

## EXTINCTION

# Avoiding ocean mass extinction from climate warming

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Global warming threatens marine biota with losses of unknown severity. Here, we quantify global and local extinction risks in the ocean across a range of climate futures on the basis of the ecophysiological limits of diverse animal species and calibration against the fossil record. With accelerating greenhouse gas emissions, species losses from warming and oxygen depletion alone become comparable to current direct human impacts within a century and culminate in a mass extinction rivaling those in Earth's past. Polar species are at highest risk of extinction, but local biological richness declines more in the tropics. Reversing greenhouse gas emissions trends would diminish extinction risks by more than 70%, preserving marine biodiversity accumulated over the past ~50 million years of evolutionary history.

**H**uman activities are altering the global climate, physically transforming habitats, and overexploiting ecosystems of land and sea (1, 2). As a result, rates of species extinction have risen above natural background levels (3, 4). Documented extinctions are largely confined to land, where industrial human impacts began earlier and remain more pervasive despite rapid growth in commercial fishing, marine pollution, and transport (5). Climate change may eventually eclipse direct local human threats by causing widespread habitat loss through changes in the thermal and chemical conditions that reach even the most remote biomes on Earth, including the deep and open ocean (6, 7). However, climate's impact on global biodiversity is challenging to observe, especially for undersampled marine environments (8), and common statistical models are difficult to validate, particularly as new climate conditions emerge (9–11).

The potential for substantial biodiversity loss is illustrated by the fossil record, where long-term diversification (12, 13) is punctuated by episodic extinctions of varying intensity (Fig. 1A and fig. S1A). The most extreme events, the “Big 5” mass extinctions, coincided with global environmental changes, although mechanisms driving biodiversity collapse remain uncertain (3). In the largest such event, the end-Permian “Great Dying,” loss of more than two-thirds of marine animal genera reduced biodiversity to near its minimum since animals first radiated (12–14). Similar environmental changes that occurred in the end-Permian, including rising temperatures and declining ocean O<sub>2</sub>, productivity, and pH, are now also underway in the Anthropocene (fig. S2; 6, 7, 14–17). Past mass extinctions provide the only empirical benchmarks for evaluating the severity and drivers of a “sixth mass extinction” (3, 18).

Here, we project global and local extinction risks for marine animals (as a percentage of species lost) on the basis of habitat loss from climate change using an ecophysiological model that predicted the severity and latitude pattern of the end-Permian extinction (17, 19). Multicentury climate and ocean conditions are simulated by a group of Earth system models that reproduce historical global warming trends (table S1; 6, 20) and project future climate changes under scenarios of high and low anthropogenic greenhouse gas emissions (Fig. 1C, inset; 6, 7, 21). Global marine biodiversity is represented through a set of >10<sup>4</sup> simulated animal species types (“ecophysio-types”; 17), defined by thermal and hypoxia tolerance traits (table S2 and fig. S3) that structure the current biogeography of diverse taxa (22–24). Model species are assigned traits with frequencies found in a global species data compilation (22), allowing predicted patterns and climatic changes in biological richness to be compared with and tested against richness observations.

Ocean habitability requires conditions to remain within a species' ecophysiological tolerances. Local O<sub>2</sub> must meet temperature-dependent metabolic demands for growth and ecological activity, imposing covarying upper temperature and lower O<sub>2</sub> limits (22, 23). A loss of aerobic habitat causes local species extirpation wherever ocean warming and O<sub>2</sub> loss drive the O<sub>2</sub> supply-to-demand ratio ( $\Phi$ ) below a species' critical threshold ( $\Phi_{crit}$ ) (17, 24, 25). Aerobic habitat losses of model species are comparable to those within the known geographic ranges of real species with corresponding traits (fig. S4). New habitat can also be gained at the cold edge of a species' range if temperatures there rise above its minimum tolerance (fig. S5; 25, 26).

Species are committed to global extinction if net habitat loss exceeds a critical fraction ( $V_{crit}$ ) beyond which a viable population cannot be sustained even if disappearance is gradual (i.e., the extinction debt) (27). This uncertain extinction threshold is varied around a central value that is calibrated by the end-Permian extinction (fig. S6; 17, 19). We also considered the widest possible range of species capacities to colonize new habitat, denoted 0 and 100% colonization (Fig. 1B; 19), using the median of these scenarios as our central extinction case.

As anthropogenic climate change accelerates, so too do projected species losses (fig. S7). The rate of these losses over time depends on the emissions scenario, which sets the pace of warming and ocean O<sub>2</sub> loss. By the latter half of this century, the divergent greenhouse gas emission scenarios will lead to markedly different climate trajectories and to growing disparities in the fraction of species lost globally (extinction) and locally (extirpation).

The eventual intensity of species losses for all emissions scenarios, climate models, and time periods is well predicted by the magnitude of global surface warming (Fig. 1, B and C). Total warming in turn is governed by cumulative emissions and varies across models with different climate sensitivities. For a given temperature change, extinction risk depends on the amount of O<sub>2</sub> lost ( $R^2 = 0.69$  to  $0.87$ , range across colonization scenarios), which also differs among models (fig. S8).

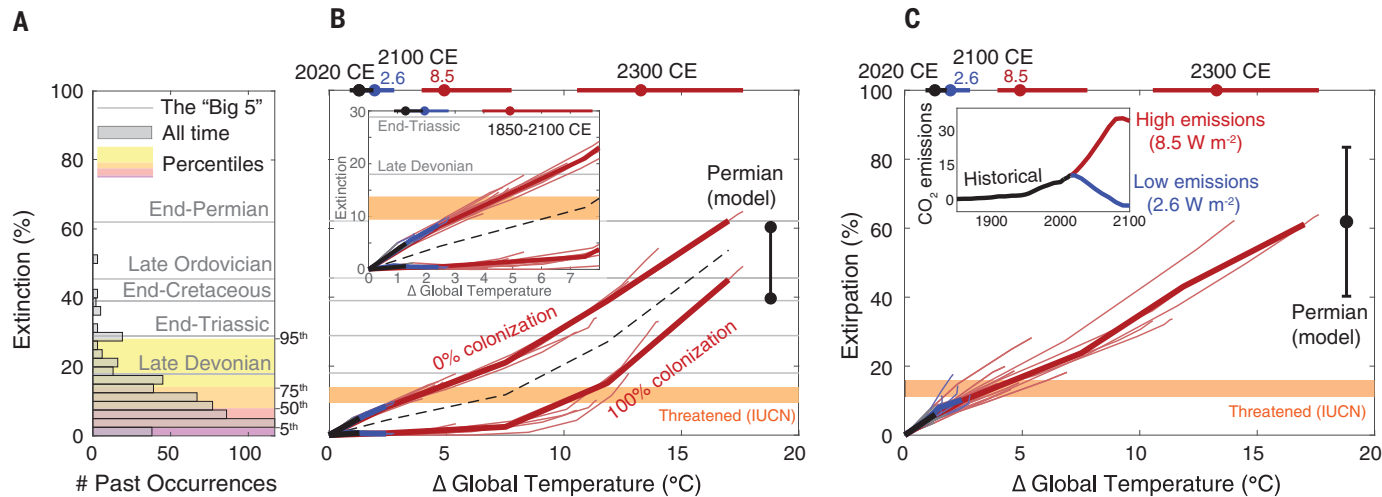
Under the low-emissions scenario, global temperature stops rising after  $\sim 1.9^\circ \pm 0.5^\circ\text{C}$  of warming [intermodel mean, SD; (6)] by the end of the century, and species losses remain close to current commitments (Fig. 1B, inset, and C). Under the high-emissions scenario, surface air warming could reach  $\sim 4.9^\circ \pm 1.4^\circ\text{C}$  by 2100 CE and  $\sim 10^\circ$  to  $18^\circ\text{C}$  over the next three centuries (6), markedly elevating losses (Fig. 1, B and C). Significant losses are also expected in another high-emissions scenario (SSP3-7.0), which yields  $8.2^\circ\text{C}$  of warming by 2300 CE ( $5.7^\circ$  to  $11.8^\circ\text{C}$ , 5 to 95% range) in a reduced-complexity model that does not simulate O<sub>2</sub> (6). Global extinction risk is higher if species cannot gain new habitat (Fig. 1B). Colonization of new regions at species' cold-edge range boundaries partially compensates for aerobic habitat loss (25) but eventually ceases to maintain habitat as warming intensifies.

We compared extinction risks from future climate change with those from current direct anthropogenic threats (fig. S9; 19) on the basis of vulnerability assessments from the International Union for Conservation of Nature (IUCN; 28). Future species losses from warming would become comparable to the sum of all anthropogenic stressors at the end of this century (Fig. 1B, inset, and C).

Under the high-emissions scenario, global extinction risks from continued warming eventually rival the severity of past mass extinctions in the fossil record and in paleosimulations

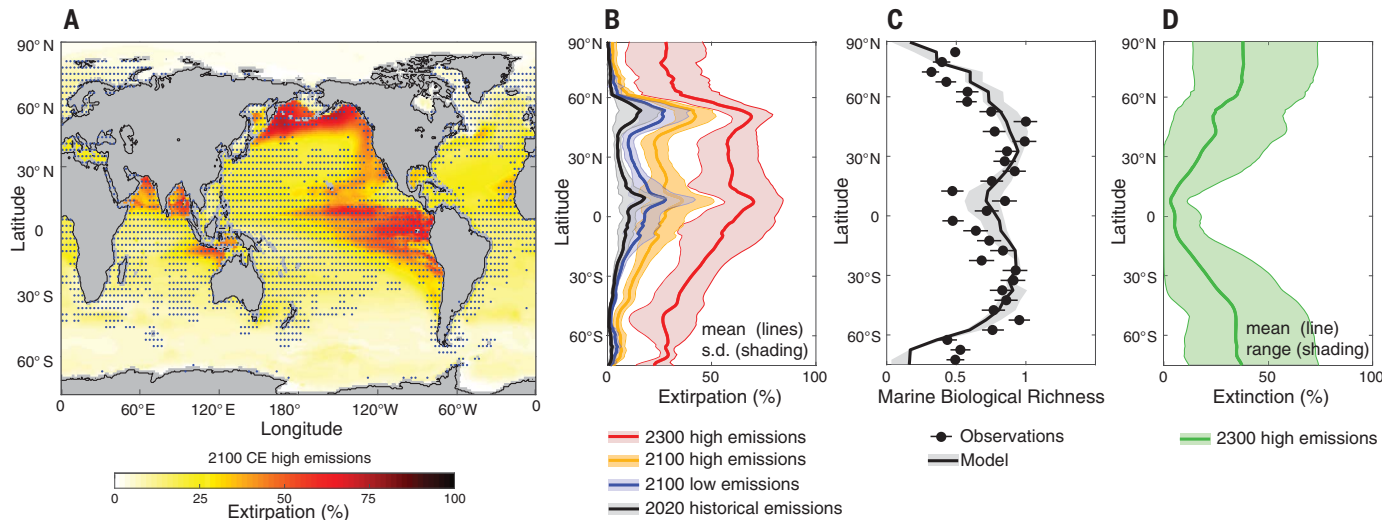
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**Fig. 1. Marine extinctions in the past and risk from climate warming.** (A) Extinction intensity (percent losses) from the fossil record of marine animal genera over the past ~542 million years (12), including the “Big 5” mass extinctions (35) (fig. S1A). (B and C) Projected global extinction (B) and global mean extirpation risks (averaged over 1° latitude × longitude, 0 to 500 m) (C) rise with increases in annual mean global surface air temperature (thick lines are intermodel averages; thin lines are individual Earth system models) and are plotted under historical greenhouse gas emissions (petagrams of carbon per year) and divergent future scenarios [(C), inset], yielding radiative forcings of 2.6 W/m<sup>2</sup> [i.e., RCP/SSP1-2.6; (6, 19, 21)] versus

8.5 W/m<sup>2</sup> in 2100 [i.e., RCP/SSP5-8.5; (6, 19, 21)]. Inset in (B) zooms in to show end of the century changes. Percent colonization refers to the fraction of new habitat that a species can instantly disperse to and inhabit (thin dashed line is the median case). Extinction risks from current anthropogenic threats are estimated from IUCN vulnerability assessments (orange bars; tables S3 and S4; 19). Simulated end-Permian extinction risks are shown across colonization scenarios in (B) and in (C) display the global mean and spatial SD of extirpation. Points and horizontal lines on the top axis show the average and range of warming across Earth system models evaluated here, respectively, for different time horizons and emissions scenarios.



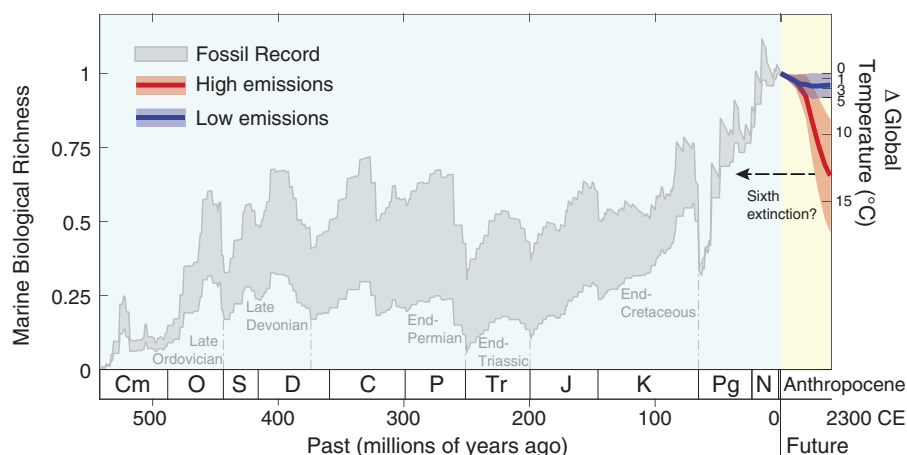
**Fig. 2. Spatial variation in species losses and marine biological richness.** (A) By 2100, regions of strong extirpations overlap past productive fisheries (blue points), where catch rates exceed the global median from 1950 to 2014 (36). (B to D) Patterns of extirpation risk (B), marine biological richness (C), and global extinction risk [(D); averaged across colonization scenarios] are shown versus latitude. Observed biological richness (number of species) estimated

using rarefaction (31) is reproduced by the trait-based habitat model applied to climatological distributions of temperature and O<sub>2</sub> (37, 38) across a range of maximum summation depths [(C) line is 500 m; shading is 0 and 5000 m; (19)]. Richness is normalized to the maximum observation. Extirpation and global extinction risks are averaged from 0 to 500 m, across Earth system models, and across longitude in (B) and (D).

(Fig. 1B). A mass extinction in this emissions scenario is projected across all potential values of the extinction threshold except in the unlikely case that the average species can maintain a viable population in <10% of their initial habitat volume (fig. S10; 19). By contrast, limiting warming to 2°C would cut the severity of extinctions by >70%, avoiding a

marine mass extinction across all extinction thresholds. Climate-driven species losses vary widely among ocean biomes, with important implications for fisheries and the patterns of biological richness (Fig. 2). These spatial patterns also provide crucial observational tests of the underlying model.

Extirpation risk is greatest where climate anomalies are strong (fig. S2) or species are living close to their ecophysiological thresholds, typically equatorward near the warm and/or low-O<sub>2</sub> edges of their ranges (Fig. 2, A and B). Vulnerable regions include highly productive ecosystems where background O<sub>2</sub> is already low, such as the north Pacific, eastern boundary



**Fig. 3. Past and potential futures of marine biological richness.** The number of marine animal genera is plotted over time from the fossil record relative to present and projected into the future on the basis of model extinction risks, averaged (lines) and varying (SD, shadings) across Earth system models and colonization scenarios. The right axis shows the change in global mean temperature for a given richness loss. Vertical dashed lines denote the “Big 5” mass extinctions. The lower fossil curve is based on Sepkoski’s *Compendium of Fossil Marine Animal Genera* (12), and the upper curve presents these data with the secular trend found in the Paleobiology Database (<https://paleobiology.org>) (fig. S12; 13). Letters indicate major stratigraphic intervals plus the current Anthropocene. Time scale differs for past and future (see fig. S1B for both plotted on the same scale).

upwelling systems, and the tropical Indo-Pacific (Fig. 2A). These regions are also home to many of the world’s most productive fisheries, which supply ~17% of humanity’s dietary protein (29). The spatial pattern of extirpation is relatively stable over time, but its magnitude steadily rises with warming (Fig. 2B). Low extirpation intensities are predicted to be evident at low and northern midlatitudes already (Fig. 2B) and may underlie the previously documented range shifts observed there (24–26, 30). Earth system models may under-represent both small-scale spatial refugia as well as short-term heat waves and related extreme events. Although these phenomena will undoubtedly modulate local impacts on some species, they are unlikely to override the broader biotic outcome from the persistent large-scale and long-term climate trends presented here.

The latitudes of strong fractional species extirpation also overlap regions of peak biological richness (Fig. 2, B and C). The number of observed marine animal species increases from the poles toward the tropics, with a reduction near the equator (31–33). The model reproduces this pattern: As temperatures rise above species’ minimum tolerances, richness increases from the poles to the tropics but decreases approaching the equator, where species reach their temperature-dependent hypoxia limits.

In contrast to local extinctions, global extinction risk is greater for polar species than for tropical ones, threatening higher-latitude richness where extirpation is weaker (Fig. 2, C and D). Species initially inhabiting the tropics can tolerate warm, low- $O_2$  waters, making them resilient to the climatic expansion of those conditions, especially for species with

high colonization ability (fig. S11). By contrast, polar species occupy a disappearing climate niche and lack habitat refugia as the climate warms. This latitudinal extinction pattern has been detected in the fossil record of the end-Permian extinction (17, 34), supporting the mechanistic basis for model projections.

The projected impact of accelerating climate change on marine biota is profound, driving extinction risk higher and marine biological richness lower than has been seen in Earth’s history for the past tens of millions of years (Fig. 3 and fig. S1). Additional climate-related threats beyond warming and  $O_2$  loss, including ocean acidification and declining primary productivity, have the potential to amplify these losses even further (6, 7, 18). However, it is not too late to enact the reductions in greenhouse gas emissions needed to avoid a major extinction event. The low-emissions scenario assumes that declines began around 2020 CE and continue thereafter (Fig. 1C, inset). Coordinated efforts to slow the local impacts of overfishing and marine pollution demonstrate the high intrinsic and economic value of preserving marine biodiversity and living resources. Realizing the fruits of these conservation efforts depends on mounting complementary societal responses to avert the greater threat posed by climate change.

#### REFERENCES AND NOTES

1. S. Díaz *et al.*, *Science* **366**, eaax3100 (2019).
2. S. L. Maxwell, R. A. Fuller, T. M. Brooks, J. E. M. Watson, *Nature* **536**, 143–145 (2016).
3. A. D. Barnosky *et al.*, *Nature* **471**, 51–57 (2011).
4. G. Ceballos *et al.*, *Sci. Adv.* **1**, e1400253 (2015).
5. D. J. McCauley *et al.*, *Science* **347**, 1255641 (2015).
6. Intergovernmental Panel on Climate Change (IPCC), *Climate Change 2021: The Physical Science Basis. Contribution of Working*

- Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge Univ. Press, 2021).
7. L. Kwiatkowski *et al.*, *Biogeosciences* **17**, 3439–3470 (2020).
8. C. Mora, D. P. Tittensor, S. Adl, A. G. B. Simpson, B. Worm, *PLOS Biol.* **9**, e1001127 (2011).
9. W. W. L. Cheung *et al.*, *Fish Fish.* **10**, 235–251 (2009).
10. J. G. Molinos *et al.*, *Nat. Clim. Chang.* **6**, 83–88 (2016).
11. C. M. Beale, J. J. Lennon, A. Gimona, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 14908–14912 (2008).
12. R. A. Rohde, R. A. Muller, *Nature* **434**, 208–210 (2005).
13. J. Alroy *et al.*, *Science* **321**, 97–100 (2008).
14. J. L. Payne, M. E. Clapham, *Annu. Rev. Earth Planet. Sci.* **40**, 89–111 (2012).
15. H. Jurikova *et al.*, *Nat. Geosci.* **13**, 745–750 (2020).
16. S. E. Grasby, B. Beauchamp, J. Kries, *Geology* **44**, 779–782 (2016).
17. J. L. Penn, C. Deutsch, J. L. Payne, E. A. Sperling, *Science* **362**, eaat1327 (2018).
18. J. L. Payne, A. M. Bush, N. A. Heim, M. L. Knope, D. J. McCauley, *Science* **353**, 1284–1286 (2016).
19. Materials and methods are available as supplementary materials.
20. S. M. Papalexiou, C. R. Rajulapati, M. P. Clark, F. Lehner, *Earth’s Futur.* **8**, e2020EF001667 (2020).
21. B. C. O’Neill *et al.*, *Geosci. Model Dev.* **9**, 3461–3482 (2016).
22. C. Deutsch, J. L. Penn, B. Seibel, *Nature* **585**, 557–562 (2020).
23. C. Deutsch, A. Ferrel, B. Seibel, H. O. Pörtner, R. B. Huey, *Science* **348**, 1132–1135 (2015).
24. E. M. Howard *et al.*, *Sci. Adv.* **6**, eaay3188 (2020).
25. M. L. Pinsky, R. L. Selden, Z. J. Kitchel, *Ann. Rev. Mar. Sci.* **12**, 153–179 (2020).
26. J. M. Sunday, A. E. Bates, N. K. Dulvy, *Nat. Clim. Chang.* **2**, 686–690 (2012).
27. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, *Nature* **371**, 65–66 (1994).
28. International Union for Conservation of Nature, “The IUCN Red List of Threatened Species, version 2019-3” (IUCN, 2019); <https://www.iucnredlist.org/>.
29. C. Costello *et al.*, *Nature* **588**, 95–100 (2020).
30. J. Lenoir *et al.*, *Nat. Ecol. Evol.* **4**, 1044–1059 (2020).
31. C. Chaudhary, H. Saedi, M. J. Costello, *Trends Ecol. Evol.* **32**, 234–237 (2017).
32. D. P. Tittensor *et al.*, *Nature* **466**, 1098–1101 (2010).
33. M. Yasuhara *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **117**, 12891–12896 (2020).
34. C. J. Reddin, Á. T. Kocsis, W. Kiessling, *Paleobiology* **45**, 70–84 (2019).
35. S. M. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* **113**, E6325–E6334 (2016).
36. D. Pauly, D. Zeller, “Sea Around Us concepts, design and data (2015); <http://www.seaaroundus.org/>.
37. R. A. Locarnini *et al.*, “World Ocean Atlas 2013, volume 1: Temperature” (NOAA, 2013); [https://www.ncei.noaa.gov/data/oceans/woa/WOA13/DOC/woa13\\_vol1.pdf](https://www.ncei.noaa.gov/data/oceans/woa/WOA13/DOC/woa13_vol1.pdf).
38. H. E. Garcia *et al.*, “World Ocean Atlas 2013, volume 3: Dissolved oxygen, apparent oxygen utilization, and oxygen saturation” (NOAA, 2014); [https://www.ncei.noaa.gov/data/oceans/woa/WOA13/DOC/woa13\\_vol3.pdf](https://www.ncei.noaa.gov/data/oceans/woa/WOA13/DOC/woa13_vol3.pdf).
39. Model output and code for: J. L. Penn, C. Deutsch, Avoiding ocean mass extinction from climate warming, Zenodo (2022); <https://doi.org/10.5281/zenodo.5899743>.

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#### SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.abe9039](https://science.org/doi/10.1126/science.abe9039)  
Materials and Methods  
Figs. S1 to S12  
Tables S1 to S5  
References (40, 41)  
MDAR Reproducibility Checklist

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