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# The state of the late Quaternary megafauna extinction debate: a systematic review and analysis

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With its origins in the late 18<sup>th</sup> and early 19<sup>th</sup> century, the question of what drove the late Quaternary megafauna extinctions remains one of science's most enduring and hotly contested debates. Once strictly the domain of archaeologists and paleontologists, the topic has attracted growing interest from other disciplines in recent decades, particularly ecologists and conservation biologists, who view these extinctions as a lens through which to inform contemporary conservation and ecosystem management strategies. Alongside this expansion, the field has seen increasing use of advanced analytical and statistical methods. Yet despite these developments, scientific opinion remains deeply divided over the cause(s) of these extinctions. Each year dozens of papers on the topic are published and along with these review articles that cover the debate or certain aspects of it. However, these reviews tend to reflect the viewpoints of their authors. Recognizing this limitation, the present study aimed to offer a more objective, data-driven overview of the field by conducting a systematic review and analysis of the literature. Specifically, we sought to: (1) trace the development of the megafauna extinction debate to understand how it has evolved over time; (2) identify key thematic and conceptual foci within the literature; and (3) use this synthesis of historical trends and interdisciplinary variation to propose a forward-looking research agenda that encourages greater engagement, discussion, integration, and collaboration across fields. Our analysis reveals strong disciplinary divides, uneven temporal and spatial research coverage, and persistent uncertainty over extinction causes. Despite recent major methodological advances, the field remains fragmented, underscoring the need for a research agenda that fosters interdisciplinary collaboration, expands field and legacy studies, as well as species-specific approaches, and integrates cutting-edge scientific and statistical techniques.

## KEYWORDS

megafauna extinctions, Pleistocene, Holocene, conservation, rewilding, biases

## Introduction

The idea that a species could completely disappear from the Earth was first proposed by naturalists in the late 18<sup>th</sup> and early 19<sup>th</sup> centuries (for a review on 19<sup>th</sup> century research into megafauna extinctions see Grayson, 1989), prompting initial efforts to explain the extinction of large mammals like mammoths, mastodons, and giant ground sloths. Early theories included catastrophic events—such as the Biblical flood (Parkinson, 1811; Buckland, 1823) and sudden glaciation (Agassiz, 1837)—as well as more gradual, climate-driven extinctions (Lyell, 1832; Dawkins, 1869). Others rejected climate-based explanations altogether, attributing megafauna losses to intensive overhunting by humans (Turner, 1799; Flemming, 1826). By the late 19<sup>th</sup> century, the debate had stalled, entering what Monjeau et al., (2017, p. 200) describe as a “phase of conceptual blockage,” as scholars increasingly favored gradual drivers for extinction, whether climatic or anthropogenic, but lacked the precise absolute dating techniques and other advanced scientific methods needed to rigorously test different hypotheses.

The debate was eventually revitalized in the mid 20<sup>th</sup> century with the development and application of radiocarbon dating (Libby, 1952). In the mid-1960's, Martin (1966, 1967), drawing on radiocarbon-dated fossils and better-resolved paleoenvironmental data, proposed his influential “overkill” model. Initially applied to North America and later to other continents as well as numerous islands, this hypothesis argued that humans armed with specialized hunting technologies quickly drove many megafauna species to extinction as they spread around the globe. Martin's work sparked widespread debate (Leakey, 1966, 1967; Martin, 1967; Martin and Wright, 1967; Martin and Klein, 1984), laying the foundation for the modern era of megafauna extinction research. As in the 19<sup>th</sup> century, most researchers today still fall into one of three broad groups: those attributing the extinctions to climate change, those advocating for human-mediated impacts, and those emphasizing some combination of the two.

The turn of the millennia ushered in a new wave of research, driven in large part by advances in scientific techniques and analytical approaches (Swift et al., 2019). Improvements in radiocarbon dating and the integration of Bayesian modelling have led to significantly refined chronologies (Stuiver et al., 1998; Higham et al., 2006; Jacobi and Higham, 2009), while innovations in luminescence and other radiometric dating techniques extended timelines beyond the limits of reliable <sup>14</sup>C dating, ~50 ka (Roberts et al., 2001; Turney et al., 2008; Price et al., 2011). The integration of ancient DNA (aDNA)—now retrievable from both fossils and sediments, and increasingly older materials (van der Valk et al., 2021; Kjær et al., 2022)—has opened new windows into megafauna population dynamics, adaptations, and extinction chronologies (Shapiro et al., 2004; Campos et al., 2010; Lorenzen et al., 2011; Collins et al., 2014; Seersholm et al., 2020; Murchie et al., 2021). Stable isotope analysis has likewise improved and expanded, offering insights into past environments and extinct species' diets and mobility (Bocherens et al., 2017; Price et al., 2017, 2017; Wooller et al., 2021; McCormack et al., 2022; Koutamanis et al.,

2023). Complementing these advances, the rise of open-access databases has enabled large-scale meta-analyses that integrate paleoclimate data, extinction timelines, and archaeological evidence to assess drivers of megafauna extinctions at continental and global scales (Sandom et al., 2014a; Saltré et al., 2016; Berti and Svenning, 2020; Stewart et al., 2021).

These and other advances have coincided with—and sometimes been driven by—a broadening interest in late Quaternary megafauna extinctions. Once largely the pursuit of paleontologists and archaeologists, these extinctions are now studied by researchers working across a range of disciplines. Much new work has focused on understanding the knock-on ecological effects of megafauna extinctions (Johnson, 2009; Gill, 2014; Galetti et al., 2018; Svenning et al., 2024) as well as the potential role of rewilding programs in mitigating these effects (Svenning et al., 2016; Cromsigt et al., 2018; Lundgren et al., 2020). Ultimately, this growing interest reflects scholarly attention toward understanding the deep-time origins and extent of human environmental impacts, aiming to apply these insights to contemporary conservation and restoration efforts (Boivin et al., 2016; Stephens et al., 2019; Ellis et al., 2021). As put by Nagaoka et al., (2018, p. 9684), not only is the subject of the late Quaternary megafauna extinctions used in “defining the boundaries of the Anthropocene and other concepts such as the Sixth Extinction” it is also at the very core of “understanding the nature of the relationship between humans and the environment.” For some scholars, the notion of an abrupt wave of extinction is cited as one thread of evidence for a fundamental shift in human behavior, one that marks the emergence of ‘modern humans’ and sets them apart from their ‘archaic hominin’ predecessors (e.g., Marean, 2015). Others, however, have suggested that human-mediated extinctions may pre-date the emergence of *Homo sapiens*, pushing back the ecological impacts of our own genus (Faurby et al., 2020; Hauffe et al., 2024; Pereira et al., 2024).

An interesting feature of the modern debate are the stark disciplinary differences in how researchers conceptualize and study megafauna extinctions (Grayson and Meltzer, 2003; Nagaoka, 2012; Nagaoka et al., 2018). A 2018 survey found that archeologists and paleobiologists largely view the cause of extinctions as unresolved, often pointing to a combination of climatic and anthropogenic factors (Nagaoka et al., 2018). In contrast, ecologists tend to consider humans, through overhunting and habitat modification, as the primary driver of extinctions. This divergence highlights the unresolved nature of the megafauna extinction debate, as well as the contrasting views that emerge from diverse disciplinary datasets, preconceptions, and theoretical frameworks. It also underscores the need for greater interdisciplinary engagement, particularly between ecologists and those working in deeper time (Louys et al., 2012; Swanson et al., 2021; Azevedo-Schmidt et al., 2025).

To gain a better understanding of the late Quaternary megafauna extinction debate—its history, evolution, and status—we conducted a quantitative systematic review and analysis of the scientific literature published since the 1950's. While the debate has been extensively explored through review articles (Barnosky et al., 2004; Wroe and Field, 2006; Louys et al., 2007; Stuart, 2015; Galetti

et al., 2018), edited volumes (Martin and Klein, 1984), and popular science books (Kolbert, 2014; MacPhee and Schouten, 2019; Edmeades, 2021; Stuart, 2021), these works tend to reflect the specific viewpoints and perspectives of their authors on what remains a highly contentious topic. Indeed, it has been noted that within the megafauna extinction debate, scholars often advocate strongly for a specific extinction hypothesis while insufficiently engaging with alternative interpretations or the broader body of research (Nagaoka et al., 2018). Recognizing this limitation, the present study sought to provide an objective, data-driven overview of the field. Specifically, we aimed to: (1) trace the development of the megafauna extinction debate to understand how it has evolved over time; (2) identify key thematic and conceptual foci within the literature; and (3) use this synthesis of historical trends and interdisciplinary variation to propose a forward-looking research agenda that encourages greater engagement, discussion, integration, and collaboration across fields.

## Methods

To conduct the systematic review, we queried two major academic databases, Web of Science (WoS) and Scopus (accessed November 2021), for articles related to the late Quaternary megafauna extinctions. Terms were searched for within keywords, titles, and abstracts of papers using the following query: “Megafauna” AND “extinction” AND (“Quaternary” OR “Pleistocene” OR “Holocene”). This search returned 596 unique articles published between 1959 and 2021. The metadata from all retrieved articles was compiled into an Excel spreadsheet, the articles randomized, and evenly distributed among three analysts (MS, CP, MZ) for review.

Each article was imported into and coded using MAXQDA (<https://www.maxqda.com/>), a qualitative data analysis software that enables text highlighting, tagging, and coding. Using these functions, we coded text in each article to answer ten pre-defined questions aimed at capturing how the late Quaternary megafauna extinctions have been conceptualized and studied through time and across different disciplines (Table 1). Articles falling outside the scope of the study were removed based on the exclusion criteria:

1. Article must relate to the Quaternary period (2.6 Ma to present).
2. Article must relate to the extinction of vertebrates.
3. Article must relate to the extinction of megafauna, however defined.
4. Article must focus on megafauna extinctions, or the findings must be related to the extinction of megafauna in some significant way.

Firstly, however, to ensure inter-analyst consistency in data extraction and analysis, a series of “training sets” was conducted. Each analyst was assigned the same set of 20 randomly selected papers from the database. Using the exclusion criteria, they

TABLE 1 The ten questions asked of each article and using Morris et al. (2022) as an example.

Question	Code example	Article example
What megafauna are being analyzed?	Tasmanian devil	This study “test[ed] whether climate change could have imposed physiological stress on the Tasmanian devil <i>Sarcophilus harrisii</i> during the mid-Holocene, when the species went extinct on mainland Australia.”
What is the geographical focus?	Australia	
What is the study scale?	Country	
What is the temporal focus?	Early to mid-Holocene	
What is the primary extinction cause(s) proposed?	Anthropogenic	This study claimed “cultural and demographic changes in the human population or competition from the dingo <i>Canis dingo</i> as the main contending hypotheses to explain mainland loss of the devil in the mid-Holocene.”
What is the secondary extinction cause(s) proposed?	None	No secondary extinction causes were proposed
What extinction cause(s) is refuted?	Climate change	This study “found no evidence of widespread negative effects of climate on physiological parameters for the devil on the mainland during its extinction window.”
What themes are discussed?	Human population density	This study discussed a human population boom at around 5000-years BP “consisting of occupation of more habitat types, technological change, more sedentary behavior and population growth.”
What data are being analyzed?	Temperature	This study used “bias-corrected data on monthly temperature (min and max), precipitation and relative humidity using PaleoView, a free software that generates paleoclimate data at different temporal scales at 2.5° x 2.5° resolution.”
How are megafauna defined?	> 45 kg	This study defined megafauna as those animals “typically weighed over 45 kg.”

independently screened the papers and coded those deemed relevant until ten papers had been analyzed. This training process was repeated twice more, with new sets of papers each time. After each round, results were compared and discussed to refine the coding approach and improve consistency in paper selection. By the third training set, all analysts consistently selected the same ten papers, demonstrating inter-analyst alignment.

After completing the training set, the analysts independently analyzed 100 articles each, for a total of 300 articles. Given that the initial literature search was conducted in November 2021, it was likely it may not be capturing the most recent trends in the field. To address this imbalance, we conducted a follow-up literature search in WoS

using the same search terms but this time focusing on the years 2022–2024. This search yielded an additional 125 articles. From these, 60 articles were analyzed as before, resulting in a total of 360 papers. A full list of the articles included in this study can be found in Appendix 1 (also available at [https://github.com/wccarleton/mfreview/blob/main/data/mf\\_review\\_papers\\_final.xlsx](https://github.com/wccarleton/mfreview/blob/main/data/mf_review_papers_final.xlsx)).

VOSviewer (version 1.6.20) was used to conduct a series of network cluster analyses based on co-authorship, citations, and keyword co-occurrence using both author and WoS keywords. We also performed a basic hierarchical clustering analysis of our coded themes using MAXQDA's in-built Code Map tool, which groups codes into clusters based on how similarly (i.e., co-occurrence in documents) codes have been applied in the data. Clusters were generated using the “map position” setting, meaning their arrangement reflects their spatial projection in two-dimensional space rather than from their exact calculated distances. To assess the through-time trend in publication volume, we divided the number of articles published each year in our sample by the total number of articles published each year in the five most common journals in our dataset (data sourced from Scopus).

Following this, we conducted a more formal quantitative analysis combining bibliometric data with codes derived from the literature. Using the NetworkX package in Python, we constructed a directed citation network where each paper is represented by a node and citations by edges. In-degree (the number of edges coming to a node) served as a proxy for internal citation counts, which we validated against broader citation metrics to assess the fidelity of our literature sample. We applied the Leiden network clustering algorithm to automatically determine the number and composition of clusters. These clusters were then quantitatively assessed in relation to three variables:

1. **Discipline**—whether clusters aligned with disciplinary categories assigned to the relevant papers. Categories were determined based on WoS Subject Categories and journal focus and, where ambiguous, by consulting the article title and abstract.
2. **Extinction Cause**—whether clusters aligned with the main extinction cause promoted by the relevant papers.
3. **Co-authorship**—whether clusters were shaped by authors citing close collaborators, leading to overlap between citation and authorship networks.

Finally, we modelled the relationship between the three variables and citation network cluster assignments using a Bayesian logit-softmax model, allowing us to quantify the contribution of each variable. To avoid excessive complexity, we used only the modal co-authorship clusters (i.e., the most frequent cluster represented among the authors of a given paper) as a potential explanatory variable for each paper. While this simplification does not capture all possible co-authorship affiliations, it provides a tractable way to test whether predominant membership in a single co-authorship cluster increases the likelihood of a paper being assigned to a specific citation network cluster.

## Results

The literature search returned 1,107 articles (Figure 1). After removing 386 duplicates, we screened 515 records, of which 360 met our inclusion criteria and were assessed. The final sample spans publications from 1959 to 2024, covers 112 journals, includes 1,783 keywords, and contributions from 1,445 authors. The articles reveal a clear growing interest in late Quaternary megafauna extinctions, with a marked surge in publications around the turn of the millennium (Figure 2C).

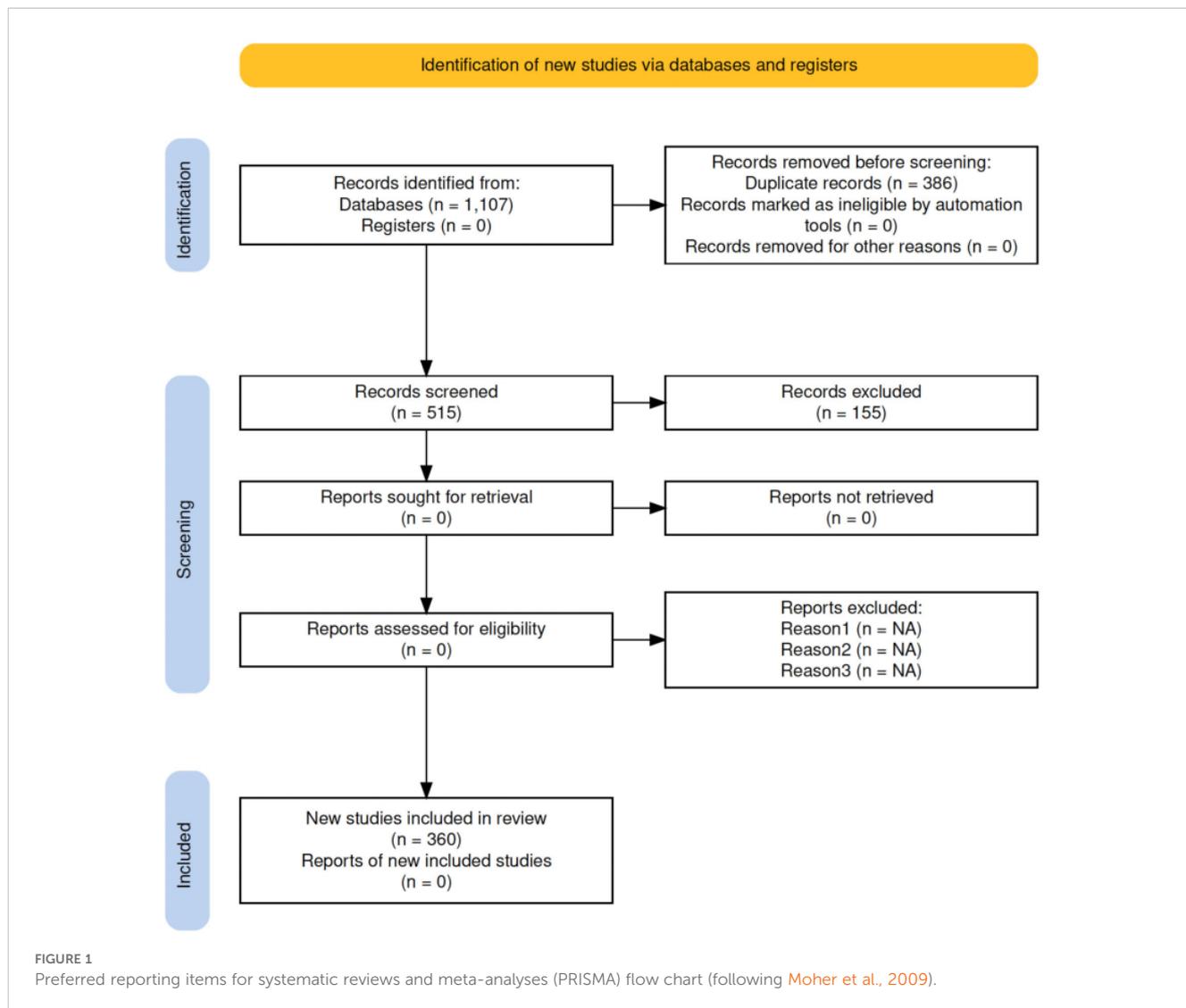
### Keyword co-occurrence, citation, and co-authorship network

Keywords were drawn from both author-assigned and WoS entries and filtered to include only those appearing at least five times. Of the 1,783 keywords, 130 met this criterion and were grouped into six clusters (Figure 3). Ignoring terms used in the initial search query, the five most commonly occurring keywords were climate change ( $n = 62$ ), mammals ( $n = 40$ ), climate ( $n = 38$ ), paleoecology ( $n = 31$ ), radiocarbon ( $n = 35$ ), and body mass ( $n = 35$ ). More recently emerging keywords include terms common in ecology and conservation biology, such as biodiversity ( $n = 12$ ), functional diversity ( $n = 6$ ), communities ( $n = 6$ ), conservation ( $n = 17$ ), and consequences ( $n = 12$ ) (Figure 4).

For the author citation network analysis, a threshold of three or more publications per author was applied, resulting in 134 individuals which grouped into six clusters (Figure 5). These clusters broadly align with both research discipline and geographic focus. For instance, cluster 4 consists mostly of ecologists, while clusters 1, 3, and 5 are largely researchers working in Eurasia, Australia, and Madagascar, respectively. Ecologists are responsible for a greater number of articles in recent years, indicated by the brighter colors in Figure 6. A further analysis of the gender of the authors, indicates that 80% ( $n = 107$ ) of the 134 authors are male, pointing to a strong gender bias within the scientific leadership of megafaunal extinction studies.

For the journal citation network analysis, a threshold of two or more publications per journal was applied, resulting in 44 journals (Figure 7). The resulting network yielded five distinct clusters, which again largely correspond to disciplinary focus. For example, ecology journals like *Ecography*, *Nature Ecology & Evolution*, and *Ecology Letters* cluster together, as do Quaternary science journals like *Quaternary International*, *Quaternary Geochronology*, and *Earth-Science Reviews*. Two particularly prominent and influential journals in our literature sample are *Quaternary Science Reviews* and *Proceedings of the National Academy of Sciences (PNAS)*, which contributed 45 and 29 publications, respectively, and exhibit strong citation links with other journals in the network. As shown in Figure 8, ecology journals have become more prominent in recent years.

For the publication citation network analysis, 338 articles were analyzed, with 22 excluded due to a lack of connections with other



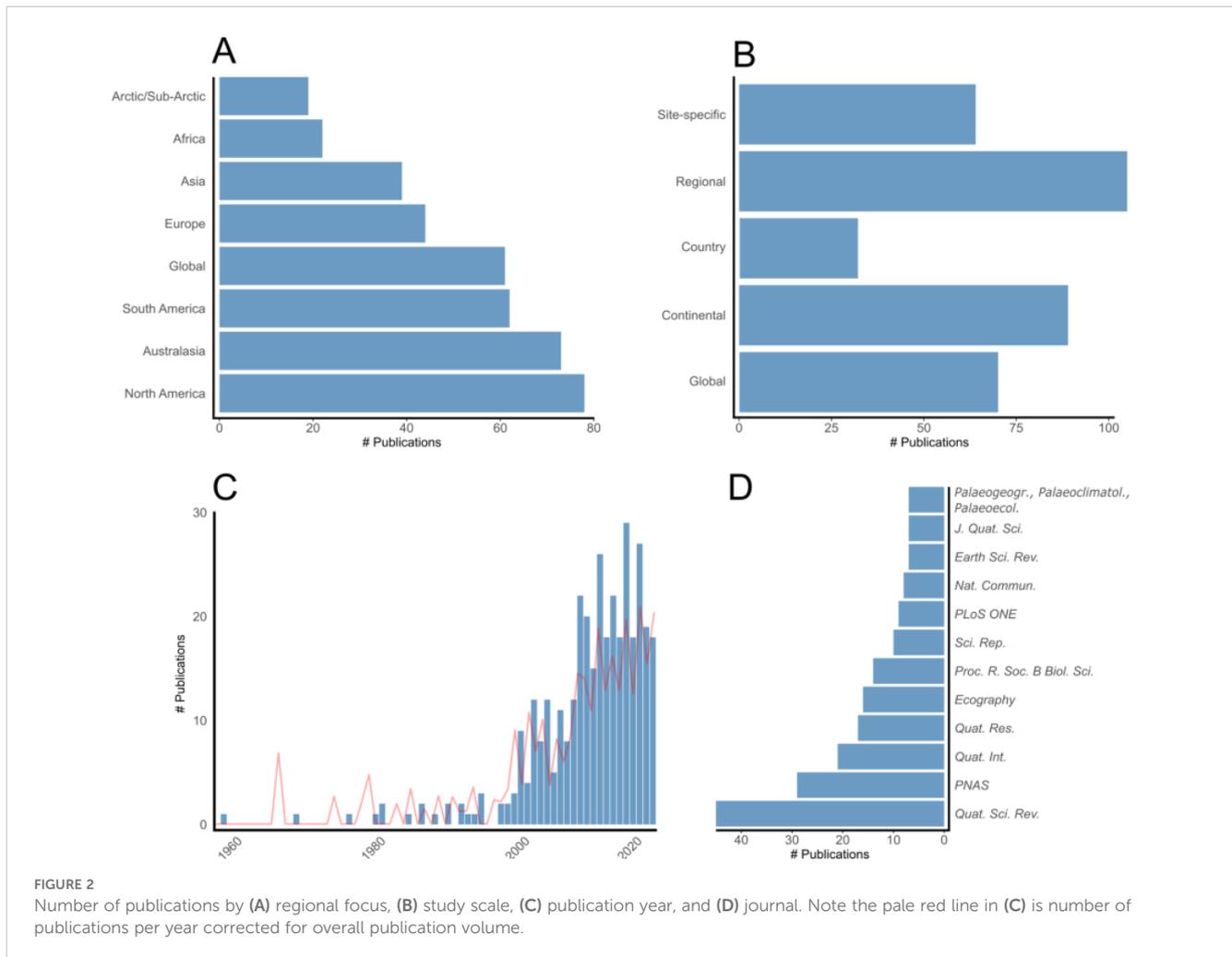
articles. This network yielded 17 distinct clusters, again revealing clear patterns reflecting disciplinary and geographic focus (Figures 9, 2D). Notably, the two review articles by Barnosky et al. (2004) and Koch and Barnosky (2006) stand out as being particularly central and influential in the debate, with a high number of citations and strong links with the broader megafauna extinction literature (Figure 9; Table 2). A comparison with the broader citation network revealed a strong correlation (Supplementary Table S1), indicating that our internal citation metrics reliably reflect the wider influence of papers. The continued publication of megafauna extinction studies in top journals such as *Nature*, *Science*, and *PNAS* highlights the perceived importance and sustained interest in this topic.

In our more formal network analysis, we used NetworkX to generate a publication citation network—a visual network of the relationship between articles based on their citations—and applied the Leiden algorithm, which identified seven distinct clusters (Supplementary Figure S1). Some of these have considerable time depth and are densely populated, while others are more recent and contain fewer papers. As with the publication citation network

above (Figure 9), citation network clusters reflect disciplinary effects (Supplementary Figure S8). Clustering also reflects proposed extinction causes: some clusters predominantly support human-driven models, others emphasize climate-driven models, and some present a more balanced mix of the three major hypotheses (Supplementary Figure S8).

Applying the Leiden algorithm to the internal co-authorship network identified 80 co-authorship clusters. To extract useable insights and limit the number of potential explanatory variables we selected the top ten clusters for subsequent analysis. These ten clusters account for approximately 80% of the total edges in the internal co-authorship network (Supplementary Figure S5) and, it is reasoned, are representative of the core ideas in the literature sample.

Plotting co-authorship cluster frequency across the internal citation clusters revealed that few co-authorship groups dominate multiple citation clusters in the internal network (Supplementary Figure S6). This suggests that much of the debate about megafauna extinctions—and the corresponding citation clusters in the broader literature—is shaped by a relatively small number of co-author communities. However, the “Other” category, which groups many



smaller and less influential author clusters, still plays a major role, dominating three of the citation network clusters.

Lastly, mapping the co-authorship network revealed a complex structure of human social networks (Supplementary Figure S4). Specifically, it exhibits a “small world network” dynamic with high clustering and short distances. In other words, this suggests that the researchers in the megafauna extinction literature are connected, without isolated groups, while still containing distinct clusters of co-authors who form tight-knit communities. The relationship between the three variables and citation network are more formally modelled using a Bayesian logit-softmax model, the results of which are provided in the Supplementary Material. The modelling indicates that citation network cluster membership is predicted by disciplinary affiliation, extinction cause, and co-authorship networks, but the strength of the effects varies by citation cluster.

## Summary of the literature

### Temporal scope, taxonomic focus, and regional patterns

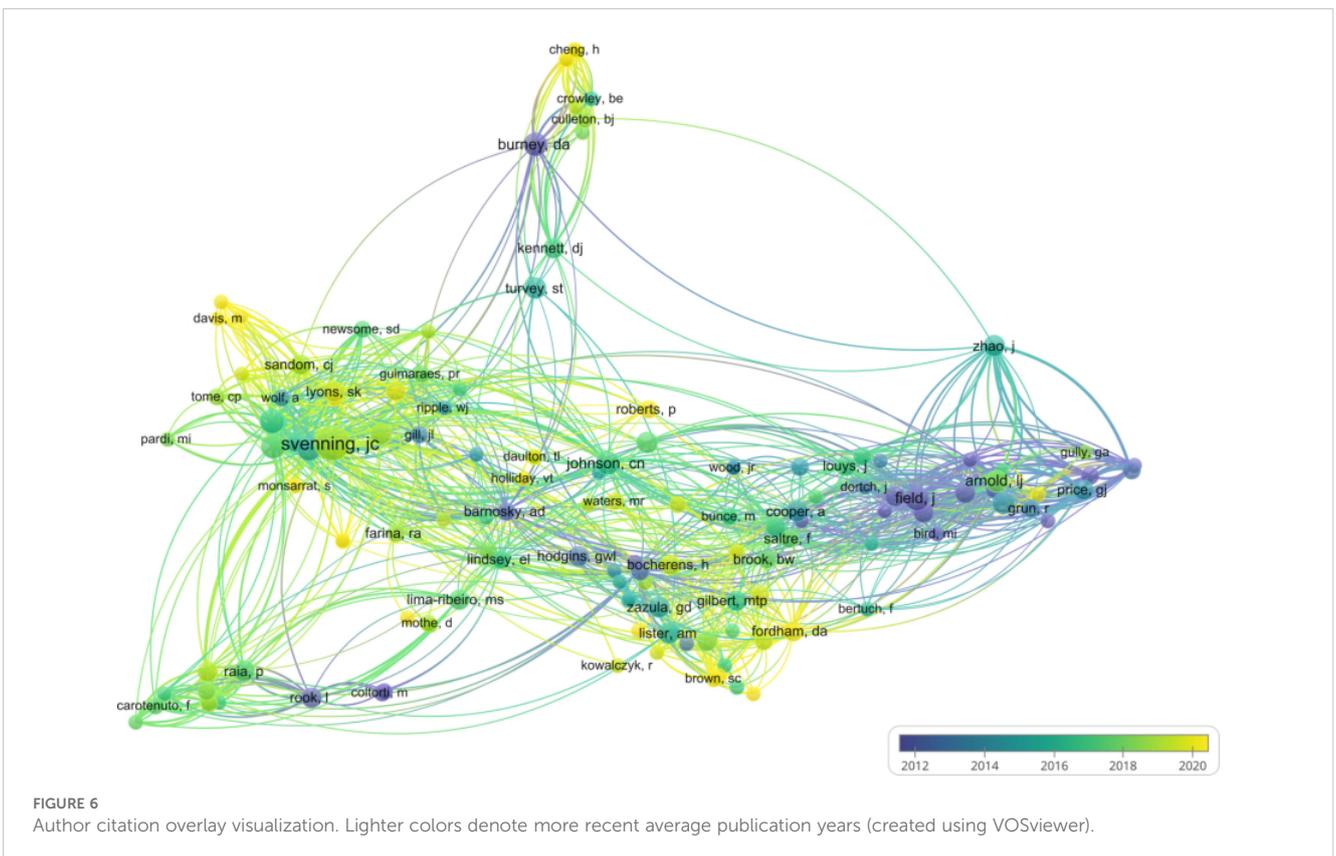
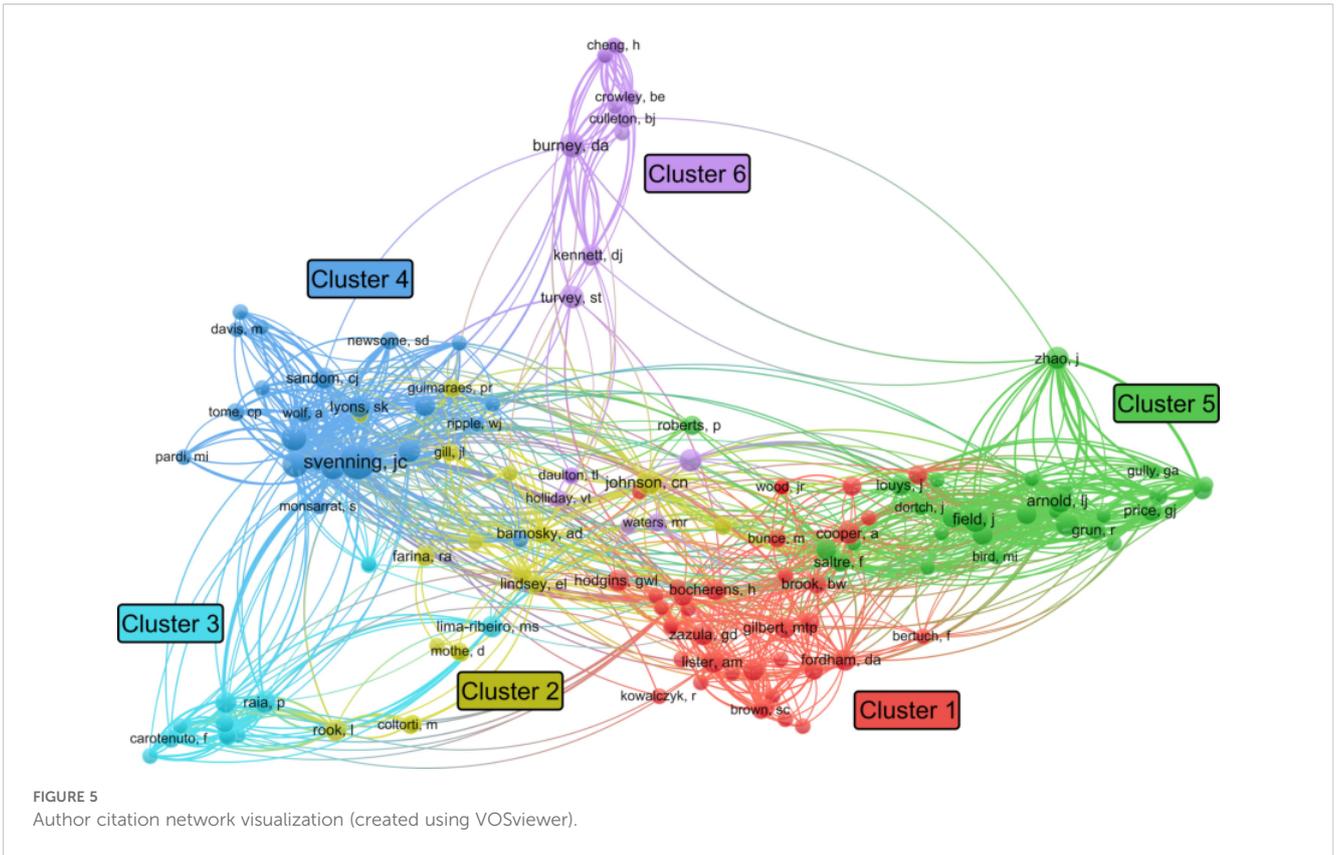
Most studies in the literature sample focused on the Late Pleistocene ( $n = 144$ ) and Late Pleistocene–Holocene transition

( $n = 146$ ). A smaller but significant number of studies focused on Holocene extinctions ( $n = 42$ ), particularly on islands such as the Caribbean and Mascarene Islands, Madagascar, Mallorca, and New Zealand (Crowley, 2010; Rawlence et al., 2012; Bover et al., 2016; Li et al., 2020). Some Holocene studies reported late survivals on the continents, such as the European wild ass (*Equus hydruntinus*) in Europe (Crees and Turvey, 2014) and the mid-Holocene extinction of the Tasmanian devil (*Sarcophilus harrisii*) on mainland Australia (Morris et al., 2022). Few studies reported extinctions that pre-date the Late Pleistocene (Hocknull et al., 2007; Prideaux et al., 2007).

Geographically, research is concentrated in regions that experienced severe megafauna losses, especially Australasia and the Americas, though coverage within these areas is uneven (Figure 2A). In North America, studies are biased toward northern latitudes and iconic sites like the La Brea Tar Pits in California (DeSantis et al., 2012; Jones and Desantis, 2017; Fuller et al., 2020; O’Keefe et al., 2023) and Hall’s Cave in Texas (Smith et al., 2016; Seersholm et al., 2020). South America is dominated by the Pampas region, due to its rich fossil record and purported evidence of butchery (Martínez et al., 2013; Chichkoyan et al., 2017; Lopes et al., 2020; Prates and Perez, 2021; Alberdi et al., 2023; Bellinzoni et al., 2024). In Australia research is concentrated in the southeast and southwest of the continent (Ayliffe et al., 2008;









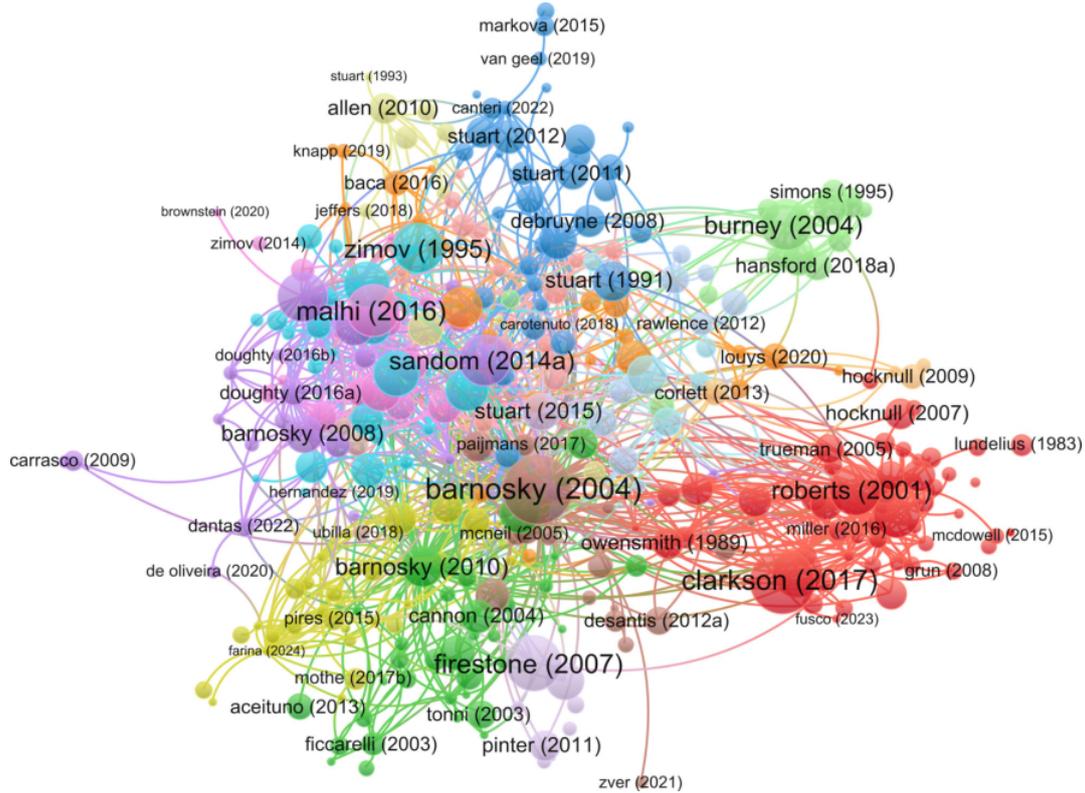
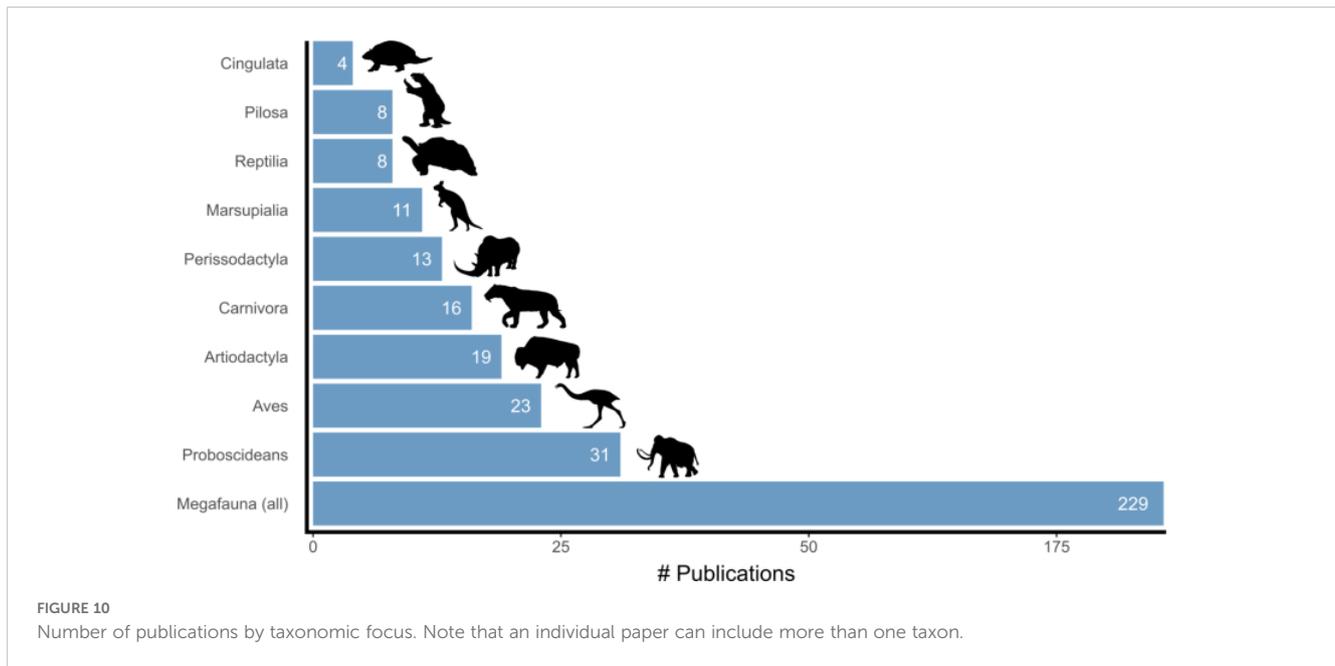


FIGURE 9  
Publication citation network visualization (created using VOSviewer).

TABLE 2 Top 10 most cited articles in our literature sample. Note that the citation counts reflect only those from within the internal network, meaning the true citation counts of these articles is much higher.

Title	Author	Year	Article type	Journal	# of citations
Late Quaternary Extinctions: State of the Debate	Koch and Barnosky	2006	Review article	<i>Annual Review of Ecology, Evolution, and Systematics</i>	117
Assessing the causes of Late Pleistocene extinctions on the continents	Barnosky et al.	2004	Review article	<i>Science</i>	112
Species-specific responses of late Quaternary megafauna to climate and humans	Lorenzen et al.	2011	Research article	<i>Nature</i>	62
Global late Quaternary megafauna extinctions linked to humans, not climate change	Sandom et al.	2014	Research article	<i>Proceedings of the Royal Society B</i>	56
A multispecies overkill simulation of the end-Pleistocene megafauna mass extinction	Alroy	2001	Research article	<i>Science</i>	55
New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago	Roberts et al.	2001	Research article	<i>Science</i>	54
Timing of Quaternary megafauna extinction in South America in relation to human arrival and climate change	Barnosky and Lindsey	2010	Review article	<i>Quaternary International</i>	50
Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America	Gill et al.	2009	Research article	<i>Science</i>	47
Megafauna and ecosystem function from the Pleistocene to the Anthropocene	Malhi et al.	2016	Review article	<i>Science</i>	43
A requiem for North American overkill	Grayson and Meltzer	2003	Review article	<i>Journal of Archaeological Science</i>	43



Westaway, 2020; Meltzer, 2020; Fariña and Vizcaino, 2024), regions (Louys et al., 2007; Bird et al., 2013), or events, such as the Younger Dryas Impact Hypothesis (Pinter et al., 2011; Powell, 2022; Holliday et al., 2023, 2024) and the timing of human arrival in Australasia (O'Connell and Allen, 2004) and the Americas (Fiedel, 2022). Some centered on ecological processes, such as the impact of Aboriginal landscape burning on Australian fauna (Bowman, 1998), while others addressed more practical and methodological issues, such as the interpretation of the *Sporormiella* record (Fiedel, 2018).

### Extinction cause(s)

Overall, the major extinction hypotheses are similarly represented in our literature sample: 82 (23%) articles cite humans as the primary driver, 82 (23%) articles cite climate as the primary driver, 71 (20%) proposed a mixed human-climate cause. A third of articles offered no explicit major driver of extinction, while only a few considered an extraterrestrial cause, such as a solar flare or comet impact (Firestone et al., 2007; LaViolette, 2011; Powell, 2022).

Breaking down extinction cause by region shows that for Australia, North America, and South America, the three extinction models are similarly represented (Figure 11C). In contrast, for Eurasia and studies of the arctic/sub-arctic, climate-based extinction models dominate. The opposite is true for global studies, which overwhelmingly promote human-driven extinction models. Almost all studies on islands advocate for human-driven extinctions, with a few proposing mixed models, particularly in the case of Madagascar.

Trends over time reveal some subtle but potentially meaningful shifts (Figure 11B). Climate-based explanations rose after the turn of the millennium, peaking at 44% of papers between 2010–2014, before declining to a low of 28% in recent years. Anthropogenic-based explanations have steadily grown, from 32% in 2000–2004 to around 38% since 2010. Mixed models were high around the turn of

the millennium, followed by a low of 19% between 2010–2014 and a steady rise to 35% in recent years.

Disciplinary differences also emerge (Figure 11A). Quaternary science tends to favor climate-based explanations (31%) over human (15%) or mixed causes (18%). In contrast, ecology journals lean more toward human-driven explanations (36%), with less support for climate (17%) or mixed causes (20%). Most archaeology papers (58%) do not propose a primary extinction cause, indicating a degree of caution or uncertainty within the field. Multidisciplinary journals, meanwhile, show a more balanced representation of extinction hypotheses.

Within each of the major hypotheses, scholars have proposed a range of mechanisms. Anthropogenic causes include general overhunting as well as more specified overkill models such as selective predation of juveniles in slow-reproducing species (McNeil et al., 2005; Brook and Johnson, 2006) and harvesting of large bird eggs (Miller et al., 2016). More recently, attention has shifted towards more indirect human pressures, especially habitat destruction and fragmentation, fire regimes, and competition with livestock (Holdaway et al., 2014; Hansford et al., 2021; Iijima et al., 2022; Adesanya Adeleye et al., 2023; O'Keefe et al., 2023).

Climate-based models typically emphasize habitat loss and vegetation change linked to glacial-interglacial cycles and abrupt climate events like the Last Glacial Maximum, Younger-Dryas, and Bølling-Allerød (Gallo et al., 2013; Huntley et al., 2013; Baca et al., 2016; Villavicencio and Werdelin, 2018; van Geel et al., 2019; Vachula et al., 2020). Transitions between forest and grassland (Field et al., 2001; Long and Yahnke, 2011; Zazula et al., 2014; Gilmour et al., 2015; Benfield et al., 2023), prolonged droughts (Hocknull et al., 2007; DeSantis et al., 2017; Kemp et al., 2019; Lewis et al., 2020; Louys and Roberts, 2020), and wetland expansion (Mann et al., 2013; Puzachenko et al., 2021) are also cited. Less commonly cited are changes in atmospheric CO<sub>2</sub> concentration, sea level rise, and volcanic eruptions (Louys et al., 2007; Faith and O'Connell, 2011; Gonzalez et al., 2014).

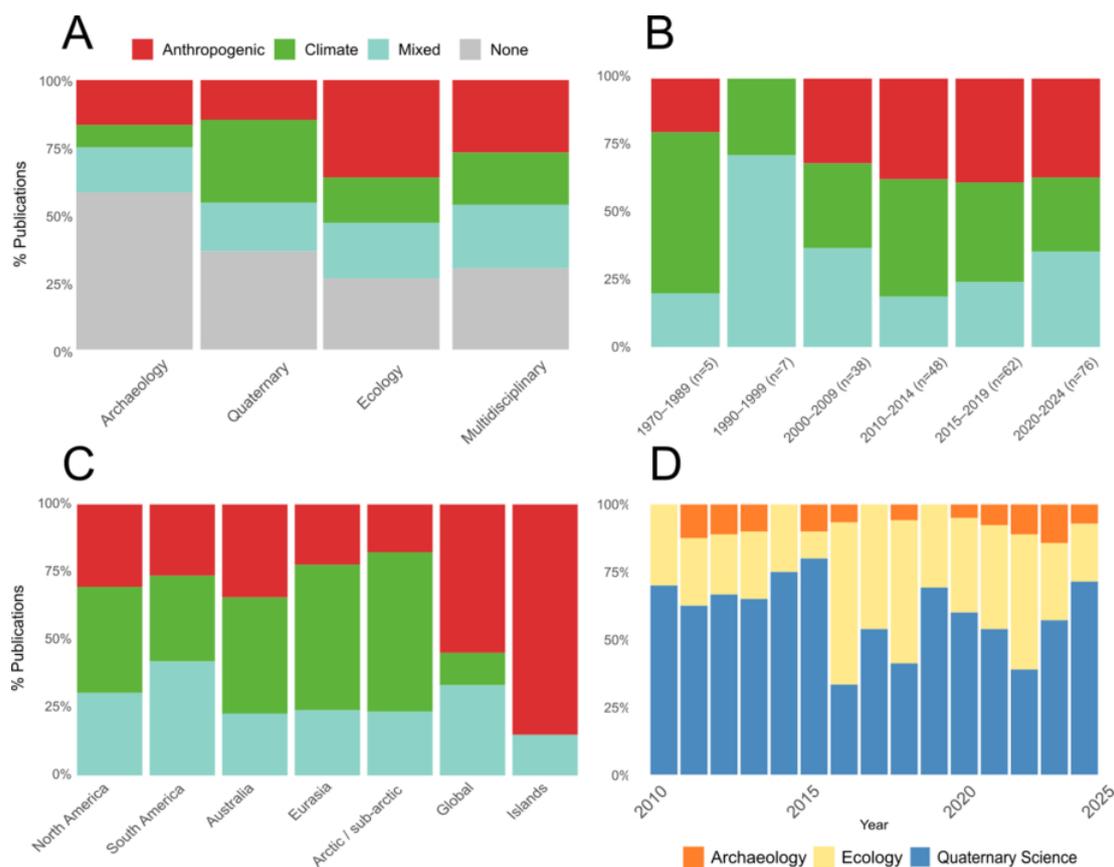


FIGURE 11

Proportion of the three key extinction hypotheses by discipline (A), time (B), region (C), and proportion of publications by discipline (D). Note for (B) earlier periods have larger time bins due to smaller sample sizes.

Many papers propose a synergistic effect, with human activity amplifying existing climate stress (Prescott et al., 2012; Gill, 2014; Mothé et al., 2017; Seersholm et al., 2020; Pilowsky et al., 2023; Fariña and Vizcaíno, 2024; Robu et al., 2024). In some instances, indirect pressures such as competition, livestock introduction, and landscape modification are implicated (Hixon et al., 2021b; O’Keefe et al., 2023); in others, humans are seen as delivering a final blow—or *coup de grâce*—to already declining megafauna populations (Lima-Ribeiro et al., 2012; Cantalapiedra et al., 2021; Fordham et al., 2024).

## Thematic clusters

Hierarchical clustering of themes appearing in at least 5% of articles returned a total of 78 codes, which we place into five distinct clusters (Figure 12). While this clustering is somewhat arbitrary as the number of clusters is manually selected, it does capture some of the major themes being discussed in the megafauna literature, both historically and more recently. Below, we outline some of the main features of these clusters, drawing only from articles within our literature sample.

### Cluster 1: Colonization, subsistence strategies, tool use, and the human role in megafauna extinctions

This cluster explores the deep-time human dimensions of megafauna extinctions, focusing on the timing and nature of human-megafauna overlap and interaction. While once difficult to demonstrate, there is now unequivocal evidence of human-megafauna coexistence across North and South America, Australia, and on several islands (Field et al., 2008; Politis and Messineo, 2008; Meltzer, 2020; Louys et al., 2021). What remains heavily debated in the literature, however, is the duration and extent of these overlaps. In Australia, for example, many researchers place the megafauna extinction “window” between 50–40 ka, coinciding with the spread of people across the continent (Roberts et al., 2001; Lopes dos Santos et al., 2013; Saltré et al., 2016, 2019). Others, however, argue the megafauna record is too patchy to support a discrete extinction window, noting that some species have last appearance dates well before this, others lack direct dates entirely, and some persisted for tens-of-thousands of years after human arrival in some regions (Wroe and Field, 2006; Faith and O’Connell, 2011; Dortch et al., 2016; Westaway et al., 2017; Price et al., 2021). Similar debates persist for the Americas (Waguespack, 2007;



impacts are discussed for a range of megafauna, including birds and reptiles (Pedrono et al., 2013; Joos et al., 2022; Kemp, 2023), megaherbivores have received particular attention owing to their role as ecosystem engineers with the ability to modify, shape, and create habitats (Owen-Smith, 1989; Johnson, 2009; Doughty, 2013; Gill, 2014; Bakker et al., 2016; Doughty et al., 2016b; Bocherens et al., 2017; Bocherens, 2018; Galetti et al., 2018; Pires et al., 2018; Pires, 2024).

Three ecological impacts appear most frequently in the literature: seed dispersal, nutrient redistribution, and fire regulation. Megaherbivores disperse more and larger seeds over longer distances and enhance germination through digestion (Kistler et al., 2015; Berti and Svenning, 2020); redistribute nutrients via feces, carcasses, and soil disturbance (Doughty et al., 2016c, 2020); and reduce fuel loads and fire intensity through browsing and trampling (Owen-Smith, 1989; Webb, 2008; Corlett, 2013; Pedrono et al., 2013; Bakker et al., 2016; Raczka et al., 2018). Their extinction has been linked to reduced plant ranges, population fragmentation, and genetic loss (Kistler et al., 2015; Doughty et al., 2016b; Pires et al., 2018; Berti and Svenning, 2020), major declines in nutrient cycling (Doughty et al., 2016c, 2020), and increased fire frequencies (Owen-Smith, 1989; Webb, 2008; Corlett, 2013; Pedrono et al., 2013; Bakker et al., 2016; Raczka et al., 2018). Other discussed impacts of megafauna extinctions include co-extinctions (Corlett, 2013; Galetti et al., 2018), reduced carbon storage (Doughty et al., 2016b; Berzaghi et al., 2023), atmospheric and climatic changes (Zimov and Zimov, 2014), and reduced microbe and pathogen dispersal (Galetti et al., 2018; Doughty et al., 2020).

### Cluster 3: Megafauna ecology, behavior, and implications for modern conservation strategies

This cluster examines how late Quaternary extinctions contribute to modern conservation and restoration strategies. Although such connections have been discussed for decades (Emslie, 1987; Owen-Smith, 1989; Bowman, 1998; Choquenot and Bowman, 1998; Barnosky et al., 2004; Wroe et al., 2004), there has been a notable rise in recent years. Perhaps the most prominent example is the use of fossil record to guide rewilding efforts (Corlett, 2013; Bakker et al., 2016; Bocherens et al., 2017; Berti and Svenning, 2020; Zeller and Göttert, 2021; Morris et al., 2022; Davoli et al., 2024) with a prominent case being Pleistocene Park in Siberia, where species like bison and muskox have been reintroduced in an attempt to restore the steppe ecosystem (Zimov and Zimov, 2014).

As part of rewilding efforts, there has been an increasing attention on trait-based rewilding, focused on restoring ecological rather than species-specific functions (Lundgren et al., 2020). This shift aligns with a growing recognition of the role of keystone species and their cascading effects on ecosystem structure and function. Compared to species-centered approaches, trait-based rewilding offers greater flexibility, allowing for the selection of ecologically suitable analogues under contemporary and future climate scenarios, and enhancing functional redundancy and ecosystem resilience (Kemp, 2023).

In response to these recent trends, Moleón et al. (2020) propose two new function-oriented megafauna concepts: ‘keystone megafauna’ and ‘functional megafauna’. Here, the term keystone megafauna refers to the megafauna species that have the strongest influence on the structure and functioning of the ecosystem they inhabit. Functional megafauna, on the other hand, is defined as “the subset of largest species of a given clade or guild that have distinctive functional traits.” A further subcategory, “apex megafauna”, refers to species so large that they were only subject to anthropogenic predation.

### Cluster 4: Ecological resilience and adaptive responses among megafauna and human populations amid changing climates and environments

This cluster examines species’ adaptability, vulnerability, and resilience in the face of climatic and anthropogenic pressures. Many studies highlight physiological and behavioral adaptations to arid, cold, or otherwise challenging environments (Wroe and Field, 2006; Larmon et al., 2019; Mann et al., 2019; Lord et al., 2020; Novaro and Walker, 2021; Dembitzer et al., 2022; Alberdi et al., 2023), as well as to specific environments and dietary niches (Webb, 2008; Martínez et al., 2013; Lanö et al., 2017; Amir et al., 2022; Smith et al., 2022; Bellinzoni et al., 2024; Hardy and Rowland, 2024; Zhang et al., 2024). Some studies attribute extinctions to limited adaptability to environmental change (Zhang et al., 2024), while others reveal that certain species were more ecologically flexible than previously assumed (Hardy and Rowland, 2024).

Advances in aDNA have transformed understanding of extinction dynamics, revealing genetic adaptations (e.g., cold-tolerant TPRA1 variants in woolly rhinoceros) and reconstructing population histories (Lord et al., 2020; Meltzer, 2020; Fiedel, 2022). While some species, like New Zealand’s moa, showed demographic stability until rapid extinction (Allentoft et al., 2014), others, like the Wrangel Island mammoths, experienced sharp declines in genetic diversity prior to extinction, perhaps related to isolation (Nyström et al., 2012).

Human adaptability is also central, with research linking dietary flexibility and technological innovation to shifting ecological conditions. Some studies suggest that specialized megafauna hunting was a response to human physiological needs (Ben-Dor and Barkai, 2024), while others link megafauna disappearances to broadening of diets and technological innovations (Dembitzer et al., 2022).

Lastly, co-evolutionary dynamics and prey naivete are frequently cited to explain geographic variation in extinction severity (Sandom et al., 2014a). In Africa and Eurasia, long-term co-existence with humans has been linked to the evolution of anti-predator behaviors in megafauna (Jukar et al., 2021). Some surviving species may have passed through an “extinction filter”, helping explain their persistence in certain human-disturbed tropical ecosystems (Amir et al., 2022).

## Cluster 5: Challenges in reconstructing the timing and drivers of megafaunal extinction

This final cluster highlights the significant biases, uncertainties, and data gaps that continue to complicate the study of late Quaternary megafauna extinctions. Frequently cited issues include the poor quality and resolution of radiocarbon dates (Meltzer and Mead, 1983; Brook and Bowman, 2002; Cupper and Duncan, 2006; Dortch et al., 2016; Kemp et al., 2019; Jukar et al., 2021), a general scarcity of well-dated fossils (Gillespie et al., 1978; Faith and O'Connell, 2011; Gill et al., 2012; Cooke et al., 2017; Fiedel, 2018; Kemp et al., 2019; Hocknull et al., 2020; Price et al., 2021), poorly resolved and spatially biased paleoclimate records (Gill et al., 2012; Kemp et al., 2019; Plint et al., 2019; Hocknull et al., 2020; Seersholm et al., 2020; Adesanya Adeleye et al., 2023), and taphonomic and stratigraphic biases, such as the Signor-Lipps effect and sediment reworking (Field, 2006; Field et al., 2008, 2013). Concerns over radiometric date reliability—particularly of pre-AMS radiocarbon dates—are particularly prevalent and have led to the development of quality ranking systems to screen for reliability (Meltzer and Mead, 1983; Burney et al., 2004; Barnosky and Lindsey, 2010; Saltré et al., 2016).

A central debate concerns the scarcity of butchery sites—the so-called “associational critique” (Cannon and Meltzer, 2008; Surovell and Grund, 2012; Aceituno et al., 2013; Jukar et al., 2019; Wolfe and Broughton, 2020; Bampi et al., 2022; Alberdi et al., 2023). On the one hand, critics argue that the lack of direct evidence of hunting undermines claims of widespread or intensive megafauna hunting (Meltzer, 2020). On the other hand, defenders argue that, considering taphonomic loss, short extinction windows, sparse human populations, and number of butchery sites for extant species, the number of butchery sites for extinct species is as expected (Surovell and Grund, 2012; Wolfe and Broughton, 2020).

Finally, this cluster explores the roles of climate and human land-use in megafauna extinctions. Many studies link glacial-interglacial shifts and altered precipitation to habitat fragmentation and megafauna loss (Reed, 1970; Webb, 2008; Stuart and Lister, 2011; Huntley et al., 2013; Mann et al., 2013; Lima-Ribeiro et al., 2014; Markova et al., 2015; Rabanus-Wallace et al., 2017; Louys and Roberts, 2020; Araújo et al., 2021; Mondanaro et al., 2021). Human practices such as burning—especially “firestick farming” in Australia and New Zealand—are implicated in major vegetation changes that may have contributed to extinctions (Bowman, 1998; Bird et al., 2013; Doughty, 2013; Holdaway et al., 2014; Perry et al., 2014, 2014; Faurby and Svenning, 2015; Westaway et al., 2017; Domic et al., 2021; Adesanya Adeleye et al., 2023). On islands like Madagascar, megafauna extinctions are often tied to agricultural expansion, forest clearance, and livestock introduction (Li et al., 2020; Hixon et al., 2021a).

## Discussion

In recent years, ecologists have become increasingly prominent voices in the megafauna extinction debate, bringing with them a growing emphasis on leveraging these extinctions to inform

contemporary ecosystem management and conservation strategies. Their contributions have introduced innovative new approaches, methodologies, and research that is more global in scope, providing novel insights not easily reachable through more traditional means. The differences in focus and emphasis are understandable given the distinct histories, training, and research priorities of different disciplines. What is less easily explained, however, is the persistent divide between ecologists and researchers in Quaternary science and archaeology over the primary drivers of late Quaternary megafauna extinctions.

This divide probably relates to the broader structural and disciplinary fragmentation within late Quaternary megafauna extinction research. Our analysis revealed a rich and expanding field, but one that remains fragmented along disciplinary lines. Ecologists, Quaternary scientists, and archaeologists tend to form research clusters, publish in discipline-specific journals, and engage primarily with their own discipline's literature. This is not wholly unsurprising given the nature of academia. However, we argue that this siloing has likely contributed to the persistent divergent interpretations and limited cross-disciplinary dialogue, despite the overlapping questions and complementary datasets.

These disagreements are not geographically or temporally uniform. For instance, our analysis revealed a broad consensus that human activity played a central role in more recent megafauna extinctions on islands like Madagascar and New Zealand, although debates persist over the precise nature and tempo of these extinctions, which has important implications for understanding the immediate human impacts on ‘pristine’ island ecosystems. In contrast, scientific opinion remains deeply divided in regions with the longest research histories, such as Australia and the Americas, despite recent claims to the contrary (Svenning et al., 2024). At the continental and global scale, recent research has been increasingly shaped by ecologists, whose use of meta-analyses seeks to model the relative contributions of climate change and human activity to megafauna extinctions. Overwhelmingly these studies find little support for climate-based extinction models but strong support for human ones (Sandom et al., 2014a; Saltré et al., 2016; Lemoine et al., 2023), which explains the growing prevalence of anthropogenic extinction models over the past decade.

This approach has drawn criticism from Quaternary scientists and archaeologists (Grayson and Meltzer, 2003; Price et al., 2018). A poorly resolved fossil record and significant dating uncertainties are seen to seriously undermine meta-analyses, while insufficient scrutiny of fossil data has led to unfortunate errors in the datasets used in models (see Price et al., 2018 for critique). In our literature sample most archaeology papers (58%) and, to a lesser extent, Quaternary science (37%) papers offer no primary extinction cause, and while this may reflect disciplinary differences in research aims, it may also reflect a greater appreciation and understanding of the biases and limitations inherent in the fossil and archaeological records.

This is perhaps best exemplified by the longstanding “associational critique”, a common debate in our literature sample, but one that has largely taken place within archaeology journals (Nagaoka et al., 2018). Despite decades of consideration, involving

the development of innovative proxies to estimate through-time fossil loss, as well as the application of novel probabilistic and theoretical frameworks to assess the expected frequency of preserved kill sites in the fossil record, there remains little consensus on the seemingly straightforward question of how many kill sites are needed to support the overkill hypothesis (Surovell and Grund, 2012; Wolfe and Broughton, 2020; Grayson et al., 2021).

This debate underscores the complex interplay of geological, temporal, demographic, and behavioral forces that influence fossil preservation and determine what is ultimately recovered and studied by paleontologists and archaeologists, one of the core themes of our literature sample. These challenges are further compounded by significant spatial and temporal gaps in the Quaternary fossil and archaeological records. As our analysis revealed, much of the Eurasian and Australian interiors remain unexplored, research in North America has been largely concentrated in the southwest and northeast, and in South America research has focused on the fossil-rich Pampas region. Several of North America's (Meltzer, 2020) and around one third of Australia's (Price et al., 2018) extinct megafauna species remain undated, while the timing of human arrival to the continents, as well as even more recently settled islands like Madagascar, remains debated.

Other thematic clusters that emerged reflect the growing influence of ecological research, particularly around the ecological ramifications of megafauna extinctions and their relevance for contemporary conservation. A key focus has been the use of late Quaternary extinctions to inform rewilding efforts, initially through the reintroduction of extirpated native species, and more recently through the introduction of non-natives as functional analogues. This research has potentially huge benefits for conservation and biodiversity restoration. However, much of it rests on assumptions of overkill and may be ignoring Quaternary science and archaeological research that could help make more accurate inferences regarding species' ecological tolerances and resilience in the face of long-term climate and human pressures.

As this analysis shows, the late Quaternary megafauna extinction debate is a rich, evolving, and methodologically diverse field. Researchers draw on an impressive range of data, from traditional zooarchaeological and paleontological records to emerging biomolecular and geochemical techniques. In many cases, megafauna researchers are not merely adopting new approaches but driving forward methodological and statistical innovations (e.g., Stewart et al., 2021; Kjær et al., 2022; Paterson et al., 2025). Yet, despite these innovations, and more than five decades of intense research, the field remains divided in its conceptual foundations and empirical base. In the following section we outline a forward-looking research agenda built around five research priorities.

## Future directions

### Fostering interdisciplinary collaboration to bridge disciplinary divides

A persistent lack of integration between the ecological sciences and the paleosciences has been previously noted, rooted in

differences in language, conceptual frameworks, methodologies, research agendas, and publications patterns, as well as institutional barriers set in academic training and departmental structures (Rull, 2010; Louys et al., 2012; Plotnick, 2012; Hsieh and Plotnick, 2020; Lister, 2021; Azevedo-Schmidt et al., 2025). Despite the overlapping research questions and complementary datasets, our analysis indicates that this division clearly extends to the late Quaternary megafauna extinction research, which has expanded in recent years to include a greater number of researchers from across a broader range of disciplinary backgrounds.

This disconnect has tangible consequences. For example, ecologists have been noted to overlook limitations in the fossil and archaeological records (Nagaoka et al., 2018), and some meta-analyses contain errors that closer collaboration with archaeologists or Quaternary scientists could have easily prevented (Price et al., 2018). Meanwhile, archaeologists and Quaternary scientists may underestimate ecological and behavioral flexibility, leading to overly simplistic interpretations of their study species and ecosystems. Even commonly used terms like “community” vary across disciplines (Louys et al., 2012), complicating data integration, while core concepts in the megafauna extinction literature—such as “prey naïveté” and “habitat disturbance”—are often invoked without clear definitions, empirical support, or engagement with the relevant records.

Even how megafauna are defined varies considerably in the literature, with body mass definitions ranging from 10 kg to over 100 kg (and over 1000 kg in the case of megaherbivores). Given the dichotomy between the need to establish a standard body-mass threshold and functional definitions of megafauna based on ecological roles (see Moleón et al., 2020), an expanded concept of megafauna may be necessary when comparing taxa from different geographical contexts (e.g., islands, continents) despite providing similar ecological functions (Hansen and Galetti, 2009).

To address these challenges, we call for greater communication, integration, and, perhaps most importantly, collaboration. Dedicated interdisciplinary events—such as conferences, workshops, and edited volumes—should be established and seek to engage ecologists, conservation biologists, Quaternary scientists, archaeologists, and policymakers. Importantly, a common language needs to be established, which will perhaps be best served by archaeologists and Quaternary scientists better situating their research within existing ecological frameworks (Rull, 2010). At the institutional level, universities and research centers should support cross-disciplinary initiatives on late Quaternary megafauna extinctions, promoting knowledge transfer and broadening researchers' exposure to different methods and perspectives. Rather than attempting to solve the debate, these efforts should seek to reframe research priorities around more integrative and actionable research questions that seek to understand the ecosystem-level effects of megafauna extinctions.

### Expanding geographical and temporal coverage through fieldwork and legacy collections

Our review highlights major geographic and temporal biases in megafauna extinction research, biases that can only be addressed by

renewed investment in field-based research. While Eurasia and North America benefit from relatively well-developed radiocarbon chronologies, regions such as Africa, Australia, and South America often lack comparable resolution (Bird et al., 2022); though efforts to build high-fidelity, open-access radiocarbon databases are gaining traction (Peters et al., 2019; Iminjili et al., 2025).

This shortage of dated material stems in part from limited fieldwork in certain regions. Unfortunately, support for fieldwork in both paleontology (Reisz and Sues, 2015; Maidment and Butler, 2025; Wang et al., 2025) and ecology (Ríos-Saldaña et al., 2018; Engel et al., 2021; Soga and Gaston, 2025) has declined in recent decades. This has been attributed to: (1) limited funding for fieldwork, which is often perceived as high risk; (2) pressure to publish quickly and in high-impact journals, which is at odds with fieldwork-based research that is often considered low impact and can take years to materialize; and (3) growing societal and environmental concerns, such as the need to reduce the ecological footprint of research and avoid helicopter or parachute science.

These pressures have led to a growing prominence of remote sensing and large-scale modelling studies, which are fast to implement, data-intensive, global in scope, and perceived as more impactful (Ríos-Saldaña et al., 2018). While such “big data” studies have yielded valuable insights into megafauna demographics and extinction chronologies, they ultimately rely on primary data that many archaeologists and paleontologists consider insufficient and heavily biased (Price et al., 2018; Meltzer, 2020).

Recent recommendations from ecologists to support field-based research are equally relevant to the paleosciences (Rafiq et al., 2024; Soga and Gaston, 2025). These include: (1) increasing and diversifying funding opportunities for long-term research projects; (2) encouraging the publication of field-based research in high-impact journals; (3) requiring meta-analyses to cite all contributing papers in the main bibliography to increase visibility and recognition of primary fieldwork; (4) broadening evaluation metrics in grant, award, and hiring decisions to better recognize field-based contributions; and (5) increasing support through institutional policies and resources through, for example, financial and regulatory backing, assisting remote teaching, and field safety and harassment training.

While more fieldwork is critical, significant gains can be made elsewhere. Many museums house large legacy collections that can now be reappraised using revised taxonomies and modern scientific techniques (Allmon et al., 2018; Parry and Eichenberg, 2024). Radiocarbon dating previously untested sites or re-dating specimens analyzed prior to the advent of high-precision AMS methods can greatly improve extinction chronologies. To highlight just one example, Knell and Lee (2020) re-dated megafauna remains from the Lamb Spring site in Colorado and found the new ages to be significantly older than those originally reported from the 1980's. Even bone fragments previously considered unidentifiable—which fill the draws and storerooms of many museums—now have the potential to be taxonomically identified using quick, cost-effective palaeoproteomics (see below).

Many legacy collections are at risk of becoming forgotten, inaccessible, or “orphaned” with unclear ownership (Parry and

Eichenberg, 2024). Efforts to identify, document, inventory, and digitize these collections are urgently needed. Globally, many museums are now engaged in efforts to digitize their massive collections, in what has been described as paleontology's “second digital revolution”. Digitization efforts at nine North American institutions revealed that their collections contain roughly 23 times more Cenozoic marine invertebrate fossil localities than currently represented in the Paleobiology Database (PBDB), suggesting that globally, perhaps only 2-3% of recorded fossil localities are publicly available (Marshall et al., 2018). Even if late Quaternary megafauna sites are better represented in such public databases, the number of undocumented sites and fossils in museums is still likely to be significant.

### Prioritizing species-specific approaches

Our analysis shows that much of the literature approaches megafauna extinction at a broad taxonomic scale, with species-specific studies lacking and disproportionately focused on a few charismatic taxa like mammoths and *Diprotodon*, while most other species receive limited attention. Although global syntheses can reveal general trends, recent work highlights the quantity and fidelity of associated dates are largely insufficient to discern patterns and possible causes of extinction (Stuart, 2015; Price et al., 2018). Instead, there is a growing recognition among many Quaternary scientists and archaeologists that extinction dynamics must be examined at the species level, within their specific environmental, climatic, and archaeological contexts.

Recent studies have highlighted the value of species-specific approaches. In their influential study, Lorenzen et al. (2011) combined aDNA, species distribution models, and the human fossil record to show that arctic and sub-arctic megafauna species each responded differently to climate change and human activity. Tejada et al. (2021) used nitrogen isotopes to show that instead of being an obligate herbivore like living sloths, the extinct Darwin's ground sloth (*Mylodon darwini*) was an opportunistic scavenger, overturning previous assumptions regarding its feeding behavior. Species-specific studies of extant fauna are equally important for generating more accurate inferences regarding the fossil record. For instance, long-term elephant enclosure experiments in Africa can provide insights into the effects of herbivory on plant dynamics (Kimuyu et al., 2014), data that is critical for understanding the ecological ramifications of megaherbivore extinctions in the past. Though, as the study of Darwin's ground sloth highlights, care must be taken when drawing comparisons between species no matter how closely related. Even members of the same species may have exhibited different behaviors in the past. For instance, a recent study using strontium isotopes ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) showed that many of eastern Africa's iconic migratory mammals (e.g., blue wildebeest) have not always undertaken long distance migrations (O'Brien et al., 2024).

By bringing the full weight of modern ecological and biological knowledge to species-specific research, combined with archaeological and paleontological knowledge of the limits of the fossil and cultural records, we can better uncover the complex human-animal-environment interactions that shaped past

extinctions, generating data more directly relevant to conservation and restoration planning (Lister, 2021; Pardi and DeSantis, 2022).

### Integrating emerging scientific methods

Our analysis shows a clear increase in the use of innovative scientific and statistical approaches in late Quaternary megafauna extinction research. Improved dating methods involving single amino acid radiocarbon dating and XAD-2 resin pretreatment can help with issues of contamination and yield more accurate ages (Gillespie et al., 2015; Zazula et al., 2017; Deviese et al., 2018; Kosintsev et al., 2019). For instance, Zazula et al. (2017) used single amino acid radiocarbon dating of hydroxyproline to demonstrate that previously published dates for western camel (*Camelops hesternus*) were erroneously young by several tens of thousands of years, likely due to carbon contamination from glue or varnish used in fossil preparation and conservation.

Multi-isotope studies and the incorporation of less commonly used isotopes such as sulfur and zinc are leading to more refined reconstructions of megafauna diets, niche partitioning, and mobility (Bourgon et al., 2020; McCormack et al., 2022; Britton et al., 2023; Pederzani et al., 2024; Heddell-Stevens et al., 2024). Compound-specific isotope analysis (CSIA), which distinguishes isotopic values across individual amino acids, has clarified the trophic position of the abovementioned Darwin's ground sloth (Tejada et al., 2021) and refined dietary insights for the short-faced bear (Kubiak et al., 2023). Despite the greater resolution provided by these approaches, their use in late Quaternary megafauna extinction does remain limited, with only a small number of articles in our literature sample using these (Fuller et al., 2020; Bellinzoni et al., 2024).

Recent years have seen a drastic increase in the application of palaeoproteomics in paleontology. In the absence of aDNA, shotgun proteomics offers an alternative means for phylogenetic placement of extinct species. Megafauna proteins older than 20 million years have now been recovered (Paterson et al., 2025) and proteomic phylogenies have helped resolved the evolutionary relationships of *Genyornis* (Demarchi et al., 2022), rhinocerotids (Welker et al., 2017; Cappellini et al., 2019; Paterson et al., 2025), sloths (Buckley et al., 2015; Presslee et al., 2019), and other megafauna. Additionally, individual sex determination can now be achieved using enamel proteins (Cappellini et al., 2019; Armaroli et al., 2025; Rey-Iglesia et al., 2025), while proteomic analysis of gut tissue samples provides direct evidence of megafauna diets (Cucina et al., 2021).

Related is Zooarchaeology by Mass Spectrometry (ZooMS), a proteomics method that allows taxonomic identification of otherwise unidentifiable bone fragments. It is high-throughput and cost effective, meaning hundreds and even thousands of specimens can be analyzed in a single study (Buckley et al., 2017b; Brown et al., 2021). ZooMS has proven valuable for expanding taxonomic resolution and identifying material suitable for further stable isotope, aDNA, and radiocarbon analysis (Buckley et al., 2017a, Buckley et al., 2017b; Antonosyan et al., 2024; Peters et al., 2025). Despite its growing global adoption, ZooMS has so far seen little direct application to late Quaternary megafauna extinctions; none of the studies in our sample employed this

widely used technique. Nonetheless, its potential is evident. For example, Antonosyan et al. (2024) recently successfully applied it to North America megafauna from museum legacy collections, while Peters et al. (2023, 2025) demonstrated protein survival beyond 50,000 years in subtropical Australia and developed peptide markers for three extinct Australian megafauna species (see also Buckley et al., 2017a).

Though still in its early stages, lipidomics holds potential as well. This technique has been used to detect hormones like testosterone in mammoth tusks (Cherney et al., 2023) and hair (Koren et al., 2018), offering unique insights into physiology and behavior. Collectively, biomolecular approaches can greatly enhance our ability to reconstruct species' biology, ecology, and evolutionary history, and are especially powerful when applied to poorly preserved or fragmentary remains that tend to dominate Quaternary fossil assemblages. Their wider integration into extinction studies could therefore substantially advance our understanding of megafauna extinctions.

Recent advancements in CT scanning and related imaging techniques (e.g., neutron scanning) has opened new avenues for non-destructive assessments of fossils (Smilg and Berger, 2015; Ziegler et al., 2020; Smith et al., 2021), though recent research cautions that micro-CT scanning may cause radiation damage in biomolecules which may impact downstream analyses (e.g., radiocarbon dating, aDNA) (Duval et al., 2025). Still, applying scanning methods such as these can be used to detect fossils encased in sedimentary material (e.g., breccia), elucidate the taphonomic and depositional histories of fossil assemblages, and minimize damage during fossil extraction (Smith et al., 2021).

On larger scales, drone-mounted LiDAR is significantly enhancing the efficiency and cost-effectiveness of field surveys (Maidment and Butler, 2025). Likewise, the integration of remote sensing with Geographical Information Systems (GIS) modelling has proven valuable for predicting the distribution of fossil-bearing sites, resulting in shorter survey times, lower costs, and substantially higher fossil recovery rates (Block et al., 2016; Maidment and Butler, 2025). Even smartphones are now fitted with 3D modelling and LiDAR software enabling rapid in-the-field scanning of sites and individual fossils and artefacts.

### Better management of modelling and uncertainty

Bringing all of these lines of evidence together will require advanced data science approaches. Answering questions about causality, for instance, requires causal modelling (McElreath, 2020), and time will be an important dimension in such models (Granger, 1980). Managing the uncertainties associated with time is paramount and previous approaches that neglect those uncertainties can no longer be considered sufficient (Carleton and Groucutt, 2021).

New Bayesian modelling approaches allow for the integration of uncertainties across datasets and can be used to account for, and propagate, measurement uncertainties and sampling uncertainties all the way through an analytical pipeline. As has been shown, simple regression models involving summed probability density functions (SPDs) and mean climate time series, can be deeply

misleading and fail to account for surprisingly large uncertainties that can be associated with both kinds of data (Carleton and Groucutt, 2021; Stewart et al., 2021, 2022; Crema, 2022).

As new approaches, like palaeoproteomics and aDNA, are added into the mix, the laboratory and sampling uncertainties associated with these approaches will have to be carefully considered. The uncertainties must be built into the models that are then used to test hypotheses about megafauna population and evolutionary dynamics. Ideally, these models will start with theoretical framing that guides modelling choices and frames models as expressions of theoretical processes (Shmueli, 2010), as opposed to data dredging and pattern recognition (hunting for correlations) that can easily distort our impressions of past ecological and human-faunal dynamics.

## Study limitations

We acknowledge several important limitations and biases that characterize our study. First, by including only English-language articles, we likely overlook important research published in other languages. Indeed, a recent survey found that much of the research on South American megafauna is published in low-reach gray literature (e.g., technical reports, working papers, government documents, academic theses) and local journals written in Latin languages (Bampi et al., 2024). This survey also revealed that more megafauna kill sites are reported in these sources than in English-language articles, suggesting that the perceived scarcity of kill sites in South America compared to North America is due to a language bias, not a lack of data. Similar biases are likely present elsewhere, such as in China and Russia, where it has been noted that few native-language archaeological publications are translated into English (Hein, 2016; Rouse et al., 2024). Consequently, our literature sample may have missed important themes and data in the megafauna extinction debate, particularly from regions like South America and China, where a significant body of research exists in native languages.

Another limitation is the narrow scope of our literature search, which was restricted to just WoS and Scopus. While these two databases are excellent for capturing peer-reviewed journal articles, they do not cover much of the literature found in global policy documents, such as reports, working papers, policy briefs, and other gray literature from think tanks, governmental agencies, and international organizations. So, while this review sought to provide an objective and comprehensive overview of the state of the field, it inevitably misses perspectives on late Quaternary extinctions from outside academia. A quick search on Policy Commons using our original search terms returned 557 publications, including 447 documents, 64 articles, nine theses, and seven books published in English, Spanish, Portuguese, German, and Welsh.

A third limitation of our study concerns the poor coverage of older articles in databases like WoS and Scopus. One of the goals of our review was to trace changes in how late Quaternary megafauna extinctions have been perceived and studied over time. However,

our literature sample included very few articles published before the turn of the millennium. More effort could have been made to locate older publications to offer a more complete view of the history of the debate.

## Data availability statement

The Python code used to prepare and analyze the data and conduct the network and citation analyses are available at <https://github.com/wccarleton/mfreview>.

## Author contributions

MS: Visualization, Data curation, Investigation, Formal analysis, Conceptualization, Project administration, Writing – review & editing, Writing – original draft, Methodology. CP: Conceptualization, Investigation, Writing – review & editing, Writing – original draft, Formal analysis. MZ: Investigation, Conceptualization, Writing – review & editing, Formal analysis. WC: Writing – review & editing, Formal analysis. PR: Writing – review & editing. NB: Writing – review & editing. HG: Writing – review & editing, Resources.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmamm.2025.1678231/full#supplementary-material>

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