Supplementary Methods

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Fossil data

We compiled dated and georeferenced fossil records for woolly mammoths (*Mammuthus primigenius*) during the Late Pleistocene and Holocene in Eurasia and North America. All records were sourced from publicly accessible databases and published literature. For each fossil we recorded information on its location, age and method used for dating, material dated and several other criteria (*1*). Because poor estimates of age can lead to erroneous inferences of the causes and consequences of past events (*2*), we assessed the age reliability of the mammoth

fossil record following the criteria devised by Barnosky and Lindsey (*3*). Records not meeting these criteria were removed from the database and not used for any further analysis. All reliable ages were calibrated using OxCal (*4*) and the IntCal13 calibration curve (*5*). Fossil data used in the analyses can be found in Appendix 3 of Fordham and Brown (*1*). The R code used to determine high-quality *M. primigenius* fossils can be found here:

https://github.com/GlobalEcologyLab/Mammoth/tree/master/extras.

To map the location of megafauna fossils in Eurasia that have been radiocarbon dated, we compiled dated and georeferenced fossil records for herbivorous Eurasian megafauna within the radiocarbon dating window from publicly accessible databases (6-10) and published literature (11). The database included many indicator species of *M. primigenius*, including (but not limited to) *Equus sp., Ovibos pallantis, Bison priscus* (12). Fossils were classified as coming from distinct sites if they were in different $0.05^{\circ} \times 0.05^{\circ}$ grid cells. We then summed the number of distinct fossil collection sites in each $1^{\circ} \times 1^{\circ}$ grid cell and mapped the density of fossil sites for the study region. The database, supporting code and metadata can be found here: https://github.com/GlobalEcologyLab/Mammoth/tree/master/extras.

Climate data

Monthly mean paleoclimate simulations were accessed using PaleoView (13) for the period 21,000 BP to the present. These paleoclimate simulations were generated by the Community Climate System Model Version 3 (CCSM3) (14-16); a global coupled atmosphere– ocean–sea ice–land general circulation model (AOGCM) that has a latitude-longitude resolution of \sim 3.75° in the atmosphere (i.e., over land and sea) and \sim 3° in the ocean and includes a dynamic global-vegetation module. We used PaleoView to generate 30-year average estimates for 5 climate variables every 25 years from 21,000 to 0 BP. These climate variables were: (i) average

minimum daily temperature in January; (ii) average maximum daily temperature in July; (iii) temperature seasonality (standard deviation [SD] mean monthly temperature \times 100); (iv) average daily precipitation in Northern Hemisphere summer (JJA) and (v) across the entire year. We chose these climatic variables because they are frequently used to model the climatic niches of large herbivores in Eurasia (11, 17), and because they directly affect their population dynamics (18). In Eurasia, summer climatic conditions can affect the survival and fecundity of coldadapted herbivores, often through forage quality (19). This is because warmer summer temperatures increase plant productivity (20). While particularly harsh winter climates can increase the mortality of Artic grazers (21, 22). The spatial resolution of the climate data sets was resampled to a 1 × 1° resolution (23). Bilinear interpolation was purposefully chosen because it retains the integrity and limitations of the original model output data, where orography is highly smoothed relative to the real-world (24).

To better capture the breadth of climatic conditions in the statistical models of climate suitability that mammoths can potentially persist in, we accessed paleoclimate simulations further back in time. To do this we used the Hadley Centre Climate AOGCM (HadCM3), which has a spatial resolution of $2.5^{\circ} \times 3.75^{\circ}$ (latitude × longitude) (25). The temporal resolution of the HadCM3 data is coarse, with climate snapshot data being available every 2,000 years for the period 80,000 BP to 22,000 BP, and snapshots every 1,000 years for the period 21,000 BP to 0 BP (25). We resampled climate snapshot data to a common $1 \times 1^{\circ}$ resolution (see above) for all climate snapshots between 60,000 BP and 21,000 BP.

Since inter-model differences between AOGCMs can be large (26) we tested the consistency of 30-year average climatic projections centered on 21,000 BP and 20,000 BP. To do this we calculated the pattern correlation, root mean square error (RMSE) and area weighted

mean error (AWME) between projections (26). There was good agreement in the spatial pattern of model projections for the chosen climatic variables ($|\mathbf{r}| > 0.8$) for the study region (1). The RMSE, and AWME between CCSM3 TraCE-21 and HadCM3 projections are shown in Appendix 4 of Fordham and Brown (1). We derived a correction factor for each variable, month, and grid cell in the HadCM3 using the differences between the TraCE-21 and the HadCM3 estimates of 30-year average climate centered on 21,000 BP. The correction factor ensured that the HadCM3 and TraCE-21 projections of temperature and precipitation for the year 21,000 BP were aligned. To do this for temperature we used an additive correction, while for precipitation we used a multiplicative correction. The approach we employed is identical to bias correcting projections for differences between modelled and observed climate, making the fundamental assumption that even if there are differences in the absolute estimates of the models, changes produced by the models are correct (13).

Matching climatic records with fossil-based inferences of past localities of *M*. *primigenius* prior to 21,000 BP avoided truncating climatic suitability in niche model projections (27), accounting for a potentially wider range of historical climatic conditions that *M*. *primigenius* could persist and thrive in. Comparisons of Outlying Mean Index (28) confirmed that climatic conditions at fossil sites prior to 21,000 BP were different and should be included in the analysis (OMI = 0.011 and 0.547, for the periods 60,000 to 21,000 BP and 21,000 to 0 BP, respectively). A lower OMI value prior to 21,000 BP suggests that climatic conditions were more typical of the climatic condition in Eurasia during this period. See below (*Niche marginality and tolerance*) for an explanation of OMI analysis.

We restricted all demographic model simulations of *M. primigenius* population and range dynamics to the period from 21,000 BP because high temporal resolution paleoclimate

reconstructions are needed to directly model ecological and evolutionary responses to past climatic and environmental change (24). An alternate approach would have been to use a stochastic weather generator to produce a synthetic time series of weather data based on observed present day weather for each grid cell and apply it to each HadCM3 millennial climate snapshot (29). However, this assumes that time-averaged weather (i.e. climate variability) does not change over long periods of time, which is unlikely to be the case (30).

Dynamic spatial structure

Climate suitability was used to define the initial spatial structure of the process-explicit simulation model by considering the ecological niche of *M. primigenius* as an n-dimensional hypervolume (*31*) across time (*32*).

Multi-temporal niche hypervolume

We intersected climate projections for each georeferenced fossil for the period ± 1 SD around the estimated age of the fossil. Therefore, each fossil had a time series of climate data associated with it. Collectively, this represents the climate history over which *M. primigenius* were likely to have been present at the fossil sites (*33*). We constructed a multi-temporal hypervolume estimate of climate suitability by combining spatiotemporal climate information associated with georeferenced and aged fossils for Eurasia and North America (see above). We removed all duplicate climates associated with presences; in these instances, all climate parameters (mean daily rainfall variables rounded to two decimal places and mean daily temperature variables rounded to one decimal place) are the same.

We tested for collinearity between climate variables and removed variables that were strongly correlated $|\mathbf{r}| > 0.7$ (34), opting for variables that have well established biological

evidence for affecting the population dynamics of large herbivores in the northern-hemisphere (18), providing strong support for their inclusion in the niche hypervolume (31). The final set of predictor variables were: (i) average minimum daily temperature in January; (ii) average maximum daily temperature in July; (iii) average daily precipitation in summer.

We measured the geometry of this 3-dimensional hypervolume with a box kernel and the Silverman bandwidth estimator using the R package 'hypervolume' (*35, 36*). The hypervolume was then checked for occupied and unoccupied hypervolume space as a potential indicator of unconsidered climate space (*37*).

Niche marginality and tolerance

To account for large uncertainties in the climatic conditions used by *M. primigenius* we exhaustively subsampled the multi-temporal hypervolume using Outlier Mean Index (OMI) analysis, focusing on measures of niche separation and niche breadth (*28*). These metrics measure the difference between the mean climate conditions in the niche sample and those in the full hypervolume (Marginality), and the variability of climatic conditions in the niche sample (Tolerance).

We did this using the R package 'ade4' (38) and data used to construct the 3-dimensional hypervolume. In contrast to other ordination techniques, OMI does not make assumptions about the shape of the species' response curves to the environment, and therefore has been applied widely in the study of climate niches of species (39, 40). Marginality is a measure of climatic specialisation, calculated using the distance between the climate conditions in the niche sample and the mean conditions of the total multi-temporal climate space. Niche samples with high marginality values occur in less common climates compared to the total multi-temporal climate space, while those with low values have non-marginal niches, occurring in climates that are

typical of multi-temporal climate space. Tolerance (or Breadth) provides an index of the variability of the climatic conditions in the niche sample. High tolerance values are associated with a wide niche breath and low tolerance values to small niche breadth.

We calculated niche samples with non-overlapping as well as overlapping hypervolumes, ensuring that the edges of the hypervolume were well represented in the niche samples (36), sampling Marginality and Tolerance between bounds of 0.0001 - 21.45 and 0.042 - 2.10 (1), respectively. This sub-sampling process resulted in 1,862 potential subsets of the full multi-temporal hypervolume (an approximation of the potential realized niche (32)), which we used to calibrate the bioclimatic envelope. This sub-sampling process, allowed the realized climatic niche for *M. primigenius* to be established using pattern-oriented methods (41).

Modelling the bioclimatic envelope

We created a bioclimatic envelope model (BEM) for *M. primigenius* using MaxEnt (42) and made spatial projections of climate suitability for the period from 21,000 to 0 BP at 25-year (generational; see below) time steps for the study region (1). Correlative approaches, which model the bioclimatic envelope of a species, assume that the distribution of a species is an unbiased spatial indicator of its ecological requirements (43). We used a standard maximum entropy method (42) to project climate suitability because it is computationally faster than the kernel density hypervolume method and produces similar results (44), because it has been shown to outperform many other BEMs (45), and because it is frequently applied to paleo contexts (23, 46). Climates not associated with a fossil occurrence were treated as potential background points. The background extent was restricted to the study region (1). The number of background points was set at up to 10 times the number of presence points (47), based on the need for a background that is representative of the climatic conditions potentially accessible to the species (48). We

used 5-fold cross validation to set a threshold for species occurrence based on maximizing the sum of sensitivity and specificity (49).

We assessed the cross-validated predictive capacity of the full multi-temporal BEM by training the model with an 80% random sample of the initial data and testing it against the remaining 20% of data. We did this 100 times and calculated the average area under the curve (AUC) of the receiver operation characteristic (ROC) and the true skill statistic (TSS). The results were: AUC = 0.998 and TSS = 0.971, indicating excellent predictive capacity (*50*).

We generated separate MaxEnt BEM models for all subsamples of the hypervolume (see above). We checked that each sample had ≥ 20 fossil occurrence records (i.e., points with unique climates) (51). Doing this resulted in thousands of model projections (n = 1,862) of spatiotemporal change in climate suitability for mammoths from 21,000 to 0 BP at 25-year (generational) time steps for the Eurasian study region.

Projections of climate suitability were scaled between 0 and 1 individually for each model following equation 1:

$$Z_i = \frac{x_i - \min(x)}{\max(x) - \min(x)} \tag{1}$$

Where x_i = climate suitability at grid cell i at time i; min(x) = threshold for species occurrence based on maximizing the sum of sensitivity and specificity; and max (x) = maximum climate suitability for any grid cell at any point in time from 21,000 to 0 BP.

Projections of climate suitability were then scaled to account for latitudinal variance in grid cell size and the proportion of the cell that is land and not ice at each time step based on sea ice and coastline reconstructions at 25 year time steps from 21,000 BP to the present day. These reconstructions came directly from the TraCE-21ka experiment, upon which PaleoView (*13*) is based.

Human density

We modelled the peopling of Eurasia by Palaeolithic humans using the Climate Informed Population Genetics Model (CISGEM), where genetic history and local demography is informed by paleoclimatic and paleo-vegetation reconstructions of net primary productivity (NPP) (*52*), which has been shown to be a primary determinant of global hunter-gatherer population densities (*53*). The model has previously been shown to reconstruct arrival times of anatomically modern humans and current-day distributions of global and regional genetic diversity (*52*, *54*). It simulates local effective population sizes (N_e) as a function of genetic history, local demography as well as primary productivity (*52*, *54*). Like other numerical models of early human migration (*55*), arrival, occupancy, and density (here N_e) are forced by spatiotemporal estimates of climate and sea level changes over the past 125 thousand years.

In CISGEM, the world is represented by a hexagonal grid, each cell approximately 100 km wide. The potential number of people who can live in each cell (its carrying capacity) is determined by reconstructions of NPP done by coupling the HadCM3 paleoclimate model (described above) to the Miami vegetation model (*56*). Every 25 years (approximately the generation time of humans), the carrying capacity is updated to allow for changes in climate, as well as sea level and ice sheet extent. At each generation, any cell that is inhabited will grow with a rate r (until it reaches the local carrying capacity), sending out migrants to other inhabited cells at rate m, or colonists to previously uninhabited cells at rate c. The relationship between carrying capacity and NPP, as well as the values of other demographic parameters, were fitted using pattern-oriented methods (*41*) using an Approximate Bayesian Computation framework (*57*). Targets for model calibration were pairwise genetic differentiation among a large panel of modern-day human populations. In other words, the demography was calibrated to produce

realistic genetic differentiation patterns across the globe. Eriksson *et al.* provide a detailed description of CISGEM parameters and procedures (*52*).

Based on the ABC fit, we took the best 4,000 parameter combinations and reconstructed population sizes through time, which were then used when modelling human impact on mammoth. For each grid cell of $1 \times 1^{\circ}$ resolution in Eurasia, we used CISGEM to calculate a time series of effective population size (N_e) from 21,000 BP to 0 BP at 25-year time steps, following a burn-in period of approximately 80 generations (2,000 years). To account for parameter uncertainty in spatiotemporal projections of N_e we ran 4,000 different models each using a unique combination of parameter settings (based on established upper and lower confidence bounds (*52*)) using Latin hypercube sampling (*58*). An upper plausible threshold for N_e was set at 500 individuals per grid-cell based on estimates of true abundance in modern-day hunter-gatherer societies (*59*). We calculated average N_e ± 1 SD for each time step at each grid cell and then generated 10,000 plausible reconstructions of human population abundance, by sampling within ± 1 SD of N_e using a triangular distribution (*60*). Stochasticity in human abundances is therefore the result of sampling established ranges for demographic parameters in CISGEM.

Process-explicit mammoth model

Bioclimatic envelope models of climate suitability and CISGEM estimates of human abundance were coupled with stochastic population models that capture extinction as well as colonization dynamics by simulating landscape-level population processes, including dispersal with source-sink dynamics. The model was coded in Program R and is available here: <u>https://github.com/GlobalEcologyLab/Mammoth</u>.

Each grid cell was modelled with a scalar-type stochastic model, which simulates the finite rate of population increase "R", its variance and the population carrying capacity (*61*). The approach has been shown to be superior at reconstructing the historical range dynamics of species compared to BEMs alone (*62*). The model was run at generational time steps (25 years, see below).

Upper abundance

The upper abundance of each cell was based on climate suitability (63). To convert climate suitability (scaled by latitude and land surface area) to upper abundance, we first assumed that the maximum area of suitable habitat in any given cell $\leq 2,443$ km² not 9,777.5 km². This approach appropriately addresses the mismatch between the spatial scale of the model and how *M. primigenius* are likely to have used the landscape (64). We set upper abundance at 1.875 mammoths km² and allowed it to vary, across models, at a rate of between 0.25 and 4 animals km². The lower estimate was taken from density estimates for African elephants (65) and the upper estimate is for a model previously published on mammoths (66).

Population growth

We used long-term population-dynamics time-series data to calculate finite rates of population increase and their variance (*67*). We fit a Ricker logistic function to a 13-year time series for African elephants (*Loxodonta africana*) in Tarangire National Park, Tanzania, from 1993 to 2005 (*68*). This time series was chosen because the population was in a state of rebound after heavy poaching prior to 1993 (*68*). This provided a mean estimate of Rmax (lambda) of 1.08 (at an annual time scale).

We scaled Rmax to the generation level by taking the exponent (1.08^{25}) and treated this as an upper estimate of Rmax in the model, with a parameter range of 1.01^{25} and 1.08^{25} (i.e., maximum R0 = 1.28 - 6.85). Generation length was set to 25 years based on Wittemyer, Daballen and Douglas-Hamilton (*69*). The decision to set 1.08^{25} as the upper estimate was based on a comparison of observed and model simulated variation in population abundance, where variation in population abundance for the generational estimate was larger than expected based on annual estimates.

We used time series data (1972 – 2000) for a population of *L. africana* at or near carrying capacity to calculate the standard deviation (SD) in population growth rate (70) = 0.44. This was used to model population fluctuations driven by environmental stochasticity (71). We calculated SD in population growth at a generational time step by repeatedly running an annual model for 500 years and then calculating the standard deviation of population growth at a generational level once the population had reached carrying capacity. Doing this resulted in an estimate of SD_{R0} of 0.175, which we treated as an upper estimate based on model simulations. The upper and lower bounds for SD_{R0} were set at 0 to 0.175.

Density dependence was modelled using a Beverton-Holt type density dependent response (72), under which most compensation in vital rates occurs at population sizes close to carrying capacity; we chose this representation because model-simulation tests using this functional form showed ecologically realistic fluctuations in abundance when carrying capacity was exceeded. This was not true for the Ricker model.

Dispersal

We assume that *M. primigenius* would have been highly mobile (*32*) based on home range and seasonal migration rates of elephants, which can exceed 150 km in a matter of days

(73, 74). Furthermore, based on allometry a 10-year old male mammoth weighing 1500 kg (based on growth curves) would have a mean dispersal rate of \sim 75km and a maximum dispersal rate of \sim 394km, with upper limits of 187 km and 750 km, respectively (75).

We modelled a mean dispersal rate of 15% of the population moving per generation at an average maximum distance of 300 km. We set upper and lower bounds on these estimates of 5 - 25% and 100 - 500 km, respectively. Dispersal was modelled using the following equation:

$$m_{ij} = \begin{cases} a^{\left(\frac{-D_{ij}}{b}\right)}, & D < D_{max} \\ 0, & D \ge D_{max} \end{cases}$$
(2)

Where movement (m) between cell *i* and *j* is a function of the parameters *a*, *b*, and *Dmax*; and *Dij* is the distance between the two populations. The parameter *a* is $0.5 \times$ the total proportion of dispersers that leave a cell at each time step and *b* and *Dmax* are modelled as one of 9 combinations depending on the estimate of D (*1*). This approach prevents large dispersal rates to closely neighbouring cells (i.e., the drainage effect) by pre-calculating a fixed proportion of individuals that should move to a given cell based on *a*, *Dmax* and *Dij*.

Allee effect

Genetic evidence suggests that *M. primigenius* experienced a negative Allee effect prior to extinction due to inbreeding (*76*). To capture this without the need of a detailed genetic submodel, we set a local quasi-extinction threshold (*64*) which made cell abundance zero if abundance fell below the Allee threshold. The range of values for the Allee effect were 0 (i.e., no Allee effect) to 500 mammoths per grid cell. The upper estimate is equivalent to 5% of max population abundance in highly suitable cell.

Environmental correlation

This was a fixed parameter in our models that was set to b = 850 km (77), where b is the decay constant of an exponential decline model. This parameter accounts for similarity in environmental fluctuations for populations located close together versus further apart.

Human hunting

We modelled human hunting of *M. primigenius* as a function of the timing of the arrival and abundance of anatomically modern humans in a given grid cell (see *Human density* above), with maximum offtake rates varying from zero to 35% of mammoth population abundance and the type varying in form, from a Type II to a Type III functional response.

We varied exploitation of *M. primigenius* by humans between zero and 35 % at equilibrium abundance (i.e., maximum abundance in a grid cell with HS = 1). Harvesting was modelled using the following functional response:

$$Functional \ response = \frac{(F \times P^z)}{(G + P^z)}$$
(3)

Where P is the density of prey population (current population size, divided by maximum population size), F is the maximal predation rate, G is a constant equal to the prey density at which predation is half-maximal, and z is a measure of the departure from maximal predation. Functional response gives the number of prey killed per predator per year.

The harvest rate (H, proportion of the prey population killed) was calculated by dividing eq. 3 by the current prey density.

$$H = \frac{\left(\frac{F \times P^{z}}{G + P^{z}}\right)}{P} \tag{4}$$

The parameterization (above) is based on considering all of the human population in a particular grid cell at maximal density as 1 predator. Thus, to get harvest rate at a particular time and grid cell, eq. 4 was multiplied by the human population density (i.e., current human population, divided by maximum human population [500 per 100km²; see above]) at that time and grid cell:

$$H' = \frac{\left(\frac{N \times F \times P^{Z}}{G + P^{Z}}\right)}{P}$$
(5)

Where N is the human population density. G was set to 0.4 (52, 55), and F varied from 0 to 0.35.

Previously Alroy (78) modelled hunting success of megafauna by setting z = 1 in the above equation. This resulted in a type II functional response. We modelled z as a variable parameter ranging from 1 to 2 (following (78)). At z = 1 the function is monotonic, under which predation is modulated only by prey density and predator satiation, implying complete naivety of prey. At z > 1.5 hunting success takes on an increasingly sigmoidal Type III functional response, under which prey become harder to hunt at low densities. This might result from prey adaptation (evolved or learned behaviour), prey switching by hunters or prey being located in refugia (79, 80). We chose not to model a numerical response because the human population in Eurasia were not obligate hunters of mammoths. This is evident by an approximately exponential long-term growth trend in Eurasia during the early-to-mid Holocene (81, 82). Fluctuations in human population during this time have been linked to climate and associated societal responses, including altered food-procurement strategies involving a wide variety of sources (83).

Latin hypercube sampling

Models built using 'best estimates' for demographic parameters and environmental attributes were varied across wide but plausible ranges using a Latin hypercube sampling to provide a robust coverage of multi-dimensional parameter space (*60*). This procedure produced

90,000 conceivable models with different combinations of rates of population growth, dispersal, climate suitability, exploitation by humans and so on, each of which we ran for a single replicate (*84*).

Latin hypercube sampling generates a stratified random subset of parameter input values for simulation, by assigning a plausible range for each parameter and sampling all subsets of its distribution once, based on subdivisions of equal probability density (*85*). With the exception of human abundance there were no best estimates, so we used uniform sampling distributions (triangular for human abundance). Appendix 3 in Fordham and Brown (*1*) shows the plausible range for each parameter used in the hypercube.

Pattern Oriented Modelling

We used pattern-orientated modelling (POM) to evaluate whether a model is adequate in its structure and parameterization to simulate mechanistic responses to climate change and exploitation in a way that realistically matches the observed outcomes (*41, 86*). Model simulations of changes in range area, extirpation patterns, total population size, and location of the last remaining population/populations (or extant populations for models where extinction did not occur prior to 3,000 BP) were assessed using a multivariate target based on inferences from the fossil record and ancient DNA.

Observed and modelled summary statistics

Changes in population size and location

We used trend in effective population size $(N_e)(1)$ as a proxy for change in total population size for mammoths (11) using Bayesian skyline plots (87). This method simultaneously estimates genealogy, demographic history, and substitution-model parameters in a single analysis, directly accounting for phylogenetic uncertainty of the inferred genealogy. Bayesian Skyline Plot permits instantaneous changes in population size to be estimated which is needed to detect rapid changes in population dynamics (*87*). Effective population size was calculated using a previously compiled dataset containing 445 radiocarbon-dated fossils (*88*). From these, 74 fossil records have associated aDNA sequences (*88*), which are available in GenBank (*89*). These were aligned using Geneious v1.9.8 (*90*) and the MUSCLE algorithm (*91*), using default settings. Radiocarbon dates were calibrated using OxCal and the IntCal13 calibration curve (*92*). We reconstructed the genealogy using BEAUti v.1.10.4 and BEAST v1.10.4 (*93*). We used the average calibrated date of each fossil record as prior information for the tip-dates, and the standard deviation to derive uncertainty in the tip-dates.

We selected a GTR + Gamma + Invariant Sites substitution model, based on Akaike's Information Criterion (AIC), done in jModelTest v2.1.10 (94). We used a strict molecular clock, a Coalescent Bayesian Skyline Tree Prior, a constant Skyline Model and the UPGMA starting tree. The Markov Chain Monte Carlo run was set with a chain length of 10⁸ and to log parameters every 10⁴ simulations to avoid possible autocorrelation during the MCMC analysis. We then analysed the output using Tracer v1.7.1 (95). Our approach is similar to the approach used by Foote, Kaschner, Schultze, Garilao, Ho, Post, Higham, Stokowska, van der Es, Embling, Gregersen, Johansson, Willerslev and Gilbert (96) to investigate changes in mammal N_e based on aDNA and contemporary sequences. The resulting estimate of N_e for woolly mammoth (*1*) mirrors estimates elsewhere (97).

We used piecewise regression to determine the inflection points for the line segments for the mean and upper and lower confidence intervals and then calculated the coefficients using the Program R package 'segmented' (*98*). Using this approach, we identified the steepest decline in the median estimate of N_e during the period 12,613 to 18,619 BP. We calculated the slope of N_e using a Theil–Sen estimator with the R package 'trend' (*99*) for this time interval. We also calculated the Thiel-Sen slope in simulated total population size for the period 12,613 to 18,619 BP (i.e., the period for which the slope of median N_e was calculated) and used this as input in our Approximate Bayesian Computation (see next section).

As a spatio-temporal target we calculated the number of sites where mammoth populations were simulated to coincide with sites from the fossil record.

Timing and location of extinction:

We estimated time and location of range-wide extinction and the extirpation pattern using a maximum-likelihood method first developed by Solow, Roberts and Robbirt (100) to correct for the Signor-Lipps effect. Using an adapted approach (101) we estimated the median time of range wide extinction to be 3798 BP (95% Confidence Levels = 4089 BP to 3450 BP) and for this to have occurred on Wrangel Island, located off the coast of Beringia. A lower estimate of ~ 3.4 k BP for the timing and location of the final extinction event corresponds with other studies (102). We calculated the time of extirpation (in years BP) for each of the simulations and then calculated the difference between the model- and fossil-based estimates. If the model-based estimate fell within the 95% Confidence Levels the difference was zero years.

We calculated the distance from the last remaining simulated population of mammoths to the site of the youngest fossil by calculating the shortest distance between two points on an ellipsoid (i.e., allowing for the non-spherical shape of the earth) using the R package 'geosphere' (*103*). Where the final extinction event was caused by the extirpation of more than one population, we calculated a weighted centroid using the simulated abundances of these locations

and then calculated the distance (in km) to the 'real' location of the final extinction event (i.e. Wrangel Island).

Approximate Bayesian Analysis

We used Approximate Bayesian Computation (ABC) analysis (57) to determine models that did well at replicating the range dynamics of woolly mammoth during the late Pleistocene and Holocene. The ABC approach to pattern-oriented modelling provides a systematic way of assessing support for different model versions and parameterisations based on available validation data, given some prior beliefs about how likely they are (*104*). The use of ABC approaches for calibrating and evaluating complex demographic-based models can embed the often-complex process of optimising model structure and parameters within an established statistical framework, thereby making the process transparent and objective (*104, 105*).

Specifically, we used ABC to fit the simulation models to data and estimate (and narrow down) the posterior distribution of model parameters. We did this using the R package 'abc' (*106*). Parameter values in the ABC analysis were the 12 demographic and niche parameters (see Appendix 4 in Fordham and Brown (*1*) for details). The summary and target statistics were treated collectively in the ABC modelling (i.e., using a multi-variate target), meaning that models were assessed on the capability to simultaneously replicate a suite of key aspects of the extinction dynamics of mammoths.

We used a neural-network-regression algorithm to construct the posterior distributions of parameters because of the high dimensionality and potential non-linearity associations between the target statistics (*106*). Targets used in the model (described above) were: (i) Thiel-Sen trend of the median N_e estimates, (ii) time of extinction, (iii) distance to last fossil record, and (iv) the number of simulated fossil sites. The number of hidden layers (n = 3) was chosen based on

assessment of the model fit to the residuals using QQ plots, whilst the accuracy of parameter estimates and sensitivity to the tolerance rate threshold (0.01 or 0.005) was assessed using the rejection method and the 'cv4abc' function (*106*) with 2,000 leave-one-out samples. Based on cross validation, we selected a tolerance rate of 0.01 to generate and compare density plots of the prior and posterior distributions and calculate credible intervals as the prediction error between the tolerances was negligible (difference in mean prediction error = 0.009).

Identifying drivers of extinction and range collapse

Models retained from the prior distribution (n = 900 models) using ABC analysis (i.e., those making up the posterior distribution of the top 1% of feasible parameterisations, as assessed by the multi-variate target from the pattern-oriented modelling) were used to generate an ensemble average (weighted by the Euclidean distance of the model from the idealised targets) of timing of extirpation (extinction at the grid cell) and total population abundance. These were verified using expert knowledge and published studies.

Statistical analysis

We assessed the role of human harvesting and climate change on the extinction of mammoths during the most recent deglaciation period using random forest classification trees, implemented with the 'ranger' package for R (*107*). Random forests have been used previously to identify the most important drivers of extinction times from multi-predictor correlative models (*77*). To do this we first discretized the period between 21 and 5 kya BP into three climatically distinct periods of time (21-15 kya BP [P1], 15-11 kya BP [P2], 11-5 kya BP [P3]) (*108*), and for each of the periods calculated a suite of metrics related to the magnitude and pace of climatic

change and human expansion. These metrics are detailed in Appendix 2 of Fordham and Brown (1).

For each period of time (P1-P3), we built and cross validated (10 repeats of 10-fold CV) a random forest model that linked climate and human variables (each modelled separately and together) to extinction risk. We modelled extinction risk as Expected Minimum Abundance (EMA) over the time period (*109*), divided by population abundance at the start of the period. All models included range area (km²) at the beginning of the focal period to account for the strong relationship between range area and EMA (*77*), and the fact that range area and population size are not necessarily linearly correlated (*110*). Candidate model sets were constructed and tested for each period of time (P1-P3), at four spatial scales (entire study region [Eurasia], Europe-only, Asia-only, and Beringia-only).

The random forest regression models were constructed with 2,000 trees, whilst the number of variables tried at each split and the minimum node size of the trees was tuned via cross validation to maximize model accuracy. Subsampling for the trees was done without replacement using 66% of the samples, whilst variable importance was calculated using unscaled permutation importance (*111*). Raw variable importance scores from the permutation approach were converted to % contribution to explained variance. This was done to allow comparisons across time and space of the importance of the variables (*112*). Interactions between the variables and EMA were assessed using Accumulated Local Effects plots, which are preferable to traditional partial dependency plots when variables are potentially correlated (*113*). Inspection of accumulative Local Effects plots showed that climate and human drivers in the model affected EMA in a logical way (*1*) (as expected *a priori* from theory), where increases in the strength of warming and human drivers resulted, in most instances, in a negative impact on EMA. The

positive relationship between EMA and some human impact parameters in P1 (21,000 BP to 15,000 BP) is likely to reflect a positive relationship between mammoth carrying capacity, and independently, human abundance, with a common set of climate attributes during the early stage of this period (see Main Text Fig. 2).

To assess the level of spatiotemporal autocorrelation between climatic and human drivers of extinction we calculated Lee's L Statistic (*114*) for each time step for the 900 selected models. Lee's L statistic was calculated using the R package 'spdep' (*115*). Lee's L statistic estimates the amount of spatial clustering present in a bivariate relationship with positive values indicating positive spatial autocorrelation, negative values indicating negative spatial autocorrelation (0 implies no relationship). Standardised spatial weights for the relationship were defined by calculating the number of nearest neighbours to each cell with a minimum and maximum distance of 100 and 500 km, respectively. The model weights from the ABC analysis were then used to calculate the weighted ensemble mean L statistic.

Timing of extirpation and probability of occurrence

To estimate and map time of extirpation we determined the final time step that each of the $1^{\circ} \times 1^{\circ}$ grid cells was occupied for each of the 900 ABC selected simulations. To generate spatiotemporal estimates of probability of occurrence, we produced binary presence/absence maps for each time step for each of the 900 ABC selected simulations. These extirpation and binary presence absence maps were then used to generate ensemble weighted average extirpation and probability of occurrence maps using the weights from the ABC analysis.

To calculate a minimum threshold for occurrence we calculated the probability of occurrence that maximized the area under the receiver operating curve for the fossil record based on predictions from a binomial GLM. To do this, we extracted the mean probability of

occurrence for each fossil across time (Fossil age \pm 1 S.D), and for 10 randomly sampled background points (48) covering the same time interval. Using 10 repeats of 10-fold cross validation, we built 100 binomial GLMs using different thresholds between 0 and 1 at 0.01 intervals. AUC was calculated for each of the models, with the smallest threshold (0.34) being chosen that maximised AUC (AUC = 0.917).

Scenario testing

A counterfactual scenario was run on the 900 selected (by ABC) simulations to confirm the impacts of human harvesting on mammoth populations. The scenario altered the harvesting rates of humans on the landscape, by prohibiting harvesting during the simulation, including the burn-in period. The effects of humans were quantified by: (i) analysing differences in scaled expected minimum abundance between the baseline and no-humans scenario; (ii) calculating the difference in grid-cell mean weighted extirpation dates between the baseline and no-humans scenario; (iii) calculating differences in regional and range-wide estimates of EMA between the baseline and no-humans scenario; and (iv) quantifying synchrony in the time series of abundances for the baseline and no-humans scenario (116, 117). Differences in EMA within each region were compared with a weighted t test in the 'weights' package for R (118). Weights were specified using the ABC weights (see above). Percent increase in survival under the nohumans scenario was calculated by comparing the number of simulations that went extinct between the baseline and no-human scenarios. Synchrony was measured as the average phase synchrony of the time series of abundances for each of the 900 models, and by finding the proportion of local minima and maxima (i.e. the peaks and troughs of abundances; peak coincidence) that were congruent in the simulations of abundance. Phase synchrony and peak coincidence was calculated using the synchrony package for R (119).

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