

10. T. Eisner *et al.*, *J. Insect Physiol.* **23**, 1383–1386 (1977).
11. H. Schildknecht, *Angew. Chem. Int. Ed. Engl.* **9**, 1–9 (1970).
12. M. W. Westneat *et al.*, *Science* **299**, 558–560 (2003).
13. J. J. Socha, M. W. Westneat, J. F. Harrison, J. S. Waters, W.-K. Lee, *BMC Biol.* **5**, 6 (2007).
14. J. J. Socha *et al.*, *J. Exp. Biol.* **211**, 3409–3420 (2008).
15. M. W. Westneat, J. J. Socha, W.-K. Lee, *Annu. Rev. Physiol.* **70**, 119–142 (2008).
16. W.-K. Lee, J. J. Socha, *BMC Physiol.* **9**, 2 (2009).
17. Materials and methods are available as supplementary materials on Science Online.
18. J. F. V. Vincent, J. E. Hillerton, *J. Insect Physiol.* **25**, 653–658 (1979).
19. O. Sotavalta, *Biol. Bull.* **104**, 439–444 (1953).
20. J. F. V. Vincent, U. G. K. Wegst, *Arthropod Struct. Dev.* **33**, 187–199 (2004).
21. J. F. V. Vincent, *Proc. R. Soc. London Ser. A* **188**, 189–201 (1975).
22. R. F. Chapman, *The Insects: Structure and Function* (Cambridge Univ. Press, Cambridge, ed. 5, 1998).

ACKNOWLEDGMENTS

Use of the Advanced Photon Source was supported by the U.S. Department of Energy, Office of Science, Office of Basic Energy Sciences, under contract DE-AC02-06CH11357. This work was supported in part by the U.S. Army Research Laboratory and the U.S. Army Research Office through the MIT Institute of Soldier Nanotechnologies under contract W911NF-13-D-0001 and in part by the National Science Foundation through the MIT Center for Materials Science and Engineering under contract DMR-08-19762. This research was funded in part by the U.S. Department of Defense, Office of the Director, Defense Research and Engineering, through the National Security Science and Engineering Faculty Fellowship awarded to C.O. under contract N00244-09-1-0064; in part by the National Science Foundation through funding awarded to W.M. under contract DEB-0908187; and in part by the U.S.

Department of Energy, Office of Science, Office of Basic Energy Sciences, under contract DE-SC0012704. Experiment data are available for download from DSpace@MIT (<https://dspace.mit.edu/>); please cite this collection using the handle hdl.handle.net/1721.1/96123.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/348/6234/563/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S3
Tables S1 and S2
Movies S1 to S3
References (23–32)

12 September 2014; accepted 16 March 2015
10.1126/science.1261166

EXTINCTIONS

Paleontological baselines for evaluating extinction risk in the modern oceans

Seth Finnegan,^{1,*} Sean C. Anderson,^{2,†} Paul G. Harnik,^{3,†} Carl Simpson,⁴ Derek P. Tittensor,^{5,6,7} Jarrett E. Byrnes,⁸ Zoe V. Finkel,⁹ David R. Lindberg,¹ Lee Hsiang Liow,¹⁰ Rowan Lockwood,¹¹ Heike K. Lotze,⁷ Craig R. McClain,¹² Jenny L. McGuire,¹³ Aaron O'Dea,¹⁴ John M. Pandolfi¹⁵

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 wide-

spread 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 (10⁵ to 10⁷ years) (5) 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 pale-

ontologically 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 (23), 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

¹Department of Integrative Biology, University of California, Berkeley, CA 94720, USA. ²Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada. ³Department of Earth and Environment, Franklin and Marshall College, Lancaster, PA 17604, USA. ⁴Department of Paleobiology, National Museum of Natural History, Washington, DC 20013, USA. ⁵United Nations Environment Programme World Conservation Monitoring Centre, Cambridge CB3 0DL, UK. ⁶Computational Science Laboratory, Microsoft Research, Cambridge CB1 2FB, UK. ⁷Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada. ⁸Department of Biology, University of Massachusetts, Boston, MA 02125, USA. ⁹Environmental Science Program, Mount Allison University, Sackville, New Brunswick E4L 1A5, Canada. ¹⁰Center for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, Blindern, N-0316 Oslo, Norway. ¹¹Department of Geology, College of William and Mary, Williamsburg, VA 23187, USA. ¹²National Evolutionary Synthesis Center, Durham, NC 27705, USA. ¹³School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA. ¹⁴Smithsonian Tropical Research Institute, 0843-03092, Balboa, Republic of Panama. ¹⁵Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, University of Queensland, St. Lucia, QLD 4072, Australia. *Corresponding author. E-mail: sethfinn@berkeley.edu †These authors contributed equally to this work.

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 wide-ranging 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 charac-

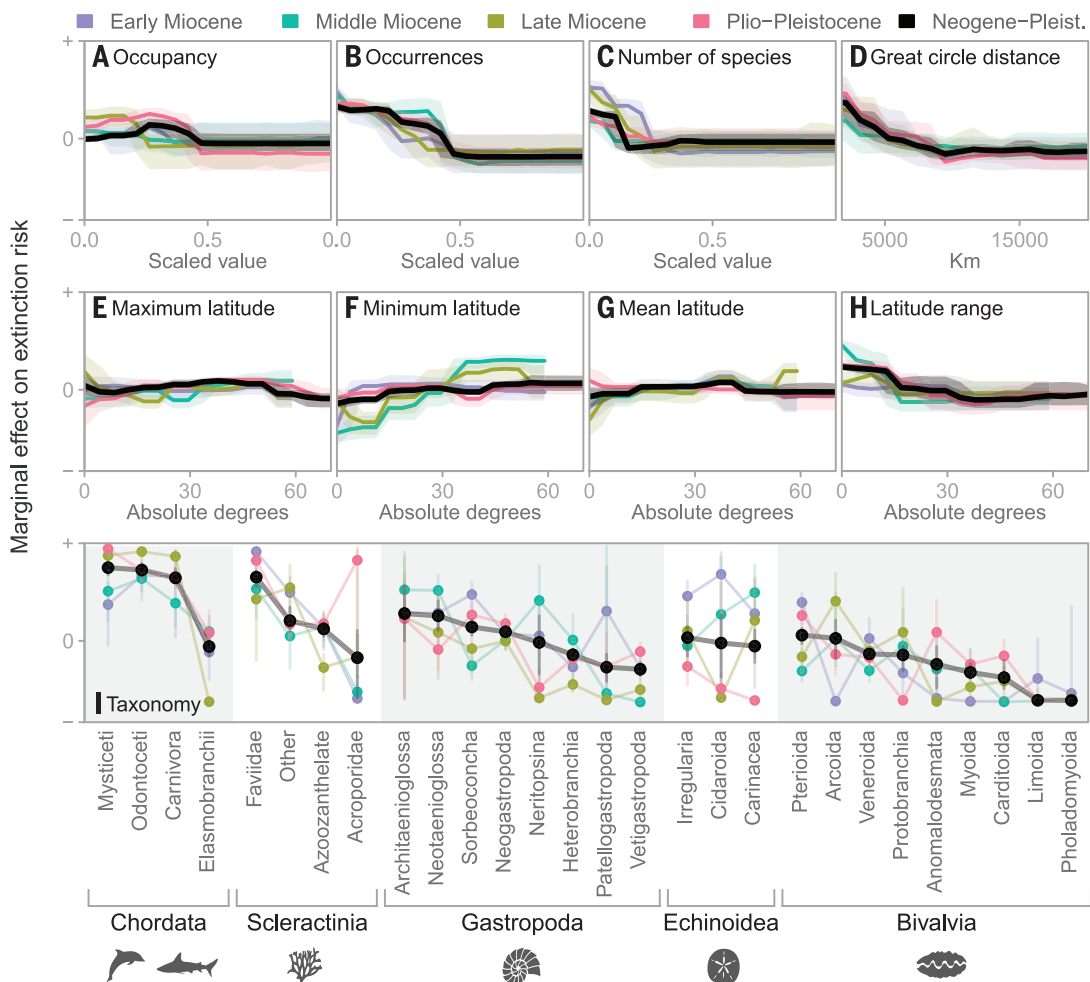
teristics are not systematically distorted by the vagaries of fossil preservation [fig. S2 (30)]. To represent taxonomic identity and its correlates, we included membership in taxonomic subgroups of ordinal to familial rank as predictors [Fig. 1 (30)].

We used generalized boosted regression models (GBMs), which perform well when relationships between predictor and response variables are nonlinear (31), 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% ($\pm 1\%$) of cases (table S3) (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

Fig. 1. Predictors of extinction risk in the marine fossil record. (A to I) Panels show scaled marginal influence of predictors on genus extinction risk for subinterval models and a model based on the entire Neogene-Pleistocene (lines: median; shaded regions: 80% confidence interval). y-axis values above 0 indicate a tendency for genera with a given predictor value to go extinct, and values below 0 indicate a tendency to survive. Occupancy, occurrences, and number of species per genus were log transformed and rescaled within each subinterval to reduce the effects of differential sampling intensity.



realms (36) [fig. S7 (30)]. 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 distribu-

tions 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

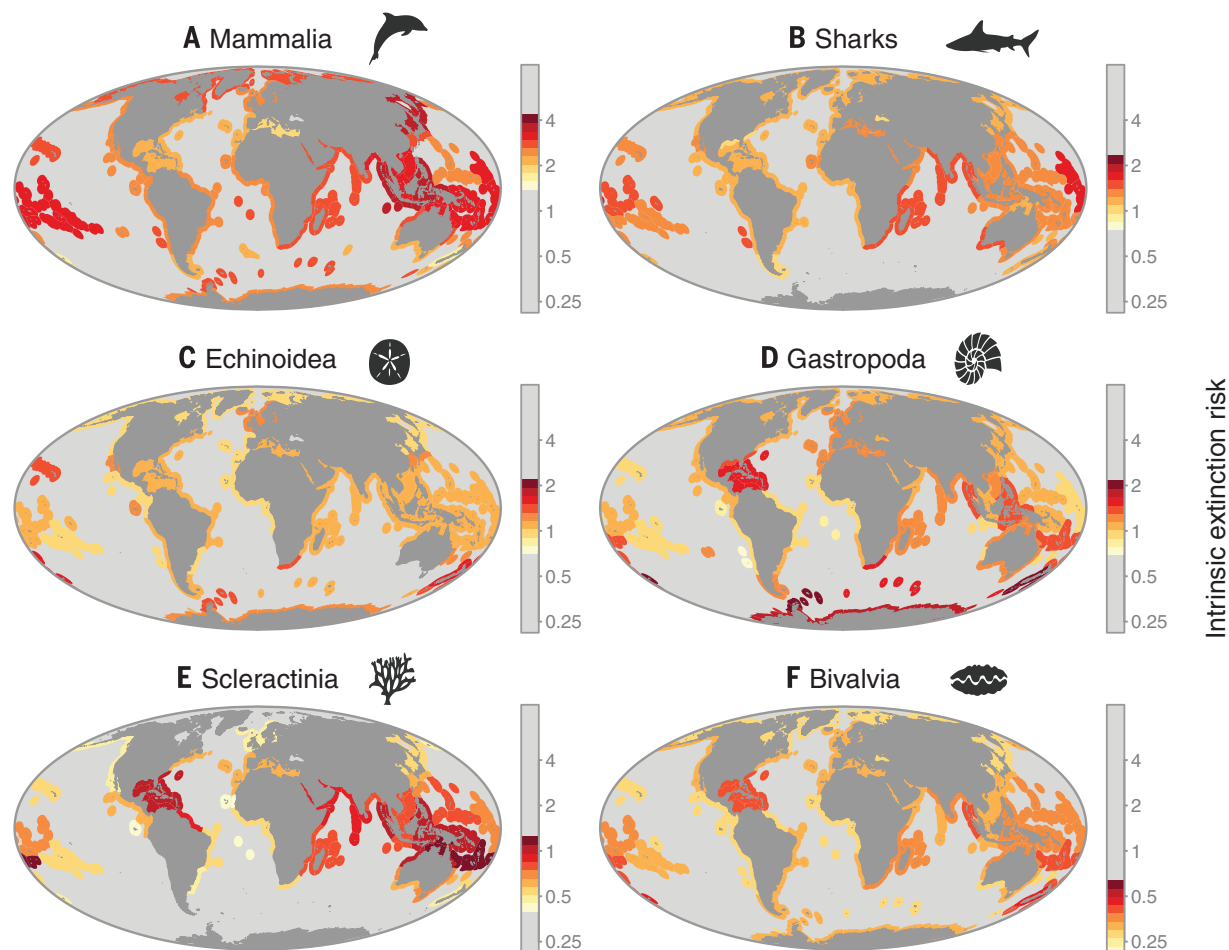


Fig. 2. Geographic distribution of mean intrinsic risk for present-day genera across coastal biogeographic provinces for six major taxonomic groups. (A to F) Scale bars indicate mean intrinsic risk as a multiple of the geometric mean across all groups. Color scales indicate a fixed threefold range of intrinsic risk centered on the geometric mean risk for a given group.

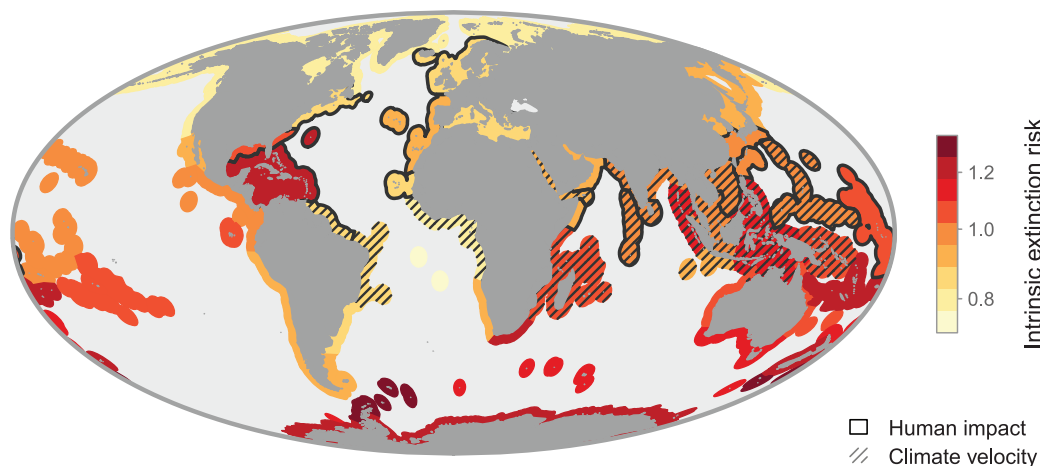


Fig. 3. Hotspots of human impact and velocity of climate change overlaid on mean intrinsic risk. Colored regions indicate mean intrinsic extinction risk of all genera that occur in a given province as a multiple of the geometric mean risk across all provinces. Outlined and hatched provinces indicate areas above the 80th percentile for mean human impact (2) and velocity of climate change (1), respectively.

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 endemism 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 overinterpreting 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 geographically 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 broad-scale geographic patterns of intrinsic risk remain after accounting for this relationship (fig. S15). Omitting all genera sampled in only a single province reduces the number of modern genera by 14% but likewise does not substantially alter broad-scale mean intrinsic risk patterns (fig. S16). Omitting the bounding-box interpolation procedure results in greater heterogeneity among adjacent provinces but also does not change the broad-scale regional differences (fig. S17). Genera with very few occurrences necessarily have limited geographic ranges, but genera with three or more occurrences exhibit the full range of great circle distances (fig. S18). Raising the minimum number of occurrences required for including a genus in the modern data set has relatively little effect on differences in intrinsic risk across provinces (figs. S19 and S20). In the fossil calibration data, marginal effects of predictor variables on extinction risk are relatively stable even when poorly preserved genera are excluded (figs. S21 to S24). Thus, per-genus and inter-provincial intrinsic risk patterns are generally conserved when a variety of culls are applied to the fossil data to address potential biases arising from incomplete sampling (figs. S25 and S26).

The preceding analyses suggest that the broad-scale intrinsic risk patterns that we report are unlikely to be artifacts of sampling heterogeneity or our modeling approach, but rather reflect the expected distribution of extinction risk if the extinction risk patterns of the past 23 million years are projected onto modern fauna. Our intrinsic risk predictions can thus be used as a baseline for determining which genera would be most

at risk, and which regions would face the greatest losses, under a prehuman extinction regime. Human activity is increasingly altering the structure and function of marine ecosystems (3), and the degree to which future extinction patterns will resemble those of the past depends on how contemporary stresses and intrinsic risk interact.

To delineate the geographic distribution of potential interactions, we compared the mean intrinsic risk of genera in each province with assessments of anthropogenic impact (2) and velocity of climate change (1) (Fig. 3 and fig. S27). Provinces characterized by the coincidence of high intrinsic risk and rapid climate shifts or elevated human impacts are located primarily in the tropics and subtropics (Fig. 3). Extratropical provinces in the Northern Hemisphere are characterized by low mean intrinsic risk and variable but often high human impact, whereas extratropical provinces in the Southern Hemisphere tend to combine high mean intrinsic risk and comparatively low current threats (Fig. 3).

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 dwarf 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 (77). Examining differences in the evolutionary lability 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 where exceptionally complete fossil records coincide with detailed modern censuses of marine populations. 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

1. M. T. Burrows *et al.*, *Science* **334**, 652–655 (2011).
2. B. S. Halpern *et al.*, *Science* **319**, 948–952 (2008).
3. J. B. C. Jackson, *Proc. Natl. Acad. Sci. U.S.A.* **105** (suppl. 1), 11458–11465 (2008).
4. J. M. Pandolfi, S. R. Connolly, D. J. Marshall, A. L. Cohen, *Science* **333**, 418–422 (2011).
5. P. G. Harnik *et al.*, *Trends Ecol. Evol.* **27**, 608–617 (2012).
6. L. McClenachan, A. B. Cooper, K. E. Carpenter, N. K. Dulvy, *Conserv. Lett.* **5**, 73–80 (2012).
7. T. P. Hughes *et al.*, *Science* **301**, 929–933 (2003).
8. N. Dulvy, Y. Sadovy, J. Reynolds, *Fish Fish.* **4**, 25–64 (2003).
9. T. J. Webb, B. L. Mindel, *Curr. Biol.* **25**, 506–511 (2015).
10. D. J. McCauley *et al.*, *Science* **347**, 1255641 (2015).
11. K. E. Jones, A. Purvis, J. L. Gittleman, *Am. Nat.* **161**, 601–614 (2003).
12. M. Cardillo, G. M. Mace, J. L. Gittleman, A. Purvis, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 4157–4161 (2006).
13. I. P. Owens, P. M. Bennett, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 12144–12148 (2000).
14. C. M. Roberts *et al.*, *Science* **295**, 1280–1284 (2002).
15. V. Parravicini *et al.*, *Ecol. Lett.* **17**, 1101–1110 (2014).
16. N. K. Dulvy *et al.*, *eLife* **3**, e00590 (2014).
17. A. D. Davidson *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 3395–3400 (2012).
18. J. S. Clark *et al.*, *Science* **293**, 657–660 (2001).
19. L. Bromham, R. Lanfear, P. Cassey, G. Gibb, M. Cardillo, *Proc. Biol. Sci.* **279**, 4024–4032 (2012).
20. N. K. Dulvy, J. K. Pinnegar, J. D. Reynolds, *Holocene Extinctions*, S. T. Turvey, Ed. (Oxford Univ. Press, Oxford, 2009), pp. 129–150.
21. A. B. Ronov, *Int. Geol. Rev.* **24**, 1365–1388 (1982).
22. S. E. Peters, *J. Geol.* **114**, 391–412 (2006).
23. J. Alroy *et al.*, *Science* **321**, 97–100 (2008).
24. D. P. Tittensor *et al.*, *Nature* **466**, 1098–1101 (2010).
25. J. W. Valentine, D. Jablonski, A. Z. Krug, K. Roy, *Paleobiology* **34**, 169–178 (2008).
26. M. Foote, J. S. Crampton, A. G. Beu, R. A. Cooper, *Paleobiology* **34**, 421–433 (2008).
27. P. G. Harnik, C. Simpson, J. L. Payne, *Proc. Biol. Sci.* **279**, 4969–4976 (2012).
28. S. C. Wang, A. M. Bush, *Paleobiology* **34**, 434–455 (2008).
29. A. Purvis, J. L. Gittleman, T. M. Brooks, *Phylogeny and Conservation* (Cambridge Univ. Press, Cambridge, 2005).
30. See supplementary materials and methods on Science Online.
31. J. Elith, J. R. Leathwick, T. Hastie, *J. Anim. Ecol.* **77**, 802–813 (2008).
32. OBIS, Data from the Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. <http://www.iobis.org> (consulted on 12 September 2012).
33. L. O. Lucifora, V. B. Garcia, B. Worm, *PLOS ONE* **6**, e19356 (2011).
34. J. Schipper *et al.*, *Science* **322**, 225–230 (2008).
35. C. L. Belanger *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 14046–14051 (2012).
36. M. D. Spalding *et al.*, *Bioscience* **57**, 573 (2007).
37. C. Mora, D. R. Robertson, *Ecology* **86**, 1771–1782 (2005).
38. W. Renema *et al.*, *Science* **321**, 654–657 (2008).
39. A. Clarke, *J. Exp. Mar. Biol. Ecol.* **366**, 48–55 (2008).
40. K. Linse, H. J. Griffiths, D. K. Barnes, A. Clarke, *Deep Sea Res. Part II Top. Stud. Oceanogr.* **53**, 985–1008 (2006).
41. M. Lyle, S. Gibbs, T. C. Moore, D. K. Rea, *Geology* **35**, 691 (2007).
42. J. W. Valentine, D. Jablonski, A. Z. Krug, S. K. Berke, *Paleobiology* **39**, 1–20 (2012).
43. D. A. Villena, A. B. Smith, *PLOS ONE* **8**, e74470 (2013).
44. D. F. Doak *et al.*, *Ecology* **89**, 952–961 (2008).

ACKNOWLEDGMENTS

This work is a product of the Determinants of Extinction in Ancient and Modern Seas Working Group supported by the National Evolutionary Synthesis Center (NSF grant EF-0905606). Additional support was provided by the Natural Sciences and Engineering Research Council of Canada (to H.K.L., S.C.A., and Z.V.F.); the National System of Investigators of the National Secretariat for Science, Technology and Innovation of Panama (to A.O.); the Australian Research Council Centre of Excellence for Coral Reef Studies (to J.M.P.); and the Deutsche Forschungsgemeinschaft (grant KI 806/7-1 to C.S.). We thank the contributors to the Paleobiology Database and to OBIS. We also thank four anonymous reviewers for insightful comments that substantially improved the quality of the manuscript. This article is Paleobiology Database contribution no. 227. All scripts and data used to conduct analyses are available at <https://github.com/seananderson/paleobaselines>.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/348/6234/567/suppl/DC1
Materials and Methods
Figs. S1 to S27
Tables S1 to S3
References (45–75)

10 January 2015; accepted 23 March 2015
10.1126/science.aaa6635