Changes in limiting factors for forager population dynamics in Europe across the Last Glacial-Interglacial Transition

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1 *Changes in limiting factors for forager population dynamics in Europe across the Last*
2 *Glacial-Interglacial Transition*

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8 **Abstract**

9 *Population dynamics set the framework for human genetic and cultural evolution. For*
10 *foragers, demographic and environmental changes correlate strongly, although the causal*
11 *relations between different environmental variables and human responses through time and*
12 *space likely varied. Building on the notion of limiting factors, namely that the scarcest resource*
13 *regulates population size, we present a statistical approach to identify the dominant climatic*
14 *constraints for hunter-gatherer population densities and then hindcast their changing*
15 *dynamics in Europe for the period between 20kyBP to 8kyBP. Limiting factors shifted from*
16 *temperature-related variables during the Pleistocene to a regional mosaic of limiting factors*
17 *in the Holocene. This spatiotemporal variation suggests that hunter-gatherers needed to*
18 *overcome very different adaptive challenges in different parts of Europe, and that these*
19 *challenges vary over time. The signatures of these changing adaptations may be visible*
20 *archaeologically. In addition, the spatial disaggregation of limiting factors from the*
21 *Pleistocene to the Holocene coincides with and may partly explain the diversification of the*
22 *cultural geography at this time.*

23 **Introduction**

24 As the link between exogenous environmental factors and organismal physiology, demography
25 is vital for understanding evolution, including cultural evolution ¹. The relevance of past
26 demography for understanding culture change in prehistory specifically has long been
27 recognised ^{2,3}. Demographic conditions impinge on cultural transmission ⁴⁻⁶ but are also clearly
28 implicated in the boom-and-bust patterns of population fluctuations – including periodic

extirpations – suggested to have characterised the demographic histories of prehistoric foragers and incipient farmers in many regions⁷⁻¹⁰. Numerous recent studies have focused on the drivers of population expansion to explain the pattern and timing of human colonisation using a variety of ecological comparative approaches^{11,12} (but see ref.¹³ for a discussion of points of concern of such approaches). Yet, as foragers have a high intrinsic growth rate, population increase is, in the absence of cultural or environmental constraints, the default demographic trajectory. Evidently, however, past populations did not grow substantially, making it particularly germane to understand the factors that curtailed population growth^{14,15}. The approach adopted here builds on the central theorem that population sizes would always be regulated by the scarcest resource: the limiting factor¹⁶.

Foragers of the recent past persisted in a wide variety of environments, from the frigid Arctic to tropical rainforests. Each environment offered particular opportunities but also posed particular challenges. While several earlier studies have pointed at temperature or seasonality as key drivers of forager demography at global or continental scales^{17,18}, the specific factors that would have capped or even depressed population size are likely to have varied in both space and time. Only in understanding these limiting factors can we begin to conduct targeted investigations of how specific forager populations may have overcome them via either population-specific genetic adaptations or the sort of ‘extra-somatic adaptations’¹⁹ that are so characteristic of human culture.

In this study, we focus specifically on forager palaeodemography in Europe from the Last Glacial Maximum (Greenland Stadial 2, GS2) to 8000 years before present (BP), a climatically volatile period also known as the Last Glacial-Interglacial Transition²⁰. Previous studies have identified broad patterns of population growth and expansion using different methods commonly used in ecological analyses^{12,21-23}. Correlations between temperature and overall population density have been identified, suggesting overall increases in energy availability as the key driver of the increase in human population size following the end of GS2¹⁷. However, regional population collapses have been suggested to have occurred asynchronously and in different places^{9,24}. This raises the question of which specific limiting factors acted on forager populations and how these limiting factors varied over space and time.

Like many related studies, we begin with the global ethnographic hunter-gatherer dataset originally assembled by Binford and now digitally available^{25,26}. We couple this to a suite of quantile Generalised Additive Models (qGAMs) to describe changes in maximum (90-

percentile) population density as a univariate function of environmental variables related to the effect of temperature and precipitation on available energy, annual variability, and productivity. We then use the downscaled centennial average-conditions of each predictor derived from a transient climatic simulation (CCSM3 SynTrace-21²⁷) and the best performing univariate qGAM models to hindcast hunter-gatherer population densities between 20ky to 8kyBP. We define the limiting environmental factor as the variable predicting the lowest population density at a given place and time. This approach allows us to query the spatial dynamics of forager limiting factors across the Last Glacial-Interglacial Transition and derive specific hypotheses as to which selection pressures acted most strongly on different forager communities in Late Pleistocene and Early Holocene Europe.

Our analysis demonstrates that the dynamics on limiting factors for forager population densities showed marked differences in space and time. Temperature-related variables were the main limiting factors during the Pleistocene, whereas the Early Holocene was characterised by a regional mosaic of limiting factors. Furthermore, our model reveals geographic differences in the limiting factors between Fennoscandia, Southern, Central, and Eastern Europe. The spatiotemporal variation in limiting factors suggests that hunter-gatherers needed to overcome very different adaptive challenges in different parts of Europe across this period of climatic and environmental change.

Results and discussion

The relation between the environmental factors explored here and population density assessed using qGAMs (**Fig. 1**) was negative for temperature seasonality, positive for effective temperature, winter/fall temperature, and unimodal for the warmest temperature. Seasonal, monthly, and extreme precipitation, and topographic heterogeneity showed an overall flat trend (**supplementary figure S1**), yet these also differed from a mean model as determined by the high deviance explained (**Table 1**).

No single environmental variable explained more than 81% of the population density variation among ethnographic foraging societies (**Table 1**). However, the performance of more complex multivariate models using machine learning approaches¹² or Structural Equation Models¹¹ that combine three or more variables perform only marginally better. The five environmental variables with the highest predictive accuracies (based on the deviance explained; **Table 1**) were Temperature of the Coldest Month; Temperature Seasonality; Winter Mean Temperature;

Effective Temperature and Mean Annual Temperature. These variables display high collinearity (Pearson correlations range between 0.83 and 0.96), suggesting that temperature overall best captures the effect of temperature minima and energy availability in relation to forager demography. Two of the variables (Temperature of the Coldest Month and Winter Mean Temperature) represent the effect of extreme cold conditions (= winter mortality) on demographic trends and/or ecological performance ^{28,29}. The other two (Mean Annual Temperature, Effective Temperature, Temperature Seasonality) relate to overall energy availability ²⁸. These factors are linked to higher environmental productivity and are expected to increase available resources, leading to higher population densities, as already suggested by a plethora of earlier studies ³⁰⁻³². Other variables related to environmental productivity have lower predictive accuracy (explained deviances < 0.79, see **Table 1**) and lower collinearity with other variables related to energy availability.

Most seasonal temperature and precipitation variables showed some of the lowest explained deviances (**Table 1**), indicating that seasonal climatology most likely did not impose a direct limit on past forager populations densities in Late Pleistocene/Early Holocene Europe (contra ¹⁸). Topographic complexity, a variable shown to influence population density in other studies ¹¹, showed only above-average predictive accuracy (**Table 1**). Like seasonal temperature and precipitation, the topographic complexity effect on population density may be indirect and mediated by variables describing available resources or climate extremes.

Besides the well-known limitations of using foragers of the recent past for reconstructing prehistoric social and demographic conditions ¹³, the issue of model truncation and non-analogy of climatic conditions present themselves as major potential caveats. Climatic non-analogy here refers to the problem of projecting models beyond the domain for which they have been calibrated ³³⁻³⁵. Model truncation refers to the incomplete characterisation of hunter-gatherer populations' total climate space ³⁶⁻³⁸ and has been a long noted limitation of ethnographic analogies for prehistoric foragers ³⁹. However, it has also been shown that the dataset assembled by Binford is not critically biased in terms of forager niche space ²⁵. Likewise, we do not see either truncation or severe non-analogy in a temporal context, as the climate space observed at different moments during the 21-to-8kyBP period show broad overlaps with the climate space used to develop our qGAMs (**Fig. 2; supplementary figure S2**). This means that our models are not unduly extrapolating into environmental regions where there is no clear indication of how population density changes as a function of evaluated

climatic variables. By the same token, it is necessary to highlight that the distributions of some paleoclimatic conditions – including all those with the highest predictive values in our models – are skewed towards the lower end of contemporary values. This is especially pronounced for the Pleistocene and variables such as maximum temperatures (**Fig. 2**), affecting our inference power on changes in population densities at these extremes.

Our models indicate that the estimated human population size in Europe was the lowest at 22kyBP (~294,000 individuals) and largest at 8kyBP (~706,000 individuals). Also, based on our model, we show that at the warmest point of the Greenland Interstadial 1 (~14.7kyBP; GI1), Europe's human population size estimated by our model was ~617,000 individuals; a number that decreased to ~607,000 individuals at the coldest point of the Greenland Stadial 1 (~11.7kyBP; GS1). Overall occupied area (number of inhabited cells) was 62.4% of the region at the end of the GS2 (~22kyBP). This number increased to ~98.8% during GI 1, decreased to ~97.7% during the GS 1, and reached the highest point (~99.8%) by the mid-Holocene (~8kyBP). Taken at face value, these values are gross overestimation of actual sustained forager land-use at this time. Forager land-use was evidently extensive, including largely empty spaces⁴⁰. By the same token, these numbers are in line with archaeologically derived trends of overall population growth and expansion during this time (red lines; **Fig. 3A**).

During the evaluated period, the mean population density in the inhabited area varied between 2.6 and 6.2 persons per 100 km² (GS2 = 2.7 p/100 km²; GI1 = 5.25 p/100 km²; GS1 = 5.17p/100 km²; mHol = 6p/100 km²; **Fig. 3A**). Although the temporal patterns in average population density derived from our limiting-factor analysis are similar to those of core area estimates by Bocquet-Appel, et al.²¹ (blue areas, **Fig. 3A**), these do not match numerically due to our focus on maximum population densities. Moreover, our population density estimates are consistent with those suggested by Tallavaara, et al.¹², and more recently Kavanagh, et al.¹¹.

The estimated pattern of human population density (**Fig. 3**) indicates a population expansion starting almost 3ky after the ice sheet began to recede from its maximum extent 22kaBP. Evaluating the spatially explicit predictions of our model, we find that at the end of the GS2, hunter-gatherer societies in Europe extended as far north as central France, southern Germany and southern parts of modern-day Ukraine (**Fig. 4A**), a pattern that is consistent with archaeological evidence for the recolonisation of Europe⁴¹⁻⁴⁴. Our models also suggest that by the end of the GS2, a relatively large proportion of the European continent may have been at least sporadically inhabited (~62%; **Fig. 4A-B**), with the Mediterranean region up to the north

of the Alps showing population densities up to 12 individuals/100 km². This restricted occurrence pattern is supported by the archaeological record ⁴⁰. Furthermore, our model indicates a persistent southwest-northeast gradient of decreasing population densities in this southern region, with the most populated areas occurring in the Iberian Peninsula and the Mediterranean region (**Fig. 4A-B**). From this point, the recolonisation of the continent began at ~17kyBP (**Fig. 3**), reaching almost all the way to Scandinavia by the start of GI1 (~14.7kyBP, **Fig. 4c**). Earlier archaeological ^{45,46} and modelling studies ²² have already suggested that this colonisation was rapid but also that it proceeded in several steps where both climate and landforms served as barriers to expansion⁴⁷. Our results expand on this discussion by highlighting that different climate variables limited human dispersal for a given location and that these limits changed over time.

Using our limiting-factor approach, we improve our understanding of demographic mechanisms in Late Pleistocene and Early Holocene European hunter-gatherer societies by highlighting the spatiotemporal changes in the main factor restricting population density (**Fig. 4F-T**; and **Fig. 5**). Our modelled population density estimates can be linked to regional or local narratives or empirical tests of changes in occurrences and population sizes (e.g., refs. ^{25,48}). The changes in limiting factors suggested in our models can be divided into three periods. The first period spans from the termination of GS2 to the onset of interstadial warming at around 15kyBP. During this period, energy availability measured as effective temperature (ET) was the main factor limiting population density across most of the continent (~50% of cells; **Fig. 5A**). Mean temperature of the warmest month (MWM) was also a strong limiting factor (~30% of cells; **Fig. 5**). However, limitations imposed by winter temperatures, could be also considered as likely limiting factors based on estimates of average conditions at a continental scale (**Fig. 5B**). The range of experienced temperature conditions, represented by ET, can thus be seen as the major limiting factor shaping human population density in Europe between GS2 and the initiation of warming associated with GI1 (**Fig. 5A**). With temperature related variables as the overwhelming limiting factor during this period (**Fig. 5B**), it is likely that the emergence of sophisticated sewing techniques and pyrotechnology ⁴⁹ facilitated the persistence and even moderate expansion of populations at this time.

The second period covers the rapid warming (GI1) as well as cooling (GS1) events between 14.7kyBP to 11.7kyBP. During this period, the importance of ET steadily decreased, and mean temperature of the warmest month (~27% of cells) and temperature seasonality (~23% of cells)

became the main factors limiting population density (**Fig. 5A**). The decrease of ET as a limiting factor indicates that during this period of rapid change, it was not temperature but energy availability (due to the link between MWM and productivity) what determined human population density in Europe (**Fig. 5B**). Our models suggest that overall population densities increased (**Fig. 3**), although a temporary reduction associated with GS1 cooling is also clear.

The last period encompasses the Early Holocene from its onset at 11.7ky to 8kyBP. Here, temperature of the warmest month increased in importance as the main limiting factor (~50% of cells; **Fig. 5A**), while the effect of ET became marginal (**Fig. 5B**). Also, temperature seasonality became a critical limiting factor in many regions (**Fig. 4I, J**). These patterns indicate a complete shift from experienced temperature conditions to available resources as the main limiting factor of European forager population densities during the Holocene. Such a shift is interesting as the Early Holocene also witnessed a significant reorganisation of forager socio-ecological systems towards more varied use of resources and more pronounced territoriality focused on spatial circumscribed and regionally available resources, and a widespread shift from immediate-return to delayed-return economies. This also aligns with the idea that decreasing territory sizes and more marked boundary formation directly relate to the spatiotemporal dynamics of resource availability ⁵⁰.

The regional disaggregation of patterns in limiting factors shows strong differences between Fennoscandia, Southern, Central, and Eastern Europe (**Fig. 4F-J**). These patterns are persistent over time, with regional shifts linked to the main feature of temperature change. In Fennoscandia and the British Isles, effective temperature was the main limiting factor for most of the Late Pleistocene. This changed after the onset of the Holocene when seasonal temperatures and precipitation became the dominant limiting factor. In Eastern and Western Europe, effective temperature was the main limiting factor at the end of the GS2 but were replaced by Winter temperature and MWM at the onset of the GI1. During the GS1 and the early Holocene, the main limiting factors were MWM and TS. In southern Europe and especially in the Mediterranean, MWM was the main limiting factor throughout most of the GS2, after which precipitation became the dominant limiting factor.

Our analyses show that the main limiting factors that limited forager population densities across the Last Glacial-Interglacial Transition in Europe changed markedly over time (**Fig. 5**) and space (**Fig. 4F-J**). We can now return to the archaeological record with these insights, searching for material culture proxies that may have allowed these past communities to

220 overcome these particular limiting factors ⁵¹⁻⁵³ . While these may have related to water
221 availability (= containers) in the Mediterranean, they are predicted to relate to temperature (=
222 clothing or pyrotechnology) in higher latitudes. Where such technologies are absent in the
223 archaeological record, we can also begin to think about population vulnerability to climatic
224 factors at regional levels. Especially in higher latitudes, population fluctuations may have
225 been pronounced at the sub-centennial scale, to the point of local population extirpations ^{9,54} .

226 Finally, the marked shift in limiting factors at the onset of the Holocene may be indicative of
227 a greater focus on resource access at a regional scale. The spatiotemporal dynamics of
228 resource availability have a direct impact on land-use, mobility, territoriality, and the
229 formation of information networks in foragers ^{50,55} . In the Holocene, regional cultural
230 signatures became more pronounced and borders between different cultural zones more
231 strongly articulated. This itself may be seen as a response to the fundamental shift in limiting
232 factors we have identified in our models.

233 Seeking correlations between environmental variables and past human population densities is
234 not a new endeavour. Following recent calls for more theoretically-informed rather than mere
235 statistical explorations of this relationship ¹³ , we highlight that while the environment can be
236 said to strongly constrain forager lifeways, precisely which aspects of the environment do so
237 at any one place and time vary. Our approach offers a robust way to infer the hierarchy of
238 limiting factors and hence provide a spatiotemporal hypothesis for major selection pressures
239 acting on forager populations in the past.

240 Independent palaeodemographic estimates broadly support our models, but many questions
241 remain. Climate models, for instance, only indirectly capture the interaction of human
242 population dynamics with changes in biodiversity and ecosystem compositions. In addition,
243 the match between modelled population densities and the field-validated presence of Late
244 Pleistocene/Early Holocene populations is not equally robust everywhere. These deviations
245 may stimulate targeted field-testing with the aim of assessing whether and why population
246 densities periodically fell short of or exceeded modelled values. In conjunction with legacy
247 data derived from archives and the literature, such fieldwork can also shed light on the
248 specific strategies these past foragers employed to mitigate the risks posed by specific
249 limiting factors.

250 Small-scale societies have a variety of adaptive options at their disposal (see ref.⁵⁶), most of
251 which can be captured through archaeological proxies ⁵⁷⁻⁵⁹ . Our limiting factor model here

serves as an explicit spatiotemporal hypothesis of which risk mitigation measures should be in use at which time and place. The successful identification of these would throw significant new light on the resilience and adaptation – or lack of it – during this climatically and environmentally tumultuous time. Finally, the marked shifts in dominant limiting factors identified in our models map into the results of Late Pleistocene/Early Holocene Earth System tipping points recently discussed by ref. ⁶⁰. It is likely that, just like analogues anthropogenic warming in the present, these periods of rapid and substantive climatic change would have created challenges for contemporaneous forager populations. In an effort to align archaeological perspectives on climate change with the quandaries of our time (cf. ⁶¹), future research would be well-advised to focus on such periods of major systemic transitions.

Methods

Models of hunter-gatherers' population density

We use ethnographic data on terrestrially adapted mobile hunter-gatherers and their climatic space ²⁵ to construct a series of statistical models that predict hunter-gatherer population density based on one of 16 climatic predictors (see **Table 1** for rezoning and source). While there are important caveats ¹³, this approach builds on multiple ethnographic studies showing a link between climate on the one hand and hunter-gatherer diet, mobility, and demography on the other ^{55,62-66}. This statistical connection is the basis of recent studies focused on building complex multivariate models of population dynamics ^{11,12,67}. A benefit of our statistical approach is that it overcomes some significant limitations, such as lack of quantitative population size data based on the archaeological record itself or genetic data, each associated with their own limitations (as reviewed in refs. ^{2,12}).

We omitted four observation classes in the original ethnographic dataset in defining the association between hunter-gatherer population density and climatic predictors. First, we removed observations associated with food producers. Second, sedentary populations or those that reside at a single location for >1 year. Third, populations using aquatic resources (>30% of their dietary protein comes from aquatic environments, as defined in ^{68,69}). Forth, we excluded all observations related to horse-riding populations. The filters employed here correspond to those used by Tallavaara, et al. ¹² to maximise the match between ethnographic data and the current knowledge of the highly mobile and overwhelmingly terrestrially oriented lifestyles of Late Pleistocene/early Holocene hunter-gatherers in Europe. The implemented

filters are less restrictive than those used by other studies that have sought to reconstruct forager population dynamics during this time ⁷⁰ and thus allow for a relatively large degree of behavioural variation. This is important given that increasing evidence of marine and lacustrine resource use is emerging for at least certain times and regions in Late Pleistocene Europe ⁷¹⁻⁷³, and that a marked diversification characterises the resource base of early Holocene foragers. Finally, these filters remove any population using external supplements to their hunter-gatherer lifestyle, resulting in a database including information on 127 populations.

We used climate data on historical averages (1970-2000) for 19-climate variables (**Table 1**) to build our ethnography-based population density models. These were obtained from the Worldclim version 2.1 ⁷⁴ at a 10-ArcMin resolution. Importantly, we used Worldclim data instead of climatic variables directly available from the ethnographic dataset to ensure comparability between climatic variables not in the database (i.e., seasonal means). Equally importantly, this approach prevents any estimation biases due to differences between the data used to define climate-density relations and paleoclimatic surfaces (*see the section estimating human populations density across the Pleistocene-Holocene transition below*) used to estimate population density changes and limiting factors over time.

Initially, we model how population densities of hunter-gatherer communities change along current environmental gradients using Quantile Generalised Additive Models (qGAMS). Modelling such dynamics using qGAMs offers a transparent way to determine the non-linear changes in different percentiles of a response variable (= population densities) to one or multiple environmental variables. This approach is commonly used in the ecological literature to determine the likelihood of occurrence or abundance of a given species under a particular environmental regime ⁷⁵⁻⁷⁹ but has never before been applied to human palaeodemography. In contrast to previous studies evaluating past human population density changes, we do not consider the synergies between multiple climatic variables when describing the relation between population densities and climate. Instead, we focus on the individual effects of evaluated variables on the top 90-percentile of population densities to identify the most pronounced limiting factor that acted on palaeodemographic growth. The tendencies in population densities as a function of environmental variables were consistent for different percentiles (see **supplementary figures S1**).

The population density derived from the ethnographic data followed a log-normal distribution, so these were log-transformed for subsequent analyses, and a gaussian response distribution

was used in our qGAMs models. Annual, monthly, and seasonal precipitation variables were similarly transformed. The ability of each of the evaluated variables to predict hunter-gatherer population densities was determined using the mean deviance explained ($1 - (\text{Residual Deviance}/\text{Null Deviance})$). These were calculated both for the whole dataset, and using a 1000-fold cross-validation approach (70% random sample for calibration and 30% for validation). All models and prediction accuracy estimates were implemented in R (version 3.6; ⁸⁰) using the *mgcv* (version 1.8.24; ⁸¹) and *qgam* (version 1.3.2; ⁸²) packages.

Estimating human populations density across the Pleistocene-Holocene transition

The monthly average temperature and annual precipitation values for Europe for the 21ky to 8kyBP period come from the CCSM3 SynTrace paleoclimate simulations ⁸³. These were bias-corrected and downscaled to $0.5^\circ \times 0.5^\circ$ following the methods described by Lorenz, et al. ⁸⁴. The paleoclimatic simulation data used here was originally generated to evaluate changes in European and North American fossil pollen data and vegetation novelty since the Last Glacial Maximum ²⁷. Source climate surfaces were aggregated to centennial means from the original decadal averages of monthly values.

Past hunter-gatherer population densities were then predicted for every 30ArcMin cell above sea level. For visualization we also show the areas covered by glaciers using the glacier extent shapefiles derived by PaleoMIST ⁸⁵. To generate 90% percentile population density estimates for each variable/century combination, only those qGAM models parametrised using the ethnographic data and current climatic conditions with cross-validated deviances above 70% were projected into past climatic conditions. As our objective was to establish the climatic variable that imposed the strongest constraints on hunter-gatherer population density at any one time, we determined the variable estimating the lowest 90%-percentile population density for a given cell at each evaluated time-period to be the limiting factor (the scarcest resource that would then limit population size cf. ¹⁶). For each evaluated time-period, we summarised the proportion of the available land area (i.e., land area not covered by ice) where each of the assessed variables was determined to be the limiting factor.

We calculated the changes in the percentage of inhabited land area in Europe during the evaluated period by estimating the proportion of the inhabited area, here defined as the region where population densities were above 1 individual per 100km². To calculate human-population size in Europe during every century, we multiplied the predicted population density

in each cell by the land area of the corresponding cell to arrive at per cell population size. We then summed these values to arrive at the total population size for each century.

Uncertainties in population density, size, occupied area, and limiting factor estimates were determined using a cross-validation approach, where model fitting was iterated 1000 times using a random sample (70%) of the ethnographic and climate data at each time step. Each model was used to hindcast populations densities, estimate the percentage of inhabited land area and human population size, and define the relevant limiting factor. Uncertainty in continental-scale estimates of population densities, occupied area and population size was determined using 95% confidence intervals. The variable selected as the limiting factor in most cross-validation folds was selected as the limiting factor.

Validation of population density estimates

To assess the validity of our population density estimations, we use the International Union for Quaternary Science (INQUA) Radiocarbon Palaeolithic Europe Database v28⁸⁶. Changes in the density of records are a useful continental-scale proxy-measurement of prehistoric population size changes and are increasingly used to describe prehistoric human population dynamics trends⁸⁷⁻⁹². We extracted proxy dates (based on ¹⁴C dates) from the INQUA Radiocarbon Palaeolithic Europe Database, aggregating these to the closest 1000 years. Our goal is to determine the match between our qGAM derived populations densities and prehistoric population occupation derived from the frequencies of radiocarbon dates between 20kaBP and 10kaBP as done by Tallavaara, et al.¹². This approach allowed validating our hindcasted estimates of absolute prehistoric population density since our model is not archaeologically informed, avoiding any possible circularity between model development and validation.

We also used site-based estimates of population density as derived using the Cologne Protocol by Schmidt, et al.²³. We focus on estimates of extended interconnected socio-economic areas (Core Areas) for five unequal time bands between 25kaBP and 11.7KaBP. Although ultimately also based on Binford²⁵, these estimates present independently derived spatially implicit estimates of population density for the Late Palaeolithic in Europe.

Data availability

375 The ‘Binford’ ethnographic database ²⁵ is available from the Database of Places, Language,
 376 Culture, and Environment (D-PLACE; <https://d-place.org/about>). Current and Late Quaternary
 377 environmental datasets are publicly available from the associated references. International
 378 Union for Quaternary Science (INQUA) Radiocarbon Palaeolithic Europe Database v28 is
 379 available from [https://pandoradata.earth/am/dataset/radiocarbon-palaeolithic-europe-database-](https://pandoradata.earth/am/dataset/radiocarbon-palaeolithic-europe-database-v28)
 380 [v28](https://pandoradata.earth/am/dataset/radiocarbon-palaeolithic-europe-database-v28). Contemporary climate databases are available from the WorldClim project
 381 (<https://www.worldclim.org>), and late-Pleistocene climate sources are available at
 382 <https://doi.org/10.6084/m9.figshare.c.4673120.v2>.

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643

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649 **Author contributions**

650 AO: Conceptualization; Methodology; Formal analysis; Resources; writing – original draft,
651 writing – review & editing; Visualization.

652 FR: Conceptualization; Methodology; writing – original draft, writing – review & editing.

653

Table 1. Variables used to generate ethnographic based models of the effect of climate on hunter-gatherer population density and summary of cross-validated deviance explained for the evaluated variables. Estimates correspond to those of a 1000-fold cross-validation approach (1000 samples of 70% training and 30% testing observations) or the full dataset

Variable name	Acronym	Units	How does the variable determine population density?	Cross-validated Deviance explained. Mean [95% CI]	Full-dataset Deviance explained
Effective Temperature *	ET	C	Energy availability	0.774 [0.8 - 0.826]	0.792
Potential Evapotranspiration **	PET	mm/yr	Energy availability	0.751 [0.8 - 0.81]	0.774
Mean Annual Temperature	MAT	C	Energy availability	0.733 [0.7 - 0.777]	0.757
Mean temperature of the Coldest Month	MCM	C	Extreme Events	0.798 [0.8 - 0.839]	0.812
Mean temperature of the Warmest Month	MWM	C	Extreme Events	0.705 [0.7 - 0.762]	0.737
Temperature Seasonality	TSeson	C	Annual Variability	0.777 [0.8 - 0.839]	0.811
Spring Mean Temperature	SpMT	C	Seasonal trends	0.789 [0.8 - 0.828]	0.804
Summer Mean Temperature	SmMT	C	Seasonal trends	0.773 [0.8 - 0.817]	0.786
Fall Mean Temperature	FMT	C	Seasonal trends	0.725 [0.7 - 0.786]	0.750
Winter Mean Temperature	WMT	C	Seasonal trends	0.765 [0.8 - 0.808]	0.782
Annual precipitation	PREC	mm/yr	Energy availability	0.701 [0.7 - 0.757]	0.712
Precipitation of the Driest Month	PDM	mm/m onth	Extreme Events	0.746 [0.7 - 0.793]	0.760
Precipitation of the Wettest Month	PDM	mm/m onth	Extreme Events	0.77 [0.8 - 0.804]	0.784
Precipitation Seasonality	PSeson	mm/m onth	Annual Variability	0.737 [0.7 - 0.772]	0.748
Spring Precipitation	SpPREC	mm/m onth	Seasonal trends	0.773 [0.8 - 0.814]	0.788
Summer Precipitation	SmPREC	mm/m onth	Seasonal trends	0.753 [0.8 - 0.8]	0.779
Fall Precipitation	FPREC	mm/m onth	Seasonal trends	0.7 [0.7 - 0.772]	0.711
Winter Precipitation	TPREC	mm/m onth	Seasonal trends	0.774 [0.8 - 0.826]	0.792
Topographic Ruggedness Index ***		m	Habitat Heterogeneity	0.751 [0.8 - 0.81]	0.774

* Calculated following ²⁵

** Calculated following on ⁹³.

*** Calculated following ⁹⁴

Figure 1. Quantile Generalised Additive Models (qGAM) describing the relation between environmental factors and population density for 10-percentiles (dashed lines), 50-percentiles (solid lines), and 90-percentiles (dotted lines). Here, only the six most limiting factors during the 22kaBP to 8kaBP are presented. Full explorations of evaluated variables presented in **Supplementary material S1**.

Figure 2. Convergence between current climatic conditions (hashed density plots) and paleoclimatic conditions at four different periods (coloured density plots). Paleoclimatic periods are Greenland Stadial 2, Greenland Interstadial 1, Greenland Stadial 1, and Holocene. As in Figure 1, only the six most limiting factors during the 22kaBP to 8kaBP are presented. Full explorations of evaluated variables presented in **Supplementary material S2**.

Figure 3. Contrast between Europe wide mean population density (top panel), and trends in key environmental variables (bottom). Estimated average population density for all Europe based on a randomization approach (top panel) are compared to archaeological population proxy based on number of calibrated radiocarbon dates for Europe between 21 and 11kyBP based on ¹² summaries of the Radiocarbon Palaeolithic Europe Database v28 ⁸⁶ (red), and core area (cf. ²³ population density mean and upper/lower estimates based on the Cologne Protocol (blue). On the bottom panel, plotted variables are: Effective temperature, Minimum temperature of the Coldest Month, and Maximum temperature of the Warmest Month.

Figure 4. Estimated human population density and range (areas where population density > 1 individual per 100km²) (A-E) and factors limiting population density (F-J) across Europe for selected times during the 22ky to 8kyBP period. (A, F) Greenland Stadial 2; (B, G) Greenland Interstadial 1; (C, H) Greenland Stadial 1 warming terminations (D, I) Holocene initiation; (E, J) Mid-Holocene. Areas in grey scale represent the glacier extent as derived by PaleoMIST⁸⁵.

Figure 5. Proportion of the ice-free area of Europe where each variable was estimated to be the factor limiting population density (A); and estimated population size based on the mean environmental conditions for each century (B). In both panels, only the six variables with the highest percentages of cells where the variable is the limiting factor are presented.

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662

Supplementary material S1 Quantile Generalised Additive Models (qGAM) describing the relation between the six most important environmental factors explored and population density for 10-percentiles (dashed lines), 50-percentiles (solid lines), and 90-percentiles (dotted lines). Title acronyms as in **Table 1**.

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Supplementary material S2. Overlap between current climatic conditions (hashed density plots) used for model building and paleoclimatic databases (coloured density plots) used to hindcast human population density for all 19-climatic variables used. Title acronyms as in Table 1.

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666