





REVIEW

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

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Received: 19 February 2025 | Revised: 12 August 2025 | Accepted: 16 August 2025

Funding: This work resulted from a series of workshops with financial support from the Leverhulme Centre for Anthropocene Biodiversity (RC-2018-021). Bethany J Allen was funded by ETH Zurich. Thomas Guillerme was funded by NERC IRF grant NE/X016781/1. Philip D. Mannion contribution was funded by The Royal Society (UF160216, URF\R\221010) and The Leverhulme Trust (RPG-2021-202). This is Paleobiology Database official publication number #533. For the purpose of open access, the lead author has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

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

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

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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 are indeed higher than at any time over the last 66 million years, that is, 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.

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

Here, we synthesize previous literature investigating both past extinctions and ongoing biodiversity change to 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 Phanerozoic mass extinctions. We follow this by discussing extinction events over the last 66 million years, that is, since the last mass extinction and when Earth's ecosystems and biodiversity have been the most similar to those of the present day. We then consider the anthropogenic extinction event, defined herein as spanning the last interglacial (~130 ka) to the present. This represents the well-established time frame of increasing human planetary influence, from the megafaunal extinction, through to the current 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 presentday 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, 278). The ambiguity in this definition has led to more quantitative interpretations, such as 75% of species becoming extinct in <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

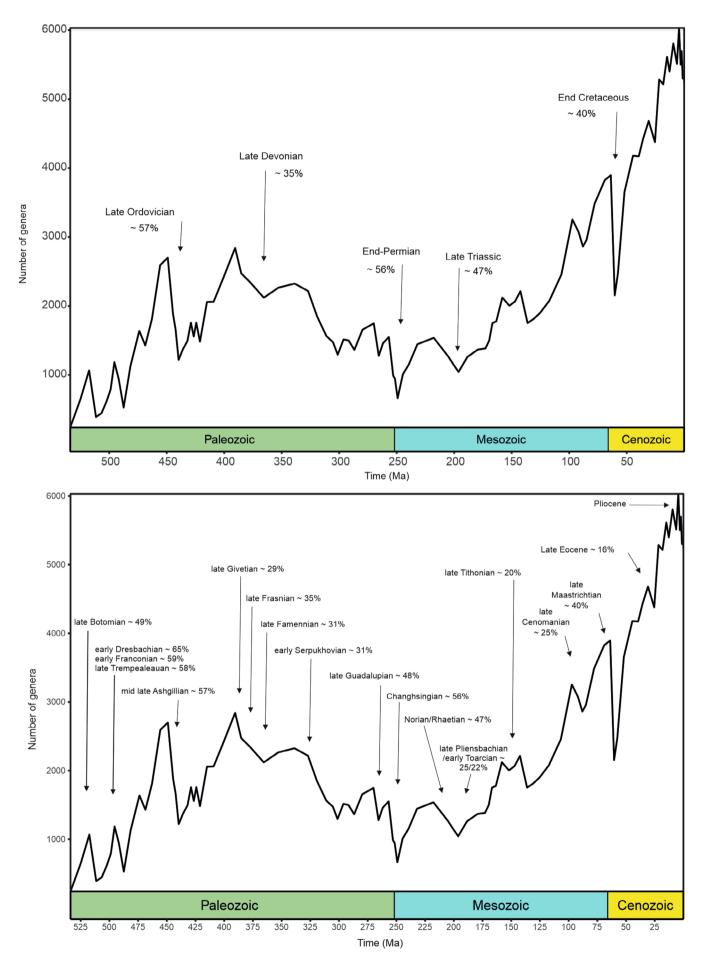


FIGURE 1 | Legend on next page.

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.

(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, that is, 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 (234-232 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 localized 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 fordeep-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 recognizable 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 hypothesized 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," that is, global cooling associated with the rapid release of sulfate 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

The most recent mass extinction event took place at the end of the Cretaceous, heralding the end of the Mesozoic and the beginning of the Cenozoic, 66 Ma. The large asteroid impact in the Yucatán Peninsula of Mexico and subsequent wildfires resulted in dust, sulfate aerosols, CO_2 , soot, and water vapor entering the atmosphere, which led to rapid, extreme climatic cooling and ocean acidification (Chiarenza et al. 2020; Hull et al. 2020; Morgan et al. 2022). An estimated 40% of genera and 76% of species were lost (Barnosky et al. 2011), including the extinction of many vertebrate and invertebrate groups, most famously the non-avialan dinosaurs and ammonites, although no taxonomic group passed through the K/Pg boundary entirely unscathed (Hallam and Wignall 1997). The process was likely rapid (Chiarenza et al. 2020), meaning that both the magnitude and rate of extinction were extremely high.

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

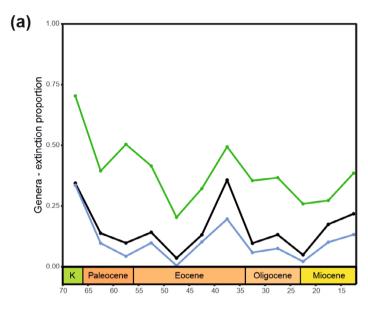
The Cenozoic fossil record provides evidence for several extinction events since the K-Pg event. Although not as devastating as the latter extinction, all of these appear to have been taxonomically, environmentally, and geographically wide-ranging, with long-term consequences for the biosphere (Figures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

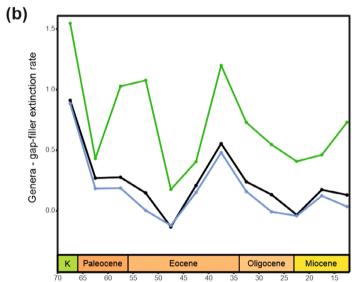
The events defining the start and end of the Eocene resulted in substantial change in the Earth's systems. The PETM saw rapid warming (>5°C global mean average increase) and ocean acidification, attributed to volcanic carbon releases within <10,000 years (Aze 2022; Harnik et al. 2012; Haynes and Hönisch 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%–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 and 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 <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 mollusks, 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 millionyear 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 toward 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). Localized extinctions at the end of the Pliocene have also been noted for Caribbean mollusks 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."





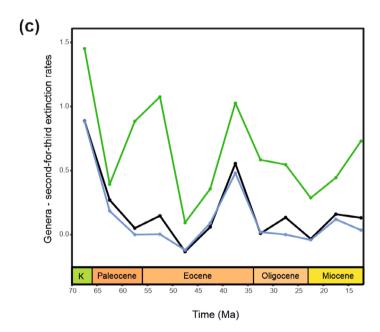


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FIGURE 2 | Proportional extinctions (a), gap-filler (b) and second-for-third extinction rate (c) using 5 my bins and genera from the Paleobiology Database (download April 2025) and the divDyn R package (Kocsis et al. 2019). Points indicate the midpoint 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 cannot be calculated for more recent bins.

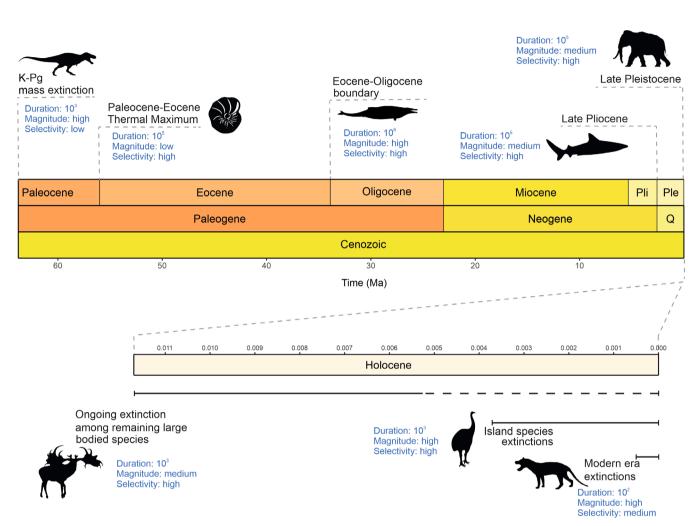


FIGURE 3 | A timeline of major Cenozoic extinction events. Produced using the R packages sepkoski (Jones 2022) and deeptime (Gearty 2024). Species silhouettes (phylopic.org contributors (M. Brea Lueiro, T.M. Keesey, S. Traver, J. Taylor) and Inês Martins) show single examples for illustrative purposes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

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 (>44kg) 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 ~1000 bird species (and any obligate parasites) resulting from human colonization (Duncan et al. 2013). Recent estimates of global bird extinctions consider that ~12% of bird species (1300-1500) 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 globalization 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%–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 modeling and data limitations. Existing scenario studies often use a single model, analyze 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 et al. (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, that is, 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 ~240-540 years. If only Critically Endangered species were lost over 500 years followed by rate continuation, estimates range from 4450 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 the 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 millionyear 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, that is, 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, that is, 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 exacerbate 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 the 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; Guillerme 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 presentday 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 and of itself, as the relative frequency of these groups has not been consistent over timethis, 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; del 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 vary 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 1400 known mammal genera over the last ~130 ka. Only 1245 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 (Pimiento et al. 2017). However, when we only consider megafauna (genera > 45 kg; 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 7 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 Saban 2025).

TABLE 1 | Summary of magnitudes estimated for Cenozoic extinction events. These are based on different taxonomic and spatial data, and thus they are not necessarily all directly comparable.

		Geographic		
Extinction event	Taxon	scope	Extinction magnitude	References
PETM	Deep sea benthic foraminifera	Local	33%-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)	Pimiento et al. (2017)
	Molluscs	Regional	49% (species)	Pimiento 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)

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 the 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 homogenization of the biosphere (Fraser et al. 2022). In addition to this early wave, simplified and often homogenized ecosystems across the globe are widely documented today (Daru et al. 2021). Current homogenization 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 (Pimiento 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.

5 | 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 appear 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 is also highly uncertain and they 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-avialan dinosaurs 66 million years ago; whether we see a mass extinction remains a choice yet to be made.

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Acknowledgements

We would like to thank Erin Saupe and Alex Dunhill for their feedback and discussions. This work resulted from a series of workshops with financial support from the Leverhulme Centre for Anthropocene Biodiversity (RC-2018-021). Bethany J. Allen was funded by ETH Zurich. Thomas Guillerme was funded by NERC IRF grant NE/X016781/1. Philip D. Mannion contribution was funded by The Royal Society (UF160216, URF\R\221010) and The Leverhulme Trust (RPG-2021-202). This is Paleobiology Database official publication number #533. For the purpose of open access, the lead author has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

Conflicts of Interest

The authors declare no conflicts of interest.

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.

References

Aberhan, M., and T. K. Baumiller. 2003. "Selective Extinction Among Early Jurassic Bivalves: A Consequence of Anoxia." *Geology* 31, no. 12: 1077–1080. https://doi.org/10.1130/G19938.1.

Allen, B. J., R. C. M. Warnock, and A. M. Dunhill. 2025. "A History of the World Imperfectly Kept": Will We Ever Know How Biodiversity Has Changed Over Deep Time. https://doi.org/10.32942/X2DD1V.

Allen, B. J., P. B. Wignall, D. J. Hill, E. E. Saupe, and A. M. Dunhill. 2020. "The Latitudinal Diversity Gradient of Tetrapods Across the Permo-Triassic Mass Extinction and Recovery Interval." *Proceedings of the Royal Society B: Biological Sciences* 287: 20201125. https://doi.org/10.1098/rspb.2020.1125.

Allison, P. A., and D. E. G. Briggs. 1993. "Paleolatitudinal Sampling Bias, Phanerozoic Species Diversity, and the End-Permian Extinction." *Geology* 21, no. 1: 65–68.

Alroy, J. 2010. "Geographical, Environmental and Intrinsic Biotic Controls on Phanerozoic Marine Diversification." *Palaeontology* 53, no. 6: 1211–1235. https://doi.org/10.1111/j.1475-4983.2010.01011.x.

Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. "Extraterrestrial Cause for the Cretaceous-Tertiary Extinction." *Science* 208, no. 4448: 1095–1108. https://doi.org/10.1126/science.208.4448.1095.

Andermann, T., S. Faurby, S. T. Turvey, A. Antonelli, and D. Silvestro. 2020. "The Past and Future Human Impact on Mammalian Diversity. *Science.*" *Advances* 6, no. 36: eabb2313. https://doi.org/10.1126/sciadv.abb2313.

Antell, G. T., R. B. J. Benson, and E. E. Saupe. 2024. "Spatial Standardization of Taxon Occurrence Data—A Call to Action." *Paleobiology* 50: 177–193. https://doi.org/10.1017/pab.2023.36.

Arcila, D., and J. C. Tyler. 2017. "Mass Extinction in Tetraodontiform Fishes Linked to the Palaeocene–Eocene Thermal Maximum." *Proceedings of the Royal Society B: Biological Sciences* 284, no. 1866: 20171771. https://doi.org/10.1098/rspb.2017.1771.

Aze, T. 2022. "Unraveling Ecological Signals From a Global Warming Event of the Past." *Proceedings of the National Academy of Sciences* 119, no. 13: e2201495119. https://doi.org/10.1073/pnas.2201495119.

Babila, T. L., D. E. Penman, C. D. Standish, et al. 2022. "Surface Ocean Warming and Acidification Driven by Rapid Carbon Release Precedes Paleocene-Eocene Thermal Maximum. *Science.*" *Advances* 8, no. 11: eabg1025. https://doi.org/10.1126/sciadv.abg1025.

Bambach, R. K. 2006. "Phanerozoic Biodiversity Mass Extinctions." *Annual Review of Earth and Planetary Sciences* 34: 127–155. https://doi.org/10.1146/annurev.earth.33.092203.122654.

Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing, and A. B. Shabel. 2004. "Assessing the Causes of Late Pleistocene Extinctions on the Continents." *Science* 306, no. 5693: 70–75. https://doi.org/10.1126/science.1101476

Barnosky, A. D., N. Matzke, S. Tomiya, et al. 2011. "Has the Earth's Sixth Mass Extinction Already Arrived?" *Nature* 471, no. 7336: 51–57. https://doi.org/10.1038/nature09678.

Benson, R. B. J., R. Butler, R. A. Close, E. Saupe, and D. L. Rabosky. 2021. "Biodiversity Across Space and Time in the Fossil Record." *Current Biology* 31, no. 19: R1225–R1236. https://doi.org/10.1016/j.cub. 2021.07.071.

Bibi, F., and J. L. Cantalapiedra. 2023. "Plio-Pleistocene African Megaherbivore Losses Associated With Community Biomass Restructuring." *Science* 380, no. 6649: 1076–1080. https://doi.org/10.1126/science.add8366.

Blackburn, T. M., C. Bellard, and A. Ricciardi. 2019. "Alien Versus Native Species as Drivers of Recent Extinctions." *Frontiers in Ecology and the Environment* 17, no. 4: 203–207. https://doi.org/10.1002/fee.2020.

Bond, D. P. G., and S. E. Grasby. 2017. "On the Causes of Mass Extinctions." *Palaeogeography, Palaeoclimatology, Palaeoecology* 478: 3–29. https://doi.org/10.1016/j.palaeo.2016.11.005.

Braje, T. J., and J. M. Erlandson. 2013. "Human Acceleration of Animal and Plant Extinctions: A Late Pleistocene, Holocene, and Anthropocene Continuum." *Anthropocene* 4: 14–23. https://doi.org/10.1016/j.ancene. 2013.08.003.

Bush, A. M., S. C. Wang, J. L. Payne, and N. A. Heim. 2020. "A Framework for the Integrated Analysis of the Magnitude, Selectivity, and Biotic Effects of Extinction and Origination." *Paleobiology* 46, no. 1: 1–22. https://doi.org/10.1017/pab.2019.35.

Button, D. J., G. T. Lloyd, M. D. Ezcurra, and R. J. Butler. 2017. "Mass Extinctions Drove Increased Global Faunal Cosmopolitanism on the Supercontinent Pangaea." *Nature Communications* 8, no. 1: 733. https://doi.org/10.1038/s41467-017-00827-7.

Calosi, P., H. M. Putnam, R. J. Twitchett, and F. Vermandele. 2019. "Marine Metazoan Modern Mass Extinction: Improving Predictions by Integrating Fossil, Modern, and Physiological Data." *Annual Review of Marine Science* 11, no. 1: 369–390. https://doi.org/10.1146/annurev-marine-010318-095106.

Carmona, C. P., R. Tamme, M. Pärtel, et al. 2021. "Erosion of Global Functional Diversity Across the Tree of Life. *Science.*" *Advances* 7, no. 13: eabf2675. https://doi.org/10.1126/sciadv.abf2675.

Carroll, T., J. H. Hatfield, and C. D. Thomas. 2023. "Globally Abundant Birds Disproportionately Inhabit Anthropogenic Environments." *bioRxiv*. https://doi.org/10.1101/2023.12.11.571069.

Carvalho, M. R., C. Jaramillo, F. de la Parra, et al. 2021. "Extinction at the End-Cretaceous and the Origin of Modern Neotropical Rainforests." *Science* 372, no. 6537: 63–68. https://doi.org/10.1126/science.abf1969.

- Ceballos, G., and P. R. Ehrlich. 2023. "Mutilation of the Tree of Life via Mass Extinction of Animal Genera." *Proceedings of the National Academy of Sciences* 120, no. 39: e2306987120. https://doi.org/10.1073/pnas.2306987120.
- Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. "Accelerated Modern Human–Induced Species Losses: Entering the Sixth Mass Extinction." *Science Advances* 1, no. 5: e1400253. https://doi.org/10.1126/sciadv.1400253.
- Chaabane, S., T. de Garidel-Thoron, J. Meilland, et al. 2024. "Migrating Is Not Enough for Modern Planktonic Foraminifera in a Changing Ocean." *Nature* 636, no. 8042: 390–396.
- Chen, Z.-Q., and M. J. Benton. 2012. "The Timing and Pattern of Biotic Recovery Following the End-Permian Mass Extinction." *Nature Geoscience* 5, no. 6: 375–383. https://doi.org/10.1038/ngeo1475.
- Chiarenza, A. A., A. Farnsworth, P. D. Mannion, et al. 2020. "Asteroid Impact, Not Volcanism, Caused the End-Cretaceous Dinosaur Extinction." *PNAS* 117, no. 29: 17084–17093. https://doi.org/10.1073/pnas.2006087117.
- Cleary, T. J., R. B. J. Benson, S. E. Evans, and P. M. Barrett. 2018. "Lepidosaurian Diversity in the Mesozoic-Palaeogene: The Potential Roles of Sampling Biases and Environmental Drivers." *Royal Society Open Science* 5, no. 3: 171830. https://doi.org/10.1098/rsos.171830.
- Close, R. A., R. B. J. Benson, E. E. Saupe, M. E. Clapham, and R. J. Butler. 2020. "The Spatial Structure of Phanerozoic Marine Animal Diversity." *Science* 368, no. 6489: 420–424. https://doi.org/10.1126/science.aav8309.
- Close, R. A., S. W. Evers, J. Alroy, and R. J. Butler. 2018. "How Should We Estimate Diversity in the Fossil Record? Testing Richness Estimators Using Sampling-Standardised Discovery Curves." *Methods in Ecology and Evolution* 9, no. 6: 1386–1400. https://doi.org/10.1111/2041-210X.12987.
- Clyde, W. C., and P. D. Gingerich. 1998. "Mammalian Community Response to the Latest Paleocene Thermal Maximum: An Isotaphonomic Study in the Northern Bighorn Basin." *Wyoming. Geology* 26, no. 11: 1011–1014.
- Congreve, C. R., A. R. Falk, and J. C. Lamsdell. 2018. "Biological Hierarchies and the Nature of Extinction." *Biological Reviews* 93, no. 2: 811–826. https://doi.org/10.1111/brv.12368.
- Cooke, R., W. Gearty, A. S. A. Chapman, et al. 2022. "Anthropogenic Disruptions to Longstanding Patterns of Trophic-Size Structure in Vertebrates." *Nature Ecology & Evolution* 6, no. 6: 684–692. https://doi.org/10.1038/s41559-022-01726-x.
- Cooke, R., F. Sayol, T. Andermann, et al. 2023. "Undiscovered Bird Extinctions Obscure the True Magnitude of Human-Driven Extinction Waves." *Nature Communications* 14, no. 1: 8116. https://doi.org/10.1038/s41467-023-43445-2.
- Corrie, J. E., and R. E. Fordyce. 2022. "A Redescription and Re-Evaluation of Kekenodon Onamata (Mammalia: Cetacea), a Late-Surviving Archaeocete From the Late Oligocene of New Zealand." *Zoological Journal of the Linnean Society* 196, no. 4: 1637–1670. https://doi.org/10.1093/zoolinnean/zlac019.
- Cowie, R. H., P. Bouchet, and B. Fontaine. 2022. "The Sixth Mass Extinction: Fact, Fiction or Speculation?" *Biological Reviews* 97, no. 2: 640–663. https://doi.org/10.1111/brv.12816.
- Cowie, R. H., P. Bouchet, and B. Fontaine. 2025. "Denying That We May Be Experiencing the Start of the Sixth Mass Extinction Paves the Way for It to Happen." *Trends in Ecology & Evolution* 40, no. 8: 722–723. https://doi.org/10.1016/j.tree.2025.06.001.
- Dal Corso, J., M. Bernardi, Y. Sun, et al. 2020. "Extinction and Dawn of the Modern World in the Carnian (Late Triassic)." *Science Advances* 6, no. 38: eaba0099. https://doi.org/10.1126/sciadv.aba0099.
- Daru, B. H., T. J. Davies, C. G. Willis, et al. 2021. "Widespread Homogenization of Plant Communities in the Anthropocene." *Nature*

- Communications 12, no. 1: 6983. https://doi.org/10.1038/s41467-021-27186-8.
- Daskalova, G. N., I. H. Myers-Smith, and J. L. Godlee. 2020. "Rare and Common Vertebrates Span a Wide Spectrum of Population Trends." *Nature Communications* 11, no. 1: 4394. https://doi.org/10.1038/s41467-020-17779-0.
- Davis, M., S. Faurby, and J.-C. Svenning. 2018. "Mammal Diversity Will Take Millions of Years to Recover From the Current Biodiversity Crisis." *Proceedings of the National Academy of Sciences* 115, no. 44: 11262–11267. https://doi.org/10.1073/pnas.1804906115.
- de Vries, D., S. Heritage, M. R. Borths, H. M. Sallam, and E. R. Seiffert. 2021. "Widespread Loss of Mammalian Lineage and Dietary Diversity in the Early Oligocene of Afro-Arabia." *Communications Biology* 4, no. 1: 1–9. https://doi.org/10.1038/s42003-021-02707-9.
- Dean, C. D., A. A. Chiarenza, and S. C. R. Maidment. 2020. "Formation Binning: A New Method for Increased Temporal Resolution in Regional Studies, Applied to the Late Cretaceous Dinosaur Fossil Record of North America." *Palaeontology* 63, no. 6: 881–901. https://doi.org/10.1111/pala.12492.
- del Monte-Luna, P., M. Nakamura, A. Vicente, et al. 2023. "A Review of Recent and Future Marine Extinctions." *Cambridge Prisms: Extinction* 1: e11. https://doi.org/10.1017/ext.2023.11.
- Dineen, A. A., M. L. Fraiser, and P. M. Sheehan. 2014. "Quantifying Functional Diversity in Pre- and Post-Extinction Paleocommunities: A Test of Ecological Restructuring After the End-Permian Mass Extinction." *Earth-Science Reviews* 136: 339–349. https://doi.org/10.1016/j.earscirev.2014.06.002.
- Duncan, R. P., A. G. Boyer, and T. M. Blackburn. 2013. "Magnitude and Variation of Prehistoric Bird Extinctions in the Pacific." *Proceedings of the National Academy of Sciences* 110, no. 16: 6436–6441. https://doi.org/10.1073/pnas.1216511110.
- Dunhill, A. M., and M. A. Wills. 2015. "Geographic Range Did Not Confer Resilience to Extinction in Terrestrial Vertebrates at the End-Triassic Crisis." *Nature Communications* 6, no. 1: 7980. https://doi.org/10.1038/ncomms8980.
- Edie, S. M., D. Jablonski, and J. W. Valentine. 2018. "Contrasting Responses of Functional Diversity to Major Losses in Taxonomic Diversity." *Proceedings of the National Academy of Sciences* 115, no. 4: 732–737. https://doi.org/10.1073/pnas.1717636115.
- Ellis, E. C., N. Gauthier, K. Klein Goldewijk, et al. 2021. "People Have Shaped Most of Terrestrial Nature for at Least 12,000 Years." *Proceedings of the National Academy of Sciences* 118, no. 17: e2023483118. https://doi.org/10.1073/pnas.2023483118.
- Erwin, D. H. 2006. "Dates and Rates: Temporal Resolution in the Deep Time Stratigraphic Record." *Annual Review of Earth and Planetary Sciences* 34, no. 1: 569–590. https://doi.org/10.1146/annurev.earth.34.031405.125141.
- Fan, J., S. Shen, D. H. Erwin, et al. 2020. "A High-Resolution Summary of Cambrian to Early Triassic Marine Invertebrate Biodiversity." *Science* 367, no. 6475: 272–277. https://doi.org/10.1126/science.aax4953.
- Faurby, S., R. Ø. Pedersen, M. Davis, et al. 2020, February 28. "MegaPast2Future/PHYLACINE_1.2: PHYLACINE Version 1.2.1. (Version v1.2.1). Zenodo." https://doi.org/10.5281/zenodo.3690867.
- Faurby, S., R. Ø. Pedersen, J.-C. Svenning, and A. Antonelli. 2022. "The Counteracting Effects of Anthropogenic Speciation and Extinction on Mammal Species Richness and Phylogenetic Diversity." *Global Ecology and Biogeography* 31, no. 9: 1810–1823. https://doi.org/10.1111/geb.13560.
- Feng, Z., H.-B. Wei, Y. Guo, et al. 2020. "From Rainforest to Herbland: New Insights Into Land Plant Responses to the End-Permian Mass Extinction." *Earth-Science Reviews* 204, no. 103: 153. https://doi.org/10.1016/j.earscirev.2020.103153.

Finnegan, S., P. G. Harnik, R. Lockwood, H. K. Lotze, L. McClenachan, and S. S. Kahanamoku. 2024. "Using the Fossil Record to Understand Extinction Risk and Inform Marine Conservation in a Changing World." *Annual Review of Marine Science* 16, no. 1: 307–333. https://doi.org/10.1146/annurey-marine-021723-095235.

Flannery-Sutherland, J. T., D. Silvestro, and M. J. Benton. 2022. "Global Diversity Dynamics in the Fossil Record Are Regionally Heterogeneous." *Nature Communications* 13, no. 1: 2751. https://doi.org/10.1038/s41467-022-30507-0.

Foster, G. L., P. Hull, D. J. Lunt, and J. C. Zachos. 2018. "Placing Our Current 'Hyperthermal' in the Context of Rapid Climate Change in Our Geological Past." *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 376, no. 2130: 20170086. https://doi.org/10.1098/rsta.2017.0086.

Foster, W. J., B. J. Allen, N. H. Kitzmann, et al. 2023. "How Predictable Are Mass Extinction Events? *Royal Society Open.*" *Science* 10, no. 3: 221507. https://doi.org/10.1098/rsos.221507.

Foster, W. J., and R. J. Twitchett. 2014. "Functional Diversity of Marine Ecosystems After the Late Permian Mass Extinction Event." *Nature Geoscience* 7, no. 3: 233–238. https://doi.org/10.1038/ngeo2079.

Fraser, D., A. Villaseñor, A. B. Tóth, et al. 2022. "Late Quaternary Biotic Homogenization of North American Mammalian Faunas." *Nature Communications* 13, no. 1: 3940. https://doi.org/10.1038/s41467-022-31595-8.

Gearty, W. 2024. "Deeptime: Plotting Tools for Anyone Working in Deep Time. (R Package Version 2.0.0)." https://CRAN.R-project.org/package=deeptime.

Gibbs, S. J., P. R. Bown, J. A. Sessa, T. J. Bralower, and P. A. Wilson. 2006. "Nannoplankton Extinction and Origination Across the Paleocene-Eocene Thermal Maximum." *Science* 314, no. 5806: 1770–1773. https://doi.org/10.1126/science.1133902.

Gibert, C., and G. Escarguel. 2017. "Evaluating the Accuracy of Biodiversity Changes Through Geologic Times: From Simulation to Solution." *Paleobiology* 43, no. 4: 667–692. https://doi.org/10.1017/pab. 2017.10.

Gordon, J. D., B. Fagan, N. Milner, and C. D. Thomas. 2024. "Floristic Diversity and Its Relationships With Human Land Use Varied Regionally During the Holocene." *Nature Ecology & Evolution* 8: 1459–1471. https://doi.org/10.1038/s41559-024-02457-x.

Greenspoon, L., E. Krieger, R. Sender, et al. 2023. "The Global Biomass of Wild Mammals." *Proceedings of the National Academy of Sciences* 120, no. 10: e2204892120. https://doi.org/10.1073/pnas.2204892120.

Guillerme, T., and N. Cooper. 2018. "Time for a Rethink: Time Sub-Sampling Methods in Disparity-Through-Time Analyses." *Palaeontology* 61, no. 4: 481–493. https://doi.org/10.1111/pala.12364.

Hallam, A., and P. B. Wignall. 1997. *Mass Extinctions and Their Aftermath*. Oxford University Press. https://doi.org/10.1093/oso/9780198549178.001.0001.

Hansford, J., J. M. Nuñez-Miño, R. P. Young, S. Brace, J. L. Brocca, and S. T. Turvey. 2012. "Taxonomy-Testing and the 'Goldilocks Hypothesis': Morphometric Analysis of Species Diversity in Living and Extinct Hispaniolan Hutias." *Systematics and Biodiversity* 10, no. 4: 491–507. https://doi.org/10.1080/14772000.2012.748697.

Harnik, P. G., H. K. Lotze, S. C. Anderson, et al. 2012. "Extinctions in Ancient and Modern Seas." *Trends in Ecology & Evolution* 27, no. 11: 608–617. https://doi.org/10.1016/j.tree.2012.07.010.

Harper, D. A. T. 2024. "Late Ordovician Mass Extinction: Earth, Fire and Ice." *National Science Review* 11, no. 1: nwad319. https://doi.org/10.1093/nsr/nwad319.

Harper, D. A. T., B. Cascales-Miñana, and T. Servais. 2020. "Early Palaeozoic Diversifications and Extinctions in the Marine Biosphere: A

Continuum of Change." *Geological Magazine* 157, no. 1: 5–21. https://doi.org/10.1017/S0016756819001298.

Hatfield, J. H., K. E. Davis, and C. D. Thomas. 2022. "Lost, Gained, and Regained Functional and Phylogenetic Diversity of European Mammals Since 8000 Years Ago." *Global Change Biology* 28, no. 17: 5283–5293. https://doi.org/10.1111/gcb.16316.

Haynes, L. L., and B. Hönisch. 2020. "The Seawater Carbon Inventory at the Paleocene–Eocene Thermal Maximum." *Proceedings of the National Academy of Sciences* 117, no. 39: 24088–24095. https://doi.org/10.1073/pnas.2003197117.

Hayward, B. W., S. Kawagata, H. R. Grenfell, A. T. Sabaa, and T. O'Neill. 2007. "Last Global Extinction in the Deep Sea During the Mid-Pleistocene Climate Transition." *Paleoceanography* 22, no. 3. https://doi.org/10.1029/2007PA001424.

Hendricks, J. R., E. E. Saupe, C. E. Myers, E. J. Hermsen, and W. D. Allmon. 2014. "The Generification of the Fossil Record." *Paleobiology* 40, no. 4: 511–528. https://doi.org/10.1666/13076.

Holland, S. M. 2017. "Structure, not Bias." *Journal of Paleontology* 91, no. 6: 1315–1317. https://doi.org/10.1017/jpa.2017.114.

Holland, S. M., K. M. Loughney, and M. Cone. 2022. "Preferential Preservation of Low-Elevation Biotas in the Nonmarine Fossil Record." *Geology* 51, no. 1: 111–114. https://doi.org/10.1130/G50579.1.

Hooker, J. J., M. E. Collinson, and N. P. Sille. 2004. "Eocene–Oligocene Mammalian Faunal Turnover in the Hampshire Basin, UK: Calibration to the Global Time Scale and the Major Cooling Event." *Journal of the Geological Society* 161, no. 2: 161–172. https://doi.org/10.1144/0016-764903-091.

Hoyal Cuthill, J. F. 2022. "Ediacaran Survivors in the Cambrian: Suspicions, Denials and a Smoking Gun." *Geological Magazine* 159, no. 7: 1210–1219. https://doi.org/10.1017/S0016756821001333.

Hull, P. M., A. Bornemann, D. E. Penman, et al. 2020. "On Impact and Volcanism Across the Cretaceous-Paleogene Boundary." *Science* 367, no. 6475: 266–272.

Hull, P. M., S. A. Darroch, and D. H. Erwin. 2015. "Rarity in Mass Extinctions and the Future of Ecosystems." *Nature* 528, no. 7582: 345–351.

Hull, P. M., and S. A. F. Darroch. 2013. "Mass Extinctions and the Structure and Function of Ecosystems." *Paleontological Society Papers* 19: 115–156. https://doi.org/10.1017/S1089332600002710.

Hulme, P. E., M. Bernard-Verdier, J. L. Bufford, and W. Godsoe. 2015. "Rapid Anthropocene Speciation Reveals Pull of the Recent: A Response to Thomas." *Trends in Ecology & Evolution* 30, no. 11: 635–636. https://doi.org/10.1016/j.tree.2015.09.009.

IPBES. 2016. "The Methodological Assessment Report on Scenarios and Models of Biodiversity and Ecosystem Services." *IPBES Secretariat* 2016: 157348.

IUCN. 2024. "The IUCN Red List of Threatened Species. (Version 2023–1)." https://www.iucnredlist.org.

Jablonski, D. 1986. "Causes and Consequences of Mass Extinctions: A Comparative Approach." *Dynamic of Extinction*: edited by D. K. Elliot, 183–229. J. Wiley.

Jablonski, D. 2004. "Extinction: Past and Present." *Nature* 427, no. 6975: 589a. https://doi.org/10.1038/427589a.

Jaramillo, C., M. J. Rueda, and G. Mora. 2006. "Cenozoic Plant Diversity in the Neotropics." *Science* 311, no. 5769: 1893–1896. https://doi.org/10.1126/science.1121380.

Jones, L. A. 2022. "Sepkoski. (Version 0.0.1.9000)." https://github.com/LewisAJones/sepkoski.

Jones, L. A., C. D. Dean, P. D. Mannion, A. Farnsworth, and P. A. Allison. 2021. "Spatial Sampling Heterogeneity Limits the Detectability

of Deep Time Latitudinal Biodiversity Gradients." *Proceedings of the Royal Society B: Biological Sciences* 288: 20202762. https://doi.org/10.1098/rspb.2020.2762.

Keller, G. 1986. "Stepwise Mass Extinctions and Impact Events: Late Eocene to Early Oligocene." *Marine Micropaleontology* 10, no. 4: 267–293. https://doi.org/10.1016/0377-8398(86)90032-0.

Kemp, D. B., and P. F. Sexton. 2014. "Time-Scale Uncertainty of Abrupt Events in the Geologic Record Arising From Unsteady Sedimentation." *Geology* 42, no. 10: 891–894. https://doi.org/10.1130/G35783.1.

Kiessling, W., and C. Simpson. 2011. "On the Potential for Ocean Acidification to Be a General Cause of Ancient Reef Crises." *Global Change Biology* 17, no. 1: 56–67. https://doi.org/10.1111/j.1365-2486. 2010.02204.x.

Koch, P. L., and A. D. Barnosky. 2006. "Late Quaternary Extinctions: State of the Debate." *Annual Review of Ecology, Evolution, and Systematics* 37: 215–250. https://doi.org/10.1146/annurev.ecolsys.34. 011802.132415.

Kocsis, A. T., C. J. Reddin, J. Alroy, and W. Kiessling. 2019. "The R Package divDyn for Quantifying Diversity Dynamics Using Fossil Sampling Data." *Methods in Ecology and Evolution* 10, no. 5: 735–743.

Krone, I. W., K. M. Magoulick, and R. M. Yohler. 2024. "All the Earth Will Not Remember: How Geographic Gaps Structure the Record of Diversity and Extinction." *Paleobiology* 50: 214–225. https://doi.org/10.1017/pab.2023.34.

Leakey, R. E., and R. Lewin. 1995. "The Sixth Extinction: Patterns of Life and the Future of Humankind. Doubleday."

Lemoine, R. T., R. Buitenwerf, and J.-C. Svenning. 2023. "Megafauna Extinctions in the Late-Quaternary Are Linked to Human Range Expansion, Not Climate Change." *Anthropocene* 44, no. 100: 403. https://doi.org/10.1016/j.ancene.2023.100403.

Lowery, C. M., P. R. Bown, A. J. Fraass, and P. M. Hull. 2020. "Ecological Response of Plankton to Environmental Change: Thresholds for Extinction." *Annual Review of Earth and Planetary Sciences* 48, no. 1: 403–429.

Lydeard, C., R. H. Cowie, W. F. Ponder, et al. 2004. "The Global Decline of Nonmarine Mollusks." *Bioscience* 54, no. 4: 321. https://doi.org/10.1641/0006-3568(2004)054[0321:TGDONM]2.0.CO;2.

Lyson, T. R., I. M. Miller, A. D. Bercovici, et al. 2019. "Exceptional Continental Record of Biotic Recovery After the Cretaceous-Paleogene Mass Extinction." *Science* 366, no. 6468: 977–983. https://doi.org/10.1126/science.aay2268.

MacLeod, K. G. 1994. "Bioturbation, Inoceramid Extinction, and Mid-Maastrichtian Ecological Change." *Geology* 22, no. 2: 139–142.

Malhi, Y., C. E. Doughty, M. Galetti, F. A. Smith, J.-C. Svenning, and J. W. Terborgh. 2016. "Megafauna and Ecosystem Function From the Pleistocene to the Anthropocene." *Proceedings of the National Academy of Sciences* 113, no. 4: 838–846. https://doi.org/10.1073/pnas.15025 40113.

Mammola, S., C. S. Fukushima, G. Biondo, et al. 2023. "How Much Biodiversity Is Concealed in the Word 'Biodiversity'?" *Current Biology* 33, no. 2: R59–R60. https://doi.org/10.1016/j.cub.2022.12.003.

Mannion, P. D., R. B. J. Benson, M. T. Carrano, J. P. Tennant, J. Judd, and R. J. Butler. 2015. "Climate Constrains the Evolutionary History and Biodiversity of Crocodylians." *Nature Communications* 6, no. 1: 8438. https://doi.org/10.1038/ncomms9438.

Marshall, C. R. 2023. "Forty Years Later: The Status of the "Big Five" Mass Extinctions." *Cambridge Prisms: Extinction* 1: e5. https://doi.org/10.1017/ext.2022.4.

Matisoo-Smith, E., R. M. Roberts, G. J. Irwin, J. S. Allen, D. Penny, and D. M. Lambert. 1998. "Patterns of Prehistoric Human Mobility in

Polynesia Indicated by mtDNA From the Pacific Rat." *Proceedings of the National Academy of Sciences* 95, no. 25: 15145–15150. https://doi.org/10.1073/pnas.95.25.15145.

Matthews, T. J., K. A. Triantis, J. P. Wayman, et al. 2024. "The Global Loss of Avian Functional and Phylogenetic Diversity From Anthropogenic Extinctions." *Science* 386, no. 6717: 55–60. https://doi.org/10.1126/science.adk7898.

McGhee, G. R., M. E. Clapham, P. M. Sheehan, D. J. Bottjer, and M. L. Droser. 2013. "A New Ecological-Severity Ranking of Major Phanerozoic Biodiversity Crises." *Palaeogeography, Palaeoclimatology, Palaeoecology* 370: 260–270. https://doi.org/10.1016/j.palaeo.2012.12.019.

McGhee, G. R., P. M. Sheehan, D. J. Bottjer, and M. L. Droser. 2004. "Ecological Ranking of Phanerozoic Biodiversity Crises: Ecological and Taxonomic Severities Are Decoupled." *Palaeogeography, Palaeoclimatology, Palaeoecology* 211, no. 3: 289–297. https://doi.org/10.1016/j.palaeo.2004.05.010.

McKinney, M. L., and J. L. Lockwood. 1999. "Biotic Homogenization: A Few Winners Replacing Many Losers in the Next Mass Extinction." *Trends in Ecology & Evolution* 14, no. 11: 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1.

Molina, E. 2015. "Evidence and Causes of the Main Extinction Events in the Paleogene Based on Extinction and Survival Patterns of Foraminifera." *Earth-Science Reviews* 140: 166–181. https://doi.org/10.1016/j.earscirev.2014.11.008.

Monarrez, P. M., N. A. Heim, and J. L. Payne. 2021. "Mass Extinctions Alter Extinction and Origination Dynamics With Respect to Body Size." *Proceedings of the Royal Society B: Biological Sciences* 288: 20211681. https://doi.org/10.1098/rspb.2021.1681.

Morgan, J. V., T. J. Bralower, J. Brugger, and K. Wünnemann. 2022. "The Chicxulub Impact and Its Environmental Consequences." *Nature Reviews Earth and Environment* 3, no. 5: 338–354. https://doi.org/10.1038/s43017-022-00283-y.

Mottl, O., S. G. A. Flantua, K. P. Bhatta, et al. 2021. "Global Acceleration in Rates of Vegetation Change Over the Past 18,000 Years." *Science* 372, no. 6544: 860–864. https://doi.org/10.1126/science.abg1685.

Nanglu, K., and T. M. Cullen. 2023. "Across Space and Time: A Review of Sampling, Preservational, Analytical, and Anthropogenic Biases in Fossil Data Across Macroecological Scales." *Earth-Science Reviews* 244, no. 104: 537. https://doi.org/10.1016/j.earscirev.2023.104537.

O'Keefe, F. R., R. E. Dunn, E. M. Weitzel, et al. 2023. "Pre-Younger Dryas Megafaunal Extirpation at Rancho La Brea Linked to Fire-Driven State Shift." *Science* 381, no. 6659: eabo3594. https://doi.org/10.1126/science.abo3594.

Otto, S. P. 2018. "Adaptation, Speciation and Extinction in the Anthropocene." *Proceedings of the Royal Society B: Biological Sciences* 285, no. 1891: 20182047. https://doi.org/10.1098/rspb.2018.2047.

Payne, J. L., J. A. A. Aswad, C. Deutsch, P. M. Monarrez, J. L. Penn, and P. Singh. 2023. "Selectivity of Mass Extinctions: Patterns, Processes, and Future Directions." *Cambridge Prisms: Extinction* 1: e12. https://doi.org/10.1017/ext.2023.10.

Pearson, P. N., I. K. McMillan, B. S. Wade, et al. 2008. "Extinction and Environmental Change Across the Eocene–Oligocene Boundary in Tanzania." *Geology* 36, no. 2: 179–182. https://doi.org/10.1130/G24308A.1.

Pearson, R. G., W. Thuiller, M. B. Araújo, et al. 2006. "Model-Based Uncertainty in Species Range Prediction." *Journal of Biogeography* 33, no. 10: 1704–1711. https://doi.org/10.1111/j.1365-2699.2006.01460.x.

Pereira, H. M., P. W. Leadley, V. Proença, et al. 2010. "Scenarios for Global Biodiversity in the 21st Century." *Science* 330, no. 6010: 1496–1501. https://doi.org/10.1126/science.1196624.

Pereira, H. M., I. S. Martins, I. M. D. Rosa, et al. 2024. "Global Trends and Scenarios for Terrestrial Biodiversity and Ecosystem Services From 1900 to 2050." *Science* 384, no. 6694: 458–465. https://doi.org/10.1126/science.adn3441.

Peters, S. 2022. "Sepkoski's Online Genus Database." https://strata.geology.wisc.edu/jack/.

Pimiento, C., C. D. Bacon, D. Silvestro, et al. 2020. "Selective Extinction Against Redundant Species Buffers Functional Diversity." *Proceedings of the Royal Society B: Biological Sciences* 287: 20201162. https://doi.org/10.1098/rspb.2020.1162.

Pimiento, C., J. N. Griffin, C. F. Clements, et al. 2017. "The Pliocene Marine Megafauna Extinction and Its Impact on Functional Diversity." *Nature Ecology & Evolution* 1, no. 8: 1100–1106. https://doi.org/10.1038/s41559-017-0223-6.

Pimm, S. L., C. N. Jenkins, R. Abell, et al. 2014. "The Biodiversity of Species and Their Rates of Extinction, Distribution, and Protection." *Science* 344, no. 6187: 1246752.

Plotnick, R. E., F. A. Smith, and S. K. Lyons. 2016. "The Fossil Record of the Sixth Extinction." *Ecology Letters* 19, no. 5: 546–553. https://doi.org/10.1111/ele.12589.

Purvis, A., K. E. Jones, and G. M. Mace. 2000. "Extinction." *BioEssays* 22, no. 12: 1123–1133.

Pym, F. C., F. Franco-Gaviria, I. G. Espinoza, and D. H. Urrego. 2023. "The Timing and Ecological Consequences of Pleistocene Megafaunal Decline in the Eastern Andes of Colombia." *Quaternary Research* 114: 1–17. https://doi.org/10.1017/qua.2022.66.

Raja, N. B., E. M. Dunne, A. Matiwane, et al. 2022. "Colonial History and Global Economics Distort Our Understanding of Deep-Time Biodiversity." *Nature Ecology & Evolution* 6, no. 2: 145–154. https://doi.org/10.1038/s41559-021-01608-8.

Raup, D. 1991. "Extinction Bad Genes or Bad Luck. WW Norton."

Raup, D. M. 1972. "Taxonomic Diversity During the Phanerozoic." *Science* 177, no. 4054: 1065–1071. https://doi.org/10.1126/science.177. 4054.1065.

Raup, D. M. 1986. "Biological Extinction in Earth History." *Science* 231, no. 4745: 1528–1533. https://doi.org/10.1126/science.11542058.

Raup, D. M., and J. J. Sepkoski. 1982. "Mass Extinctions in the Marine Fossil Record." *Science* 215, no. 4539: 1501–1503. https://doi.org/10.1126/science.215.4539.1501.

Roopnarine, P. D. 2006. "Extinction Cascades and Catastrophe in Ancient Food Webs." *Paleobiology* 32, no. 1: 1–19. https://doi.org/10.1666/0094-8373(2006)032[0001:ECACIA]2.0.CO;2.

Sahney, S., and M. J. Benton. 2008. "Recovery From the Most Profound Mass Extinction of All Time." *Proceedings of the Royal Society B: Biological Sciences* 275, no. 1636: 759–765. https://doi.org/10.1098/rspb. 2007.1370.

Sansom, R. S., S. E. Gabbott, and M. A. Purnell. 2010. "Non-Random Decay of Chordate Characters Causes Bias in Fossil Interpretation." *Nature* 463, no. 7282: 797–800. https://doi.org/10.1038/nature08745.

Säterberg, T., S. Sellman, and B. Ebenman. 2013. "High Frequency of Functional Extinctions in Ecological Networks." *Nature* 499, no. 7459: 468–470. https://doi.org/10.1038/nature12277.

Sayol, F., R. S. C. Cooke, A. L. Pigot, et al. 2021. "Loss of Functional Diversity Through Anthropogenic Extinctions of Island Birds Is Not Offset by Biotic Invasions. *Science.*" *Advances* 7, no. 46: eabj5790. https://doi.org/10.1126/sciadv.abj5790.

Schulte, P., L. Alegret, I. Arenillas, et al. 2010. "The Chicxulub Asteroid Impact and Mass Extinction at the Cretaceous-Paleogene Boundary." *Science* 327, no. 5970: 1214–1218. https://doi.org/10.1126/science. 1177265.

Seebens, H., T. M. Blackburn, P. E. Hulme, et al. 2021. "Around the World in 500 Years: Inter-Regional Spread of Alien Species Over Recent Centuries." *Global Ecology and Biogeography* 30: 1621–1632. https://doi.org/10.1111/geb.13325.

Seersholm, F. V., D. J. Werndly, A. Grealy, et al. 2020. "Rapid Range Shifts and Megafaunal Extinctions Associated With Late Pleistocene Climate Change." *Nature Communications* 11, no. 1: 2770. https://doi.org/10.1038/s41467-020-16502-3.

Sepkoski, J. J. 1981. "A Factor Analytic Description of the Phanerozoic Marine Fossil Record." *Paleobiology* 7, no. 1: 36–53. https://doi.org/10.1017/S0094837300003778.

Sepkoski, J. J. 1986. "Phanerozoic Overview of Mass Extinction." In *Patterns and Processes in the History of Life*, edited by D. M. Raup and D. Jablonski, 277–295. Springer. https://doi.org/10.1007/978-3-642-70831-2_15.

Sepkoski, J. J. 2002. "A Compendium of Fossil Marine Animal Genera." *Bulletins of American Paleontology* 363: 1–560.

Signor, P., and J. Lipps. 1982. "Gradual Extinction Patterns and Catastrophes in the Fossil Record." *Geological Society of America, Special Paper* 190: 291–296.

Silvestro, D., N. Salamin, and J. Schnitzler. 2014. "PyRate: A New Program to Estimate Speciation and Extinction Rates From Incomplete Fossil Data." *Methods in Ecology and Evolution* 5, no. 10: 1126–1131. https://doi.org/10.1111/2041-210X.12263.

Smith, A. B., A. S. Gale, and N. E. A. Monks. 2001. "Sea-Level Change and Rock-Record Bias in the Cretaceous: A Problem for Extinction and Biodiversity Studies." *Paleobiology* 27, no. 2: 241–253.

Smith, A. B., and A. J. McGowan. 2007. "The Shape of the Phanerozoic Marine Palaeodiversity Curve: How Much Can Be Predicted From the Sedimentary Rock Record of Western Europe?" *Palaeontology* 50, no. 4: 765–774. https://doi.org/10.1111/j.1475-4983.2007.00693.x.

Smith, T. J., R. S. Sansom, D. Pisani, and P. C. J. Donoghue. 2023. "Fossilization Can Mislead Analyses of Phenotypic Disparity." *Proceedings of the Royal Society B: Biological Sciences* 290: 20230522. https://doi.org/10.1098/rspb.2023.0522.

Spalding, C., and P. M. Hull. 2021. "Towards Quantifying the Mass Extinction Debt of the Anthropocene." *Proceedings of the Royal Society B: Biological Sciences* 288: 20202332. https://doi.org/10.1098/rspb. 2020.2332.

Speijer, R. P., C. Scheibner, P. Stassen, and A.-M. M. Morsi. 2012. "Response of Marine Ecosystems to Deep-Time Global Warming: A Synthesis of Biotic Patterns Across the Paleocene-Eocene Thermal Maximum (PETM)." *Austrian Journal of Earth Sciences* 105, no. 1: 6–16.

Stanley, S. M. 2016. "Estimates of the Magnitudes of Major Marine Mass Extinctions in Earth History." *Proceedings of the National Academy of Sciences* 113, no. 42: E6325–E6334. https://doi.org/10.1073/pnas.1613094113.

Stewart, M., W. C. Carleton, and H. S. Groucutt. 2021. "Climate Change, Not Human Population Growth, Correlates With Late Quaternary Megafauna Declines in North America." *Nature Communications* 12, no. 1: 965. https://doi.org/10.1038/s41467-021-21201-8.

Stigall, A. L. 2019. "The Invasion Hierarchy: Ecological and Evolutionary Consequences of Invasions in the Fossil Record." *Annual Review of Ecology, Evolution, and Systematics* 50 50: 355–380. https://doi.org/10.1146/annurev-ecolsys-110617-062638.

Sun, J., X. Ni, S. Bi, et al. 2014. "Synchronous Turnover of Flora, Fauna and Climate at the Eocene–Oligocene Boundary in Asia." *Scientific Reports* 4, no. 1: 7463. https://doi.org/10.1038/srep07463.

Svenning, J.-C., R. T. Lemoine, J. Bergman, et al. 2024. "The Late-Quaternary Megafauna Extinctions: Patterns, Causes, Ecological Consequences and Implications for Ecosystem Management in the

Anthropocene." Cambridge Prisms: Extinction 2: e5. https://doi.org/10. 1017/ext.2024.4.

Tennant, J. P., P. D. Mannion, P. Upchurch, M. D. Sutton, and G. D. Price. 2017. "Biotic and Environmental Dynamics Through the Late Jurassic–Early Cretaceous Transition: Evidence for Protracted Faunal and Ecological Turnover." *Biological Reviews* 92, no. 2: 776–814. https://doi.org/10.1111/brv.12255.

Thomas, C. D. 2015. "Rapid Acceleration of Plant Speciation During the Anthropocene." *Trends in Ecology & Evolution* 30, no. 8: 448–455. https://doi.org/10.1016/j.tree.2015.05.009.

Thomas, C. D. 2020. "The Development of Anthropocene Biotas." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 375, no. 1794: 20190113. https://doi.org/10.1098/rstb.2019.0113.

Thuiller, W., M. Guéguen, J. Renaud, D. N. Karger, and N. E. Zimmermann. 2019. "Uncertainty in Ensembles of Global Biodiversity Scenarios." *Nature Communications* 10, no. 1: 1446. https://doi.org/10.1038/s41467-019-09519-w.

Tibshirani, B. E. R. J. 1994. *An Introduction to the Bootstrap*. Chapman and Hall/CRC. https://doi.org/10.1201/9780429246593.

Tierney, J. E., J. Zhu, M. Li, et al. 2022. "Spatial Patterns of Climate Change Across the Paleocene–Eocene Thermal Maximum." *Proceedings of the National Academy of Sciences* 119, no. 42: e2205326119. https://doi.org/10.1073/pnas.2205326119.

Tomašových, A., S. Dominici, R. Nawrot, and M. Zuschin. 2023. "Conservation Palaeobiology of Marine Ecosystems." In *Temporal Scales, Sampling Designs and Age Distributions in Marine Conservation Palaeobiology*, edited by R. Nawrot, S. Dominici, A. Tomašových, and M. Zuschin. Geological Society of London. https://doi.org/10.1144/SP529-2022-361.

Turvey, S. 2009. Holocene Extinctions. OUP Oxford.

Turvey, S. T., and J. J. Crees. 2019. "Extinction in the Anthropocene." *Current Biology* 29, no. 19: R982–R986.

Urban, M. C. 2015. "Accelerating Extinction Risk From Climate Change." *Science* 348, no. 6234: 571–573. https://doi.org/10.1126/science.aaa4984.

van Woesik, R., E. C. Franklin, J. O'Leary, T. R. McClanahan, J. S. Klaus, and A. F. Budd. 2012. "Hosts of the Plio-Pleistocene Past Reflect Modern-Day Coral Vulnerability." *Proceedings of the Royal Society B: Biological Sciences* 279, no. 1737: 2448–2456. https://doi.org/10.1098/rspb.2011.2621.

Vermeij, G. J. 1991. "When Biotas Meet: Understanding Biotic Interchange." *Science* 253, no. 5024: 1099–1104. https://doi.org/10.1126/science.253.5024.1099.

Vilhena, D. A., and A. B. Smith. 2013. "Spatial Bias in the Marine Fossil Record." *PLoS One* 8, no. 10: e74470. https://doi.org/10.1371/journal.pone.0074470.

Wagner, P. J., and J. D. Marcot. 2013. "Modelling Distributions of Fossil Sampling Rates Over Time, Space and Taxa: Assessment and Implications for Macroevolutionary Studies." *Methods in Ecology and Evolution* 4, no. 8: 703–713. https://doi.org/10.1111/2041-210X.12088.

Waller, N. L., I. C. Gynther, A. B. Freeman, T. H. Lavery, and L. K.-P. Leung. 2017. "The Bramble Cay Melomys *Melomys rubicola* (Rodentia: Muridae): A First Mammalian Extinction Caused by Human-Induced Climate Change?" *Wildlife Research* 44, no. 1: 9–21. https://doi.org/10.1071/WR16157.

Weppe, R., F. L. Condamine, G. Guinot, J. Maugoust, and M. J. Orliac. 2023. "Drivers of the Artiodactyl Turnover in Insular Western Europe at the Eocene–Oligocene Transition." *Proceedings of the National Academy of Sciences* 120, no. 52: e2309945120. https://doi.org/10.1073/pnas.2309945120.

Wiens, J. J., and K. E. Saban. 2025. "Questioning the Sixth Mass Extinction." *Trends in Ecology & Evolution* 40, no. 4: 375–384.

Wilmshurst, J. M., T. L. Hunt, C. P. Lipo, and A. J. Anderson. 2011. "High-Precision Radiocarbon Dating Shows Recent and Rapid Initial Human Colonization of East Polynesia." *Proceedings of the National Academy of Sciences* 108, no. 5: 1815–1820. https://doi.org/10.1073/pnas. 1015876108.

Yao, W., A. Paytan, and U. G. Wortmann. 2018. "Large-Scale Ocean Deoxygenation During the Paleocene-Eocene Thermal Maximum." *Science* 361, no. 6404: 804–806. https://doi.org/10.1126/science.aar8658.

Ying, R., F. M. Monteiro, J. D. Wilson, M. Ödalen, and D. N. Schmidt. 2024. "Past Foraminiferal Acclimatization Capacity Is Limited During Future Warming." *Nature* 636, no. 8042: 385–389.