NATURE | REVIEW

Has the Earth’s sixth mass extinction already arrived?

Anthony D. Barnosky, Nicholas Matzke, Susumu Tomiya, Guinevere O. U. Wogan, Brian Swartz, Tiago B. Quental, Charles Marshall, Jenny L. McGuire, Emily L. Lindsey, Kaitlin C. Maguire, Ben Mersey & Elizabeth A. Ferrer

Nature **471**, 51–57 (03 March 2011) doi:10.1038/nature09678
Published online 02 March 2011

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.

Subject terms: Palaeontology Environmental science Ecology Earth science

Introduction

Of the four billion species estimated to have evolved on the Earth over the last 3.5 billion years, some 99% are gone[1]. That shows how very common extinction is, but normally it is balanced by speciation. The balance wavers such that at several times in life’s history extinction rates appear somewhat elevated, but only five times qualify for ‘mass extinction’ status: near the end of the Ordovician, Devonian, Permian, Triassic and Cretaceous Periods[2, 3]. These are the ‘Big Five’ mass extinctions (two are technically ‘mass depletions’)[4]. Different causes are thought to have precipitated the extinctions (Table 1), and the extent of each extinction above the background level varies depending on analytical technique[4, 5], but they all stand out in having extinction rates spiking higher than in any other geological interval of the last ~540 million years[3] and exhibiting a loss of over 75% of estimated species[2].

Table 1: The ‘Big Five’ mass extinction events

Increasingly, scientists are recognizing modern extinctions of species[6, 7] and populations[8, 9]. Documented numbers are likely to be serious underestimates, because most species have not yet been formally described[10, 11]. Such observations suggest that humans are now causing the sixth mass extinction[10, 12, 13, 14, 15, 16, 17], through co-opting resources, fragmenting habitats, introducing non-native species, spreading pathogens, killing species directly, and changing global climate[10, 12, 13, 14, 15, 16, 17, 18, 19, 20]. If so, recovery of biodiversity will not occur on any timeframe meaningful to people: evolution of new species typically takes at least hundreds of thousands of years[21, 22], and recovery from mass extinction episodes probably occurs on timescales encompassing millions of years[5, 23].

Although there are many definitions of mass extinction and gradations of extinction intensity[4, 5], here we take a conservative approach to assessing the seriousness of the ongoing extinction crisis, by setting a high bar for recognizing mass extinction, that is, the extreme diversity loss that characterized the very unusual Big Five (Table 1). We find that the Earth could reach that extreme within just a few centuries if current threats to many species are not alleviated.

Data disparities

Only certain kinds of taxa (primarily those with fossilizable hard parts) and a restricted subset of the Earth's biomes (generally in temperate latitudes) have data sufficient for direct fossil-to-modern comparisons (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[24]. Also relevant is that not all of the partially evaluated clades have had their species sampled in the same way: some are randomly subsampled[25], 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).

Box 1: Severe data comparison problems

Full box

Table 2: Methods of comparing present and past extinctions

Defining mass extinctions relative to the Big Five

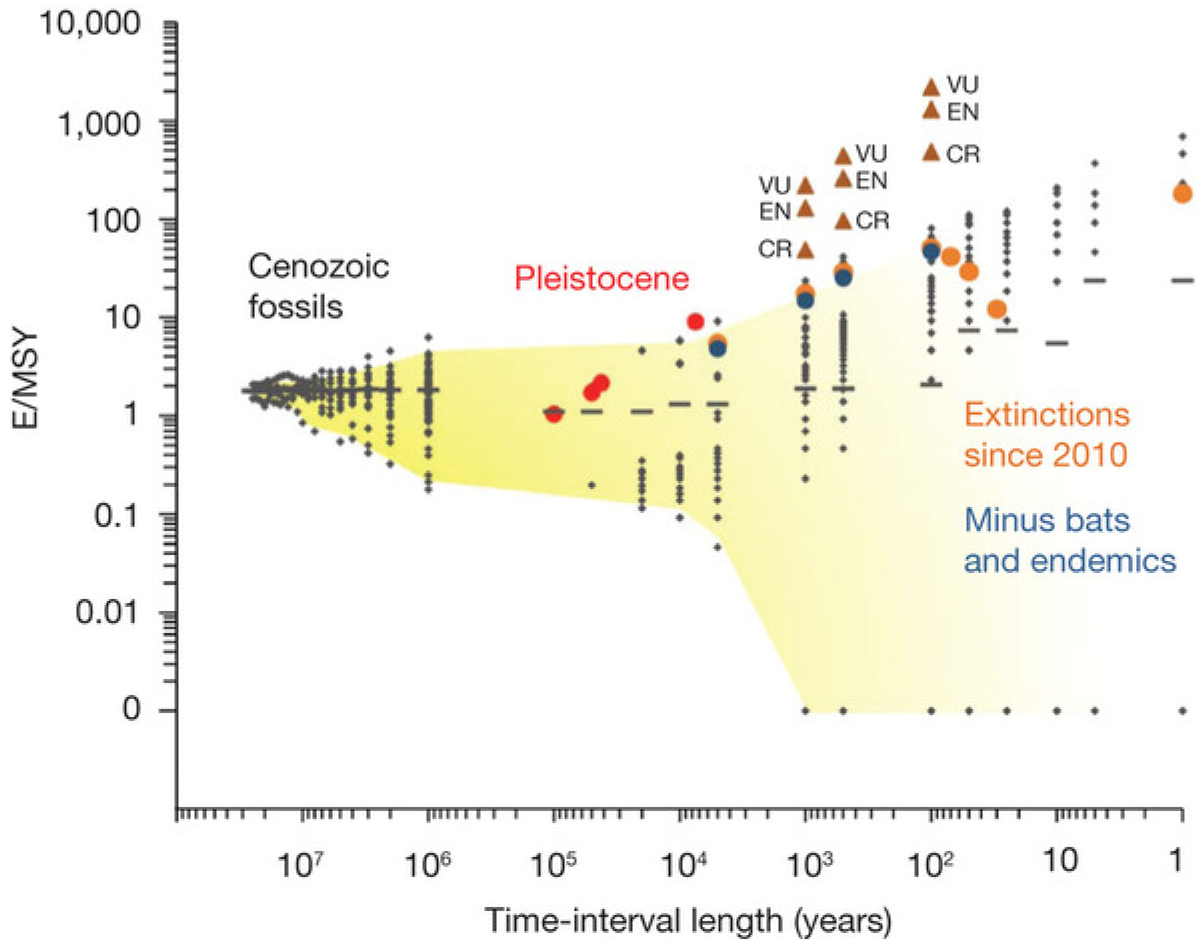
Extinction involves both rate and magnitude, which are distinct but intimately linked metrics[26]. Rate is essentially the number of extinctions divided by the time over which the extinctions occurred. One can also derive from this a proportional rate—the fraction of species that have gone extinct per 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[3]. Recent studies suggest that the Devonian and Triassic events resulted more from a decrease in origination rates than an increase in extinction rates[4, 5]. Either way, the standing crop of the Earth's species fell by an estimated 75% or more[2]. 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[12, 14, 15, 16, 17] 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[28, 29]. 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 palaeontology databases[30, 31] 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 ≈ 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[32, 33] (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 23) in less-than-50-year time bins. (3) In the scenario where currently 'threatened' species[34] would ultimately go extinct even in as much as a thousand years, the resulting rates would far exceed any reasonable estimation of the upper boundary for variation related to interval length. The same applies if the extinction scenario is restricted to only 'critically endangered' species[34]. This does not imply that we consider all species in these categories to be inevitably destined for extinction—simply that in a worst-case scenario where that occurred, the extinction rate for mammals would far exceed normal background rates. Because our computational method maximizes the fossil background rates and minimizes the current rates (see Fig. 1 caption), our observation that modern rates are elevated is likely to be particularly robust. Moreover, for reasons argued by others[27], the modern rates we computed probably seriously underestimate current E/MSY values.

Figure 1: Relationship between extinction rates and the time interval over which the rates were calculated, for mammals.



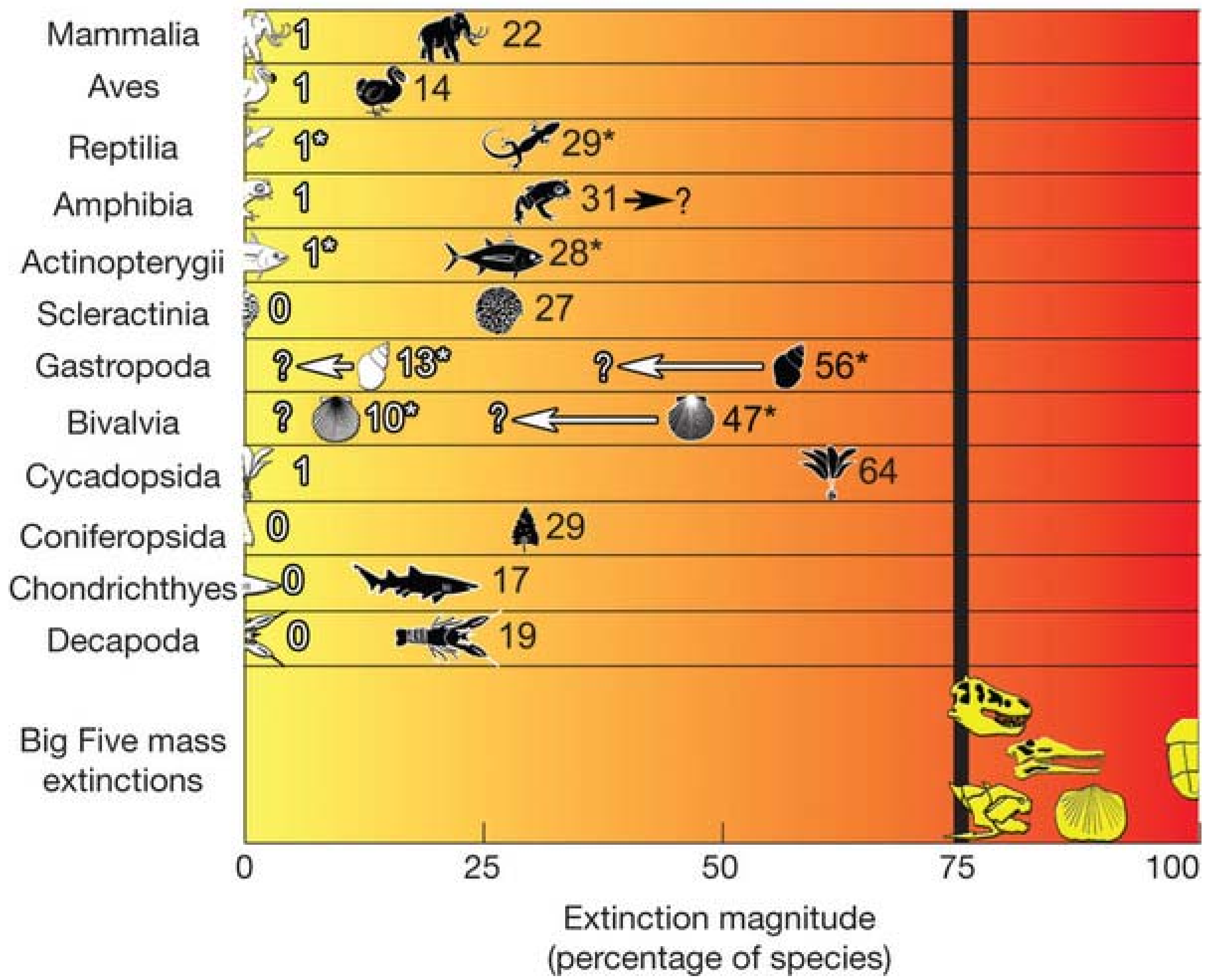
Each small grey datum point represents the E/MSY (extinction per million species-years) calculated from taxon durations recorded in the Paleobiology Database[30] (million-year-or-more time bins) or from lists of extant, recently extinct, and Pleistocene species compiled from the literature (100,000-year-and-less time bins)[6, 32, 33, 89, 90, 91, 92, 93, 94, 95, 96, 97]. 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 km^2 as recorded by the IUCN[6], all species restricted to islands of less than 105 km^2, 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 count[30]). 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 Database[30], 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 computed 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.

Another approach is simply to ask whether it is likely that extinction rates could have been as high in many past 500-year intervals as they have been in the most recent 500 years. Where adequate data exist, as is the case for our mammal example, the answer is clearly no. The mean per-million-year fossil rate for mammals we determined (Fig. 1) is about 1.8 E/MSY. To maintain that million-year average, there could be no more than 6.3% of 500-year bins per million years (126 out of a possible 2,000) with an extinction rate as high as that observed over the past 500 years (80 extinct of 5,570 species living in 500 years). Million-year extinction rates calculated by others, using different techniques, are slower: 0.4 extinctions per lineage per million years (a lineage in this context is roughly equivalent to a species)[35]. To maintain that slower million-year average, there could be no more than 1.4% (28 intervals) of the 500-year intervals per million years having an extinction rate as high as the current 500-year rate. Rates computed for shorter time intervals would be even less likely to fall within background levels, for reasons noted by ref. 27.

Magnitude

Comparisons of percentage loss of species in historical times[6, 36] to the percentage loss that characterized each of the Big Five (Fig. 2) need to be refined by compensating for many differences between the modern and the fossil records[2, 37, 38, 39]. Seldom taken into account is the effect of using different species concepts (Box 1), which potentially inflates the numbers of modern species relative to fossil species[39, 40]. A second, related caveat is that most assessments of fossil diversity are at the level of genus, not species[2, 3, 37, 38, 41]. Fossil species estimates are frequently obtained by calculating the species-to-genus ratio determined for well-known groups, then extrapolating that ratio to groups for which only genus-level counts exist. The over-75% benchmark for mass extinction is obtained in this way[2].

Figure 2: Extinction magnitudes of IUCN-assessed taxa [6] in comparison to the 75% mass-extinction benchmark.



Numbers next to each icon indicate percentage of species. White icons indicate species 'extinct' and 'extinct in the wild' over the past 500 years. Black icons add currently 'threatened' species to those already 'extinct' or 'extinct in the wild'; the amphibian percentage may be as high as 43% (ref. 19). Yellow icons indicate the Big Five species losses: Cretaceous + Devonian, Triassic, Ordovician and Permian (from left to right). Asterisks indicate taxa for which very few species (less than 3% for gastropods and bivalves) have been assessed; white arrows show where extinction percentages are probably inflated (because species perceived to be in peril are often assessed first). The number of species known or assessed for each of the groups listed is: Mammalia 5,490/5,490; Aves (birds) 10,027/10,027; Reptilia 8,855/1,677; Amphibia 6,285/6,285, Actinopterygii 24,000/5,826, Scleractinia (corals) 837/837; Gastropoda 85,000/2,319; Bivalvia 30,000/310, Cycadopsida 307/307; Coniferopsida 618/618; Chondrichthyes 1,044/1,044; and Decapoda 1,867/1,867.

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 birds[2, 33, 35, 42, 43, 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 event[43], but only 1% of today's species have even been assessed[6], 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 important[25].

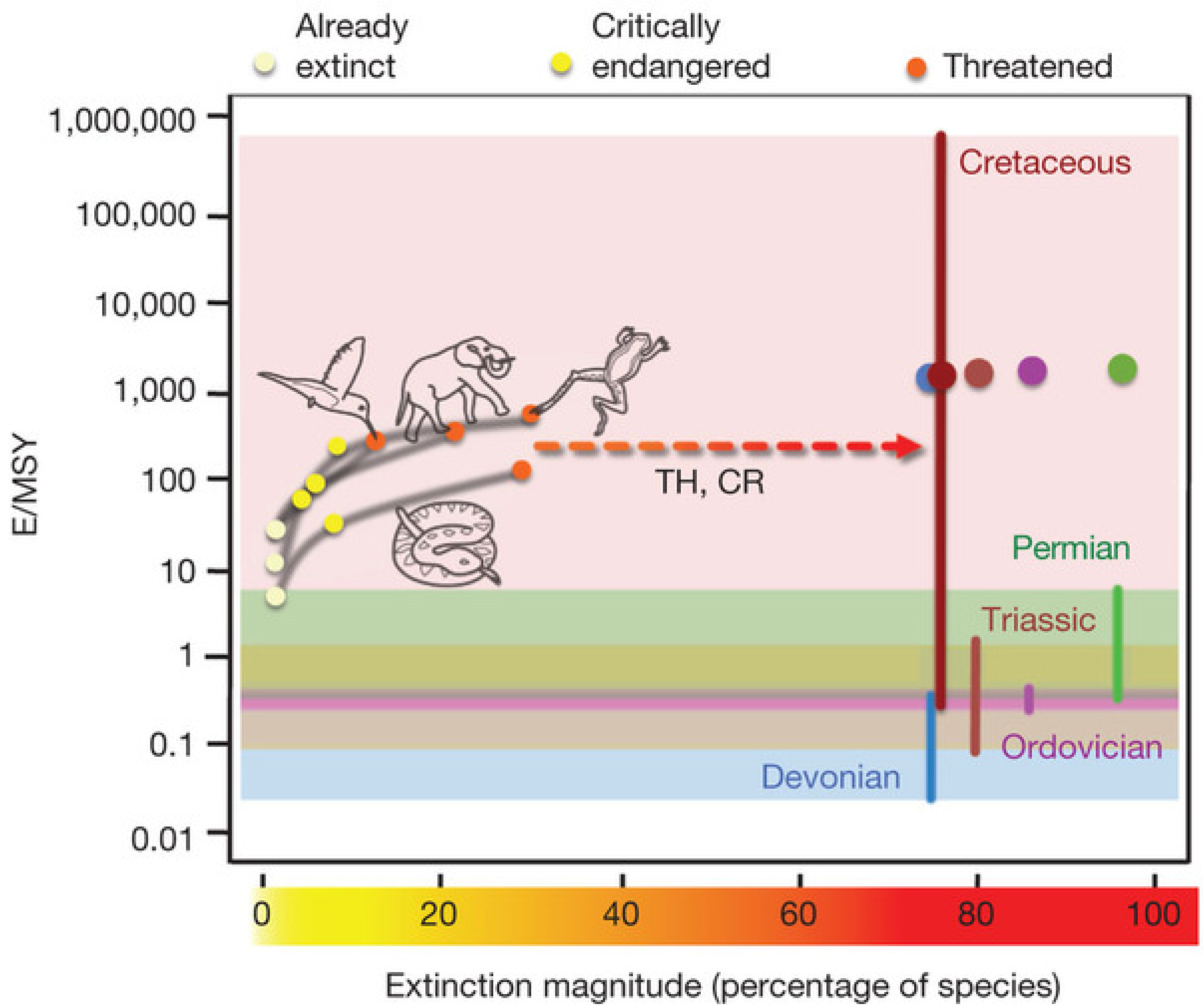
For a very few groups, modern assessments are close to adequate. Scleractinian corals, amphibians, birds and mammals have all known species assessed[6] (Fig. 2), although species counts remain a moving target[27]. In these groups, even though the percentage of species extinct in historic time is low (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 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[30, 31, 45]. An additional, new approach models how much extinction can be expected under varying scenarios of human impact[7]. 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[27]) 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).

Figure 3: Extinction rate versus extinction magnitude.



Vertical lines on the right illustrate the range of mass extinction rates (E/MSY) that would produce the Big Five extinction magnitudes, as bracketed by the best available data from the geological record. The correspondingly coloured dots indicate what the extinction rate would have been if the extinctions had happened (hypothetically) over only 500 years. On the left, dots connected by lines indicate the rate as computed for the past 500 years for vertebrates: light yellow, species already extinct; dark yellow, hypothetical extinction of 'critically endangered' species; orange, hypothetical extinction of all 'threatened' species. TH: if all 'threatened' species became extinct in 100 years, and that rate of extinction remained constant, the time to 75% species loss—that is, the sixth mass extinction—would be ~240 to 540 years for those vertebrates shown here that have been fully assessed (all but reptiles). CR: similarly, if all 'critically endangered' species became extinct in 100 years, the time to 75% species loss would be ~890 to 2,270 years for these fully assessed terrestrial vertebrates.

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 useful basis of comparison, two different hypothetical approaches are possible. The first assumes that the Big Five extinctions took place suddenly and asks what rates would have produced their estimated species losses within 500 years (Fig. 3, coloured dots on the right). (We emphasize that this is a hypothetical scenario and that we are not arguing that all mass extinctions were sudden.) In that scenario, the rates for contemporary extinctions (Fig. 3, light yellow dots on the left) are slower than the rates that would have produced each of the Big Five extinctions in 500 years. However, rates that consider 'threatened' species as inevitably extinct (Fig. 3, orange dots on the left) are almost as fast as the 500-year Big Five rates. Therefore, at least as judged using these vertebrate taxa, losing threatened species would signal a mass extinction nearly on par with the Big Five.

A second hypothetical approach asks how many more years it would take for current extinction rates to produce species losses equivalent to Big Five magnitudes. The answer is that if all 'threatened' species became extinct within a century, and that rate then continued unabated, terrestrial amphibian, bird and mammal extinction would reach Big Five magnitudes in ~240 to 540 years (241.7 years for amphibians, 536.6 years for birds, 334.4 years for mammals). Reptiles have so few of their species assessed that they are not included in this calculation. If extinction were limited to 'critically endangered' species over the next century and those extinction rates continued, the time until 75% of species were lost per group would be 890 years for amphibians, 2,265 years for birds and 1,519 years for mammals. For scenarios that project extinction of 'threatened' or 'critically endangered' species over 500 years instead of a century, mass extinction magnitudes would be reached in about 1,200 to 2,690 years for the 'threatened' scenario (1,209 years for amphibians, 2,683 years for birds and 1,672 years for mammals) or ~4,450 to 11,330 years for the 'critically endangered' scenario (4,452 years for amphibians, 11,326 years for birds and 7,593 years for mammals).

This emphasizes that current extinction rates are higher than those that caused Big Five extinctions in geological time; they could be severe enough to carry extinction magnitudes to 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[7, 20, 25, 34].

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[46].

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 population structure considered 'normal' on the current landscape has in fact already suffered diversity declines relative to conditions a few thousand years ago[47, 48]. Likewise, the fossil record shows that species richness and evenness taken as 'normal' today are low compared to pre-anthropogenic conditions[10, 27, 32, 33, 42, 45, 49].

Selectivity

During times of normal background extinction, the taxa that suffer extinction most frequently are characterized by small geographic ranges and low population abundance[38]. However, during times of mass extinction, the rules of extinction selectivity can change markedly, so that widespread, abundant taxa also go extinct[37, 38]. Large-bodied animals and those in certain phylogenetic groups can be particularly hard hit[33, 50, 51, 52]. In that context, the reduction of formerly widespread ranges[8] and disproportionate culling of certain kinds of species[50, [51, 52, 53] 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[54, 55, 56, 57]. 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[58, 59] 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 [60].

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 CO_2 levels continue to rise, habitat fragmentation, pollution, overfishing and overhunting, invasive species and pathogens (like chytrid fungus), and expanding human biomass[6, 7, 18, 20] 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[7, 20], especially given the feedbacks between individual stressors[56].

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 phylogenetic 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.

Our examination of existing data in these contexts raises two important points. First, the recent loss of species is dramatic and serious but does not yet qualify as a mass extinction in the palaeontological sense of the Big Five. In historic times we have actually lost only a few per cent of assessed species (though we have no way of knowing how many species we have lost that had never been described). It is encouraging that there is still much of the world’s biodiversity left to save, but daunting that doing so will require the reversal of many dire and escalating threats[7, 20, 61, 62, 63].

The second point is particularly important. Even taking into account the difficulties of comparing the fossil and modern records, and applying conservative comparative methods that favour minimizing the differences between fossil and modern extinction metrics, there are clear indications that losing species now in the ‘critically endangered’ category would propel the world to a state of mass extinction that has previously been seen only five times in about 540 million years. Additional losses of species in the ‘endangered’ and ‘vulnerable’ categories could accomplish the sixth mass extinction in just a few centuries. It may be of particular concern that this extinction trajectory would play out under conditions that resemble the ‘perfect storm’ that coincided with past mass extinctions: multiple, atypical high-intensity ecological stressors, including rapid, unusual climate change and highly elevated atmospheric CO_2. 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.

References

1. Novacek, M. J. *The Biodiversity Crisis: Losing What Counts* (The New Press, 2001)
2. Jablonski, D. Extinctions in the fossil record. *Phil. Trans. R. Soc. Lond. B* **344**, 11–17 (1994)
   This paper summarizes, from a palaeontological perspective, the difficulties of comparing the past and present extinctions.
3. Raup, D. M. & Sepkoski, J. J. Mass extinctions in the marine fossil record. *Science* **215**, 1501–1503 (1982)
   This is a statistical assessment of the Big Five extinction rates relative to background rates.
4. Bambach, R. K. Phanerozoic biodiversity mass extinctions. *Annu. Rev. Earth Planet. Sci.* **34**, 127–155 (2006)
   This paper discusses the definition of mass extinctions and mass depletions, and the relative role of origination versus extinction rates in causing the diversity reductions that characterize the Big Five.
5. Alroy, J. Dynamics of origination and extinction in the marine fossil record. *Proc. Natl Acad. Sci. USA* **105**, 11536–11542 (2008)
6. IUCN. International Union for Conservation of Nature Red List 〈http://www.iucn.org/about/work/programmes/species/red_list/〉 (2010)
7. Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501 (2010)
8. Ceballos, G. & Ehrlich, P. R. Mammal population losses and the extinction crisis. *Science* **296**, 904–907 (2002)
9. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. Population diversity: its extent and extinction. *Science* **278**, 689–692 (1997)
10. Dirzo, R. & Raven, P. H. Global state of biodiversity and loss. *Annu. Rev. Environ. Resour.* **28**, 137–167 (2003)
    This paper is an overview of the taxonomic and spatiotemporal patterns of biodiversity and the magnitude of the current biodiversity crisis.
11. Joppa, L. N., Roberts, D. L. & Pimm, S. L. How many species of flowering plants are there? *Proc. R. Soc. Lond. B* doi:10.1098/rspb.2010.1004 (2010)
12. Leakey, R. & Lewin, R. *The Sixth Extinction: Patterns of Life and the Future of Humankind* (Doubleday, 1992)

13. Wake, D. B. & Vredenburg, V. T. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl Acad. Sci. USA* **105**, 11466–11473 (2008)

14. May, R. M., Lawton, J. H. & Stork, N. E. in *Extinction Rates* (eds Lawton, J. H. & May, R. M.) Ch. 1, 1–24 (Oxford University Press, 1995)
This paper compares fossil-background and recent extinction rates and explains the numerous assumptions that are required for the comparison.

15. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science* **269**, 347–350 (1995)
This paper explains and uses the E/MSY metric to compare the fossil-background, current, and predicted future extinction rates.

16. Myers, N. Mass extinctions: what can the past tell us about the present and future? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **82**, 175–185 (1990)

17. Pimm, S. L. & Brooks, T. M. in *Nature and Human Society: The Quest for a Sustainable World* (eds Raven, P. H. & Williams, T.) 46–62 (National Academy Press, 1997)

18. Barnosky, A. D. *Heatstroke: Nature in an Age of Global Warming* 1–269 (Island Press, 2009)

19. Vredenburg, V. T., Knapp, R. A., Tunstall, T. S. & Briggs, C. J. Dynamics of an emerging disease drive large-scale amphibian population extinctions. *Proc. Natl Acad. Sci. USA* **107**, 9689–9694 (2010)

20. Hoffmann, M. *et al.* The impact of conservation on the status of the world's vertebrates. *Science* **330**, 1503–1509 (2010)

21. Avise, J. C., Walker, D. & Johns, G. C. Speciation durations and Pleistocene effects on vertebrate phylogeography. *Proc. R. Soc. Lond. B* **265**, 1707–1712 (1998)

22. Weir, J. T. & Schluter, D. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574–1576 (2007)

23. Lu, P. J., Yogo, M. & Marshall, C. R. Phanerozoic marine biodiversity dynamics in light of the incompleteness of the fossil record. *Proc. Natl Acad. Sci. USA* **103**, 2736–2739 (2006)

24. Vié, J.-C., Hilton-Taylor, C. & Stuart, S. N. (eds) *Wildlife in a Changing World—An Analysis of the 2008 IUCN Red List of Threatened Species* 180 (IUCN, 2009)

25. Baillie, J. E. M. *et al.* Toward monitoring global biodiversity. *Conserv. Lett.* **1**, 18–26 (2008)

26. Şengör, A. M. C., Atayman, S. & Özeren, S. A scale of greatness and causal classification of mass extinctions: implications for mechanisms. *Proc. Natl Acad. Sci. USA* **105**, 13736–13740 (2008)

27. Pimm, S., Raven, P., Peterson, A., Sekercioglu, Ç. H. & Ehrlich, P. R. Human impacts on the rates of recent, present, and future bird extinctions. *Proc. Natl Acad. Sci. USA* **103**, 10941–10946 (2006)

28. Foote, M. Temporal variation in extinction risk and temporal scaling of extinction metrics. *Paleobiology* **20**, 424–444 (1994)
This paper addresses the effect of interval length on extinction metrics using simulations.

29. Foote, M. & Raup, D. M. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* **22**, 121–140 (1996)

30. PBDB. The Paleobiology Database 〈http://paleodb.org/cgi-bin/bridge.pl〉 (2010)

31. NEOMAP. The Neogene Mammal Mapping Portal 〈http://www.ucmp.berkeley.edu/neomap/〉 (2010)

32. Barnosky, A. D. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proc. Natl Acad. Sci. USA* **105**, 11543–11548 (2008)

33. Koch, P. L. & Barnosky, A. D. Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* **37**, 215–250 (2006)

34. Mace, G. M. *et al.* Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* **22**, 1424–1442 (2008)
This paper explains the methodology used by the IUCN to assess the extinction risks of extant species.

35. Alroy, J. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 285–311 (1996)

36. Stork, N. E. Re-assessing current extinction rates. *Biodivers. Conserv.* **19**, 357–371 (2010)

37. Jablonski, D. Lessons from the past: evolutionary impacts of mass extinctions. *Proc. Natl Acad. Sci. USA* **98**, 5393–5398 (2001)

38. Jablonski, D. Extinction and the spatial dynamics of biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 11528–11535 (2008)

39. Purvis, A., Jones, K. E. & Mace, G. M. Extinction. *Bioessays* **22**, 1123–1133 (2000)

40. Agapow, P.-M. *et al.* The impact of the species concept on biodiversity studies. *Q. Rev. Biol.* **79**, 161–179 (2004)

41. Alroy, J. *et al.* Phanerozoic trends in the global diversity of marine invertebrates. *Science* **321**, 97–100 (2008)

42. Steadman, D. W. *Extinction and Biogeography of Tropical Pacific Birds* (University of Chicago Press, 2006)

43. Raup, D. M. & Jablonski, D. Geography of end-Cretaceous marine bivalve extinctions. *Science* **260**, 971–973 (1993)

44. Regan, H. M., Lupia, R., Drinnan, A. N. & Burgman, M. A. The currency and tempo of extinction. *Am. Nat.* **157**, 1–10 (2001)

45. Carrasco, M. A., Barnosky, A. D. & Graham, R. W. Quantifying the extent of North American mammal extinction relative to the pre-anthropogenic baseline. *PLoS ONE* **4**, e8331 (2009)
This paper uses species-area relationships based on fossil data to demonstrate that the recent biodiversity baseline for mammals is substantially depressed with respect to its normal condition.

46. Quental, T. B. & Marshall, C. R. Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* **25**, 434–441 (2010)

47. Anderson, C. N. K., Ramakrishnan, U., Chan, Y. L. & Hadly, E. A. Serial SimCoal: a population genetics model for data from multiple populations and points in time. *Bioinformatics* **21**, 1733–1734 (2005)

48. Ramakrishnan, U. & Hadly, E. A. Using phylochronology to reveal cryptic population histories: review and synthesis of four ancient DNA studies. *Mol. Ecol.* **18**, 1310–1330 (2009)
This paper uses a hypothesis-testing framework to reveal population histories and compare past populations to present ones.

49. Blois, J. L., McGuire, J. L. & Hadly, E. A. Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature* **465**, 771–774 (2010)

50. Cardillo, M. *et al.* Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241 (2005)

51. Davies, T. J. *et al.* Phylogenetic trees and the future of mammalian biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 11556–11563 (2008)

52. Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE* **2**, e296 (2007)

53. Russell, G. J., Brooks, T. M., McKinney, M. M. & Anderson, C. G. Present and future taxonomic selectivity in bird and mammal extinctions. *Conserv. Biol.* **12**, 1365–1376 (1998)

54. Erwin, D. H. The Permo-Triassic extinction. *Nature* **367**, 231–236 (1994)

55. Arens, N. C. & West, I. D. Press-pulse: a general theory of mass extinction? *Paleobiology* **34**, 456–471 (2008)

56. Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460 (2008)

57. Jablonski, D. in *Dynamics of Extinction* (ed. Elliott, D. K.) 183–229 (Wiley, 1986)

58. Alvarez, L. W., Alvarez, W., Asaro, F. & Michel, H. V. Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* **208**, 1095–1108 (1980)

59. Schulte, P. *et al.* The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science* **327**, 1214–1218 (2010)

60. Prauss, M. L. The K/Pg boundary at Brazos-River, Texas, USA—an approach by marine palynology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **283**, 195–215 (2009)

61. GBO3. *Global Biodiversity Outlook 3* 94 (Secretariat of the Convention on Biological Diversity, 2010)

62. Mace, G. *et al.* in *Millenium Ecosystem Assessment, Ecosystems and Human Well-being: Biodiversity Synthesis* (eds Ceballos, S. L. G., Orians, G. & Pacala, S.) Ch. 4, 77–122 (World Resources Institute, 2005)

63. Cardillo, M., Mace, G. M., Gittleman, J. L. & Purvis, A. Latent extinction risk and the future battlegrounds of mammal conservation. *Proc. Natl Acad. Sci. USA* **103**, 4157–4161 (2006)

64. Sepkoski, J. J. in *Global Events and Event Stratigraphy in the Phanerozoic* (ed. Walliser, O. H.) 35–51 (Springer, 1996)

65. Sheehan, P. M. The Late Ordovician mass extinction. *Annu. Rev. Earth Planet. Sci.* **29**, 331–364 (2001)

66. Sutcliffe, O. E., Dowdeswell, J. A., Whittington, R. J., Theron, J. N. & Craig, J. Calibrating the Late Ordovician glaciation and mass extinction by the eccentricity cycles of Earth's orbit. *Geology* **28**, 967–970 (2000)

67. Sandberg, C. A., Morrow, J. R. & Zlegler, W. in *Catastrophic Events and Mass Extinctions: Impacts and Beyond* (eds Koeberl, C. & MacLeod, K. G.) 473–387 (Geological Society of America Special Paper 356, GSA, 2002)

68. McGhee, G. R. *The Late Devonian Mass Extinction* 1–302 (Columbia University Press, 1996)

69. Murphy, A. E., Sageman, B. B. & Hollander, D. J. Eutrophication by decoupling of the marine biogeochemical cycles of C, N, and P: a mechanism for the Late Devonian mass extinction. *Geology* **28**, 427–430 (2000)

70. Algeo, T. J., Scheckler, S. E. & Maynard, J. B. in *Plants Invade the Land: Evolutionary and Environmental Approaches* (eds Gensel, P. G. & Edwards, D.) 213–236 (Columbia University Press, 2000)

71. Berner, R. A. Examination of hypotheses for the Permo-Triassic boundary extinction by carbon cycle modeling. *Proc. Natl Acad. Sci. USA* **99**, 4172–4177 (2002)

72. Payne, J. L. *et al.* Calcium isotope constraints on the end-Permian mass extinction. *Proc. Natl Acad. Sci. USA* **107**, 8543–8548 (2010)

73. Knoll, A. H., Bambach, R. K., Payne, J. L., Pruss, S. & Fischer, W. W. Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* **256**, 295–313 (2007)

74. Hesselbo, S. P., McRoberts, C. A. & Palfy, J. Triassic-Jurassic boundary events: problems, progress, possibilities. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **244**, 1–10 (2007)

75. Ward, P. D. *et al.* Sudden productivity collapse associated with the Triassic-Jurassic boundary mass extinction. *Science* **292**, 1148–1151 (2001)

76. Archibald, J. D. *et al.* Cretaceous extinctions: multiple causes. *Science* **328**, 973 (2010)

77. Keller, G. Cretaceous climate, volcanism, impacts, and biotic effects. *Cretac. Res.* **29**, 754–771 (2008)

78. Mukhopadhyay, S., Farley, K. A. & Montanari, A. A short duration of the Cretaceous-Tertiary boundary event: evidence from extraterrestrial helium-3. *Science* **291**, 1952–1955 (2010)

79. Royer, D. L. CO_2-forced climate thresholds during the Phanerozoic. *Geochim. Cosmochim. Acta* **70**, 5665–5675 (2006)

80. McCallum, M. L. Amphibian decline or extinction? Current declines dwarf background extinction rate. *J. Herpetol.* **41**, 483–491 (2007)

81. Rosenzweig, M. L. Loss of speciation rate will impoverish future diversity. *Proc. Natl Acad. Sci. USA* **98**, 5404–5410 (2001)

82. Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145–148 (2004)

83. Pimm, S. L. & Raven, P. H. Extinction by numbers. *Nature* **403**, 843–845 (2000)

84. Sinervo, B. *et al.* Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899 (2010)

85. Roelants, K. *et al.* Global patterns of diversification in the history of modern amphibians. *Proc. Natl Acad. Sci. USA* **104**, 887–892 (2007)

86. Raup, D. M. A kill curve for Phanerozoic marine species. *Paleobiology* **17**, 37–48 (1991)

87. Foote, M. Estimating taxonomic durations and preservation probability. *Paleobiology* **23**, 278–300 (1997)

88. Rabosky, D. L. Extinction rates should not be estimated from molecular phylogenies. *Evolution* **64**, 1816–1824 (2010)

89. Barnosky, A. D. & Lindsey, E. L. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quat. Int.* **217**, 10–29 (2010)

90. Turvey, S. T. *Holocene Extinctions* (Oxford University Press, 2009)

91. Faith, J. T. & Surovell, T. A. Synchronous extinction of North America’s Pleistocene mammals. *Proc. Natl Acad. Sci. USA* **106**, 20641–20645 (2009)

92. Surovell, T., Waguespack, N. & Brantingham, P. J. Global archaeological evidence for proboscidean overkill. *Proc. Natl Acad. Sci. USA* **102**, 6231–6236 (2005)

93. Finlayson, C. *et al.* Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* **443**, 850–853 (2006)

94. Morwood, M. J. *et al.* Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* **431**, 1087–1091 (2004)

95. Orlova, L. A., Vasil’ev, S. K., Kuz’min, Y. V. & Kosintsev, P. A. New data on the time and place of extinction of the woolly rhinoceros *Coelodonta antiquitatis* Blumenbach, 1799. *Dokl. Akad. Nauk* **423**, 133–135 (2008)

96. Reumer, J. W. F. *et al.* Late Pleistocene survival of the saber-toothed cat *Homotherium* in Northwestern Europe. *J. Vertebr. Paleontol.* **23**, 260–262 (2003)

97. MacPhee, R. D. E. *Extinctions in Near Time: Causes, Contexts, and Consequences* (Kluwer Academic/Plenum Publishers, 1999)

Download references

Acknowledgements

S. Beissinger, P. Ehrlich, E. Hadly, A. Hubbe, D. Jablonski, S. Pimm and D. Wake provided constructive comments. Paleobiology Database data were contributed by M. Carrano, J. Alroy, M. Uhen, R. Butler, J. Mueller, L. van den Hoek Ostende, J. Head, E. Fara, D. Croft, W. Clyde, K. Behrensmeyer, J. Hunter, R. Whatley and W. Kiessling. The work was funded in part by NSF grants EAR-0720387 (to A.D.B.) and DEB-0919451 (supporting N.M.). This is University of California Museum of Paleontology Contribution 2024.

Author information

Affiliations

Department of Integrative Biology, University of California, Berkeley, California 94720, USA

Anthony D. Barnosky,Nicholas Matzke,Susumu Tomiya,Guinevere O. U. Wogan,Brian Swartz,Tiago B. Quental,Charles Marshall,Jenny L. McGuire,Emily L. Lindsey,Kaitlin C. Maguire,Ben Mersey &Elizabeth A. Ferrer

University of California Museum of Paleontology, California, USA
Anthony D. Barnosky,Susumu Tomiya,Brian Swartz,Tiago B. Quental,Charles Marshall,Jenny L. McGuire,Emily L. Lindsey,Kaitlin C. Maguire &Elizabeth A. Ferrer

University of California Museum of Vertebrate Zoology, California, USA
Anthony D. Barnosky,Susumu Tomiya,Guinevere O. U. Wogan &Jenny L. McGuire

Human Evolution Research Center, California, USA
Ben Mersey

Present address: Departamento de Ecologia, Universidade de São Paulo (USP), São Paulo, Brazil
Tiago B. Quental

Present address: National Evolutionary Synthesis Center, 2024 W. Main Street, Suite A200, Durham, North Carolina 27705, USA.
Jenny L. McGuire

Contributions
All authors participated in literature review and contributed to discussions that resulted in this paper. A.D.B. planned the project, analysed and interpreted data, and wrote the paper. N.M. and S.T. performed key data analyses and interpretation relating to rate comparisons. G.O.U.W., B.S. and E.L.L. assembled critical data. T.B.Q. and C.M. provided data, analyses and ideas relating to diversity dynamics and rate-magnitude comparisons. J.L.M. helped produce figures and with N.M., S.T., G.O.U.W., B.S., T.B.Q., C.M., K.C.M., B.M. and E.A.F. contributed to finalizing the text.

Competing financial interests
The authors declare no competing financial interests.

Corresponding author
Correspondence to: Anthony D. Barnosky

Comments

2011-03-15 02:01 AM

Gregory Ryskin said: The percentage of species lost in a mass extinction is not the right statistic to consider. Instead, one should compare the mortality statistics at the level of individuals; this paints a completely different picture. See Abrupt global events in the Earth's history: a physics perspective

2011-04-05 07:30 AM

Mark Thompson said: I agree with your point Ryskin and this is an error that creeps up in conservation literature and the analysis on rates of extinction. However, the notion of individuality in the hierarchical view of life may help in this regard (i.e., treating species as individuals – Ghislen, Hull and Gould wrote extensively on this topic). I have several concern about using species or even genera to examine rates of extinction over time.

Foremost, as you point out it is not the right statistic, but for reasons that pertain to ecosystem services. If we are interested in biodiversity loss conservation biologists need to start thinking beyond the species category and look at the functional diversity as Peter Kareiva has written about for biodiversity 'cold spots'. I live in Prince George BC – we have very few species of amphibians, one salamander species only. However, this single salamander species holds a great amount of biomass and functional utility in our forests. Not only does it contribute to the knowledge of what salamanders are about for conservation efforts that can reach people in a very direct way, they are more important because we lack ecological exchangeability through redundant eco-type that could take its place if lost. Gerardo Ceballos & Paul Ehlrich wrote about population losses in mammals (http://www.sciencemag.org/content/296/5569/904) and correctly state that the population levels of biodiversity as the more sensitive indicator of natural capital – this is where the bulk of the functional biomass is concentrated. Saving species hotspots is not necessarily the most effective way to for conservation biologists to realize their goals to conserve biodiversity.

Moreover, Peter Ward has written about the nature of biodiversity over time in his paper 'The Father of All Mass Extinctions'. "It has long been argued that endemic centers are among the most important places to save. But the point is that endemic centers exist because they have not produced large numbers of successful species. Endemic centers are often living museums of very ancient species that do not have much potential for future evolution." Hence, we have a new emergent context to deal with in the Anthropocene and looking at species diversity in isolation to set conservation targets can put us well off the mark. If you look at population losses, estimated to be 20X the rate of species loss, I think the situation looks even more dire than Barnosky indicates in this article.

Subscribe to comments

Nature ISSN 0028-0836 EISSN 1476-4687