

# Using the Fossil Record to Understand Extinction Risk and Inform Marine Conservation in a Changing World

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## Keywords

conservation paleobiology, extinction, fossil record, climate change, human impact, marine conservation

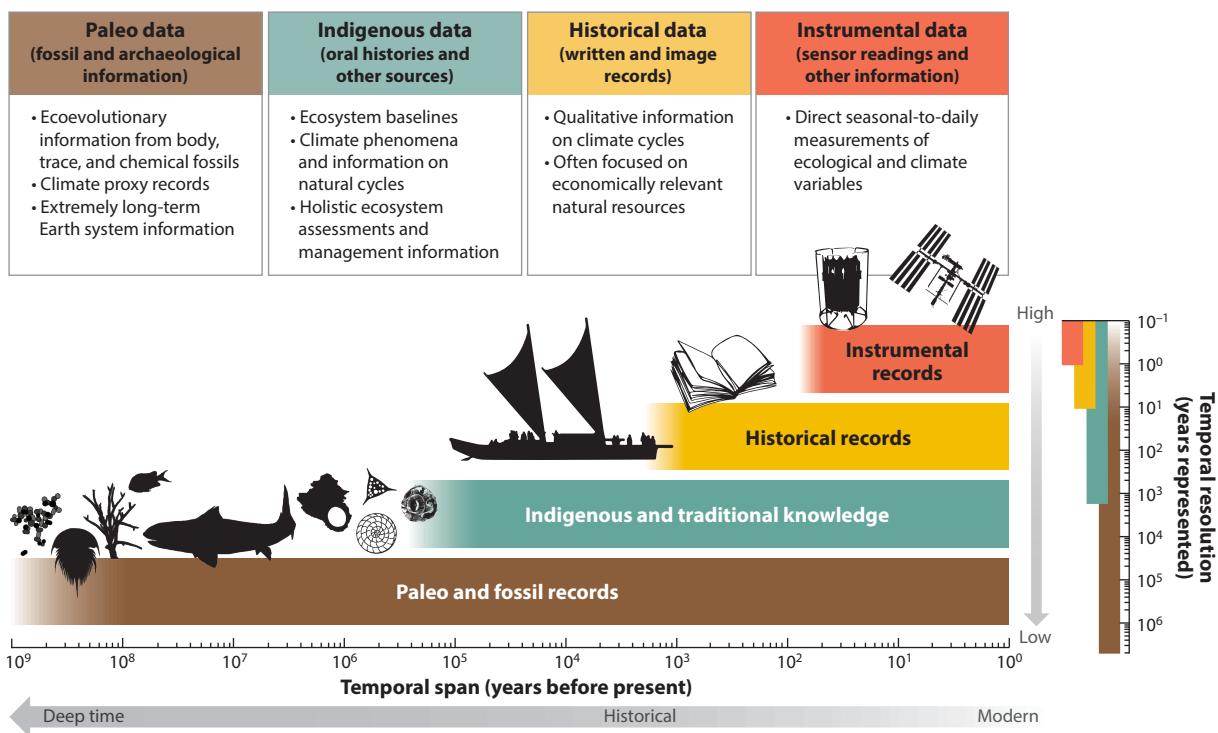
## Abstract

Understanding the long-term effects of ongoing global environmental change on marine ecosystems requires a cross-disciplinary approach. Deep-time and recent fossil records can contribute by identifying traits and environmental conditions associated with elevated extinction risk during analogous events in the geologic past and by providing baseline data that can be used to assess historical change and set management and restoration targets and benchmarks. Here, we review the ecological and environmental information available in the marine fossil record and discuss how these archives can be used to inform current extinction risk assessments as well as marine conservation strategies and decision-making at global to local scales. As we consider future research directions in deep-time and conservation

paleobiology, we emphasize the need for coproduced research that unites researchers, conservation practitioners, and policymakers with the communities for whom the impacts of climate and global change are most imminent.

## 1. INTRODUCTION AND GOALS

Ongoing climate and environmental changes are a shared social, political, and scientific challenge that requires collaboration across disciplines to fully understand and address short- and long-term consequences. The current changes are unprecedented in human experience and will unfold over thousands of years; thus, understanding their long-term consequences requires synthesizing data at many timescales, from short-term experimental manipulations to macroevolutionary patterns in deep time (Figure 1). The fossil record is particularly important for informing our understanding of extinction risk due to the paucity of observations on recent marine extinction events. While the



**Figure 1**

Sources of data necessary for understanding the long-term response of marine ecosystems to current and future global environmental change. A combination of diverse data sources allows reconstruction of biological and environmental time series that span a wide array of timescales and vary markedly in their resolution. Although some fossil data can be resolved as finely as subseasonally, most fossil records are appreciably coarser. Because of limitations in temporal resolution and span inherent in each of these sources of data, integrative approaches have the greatest potential to provide long-term quantitative, qualitative, and holistic records of ecosystem states from deep time through the present day. Organism silhouettes obtained from PhyloPic (<https://phylopic.org>) (Public Domain Mark 1.0/CC0 1.0/CC BY 3.0/CC BY 4.0/CC BY-SA 3.0), including images created by James St. John and T. Michael Keesey (Anthozoa), Matt Crook (diatoms), Ben Moon (Foraminifera), and Richard Lampitt and Jeremy Young/NHM (vectorization by Yan Wong) (Haptophyta). This figure is licensed under a Creative Commons Attribution-ShareAlike 4.0 International (CC BY-SA 4.0) license.

majority of species that have ever lived are now extinct, only approximately 20 historical global marine extinction events are known, although there have been many regional extirpations (Dulvy et al. 2009, Harnik et al. 2012a). Beyond providing insight into extinction processes, the fossil record can be a valuable source of information about the historical ranges and abundance of extant species as well as ecosystem structure and function under environmental conditions different from those of the present (i.e., no-analog systems), including those expected in a warmer future.

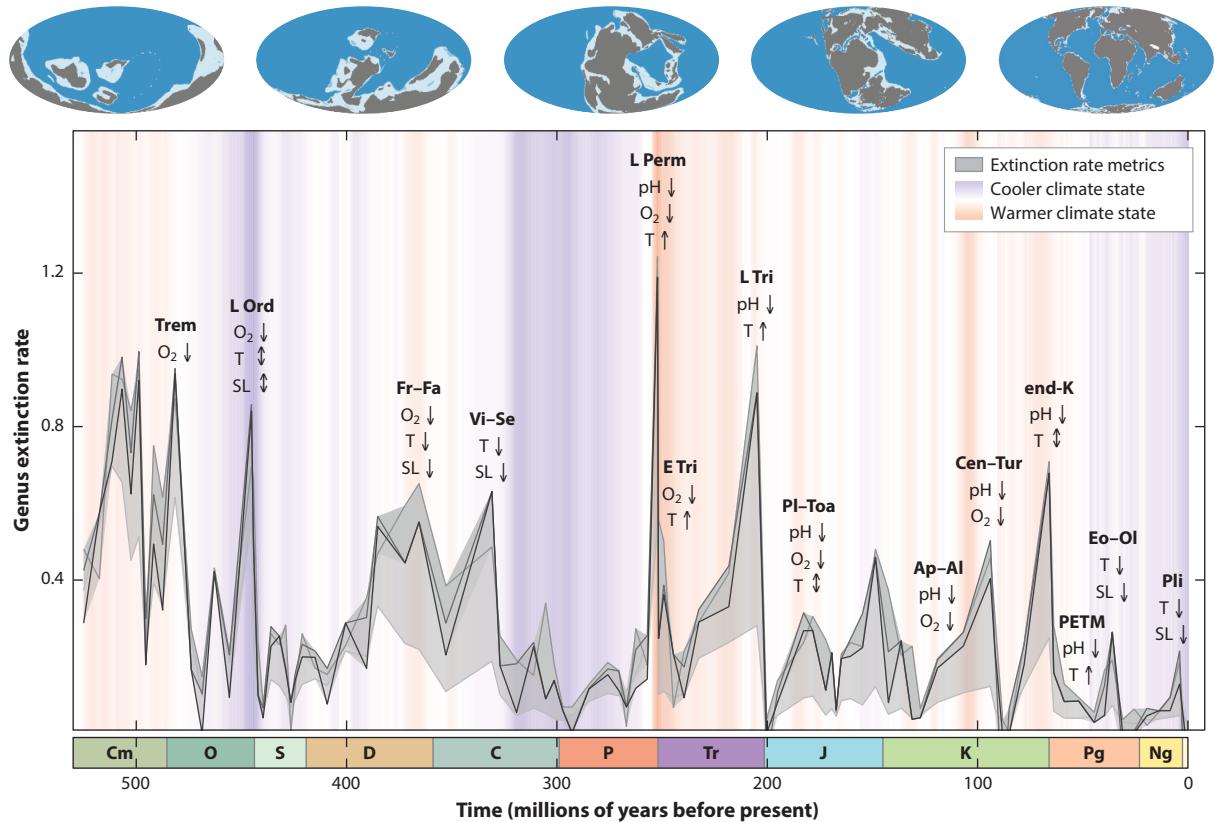
The aim of this review is to provide marine scientists, conservation practitioners, and managers a comprehensive overview of the information we can derive from the marine fossil record and the major lessons it can teach us about past extinction events that can inform our understanding of present and future marine ecosystems (Section 2). We highlight how paleontological data can be used to inform extinction risk assessments as well as marine conservation strategies and decision-making at global to local scales (Section 3). Lastly, we discuss avenues for further research in the growing field of conservation paleobiology (Section 4). In doing so, we hope to encourage more, and deeper, collaborations between modern biologists and paleobiologists to promote the cross-disciplinary understanding of marine ecosystems required to meet the challenges of the present and those in the future.

## 2. INFORMATION AVAILABLE IN THE MARINE FOSSIL RECORD

The term fossil carries a connotation of antiquity, but in the broadest sense fossils are simply the enduring remains of once-living organisms. It is a common misconception that fossils are always altered; many marine organisms produce shells and bones that may be preserved with their primary mineralogy, and sometimes even with primary organic compounds, for tens to hundreds of millions of years (Kidwell & Holland 2002). Here, we use the term fossil to refer to any organismal remains with the potential for long-term preservation, regardless of age. Both ancient and recent fossils are relevant for our purposes: The deep-time fossil record extends back hundreds of millions of years and provides insight into past environmental changes and extinctions (Figure 2), while many studies in the growing fields of conservation paleobiology and historical ecology use death assemblages (DAs) of organisms that lived within the past few hundred or thousand years to track historical changes and contextualize modern ecosystems (Dietl et al. 2015, Harnik et al. 2012a, Lotze & McClenahan 2014).

Fossilization is often thought of as a rare event, and the probability of any given individual being fossilized is low, but preservation probabilities vary considerably across taxa and environments. For mineralizing organisms that occur in marine shelf and slope environments where sedimentation rates are highest, the percentage of species that preserve as fossils can be high (Kidwell 2013). For example, 80% of bivalve and gastropod species currently known to exist in southern California and northern Baja California are also known from the region's Pleistocene fossil record (Valentine 1989). Globally, 76% of living marine bivalve genera and subgenera (Valentine et al. 2006) and more than 50% of extant elasmobranch genera (Paillard et al. 2021) are known from the fossil record. In general, mollusks and other well-skeletonized benthic invertebrates (such as corals and brachiopods) and pelagic biomimicry (such as foraminifera, coccolithophorids, diatoms, and radiolarians) have the most complete records (Lloyd et al. 2012, Payne & Heim 2020) (Figures 3 and 4). Fossils have been recovered from around the world (Figure 4), and spatiotemporal information about these occurrences are increasingly available electronically through international database efforts such as the Paleobiology Database (<https://paleobiodb.org>), Neptune (<https://nsb.mfn-berlin.de>), and Neotoma (<https://www.neotomadb.org>).

Recently dead material can be preserved in surficial sediment on the seafloor for decades to centuries (Kidwell 2013), and sediment cores can extend these records back over millennia.

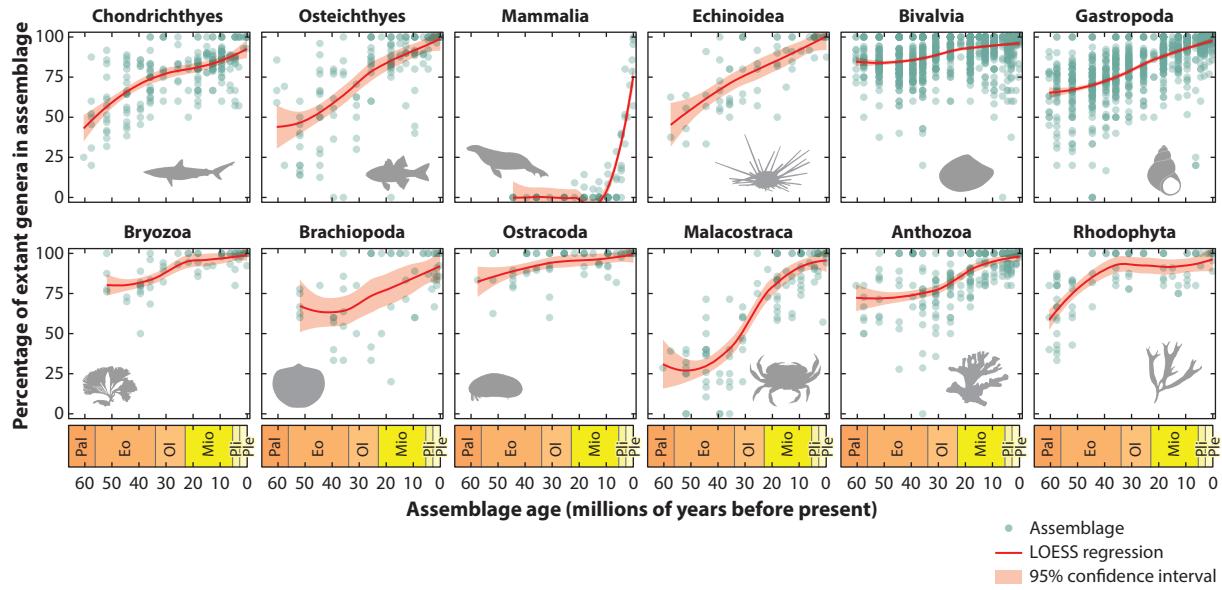


**Figure 2**

Extinction rates of marine animal and protist genera through geologic time. Gray lines and areas represent four different rate metrics (Kocsis et al. 2019) applied to occurrences in the Paleobiology Database (<https://paleobiodb.org>). Modern extinction rate estimates are not shown because comparing rates estimated at very different observational timescales is inherently problematic (Spalding & Hull 2021). Background colors indicate long-term mean climate state (Scotese et al. 2021). Paleogeographic maps at representative intervals (Scotese & Wright 2018) are shown at the top. Major and some minor extinction events are indicated along with associated changes in temperature (T), oxygenation (O<sub>2</sub>), acidification (pH), and shallow marine habitat due to sea level change (SL). Extinction event abbreviations: Trem, Tremadocian; L Ord, Late Ordovician; Fr-Fa, Frasnian–Famennian; Vi-Se, Viséan–Serpukhovian; L Perm, Late Permian; E Tri, Early Triassic; L Tri, Late Triassic; PI-Toa, Pliensbachian–Toarcian; Ap-Al, Aptian–Albian; Cen-Tur, Cenomanian–Turonian; end-K, Cretaceous–Paleogene; PETM, Paleocene–Eocene Thermal Maximum; Eo-OI, Eocene–Oligocene; Pli, Pliocene. Geologic period abbreviations: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene. For further description of data processing and analyses, see the **Supplemental Material**.

**Supplemental Material >**

Time averaging of fossils (i.e., mixing together of individuals that lived at different times) occurs because skeletal remains accumulate and can remain near the sediment–water interface for hundreds to thousands of years. Scales of time averaging vary from years in areas of high sedimentation and low biotic or physical disturbance to millennia in areas of low sedimentation or increased disturbance (Kidwell 2013). Time averaging can be measured by direct dating of skeletal remains via <sup>14</sup>C or amino acid racemization. Although surface assemblages of marine fossils commonly include individuals that lived long before the sampling event, the DA is typically dominated by recently dead individuals (Kidwell 2013). While time averaging has the potential to distort species abundance and limit temporal resolution, it can also be beneficial in some contexts. Time-averaged marine DAs can provide a more accurate census of the living community than live



**Figure 3**

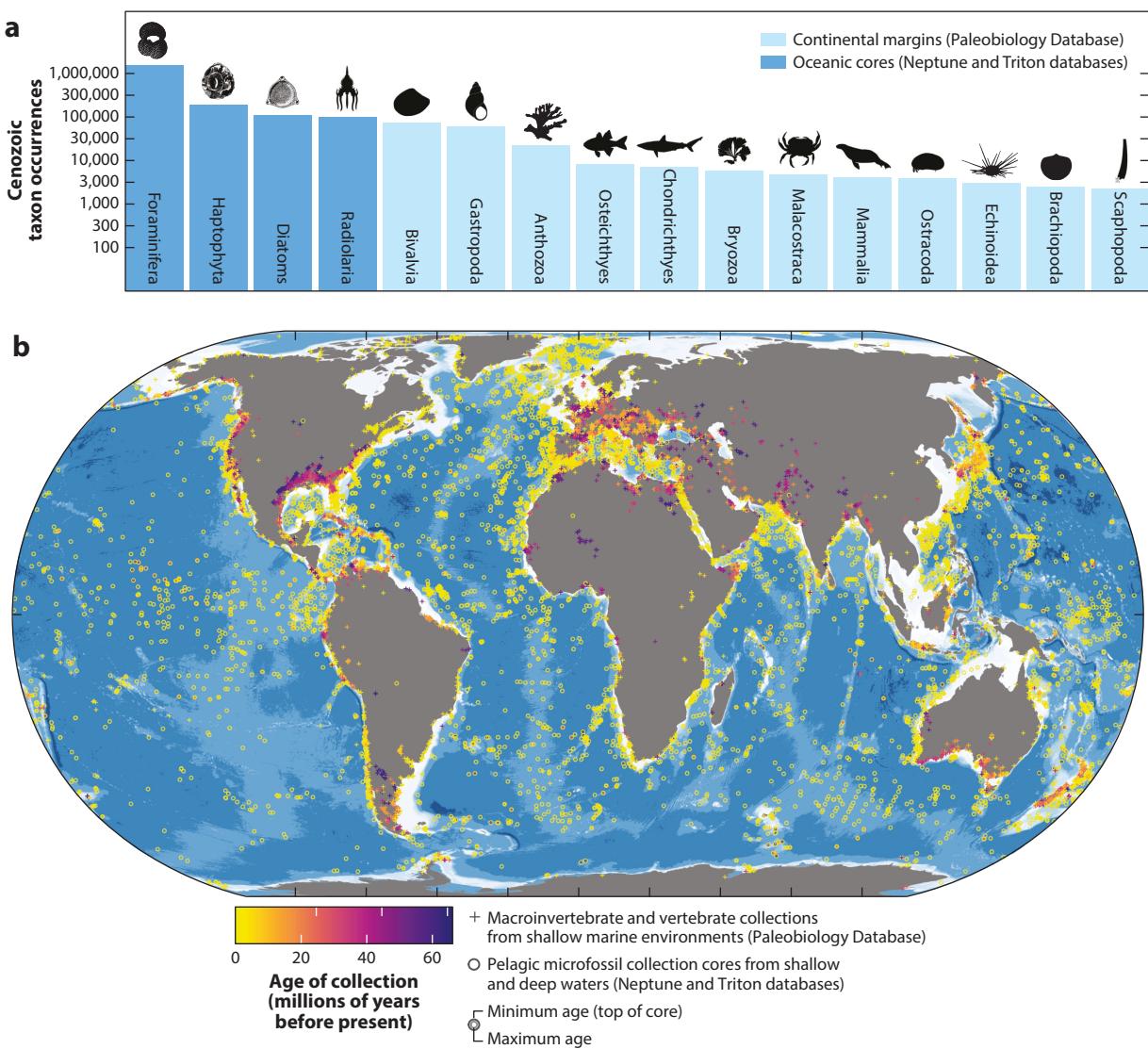
Percentages of genera in Cenozoic fossil assemblages that are still extant today. Each point represents an assemblage from a stratigraphic unit (formation or member) containing occurrences for five or more genera in the Paleobiology Database (<https://paleobiodb.org>). The figure is restricted to select groups with relatively high preservation potential. Red lines and shaded areas are LOESS (locally estimated scatterplot smoothing) regressions and 95% confidence intervals. The rate at which the percentage of extant genera declines in progressively older assemblages is primarily a function of extinction rate. Geologic epoch abbreviations: Pal, Paleocene; Eo, Eocene; Ol, Oligocene; Mio, Miocene; Pli, Pliocene; Ple, Pleistocene. For further description of data processing and analyses, see the **Supplemental Material**. Organism silhouettes obtained from PhyloPic (<https://phylopic.org>) (CC0 1.0/CC BY 3.0/CC BY-SA 3.0), including images created by Noah Schlottman (from a photo by Hans De Blauwe) (Bryozoa), Didier Descouens (vectorization by T. Michael Keesey) (Echinoidea), Maxime Dahirel (Ostracoda), Harold N. Eyster (Malacostraca), and Jakovche (Mammalia). This figure is licensed under a Creative Commons Attribution-ShareAlike 4.0 International (CC BY-SA 4.0) license.

collections, simply because they yield larger sample sizes and average out short-term variability and local patchiness (Tomašových & Kidwell 2009).

Recent and deep-time fossil records can provide a wealth of information on the biotic and abiotic factors that affect species extinction risk. A common misconception is that the only information that can be derived from the fossil record is the time period during which a particular taxon existed (i.e., the stratigraphic range between its oldest and youngest fossil occurrences). Although stratigraphic range data were the basis for early studies of extinction (Raup & Sepkoski 1982), modern paleontological studies incorporate many other types of data that are more comparable to those studied by marine biologists. Biotic information preserved in these records include presence, relative abundance, geographic distribution, body size, and traces of biotic interactions (Bottjer 2016). Data on abiotic factors, including temperature, salinity, oxygen levels, pH, nutrients, and contaminants, can commonly be reconstructed via geochemical, sedimentological, or paleontological proxies (Lotze et al. 2022, Peharda et al. 2021).

Geographic ranges and habitat breadths can be reconstructed from fossils with reasonable fidelity. The present-day geographic ranges of extant taxa are generally strongly correlated with their Pliocene-to-recent geographic ranges (Finnegan et al. 2015), and modeling studies indicate that the geographic ranges of many extinct taxa can be reliably estimated with fossil occurrence data (Darroch & Saupe 2018); the ranges of taxa that have low inherent preservation potential, or that inhabit environments poorly represented in the sedimentary record, will tend to be

**Supplemental Material** >



**Figure 4**

The (a) taxonomic composition and (b) geographic distribution of Cenozoic marine fossils (66 Ma to present) currently included in three international marine fossil databases. Blue bars indicate the number of documented fossil occurrences. Points indicate the locations of fossil collections, and the colors denote their ages. Crosses indicate macroinvertebrate and vertebrate collections, primarily from shallow marine environments (<200 m), as recorded in the Paleobiology Database (<https://paleobiodb.org>). Circles indicate pelagic microfossil collections in cores collected in shallow and deep water, as recorded in the Neptune (<https://nsb.mfn-berlin.de>) and Triton (Fenton et al. 2021) databases. Outer circle colors indicate minimum ages (top of core), and inner circle colors indicate maximum ages when available. Points on land indicate areas that were submerged during the Cenozoic. The density of points in wealthy, industrialized countries is primarily an artifact of historical sampling intensity, not the relative richness of the fossil record in these regions (Raja et al. 2022). Likewise, variation among groups in numbers of occurrences reflects differences in sampling effort and preservation as well as abundance and distribution. Note that the y axis of panel a is log scaled. For further description of data processing and analyses, see the **Supplemental Material**. Organism silhouettes obtained from PhyloPic (<https://phylopic.org>) (Public Domain Mark 1.0/CC0 1.0/CC BY 3.0/CC BY-SA 3.0), including images created by Noah Schlottman (from a photo by Hans De Blauwe) (Bryozoa), Didier Descouens (vectorization by T. Michael Keesey) (Echinoidea), Richard Lampitt and Jeremy Young/NHM (vectorization by Yan Wong) (Haptophyta), Maxime Dahirel (Ostracoda), Harold N. Eyster (Malacostraca), and Jakovche (Mammalia). This figure is licensed under a Creative Commons Attribution-ShareAlike 4.0 International (CC BY-SA 4.0) license.

underestimated. Likewise, habitat breadths can be estimated from the variety of depositional environments in which fossils of a given lineage occur. Wave and current energy, relative depth, and substrate type can be reconstructed from sedimentary deposits, but it is also possible to determine surface and bottom temperature, productivity, and dissolved oxygen concentration at the seafloor from geochemical and biological proxies (Hönisch et al. 2012, Veizer & Prokoph 2015). For fossils that grow by marginal accretion, aspects of the local environment such as temperature can be reconstructed at very high temporal resolution (e.g., annual to daily) using geochemical data (Peharda et al. 2021).

Relative abundance and taxonomic diversity trends are also reflected in fossil assemblages. Rank-order abundance patterns of mineralizing species are fairly well preserved in recent fossil assemblages, and when they disagree with abundances in the living community, this is often due to recent biotic change and not preservation bias (Kidwell 2007). Likewise, in the deep-time record, abundance patterns of calcifying taxa are not attributable to differences in mineralogy or durability, which potentially affect preservation (Behrensmeyer et al. 2005). Thanks to the recent development of inexpensive, high-throughput  $^{14}\text{C}$  dating methods, changes in abundance structure, especially in dominant taxa, can be tracked at higher resolution than the overall scale of time averaging (Tomašových et al. 2016). Spatial and environmental diversity gradients and their changes through time can also be assessed with fossils. Although skeletal material can be moved by waves and currents, out-of-habitat transport is generally rare and easily recognized (Kidwell 2008).

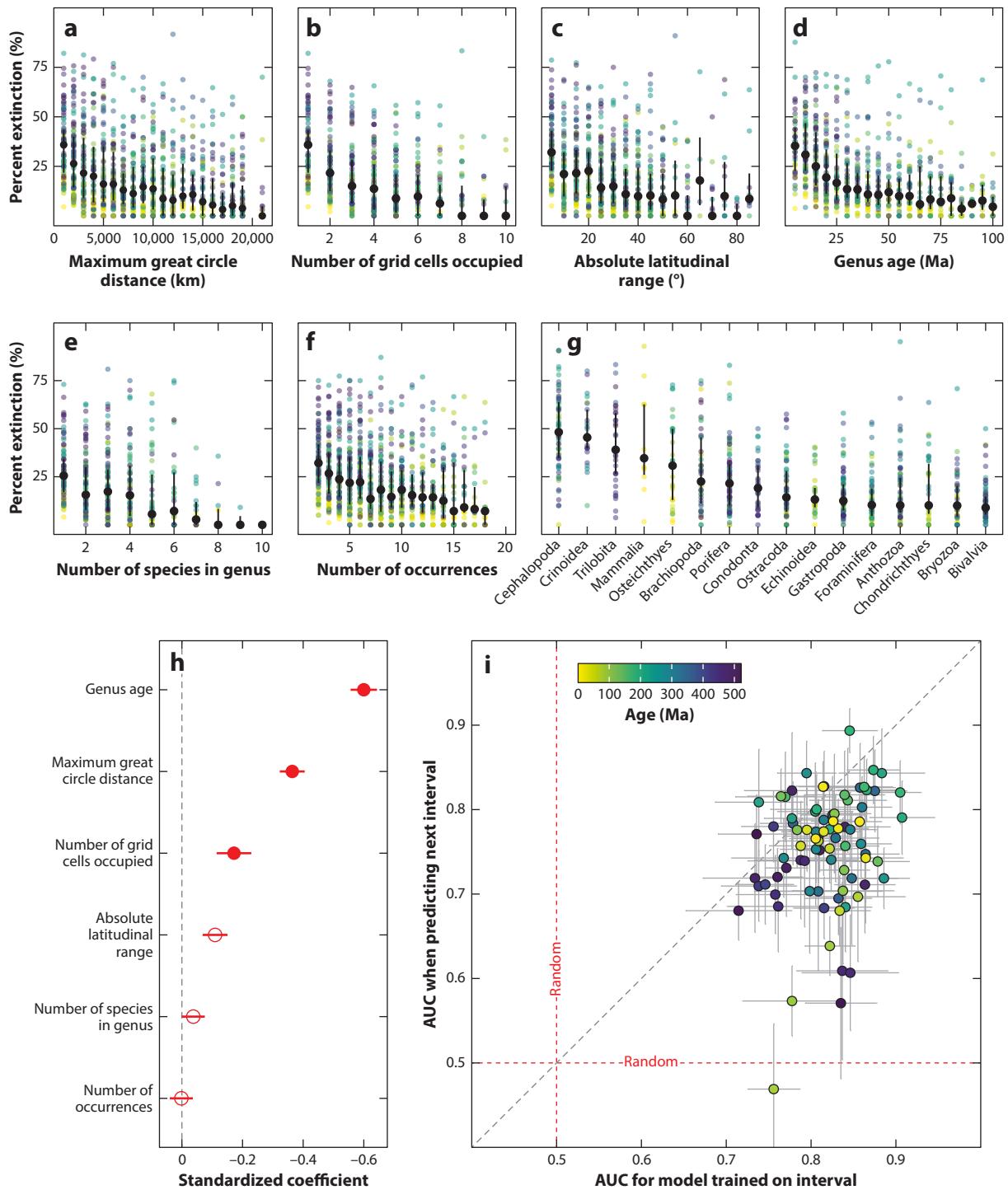
Body size, trophic ecology, and other aspects of life history can also be derived from fossils (Harnik et al. 2017, Palmer et al. 2021, Payne & Heim 2020). Automated and machine-learning methods (Hsiang et al. 2018, 2019) enable the efficient collection of individual-level body size and morphology data to assess intraspecific and community-level variation. Life history characteristics such as growth rate, reproductive mode, time to maturation, life span, and season of mortality can be estimated for taxa that grow by marginal accretion or in discrete molts. Metabolic rates can be estimated based on allometric size scaling and comparison with living relatives, and may also be constrained by geochemical data (Payne et al. 2014, Peharda et al. 2021). Trophic level can be constrained from knowledge of living relatives or from functional morphology (Dunne et al. 2008) and isotopic analysis of skeletal-bound organic nitrogen and carbon in sufficiently well-preserved fossils (Casey & Post 2011). Analyses of modern marine food webs show that important aspects of food web structure can be recovered from data restricted to taxa with high preservation potential (Dunne et al. 2008, Roopnarine & Dineen 2018). Taken together, the above examples highlight the diversity of ecological and environmental information available in marine fossil records.

A common use of the fossil record is to take extinction rates estimated from intervals of background or mass extinction in deep time as a baseline of comparison for extinction rate estimates from an ongoing sixth mass extinction. The desire to make such comparisons is understandable, but the great disparity in observational timescale between the deep-time fossil record and the modern, along with the unavoidable dependence of extinction rate estimates on observational timescale, renders this a largely futile exercise that is likely to be misleading (Spalding & Hull 2021).

### 3. LESSONS FROM PAST EXTINCTIONS

#### 3.1. Traits That Affect Extinction Risk in Fossil Taxa

The fossil record provides unequivocal evidence that some lineages have characteristically higher speciation and extinction rates than others (Wang & Bush 2008) (**Figure 5g**), implying that extinction risk is influenced by traits that are often shared among related species. Aspects of



(Caption appears on following page)

**Figure 5 (Figure appears on preceding page)**

General determinants of genus extinction risk in the Phanerozoic marine fossil record (550 Ma to present), based on analysis of occurrences in the Paleobiology Database (<https://paleobiodb.org>). Panels *a*–*g* show relationships between proportional extinction and (*a*) maximum great circle distance, (*b*) number of occupied equal-area grid cells, (*c*) absolute latitudinal range, (*d*) genus age (time since first occurrence), (*e*) species richness (number of species in genus), (*f*) number of occurrences, and (*g*) taxonomic affinity for genera sampled in 91 geologic stages (median stage duration of 5.2 million years). The color scale (shown in panel *i*) indicates age. Panel *h* reports coefficient estimates from mixed-effects logistic regression models that included taxonomic group as a random effect and the remaining predictors as fixed effects. Panel *i* shows the accuracy of stage-specific models when classifying genera as becoming extinct or surviving in the stage on which they were trained (*x* axis) and in the following stage (*y* axis). Accuracy is measured as the area under the receiver operating characteristic curve (AUC), which gives the probability that a randomly selected extinct genus will be assessed as having greater extinction risk than a randomly selected surviving genus. Models that include these predictors are able to correctly rank extinctions and survivors on average ~81% of the time in the stages on which they were trained and ~76% of the time when making predictions for the following stage. The relatively high accuracy of these models implies that certain factors have been consistently important determinants of extinction across a range of conditions and can be used to predict current and future risk. For further description of data processing and analyses, see the **Supplemental Material**.

geographic range are the most consistent determinants of extinction risk: Narrowly distributed taxa almost always exhibit higher risk than more broadly distributed taxa (Payne & Finnegan 2007) (**Figure 5a,b**), and this pattern is observed in most groups that have been examined (Harnik et al. 2012b). Geographic range is also a consistent predictor throughout events characterized by markedly different types of environmental change (Harnik et al. 2012b, Orzchowski et al. 2015) (**Figure 5a,b**), though it may contribute less during mass extinctions (Jablonski 2005, Payne & Finnegan 2007), perhaps because of the global extent of environmental stressors. Species richness is also often associated with genus extinction risk, but this appears to primarily reflect the positive correlation between species richness and genus geographic range (Finnegan et al. 2008, Payne & Finnegan 2007). These paleontological results are robust to a variety of potential biases and provide empirical support for the use of range size in current risk assessments (e.g., the IUCN Red List of Threatened Species; <https://www.iucnredlist.org>).

**Supplemental Material >**

Species abundance is another criterion used in current risk assessments (e.g., the IUCN Red List of Threatened Species). In general, paleontological studies have found that the relationship between local abundance and extinction risk is either nonlinear or not statistically significant after controlling for the effects of geographic range size (Harnik 2011, Harnik et al. 2012b). This may reflect either a true decoupling between local abundance and extinction risk or the temporal resolution of the deep-time fossil record, which may be unable to resolve a short-term population decline preceding extinction. Consequently, no studies have used deep-time fossil abundance data to calibrate extinction risk models for extant taxa.

Body size is associated with risk status in some groups today, particularly larger-bodied species subject to overexploitation (Dulvy et al. 2009, McClenachan et al. 2016). In contrast, larger-bodied marine taxa were not at elevated risk in the geologic past; instead, smaller-bodied taxa were generally at greater risk, after controlling for geographic range size and potential sampling biases (Payne & Heim 2020, Payne et al. 2016). Body size is correlated with many traits (e.g., fecundity and trophic level), and consequently relationships with extinction risk can vary markedly in direction in different groups and may reflect different underlying processes. One study of extinction selectivity found that the effect of body size on risk could be comparable to that of range size, but because the sign of this relationship varied across different groups of Cenozoic bivalves, size seemed to have no overall effect (Harnik 2011).

Some traits used in current risk assessments are unlikely to be preserved in the fossil record (e.g., fecundity). However, such traits may vary among clades, and paleontological studies have observed consistent clade-level differences in risk—for example, the estimated mean extinction probability of cephalopods is four times higher than that of other mollusk classes (Wang & Bush

2008)—which likely reflects differences in unmeasured traits (**Figure 5g**). Consequently, taxonomic identity has been considered a latent variable for traits that affect risk but cannot be directly determined from fossils (Collins et al. 2018, Finnegan et al. 2015). Finnegan et al. (2015) found that taxonomic identity and geographic range size were the two most important predictors of risk over the past 23 million years, with marine mammals at much greater risk than various marine invertebrate groups, but considerable variation in risk also existed among closely related families (e.g., corals).

The time since a taxon's first appearance in the geologic record is another frequently observed but poorly understood determinant of risk in deep time; in most intervals, younger taxa exhibit higher extinction rates than older taxa in the same group (Crampton et al. 2016, Finnegan et al. 2008) (**Figure 5d**). The association between taxon age and risk is largely independent of age covariates such as geographic range size or species richness (Finnegan et al. 2008), implying that an incumbent advantage somehow plays a role in survivorship on geologic timescales, although this advantage seems to be reduced during some mass extinctions (Crampton et al. 2016, Finnegan et al. 2008). Age and extinction risk are not associated among extant marine genera, which suggests that current risk patterns differ from those that dominated in the geologic past, that current risk patterns more closely resemble selectivity during past mass extinctions, or that survivorship advantages associated with taxon age are not captured by current assessment criteria (Werbin et al. 2018).

### 3.2. Potential Fossil Analogs for Current and Future Environmental Changes

Global environmental changes have been associated with elevated extinction rates throughout the history of life (**Figure 2**). These past events provide information about extinction risks associated with specific types of environmental perturbation. Although the driver of current global changes is human activity, many of the resulting environmental conditions, particularly ocean warming, deoxygenation, and acidification, have analogs in the deep-time fossil record. Volcanism in the late Permian (~252 Ma), for example, released massive volumes of greenhouse gases into the coupled atmosphere–ocean system at rates estimated as slower than, but within an order of magnitude of, current injection rates (Cui et al. 2021). This led to rapid warming of the surface ocean, widespread anoxia, elevated hydrogen sulfide in shallow waters, and a drastic reduction of metabolically viable habitat for many marine groups (Penn et al. 2018). Up to 80–90% of marine animal species are estimated to have gone extinct during this event. The hardest-hit groups were relatively inactive calcifiers with poorly buffered respiratory physiology (Clapham 2017, Clapham & Payne 2011), implying that both ocean acidification and other changes in seawater chemistry were important extinction drivers. Higher-latitude faunas exhibited elevated extinction rates, possibly because tropical faunas experienced warm, low-oxygen conditions more frequently before the event (Penn et al. 2018).

Other extinction events linked to volcanically driven greenhouse warming, deoxygenation, and potential ocean acidification occurred throughout the Mesozoic and Cenozoic Eras (~252 to 0 Ma) (Clapham & Renne 2019, Reddin et al. 2021, Tian et al. 2021) (**Figure 2**). Some commonalities can be discerned across these events (Harnik et al. 2012a, Reddin et al. 2021). For example, motile taxa preferentially survived the Late Permian and Late Triassic (Clapham 2017), consistent with expectations that motile organisms have a greater aerobic scope than sessile organisms. Similarly, pelagic predators and benthic groups with photosymbionts (Dunhill et al. 2018) were preferentially impacted by the Late Triassic and Toarcian events, although why remains unclear. Biotic responses also varied considerably across some of these climatic events. For example, reef ecosystems collapsed during both the Late Permian and Late Triassic extinctions (Kiessling &

Simpson 2011), yet selective extinction of heavily calcifying groups was observed only during the End Permian. Likewise, extinction risk varied latitudinally during the Late Triassic, but tropical faunas were most heavily affected, in contrast to the Late Permian event (Reddin et al. 2019). The Paleocene–Eocene Thermal Maximum has received particular attention as a potential analog for current rapid warming (Kender et al. 2021, Tian et al. 2021), but unlike some Mesozoic hyperthermal events, it caused relatively few extinctions. Among well-studied taxa, only deep-sea benthic foraminifera experienced globally elevated extinction rates (Arreguín-Rodríguez et al. 2022), whereas shallow marine benthos exhibited little long-term change (Ivany et al. 2018). Such variation in species response to superficially similar perturbations through geologic time may be attributable to lower rates and/or magnitudes of greenhouse gas injection but may also depend on the background climate state within which hyperthermals occur: An event occurring during a warm state will push species closer to their thermal–aerobic tolerance limits than a comparable-magnitude event during a relatively cool state (Arreguín-Rodríguez et al. 2022, Mathes et al. 2021). Long-term changes in physical and biological boundary conditions, such as the diversification and expansion of planktonic calcifiers and consequent increase in the acid-buffering capacity of the deep oceans (Ridgwell 2005), may also act to reduce the biodiversity impacts of some environmental stressors. Differentiating among these possible explanations for disparate biotic responses will be essential for understanding the implications of previous hyperthermal events for modern marine ecosystems.

Studies of global-scale extinction patterns can be difficult to apply in the regional context in which much conservation planning and implementation occur. However, the fossil record also provides many regional- and community-scale case studies in how ecological communities have responded to past climate perturbations. These studies collectively confirm that warming episodes have often been associated with increased rates of continental weathering and primary production and with deoxygenation of shelf environments, and that climatically forced changes in the distribution of benthic dissolved oxygen have been a major driver of benthic community turnover and extirpation throughout Earth history (Martindale & Aberhan 2017, Moffitt et al. 2015). Reductions in mean body size and mean trophic level are often observed during these events, consistent with studies of modern benthic dissolved oxygen gradients (Sperling et al. 2016).

Finally, paleontological data can provide a window into the biotic impacts of a broader array of environmental conditions than is available from modern or historical observational records. These extranormal states are typically referred to as nonanalog systems, as they are representative of environmental conditions or ecological communities that are compositionally distinct from those of modern systems. To date, past nonanalog systems have provided insight into the potential environmental and ecosystem states projected to occur as a result of global warming under a range of emission scenarios (Burke et al. 2018). Past nonanalog systems can be used to constrain the impacts of predicted warming on global systems as well as provide regional examples of the ecosystem and climate reorganizations expected at specific warming stages (Dowsett et al. 2013, Fischer et al. 2018).

#### 4. INFORMING MARINE CONSERVATION AND DECISION-MAKING

Making informed conservation decisions requires an understanding of change over long time periods (Dietl et al. 2015), and conservation targets often depend on the baseline used to estimate change (Grace et al. 2019, McClenachan et al. 2012). We focus first on the deep-time fossil record and then describe the ways in which more recent fossil records can be used to set baselines for management and restoration of specific regional- to local-scale ecosystems and particular species of concern.

## 4.1. Using Deep-Time Fossil Data to Assess Risk: Identifying Regions or Taxa for Prioritization

The deep-time fossil record is most useful for assessing extinction risk at broader geographic and taxonomic scales. Research at these larger temporal and spatial scales can help refine predictive extinction and ecological niche models and can have applications in the context of global priority setting for conservation.

**4.1.1. Assessing extinction vulnerability.** Relationships between traits and extinction risk have been quantified from deep-time fossil records and used to predict the vulnerability of extant taxa based on their present-day traits. These broad-scale vulnerability estimates can be used in conservation efforts by identifying geographic regions or taxonomic groups that are more vulnerable. For example, Finnegan et al. (2015) and Collins et al. (2018) identified marine biogeographic provinces with high proportions of vulnerable taxa based on models calibrated on the Cenozoic fossil record. These regions include tropical hot spots of present-day marine biodiversity (e.g., the Coral Triangle) as well as the polar Southern Ocean. These patterns emerge because of high endemicity as well as faunal composition; these regions contain a greater proportion of clades that have exhibited elevated extinction rates through deep time. These comparisons of relative vulnerability, when combined with data on current stressors (Halpern et al. 2008, 2015), highlight regions where more vulnerable faunas currently face rapidly warming seas (Collins et al. 2018) and biological invasions (Aronson et al. 2015). Fossil-informed vulnerability estimates for present-day species can be incorporated into decision-making processes in much the same way that estimates of anthropogenic impact (Halpern et al. 2008, 2015) have been used in global prioritization efforts (Asaad et al. 2018). With the scarcity of risk assessments for extant marine animals, vulnerability estimates calibrated using fossil data can help prioritize which species designated as data deficient should undergo formal assessment or biological monitoring.

**4.1.2. Evaluating risk criteria.** Paleontological analyses of deep-time extinction risk can aid conservation decision-making by ground-truthing variables hypothesized to affect extinction risk among extant fauna. For example, the consistent association between geographic range size and extinction risk through geologic time and across marine taxa (Harnik et al. 2012b, Payne & Finnegan 2007) provides empirical support for the use of geographic range as a criterion in current risk assessments. In contrast, relative abundance and population size do not consistently predict extinction risk through geologic time (Harnik 2011, Harnik et al. 2012b), especially when other characteristics (such as range size) are accounted for. Geographic occurrence data may provide a more robust estimate of vulnerability than abundance data, which is encouraging given the dearth of population time series for nonexploited marine animals. Recent studies have also investigated physiological responses to warming and deoxygenation, using relationships observed experimentally in extant species to hindcast extinction risk during analogous events in deep time (Penn et al. 2018). Congruence between extinction patterns predicted from coupled climate–physiology models and empirical observations of the fossil record indicates that biota at high latitudes are especially vulnerable to projected ocean warming and deoxygenation.

Most taxonomic groups exhibit relatively consistent differences in extinction and speciation rates in the fossil record (Wang & Bush 2008) (**Figure 5g**). This fact, combined with the consistent importance of geographic range size in risk under different environmental conditions, means that models trained on extinction patterns in the past can predict which taxa will go extinct in a given interval of time with moderate accuracy (Finnegan et al. 2015, Smits & Finnegan 2019) (**Figure 5i**). This pattern implies that the factors influencing extinction risk tend to be broadly consistent through time, even in the face of changing boundary conditions. Exceptions include

rare intervals of rapid, global, and large-magnitude climate and environmental change (Figure 2), during which extinction may be less selective (Cole & Hopkins 2021, Payne & Finnegan 2007) or selective on different factors (Jablonski 1986). However, even models based on these intervals usually yield better-than-random risk predictions for the succeeding interval (Figure 4*i*).

**4.1.3. Refining spatial distribution models.** For extant species, the fossil record presents an opportunity to hindcast past geographic distributions under different climate and environmental regimes and thereby test the performance of ecological niche models. These models are increasingly used to predict future risk in response to environmental conditions projected over ecological to evolutionary timescales (Maguire et al. 2015, Myers et al. 2015). Models based only on modern distributions assume that the occupied niche of a species (the range of environmental conditions within which it maintains viable populations at present) is a good indicator of its fundamental niche (the range of conditions within which it could maintain viable populations); this assumption may not be valid for species with actively expanding or contracting ranges. These models also assume that the fundamental niche of a species is static on centennial to millennial timescales and will not evolve with a changing fitness landscape. The few studies that have attempted to hindcast the past distributions of extant marine species, based primarily on their realized thermal niches, have generally found high concordance between predicted and observed ranges (Antell et al. 2021; Saupe et al. 2014a,b), implying that thermal niches are often conserved on  $10^5$ – $10^6$ -year timescales (Reddin et al. 2021). Niche estimates and information about their stability through time could be directly incorporated into predictive models of extinction risk.

**4.1.4. Identifying new risk criteria.** Paleontological studies also offer new criteria that can be incorporated into current risk assessments. For example, because a taxon's geographic range size waxes and wanes over time, Kiessling & Kocsis (2016) proposed that geographic range trajectories of extant taxa could be estimated from fossil data and incorporated into present-day risk assessments: To the extent that geographic range trajectories are deterministic (an open question depending on the characteristic timescales of the processes driving them), taxa with ranges that have declined through recent geologic time may be more vulnerable to extinction now or in the near future. Similarly, comparisons between fossil and present-day patterns of extinction risk in corals have identified morphological traits associated with past risk (Raja et al. 2021) that could potentially be used to refine current risk assessments. Finally, comparisons of present and past risk estimates (Payne et al. 2016, Raja et al. 2021) may conflict. Some of these mismatches can be attributed to differences in present-day and past extinction drivers (e.g., overfishing of extant species). In other instances, these discrepancies result from uncertainty regarding which traits are most important in predicting extinction and highlight opportunities for further refinement of assessment criteria.

## 4.2. Fossil Assemblages Provide a Record of Recent Ecological and Environmental Change

As the scale of analysis shifts from deep-time to recent fossil records and becomes increasingly regional to local in scope, there are greater opportunities to connect paleontological data to specific conservation actions. Here, we provide examples of recent studies that use near-time fossil records to monitor, manage, and restore marine ecosystems.

**4.2.1. Extending records of biomonitoring.** Biological monitoring in marine ecosystems is limited to the past century, beginning long after the onset of anthropogenic disturbance, which limits understanding of the magnitude and drivers of change. Because DA accumulation is

ongoing in many habitats, the recent fossil record can extend biomonitoring records back by millennia, at a decadal or subcentennial resolution. For example, biomonitoring of the benthic fauna on the southern Californian shelf dates back 60 years, recording biotic response to massive changes in water quality (Allen et al. 2007). In collaboration with the Los Angeles County Sanitation Districts, researchers used DAs to extend this record back thousands of years and determined that extreme ecological changes occurred long before twentieth-century urbanization, fishing, and climate change (Kokesh et al. 2022a, Leonard-Pingel et al. 2019, Tomašových & Kidwell 2017). Massive sediment pollution in the 1800s, likely associated with livestock grazing, drove the extirpation of an offshore shell-gravel community dominated by filter feeders that had persisted for millennia. Siltation produced a modern muddy, depauperate community composed primarily of deposit feeders, an ecological shift that went unrecognized until DA material was available (Tomašových & Kidwell 2017).

The longer timescales and broader geographic scales available through fossil datasets provide critical context for modern biomonitoring. For example, Martinelli et al. (2017) used data from live surveys in north-central Chile with DAs, combined with older fossil material spanning 300 ky, to track ecological changes in molluscan assemblages; the results demonstrated that the benthic community was largely resilient to climate change, with little to no change recorded until harvest pressure increased in recent years. O'Dea et al. (2020) took advantage of an 11-hectare area of fossilized coral from the mid-Holocene (7.2–5.6 ka) in Panama to assess both spatial and temporal variability in coral community structure. While the fossilized reefs showed little to no temporal variability before human settlement, they exhibited significant spatial variability. Spatial variability in Holocene reefs (i.e., historical range of variability) showed little overlap between Holocene and modern coral reef community composition or structure (O'Dea et al. 2020). These near-time approaches provide estimates of both temporal and spatial variability, often in conjunction with assessments of environmental drivers.

**4.2.2. Establishing biotic baselines.** The majority of studies that apply fossil data to marine conservation seek to establish baselines for management or restoration (Hong et al. 2021, 2022; Leonard-Pingel et al. 2019; Tomašových & Kidwell 2017). Recent paleoecological data can help establish targets for recovery or set benchmarks for managing human extraction. For example, sharks have been intensively fished for centuries; analysis of fossil dermal denticles established a 7,000-year baseline demonstrating that Caribbean sharks were three times more abundant prior to exploitation (Dillon et al. 2021). Shark conservation efforts explicitly rely on such baselines to advocate for protection, including local marine protected areas (Caribb. Shark Coalit. 2020). In another example, fossil fish ear stones in the upper Gulf of California revealed that the Gulf corvina (*Cynoscion othonopterus*), a commercially harvested fish, used the Colorado River estuary as a juvenile nursery throughout the past century (Rowell et al. 2005), until dams eliminated the habitat. Fossil data, when collected via bulk sampling, can be used to establish community-level baselines. For example, the benthic bivalve community of the Colorado River Delta boasts a centuries-long record that Dietl & Smith (2017) used to quantify the effects of river diversion in the past century. The authors noted that data on DA abundance could be used to assess the efficacy of mitigation strategies, including pulsed river flows.

Body size distribution of populations is another important metric of human impact (e.g., Graham et al. 2005) preserved in the recent fossil record. Analyses of 1,000 years of archaeological conch middens in Caribbean Panama demonstrated a shift toward smaller individuals, with earlier ages at maturity (O'Dea et al. 2014). Fisheries management relies on information on size structure to determine reference points for unexploited populations (Sathianandan 2017). For example, the size distribution of abalone species is well documented from middens spanning 10,000 years in

California's Channel Islands (Haas et al. 2019). This information is directly relevant to recovery planning, as size frequency is a key criterion in the California Abalone Recovery and Management Plan (Calif. Dep. Fish Game Mar. Reg. 2005).

DAs can accurately record the timing and effects of biological invasions, many of which may be unrecognized in biomonitoring data. For example, DA samples from Kingston Harbor in Jamaica record at least two molluscan invasions in the past 20 years (Kokesh & Stemann 2023). The invasion of the Asian green mussel (*Perna viridis*) at the end of the twentieth century is recorded faithfully in the surficial record, along with a short-lived peak in abundance and an associated decline in mangrove oyster (*Crassostrea rhizophorae*) populations. Similarly, DAs from the Po River Delta in Italy document the invasion of the bivalve *Anadara transversa* in the 1970s, followed by a lag in establishment due to metal contamination (Albano et al. 2018). *A. transversa* occurred in the northern Adriatic Sea for 20 years, but it failed to reach reproductive size until water quality improved.

Fossils can elucidate the ecological function of key species in the past and contribute to restoration. As government agencies and nonprofit organizations shift to framing goals based on ecological function, the recent fossil record can play a much larger role than it currently does. For example, fossil oyster reefs dating back to 500 ka demonstrated that these past populations were composed of significantly larger, more abundant individuals (Kusnerik et al. 2018) that filtered water an order of magnitude more efficiently than today's reef (Lockwood & Mann 2019). Chesapeake Bay oyster restoration goals explicitly include the restoration of filtration capacity, legally mandated to reduce dissolved nutrients in the bay (NOAA Fish. 2021). Fossils can also reveal ecosystem interactions over time, including trophic links and predator-prey relationships. For example, analysis of sediment cores in the Caribbean over 3,000 years demonstrated that coral accretion rates are driven by the abundance of parrotfish, key herbivores that graze on the algae that directly compete with coral (Cramer et al. 2017). Together with present-day data on parrotfish abundance and coral cover over the last several decades (Jackson et al. 2014) and experimental work showing the mechanism of these interactions (Steneck et al. 2014), this information builds a strong case for the prioritization of parrotfish for conservation. Parrotfish protections have successfully been implemented in several Caribbean countries [e.g., the Belize Fisheries (Nassau Grouper and Species Protection) Regulations, Statut. Instr. 49 (2009)]. Similarly, fossil data can reveal complex interactions among species, including humans, in nearshore marine ecosystems. For example, as sea otters have begun to recover from centuries of intensive commercial hunting along the west coast of North America, questions of appropriate baselines have emerged. In British Columbia, archaeological analyses show that Indigenous peoples maintained Late Holocene sea otter populations well below carrying capacity, which effectively mediated the keystone role of sea otters in nearshore ecosystems and enhanced the productivity of important fisheries, such as mussels (Slade et al. 2022). As otters recover in these ecosystems, questions of social justice and First Nations sovereignty have emerged; recovering sea otters facilitate kelp forest growth and thereby augment offshore recreational fisheries dominated by non-First Nations men, while feeding on nearshore shellfish fisheries dominated by First Nations women (Levine et al. 2017). These key conservation questions are closely linked to notions of past baselines as well as ecological interactions (Menzies 2015, Reeder-Myers et al. 2022).

Few studies have actually used DA data to assess restoration progress. Leonard-Pingel et al. (2019) determined that shelf communities off the southern California coast have shown little recovery from sewage outflow, despite large-scale mitigation efforts since the early 1970s. Interestingly, DA material did reveal a short-lived increase in chemosymbiotic taxa in the early twentieth century, before biomonitoring began (Leonard-Pingel et al. 2019). Although this particular case study did not identify progress toward recovery, it validates the overall approach.

**4.2.3. Identifying conservation and restoration priority sites.** Data from recent fossil assemblages have also been used to prioritize sites for protection or restoration. In one example, archaeological data were used to identify optimal sites for outplanting endangered black abalone in California’s Channel Islands (Braje et al. 2015). Shell-midden material made it possible to identify sites that supported dense abalone populations in the past and offer optimal environmental conditions in the present, but where populations were decimated by overharvesting. In another example, O’Dea et al. (2020) were the first to flag modern coral communities at Punta Caracol (Panama) for protection ahead of other reefs, because reefs at this site have persisted relatively unchanged for more than 800 years. The composition of these communities today falls within their historical range of compositional variability, in contrast to the compositions of most other Caribbean reefs, which have undergone pronounced change. Similarly, the collapse of the shell-gravel ecosystem offshore southern California documented from DA material allowed Tomašových & Kidwell (2017) to emphasize the crucial importance of protecting the relict shell-gravel habitats that remain in the vicinity of the Channel Islands.

**4.2.4. Environmental proxies and disentangling extinction drivers.** Environmental proxy data, including temperature, salinity, pH, and oxygenation, can be assessed directly from recent fossils or sediments and compared with ecological data over time or space. Such comparisons make it possible to disentangle the relative effects of various environmental drivers and, in some situations, specific human activities on marine communities. For example, in highly urbanized sites near Hong Kong, analysis of shallow marine ostracode communities over the last century revealed different drivers of change at regional and local scales. While both human and nonhuman factors correlated spatially with changes in taxon dominance, regional patterns reflected monsoonal influence and dam building, whereas local patterns correlated with metal pollution (Hong et al. 2021, 2022). These approaches sometimes highlight the resiliency of marine ecosystems to human activities. For example, molluscan DAs from the Persian Gulf revealed no evidence of community shifts based on sediment contamination or distance from oil platforms (Albano et al. 2016).

Local- and regional-scale studies also provide insights into rates of community disassembly and reassembly following larger environmental shifts. Pleistocene–Holocene glacial–interglacial cycles provide a particularly valuable opportunity; time series in single locations can examine community stability or lack thereof following multiple perturbations. For example, the ecological structure of Barbados reefs remained relatively stable for at least 95 ky, through multiple glacial–interglacial cycles (Pandolfi & Jackson 2006); massive ecological changes were restricted to recent anthropogenic impacts. In the northern Adriatic, molluscan communities also exhibit a striking degree of ecological similarity between the last interglacial interval (~125 ka) and the Holocene interglacial, with much larger compositional differences separating those from present-day communities (Kowalewski et al. 2015). These studies suggest that changes in marine communities reflect both climate and other, more direct anthropogenic impacts, with the effects of the latter dwarfing the former in recent time series.

In addition to biotic restoration, DA material can provide targets for abiotic or environmental restoration. One of the longest-term and most successful applications of recent fossil data involves the reconstruction of salinity regimes in the Greater Everglades Ecosystem and Florida Bay (Jones et al. 2019, Marshall et al. 2020, Wingard et al. 2017). This region experienced extensive canal development in the early twentieth century, well before water quality data were collected. As a result, wetland managers have turned to DA material, which dates back 200 years, to reconstruct changes in molluscan dominance, which in turn provide a spatially resolved record of hydrologic changes. These indicators form the foundation of abiotic restoration targets for federal and state

agencies associated with the Comprehensive Everglades Restoration Plan in Florida Bay (Wingard et al. 2017).

## 5. TOWARD CONSERVATION FUTURES

Paleontology and related disciplines, such as archaeology and historical ecology (Lotze & McClenachan 2014), are critical to generating the long-term records needed to contextualize modern extinction risk and to project future impacts under different environmental change scenarios (Burke et al. 2018, Dietl et al. 2015). While fossil data hold significant promise for informing conservation strategies, much paleontological research takes place without direct connection to the communities impacted by conservation efforts. As we look toward future research directions in conservation paleobiology, we highlight the need for coproduced research that unites paleontologists, marine scientists, conservation practitioners, and policymakers with the communities for whom the impacts of climate and global change are most imminent (Latulippe & Klenk 2020, Turnhout et al. 2020).

### 5.1. Conservation Paleobiology Must Involve Coproduction of Knowledge

Coproduction methods are increasingly recognized as critical for making scientific practice responsive to broader societal needs and for informing policy decisions (Beier et al. 2017, Irwin et al. 2018). Coproduction is a collaborative, iterative process that utilizes multiple knowledge systems to develop actionable knowledge (Mach et al. 2020, Turnhout et al. 2020). This process can occur from distinct perspectives (Arnstein 1969, Rosen & Painter 2019), with some coproduced research operating within conventional academic structures (Turnhout et al. 2020) and other studies centering research within community contexts (David-Chavez & Gavin 2018). Coproduction best practice calls for moving toward establishing collaborative efforts centered in community needs to allow for innovative and actionable knowledge production (Turnhout et al. 2020).

Despite growing awareness of the need for heightened coproduction across related sciences, this practice remains relatively rare within paleobiology. Even in subfields of paleobiology that are considered more applied, such as conservation paleobiology, assessments show that the great majority (~90%) of studies do not have readily identifiable, tangible applications (Groff et al. 2023). This implementation gap likely has detrimental impacts on the perceived relevance of paleontology to important global issues such as climate change policy (Kiessling et al. 2023). We suggest that this gap can be bridged by an increased emphasis on coproduction, where the communities most impacted by research outcomes codesign, undertake, and analyze the research along with academic or professional scientists. As equal members of the research team, these partners can develop study questions and ensure that data are relevant to their needs, allowing for uptake in data-driven policy. Rather than asking what decision-makers can take from paleontological data, we encourage marine and conservation paleontology researchers to ask how they can support community-led decision-making.

While marine conservation includes numerous examples of successful community-focused research, most paleontological research involves transdisciplinary collaborations among academics and research practitioners (e.g., marine paleontologists, archaeologists, and ecologists) that produce syntheses to inform marine conservation and management. For example, teams of paleontologists and marine biologists used fossil data to map extinction risk and identify which ocean areas might be most vulnerable to climate change and other human impacts (Finnegan et al. 2015, Harnik et al. 2012a). This example shows how collaborations can combine multiple data types to cocreate syntheses necessary for understanding ecosystem dynamics over deep time and into the future.

Examples of community-centered coproduction in marine conservation paleobiology are rare. Cases in which fossil data have been used to provide decision-making support include collaborations with Indigenous and traditional rights holders to restore sea gardens by the Coast Salish First Nation (WSÁNEĆ Leadersh. Counc. 2023) and the Swinomish Tribe (<https://www.swinomish-climate.com>). Information on the age of clam gardens (Smith et al. 2019), past productivity (Groesbeck et al. 2014), and impact on coastal biota was utilized to build support for Indigenous-led ecosystem goals (Haggan et al. 2004). In Chesapeake Bay, the Nansemond Indian Nation incorporated paleontological information on the body size, distribution, and harvesting of oyster species (Jenkins & Gallivan 2020, Schulte 2017) to inform river stewardship efforts tied to cultural revitalization (Bass 2021). Ongoing academic efforts to coproduce actionable paleontological research include working group projects supported by the Conservation Paleobiology Network (<https://conservationpaleorcn.org>) and the growing cohort of Indigenous paleontologists who lead place-based research relevant to conservation (Razanatsoa et al. 2021). These incipient efforts deserve greater attention and energy from academics, particularly as federal agencies increase calls for the incorporation of Indigenous and traditional knowledge in research, policy, and decision-making (Sea Grant Newt. 2018, White House Counc. Environ. Qual. 2022). As awareness of the importance of coproduction grows, efforts should ensure that research is led by the communities where data are collected and who will be directly impacted by decision-making outcomes (but see David-Chavez & Gavin 2018). Careful implementation of coproduction with Indigenous peoples is particularly important when conservation paleobiology has implications for Indigenous fisheries and where fossil data can be used to promote Indigenous sovereignty in resource management and conservation and the return of rights to Indigenous communities.

## 5.2. Avenues for Future Research Involving Recent Fossil Records

Some of the most exciting avenues for future research in marine conservation paleobiology focus on recent fossil records, often preserved in the same environment as the modern ecosystem. At sites that are biologically monitored, workflows typically involve separating live- from dead-collected material and discarding the latter. We strongly recommend that managers archive this dead material for future analyses. In Puget Sound, Chesapeake Bay, and southern California, partnerships among managers and paleontologists at state, federal, nonprofit, and academic institutions have made it possible for DA material to be archived in conjunction with live-collected benthic macrofauna (Kokesh et al. 2022b, Lockwood & Chastant 2006, Tomašových & Kidwell 2017). This DA material is likely to provide a much longer timescale and a more representative sample of the local fauna than the living population, in part due to sampling effects (Kidwell 2013). This approach could provide a wealth of information on rare species, invasive taxa, short-term responses to environmental shifts, and progress toward restoration.

Seasonal and annual biomonitoring is used by managers not only to document ecological degradation but also to assess the effects of restoration practices. For taxa and ecosystems in the early stages of intervention, the likelihood that biomonitoring will capture rare taxa is low, and live sampling of those taxa may work against conservation goals. Sampling of the DA is not as temporally resolved, but it is often cheaper and easier, and it requires fewer samples than sampling the living population, without the issue of harvesting rare taxa. Small-scale community change is readily recorded in the DA, making it possible to determine the efficacy of restoration efforts. Future work should use these approaches to assess the effects of a variety of restoration practices, including water release from dams (Dietl & Smith 2017), pollution controls, riparian buffers, living shoreline construction, and no-harvest sanctuaries and marine protected areas.

For many marine ecosystems, collection of the DA would make it possible to assess biotic shifts during important socioecological transitions, including colonization, agricultural and industrial

shifts, and warfare. Efforts to synthesize long-term global change in coastal ecosystems identified colonial occupation and settlement as key periods for change in ecosystems, including coral reefs (Muraoka et al. 2022) and estuaries (Lotze et al. 2006). These transitions are often complex (Wilson 2021) and rapid on geologic timescales, but they leave behind a rich sedimentary record that is commonly mined for paleoclimatic proxies. Far less attention has been paid to the fossil material preserved in the same context, which would make it possible to track biotic response, especially in the absence of monitoring data. As Indigenous peoples and marine science partners seek to reconstruct the consequences of harvesting and land-use practices across Indigenous, colonial, industrial, and postindustrial communities, these fossil materials will be essential for quantifying changes across the entire ecosystem.

The DA record, when assessed in the context of geochemical, paleoclimate, age, and archaeological data, is a vital tool for determining the relative impacts of a variety of human-driven environmental changes. This type of approach is yielding fascinating results in ecosystems with long-term records of Indigenous settlement (e.g., Reeder-Myers et al. 2022) and urban ecosystems such as Hong Kong harbors (Hong et al. 2021, 2022). In recent years, the development of geochemical and molecular biochemical tools has exploded, making it possible to reconstruct recent records of population and functional ecology within a complex abiotic context. In Chesapeake Bay, for example, paleontologists and archaeologists now have the ability to track nutrient loading in oysters at a seasonal or monthly level, reaching back more than 3,000 years (Black et al. 2017). These high-resolution environmental proxies directly relate to functional ecology and can be used to quantify ecosystem function over much longer timescales and across multiple repeated climate shifts. Perhaps the most exciting development pertaining to recent fossil material is the rapid advancement over the past few decades in methods for extracting environmental DNA (eDNA), ancient DNA (aDNA), and sedimentary ancient DNA (sedaDNA) (Angeles et al. 2023, Armbrecht 2020, Scott et al. 2022, Torti et al. 2015). These approaches require refinement (Edwards 2020), and many marine environments are challenging for the preservation of DNA, but in some situations they allow access to genetic material preserved in bone, shell, plant material, and sediment, facilitating studies of population genetic changes at decadal, centennial, and millennial scales. sedaDNA has already been used, for example, to reconstruct marine biodiversity over the past two centuries in an industrialized bay in Europe, revealing the biotic impacts of pollution in the early twentieth century, prior to monitoring efforts (Angeles et al. 2023). aDNA and sedaDNA may eventually also be able to provide information on long-term changes in the genetic diversity and population size and structure of selected species.

### 5.3. **Avenues for Future Research Involving Deep-Time Fossil Records**

Critical questions remain regarding the ecological and environmental drivers of past marine extinctions. Addressing these is necessary if we are to effectively use information in the deep-time fossil record to anticipate and mitigate the impacts of current and future anthropogenic environmental change on marine biodiversity. Although environmental changes analogous to present conditions and future projections occurred multiple times in the geologic past, patterns of extinction selectivity vary considerably across these intervals of ocean warming, deoxygenation, and acidification (e.g., Clapham & Payne 2011, Ivany et al. 2018). To what extent do these varied responses reflect differences in the rate or magnitude of greenhouse gas injection during these events, stochastic ecological responses to complex environmental forcing, or secular changes in global boundary conditions through geologic time? Studies seeking to address this question will also need to consider how spatiotemporal and taxonomic variation in the preserved and sampled fossil record affects deep-time selectivity patterns. Focusing on effect sizes and relevance for

projections can help to make deep-time extinction studies more accessible to policymakers (Kiessling et al. 2023).

Although many paleontological analyses provide empirical support for traits widely used in current risk assessments, discrepancies have been noted in the few studies that explicitly compared modern and fossil risk estimates (Payne et al. 2016, Raja et al. 2021). Understanding why these differences exist is critical for determining future vulnerability to global change. To what extent do observed differences result from changes in stressors over time, and specifically threats like overexploitation that lack a geologic analog? Although many predatory species are currently at greater risk due to overexploitation (Dulvy et al. 2009, Harnik et al. 2012a, Lotze et al. 2006), few studies have examined the influence of trophic level on extinction risk in deep time. Determining whether species at higher trophic levels are at greater risk even in the absence of exploitation is important given evidence that the impacts of climate-driven declines in primary productivity are amplified at higher trophic levels (Kwiatkowski et al. 2019). Analyses of trophic structure in deep time are increasingly feasible; recent paleontological studies have shown that microvertebrate remains such as dermal denticles, otoliths, and fish teeth can accurately record changes in predator relative abundance and functional diversity through time (Cramer et al. 2017, Dillon et al. 2021, Pimiento et al. 2017, Sibert et al. 2017). These approaches complement an expanding set of geochemical proxies capable of estimating trophic level and shifts in trophic level over space and time (Kast et al. 2022, Lueders-Dumont et al. 2018). Finally, more study is needed to understand the persistent influence of taxon age on extinction risk in deep time and its significance, if any, for evaluating current risk.

While extinction has been the subject of considerable paleontological research, there is much we can also learn about the future of marine ecosystems by studying the characteristics of surviving species in the past. Analyses of Pleistocene fossils, for example, can predict which shallow-water species are likely to expand their geographic distributions during warming (Orzechowski & Finnegan 2021). Similarly, studies focused on ocean deoxygenation in deep time can elucidate which traits are observed in species tolerant of such conditions. Given recent reductions in dissolved oxygen concentrations in many regions, such paleontological analyses provide a model for expected functional shifts ground-truthed by comparing the functional diversity of living communities with DAs that accumulated historically under more oxygenated conditions. These approaches can be used to predict which species are likely to thrive in the face of anthropogenic environmental change and the resulting consequences for the functional ecology of marine ecosystems.

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