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Vegetation responses to abrupt climatic changes during the Last Interglacial Complex (Marine Isotope Stage 5) at Tenaghi Philippon, NE Greece

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A research paper for Quaternary Science Reviews

Abstract

The discovery that climate variability during the Last Glacial shifted rapidly between climate states has intensified efforts to understand the distribution, timing and impact of abrupt climate change under a wide range of boundary conditions. In contribution to this, we investigate the nature of abrupt environmental changes in terrestrial settings of the Mediterranean region during the Last Interglacial Complex (Marine Isotope Stage [MIS] 5) and explore the relationships of these changes to high-latitude climate events. We present a new, temporally highly resolved (mean: 170 years) pollen record for the Last Interglacial Complex from Tenaghi Philippon, north-east Greece. The new pollen record, which spans the interval from 130,000 to 65,000 years ago, forms part of an exceptionally long polleniferous sediment archive covering the last 1.35 million years.

The pollen data reveal an interglacial followed by alternating forest and steppe phases representing the interstadials and stadials of the Early Glacial. Superimposed on these millennial-scale changes is evidence of persistent sub-millennial-scale variability. We identify ten high-amplitude abrupt events in the pollen record, characterised by rapid contractions of closed forest to open steppe environment and interpreted to indicate major changes in moisture availability and temperature. The contractions in forest cover on millennial timescales appear associated with cooling events in the Mediterranean Sea, North Atlantic and Greenland regions, linked to the Dansgaard-Oeschger (DO) cycles of the Early Glacial. On sub-millennial timescales, the pattern of changes in forest cover at Tenaghi Philippon display a structure similar to the pattern of short-lived precursor and rebound-type events detected in the Greenland ice-core record. Our findings indicate that persistent, high-amplitude environmental variability occurred throughout the Early Glacial, on both millennial and submillennial timescales. Furthermore, the similarity of the pattern of change between Tenaghi Philippon and Greenland on sub-millennial timescales suggests that teleconnections between the high-latitudes and the Mediterranean region operate on sub-millennial timescales and that some

terrestrial archives, such as Tenaghi Philippon, are particularly sensitive recorders of these abrupt climate changes.

Keywords

Abrupt climate change; Mediterranean region; palaeoclimate; Last Interglacial Complex; Eemian; Early Glacial; Weichselian; pollen; Greece;

Highlights

- Centennial-scale climate variability is detected throughout MIS 5 in NE Greece
- Precursor/rebound events detected in Greenland are also seen at Tenaghi Philippon
- Mediterranean vegetation variability corresponds to supra-regional climate variability
- Close coupling between North Atlantic, Greenland, Mediterranean climate variability

1. Introduction

The late Pleistocene is an ideal interval to decipher the expressions, mechanisms and feedbacks of climate change because of the relatively high abundance of accessible palaeoclimate archives and the existence of pronounced climate fluctuations under both glacial and interglacial boundary conditions. Certain intervals during the late Pleistocene have been the focal point of much research: the peak warmth of the Last Interglacial (Marine Isotope Stage [MIS] 5e) (e.g. CAPE-Last Interglacial Project Members 2006), rapid climate variability of MIS 4 to 2 (e.g. Fletcher et al. 2010, Müller et al. 2011), the Last Glacial Maximum (e.g. Harrison and Prentice 2003, Clark et al. 2009) and the Last Glacial-Holocene transition (e.g. Clark et al. 2012, Muschitiello and Wohlfarth 2015). Although these extreme intervals are important for our understanding of the climate system, they do not provide a complete representation of the range of boundary conditions of an interglacial-glacial cycle. The focus of our paper, therefore, is the Last Interglacial Complex from 130,000 – 70,000 thousand years before present (130 – 70 ka), including the Last Interglacial (MIS 5e) and Early Glacial (MIS 5d-a) interval and occurring before the onset of the well-studied climate variability of MIS 4 to 2. The Early Glacial (the Early Weichselian in Europe) is characterised by increasing global ice volume and two stadials and interstadials, equivalent to MIS 5d and 5b, and 5c and 5a, respectively (Shackleton 1969, Shackleton et al. 2003). The broad climate characteristics of the Early Glacial interval of MIS 5 are relatively well-established from a large number of marine, terrestrial and ice-core proxy datasets from different archives across Europe and the North Atlantic region (e.g. Sánchez-Goñi et al. 1999, NGRIP-Members 2004, Helmens 2014). However, what is particularly interesting about the Early Glacial are the abrupt climate events that have been detected in temporally more highly resolved proxy datasets (e.g. Drysdale et al. 2007, Capron et al. 2010, Incarbona et al. 2010, Boch et al. 2011), which to date have received less research focus than the Dansgaard-Oeschger (DO) cycles and the Heinrich events of the Last Glacial (MIS 4 to 2) (Dansgaard et al. 1993, Grootes et al. 1993).

Since the discovery of DO cycles for the Last Glacial period there has been a proliferation of studies investigating the nature and causes of abrupt climate change (e.g. Sánchez-Goñi and Harrison 2010, and references therein). The language used to describe and define abrupt climate change can, however, cause confusion, which prompts the need to standardise the terms applied. In the classical review of Alley et al. (2000), abrupt climate change is described to occur "when the climate system is forced to cross some threshold, triggering a transition to a new state at a rate determined by the climate system itself and faster than the cause". This definition, which was later adopted by the Intergovernmental Panel on Climate Change (Meehl et al. 2007) and is widely followed in the description of abrupt events of the Last Glacial (e.g. Sánchez-Goñi and Harrison 2010), is therefore also used in this paper.

Evidence from the Greenland ice cores indicates that the Early Glacial was characterised by lower-frequency DO events followed by long interstadials (NGRIP-Members 2004). In addition, sub-millennial variability characterised by abrupt warming prior to DO events (so-called "precursor events" (Capron et al. 2010)), warming events towards the end of interstadials ("rebound events" (Capron et al. 2010)), and abrupt cooling episodes within interstadials are detected in the ice core records (Capron et al. 2010). DO cycles have been detected in Early Glacial terrestrial records throughout Europe (e.g. Allen et al. 2000) but few of these records have a temporal resolution sufficient to resolve the sub-millennial features detected in the Greenland ice cores. An exception is a radiometrically-dated composite speleothem record from the northern rim of the Alps (Switzerland and Austria) that provides a fragmented, but high-resolution $\delta^{18}O$ record for 118 – 64 ka (Boch et al. 2011). This record exhibits a similarity to the DO cycles known from Greenland in terms of timing, duration and relative amplitude of the cycles as well as in the presence of sub-millennial features. The similarity between the two records presents a strong case for synchronous climate between Greenland and central Europe during the Early Glacial, within the limits of dating uncertainties (Boch et al. 2011). Whether the sub-millennial features of the Early Glacial DO cycles are present in other European terrestrial archives is yet unclear due to a lack of suitably high-resolution, continuous records. The waxing and waning of Pleistocene ice sheets mean that terrestrial records, particularly in northern and central Europe, are often fragmentary due to the erosive action of ice sheets (de Beaulieu et al. 2001, Müller et al. 2003). With relatively ice-free conditions persisting even during glacial intervals at low altitudes in southern Europe, archives from these regions can provide continuous records of environmental change through the full range of climatic boundary conditions (e.g. Wijmstra 1969, Tzedakis et al. 1997, Brauer et al. 2007, Roucoux et al. 2008, Sadori et al. 2016).

One such archive is Tenaghi Philippon, north-east Greece, which has yielded a polleniferous sequence spanning the last 1.35 million years (Tzedakis et al. 2006, Pross et al. 2015). The enormous potential of this site for palynological research was first demonstrated by T.A. Wijmstra and colleagues in the 1960s to 80s when they generated an orbital-scale-resolution pollen dataset for the entire sequence (Wijmstra 1969, Wijmstra and Smit 1976, van der Wiel and Wijmstra 1987b, van der Wiel and Wijmstra 1987a). The resulting record of vegetation change, which was found to exhibit a close correspondence with deep-sea records (Wijmstra and Groenhart 1983), highlighted the stratigraphical completeness of the Tenaghi Philippon archive. The relatively low temporal resolution of this seminal record precludes the detection of abrupt changes, but centennial-scale analyses of new core material recovered in 2005 and 2009 (Pross et al. 2007, Pross et al. 2015) demonstrate that the vegetation at Tenaghi Philippon was highly sensitive to millennial-, centennial-, and decadal-scale climate change during both glacials and interglacials (Pross et al. 2009, Fletcher et al. 2013, Milner et al. 2013). The close fidelity between vegetation changes at Tenaghi Philippon and DO events in Greenland ice cores (Müller et al. 2011) highlights the potential of the Tenaghi Philippon archive to detect abrupt variability seen in North Atlantic, higher-latitude climate records, and therefore to test for climatic teleconnections between the higher and lower latitudes.

This paper: i) investigates the characteristics of abrupt climate change during the Early Glacial in north-east Greece by reconstructing a centennial-scale record of vegetation change at Tenaghi Philippon, and ii) examines how the changes in the vegetation record relate to high-latitude climate events, such as the sub-millennial features identified in the DO cycles. Selected pollen data for the Last Interglacial from this site were previously presented by Milner et al. (2012, 2013). The complete pollen dataset for the Last Interglacial underlying these papers together with the previously unpublished Early Glacial data presented here creates a new high-resolution pollen record for the entire Last Interglacial Complex (MIS 5) from Tenaghi Philippon.

2. Regional Setting

Tenaghi Philippon (42 m a.s.l., Figure 1) is a 55 km^2 large sub-basin of the Drama Basin, an intermontane tectonic graben in the western part of the Rhodope Massif. Whereas marine and deltaic sediments were deposited during the Pliocene when the graben was connected to the Parathethys Sea, fluvial and lacustrine sediments were deposited during the Early Pleistocene across large parts of the Drama Basin. The lake shallowed and was replaced by marshes (Filippidis et al. 1996), which marks the start of the formation of peat in the Tenaghi Philippon sub-basin from 1.35 Ma (van der Wiel and Wijmstra 1987b, Tzedakis et al. 2006), including the core interval presented in this paper. The peat from Tenaghi Philippon is predominantly formed from Cyperaceae and continued accumulating, with intercalated lake sediments, until the area was drained for agricultural use between 1931 and 1944. A detailed review of the characteristics and the geological evolution of the Tenaghi Philippon archive has been provided by Pross et al. (2015).

The Drama Basin is bounded by mountains up to ca. 2200 m high. These mountains include the Symvolon Range (477 m) in the southeast, the Phalakron Range (2232 m) in the north, the Menikion (1963 m) and Pangaion (1956 m) ranges in the west and southwest, and the Lekanis mountains (1150 m) in the east. The Tenaghi Philippon sub-basin is predominantly fed by groundwater and runoff from the surrounding mountains. The climate of the region is Mediterranean with warm, dry summers and mild, wet winters: at the nearby Amygdaleonas meteorological station (40° 56’ N, 24° 25’ E; 62.8 m a.s.l.) mean January temperature is 3.4 °C, mean July temperature 23.9 °C and annual precipitation 600 mm. The warm, dry summers are linked to the extension of the Azores High, and the winter precipitation is predominantly controlled by Mediterranean cyclogenesis and penetration of westerly storm tracks into southern Europe (Dünkeloh and Jacobeit 2003, Lionello et al. 2006).

The more northerly position of Tenaghi Philippon compared to central Greece creates cooler winters due to increased continental influence, and activity of the Siberian High can create outbreaks of continental polar air, leading to episodes of cold, dry and stable weather in winter and early spring (Saaroni et al. 1996).

Before the region was cultivated, the wetter parts of the basin were dominated by local wetland and peat-accumulating taxa, such as Nymphaea alba L., Polygonum amphibium L., Phragmites communis Trin., Typha angustifolia L., with associated wetland trees Alnus sp. Betula pendula Roth., Populus sp. and Salix sp. (Pross et al. 2015). In the region today, sclerophyllous scrub dominates the lowland areas surrounding the Drama Basin up to elevations of 250 m a.s.l. with evergreen Quercus (Quercus ilex L., Q. coccifera L.), Pistacia terebinthus L., Juniperus sp., Cistus monspeliensis L., and Arbutus unedo L. Evergreen Quercus continues into the scrub woodland zone above 300 m with Carpinus orientalis Mill., Castanea sativa Mill., and Vitis sylvestris C.C.Gmel. Above 450 m deciduous Quercus (Q. fraineto Ten., Q. pubescens Willd., Q. petraea (Matt.) Liebl.) becomes more common with Ostrya carpinifolia Scop., Corylus avellana L., Acer sp., Cornus mas L. and Tilia tomentosa (Moench). At higher altitudes (> 600 m) Pinus nigra J.F.Arnold occurs with Abies alba Mill. and Fagus L., and sub-alpine and alpine meadows occur above the tree line at ~1600 m (Wijmstra 1969, Pross et al. 2015, and references therein).

3. Material and Methods

3.1. Core recovery

Core TP-2005 (40° 58’ 24” N, 24° 13’ 26” E; 60 m length) was drilled in 2005 near the previously-studied TF-II site of Wijmstra (1969). The interval presented here, comprising the Last Interglacial Complex, spans from 19.00 to 33.92 m under the present surface. The Last Interglacial Complex was identified in the TP-2005 core by alignment of preliminary, lower-resolution pollen data to the SPECMAP stack and pollen data from core TF-II (Pross et al. 2007). The transition between the penultimate glacial and the Last Interglacial occurs across a core segment change (at 33.0 m) and the soft sediments at this depth decreased core recovery. As a result of the lower core recovery for this core section, we used samples from a parallel core (TP-2005b) for the interval from 33.00 to 33.92 m. The TP-2005 core displays no evidence of other breaks in accumulation.

3.2. Palynological analyses

Palynological samples were analysed every four centimetres for the interval presented here, which extends from the end of the Saalian glacial (MIS 6) to the Early Weichselian (start of MIS 4), totalling 373 samples. The sampling distances are five-fold smaller than the earlier palynological analysis of Wijmstra (1969) and yield a mean temporal resolution of 170 years (minimum=59, maximum=957, median=118 years) based on the age model described below. Pollen and spores were extracted following conventional methods (Berglund and Ralska-Jasiewiczowa 1986) including treatment with HCl, NaOH and acetolysis to remove carbonates, humic acids, and cellulose, respectively. Pollen counts were performed using a Leica compound light microscope at a magnification of 400× and 1000× when finer detail was required for identification. Where possible, pollen grains were identified to species level. Pollen identifications were based on Reille (1992), Beug (2004) and reference material. Nomenclature follows Flora Europea (Tutin et al. 1964-1980).

Quercus pollen was divided into deciduous (d) (which includes some semi-evergreen species) and evergreen (eg) morphotypes (Moore et al. 1991). In this paper, Ostrya includes Ostrya carpinifolia and Carpinus orientalis, and Carpinus refers to Carpinus betulus. A minimum of 300 pollen grains were counted per sample excluding Gramineae, aquatic and local wetland taxa, pteridophyte and algal spores, and indeterminate grains. Aquatic and local wetland taxa include Cyperaceae, Polygonaceae, Typhaceae, Lythrum, pteridophytes, Sphagnum, Nymphaea, Nuphar, Myriophyllum, Stratiotes-type, Menyanthes, Utricularia, and Potamogeton. Gramineae pollen grains were excluded from the pollen sum because of the morphological similarities of pollen from local wetland Phragmites and pollen from other, dryland grasses in the regional pollen rain. Throughout its evolution from ~1.35 Ma onwards, the Tenaghi Philippon sub-basin has predominantly been a wetland marsh environment, dominated by Cyperaceae and associated marsh taxa (Pross et al. 2015). Phragmites likely colonised the wetter parts of the basin, as can still be observed today, and the Gramineae pollen counts (which include Phragmites) therefore represent pollen from both local sources and more distal parts of the basin. Based on the observations that the locally sourced pollen signal at a site becomes weaker with increasing basin size (Sugita 1993), sites with a large catchment area such as Tenaghi Philippon are dominated by regional pollen rain. Hence, the pollen source area for the TP-2005 core can be assumed to integrate the local vegetation signal from the basin floor and the signal from the surrounding mountain slopes.

3.3. Biomisation and interpretation of pollen data

Eight pollen assemblage superzones sensu Tzedakis (1994) were assigned to the pollen data on the basis of large-scale shifts in the abundance of pollen (superzones A – H). Local stratigraphical names used throughout the text incorporate those defined by Wijmstra (1969) for the low-resolution TF-II pollen record.

The interpretation of pollen data in terms of vegetation is based on the abundance of arboreal pollen (AP), and the composition of taxa. Biomes were assigned to the pollen data in order to investigate changes in the general character of the regional vegetation, particularly the variations between temperate deciduous forest, cool mixed forest, broad-leaved evergreen/warm mixed forest, and steppe biomes. Our biomisation method follows that outlined by Prentice et al. (1992, 1996). A biome is assigned to each pollen sample based on the abundance of each plant functional type represented in the sample. The percentage of AP in the forested samples provides some indication of the extent of forest cover: forest samples with AP < 70 % are likely to represent a mixed forest-steppe environment, classified as 'wooded steppe' by Allen et al. (2000) based on modern pollen-vegetation relationship observations. Wooded steppe reflects a landscape with an open tree canopy or patchy woodland cover (Allen et al. 2000).

The climatic interpretation of pollen data is based on the bioclimatic limits of the biomes and individual indicator taxa. Moisture availability is the principal abiotic factor controlling tree growth in the Mediterranean region (Rey and Alcántara 2000, Castro et al. 2004). The annual precipitation threshold for tree population survival is approximately 300 mm (e.g. Zohary 1973), and the limit between forest and non-forest environments typically occurs at an actual to equilibrium evapotranspiration of 65 % (Prentice et al. 1992). Changes in temperature predominantly influence the composition of the vegetation, particularly with regard to the abundance of frost-intolerant Mediterranean taxa and the relative importance of cold-tolerant montane taxa such as Pinus and Betula.

3.4 Identification of abrupt events

To identify abrupt changes in vegetation at Tenaghi Philippon, we followed the method used by Fletcher et al. (2013). We calculated the first derivative of the AP percentages against age to identify the events of abrupt expansion and contraction of forest populations. High-amplitude forest expansion/contraction events were defined as AP increases/decreases of ≥ 20 % between samples, whereas lower-amplitude forest expansion/contraction events were defined as AP increases/decreases of 10 – 20 %.

3.5. Chronology

Because absolute age control is currently unavailable for the MIS 5 section of the TP-2005 core, the age model has been developed using a stepping-stone correlation strategy similar to the approach successfully applied to other records of the last 130,000 years in the Mediterranean region (Tzedakis et al. 2002a, Margari et al. 2009) and notably also for the MIS 9 – 7 section of the TP-2005 core (Fletcher et al. 2013).

Details of the chronology have been previously published (Milner et al. 2012), but are summarised here for reference. We developed a new chronology for the marine core MD95-2042 from the Iberian margin by aligning its planktonic $\delta^{18}O$ record (Shackleton et al. 2000) to the synthetic Greenland record of Barker et al. (2011). The TP-2005 pollen data were then aligned with the pollen record from core MD95-2042 (Figure 2, Sánchez-Goñi et al. 1999). The midpoints of major transitions in AP in the Tenaghi Philippon record were aligned to the midpoints of major transitions in AP in the MD95-2042 pollen record. The resulting age-control points are listed in Table 1, and the alignment of the records is shown in Figure 2. The similarity between the pollen records from cores MD95-2042 and TP-2005 in terms of the sequence and pattern of events suggests that the climatic patterns of Iberia and Greece were similar. By aligning the two records we assume that tree populations changed synchronously between south-west Iberia and north-east Greece. The use of total temperate tree pollen as the basis for correlation, rather than a single pollen taxon, circumvents the potential effect that the presence of different species in the two locations could have on the timings of the changes recorded. Previous research has found that vegetation response to North Atlantic climate change was rapid and effectively synchronous (within the limits of sampling resolution) across southern Europe (Roucoux et al. 2001, Sánchez-Goñi et al. 2002, Tzedakis et al. 2002b). The assumption of synchronous vegetation change across southern Europe is based on two factors. Firstly, the regional air flow has a predominantly westerly direction, which helps to rapidly transmit climate variability across southern Europe (Tzedakis et al. 1997). Secondly, the continued persistence of temperate trees during glacial intervals throughout southern Europe ensures there is little, if any, migrational lag in the vegetation response to climatic forcing when conditions become suitable for the expansion of woodland (Allen et al. 1999, Sánchez-Goñi et al. 2000, Sánchez-Goñi et al. 2002, Tzedakis et al. 2004).

Inherent in the age model are the uncertainties in the Barker et al. (2011) timescale for this interval from absolute dating and tuning errors. These errors result in a combined uncertainty of between 0.49 and 1.59 kyr (minimum=0.49, maximum=1.59, median=1.07 kyr for eleven age control points) for the Last Interglacial and Early Glacial (Barker et al. 2011). Further uncertainties relating to the resolution of TP-2005 and the relative alignment between records are shown in Table 1, following methods outlined by Govin et al. (2015). Combined uncertainty for the TP-2005 age model ranges between 1.03 and 2.77 kyr. Despite these uncertainties, the age model can be considered to be the best currently possible in the absence of tephrochronological analysis or radiometric dating of the TP-2005 core for this interval.

5. Results

5.1. Long-term environmental change

The TP-2005 pollen data for the Last Interglacial and Early Glacial (MIS 5) show a pattern of alternating development of forest and xerophytic steppe vegetation (Figure 3, Table 2). Approximately 65 % of the pollen samples are classified as forest (n = 244) and 35 % of the samples are classified as steppe (n = 129), as determined by the biome classifications. The forest intervals are dominated by deciduous Quercus pollen, which often reaches > 50 % of the pollen assemblage. With the exception of Pinus, which is a sub-dominant taxon, pollen from all other tree taxa occur in low abundances (typically < 10 %). Steppe intervals are characterised by the xerophytic herbs Artemisia (typically > 50 %), Chenopodiaceae (typically ≥ 15 %) and other Amaranthaceae. Gramineae pollen are also abundant during the steppe intervals. The abundance of tree taxa during steppe intervals varies from almost completely absent (e.g. Lydia II stadial, Figure 4) to approximately 30 % (e.g. second part of the Drama interstadial, Figure 4). Pinus is the dominant tree taxon during steppe intervals, although small populations of Quercus and other tree taxa such as Betula, Alnus and Juniperus are also present. Wooded steppe intervals (i.e. samples classified as forest biome but with <70 % AP) account for 10 % of all samples (n = 38). These intervals typically have an increased abundance of Pinus alongside Quercus, compared to the forested intervals with AP >70%, and trees are assumed to be scattered across the landscape with dense woodland restricted to locally suitable spots (such as gorges or low altitudes), with higher values of AP representing more widespread or dense forest in the pollen catchment.

The alternating development of forest and steppe vegetation in the TP-2005 pollen record represents alternating warm/wet and cold/dry sub-stages of the Last Interglacial Complex (MIS 5). Southern European pollen stages have been previously correlated to the sub-stages of MIS 5 (e.g. Turon 1984, Sánchez-Goñi et al. 1999). We adopt the same correlation scheme here and align the Tenaghi Philippon local stratigraphical names to the European stage names. The Pangaion interglacial is the longest and most floristically diverse forested interval from 128.5 to 112.3 ka and it is equivalent to the Eemian interglacial (approximately coeval with MIS 5e). The Lydia I cold and dry interval from 112.3 to 109 ka is equivalent to the Meliséy I stadial and the ice volume maximum of MIS 5d. The Doxaton and Drama intervals from 109 to 87.4 ka trace the development of temperate forest of an interstadial with a diverse arboreal flora, correlating to St Germain Ia and Ic and broadly equivalent to MIS 5c, and separated by a cold and dry interval from 105.8 to 102.1 ka associated with the Montaigu event in Europe (Woillard 1978). Following the Drama interstadial, the cold and dry interval of Lydia II from 87.4 to 83.3 ka is equivalent to the Meliséy II stadial and the ice volume maximum of MIS 5b. The final prolonged forested interval of Elevtheroupolis from 83.3 to 78.3 ka is associated with the St Germain II interstadial and MIS 5a and the subsequent fluctuations from 78.3 to 66.5 ka during the Dendrakia interval are associated with the Ognon-Stadial phases (Sánchez-Goñi et al. 1999) at the end of MIS 5a and transition to MIS 4.

5.2. Abrupt environmental change

Changes in the AP percentages in the TP-2005 record during the Last Interglacial and Early Glacial indicate forest contractions and expansions on millennial and sub-millennial timescales (Figure 4). There may have been shorter-lived events in the vegetation which this record cannot detect (i.e., those with a period of half the sampling interval or lower). Ten high-amplitude contraction events are recorded, represented by decreases in AP of ≥ 20 % and indicating major shifts in regional arboreal cover. Two high-amplitude forest contractions marked the onset of prolonged stadial conditions: A2 and E6 before the onset of Lydia I and II, respectively (Figure 4). Other contraction events occurred within interstadial or interglacial forested intervals, either representing short-term expansions of steppe vegetation interrupting the general dominance of temperate or cold mixed forest (e.g. G2 and G3 during the Elevtheroupolis interstadial; Figure 4), or representing the start of longer-term expansions of steppe vegetation during an interstadial interval (e.g. E1 during the Drama interstadial; Figure 4). The high-amplitude events are characterised by a reduction in temperate tree taxa and a dominance of Artemisia and Chenopodiaceae. Some of the contraction events saw the almost complete disappearance of temperate tree taxa (e.g. E4 during the Drama interstadial; Figure 4). Eleven low-amplitude contraction events occurred during the Early Glacial, represented by decreases of AP percentages by 10 – 20 % and indicating more minor changes in arboreal cover (Figure 4). These events were characterised by either (i) a change in dominance from temperate woodland to steppe but with the change occurring over longer timescales, and with a greater persistence of tree taxa (e.g. C1 marking the end of the Doxaton interval; Figure 4), or (ii) a reduction in temperate woodland and expansion of Pinus and steppe vegetation, but without a shift in the vegetation dominance (e.g. G4 – G8 during the Elevtheroupolis interstadial during which Quercus and temperate woodland continued to dominate; Figure 4).

6. Discussion

6.1. Environmental change at Tenaghi Philippon in a European and North Atlantic context

The pollen data from TP-2005 present a striking record of environmental change throughout the Last Interglacial and Early Glacial. Major shifts between forest and steppe vegetation indicate pronounced changes in temperature and moisture availability. All major vegetation events detected in our new pollen data are documented in palaeoclimatic records from the North Atlantic realm: intervals of low forest cover at Tenaghi Philippon are linked to intervals of reduced sea surface temperatures in the Mediterranean Sea and North Atlantic, and intervals of high forest cover at Tenaghi Philippon are linked to intervals of high sea surface temperatures in the respective areas (Figure 5). This correspondence suggests a close coupling between the Mediterranean and the North Atlantic realm (Figure 5). Teleconnections between these regions are not fully understood, but can be explained through reorganisation of oceanic and atmospheric circulation (e.g. McManus et al. 2002, Rohling et al. 2002, Martrat et al. 2004, Incarbona et al. 2010). Cold events in the North Atlantic are associated with a reduction in North Atlantic Deep Water formation, reduction in the intensity of the Atlantic Meridional Overturning Circulation (AMOC) and a southward expansion/intensification of the polar vortex (Mayewski et al. 1997). Such conditions would cause lower sea surface temperatures, increased southerly outbreaks of polar air and increased frequency of north-westerlies in the Mediterranean (Cacho et al. 1999, Rohling et al. 2002). Evidence for prominent dry events are detected in lake records from southern Europe (e.g. Regattieri et al. 2015), and the reduction in temperature and moisture would lead to a contraction of temperate taxa and expansion of steppe at Tenaghi Philippon and throughout southern Europe (Figure 5). Interestingly, the TP-2005 pollen record appears more responsive to regional cooling events than the nearby pollen records from Ioannina in northwest Greece (470 m a.s.l.) and Lago Grande di Monticchio in southern Italy (656 m a.s.l.) (Figure 1). Although the overall trend in vegetation change between the three sites is similar

(Figure 5), the vegetation at Tenaghi Philippon appears to have reacted more sensitively to climate forcing, potentially due to a threshold response to temperature and moisture availability.

6.2 Sub-millennial change at Tenaghi Philippon

What is particularly interesting about the Tenaghi Philippon pollen record is how it can contribute to the discussion on sub-millennial-scale variability during the Early Glacial. Exploration of teleconnections between the high- and mid-latitudes on sub-millennial timescales has been hindered by a lack of high-resolution records from sites that are particularly sensitive to climate change. Our new high-resolution pollen record from Tenaghi Philippon allows us to investigate whether the sub-millennial climate forcing documented in the NGRIP ice core and the partially fragmented speleothem record from central Europe (Capron et al. 2010, Boch et al. 2011) also extended into southern Europe.

6.2.1. Precursor Events

The clearest similarity between Tenaghi Philippon and the higher-latitude North Atlantic realm on sub-millennial timescales emerges for a warming-cooling fluctuation within the Adriani interval, 105.8 to 102. 1 ka (corresponding to GS24 in the NGRIP Greenland ice core, Figure 5). At Tenaghi Philippon, this fluctuation is characterised by an abrupt expansion of mixed Quercus-Pinus forest (event D1, Figure 4) before a return to a steppe-dominated landscape. In European pollen records, the Montaigu Event (equivalent to the Adriani and GS 24, Figure 5) is identified as an expansion of steppe with Pinus (Reille et al. 1992), but very few pollen records are yet available in a temporal resolution that is high enough to detect variability within this interval. At some southern European sites, temperate taxa persisted throughout the Montaigu event, such as at Ioannina (Tzedakis et al.

2002b), Lago Grande di Monticchio (Brauer et al. 2007) and the Iberian margin (Sánchez-Goñi et al. 1999) (Figure 5). However, our data from the TP-2005 core represents the first European vegetation record to date providing a clear expression of a short-lived warming and cooling fluctuation during the Montaigu Event (D1, Figure 4). We need to turn to other palaeoclimatic records to establish the geographical extent of this variability. A similar pattern of warming-cooling to that in the TP-2005 pollen record during the Adriani interval is evident in the $\delta^{18}O$ speleothem record from Corchia cave in north-west Italy (Drysdale et al. 2007), the abundance of the planktonic foraminifera Globigerinoides ruber in the central Mediterranean Sea (Sprovieri et al. 2006), the planktonic $\delta^{18}O$ record of core MD95-2042 off the Iberian margin (Shackleton et al. 2000), the $\delta^{18}O$ in the NALPS speleothem record of central Europe (Boch et al. 2011), and the $\delta^{18}O$ record from Greenland ice core (NGRIP-Members 2004). This suggests that the observed signal occurs supra-regionally. In the NGRIP ice core, rapid increases and decreases in $\delta^{18}O$ values occurring shortly (ca. 1 kyr) before some interstadials have been referred to as precursor events (Capron et al. 2010). They are thought to reflect climatic changes resulting from variations in the intensity of the AMOC caused by variations in freshwater influx during strong northern summer insolation before the onset of interstadials (Capron et al. 2010). The similarity of the changes in the TP-2005 pollen record and the NGRIP $\delta^{18}O$ signal (Figure 6) suggests that precursor events were widespread throughout the North Atlantic realm and extended into the mid-latitudes of the European continent. The mechanism driving this teleconnection can be explained through variations in AMOC intensity, which would affect the meridional extent of the main atmospheric circulation features in the Northern Hemisphere. Expansions and/or intensifications of the polar vortex and winter-type circulation features occurring during intervals of reduced AMOC intensity would transmit climate variability throughout the North Atlantic realm and towards the mid-latitudes, similar to that seen during the DO cycles of the Last Glacial (e.g. Rohling et al. 2003, Martrat et al. 2007, Müller et al. 2011, Sprovieri et al. 2012). There is evidence of further precursor-type events in the TP-2005 pollen record during the onset of the

Elevtheroupolis interstadial at 83.3 ka corresponding to the NGRIP record (blue bars, Figure 6).Together with a similar pattern of variability in the NALPS speleothem record (Boch et al. 2011), the Iberian margin (Shackleton et al. 2000) and the central Mediterranean sea records (Sprovieri et al. 2006), this suggests that pre-interstadial variability was a widespread feature of the Early Glacial in the Mediterranean region and the North Atlantic realm.

6.2.2. Rebound Events

The pollen record from Tenaghi Philippon suggests that not only are the onset of interstadials characterised by pronounced variability, but so too are the end of interstadials. Variability at the end of interstadials is most pronounced during the Drama interstadial at Tenaghi Philippon (102.2 to 87.4 ka in TP-2005, approximately equivalent to MIS 5c, Figure 4). Here, peak interstadial conditions from ca. 102 ka onwards ended abruptly at 95.9 ka with a pronounced contraction of forest (E1, Figure 4), indicating a severe reduction in moisture availability and temperatures. After an interval of steppe vegetation for ca. 2.5 kyr, forests subsequently re-expanded and persisted until the onset of the Lydia II stadial (E6 at 87.4 ka, Figure 4). The increase in AP in TP-2005 at the end of the Drama interstadial suggests that moisture availability and temperature increased sufficiently during this interval to support extensive temperate woodland. The pollen records from Ioannina and Lago Grande di Monticchio do not detect clear variability at this time (Figure 5). However, evidence for a similar cool-warm sequence in other palaeoclimate records from the North Atlantic realm (Figure 5) indicates that the vegetation changes at Tenaghi Philippon reflect a supra-regional signal. The proposed correlation is as follows: the steppe expansion at Tenaghi Philippon, identified by event E1 in the TP-2005 record (Figure 4), corresponds with cold event C22 in Mediterranean and North Atlantic marine records and GS 23 in Greenland ice cores, which marked the culmination of a long gradual cooling of the interstadial GIS 23 (Figure 5). The re-expansion of temperate woodland at

Tenaghi Philippon at ca. 93 ka corresponds with a warming detected in marine records from the central Mediterranean (Sprovieri et al. 2006) and the North Atlantic (referred to as W22, McManus et al. 1994), and a rebound event GIS 22 in NGRIP ice core (Capron et al. 2010) (Figure 5). Rebound events are thought to be caused by an enhancement of the AMOC related to prolonged cooling affecting salinity and precipitation through reduced temperatures and sea-ice formation in the North Atlantic (Capron et al. 2010). An enhanced AMOC would transmit additional warmth and moisture to the mid-latitudes providing an explanation for the expansion of temperate woodland at Tenaghi Philippon. If rebound-events are pervasive features of the Early Glacial in the mid-latitudes, we would expect to see a rebound-type event at the end of the second interstadial of the Early Glacial (MIS 5c) similar to that detected in the NGRIP ice core record during GIS 21 (Capron et al. 2010). Although the variability at the end of the Elevtheroupolis interstadial in the TP-2005 record is less pronounced than for the Drama interstadial, there is indeed evidence of a short rebound-type event at ca. 78 ka. A contraction (G9, Figure 4) and subsequent recovery of temperate woodland indicates a shift between cold/arid and warm/wet climate that occurred at the end of the interstadial. There is some variability in the Lago Grande di Monticchio pollen at this time (Figure 5), but a clearer sequence of climatic change shortly before cold event C20 is documented in a central Mediterranean Sea planktonic foraminifera palaeoclimate record (Sprovieri et al. 2006) and the NALPS speleothem record from central Europe (Boch et al. 2011). The evidence of variability at this time and the potential similarity between the NGRIP and TP-2005 records (grey bars, Figure 6) suggests that a rebound-type event at the end of MIS 5c may have been widespread across the Mediterranean region and North Atlantic realm.

Interestingly, the rebound event at the end of the Drama interstadial at Tenaghi Philippon, marked by the re-expansion of forest, was not climatically stable, but was instead characterised by short-lived high-amplitude cold events. The first of these events (E4, Figure 4) was characterised by a reduction of temperate taxa to below 1 %. The near-elimination of temperate taxa indicates a period of intense cold and/or aridity. The second event (E5, Figure 4) was characterised by a transient reduction of temperate taxa to 2 %, indicating a similarly pronounced cold/arid episode. Many palaeoclimate datasets available for this interval are not sufficiently temporally resolved to identify such abrupt cooling (Figure 5). However, there are several palaeoclimate records indicating that the cooling observed in the TP-2005 record is part of a supra-regional signal of climatic variability: (i) A cooling bisecting the warm interval between C22 and C21 is recorded in a central Mediterranean Sea planktonic foraminifera record (Sprovieri et al. 2006, Figure 6); (ii) Two cooling episodes are seen in the NALPS speleothem record where they are referred to as GIS 22 transient cooling I and II (Boch et al. 2011); and (iii) A pronounced cooling event is detected during GIS 22 in the NGRIP record (NGRIP-Members 2004, Figure 6). Taken with the new data from the TP-2005 record, the evidence suggests there were widespread intermittent cooling episodes during the rebound event on sub-millennial timescales, potentially linked to unstable ice sheets and freshwater influx affecting heat and moisture transfer to the mid-latitudes.

6.2.3. Additional cooling events

Additional sub-millennial cooling events that do not conform to the rebound/precursor structure also occurred during the Early Glacial at Tenaghi Philippon. In particular, the Elevtheroupolis interstadial was characterised by multiple low-amplitude forest contractions (G1 – G8, Figure 4) suggesting more frequent episodes of cooler and/or drier climate during the final interstadial of MIS 5. There is only very muted variability in the vegetation records from Ioannina and Lago Grande di Monticchio during this interstadial, suggesting a different sensitivity of the ecosystem at these sites. However, a similar variability, including a pronounced cold event, is documented in Globigerinoides ruber abundances in the central Mediterranean Sea (Sprovieri et al. 2006, Figure 5), suggesting cooling occurred over a wide area. Although there is variability superimposed on the gradual cooling trend of the NGRIP ice core data during GIS 21, it is difficult to discern any clear corresponding cooling events (Figure 5).

The most pronounced sub-millennial cooling in the NGRIP ice core record during MIS 5 occurred during GIS 24, corresponding to the Doxaton interval in the TP-2005 pollen record. At Tenaghi Philippon, the Doxaton interval was characterised by a forest landscape with small patches of Mediterranean woodland (Figure 4). The mid-point of the interstadial was marked by an expansion of Pinus and Artemisia for ca. 500 years at 107.5 ka, suggesting temporarily reduced temperature and/or moisture availability. A cooling event during this interval has not previously been detected in Greece, but is documented in a number of European terrestrial records: a boreal forest expansion at Grande Pile in eastern France (Woillard 1978), a 300-year cooling episode at Ribains in south-east France (Rioual et al. 2007), an arid interval at Corchia, north-west Italy (Drysdale et al. 2007), and a brief cooling episode in the NALPS speleothem record (Boch et al. 2011). An intra-interstadial fluctuation during this interval is also detected in marine records from the North Atlantic (e.g. McManus et al. 1994) and the central Mediterranean Sea (Sprovieri et al. 2006, Figure 6). For Greenland, the NGRIP ice core data indicate a rapid drop in surface air temperatures bisecting GIS 24 and lasting ca. 200 years (NGRIP-Members 2004). This transient temperature decline was likely associated with instabilities in the AMOC caused by variations in freshwater discharge or enhanced precipitation (Capron et al. 2010). Simultaneous changes in CH_4 concentrations indicate widespread changes in the biosphere and hydrological cycle, similar to the effects of the 8.2 ka climatic event of the Holocene (Alley et al. 1997, Thomas et al. 2007). However, although the cooling during GIS 24 in the NGRIP $\delta^{18}O$ record shows similarities to the TP-2005 pollen record (Figure 6), the climate change was not severe enough to trigger large-scale changes in vegetation cover at Tenaghi Philippon. The new TP-2005 data therefore suggest that the cooling in southern Europe was less severe than the 8.2 ka event of the Holocene, which is marked by a ~35 % decrease in temperate taxa at Tenaghi Philippon (Pross et al. 2009) compared to only ~15 % during the Doxaton interstadial.

The widespread evidence for a cooling throughout Europe and the North Atlantic realm during GIS 24 supports the proposed mechanism of changes in the AMOC, which could result in the transmission of cooler conditions across Europe through the expansion/intensification of the polar vortex and enhancement of winter-type circulation patterns. However, the magnitude of the cooling was not uniform throughout the region.

7. Conclusions

We investigated the nature of abrupt climate change in north-east Greece during the Early Glacial through the use of new high-resolution pollen data from Tenaghi Philippon (core TP-2005), in order to understand how changes in vegetation relate to high-latitude events on millennial and sub-millennial timescales. The presented pollen record, spanning from 130 to 65 ka and encompassing the Last Interglacial and Early Glacial, reveals a striking pattern of vegetation change during the Last Interglacial Complex: multiple temperate tree population crashes and expansion of xerophytic Artemisia-Chenopodiaceae steppe indicate that pronounced decreases in temperature and moisture availability occurred on both millennial and sub-millennial timescales during this interval. We identify ten high-amplitude abrupt shifts in vegetation on sub-millennial timescales, and eleven low-amplitude changes. The number of abrupt shifts in vegetation indicates higher climate variability during the Early Glacial period in north-east Greece than the millennial-scale changes seen by the succession of interstadial-stadials and DO cycles recorded in palaeoclimatic archives throughout Europe and the North Atlantic realm.

Event-stratigraphic correlation indicates that the vegetation changes at Tenaghi Philippon correspond to changes in temperature proxies in the Mediterranean and North Atlantic regions. Hitherto, explorations of teleconnections between the high- and mid-latitudes on sub-millennial timescales have been hindered by a lack of high-resolution records from sites that are particularly sensitive to supra-regional climate change. Comparison of our high-resolution TP-2005 pollen record to other palaeoclimate records indicates evidence of teleconnections persisting between mid- and high-latitudes on both millennial and sub-millennial timescales during the Early Glacial. Of particular note is the evidence of precursor- and rebound-type events at Tenaghi Philippon, similar to the climatic changes detected in the Greenland ice core records. These sub-millennial features of the DO cycles create a pattern of interstadial variability, and our findings indicate that they were a widespread and pervasive feature of the Early Glacial. Mechanisms similar to those operating on millennial timescales during the DO cycles provide a plausible explanation for rapid transmission of climate change across the North Atlantic and European region on sub-millennial timescales; namely, variations in the intensity of the Atlantic Meridional Ocean Circulation and polar vortex affecting transport of heat and moisture to the mid-latitudes.

Our results provide further evidence that changes in the northern high-latitudes can have far-reaching consequences, affecting climate and ecosystems in the mid-latitudes. In comparison to other southern European pollen records (e.g. Ioannina and Lago Grande di Monticchio), the vegetation at Tenaghi Philippon seems particularly sensitive to oceanic and atmospheric systems under a range of boundary conditions and on different timescales. Our results underscore the necessity for further analysis of palaeoclimatic records from sites that are particularly sensitive to climate change in order to improve our understanding of teleconnections and climate-ecosystem interactions on sub-millennial timescales.

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FIGURE 1. Location of Tenaghi Philippon (TP-2005) and key sites mentioned in the text. Ioannina (Greece, I-284); Lago Grande di Monticchio (Italy, LGdM); Corchia (Italy); ODP Site 963 Hole A (Central Mediterranean Sea, ODP-963); core MD95-2042 (Iberian margin); caves sites at the northern rim of the Alps (NALPS); ODP Site 980 (North Atlantic); NGRIP ice core (Greenland).

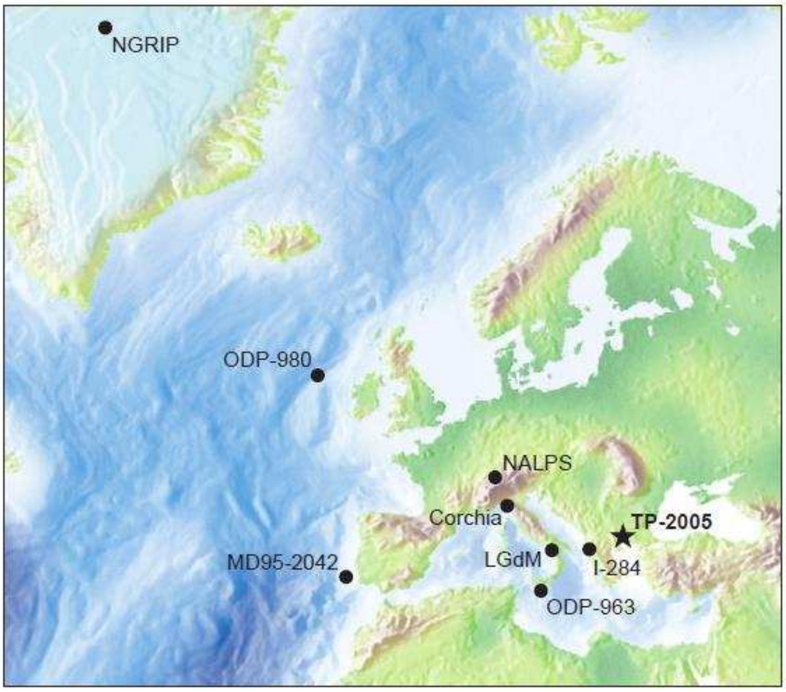


FIGURE 2. Age model for the Last Interglacial Complex interval from the Tenaghi Philippon TP-2005 core based on the alignment to the arboreal pollen percentage curve in marine core MD95-2042 from the Iberian margin. (a) Sediment accumulation rate (SAR) and location of age control points (diamonds) for core TP-2005. (b) Temperate tree pollen percentages for TP-2005. (c) Temperate tree pollen percentages from core MD95-2042 (Sánchez-Goñi et al. 1999). (d) Planktonic $\delta^{18}O$ foraminifera data from MD95-2042 (Shackleton et al. 2000).

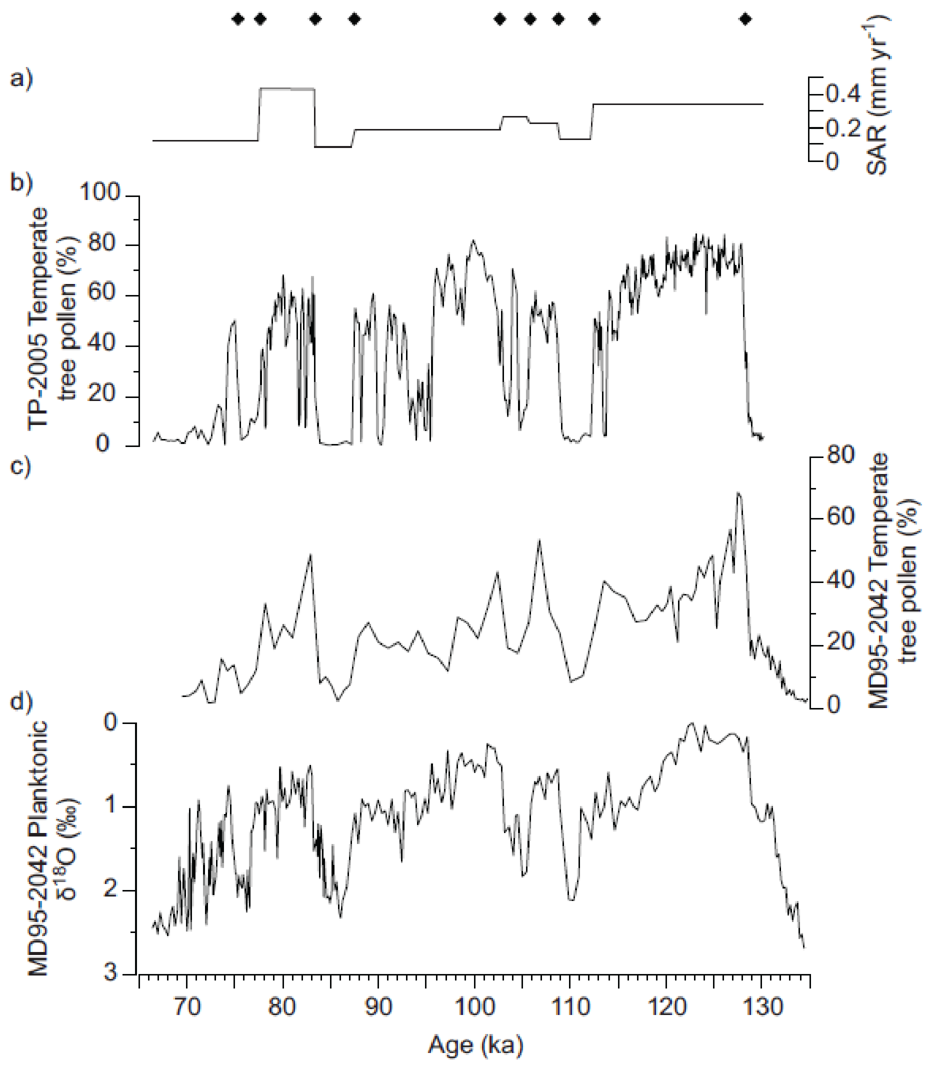


FIGURE 3. Pollen record for the Last Interglacial Complex interval from core TP-2005. Percentage of pollen taxa plotted against age. Newly introduced pollen superzones and local interval names are also shown. AP and NAP refer to arboreal and non-arboreal pollen, respectively.

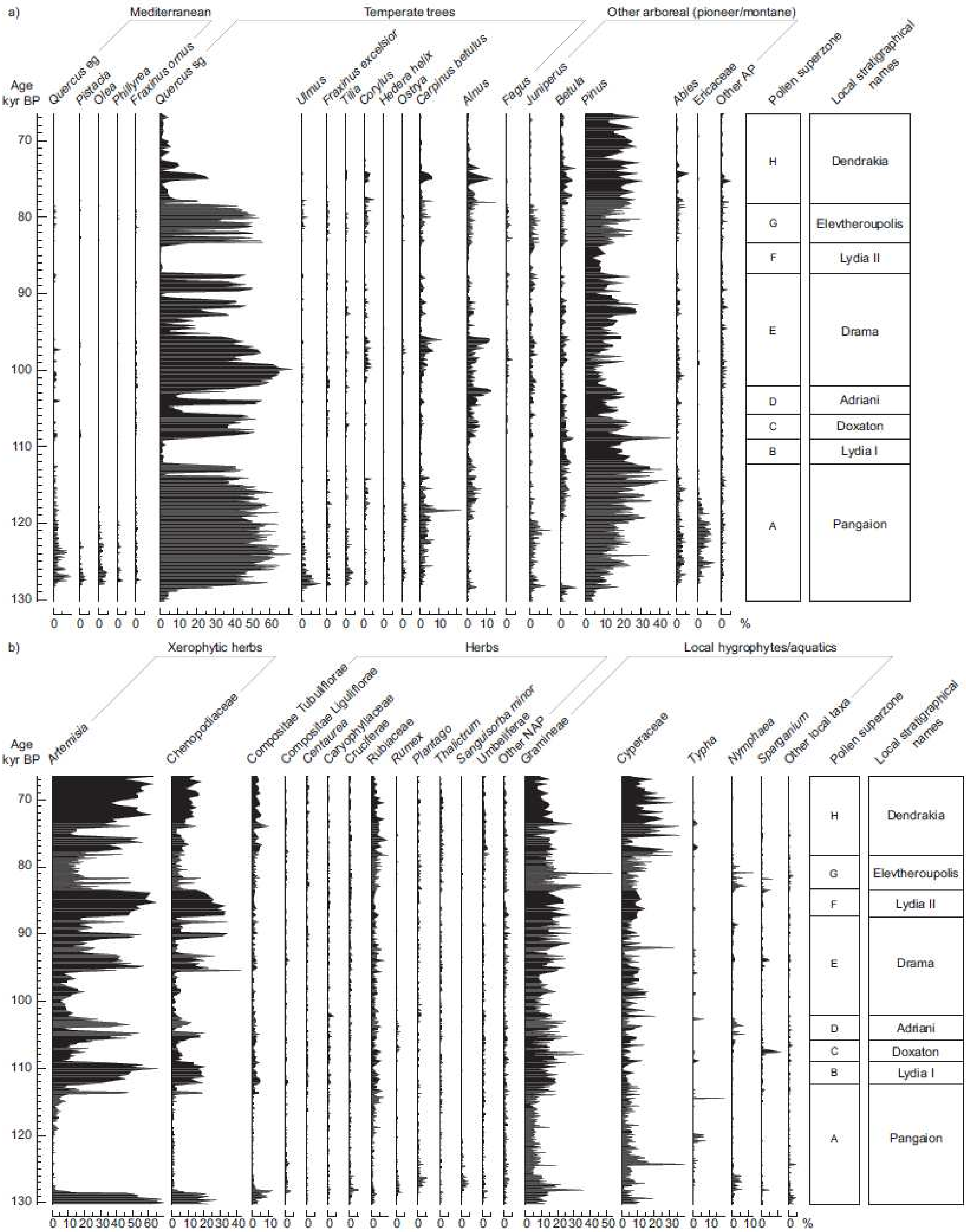

a)
Mediterranean
Temperate trees
Other arboreal (pioneer/montane)
Age kyr BP
Quercus eg
Pistacia
Olea
Phillyrea
Fraxinus ornus
Quercus sg
Ulmus
Fraxinus excelsior
Tilia
Corylus
Hedera helix
Ostrya
Carpinus betulus
Alnus
Fagus
Juniperus
Betula
Pinus
Abies
Ericaceae
Other AP
Pollen superzone
Local stratigraphical names
H
Dendrakia
G
Elevtheroupolis
F
Lydia II
E
Drama
D
Adriani
C
Doxaton
B
Lydia I
A
Pangaion
%
b)
Xerophytic herbs
Herbs
Local hygrophytes/aquatics
Age kyr BP
Artemisia
Chenopodiaceae
Compositae Tubuliflorae
Compositae Liguliflorae
Centaurea
Caryophyllaceae
Cruciferae
Rubiaceae
Rumex
Plantago
Thalictrum
Sanguisorba minor
Umbelliferae
Other NAP
Gramineae
Cyperaceae
Typha
Nymphaea
Sparganium
Other local taxa
Pollen superzone
Local stratigraphical names
H
Dendrakia
G
Elevtheroupolis
F
Lydia II
E
Drama
D
Adriani
C
Doxaton
B
Lydia I
A
Pangaion
%

FIGURE 4. Pollen percentages for selected pollen groups, biome reconstruction and identification of abrupt events during the Last Interglacial Complex as documented in core TP-2005. (a) First derivative (AP`) of arboreal pollen percentages against age, highlighting forest expansion and contraction events. High-amplitude forest contraction events (≥ 20 % decrease in AP, solid line) and low-amplitude forest contraction events (10 – 20 % decrease in AP, dashed line) are marked and numbered. (b) Pollen from arboreal taxa, temperate tree taxa (arboreal taxa excluding Pinus, Juniperus and Betula), and Mediterranean taxa (evergreen Quercus, Olea, Pistacia, Phillyrea) are plotted against age with reconstructed biomes represented by symbols. Pollen superzones, local interval names and approximate MIS equivalent sub-stages are also shown.

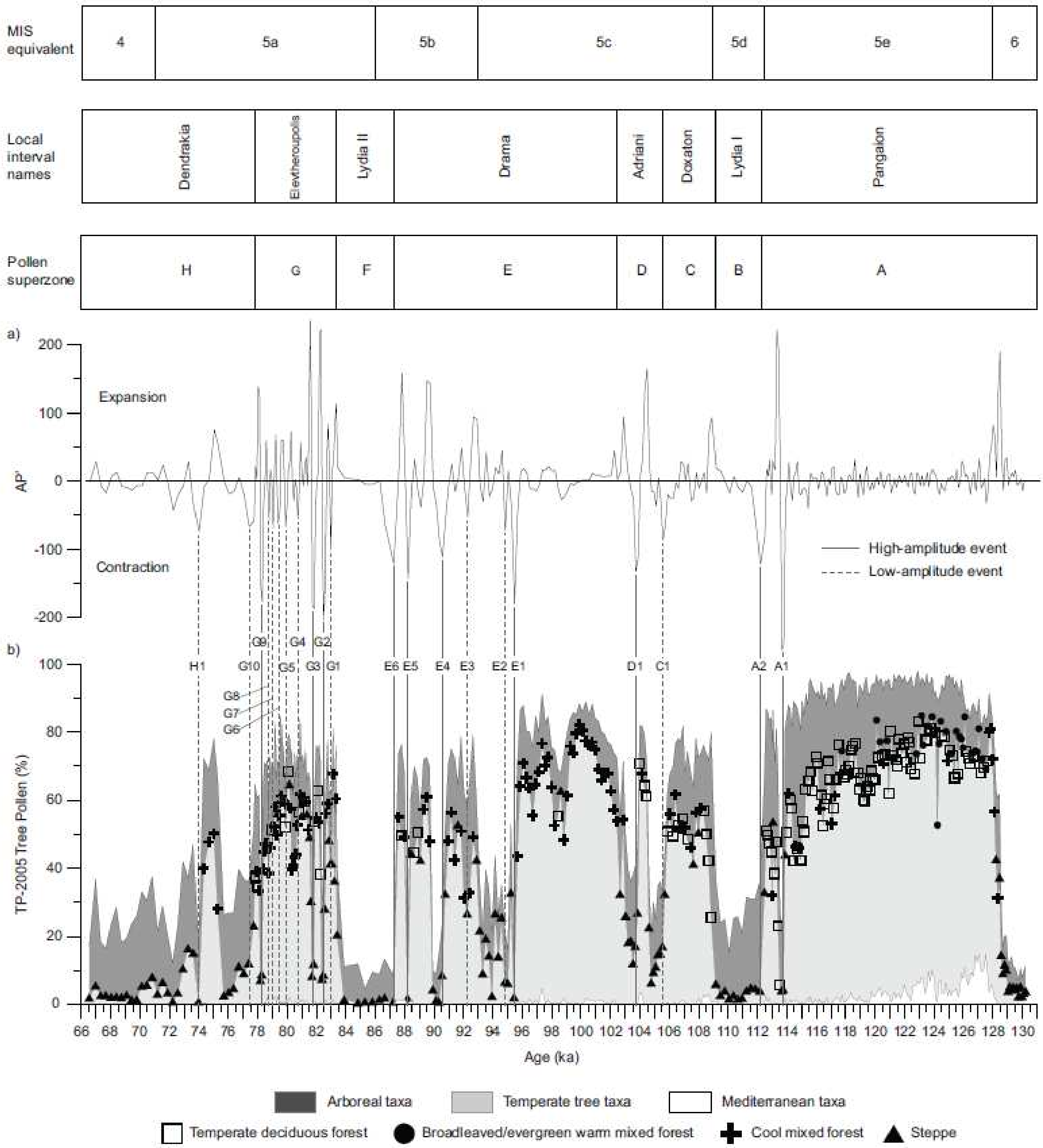
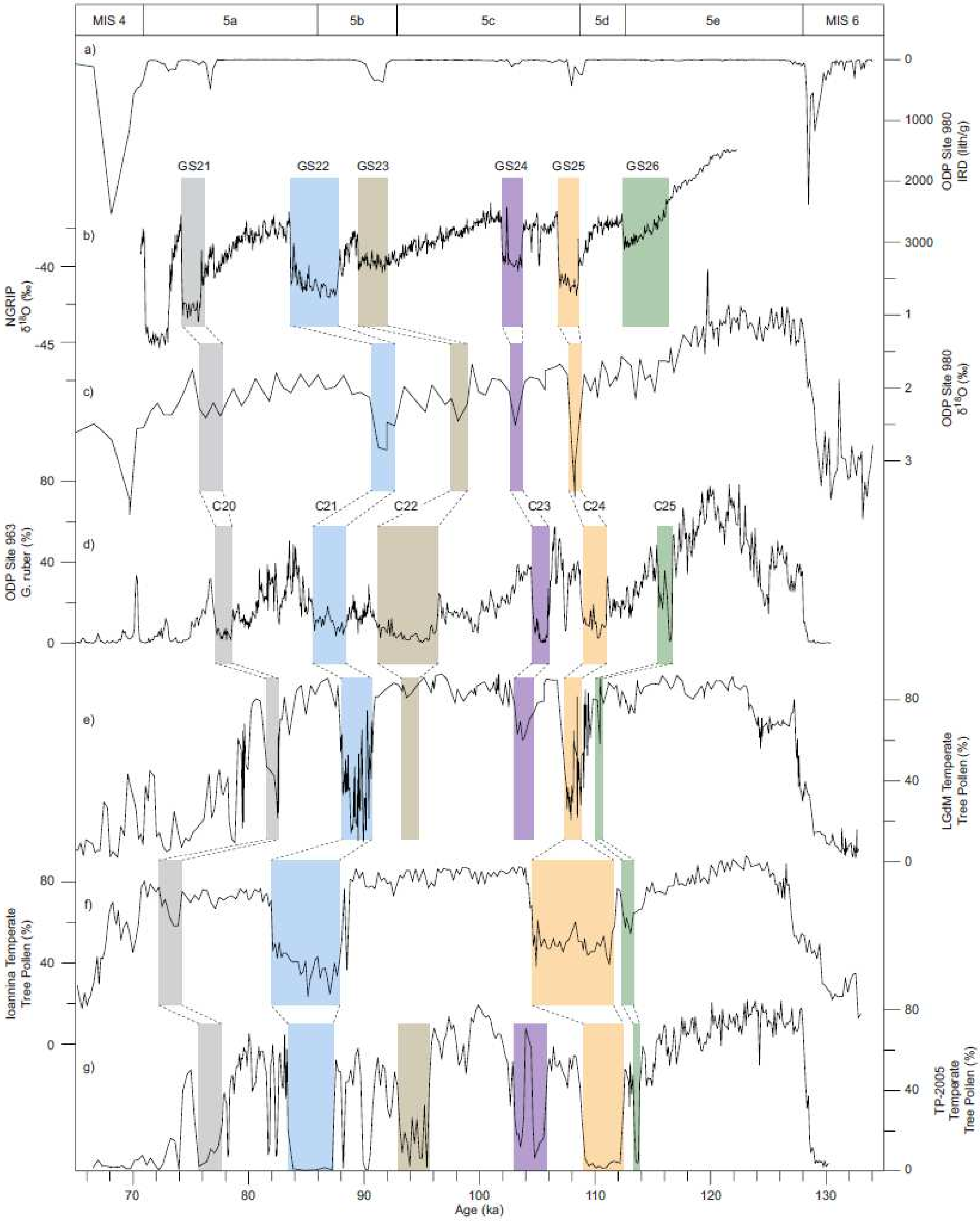


FIGURE 5. Pollen record for the Last Interglacial Complex from core TP-2005 compared with coeval climate proxy records from the Mediterranean region, North Atlantic and Greenland. (a) Ice-rafted debris (IRD) at ODP Site 980 in the subpolar North Atlantic (Oppo et al. 2006). (b) $\delta^{18}O$ of NGRIP Greenland ice core (NGRIP-Members 2004). (c) $\delta^{18}O$ of planktonic foraminifera at ODP Site 980, subpolar North Atlantic (Oppo et al. 2006). (d) Planktonic foraminifera Globigerinoides ruber record from ODP Site 963, central Mediterranean Sea (Sprovieri et al. 2006).

(e) Percentage of temperate tree pollen at Lago Grande di Monticchio (Brauer et al. 2007). (f) Percentage of temperate tree pollen at Ioannina (Tzedakis et al. 2002b). (g) TP-2005 percentage of temperate tree pollen. The MIS substages have been ascribed following Martrat et al. (2004). Cold events identified in the North Atlantic and Greenland are highlighted by coloured bars and labelled on graph (b) and (d), and correlation to potential associated events at other sites are highlighted using the same colours and correlation lines. All records are plotted on their original age models.



MIS 4
5a
5b
5c
5d
5e
MIS 6
a)
b)
c)
d)
e)
f)
g)
GS21
GS22
GS23
GS24
GS25
GS26
C20
C21
C22
C23
C24
C25
NGRIP δ18O (‰)
ODP Site 980 IRD (lith/g)
ODP Site 980 δ18O (‰)
ODP Site 963 G. ruber (%)
LGdM Temperate Tree Pollen (%)
Ioannina Temperate Tree Pollen (%)
TP-2005 Temperate Tree Pollen (%)
Age (ka)

FIGURE 6. Sub-millennial features of MIS 5 identified in the TP-2005 pollen data and proposed correlation to the NGRIP ice core. (a) $\delta^{18}O$ of NGRIP Greenland ice core (NGRIP-Members 2004). (b) TP-2005 percentage of temperate arboreal pollen. The warm Greenland interstadials within the DO cycles are indicated by numbers. Abrupt sub-millennial rebound- and precursor-type events identified in TP-2005 and NGRIP are highlighted by coloured bars (rebound events highlighted by grey bars, precursor events by blue bars). Additional cooling events discussed in the text are marked by arrows.

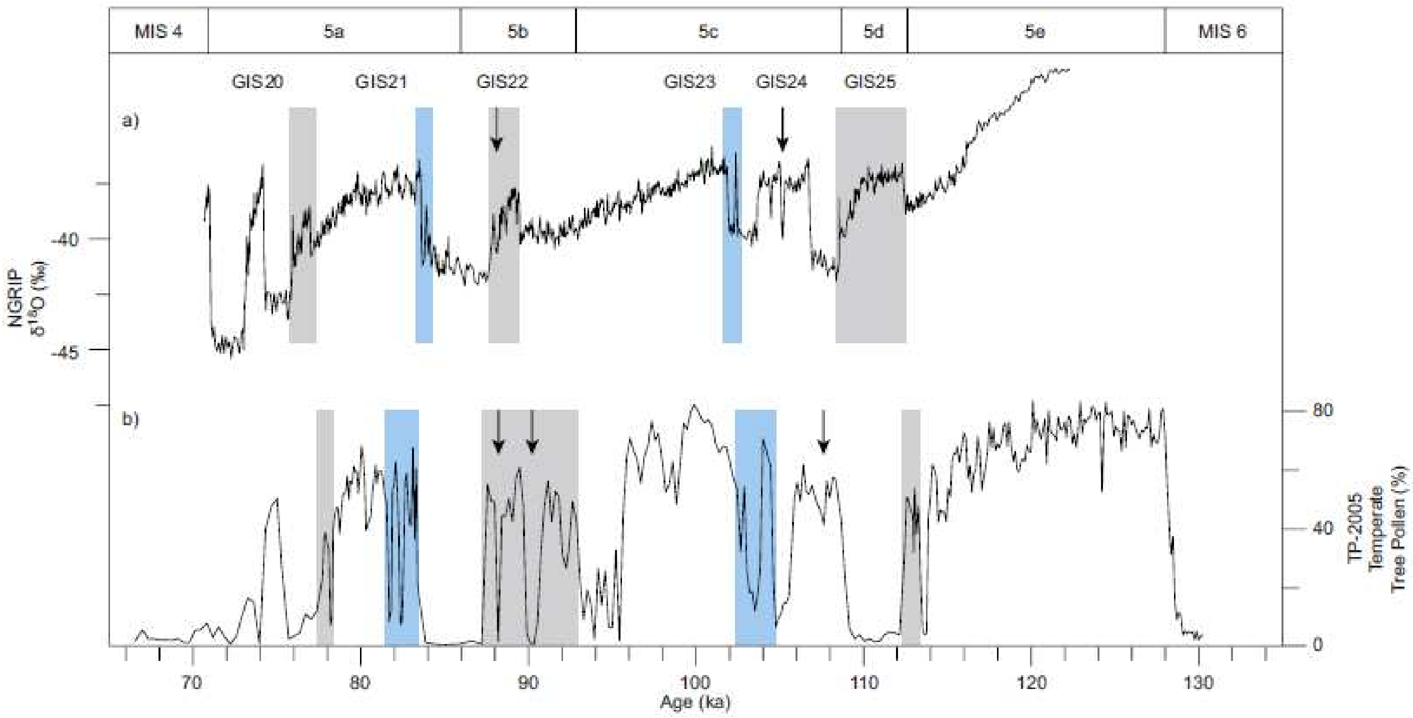


TABLE 1. Age control points used in the correlation of cores TP-2005 and MD95-2042 for the Last Interglacial and Early Glacial. The stratigraphical location of the age control points are shown in Figure 2, and represent the mid-transitions for the onset and end of the interglacial (Pangaion), interstadials (Doxaton-Drama and Elevtheroupolis) and stadials (Lydia I and II) in the pollen records. The estimated uncertainties associated with the age control points are provided: relative error is derived from the quadratic sum of resolution and relative alignment uncertainty, combined age uncertainty is derived from the quadratic sum of dating error of reference chronology and relative uncertainty (following Govin et al. 2015).

Depth (m)	**Age (ka)**	**Dating error of reference chronology (kyr)**	**TP-2005 Resolution (±1 kyr)**	**Relative alignment uncertainty (kyr)**	**Relative error (kyr)**	**Combined uncertainty (kyr)**
19.76	73.26	0.66	0.30	0.73	0.79	1.03
19.99	75.27	0.82	0.29	0.75	0.81	1.16
20.28	77.71	0.82	0.14	0.95	0.96	1.27
22.72	83.39	1.31	0.18	0.95	0.97	1.64
23.06	87.46	0.69	0.27	1.92	1.94	2.06
25.98	102.97	1.07	0.15	1.05	1.07	1.52
26.68	105.70	1.59	0.15	2.25	2.26	2.77
27.40	108.86	1.59	0.20	2.2	2.21	2.73
27.88	112.45	1.59	0.14	2.21	2.22	2.74
33.26	128.28	1.42	0.11	0.99	1.00	1.74

TABLE 2. Main palynological characteristics of the Last interglacial and Early Glacial from core TP-2005 including maximum temperate tree pollen percentage, dominant biomes, and climatic interpretation. Biome abbreviations: TEDE: temperate deciduous forest, WAMX: broadleaved/evergreen warm mixed forest, COMX: cool mixed forest, STEP: steppe. Quercus (d) and (eg) refers to deciduous and evergreen morphotypes of Quercus, respectively. Vegetation changes during the Last Interglacial (Pangaion, superzone A) were discussed by Milner et al. (2012, 2013) but are included in the description here for context.

Super-zone	Local Interval Name	Basal depth (m)	Age (duration) (ka)	Main pollen components	Max. Temperate tree (%)	Dominant biomes	Climatic interpretation
H	Dendrakia	20.54	78.3–66.5 (11.8)	Artemisia and Chenopodiaceae, with fluctuations in Quercus (d) and Pinus	50	STEP / COMX	Cold and dry
G	Elevtheroupolis	22.70	83.3–78.3 (5)	Quercus (d), Pinus, Artemisia and Chenopodiaceae, with low percentages of Corylus, Carpinus, Abies, Alnus	68	COMX	Cool and humid
F	Lydia II	23.06	87.4–83.3 (4.1)	Artemisia and Chenopodiaceae	2	STEP	Cold and dry
E	Drama	25.82	102.1–87.4 (14.7)	Quercus (d) with Corylus, Carpinus and Alnus, and increasing presence of Pinus, Artemisia and Chenopodiaceae	82	COMX	Cool and humid
D	Adriani	26.70	105.8–102.1 (3.7)	Artemisia and Chenopodiaceae with fluctuation in Quercus (d)	71	STEP	Cold and dry
C	Doxaton	27.42	109.0–105.8 (3.2)	Quercus (d) and Pinus	62	TEDE	Warm and humid
B	Lydia I	27.86	112.3–109.0 (3.3)	Artemisia and Chenopodiaceae	6	STEP	Cold and dry
A	Pangaion	33.34	128.5–112.3 (16.2)	Quercus (d) with Ulmus, Quercus (eg), Olea and Phillyrea; Abies, Ericaceae, Carpinus and Corylus; and Pinus	85	TEDE / WAMX	Warm and summer-dry to warm and humid