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The Greatest Extinction Event in 66 Million Years? Contextualising Anthropogenic Extinctions

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1 **The greatest extinction event in 66 million years? Contextualising anthropogenic**
2 **extinctions**

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7 Running Title: Contextualising anthropogenic extinctions

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27 **Abstract**

28 Biological communities are changing rapidly in response to human activities, with the high
29 rate of vertebrate species extinction leading many to propose that we are in the midst of a
30 sixth mass extinction event. Five past mass extinction events have commonly been identified
31 across the Phanerozoic, with the last occurring at the end of the Cretaceous, 66 million
32 years ago (Ma). However, life on Earth has always changed and evolved, with most species
33 ever to have existed now extinct. The question is, are human activities increasing the rate
34 and magnitude of extinction to levels rarely seen in the history of life? Drawing on the
35 literature on extinctions primarily over the last 66 million years (i.e. the Cenozoic), we ask:
36 (1) what comparisons can meaningfully be drawn? and (2) when did the Earth last witness
37 an extinction event on this scale? We conclude that, although challenging to address, the
38 available evidence suggests that the ongoing extinction episode still falls a long way short of
39 the devastation caused by the bolide impact 66 Ma, but that it has likely surpassed most
40 other Cenozoic events in magnitude, with the possible exception of the Eocene–Oligocene
41 transition (34 Ma), about which much uncertainty remains. Given the number of endangered
42 and at-risk species, the eventual magnitude of the current event will depend heavily on
43 humanity's response and how we interact with the rest of the biosphere over the coming
44 millennia.

Keywords: mass extinction, sixth mass extinction, Anthropocene, Cenozoic, extinction, biodiversity

1 INTRODUCTION

Human activities have resulted in rapid and far-reaching changes to global biodiversity (Ellis *et al.* 2021; Thomas 2020). This includes the extinction of almost two thirds of terrestrial vertebrate megafauna (Svenning *et al.* 2024; Turvey and Crees 2019), and the mass movement of species across the globe (Thomas 2020), with major impacts seen since at least the Late Pleistocene (~ 130,000 years ago) and forecast far into the future (Andermann *et al.* 2020; Davis *et al.* 2018; Ellis *et al.* 2021; Gordon *et al.* 2024; Matthews *et al.* 2024). Based on comparisons with background estimates from the fossil record, the rate at which species are currently going extinct has led many scientists to propose that we are now entering a sixth mass extinction (Barnosky *et al.* 2011; Ceballos *et al.* 2015; Leakey and Lewin 1995; Pimm *et al.* 2014). The Earth has experienced multiple climatic and environmental perturbations, including five such ‘events’ across the Phanerozoic (the last 541 million years) interpreted as mass extinctions. The most recent of these occurred at the Cretaceous/Paleogene (K/Pg) boundary, 66 million years ago (Ma). Uncertainty remains as to whether the current extinction rate and magnitude is indeed higher than at any time over the last 66 million years i.e. the Cenozoic (Barnosky *et al.* 2011; Cowie *et al.* 2022), and if they are already comparable to those associated with events such as the bolide impact that ended the age of the non-avian dinosaurs at the K/Pg boundary (e.g. Chiarenza *et al.* 2020) or the large-scale volcanic activity thought responsible for the end-Permian Great Dying, 252 Ma (e.g. Chen and Benton 2012). Put more simply, is the Earth currently experiencing a mass extinction event, or one only severe on human timescales? This is important to answer if we want to use the past as an analogue for understanding and predicting the scale of the ongoing biodiversity crisis, including recovery times and long-term ramifications to the biosphere.

71 More than 99% of all species that have ever existed are now extinct, with extinction being a
72 fundamental evolutionary process, however definitions and detections can prove challenging
73 (Jablonski 2004; Raup 1991). The exact timing of extinction is difficult to determine both in
74 the present and in the past (Purvis *et al.* 2000). The loss of a population from a particular
75 geographic area (i.e. local extinction or extirpation) may or may not be a precursor to global
76 extinction (Congreve *et al.* 2018), while knowledge of the distribution of all populations of a
77 species is also rare (e.g. Pearson *et al.* 2006). Species also become “functionally” extinct
78 long before this point. Functional extinction occurs when a population becomes so low that it
79 has limited impacts on other species, due to its rarity, and where recovery is no longer
80 realistic (e.g. due to various Allee effects or continued environmental changes that led to the
81 original decline [e.g. Säterberg *et al.* 2013]). Over longer time periods the issues of
82 pseudoextinction and Lazarus taxa are encountered. Pseudoextinction occurs when all the
83 members of a species are lost but their descendants survive as a daughter species,
84 highlighting the issue of species delineation, and the extent to which this is comparable
85 between fossil and living taxa (Raup, 1991). Lazarus taxa disappear from the fossil record,
86 assumed to be extinct, but are then detected in a later time period indicating a lack of
87 detection rather than genuine absence (Jablonski, 1986).

88 Here, we synthesise previous literature investigating both past extinctions and ongoing
89 biodiversity change to place the period of anthropogenic extinctions in the wider geological
90 context. To do this, we start by examining the events traditionally seen as the largest of all
91 extinction events – the five Phanerozoic mass extinctions. We follow this by discussing
92 extinction events over the last 66 million years, i.e. since the last mass extinction and when
93 Earth’s ecosystems and biodiversity have been the most similar to those of the present day.
94 We then consider the anthropogenic extinction event, defined herein as spanning the last
95 interglacial (~ 130 ka) to the present. This represents the well-established time frame of
96 increasing human planetary influence, from the megafaunal extinction, through to the current
97 period where humans have modified the planet to such an extent that our influence is

inescapable (Thomas 2020; Svenning *et al.*, 2024). We then discuss the challenges of making meaningful comparisons given the contrasting biases between the fossil record and present-day biodiversity data, explore comparisons that can be made, and finish by discussing what these mean for the future of biodiversity. By reviewing the evidence we address the central hypothesis that the ongoing anthropogenic extinction event is comparable in magnitude and rate to past events considered mass extinctions.

2 EXTINCTIONS PAST, PRESENT AND FUTURE

2.1 The 'Big Five'

Although there will always be species extinctions, some time periods are known for their atypically high rates (extinction events), with the greatest of these being labelled 'mass extinctions'. However, such events are difficult to define. One commonly cited 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 (geologically) 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 (Figure 1). These events are: (1) the Late Ordovician mass extinction (~445 Ma); (2) the prolonged 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 (K-Pg) mass extinction (~66 Ma) (Raup and Sepkoski 1982).

The extent to which the ‘Big 5’ are genuinely distinct from other extinction events is debated, given that the Phanerozoic has been punctuated by many smaller scale and often less well-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 diversity losses during the Late Devonian and Late Triassic being at least partially attributable to reductions in origination rates (Bambach 2006). On the other hand, Bambach (2006) identified at least 18 substage intervals across the Phanerozoic that could be seen as mass extinctions using a marine genus-level compendium (Figure 1). This means that all detectable spikes in extinction rate could be considered mass extinctions, or the term could be reserved for the largest three (i.e. Late Ordovician, Permian-Triassic and Cretaceous-Paleogene), which are distinct extinction anomalies even when accounting for various data constraints (see 3).

Consideration must also be given to the other elements of the definition, i.e. multiple geographically widespread higher taxa disappearing within a relatively short time (Sepkoski, 1986). This again has proven contentious, especially as most studies have been reliant on compilations dominated by the best-preserved marine taxa (Figure 1), with terrestrial extinction rates harder to quantify due to the sparser fossil record (e.g. Benson *et al.* 2021). Some events not viewed as mass extinctions have resulted in significant global changes, such as the Carnian Pluvial Episode (234 to 232 Ma), which saw the 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 or taxonomically restricted (Arcila and Tyler 2017; MacLeod 1994), or primarily affected organisms with particular traits (Aberhan and Baumiller 2003; Pimiento *et al.* 2017; Pym *et al.* 2023). Past diversity is usually measured at the level of genera, rather than species, with the challenge of identifying species, among other factors, resulting in the proliferation of genus-level palaeobiological analysis (Hendricks *et al.* 2014). Conversion of genus level estimates into species loss

creates further complications, with factors such as the phylogenetic clustering of extinctions having a major role (Stanley 2016). Uncertainty also arises because a widespread genus in the fossil record could be represented by one of a few widespread species, or by very large numbers of more localised species with different biogeographic ranges (Hallam and Wignall 1997).

Understanding the rate of extinction is as important as estimating its magnitude. The 'highest' temporal resolution that can be reliably reached for deep-time estimates such as those used for the 'Big Five' is often on the order of hundreds of thousands to millions of years (Erwin 2006). Particularly complete geological sections and advanced methodological approaches have resulted in higher resolutions (e.g. Dean *et al.* 2020; Fan *et al.* 2020; Lyson *et al.* 2019) but these are uncommon and difficult to correlate in order to gain a picture of the rapidity of the event on a global scale. Extinction events are, however, increasingly being perceived as pulses (Spalding and Hull 2021), which only appear to be gradual (smooth) increases in extinction rates when averaged over longer periods of time. High resolution data (i.e. comparable to that used when considering anthropogenic extinctions) would capture these peaks in extinction rate, but coarser data (i.e. which characterises most of the fossil record) would produce a lower rate, averaged over a longer period of time, 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 decline in Cretaceous North American dinosaurs (Dean *et al.* 2020). In other cases, an extinction event with a large magnitude (i.e. a large reduction in standing diversity) might only have a limited impact on ecological processes at any given time if the species turnover took place gradually over a long period. A slow decline in generic diversity over one or more million years in the fossil record, for example, may represent a recognisable anomaly, but might not be seen as an extinction event or crisis on a decadal to millennial timescale (Bambach 2006). To try and resolve this, attempts have been made to estimate the temporal duration of heightened extinction rates based on the hypothesised

causes. For example, the K-Pg event is considered to have been geologically instantaneous because of the rapid cessation of photosynthesis caused by the consequent 'impact winter', i.e. global cooling associated with the rapid release of sulphate aerosols (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 (Harper 2024).

Defining mass extinctions and comparing events to one another 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 (e.g. Foster *et al.* 2023). Rate and magnitude changes alone are unlikely to meaningfully capture the consequences of such events for Earth systems and the 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 discussions of whether the present day represents a potential 'Big Sixth' mass extinction, and therefore the greatest extinction event in the last 66 million years. Nonetheless, it is possible to conclude that all of the 'Big Five' mass extinctions were characterised by the Earth's physical and then biological conditions deviating outside the range previously experienced, leading many species to disappear in each case.

While there has been much debate on the threshold that defines a mass extinction (Barnosky *et al.*, 2011; Marshall, 2023), there is even less consensus on what distinguishes a smaller, non-mass extinction, from the 'normal' background rate of extinction. One possibility is to consider extinction rates to constitute an 'event' when they substantially exceed the background extinction rate but fail to reach the threshold of a mass extinction. This definition is how we have selected smaller extinction events for discussion below.

2.2 The last 66 million years

204 The most recent mass extinction event took place at the end of the Cretaceous, heralding
205 the end of the Mesozoic and the beginning of the Cenozoic, 66 Ma. The large asteroid
206 impact in the Yucatán Peninsula of Mexico and subsequent wildfires resulted in dust,
207 sulphate aerosols, CO₂, soot and water vapour entering the atmosphere, which led to rapid,
208 extreme climatic cooling and ocean acidification (Chiarenza *et al.* 2020; Hull *et al.* 2020;
209 Morgan *et al.* 2022). An estimated 40% of genera and 76% of species were lost (Barnosky *et*
210 *al.* 2011), including the extinction of many vertebrate and invertebrate groups, most famously
211 the non-avian dinosaurs and ammonites, although no taxonomic group passed through the
212 K/Pg boundary entirely unscathed (Hallam and Wignall 1997). The process was likely rapid
213 (Chiarenza *et al.* 2020), meaning that both the magnitude and rate of extinction were
214 extremely high.

215 Major losses in taxonomic groups that were dominant during the Cretaceous mean that
216 much of the floral and faunal composition of present-day ecosystems originated in the
217 Cenozoic (Finnegan *et al.* 2024). Although Cenozoic extinction events were of lower
218 magnitude than some others that preceded them, they are likely to have been the most
219 comparable to present-day extinctions in terms of the ecosystems and higher taxa involved.
220 As such, although we draw on deeper time comparisons, our primary focus in this
221 contribution is on the Cenozoic.

222 The Cenozoic fossil record provides evidence for several extinction events since the K-Pg
223 event. Although not as devastating as the latter extinction, all of these appear to have been
224 taxonomically, environmentally, and geographically wide-ranging, with long-term
225 consequences for the biosphere (Figures 2-3). These are the Paleocene-Eocene Thermal
226 Maximum (~ 56 Ma), the Eocene-Oligocene transition (~ 34 Ma), and the Pliocene to
227 Pleistocene transition (~ 2.6 Ma) (Bambach 2006; Finnegan *et al.* 2024; Harnik *et al.* 2012).

228 The events defining the start and end of the Eocene resulted in substantial change in the
229 Earth's systems. The PETM saw rapid warming (> 5 °C global mean average increase) and

ocean acidification, attributed to volcanic carbon releases within < 10,000 years (Aze 2022; Harnik *et al.* 2012; Haynes and Hönisch 2020; Tierney *et al.* 2022). This led to turnover in many communities 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 magnitude of extinction in the latter group, which had been relatively unscathed by the K-Pg event but suffered a decline at the PETM (33 to 65% of species lost [Speijer *et al.* 2012]) unparalleled in the rest of its Cenozoic timeline (Hallam and Wignall 1997). The current evidence suggests that although geographically widespread (e.g. Babila *et al.* 2022), high extinction magnitudes were restricted to marine taxa sensitive to the rapid warming, acidification, and deoxygenation of oceanic water, with only limited evidence for terrestrial plant and mammal extinctions (Clyde and Gingerich 1998; Jaramillo *et al.* 2006; Yao *et al.* 2018).

Global cooling at the end of the Eocene (~ 34 Ma) 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, and the event appears more clearly in fossil record analyses (Figures 1-2), but it is challenging to narrow down the event's duration and the concurrence of regional changes. For example, elevated extinction magnitudes are found for some groups of foraminifera, with planktonic forms suffering one of their worst extinction events (Pearson *et al.* 2008; Lowery *et al.*, 2020). Foraminifera extinctions are estimated at less than 15% of species at the Eocene-Oligocene boundary, but are 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 an interval of at least 1 million years (Lowery *et al.*, 2020) and perhaps up to 14 million years in duration for some groups (Hallam and Wignall 1997). The diversity of early stem whales ('archaeocetes') also appears to have declined across the Eocene-Oligocene transition (Corrie and Fordyce 2022). In the terrestrial realm, there is evidence for relatively rapid continental-scale

extinctions in mammals (de Vries *et al.* 2021; Hooker *et al.* 2004; Weppe *et al.* 2023), with magnitude estimates for western Europe's endemic artiodactyls being as high as 77% of species (62% genera) lost over a million-year period (Weppe *et al.* 2023). There is also evidence for diversity declines in reptilian groups, at least in Europe and North America (Cleary *et al.* 2018; Mannion *et al.* 2015). Increased extinction in South American plants has also been documented (Jaramillo *et al.* 2006). Overall, however, evidence points towards a prolonged, and potentially spatially heterogeneous, species turnover in response to global cooling and changing aridity (Hallam and Wignall 1997; Mannion *et al.* 2015; Sun *et al.* 2014).

Global cooling again coincided with elevated extinction rates as the Pliocene transitioned into the Pleistocene (2.6 Ma), with marine megafauna particularly strongly affected. It is estimated that 36% of the 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 currently identify a major global event, with extinctions unfolding over multi-million-year time scales.

In summary, the current evidence suggests that many of the perceived extinction events in the Cenozoic may have been a drawn-out series of localised and shorter-term events that, in combination, resulted in large global turnover. The K-Pg and Eocene-Oligocene have the clearest evidence for impacts across a wide range of taxa and environments as well as the highest magnitude. The K-Pg and PETM, however, are the strongest candidates for relatively rapid rates meaning that changes in the global flora and fauna may have been perceivable on time scales more similar to those thought to characterise the proposed present-day 'sixth mass extinction'.

2.3 The anthropogenic 'sixth mass extinction'

A fundamental question is 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 earliest evidence of anthropogenic disturbance is denoted by the extinction of the terrestrial megafauna. This starting point is not, however, free of controversy as it relies on resolving the major drivers behind the Late Pleistocene extinctions. Nearly two thirds of megafaunal vertebrate genera (> 44 kg) became extinct by the end of the Pleistocene (11.7 ka) (Turvey and Crees 2019; Svenning *et al.*, 2024). Although this extinction rate is relatively high and the global impacts broad, the overall magnitude of this initial wave of extinction was limited due to its taxonomic and trait-based (body size, terrestrial) selectivity. Whilst the temporal co-occurrence of the extinctions with the spread of *Homo sapiens* across Earth's surface heavily implicates humans as a significant contributor to the event (Barnosky *et al.* 2004; Lemoine *et al.* 2023), the extent of the role of the individual versus combined contributions of climate versus human hunting and landscape modification (e.g. O'Keefe *et al.* 2023) in the late Pleistocene megafaunal extinction event is still debated, especially in relation to the fates of individual species (Lemoine *et al.* 2023; Seersholm *et al.* 2020; Stewart *et al.* 2021).

During the early Holocene (Holocene: 11.7 ka to present) humans spread to increasingly isolated islands. People, along with their commensals, such as nest predating rats, reached even remote islands, finding large numbers of island endemics (e.g. flightless birds) vulnerable to these new threats. Humans are thought to have expanded across the Pacific in the last 3.5 ka (Matisoo-Smith *et al.* 1998) and into East Polynesia within the last 1 ka (Wilmshurst *et al.* 2011), with the estimated extinction of ~1,000 bird species (and any obligate parasites) resulting from human colonisation (Duncan *et al.* 2013). Recent estimates of global bird extinctions consider that ~ 12% of bird species (1,300 - 1,500) have become extinct in the last ~ 130 ka with the majority of these being island species (Cooke *et al.* 2023; Matthews *et al.*, 2024). 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 (Hansford *et al.* 2012). This combination of drivers expanded the taxonomic and geographic breadth of extinctions, overall contributing to a larger magnitude event. As human populations and transport capabilities increased during the modern period (post-1500), hunting and the spread of human-associated species continued, leading to further extinctions (Turvey 2009; Turvey and Crees 2019). An increasing number of species were transported by trade and other human activities, with major increases in inter-regional spread after 1800 AD (Seebens *et al.*, 2021). This was compounded by the acceleration and globalisation of habitat loss, as land was cleared for livestock, agriculture, and settlements (Gordon *et al.* 2024; Mottl *et al.* 2021).

The high prevalence of localised island species among the list of human caused extinctions raises issues of how these waves of extinction will be seen through the fossil record. The magnitude of the current extinction rate would be underestimated by 66 to 98%, as nearly 30% of tetrapod species have little chance of fossilisation as they are not located in areas with long-term deposition (Krone *et al.* 2024). This underlines the fact that differences in preservation potential in the fossil record introduce biases as to which groups of organisms can effectively be studied and compared (Sansom *et al.* 2010). It is also clear that apparent extinctions in the fossil record may actually be periods of persistent rarity where a taxon is simply no longer detected due to reduced abundance (Hull *et al.* 2015).

2.4 An uncertain future

The Bramble Cay melomys (*Melomys rubicola*) is the first mammal species for which its extinction has been almost entirely attributed to anthropogenic climate change, as erosion and storms beset its only known island population (Waller *et al.* 2017). Climate change, including severe weather, has already been implicated in the extinction (or extinction in the wild) of at least 41 species (IUCN 2024). A meta-analysis considering published estimates of

extinction risk and representative concentration pathways for the 21st century, predicted that 3°C warming will result in an estimated 8.5% of species becoming extinct, with a rise of 4.3°C increasing this to 16% (Urban 2015). Indeed, groups that have exhibited high extinction rates under climatic change in the past such as foraminifera are already starting to show declines in abundance and biomass as well as range shifts (Chaabane et al., 2024; Ying et al., 2024). Alongside climate change, land and sea use, as well as human appropriation of net primary productivity, continue to rapidly change the planet. 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 use different projections for future land-use and climate when comparing multiple models (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. Nonetheless, despite the large range of estimated extinction levels, nearly all projections indicate large numbers of additional species-level extinctions, but none of them predicts extinction levels as high as 75% of species (given current, known threats).

Assuming losses of all threatened species, added to those already extinct (or extinct in the wild) since 1500 AD, Barnosky (2011) estimated species losses of on average 32% (ranging

from 14% in birds to 64% in cycads). Using a Late Pleistocene baseline, Davis *et al.* (2018) estimated that a century from now we will have lost 16% of mammal species over the last 130 ka. 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, i.e. 75% species losses. Assuming the loss of all threatened species within the first century with high rates still continuing after, a mass extinction would be reached for terrestrial amphibians, mammals, and birds in ~ 240 to 540 years. If only 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). A range of estimates has been produced by different studies depending on the data and assumptions made (Wiens and Saban, 2025). On this basis, for mass extinction levels 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. However, this likely requires new threatening processes, extinction cascades or ecosystem tipping points to emerge in future, given that high rates would need to continue even after the loss of all currently threatened species to reach the 75% threshold for assessed groups (Wiens and Saban, 2025). Unknown extinctions also clearly hamper the accuracy of any estimates (Cowie *et al.*, 2025). Future scenarios are highly uncertain, and this hinders our ability to predict future extinction risk, particularly when many of the relevant processes are likely non-linear. It is clear therefore that projections of a sixth mass extinction are heavily contingent on the assumptions made.

The other side of this coin is speciation. Humans have moved species around the planet across distances and at rates exceeding those of past biotic interchanges such as the Great American Biotic Interchange (Stigall 2019). As these new populations adapt to novel surroundings, they often contribute to the extinction of other species, as evidenced by our discussion of island extinctions above; furthermore, it is estimated that introduced species

have contributed to 25% of plant extinctions and 33% of animal extinctions documented by the IUCN (Blackburn et al., 2019). They might also be expected to form new species over time, a process that could be accelerated by the strength of anthropogenic selection pressures and hybridisation (Thomas 2015). However, the extent to which this could offset losses is heavily 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 loss of global phylogenetic diversity for an extended period (Faurby *et al.* 2022). On million-year time scales, heightened speciation rates are hypothesised as ecosystems recover in the aftermath of extinction events (Chen and Benton 2012), as empty niche space is refilled. How such a mechanism could operate under the rapid anthropogenic drivers of change is unknown, especially as niche space and resources have been disproportionately channelled from many species into one, i.e. *Homo sapiens*. In sum, conservation of at-risk species and the resilience of remaining species will likely reduce species-level extinction rates, but extinction will undoubtedly continue under ongoing climatic changes, ongoing species introductions, and as-yet unimagined future human pressures.

3 BIASES AND UNCERTAINTY

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). Accurately comparing ecosystems through time is a substantial challenge that requires comprehensive consideration of fossil record biases, i.e. biological, environmental and research biases which systematically and non-randomly skew the available fossil record (Alroy 2010; Nanglu and Cullen 2023; Raup 1972). Understanding and addressing these biases is therefore essential for us to accurately quantify past extinction rates, and make clearer comparisons with those of the present and future.

3.1 Temporal inconsistency

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 and time (Holland *et al.* 2022; Smith and McGowan 2007). Rocks that are preserved are prone to destruction in non-uniform ways (e.g. subduction), producing a geological record that is incomplete, 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 information distortion, with geographic and societal (Raja *et al.* 2022) factors substantially impacting our perception of past events.

All of these factors have particularly noticeable effects on estimation of the rates and durations of ‘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 (e.g. Ediacaran extinctions, Hoyal Cuthill 2022; Jurassic-Cretaceous boundary, Tennant *et al.* 2017). In addition, the synthesis required to detect large-scale events is hampered by the differences in temporal sampling between different studies which have a substantial impact on measuring diversity through time (Dean *et al.* 2020; Gibert and Escarguel 2017; Guillaume and Cooper 2018; Smith *et al.* 2023).

The timing of extinction is highly dependent on the definition of the taxonomic entity being described: this means that inferred extinction rates can be affected by differences in species definitions between clades, and between living and fossil taxa. In its most extreme form, modern phylogenetic methods have resulted in the ability to split species based predominantly on their genetic diversity, an option not open for fossil remains. As already discussed, the majority of paleobiological studies are focused at the genus level (Hendricks *et al.*, 2014), in contrast to present-day biodiversity which is typically discussed in terms of species. Our varying ability to resolve different taxonomic groups to species level also has a temporal effect in of itself, as the relative frequency of these groups has not been consistent

over time - this, combined with heterogenous preservational biases, means that the diversity of certain taxonomic groups is more difficult to estimate than others, providing a challenge to global biodiversity estimates as clades wax and wane. There are also clear temporal patterns in terms of which groups are studied, and these issues are not restricted to paleontological analyses; most studies of current biodiversity are also taxonomically limited (Cowie *et al.*, 2025; Mammola *et al.* 2023; Wiens and Saban, 2025). One such challenging issue for comparison is our lack of knowledge on modern marine extinctions (Harnik *et al.* 2012; Monte-Luna *et al.* 2023), whereas enumeration of many extinction events in deep time relies on changes in marine genera due to their relatively high preservation potential (Plotnick *et al.* 2016).

3.2 Spatial inconsistency

Spatial heterogeneity in fossil data can generate uncertainties that are as large as those associated with temporal gaps in the geological record (Allison and Briggs 1993; Antell *et al.* 2024; Close *et al.* 2020; 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 impacted by historical legacies (Raja *et al.* 2022). This changing patchwork of spatial data has a substantial impact on our understanding and interpretation of extinction events. Given that the geographic distributions of species and ecosystems have responded to changing environmental conditions throughout time, there is a risk of conflating ecological and evolutionary adjustments to the new conditions with global extinction. For example, did a species become extinct between two successive time periods, or is its preferred environment no longer represented in the fossil record (Smith *et al.* 2001)? Conversely, an integrated fossil record at the global scale may underestimate the magnitude of regional changes (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).

4 MEANINGFUL COMPARISONS

To compare extinction events requires consideration of the available data quality, magnitude, duration, and selectivity of each extinction event. To make future predictions we must also consider common drivers: which influences are known to be able to cause major shifts in the biosphere? It is difficult to both understand past extinction events and, perhaps more importantly, to make fair and meaningful comparisons between extinction events (e.g. Tomašových *et al.* 2023). Although methodological approaches exist to combat at least some of these biases (e.g. PyRate, subsampling, spatial partitioning (Close *et al.* 2018; Silvestro *et al.* 2014; Tibshirani 1994; Allen *et al.* 2025)), the drawing of well-supported comparisons between different time periods is always likely to remain heavily caveated. Because it is clear that our knowledge is incomplete, we therefore need to be circumspect and make the most of the multiple lines of evidence that are available.

4.1 Extinction drivers

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, how comparable are the volume and rate (Foster *et al.* 2018)? Although the sources of atmospheric changes differ (e.g. fossil fuels versus volcanic activity), it is clear that warming has been a key extinction driver in most major past events, with accompanying acidification and anoxia in the oceans (Bond and Grasby 2017; Calosi *et al.* 2019; Harnik *et al.* 2012). This underlines the importance of emissions to the unfolding extinction event. Other similarities can also be observed: for example, large community restructuring has occurred in past biotic interchanges (i.e. during the exchange of species when barriers between

separated landmasses or oceans are removed), which parallels anthropogenic species introductions; however, the rate and volume are likely far greater at present (McGhee *et al.* 2013; Vermeij 1991). Other anthropogenic drivers are more difficult to match with past extinction events. The degree of novel predation generated by humans may have some parallels in past biotic interchange but the rate and extent are likely uniquely high. The rapid and extensive changes in land and sea-use (human versus Earth system mediated) are probably only surpassed by cataclysms such as the K-Pg event, with other events experiencing these on far slower timescales. However, many of the key measures and consequences of extinction events have similarities between the present day and those seen in the geological record.

4.2 Extinction magnitudes

The magnitude of an extinction event is often calculated as the proportional reduction in the number of taxa (e.g. genera or species) or the proportion of taxa surviving into the time bin or period after an event (Table 1, Figure 2). Mammals provide our highest resolution information on anthropogenic extinctions. The PHYLACINE database (Faurby *et al.* 2020) records 1,400 known mammal genera over the last ~130 ka. Only 1,245 of these are estimated to still be extant in the wild, giving an approximate loss of 11% of mammal genera globally. This is less than the 62% genus loss estimated for western European endemic artiodactyls across the Eocene-Oligocene transition (Weppe *et al.* 2023), but the latter is only a subset of the late Eocene mammal fauna, whereas the 11% loss of Recent mammal genera is a global estimate. The latter is also less than the 36% loss of Pliocene marine megafaunal genera (Pimienta *et al.* 2017). However, when we only consider megafauna (genera > 45kg; Malhi *et al.* 2016) in our estimate of Recent mammalian losses (43%), this exceeds that of the Pliocene. 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 16% late Eocene genus extinction reported by Bambach (2006). However, data comparability is again an issue: Bambach's (2006) estimates are across a wide range of marine taxa and not just a

single group, and they do not account for sampling heterogeneity. Raw proportions of genus extinction based on all taxa and across just mammals and reptiles in the Paleobiology Database (<https://paleobiodb.org/> [accessed 23rd April 2025]) also indicate very high losses at the end of the Eocene, a pattern that holds across multiple measures (Figure 2). These are, however, based on 5 million year time bins, with this coarse resolution allowing more extinction accumulation as the time period is longer. Such comparisons show some of the issues already highlighted around the challenges of comparison between past and present data.

4.3 Extinction rates

We would expect the 130 kyr time scale used here for anthropogenic extinctions to be short compared to some other documented extinction events. However, the duration and dynamics of past extinctions are mostly unresolved, with some authors estimating a similar 100 kyr scale duration for the PETM (Molina 2015; Speijer *et al.* 2012). The K-Pg is thought to have had a more rapid 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 100-fold if its duration was 50,000 years rather than seven million years (Marshall 2023). Since ‘short-sharp’ events of 100,000 or fewer years tend to become temporally averaged into ‘longer-gradual’ geological events in the fossil record, it is extremely difficult to draw firm conclusions about the tempo of most past mass extinction events. Rate-duration deductions therefore inevitably come with high levels of uncertainty. This is especially true for many of the estimates used to examine the ‘Sixth mass extinction’, with most authors focusing on just the wave of extinctions that have taken place over the last 500 years (e.g. Ceballos *et al.* 2015), a drastically different temporal resolution to the baseline data used as a comparator (Wiens and Saben, 2025). Rate analyses indicate that the K-Pg event and the start and end of the Eocene saw the highest extinction rates (Figure 2), but their duration is uncertain and therefore currently not comparable to the modern record. Such drastic differences in

temporal resolution make solely quantitative comparisons highly unreliable, unless enforced with other contextual information such as drivers and mechanisms.

4.4 Extinction selectivity

Another key aspect traditionally used to compare events is extinction selectivity. Range size is considered a key attribute, with some evidence that geographically restricted species are usually at higher risk. This, however, does not appear to hold consistently across all mass extinctions (Dunhill and Wills 2015; Foster *et al.* 2023; Payne *et al.* 2023). The current event shows a preferential loss of small ranged species, with the loss of island endemics being a prominent example (e.g. Cooke *et al.* (2023)), but extinctions from small oceanic islands and of small ranged species in general are typically not detected in the deep time fossil record (Plotnick *et al.* 2016). However, earlier waves of anthropogenic extinction such as the loss of the terrestrial megafauna, resulted in the loss of once widespread species, and population trends over the last few decades cannot be explained by geographic range size (Daskalova *et al.* 2020; Malhi *et al.* 2016). Range contractions and population reductions in widespread species can result in more species being rare. This may leave them more vulnerable to extinction in future, but in turn, would also likely result in fewer species being preserved, which would be perceived as a mass extinction by future paleobiologists working only with the fossil record (Hull *et al.* 2015). Body size selectivity is often identified with anthropogenic extinctions (Purvis *et al.* 2000), again exemplified by the terrestrial megafaunal extinctions. However, this link between body size and extinction is not seen in all events (Monarrez *et al.* 2021; but see K-Pg; Payne *et al.* 2023). Assessing these factors mechanistically, both body size and range size are related to demography, with large species and those with restricted ranges usually having smaller populations, and, in the case of large species, lower reproductive rates. Smaller populations and reduced ability to rapidly replenish them make species susceptible to overharvesting, which is perhaps a unique driver to the current extinction event.

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 that current patterns of selectivity may not hold as the event increases in magnitude. For example, amphibian extinctions due to infection by chytrid fungus are not specifically associated with body size. 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). As the magnitude increases, the chances of losing higher taxonomic groups increases under a random process ('Field of bullets' (Raup 1991)), but for this to be achieved at lower magnitudes, the process would have to differ strongly from random (i.e. some form of selectivity). However, as yet, no clear patterns in the degree or type of selectivity have been found in common across mass extinctions (Bush *et al.* 2020; Foster *et al.* 2023; Payne *et al.* 2023).

4.5 Biosphere regime shift

When considering anthropogenic extinctions, the loss of the megafauna and the processes they regulated can be seen as part of a simplification and homogenisation of the biosphere (Fraser *et al.* 2022). In addition to this early wave, simplified and often homogenised ecosystems across the globe are widely documented today (Daru *et al.* 2021). 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 human transportation across the world. This bears strong similarities to the "disaster faunas" 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 mass extinction (Sahney and Benton 2008). 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 event (Alvarez *et al.* 1980), but it has proven difficult to quantify (Roopnarine 2006).

Community and ecosystem restructuring is also studied by the analysis of changes 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 predictions of future extinction risk (Carmona *et al.* 2021; Hatfield *et al.* 2022; Sayol *et al.* 2021). Although evidence is mixed on whether past extinctions removed entire functional groups (Dineen *et al.* 2014; Edie *et al.* 2018; Foster and Twitchett 2014), they did reduce functional redundancy, with fewer species performing any particular function (Pimienta *et al.* 2017, 2020). In the cases of the end-Permian and end-Cretaceous mass extinctions, regime shifts are thought to have taken place, with pre-extinction and post-extinction faunas and floras having different structures, for example the restructuring of tropical forests post K-Pg (Carvalho *et al.* 2021; Feng *et al.* 2020). 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 the biosphere with such levels of reorganisation perhaps not seen since the recovery from the K-Pg.

4 CONCLUSIONS

The available evidence suggests that the current extinction rate is approaching or even surpassing that seen across earlier Cenozoic events, at least for certain groups. Both the taxonomic and geographic breadth also appears to be greater than other Cenozoic events and it is clear that human influence has grown rapidly and become global. The magnitude recorded so far, however, suggests that anthropogenic extinctions are still far below that of the larger pre-Cenozoic mass extinction events, such as those that marked the end-Permian and end-Cretaceous. The Eocene-Oligocene transition, 34 million years ago, appears to be the nearest contender for the largest Cenozoic extinction event, but comparison to the

current anthropogenic extinction event is heavily hampered by the lack of high resolution data. Nevertheless, the available evidence suggests that the Eocene-Oligocene event occurred on a million-year timescale and was staggered spatiotemporally and taxonomically. Comparisons of extinction events across deep time will always remain deeply caveated and uncertain though, even with rapidly improving methods and accumulating data. However, the future of anthropogenic pressures are also highly uncertain and are not expected to subside for at least many decades, and some, such as climatic change, are expected to increase. The current extinction event 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 sea/land-use and climatic change will have a substantial impact on the magnitude of the current extinction event. Precluding major reductions in the current extinction rate, we are witnessing what will become the greatest extinction event since the demise of the non-avian 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.

Conflict of interest statement

None

Data availability statement

Sepkoski's compendium (Figure 1) was reproduced using the R package `sepkoski`. Genus level records were from the Paleobiology Database <https://paleobiodb.org> (Downloaded 23rd April 2025) and plotted (Figure 2) using the R package `divDyn`.

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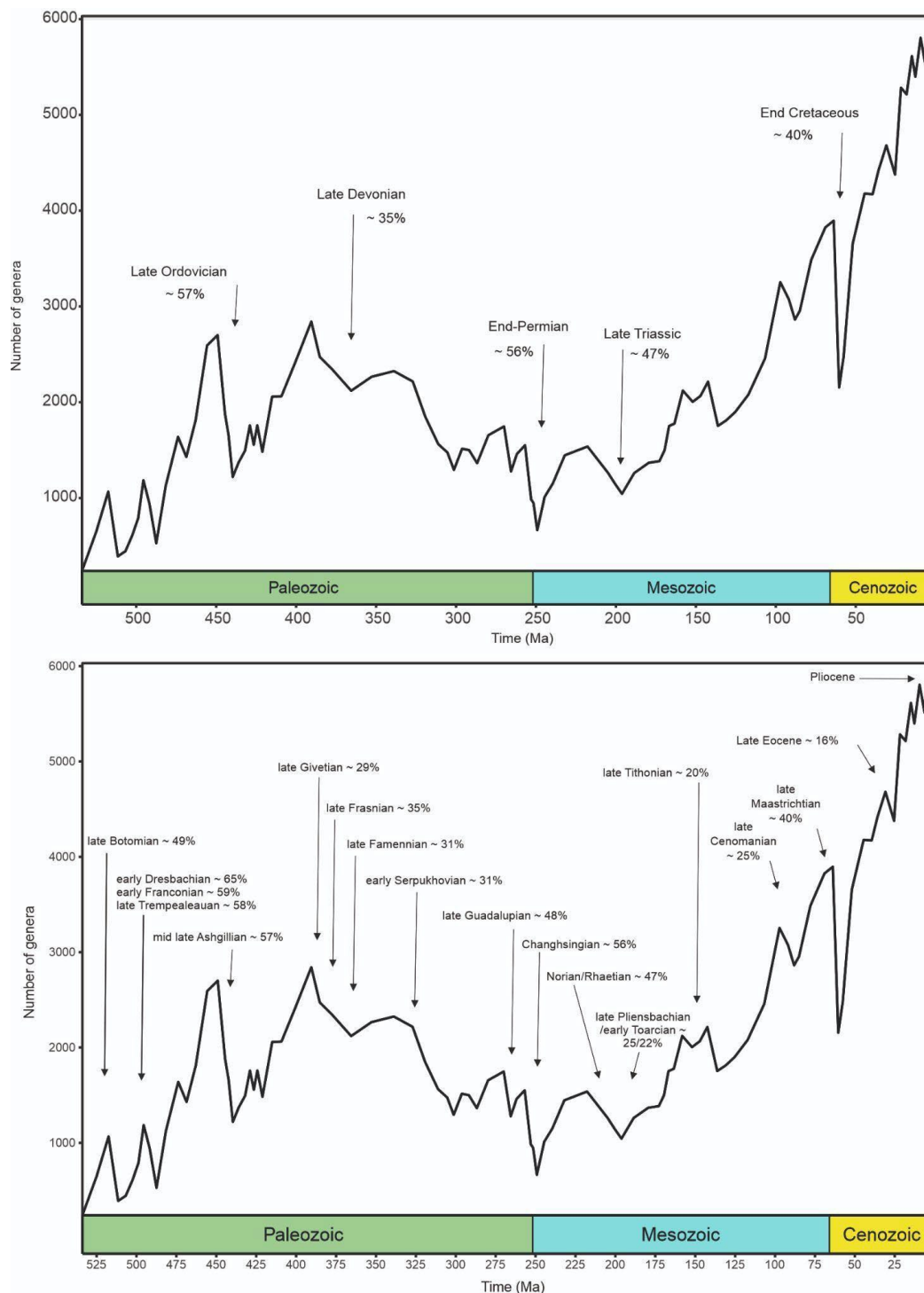
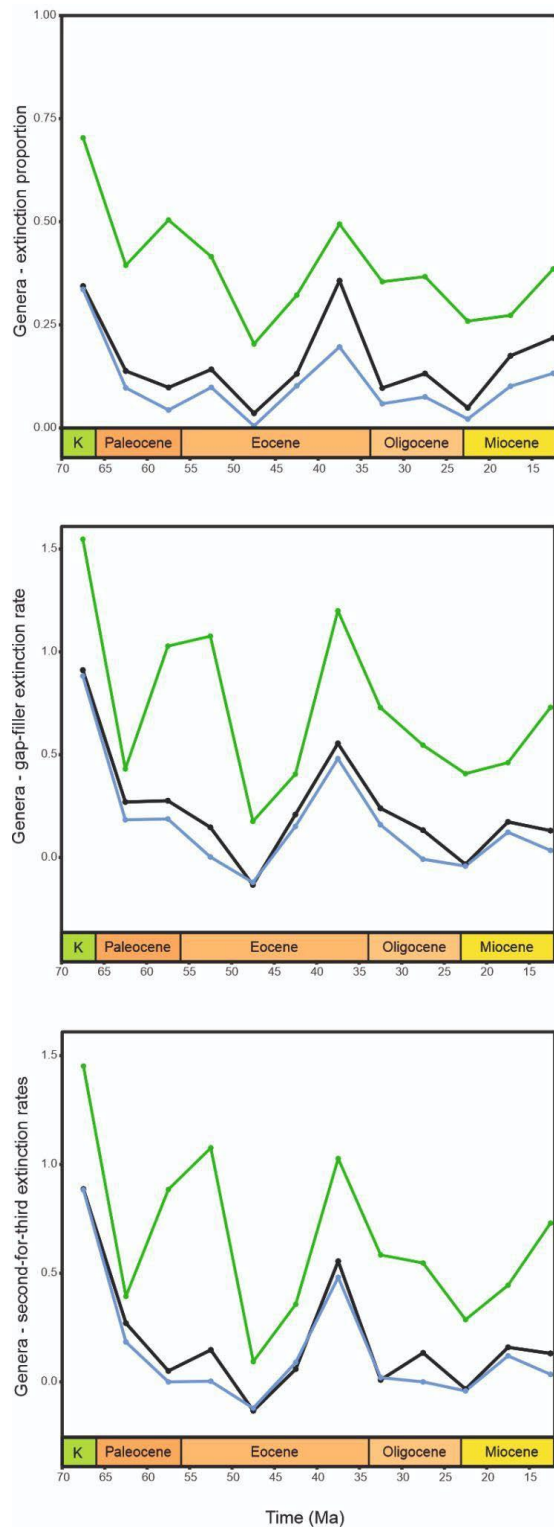


FIGURE 1 - Number of fossil marine animal genera over the Phanerozoic based on Sepkoski's compendium (Peters 2022; Sepkoski 1981, 2002). Reproduced using the R packages sepkoski (Jones 2022) and deeptime (Gearty 2024). In the top panel the arrows indicate the Big Five mass extinction events with estimates of the percentages of genera becoming extinct. The bottom panel shows the 18 sub-stage intervals identified by Bambach (2006). A percentage of extinct genera was not given for the Pliocene.



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FIGURE 2 - Proportional extinctions, gap-filler and second-for-third extinction rate using 5 my bins and genera from the Paleobiology Database (download April 2025) and the divDyn R package (Kocsis *et al.*, 2019). Points indicate the midpoint of each bin. Individual records were assigned based on the midpoint of their potential date. Black indicates all genera, blue genera from predominantly marine taxonomic groups and green mammals and reptiles. Records missing genus information and singletons were not considered. Due to the resolution these can not be calculated for more recent bins.

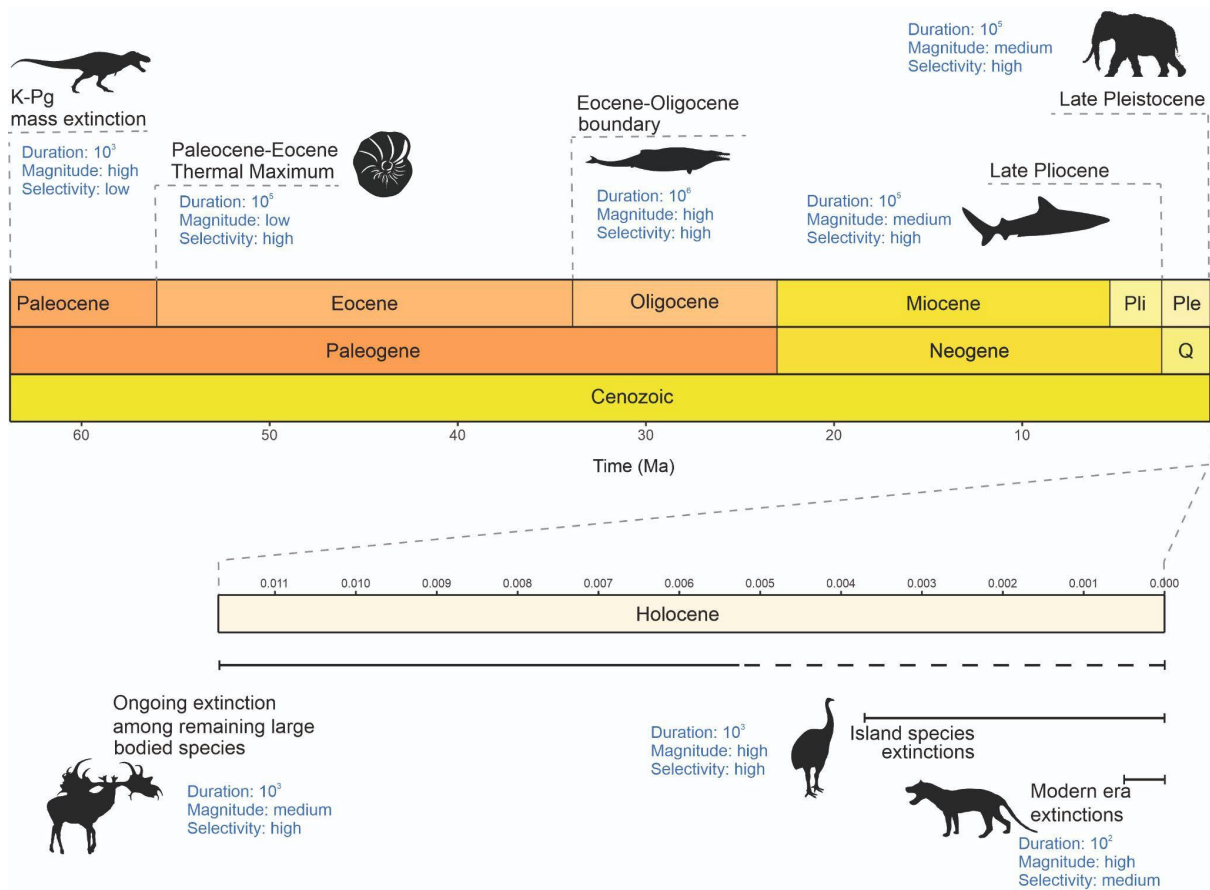


FIGURE 3 - A timeline of major Cenozoic extinction events. Produced using the R packages sepkoski (Jones 2022) and deeptime (Gearty 2024). Species silhouettes (phylopic.org contributors (M. Brea Lueiro, T.M. Keeseey, S. Traver, J. Taylor) and Inês Martins) show single examples for illustrative purposes and are not intended to be comprehensive.

1299 **Table 1** - Summary of magnitudes estimated for Cenozoic extinction events. These are
1300 based on different taxonomic and spatial data, and thus they are not necessarily all directly
1301 comparable.

| Extinction event | Taxon | Geographic scope | Extinction magnitude | Reference |
|------------------|---|------------------|---|------------------------------------|
| PETM | Deep sea benthic foraminifera | Local | 33 to 65% (species) | Speijer et al., (2012) |
| Eocene-Oligocene | Marine animals | Global | 15.6% (genera) | Bambach, (2006) |
| | Planktonic foraminifera | Regional | < 15% (species) | Keller, (1986) |
| | Endemic artiodactyls | Local | 77% (species) 62% (genera) | Weppe et al., (2023) |
| Plio-Pleistocene | Marine animals | Global | Ranging by taxonomic group 0.5% to > 11% (genera) | Bambach, (2006) |
| | Marine megafauna | Global | 36% (genera) | Pimienta et al., (2017) |
| | Molluscs | Regional | 49% (species) | Pimienta et al., (2020) |
| | Corals | Regional | 42% (genera) | van Woesik et al., (2012) |
| Anthropogenic | Mammals (since last interglacial) | Global | 11% (genera) | Derived from Faurby et al., (2020) |
| | Mammalian megafauna (since last interglacial) | Global | 43% (genera) | Derived from Faurby et al., (2020) |
| | Mammalian megafauna (Late Quaternary) | Regional | 21% (Africa) to 88% (Australia) (genera) Continental median= 72% | Koch and Barnosky (2006) |
| | Birds (since last interglacial) | Global | 12% (species) | Cooke et al., (2023) |
| | Pacific Island landbirds (Holocene) | Local | 0 to 100% (species) Island median = 66.5% | Braje and Erlandson, (2013) |

| | | | | |
|--|---|----------|-----------------------------|------------------------------|
| | Pacific Island land snails (since human occupation) | Regional | Approximately 50% (species) | Lydeard et al., (2004) |
| | Tetrapods (since 1500) | Global | 1% (genera) | Ceballos and Ehrlich, (2023) |

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