The greatest extinction event in 66 million years?

Jack H Hatfield[1,2*+], Bethany J Allen[3,4], Tadhg Carroll[1,2,5], Christopher D Dean[6], Shuyu Deng[1,2], Jonathan D Gordon[1,2,7], Thomas Guillerme[8], James P Hansford[9,6], Jennifer F Hoyal Cuthill[10], Philip D Mannion[6], Alexander RD Payne[1,2], Inês S Martins[1,2], Amy Shipley[11], Chris D Thomas[1,2], Jamie B Thompson[12], Lydia Woods[11], Katie E Davis[2+]

* jack.hatfield@york.ac.uk

[+] These authors contributed equally

[1] Leverhulme Centre for Anthropocene Biodiversity, University of York, York, UK

[2] Department of Biology, University of York, York, UK

[3] Department of Biosystems Science and Engineering, ETH Zurich, Basel, Switzerland

[4] Computational Evolution Group, Swiss Institute of Bioinformatics, Lausanne, Switzerland

[5] Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK

[6] Department of Earth Sciences, University College London, London, UK

[7] Department of Archaeology, University of York, York, UK

[8] School of Biosciences, University of Sheffield, Sheffield, UK

[9] Institute of Zoology, Zoological Society of London, London, UK

[10] School of Life Sciences, University of Essex, Colchester, UK

[11] School of Earth and Environment, University of Leeds, Leeds, UK

[12] School of Biological Sciences, University of Reading, Reading, UK

Abstract

Biological communities are changing rapidly in response to human activities, with the high rate of vertebrate species extinction leading many to propose that we are in the midst of a sixth mass extinction event. Five past mass extinction events have most commonly been emphasised across the Phanerozoic, with the last occurring at the end of the Cretaceous, 66 million years ago. Life on Earth has, however, always changed and evolved, with most of the species known to have existed now extinct. The question is, are human activities increasing the rate and magnitude of extinction into realms rarely seen in life history? Considering the literature on extinctions, predominantly over the last 66 million years, we ask what comparisons can be meaningfully drawn and when the Earth last witnessed an extinction event on this scale. We conclude that the available evidence suggests that the current event has likely surpassed most other events during the Cenozoic with the exception of the Eocene-Oligocene event for which much uncertainty remains. Currently we are still a long way short of the devastation caused by the bolide impact 66 million years ago. Given the number of endangered and at risk species, the current event is still in progress and much will depend on how humanity interacts with the rest of the biosphere over the coming millennia.

Main

Human activities have resulted in rapid and far-reaching changes to global biodiversity, including the extinction of almost two thirds of vertebrate megafauna (Turvey and Crees 2019), the movement of species across the globe (Thomas 2018), and our influence on the changing climate (Allen *et al.* 2024), with major impacts seen throughout human history and forecast long into the future (Davis *et al.* 2018; Ellis *et al.* 2021; Gordon *et al.* 2024). The rate at which species are going extinct as a result of these impacts has led many scientists to propose that we are now entering a sixth mass extinction focusing on comparisons between current rates and background rate estimates from the fossil record (Barnosky *et al.* 2011; Ceballos *et al.* 2015; Leakey and Lewin 1995; Pimm et al. 2014). The fact that we are witnessing elevated extinction rates is well established but it is not yet clear where the effects of human actions sit in the context of past extinctions, in terms of the rate of loss, the duration of those losses, and the total magnitude. The Earth has experienced multiple climatic and geological perturbations, and hence it is important to assess whether the recent extinction rate and magnitude is indeed higher than at any time over the last 66 million years (Barnosky *et al.* 2011; Cowie *et al.* 2022), or if extinction rate and magnitude are already comparable to those associated with events such as the bolide impact that ended the age of the non-avian dinosaurs (K-Pg) or the large-scale volcanic activity thought responsible for the end Permian Great Dying. Is the Earth currently experiencing a major extinction event, or one only severe on human timescales?

Comparing extinction rates over geological timescales, however, presents numerous difficulties. Data derived from the fossil record is intrinsically different from our knowledge of living species in many ways, including its resolution (spatial, temporal, taxonomic) and the extent to which sampling is biased towards particular species groups and environments. Environments are also not static, and direct comparisons between ancient and modern ecosystems, including how to quantify reasonable expectations of their relative capacity to sustain biodiversity under comparable environmental constraints, are not always straightforward (Dillon *et al.* 2023).

Additional challenges are the differing durations of extinction events, combined with the temporal resolution of the data. The present-day extinction event has by most definitions only lasted for a short time on geological time scales (a few hundred thousand years or less), with a relatively high frequency of data available, and is unfinished. In contrast, the majority of extinction events, especially those caused by global climatic changes, have occurred over much longer time frames. They may also have taken place as a series of extinction rate spikes or pulses linked to different drivers and changes, occurring as part of a more extended extinction event. If so, brief extinction spikes might have occurred before, but would be difficult to detect from the temporal resolution of the fossil record. Indeed, the extinction events bounding the Eocene, approximately 59 and 33.9 Ma, may have unfolded on a 100 ky time frame (Molina 2015; Speijer *et al.* 2012). It is therefore crucial to first examine how an extinction event is defined and how the magnitudes and rates are considered and compared.

Here, we draw on a diverse range of data from both past extinctions and ongoing biodiversity change to better place the period of Anthropogenic extinctions in the wider geological context. To do this we start by examining the events traditionally seen as the largest of all extinction events - the five mass extinctions. We follow this by discussing the last 66 million years, the time at which we have perhaps the best data resolution and Earth's ecosystems and biodiversity are the most similar to those of the present. We then consider the Anthropogenic extinction event here, defined as spanning the last interglacial (~ 130 ka) to the present. This represents the well-established time frame of increasing human planetary influence, from the changing of planetary processes with the megafaunal extinction to the current period where humans have modified the planet to such an extent that our influence is inescapable (Thomas 2020). Next, we discuss the challenges of making meaningful comparisons given the contrasting biases between the fossil record and modern biodiversity data, before exploring what comparisons can be made, and finish by discussing what these mean for the future of biodiversity. We conclude that humans may well be in the process of generating the greatest magnitude extinction event for 66 million years, but that much still depends on the actions taken in the decades and centuries to come.

EXTINCTIONS PAST, PRESENT AND FUTURE

The "Big Five"

Extinction is a fundamental evolutionary process. In fact, more than 99% of all species that have ever existed are now extinct (Jablonski 2004; Raup 1992). Some time periods, however, are known for their atypically high rates of extinctions (extinction events), with the greatest of these being labelled "mass extinctions". However, such events are hard to define with different criteria favoured. One definition of a mass extinction event is a *"substantial* *increase in the amount of extinction suffered by more than one geographically wide-spread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity"* (Sepkoski 1986, p. 278). The ambiguity in this definition has led to more quantitative interpretations such as 75% of species becoming extinct in less than 2 million years (Barnosky *et al.* 2011). Through their dramatic impact on both species and ecosystems, over relatively short periods of time, these events have undoubtedly shaped the evolutionary history of life on Earth across the past ~550 million years (Hull and Darroch 2013; McGhee *et al.* 2004; Raup and Sepkoski 1982). Only five instances are believed to have been this devastating and widespread, and are often described as the "Big Five" mass extinctions. These events are: (1) the Late Ordovician mass extinction (~445 Ma); (2) the Late Devonian mass extinction(s) (~370-360 Ma); (3) The Permian-Triassic mass extinction (~252 Ma); (4) the Late Triassic mass extinction (~201 Ma), and (5) The Cretaceous-Paleogene mass extinction (~66 Ma - K-Pg) (Figure 1) (Raup and Sepkoski 1982).

The extent to which the 'Big 5' are genuinely distinct is debated, given that the Phanerozoic has been punctuated by many supposedly smaller scale and often lesser-known extinction events (Raup 1986), with constantly fluctuating rates suggesting a continuum of extinction episodes (Harper *et al.* 2020). Only the Late Ordovician, Permian-Triassic and Cretaceous-Paleogene extinctions stand out on magnitude alone, with the Late Devonian and Late Triassic being at least partially attributable to reductions in origination (Bambach 2006). On the other hand, Bambach (2006) identified at least 18 substage intervals that could meet the criteria of mass extinction using a genus compendium. This means that all detectable spikes in extinction could be considered mass extinctions, or the term could be reserved for the largest three, apparent even when accounting for various data constraints (see past uncertainties and fossil record biases). Consideration must also be given to the other elements of the definition - multiple geographically widespread higher taxa and relatively short time. Some of the extinctions not viewed as mass extinctions have resulted in significant global changes, such as the Carnian Pluvial Episode (234 to 232 Ma), which saw large-scale loss of genera but also major diversification, resulting in substantial turnover (Dal Corso *et al.* 2020). Many known extinction events are also more geographically restricted or are restricted to particular clades (Arcila and Tyler 2017; Sibert and Rubin 2021; MacLeod 1994) or a selection of particular traits (Aberhan and Baumiller 2003; Pimiento *et al.* 2017; Pym *et al.* 2023). It must, however, be noted that because diversity is usually measured at the level of genera and not species, a notable drop in generic diversity could mean that the geographic spread is considerable, as many genera contain multiple species with different biogeographic ranges (Hallam and Wignall 1997).

Understanding of the rate of extinctions is also extremely important, especially in the context of current biodiversity. What may appear to be an extinction event with a large magnitude (large reduction in standing diversity) could be biologically insignificant on ecological timescales, if it took place steadily over a long time scale. A slow decline in populations over the million year timescales found in the fossil record may look drastic if seen via the geological record, but would not be seen as an extinction event or crisis by any observer at the time (Bambach 2006). Extinction events, however, are being increasingly perceived as pulses (Spalding and Hull 2021), meaning a series of rapid events rather than a prolonged slight increase in rate. A high resolution record for global scale events is however not a possibility. To try and resolve this, attempts have been made to estimate the temporal component based on the hypothesised causes. For example, the K-Pg is believed to be rapid due to the rapid cessation of photosynthesis caused by the impact winter and global cooling from rapid sulphate aerosol release (Morgan *et al.* 2022; Schulte *et al.* 2010). The Late Ordovician, in contrast, is seen as at least two distinctive pulses attributed to cooling, glaciation and changes in ocean chemistry (Bambach 2006).

Defining mass extinctions and comparing between events is therefore a complex and sometimes subjective process. Given the complex causes and consequences, even the largest extinctions that we know of, the “Big Five” are very different to one another and have nuanced trajectories. Using rate and magnitude changes alone are unlikely to meaningfully reveal the changes wrought on the planet and its biosphere. Attempts to categorise what is, in effect, a continuous scale may in this case not be useful. This complexity and continuum of magnitudes of extinction 'events' complicates the discussions of whether the present day represents a potential Big Sixth mass extinction, and therefore represents the greatest extinction event in the last 66 million years.

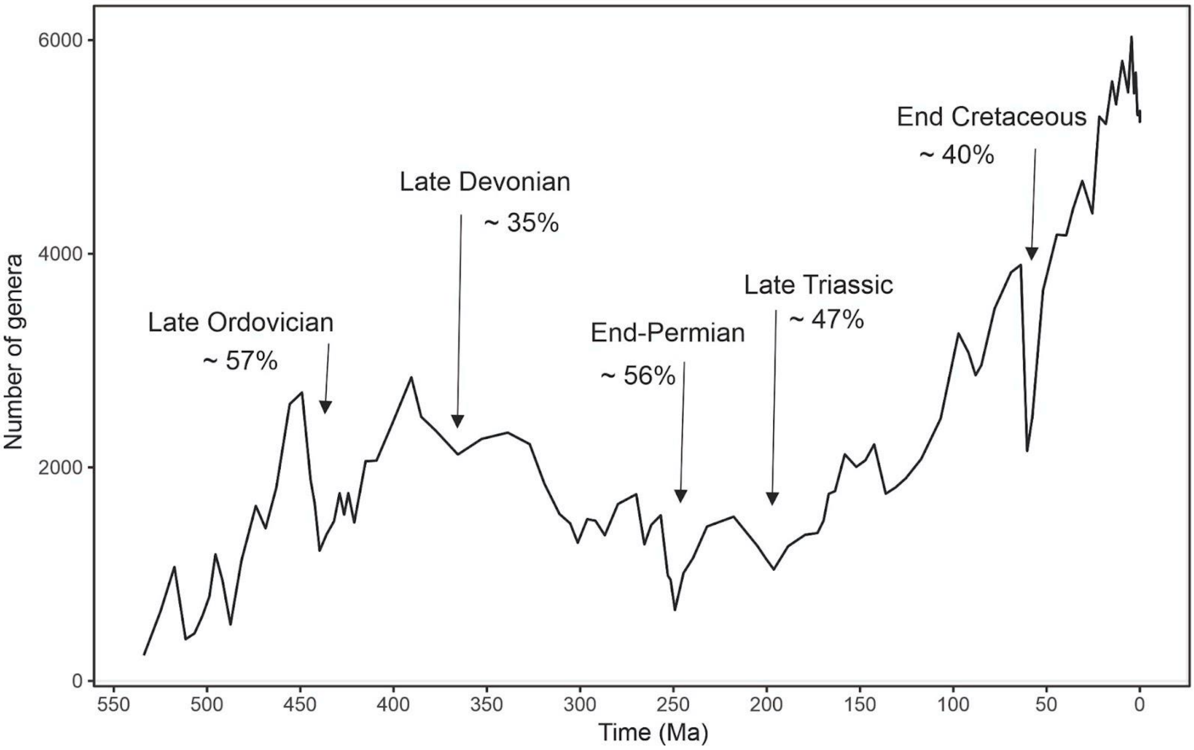

Figure 1 - Number of fossil marine animal genera over the Phanerozoic based on Sepkoski's compendium (Peters 2022; Sepkoski 1981, 2002). Reproduced using the R package sepkoski (Jones 2022). Arrows indicate the Big Five mass extinction events with percentage genera extinction estimates given based on Barnosky *et al*., (2011).

The last 66 million years

The most recent mass extinction event took place at the end of the Cretaceous period, heralding the end of the Mezozoic and the beginning of the Cenozoic, 66 million years ago. The large asteroid impact in the Yucatán Peninsula and subsequent wildfires resulted in dust, sulphate aerosols, CO_2, soot and water vapour entering the atmosphere which led to rapid climatic cooling (followed by warming after the immediate impact winter) and ocean acidification (Chiarenza *et al.* 2020; Morgan *et al.* 2022). An estimated 40% of genera and 76% of species were lost (Barnosky *et al.* 2011). The process was likely very rapid (Chiarenza *et al.* 2020), meaning that both the magnitude and rate of extinction were extremely high. Many vertebrate and invertebrate groups were lost, most famously the non-avian dinosaurs and ammonites, with rapid changes in many taxonomic groups such as planktonic foraminifera (Hallam and Wignall 1997).

Changes in species community structures and Earth systems mean that predicting modern events based on past extinctions faces substantial limitations (Foster *et al.* 2023). Major losses in dominant vertebrate and invertebrate groups during the K-Pg extinction mean that much of the modern flora, fauna and ecosystems originated in the Cenozoic (Finnegan *et al.* 2024). Cenozoic extinction events are therefore likely the most comparable to modern extinctions due to the similarities in ecosystems and species. The continental configuration has also remained relatively consistent even if sea levels have fluctuated with temperature and glaciation. In other ways however, earlier Era comparisons have clear benefits. For example extinction events following the fifth mass extinction have been less severe than many that have preceded them. When it comes to drivers of change, it can also be argued that current climate warming is not well paralleled by other Cenozoic events as most involve cooling not warming. Therefore, although we primarily focus here on the Cenozoic, deeper time comparisons are useful in a number of cases.

Analysis of the fossil record has revealed multiple Cenozoic extinction events, less severe than the K-Pg but still large enough to have long-term consequences for the biosphere. The most prominent of these are the Paleocene-Eocene Thermal Maximum (~ 56 Ma), the Eocene-Oligocene (~ 34 Ma) and the Pliocene (5.3 - 1.8 Ma) (Bambach 2006; Finnegan *et al.* 2024; Harnik *et al.* 2012; Hoyal Cuthill *et al.* 2020).

The events defining the start and end of the Eocene resulted in substantial change in the Earth's systems. The Paleocene- Eocene Thermal Maximum (PETM ~ 56 Ma) saw rapid warming and ocean acidification (Harnik *et al.* 2012) attributed to volcanic activity (Haynes and Hönisch 2020) which lead to turnover in many assemblages and elevated extinction rates for metazoan reef species (Kiessling and Simpson 2011), calcareous nannoplankton (Gibbs *et al.* 2006) and benthic foraminifera (Speijer *et al.* 2012). The event is perhaps most notable for the high levels of extinction in benthic foraminifera, a group that had been relatively unscathed by the K-Pg but seems to have suffered a decline at the PETM unparalleled in the rest of their Cenozoic timeline (Hallam and Wignall 1997). The current evidence suggests that although geographically widespread, high extinction levels were restricted to marine taxa sensitive to the rapid warming and acidification with some evidence for plant and mammal extinctions (Clyde and Gingerich 1998; Jaramillo *et al.* 2006).

Global cooling at the end of the Eocene (34 million years ago) is believed to have caused the Eocene-Oligocene extinction event (Harnik *et al.* 2012). In comparison with the PETM, there is more evidence that both the marine and terrestrial realms were strongly affected, but it is challenging to narrow down the event's duration and the concurrence of regional changes. For example, elevated extinction rates are found for some groups of foraminifera (Pearson *et al.* 2008): these are estimated to be less than 15% at the Eocene-Oligocene boundary, but higher when combined with other Late Eocene extinctions (Keller 1986). Similar patterns are reported for calcareous nannoplankton and molluscs which both show a drawn-out loss and turnover, with marine extinctions extended across as many as 14 million years (Hallam and Wignall 1997). In the terrestrial realm, there is evidence for relatively rapid continental-scale mammal extinctions (de Vries *et al.* 2021; Hooker *et al.* 2004; Weppe *et al.* 2023), with estimates for Western Europe's endemic artiodactyls being as high as 77% of species (62% genera) lost in a million year period (Weppe *et al.* 2023). Increased extinction rates in South American plants has also been documented (Jaramillo *et al.* 2006). Overall, however, evidence points towards a prolonged species turnover in response to global cooling and changing aridity (Hallam and Wignall 1997).

Global cooling again caused elevated extinction rates as the Late Pliocene moved into the Pleistocene (2.6 million years ago), with marine megafauna particularly affected (Pimiento *et al.* 2017). It is estimated that 36% of Pliocene marine megafaunal genera did not survive into the Pleistocene (Pimiento *et al.* 2017). Localised extinctions at the end of the Pliocene have also been noted for Caribbean molluscs and corals (Pimiento *et al.* 2020; van Woesik *et al.* 2012) as well as the loss of many terrestrial African megaherbivores (Bibi and Cantalapiedra 2023) and benthic foraminifera (Hayward *et al.* 2007). Again, however, it is difficult to identify a major global event from current evidence with extinctions unfolding over multi-million year time scales. Extinctions in some groups may span the Late Pliocene into the Mid-Pleistocene in response to changing sea-levels and global cooling.

The current evidence suggests that many of the perceived extinction events in the Cenozoic may have been a drawn-out series of smaller localised events that, in combination, result in large global turnover. The K-Pg and Eocene-Oligocene have the clearest evidence for impacts across a wide range of taxa. The K-Pg and PETM, however, are the strongest candidates for relatively rapid changes in the global flora and fauna that may have been perceivable on time scales more similar to those employed by researchers of the “sixth mass extinction”.

The Anthropogenic “sixth mass extinction”

A fundamental question behind understanding the potential of a currently ongoing mass extinction is establishing precisely when *Homo sapiens* started to significantly alter global systems and cause a spike in species extinctions. There are multiple phases of influence throughout the evolution of humans but for many the beginnings of large-scale significant influences on planetary processes was the extinction of the megafauna. As a starting point this is however not free of controversy as it relies on resolving the major drivers behind the extinction of the Pleistocene megafauna. Nearly two thirds of megafaunal vertebrates (> 44 kg) became extinct by the end of the Pleistocene (11.7 ky) (Turvey and Crees 2019) with mammals being the group worst affected: around 11% of mammal genera and 6% of species, of all sizes, have gone extinct since the last interglacial (~ 130 ky) (Faurby *et al.* 2020). Although this extinction rate was relatively high and the global impacts broad, the overall magnitude of this event was limited due to its taxonomic and trait-based (body size) selectivity. Whilst the temporal co-occurrence of the extinctions with the spread of human populations across Earth's surface heavily implicates humans as a significant part of the event (Barnosky *et al.* 2004; Lemoine *et al.* 2023), the extent of the role of climate versus human hunting in the late Pleistocene megafaunal extinction event is still debated (Lemoine *et al.* 2023; Seersholm *et al.* 2020; Stewart *et al.* 2021).

Further human influence on extinctions came as humans spread to new landmasses, which continued into the Holocene. People, along with their commensals such as nest predating rats, reached remote islands, finding large numbers of island endemics ill equipped to cope with these new threats (e.g. flightless birds). Humans are believed to have expanded across the Pacific after 3,500 cal yr BP (Matisoo-Smith *et al.* 1998) and into East Polynesia after ~1,000 cal yr BP (Wilmshurst *et al.* 2011), leading to the extinction of ~1,000 bird species (and any obligate parasites) over the period from the first human arrival to European colonisation (Duncan *et al.* 2013). Recent estimates of global bird extinctions to date, estimate that ~ 12% of bird species (1,300 - 1,500 species) have become extinct in the last 126 ky (Cooke *et al.* 2023). Island mammals were also lost, with regions such as the Caribbean and Madagascar strongly affected (Turvey 2009; Turvey and Crees 2019). In some cases, both the largest and smallest species became extinct, potentially in response to different drivers (human hunting disproportionately impacted large slow reproducing species and small species suffered from introduced species competition and predation) (Hansford *et al.* 2012). This combination of drivers expanded the taxonomic and geographic breadth of extinctions, overall contributing to a larger event.

As human populations and the capabilities of transport technology increased during the modern period, the hunting of many species and the introduction and spread of human-associated species continued, leading to further extinctions (Turvey 2009; Turvey and Crees

2019). This was further compounded by the acceleration and globalisation of habitat loss, caused by land-use change, as growing human populations and consumption cleared land for livestock, agriculture and settlements (Gordon *et al.* 2024; Mottl *et al.* 2021). Agricultural expansion and logging are now the most common risks to assessed vertebrate species (Munstermann *et al.* 2022). The expansion of these drivers and the increasing list of historic extinctions has thus fed into the proposal of a sixth mass extinction.

The IUCN Red List documents modern period extinctions occurring since 1500 (IUCN 2024). For most species groups, the percentage of species documented by the IUCN as extinct is in single figures (Barnosky *et al.* 2011). As discussed above, the inclusion of extinctions since the last interglacial in estimates does not result in a drastic rise, even when the figure for mammals is calculated at the genus level. These estimates are still complicated by data deficiencies and the large number of species currently classed as threatened with uncertain futures. This makes attempts to try and predict the fate of these species very important when quantifying the current extinction event.

An uncertain future

The Bramble Cay melomys (*Melomys rubicola*) has been designated the first mammal recorded to have become extinct due to Anthropogenic climate change as erosion and storms beset its only known island population (Waller *et al.* 2017). Indeed, climate change and severe weather events have already been implicated in the extinction (or extinction in the wild) of at least 41 species (IUCN 2024). A meta-analysis of published estimates found that 3°C warming will result in an estimated 8.5% of species becoming extinct with a higher rise of 4.3°C resulting in a figure of 16% (Urban 2015). Alongside and inextricably linked with climate change, human influence on land and sea use, as well as appropriation of net primary productivity, has increased rapidly through the Holocene, resulting in substantial effects on other species (Ellis *et al.* 2021; Haberl *et al.* 2014). Future biodiversity is therefore highly dependent on socioeconomic scenarios. Using diverse sets of these socioeconomic trajectories of human development and policy choices, several studies have explored future biodiversity trends, often finding an acceleration of extinction rates attributed to land-use and climate change (IPBES 2016; Pereira *et al.* 2010, 2024), but they also have been hampered by modelling and data limitations. Existing scenario studies often use a single model, analyse a single facet of biodiversity, or when comparing multiple models use different projections for future land-use and climate (IPBES 2016). It is therefore not surprising that the sources of uncertainty in these scenarios are numerous and difficult to ascertain (Thuiller *et al.* 2019). A recent extensive model intercomparison (Pereira *et al.* 2024), showed that even when controlling for some of these aspects, substantial variation in outcomes can still be linked to both our choice of models and projections. Since these models, and similar studies, used different sources of biodiversity and driver data of varied structure, resolution and coverage (e.g. taxonomic, temporal, spatial), it is unsurprising that current predictions of extinction risks also vary widely depending on the focus of each study.

Another source of uncertainty are conservation efforts. Although they have prevented some vertebrate extinctions, prevention has failed in other cases, regardless of efforts and international legislation, or only managed to slow rather than reverse declines, leading to calls for biodiversity conservation to be scaled up (Bolam *et al.* 2021; Langhammer *et al.* 2024). Failure to meet previous biodiversity targets, and the need for an easily communicated aim, has led some to propose a target of less than 10 extinctions per year over the next 100 years across the 2 million described species (Rounsevell *et al.* 2020). Such a target may be rather ambitious considering future extinction estimates using species extinction risks based on IUCN categories derived from factors such as population change and species distribution.

Barnosky *et al.* (2011) assumed the loss of all species deemed “threatened”, alongside those already known to be extinct (“extinct” or “extinct in the wild” since 1500), providing estimated species losses ranging from 14% in birds to 64% in cycads. Davis *et al.* (2018) focused only on mammals but used a Late Pleistocene baseline of 130ky (which provides a conservative estimate missing earlier extinctions) and an extinction probability over 100 years based on

IUCN categories. Projecting 100 years forward from present, they estimated a loss of 16% of mammal species. These estimates, however, require many assumptions, predominantly that current extinction probabilities and rates will continue, and that IUCN categories are largely accurate. Barnosky *et al.* (2011) took this further and asked how long it would take for the percentage of species lost to reach “mass extinction” levels. Assuming the loss of all threatened species within a century and these same rates continuing, a mass extinction (defined as 75% species extinction) would be reached for terrestrial amphibians, mammals and birds in ~ 240 to 540 years. On the other end of their scale, if critically endangered species were lost over 500 years followed by rate continuation, estimates range from 4,450 to 11,330 years across groups for the 75% threshold to be reached (Barnosky *et al.* 2011). This means that if mass extinction levels are to be reached, high extinction rates must be maintained for either a few centuries or a few millennia depending on the rate at which already threatened species are lost. It is clear therefore that projections of a sixth mass extinction are heavily contingent on the assumptions made.

To reach the widely referenced mass extinction level of 75% species extinction, numbers of extinctions would have to far exceed the number of species currently threatened for most groups according to most studies (e.g. 45% of angiosperms (Bachman *et al.* 2024)). Losses based on current extinction risk would be highly unevenly spread across geography and taxonomy with ungulates and islands particularly affected (Faurby *et al.* 2022). In addition, the loss of all at-risk species within a century would likely require extinction drivers growing in severity (e.g climate change) or new as-yet-unknown extinction drivers, unless the current extinction debt is already high (i.e., the number of species unalterably committed to extinction by past events). If climate change happens rapidly, extinction rates could increase as species fail to keep pace. The need for large-scale climate adaptation could also impact conservation efforts and funding, especially if there is a mismatch between climate mitigation and adaptation solutions and biodiversity protection. On the other hand, as the species most threatened by current anthropogenic extinction drivers are lost (such as slowly reproducing land mammals, non-native predator-sensitive flightless island birds, or chytrid-susceptible amphibian groups), rates may decrease. With a higher proportion of remaining species exhibiting some tolerance of anthropogenic global change, extinction rates could be expected to reduce. If coupled with the passing of peak land-use due for example to advanced in the food production system (Thomas 2022) and successful navigation of complex changes in global human population (Marini *et al.* 2024) as well as the success of calls for increasing conservation efforts and financing, extinction rates may fall before percentage species losses reach the levels of the larger extinction events.

The other side of this coin is the potential for future speciation. Humans have moved species around the planet with many aspects comparable to past biotic interchanges such as the Great American Biotic Interchange (Stigall 2019). As these new populations adapt to novel surroundings they might be expected to form new species, a process that could be extradited by the strength of anthropogenic selection pressures and hybridisation (Thomas 2015). The extent to which this could offset losses is hotly debated (Hulme *et al.* 2015; Thomas 2015). New species may compensate to some extent for taxonomic and functional diversity, but are unlikely to replenish the lost phylogenetic diversity for many thousands of years (Faurby *et al.* 2022). For example, although in some aspects the Dingo (*Canis lupus dingo*) could be considered a replacement for the Thylacine (*Thylacinus cynocephalus*), the Dingo does not compensate for the loss of the unique marsupial wolf in terms of phylogenetic diversity (Faurby *et al.* 2022). On longer time scales, speciation events are hypothesised to follow extinction events (Chen and Benton 2012) as empty niche space is refilled. How such a mechanism could operate in the current case is unknown, especially as niche space and resources have been channelled from many species into one - *Homo sapiens*. Given the major uncertainties faced when modelling the future, researchers have aimed to use the past for both context and comparisons, generating its own challenges.

LIMITATIONS AND COMPARISONS

To compare mass extinctions we must look at the factors that define them - the available data quality, magnitude, duration, selectivity and the resulting amount of global and ecosystem change. To make future predictions we must also consider common drivers: which influences are known to be able to cause major shifts in the biosphere?

Past uncertainties and fossil record biases

The structure of the available fossil record (Holland 2017), and the subsequent sampling of fossil material from it, fundamentally impacts what we can ascertain about past extinctions (Signor and Lipps 1982). Therefore, providing accurate comparisons of ecosystems through time is a substantial challenge requiring comprehensive consideration of fossil record biases - biological, environmental and anthropogenic factors which systematically and non-randomly skew the available fossil record (Alroy 2010; Nanglu and Cullen 2023; Raup 1972). At a fundamental level, the deposition of fossil-bearing rocks is driven by a variety of geological and environmental factors that are non-continuous and non-evenly distributed across space or time (Holland 2023; Holland *et al.* 2022). Rocks that are preserved are prone to destruction in ways (e.g subduction) that are also non-uniform. As such, the resulting global geological record we have today is incomplete and biased, and consequently temporally and spatially coarse and uneven (Benson *et al.* 2021; Vilhena and Smith 2013; Wagner and Marcot 2013). Subsequent sampling processes of fossiliferous material from this record further exacerbates this process of information distortion, with geographic and anthropogenic (Raja *et al.* 2022) factors significantly impacting our perception of past events.

Understanding the speed of extinction events is crucial for recognising both the drivers and impacts of species loss. In general, however, the ‘highest’ temporal resolution that can be reliably reached is on the order of hundreds of thousands to millions of years (Erwin 2006). Particularly complete geological sections (Antell *et al.* 2021) and advanced methodological approaches (Dean *et al.* 2020; Fan *et al.* 2020) have resulted in higher resolutions, although the utilisation of bins spanning millions of years is common practise within palaeontological studies in response to temporal uncertainty (e.g. Flores *et al.* 2023). This is problematic when trying to compare extinction rates due to the assumed pulse based dynamic of extinction (Spalding and Hull 2021). High resolution data (like the hundred to thousand year data used when considering anthropogenic extinctions) would capture these peaks in extinction rate but courser data (like most of the fossil record) would produce a lower rate, as extinction pulses would be inextricably combined with periods of low or background extinctions. This issue has been shown to impact perceptions of deep-time fluctuations in diversity, such as the Campanian-Maastrichtian diversity decline in North American dinosaurs (Dean *et al.* 2020). The often course resolutions available are also non-continuous and non-uniform in regard to stratigraphy and deposition, resulting in a record with gaps of varying lengths (Kowalewski and Bambach 2008). The record might be present, then absent, then present again, without a clear idea of the swiftness or process of an event; in fact, the majority of the geological record is composed of hiatus, and so non-uniform sedimentation rates therefore set a limit on the possible temporal resolution of the stratigraphic record (Kemp and Sexton 2014; Kowalewski and Bambach 2008). Equally, the geological record could be available but be sediment poor or entirely inadequate for fossil preservation due to local taphonomic conditions or variable preservation potential inherently related to the specific environment (e.g. Holland *et al.* 2022). All of these factors also vary somewhat systematically through both time and space, rendering simple corrections impossible.

This range of completeness, variability and quality of the data through time has been shown to have noticeable effects on estimation of the rates and durations of rapid events (Kemp and Sexton 2014). A lack of available data can result in ‘contentious’ extinction events; either through an inability to distinguish between poor sampling within an interval or a loss of species. This means that many apparent extinction events may only be considered well supported when accompanied by other evidence of global change (e.g. Jurassic-Cretaceous boundary, Tennant *et al.* 2017; Olson’s Extinction, Brocklehurst *et al.* 2017; Ediacaran extinctions, Hoyal Cuthill 2022). In addition, the synthesis required to detect large scale events is hampered by effectively disparate data bins which have a large impact on measuring biological diversity through time (Dean *et al.* 2020; Gibert and Escarguel 2017; Guillerme and Cooper 2018; Smith *et al.* 2023).

Whilst the impact of temporal variation in the quality and completeness of the geological record has historically been a key focus of analytical palaeobiology, it has only been established in recent years that spatial heterogeneity in fossil data can be an equally large issue for assessing diversity change through time (Allison and Briggs 1993; Antell *et al.* 2024; Close *et al.* 2017, 2020a, 2020b; Vilhena and Smith 2013). The number, spread and size of geographic regions and environments that are represented in the fossil record varies substantially and non-uniformly through time, and the subsequent sampling of these localities is also inherently impacted by geographically-varying anthropogenic processes and historical legacies (Raja *et al.* 2022). This changing patchwork of spatial data has large impacts on our understanding and interpretation of extinction events.For example, did a species become extinct between two successive time periods, or are we no longer preserving its preferred environment (Smith *et al.* 2001)? The spatial distribution of fossil occurrences may also give the false perception of global impacts, where in fact extinction and origination rates could show more regionally significant patterns (Flannery-Sutherland *et al.* 2022). Particular latitudes also show correlated increases in outcrop area, diversity and collector effort during different time intervals, impacting our ability to understand macroecological patterns such as the latitudinal diversity gradient (Allen *et al.* 2020; Allison and Briggs 1993; Jones *et al.* 2021; Vilhena and Smith 2013).

The choice of operational taxonomic unit varies depending on the context and the clades of interest, with the use of genera widespread in paleobiology, whereas species are the unit of focus of most modern day ecological analyses. Avoiding polyphyletic and paraphyletic genera is a challenge with only fossil remains, but resolving species is an even greater challenge which, among other factors, has led to the proliferation of genus level analysis (Hendricks *et al.* 2014). Conversion of genus level estimates into a magnitude of species loss creates further complications, with factors such as the phylogenetic clustering of extinctions having a major role (Stanley 2016). This means that the 75% species loss criteria for a mass extinction may exclude most of the current “Big Five” under alternate analysis (Stanley 2016). On the other hand, analysis of fossilisation potential has shown that large amounts of species loss are not likely to be reflected in the fossil record. The magnitude of the current extinction rate would be perceived as far lower (a 66 to 98% underestimate) as nearly 30% of tetrapod species have no chance of fossilisation (Krone *et al.* 2024). This underlines the fact that differences in preservation in the fossil record introduce biases on which groups of organisms can effectively be studied and compared (Sansom *et al.* 2010).

Given this wide range of factors, it is difficult to both understand individual extinction events and, more importantly, difficult to compare between extinction events and even between different taxonomic groups during the same event. Although methodological approaches exist to combat at least some of these biases (e.g. PyRate, subsampling, spatial partitioning (Close *et al.* 2018, 2020b; Silvestro *et al.* 2014; Tibshirani 1994)), the drawing of well-supported comparisons between different time periods is always likely to remain majorly caveated. These issues are not caused by past data alone; most studies of current biodiversity are taxonomically limited (Mammola *et al.* 2023). One such challenging issue for comparison is our lack of knowledge on modern marine extinctions (Harnik *et al.* 2012; Monte-Luna *et al.* 2023) as the classification of many extinction events in deep time relies on changes in marine genera due to relatively high preservation potential. However, while it is clear that our knowledge is incomplete, we therefore need to make the most of the information we do have, and use multiple lines of evidence in conjunction to make the most robust conclusions possible.

Drawing comparisons

The magnitude of an extinction event is often calculated as the proportional reduction in the diversity of genera (Table 1). It is, however, complicated to measure, as it requires comparable estimates of genera richness from before and after an event of interest. The best information on the current extinction we have is for mammals. The PHYLACINE database (Faurby *et al.* 2020) records a total of 1,400 mammal genera known, between ~130,000 years ago to the present. Only 1,245 of these are estimated to still be extant in the wild, giving an approximate loss of 11% of mammal genera. This is less than the estimate for Western European endemic artiodactyls at the Eocene-Oligocene boundary (Weppe *et al.* 2023), but it must be noted that Western European endemic artiodactyls are only a subset of the Late Eocene mammal fauna where as 11% of mammal genera is a global estimate. The 11% is also less than the 36% loss of Pliocene marine megafaunal genera (Pimiento et al. 2017). In this case however we can apply a megafauna filter of > 45kg (Malhi *et al.* 2016) to the PHYLACINE data, resulting in an estimate that exceeds that of the Pliocene marine megafaunal extinction. The original value of 11% would also exceed the 8% estimate of genus extinctions outside of peak Cenozoic intervals and not be far short of the 15.6% Late Eocene genus extinction reported by Bamach (2006). The issue with these later comparisons is that Bamach’s estimates are across a wide range of marine taxa and not just a single group. Such comparisons therefore show some of the issues already highlighted around the challenges of comparison between past and present data.

As noted, much of the evidence for a sixth mass extinction focuses on rates which are challenging to compare between the typically high resolution modern data and the coarser resolution available for the past. We would expect the 130,000 year time scale used here for anthropogenic extinctions to be rather short compared to other documented extinction events, which in combination with the considerable magnitude would result in a higher extinction rate. However, the duration of past extinctions is currently mostly unresolved with some authors estimating a similar scale duration for the PETM (Molina 2015; Speijer *et al.* 2012). The K-Pg is thought to have had a faster extinction rate with most extinctions happening over a very short duration due to the impact winter caused by the bolide (Chiarenza *et al.* 2020; Marshall 2023). Late Triassic extinction rates may also have been underestimated by 100 times if the duration was 50,000 years and not seven million

(Marshall 2023). Some have also suggested that smaller events may have also been more rapid than previously thought, with Molina (2015) suggesting that the marine extinction spikes at the start and end of the Eocene may have durations of only 100,000 years. It is, however, clear that based on the available evidence, calculation of the duration (and therefore the associated extinction rates) of extinction events cannot be done with a high level of precision.

Table 1 - Summary of extinction magnitude reported for Cenozoic extinction events. It should be noted that extinction magnitudes provided by studies not at the global scale may contain both global and local extinctions so are not directly comparable to global estimates.

Extinction event	Taxon	Geographic scope	Extinction magnitude	Reference
PETM	Deep sea benthic foraminifera	Local studies	33 to 65% of spp	Speijer et al., (2012)
Eocene-Oligocene	Marine animals	Global	15.6% of genera	Bambach, (2006)
	Planktonic foraminifera	Regional	< 15% of spp	Keller, (1986)
	Endemic artiodactyls	Local	77% of spp 62% of genera	Weppe et al., (2023)
Plio-Pleistocene	Marine animal taxa	Global	< 0.5 % to > 11% of genera	Bambach, (2006)

	Marine megafauna	Global	36% of genera	Pimiento et al., (2017)
	Molluscs (Late Pliocene and Pleistocene)	Regional	49% of spp	Pimiento et al., (2020)
	Coral	Regional	42% of genera	van Woesik et al., (2012)
Anthropogenic	Mammals (since last interglacial)	Global	11% of genera	Derived from Faurby et al., (2020)
	Mammalian megafauna (Late Quaternary)	Continental	21% (Africa) to 88% (Australia) of genera	Koch and Barnosky (2006)
	Birds (since last interglacial)	Global	12% of bird spp	Cooke et al., (2023)
	Pacific Island landbirds (Holocene)	Local	0 - 100% of spp	Braje and Erlandson, (2013)
	Tetrapods (since 1500)	Global	1% of genera	Ceballos and Ehrlich, (2023)

Another key aspect traditionally used to compare events is extinction selectivity. Logically larger extinction events would be thought to be less selective than their smaller counterparts, as a high-magnitude high-selectivity event would require very high extinction proportions in some taxonomic or functional groups combined with extremely low values for others (Bush *et al.* 2020). However, as yet, no clear patterns in the degree or type of selectivity have been found in common across mass extinctions or that clearly differentiate them from other events (Bush *et al.* 2020; Foster *et al.* 2023; Payne *et al.* 2023). Some evidence suggests that geographic range size may be important, with smaller range species being at higher risk, but this does not appear to hold consistently across mass extinctions (Dunhill and Wills 2015; Foster *et al.* 2023; Payne *et al.* 2023). The current event does show a preferential loss of small ranged and endemic species, with the loss of island endemics being a prominent example (e.g. Cooke *et al*. (2023), but with the caveat of these being at species not genus level). Other aspects, such as the megafaunal extinction which resulted in the loss of once widespread species, and population trends over the last few decades, are not explained by geographic range size (Daskalova *et al.* 2020; Malhi *et al.* 2016). The pattern of losses so far is still skewed towards range-restricted species, contrasting with the patterns reported for mass extinctions but this may change as the event unfolds.

The loss of the megafauna and the rapid decline in larger species, for example the marine mammal declines and extinctions of the 19th and 20th centuries (Dulvy *et al.* 2009), shows there are other selective forces at play. Alongside range size, body size is another attribute widely hypothesised to be selected upon. This may also be unusual given the link between body size and extinction was not seen in some other events (Monarrez *et al.* 2021; but see K-Pg; Payne *et al.* 2023). Extinction probability for marine genera in previous extinction events was not higher for larger species but there is a clear size influence on extinction risk for modern extinctions (Payne *et al.* 2016). The spatial extent and intensity of human influence means that extinctions are unlikely to be confined to a particular taxonomic group or geographic location and current patterns of selectivity may not hold as the event increases in magnitude. The detected size selectivity when it comes to extinction risk would be an issue if it continues with increasing magnitude. The disproportionate loss of large species has, and will, restructure ecosystems which could mean the consequences and following recovery from the current event may differ from those proceeding (Cooke *et al.* 2022; Malhi *et al.* 2016).

Extinction events of high magnitude and/or high selectivity can result in significant restructuring of the biosphere, with mass extinctions leading to wholesale shifts in the composition of flora and fauna globally. Extinctions and extirpations of species can profoundly influence ecological and evolutionary processes. Their loss can destabilise ecosystems, alter nutrient cycling, and impact food webs driving trophic collapse (Roopnarine 2006). On an evolutionary timescale, they can also be a catalyst for the emergence of new species as niches are vacated, creating new opportunities for adaptive radiations, although such diversity recoveries may show delays (Kirchner and Weil 2000). The fossil record demonstrates that species communities have undergone continual iterative change, disappearing and reforming with new species compositions, but with strong functional similarities, underscoring the resilience and dynamic nature of ecosystems across long time scales (Cooke *et al.* 2022). Extinction is merely part of the evolutionary process in the long-term, but can be disastrous for particular ecosystem configurations over shorter periods of time. It is this shorter period of time, however, that is of concern to humanity as the ecosystems of the world provide the natural resources necessary for our survival. When considering the consequences of anthropogenic extinctions, the loss of the world’s megafauna is almost certainly the best understood due to their charismatic nature and tendency to be more prevalent and easily identifiable in the fossil record. These records tell an important story of transformation of globally significant ecosystems in response to their extinction. Including the altered vegetation composition (Gill *et al.* 2009), the decline of arctic permafrost driving accelerated climatic change (Zimov 2005) and the limitation of phosphorus and nitrogen within and across biomes (Doughty *et al.* 2016). This loss of large species and the subsequent alteration of global cycles is likely to have also followed the Pliocene megafaunal extinction in the marine realm (Pimiento *et al.* 2017).

The loss of the megafauna and the processes they governed can be seen as part of a simplification and homogenisation of the biosphere (Fraser *et al.* 2022). Simplified and often homogenised ecosystems across the globe are widely documented today (Daru *et al.* 2021). This is similar to the disaster fauna of the past (Button *et al.* 2017), with generalist species thriving in the wake of extinction events. Perhaps the most famous example is *Lystrosaurus*, a bulky herbivore that became dominant following the end Permian extinction (Sahney and Benton 2008). Current homogenisation is attributed to increasingly widespread generalist taxa (McKinney and Lockwood 1999) as well as species able to prosper on a highly human-dominated globe (Carroll *et al.* 2023). In addition, many species have become globally widespread due to direct transportation (intentional or not) across the world by humans. Other changes in species community complexity and structure could result from cascading effects through food webs and other forms of species interaction (e.g. mutualisms and competition) which are of mounting concern for current conservation efforts. Looking at past extinctions, trophic cascades have been discussed as a potential mechanism exacerbating the K-Pg (Alvarez *et al.* 1980), but it has proven hard to quantify (see Roopnarine 2006 for a review).

Community and ecosystem restructuring is also studied by the analysis of changing in functional space, altering the range of ecological roles filled. Loss of functional space and particular functional groups is widely seen in the current extinction event and in future extinction risk predictions (Carmona *et al.* 2021; Hatfield *et al.* 2022; Sayol *et al.* 2021). Although evidence is mixed on whether past extinctions removed entire functional groups from communities (Dineen *et al.* 2014; Edie *et al.* 2018; Foster and Twitchett 2014), they did reduce functional redundancy, with fewer species performing any particular function (Pimiento *et al.* 2017, 2020). In the cases of the end-Permian and end-Cretaceous mass extinctions, regime shifts are considered to have taken place, with pre-extinction and post-extinction faunas and floras having different community structures, for example the restructuring of tropical forests post K-Pg (Carvalho *et al.* 2021; Feng *et al.* 2020; Foster *et al.* 2023). Human activities have disrupted long standing vertebrate size structure patterns (Cooke *et al.* 2022) and created a mammalian biomass overwhelmingly composed of humans and domesticates (Greenspoon *et al.* 2023). This represents a large-scale restructuring of species assemblages and with such levels of reorganisation not seen since the recovery from the K-Pg.

The extent to which the drivers of extinction in deep time are comparable to human-induced environmental changes in the present is debated (e.g. Otto (2018)). For example, although greenhouse gas emissions play a key role in both present and past climatic changes, there is debate about how comparable the volume and rate of emissions are (Foster *et al.* 2018). Although the sources of atmospheric changes differ (anthropogenic climate change versus past volcanic activity), it is clear that warming has been a key extinction driver in most major past events, with the accompanying acidification and anoxia in the oceans (Bond and Grasby 2017; Calosi *et al.* 2019; Harnik *et al.* 2012). This underlines the importance of continuing human greenhouse gas emissions to the unfolding extinction event. Other similarities can also be observed: for example, large community restructuring has in the past been seen in biotic interchanges (the exchange of species when barriers between separated landmasses or oceans are removed), which parallels anthropogenic species introductions (McGhee *et al.* 2013; Vermeij 1991).

CONCLUSIONS

The available evidence suggests that the current extinction rate is higher and that the magnitude is at least for certain groups, approaching those seen across all other Cenozoic events. The taxonomic and geographic breadth also seems to be greater than the other Cenozoic events. It is also clear that human influence has grown rapidly and is global, with far reaching global change. Many of these anthropogenic pressures are not expected to subside for at least many decades, and some such as climate change, are expected to increase. If extinctions continue in a similar fashion, with the loss of currently threatened species, doubt that this event represents the greatest since the K-Pg will be ever diminishing. The magnitude recorded so far suggests that anthropogenic extinctions are still far behind the larger extinction events of the past such as the end-Permian and end-Cretaceous. This extinction event, however, is still unfolding, and whether the severity reaches that seen in the past will depend heavily on the fate of species now rare or otherwise considered at risk. As we move forward, the amount of anthropogenic land-use and climatic change will have a great impact on the magnitude of the current extinction event. We are likely witnessing what will become the greatest extinction event since the downfall of the dinosaurs 66 million years ago; whether we see a mass extinction remains a choice yet to be made.

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Author Contribution statement

JHH and KED drafted the first version of this manuscript. All authors contributed to workshop discussions, the drafting of individual sections and provided edits and suggestions for the final version.

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Conflict of Interest statement

None

Data Availability statement

Data availability is not applicable to this article as no new data were created or analysed in this study. All data presented is available from the sources cited.

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