FRONTIERS OF BIOGEOGRAPHY
The scientific journal of
The International Biogeography Society

Frontiers of Biogeography 18, 2025,
e135081 | DOI 10.21425/fob.18.135081

RESEARCH ARTICLE

Europe's lost landscape sculptors: Today's potential range of the extinct elephant *Palaeoloxodon antiquus*

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Editor Janet Franklin
Received 20 August 2024 ♦ **Accepted** 27 February 2025 ♦ **Published** 23 April 2025

Abstract

The straight-tusked elephant (*Palaeoloxodon antiquus*) was amongst the largest herbivores once engineering the European landscape on a continental scale. In combination with the glacial-interglacial cycles of the Pleistocene, the species was an integral part of the control regimes that shaped European flora and fauna. With the human-facilitated extinction of the straight-tusked elephant, these landscape-forming processes were lost during the last Glacial-Interglacial cycle. Given today's climate, could straight-tusked elephants still be part of modern ecosystems in Europe? And if yes, where? Answers to these questions can support nature conservation in preserving species and ecosystems historically adapted to these lost control regimes.

We reconstructed the realised niche of the straight-tusked elephant by allocating a novel compilation of fossil occurrences to either cold or warm stages, based on their assignment to Marine Isotope Stages. Further, we quantified the past potential distribution of the straight-tusked elephant since its extinction and its current potential distribution given the modern climate. Results show that the elephant could have persisted in the Mediterranean Basin until today and that modern climate across Central and Western Europe, excluding the Alps, as well as in the Mediterranean, is highly suitable for its occurrence.

Our results show that, without human-induced extinctions, European fauna would comprise extinct megafauna, acting as ecosystem engineers on a continental scale. Local rewilding initiatives aim at restoring these lost processes, but potentially cannot achieve lasting ecological effects on comparable scales.

Highlights

- The current European climate would still be suitable for the extinct straight-tusked elephant (*Palaeoloxodon antiquus*).
- The straight-tusked elephant could have persisted during the last Glacial-Interglacial cycle, considering past climate.
- Conserving the ecosystems shaped by the top-down ecosystem functions executed by the straight-tusked elephant in Europe may be especially promising in regions where the elephant could still exist today.
- Using reference cold and warm stages, based on Marine Isotope Stages in a Species Distribution Modelling framework, is a promising attempt to overcome dating uncertainties inhibiting more specific niche reconstructions of extinct species.

Keywords

Fossil, Late Quaternary Extinctions, Megafauna, Rewilding, Species Distribution Model

Introduction

Human-facilitated extinctions of large herbivores, so-called megafauna (defined as animals with a body mass ≥ 45 kg), lastingly altered biodiversity patterns and ecosystem structures (Allen et al. 2010; Faurby and Svenning 2015; Galetti et al. 2018; Bergman et al. 2023). Despite growing evidence for and acceptance of the assumption that megafaunal species could still exist today had they not been extinct, we still face difficulties in reconstructing and quantifying the niche of these extinct mammals precisely due to uncertainties inherent to palaeontological data (Varela et al. 2011; Faurby and Svenning 2015). Detailed knowledge of the niche of extinct species enables us to improve predictions on where the extinct species could still live today. Such regions can be particularly suitable for conserving ecosystem types or species that have been historically adapted to and selected for by the control regimes of extinct megafauna (Johnson 2009; Estes et al. 2011; Bakker et al. 2016). Furthermore, comparing niches of extinct species and their living relatives can help to understand extinction, evolutionary advantages and adaptation potentials (Fordham et al. 2024).

The straight-tusked elephant (*Palaeoloxodon antiquus*) dominated faunal assemblages of Central and Western Europe as one of the largest herbivores during the Interglacial periods of the Pleistocene (Koenigswald 2003, 2007; Johnson 2009). The species first originated in Africa before it entered Eurasia through the Levant ca. 800,000 to 600,000 years ago (Lister 2004). *P. antiquus* survived various Glacial-Interglacial cycles, but became extinct ca. 50,000 to 34,000 years ago, with the last local populations in the Iberian and the Mediterranean (Stuart 2005; Stuart and Lister 2007). Humans eventually drove the straight-tusked elephant to extinction, but presumably only when environmental changes had caused a reduction in population size and geographical range (Stuart 1991, 1999, 2005; Barnosky et al. 2004; Gaudzinski-Windheuser et al. 2023). During the approximately 700,000 years before its extinction, the straight-tusked elephant likely prevailed in the Mediterranean Region due to suitable environmental conditions during Interglacial as well as Glacial periods. Likewise, there is abundant information on the migration and occurrence of the straight-tusked elephant in Central, Western and Eastern Europe during interglacial climate conditions (Koenigswald 2003, 2007; Pushkina 2007).

The species is generally described as adapted to temperate climate conditions in woodlands or mixed habitats with a mixed browse and graze diet (Lister 2004). Tooth microwear analyses propose that individuals of the species turned from graze-dominated mixed feeders into leaf browsers over the course from the Middle Pleistocene to the Late Pleistocene. This dietary breadth allowed for an adaptation to different environmental and vegetational circumstances (Rivals et al. 2012). Morphological reconstructions of fossil finds draw an impressive picture of an elephant which, as an adult male, can grow to about 370–450 cm high while weighing about 10–15 tonnes and having body hair comparable to the extant *Elephas maximus* (Palombo et al. 2010; Schauer 2010; Larramendi 2016). DNA analyses identified the African forest elephant (*Loxodonta cyclotis*) and the African bush elephant (*Loxodonta africana*) as the closest extant relatives of *P. antiquus* (Meyer et al. 2017; Palkopoulou et al. 2018). Extant elephants are ecosystem engineers that substantially impact their environment by trampling, digging, burrowing etc. (Pringle 2008; Haynes 2012). Keeping these ecosystem functions in mind and recognising the physical size of the straight-tusked elephant, the extinct species must have been a comparable ecosystem engineer. In combination with the alternating interglacial and glacial periods during the Pleistocene, these abiotic and biotic controls presumably established a mosaic of dense and light wooded landscapes in Europe (Bradshaw et al. 2003; Allen et al. 2010; Bråthen et al. 2021; Pearce et al. 2023).

In this study, we aim to quantify the realised environmental niche of the extinct straight-tusked elephant by combining its fossil record with palaeoclimate reconstructions. We chose the species as a model species because of its presumably distinctive role in shaping European ecosystems during the Pleistocene. Moreover, the fossil record of the straight-tusked elephant comprises over a hundred finds in Eurasia, which we consider an adequate dataset for niche reconstruction. Generally, occurrences of fossils are often rare and scattered across time, as well as hard to date accurately. These circumstances make it difficult to correlate fossil finds with precise palaeoclimate reconstructions directly (Varela et al. 2011; Nanglu and Cullen 2023). Moreover, precise and high-resolution palaeoclimate reconstructions typically focus on specific time intervals. To address these issues, fossil occurrences can be grouped into Marine Isotope Stages (MIS), which correspond to glacial or interglacial periods characterised by distinct environmental conditions. Moreover, the repeatedly occurring glacial and interglacial periods of the Pleistocene are characterised by comparable environmental conditions to each other (Lisiecki and Raymo 2005). Thus, MIS allow for comparing long, non-consecutive periods in time during which similar environmental conditions prevailed. This holds true not only for the past, but also for the present: by identifying reference periods in the past during which environmental conditions must have been comparable to today, palaeontology can add to understanding the history of today's ecosystems and discover processes relevant to nature conservation today.

We hypothesised that the straight-tusked elephant could have persisted in the European climate of the past 45,000 years and that current climatic conditions in Western and Central Europe would be suitable for the straight-tusked elephant, based on range reconstructions of Faurby and Svenning (2015). This study hence quantified the realised environmental niche of the straight-tusked elephant (*Palaeoloxodon antiquus*) by linking fossil occurrences to environmental gradients of either cold or warm stages within a Species Distribution Model (SDM) framework. We compiled a new list of fossil finds of the straight-tusked elephant to increase the amount of data available for our analysis. By pooling fossil occurrences into cold and warm stages, we ensured that the resulting dataset had sufficient occurrences associated with comparable environmental conditions to estimate the species' realised niche robustly. Furthermore, the pooling enabled us to use precise palaeoclimate reconstructions that are only available for specific time intervals of the Pleistocene. We then predicted the geographic distribution of the straight-tusked elephant in 1,000-year steps since its potential extinction using a spatially coarser palaeoclimate dataset. We estimated the current potential distribution using a high-resolution dataset for modern climate.

Given the past climate, the straight-tusked elephant could have persisted in a distinctly reduced and fragmented suitable habitat in Europe during the Last Glacial Maximum (LGM). Given the current climate, the straight-tusked elephant could still exist in large parts of Europe today. In these regions, the conservation of ecosystem types and floral species that are adapted to the control regimes of extinct megafauna may be especially promising. It is generally recognised that ecological processes driving adaptation and selection in nature have changed since the Quaternary and that humans have had a considerable share in this change. As today's flora and fauna have been shaped by Quaternary processes, understanding these altered processes is crucial for adopting adequate nature conservation measures (Delcourt and Delcourt 1988; Otto 2018; Rull 2020).

Materials and methods

The primary analysis of the study is a Species Distribution Model (SDM), a standard method in neo-ecological research (Fig. 1). The first step of the analysis is to construct a realised niche of species, based on its known occurrence in environmental space. Then, the species distribution is estimated in the region of interest, based on the geographical distribution of the environmental space (Guisan and Zimmermann 2000). Since the straight-tusked elephant is an extinct species, our analysis is based on its fossil record and reconstructed palaeoclimate data. Applying SDMs to palaeontological data and estimating realised niches of extinct species is challenging because of many biases inherent to palaeontological data (Varela et al. 2011). The following sections will explain in detail which modelling assumptions we made to meet and overcome these challenges.

Occurrence data of the straight-tusked elephant (*Palaeoloxodon antiquus*)

We can only use a fossil occurrence of the straight-tusked elephant in our SDM framework if we can confidently match it with the environmental space in which the individual corresponding to the fossil must have lived. The environmental space is determined by when and where the individual has lived. First, we assume that the site of find of the fossil lies within the home range of the individual. Hence, only fossil finds with recent coordinates specifying the site of find are part of our dataset. Second, determining confidently when the individual has lived is difficult because ages of fossils are typically estimated with uncertainties many times greater than the lifespan of the species. Ages of fossils that originated during the past ~ 50,000 years can be determined quite accurately by the Accelerator Mass Spectroscopy (AMS) radiocarbon (^{14}C) dating method (Zhang et al. 2019), but the majority of fossils of the straight-tusked elephant originated earlier. Age estimates for older fossils are often obtained, based on index fossils and other stratigraphic or environmental evidence. This also includes the assignment of fossils to MIS, which enables researchers to correlate the fossil findings with a specific climatic context. We use this assignment to MIS that represent cold or warm stages to overcome dating uncertainty. The MIS assignment allows for a reasonable inference of the prevailing climate during the time of deposition – even when precise dating is unavailable – and reduces the complexity associated with interpreting ambiguous dating results. Thus, only fossil finds of the straight-tusked elephant that had age estimates falling within a MIS or were confidently attributed to either a cold or a warm stage, are part of our dataset.

Data on fossil occurrences of the straight-tusked elephant (*Palaeoloxodon antiquus*) (Zeonodo repository: 10.5281/zenodo.10953345) were synthesised from an exhaustive literature review including archaeological sites that contain fossil remains of the straight-tusked elephant, the New and Old Worlds Database of fossil mammals (NOW; http://nowdatabase.org/now/database) (The NOW Community 2023) and the Paleobiology Database (PBDB; http://paleobiodb.org/#) (Fig. 1A). German, English, French, Italian, Spanish and Portuguese literature were included. Language barriers aggravated the review of archaeological sites, especially in the East, including Eurasia and the Middle East. Therefore, data in these regions are primarily based on synoptic articles available in English (Markova 2000, 2007; Pushkina 2007; Mauch Lenardić 2012; Pawłowska 2015; Zastrozhnov et al. 2018). Stated age determinations included absolute dating methods (Uranium Series, Electron Spin Resonance, Thermoluminescence, Optically Stimulated Luminescence, Amino Acid Racemization, Radiocarbon), palaeomagnetism, biostratigraphical as well as archaeological considerations. To avoid duplicates originating from merging data from different sources, we applied the following additional curation steps only to the fossil finds that fulfilled the aforementioned criteria on geographical information and age estimation: fossil finds with identical site names, coordinates (up to two decimal places) and age estimates were considered as identical records. For fossil finds from sites near one another within one country, references recorded in the databases were compared with the results of the literature review. Metadata such as site name, age estimates and cross-reference to author groups were compared to rank fossil finds as "no duplicate", "likely no

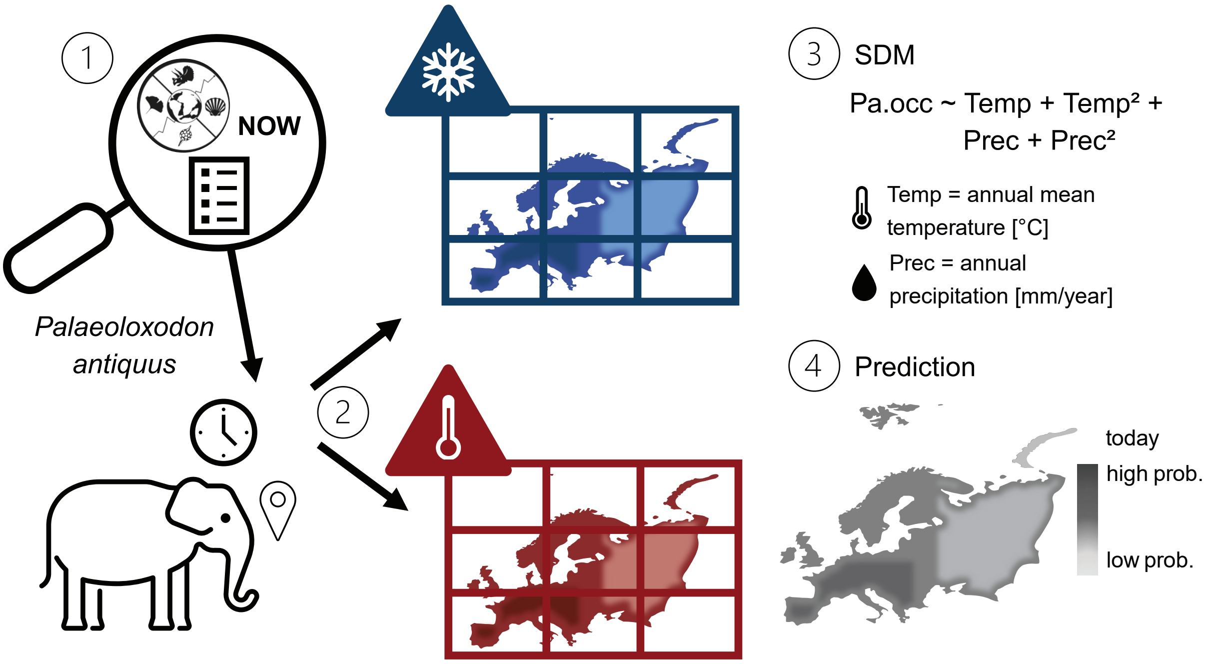

Figure 1. Schematic sketch of the methodological workflow. **A.** Data collection from existing literature, the New and Old Worlds Database of fossil mammals (NOW) and the Paleobiology Database (PBDB) as well as preprocessing. **B.** Matching the fossil occurrences of the straight-tusked elephant (*Palaeoloxodon antiquus*) with known age and location information to the respective local environmental conditions of either a cold or a warm stage. **C.** Building the Species Distribution Model (SDM). **D.** Predicting the potential distribution of the straight-tusked elephant in Europe, given the modern climate.

duplicate", "likely duplicate" or "duplicate". Consistency in naming sites of fossil finds within similar author groups was assumed. Only fossil finds ranked as "no duplicate" or "likely no duplicate" were used in the SDM (Zeonodo repository: https:/doi.org/10.5281/zenodo.10953345).

Overall, we found 288 reported occurrences of the straight-tusked elephant in Eurasia, out of which 119 could be confidently attributed to one MIS and contained precise geographical information about the site of the fossil find (Fig. 2). One hundred and five of these occurrences originated from interglacial sediments, whereas only 14 occurrences originated from glacial sediments. The oldest fossils of the straight-tusked elephant were attributed to MIS 19, whereas the youngest fossils of the straight-tusked elephant were attributed to MIS 3. Most interglacial occurrences were attributed to MIS 5, which started 130,000 years ago and ended 71,000 years ago and describes the Last Interglacial Period (Fig. 3).

Assigning fossils of the straight-tusked elephant to environments of cold or warm stages

The chronostratigraphic division of the Pleistocene into MIS has been under constant reappraisal and development and has, thus, not always been used consistently (Lisiecki and Raymo 2005; Railsback et al. 2015). What appears universally accepted is that, at a 100,000-cyclicity, a sharp transition from glacial to interglacial conditions occurred during the Mid-Pleistocene (Past Interglacials Working Group of PAGES 2016). However, the transition back to glacial conditions is less obvious and, thus, the exact duration of Interglacial stages remains under debate (Past Interglacials Working Group of PAGES 2016). In the MIS nomenclature, Glacial stages are even-numbered, while Interglacial stages are odd-numbered (Railsback et al. 2015; Past Interglacials Working Group of PAGES 2016), except MIS 3, which is generally accepted to be no Interglacial stage (Railsback et al. 2015) and, thus, was handled as a glacial stage in our analysis. We followed the general attribution of odd-numbered MIS to Interglacial stages (i.e. warm stage) and even-numbered MIS to Glacial stages (i.e. cold stage) (Fig. 1B). Consequently, some fossil occurrences originating from climatic transition phases were probably assigned to more extreme climatic conditions of either a warm or a cold stage, which could lead to overestimating the species' tolerance to climatic extremes.

Another reason for pooling the fossil finds into warm or cold stages is that, in this way, we can use the spatially highest resolved palaeoclimate reconstructions that are typically only available for specific intervals of the past, i.e. the LGM or the Last Interglacial period (Otto-Bliesner et al. 2006; Karger et al. 2017). Our underlying assumption is that the environmental conditions among warm and cold stages during the lifespan of the straight-tusked elephant were comparable. This assumption is backed up by global dO18 reconstructions and their concurrence with chrono-stratigraphical evidence from Central Europe (Fig. 3) (Lisiecki and Raymo 2005; Szymanek and Julien 2018). While temporally higher resolved reconstructions of past climate exist, they lack spatial accuracy (Krapp

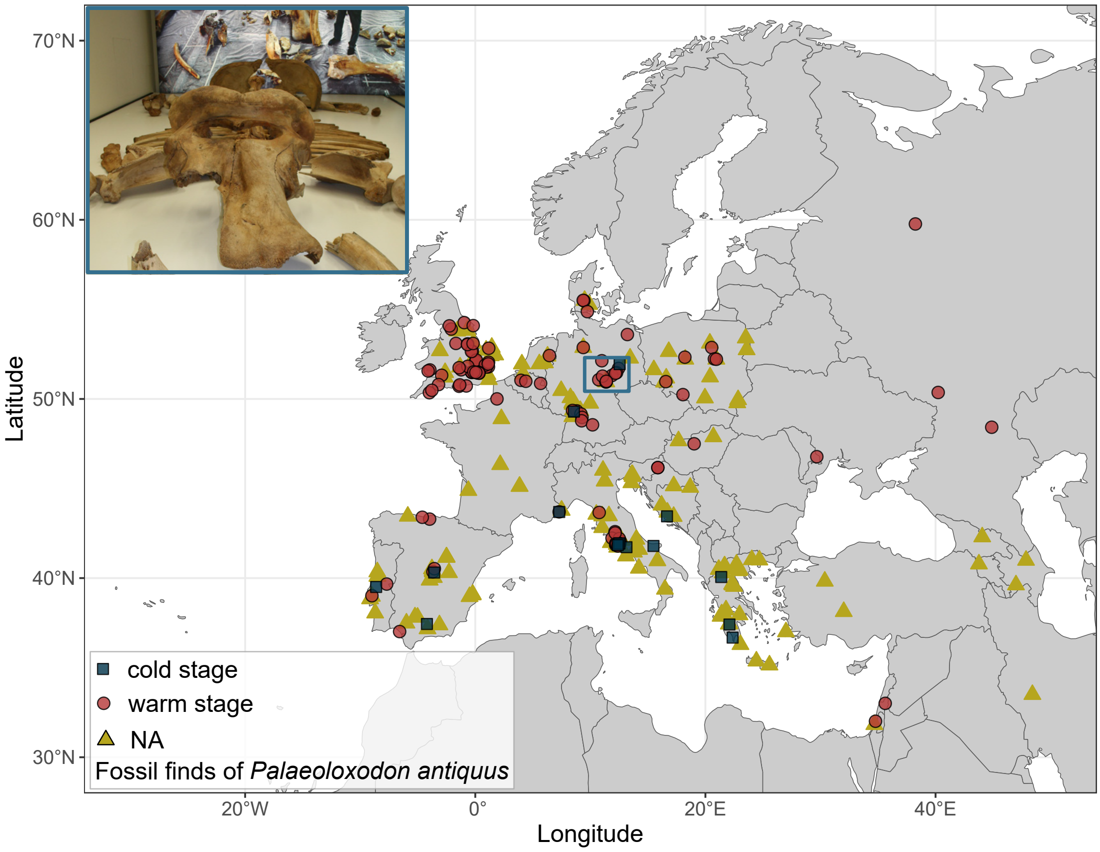

Figure 2. All sites of the find of fossils of the straight-tusked elephant (*Palaeoloxodon antiquus*) (n = 288). Red triangles represent the findings assigned to a warm stage, i.e. Interglacial Periods (n = 105). Blue squares represent the findings assigned to a cold stage, i.e. Glacial Periods (n = 14) and yellow dots represent findings that could not be assigned confidently to either a warm or a cold stage and, thus, were excluded from the analysis (n = 169). The picture shows a skeleton of *P. antiquus* from Neumark-Nord 1, Germany (taken and cropped from Einsamer Schütze/Wikimedia Commons CC BY-SA 2010). Its geographic location is indicated by the blue rectangle in the map.

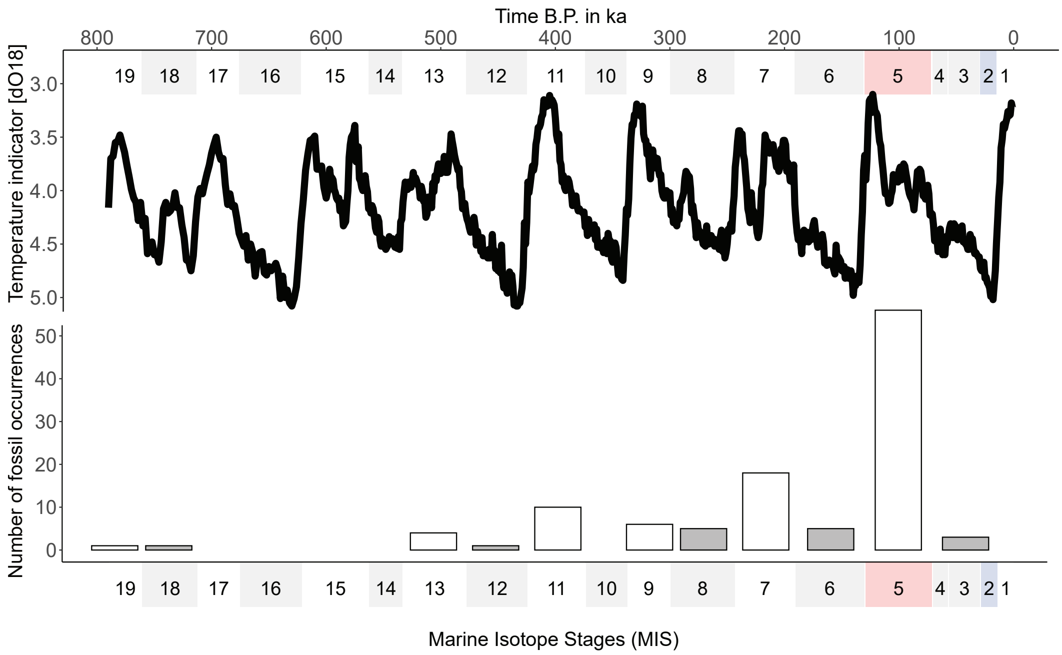

Figure 3. Upper half: Reconstructed temperature fluctuations, based on the dO18 proxy (Lisiecki and Raymo 2005) for the assumed period in which the straight-tusked elephant (*Palaeoloxodon antiquus*) lived in Europe. Lower half: Number of *P. antiquus* fossil occurrences used in the analysis per MIS. White-shaded MIS represent interglacial periods and grey-shaded MIS represent glacial periods. Red indicates MIS5, i.e. the Last Interglacial, used as a climatic reference for warm stages. Blue indicates MIS2, i.e. the Last Glacial Maximum, used as a climatic reference for cold stages.

et al. 2021). Given the fact that ages of fossils cannot be determined with pinpoint accuracy anyhow, we argue that reconstructing the realised environmental niche of the straight-tusked elephants from reconstructions of mean environmental conditions during warm and cold stages are appropriate approximations of past living environments.

Environmental data

Georeferenced climate data from the Last Glacial Maximum (LGM) supplied by CHELSA served as a proxy for cold stages (Karger et al. 2017), while data from the Last Interglacial served as a proxy for warm stages (Otto-Bliesner et al. 2006). CHELSA data on the current climate was used for inferences about today's potential distribution of the straight-tusked elephant in Europe (Karger et al. 2017). All data were downloaded pre-processed from www.paleoclim.org on 23.02.2024 (Brown et al. 2018). The data included the bioclim variables bio_1, i.e. annual mean temperature in °C × 10, and bio_12, i.e. annual precipitation in mm/year, for each time period at the same spatial extent and resolution (2.5 × 2.5 arcmins). The data were cropped to a spatial extent of xmin = -15, xmax = 50, ymin = 30 and ymax = 70 covering Eurasia (Suppl. material 1). Temperature values were divided by ten to obtain values in °C. Notably, the straight-tusked elephant has already been extinct during the LGM. However, we decided to use the LGM dataset for the reasons and assumptions mentioned in the previous section. We also ran the model on a coarser climate dataset from MIS6, from which fossils of the straight-tusked elephant were found, and did not obtain distinctly different results (Suppl. material 1).

We predicted the potential distribution of the straight-tusked elephant in 1,000-year steps since its extinction using the climate dataset by Krapp et al. (2021). The dataset spans the past 45,000 years to the present, i.e. 1950, and was downloaded through the R package pastclim (Krapp et al. 2021; Leonardi et al. 2023). The spatial resolution of this dataset is 30 × 30 arcmins and, thus, lower than the resolution of the datasets used for training our model. It was cropped to the same spatial extent as the other environmental datasets. Temperature values were already stated in °C.

We included annual mean temperature and annual precipitation as the essential independent variables in the SDM, as reconstructions of temperature are considered more reliable than reconstructions of precipitation and mean values are considered more reliable than extreme values (Kageyama et al. 2006; Harrison et al. 2015; Karger et al. 2023). Nevertheless, we further included precipitation as a predictor variable since the distribution of extant elephants appears to be constrained by water availability and vegetation characteristics (Chamaillé-Jammes et al. 2007; Smit et al. 2007; De Knegt et al. 2011). Since environmental conditions influence the productivity and composition of vegetation, the responsiveness of the species to precipitation variables can mask its response to food availability. Specifically, during glacial stages, not only lower temperatures, but also lower atmospheric CO_2 levels are affecting primary production. While lower temperatures generally increase the water use efficiency of plants, lower CO_2 levels decrease the very same. These opposing effects may cancel each other out but can evidently change the composition of vegetation communities in specific landscapes (Cowling et al. 2020; Grobler et al. 2023). Thus, the correlation between environmental variables and the presence of the species may be partially indirect and mask the direct correlation with food availability that most likely differed between cold and warm stages, while our model assumes a similar response of the species across both stages.

Species distribution modelling

We modelled the environmental niche of the straight-tusked elephant using a binomial generalised linear model (GLM) that predicted the likelihood of occurrence of the straight-tusked elephant in a respective raster cell, based on fossil finds and the climate variables of annual mean temperature and annual precipitation (Fig. 1C, D). We implemented explanatory variables as polynomials to allow for a hump-shaped relationship between species occurrence and climate (for detailed information on using GLMs in SDM, see Guisan and Zimmermann (2000) and Guisan et al. (2002)).

A GLM requires absence values to predict the likelihood of occurrence given a specific combination of climatic variables. We used two different approaches to create 106 random pseudo-absences for warm stages and 15 random pseudo-absences for cold stages. The first approach was to randomly draw raster-cell values from our two climatic datasets (see result in Suppl. material 1). For the second approach, we narrowed down the spatial extent from which pseudo-absences were randomly drawn to the area in which fossil occurrences were found in Europe (extent of xmin = -11, xmax = 68, ymin = 22.5 and ymax = 61) (see results in Result section). Further, high similarity in dispersal barriers, competition and further biotic factors during the former lifetime of the straight-tusked elephant and today were assumed.

All analyses were implemented in R (version 4.3.2) (R Core Team 2023) using the packages tidyverse (version 2.0.0) (Wickham et al. 2019), sf (version 1.0.15) (Pebesma 2018), raster (version 3.6.26) (Hijmans et al. 2023b) and dismo (version 1.3.14) (Hijmans et al. 2023a), terra (version 1.7.65) (Hijmans et al. 2024) and pastclim (version 2.0.0) (Leonardi et al. 2023).

Results

Current potential distribution of the straight-tusked elephant

The current potential distribution of the straight-tusked elephant (*Palaeoloxodon antiquus*) is centralised in Western and Central Europe (Fig. 4). The modern climate would be highly suitable for the straight-tusked elephant along the West Coast of Europe, reaching into the interior up to the Alps and in Great Britain. The northernmost current potential distribution spanned all Denmark, including the southern area of Sweden. In southern Sweden and Eastern European countries, the predicted likelihood of occurrence for the straight-tusked elephant was still high and gradually declined towards Russia. In the Southeast, the current potential distribution extended slightly further than the Black Sea. The current southernmost potential distribution spanned all Türkiye, with a higher likelihood of presence at the coasts than in the country's interior.

The probability of presence was also high at the coastline of the Levantine and parts of the North African Mediterranean coastline, but depicted a clear cut towards the continental interior. The modern climate would also be highly suitable for the straight-tusked elephant in the Mediterranean Region, comprising Greece, Italy and the Balkan Region, as well as the Iberian Peninsula. In general, the modern climate along the coastlines of Europe, as well as in Western and Central Europe, would be highly suitable for the straight-tusked elephant. Meanwhile, the likelihood of occurrence for straight-tusked elephants was much lower in mountainous regions (the Alps, the Caucasus Mountains, the Carpathians and the Pyrenees) (Fig. 4). The same pattern was obtained when pseudo-absences were sampled randomly from the entire study area (Suppl. material 1).

Potential distribution of the straight-tusked elephant during the Last Glacial Maximum (LGM)

Climatic conditions during the LGM were fragmenting the suitable habitat for the straight-tusked elephant (Fig. 5).

Between 34,000 and 18,000 years ago, the potential distribution of straight-tusked elephants in Europe was the lowest. 14,000 years ago, climatic conditions offered a suitable habitat for the straight-tusked elephant at comparable scales to those of 46,000 years ago. Hence, for over 30,000 years, climatic change had distinctly reduced the suitable habitat for straight-tusked elephants in Europe. The SDM highlights the Mediterranean coastlines, including the African and Turkish coasts, as the most suitable habitat for the straight-tusked elephant during this period (Fig. 5; Suppl. material 1).

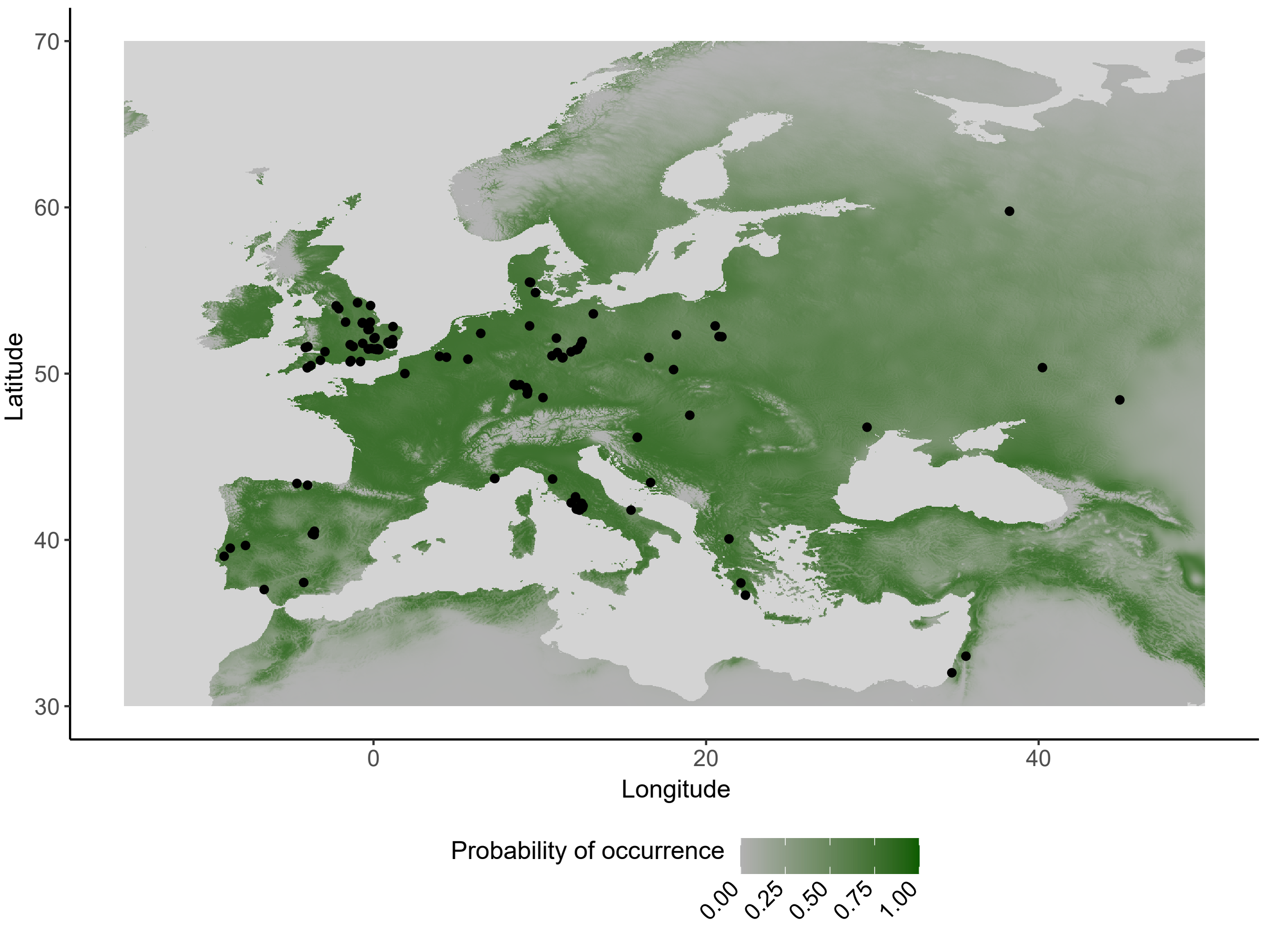

Figure 4. Current potential distribution of the straight-tusked elephant (*Palaeoloxodon antiquus*) in Europe. The probability of occurrence ranges from 0.0 (grey regions) to 1.0 (strong green regions). Black points indicate sites of finding *P. antiquus* fossils that were used to train the species distribution model. Note that the probability of occurrence is a relative indicator, with the absolute value defined by the ratio between presence and absence points.

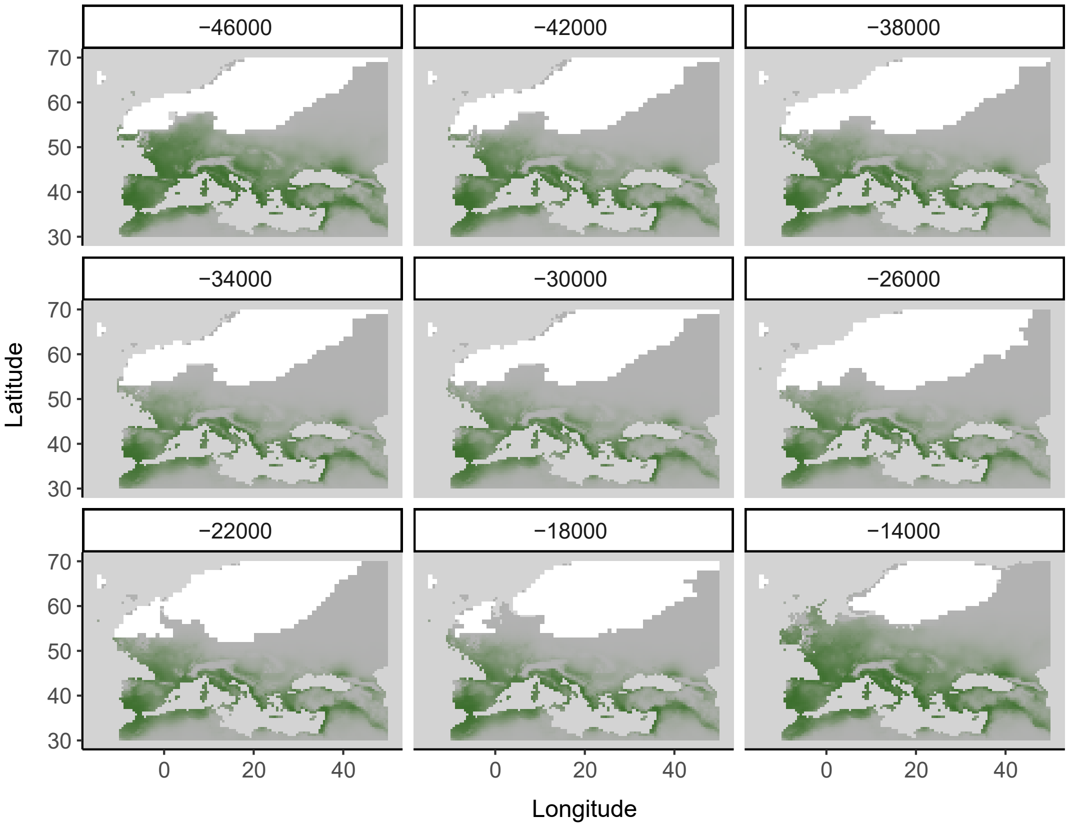

Figure 5. Potential distribution of the straight-tusked elephant (*Palaeoloxodon antiquus*) during and after its extinction in Europe. The probability of occurrence ranges from 0.0 (grey regions) to 1.0 (strong green regions). Ice sheets are plotted in white. Note that the probability of occurrence is a relative indicator, with the absolute value defined by the ratio between presence and absence points. The titles of the panels state the time before present, i.e. 1950.

Discussion

For nearly a million years, the straight-tusked elephant (*Palaeoloxodon antiquus*) roamed Europe and profoundly shaped its ecosystems (Palombo et al. 2010; Schauer 2010). Seasonal climate likely drove their migration dynamics, as observed in their living relatives, connecting diverse landscapes across the continent (Koenigswald 2003; Bohrer et al. 2014). By browsing intensively in specific regions for limited periods, they modified local vegetation, dispersed seeds and cycled nutrients on a continental scale (Owen-Smith 1999; Pringle 2008; Blake et al. 2009; Johnson 2009; Doughty et al. 2016; Pires et al. 2018). The removal of this keystone species from ecosystems due to extinction — likely driven by climatic shifts and human pressures — triggered significant ecological consequences. Vegetation structures transformed, trophic systems were downgraded and the loss of interconnected ecological interactions resulted in co-extinctions (Estes et al. 2011; Terborgh 2013; Bakker et al. 2016; Svenning et al. 2016; Galetti et al. 2018).

Our results show that much of Europe, where the straight-tusked elephant once thrived, would remain climatically suitable for this species today, highlighting the potential of these regions to support ecosystems adapted to the lost control regimes of extinct megafauna. This finding is in line with existing range estimates of the straight-tusked elephant based on fossil co-occurrence, but reports a more nuanced picture of the currently suitable habitat (Faurby and Svenning 2015; Suppl. material 1). Further, our predictions of the potential distribution of the straight-tusked elephant during the LGM support the notion that climatic conditions during Glacial periods forced straight-tusked elephants back to the Mediterranean Basin, but did not impede their survival in Europe (Stuart 1991, 1999, 2005; Barnosky et al. 2004). Evidence is thus growing that megafauna, which had lived in most parts of Europe and shaped vegetation structures before human arrival, could still persist today (Johnson 2009; Sandom et al. 2014; Bakker et al. 2016; Markova and Puzachenko 2018). Multiple sources of evidence, such as fossil pollen records or faunal fossil finds, support the assumption that European ecosystems consisted of more open woodland patches and larger herbivore populations during the Last Interglacial Period (MIS5e, 129,000–126,000 years ago) than in the early Holocene (Sandom et al. 2014; Markova and Puzachenko 2018; Pearce et al. 2023). Moreover, European plant species adapted to more open habitats, such as the diverse groups of forbs, would presumably profit from megafaunal activities comparable to those of the Pleistocene (Bråthen et al. 2021). Modern conservation strategies in Europe, which primarily aim to shield biodiversity from human activities through protected areas (European Commission 2022), likely fail to re-establish the lost control regimes that large megafauna exerted in the past (Perino et al. 2019). Restoring these ecological processes would require a paradigm shift in how we approach biodiversity conservation and ecosystem management.

Rewilding complex ecosystems could constitute such a shift, offering a promising approach to restoring ecological processes and biodiversity in regions where megafauna like the straight-tusked elephant once thrived (Perino et al. 2019). Rewilding emphasises the restoration of self-sustaining and complex ecosystems by re-instating natural processes and, where appropriate, re-introducing missing species (Carver et al. 2021; Mutillod et al. 2024). Current rewilding initiatives have introduced large herbivores such as bison, cattle and wild horses in an attempt to re-establish lost control regimes in ecosystems (Cromsigt et al. 2018; Dvorský et al. 2022; Hart et al. 2023). However, the effectiveness of such surrogates in fully replicating the ecological roles of extinct megafauna, such as the straight-tusked elephant, is debated for at least three non-mutually exclusive reasons (Hart et al. 2023; Pringle et al. 2023; Lundgren et al. 2024).

[1] While the climate may still be suitable, the ecological processes shaping adaptation and selection in nature have shifted considerably since the Quaternary, mainly due to human influences (Otto 2018; Rull 2020). Additionally, co-extinctions of other species that depended on the straight-tusked elephant, for example, predators, parasites or dung beetles, followed its extinction (Galetti et al. 2018). Thus, whole ecological networks and their ecological dynamics no longer exist today. Whether the re-introduction of single megafaunal species would re-establish the lost control regimes of these past ecological networks remains in question.

[2] Large-scale migration dynamics that once connected European ecosystems are no longer feasible in today's fragmented landscapes. Unlike in the past, where straight-tusked elephants migrated across the continent in response to seasonal changes, current rewilding initiatives are limited to confined spaces (Cromsigt et al. 2018; Dvorský et al. 2022; Hart et al. 2023). Consequently, essential spatial processes such as seed dispersal and nutrient redistribution remain inhibited. The dense human population and extensive infrastructure in Europe further impede the re-establishment of continental-scale migrations. Attempts to restore such dynamics would not only be impractical, but could also lead to significant societal conflicts, as observed with large herbivore migrations in other parts of the world (Hoare 2000; Shaffer et al. 2019; Hart et al. 2023).

[3] The functional space of rewilded faunal assemblages often just partially overlaps with the functional space of extinct faunal assemblages. Rewilding can expand the functional space of current faunal assemblages and increase their similarity to those of extinct communities (Lundgren et al. 2020, 2024; Hedberg et al. 2022), but the largest herbivores are frequently found to be functionally irreplaceable. Therefore, entirely substituting the ecological roles of extinct megafauna remains challenging (Pringle et al. 2023).

While rewilding efforts are, therefore, promising and valuable, their ability to fully restore the ecological roles of extinct megafauna is inherently limited by the profound changes in landscape structure, species interactions and migration dynamics that have reshaped modern ecosystems. Comparisons of the straight-tusked elephant's reconstructed niche with that of its closest living relatives, *L. cyclotis* and *L. africana*, reveal that the extinct species occupied colder habitats. The precipitation niche of the straight-tusked elephant is narrow and centres around lower mean precipitation levels, but lies within the precipitation niche of its living relatives (Suppl. material 1). While other extant elephants might share a closer environmental overlap, this highlights the difficulty of identifying species capable of fulfilling the environmental and functional roles of extinct ecosystem engineers. Hence, it remains questionable whether the re-introduction of large herbivores can fully re-establish the ecological functions and dynamics of species like the straight-tusked elephant once shaped on a continental scale.

Our analysis has several limitations and potential biases that warrant consideration. Recent studies have demonstrated that seasonal extremes of climatic variables, rather than annual means, play a significant role in determining the geographical distributions of extant elephants (Zacarias and Loyola 2018; Kanagaraj et al. 2019; Dejene et al. 2021) and likely influenced the distributions of extinct megafauna as well (Koenigswald 2003). Consequently, our results may underestimate the realised niche of the straight-tusked elephant, as seasonal extremes might better explain some fossil occurrences. However, the uncertainties inherent in reconstructed palaeoclimatic variables may limit the accuracy of models that include these factors. Further, the species distribution model employed here makes simplified assumptions about the relationship between environmental variables and the occurrence of the straight-tusked elephant. While increasing model complexity by incorporating additional variables or seasonal extremes could refine niche estimates, such approaches depend on assumptions that uncertainties in palaeoecological data are negligible — a premise that is difficult to justify given the high dating uncertainties and inherent biases in fossil and climate data. Further, our SDM only considers environmental, but not biotic predictors. Other neighbouring proboscideans may have limited the natural distribution of the straight-tusked elephant (but see Lister (2004), Rivals et al. (2012) and Saarinen and Lister (2016)). For instance, *Mammuthus* dominated the so-called glacial faunal assemblage in Eastern Europe and Siberia (Koenigswald 2003) and several related species are also reported from Asia, for example, *Palaeoloxodon turkmenicus*, *Palaeoloxodon namadicus* and *Palaeoloxodon naumanni* (Pushkina 2007). Nevertheless, we believe that our model's balance of simplicity and confidence in the data provides a robust framework for interpreting patterns in the available evidence. Finally, discrepancies between empirical findings from the fossil record and our model predictions might suggest limitations in our approach to fully capturing the realised niche of the straight-tusked elephant. For instance, while our model predicts high probabilities of the straight-tusked elephant's presence in regions such as southern Sweden, the Baltic countries, Ireland and North Africa, no fossil evidence currently supports these occurrences. In some cases, such as Sweden and the Baltics, glacial activity may have prevented fossil preservation, while in North Africa, competition or hybridisation with other proboscideans may have limited the species' establishment despite suitable habitat (Palkopoulou et al. 2018). Furthermore, the taxonomy of *P. antiquus* has been revised repeatedly and first evidence suggests that both the Asian and the European straight-tusked elephants may belong to the same population (Lin et al. 2023). If one population of straight-tusked elephants was widely distributed across Eurasia, then their niche was most likely wider than reconstructed in this study. While our findings provide valuable insights into the potential distribution and realised niche of the straight-tusked elephant, they also highlight the complexities and uncertainties inherent in reconstructing past ecological dynamics, underscoring the need for continued refinement of models and further exploration of the fossil record. Finally, we believe that improving data availability and quality in palaeontology offers vast potential to contribute to a general understanding of modern ecosystems essential for their conservation.

Conclusions

To conclude, our findings suggest that, under current climatic conditions, European ecosystems could include extinct megafauna, such as the straight-tusked elephant. Ecosystems shaped by the control regimes of such megafauna may still possess the resilience and capacity for self-sustainability today. However, while megafauna diversity and distribution are notably reduced compared to the Pleistocene, protecting nature from human interference alone does not restore the lost control regimes. Rewilding, though promising, must be approached with caution due to two key challenges: first, our understanding of the ecological processes that have shaped modern ecosystems, particularly the role of megafaunal ecosystem engineers, remains incomplete. Second, the re-introduction of large herbivores as surrogates for extinct megafauna is unlikely to fully replicate the ecological functions and dynamics once driven by species like the straight-tusked elephant due to profound changes in landscape structure, species interactions and migration dynamics that have reshaped contemporary ecosystems. Thus, while rewilding can diversify functional space in current ecosystems, its potential to fully restore the intricate ecological roles of extinct species on a continental scale remains in question.

Acknowledgements

F.G., G.M. and M.J.S. were supported by the Deutsche Forschungsgemeinschaft (KI 806/16–1 and STE 2360/2-1) embedded in the Research Unit TERSANE (FOR 2332: Temperature-related stressors as a unifying principle in ancient extinctions). We sincerely thank our anonymous reviewers and our editor Janet Franklin for their constructive and insightful feedback, which has significantly improved this manuscript. Funded by the Open Access Publishing Fund of the University of Bayreuth.

Author contributions

Study design: MJS, CM, FG, GM; Data collection: CM, PP, FG; Data analysis: FG, CM, GM, MJS; Visualisation: FG, PP, MJS; Writing: FG, CM, GM, PP, MJS; Editing and Approving: FG, PP, GM, MJS, CM.

Data accessibility statement

All data and R scripts are publicly available on Zenodo (10.5281/zenodo.10953345). Fossil occurrences of the straight-tusked elephant (*Palaeoloxodon antiquus*) that are presently not entered in the Paleobiology Database (PBPDB, https://paleobiodb.org/#/), but are part of our compiled data, will be entered in the PBDB.

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Supplementary materials

Supplementary material 1

Supplementary figures S1–S10 (.docx)

Link: https://doi.org/10.21425/fob.18.135081.suppl1