



Coupled ocean–land millennial-scale changes 1.26 million years ago, recorded at Site U1385 off Portugal



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ABSTRACT

While a growing body of evidence indicates that North Atlantic millennial-scale climate variability extends to the Early Pleistocene, its impact on terrestrial ecosystems has not been established. Here we present ultra-high resolution (70–140 year) joint foraminiferal isotopic and pollen analyses from IODP Site U1385 off Portugal, focusing on a short glacial section of Marine Isotope Stage 38, ~1.26 million years ago. Our records reveal the presence of millennial-scale variability in the coupled ocean–atmosphere–land system in the North Atlantic and provide the first direct evidence for the response of western Iberian vegetation to abrupt climate changes in the Early Pleistocene. The magnitude and pacing of changes bear significant similarities to Dansgaard–Oeschger variability of the last two glacials.

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1. Introduction

The recognition of the extreme and widespread nature of millennial-scale climate variability in the North Atlantic region during the last glacial (e.g. Dansgaard et al., 1993; Bond et al., 1993) raised important questions about the geographical extent of such changes and their impact on terrestrial ecosystems. High-frequency oscillations in pollen values had been known from southern European sequences extending to the last glacial, but a close temporal link with North Atlantic changes was only established after comparing pollen and marine proxies within the same deep-sea sequences off Portugal (Sánchez Goñi et al., 2000; Roucoux et al., 2001). Further work has shown that millennial-scale variability is a pervasive feature of the last 800 kyr (e.g. McManus et al., 1999; Jouzel et al., 2007; Margari et al., 2010; Barker et al., 2011), but its amplitude can be influenced by different boundary conditions.

More recent evidence has shown that millennial-scale variability extends to the Early Pleistocene (e.g. Raymo et al., 1998), a period characterized by 41-kyr glacial–interglacial cycles and maximum ice volumes ranging between one- and two-thirds of the Last Glacial Maximum value (e.g. Ruddiman et al., 1986; Shackleton, 1995; Elderfield et al., 2012). Records from the North Atlantic document the presence of ice-rafted detritus (IRD) and attendant changes in the meridional overturning circulation (MOC) on millennial timescales during the Early Pleistocene

(e.g. Raymo et al., 1998; Mc Intyre et al., 2001; Kleiven et al., 2003; Bailey et al., 2012). Hodell et al. (2008) suggested that major iceberg discharges from the Laurentide Ice Sheet via the Hudson Strait (Heinrich events) were initiated from Marine Isotope Stage (MIS) 16 onwards, possibly representing the crossing of a threshold in ice thickness, leading to ice instability; prior to MIS 16, IRD events are of lower amplitude, higher frequency and different lithology compared to classic Heinrich events. The question that arises is whether small differences in the character of ice discharges and mean climate state could lead to differences in the extent of their downstream impact, including the vegetation response.

This poses significant challenges for terrestrial archives to capture the effects of such changes. In Europe, several pollen records cover parts of the Early Pleistocene, but lack either the required resolution to detect centennial/millennial events and/or the chronological precision to establish a cause and effect relationship with records of North Atlantic variability (e.g. Elhai, 1969; Suc and Popescu, 2005; Tzedakis et al., 2006; Leroy, 2008; Muttoni et al., 2007; Popescu et al., 2010). The few joint marine–terrestrial studies (e.g. Joannin et al., 2007, 2011) circumvent correlation issues, but do not have the required detail to resolve millennial-scale variability. Further afield, detailed lithological and pollen records from Hequing Basin, southwestern China show pervasive millennial-scale changes in the Early Pleistocene (An et al., 2011), but how this is related to North Atlantic variability remains difficult to establish. Here an attempt is made to address these challenges by generating detailed foraminiferal-isotopic and pollen records in a marine core off Portugal.

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2. Design of study and aim

In recent years, the Portuguese Margin has emerged as a prime location for tracing millennial-scale variability and undertaking land–sea comparisons. This is a direct consequence of its geographic position and hydrographic setting. A key aspect is that sites are located near the continent, where the combined effects of the Tagus River and a narrow continental shelf lead to the rapid delivery of terrestrial material, but deep enough to generate high-quality isotopic records that are pertinent to basin-wide phenomena. Joint pollen and foraminiferal isotope analyses in the same marine core have allowed the in situ assessment of phase and amplitude relationships between terrestrial and ocean changes, bypassing timescale and correlation uncertainties. This has established the immediate response of vegetation to millennial-scale variability during recent glacials (e.g. Sánchez Goñi et al., 2000; Roucoux et al., 2001, 2006; Tzedakis et al., 2004; Margari et al., 2010, 2014). Further work has revealed a strong coherence between changes in tree populations and atmospheric CH₄ concentrations on orbital and millennial timescales, reflecting a close coupling between low- and mid-latitude hydrological changes via shifts in the mean latitudinal position of the Intertropical Convergence Zone (ITCZ) (Tzedakis et al., 2004, 2009).

A significant new opportunity has now arisen from deep-sea drilling on the Portuguese Margin (Fig. 1). Integrated Ocean Drilling Project (IODP) Site U1385 provides a sediment sequence that extends back to ~1.45 million years ago (Hodell et al., 2013a, 2015) and has the potential to become the prime archive to gain insights into the nature of millennial-scale variability and their effects on western Iberian ecosystems during the Early Pleistocene. The aim of this study is to provide the first unequivocal evidence for a direct link between North Atlantic climate variability and vegetation response during an Early Pleistocene glacial. To do this, we have undertaken ultra-high resolution planktonic foraminiferal and pollen analyses (70 and 140 year, respectively) from a 1-m section at the transition into MIS 38 (Fig. 2). MIS 38 represents a typical glacial of the 41-kyr world with sea-level lowstands of about 20–70 m below present (Elderfield et al., 2012), which falls within the ice-volume window of millennial instability of the 100-kyr world (Chapman and Shackleton, 1999; McManus et al., 1999; Thompson

and Goldstein, 2006). Our study interval occurs at the point where unadjusted benthic $\delta^{18}\text{O}$ values in *Cibicidoides wuellerstorfi* begin to exceed 3.5‰ (Fig. 2), representing the crossing of the ‘ice-volume threshold’ of McManus et al. (1999) beyond which iceberg discharges and sea surface temperature oscillations are amplified. XRF analyses from that interval (Hodell et al., 2015) show high-frequency oscillations in lithological composition, corroborating the presence of millennial-scale variability.

3. Materials and methods

Site U1385 was recovered from the same location (37°34'N, 10°7'W; 2578 m water depth) as core MD01-2444 (Fig. 1), which has provided detailed records of the last two glacials (Vautravers and Shackleton, 2006; Martrat et al., 2007; Skinner and Elderfield, 2007; Margari et al., 2010, 2014; Hodell et al., 2013b). Four holes were cored to ~150 m below seafloor. The sediments are uniform, representing one lithological unit of nannofossil muds and clays, with varying proportion of biogenic carbonate material; sediment accumulation rates are high (11 cm/kyr) (Hodell et al., 2015). XRF analyses at 1-cm resolution have been undertaken in all four holes, thereby permitting accurate hole-to-hole correlation and construction of a complete spliced stratigraphic section containing no notable gaps or disturbed intervals (Hodell et al., 2015). Foraminiferal isotopic analyses at 20-cm intervals have been completed for the entire sequence and confirm the existence of all isotope stages to MIS 47 (Hodell et al., 2015).

Isotopic analysis of planktonic foraminifera was undertaken at 1-cm intervals from 142.10 to 143.10 revised metre composite depth (rmcd) of Hole D. Samples were wet sieved at 63 μm and dried in an oven at 50 °C. Stable isotopes were measured on the planktonic foraminifera *Globigerina bulloides* picked from the 250 to 355 μm size fraction. Foraminifer tests were crushed and soaked in a solution of 1% H₂O₂ for 30 min in individual vials. Acetone was added and the samples placed in an ultra-sonic bath for 10 s, after which the liquid was carefully decanted to remove any contaminants. The samples were dried in an oven at 50 °C overnight. Isotopic analysis of the samples was performed on a VG SIRA mass spectrometer with a Multicarb system for samples of >80 μg mass. Analytical precision is estimated to be $\pm 0.08\text{‰}$ for $\delta^{18}\text{O}$. For smaller samples (<80 μg), measurements were performed on a ThermoScientific MAT253 mass spectrometer fitted with a Kiel device. Analytical precision is estimated to be $\pm 0.08\text{‰}$ for $\delta^{18}\text{O}$ measurements. Results are reported relative to V-PDB.

Pollen analysis was undertaken at 2-cm intervals over the same 1-m section (142.10–143.10 rmcd) of Hole D. Samples were ~7 g, initially split in three tubes, combined into one at the final stages. Pollen preparation followed standard procedures, including boiling in 10% HCl to remove carbonates, 10% KOH to remove humic acids and 40% HF to remove silicates. Fine sieving, through a mesh of 10 μm or less, was not used as it has been found to result in a loss of pollen, particularly Gramineae. Residues were mounted in silicone oil for microscopic analysis at magnifications of $\times 400$, $\times 630$ and $\times 1000$. Pollen identification was carried out at the lowest possible taxonomic level, and nomenclature follows Flora Europaea (Tutin et al., 1964–1980). Abundances are expressed as percentages of the main sum (marine pollen sum of minimum 100 grains per sample), which includes all pollen except *Pinus*, Pteridophyte spores and aquatics. *Pinus* is conventionally excluded from the main sum, as it is strongly over-represented in marine sediments because of its extensive dispersal ability and buoyancy (Hopkins, 1950). Pollen studies from continental shelf sequences suggest that palynomorph transport to these areas is controlled primarily by fluvial and secondarily by aeolian processes (Chmura et al., 1999). In the Portuguese Margin, aeolian pollen transport is limited by the direction of the prevailing offshore winds and pollen is mainly transported to the abyssal site by the sediments carried by the Tagus River (Sánchez Goñi et al., 2000). Comparison of modern marine and terrestrial samples along western Iberia has shown that the marine pollen assemblages provide an integrated picture of the regional

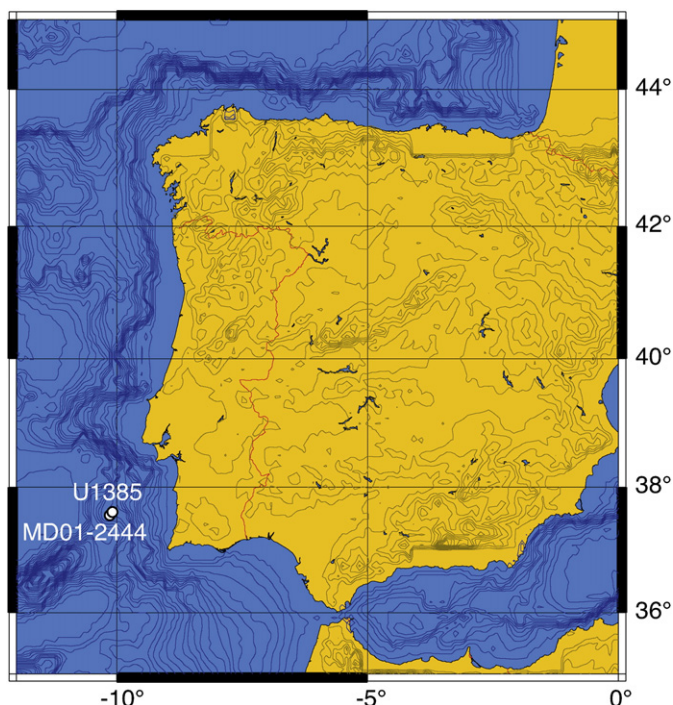


Fig. 1. Location of sites discussed in text.

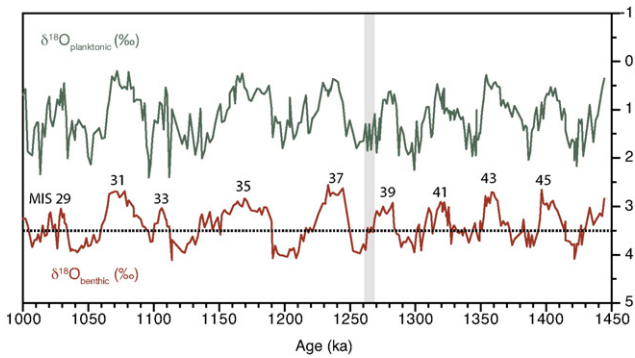


Fig. 2. Low-resolution benthic (*Cibicidoides wuellerstorfi*) and planktonic (*Globigerina bulloides*) $\delta^{18}\text{O}$ from Site U1385 (Hodell et al., 2015), spanning part of the Early Pleistocene. Marine Isotope Stages are indicated. Shaded area denotes interval of interest. The 3.5‰ in benthic $\delta^{18}\text{O}$ threshold of McManus et al. (1999) is also shown.

vegetation of the adjacent continent (Naughton et al., 2007). Pollen zones are informally defined as ‘U1385-MIS38-a’, etc.; as analyses proceed above and below the study interval, the numbering system may need to be amended in future. As in previous work on the Portuguese Margin, the category “temperate trees” comprises deciduous trees, conifers (*Abies*, *Cedrus*) and Mediterranean sclerophylls (evergreen *Quercus*, *Olea*, *Phillyrea*, *Pistacia*), and excludes *Juniperus*, *Betula* and *Pinus*.

Hodell et al. (2015) have constructed an astronomical timescale for U1385, by tuning variations in sediment colour to precession. Spectral analysis of lightness (L^*) in the depth domain showed significant cycles at 2.5 m and 2 m, thought to reflect precession periods of ~23 and 19 kyr, respectively, while a bandpass filter revealed an amplitude modulation that closely matched the eccentricity modulation of precession. The U1385 record was thus tuned by correlating peaks in L^* to the precession index assuming a 3-kyr lag on the basis of radiocarbon ages at the onset of the Holocene (Hodell et al., 2015).

4. Results

Inspection of the pollen diagram (Fig. 3) shows five zones (U1385-MIS38 a, c, e, g, i) characterized by relatively higher temperate tree pollen values (up to 30%), mainly deciduous *Quercus* and to a lesser extent Mediterranean sclerophylls (mainly evergreen *Quercus* and *Olea*), separated by zones of higher pollen values of steppe/semi-desert plants (*Artemisia*, *Chenopodiaceae*, *Graminae*). Hints of a vegetation succession with early expansions of deciduous oaks and Mediterranean sclerophylls, followed by later increases in *Carpinus betulus* or *Ericaceae* are discernible in some of the forested zones. Sporadic occurrences of ‘Tertiary relicts’ (*Zelkova*, *Pterocarya*, *Carya*, *Parrotia*, *Tsuga*, *Liquidambar*) now extinct in Iberia (Postigo-Mijarra et al., 2010) are recorded.

The planktonic $\delta^{18}\text{O}$ record (Fig. 4) also shows a series of oscillations, with values ranging between 0.7 and 2.3‰. Intervals of lower planktonic $\delta^{18}\text{O}$ values, centred at ~1268.7, 1267.7, 1266.4, 1264.8, 1262.9 thousand years ago (ka), are coeval with increases in temperate tree pollen, denoting interstadial conditions. Intervening stadials characterized by higher planktonic $\delta^{18}\text{O}$ values correspond to increased pollen percentages of steppe/semi-desert taxa. Comparison with changes in sediment composition as reflected by XRF analyses (Hodell et al., 2015), shows that the stratigraphic intervals of high (low) temperate tree pollen values and lower (higher) planktonic $\delta^{18}\text{O}$ values correspond to increases (decreases) in the ratio of biogenic (Ca) to detrital (Ti) sediments (Fig. 4). Late/Middle Pleistocene millennial-scale changes in Ca/Ti have been thought to reflect variations in carbonate productivity (Hodell et al., 2013b) and/or detrital sedimentation (Lebreiro et al., 2009). The close correspondence between temperate tree values on one hand and the Ca/Ti ratio may point to a causal link, whereby expanded vegetation cover during times of moisture availability prevented increased erosion and discharge of detrital material by

the Tagus River. Alternatively, the two signals may represent independent but synchronous responses to climate forcing.

Taken together, these records provide the first evidence of millennial-scale changes in the coupled ocean–atmosphere–land system and the immediate response of vegetation to abrupt climate variability in the Early Pleistocene. Previous work has linked reductions in southern European winter precipitation to southward shifts in the mean position of the ITCZ (Tzedakis et al., 2009), reflecting the influence of increased high-latitude land- or sea-ice (Chiang and Bitz, 2005). More specifically, disruption of the Atlantic MOC produces a southward displacement of the ITCZ, which leads to cold and dry conditions in southern Europe and expansion of steppe/semi-desert communities. During interstadials the ITCZ shifts northwards, bringing southern Europe under the influence of the zone of subtropical descent in summer and mid-latitude westerlies in winter, leading to pronounced Mediterranean summer-dry, winter-wet conditions, as reflected by the increased values of deciduous *Quercus* and Mediterranean sclerophylls. By analogy with the Late/Middle Pleistocene, therefore, our records suggest that hydrological changes via shifts in the mean latitudinal position of the ITCZ were also a feature of the Early Pleistocene. This implies that iceberg discharges into the North Atlantic and associated MOC disruption were of sufficient magnitude to lead to changes in the Atlantic cross-equatorial surface ocean temperature gradient on millennial timescales.

5. Comparisons with Late/Middle Pleistocene records

Finally, we place the Early Pleistocene changes within the context of millennial-scale variability of the Late/Middle Pleistocene. Fig. 5 juxtaposes the U1385 planktonic $\delta^{18}\text{O}$, temperate tree and *Artemisia*-*Chenopodiaceae* pollen records with those from two 20-kyr windows of MIS 3 (including Heinrich Stadials (HS) 5 and 4 and Dansgaard-Oeschger (D–O) stadials–interstadials) and early MIS 6 (only D–O stadials–interstadials) from adjacent core MD01-2444 (Margari et al., 2010). With respect to planktonic $\delta^{18}\text{O}$ records, the maximum amplitude of changes is similar in all three intervals. The isotopic record bears a striking resemblance to the MIS 38 succession of stadials and interstadials to that of a MIS 3 Bond cycle from D–O 12 to 8, but it is missing the more extreme values associated with HS4 (Fig. 5). The MIS 38 temperate tree pollen record, on the other hand, does not resemble a Bond cycle as clearly, but bears more similarities to the MIS 6 pollen record, in terms of the absolute values reached, though stadials were longer in MIS 6 (Margari et al., 2010). MIS 38 maxima in *Artemisia*-*Chenopodiaceae*, an indicator of extreme aridity, are not as high as those associated with Heinrich events, but higher than most D–O stadials of MIS 3. Substantial expansions of steppe taxa have been noted before in Early Pleistocene terrestrial pollen records from Iberia (e.g. Leroy, 2008; González-Sampérez et al., 2010), but never before placed in such a detailed climatostratigraphical context. The amplitude of the U1385 vegetation changes, even at such an early stage of the glacial, suggests that climate changes associated with stadial conditions exceeded the tolerance thresholds of most trees on the adjacent landmass. Further analyses over the entire MIS 38 stage and additional cold stages will be able to provide a wider perspective on these changes.

6. Conclusions

We have undertaken ultra-high resolution joint pollen and planktonic foraminiferal isotope analyses on a short section of early MIS 38 (~1262–1269 ka) from IODP Site U1385 on the Portuguese Margin. The generated datasets provide the first evidence for a direct link between North Atlantic climate variability and vegetation response during the Early Pleistocene. By analogy with the Late/Middle Pleistocene (Tzedakis et al., 2009), hydrological changes indicated by the pollen record imply shifts in the mean latitudinal position of the ITCZ, as a result of variations in the strength of the MOC. The magnitude and pacing of

U1385

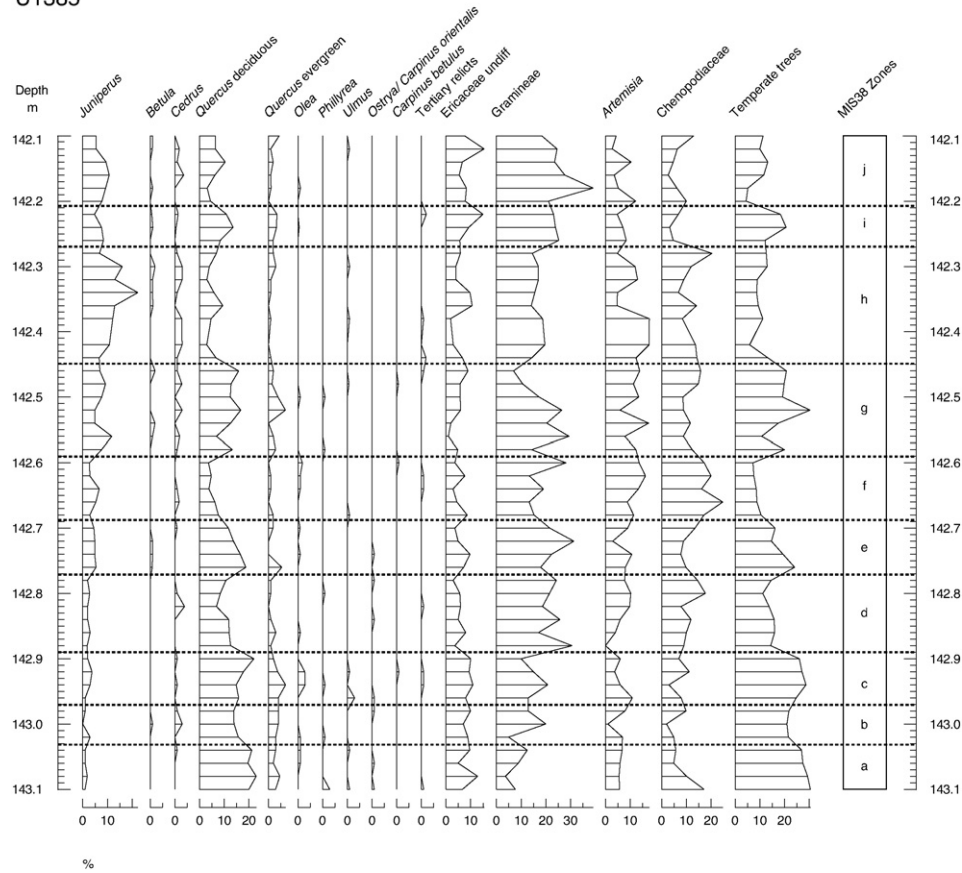


Fig. 3. Pollen diagram of 142.10–143.10 rcmd of core U1385, showing selected taxa. Informal zonation scheme indicated.

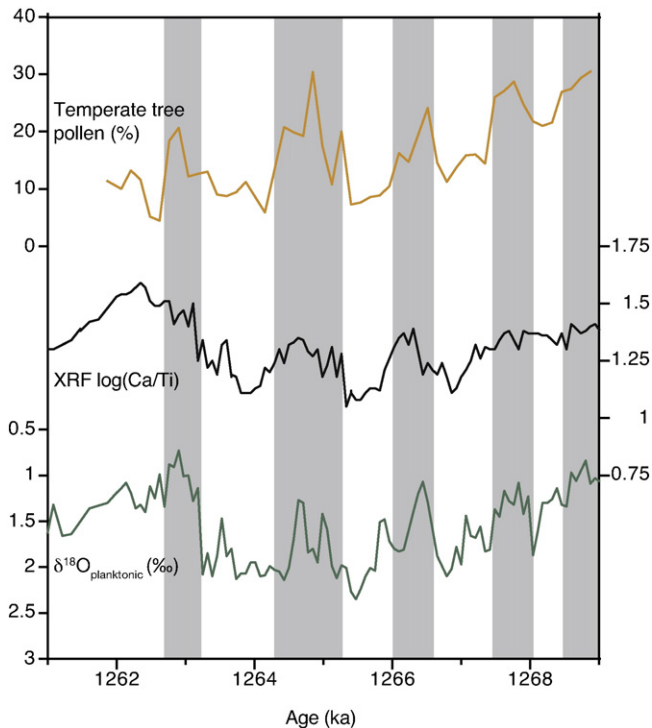


Fig. 4. Comparison of planktonic $\delta^{18}\text{O}$, $\log(\text{Ca}/\text{Ti})$ and temperate tree pollen records from U1385 over the interval of interest, plotted against time.

climate instability bear significant similarities to Dansgaard–Oeschger variability of the Late/Middle Pleistocene. While climate shifted from a state of interglacial dominance in the Early Pleistocene to increasingly residing in a glacial state in the Middle and Late Pleistocene (Berger et al., 1999; Crowley and Hyde, 2008), at intermediate-scale variability the mode and tempo of millennial-scale variability appears to be very similar between the ‘41-kyr world’ and the ‘100-kyr world’.

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References

- An, Z.S., Clemens, S.C., Shen, J., Qiang, X.K., Jin, Z.D., Sun, Y.B., Prell, W.L., Luo, J.J., Wang, S.M., Xu, H., Cai, Y.J., Zhou, W.J., Liu, X.D., Liu, W.G., Shi, Z.G., Yan, L.B., Xiao, X.Y., Chang, H., Wu, F., Ai, L., Lu, F.Y., 2011. Glacial–interglacial Indian summer monsoon dynamics. *Science* 333, 719–723.
- Bailey, I., Foster, G.L., Wilson, P.A., Jovane, L., Storey, C.D., Trueman, C.N., Becker, J., 2012. Flux and provenance of ice-rafted debris in the earliest Pleistocene sub-polar North Atlantic Ocean comparable to the last glacial maximum. *Earth Planet. Sci. Lett.* 341–344, 222–233.
- Barker, S., Knorr, G., Edwards, L., Parrenin, F., Putnam, A.E., Skinner, L.C., Wolff, E., Ziegler, M., 2011. 800,000 years of abrupt climate variability. *Science* 334, 347–351.
- Berger, A., Li, X.S., Loutre, M.F., 1999. Modelling northern hemisphere ice volume over the last 3 Ma. *Quat. Sci. Rev.* 18, 1–11.

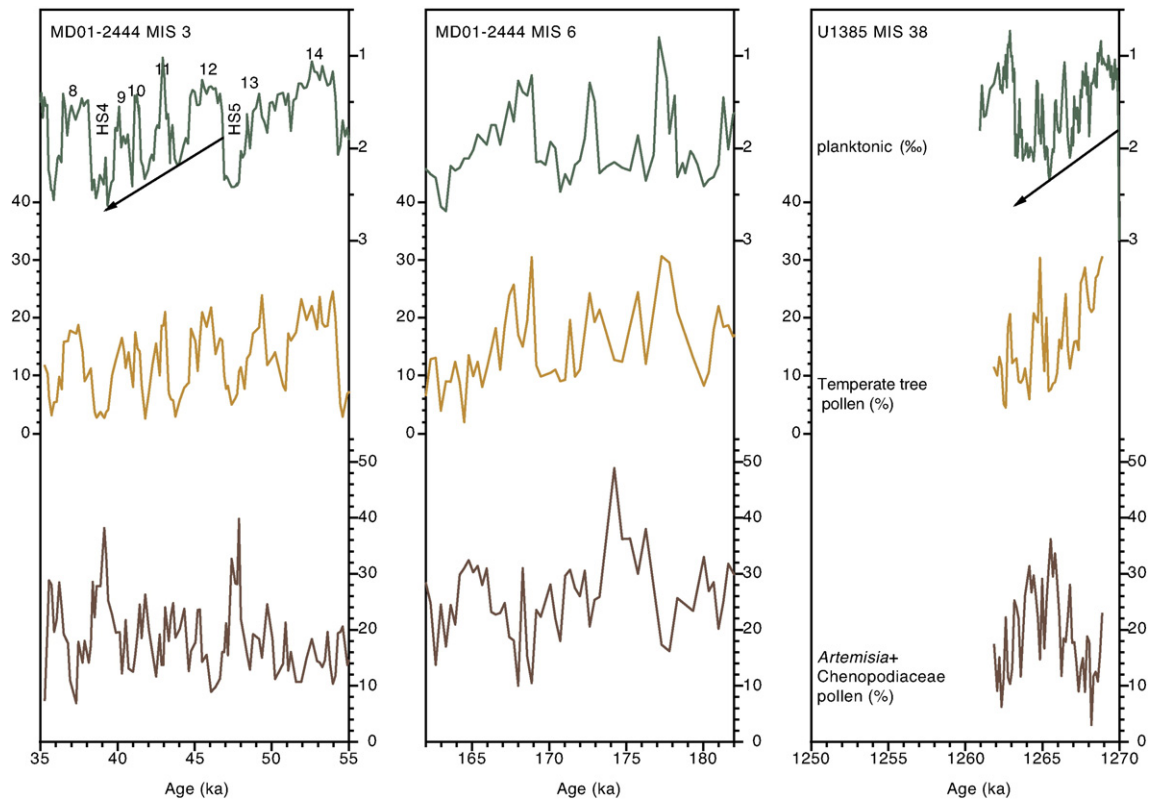


Fig. 5. Comparison of planktonic $\delta^{18}\text{O}$, temperate tree and *Artemisia*-*Chenopodiaceae* pollen records from core MD01-2444 (MIS 3 and MIS 6) (Margari et al., 2010) and U1385 (MIS 38) this study.

- Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., Bonani, G., 1993. Correlations between climate records from North-Atlantic sediments and Greenland ice. *Nature* 365, 143–147.
- Chapman, M.R., Shackleton, N.J., 1999. Global ice-volume fluctuations, North Atlantic ice-raftering events, and deep-ocean circulation changes between 130 and 70 ka. *Geology* 27, 795–798.
- Chiang, J.C.H., Bitz, C.M., 2005. Influence of high latitude ice cover on the marine Inter-tropical Convergence Zone. *Clim. Dyn.* 25, 477–496.
- Chmura, G.L., Smirov, A., Campbell, I.D., 1999. Pollen transport through distributaries and depositional patterns in coastal waters. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149, 257–270.
- Crowley, T.J., Hyde, W.T., 2008. Transient nature of late Pleistocene climate variability. *Nature* 456, 226–230.
- Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahljensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjornsdottir, A.E., Jouzel, J., Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–220.
- Elderfield, H., Ferretti, G., Greaves, M., Crowhurst, S., McCave, I.N., Hodell, D., Piotrowski, A.M., 2012. Evolution of ocean temperature and ice-volume through the Mid-Pleistocene climate transition. *Science* 337, 704–709.
- Elhai, J., 1969. La Flore sporo-pollinique du gisement villafranchien de Senèze (Massif Central-France). *Pollen Spores* 11, 127–139.
- González-Sampériz, P., Leroy, S.A.G., Carrión, J.S., Fernández, S., García-Antón, M., Gil-García, M.J., Uzquiano, P., Valerogarcés, B., Figueiral, I., 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. *Rev. Palaeobot. Palynol.* 162, 427–457.
- Hodell, D.A., Channell, J.E.T., Curtis, J.H., Romero, O.E., Röhl, U., 2008. Onset of “Hudson Strait” Heinrich events in the eastern North Atlantic at the end of the middle Pleistocene transition (~640 ka)? *Paleoceanography* 23, PA4218.
- Hodell, D.A., Lourens, L., Stow, D.A.V., Hernández-Molina, J., Alvarez Zarikian, C.A., the Shackleton Site Project Members, 2013a. The “Shackleton Site” (IODP Site U1385) on the Iberian Margin. *Sci. Drill.* 16, 13–19.
- Hodell, D., Crowhurst, S., Skinner, L., Tzedakis, P.C., Margari, V., MacLaghlan, S., Rothwell, G., 2013b. Response of Iberian Margin sediments to orbital and suborbital forcing over the past 420 kyr. *Paleoceanography* 28, 1–15. <http://dx.doi.org/10.1002/palo.20017>.
- Hodell, D., Lourens, L., Crowhurst, S., Konijnendijk, T., Tjallingii, R., Jiménez-Espejo, F., Skinner, L., Tzedakis, P.C., Shackleton Site Project Members, 2015. A reference time scale for Site U1385 (Shackleton Site) on the SW Iberian Margin. *Glob. Planet. Chang.* 133, 49–64.
- Hopkins, J., 1950. Different flotation and deposition of conifer and deciduous pollen. *Ecology* 31, 633–641.
- Joannin, S., Quillévéré, F., Suc, J.-P., Lécuyer, C., Martineau, F., 2007. Early Pleistocene climate changes in the central Mediterranean region as inferred from integrated pollen and planktonic foraminiferal stable isotope analyses. *Quat. Res.* 67, 264–274.
- Joannin, S., Bassinot, F., Combourieu Nebout, N., Peyron, O., Beaudouin, C., 2011. Vegetation response to obliquity and precession forcing during the Mid-Pleistocene Transition in Western Mediterranean region (ODP site 976). *Quat. Sci. Rev.* 30, 280–297.
- Jouzel, J., Masson-Demotte, V., Cattani, O., Dreyfus, G., Falourd, S., Hoffmann, G., Minster, B., Nouet, J., Barnola, J.M., Chappellaz, J., Fischer, H., Gallet, J.C., Johnsen, S., Leuenberger, M., Loulergue, L., Luethis, D., Oerter, H., Parrenin, F., Raisbeck, G., Raynaud, D., Schilt, A., Schwander, J., Selmo, E., Souchez, R., Spahni, R., Stauffer, B., Steffensen, J.P., Stenni, B., Stocker, T.F., Tison, J.L., Werner, M., Wolff, E.W., 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science* 317, 793–796.
- Kleiven, H.E., Jansen, E., Curry, W.B., Hodell, D.A., Venz, K., 2003. Atlantic Ocean thermohaline circulation changes on orbital to suborbital timescales during the mid-Pleistocene. *Paleoceanography* 18, 1008 (13PP).
- Lebreiro, S.M., Voelker, A.H.L., Vizcaino, A., Abrantes, F.G., Alt-Epping, U., Jung, S., Thouveny, N., Gracia, E., 2009. Sediment instability on the Portuguese continental margin under abrupt glacial climate changes (last 60 kyr). *Quat. Sci. Rev.* 28, 3211–3223.
- Leroy, S.A.G., 2008. Vegetation cycles in a disturbed sequence around the Cobb-Mountain subchron in Catalonia. *J. Paleolimnol.* 40, 851–868.
- Margari, V., Skinner, L.C., Tzedakis, P.C., Ganopolski, A., Vautravers, M., Shackleton, N.J., 2010. The nature of millennial-scale climate variability during the past two glacial periods. *Nat. Geosci.* 3, 127–131.
- Margari, V., Skinner, L.C., Hodell, D.A., Martrat, B., Toucanne, S., Grimalt, J.O., Gibbard, P.L., Lunkka, J.P., Tzedakis, P.C., 2014. Land-ocean changes on orbital and millennial timescales and the penultimate glaciation. *Geology* 42, 183–186.
- Martrat, B., Grimalt, J.O., Shackleton, N.J., de Abreu, L., Hutterli, M.A., Stocker, T.F., 2007. Four climatic cycles of recurring deep and surface water destabilizations on the Iberian Margin. *Science* 317, 502–507.
- Mc Intyre, K., Delaney, M.L., Ravelo, A.K., 2001. Millennial-scale climate change and oceanic processes in the late Pliocene and early Pleistocene. *Paleoceanography* 16, 535–543.
- McManus, J.F., Oppo, D.W., Cullen, J.L., 1999. A 0.5-million-year record of millennial-scale climate variability in the North Atlantic. *Science* 283, 971–975.
- Muttoni, G., Ravazzi, C., Breda, M., Pini, R., Laj, C., Kissel, C., Mazaud, A., Garzanti, E., 2007. Magnetostratigraphic dating of an intensification of glacial activity in the southern Italian Alps during Marine Isotope Stage 22. *Quat. Res.* 67, 161–173.
- Naughton, F., Sánchez Goñi, M.F., Desprat, S., Turon, J.-L., Duprat, J., Malaizé, B., Joli, C., Cortijo, E., Drago, T., Freitas, M.C., 2007. Present-day and past (last 25,000 years) marine pollen signal off western Iberia. *Mar. Micropaleontol.* 62, 91–114.
- Popescu, S.-M., Biltekin, D., Winter, H., Suc, J.-P., Melinte-Dobrinescu, C., Klotz, S., Rabineau, M., Combourieu-Nebout, N., Clauzon, G., Deaconu, F., 2010. Pliocene and Lower Pleistocene vegetation and climate changes at the European scale: long pollen records and climatostratigraphy. *Quat. Int.* 219, 152–167.
- Postigo-Mijarra, L.M., Morla, C., Barrón, E., Morales-Molino, C., García, S., 2010. Patterns of extinction and persistence of Arctotertiary flora in Iberia during the Quaternary. *Rev. Palaeobot. Palynol.* 162, 416–426.

- Raymo, M.E., Ganley, K., Carter, S., Oppo, D.W., McManus, J., 1998. Millennial-scale climate instability during the early Pleistocene epoch. *Nature* 392, 699–702.
- Roucoux, K.H., Shackleton, N.J., de Abreu, L., Schonfeld, J., Tzedakis, P.C., 2001. Combined marine proxy and pollen analyses reveal rapid Iberian vegetation response to North Atlantic millennial-scale climate oscillations. *Quat. Res.* 56, 128–132.
- Roucoux, K.H., Tzedakis, P.C., de Abreu, L., Shackleton, N.J., 2006. Climate and vegetation changes 180,000 to 345,000 years ago recorded in a deep-sea core off Portugal. *Earth Planet. Sci. Lett.* 249, 307–325.
- Ruddiman, W.F., Raymo, M., McIntyre, A., 1986. Matuyama 41,000-year cycles: North Atlantic Ocean and Northern Hemisphere ice sheets. *Earth Planet. Sci. Lett.* 80, 117–129.
- Sánchez Goñi, M.F., Turon, J.-L., Eynaud, F., Gendreau, S., 2000. European climatic response to millennial-scale changes in the atmosphere–ocean system during the last glacial period. *Quat. Res.* 54, 394–403.
- Shackleton, N.J., 1995. New data on the evolution of Pliocene climatic variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution*. Yale University, New Haven, pp. 242–248.
- Skinner, L.C., Elderfield, H., 2007. Rapid fluctuations in the deep North Atlantic heat budget during the last glacial period. *Paleoceanography* 22, PA1205.
- Suc, J.-P., Popescu, S.-M., 2005. Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma. In: Head, M.J., Gibbard, P.L. (Eds.), *Early-Middle Pleistocene Transitions: The Land–Ocean Evidence*. Geological Society of London, Special Publication 247, pp. 147–158.
- Thompson, W.G., Goldstein, S.L., 2006. A radiometric calibration of the SPECMAP time-scale. *Quat. Sci. Rev.* 25, 3207–3215.
- Tutin, T.G., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1964–1980. *Flora Europaea*, 5 volumes (5 volumes) Cambridge University Press, Cambridge.
- Tzedakis, P.C., Roucoux, K.H., de Abreu, L., Shackleton, N.J., 2004. The duration of forest stages in southern Europe and interglacial climate variability. *Science* 306, 2231–2235.
- Tzedakis, P.C., Hooghiemstra, H., Pälike, H., 2006. The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quat. Sci. Rev.* 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 Planet. Sci. Lett.* 277, 307–317.
- Vautravers, M., Shackleton, N.J., 2006. Centennial scale surface hydrology off Portugal during Marine Isotope Stage 3: insights from planktonic foraminiferal fauna variability. *Paleoceanography* 21, PA3004.