The role of climate in the spread of modern humans into Europe

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ABSTRACT

The spread of anatomically modern humans (AMH) into Europe occurred when shifts in the North Atlantic meridional overturning circulation triggered a series of large and abrupt climate changes during the last glacial. However, the role of climate forcing in this process has remained unclear. Here we present a last glacial record that provides insight into climate-related environmental shifts in the eastern Mediterranean region, i.e. the gateway for the colonisation of Europe by AMH. We show that the environmental impact of the Heinrich Event H5 climatic deterioration c. 48 kyr ago was as extreme as that of the glacial maximum of Marine Isotope Stage (MIS) 4 when most of Europe was deserted by Neanderthals. We argue that Heinrich H5 resulted in a similar demographic vacuum so that invasive AMH populations had the opportunity to spread into Europe and occupy large parts before the Neanderthals were able to reoccupy this territory. This spread followed the resumption of the Atlantic meridional overturning circulation at the beginning of Greenland Interstadial (GIS) 12 c. 47 kyr ago that triggered an extreme and rapid shift from desert-steppe to open woodland biomes in the gateway to Europe. We conclude that the extreme environmental impact of Heinrich H5 within a situation of competitive exclusion between two closely related hominids species shifted the balance in favour of modern humans.

1. Introduction

Located in an intermediate position between the higher-latitude (i.e., influenced by the westerlies) and lower-latitude (i.e., monsoonally influenced) climate systems, the eastern Mediterranean region is highly sensitive to short-term climate variability. This sensitivity is well documented for the early to fully developed interglacial state of the Holocene (Rohling et al., 2002; Kotthoff et al., 2008a). The influence of short-term climatic forcing during that time is known to have affected late prehistoric to early historic cultures in the eastern Mediterranean region (Weiss et al., 1993; Pross et al., 2009). Markedly less information is available on the potential role of climate forcing on human population dynamics during the last glacial, notably the dispersal of AMH from Africa and their subsequent colonisation of Eurasia. With regard to the immigration of AMH into Europe, the eastern Mediterranean region is of particular interest because it served as a gateway in this process (Fig. 1). The archaeological evidence and the preference for migration routes along coastlines and rivers have shown that AMH used the south-eastern gateway to colonise Europe (Bar-Yosef, 2002; van Andel et al., 2003; Mellars, 2006). The scarcity of sufficiently resolved, chronologically well constrained terrestrial climate data from that region has, however, precluded insights into potential relationships between climatic forcing and the migration of AMH into Europe. In order to identify the environmental conditions under which AMH migrated into Europe, we have generated a well-dated, centennial-scale-resolution pollen record spanning MIS 2—4 based on a new core from the classical site of Tenaghi Philippon (Supplementary information) in NE Greece (Fig. 1). Given the proximity to glacial refugia of temperate plants (Tzedakis et al., 2002), the Tenaghi Philippon archive is ideally suited to record abrupt climate improvements during glacials since the vegetation response to climatic forcing occurred without significant migration lags.

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2. Stratigraphy and chronology

The new Tenaghi Philippon core (40°58′24″ N, 24°13′26″ E, 40 m asl) holds a terrestrial archive that is preserved mainly in fen-peat and comprises the last c. 300 kyr BP continuously (Fig. 2). The chronology of the core interval covering MIS 1–4 is based on 20 AMS 14C dates (Table 1), tephrostratigraphy, and, beyond the range of 14C dating, tuning of its pollen record to the SPECMAP curve (Martinson et al., 1987). All age data yield an internally consistent chronology with a very good agreement between all three independent methods. Table 1

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<th>Depth (m)</th>
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<th>Calendar age (yrs BP)</th>
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<td>1906 ± 30</td>
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<td>6391 ± 53</td>
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<td>7297 ± 67</td>
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Fig. 1. Migration route of modern humans from Africa into Europe when sea-level was 70 m below present (brown coastline) as realized at 48 kyr BP (Siddall et al., 2003) during early MIS 3. Black dots mark palaeoanthropological sites (Supplementary Table S2) relevant for the migration route: BT = Boker Tachtit, Ke = Kebara, KA = Ksar ‘Aqil, Üç = Üçağızlı, BK = Bacho Kiro, Te = Temnata, BB = Brno-Bohunice. Black dots with numbers indicate sites with dating results (in kyr before present) relevant for the timing of the migration process. Black squares mark relevant palaeoenvironmental reconstruction sites: TP = Tenaghi Philippon, MD9501, So = Soreq, ML = Megali Limni, Io = Ioannina, Mo = Monticchio.

Fig. 2. Stratigraphy and chronology of the core Tenaghi Philippon TP-2005. (A) SPECMAP chronology (Imbrie et al., 1984). (B) Overview pollen record of the 60 m core TP-2005 (Pross et al., 2007); taxa are grouped according to their climatic requirements (Fig. 3). (C) Age-depth curve for the interval from MIS 1 to 4; Black dots indicate AMS 14C dates converted into calendar ages (Table 1). White squares indicate reported ages of identified tephra layers, i.e. Y-2 tephra derived from Cape Riva eruption on Santorini, and Y-5 tephra from Campanian Ignimbrite eruption in southern Italy (Figs. S1, S2). Note, the MIS 4/5 boundary is situated at 19 m depth.
consistent age-depth model (Fig. 2c). The $^{14}$C ages were converted into calendar years following Weninger and Jöris (2008). The tephra layers were geochemically characterised and correlated with tephras from known eruptions (Supplementary Figs. S1, S2). The tephra layer at 7.61 m depth represents the Y-2 tephra derived from the Cape Riva eruption on Santorini, dated at 21,950 cal yr BP (Wulf et al., 2002). The tephra layer between 12.87 and 12.64 m represents the Y-5 tephra, which resulted from the Campanian Ignimbrite eruption in southern Italy at 39.3+/−0.1 kyr BP (De Vivo et al., 2001). The MIS 4/5 boundary, equivalent to 73 kyr BP (Martinson et al., 1987), was used as a tuning point beyond the range of $^{14}$C dating; based on palynological data, it corresponds to a depth of 19 m (Fig. 2).

3. Last glacial climate-related environmental shifts in the eastern Mediterranean region

Our centennial-scale-resolution pollen record (Fig. 3) shows a series of strong, short-term increases of total tree taxa percentages that punctuate the otherwise high percentages of desert-steppe biomes (yellow curve) in the eastern Mediterranean region during the last glacial. From left to right: converted absolute dating results (Table 1), depth scale, main diagram (tree taxa percentages plotted from left to right, herb taxa percentages from right to left), silhouette curves indicate percentages of selected taxa, MIS = Marine Isotope Stages. The record is based on 457 samples; a mean of 442 pollen grains was analysed per sample; average sample spacing is 3.3 cm, and average temporal resolution is 144 years.

![Vegetation dynamics during the last glacial as documented in the pollen record from the site Tenaghi Philippou. The pollen record shows a series of interstadials characterised by short-term spreads of tree populations (green and red curves) that interrupted the generally dominance of desert-steppe biomes (yellow curve) in the eastern Mediterranean region during the last glacial. Frost-sensitive Mediterranean tree taxa such as evergreen Quercus, frequently found during MIS 5 and MIS 1 (Fig. 2), were almost constantly absent throughout MIS 2–4 (Fig. 3), which suggests that serious](image-url)
winter frosts occurred regularly during glacial times. In contrast, deciduous tree taxa requiring warm summers such as summergreen *Quercus* were frequently present during interstadials in MIS 3. At the Ioannina site (Tzedakis et al., 2002), located on the west-facing flank of the Pindus range in western Greece (Fig. 1), summergreen *Quercus* was frequently present even during stadials and full glacial conditions in MIS 2 and 4. Hence, a lack of summer warmth was rather not the factor limiting tree growth in the region during the last glacial. Instead, the general dominance of dry steppe biomes, as indicated by the high percentages of *Artemisia* and Chenopodiaceae (Fig. 3), shows that the availability of precipitation was the limiting factor for tree growth. Therefore, the strong spread of tree populations during interstadials was most likely facilitated by short-term increases of precipitation that interrupted the otherwise arid environments of the eastern Mediterranean region during the last glacial.

The absolute dating results show that all interstadials at Tenaghi Philippon can be linked with Greenland interstadials, although there are partially offsets to the NGRIP chronology that appear strongest close to limit of 14C dating (Fig. 4). Since the last glacial climate variability in Europe has been demonstrated to be in phase with that in Greenland (Sánchez Goñi et al., 2002; Spötl et al., 2006; Fleitmann et al., 2009) we argue that these offsets do not represent real phase differences, but result from limitations associated with 14C dating. Hence, the Tenaghi Philippon site contributes a long, high-resolution, chronologically well constrained last glacial pollen record that is representative for climate-related environmental shifts in the eastern Mediterranean region.

4. Influence of environmental changes on the migration of anatomically modern humans from Africa into Europe

The Tenaghi Philippon record covers the entire interval from the dispersal of AMH from Africa to the colonisation of Europe. Because Tenaghi Philippon is located within the gateway used by AMH to colonise Europe (Fig. 1), the vegetation data from that site are instrumental in identifying the climatic and environmental changes that influenced this migration process.

The ultimately successful dispersal of modern humans from Africa has been dated, using archaeological evidence, to between approximately 60 and 50 kyr BP (Mellars, 2006). For this interval, the δ18O record of surface dwelling planktonic foraminifers from core MD9501 (Almogi-Labin et al., 2009) in the Levantine Sea (Fig. 1) shows anomalously low values between c. 55 and 49 kyr BP (Fig. 5c), indicating the formation of Sapropel S2 as a consequence of surface-water freshening in the eastern Mediterranean Sea related to enhanced Nile runoff. These processes are a response to circulation and the associated strong increase in sea-surface temperature (Bond et al., 1993; Bauch et al., 2001) facilitated an enhanced moisture load of the westerlies on their track into Europe.

Other pollen records from the region such as Kopais (Tzedakis, 1999; Tzedakis et al., 2004), Ioannina (Tzedakis et al., 2002), GeoFü SL152 (Kotthoff et al., 2008b), Megali Limni (Margari et al., 2009) agree well with the Tenaghi Philippon record when the influence of local factors, e.g. altitude and topographic variability, on plant taxa composition at the respective sites is taken into account. Therefore, the Tenaghi Philippon pollen record is instrumental in identifying the climatic and environmental changes that influenced this migration process.
the orbitally induced summer insolation maximum at 58 kyr BP (Fig. 5d) that resulted in a northward movement of the Intertropical Convergence Zone and the extension of monsoonal summer rainfalls into the otherwise hyper-arid Sahara in northern Africa (Rossignol-Strick et al., 1982). Thus, as was the case in the early Holocene during formation of Sapropel S1, a humid period prevailed in northern Africa during Sapropel S2 formation between c. 55 and 49 kyr BP. We argue that this North African humid period facilitated the successful dispersal of AMH from Africa.

Our argument is corroborated by the earliest palaeolithic industry in the eastern Mediterranean of MIS 3 that is a candidate for manufacture by AMH, found at the site of Boker Tachtit in Sinai (Fig. 1) and dated to 51.0 ± 3.4 kyr cal BP (Marks, 1983; Bar-Yosef, 2002; Supplementary Table S2). During that time, conditions were also humid and mild in the eastern Mediterranean as indicated by the vegetation data from Tenaghi Philippon (Fig. 5b) and the precipitation proxy-record from the Soreq cave speleothem (Bar-Matthews et al., 2000) for the GIS 14/13 interval. Triggered by the resumption of the North Atlantic meridional overturning circulation (Bond et al., 1993; Bauch et al., 2001) the climate improvement connected to GIS 14/13 also brought moist and mild environmental conditions over large parts of Europe (Allen et al., 1999; Sánchez Goñi et al., 2002; Fletcher et al., 2010). Because of the coincidence of the orbitally induced North African humid period between c. 55 and 49 kyr BP with the humid and mild conditions in the Near East and in Europe during GIS 14/13 (Fig. 5) as triggered by the North Atlantic circulation, natural environments were exceptionally favourable for AMH to migrate directly into Europe already at that time.

The scenario of an initial AMH movement into Europe during GIS 14/13 is supported by the earliest industry attributed to modern humans in Europe, found at the site of Brno-Bohunice in the Czech Republic (Fig. 1) and dated to a weighted mean of 48.2 ± 1.9 kyr BP (Richter et al., 2008; Supplementary Table S2), and by the similarity of its Bohunician industry with the Emiran industry of Boker Tachtit (Richter et al., 2008; Hoffecker, 2009). Since 5 of the 11 thermoluminescence dates performed on burned flints from the Bohunian industry plot within the interval of late GIS 14/13 (Richter et al., 2008) when environmental conditions were favourable, we propose an initial AMH movement into Europe during that time. However, this movement was preceded by Neanderthal populations moving back from their southern refuges into Central and Northern Europe during milder climate conditions in the interval from GIS 17 to mid GIS 14/13. Substantial indigenous populations were therefore present in Europe (van Andel et al., 2003), forming a competitive barrier to the further expansion of
AMH during late GIS 14/13. The decisive environmental event in this situation of competition between two closely related hominin species was the sharp climatic deterioration of Heinrich Event H5 at c. 48 kyr BP.

Heinrich Event H5 brought a collapse of the Laurentide ice sheet and the release of a huge amount of icebergs into the North Atlantic (Broecker, 1994) which even reached the coastlines of Europe (Sánchez Goñi et al., 2002). This event triggered a disruption of the North Atlantic meridional overturning circulation and an extreme climate deterioration with cold and/or dry conditions over Europe (Allen et al., 1999; Sánchez Goñi et al., 2002; Müller et al., 2003). Our vegetation data from Tenaghi Philippou reveal that the impact of Heinrich H5 was as extreme as the glacial maximum of MIS 4 (Fig. 5b) when most parts of Europe were deserted by Neanderthals (van Andel et al., 2003). Therefore, we argue that there was a demographic vacuum in most of Europe during the centuries-long Heinrich H5 event. In the mid-latitudes of Europe, the impact of H5 was mainly through a strong temperature decline (Müller et al., 2003), whereas drought was the critical issue in the Mediterranean as documented by the records Tenaghi Philippou (Figs. 4 and 5), Megali Limni (Margari et al., 2009), and MD95-2043 in the Alboran Sea (d’Errico and Sánchez Goñi, 2003). The lake level data for Lake Lisan (Bartov et al., 2002), the huge precursor of the Dead Sea, suggest, however, that the freshwater capacity in the NW Levant was still sufficient to sustain large AMH populations close to the gateway to Europe.

With the subsequent climate improvement at the onset of GIS 12, c. 47 kyr BP, triggered by the rapid resumption of the North Atlantic meridional overturning circulation (Bond et al., 1993), environments in the gateway to Europe changed quickly from desert-steppe into open forest biomes (Fig. 4), which comprised apart from Pinus mainly summergreen Quercus, but also minor percentages of Corylus, Ulmus, Tilia, and even evergreen Quercus (Fig. 3). The occurrence of these taxa indicates warm summers with a mean temperature of ∼17 °C during the warmest month and mild winters with a mean temperature of >3 °C during the coldest month (Frenzel, 1991; Barbero et al., 1992). Due to this rapid and extreme climate improvement the invasive AMH populations that persisted through Heinrich H5 in the refuge of the NW Levant had the opportunity to spread into Europe and occupy large parts in the centre and north of the continent before the sedentary Neanderthals were able to reoccupy this territory. This scenario is consistent with the finding that migration and settlement choices of early AMH show clear preferences for mild climate conditions (Davies and Gollop, 2003), and the similarity of artefact assemblages found at Bacho Kiro and Tennmata Cave in SE Europe (Fig. 1) with those of Boker Tachtit, Keser ‘Aqil, and ‘Uçagızlı in the Levant (Hoffecker, 2009).

In contrast to the situation after the glacial maximum of MIS 4 when understrengthened Neanderthal populations could recover without competition by AMH during the milder climate conditions in the interval from GIS 17 to mid GIS 14/13 (Fig. 5b), the Heinrich H5 climate deterioration resulted in a demographic vacuum that occurred when an invasive human species that had already rapidly colonised SE Asia and Australia was at the gateway to Europe. We conclude that the extreme environmental impact of Heinrich Event H5 at c. 48 kyr BP as documented at Tenaghi Philippou within a situation of competitive exclusion between two closely related hominids species shifted the balance in favour of modern humans.

During the further colonisation of Europe by AMH, the impact of subsequent extreme climate changes caused environmental conditions to switch repeatedly—in some cases within one human generation—from those supporting open forest biomes during Greenland stadials to dry steppe or tundra biomes during Greenland stadials and vice versa. Adaptation to such abrupt environmental changes is a hallmark of AMH and was achieved through innovation in both technology and social organisation to create a dispersal specialist with a global distribution (Gamble, 2009).

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Appendix. Supplementary information

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quascirev.2010.11.016.

References


Gamble, C., 2009. Human display and dispersal: a case study from biotidal Britain in the middle and upper pleistocene. Evolutionary Anthropology 18, 144–156.


