RESEARCH ARTICLE

Global Ecology and Biogeography   A Journal of Macroecology   WILEY

Range and extinction dynamics of the steppe bison in Siberia: A pattern-oriented modelling approach

Julia A. Pilowsky[1,2] | Sean Haythorne[1,3] | Stuart C. Brown[1,4] | Mario Krapp[5,6] | Edward Armstrong[7] | Barry W. Brook[8] | Carsten Rahbek[2,9,10,11] | Damien A. Fordham[1,2,11]

[1]The Environment Institute and School of Biological Sciences, University of Adelaide, Adelaide, South Australia, Australia

[2]Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Copenhagen Ø, Denmark

[3]School of BioSciences, University of Melbourne, Melbourne, Victoria, Australia

[4]Section for Evolutionary Genomics, Globe Institute, University of Copenhagen, Copenhagen K, Denmark

[5]Antarctic Research Centre, Victoria University of Wellington, Wellington, New Zealand

[6]GNS Science, Lower Hutt, New Zealand

[7]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

[8]School of Biological Sciences and Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage, University of Tasmania, Hobart, Tasmania, Australia

[9]Danish Institute for Advanced Study, University of Southern Denmark, Odense, Denmark

[10]Institute of Ecology, Peking University, Beijing, China

[11]Center for Mountain Biodiversity, Globe Institute, University of Copenhagen, Copenhagen Ø, Denmark

Correspondence
Julia A. Pilowsky and Damien A. Fordham, The Environment Institute and School of Biological Sciences, University of Adelaide, Adelaide, SA 5005, Australia.
Email: julia.pilowsky@adelaide.edu.au (J.A.P.) and damien.fordham@adelaide.edu.au (D.A.F.)

Abstract

Aim: To determine the ecological processes and drivers of range collapse, population decline and eventual extinction of the steppe bison in Eurasia.

Location: Siberia.

Time period: Pleistocene and Holocene.

Major taxa studied: Steppe bison (*Bison priscus*).

Methods: We configured 110,000 spatially explicit population models (SEPMs) of climate–human–steppe bison interactions in Siberia, which we ran at generational time steps from 50,000 years before present. We used pattern-oriented modelling (POM) and fossil-based inferences of distribution and demographic change of steppe bison to identify which SEPMs adequately simulated important interactions between ecological processes and biological threats. These "best models" were then used to disentangle the mechanisms that were integral in the population decline and later extinction of the steppe bison in its last stronghold in Eurasia.

Results: Our continuous reconstructions of the range and extinction dynamics of steppe bison were able to reconcile inferences of spatio-temporal occurrence and the timing and location of extinction in Siberia based on hundreds of radiocarbon-dated steppe bison fossils. We showed that simulating the ecological pathway to extinction

for steppe bison in Siberia in the early Holocene required very specific ecological niche constraints, demographic processes and a constrained synergy of climate and human hunting dynamics during the Pleistocene–Holocene transition.

Main conclusions: Ecological processes and drivers that caused ancient population declines of species can be reconstructed at high spatio-temporal resolutions using SEPMs and POM. Using this approach, we found that climatic change and hunting by humans are likely to have interacted with key ecological processes to cause the extinction of the steppe bison in its last refuge in Eurasia.

KEYWORDS

climate change, distribution, extinction dynamics, mechanistic model, metapopulation, palaeoclimate, range shift, spatially explicit population model, steppe bison, synergistic threats

1 | INTRODUCTION

Several hypotheses have been proposed for how extinctions manifest in space and time (Davidson et al., 2009; Owens & Bennett, 2000), but generalities across landscapes and time periods have been difficult to formulate (Laliberte & Ripple, 2004). Theories of range shifts, population declines and extinctions are now being tested directly using historical and palaeo-reconstructions (Fordham et al., 2021, 2022), permitting inferences of how biodiversity is likely to respond to future environmental change (Fordham et al., 2020). However, reconstructing past demographic changes at landscape scales poses unique modelling challenges, including the reliance on indirect proxies to draw inferences about range collapses and the timing and location of extinction (Dietl et al., 2015); uncertainty in reconstructions of past climates (Rutherford et al., 2005) and human-driven environmental threats (Ellis et al., 2021; Pilowsky, Manica, et al., 2022); and a lack of information on the ecological lifestyles and traits of many species (Fordham et al., 2016).

Some of these issues can be addressed, at least in part, using process-explicit models, particularly if they are combined with pattern-oriented modelling (POM) techniques (Box 1). Process-explicit models simulate ecological and evolutionary mechanisms responsible for spatio-temporal patterns of biodiversity (Pilowsky, Colwell, et al., 2022). These mechanisms include extirpation, movement, ecological interactions, adaptation and speciation. Unlike correlative approaches, such as species distribution models, process-explicit models establish causal links between process and pattern (Urban et al., 2016). However, high data demand and model complexity have meant that, to date, they have been used less frequently in studies of the structure and dynamics of patterns of biodiversity. This is steadily changing, owing to increased data availability, computational power (Pilowsky, Colwell, et al., 2022) and a growing need for stronger inferences about the causes of contemporary and ancient changes in biodiversity (Fordham et al., 2020; Pontarp et al., 2019; Rangel et al., 2018).

POM methods (Grimm & Railsback, 2012) can directly address some of the problems of data availability and subsequent parameter uncertainty in process-explicit models of species distributions

---

BOX 1   Biodiversity modelling terms

Approximate Bayesian computation (ABC): A statistical technique that uses Bayesian statistics to estimate the distributions of model parameters by comparing simulated probability distributions of summary statistics against their observed distributions (Beaumont et al., 2002).

Correlative models: Models that statistically relate environmental variables to observation data in order to infer biological patterns (Pilowsky, Colwell, et al., 2022).

Pattern-oriented modelling (POM): An approach for optimizing model parameters using independent validation targets (Grimm et al., 2005).

Process-explicit models: Models that represent the dynamics of an ecological system as explicit functions of the processes that drive change in that system. Also known as process-based and mechanistic models (Connolly et al., 2017).

Spatially explicit population models (SEPMs): Process-explicit models that simulate mortality, reproduction and movement in a network of populations on a landscape map (Dunning Jr et al., 1995).

---

and community dynamics (Canteri et al., 2022; Fordham et al., 2022; Rangel et al., 2018). Although POM was first used in ecology and evolution to optimize uncertain parameters in individual- and agent-based models (Thulke et al., 1999), it has since been used to simulate demographic change using spatially explicit population models (Canteri et al., 2022; Fordham et al., 2022), genetic diversification in lineages of species (Knowles & Alvarado-Serrano, 2010), changes in community structure (Colwell & Rangel, 2010) and evolutionary shifts in populations (Barnes & Clark, 2017). It uses optimization routines to determine model parameter values based on observed (or inferred, if operating across palaeo time frames) empirical patterns (Grimm & Railsback, 2012), increasing the likelihood of capturing

key biological processes in model simulations. This strategy assumes that observed patterns are fingerprints of underlying ecological and evolutionary processes, enabling models to be parameterized initially using uncertain but plausible information on these processes (Gallagher et al., 2021).

Despite offering new opportunities to gain a better understanding of the mechanisms that regulate biodiversity under past climate and environmental change, POM methods are only now being used in conjunction with spatially explicit population models (SEPMs) to reconstruct species' range and extinction dynamics over palaeo time-scales (but see Canteri et al., 2022; Fordham et al., 2022). SEPMs simulate movement, mortality and reproduction in networks of populations over time (Anderson et al., 2009; Hanski, 1998), allowing the identification of ecological mechanisms and threats that caused ancient extinctions and range collapses (Canteri et al., 2022). POM optimization is done using patterns inferred from the fossil record and ancient DNA (Fordham et al., 2022). Here, we show the utility of combining POM methods with SEPMs to reconstruct and disentangle the extinction dynamics of the steppe bison (*Bison priscus*) in Eurasia. The approach uses multiple rounds of SEPM optimization to reconstruct continuously the interactions between the ecological lifestyle and demography of steppe bison and drivers of global change (climatic change and human activities) over a period going back 50,000 years. We do this using the R package PALEOPOP v2.1.0 (Haythorne et al., 2021) that we developed as an extension to POEMS (Fordham et al., 2021), adding important new functionality for modelling species range dynamics over multi-millennial time-scales.

The steppe bison was one of the many large herbivores that dominated the "mammoth steppe" biome of the Ice Age (Guthrie, 1989), all of which declined in range size as the mammoth steppe was replaced by a taiga–tundra ecotone during the Pleistocene–Holocene transition (Lorenzen et al., 2011; Markova et al., 2015). The relative abundance of steppe bison (based on reconstructions of effective population size) peaked during the late Pleistocene (Shapiro et al., 2004), when the mammoth steppe was maximally distributed (Anderson & Lozhkin, 2001), with regional extinction in Eurasia at *c.* 8.7 kilo-years before present (kyr BP) (Boeskorov et al., 2016) and global extinction in North America some 6–8 kyr later (Shapiro et al., 2004). In Eurasia, isotopic analysis of late Pleistocene fossils shows that the steppe bison was a strict grazer that did not migrate seasonally (Julien et al., 2012). Here, they competed with the European bison (*Bison bonasus*) for ecological dominance until climate-induced vegetation change following the Last Glacial Maximum [LGM; a period from 26.5 to 19 kyr BP (Clark et al., 2009)] restricted the less ecologically flexible steppe bison to Siberia (Soubrier et al., 2016).

The processes leading to the megafaunal extinctions of the mammoth steppe during the late Pleistocene and early Holocene are uncertain, with intense debate regarding the timing, location and the roles of human hunting and climatic change (Mann et al., 2019; Stuart, 2015; Wang et al., 2021). Here, we configure 110,000 SEPMs of climate–human–steppe bison interactions in Siberia, which we test against inferences of demographic change and range collapse inferred from fossils using POM methods. Our continuous reconstructions of the range and extinction dynamics of steppe bison from 50 kyr BP reveal the ecological processes and threats that led to the demise of the steppe bison in its last stronghold in Eurasia at *c.* 9 kyr BP.

2 | MATERIALS AND METHODS

The steppe bison is an extinct species of bison that was once widespread in the steppe of the Northern Hemisphere (Markova et al., 2015). Its relative abundance (based on reconstructions of effective population size) peaked during the late Pleistocene (Shapiro et al., 2004), when the mammoth steppe biome was maximally distributed (Anderson & Lozhkin, 2001), and it became regionally extinct in Eurasia *c.* 8.7 kyr BP (Boeskorov et al., 2016). We simulated the ecological pathway to extinction for the steppe bison in Siberia.

2.1 | PALEOPOP

PALEOPOP is an object-oriented R package (Haythorne et al., 2021) that we developed to simulate range and extinction dynamics of species over multiple millennia, enabling causal insights into likely past driver–state relationships. PALEOPOP uses a lattice-grid population model to simulate ecological processes (demography and ecological requirements) and their interactions over long temporal scales. PALEOPOP is an extension to the R package POEMS v.1.0.1 (Fordham et al., 2021), which implements SEPMs and POM methods to identify ecological processes of range shifts and extinctions (Figure 1). PALEOPOP adds three major features to POEMS: (1) the capacity to simulate long-term processes of landscape change (sea level rise; movement of glacial ice sheets) occurring over glacial–interglacial cycles; (2) a palaeo-population simulator optimized for simulating demographic change resulting from metapopulation and dispersal dynamics over multiple millennia; and (3) a palaeo-results object suitable for storing the data-heavy output from the palaeo-population simulator.

2.2 | Steppe bison niche

2.2.1 | Fossil data

We gathered radiocarbon-dated data on steppe bison fossils from the palaeontological literature (for details, see Supporting Information Appendix S1). We regularized inconsistent and outdated species names, discarding any records where the species was ambiguous (e.g., "bison" without clear indicators of whether it was the steppe bison or another bison species). In cases where a site name was available but latitude and longitude were not, we compared maps from the source literature against OpenStreetMap and Google Earth to geocode locations
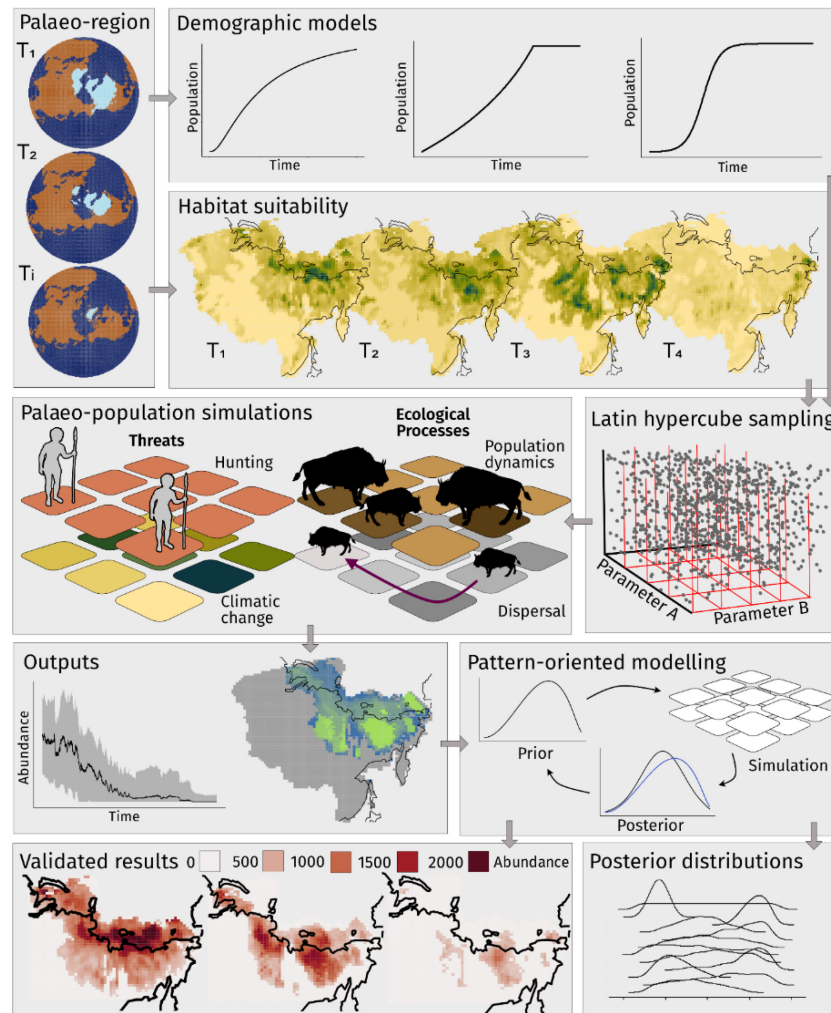
FIGURE 1 Modelling species range dynamics over palaeo time-scales. The modelled dynamic palaeo-region changes temporally owing to climatic change and associated rising sea levels and melting ice sheets. Spatially explicit population models (SEPMs) are built by coupling a demographic model with a grid-lattice-type spatial structure of habitat suitability. Latin hypercube sampling is used to sample SEPM parameter space exhaustively, resulting in tens of thousands of parameter combinations, each of which is used to parameterize an SEPM. The palaeo-population simulations include ecological processes (including dispersal and extinction) responding to key threats of human hunting and climatic change. These simulations reconstruct outputs of past population size and abundance maps. Pattern-oriented modelling (POM) is used to identify models that reconcile patterns of demographic change inferred from palaeo-archives. This involves optimizing values of SEPM parameters by comparing the distributions of posterior and prior parameter ranges (posterior distributions) for successive iterations of model building and testing. Models that do best at simulating inferred patterns of range and extinction dynamics are used to generate validated projections.

manually. The quality of all radiocarbon dates was assessed based on stratigraphy, association and the material dated. We retained 378 records rated as "reliable" (Barnosky & Lindsey, 2010). We calibrated these radiocarbon dates using the OxCal v.4.4 tool (Ramsey, 2017) and the IntCal13 curve (Reimer et al., 2013), which returned calibrated age and standard deviation estimates. The fossil record can be accessed from Figshare (Pilowsky et al., 2021).

2.2.2 | Climate data

Palaeoclimate simulations of precipitation, temperature and latent heat flux used to model the ecological niche of the steppe bison

(see below) are from the HadCM3B coupled ocean–ice–atmosphere model (Valdes et al., 2017). These palaeoclimate simulations incorporate monthly and interannual climate variability (directly from model output) and millennial-scale variability (by assimilating model and Greenland ice core data) and have been downscaled to 0.5° × 0.5° spatial resolution (Armstrong et al., 2019). We extracted monthly data for the study region of Siberia (Supporting Information Appendix S1, Figure S1.1) from 50 to 5 kyr BP and generated 30-year averages at a 12-year (generational; see description of the process-explicit model below) time step for: (1) total annual precipitation; (2) mean boreal winter (DJF) temperature; and (3) total evapotranspiration during boreal spring and summer (MAMJJA). Evapotranspiration (ET) was calculated by dividing the average monthly latent heat

flux by the latent heat of vaporization based on average monthly temperatures:

$$ET_{(mm/month)} = \left(\frac{\text{heat flux}}{(2.501 - 0.00237 \times \text{temperature}) \times 1 \times 10^6} \right) \times 86,400 \times 30 \tag{1}$$

where heat flux and temperature are the modelled monthly heat flux (in watts per square metre) and temperature (in degrees Celsius) for each month.

The mean temperature of the coldest month, mean temperature of the warmest month and annual precipitation have been used previously to model the ecological niche and distribution of high-latitude herbivores, including the steppe bison (Lorenzen et al., 2011) and the American bison (*Bison bison*) (Metcalf et al., 2014). This is because the temperature variables are likely to capture the upper and lower thermal limits of the species, and precipitation drives demographic rates in extant bison species (Koons et al., 2012). Given that spring and summer evapotranspiration was moderately correlated with the temperature of the warmest month (Kendall's $\tau = .548$), we chose to model only spring and summer evapotranspiration because it captures better the structure of vegetation available as forage in the warmer months (Guthrie, 2006). We used average temperature across all boreal winter months (DJF) instead of only the coldest month, because it captures better the stressors and limitations created by winter conditions (DelGiudice et al., 1994, 2001). None of the three variables were correlated with each other by more than Kendall's $\tau = .5$.

2.2.3 | Niche model

We generated continuous habitat suitability maps (based on probability of occurrence) for the steppe bison in Siberia from 50 to 5 kyr BP using ecological niche models (Nogués-Bravo, 2009). To do this, we paired fossil occurrences with our three selected climate variables, accounting for dating uncertainty (Fordham et al., 2022). Climate data were paired spatially, as determined by the grid cell where the fossil occurred, and temporally, as determined by the band of uncertainty [±2SD, which is commonly used for calibrated radiocarbon date distributions (Blaauw, 2010)] around the calibrated radiocarbon date. We removed any duplicate climate data created by two fossil occurrences falling within identical or overlapping spatio-temporal bins (Canteri et al., 2022). We used this climate dataset to create a full (multi-temporal) Gaussian hypervolume, optimized for appropriate bandwidth (Blonder et al., 2018), which provided an estimate of the fundamental niche of steppe bison (Nogués-Bravo, 2009).

Given that the realized climatic niche of steppe bison is likely to be a subset of its fundamental niche (Soberón & Nakamura, 2009), we thoroughly subsampled the full hypervolume of potentially livable climatic conditions (Supporting Information Appendix S1, Figure S1.2) and determined the realized niche using SEPMs and POM (see section 2.4 below). We did this by cutting the full hypervolume into

smaller hypervolumes ($n = 1000$) of different volumes and marginalities (climatic specialization) using outlying mean index analysis (Dolédec et al., 2000). We projected the hypervolumes back into geographical space, creating time series of maps of habitat suitability based on the probability density of the climate hypervolume at the set of environmental conditions in each grid cell (77.8 km × 71.0 km grid cell resolution) from 50 to 5 kyr BP. We scaled the suitability scores of each projection to a zero to one interval, based on the 95th percentile of maximum habitat suitability values in grid cells across time and space.

2.3 | Palaeolithic humans

The expansion of Palaeolithic humans into northern Eurasia was modelled using a process-explicit climate-informed spatial genetic model (CISGEM) that has been shown accurately to reconstruct the dispersal of *Homo sapiens* out of Africa (Eriksson et al., 2012). CISGEM simulates local effective population size (N_e) based on a cellular demographic model, with carrying capacity modulated by net primary productivity. We ran CISGEM from 120 kyr BP to the present using the HadCM3B ocean–ice–atmosphere model (Valdes et al., 2017) and 4950 parameter combinations that had previously been shown to reconstruct patterns of human migration and growth robustly (Eriksson et al., 2012). We calculated the mean and variance of the 4950 simulation results (Supporting Information Appendix S1, Figure S1.3) and scaled the projections of N_e between zero and one (taking an approach identical to the scaling of steppe bison habitat suitability projections). We then resampled the outputs from the time step of CISGEM (25 years) to the time step of the bison simulations (12 years). To parameterize human hunting in our demographic models, we generated 50,000 potential trajectories of relative human density (using relative N_e as a proxy) in Siberia by sampling a lognormal distribution of relative effective population size (based on the mean and variance of the 4950 simulations), accounting for spatially autocorrelated stochasticity (see Supporting Information Appendix S1 for an extended description of the methods used to reconstruct human densities in Siberia).

2.4 | Process-explicit model

We generated an SEPM in PALEOPOP that simulated the ecological processes of movement and demographic change (extinction), responding to shifting climates, sea levels, ice sheets and human hunting. Key ecological processes we modelled for the steppe bison included density-dependent population growth, dispersal and source–sink dynamics. These processes were simulated at generational time steps (12 years) using scalar-type SEPMs (Fordham et al. 2018). Habitat suitabilities from the potential realized niche models were used to structure the metapopulation by providing estimates of relative upper abundance in space and time (Fordham et al., 2022), assuming no adaptation to climatic or environmental change over the

course of the simulation. Simulations were run at 12-year time steps from 50 to 5 kyr BP. To ensure stable metapopulation dynamics at the beginning of the simulation (Fordham et al., 2018), all simulations were preceded by a burn-in period of 100 generations, whereby grid cell upper abundance values were held at 50 kyr BP values for the burn-in period.

2.4.1 | Demography

Demographic rates for congeneric species (*B. bison* and *B. bonasus*) were used as surrogates for the steppe bison (Fordham et al., 2016). We estimated the maximum annual growth rate and its variance using time series data for *B. bison* and *B. bonasus* (for details, see Supporting Information Appendix S1). We scaled these growth rates to a generational time step based on the 12-year generation length of *B. bison* (Pacifici et al., 2013). After testing the stability of population dynamics with different density dependence functions, we modelled population growth with Ricker logistic density dependence (Ricker, 1954), with the carrying capacity dependent on the habitat suitability in a given grid cell. At a habitat suitability of one, the carrying capacity was equal to the maximum density (Table 1), reducing with lower suitability scores. We modelled a negative Allee effect, using a quasi-extinction threshold below which populations immediately dropped to zero (Fordham et al., 2018).

We simulated natal dispersal based on empirical estimates for *B. bison* (Jung, 2017). Between 5 and 25% of the population dispersed per generation, with a maximum dispersal distance of 100–500 km (Table 1). A dispersal friction landscape (Adriaensen et al., 2003) based on ice sheet reconstructions was used to ensure that bison dispersed only through ice-free grid cells. Human hunting was simulated based on relative abundance (see above). The harvest

z parameter shaped the hunting function from a type II ($z = 1$) to type III ($z = 2$) functional response (Brook & Bowman, 2002), with the maximum harvest set from 0 to 35% (Fordham et al., 2022). All demographic parameters are described in more detail in the Supporting Information (Appendix S1).

2.4.2 | Model simulations

To address parameter uncertainty, which is inevitably high for extinct species (Brook & Bowman, 2004), we created 50,000 unique SEPM parameterizations using Latin hypercube sampling (Stein, 1987), drawing samples from uniform prior distributions for 11 model parameters (Table 1). This stratified sampling of the priors allowed us to generate a large suite of SEPMs, covering the parameter space of demographic processes, ecological requirements (based on realized niche breadth and specialty) and hunting pressure. We selected realized niches to generate the carrying capacity landscapes in each simulation. Each sampled combination of parameters, including niche estimates, was integrated into an SEPM and simulated for a single replicate (Fordham et al., 2022). Fifty thousand simulations took 214 h in parallel on an eight-core Windows machine with a 3.6 GHz processor.

2.5 | Pattern-oriented modelling

2.5.1 | Validation targets

POM (Grimm et al., 2005) was used to evaluate different SEPM parameterizations. Simulations were validated using POM methods by comparing simulated estimates of spatio-temporal occurrences in Siberia, and the timing and location of extinction, with

Parameter	Mean prior	Mean posterior
Ecological niche		
Niche volume	0.5 (0–1)	0.438 (0.332–0.775)
Niche outlier marginality index (OMI)	0.5 (0–1)	0.197 (0.166–0.237)
Human harvesting		
Maximum harvest (%)	17.5 (0–35)	25.3 (9.5–34.1)
Harvest function (z)	1.5 (1–2)	1.46 (1.04–1.89)
Human density (p)	0.5 (0–1)	0.782 (0.585–0.984)
Movement		
Dispersing fraction	0.15 (0.05–0.25)	0.212 (0.121–0.249)
Maximum dispersal distance (km)	300 (100–500)	419 (285–495)
Population model		
Maximum growth rate (r)	2.07 (1.31–2.84)	2.066 (1.566–2.816)
Variance of growth rate	0.123 (0–0.245)	0.172 (0.095–0.228)
Allee effect (abundance threshold)	250 (0–500)	212 (126–298)
Maximum density (bison per grid cell)	1875 (500–3250)	2542 (1840–3203)

TABLE 1 Parameter distributions: The prior and posterior means, minima and maxima are shown for parameters in the process-explicit model of steppe bison range and extinction dynamics

Note: All priors are uniformly distributed. For details, see Materials and Methods.

fossil-based inferences (Supporting Information Appendix S1). We estimated the timing of extinction in Siberia from the fossil record to be 8734 yr BP (95% confidence interval: 8810–8657 yr BP) using a Gaussian-resampled, inverse-weighted method (Bradshaw et al., 2012) that accounts for the Signor–Lipps effect (Signor et al., 1982). We estimated the extinction location to be in the Lena River basin, based on the youngest fossil (Pilowsky et al., 2021). To calculate spatio-temporal occurrence, we set a spatio-temporal window of uncertainty around each steppe bison fossil in our study region ($n = 31$), then quantified the agreement between simulated and inferred occurrence. The spatial window was based on the grid cell and its eight nearest neighbours, and the temporal band of uncertainty was based on ±2SD of the calibrated date. The same temporal band of uncertainty was used to quantify climatic conditions for the multi-temporal niche. A simulated presence of bison within the inferred window of occurrence was treated as a correctly simulated occurrence.

2.5.2 | Statistical procedure

POM was done in the R package ABC v.2.1 (Csilléry et al., 2012) using approximate Bayesian computation with the rejection algorithm to select the 100 best models. All summary metrics for analysis were scaled based on their standard deviations (van der Vaart et al., 2015). The POM procedure was repeated using informed priors from previous model runs. This was done until Bayes factors indicated that the posteriors had converged (Supporting Information Appendix S2, S2.1). The procedure involved running four additional rounds of 10,000 simulations each, selecting the best 100 models each time and using the posterior distributions as the priors for the subsequent round. Posterior predictive checks were done to determine whether the posterior distributions resulted in a good resemblance between simulated and observed data (Gelman et al., 2014).

2.6 | Counterfactual scenarios

Counterfactual scenarios create possible alternatives to what occurred historically (Mondal & Southworth, 2010). We used counterfactual analysis to determine the consequences of rates of past climatic change and hunting by humans on the decline and extinction of steppe bison in Siberia (Fordham et al., 2022). We created an optimized ensemble based on the 100 best models selected from the final round of simulations, which served as a "baseline scenario" (non-counterfactual) of what is historically likely to have occurred in Siberia based on our POM approach. We used this optimized ensemble of models to simulate two counterfactual scenarios: no harvest, which modelled no hunting of steppe bison by humans from 50 kyr BP (i.e., steppe bison responding only to climate change); and constant climate, which held climatic suitability for steppe bison in Siberia at LGM values from 21 kyr BP to the end of the simulation. For the constant climate scenario, the density of humans remained dynamic. Demographic and ecological parameters for the counterfactual

scenarios were generated using random draws from the posterior distributions of the optimized ensemble model, using the Latin hypercube sampling approach described above. The counterfactual and baseline scenarios were compared using 10,000 simulations per scenario.

3 | RESULTS

Our validated simulations showed that the range of the steppe bison in Siberia contracted in a north-easterly direction until 33 kyr BP, when the range fragmented into smaller populations (Figure 2). This fragmentation continued through the Pleistocene–Holocene transition, resulting in only refugial populations in north-eastern Siberia from 11 kyr BP (Supporting Information Movie S1). The time of extinction in Siberia was simulated to occur at 7.4 kyr BP (±1.5 kyr BP), based on the ABC-weighted average of the best 100 process-explicit models. The oldest end of the window of uncertainty in our simulated estimate of time of extinction overlapped with the time of extinction based on the fossil record (8.81–8.66 kyr BP; see Materials and Methods). The youngest end overlapped with independent environmental DNA evidence of prolonged persistence of steppe bison in north-eastern Siberia, with the youngest inference of occurrence being at 6.4 ± 0.6 kyr BP (Wang et al., 2021). This ensemble of "best models" projected the last surviving population to be in the east Siberian highlands, occurring *c.* 500 km from the last known fossil, located at Batagaika in the Lena River valley (Murton et al., 2017).

The capacity of SEPMs to simulate fossil-based inferences of timing and location of extinction was high after five iterations of POM (Figure 3). Bayes factors showed convergence in prior and posterior distributions after these five iterations of POM (all Bayes factors were less than one; Supporting Information Appendix S2, Figure S2.1). Posterior predictive checks showed that these posterior parameter distributions resulted in reasonable resemblance between simulated and observed data for extinction location and extinction time ($p > .01$; Supporting Information Appendix S2, Table S2.1). However, there was a poorer fit between the simulated spatio-temporal occurrence of bison at fossil sites and the observed fossil-based inference of spatio-temporal occurrence ($p < .01$).

3.1 | Posterior distributions of model parameters

Comparison of posterior and prior parameters showed that accurately reconstructing inferences of range contraction and the timing and location of extinction from the fossil record required specific demographic and niche constraints and hunting pressure (Figure 4). Posterior distributions showed that specific niche requirements were needed to reconstruct the range and extinction dynamics of steppe bison. The posterior distributions for niche volume and outlying mean index (Table 1) indicated that steppe bison in Siberia fulfilled a subset of core climatic conditions available to the species across its entire multi-temporal range. This was shown by a small-to-medium
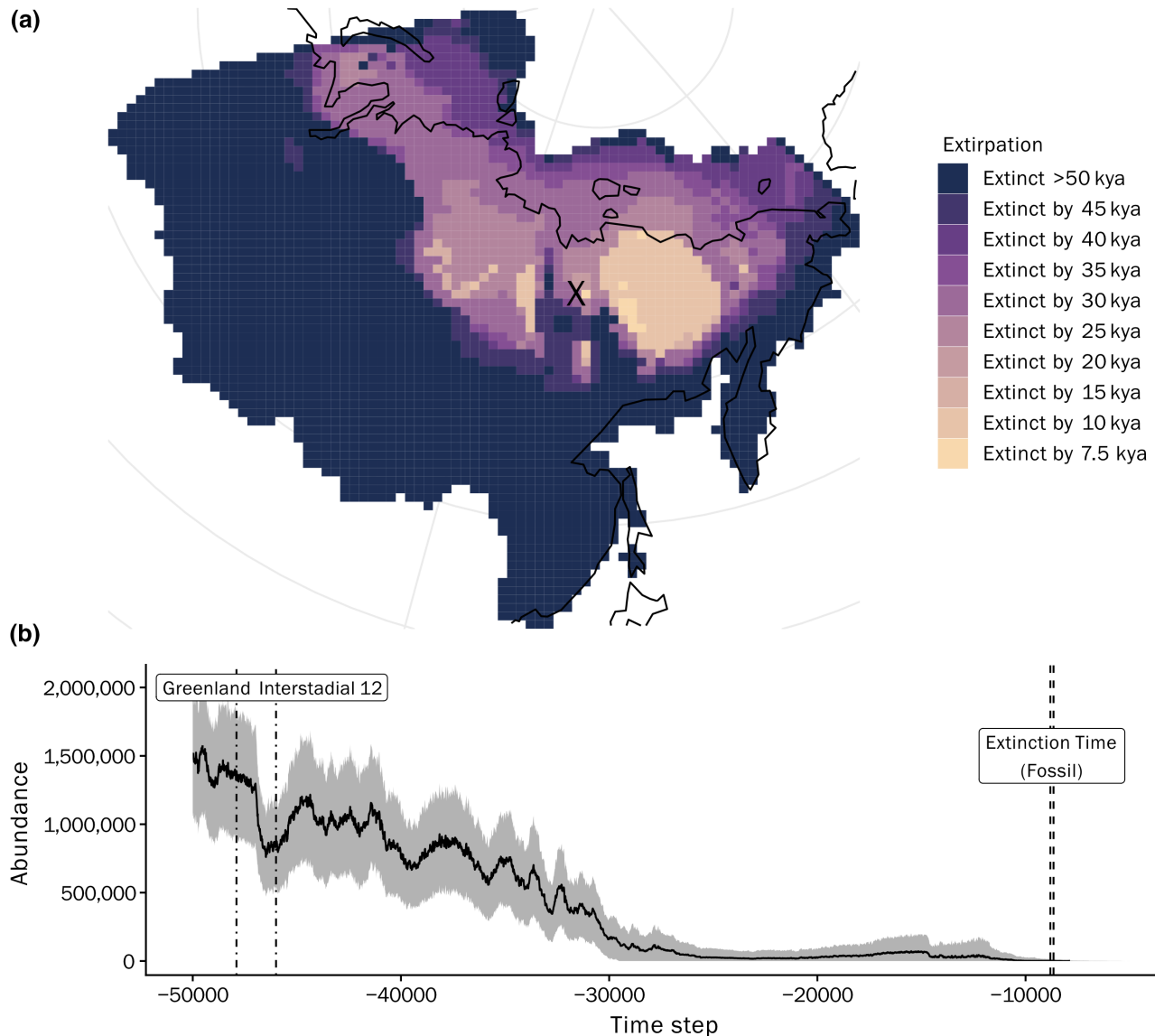
(a)

(b)

FIGURE 2 Validated reconstruction of the extinction of the steppe bison in Siberia. (a) The map shows the multi-model average estimate of the time of extirpation for the best models according to pattern-oriented modelling. The location of the site of extinction based on fossil data is marked with a cross. (b) The time series shows simulated total population size for steppe bison in Siberia. Vertical lines show extinction time as estimated from the fossil record and Greenland interstadial 12. The latter is a period of climatic warming between 47.9 and 46.0 kyr BP.

niche volume (60% of the full multi-temporal niche volume) and small outlying mean index. Among demographic processes, the posterior distributions showed that a high variance in growth rate, a medium-sized Allee effect, high maximum density and high dispersal (in terms of both maximum dispersal distance and dispersing fraction) were important for reconstructing range and extinction dynamics of the steppe bison in Siberia (Table 1). Furthermore, hitting validation targets required high human densities and high rates of harvest (Table 1).

3.2 | Counterfactual scenarios

In a no hunting scenario, the total population size of steppe bison in Siberia was higher throughout the simulation compared with the baseline (with hunting), and they did not go extinct before the end of the

simulation at 5 kyr BP (Figure 5). Before 30 kyr BP in the no hunting scenario, the range of the steppe bison extended further south and west, fragmenting into smaller subpopulations only in the final 5000 years of the simulation (Supporting Information Movie S1). In a constant climate scenario, in which the climate was unvarying from 21 kyr BP, total population size stabilized at 19 kyr BP (Figure 5), while the range contracted to two large subpopulations that were linked by dispersal, both of which persisted to the end of the simulation (Supporting Information Movie S1).

Neither of the counterfactual scenarios did as well as the baseline model at predicting the timing and location of extinction (Supporting Information Appendix S2, Figure S2.2). Models without human hunting (no hunting scenario) were generally better able to simulate spatio-temporal occurrence than the constant climate and baseline scenarios. This was because the absence of hunting
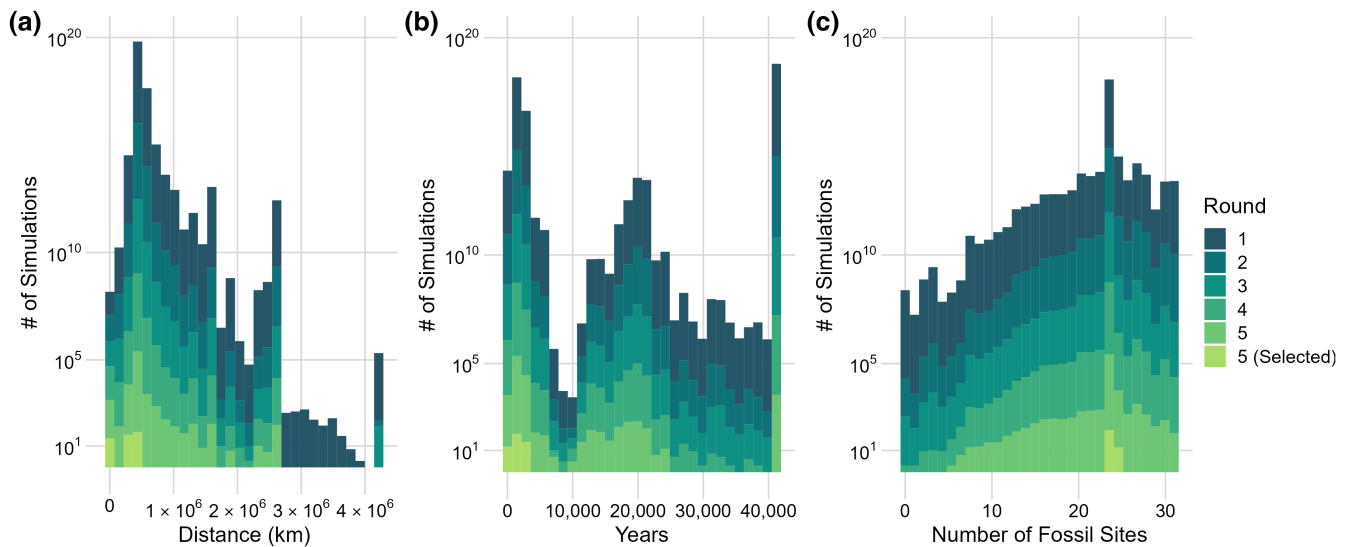
FIGURE 3 Reconstructions of validation targets using pattern-oriented modelling (POM). Validation targets for POM are: (a) extinction location, evaluated by difference (in kilometres) between simulated extinction location and the location based on the youngest fossil; (b) extinction time, evaluated by difference (in years) between simulated and inferred time of extinction based on the fossil record; and (c) fossil-based occurrence, evaluated by the number of sites where spatio-temporal occurrence is simulated correctly. For (a) and (b), the target for POM was zero (no difference between simulated and target value). For (c), the target was 31, which is equal to the total number of fossil occurrence sites. Different colours show five successive iterations of POM. For further details, see the Materials and Methods.
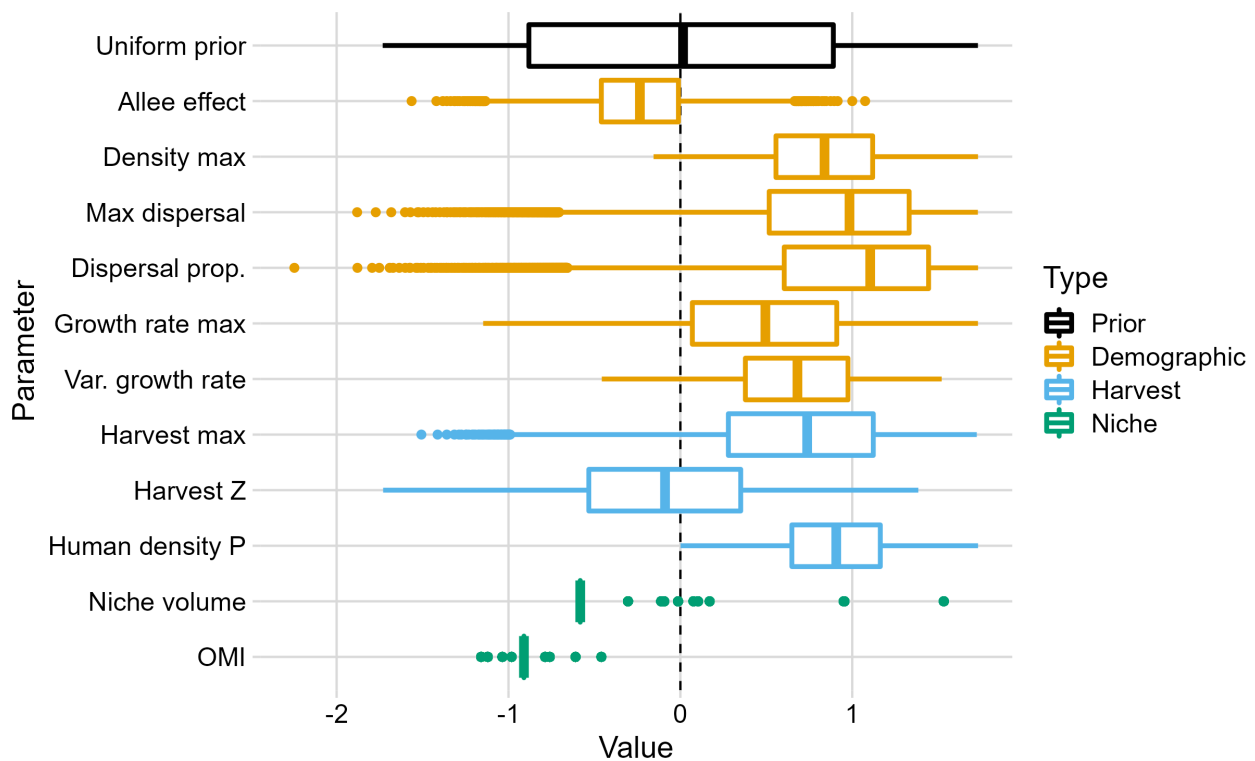

FIGURE 4 Regression-adjusted posterior distributions for parameters. Maximum (max) dispersal distance and the fraction of bison that dispersed in each generation (dispersing fraction) combine to simulate dispersal. Maximum density of bison in each grid cell, Allee effect, variance (var.) and maximum growth rate all interact to simulate population growth. Human density (relative human density), harvest z (shape of the harvest function) and maximum harvest (maximum proportion of bison hunted) determine the hunting rate. Volume and outlying mean index (OMI) are measures of climatic niche space (the size of the climatic niche and the marginality of climatic preferences, respectively). All prior distributions were uniform. Parameters are described in more detail in the Materials and Methods. Unscaled parameter ranges are provided in Table 1.
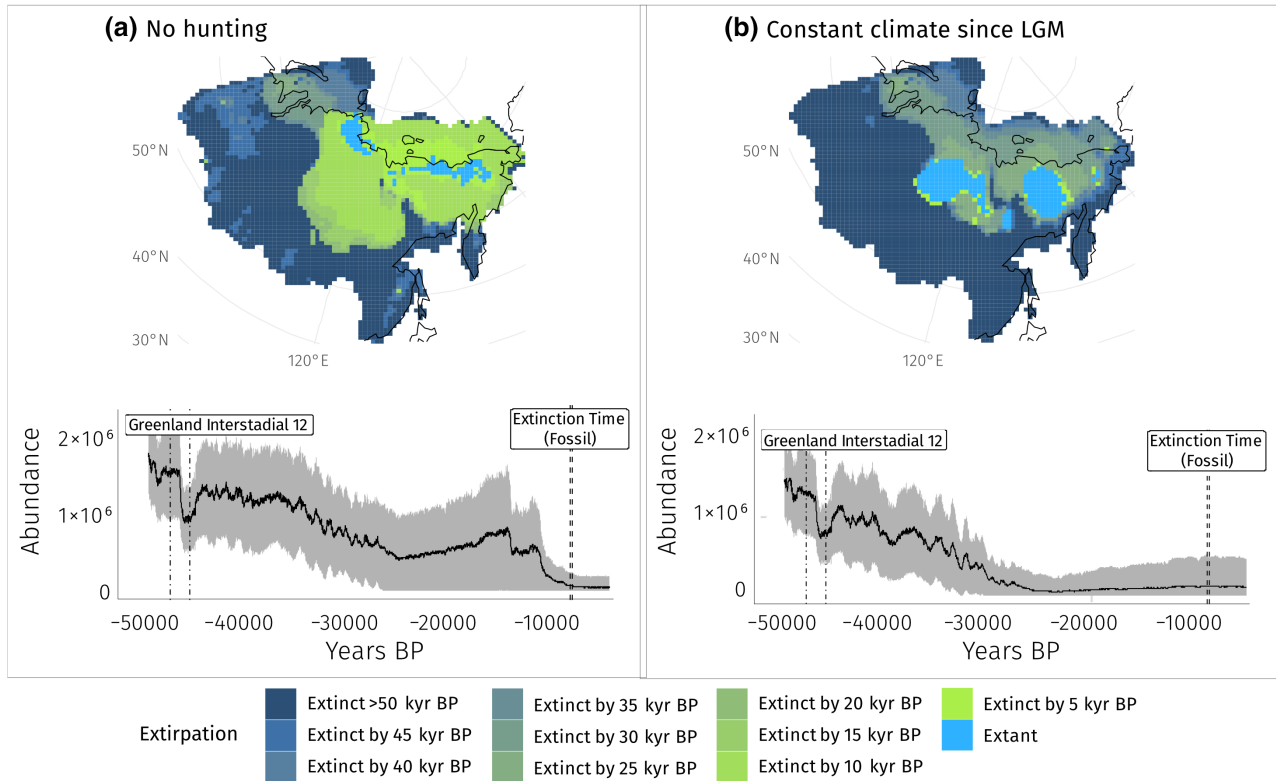
FIGURE 5 Alternative scenarios of extirpation and population decline. Counterfactual scenarios simulate: (a) climate change but no human harvesting of bison (no hunting); and (b) no climate change from 21 kyr BP, but harvesting of bison before and after that time [constant climate since Last Glacial Maximum (LGM)]. Maps show when populations in each grid cell went extinct locally. Populations that survived to the end of the simulation are shown in bright blue (extant). Line graphs show the simulated trajectories of total abundance in Siberia (±1SD). They include timing of Greenland interstadial 12 and timing of extinction in Siberia inferred from fossils. For details, see Figure 2.

by humans resulted in larger areas of occupied habitat in Siberia through time (Supporting Information Movie S1).

4 | DISCUSSION

We were able to reconcile inferences of spatio-temporal occurrence and the timing and location of extinction for steppe bison in Siberia based on hundreds of radiocarbon-dated fossils. Our ensemble of "best models" projected extinction to have occurred in the east Siberian highlands at 7.4 kyr BP, occurring on average 1300 years after the fossil estimate. This is consistent with fossil-based estimates of extinction often being hundreds to thousands of years earlier than the likely timing of the extinction event (Haile et al., 2009; Wang et al., 2021), because they represent the last time that a species was abundant (Mann et al., 2019). We show that simulating the ecological pathway to extinction for steppe bison in its last refuge in Eurasia required very specific ecological niche constraints, demographic processes and hunting dynamics. It also required these processes to respond to climatic change, human abundance and their interaction during the Pleistocene–Holocene transition. Counterfactual scenarios confirmed that human hunting and climatic change were both pivotal long-term drivers of regional extinction for the steppe bison in Siberia and, most probably,

Eurasia more generally. These results demonstrate how SEPMs and POM methods can be used in macroecology and palaeoecology to disentangle the mechanisms that were integral in the decline and later extinction of species.

The processes leading to the megafauna extinctions of the late Pleistocene and early Holocene are uncertain, with intense debate on the roles of human hunting and climatic change (Mann et al., 2019; Stuart, 2015). The steppe bison was an iconic herbivore that dominated the "mammoth steppe" of the Ice Age Arctic (Guthrie, 1989). Although the timing, location and causes of megafaunal extinctions in this biome are contested (Cooper et al., 2015; Koch & Barnosky, 2006; Stuart, 2015), our process-explicit models show that a synergy of climatic change and exploitation by humans most probably drove the steppe bison, and perhaps other herbivores of the mammoth steppe, to extinction during the late Pleistocene and early Holocene.

POM revealed the ecological processes that regulated the extinction dynamics of steppe bison. Reconstructing fossil-based evidence of spatio-temporal occurrence and extinction in the northern Lena River valley requires steppe bison to have an ecological niche volume of 59–74% of the size of the full multi-temporal niche (Nogués-Bravo, 2009). This reduced niche volume has low marginality (Dolédec et al., 2000), meaning that the ecological niche for steppe bison in Siberia represented the core climatic preferences of steppe bison more generally. Among demographic processes,

dispersal and the effect of small population size on extirpation are likely to have influenced the range and extinction dynamics of steppe bison. Hitting our multivariate validation target required a pronounced Allee effect and the capacity for high dispersal, among other demographic constraints. Evidence for an Allee effect at low population densities has been found in natural populations of other temperate and polar ungulates: bighorn sheep (*Ovis canadensis*), chamois (*Rupicapra rupicapra*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*) and woodland caribou (*Rangifer tarandus*) (Kramer et al., 2009). This has been attributed largely to cooperative defence and predator satiation reducing mortality at high densities, although mate selection at low density could also be a factor (Kramer et al., 2009). A high capacity for movement, including long-distance dispersal, was also needed to reconstruct inferences of demographic change from the fossil record. Research on American bison has shown that they migrate seasonally in response to forage availability in winter (Gates & Larter, 1990). They will also disperse towards unoccupied habitat when population densities become high (Plumb et al., 2009).

Reconciling inferences of range collapse and extinction from the palaeo-record required hunting by humans. More specifically, humans needed to be found in medium to high regional densities (based on projections for Siberia), with high harvest offtake. Holding the hunting of bison constant to zero exploitation and analysing the effect of this constraint on dynamic processes and emergent patterns revealed that human hunting was a crucial and chronic driver of extinction of steppe bison in Siberia. Without hunting by humans, steppe bison maintained a wider distribution and larger population size and did not go extinct by 5 kyr BP (the end of the simulation). Instead, bison persisted in two small subpopulations in the far north of Siberia with suitable climatic conditions. This finding aligns with archaeological evidence showing that human hunters in Siberia relied heavily on bison prey during the Pleistocene–Holocene transition (Vasil'ev, 2003) and that bison were disproportionately selected by hunters (Pushkina & Raia, 2008).

Keeping climatic conditions constant for steppe bison (but not humans) since the LGM in the constant climate counterfactual scenario showed that hunting alone could not have driven the steppe bison to extinction. Without deglacial warming negatively affecting range and abundance, steppe bison were projected to be at large abundances at 5 kyr BP despite hunting by humans. Taken together, our counterfactual hypotheses of the drivers of range collapse and extinction of steppe bison show that human hunting and climatic change were important determinants of the ecological pathway to extinction for steppe bison in Siberia. This association is likely to have been synergistic, with humans accelerating the range collapse of steppe bison during the Pleistocene–Holocene transition, hastening the extirpation of populations that had become fragmented owing to deglacial warming and associated shifts in vegetation. A similar mechanistic explanation has been proposed for the extinction of the woolly mammoth (Fordham et al., 2022).

Although we have shown that the application of POM methods to process-explicit modelling provides a powerful approach

for continuously reconstructing range dynamics over thousands of years, the approach is only as accurate as the validation targets being used. Our validation targets were independent from the data used to parameterize the model. They captured a hierarchy of demographic responses (Gallagher et al., 2021), and they were estimated robustly using statistical techniques applied to fossil data (Bradshaw et al., 2012). Therefore, we have confidence in our POM and results, including the posterior distributions for model parameters and their multi-model averaged projections of range and extinction dynamics (Grimm & Railsback, 2012). However, for many other species, an abundant and spatially representative fossil record will not be available to optimize SEPMs of species range dynamics using POM. Here, other types of palaeo-validation data could be considered, including ancient DNA estimates of past population change (Fordham et al., 2014) and inferences of spatio-temporal occurrence from environmental DNA in sediments and ice cores (Wang et al., 2021). For threatened species or for species that went extinct recently (such as the thylacine in Australia), historical sightings can provide important sources of validation data (Fordham et al., 2021).

Posterior predictive checks of our process-explicit model showed that the posterior ranges of model parameters reconstruct extinction time and location reasonably well (Gelman et al., 2014). However, it was more difficult to reconcile fossil evidence of spatio-temporal occurrence. Indeed, this target was easier to reconstruct in simulations without human hunting, because in the no hunting scenario, steppe bison maintained larger ranges through time. Larger ranges resulted in occurrence being higher not only at fossil sites, but also in areas that were unlikely to have been habitable by steppe bison during periods in the past. It is possible that the difficulty with correctly simulating spatio-temporal occurrence at fossil sites could stem from the hunting dynamics in our process-explicit model. These dynamics were relatively simple, not accounting for technological developments that are likely to have occurred during the time frame of the simulation (Goebel, 2002). The wide posterior range for the functional response of human hunting of steppe bison extends from the selected best models having a diverse range of hunting strategies, suggesting that a variety of parameter values can give a close fit to inferences of extinction dynamics from the fossil record. Also, the model we used to simulate the peopling of Siberia (and Eurasia more generally in CISGeM) does not account for topography, which could have caused barriers to movement, particularly in the Siberian highlands (Eriksson et al., 2012), affecting spatio-temporal harvest rates.

Our process-explicit modelling shows that climatic change and hunting by humans in Siberia during the late Pleistocene and early Holocene is likely to have interacted with key ecological requirements and demographic processes of steppe bison to cause their extinction in Eurasia during the early Holocene. Moreover, it shows that process-explicit models validated with POM methods can continuously simulate the ecological processes and drivers that cause the population declines of species over many millennia, in addition to the final extinction event. Although synthesis of long- and short-term causes of population decline (Caughley, 1994) remains rare, the

integrated computational framework used here provides new opportunities to establish ecological pathways to extinction over long time periods. If applied to a diverse range of species, generalities in ecological processes of extinction could be identified.

DATA AVAILABILITY STATEMENT

The data used for the analysis is available on Figshare (DOI: 10.6084/m9.figshare.17059592.v2) and an example of the R code is available on Zenodo (DOI: 10.5281/zenodo.7098687).

ORCID

Julia A. Pilowsky https://orcid.org/0000-0002-6376-2585
Stuart C. Brown https://orcid.org/0000-0002-0669-1418
Mario Krapp https://orcid.org/0000-0002-2599-0683
Edward Armstrong https://orcid.org/0000-0001-9561-0159
Barry W. Brook https://orcid.org/0000-0002-2491-1517
Carsten Rahbek https://orcid.org/0000-0003-4585-0300
Damien A. Fordham https://orcid.org/0000-0003-2137-5592

REFERENCES

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning, 64*(4), 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Anderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences, 276*(1661), 1415–1420. https://doi.org/10.1098/rspb.2008.1681

Anderson, P. M., & Lozhkin, A. V. (2001). The stage 3 interstadial complex (Karginskii/middle Wisconsinan interval) of Beringia: Variations in paleoenvironments and implications for paleoclimatic interpretations. *Quaternary Science Reviews, 20*(1–3), 93–125. https://doi.org/10.1016/S0277-3791(00)00129-3

Armstrong, E., Hopcroft, P. O., & Valdes, P. J. (2019). A simulated northern hemisphere terrestrial climate dataset for the past 60,000 years. *Scientific Data, 6*(1), 1–16. https://doi.org/10.1038/s41597-019-0277-1

Barnes, R., & Clark, A. T. (2017). Sixty-five million years of change in temperature and topography explain evolutionary history in eastern north American plethodontid salamanders. *The American Naturalist, 190*(1), E1–E12. https://doi.org/10.1086/691796

Barnosky, A. D., & Lindsey, E. L. (2010). Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International, 217*(1), 10–29. https://doi.org/10.1016/j.quaint.2009.11.017

Beaumont, M. A., Zhang, W., & Balding, D. J. (2002). Approximate Bayesian computation in population genetics. *Genetics, 162*(4), 2025–2035. https://doi.org/10.1093/genetics/162.4.2025

Blaauw, M. (2010). Methods and code for "classical" age-modelling of radiocarbon sequences. *Quaternary Geochronology, 5*(5), 512–518. https://doi.org/10.1016/j.quageo.2010.01.002

Blonder, B., Morrow, C. B., Maitner, B., Harris, D. J., Lamanna, C., Violle, C., Enquist, B. J., & Kerkhoff, A. J. (2018). New approaches for delineating n-dimensional hypervolumes. *Methods in Ecology and Evolution, 9*(2), 305–319. https://doi.org/10.1111/2041-210X.12865

Boeskorov, G. G., Potapova, O. R., Protopopov, A. V., Plotnikov, V. V., Agenbroad, L. D., Kirikov, K. S., Pavlov, I. S., Shchelchkova, M. V., Belolyubskii, I. N., Tomshin, M. D., Kowalczyk, R., Davydov, S. P., Kolesov, S. D., Tikhonov, A. N., & van der Plicht, J. (2016). The Yukagir Bison: The exterior morphology of a complete frozen mummy of the extinct steppe bison, Bison priscus from the early Holocene of northern Yakutia, Russia. *Quaternary International, 406*, 94–110. https://doi.org/10.1016/j.quaint.2015.11.084

Bradshaw, C. J. A., Cooper, A., Turney, C. S. M., & Brook, B. W. (2012). Robust estimates of extinction time in the geological record. *Quaternary Science Reviews, 33*, 14–19. https://doi.org/10.1016/j.quascirev.2011.11.021

Brook, B. W., & Bowman, D. M. J. S. (2002). Explaining the Pleistocene megafaunal extinctions: Models, chronologies, and assumptions. *Proceedings of the National Academy of Sciences, 99*(23), 14624–14627. https://doi.org/10.1073/pnas.232126899

Brook, B. W., & Bowman, D. M. J. S. (2004). The uncertain blitzkrieg of Pleistocene megafauna. *Journal of Biogeography, 31*(4), 517–523. https://doi.org/10.1046/j.1365-2699.2003.01028.x

Canteri, E., Brown, S. C., Schmidt, N. M., Heller, R., Nogues-Bravo, D., & Fordham, D. A. (2022). Spatiotemporal influences of climate and humans on muskox range dynamics over multiple millennia. *Global Change Biology.* https://doi.org/10.1111/gcb.16375

Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology, 63*(2), 215–244. https://doi.org/10.2307/5542

Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., & McCabe, A. M. (2009). The last glacial maximum. *Science, 325*(5941), 710–714. https://doi.org/10.1126/science.1172873

Colwell, R. K., & Rangel, T. F. (2010). A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1558), 3695–3707. https://doi.org/10.1098/rstb.2010.0293

Connolly, S. R., Keith, S. A., Colwell, R. K., & Rahbek, C. (2017). Process, mechanism, and modeling in macroecology. *Trends in Ecology & Evolution, 32*(11), 835–844. https://doi.org/10.1016/j.tree.2017.08.011

Cooper, A., Turney, C., Hughen, K. A., Brook, B. W., McDonald, H. G., & Bradshaw, C. J. (2015). Abrupt warming events drove late Pleistocene Holarctic megafaunal turnover. *Science, 349*(6248), 602–606. https://doi.org/10.1126/science.aac4315

Csilléry, K., François, O., & Blum, M. G. B. (2012). abc: An R package for approximate Bayesian computation (ABC). *Methods in Ecology and Evolution, 3*(3), 475–479. https://doi.org/10.1111/j.2041-210X.2011.00179.x

Davidson, A. D., Hamilton, M. J., Boyer, A. G., Brown, J. H., & Ceballos, G. (2009). Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Sciences, 106*(26), 10702–10705. https://doi.org/10.1073/pnas.0901956106

DelGiudice, G. D., Moen, R. A., Singer, F. J., & Riggs, M. R. (2001). Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. *Wildlife Monographs, 147*, 1–60.

DelGiudice, G. D., Singer, F. J., Seal, U. S., & Bowser, G. (1994). Physiological responses of Yellowstone bison to winter nutritional deprivation. *The Journal of Wildlife Management, 58*(1), 24–34. https://doi.org/10.2307/3809545

Dietl, G. P., Kidwell, S. M., Brenner, M., Burney, D. A., Flessa, K. W., Jackson, S. T., & Koch, P. L. (2015). Conservation paleobiology: Leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth and Planetary Sciences*, *43*(1), 79–103. https://doi.org/10.1146/annurev-earth-040610-133349

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: A new method. *Ecology*, *81*(10), 2914–2927. https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2

Dunning, J. B., Jr., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H., & Stevens, E. E. (1995). Spatially explicit population models: Current forms and future uses. *Ecological Applications*, *5*(1), 3–11. https://doi.org/10.2307/1942045

Ellis, E. C., Gauthier, N., Goldewijk, K. K., Bird, R. B., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(17), e2023483118. https://doi.org/10.1073/pnas.2023483118

Eriksson, A., Betti, L., Friend, A. D., Lycett, S. J., Singarayer, J. S., von Cramon-Taubadel, N., Valdes, P. J., Balloux, F., & Manica, A. (2012). Late Pleistocene climate change and the global expansion of anatomically modern humans. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(40), 16089–16094. https://doi.org/10.1073/pnas.1209494109

Fordham, D. A., Akçakaya, H. R., Alroy, J., Saltré, F., Wigley, T. M. L., & Brook, B. W. (2016). Predicting and mitigating future biodiversity loss using long-term ecological proxies. *Nature Climate Change*, *6*(10), 909–916. https://doi.org/10.1038/nclimate3086

Fordham, D. A., Bertelsmeier, C., Brook, B. W., Early, R., Neto, D., Brown, S. C., Ollier, S., & Araújo, M. B. (2018). How complex should models be? Comparing correlative and mechanistic range dynamics models. *Global Change Biology*, *24*(3), 1357–1370. https://doi.org/10.1111/gcb.13935

Fordham, D. A., Brook, B. W., Moritz, C., & Nogués-Bravo, D. (2014). Better forecasts of range dynamics using genetic data. *Trends in Ecology & Evolution*, *29*(8), 436–443. https://doi.org/10.1016/j.tree.2014.05.007

Fordham, D. A., Brown, S. C., Akçakaya, H. R., Brook, B. W., Haythorne, S., Manica, A., Shoemaker, K. T., Austin, J. J., Blonder, B., Pilowsky, J., Rahbek, C., & Nogues-Bravo, D. (2022). Process-explicit models reveal pathway to extinction for woolly mammoth using pattern-oriented validation. *Ecology Letters*, *25*(1), 125–137. https://doi.org/10.1111/ele.13911

Fordham, D. A., Haythorne, S., Brown, S. C., Buettel, J. C., & Brook, B. W. (2021). Poems: R package for simulating species' range dynamics using pattern-oriented validation. *Methods in Ecology and Evolution*, *12*(12), 2364–2371. https://doi.org/10.1111/2041-210X.13720

Fordham, D. A., Jackson, S. T., Brown, S. C., Huntley, B., Brook, B. W., Dahl-Jensen, D., Gilbert, M. T. P., Otto-Bliesner, B. L., Svensson, A., Theodoridis, S., Wilmshurst, J. M., Buettel, J. C., Canteri, E., McDowell, M., Orlando, L., Pilowsky, J., Rahbek, C., & Nogues-Bravo, D. (2020). Using paleo-archives to safeguard biodiversity under climate change. *Science*, *369*(6507), eabc5654. https://doi.org/10.1126/science.abc5654

Gallagher, C. A., Chudzinska, M., Larsen-Gray, A., Pollock, C. J., Sells, S. N., White, P. J. C., & Berger, U. (2021). From theory to practice in pattern-oriented modelling: Identifying and using empirical patterns in predictive models. *Biological Reviews*, *96*(5), 1868–1888. https://doi.org/10.1111/brv.12729

Gates, C. C., & Larter, N. C. (1990). Growth and dispersal of an erupting large herbivore population in northern Canada: The Mackenzie wood bison (Bison bison athabascae). *Arctic*, *43*(3), 231–238.

Gelman, A., Hwang, J., & Vehtari, A. (2014). Understanding predictive information criteria for Bayesian models. *Statistics and Computing*, *24*(6), 997–1016. https://doi.org/10.1007/s11222-013-9416-2

Goebel, T. (2002). The "microblade adaptation" and recolonization of Siberia during the late upper Pleistocene. *Archaeological Papers of the American Anthropological Association*, *12*(1), 117–131. https://doi.org/10.1525/ap3a.2002.12.1.117

Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: A "multi-scope" for predictive systems ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1586), 298–310. https://doi.org/10.1098/rstb.2011.0180

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T., & DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, *310*(5750), 987–991. https://doi.org/10.1126/science.1116681

Guthrie, R. D. (1989). *Frozen Fauna of the mammoth steppe: The story of blue babe*. University of Chicago Press.

Guthrie, R. D. (2006). New carbon dates link climatic change with human colonization and Pleistocene extinctions. *Nature*, *441*(7090), 207–209. https://doi.org/10.1038/nature04604

Haile, J., Froese, D. G., MacPhee, R. D. E., Roberts, R. G., Arnold, L. J., Reyes, A. V., Rasmussen, M., Nielsen, R., Brook, B. W., Robinson, S., Demuro, M., Gilbert, M. T. P., Munch, K., Austin, J. J., Cooper, A., Barnes, I., Möller, P., & Willerslev, E. (2009). Ancient DNA reveals late survival of mammoth and horse in interior Alaska. *Proceedings of the National Academy of Sciences*, *106*(52), 22352–22357. https://doi.org/10.1073/pnas.0912510106

Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*(6706), 41–49. https://doi.org/10.1038/23876

Haythorne, S., Pilowsky, J. A., Brown, S., & Fordham, D. (2021). Paleopop: Pattern-oriented modeling framework for coupled niche-population paleo-climatic models (v.2.1.2) [Computer software]. https://CRAN.R-project.org/package=paleopop

Julien, M.-A., Bocherens, H., Burke, A., Drucker, D. G., Patou-Mathis, M., Krotova, O., & Péan, S. (2012). Were European steppe bison migratory? 18O, 13C and Sr intra-tooth isotopic variations applied to a palaeoethological reconstruction. *Quaternary International*, *271*, 106–119. https://doi.org/10.1016/j.quaint.2012.06.011

Jung, T. S. (2017). Extralimital movements of reintroduced bison (Bison bison): Implications for potential range expansion and human-wildlife conflict. *European Journal of Wildlife Research*, *63*(2), 35. https://doi.org/10.1007/s10344-017-1094-5

Knowles, L. L., & Alvarado-Serrano, D. F. (2010). Exploring the population genetic consequences of the colonization process with spatio-temporally explicit models: Insights from coupled ecological, demographic and genetic models in montane grasshoppers. *Molecular Ecology*, *19*(17), 3727–3745. https://doi.org/10.1111/j.1365-294X.2010.04702.x

Koch, P. L., & Barnosky, A. D. (2006). Late Quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 215–250. https://doi.org/10.1146/annurev.ecolsys.34.011802.132415

Koons, D. N., Terletzky, P., Adler, P. B., Wolfe, M. L., Ranglack, D., Howe, F. P., Hersey, K., Paskett, W., & du Toit, J. T. (2012). Climate and density-dependent drivers of recruitment in plains bison. *Journal of Mammalogy*, *93*(2), 475–481. https://doi.org/10.1644/11-MAMM-A-281.1

Kramer, A. M., Dennis, B., Liebhold, A. M., & Drake, J. M. (2009). The evidence for Allee effects. *Population Ecology*, *51*(3), 341–354. https://doi.org/10.1007/s10144-009-0152-6

Laliberte, A. S., & Ripple, W. J. (2004). Range contractions of north American carnivores and ungulates. *Bioscience*, *54*(2), 123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2

Lorenzen, E. D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K. A., Ugan, A., Borregaard, M. K., Gilbert, M. T. P., Nielsen, R., Ho, S. Y. W., Goebel, T., Graf, K. E., Byers, D., Stenderup, J. T., Rasmussen, M., Campos, P. F., Leonard, J. A., Koepfli, K.-P., ... Willerslev, E. (2011). Species-specific responses of late Quaternary megafauna to climate and humans. *Nature*, *479*(7373), 359–364. https://doi.org/10.1038/nature10574

Mann, D. H., Groves, P., Gaglioti, B. V., & Shapiro, B. A. (2019). Climate-driven ecological stability as a globally shared cause of late Quaternary megafaunal extinctions: The plaids and stripes hypothesis. *Biological Reviews*, *94*(1), 328–352. https://doi.org/10.1111/brv.12456

Markova, A. K., Puzachenko, A. Y., van Kolfschoten, T., Kosintsev, P. A., Kuznetsova, T. V., Tikhonov, A. N., Bachura, O. P., Ponomarev, D. V., van der Plicht, J., & Kuitems, M. (2015). Changes in the Eurasian distribution of the musk ox (*Ovibos moschatus*) and the extinct bison (*Bison priscus*) during the last 50 ka BP. *Quaternary International*, *378*, 99–110. https://doi.org/10.1016/j.quaint.2015.01.020

Metcalf, J. L., Prost, S., Nogues-Bravo, D., DeChaine, E. G., Anderson, C., Batra, P., Araujo, M. B., Cooper, A., & Guralnick, R. P. (2014). Integrating multiple lines of evidence into historical biogeography hypothesis testing: A Bison bison case study. *Proceedings of the Royal Society B-Biological Sciences*, *281*(1777), 20132782. https://doi.org/10.1098/rspb.2013.2782

Mondal, P., & Southworth, J. (2010). Evaluation of conservation interventions using a cellular automata-Markov model. *Forest Ecology and Management*, *260*(10), 1716–1725. https://doi.org/10.1016/j.foreco.2010.08.017

Murton, J. B., Edwards, M. E., Lozhkin, A. V., Anderson, P. M., Savvinov, G. N., Bakulina, N., Bondarenko, O. V., Cherepanova, M. V., Danilov, P. P., Boeskorov, V., Goslar, T., Grigoriev, S., Gubin, S. V., Korzun, J. A., Lupachev, A. V., Tikhonov, A., Tsygankova, V. I., Vasilieva, G. V., & Zanina, O. G. (2017). Preliminary paleoenvironmental analysis of permafrost deposits at Batagaika megaslump, Yana uplands, Northeast Siberia. *Quaternary Research*, *87*(2), 314–330. https://doi.org/10.1017/qua.2016.15

Nogués-Bravo, D. (2009). Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, *18*(5), 521–531. https://doi.org/10.1111/j.1466-8238.2009.00476.x

Owens, I. P. F., & Bennett, P. M. (2000). Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences*, *97*(22), 12144–12148. https://doi.org/10.1073/pnas.200223397

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Marasini, G. G., Visconti, P., & Rondinini, C. (2013). Generation length for mammals. *Nature Conservation-Bulgaria*, *5*, 87–94. https://doi.org/10.3897/natureconservation.5.5734

Pilowsky, J. A., Colwell, R. K., Rahbek, C., & Fordham, D. A. (2022). Process-explicit models reveal the structure and dynamics of biodiversity patterns. *Science Advances*, *8*(31), eabj2271. https://doi.org/10.1126/sciadv.abj2271

Pilowsky, J. A., Haythorne, S., Brown, S. C., Krapp, M., Armstrong, E., Brook, B. W., Rahbek, C., & Fordham, D. A. (2021). *Quality-controlled carbon-14 dates of steppe bison (Bison priscus) fossils* [Data set]. figshare. https://doi.org/10.6084/M9.FIGSHARE.17059592.V2

Pilowsky, J. A., Manica, A., Brown, S. C., Rahbek, C., & Fordham, D. A. (2022). Simulations of human migration into North America are more sensitive to demography than choice of palaeoclimate model. *Ecological Modelling*, *473*, 110115. https://doi.org/10.1016/j.ecolmodel.2022.110115

Plumb, G. E., White, P. J., Coughenour, M. B., & Wallen, R. L. (2009). Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation*, *142*(11), 2377–2387. https://doi.org/10.1016/j.biocon.2009.05.019

Pontarp, M., Bunnefeld, L., Cabral, J. S., Etienne, R. S., Fritz, S. A., Gillespie, R., Graham, C. H., Hagen, O., Hartig, F., Huang, S., Jansson, R., Maliet, O., Münkemüller, T., Pellissier, L., Rangel, T. F., Storch, D., Wiegand, T., & Hurlbert, A. H. (2019). The latitudinal diversity gradient: Novel understanding through mechanistic eco-evolutionary models. *Trends in Ecology & Evolution*, *34*(3), 211–223. https://doi.org/10.1016/j.tree.2018.11.009

Pushkina, D., & Raia, P. (2008). Human influence on distribution and extinctions of the late Pleistocene Eurasian megafauna. *Journal of Human Evolution*, *54*(6), 769–782. https://doi.org/10.1016/j.jhevol.2007.09.024

Ramsey, C. B. (2017). *OxCal program, version 4.3. Oxford radiocarbon accelerator unit*. University of Oxford.

Rangel, T. F., Edwards, N. R., Holden, P. B., Diniz-Filho, J. A. F., Gosling, W. D., Coelho, M. T. P., Cassemiro, F. A. S., Rahbek, C., & Colwell, R. K. (2018). Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science*, *361*(6399), eaar5452. https://doi.org/10.1126/science.aar5452

Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Ramsey, C. B., Buck, C. E., Cheng, H., Edwards, R. L., & Friedrich, M. (2013). IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, *55*(4), 1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, *11*(5), 559–623. https://doi.org/10.1139/f54-039

Rutherford, S., Mann, M. E., Osborn, T. J., Briffa, K. R., Jones, P. D., Bradley, R. S., & Hughes, M. K. (2005). Proxy-based northern hemisphere surface temperature reconstructions: Sensitivity to method, predictor network, target season, and target domain. *Journal of Climate*, *18*(13), 2308–2329.

Shapiro, B., Drummond, A. J., Rambaut, A., Wilson, M. C., Matheus, P. E., Sher, A. V., Pybus, O. G., Gilbert, M. T. P., Barnes, I., Binladen, J., Willerslev, E., Hansen, A. J., Baryshnikov, G. F., Burns, J. A., Davydov, S., Driver, J. C., Froese, D. G., Harington, C. R., Keddie, G., ... Cooper, A. (2004). Rise and fall of the Beringian steppe bison. *Science*, *306*(5701), 1561–1565. https://doi.org/10.1126/science.1101074

Signor, P. W., Lipps, J. H., Silver, L. T., & Schultz, P. H. (1982). Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*, *190*, 291–296.

Soberón, J., & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, *106*(Supplement 2), 19644–19650. https://doi.org/10.1073/pnas.0901637106

Soubrier, J., Gower, G., Chen, K., Richards, S. M., Llamas, B., Mitchell, K. J., Ho, S. Y. W., Kosintsev, P., Lee, M. S. Y., Baryshnikov, G., Bollongino, R., Bover, P., Burger, J., Chivall, D., Crégut-Bonnoure, E., Decker, J. E., Doronichev, V. B., Douka, K., Fordham, D. A., ... Cooper, A. (2016). Early cave art and ancient DNA record the origin of European bison. *Nature Communications*, *7*(1), 13158. https://doi.org/10.1038/ncomms13158

Stein, M. (1987). Large sample properties of simulations using Latin hypercube sampling. *Technometrics*, *29*(2), 143–151. https://doi.org/10.1080/00401706.1987.10488205

Stuart, A. J. (2015). Late quaternary megafaunal extinctions on the continents: A short review. *Geological Journal*, *50*(3), 338–363. https://doi.org/10.1002/gj.2633

Thulke, H.-H., Grimm, V., Müller, M. S., Staubach, C., Tischendorf, L., Wissel, C., & Jeltsch, F. (1999). From pattern to practice: A scaling-down strategy for spatially explicit modelling illustrated by the spread and control of rabies. *Ecological Modelling*, *117*(2), 179–202. https://doi.org/10.1016/S0304-3800(98)00198-7

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., Meester, L. D., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), aad8466. https://doi.org/10.1126/science.aad8466

Valdes, P. J., Armstrong, E., Badger, M. P. S., Bradshaw, C. D., Bragg, F., Crucifix, M., Davies-Barnard, T., Day, J. J., Farnsworth, A., Gordon, C., Hopcroft, P. O., Kennedy, A. T., Lord, N. S., Lunt, D. J., Marzocchi, A., Parry, L. M., Pope, V., Roberts, W. H. G., Stone, E. J., ... Williams, J. H. T. (2017). The BRIDGE HadCM3 family of climate models: HadCM3@Bristol v1.0. *Geoscientific Model Development*, *10*(10), 3715–3743. https://doi.org/10.5194/gmd-10-3715-2017

van der Vaart, E., Beaumont, M. A., Johnston, A. S. A., & Sibly, R. M. (2015). Calibration and evaluation of individual-based models using approximate Bayesian computation. *Ecological Modelling*, *312*, 182–190. https://doi.org/10.1016/j.ecolmodel.2015.05.020

Vasil'ev, S. A. (2003). Faunal exploitation, subsistence practices and Pleistocene extinctions in Paleolithic Siberia. *Deinsea*, *9*(1), 513–556.

Wang, Y., Pedersen, M. W., Alsos, I. G., De Sanctis, B., Racimo, F., Prohaska, A., Coissac, E., Owens, H. L., Merkel, M. K. F., Fernandez-Guerra, A., Rouillard, A., Lammers, Y., Alberti, A., Denoeud, F., Money, D., Ruter, A. H., McColl, H., Larsen, N. K., Cherezova, A. A., ... Willerslev, E. (2021). Late quaternary dynamics of Arctic biota from ancient environmental genomics. *Nature*, *600*, 86–92. https://doi.org/10.1038/s41586-021-04016-x

BIOSKETCH

We are an interdisciplinary team of macroecologists, ecological modellers, evolutionary biologists and climate scientists interested in developing process-explicit models to improve our understanding of the mechanisms responsible for the distributions of organisms, communities and ecosystems in space and time.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.