Paleontological baselines for evaluating extinction risk in the modern oceans

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Marine taxa are threatened by anthropogenic impacts, but knowledge of their extinction vulnerabilities is limited. The fossil record provides rich information on past extinctions that can help predict biotic responses. We show that over 23 million years, taxonomic membership and geographic range size consistently explain a large proportion of extinction risk variation in six major taxonomic groups. We assess intrinsic risk—extinction risk predicted by paleontologically calibrated models—for modern genera in these groups. Mapping the geographic distribution of these genera identifies coastal biogeographic provinces where fauna with high intrinsic risk are strongly affected by human activity or climate change. Such regions are disproportionately in the tropics, raising the possibility that these ecosystems may be particularly vulnerable to future extinctions. Intrinsic risk provides a prehuman baseline for considering current threats to marine biodiversity.

overfishing, habitat loss, pollution, climate change, and ocean acidification (1–4) pose intensifying threats to marine ecosystems, leading to concerns that a wave of marine extinctions may be imminent (5–10). In contrast to the terrestrial realm (11–13), little is known about the distribution of extinction vulnerability among marine taxa. Formal threat assessments have been conducted for a small and taxonomically biased subset of marine species (5, 9). These assessments are based primarily on the current distribution of species and their exposure to modern threats (14–17), but longer-term baseline data are a key component of any forecasting effort (18, 19). Knowledge of past extinction patterns is critical for predicting the factors that will determine future extinction vulnerability. This knowledge can only come from the fossil record. Historical records are fragmentary for the marine realm, and few extinctions have been directly documented (5, 20). However, thick sequences of fossil-rich marine sediments are widespread on all continents (21, 22) and chronicle the waxing, waning, and extinction of taxa within many ecologically important groups. The environmental drivers of current and future extinctions may differ from those of the past (5), but the considerable variation in rates and drivers of extinction over geological time scales (102 to 106 years) provides an opportunity to determine whether there are predictors of extinction vulnerability that have remained consistent despite this variation. Such predictors can complement current risk assessments by identifying taxa that we expect to be especially vulnerable to extinction, given the macroevolutionary histories of taxa with similar characteristics. Here we construct models of extinction risk—defined as the probability of a fossil taxon being classified as extinct on the basis of its similarity to other fossil taxa—that went extinct over the same interval of time—and use these models to evaluate the baseline extinction vulnerabilities of extant marine taxa. We use the term “intrinsic risk” to refer to paleontologically calibrated estimates of baseline vulnerability for modern taxa.

We base our intrinsic risk evaluation on analyses of observed extinctions over the past 23 million years (Neogene-Pleistocene). We chose this interval to maximize faunal and geographic comparability between the modern and fossil data sets. The Neogene-Pleistocene fossil record is dominated by groups that are still extant and diverse, with continental configurations relatively similar to those of the present day. This interval also encompasses multiple extinction pulses and major changes in climatic and oceanographic conditions (e.g., contraction of the tropics, glacial-interglacial cycles, and associated changes in sea surface temperature and sea level) and is thus ideal for evaluating the consistency of extinction risk predictors. Using the Paleobiology Database (22), we analyzed Neogene-Pleistocene extinctions in six major marine taxonomic groups (bivalves, gastropods, echinoids, sharks, mammals, and scleractinian corals) for a total of 2897 fossil genera (table S1). We focused on these groups because they are generally well preserved in the fossil record (fig. S1) and are comparatively well sampled in modern coastal environments. Furthermore, these groups include several speciose
clades that exhibit well-known global marine biodiversity gradients and collectively represent a broad sample of marine ecological, phylogenetic, and functional diversity (24, 25).

Geographic range size (26, 27) and taxonomic identity (27, 28) are some of the most consistent predictors of extinction risk in the marine fossil record—the former presumably because widespread taxa are less susceptible to habitat loss and local disturbances, and the latter because many traits that influence extinction risk are correlated with phylogeny (29). We therefore evaluated seven metrics of geographic distribution and occurrence frequency [Fig. 1 and table S2 (30)] as potential predictors of extinction risk for fossil genera in four Neogene-Pleistocene subintervals (Early Miocene, Middle Miocene, Late Miocene, Plio-Pleistocene). Ideally, risk would be assessed for species, but species durations and geographic ranges in the fossil record are often poorly known. Hence, in keeping with many previous paleobiological analyses, we analyzed genera and included the number of species per genus as a potential extinction predictor [Fig. 1 (30)]. Strong positive correlations between fossil and modern predictor values for the 1163 genera that are sampled in both the Plio-Pleistocene fossil record and modern biogeographic databases suggest that relative differences among genera in these characteristics are not systematically distorted by the vagaries of fossil preservation [fig. S2 (30)]. To represent taxonomic identity and its correlates, we included membership in taxonomic subgroups of ordinal to familial rank as predictors [Fig. 1 (30)].

We used generalized boosted regression models (GBMs), which perform well when relationships between predictor and response variables are nonlinear (30), to evaluate extinction risk in each Neogene-Pleistocene subinterval (30). All subinterval models performed significantly better than chance (AUC = 0.71 to 0.82) when predicting one-third of the data that were withheld when building test models (fig. S3). A model built on the entire Neogene-Pleistocene data set correctly identified genera that went extinct as having higher risk than those that survived in 87% (11%) of cases (table S1) (30). Partial dependence plots show that many extinction risk patterns are common to all subintervals (Fig. 1). Geographic range size (great circle distance) and especially taxonomic group have a strong influence on extinction risk in all subintervals (Fig. 1 and fig. S4). The consistency of between-group differences throughout the Neogene-Pleistocene interval implies that important extinction risk factors are phylogenetically conserved (29). An alternative hypothesis, that between-group extinction risk differences reflect differences in preservation potential, is not supported (fig. S5).

We further evaluated the consistency of extinction risk patterns across geological time by comparing the extinction risk of a genus estimated by a model calibrated on the subinterval in which it was sampled to the extinction risk of the same genus estimated by a model calibrated on a different subinterval (fig. S6). Spearman rank-order correlations of genus extinction risk estimates for the 12 comparisons range from 0.70 to 0.79 (all P < 0.001, fig. S6). Thus, all subinterval-specific models yield similar and strongly correlated genus risk predictions despite subinterval-to-subinterval variation in the environmental drivers of extinction and in the sampling of the fossil record.

The consistency of extinction risk patterns through more than 23 million years suggests that the fossil record can provide meaningful constraints on the distribution of intrinsic risk across modern marine genera. We therefore measured the same predictors that were included in the paleontological models (Fig. 1) for 2615 extant marine genera belonging to the same six taxonomic groups that are recorded either in the OBIS database (32) or in species range maps (33, 34) [fig. S7 and table S1 (30)]. Before calculating geographic range predictors, we smoothed sampling heterogeneity across regions using a minimum bounding box procedure (35) to interpolate genus occurrences within 12 coastal biogeographic...
We then used the model built on the entire Neogene-Pleistocene (Fig. 1) to predict intrinsic risk for contemporary genera (fig. S8). We averaged intrinsic risk predictions for all genera sampled in 62 coastal biogeographic provinces (36) (fig. S9) to map the modern distribution of intrinsic risk (Fig. 2).

Our maps show that many provinces with the highest mean intrinsic risk are located in the tropics, particularly in the diverse tropical Indo-Pacific and Western Atlantic (Fig. 2). This pattern is not driven by innate differences in extinction regime between tropical and extratropical environments—genera with exclusively extratropical distributions exhibit higher proportional extinction than those with ranges that include the tropics in most Neogene-Pleistocene subintervals [Fig. 1F and fig. S10D (23)]. The elevated mean intrinsic risk of some tropical provinces instead reflects the macroecological and macroevolutionary characteristics of some tropical genera. Tropical
provinces generally host a greater proportion of genera belonging to relatively extinction-prone groups such as faviid corals and also tend to have proportionally more genera with narrow geographic ranges (fig. S11 (30)). The latter pattern may be driven by habitat heterogeneity in regions with numerous islands and associated reefs (37), which have been argued to promote endemism (38).

In the polar regions, the mean intrinsic risk of gastropods is high in the Antarctic relative to that of the Arctic (fig. 2), again reflecting high endemcity in this province (39, 40), isolated for more than 30 million years by circumpolar currents (41).

We highlight these large-scale patterns but caution against interpreting province-to-province variation. The range of intrinsic risk within a given province far exceeds the range of mean intrinsic risk between provinces (fig. S12). Furthermore, sampling is taxonomically and geo-taxonomically uneven in both the Paleobiology Database (42, 43) and OBIS (24), and such heterogeneity could bias our understanding of intrinsic risk distributions by distorting the observed geographic ranges of fossil and extant genera. It is possible, for example, that heavily sampled provinces contain a greater proportion of "pseudoendemic" genera that have not been sampled in other provinces in which they occur. Some groups exhibit positive relationships between modern sampling effort (as measured by total genus occurrences in OBIS) and mean intrinsic risk of provinces (figs. S13 and S14), but the same relationship and range of great circle distances (fig. S18). Raising the probability of provinces generally host a greater proportion of genera with narrow geographic ranges is high in the Antarctic relative to that of the Arctic (fig. 2), again reflecting high endemcity in this province (39, 40), isolated for more than 30 million years by circumpolar currents (41).

The implications of these broad-scale patterns for the future of coastal marine ecosystems will depend on how intrinsic risk and current threats interact to determine future extinction risk. For example, additive interactions would lead to extinction rates in some tropical regions exceeding those expected from human impacts alone, whereas multiplicative interactions would also raise the prospect of unforeseen ecological consequences (44). In other cases, such as the highly impacted coastal ecosystems of the North Atlantic, anthropogenic impacts may overwhelm intrinsic risk effects and leave a distinctly human fingerprint on future extinctions.

Understanding how intrinsic risk and current threats interact will involve disentangling the traits that underlie intrinsic risk differences. Potentially important life-history and ecological correlates of taxonomic identity include body size, larval mode, fecundity, life span, habitat preference, and trophic position, all of which are important predictors in modern risk assessments (27). Examining differences in the evolutionary stability of these traits across taxa (29) may also illuminate the drivers of intrinsic risk variation and inform predictions about the potential response times of taxa to current and future environmental change.

Our approach provides a flexible analytical framework that can be extended to incorporate additional risk predictors as data become available, and can be adapted to focus on specific taxa or regions of interest when possible. This approach complements the fossil records as a whole and observed modern species trends. Integrating modern threat assessments with long-term baseline data provided by the fossil record has potential to inform conservation planning—identifying taxa and ecosystems of potential conservation concern and teasing apart the ways in which extinction regimes in modern human-impacted ecosystems differ from those that prevailed in the geologic past.

REFERENCES AND NOTES

30. See supplementary materials and methods on Science Online.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Figs. S1 to S27
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References (45–75)

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Recognizing the threat of additive risk
Humans are accelerating the extinction rates of species in both terrestrial and marine environments. However, species extinctions have occurred across time for a variety of other reasons. Finnegan et al. looked at the extinction rates across marine genera (groups of species) over the past 23 million years to determine intrinsic extinction rates and what traits or regions correspond to the highest rates. Combining patterns of intrinsic extinction with regions of high anthropogenic threat revealed taxa and areas, particularly in the tropics, where the risk of extinction will be especially high.

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