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Hominin Evolution in the Middle-Late Pleistocene

Fossils, Adaptive Scenarios, and Alternatives

by Osbjorn M. Pearson

Hominins from Europe and Africa shed light on functional adaptations and other aspects of lifeways during the Middle Paleolithic. By the end of that time span, Neanderthals and modern humans clearly differed physically and perhaps behaviorally. Explanations of the anatomical differences have largely focused on adaptation (directional selection) to climate and habitual activity, but it is hard to rule out the alternative of genetic drift. Drift would have accelerated during periods of low population numbers, while selection operates best when populations are large and expanding. Demographic changes almost certainly tracked climatic conditions in both continents. Environmental and genetic data suggest that European hominins were primarily shaped by drift, while both factors operated in Africa.

The period of time between 250 and 35 ka witnessed the emergence of Neanderthals in western Eurasia, modern humans in Africa, and, at around 60 ka, the spread of modern humans into Eurasia, where they replaced archaic humans, albeit with a small amount of interbreeding. Interpretations of these events have tended to focus on different anatomical and cultural adaptations as the key underlying forces responsible for producing the differences between modern humans and Neanderthals. The alternative, that genetic drift drove some or perhaps many of the anatomical changes, has long been recognized (Howell 1957) but has received less emphasis.

The time is ripe for a reconsideration of scenarios for adaptive change because of the accumulation of a critical mass of new evidence from paleoecology, genetics, anatomy, and chronology. Paleoclimatic records provide insights into why at least some of the morphological and genetic evolution may have occurred. In this paper, I argue that climate and population genetics are linked. Climate affects ecological productivity and biomass, which in turn affects human population numbers. Changes in population size have predictable consequences for the expected rate of neutral genetic change.

The general outline of the evolution of modern humans and Neanderthals is well known (Arsuaga 2010; Arsuaga et al. 1997; Hublin 2009; Martínón-Torres et al. 2012; Stringer

2007, 2011). Both populations diverged from a common ancestor around 350,000 years ago as gauged by both genetic differences (Green et al. 2010) and divergence in cranial dimensions modeled as the result of neutral evolution (Weaver, Roseman, and Stringer 2008).¹ There is less agreement about the deeper phylogeny of these lineages and related forms from the late Lower through early Middle Pleistocene, but that period predates the central focus of this paper. Key anatomical differences between Neanderthals and modern humans include both the differential retention of primitive features in each lineage as well as new features (apomorphies) in each.

In Europe, the Neanderthal lineage evolved a series of apomorphies, including midfacial prognathism, a posterior position of the mental foramen, a retromolar gap in the mandible, a broad suprainiac fossa that is oval in form, a large juxtamastoid process coupled with a small mastoid process, an occipital bun, double-arched browridges that are reduced in absolute volume and vertical thickness compared with those of Middle Pleistocene hominins, and a substantially larger brain than those of most Middle Pleistocene hominins

1. Recent papers have produced a range of estimates for when the ancestors of Neanderthals and modern humans split, ranging from ~835 ka for the average divergence for autosomal sequences (Green et al. 2010) to estimates of 270–400 ka for the population (rather than DNA sequence) divergence time (Green et al. 2010) based on the same data. Other authors have calculated additional estimates for the divergence times between Neanderthals, Denisovans, and modern humans (e.g., Harris and Nielsen 2013; Li, Mulliken, and Reich 2010; Meyer et al. 2012; Reich et al. 2010). It is important to note that estimates of DNA divergence dates generally precede (often substantially) estimates of population divergence.

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(Hublin 2009; Stringer 2007). Hublin (2009) considers that the full set of Neanderthal features were present by oxygen isotope stage (OIS) 7,² and 3-D morphometric analyses of the face, temporal bone, and posterior cranial vault corroborate this view (Harvati, Hublin, and Gunz 2010). This suite of Neanderthal features had become common in European hominins by OIS 5, including the specimens from Krapina and Saccopatore, and they became even more frequent in OIS 4–3. This gradual increase in similarity to late Neanderthals has been dubbed the “accretion model” and may have unfolded as a single, long trend or perhaps in two pulses (Hublin 2009). A similar pattern applies to the evolution of Neanderthal postcranial morphology (Trinkaus 1983, 2006). Scenarios for the evolution of Neanderthal postcranial morphology have tended to emphasize adaptation to either the need to produce large amounts of physical force or to preserve heat in a cold climate.

The problem of whether Sima de los Huesos is young (ca. 350 ka) or old (500–600 ka) complicates scenarios for the pace of evolutionary change in Europe (Stringer 2012). The Sima de los Huesos sample shows mosaics of Neanderthal and non-Neanderthal morphology in virtually all aspects of its morphology (Arsuaga et al. 1997). Recently Martínón-Torres and colleagues (2012) have shown that the sample has very Neanderthal-like teeth; some of the nonmetrical features are even more common in the Sima de los Huesos sample than in late, “classic” Neanderthals from OIS 4 to OIS 3, which casts doubt on simple models of a steady increase in Neanderthal features over time. Recent alternative hypotheses that accept the greater antiquity for Sima de los Huesos have proposed the presence of two lineages in Europe until 300–400 ka (García and Arsuaga 2011) or complicated scenarios of local extinction, recolonization, and admixture of two or more populations (Dennell, Martínón-Torres, and Bermúdez de Castro 2011).

While Neanderthals evolved in Europe, hominins in Africa evolved gradually toward a modern form (Bräuer 2008; Pearson 2008; Rightmire 2009). Modern human apomorphies include a larger brain than generally observed in African crania dating to 300 ka or before; a more globular cranium (Lieberman 2011; Lieberman, McBratney, and Krovitz 2002) with more bossed parietals and an enlarged temporal lobe (Lieberman 2011); an altered trajectory of endocranial growth relative to Neanderthals (Gunz et al. 2012); a vertically short face tucked beneath the frontal lobe (Lieberman 2011); retention of a canine fossa into adulthood; and the presence of a projecting chin on the mandible (Stringer 2002, 2007). The earliest crania that demonstrate the full suite of modern fea-

2. Both ice cores from Greenland and Antarctica as well as deep-sea cores (and other data) help to reconstruct long-term patterns of climate change. Many authorities prefer the term “marine isotope stage” for this sequence because the marine sequence is the longest and most complete, but in light of the importance of ice cores in illuminating the last 300 kyr, I have used the older and more inclusive oxygen isotope stage (OIS) throughout this paper.

tures are Omo I, dated to 195 ka (Brown, McDougall, and Fleagle 2012; Day and Stringer 1991; McDougall, Brown, and Fleagle 2005), and the Herto crania at 150–160 ka (Clark et al. 2003; White et al. 2003).

Advances in imaging, especially synchrotron x-rays, which allow researchers to peer inside teeth and count daily increments of enamel accretion (Smith and Tafforeau 2008), have revealed that Neanderthal children matured more rapidly than modern children (Smith et al. 2010). Neanderthals thus bear a closer resemblance to the ancestral condition of even more rapid dental skeletal maturation of *Homo erectus* (Dean and Smith 2009; Dean et al. 2001; Graves et al. 2010). In contrast, the mandibular dentition of Jebel Irhoud 3, a juvenile late archaic hominin from Morocco dating to 160 ka with affinities to modern humans (Hublin 2001; Hublin and Tillier 1981), preserves evidence of a slower, modern pace of dental development (Smith et al. 2007).

Both African and European Middle Pleistocene hominins tended to be medium to tall in stature (Carretero et al. 2012) and very heavy for height relative to modern hunters and gatherers (Churchill et al. 2012; Kappelman 1996). A more slender physique typified Omo I from Africa (Pearson et al. 2008) and the early modern humans from Skhul and Qafzeh in Israel (Carretero et al. 2012; Ruff, Trinkaus, and Holliday 1997). Neanderthals remained at least 20% heavier relative to modern human foragers of similar height (Kappelman 1996; Ruff, Trinkaus, and Holliday 1997). Carretero et al. (2012) proposed that this reduction in body mass may have been an evolutionary adaptation to a lifestyle that favored energy efficiency. The stature of early modern humans from the Levallois-Mousterian of the Levant and the Gravettian of Europe is particularly striking relative to Neanderthals and almost all other samples from Europe before the twentieth century (Carretero et al. 2012).

Adaptation or Drift?

Over the last 50 years, the dominant view of the differences between Neanderthals and modern humans has been that the dissimilarities in anatomy reflected adaptive differences shaped by natural selection to meet specific challenges. Coon (1962), for example, argued that the enormous nose of Neanderthals had evolved to warm glacial air. Trinkaus’s (1983) influential analysis of the Shanidar Neanderthals emphasized that Neanderthal morphologies met adaptive needs for greater strength or leverage relative to modern humans. Trinkaus argued that many distinctive facial features of Neanderthals and their relatively large canines and incisors were adaptations for increased amounts of anterior biting. Some of the adaptive hypotheses have not received experimental support. For example, building on previous observations by Hylander (1977) about Neanderthal and Inuit noses, Rae, Koppe, and Stringer (2011) found no evidence that the Neanderthal face is cold adapted. Similarly, Clement, Hillson, and Aiello (2012) found

no, or at best ambiguous, support for the hypothesis that Neanderthal faces were specially shaped to resist anterior dental loading.

The evidence that Neanderthal bodies were adapted to a cold climate lies in their wide hips, shortened distal limb segments, short limbs relative to trunk length, and large articular surfaces and thick long bone shafts, all of which characterize recent humans whose ancestors have lived in cold climates for thousands of years (Holliday 1997; Pearson 2000; Ruff 1994). Wide hips and robust long bones were already present in the Sima de los Huesos sample (Arsuaga et al. 1999; Bonmatí et al. 2010) and may have been the primitive condition for Middle Pleistocene *Homo* (Arsuaga et al. 1999). Wide hips may have also been inherited from *Homo erectus* (Simpson et al. 2008) rather than appearing as an evolutionary novelty in Middle Pleistocene hominins.

Recently, Betti, von Cramon-Taubadel, and Lycett (2012) demonstrated that variance within pelvic dimensions of living humans tracked population history (distance from Africa) rather than climate while variance in the dimensions of the femur and tibia correlated with minimum annual temperature rather than population history. The implications of these findings are that contrary to previous conclusions (Ruff 1994), pelvic form appeared to have followed a pattern of largely neutral evolution like most human cranial dimensions (Betti et al. 2009, 2010; Roseman 2004; Weaver, Roseman, and Stringer 2007, 2008). Given congruent estimates for stature based on femurs and tibiae, the Sima de los Huesos sample appears to have less shortened distal limb segments than Neanderthals (Carretero et al. 2012), which provides some evidence that European hominins evolved more cold adapted proportions over time. In a review of 75 distinctive cranial, dental, and postcranial features of early modern humans and Neanderthals, Trinkaus (2006) concluded that only one quarter were unique to Neanderthals while twice that many were unique to modern humans, a finding that means that Neanderthal morphology had remained fairly primitive while early moderns were much more derived. This could provide evidence that early modern humans had shifted to different niches than archaic humans and had experienced a substantial pulse of selection that tailored them for their new habits.

Genetic drift provides an alternative explanation for morphological divergence (Howell 1957). Although this hypothesis has been marginalized historically, recent reviews have emphasized its potential importance (e.g., Hublin 2009). Weaver, Roseman, and Stringer (2007, 2008) demonstrated that if one applies a model of neutral evolution to expected divergence in cranial dimensions, the observed morphological divergence between humans and Neanderthals could be explained solely as the result of genetic drift over the last 350 kyr. In addition, some recent approaches to cultural innovations also emphasize the role of chance, especially if change is dependent on population size and density (e.g., Powell, Shennan, and Thomas 2009; Shennan 2001). These results

are exciting and motivate one to take a closer look at some of the recent genetic advances.

Genetics

Views of the origin of modern humans and our divergence from Neanderthals have been profoundly and perhaps decisively influenced by genetic data from living humans as well as ancient DNA (aDNA) from Neanderthals. The completion of a draft of the Neanderthal nuclear genome (Green et al. 2010) and recovery and analysis of nuclear and mitochondrial DNA from “Denisovans,” a third lineage that separated from modern humans slightly before Neanderthals (Meyer et al. 2012; Reich et al. 2010), stand out as signal achievements. These discoveries have decisively answered the question of whether interbreeding occurred between modern and archaic humans (it did in both cases) and opened new windows on which genes may have been involved in producing evolutionary novelties in both modern humans and Neanderthals.

Analysis of autosomal DNA indicates a divergence time between modern human and Neanderthal populations of 270–440 ka (Reich et al. 2010). Work on aDNA has also shed more light on Neanderthal population history, suggesting a marked bottleneck among their ancestors sometime before the time of the Mezmaiskaya neonate, 60–70 ka (Reich et al. 2010), and another bottleneck after 48 ka (Dalén et al. 2012). Furthermore, all Neanderthal mtDNAs share a common ancestor approximately 100 ka and a common ancestor with modern humans ~500 ka (Reich et al. 2010).

Modes of Genetic Evolution

At the genetic level, two of the fundamental means by which evolution can occur are natural selection (referred to subsequently simply as “selection”) and genetic drift. The two processes are not mutually exclusive, and both often act on a population at the same time. Selection generally works on a given gene only if different alleles exist and one confers higher fitness than another, although epistasis (the interdependence of genes to produce a phenotype) may produce a shifting target for selection. The ultimate source of new alleles is mutation, which occurs rarely. Most mutations are either neutral (and have no effect on natural selection) or harmful (by interfering with gene function and thus causing deleterious effects to the organism); only a small number of mutations prove to be beneficial. Most selection pressures that have actually been observed in nature are weak in strength; alleles under strong positive selection rapidly move to fixation while alleles under strong negative selection are rapidly removed from a population (Futuyma 1986).

In a larger population, one expects more of the rare, favorable mutations to arise simply because the number of new mutations varies with population size (Cochran and Harpending 2009; Hawks et al. 2007). Large populations also tend to moderate, often to a great degree, the effects of drift. Thus,

large populations provide favorable conditions for the production of new, beneficial mutations; large and growing populations provide the most fertile ground for new mutations to arise and increase in frequency.

Under a neutral model of evolution, most new mutations are lost to drift (especially in small or numerically stable populations). In growing populations, new mutations are more likely to be preserved, while in shrinking populations they are more likely to be lost because of drift (Harpending et al. 1993, 1998). Drift slows in large populations but accelerates in small populations and can override the signal of all but the strongest selective pressures. As a result, population size emerges as a key variable in both selection and drift. Estimating population size in the past is difficult and invariably requires one to make a series of assumptions that are open to criticism. The problem may not be intractable, however, because during the Middle and Upper Pleistocene, recurrent 100,000-year-long glacial cycles drove climate change and almost certainly affected hominin populations.

Geology and Paleoclimate

The climate in Europe in the Middle-Upper Pleistocene was dominated by a high-amplitude 100,000-year cycle that appears to have been determined by the eccentricity cycle in the earth's orbit around the sun (deMenocal 2004). The glacial cycles show up very clearly in oxygen isotope values from deep-sea cores and ice cores from Greenland and Antarctica (deMenocal 2004). The paleoclimate of Africa presents a more complicated picture but one that is ultimately related to orbital dynamics because of changes in air circulation and rainfall that arose as consequences of the amount of solar radiation (insolation) that reached the earth (Siddall et al. 2010; Trauth, Larrasoana, and Mudelsee 2009). In Africa, oscillations in precipitation were more crucial than temperature, and paleoclimatic records show that precipitation fluctuated dramatically in Africa during the Pleistocene.

Records of dust flux from deep-sea cores such as ODP 721/722 in the Arabian Sea and ODP 659 off of the coast of Mauritania can serve as proxies for precipitation in East Africa and the western Sahel and southern Sahara (deMenocal 2004; Trauth, Larrasoana, and Mudelsee 2009). The record stems from long-standing patterns of atmospheric circulation. In June, July, and August, clockwise-circulation monsoonal winds blow moisture onshore in Somalia from the Indian Ocean and carry dust from Somalia into the Arabian Sea. During the same months the southerly Shamai winds scour dust off of the Arabian Peninsula and deposit it in the Arabian Sea. The dust-flux record from the Arabian Sea, ODP 721/722, therefore records both of these influences. Site ODP 659, off of the coast of Mauritania and Western Sahara, receives a substantial amount of its dust from the southern Sahara and northern Sahel during these months. During December, January, and February, the direction of air circulation reverses over East Africa, and the Trade Winds blow air onshore over

East Africa and across the Sahel and much of the Sahara from a northeasterly counterclockwise direction. Site ODP 659 also receives dust from Western Sahara and portions of the northern Sahara during these months.

Ample precipitation over East Africa and the southern Sahara and Sahel promote the growth of vegetation, which decreases the amount of dust that winds scour off of the land. Periods of decreased precipitation diminish the amount of vegetation and dependent biomass (including humans) and produce more dust. The Arabian Sea dust core shows a 100,000-year oscillation between wet and dry with the most intense and long-lasting dry periods corresponding to the major glacial advances in the Northern Hemisphere (fig. 1). Major dry phases would have been guaranteed to produce greatly expanded Sahara and Kalahari deserts and unfavorable conditions for human habitation. This seems to have happened many times in the past, with conditions in OIS 2 serving as a case in point (Brooks and Robertshaw 1990; Deacon and Lancaster 1988). In addition, cores and seismology of several of the oldest East African great lakes, especially Lakes Malawi and Tanganyika, have shown that substantial portions of tropical Africa south of the equator experienced severe droughts over the last 200 kyr that would not have been inferred from the oxygen isotope curve (Burnett et al. 2010; Cohen et al. 2007; Scholz et al. 2011), although the effects of these droughts appear to have been mitigated or absent at the equator and cannot be generalized to the whole of Africa (Blome et al. 2012). Some of the reconstructed lake levels (e.g., for Lake Malawi) do not closely follow the dust curves (fig. 2), suggesting yet another layer of complexity in the climatic record.

In Europe, major glaciations appear to have pushed hominins out of the northern European plain and Britain and into southern refugia along the Mediterranean Sea (Dennell, Martín-Torres, and Bermúdez de Castro 2011; Stringer 2006). Very wet and warm periods in Europe produced dense forests that may have also been unfavorable habitat (Roebroeks, Conard, and Van Kolfschoten 1992), although interstadial periods seem to have been far more favorable for hominin populations than the coldest periods of glaciations.

Predictions

The direct influence of climatic conditions on population sizes in Europe and Africa allows a series of predictions about the relative ability of selection and drift to produce changes in hominin populations. Periods of large-scale glacial advance in Europe should produce periods of stress and low population numbers and rapid genetic drift in Neanderthals. In contrast, periods of warmer but not yet heavily forested conditions would have supported a higher biomass of large herbivores and the humans who preyed on them (Roebroeks, Conard, and Van Kolfschoten 1992), thus producing an increase in hominin population numbers and a decelerated rate of drift.

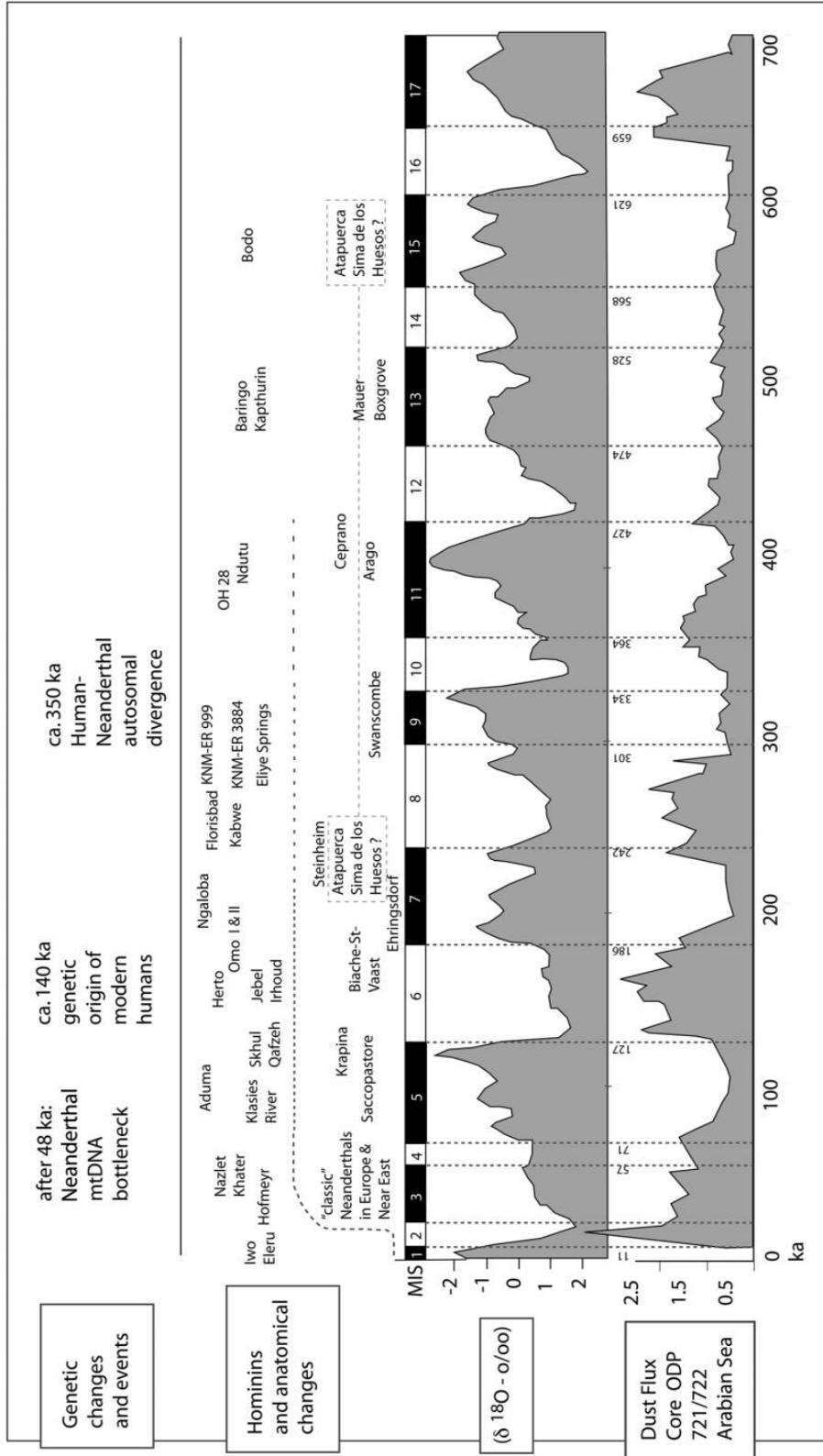


Figure 1. Key events in genetic evolution, ages of fossil specimens, oxygen isotope stage (OIS) curves, and dust-flux data from the Arabian Sea. OIS curves adapted from Klein (2009); dust-flux curves from Donges et al. (2012).

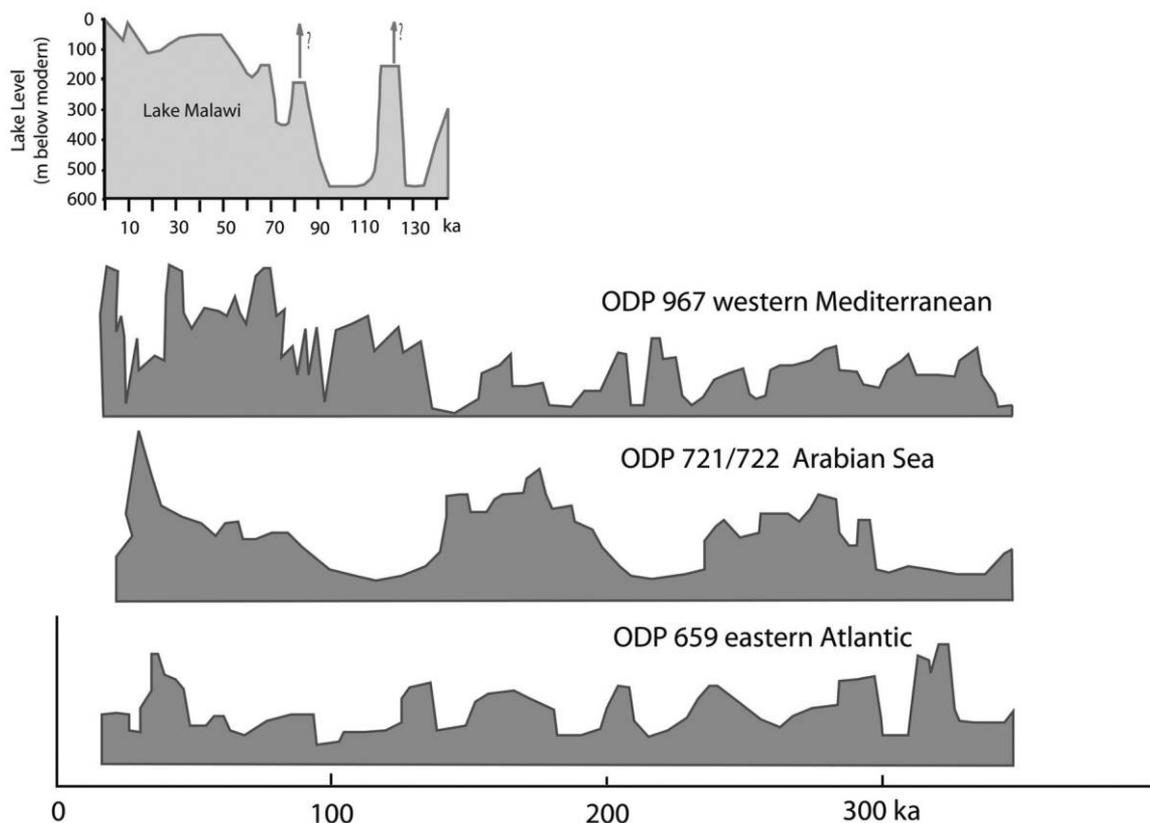


Figure 2. Water levels in Lake Malawi over the last 145,000 years and 300,000 years of dust flux from different sea cores. Water levels adapted from Scholz et al. (2011); dust-flux data after Donges et al. (2012).

Mellars and French (2011) have argued that Neanderthals in southwestern France had population numbers during the Würm Glaciation (OIS 4–3) that totaled approximately one-tenth (actually 1/9) as many individuals as the later Aurignacian occupation, although many of the assumptions that led to this conclusion have been challenged (Dogandžić and McPherron 2013) and defended (Mellars and French 2013). Mellars and French (2011) refrained from proposing an estimate of the number of individuals this would have involved, but Bocquet-Appel et al.'s (2005) model for human population in Upper Paleolithic Europe produced an estimate of the population of Europe during the Aurignacian of 4,424 people (95% confidence interval [CI]: 1,738–28,359). If one accepts Bocquet-Appel et al.'s (2005) estimates for the Aurignacian and extends Mellars and French's (2011) conclusions to the whole of Europe, it would imply that the Neanderthal population of Europe only totaled 492 individuals (95% CI: 193–3,151). Reviewing previous estimates of Neanderthal population numbers, Dennell, Martínón-Torres, and Bermúdez de Castro (2011) proposed the Neanderthal population of Europe totaled 3,000–5,000 during interstadials and 1,500–2,500 during the depths of glacial advances, when Neanderthal populations were confined to refugia in Iberia,

Italy, and the Balkans. At the higher end of estimates, Sørensen (2011) proposed a population of less than 10,000 individuals during the Eemian interglacial (OIS 5e), when Neanderthal numbers and inhabited territory may have been at a peak. Such low numbers would make sense given the large territories required for the Neanderthal specialization on large-bodied prey (Stiner 2013). If these remarkably low population numbers are accurate, Neanderthals may never have been numerous enough to experience conditions in which there were enough individuals for favorable mutations to arise at a brisk pace. Rather, they may have been skirting the edge of extinction for most of their existence, generally losing genetic diversity as they did so. Neanderthals may have only rarely experienced periods of population growth and range expansion.

New data from the Denisovan genome from Siberia (Meyer et al. 2012) suggest that this population also had a strikingly low long-term effective population size of approximately $N_e = 1,667$ individuals for the period between 400 and 100 ka (Li, Patterson, and Reich 2012). It is important to bear in mind that effective population size can be different from (and sometimes lower by an order of magnitude or more) census size (the actual number of individuals) and that N_e approx-

imates the harmonic mean of the number of breeding individuals over time. Nevertheless, for an effective population size to shrink from 16,667 before 400 ka to 1,667 after 400 ka as the Denisovans did and apparently remained (Li, Patterson, and Reich 2012), the population must have crashed to 1,667 individuals (or fewer) one or more times.

Lest one think that Neanderthals and Denisovans were fundamentally different from modern humans in the face of climatic instability, it is important to realize that some recent research to model effective population size in modern human populations based on genomic data suggests that both the ancestors of living Europeans and Chinese experienced one or more severe bottlenecks between 40 and 20 ka such that the effective population size of each of these populations shrank to a size of approximately $N_e = 1,200$ during this interval before rebounding to a higher size (to N_e between 11,000 and 50,000) during the Holocene (Li and Durbin 2011). This result implies that similar dynamics, likely attributable to climatic cycles, affected archaic and modern populations in Eurasia in very similar ways.

Recently, a number of authors have stressed that climatic deterioration in Europe and the Near East could have led to the local extinction of populations (Dennell, Martínón-Torres, and Bermúdez de Castro 2011; Hublin and Roebroeks 2009; Shea 2011; Stewart and Stringer 2012; Stringer 2006). Britain, in particular, seems to have been abandoned with each major glacial advance and then reoccupied, at least as long as a land bridge connected it to the continent (Stringer 2006). Heinrich events, short periods of extreme cold followed by rapid warming, during glaciations may have posed especially difficult challenges for hominins in Europe (Stewart and Stringer 2012) and perhaps contributed to a contraction in the range of Neanderthals in southern Iberia and the spread of modern humans bearing Aurignacian technology into France and northern Spain (d'Errico and Sánchez Goñi 2003).

In Africa, especially in East Africa, biomass and human population size were much more dependent on the availability (and predictability) of precipitation, and the dust-flux data from deep-sea cores provide an accessible gauge of precipitation (deMenocal 2004; Rohling et al. 2013). Periods of low dust flux indicate more precipitation, more vegetation, more animal biomass, and more people. During these times selection would logically have more power to create phenotypic change, and genetic drift would be less influential. Periods of high dust flux correspond to less precipitation, less vegetation, fewer people, and thus rapid genetic drift. The scale of the effect of climatic changes on human populations is clearly apparent in the dramatic decrease in the number of sites in the Last Glacial Maximum in East Africa (Brooks and Robertshaw 1990); difficulties for human populations likely continued even after that, including evidence of the desiccation of Lake Victoria until ca. 14.5 ka (Williams et al. 2006) and the desiccation of Lake Tana around the same time (Lamb et al. 2007; Marshall et al. 2011).

If selection was the crucial factor driving change in the

lineages of Neanderthals or modern humans, then major changes in anatomy in each lineage should emerge during periods that favor large population numbers. On the other hand, if drift was the key force in driving the divergence of Neanderthals and early modern humans, then key evolutionary events and appearance of new morphologies should appear during or immediately after periods of low population numbers. As new morphologies may be effectively invisible in the fossil record during periods of contracted population size, they may, in fact, appear in the record only slightly later, once population sizes had rebounded.

Any test of these hypotheses faces practical limitations, including an incomplete fossil record, poor dating of some fossils, and inadequate resolution of current methods in pinpointing morphological or genetic changes to exact spots in the 100,000-year glacial and faster insolation cycles. Margins of error for dates for fossils or genetic events may overlap both favorable and unfavorable periods of climatic cycles. A further difficulty particular to Africa lies in the variability of dust-flux records: different patterns occur in different cores around Africa (fig. 2). For the sake of argument, I assume in this paper that the record of dust flux from the Arabian Sea is the most relevant to the origin of modern humans, but this issue is certainly open to debate. As a case in point, Blome et al. (2012) synthesized paleoclimatic records for the whole of Africa using multiple proxies, including terrestrial, lacustrine, and oceanic data (fig. 3). The resulting synthesis depicts a mosaic of wet and dry periods that are frequently asynchronous between regions and do not correspond in a consistent way to the OISs. Their results for East Africa are perhaps the most useful for inferences regarding the origin and dispersal of modern humans. Likewise, Rohling et al. (2013) present multiproxy data for the Mediterranean and Red Sea regions, two areas that were crucial for hominin dispersals from (and perhaps into) Africa during the last 500 kyr. The arrows in figure 3 extend the analyses of Blome et al. (2012) by indicating possible population expansions within Africa and possible expansions into Arabia during the windows of opportunity described by Rohling et al. (2013). In each case, populations can be inferred to have spread from regions with favorable climate and thus presumably comparatively high human population density into regions previously nearly devoid of people but with newly favorable climatic conditions.

Results

Comparison of the time lines of paleoclimate, the fossil record, and genetic divergences and bottlenecks provide a rough check of whether key events occur in periods favorable for large population numbers or in periods unfavorable for large populations (fig. 1). In many cases, the relationships are highly suggestive, but problems remain.

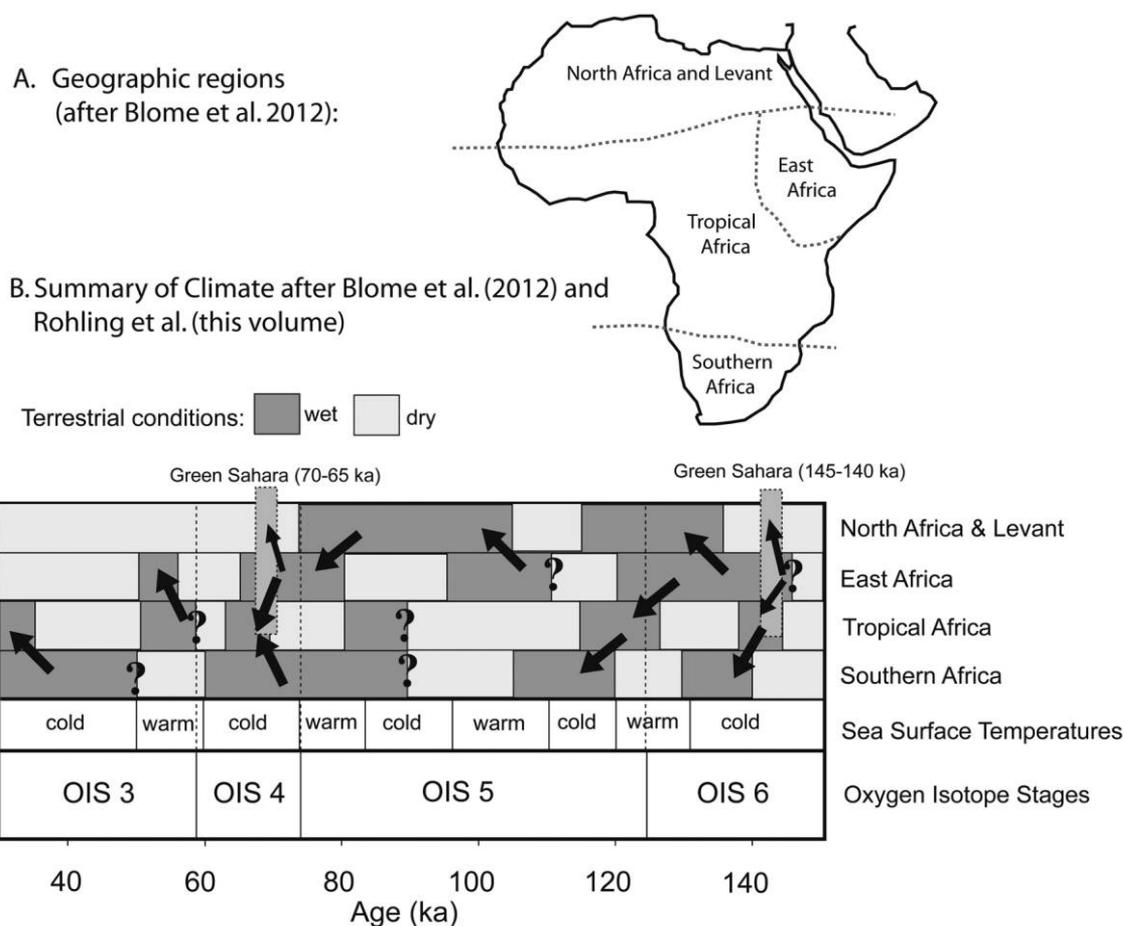


Figure 3. A, Geographical regions in Africa adapted from Blome et al. (2012, with permission from Elsevier). B, Climate in Africa adapted from Blome et al. (2012, with permission from Elsevier) with two periods of a wet Sahara coinciding with periods of low sea level (following Rohling et al. 2013) indicated. The arrows show possible directions of colonization from regions of higher population density into adjacent areas. Question marks symbolize that the geographic source of the colonizing population is uncertain (and thus, one might assume, largely of local origin).

Europe

The age of the fossils from Sima de los Huesos is a key problem for making sense of the tempo and mode of hominin evolution in Europe over the last 500 kyr (Stringer 2012). If the Sima de los Huesos dates to 500–600 ka (Bischoff et al. 2007), then one can conclude the features characteristic of the later, “classic” Neanderthals dating to OIS 4–3 increased in frequency very slowly within the Neanderthal lineage. Hominins with the full suite of Neanderthal cranial traits appear by OIS 7 (Hublin 2009), but a further pulse of change made western European Neanderthals from OIS 4–3 especially distinctive. It is difficult to tell whether this apparently late inflection in the rate of “Neanderthalization” was the result of selection within a large population during OIS 5 or of rapid drift in a small population during OIS 4–3.

Neanderthal mtDNA sequences provide support for a late bottleneck in their population. A recent analysis of the ancient

mtDNA of a Neanderthal from Valdegoba, Spain, dating to 48.5 ka, shows that all Neanderthal mtDNA sequences post-dating this time formed a compact, monophyletic group within the known Neanderthal sequences (Dalén et al. 2012). These late, western Neanderthal mtDNA sequences have a coalescent age of 58 ka (the end of OIS 4) with a 95% CI 54–77 ka. A severe population bottleneck (or selection, which may be less likely) could produce such a pattern. Dalén and colleagues (2012) conducted an Approximate Bayesian Computation Analysis to test demographic models of neutral evolution that were the most likely to produce this pattern of greatly reduced diversity. The results showed that the most probable scenario (isolation and drift in the western and eastern populations of Neanderthals at 48 ka) would have involved an effective population size (N_e) of western Neanderthals of only 300 females, a marked reduction from the estimate for the eastern subpopulation ($N_e = 2,000$ females).

The effective population size for the autosomal genes in the entire population is expected to be four times that of mtDNA (i.e., $N_e = 1,200$ and $8,000$ in the western and eastern sub-populations, respectively). The usual cautions about the difference between census size and N_e apply, but one is left with the strong impression that western European Neanderthals experienced a major population crash during OIS 4.

A second possibility for Europe is that the fossils from the Sima de los Huesos date to only around 350 ka. Stringer (2012) argues that the younger age is supported by the mosaic presence of many distinctive Neanderthal cranial, dental, and postcranial features in the sample. These features are similarly common in European fossils dating to 300–200 ka but much more rare (or absent) in earlier fossils from other sites in Europe. Stringer (2012) also notes that an age of 600–500 ka for the Sima de los Huesos fossils would place them earlier than the estimated population divergence times for the ancestors of modern humans and Neanderthals and that the dated spelothems may, in fact, have been breached by a flow of younger sediments within the cave so that younger strata containing the hominins now underlie an only partially complete but older spelothem. However, Spanish researchers prefer the older date, noting that the younger age is contradicted by fossil fauna from the same deposit as the hominins, including relatively primitive fossils of *Ursus deningeri* and the vole *Clethrionomys acrorhiza* (García and Arsuaga 2011). Nevertheless, if the hominins from Sima de los Huesos date to around 350 ka, the time span for drift would be cut in half, implying a more rapid pace of Neanderthalization later in the sequence. If this was the case, much of the genetic and morphological change may have been concentrated in bursts of drift that corresponded to major contractions in Neanderthal numbers during OIS 8, 6, and 4. A shortened time span would also create a stronger association between expansion in brain size and adoption of Middle Paleolithic technologies between 300 and 200 ka.

Africa

The Arabian Sea dust core shows a long relatively wet and stable period between 640 and 427 ka. This period is associated with the first appearance of *Homo heidelbergensis* (or *Homo rhodesiensis*, if this name is to be preferred) in Africa (i.e., the Bodo cranium, dated to 600 ka; Clark et al. 1994; Rightmire 1996) and, intriguingly, marked technological advances represented by precociously early blade production and core technology in the Kapthurin Formation at Lake Baringo (Johnson and McBrearty 2010; Tryon and McBrearty 2006). It is possible that large population sizes in Africa during much of the Middle Pleistocene drove both cultural innovations and anatomical evolution via positive selection on beneficial new mutations.

The dust core also indicates marked dry periods in East Africa during OIS 8 (301–242 ka), OIS 6 (186–127 ka), and OIS 4–2 (71–12 ka), although Blome et al. (2012) suggest

that the last interval in East Africa was interrupted by a wet period around 55–50 ka. The origin of modern humans dates to OIS 6. The first fossils of recognizably modern form date to 195–160 ka (i.e., the end of OIS 7 and into OIS 6). All extant mtDNA sequences coalesce to a common ancestor at 140–210 ka (Behar et al. 2008), and Y chromosomes coalesce at 141.5 ± 15.6 ka (Cruciani et al. 2011), although an extremely rare Y-chromosome haplotype from an African American man was recently reported that coalesces with other Y chromosomes at 338 ka (Mendez et al. 2013). OIS 6 has been likened to the hyperarid conditions of the Last Glacial Maximum in OIS 2 (Deacon and Lancaster 1988), which featured greatly decreased archaeological visibility of human populations in much of Africa (Brooks and Robertshaw 1990). Genetic drift would be expected to be the dominant factor during such a period, but it is worth reiterating that African climate was a complex and regionally variable mosaic (Blome et al. 2012).

Indirect evidence from autosomal genes also supports the hypothesis that the African ancestors of modern humans experienced a major population bottleneck during this period. Fagundes et al. (2007) simulated several scenarios for the origin of modern humans with a sample of 50 autosomal loci that were subsequently compared with observed patterns of variation in human nuclear loci. They found the best correspondence to observed patterns of human genetic variation in a model that features an origin of modern humans in Africa followed by exponential population growth, expansion from Africa and replacement of archaic hominins outside of Africa (specifically in Asia in their model) followed by exponential population growth in Asia, and finally a migration from Asia to the Americas followed by a final burst of exponential population growth in the New World. The best-fitting model produced a series of posterior estimates for demographic and historical parameters, including the age of the speciation event that produced modern humans (median: 141,455; 95% CI: 103,535–185,642), the age of the migration from Africa (median: 51,102; 95% CI: 40,135–70,937), the age of the colonization of the Americas (median: 10,280; 95% CI: 7,647–15,945), the size of the archaic African population (median: 12,772; 95% CI: 6,604–20,211), the population size during the bottleneck during speciation (median: 600; 95% CI: 76–1,620), the size of the bottleneck when leaving Africa (median: 462; 95% CI: 64–1,224), and the size of the bottleneck when leaving Asia to settle the Americas (median: 452; 95% CI: 71–1,280).

Not all of the genetic data supports the conclusion that a population bottleneck produced modern humans, and some of the data strongly contradict that hypothesis. Using data from complete genomes of several modern men comprising two Yoruba, three Europeans, one Chinese, and one Korean, Li and Durbin (2011) applied population genetics models to infer changes in human effective population size over the last million years. Intriguingly, their data showed no evidence of a bottleneck between 200 and 100 ka. In fact, their results

show growth in effective population size from ~450 ka until 120–150 ka and very similar histories (and likely shared histories in an ancestral source population) of Yoruban, eastern Asian, and European population size before 60 ka. After that, all three populations experienced bottlenecks, although the one that affected the ancestors of the Yoruba appears to have been less severe and allowed an earlier recovery.

Likewise, by applying a population genetics model to expectations for (neutral) change in cranial dimensions, Weaver (2012) showed that crania that had dimensions that differed by one standard deviation from modern crania could be expected by around 165 ka, which corresponds reasonably well to when most researchers agree that modern (or nearly modern) humans appear in the East African fossil record. Weaver's model, however, assumes a constant effective population. A potential explanation for the apparent lack of a contraction in the effective population size of the ancestors of modern humans in Africa is that if there were in fact bottlenecks within a subdivided population in Africa, following the bottlenecks, members of dissimilar populations mixed extensively, restoring to the resulting population much of the genetic variation that existed before each bottleneck. The complex mosaic of favorable climates over time in different parts of Africa reported by Blome et al. (2012) may have provided the right conditions for this sort of mechanism (fig. 3).

Given that both climatic and genomic data suggest a bottleneck in East Africa and Arabia after 60 ka, it is highly likely that a substantial amount of genetic drift occurred in the population of modern humans as they left Africa or for a period of time immediately afterward. As a result, outbreeding would have been highly favorable if heterozygosity was greatly increased by these events, especially for loci such as the major histocompatibility complex, in which alleles from archaic Eurasian populations are far more frequent in populations outside of Africa than they are in other loci (Abi-Rached et al. 2011).

Low lake levels in Lake Malawi and Lake Tanganyika and high levels of dust flux suggest generally unfavorable conditions for human population growth in tropical Africa during much of OIS 5 (Blome et al. 2012; Scholz et al. 2011). The result was likely relatively rapid genetic drift and population differentiation among modern humans in Africa. Another population contraction in most of Africa in OIS 2 probably accounts for late (Holocene or terminal Pleistocene) appearance of crania that have cranial metrics that cannot be distinguished from one or more extant populations (De Villiers and Fatti 1982; Habgood 1989). Early Holocene (and likely from the end of OIS 2) human remains show evidence of strong morphological differentiation among African populations. The spread of pastoralism and agricultural populations in Africa has blurred or erased these stark distinctions (Tishkoff et al. 2009). For Africa, then, the dust-core and genetic data suggest that selection may have been important from 600–400 ka, but periods of drift had more potential to be the dominant influence thereafter.

Conclusions

As a result of this comparison of records of paleoclimate, morphological change, and genetic change, it seems apparent that many of the observed changes leading to Neanderthals were more likely to have been the products of drift than selection, whereas both drift and selection may have been important in the emergence of modern humans. Many of the key events appear to date to periods in which population sizes were greatly reduced and genetic drift would have been rapid. The picture that emerges is one of human population history that was highly (although almost certainly not exclusively) contingent on climatic changes.

One prominent example of this dependence on climate comes from mtDNA intramatch distributions that show rapid population growth in Africa at ca. 80 ka (Harpending et al. 1993, 1998; Sherry et al. 1994); estimates of lake levels from Lakes Malawi and Tanganyika show a return of wet conditions at the same time (Burnett et al. 2010; Scholz et al. 2011), although the pattern of wet and dry periods for Africa as a whole forms a complex mosaic that frequently departs from the pattern observed in Lakes Malawi and Tanganyika (Blome et al. 2012). Rohling et al. (2013) demonstrate that favorable conditions combining low sea levels with elevated levels of precipitation to support terrestrial biomass (including humans) would have facilitated movements across the Bab-el-Mendab strait between East Africa and Arabia only in narrow windows of time, the latest of which dates to 70–65 ka. These patterns help to illuminate a particularly irksome issue in research on the origin of modern humans: the question of why modern humans only expanded out of Africa at 50–60 ka if “anatomically modern” morphology arose between 200 and 150 ka (e.g., Klein 2009). The answer seems to be that climatic conditions did not favor a large, interconnected population in Africa between 125–ca. 80 ka because each region experienced one or more dry periods during this interval (Blome et al. 2012). Many of the famous cultural advances associated with the Upper Paleolithic and Late Stone Age are also likely to have depended on population size and density (Powell, Shennan, and Thomas 2009; Premo and Kuhn 2010).

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