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Campanian Ignimbrite tephra reveals asynchronous vegetation responses to abrupt climate change in the eastern Mediterranean region

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ABSTRACT

The timing and rate of ecosystem response to abrupt climate change is a product of numerous complex interactions between biotic and abiotic drivers. Palaeoecological studies from long sedimentary records, particularly those that span periods of dynamic climate such as the last glacial cycle, can help to contextualise ecosystem responses to climate variability through time. Detailed studies that compare proxy data from multiple sites, with high chronological precision, have the potential to ascribe mutual climate drivers, and, therefore, track spatiotemporal variability in ecosystem responses. Here, we interrogate the vegetation impact of past climate change in the eastern Mediterranean, using three sub-centennially resolved pollen archives from Greece. The widespread Campanian Ignimbrite (CI/Y-5; ca. 39.85 ka BP) tephra marker is used as an isochron to directly correlate pollen records from Ioannina (NW Greece), Tenaghi Philippon (NE Greece), and Megali Limni (NE Aegean). Our results reveal spatiotemporal variability in the timing of vegetation response in the Mediterranean to climate forcing across Heinrich Stadial 4 (40.2–38.3 ka BP), a period of known abrupt climatic change. We identify a decline in tree pollen in all three sites, likely related to the onset of enhanced regional aridity, with vegetation at Tenaghi Philippon responding prior to the CI/Y-5, in contrast to at Megali Limni and Ioannina, where much of the vegetation change occurs following tephra deposition.

1. Introduction

Archives of past climate and environmental change from throughout the North Atlantic provide evidence for repeated, millennial-scale oscillations during the last glacial period. Rapid climatic changes have been observed between cool (stadial) and warm (interstadial) periods across a range of marine (e.g. Cacho et al., 1999), terrestrial (e.g. Allen et al., 1999), and ice core records (e.g. Rasmussen et al., 2014). Ice rafted debris (IRD) layers within North Atlantic marine sequences provide evidence of at least six large-scale iceberg discharge events, termed Heinrich events (HEs; see Hemming, 2004), which overprint the millennial-scale Dansgaard-Oeschger (D-O) cycles observed in Greenland and the North Atlantic (Bond et al., 1993; Rasmussen et al., 2003). HEs are, across a range of proxy records from the last glacial cycle, shown to be associated with some of the most pronounced D-O coolings, termed “Heinrich Stadials” (HSs; Barker et al., 2009). Strong evidence links last glacial climate oscillations to changes in the strength and structure of the Atlantic Meridional Overturning Circulation (AMOC; see Menviel et al., 2020). Whilst the behaviour of AMOC across this interval is complex, it is often simplified as falling into three distinct circulation modes (stadial mode, interstadial mode, and Heinrich mode), each associated with a different climate state (stadials, interstadials, and Heinrich stadials respectively; see Rahmstorf, 2002). Under Heinrich mode, associated with iceberg rafting and large resultant freshwater input top the North Atlantic, AMOC was significantly weakened (Henry et al., 2016).

Given the rapid nature of climate change across HSs, studies of terrestrial ecological responses can provide insights into the complex teleconnections that govern spatial patterns of climate variability (e.g. Naughton et al., 2009; Sánchez Goñi et al., 2008). Understanding the

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complex spatiotemporal expression of ecological response to past climate change is particularly important when considering present-day weakening of ocean circulation (Caesar et al., 2021). Here, we interrogate the expression and sequencing of terrestrial vegetation responses in Greece, on the periphery of the North Atlantic climate system, to stadial cooling at the onset of Heinrich Stadial 4 (HS4; 40.2 to 38.3 ka, *sensu* Sanchez Goñi and Harrison, 2010).

IRD fluxes within North Atlantic marine sediments suggest Heinrich Event 4 (HE4) was the largest iceberg discharge event during the last glacial in terms of ice volume (Hemming, 2004). High-resolution studies across the HS4 interval, derived from a range of circum-Atlantic paleoclimate archives, suggest that the stadial was not a stationary, prolonged cooling, but rather a gradual stadial cooling followed by more extreme, shorter-lived, HE-driven cooling (e.g. Margari et al., 2020). In the Greenland ice-core oxygen isotope record (Fig. 1a) HSs resemble regular D-O stadials (Rasmussen et al., 2014). However, ice core δ^{17}O-excess records reveal a two-stage onset of stadial conditions, with initial cooling followed by an intermediate phase marked by rapid fluctuations in δ^{17}O-excess related to lower-latitude climate dynamism (Fig. 1b; Guillevic et al., 2014).

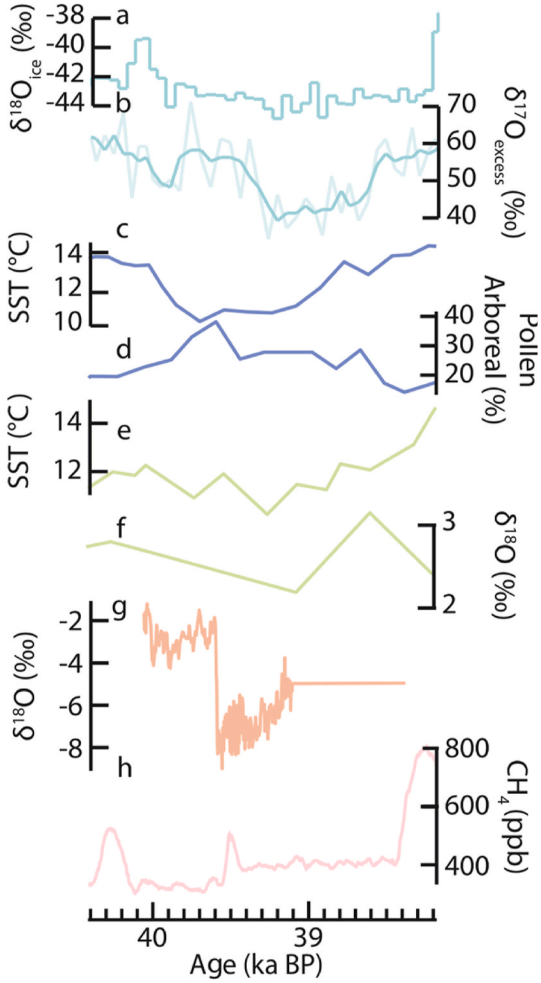

Fig. 1. Compilation of circum-Atlantic HS4 proxy records, including: NEEM (Greenland; Guillevic et al., 2014) ice core (a) δ^{18}O and (d) δ ^{17}O-excess data; MD01-2444 marine core (Iberian Margin; Margari et al., 2020) (c) reconstructed SST reconstructed from C37 alkenones, (d) arboreal pollen; MD95-2043 marine core (Western Mediterranean; Cacho et al., 2002; Fletcher and Sánchez Goñi, 2008) (e) reconstructed SST and (f) δ^{18}O (*G. bulloides*); Toca da Boa Vista (Brauer et al., 2000) speleothem (g) δ^{18}O; WAIS (Antarctica; Rhodes et al., 2015) ice core (h) CH_4. MD01-2444 and WAIS data are plotted on the WD2014 timescale, NEEM data are plotted against GICC05, and MD95-2043 and TBV data are plotted on their own, published timescales.

In North Atlantic marine sequences, HSs are associated with more extreme impacts than D-O stadials. Proxy reconstructions which span HSs reveal major deep water circulation changes, strengthening of monsoon winds, and a shift to pollen assemblages which suggest colder, more arid conditions than conventional D-O stadials (Cacho et al., 2000; Sánchez Goñi et al., 2000; Roucoux et al., 2001). In particular, sea surface temperature (SST) reconstructions from marine core MD01-2444 (Fig. 1c) reveal a short cooling phase was followed by an interval of maximum cooling and aridity (Fig. 1d; Margari et al., 2020). A similar pattern is seen in the Western Mediterranean, where the initial cooling is followed by a period of enhanced cooling with evidence of sub-polar water incursion to the Mediterranean basin (Fig. 1e–f; Cacho et al., 2002). Pollen records from the same marine cores demonstrate that the terrestrial biosphere responded rapidly and in-phase with SST changes during HSs (Margari et al., 2020; Fletcher and Sánchez Goñi, 2008).

A multi-stage onset to HS4 is not exclusive to archives proximal to the North Atlantic. Brazilian speleothem sequences also record multi-stage variability in the South American summer monsoon (Fig. 1g; Wendt et al., 2019). The broader effects of North Atlantic climate forcing on global air masses is, likewise, echoed in detailed atmospheric CH_4 reconstructions from Antarctica (Fig. 1h; Rhodes et al., 2015).

Climate and environmental responses to HS4 have been identified in terrestrial sequences from the central and eastern Mediterranean (e.g. Tzedakis et al., 2004), however, lack of robust geochronological control has, until now, limited the assessment of relative leads and lags in proxy response. We take advantage of the widespread 39.85 ka Campanian Ignimbrite (CI/Y-5) tephra marker to precisely correlate three centennially resolved pollen records from eastern Mediterranean terrestrial sequences that span HS4. The presence of a time-synchronous marker horizon, present in all three records and close to the onset of HS4 cooling, provides a unique opportunity to test the synchroneity of vegetation responses between three pollen sequences downstream of the North Atlantic climate realm.

The Campanian Ignimbrite (CI/Y-5) tephra marker was produced during an eruption of Campi Flegrei, Italy, that has been dated to 39.85 ± 0.14 ka BP (Giaccio et al., 2017), which is approximately coeval with the onset of HS4. Stratigraphic evidence in marine and terrestrial records has shown that the two events were not causally linked (Lowe et al., 2012). The close timing of HS4 and the CI eruption, however, provides an opportunity to use the tephra marker to interrogate environmental responses to HS4. Amongst the largest known Quaternary eruptions, the CI produced a tephra deposit, sometimes distally termed the Y-5, which fell over an area of 3.5 million km^2 (Costa et al., 2012, Fig. 2a) within the hours to days following the eruption. The CI/Y-5 tephra marker has been identified in a range of marine and terrestrial sediment sequences in the central and eastern Mediterranean and has been used as a chronostratigraphic marker (isochron) for both dating and direct correlation of Quaternary archives (e.g. Lowe et al., 2012). The CI/Y-5 tephra is found as a cm-scale visible tephra layer at the three study sites considered in this study: Ioannina (McGuire et al., 2022), Tenaghi Philippon (Wulf et al., 2018), and Megali Limni (Margari et al., 2007).

2. Study sites

Ioannina (39°39′00.0"N, 20°53′24.0"E; 470 m a.s.l.) is a lake located within a karstic basin in the Epirus region of NW Greece (Fig. 2). The basin floor is 35 km on its longest axis, although through artificial drainage the lake itself is currently reduced to ca. 11 km in length. The basin is bounded by the Pindus Mountains to the east, and the Tomarokhoria Plateau to the southwest. In the present-day, Ioannina, and the Epirus region more broadly, receives much higher precipitation throughout the year (Fig. 2) than lowland and more easterly regions, largely due to the orographic uplift of moist warm air from the nearby

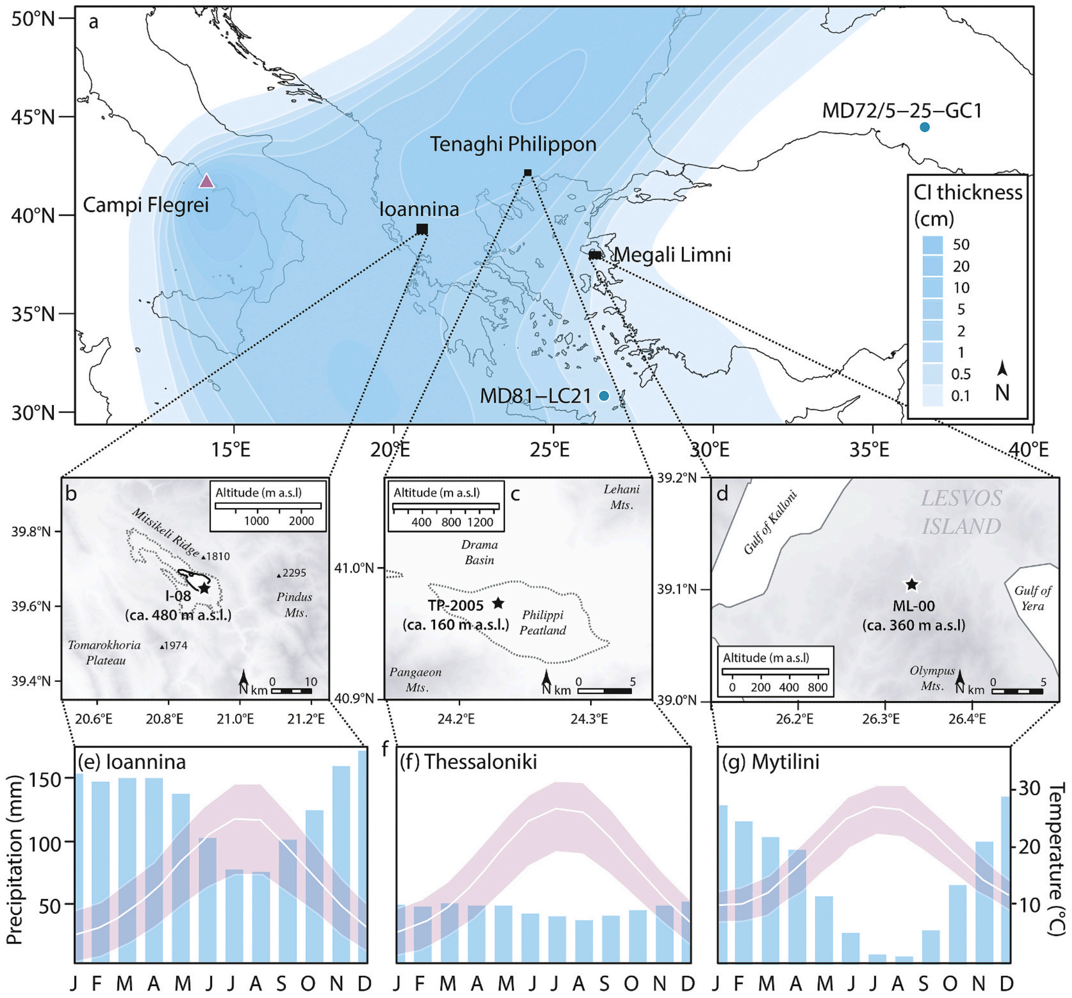

Fig. 2. Maps showing: (a) the location of sites mentioned in the text, overlain by the simulated dispersal of the plinian and co-ignimbrite phase of the Campanian Ignimbrite eruption, after Marti et al. (2016) with relief maps showing core locations within (b) the Ioannina Basin, (c) the Drama Basin, and (d) Lesvos Island, alongside nearby HNMS climate data from (e) Ioannina 1956–2010, (f) Thessaloniki 1959–2010, and (g) Mytillini 1955–2010 from HNMS (http://emy.gr/emy/en/climatology/climatology_city).

Ionian and Adriatic seas. The present-day vegetation at the site, outside of the intensively farmed basin floor, includes *Juniperus communis* scrubland, with dense stands of *Quercus coccifera* and *Pinus nigra* on the lower mountain slopes (Roucoux et al., 2008). Beyond the immediate surrounds of the lake, vegetation follows a distinct altudinal gradient in nearby valleys. At lower altitudes vegetation is characterised by mixed woodlands (evergreen and deciduous *Quercus*, along with *Carpinus* spp., *Ostrya carpinifolia*, *Corylus* spp., and *Salix* spp.) with increased *Pinus* and *Juniperus* at altitude (Roucoux et al., 2008). At higher altitudes (>1,000 m a.s.l.) *Fagus sylvatica* and *Abies cephalonica* grow, interspersed with sparse, low-growing *Juniperus* spp. Scrub (Roucoux et al., 2008).

The lake Ioannina sediment record has been the focus of multiple palynological investigations over the last 50 years, commencing with early work to support archaeological investigations in the Epirus region by Bottema (1974). Subsequent work focused on reconstructing palaeoecological change within the long core sequences I-249 (Fig. 3; Tzedakis, 1993; Tzedakis, 1994) and I-284 (e.g. Frogley et al., 1999, 2009; Lawson et al., 2004; Roucoux et al., 2008, 2011; Tzedakis et al., 2006) which span multiple glacial-interglacial cycles. Due to the large size of the basin, it is likely pollen deposited in the lake centre recorded in, for example, core I-284 reflects mostly the regional vegetation, with a smaller component reflecting the local vegetation sourced from the lake margins (Lawson et al., 2004; Roucoux et al., 2011).

Across the last glacial cycle, the palynological assemblages of Ioannina sediments are divided by Tzedakis et al. (2006) into three broad vegetation types: forest communities where arboreal pollen (AP) exceeds 70% of the terrestrial pollen sum; communities of intermediate forest cover where AP is between 40 and 70%, and open vegetation communities containing scattered trees where AP is between 20 and 40% (Fig. 3). Tree populations persisted at Ioannina throughout the last glacial, when cold stage tree populations were made up predominantly of deciduous *Quercus* and *Pinus* (>15 and > 10% respectively), with other trees such as *Abies*, *Ulmus*, *Corylus*, *Carpinus*, and *Ostrya* continuously present at lower abundances (Tzedakis, 1993; Tzedakis et al., 2006). Tzedakis et al. (2004) identify millennial-scale expansions and contractions of tree populations recorded in the Ioannina sequence which were similar in frequency to North Atlantic climate variability, with repeated intermediate declines in AP interspersed with infrequent larger decreases. The lowest AP values at Ioannina are argued to correlate with AP minima in the Alboran Sea pollen records, which are interpreted to be synchronous with HEs (Tzedakis et al., 2006).

The **Tenaghi Philippon** (40°58′24″N, 24°13′26″E; 40 m a.s.l.) site is in the Drama Plain in the northeast of the Greek mainland. Whilst the temperature regime at the site is similar to Ioannina, precipitation is much lower, with a mean annual precipitation of 600 mm (Fig. 2), increased continental influence in the region drives anomalously cold and windy episodes during winter due to southward migration of polar air masses from the Siberian High (Pross et al., 2009). The area today is

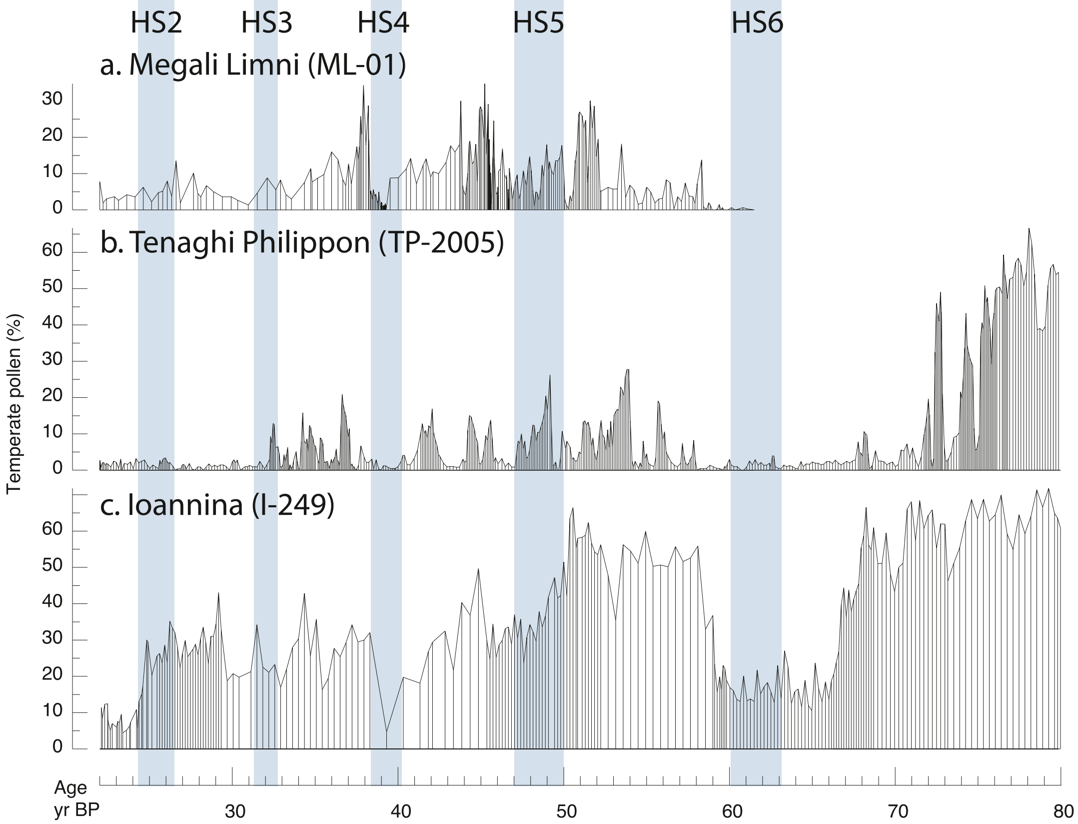

Fig. 3. Temperate tree pollen percentages, redrawn from previously published pollen records from the (a) Megali Limni (ML; Margari et al., 2009), (b) Tenaghi Philippon (TP-2005; Müller et al., 2011; Koutsodendris et al., 2023), and (c) Ioannina (I-249; Tzedakis, 1993) sites. Blue shading denotes timing of Heinrich Stadials in the North Atlantic *sensu* Sanchez Goñi and Harrison (2010).

almost completely cultivated land following artificial drainage. The present-day regional vegetation in the Drama Basin varies with altitude, with low altitudes dominated by thermophilous scrub formations (evergreen *Quercus* spp., *Pistacia terebinthus*, *Cistus* spp.), mid-altitudes are primarily associated with mixed Mediterranean woodlands (deciduous *Quercus* spp., *Carpinus orientalis*, *Castanea sativa*), and montane tree communities dominant at higher altitudes (*Pinus sylvestris*, *Picea abies*, *Fagus sylvatica*, and *Betula pendula*) (Fletcher et al., 2013).

The sediment sequence at Tenaghi Philippon, which has a depth of ca. 200 m, is composed of peats, gyttja, lake marls and clays (Pross et al., 2015). Initial investigations from the site (e.g. Wijmstra, 1969; van der Wiel and Wijmstra, 1987) demonstrated Tenaghi Philippon sediment sequences span several glacial-interglacial cycles (ca. 1.4 Ma), with interglacials marked by high AP and glacials by low AP. The large size of the Tenaghi Philippon basin suggests that the pollen in TP-2005, as at Ioannina, is dominated by regional pollen, with some local peatland taxa represented (Pross et al., 2015). Koutsodendris et al. (2023) identify two main alternating vegetation regimes across a 500-0 ka pollen record from Tenaghi Philippon: an open cold-stage vegetation dominated by steppe biomes where tree pollen is below 35%, and warm-stage forest vegetation where tree pollen is above 65% (Fig. 3). During the last glacial, as at Ioannina, millennial-scale short-term expansions of tree populations interrupted the general dominance of dry steppe taxa such as *Artemisia* and Chenopodiaceae (Koutsodendris et al., 2023). Periods of higher AP, such as maxima at ca. 53 ka BP, have been linked to short-term increases in precipitation at the site.

Megali Limni (39°06′00.0"N, 26°19′12.0"E; 323 m a.s.l.), a palaeolake basin on upland Lesvos Island in the northeastern Aegean Sea, covers ca. 1.48 km^2, with a modern catchment ca. 13 km^2. Bounded by hills, the basin is located within a V-shaped valley of fluvial origin that was blocked at its southern end by a landslide to form a lake basin (Margari, 2004). The basin is situated in an area characterised by serpentine soils, which are primarily relatively deep (70–120 cm) clays with high water retention capacity (Kosmas et al., 2000). Present-day rainfall at the site is highly seasonal, with similarly wet winters to Ioannina, yet much drier summers (Fig. 2). In the present day, the site is used as agricultural land, surrounded by *Pinus brutia* forest.

Palynological investigation of the last glacial cycle at Megali Limni by Margari et al. (2009) reveals several oscillations between steppe, forest-steppe, and forest, which are interpreted as occurring in concert with North Atlantic millennial-scale variability (Fig. 3). The local vegetation during late Marine Isotope Stage 4 was grassland/steppe, indicating cold and arid conditions, with increased AP during last glacial interstadials, suggesting increases in tree population extent, precipitation, and temperature. During stadial periods, as at Ioannina and Tenaghi Philippon, *Artemisia* and Chenopodiaceae increase, suggesting enhanced aridity, with the most extreme contractions in tree populations recorded during stadials corresponding to HEs.

3. Methods

To evaluate regional variability in ecosystem responses to HS4-associated cooling, we have generated a new 5.3 m long centennially resolved pollen record for Ioannina that captures vegetation changes ca. 1.5 ka before and after the onset of HS4. We compare our new data to the previously published pollen records from Tenaghi Philippon (TP-2005; Müller et al., 2011; Koutsodendris et al., 2023) and Megali Limni (ML; Margari et al., 2009) using the CI/Y-5 for correlation.

3.1. Pollen analysis

Our new Ioannina pollen record was generated using core I-08, a 38 m sediment core recovered in 2008 from a single borehole at the edge of the present-day lake basin, using a truck-mounted drill (recovery >90%). The sequence primarily consists of carbonate clay and silt, with sand between 21.00 and 19.71 m. The full I-08 tephra record, which identified the CI/Y-5 tephra at 30.14 m depth, has been published by McGuire et al. (2022).

Uniform 0.5 cm^3 subsamples were taken for pollen analysis with 2 cm sample spacing between 31.98 and 28.67 m depth. An exotic spike of *Lycopodium* marker spores was added prior to sample preparation following Stockmarr (1971). Preparation followed standard palynological techniques including the treatment with 7% HCl, 10% NaOH, 60% HF and acetolysis. A minimum of 300 pollen grains of terrestrial plant origin (excluding pteridophytes) were counted in each sample following the recommendation of Maher (1972). Poaceae has been excluded from the terrestrial sum, as Ioannina is a large lake basin with abundant peripheral wetlands, meaning grasses can dominate the assemblage regardless of prevailing climate and environmental regimes (Lawson et al., 2004).

Identification of pollen grains is based on Beug (2004), Chester and Raine (2001), and laboratory reference collections, particularly the Godwin pollen collection in the Department of Geography, University of Cambridge. The percentages of taxa were calculated relative to the sum of total terrestrial pollen, which excludes Poaceae, aquatic plants, spores, and algae, with *Lycopodium* counts used to calculate pollen concentrations. Pollen groupings, where taxa are grouped according to shared ecological characteristics, are outlined in Table S1.

3.2. *Age-depth modelling*

We develop a linked age-depth model, which we use to update the chronologies for each of the sites to ensure our comparisons are internally consistent. The central chronology we use is that of Tenaghi Philippon (TP-2005), which incorporates 20 ^{14}C dates from the original chronology of Müller et al. (2011) and 54 ^{14}C dates from Staff et al. (2019). Also incorporated are the CI/Y-5, Masseria del Monte/Y-3, and Vallone del Gabellotto/E−1 tephra markers (Wulf et al., 2018). The CI/Y-5 tephra horizon is used for direct temporal correlation of sites in this study. The CI eruption has been directly dated using Ar/Ar to 39.85 ± 0.14 ka BP (Giaccio et al., 2017). We import the Giaccio et al. (2017) age into the Tenaghi Philippon TP-2005 age-depth model using the OxCal C_Date function at the upper bound of the tephra deposit at 12.64 m depth (Wulf et al., 2018). When incorporated in the TP-2005 age model, the CI/Y-5 tephra marker age is remodelled to ca. 39,650 cal BP (2-σ calendar age range: 39,911 to 39,461 cal BP; Fig. S1) through Bayesian inference based on the surrounding radiocarbon ages.

To facilitate direct correlation between the sites we use the modelled Tenaghi Philippon posterior probability function for the CI/Y-5 tephra marker output by the TP-2005 *P_Sequence* model within the age models created for I-08 and ML. Our alignment approach provides a consistent and robust means to compare the sites without removing important geochronological data from the well-resolved TP-2005 age model. Chronologies for the Ioannina (I-08), Megali Limni (ML) were remodelled using Bayesian *P_Sequence* deposition models (Bronk Ramsey, 2008), implemented in OxCal v. 4.4. utilising the IntCal20 calibration curve (Bronk Ramsey, 2009; Reimer et al., 2020). The Ioannina chronology uses published tephra (McGuire et al., 2022) and radiocarbon (Jones et al., 2013) age estimates. Similarly, our updated Megali Limni chronology utilises a combination of radiocarbon and tephra ages (Margari et al., 2007, 2009). For tephra deposits with a thickness >1 cm, depths below the tephra deposit are adjusted to account for the thickness of the deposit in that sequence.

Given that primary volcanic ash-fall layers form time-synchronous markers, the occurrence of the CI/Y-5 tephra as a visible layer across all three sites (Ioannina, McGuire et al., 2022; Tenaghi Philippon, Wulf et al., 2018; Megali Limni, Margari et al., 2007) allows direct correlation of the three sequences independent of other geochronological control. To understand the duration of the changes observed, however, and to provide some insight into the rate at which the changes identified within the proxy record occur, it is necessary to develop age-depth models for the sequences. Through this, we produce a linked age-depth model, combining the chronological modelling of the three sites, to ensure the model-age of the CI/Y-5 in each sequence is consistent (Fig. 7). A combined age-depth model ensures that other chronological control, in this instance radiocarbon dates and other tephrochronological information, does not result in different ages being ascribed to the CI/Y-5 tephra marker.

4. Results

4.1. *Pollen records*

In this section we present the results of our new, high-resolution pollen study of the I-08 core across the HS4 window. We then go on to consider the timing of the vegetation change at Ioannina, as recorded in our new I-08 pollen record, and compare it to previously published records from Tenaghi Philippon and Megali Limni surrounding the CI/Y-5 tephra marker. We present all three records using their revised, linked, age-depth models.

Our new **Ioannina** record (Fig. 4) is resolved to sub-centennial scale, an order-of-magnitude greater than previous records from the site across the same temporal window. In the I-08 record, sediments directly below the CI/Y-5 tephra unit (30.21–29.93 m depth) contain ca. 40% tree pollen, predominantly made up of deciduous *Quercus*, with some *Abies*, and *Pinus*. Abundances of steppe taxa *Artemisia* and Chenopodiaceae are low, accounting for less than <30 % terrestrial pollen. Between 30.27 and 30.20 m depth there is a drop in deciduous *Quercus* from ca. 35% of the terrestrial sum, values similar to Holocene levels (Tzedakis, 2002; Lawson et al., 2004), to ca. 20% of the terrestrial pollen sum.

Above the CI/Y-5 unit, there is a more substantial decline in deciduous *Quercus* to <10 %. The decline in oak is reflected across all tree pollen taxa, and we see the complete disappearance of *Abies, Carpinus*, and *Corylus.* In concert with the decline in tree pollen, there is an expansion in *Artemisia* and other herbaceous taxa, although there is no concurrent large expansion in Chenopodiaceae. The ca. 10% AP minimum between 29.9 and 29.8 m depth, is amongst the lowest observed at Ioannina in records which span at least the last two full climatic cycles (Tzedakis et al., 2006; Lawson et al., 2004; Roucoux et al., 2008; Roucoux et al., 2011), approaching the ca. 8 % AP minimum ca. 24 ka BP associated with the last glacial maximum (Lawson et al., 2004) and the 8 % temperate tree pollen (AP minus *Pinus*, *Juniperus,* and *Betula*) recorded between ca. 177 and 158.5 ka associated with cooling during MIS 6 (Roucoux et al., 2011).

In the record from **Tenaghi Philippon** (Fig. 5) an AP decline commences at 13.2 m depth, over 20 cm below the visible CI/Y-5 tephra layer, which has its base at 12.86 m. Deciduous *Quercus* and *Pinus* decline in unison, whilst trace occurrences of *Juniperus* persist. The AP minimum is reached just below the CI, and values remain low in the sediments immediately above. The highest values of *Artemisia* at Tenaghi Philippon follow the deposition of the CI/Y-5, above which they begin to decline. As with the Ioannina record, values of AP in sediments around the CI/Y-5 marker, and thus broadly synchronous with HS4, are amongst the lowest recorded at the site, and are similar to values from the late glacial, as well as across earlier glacial stages such as MISs 6, 8, 10, and 12 (Fletcher et al., 2013; Koutsodendris et al., 2023). The relative timing of the tree population decline, however, is different to that recorded at Ioannina: a dramatic decline in tree populations at Tenaghi Philippon occurred prior to the CI eruption, whilst at Ioannina tree population decline continues through, and reaches a minimum following, the eruption, suggesting a diachronous vegetation response between the two sites.

Finally, the pollen record from **Megali Limni** also records a dramatic contraction in AP *across* the CI/Y-5 marker (Fig. 6), which lies between

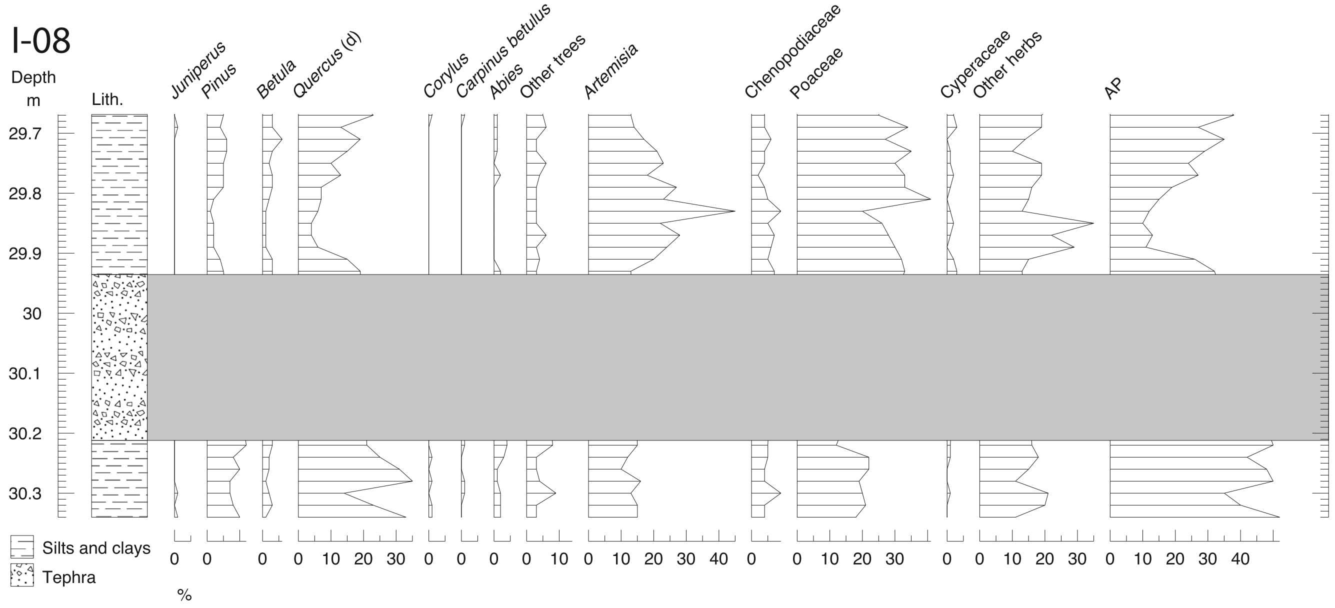

Fig. 4. Summary pollen diagram for the I-08 Ioannina core for sediments surrounding the CI tephra marker, showing percentage of terrestrial pollen concentration plotted against depth. The grey shaded area denotes the depths of the CI tephra marker (see McGuire et al., 2022).

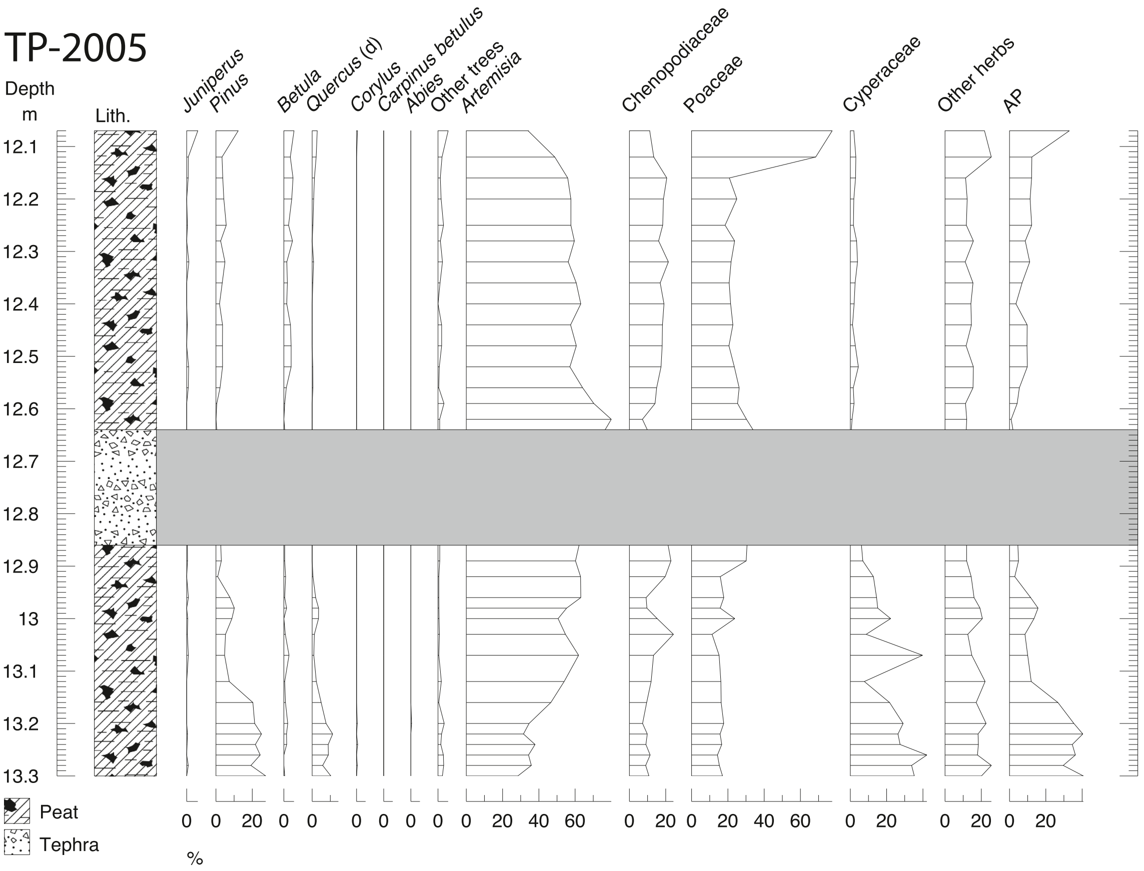

Fig. 5. Summary pollen diagram for the TP-2005 Tenaghi Philippon core for sediments surrounding the CI tephra marker, showing percentage of terrestrial pollen concentration plotted against depth, after Müller et al. (2011) and Koutsodendris et al. (2023). The grey shaded area denotes the depths of the CI tephra marker (see Wulf et al., 2018).

7.61 and 7.5 m depth. Most notably, whilst the samples below the CI/Y-5 marker (from 7.65 m depth upwards) show a decline in *Pinus* (from ca. 40 to 20 %), a further contraction in tree populations, including deciduous *Quercus* and *Pinus* happens across the deposition of the CI/Y-5. There is a decline in tree taxa, particularly *Pinus*, between the sample immediately underlying the visible tephra unit ca. 7.6 m depth and the sample immediately above it at 7.5 m depth. In contrast to Ioannina and Tenaghi Philippon, there is no substantial change in steppe taxa, with

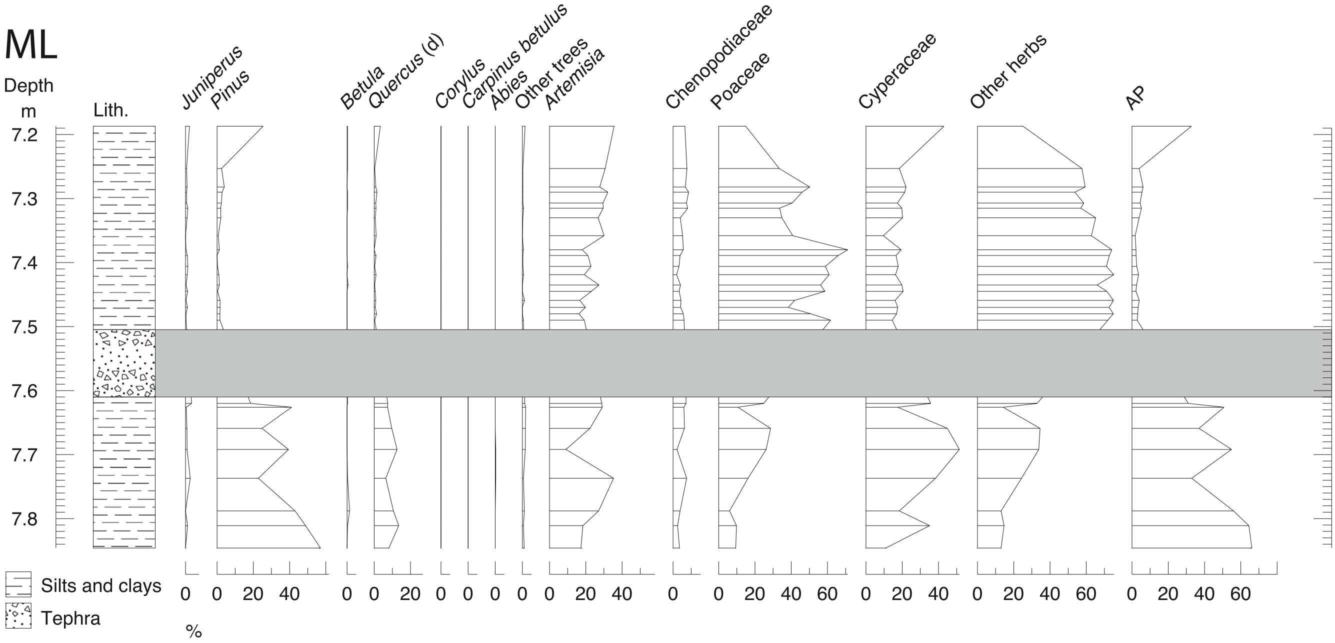

Fig. 6. Summary pollen diagram for the Megali Limni (ML) core for sediments surrounding the CI tephra marker, showing percentage of terrestrial pollen concentration plotted against depth, after Margari et al. (2009). The grey shaded area denotes the depths of the CI tephra marker (see Margari et al., 2007).

only small oscillations in *Artemisia* and Chenopodiaceae pollen assemblages. At both the lake sites, Ioannina and Megali Limni, there is an increase in Poaceae pollen abundance across HS4.

To summarise, all three records show declining tree pollen in sediments close to the CI/Y-5 tephra marker, however, the pattern and timing of vegetation change varies between the sites. At Ioannina, whilst there is a gradual decline in tree pollen, particularly in deciduous *Quercus*, the most abrupt vegetation response, and the tree pollen minimum, occurs above the CI/Y-5. At Megali Limni, change occurs on both sides of the CI/Y-5 tephra, and, as at Ioannina, the minimum in tree pollen abundance is reached above the tephra marker. At Tenaghi Philippon, by contrast, tree pollen minima have already been reached prior to deposition of the CI/Y-5, and tree pollen percentages remain low above the tephra layer.

4.2. Chronology

Fig. 7 shows our revised Bayesian age-depth models for Ioannina, Tenaghi Philippon and Megali Limni, linked with a consistent age for the CI/Y-5 of 39,911 to 39,461 cal BP (2-σ calendar age range), taken from the TP-2005 age model. The uncertainty associated with all three age models increases with distance from the CI/Y-5 tephra marker (Fig. 8), which has the lowest chronological uncertainty of all the dates incorporated in the age-depth models. In the Tenaghi Philippon sequence, intensive radiocarbon dating in 2 m of sediment underlying the CI/Y-5 (see Staff et al., 2019) ensures, at most, centennial-scale uncertainties between ca. 47,300 and 39,600 cal BP. However, the resolution of the dating is lower above the CI/Y-5, and thus age uncertainties are larger, up to millennial-scale, in this section of the record (Fig. 8). Similarly, in both the Ioannina and Megali Limni sequences, the CI eruption age control provides a high degree of chronological certainty across the H4 interval. Critically, at the depth of the CI/Y-5 tephra in each sequence the precision of inter-site comparisons is reduced to zero, allowing the relative timing of tree decline to be precisely compared between the three records.

5. Discussion

5.1. The timing of vegetation response to HS4

When plotted against modelled age, the I-08, TP-2005, and ML pollen records (Fig. 9) all reveal marked contractions in temperate and pioneer tree pollen ca. 40 ka BP, which we interpret here as a vegetation response to regional cooling and drying associated with Heinrich Stadial 4. Here, we discuss the character of the vegetation response recorded in our new Ioannina record, drawing on earlier pollen studies at the site, before considering the timing of ecological response across the HS4 window at each site.

Our new Ioannina record (I-08), the sub-centennial resolution of which is an order-of-magnitude greater than earlier records from the site across the same temporal window, provides new insights into the extent of vegetation response to HS4 at the site. Firstly, as hinted in earlier records (e.g. Tzedakis et al., 2004, Fig. 3) the tree pollen minimum ca. 40 ka BP is markedly lower than any other millennial-scale contraction observed across the last glacial cycle at the site. The persistence of low (>10 %) tree pollen concentrations across multiple pollen samples in I-08 suggests a pronounced reduction in the extent of tree population, shown most clearly by the decline in deciduous *Quercus*. The expansion of steppe taxa, including *Artemisia* and Poaceae, suggests the forest cover was replaced by steppe, driven by HS4 drying. Based on our age-depth model, this collapse in tree populations was sustained for ca. 120 years, at which point populations recover rapidly.

Vegetation response at the site to climatic change during HS4 appears to occur across the CI/Y-5 tephra layer. Whilst temperate tree taxa, such as deciduous *Quercus,* begin to decline prior to the deposition of the CI/Y-5, tree populations continue to decline until ca. 100 years after the Campanian Ignimbrite eruption, at which point they reach their minimum. Unlike in previous studies from the site, where this minimum is seen in a single sample, in our new I-08 record the contraction in temperate tree pollen is maintained across multiple samples, suggesting sustained forest collapse in much of the basin for at least a century. Although the age model uncertainty does not allow for much more than a broad understanding of the rate of this change, initial temperate tree pollen declines by 8% over a ca. 210-year window in sediments above the CI/Y-5 and decline by 15% over ca. 150 years in sediments

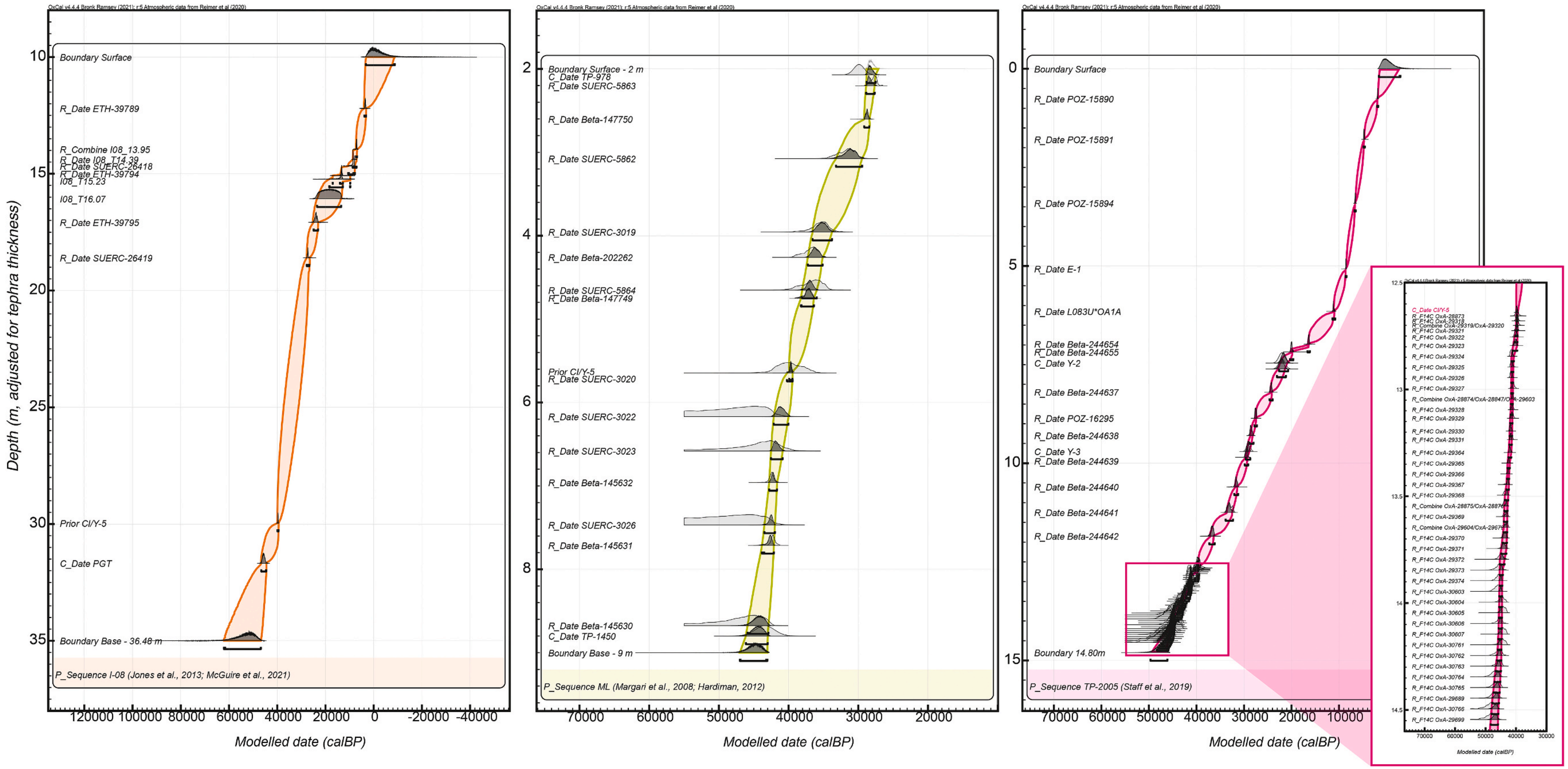

Fig. 7. Depth plots showing the new I-08, ML, and TP-2005 OxCal P_sequence depositional models. Interpolation and posterior probability density functions are shown at 95.4% confidence limits. Asterisks denote the CI/Y-5 within the model, which is used to link the three chronologies. Full chronostratigraphic information, and the code used to build the model, is available at https://github.com/amy-mcg/McGuire_HS4.

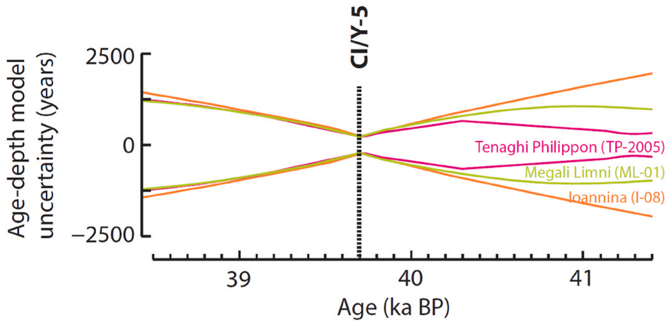

Fig. 8. Age-model 95% uncertainty for Ioannina (I-08), Tenaghi Philippon (TP-2005), and Megali Limni (ML) plotted against age.

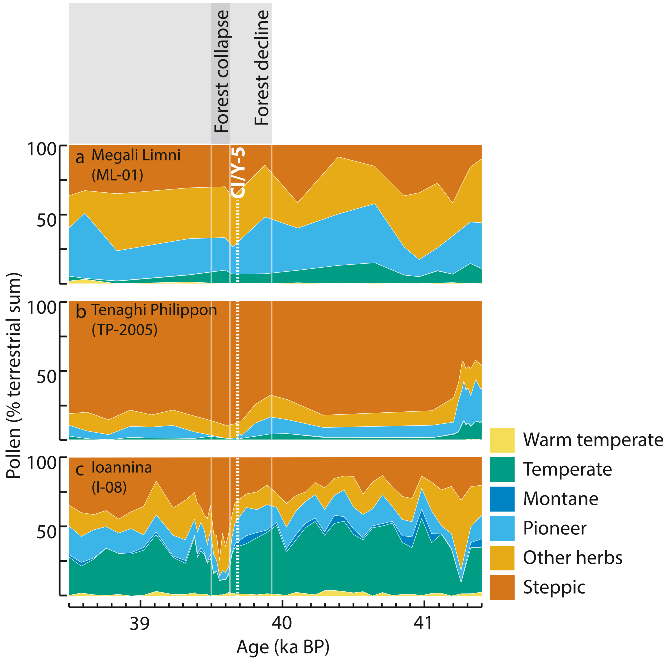

Fig. 9. Comparison of the timing of vegetation response to HS4 observed at (a) Ioannina (I-08), (b) Tenaghi Philippon (TP-2005), and (c) Megali Limni (ML). Shading indicates the timing of forest minimum at Tenaghi Philippon (associated with regional forest decline) relative to Ioannina (associated with forest collapse).

immediately overlying the tephra marker. If we are to infer this as a gradual initial decline, followed by a subsequent rapid collapse in tree populations, this is at odds with our current understanding of millennial-scale climate change in the Mediterranean region where, broadly, it is assumed that stadial and interstadial onsets are rapid due to close coupling of the regional climate with that of the North Atlantic climate realm, driven by migration of the eddy-driven polar jet stream (e.g. Stadelmaier et al., 2024).

The gradual initial vegetation response to stadial drying at Ioannina may be related to the distinct character of the lake catchment and the Pindus region, where topographic complexity provides an array of habitats, perhaps sheltered or south-facing areas, which would remain sufficiently wet due to orographic rainfall, in which temperate vegetation was able to persist while at the regional scale, precipitation declined. The presence of these microclimatic refugia may have delayed and/or limited the response of vegetation to increased regional aridity because, locally, conditions remained sufficiently wet for temperate trees to survive (Tzedakis et al., 2004). Furthermore, the presence of refugia capable of sustaining deciduous vegetation even during times of climatic extremes, such as HS4, would have facilitated the rapid recovery of tree populations in the Ioannina catchment (see Tzedakis et al., 2006).

The gradual initial tree population decline, followed by an abrupt phase of vegetation collapse, could also reflect the structure of stadial onsets in other records, particularly HSs. For example, in multiproxy analysis of HS4 and HS5 in marine sediments from the Iberian Margin Margari et al. (2020) identify considerable structure, which contrasts to the uniform cooling seen across non-Heinrich stadials. In the Iberian Margin sequences, HSs begin with a short transitional cooling phase, followed by an interval of maximum cooling and aridity. Our uniquely resolved I-08 pollen record may express this same sequencing, with a slow initial decline in tree pollen, responding to early-HS gradual increased aridity, followed by a rapid, sub-centennial decline, which appears to reflect local forest collapse (Fig. 9).

The pattern and timing of vegetation responses at Tenaghi Philippon presents a contrast to those at Ioannina. In the TP-2005 record tree populations disappear rapidly, and almost completely (<5 %), prior to the CI, representing the most extreme decline observed during the last glacial record (Koutsodendris et al., 2023). Thus, the vegetation response at Tenaghi Philippon is more rapid, and earlier, than at the Ioannina site. Tree populations at Tenaghi Philippon, in the low relief Drama Basin (Fig. 2c), would have been growing in conditions towards the low end of their moisture tolerance even during the, regionally, wetter phases of the last glacial (Tzedakis et al., 2004; Koutsodendris et al., 2023). The proximity of temperate taxa to their lower moisture limits may explain why forest cover contracted rapidly in response to increased aridity at the site during HSs (Tzedakis et al., 2004; Müller et al., 2011).

A marked difference between the HS4 contraction in tree populations at Tenaghi Philippon and tree population contractions associated with previous and subsequent stadials is the duration of tree population minimum. Tree populations only expanded again after ca. 5,000 years (Fig. 3), which is more than 2,000 years after the end of HS4 as dated in the North Atlantic (HS4; 40.2 to 38.3 ka, *sensu* Sanchez Goñi and Harrison, 2010). Given that HS4 is associated with the most prolonged stadial conditions during the last glacial cycle, it may be that tree populations in NE Greece, including in areas where less resilient taxa which were typically able to persist through less arid stadial periods, were unable to survive the harsh HS4 climate. If that was the case, recovery of tree populations would have been reliant on the spread of trees from more distant stadial refugia, which could explain the slow pace of tree population recovery. Alternatively, it may be that the harsh conditions, particularly the extreme aridity, which would have limited the growth of temperate taxa, were sustained at the site for the entire 5,000-year interval.

At Megali Limni, as at Ioannina, tree pollen decline continues following the deposition of the CI, with a contraction in *Pinus* and *Juniperus*. The Megali Limni record suggests an initial decline in forest cover prior to the deposition of the CI/Y-5, however, due to sample resolution, it is challenging to say whether there is evidence of a sustained decline. Tree populations persist at Megali Limni across many millennial-scale climate cycles (Margari et al., 2009), in contrast to the strong contraction of temperate woodland taxa associated with stadial cooling and drying at TP. The full pollen record from Megali Limni (ML; Fig. 3), which spans ca. 60 to 20 ka BP, suggests that, as at Ioannina, HEs have a more pronounced effect on tree populations than D-O stadials (Margari et al., 2009). There is a more pronounced reduction of tree cover during HS4 at both Ioannina and Megali Limni relative to other HSs at the sites. At both sites, the reduction in tree cover is similar to that seen at both sites across the last glacial maximum, hinting at the severity of drying across the region during HS4.

A final interesting feature of the Ioannina (Fig. 4) and Megali Limni (Fig. 6) records are the changes in Poaceae pollen concentration across HS4. In both sites there is an abrupt increase grass pollen in the sample overlying the CI/Y-5 relative to the sample underlying the tephra marker. In these sites, Poaceae has two potential sources: an increase in grassland within the catchment, or the expansion of wetlands on the lake margins, associated with taxa such as *Phragmites*, in the Poaceae family. If it is the former, increased grassland within the pollen source region, this further reflects an expansion of steppe environments at the sites. If it is the latter, this suggests an abrupt change in lake level at the sites. Whilst diatom studies have not been undertaken at Megali Limni, detailed, multi-core diatom studies from the Ioannina site demonstrate marked lake level fluctuations associated with aridity during the LGM, followed by a wetter late glacial interstadial, with increased lake levels during the Younger Dryas stadial (Wilson et al., 2008; Jones et al., 2013). Similarly, diatom analysis across the penultimate deglaciation at Ioannina suggests multiple oscillations in lake level, which Wilson et al. (2008) link to the regional influence of abrupt changes in North Atlantic conditions. Regardless of what caused the increase in Poaceae within the sediments across the CI/Y-5, it seems likely that the increase in Poaceae, whether a result of changes in lake level or an expansion in steppe environments within the catchments, are a consequence of enhanced regional aridity. This is not the case at Tenaghi Philippon, where there is a decline in Poaceae as part of a longer term, more gradual change, also reflected in the *Artemisia* curve. Overall, changes in Poaceae at Tenaghi Phillipon are less pronounced, partly due to the differing sedimentary context of the site, and as Poaceae is not as abundant at this site, in this interval.

Given the importance of stratigraphy to our argument, it is important to consider whether the changes observed in the pollen spectra, particularly in abundant taxa such as Poaceae, *Artemisia,* and *Quercus*, are an artifact of coring-related disturbance, particularly above and below the poorly consolidated tephra layer. Across all sites, changes in the pollen spectra reveal declining tree populations (interpreted from both relative abundance and concentration of tree pollen) occurred in tandem with expansions in steppe taxa more resilient to cooling and drying. Thus, it is unlikely that rapid changes in vegetation composition are an artifact of coring processes, which would be unlikely to produce pollen spectra which make ecological sense.

Furthermore, the sediment stratigraphy of the cores does not suggest coring or post-depositional alteration of the sequences. At Ioannina, laminations in the I-08 sequence both above and below the Campanian Ignimbrite tephra marker suggest minimal coring-related disturbance, supported by cryptotephra analysis, which demonstrate a marked, exponential, decline in tephra content in sediments immediately underlying and overlying the CI/Y-5 (McGuire et al., 2022). Similarly, at Tenaghi Philippon, Wulf et al. (2018) identify tephra glass shards that have undergone post-depositional reworking in overlying sediments, however they argue that the processes responsible for tephra reworking should have had no effect on the pollen data. Finally, at Megali Limni sediments are organic-rich clays with no lithological evidence of disturbance. We rule out post-depositional bioturbation as a driver, as sediment mixing would be expected to make changes in the pollen spectra appear more gradual, as opposed to more abrupt. Thus, we argue the rapid variability observed in the pollen records is not a consequence of taphonomy, and instead reflects real, abrupt, vegetation changes at the three sites.

5.2. *Site-specific or regional drivers of vegetation change?*

Vegetation records from throughout the Mediterranean region have long suggested that Heinrich Stadials drive more extreme ecosystem responses than D-O stadials. Tzedakis et al. (2004) suggest that the marked vegetation response at Ioannina across HSs is associated with the entrance of polar water through the Strait of Gibraltar (Cacho et al., 1999; Fletcher and Sánchez Goñi, 2008). Since surface waters in the Eastern Mediterranean Sea derive from the same Atlantic Water Stream as the Western Mediterranean (Pinardi and Masetti, 2000), the input of cooler, polar waters should propagate to the Eastern Mediterranean basin. Cooler surface waters in the Mediterranean Basin would have reduced evaporation, and thus the moisture content of low-pressure systems moving across the nearby seas, intensifying the aridity at sites such as Ioannina where precipitation is driven by uplift of moisture-laden air masses (Tzedakis et al., 2004). The relationship between SST and precipitation has been observed in the present day, where precipitation in the eastern Mediterranean region is sensitive to changes in sea surface temperatures (SSTs), with increased SSTs linked to increased rainfall (Turuncoglu, 2015).

The CI/Y-5 tephra provides a precise chronological tie-point between the TP-2005, ML, and I-08 sequences, and reveals that vegetation responses to the onset of HS4 were time-transgressive within Greece (Fig. 9). The tree pollen minimum at Tenaghi Philippon predates the deposition of the CI/Y-5 tephra marker by ca. 50 years, whereas at Ioannina and Megali Limni the tree pollen minimum lags deposition of the CI/Y-5 marker by ca. 100 years. Even considering the uncertainties associated with our age-depth models (Fig. 8), the CI/Y-5 tephra marker provides unequivocal evidence that the eradication of tree populations occurs earlier at Tenaghi Philippon than the tree population contractions seen at Ioannina and Megali Limni.

Whilst site-specific vegetation characteristics provide some explanation for the offset in the timing of the tree population pollen minimum, it is also important to consider the nature of climatic change across HS4. Numerous records (Fig. 1) suggest that HS4 is not just an initial cooling followed by a sustained stable cold climate throughout the stadial. Instead, records from the North Atlantic and its periphery (e.g. Fletcher and Sánchez Goñi, 2008) point at a multi-stage onset where an initial cooling, as seen during D-O stadials, is followed by the more extreme cooling associated with the onset of ice rafting in the North Atlantic, and AMOC entering Heinrich mode (*sensu* Rahmstorf, 2002). Given the broader vegetation histories from the individual sites, the onset of stadial cooling is typically more rapid, and tree population decline more marked, at Tenaghi Philippon than at Ioannina and Megali Limni (Tzedakis et al., 2004; Margari et al., 2009; Müller et al., 2011).

Earlier work by Lowe et al. (2012) found that the onset of HS4 aridity predates deposition of the CI/Y-5 tephra marker. In particular, dust indices from Aegean Sea core MD81-LC21 signal increased aridity prior to the CI eruption (Lowe et al., 2012). Similarly, we see a decline in tree pollen, coupled with a rise in steppe taxa, in all three records, which provides evidence of cooling/aridity prior to the deposition of the CI/Y-5 across the region. Most notably, in the TP-2005 record (Fig. 5), tree pollen is close to its minimum prior to the CI. It may be that at Tenaghi Philippon, where trees are closer to their moisture tolerance limit, the onset of regional aridity prior to the CI/Y-5 eruption was enough to drive close to complete tree population decline, while at Ioannina and Megali Limni, tree population extent was declining but the change was not as pronounced.

Regional climatic changes, particularly in aridity, may also explain the offset in timing of tree pollen minimum at Tenaghi Philippon relative to Ioannina and Megali Limni (Fig. 9). As highlighted, tree population decline at Tenaghi Philippon ca. 41 ka BP, below the CI/Y-5 tephra layer, is related to the earliest stage of HS4, where cooling and drying is similar to that associated with a typical D-O stadial. Subsequently, the almost unprecedented, sustained tree population contraction observed at Megali Limni and Ioannina ca. 39.65 ka BP, recorded above the CI/Y-5 in both records, is a response to the onset of extreme cooling and drying at the site associated with AMOC shutdown during HE4. Such a mechanism may also explain why there is a decline in deciduous *Quercus* below the CI/Y-5 at Ioannina (Fig. 4), and a decline in *Pinus* and deciduous *Quercus* below the CI/Y-5 at Megali Limni (Fig. 6).

The Mediterranean basin has a rich variety of pollen records from a range of palaeoenvironmental contexts, which can also provide insights into the nature of vegetation responses to HS4 in the region. For example, the pollen record from the varved lake record of Lago Grande di Monticchio (Italy; Allen et al., 1999) shows a decrease in arboreal pollen ca. 40.8 ka BP, prior to deposition of the CI/Y-5 tephra (Fig. 10). Detailed analysis of the pollen assemblage is sediments immediately

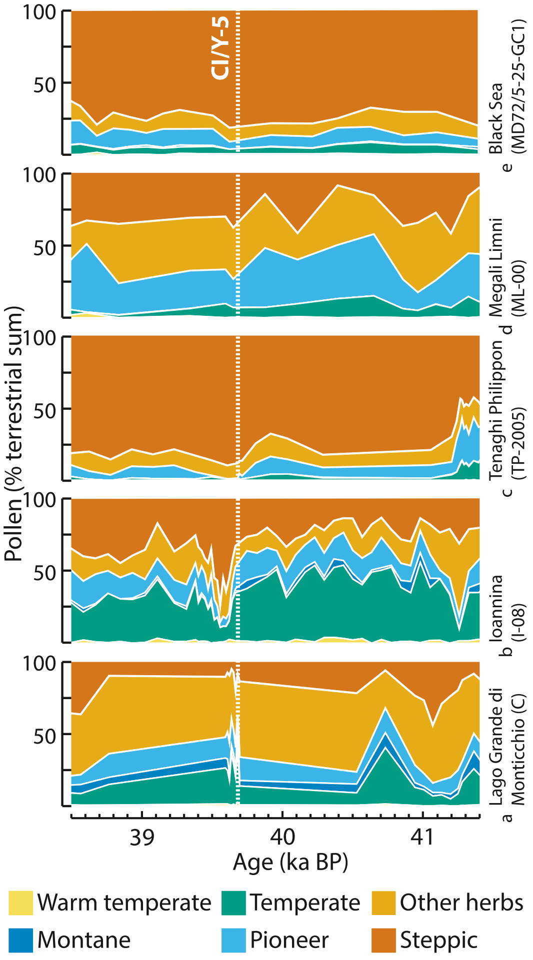

Fig. 10. Comparison of the timing of vegetation response to HS4 observed at (b) Ioannina (I-08), (c) Tenaghi Philippon (TP-2005), and (d) Megali Limni (ML) to pollen records from (a) Lago Grande di Monticchio, Italy (Allen et al., 1999) and (e) Black Sea core MD72/5-25-GC1 (Shumilovskikh et al., 2014).

overlying the CI/Y-5 tephra suggests there was a decline in vegetation productivity associated with the eruption, however, Poaceae, *Artemisia* and Chenopodiaceae remain the dominant taxa at the site. High tephra inputs associated with an increase in regional volcanism prior to the Campanian Ignimbrite eruption (e.g. Wutke et al., 2015; Vineberg et al., 2023) almost certainly shape the pollen assemblage at Lago Grande di Monticchio across HS4 (Allen and Huntley, 2018), making direct comparison challenging. Further eastward, pollen records from the Black Sea (Shumilovskikh et al., 2014, Fig. 10e) do not record a strong vegetation response across the HS4 window, although there is a minimum in tree pollen taxa following the CI/Y-5, in line with the timing of tree pollen minima recorded at Ioannina and Megali Limni.

At present, there are few palaeoclimate reconstructions, beyond vegetation records, which are of sufficient resolution to interrogate variability within HSs. To conclusively demonstrate whether the vegetation responses at Ioannina and Megali Limni lag that seen at Tenaghi Philippon due to (i) site-specific factors or (ii) the onset of the “Event” stage of HS4, marked by polar water incursion to the Mediterranean, further evidence is needed. In the nearby Black Sea, SSTs are shown to have declined during HS4, with an SST minimum identified alongside the deposition of the CI/Y-5 tephra marker (Wegwerth et al., 2015); however, the multi-centennial resolution of the study precludes precise comparison with our archives. Going forward, pan-Mediterranean SST reconstructions demonstrating the propagation of Heinrich forcing beyond the Western Mediterranean (e.g. Rodrigo-Gámiz et al., 2014) could offer a useful perspective, however achieving sub-centennial resolution across the HS4 interval in marine archives is challenging.

Finally, model outputs may provide some evidence that the timing of vegetation response between our three sites is a product of the multi-stage structure of HS4. Margari et al. (2020) demonstrate enhanced cooling and drying across the Iberian Margin during periods of freshwater forcing, with similar responses shown across the Mediterranean region. A challenge arises, however, in comparing models of HSs to typical D-O stadials, as the latter are typically synthesised in models using the same freshwater forcing that drives Heinrich Events. As models get better at capturing D-O variability independently of freshwater AMOC forcing (e.g. Malmierca-Vallet et al., 2023), detailed comparisons of HSs relative to other millennial-scale coolings may be possible.

5.3. *The use of tephra layers as a chronostratigraphic alignment tool*

Here, we have utilised tephrostratigraphic alignment to provide new insights into the leads and lags in proxy responses to past climate change between different sites. As discussed, our findings suggest that the proxy (in this case, pollen) signal at the three sites is either highly localised, or that the vegetation at the different sites is responding to different climatic drivers. Our findings reinforce the argument that we should not exclusively date our archives through aligning vegetation records to other proxy records of climate change. We show here that pollen responses, even in large basins where we can assume a regional signal, reflect the intrinsic character of the ecosystem within that basin, and factors such as proximity to glacial refugia, local microclimates, and broader climatic setting, make the response recorded in the pollen record highly site-specific. We have clearly demonstrated that some ecosystems will respond more quickly than others to regional climate change, although we have been unable to argue conclusively whether this is due to differing ecosystem characteristics, or the nature of the past climate change itself.

We accept, however, that in some instances, where no other chronostratigraphic control is possible, alignment of proxy records to orbital parameters or regional climate reconstructions are the only way to develop age models for Quaternary sequences. It is beyond the scope of this paper to review all the inherent uncertainties associated with tuning records (see Blaauw [2012] for a detailed discussion). We would, however, like to highlight the need for transparency when aligning archives. Whilst chronostratigraphic alignment of the pollen record, to either a regional climate record or orbital parameters, is a powerful technique to answer questions about the character of a vegetation response to past climatic variability, such approaches do not allow a detailed interrogation of the relative timing and pace of these ecosystem responses between records.

We also highlight some of the limitations of tephra layers as a correlation tool. Firstly, whilst a single tephra marker can coincide closely with a known climate oscillation, many tephra markers do not. The Campanian Ignimbrite, being a large eruption with widely distributed tephra deposits, provides a useful isochron to interrogate HS4, and the timing of local responses to this regional climate event; however, it only provides a single time-horizon that can only be used to interrogate proxy responses over a limited temporal window. Whilst similar markers have been identified, such as the 12.1 ka Vedde Ash which has been used to demonstrate time-transgressive climatic amelioration during the Younger Dryas cold period (Lane et al., 2013), such markers are rare. Therefore, we cannot rely on tephra frameworks alone for robust interrogations of leads and lags in proxy responses to global climate change. Development of other climate-independent chronological techniques which provide similar precision, such as the use of the ^{10}Be for precise chronostratigraphic alignment (e.g. Czymzik et al., 2020), or the identification of Miyake events (rapid atmospheric ^{14}C variations, e.g. Miyake et al., 2013) within a broader range of sequences, will help us better interrogate time-transgressive proxy responses to past climate change.

Tephrochronological data, particularly where it is of far greater precision than other geochronological data, is also of limited utility beyond the immediately overlying and underlying sediments. That is to say, with increasing distance from the tephra marker, the age-depth model becomes more uncertain (Fig. 8), and thus using tephra markers to provide insights such as rates of change, is limited by the same chronological uncertainties inherent in other dating approaches. Short of identifying multiple tephra layers, which is often not possible, it is necessary to rely upon other, less precise, dating techniques. Thus, whilst extremely useful in identifying leads and lags within proxy response, other approaches such as varve stratigraphy (e.g. Allen et al., 1999) or detailed radiocarbon analyses (e.g. Staff et al., 2019) are more helpful when determining rates and durations.

6. Conclusions

The Campanian Ignimbrite (CI/Y-5) tephra marker provides an invaluable isochronous tie-point with which to interrogate the temporal and spatial variability of proxy responses to HS4 in the Mediterranean, providing opportunities for detailed terrestrial and marine correlations. We use the CI/Y-5 tephra to align three well-resolved pollen sequences from disparate, and environmentally different, regions of Greece. Our findings suggest that ecological responses to Heinrich forcing in the Mediterranean are not synchronous, with some sites recording earlier vegetation responses than others.

Our results demonstrate the ability of tephra markers to identify leads and lags in proxy responses between sites. In doing so, we reiterate the importance of independently dating archives when seeking to compare the timing of environmental responses to past climate change. We also highlight the role of site-specific characteristics in shaping the proxy response, and thus the need to develop multiple lines of proxy evidence to fully characterize the nature of climate and environmental response across a single region. New, sub-centennial records of regional climate change, particularly proxies for past temperature and precipitation variability, are necessary if we are to understand more fully the vegetation response at the individual sites.

CRediT authorship contribution statement

Amy M. McGuire: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Christine S. Lane:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Katherine H. Roucoux:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Ian T. Lawson:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Andreas Koutsodendris:** Writing – review & editing. **Jörg Pross:** Writing – review & editing. **Vasiliki Margari:** Writing – review & editing. **Polychronis C. Tzedakis:** Resources, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Amy McGuire reports financial support was provided by University of Cambridge. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All code is included in the supplementary, and new pollen data will be uploaded to PANGAEA and Neotoma following publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.108714.

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