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Body size evolution through shifting climatic conditions in Mesozoic dinosaurs

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Abstract: Body size evolution is commonly associated with climate change. For example, birds and mammals have been found to decrease in size with anthropogenic global warming. Recent studies have inferred distinct shifts in climatic niche preferences among the three major dinosaur clades. Following the Early Jurassic Toarcian extinction event (Jenkyns Event), sauropods increasingly occupied warmer and drier environments, while theropods shifted toward cooler and wetter climates. Ornithischians showed a similar pattern to theropods, but much later, coinciding with the Late Cretaceous Cenomanian/Turonian boundary. We apply phylogenetic comparative methods to test whether shifts in preferred climatic niches are coupled with dinosaur body size evolution. We find no support for a correlation between body size and local palaeotemperature, seasonality, or mean annual precipitation (MAP) among species in any dinosaur clade, before or after shifts in preferred climatic niches. With this original dataset, we find that larger eusauropod body sizes are weakly correlated with lower MAP after the Jenkyns Event. However, this trend is not recovered when using a larger and more recent dataset of eusauropods, demonstrating that the strength of such climate–size relationships is subject to sampling intensity. Our findings highlight the complex role of climate on body size evolution and how the detection of macroevolutionary patterns is influenced by sample size.

Key words: dinosaur, Mesozoic, palaeoclimate, biogeography, thermophysiology, body size.

CLIMATIC variation induces selective pressures on animal lineages as they evolve and disperse, controlling their geographic ranges and affecting how ecosystems are structured and distributed across the planet (Condamine *et al.* 2012). Climate has long been hypothesized to play a role in body size evolution, but the extent and capacity of this role remain subject to debate. A warming climate is often thought to correlate with changes in body size, though the directionality of this change depends on the clade of interest and can vary immensely (Brown *et al.* 1993; Makarieva *et al.* 2005; Ohlberger 2013; Riemer *et al.* 2018; Kozłowski *et al.* 2020). For example, ectotherms might be expected to become larger in warmer climates given their metabolic dependence on external heat sources, a trend observed in some extant snakes and lizards at the intraspecific level (Ashton & Feldman 2003). However, an increase in body size with temperature is not universally observed among ectothermic poikilotherms intraspecifically (Belk & Houston 2002; Ashton & Feldman 2003; Adams & Church 2008; Zamora-Camacho *et al.* 2014) or interspecifically (Feldman & Meiri 2014; Meik *et al.* 2024; Vicent-Castelló *et al.* 2025), raising questions about the underlying mechanisms of such varied patterns. Cenozoic turtles expanded their latitudinal ranges during warmer intervals (Chiarenza *et al.* 2023; Sterli *et al.* 2024), yet temperature does not appear to explain body size variation among species (Cadena *et al.* 2012; Farina *et al.* 2023). Four

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species of western North American rattlesnakes are larger in wetter and cooler environments, but this may be linked to increased resource availability, with temperature playing only a secondary role (Meik *et al.* 2024). Larger body sizes in two sister clades of lacertid lizards (the Eremiadini and Lacertini) are correlated with different climatic variables: colder temperatures and lower precipitation seasonality, respectively (Vicent-Castelló *et al.* 2025). In contrast, body size in the closely related Gallotinae could not be explained by any tested climatic variable (Vicent-Castelló *et al.* 2025). These studies demonstrate that the effect of temperature on ectotherm body size evolution is context-dependent; cooler temperatures can increase precipitation, which in turn increases the availability of resources and energy facilitating growth to larger sizes (Blois *et al.* 2008; Meik *et al.* 2024; Vicent-Castelló *et al.* 2025). Clearly, regardless of thermophysiology, the role of climate in influencing body size evolution is complex.

Studies on relationships between climate and body size have found mixed results across different clades. This variability stems partly from the complex ways in which climate influences body size evolution, as previously described, and partly from the diverse methodologies employed to investigate these relationships. These methods include regression analyses at higher taxonomic (Brehm & Fiedler 2004; Berke *et al.* 2013), interspecific (Feldman & Meiri 2014; Baldwin *et al.* 2023; Wilson *et al.* 2024; Vicent-Castelló *et al.* 2025), and intraspecific (Belk & Houston 2002; Adams & Church 2008) levels; meta-analyses of intraspecific correlation strengths with latitude (Ashton & Feldman 2003); correlations with latitude at the community level (Blackburn & Gaston 1996); and redundancy analyses that account for spatial autocorrelation (Meik *et al.* 2024). Each of these approaches inherently tests for associations between body size, latitude, and climate at different scales. Reviews have suggested that body size patterns in relation to climate and latitude can be studied at any scale, though intraspecific relationships tend to be stronger than interspecific ones (Blackburn *et al.* 1999; Meiri 2011; Shelomi 2012). This is likely to be due to the context-dependent nature of climate's effects on body size across species, as well as the multitude of biotic and abiotic factors influencing body size evolution. Furthermore, we might expect different mechanisms (e.g. temperature, resource availability) to influence body size at varying scales. At the macroevolutionary scale, if climate change (e.g. temperature, seasonality, or precipitation) repeatedly selects for an increase or decrease in body size within a clade, we might detect coincident changes in body size and occupied climate across branches in a phylogenetic tree. Previous reviews have advocated for using such phylogenetic approaches when analysing interspecific climate–size relationships (Blackburn *et al.* 1999; Chiarenza 2024).

In this study, we use phylogenetic regression models to test for an interspecific relationship between body size and palaeoclimate in a globally distributed sample of Mesozoic dinosaurs. We also employ another phylogenetic approach that tests whether ancestral changes in body size along branches correlate with changes in climate (Wilson *et al.* 2024). In other words, do lineages exhibiting increases or decreases in size also show correlated shifts in climate? Our model additionally allows for shifts in evolutionary rate along branches; a necessity given the variable rates of body size evolution and climatic niche expansion recorded for non-avialan dinosaurs (Benson *et al.* 2018; Chiarenza *et al.* 2024; Dunne *et al.* 2023). We demonstrated the efficacy of this model in Wilson *et al.* (2024), where we found a negative correlation between body mass and local mean annual temperature in extant birds (median Bayesian posterior slope (β) = −0.0036, median $R^2 = 0.13$), consistent with recent research on avian body size evolution (Baldwin *et al.* 2023). However, we did not detect a considerable temperature effect in extant terrestrial mammals (Bayesian 95% credible interval of $R^2 = -0.0005, 0.024$; Wilson *et al.* 2024). We found no support for a positive relationship between latitude and body size across our robust datasets for extant birds and mammals, contrary to the predictions of Bergmann's rule. We further demonstrated the model's efficacy using Ursidae (bears) as a case study. Absolute latitude explained 75% of body mass variation among eight ursid species (Wilson *et al.* 2024). The effects of latitude and climate on body size evolution can be small but still detectable at the phylogenetic scale, consistent with previous reviews of interspecific correlations between climate and body size (Blackburn *et al.* 1999; Meiri 2011).

Recent work has demonstrated distinct shifts in habitat preference as a function of climate among the major dinosaur clades, with theropods and ornithischians inhabiting cooler and wetter inferred climates that are hypothesized to coincide with the evolution of endothermy (Chiarenza *et al.* 2022, 2024). In contrast, eusauropod sauropodomorphs became more restricted to warmer and drier environments, a pattern proposed to be associated with poikilothermy (Chiarenza *et al.* 2022, 2024; Dunne *et al.* 2023). These shifts in dinosaur habitat occupation appear to have changed following two key Mesozoic climate events (Fig. 1): for sauropods and theropods, the early Toarcian extinction (or Jenkyns Event) at about 183 million years ago (Ma), and for ornithischians, the Cretaceous Thermal Maximum around the Cenomanian/Turonian boundary at 93.9 Ma (Chiarenza *et al.* 2022, 2024). We aim to assess whether these patterns are associated with changes in body size by testing

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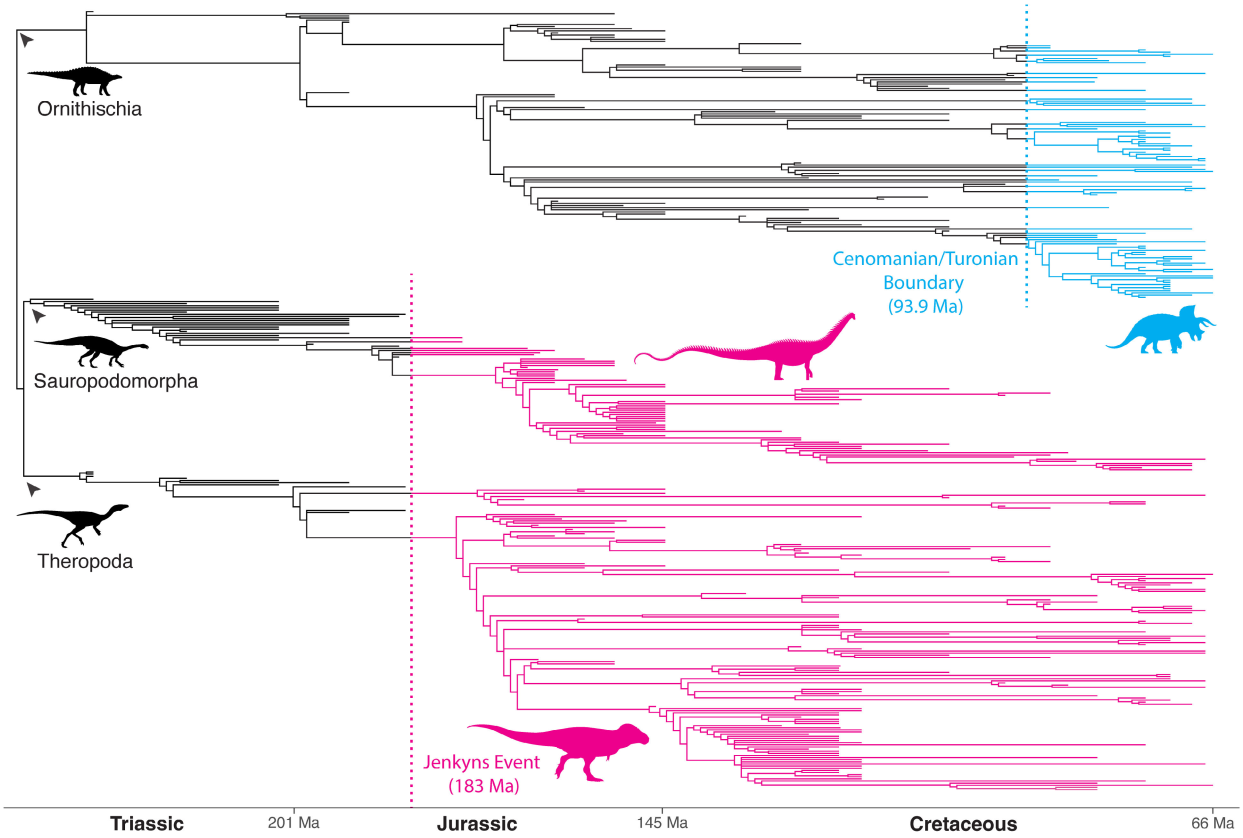

FIG. 1. Mesozoic dinosaur phylogeny. Coloured branches and silhouettes represent taxa following the climate events for which the respective clades are proposed to have been significantly impacted. Blue: Cenomanian/Turonian boundary (93.9 Ma); pink: Jenkyns Event (183 Ma). Ornithischians represented by the black *Scelidosaurus* (Gareth Monger; CC BY 3.0) and blue *Triceratops* silhouette (Jagged Fang Designs; CC0 1.0), sauropodomorphs by the black *Plateosaurus* (Mike Taylor; CC0 1.0) and pink *Diplodocus* silhouette (Jagged Fang Designs; CC0 1.0), and theropods by the black *Coelophysis* (Will Toosey; CC BY 4.0) and pink *Tyrannosaurus* silhouette (Jack Mayer Wood; CC BY 3.0).

for an effect of climate on dinosaur body size evolution, both before and after these proposed shifts in climatic preferences for each clade. We enlist a suite of climatic variables, consisting of mean annual temperature (MAT), warm-month mean temperature (WMMT), cold-month mean temperature (CMMT), seasonality (WMMT–CMMT), and mean annual precipitation (MAP), seeking to capture the complex role of climate on body size evolution.

MATERIAL & METHOD

Dinosaur body size, palaeo-occurrence & climate data

We collected femoral circumferences (in mm), a proxy for body mass (Benson *et al.* 2018), and palaeogeographic data for 339 dinosaur species from Benson *et al.* (2018) and O'Donovan *et al.* (2018). O'Donovan *et al.* obtained the palaeogeographic data from the Paleobiology Database (PBDB; https://paleobiodb.org), which converts the present-day latitudes and longitudes of fossil occurrences into palaeolatitude and palaeolongitude values using GPlates software (Müller *et al.* 2018). To ensure our palaeogeographic locations were estimated consistently, we used the Getech Plc. plate model to produce palaeorotations for each sample site from the PBDB through time. A state-of-the-art coupled Atmosphere–Ocean General Circulation Model (AOGCM), HadCM3L-M2.1aD (Valdes *et al.* 2017; Wilson *et al.* 2024), was employed using realistic time-dependent boundary conditions to understand the impact of climate change throughout the Mesozoic. Both the atmospheric and oceanic component models have a resolution of 3.75° longitude by 2.5° latitude, with 19 hybrid levels in the atmosphere and 20 vertical levels in the ocean. Getech Plc. provided stage-specific palaeogeographies (topography, bathymetry, land-sea distribution; Lunt *et al.* 2016). We derived $p\mathrm{CO}_2$ for each time period from proxy-CO_2 data (Foster *et al.* 2017; Rae *et al.* 2021) and solar luminosity from

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Gough (1981). Critically, HadCM3L-M2.1aD includes a recent update to the cloud physics that better resolves high latitude warmth in line with proxy evidence, while also producing an accurate pre-industrial climate (Fenton *et al.* 2023; Malanoski *et al.* 2024; Sun *et al.* 2024). Palaeoclimate data were inferred using an updated version of the UKMO HadCM3 family, a coupled AOGCM, with a lower resolution ocean component (specifically HadCM3BL-M2.1aD, following the nomenclature of Valdes *et al.* 2017). For additional information concerning the specific predictive performance of the climate model, see Wilson *et al.* (2024) and Malanoski *et al.* (2024).

A phylogenetic approach to test climate – body size relationships

To assess the relationship between body size and predicted local climate, we conducted Bayesian phylogenetic independent contrast regressions using $\log_{10}$-transformed femoral circumference as the dependent variable. We tested five different climate variables as our primary independent variables: mean annual temperature (MAT), cold-month mean temperature (CMMT), warm-month mean temperature (WMMT), seasonality (WMMT–CMMT), and $\log_{10}$-transformed mean annual precipitation (logMAP). These were obtained from the HadCM3BL-M2.1aD model (Valdes *et al.* 2017; Wilson *et al.* 2024). We used the dinosaur phylogeny from Benson *et al.* (2018) and ran separate analyses for each major Mesozoic dinosaur clade (sample sizes for taxa with femoral circumferences and occurrence data: n = 120 ornithischian, 72 sauropodomorph, and 147 theropod taxa). Given the evidence for shifts in climate preferences across all three clades, we ran additional analyses, limiting the analysed species to those dated after the climatic event of interest. For sauropodomorphs and theropods, this shift coincides with the early Toarcian extinction event (or Jenkyns Event) at around 183 Ma. For ornithischians, it coincides with the Cenomanian/Turonian (C/T) boundary at 93.9 Ma, which is associated with the Cretaceous Thermal Maximum (Chiarenza *et al.* 2024). These post-climate event analyses reduced the sample sizes to 77 ornithischians, 50 eusauropod sauropodomorphs, and 138 theropods.

Our analyses were supplemented with estimated body masses and a recently published sauropodomorph phylogeny (D'Emic 2023). This consensus tree was grafted from several previous phylogenetic analyses with additional taxa (n = 169 sauropodomorphs, 157 post-Jenkyns Event). We repeated D'Emic's (2023) procedure for time-calibrating the phylogeny, which uses a branch-scaling method based on the number of character changes and ages of fossil taxa (Forey 1988), later adapted by Brusatte *et al.* (2008). Future studies could account for the uncertainty in estimated node ages by inferring a distribution of time-scaled trees using Bayesian tip-dating methods, such as the fossilized birth–death model (Stadler *et al.* 2018).

We then compared the likelihood support of these regression models against phylogenetic independent contrasts models on femoral circumference alone (equivalent to an intercept-only null model) and regression models including a regional and time-specific fossil occurrence count as a measure of spatiotemporal fossil sampling intensity (described in more detail below). Model selection was based on Bayes factors (BF), where

$$\mathrm{BF} = 2 \times (\log\ \text{marginal likelihood Model 1} \\ - \log\ \text{marginal likelihood Model 2}).$$

A BF score >2 indicates good support for Model 1 over Model 2.

We further applied a variable-rate regression model, which uses a reversible-jump Markov-chain Monte Carlo (RJMCMC) algorithm to propose branch-specific and clade-wide shifts from a background phylogenetic variance (or rate of evolution) without *a priori* specification (Venditti *et al.* 2011; Baker *et al.* 2016). In the context of a regression model, these 'rate shifts' describe changes in the residual variance of the climate – body size relationship inferred across the tree. These variable-rate regression models were compared to the final uniform-rate models chosen through our model selection procedure using Bayes factors, as described above. We conducted our phylogenetic regression analyses using BayesTraits v4.0.0 (Pagel *et al.* 2004; Meade & Pagel 2023). However, in cases where we find no relationship between body size and climate, we refrain from interpreting specific estimates of evolutionary rates. All analyses ran for 12 500 000 iterations with a 2 500 000-iteration burn-in and sampling frequency of 1000. Convergence in the model likelihoods was evaluated using the program Tracer v1.7.2 (Rambaut *et al.* 2018). We estimated log marginal likelihoods using the Stepping Stone algorithm (Xie *et al.* 2011), with 100 stones sampled every 1000 iterations. In addition, we assessed the statistical significance of each regression coefficient by calculating the proportion of slope (β) parameter estimates that crossed a value of 0 (p_{MCMC}). A low p_{MCMC} indicates that a considerable proportion of the slope estimates deviates from a flat line. To account for the variation in climate variables across a taxon's geographic range, our model implements a Bayesian reversible-jump Markov-chain Monte Carlo (RJMCMC) procedure to randomly sample estimates of each palaeoclimate variable for 120 species found in multiple localities.

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To visualize the relationship between lineage shifts in climatic occupation and body size, we used the branch-wise plotting scheme developed in Wilson *et al.* (2024). These plots illustrate the magnitude and direction of ancestral changes in body size relative to a given climate variable. This was achieved by calculating the amount of ancestral change along each branch of a phylogeny, while accounting for variable rates of evolution. Univariate variable-rate analyses were run separately for each dependent and independent variable, while accounting for multiple occurrence data, and producing a posterior distribution of trees scaled by the rate of evolution along each branch. We then acquired the rate-scaled majority-rules consensus trees for each variable and estimated the maximum likelihood ancestral states of each node using the 'fastAnc' function in the R package 'phytools' (Revell 2023). Ancestral changes along each branch were then calculated by taking the difference between the estimated ancestral state of each node and its immediate descendants. If the evolution of body size was coupled with changes in occupied climate at the lineage level, we would expect a linear relationship between the branch-wise ancestral changes for each variable (Wilson *et al.* 2024). We tested for a linear relationship using a Bayesian generalized linear mixed model in the R package MCMCglmm v2.36 (Hadfield 2010; R Core Team 2024), with a random effect on the ancestral node of each branch to account for potential non-independence in rates of evolution (Sakamoto & Venditti 2018). MCMCglmm analyses were run for 1 000 000 iterations with a 10 000-iteration burn-in and sampling frequency of 500. We used default priors for the fixed effects with a diffuse normal distribution centred around 0 ($\mu = 0$) and a large variance ($\sigma^2 = 10^8$). For the variances of the random effects, we applied inverse-Gamma distributions with both shape (α) and scale (β) parameters equal to 0.01. Convergence in the model likelihoods, fixed effects, and random effects was evaluated using the plot function in R. We also calculated marginal and conditional R^2 values, which respectively measure the variance explained by the fixed effects and all model effects (fixed and random effects).

Spatiotemporal size sampling bias metric

Body size may correlate with the number of fossil occurrences in a particular region and time, especially if regions with fewer fossils are less likely to record small-bodied taxa. Fossil preservation often favours large-bodied taxa in dinosaur-dominated assemblages, an issue that has been clearly demonstrated in Late Cretaceous North America (Brown *et al.* 2022). To investigate such an effect on our results, we followed the approach of Wilson *et al.* (2024) by compiling the number of unique terrestrial tetrapod occurrences across nine 20-degree palaeolatitudinal zones, which were further subdivided by geochronological age. Following a protocol by Dunne *et al.* (2021), we removed taxonomically unidentifiable fossils and non-body fossil occurrences. Based on their average age and palaeolatitude, we assigned each taxon a geographic- and time-specific occurrence count as an additional independent variable. It is important to recognize that this metric does not capture all types of sampling bias that may have influenced our results (see Discussion). Furthermore, it will only detect a bias if there is a linear effect that increases or decreases the average estimated body size. For example, we may hypothesize a positive relationship if increased sampling in each formation is more likely to recover large individuals. Alternatively, the correlation would be negative if sampling recovered more smaller-bodied taxa that are typically less likely to have been preserved or discovered. Despite these potential size biases, we still expect that our analyses can test whether the known variation among generally larger-sized dinosaurs (e.g. eusauropods) is correlated with environmental variables. We assessed the statistical support for a correlation with our spatiotemporal sampling metric by comparing it to a regression model excluding the metric using Bayes factors (described above).

RESULTS

Our model selection process supported models including only body size ($\log_{10}$ femoral circumference) and the given climate variable for each clade. These models outperformed an intercept-only null model and a model which included an additional sampling bias metric (number of tetrapod occurrences) (BF = 5.38–27.07; Table S1). See Supporting Information for further details about our model selection process. Our final regression analyses show no relationship between body size and any of the five tested climate variables among all species in the three Mesozoic dinosaur clades (p_{MCMC} = 0.072–0.497; Table S2).

We also found no support for a relationship between body size and climatic variables in post-Cretaceous-Thermal-Maximum ornithischians or the post-Jenkyns-Event theropods (p_{MCMC} = 0.05–0.759; Table S3). For eusauropod sauropodomorphs following the Jenkyns Event, there was no evidence for a correlation with temperature or seasonality (p_{MCMC} = 0.081–0.482; Table S3). However, we did find that eusauropods were larger in more arid regions or low logMAP (median $\beta = -0.0878$ [95% CI = -0.146, -0.0197], $p_{MCMC} = 0.008$). Specifically, with every mm decrease in MAP, there is an

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associated 0.714–0.956 mm ($10^{-0.146}$ and $10^{-0.0197}$, respectively) increase in femoral circumference in the post-Jenkyns Event eusauropods. MAP also explains 17.8% of the variation in body size among post-Jenkyns Event eusauropods on average (median $R^2 = 0.178$ [95% CI = 0.00943, 0.379]). However, supplemental analyses using a larger sample of post-Jenkyns Event eusauropods from D'Emic (2023) show no relationship between body mass and logMAP ($p_{MCMC} = 0.197$; Table S4). When we restrict our analyses to the taxa overlapping with the dataset of Benson *et al.* (2018) (n = 50 sauropodomorphs, 44 post-Jenkyns Event eusauropods), we again find an inverse relationship with logMAP. This suggests that the relationship between eusauropod body size and logMAP is better explained by incomplete sampling.

In contrast to our phylogenetic regression analyses, the estimated ancestral changes in body size and local MAT are inversely correlated among ornithischian lineages after the Cretaceous Thermal Maximum. This finding is consistent with a greater preference for cooler environments (mean $\beta = -0.0082$ [95% CI = −0.013, −0.0039], $p_{MCMC} < 0.0005$; Fig. 2B). Branch-wise changes in temperature preference along phylogenetic branches explain 7.8% of the branch-wise changes in ornithischian body size after the Cretaceous Thermal Maximum (median marginal $R^2 = 0.078$). This represents an increase compared to when all ornithischian branches are considered (mean $\beta = -0.0039$ [95% CI = −0.0071, −0.0012], $p_{MCMC} = 0.014$, median marginal $R^2 = 0.026$; Fig. 2A). Here, we determined which branches dated before or after each relevant climatic event using the descendant node ages of each branch. We see a marginally non-significant relationship between ancestral size and local MAT changes among all sauropodomorph lineages (mean $\beta = -0.0031$ [95% CI = −0.0065, −0.00021], $p_{MCMC} = 0.053$, median marginal $R^2 = 0.028$; Fig. 2C). Notably, we find no correlation with ancestral changes in MAT among eusauropod branches after the Jenkyns Event ($p_{MCMC} = 0.48$; Fig. 2D). There is no relationship between ancestral changes in body size and MAT among theropod lineages after the Jenkyns Event ($p_{MCMC} = 0.17$; Fig. 2F). We also found little evidence that ancestral changes in logMAP had a strong effect on body size for any clade after shifts in preferred climatic niche ($p_{MCMC} = 0.077$–0.18) (Fig. 3).

DISCUSSION

Effect of taxonomic sampling

Any sufficiently large dataset can be arbitrarily divided into subgroups that exhibit different patterns from the overall data. This is commonly referred to as Simpson's paradox and is cautioned against by Wilson *et al.* (2024) with regard to ecogeographic rules (e.g. Bergmann's rule). However, such tests can be meaningful if appropriately guided by *a priori* hypotheses (e.g. a shift in the relationship between body size evolution and climatic changes following the Jurassic Jenkyns Event). Our finding that larger eusauropod body sizes are related to lower MAP after the Jenkyns Event appears to be one such case, as our supplemental analysis of the larger D'Emic (2023) dataset recovered no relationship. This highlights how results can drastically change with an increased sample size, and even a few taxa can act as outliers at such low resolution. We also conducted a set of analyses using the phylogeny and data from D'Emic (2023), restricting the analyses to taxa that overlap with the Benson *et al.* (2018) dataset. These analyses yielded broadly consistent results with our initial analyses (Table S4). To further demonstrate that these findings cannot be attributed to the use of different phylogenies, we additionally ran analyses using the tree from Benson *et al.* (2018) and data from D'Emic (2023). These analyses yielded consistent results with those using the D'Emic (2023) tree. The data from Benson *et al.* (2018) in our initial analyses were femoral circumferences, rather than body mass estimates, as in the D'Emic (2023) data. Despite this difference, the estimated slopes from both sets of analyses were negative.

These analyses revealed that the inverse relationship between eusauropod body size and MAP is only statistically significant when analysing the taxa in the Benson *et al.* (2018) dataset, regardless of the phylogeny that is used. This highlights the importance of analysing the most complete taxonomic sampling available in such macroevolutionary studies. Such macroevolutionary studies are inherently limited to taxa that can be reliably placed on a phylogeny. However, the use of grafted supertrees or the placement of taxa as polytomies based on taxonomic assignment, as was done in D'Emic (2023) for sauropodomorphs, offers possible solutions to circumvent this limitation. Future studies should examine the strength of these size–climate relationships with more comprehensive phylogenies of ornithischians and theropods.

Effect of fossil preservation & sampling biases

Our model selection results found no linear relationship between body size and the number of terrestrial vertebrate fossil occurrences in each time and geographic region. This does not mean that fossil sampling bias is absent. Studies have extensively demonstrated the influence of disproportionate fossil sampling in different geographic regions on comparative analyses of diversification and biogeography (Benson & Upchurch 2013;

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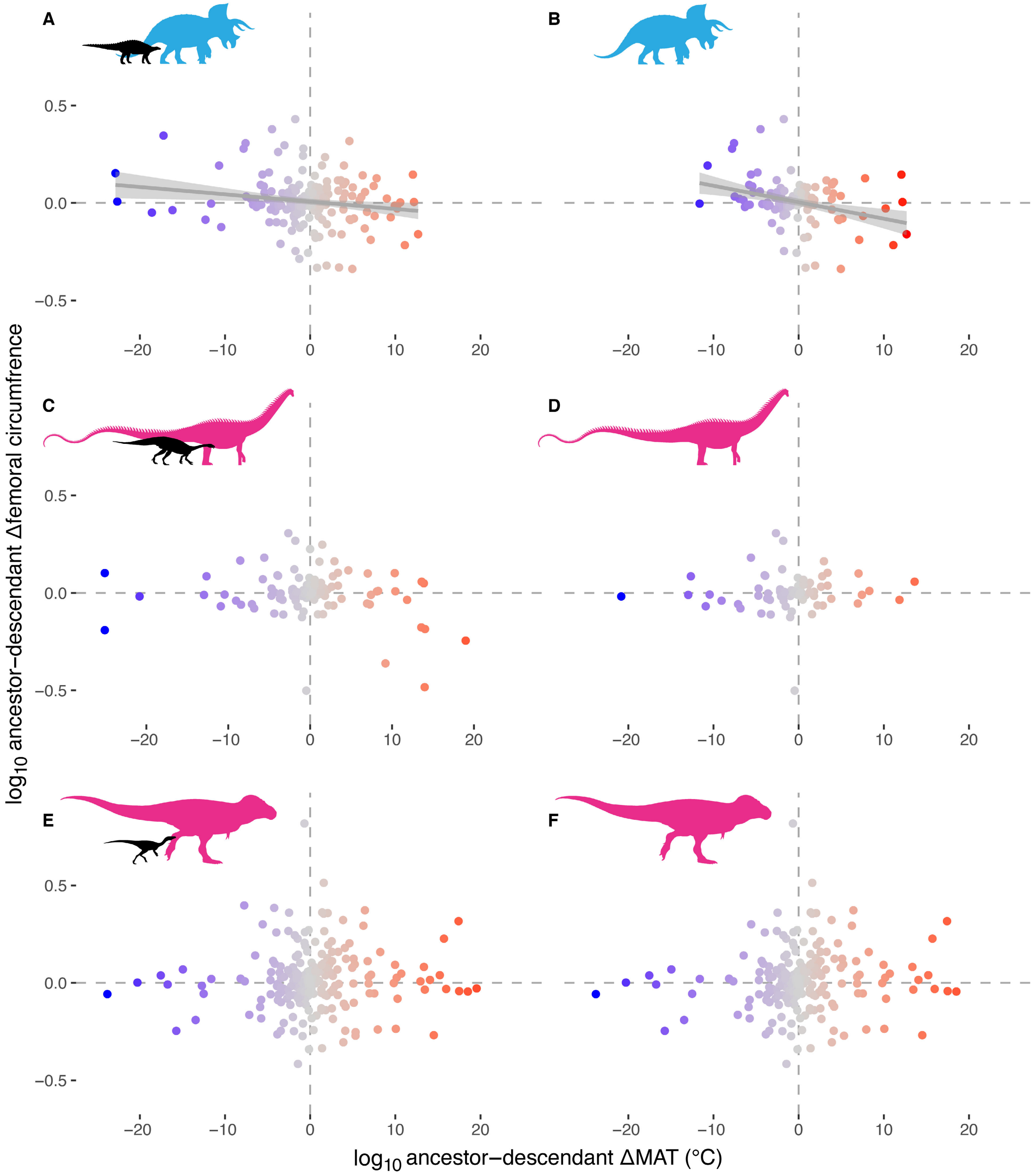

FIG. 2. Estimated changes in femoral circumference ($\log_{10}$) as a function of changes in mean annual temperature (°C) along branches of the Benson *et al.* (2018) dinosaur phylogeny in: A, all ornithischians; B, ornithischians following the Cenomanian/Turonian boundary; C, all sauropodomorphs; D, sauropodomorphs following the Jenkyns Event; E, all theropods; F, theropods following the Jenkyns Event. Best-fit lines (grey) and standard errors (light grey) are shown for cases with inferred size–temperature relationships at the branch level. (Silhouettes: A–B, *Scelidosaurus*, Gareth Monger, CC BY 3.0; *Triceratops*, Jagged Fang Designs, CC0 1.0; C–D, *Plateosaurus*, Mike Taylor, CC0 1.0; *Diplodocus*, Jagged Fang Designs, CC0 1.0; E–F, *Coelophysis*, Will Toosey, CC BY 4.0; *Tyrannosaurus*, Jack Mayer Wood, CC BY 3.0.)

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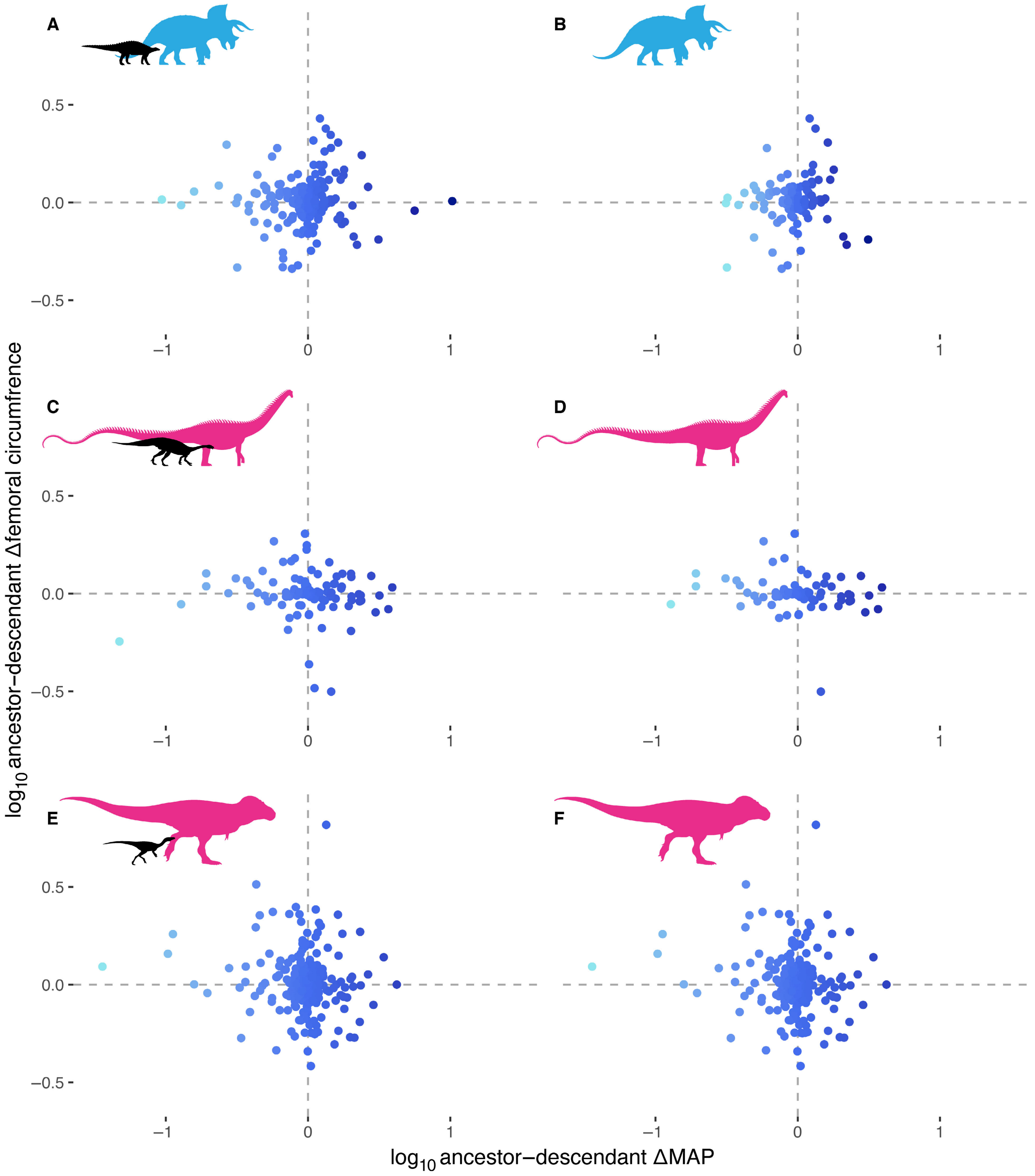

FIG. 3. Estimated changes in femoral circumference (log$_{10}$) as a function of changes in mean annual precipitation (log$_{10}$) along branches of the dinosaur phylogeny in: A, all ornithischians; B, ornithischians following the Cenomanian/Turonian Boundary; C, all sauropodomorphs; D, sauropodomorphs following the Jenkyns Event; E, all theropods; F, theropods following the Jenkyns Event. (Silhouettes: A–B, *Scelidosaurus*, Gareth Monger, CC BY 3.0; *Triceratops*, Jagged Fang Designs, CC0 1.0; C–D, *Plateosaurus*, Mike Taylor, CC0 1.0; *Diplodocus*, Jagged Fang Designs, CC0 1.0; E–F, *Coelophysis*, Will Toosey, CC BY 4.0; *Tyrannosaurus*, Jack Mayer Wood, CC BY 3.0.)

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Gardner *et al.* 2019; Close *et al.* 2020; Jones *et al.* 2021). For instance, more Mesozoic terrestrial vertebrate fossils come from mid-to-high latitudes and the Cretaceous (Wilson *et al.* 2024; Maidment & Butler 2025). In addition to preservation biases, historical and socioeconomic factors have also favoured the collection and curation of fossils from those regions (Raja *et al.* 2022). Our spatiotemporal sampling bias metric aimed to test for a bias in the average body size of more densely sampled localities. However, our results suggest that increased sampling increases body size variation among taxa without an average increase or decrease in size (Wilson *et al.* 2024).

Effect of other biases

High-resolution spatiotemporal sampling may be necessary to detect ecogeographic relationships across macroevolutionary timescales. Wilson *et al.* (2024) tested for a correlation between body size and temperature in 5496 extant birds and 2305 extant mammals. Even with these large sample sizes of contemporaneously occurring species, we detected only a weak signal in extant mammals (statistically significant but with an $R^2 \approx 0$) and a moderate signal in extant birds. This suggests that we cannot rule out the possibility that Mesozoic dinosaur body sizes were weakly, or even moderately, influenced by climate without examining more densely sampled datasets. The stratigraphic control of such data is necessary, given that most non-avialan dinosaur species are not contemporaneous, unlike studies on extant birds and mammals. Despite the expectations of Bergmann's rule, Wilson *et al.* (2024) found that most non-avialan dinosaur taxa from the Late Cretaceous Prince Creek Formation were comparable in size to close relatives from near-contemporaneous lower-latitude formations. However, additional data are needed to improve body size estimates for taxa in the formation.

The use of different body size proxies has also led to inconsistent findings (Bailey *et al.* 2020). Body mass may be a poor proxy, as changes in body mass can reflect alterations in either structural size or body condition, an issue which has also been observed in other studies (Canale *et al.* 2016). Bailey *et al.* (2020) found that using body mass yielded opposite results from when structural size and body condition were analysed independently. While this is less problematic for studies on extinct organisms, as body mass estimates are derived from skeletal proxies rather than directly measured, it nevertheless highlights the importance of consistency in body size measures when comparing study results. The findings of Canale *et al.* (2016) further emphasize the value of using multiple body size proxies when available, as they found that changes in overall body size and body mass can be decoupled, exhibiting different sensitivities to climatic variation. In such scenarios, relying on only one body size metric could lead to misleading patterns that do not accurately characterize changes within a given population or species.

Estimates of body mass for extinct species introduce a range of additional confounding factors. These estimates are often based on only a few specimens, or sometimes even only a single partial specimen, and thus cannot fully capture the true body size variation within a species (Gayford *et al.* 2024). Studies on extant species indicate that body size varies more dramatically within larger species of mammals and birds, possibly because size variation in smaller animals is more heavily constrained by energetic and functional limitations (Hallgrímsson & Maiorana 2000). Environmental factors may also influence intraspecific body size variability; for example, tropical birds exhibit lower intraspecific body variability, hypothesized to be related to more stable climates and resources (Read *et al.* 2018). Additionally, body size variation within species can dramatically change in relatively short time scales. For example, intraspecific body size variation has been shown to have rapidly increased in many North American birds and mammals (30.67% and 9.59%, respectively) since 1880, potentially in response to anthropogenic climate change (Zheng *et al.* 2023). This has major implications for the fossil record, where a single formation can represent hundreds to potentially millions of years of evolutionary time that may have experienced major fluxes in climate.

Beyond intraspecific variation, ontogenetic change should also be considered when studying the body sizes of extinct species (Chapelle *et al.* 2025). Dinosaurs underwent dramatic body size transformations throughout ontogeny, with *Tyrannosaurus rex* growing up to 8000 kg in 35–40 years (Woodward *et al.* 2026). However, while ontogenetic series are known for some species (Horner *et al.* 2000; Horner & Goodwin 2006; Wilson & Scannella 2021), this is rare, and most extinct taxa are only known from single, incomplete specimens. Consequently, the actual size range of many extinct species is not well-represented by the fossil record. For example, the largest-known Triassic theropods are represented by individuals that were still rapidly growing, and their maximum potential body sizes have been shown to be much larger than the body fossil record suggests (Griffin & Nesbitt 2020). Indeed, it is unlikely that we have sampled specimens at or near the maximum body size for some species (Mallon & Hone 2024). Even adult body mass can fluctuate dramatically throughout a given year, especially in hibernating species. For example, coastal brown bear females were observed to lose upwards of 73 kg over the course of a single winter (Hilderbrand *et al.* 2000).

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Our study attempted to account for variation in body size by allowing our model to sample from multiple femoral circumference measurements for multiple species. However, future studies could improve on this by sampling additional body size proxies or by using phylogenetically informed predictions to incorporate distributions of body size values (Organ *et al.* 2011).

Sauropod fossil record

Our finding that there is no clear effect of climate on the evolution of sauropod body size following the Jenkyns Event is largely consistent with the fossil record. Sauropods showed an increased preference for warm and dry climates in the Jurassic while shifting toward a preference for higher seasonal precipitation in later diverging groups (Chiarenza *et al.* 2024; Dunne *et al.* 2023). Some of the largest sauropods come from such environments, including the Late Jurassic Morrison Formation of the Western United States (Noto & Grossman 2010; Chiarenza *et al.* 2022) and the Late Cretaceous Huincul Formation of Argentina (Coria & Currie 2006; Chiarenza *et al.* 2024). Morrison Formation sauropods include *Diplodocus hallorum*, which at an estimated 50+ m long and weighing *c.* 14.5 tonnes, is among the largest dinosaurs, in terms of body length, from North America and the world (D’Emic 2023; Woodruff *et al.* 2024). *Argentinosaurus huinculensis* comes from the Huincul Formation and is considered to be one of the largest terrestrial animals ever to have existed, with some body mass estimates exceeding 90 tonnes (Mazzetta *et al.* 2004; Benson *et al.* 2014). The titanosauriform *Chubutisaurus insignis* from the arid Bayo Overo Member of the Cerro Barcino Formation is one of the largest sauropods in the Benson *et al.* (2018) dataset, with body mass estimates ranging up to *c.* 30 tonnes (Benson *et al.* 2018; D’Emic 2023). Additionally, several ‘dwarf’ sauropods from the Hateg Basin, once thought to be part of a larger miniaturized fauna due to limited resources resulting in ‘island dwarfism’, reveal the smallest weighing just 1 tonne and measuring no more than 3 m (Díaz *et al.* 2025). Aside from resource availability, this would agree with expectations for sauropod body size based on our analyses, given the subtropical climate (Benton *et al.* 2010). However, a recently discovered titanosaur from the fauna, *Uriash kadici*, may have weighed 10 tonnes and exceeded 11 m in length (Díaz *et al.* 2025).

Likewise, there are plenty of giant sauropods from less arid formations. For example, the giant titanosaur *Patagotitan mayorum*, weighing up to an estimated 86 tonnes (69 tonnes ±17 tonnes; Carballido *et al.* 2017), comes from the uppermost Cerro Castaña Member of the Cerro Barcino Formation, which is interpreted as having higher humidity and weaker seasonality than the lower units of the formation, such as the Bayo Overo Member, that were drier and more seasonal (Krause *et al.* 2020).

Ornithischians & theropods

Following the Jenkyns Event, some theropod taxa retained a preference for warmer and drier environments, whereas other taxa inhabited cooler, wetter, and more seasonal climates (Chiarenza *et al.* 2024). Ornithischians showed a similar shift toward cooler, wetter, and more seasonal environments, but about 80 million years later, following the Cretaceous Thermal Maximum (Chiarenza *et al.* 2024). Despite this substantial geographic and climatic range expansion, we found no correlation between climate and body size in either group. However, we found a significant association between ancestral increases in size and decreases in local palaeotemperature along ornithischian branches after the Jenkyns Event. This suggests that an expansion toward cooler climates may have driven the rate or amount of change in body size along ornithischian lineages, but not their interspecific variation in size at any given time.

As Chiarenza *et al.* (2024) noted, this aligns with the fossil record, which indicates that only theropods and ornithischians inhabited high-latitude, cold-weather environments. For instance, the Prince Creek Formation in northern Alaska, the northernmost Cretaceous terrestrial ecosystem, was located at a palaeolatitude of 80–85°N. Residents there are estimated to have endured a cold month mean temperature of around −2°C (Druckenmiller *et al.* 2021). In line with our findings, both here and in our previous study (Wilson *et al.* 2024), this colder climate does not appear to have influenced the variation of body sizes among dinosaurs inhabiting the ecosystem, as dinosaurs from the Prince Creek Formation are comparable in size to their relatives from more southerly Late Cretaceous North American localities (Druckenmiller *et al.* 2021; Wilson *et al.* 2024). Alternatively, the relatively milder latitudinal temperature gradients of the Mesozoic (despite evidence of occasional freezing temperatures) may not have been sufficient to necessitate larger body sizes for heat retention (as predicted by Bergmann’s rule).

CONCLUSION

Climatic gradients affect species distributions and ecosystem structure. Global climate change influences biogeography, leading to observable patterns in ecologically relevant traits, such as body size. These patterns have long been used to formulate hypotheses regarding the mechanisms underlying the distribution of extant animals. Recent studies have inferred distinct shifts in climatic niche

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preferences among the three major dinosaur clades, coinciding with the Jenkyns Event and the Cenomanian/Turonian boundary. We investigated whether these shifts in preferred climatic niches were coupled with dinosaur body size evolution, finding no evidence for a correlation between body size and multiple climate variables either before or after these events. There is some evidence that the rate or magnitude of change in palaeotemperature may have driven increases in body size among ornithischians after the Jenkyns Event. However, we also demonstrate that the detection of such macroevolutionary patterns is greatly influenced by sample size, warranting further study with more comprehensive body size datasets and phylogenies.

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DATA ARCHIVING STATEMENT

All data included in this study are available in Zenodo: https://doi.org/10.5281/zenodo.14579710

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.70068):

Table S1. Model selection results for phylogenetic comparative analyses.
Table S2. Results of the variable-rate independent contrasts regression models for all Mesozoic ornithischians, sauropodomorphs and theropods.
Table S3. Results of the variable-rate independent contrasts regression models for ornithischians, theropods, and eusauropod sauropodomorphs following significant shifts in temperature optima (according to Chiarenza *et al.* 2024).
Table S4. Results of comparisons with data from D'Emic (2023) and Benson *et al.* (2018) of the uniform-rate independent contrasts regression models for sauropodomorphs and eusauropod sauropodomorphs following the Jenkyns event (JE).
Table S5. Results of the branch-wise generalized linear mixed models for all ornithischian, sauropodomorph, and theropod branches.
Table S6. Results of the branch-wise generalized linear mixed models for ornithischian, theropod, and eusauropod sauropodomorph branches following significant shifts in temperature optima (according to Chiarenza *et al.* 2024).

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