BOREAS An international journal of Quaternary research

Marine Isotope Stage 11c in Europe: Recent advances in marine–terrestrial correlations and their implications for interglacial stratigraphy – a review

IAN CANDY, DULCE OLIVEIRA, DANIEL PARKES, JENNIFER SHERRIFF AND DAVID THORNALLEY

BOREAS

Candy, I., Oliveira, D., Parkes, D., Sherriff, J. & Thornalley, D.: Marine Isotope Stage 11c in Europe: Recent advances in marine–terrestrial correlations and their implications for interglacial stratigraphy – a review. *Boreas*. https://doi.org/10.1111/bor.12656. ISSN 0300-9483.

The interglacial known as MIS 11c (*c.* 426 000–396 000 years ago) receives intensive international interest because of its perceived role as an analogue for the current interglacial and its importance for understanding future climate change. Here we review the current understanding of the stratigraphy of this interglacial in Europe. This study considers (i) the evidence for the environmental history of this interglacial as reconstructed from the varved lake records from northern Europe, (ii) the climate history of MIS 11c as preserved in the long pollen records of southern Europe and (iii) a comparison of both of these with marine records from the North Atlantic. The result of this review is a discussion of the evidence for millennial and centennial scale climate change found in European records of MIS 11c, the patterns of warming that are seen across this interglacial and the discrepancy in aspects of the duration of this interglacial that seems to exist between the marine and terrestrial records of this warm period. A review of the recent advances in the study of MIS 11c in Europe confirms its importance for understanding both the past evolution of the Holocene and the future patterns of long-term climate change.

Ian Candy (ian.candy@rhul.ac.uk), Department of Geography, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK; Dulce Oliveira, Centre of Marine Sciences (CCMAR/CIMAR LA), Campus de Gambelas, Universidade do Algarve, Faro 8005-139, Portugal and Divisão de Geologia e Georecursos Marinhos, Instituto Português do Mar e da Atmosfera (IPMA), Av. Doutor Alfredo Magalhães Ramalho 6, 1495-165 Algés, Portugal; Daniel Parkes, Department of Geography, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK and Department of Geography, University College London, North-West Wing, Gower St, London WC1E 6BT, UK; Jennifer Sherriff, Department of Geography, King's College London, 40 Bush House, London WC2B 4BG, UK; David Thornalley, Department of Geography, University College London, North-West Wing, Gower St, London WC1E 6BT, UK; *received 30th April 2023, accepted 8th March 2024.*

The interglacial known as MIS 11c (*c.* 426 000–396 000 years ago) has long attracted intensive study from the palaeoclimate community (Droxler & Farrell 2000; Loutre & Berger 2003; Droxler *et al.* 2003a; Candy *et al.* 2014; Tzedakis *et al.* 2022). Much of the interest around MIS 11c is related to the fact that it was long regarded as the closest analogue to the current interglacial, based on the similarity in the orbital parameters of these two intervals (see Droxler *et al.* 2003a and references therein). While still discussed in this context, it is now increasingly clear that MIS 11c is a relatively 'unique' interglacial, certainly within the Middle and Late Pleistocene, and that it is these 'unique' aspects that make this interval of international interest (Tzedakis *et al.* 2022). These unique aspects include, but are not restricted to (i) the extended duration of MIS 11c (*c.* 30 000 years) spanning two precession cycles with no intervening climatic cooling (Berger & Loutre 2002; Loutre & Berger 2003), (ii) the collapse of large parts of the Greenland Ice Sheet and associated globally high sea levels of up to 14 m above present (Raymo & Mitrovica 2012; Reyes *et al.* 2014; Dutton *et al.* 2015; Robinson *et al.* 2017), (iii) abrupt shifts in atmospheric carbon dioxide concentrations (Nehrbass-Ahles *et al.* 2020) and (iv) boundary conditions that consisted of such aspects as the persistence of relatively high CO_2 levels over an unusually long period. MIS 11c sequences, in Europe at least, contain the most compelling evidence for abrupt climate events in any pre-Holocene interglacial (Candy *et al.* 2014). Much of the narrative regarding MIS 11c has, as witnessed by the recent review article of Tzedakis *et al.* (2022), focussed on long continuous records (i.e. marine or lacustrine sequences) that have absolute chronologies based upon orbital tuning or, in the case of the long Antarctic ice-core records (EPICA 2004), chronologies based around ice accumulation and ice flow models. This allows direct comparisons to be made between the palaeoenvironmental records derived from each of these sequences.

Such a narrative negates, however, the integration of palaeoenvironmental data from high-resolution records that span MIS 11c but are not part of the group of long continuous palaeoclimate records that are commonly used to make inferences about interglacial climates (Koutsodendris *et al.* 2011, 2012; Candy *et al.* 2014). This is because records which only span short sections of time, e.g. a single interglacial, cannot be orbitally tuned; consequently they often lack a high-resolution absolute chronology that would allow direct correlation to other sequences. This is particularly true for time intervals, such as MIS 11c, which lie beyond, or at the limit of, conventional dating techniques (Candy *et al.* 2014). This is a significant issue in Europe, as annually laminated (varved) lake records of MIS 11c are abundant in this region (Turner 1970; Müller 1974; Nitychoruk

DOI 10.1111/bor.12656

et al. 2005; Koutsodendris *et al.* 2012; Tye *et al.* 2016) and offer some of the highest resolution records of this interglacial anywhere in the world. However, owing to their lack of an orbitally tuned chronology, the annual resolution they offer is unconstrained. Consequently, these records allow annual-scale reconstructions of vegetation and climatic shifts within MIS 11c but lack the chronology to allow these changes to be correlated with those observed in marine and ice-core records (see Koutsodendris *et al.* 2012 and Candy *et al.* 2021 for discussion). As a result, our understanding of MIS 11c palaeoclimate and palaeoenvironments currently overlooks the high-resolution data that many European sequences can offer.

This paper aims to synthesize recent developments in our understanding of MIS 11c in Europe with a particular focus on attempts to correlate and/or synchronize the European terrestrial record with North Atlantic marine cores. The advantage of such an approach is that it allows the use of the annual and seasonal resolution palaeoclimate records of MIS 11c in Europe to investigate some of the climatic shifts preserved in much lower resolution in the marine and ice-core records. This paper is not a comprehensive review of MIS 11c in Europe; such a review was presented in Candy *et al.* (2014) and in many key areas the fundamental observations of that review have not changed. This review is focussed on two key themes which have greatly advanced across the last 10 years: (i) the approaches that are employed to correlate terrestrial records of MIS 11c in Europe with marine core records of the North Atlantic; and (ii) the improved understanding of European MIS 11c palaeoclimates that these correlations have allowed. This paper will focus mainly on European lake sequences as these provide the highest resolution, continuous sequences currently available. The study begins by summarizing the key lacustrine sequences spanning MIS 11c in Europe and discussing the difference between those of southern Europe and the Mediterranean and those of northern Europe. The paper then considers the varved sequences of northern Europe, their correlation with marine sequences and what this correlation means for MIS 11c palaeoclimates in this region. The records of the Mediterranean/southern Europe are then discussed in a similar fashion. The paper concludes by comparing the palaeoenvironments and palaeoclimates of MIS 11c in northern and southern Europe and identifying key research questions for future studies.

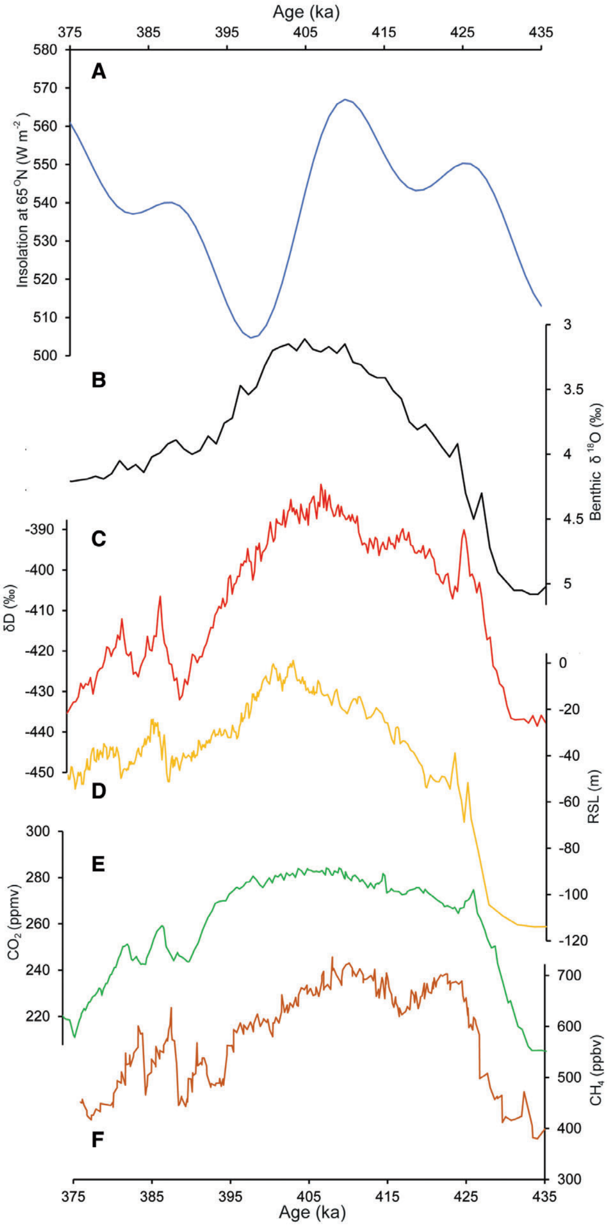

Fig. 1. The structure of MIS 11c as preserved in multiple palaeoclimatic records. A. Northern Hemisphere insolation (June 65°N) (Berger & Loutre 1991). B. LR04 stacked benthic δ^{18}O record that broadly equates to global ice volume (Lisiecki & Raymo 2005). C. EPICA Dome C deuterium record of air temperature over Antarctica (Jouzel *et al.* 2007). D. Sea-level changes relative to present-day values (Rohling *et al.* 2010). E. High-resolution carbon dioxide record from EPICA Dome C (Nehrbass-Ahles *et al.* 2020). F. High-resolution methane record from EPICA Dome C (Nehrbass-Ahles *et al.* 2020).

The palaeoclimatic character and structure of MIS 11c

The most widely discussed climatic attribute of MIS 11c is its extended duration in contrast to all other late Middle and Late Pleistocene interglacials (see Droxler *et al.* 2003b; Candy *et al.* 2014; PAGES 2016; Tzedakis *et al.* 2022). This is best observed in long marine and Antarctic ice-core records which indicate the persistence of interglacial conditions for between 25 000 and 30 000 years (Fig. 1; McManus *et al.* 1999; EPICA 2004; Tzedakis *et al.* 2022). Such a duration means that MIS 11c spans two insolation peaks, the first at *c.* 425 000 and the second at *c.* 410 000 years (Fig. 1A). The continuation of interglacial conditions across this time interval, despite a decline in insolation (clearly seen in June

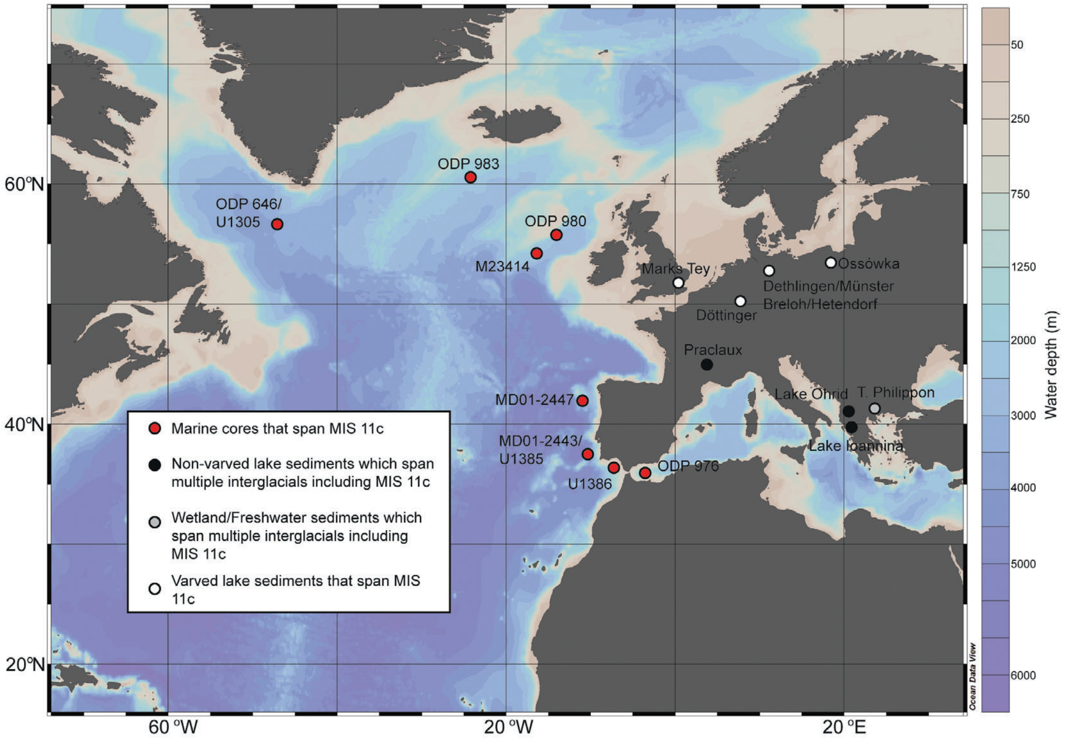

Fig. 2. Location of key records that contain proxy evidence for MIS 11c palaeoenvironment. Map produced using OCEANVIEW data and viewer.

insolation at 65°N), is probably due to the astronomical configuration (i.e. long-lasting low eccentricity, near antiphase between obliquity and precession and damped precession) and the persistence of relatively high levels of atmospheric CO_2 (~280 ppm) across this interval that allowed prolonged interglacial conditions throughout MIS 11c (Fig. 1E; Yin & Berger 2015; Tzedakis *et al*. 2022). The majority of marine and ice-core records, and some long lake sequences, indicate that the thermal maximum of MIS 11c occurred in association with the second insolation peak (Tzedakis *et al*. 2022). Equally, it appears that global ice volume underwent a persistent reduction across MIS 11c with peak sea level, and hence the ice-mass minima, occurring at *c*. 405 000 years (Fig. 1B, D; Lisiecki & Raymo 2005; Rohling *et al*. 2010). There is a general consensus that the MIS 11c sea-level highstand was significantly greater, ~+14 m, than that of the Holocene (Raymo & Mitrovica 2012; Roberts *et al*. 2012), indicating that parts of both the Greenland Ice Sheet and West Antarctic Ice Sheet decayed during this interglacial. It has been proposed, most convincingly through modelling studies (Robinson *et al*. 2017), that the large-scale ice sheet wastage that occurred during MIS 11c was a function of the extended duration of this interglacial rather than due to the occurrence of extreme warmth. Indeed, there is no consistent pattern from palaeoclimatic records from MIS 11c to suggest the interval was a period of exceptional warmth or characterized by temperatures similar to the Holocene (see Candy *et al*. 2014 for discussion).

MIS 11c in European lake sequences

The palaeoenvironments of MIS 11c in Europe are preserved in a range of sedimentary archives that include lake sequences, fluvial deposits, cave sediments, tufa accumulations and raised beaches (see Candy *et al*. 2014 but also more recently Sherriff *et al*. 2021). While these sequences can provide a wide range of multiproxy reconstructions of MIS 11c, many of them are characterized by intermittent, discontinuous sedimentation. Consequently, the palaeoenvironmental evidence that they generate frequently provides high-resolution data of snapshots of time within MIS 11c, separated by hiatuses of unknown duration (Candy *et al*. 2010). Good examples of this would be the site of Swanscombe, within the Thames terrace river sequence (White *et al*. 2013), and cave sequences of central and northern Spain, e.g. Aridos, Ambrona and Gran Dolina (Blain *et al*. 2015). In both cases detailed palaeoenvironmental records have been generated that enhance our understanding of MIS 11c in these regions; however, the episodic nature of deposition in these locations means that they are not suitable for the production of continuous climate records.

In this review we focus on lake sediment records as these environments are characterized by relatively consistent sedimentation and consequently result in the accumulation of quasi-continuous records (Fig. 2). Koutsodendris *et al.* (2012) provide a useful review of the location of key MIS 11c lacustrine sequences in Europe which, in summary, can be divided into three geographical groups. The first of these is a northern group of sites that are found at or above 50°N in Poland, Germany, Denmark and south/central Britain. These sites are primarily lake sequences that have accumulated in topographic lows that were formed during the preceding glacial stage MIS 12 as a result of subglacial scour or sedimentation around dead ice features (Candy *et al.* 2014). The southern limit of these sites is, therefore, restricted by the ice limits achieved during MIS 12. The second of these groups occurs in southern Germany, southern France and Switzerland, lying between 44 and 47°N and typically comprises lake basins formed as a result of either glacial processes (from Alpine ice masses) or the formation of volcanic crater lakes. The final group occurs in southern Europe and is heavily biased towards a group of sites that occur in wetlands and lakes that have developed within basins that are undergoing tectonic subsidence. These sites occur between 38 and 42°N in the eastern Mediterranean. Since the publication of Koutsodendris *et al.* (2012) detailed work has been carried out on the Lake Ohrid record (Kousis *et al.* 2018), a further site from the eastern Mediterranean which has again formed in association with a subsiding basin. Across these geographical groups, the key proxy that has been applied to these lacustrine sequences is fossil pollen and the shifts in the vegetation assemblages it records. Several marine pollen records from the Iberian margin, MD01-2447, MD01-2443, IODP U1385 and IODP U1386 (Desprat *et al.* 2005, 2017; Tzedakis *et al.* 2009; Oliveira *et al.* 2016; Hes *et al.* 2022), and a recent pollen record from the Western Alboran Sea, ODP Site 976 (Sassoon *et al.* 2023), have also aided the understanding of MIS 11c palaeoenvironments in temperate southern Europe and the Mediterranean. These sites preserve fossil pollen which has been transferred into the marine realm by major river systems and/or wind and has allowed for vegetation change in southwestern Europe to be reconstructed during this interglacial.

The diverse nature of these MIS 11c lake sequences means that understanding the stratigraphy and palaeoenvironmental history of this interglacial presents different challenges depending upon whether the focus of research is in northern or southern Europe. In southern Europe, the accumulation of sediments within subsiding basins means that these sites provide relatively continuous histories of much of the Middle and Late Pleistocene (Tzedakis *et al.* 1997, 2001, 2022). Consequently, peaks and troughs in the pollen record can be orbitally tuned, providing a continuous chronology for each of the sequences. This is augmented by independently dated tephra horizons in sequences such as Lake Ohrid and Tenaghi Philippon (Kousis *et al.* 2018; Vakhrameeva *et al.* 2018). Currently, the resolution at which pollen has been analysed in many of these sequences is at a millennial to multicentennial scale for MIS 11c, a resolution of *c.* 500 years in Lake Ohrid (Kousis *et al.* 2018) and *c.* 800–1800 years in Tenaghi Philippon (Ardenghi *et al.* 2019). Marine pollen data from the Iberian margin and the Alboran sea have also been published but, again, at a multicentennial scale resolution and constrained by an orbital chronology (Desprat *et al.* 2005, 2017; Tzedakis *et al.* 2009; Oliveira *et al.* 2016; Hes *et al.* 2022; Sassoon *et al.* 2023). These sites are, therefore, ideal for establishing long-term trends in vegetation development and identifying millennial-scale climate oscillations.

In contrast, numerous lake sequences from northern Europe (>50°N) are annually laminated, or varved, allowing for potential reconstructions of vegetation change at a sub-decadal scale (Nitychoruk *et al.* 2005; Koutsodendris *et al.* 2010, 2012; Tye *et al.* 2016; Candy *et al.* 2021). Such sites show the most convincing evidence for centennial-scale abrupt climate change in MIS 11c and, in fact, in any pre-Holocene interglacial (Candy *et al.* 2014). However, these records are limited by the fact they rarely cover a sufficient period of time to allow for orbital tuning. In many cases these sequences span the latter stages of MIS 12, MIS 11c and the onset of the subsequent cold period (see Koutsodendris *et al.* 2012, although see Nitychoruk *et al.* 2005; Hrynowiecka *et al.* 2019; Górecki *et al.* 2022 for Polish records which are an exception to this). These sequences, therefore, preserve high-resolution records of MIS 11c but the shifts in vegetation assemblage that they record are 'floating' in time and cannot be reliably correlated/synchronized with the orbitally tuned marine records of the North Atlantic or the long lake/wetland records of southern Europe. Early work on these sites generated, for the most part, low-resolution pollen records, however, several key studies (e.g. Turner 1970) and more recent work (Nitychoruk *et al.* 2005; Koutsodendris *et al.* 2010, 2012, 2013; Tye *et al.* 2016; Hrynowiecka *et al.* 2019; Górecki *et al.* 2022) have been able to generate high-resolution records of MIS 11c vegetation evolution. The sites located between 44 and 47°N have neither orbitally tuned chronologies nor convincing varve-based chronologies. The low resolution of these records means that while they will be referred to, they will not be discussed in great detail here. Consequently, this paper will discuss advances in our understanding of the stratigraphy of MIS 11c in Europe through a synthesis of recent publications from southern Europe (36–42°N) and Europe north of 50°N.

The vegetation history of MIS 11c in Europe north of 50°

Interglacial vegetation succession

MIS 11c in northern Europe is represented by deposits of the Hoxnian (UK), Holsteinian (German) and Mazovian

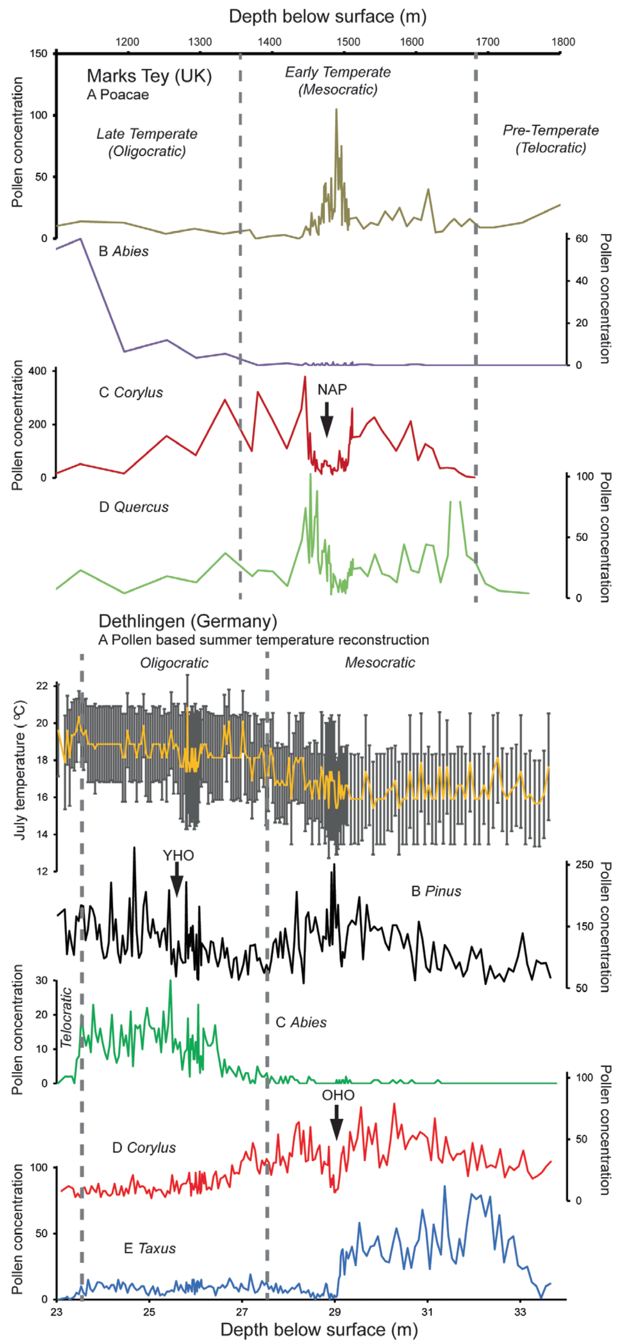

Fig. 3. Pollen data spanning MIS 11c from Marks Tey (top) and Dethlingen (bottom). The graphs show pollen percentage data from selected taxa and July temperature reconstructions (derived from pollen data) for Dethlingen. Marks Tey data from Tye *et al.* (2016) and Candy *et al.* (2021) and Dethlingen from Koutsodendris *et al.* (2010, 2012). Abrupt events are indicated with a black arrow.

(Poland) interglacial (Turner 1998; Nitychoruk *et al.* 2005; Koutsodendris *et al.* 2010, 2012). The vegetational history of this interglacial in these regions has been widely discussed, but in summary (Fig. 3), it follows the four stage idealized pattern of interglacial vegetation succession. These stages are: pre-temperate (protocratic), early temperate (mesocratic), late temperate (oligocratic) and post temperate (telocratic) (Iversen 1958; Andersen 1966; Turner & West 1968; Birks 1986). In Hoxnian sequences of central and southern England (see West 1956, 1970, 1980 for details) the pre-temperate phase (Ho I) was dominated by pioneer species (*Betula* and *Pinus*) that re-colonized the landscape after the end of preceding (Anglian) glacial stage. The early temperate phase (Ho II) was characterized by the expansion of temperate, deciduous woodland, dominated by *Quercus*, *Ulmus*, *Tilia*, *Alnus* and *Corylus*, which vary in their relative proportions during Ho II. The late temperate phase (Ho III) is characterized by declines in the abundance of many of the deciduous woodland taxa (i.e. *Quercus* and *Ulmus*) and the progressive dominance of *Abies*. The shift to boreal woodland and the opening up of the landscape (as witnessed by an increase in Poaceae) characterizes the post-temperate phase (Ho IV).

Holsteinian/Mazovian sequences show similar patterns of development (Turner 1998), particularly the dominance of *Abies* in the oligocratic phase; however, variations in the role of different woodland taxa exist between the British and European sequence. This is primarily a reflection of the difference between the more maritime (Britain) vs. the more continental (central Europe) climate. At sites such as Dethlingen in Germany (Fig. 3) the mesocratic phase was dominated by temperate woodland (*Taxus*, *Carpinus*, *Quercus* and *Corylus*) although the presence of *Picea* throughout these zones is often used to indicate the potential existence of strongly seasonal conditions (Koutsodendris *et al.* 2010). The oligocratic phase is characterized by the establishment of a *Carpinus–Abies* woodland and the expansion of evergreen trees at the expense of deciduous taxa. A similar succession is seen in Polish sites, such as Ossówka, where an early temperate woodland (*Taxus*, *Fraxinus Carpinus*, *Quercus* and *Corylus*) is replaced by a *Carpinus–Abies* dominated woodland (Nitychoruk *et al.* 2005).

In both central/southern England and continental Europe it has been proposed that the thermal maximum of the interglacial occurred during the late temperate/oligocratic phase (Candy *et al.* 2014). In the case of sites in central England, this suggestion is made on the basis that thermophilous plant species indicative of summer temperatures that are in excess of those of the present day (e.g. *Trapa natans*) are found in deposits of Ho III (Candy *et al.* 2010, 2014). Furthermore, studies that have used pollen spectra as a basis for modelling palaeotemperatures and palaeoprecipitation in past interglacials indicate that the warmest temperatures during the Holsteinian occurred during the oligocratic phase (Fig. 3), again in association with the *Carpinus–Abies* dominated woodland (Kühl & Litt 2007; Koutsodendris *et al.* 2012). It has long been argued that the transition from the early temperate/mesocratic to late temperate/oligocratic phase is most likely a function of long-term ecological succession, in association with factors such as declining soil quality and acidification, alongside regional climatic trends (West 1956; Turner 1970; Koutsodendris *et al*. 2010).

The duration of MIS 11c in northern Europe

A number of Hoxnian/Holsteinian/Mazovian lake sequences in northern Europe have been shown to be varved (see Turner 1970; Müller 1974; Nitychoruk *et al*. 2005; Koutsodendris *et al*. 2010; Tye *et al*. 2016). The combination of varve counting and pollen analysis allows the duration of the persistence of interglacial woodland in this region to be estimated. In Holsteinian varved sequences from Germany, such as Hetendorf and Munster-Breloh, along with more recent studies at Dethlingen, counting of annual laminations has indicated that the interglacial woodland phase of MIS 11c persisted for *c*. 15 000–16 000 years (see Koutsodendris *et al*. 2012, 2013). This is consistent with estimated varve counts at Ossówka which suggest that the woodland phase in the Mazovian persisted for *c*. 16 000 years (Nitychoruk *et al*. 2005). This makes the Holsteinian/-Mazovian an interglacial of relatively long duration in comparison with other interglacials for which varve chronologies exist, for example, it is estimated that woodland conditions persisted during the Eemian for *c*. 13 000 years (Turner 1998; Caspers *et al*. 2002). It does, however, make the duration of the Holsteinian/-Mazovian shorter, by between 9000 and 14 000 years, than MIS 11c as it is expressed in marine and ice-core records (EPICA 2004). Koutsodendris *et al*. (2010, 2012, 2013) explained this discrepancy by arguing that the Holsteinian/Mazovian *sensu stricto* did not correlate with the entirety of MIS 11c but rather with the second, and youngest, insolation peak of this interval. This suggestion means that the development of fully interglacial woodland in Europe occurred post 415 000 years and that peak interglacial conditions in northern Europe align with the thermal maximum of MIS 11c as seen in marine and ice-core records. However, this correlation also means that, in northern Europe, the first half of MIS 11c, associated with the first insolation peak, must have been a period when an open landscape, devoid of temperate woodland, persisted for many thousands of years after the onset of MIS 11c, under conditions that, while not representing the thermal maximum, were comparable in warmth to those of the present day and other interglacial periods.

The argument for a 'short' woodland phase for the Holsteinian/Mazovian interglacial is in contrast with estimates of the duration of the woodland phase of the Hoxnian interglacial of southern Britain based on varve counting from the site of Marks Tey. Work by Shackleton & Turner (1967) and Turner (1970) has argued that the varved lake sediments at this site allow the duration of the Hoxnian interglacial to be estimated at *c*. 30 000 years. While this is consistent with the length of MIS 11c, as calculated from orbitally tuned marine records, the Marks Tey sequence is not ideally suited to the construction of quantified estimates of interglacial duration (see Tye *et al*. 2016 for discussion). There are three reasons for this. Firstly, the original work on Marks Tey was not based on high-precision counting of varves at the microscopic level but visual estimates of approximate varve numbers. More recent work on the Marks Tey sequence has shown that some parts of this record, while laminated, are not convincingly varved and cannot, therefore, be reliably used to estimate the duration of sedimentation (Tye *et al*. 2016; Candy *et al*. 2021). Secondly, the section of the Marks Tey sequence that can be proved to be varved can be shown to contain, when subjected to high-resolution lamination counting at the microscopic level (Tye *et al*. 2016; Candy *et al*. 2021), substantially fewer years' worth of sedimentation than was initially estimated by Shackleton & Turner (1967) and Turner (1970). This suggests that these previous suggestions of the Hoxnian interglacial duration were overestimates. Finally, the upper part of the Hoxnian succession at Marks Tey has been intensely brecciated by post-depositional processes (Turner 1970; Tye *et al*. 2016). The varves in this section of the sequence are not intact. Consequently, the time interval in which these sediments are recording is based on the approximate thickness of the section and an estimate of the number varves contained within, rather than absolute varve counting (Shackleton & Turner 1967). In summary, while Marks Tey is frequently cited as providing evidence for a *c*. 30 000-year duration of the Hoxnian interglacial, recent work has shown that this sequence should not be used in this way and any estimate of interglacial duration derived from this sequence should be treated with caution.

Abrupt climate change during MIS 11c in northern Europe

The Hoxnian/Holsteinian/Mazovian pollen records of northern Europe provide some of the most convincing evidence for abrupt ecosystem instability in any pre-Holocene interglacial (Figs 3, 4). In Holsteinian/Mazovian sequences two short-lived ecological events (Fig. 3), characterized by the regression of temperate woodland taxa and the expansion of pioneer woodland species (i.e. *Betula* and *Pinus*), are routinely preserved (Müller 1974 cited in Kukla 2003; see Koutsodendris *et al*. 2012 for a more recent review). The earlier of these, the Older Holsteinian Oscillation (OHO), is the more clearly expressed and occurred late in the mesocratic phase of interglacial vegetation succession (Koutsodendris *et al*. 2012). The latter of these, the Younger Holsteinian Oscillation (YHO), is more subdued and occurred late within the oligocratic phase of interglacial vegetation succession (Koutsodendris *et al*. 2012). When these oscillations are recorded in varved sequences it is possible to estimate their durations and they are of apparent centennial-scale. For example, the OHO in Dethlingen is

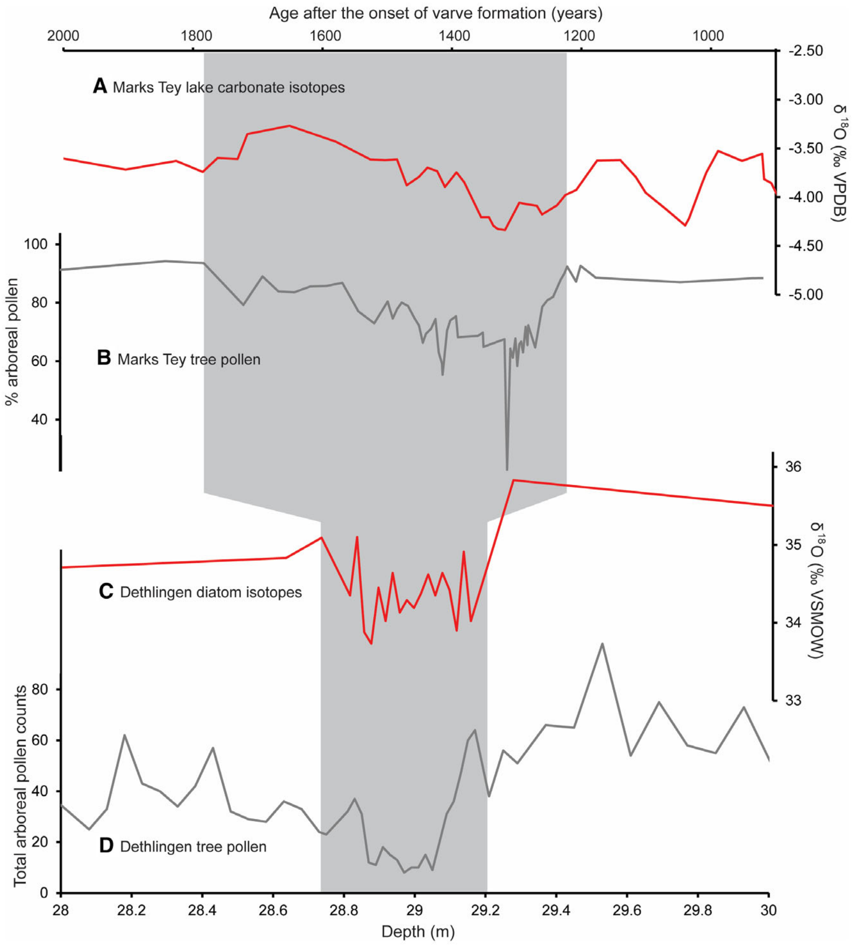

Fig. 4. High-resolution structure of the NAP (A and B, top) and OHO (C and D, bottom) in Marks Tey (Tye *et al.* 2016; Candy *et al.* 2021) and Dethlingen (Koutsodendris *et al.* 2010, 2012). The pollen data are selected to show the clearest expression of the events, arboreal pollen (percentage, AP) in the case of Marks Tey and arboreal pollen (total counts) in the case of Dethlingen. It is important to note that the δ^{18}O values for the two sites are generated from different materials for the two sites, endogenic carbonate (Marks Tey, A) and diatom silica (Dethlingen, C). High-resolution δ^{18}O analysis of diatoms was only undertaken across the Older Holsteinian Oscillation (OHO) with much lower resolution analysis before and after the event; the straight lines before and after the OHO data, therefore, represent the continuation of the data series to the next available point (Koutsodendris *et al.* 2012).

estimated to last for *c.* 220 years whereas the YHO is estimated to last for *c.* 660 years (Koutsodendris *et al.* 2012, 2013). The fact that both the OHO and the YHO are found at similar points in the vegetation history of the Holsteinian/Mazovian and are routinely observed in multiple sites across northern Germany and Poland has been used to imply that they represent a vegetation response to an abrupt climatic shift (Koutsodendris *et al.* 2012). The OHO has been suggested to reflect a significant cooling event, particularly characterized by a decline in winter temperatures, while the YHO has been suggested to reflect a decline in summer temperatures and/or annual precipitation levels (Koutsodendris *et al.* 2012). In the Hoxnian pollen records of central/eastern England a regression event occurred at a similar point in the pollen stratigraphy to the OHO (i.e. late in the mesocratic/early temperate phase) but here it is characterized by an increase in grass pollen (Poaceae) at the expense of all tree taxa (West 1956; Turner 1970; Coxon 1985; Candy *et al.* 2014). The expansion of non-arboreal taxa has been used to refer to this event as the non-arboreal pollen (NAP) phase (Figs 3, 4). High-precision varve counting (Candy *et al.* 2021) has shown that the duration of this event was significantly longer than its continental counterpart with *c.* 560 varve years elapsing between the first decline in tree pollen to the full recovery of the ecosystem to its pre-NAP phase state. The discussion of the OHO/NAP phase is here, and in recent studies, focussed on the record of this event preserved at Dethlingen and Marks Tey. This focus is a function of the fact that these two sites offer the highest resolution record of this event and have investigated change across this event using a range of different proxies. It is important to acknowledge, however, that the pattern of change seen at Marks Tey and Dethlingen is consistent with that preserved in lower resolution records from the same regions (i.e. Hoxne, Athelington, Hetendorf and Münster Breloh).

In records of the NAP phase in the British record of the Hoxnian the clearest vegetation response is seen in the expansion and contraction of Poaceae and *Corylus*, respectively. This is because, in percentage pollen terms, these two taxa show the biggest response. However, it is important to note that in high-resolution pollen diagrams of this event (see Tye *et al*. 2016) all deciduous tree species show a decline but this is less apparent because those taxa have lower overall percentages. For example, the percentage pollen concentrations of both *Quercus* and *Ulmus* reach their lowest levels during the NAP phase, dropping to ~1% from pre-event levels of ~10%. The impact on these taxa is much shorter lived than in the case of *Corylus*; however, it is clear that this event impacted the majority of tree species. The fact that the clearest response to this event is seen in *Corylus* is partly because this taxa has a high pollen production rate but also because, as in the case of the 8200-year event in Ireland (Holmes *et al*. 2016), this taxon is part of the understorey and its decline is not simply a response to temperature/precipitation change but also to the loss of the canopy that is a key part of its environment. In many aspects, the NAP phase has strong similarities to the OHO as, at sites such as Dethlingen, all deciduous tree species decline, in both percentage abundance and concentration, during this event. As highlighted earlier, the major difference in the ecological response to this event is that, in most German sites, this deciduous woodland is replaced by pioneer species such as *Picea* and *Betula* with a much smaller response in Poaceae than is seen at Marks Tey, for example. Records from Poland show a similar vegetation response to the OHO to that seen in the German sites but this interval is also characterized by an increase in *Larix* along with *Picea* and *Betula* (Krupinski 1995 cited in Koutsodendris *et al*. 2010, 2012).

In the absence of absolute dating estimates for these sequences, Koutsodendris *et al*. (2012) have suggested two possible ages for the OHO/NAP phase, both of which are based on tying the patterns of vegetation development seen in the Holsteinian sequences of Germany with marine records of the North Atlantic and insolation curves. The first of these approaches involved synchronizing the expansion of deciduous woodland in central Europe with the onset of MIS 11c; this yielded an age estimate of 418 000 years for the OHO. The second approach involved correlating the expansion of deciduous woodland in central Europe with the second, and larger, of the two summer insolation peaks that occurred in MIS 11c and this yielded an age estimate of 408 000 years for the OHO. Koutsodendris *et al*. (2012) favoured the second of these two scenarios as the correlation of woodland expansion with major insolation peaks is consistent with our understanding of climate/ecosystem dynamics.

The presence of charcoal at the beginning of the NAP phase at sites such as Marks Tey led some researchers to suggest that this event reflected a wildfire (Turner 1970). However, a recent study by Candy *et al*. (2021) has provided two lines of evidence to support a climatic driver for the NAP phase. Firstly, the summer lamination of each varve in the Marks Tey sequence consists of endogenic carbonate (Turner 1970) which can be analysed for the oxygen isotope ratio ($\delta^{18}O$) a technique that, in lake sequences, is routinely used as a palaeoclimatic proxy (Marshall *et al*. 2002, 2007; Blockley *et al*. 2018). The onset of the NAP phase is coincident with a significant decline in $\delta^{18}O$ values (Fig. 4), of the order of ~0.8‰, with these low $\delta^{18}O$ values persisting for 185 years (Candy *et al*. 2021). In British Quaternary lake sequence such a decline in $\delta^{18}O$ values is commonly interpreted as an abrupt cooling event while the magnitude of the isotopic decline is consistent with that seen in association with abrupt events of the Holocene, such as the 8200-year event (see Marshall *et al*. 2007). The only other site where high-resolution $\delta^{18}O$ values analysis has been carried out across the OHO/NAP phase is at Dethlingen (Koutsodendris *et al*. 2012). Here endogenic carbonate is absent and $\delta^{18}O$ analysis of diatom tests, a technique more likely to be affected by detrital contamination than carbonate analysis, was undertaken and showed a decline in $\delta^{18}O$ values of the order of ~1‰ (Fig. 4). This again supports a climatic origin for MIS 11c vegetation shifts in the early temperate/mesocratic phase of vegetation succession. Frustratingly, such techniques do not allow the quantification of the scale of temperature change that these proxies record. $\delta^{18}O$ values in lake carbonates are a function of multiple environmental factors and while temperature is likely to be the driving control it is not the only one and cannot, therefore, be isolated. Techniques that are routinely used to quantify temperature change during abrupt events in Lateglacial and Holocene sequences, i.e. chironomids, have rarely been applied to MIS 11c sequences (although see Horne *et al*. 2023).

Secondly, Candy *et al*. (2021) presented a major advance in our understanding of European interglacial landscapes/succession by co-locating a geochemically fingerprinted tephra layer in both the Marks Tey sequence and within the MIS 11c section of ODP 980 in the North Atlantic (Oppo *et al*. 1998; McManus *et al*. 1999). This has allowed the first direct synchronization to be made between a varved record of interglacial vegetation history from northern Europe with a marine record of changing climate and oceanographic processes during the same warm period. This synchronization allows the LR04 timescale that exists for ODP 980 to be imported to the Marks Tey varve record, giving an estimated age of the tephra as 415 365–415 145 years and the onset of the NAP phase as 414 780–414 480 years, an age that is more consistent with the first scenario proposed by Koutsodendris *et al*. (2012). The use of this tephra to synchronize the

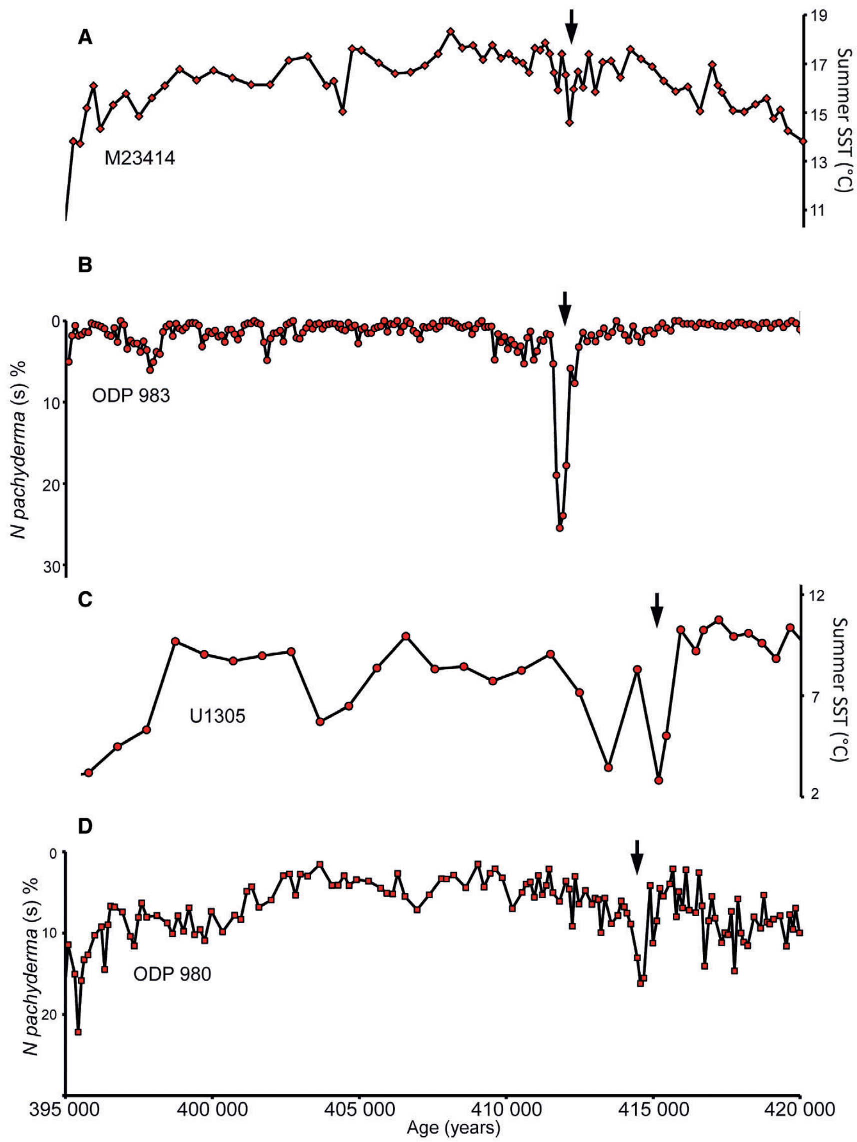

Fig. 5. Expression of abrupt cooling events in four North Atlantic records. A. Foraminifera-based sea surface temperature reconstructions from M23414. B. *Neogloboquadrina pachyderma* (s) from ODP 983 (Barker *et al*. 2015). C. Foraminifera-based sea surface temperature reconstructions from U1305 (Irvali *et al*. 2020). D. *N. pachyderma* (s) from ODP 980 (Oppo *et al*. 1998; McManus *et al*. 1999).

varved lake and marine records shows evidence for a decline in lake carbonate δ^{18}O values, in the Marks Tey sequence, and a coincident increase in percentage of *Neogloboquadrina pachyderma* (s), in the ODP 980 record (Oppo *et al*. 1998; McManus *et al*. 1999). Both of these shifts are best explained by NAP the onset of colder conditions, cooling air temperatures in the case of Marks Tey and cooling sea-surface temperatures (SSTs) in the case of ODP 980. Consequently, this tephra correlation indicates that at *c*. 414 500 years a regional cooling event occurred that caused an abrupt decline in both air temperatures and SSTs in northern Europe and the North Atlantic. This cooling event is now observable in multiple records, between 415 000 and 412 000 years, from the northeastern Atlantic (Fig. 5; e.g. ODP 980, 983 and M23414; Oppo *et al*. 1998; McManus *et al*. 1999; Barker *et al*. 2015; Kandiano *et al*. 2017) with evidence for a comparable timing, but longer duration event in the northwestern Atlantic (U1305; Irvali *et al*. 2020). When the Holsteinian/Mazovian records of the OHO are also taken into consideration, this indicates that this event was regionally extensive across a large part of the North Atlantic and western and central Europe. It is also noticeable that recent tephrostratigraphic work from the Maar Lake at Dottinger has not only shown that the interglacial recorded at this site can be correlated with MIS 11c, rather than MIS 9 as previously suggested (Diehl & Sirocko 2007), but has also shown that the evidence for the OHO at this site occurred early in the interglacial, closer to the estimated age of 414 500 years than to the estimate of 408 000 years (Arias *et al*. 2023).

In contrast to the OHO/NAP phase, the YHO is more enigmatic, given it is well recorded in German and Polish sequences (Nitychoruk *et al*. 2005; Koutsodendris *et al*. 2012; Hrynowiecka *et al*. 2019), but currently unknown from any Hoxnian record in Britain or any North Atlantic marine core (Candy *et al*. 2014). In Britain, many Hoxnian sequences are incomplete owing to the fact that lake basins were infilled with sediment prior to the end of the interglacial or, as in the case of Marks Tey, heavily affected by post-depositional alteration in the upper parts of the lake beds (Turner 1970; Candy *et al*. 2014). This means that the late temperate (oligocratic) phase, within which evidence for the YHO should be found, is poorly represented in this region. Only at rare sites, such as Athelington in Suffolk (Coxon 1985), do Hoxnian sequences record the entirety of this interglacial *in situ*. However, to date Athelington has not been analysed for pollen, or any proxy, at sufficiently high resolution to testify to the presence of this climatic event in England. No convincing evidence currently exists for a younger climatic event in North Atlantic marine cores; however, given that evidence from Holsteinian/Mazovian sequences would suggest that this event was more muted than the OHO/NAP phase it may be that marine proxies are either not sufficiently sensitive or not analysed in sufficiently high resolution to detect this event. The varve chronologies from German Holsteinian sequences indicate, however, that *c*. 3500–4500 years elapsed between the end of the OHO and the onset of the YHO (Koutsodendris *et al*. 2012, 2013). Considering the tephra correlation outlined above, this would indicate an approximate age of *c*. 410 000 years for the YHO.

The vegetation history of MIS 11c in southern Europe between 36 and 42°N

Interglacial vegetation dynamics in southwestern Europe

The vegetation evolution in southwestern Europe during MIS 11c has been recorded in a number of cores from the Iberian margin (Desprat *et al*. 2005, 2017; Tzedakis *et al*. 2009; Oliveira *et al*. 2016; Hes *et al*. 2022) and the ODP Site 976 sequence from the Alboran Sea (Sassoon *et al*. 2023) (Fig. 6). The base of the MD01-2443 core occurs at around the MIS 12/11 transition while MD01-2447 records vegetation shifts from 422 000 years onwards and, consequently, both sites cover the period from MIS 11c onwards (Desprat *et al*. 2005, 2017; Tzedakis *et al*. 2009). U1385 records the MIS 12/11 transition onwards; however, owing to either a sedimentary hiatus or a locally condensed record the interval between 431 000 and 415 000 years is represented by only four sampling points (Oliveira *et al*. 2016). Site U1386 covers this time interval and sheds light on the SW Iberian vegetation changes between 433 000 and 404 000 years. The ODP Site 976 pollen record encompasses the MIS 12/11 transition and covers the entire MIS 11 (Sassoon *et al*. 2023). These records provide palaeoenvironmental data at varying sub-millennial resolution, with the exception of the zone of low sedimentation rate in U1385 mentioned above.

These records all show an expansion of woodland species in southwestern Europe that occurred at the onset of MIS 11c in association with Termination V (Fig. 6). Although the magnitude of forest development was regionally specific (Desprat *et al*. 2017; Sánchez Goñi *et al*. 2018; Hes *et al*. 2022), this is in contrast with the suggested pattern of MIS 11c vegetation succession in northern Europe, where it is proposed that woodland development had not occurred until after 415 000 years (Koutsodendris *et al*. 2010, 2012). The MIS 11c section is represented by the Vigo interglacial in the northern site MD01-2447, which records that the forested conditions during this interval last for *c*. 27 000 years, between 422 000 and 395 000 years (Desprat *et al*. 2005, 2017). The pollen record of the Vigo interglacial indicates that the warmest conditions, i.e. the thermal maximum occurred at *c*. 410 000–405 000 years (Desprat *et al*. 2005, 2017). This is proposed on the basis of the contraction in pioneer species and the expansion of Mediterranean taxa that occurred during this zone. Two millennial-scale forest decline events that appear to have affected the forest history of this region, observable through the reduction in percentage temperate and humid tree taxa, are recorded in this interval, one centred at 411 000 and one at 406 000 years (Desprat *et al*. 2005, 2017).

MD01-2443 shows some similarity with the record of MD01-2447 (Fig. 6), albeit at a higher resolution (Tzedakis *et al*. 2009). This record shows that temperate woodland had become fully established, after the onset of MIS 11c, by at least 420 000 years. A pronounced decline in temperate woodland occurred during MIS 11c, with temperate tree populations reaching a minimum at *c*. 415 000 years (Tzedakis *et al*. 2009), which may correspond to the first decline recorded in the Vigo interglacial within the chronological uncertainties (Desprat *et al*. 2017). This decline persisted for several thousand years, while a more short-lived but still millennial-scale decline also occurred at 406 000 years. Finally, the peak in temperate and Mediterranean taxa, which should correspond with the thermal maximum of the interglacial, occurred between 410 000 and 405 000 years (Tzedakis *et al*. 2009), a timing that is also consistent with that of the Vigo interglacial (Desprat *et al*. 2005, 2017). The record of U1385 is broadly consistent with that of both MD01-2443 and MD01-2447 although the hiatus/condensed section early in MIS 11c makes a direct comparison of the early part of this interglacial problematic (Oliveira *et al*. 2016). The peak

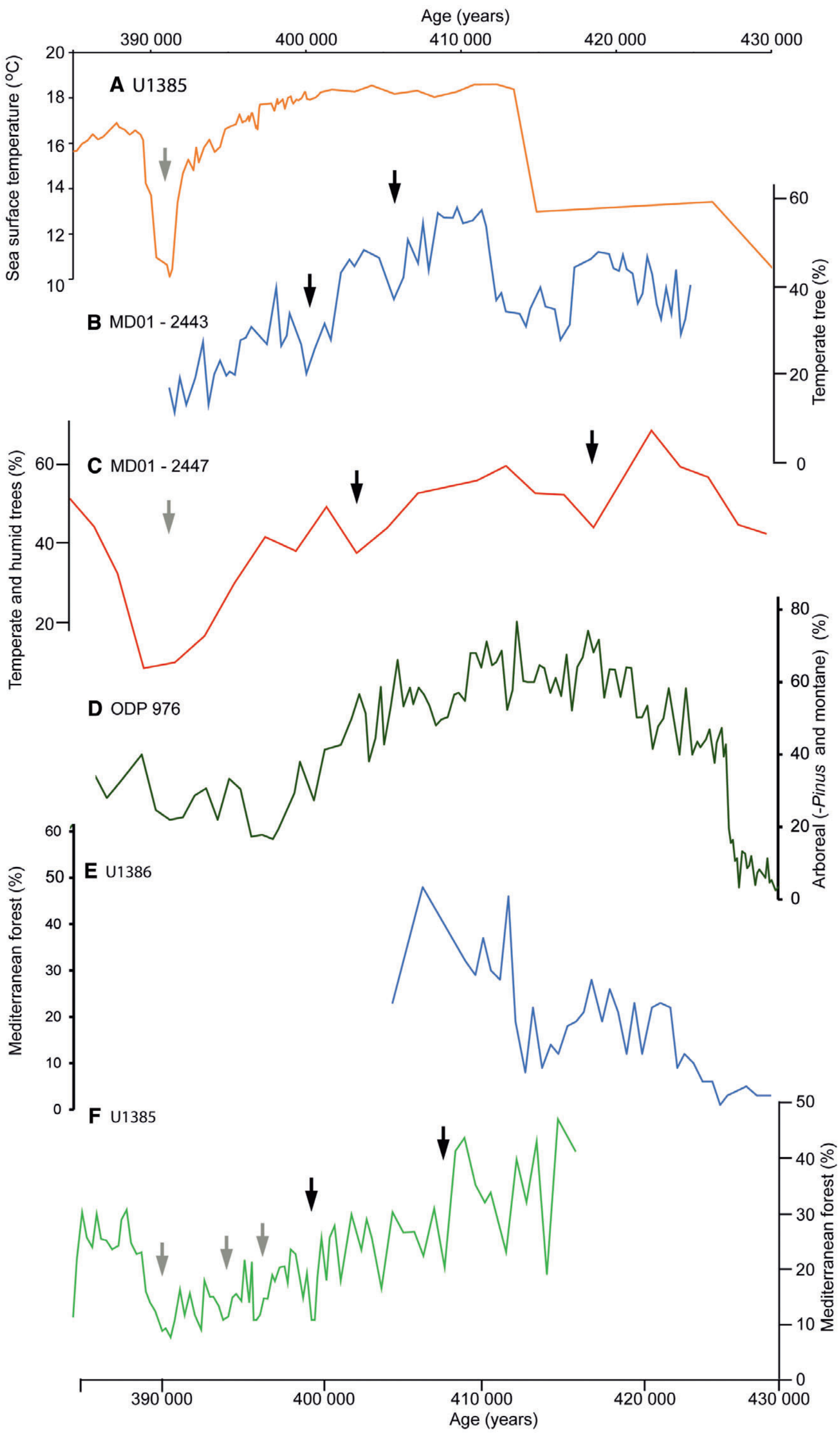

Fig. 6. Palaeoclimate records of MIS 11c from southwest Europe. A. Alkenone-based sea surface temperature record from U1385 (Rodrigues *et al.* 2011); note the presence of a sedimentary hiatus/reduced sedimentation in early MIS 11c and hence the limited number of data points spanning this interval. B. Percentage temperate tree pollen from MD01-2443 (Tzedakis *et al.* 2009). C. Percentage temperate and humid tree pollen from MD01-2447, the 'Vigo' interglacial (Desprat *et al.* 2005). D. Percentage arboreal pollen (minus *Pinus* and montane taxa) from ODP 976 (Sassoon *et al.* 2023). E. Percentage Mediterranean forest taxa (Hes *et al.* 2022). F. Percentage Mediterranean forest as recorded in U1385 (Oliveira *et al.* 2016). Black arrows indicate the presence of abrupt events, as indicated by respective authors, within MIS 11c, while grey arrows indicate the presence of abrupt events, as indicated by respective authors, within MIS 11 post-MIS 11c.

in percentage Mediterranean forest and Mediterranean taxa has been used, however, to suggest a thermal maximum between 414 000 and 408 000 years within the Sines interglacial, which is consistent with the other Iberian margin cores, including the U1386 record that also defines a more precise onset of the Mediterranean forest at 424 000 years (Hes *et al.* 2022). In line with previous work, the recent southernmost record, ODP site 976, shows a similar response of the vegetation during the MIS 12/11 transition and MIS 11c but the thermal maximum reflected by the optimum of temperate and Mediterranean taxa covers a longer time period, from 426 000 to 400 000 years (Sassoon *et al.* 2023).

The pollen sequences from U1385 and ODP Site 976 provide consistent evidence for abrupt vegetation shifts (Fig. 6) across MIS 11c on millennial timescales (Oliveira *et al.* 2016; Sassoon *et al.* 2023). Both record the strongest decline in tree population at *c.* 408 000 years, which can be correlated with the 406 000-year event seen in MD01-2443 and MD01-2447 (Tzedakis *et al.* 2009; Desprat *et al.* 2017). Oliveira *et al.* (2016) have argued that as the age of the 408 000-year event closely matches the age estimated for the OHO/NAP phase by Koutsodendris *et al.* (2012), this could be evidence for the expression of the same event in southern Europe. However, this correlation now has to be considered in the light of the recent tephra work of Candy *et al.* (2021) which shows that the timing of the OHO/NAP phase as proposed by Koutsodendris *et al.* (2012), i.e. 408 000 years, needs to be re-evaluated. As highlighted by Oliveira *et al.* (2016), however, if the 408 000-year event seen in U1385 is the southern European correlative of the OHO/NAP phase, this event appears to have had a different long-term impact on the ecosystems of the region. Whereas tree populations and vegetation assemblages recovered to pre-event levels after the OHO/NAP phase in northern Europe, the opposite is true for the records from U1385, MD01-2443, MD01-2447 and ODP Site 976, with percentage tree pollen levels never recovering to those levels that existed prior to the 408 000-year event (Tzedakis *et al.* 2009; Oliveira *et al.* 2016; Desprat *et al.* 2017; Sassoon *et al.* 2023). In the Iberian margin records and ODP Site 976, clearly defined millennial-scale abrupt shifts in vegetation occur after the main interglacial phase in late MIS 11, such as a final abrupt forest decline at *c.* 399 000 years; however, these are beyond the scope of this review.

Interglacial vegetation succession in southeastern Europe

In the eastern Mediterranean, the key records come from Lake Ohrid (Kousis *et al.* 2018), Lake Ioannina (Tzedakis 1993; Tzedakis *et al.* 1997), Lake Kopais (Okuda *et al.* 2001) and the wetlands of Tenaghi Philippon (Tzedakis *et al.* 2006; Ardenghi *et al.* 2019). Of these sequences, it is the Lake Ohrid record that has the highest resolution record of MIS 11c (1 sample per *c.* 477 years). This record indicates that a rapid expansion of temperate tree taxa and Mediterranean taxa occurred at *c.* 425 000 years (Fig. 7), indicating that, as is the case for southwestern Europe, forest expansion in southeastern Europe occurred in close association with the onset of MIS 11c (Kousis *et al.* 2018). Between 425 000 and 414 000 years the woodland was dominated by temperate and Mediterranean taxa but from 414 000 to 406 000 years, while temperate forests still dominated, an increasing abundance of *Abies*, *Picea* and *Pinus* occurred (Kousis *et al.* 2018). Pollen-based temperature reconstructions of this period indicate that this was the warmest part in the entirety of MIS 11c with maximum reconstructed temperatures being reached between 415 000 and 412 000 years (Kousis *et al.* 2018). The later part of MIS 11c in this record is characterized by two millennial-scale expansions of *Artemisa*, Poaceae and Chenopodiaceae, at the expense of woodland taxa; these occurred at 406 000–404 000 years and 401 000–399 000 years (Kousis *et al.* 2018). The interval between these two events, 404 000–401 000 years, is characterized by a recovery of temperate forests (Kousis *et al.* 2018). Consequently, MIS 11c at Lake Ohrid is characterized by an early/middle part of the interglacial (425 000–406 000 years) defined by *c.* 19 000–18 000 years of relatively stable woodland (that sees succession from mesocractic to oligocratic assemblages) followed by abrupt shifts in vegetation during the latter part of the interglacial.

The lower resolution analysis from Tenaghi Philippon (Fig. 7) shows that arboreal pollen dominates for the entirety of MIS 11 but that when *Pinus* is subtracted from the arboreal pollen total, to give percentage temperate taxa, the interglacial woodland had begun to decline by 405 000 years and had reached a minimum by *c.* 400 000 years (Tzedakis *et al.* 2001, 2006). This is supported by more recent work that demonstrates that the percentage of arboreal pollen (minus *Pinus*, *Juniperus* and *Betula*) began to increase to above 50% at *c.* 424 000 years and stayed above that level until *c.* 403 000 years (Ardenghi *et al.* 2019). This indicates the persistence of a dominance of temperate woodland taxa for *c.* 19 000 years, consistent with the duration of temperate/-Mediterranean taxa at Lake Ohrid. The MIS 11c pollen record from Lake Ioannina shows a broadly similar vegetation history to that of Tenaghi Philippon, although less work has been carried out on this interval in this record.

The resolution of the MIS 11c pollen record at Tenaghi Philippon has not, until recently, been sufficient to investigate millennial/centennial-scale vegetation shifts with any great degree of precision; however, two short-lived periods of arboreal pollen (minus *Pinus*, *Juniperus* and *Betula*) reduction occurred in late MIS 11c/early MIS 11b (see Ardenghi *et al.* 2019). While the timing of these vegetation shifts occurred in the same stratigraphic setting as the comparable events seen in the Lake Ohrid record, the age–depth model of the two records would indicate that they are not synchronous. Whether this is because the events are truly asynchronous or they are synchronous within the uncertainties of each sequence

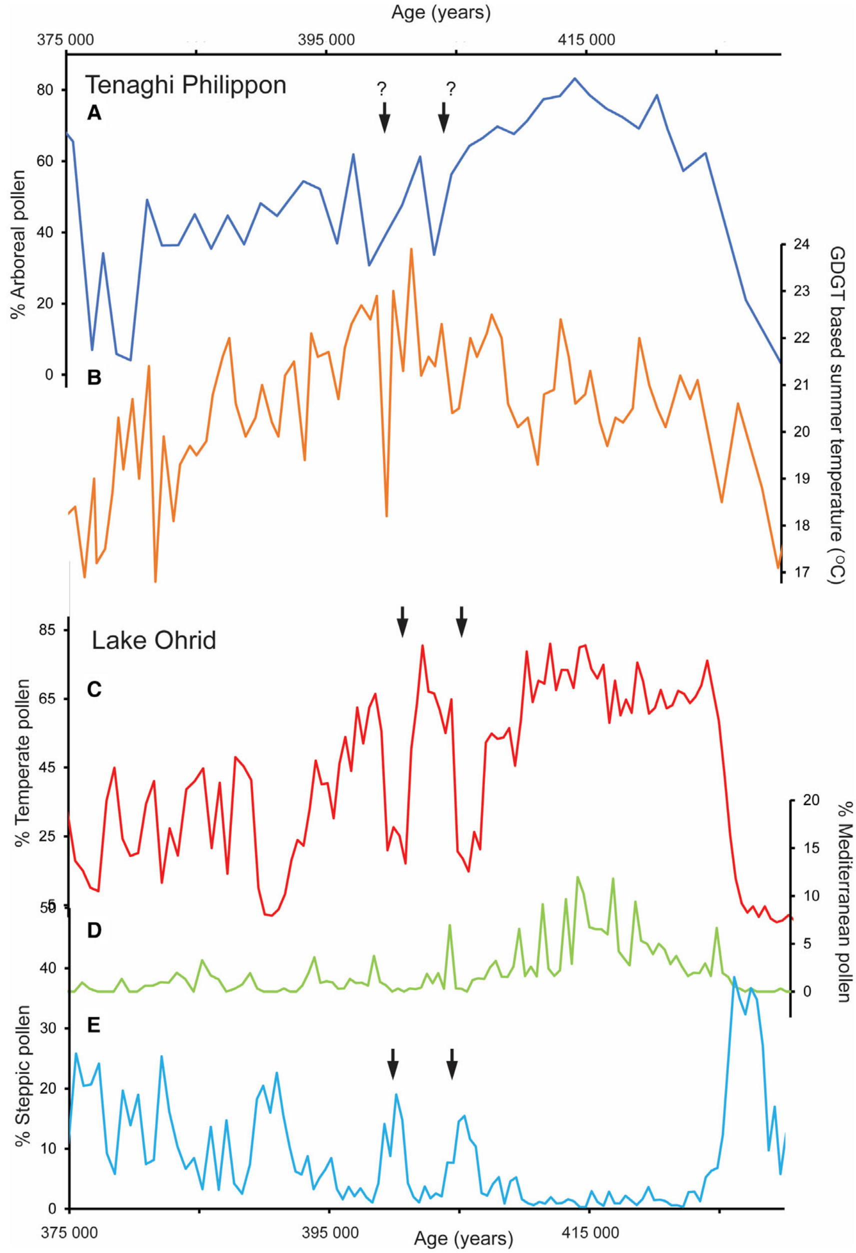

Fig. 7. Palaeoclimate records of MIS 11c from southeast Europe. A. Percentage arboreal pollen (minus *Pinus*, *Betula* and *Juniperius*) from T. Philippon (Ardenghi *et al*. 2019). B. GDGT-based temperature reconstructions (Ardenghi *et al*. 2019). C–E. Percentage pollen data of different ecological groups from Lake Ohrid (Kousis *et al*. 2018).

age-depth model is not possible to establish. It is worth noting, however, that although, in Tenaghi Philippon, late MIS 11c events are characterized by reduced percentage arboreal pollen (minus *Pinus*, *Juniperus* and *Betula*), overall arboreal pollen values do not decline, indicating that these events are characterized by an expansion of pioneer woodland species at the expense of more temperate taxa (Tzedakis *et al*. 2001, 2006; Ardenghi *et al*. 2019). In contrast, the events in Lake Ohrid are characterized by expansion in steppic taxa, at the expense of all woodland species (Kousis *et al*. 2018). It is likely that this difference in response is a function of the topographic setting of each site with tree species, both temperate and pioneer taxa, in the relatively high-altitude Lake Ohrid region being more vulnerable to environmental shifts than the woodland assemblages at the low-lying site of Tenaghi Philippon. A recent study (Koutsodendris *et al*. 2023) has, however, shown that a cooling event, marked by a decrease in the percentage of tree pollen and an associated increase in steppic elements, occurred at 416 000 years, the timing of which is not inconsistent with that of the OHO/NAP phase.

Discussion

Abrupt events within MIS 11c in Europe

Currently, the main records of MIS 11c from Europe all show evidence of abrupt change during this interglacial; however, there is a difference between the evidence and nature of such events in southern and northern Europe. In northern Europe, there is evidence for at least two centennial-scale regressions in temperate woodland taxa: one during the mesocratic (early temperate) phase, the OHO/NAP phase, and one during the oligocratic (late temperate) phase, the YHO. These regressive phases, therefore, occur under fully interglacial conditions and, in the case of the YHO, during the thermal maximum of this interval (Fig. 3). In southern Europe there is evidence for millennial-scale abrupt events and these are typically found towards the end of the interglacial, but still during fully interglacial conditions, and during the transition to MIS 11b (Figs 6, 7). Consequently, these events seem to be more closely associated with the climatic downturn in the late part of MIS 11c and towards the end of the interglacial.

There has long been a discussion in the literature about the cause of the NAP phase in England, with authors having argued the potential role of browsing by megafauna, natural wildfire and/or anthropogenic burning (see Turner 1970; James 1989; Candy *et al.* 2014). There now seems, however, very little doubt that the NAP phase is a vegetation response triggered by abrupt climate cooling (Candy *et al.* 2021). This is proposed for the following reasons. Firstly, a clear shift in the δ^{18}O value of lake carbonates occurred in direct association with the onset of the NAP phase at Marks Tey (Candy *et al.* 2021). As mentioned earlier both the pattern and magnitude of this shift are best explained by the occurrence of a centennial-scale cooling event at the same point as the NAP phase (Candy *et al.* 2021). Secondly, the Marks Tey/ODP 980 tephra correlation shows a synchronous response in air temperatures over southern England, as witnessed by the shift in carbonate δ^{18}O values at Marks Tey, and sea surface temperatures, as evidenced by the increase in percentage *N. pachyderma* (s) in ODP 980 (Candy *et al.* 2021). Finally, multiple coring sites across the North Atlantic record this SST cooling event, implying that it had far-reaching spatial impacts, rather than being a more local phenomenon (Kandiano *et al.* 2017; Barker *et al.* 2019; Candy *et al.* 2021). Given that the NAP phase seems to be part of a regional-scale cooling event it seems reasonable to assume that the OHO is a vegetation response to the same climatic shift and is effectively synchronous with these other records. This approach has also been applied in southern Europe where studies by Vakhrameeva *et al.* (2021) have co-located MIS 11c tephras in Tenaghi Philippon and ODP 964; however, so far this has not yielded the co-correlation of evidence for abrupt climate change that has been achieved in the North Atlantic.

Currently, it is unclear what the driver of this event is; however, it seems likely to be triggered by changes in North Atlantic circulation (see Candy *et al.* 2021). As well as seeing a clear expression in the North Atlantic and western/central parts of northern Europe, regions that are particularly vulnerable to changes in the Atlantic Meridional Overturning Circulation (AMOC), the timing of this event, *c.* 414 000 years, is consistent with the timing of a well-defined jump in Antarctic ice-core records of atmospheric carbon dioxide concentrations (Nehrbass-Ahles *et al.* 2020). Such a jump, known as a carbon dioxide jump, has been proposed as a possible response to changing strength in the AMOC (Nehrbass-Ahles *et al.* 2020). Further support for a weakening of the AMOC during this event is provided by deep ocean marine sediment cores from the western subpolar and subtropical North Atlantic (Poli *et al.* 2000; Hall & Becker 2007; Galaasen *et al.* 2020). These studies document during MIS 11c a number of low benthic foraminiferal δ^{13}C events – interpreted to be recording deep ocean seawater δ^{13}C, and lower percentage $CaCO_3$ in the sediment, which is, in part, controlled by the corrosivity of bottom water. These events are interpreted as periods where there was a reduction in the influence of North Atlantic Deep Water, which may occur during a weakening of the AMOC. In several of these records, one of the most prominent events during MIS 11c occurs at ~412 000–414 000 years, which is consistent with the ice-core carbon dioxide jump age, providing mutually supporting evidence for an AMOC weakening at this time.

As MIS 11c is the interglacial with the most convincing evidence for largescale wastage of the Greenland Ice Sheet (Reyes *et al.* 2014), it is tempting to relate this event to cryospheric changes. However, the chronologies associated with the marine cores that have the best evidence for Greenland Ice Sheet dynamics, e.g. ODP 646 and MD99-2227 (de Vernal & Hillaire-Marcel 2008; Reyes *et al.* 2014), are not as precise as those in other regions of the North Atlantic, i.e. ODP 980, making it difficult to establish the relationship between this abrupt event and ice-sheet wastage. There is no clear evidence for the YHO in either the British record or the North Atlantic record of MIS 11c. In the case of Britain, this is probably due to the absence of well-preserved sediments covering this period, while in the case of North Atlantic marine cores this is more likely to be a reflection of the subdued nature of the YHO but could also reflect the fact that this event had no oceanic trigger and, therefore, has limited expression in marine records from this region. It should be noted that, in records such as M23414, there is potential evidence for two discrete cold events in the North Atlantic between 414 000 and 410 000 years which could potentially correspond to the OHO and YHO (Kandiano *et al.* 2017).

There is limited evidence in southern Europe for any vegetation shift/climatic event that is comparable with the

OHO/NAP phase or the YHO (although see the recent work of Koutsodendris *et al.* 2023 from Tenaghi Philippon). As these two events are centennial in scale this may simply reflect the fact that none of the southern European sequences described above have the resolution to record such short-lived phenomena. The suggestion that correlatives of the OHO/NAP phase may be found in U1385/ODP 976 (Oliveira *et al.* 2016; Sassoon *et al.* 2023) and MD01-2443/MD01-2447 (Tzedakis *et al.* 2009; Desprat *et al.* 2017), at ages of 408 000 and 406 000 years (Fig. 6), is now queried on the basis of the new age of 414 000 years that is now proposed for the NAP phase. Whether this age discrepancy is because the Iberian margin/Alboran Sea and the Marks Tey record are genuinely recording different events or the uncertainties in the age-depth models of each record are such that the differences in absolute age estimates can be explained by age error is currently unclear. In MD01-2447 there is evidence for a strong reduction in the percentage of temperate and humid tree species during the main part of MIS 11c, during the Vigo interglacial, between *c.* 412 000 and 410 000 years (Desprat *et al.* 2005, 2017). Furthermore, the decline in percentage temperate and Mediterranean pollen in MD01-2443 between 417 000 and 412 000 years is broadly synchronous with that seen in the Vigo interglacial within the age uncertainties (Tzedakis *et al.* 2009). Both records show that this forest decline persisted for several millennia; therefore, it is unlikely to be comparable with the centennial-scale shifts seen in northern European pollen records. Tzedakis *et al.* (2009) have proposed that the close linkage between vegetation shifts in the MD01-2443 record and CH_4 concentrations in the Antarctic ice-cores would imply that changes in the position of the ITCZ are likely to drive these changes in southern European vegetation, a mechanism in strong contrast to the changes in AMOC proposed as a driver for the OHO/NAP phase (Candy *et al.* 2021). It is possible that the event in the Vigo interglacial centred at 411 000 years is also, therefore, a response to shifts in tropical circulation systems. Moreover, it is important to note that none of the MIS 11c forest events seen in records of southern Europe appear to have an expression in the SST records of the Iberian margin or in the mid-to-high latitudes of the North Atlantic suggesting that these events are not primarily related to high-latitude processes (Oliveira *et al.* 2016). This is, again, in contrast with the relationship between North Atlantic SSTs and vegetation response in northern Europe during the NAP phase. Recently, Sánchez Goñi *et al.* (2018) have proposed that these events detected at Site U1385 may have been driven by low-latitude forcing mechanisms on the basis of the dominant cyclicity of *c.* 10 000 years found in the pollen record of Site U1385. This cyclicity has been linked to the impact of the second harmonic of precession which may have led to meridional shifts in the temperate westerlies and consequent drying in SW Iberia (Sánchez Goñi *et al.* 2018).

No MIS 11c records from the eastern Mediterranean appear to record anything comparable with the OHO/NAP phase or YHO, although this, again, could be a function of the resolution of the records. Many of these sequences, however, record abrupt vegetation shifts in the later part of MIS 11c, a feature common to many records from the Iberian margin (Kousis *et al.* 2018). These events typically occur post-400 000 years and are associated with the climatic downturn and cooling of the climate that occurred after the thermal maximum of the interglacial (Fig. 7). While SST records, MD03-2699 (Voelker *et al.* 2010; Rodrigues *et al.* 2011) and U1385 (Oliveira *et al.* 2016) show that these events occurred against a backdrop of cooling conditions, the proxy data suggest gradual cooling with no obvious abrupt cold events occurring in association with these vegetation shifts. This cooling is also recorded in the increasing percentage of *N. pachyderma* (s) in MD01-2447 from 402 000 years onwards, although no ice-rafted detritus (IRD) is present in these records until after 390 000 years, once the colder conditions of MIS 11b had become established (Desprat *et al.* 2005). This pattern of cooling is also seen in the biomarker-based temperature reconstruction from Tenaghi Philippon which records falling temperatures from 400 000 years onwards (Ardenghi *et al.* 2019). While the highest resolution pollen records of MIS 11c from southeastern and southwestern Europe, Lake Ohrid and U1385 respectively, record a similar stratigraphy, i.e. the occurrence of two clearly defined contractions of temperate and/or Mediterranean taxa post 406 000 years, the absolute timing of these records are not, apparently synchronous. However, accepting minor, inevitable offsets in the timing of potentially equivalent events in other archives as they arise from age-model uncertainties, an impact of the Lake Ohrid 11-1 event on vegetation is clearly documented in pollen records from the Iberian margin.

In summary, there is evidence for abrupt centennial-scale events during the early to middle part of MIS 11c in the pollen records of northern Europe and, in the case of the OHO/NAP phase, these appear to be: (i) synchronous with declines in North Atlantic SSTs, and (ii) driven by changes in the AMOC. In southern Europe only millennial-scale events are currently known with the most convincing evidence for these being found during the cooling phase that occurred after the climatic peak of the interglacial. These events are characterized by significant ecological shifts but do not appear to have occurred in association with any declines in SST or increases in IRD. In SW Iberian marine pollen records (MD01-2443, MD01-2447 and U1385) evidence exists for millennial-scale shifts in vegetation assemblage but this has been proposed to be driven by moisture changes resulting from shifts in atmospheric circulation controlled by low-latitude processes rather than changes in

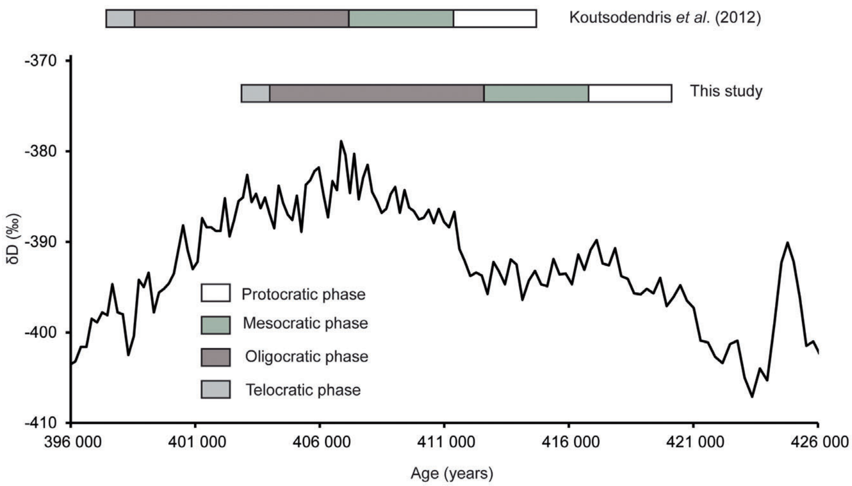

Fig. 8. Comparison between the stage of vegetation succession in northern Europe and a palaeoclimatic record of MIS 11c. Top is the correlation based upon linking the maximum woodland expansion of Holsteinian records with the thermal maximum of MIS 11c (after Koutsodendris *et al.* 2010). Bottom is the correlation based on the tephra correlation of Candy *et al.* (2021) and the varved estimates of the duration of forest stages (Koutsodendris *et al.* 2010, 2012, 2013). The duration of the different vegetation stages is based on the compilation of German sequences only (Koutsodendris *et al.* 2010, 2012, 2013) as the incomplete nature of some varved records (i.e. Marks Tey) and the lack of high-resolution, quantified varve counts (Ossówka) makes the incorporation of estimates from other sites problematic.

North Atlantic ocean circulation (Tzedakis *et al.* 2009; Sánchez Goñi *et al.* 2018).

Resolving the marine and terrestrial record of MIS 11c in Europe

While the orbitally tuned records of southern Europe allow the timing of environmental changes in MIS 11c to be directly compared with records derived from Antarctic ice cores and long marine records, this has not been possible for MIS 11c records in northern Europe. Here, however, we directly correlate the record of vegetation succession for the Holsteinian interglacial with a range of orbitally tuned records on the basis that: (i) the tephra from Marks Tey allows an absolute age to be derived for the NAP phase through correlation with the LR04 age model associated with ODP 980 (Candy *et al.* 2021); (ii) the NAP phase and the OHO represent vegetation responses to the same event (Koutsodendris *et al.* 2012); and (iii) varve counting at Dethlingen allows the timing of shifts in forest history before and after the OHO (Koutsodendris *et al.* 2012) to be directly compared with orbitally tuned records. Using a composite of varved records from the same region of Germany, incorporating the sites of Dethlingen, Munster Breloh and Hetendorf, Koutsodendris *et al.* (2012, 2013) have suggested that woodland expansion began approximately 6000 years prior to the onset of the OHO. While mesocratic forest became established in northern Europe (*c.* 50–55°N) *c.* 3000 years before the OHO, the onset of boreal woodland development (the protocratic or pre-temperate phase) began at least 2200 years before that. In conjunction with the age of the OHO of 414 000 years (imported from the Marks Tey tephra correlation) this would place the onset of boreal woodland development at 420 000 years and the beginning of the mesocratic phase at 417 000 years (Fig. 8). This correlation would suggest that the timing of woodland expansion post-MIS 12 is broadly consistent between northern and southern Europe occurred at the start of MIS 11c. The age of 420 000 for northern Europe is broadly comparable with the age of 426 000/425 000 years for southern Europe (Desprat *et al.* 2005; Tzedakis *et al.* 2009; Hes *et al.* 2022; Sassoon *et al.* 2023), i.e. both regions indicate that woodland expansion began early within and close to the onset of MIS 11c. The slightly later date, by a few millennia, of woodland expansion in northern Europe probably occurred because of the existence of a lag between the onset of warming and the migration into the area of tree species from more southerly latitudes.

At Dethlingen the mesocratic phase was re-established after the OHO and persisted for *c.* 630 years before the onset of the oligocratic phase which, in turn, persisted for 8500 years (Koutsodendris *et al.* 2012, 2013). The end of the oligocratic phase saw the onset of the telocratic phase which persisted for at least 1000 years before the end of the interglacial (Koutsodendris *et al.* 2013). This varve-based estimate of vegetation history would indicate that oligocratic woodland developed at around 413 000 years and persisted until 405 000 years after which cooling led to the development of telocratic woodland (Fig. 8). When these timings are compared with North Atlantic records such as ODP 980 and M23414, this pattern of vegetation succession is consistent with patterns of warming and cooling at these latitudes. Percentage concentrations of *N. pachyderma*

(s) begin to increase in ODP 980 from *c*. 405 000 years onwards while foraminifera-based SST estimates from M23414 show that SST begin to decrease from a similar point onwards (Oppo et al. 1998; McManus *et al*. 1999; Kandiano *et al*. 2017; Candy *et al*. 2021). This correlation refutes the suggestion of Koutsodendris *et al*. (2013) that a major asynchroniety existed between the onset of interglacial woodland development between southern and northern Europe and the requirement of the existence of an extended interval of open grassland during the early part of MIS 11c. The correlation presented here proposes a more unified response of European ecosystems to the warming associated with the onset of MIS 11c.

The timing of the thermal maximum of MIS 11c in Europe

There is a consistent pattern, across southern Europe pollen records, that the thermal maximum of MIS 11c occurred in the middle to late part of the interglacial with estimates of 410 000–405 000 years (MD01-2447, Desprat *et al*. 2005, 2017; MD01-2443, Tzedakis *et al*. 2009), 414 000–408 000 years (Site U1385, Oliveira *et al*. 2016) and 414 000–406 000 years (Lake Ohrid, Kousis *et al*. 2018). The correlation of northern European MIS 11c with orbitally tuned chronologies through tephrostratigraphy (see above) now shows that this pattern is also consistent for this region. It has long been proposed that the warmest conditions in northern Europe during MIS 11c occurred during the oligocratic/late temperate phase. This is based on the distribution of the fossils of thermophilous flora and fauna within British Hoxnian records (Candy *et al*. 2014) and the output of pollen-based temperature reconstruction from Holsteinian sequences in Germany (Kühl & Litt 2007; Koutsodendris *et al*. 2010, 2012). This varve-based model of vegetation development indicates that the oligocratic phase existed from 413 000 to 405 000 years, consistent with the pattern seen across the Mediterranean region. This timing is also consistent with the timing of peaks in CO_2 and CH_4 (as seen in Antarctic ice-core records), temperature maxima from a range of marine and ice-core records and the age of the global ice-volume minimum for this interglacial, as seen in LR04 (see Tzedakis *et al*. 2022).

Duration of MIS 11c conditions in Europe

There still exists a paradox regarding the duration of interglacial conditions during MIS 11c. The varved records from both Holsteinian and Mazovian records, which are likely to be the most robust estimates of interglacial duration that we have, indicate that interglacial conditions persisted for *c*. 15 000–16 000 years, which is half the estimated duration of 32 000 years that is normally cited for MIS 11c in marine δ^{18}O records (Nitychoruk *et al*. 2005; Koutsodendris *et al*. 2012). The use of pollen records as an indicator for interglacial conditions is likely to result in interglacial durations of slightly shorter lengths in northern latitudes simply because: (i) the onset of interglacial conditions will lag those seen in more southerly latitudes because of the time required for the migration northwards of tree populations; and (ii) the onset of cooling is likely to be more profound in northern latitudes leading to an earlier break up of woodland conditions. However, this 'short duration' is still difficult to reconcile with sites from southern Europe such as ODP site 986 where the MIS 11c has been proposed to last for *c*. 26 000 years. While sites such as Dottinger Maar Lake (Germany) and Ossówka (Poland) do present evidence for a longer interglacial duration, closer to 26 000 years these estimates from the former are partially produced by tuning between records (Arias *et al*. 2023) and the latter does not have a quantified varve chronology (Nitychoruk *et al*. 2005, 2006). At sites like Lake Ohrid a stable temperate and Mediterranean taxa dominated woodland persisted for *c*. 18 000 years prior to the millennial-scale regressive events that occurred late in MIS 11c (Kousis *et al*. 2018). The duration of stable woodland conditions at sites like Lake Ohrid is, therefore, more consistent with the record of northern Europe, indicating that this is not simply a discrepancy based on latitude. It is possible that the comparatively short-lived interglacial duration recorded in northern and central Europe could reflect the fact that these records do not preserve the entirety of MIS 11c. In this model, the expansion of cold-adapted vegetation at the end of these sequences would not represent the end of the interglacial but the onset of an abrupt, late MIS 11c climatic event, similar to those that are found in MIS 11c records of southern Europe (Kousis *et al*. 2018). This model requires the lacustrine basins of Holsteinian/Mazovian age to be infilled with sediment before the end of MIS 11c.

It is likely that this paradox can only be addressed through the development of a greater number of independent controls in orbitally tuned sequences. MIS 11c is notorious for problems regarding orbitally tuned chronologies because of the occurrence of fewer reliable tie points when compared with interglacials with more distinctive climatic structures, such as MIS 5e (Desprat *et al*. 2005; Candy *et al*. 2014). This may lead to age discrepancies of several 1000 years which could begin to account for the inconsistency of estimates of interglacial duration from across Europe. That is not to say that this discrepancy is not, simply that independent age controls would provide an excellent step forward in addressing the question. The impact of tephra work both through direct correlation of varved lake sequences and marine records, in the case of northern Europe (Candy *et al*. 2021; Vakhrameeva *et al*. 2021; Arias *et al*. 2023), and the generation of radiometric dates, in the case of Lake Ohrid (Kousis *et al*. 2018), has shown the potential power of such analysis and should be targeted in the future.

Tephrostratigraphy and future research in European records of MIS 11c

This study has summarized the current state of our understanding of the climate history of MIS 11c across Europe; however, it is clear that major limitations to this understanding still exist. As this study has shown, a major part of this is the discrepancy between the record of abrupt climate change in northern and southern Europe. This discrepancy is difficult to resolve without improved chronological studies. In particular, while a combination of orbital tuning and tephrostratigraphy has produced high-resolution chronologies for MIS 11c sequences in southern Europe, the fragmented and chronologically 'floating' nature of similar sequences in northern Europe makes it difficult to establish whether records of abrupt events found in these regions correlate or represent spatial differences in climate history. A major advance in MIS 11c studies over the past 5 years is the expansion of tephra studies (Candy *et al.* 2021; Vakhrameeva *et al.* 2021; Arias *et al.* 2023). The identification of tephra in the lake sequences of Marks Tey and Dottinger has allowed the synchronization of records with North Atlantic marine cores, in the case of the former, and robust correlation with MIS 11c, in the case of the latter. Equally, recent advances in the tephrostratigraphy of MIS 11c in southern Europe have allowed direct correlations to be made between lake and marine records. It is hoped that future studies will develop this technique further and allow more robust terrestrial–marine correlations to be made and to improve the comparison of MIS 11c sequences between northern and southern Europe.

Conclusions

Europe has a particularly rich record of sites that provide, through high-resolution pollen analysis, detailed information on the climate and environments of MIS 11c. This review has shown that our current state of knowledge makes it possible to draw the following conclusions regarding this interglacial:

- There is abundant evidence for climatic instability in MIS 11c sequences in Europe at both centennial and millennial time scales. Currently, it would appear that records in northern Europe provide strong evidence for abrupt climate events on centennial timescales and that these events occur under fully interglacial conditions and are probably associated with changes in AMOC. Southern Europe contains greater evidence for millennial-scale climate change during the cooling at the end of the interglacial. However, a growing body of evidence has shown that these millennial-scale forest declines have occurred under fully interglacial conditions, probably driven by low-latitude forcing mechanisms. Part of the discrepancy between northern and southern European records of MIS 11c may reflect the resolution of the available records and the section of the interglacial that is best preserved in each region.
- There is remarkable consistency across Europe regarding the timing of key aspects of vegetation succession during MIS 11c. In both northern Europe the onset of woodland expansion is closely tied to the onset of MIS 11c and the climatic amelioration that occurred across Termination V. It is likely that the onset of woodland expansion began later in northern Europe, by a few millennia, probably as a result of the lag between climatic amelioration and the northward migration of more thermophilous tree species, a pattern of response that is likely to be less significant in southern Europe.
- Furthermore, there appears to be remarkable consistency across Europe with respect to the timing of the thermal maximum of the interglacial. This appears to uniformly occur in the middle to late part of the interglacial between *c.* 415 000 and 405 000 years. This is consistent with global patterns of interglacial warmth, ice volume and greenhouse gas concentrations seen in a wide range of palaeoclimate archives.
- There exists some discrepancy between the estimates of interglacial duration across Europe with northern Europe being characterized by a 'shorter' interglacial (*c.* 16 000 years) than southern Europe where a 'longer' interglacial persisted, in some regions, for up to 27 000 years. It is unclear whether this discrepancy reflects a regional difference in the duration of interglacial warmth or is an artefact of the problem of chronology construction that is particularly acute for MIS 11c. Only further geochronological work will address this issue.

Acknowledgements. – This review represents contributions from the RCUK through the research studentships that were awarded to JS (AHRC; Block Grant 796) and DP (NERC; London DTP NE/S007229/1). The contribution of DP to this paper was supported by funding from the NERC London DTP. DO acknowledges funding from FCT (UIDB/04326/2020-doi: 10.54499/UIDB/04326/2020, CEECIND/02208/2017).

Author contributions. – IC, JS and DP reviewed the European terrestrial records of MIS 11 particularly the British Isles, DP and DT reviewed the marine records of the North Atlantic, DO and IC reviewed the vegetational records of MIS from southern Europe.

Data availability statement. – This review represents contributions from the RCUK through the research studentships that were awarded to JS (AHRC) and DP (NERC). All data presented here have been previously published and is either available through Pangaea, National Oceanic and Atmospheric Association or the supplementary information of the individual publications.

References

Andersen, S. T. 1966: Interglacial vegetational succession and lake development in Denmark. *Palaeobotanist 15*, 117–127.

Ardenghi, N., Mulch, A., Koutsodendris, A., Pross, J., Kahmen, A. & Niedermeyer, E. M. 2019: Temperature and moisture variability in the eastern Mediterranean region during Marine Isotope Stages 11–10 based on biomarker analysis of the Tenaghi Philippon peat deposit. *Quaternary Science Reviews 225*, 105977, https://doi.org/10.1016/j.quascirev.2019.105977.

Arias, S. F., Förster, M. W. & Sirocko, F. 2023: Rieden tephra layers in the Dottinger Maar lake sediments: implications for the dating of the Holsteinian interglacial and Elsterian glacial. *Global and Planetary Change 227*, 104143, https://doi.org/10.1016/j.gloplacha.2023.104143.

Barker, S., Chen, J., Gong, X., Jonkers, L., Knorr, G. & Thornalley, D. 2015: Icebergs not the trigger for North Atlantic cold events. *Nature 520*, 333–336.

Barker, S., Knorr, G., Conn, S., Lordsmith, S., Newman, D. & Thornalley, D. 2019: Early interglacial legacy of deglacial climate instability. *Paleoceanography and Paleoclimatology 34*, 1455–1475.

Berger, A. & Loutre, M. F. 1991: Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews 10*, 297–317.

Berger, A. & Loutre, M. F. 2002: An exceptionally long interglacial ahead? *Science 297*, 1287–1288.

Birks, H. J. B. 1986: Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. *In* Berglund, B. E. (ed.): *Handbook of Holocene Palaeoecology and Palaeohydrology*, 3–65. Wiley, Chichester.

Blain, H. A., Lozano-Fernández, I., Ollé, A., Rodríguez, J., Santonja, M. & Pérez-González, A. 2015: The continental record of Marine Isotope Stage 11 (Middle Pleistocene) on the Iberian Peninsula characterized by herpetofaunal assemblages. *Journal of Quaternary Science 30*, 667–678.

Blockley, S., Candy, I., Matthews, I., Langdon, P., Langdon, C., Palmer, A., Lincol, P., Abrook, A., Taylor, B., Conneller, C., Bayliss, A., MacLeod, A., Deeprose, L., Darvill, C., Kearney, R., Beavan, N., Staff, R., Bamforth, M., Taylor, M. & Milner, N. 2018: The resilience of postglacial hunter-gatherers to abrupt climate change. *Nature Ecology and Evolution 2*, 810–818.

Candy, I., Rose, J., Coope, G. R., Lee, J. R., Parfitt, S. P., Preece, R. C. & Schreve, D. C. 2010: Pronounced climate warming during early Middle Pleistocene interglacials: investigating the mid-Brunhes event in the British terrestrial sequence. *Earth Science Reviews 103*, 183–196.

Candy, I., Schreve, D. C., Sherriff, J. & Tye, G. J. 2014: Marine Isotope Stage 11: palaeoclimates, palaeoenvironments and its role as an analogue for the current interglacial. *Earth-Science Reviews 128*, 18–51.

Candy, I., Tye, G., Coxon, P., Hardiman, M., Matthews, I. & Palmer, A. 2021: A tephra-based correlation of marine and terrestrial records of MIS 11c from Britain and the North Atlantic. *Journal of Quaternary Science 36*, 1149–1161.

Caspers, G., Merkt, J., Müller, H. & Freund, H. 2002: The Eemian interglaciation in northwestern Germany. *Quaternary Research 58*, 49–52.

Coxon, P. 1985: A Hoxnian interglacial site at Athelington, Suffolk. *New Phytologist 99*, 611–621.

Desprat, S., Oliveira, D., Naughton, F. & Sánchez Goñi, M. F. 2017: L'étude du pollen des séquences sédimentaires marines pour la compréhension du climat: l'exemple des périodes chaudes passée. *Quaternaire 28*, 259–269.

Desprat, S., Sánchez Goñi, M. F., Turon, J. L., McManus, J. F., Loutre, M. F., Deprat, J., Malaize, B., Peyron, O. & Peypouquet, J. P. 2005: Is vegetation responsible for glacial inception during periods of muted insolation changes? *Quaternary Science Reviews 24*, 1361–1374.

Diehl, M. & Sirocko, F. 2007: A new Holsteinian record from the dry Maar at Döttingen (Eifel). *In* Sirocko, F., Claussen, M., Sánchez-Goñi, M. F. & Litt, T. (eds.): *The Climate of Past Interglacials*, 397–416. *Developments in Quaternary Science 7*. Elsevier, Amsterdam.

Droxler, A. W. & Farrell, J. W. 2000: Marine Isotope Stage 11 (MIS 11): new insights for a warm future. *Global and Planetary Change 24*, 1–5.

Droxler, A. W., Alley, R. B., Howard, W. R., Poore, R. Z. & Burckle, L. H. 2003a: Unique and exceptionally long interglacial Marine Isotope Stage 11: window into Earth warm future climate. *In* Droxler, A. W., Poore, R. Z. & Burckle, L. H. (eds.): *Earth's Climate and Orbital Eccentricity: The Marine Isotope Stage 11 Question*, 1–14. *Geophysical Monograph Series 137*. Blackwell Publishing Ltd, Hoboken.

Droxler, A. W., Poore, R. Z. & Burckle, L. H. (eds.) 2003b: *Earth's Climate and Orbital Eccentricity: The Marine Isotope Stage 11 Question*. *Geophysical Monograph Series 137*, 240 pp. American Geophysical Union, Washington.

Dutton, A., Carlson, A. E., Long, A. J., Milne, G. A., Clark, P. U., DeConto, R., Horton, B. P., Rahmstorf, S. & Raymo, M. E. 2015: Sea-level rise due to polar ice-sheet mass loss during past warm periods. *Science 349*, aaa4019, https://doi.org/10.1126/science.aaa4019.

EPICA Community Members 2004: Eight glacial cycles from an Antarctic ice core. *Nature 429*, 623–628.

Galaasen, E. V., Ninnemann, U. S., Kessler, A., Irvali, N., Rosenthal, Y., Jerry, T., Bouttes, N., Roche, D. M., Kleiven, H. & Hodell, D. 2020: Interglacial instability of North Atlantic Deep Water ventilation. *Science 367*, 1485–1489.

Górecki, A., Żarski, M., Drzewicki, W., Pleśniak, Ł., Zalewska-Gałosz, J. & Hrynowiecka, A. 2022: New climatic oscillations during MIS 11c in the record of the Skrzynka II site (Eastern Poland) based on palynological and isotope analysis. *Quaternary International 632*, 4–20.

Hall, I. & Becker, J. 2007: Deep Western Boundary Current variability in the subtropical northwest Atlantic Ocean during marine isotope stages 12–10. *Geochemistry, Geophysics, Geosystems 8*, 1–14.

Hes, G., Sánchez Goñi, M. F. & Bouttes, N. 2022: Impact of terrestrial biosphere on the atmospheric CO_2 concentration across Termination V. *Climate of the Past 18*, 1429–1451.

Holmes, J. A., Tindall, J., Roberts, N., Marshall, W., Marshall, J. D., Bingham, A., Feeser, I., O'Connell, M., Atkinson, T., Jourdan, A. L. & March, A. 2016: Lake isotope records of the 8200-year cooling event in western Ireland: comparison with model simulations. *Quaternary Science Reviews 131*, 341–349.

Horne, D. J., Ashton, N., Benardout, G., Brooks, S. J., Coope, G. R., Holmes, J. A., Lewis, S. G., Parfitt, S. A., White, T. S., Whitehouse, N. J. & Whittaker, J. E. 2023: A terrestrial record of climate variation during MIS 11 through multiproxy palaeotemperature reconstructions from Hoxne, UK. *Quaternary Research 111*, 21–52.

Hrynowiecka, A., Żarski, M. & Drzewicki, W. 2019: The rank of climatic oscillations during MIS 11c (OHO and YHO) and post-interglacial cooling during MIS 11b and MIS 11a in eastern Poland. *Geological Quarterly 63*, 375–394.

Irvali, N., Galaasen, E. V., Ninnemannm, U. S., Rosenthal, Y., Born, A. & Kleiven, H. F. 2020: A low climate threshold for south Greenland ice sheet demise during the Late Pleistocene. *Proceedings of the National Academy of Sciences of the United States of America 117*, 190–195.

Iversen, J. 1958: The bearing of glacial and interglacial epochs on the formation and extinction of plant taxa. *Uppsala Universitets Årsskrift 6*, 210–215.

James, S. R. 1989: Hominid use of fire in the Lower and Middle Pleistocene: a review of the evidence. *Current Anthropology 30*, 1–26.

Jouzel, J. and 32 others. 2007: Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science 317*, 793–796.

Kandiano, E. S., van der Meer, M. T. J., Schouten, S., Fahl, K., Damste, J. S. S. & Bauch, H. A. 2017: Response of the North Atlantic surface and intermediate ocean structure to climate warming of MIS 11. *Nature Communications 7*, 46192, https://doi.org/10.1038/srep46192.

Kousis, I., Koutsodendris, A., Peyron, O., Leicher, N., Francke, A., Wagner, B., Giaccio, B., Knipping, M. & Pross, J. 2018: Centennial-scale vegetation dynamics and climate variability in SE Europe during Marine Isotope Stage 11 based on a pollen record from Lake Ohrid. *Quaternary Science Reviews 190*, 20–38.

Koutsodendris, A., Brauer, A., Pälike, H., Müller, U. C., Dulski, P., Lotter, A. F. & Pross, J. 2011: Sub-decadal- to decadal-scale climate cyclicity during the Holsteinian interglacial (MIS 11) evidenced in annually laminated sediments. *Climate of the Past 7*, 987–999.

Koutsodendris, A., Dakos, V., Fletcher, W. J., Knipping, M., Kotthoff, U., Milner, A. M., Müller, U. C., Kaboth-Bahr, S., Kern, O. A., Kolb, L. & Vakhrameeva, P. 2023: Atmospheric CO_2 forcing on Mediterranean biomes during the past 500 kyrs. *Nature Communications 14*, 1664, https://doi.org/10.1038/s41467-023-37388-x.

Koutsodendris, A., Lotter, A. F., Kirilova, E., Verhagen, F. T., Brauer, A. & Pross, J. 2013: Evolution of a Holsteinian (MIS 11c) palaeolake based on a 12-ka-long diatom record from Dethlingen (northern Germany). *Boreas 42*, 714–728.

Koutsodendris, A., Muller, U. C., Pross, J., Brauer, A., Kotthoff, U. & Lotter, A. F. 2010: Vegetation dynamics and climate variability during the Holsteinian interglacial based on a pollen record from Dethlingen (northern Germany). *Quaternary Science Reviews 29*, 3298–3307.

Koutsodendris, A., Pross, J., Muller, U. C., Brauer, A., Fletcher, W. J., Kuhl, N., Kirilva, E., Verhagen, T. M., Lucke, A. & Lotter, A. F. 2012: A short-term climate oscillation during the Holsetinian interglacial (MIS 11c): an analogy to the 8.2 ka climatic event? *Global and Planetary Change 92–93*, 224–235.

Krupinski, K. M. 1995: Pollen stratigraphy and succession of vegetation during the Mazovian interglacial based on studies of sediments from Podlasie. *Acta Geographica Lodziensia 70*, 1–200.

Kühl, N. & Litt, T. 2007: Quantitative time-series reconstructions of Holsteinian and Eemian temperatures using botanical data. *In* Sirocko, F., Claussen, M., Sánchez-Goñi, M. F. & Litt, T. (eds.): *The Climate of Past Interglacials*, 239–254. *Developments in Quaternary Science 7*. Elsevier, Amsterdam.

Kukla, G. 2003: Continental records of MIS 11. *In* Droxler, A. W., Poore, R. Z. & Burckle, L. H. (eds.): *Earth's Climate and Orbital Eccentricity: The Marine Isotope Stage 11 Question*, 207–211. *Geophysical Monograph Series 137*. American Geophysical Union, Washington.

Lisiecki, L. E. & Raymo, M. E. 2005: A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography 20*, PA1003, https://doi.org/10.1029/2004pa001071.

Loutre, M. F. & Berger, A. 2003: Marine Isotope Stage 11 as an analogue for the present interglacial. *Global and Planetary Change 762*, 1–9.

Marshall, J. D., Jones, R. T., Crowley, S. F., Oldfield, F., Nash, S. & Bedford, A. 2002: A high resolution late glacial isotopic record from Hawes Water, Northwest England. Climate oscillations, calibration and comparison of palaeotemperature proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology 185*, 25–40.

Marshall, J. D., Lang, B., Crowley, S. F., Weedon, G. P., van Calsteren, P., Fisher, E. H., Holme, R., Holmes, J. A., Jones, R. T., Bedford, A., Brooks, S. J., Bloemendal, J., Kiriakoulakis, K. & Ball, J. D. 2007: Terrestrial impact of abrupt changes in the North Atlantic thermohaline circulation: early Holocene, UK. *Geology 35*, 639–642.

McManus, J. F., Oppo, D. W. & Cullen, J. L. 1999: A 0.5 million year record of millennial-scale climate. *Science 283*, 971–974.

Müller, H. 1974: Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der holstein-zeitlichen Kieselgur von Munster-Breloh. *Geologisches Jahrbuch A 21*, 107–140.

Nehrbass-Ahles, C., Shin, J., Schmitt, J., Bereiter, B., Joos, F., Schilt, A., Sdhmidely, L., Silva, L., Teste, G., Grilli, R., Chappelaz, J., Hodell, D., Fischer, H. & Stocker, T. F. 2020: Abrupt CO_2 release to the atmosphere under glacial and early interglacial climate conditions. *Science 369*, 1000–1005.

Nitychoruk, J., Bińka, K., Hoefs, J., Ruppert, J. & Schneider, J. 2005: Climate reconstruction for the Holsteinian Interglacial in eastern Poland and its comparison with isotopic data from Marine Isotope Stage 11. *Quaternary Science Reviews 24*, 631–644.

Nitychoruk, J., Bińka, K., Ruppert, H. & Schneider, J. 2006: Holsteinian interglacial = marine isotope stage 11? *Quaternary Science Reviews 25*, 2678–2681.

Okuda, M., Yasuda, Y. & Setoguchi, T. 2001: Middle to Late Pleistocene vegetation history and climatic changes at Lake Kopais, Southeast Greece. *Boreas 30*, 73–82.

Oliveira, D., Desprat, S., Rodrigues, T., Naughton, F., Hodell, D., Trigo, R., Rufino, M., Lopes, C., Abrantes, F. & Sánchez Goñi, M. F. S. 2016: The complexity of millennial-scale variability in southwestern Europe during MIS 11. *Quaternary Research 86*, 373–387.

Oppo, D. W., McManus, J. F. & Cullen, J. L. 1998: Abrupt climate events 500,000 to 340,000 years ago: evidence from subpolar North Atlantic sediments. *Science 279*, 1335–1338.

Past Interglacials Working Group of PAGES 2016: Interglacials of the last 800,000 years. *Reviews of Geophysics 54*, 162–219.

Poli, M. S., Thunell, R. C. & Rio, D. 2000: Millennial-scale changes in North Atlantic Deep Water circulation during marine isotope stages 11 and 12: linkage to Antarctic climate. *Geology 28*, 807–810.

Raymo, M. E. & Mitrovica, J. 2012: Collapse of polar ice sheets during the stage 11 interglacial. *Nature 483*, 453–456.

Reyes, A. V., Carlson, A. E., Beard, B. L., Hatfield, R. G., Stoner, J. S., Winsor, K., Welke, B. & Ullman, D. J. 2014: South Greenland ice-sheet collapse during Marine Isotope Stage 11. *Nature 510*, 525–528.

Roberts, D. L., Karkanas, P., Jacobs, Z., Marean, C. W. & Roberts, R. G. 2012: Melting ice sheets 400,000 yr ago raised sea level by 13m: past analogue for future trends. *Earth and Planetary Science Letters 357–358*, 226–237.

Robinson, A., Alvarez-Solas, J., Calov, R., Ganopolski, A. & Montoya, M. 2017: MIS-11 duration key to disappearance of the Greenland ice sheet. *Nature Communications 8*, 1–7.

Rodrigues, T., Voelker, A. H. L., Grimalt, J. O., Abrantes, F. & Naughton, F. 2011: Iberian Margin sea surface temperature during MIS 15 to 9 (580-300 ka): glacial suborbital variability versus interglacial stability. *Paleoceanography 26*, PA1204, https://doi.org/10.1029/2010PA001927.

Rohling, E. J., Braun, K., Grant, K., Kucera, M., Roberts, A. P., Siddall, M. & Trommer, G. 2010: Comparison between Holocene and Marine Isotope Stage-11 sea-level histories. *Earth and Planetary Science Letters 291*, 97–105.

Sánchez Goñi, M. F., Desprat, S., Fletcher, W. J., Morales-Molino, C., Naughton, F., Oliveira, D., Urrego, D. & Zorzi, C. 2018: Pollen from the deep-sea: a breakthrough in the mystery of the ice ages. *Frontiers in Plant Science 9*, 38, https://doi.org/10.3389/fpls.2018.00038.

Sassoon, D., Lebreton, V., Combourieu-Nebout, N., Peyron, O. & Moncel, M. H. 2023: Palaeoenvironmental changes in the southwestern Mediterranean (ODP site 976, Alboran sea) during the MIS 12/11 transition and the MIS 11 interglacial and implications for hominin populations. *Quaternary Science Reviews 304*, 108010, https://doi.org/10.1016/j.quascirev.2023.108010.

Shackleton, N. J. & Turner, C. 1967: Correlation between marine and terrestrial Pleistocene successions. *Nature 216*, 1079–1082.

Sherriff, J. E., Schreve, D. C., Candy, I., Palmer, A. P. & White, T. S. 2021: Environments of the climatic optimum of MIS 11 in Britain: evidence from the tufa sequence at Hitchin, southeast England. *Journal of Quaternary Science 36*, 508–525.

Turner, C. 1970: The Middle Pleistocene deposits at Marks Tey, Essex. *Philosophical Transactions of the Royal Society of London B257*, 373–440.

Turner, C. 1998: Volcanic maars, long Quaternary sequences and the work of the INQUA subcommission on European Quaternary stratigraphy. *Quaternary International 47*, 41–49.

Turner, C. & West, R. G. 1968: The subdivision and zonation of interglacial periods. *Eiszeitalter und Gegenwart 19*, 93–101.

Tye, G. J., Sherriff, J., Candy, I., Coxon, P., McClymont, E. & Schreve, D. C. 2016: The δ^{18}O stratigraphy of the Hoxnian lacustrine sequence at Marks Tey, Essex, UK: implications for the climatic structure of MIS 11 in Britain. *Journal of Quaternary Science 31*, 75–92.

Tzedakis, P. C. 1993: Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature 364*, 437–440.

Tzedakis, P. C., Andrieu, V., de Beaulieu, J.-L., Birks, H. J. B., Crowhurst, S., Follieri, M., Hooghiemstra, H., Magri, D., Reille, M., Sadori, L., Shackleton, N. J. & Wijmstra, T. A. 2001: Establishing a terrestrial chronological framework as a basis for biostratigraphical comparisons. *Quaternary Science Reviews 20*, 1583–1592.

Tzedakis, P. C., Andrieu, V., de Beaulieu, J.-L., Crowhurst, S., Follieri, M., Hooghiemstra, H., Magri, D., Reille, M., Sadori, L., Shackleton, N. J. & Wijmstra, T. A. 1997: Comparison of terrestrial and marine records of changing climate of the last 500,000 years. *Earth and Planetary Science Letters 150*, 171–176.

Tzedakis, P. C., Hodell, D. A., Nehrbass-Ahles, C., Mitsui, T. & Wolff, E. W. 2022: Marine Isotope Stage 11c: an unusual interglacial. *Quaternary Science Reviews 284*, 107493, https://doi.org/10.1016/j.quascirev.2022.107493.

Tzedakis, P. C., Hooghiemstra, H. & Pälike, H. 2006: The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quaternary Science Reviews 25*, 3416–3430.

Tzedakis, P. C., Pälike, H., Roucoux, K. H. & de Abreu, L. 2009: Atmospheric methane, southern European vegetation and low-mid latitude links on orbital and millennial timescales. *Earth and Planetary Science Letters 277*, 307–317.

Vakhrameeva, P., Koutsodendris, A., Wulf, S., Fletcher, W. J., Appelt, O., Knipping, M., Gertisser, R., Trieloff, M. & Pross, J. 2018: The cryptotephra record of the Marine Isotope Stage 12 to 10 interval (460–335 ka) at Tenaghi Philippon, Greece: exploring chronological markers for the Middle Pleistocene of the Mediterranean region. *Quaternary Science Reviews 200*, 313–333.

Vakhrameeva, P., Koutsodendris, A., Wulf, S., Portnyagin, M., Appelt, O., Ludwig, T., Trieloff, M. & Pross, J. 2021: Land-sea correlations in the Eastern Mediterranean region over the past c. 800 kyr based on macro-and cryptotephras from ODP Site 964 (Ionian Basin). *Quaternary Science Reviews 255*, 106811, https://doi.org/10.1016/j.quascirev.2018.09.019.

de Vernal, A. & Hillaire-Marcel, C. 2008: Natural variability of Greenland climate, vegetation, and ice volume during the past million years. *Science 320*, 1622–1625.

Voelker, A. H. L., Rodrigues, T., Billups, K., Oppo, D., McManus, J., Stein, R., Hefter, J. & Grimalt, J. O. 2010: Variations in mid-latitude North Atlantic surface water properties during the mid-Brunhes (MIS 9-14) and their implications for the thermohaline circulation. *Climate of the Past 6*, 531–552.

West, R. G. 1956: The Quaternary deposits at Hoxne, Suffolk. *Philosophical Transactions of the Royal Society of London B24*, 265–356.

West, R. G. 1970: Pollen zones in the Pleistocene of Great Britain and their correlation. *New Phytologist 69*, 1179–1183.

West, R. G. 1980: Pleistocene forest history in East Anglia. *New Phytologist 85*, 571–622.

White, T. S., Preece, R. C. & Whittaker, J. E. 2013: Molluscan and ostracod succession from Dierden's Pit, Swanscombe: insights into the fluvial history, sea-level record and human occupation of the Hoxnian Thames. *Quaternary Science Reviews 70*, 73–90.

Yin, Q. & Berger, A. 2015: Interglacial analogues for the Holocene and the natural near future. *Quaternary Science Reviews 120*, 28–46.