



# The effect of geographic range and climate on extinction risk in the deep-time amphibian fossil record

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## ARTICLE INFO

### Keywords:

Oxygen isotopes  
Environmental variability  
Latitudinal gradient  
Traits  
Temporal stability

## ABSTRACT

Geographic range is of crucial importance concerning the extinction risk of species. However, our understanding of how the influence of this trait on extinction risk has varied through Earth history and across different climate regimes is still rather unexplored. This is especially true for taxa that are currently of strong interest in conservation biology, displaying a strong mismatch between paleontological studies and modern efforts to quantify the extinction risk of threatened species. We herein calculated a continuous measure for the connection of geographic range and extinction risk in the deep-time amphibian fossil record. Furthermore, we evaluated the impact of climate on this connection, using two climate proxies derived from oxygen isotope data (global relative temperature change and variations in the latitudinal temperature gradient). We show that geographic ranges tended to be larger during times of comparatively small latitudinal temperature gradients. Moreover, the strength of geographic range influencing extinction risk fluctuated temporally, but remained positive at all times. The variation in range size impact on extinction risk showed a strong connection with the latitudinal temperature gradient. Our findings indicate that geographic range persists as a factor influencing species' extinction risk through all times. However, geographic range seemed less important during times of higher environmental variability. Reasons might be the restriction of species ranges due to environmental constraints, causing ranges to become more similar and therefore lose relative importance in buffering for extinction risk, while other factors gain in importance. Simultaneously, similar ranges might be more prone to alteration by e.g. conservation biases (related to sedimentary deposition and fossilization) in relation to their real range size, resulting in a smaller signal-to-noise ratio, potentially affecting the correlation strength. We show that trait-extinction risk dynamics can vary in their intensity, and that specifically the observed impact of geographic range on extinction risk can vary with climatic changes.

## 1. Introduction

Among the factors that influence the extinction risk of a species, geographic range has been shown to be of paramount importance across a large number of different taxa, both in living species and in the deep-time fossil record (Finnegan et al., 2015; Harnik, 2011; Kiessling and Aberhan, 2007; Kiessling and Kocsis, 2016; Purvis et al., 2000; Sodhi et al., 2008; Tietje and Rödel, 2018). Not surprisingly, geographic range is thus also the main factor used to assess the extinction risk for living species in the IUCN Red List assessment procedure (IUCN, 2012). Given its importance across taxa, time and ecosystems, the influence of geographic range on extinction risk seems persistent; and a large range proves beneficial for a species' survival. Nevertheless, potential changes in the range size–extinction risk connection across time have been

assessed mostly for marine invertebrates (Payne and Finnegan, 2007; Foote et al., 2008; Harnik et al., 2012; Orzechowski et al., 2015; but also Dunhill and Wills, 2015). These studies focus on taxa which are not the principal foci of current conservation efforts, while modern conservation studies would benefit from paleontological counterpart studies for cross-validation of results and to provide a perspective on extinction dynamics on long timescales. We try to bridge this mismatch between paleontology and conservation by focusing on the connection of geographic range and extinction risk under changing climatic conditions in amphibians, which are a main focus of conservation activities today. Amphibians are currently globally threatened (Ceballos et al., 2017) and might, as ectothermic terrestrial vertebrates, exhibit different dynamics than marine invertebrates, particularly in response to environmental changes.

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The strong connection between geographic range and extinction risk intuitively makes sense, as a large geographic range allows to buffer declines, or even extinctions, of local populations. For instance, local populations may be impacted by unforeseen rapid environmental changes like flooding, volcanic activity, or the arrival of a new competitor, predator, parasite or disease (Kats and Ferrer, 2003; Bower et al., 2019; Jones, 2012; Scheele et al., 2019; Walls et al., 2013; Wilting et al., 2012). Declines or extinctions on a local scale, can either be reversed by filling up the gaps with migrating individuals from other (meta-)populations (Green, 2005), or the taxon simply survives with an altered range (Wiens, 2016).

Among the factors that affect the geographic range of a species are intrinsic traits like dispersal ability and body size (Gaston, 2003; Gaston and Blackburn, 2008; Penner and Rödel, 2019; Sodhi et al., 2008). Concerning extrinsic factors impacting range size, climate has been shown to be one of the most significant factors dictating the limits of the geographic distribution of species (Caughley et al., 1987; Gaston, 2003; Estrada et al., 2015). Whether climatic variables affect exclusively the geographic range itself, or if they also alter the effect strength with which the geographic range is influencing extinction risk over time has been tested in only a few studies. In a meta-analysis Orzechowski et al. (2015) investigated the environmental influence on the extinction selectivity and geographic range in fossil marine bivalves and gastropods, and found no effect. Payne and Finnegan (2007) however, detected a decrease in the association strength of geographic range and survivorship of marine invertebrates during mass extinction events.

Here we assess the interaction of geographic range with extinction risk for amphibian species in deep-time and relate the patterns in this interaction to two global climate proxy records based on carbonate shell geochemistry. The two climate proxies we used are 1) low-latitude oxygen isotope data, which reflects long-term trends in relative global temperature; greenhouse vs. icehouse modes (Zachos et al., 2001; Prokoph et al., 2008; Veizer and Prokoph, 2015), and 2) the difference between high and low-latitude oxygen isotope data, which represents a measure of the global latitudinal temperature gradient and variations therein. Both climate proxies align well with the current understanding of climatic trends throughout the Phanerozoic (Kidder and Worsley, 2010; Hay and Floegel, 2012; Veizer and Prokoph, 2015). This study yields insights into the interplay of geographic range, climate, and the connection of geographic range and extinction risk under differing climatic conditions in the amphibian fossil record.

## 2. Material and methods

### 2.1. Data

#### 2.1.1. Species data

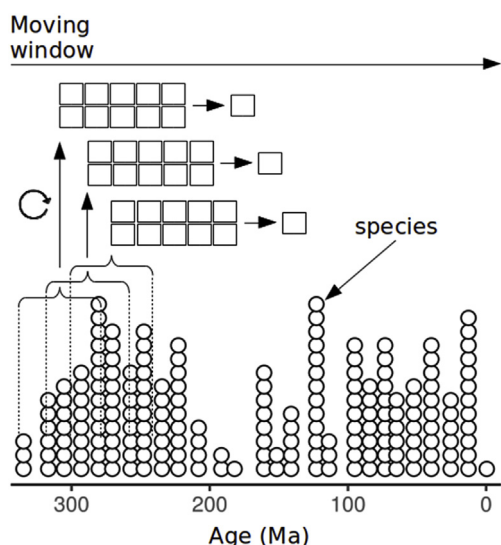
We used the amphibian dataset from Tietje and Rödel (2018). This dataset includes stratigraphic range (duration) and geographic range for 353 extinct amphibian species which were calculated from 1049 occurrences from the Paleobiology Database and the literature (for a complete list of references see Tietje and Rödel, 2018). For an overview see Figure S1. The data cover lissamphibian groups including their potential stem-taxa, Temnospondyli as well as Lepospondyli (see Tietje and Rödel, 2017 for more detailed information), dating back 339 million years. Species duration was calculated as the time between the midpoints of the youngest and oldest stratigraphic unit (geological stages) in which a species occurred, rounded to the next full million years. The geographic range for each species was calculated as maximum great circle distance, which represents the shortest distance between two points on the surface of a sphere (Kiessling and Aberhan, 2007) and has shown to be suitable to reconstruct spatial range from sparse occurrence point data (Darroch and Saupe, 2018). Great circle distances were calculated for each geologic stage within a species lifespan. The maximum extent ever achieved by a species over its

lifespan was used as its geographic range for further analysis. Therefore, the final dataset comprises one value for the duration and geographic range for each species, as well as the mean species age. As we were mainly interested in latitudinal aspects of geographic range and climate, we additionally ran the analysis using the latitudinal range as an alternative measure for geographic range to account for differences between these metrics.

#### 2.1.2. Climate data

We used the oxygen isotope data ( $\delta^{18}\text{O}$ ; on the VPDB-scale) based on carbonate shells from organisms (bivalves, belemnites, brachiopods and foraminifera) living at shallow water depths provided by Veizer and Prokoph (2015), thereby reflecting the surface water conditions. Each isotope value is referenced to the geologic stage (GTS, 2012) and comes with information on the climatic zone (temperate, arctic, tropical, and subtropical). For global average climatic trends, we use exclusively oxygen isotope data from low paleolatitude surface oceans as defined in Veizer and Prokoph (2015). The selection of surface water species is necessary to connect the Cretaceous-recent dataset with the pre-Cretaceous dataset, where the latter consists exclusively of shallow water taxa from shelf environments and epicontinental seas. Although this dataset stacks  $\delta^{18}\text{O}$  measured on the shells produced by different taxonomic groups, systematic  $\delta^{18}\text{O}$  offsets (so-called “vital effects”) between those fossils groups are relatively small comparative to the overall scatter in the dataset (Veizer and Prokoph, 2015). By doing so, we create a more-or-less continuous climate proxy record that is representative for one environment (low-latitude surface waters), which is sensitive to secular climatic trends, and unbiased by artifacts generated through the inclusion of climatic signals specific to certain environments (i.e. cooler deep water vs. warm upper water column conditions). Moreover, low-latitude oceans are a principal driving force of solar heat distribution from the equator to the poles, and thereby control general atmospheric circulation (Chiang, 2009). Hence, long-term first-order trends in the low paleolatitude surface water  $\delta^{18}\text{O}$  ( $\delta^{18}\text{O}_{\text{low-latitude}}$ ) record can be regarded as a monitor of climate evolution that is directly relevant to changes in the global amphibian population over long geological timescales.

The latitudinal  $\delta^{18}\text{O}$  gradient ( $\Delta^{18}\text{O}_{\text{high-low-latitude}}$ ) was calculated for the last 110 million years from planktic foraminifera by calculating the difference between high (58°–90° N/S paleolatitude) and low (15°S–15°N paleolatitude) latitude data, as a second source of paleoclimate information. This record would be largely a reflection of the latitudinal temperature gradient, although other factors do as well control latitudinal differences in seawater  $\delta^{18}\text{O}$  composition (Tindall et al., 2010). Besides the control of global average temperatures, this latitudinal temperature gradient is thought to be dictated by secondary processes, such as the continental configuration, oceanic circulation patterns and the presence of land ice (Bjerrum et al., 2001; Poore et al., 2011), so this record might be a more sensitive monitor of latitudinal temperature differences important for the distribution of amphibian habitats. To accommodate for the before cited uncertainties in  $\delta^{18}\text{O}$  composition we restrict this record to the last 110 million years where continental configuration, circulation patterns, and climate evolution are best constrained, but also as older carbonate shell records are scarce before this time. Moreover older carbonate shell records consisting of bivalves, brachiopods and belemnites from shelf and epicontinental settings might be unrepresentative of the latitudinal temperature gradient due to restricted exchange of water with the open ocean, and are therefore more likely to be influenced by riverine influxes. These influxes can lead to local isotope values different from the open ocean, which would not be representative for the general climatic conditions (Marshall, 1992; Holmden et al., 1998; Harzhauser et al., 2007). This effect is exaggerated by repeated evaporation-precipitation cycles, and associated isotope fractionation during phase transitions, that successively deplete meteoric water in  $^{18}\text{O}$  during transport towards the high-latitude (Marshall, 1992). Hence, high-latitude isotope data older than



**Fig. 1.** Schematic representation of the moving window approach. Each dot represents the mean age of a species and has a corresponding geographic range and duration. A window size that ensures a specified minimum sample size (at least 10 in our case) at all times is chosen and moved along the temporal axis. At each 1 million year step, repeated subsampling with replacement is performed (100 repetitions). For each subsample, we calculate either the median and median absolute deviation (isotope data), or the Spearman rank correlation (geographic range and duration data).

ca. 110 million years, that predominantly originate from shallow water settings, could be compromised, which makes a  $\delta^{18}\text{O}$  gradient as a sensitive proxy of prevalent climatic conditions less reliable.

### 3. Methods

Prior to all calculations, isotope values were corrected for  $^{18}\text{O}$  depletion (Phanerozoic trend, “secular shift”) using the equation provided by [Veizer and Prokoph \(2015\)](#). To cancel out the temporally and quantitatively uneven spread of data in the isotope dataset, we calculated median isotope values using a moving window approach including a subsampling routine ([Schobben et al., 2017](#)), which divides the temporal axis of the data into an evenly sized grid and moves a window over this grid in small steps (one million years), repeating the same analysis in each time interval ([Fig. 1](#)). Window size was chosen as 25 million years to maintain a minimum sample size of ten in each window. Additionally, within each window the data was repeatedly subsampled ( $n = 100$ ) to the sample size of the minimum number of isotope values contained in all windows, the final value being the median  $\delta^{18}\text{O}$  of all subsamples. Additionally, the median absolute deviation was calculated from the 100 medians as an error measure for the final median. The moving window procedure acts as a smoother which accounts for temporal unevenness of data, while the internal subsampling procedure accounts for quantitative differences in the data.

We split the isotope data into two sets, according to the climatic zone information given by [Veizer and Prokoph \(2015\)](#). “Arctic” and “temperate” labeled data points were used to calculate the high-latitude temperatures, data points labeled with “tropical” to calculate low-latitude temperatures. The moving window approach was applied to both datasets. The temperature gradient was calculated as the difference between the two resulting curves from high and low-latitudes. Data labeled as subtropical were not used for the temperature gradient due to potentially high evaporation in these areas, which can lead to falsely increased  $\delta^{18}\text{O}$  values, known as the cool tropic paradox ([D’Hondt and Arthur, 1996](#)). Following the same procedure, we calculated additional climate proxies to provide support for our approach of using exclusively

surface water oxygen data; the median deep sea  $\delta^{18}\text{O}$  curve. Comparing the median deep sea  $\delta^{18}\text{O}$  record with the median surface  $\delta^{18}\text{O}$  record gives insights if the surface water  $\delta^{18}\text{O}$  follows global climatic trends ([Zachos et al., 2001](#)). Additionally, deep sea water formation usually takes place at high-latitudes ([Rahmstorf, 2002](#)), however, differences between the deep sea  $\delta^{18}\text{O}$  and the high-latitude surface  $\delta^{18}\text{O}$  records can potentially point at regional variations in the deep sea water formation, where variations in deep water formation seems to be intimately linked with the hydrological cycle ([Marotzke and Willebrand, 1991](#)). Paleontological (i.e. geographic range and duration) and climate data were combined by picking the closest temperature or temperature gradient value for each species mean age.

To estimate a continuous measure for the connection of geographic range and duration, we calculated the correlation between the geographic range and duration following the same moving window approach as for the isotope data. Window size was 50 million years to ensure a minimum sample size of ten. As for the isotope data, the moving window procedure accounts for the temporally and quantitatively uneven spread of species occurrences. The resulting correlation curve was used to test the connection with the global average relative temperature and the latitudinal  $\delta^{18}\text{O}$  gradient. Time-series data (i.e. climate data) were used in their original form without accounting for autocorrelation as to preserve the inherent information about relatively warmer and colder climatic conditions, which would be lost by e.g. first differencing or further detrending the climate proxies. Normality of numerical variables was tested using Shapiro-Wilk normality test. As none of the variables show normal distribution, we used Spearman rank correlation test for correlation analysis. All analysis were done in R version 3.6.0 (Planting of a Tree). Data and R files to replicate this study are fully available on <https://doi.org/10.5281/zenodo.3497434>.

### 4. Results

#### 4.1. Correlation strengths among climate proxy and geographic range data

A statistical evaluation of the climate proxy and paleontological datasets by means of Spearman rank correlation is summarized in [Table 1](#). Deep-sea  $\delta^{18}\text{O}$ , the usual reference for mainly Cenozoic climatic trends ([Fig. 2d](#)) ([Zachos et al., 2001](#)), strongly correlates with the low-latitude surface  $\delta^{18}\text{O}$  ([Fig. 2a](#)) as well as with the high-latitude  $\delta^{18}\text{O}$  ([Fig. 2c](#)). Conversely, no correlation is observed between low-latitude surface  $\delta^{18}\text{O}$  and the latitudinal  $\delta^{18}\text{O}$  gradient.

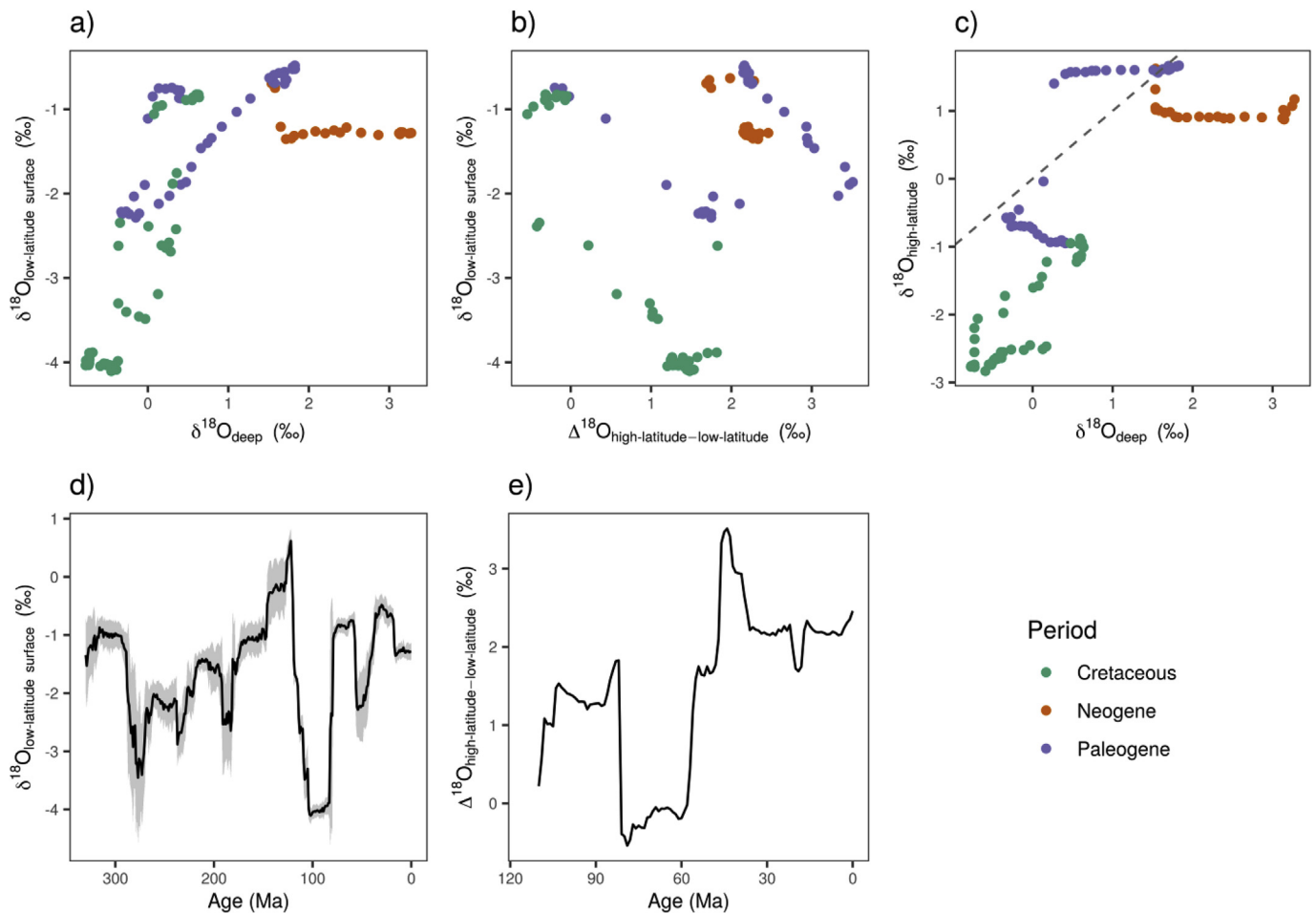
Co-variance of geographic range and species duration was signified by moderately strong correlation strength. We obtained weak and moderately negative correlation strengths between geographic range and low-latitude surface  $\delta^{18}\text{O}$  (global relative temperature trends), and  $\Delta^{18}\text{O}_{\text{high-low-latitude}}$  (latitudinal gradient), respectively ([Fig. S3](#)). As a last

**Table 1**

Spearman rank correlation values for climate proxies and geographic range, showing correlation strength ( $\rho$ ), the p-value of the correlation, the sample size (n) and the age range of the data points. Significant values are highlighted bold.

y vs. x	$\rho$	p-value	n	age range (Ma)
$\delta^{18}\text{O}_{\text{low-latitude surface}} \sim \delta^{18}\text{O}_{\text{deep}}$	<b>0.73</b>	< 0.001	117	117–0
$\delta^{18}\text{O}_{\text{deep}} \sim \delta^{18}\text{O}_{\text{high-latitude}}$	<b>0.80</b>	< 0.001	111	111–0
$\delta^{18}\text{O}_{\text{low-latitude surface}} \sim \Delta^{18}\text{O}_{\text{high-low latitude}}$	0.12	0.209	111	111–0
duration ~ geographic range *	0.57	–	333	333–0
geographic range ~ $\delta^{18}\text{O}_{\text{low-latitude surface}}$	–0.04	0.599	353	339–0
geographic range ~ $\Delta^{18}\text{O}_{\text{high-low-latitude}}$	–0.30	< 0.010	353	339–0
$\delta^{18}\text{O}_{\text{low-latitude surface}} \sim \rho_{\text{geographic range-duration}}$	–0.23	< 0.001	331	331–0
	–0.20	< 0.050	111	111–0
$\Delta^{18}\text{O}_{\text{high-low-latitude}} \sim \rho_{\text{geographic range-duration}}$	–0.71	< 0.001	111	111–0

\*The median of all values contained in the continuous correlation measure, the results of the moving window approach.



**Fig. 2.** Carbonate-oxygen isotope data from Prokoph and Veizer (2015). a) Low-latitude surface water  $\delta^{18}\text{O}$  and deep water  $\delta^{18}\text{O}$ . b) Low-latitude surface water  $\delta^{18}\text{O}$  and  $\Delta^{18}\text{O}_{\text{high-latitude-low-latitude}}$  (latitudinal  $\delta^{18}\text{O}$  gradient); the difference between surface high-latitude and low-latitude  $\delta^{18}\text{O}$ . c) High-latitude surface water  $\delta^{18}\text{O}$  and deep water  $\delta^{18}\text{O}$ . Dashed line represents  $f(x) = x$ . d) Median low-latitude surface water  $\delta^{18}\text{O}$  over time. The grey area is the median absolute deviation for the median values. e) Latitudinal  $\delta^{18}\text{O}$  gradient based on subtracting low-latitude from high-latitude surface water  $\delta^{18}\text{O}$  over time.

step, we looked at the connection between the correlative strength of duration with geographic range and the two climate proxies used in this study, which yielded a weak and a strongly negative correlation, respectively (Table 1). Limiting correlation and low-latitude surface  $\delta^{18}\text{O}$  data to the temporal range of the  $\Delta^{18}\text{O}_{\text{high-latitude-low-latitude}}$  dataset showed no difference in the connection (Table 1).

#### 4.2. Temporal trends in climate data and correlation strength between geographic range and duration

The correlative strength ( $\rho$ ) between geographic range and species duration ( $\rho_{\text{geographic range-duration}}$ ) ranged between 0.38 and 0.65 for 50% (lower and upper quantile, respectively) of the sample population (cf. median  $\rho$  Table 1). Fig. 3 displays the temporal pattern in the correlation and shows that it remained relatively stable around its median value of 0.57 (Table 1) from the Carboniferous to the Middle Triassic. From the Triassic–Jurassic up to the Late Jurassic,  $\rho_{\text{geographic range-duration}}$  rose above the median background value, where after a steep drop marked the latest Jurassic with an almost total eclipse of the correlative strength, and remaining low up to 100 Ma (base of the Late Cretaceous). A steep rise in  $\rho_{\text{geographic range-duration}}$  was followed by a long period of stable and high correlative strength. Only during the Middle Paleogene, a steady decrease of  $\rho_{\text{geographic range-duration}}$  with a persistent decline for the remainder of the Paleogene was evident. The Neogene showed the lowest values  $\rho_{\text{geographic range-duration}}$  of the record.

Comparing the correlation curve with the two climate proxies, we

found a strong covariance between the two most notable minima in the  $\rho_{\text{geographic range-duration}}$  record and transitions from low to high  $\delta^{18}\text{O}_{\text{low-latitude surface}}$  during the Early Cretaceous and the last 45 Myr of the Cenozoic (Fig. 4a & Table 1). Conversely low  $\delta^{18}\text{O}_{\text{low-latitude surface}}$  were generally associated with higher values of  $\rho_{\text{geographic range-duration}}$ . Upon comparing the  $\rho_{\text{geographic range-duration}}$  record with the latitudinal  $\delta^{18}\text{O}$  gradient, a similar but stronger pattern emerged where a large latitudinal  $\delta^{18}\text{O}$  gradient was mirrored by low  $\rho_{\text{geographic range-duration}}$  values (Fig. 4b, Table 1).

When applying latitudinal range size as an alternative measure for geographic range, we found that it strongly correlated with the maximum great circle distance for our data ( $\rho = 0.79$ ,  $p < 0.001$ ), resulting in very similar results for the entire analysis (Table S1; Fig. S5 & S6).

## 5. Discussion

A common aim of conservation paleobiology is to make inferences from the past for the present and future (Dietl and Flessa, 2011, 2017; O'Dea et al., 2017). Considering that the previous statement assumes temporal stability of the studied traits, it is essential to test if biotic interactions in the past resemble interactions today. Here we show that for the last 330 million years geographic range of amphibians was positively correlated with species longevity. Although the general influence of geographic range on extinction risk seems consistent, we did observe variations in the interaction strength, which seemed connected

with geochemical climate proxy data.

The quality of the fossil record is a main factor which sets the frame for paleontological studies, and the comparatively small scope of the amphibian record in particular is most likely one of the reasons for the mismatch between studies in paleontology and conservation biology. However, we did not find indications that our results are artifacts rather than real signals, for the following reasons. First, geographic ranges and species durations show only minor fluctuations over time (Fig. S1), and between the major taxonomic groups (Fig. S4), suggesting no major disruptions in the amphibian fossil record which might lead to the fluctuations in the geographic range influence on extinction risk as shown in Fig. 3. Furthermore, geographic ranges of species are independent from the total of occurrences in each geology stage (Fig. S2a), and therefore likely represent a real signal rather than an effect caused by the sampling extent. However, we observed temporal fluctuations in the abundance of occurrences (Fig. S2b), which we account for by smoothing our data with the moving window procedure. Interestingly, the peaks in the temporal pattern of occurrences do not coincide with shifts in the correlation pattern, which in combination with the lack of major differences in geographic range sizes suggests this pattern to be of negligible importance for our analysis. Lastly, additional support was added to our results by repeating the analysis with latitudinal range as a second geographic range measure, which concentrates entirely on the latitudinal aspect of the correlation and therefore rules out that the correlation might be spurious and driven by e.g. longitudinal variations, which would not necessarily be connected to climatic conditions. Although, the fossil record used for this study might be limited in quantity, we do not detect signs of strong biases, which makes us confident that our results represent real ecological signals.

The continued positive correlation between geographic range and extinction risk underlines the ubiquitous influence of geographic range, even under differing environmental conditions. This supports geographic range as a useful measure for extinction risk of living species, as it is included in the current assessment procedures of the IUCN Red List (IUCN, 2012). Our results support Orzechowski et al. (2015) and Finnegan and Payne (2007), who found that the geographic range remained a persistent factor for extinction selectivity for marine gastropods and bivalves over the last 540 million years. However, in contrast to Orzechowski et al. (2015), we observed a link between the variation of the influence strength of the geographic range and the climate proxies.

Adding two climate proxies, average  $\delta^{18}\text{O}_{\text{low-latitude surface}}$  and the latitudinal  $\delta^{18}\text{O}$  gradient, to our analysis suggests that the average global climate ( $\delta^{18}\text{O}_{\text{low-latitude surface}}$ ) only had a minor effect on the correlation pattern (Fig. 4a), and no measurable effect on the geographic range of species itself, which agrees with Orzechowski et al. (2015). In contrast, the latitudinal  $\delta^{18}\text{O}$  gradient was strongly negatively correlated with the temporal variations in the correlation of geographic range and duration (Fig. 4b, Table 1), and moderately correlated with the geographic range itself (Fig. S3b, Table 1). The differing connections between these two climate proxies and the temporal correlation pattern underline the lack of correlation we observed between them (Table 1 & Fig. 2b). While the latitudinal  $\delta^{18}\text{O}$  gradient is usually expected to follow the global trend (Tindall et al., 2010), several effects might cause the detachment of the two climate records; the continental configuration, oceanic circulation patterns and the presence of land ice (Bjerrum et al., 2001; Poore et al., 2011). Detachment is also clear from Fig. 2c, as deep water  $\delta^{18}\text{O}$  can deviate to more positive values than the expected 1:1 relation with high-latitude surface  $\delta^{18}\text{O}$ , where it is considered that the 1:1 relation would be the result of deep-water formation occurring at high-latitudes. So, even though  $\delta^{18}\text{O}_{\text{deep}}$  and  $\delta^{18}\text{O}_{\text{high-latitude}}$  (Table 1) correlated well, suggesting an overriding control by secular climate trends on the latitudinal  $\delta^{18}\text{O}$  gradient, anomalous heavy  $\delta^{18}\text{O}_{\text{deep}}$  data, e.g. in the Cretaceous, suggest a different mode of deep water formation. Veizer and Prokoph (2015)

implied that this Cretaceous signal can be best reconciled with deep-water formation at low-latitudes, where land-locked basins of the Tethys ocean could generate hypersaline water masses, dense enough to fuel a halothermal mode of ocean circulation, instead of a thermohaline mode, as we observe in today's ocean. Hence, we argue that the latitudinal temperature gradient could therefore provide additional information about past climatic conditions relevant to the amphibian record. More so, ocean circulation has a key control on surface currents and is thereby an important aspect in the interaction of the ocean with the atmosphere and global heat distribution, thus controlling the prevailing regional terrestrial climate systems (e.g. the effect of the modern Gulf Stream on NW Europe) (Marotzke and Willebrand, 1991; Rahmstorf, 2002). The latitudinal  $\delta^{18}\text{O}$  gradient might therefore be a more sensitive gauge of climatic parameters (e.g. precipitation patterns and fluctuations in daily and seasonal temperatures) that control global environmental variability, which ultimately contributes to the distribution limits of a species according to its environmental niche (Caughley et al., 1987; Gaston, 2003; Diffenbaugh and Field, 2013; Estrada et al., 2015). Our results suggest that a higher environmental variability trims the latitudinal boundaries for species distributions, leading to generally smaller geographic ranges. This is supported by our observation that geographic ranges were larger when the latitudinal  $\delta^{18}\text{O}$  gradient was small (Fig. S3b). These results also align with findings by Tomašových et al. (2015) who also demonstrate the importance of temperature in setting range limits.

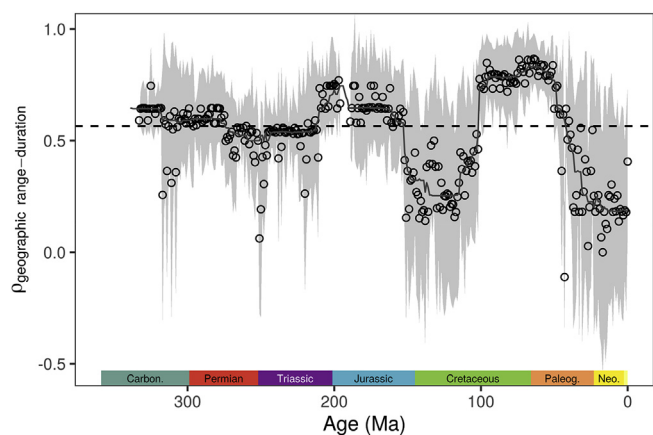
However, the latitudinal  $\delta^{18}\text{O}$  gradient had the strongest connection not with geographic range itself, but with its correlation with species durations (Table 1). Two scenarios may explain how the temperature gradient might cause the observed variation in the correlation strength of geographic range and duration.

First, under a general spatial restriction due to environmental conditions (i.e. a large latitudinal temperature gradient), the potential of the geographic range to buffer for extinction risk might not unfold its full effect, as the differences in ranges between species are rather small due to the lower upper limit (i.e. the species with the largest range at that time). Low variability in this trait might eventually lead to a decrease in relative importance of the geographic range in relation to other beneficial traits. This is supported by Chen et al. (2019), who showed that geographic range had stronger influence on extinction risk in small-ranging amphibian species compared to species with larger ranges, while also detecting differences in other trait influences between these two geographic range groups. We cannot determine the mechanisms behind these observed patterns, however we suppose a more complex interplay of factors linked to geographic range, e.g. body size or dispersal ability, might be responsible, as these factors usually show close connections in amphibians (Penner and Rödel, 2019).

One might as well argue that range size would be especially beneficial for survival during times of high environmental variability, as it requires true generalists with large niche breadths.

Smaller climatic zones and therefore suitable habitats might have higher levels of interspecific competition due to the limited available area. Therefore, the ability to cope with competitors and exploit limited resources become comparatively more important for survival. On the other end, limited competitive qualities might be compensated with a large geographic range, raising the importance of this trait for extinction risk as soon as the environmental conditions allow for a wider spread. However, an increase in competition in small suitable areas is likely most relevant for phases of shifting climatic conditions, as species richness itself is strongly affected by environment heterogeneity (Stein et al., 2014), which would make increased competition a rather short-term effect until species richness has adapted.

An additional explanation for variations in the correlation strength between the geographic range and duration is a decrease in the signal-to-noise ratio rather than the importance of geographic range itself. When geographic ranges become generally smaller, caused by a large temperature gradient (Fig. S3b), the distances between the ranges of



**Fig. 3.** Correlation of geographic range and duration of species (Spearman's rank correlation) assessed via a moving window approach. Larger absolute values indicate a stronger influence of geographic range, while smaller absolute values closer to zero indicate less influence. Window size was 25 million years, within each window we applied a subsampling routine ( $n = 100$ ) to the size of the minimum number of data points contained in all windows, the final value being the median of all subsamples. The grey area depicts the median absolute deviation from the median correlation. The grey line is the moving average of the correlation values using a window size of 20 Myr. The dashed line is the median of all correlation values.

each species become smaller too (i.e. signal). As Spearman's correlation test is rank-based, potential incompleteness of the fossil record (i.e. noise) can more easily distort the actual rank order of species under these conditions, resulting in a smaller correlation. This effect would not require changes in preservation or fossil record quality over time, but is simply based on the degree of homogeneity of geographic range data.

A limitation of our study is the temporal and spatial resolution of the data, which might be the reason why we observe one major drop in the temperature gradient around 80 million years that is not mirrored by the correlation pattern (Fig. 4a). It is also possible that climate proxies might not always properly display the local conditions that apply to these species, due to for example the continental configuration. More short-term climatic fluctuations in terrestrial systems might as well not be recorded, as our climate proxies reflect relative trends in ocean temperature and global climate, where the ocean has a larger heat capacity than landmasses and is therefore less susceptible to short-term fluctuations (Diffenbaugh and Field, 2013). As a result, short time scale climatic changes, perturbing terrestrial environments and ecosystems, might have only had a limited effect on the contemporaneous marine environment. However, we argue that large scale patterns in the climate proxies point to changes in the prevailing climate modes that would have had the potential to influence biotic interactions. Other studies support this notion and have already shown a long-term coupling between environmental changes and biodiversity (Hannisdal and Peters, 2011).

The amphibian fossil record shows some major taxonomic turnovers, like the end of the small bodied Lepspondyli at the Permian-Triassic boundary, the following rise of generally large bodied temnospondyls, and their demise, followed by the rise of the mostly smaller lissamphibians around the Triassic-Jurassic boundary (Schoch, 2014). This sequential rise and fall of major amphibian orders has the potential to create phylogenetically rather than environmentally driven results, both for the correlation pattern and the geographic range and duration themselves. Comparing the three factors geographic range, duration, and correlation strength of both factors between the major taxonomic orders however revealed only mild differences for correlation and duration, and no difference for the geographic range (Fig. S4). Those groups showing differences in median correlation strength occurred

around the same time in the fossil record, and most differences in duration are caused by Allocaudata, a group comprising just eleven species. We therefore argue that existing phylogenetic signal should be negligibly small. Given that these major taxonomic groups also encompass differing life habits from fully aquatic small salamanders to mostly terrestrial, gigantic temnospondyls, we do not expect preservation or sampling biases to have a strong effect on our results.

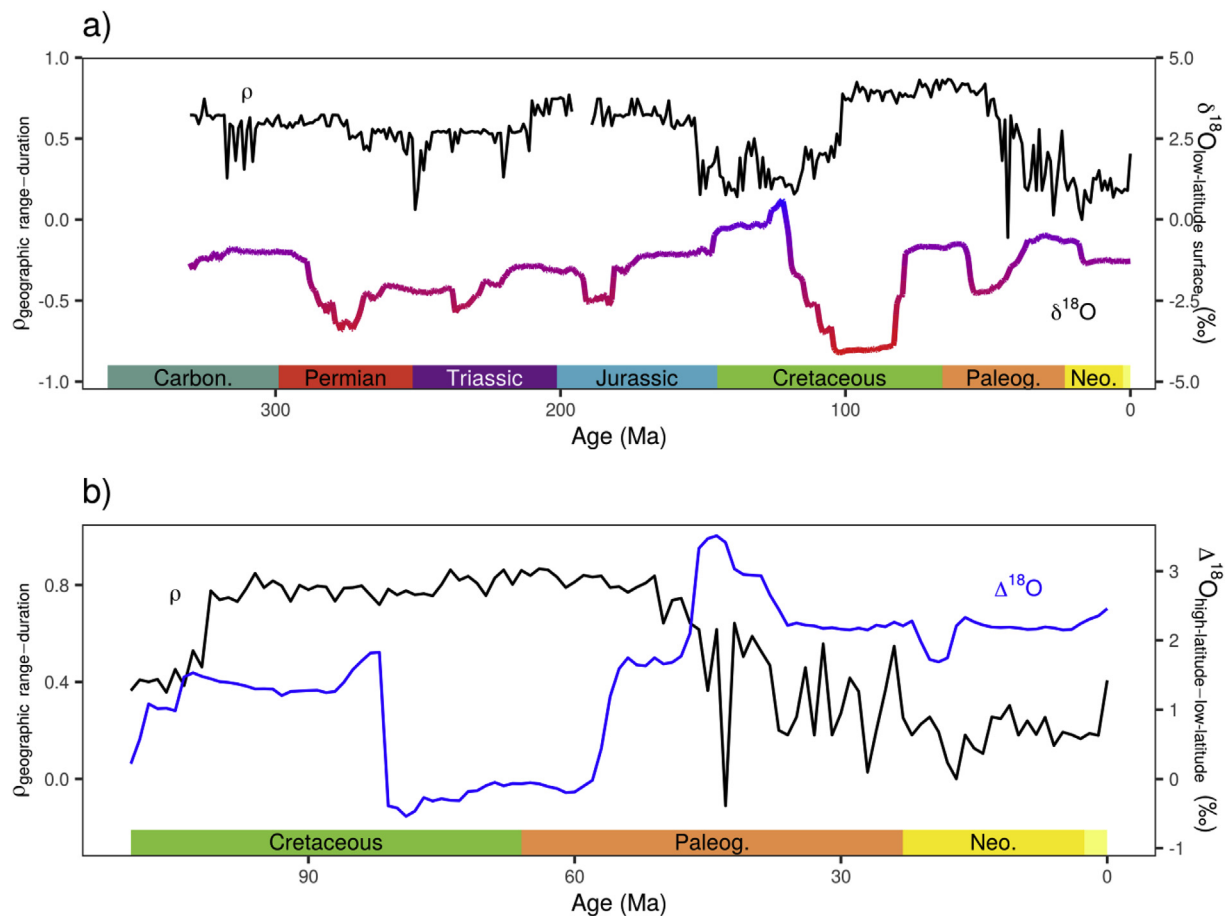
In contrast to some studies on marine invertebrates (Finnegan and Payne, 2007) and terrestrial tetrapods (Dunhill and Wills, 2015), we did not find a weakening of the geographic range–extinction risk connection around the last three mass extinction events (Permian–Triassic, Triassic–Jurassic, Cretaceous–Paleogene). Moreover, the long-term temporal trends in  $\rho_{\text{geographic range–duration}}$  suggest a stronger link between those variables compared to the Neogene and Quaternary, thereby hinting at a stronger influence of the geographic range–extinction risk connection during these past intervals than today (Fig. 4a). Intriguingly, the small proportion (17%) of species in our data with last appearances within a three million year interval around mass extinction events agrees with the common perception that amphibians were generally less affected than other tetrapod clades by these events (Schoch, 2014). Naturally we cannot rule out durations to be shortened by preservation and sampling effects (Signor-Lipps effect), which might affect this observation and mask a stronger effect of mass extinctions on the fossil record of amphibians. In addition, the difference in timescale over which those mass extinctions unfold ( $< 1$  Myr) comparative to the multi-million year record studied here, suggests that the here found geographic range–extinction risk connection might be of importance on both long and short timescales. Although not readily discernible in our broad-scale  $\delta^{18}\text{O}$  low-latitude surface record (Fig. 4a), probably because of their short duration, past extinction events have been connected with rapid warming events (Ruhl et al., 2011; Joachimski et al., 2012; Schobben et al., 2014; Vellekoop et al., 2014; Barnet et al., 2018), which some argue to be analogous to current human-driven climate change (Barnosky et al., 2011). However, as the Neogene and Quaternary  $\rho_{\text{geographic range–duration}}$  is low compared to the average correlation in the amphibian fossil record (Fig. 4a), the baseline for current climate-driven impact on amphibians might be different than in those past mass extinctions. Even though geographic range is an important determinant of extinction risk, caution needs to be taken when formulating conservation strategies, as an over-reliance on this single parameter might not always be justified, given the possible fluctuations in the strength of its influence, potentially caused by environmental parameters.

## 6. Conclusions

Geographic range is an important parameter used in the extinction risk assessment procedure for the IUCN Red List. Although the link between geographic range and species survival success seems valid today, the stability of this link in relation to changing environmental and climatic conditions is of particular importance given current and future predicted human-induced climate change. Hence, the main objective of this study is to assess the validity of this rule. We do this by looking at long-term changes in geographic range influence on extinction risk in one of the most critically endangered taxonomic groups: the amphibians. Our study provides validation for the usage of geographic range as a measure for extinction risk in living amphibian species, even under most differing environmental conditions. However, we also emphasize that trait-extinction risk dynamics can vary in their intensity, and that specifically the observed impact of geographic range on extinction risk can vary with climatic changes.

## Data availability

All data and R code to replicate this study are available on <https://doi.org/10.5281/zenodo.3497434>.



**Fig. 4.** Temporal changes in correlation strength of geographic range and duration of species, plotted with oxygen isotope data; a) median low-latitude  $\delta^{18}\text{O}$  and b) latitudinal  $\delta^{18}\text{O}$  gradient. Colored lines show the climate proxy data, black lines show the correlation strength ( $\rho$ ) between the geographic range and the duration (stratigraphic range) of species. Note the different time scales between a) and b). Missing values in a) indicate a failure to calculate Spearman correlation values in these time bins due to a lack of variability in the data.

#### Authors' contributions

Data collection and analysis were performed by MT. MT, MS and MOR contributed in writing the manuscript. All authors contributed substantially to the design of the study.

#### Funding

MT was supported by the innovation-fund of the Museum für Naturkunde Berlin.

#### Declarations of competing interest

None.

#### Acknowledgements

We thank the numerous contributors to the Paleobiology Database for entering their data and making quantitative studies like this one possible in the first place. We also thank Alex Dunhill and one anonymous reviewer for their work reviewing and thereby improving our manuscript. This is Paleobiology database publication number 352.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2019.109414>.

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