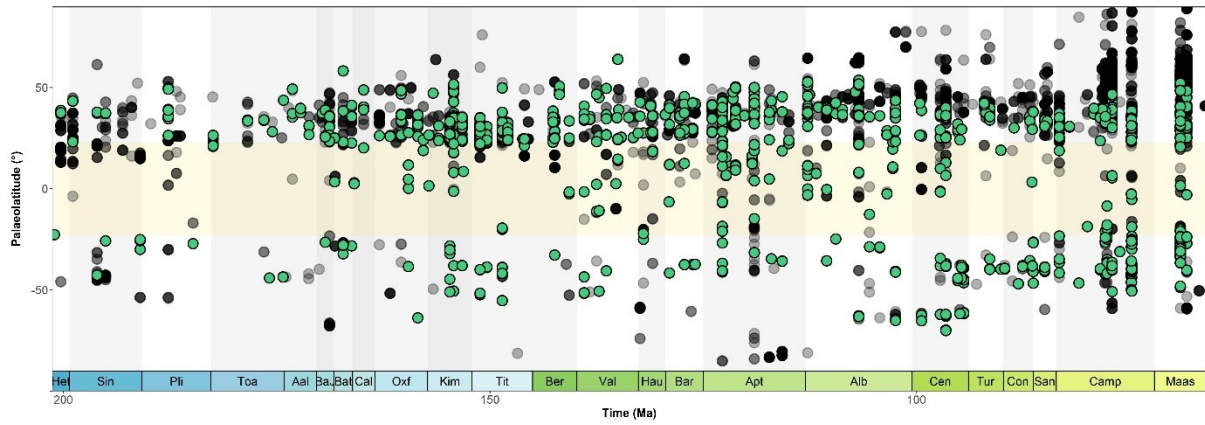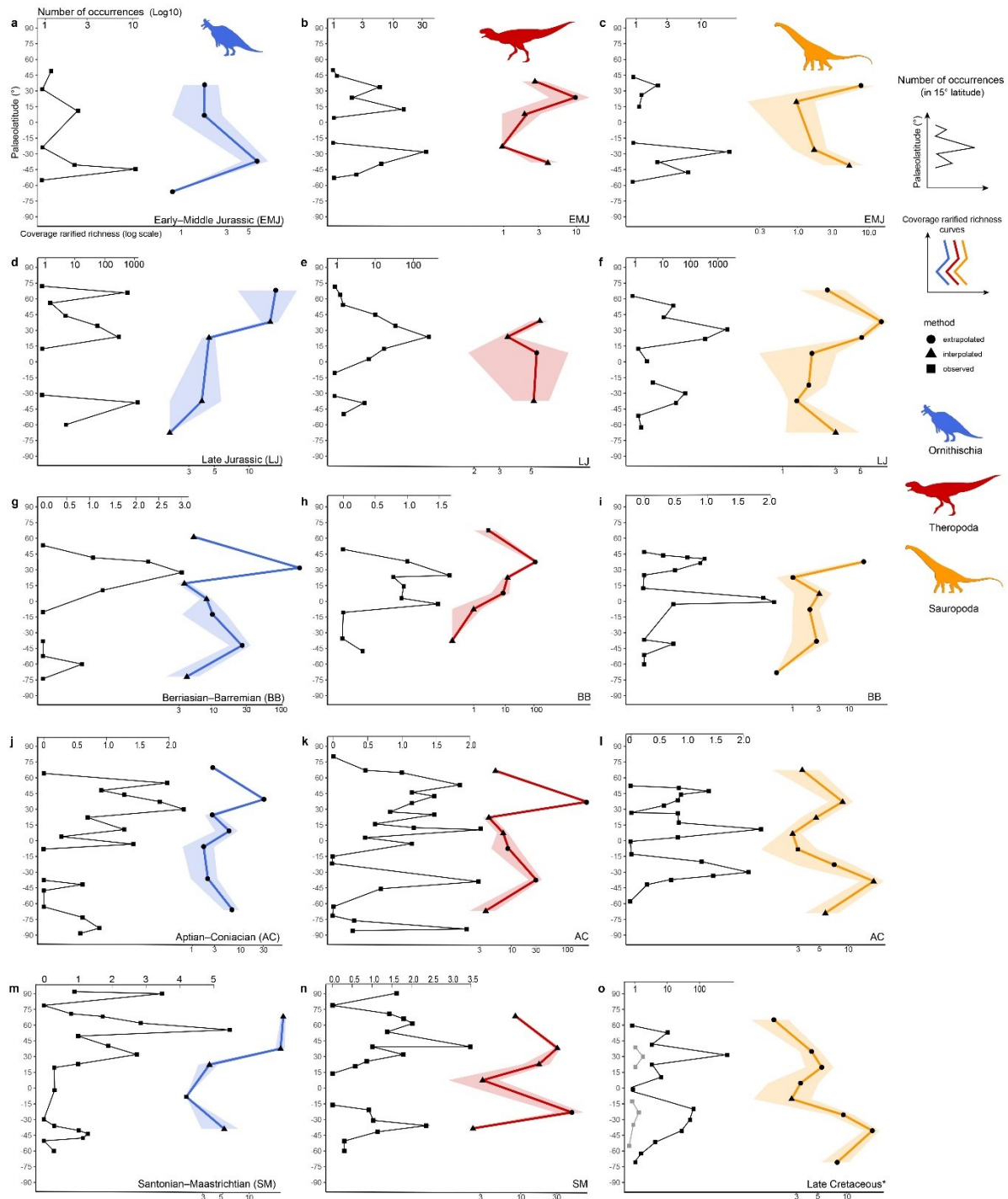**Figure 3. Latitudinal subsampled non-avian dinosaur (genera) richness from Jurassic–Cretaceous.** Intervals depicted are at a quorum of 0.4 for latitudinal bins (top x-axis). A–C, EMJ, Early–Middle Jurassic; D–F, LJ, Late Jurassic; G–I, BB, Berriasian–Barremian; J–L, AC, Aptian–Coniacian, M–N, SM, Santonian–Maastrichtian; The asterisk (*) in o indicates the use of a coarser Epoch-based bin (Late Cretaceous) for sauropods given the very low number of occurrences in each latitudinal bin in the Santonian–Maastrichtian interval (grey line with squares in o). Also included are latitudinal raw occurrences for 15° (black lines, y-axis) as an indicator of

underlying data quality. Unfilled points are contributed to by <10 collections. See also Figures S1–S3. **Related to Data S1**
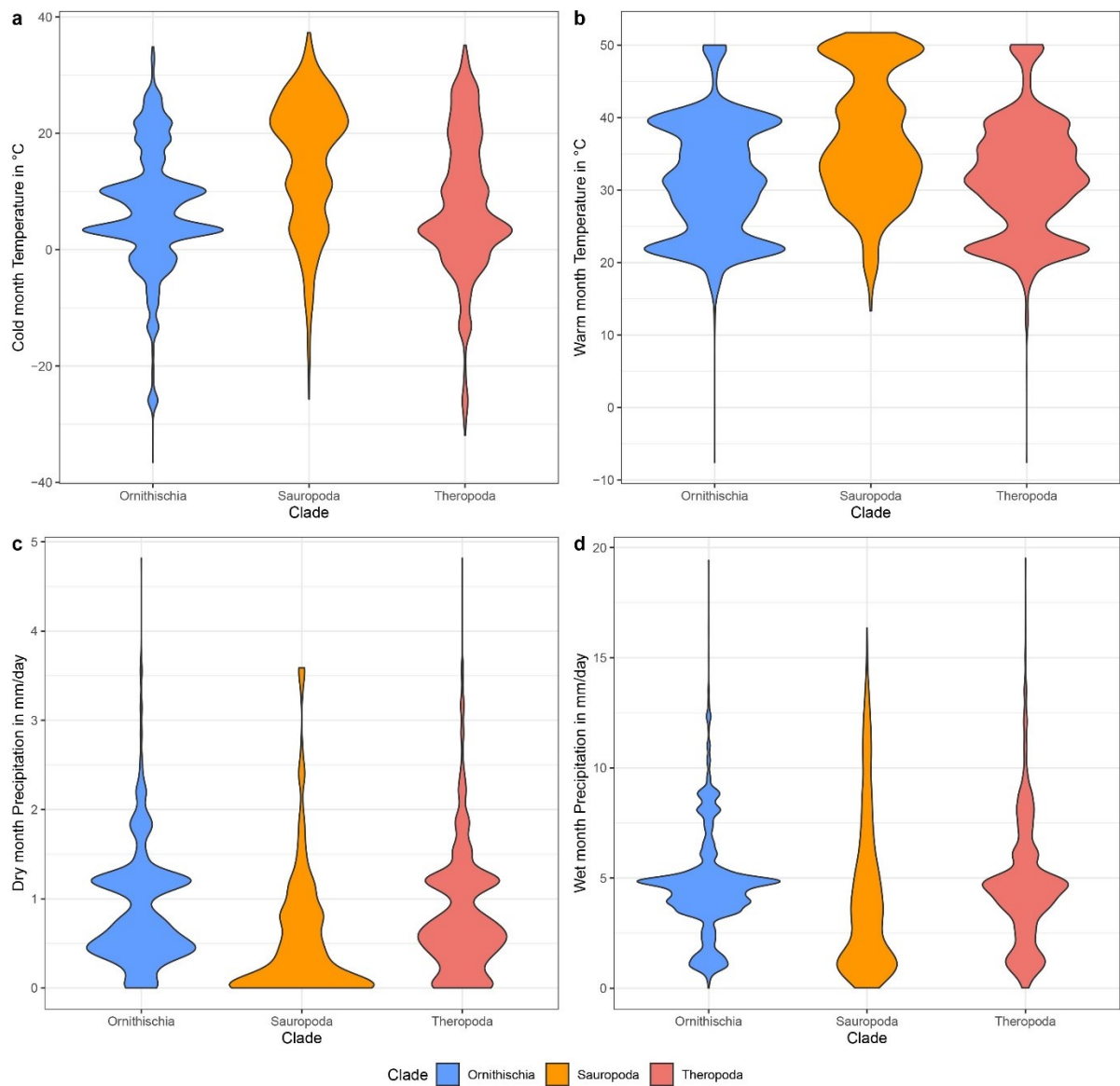
Figure 4. Violin plots illustrating the Jurassic–Cretaceous palaeoclimatic niche occupation of the three main dinosaur subclades. Blue color represents Ornithischia, orange represents Sauropoda and red non-avian Theropoda. Variables represented are temperature in Celsius (°C) of the cold (A) and warm (B) months, and precipitation values of the dry (C) and wet (D) months in mm/day. See also Figure S4. **Related to Data S1 and Data S2.**
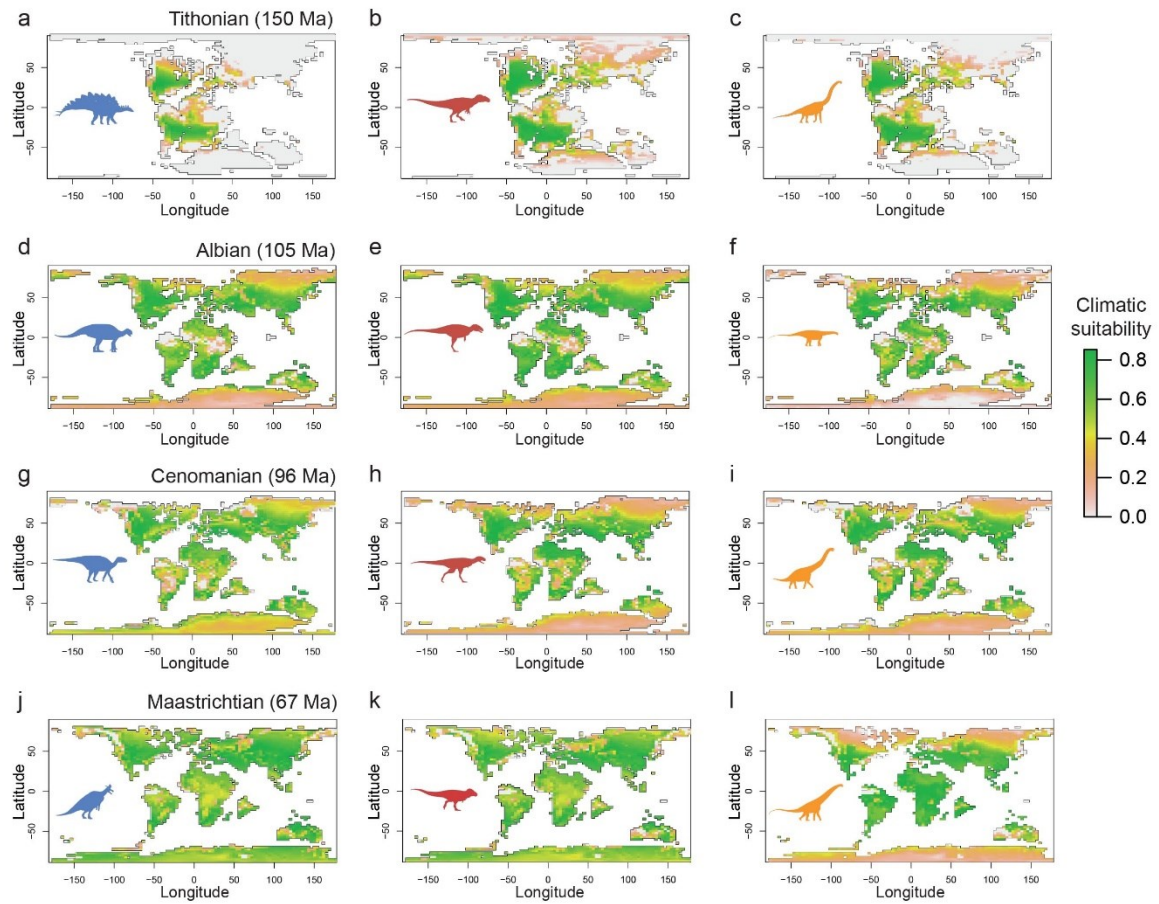
Figure 5. Palaeogeographic maps of climatic suitability during different stages of the Mesozoic for non-avian dinosaurs. Blue color represents Ornithischia, orange represents Sauropoda and red non-avian Theropoda. Stages represented are: A–C, Tithonian; D–F, Albian; G-I, Cenomanian; J–L, Maastrichtian. **Related to Data S1 and Data S3.**
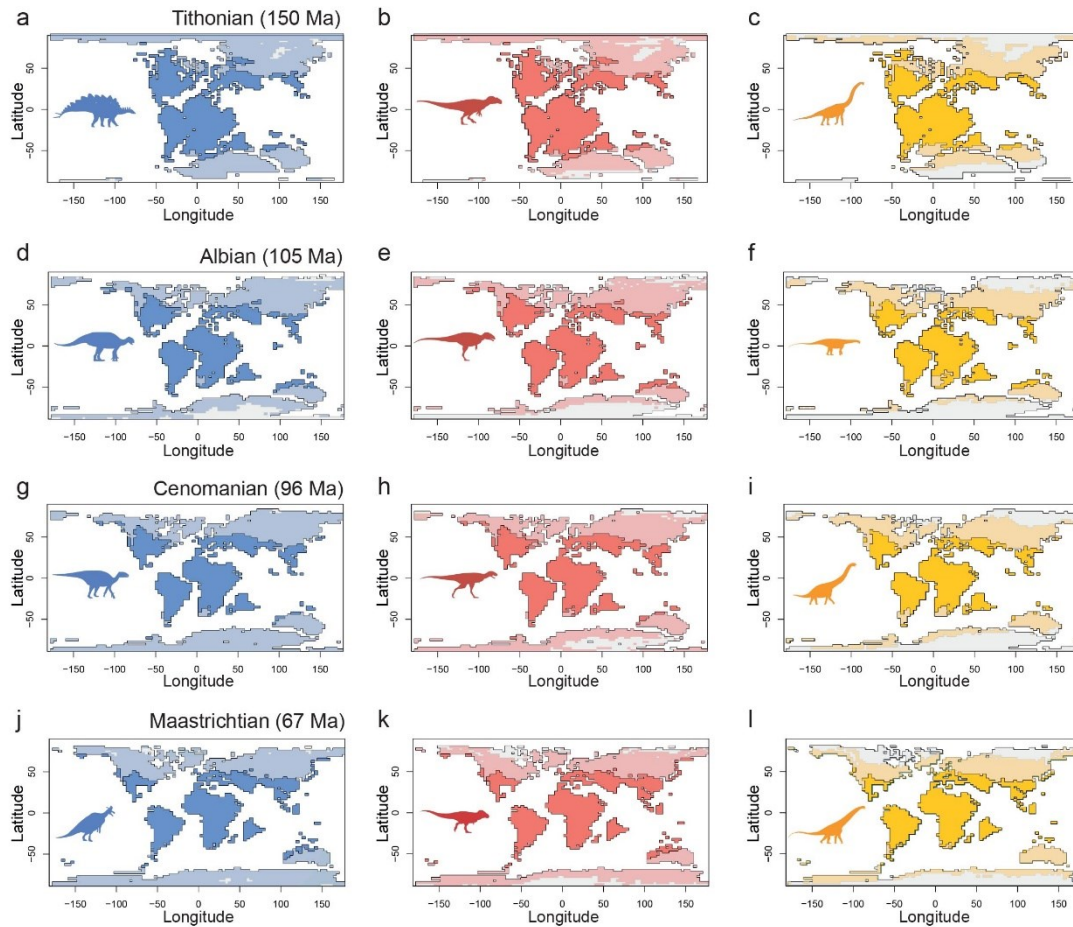
Figure 6. Spatial projections on Mesozoic palaeogeographies of the climatic niche occupied by dinosaur subclades. Shaded colors represent the climatic niche occupied (absolute maximum and minimum values, i.e. larger climatic niche) while darker colors portray the 1st and 3rd quartile (smaller climatic niche) of their thermal range occupation in the temperature of the coldest month GCM-spatially explicit variable layer. Stages represented are: A–C, Tithonian; D–F, Albian; G-I, Cenomanian; J–L, Maastrichtian. **Related to Data S1 and Data S2.**

Table 1. Results for the Kruskal-Wallis and Dunn's test. Abbreviations: n, number of observations; p.adj, adjusted p-values for multiple comparisons; sa, sample size-adjusted tests. Asterisks indicate significance levels based on p-values, with '*' significant at p ≤ 0.05, '**' significant at p ≤ 0.01, '***' significant at p ≤ 0.001, and '****' significant at p ≤ 0.0001; ns indicate non-significant results. **Related to Figures 4, S4 and Data S2.**

| Climatic variable	group 1	group 2	n 1	n 2	Statistic	p	p.adj	p.adj.signif
Cold month mean Temperature (°C)	Ornithischia	Sauropoda	6210	2008	27.926203	1.28E-171	3.85E-171	****
Cold month mean Temperature (°C)	Ornithischia	Theropoda	6210	5752	3.371784	0.00074683	0.00224049	**
Cold month mean Temperature (°C)	Sauropoda	Theropoda	2008	5752	-25.27795	5.58E-141	1.68E-140	****
Warm month mean Temperature (°C)	Ornithischia	Sauropoda	6210	2008	24.084834	3.60E-128	1.08E-127	****
Warm month mean Temperature (°C)	Ornithischia	Theropoda	6210	5752	1.1738336	0.240461689	0.72138507	ns
Warm month mean Temperature (°C)	Sauropoda	Theropoda	2008	5752	-23.02518	2.61E-117	7.83E-117	****
Dry month Precipitation (mm/day)	Ornithischia	Sauropoda	6210	2008	-26.74871	1.28E-157	3.83E-157	****
Dry month Precipitation (mm/day)	Ornithischia	Theropoda	6210	5752	-5.571917	2.52E-08	7.56E-08	****
Dry month Precipitation (mm/day)	Sauropoda	Theropoda	2008	5752	22.558448	1.11E-112	3.33E-112	****
Wet month Precipitation (mm/day)	Ornithischia	Sauropoda	6210	2008	-13.78299	3.23E-43	9.68E-43	****
Wet month Precipitation (mm/day)	Ornithischia	Theropoda	6210	5752	-2.60553	0.00917322	0.02751966	*
Wet month Precipitation (mm/day)	Sauropoda	Theropoda	2008	5752	11.811327	3.41E-32	1.02E-31	****
Cold month mean Temperature (°C) [sa]	Ornithischia	Sauropoda	6210	2008	3546437	1.60E-186	4.80E-186	****
Cold month mean Temperature (°C) [sa]	Ornithischia	Theropoda	6210	5752	17335519	0.005	0.016	*
Cold month mean Temperature (°C) [sa]	Sauropoda	Theropoda	2008	5752	7845850	5.21E-127	1.56E-126	****
Warm month mean Temperature (°C) [sa]	Ornithischia	Sauropoda	6210	2008	3993274	2.72E-130	8.16E-130	****
Warm month mean Temperature (°C) [sa]	Ornithischia	Theropoda	6210	5752	17657438	0.282	0.846	ns
Warm month mean Temperature (°C) [sa]	Sauropoda	Theropoda	2008	5752	7743708	5.58E-115	1.67E-114	****
Dry month Precipitation (mm/day) [sa]	Ornithischia	Sauropoda	6210	2008	8743126	1.24E-162	3.72E-162	****
Dry month Precipitation (mm/day) [sa]	Ornithischia	Theropoda	6210	5752	18870479	8.05E-08	2.41E-07	****
Dry month Precipitation (mm/day) [sa]	Sauropoda	Theropoda	2008	5752	3867455	4.55E-108	1.36E-107	****
Wet month Precipitation (mm/day) [sa]	Ornithischia	Sauropoda	6210	2008	7536688	3.54E-45	1.06E-44	****
Wet month Precipitation (mm/day) [sa]	Ornithischia	Theropoda	6210	5752	18321226	0.014	0.043	*
Wet month Precipitation (mm/day) [sa]	Sauropoda	Theropoda	2008	5752	4785294	2.15E-30	6.45E-30	****

STAR★Methods

RESOURCE AVAILABILITY

Deposited data

Dinosaur fossil occurrences and climate variables used in this study	This study	Data S1
Ecological niche models (DOMAIN/Bioclim) used in this study	DOI: 10.6084/m9.figshare.16930186	Data S3

Software and algorithms

R package mapast V 0.1	https://rdrr.io/github/macroecology/paleoMap/man/mapast-R-package.html.	N/A
R package iNEXT V 2.0.20	https://cran.r-project.org/web/packages/iNEXT/index.html	N/A
R package rstatix V 0.7.0	https://cran.r-project.org/web/packages/rstatix/index.html	N/A
R package dismo V 1.3-5	https://cran.r-project.org/web/packages/dismo/index.html	N/A
R package stats V 4.2.0	https://stat.ethz.ch/R-manual/R-devel/library/stats/html/00Index.html	N/A
R package ggplot2 V 3.3.5	https://cran.r-project.org/web/packages/ggplot2/index.html	N/A
R package raster V 3.5-2	https://cran.r-project.org/web/packages/raster/index.html	N/A

Materials availability

This study did not generate new unique materials.

Data and code availability

The fossil occurrence data and related climatic variables are available as Data S1. Data S2 is a Microsoft Excel file with the summary of each dinosaurian climatic variables (ranges). General Circulation Models and palaeoclimate data used here come from the BRIDGE group and are available at: http://www.bridge.bris.ac.uk/resources/simulations). The ecological niche models are deposited in the public repository FigShare (figshare.com), and available under a CC BY 4.0 licence at this DOI: 10.6084/m9.figshare.16930186.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Not applicable

METHODS DETAILS

Dinosaur occurrence dataset

A global dataset of Jurassic–Cretaceous (Hettangian–Maastrichtian) dinosaur occurrences and collections was downloaded from the Paleobiology Database (paleobiodb.org, accessed 23rd September 2019). Datasets for palaeodiversity analyses were further accessed until the 23rd July 2021 for sensitivity tests. These data represent the current published knowledge on the global occurrences and taxonomic opinions of Dinosauria. Although we vetted for spurious taxonomic occurrences and checked the spatial distribution of Paleobiology Database entries, single data points might have been missed either in the online compiled dataset or during data checking and vetting procedures. For the palaeodiversity analyses, the occurrence dataset was filtered to remove marine and parataxonomic taxa (e.g. eggs and trace fossils; the latter retained for the habitat suitability modelling analyses, as reported below). As some stratigraphic incongruencies emerged regarding some occurrences, we checked and reassigned them to the most accurate chronostratigraphic framework following the most recent palaeontological data/stratigraphic re-evaluation. For example, several occurrences of North American sauropods previously assigned to the Campanian have recently been recalibrated to the late Maastrichtian[131]. Similarly, the dinosaur-rich Adamantina Formation in Brazil has been considered as Turonian–Santonian by some authors[132], but there is a growing consensus that it can be dated to the late Campanian–early Maastrichtian[133]. This updated information was also integrated in the Paleobiology database (PBDB; paleobiodb.org) by one of us (PDM). The dataset was partitioned into the three main dinosaur clades: Ornithischia, Sauropoda, and Theropoda, vetting and retaining valid ichnotaxa down to these taxonomic levels. The dataset comprises 7067 fossil collections containing 14356 occurrences, which after data cleaning and vetting accounted for 12939 representing 6019 ornithischians, 2154 sauropods, and 4766 theropods. Palaeorotations of present-day coordinate data were performed using EarthByte via the PaleoGIS extension for ArcGIS according to the plate models of Seton et al.[134]. Ancient coastlines for the Jurassic–Cretaceous interval were accessed using the R package 'mapast'[135]. Data preparation and analyses were conducted within R v. 3.6.0–4.0.5.

Palaeodiversity and sampling analyses

We computed coverage-based sampling standardised richness at genus level for the three main dinosaur subgroups: Ornithischia, Sauropoda, and Theropoda. We used shareholder quorum subsampling (SQS), using a coverage-based extrapolation approach to reconstruct latitudinal genus richness. This method, first introduced by Alroy[136,136–138], is a subsampling methodology that uses a frequency-distribution coverage (the measure of sample completeness is estimated using Good's u[139]). This

approach is used to theoretically 'equalise' between different assemblages that are heterogeneously sampled, in principle, making them less biased. The SQS method was applied following the procedure outlined by Dunne et al.[29,140] via the R package iNEXT (iNterpolation/EXTrapolation[141]), which uses the analytical corrections from Chao & Jost[142], yielding confidence intervals that allow coverage-based extrapolation (using the Chao1 estimator), in addition to interpolation, based on incidence frequency of the occurrence data (i.e. whether or not a taxon is present in a collection). As noted by previous authors (e.g.[134,140]), relative taxonomic richness trends can change at different quorum levels, and in particular to level down at higher levels. For this reason, different quorum levels (0.3–0.7) were investigated, including the baseline of 0.4 recommended by Alroy[137], to sufficiently represent relative changes in diversity[74,98,143], and in order to explicitly represent the volatility of relative trends. We binned the latitudinal occurrences in 15° spatial bands, with a coarser 45–90° band in each hemisphere due to the very sparse sampling at these high palaeolatitudes (see Dunne et al.[29] for a similar approach). Since the low amount of collections in some latitudinal bins made SQS extrapolation inoperable at high quorum levels, only a quorum level of 0.4 is presented in the results (Figure 3).

Given the further division into latitudinal bins and the scarcity of sampling in some geologic stages compared to others, we used time bins representing multiple stages to reach an adequate number of occurrences to analyse via SQS. Given the lower number of fossil occurrences in the Early and Middle Jurassic, we combined these two bins in a single Early–Middle Jurassic unit (Hettangian–Callovian). In addition to the Early–Mid Jurassic and Late Jurassic (Oxfordian–Tithonian, 163–145 Ma), the Berriasian–Barremian (145–125 Ma), Aptian–Coniacian (125–86 Ma), and Santonian–Maastrichtian (86–66 Ma) were used for the Cretaceous Period. We subdivided the Cretaceous into these three bins to potentially better reflects the macro-geologic depositional regimes that underly fossil preservation in terrestrial systems of these stages[144–147], although at the expense of poorer sampling in each time bin. Counts of taxonomic occurrences in latitudinal bins were used as proxies for underlying sampling effort for palaeodiversity curves and were computed in ggplot2[148].

Palaeoclimate models

GCM-derived palaeoclimate data used here come from the BRIDGE group[149] (http://www.bridge.bris.ac.uk/resources/simulations). These climate simulations were carried out using the coupled AOGCM [HadCM3L-M2.1[150]]. HadCM3L has contributed to the Coupled Model Intercomparison Project experiments, demonstrating skill at reproducing the modern-day climate[150,151] and has been used for an array of different paleoclimate experiments showing skill in simulating past climates[149,152,153]. These GCMs have been used in other recent Mesozoic palaeobiogeographic studies[23,29,46] and further details on model settings, constraints and uncertainties can be found there or in Lunt et al.[149] and Farnsworth et al.[154]. Variables include cold and warm mean 2 meter temperature in °C and precipitation of the dry and wet month mean in mm/day, originally provided at a spatial resolution of 2.75°×3.25° degrees and downscaled at 0.5°×0.5° utilising the Getech Plc. paleogeography in order to produce the topographic

and bathymetric boundary conditions required by the model. The sub-grid scale orographic features of the topography are calculated within the model, enabling finer scale features to have an impact on the climate signal. CO_2 is set at 1120 ppm for each geologic stage and is within the estimated range from that of Foster et al.[155] for the Cretaceous and of Breecker et al.[156] and Franks et al.[157] for the Jurassic. Solar luminosity is calculated for each geologic stage[158], and we use a modern-day orbital configuration. Each simulation is run for 1422 model years and reaches quasi-surface equilibrium. Both regional and large-scale circulation (and associated energy and momentum fluxes), as well as temporal fluctuations, are also resolved and are important determinants of climate. Further details on the implications of these palaeoclimatic modelling constraints on Mesozoic habitat suitability modelling are discussed in the method description (see also the supplementary information) in Chiarenza et al.[23,46], Dunne et al.[95] and Waterson et al.[159], and the effects of some of these constraints (e.g. boundary conditions, such as CO_2 content) in Farnsworth et al.[154].

QUANTIFICATION AND STATISTICAL ANALYSIS

In order to compare the co-occurring climatic variables of the three dinosaurian subclades, testing whether the median or their distributions were significantly different (i.e. null hypothesis coinciding with the observation of equivalence of their medians), we used the Kruskal-Wallis test[160] for two independent groups of samples. This non-parametric test is implemented in R with the base function kruskal.test() of the stats package from the R core team[161]. Using the outputs from the Kruskal-Wallis test, we then used the Multiple Pairwise Wilcox test to highlight which group significantly differs from the other subsets of observations. This test is also implemented in R using the function pairwise.wilcox.test(). To further determine the extent to which the independent variables differ from each other in the subsets and the effect of different sample sizes in the significance of the outcomes (using η [eta squared] as a measure for the Kruskal-Wallis test effect size[162]), we used the Dunn's test [163], a post-hoc analysis for multiple comparisons implemented with a correction to control the experiment-wise error rate and available with the R package rstatix[164]. Results of these tests were plotted in Figure S4 and included in Table 1. All analyses were conducted in R version 3.6.1– 4.0.5 (R Core Team, 2019–2021).

Habitat suitability modelling

To evaluate climatic suitability, we used a two-pronged approach: building a simple habitat suitability model for each dinosaurian subclade in each time interval and spatially projecting their climatic envelopes based on the aforementioned climatic niche filling quantification analysis. We implemented the DOMAIN algorithm[51] using the R package dismo[165], an ecological niche model which uses the Gower distance to measure climatic suitability. The DOMAIN algorithm quantifies the distance between the climatic conditions of the pixels on the map and the closest species observation (in the n-dimension environmental space, not geographically). Although this model is

generally considered as a coarse niche modelling technique[166,167], it has the advantage of simple implementation and minimal assumptions. Given the coarse spatial and temporal resolution of our dataset, combined with our interest of creating suitability maps based purely on climate, we preferred this simple modelling approach compared to other recently implemented ecological niche and habitat suitability modelling, such as that previously employed by our team in the past[23,46,168–170], where limitations and assumptions for these kind of approaches are also discussed. For the climatic envelope approach, we reclassified our stage-specific climatic layers based on the 1st and 3rd quartile (smaller niche) of their thermal range occupation, following our climatic niche occupation analyses (Figures 4 and S4), and the broader absolute maximum and minimum values (larger niche) in the same distribution (Figure 6). Spatial reclassification of habitat suitability maps was implemented with the R package raster[171].

ADDITIONAL RESOURCES

Data S1. Related to Figures 1–6 and S1–S3. Dinosaur fossil occurrences and climate variables used in this study.

Data S2. Related to Figures 4, 6 and S4. Summary statistics of dinosaurian climatic variables (ranges).

Data S3. Related to Figure 5. Ecological niche models (DOMAIN/Bioclim) used in this study are available on FigShare under CC BY 4.0 licence (DOI: 10.6084/m9.figshare.16930186).

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