Hominin variability, climatic instability and population demography in Middle Pleistocene Europe

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ABSTRACT

We propose a population model for Middle Pleistocene Europe that is based on demographic "sources" and "sinks". The former were a small number of "core" or populations in glacial refugia in southern Europe from which hominins expanded northwards in interstadial and interglacial periods; occupation outside glacial refugia would have been restricted to warm or temperate periods, and populations at the northern limit of the Middle Pleistocene range would have been "sink" populations in that they depended upon recruitment from source populations further south. Southwest Asia would also have been a likely source of immigrant, source populations. We argue as an alternative to an "ebb and flow" model in which groups retreated to refugia when conditions worsened that local extinction outside refugia would have been frequent. In extreme situations, Europe may have been a population "sink" (i.e. unpopulated) that was replenished from source populations in Southwest Asia. We suggest that this pattern of repeated colonisation and extinction may help explain the morphological variability of European Middle Pleistocene hominins, particularly *Homo heidelbergensis* and its apparent non-lineal evolution towards *Homo neanderthalensis*.

1. Introduction

Europe has the best-documented record in the world regarding its Middle Pleistocene inhabitants, their tool-kits and way of life, and their climatic and environmental contexts. In addition to the annual and gradual accretion of new excavations, surveys and analyses, there have been some spectacular recent discoveries, notably the new mandible from the Sima del Elefante, Atapuerca, Spain, that now extends the time-depth of the European populations to ≥1.2 Ma (Carbonell et al., 2008), and the evidence from Pakefield, UK, that indicates that hominins extended their range (even if briefly) to at least 53°N in northern Europe ca 700 ka (Parfitt et al., 2005). Notwithstanding these advances, numerous challenges remain for explaining the nature of settlement and hominin evolution in Early and Middle Pleistocene Europe. Here, we look at two problems in particular, and suggest how these might be investigated. The first is how hominin populations responded to frequent and often severe climatic and environmental disruption; and the second is how these responses might

help explain the morphological variability of its inhabitants. Each can be outlined in turn.

2. Setting the issues: hominin variability and environmental disruption

2.1. The climatic and environmental record: instability and environmental fragmentation

As has been amply demonstrated over the last three decades, there were numerous, generally muted cool periods with an average duration of 41 ka in the Early Pleistocene, and five major cold periods in the Middle Pleistocene, each of which lasted ca 100 ka (see Fig. 1). The Middle Pleistocene Transition (MPT) between these two climatic regimes began with an increase in global ice volume from ca 922 to 882 ka and ended with the onset of a 100-ka cycle of glaciations and interglacials at ca 640 ka (Mudelsee and Schultz, 1997; Heslop et al., 2002; Li et al., 2008). The earliest glaciation across northern Europe occurred in Marine Isotope Stage (MIS) 16, ca 650–620 ka (Head and Gibbard, 2005: 13). With the partial exception of the unusually long interglacial, MIS 11 (423–362 ka), Middle Pleistocene interglacials were relatively short, and conditions considerably colder than the present have dominated the last 600 ka.

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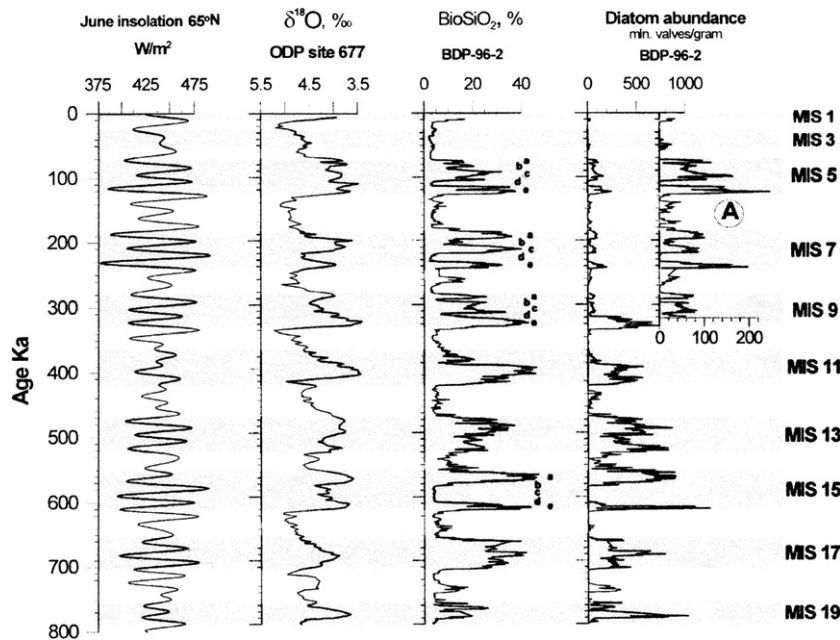
Fig. 1. The climatic record of Lake Baikal over the last 800 ka. This shows clearly the dominant features of Middle Pleistocene climate in continental Eurasia: ca six long periods (average duration, 100 ka) of severe cold climate interspersed by short warmer episodes of interglacial or interstadial climate. These contrasts would have been the main driving force behind hominin settlement in Middle Pleistocene Europe and Asia. Source: Khursevich et al. (2001), Fig. 1.

There were also numerous short but severe climatic oscillations within glacial and occasionally, interglacial stages which show that Pleistocene climates were inherently unstable. The best known are the short and cold Heinrich Events that were first detected in the Upper Pleistocene sections of North Atlantic marine cores (Heinrich, 1988), but which are now known from several other Upper Pleistocene sources, including the GISP2 ice core record from Greenland (Shackleton et al., 2004), the speleothem record of Soreq Cave, Israel (Bar-Matthews et al., 2003), and the Loess Plateau of North China (Liu and Ding, 1998). Similar short but severe oscillations are now known from earlier periods. As example, North Atlantic marine cores show numerous short but extremely cold events (usually during cold phases) during the Middle Pleistocene (see Fig. 2) that had a similar intensity to the Heinrich events that are recorded for the last glaciation in the Greenland ice cores (Oppo et al., 1998; McManus et al., 1999; Kandiano and Bauch, 2003). Similar millennia-length oscillations are recorded in the Early and Middle Pleistocene parts of the loess sequences of the Chinese Loess Plateau (Lu et al., 1999) and the EPICA Dome C ice cores of Antarctica (Lüthi et al., 2008). These short but severe climatic oscillations of a few millennia probably disrupted hominin settlement in mid-latitudes as much as the better known, longer shifts between glacials and interglacials, and also need to be incorporated into models of early hominin settlement and evolution in Europe.

A great deal is known from a wide variety of terrestrial sources about how the fauna and flora of Europe responded to each major shift from glacial to interglacial climate, and back again (see e.g. Candy and Schreeve, 2007). Although some regions, such as northern Europe, are much better documented than others, it has been possible to reconstruct the major vegetational zones of Europe at various glacial and interglacial stages: two examples are shown in Figs. 3 and 4. Broadly speaking, as ice sheets expanded over northern Europe during a cold phase, vegetational zones shifted southwards, so that all parts of Europe that were occupied by hominins experienced major environmental shifts from, for example, steppe grassland to open woodland, or from deciduous to coniferous forest. Animal populations also responded in the same

way, so that "northern" species occasionally extended as far south as the Mediterranean, and "warm" species such as hippopotamus occasionally extended into Britain. Hominins too would have had to respond to these shifts in the type, availability and productivity of resources across the European peninsula. The most severe of these shifts towards a colder climate would have resulted in the formation of a small number of vegetational and mammalian glacial refugia in southern Europe. (Cold-adapted species such as lemmings, mammoths and musk-oxen would have had their own interglacial refugia in northern Russia and Siberia during the warmest parts of interglacials, but these are not relevant to Middle Pleistocene hominins). The main glacial refugia during the last glaciation were in the Balkans, the Italian peninsula, and Iberia, with perhaps subsidiary ones north of the Alps (Taberlet et al., 1998; Hewitt, 1999: 104). When the climate ameliorated in the Holocene for warm-tolerant species, these regions were the main bases from which re-colonisation took place. According to Hewitt
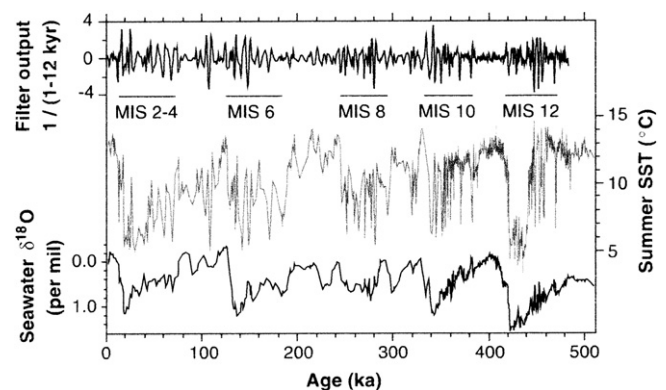

Fig. 2. Summer sea-surface temperatures and seawater δ18O in the last 500 ka from site 980, North Atlantic. This clearly shows numerous short-term, sub-Milankovich-length climatic fluctuations within major isotopic stages, and these short-term changes need to be factored into investigations of Middle Pleistocene hominin settlement in Eurasia. Source: McManus et al. (1999), Fig. 3.
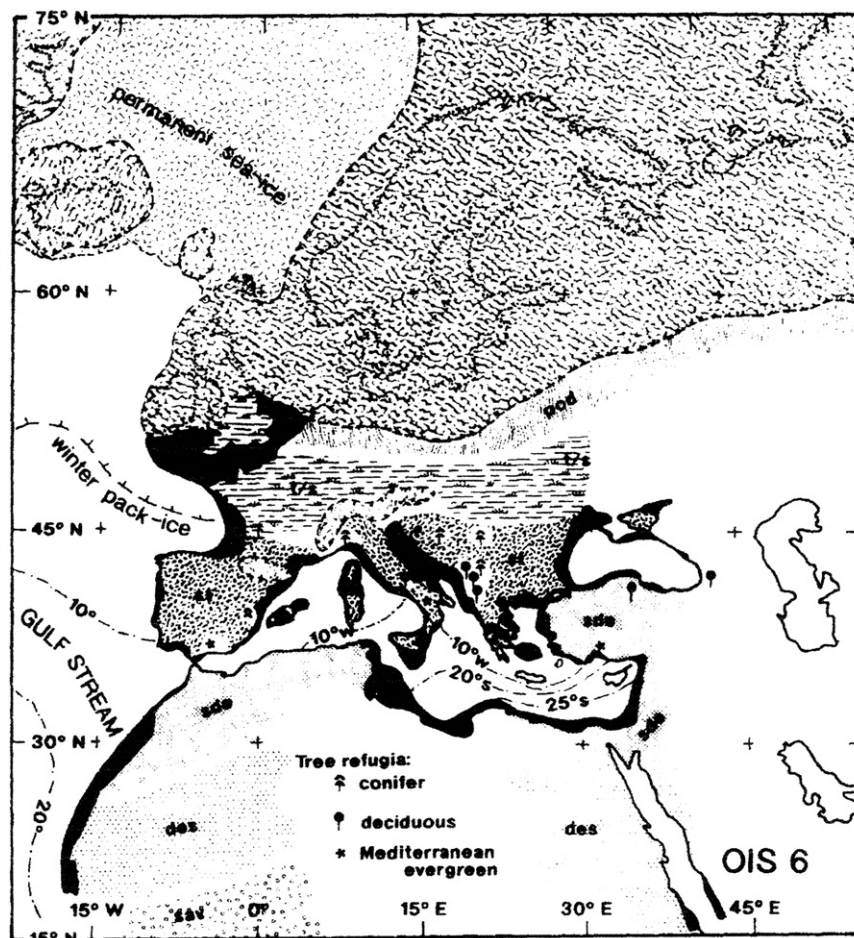
Fig. 3. Reconstructed vegetational habitats in Europe and North Africa during the penultimate glaciation (MIS 6). This figure and Fig. 4 show the range of environmental conditions experienced by hominins before 100 ka. Although no two ice ages were identical, each would have been dominated by major ice sheets over the British Isles, Scandinavia and northern Europe, with polar desert and cold steppe further south, and trees largely confined to major refugia in Iberia, Italy and the Balkans. Key: cloudy pattern = ice sheets; black = emerged coastal plains. Palaeoenvironments: pod = polar desert; t/s = tundra and cold steppe mosaic; st = arid cold steppe; med = Mediterranean evergreen woodland; sde = semi-desert; des = desert. Coastline in based on an isobath of −100 m. Source: Andel and Tzedakis (1996), Fig. 6.

(1999: 104), the Balkans formed the most important of these refugia in providing species for North European Holocene colonisation in nine out of 11 instances; the Pyrenees blocked expansion out of an Iberian refugium in four of 11 cases, whereas the Alps effectively blocked expansion from the Italian peninsula in eight out of 11 instances. Hominins would probably have responded in much the same way: a contraction of range into a small number of lowland glacial refugia in southern Europe, and subsequent expansion from them in warmer periods

2.2. The fossil hominin record

There is a general but by no means unanimous consensus that most Middle Pleistocene hominins should be classified as either *Homo heidelbergensis* (e.g. Arsuaga et al., 1993, 1997; Stringer, 1993) or *Homo neanderthalensis* (Hublin, 1988; Bermúdez de Castro et al., 2009; Hublin and Roebroeks, 2009), rather than, as suggested a few years ago, as either "late *Homo erectus*" (e.g. Vlacek, 1978; Wolpoff, 1980) or "archaic *Homo sapiens*" (see e.g. Stringer et al., 1979; Gamble, 1986). These debates reflect the usual problems of a fragmented, and sometimes poorly-dated set of material, a lack of agreement over how elastic each of these taxa should be (e.g. at what point does a "late *H. erectus*" become something else), and how an anagenetic lineage should be subdivided – assuming of course that human evolution in Middle Pleistocene Europe

proceeded along anagenetic lines. The term "*H. heidelbergensis*" is thus a convenient abbreviation for a longer statement along the lines that whilst most European Middle Pleistocene hominin specimens share some features with *H. erectus*, *H. neanderthalensis* and even some specimens regarded as "archaic *H. sapiens*" – leaving aside for the moment how each is or can be defined – they seem nonetheless to be sufficiently distinct to be placed in a separate category that was ancestral in Europe to Neanderthals. Under the convention of taxonomic priority, this category has to be *H. heidelbergensis* as a result of Schoetensack's decision in 1907 to apply this term to the Mauer mandible, which is thus the type fossil of this species.

As even cursory reading shows, two problems persist in the use of this term. The first is the geographical extent of *H. heidelbergensis*. Is it only found in Europe?; or Europe and Southwest Asia?; Europe, Southwest Asia and Africa?; or Europe, East and possibly North Africa and/or North China and/or India?; or Europe and Asia, but not Africa? In-depth discussion of this issue is beyond the remit of this paper, but the case for restricting its usage to only Europe and Southwest Asia has been made by Dennell (2009: 465–468) and Dennell et al. (submitted), for those interested in the rationale for that argument: our view is strongly that the term *H. heidelbergensis* should be restricted to Southwest Asia and Europe.

The second problem is that the European specimens that are now commonly assigned to *H. heidelbergensis* are highly variable,
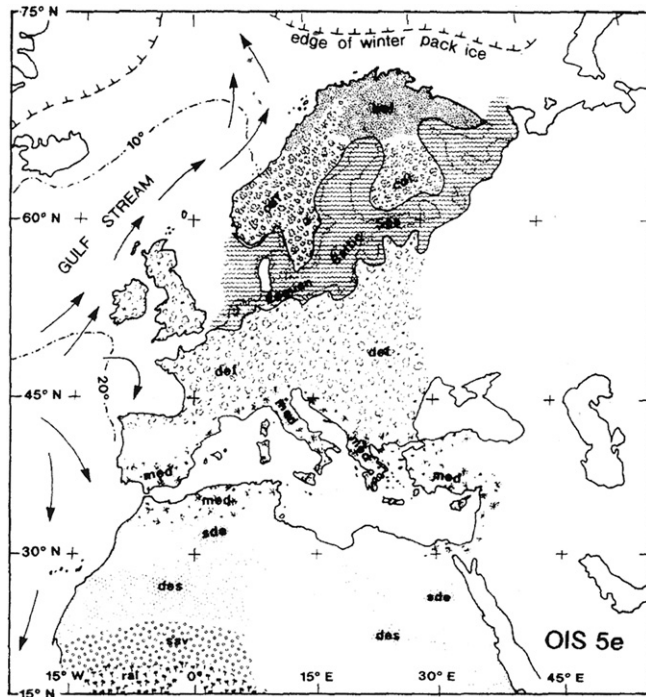
Fig. 4. Reconstructed vegetational habitats in Europe and North Africa during MIS 5e. Although the peak of the Last Interglacial appears to have been exceptionally warm, it was broadly similar to earlier interglacials in that Europe was largely ice-free, and extensively wooded. Note that Scandinavia in MIS5e was temporarily an island. Key: bof = boreal forest; cdf = coniferous and deciduous forest; eec = deciduous forest; Med = Mediterranean evergreen woodland; sde = semi-desert; des = desert; sav = Sahelian parkland; rai = African rainforest. Source: Andel and Tzedakis (1996), Fig. 9.

and (as shown below), the path to becoming a Neanderthal was not straightforward during the Middle Pleistocene. Apart from the lack of a reliable, precise chronological framework for each pre-Neanderthal specimen, the combination of primitive and derived traits appears to be random and cannot be ordered into a chronological sequence (Bermúdez de Castro et al., 2009). Part of our concern in this paper is to indicate how this variability within *H. heidelbergensis* can be modelled in terms of population and environmental dynamics in response to climatic and environmental disruption.

2.3. European Middle Pleistocene hominin variability

The degree of morphological variability in the European Middle Pleistocene fossil hominin record shows three features. First, although the Early Pleistocene populations of Europe (*Homo antecessor*) were initially proposed as the best candidate to represent the last common ancestor of both the *H. sapiens* and *H. neanderthalensis* lineages (Bermúdez de Castro et al., 1997), the "geometry" of this relationship needs a deeper assessment, as there is some evidence of population discontinuity between the Early and the Middle Pleistocene populations of Europe (Bermúdez de Castro et al., 2003). *H. heidelbergensis* is thus likely to have been an immigrant into Europe, although (as explored below), some genetic linkage to *H. antecessor* cannot be excluded. Secondly, there was no simple, unilineal development within *H. heidelbergensis* towards being a Neanderthal. Thirdly, the climatic and environmental record also shows that both *H. antecessor* and *H. heidelbergensis* evolved under conditions that rarely allowed long-term, stable adaptations. Certainly in northern Europe, hominin occupation is known to have been infrequent and intermittent, with Britain

abandoned for perhaps 80% of the last 500,000 years (Stringer, 2006). Even in areas further south and in most upland regions, population wipe-outs and re-locations must have been frequent. As stated elsewhere, "The early hominin settlement of Asia is thus a repeated theme of regional expansion and contraction, re-colonisation and abandonment, integration and isolation" (Dennell, 2009: 475); the same appears true of Europe.

3. "Core" and "peripheral" populations

If, as seems probable, the early Palaeolithic settlement of Europe and Asia was characterized by frequent spatial and geographic discontinuities (Dennell, 2003), there should have been a few core hominin populations that survived glacial maxima, but several peripheral ones that were viable only during interglacial or interstadial periods. The archaeological test for determining whether a region was a glacial refugium and was therefore occupied by a core population during the coldest part of a glacial cycle lies in its palaeoclimatic record: if a region was occupied during the coldest part of a glacial cycle, it would qualify as a glacial refugium with a core population; if not, it would be a region of peripheral settlement. Two general questions need to be asked at this point concerning the existence and location of these core populations and glacial refugia.

3.1. Did Europe always have core populations – i.e. at what point was it "permanently" colonised?

During recent debates over the "long" versus "short" chronology in Europe (Roebroeks and Kolfschoten, 1994; Dennell and Roebroeks, 1996), an important contrast was often drawn between the settlement records of northern and southern Europe. Northern Europe, it was argued, was occupied later than southern Europe, and was not colonised in the sense that occupation was restricted to interglacial periods and possibly the early and final parts of a glaciation. The implicit assumption here was that southern Europe was occupied continuously throughout the Middle and possibly the late Early Pleistocene. Attention was thus focused on determining when southern Europe was first colonised from the age of the earliest reliable, well-dated archaeological and/or hominin piece of evidence. It is, however, an untested assumption that hominins continuously occupied southern Europe after they had first entered it. The question "When was Europe first colonised?" might perhaps be rephrased "How often was Europe uninhabited after hominins first entered it?". We do not know the answer at present because there are too few finds from southern Europe with the necessary palaeoclimatic information to establish whether hominins survived every glacial maximum, but we should not exclude the possibility that Europe may have been completely uninhabited during the maxima of, for example, MIS 16, 14, 12 and perhaps more recent glacial periods. In this context, it is particularly interesting that recent evidence indicates that the earliest indications of hominins in the Orce Basin and at Atapuerca all occurred in mild, interglacial periods (Blain et al., 2008, 2009; Agustí et al., 2009). This might indicate that during the Early Pleistocene, the Iberian Peninsula was repeatedly colonised in warm periods and then abandoned in cold ones. If so, the "core" populations would have been further east, in Italy, the Balkans or even in Southwest Asia.

3.2. If there were core populations in Europe during a glacial–interglacial cycle, where were they?

As indicated above, the core populations of Middle Pleistocene Europe were probably in glacial refugia in southern Europe. An

inescapable aspect of European geography is that its southern border is immutable because of the Mediterranean; as glacial refugia had to be in southern Europe, there are few obvious alternatives to the Balkans, Italy and Iberia as refugia. (There may of course have been supplementary glacial refugia that were occupied throughout most of a glacial period, such as Southwest France and a few areas north of the Alps such as southern Germany). We do not know whether all, some, or none of these glacial refugia were used in each glacial period; some glaciations were more severe than others or had differing regional impacts, and hominins gradually improved their survival abilities over the last million years. For example, the development of co-operative big-game hunting and the use of fire after 500 ka undoubtedly enhanced the chances that hominins could survive the severest parts of a glacial period in regions that their predecessors could not.

Under such conditions of repeated colonisation and abandonment, population isolation and fragmentation, we might expect to find evidence of several palaeospecies in Middle Pleistocene Europe: as Tattersall (1996: 53) observed, "The isolation of infra-specific populations is thus a prerequisite for speciation, and the occasions for such isolation can rarely have occurred more frequently than during the dramatic climatic and glacio-eustatic fluctuations of the Pleistocene". Interestingly, however, taxonomic unity was maintained, albeit with considerable degree of variability. Here, we explore how this might have happened.

3.3. "Demes" in Middle Pleistocene Europe

Howell (1996, 1999) usefully discussed how the paleodeme, or p-deme, should be the basic unit of study of early hominins. He described demes as "the basic stuff of the hominin fossil record"; "demes (sometimes as isolates) constitute subspecies", "the aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species" (Howell, 1999: 8–9). As

Table 1
Chronology of some of the relevant hominin sites mentioned in the text.

Site	Hominin	Dating	Source
Sima del Elefante, Spain	*H. antecessor*	ca 1.2 Ma	Carbonell et al., 2008
Gran Dolina-TD6, Spain	*H. antecessor*	ca 960 ka	Berger et al., 2008
Mauer, Germany	*H. heidelbergensis*	ca 640 ka	Hambach 1996
Sima de los Huesos, Spain	*H. heidelbergensis*	>530 ka	Bischoff et al., 2007
Ceprano, Italy	*H. cepranensis*	ca 460 ka	Muttoni et al., 2009
Arago, France	*H. heidelbergensis*	ca 450 ka	Lumley and Lumley, 1971
Montmaurin, France	*H. heidelbergensis*	ca 400 ka	Billy and Vallois, 1977
Steinheim, Germany	*H. heidelbergensis*	ca 350 ka	Delson et al., 2000
Petralona, Greece	*H. heidelbergensis*	200–350 ka	Delson et al., 2000
Swanscombe, UK	*H. heidelbergensis*	ca 350–250 ka	Delson et al., 2000
Pontnewydd, UK	*H. neanderthalensis*	ca 200 ka	Green et al., 1981
Hortus, France	*H. heidelbergensis*	ca 110–120 ka	Lumley, 1973
Krapina, Croatia	*H. heidelbergensis*	ca 120–140 ka	Rink et al., 1995

Notes: the dates shown here are ones that we rely upon in this paper. Several of these dates and specimens are problematic and come with health warnings. The date of 640 ka for Mauer lacks independent verification, and is considerably older than the often-used estimate of ca 500 ka (see e.g. Roebroeks and Kolfschoten, 1994). The date of >530 ka for Sima de los Huesos is considerably older than the previous estimate of ca >350 and perhaps 400–500 ka but is used here until refuted. The re-dating of *H. cepranensis* from ca 1 Ma (see Ascenzi et al., 2000; Manzi et al., 2001; Manzi, 2004) to ca 460 ka raises major issues concerning the late persistence of this taxon, and the identity of the hominin that made the Italian Acheulean. The age of Petralona is impossible to establish in the absence of stratigraphic and contextual information, and only a general estimate of its age range is possible.

Trinkhaus (1990) put it: "the best approach …. is probably one that regards the available fossil samples (or specimens) as representative of prehistoric populations or lineages acting as portions of dynamic evolutionary units". Howell (ibid.) recognised three p-demes in the European fossil hominin record before MIS 7. The first was Atapuerca-Gran Dolina (i.e. *H. antecessor* from TD [Trinchera Dolina] 6); the morphology "is distinctive and seemingly divergent from less ancient European counterparts" Howell (ibid.); he also suggested that the Ceprano cranium might also be included in this p-deme (see below). The second and third p-demes are both within the palaeospecies *H. heidelbergensis*. One was primarily represented by the Mauer type specimen and the material from Arago: "this p-deme is distinguished by an idiosyncratic (regional) mosaic of some (sym)plesiomorphic cranial, gnathic, and post-cranial features coupled with derived (apomorphic) features of other aspects of cranium (fronto-parietal elements, facial skeleton) and mandible (symphysis, and ramus, dentition) which may approximate structures characteristic of subsequent Neanderthals". Howell (ibid.) suggested that a miscellany of specimens might be included in this group, notably the tibia diaphysis from Boxgrove, the mandible fragment from Visogliano, and a femoral diaphysis from Venosa–Notachiroco. The third group he termed Petralona/Atapuerca (i.e. Sima de los Huesos), and suggested it might also include the Montamaurin–La Niche mandible, the Vértesszöllös occipital and dental elements, the Steinheim, Swanscombe and Bilzingsleben crania, and maybe also the skeleton at Altamura, Italy, that is encased in a flowstone. (Additional possible candidates included various cranial and postcranial Italian specimens from Prince Cave, Liguria, Casto di Guido, Cava Pompi, Casal de' Pazzi, Sedia del Diavolo, and Ponte Mammalo). In his view (ibid., p. 17), "This p-deme reveals persistence of some plesiomorphic features, but substantially stronger and widespread expression of Neandertal synapomorphies". It is interesting to note that the two p-demes that Howell recognised with *H. heidelbergensis* overlap in both space and time: both are represented in southern as well as northern Europe, and each has a considerable time-depth. One of the *H. heidelbergensis* p-demes includes specimens like Mauer and Arago that are separated by a time gap of about 200 ka (see Table 1 for the ages of some of the sites relevant to this discussion). Similarly, the Petralona/Atapuerca p-deme includes fossils with ages that differ by perhaps more than 300 ka. Because of their spatial overlap, neither can strictly be regarded as "local populations of a species inhabiting a geographic subdivision of the range of the species". The disparity in the geographic and temporal frame of the fossil populations included in each of the *H. heidelbergensis* p-demes described by Howell (1999) is also present in the Gran Dolina-TD6/Ceprano p-deme. A recent study (Muttoni et al., 2009) has provided a significantly younger age for the Ceprano calvaria (ca 460 ka) in comparison with the ca 960 ka obtained for the TD6 level (Berger et al., 2008).

Our own assessment of these p-demes is outlined below in Section 4.1.

3.4. demes, population islands, and tidal islands

In studies of modern populations, demes can be studied as independent breeding populations, as "the aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species" (Howell, ibid.). In palaeoanthropology, we need to factor in time over a geological time-scale (i.e. over several thousand generations), and in Pleistocene Europe, we have also to factor in climatic and environmental disruption, leading to frequent population fragmentation and recombination. In some situations, there may have been prolonged periods of isolation with high levels of intra-breeding within groups, or integration with high levels of

interbreeding between groups; there would also have been local and regional extinction events, and substantial demographic discontinuity in many parts of Europe outside long-term refugia: p-demes would never have been static groupings.

It is unlikely that populations within demes could have survived prolonged isolation, even if sufficiently large to be reproductively viable. Conservation studies indicate that high rates of inbreeding are associated with high rates of extinction because of the loss of heterozygosity and a reduction in the overall fitness of the population by decreasing reproductive rates and increasing susceptibility to pests, predators and/or environmental change (see e.g. Frankham, 1995: 796). Although it is initially attractive to model demes as recognisable "islands" of independent breeding populations, it is more appropriate to envisage them as "tidal islands"; that is to say, they were sometimes isolated (as e.g. at the height of a glacial phase and confined to a refugia) and at other times, able to interbreed with other demes – as in the optimal parts of interglacials or interstadials, when populations expanded to their maximum extent; some may also have "drowned", i.e. become extinct. The genetic tide thus ebbed and flowed as the environment and climate alternated between cold periods of high environmental stress and low productivity, and warm periods of lessened environmental stress and high biological productivity

3.5. "Sources" and "sinks"

As a very interesting approach, Eller et al. (2004) and Hawks (2009) have proposed that Pleistocene populations dynamics can be modelled as "sources and sinks". "Source-sink dynamics" is a theoretical ecological model originally developed by Pulliam (1988) to describe how variation in habitat quality may affect the growth or decline of a population. To quote Hawks: "a population sink is a region where the average rate of reproduction is below replacement levels. This region can remain populated only if individuals migrate in from other places. The places that reproduce above replacement are called population sources". He notes also: "there is no reason why the source-sink dynamic need have been constant [over Neanderthal evolution] …. Investigating the boundary conditions of the source-sink model and its correspondence to autosomal genetic results would be helpful".

The population sources are likely to have been in the South and Southeast European refugia mentioned above (or in Southwest Asia if Europe was abandoned altogether) because it from these that subsequent expansion occurred. These refugia are of fundamental importance to understanding the natural history of Europe, and doubtless also its Palaeolithic record. As Bennett et al. (1991: 111) note: "Only the genotypes in southern sites where populations can survive the whole glacial/interglacial cycle are likely to persist. … If a tree species becomes extinct in southern Europe, at any point in a glacial/interglacial cycle, it will ultimately become extinct everywhere, regardless of what the population in northern Europe is like at the time of extinction in southern Europe. The evidence suggests that for most European tree species there is no return movement". The same is likely to be true of hominins: if populations in the refugia in South and Southeast Europe became extinct, then so would those in the rest of Europe.

As an initial step in exploring the palaeo-demography of Middle Pleistocene Europe, we can regard the p-demes that are evidenced in the European record as the outcomes of this dynamic between population sources and sinks. We will never fully understand the precise histories of these demes, but we can suggest how variability arose at a demic level within a variable taxon that is defined by inherited genetic characteristics that altered the phenotype. To use an analogy, the p-deme is the outcome in a systems model of a black box that contains the combination of climatic,

environmental, and demographic factors that produced it; these factors can include prolonged periods of isolation from and/or, occasional interbreeding with other demes, short-term catastrophies (such as the extinction of some groups within a deme and the ensuing loss of genetic variability), repeated expansion and contraction of the demic range (with varying opportunities for isolation and interbreeding), and so on. Under conditions of demic expansion, Hawks (2009) suggested: "The continual migration from sources to sinks creates a genetic gradient. Individuals sampled at any given time in the population sink are overwhelmingly likely to have ancestors not in the sink but in one or more source populations". This statement outlines a much more dynamic and complex scenario, in which it would be possible to fit the similarities between geographic and/or temporally distant populations as far as they constitute a "sink and source complex".

4. Towards a model

We consider first, our own assessment of the p-demes in Middle Pleistocene Europe, and then propose how repeated population expansion and contraction between sources and sinks in response to climatic and environmental shifts might have resulted in the type of phenotypic variability exhibited by Middle Pleistocene European hominins.

4.1. First, our own (short) assessment of the European p-demes before MIS 7

Dating is critically important to any assessment of evolutionary trends within the European Middle Pleistocene hominin sample, but remains problematic with respect to several important discoveries. The dates that are preferred in this paper are listed in Table 1, along with various caveats regarding individual finds. As indicated, the dating of Mauer – the type specimen of *H. heidelbergensis* – is uncertain, and there is no obvious way of preferring the estimated age of 640 ka over the commoner one of ca 500 ka. The age of the Sima de los Huesos continues to be debated, but we accept the latest estimate that its minimum age is 530 ka until this is falsified. The re-dating of Ceprano to around half its previous age raises major currently unsolvable problems over the status (and persistence) of *Homo cepranensis* and the identity of the hominins that made the Italian Acheulean. Other finds are dated to within very broad limits, notably Petralona and Swanscombe, and the age of others such as Altamura remain unknown.

Nevertheless, we agree in general terms, with Howell (1999) that the Middle Pleistocene European populations cannot be organised into consistent geographic or chronological demes. More specifically, they cannot be organised along a chronological scale from "less to more" Neanderthal. As explained below, all these hominin populations (with possibly the exceptions of Ceprano and the isolated occipital from Vértesszöllös, Hungary) show Neanderthal traits, but the degree of neanderthalisation and the skeletal part that shows the derived conformation varies from group to group, and populations like Sima de los Huesos (>530 ka) appear to be more Neanderthal than some later Middle Pleistocene ones such as Arago in France.

Most European fossil remains from this period exhibit one or more derived cranial traits shared exclusively with Neanderthals. This rule applies to the most complete specimens, such as the skulls from Steinheim, Petralona, Arago, Swanscombe, and Atapuerca-Sima de los Huesos (SH) sites. The Arago 21 specimen exhibits a clear midfacial projection, with an extended maxilla and a Neanderthal-like lower rim of the nasal cavity. The Petralona cranium also shows midfacial projection, less marked than in Arago 21, but within the limits of the Neanderthal variation. The Steinheim

cranium presents a Neanderthal-like supraorbital torus, a wide nasal aperture, and certain midfacial prognathism. Concerning the occipital bone, the Bilzingsleben, Vértesszöllös, and Petralona specimens do not exhibit a suprainiac fossa or a bilateral development of the torus, which are considered Neanderthal derived traits, but the Swanscombe hominin displays a Neanderthal-like suprainiac fossa (a centrally placed elliptical depression with a pitted floor). The most extreme example about the variability of the Middle Pleistocene specimens would come from the Italian locality of Ceprano. Despite its taxonomic uncertainty, the Ceprano calvaria was regarded as representative of one of the oldest hominins that populated Europe (see e.g. Manzi, 2004). A recent analysis has yielded a significantly younger age (Muttoni et al., 2009; see Table 1) despite its morphological primitiveness. This fossil could be a good example of the lack of linearity in the neanderthalization process defended in this manuscript and/or it could evidence the late survival, until the Middle Pleistocene, of an earlier European lineage. In both cases, population isolation and fragmentation would have worked as key factors.

Similarly to the cranial remains, the dentognathic evidence exhibits a highly variable combination of Neanderthal and primitive traits. Paradoxically, and despite being the holotype of *H. heidelbergensis*, it is difficult to link the Mauer mandible with other European Middle Pleistocene specimens because of its large ramus breadth and heavy appearance (Rightmire, 1998). However, Rosas and Bermúdez de Castro (1998) have demonstrated that the Mauer mandible bears a set of characteristics that are the structural basis on which Neanderthals apomorphies were eventually fully developed. Furthermore, the dental proportions of the Mauer mandible, especially the buccolingual dimensions with respect to the total dental size are similar to those of Neanderthals (Bermúdez de Castro et al., 1999). Although the Arago 13 mandible exhibits a primitive pattern, the Arago 2 specimen, as well as the Montmaurin mandible also show clear Neanderthal derived traits, such as the position of the lateral prominence or the medial position of intersection between the mandibular notch and the condyle (Rosas, 2001).

The most representative sample of the Middle Pleistocene comes from the Sima de los Huesos site (Burgos, northern Spain), which has provided >80% of the Middle Pleistocene world-wide record for the genus *Homo* (Bischoff et al., 2007). Although the last age estimate (>530 ka) obtained for the Atapuerca-SH site (Bischoff et al., 2007) is difficult to fit the in evolutionary schemes of some researchers about the Neanderthal lineage, the data are robust and consistent with other chronological and stratigraphic studies in progress in the site. All these data would still point to the Atapuerca-SH site as one of the earliest localities with hominin evidence in the European Middle Pleistocene. According to Arsuaga et al. (1997), the SH crania show a number of primitive features lost in the Upper Pleistocene Neanderthals, especially in the braincase, but also in the facial skeleton. Other traits, such as the morphology of the occipital bone or the midfacial topography are considered transitional to the Neanderthal morphology, whereas other traits are close to what is found in Neanderthals. It is interesting to note that whereas some cranial regions such as the supraorbital morphology and the midface closely resemble the anatomy of Neanderthals, other parts exhibit an almost totally primitive aspect, such as the temporal bone (Martínez and Arsuaga, 1997). The SH mandibles also exhibit a clear Neanderthal morphological pattern, including a posterior position of the mental foramen, marginal tubercle and lateral prominence, as well as a well-developed retromolar space (Rosas, 2001).

Regarding the dentition, a peculiarity of the Atapuerca-SH hominins is the reduced size of their premolars and molars. On average, the dimensions of the mandibular posterior teeth (P4–M3) are similar to those of modern humans. In contrast, the size of the lower and upper incisors, canines and third premolars are comparable to that of late Pleistocene Neanderthals (Bermúdez de Castro, 1993). Thus, the SH lower dentition shows a strong imbalance between the anterior and posterior teeth in relation to modern humans, and even with regard to other Middle Pleistocene hominins and Neanderthals. SH hominins show high percentages of strong labial convexity and prominent basal eminence in their upper central incisors, characteristics that are typical of Neanderthals. Upper lateral incisors from SH display a particular shovel shape we have coined "triangular shovel shape" (Lumley, 1973; Martinón-Torres, 2006; Martinón-Torres et al., 2006), that is typical and exclusive of European Middle Pleistocene and Neanderthal populations (e.g. Hortus and Krapina) (although incipient forms of it can be traced back in *H. antecessor* and *H. erectus* species). SH upper canines are also characterized by "mass additive" traits (term by Irish [1998]), with high percentages of shovel shape, mesial canine ridge and prominent lingual tubercle, overlapping with Neanderthal populations in their distributions (Martinón-Torres, 2006). SH hominins, like European Middle Pleistocene populations and Neanderthals do not express *cingulum* in their canines and premolars. Interestingly, specimens such as those from Arago present a vestige of this buccal platform, which is still fully present in the Atapuerca-TD6 populations (Bermúdez de Castro et al., 1999; Bermúdez de Castro et al., 2003). Lower first premolars in the SH sample present a characteristic conformation typical of the Neanderthal lineage but even more pronounced than in classic Neanderthals, while Arago specimens and teeth from Krapina and Le Moustier, present more primitive conformations (Gómez-Robles et al., 2008). The majority of the lower molars of SH hominins show a deep pit-like anterior fovea in typical combination with a strong mid-trigonid crest, almost constant in European Neanderthals such as La Quina, Krapina or l'Hortus but, interestingly, this crest is absent in Mauer, the holotype of *Homo heidelbergensis.* The characteristic shape of Neanderthal upper first molars, with a bulging hypocone protruding in a rhomboidal contour (Bailey and Lynch, 2005) can be traced back to the Early Pleistocene specimens (Gómez-Robles et al., 2007) and is a constant in the Middle Pleistocene groups. Finally, some SH lower molars do not express a C5, an exceptional circumstance in the Middle Pleistocene European populations (Bermúdez de Castro, 1987; Martinón-Torres, 2006). In summary, we can state that regarding the dentition, SH hominins do not lack any dental trait that is usually considered as typical of *H. neanderthalensis* and all the dental traits described in the SH hominins form part of what are called typically Neanderthal traits (Bermúdez de Castro, 1988, 1993; Martinón-Torres, 2006). The majority of these dental traits (with the exception of their first lower premolar [Martinón-Torres et al., 2006], first upper molar [Gómez-Robles et al., 2007] and upper lateral incisor conformations [Martinón-Torres, 2006; Martinón-Torres et al., 2006, 2007a,b]) are not apomorphies, but characteristic of the Neanderthal lineage due to their high frequencies and their particular combination (Bailey, 2002; Martinón-Torres, 2006).

Thus, while the Sima de los Huesos populations exhibit a fully Neanderthal pattern in both dental morphology and proportions (Bermúdez de Castro, 1988, 1993; Martinón-Torres, 2006), other early Middle Pleistocene fossils like the Mauer mandible (ca 640 ka) lack some of the distinctive morphological traits of other European Middle Pleistocene populations (Rosas and Bermúdez de Castro, 1998; Rosas, 2001; Mounier et al., 2009). Similarly, the Arago hominins (ca 450 ka vs. >540 ka of SH) are anomalous compared with SH and later Neanderthals, and Arago 13 "shows a combination of the 'Gran Dolina and Sima de los Huesos' dental traits" (Bermúdez de Castro et al., 2003: 1423). Thus, some later pre-Neanderthals such as Arago appear to be "less Neanderthal" than chronologically older specimens such as Sima de los Huesos.

In addition, other late Middle Pleistocene specimens from Europe, like the Pontnewydd teeth (ca 200 ka), characterized for being similar to those of Upper Pleistocene Neanderthals (Green et al., 1981) have shown significant similarities with the much earlier fossils from Sima de los Huesos (Martinón-Torres, 2006; Gómez-Robles et al., 2007). Given its clear Neanderthal character despite its early chronology, it is likely that the SH population played a major role as a core or source population for the Neanderthal gene pool.

From all this, we can conclude that is highly difficult – if not impossible – to organize the Middle Pleistocene populations into morphological demes that are spatially and/or temporally consistent. With this outline of a basic palaeo-demography in mind, we now show how changes in boundary conditions between sinks and sources could help explain variability within the *H. heidelbergensis* taxon. First, we need to consider some properties of effective and census populations.

4.2. Effective and census populations

Estimates of Palaeolithic population sizes are usually based on analogies with modern hunter-gatherers or, for early hominin populations, apes or social carnivores (see e.g. Antón and Swisher, 2004; Arcadi, 2006). Bocquet-Appel et al. (2005) attempted to estimate European Upper Palaeolithic population sizes by reference to modern hunter-gatherer population densities and numbers of archaeological sites, and suggested that the meta-population level was ca 4400–5900, or with a 95% confidence level, between 1700 and 37,700. Hublin and Roebroeks (2009: 3) cite estimates of 470–750 for the Mousterian of Acheuelean Tradition and 1240–1940 for the MIS 3 Central European Micoquian. These estimates refer to conditions in the Upper Pleistocene, when climates were often considerably colder than the present, and population levels during interglacials were probably considerably higher. However, our main concern in this paper is with the size of core populations when conditions were at their most severe during the harshest parts of a glacial period. Middle Pleistocene European population levels are most unlikely to have been higher than in the Upper Palaeolithic, and a level of 3000–5000 might seem reasonable in interstadial periods, and perhaps 1500–2500 in very cold periods when they were confined to glacial refugia. If we assume that Middle Pleistocene populations comprised small subsistence groups of 25 hominins, there might have been only 60–100 in full glacial periods in glacial refugia, but 120–200 in interstadia. (If average group sizes are assumed to have been ca 50, these numbers would of course be halved). On the assumption that ca 40% of the population were of reproductive age, the effective breeding population is unlikely to have been more than 600–1000 in full glacial times, and perhaps 1200–2000 during interstadia. (However, the likely proportion is likely to have been much lower if mating was constrained by incest and other taboos; in small kin-based groups, exogamous mating would have been unavoidable if incestuous relationships were disallowed). The size of Middle Pleistocene mating networks, and the means by which they were maintained, can only be guessed at. If, however, the distances over which lithic materials were routinely transported is taken as a proxy indicator of exchange and information networks (see e.g. Roebroeks et al., 1988; Gamble, 1999), Middle Pleistocene social and reproductive networks appear to have been far smaller than those evidenced in the Upper Palaeolithic, with the implication that most mates were drawn from a small and tightly constrained pool. Estimates of the kind given above can only be suggestions, but help reinforce the point that early Palaeolithic population levels, densities, and growth rates were probably extremely low. The interesting issue is how enough groups (or groupings of groups) maintained sufficient genetic viability to result

in long-term phenotypic survival. Here, we need discuss the relationship between effective and total population size.

Eller et al. (2004) discuss an interesting paradox that arises in discussions of multi-regional evolution of modern humans. They point out that "multi-regional evolution requires large numbers of humans to have existed at any one time, but genetic data reflect a small population size throughout human prehistory". If one takes, for example, estimates of Pleistocene population size based on demographic models of hunter-gatherer population densities across the whole of Eurasia, a figure of between 500,000 and 1,000,000 appears reasonable for interglacial conditions. Of these, ca one third to a half should be of reproductive age, and thus the effective population size – i.e. that required to maintain genetic viability – would be ca 167,000–500,000. However, genetic data indicate a much smaller inbreeding population size of only ca 10,000 individuals. That figure would imply absurdly low population densities of ca 1 individual per 30,000 sq km, or "a home range the size of West Virginia" (Eller et al., ibid. 692). On that basis, the multi-regional model of modern human origins is deemed by many to be genetically impossible; indeed, it is almost impossible to envisage how Eurasia could have been colonised by such small numbers of individuals during the Middle Pleistocene. However, they showed that a small effective population size could be reconciled with a high census size under a model of high rates of population extinction and re-colonisation. Their model requires that – as suggested here – "Pleistocene human populations were small, isolated, and susceptible to population extinction" (ibid., 701–2). As has been shown mathematically, the effective size of a population decreases relative to the total census size under conditions of fragmentation (Whitlock and Barton, 1997). Population isolation cannot be sustained over numerous generations; however, without increasing the risk of local extinction, so varying rates of inter-demic genetic exchange have to be allowed for. Although island populations are relatively easy to model because they can be treated as self-contained and inbreeding, the Pleistocene demographic landscape probably comprised (as suggested above) demic "tidal islands" that were periodically linked to, and merged with, other demic groups.

4.3. Demic expansion and mixing

The pattern of hominin occupation in northern Europe is a repeated one of colonisation and abandonment, as evidenced best by the British evidence (see e.g. Stringer, 2006), and shown schematically in Fig. 5. This shows an initial colonisation event, followed by five distinct extinction and re-colonisation events. (Extinction here indicates that occupation ceases; the inhabitants may have withdrawn further south, or more probably [as argued below] become extinct). Fig. 6 shows schematically how three isolated p-demes in glacial refugia might have reacted to the onset of a warm period. As seen, the initial onset of warm conditions enabled each to expand, and two of these overlapped and could thus exchange genes. Over time, each deme could fission, and then establish daughter "source" populations further north. In this figure, two of these were derived from different source populations, but now overlapped and were able to interbreed; the third (derived from two demes) remained isolated. At the maximum extent of this dispersal event, further expansion occurred northwards; two of these populations overlapped, and the third remained separate. All three were probably "sink" populations in the sense that they needed recruitment from source populations further south to remain genetically viable.

An important point to emphasis in this model is that the process of colonisation, extinction and re-colonisation need not have been identical in each climatic cycle; as Bennett and Provan (2008: 2450) note with regard to plant species, we do not know if those species
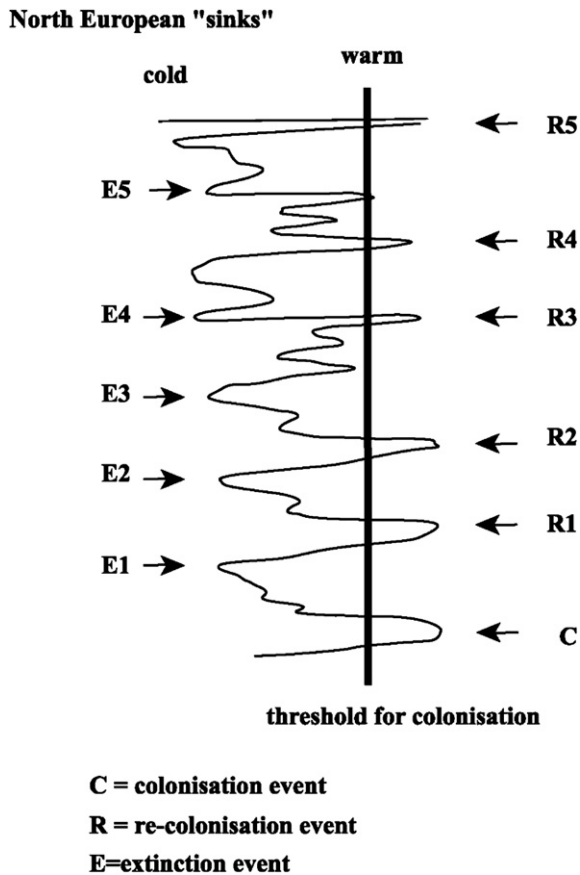
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North European "sinks"

Fig. 5. Colonisation, extinction, and "sink" populations in Middle Pleistocene northern Europe. This is a schematic representation of "sink" populations at the northern limit of their range responded to the warm-cold shifts that occurred repeatedly throughout the Middle Pleistocene. An initial colonisation event in a warm period is followed by extinction in a cold one, and re-colonisation in a subsequent warm period. This pattern of re-colonisation and extinction is repeated here five times, in a manner similar to that seen in the British Isles.

Fig. 6. Population expansion and demic inter-mixing. This is a schematic representation of how population fragmentation, dispersal and recombination could lead to the type of demic variability exhibited by *H. heidelbergensis* during the Middle Pleistocene. The solid circles denote demes during cold periods when populations contract into refugia; the dashed circles indicate interglacial or interstadial conditions when expansion from them is possible. Here, the bottom row indicates three demes in refugia in South and Southeast Europe. Each is separated in glacial conditions, but in interglacial conditions, demes b and c overlap. The middle row indicates how each expands in interglacial times and becomes a source population: here, demes 2a and 2b overlap, but 2c (derived originally from demes b and c) remains isolated. The top row indicates the maximum expansion during an interglacial; here, deme 3a (derived from demes 2a and 2b) is isolated, but demes 3b and 3c overlap, although each has a different ancestry.

that have a record of expansion did so in every interglacial, or whether expanding populations came from different refugia. Hewitt (1999: 105) suggests there are three common models of how a species re-colonised northern Europe from refugia: the simplest is the grass-hopper model, as this species colonised most of Europe from a Balkan refugia; more complex is the brown bear model involving expansion from refugia in Iberia and the Balkans but not Italy; and more complex still is the hedgehog model, which expanded from all three main refugia in Iberia, Italy and the Balkans. Other scenarios can easily be envisaged. Hominins could have behaved at different times as grass-hoppers, hedgehogs or bears in their mode of re-colonisation, or (as suggested below) exhibited more complex patterning, with immigration from Southwest Asia as an important additional factor.

The demic expansions and mixing described within the source-sink concept allows the existence and persistence of a population even in circumstances of local maladaptation (Dias, 1996). The permanent migration of individuals or p-demes from source to sink habitats may lead to a stabilization of the overall demographic system despite the low demographic density and threats to survival (e.g. severe climatic oscillations).

4.4. Refugia – "arks" or "life boats"?

One common assumption implicit in many discussions of how Palaeolithic groups in northern Europe responded to a deteriorating
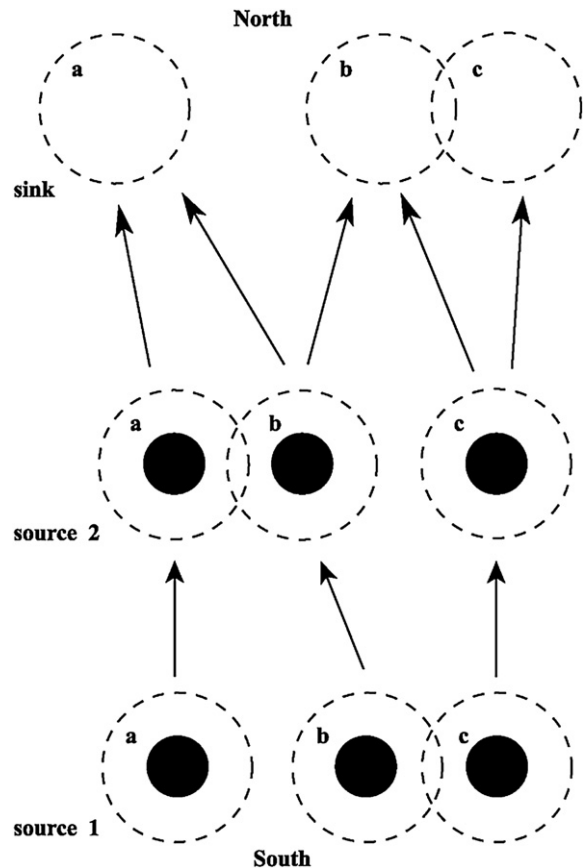
climate is that they simply retreated to refugia, where they could reside until conditions improved. These refugia thus functioned as "arks", where hominins (and other mammals) sought refuge until conditions improved. In our view, this is extremely unlikely: when biological productivity in northern latitudes (or at higher altitudes) dropped as conditions worsened, it seems unlikely that hominin (and other mammalian groups) could simply relocate to southern (or lowland) areas that would also have been experiencing environmental stress. Instead of envisaging that populations could remain stable at a continental level by using refugia as "arks", it seems much more likely that they fluctuated considerably along the lines indicated by Bocquet-Appel et al. (2005), with peaks in warm periods and troughs in cold ones. Refugia are more likely to have been "life boats", in which space was limited to local populations that had a higher chance of survival, and regional extinction seems much a more likely outcome for those elsewhere. We thus agree wholeheartedly with Hublin and Roebroeks's (2009) recent suggestion that rather than a simple "ebb and flow" model for Neanderthal occupation, implying north to south migration of populations when the climatic conditions became severe, local extinctions followed by re-colonisation would have played a major role in shaping these groups. According to them, these repeated

regional extinctions of Neanderthal populations would have led to repeated genetic bottlenecks, the survival in southern Europe of a non-random sample, and a subsequent reduction of the variability in the Neanderthal lineage. However, while we agree that local extinctions may be an important phenomenon to explain the homogeneity of the classic Neanderthals, we believe that in the early stages of this evolutionary lineage, a degree of interbreeding between demes was not only possible but was responsible for the high variability of the Middle Pleistocene populations. A pattern purely based on local extinctions maintained throughout the Middle Pleistocene would have implied a faster decline in the morphological variability and a steadier fixation of the Neanderthal traits through processes such as random allelic variation and genetic drift. However, the classic Neanderthals do not appear until the Upper Pleistocene and during a considerable period of hundreds of thousand years, the European populations maintained a high degree of morphological variability.

4.5. Closed versus open systems

Although this paper is primarily about Middle Pleistocene Europe, the continent was not a closed system, but instead one that was periodically (and probably most frequently during interglacial and interstadial conditions) open to immigration (or re-colonisation if it was totally depopulated during a glacial maximum) from refugia in Southwest Asia such as the Levant or Caucasus. The most likely route of entry into Europe is likely to have been through western Turkey into the Balkans, although some immigration from north of the Black Sea cannot be excluded. There is no evidence that hominins prior to modern humans crossed the Straits of Gibraltar (see e.g. O'Regan et al., 2006). Sadly, the Middle Pleistocene fossil hominin record for Southwest Asia is derisory compared to that from Europe, and limited to specimens with little taxonomic merit, such as the Zuttiyeh cranium, Israel, that is probably ca 300 ka (Bar-Yosef, 1998), and the recent undated fragment from western Turkey that was embedded in travertine and found during tile-cutting (Kappelman et al., 2008). A mandible fragment from Azyk, Azerbaijan, that is probably mid-Middle Pleistocene in age has been tentatively assigned to H. heidelbergensis (Howells, 1980), and at least indicates its presence in Southwest Asia.

Despite the small number and poor quality of evidence from this region, we hypothesise that it was a potential source of variability among Middle Pleistocene hominin populations in Europe (arguments in support of this source population in Southwest Asia can be found in Dennell et al., submitted). Successive migrations of hominins into Europe during environmentally suitable periods of the Middle Pleistocene would thus have provided further influxes of genetic and phenotypic variability (see Fig. 7). Thus, Europe could have worked as a "true" sink (i.e. it needed high immigration rates to maintain its population) or as a pseudo-sink (capable of surviving with a small population and without immigration, but able to accommodate incoming populations [see Watkinson and Sutherland, 1995]). As suggested above, populations in all the main glacial refugia might occasionally have become extinct, in which case Europe would then have been re-colonised from refugia in Turkey, the Levant, or other parts of Southwest Asia. The possibility of an inversion between source and sink has been also described (Dias, 1996). As an example, climate fluctuations or natural disasters may not affect all the habitats to the same degree, and some patches that were working as source regions may temporary become sinks, allowing intricate patterns of inter-demic breeding and consequently a high phenetic variability. We should not forget that the range contraction of a species is not the same as range contraction of all its groups. In fact, taking into account the low density of Upper Pleistocene populations, and the low probability
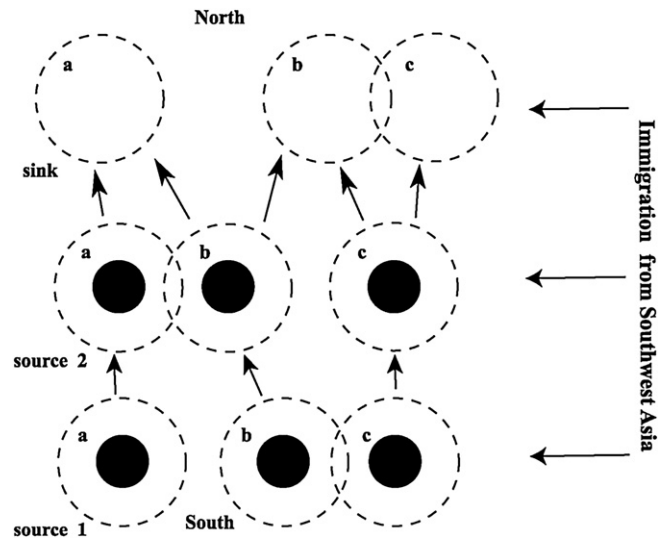

Fig. 7. Middle Pleistocene Europe as an open demic system. In this figure, Europe is treated as an open system, whereby immigration by *H. heidelbergensis* is likely under suitable conditions (usually during interglacials and interstadials) from Southwest Asia, either via western Turkey and perhaps also from north of the Black Sea. As populations in Southwest Asia would have undergone their own internal development (genetic drift, bottle necks, natural selection, etc.), each incoming population would be slightly different from its predecessors, and this too would increase the phenotypic variability among the European Middle Pleistocene inhabitants. Southwest Asia is defined as a CADE (central area for dispersals in Eurasia) by Dennell et al. (submitted).

of random-mating processes among Early and Middle Pleistocene groups, we should consider the possibility of other population dynamics, including competition. With these low demographic densities, the average rate of reproduction of these groups was probably not enough for replacement levels, underlining the necessity of continual migrations from source regions or populations to maintain the demographic level (Enflo et al., 2001). As suggested by Hawks (2009), it is unlikely that those small sized groups were capable of occupying the Western part of Eurasia and remaining as a cohesive species purely via gene flow. The climatic oscillations of the Middle Pleistocene make it likely that replacement and migrational waves would have been the pattern of peopling Europe at that time, and contributed to its small effective population size (Green et al., 2008). As suggested by Hublin and Roebroeks (2009: 5) "With the first substantial occupation of temperate Pleistocene Eurasia from the Middle Pleistocene onward, …. regional extinction and re-colonisation …. may have been an important demographic factor in the history of humankind, possibly for the first time at such a large scale".

A model based on repeated extinction and re-colonisation can involve a number of colonist or kin-structured migrations (Eller et al., 2001). Both the 'source' and the 'peripheral' populations can undergo genotype changes by mutation and natural selection so the migrational waves may present their own anatomical variations whilst still being able to mix with peripheral demes. In this context, we cannot disregard the probability that the apparently random mosaic pattern between archaic and derived populations during the Middle Pleistocene is in fact the result of local divergences and later recombination among some groups. These migrational waves would have created genetic gradients in the 'sink' populations. Thus, the 'sink' populations may have ancestors not only in the 'sink' but also in the source populations (Hawks, 2009). This could be theoretically translated to a morphological level, resulting in demes with mixture of primitive and derived traits, as it happens in Middle Pleistocene European populations (Arsuaga et al., 1997). This non-linear pattern of demes interaction could even allow the

mixture of Neanderthals with their own ancestors (a scenario already pointed out by Pääbo, 2009). This, in turn, could be an underlining reason for the impossibility of aligning in a chronological sequence the primitive and derived traits of Middle Pleistocene populations (i.e. chronologically later pre-Neanderthals look "less Neanderthal" than chronologically older specimens).

4.6. Ancestors and descendants

One interesting possibility of the model proposed here is that in some situations, populations of a palaeospecies that were ancestral to another could have interbred with their own descendants. Despite belonging to different taxonomic species, the scenario of a possible interbreeding between Neanderthals and their own ancestors, the European Middle Pleistocene populations, has been already suggested by Pääbo (2009) This pattern of interbreeding could partially explain the random combination of plesiomorphies and apomorphies in the hominin groups that inhabited Europe during this period. In the same line, we suggest that interbreeding between the European Middle Pleistocene populations of *H. heidelbergensis* and their possible ancestors (*H. antecessor*) cannot be totally discounted (Bermúdez de Castro et al., 2003; Dennell et al., submitted), especially in the early stages of their speciation, when a less derived conformation is to be expected. In this hypothetical scenario, part of the *H. antecessor* gene pool could have developed in isolation as a separate deme (and even persisted in the Middle Pleistocene as fossils like Ceprano may indicate), but another part developed anagenetically into *H. heidelbergensis*. At some point, each deme colonised a new region. Here, the colonies could have overlapped, genetic exchange could have occurred and (assuming that offspring were fertile) a hybrid palaeospecies could have developed. This scenario is shown in Fig. 8.

5. Discussion

The variability of *H. heidelbergensis* in Middle Pleistocene Europe has been largely regarded as a taxonomic nuisance that is best left to physical anthropologists to resolve, and not as a topic that has a wider relevance to studies of hominin settlement histories. As we have tried to show, the climatic and environmental instability of Europe were probably major factors in causing much of the variability of this taxon, and provides also an explanation of how phenotypic uniformity arose but without resulting in speciation. This is perhaps surprising, as allopatric speciation would be expected under conditions of prolonged fragmentation and isolation. Instead, the European fossil hominin and climatic record for the Middle Pleistocene provides an example of how and why distinct demes occurred that overlapped in space and time whilst remaining within a single palaeospecies. The migrational pattern described here by a source and sink model would allow the existence and persistence of the Middle Pleistocene populations despite a low demographic density and negative environmental conditions. This pattern may have led to the stabilization of the demographic system despite the cyclic deterioration of the habitat. Inter-demic mixing would have allowed a higher genetic and phenetic variability despite the isolation and local extinctions of these groups. Eventually, maintained isolation and repeated genetic bottlenecks (particularly pronounced with the last glaciation) could have led to a drastic reduction of the variability and phenotype of the classic Neanderthals (Hublin and Roebroeks, 2009) and (as possibilities that need to be explored in more detail), insufficient genetic viability and eventual extinction.

The settlement pattern outlined here that was based on a small number of glacial refugia in southern Europe that contained the "core" populations that survived most, and possibly, all the glacial
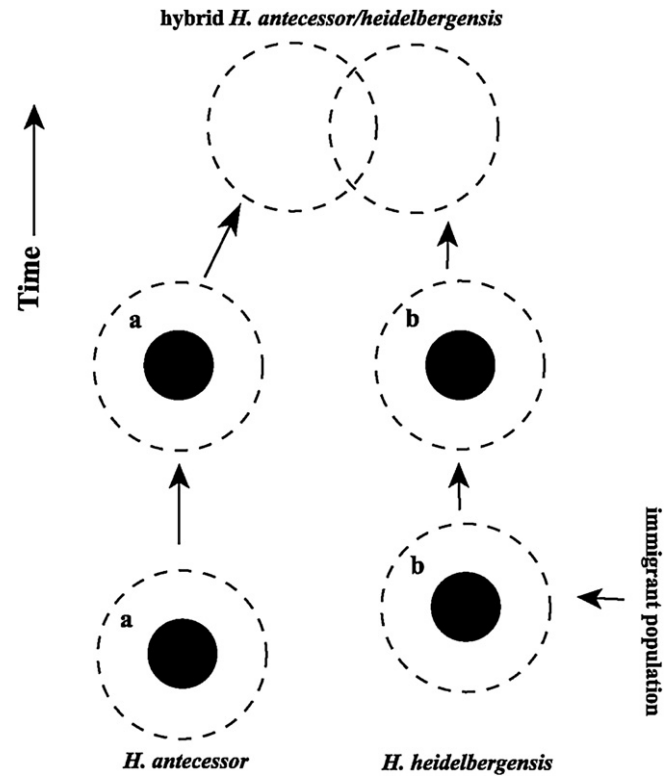

Fig. 8. Ancestors and descendants. This figure shows schematically how a palaeospecies that is ancestral to one palaeospecies might interbreed with some of its descendants. In this example, part of the *H. antecessor* gene pool (bottom) develops in isolation as a separate deme, but another part develops anagenetically into *H. heidelbergensis* (middle). In the top part of the diagram, each colonises a new region. Here, the colonies overlap, genetic exchange occurs and (assuming that offspring are fertile) a hybrid palaeospecies develops.

maxima of the Early and Middle Pleistocene permit one further observation about the European fossil hominin record. If the main glacial refugia were in the Balkans, the Italian Peninsula and Iberia, it follows that hominin specimens from outside these regions should represent peripheral populations that did not necessarily leave descendants. This may help explain some of the problems in linking them all to a simple set of ancestor-descendant relationships, as some may have been dead-ends if, as suggested here, population extinction was a more likely outcome than a simple ebb and flow model of populations out of and back into glacial refugia. Of the likely core regions that contain hominin specimens, the Balkans are represented by only the Petralona specimen which is more or less undateable and devoid of any palaeo-environmental context, and the end-Middle Pleistocene Neanderthal sample from Krapina. The only pre-Upper Pleistocene specimen from Italy that is well-studied and well-dated is the Ceprano specimen of *H. cepranensis*, which now seems highly anomalous if it indeed dates to the mid-Middle Pleistocene. This leaves the Iberian Peninsula, which now has a very rich fossil record, thanks to the numerous discoveries at Atapuerca. However, as noted above, the evidence from Sima del Elefante and Gran Dolina appears to indicate that hominins were present in interglacial periods, as also in the Orce Basin, so these might not represent core populations. The key sample is of course the Sima de los Huesos sample of 28 individuals; although its palaeoclimatic context is unknown, we should bear in mind the possibility that even this sample might not have been a "core" population. Until we have a clearer idea of the "core" populations of Early and Middle Pleistocene Europe, we will continue to face problems in identifying the evolutionary links between specimens.

The demographic model proposed here also has a wider relevance to studies of other Middle Pleistocene populations in comparable settings. China is one example, on the other side of the Eurasian landmass. In Middle Pleistocene China, the primary inhabitant was *H. erectus* s.s. (most famously represented at Locality 1, Zhoukoudian), and late Middle Pleistocene specimens are often referred to by Chinese and a few western researchers as "archaic *H. sapiens*". (Some western researchers also claim that specimens such as Dali and Jinnuishan should be classified as *H. heidelbergensis* (see Rightmire, 2001), in which case there may have been at least two contemporaneous hominin species), The climatic record for China is very similar to that from Europe in showing numerous interglacial and interstadial episodes, and its fauna and flora responded in the same way by repeated expansion and contraction. There is also evidence of morphological heterogeneity among the hominin populations. For example, Howell (1999) suggested that Yunxian/Lantian, Locality 1 Zhoukoudian, Dali, Jinnuishan, Maba (which he also grouped with the Hathnora specimen from India) should each be regarded as a separate deme. More recently, Liu et al. (2005) have suggested that Hexian and Tangshshan (Nanjing) show some differences from the Locality 1 hominins, and Durban et al. (2005) have also concluded that there are major differences between the Hexian specimen and Locality 1, Skull V. The pattern of hominin settlement and evolution in Middle Pleistocene China may not differ greatly from that in Europe.

6. Memes and demes

As a final point, our model of population fragmentation, recombination, extinction and expansion may help explain some of the variability that is evident in Middle Pleistocene lithic assemblages, particularly in northern Europe. If, as we suggest, northern Europe was repeatedly re-colonised (and probably from different directions) by groups that usually became extinct when conditions deteriorated, it is perhaps unsurprising that there is evidence of different lithic "traditions" (particularly Acheulean and Clactonian ones) and a non-linear pattern of development within them. Lithic variability may thus have resulted from demographic discontinuities and regroupings under conditions of repeated instability.

7. Conclusions

Four main points arise from this paper. The first is the need to view holistically the variability of European pre-Neanderthal populations in of Europe in relation to the highly unstable climatic and environmental conditions that prevailed throughout the Early and Middle Pleistocene. When viewed in this way, the variability of *H. heidelbergensis* is an unsurprising outcome of repeated dispersal, fragmentation, regional extinction, and recombination. Secondly, we suggest that we need to move beyond a simple "ebb and flow" model for Middle Pleistocene Europe, in which populations expanded northwards in favourable circumstances, and then retreated southwards into refugia when conditions deteriorated. A more realistic approach is to view populations as "sources" or "sinks" – the former in South and Southeast Europe giving rise to and helping to sustain the latter in Central and northern Europe, which would have experienced high rates of local extinctions and wipe-outs but also some mixing between sink survivors and source inhabitants. In this model, glacial refugia were not areas to which groups retreated, but areas where some populations survived. Refugia are thus better regarded as core populations (see e.g. Dennell, 2009: 475) or as genetic bottlenecks: as Bennett and Provan (2008: 2453) point out, renaming refugia as bottlenecks has the considerable advantage of indicating population continuity in that populations go through bottlenecks but come out through refugia. When viewed in this way, the Middle Pleistocene record for hominins might not have been structurally very different from that of trees, which "on the Quaternary time-scale resemble the periodic irruptions, followed by population collapse, of lemming populations .... north European tree species are really not 'adapted' in any particular way to the changing climates of the Quaternary. They exist, for the most part, as small, local populations, which increase dramatically when climates changes in their favour. Since the climate changes are not permanent, the new populations ultimately become extinct" (Bennett et al., 1991: 111). Thirdly, the Balkans were probably one of the principal hominin refugia (or bottlenecks, or core areas of settlement) in Middle Pleistocene Europe, yet almost nothing is so far known of their settlement history: this imbalance in data coverage needs to be addressed as a major priority. Finally, we suggest that although Palaeolithic Europe is often treated as a closed system, it needs to be seen as an open-ended one at the western end of the Eurasian landmass that experienced frequent episodes of immigration throughout the Pleistocene; there may even have been times during the past million years when Europe was completely depopulated and then re-colonised.

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