PALEOECOLOGY

Climate change is an important predictor of extinction risk on macroevolutionary timescales

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Anthropogenic climate change is increasing rapidly and already impacting biodiversity. Despite its importance in future projections, understanding of the underlying mechanisms by which climate mediates extinction remains limited. We present an integrated approach examining the role of intrinsic traits versus extrinsic climate change in mediating extinction risk for marine invertebrates over the past 485 million years. We found that a combination of physiological traits and the magnitude of climate change is necessary to explain marine invertebrate extinction patterns. Our results suggest that taxa previously identified as extinction resistant may still succumb to extinction if the magnitude of climate change is great enough.

The climate has changed rapidly over the past several decades (1), and this is projected to continue into the coming centuries (2, 3). Changes in climate are already affecting modern biodiversity (4–6) and are expected to continue to alter biodiversity in the future (7). Substantial biodiversity loss has also been linked to past changes in climate (7–10); however, relatively little is known regarding the effect of climate change on extinction risk for taxa over Phanerozoic timescales or how the rate and magnitude of climate change affect extinction risk compared to other known extinction predictors. Determining the traits that promote or inhibit extinction provides critical insight on the causal mechanisms generating biodiversity over geological time scales (11, 12) and may help identify species at risk of extinction today (13–16).

Previous work has identified correlates of extinction in modern and ancient taxa, including abundance (17, 18), body size (15, 19, 20), niche breadth (21–26), thermal tolerance (15, 22, 27, 28), and geographic range size (11, 12, 17, 18, 22, 28–30). The latter trait in particular has been identified as a key predictor of extinction over the Phanerozoic (11, 14, 17, 20, 29). Despite this important past work, tests of extinction determinants over macroevolutionary timescales have been conducted for only a few predictor variables and are often tested in isolation, limiting our understanding of evolutionary drivers and our ability to forecast the effects of anthropogenic climate change on biodiversity.

Thermal tolerance, for example, has been posited to affect the vulnerability of species to anthropogenic climate change today (31–34) and in the past (27) but has not been assessed over Phanerozoic timescales relative to other extinction risk predictors. We hypothesize that the thermal tolerance of a taxon influences its risk of extinction as this trait mediates responses to climate change and because fossil data suggest extinction patterns tend to vary latitudinally (35–37). We additionally hypothesize that the magnitude of climate change experienced by a taxon will affect its extinction risk. The rate and magnitude of current climate change are considered significant threats to global biodiversity (2), with myriad impacts already observed (5). Critically, however, the degree to which taxon-specific climate change estimates are able to predict extinction remains unknown, including whether this extrinsic factor is a stronger predictor of extinction than traits intrinsic to taxa, such as geographic range size or body size.

Paleontological occurrence data and predictors of extinction

We use three novel approaches to quantify thermal tolerance and the magnitude of climate change experienced by taxa for 9264 genera in 81 stages across the Phanerozoic (Fig. 1 and fig. S2). We assessed thermal tolerance by estimating the realized thermal preference and realized thermal niche breadth for each taxon. Realized thermal preference is estimated as the absolute deviation in occupied temperature from the median occupied temperature for a stage, whereas realized thermal niche breadth is estimated as the occupied range of temperatures for a taxon, representing degree of climate specialization (38) (see SM, methods and materials) (39).

We compare proxies for thermal physiology to known correlates of extinction, including geographic range size and body size, to examine their relative weights in governing macroevolutionary dynamics over the past 485 million years (Ma), while recognizing the complex interactions between variables (40, 41). Using the Paleobiology Database (42), we focus on nine classes of marine invertebrates belonging to Cephalopoda, Gastropoda, Echinoidea, Crinoidea, Trilobita, Ostracoda, Bival-

via, and the brachiopods Rynchonellata and Strophemenata. Marine invertebrates are well suited for our analyses because they are regarded as the most complete and reliable constituents of the fossil record (43), and their geographic ranges are thought to closely approximate their true thermal tolerances based on the correlation between realized and fundamental thermal niches calculated through lab experiments in marine ectotherms (32, 44).

Paleoclimate reconstruction

Spatial estimates of past climate used in the calculation of extinction risk predictors [see SM, methods and materials (39), data S1, and fig. S1] were derived from new HadCM3 climate simulations for 81 stages over the Phanerozoic (Fig. 1). These simulations improve on those in Valdes et al. (45) in a number of ways, including tuning of climate model variables (46) so that the model has increased polar amplification during past climates (47) and more realistic prescribed pCO_2 during the Cenozoic (48) (fig. S1). This climate model is appropriate for this study, as it successfully simulates the polar warmth of the early Eocene and Cretaceous and produces accurate simulations of the Last Glacial Maximum and preindustrial climates (49). We use several versions of these climate simulations to test the sensitivity of our results to the climate model input [see SM, methods and materials (39) and fig. S5].

Statistical model parametrization

We examined patterns of extinction selectivity over the Phanerozoic for a combined total of 292,940 spatially and temporally unique fossil occurrences using generalized linear mixed effects models that accounted for variance in selectivity temporally and taxonomically (see SM, methods and materials (39), table S1, and figs. S2 and S3). Patterns of extinction were modeled as a function of five predictors, both with (table S8) and without interaction terms, including geographic range size, body size, absolute realized thermal preference, realized thermal niche breadth, and the absolute value of taxon-specific climate change estimates (Fig. 1). Trait estimates were based on both jackknife and bootstrap subsampling to mitigate potential spatial and sample size biases [see SM, methods and materials (39) and fig. S4]. Analyses were performed at both the generic and species level (50). We focus here on generic-level patterns because species-level measures and temporal ranges are often poorly constrained on macroevolutionary timescales (13, 51), although modeled results were consistent across both approaches (table S6).

Extinction selectivity patterns

The best model for all combinations of predictors based on AIC (52, 53) was the most saturated, with all predictors significant at $\alpha < 0.05$

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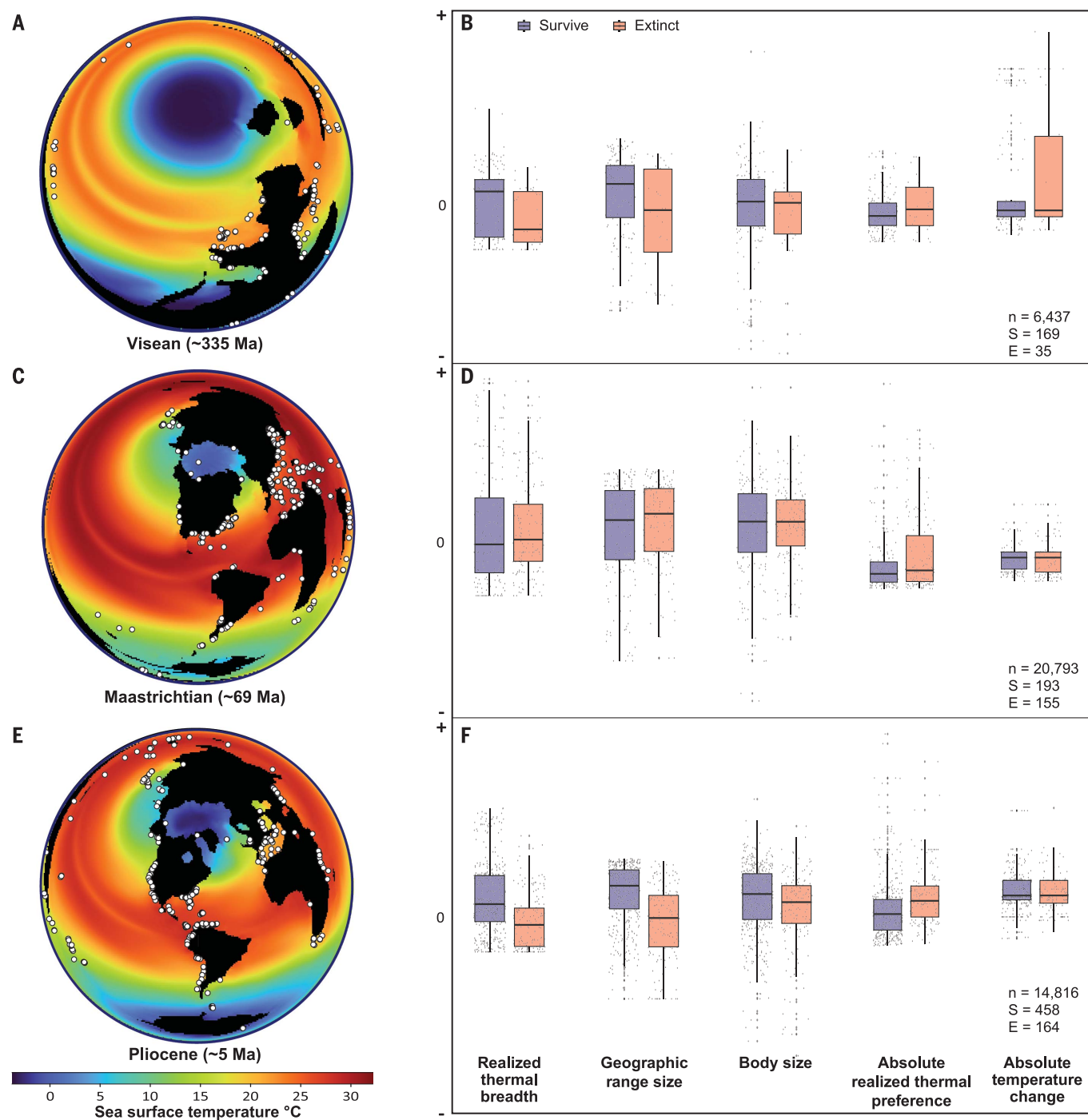
Fig. 1. Sea surface temperature estimates and predictor variable distributions for Phanerozoic taxa. (**A**, **C**, and **E**) Sea surface temperature estimates for the Visean (335 Ma), Maastrictian (69 Ma), and Pliocene (5 Ma) using the HadCM3 coupled atmosphere-ocean generalized circulation model, overlaid with taxon occurrences (white dots) used in estimating predictors in (**B**, **D**, and **F**). Boxplots of taxon trait estimates for taxa that survived versus those that went extinct in the (B) Visean, (D) Maastrictian, and (F) Pliocene, where the line represents the median, the black dots the estimates for each genus, and the whiskers the 95% confidence interval (CI) estimates. The variables were centered and standardized to enable direct comparison between distributions for each predictor, so a value of 0 indicates the mean estimate, positive values represent values greater than the mean, and negative values indicate values less than the mean. N, number of unique taxon occurrences in the stage; S, number of survivors; E, number of taxa that go extinct in the respective time interval.

and a model weight of 0.98 (*52*) (Fig. 2 and table S3). Model results were robust to the choice of subsampling approach [see SM, methods and materials (*39*), fig. S4, and tables S4 and S5], to the taxonomic rank of analysis (species or genus; table S6), and to different climate model simulations used to characterize our thermal traits [see SM, methods and materials (*39*) and fig. S5], corroborating the importance of these variables in regulating macroevolutionary patterns over 485 Ma. Furthermore, power analyses conducted on

simulated datasets suggest that our model can reliably detect selectivity signals for all five predictors [see SM, methods and materials (*39*)].

The absolute magnitude of climate change experienced by a taxon emerged as an important predictor of extinction risk in the best-supported model, suggesting that taxa exposed to greater climate change preferentially went extinct. This extrinsic environmental trait showed the same strength of correlation with extinction risk as did realized thermal niche breadth, realized thermal preference, and body size, evidenced by the overlap in confidence intervals

for coefficient estimates (Fig. 2, fig. S4, and table S3). The only trait with a stronger signal of selectivity was geographic range size. Geographic range size was also the most important predictor, even when controlling for sample size (fig. S4), since the coefficient of −0.44 was larger than the second largest of −0.29 for body size and realized thermal niche breadth (Fig. 2 and table S3). This supports past work that found that smaller-ranged species are consistently more vulnerable to extinction on geological timescales (*15, 18, 22, 29*) (Fig. 2).

Using spatiotemporal estimates of climate change experienced by each taxon [see SM, methods and materials (*39*) and Fig. 1], we find that a localized mean annual temperature change of ~7°C across stages could greatly increase a taxon's probability of extinction, calculated as the temperature when the marginal effects are greater than zero (Fig. 2). This threshold is slightly higher than that found by Song *et al.* (*54*), who suggested that an increase of 5.2°C could result in a mass extinction in the modern era. However, Song and colleagues (*54*) used globally averaged rates of climate change
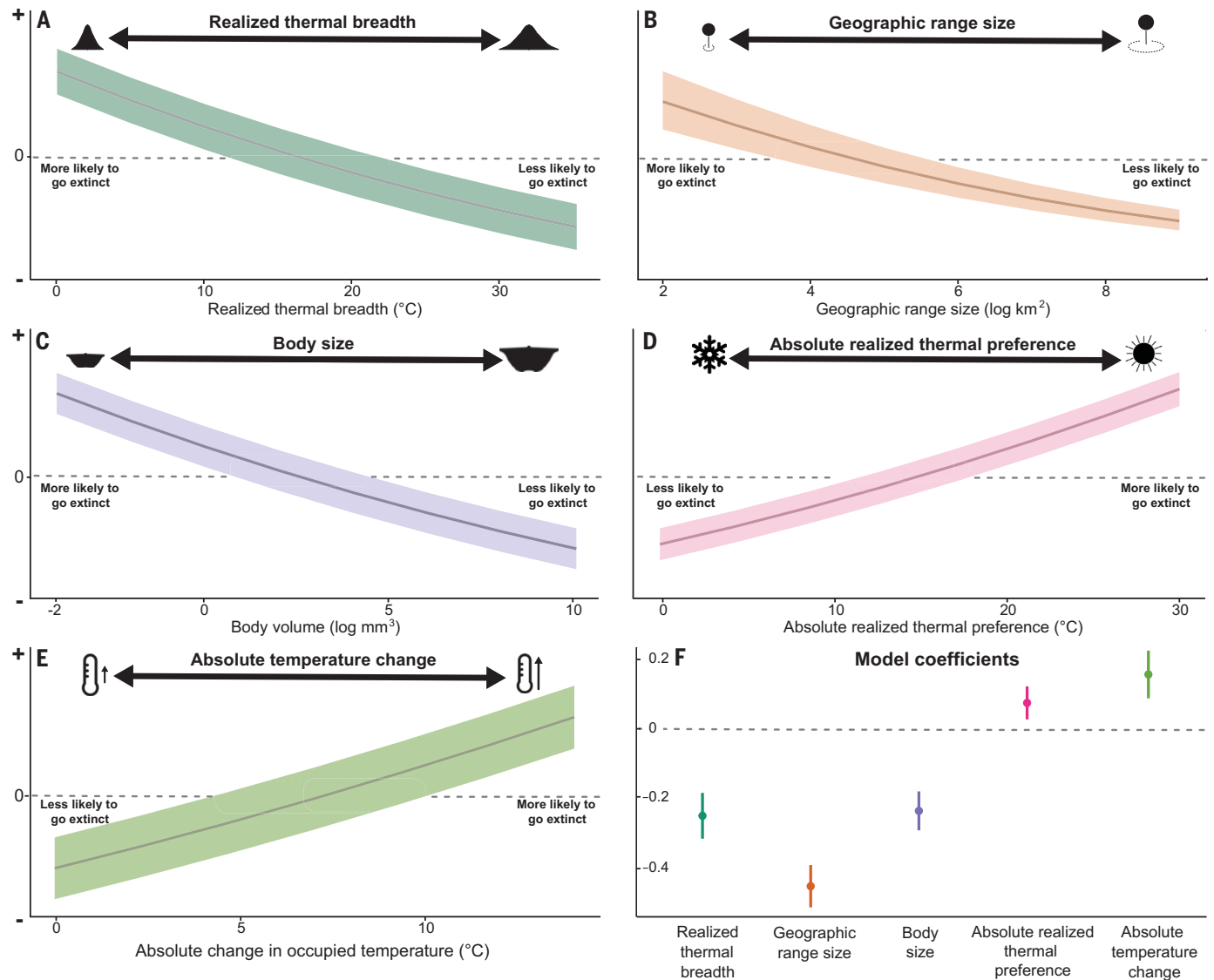
Fig. 2. Extinction risk estimates for each predictor variable included in the best-supported model. (**A** to **E**) Marginal effects plots for each predictor variable in the best model. The *y*-axis corresponds to the scaled probability of a taxon going extinct with a given trait value, holding the other predictors constant [see SM, methods and materials (*39*)]. The dark lines correspond to the median estimate and the shaded regions the 95% CI. Positive values indicate greater probability for extinction at the given predictor values and negative values indicate a taxon is less likely to go extinct at the given predictor values. (D) Realized thermal preference

was measured as the absolute value of the deviation of a taxon's median occupied temperature from the median occupied temperatures of all taxon occurrences within a stage. (E) The absolute value of climate change experienced by each unique taxon was calculated from a given stage (n) to stage n+1. (F) Extinction selectivity in log-odds for each predictor variable. The *y*-axis corresponds to the probability of extinction in log-odds. Positive values indicate a positive relationship with extinction risk and negative values indicate an inverse relationship with extinction risk (refer to table S3 for the detailed coefficients).

to predict magnitude of extinction over the Phanerozoic rather than the taxon-specific magnitude of localized climate change used here.

Realized thermal niche breadth and realized thermal tolerance were both strong and consistent predictors of extinction risk over the Phanerozoic (Figs. 1 and 2). These results are robust to the number of occurrences used to estimate thermal tolerance [see SM, methods and materials (39) and fig. S4]. Taxa that occupied climatic extremes were more extinction prone than taxa occupying more thermally intermediate isotherms (Fig. 2), suggesting a significant evolutionary advantage for taxa living in temperate isotherms over those living near the equator or at the poles. This pattern is congruent with past studies that found that taxa adapted to living in climatic extremes were more prone to extinction during hyperthermal events (27, 35, 55, 56), which could be explained by the loss of thermal habitat (ecophysiotypes) at the poles and equator due to climate change (9, 56).

Taxa with narrower thermal breadths were more susceptible to extinction than taxa with broader thermal tolerances in the best-supported model (Fig. 2), and this trait was equal in importance to realized thermal tolerance in explaining patterns of extinction over the Phanerozoic (Fig. 2). The strength of this correlate suggests that extinctions are physiologically selective based on thermal limits. However, it is important to note that the thermal breadth of a taxon is mediated by both temperature and oxygen availability, which increased over the Phanerozoic, as well as other biotic factors such as competition and nutrient availability (8, 56–58). Based on our models, taxa with narrow realized thermal breadths of less than 15°C may be at greatest risk of extinction (Fig. 2).

Body size was a significant predictor of extinction in the best-supported model, with smaller-bodied marine invertebrates more prone to extinction on geological time scales (Fig. 2 and table S3), consistent with previous studies (15, 20). Body size, however, had a relatively small effect on patterns of extinction over the Phanerozoic compared to geographic range size, especially when controlling for sample size (fig. S4). This pattern is surprising considering that body size is often regarded as one of the primary traits selected for during extinction events (11, 14, 20, 59). The relatively weak predictive performance of body size could result from methodological constraints, which required us to assume that body size was constant over time for a taxon. Thus, we were unable to identify any reductions in body size that may have occurred prior to extinction events. We also tested whether the inclusion of small-bodied taxa such as ostracods had an impact on body size selectivity and found no change in overall patterns when excluding ostracods (tables S3 and S7).

Many of the predictors considered here may interact to influence taxon extinction risk (34, 40, 41, 60), despite their low collinearity (table S2). For example, species that have both small geographic ranges and narrow niche breadths may be even more susceptible to extinction than a taxon with either a small geographic range or a narrow niche breadth. We therefore ran an additional stepwise model selection procedure considering all combinations of two- and three- way interaction terms for the five predictor variables ($n = 32$ predictors). All five main effect predictors remain statistically significant in these models, with significant interactions found between geographic range size and realized thermal tolerance, geographic range size and realized thermal niche breadth, and geographic range size and body size [see SM, methods and materials (39)]. The overall best model was found to contain the five main effect variables plus the three significant interaction terms (table S8). Therefore, there are likely cumulative impacts of these variables on extinction risk, where the importance of one variable in predicting extinction outcomes can increase or decrease depending on the level of another term.

Discussion

Our analyses suggest that intrinsic, taxon-specific traits were insufficient to explain empirical patterns in extinction dynamics over the Phanerozoic, and that the magnitude of climate change should also be considered. Climate change affected taxa within a stage regardless of their traits (table S8), although its impact varied spatially. For example, localized temperature changes may have exceeded 14°C (data S1) for some taxa during the Late Permian, which potentially explains why some species with large geographic ranges and realized thermal breadths (i.e., species predicted to be buffered from extinction) go extinct, especially during mass extinction events that are often characterized by severe climate perturbations (fig. S2). However, we do find a decrease in extinction selectivity during mass extinction intervals (fig. S2), similar to that found by past studies (20). The effect of climate change on a taxon's risk of extinction is likely mediated by additional factors, including a taxon's dispersal ability and the shape and orientation of shallow marine habitat (61).

Although proxies of thermal physiology emerged as important predictors in our model, geographic range size was the strongest correlate of extinction over the Phanerozoic, consistent with previous studies that found that realized thermal niche breadth and geographic range size can be decoupled (22, 62). However, the effects of geographic range are complex and may be more or less important based on the other predictors included here (table S8). Geographic range size may be a strong and consistent predictor of extinction because this trait

emerges from the effects of many other factors, including climatic tolerances, dispersal ability, nutrient availability, and biotic interactions (17, 18). Moreover, a larger geographic range size could serve as a buffer against localized perturbations (be they abiotic or biotic in nature), as regional events would be unlikely to affect all populations equally (22, 29). Thus, large geographic range size may buffer taxa from stochastic events, which could lead to extinction independent of thermal niche breadth.

Model uncertainty

The extinction risk models presented here represent our current best estimate for constraints on marine invertebrate extinction over the Phanerozoic and serve as a framework for future work incorporating additional parameters. For example, other intrinsic traits and factors, such as abundance (17, 18), might affect extinction risk over geological timescales. These factors, however, are difficult to characterize for extinct taxa spanning millions of years. Abundance in particular is challenging to determine even in the modern era (17), and thus we focus only on traits that can be estimated more reliably. In addition, there are many other potential extrinsic drivers not considered here, such as anoxia (8), euxinia, and ocean acidification (63). These extrinsic factors may be especially important during mass extinction events (63), but geochemical proxies are not available in our climate models and difficult to estimate over the Phanerozoic.

Our analyses may also be affected by uncertainty in both paleogeographic reconstructions—especially pre-Jurassic (45, 64)—and climate simulations (49), as the physiological and extrinsic predictors are based on proxies for spatiotemporal climate that contain uncertainty [see SM, methods and materials (39)]. New paleoclimate estimates may impact our understanding of extinction correlates over Phanerozoic timescales. However, the insensitivity of our results to different climate model boundary conditions suggests that our patterns may be robust to some degree of climate model uncertainty (fig. S5).

Finally, the temporal resolution of our stage-level analyses may affect our ability to compare changes in climate between the past and present (65, 66). However, our analyses find a robust selectivity signal that has persisted over 485 Ma (Fig. 2 and fig. S2), despite major changes in boundary conditions (61, 67, 68), suggesting that the determinants of extinction risk studied here may be present regardless of temporal scale.

Conclusions

The predictable nature of extinction on geological timescales, despite major variations in boundary conditions, environment, biota, and extinction magnitude, is notable. Our results

have implications for understanding the fate of biodiversity in response to changing climate today and into the future. Based on our models, taxa with narrow realized thermal breadths of less than 15°C, living predominantly in the poles or tropics, are likely to be at greatest risk of extinction (Fig. 2). These results reinforce the importance of climate in driving extinction on macroevolutionary timescales (8–10, 69). We find that extinction dynamics over the past 485 Ma cannot be explained fully without considering the magnitude of climate change in addition to the other physiological and taxonomic trait predictors. Our baseline extinction risk estimates derived from the geological past suggest that biodiversity may face a harrowing future given projected climate change estimates (2), which could be made worse when interacting with other anthropogenic extinction drivers (5, 13).

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SUPPLEMENTARY MATERIALS

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Data S1