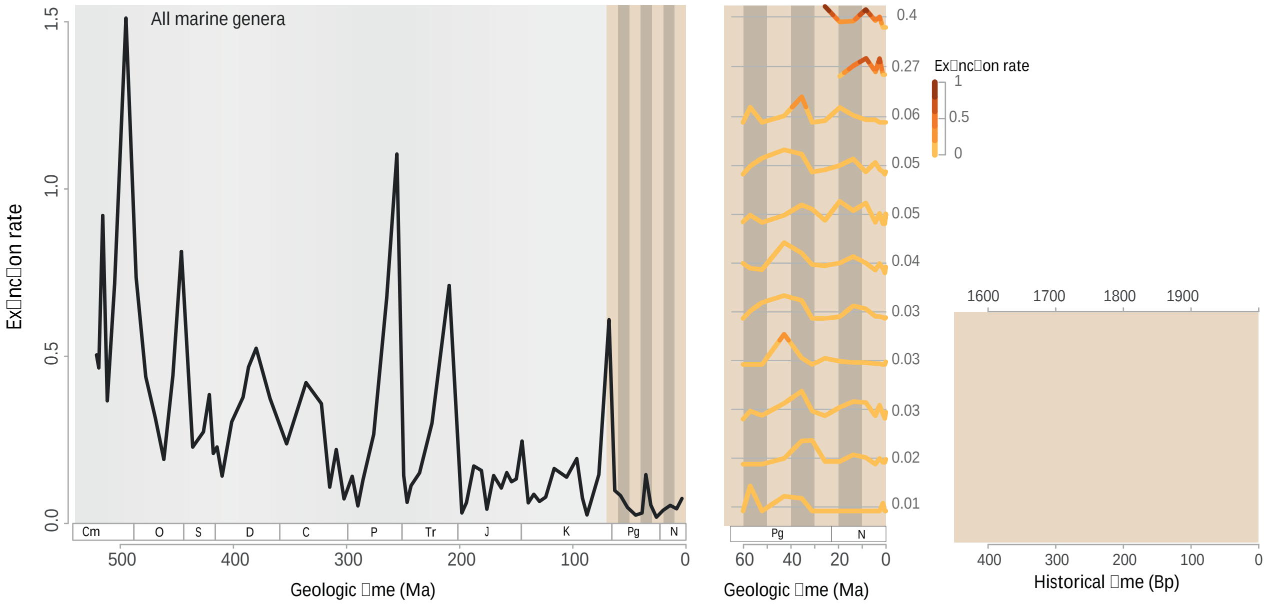

historical data offer insights into marine extinctions over multiple scales and under different environmental conditions, some of which are partly comparable to predicted future environmental states. Our comparisons reveal the many opportunities and challenges of combining data for ancient and modern organisms in an effort to better understand and predict the impact of current and future environmental changes on extinction risk in the sea.

[illegible]

The fossil record

Extinctions are a primary feature of the marine fossil record (Figure 1a). Although mass extinction events were important drivers of macroevolutionary change [22], most marine organisms (>90%) went extinct during intervals characterized by 'background' extinction rates (Figure 1a; Box 1) [12,13,23]. This long record of extinctions provides many opportunities to assess the environmental conditions and biological characteristics that can lead to elevated risk.

One conspicuous trend in the marine fossil record is the overall decline in background extinction rates towards the present-day (Figure 1a). This decline reflects the loss of extinction-prone lineages, which, combined with variation in origination rates, led to marked changes in the composition of marine ecosystems over time [24]. Recovery from the end-Permian [251 million years ago (Ma)] and end-Cretaceous extinctions (65 Ma) involved the diversification of clades that are the major constituents of marine communities today. Thus, because of their ecological and evolutionary similarities, data for the past 65 million years might be most informative for understanding current and future extinction risk.

Extinction rates varied considerably over the past 65 million years (Figure 1b), with congruent extinction peaks at some times for some clades (e.g., elevated rates 34 Ma for several groups associated with a transition from greenhouse to icehouse climates [25]), and incongruent peaks at other times. On average, extinction rates differ markedly among major clades, with marine mammals [cetaceans and marine carnivorans (pinnipeds and aquatic mustelids)] going extinct at rates more than ten times those of most invertebrates (Figures 1b and 2a). Extinction rates also vary among invertebrates: the mean extinction rate for scleractinian corals is approximately twice that of bivalves and five times that of brachiopods (Figures 1b and 2a). This temporal and phylogenetic heterogeneity in rates provides an opportunity to dissect the factors associated with elevated extinction risk among past marine organisms [26–28]. Moreover, when integrated species lags behind that of terrestrial species: out of the 41 500 assessed species in 2007 only 1500 were marine, with another 1500 marine species added by 2008 [38]. This included complete assessments of sharks and rays, groupers, reef-building corals, seabirds, marine mammals, and sea turtles (Figure 2c). Since then, assessments for all mangroves [19], seagrasses [18], and tunas [17] have been completed (Figure 2c), and the International Union for the Conservation of Nature (IUCN) aims to have 20 000 marine species assessed by 2012 [38]. Nevertheless, assessments for many groups are incomplete or entirely lacking (Figure 2c).

marine,

marine,

Comparing extinctions through time

Although overall background extinction rates have declined throughout the fossil record, there have been many periods of enhanced extinction rates (Figure 1). Currently, the Earth is

[11,33,43], followed by habitat loss and, to a lesser extent, pollution and climate change (Table 1). Of 168 marine, estuarine, and diadromous (i.e., migrating between fresh and salt waters) species listed or considered for listing under the US Endangered Species Act (ESA) in 2004, 81% were affected by overexploitation [42]. Historically, exploitation was associated with 55% of local extirpations and global extinctions [11] and 96% of depletions and extirpations have particularly strong effects on associated species. In the Wadden Sea, for example, loss of such habitat contributed to 70% of the 25 species extirpations in historical time [34]. In the fossil record, the loss of shallow marine habitat due to falling sea level has been associated with elevated extinction rates [13] and biodiversity loss [49]. For example, sea-level fall driven by global cooling was associated with elevated extinction during the end-Ordovician (444 Ma) [50] and Eocene–Oligocene (34 Ma) [51] (Table 1), but not during the most recent glacial–interglacial cycles (1 Ma) [52,53] (Box 2). This might reflect a difference in starting conditions: the Late Ordovician and late Eocene were characterized by greenhouse conditions with extensive continental flooding, whereas the Pliocene–Pleistocene transition occurred in a world with minor continental flooding that had already cooled considerably from the early Cenozoic.

Global warming and associated stressors

Global warming and ocean acidification, which are of growing concern today and for the future [3,4,38], were important factors in some ancient extinctions [27,28] but played little role in historical extinctions (Table 1, Box 2) [11,33,34]. Geochemical and paleontological evidence suggests that four of five global reef crises and three of five mass extinctions in the fossil record were 0-.47s4Tm()Tj/F51Tf9.464

deep-water benthic foraminiferan species went extinct, whereas other microfossil groups were relatively unaffected [54]. Today, climate warming and acidification pose increasing threats to corals [4,14,55], warming and sea-level rise to seagrasses and mangroves [18,19], and many species show range shifts, local extirpations, and invasions in response to changes in ocean temperature [56,57].

Anoxia and pollution

Anoxia is another important driver of extinction risk in both modern and ancient seas (Table 1). In addition to direct toxicity, oxygen depletion of bottom waters can lead to large-scale habitat loss [58]. In historical and modern times, bottom-water anoxia driven by excessive nutrient loading and decomposition of organic matter has led to some extirpations in estuarine and coastal waters [11,33,42]. Widespread anoxia is also associated with several major extinctions in the fossil record (Table 1), triggered by elevated atmospheric CO_2, global warming, diminished thermohaline circulation, and eutrophication [59]. Other forms of pollution (e.g., pesticides and toxic algal blooms) have also contributed to historical extinctions and current risk [11,15,33,38,42], but identifying definitive examples of these in the fossil record is challenging.

Synergistic effects

In the near future, most human impacts in the ocean will increase, and the effects of climate change will interact with existing threats, such as overexploitation and habitat loss [4,10,60]. There is great uncertainty about how these cumulative impacts will interact to affect marine species and ecosystems; if already severely stressed, their resilience to further change can be greatly reduced [8,61,62]. Historical assessments show that multiple human impacts were involved in approximately 40% of extirpations in the Wadden Sea [34] and 42% of extirpations in estuaries and coastal seas worldwide [33]. This usually involved the combination of overexploitation and habitat loss and, to a lesser extent, pollution. In the fossil record, many extinction events were associated with multiple stressors that might have acted synergistically. For example, the end-Permian extinction is associated with warming, acidification, and anoxia [27,28,41]. Further study of past extinctions caused warming and acidification can identify threshold rates below which carbonate saturation was well buffered (>10 000 years) [6] and warming and acidification had little effect on reef diversity and growth versus episodes of more rapid change associated with reef declines and extinction (Box 2) [4].

Third, in terms of the biological correlates of marine extinctions, it appears that body size has been strongly associated with historical and current risk, whereas geographic range has been one of the strongest correlates in the fossil

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