

Species-specific responses of Late Quaternary megafauna to climate and humans

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Despite decades of research, the roles of climate and humans in driving the dramatic extinctions of large-bodied mammals during the Late Quaternary period remain contentious. Here we use ancient DNA, species distribution models and the human fossil record to elucidate how climate and humans shaped the demographic history of woolly rhinoceros, woolly mammoth, wild horse, reindeer, bison and musk ox. We show that climate has been a major driver of population change over the past 50,000 years. However, each species responds differently to the effects of climatic shifts, habitat redistribution and human encroachment. Although climate change alone can explain the extinction of some species, such as Eurasian musk ox and woolly rhinoceros, a combination of climatic and anthropogenic effects appears to be responsible for the extinction of others, including Eurasian steppe bison and wild horse. We find no genetic signature or any distinctive range dynamics distinguishing extinct from surviving species, emphasizing the challenges associated with predicting future responses of extant mammals to climate and human-mediated habitat change.

Towards the end of the Late Quaternary, beginning around 50,000 years ago, Eurasia and North America lost approximately 36% and 72% of their large-bodied mammalian genera (megafauna), respectively¹. The debate surrounding the potential causes of these extinctions has focused primarily on the relative roles of climate and humans^{2–5}. In general, the proportion of species that went extinct

was greatest on continents that experienced the most dramatic climatic changes⁶, implying a major role of climate in species loss. However, the continental pattern of megafaunal extinctions in North America and Australia approximately coincides with the first appearance of humans, suggesting a potential anthropogenic contribution to species extinctions^{3,5}.

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Demographic trajectories of different taxa vary widely and depend on the geographic scale and methodological approaches used^{3,5,7}. For example, genetic diversity in bison^{8,9}, musk ox¹⁰ and European cave bear¹¹ declines gradually from approximately 50,000–30,000 calendar years ago (kyr BP). In contrast, sudden losses of genetic diversity are observed in woolly mammoth^{12,13} and cave lion¹⁴ long before their extinction, followed by genetic stability until the extinction events. It remains unresolved whether the Late Quaternary extinctions were a cross-taxa response to widespread climatic or anthropogenic stressors, or were a species-specific response to one or both factors^{15,16}. Additionally, it is unclear whether distinctive genetic signatures or geographical range-size dynamics characterize extinct or surviving species—questions of particular importance to the conservation of extant species.

To disentangle the processes underlying population dynamics and extinction, we investigate the demographic histories of six megafauna herbivores of the Late Quaternary: woolly rhinoceros (*Coelodonta antiquitatis*), woolly mammoth (*Mammuthus primigenius*), horse (wild *Equus ferus* and living domestic *Equus caballus*), reindeer/caribou (*Rangifer tarandus*), bison (*Bison priscus/Bison bison*) and musk ox (*Ovibos moschatus*). These taxa were characteristic of Late Quaternary Eurasia and/or North America and represent both extinct and extant species. Our analyses are based on 846 radiocarbon-dated mitochondrial DNA (mtDNA) control region sequences, 1,439 directly dated megafaunal remains and 6,291 radiocarbon determinations associated with Upper Palaeolithic human occupations in Eurasia. We reconstruct the demographic histories of the megafauna herbivores from ancient DNA data, model past species distributions and determine the geographical overlap between humans and megafauna over the past 50,000 years. We use these data to investigate how climate change and anthropogenic impacts affected species dynamics at continental and global scales, and contributed to the extinction of some species and the survival of others.

Responses differ among species and continents

The direct link between climate change, population size and species extinctions is difficult to document¹⁰. However, population size is probably controlled by the amount of available habitat and is indicated by the geographical range of a species^{17,18}. We assessed the role of climate using species distribution models, dated megafauna fossil remains and palaeoclimatic data on temperature and precipitation. We estimated species range sizes at the time periods of 42, 30, 21 and 6 kyr BP as a proxy for habitat availability (Fig. 1 and Supplementary Information section 1). Range size dynamics were then compared with demographic histories inferred from ancient DNA using three distinct analyses (Supplementary Information section 3): (1) coalescent-based estimation of changes in effective population size through time (Bayesian skyride¹⁹), which allows detection of changes in global genetic diversity; (2) serial coalescent simulation followed by approximate Bayesian computation, which selects among different models describing continental population dynamics; and (3) isolation-by-distance analysis, which estimates potential population structure and connectivity within continents. If climate was a major factor driving species population sizes, we would expect expansion and contraction of a species' geographical range to mirror population increase and decline, respectively.

We find a positive correlation between changes in the size of available habitat and genetic diversity for the four species—horse, reindeer, bison and musk ox—for which we have range estimates spanning all four time-points (the correlation is not statistically significant for reindeer: $P = 0.101$) (Fig. 2 and Supplementary Information section 4). Hence, species distribution modelling based on fossil distributions and climate data are congruent with estimates of effective population size based on ancient DNA data, even in species with very different life-history traits. We conclude that climate has been a major driving force in megafauna population changes over the past 50,000 years. It is

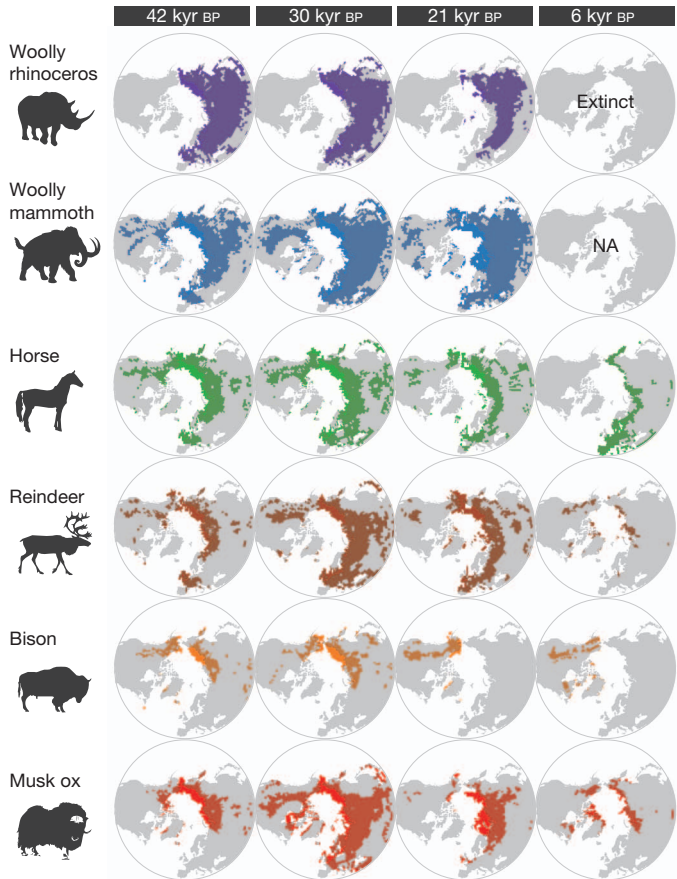


Figure 1 | Modelled potential ranges of megafauna species at 42, 30, 21 and 6 kyr BP. Ranges were modelled using the megafauna fossil record and palaeoclimatic data for temperature and precipitation; ice sheet extent was not included as a co-variable. Range measurements were restricted to the regions for which fossils were used to build the models, rather than all potentially suitable Holarctic area. NA, not available.

noteworthy that both estimated modelled ranges and genetic data are derived from a subset of the entire fossil record (Supplementary Information sections 1 and 3). Thus, changes in effective population size and range size might change with the addition of more data, especially from outside the geographical regions covered by the present study. However, we expect that the reported positive correlation will prevail when congruent data are compared.

The best-supported models of changes in effective population size in North America and Eurasia during periods of dramatic climatic change over the past 50,000 years are those in which populations increase in size (Fig. 3 and Supplementary Information section 3). This is true for all taxa except bison. However, the timing is not synchronous across populations. Specifically, we find highest support for population increase beginning approximately 34 kyr BP in Eurasian horse, reindeer and musk ox (Fig. 3a). Eurasian woolly mammoth and North American horse increase before the Last Glacial Maximum (LGM) approximately 26 kyr BP. Models of population increase in woolly rhinoceros and North American woolly mammoth fit equally well before and after the LGM, and North American reindeer populations increase later still. Only North American bison shows a population decline (Fig. 3b), the intensity of which probably swamps the signal of global population increase starting at approximately 35 kyr BP identified in the skyride plot (Fig. 2a).

These increases in effective population size probably reflect responses to climate change. By 34 kyr BP, the relatively warmer Marine Isotope Stage (MIS) 3 interstadial marked the transition to cold, arid full-glacial conditions of MIS 2, which began approximately

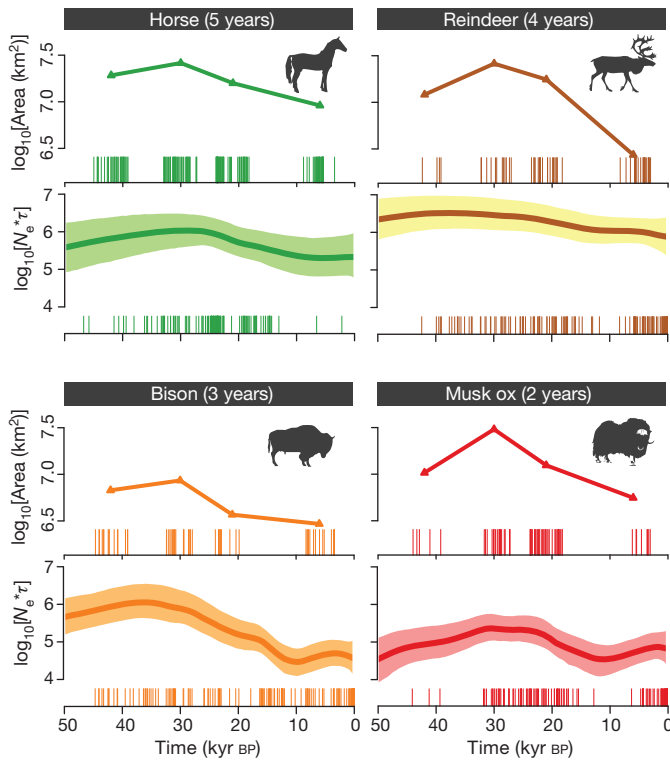


Figure 2 | Temporal changes in global genetic diversity and range size in horse, bison, reindeer and musk ox. The x-axis is in calendar years; the y-axis is the product of effective population size and generation time ($N_e\tau$). Generation times are given in parentheses. Comparable estimates of associated range sizes (square kilometres) are from Fig. 1. The temporal span of the radiocarbon-dated samples used in each approach is shown as vertical lines below each panel; each line represents one dated individual.

30 kyr BP^{20,21}. Although the pre-LGM density of humans in Siberia remains uncertain, Pleistocene archaeological sites in the Siberian far north are scarce²² and humans were presumably absent from North America before at least 15 kyr BP²³. These point to climate, rather than

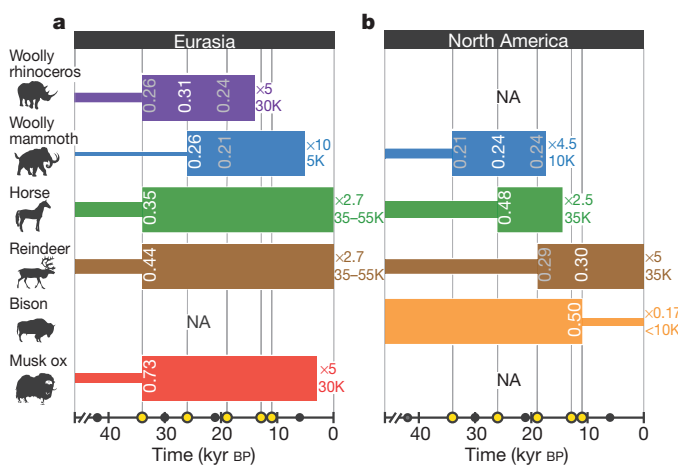


Figure 3 | Best-supported demographic models inferred by approximate Bayesian computation model-selection. a, Eurasia; b, North America. Grey dots on the time axis indicate periods with range size estimates. Yellow dots indicate the periods of demographic increase or decline, which were tested against each other in the approach. White values inside coloured bars reflect support for the best-supported model (for example, Eurasian woolly mammoth, increase at 26 kyr BP). The intensity of increase or decline (for example, $\times 10$) and effective population size at the time of the youngest sample (for example, 5,000 individuals) are shown. We indicate in grey cases where multiple models received similar levels of support.

humans, as the key driver of these species-specific and, in some cases, continent-specific demographic changes. This conclusion is supported by the significant correlations between modelled range sizes and effective population sizes (Fig. 2).

Modes of extinction

Both woolly rhinoceros and woolly mammoth suffered global extinctions during the Late Quaternary. Neither shows evidence of a decline in genetic diversity leading to their extinction at either continental or global scales (Supplementary Figs 3.2 and 3.6). However, the fossil records of the two species differ: woolly rhinoceros remains widely distributed across Eurasia until it disappears from the fossil record approximately 14 kyr BP (Supplementary Fig. 2.2), whereas the woolly mammoth range retreats northwards during its last millennia (Supplementary Figs 2.3 and 5.2c, d). We find increased isolation-by-distance preceding extinction (Supplementary Fig. 3.1 and Supplementary Information section 3), suggesting that populations of both species became increasingly fragmented, although the results are not statistically significant for woolly mammoth. The high and sustained levels of genetic diversity in these species might reflect the fixation of multiple distinct haplotypes in increasingly isolated and diminishing subpopulations. For woolly mammoth, this pattern is also supported by fossil evidence²⁴.

Our data suggest similar possibilities of increased isolation-by-distance before the extinctions of musk ox in Eurasia (approximately 2.5 kyr BP^{25,26}) and of steppe bison in the north of the North American plains, which potentially survived until only a few hundred years ago⁸ (Supplementary Fig. 3.1). Such fragmentation is commonly observed in wide-ranging species undergoing population decline, owing to populations aggregating in patches of high-quality habitat²⁷. In contrast, we find low levels of isolation-by-distance in wild horse and in Eurasian and North American reindeer, suggesting these populations remained relatively panmictic over time.

Disentangling the roles of climate and humans

To evaluate the potential role of humans in the local and global megafauna extinctions, we measured the following: (1) the spatial overlap between the modelled range of each megafauna species and the Eurasian Palaeolithic archaeological record at 42, 30 and 21 kyr BP; (2) the presence of megafauna remains in Palaeolithic archaeological assemblages from Europe (48–18 kyr BP) and Siberia (41–12 kyr BP); and (3) variation in fossil abundance and the temporal and spatial distributions of known Palaeolithic archaeological sites and the Eurasian megafauna fossil record at 1,000-year intervals. For the last category, we added 1,557 indirectly dated megafaunal remains to the 1,439 directly dated specimens to increase sample sizes. Although associated with greater age-estimate uncertainties, the integrity of each of the indirectly dated samples was evaluated before inclusion following the guidelines listed in Supplementary Information section 5.

Woolly rhinoceros and Eurasian woolly mammoth experience a five- to tenfold increase in effective population size between 34 kyr BP and 19 kyr BP (Fig. 3), at least 10,000 years after first human contact as inferred from the overlap between estimated ranges and archaeological sites (Supplementary Figs 1.2 and 1.5). This result directly contradicts models of population collapse from human overkill (blitzkrieg)² or infectious diseases following the first human contact (hyperdisease)²⁸.

We find no evidence that Palaeolithic humans greatly impacted musk ox populations, in agreement with previous conclusions that humans were not responsible for the extinction of musk ox in Eurasia¹⁰. Musk ox remains are found in only 1% of European archaeological sites and 6% of Siberian sites, and do not overlap noticeably in range with Palaeolithic humans in either Europe or Siberia (Fig. 4). However, the decline in the potential range of musk ox by 60% between 21 and 6 kyr BP (Fig. 1), the increase in isolation-by-distance at 19 kyr BP (Supplementary Fig. 3.1 and Supplementary Table 3.3) and the positive correlation between climate-driven range size and genetic diversity (Fig. 2b) all point

towards climate as the main driver of musk ox population dynamics, including the decrease in genetic diversity after the LGM (Fig. 2a). The importance of climate is further supported by the physiology of musk ox, which might be a more sensitive indicator of environmental warming than the other species. Musk ox has extreme temperature sensitivity and is unable to tolerate high summer temperatures; the 10 °C summer isotherm approximates the southern limit of its present-day range²⁹.

We find little regional overlap between Palaeolithic humans and woolly rhinoceros in Siberia after the LGM (that is, after 20 kyr BP); the species is found in fewer than 11% of Siberian archaeological sites during this time (Fig. 4). This suggests that woolly rhinoceros was not a common prey species for humans, and that overhunting is an unlikely explanation for their extinction in Siberia. However, we note that geographical overlap existed between humans and woolly rhinoceros in Europe during the two millennia preceding extinction (Fig. 4), and therefore cannot exclude the hypothesis that humans influenced the final collapse of the species in this region. The continued presence of woolly rhinoceros in the fossil record throughout Siberia and parts of Europe up until the species extinction event (Supplementary Fig. 2.2) suggests that the final collapse of the species was synchronous across its range.

The data from woolly mammoth are inconclusive about the causes of extinction. We find that the range of Eurasian woolly mammoth

overlaps continuously with humans throughout the Palaeolithic (Fig. 4), in agreement with previous results based on a more limited data set³⁰. Woolly mammoth remains are found in 40% and 35% of all European and Siberian Palaeolithic sites, respectively, and mammoth subsistence hunting by Clovis peoples in North America has been documented³¹. However, the prevalence of woolly mammoth in Siberian sites declines after the LGM (43% of sites before 19 kyr BP compared with 30% after; Fig. 4). This decline could indicate a northward range shift of woolly mammoth ahead of humans³⁰ (Fig. 5.2c, d), an increasing scarcity of woolly mammoths in southern Siberia or an increasing human preference for other prey species.

In wild horse, the large mid-Holocene range of over 9 million km² (Fig. 1 and Supplementary Table 1.3) suggests the potential for a large Eurasian population at this time, and is not consistent with climate driving the final disappearance of the species in the wild. Rather, the decline in genetic diversity observed after the LGM in horse and bison, and to a lesser degree in reindeer (Fig. 2), might reflect the impact of expanding human populations in Europe and Asia. The presence of the three species in the archaeological record suggests that their populations are more likely to have been influenced by humans. Bison and horse are the most common megafauna herbivores found in archaeological sites (Fig. 4), with horse present in 58% and 66% of European and Siberian sites, respectively. Furthermore, horse shows extensive geographical

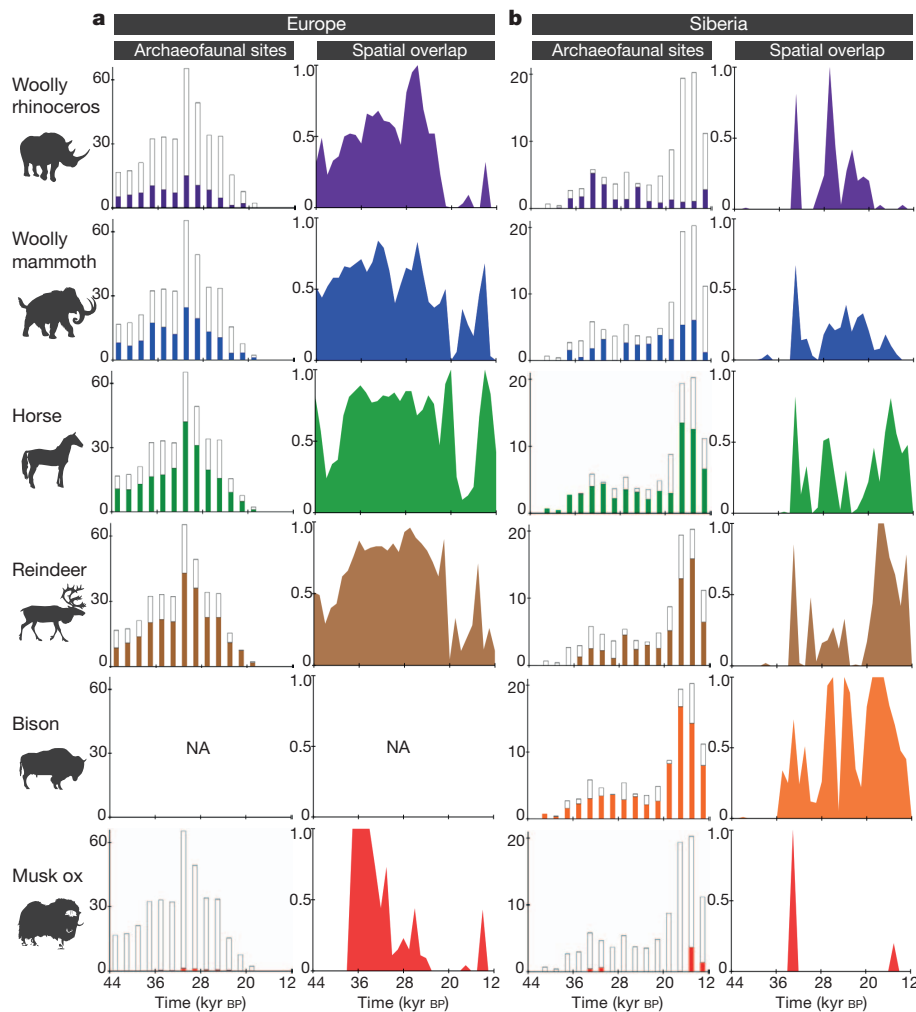


Figure 4 | Spatial and temporal association between megafauna and Upper Palaeolithic humans. **a**, Europe; **b**, Siberia. Column graphs represent known cultural occupations containing at least one of the six species, averaged over 2,000-year time bins; data span 48–18 kyr BP for Europe and 41–12 kyr BP for Siberia. Open bars indicate the number of archaeofaunal sites, filled bars

represent the frequency of each species in the binned assemblages. Area graphs show the fraction of megafauna surface area shared with humans at 1,000-year intervals, calculated from the mean \pm one standard deviation of latitude and longitude; data represented in Supplementary Fig. 5.2. Graphs use coordinates of data associated with both direct and indirect dates.

overlap with humans in both Europe and Siberia after the LGM, although large population sizes might have insulated horses to some extent from the effects of selective hunting by humans.

In bison, the pre-human decline in genetic diversity starting approximately 35 kyr BP and the strong correlation between range size and genetic diversity (Fig. 2) indicate climate as a main driver of demographic change. This conclusion is supported by the fivefold decline in effective population size (Fig. 3) and increased isolation-by-distance approximately 11 kyr BP in North America (Supplementary Fig. 3.1 and Supplementary Table 3.3). The timing of these demographic changes coincides with the pronounced climatic shifts associated with the Pleistocene/Holocene transition³², although they also coincide with fossil evidence of growing populations of potential competitors such as *Alces* and *Cervus*³³. The accelerated rate of decline in genetic diversity after approximately 16 kyr BP (Fig. 2) is coincident with the earliest known human expansion in the Americas²³, and the significant presence of bison in 77% of the Siberian archaeological assemblages points to their popularity as a prey species (Fig. 4).

Reindeer are the most abundant of the six taxa today. As with horse, they show continuous geographical overlap with Palaeolithic humans in Eurasia (Fig. 4). Reindeer are common in both European and Siberian Palaeolithic assemblages, are found in 67% of Siberian sites after the LGM and were an important prey species for humans in both Eurasia and North America³⁴. Unlike bison and horse, the potential range of reindeer declines by 84% between 21 and 6 kyr BP (Fig. 1 and Supplementary Table 1.3). Despite the apparently detrimental influences of both humans and climate change, wild and domestic reindeer currently number in the millions across the Holarctic³⁵. Although individual populations are affected by changing climate³⁶, the species is not currently under threat of extinction. The success of reindeer may be explained by high fecundity³⁷ and ecological flexibility³⁸. In addition, continued low levels of isolation-by-distance suggest high mobility and near-panmixia of populations over millennia (Supplementary Fig. 3.1 and Supplementary Table 3.3).

Conclusions

We find that neither the effects of climate nor human occupation alone can explain the megafauna extinctions of the Late Quaternary. Rather, our results demonstrate that changes in megafauna abundance are idiosyncratic, with each species (and even continental populations within species) responding differently to the effects of climate change, habitat redistribution and human encroachment. Although reindeer remain relatively unaffected by any of these factors on a global scale, climate change alone explains the extinction of Eurasian musk ox and woolly rhinoceros, and a combination of climatic and anthropogenic effects appears to be responsible for the demise of wild horse and steppe bison. The causes underlying the extinction of woolly mammoth remain elusive.

We have shown that changes in habitat distribution and population size are intrinsically linked over evolutionary time, supporting the view that populations of many species will decline in the future owing to climate change and habitat loss. Intriguingly, however, we find no distinguishing characteristics in the rate or pattern of decline in those species that went extinct compared with those that have survived. Our study demonstrates the importance of incorporating lessons from the past into rational, data-driven strategies for the future to address our most pressing environmental challenges: the ongoing global mass-extinction of species and the impacts of global climate change and humans on the biodiversity that remains.

METHODS SUMMARY

Our data comprise 846 radiocarbon-dated ancient mitochondrial DNA sequences, 1,439 directly dated and 1,557 indirectly dated megafauna specimens, and 6,291 dated remains associated with Upper Palaeolithic humans in Eurasia. For population genetic analysis, we used the following: (1) the Bayesian skyride approach²⁰ to estimate the global demographic trajectory of each species over the

past 50,000 years; (2) serial-coalescent simulations and the approximate Bayesian computation model-selection approach³⁹ to assess demographic change in Eurasia and in North America, and in the global data set; (3) isolation-by-distance to investigate changes in population structure over time in the two continental subpopulations. Palaeoclimatic estimates of precipitation and temperature were used to model the potential geographical range of each species at 42, 30, 21 and 6 kyr BP, using only contemporaneous radiocarbon-dated megafauna fossils (± 3 kyr) for each period. Range measurements were restricted to Holarctic regions for which fossils were used to build the models. Using a Bayesian hierarchical modelling framework, these changes in range size were compared with changes in effective population size estimated from the Bayesian skyrides. To assess the spatial and temporal association between humans and megafauna, we (1) analysed variations in fossil abundance and spatial and temporal overlap between the human Upper Palaeolithic and megafauna fossil records in Europe and Siberia, (2) inferred the area of overlap between the human data from (1) and the megafauna ranges at 42, 30 and 21 kyr BP, and (3) assembled a list of the cultural occupations in Europe and Siberia with megafauna presence, to determine which taxa were directly associated with Palaeolithic humans. For details on methods see Supplementary Information.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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- Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L. & Shabel, A. B. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* **306**, 70–75 (2004).
- Martin, P. S. in *Quaternary Extinctions: A Prehistoric Revolution* (eds Martin, P. S. & Klein, R. G.) 364–403 (Univ. Arizona Press, 1984).
- Alroy, J. A. multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* **292**, 1893–1896 (2001).
- Stuart, A. J., Kosintsev, P. A., Higham, T. F. G. & Lister, A. M. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. *Nature* **431**, 684–689 (2004).
- Koch, P. L. & Barnosky, A. D. Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Syst.* **37**, 215–250 (2006).
- Nogués-Bravo, D., Ohlemüller, R., Batra, P. & Araújo, M. B. Climate predictors of Late Quaternary extinctions. *Evolution* **64**, 2442–2449 (2010).
- Haile, J. et al. Ancient DNA reveals late survival of mammoth and horse in interior Alaska. *Proc. Natl Acad. Sci. USA* **106**, 22363–22368 (2009).
- Shapiro, B. et al. Rise and fall of the Beringian steppe bison. *Science* **306**, 1561–1565 (2004).
- Drummond, A. J., Rambaut, A., Shapiro, B. & Pybus, O. G. Bayesian coalescent inference of past population dynamics from molecular sequences. *Mol. Biol. Evol.* **22**, 1185–1192 (2005).
- Campos, P. F. et al. Ancient DNA analyses exclude humans as the driving force behind Late Pleistocene musk ox (*Ovibos moschatus*) population dynamics. *Proc. Natl Acad. Sci. USA* **107**, 5675–5680 (2010).
- Stiller, M. et al. Withering away—25,000 years of genetic decline preceded cave bear extinction. *Mol. Biol. Evol.* **27**, 975–978 (2010).
- Barnes, I. et al. Genetic structure and extinction of the woolly mammoth, *Mammuthus primigenius*. *Curr. Biol.* **17**, 1–4 (2007).
- Debruyne, R. et al. Out of America: ancient DNA evidence for a new world origin of Late Quaternary woolly mammoths. *Curr. Biol.* **18**, 1320–1326 (2008).
- Barnett, R., Yamaguchi, N., Barnes, I. & Cooper, A. The origin, current diversity, and future conservation of the modern lion (*Panthera leo*). *Proc. R. Soc. B* **273**, 2159–2168 (2006).
- Guthrie, R. D. Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* **426**, 169–171 (2003).
- Grayson, D. K. Deciphering North American Pleistocene extinctions. *J. Anthropol. Res.* **63**, 185–214 (2007).
- Andrewartha, H. G. & Birch, L. C. *The Distribution and Abundance of Animals* (Univ. Chicago Press, 1954).
- Borregaard, M. K. & Rahbek, C. Causality in the relationship between geographic distribution and species abundance. *Q. Rev. Biol.* **85**, 3–25 (2010).
- Minin, V. N., Bloomquist, E. W. & Suchard, M. A. Smooth skyride through a rough skyline: Bayesian coalescent-based inference of population dynamics. *Mol. Biol. Evol.* **25**, 1459–1471 (2008).
- Zazula, G. D. et al. Ice age steppe vegetation in east Beringia. *Nature* **423**, 603 (2003).
- Zazula, G. D., Froese, D. G., Elias, S. A., Kuzmina, S. & Mathewes, R. W. Arctic ground squirrels of the mammoth-steppe: paleoecology of Late Pleistocene middens (~24,000–29,450 ¹⁴C yr BP), Yukon Territory, Canada. *Quat. Sci. Rev.* **26**, 979–1003 (2007).
- Pitulko, V. V. et al. The Yana RHS site: humans in the Arctic before the last glacial maximum. *Science* **303**, 52–56 (2004).
- Goebel, T., Waters, M. R. & O'Rourke, D. H. The Late Pleistocene dispersal of modern humans in the Americas. *Science* **319**, 1497–1502 (2008).

24. Stuart, A. J., Sulerzhitsky, L. D., Orlova, L. A., Kuzmin, Y. V. & Lister, A. M. The latest woolly mammoths (*Mammuthus primigenius* Blumenbach) in Europe and Asia: a review of the current evidence. *Quat. Sci. Rev.* **21**, 1559–1569 (2002).
25. Vereshchagin, N. K. Prehistoric hunting and the extinction of Pleistocene mammals in the USSR. *Proc. Zool. Inst. Russ. Acad. Sci.* **69**, 200–232 (1971).
26. Kuznetsova, T. V., Sulerzhitsky, L. D., Siebert, C. & Schirmermeister, L. (2001) in *La Terra degli Elefanti* (eds Cavarretta, G. Giola, P., Mussi, M. & Palombo, M. R.) *The World of Elephants, Proc. 1st Int. Congr.* 289–292 (2001).
27. Wilson, R. J., Thomas, C. D., Fox, R., Roy, D. B. & Kunin, W. E. Spatial patterns in species distributions reveal biodiversity change. *Nature* **432**, 393–396 (2004).
28. MacPhee, R. D. E. & Marx, P. A. in *Natural Change and Human Impact in Madagascar* (eds Goodman, S. M. & Patterson, B. D.) 169–217 (Smithsonian Institution Press, 1997).
29. Tener, J. S. Muskoxen in Canada: a biological and taxonomic review. *Canadian Wildlife Service Monograph Series No. 2* (1965).
30. Ugan, A. & Byers, D. A global perspective on the spatiotemporal pattern of the Late Pleistocene human and woolly mammoth radiocarbon record. *Quaternary Int.* **191**, 69–81 (2008).
31. Surovell, T. A. & Waguespack, N. M. How many elephant kills are 14? Clovis mammoth and mastodon kills in context. *Quaternary Int.* **191**, 82–97 (2008).
32. Zielinski, G. A. & Mershon, G. R. Paleoenvironmental implications of the insoluble microparticle record in the GISP2 (Greenland) ice core during the rapidly changing climate of the Pleistocene–Holocene transition. *Geol. Soc. Am. Bull.* **109**, 547–559 (1997).
33. Guthrie, R. D. New carbon dates link climatic change with human colonization and Pleistocene extinctions. *Nature* **441**, 207–209 (2006).
34. Farnell, R. *et al.* Multidisciplinary investigations of alpine ice patches in southwest Yukon, Canada: paleoenvironmental and paleobiological investigations. *Arctic* **57**, 247–259 (2004).
35. Williams, T. M. & Heard, D. C. World status of wild *Rangifer tarandus* population. *Rangifer* **1** (special issue), 19–28 (1986).
36. Joly, K., Klein, D. R., Verbyla, D. L., Rupp, T. S. & Chapin, F. S. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography* **34**, 345–352 (2011).
37. Skogland, T. The effects of density-dependent resource limitation on the demography of wild reindeer. *J. Anim. Ecol.* **54**, 359–374 (1985).
38. Leader-Williams, N. *Reindeer on South Georgia* Ch. 1, 3–18 (Cambridge Univ. Press, 1988).
39. Beaumont, M. in *Simulations, Genetics and Human Prehistory* (eds Matsumura, S., Forster, P. & Renfrew, C.) 134–154 (McDonald Institute for Archaeological Research, 2008).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions E.W. conceived and headed the overall project. C.R. headed the species distribution modelling and range measurements. E.D.L. and J.T.S. extracted, amplified and sequenced the reindeer DNA sequences. J.B. extracted, amplified and sequenced the woolly rhinoceros DNA sequences; M.H. generated part of the woolly rhinoceros data. J.W., K.-P.K., J.L. and R.K.W. generated the horse DNA sequences; A.C. generated part of the horse data. L.O., E.D.L. and B.S. analysed the genetic data, with input from R.N., K.M., M.A.S. and S.Y.W.H. Palaeoclimate simulations were provided by P.B., A.M.H., J.S.S. and P.J.V. The directly dated spatial latitudinal/longitudinal megafauna locality information was collected by E.D.L., K.A.M., D.N.-B., D.B. and A.U.; K.A.M. and D.N.-B. performed the species distribution modelling and range measurements. M.B. carried out the gene–climate correlation. A.U. and D.B. assembled the human Upper Palaeolithic sites from Eurasia. T.G. and K.E.G. assembled the archaeofaunal assemblages from Siberia. A.U. analysed the spatial overlap of humans and megafauna and the archaeofaunal assemblages. E.D.L., L.O., B.S., K.A.M., D.N.-B., M.K.B., A.U., T.G. and K.E.G. wrote the Supplementary Information. D.F., G.Z., T.W.S., K.A.-S., G.B., J.A.B., D.L.J., P.K., T.K., X.L., L.D.M., H.G.M., D.M., M.M., E.S., M.S., R.S.S., T.S., E.S., A.T., R.W. and A.C. provided the megafauna samples used for ancient DNA analysis. E.D.L. produced the figures. E.D.L., L.O. and E.W. wrote most of the manuscript, with input from B.S., M.H., D.N.-B., K.A.M., M.T.P.G., C.R., R.K.W., A.U. and the remaining authors.

Author Information Mitochondrial DNA sequences are deposited in GenBank under accession numbers JN570760–JN571033. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to E.W. (ewillerslev@snm.ku.dk).

METHODS

Data. Mitochondrial DNA sequences and accelerator mass spectrometry radiocarbon dates were collected from the past and present geographical ranges of six megafauna herbivores from Eurasia and North America: woolly rhinoceros (*Coelodonta antiquitatis*), woolly mammoth (*Mammuthus primigenius*), horse (wild *Equus ferus* and living domestic *Equus caballus*), reindeer/caribou (*Rangifer tarandus*), bison (*Bison priscus/Bison bison*) and musk ox (*Ovibos moschatus*) (Supplementary Fig. 2.1 and Supplementary Information sections 2 and 3). Our data comprise 846 radiocarbon-dated ancient mitochondrial DNA sequences (274 of which are new), 1,439 directly dated megafauna specimens (357 of which are new) and 6,291 dated remains associated with Upper Palaeolithic humans in Eurasia. In one analysis of the spatial and temporal association between humans and megafauna detailed below, we included an additional 1,557 indirectly dated megafaunal remains.

Species distribution modelling. We assessed changes in potential range size of each species over the past 50,000 years using 829 radiocarbon-dated megafauna fossils calibrated with the IntCal09 calibration curve⁴⁰ and palaeoclimatic estimates of precipitation and temperature⁴¹. Potential ranges were estimated for the four periods for which palaeoclimatic data are available, 42, 30, 21 and 6 kyr BP, using only contemporaneous fossils (± 3 kyr) for each period (Supplementary Fig. 1.2). We compared temporal changes in potential range size (from species distribution models) and genetic diversity (from Bayesian skyrides¹⁹) during the past 50 kyr BP to assess the relation between these independent proxies of population size. If climate were a major driver of changes in population size, we would expect these two measures to be positively correlated. Estimating past ranges using species distribution models can be affected by an incomplete or biased fossil record as well as inaccuracies in the palaeoclimate simulations used in the models; uncertainties associated with these issues are depicted in our estimates of range size and how it correlates to genetic diversity (Supplementary Fig. 4.3). Range measurements were restricted to regions for which fossils were used to build the models, rather than all potentially suitable Holarctic areas. Fossil localities represent a subset, rather than an exhaustive search, of the literature available, and modelled ranges consequently represent a subset of the entire past distribution of the species. Too few fossils were available to estimate the potential ranges of woolly rhinoceros and woolly mammoth at 6 kyr BP, as the former was extinct and the latter was restricted to two island populations. Thus, too few periods with range estimates for these two species precluded statistical comparison with the genetic data, which spanned 50,000 years. For further details see Supplementary Information sections 1 and 4.

Ancient genetic analysis. We used three analytical approaches capable of incorporating serially sampled data to reconstruct the past population dynamics of each megafauna herbivore species. (1) The Bayesian skyride approach¹⁹ estimates changes in genetic diversity through time as a proxy for effective population size, and was used to estimate the global demographic trajectory of each species. Because these data sets comprise samples from both a broad temporal and geographical extent, it is likely that they violate, at least during some of their

evolutionary history, the assumption of panmixia made by the coalescent models currently implemented in BEAST⁴². However, the skyride makes the least stringent prior assumptions among these coalescent models, and therefore is the most likely to accommodate the temporal changes in structure that might characterize each of these species. (2) Serial-coalescent simulations and the approximate Bayesian computation model-selection approach³⁹ were used to test for demographic change in the continental subpopulations (Eurasia and North America) and in the global data set. Time points were chosen to represent midpoints between the four periods (42, 30, 21 and 6 kyr BP) for which we modelled potential megafauna ranges, and periods of dramatic climatic changes: the beginning (26 kyr BP) and end (19 kyr BP) of the LGM, the onset of the Younger Dryas (12.9 kyr BP) and the beginning of the Holocene (11 kyr BP). (3) Isolation-by-distance was used to test for changes in population structure over time in the continental subpopulations. Note that as with the species distribution models, the demographic events inferred from the ancient DNA data are conditional upon the samples included in the analysis. Hence, although we use the broad geographical terms of Eurasia and North America, the regions are limited to the localities covered by the sequenced samples (Supplementary Fig. 2.1). For further details on the genetics data see Supplementary Information section 2. For further details on the statistical analysis see Supplementary Information section 3.

Spatial association between megafauna and Palaeolithic humans. The presence of humans within the range of a species might directly or indirectly influence the capacity of the species to occupy that habitat. As a proxy for human impact, we assessed the spatial and temporal association between humans and megafauna using three approaches. (1) We compiled the human Upper Palaeolithic fossil record (50–12 kyr BP), including 6,291 radiocarbon determinations associated with human occupations in Europe and Siberia. We analysed variations in fossil abundance and spatial and temporal overlap at 1,000-year intervals between humans and the megafauna fossil record. To increase sample sizes for this particular analysis, we augmented the 1,439 directly dated megafauna specimens with an additional 1,557 indirectly dated megafaunal remains. Although associated with greater age-estimate uncertainties, the integrity of each indirectly dated sample was evaluated before inclusion following the guidelines listed in Supplementary Information section 5. (2) We inferred the area of overlap between the archaeological record from (1) and the megafauna ranges at 42, 30 and 21 kyr BP estimated using species distribution models. (3) We assembled a list of 380 cultural occupations in Europe (48–18 kyr BP) and 98 sites in Siberia (41–12 kyr BP) with megafauna presence, to determine which taxa were directly associated with Palaeolithic humans. For further details see Supplementary Information section 5.

40. Reimer, P. J. *et al.* IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* **51**, 1111–1150 (2009).
41. Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. & Araújo, M. B. Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biol.* **6**, e79 (2008).
42. Drummond, A. J. & Rambaut, A. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7**, 214 (2007).