REVIEW

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Rarity in mass extinctions and the future of ecosystems

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The fossil record provides striking case studies of biodiversity loss and global ecosystem upheaval. Because of this, many studies have sought to assess the magnitude of the current biodiversity crisis relative to past crises—a task greatly complicated by the need to extrapolate extinction rates. Here we challenge this approach by showing that the rarity of previously abundant taxa may be more important than extinction in the cascade of events leading to global changes in the biosphere. Mass rarity may provide the most robust measure of our current biodiversity crisis relative to those past, and new insights into the dynamics of mass extinction.

It has become commonplace to refer to the modern biodiversity crisis as the 'sixth mass extinction'[1,2]. With three short words, we place the biotic and environmental disturbance created by mankind on par with the greatest biodiversity crises of the past half billion years. This is a comparison that demands close attention as the 'Big Five' mass extinctions include truly catastrophic events[3,4], the biggest of which resulted in the inferred extinction of $>75\%$ of species alive at the time[1,4]. In addition, mass extinctions have shaped the evolutionary history of the planet[5–7]. Organisms that were ecologically dominant before a mass extinction frequently do not survive, and rarely enjoy the same levels of dominance in the aftermath[6,8]. However, there are fundamental differences between the types of data upon which past mass extinctions have been identified, and those upon which the current biodiversity crisis is being assessed. That is, abundant marine fossil genera on multi-million year timescales for the former[9,10], and (often rare) terrestrial species on decadal to centennial timescales for the latter[1]. So the question is critical: are we currently in the midst of the 'sixth' mass extinction, and can we develop an appropriate metric for the comparison of ancient and modern biotic crises?

The Big Five mass extinctions were profoundly disruptive events with effects extending far beyond the loss of taxonomic diversity[11–15]. In addition to extinction, all major mass extinctions are also characterized by prolonged intervals of ecological change[12,16]. Ecosystems are comprised of interacting networks of biotic and biophysical components, including taxa, nutrients, and their trophic and non-trophic interactions[17]. Species loss and ecosystem reassembly during mass extinction is unsurprising given the disruption of ecological networks[18]. For hundreds of thousands to millions of years after mass extinctions, a series of short-lived, low-diversity and (at times) low productivity ecosystems dominate[16,19,20]. Large-bodied taxa often become dwarfed, or are replaced by small-bodied taxa[21,22]. Previously dominant groups may be supplanted in the evolutionary diversifications that follow[23–25], as new, diverse ecosystems are built[26]. The largest extinction intervals result in permanent state changes in the structure of ecosystems, as well as the character of the flora and fauna that dominate them[5,25,27]. Mass extinctions, therefore, not only punctuate the history of life, they also forever alter its trajectory.

In this light, the fossil record of mass extinctions is an important laboratory for understanding the effects of current environmental change on global ecosystem structure and function[28]. A key question is: how do minor biodiversity crises become mass extinctions? And, why do mass extinctions tend to coincide with permanent state changes in global ecosystems? To date, studies have considered these issues by comparing projected rates of modern species loss and rates estimated from the fossil record[1,11,29]—a method complicated by the need to extrapolate across temporal scales and abrupt state changes. Here, we propose a different approach, and consider whether the loss of species abundance—mass rarity—might have characterized past mass extinctions as they were occurring. Rarity is important for two reasons: first, because it more accurately reflects function in ecological networks[30] and thus mass rarity (rather than mass extinction) may be a primary driver of the events and patterns associated with the mass disappearance of fossils from the fossil record. Second, the extent to which previously common taxa have become rare offers a direct metric of the size of the present biotic crisis. There may be no need to project current extinction rates in order to get a sense of the future of ecosystems. Mass rarity may be all that is needed to forever change the biosphere.

From past abundance to current rarity

Humans have reduced the abundance of many historically common species. This increased rarity has been achieved through wholesale reduction in geographic ranges and/or population sizes, through modification of terrestrial habitats, appropriation of primary productivity for humanity, overexploitation and pollution, among other factors[31–33]. On land, widespread evidence exists for ongoing habitat loss and population declines globally[31,34]. This includes, for instance, a 20% decline in habitat specialist populations monitored by the Wild Bird Index since the 1980s, and continuing declines in the IUCN Red List Index of species survival aggregated across birds, mammals, amphibians and corals[31]. Likewise, most fished coral reefs support less than half the expected fish biomass[35], with long-term declines in the abundance of reef taxa since first human contact[36]. Among subsets of mammals, birds, butterflies, and highly mobile pelagic predators, more than 50% of the taxa studied have experienced range contractions in the last decades to centuries[37–39]. Yet to date, the absolute number of recorded species extinctions is dwarfed by those inferred for mass extinctions in the geological past[1,11] and local declines in species richness are equivocal[33,40]. However, the extent of abundance loss is not equivocal, nor is the effect of land use[34]. Mass rarity, that is the reduction in geographic range and/or numerical abundance of a species globally, seems to be one or more orders of magnitude more severe than extinctions to date[41–44], and is an urgent conservation priority for both species and ecosystems[38,45–47]. What remains a major unknown, however, is how global mass rarity today relates to the biotic crisis recorded in the fossil record, and what sustained mass rarity might mean for the future of ecosystems.

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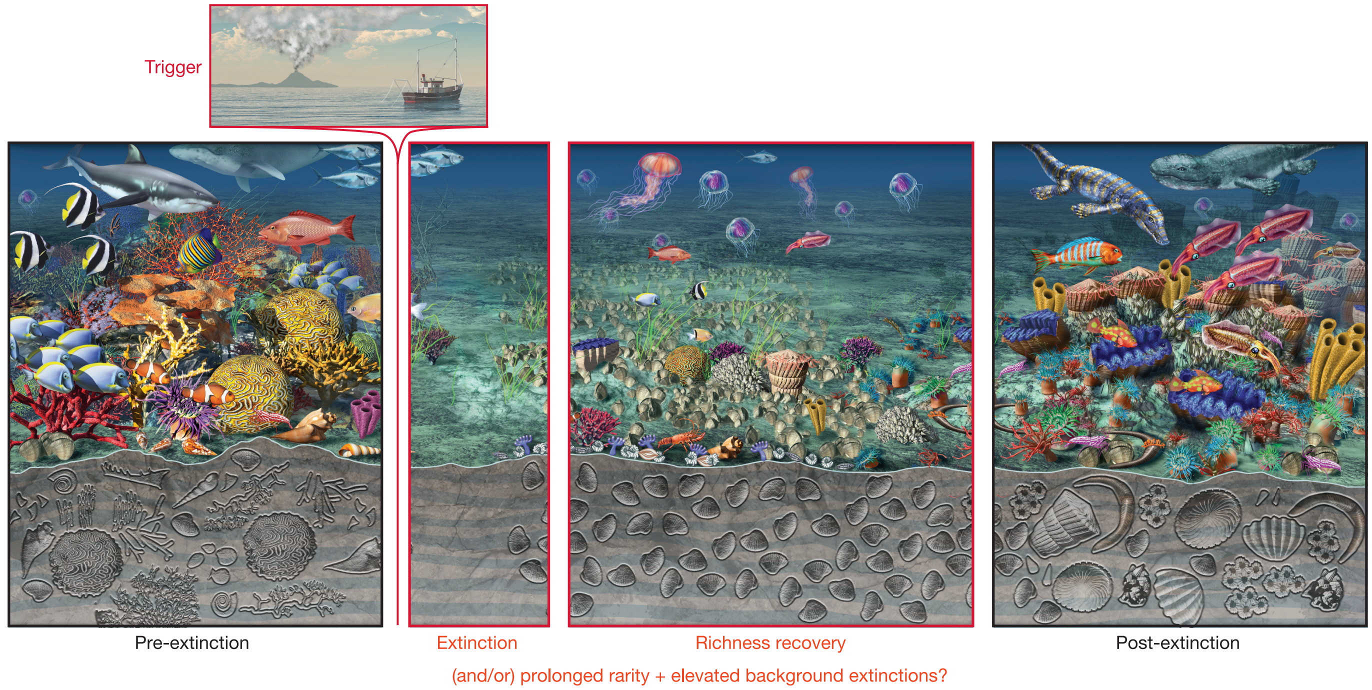


Figure 1 | Mass rarity and mass extinction are indistinguishable in the fossil record, and may have the same ecosystem effects. Anthropogenic activities have led to mass rarity of many previously abundant flora and fauna (right to middle). Mass rarity can look like mass extinction in the fossil record because the previously abundant taxa become so rare as to no longer be readily observed (bottom). Previously abundant and ecologically important groups, such as ecosystem engineers may not actually become extinct, but decline below the abundance threshold required for them to perform their ecological roles, becoming ecological 'ghosts'. Chance reassembly after mass rarity could lead to drastically different ecosystem structure and function even with minimal extinction (right)—raising the question of what the future might hold. Artwork courtesy of Nicolle R. Fuller, Sayo-Art.

We suggest that global rarity today (that is recent mass rarity, not the local rarity of most species in ecological studies as in ref. 48) may already be equivalent to intervals of pervasive fossil disappearance (Fig. 1). This is because the fossil record, particularly as it is preserved and studied across extinction boundaries (Box 1), primarily records the dynamics of durably skeletonized, geographically widespread, abundant taxa, and not the absolute presence or absence of all species originally in that ecosystem. When taxa are rare they can be missed, and when events are rapid, the order and importance of different factors can be hard to interpret.

The vast majority of species evolve, exist and become extinct without being preserved as fossils[49–51]. The fossil record is instead dominated by species that inhabit environments with high preservation potential. Such environments include those in which sediment accumulates, such as in (or around) lakes, rivers, swamps, marine basins, or reef tracts[52]. Even in such areas, most species stand little chance of being preserved. Rather, the fossil record is dominated by those taxa possessing heavily mineralized hard parts, such as teeth, bone or shells[51]. Organisms that are very small, entirely soft-bodied, or occur in ephemeral habitats are rarely preserved[49–51]. Additionally, as in living ecosystems, species that exist over a broad geographic range and in large numbers have a higher probability of being found than species that are rare and/or geographically restricted.

As a consequence, the fossil record of abundant, widespread, hard-bodied, marine taxa shapes our paleontological perspective of the long-term dynamics of life[10] (see Box 1). By definition, a mass extinction is an interval of time characterized by elevated rates of extinction relative to background intervals[14,15]. In practice, however, they are identified by the geologically sudden disappearance of abundant, long-lived genera (or higher order taxa) from global-scale compilations of fossil occurrences of biomineralizing taxa[9,10].

The often-discussed 'Big Five' mass extinction events were first recognized in this way from the shelly marine fossil record: the end Ordovician (~445 million years ago (Ma)), end Devonian (~375 Ma), Permo–Triassic (PT; 251 Ma), Triassic–Jurassic (TJ; 199 Ma), and Cretaceous–Palaeogene (KPg; 66 Ma)[10,15], although marine and terrestrial extinctions have subsequently been shown to often go hand-in-hand[53].

Detecting and predicting the ultimate severity of a mass extinction as it is happening requires a detailed understanding of the triggers and feedbacks of the extinction interval—the geologically brief interval of time when previously abundant fossil taxa disappear en masse (see Extinction in Fig. 2). Assessments of the severity of the current biodiversity crisis relative to those of the past presuppose an understanding of these geologically near-instantaneous events (Box 1). So, how much is actually known?

Changing the world

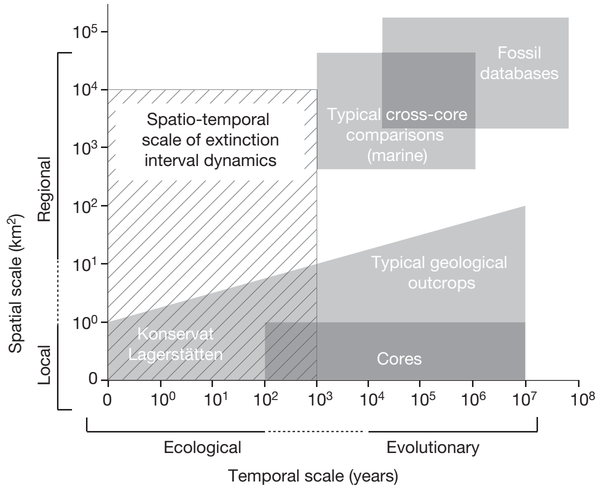
Extinction intervals involve a primary trigger, secondary feedbacks, ecological transitions, and extinction (Fig. 2)[18]. The primary trigger (or set of triggers) is the environmental disturbance(s) that precipitates the mass extinction—including, for instance, asteroid impact or massive volcanism[12]. A primary trigger need not drive many species extinct, as per the classic view of mass extinctions (Fig. 3a, scenario 1). Rather, it need only cause sufficient disturbance for processes like extinction debt[54,55] or ecological collapse[18] to result in mass secondary extinctions (Fig. 3b, scenario 2). A primary trigger might produce widespread rarity of formerly dominant taxa, thereby greatly elevating rates of background extinction for these taxa (Fig. 3c, scenario 3), or could directly cause the extinction of all species lost in a given interval. In addition, ecological turnover may precede the loss of taxa (that is, be driven by the primary trigger) or follow it (that is, result from the loss of species during extinction).

The brevity of mass extinctions (Box 1), combined with the time-averaged nature of the fossil record, currently precludes an understanding of the relative contribution of these four processes (Fig. 3). This makes it very difficult to use fossil data to disentangle alternative scenarios of the dynamics of mass extinctions: 'trigger kills all' (Fig. 3a), 'trigger sparks feedbacks and secondary extinctions' (Fig. 3b), and 'trigger drives mass rarity and elevated extinction risk' (Fig. 3c). We have little information yet about the relative importance of primary and secondary extinctions or mass rarity during past events.

BOX 1

The scale of extinction dynamics

Extinction intervals are extremely short (Fig. 2), even geologically instantaneous, relative to the typical resolving power of the fossil record[112] (see Box Figure). The three mass extinction events with the best geochronologic constraints on their duration (PT, TJ and KPg) all occurred on time scales on the order of 10^3–10^4 years[18,113–115]. In exceptional circumstances, rapid sedimentation may preserve a temporally detailed record of a mass extinction in a local region[114]. However, taphonomic and sedimentological processes typically time-average accumulations of shell material such that individual samples will represent communities mixed over 10^3–10^4 year intervals. We consider events 'geologically instantaneous' if they occur on timescales at or below the resolution of the records used to study them (here 10^3–10^4 years). While exceptional 'snapshots' of the fossil seafloor during a single moment of time do exist (that is, Konservat Lagerstätten), they are so infrequent that they rarely figure in studies of mass extinctions, and none have yet been discovered crossing a major extinction boundary. The global paleontological and marine core compilations that are so key for detailing the broader patterns of extinction, currently lack the temporal resolution needed to disentangle the dynamics within the extinction interval. The unavoidable conclusion is that the 'pixel size' of the fossil record may be too temporally coarse, or spatially restricted, to resolve the most important processes during the extinction phase.



Box Figure Mismatch in the spatio-temporal scale of ecosystems collapse and the resolving power of the fossil record. The fossil record provides detailed records of macroevolutionary processes occurring at many spatial and temporal scales (shaded regions). The dynamics of extinction intervals occur on spatial and temporal scales just beyond those that are readily documented (striped box).

To be clear, these three scenarios are distinguished by the internal dynamics of the extinction interval (Figs 1 and 3). In scenario 1, the extinction of well-fossilized taxa is driven by the trigger and coincides with, or even precedes, major environmental change. In scenarios 2 and 3, mass extinction is delayed—being driven by secondary feedbacks or elevated background extinction risk, respectively—after profound ecological disruption.

Comparing the present crisis to those that have occurred in the past requires knowing which of these scenarios is typical or dominant, as each involves distinct patterns of feedback, propagation of risk, and timing of extinction. To date, palaeontologists have acted on the implicit assumption that the first scenario is correct (with rare exceptions, as in refs 18, 56, 57), when all the fossil record indicates—at a minimum—is that there must have been a geological instantaneous loss in the abundance of previously dominant taxa at the extinction boundary (the third scenario). The relative importance of these scenarios during the extinction interval cannot be disentangled by standard quantitative paleontological approaches, like those used to estimate species ranges or to control for uneven sampling in diversity dynamics[58], because the timescale of the extinction interval is much shorter than the uncertainty intervals associated with these approaches.

That said, the dynamics of modern ecosystems support the inference that mass rarity can drive permanent ecosystem change. Taxa need not go locally or globally extinct to destroy the links in an ecological network. Rather, species simply have to become so rare as to be ecologically insignificant[59,60]. For instance, in the Chesapeake Bay changes in land use (runoff, sedimentation and nitrification) and overfishing of oysters in the 19th and 20th centuries contributed to shift from a highly productive estuarine ecosystem with thriving oyster, crab and fish fisheries, to a eutrophic, oxygen-depleted, bacterially dominated system[61,62]. Likewise, overfishing of North Atlantic cod similarly resulted in a shift from a fish (cod)-dominated system to one dominated by invertebrates (shrimps, crab and lobster[59,63]). In the Caribbean, coral reefs collapsed after centuries of overfishing and pollution compounded by warming, coral bleaching, disease and invasive species, with widespread replacement of corals by macroalgae[36,61,64]. In each case, the new structure seems to be an alternative stable state, as extensive management efforts have been unable to restore historic ecosystem structure[60,65].

The fossil record likewise documents examples of profound ecosystem change owing to shifts in the relative abundance (not just presence or absence) of taxa, including many of the turnovers in dominant reef builders[66,67], the rise of angiosperms[68] and C4-grasses[69], and during past biodiversity crises (see discussion below). In short, there is no a priori reason to believe that the extirpation of species drives observed ecosystem changes at mass extinction boundaries—global mass rarity may be as plausible a mechanism for ecosystem change as mass extinction. This being the case, we suggest that the extent of mass rarity might be the best metric for comparing the current crisis to those in the fossil record.

The kill mechanism need only make the common rare

Although palaeontologists have focused on extinction more than rarity, they have identified unusual phenomena associated with rarity during mass extinction episodes. Rarity matters because geographically or numerically restricted taxa typically have a relatively small probability of being preserved in the fossil record, or being recovered by palaeontologists[70]. A species that undergoes a drastic reduction in population size, or contraction in range size, can thus appear to be 'extinct' in the fossil record, until that population either recovers, or eventually dies out entirely[71,72].

Species that disappear from the fossil record—sometimes repeatedly, and often for millions of years—only to subsequently reappear are called 'Lazarus' taxa[72]. Such taxa are known from each of the Big Five mass extinctions boundaries[72]. They include a variety of clades with high preservation potential, such as molluscs across the PT extinction[73], brachiopods across the Ordovician–Silurian[74] and KPg[75] extinctions, and ostracods across the late Devonian extinction[76]. Outside of extinction boundaries, once-abundant taxa can also vanish from the fossil record for 10^5–10^6 years without extinction, owing to rarity. Striking examples include the coelacanth fishes (currently extant; ~70 million year fossil gap[77]) and the once widely abundant marine algae *Cyclagelosphaera* (currently extant; 54 million year fossil gap[78]).

Another example of extinction-related rarity is found in species that persist in low numbers through an extinction interval before dying out in the aftermath—a phenomenon known as 'Dead Clades Walking'[79,80].

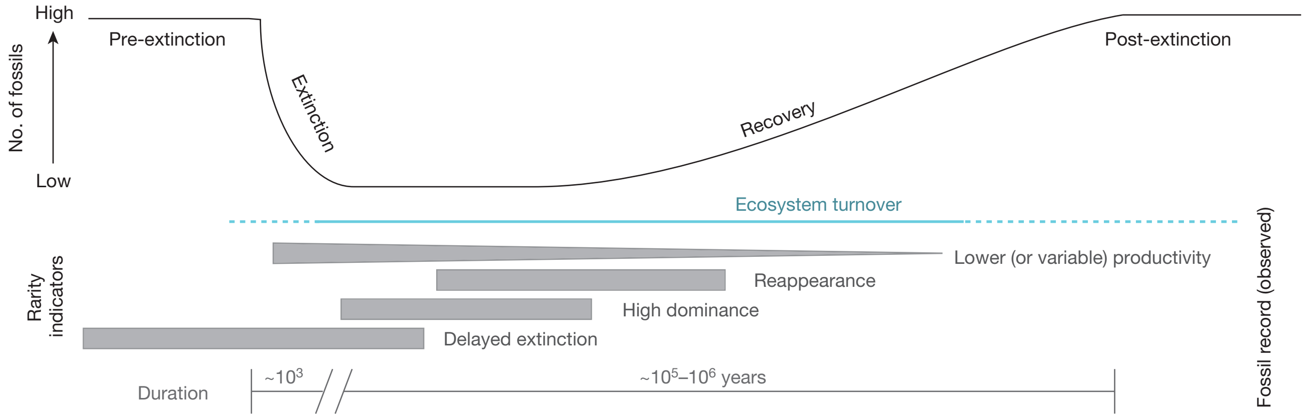


Figure 2 | The sequence of taxonomic and ecosystem events across extinctions is unclear. Extinction intervals have four recognized phases (at the top: pre-extinction, extinction, recovery, post-extinction), based on the richness of fossils preserved. The relationship between fossil diversity and changes in ecosystem structure and function is unclear and may precede, coincide with, or follow the lost fossil diversity (blue solid to dashed line). A wide variety of palaeontological phenomena (grey boxes) document pervasive rarity as a feature of past mass extinctions. Most are widely accepted phenomena, with only the evidence for lowered productivity still debated within and among events[56,87–91].

A frequently cited case is that of bellerophontid gastropods after the PT extinction[81]. More generally, an estimated 10–20% of the genera surviving extinction intervals die out before global biodiversity recovers[79]. For other taxa we might imagine that the sudden loss of fossils across a boundary is driven by extinction or by persistent rarity. For the second case, rarity and range contractions at extinction boundaries can be followed by eventual extinction, long disconnected from the last fossil occurrence.

Three final attributes of past mass extinctions support the hypothesis of pervasive mass rarity. These features include the short-lived dominance of post-extinction taxa, the rarity of previously widespread habitats, and evidence for decreased primary productivity in the wake of extinctions. Those species that dominate assemblages immediately after extinctions are know as ‘bloom taxa’[16]. They have been recognized from the major, as well as many minor, extinction events[16,20,71,82,83]. The ecological success of post-extinction dominants in the unusual ecosystems characterizing

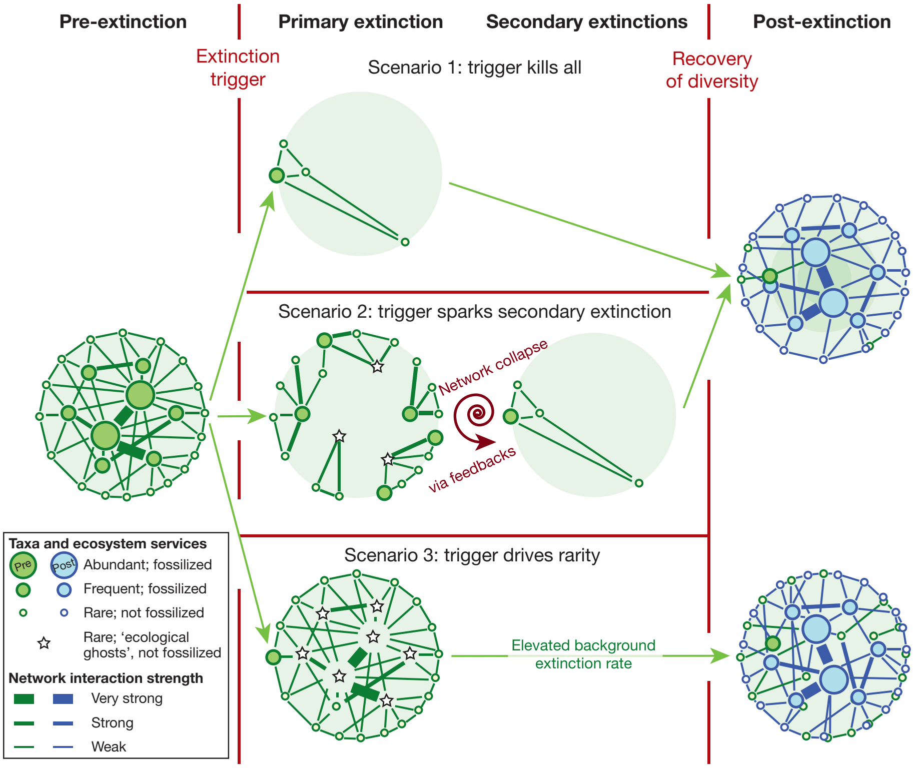


Figure 3 | The geological brevity of mass extinctions makes it difficult to discern the relative importance of various processes. Mass extinction intervals are geologically instantaneous, making it difficult to measure the processes responsible for determining the size and ecological impact of any event. Three major extinction interval scenarios are (top) scenario 1: the primary extinction trigger directly kills off the pre-extinction taxa, with the size and impact of extinction determined by trigger; (middle) scenario 2: the extinction trigger kills key taxa (or environmental resources) with feedbacks leading to secondary extinctions; or (bottom) scenario 3: the trigger makes many species rare, many of which go extinct, and when abundant populations recover, the ecosystem, by chance, is structured differently. In scenarios 2 and 3 the decreased abundance in key taxa is sufficient to diminish their ecological effect (they become ecological ghosts) and precipitates further ecosystem collapse through secondary extinction and feedbacks. Also note that the primary trigger can be called the ‘kill-mechanism’ and include multiple coincident disturbances.

extinction aftermaths coincides with the prolonged rarity of all other taxa[16,83,84]. At the same time, pre-extinction habitats themselves often become rare or altered, as revealed by changes in the composition, continuity and texture of common sedimentary rock types[20,73,85]. In addition, the rate of sediment accumulation is often much lower during and after the extinction interval (for example, prolonged low sedimentation after the PT[86]), a feature due at least in part to the low abundance of fossil-forming organisms (as for pelagic sediments after the KPg[87]). This, and other lines of evidence[56,87–89], have been used to argue for some suppression of primary productivity in the aftermath of extinctions—although to what extent this is true is still hotly debated[90,91]. Regardless, these lines of evidence indicate that pervasive rarity of formerly abundant taxa is unifying feature of extinctions and their aftermaths.

This evidence for mass rarity during past extinction events is surprisingly similar to the widespread rarity of previously common flora and fauna today. The modern ocean is full of ecological 'ghosts'—taxa that are so rare they no longer provide past ecological services[36,38,92,93]. Mass rarity includes local, often remarkable, declines in species abundance, as well as range contractions (as reviewed in refs 38 and 44). For those species with excellent historical and fossil records, like Caribbean corals, the recent population collapse contrasts with the marked resilience to past climatic perturbation[36,94,95]. What's more, the loss of species abundance is known to, at times, have cascading effects on ecosystem structure and function[45], and extinction debt may cause extinction hundreds[96] to millions[97] of years after an environmental perturbation. In this light, the paucity of extinctions in the oceans to date should not be viewed as a sign of the relative health of marine ecosystems[11,38]—rarity itself may be the most direct metric of how close global ecosystems are to a permanent state shift.

Saving the fossil record of today

The effect of humanity is so pervasive[32,36,93] that we are leaving a globally recognizable mark in the rock record[98,99]. Some scientists are seeking to formally recognize this moment as the 'Anthropocene'[100,101]—defining it as the epoch of human-dominated earth systems[98,99]. As we consider humanity's effect on the biosphere, we must recognize that this history is still being written in stone and it remains ours to shape. Thus our hypothesis of past mass extinctions as mass rarity events offers a to-do list for avoiding the ecological aftermath of catastrophic and global biotic crises.

For ecologists and conservation biologists, we have argued that, on timescales comparable to those studied today, past mass extinction events may have been characterized by the geologically instantaneous mass rarity of previously abundant, widespread, well-preserved species. This argument is supported by the nature of the rock record, in which the observed presence or absence of a fossil species depends as much on its abundance as its existence. The rarity of previously common taxa is the only factor tied with certainty to the profound ecological change observed across extinction boundaries. And rarity alone may be enough to drive permanent shifts in the earth system—long before 'rare' turns into 'extinct'. Because of this, we argue that changes in the abundance and ranges of previously common taxa provide an additional, potentially more accurate, metric of the severity of the current biotic crisis relative to those in the past than do extrapolated extinction rates.

To date, the majority of extinction studies have been biased towards terrestrial species and charismatic megafauna[102,103] and we know relatively little about changes in the abundance and ranges of the shelly marine invertebrates that would provide a direct link to mass extinctions in the fossil record[104]. Rarity of previously common taxa matters. In order to avoid a mass-extinction-like fossil record, we need to increase the population size and geographic range of once-abundant taxa and trophic groups (that is, reverse defaunation and defloration) and minimize the geographic extent of habitat destruction.

From custodians of deep time[105], we need quantitative assessments of the fossil record of the present and future earth in order to accurately size up current biotic changes with the same filter through which we see the past. Equally important will be studies of the dynamics and resilience of full ecological networks (not just trophic food webs) during massive perturbations. Spatially explicit models of the various extinction scenarios (Fig. 3) would likewise aid in distinguishing among the potential mechanisms at play during mass extinctions[18]. Ongoing efforts to build palaeontological data archives[106] and to collect finely resolved records from extinction boundaries[19,90,91] are likewise key, as they provide the means to globally test emergent predictions on relevant timescales and key processes, like geographic rarity, on others[107,108]. Finally, the fossil record offers numerous examples of ecosystem change with and without fossil extinctions[109,110]. How and why this occurs is a key question to address if we are to predict, and avoid, a state shift in the structure and function of our biosphere in the years to come[110]. Although extinctions are rare[44], the ecological ghosts of oceans past already swim in emptied seas[11,111].

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