

Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe

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Abstract

The vegetation and the climatic context in which the first hominins entered and dispersed in Europe during the Early Pleistocene are reconstructed, using literature review and a new climatic simulation. Both in situ fauna and in situ pollen at the twelve early hominin sites under consideration indicate the occurrence of open landscapes: grasslands or forested steppes. The presence of ancient hominins (*Homo* of the *erectus* group) is only possible at the transition from glacial to interglacial periods, the full glacial being too cold for them and the transition interglacial to glacial too forested. Glacial-interglacial cycles forced by obliquity showed paralleled vegetation successions, which repeated c. 42 times during the course of the Early Pleistocene (2.58-0.78 Ma), providing 42 narrow windows of opportunity for hominins to disperse into Europe.

The climatic conditions of this Early Pleistocene protocratic vegetation are compared with a climatic simulation for 9 ka ago without ice sheet, as this time period is so far the best analogue available. The climate at the beginning of the present interglacial displayed a stronger seasonality than now. Forest cover would not have been hampered though, clearly indicating that other factors linked to refugial location and soils leave this period relatively free of forests. Similar

situations with an offset between climate and vegetation at the beginning of interglacials repeated themselves throughout the Quaternary and benefitted the early hominins when colonising Europe.

The duration of this open phase of vegetation at the glacial-interglacial transition was long enough to allow colonisation from the Levant to the Atlantic.

The twelve sites fall within rather narrow ranges of summer precipitation and temperature of the coldest month, suggesting the hominins had only a very low tolerance to climate variability.

Key words

Vegetation, climatic modelling, Early Pleistocene, hominin dispersal, Europe, pollen

1 Introduction

As *Homo erectus* groups left Africa via the Levant and as they reached SW Turkey, they entered a completely new world, unfamiliar to them and to which they had to adapt. What were the vegetation and the climate at the sites where they first lived? Utilising palynology and climatic modelling, this paper attempts to establish the types of vegetation that would allow them to thrive and the climatic limits within which they subsisted in Europe and SW Asia.

One of the most frequent causes referred to for early hominins leaving Africa is climatic change in their homeland by aridification, for example the enlargement of the Saharan belt. This has been illustrated in the cores of ODP site 658, off the coast of Mauritania (21 ° N, 19 ° W) (Leroy and Dupont, 1994; Dupont and Leroy, 1995). The main steps of aridification identified in that long pollen record (3.7 to 1.7 and 0.7 Ma to the present) are 3.5-3.2 and 2.6 Ma ago. For East Africa, much less palynological information is available. Bonnefille (1995) has summarised the numerous attempts at extracting pollen from hominin sites and concluded on aridification steps at 3.2, 2.35 and 1.8 Ma.

Figure 1 here

H. erectus, or perhaps *H. habilis*, are the first hominins to occupy Europe with a date of arrival that is still debated but probably around the Olduvai subchron (1.94-1.79 Ma) (Lordkipanidze et al., 2007). However because of the scarcity of sites causing a strong sampling error, it is possible that this first arrival occurred earlier, but probably not before the Gauss-Matuyama transition at 2.58 Ma (Mithen and Reed, 2002). The main periods of mammal migrations out of Africa have been linked to periods of rapid environmental changes. The most important one is at 2.58 Ma. This date is now recognised by the International Commission of Stratigraphy as the start of the Quaternary and the Pleistocene (Leigh Mascarelli, 2009). It corresponds to the “Elephant-*Equus* event” (Arribas and Palmqvist, 1999). The next most important period of change is from the Jaramillo subchron (1.19-0.99 Ma) to the Matuyama–Brunhes transition (0.78 Ma). It corresponds to the “end-Villafranchian” dispersal Event (Arribas and Palmqvist, 1999). From the faunal point of view, an additional event, i.e. the Wolf event or *Homo* event, is recognised, that is however not significantly marked in climatic changes. The arrival of several African carnivores is recognised in Europe, including the genus *Homo*, at 1.8-1.6 Ma with

Asian ruminants ([Arribas and Palmqvist, 1999](#)). These major mammal turnovers were accompanied in East Africa by aridification ([Arribas and Palmqvist, 1999](#)). These main steps fit well the conclusions drawn from pollen analyses.

In order to survive in the colder climates of Europe, one would benefit from the use and control of fire. No evidence of the use of fire has however emerged so far from the Early Pleistocene sites of Europe. One has to wait until the Middle Pleistocene for controlled use of fire (e.g. 400 ka ago in [Gowlett, 2006](#)). However in northern Israel, evidence, such as burnt flints organised in recognisable patterns linked to hearths, shows that hominins could start a fire by 790-690 ka ago ([Alperson-Afil, 2008](#)). During the end of the Early Pleistocene, the first signs of active hunting emerge. Clear instances of hunting have been identified in the fauna of Atapuerca, Gran Dolina, TD6 ([Villa and Lenoir, 2009](#)) (Figs 1 and 2). It has been suggested that occupation was at first intermittent, with populations dying out ([Dennell, 2003](#)).

Figure 2 here

As hominins colonised Europe they would minimise the changes they had to make in order to adapt step by step. One of the factors favouring their presence suggested so far is open landscape similar to African ones with large herbivore herds, such as bison and equids ([Dennell, 2003](#)). The presence of large carnivores has been suggested by some to be favourable as large sabre-tooth felids would have left flesh on carcasses that hominins could then access before smaller predators and scavengers ([Arribas and Palmqvist, 1999](#)). Others have seen these large carnivores as competitors that would have stopped the spread of hominins. In any case, large herbivore herds are a requirement for hominin survival, which themselves require open spaces for feeding and migrating.

Only few sites where the presence of ancient hominins has been confirmed are available, either in the form of skeletal or artefact remains. Twelve sites are considered in this study: Dmanisi in Georgia, Bogatyri in southern Russia, Pirro Nord, Ceprano and Ca' Belvedere di Monte Poggiolo in Italy, Le Vallonnet, Lunery-Rosières, Pont-de-Lavaud à Eguzon-Chantôme and Lézignan-la-Cèbe in France, Atapuerca (Sima del Elefante and Gran Dolina) and Orce (Barranco León and Fuentenueva-3) in Spain (references in Table 1). For their geographical positions see Figure 1.

Table 1 here

The aims of this paper are to:

- provide the vegetation setting for the Early Pleistocene (2.58 to 0.78 Ma) in Europe with emphasis on periods of vegetation cover opening;
- review what is known of the vegetation at the time and location of hominin finds; if no information is available in situ, information from the closest pollen sites were derived to get the best estimation for the in situ vegetation; and
- establish the climatic parameters which are common to the sites of ancient hominin occupation and that would represent the limits in which the hominins lived.

2 Vegetation setting for Early Pleistocene of Europe

Many review papers have dealt with vegetation in the Early Pleistocene ([Suc and Popescu, 2005](#); [Leroy, 2007](#); [Tzedakis, 2009](#)). Here, the focus is on showing that despite a dense forest cover during most of this period, the landscape opened up regularly, albeit briefly, during glacial times. There is an overall trend over the Early Pleistocene to slightly cooler conditions ([Lisiecki and Raymo, 2005](#)) reflected in the progressively longer periods of opening of the vegetation in the glacial periods.

For nearly two million years during the northern hemisphere ice ages, $\delta^{18}\text{O}$ fluctuations representing global ice volume had a periodicity of 41 ka ([Lisiecki and Raymo, 2005](#); [Ruddiman, 2006](#)). The numbering of obliquity-forced cycles in the Early Pleistocene in the oxygen isotope stratigraphy from marine oxygen isotope stage (MIS) 103 to 19 reflects the 42 glacial-interglacial cycles. In the eastern Mediterranean region, a vegetation record from Rhodos indicates that the forcing of the vegetation cycles is dominated by obliquity over precession ([Joannin et al., 2007](#)). At Semaforo, south Italy, spectral analyses on a pollen record have revealed a dominant obliquity forcing, modulated by precession ([Klotz et al., 2006](#)). Site ODP 658 (of the coast Mauritania) also indicates a predominant forcing on vegetation by obliquity during the Early Pleistocene ([Dupont and Leroy, 1995](#)). So from this brief review we can see that the fluctuation in the oxygen isotope curves have been paralleled in the vegetation. Therefore one may safely say that there were c. 42 cycles of vegetation change in the Early Pleistocene (Fig. 3).

Figure 3 here

Vegetation goes through consecutive phases of colonisation and succession from early interglacial to the end of interglacial periods (Leroy, 2007): eg in Semaforo, southern Italy (Combourieu-Nebout, 1993), and Nogaret, south of France (Leroy and Seret, 1992). The succession may be schematised as a sequence of open vegetation, dry open woodland, deciduous forest, mixed forest and humid conifer forest before returning to open vegetation (Fig. 3) (Leroy and Ravazzi, 1997).

The vegetation of the Early Pleistocene is characterised by closed forests over a large part of the climatic cycle, even in the southern peninsulas of Europe. The pollen records are for example 1) in Spain: Garraf 1, Bòbila Ordis and ODP 976, see also González-Sampériz et al. (submitted); 2) in France: Senèze, Ceyszac; 3) in Italy: Stirone, Semaforo, Lefte, Pietrafitta, Montalbano Jonico; and 4) in Greece: Tenaghi Philippon (references in caption of Fig. 1 and age span in Fig. 2). All have fairly closed interglacial vegetation with the exception of the marine site ODP 976 in the Sea of Alboran, which records both the open vegetation of S. Iberia and N. Africa. Tenaghi Philippon from its base at 1.35 Ma already shows longer steppic periods (glacials) than more western sites of the same age (Tzedakis et al., 2006). This reflects an eastwards gradient of increased continentality and aridity.

The interglacial-glacial transitions are characterised in many places by dense conifer forests (*Tsuga*, *Abies* and/or *Picea*).

The forests were open for two reasons (Fig. 3). First during the glacial periods, the low temperatures and/or arid conditions were the limiting factor. Glacial periods with nearly no trees have been recorded from the beginning of the Early Pleistocene; for example the glacials of Semaforo between ~2.46 and ~2.11 Ma (Klotz et al., 2006), the two glacial periods of Bernasso between c. 2.16 and 1.96 Ma (Leroy and Roiron, 1996), the glacial period of St Macaire in the late Early Pleistocene (Leroy et al., 1994) and the glacials of Tenaghi Philippon from 1.35 Ma (van der Wiel and Wijmstra, 1987).

Secondly the transitions to the interglacials were open because, despite improved climate conditions, trees needed time to come out of refugia. An open landscape with scattered trees (grasslands, steppes and/or forested steppes) at the transition from glacial to interglacial is visible in many diagrams, for example the forest-steppe of Tenaghi Philippon in north eastern Greece (Wijmstra et al., 1990), the open woodland at the beginning of the interglacial of Nogaret at 1.88 Ma (Leroy

and Seret, 1992), the forest-steppe of Leffe (Ravazzi and Rossignol-Strick, 1995), the forest-steppe phases of Senèze (Elhaï in Ablin, 1991) and the Mediterranean woodlands of Ceysac (Ablin, 1991) (Fig. 2).

In conclusion, it has been shown that the dense Pliocene forests opened up during 42 climatic cycles in the Early Pleistocene with progressively longer glacials leading to longer periods with open vegetation (forested steppe and open Mediterranean like woodlands) at the transitions between glacials to interglacials. Therefore windows of opportunity for hominin colonization were repeated and increased in length during the Early Pleistocene.

3 Vegetation at the sites of ancient hominin finds

This potential use of the open landscape at the glacial-interglacial transition by hominins to expand into Europe is in this section compared to information derived from the ancient hominin sites themselves, either from the fauna found at those sites, which can be diagnostic of an environment, or more directly from pollen spectra from hominin levels.

Figure 4 here

Table 1 lists the sites of hominin finds considered in this study. Some information on past environment can be derived already from the fauna found at many of those sites. For all the sites where faunal information is available (except Sima del Elefante in Atapuerca) (Fig. 4), the fauna indicates environments with diverse co-existent ecosystems (from steppe to forest), with forested steppe, or completely open environments. Based on this analysis, it is clear that the sites of early hominins were not located in dense forests.

Table 2 here

Table 2 presents a synthesis of vegetation reconstruction by palynology from the levels where hominin finds have been made. Hardly more than half the sites have delivered good quality pollen spectra directly associated with the hominin remains/artefacts. This is due to the taphonomy of these sites that is often not suitable for the preservation of pollen grains, which require anoxic conditions and fine-grained sediment for optimal preservation. The sites with pollen preservation reveal a rather open environment often of Mediterranean style. One exception is Eguzon-Chantôme, west France, where human settlements seem to have occurred

during forested interstadials or forested transition periods ([Despriée et al., 2006](#); pers. comm., Aug. 2009) (Fig. 4).

Table 3 here

Table 3 is an attempt to improve on the vegetation reconstructions made in the previous two tables by including information derived from other sites of the same age or similar ages that are in the vicinity of the hominin sites. Most of these other pollen sites are located 230- 300 km away, often in other ecosystems. For some hominin sites the closest good pollen sites are even further away, as far as ~600 km. Nevertheless the point is that most of those sites indicate that the climate was periodically changing in the region in the Early Pleistocene. They show periods of landscape opening in addition to the full glacial conditions. However the vegetation types for the exact time of nearby hominin settlements cannot be fully derived because of uncertainties in dating.

4 How many potential phases of expansion into Europe?

Speed and distance of migration are interesting to debate in relation to the length of favourable periods within a glacial-interglacial cycle (41 ka). [Lewin and Foley \(2004\)](#) have suggested that 16 km per *H. erectus* generation would be a reasonable average when travelling eastward along the same vegetation and climate zones. In their example it would have taken 25,000 yr to reach Java from East Africa.

Although other routes of migration to Europe have been mentioned, such as Gibraltar and Sicily, the Levant remains the most probable. For the colonisation of Europe from Africa, or, better, the northern tip of the Levant that can be seen as a northward projection of the vegetation and climate of Africa, a slightly slower speed of migration of 1 km per year or less is suggested because of the novelty of the environment and the need to adapt to it. To cover the distance from SE Turkey near the Syrian desert (e.g. Gaziantep) to Tbilisi (Georgia), 800 km, and from Gaziantep to Granada (S. Spain), 5200 km, it would have taken 800 and 5200 years respectively. Therefore even if a slightly longer time was necessary, this could easily be done within the optimal part of the climatic cycle (open). In other words, distance and speed of migration are not limiting factors. This speed of colonisation is in agreement with attempts using spatial ecology models to understand the arrival

date of hominins in Europe in terms of factors such as vegetation, continental configuration and distance from the African source ([Mithen and Reed, 2002](#); [Hughes et al., 2007](#)).

An expansion into Europe could have happened within each Early Pleistocene climatic cycle, which would have allowed recolonisation after the disappearance of the hominin population, or replenished a failing population (Fig. 3).

5 Climatic parameters shared by ancient hominin sites

Our analysis using climatic simulations done by Global Circulation Models aims at narrowing down the climatic parameters common to the twelve hominin sites. No climatic simulations using Global Circulation Models are however available at a reasonable resolution for the Early Pleistocene glacials, interglacials or intermediate periods. For the glacial-interglacial transitions, the next best time period would then be at 9 ka ago.

During the c. 42 climatic cycles of the Early Pleistocene, the ice sheets were smaller and a diverse range of different orbital configurations occurred. Moreover, the CO₂ content of the air is not known as the oldest ice core stops at 740 ka ago ([EPICA community members, 2004](#)). Therefore using the 9 ka simulation is not fully adequate, but is the best available, especially when modified to take into consideration the smaller ice sheets in the Early Pleistocene. What remains similar between the Holocene and other Quaternary cycles is the offset between the early climatic optimum and the later vegetation optimum.

5.1 Early Holocene climate

At the beginning of the Holocene, pollen analyses show the progressive colonisation of open landscapes by trees coming out of refugia ([Huntley, 1990](#)). This phase of colonisation is often termed a protocratic phase following the definition of Iversen ([Roberts, 2002](#)) and is characterised by open woodland over most of Europe.

Because of the distribution of the insolation over the planet at 9 ka, the climate of Europe is rapidly becoming warmer than now making it relatively drier than now in many places. [Renssen et al. \(2009\)](#) have suggested that the delayed melting of the Laurentide icesheet has counteracted this orbital warming by providing a cooler climate than otherwise expected. In a simulation for 9 ka using

the ECbilt model, Europe remains nevertheless clearly warmer by 1 to 5 °C than at present and shows an early thermal optimum (Renssen et al., 2009). The thermal maximum was earlier in south-eastern than south-western Europe (Renssen et al., 2009).

5.2 Comparison of the 9 ka glacial-interglacial transition and present climates

We used a 9 ka simulation with the atmospheric general circulation model ECHAM5 (resolution T31, 19 levels) coupled with the ocean general circulation MPI-OM (with 40 levels and a dynamic-thermodynamic sea-ice component) and a dynamic vegetation model (Mikolajewicz, 2009) in which only the earth orbital parameters and greenhouse gas concentrations have been changed, in order to be closer to Early Pleistocene conditions, i.e. without an ice sheet and its melting. In the discussion below, this simulation is called: 9kaMOD. The 0.5° grid climatology for the present was obtained from “the CLIMATE database version 2.1 (W. Cramer, Potsdam, pers. comm.)” (www.pik-potsdam.de/~cramer/climate.html) (Leemans and Cramer, 1991) for a simple downscaling of the low-resolution model results (Leroy and Arpe, 2007).

Figure 5 here

The results are the following. For the 9kaMOD simulations, temperature difference maps show cooler winters and springs (around 1°C) and warmer summers (exceeding 3°C in places), which means a higher seasonality than at present (Fig. 5). Annual mean temperatures are however hardly changed between the present and 9kaMOD (less than 0.5°C). Also the annual precipitation (Fig. 6) shows very small differences between the present and 9kaMOD. Wetter conditions of more than 2 mm/month (average for the year) were found only for the Middle East and the Atlantic west of Portugal, though only the increases south of Greece and Turkey are of significance. At the seasonal scale, spring is wetter all over Europe by up to 6 mm/month, which is, however, small compared to the actual amounts (Fig. 6). Wetter winters occur in the south of Greece and Turkey, reaching 10 mm/month, in areas of more than 50 mm/month. This hardly changes the patterns of total precipitation maps.

Figure 6 here

According to the 9kaMOD simulation, the climate then was not very different

from the present one, but with a slightly larger seasonality. The Koeppen diagrams for the hominin sites show very small differences between 9kaMOD and the present for precipitation but clearly warmer summers, perhaps by 3 °C (Fig. 7). All sites, except the two northern French ones, show slightly higher spring precipitation. Overall at 9kaMOD, the seasonality was higher.

Figure 7 here

After applying a simple down-scaling as done in [Leroy and Arpe \(2007\)](#), the temperature of the coldest month (Fig. 8, upper panel) shows the well-known gradient from south to north modified by continentality, i.e. with warmer winters in the west along the Atlantic coast and colder ones in the east. Also the orographic impacts are clearly indicated with cooler temperatures over high grounds. The hominin sites (indicated by circles) can be found in a relatively small belt with minimum temperatures between 0 and 6 °C except that in Georgia. The latter deviation from the norm is probably due to the fact that a 0.5° grid is too coarse for the highly structured topography in that area.

Figure 8 here

Another important variable for life is precipitation. In Fig. 8, lower panel, the summer precipitation (JJA) is shown after a down-scaling. One sees the typical maxima around the Alps, Carpathians and Caucasus and very low values around the Mediterranean, especially Arabia. As with the minimum temperatures, all hominin sites are gathered within a narrow band, for precipitation between 30 and 60 mm/month. As already demonstrated in Fig. 7, the climate at the hominin sites had no summer drought, just a summer minimum.

In the maps for the differences between the temperature of the coldest and the warmest month (not illustrated), the sites fall between values of 16 and 26 °C, which is a very large range. The two sites in eastern Europe show the largest range with values of around 26 °C, whereas the lowest range can be found at the sites in western France with only 17 °C. Because of this large variability in the temperature range between summer and winter, this variable seems to be only of small importance for hominin dispersal.

5.3 Hominin sites and simulated tree distribution

The two variables, minimum temperature and summer precipitation, have been successfully used by [Leroy and Arpe \(2007\)](#) as the main limiting factors for

summer-green tree growth. In the Early Pleistocene, the climate over most of the climatic cycle might have been different (shifted to higher temperatures by a few degrees) from the present and especially the glacial-interglacial transitions might have been warmer than those of 9kaMOD. The data shown here should therefore not be taken as absolute values. Nevertheless the patterns may have been similar.

Figure 9 here

The present and the 9 ka time are towards the middle between the glacial and the interglacial extremes. Earlier in the cycle, i.e. nearer the glacial period maxima, the climate would have been cooler and drier and the limits for tree growth would put the hominin sites nearer to the border line of possible tree growth that would be more favourable for their expansion. But at both 9 ka and now the hominin sites are in areas where forest could have been present according to the climate (Fig. 9), but not during the Last Glacial Maximum. This apparent contradiction between the model and the information derived from in situ floral and faunal observations, i.e. open landscapes, is further discussed in section 6.2.

6 Discussion

6.1 Quantification and simulation of climate in the Early Pleistocene

A quantification of the climate from vegetation using the 'Climatic Amplitude Method' suggests that the Early Pleistocene interglacials were a few degrees warmer than at present and similar to the Pliocene ([Fauquette et al., 1998](#)). In the Mediterranean marine pollen record of Semaforo (south Italy) covering the period from ~2.46 to ~2.11 Ma, the reconstruction reveals higher temperatures by at least 2.8 °C in annual mean and 2.2 °C in winter temperatures, and 500 mm more in annual mean precipitation during the interglacials as compared to the present-day climate ([Klotz et al., 2006](#)). During the glacial periods, temperatures are generally lower as compared to the present-day climate in the record of Semaforo, but precipitation is similar.

The use of the Mutual Climatic Range method on reptiles and amphibians at Gran Dolina, Atapuerca ([Blain et al., 2009](#)) reconstructs a temperature range of 10-13 °C and precipitation range of 800-1000 mm/year for the hominin levels. When compared with the down-scaled 9kaMOD values of 13.4 °C and 680 mm/year (Fig.

7), only a slight difference appears, which could result from the fact that the model data represent 0.5° grid mean values while the estimates from fauna findings are point values. Also one should not expect exactly the same climate at 9kaMOD as during the Early Pleistocene hominin settlement. Only a climatic model simulation for the Early Pleistocene glacial-interglacial transition validated by data would help to improve the present results using the 9 kaMOD.

6.2 Open woodland position in the Early Pleistocene vegetation cycles

The vegetation of Europe, even in its low latitudes, consisted for the most part of the glacial-interglacial cycles of dense forests, i. e. deciduous, mixed or coniferous. The glacials were characterised, although briefly, by a clear opening of the landscape. Rare exceptions to this have been noted, such as the site of Stirone in the Po valley which throughout its sequence shows more of the characteristics of a dense forest of the mid European forest and less those of a Mediterranean region ([Fauquette and Bertini, 2003](#)).

The next most open part of the climatic cycle, outside the severe conditions of the full glacials, is at the transition between glacials to interglacials. Interstadial periods should also be considered but they are less well documented in the pollen records of the Early Pleistocene.

A survey of the faunal and floral information derived from the sites of ancient hominin occupation indicates that most sites were indeed occupied during the glacial-interglacial transition in a climatic cycle. This suits their need to access large herbivore herds in open landscapes.

6.3 Causes for the open landscape

The vegetation was still open at the beginning of the Holocene interglacial as well as Early Pleistocene ones. The causes for this cannot be only climatic, as the model indicates that the climatic conditions were very favourable. The difference between the climate at the beginning and at the end of an interglacial is rather small, as we have just highlighted for the Holocene. The extent of possible tree growth for the present and 9kaMOD was plotted using the limits chosen by [Leroy and Arpe \(2007\)](#). All hominin sites lie well within the areas of high likelihood of tree growth, even for warm-loving trees (Fig. 9).

During the c. 42 climatic cycles of the Early Pleistocene, all possible orbital configurations occurred. This may have had an influence on the duration of the transition. But palaeodata show that the opening is a characteristic of most cycles (whatever the orbital configuration) and therefore other factors have contributed to delay the tree colonisation of this open landscape. The causes frequently cited for the early Holocene are such as rates of dispersals from refugia, location of glacial refugia, soil development and competition between species (Roberts, 2002; Leroy and Arpe, 2007). These causes also apply to the Early Pleistocene.

6.4 Climatic conditions at the hominin sites

Rolland (2001) has already suggested severe winters as a cause for the lag behind Asia for the peopling of Europe. Cold temperatures would have limited the expansion of hominins as they were still largely an African species. Moreover the first waves of colonisers did not have the control of fire yet. Our analysis indicates that the sites are located within the narrow limits of the temperature of the coldest month, i.e. T_{\min} , between 0 and 6 °C, with, therefore, very few days of frost, but with a distinctively cold winter.

Hominins also needed to have a continuous supply of meat from herbivore herds, obtained initially by scavenging and much later by hunting; so the summers should not have been too dry for plants growth, especially grass. On the other hand the climate should not have been too humid as otherwise a too dense vegetation would have stood in the way of herbivore herds.

Figure 10 here

What are striking are the narrow ranges of summer precipitation and of the temperatures of the coldest month, common to all sites (Fig. 10), while the temperature of the warmest month and the seasonality were of lesser importance.

The climate reconstructions (higher precipitation and temperature than today) made from pollen, reptiles and amphibians in absolute numbers diverged only slightly from the value extracted from the model simulation at the one available site and the narrow range of climatic conditions found for the twelve sites probably constitutes a robust result from this study. This information will be relevant for further attempts to refine the ecological niche of the *H. erectus* group.

6.5 Consequences for dispersal

In Asia, Dennell (2004) suggests that dispersal were probably intermittent, often discontinuous. Initially colonisation was confined to warm grasslands and open woodlands across southern Asia following the same climate and vegetation latitudinal band from the west to the east. Therefore the part of the climatic cycle that was favourable for hominin dispersal in Asia was probably longer than in Europe (owing to the similarity of the ecosystems), and came earlier in the Early Pleistocene (as requiring less adaptation).

The 9kaMOD simulation for Europe, having identified a narrow range of summer precipitation and of the temperature of the coldest month, indicates that, at the beginning of dispersals, only a narrow set of climatic factors were suitable to the early hominins. This suggests that hominins most likely disappeared from Europe as soon as the conditions deviated too much from the above and reinforces the hypothesis that the earlier occupation of Europe was only intermittent ([Bar-Yosef and Belfer-Cohen, 2001](#)), until they became able to adapt to a wider range of climatic conditions. New climatic, biological or cultural conditions, such as fire control, were required before they could permanently occupy Europe.

So far the archaeological evidence shows that intermittent colonisation occurred in the second half of the Early Pleistocene, but our analysis shows that it could have started earlier ([Hughes et al., 2007](#); [Scott and Gibert, 2009](#)) and happened up to 42 times within the Early Pleistocene. Moreover a narrow geographical corridor of optimal climatic and vegetation conditions has been identified where potential new findings are expected (Fig. 10).

7 Conclusions

The Early Pleistocene landscape of Europe was open at times of hominin occupation. This was found at glacial-interglacial transitions, not at the interglacial-glacial transitions.

The 9kaMOD climatic simulation, i.e. without an ice sheet and its melting to make it more similar to Early Pleistocene conditions, shows that, although climatic conditions were already favourable to tree colonisation, this was considerably delayed. The lag of the vegetation optimum behind the climatic optimum in each interglacial provided a window of opportunity for the dispersal of large herbivore

herds and hominins.

The offset between the climatic and vegetation optima repeated itself throughout the Quaternary and provided ideal conditions for the early hominins within each climatic cycle. The short window was nevertheless long enough to allow colonisation from the Levant to the Atlantic.

Dispersal events could have occurred 42 times during the course of the Early Pleistocene, until hominins became able to maintain themselves through the various climatic conditions of a full climatic cycle.

The early hominins probably had a narrow range of tolerance to climate variability. The corridor of optimal climatic conditions can be used to narrow down the area where further hominin sites should be searched for.

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10 Figure captions

Fig. 1: Location of the sites mentioned in the paper.

Circles for hominin sites –

B&F: Barranco León and Fuentenueva-3 ([Scott et al., 2007](#)), **Bg:** Bogatyri ([Bosinski, 2006](#)), **Cep:** Ceprano ([Manzi et al., 2001](#)), **D:** Dmanisi ([Gabunia et al., 2000](#)), **E:** Eguzon-Chantôme ([Despriée et al., 2009](#)), **GD:** Gran Dolina ([Cuenca-Bescós and García, 2007](#)), **L:** Le Vallonnet ([de Lumley, 1988](#)), **LC:** Lézignan-le-Cèbe ([Crochet et al., 2009](#)), **Lu:** Lunery-Rosières ([Despriée et al., 2009](#)), **MP:** Monte Poggiolo ([Falguères, 2003](#)), **Pir:** Pirro Nord ([Arzarello et al., 2007](#)), **Si:** Sima del Elefante ([Cuenca-Bescós and García, 2007](#)).

Triangles for sites with information concerning plants near hominin sites – **BN:** Bernasso ([Leroy and Roiron, 1996](#)), **BO:** Bòbila Ordis ([Leroy, 2008](#)), **Cey:** Ceysac ([Ablin, 1991](#)), **Ga:** Garraf 1 PII & PIII ([Suc and Cravatte, 1982](#)), **Le:** Lefte ([Muttoni et al., 2007](#)), **MJ:** Montalbano Jonico ([Joannin et al., 2008](#)), **N:** Nogaret ([Leroy an Seret, 1992](#)), **Pie:** Pietrafitta ([Lona and Bertoldi, 1973](#)), **Sem:** Semaforo ([Combourieu-Nebout, 1993](#)), **Sen:** Senèze (Elhaï in [Roger et al., 2000](#)), **SM:** Saint-Macaire ([Leroy et al., 1994](#)), **St:** Stirone ([Bertini, 2001](#)), **T:** Tenaghi Philippon ([van der Wiel and Wijmstra, 1987](#); [Tzedakis et al., 2006](#)), **976:** ODP site 976 ([Joannin, 2007](#)).

Fig. 2: Climato-stratigraphic framework for the sites of early hominin occupation in Europe and some key pollen sites mentioned in this paper ([Leigh Mascarelli, 2009](#); [Head and Gibbard, 2005](#)). CM: Cobb Mountain subchron. MIS: Marine oxygen isotopic stages. Site abbreviation see figure 1. Vertical dash line indicates the age of hominin findings with its range of uncertainty. Horizontal numbers indicate MIS stages when known.

Fig. 3: Vegetation cycles in the Early Pleistocene. Top: Schematic succession of vegetation in Europe during climatic cycles forced by obliquity. Middle: Optimal conditions (open vegetation but not cold) for hominin expansion in the boxes with heavy frame superimposed on climatic cycles. Bottom: Climatic cycles. Position of dispersal events from [Arribas and Palmqvist \(1999\)](#).

Fig. 4: Vegetation at the twelve hominin sites. The site in northern Spain represents 2 sites close to each other. Square: open vegetation; No symbol: not known; Triangle: forested; inner symbols: from pollen; outer symbols: from fauna.

Fig. 5: 2 m temperature differences between 9 kaMOD and the present during the course of the four seasons and the annual mean. Contours at +/- 0.5, 1., 1.5, 2, 3, 4, 5 °C. For the annual mean also a 0.2 contour is given. Negative values are dashed, shading for >1 and < -1 °C

Fig. 6: Precipitation differences between 9 ka and the present during the four seasons and the annual mean. Units: mm/month, means over 3 or 12 months respectively are shown. Contours at +/- 1, 2, 3, 4, 5, 6, 7, 10, 15 mm/month, negative values are dashed, shading for >2 and < -2mm/month.

Fig. 7: Koeppen diagrams for the 9 kaMOD (thick lines) and the present-day climatic (thin lines) conditions in the twelve hominin sites. Dashed lines: precipitation, solid lines: temperature. The temperature scale is given on the right.

Fig. 8: Down-scaled temperature of the coldest month (top) and the summer precipitation (bottom) in simulations for 9 kaMOD. Circles: hominin sites. Contours for temperature every 3 °C, shading for > 6 and <0 °C. Contours for precipitation at 10, 30, 60, 100, 150 mm/month, shading for >60 and < 30 mm/month.

Fig. 9: Likelihood of growth of warm-loving trees resulting from the combination of temperature of the coldest month, summer precipitation and growing degree days. Top: now. Middle: 9 kaMOD. Bottom: Last Glacial maximum. The higher the values (darker shading), the higher the likelihood of tree growth. < 1 (no shading) means no tree growth (see Leroy and Arpe, 2007, for further details). Circles for hominin sites.

Fig. 10: Geographical corridor of similar climate in the 9kaMOD simulations. Grey areas: Temperature of coldest month ranging from 0 to 6 °C or summer precipitation (average for JJA) ranging from 30 to 60 mm/month. Dark gray areas: both the summer precipitation and the minimum temperature criteria are fulfilled. Dots: hominin sites, they are clustered in the dark gray areas.

11 Tables

Table 1: Hominin sites and information on the palaeo-environments derived from

fauna.

Table 2: Vegetation reconstructions made at the levels with hominin finds. Medit.:
Mediterranean.

Table 3: Pollen sites as close as possible in time and space to hominin sites for
extra information on vegetation. Medit.: Mediterranean. Intergl.: interglacial.