Extinction of the woolly mammoth in Beringia has long been subject to research and speculation. Here we use a new geo-referenced database of radiocarbon-dated evidence to show that mammoths were abundant in the open-habitat of Marine Isotope Stage 3 (~45–30 ka). During the Last Glacial Maximum (~25–20 ka), northern populations declined while those in interior Siberia increased. Northern mammoths increased after the glacial maximum, but declined at and after the Younger Dryas (~12.9–11.5 ka). Remaining continental mammoths, now concentrated in the north, disappeared in the early Holocene with development of extensive peatlands, wet tundra, birch shrubland and coniferous forest. Long sympatry in Siberia suggests that humans may be best seen as a synergistic cofactor in that extirpation. The extinction of island populations occurred at ~4 ka. Mammoth extinction was not due to a single cause, but followed a long trajectory in concert with changes in climate, habitat and human presence.
Woolly mammoth (*Mammuthus primigenius* Blum.) were abundant in Beringia during the late Pleistocene before disappearing in the Holocene, and their extinction remains of wide interest and speculation1–13. The Pleistocene environment they occupied is often referred to as ‘mammoth steppe’, although the nature and chronology of this habitat has been debated14–19. Extinction has been attributed to one or a combination1,2,3,8 of factors including over-hunting by humans1,5,7,13, ecological displacement during the transition from the Last Glacial Maximum (LGM) to the warm and stable Holocene1,6,9, or impact by an extraterrestrial object11 at the time of the Younger Dryas (YD) climatic oscillation.

We reconstructed the detailed pattern of extinction in Beringia, the last redoubt of the mammoths, and examine these various extinction hypotheses by comparing spatially and temporally the changes in mammoth populations relative to environmental changes over the past 45 ka (45,000 cal. years before present) using a georeferenced radiocarbon database of 1,323 woolly mammoth dates, 658 peatland initiation dates, 447 tree and wood macrofossil dates, 576 dates from Paleolithic archaeological sites (~ 45ka–10ka), palynological records and genetic data.

**Results**

**Patterns of Mammoth Abundance during MIS 3.** Of the 1,323 mammoth radiocarbon dates, 377 are infinite in age or classified as potentially >45 ka. Finite-age mammoth remains are abundant from Marine Isotope Stage 3 (MIS 3), and notably common at northern sites, suggesting more favourable conditions for woolly mammoths in northernmost Asia and adjacent North America between ~30 to 45 ka than during the subsequent LGM (Figs 1–3). Mitochondrial DNA for Siberian woolly mammoths suggests that two distinct clades were extant during MIS 3 (ref. 15) (Supplementary Fig. S1). Paleolithic human sites in Asien Beringia and particularly its southern periphery are widely present during MIS 3 and demonstrate a long sympatry between humans and woolly mammoths in that region (Figs 1 and 2).

Maximum temperatures in Beringia during MIS 3 were slightly lower (< 2 to 3 °C) than during the Holocene19. June insolation was lower than the Holocene and December insolation was roughly equal (Fig. 1). Northerly areas supported a mosaic of open graminoid and herbaceous vegetation with shrubland. Conifers were present in interior areas12, although likely not as abundant as during the Holocene (Figs 1 and 4). A peak in the northern woolly mammoth populations during MIS 3 is consistent with the known ecology of the species and is supported by recent climate suitability modelling7. Mammoths were open vegetation-adapted with diets dominated by graminoids and soft-shoots of selected woody plants such as willow (*Salix*)14,19. Conifer trees, although found in the stomachs of some woolly mammoths, are not nutritious browse. Birch (*Betula*) can be toxic to cecal digesters, such as mammoths, which lack a rumen for detoxification5,18. While grasses and willows were plentiful, birch was less abundant as during the Holocene (Figs 1 and 4). A peak in the northern woolly mammoth populations during MIS 3 is consistent with the known ecology of the species and is supported by recent climate suitability modelling7. Mammoths were open vegetation-adapted with diets dominated by graminoids and soft-shoots of selected woody plants such as willow (*Salix*)14,19. Conifer trees, although found in the stomachs of some woolly mammoths, are not nutritious browse. Birch (*Betula*) can be toxic to cecal digesters, such as mammoths, which lack a rumen for detoxification5,18. While grasses and willows were plentiful, birch was less abundant as during the Holocene (Figs 1 and 4). A peak in the northern woolly mammoth populations during MIS 3 is consistent with the known ecology of the species and is supported by recent climate suitability modelling7. 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and shrubby vegetation including willows (Figs 1 and 4). Before the subsequent full development of large peatlands, dense birch cover and conifer forest (Figs 1–4), these conditions would have promoted woolly mammoth population growth in the north. Populations in southern Siberia were, in contrast, declining relative to LGM levels, probably because of conifer forest and

![Figure 1](https://example.com/figure1.png)

**Figure 1 | Comparative time series of woolly mammoth abundance.** Comparative time-series of orbital forcing, environmental factors, Paleolithic human sites and woolly mammoth abundance. (a) General boundaries of marine isotope stages (MIS 1,2,3) and June (orange) and December (dark blue) insolation variations at 60°N. The timing of the YD is indicated. (b) Arctic surface temperatures as represented in Greenland GISP2 ice core (light blue). (c) Pollen/spore accumulation rates for Poaceae (grass), Salix (willow), Betula (birch), coniferous trees, and Sphagnum in northeastern Asia (Sosednee Lake, grey) and Alaska (Joe Lake, black). (d) Radiocarbon age probability plots for wetland/peatland initiation dates (olive green and black), and Betula (birch) (light blue) and treeline conifer macrofossils (lime green). Probability plot of radiocarbon ages from coniferous tree macrofossils from central Siberia is presented in blue. (e) Cumulative probabilities (sum probability in 100-yr periods) of northern Eurasian Paleolithic dates and occupation episodes (blue) per 1,000-year periods and cumulative probabilities of early Alaska-Yukon human occupation sites (red). The cumulative probabilities are overlain on simple histograms of the number of dates per 5,000-year interval (dark red). All human site data series are terminated at 10 ka. (f) Cumulative probabilities of northern Asian and northwestern North American woolly mammoth remains (yellow) overlain on simple histograms of the number of dates per 5,000-year interval (dark yellow). Histograms are divided by continental sites (yellow) and island sites (grey). Histograms are included as cumulative probability curves are prone to age-dependent bias as explained in Supplementary Information. For data sources and calculations, see Methods and Supplementary Data 1.
peatland development and possibly greater human hunting pressures (Figs 1–4). The geographic distribution of the Asian population density was shifting back to a pattern of higher density in the north. However, unlike MIS 3, the more southerly populations seem to have disappeared almost entirely by ~12.5 ka (Figs 1–3).

**Ultimate decline and Holocene extinction.** A steep decline in woolly mammoths in northern North America occurred around the time of the YD at ~12.9 ka and in northern Asia, during the subsequent continued development of extensive birch cover, peatlands and conifer forest (Figs 1–4). Temperature reconstructions suggest a rapid cooling of 3.5°C to 8.9°C in portions of Alaska during the YD. However, climatic and vegetation impacts were regionally variable, and there is no clear vegetation change in the pollen records, presented here, that can be ascribed to the YD (Figs 1 and 4). Even in the face of vegetation resilience, a very rapid cooling could...
have been more deleterious to large mammals that remain active year round. Stable isotope studies of woolly mammoth remains suggest that they did not migrate appreciable distances, and confined latitudinal ranges would possibly have made them vulnerable in areas with pronounced cooling. In the absence of information on the specifics of mammoth physiology, the potential impacts of such an oscillation, however, remain uncertain. North American mammoth populations do seem to have declined coincidentally with the YD (Fig. 1), but such a decline is not as clear for Asia. Although it’s potential impact on mammoths is still to be resolved, it is notable that a rapid climatic oscillation analogous to the YD does not appear to have occurred during the earlier MIS 6–MIS 5 glacial–interglacial transition through which *M. primigenius* survived.

Dated mammoth remains from after the YD come from northernmost Eurasia and Arctic islands (Continental Northern Asia = 5, Arctic Islands = 112). Small continental populations of woolly mammoth certainly were present after the YD, but trajectory of these populations towards extinction was being driven by changing habitat and perhaps also through human hunting that had spread to North America (Figs 1–3). Graminoid, willow and drier herbaceous cover decreased in concert with the establishment of deleterious birch shrubland/woodland throughout Beringia, development of extensive peatlands and wet tundra, and expansion of conifer forest including areas north of the modern treeline across Eurasia as far as the present coastline (Figs 1–4).

Pressure from hunting was also present, as contemporary Palaeolithic sites are numerous in both Siberia and now in northwestern North America (Figs 1–3). Modelling studies show that given the environmental stresses at the time, even limited hunting by humans could have significantly contributed to woolly mammoth extinction. Humans may have been even more widespread by this time than the radiocarbon database of Palaeolithic sites.
captures. Although chronological control of older paleoenvironmental records presents uncertainties, ancestral mammoths had survived decreased grasslands, increased peatlands and extensive birch shrubland and conifer range expansion during the time of MIS 5 (ref. 35) (Fig. 4). However, the magnitude of the decrease in grassland and increase of pine during the Holocene and MIS 5 seems to be not typical of the earlier MIS 7 interglacial in northern Asia32,33 (Fig. 4).

The geographic pattern of Beringian mammoth extinction, seems to be one of the final populations existing on the northern periphery of a once more extensive range33 (Figs 2 and 3). This pattern is consistent with the open vegetation available on the fringes of the continents and perhaps less intense human hunting there. As sea-level rose during the Late Glacial and Early Holocene, some of these northern mammoth populations were isolated on what became Wrangel Island and the Pribilof Islands30–32. The last surviving mammoths on Wrangel Island may have been driven to extinction by stochastic factors related to their being a small and isolated population, hunting by newly arrived humans or disease33. They may also have been affected by cooling during the Neoglacial, which is evident in treeline retreat across northern Eurasia at ~4 ka (ref. 36). Unfortunately, it seems that no mammoths were left on continental Asia to take advantage of opening of vegetation as treeline retreated after 4 ka.

Discussion

Not one, but several factors would have made the present interglacial particularly challenging for woolly mammoths in Beringia: the preceding declines in northern populations during the LGM; the rapid and relatively early development of unpalatable birch shrubland; wet tundra and extensive peatlands/wetlands followed by the expansion of conifer forest and woodland to the continental margins in Eurasia; the presence of modern humans not only in Siberia, but now also in North America; and the sudden, but regionally differing, impacts of the YD oscillation. The relative importance of these specific forces may never be wholly resolvable, and was likely regionally variable, but combined, they provided the lethal intersection1 of factors to drive the woolly mammoths to extinction in continental Beringia with relucTable populations hanging on for several millennia on isolated Arctic islands. That final extinction of the island populations signalled the conclusion of the long sunset of the woolly mammoths in Beringia after over 20,000 years of multiple environmental challenges related to changes in climate, habitat and human predation.

Care must be taken in the use of large radiocarbon data sets, and debate exists over the best approaches41–44. We have avoided known apatite bone dates for mammoths (Supplementary Data 1), attempted to select archaeological dates with clear context and further mitigate problems in the dating of Asian sites by using occupation-age estimates (see below) that are often based on multiple dates, and we have only incorporated dates from laboratories that we believe participated in either international or internal Soviet/Russian multi-lab intercomparisons. Overlapping issues may still persist with individual dates, but we believe the total numbers, incorporated in the analysis, portray overall general records of abundance and geographic patterns with acceptable fidelity.

Archaeological dates and Eurasian occupation episodes. The dates for Paleolithic sites are from a number of sources34–36, and those from Eurasian Paleolithic sites were used to calculate occupation-episode estimates for 1,000-year time-slices to remove any bias introduced by sites that have many dates for a single occupation period owing to the employed sampling and dating method45–47. The occupation episode totals for each time-slice represent the number of geographically discrete sites that have dates indicating human presence during that time period.

Other paleoenvironmental data sets and chronologies. Online data for June and December insolation variations at 60°N (ref. 48), temperature and oxygen stable isotope records from the Greenland GISP2 and NGRIP ice cores49,50,51,52, deuterium stable isotope record from the Antarctica EPICA Dome C ice core53,54, and the pollen and spore data for the Joe Lake and Sosednaya Lakes cores35,55 were obtained from the NOAA National Climate Data Center site (www.ncdc.noaa.gov/paleo).

Additional data for Sosednaya Lake were provided by Dr Pat Anderson. Chronologies were constructed by fitting a cubic spline to the sediment age-depth relationship based on calibrated29 radiocarbon dates. Pollen and spore concentrations for Lake El’gygytgyn were received in digital format courtesy of Drs Anatoly Lohkhin and Pat Anderson and are from 2005. As presented, they may differ slightly in terms of pollen sum used to calculate percentages, details of counts and subsamples represented in previously published form55. There has been previous discussion regarding the chronology for Lake El’gygytgyn19,34–36, and we use an updated chronology incorporating orbital tuning provided by Drs Norbert Nowaczyk and Julie Brigham-Grette.PEAT/wetland initiation and wood macrofossil dates are from several sources19,36,56,57.

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