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The Extinction Risk–Range Change Relationship: Evidence From the Fossil Record

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ABSTRACT

Aim: Climate change is a major driver for the wave of species extinctions predicted for this century. Extinction risk assessments are often estimated from climate-driven reductions in the geographic ranges of species. However, the empirical relationship between extinction risk and range change remains unclear because few extinctions are observed in the Holocene. Using fossil evidence, this study investigates how extinction risk changes with the percentage change in geographic range of a genus over multi-million-year timescales.

Location: Fossil evidence is derived from the Paleobiology Database, which documents global fossil occurrences.

Time Period: We examine Neogene to Holocene (23–0 Ma) occurrences of marine genera.

Major Taxa Studied: The dataset includes six marine classes—Bivalvia, Echinoidea, Gastropoda, Mammalia, Anthozoa and Chondrichthyes—encompassing 1215 genera.

Methods: A Bayesian hierarchical weighted generalized additive model was implemented to analyse 2600 range change observations on a multi-million-year timescale.

Results: Results show that extinction risk increases non-linearly with range loss and differs between taxa. Responses vary broadly between taxonomic classes. Model comparisons indicate extinction risk is best explained by the interaction between absolute range and range change. With constant absolute range, however, extinction risk does not consistently increase with range loss. Alternative binning and weighting schemes revealed systematic effects on extinction risks.

Main Conclusions: Extinction risk increases with range loss, but this relationship is strongly modulated by absolute range and varies across taxa. For a given absolute range, the effect of range loss on extinction risk largely disappears, suggesting greater vulnerability in small-ranged taxa (and v.v.). However, model comparison indicated that extinction risk is best explained when both absolute range size and range change are included, implying both capture complementary aspects of vulnerability. By linking extinction dynamics to both absolute range and range change, our results provide a deep-time perspective on the mechanisms underlying genus persistence and vulnerability.

1 | Introduction

The extinction and survival of organisms through times of changes in climate, habitat or due to catastrophic events is an ongoing process since the origin of life (Seilacher 1984; Brasier and Donovan 1989; Sokolov and Fedonkin 2005). Understanding the mechanisms behind this process is crucial especially in today's context of the human-induced and rapid progressing climate change, which is threatening species, biodiversity and whole ecosystems (Urban 2015; Zurell et al. 2023). Losses of ecosystem functions affect wildlife but also lead to severe impairments for human society (Dietz et al. 2020). Particularly 'geographic range', that is, the size of an area a taxon occupies, is often indicated as an important predictor of extinction risk in the fossil record (Kiessling and Aberhan 2007; Payne and Finnegan 2007; Harnik et al. 2012). The general finding is that taxa with smaller geographic ranges are more likely to become extinct (Harnik et al. 2012).

While there is hence clear evidence for a link between extinction risk and absolute range (Kiessling and Aberhan 2007; Payne and Finnegan 2007; Harnik et al. 2012), the IUCN (2022) and IPCC (2022) describe the endangerment status of species using geographic range loss (the percentage change in the size of an area a taxon occupies over time; IUCN Red List criterion A). A species is considered 'critically endangered' if it has experienced a range reduction of 80% or more, leading to an extinction probability exceeding 50% within the short term (10–100 years). It is classified as 'endangered' if it has undergone a range reduction of at least 50%, resulting in an extinction risk of over 20% in the near future (10–100 years) (IUCN 2025). Earlier studies have shown that changes in geographic range are important for understanding extinction dynamics (Kiessling and Kocsis 2016; Smith et al. 2025). However, the exact nature of this relationship, particularly how range loss translates into extinction risk, remains underexplored (Zurell et al. 2023).

Existing extinction risk predictions based on geographic range often use SDMs (species distribution models; Urban 2015; Warren et al. 2018). However, while classifying a species according to the IUCNs endangerment status can be done with well-constructed SDMs, it is considered more problematic to use SDMs to predict the likelihood of species becoming extinct (Zurell et al. 2023). The scarcity of documented species extinctions in recent times, especially those that can be confidently attributed to climate change (IPCC 2022) further restrict the predictive power of this approach.

Using the fossil record to investigate extinction mechanisms can help to enhance our understanding and resolve data deficiency issues that result from limited availability of suitable ecological data. The fossil record consists of fossil occurrence data as well as a multitude of biological, biostratigraphical and geochemical proxies. It provides information on the appearance and extinction of evolutionary lineages, community assembly and environmental conditions. It documents numerous climate-induced extinctions which provide an opportunity to enhance our understanding of extinction dynamics and mechanisms, thereby harbouring substantial informative potential for conservation efforts (Jablonski 1999; Dietl and Flessa 2009; Calosi et al. 2019; Kiessling et al. 2019; Fordham et al. 2020). Future extinction risk predictions would benefit from an integrative approach using ecological and palaeontological data and methods together as has been done in studies such as Finnegan et al. (2015) and Raja et al. (2021). First integrative databases are being developed to unite datasets across different temporal scales (e.g., Dornelas et al. 2018; Smith et al. 2023). Such work advances our ability to maximize the predictive potential of these datasets, since one of the primary limitations hindering the application of palaeontological data in conservation contexts is the enormous difference in timescales between ecological and palaeontological records. These differences in timescales lead to disparities in observed rates and magnitudes of macroecological and environmental processes (Smith et al. 2023). The rates of change of any unsteady process typically appear to be slower when measured over long time intervals affecting perceptions of many ecological and environmental change processes (Kemp et al. 2015; Spalding and Hull 2021; Smith et al. 2023). Therefore, it is crucial to thoughtfully evaluate the applicability and relevance of patterns observed in palaeontological records when transferring it in today's context.

Here we test whether genera that experienced severe losses in geographic range are more likely to go extinct in the subsequent time interval. Additionally, we examine whether absolute range size influences extinction risk, that is, whether genera with smaller ranges are more likely to go extinct than those with larger ranges. To address these questions, we analyse Neogene to Holocene (23–0 million years) occurrences of marine animal genera documented in the Paleobiology Database (PBDB 2023) (Figure 1). Although an explicit test of how timescale influences the relationship between geographic range dynamics and extinction risk would be desirable, such an analysis is not yet possible because the integrative BioDeepTime database (Smith et al. 2023) does not extend far enough back in time. We therefore analyse a PBDB-derived dataset that has already underpinned related studies of marine extinction risk patterns and their implications for extinction risk assessments (e.g., Finnegan et al. 2015). Percent geographic range changes between adjacent time intervals were estimated for each genus, and the relationship between range change and extinction risk was examined using a Bayesian hierarchical weighed generalised additive model. The hierarchical part of the model incorporates taxonomic classes to investigate the importance of taxonomic identity/phylogeny in this regard. Our study aims to contribute to a more detailed understanding of the extinction risk–geographic range change relationship on multi-million-year timescales. A direct comparison of the results of this study with the IUCN (2022) criteria is not feasible due to the limited temporal resolution of fossil data at the global scale (~2–5 Ma time bins vs. the 10–100 year timespan stated by the IUCN) and the genus-level taxonomic resolution of many fossil occurrence records (but see Section 2.6 below). However, understanding the ultimate fates of evolutionary lineages in the face of environmental change requires assessment and projection over much longer timescales, and we view our findings as a contribution towards this goal.

2 | Materials and Methods

2.1 | Data and Data Cleaning

The data was downloaded in March 2023 from the Paleobiology Database (PBDB 2023) to reconstruct the dataset from Finnegan et al. (2015), which includes six major well-skeletonized

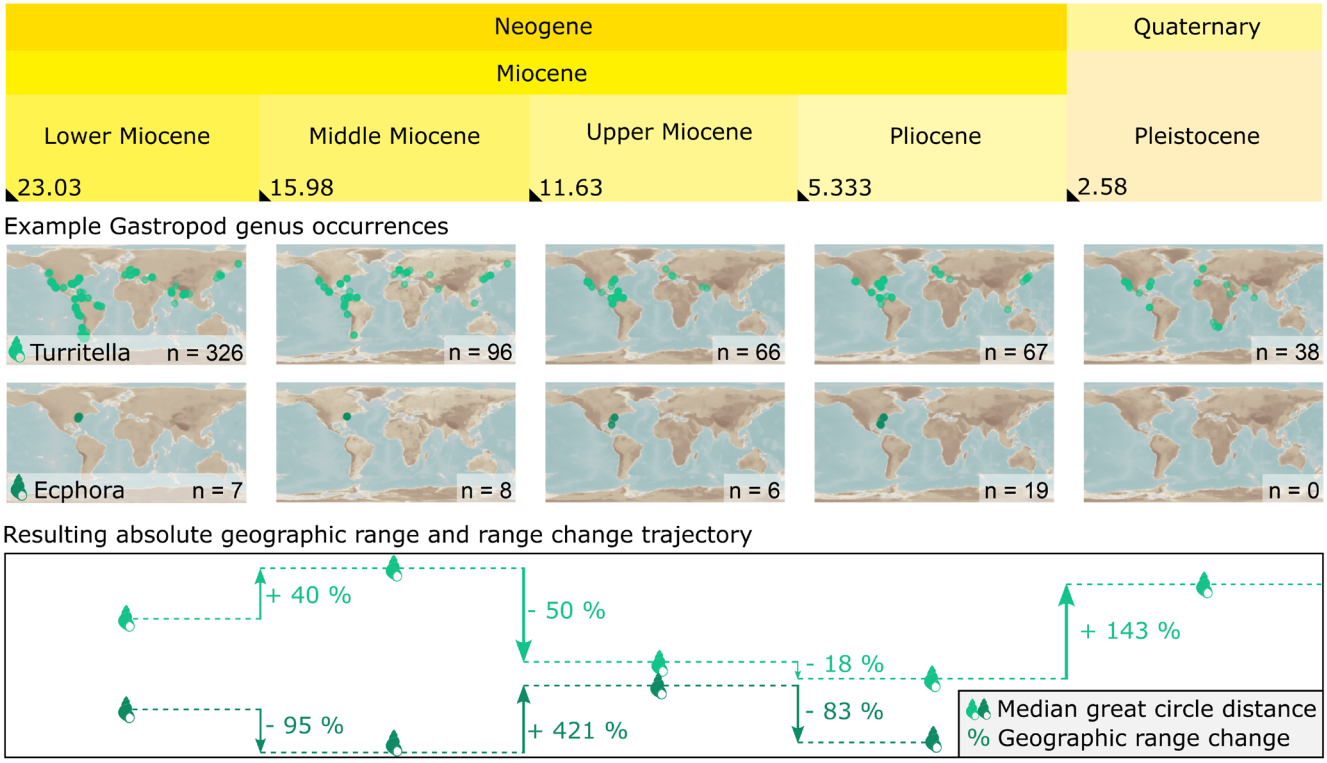

FIGURE 1 | Schematic overview of the temporal resolution and methodological approach by visualising the occurrences of two example genera and their geographic range change throughout the studied periods. The temporal resolution visible in this plot reflects the binning used in the models on stage level.

marine taxonomic groups: Bivalvia, Echinoidea, Gastropoda, Mammalia, Scleractinian corals and Chondrichthyes, spanning the Neogene to Holocene interval. This dataset is well-suited for the analysis of geographic range and extinction risk due to the selection of well-preserved taxa and a temporal resolution that involves several climatic transitions and smaller extinction pulses (Finnegan et al. 2015).

Data were cleaned to select occurrences on genus level (but analysis was repeated on species level, see Section 2.4 below). Multiple occurrences of a genus within a collection were removed, and the data was binned to stratigraphic stage level (Gradstein et al. 2020) (Figure 1). A temporal grain on stage level, corresponding to approximately 5 Ma time bins on average, provides a balance between sufficient data density and comparably short time steps. Temporal binning was conducted with the divDyn package in R (Kocsis et al. 2019; R-Core-Team 2023). Occurrences with missing palaeo-coordinates and occurrences with too much temporal uncertainty to be confidently binned at stage level were removed. Stages were restricted to the temporal period from the Neogene–Holocene, and singletons (genera occurring only within a single time interval) were excluded.

2.2 | Geographic Range Change and Extinction Signal

The calculation of median absolute geographic range was implemented for each genus in each bin separately based on great circle distance (sf package; Pebesma and Bivand 2023). In this study, we use the term geographic range to refer to the spatial extent of a taxon's distribution, expressed as a distance-based measure rather than a polygonal area. Thus, when we speak of 'range', we imply its size, not its shape. Our metric aims to capture the minimum preserved extent of a genus in the fossil record, calculated as the median great-circle distance between occurrences within a time bin. Here absolute range refers to a taxa's minimum relative range across the different temporal bins, which—given the incompleteness of the fossil record—we treat as a minimum estimate. Great circle distance was calculated for each combination of points within a bin and genus by creating a distance matrix. The median distance for every group (genus and temporal bin) was extracted (see Appendix Figure 1.1 in Supporting Information for model results with maximum distances). We chose median over maximum distances, as maximum great circle distances increase the apparent frequency of extreme range contractions (> 95%), which we attribute to sampling artefacts (i.e., apparent range 'jumps' caused by the disappearance of single outlier occurrences). Comparisons with only one occurrence available were omitted. Although studies found other methods such as convex hulls to perform slightly better, great-circle distance was only marginally less effective under sparse sampling conditions (Darroch and Saupe 2018; Darroch et al. 2020), making it nevertheless an appropriate and robust choice given the limited number of occurrences for many genera in our dataset. Further, while alternative approaches such as latitudinal range may be conceptually linked to environmental tolerances, we favoured a distance-based approach that incorporates all available spatial information, given the clustered and uneven nature of fossil occurrence data.

Geographic range change was calculated as the percentage change in the absolute geographic range between consecutive bins (see Appendix Figure 1.2 in Supporting Information for a violin plot of the data distribution across −100 to +100% range change). First occurrence bins were removed from consideration because there is no preceding geographic range value to compare them to. Finally, geographic range change values were log-transformed as extreme values could interfere with the posterior chain of the model. Range change values were back transformed after fitting the model. Log ratios are used to calculate symmetrical metrics of temporal change as commonly employed in ecological studies (e.g., Vellend et al. 2013; Chase et al. 2019; Blowes et al. 2024).

The extinction signal was coded as a binary value for each genus-time bin combination. Genera occurring in a given time bin were assigned a zero (survival) if they were also sampled in subsequent intervals and a one (extinction) if they were last sampled in that time bin. This approach assumes that time bins of last occurrence correspond to times of extinction, acknowledging that some proportion of genera with last occurrences in a given bin in fact persisted into subsequent bins but are never sampled again. Genera that continued to appear into the Holocene were presumed to be extant and, consequently, were not attributed a one. The data were cleaned from singletons again and weights were calculated by counting the number of occurrences in each group (per genus and temporal bin). The model will assign higher importance to values calculated from a larger number of occurrences, aiming to account for discontinuous sampling/sampling bias.

2.3 | Statistical Models

2.3.1 | Geographic Range Change Only Model

The evaluation of the data was done using a Bayesian hierarchical weighted generalised additive model using the 'brm()' function (brms package; Bürkner 2017), specifying a binomial family with a logit link function to model the binary extinction signal. The formula was structured as follows:

$$extinction \mid weights(number\ of\ occurrences) \sim s(range\ change) + (range\ change \mid class)$$

with the variable *extinction* being the extinction signal of each genus, *number of occurrences* representing the number of occurrences in each group (per genus and temporal bin) and *range change* are the log-transformed geographic range changes in percent. The component *extinction | weights(number of occurrences)* depicts the weighing. It assigns a certain importance to the values depending on how many occurrences the value is based on (raw genus occurrence counts per temporal bin); the more occurrences the greater the weight. We explored other weighting schemes to assess potential effects of weighting. These model results can be found in Appendix Figures 1.3–1.5 in Supporting Information. The hierarchical component of the model is represented by *(range change | class)*. This component allows us to model all taxonomic classes at the same time, but each class is assigned its own trend. This way our model represents a compromise between a fully pooled and a completely un-pooled model by pooling less-sampled groups towards estimates of better sampled groups. This helps to identify potential differences between classes in their response to geographic range change. The component *s(range change)* builds on the 's()' function (mgcv package; Wood 2017), and constitutes the additive part of the model. It models the independent variable *range change* via thin plate regression splines so that the trend does not have to follow a predetermined pattern (linear, exponential, etc.), allowing for a trend that precisely fits the signal indicated by the data.

2.3.2 | Absolute Geographic Range Only Model

To ensure comparability and verify the model's outputs against other studies using absolute geographic range (as opposed to % geographic range change from previous stage) (e.g., Finnegan et al. 2015; Malanoski et al. 2024), we implemented a model incorporating absolute geographic range (see Appendix Figure 1.7 in Supporting Information).

Absolute-range-only model:

$$extinction \mid weights(number\ of\ occurrences) \sim s(absolute\ range) + (absolute\ range \mid class)$$

2.3.3 | Combined and Interaction Model

A combined and an interaction model including both absolute range and range change was set up and later used in a model comparison to test the predictive power of each model.

Combined model:

$$extinction \mid weights(number\ of\ occurrences) \sim s(range\ change) + (range\ change|class) + s(absolute\ range)$$

Interaction model:

$$extinction \mid weights(number\ of\ occurrences) \sim s(range\ change) + (range\ change|class) * s(absolute\ range)$$

2.3.4 | Model Comparison

We tested four alternative models to evaluate the relative importance of geographic range change and absolute range in predicting extinction risk: (1) a simple range-change-only model, (2) an absolute-range-only model, (3) a combined additive model (absolute range + range change) and (4) an interaction model (absolute range * range change). The model comparison was performed using the functions 'loo' and 'loo_compare' (loo package; Vehtari et al. 2024). Loo is a function specifically for Bayesian models based on the leave-one-out cross-validation (LOO-CV) by using Pareto Smoothed Importance Sampling (PSIS) (Vehtari et al. 2024). This method estimates the expected log predictive density, which reflects the model's ability to generalize beyond the observed data. Models were compared using 'loo_compare', which ranks them based on their predictive accuracy and provides uncertainty estimates for the differences. Models with higher elpd_loo values (or lower Δelpd) are considered to have better predictive accuracy. This approach allowed us to evaluate

the relative predictive performance and select the model that best balances goodness of fit and generalizability. In addition, the Bayesian R^2 was calculated using the function 'r2_bayes' of the performance package (Lüdecke et al. 2021). It is defined as the ratio of the variance of predicted values to the sum of the variance of predicted values and the expected variance of the errors (Gelman et al. 2019).

2.4 | Species Level Analysis

The analysis was repeated using only species-level occurrence data with the range-change-only model (see Appendix Figure 1.10 in Supporting Information). The data set, data cleaning and statistical evaluation were the same as for the genus level analysis, but occurrences with a higher taxonomic rank (genus, etc.) than species level were excluded. Since many occurrences in the Paleobiology Database are only resolved to genus level, the resulting data set consisted of 741 species with a total of 1061 calculated range changes. For example, while we were able to analyse 28 genus-level range changes in Echinoidea, we were able to analyse only 2 species-level range changes. Accordingly, the results are based on a comparatively small data set and should be interpreted with caution (see Appendix Figure 1.2 in Supporting Information).

The degree to which genus-level and species-level analyses can be directly compared has been a topic of debate (Pandolfi 2001; Hendricks et al. 2014; Albano et al. 2016) and is often dependent on the research question. In conservation contexts, for example, Hadly et al. (2009) found genus-level data to be reliable for predicting mammalian responses to environmental changes. Similarly, Yu et al. (2022) emphasized the importance of higher taxonomic level (e.g., genus) analysis to bring ecological and evolutionary insights into conservation. These studies underscore the relevance of conducting analyses at the genus level. In our study, we therefore focus primarily on genus-level patterns, as the greater data availability at this taxonomic level makes the results more robust and thus potentially more informative even for understanding species-level processes.

2.5 | Temporal Grain

One analytical challenge in our statistical model pertains to the temporal grain. Some range changes were calculated over shorter or longer time intervals, reflecting the variability in stage lengths. This variability can influence the results as range changes observed over shorter time would be expected to involve less change than range changes observed over longer intervals. To address this concern, we changed the binning of the data from stages to 7 Ma time bins. The model now covers the time interval from 35 to 0 Ma. The model structure remained the same. This approach allows us to better understand and interpret the influence of the temporal variability at play. The results of this model can be found in the Appendix Figures 1.17 and 1.18 in Supporting Information.

There is a fundamental trade-off between temporal grain and the accuracy of apparent geographic ranges. Short time bins include fewer fossil occurrences and therefore apparent geographic ranges are more likely to substantially underestimate true ranges at any given time. Long time bins capture a larger number of occurrences and therefore often broader apparent geographic ranges but because true geographic ranges can change on relatively short timescales there is a greater risk that apparent geographic ranges overestimate true geographic ranges at any given time. To assess the effect of temporal resolution, we repeated the analysis using 1 Ma bins. While finer binning may improve comparability with modern ecological processes, it also increases sampling variability due to fewer occurrences per bin, leading to contractions of apparent range. This inflates the number of range changes and flattens the extinction risk signal. In the 1 Ma model, the number of survivals increased approximately fivefold while extinctions remained constant, shifting the ratio and weakening the signal. Given the low background extinction rate in the Neogene, meaningful interpretation at this resolution would likely require a larger, taxonomically finer and extinction-rich dataset. The results of the 1 Ma binning analysis are provided in the Appendix Figures 1.19 and 1.20 in Supporting Information. This is underlined by Smith et al. (2025) who also examined the role of geographic range dynamics in predicting extinction risk and found that coarser temporal binning tends to improve model performance. Smith et al. (2025), working with microplankton species and bin sizes ranging from 0.1 to 1 Ma, reported that the explanatory power of occupancy and occupancy change increased with larger bin sizes, attributing this to reduced noise and greater statistical power.

2.6 | Weights

To evaluate the impact of weighting by number of occurrences, we repeated the analysis without weights, with inverse weights and with log transformed weights. The weighting is intended to help mitigate sampling artefacts, particularly in poorly sampled genera where the disappearance of a single occurrence can cause disproportionate range reductions. However, it may also bias the analysis towards common species and obscure signals from rarer taxa. This is further complicated by potential regression-to-the-mean effects, which would imply common species to be more likely to decline. The log transformed weights may represent a good compromise here, between accounting for sampling bias and the regression-to-the-mean effect. The results of these analyses are provided in Appendix Figures 1.3–1.5 in Supporting Information. Findings indicate that the results retained the same overall pattern, although the increase in extinction risk at higher levels of range loss appears less steep. This suggests that while the weight approach affects the scale of the effect, it does not alter the qualitative conclusions.

2.7 | Subsampling

In addition to the weighting, we further evaluate the influence of sampling bias and potential regression-to-the-mean effects by conducting a subsampling analysis based on genus-level occurrence counts. Genera with fewer than 10 occurrences per temporal bin were classified as rare, and those with more than 14 as common. The results showed that common genera exhibited steeper slopes linking geographic range loss to extinction signal, while rare genera showed flatter relationships (see Appendix Figures 1.6 and 1.7 in Supporting Information). This pattern may

reflect regression-to-the-mean effects in common taxa, which are more likely to decline in their range. However, it could also result from increased sampling noise in rare genera, where the loss of a single occurrence can disproportionately affect estimated range size. Because these effects are difficult to disentangle with the available data, and sampling variability appears to pose the stronger bias, we retained the weighting by number of occurrences.

2.8 | Limitations of the Fossil Record

The structure of the paleontological record (Foote and Sepkoski 1999) imposes important constraints on our analyses which complicate direct comparison with modern risk assessments. The relatively course temporal resolution of global stratigraphic stages means that geographic ranges of genera are time-averaged at million-year timescales. This resolution does not capture the full variation in species or genus abundance observed over shorter time scales (Kemp et al. 2015). Even the finest-scale fossil samples are time-averaged to some extent (Kowalewski et al. 1998). However, this averaging can be both a limitation and a strength, while it obscures short-term dynamics, it enhances the ability to detect long-term ecological and environmental trends (Kowalewski et al. 1998). Therefore, the extinction risks presented do not reflect contemporary risk percentages, due to the effect of observing different evolutionary rates at longer vs. shorter time scales caused by the non-monotonic nature of evolutionary rates of change (Kemp et al. 2015; Kiessling et al. 2023). Due to discontinuous preservation, caused by sedimentary processes and varying taphonomic potentials, as well as discontinuous sampling in time and space (Behrensmeyer et al. 2000; Benton et al. 2000; Vilhena and Smith 2013; Raja et al. 2022) both geographic and stratigraphic ranges of genera should be regarded as minimal estimates. In particular, the preserved geographic ranges (reconstructed as great-circle distances, GCD) represent a truncated version of the original range, and the degree of truncation likely varies through time due to shifting sedimentary deposition centres and across taxa due to differences in taphonomic potential (e.g., disarticulation and post-mortem scattering in groups with multi-element skeletons). While absolute range sizes are notoriously difficult to be preserved consistently, studies have shown that relative geographic range size (i.e., rank order among taxa) has a surprisingly high preservation potential (Darroch et al. 2020, 2022; Casey et al. 2021). Studies therefore support that paleogeographic ranges, despite their limitations, can reliably reflect relative range dynamics and offer valuable insights into macroevolutionary patterns, provided that temporal resolution and taphonomic biases are carefully considered (Darroch et al. 2020, 2022; Casey et al. 2021).

It is also important to recognize that the duration of stratigraphic stages throughout the Neogene is not uniform, ranging from ~2.5 to ~7 Ma. This variability in duration may impact the observed changes in geographic range between stages. Specifically, shorter stages are likely to encompass less occurrence, which could result in the documentation of smaller geographic ranges.

To minimize the potential effects of range underestimation, we assigned weights proportional to the total number of occurrences of each genus, so that well sampled genera have a greater influence on model coefficient estimates than poorly sampled genera. Furthermore, we built a model using 7 Ma bins instead of stages to test the impact of inconsistent time between bins (see Appendix Figures 1.17 and 1.18 in Supporting Information).

3 | Results

The raw data exhibit a strongly skewed structure (Figure 2, see also Appendix Figures 1.21 and 1.22 in Supporting Information): most genera occupy small absolute ranges (< 1000 km) and the densest observations correspond to contractions (−100% to 0%). The log/pseudo-log view reveals a secondary cluster near ~1000 km absolute range with negative range changes and shows that extreme expansions (> +300%) are uncommon.

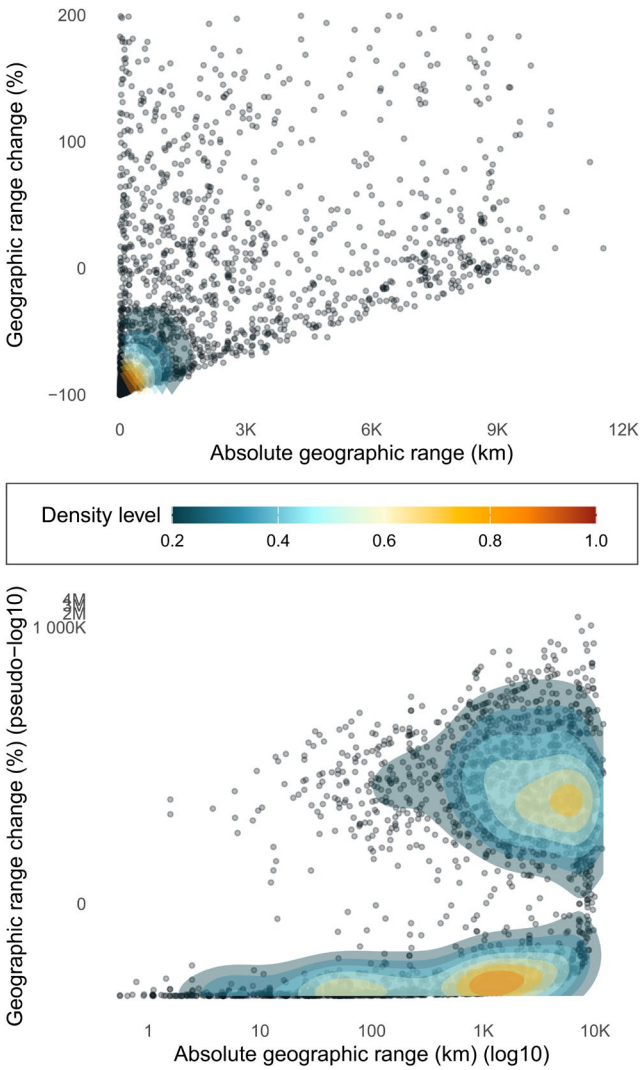

FIGURE 2 | 2D-Kernel-Density plots showing the density of occurrences across absolute geographic range and range change. Density levels are represented by a colour gradient. Dots represent the raw data points. The upper plot shows the data with linear axes and is restricted to −100% to +200% range change. The lower plot shows all data points (no restriction on axes) with $\log_{10}$/pseudo-$\log_{10}$ transformed axes.

To statistically evaluate the relationship between extinction risk and geographic range change, we implemented four models: a range-change-only model, an absolute-range-only model, a combined additive model and an interaction model. All models revealed a non-linear increase in extinction risk with geographic range loss (Figure 3, see also Appendix Figures 1.9 and 1.11 in Supporting Information). Positive range changes do not show any increase in extinction risk. The general trend for all classes appears to be similar, with almost no increase in extinction risk between 0% and 50% range loss. Starting from 50% range loss, the overall trend then shows a rapid increase in extinction risk with increasing range loss (Table 1), ending in a slight drop in extinction risks at around > 95% range loss. The class-specific trends show distinct patterns for each class and each model with clear differences in their baseline extinction risk also when gaining geographic range (see Appendix Figure 1.6 in Supporting Information). The extinction response to geographic range loss is comparable in most classes, except for the echinoids. However, this class should be interpreted cautiously given its small sample size ($n = 28$). Echinoidea show the lowest response to range loss of all classes for the interaction and range-change-only model, followed by Mammalia (Figure 4, Table 1). The class Anthozoa and Bivalvia exhibit the highest sensitivities to range loss in both models (Figure 4, Table 1).

Results from the absolute-range-only model are similar to those from previous studies (e.g., Finnegan et al. 2015). Compared to the range-change-only model, the class-specific patterns are less distinct, forming two clusters: Chondrichthyes, Echinoidea and Mammalia group together, while Anthozoa, Bivalvia and Gastropoda form another cluster. The overall trend is less clear, marked by a sudden increase in extinction risk starting at absolute ranges of around < 1000 km (see Appendix Figure 1.7 in Supporting Information).

The combined additive model (Appendix Figure 1.15 in Supporting Information) and the interaction model (Figure 5) reveal that absolute range dominates extinction risk predictions. When absolute range is held constant, the effect of range change largely disappears (Figure 5b). This suggests that the apparent influence of range contraction is mediated by its relationship with absolute range size. Genera with small ranges consistently exhibit higher extinction probabilities than those with large ranges, regardless of percentage range loss (Figure 5b). It can also be seen that there is no clear change in extinction risk with higher range losses for genera with equal range size. The plots for small, medium and large ranged genera indicate two clusters of classes as also visible in the model without constant absolute ranges (Figure 3). However, the conditional effect trends appear to be nearly flat at extinction risks of up to 20% for large ranged, up to 40% for medium ranged and up to 80% for small range genera.

Model adequacy was tested by performing a model comparison (loo) between the geographic range-change-only model, the absolute-range-only model and the combined/interaction models including both absolute geographic range and geographic range change as independent variables. The comparison identified the interaction model (absolute geographic range * geographic range change) as the best model, followed by the combined additive model (absolute + range change) (Table 2). The proportion of variance explained for new data (Bayesian R^2; Gelman et al. 2019) is highest for the interaction model (Table 2), suggesting that the interaction model is more effective at explaining the observed variability in the data and, therefore, more accurate in making predictions than the other models. This outcome reflects the underlying data structure: most observations cluster at small absolute ranges and large contractions, meaning percentage range loss alone cannot fully explain extinction risk because its effect depends on the starting range size. The models that condition on absolute range and its interaction with range change account for this dependency, whereas the model based only on percentage change or only on absolute range ignores it. The interaction model is therefore viewed as the most appropriate in the context of this study.

To assess the influence of temporal grain on extinction risk estimates, we repeated the analysis using the simple range-change-only model with alternative binning schemes (7 Ma and 1 Ma intervals). The model considering the inconsistent temporal grain, by creating 7 Ma bins, revealed a non-linear increase towards higher range losses and a similar result for the baseline extinction risks of each class. The response of each class to a range loss of 50% to 95% also unveiled a generally comparable pattern; however, the percentages in range loss response deviate notably from the range-change-only stage level model (see Appendix Figure 1.18 and Table 1.1 in Supporting Information). The classes Anthozoa, Bivalvia and Chondrichthyes continue to exhibit the highest responses. Even though Anthozoa show in comparison a lower response with around 252% compared to 518% in the simple model. Chondrichthyes and Echinoidea, on the other hand, exhibit a significantly higher response with 678% and 1900%, respectively. However, due to the small sample size, the result for Echinoidea should be interpreted with caution.

The high-resolution range-change-only model using 1 Ma temporal bins reveals a weak, almost flat relationship to range loss but shows a comparable pattern for baseline extinction risks. Notably, Chondrichthyes now show lower baseline risks and group with the invertebrate classes. The response of each class to a 50% to 95% range loss is notably lower, but the pattern largely mirrors the range-change-only stage level model (see Appendix Figure 1.20 and Table 1.1 in Supporting Information). Anthozoa (50% response) and Chondrichthyes (32%) continue to exhibit the strongest responses. The key difference to the stage level model is that Bivalvia now show the lowest response to range loss (2%), replacing Echinoidea in that position.

Additional figures visualizing the distribution of the raw data as well as alternative models using, for example, maximum great-circle distance, differing weighting schemes and taxonomic resolutions can be found in Appendix S1.

4 | Discussion

4.1 | Primary Finding and Conceptual Synthesis

Our analyses indicate that extinction risk is best explained by the joint effects of absolute geographic range and geographic range change, with the interaction model (absolute range * range change) outperforming the combined additive,

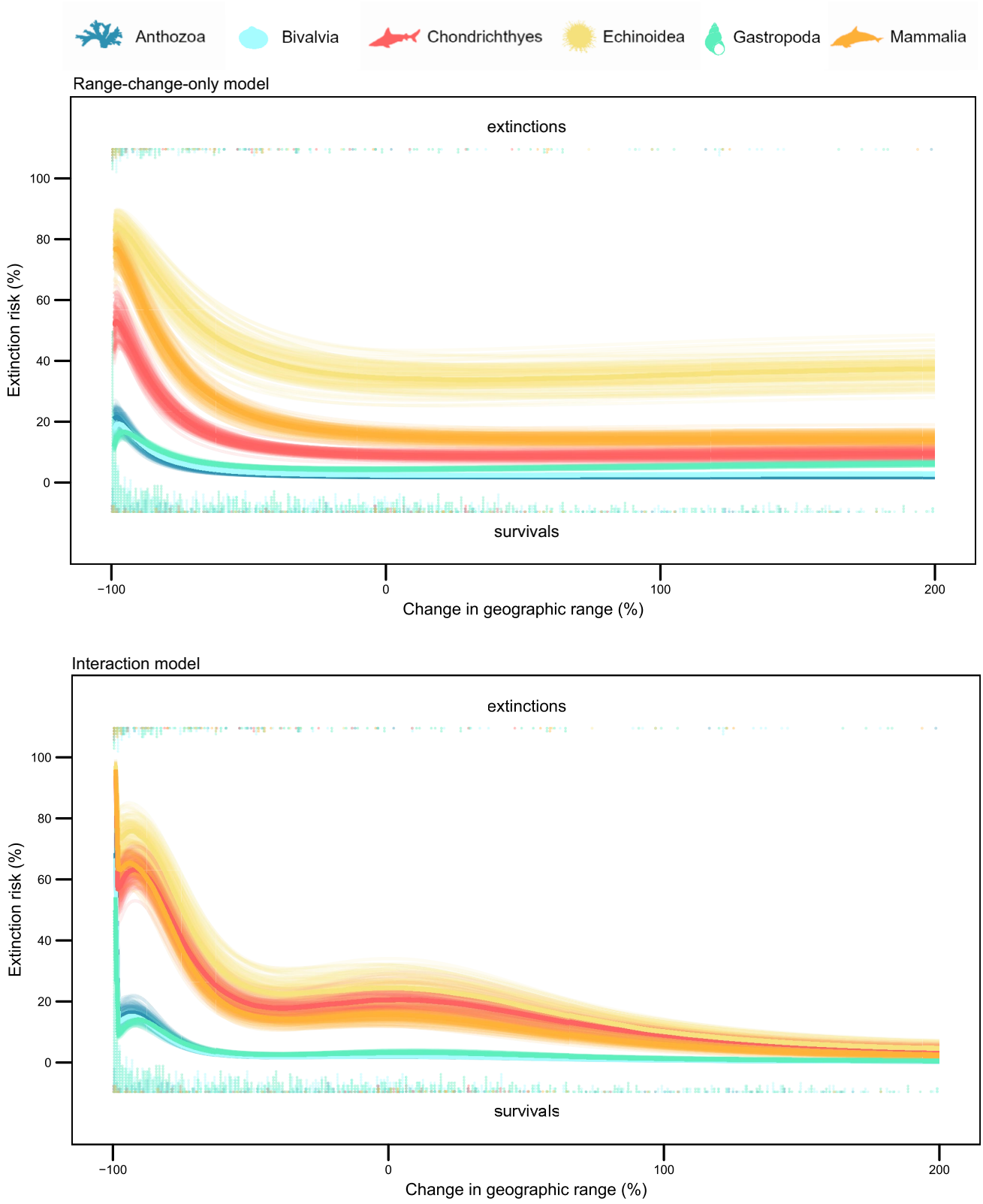

FIGURE 3 | Change in extinction probability ('risk') with geographic range loss for 6 marine taxonomic classes based on the range-change-only (upper plot) and interaction model (lower plot). The temporal period covers fossil data from Neogene to Holocene period (23–0 Ma) using stage-level temporal bins. The thin lines are draws from the posterior distribution. The thick lines represent the median of those draws. The dots visualize the distribution of observed extinctions and survivals per class.

TABLE 1 | Median extinction risk percentages for 50%, 80% and 95% range loss and median range loss responses based on the range-change-only and interaction model with stage level resolution.

		Range-change-only model		Interaction model	
Class	Range change (%)	Extinction risk (%)	Response to range loss (%)	Extinction risk (%)	Response to range loss (%)
Anthozoa	−95	18	518	50	
Anthozoa	−80	7		22	218
Anthozoa	−50	3		17	
Bivalvia	−95	18	409	48	
Bivalvia	−80	8		21	224
Bivalvia	−50	4		15	
Chondrichthyes	−95	50		90	
Chondrichthyes	−80	26	290	74	33
Chondrichthyes	−50	13		68	
Echinoidea	−95	82		94	
Echinoidea	−80	64	90	81	28
Echinoidea	−50	43		75	
Gastropoda	−95	17		43	
Gastropoda	−80	10	217	22	127
Gastropoda	−50	5		19	
Mammalia	−95	73		90	
Mammalia	−80	45	224	71	47
Mammalia	−50	22		62	

absolute-range-only and range-change-only alternatives (Table 2). This is supported by leave-one-out cross-validation and Bayesian R^2 (Section 2; Table 2), which together show the interaction model's highest predictive accuracy and variance explained for new data. This outcome is reflected by the underlying data structure (Figure 2): most observations cluster at small absolute ranges and large contractions, meaning percentage range loss alone cannot fully explain extinction risk because its effect depends on the starting range size. Models that condition on absolute range and its interaction with range change account for this dependency. In practical terms, this means that range contractions do not exert a uniform effect; their impact depends on the absolute range size a taxon occupies. Large-ranged genera can sustain sizable percentage losses while retaining viable habitat, whereas small-ranged genera are vulnerable even to modest contractions, an interpretation consistent with previous findings that small absolute ranges increase risk and that range size is a first-order buffer against local environmental disturbances (Harnik et al. 2012).

This framework reconciles two seemingly conflicting results. First, the range-change-only model (and marginal effect plots) shows a non-linear increase in extinction risk with increasing percentage range loss while positive range changes show no corresponding rise in risk (Figure 3), a pattern also broadly consistent with the other more complex models. Second, conditional plots from the better-performing interaction and combined additive models demonstrate that when absolute range is held constant, the range loss effect largely flattens (Figure 5b). In other words, the apparent global increase in risk with percentage loss in the marginal view reflects the uneven distribution of absolute range along the range-loss axis: small-ranged genera disproportionately occupy the high-loss portion of the gradient, while large-ranged genera cluster towards lower losses. The raw data make this coupling explicit (Figure 2), where the strongest percentage declines occur predominantly among small-ranged genera. Taken together, these results argue against relying on percentage range loss in isolation and instead support a conditional, interaction-based understanding of spatial vulnerability across multimillion-year timescales.

4.2 | Taxonomic Differences and Trait Mediation

The relationship between range change and extinction risk is taxon dependent. In our data, Anthozoa exhibit the highest sensitivity to range loss, whereas Echinoidea show the weakest response; other classes are intermediate (Figure 4). This finding, along with the observation of distinct baseline extinction risks for the individual classes, emphasizes the significance of

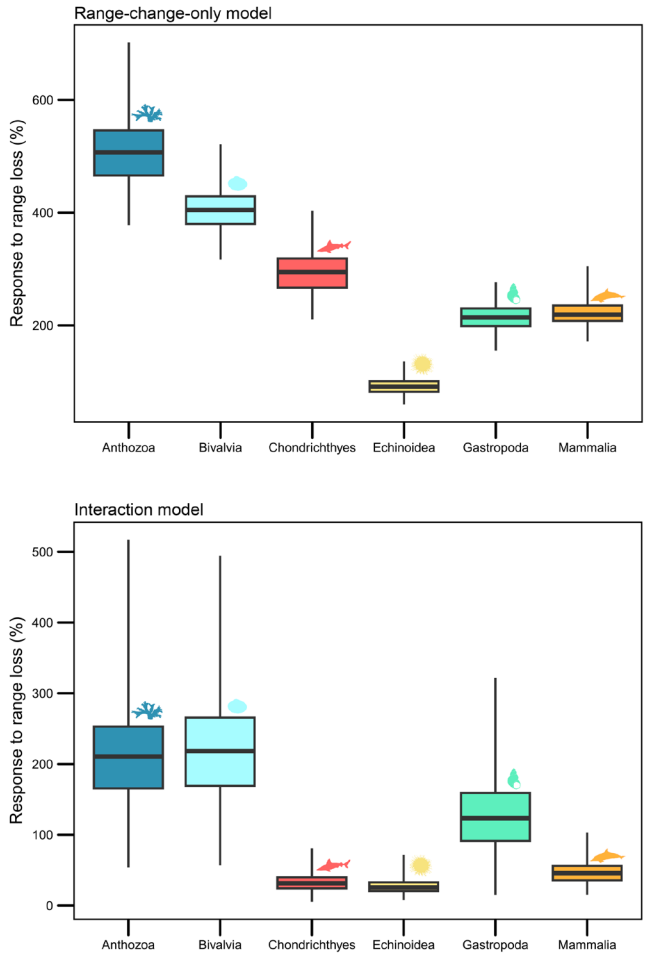

FIGURE 4 | Response of each class to range loss, calculated as the % increase in extinction risk from 50% to 95% range loss. Upper plot shows results for the range-change-only model. Lower plot shows the interaction model.

taxonomic identity and/or phylogeny in extinction risk assessments, as supported by previous studies (Wang and Bush 2008; Harnik et al. 2012; Finnegan et al. 2015). The apparent role of phylogeny in influencing extinction risk can be attributed to underlying variations in traits and macroevolutionary differences such as life cycle speed, reproduction modes, body size, or physiology (Van M. Savage et al. 2004; Purvis et al. 2005; Chichorro et al. 2019; Reddin et al. 2020) (although we cannot rule out the possibility that it also reflects differences in taxonomic practice). These drivers can be expected to operate across timescales and would thus also influence extinction risk–range dynamics today. Accounting for taxonomic identity/phylogeny could therefore enhance the accuracy of extinction risk assessments.

4.3 | Temporal Scale and Sensitivity to Binning

Temporal grain strongly influences the observable link between range dynamics and extinction risk. Re-binning to equal size 7 Ma intervals retained overall qualitative patterns in baseline risks but altered effect magnitudes, with some groups (e.g., Chondrichthyes, Echinoidea) showing higher responses than in the stage-level analysis, while Anthozoa's response decreased (Appendix Table 1.1; Figures 1.17 and 1.18 in Supporting Information). This demonstrates that variations in time intervals resulting from binning the data to stratigraphic stages can indeed have an impact on the results. However, it does not alter the primary conclusion. The reason for this observed effect of binning is that changes observed over longer time intervals tend to be more significant than those occurring over shorter periods (more time = more change). Genera that primarily occur over short stages may exhibit less range change but show a higher sensitivity to range loss. This can be attributed to the observed 'small' range changes throughout these short time intervals which would statistically lead to a high response to range loss in case of an extinction (small range loss + extinction = high sensitivity to range loss).

In contrast, 1 Ma bins weakened the extinction signal: survivals increased five-fold while the number of extinctions remained the same, inflating apparent range-change events and flattening risk gradients (Section 2; Appendix Figures 1.19 and 1.20 in Supporting Information). This reflects the general statistical principle that coarser bins reduce sampling noise and increase power for macroevolutionary signals (Smith et al. 2025). Accordingly, while directional inferences are robust to moderate changes in temporal grain, inference strength and class-specific magnitudes are grain dependent, underscoring the need to match bin size to data density and the ecological process of interest. Our results thus highlight the need for larger and taxonomically finer resolved deep-time data sets for macrofaunal taxa when targeting ≤ 1 Ma temporal resolution.

4.4 | Extreme Range Loss (> 95%)

At very high range losses (> 95%), we observed a slight decline in extinction risk, particularly in gastropods and chondrichthyans (Figure 3). This decline is not a statistical artifact, such as an edge effect from the smoothing spline fit, as the raw geographic range data includes genera that survive range losses of over 95%. We also ameliorated issues with geographic range calculations from spatial clustering (multiple occurrences at the same location) or extremely distant (intercontinental) occurrences by omitting the most distant occurrence per genus-bin group and filtering out proximal coordinates (≤ 0.3° difference) in separate analyses. Interestingly, the decline is not visible when running the model with large-ranged taxa only (see Appendix Figure 1.16 in Supporting Information)—therefore we think it is an artifact resulting from mixing genera with broad and narrow geographic ranges. Genera that originally possess extensive ranges can experience higher range losses and still retain a larger habitat compared to those with initially limited ranges and low range losses. Consequently, even after a significant percentage of range reduction, large-ranged genera may still have a higher survival chance than small-ranged taxa that have experienced less percentage decrease. This disparity in the initial range sizes could lead to the observed drop in extinction risks among genera with the most pronounced range losses.

4.5 | Implications for Forecasting and Conservation Assessments

Our results indicate that on multi-million-year timescales percentage range loss alone is not a reliable predictor of extinction

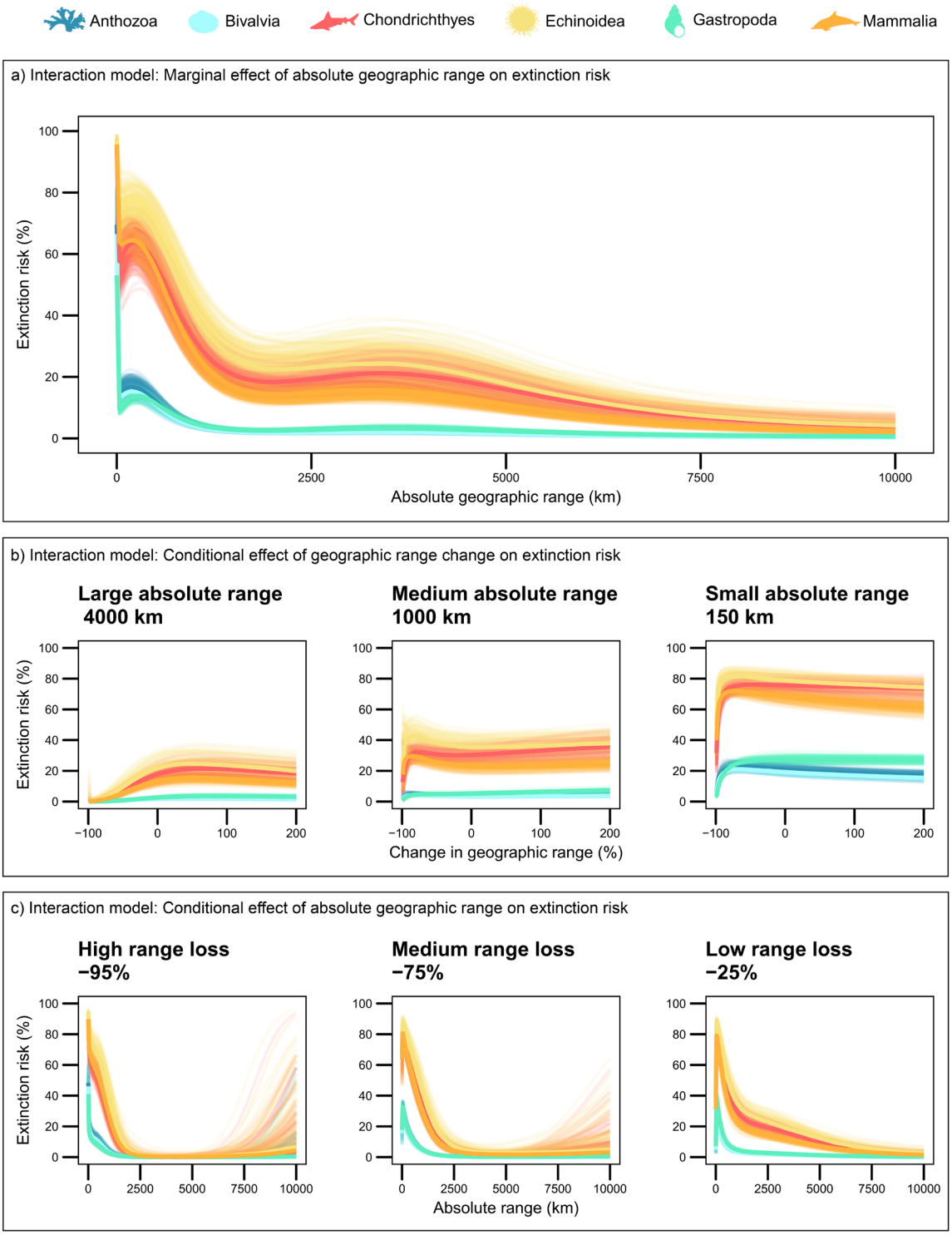

FIGURE 5 | Interaction model (absolute geographic range ∗ geographic range change). The temporal period covers fossil data from Neogene to Holocene period (23–0 Ma) using stage level temporal bins. (a) Output of the model displaying the marginal effect of geographic range change on extinction risk. (b) Output of the model displaying the conditional effect of geographic range change on extinction risk for varying constant values of absolute geographic range (small, medium, large). (c) Output of the model displaying the conditional effect of absolute geographic range on extinction risk for varying constant values of geographic range change (−25%, −75%, −95%).

risk, indicating the importance of rate and temporal context of range change. This interpretation has direct implications for predicting extinction under climate change. In modern systems, where range contractions can be tracked over decades, a sustained rate of decline is a strong warning signal of elevated extinction risk (e.g., Wilson et al. 2005). In contrast, contractions reconstructed from fossil data integrate processes over millions of years—geological, evolutionary and macroecological (Darroch et al. 2022) —which blur short-term ecological signals. Paleogeographic ranges are shaped by nested biotic

TABLE 2 | Conditional and marginal R^2 calculated using the function r2_bayes of the performance package (Lüdecke et al. 2021) and the estimated difference and standard error of the expected leave-one-out prediction errors using the function 'loo' (loo package; Vehtari et al. 2024). The lower the loo value, the better the model explains the data.

Models	Range-change-only	Absolute-range-only	Change + absolute range	Change * absolute range
Conditional R^2	0.070	0.116	0.143	0.150
Marginal R^2	0.102	0.184	0.225	0.245
Loo: expected log predictive density difference	−994.861	−214.343	−69.338	0.000
Loo: standard error difference	157.116	74.224	53.184	0.000

and abiotic processes acting across temporal scales from hours to millions of years and are inherently time-averaged (Kowalewski et al. 1998; Darroch et al. 2022). This means that range contractions observed in deep-time may reflect long-term environmental shifts, dispersal barriers or macroevolutionary trends, rather than acute ecological stress (Darroch et al. 2022). Hence, we interpret that while deep-time range histories provide valuable context for understanding extinction selectivity, they may have limited use for forecasting near-future extinctions, not because the fossil record is intrinsically flawed, but because the underlying temporal scales and processes differ.

Yet, the predictive value of long-term range trajectories may depend on the taxonomic and ecological context. Smith et al. (2025) demonstrated that in pelagic microplankton, both standing occupancy and its change remain statistically significant predictors of extinction at ≤ 1-million-year resolutions. Notably, the predictive power of range change increased with coarser temporal binning, implying that persistent environmental forcing or legacy effects can be captured at long timescales. This contrasts with our findings for benthic and nektonic macrofaunal taxa (see Appendix Figures 1.19 and 1.20 in Supporting Information) and earlier results by Kiessling and Kocsis (2016), where coarse temporal resolution limited predictive capacity and absolute range dominated as the main driver of extinction risk.

These differences likely arise from fundamental ecological and preservational contrasts between pelagic microfossils and macrofaunal taxa. Microplankton, which are passively dispersed and respond smoothly to global environmental changes, exhibit more continuous and directionally consistent range shifts (Villarino et al. 2018; Lowery et al. 2020). Their high abundance and ecological breadth facilitate the detection of long-term occupancy trends. In contrast, macrofaunal taxa are more strongly affected by local environmental variability and biotic interactions (Fronhofer et al. 2018). Their ranges can shift abruptly, fragment, or recover and such episodic dynamics are less likely to be preserved in time-averaged fossil records. Consequently, while microfossil data may capture long-term climatic legacies, macrofossil datasets require higher temporal and spatial resolution to disentangle short-term ecological responses from long-term evolutionary and taphonomic noise.

Three implications emerge from our deep-time perspective:

1. Relying on percentage range change (or absolute range) alone is not sufficient to infer macro-evolutionary extinction risk. Over multimillion-year timescales, absolute range and its interaction with range change dominate.
2. Range contractions matter most for small-ranged taxa. Absolute range size acts as a first-order buffer against environmental disturbances; hence, underlining the importance of accounting for absolute range in modern assessments.
3. Rate of range change is important because temporal scale strongly affects the magnitude and detectability of extinction risk, highlighting the need to align temporal resolution with ecological processes of interest and data density.

5 | Conclusion

Our study offers a deep-time perspective on how extinction risk relates to geographic range change. Although marginal analyses suggest a non-linear increase in risk with percentage range loss, this pattern largely disappears at equal absolute ranges, indicating that absolute range size dominates extinction risk over multi-million-year timescales. Taxonomic differences persist, and temporal grain strongly influences effect magnitudes, but the qualitative pattern remains robust. Small-ranged taxa are consistently more vulnerable than large-ranged taxa, regardless of percentage loss. Crucially, model comparison indicates that neither absolute range nor range change in isolation is sufficient to predict extinction—predictive performance is best only when both are modelled jointly via their interaction. These findings caution against using absolute range or percentage range change alone as a predictor of extinction risk and underscore the importance of considering both as well as the rate or persistence of decline. While macrofaunal fossil data provide valuable insights into long-term selectivity mechanisms, their predictive capacity for near-future extinctions is limited because underlying processes and timescales differ. Bridging these scales will require higher resolved macrofaunal fossil data and integrative frameworks that combine paleontological, ecological and physiological information to refine our understanding of how spatial dynamics shape biodiversity loss.

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The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70226-sup-0001-supinfo.docx.