

Impact of environmental barriers on temnospondyl biogeography and dispersal during the Middle–Late Triassic

by RAPHAEL MORENO^{1,2,*} , EMMA M. DUNNE³ , EUDALD MUJAL^{1,4} , ALEXANDER FARNSWORTH^{5,6} , PAUL J. VALDES⁵  and RAINER R. SCHOCH^{1,2} 

¹Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany; raphael.moreno@smns-bw.de

²Fachgebiet Paläontologie, Institute für Biologie, Universität Hohenheim, 70599 Stuttgart, Germany

³GeoZentrum Nordbayern, Friedrich-Alexander Universität Erlangen–Nürnberg (FAU), 91054 Erlangen, Germany

⁴Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/de les columnes, s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Catalonia, Spain

⁵School of Geographical Sciences, University of Bristol, University Rd, Bristol BS8 1SS, UK

⁶State Key Laboratory of Tibetan Plateau Earth System, Resources and Environment (TPESRE), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Lincui Road, Chaoyang District, Beijing 100101, China

*Corresponding author

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Abstract: Temnospondyls had a remarkable worldwide distribution throughout the Triassic at a time of periodic arid climates, and were a stable component of Triassic terrestrial ecosystems. Given the postulated ancestral relationship between temnospondyls and modern lissamphibians it is pertinent to recognize that the group may have exhibited some degree of ecological resilience and adaptability. Despite this higher level of plasticity, temnospondyls might still have been susceptible to environmental and climate changes. Although fossil sites are distributed sporadically, we try to circumvent the present geographical and geological biases by combining actual fossil occurrences with environmental conditions derived from general circulation models. Here, we employ species distribution modelling to examine the

palaeogeographic and palaeoclimatic distribution of European temnospondyls during the transition from Middle to Late Triassic. The model shows different suitable areas for temnospondyl habitats that give new potential insights on the biogeographic distribution patterns and dispersal potential. We suggest that the Central European Basin functioned as a focal point for Triassic temnospondyl diversification and spread. Moreover, this paper provides the first application of species distribution modelling for Triassic temnospondyls and aids in understanding their climatic niche occupation and evolution.

Key words: Temnospondyli, Triassic, species distribution model, biogeography, palaeobiology, palaeoclimate.

THE diverse group of temnospondyls includes *c.* 200 genera and spans a time range over 220 million years, from the early Carboniferous to the Early Cretaceous (Schoch & Milner 2014). Temnospondyls are abundant tetrapods in the Triassic (251–201 Ma) fossil record and are widely spread in the global fossil record, with rich assemblages on every continent (Schoch 2000a). Based on this widespread distribution and temporal stability, temnospondyls have been used in correlative studies of Triassic tetrapod assemblages (Lucas 2020). Due to their divergent modes of life, temnospondyls cover a wide range of ecological niches, in both the terrestrial and aquatic realms (Rinehart *et al.* 2023). This diversity in lifestyle and ecology and their potential evolutionary connection to modern Lissamphibia could give insight into amphibian evolution in response to substantial changes of environmental conditions such as those of the Triassic.

The ancestral origins of Stereospondylomorpha were reconstructed by Eltink *et al.* (2019) as having arisen in Laurasia with the first occurrence of the group documented in the early Permian. With Platyoposauridae, originating in eastern Europe during the late early Permian, temnospondyls underwent their first widespread geographical distribution into northwestern Gondwana, overcoming the Central Pangaeian Mountains in the process. The origin of the more derived stereospondyls and their descendants were reconstructed to have occurred in present day Africa, while the region where the ancestors of capitosaurids and trematosaurids originated remains obscure. It was probably located either in Africa or (eastern) Europe and the group then gained a cosmopolitan distribution burst during the Induan (Eltink *et al.* 2019). Complementary to the analyses of Eltink *et al.* (2019), Gee *et al.* (2023) discussed the biogeographic implications

of the temnospondyl assemblages of high latitude Gondwana. While some clades of Early Triassic temnospondyls such as lydekkerinids appear to have been globally distributed (depending on the applied taxonomic framework), some other clades such as chigutisaurids or lapillopsids are restricted to the southern regions of Pangaea (Gee *et al.* 2023). These authors note an apparent distributional disparity between aquatic-adapted and more terrestrial-adapted clades, whereby aquatic groups such as brachyopids or capitosaurids were more capable of crossing the geographic or climatic barriers in the equatorial regions of Pangaea than more terrestrial groups such as lapillopsids (Gee *et al.* 2023). The biogeographic distribution of temnospondyls is therefore linked to their inferred ecology and lifestyle. Historically, the biogeography of temnospondyls was first studied by Irving & Brown (1964, 1966) and later by Cefelli (1980). Through a combination of fossil occurrence data with palaeomagnetic data, the palaeolatitudinal distribution of temnospondyls was analysed in different time intervals from the Carboniferous to the Triassic. Irving & Brown (1964) specifically chose temnospondyls for their study because of their well-defined and continuous fossil record from the Late Palaeozoic to the Early Mesozoic. Cefelli (1980) then updated and added to the original dataset used by Irving & Brown (1964), to include additional regions not considered in the prior study. The results of Cefelli (1980) indicated that the highest diversity of the group was around mid-palaeolatitudes, contrasting with the pattern observed in the Palaeozoic where diversity was highest in equatorial regions. This pattern was attributed to what were presumed to be more uniform climate conditions in the Triassic (Cefelli 1980). With advancements in computational power, the development of more sophisticated methodologies allow for more integrative approaches to study biogeographic distributions.

Species distribution modelling (SDM) is an effective tool to identify the distribution of species in space and time (Varela *et al.* 2011). In the literature the terms SDM or ecological niche modelling (ENM) are used most often to refer to a set of comprising algorithms that model the distribution of species while also connecting them with the concept of ecological niches (Sillero 2011). In recent years this technique has found a wider application in the field of palaeontology to answer ecological and evolutionary questions in deep time (Haywood *et al.* 2019). Earlier in the 2010s, this technique found a use in a Recent palaeontological context (Graham *et al.* 1996; Svenning *et al.* 2011), but authors have previously successfully applied this approach deep into the Phanerozoic as well (Stigall 2012; Myers *et al.* 2015; Waterson *et al.* 2016; Chiarenza *et al.* 2019, 2020, 2021).

Palaeontology however, poses unique challenges to the applicability of SDM. To be able to estimate

palaeobiogeographic shifts in the diversity of temnospondyls it is essential to recognize the possibility of sampling biases in the data. These biases can be geological, taphonomic, geographic or anthropological in nature (Dunhill *et al.* 2014; Raja *et al.* 2022). Fossil occurrences are not only bound by the presence of rock outcrops and fossiliferous strata but also by accessibility of land area or specific human research interests. As pointed out by Szczygielski & Sulej (2023), large areas of unsampled territory in the inland regions of Pangaea make it difficult to assess palaeobiogeographic patterns through the direct fossil record. While taphonomic biases, such as availability of favourable facies for fossil preservation, limit our knowledge of the real distribution, the combination of these with simulated climate data from general circulation models pose the opportunity for a simulated approximation of the palaeobiogeographic distribution of these taxa.

TEMNOSPONDYL BIOGEOGRAPHY

Temnospondyls are a common component of tetrapod assemblages throughout the Triassic and occur on all continents. During the Middle and Late Triassic, the stereospondyls formed the dominant clade of temnospondyls, reaching a worldwide distribution (Schoch & Milner 2014).

In the Middle Triassic, capitosauroids are present in Southeast Asia (Wu *et al.* 2022), Russia (Tverdokhlebov *et al.* 2003), Europe (Schoch & Werneburg 1999), northern Africa (Dahoumane *et al.* 2016), India (Bandyopadhyay & Sengupta 1999) and North America (Sues *et al.* 2021) in the northern hemisphere. Trematosauridae are found in Europe (Schoch & Werneburg 1999), northern Africa (Soussi *et al.* 2017), India (Welles 1993) and North America (Sues *et al.* 2021), while plagiosaurids are identified in Russia (Tverdokhlebov *et al.* 2003), Europe (Schoch & Werneburg 1999) and the arctic region (Lowy 1949). Brachyopids are only present in India (S. Chakravorti, unpub. data) and North America (Schoch & Milner 2000), while chigutisaurids only occur in the southern hemisphere in the Middle Triassic. In the southern hemisphere, Capitosauria are widespread in South Africa (Smith *et al.* 2020), Australia (Poropat *et al.* 2023) and Antarctica (Sidor *et al.* 2023). Trematosaurids and brachyopids occur in the fossil assemblages of South Africa (Smith *et al.* 2020) and Australia (Poropat *et al.* 2023), while Chigutisauridae and Plagiosauridae only occur in Australia (Poropat *et al.* 2023) and Antarctica (Gee & Sidor 2022) respectively. Indeterminate material has been recovered from South America (Otero *et al.* 2023).

During the early parts of the Late Triassic, climatic conditions shifted from a dry to a more humid climate.

This shift in climate led to dynamic changes in biogeography, diversification and ecology among various groups of tetrapods (Benton *et al.* 2018; Benton & Wu 2022). This increase in humidity during the Carnian Pluvial Event (CPE; Dal Corso *et al.* 2020) affected temnospondyls through the development of widespread wet environments that favoured the colonization of various regions across Pangaea.

In the Late Triassic, capitosauroids had a reduced geographical distribution with occurrences in Southeast Asia (Shi *et al.* 2023), Europe (Schoch & Milner 2000) and the arctic region (Kear *et al.* 2015) in the northern hemisphere, and Argentina (Martínez *et al.* 2012) and South Africa (Peacock *et al.* 2017) in the southern hemisphere. Trematosauridae also show reduced habitation across continents, only inhabiting Europe (Schoch & Milner 2000) and North America (Sues & Schoch 2013) in the northern hemisphere and disappearing completely from the southern hemisphere. Metoposaurids first occurred in the early Late Triassic and developed a widespread distribution, ranging from Europe (Sulej 2002), North America (Gee *et al.* 2019; Gee & Jasinski 2021; Gee & Kufner 2022), northern Africa (Buffa *et al.* 2019), India (Chakravorti & Sengupta 2019) to indeterminate reports in South Africa (Barrett *et al.* 2020). Similar to trematosauroids, Plagiosauridae also disappear from the fossil record of the southern hemisphere and members of the group are restricted to Southeast Asia (Nonsrirach *et al.* 2021), Europe (Schoch & Milner 2000) and the arctic region (Marzola *et al.* 2018) during the Late Triassic. Chigutisauridae expanded their geographical range during the Late Triassic to India (Chakravorti & Sengupta 2023), South America (Martínez *et al.* 2012) and South Africa (Viglietti *et al.* 2020), while potentially disappearing from their Middle Triassic habitats in Australia. Pledge (2013) mentioned indeterminate material from a potential chigutisaurid from the Late Triassic of South Australia, but the precise stratigraphic location of this find is not entirely clear as Hart *et al.* (2023) referred it to the Lower Triassic. In a similar vein, brachyopids became endemic to South Africa (Peacock *et al.* 2017) in the Late Triassic.

This distribution pattern indicates that while some temnospondyl groups were widespread across Pangaea, others had a more restricted distribution, which could have been influenced by factors such as climatic conditions, geographical barriers and ecological niches. The presence of certain groups in specific areas suggests that there were distinct biogeographical regions, even within the supercontinent Pangaea, which may have led to varied evolutionary paths for these ancient amphibians. This distributional shift is remarkably highlighted in the Indian Maleri Formation, where metoposaurids, a clade found predominantly in the northern hemisphere, were replaced by chigutisauroids which only occur in the southern

hemisphere at the Carnian–Norian boundary (Sengupta 1995; Chakravorti & Sengupta 2023).

Nonetheless, comparable habitats were present in different regions of Pangaea (e.g. the Anisian Moenkopi Formation of North America and the Buntsandstein of Central Europe, Haque *et al.* 2021) harbouring similar temnospondyl faunas. Furthermore, lithological evidence differs for the fossil occurrences of each group. A clear higher abundance of Capitosauria in sandstones, compared to siltstones, mudstones or carbonates, indicates a wide range of potential occupied habitats with a preference for fluvial or deltaic environments for this clade (Schoch & Werneburg 1999). In contrast, Trematosauridae, Metoposauridae and Plagiosauridae occur in varied lithologies with a more even distribution across lithological (i.e. environmental) regimes, suggesting the occupation and niche partitioning of a wide range of preferred habitats specific to the individual clade or species, including lacustrine, fluvial, deltaic (Schoch & Milner 2014) and in some rare cases even potentially marine environments (Kear *et al.* 2015).

Here, we employ SDM to describe changes in the palaeobiogeographical distribution of temnospondyls throughout the Middle to Late Triassic by combining real world fossil occurrences with environmental data from general circulation models. By searching for regions with similar climatic conditions as seen in the back-rotated fossil localities we try to assess distributional patterns detached from present taphonomic biases. Investigation of climate range conditions occupied by the studied groups reinforce the results of the SDM and further indicate differences in niche occupation and dispersal potential.

MATERIAL & METHOD

Occurrence data

A comprehensive dataset comprising occurrences of Middle to Late Triassic temnospondyl amphibians was downloaded from the Paleobiology Database (PBDB, <https://paleobiodb.org/>, accessed December 2021) using the R package *velociraptor* (v1.1.0; Zaffos 2019) within the R environment (v4.1.0; R Core Team 2021). To extract this data, the API was queried using the taxonomic group name ‘Temnospondyli’ and the time intervals ‘Anisian’ to ‘Rhaetian’. These data were complemented with additional occurrences from current published literature which are not currently featured in the PBDB, for example, due to constraints around entering specimen-level data in the PBDB (see Table S1). This resultant dataset consists of 437 unique temnospondyl occurrences. To make these data compatible with

explanatory variables from palaeogeographic general circulation models, the occurrence points were matched to standardized geological stage-level resolution using the R package *divDyn* (v0.8.1; Kocsis *et al.* 2019). Lastly, the occurrence records were binned into three intervals based on the respective geological stages from the Anisian to the Carnian. To examine a more representable sample size we combined the groups ‘Capitosauria’ (5 families: Capitosauridae, Cyclotosauridae, Heylerosauridae, Mastodonsauridae, Paracyclotosauridae), ‘Trematosauridae’ (1 family: Trematosauridae), ‘Metoposauridae’ (2 families: Almasauridae, Metoposauridae) and the family Plagiosauridae into the category of Temnospondyli. Most of the occurrences outside of the Central European Basin (CEB) recorded in the dataset used here are located around the equatorial regions of Pangaea or along coastlines, leaving the inland regions mostly unsampled. Due to their sparse and more regionally restricted fossil record during the target intervals, we omitted the occurrence points of brachyopids and chigutisaurids from the analysis. To fit these present-day coordinates to their respective palaeogeographic location, we rotated the coordinates to their Mesozoic positions using R packages *rgplates* (v0.1.0; Kocsis & Raja 2021a) and *chronosphere* (v0.4.1; Kocsis & Raja 2021b). Since the climatic layers we used have been produced using the Scotese & Wright (2018) rotation model, the same model has been applied here to reconstruct the palaeocoordinates of our occurrences. These same packages were used to create palaeogeographic maps displaying the distribution of temnospondyl occurrences across the globe (Fig. 1).

Palaeoclimatic reconstructions

The climatic model outputs used to produce the SDMs are provided by the Bristol Research Initiative for Dynamic Global Environment group (BRIDGE; <http://www.bristol.ac.uk/geography/research/bridge>). These palaeogeographic general circulation models use a wide variety of specific parameters to simulate climate in deep time (Valdes *et al.* 2017, 2021). The model data used here belong to the HadCM3 family (Gordon *et al.* 2000; Pope *et al.* 2000; Valdes *et al.* 2021), and more specifically the model HadCM3BL-M2.1aD (Valdes *et al.* 2017, 2021). For a more detailed description of the model used see Valdes *et al.* (2017, 2021). The original output layers had a horizontal resolution of $3.75^\circ \times 2.5^\circ$, which results in a global grid of 96×73 cells (Valdes *et al.* 2021). To achieve a finer resolution grid to better fit the extend of the occurrence data, these global grid cells were interpolated to a horizontal resolution of $0.5^\circ \times 0.5^\circ$ grid, resulting in a global grid of 720×360 cells using the R package *ncdf4* (v1.18; Pierce 2021) with the bilinear method. The average

grid box size is roughly 55 km. We then extracted the climatic variables from the model output files that the BRIDGE group provides.

The variables to be used in this study were chosen in accordance with physiological relevancy to the species or genera in question (Antczak & Bodzioch 2018). Mean annual surface temperature and mean annual precipitation are used commonly in other palaeoclimatic studies (Dunne *et al.* 2021). To avoid overfitting of the model (Peterson 2011) due to the limited amount of data points available we used three climatic variables to establish our model: (1) mean annual air temperature at 1.5 m height; (2) mean annual precipitation; and (3) relative humidity at 1.5 m height. Variance inflation factor (VIF) analysis was applied to remove multicollinearity between explanatory variables. Subsequently, mean annual temperature and relative humidity showed high VIF values of 15. To reduce VIF values, relative humidity was thence excluded from model building. Previous authors (Sodhi *et al.* 2008; Girardello *et al.* 2010; Ficetola & Maiorano 2016) have shown that the distribution/physiology of extant amphibians is affected by temperature and precipitation. Using modern day amphibian distributions as a proxy for temnospondyl dispersion, it is likely that the two chosen variables impacted these early amphibian ancestors (Antczak & Bodzioch 2018).

Plots were constructed to visualize the range of palaeoclimatic conditions each group (Capitosauria, Trematosauridae, Metoposauridae, Plagiosauridae) occurred in. These plots, named ‘raincloud plots’, use boxplots and density plots to provide a summary of the distribution, central tendency, and spread of a dataset. The climate variables mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted from the climate model output described above and plotted in R using functions in the R package *ggplot2* (v3.4.4; Wickham *et al.* 2023). The data were divided into two to match the climate model time-binning format bins: (1) Middle Triassic (Anisian–Ladinian); and (2) Late Triassic (Carnian).

Species distribution modelling

The models were fully analysed in the R Studio Environment, with R (v4.1.0; R Core Team 2021), using the R package *biomod2* (v. 3.5.1; Thuiller *et al.* 2021). In *biomod2*, multiple algorithms are included to predict habitat suitability for a species. We generated MaxEnt (Phillips *et al.* 2006), Generalized Linear Models (GLM; McCullagh 1984), randomForest (RF; Breiman 2001) and Surface Range Envelope (SRE, equivalent to BIOCLIM; Busby 1991) models to cover a range of potential variability between algorithms. All output models were combined into a consensus ensemble model that has primarily been used in this study.

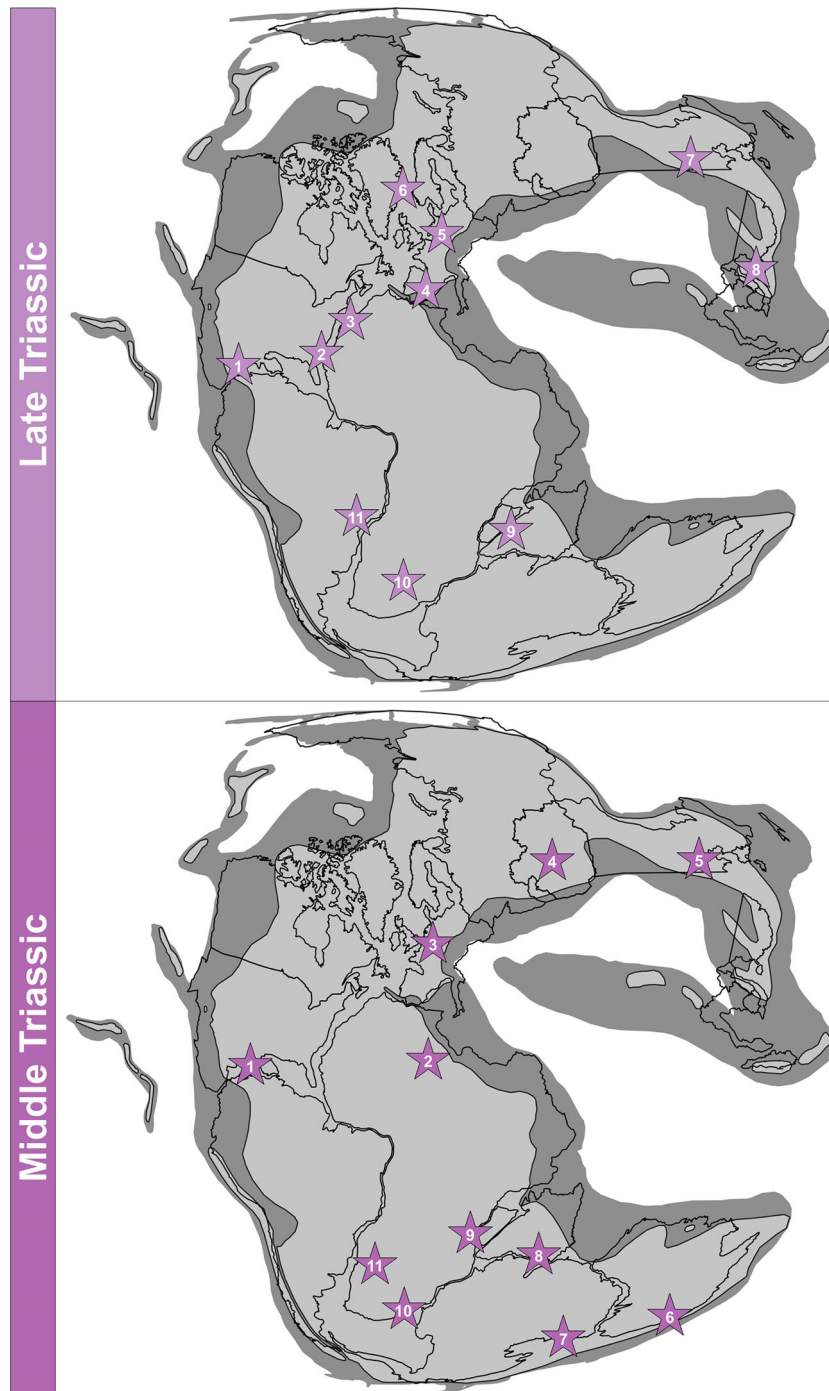


FIG. 1. Distribution of fossil localities containing temnospondyl fossils during the Middle and Late Triassic. *Middle Triassic localities:* 1, Arizona, USA; 2, Algeria; 3, Europe; 4, Russia; 5, northern China; 6, New South Wales, Australia; 7, Antarctica; 8, India; 9, Tanzania; 10, South Africa; 11, Namibia. *Late Triassic localities:* 1, Arizona, USA; 2, Pennsylvania, USA; 3, Morocco; 4, Iberian Peninsula; 5, Central Europe; 6, Greenland, Svalbard; 7, northern China; 8, Thailand; 9, India, Madagascar; 10, South Africa; 11, Argentina, Brazil. Base maps modified after Scotese & Wright (2018) and Kocsis & Scotese (2021).

To enable the use of presence-background algorithms, three selections of 1000 randomly picked pseudo-absences were conducted. For model building, the default settings

were used for GLM and SRE. To build models with the RF approach we ran 1000 iterations and computed classification trees. To choose the parameters that best fit our

dataset for the MaxEnt algorithm we used the R package ENMeval (Kass *et al.* 2021). We chose to use the model parameters given with the lowest possible delta Akaike information criterion (AICc; Burnham & Anderson 2002) with the feature class set to linear, the regularization multiplier set to 3, and a default prevalence of 0.5.

For each method, 50 evaluation runs were conducted with a 70–30 data split of our occurrence dataset for calibration and evaluation purposes. Area under the receiver operators curve (AUC; Hanley & McNeil 1982), true skill statistics (TSS; Allouche *et al.* 2006) and Cohen's kappa (Cohen 1960) were used for model evaluation. In the process of modelling, presences and background were weighted equally. For the resulting ensemble model building, a total consensus model with a mean of probabilities and a confidence interval of 0.05 was chosen to combine all models created in the previous steps.

In total multiple models combining four time-bins were projected: (1) Anisian–Ladinian (245–240 Ma); (2) Ladinian – early Carnian (240–234 Ma); (3) early Carnian – late Carnian (234–232 Ma). Lastly, the produced consensus ensemble models of each of the three time-slice were modified using the RangeSize function. The rate of change for potential suitable habitat by the species (in this study the combined group Temnospondyli) is correlated to the habitat lost or gained. Species range change maps (SRC) estimate habitat suitability changes when comparing different time slices of models that have been projected into future projection scenarios (Thuiller *et al.* 2021).

RESULTS

Model uncertainties

When applied to the fossil record, SDMs offer valuable insights into the biogeographic distribution patterns of extinct taxa in times of changing climates. Due to biases and the inherent incompleteness of the fossil record (Behrensmeyer *et al.* 2000), species occurrence data require critical evaluation for reliability. The combination of these data points with palaeoclimatic reconstructions potentially further introduces spatial and temporal uncertainties in later projection scenarios (Cao *et al.* 2019; Buffan *et al.* 2023). Constraints in spatial (Varela *et al.* 2011) and temporal (Maguire & Stigall 2009; Svenning *et al.* 2011)

resolutions might influence insights on small-scale environmental and ecological complexities and therefore require careful interpretation.

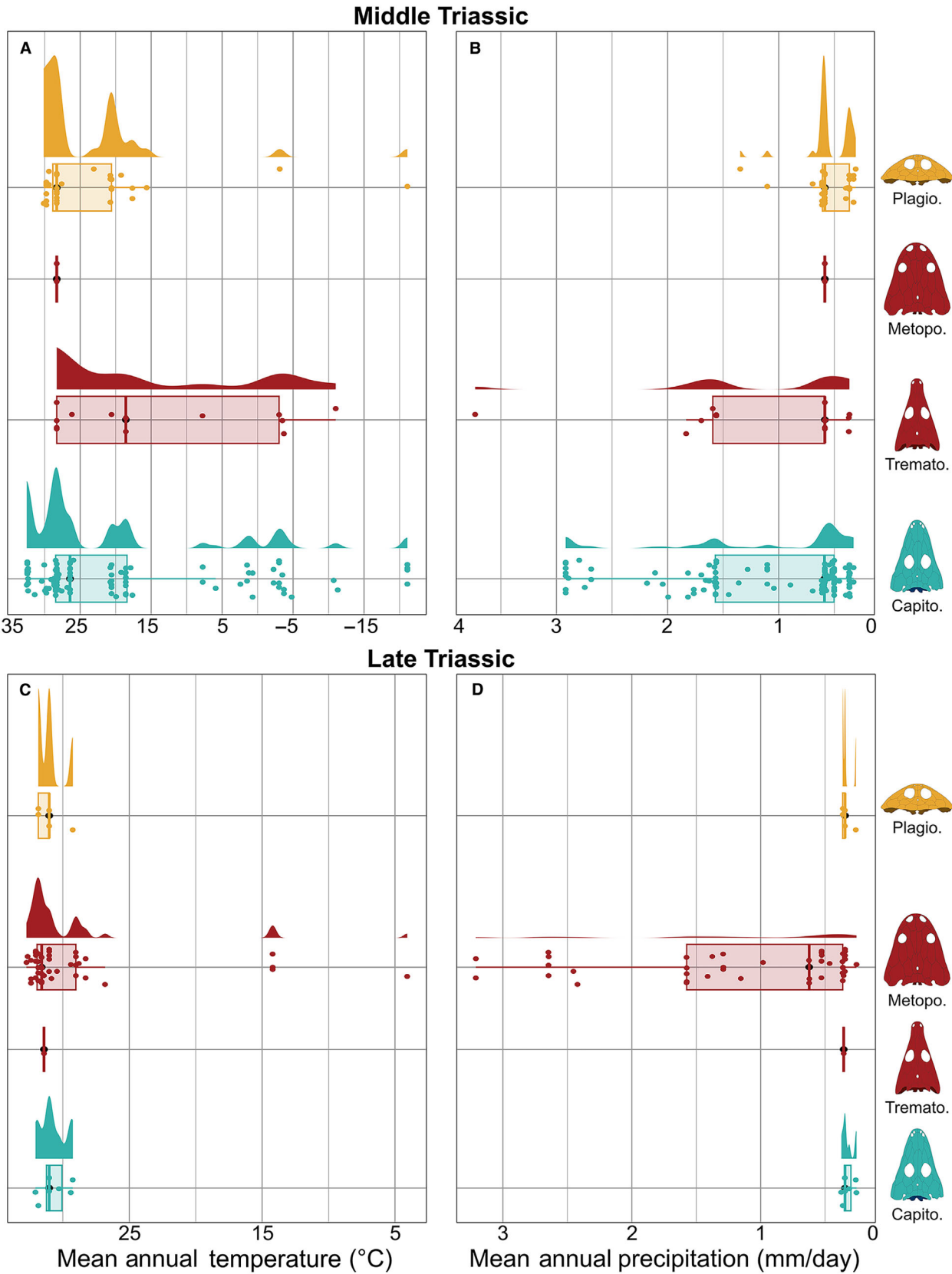
Nonetheless, SDMs remain valuable in a palaeontological context due to their implicit facilitation of testable hypotheses. Assumptions on a species past distribution can continuously be refined with new fossil data and enhanced palaeoclimate models (Guisan *et al.* 2017). Further, SDMs are an effective tool to detect and inform about broad-scale predictions and relative differences in distributions across changing climates and thereby providing valuable insights to biological responses to shifting environmental conditions (Pearson & Dawson 2003).

Despite these ambiguities, the simulations conducted herein provide important perspectives on the biogeographic patterns of deep-time taxa.

Model results

Across the Middle to Late Triassic, temnospondyls shift their geographic range. In the Middle Triassic, temnospondyls had a wide geographic range, occurring across southern and northern palaeolatitudes (Fig. 1). In the Late Triassic, this range became more restricted to lower and mid-palaeolatitudes (Fig. 1). Across this interval, the different temnospondyl groups show variations in the range of climatic conditions in which they occur. In the Middle Triassic, Capitosauria occur across a broad range of mean annual temperature (MAT) and mean annual precipitation (MAP) values (Fig. 2A, B). The group containing Trematosauridae and Metoposauridae occurs across similarly broad ranges of MAT and MAP, but their median occurrence is in cooler regions compared to Capitosauria (Fig. 2A). Plagiosauridae occur across a similar range of MAT and MAP values as Capitosauria, also preferring warmer temperatures. All groups prefer areas with low MAP, with plagiosaurids having the most restricted range of precipitation values (Fig. 2B). In the Late Triassic, Capitosauria occur across a much more constricted range of MAT and MAP values, yet still prefer warmer temperatures and areas with low precipitation (Fig. 2C, D). The same is true for Plagiosauridae (Fig. 2C, D). Trematosaurids and metoposaurids occupy similar ranges as in the Middle Triassic (Fig. 2), however, the majority now prefer warmer temperatures than in the Middle Triassic and occur across a wider range of

FIG. 2. Raincloud plots displaying the range of mean annual temperature (MAT) and mean annual precipitation (MAP) in the Middle Triassic (A, B) and the Late Triassic (C, D). The boxplots for each group are accompanied by density plots for each group. Raw climate values for occurrences can be found in Table S1. Capitosauria (Capito.) are represented as skulls of *Mastodonsaurus giganteus*, Trematosauridae (Tremato.) are represented as skulls of *Trematolestes hagdorni*; Metoposauridae (Metopo.) as skulls of *Metoposaurus diagnosticus*; and Plagiosauridae (Plagio.) as skulls of *Gerrhotraxon pulcherrimus*.



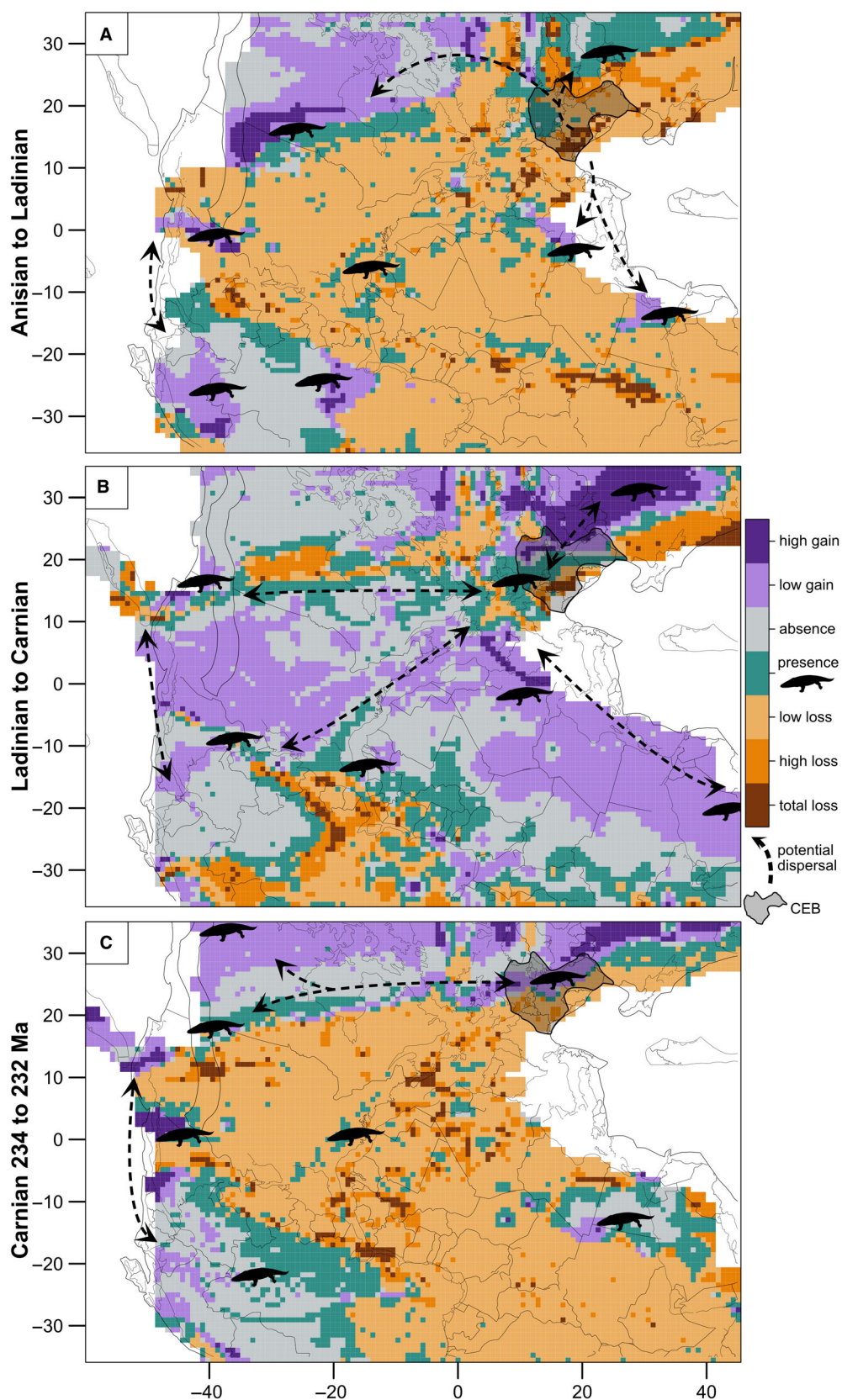


FIG. 3. Species range change (SRC) maps for the computed scenarios and combined temnospondyl occurrences. A, Anisian to Ladinian. B, Ladinian to Carnian. C, Carnian 234 Ma to Carnian 232 Ma. Interpretive dispersal trajectories (arrows) were added manually on the basis of the model results to connect regions of high habitat suitability. Temnospondyl presence is indicated by a generic capitosauroid silhouette. The modelling output focuses on central Pangaea. Purple shades indicate an increase in suitable habitat, while orange shades show a loss of suitable habitat. Areas of teal colour show regions populated by temnospondyls but in varying abundance. Differences in range size per simulated time interval are reported in Table 1 as predicted numbers of pixels lost, gained or stable, and percentages thereof. Shape of the CEB after Bachmann (2021); base map modified from Scotese & Wright (2018).

TABLE 1. Range size differences per simulated time interval.

Time interval	Loss (px)	Absence (px)	Presence (px)	Gain (px)	PercLoss (%)	PercGain (%)	Species range change (%)
Anisian–Ladinian	6	7	3	11	66.7	122.2	55.6
Ladinian–Carnian	68	64	57	50	54.4	40	−14.4
Carnian (234–232 Ma)	13	11	7	12	65	60	−5

Loss, Absence, Presence and Gain are reported in numbers of pixels affected. PercLoss, PercGain and SpeciesRangeChange are reported in percentage of pixels.

precipitation values than any other group (Fig. 2C, D). It is noteworthy that in the Middle Triassic the sole representative of the Metoposauridae is *Callistomordax kugleri* (Schoch 2008) from the Ladinian of Germany, reflecting the evolutionary history of metoposaurids, while the only Late Triassic trematosaurids are *Calamops paludosus* (Sues & Schoch 2013) and *Hyperkynodon keuperinus* (Schoch *et al.* 2002).

Simulating the time interval from the Anisian to the Ladinian shows a total loss of temnospondyl habitats in the Central European Basin (CEB), with accompanying extended areas of low to high habitat loss in the vicinity, reaching to a maximum of 30°N palaeolatitude along the eastern coastline of Pangaea (Fig. 3A). Small isolated areas of increasing habitat suitability appear around the palaeoequator and south to −10° palaeolatitude on the eastern coast of Pangaea. The western coast of Pangaea gains suitable habitat in central western and northwestern areas of present-day North America, as well as in the northern regions of South America. This indicates that these areas are likely to have been connected. Inland regions, as well as areas bordering on the eastern coast of Pangaea, experience a general decrease in temnospondyl habitat suitability, where only small remnants or potential refugia of temnospondyls stay present during this time interval (Fig. 3).

Considering habitational changes from the Ladinian to the Carnian, the model predicts habitat loss within the CEB (Fig. 3B). This habitat loss is probably due to the onset of the Gipskeuper ingression and stretches along south–westward through the entire CEB. Following the borders of areas with high habitat loss, the model predicts a minor decrease of temnospondyl presence. Area of

habitat loss extends along the northeastern coast of Pangaea up to a palaeolatitude of 30°N and beyond, going from Ladinian to Carnian. To the north of the CEB, an increase in suitable habitat conditions is indicated in the region of present-day east coast of Greenland and the Baltic region. South of the CEB, a large region of increased suitable habitat extends from the equator up to the 20°S palaeolatitude following the eastern coastline of Pangaea. A corridor following latitude of 20°N in an east–west direction shows less optimal conditions, but indicates potential connectedness of temnospondyl populations between the eastern and western coastlines of Pangaea on the adjacent areas. The area of increased suitable habitat in present day North America can be seen as extension of the suitable climates observed on the eastern coast of Pangaea. A pathway between present-day North America and western Africa indicates temnospondyl presence in this area. Inland regions in Central Pangaea underwent a decrease in suitable habitat in this period.

Given the relative duration of the Carnian, combined with the comparably high resolution of its fossil record, a simulation of the transition between the two substages of the Carnian was performed (Fig. 3C). In the CEB this time period reflects the transition between the Gipskeuper ingressions during the deposition of the Grabfeld Formation and the onset of the Stuttgart Formation of present-day Germany that is representative of the Carnian Pluvial Event (CPE; Dal Corso *et al.* 2020). Changes in habitat suitability from 234 to 232 Ma show an increase relative to the previously simulated time interval, especially in the southern parts of the CEB as well as increase in the northwest of the basin (Fig. 3C). The corridor

following the palaeolatitude of 20°N in east–west direction is still present in this interval, hinting at persistent climatic conditions in the Middle and Late Triassic in the area. Bordering areas to the west signal strong increase of suitable habitat, indicate connectedness and highly suitable conditions for temnospondyls along the west coast of Pangaea up to 30° south of the palaeoequator. Inland regions, as well as regions following the eastern coast of Pangaea, show a decrease in suitable habitat compared to the previous time interval, except for areas in present day Egypt and Jordan and small isolated remnants between present day North America and northern Africa (Fig. 3C). Habitat suitability seems to recover slightly going from Ladinian to the Carnian 232 Ma step in the CEB. The area on the western coast of Pangaea retains the increase in habitat suitability in this time interval, indicating favourable environmental conditions in that region. Despite the increase of habitat suitability in numerous areas of central Pangaea, the overall area shows a decreasing trend during the Middle to Late Triassic transition with a loss of habitat suitability of 5–14%, while the climatic conditions led to a general increase in suitable habitat of over 50% during the Middle Triassic (Table 1).

DISCUSSION

Habitat suitability and geographical context

The SDMs document the changes in temnospondyl biogeography across the Middle to Late Triassic, and highlight the impact of environmental and climate changes.

Across all simulated time intervals, unfavourable habitat conditions in areas of present-day fossil localities were predicted when investigating the time interval from Anisian to Ladinian, and Ladinian to Carnian 232 Ma inside the CEB. With respect to fossil sites outside of the CEB, all simulations predicted at least a slight increase in habitat suitability in the areas around the North American Moenkopi and Chinle formations. Habitat suitability in areas of the Zarzaitine Group of Algeria and Argana Group of Morocco and the region of the Upper Triassic Chatham Group of North Carolina are predicted as small patches during the early and the late simulated time interval, but showed extended areas during the intermediate step. The simulation of the transition from the Ladinian to the Carnian connects the suitable regions of southwestern USA with those found in North Carolina and the Moroccan Argana Basin by predicting a slight increase in range size expansion across the North American continent. Both the Moenkopi Formation of southwestern USA and the Zarzaitine Group of Algeria are significantly older than the Ladinian Lower Keuper of the

CEB. While the Argana Group, Chatham Group and Chinle Formation all date younger than the Lower Keuper of the CEB, the simulation of the time interval going from the Ladinian to the Carnian seems to indicate favourable conditions during this time interval as well, hinting at hypothetical good habitat conditions during the entire Triassic in those regions.

Latitudinal patterns

The Anisian localities of England mainly encompass temnospondyls of the clade Capitosauria with remains of the closely related capitosaur *Procyclusaurus*, *Eocyclosaurus*, *Mastodonsaurus* and *Stenotosaurus* from this area (Schoch & Milner 2000; Schoch *et al.* 2023), while the Anisian Moenkopi Formation of North America (Haque *et al.* 2021) feature coeval remains of *Eocyclosaurus* and *Quasicyclosaurus* (Schoch 2000b). Anisian strata of the same age from Germany feature capitosaur remains as well, including *Eocyclosaurus*, *Mastodonsaurus* and *Stenotosaurus* (Schoch *et al.* 2023; Schoch & Moreno 2024). This presence of fossil remains in the according coeval fossil deposits from the lower Middle Triassic suggest the distribution and range size of capitosaur to follow the corridor along palaeolatitude of 20°N. Connecting the presence of *Calmasuchus* (Fortuny *et al.* 2011) of the Iberian Peninsula with the occurrences of *Parotosuchus* and *Wellesaurus* in the Anisian Zarzaitine Group of Algeria provides a link between the regions of Europe and northern Africa and suggests that capitosaur extended their habitat in north–south direction all the way from northern Africa to the Anisian Muschelkalk Group of Winterswijk (Oosterink & Diepenbroek 1990) in the Netherlands, and potentially into the Ural regions. Recent finds of Ladinian temnospondyl material from the Shaanxi Province, China (Wu *et al.* 2022) are coeval with the Kupferzell and Vellberg-Eschenau deposits of southern Germany (Schoch & Seegis 2016; Schoch *et al.* 2022) and extend the biogeographical range of capitosaur into the North China block as early as the Middle Triassic. This distributional pattern suggests widespread aquatic pathways extending along the coastline from the CEB over the Ural into the Ordos Basin (Fig. 4). During the Anisian, trematosaur members are restricted to the fluvial–lacustrine deposits of the Zarzaitine Group before expanding their distributional range northwards into the CEB in the following Ladinian period, indicating a change of environment favouring the living conditions for these genera in that region. Based on putative marine affinities (Fortuny *et al.* 2017) for the derived lonchorhynchines (*Wantzosaurus*, *Aphaneramma*) it appears plausible that some trematosaurs could have utilized aquatic pathways of varying salinity levels as potential pathways

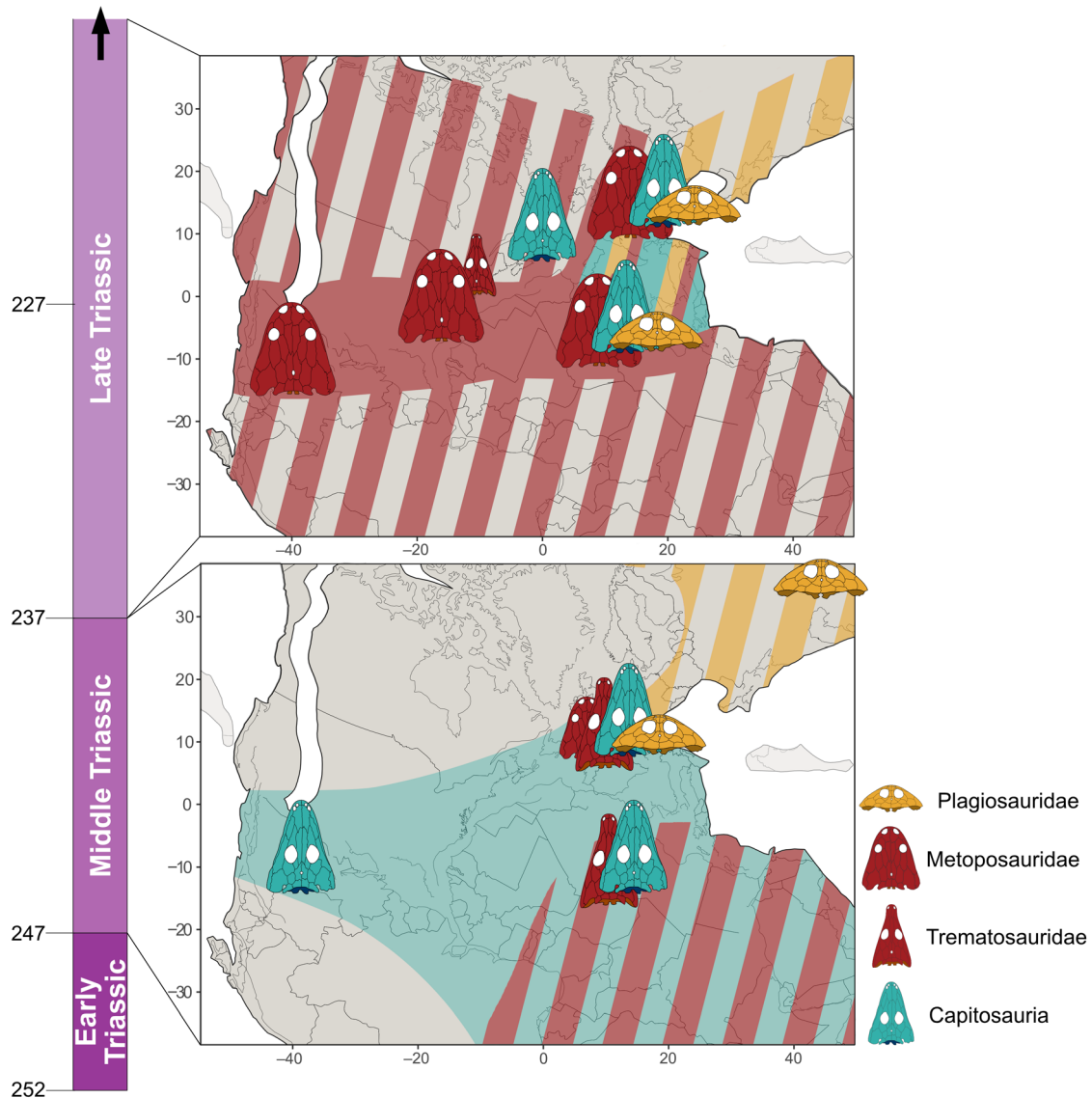


FIG. 4. Global distribution of temnospondyl clades across Pangaea during the Triassic and estimated range size of different temnospondyl clades inferred from real world fossil localities and habitat suitability maps connecting those regions in the study area. Full coloured areas show occupied region backed by real world fossil localities for the various groups of temnospondyls analysed, while striped areas connect geographically more distant fossil localities. In these cases, occurrence can only be assumed based on the results shown in Figure 3. Capitosauria are represented as skulls of *Mastodonsaurus giganteus*; Trematosauridae as skulls of *Trematolestes hagdorni*; Metoposauridae as skulls of *Metoposaurus diagnosticus*; and Plagiosauridae as skulls of *Gerrothorax pulcherrimus*. Base map modified from Scotese & Wright (2018); time scale adapted from Cohen *et al.* (2013) v2022/10.

for migration. Plagiosauridae are restricted to the Muschelkalk bonebed in the Germanic Basin in the early Ladinian (Schoch & Werneburg 1999) potentially indicating their higher tolerance for environmental influences.

In the following Late Triassic, capitosaurids show reduced distributional range size restricting their habitat to Laurasia (Schoch & Milner 2000), inferring worsening habitat conditions in regions of Pangaea where this clade had previously been widely distributed around the

Ladinian–Carnian transition (Fig. 4). Following further habitat reduction into the CEB and adjacent regions, capitosaurids started expanding their biogeographical range again into Asia during the Carnian–Norian (Nonsrirach *et al.* 2021; Shi *et al.* 2023). The faunas of North America and northern Africa are dominated by metoposaurids (Fig. 4). The genera *Anaschisma*, *Apachesaurus* and *Buettnererpeton* are distributed in North America and *Almasaurus*, *Arganasaurus* and *Dutuitosaurus* in Morocco

(Buffa *et al.* 2019). In the CEB, large trematosaurids and metoposaurids can be found (*Hyperkynodon*, *Metoposaurus*). While trematosaurids seem to have a restricted distributional range and are confined to the CEB and the east coast of North America, the range of metoposaurids seems to extend laterally across Central Pangaea. This wide disparity in range size suggests significant differences in ecological needs of both families. Plagiosauridae remained restricted to the CEB during the early stages of the Late Triassic, but extended their distribution northwards into Greenland during the Norian (Jenkins *et al.* 2008; Clemmensen *et al.* 2015), indicating a general lack of necessity or ability to extend their distributional range. Plagiosaurs are adapted to ecological niches different from those of capitosaurids and trematosaurids, while also able to inhabit a wider range of aquatic habitats (Fortuny *et al.* 2017) with *Gerrothorax pulcherrimus* being capable to endure various conditions for a wider range of inhabited areas (Sanchez & Schoch 2013). Despite being able to adapt to different ecological environments, plagiosaurs are only found in very narrow temperature and precipitation ranges, which in turn significantly limits their dispersal potential (Fig. 2).

Abiotic controls on geographical distribution

The geographical distribution of species is controlled by both biotic and abiotic conditions. In particular, the presence of physical barriers and therefore the accessibility for dispersal contribute largely to the dispersal potential of an animal (Peterson 2011; Saupe *et al.* 2012; Anderson 2013). In the case of fossil taxa geological, taphonomical and anthropological biases might obfuscate the true distribution of these taxa.

In the Middle Triassic, all groups occur across a wide range of temperatures and precipitation values (Fig. 2). However, in the Late Triassic, the ranges of both the Capitosauria and Plagiosauridae become more restricted, while the Trematosauridae and Metoposauridae remains comparatively broad (Fig. 2). This shift in occupied climatic ranges occurs at the same time as a decrease in suitable temnospondyl habitat, as outlined above (Fig. 3). This might indicate that Trematosauridae and Metoposauridae had a greater dispersal ability than the other temnospondyl groups, which allowed them to increase their geographical range towards the end of the Late Triassic, in spite of changing climatic conditions.

Palaeobiogeographical analysis indicates a cosmopolitan distribution for certain clades of Triassic tetrapods, including capitosaurid temnospondyls during the Middle Triassic (Ezcurra 2010). This pattern substantiates the absence of geographic barriers during this time period (Scotese & Wright 2018). Instead, observed biogeographic

provinces were proposed to be primarily shaped by climatic factors influencing regional climates and seasonality (Ezcurra 2010; Whiteside *et al.* 2011, 2015; Griffin *et al.* 2022). This apparent conundrum between cosmopolitan distribution and existing biogeographic provinces can be rationalized by the influence of climatic barriers. During the Middle Triassic, strong climatic barriers for dispersal persisted and first started to dampen with the onset of the CPE (Griffin *et al.* 2022). Diminishing climatic barriers might have been driven by shifts in global climate patterns. Less restrictive and generally more pandering climatic conditions favoured non-capitosaurid temnospondyls to expand from their endemic regions into higher latitudes. Proposed prominent humid conditions in this part of Pangaea (Stefani *et al.* 2010; Mazaheri-Johari *et al.* 2021) support this interpretation and fit the required habitat suitability for temnospondyls. Biogeographic connectedness analysis (Button *et al.* 2017) has shown a declining trend from the Ladinian to the early Late Triassic, and a stagnating trend from the early Late Triassic to the late Late Triassic in Laurasia. A rising trend during this period is observed in Gondwana. This indicates increasing endemism during the Late Triassic in the northern parts of Pangaea and the development of a different distinct fauna in the southern parts (Button *et al.* 2017). Moreover, latitudinal variation has been identified as a major force behind the palaeogeographic distribution and provincialism of tetrapods during the Triassic (Ezcurra 2010; Dunne *et al.* 2021).

For the Late Triassic, the North American Newark Basin records lacustrine deposits (Whiteside *et al.* 2011) that provide the abiotic foundation for temnospondyl range expansion into this region. Biotic interactions could have played a key role in relation to dispersal potential and abiotic interaction explaining why temnospondyls lost significant suitable habitational area across the simulated time interval. However, since biotic interactions have not been considered during the modelling process, this interpretation is based purely on the fossil record and the accompanied faunas of previously described fossil localities. In the case of the Late Triassic Metoposauridae, Brusatte *et al.* (2015) noted the presence of *Metoposaurus* in assemblages featuring phytosaurs in similar but not identical latitudinal ranges. Recently, Griffin *et al.* (2022) identified a new Carnian dinosaur-bearing assemblage in Zimbabwe connecting coeval assemblages from South America and India. This newly found assemblage strengthens the hypothesis that these animals dispersed along these latitudinal climatic zones. Based on their results, it seems reasonable to suggest that the temnospondyl families examined in this study potentially dispersed similarly as is shown by the herein described simulations thereby dependent on existing connected aquatic environments.

Future prospects

With the recent discovery of a new benthosuchid from the Early Triassic of Brazil (Pinheiro *et al.* 2024) challenging the long-believed endemism of this family in the East European Platform (Schoch 2000a) and suggesting a biogeographical connection between these far regions of Pangaea, it is evident that many aspects of the evolutionary history of temnospondyls are still to be discovered. Applying a palaeoclimatic framework to the ever-growing direct fossil record might be key to understanding the complex broader biogeographical patterns of the group. There are multiple lines of evidence showing that abiotic factors influence the distribution of Triassic tetrapods (Ezcurra 2010; Dunne *et al.* 2021); the new insights gained from the present study add to these observations and indicate that changes in abiotic conditions are a clear pressure on the distribution of Middle and Late Triassic temnospondyls. It is therefore evident that employing distribution modelling techniques across the evolutionary history of the group, in their full geographic and taxonomic extent from the Carboniferous to the Cretaceous, in future studies will aid in unveiling the complexities of these early amphibians.

CONCLUSION

By combining occurrence data for Middle and Late Triassic temnospondyl amphibians with climatic data from palaeogeographic general circulation models, we documented changes in the biogeographic distribution of different temnospondyl clades across changing climates from humid to arid conditions. The simulations connect fossil localities across Pangaea and allow for interpretation of putative migration pathways in times of dynamic climates and uncertain environmental circumstances for this group. As shown by previous studies (Peterson 2011; Anderson 2013), the geographic distribution of a species is controlled by biotic and abiotic conditions and the potential to disperse due to the lack of physical barriers. Abiotic conditions favourable for temnospondyl distribution include areas with generally low seasonality and relatively high temperatures (Dunne *et al.* 2021). These regional climatic zones must be accompanied by fresh or brackish water systems to allow the dispersion of the aquatic temnospondyl clades simulated in this study. Connected bodies of water must have been present on the local to regional level as seen in the Central European Basin (CEB), with the Lower Keuper delta (Wurster 1968; Nitsch 2015), or the Great Lakes of the Newark Basin (Olsen 2010). Northward migration of capitosaur and trematosaur from Gondwana up to Greenland in the early Middle Triassic is followed by

coexistence of both clades in the CEB. This region of Pangaea could have served as a focal point for further dispersion for both clades in the following periods of the Triassic. The CEB was connected to other terrestrial basins of Laurentia (Schoch 2000a; Scotese & Wright 2018; Kocsis & Scotese 2021). This setting opened up possibilities for eastward expansion of territory of capitosaur into the China block through the Ural regions along the coastline and the Triassic Boreal Ocean delta plain (Klausen *et al.* 2019), and westward expansion along the diminished Central Pangaeic Mountain Range (Scotese & Wright 2018) and along the palaeolatitude of 20°N for trematosaurid temnospondyls respectively. The biogeographic patterns described in this study open the way to further evaluate the processes of dispersal and vicariance. While both play a role in the occupation of new territories, the interplay of both processes offers extensive opportunity for future research endeavours.

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Author contributions. **Conceptualization** R Moreno (RM); **Formal Analysis** RM (lead), E Dunne (ED); **Investigation** RM (lead); **Methodology** RM (lead), ED; **Resources** A Farnsworth (AF), PJ Valdes (PJD); **Software** RM (lead), ED; **Supervision** RR Schoch (RRS); **Visualization** RM; **Writing – Original Draft preparation** RM; **Writing – Review & Editing** RM (lead), ED, E Muijal, AF, PJD, RRS.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12724>):

Table S1. Data used to produce Figures 1 and 2, and the species distribution models (Fig. 3).

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