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SECTION S1: Species distribution modelling

1.1 Introduction

Species distribution models, or SDMs, have been developed over the last three decades to address our incomplete knowledge of species distributions, a challenge described as the "Wallacean shortfall"¹. While primarily developed to estimate the current distribution of species for which we have incomplete sampling, SDMs have also been heavily utilized over the last decade to forecast species future distributions due to modern climate change². They may also be a promising tool for reconstructing the distribution of species in past time periods³ for which varying sampling intensity and bias in the fossil record are more significant problems than in the distribution data from current ecological sampling schemes.

Species distribution models are deeply rooted in niche theory^{4,5} (see also Soberón⁶ for a recent study on niche theory and SDMs) and gradients analysis^{7,8}. They link ecological theory and statistics under the principle that species abundance and population performance, which control species distributions, change across environmental gradients^{9,10}, by relating the distribution of species and the environmental conditions in which they occur in an *n-*dimensional environmental space, in which each dimension is an environmental variable, to statistically describe the environmental niche of a species (or the climatic niche if only climatic variables are used). The modelled species niche can be transferred into geographical space where each grid cell (or unit of space) is assigned specific values of the environmental parameters used to define the species niche. The methodological approach, which transfers the species niche from environmental to geographical space is rooted in the duality between Hutchinson's "niche" and "biotope"11. Under climate change, the spatial extent of suitable climatic conditions for a given species can increase or decrease, driving changes in the distribution of that species. For example, a large reduction in the availability of suitable climate conditions would be expected to cause a reduction in a species' realised distribution, thus contributing to a reduction of population size and a potential increase in extinction risk 12 .

To relate changes in the megafauna species' (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*)) distributions against estimates of effective population size from the Bayesian skyride models (see Supplementary Information section S3), we used SDMs to estimate range sizes for each

species through the late Quaternary. In practice, SDMs reconstruct species' geographic distributions by relating species' presence records (in this case, fossil locality data) to a set of environmental predictors (e.g., temperature and rainfall) to map a species' geographic range using a geographic information system (GIS)¹³. Strong enthusiasm for incorporating SDMs in a variety of biological studies has resulted in intense scrutiny of the method's theoretical assumptions¹⁴. Paramount is recognising the difference between a species' fundamental niche, the full set of conditions in which a species can survive long-term, and the realised niche, the subset of the fundamental niche that is actually occupied at a given time⁵ and upon which SDMs are based. SDMs are generated using climatic data¹⁵, but a species' realised niche is also determined by other factors (such as barriers to dispersal). Projecting an SDM onto past or future climate surfaces, as is common in climate change studies, may ignore those limits while assuming a species will exist in all places with favourable climatic conditions, and that the niche is static through evolutionary time—assumptions which need to be explored for many species¹⁴. Further, combinations of climatic variables with no analogues in other time periods may result in underestimation of a species' ecological and geographic range in past or future projections¹⁶.

Therefore, range size estimates to be compared with the genetic data (results in Fig. 2 in main text) were modelled using only locality and climate data from the same time periods (42, 30, 21 and 6 kyr BP); SDMs from one time period were not projected onto earlier or later periods, and range measurements were restricted to regions for which fossils were used to build the models, rather than all potentially suitable Holarctic area. This approach allowed us to circumvent assumptions regarding climatic niche stasis through time, as well as the effects of dispersal limitations which might have prevented species from reaching areas of otherwise suitable habitat.

1.2 Palaeoclimate data

Late Quaternary climatic conditions are simulated using Atmospheric-Ocean coupled General Circulation Models (hereafter AOGCMs). An AOGCM is a set of equations simulating the dynamics of the ocean and the atmosphere under certain environmental conditions (i.e. $CO²$ concentration, ice sheet extent) to provide estimates of past climatic parameters (e.g., rainfall or temperature). Each AOGCM differs slightly in both the absolute values of estimated climatic conditions and in the geographical distribution of those conditions. To assess the effect of AOGCM choice on species' distributions and the subsequent relationship between range size and effective population size, we simulated past climatic conditions using two different AOGCMs: GENESIS2 and HadCM3.

1.2.1 GENESIS2

Four GENESIS2 simulations were used: two for Marine Isotope Stage 3 (MIS 3), one for the Last Glacial Maximum (LGM; ~21 kyr BP) and one for the mid-Holocene (~6 kyr BP). The Marine Isotope Stage 3 (MIS 3) simulations represent the warmer middle part (~42 kyr BP) and colder later part (~30 kyr BP) of MIS 3. Carbon dioxide levels were specified at 200 ppm for the MIS 3 and LGM simulations¹⁷ and 280 ppm for the mid-Holocene simulation¹⁸. Sea surface temperatures (SSTs) for the MIS 3 and LGM simulations were taken primarily from CLIMAP¹⁹, with modifications from GLAMAP-2000 and other sources²⁰. SSTs for the mid-Holocene simulation were prescribed at present-day values²¹. In all cases, insolation was calculated using orbital parameters^{22,23}. All simulations were spun up to equilibrium; results are 10-year averages.

Comparison of GENESIS2 model output to proxy data shows that temperatures in Europe are accurate to within $\pm 1^{\circ}$ C for the mid-Holocene and $\pm 2^{\circ}$ C for the LGM²⁴. For Oxygen Isotope Stage 3, ²⁵ found that GENESIS2 temperatures in southern Europe agree well with proxy data but were 3-4°C too warm in Northern Europe. Comparison of present day GENESIS2 model output with observations suggests that variability in Europe can be extrapolated to all of northern Eurasia and North America²⁶. We are unaware of any GENESIS2 model-data comparisons for palaeoprecipitation. However, for present-day northern Eurasia and North America the model is accurate to within ± 1 mm day⁻¹ when compared to observations²⁶. Atmospheric carbon dioxide boundary conditions are well-constrained^{$27,28$}.

1.2.2 HadCM3

A second set of climate model outputs for the same Quaternary periods, the warmer middle part (~40 kyr BP) and colder later part (~32 kyr BP) of MIS 3, LGM and the Mid-Holocene were derived from the Hadley Centre Coupled Climate Model Version 3 (HadCM3). The simulations form part of the ensemble presented in 29 . The particulars of HadCM3 are well documented³⁰. HadCM3 was one of the first coupled atmosphere-ocean climate models which required no flux corrections, even for simulations of a thousand years or more³¹. The climate model consists of a linked atmospheric model, ocean model and sea ice model. In HadCM3 the horizontal resolution of the atmosphere model is 2.5 degrees latitude by 3.75 degrees longitude. This gives a grid spacing at the equator of 278 km in the north-south direction and 417 km east-west and is approximately comparable to a T42 spectral model resolution. The atmospheric model consists of 19 layers. The spatial resolution over the ocean in is $1.25^\circ \times 1.25^\circ$ and the model has 20 layers. The atmospheric

model has a time step of 30 minutes and includes a radiation scheme that can represent the effects of minor trace gases³². A parameterization of simple background aerosol climatology is also included³³. The convection scheme is that of 34 . A land-surface scheme includes the representation of the freezing and melting of soil moisture. The representation of evaporation includes the dependence of stomatal resistance on temperature, vapour pressure and $CO²$ concentration³⁵.

The ocean model includes the use of the Gent-McWilliams mixing scheme³⁶. There is no explicit horizontal tracer diffusion in the model. The horizontal resolution allows the use of a smaller coefficient of horizontal momentum viscosity leading to an improved simulation of ocean velocities. The sea ice model is a simple thermodynamic scheme and contains parameterizations of ice drift and leads (Polynyas 37).

For the MIS 3, LGM and mid-Holocene, orbital parameters are taken from ²³. Atmospheric concentrations of CO_2 were taken from the Vostok ice core record³⁸ and CH₄, and N₂O were taken from EPICA³⁹. All ice-core data were on the same EDC3 timescale⁴⁰.

Ice-sheet reconstructions are developed from the ICE5G model⁴¹, which includes a detailed evolution of the ice thickness, extent and continental isostatic rebound for the whole period from the LGM to the modern at 500-year intervals. Using standard linear interpolation techniques, this dataset was used to calculate, at the scale of the climate model, the total continental elevation (including the direct thickness of the ice sheets plus the effects of isostatic adjustment), bathymetry (including isostatic changes), ice-area extent, and land sea mask for the LGM and mid-Holocene. To ensure consistency with pre-industrial boundary conditions an anomaly-based method was used to calculate palaeogeographic boundary conditions. In this method, for anomalies of a particular time-slice, palaeogeography minus pre-industrial ICE-5G data are then added to our model preindustrial geographical boundary conditions. The geographical extent and heights of the major ice sheets prior to the LGM were based on 42 , which included a calculation of the pre- and post-glacial ice. Singarayer and Valdes²⁹ used the SPECMAP⁴³ record of $d^{18}O$ history to constrain the evolution of the volume of land ice from the last interglacial up to the LGM.

Each simulation was integrated for approximately 200 years, a sufficient period of time to bring the surface climatology to equilibrium, with the final 30 years used to calculate the required climatological mean. The version of HadCM3 used does not include interactive vegetation, so all simulations use the same pre-industrial vegetation boundary condition. Similarly, aerosol loading in the model is unchanged and does not account for changes in dust during the cycle.

Using HadCM3, we obtain reasonable estimates of the global temperature glacial/interglacial range as well as trends in polar regions, although the magnitude of change at high latitudes is underestimated, as other similar models have found for the $LGM²⁹$. HadCM3 produces a pattern of cooling for the LGM which are broadly consistent with the findings from simpler models and palaeoclimatic data⁴⁴. HadCM3 performance in simulating both the LGM and mid-Holocene have been evaluated and are recognised as being either good or generally comparable with other climate models run for the same time intervals 45 .

1.2.3 Palaeoclimate variables

From both AOGCM datasets, three variables (Supplementary Figure S1.1) were selected to describe the potential distribution of each species: mean temperature of the coldest month (°C), mean temperature of the warmest month (°C), and annual precipitation (mm). Temporal trends in these climatic variables are similar between the two AOGCMs (Supplementary Figure S1.2). Palaeoclimatic simulations for GENESIS2 are at a 2×2-degree spatial resolution; palaeoclimatic simulations for HadCM3 are resampled at a 2×2-degree resolution. This conservative variable set was selected to balance the number of species occurrences versus the number of climatic variables used to calibrate species' realised climatic niches. Using many climatic variables to model the potential distribution of a species using few presence records (e.g., fossil localities) is likely to lead to model over-fitting, yielding a misrepresentation of the geographical distribution of the modelled species⁴⁶. Given the constraint of using only a small number of climatic variables, we aimed to capture the upper and lower thermal limits of each species, as well as a moisture variable. Previous applications of SMDs have used similar limited sets of climatic variables as predictors of megafauna distributions³. All figures presented in the main text were generated using climate variables from GENESIS2.

Supplementary Figure S1.1. Palaeoclimatic data (GENESIS2) for annual precipitation (mm), average temperature of the warmest month (°C), average temperature of the coldest month (°C) and the fossil record were used to estimate species potential ranges.

Supplementary Figure S1.2. Average climatic temporal trends across the Holartic based on GENESIS, left, and HadCM3, right, AOGCMs. Green (lower) lines indicate mean temperature of the coldest month (°C), red (upper) lines indicate mean temperature of the warmest month (°C), and blue bars indicate annual precipitation (mm).

1.3 Megafauna locality data

For each species, ¹⁴C-dated fossil localities from Eurasia and North America were obtained for the following calendar time intervals: 45–39, 33–27, 24–18 and 9–3 kyr BP. Radiocarbon dates (uncalibrated 14 C dates) were calibrated into calendar years using the IntCal09 calibration curve⁴⁷ using the OxCal 4.1 online calibration resource (https://c14.arch.ox.ac.uk). The 829 fossil localities included data from sequenced specimens (Supplementary TableS6.2-6.4), supplemented with fossil localities from the literature (Supplementary Table S6.1); The majority of the 829 localities used for the Species Distribution Models (SDMs) were compiled from synthetic works, rather than the original papers in which the dates were first presented, so we were unable to evaluate our data by fossil context, dated material or dating method⁴⁸. However, the vast majority (98%) of the 829 localities used were from directly dated (standard or AMS) animal remains; thus, if we assume that most dates were from bone collagen, dung, hide or hair, we anticipate that most of our directly dated samples would rank an 11 or 12 on the scale proposed by 48 . Given the breadth of the time bins used—6,000 calibrated years—the difference between dating methods should have little impact on our results, as this is significantly greater than the differences between conventional and AMS dates observed by ⁴⁸.

The list of localities is not and was not intended to be exhaustive, but was meant to cover at least those regions with genetic data to enable comparison of the estimates of potential range size and estimated effective population size. Therefore, modelled species ranges are not intended to fully represent past species distributions in great detail, and may under-represent the species' actual range in areas for which we have little data. Fossil localities are indicated in Supplementary Fig. S1.3. Data were only included where the literature contained explicit geographic coordinates or detailed site descriptions which could be located at http://toolserver.org/~geohack/. As each set of geographical coordinates relates to a specific dated fossil, localities are duplicated where more than one dated fossil has been found.

For woolly mammoth, all known fossils dating from 9–3 kyr BP are from Wrangel Island^{49,50}, with the exception of one known specimen from St. Paul Island⁵¹. This fossil distribution, consisting of two unique localities, is insufficient data with which to generate species distribution models, and so

no distribution is presented for the woolly mammoth at 6 kyr BP, even though the species was not yet extinct.

Supplementary Figure S1.3. Megafauna potential range at 42, 30, 21 and 6 kyr BP estimated from palaeoclimatic data (GENESIS2) and dated fossils for each species, represented by white dots.

Range measurements were restricted to regions for which fossils were used to build the models, rather than all potentially suitable Holarctic area. Contemporaneous Palaeolithic human sites for each period are represented by black dots. No or too few fossils were available for woolly rhinoceros and mammoth to estimate their ranges at 6 kyr BP.

Horse

1.4 Species distribution modelling

1.4.1 Model algorithms

Species distribution model (SDM) projections are sensitive to the different statistical techniques used to describe and project species' potential ranges. Mahalanobis Distance $(MD)^{52}$, a strict presence-only method, was used to model the 42, 30, 21 and 6 kyr BP distributions of each species. MD is a simple envelope technique that provides a strict presence-only measure of environmental distance, which is calculated in relation to an optimum climatic point, defined as the centroid for all occurrence points in the total climatic space. The distance between this "optimum" and the observed climatic values for each species presence is inverse to the suitability of the climate at that site. MD produces an ellipsoidal envelope around the climatic optimum space by taking into account the covariance among climatic variables.

While a variety of methods are available for modelling species distributions, certain characteristics of the fossil record help to narrow the range of algorithms from which to select. First, the fossil record provides information about the presence of species, but not about their absence, and so presence-absence algorithms must be discarded. Other well-known, more complex algorithms such as $GARP⁵³$ or Maxent⁵⁴ could be used because they generate pseudo-absences against which to test the models. However, different procedures for calculating pseudo-absences can yield significantly different modelled species ranges^{55,56}. In addition, bias in the fossil record is not simply a result of sampling effort, as with extant species, but of unevenly distributed geomorphological conditions affecting the fossilisation and persistence of remains through time, making selection of the study area on which to calculate pseudo-absences far more challenging for fossil data than for extant species for which the extent of the distribution is often known to some degree⁵⁵. After these methods are discarded, the remaining suitable algorithms are restricted to simple presence-only methods based on environmental distances to a climatic optimum, which have been shown to handle bias in the fossil record better than more complex algorithms⁵⁷. Specifically, MD has been shown to perform better than other presence-only methods in a recent comparative study⁵⁸. It has been successfully used for palaeobiology studies^{3,57,59} and is specifically recommended⁵⁷ for modelling potential species distributions using the fossil record.

1.4.2 Model implementation and performance

Species' distributions used to estimate range size (see below) were modelled using only locality and climate data from the same time periods (42, 30, 21 and 6 kyr BP). A minimum of five dated fossil localities per species/time period were used to build the models⁶⁰ (Supplementary Table S1.1). Modelling was implemented using the openModeller cross-platform modelling interface⁶¹. Each species/time period was modelled with both methods using all available locality data to build the model using both GENESIS2 and HadCM3.

To assess the impact of using a limited subset of the known fossil record on model performance for each species, we performed ten independent model runs in which a different randomly selected 75% of the data were used to build the model and 25% were used to test it each time. This evaluation does not assess the accuracy of model predictions—independent evaluation data (e.g., genetic data or additional fossils) would be required for this purpose. Rather, it provides a measure of internal consistency among repeated runs. Model performance was assessed using the Area Under the (Receiver Operating Characteristic) Curve (AUC; see 62 for a review on the advantages and disadvantages of using the AUC as a performance measure). Scores >0.75 are typically considered adequate for species distribution modelling⁶³. Random sub-set model runs were performed using GENESIS2. Species distribution models yielded consistently high AUC values under testing, with only two species/time period yielding a coefficient of variation in AUC greater than 5% (bison and musk ox, 42 kyr BP; Supplementary Table S1.2). This suggests that model performance was relatively robust.

Supplementary Table S1.1. Total number of samples used to build the SDM for each species/ time period. Some localities had multiple dated samples, and the number of unique localities is given in parentheses.

Supplementary Table S1.2. AUC scores for ten model runs using a unique 75% and 25% of the data for building and testing the model, respectively (GENESIS2). Mean AUC, standard deviation and coefficient of variation (CV) are indicated.

1.4.3 Measuring range size

To calculate modelled range size for each species/time period, the continuous suitability values mapped by openModeller were converted into deciles and the upper decile (suitability >0.9), the area of most suitable climate conditions, was used to map modelled range size (following a similar approach to 3). Assuming that only the areas with the highest suitability constituted the potential range is a conservative approach which should prevent overestimation of range sizes. Because all species were not present throughout the Holarctic for all periods, the Holarctic was divided into 3 regions: Europe, Asia and North America. Modelled ranges were cropped to exclude non-land areas and to match those regions for which fossil localities were used to generate the models (e.g., if no fossils were available from North America for a given period, as for the woolly rhinoceros, climatically suitable range from North America was excluded from the range size estimate). This ensured that aDNA and species distribution modelling methods were testing hypotheses relating to

the geographic space actually occupied by each species at a given time as indicated by the fossil record. Cropping was conducted in R^{64} using the package sp⁶⁵. Species ranges were then measured (in square kilometres) using IDRISI Taiga (Clark Labs, Worcester, MA, USA).

Distributions for the six megafauna herbivores, reconstructed using SDMs for the periods 42, 30, 21 and 6 kyr BP, contracted in size from 30 kyr BP to the present for all species, although the severity of contraction varies substantially among taxa (Supplementary Table S1.3, Supplementary Fig. S1.3). While the absolute area of species ranges modelled using GENESIS2 and HadCM3 differ, as expected, trends of range expansion and contraction through time are consistent between AOGCMs (Supplementary Figure S1.4). Estimates of range size based on HaDCM3 also shows a significant correlation with estimated effective population size (Section S4; Supplementary Figure S4.3).

Supplementary Table S1.3. Area of potential species' range (climatic suitability ≥ 0.9 .), rounded to the nearest $50,000 \text{ km}^2$.

Supplementary Figure S1.4. Estimated potential range size in km² for all 6 species at 42, 30, 21 and 6 kyr BP, modelled using the GENESIS2 (solid line) and HadCM3 (dotted line) AOGCMs. While the absolute area of species ranges differ, temporal trends in range size are consistent between AOGCMs.

1.4.4 Sensitivity of range size estimates to fossil record uncertainty

Species Distribution Models are sensitive to the initial conditions used to calibrate the models. When modelling the past distributions of extinct and extant species, initial conditions include the historical climatic data and the distribution of the fossil record. Above we address the effect of using different AOGCMs for estimating range size, but the fossil record is an incomplete and often biased representation of the past distribution of species which can also bias our results Therefore, to incorporate this uncertainty in the estimation of potential range size into the correlation between effective population size and geographic range size (Supplementary Information section S4) we performed ten additional independent model runs using GENESIS2, in which a different randomly selected 90% set of the localities was used to build the model each time. Modelled ranges from the 90% random sub-set runs were cropped and measured as described in S1.4.2. We found a positive correlation between changes in the size of available habitat and genetic diversity for the four species for which we have range estimates spanning all four time-points (although the correlation was not statistically significant for reindeer: $p = 0.101$; Supplementary Information section S4).

1.4.5 Sensitivity of range sizes to radiocarbon dating error

Radiocarbon dates associated with indirectly-dated fossils are considered less reliable than those for which the specimen of interest itself is dated⁴⁸ although in some cases (e.g., reindeer, 21 kyr BP, Spanish localities) indirectly-dated fossils can represent important extensions of a species' geographic distribution for which directly-dated fossils are unavailable. Furthermore, for reindeer, ten indirectly-dated specimens from North America were included in the analysis, as the published DNA sequences from the samples⁶⁶ were included in the genetic analysis. To examine whether the incorporation of 16 indirectly-dated fossils (ten reindeer, six bison) is likely to have influenced the detected trends in range size through time, we re-ran the models for these species excluding the indirectly-dated specimens (from Supplementary Tables S6.1 and S6.4) using GENESIS2. While the absolute area of species ranges differ, as in the random sub-set model runs, consistent temporal trends of range expansion and contraction through time are detected with these 16 specimens included and excluded (Supplementary Figure S1.5). Incorporating these new measurements into the correlation analysis did not affect the strength of the correlation between range size and effective population size, which was still significant (Supplementary Table S4.).

Supplementary Figure S1.5. Estimated potential range size in km^2 for reindeer and bison at 42, 30, 21 and 6 kyr BP, modelled using all (solid line) and only directly-dated (dotted line) fossil localities (GENESIS2). While the absolute area of species ranges differ, temporal trends in range size are consistent between fossil datasets used.

1.5 Human presence within modelled ranges

To calculate the density of Palaeolithic human fossil sites (bones, artefacts and charcoal) within the modelled geographic range for each species/time period, human fossil localities from the calendar time intervals 45–39, 33–27 and 24–18 kyr BP were overlaid on species' modelled ranges (GENESIS2) for 42, 30 and 21 kyr BP, respectively. Human radiocarbon data were derived from the INQUA Palaeolithic Radiocarbon Database v. 11 for Europe⁶⁷ and from ⁶⁸ for Siberia. Details on these radiocarbon determinations and their selection can be found in the associated citations and in Supplementary Information section S5. The most recent period (6 kyr BP) was excluded because localities were only compiled for >9 kyr BP in some data sets.

Palaeolithic human localities (Supplementary Fig. S1.3) were mapped on top of SDM results in IDRISI Taiga to identify grid cells within each species' measured range in which humans were present. Grid cells were then converted into area (km^2) to calculate the extent of each species' range occupied by humans (Supplementary Fig. S1.6).

Supplementary Figure S1.6. Overlap (km²) between megafauna and humans at 42, 30 and 21 kyr BP. Palaeolithic human localities were mapped on top of species ranges (GENESIS2), and grid cells in which humans were present were converted into area to calculate the extent of each species' range occupied by humans. Column height indicates estimates of megafauna range size; the black portion represents area of human/megafauna overlap.

1.6 Discussion

The key goal for this portion of our study was to relate changes in the megafauna species distributions to estimates of effective population size from the Bayesian skyride models (see Supplementary Information section S4). We used SDMs to estimate the potential range size for each species at four periods for which we have palaeoclimatic data, using a subset of the fossil record. The fossil list was not intended to be an exhaustive survey of all known locations for each species; rather, we targeted the fossil record for data within the same regions for which genetic data were sampled, so that SDMs and Bayesian skyride models could be explicitly compared. Modelled distributions are therefore unlikely to capture the full known distributions for some species (e.g., bison).

We have taken a conservative approach to modelling the distributions of each species; by using only contemporaneous data to build each model, rather than projecting a species' modelled climatic niche from one period to the next, we are able to avoid two potential pitfalls for SDMs: species-

climate equilibrium and climatic niche stability through time¹⁴. Species-climate equilibrium is the assumption that a species is in equilibrium with its climate, or that a species will exist in all places in which climatic conditions are favourable for its long-term survival 69 . However, many factors other than climate shape a species' ecological niche; these include barriers to dispersal, interactions with other species, and historical contingency⁷⁰, and any of these factors may result in a species' distribution being out of equilibrium with its climatic niche. For example, moist conditions on the Bering land bridge have been implicated as a barrier to dispersal to steppe-tundra species such as the woolly rhinoceros, which was adapted to drier conditions⁷¹, even though suitable habitat likely existed on both sides of the strait. Likewise, niche stability through time is the assumption that a species maintains the same climatic niche, with no niche evolution (e.g., behavioural or physiological adaptation) taking place between periods of interest. While this assumption is likely to be true for some species, resulting in either extinction or tracking of suitable conditions under periods of climate change, it will not hold true for all species. Although our fossil data are limited for some species for certain periods, we maintain that building a discrete SDM for each time period, rather than projecting the distribution from those periods for which we have more data, is more relevant for comparison with the genetic data because it represents a species' realised distribution for a given time, rather than a potentially incomplete measure of the species' climatic niche.

SECTION S2: Megafauna ancient DNA extraction, amplification and sequencing

2.1 Megafauna samples

Ancient mitochondrial DNA control region (mtDNA CR) data sets were generated for woolly rhinoceros (*Coelodonta antiquitatis*), wild horse (*Equus ferus*; the fossil species *E. lambei* has been determined to be genetically indistinguishable from *E. ferus*, based upon ⁷², hence the latter name takes precedence), and reindeer (known as caribou in North America, *Rangifer tarandus*). Subfossil samples of bone, tooth and horn were collected across northern Eurasia and North America, including the Canadian Arctic Archipelago and Greenland (Supplementary Fig. S2.1, Supplementary Tables S6.2, S6.3, S6.4). Woolly rhinoceros was only sampled in Eurasia, as the species has never been found in the New World. Sequences data sets from woolly mammoth, bison and musk ox were downloaded from GenBank (Supplementary Information section S3).

2.2 Accelerator Mass Spectrometry dating

A total of 353 Accelerator Mass Spectrometry (AMS) radiocarbon dates were obtained for woolly rhinoceros (n = 136), wild horse (n = 72) and reindeer (n = 145) from the commercial facilities offered by the Oxford Radiocarbon Accelerator Unit, UK (AMS ID: OxA), AMS 14C Dating Centre, Institut for Fysik og Astronomi, Aarhus University (AMS ID: AAR), Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectrometry (AMS ID: CAMS), and NSF Arizona AMS Facility, Physics Department, University of Arizona (AMS ID: AA) (Supplementary Tables S6.2, S6.3, S6.4).

All radiocarbon dates, including those already published, were calibrated using the IntCal09 calibration curve⁴⁷ and the OxCal 4.1 online calibration resource (https://c14.arch.ox.ac.uk). Samples with infinite radiocarbon dates and radiocarbon dates past the IntCal09 calibration curve $(c. >43,000$ ¹⁴C years before present, depending on the error of the date) were not included in the statistical analyses. Samples where the standard error of the calibrated date fell outside the calibration curve were omitted. Of the 353 new radiocarbon dates generated for this study, 16% were omitted from further analysis as their dates lay beyond the calibration curve or had infinite dates. All samples are discussed as kyr BP throughout the text, where kyr BP is defined as calendar thousand years before the present.

Supplementary Figure S2.1. Polar view of the Holarctic, with Eurasia to the right, indicating the DNA sample localities of the six megafauna species. New data sets were generated for woolly rhinoceros, horse and reindeer; further information in Supplementary Tables S6.2, S6.3, S6.4.

Supplementary Fig. 2.2. The woolly rhinoceros fossil record, including the 136 new radiocarbon dates generated for this study, plotted against latitude (top) and longitude (bottom) coordinates . Data are presented in Supplementary Tables S6.1 and S6.2. The species was present throughout Siberia right up until its disappearance from the fossil record. X-axis in calendar years BP, 1-sigma errors of the calibrated dates are included.

Supplementary Fig. 2.3. The woolly mammoth fossil record plotted against latitude (top) and longitude coordinates (bottom). The species was present throughout Siberia right up until its disappearance from the fossil record. X-axis in calendar years BP, 1-sigma errors of the calibrated dates are included.

2.3 Sequence generation

Stringent ancient DNA protocols were followed to avoid contamination from modern DNA and to assure reliability of results. All DNA extractions and PCR set-ups were performed in a dedicated ancient DNA facility isolated from multi-copy PCR work. PCR amplification, cloning and sequencing were performed at a separate DNA facility.

Ancient DNA sequences were obtained using the extraction procedures reported in 73 .

DNA was PCR amplified using overlapping fragments ranging in length from 80–560 bp, depending on the condition of the specimen, and the species being sequenced. Primers were designed to span the entire HVR-1 of the mitochondrial control region. PCR amplifications were performed in 25 µl volumes, using 1xPCR buffer, 2 mM of MgSO4, 2.0 mg/ml Bovine Serum Albumin (BSA), 0.4 μ M of each primer, 1 μ M of dNTPs, and 5U of High Fidelity Platinum Taq (Invitrogen, Carlsbad, CA). Cycling conditions were: 94˚C for 2 min, 50–70 cycles of 94˚C for 30 sec, 43–63˚C for 30 sec, and 68˚C for 45 sec, followed by 72˚C for 7 min. We included blank extraction controls and blank PCR controls in each reaction. Primer sequences and PCR-annealing temperatures are listed in Supplementary Table S2.1.

PCR products were subsequently purified with either the Invitek PCRapace PCR Purification Kit (Invitek, Berlin, Germany) or the QIAquick PCR purification kit (Qiagen, Valencia, CA), according to manufacturers' instructions. At least two independent PCRs were carried out for each fragment, and the products were either direct sequenced or cloned using TOPO TA cloning kit for sequencing (Invitrogen), with a minimum of six clones sequenced for each fragment. The overlapping of the PCR fragments resulted in a high degree of sequence replication. The sequences were obtained through the commercial service offered by Macrogen (Macrogen, Seoul, South Korea) and by inhouse sequencing at Department of Biology, University of Copenhagen, Denmark. DNA sequences were subsequently edited by eye and aligned using Se-Al version 2.0A11 (A. Rambaut, University of Edinburgh). To investigate and account contamination and for errors caused by damage or sequencing, 79% of all consensus sequences were replicated.

The data sets resulted in 274 new mtDNA sequences, including 55 woolly rhinoceros, 115 wild horse and 104 reindeer. Sequences have been submitted to GenBank with the accession numbers JN570760-JN571033, corresponding sample numbers are listed in Supplementary Tables S6.2, S6.3 and S6.4.

Supplementary Table S2.1. Primer sequences and annealing temperatures for woolly rhinoceros,

horse and reindeer.

SECTION S3: Megafauna ancient DNA sequence analysis

3.1 Data retrieval and filtering

In addition to the 274 new mitochondrial DNA (mtDNA) control region sequences of woolly rhinoceros, wild horse and reindeer generated for this study (Supplementary Information section S2), we retrieved mtDNA control region sequences of mammoth (*Mammuthus primigenius*), bison (*Bison priscus/Bison bison*), and musk ox (*Ovibos moschatus*) from GenBank (Supplementary Fig. S2.1). We also augmented the horse and reindeer data sets with additional modern and ancient sequences from GenBank (Supplementary Tables S6.3, S6.4). To summarise the global diversity of modern horse breeds, we collected 140 sequences from 28 domestic breeds (*Equus caballus*), which all had at least five sequences available: Akhak Teke, Arabian, Baise, Belgian, Caspian, Cheju, Chinese, Cleveland, Clydesdale, Debao, Exmoor, Friesian, Garrano, Haflinger, Irish, Kerry, Lusitano, Mesenskay, Mongolian, Noriker, Orlov, Pottoka, Pura, Shetland, Sorraia, Vyatskaya, Yakut, and Thoroughbred. Similarly, to summarise the global diversity of modern wild reindeer, we collected all the wild reindeer sequences available in GenBank. We grouped these into regions representing Europe, Northeast Siberia, Alaska/Yukon and the Canadian Archipelago. Due to a lack of frequency information for the limited number of sequences from the rest of the US and Canada, we grouped these together as a fifth region. Four sequences were randomly selected from each region, yielding a total of 20 modern wild reindeer sequences. In addition, we sequenced seven new modern mtDNA sequences from Urals/western Siberia and Taimyr Peninsula (Supplementary Table S6.4), as no sequences > 210 bp were available from either of these regions in GenBank (sequences published by 74 were not included as they are ≤ 150 bp long).

We calibrated the radiocarbon dates of the sequences prior to analysis. This enabled direct comparison with the range sizes (Supplementary Information section S1), which are estimated in calendar years. Hence, prior to analysis, all published sequences with infinite radiocarbon dates or with finite radiocarbon dates too old to be calibrated using the IntCal09 curve⁴⁷ ($>c$, 43,000) radiocarbon years BP, depending on the range of the radiocarbon error) were discarded from the data sets.

Sequence data sets from each species were aligned using $MUSCLE^{75}$ and checked manually using SeaView v4.2.11⁷⁶. Sequences with substantial levels of missing data after processing at (nucleotide) sites that were polymorphic among the rest of the sequences, were automatically pruned from the data sets using a home-made Perl script. Similarly, sites with a substantial level of missing or ambiguous sites (Y, R, N, ?) were discarded from the remaining sequence subsets. These filtering steps resulted in both the removal of sequences with large numbers of ambiguous/missing

bases and shorter alignments. The final mtDNA CR data sets were: woolly rhinoceros (55 seq, 348bp), mammoth (82 seq, 705bp), horse (151 seq, 288bp; 136 seq when modern domestics are excluded), reindeer (162 seq, 415bp), bison (140 seq, 549bp) and musk ox (128 seq, 633bp) (Supplementary Table S3.1), with the data sets of mammoth, bison and musk ox being reduced from those previously reported^{73,77,78} (Supplementary Table S3.2).

Supplementary Table S3.1. Summary statistics of the six megafauna DNA data sets. The Eurasian horse data set is represented both with and without the modern domestic samples. Table includes information on time bins used in the ABC and isolation-by-distance (IBD) analyses and number of sequences included in each time bin. Note that the temporal span of the time bins and sample size of each differs between the two analytical methods, as we used a minimum of three samples per time bin in ABC and a minimum of three sample localities per time bin in IBD. Because we had fewer sample localities than samples, time bins from the ABC analysis were pooled in the IBD analysis in some instances. S represents the number of polymorphic sites, π represents nucleotide diversity. The IBD p-values were determined from a randomization test with the next time-bin.

Sequence Length: 348bp

Mutation Rate Prior: Normal 0.00103355,0.000325 (substitution per generation per locus) Generation Time: 7 years

Sequence Length: 705bp

Mutation Rate Prior: Normal 0.001053,0.0003666 (substitution per generation per locus) Generation Time: 20 years

Sequence Length: 288bp

Mutation Rate Prior: Normal 0.0003988,0.00017 (substitution per generation per locus)

Generation Time: 5 years

Sequence Length: 415bp

Mutation Rate Prior: Normal 0.00060125,0.00016 (substitution per generation per locus) Generation Time: 4 years

Sequence Length: 549bp

Mutation Rate Prior: Normal 0.00102443,0.00025 (substitution per generation per locus)

Generation Time: 3 years

\$ between each American time-bin and the unique Eurasian time-bin

Sequence Length: 633bp

Mutation Rate Prior: Normal 0.00097355,0.0002 (substitution per generation per locus)

Generation Time: 2 years

\$ between each Eurasian time-bin and the unique American time-bin

Supplementary Table S3.2. Differences in sample size between original published (unfiltered) and filtered data sets of woolly mammoth, bison and musk ox.

* Relative to the sequence length before filtering

3.2 Genetic analysis

Summary statistics

We grouped the sequence data sets of each species into geographic and temporal bins to calculate summary statistics for the serial coalescent simulations. Sequences were separated into Eurasia or North America and assigned to sequential time bins within each continent (Supplementary Table S3.1). Because woolly rhinoceros was found exclusively in Eurasia, we (i) analysed a single Eurasian time-series; and (ii) grouped samples west of 90ºE and east of 102ºE in two separate geographic units, as no wolly rhinoceros have ever been recovered in between.

Summary statistics were computed using Arlequin 3.5⁷⁹ (Tajima's D and Fst) and dnaSP $v5^{80}$ (number of segregating sites, nucleotide diversity per site and haplotypic diversity). Time bins were selected to test for different population models of demographic expansion or decline at various time points during the past 50,000 years and to test for possible shifts in geographic structure using isolation-by-distance. Due to variations among species in the temporal coverage of samples, the

number of sequences in each continent and within each time bin differed among data sets. Time bins were designed to include a minimum number of three sequences each (average = 15.8, range 3–58).

To avoid over-representation of modern domestic horse sequences in subsequent analyses and to minimise computation time for serial-coalescent simulations and Bayesian skyrides, we generated random subsets of the data available on GenBank. In horse, we generated ten random data sets of 13 sequences from the subset of 140 sequences selected from Genbank. Two of the new sequences generated in this study were recovered from Neolithic Eurasian horses (specimens JW191 and JW25; Supplementary Table S6.3) and were added to the domestic data set, and we subsequently estimated summary statistics independently for each of the ten data sets. The final summary statistic vector for Eurasian Neolithic horses (time bin 11–0 kyr BP) was determined as the average of the summary statistics recovered from the ten independent data sets of 15 sequences. The procedure used for the incorporation of modern reindeer is discussed in section S3.1 above.

Isolation-by-distance (IBD)

We tested for temporal changes in the level of isolation-by-distance (IBD) within each species by calculating the correlation between pairwise genetic and geographic distances within and between consecutive time bins (Supplementary Table S3.3). Each time bin included a minimum of three geographically distinct sample localities; hence, the number of sequences in each time bin differed among species due to different sampling regimes (Supplementary Fig. S3.1). Of note, the temporal span of the time bins differed from those used in the ABC analysis because some of the ABC time bins were pooled for the IBD analysis due to small locality number; e.g., we pooled samples from $>$ 34 kyr BP (n = 4) and 34–26 kyr BP (n = 6) in North American reindeer, as they represented two localities each.

Geographic distances were estimated from latitude and longitude using the haversine formula and a spherical-earth approximation, ignoring hills. We corrected the pairwise-distance estimates among sequences for differences in calendar age of the samples following ⁸¹ and used the mutation rate average used in the serial-coalescent simulations (Supplementary Table S3.1). Hence, if two specimens were separated in time and space, only geographic distance and not sample age contributed to their genetic distance, assuming a constant clock and constant population size. Correlation coefficients were estimated in the R statistical package^{64} for each time bin and the significance of change in correlation between two successive time bins was tested through a randomisation approach using 10,000 pseudo-replicates. Briefly, for two successive time bins with

N_A and N_B sequences, pseudo-replicates were generated randomly by sampling (without replacement) N_A and N_B sequences from the merged pool of N_A and N_B sequences, and the difference in correlation coefficients was recorded. The re-sampling procedure provided an empirical estimate of the difference between correlation coefficients, assuming no change in population structure; the observed difference in correlation coefficients was compared against the re-sampling distribution to test for significance at the 5%-level (one-sided test). Pseudo-replicates were generated using a home-made Perl script and distributions were analysed using R.

Supplementary Table S3.3. Changes in isolation-by-distance through time for the continental populations in Eurasia and North America and for the gobal data (EurA $+$ NA). The correlation coefficients observed between geographic distances and pairwise genetic distances are reported for each megafauna species and for each time bin where a minimum number of five sequences were available (top line of each population panel). Genetic distances were estimated after correcting for time differences between sequence pairs. The significance of the changes in correlation coefficients between two successive time periods was tested through a randomization procedure and corresponding p-values are indicated. Significant tests (5%-level) are marked with an asterisk. Time bins are in thousands of years before present.

Supplementary Figure S3.1. Isolation-by-distance analysis of continental populations in Eurasia (EurA) and North America (NA). Correlation between genetic (calculated as nucleotide diversity corrected for temporal age) and geographic distance among samples within each time bin is indicated by the colour intensity, with values shown in Supplementary Table S3.3. The darker the colour, the stronger the correlation between geographic and genetic distance. Sample size of each time bin is indicated and an asterisk marks significant change in isolation-by-distance between consecutive bins. Crosses mark species extinction times; mainland (older) and island (younger) mammoth extinctions are included.

Approximate Bayesian Computation (ABC) and model selection

Serial-coalescent simulations (1,000,000 iterations per model) were performed using Bayesian Serial SimCoal (http://www.stanford.edu/group/hadlylab/ssc/) on a series of nine to 16 population models per species (Supplementary Fig. S3.2, Supplementary Table S3.4). Simulations were run on three data sets: (i) Eurasia; (ii) North America; and (iii) global. For woolly rhinoceros, simulations were run only for Eurasia, as the species was never found in North America. We tested a total of 217 models, resulting in 217 million serial-coalescent simulations. The K2P+Γ mutation model was used in all simulations, using the average of the posterior distributions for kappa (transition/transversion ratio) and alpha (gamma shape) estimated by BEAST. Similarly, we used the normal posterior distributions recovered from BEAST as a prior for the mutation rates (Supplementary Table S3.1). Using the age of first reproduction as a rough proxy for generation time, we assumed that generation times were: woolly rhinoceros (seven years, based on extant rhinoceros species), mammoth (20 years, based on extant elephants⁷⁸), wild horse (five years, based on Przewalski's horse⁸²), reindeer (four years⁸³), bison (three years⁸⁴) and musk ox (two years⁷³).

In all models, the effective population size at first generation was randomly sampled at each iteration from a uniform prior ranging from 1,000 to 100,000 individuals. The first model consisted of a panmictic deme with constant effective population size (Supplementary Fig. S3.2). In a second series of models, we simulated an instantaneous demographic expansion (uninformative prior, up to 10-fold) or decline (uninformative prior, down to 0.1-fold) occurring at a fixed and unique time in the past (34, 26, 19, 12.9, 11 kyr BP). These time points were chosen for the following reasons. They represented midpoints between the periods from which we have palaeoclimatic data and potential range size estimates of each species (42, 30, 21, 6 kyr BP). Also, some of them represented periods of putative climatic change, such as the beginning of the Last Glacial Maximum (LGM; 26 kyr BP), the end of the LGM (19 kyr BP), the onset of the Younger Dryas (12.9 kyr BP), and the beginning of the Holocene (11 kyr BP). Two additional models, an instantaneous expansion at 26 kyr BP followed by a decline at 19 kyr BP, and the reverse scenario (population decline at 26 kyr BP followed by an expansion at 19 kyr BP), were considered; these models were introduced to mimic demographic events possibly driven by climatic changes around the time of the LGM. With a final set of models, we aimed a final set of models at testing population subdivision between continents at 19 kyr BP (the end of the LGM) or at 11 kyr BP (the inundation of the Bering land bridge, which put an end to gene flow between continents). For woolly rhinoceros, which did not colonise the Americas, we assumed subpopulations to be west of 90ºE and east of 102ºE. Alternatively, we assumed that population subdivision was of an older date (uniform prior, 60–75 kyr BP), followed by different episodes of isolation and migration between continents. No

symmetry in migration rates was assumed and migration frequencies were randomly sampled from a uniform distribution of 0-0.01 per generation.

Approximate Bayesian Computation (ABC) analyses were performed for each model using nucleotide diversity, Tajima's D, haplotypic diversity, and Fst (except in single-continent analyses) as a vector of summary statistics. We used a tolerance region of 0.1% of all simulations and the R makepd4() function. Note that, to match the Bayesian Serial SimCoal output, the observed haplotypic diversity values were converted and multiplied by a factor $(n-1)/n$, with n being the number of sequences considered in a given time bin. Finally, the posterior probability of all N_M models was estimated using categorical regression and the R calmod() function following Beaumont⁸⁵. This procedure takes advantage of the weighted regression framework and treats a model indicator as a categorical variable that can take values ranging from 1 to N_M . R functions for ABC and categorical regression are available online at http://www.rubic.rdg.ac.uk/~mab/stuff/. Support values of the models tested in each continental population and the global species data sets are shown in Supplementary Table S3.4.

To test if the number of samples within each time bin influenced the associated estimate of nucleotide diversity, we used Spearman's ranked correlation coefficient and the R statistical package⁶⁴. Similarly, we tested the correlation between the temporal distribution of samples and nucleotide diversity. This was done by calculating the temporal distance from each sample within a time bin to the median sample age of that time bin, and correcting for sample size. Plots of nucleotide diversity against sample size and temporal span are shown in Supplementary Figs S3.3 and S3.4. We did not find any correlation.

Supplementary Figure S3.2. Simulated demographic models tested against the observed data using the ABC model-selection approach. A maximum of 16 models were tested per species. Migrations between continents is indicated in light grey. Results in Supplementary Table S3.4. **Supplementary Table S3.4.** Simulated demographic models tested against the observed data using the ABC model-selection approach. Models were run for Eurasia, North America and the global data set. A maximum of 16 different models were simulated for each species; two-population models were only analysed with the global data and encompass Eurasia and North America as separate populations, with or without migration (Supplementary Fig. S3.2). Support values for the different models are shown, and sum to 1 across all models within each data set. Values > 0.2 are in bold. Horses were analysed both with and without domestics.

Supplementary Fig. S3.3. Plots of sample size against nucleotide diversity (π) for each time bin; data from Supplementary Table S3.1. Dots represent Eurasia, triangles represent North America. In woolly rhinoceros, which is not present in North America, the two populations are from west of 90ºE (dots) and east of 102ºE (triangles); crosses represent the pooled Eurasian data. The p-value of Spearman's correlation test is indicated in the top right-hand corner of each plot, and is based on all data points within each species.

Supplementary Fig. S3.4. Plots of temporal span of samples within each time bin (average pairwise distance is in calendar years) against nucleotide diversity (π) ; data from Supplementary Table S3.1. The temporal span was calculated by summing the distance between each sample within a time bin and the temporal median, and dividing by the number of samples. Dots represent Eurasia, triangles represent North America. In woolly rhinoceros, which is not present in North America, the two populations are from west of 90ºE (dots) and east of 102ºE (triangles); crosses represent the pooled Eurasian data. The p-value of Spearman's correlation test is indicated in the top right-hand corner of each plot, and is based on all data points within each species.

Bayesian skyride plots

To explore the evolutionary history of the six species, we estimated the genealogical relationships of the sequences using the Bayesian phylogenetic inference package BEAST v1.5.4 86 , which allows the simultaneous estimation of demographic and evolutionary parameters. For each data set we performed analyses both with and without the post-mortem damage (PMD) model, which accounts for additional substitutions at the terminal branches that may be due to DNA damage⁸⁷. For each model, we assume the HKY+Γ model of nucleotide substitution and the strict molecular clock, with the evolutionary rate calibrated using the age (calibrated radiocarbon date or sampling date) of each sequence in the data set. For all analyses, two MCMC chains were run for 30–200 million iterations each, with samples drawn from the posterior every 5,000 iterations. Convergence to stationarity and mixing were evaluated using Tracer⁸⁸. The first 10% of runs were discarded as burn-in and the remainder of posterior samples from the two runs were combined. As a coalescent prior we assumed the skyride demographic model⁸⁹, which accommodates uncertainty in the demographic and phylogeographic history of each species. Although in many cases a constant population size model may be the simplest model to use, the skyride model is the most flexible coalescent model currently available in the BEAST package. In addition, the skyride model allows the estimation of theta, which approximates the effective population size, confounded by population structure, throughout the history of the sampled genealogies. Theta is proportional to the effective population size unless there is substantial structure or if sampling is biased^{90,91,92}. For some taxa, other demographic models, such as the constant population size and exponential growth/decline model, were also evaluated. In all cases, comparison between models was performed using Bayes factors⁹³.

3.3 Results and discussion

Data sets

Although some analyses were more flexible than others in terms of missing data, it was necessary to prune all the data sets in terms both of number of sequences and the number of (nucleotide) sites as described in section 3.1. First, to compare the genetic data and the results of the species distribution models (Supplementary Information section S1), it was necessary to calibrate the radiocarbon dates generated from each fossil to reflect calendar years, and samples > *c*. 43,000 radiocarbon years before present (BP) were discarded as they fell beyond the IntCal09 calibration curve47. This resulted in a significant decrease in the number of specimens in some data sets. In musk ox, for example, almost all northeast Siberian sequences (which include a distinct genetic clade⁷³), were excluded from our analyses as they could not be calibrated. Second, the Serial

SimCoal software does not accept missing sites, and we therefore filtered the data for these prior to analysis (see section S3.1). To ensure that the results from the three different analytical approaches (IBD, ABC, and BEAST) were directly comparable, we used the filtered data sets in all analyses. For differences in number of sequences and sites between the published and filtered data sets used in our analyses, see Supplementary Table S3.2.

Isolation-by-distance

We find a significant increase in IBD in Eurasian woolly rhinoceros and musk ox after 19 kyr BP, and in North American bison after 11 kyr BP (Supplementary Fig. S3.1, Supplementary Table S3.3). Although not significant, Eurasian mammoth also show an increase in the correlation between genetic and geographic distance after 19 kyr BP. Eurasian and North American reindeer and Eurasian wild horse show no changes in IBD over time, and IBD decreases in North American horse prior to the LGM. We note that although we interpret high levels of IBD as increased structuring within populations, temporal changes in genetic diversity could also be caused by local extinctions and replacements by genetically divergent populations.

Approximate Bayesian Computation and model selection

In eight of the nine continental populations, we find maximal support for models of population expansion using the ABC model-selection approach (Supplementary Table S3.4). The intensities of the increases range from 2.5 to 10-fold across populations; distribution plots of intensity estimates for the best-fit model are shown in Supplementary Figure S3.5. Bison is the only species with a well-supported signal of decline; in all other populations, models of decline are supported by posterior probabilities of ≤ 0.03 , where the support across all given models sums to 1 (Supplementary Table S3.4). The posterior probability values of the expansion models are 4–10x the values of the models of decline. In woolly rhinoceros and North American mammoth, models of expansion at 35/34, 26 and 19 kyr BP yield similar levels of support, and we are therefore unable to conclude the exact timing of the event. Similarly, we find high levels of support for population expansion at 19 and 11 kyr BP in North American reindeer. In Eurasian reindeer and musk ox, we find high support (0.44 and 0.73, respectively) for an expansion at 34 kyr BP. Interestingly, in the global populations of woolly mammoth and musk ox, we find highest support for two-population models with migration between Eurasia and North America, where the onset of migrations coincides with the timing of expansion in the continental populations (Supplementary Table S3.4). Furthermore, the end of migration at 11 kyr BP in musk ox coincides with the inundation of the

Bering land bridge, which prevented migration between continents. We could not test this timing (11 kyr BP) in mammoth, due to a lack of younger samples from North America. The estimates of effective population size at first generation were similar across populations within species (Fig. 3 in main text). Distribution plots of Ne estimates of the best-fit model are included in Supplementary Figure S3.5. We ran the ancient horse data set both with and without the modern domestic sequences, and results remained consistent (Supplementary Table S3.4).

Supplementary Figure S3.5a. Density plots of the parameter estimates in the ABC modelselection approach in the Eurasian populations. Parameter estimates of intensity and effective population size (Ne) are shown for the model with highest support. (a) Woolly rhinoceros, population increase at 26 kyr BP, (b) Woolly mammoth, population increase at 26 kyr BP, (c) Horse, population increase at 34 kyr BP, (d) Reindeer, population increase at 34 kyr BP, (e) Musk ox, population increase at 34 kyr BP. Support for all demographic models tested are shown in Supplementary Table S3.4.

Supplementary Figure S3.5a. Continued.

Supplementary Figure S3.5b. Density plots of the parameter estimates in the ABC modelselection approach in the North American populations. Parameter estimates of intensity and effective population size (Ne) are shown for the model with highest support. (a) Woolly mammoth, population increase at 26 kyr BP, (b) Horse, population increase at 26 kyr BP, (c) Reindeer, population increase at 11 kyr BP, d) Bison, population decline at 11 kyr BP. Support for all demographic models tested are shown in Supplementary Table S3.4.

Bayesian skyride plots

All skyrides can be seen in Figure 2 of the main text and in Supplementary Figures S3.6 and S3.7. For bison and musk ox (Fig. 2 in main text), the skyride estimates of changes in diversity through time differ slightly from those reported previously^{73,78,94}. This is due to our data-filtering approach, where sequences and missing sites were pruned prior to the analysis. The additional signals of expansion reported in the published studies of bison and musk ox both occurred prior to 43,000 radiocarbon years BP. Because we exclude the older samples, we do not recover the expansion signal. However, as the time period falls outside the scope of our study, which is focused on changes that occur within the most recent 50,000 years, our results are not influenced by this omission.

For horses, excluding the domestic sequences resulted in no change to the estimated demographic trajectory (Supplementary Fig. S3.7).

For some data sets, visual inspection of the skyride plots suggests that a constant population size demographic model would be a reasonable fit to the data. Bayes Factor tests (data not shown) indicate that constant population size models are a better fit to both the mammoth and woolly rhinoceros. However, because these data sets comprise samples from both a broad temporal and geographic extent, it is likely that they violate, at least during some of their evolutionary history, the assumption of panmixia made by the coalescent models used in BEAST. The skyride plot provides the most flexibility of the coalescent models currently implemented in BEAST, and therefore is the most likely to accommodate the temporal changes in structure that likely characterised each of these species. The results of these analyses (wide confidence intervals and an inability to reject simpler, constant-size model) indicate that several of the data sets simply contain too little evolutionary information to be characterised using this approach.

Supplementary Figure S3.6. Temporal changes in global effective population size and generation time (Ne $*$ τ) and potential range size in (a) woolly rhinoceros and (b) woolly mammoth. Each species panel includes the demographic trajectory of the past 50,000 years inferred from BEAST and the area of potential range size (km^2) at 42, 30 and 21 estimated using species distribution models; range sizes could not be calculated at 6 kyr BP due to insufficient fossil localities (Fig. 1 in main text; Supplementary Information section S1). We assume a generation time of seven years in woolly rhinoceros and 20 years in woolly mammoth. Radiocarbon-dated samples used in each approach are shown as vertical lines below each panel; each line represents one dated individual.

Population size **Supplementary Figure S3.7.** Temporal changes in global effective population size and generation time (Ne $*$ τ) in wild horse (a) including modern domestics (b) excluding modern domestics. Radiocarbon-dated samples used in the analysis are shown as vertical lines below the skyride in (a). We assume a generation time of five years.

SECTION S4: Gene-climate correlation

4.1 Method

The relationship between temporal changes in potential range size and changes in genetic diversity, used as a proxy for effective population size, over the past 50,000 years was evaluated in a Bayesian hierarchical modelling framework. The range size estimates were based on the results from species distribution models for four time periods with available climatic conditions (42, 30, 21 and 6 kyr BP; Supplementary Information section S1). The estimates of genetic diversity were extracted from the skyride analysis of genetic diversity based on the ancient DNA samples (Supplementary Information section S3). We estimated the relationship for the four species from which we had potential range size estimates for all four time periods: horse, reindeer, bison and musk ox. We were not able to estimate the potential range sizes of woolly rhinoceros and woolly mammoth at 6 kyr BP, as woolly rhinoceros went extinct *c*. 13 kyr BP and we did not have sufficient fossil localities for woolly mammoth at 6 kyr BP, when it was restricted to small island relict populations (Supplementary Information section S1).

Genetic diverstity estimates from BEAST are reported as a set of lines, where each line is an independent estimate of the trend in genetic diversity for the sampled population (Supplementary Fig. S4.1). These are usually summarized (e.g., by Tracer⁸⁸) as a mean with a relatively large 95% Bayesian probability interval. However, it would be misleading to base further regression analysis on these mean values, as it would underestimate the uncertainty of the genetic diversity estimates.

To incorporate this uncertainty, we sampled 1,000 individual skyrides from the posterior distribution, available from the BEAST log files. For each of these, we calculated the mean genetic diversity of 6 ka intervals centred around the dates for which we had simulations of global climate (45–39, 33–27, 24–18 and 9–3 kyr BP; Supplementary Information section S1). We then carried out 5,000 individual Bayesian hierarchical linear regressions of these values on the estimated range sizes, and combined the resulting posterior distributions of the regression parameters to yield the final parameter estimates.

To incorporate the uncertainty in the projections of range size due to potential bias in the fossil record, we generated ten species distribution models for each species/time period, randomly subsampling 90% of the fossil localities for each of 10 model runs (see Supplementary Information section S1) using climate variables from GENESIS2. For each of these ten models, plus the full

model (all localities), we measured the size of the projected range. Within each of the 5,000 individual linear regressions, the climatic range size at each time point was sampled randomly from the set of potential range sizes.

Supplementary Figure S4.1. Fifty randomly selected skylines for musk ox extracted from BEAST. Though there is an apparent overall trend, there is also considerable variation in the trajectory of each line.

The WinBUGS model used a common prior for the regression slopes for all four species, and independent priors for the intercepts. The biological rationale for this model is that although species exhibit positive temporal relationships between range size and abundance, the exact parameters of this relationship have been found to vary between different species⁹⁵. Thus, points for different species may not simply be pooled. Using a hierarchical model for the regression slope allows a combined analysis of the regression slopes without enforcing a common intercept.

The WinBugs model used was:

```
Model
{	
         for (i in 1:N) 
        \{pos[i] \sim \text{dnorm}(mul[i], tau)mu[i] <- alpha[species[i]] * bioms[i] + beta[species[i]]
         } 
         for (j in 1:Nspec) 
\{alpha[i] \sim \text{dnorm}(mu.alpha, tau.alpha)beta[j] \sim dnorm(0, 1.0E-6)
 } 
        tau \sim dgamma(0.001, 0.001) sigma <- 1/sqrt(tau) 
        sigma.alpha \sim dunif(0,100)
        tau.alpha <- 1/(sigma.alpha*sigma.alpha) 
       mu.alpha \sim dnorm(0, 1.0E-6)
}
```
In WinBUGS, the Gibbs sampler was run in three individual chains for 50,000 iterations. The first 25,000 iterations were discarded as burn-in, and the remaining 25,000 were thinned by 1:25 to 1,000. Of these three chains of 1,000 values, 200 iterations were picked randomly and saved, resulting in 200 values times 5,000 skylines = 1,000,000 simulated values from the posterior distributions. These values represent a full sample of the posterior distribution for the relationship between the two variables, and incorporate error estimates from both the skyride analysis and the SDM-projected climatic range sizes.

4.2 Results

The results of a Bayesian analysis are probability distributions that reflect the degree of belief in the estimated parameters. To make the results comparable to the results of standard frequentist regression tests, we report the proportion of the posterior density of the slopes that is lower than zero. This is comparable to the p-value from a standard one-tailed t-test. The results are summarized in Supplementary Table S4.1 and Supplementary Figure S4.2.

Supplementary Table S4.1. Summary of the posterior parameters of the Bayesian hierarchical model. SE is the standard deviation of the posterior distribution. Here p represents the proportion of values that are below 0, and is comparable to the p-value from a standard one-tailed test. Range data are modelled using the GENESIS2 climatic simulations.

Supplementary Figure S4.2. Relationship between Ne*τ and range size (modelled with GENESIS2), summarized as posterior probability distributions of regression slopes from a Bayesian hierarchical regression. The proportion of probability densities below zero (analogous to a onetailed p-value) can be seen in Supplementary Table S4.1.

The distributions of the six megafauna herbivores, reconstructed using SDMs for the periods 42, 30, 21 and 6 kyr BP, decreased in size from 30 kyr BP to the present for all species, although the severity of decline varies substantially among taxa (Supplementary Fig. S1.3). These trends are mirrored by genetic diversity in four of the six species, where there is a strong positive correlation

for horse, bison and musk ox, and a positive relationship for reindeer (Supplementary Fig. S4.3). Of note, due to the large confidence intervals, the slope for reindeer would not be considered significant when the posterior distribution is compared to a one-tailed significance value of 0.05. A positive correlation between range size and genetic diversity is consistent with ecological theory: the relationship between geographic distribution (range size) and species abundance is one of the best-documented patterns in macroecology⁹⁶. These findings support the validity of climatic range as a proxy for range size, and of genetic diversity as a proxy for effective population size. The observation that effective population size is dependent on climate also strongly supports a role for climate in driving the population dynamics of megafauna species.

which we had sufficient data for a correlation analysis, modelled using GENESIS2. Genetic **Supplementary Figure S4.3.** Correlation between Ne*τ and range size for the four species for diversity is shown as the mean and standard deviation of the 1,000 values used in the regression analysis. The mean values of slope and intercept (Supplementary Table S4.1) were used to draw the trendlines. Error bars represent measures of uncertainty: range sizes calculated using ten random 90% subsets of fossil localities per period (horizontal bars) and posterior probabilities of Ne*τ (vertical bars) (S1 and S4).

To assess whether the analysis was robust with the inclusion of the data available for woolly rhinoceros and woolly mammoth, for which we did not have range size estimates at 6 kyr BP, we repeated the analysis with the three potential range size data points (42, 30, 21 kyr BP) for these two species. As expected, due to wide probability intervals of the skyrides for woolly rhinoceros and woolly mammoth (Supplementary Fig. S3.6), no relationship was detected for these two species, and the results for the remaining four species did not change.

4.3 Assessing effect of AOGCM choice

To specifically assess the effect of AOGCM choice on species' ranges (horse, reindeer, bison and musk ox) and the subsequent relationship between range size and effective population size, we also measured potential ranges modelled with an alternative Atmospheric-Ocean coupled General Circulation Model, HadCM3. The correlation between these alternative range size estimates and the estimates of genetic diversity is comparable to those for GENESIS2, and are shown in Supplementary Table S4.2 and Supplementary Figures S4.4 and S4.5. The species distribution model was run for the full set of fossil localities only (i.e. no subsampling was performed), and the genetic diversity data was represented by 1,000 different BEAST trees.

Supplementary Table S4.2. Summary of the posterior parameters of the Bayesian hierarchical model. SE is the standard deviation of the posterior distribution. Here p represents the the proportion of values that are below 0, and is comparable to the p-value from a standard one-tailed test. Range data are modelled using HadCM3.

Supplementary Figure S4.4. Relationship between Ne*τ and range size (modelled with HadCM3), summarized as posterior probability distributions of regression slopes from a Bayesian hierarchical regression. The proportion of probability densities below zero (analogous to a one-tailed p-value) can be seen in Supplementary Table S4.2.

Supplementary Figure S4.5. The relationship between $Ne^* \tau$ and range size for the four species for which we had sufficient data for a correlation analysis, modelled using HadCM3. Genetic diversity is shown as the mean and standard deviation of the 1,000 values used in the regression analysis. The mean values of slope and intercept (Supplementary Table S4.2) were used to draw the trendlines.

4.4 Influence of sample distribution and -size on results

The positive correlation observed between geographic range and genetic diversity could potentially be caused by the spatial distribution of samples and sample size, so the wider the distribution, the more palaeohabitats covered and consequently the larger the forecasted range. Similarly, the genetic diversity may increase with the number of samples and the geographic range covered. To investigate the effect of sample distribution, we calculated the mean pairwise geographic distance between all samples within each of the four time bins (45–39, 33–27, 24–18 and 9–3 kyr BP). Geographic distances were calculated between the LAT/LON coordinates using the Haversine formula and ignoring hills. For species present in both North America and Eurasia, pairwise distances between continents were rooted through Beringia (LAT 66.07, LON -168.92) to avoid crossing of the North Pole. To account for differences in sample size between time bins, we

averaged the pairwise distances by the number of samples. However, due to differences in the number of samples from each locality, we also averaged the geographic distances within each time bin by number of unique localities. As a third measure of spatial distribution, we calculated the distance between the two furthermost samples within each timebin. To asses the influence of sample number (disregarding spatial distribution), we estimated the correlation between estimates and sample size.

The distribution measures were compared to the mean values of genetic diversity and potential range size estimated for each time bin. To ensure that comparisons with our results were unbiased, we used the same WinBUGS hierarchical regression model to perform the correlations, and summarized our results by the proportion of the posterior distribution of slope values that are below 0 (see above). The results are presented in Supplementary Table S4.3. All posterior probability intervals include 0, indicating that the relationship between population and range size is unaffected by any relationship with the geographic distribution and number of samples.

Supplementary Table S4.3. Summary of Bayesian hierarchical linear regression models between measures of sampling (rows) and genetic diversity or range size (columns). Numbers indicate the proporation of the posterior density for the regression slope that lies below 0, and is thus comparable to the "p"-values given for the effective population size - range size correlation and to one-sided p values in frequentist statistics.

To investigate whether the inclusion of 16 non-directly dates reindeer and bison samples (Supplementary Information section S1) influenced the positive relationship between range size and genetic diversity, we repeated the correlation analysis using GENESIS2 range sizes estimated with those data excluded. The significance of the correlation was not affected (Supplementary Table S4.4).

Supplementary Table S4.4. Summary of the posterior parameters of the Bayesian hierarchical model, with range sizes estimated using only directly-dated fossils for all species. Range data are modelled using GENESIS2. Here p is the proportion of probability densities below zero and is analogous to a one-tailed p-value.

SECTION S5: Temporal and spatial overlap of humans and megafauna

5.1 Introduction

To compare the temporal and geographic distribution of humans and megafauna in Europe and Siberia, we use dated faunal remains and radiocarbon determinations from human occupations for which we have latitude and longitude data. The basic premise is that the frequencies of dated sites or faunal remains can be used as a rough proxy for human or fauna population size at different points in time^{97,98,99}. Differences in their geographic and temporal distribution were used to investigate whether humans and megafauna occupied similar areas at similar points in time and whether higher frequencies of humans were associated with lower frequencies of faunas, as one might expect if humans were directly or indirectly impacting the large animals.

5.2 Data collection

Fanual materials (n=2,996) come from a number of sources. Half (n=1,439) are directly-dated specimens used in this paper (Supplementary Information sections S1, S2) or summarized in 97,98,100,101. An additional 1,557 specimens come from indirectly-dated palaeontological deposits and archaeofaunas. In Europe, these are primarily from sources compiled as part of the Stage 3 Project¹⁰². In Siberia, they come from sources cited in Supplementary Table S6.5. The indirectlydated faunal material was included for multiple reasons. Firstly, the integrity of these data were good (see handling of samples below) and were comparable to the European human data. Secondly, had we not included the indirectly-dated information, we would ignore large amounts of data indicating the presence of the six megafauna species at particular points in time and in conjunction with humans. If we ignored these because they are not directly dated, our sample of direct material would be biased. Finally, including the indirectly-dated specimens considerably increased our samples sizes; without these data included, musk ox in Europe and bison in Siberia were uninformative, due to the rarity of their occurrences in the fossil record.

These indirect dates apply only to determinations of geographic overlap and temporal trends in radiocarbon frequencies as outlined in this section, and are presented within the main text. We also provide a replicate analysis using directly-dated only material for comparison, with similar results (Supplementary Fig. S5.2). The potential range size estimates used in the analysis of overlap between humans and megafauna ranges at 42, 30 and 21 kyr BP used directly-dated materials only

(except 16 indirect dates, discussed in Supplementary Information section S1), and provide another, quasi-independent assessment of these same patterns.

Indirectly-dated megafauna specimens from Europe

In Europe, data were selected from the Stage 3 database provided they met a number of criteria. 1) Ages had to be associated with the presence of one of the five key taxa being studied in Europe (woolly rhinoceros, woolly mammoth, horse, reindeer and musk ox). 2) All ages had to be clearly identified as being radiocarbon determinations (standard or AMS) or, in a few cases, had to come from organic materials that could reasonably be inferred to have been radiocarbon-dated; luminescence and uranium-thorium dates were excluded. 3) Each radiocarbon age had to have associated latitude and longitude information, lab codes and reported errors less than 10% of mean ages. All ages greater than 45,000 radiocarbon years before present were also excluded. 4) Any radiocarbon determinations that were directly associated with a given taxon were identified and assigned correctly. For example, a deposit containing horse, reindeer and woolly rhinoceros might be placed at 27,000 BP based on the dating of a horse tibia. The horse would be identified as "directly dated" and tallied with the directly dated specimens, while the other two taxa would be assigned an age of 27,000 BP but be considered "indirectly dated". These indirect radiocarbon ages were then combined with the directly-dated material and compared to trends in human radiocarbon frequencies. Note because of the temporal focus of the Stage 3 Project, the data on early European faunas (prior to 20–18 kyr BP) is actually somewhat richer than that for later periods.

Archaeofaunal data from Europe and Siberia

A further subset of purely archaeological faunas was also identified and their temporal trends examined (Figure 4 in main text). In the case of the Stage 3 data from Europe, radiocarbon ages were tallied only when associated with archaeological stone tool industries. To make the data comparable to the Siberian dataset, information was summarized by occupation (n=380) rather than individual radiocarbon age, with occupations assigned primarily on the basis of excavation layers identified in the Stage 3 database. When detailed information on individual sites and excavations was lacking, multiple radiocarbon ages within occupations were averaged, but not weighted or pooled.

The Siberian data were compiled from 98 radiocarbon-dated cultural occupations of 68 Upper Palaeolithic archaeological sites, each of which listed at least one of the six megafuna species. The

data and references are listed in Supplementary Table S6.5. An important note is that the radiocarbon dates presented are again not necessarily direct dates on a megafauna specimen, but are dates from materials (e.g., charcoal or even some other animal bone) associated with the listed species. The sites range in age from *c*. 41–12 thousand calendar years ago (kyr BP) and geographically come from the Ob', Yenisei, and Lena River basins as well as the eastern Transbaikal and far northeast Russia. All of these cultural occupations are interpreted to represent Upper Palaeolithic occupations. Middle Palaeolithic occupations were excluded. There are a few other notable Upper Palaeolithic assemblages with rich faunal records that were not included in the analysis; these are sites or occupations with no associated radiocarbon ages (e.g., the later Upper Palaeolithic occupations at the Krasnyi Iar sites, layer 8 at Diuktai Cave), only infinite dates (e.g., Makarovo-4), or problematic radiocarbon chronologies (e.g., Mogochino, Studenoe-1).

All taxonomic identifications were done by primary investigators of the archaeological sites. In most cases, published archaeological reports describing these sites provide only "kitchen lists" of faunal taxa present, while detailed statistics like number of individual specimens present (NISP) or minimum number of individuals (MNI) are not reported (although there are some notable exceptions, for example^{103,104,105,106}; information included in Supplementary Table S6.5). Identifications reported in the primary literature are often at the genus level, which is not a problem for *Coelodonta*, *Mammuthus*, *Bison*, and *Rangifer*, but it means that some of the remains identified as *Equus* could include *E. hemionus*, the Asiatic wild ass. Similarly for musk ox, multiple species may occur, including *Ovibos moschatus* and *O. pallantis* $\binom{106,107}{n}$.

Dates were gathered from the primary literature, including dates on animal bone, charcoal and other organic materials associated with Palaeolithic artifacts or features. Dates from non-cultural layers (e.g., from above or below a cultural layer) or from problematic materials (e.g., soil organics) were omitted, as were obviously aberrant dates (i.e., those that were clearly discordant from other dates in the same occupation, or were not in accord with other occupations of the same site). Multiple dates from the same occupations were averaged, using the method described by ¹⁰⁸. This was done to keep occupations with multiple dates (for example, Mal'ta, which has 13 radiocarbon dates for the same cultural layer) from weighing more heavily in the analysis than occupations with single dates. Latitude and longitude data were obtained using published descriptions of site locations and Google Earth.

Human data

Siberian human occupations come from ¹⁰⁹. The authors provide list of 516 georeferenced radiocarbon dates from 129 archaeological sites, along with summaries by individually-dated component. The radiocarbon ages for each occupational component were used here (n=233).

European human radiocarbon ages come from the INQUA Palaeolithic Radiocarbon Database, v. 11⁶⁷. These data represent over 7,000 radiocarbon determinations from more than 1,500 sites. Due to the size and diverse nature of the INQUA data set, radiocarbon ages were not aggregated by archaeological occupation as done in Siberia. The data were cleaned for obvious errors, however, including: a) using only ages between 45,000 and 7,500⁻¹⁴C years BP, b) excluding all ages without latitude and longitude data, c) excluding all ages without associated 14 C errors, d) excluding all ages without lab codes, e) excluding dates of palaeontological deposits and f) excluding any determination with an error greater than 10% of the mean. A handful of discordant dates were also removed, mostly very young dates from purportedly old deposits. Although most sites have only a handful of ages, a few sites have many. These few sites are long, continuously occupied stratigraphic sequences, and the multiple ${}^{14}C$ determinations generally span the EpiPalaeolithic to Middle Palaeolithic $(c. 45-12,000¹⁴C$ years BP) rather than being clustered in individual occupations. They are not biased geographically, and include sites in England, Spain, France, Germany and Russia.

This yielded a total of 5,875 ages from over 1,461 sites in Europe. These include those produced by both anatomically modern *Homo sapiens sapiens* and archaic *Homo sapiens neanderthalensis*, the latter typically being associated with Middle Palaeolithic, Mousterian stone-tool industries. Although the Neandertals disappeared from most of Europe by 30,000 years ago, current interpretations suggest they were top-tier predators and should therefore have impacted megafauna populations when and where they were present $110,111,112$.

While we were unable to aggregate the European human data as done in Siberia, we were able to assess the use of individual determinations by comparing patterns in the data provided by 68 . In that case, frequencies of individual 14C determinations and dated components per 500-year interval are very tightly correlated ($r=907$, $t=17.2$, $df=64$, $p<0.01$; Supplementary Fig. S5.1) and the same is expected to hold true for Europe.

Supplementary Figure S5.1. Comparison of ¹⁴C trends by aggregation method. Data points represent the binned, calibrated radiocarbon probabilities per 500-year interval for each data set (dated occupation; individual ${}^{14}C$ determinations). Periods with high numbers of individual radiocarbon dates also have high numbers of independent, dated occupations.

5.3 Data analysis

Summarizing radiocarbon frequencies and geographic data

To compare frequencies of different taxonomic groups, radiocarbon ages for all dated components, individual radiocarbon ages (European humans), or dated megafauna were summed in 500 calendar-year intervals from 50,000–0 BP (blocks 0-499 BP; 500-999 BP; 1,000-1,499 BP; etc.). Rather than using dated midpoints, the various radiocarbon ages were first calibrated using Calib 6.0 and the IntCal09 calibration curve¹¹³. A script was then used to collapse the year-by-year probabilities output by Calib 6.0 (options, write distribution files = "yes") into 500-year blocks using R^{64} . This allowed us to use moderately-sized time intervals without worrying about larger errors associated with many determinations, the correct assignment of ages that fall close to interval divisions, or the non-normal distribution of the underlying, calibrated dates.

Mean latitudes and longitudes and their standard deviations were also calculated using the probability of a determination falling into a 500-year interval to weight its contribution. Thus dates that were highly likely to fall in a particular interval contributed heavily to estimates of the average latitude/longitude, while a determination that had a small possibility of falling in an interval

contributed little. Graphs of mean latitude and longitude for dated faunas and archaeological sites from Europe and Siberia are shown in Supplementary Figure S5.2. The area shared by humans and faunas at specific time intervals was approximated by identifying the latitudinal and longitudinal extent of the region held in common between them per interval (using mean lat/long \pm 1sd), calculating its area, and expressing it as a percentage of the area occupied by the a given taxon (again at mean lat/long \pm 1sd). These data and variation in location is discussed in the primary text and shown in Figure 4.

Timespan of comparison

Radiocarbon data were initially binned and mean latitudes and longitudes calculated across the entire IntCal09 sequence (50,000–0 calendar years BP), but trends in calibrated radiocarbon frequencies were compared across a smaller time range. First, no data were considered for periods beyond 45 kyr BP. Underlying ${}^{14}C$ data were too few for most taxa and regions, and the reliability of such dates more questionable. The younger end of the sequence was held at 12 kyr BP, the period by which most of the megafauna other than reindeer had substantially declined and the frequency of Palaeolithic occupations also drops off. Supplementary Figures S5.3 and S5.4 show the temporal distribution of binned, calibrated radiocarbon frequencies for the two regions using directly dated faunas only and with indirectly dated faunas included.

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Supplementary Figure S5.2. Plots showing latitudinal and longitudinal overlap between megafauna (coloured shading) and human (grey shading) calibrated radiocarbon ages, A. Europe direct dates only, B. Europe indirect dates added, C. Siberia direct dates only, D. Siberia indirect dates added. Error bars are \pm 1s.d.

Supplementary Figure S5.3a. European radiocarbon frequencies, humans and directly dated faunas only.

Supplementary Figure S5.3b. European radiocarbon frequencies, indirectly dated faunas included.

Supplementary Figure S5.4a. Siberian radiocarbon frequencies, humans and directly dated faunas only. The first panel shows the paeleoclimate data for the corresponding period.

Supplementary Figure S5.4b. Siberian radiocarbon frequencies, indirectly dated faunas included. The first panel shows the paeleoclimate data for the corresponding period.

5.4 Comparing radiocarbon frequencies of humans and megafauna

We compare radiocarbon frequencies among taxa after accounting for the possible effects of taphonomy and climate, following methods outlined in $97,98$ and 114 . Our chosen climate proxy was Shackleton's 24MD952042 North Atlantic benthic ¹⁸O core, corrected to the SFCP2005 timescale^{115,116} (variable, ¹⁸O; first panel in Fig. S5.4a,b). This is the same fine-grained proxy used in the previously cited studies, is appropriate for comparing trends in geographically widespread locations and mirrors but is less noisy than the Greenland ice-cores.

To incorporate issues of taphonomy and preservation in the human data, we used the model proposed by 117. Their formula calculates an expected number of observations at time *t* for a constant, random phenomenon suffering solely taphonomic losses. We converted this to an estimate of the proportion of original observations surviving at each 500-year interval midpoint (12,250 calendar years BP; 12,750 calendar years BP; etc.) as N_t/N_0 . These values scale between 0 and 1, decline in a curvilinear fashion, and were used as predictors in our regression models (variable, Surv). Fits were slightly better than simple log transforms, with somewhat more variation across intermediate values but a reduced tendency to overestimate extremes. While this approach differs from that advocated by the original authors, we argue that it is more appropriate in cases such as ours, where similar taphonomic histories cannot be assumed for all sequences¹¹⁸.

As an ancillary measure, we also calculated the absolute difference (variable, AbsDif) between radiocarbon and calendar years for each interval using the IntCal09 curve. For example, the period from 29–28.5 kyr BP corresponds to 24.146–23.743⁻¹⁴C years BP (ignoring error). The corresponding radiocarbon interval is thus 403 years long, or 97 years shorter than the corresponding calendar span. This interval would have a measure of "-97". Exactly equal intervals would have a value of "0" assigned, etc. These measures were meant to provide a check on possible over- or underrepresentation of parts of the calendar due to differences in atmospheric ${}^{14}C$ production. A file containing the benthic 18 O sequence, calculated survivorship and 14 C/calendar differences is provided in the supplemental archive ("climtaph.csv").

Comparison among taxa in Siberia and Europe were based on partial correlations after controlling for the three variables just mentioned. This was done using the residuals from a multiple regression of calibrated radiocarbon frequency (variable, ${}^{14}C$; the binned sums) against each main effect and allowing for a survivorship by climate interaction $({}^{14}C \sim \text{Surv} + {}^{18}O + \text{AbsDiff} + \text{Surv}.{}^{18}O)$. We then looked at how human frequencies compared with those of other faunas. In Europe, comparisons
using indirectly dated faunas were done only after excluding 676 radiocarbon determination from the INQUA human database that were also found in the Stage 3 archaeofaunas.

While not perfect, the overall behaviour of the models is good to very good in most cases, although the actual amount of variation explained by the taphonomic and climate variables varies substantially and the residuals in some taxa and regions still deviate from normal. Examples of such deviations includes higher than expected frequencies of human occupations at the Pleistocene-Holocene boundary, high frequencies of several indirectly-dated European faunas around 32 kyr BP (Fig. S5.3b), and the irregular behavior of several directly dated taxa such as European musk ox and, to a lesser extent, European horse and Siberian bison. In the latter cases this clearly results from the substantial gaps in the 14 C record (Supplementary Fig. S5.3a) and one should be cautious when drawing inferences from these data.

Partial correlation coefficients for humans versus European and Siberian faunas are presented in Supplementary Table S5.1. After controlling for the possible influence of climate and taphonomic losses, there appears to be little relationship between humans and any of the faunas other than mammoth and perhaps Siberian musk ox (Figure S5.5a,c). There is also little relationship among changes in the frequencies of dated faunas. Again, part of this is due to the small sample sizes of many directly dated taxa.

If the indirectly dated materials are included, changes in the frequency of dated faunas and humans in Europe become more positively correlated (Supplementary Table S5.1b; Supplementary Fig. S5.5b,d) and higher yet for OIS 3 material only (45–22 kyr BP). Correlations among faunas other than musk ox also become very high (.85 $\leq r \leq$.95). In Siberia, residual radiocarbon frequencies of humans and faunas other than musk ox also become moderately but positively correlated, echoing previously reported patterns identified for humans and woolly mammoths $97,98$. The relationship with humans reflects the incorporation of archaeological faunas, particularly the OIS 3 faunas in Europe, while the higher correlations among faunas reflect the fact that many of these animals regularly co-occur within particular archaeological deposits. The frequencies of archaeological faunas and non-faunal archaeological deposits remain highly correlated throughout OIS 3, including both broad increases from 45 kyr BP to roughly 30 kyr BP and general declines between 30 and 22 kyr BP (r=.82), and it would be interesting to see if these continued past the Last Glacial Maximum. While suggestive of some common driver for humans and faunas, this strong, positive relationship cannot be read as absolute proof that both humans and faunas were more common at certain times, since people might be expected to preferentially incorporate larger animals even if the latter were in decline.

Regardless, these changes are not the clear-cut indicator one would expect if people were negatively impacting these megafauna; more human occupations do not appear to lead to fewer occurences of any taxon. These results are not necessarily surprising given the often limited overlap in their ranges (Fig. 4 in main text, Supplementary Fig. S5.2). Humans and musk ox tend to be found in very different regions of Europe and Siberia, and in Siberia woolly rhino and woolly mammoth appear to shift their ranges northward even as human distribution remains fairly constant through 12,000 kyr BP. Opportunities for humans to impact these taxa may have been limited as a result. These results do not deny humans a role in the eventual extinction of any taxon and will merit reconsideration as additional remains are uncovered. However, they do cast doubt on whether such extinctions occurred solely as a consequence of human impact.

Supplementary Table S5.1a. Partial correlations between the frequency of dated humans and faunas per 500-year time period after controlling for climate and taphonomy. Residuals based on the model described in the text using directly dated faunas only.

Supplementary Table S5.1b. Partial correlations between the frequency of dated humans and faunas per 500-year time period after controlling for climate and taphonomy. Residuals based on the model described in the text using directly and indirectly dated faunas.

Supplementary Figure S5.5a. Scatterplot of residual ¹⁴C frequencies for Europe. "ho" horse; "hu" human; "mo" musk ox; "rd" reindeer; "rh" woolly rhino; "wm" woolly mammoth. Directly dated material only.

Supplementary Figure S5.5b. Scatterplot of residual ¹⁴C frequencies for Europe. "bi" bison; "ho" horse; "hu" human; "mo" musk ox; "rd" reindeer; "rh" woolly rhino; "wm" woolly mammoth. Indirect dates included.

Supplementary Figure S5.5c. Scatterplot of residual 14C frequencies for Siberia. "bi" bison; "ho" horse; "hu" human; "mo" musk ox; "rd" reindeer; "rh" woolly rhino; "wm" woolly mammoth. Direct dates only.

Supplementary Figure S5.5d. Scatterplot of residual ¹⁴C frequencies for Siberia. "bi" bison; "ho" horse; "hu" human; "mo" musk ox; "rd" reindeer; "rh" woolly rhino; "wm" woolly mammoth. Indirect dates included.

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SECTION S6: Data tables and sample information

Table S6.1. Dated fossil localities of the six megafauna species used to build the species distribution models; woolly rhinoceros (WR), woolly mammoth (MAM), wild horse (HRS), reindeer (RD), bison (BIS) and musk ox (MOX). Most specimens are directly dated; n/a in the AMS ID column indicates indirectly-dated specimens. In addition, woolly rhinoceros, horse and reindeer fossils with calibrated ages within 45–39, 33–27, 24–18 and 9–3 kyr BP from Supplementary Tables S6.2, S6.3 and S6.4 were included in the analysis. References follow below the table.

Supplementary Table S6.1 references

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Supplementary Table S6.2. Woolly rhinoceros (*Coelodonta antiquitatis*) sample information, listed by calibrated radiocarbon age. Data include radiocarbon age, locality information, and institution currently housing the sample. BC denotes radiocarbon dates beyond the calibration curve. Information on new radiocarbon dates and the GenBank accession numbers of new sequences (JN570760–JN570863) are included. Institution abbreviations used in Supplementary Tables S6.2, S6.3 and S6.4 are listed below.

AMNH: American Museum of Natural History, New York, USA

CGG: Center for GeoGenetics, Natural History Museum, University of Copenhagen, Denmark

CMC: Canadian Museum of Civilization, Gatineau, Quebec, Canada

CMN: Canadian Museum of Nature, Gatineau, Quebec, Canada

EPQ: Department Of Early Prehistory and Quaternary Ecology, Tuebingen

GIN RAS: Geological Institute, Moscow, Russian Academy of Sciences, Russia

GYW: Government of Yukon, Dept. Turism and Culture, Whitehorse

IPAE RAS: Zoological museum of Institute of Plant and Animal Ecology, Ekaterinburg, Russian Academy of Sciences, Russia

KIC: Khatanga Ice Cave, Taimyr Peninsula, Russia

KU: Kansas University

MPI EVA: Max Plank Institute, Leipzig, Germany

PIN RAS: Paleontological Institute, Moscow, Russian Academy of Sciences, Russia

ZIN RAS: Zoological Institute, St. Petersburg, Russian Academy of Sciences, Russia

ZMK: Zoological Museum, University of Copenhagen, Denmark

Supplementary Table S6.3. Horse *(Equus ferus*) sample information, listed by calibrated radiocarbon age. Data include radiocarbon age, locality information, and institution currently housing the sample. Information on new radiocarbon dates and GenBank accession numbers of new sequences (JN570919–JN571033) are included. Some DNA sequences were generated from specimens with published radiocarbon dates; these references follow below the table.

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Supplementary Table S6.4. Reindeer (*Rangifer tarandus*) sample information, listed by calibrated radiocarbon age. Data include radiocarbon age, locality information and institution currently housing the sample. BC denotes radiocarbon dates beyond the calibration curve. Information on new radiocarbon dates and GenBank accession numbers of new sequences (JN570760–JN570863) are included. GenBank accession numbers of previously published sequences used in the genetic analysis are included. References follow below the table.

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Supplementary Table S6.5. Megafaunal taxa present in Upper Palaeolithic archaeological sites of Siberia, by calibrated radiocarbon age. Table includes information on the minimum number of megafauna individuals reported at each site (NISP). The data are presented in Figure 4 of the main text. References are listed below table.

*May include *Equus hemionus*.

†Radiocarbon age is average of two or more.

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