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Estimates of Upper Palaeolithic meta-population size in Europe from archaeological data

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Abstract

Three databases (2961 georeferenced archeological sites, simulated climatic variables simulating a typical "warm" phase of the isotopic stage 3 (IOS3 project), and ethnographic of hunter–gatherers (HG)) were used to estimate the size, growth rate and kinetics of the metapopulation of HG during four periods of the Upper Paleolithic in Europe. The size of the metapopulation was obtained by multiplying a demographic density (per 100 km^2) by the size of the population territory of HG. Demographic density for each period was calculated by successively backprojecting a reference density obtained for the Late Glacial with inter-period growth rate of the archeological sites. From the Aurignacian to the Glacial Maximum, the metapopulation remained in a positive quasi-stationary state, with about 4400–5900 inhabitants (95% confidence interval (CI95%): 1700–37,700 inhabitants). During the Glacial Maximum, the metapopulation responded to the cold: (i) by moving the northern limits of its maximum expansion zone towards the low latitudes by 150–500 km from west to east, (ii) by concentrating in few refuge zones (mainly Périgord, Cantabria and the Ibérian coasts), (iii) by becoming perhaps distributed in smaller groups than during the pre and post Glacial Maximum. The metapopulation reached 28,800 inhabitants (CI95%: 11,300–72,600) during the mid-Late Glacial recolonisation.

Keywords: Upper Palaeolithic demography; Refuge zones; Space–time density of archaeological sites; Palaeodemography

We know that there is a relationship between the historically known population density of hunter–gatherers (HG) and climatic and ecological variables [6,7,18]. Those variables have an influence on primary and secondary biomass and hence on the density of prey, which in turn influences the density of hunter–gatherer populations. With the relationship between climate and demography, which is assumed to have remained roughly constant over the recent past, at least two approaches can be used to reconstitute prehistoric demography. The first, using reference ethnographic and environmental databases, involves estimating demographic variables directly from reconstituted climatic and ecological maps, without taking account of the archaeological data. This is the approach adopted by Binford [6] who has provided an estimation of the world population of HG by ecological zones during the Mesolithic. Another approach starts from the archaeological data. Looking at a distribution of archaeological sites on a geographical map, there are evident variations

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in site density by zones. In some zones, site density is high, in others it is low or nil. It seems reasonable to assume that zones with a large number of sites would also have had a relatively large population; zones with no sites would have been unpopulated. The same approach has already been used on a continental scale, in Australia [23], and on a regional scale [3]. The relationship between climate and demography is used by taking account of variations in the density of the archaeological information on the map. This is the approach we have used here to estimate the size, growth rate and kinetics of the metapopulation of HG during four periods of the Upper Palaeolithic in Europe. The research further explores the approach first developed by Bocquet-Appel and Demars [4,5].

This paper begins with a description of the three databases which were used in the research: (i) georeferenced archeological sites, (ii) simulated climatic variables in a typical "warm" phase of the isotopic stage 3 in Europe, and (iii) ethnographic data on HG. The latter provides the reference relationship between demography and climate. We then describe the approach used to estimate a demographic variable from the archaeological data. The size of the metapopulation is obtained by multiplying a demographic density by the size of the area representing the territory occupied by the HG. The questions which will be addressed are the following: what size were hunter–gatherer metapopulations during the four periods and how were they distributed geographically? Under severe climatic constraints (and their subsequent slackening), what was the demographic response to the climatic variation, in terms of the size of the metapopulation, the size of its settlement units and its geographical kinetics? Finally, do geographical patterns of population distribution, as estimated from archaeological data, coincide with genetic patterns of DNA*mt* distribution and linguistic patterns of proto-language distribution prior to the Glacial Maximum?

1. The data

1.1. Archaeological data

The archaeological database covers 2961 georeferenced sites, drawn from an exhaustive search in the literature (see Fig. 1). The database covers Europe up to longitude 40 °E, with some isolated sites beyond. It was first subdivided into four chronological periods BP, identified by lithic industries: Aurignacian at 40–29 ka BP (40.36–31.04 ka cal BC), Gravettian at 29–22 ka BP (31.04–23.50 ka cal BC), Lower Magdalenian and Solutrean at 22–16.5 ka BP (23.5–17.18 ka cal BC), Middle, Upper and Final Magdalenian, Hamburgian

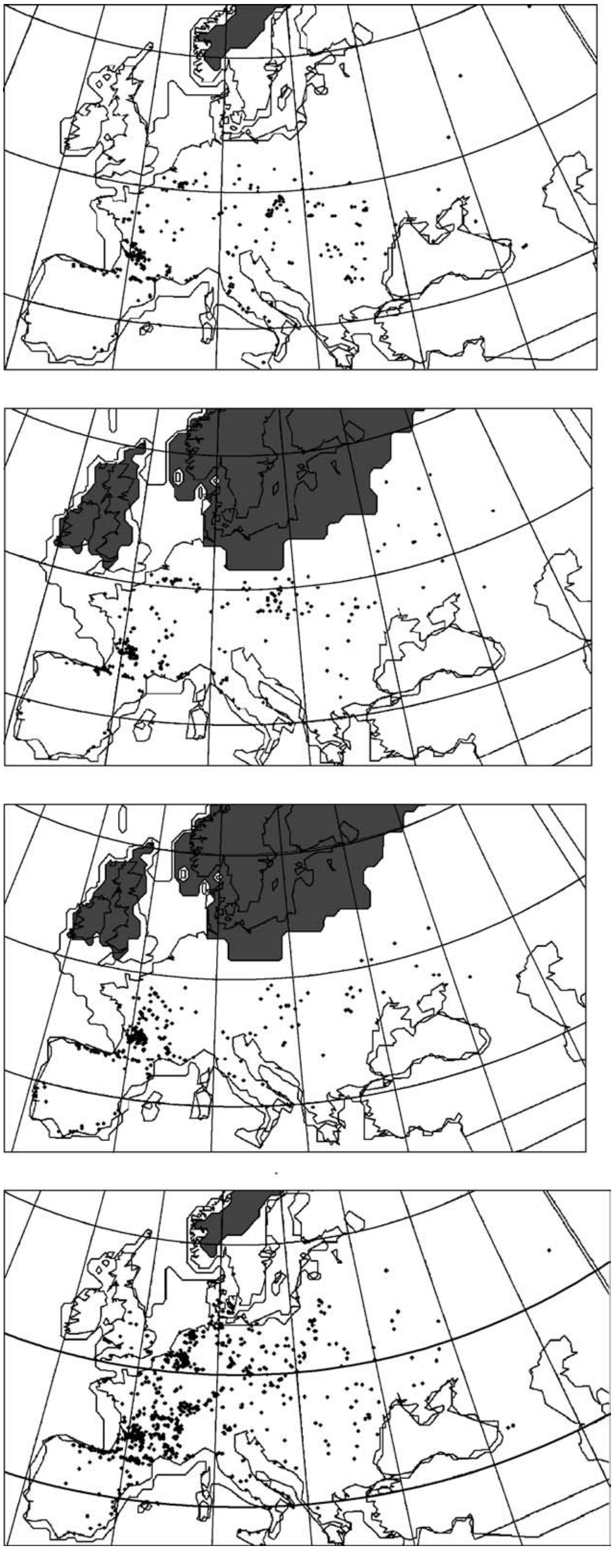

Fig. 1. Site distribution over old coastlines (IOS3 warm phase) and present-day coastlines minus islands (called *coinciding zone*) for four periods. From top to bottom: Aurignacian, Gravettian, Glacial Maximum and Late Glacial.

and Creswellian 16.5–11.5 ka BP (17.18–11.36 ka cal BC). These four chronological periods were, respectively, named the Aurignacian, Gravettian, Glacial Maximum and Late Glacial. Since demographic rates have to be calculated from durations between periods, the dates were calibrated [16,17]. The purpose of our work is to estimate demographic variables, in particular for growth rate, for which, over a pluri-millenial duration, very small values were expected. For statistical reasons, the size of sample sites, their number, were given priority over the chronological definition of the periods. To refine the chronology, we would have needed to use only radiometrically dated sites, which would have reduced the sample size considerably, as well as the accuracy of the estimated space–time distribution of the archaeological markers. To try to detect a pattern of mobility in the data, the sites were subdivided into large (>1000 tools) and small sites (≤ 1000 tools). Large sites are assumed to represent more permanent hunting settlements than small sites (see Table 2). Any individual site may have experienced a certain rate of curation, re-use and re-visiting. However, these rates can be regarded as proportional to the size of the sites themselves. Their influence on under- or over-weighting of sites can thus be regarded as negligible. It is nevertheless possible that there is an under-weighting, of archaeological origin, of the size of the "large" sites relative to the "small" sites, in terms of the number of tools. The very size of "large" sites has, perhaps, made the archaeologists less demanding in the past regarding the exhaustiveness of material recovery, in comparison with small sites today where all material is recovered. We do not see what can be done here.

1.2. Climate data

These are represented in simulations carried out for Europe by the Oxygen Isotope Stage 3 project (IOS3) research group [29,30]. These simulations have produced values on a $60 \times 60\ \mathrm{km}^2$ grid up to longitude 40°E. They provide about 30 variables altogether, including air and ground temperatures, precipitation, evapotranspiration, wind temperature and wind speed, snow-cover, relative humidity, wind chill, cloud cover, etc. Here, we have used the group of simulations that represent a typical "warm" episode, according to the authors [30], which was attributed to the Late Glacial, and to 21 ka BP. The adjective "warm" should not be misunderstood: a glacier covered a large part of Scandinavia at the time and the sea level was approximately 30 m below the current level.

In term of biomes, one of the main conclusions of this research is that:

"mosaics with patchy woodland, or parkland/savannah-like vegetation with scattered individual trees, dominated across much of Europe during the warm DO [Dansgaard/Oeschger] events. The herbaceous matrix of these landscapes was apparently comprised of a no-analogue mixture of taxa characteristic of steppe, tundra and temperate grasslands. Given the high insolation, the relatively high NPP [net primary productivity = primary biomass] simulated by the model may accurately reflect highly productive no-analogue herbaceous vegetation. Such vegetation, with scattered trees or woodland stands, might plausibly have provided the primary production necessary to support the large grazing and browsing herbivores…" [14: 99].

"It must, therefore not be assumed that the glacial environmental conditions in mid-latitude Europe were similar to those of northern Canada, Lapland and Siberia today." [14: 81].

Simulations of biomes are regarded as a failure by their authors [14], but not simulations of the bioclimatic variables, representing insulation and NPP, which do not necessarily determine present-day biomes. Consequently, among the simulated climatic variables, we used the hottest and coldest months of the year, which make it possible to calculate an index of insolation and warmness, called effective temperature (ET; [2,6]), and the net primary productivity (NPP, termed net annual above ground productivity, NAGP, in [6: 79]), available in the ethnographic database. The uniformitarian assumption predicts that, for reasons of evolutionary ecology, the demographic geographical pattern of the Upper Paleolithic (UP) in Eurasia, especially latitudinal, would be similar to that observed in ethnographic HGs living under roughly similar environmental conditions. We do not know the UP demographic pattern, since we are trying to estimate it, but we do know the pattern of the accompanying co-variables, such as the correlation between higher latitudes and more elaborate technology or a higher proportion of meat in the diet [27]. These two variables fit the uniformitarian prediction [19]. Along with latitude, climate is the other exogenous cause of demographic variation. Moving on to the UP demography, an HG ethnographic reference sample is thus necessary, as it is supposed to express the relationship between climate and demography. This sample is represented by ethnographic demographic data from North America, before contact with the West [6,13,20]. Adding to this theoretical reason is the historical filiation of the economic systems of the Late Glacial Eurasian HG and North-American ethnographic populations, resulting from an expansion of the recolonisation area that began in the Late Glacial. Around 20 ka BP, the continuum of HG in the mean and high latitudes in Eurasia expanded into North America, reflecting a relationship between demography and climate. This relationship must have been robust since it conditions the stability of the metapopulation over a very long period. For historical reasons, only the American side of the continuum has reached us via ethnography. It is therefore natural to assume that the best demography-climate information for the extinct Eurasian metapopulation is provided by the surviving American part of the ethnography.

A bias can appear in the ethnographic HG data for two main historical reasons: (i) contamination of the economic system of the HG populations by that of horticulturist-farmers (HF), (ii) epidemic impact of contact with the west (1492 AD). At the time of contact, the majority of HG ethnographic populations were at the stage of simple sporadic exchange with HF populations [25], the latter being localized in the south–south-west of North America. The functioning of the HG populations, in terms of economic production and territoriality, was therefore scarcely influenced by the HF.

The epidemic impact of the western contact, whether direct or indirect and pre- or post-contact, on the ethnographic demographic density at the time of the contact and on the possible under-evaluation that results, has given rise to much discussion. The prevailing view is that there were no continent-wide or pan-regional epidemics during the 16th century (for a summary, see [22,24,26]), for reasons that were at once geographical (barriers of buffer zones or deserts in the southwest and southeast), sociological (numerous HF populations vs small HG populations) and colonial. The numerous HF populations in the south-west of North America were more affected than the smaller HG populations in the high latitudes. A moderate impact of western contact on the evaluations, tending towards under-evaluation, is therefore possible. Among the various demographic evaluations, we chose to work with the highest (given by [6]). On the other hand, it is also possible that an intensification of hunting productivity, during the 10 ky between the Late Glacial and the XVIIth AD the present, slightly raised the ethnographic demographic density. We do not know whether these two hypothetical influences, both undoubtedly moderate, may have offset each other.

A comment is needed here: in the ethnographic data, to estimate the size of a population territory of HG from the information they provide, there is an ideological and practical difficulty, which can be summarized as:

> "Tenure in hunting gathering societies is not a surface area, but of sites and paths within a landscape" [15: 153].

This points to a possible difficulty in estimating a demographic density per unit area in a one-dimensional space rather than per two-dimensional unit area on a surface. Nevertheless, from heterogeneous ethnographic data, theoretically predictable relationships are observed, such as pluviometry and demography [7] or percentage of hunting and territory size [18: Figs. 4–8]. It is very unlikely that these coincidences are accidental. It can therefore be assumed that the ethnographic data, representing an enumeration per unit area, are correct overall. We do not have any other ethnographic data providing the size of the areas in which the HG populations lived. It is likely that ethnologists were not unaware of these questions of territory and integrated them in their estimates of densities. If not, we need to find other improbable evidence of ethnographic census data. In a critical study on the use of HG ethnological analogies, Stiles [25], taking a prehistoric perspective, considers the groups of sub-Arctic HG as a

> "fairly reasonable analogue for the settlement and subsistence patterns of northern European Late Pleistocene humans" [25: 58]

The demography of anatomically modern humans (AMH), under specified ecosystem and production system conditions, could not have been of a radically different nature to that of other groups of AMH living under roughly identical conditions.

2. Archeological data and demographic inference

To estimate demographic variables, it seemed natural to use the space-time distribution of archaeological remains. The following hypotheses were set forth:

(i) After more than one century of excavations, i.e. of information extraction by archaeologists, archaeological pressure is roughly uniform across Europe,
(ii) For an homogeneous cultural period: the density of the archaeological remains is roughly proportional to that of the population,
(iii) There is a linear and uniform relationship between the density (numbers per unit of time) and the distribution (location on the map) of archaeological information and population density and its distribution,
(iv) The variation in generating populations corresponds to the variation in density and archaeological distribution over space and time.

A question arises as to the validity of hypothesis (i) above. Does the space-time heterogeneity of the observed distribution of the archeological sites represent the effect of heterogeneous historical conditions of archaeological practice among European nations, rather than the traces, in cumulative density, of the metapopulation's activity during different periods? The number of archeological sites contained on Earth is not inexhaustible. Underlying geological sediments, are finite distributions of sites. Under the hypothesis of a roughly uniform pressure of archaeological discoveries on the map, covering a sufficiently long time period and a finite number of remains, one must expect that the characteristics of unobserved distributions will eventually appear, including in particular one very simple characteristic: exhaustion of the distributions. Fig. 2 shows the distribution histograms of the years of discovery, from the earliest until 1990, of 979 archeological sites from the sample obtained from the literature, in three major regions in Europe: France (for reasons of historical antiquity and density), the rest of Europe and the European part of the former USSR. After more than 120 years of archaeological pressure, starting at an earlier or later time according to region, a very similar distribution pattern of discoveries is evident. This is characterized by a period of continuous increase in discoveries, with some fluctuations in France, culminating in 1950–1970 in the three regions and followed by a general decline. We interpret this decline in discovery frequencies as a signal of the exhaustion of distributions, and the simultaneity of the signal in the three regions as an indication of archaeological pressure becoming roughly uniform over the duration. Fig. 2 suggests that sites still to be discovered will not fundamentally modify the space–time pattern of the sites which have already been found.

The geographical distribution of remains makes it possible to delimit areas occupied by populations, i.e. territories (see below). Chronological variations in the size of areas (expansion or contraction) are indicative of population sizes and their geographical kinetics. Space–time variations in densities and archaeological distribution allow us to infer demographic parameters, in particular for growth rates. The density of archaeological information can be expressed in different ways, depending on which cultural items per unit area are of interest to the study, e.g. whole sites, "small" sites, "large" sites, enclosures, cemeteries, etc. In this study, the unit of information is the whole archeological site divided into small and large sites.

According to hypotheses (i) and (ii) above, a succession of growth rates is obtained from the inter-period growth proportion in space–time densities of the archeological sites (total). The succession is considered to be that of the metapopulation. Then, from a reference ethnographic demographic density assigned to the most recent prehistoric period of the Late Glacial, the demographic densities of posterior periods are obtained by successively retro-projecting the growth rates onto the corresponding demographic densities. For each

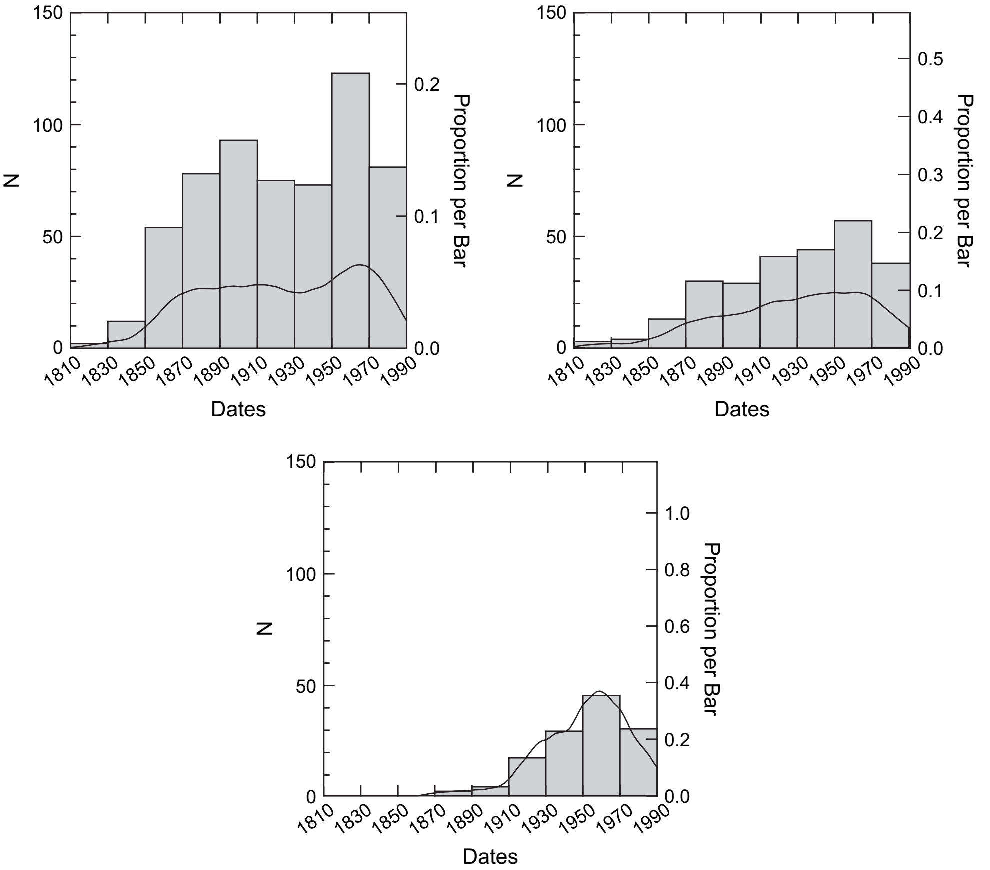

Fig. 2. Chronological distribution of the discovery year of 979 archeological sites from the Upper Paleolithic, in three major geographical zones in Europe. From left to right: France: 593 sites; rest of Europe: 259 sites; former European USSR: 127 sites. The curve represents the Loess fit (tension $\alpha = 0.5$) of the original distribution of density of discovery years in the chronology.

period, demographic size is then obtained by multiplying the demographic density by an area size, i.e. the size of the population territory of HG. Two estimation difficulties arise here: (i) the reference demographic density from which the series of estimates is initiated, which was discussed above, (ii) the size of the population territory in each time period.

During isotopic stage 3, because of cooling and isostatic variation, emersed land areas were appreciably larger than now. The coastlines, which were used to determine the size of past areas, are those corresponding to IOS3 climatic simulations. We have taken the hypothesis that the size of the territory on which the HG populations were distributed is roughly identical to that of the distribution area of the archaeological sites that these populations produced. For a given period, the archaeological area is obtained by modelling the geographical distribution of sites, using bivariate non-parametric kernel density estimators (Epanechnikov function, proportion $\alpha = 0.5$). The variation in proportion parameter α of the kernel function, i.e. of the quantity of information taken into account in the window of the local estimate, in the range of $\alpha = 0.5$–0.4, has only a slight effect on the modelling. Smaller values for the proportion parameter ($\alpha = 0.3$ and 0.2) have the effect of coming closer to the fluctuations of the local density of points by the kernel function, and thus narrowing the size of the archaeological area; an increase in $\alpha > 0.6$ has the opposite effect. The values $\alpha = 0.4$–0.5 seem reasonable empirical values to express the local detail of the site density while integrating the configuration of the overall pattern of dispersion. Next, the modelled distribution of the geographical density of sites is superimposed over the maps of IOS3 bioclimatic simulations: the warm episode in the Late Glacial and Aurignacian, the 21 ky for the Glacial Maximum and the Gravettian. The limit of each modelled distribution, minus the areas possibly occupied by the sea, represents the *archaeological territory*. By using a kernel function, the limits of the archaeological territory are as close as reasonably possible to the geographical distribution of sites, the only direct tangible data likely to indicate a territory.

The estimation procedure is therefore as follows:

1 *Reference demographic density:* An ethnological reference demographic density is estimated, with its confidence interval (CI95%), and assumed to represent the mid-Late Glacial. The Late Glacial is represented climatically by the warm simulation produced by the IOS3 project.
2 *Growth rate:* Growth rates are calculated for the three inter-periods of archeological site densities in space and time.
3 *Back-projection of the growth rates onto the reference demographic density:* From the reference demographic density and its CI95% estimated for the Late Glacial in step 1, the demographic densities (per 100 km^2) and their corresponding CI95% were calculated for each of the mid-periods following the Late Glacial, by back-projection the growth rates obtained in step 2.

For each period:

4 *Size of the total area in mid-period:* This is the archaeological territory obtained by the procedure described above.
5 *Meta-population size:* The densities estimated in step 3 were multiplied by the corresponding archaeological territories obtained in step 4.

These steps are detailed below.

2.1. Reference demographic density estimated for the Late Glacial (number of inhabitants/km^2)

The bioclimatic area occupied by the continuum of North-American ethnographic foragers is large (see [6,18]). Within this area, a demographic zone of reference was circumscribed starting from a bioclimatic criterion. A group of HG was selected if its variables NPP = NAGP (called NPP hereafter) and ET fell within the boundaries that are estimated as viable for the Late Glacial. As indicated above, these variables are regarded as realistic by their authors. To determine the viable limits for the Late Glacial, the geographical distributions of archeological sites from this period and the bioclimatic variables ET and NPP simulated were superimposed. The rounded-up minimum and maximum values for the boundaries of the bioclimatic variables were determined so as to take in roughly 90% of the geographical distribution of the archeological sites (see Fig. 3), i.e. $10. \le \text{ET} \le 12.50$; $150 \le \text{NPP} \le 350$.

Five HG groups fell within these boundaries, out of more than 300 given by Binford [6], after eliminating mounted hunters, who did not exist in the Late Glacial. In these groups were the Harney Valley Paiutes, located after forced displacement in 1879. This group was not retained. The 4 selected groups are given in Table 1. Their densities can be regarded as demographic samplings of a distribution of unknown but estimable densities, in the area between the ET and NPP boundaries. We know that the population sizes, and therefore also their densities, are log-normally distributed [21]. From the n (= 4) samples, the parameters (maximum likelihood estimates) of lognormal distribution (Shapiro–Wilk test statistic for normality = 0.8876, p-value = 0.3725) are $\mu = -0.32595$ for the average and $\sigma = 0.58341$ for the standard deviation.

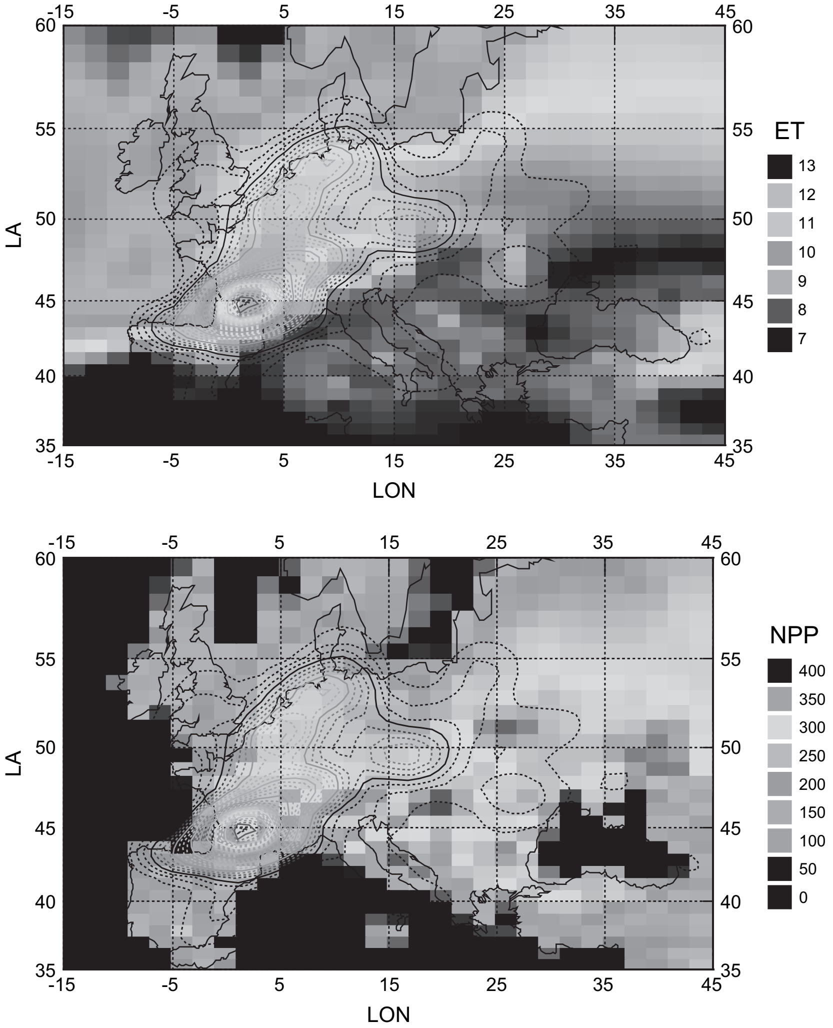

Fig. 3. Density of the geographical distribution of 1699 archeological sites from the Late Glacial, smoothed by a kernel function (Epanechnikov function, tension $\alpha = 0.5$), superimposed over bioclimatic variables from the simulation of a warm "Dansgaard/Oeschger" episode typical of IOS3. Top: effective temperature (ET) calculated from the hottest and coldest months of the year; bottom: net primary productivity (NPP). The dark continuous line for site distribution contains approximately 90% of the distribution; the outer dotted line contains 100% of the site distribution.

The limits of the confidence interval $1 - \alpha = 95\%$ of μ are given by a Student distribution: $\mu \pm t_{\alpha,\ n-1}\sigma/\sqrt{n}$, which, in terms of demographic density (to 100 km^2), produces an average of 0.722 inhabitants and lower and upper limits of IC95% of 0.285–1.825 inhabitants, respectively (see Fig. 4). The sample of 4 ethnographic reference groups is very small. For comparison, we also took the average demographic density of 0.99 inhabitants (per 100 km^2) obtained from the 10 ethnographic groups for the vegetation class called "*Dry boreal parkland (BPK-23)*" by Binford [6: 96 and 147], although we do not have the individual values. This figure of 0.99 inhabitants (per 100 km^2) is within the limits of IC95% of the reference density distribution and corresponds to 71% of its cumulative density (as against 50% for the average figure of 0.722).

Table 1
Reference ethnographic sample [6]

Ethnic group	Population size	Area ($\times$100 km^2)
Chippewyan	2850	6194
Han	1000	550.8
Mountain	780	1000
Naskapi	400	960

2.2. Growth rate

The space–time density of the archeological sites in a period t, D_t, is obtained by dividing the number of sites, N_t, by the duration of the period, d_t, and by the size of the coinciding zone, s_t (delimited by current

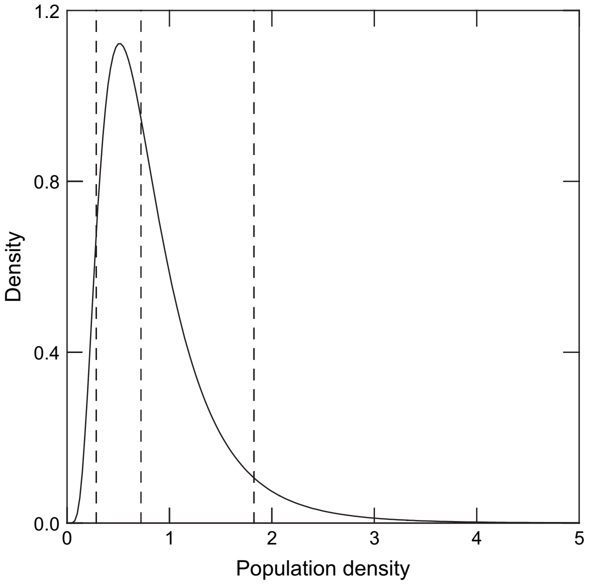

Fig. 4. Lognormal distribution of demographic densities (for 100 km^2), with sampled average and standard deviation $\mu = -0.32595$ and $\sigma = 0.58341$, respectively. In terms of demographic density, the three vertical dotted lines represent, successively from the right, the lower limit of the confidence interval at 95% (IC95%) for the average, the estimated average and the upper limit of IC95%.

coastlines minus islands; [4,5]). The density is therefore $D_t = N_t/d_t s_t$, which can be interpreted as an average geographical density in mid-period. The proportion of growth, from period $t-a$ years to period t, is given by $\lambda = D_t/D_{t-a}$, from which the growth rate $r = \lambda^{1/a} - 1$ is obtained.

The data from which the growth rates were computed are given in Tables 2–5 (see Fig. 1). These growth rates are very low (of the order of 1.0 E-5). Such rates are not always calculable in contemporary data. Total growth rates range from 1 to 5 per hundred thousand in the Aurignacian/Gravettian to 17 per hundred thousand during the Glacial Maximum/Late-Glacial expansion (Tables 3 and 4). In spite of a very strong climatic constraint beginning at the very start of the Upper Paleolithic, the metapopulation remained quasi-stationary from the Aurignacian to Glacial Maximum, growing only slightly.

The growth rate is multiplied by 3.5 in the Late Glacial. The growth rates for "large" and "small" sites show an interesting variation in relation to each other. Whereas the number of small sites increases or remains quasi-stationary from the Gravettian to the Glacial Maximum, that of the large sites decreases (see Table 4). This is in fact the only time when a reduction is observed in the data. How should we interpret this reduction? In the ethnographic data, it is well known that the sociological pattern of fusion–fission among HG follows a seasonal pattern, with fusion in seasons (periods) of abundance and fission in seasons (periods) of scarcity. This pattern of dispersion is interpreted as an intention to maximize the relationship with resources, which become micro-local during periods of scarcity. By analogy, the natural interpretation of the negative growth rates for the large sites at the Gravettian-Glacial Maximum is that, under the glacial constraint, the metapopulation tended to become distributed into smaller groups, on average, than during the previous period.

2.3. Back-projection of growth rates onto the reference demographic density

To estimate demographic densities for the periods before the Late Glacial, the growth rates (total dataset) were back-projected sequentially from the reference demographic density of the Late Glacial. Calculations and results are given in Tables 4 and 5.

2.4. Total area size in mid-period

The size of the archaeological territory is taken to represent the area in which the metapopulation is distributed.

2.5. Size of the metapopulation

Due to the uncertainty as to the reference ethnographic demographic information, the confidence interval CI95% is relatively large. From the Aurignacian to the Glacial Maximum estimates range from 4500 to 38,000 inhabitants to 11,300–72,600 inhabitants in the Late Glacial, with average values ranging from 4400 to 5900 inhabitants until the Glacial Maximum, then rising to 29,000 inhabitants in the Late Glacial. These figures

Table 2
Distribution of the archeological sites during the four periods

	Dates BP (ky)	Dates calibrated[a] (ky)	Duration calibrated (years)	Number of large sites	Number of small sites	Total sites
Aurignacian	40.0–29.0	40.36–31.04	9320	39	436	475
Gravettian	29.0–22.0	31.04–23.50	7540	49	346	395
Glacial Maximum	22.0–16.5	23.50–17.18	6320	27	365	392
Late Glacial	16.5–11.5	17.18–11.36	5820	130	1569	1699
Total				245	2716	2961

[a] Jöris and Weninger [16,17].

Table 3
By period, area sizes of the coinciding zone and of the archaeological territory

	Coinciding zone ($\times 100\ \text{km}^2$)	Archaeological territory ($\times 100\ \text{km}^2$)	λ large sites (‰)	λ small sites (‰)	λ total sites (‰)
Aurignacian	24,200	26,332	–	–	–
Gravettian	22,800	26,100	1.64837	1.04115	1.09100
Glacial Maximum	19,200	22,900	0.78064	1.49453	1.40597
Late Glacial	32,800	39,800	3.06056	2.73244	2.75504

λ-value of the proportional increase in archaeological sites between periods in the coinciding zones.

Table 4
Estimated growth rates (r) between periods in the coinciding zones

	Interval between calibrated mid-periods	Large sites (r)	Small sites (r)	Total sites (r)
Aurignacian–Gravettian	8430	5.9e–005	4.8e–006	1.0e–005
Gravettian–Glacial Maximum	6930	–3.5e–005	5.8e–005	4.9–005
Glacial Maximum–Late-Glacial	6070	0.00018	0.00016	0.00017

are of the same order of magnitude as those already estimated for a smaller area of the European Northern corridor [4,5].

3. Discussion

The site distribution represents the cumulative space density over a period. Its boundaries are therefore those of its maximum rather than of its average dispersion. These two boundaries may coincide if the area stays the same, which is not very likely. We do not see what we should do here to express the average area. The effect of using the archaeological territory over the demographic estimate would be an over-estimation of the metapopulation size. Fig. 5 shows the average demographic estimates fitted to the 3D space-time densities of archaeological sites on a square grid $2.5° \times 2.5°$, smoothed by a the same kernel function as described above. Several archaeological accretion zones appear, which are therefore also demographic. During the Aurignacian and Gravettian, the locations and the overall geographical pattern of the accretion zones are practically identical, with a main zone located in present-day Aquitaine (zone 1) and 3 other smaller zones, located respectively in present-day Belgium (zone 2), north of the Carpathians in Moravia (zone 3) and along the River Don (zone 4). From the centre of the zones, geographical distances as the crow flies are, respectively, 714 km (zones 1–2, Aquitaine–Belgium), 864 km (zones 2–3, Belgium–Moravia), 1337 km (zones 1–3, Aquitaine–Moravia) and 2800 km (zones 1–4, Aquitaine–Don). The geographical distance between zone 1 (Aquitaine) and a zone 5 which appears in southern Spain during the Last Glacial Maximum is 890 km. These accretion zones are geographically quite distant from each other, for hunters–gatherers who could only travel on foot must and therefore correspond to local populations. There is a strong continental gradient in all the periods. To within one factor, according to assumption (iv) given above, these four graphs represent the space–time density of the metapopulation and its settlement kinetics, in particular for contraction/recolonisation during IOS3, on a chronological resolution scale of about 7.25 ka.

With time, archaeological information tends to degrade. All other factors being equal, old sites are rarer than recent ones. There is therefore a possibility that the growth rates obtained mainly reflect the loss of archaeological information over time, so that this loss becomes a confounding variable that obscures possibilities for estimating the growth rate. It should be pointed out, however, that the markers of archeological sites are those of lithic industry, which are highly resistant to physical decay. Fig. 6 shows the cumulative sum of the sites with the time. Assuming a linear loss of archaeological information over time, the accumulated archaeological information should be chronologically aligned. This hypothesis was rejected, but only at the limit of the usual of significance ($r^2 = 0.853$, $F = 11.602$, $P = 0.0764$). It is therefore not rejected absolutely.

The distribution of the archeological sites in space and time over four major chronological periods does not allow demographic analysis to a resolution of less than about 7.25 ka, which is relatively coarse. This analysis thus expresses a long-term demo-geographical trend. Recently, the chronological distribution of 14C dates

Table 5
Estimated size of the metapopulation in four chrono-typological periods

	Demographic density ($100\ \text{km}^2$)			Population size		
	Average	Minimum, –CI47.5%	Maximum, +CI47.5%	Average	Minimum, –CI47.5%	Maximum, +CI47.5%
Aurignacian	0.168	0.066	1.077	4424	1738	28,359
Gravettian	0.183	0.072	1.172	4776	1879	30,589
Glacial Maximum	0.257	0.101	1.646	5885	2313	37,693
Late Glacial	0.722	0.285	1.825	28,736	11,343	72,635

has been used as a proxy for timing and settlement between regions during the Late Glacial in Western Europe [11,12]. The chronological resolution of the distribution of 14C dates (<0.5 ka) is much higher than the chrono-typological resolution used in this study. But it may be assumed that these distributions are partially biased by historical archaeological practices (regional or national) relative to 14C dating. For example, the Paviland cave, which contained a few hundred tools [9], has produced 54 14C dates [1], while the Madeleine cave, with thousands of tools in 23 principal layers, has produced only 4 dates [8]. This has even led to a paradox in which the most important archeological sites of the Upper Paleolithic, in terms of the quantity of space–time information, undoubtedly provide proportionally fewer 14C dates than the less important sites. Nevertheless, the signal-to-noise ratio seems favorable when it is based on hundreds of geographically dispersed data, and the approach seems robust enough to detect major population-related events. However, noise increases as

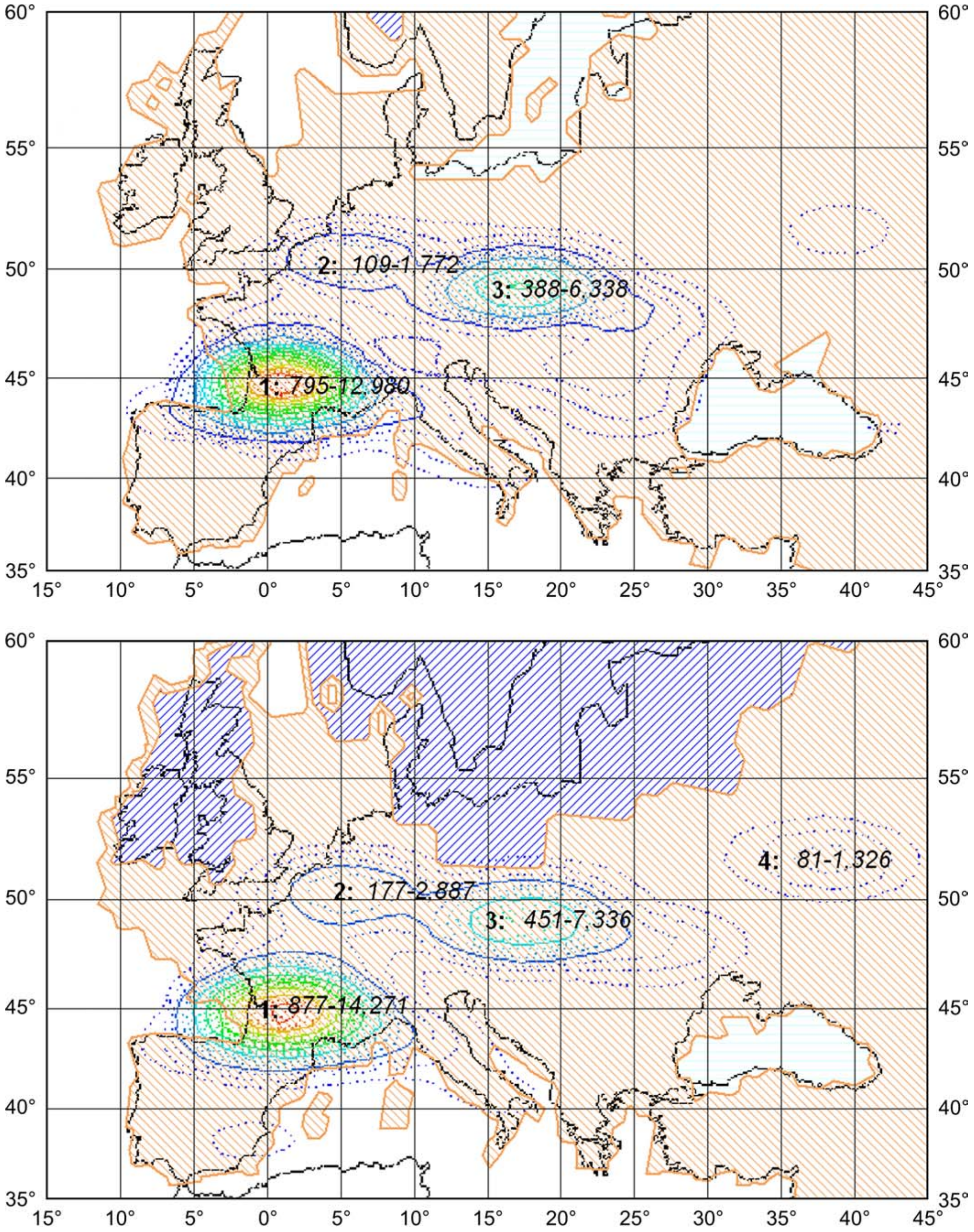

Fig. 5. Estimate of the regional distribution of the metapopulation of hunter–gatherers during four periods of the Upper Palaeolithic in Europe, superimposed on the IOS3 project maps. From top to bottom: Aurignacian, Gravettian, Last Glacial Maximum and Late Glacial. The boundaries (in black) of the accretion zones, with the corresponding numbers, account for roughly 90% of the distribution of the local population.

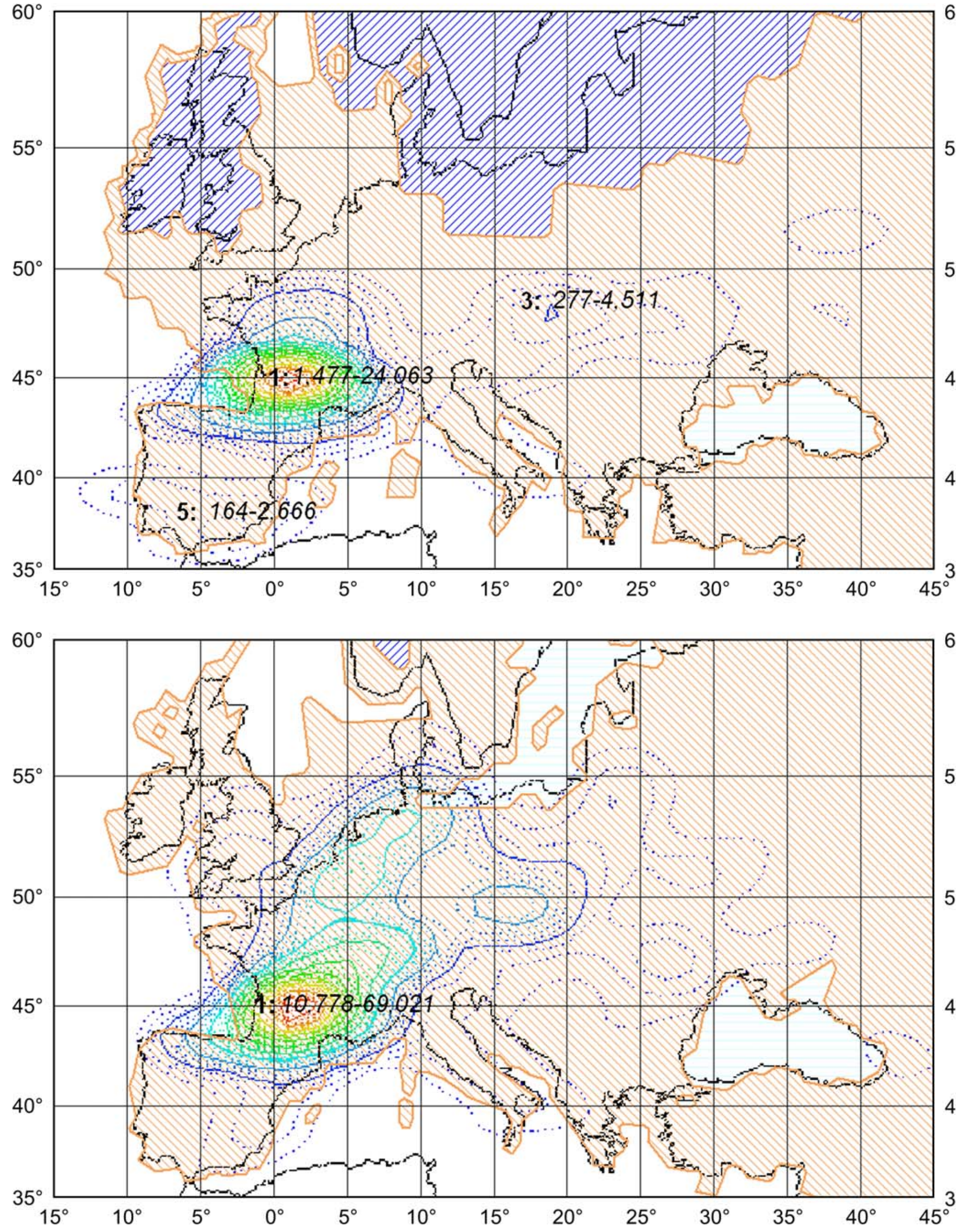

Fig. 5 (*continued*)

the quantity of data decreases. To decrease the noise, the sample size has to be increased but in addition, the number of 14C dates of an archeological site should be weighted by the quantity of information that this site represents relative to the others. In sum, the archeological sites, dated or not, give better geographical sampling but with relatively low chronological resolution, while 14C dates produce a much better chronological resolution but with less control over sampling quality over space and time.

This study did not take into account the rapid DO climatic fluctuations during IOS3, which were brought to light by core samples from Greenland (GISP2) [29]. A DO fluctuation may have produced a temperature fluctuation of about +10 °C in 250 years, i.e. in the context of IOS3, a sudden warming followed by cooling. On the ice-barriers, because of their mass, the DO effect was gradual, i.e. there was no significant rise in sea level. But the DO effect on vegetation and ungulate herds, which react rapidly, was not necessarily gradual. During the DO events, a kind of pulsation of primary and secondary biomass should therefore be considered. This would have been multidirectional, moving towards new, rapidly recolonised ecological zones, but would mainly

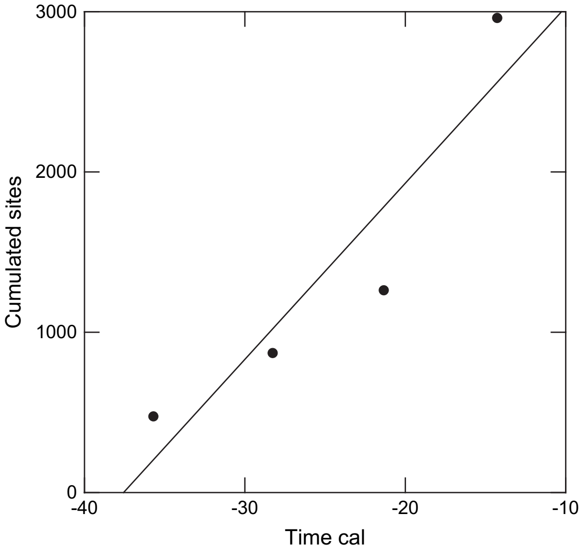

Fig. 6. Cumulative sum of the sites over time. Assuming a linear loss of information over time, the data points should be aligned. The relationship is at the limit of the usual level of significance ($r^2 = 0.853$, $F = 11.602$, $P = 0.0764$).

have run in a north–north-easterly direction before returning towards the initial zones after about 250 years. Archaeological traces of these pulsations should be found at the geographical limits of the occupied areas, which would possibly be represented by isolated sites far away from the areas of usual settlement. Without 14C dates, these events cannot be detected in the archaeological data. From 37.5 ka BP to 20 ka BP, two DO events are recorded. It is difficult to measure their demographic impact, which may tend towards failed recolonisation followed by a withdrawal. Dated sites, which could be contemporary with these DO events, should be re-analysed as sites showing evidence of a massive ecological crisis.

The archaeological data show traces of a considerable population expansion during the Late Glacial. What were the main sources of this expansion? The most likely candidates are the Aquitaine and the Cantabrian Pyrenean zones, due to the high density of archaeological sites at the Glacial Maximum. We should indicate that recently published genetic mtDNA data [10,28] show variant frequencies centred on the south-west of France and the north-east of Spain. This is interpreted as evidence of recolonisation after the Glacial Maximum at around 14.4 ± 4.8 ka. Finally, it seems that relics of a proto-language, Vasquon, are widely distributed in Europe, and draw their source in the Basque area [31]. The genetic and linguistic data both point to the same geographical regions. There are grounds for considering that the Aquitaine and French-Cantabrian refuge zone, which is well attested by archaeology, may have been the principal source of these data, in other words of Late Glacial recolonisation.

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