Has the Earth’s sixth mass extinction already arrived?

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Palaeontologists characterize mass extinctions as times when the Earth loses more than three-quarters of its species in a geologically short interval, as has happened only five times in the past 540 million years or so. Biologists now suggest that a sixth mass extinction may be under way, given the known species losses over the past few centuries and millennia. Here we review how differences between fossil and modern data and the addition of recently available palaeontological information influence our understanding of the current extinction crisis. Our results confirm that current extinction rates are higher than would be expected from the fossil record, highlighting the need for effective conservation measures.

Table 1 | The ‘Big Five’ mass extinction events

<table>
<thead>
<tr>
<th>Event</th>
<th>Proposed causes</th>
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<tbody>
<tr>
<td>The Ordovician event44-46 ended ~443 Myr ago; within 3.3 to 1.9 Myr 57% of genera were lost, an estimated 86% of species.</td>
<td>Onset of alternating glacial and interglacial episodes; repeated marine transgressions and regressions. Uplift and weathering of the Appalachians affecting atmospheric and ocean chemistry. Sequestration of CO₂.</td>
</tr>
<tr>
<td>The Devonian event44,67-70 ended ~359 Myr ago; within 29 to 2 Myr 35% of genera were lost, an estimated 75% of species.</td>
<td>Global cooling (followed by global warming), possibly tied to the diversification of land plants, with associated weathering, paedogenesis, and the drawdown of global CO₂. Evidence for widespread deep-water anoxia and the spread of anoxic waters by transgressions. Timing and importance of bolide impacts still debated.</td>
</tr>
<tr>
<td>The Permian event61-71 ended ~251 Myr ago; within 2.8 Myr to 160 Kyr 56% of genera were lost, an estimated 96% of species.</td>
<td>Siberian volcanism. Global warming. Spread of deep marine anoxic waters. Elevated H2S and CO₂ concentrations in both marine and terrestrial realms. Ocean acidification. Evidence for a bolide impact still debated.</td>
</tr>
<tr>
<td>The Triassic event64,72 ended ~200 Myr ago; within 8.3 Myr to 600 Kyr 47% of genera were lost, an estimated 80% of species.</td>
<td>Activity in the Central Atlantic Magmatic Province (CAMP) thought to have elevated atmospheric CO₂ levels, which increased global temperatures and led to a calcification crisis in the world oceans.</td>
</tr>
<tr>
<td>The Cretaceous event65,73-75 ended ~65 Myr ago; within 2.5 Myr to less than a year 40% of genera were lost, an estimated 76% of species.</td>
<td>A bolide impact in the Yucatán is thought to have led to a global cataclysm and caused rapid cooling. Preceding the impact, biota may have been declining owing to a variety of causes: Deccan volcanism contemporaneous with global warming; tectonic uplift altering biogeography and accelerating erosion, potentially contributing to ocean eutrophication and anoxic episodes. CO₂ spike just before extinction, drop during extinction.</td>
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Severe data comparison problems

**Box 1**

**Severe data comparison problems**

**Geography**

The fossil record is very patchy, sparsest in upland environments and tropics, but modern global distributions are known for many species.

A possible comparative technique could be to examine regions or biomes where both fossil and modern data exist—such as the near-shore marine realm including coral reefs and terrestrial depositional lowlands (river valleys, coastlines, and lake basins). Currently available databases could be used to identify modern taxa with geographic ranges indicating low fossilization potential and then extract them from the current-extinction equation.

**Taxa available for study**

The fossil record usually includes only species that possess identifiable anatomical hard parts that fossilize well. Theoretically all living species could be studied, but in practice extinction analyses often rely on the small subset of species evaluated by the IUCN. Evaluation following IUCN procedures places species in one of the following categories: extinct (EX), extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC) or data deficient (DD), information insufficient to reliably determine extinction risk. Species in the EX and EW categories are typically counted as functionally extinct. Those in the CR plus EN plus VU categories are counted as ‘threatened’. Assignment to CR, EN or VU is based on how high the risk of extinction is determined to be using five criteria (roughly, CR probability of extinction exceeds 0.50 in ten years or three generations; EN probability of extinction exceeds 0.20 in 20 years or five generations; VU probability of extinction exceeds 0.10 over a century).

A possible comparative technique could be to use taxa best known in both fossil and modern records: near-shore marine species with shells, lowland terrestrial vertebrates (especially mammals), and some plants. This would require improved assessments of modern bivalves and gastropods. Statistical techniques could be used to clarify how a subsample of well-assessed taxa extrapolates to undersampled and/or poorly assessed taxa.

**Taxonomy**

Analyses of fossils are often done at the level of genus rather than species. When species are identified they are usually based on a morphological species concept. This can result in lumping species together that are distinct, or, if incomplete fossil material is used, over-splitting species. For modern taxa, analyses are usually done at the level of species, often using a phylogenetic species concept, which probably increases species counts relative to morphospecies.

A possible comparative technique would be to aggregate modern phylogenetic species into morphospecies or genera before comparing with the fossil record.

**Assessing extinction**

Fossil extinction is recorded when a taxon permanently disappears from the fossil record and underestimates the actual number of extinctions (and number of species) because most taxa have no fossil record. The actual time of extinction almost always postdates the last fossil occurrence. Modern extinction is recorded when no further individuals of a species are sighted after appropriate efforts. In the past few decades designation as ‘extinct’ usually follows IUCN criteria, which are conservative and likely to underestimate functionally extinct species. Modern extinction is also underestimated because many species are unevaulated or undescribed.

A possible comparative technique could be to standardize extinction counts by number of species known per time interval of interest (proportional extinction). However, fossil data demonstrate that background rates can vary widely from one taxon to the next, so fossil-to-modern extinction rate comparisons are most reliably done on a taxon-by-taxon basis, using well-known extant clades that also have a good fossil record.

**Time**

In the fossil record sparse samples of species are discontinuously distributed through vast time spans, from $10^3$ to $10^6$ years. In modern times we have relatively dense samples of species over very short time spans of years, decades and centuries. Holocene fossils are becoming increasingly available and valuable in linking the present with the past.

A possible comparative technique would be to scale proportional extinction relative to the time interval over which extinction is measured.

(Box 1). Fossils are widely acknowledged to be a biased and incomplete sample of past species, but modern data also have important biases that, if not accounted for, can influence global extinction estimates. Only a tiny fraction (~2.7%) of the approximately 1.9 million named, extant species have been formally evaluated for extinction status by the International Union for Conservation of Nature (IUCN). These IUCN compilations are the best available, but evaluated species represent just a few twigs plucked from the enormous number of branches that compose the tree of life. Even for clades recorded as 100% evaluated, many species still fall into the Data Deficient (DD) category. Also relevant is that not all of the partially evaluated clades have had their species sampled in the same way; some are randomly subsampled, and others are evaluated as opportunity arises or because threats seem apparent. Despite the limitations of both the fossil and modern records, by working around the diverse data biases it is possible to avoid errors in extrapolating from what we do know to inferring global patterns. Our goal here is to highlight some promising approaches (Table 2).

**Defining mass extinctions relative to the Big Five**

Extinction involves both rate and magnitude, which are distinct but intimately linked metrics. Rate is essentially the number of extinctions divided by the time over which the extinctions occurred. One can also derive from this a proportional rate—the fraction of species that have gone extinct per unit time. Magnitude is the percentage of species that have gone extinct. Mass extinctions were originally diagnosed by rate: the pace of extinction appeared to become significantly faster than background extinction. Recent studies suggest that the Devonian and Triassic events resulted more from a decrease in origination rates than an increase in extinction rates. Either way, the standing crop of the Earth’s species fell by an estimated 75% or more. Thus, mass extinction, in the conservative palaeontological sense, is when extinction rates accelerate relative to origination rates such that over 75% of species disappear within a geologically short interval—typically less than 2 million years, in some cases much less (see Table 1). Therefore, to document where the current extinction episode lies on the mass extinction scale defined by the Big Five requires us to know both whether current extinction rates are above background rates (and if so, how far above) and how closely historic and projected biodiversity losses approach 75% of the Earth’s species.

**Background rate comparisons**

Landmark studies that highlighted a modern extinction crisis estimated current rates of extinction to be orders of magnitude higher than the background rate (Table 2). A useful and widely applied metric
has been E/MSY (extinctions per million species-years, as defined in refs 15 and 27). In this approach, background rates are estimated from fossil extinctions that took place in million-year--or more time bins. For current rates, the proportion of species extinct in a comparatively very short time (one to a few centuries) is extrapolated to predict what the rate would be over a million years. However, both theory and empirical data indicate that extinction rates vary markedly depending on the length of time over which they are measured. Extrapolating a rate computed over a short time, therefore, will probably yield a rate that is either much faster or much slower than the average million-year rate, so current rates that seem to be elevated need to be interpreted in this light.

Only recently has it become possible to do this by using paleontological databases combined with lists of recently extinct species. The most complete data set of this kind is for mammals, which verifies the efficacy of E/MSY by setting short-interval and long-interval rates in a comparative context (Fig. 1). A data gap remains between about one million and about 50 thousand years because it is not yet possible to date extinctions in that time range with adequate precision. Nevertheless, the overall pattern is as expected: the maximum E/MSY and its variance increase as measurement intervals become shorter. The highest rates are rare but low rates are common; in fact, at time intervals of less than a thousand years, the most common E/MSY is 0. Three conclusions emerge. (1) The maximum observed rates since a thousand years ago (E/MSY $\approx 24$ in 1,000-year bins to E/MSY $= 693$ in 1-year bins) are clearly far above the average fossil rate (about E/MSY $= 1.8$), and even above those of the widely recognized late-Pleistocene megafaunal diversity crash$^{33,35}$ (maximum E/MSY $= 9$, red data points in Fig. 1). (2) Recent average rates are also too high compared to pre-anthropogenic averages: E/MSY increases to over 5 (and rises to data points in Fig. 1). (2) Recent average rates are also too high compared to pre-anthropogenic averages: E/MSY increases to over 5 (and rises to data points in Fig. 1). (2) Recent average rates are also too high compared to pre-anthropogenic averages: E/MSY increases to over 5 (and rises to data points in Fig. 1).

The molecular phylogenies method assumes that diversification rates are constant through time and can be partitioned into originations and extinctions without evidence from the fossil record. Recent work has demonstrated that disentanglement of diversification from extinction rates by this method is difficult, particularly in the absence of a fossil record, and that extinction rates estimated from molecular phylogenies of extant organisms are highly unreliable when diversification rates vary among lineages through time.

Fuzzy Math attempts to account for different biases in fossil and modern samples and uses empirically based fossil background extinction rates as a standard for comparison: 0.25 species per million years for marine invertebrates, determined from the ‘kill-curve’ method, and 0.21 species to 0.46 species per million years for North American mammals, determined from applying maximum-likelihood techniques. The molecular phylogenies method assumes that diversification rates are constant through time and can be partitioned into originations and extinctions without evidence from the fossil record. Recent work has demonstrated that disentanglement of diversification from extinction rates by this method is difficult, particularly in the absence of a fossil record, and that extinction rates estimated from molecular phylogenies of extant organisms are highly unreliable when diversification rates vary among lineages through time.

Comparison of modern short-term rates with fossil long-term rates indicate highly elevated modern rates, but does not take into account interval-rate effect.

**Table 2 | Methods of comparing present and past extinctions**

<table>
<thead>
<tr>
<th>General method</th>
<th>Variations and representative studies</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compare currently measured extinction rates to background rates assessed from fossil record</td>
<td>E/MSY$^*$</td>
<td>7, 10, 15, 27, 62</td>
</tr>
<tr>
<td></td>
<td>Comparative species duration (estimates species durations to derive an estimate of extinction rate)$^<em>$$^</em>$</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Fuzzy Math$^{**}$</td>
<td>44, 80</td>
</tr>
<tr>
<td></td>
<td>Interval-rate standardization (empirical derivation of relationship between rate and interval length over which extinction is measured provides context for interpreting short-term rates)$^*$</td>
<td>This paper</td>
</tr>
<tr>
<td>Use various modelling techniques, including species-area relationships, to assess loss of species</td>
<td>Compare rate of expected near-term future losses to estimated background extinction rates$^{**}$</td>
<td>7, 10, 14, 15</td>
</tr>
<tr>
<td></td>
<td>Assess magnitude of past species losses$^{**}$</td>
<td>42, 45</td>
</tr>
<tr>
<td></td>
<td>Predict magnitude of future losses. Ref. 7 explores several models and provides a range of possible outcomes using different impact storylines$^{**}$</td>
<td>7, 14, 15, 27, 36, 62, 81–84</td>
</tr>
<tr>
<td>Compare currently measured extinction rates to mass-extinction rates</td>
<td>Use geological data and hypothetical scenarios to bracket the range of rates that could have produced past mass extinctions, and compare with current extinction rates (assumes Big Five mass extinctions were sudden, occurring within 500 years, producing a ‘worst-case scenario’ for high rates, but with the possible exception of the Cretaceous event, it is unlikely that any of the Big Five were the fast)$^{**}$</td>
<td>This paper</td>
</tr>
<tr>
<td>Assess extinction in context of long-term clade dynamics</td>
<td>Map projected extinction trajectories onto long-term diversification/ extinction trends in well-studied clades$^{**}$</td>
<td>This paper</td>
</tr>
<tr>
<td>Assess percentage loss of species</td>
<td>Use IUCN lists to assess magnitude or rate of actual and potential species losses in well-studied taxa$^{**}$</td>
<td>This paper and refs 6, 7, 10, 14, 15, 20, 36 and 62</td>
</tr>
<tr>
<td>Use molecular phylogenies to estimate extinction rate</td>
<td>Calculate background extinction rates from time-corrected molecular phylogenies of extant species, and compare to modern rates</td>
<td>85</td>
</tr>
</tbody>
</table>

$^*$ Assumptions that conclusions from well-studied taxa illustrate general principles.

$^{**}$ Assumes that the relationship between number and kind of species lost in study area can be scaled up to make global projections.
Figure 1 | Relationship between extinction rates and the time interval over which the rates were calculated, for mammals. Each small grey datum point represents the E/MSY (extinction per million species-years) calculated from taxon durations recorded in the Paleobiology Database²⁶ (million-year-or-more time bins) or from lists of extant, recently extinct, and Pleistocene species compiled from the literature (100,000-year-and-less time bins)³²,²³,³⁹⁻⁴⁷. More than 4,600 data points are plotted and cluster on top of each other. Yellow shading encompasses the ‘normal’ (non-anthropogenic) range of variance in extinction rate that would be expected given different measurement intervals; for more than 100,000 years, it is the same as the 95% confidence interval, but the fading to the right indicates that the upper boundary of ‘normal’ variance becomes uncertain at short time intervals. The short horizontal lines indicate the empirically determined mean E/MSY for each time bin. Large coloured dots represent the calculated extinction rates since 2010. Red, the end-Pleistocene extinction event. Orange, documented historical extinctions averaged (from right to left) over the last 1, 30, 50, 70, 100, 500, 1,000 and 5,000 years. Blue, attempts to enhance comparability of modern with fossil data by adjusting for extinctions of species with very low fossilization potential (such as those with very small geographic ranges and bats). For these calculations, ‘extinct’ and ‘extinct in the wild’ species that had geographic ranges less than 500 km² as recorded by the IUCN⁵, all species restricted to islands of less than 10⁵ km², and bats were excluded from the counts (under-representation of bats as fossils is indicated by their composing only about 2.5% of the fossil species count, versus around 20% of the modern species count⁶⁰). Brown triangles represent the projections of rates that would result if ‘threatened’ mammals go extinct within 100, 500 or 1,000 years. The lowest triangle (of each vertical set) indicates the rate if only ‘critically endangered’ species were to go extinct (CR), the middle triangle indicates the rate if ‘critically endangered’ + ‘endangered’ species were to go extinct (EN), and the highest triangle indicates the rate if ‘critically endangered’ + ‘endangered’ + ‘vulnerable’ species were to go extinct (VU). To produce Fig. 1 we first determined the last-occurrence records of Cenozoic mammals from the Paleobiology Database²⁶, and the last occurrences of Pleistocene and Holocene mammals from refs 6, 32, 33 and 89–97. We then used R-scripts (written by N.M.) to compute total diversity, number of extinctions, proportional extinction, and E/MSY (and its mean) for time-bins of varying duration. Cenozoic time bins ranged from 25 million to a million years. Pleistocene time bins ranged from 100,000 to 5,000 years, and Holocene time bins from 5,000 years to a year. For Cenozoic data, the mean E/MSY was calculated using the average within-bin standing diversity, which was calculated by counting all taxa that cross each 100,000-year-boundary within a million-year bin, then averaging those boundary-crossing counts to compute standing diversity for the entire million-year-and-over bin. For modern data, the mean was computed using the total standing diversity in each bin (extinct plus surviving taxa). This method may overestimate the fossil mean extinction rate and underestimate the modern means, so it is a conservative comparison in terms of assessing whether modern means are higher. The Cenozoic data are for North America and the Pleistocene and Holocene data are for global extinction; adequate global Cenozoic data are unavailable. There is no apparent reason to suspect that the North American average would differ from the global average at the million-year timescale.

Potentially valuable comparisons of extinction magnitude could come from assessing modern taxonomic groups that are also known from exceptionally good fossil records. The best fossil records are for near-shore marine invertebrates like gastropods, bivalves and corals, and temperate terrestrial mammals, with good information also available for Holocene Pacific Island birds⁶,²³,³³,³⁵,³⁶,³⁹⁻⁴⁴. However, better knowledge of understudied modern taxa is critically important for developing common metrics for modern and fossil groups. For example, some 49% of bivalves went extinct during the end-Cretaceous event⁶, but only 1% of today’s species have even been assessed², making meaningful comparison difficult. A similar problem prevails for gastropods, exacerbated because most modern assessments are on terrestrial species, and most fossil data come from marine species. Given the daunting challenge of assessing extinction risk in every living species, statistical approaches aimed at understanding what well sampled taxa tell us about extinction risks in poorly sampled taxa are critically important²².

For a very few groups, modern assessments are close to adequate. Scleractinian corals, amphibians, birds and mammals have all known species assessed² (Fig. 2), although species counts remain a moving target²⁷. In these groups, even though the percentage of species extinct in historic time is low (zero to 1%), 20–43% of their species and many more of their populations are threatened (Fig. 2). Those numbers suggest that we have not yet seen the sixth mass extinction, but that we would jump from one-quarter to halfway towards it if ‘threatened’ species disappear.

Given that many clades are undersampled or unevenly sampled, magnitude estimates that rely on theoretical predictions rather than empirical data become important. Often species-area relationships or allied modelling techniques are used to relate species losses to habitat-area losses (Table 2). These techniques suggest that future species extinctions will be around 21–52%, similar to the magnitudes expressed

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in Fig. 2, although derived quite differently. Such models may be sensitive to the particular geographic area, taxa and species-area relationship that is employed, and have usually used only modern data. However, fossil-to-modern comparisons using species-area methods are now becoming possible as online palaeontological databases grow. An additional, new approach models how much extinction can be expected under varying scenarios of human impact. It suggests a broader range of possible future extinction magnitudes than previous studies, although all scenarios result in additional biodiversity decline in the twenty-first century.

Combined rate–magnitude comparisons

Because rate and magnitude are so intimately linked, a critical question is whether current rates would produce Big-Five-magnitude mass extinctions in the same amount of geological time that we think most Big Five extinctions spanned (Table 1). The answer is yes (Fig. 3). Current extinction rates for mammals, amphibians, birds, and reptiles (Fig. 3, light yellow dots on the left), if calculated over the last 500 years (a conservatively slow rate), are faster than (birds, mammals, amphibians, which have 100% of species assessed) or as fast as (reptiles, uncertain because only 19% of species are assessed) all rates that would have produced the Big Five extinctions over hundreds of thousands or millions of years (Fig. 3, vertical lines).

Would rates calculated for historical and near-time prehistoric extinctions result in Big-Five-magnitude extinction in the foreseeable future—less than a few centuries? Again, taking the 500-year rate as a possible extinction rate would have been if the extinctions had happened hypothetically over only 500 years (Fig. 3, light yellow dots on the left). On the right illustrate the range of mass extinction rates ($E/MSY$) that would produce the Big Five benchmark in as little as three centuries. It also highlights areas for much-needed future research. Among major unknowns are (1) whether ‘critically endangered’, ‘endangered’ and ‘vulnerable’ species will go extinct, (2) whether the current rates we used in our calculations will continue, increase or decrease; and (3) how reliably extinction rates in well-studied taxa can be extrapolated to other kinds of species in other places.

The backdrop of diversity dynamics

Little explored is whether current extinction rates within a clade fall outside expectations when considered in the context of long-term diversity dynamics. For example, analyses of cetacean (whales and dolphins) extinction and origination rates illustrate that within-clade diversity has been declining for the last 5.3 million years, and that that decline is nested within an even longer-term decline that began some 14 million years ago. Yet, within that context, even if ‘threatened’ genera lasted as long as 100,000 years before going extinct, the clade would still experience an extinction rate that is an order of magnitude higher than anything it has experienced during its evolutionary history.

The fossil record is also enabling us to interpret better the significance of currently observed population distributions and declines. The use of ancient DNA, phylochronology and simulations demonstrate that the phylogenetic structure considered ‘normal’ on the current landscape has in fact already suffered diversity declines relative to conditions a few thousand years ago. Likewise, the fossil record shows that species richness and evenness taken as ‘normal’ today are low compared to preanthropic conditions.

Selectivity

During times of normal background extinction, the taxa that suffer extinction most frequently are characterized by small geographic ranges and low population abundance. However, during times of mass extinction, the rules of extinction selectivity can change markedly, so that widespread, abundant taxa also go extinct. Large-bodied animals and those in certain phylogenetic groups can be particularly hard hit. In that context, the reduction of formerly widespread ranges and disproportionate culling of certain kinds of species may be...
particularly informative in indicating that extinction-selectivity is changing into a state characterizing mass extinctions.

**Perfect storms?**

Hypotheses to explain the general phenomenon of mass extinctions have emphasized synergies between unusual events (23, 24). Common features of the Big Five (Table 1) suggest that key synergies may involve unusual climate dynamics, atmospheric composition and abnormally high-intensity ecological stressors that negatively affect many different lineages. This does not imply that random accidents like a Cretaceous asteroid impact (25, 26) would not cause devastating extinction on their own, only that extinction magnitude would be lower if synergistic stressors had not already ‘primed the pump’ of extinction (27).

More rigorously formulating and testing synergy hypotheses may be especially important in assessing sixth mass extinction potential, because once again the global stage is set for unusual interactions. Existing ecosystems are the legacy of a biotic turnover initiated by the onset of glacial–interglacial cycles that began ~2.6 million years ago, and evolved primarily in the absence of Homo sapiens. Today, rapidly changing atmospheric conditions and warming above typical interglacial temperatures as CO₂ levels continue to rise, habitat fragmentation, pollution, overfishing and overhunting, invasive species and pathogens (like chytrid fungus), and expanding human biomass (28, 29) are all more extreme ecological stressors than most living species have previously experienced. Without concerted mitigation efforts, such stressors will accelerate in the future and thus intensify extinction (27), especially given the feedbacks between individual stressors (29).

**View to the future**

There is considerably more to be learned by applying new methods that appropriately adjust for the different kinds of data and timescales inherent in the fossil records versus modern records. Future work needs to: (1) standardize rate comparisons to adjust for rate measurements over widely disparate timescales; (2) standardize magnitude comparisons by using the same species (or other taxonomic rank) concepts for modern and fossil organisms; (3) standardize taxonomic and geographic comparisons by using modern and fossil taxa that have equal fossilization potential; (4) assess the extinction risk of modern taxa such as bivalves and gastropods that are extremely common in the fossil record but are at present poorly assessed; (5) set current extinction observations in the context of long-term clade, species-richness, and population dynamics using the fossil record and phyleogenetic techniques; (6) further explore the relationship between extinction selectivity and extinction intensity; and (7) develop and test models that posit general conditions required for mass extinction, and how those compare with the current state of the Earth. The huge difference between where we are now, and where we could easily be within a few generations, reveals the urgency of relieving the pressures that are pushing today’s species towards extinction.

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