Demographic estimates of hunter-gatherers during the Last Glacial

Maximum in Europe against the background of palaeoenvironmental data

1. Introduction

This study aims to better understand population dynamics during the Last Glacial Maximum (LGM). In an interdisciplinary approach, it combines data from climatic modelling, geomorphology and archaeology. However, similar periods defined in archaeology and climatology are rarely exactly synchronous and the LGM is no exception. Following the EPILOG (Environmental Processes of the Ice-Age: Land, Oceans, Glaciers) project (cf. Mix et al., 2001), the LGM is defined as a period “reasonably close to an equilibrium state of climate” (Ibid., 629) comprising the maximum extent of global ice-shields and excluding short-term climatic extremes. Archaeologically, the LGM is associated with the Solutrean, Badegoulian, and Early Epigravettian (Djindjian et al., 1999). To strike a compromise between these conventions, the temporal boundaries of this study are set to 25,000 and 20,000 calBP. This allows for the integration of almost all sites assigned to the above-mentioned industries, while ensuring that the modelled palaeoclimate data can be considered representative of the period in question, since climatic conditions have been rather stable.

It is important to stress that our estimates rely on the actual state of knowledge and the sites used in our calculations are considered a representative sample of all LGM sites known today. The distribution of sites in Figure 1 indicates that the settlement pattern during the LGM was spatially heterogeneous and clusters of sites alternate with empty areas. It is disputed whether this pattern reflects prehistoric reality or is mainly the result of taphonomic processes, research intensity and accessibility (e.g. Rigaud and Simek, 1987; Straus, 1990, 93;

Straus et al. 2000, 554f., 2002, 1404f.; Bocquet-Appel et al., 2005, 1659f.; Maier 2015, 84f.). Adopting the one or the other point of view has major consequences for palaeodemographic estimates, since the latter scenario produces much higher values than the former. Our opinion is that the gaps in the distribution of sites are meaningful, at least in well investigated areas with a good accessibility of open-air sites, such as France or western Central Europe. This is because species, including *Homo sapiens*, are usually distributed unevenly, since geographic conditions and resources vary across space (e.g. Zhang et al., 2014). These differences in distribution should be reflected in the number of sites left per area. This is illustrated by the fact that newly discovered sites are repeatedly located in areas where other sites of the same age are already known. They are very rarely (if at all) situated in previously empty areas (e.g. Holzkämper et al., 2014; Rozoy, 1988, 143; for examples of the LGM compare distribution maps in Straus et al. 2000, Bocquet-Appel et al., 2005; Banks et al., 2009; Schmidt 2015 and this paper; for other examples compare e.g. Hahn, 1977; Otte, 1981; Rozoy, 1988, Bocquet-Appel et al., 2005; Kozłowski, 2015; Kretschmer, 2015). It is therefore consistent to assume that the overall site distribution in well-researched areas is not going to change fundamentally in the future (cf. Bocquet-Appel et al., 2005). However, in areas of less intensive research and – probably even more crucially – high relief intensity or extensive sediment cover, the reliability of gaps in the distribution of sites is limited. Regionally differentiated correction curves for taphonomic loss in terrestrial archives as proposed by Surovell et al. (2009) would be very helpful in this regard. However, such curves are currently not available.

Having defined the temporal and climatic frame and excluded taphonomy as a main agent in the formation of the observed large-scale site pattern, the question arises what this pattern means in terms of demography as well as if and how adaptations of LGM hunter-gatherers to different regions and climatic conditions influences the structure of the population. To address this question, we estimate the total number as well as the density of people in different regions and establish a relationship between the locations of sites and the

palaeoenvironmental conditions by extracting the environmental parameters for the observed sites from the palaeoclimate model data using logistic regression. Together with data on the distributions of permafrost, forests and loess, we assess the impact of environmental factors on the settlement pattern of hunter-gatherers during the LGM on both a continental and a regional scale. A comparison of the regional differences in population density and palaeoenvironmental conditions enables us to critically assess the quality of our estimates.

2. Material and Methods

The palaeodemographic estimates used in this study are based on information from 396 archaeological sites located between 10° W and 30° E and 35° N and 55° N, and which are dated either radiometrically to the period between 25,000 and 20,000 years calBP and/or are typologically attributed to the Solutrean, Badegoulian or Epigravettian. If only radiometrically dated sites were considered, the sample size in most regions would be too small for statistical analysis. The database was compiled from an extensive literature survey and contains information on the geographic position and, if available, raw material composition of the lithic assemblages (Maier and Zimmermann, 2015).

The climatic data used in this study are obtained from different Earth System Model (ESM) runs of the Coupled Model Intercomparison Project (CMIP5; Taylor et al., 2012). The ESM palaeoclimate simulations for the LGM are from the model runs of the Palaeoclimate Modelling Intercomparison Project (PMIP3; Braconnot et al., 2012). In comparison to the CMIP5 runs, the boundary conditions and the model parameters for PMIP3 are set according to the best estimates of palaeoconditions. These include the LGM-coastline, extension of ice sheets, orbital parameters and atmospheric trace gas concentrations. An overview of the ESM

simulations used in this study is given in Table 1. Data for temperature at 2 m above ground surface and precipitation are available at monthly intervals. For analysis of palaeoclimate conditions, we use the simulations of the Max Planck Institute for Meteorology ESM (MPI-ESM-P) and the ensemble statistics of all ESMs participating in PMIP3. For the ensemble analysis, the model outputs of all model simulations are interpolated onto the (MPI-ESM-P) grid, which has an intermediate resolution among the ESMs participating in PMIP3.

2.1. Protocol for palaeodemographic estimates

Most palaeodemographic studies rely on counts or frequency distributions of certain features, such as sites, tools, or radiocarbon dates as proxy data for their estimates (e.g. Mellars and French, 2011; Shennan et al., 2013; French and Collins, 2015). These approaches have the disadvantages of being very sensitive to missing values or newly discovered evidence. Our protocol (Fig. 2), in contrast, relies on density-based delimitations of areas with intensive settlement activity. Since new sites are usually discovered near known sites of the same age (see above) the outlines of these areas are quite stable. Generally, the method is fairly robust with regard to the detection of new sites as has been demonstrated by Wendt et al. (2010, 307ff.; see also Zimmermann et al., 2009a, 13).

Our protocol was initially designed to determine population densities of sedentary communities (Zimmermann et al., 2005, 2009a, 2009b; Hilpert et al., 2008; Wendt et al., 2010; Schlummer et al., 2014) and subsequently adjusted to meet the requirements of mobile societies (Kretschmer, 2015). In brief, the protocol combines different methods implemented in geographic information systems in a density-based upscaling approach, i.e. transferring data from individual sites to the spatial scale of archaeological cultures (for general problems of upscaling see Schlummer et al., 2014). Using MapInfo pro v.10, point data of the geographic location of each site is transferred into extensive site density estimates by

constructing largest empty circles (LEC) (Preparata and Shamos, 1988) between the vertices of Thiessen polygons and their closest three sites. The lengths of the circles' radii then serve as a measure of site density and are interpolated using kriging (Haas and Viallix, 1976). The interpolated densities are transferred to isolines which comprise areas with the same lower threshold value of site density (cf. Malmer, 1962). Eventually, the "Optimal Isoline" (OI) is identified. In our model, it delimits the economic core areas of hunter-gatherers and thus should encircle as less empty space between sites as possible. These so called "settlement areas" show a frequent and intensive use over generations. Ideally, they include all residential sites and most of the complementary sites that originated in the context of logistical mobility (Binford, 1980; Kelly, 1983). Sites of raw material extraction or hunting stays outside the settlement areas are conceptualised either as the result of logistical mobility in the periphery or residential mobility between settlement areas. The OI is determined using the heuristic criterion of the maximal increase of space (Zimmermann et al. 2005, 53f.). The area encircled by the isolines increases with growing distances between the sites. Peaks in the distribution of increasing encircled spaces thus mirror changes in site density and thereby help to delimit settlement areas. Additionally, it is often observed that about three quarters of all sites are enclosed by the OI.

As an independent measure, we determine raw material catchments to approximate areas exploited by regional groups (Demars, 1998; Maier, 2015). Supposing an aggregated and predictable resource distribution during the LGM, we follow Kelly (1995, 161 ff.) in assuming non-overlapping exploitation areas. We also assume an embedded procurement (cf. Binford 1979, 259) of lithic raw materials with exchange playing, if at all, only a marginal and thus negligible role for our estimates (cf. Floss 1994, 320ff.). Catchments are estimated by creating polygons whose edges connect a site with its attested raw material sources (Fig. 2). For this study, information on raw materials was available for 25 sites and is restricted to

129 two larger regions. In order to account for the missing information, we transfer the observed
130 data to those areas from where no data could be obtained. On this large scale, differences in
131 raw material quality do not seem to have major effects on the size of the catchments, which
132 we divided in two groups using again the criterion of the maximal increase of space. Smaller
133 catchments (n=8) are thought to represent daily activities (including foraging trips), whereas
134 larger catchments (n=17) represent seasonal activities and are thus a more suitable indicator
135 for regional groups. These regional groups can likely be correlated with Binford's "GROUP2"
136 units, representing the number of people living together during the most aggregated phase of
137 the annual fission and fusion cycles (Binford, 2001, 117). To assess the area exploited by
138 these GROUP2 units, the median values as well as the 1st and 3rd quartile of the larger
139 catchments are calculated.

140 Many arguments exist for and against the use of ethnographic data in archaeological research
141 (e.g. Binford, 1972, 1980, 1982, 1983, 2001; Clarke, 1972; Wobst, 1978; Gamble, 1986;
142 Kelly, 1995; van Reybrouck, 2000; Wiermann, 2000; French, 2015). Since studies which do
143 not include ethnographic observations usually only give relative statements of population
144 dynamics without providing absolute numbers (e.g. Jochim 1987; Straus et al., 2002; Bocquet-
145 Appel and Demars, 2002; Mellars and French, 2011; Shennan et al., 2013; French and
146 Collins, 2015), we think that ethnographic data is a permissible source of information for our
147 research purpose (see also Bocquet-Appel and Demars, 2000; Bocquet-Appel et al., 2005).
148 We use absolute counts of persons per group of 16 selected, non-mounted hunter-gatherer
149 communities (15 from North America; 1 from South America) with living conditions
150 presumably comparable to those in Palaeolithic Europe. That is living at high latitudes in
151 steppe environments and having a subsistence based on at least 60% terrestrial animals. The
152 median value for a GROUP2 unit is thus found at 43 persons (for a detailed discussion of
153 selection criteria see Kretschmer, 2015).

To estimate a minimum, median and maximum number of regional groups per settlement area, we divide the area inside the OI by the area of the raw material catchments. This is because we do not expect more than one hunter-gatherer group exploiting the same area, given the presumably aggregated and predictable resource distribution at that time (Kelly 1995, 161 ff.). To visualize possible uncertainties, we use the 1st, 2nd and 3rd Quartile of the area of the raw material catchments according to

$$N_{gmin} = \frac{A_{OI}}{A_{Q3}} \quad N_{gmed} = \frac{A_{OI}}{A_{med}} \quad N_{gmax} = \frac{A_{OI}}{A_{Q1}} \quad (1)$$

Here, N_g is the number of groups, A_{OI} the area enclosed by an OI, and A_{Q3} , A_{med} , and A_{Q1} the minimum, median, and maximum areas of raw material catchments. To calculate minimum, median and maximum estimates of population size P_o , the number of groups is multiplied by this median value L (43 persons).

$$P_{o_{min}} = N_{gmin} \cdot L \quad P_{o_{med}} = N_{gmed} \cdot L \quad P_{o_{max}} = N_{gmax} \cdot L \quad (2)$$

Minimum, median and maximum estimates for two population densities are calculated as follows:

$$D_{smin} = \frac{P_{o_{min}}}{A_{OI}} \quad D_{smed} = \frac{P_{o_{med}}}{A_{OI}} \quad D_{smax} = \frac{P_{o_{max}}}{A_{OI}} \quad (3)$$

where D_s is the population density in a settlement area. The areas encircled by OIs can either be considered individually, or – if raw material catchments link two or more settlement areas – collectively. Another possibility is to consider the averaged population density of a map section, D_m , including areas enclosed by OIs and the empty zones between OIs.

$$D_{mmin} = \frac{P_{o_{min}}}{A_m} \quad D_{mmed} = \frac{P_{o_{med}}}{A_m} \quad D_{mmax} = \frac{P_{o_{max}}}{A_m} \quad (4)$$

2.2 The calculation of preference scores

Rainfall, temperature, and elevation are probably the most important environmental parameters that influence human survival. Food and water supply are directly related to rainfall and temperature, while elevation is a descriptor of the topographic constraint to human mobility. To test the correlation between site location and rainfall/temperature, we apply the correlation test after Best and Roberts (1975) using the `cor.test` R function (R core team 2014) and find that occupation is significantly related to these factors ($p < 0.01$). Therefore, we are confident that these factors play a role in human occupation, and special attention is given to them in the following calculation.

First, we examine the Probability Density Functions (PDF) of model-ensemble mean annual air temperature (MAAT) T , mean annual precipitation (MAP) R , and elevation H , at the archaeological sites (as well as their PDFs based on individual models, not shown), in order to determine the most and least preferred conditions for LGM hunter-gatherers. Optimal fitting is performed to the distributions of the three quantities. As seen in Fig. 3, both T and R are Gauss distributed, with a PDF with the form

$$p(X) = \frac{1}{\sqrt{2\pi}\sigma_X} \exp\left(-\frac{(X - \bar{X})^2}{2\sigma_X^2}\right) \quad \text{for } X = T, R \quad (5)$$

Using the maximum likelihood method, it is found that for the PDF of MAAT, the mean value is $\bar{T} = 5.3^\circ\text{C}$ and the standard deviation is $\sigma_T = 3.9^\circ\text{C}$. Likewise, for the PDF of MAP, the mean value is $\bar{R} = 829.7\text{ mm}$ and the standard deviation is $\sigma_R = 205.9\text{ mm}$. The PDF of elevation, in contrast, can be well approximated by a Gamma distribution with the form

$$p(H) = \frac{1}{b^a \Gamma(a)} H^{a-1} e^{-\frac{H}{b}} \quad (6)$$

with a shape parameter $a = 1.7$ and a scaling parameter $b = 135.1\text{ m}$.

As the archaeological sites cover an extensive area, the environmental conditions were probably substantially varied in different regions, in particular between the western part of

Europe (centred over Southern France) and the eastern part (centred over the Carpathian Basin). Due to the presence of the Scandinavian ice sheet, the temperature over Europe increased from northeast to southwest. To take into consideration of these differences, we divided the archaeological sites by a line that runs roughly in parallel with the isothermals and at the same time corresponds to an allocation of the sites to the Solutrean/Badegoulian (West) and the Early Epigravettian (East). The line is defined by

$$\varphi = -\frac{6}{7}\lambda + \frac{390}{7} \quad (7)$$

where φ is latitude and λ is longitude (Fig. 1). The statistic parameters for the PDFs of MAAT, MAP and elevation are estimated using the data for all archaeological sites (Case-A), the West group sites (Case-W) and the East group sites (Case-E) (Table 2).

211

Based on the above derived PDFs, we can quantify the conditions, which hunter-gatherers in Western and Central Europe preferred. To this end, we define a lower and an upper limit for each variable. Using temperature as an example and suppose $T_{\min} = P^{-1}(0.005)$ and $T_{\max} = P^{-1}(0.995)$ with $P(T)$ being the probability distribution function for T , hunter-gatherers are assumed to have avoided cases of $T \leq T_{\min}$ or $T \geq T_{\max}$. Similarly parameters are set for MAP and elevation (Table 2).

218

A logistic regression method is then applied to estimate the probability of human presence in the study domain. First, the locations of all observed archaeological sites are assigned to have the probability one ($P = 1$), while the areas with either T , R or H being beyond the corresponding limits have the probability zero ($P = 0$). The probability of human presence for the remaining areas is then estimated using logistic regression, by fitting the

probability P to a score, S , which describes the optimality of the climate/environmental conditions for hunter-gatherer presence.

The procedure for computing S is as follows. First, the individual scores for temperature, rainfall and elevation, namely, S_T , S_R and S_H , are defined. These scores range between 1 (best) and 0 (worst). A weighted average of the individual scores leads to the total potential score, S , that also ranges between 1 (optimal/desired conditions) and 0 (hostile/rejected conditions). Based on tests of various averaging techniques, we adopted in this study the geometric mean of the individual scores, S_T , S_R and S_H as the total score S ,

$$S = (S_T S_R S_H)^{1/3} \quad (8)$$

The individual scores are also computed on the basis of the corresponding PDFs because, using MAAT as example, the temperature range with the highest probability also implies the most optimal temperature range for hunter-gatherer presence, and hence the highest temperature score, S_T . As temperature is Gauss distributed, the highest temperature score is centred at $\bar{T}$. Following this understanding, S_T is computed as follows:

- (1) The probability range $P_0 = 0.005$ and $P_N = 0.995$ is divided into $N = 20$ equal probability intervals with

$$\Delta P = \frac{P_N - P_0}{N}; \quad P_i = P_{i-1} + \Delta P \quad i = 1, N-1 \quad (9)$$

- (2) The temperature values, T_i , corresponding to P_i are found from the inverse probability function

$$T_i = P^{-1}(P_i) \quad (10)$$

- (3) The average PDF for each temperature interval is calculated with

$$p_i = \frac{1}{T_i - T_{i-1}} \int_{T_{i-1}}^{T_i} p(T) dT \quad (11)$$

- (4) Finally, the temperature score for temperature interval i , $S_{T,i}$, is computed as

$$S_{T,i} = p_i / p_{i,\max} \quad (12)$$

249

250 The same procedure is applied to compute S_R and S_H . Given the scores, $S_{T,i}$, $S_{R,j}$ and $S_{H,k}$, the
251 score for a combination of temperature range i , rainfall range j and elevation range k is
252 computed following Equation (8). By doing so, the spatial pattern of optimality of
253 environmental conditions for hunter-gatherers is determined. The logistic fitting of the
254 probability of human presence against the score provides an estimate of the spatial pattern of
255 the probability of human presence. For reasons outlined above, the logistic fittings are done
256 for Case-A, Case-W and Case-E.

257

258

259 2.3 Palaeoenvironmental data

260 The considered palaeoenvironmental data are loess distribution, permafrost boundary, and
261 timberline. The loess distribution in Europe is redrawn after Haase et al. (2007) and displayed
262 in Fig. 1. According to various authors, trapping of dust (loess) is related to vegetation cover
263 (e.g. Tsoar and Pye, 1987; Danin and Ganor, 1991; but see also Svirčev et al. 2013).
264 Therefore, the northern border of the loess distribution probably coincides with the northern
265 fringe of vegetation. The reconstructed sporadic and continuous permafrost boundary is
266 inferred from the distribution of relict permafrost features, particularly that of ice wedge casts
267 and polygons as well as involutions occurring at MAAT around -4°C (Washburn, 1979; Karte,
268 1983; Baulin, 1992; Velichko and Nechaev, 1992). It needs to be mentioned that
269 Vandenberghe et al. (2014) summarised the results concerning the last permafrost maximum
270 on the northern hemisphere and assume for permafrost in Europe MAAT of -8°C ($\pm 2^{\circ}$).
271 However, since the -4°C threshold is still generally accepted, we will use this value for our
272 study. The northern timberline roughly coincides with the $10\text{-}12^{\circ}\text{C}$ isotherm (Grichuk 1992).
273 This does not exclude the presence of scattered stands of trees north of this line, particularly

in climatically favourable regions such as valleys in the Carpathians (Willis and van Andel 2004). However, it delimits the distribution of larger forests to the north.

3. Results and Discussion

The Optimal Isoline is found at a Largest Empty Circle radius of 43 km (Fig. 1). The total number of people living in Western and Central Europe during the LGM is estimated to range roughly between about 1,400 and 6,300 persons at a time (Table 3). The Franco-Cantabrian region shows the highest population, comprising 750-3,600 persons and 0.6-2.7 persons per 100 km². The next highest values are estimated for southern Spain and the lower Rhône valley (100–500 persons; 0.6-2.7 p/km²), as well as Portugal and the upper Seine valley (90-430 persons; 0.6-2.7 p/km²). North of the Alps, very few sites attest an ephemeral presence of people, but none allow the inference of prolonged settlement activities. Maybe minor climatic fluctuations fostered short-termed advances into these areas as well as into northern France and central Iberia. West of 30° E, the northern limit of the site distribution does not exceed 50° N and roughly coincides with the northern limit of loess distribution (Fig. 1). In eastern Central Europe (Czech Republic, Hungary and Poland) and in the Prut region (Moldova and NE Romania), the few site clusters that exist attest the presence of hunter-gatherers with estimates of about 50 people occupying each region. In other regions with continuous occupation, such as Central and Southern Italy or Greece, the density of sites is – also due to inconclusive typological compositions – too low to arrive at reliable estimates. In comparison with estimates on the Magdalenian (Kretschmer, 2015) and work in progress on the Aurignacian and Gravettian, the derived data is very consistent.

299

300 *3.1 Evaluation of the climatic model*

301 In general, the models reproduce mean temperature conditions during the LGM
302 considerably well. However, a notable northward displacement of the -4°C isotherm can be
303 observed when compared to the reconstructed continuous permafrost boundary (Fig. 4).
304 Additionally, there is a slightly greater variability of the -4°C isotherm over the western part
305 of Europe, while over the eastern part the variability of the -4°C isotherm location is reduced.
306 This can be explained by the variability of the North Atlantic stormtrack (Hoskins and Valdes,
307 1990), that influences climate conditions particularly in Western Europe, under glacial
308 conditions (Hofer et al., 2012) in the different models. Given the resolution which is
309 approximately $200 \times 200 \text{ km}^2$, the offset of 200–400 km is considered acceptable.

310 A comparison between the timberline and the 10°C isotherm for the warmest month,
311 consistently July for all Earth system Models (ESM), again shows the capability of the
312 different ESMs to reproduce climatic conditions during this glacial period (Fig. 5). Exceptions
313 are the CNRM-CM5 (Fig. 5c) and MRI-CGCM3 (Fig. 5h) models, which apparently exhibit
314 much warmer temperatures for July compared to the other ESMs. It is also obvious that the
315 10°C isotherm and the timberline diverge farther towards the East. The reason for the
316 divergence might derive from the fact that the polar forest line is a thermally determined
317 distribution boundary that is generally defined by the mean July temperature (Walter and
318 Breckle, 1994) or the warmest month isotherm of $10\text{--}12^{\circ}\text{C}$. According to Körner (2012) and
319 Körner and Paulsen (2004), this parameter is not suitable in all parts of the world. Also the
320 mean annual air temperature (MAAT) is weakly correlated to the forest line because it
321 includes temperatures from the non-growing season which play a minor role for tree growth
322 (Körner, 2012). In addition, there is a boundary beyond which aridity limits tree growth. In
323 regions where there is no permafrost providing an additional source of humidity, the
324 precipitation during the LGM might be too low to allow tree growth.

3.2. *Evaluation of the palaeodemographic estimates*

Western Europe is doubtlessly the best-researched area with regard to the Palaeolithic. At the same time, sediment accumulation since the LGM is moderate to low. Thus, we deem the observed site pattern as fairly representative of actual LGM land-use. For the eastern part, the situation is different. Thick loess covers are present in many areas, such as the Carpathian basin, unless the slope gradient is too steep for sediment accumulation and fosters erosion, as is the case in the Carpathian Mountains. Given that the extensive overlaps of raw material catchments suggest a frequent usage of the areas, which today are void of archaeological remains (Fig. 1), it appears likely that loess cover and erosion bias the archaeological record significantly. Thus, we consider our estimates for the western part quite reliable, whereas the numbers for the eastern part are certainly minimum estimates.

The only other study providing estimates of absolute numbers of people for the LGM so far is the investigation of meta-population sizes in the European Upper Palaeolithic by Bocquet-Appel et al. (2005). A comparison of results is thus necessary, although the time range of the LGM is set differently in both studies: 23,500 – 17,000 calBP in Bocquet-Appel et al. (2005) and 25,000 – 20,000 calBP in this study. Our estimates range roughly between 1,400 and 6,300 persons, whereas those of Bocquet-Appel et al. (2005) range between 2,300 and 37,700 people with an average value of about 5,800 persons. The maximum value of nearly 38,000 people is probably the result of neglecting the gaps in the distribution of sites and thus in our view a clear overestimate of the past population. However, leaving the maximum value aside, both results are in good accordance.

3.3 Preferred and tolerated environments during the LGM

Humans are versatile when it comes to adapting to different environmental conditions (cf. Binford, 2001, Table 4.01). Therefore, an objectively discernible optimal environment for Palaeolithic hunter-gatherers does not exist. However, depending on subsistence strategy, there probably are threshold values below or above which human presence becomes unlikely. The distribution of sites shows pronounced differences with regard to environmental setting, indicating differences in preferred and tolerated conditions in Western and Central Europe. Also interesting in this regard is the differences between the sizes of the settlement areas and the areas with high preference scores. If the gaps in the site distribution are taken seriously, this indicates that only a small part of the potentially favourable area was exploited in a continuous fashion.

Conspicuously, the areas highlighted by the preference score for sites in Central and Western Europe are almost mutually exclusive. The habitats favoured by Solutrean and Badegoulian hunter-gatherers in the western part are located exclusively outside the range of continuous permafrost (Fig. 6) with MAAT between 0.5°C and 13.7°C and mean annual precipitation (MAP) between 500 and 1300 mm (Table 2). Figure 6 shows that good to optimal conditions for this adaptation (score ≥ 0.5) can be found between 40° N and 45° N and in Brittany. A conspicuous feature of Western Europe is that the settlement area of the largest regional population, located in Franco-Cantabria (Fig. 1), is bisected by the timberline with suitable conditions for tree growth in favourable areas of the southern part. For the northern part, stands of trees are likely in sheltered locations along the Dordogne and Vézère rivers. This suggests that people had adapted to rather temperate and moist climatic conditions, which allowed for the presence of scattered stand of trees in the landscape.

Early Epigravettian hunter-gatherers, in contrast, seem to have favoured a very different environmental setting (Fig. 7). As is the case in France, most sites are located north of the timberline. However, most sites are also located well north of the southern limit of

continuous permafrost. The preferred MAAT range is between -7.7°C and 10.3°C and MAP is between 260 and 1000 mm. Early Epigravettian hunter-gatherers thus had adapted to a cold and rather dry climate, and a largely treeless landscape with tundra and steppe elements prevailing. Good to optimal conditions for this adaptation are found between about 45°N and 50°N . Conspicuously, the northern fringe of site distribution at about 50°N coincides roughly with the northern extent of the loess cover. In light of the assumption that the northern loess border can be interpreted as indicative of the northern fringe of vegetation (see above), it seems that Early Epigravettian hunter-gatherers also used – at least during summer – the northernmost areas of their biome (cf. Heidenreich, 2014 for similar land-use in the Palaeolithic record of Alaska). Since sites in Germany are located in areas ranked as favourable for the Central European sites but unfavourable from a Western European point of view, it can be suggested that these few sites represent the western fringe of the Central European LGM ecumene. In this regard, the lack of sites in the central Balkan Peninsula is also of interest, since Croatia, Serbia and western Bulgaria are also highlighted as not matching the Central European preferences.

These finds shed new light on the discussion on LGM refugia in Europe (e.g. Jochim, 1987; Rigaud and Simek, 1990; Bennett et al., 1991; Straus, 2000; Willis et al., 2000; Stewart and Lister, 2001; Taberlet and Cheddadi, 2002; Willis and van Andel, 2004; Svenning et al. 2008; Schmidt et al., 2012). Usually, those areas are seen as LGM refugia for human populations that could also sustain tree growth and some rather temperate animal species. However, the different adaptations of hunter-gatherer communities in Eastern and Western Europe might suggest that also areas that did not provide conditions for trees and/or temperate animals could serve as a refugium where human populations could, at least for a certain time, survive.

An interesting approach to analyse human tolerance towards environmental factors has been proposed by Banks et al. (2006, 2008, 2009, 2011). In their 2008 study, they used ecological niche modelling to identify the limits of where hunter-gatherers could survive during the LGM to predict the potential extents of the Solutrean and the Early Epigravettian, and to evaluate the impact of environmental factors on their distribution. Although Banks et al. have focused on a shorter period within the LGM (22,000-20,000 calBP), a comparison of our results seems reasonable.

Banks et al. (2008) identify a clear northern boundary of the habitable area, which roughly follows the Loire valley and the southern fringes of the Alps and Carpathian Mountains and approximately coincides with the permafrost boundary. While our results confirm this observation for Western Europe, the area with a preference score ≥ 0.5 in Central Europe clearly extends beyond that border and up to 50° N. If there was a clear boundary of habitable area during the LGM, it would have been around this latitude, which, given the loess distribution, probably roughly coincides with the northern fringe of vegetation. However, there are about a dozen cases of recent hunter-gatherers living in environments colder than a MAAT of -7.7°C and dryer than a MAP of 260 mm (Binford. 2001, Table 401).

Banks et al. (2008) find that the ecological niches of the Solutrean and the Early Epigravettian overlap broadly, but with the difference that the Solutrean population could occupy cooler and more humid environments. Our data contradict this finding and show instead that that Early Epigravettian people were adapted to considerably colder conditions than Solutrean hunter-gatherers. These contradictory findings are probably a result of the different sample sizes. A period of only 2000 years is too short for the resolution of the archaeological data of the LGM. Although AMS dates may achieve a reasonable resolution, sites with conventional dates and, even more pronounced, only typological information do not. Dismissing typologically dated sites in periods of such small site counts as the LGM,

427 means to be left with a probably non-representative sample. Therefore, we deem our results
428 more reliable.

429

430

431 **4. Conclusions**

432

433 Climate seems to have played an important role for hunter-gatherers in Europe during the
434 LGM, inasmuch as it sets the parameters for certain subsistence strategies. This is not
435 surprising, however, the degree of difference between the conditions preferred in Western and
436 Central Europe is remarkable. These results are best interpreted in terms of two different
437 adaptations. The western community preferred a rather temperate and moist biome with a
438 MAAT of 7°C and MAP of 900 mm. Virtually all sites are located south of the permafrost
439 boundary. Open landscape was preferred, but the presence of scattered stands of trees in the
440 landscape was also tolerated. Here, the largest population can be identified in Franco-
441 Cantabria, comprising between 750 and 3,600 people with an estimated density between 0.6
442 and 2.7 persons per 100km² within the settlement areas. In Central Europe, in contrast, people
443 were adapted to a colder and drier biome with a MAAT of 1°C and MAP of 600 mm. Here,
444 most sites are located north of both the timberline and the permafrost boundary. Since
445 environments with tree growth were apparently avoided, the lack of sites in the central
446 Balkans appears credible. The estimated absolute number of people in the East ranges
447 between 60 and 100 people with a density between 0.1 and 0.2 persons per 100 km² within the
448 settlement areas. Thus, the number and density of people in Western and Central Europe
449 seems to have differed by orders of magnitude. Since ungulate biomass is dependent on the
450 net primary production which in turn is directly correlated with precipitation, the higher
451 amount of rainfall in Western Europe probably provided a richer background of resources

than Central Europe. It is thus likely that the low population number in Central Europe is part of an adaptation to this environment.

Due to extensive loess covers, these estimates for Central Europe are certainly minimum numbers. However, even doubled this would still be a comparatively small population raising the question of whether a community of that size could form a viable population under such environmental conditions (cf. Wobst, 1973; Moore, 2003; Smith, 2014). Large raw material catchments point to long-distance movements within the range of logistical mobility, which indicate the need to cover large areas to satisfy daily needs. These movements, in turn, probably foster extensive mating networks between distant groups and by increasing the number of eligible mates counteract the threat of extinction. However, already smaller disturbances – be they social or environmental – could probably cause those networks to lose their balance and eventually to break down (see e.g. Schmidt et al. 2012 for an example of the assumed correlation on the Iberian Peninsula). Very few sites located between 15°E and 20°E and 45°N and 50°N are dated to between 22,000 and 20,000 calBP or 17,000 and 18,000 BP, except perhaps for Grubgraben at the southern fringe of that area (cf. Terberger, 2013). It could therefore be assumed that the population in western Central Europe eventually collapsed around 22,000 calBP, whereas dates from the Prut region (e.g. Cosautsi, Mitoc Malul Galben, Molodova 5) suggest that people continued to live there.

This study is as an initial effort to understand the demographic development during the Palaeolithic on a regional scale. Future research will be necessary to further improve the chronological and spatial resolution and to integrate social factors in the understanding of population dynamics on spatially and temporally smaller scales.

Acknowledgments:

477 We thank Jean-Pierre Bocquet-Appel (EPHE, CNRS), Anja Duwe and Andreea Darida
478 (University of Cologne) for granting access to and compiling data on site distribution and
479 dating, Wei Chu (University of Cologne) for constructive criticism and to Jayson Orton for
480 proofreading. We acknowledge the World Climate Research Programme's Working Group on
481 Coupled Modelling, which is responsible for CMIP, and we thank the climate modelling
482 groups (listed in Table 1 of this paper) for producing and making available their model output.
483 For CMIP the U.S. Department of Energy's Program for Climate Model Diagnosis and
484 Intercomparison provided coordinating support and led development of software
485 infrastructure in partnership with the Global Organization for Earth System Science Portals.
486 We thank Qian Xia for supporting the logistic-regression analysis and Robert Rauterkus (both
487 University of Cologne), Heiko Lindner (RWTH Aachen University) for data preparation and
488 Nicole Böhl (University of Erlangen-Nürnberg) for graphic support. We also thank our
489 reviewers for the most appreciated comments. This is a publication of the Collaborative
490 Research Centre (CRC) 806 of the German Research Foundation (DFG).

491 **References**

- 492 Banks, W.E., d’Errico, F., Dibble, H., Krishtalka, L., West, D., Olszewski, D.I.,
 493 Peterson, A.T., Anderson, D.G., Gillam, J.C., Montet-White, A., Crucifix, M.,
 494 Marean, C.W., Sanchez-Goni, M.-F., Wolfarth, B., Vanhaeran, M., 2006. Ecocultural
 495 niche modeling: new tools for reconstructing the geography and ecology of past
 496 human populations. *PaleoAnthropology* 4, 68–83.
- 497 Banks, W.E., d’Errico, F., Peterson, A.T., Vanhaeren, M., Kageyama, M., Sepulchre, P.,
 498 Ramstein, G., Jost, A., Lunt, D., 2008. Human ecological niches and ranges
 499 during the LGM in Europe derived from an application of eco-cultural niche
 500 modeling. *Journal of Archaeological Science* 35, 481–491.
- 501 Banks, W.E., Zilhão, J., d’Errico, F., Kageyama, M., Sima, A., Ronchitelli, A., 2009.
 502 Investigating links between ecology and bifacial tool types in Western Europe
 503 during the Last Glacial Maximum. *Journal of Archaeological Science* 36, 2853–2867.
- 504 Banks, W.E., Aubry, T., d’Errico, F., Zilhão, J., Lira-Noriega, A., Peterson, A.T., 2011. Eco-
 505 cultural niches of the Badegoulian: Unraveling links between cultural adaptation and
 506 ecology during the Last Glacial Maximum in France. *Journal of Anthropological*
 507 *Archaeology* 30, 359–374.
- 508 Baulin, V.V., Danilova, N.S., Nechayev, V.P., Péwé, T.L., Velichko, A.A., 1992. Glaciation
 509 and permafrost – maximum cooling of the last glaciation. In Frenzel, B., Pecsli, M.,
 510 Velichko, A. A. (Eds.), *Atlas of paleoclimates and paleoenvironments of the northern*
 511 *hemisphere – Late Pleistocene – Holocene*. Gustav Fischer Verlag, Stuttgart, p. 49.
- 512 Bennett, K. D., Tzedakis, P. C., & Willis, K. J., 1991. Quaternary refugia of north European
 513 trees. *Journal of Biogeography* 18, 103–115.
- 514 Best, D.J., Roberts, D. E., 1975. Algorithm AS 89: The Upper Tail Probabilities of Spearman's
 515 rho. *Applied Statistics* 24, 377–379.

516 Binford, L.R., 1972. Contemporary model building: paradigms and the current state of
517 Palaeolithic research. In: Clarke, D.L. (Ed.), *Models in Archaeology*. Methuen,
518 London, pp. 109-166.

519 Binford, L. R., 1979. Organization and formation processes: Looking at curated technologies.
520 *Journal of Anthropological Research* 35 (3), 255–273.

521 Binford, L.R., 1980. Willow smoke and dogs' tails: hunter-gatherer settlement systems and
522 archaeological site formation. *American Antiquity* 45 (1), 4-20.

523 Binford, L.R., 1982. The archaeology of place. *Journal of Anthropological Archaeology* 1, 5-
524 31.

525 Binford, L.R., 1983. *In pursuit of the past*. Thames and Hudson, London.

526 Binford, L.R., 2001. Constructing frames of reference. An analytical method for
527 archaeological theory building using hunter-gatherer and environmental data sets.
528 University of California Press, Berkeley.

529 Bocquet-Appel, J.-P., Demars, P.-Y., 2000. Population Kinetics in the Upper Palaeolithic in
530 Western Europe. *Journal of Archaeological Science* 27, 551-570.

531 Bocquet-Appel, J.-P., Demars, P.-Y., Noiret, L., Dobrowsky, D., 2005. Estimates of Upper
532 Palaeolithic meta-population size in Europe from archaeological data. *Journal of*
533 *Archaeological Science* 32, 1656-1668.

534 Braconnot P., Harrison, S.P., Kageyama, M., Bartlein, P.J., Masson-Delmotte, V., Abe-Ouchi,
535 A., Otto-Bliesner, B., Zhao, Y., 2012. Evaluation of climate models using palaeoclimatic
536 data. *Nat. Clim. Change* 2, 417–424.

537 Clarke, D.L., 1972. Models and paradigms in contemporary archaeology. In: Clarke, D.L.
538 (Ed.), *Models in Archaeology*. Methuen, London, pp. 1-60.

539 Danin, A., Ganor, E., 1991. Trapping of airborne dust by mosses in the Negev Desert,
540 Israel. *Earth Surface Processes and Landforms* 16, 153-162.

541 Demars, P.-Y., 1998. Circulation des silex dans le nord de l'Aquitaine au Paléolithique
 542 supérieur: l'occupation de l'espace par les derniers chasseurs-cueilleurs. *Gallia*
 543 *Préhistoire* 40, 1-28.
 544 Djindjian, F., Kozłowski, J., Otte, M., 1999. Le Paléolithique supérieur en Europe. Armand
 545 Colin, Paris.
 546 Floss, H., 1994. Rohmaterialversorgung im Paläolithikum des Mittelrheingebietes. Habelt,
 547 Bonn.
 548 French, J.C., Collins, Ch., 2015. Upper Palaeolithic population histories of Southwestern
 549 France: a comparison of the demographic signatures of ^{14}C date distributions and
 550 archaeological site counts. *Journal of Archaeological Science* 55, 122-134.
 551 Gamble, C.S., 1986. The Palaeolithic settlement of Europe. Cambridge University Press,
 552 Cambridge.
 553 Grichuk, V. P., 1992. Main types of vegetation (ecosystems) for the maximum cooling of the
 554 last glaciation. In: Frenzel, B., Pécsei, B. Velichko, A.A. (Eds.), *Atlas of Palaeoclimates*
 555 *and Palaeoenvironments of the Northern Hemisphere*. INQUA/Hungarian Academy of
 556 Sciences, Budapest, pp. 123-124.
 557 Haas, A.G., Viallix, J.R., 1976. Krigeage applied to geophysics: The answer to the problem of
 558 estimates and contouring. *Geophysical Prospecting* 24, 49–69.
 559 Haase, D., Fink, J., Haase, G., Ruske, R., Pécsi, M., Richter, H., Altermann, M., Jäger, K.-D.,
 560 2007. Loess in Europe—its spatial distribution based on a European Loess Map, scale
 561 1:2,500,000. *Quaternary Science Reviews* 26, 1301-1312.
 562 Hahn, J., 1977. Aurignacien. Das ältere Jungpaläolithikum in Mittel- und Osteuropa.
 563 *Fundamenta A9*. Böhlau, Köln.

564 Heidenreich, S., 2014. Lithic Technologies, Functional Variability, and Settlement Systems in
 565 Late Pleistocene Beringia – New Perspectives on a Colonization Process. Ph.D.
 566 Dissertation, University of Erlangen-Nürnberg. urn:nbn:de:bvb:29-opus4-52087.

567 Hilpert, J., Wendt, K.P., Zimmermann, A., 2008. A hierarchical model of scale levels for
 568 estimations of population densities. In: Posluschny, A., Lambers, K., Herzog, I. (Eds.),
 569 Layers of Perception. Proceedings of the 35th International Conference on Computer
 570 Applications and Quantitative Methods in Archaeology (CAA), Berlin, Germany, April
 571 2–6, 2007 (Kolloquien zur Vor- und Frühgeschichte, Vol. 10). Habelt, Bonn, pp. 245-251.

572 Hofer, D., Raible, C.C., Dehnert, A., Kuhlemann, J., 2012. The impact of different glacial
 573 boundary conditions on atmospheric dynamics and precipitation in the North Atlantic
 574 region. *Clim. Past* 8, 935-949, doi:10.5194/cp-8-935-2012.

575 Holzkämper, J., Maier, A., Koch, I., 2014. Ergebnisse einer Suche nach Aurignacien- und
 576 Magdalénien-Fundstellen in Nordrhein-Westfalen. *Archäologisches*
 577 *Korrespondenzblatt* 44, 3, 293 – 306.

578 Hoskins B.J., Valdes, P.J., 1990. On the existence of storm-tracks. *J. Atmos. Sci.* 47, 1854–
 579 1864.

580 Jarvis A., Reuter, H.I., Nelson, A., Guevara, E., 2008. Hole-filled seamless SRTM data V4,
 581 International Centre for Tropical Agriculture (CIAT), available from
 582 <http://srtm.csi.cgiar.org>.

583 Jochim, M., 1987. Late Pleistocene refugia in Europe. In: O. Soffer (Ed.), *The Pleistocene old*
 584 *world. Regional perspectives*. Plenum Press, New York, pp. 317–331.

585 Karte, J., 1983. Periglacial phenomena and their significance as climatic and edaphic
 586 indicators. *Geo. Journal* 7 (4), 329-340.

587 Kelly, R.L., 1983. Hunter-gatherer mobility strategies. *Journal of Anthropological Research*
 588 39, 277-306.

589 Kelly, R.L., 1995. *The foraging spectrum. Diversity in hunter-gatherer lifeways.* Smithsonian
 590 Institution Press, Washington, London.

591 Körner, C., 2012. *Alpine Treelines, Functional Ecology of the Global High Elevation Tree*
 592 *Limits.* Springer, Basel.

593 Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. *J.*
 594 *Biogeogr.* 31, 713–732.

595 Kozłowski, J.K., 2015. The origin of the Gravettian. *Quaternary International* 359-360, 3-18.

596 Kretschmer, I., 2015. *Demographische Untersuchungen zu Bevölkerungsdichten, Mobilität*
 597 *und Landnutzung im späten Jungpaläolithikum.* Kölner Studien zur prähistorischen
 598 *Archäologie, Vol. 6, Marie Leidorf, Rhaden/Westf.*

599 Maier, A., 2015. *The Central European Magdalenian. Regional Diversity and Internal*
 600 *Variability. Vertebrate Paleobiology and Paleoanthropology.* Springer, New York.

601 Maier, A., Zimmermann, A., 2015. CRC806-E1 LGM-Sites Database V-20150313. CRC806-
 602 Database, DOI: 10.5880/SFB806.12 <<http://dx.doi.org/10.5880/SFB806.12>>

603 Malmer, M. P., 1962. *Jungneolithische Studien.* Habelt, Bonn.

604 Mellars, P., French, J.C., 2011. Tenfold population increase in Western Europe at the
 605 Neandertal-to-Modern Human transition. *Science* 333, 623.

606 Mix, A.C., Bard, E., Schneider, R., 2001. Environmental processes of the ice age: land,
 607 oceans, glaciers (EPILOG). *Quaternary Science Reviews* 20, 627-657.

608 Moore, J.H., 2003. Kin-based crews for interstellar multi-generational space travel. In:
 609 Kondo, Y., Bruhweiler, F., Moore, J.H., Sheffield, C. (Eds.), *Interstellar Travel and*
 610 *Multi-Generational Space Ships.* Apogee Books, Wheaton, pp. 81–88.

611 Otte, M., 1981. *Le Gravettien en Europe Centrale. Dissertationes Archaeologicae Gandenses*
 612 *20. De Tempel, Brugge.*

613 Preparata, F.P., Shamos, I.S., 1988. Computational Geometry: An Introduction. Springer, New
614 York.

615 R Core Team 2014. R: A language and environment for statistical computing. R Foundation
616 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

617 Rigaud, J.-P., Simek, J. F., 1987. “Arms too short to box with God”. Problems and prospects
618 for Paleolithic prehistory in Dordogne, France. In: O. Soffer (Ed.), The Pleistocene old
619 world. Regional perspectives. Plenum Press, New York, pp. 47–61.

620 Rigaud, J.-P., Simek, J. F., 1990. The last pleniglacial in the south of France (24 000-14 000
621 years ago). In: Soffer, O. Gamble, C. (Eds.), The world at 18 000 BP. Volume 1, High
622 Latitudes. Unwin Hyman, London, pp. 69-86.

623 Rozoy, D. J.-G., 1988. Le Magdalénien en Europe: démographie, groups régionaux. Bulletin
624 Société Préhistorique du Luxembourg, 10, 139–158.

625 Schlummer, M., Hoffmann, T., Dikau, R., Eickmeier, M., Fischer, P., Gerlach, R.,
626 Holzkämper, J., Kalis, A.J., Kretschmer, I., Lauer, F., Maier, A., Meesenburg, J.,
627 Meurers-Balke, J., Münch, U., Pätzold, S., Steininger, F., Stobbe, A., Zimmermann,
628 A., 2014. From point to area: Upscaling approaches for Late Quaternary
629 archaeological and environmental data. Earth-Science Reviews 131, 22-48.

630 Schmidt, I., 2015. Solutrean points of the Iberian Peninsula. Tool making and using behaviour
631 of hunter-gatherers during the Last Glacial Maximum. BAR International Series 2778.
632 British Archaeological Reports, Oxford.

633 Schmidt, I., Bradtmöller, M., Kehl, M., Pastoors, A., Tafelmaier, Y., Weninger, B., Weniger,
634 G-Ch., 2012. Rapid climate change and variability of settlement patterns in Iberia
635 during the Late Pleistocene. Quaternary International 274, 179–204.

636 Shennan, S., Downey, S.S., Timpson, A., Edinborough, K., Colledge, S., Kerig, T., Manning,
637 K., Thomas, M.G., 2013. Regional population collapse followed initial agriculture

638 booms in mid-Holocene Europe. *Nature Communications* 4, Article number: 2486
 639 doi:10.1038/ncomms3486.

640 Smith, C.M., 2014. Estimation of a genetically viable population for multigenerational
 641 interstellar voyaging: Review and data for project Hyperion. *Acta Astronautica* 97, 16-
 642 29.

643 Stewart, J. R., & Lister, A. M., 2001. Cryptic northern refugia and the origins of the modern
 644 biota. *Trends in Ecology and Evolution* 16, 608–613.

645 Straus, L. G., 1990. The Last Glacial Maximum in Cantabrian Spain: the Solutrean. In: Soffer,
 646 O. Gamble, C. (Eds.), *The world at 18 000 BP. Volume 1, High Latitudes*. Unwin
 647 Hyman, London, pp. 89-108.

648 Straus, L. G., Bicho, N., Winegardner, A. C., 2000. The Upper Palaeolithic settlement of
 649 Iberia: first-generation maps. *Antiquity*, 74, 553–566.

650 Straus, L.G., González Morales, M.R., Fano Martínez, M.Á., García-Gelabert, M.P., 2002.
 651 Last Glacial human settlement in Eastern Cantabria. *Journal of Archaeological Science*
 652 29, 1403-1414. Surovell, T.A., Finley, J.B., Smith, G.M., Brantingham, P.J., Kelly, R.,
 653 2009. Correcting temporal frequency distributions for taphonomic bias. *Journal of*
 654 *Archaeological Science* 36, 1715-1724.

655 Svenning, J.-C., Normand, S., & Kageyama, M., 2008. Glacial refugia of temperate trees in
 656 Europe: Insights from species distribution modelling. *Journal of Ecology* 96, 1117–
 657 1127.

658 Svirčev, Z., Marković, S. B., Stevens, T., Codd, G. A., Smalley, I., Simeunović, J., Obreht, I.,
 659 Dulić, T., Pantelić, D., Hambach, U., 2013. Importance of biological loess crusts for
 660 loess formation in semi-arid environments. *Quaternary International* 296, 206-215.

661 Taberlet, P., & Cheddadi, R., 2002. Quaternary refugia and persistence of biodiversity.
 662 *Science* 297, 2009–2010.

663 Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An Overview of CMIP5 and the experiment
664 design. *Bull. Amer. Meteor. Soc.* 93, 485-498.

665 Terberger, T., 2013. Le Dernier Maximum glaciaire entre le Rhin et le Danube, un réexamen
666 critique. In: Bodu, P., Chehmana, L., Klaric, L., Mevel, L., Soriano, S., Teyssandier, N.
667 (Eds.), *Le Paléolithique supérieur ancien de l'Europe du Nord-Ouest Réflexions et*
668 *synthèses à partir d'un projet collectif de recherche sur le centre et le sud du Bassin*
669 *parisien. Actes du colloque de Sens (15-18 avril 2009). Mémoire de la Société*
670 *Préhistorique française* 56. Paris, pp. 415–443.

671 Tsoar, H., Pye, K., 1987. Dust transport and the question of desert loess formation.
672 *Sedimentology* 34, 139-153.

673 Vandenberghe, J., French, H.M., Gorbunov, A., Marchenko, S., Velichko, A.A., Jin, H., Cui,
674 Z., Zhang, T., Wan, X., 2014. The Last Permafrost Maximum (LPM) map of the
675 Northern Hemisphere: permafrost extent and mean annual air temperatures, 25–17 ka
676 BP. *Boreas* 43, 652–666.

677 van Reybrouck, D., 2000. Beyond ethnoarchaeology? A critical history on the role of
678 ethnographic analogy in contextual and post-processual archaeology. In: Gramsch, A.
679 (Ed.), *Vergleich als archäologische Methode. Analogien in den Archäologien.* BAR
680 *International Series* 825. Archaeopress, Oxford, pp. 39-51.

681 Velichko, A.A. and Nechaev, V.P., 1992. Assessment of permafrost dynamics in Northern
682 Eurasia under global climate change. *Dokl. Akad. Nauk* 3, 667–671.

683 Washburn, A.L., 1979. *Geocryology: A survey of periglacial processes and environments.*
684 Arnold, London.

685 Walter, H., Breckle, S.W., 1994. *Spezielle Ökologie der Gemäßigten und Arktischen Zonen*
686 *Euro-Nordasiens. Ökologie der Erde, 3.* Spektrum, Jena.

- 687 Wendt, K.P., Hilpert, J., Zimmermann, A., 2010. Landschaftsarchäologie III. Untersuchungen
688 zur Bevölkerungsdichte der vorrömischen Eisenzeit, der Merowingerzeit und der
689 späten vorindustriellen Neuzeit an Mittel- und Niederrhein. Mit Beiträgen von S.
690 Ickler, H. Nortmann, B. Päffgen, F. Siegmund, P. Tutlies. Berichte der Römisch-
691 Germanischen Kommission 91, 217-338
- 692 Wiermann, R.R., 2000. Hinter'm Horizont geht's weiter... Vom Nutzen der ethnographischen
693 Analogie für die Urgeschichtsforschung. In: Gramsch, A. (Ed.), Vergleichen als
694 archäologische Methode. Analogien in den Archäologien. BAR International Series
695 825. Archaeopress, Oxford, pp. 113-118.
- 696 Willis, K. J., Rudner, E., & Sümegi, P., 2000. The full-glacial forests of central and
697 southeastern Europe. Quaternary Research, 53 , 203–213.
- 698 Willis, K.J., van Andel, T.H., 2004. Trees or no trees? The environment of central and eastern
699 Europe during the Last Glaciation. Quaternary Science Reviews 23, 2369-2387.
- 700 Wobst, H.M., 1973. Boundary conditions for Palaeolithic social systems: a simulation
701 approach. American Antiquity 39, 303–309.
- 702 Wobst, H. M., 1978. The archaeo-ethnology of hunter-gatherers or the tyranny of the
703 ethnographic record in archaeology. American Antiquity, 43 (2), 303-309.
- 704 Zhang, Z., Xiao, R., Shortridge, A., Wu, J. 2014. Spatial point pattern analysis of human
705 settlements and geographical associations in eastern coastal China – A case study.
706 International Journal of Environmental Research and Public Health, 11, 2818-2833.
- 707 Zimmermann, A., Richter, J., Frank, Th., Wendt, K.P., 2005. Landschaftsarchäologie II:
708 Überlegungen zu Prinzipien einer Landschaftsarchäologie. Berichte der Römisch-
709 Germanischen Kommission 85, 2004, 37-95.
- 710 Zimmermann, A., Wendt, K.P., Frank, Th., Hilpert, J., 2009a. Landscape Archaeology in
711 Central Europe. Proceedings of the Prehistoric Society 75, 1-53.

712 Zimmermann, A., Hilpert, J., Wendt, K.P., 2009b. Estimations of population density for
713 selected periods between the Neolithic and AD 1800. Human Biology, 81 (2-3), 357-
714 380.
715
716

717 **Table captions**

718

719 **Table 1.** List of models, institutions and horizontal resolution used in the analyses in this
720 study.

721 For each model the experiment with coding r1i1p1 is used.

722

723 **Table 2.** Probability density function parameters of model-ensemble averaged MAAT, MAP
724 and elevation.

Mean value, standard deviation as well as lower and upper limits for each variable for all sites (Case-A) as well as for sites in western (Case-W) and eastern part (Case-E) of the investigated area.

725 **Table 3.** Regionally differentiated results of the palaeodemographic estimates.

RM: raw material catchment, OI: Optimal Isoline, nGroups: number of GROUP2 units within area of OI, P: absolute number of people within OI, D_s : population density within OI, D_m : population density in map section (1,200,000 km²).

Figure captions

726

Fig. 1: Sites (black dots), Optimal Isoline (43 km, red line) and raw material catchments (hatched polygons) for the Last Glacial Maximum against the distribution of loess (redrawn after Haase et al. 2007). The short-dashed line indicates the map section used to calculate population densities (ca. 1,200,000 km²). The long-dashed line marks our separation of the western and an eastern part of the investigated area.

Fig. 2: Overview of the data and methods used to calculate the population estimates.

727 **Fig. 3:** Distributions of MAAT, T , annual precipitation, R , and elevation, H , at the
728 archaeological sites considered in this study, showing Gauss distributions for T and R , and
729 Gamma distribution for H , and providing upper and lower limits for T (-5.3 and 16.0 °C), R
730 (430 and 1192 mm), and H (7 and 911 m).

731

732 **Fig. 4:** MAAT for (a) LGM-ensemble and (b)-(h) individual ESMs. The dashed blue line
733 depicts the -4°C isotherm, hypothesized as annual mean temperature assigned to permafrost
734 conditions. The light blue line marks the reconstructed continuous permafrost boundary after
735 Baulin (1992). LGM-boundary conditions: LGM-coastlines (green-white dashed line used for
736 climate modelling) and extent of Fennoscandian ice sheet according to PMIP3-standards.

737

738 **Fig. 5:** Mean temperature of the warmest month for (a) LGM-ensemble and (b)-(h) individual
739 ESMs. The dashed blue line depicts the modelled 10°C isotherm, the dashed purple line
740 depicts the modelled 12°C isotherm, giving a range for the hypothesized limit of tree growth.
741 The solid green line marks the reconstructed timberline (after Grichuk 1992). LGM-boundary
742 conditions as in Figure 3.

743 **Fig. 6:** Preference-scores for the western part of the investigated area. The blue line indicates
744 the southern border of continuous permafrost, green line indicates the northern timberline.
745 The grey areas mark the extent of glaciers.

746

747 **Fig. 7:** Preference-scores for the eastern part of the investigated area. The blue line indicates
748 the southern border of continuous permafrost, green line indicates the northern timberline.
749 The grey areas mark the extent of glaciers.

Tables

Table 1

	Model name	Model institution	Hor. resolution (grid points)
1	CCSM4	National Center for Atmospheric Research, US/Dept. of Energy/NSF	288 x 192
2	CNRM_CM5	Centre National de Recherches Météorologiques/Centre Européen de Recherche et Formation Avancée en Calcul Scientifique, France	256 x 128
3	FGOALS_g2	LASG, Institute of Atmospheric Physics, Chinese Academy of Sciences; and CESS, Tsinghua University, China	128 x 60
4	IPSL-CM5A-LR	Institut Pierre-Simon Laplace, France	96 x 95
5	MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies, Japan	128 x 64
6	MPI-ESM-P	Max Planck Institute for Meteorology, Hamburg, Germany	196 x 98
7	MRI-CGCM3	Meteorological Research Institute, Tsukuba, Japan	320 x 160

Table 2

Temperature	$\bar{T}$ (°C)	σ_T (°C)	$T_{\min}$ (°C)	$T_{\max}$ (°C)
Case-A	5.326	3.9324	-4.8033	15.455
<u>Case-W</u>	<u>7.1033</u>	<u>2.5756</u>	<u>0.46886</u>	<u>13.738</u>
Case-E	1.3236	3.4993	-7.6899	10.337
Rainfall	$\bar{R}$ (mm)	σ_R (mm)	$R_{\min}$ (mm)	$R_{\max}$ (mm)
Case-A	829.74	205.88	299.42	1360.1
<u>Case-W</u>	920.01	161.2	504.79	1335.2
Case-E	626.46	140.31	265.06	987.86
Topography	a (shape)	b (scale)	$H_{\min}$ (m)	$H_{\max}$ (m)
Case-A	1.6544	135.1349	7	911
<u>Case-W</u>	1.4936	144.25	5.0826	924.01
Case-E	2.231	108.29	15.894	852.56

Table 3

Region	Q	OI	A _{RM}	A _{OI}	N _g	P	D _s	D _m
	1		1593	15883	10.0	429	0.027	
Portugal	2	43	3089	15883	5.1	221	0.014	
	3		7725	15883	2.1	88	0.006	
	1		1593	17395	10.9	469	0.027	
S-Spain	2	43	3089	17395	5.6	242	0.014	
	3		7725	17395	2.3	97	0.006	
	1		1593	8128	5.1	219	0.027	
SE-Spain	2	43	3089	8128	2.6	113	0.014	
	3		7725	8128	1.1	45	0.006	
	1		1593	7183	4.5	194	0.027	
E-Spain	2	43	3089	7183	2.3	100	0.014	
	3		7725	7183	0.9	40	0.006	
	1		1593	5363	3.4	145	0.027	
NE-Spain	2	43	3089	5363	1.7	75	0.014	
	3		7725	5363	0.7	30	0.006	
	1		1593	135574	85.1	3659	0.027	
Franco-Cantabria	2	43	3089	135574	43.9	1887	0.014	
	3		7725	135574	17.6	755	0.006	
	1		1593	19114	12.0	516	0.027	
S-France	2	43	3089	19114	6.2	266	0.014	
	3		7725	19114	2.5	106	0.006	
	1		1593	6017	3.8	162	0.027	
Provence/Liguria	2	43	3089	6017	1.9	84	0.014	
	3		7725	6017	0.8	33	0.006	
	1		1593	16205	10.2	437	0.027	
Upper Seine valley	2	43	3089	16205	5.2	226	0.014	
	3		7725	16205	2.1	90	0.006	
	1		17937	22159	1.2	53	0.002	
Central Europe	2	43	29370	22159	0.8	32	0.001	
	3		31928	22159	0.7	30	0.001	
	1		20796	22392	1.1	46	0.002	
Prut	2	43	29370	22392	0.8	33	0.001	
	3		31288	22392	0.7	31	0.001	
	1				147.2	6330	0.023	0.005
Total	2			275413	76.2	3057	0.011	0.002
	3				31.3	1346	0.005	0.001

LGM-Ensemble

LGM-CCSM4

LGM-CNRM-CM5

LGM-FGOALS-g2

LGM-IPSL

LGM-MIROC

LGM-MPI-ESM

LGM-MRI-CGCM3

LGM-Ensemble

LGM-CCSM4

LGM-CNRM-CM5

LGM-FGOALS-g2

LGM-IPSL

LGM-MIROC

LGM-MPI-ESM

LGM-MRI-CGCM3