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Rising atmospheric CO_2 concentrations: the overlooked factor promoting SW Iberian Forest development across the LGM and the last deglaciation?

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Abstract:

Across the last deglaciation, the global atmospheric concentration of carbon dioxide (pCO_2) increased from ~180 to ~280 ppm. However, the impact of pCO_2 changes on vegetation across the last deglaciation remains poorly understood. Under full glacial low pCO_2, plants experienced constraints on photosynthesis. Therefore, a significant reduction in pCO_2 limitation should have impacted local and regional vegetation dynamics across deglaciation. We hypothesise that deglacial pCO_2 rise could have (1) led to a gradual reduction of the physiological constraint promoting forest response when moisture availability was sufficient, despite low temperatures; and (2) amplified the response of forest development to warmer and wetter conditions. The high-resolution analysis of terrestrial (pollen, C_{29}:C_{31} organic biomarker) and marine (alkenone-derived Sea Surface Temperature, $C_{37:4}$%, and long-chain n-alkanes ratios) indicators, using a direct land-sea direct comparison, in the Iberian margin site Integrated Ocean Drilling Program (IODP) U1385 ("Shackleton site") throughout the Last Glacial Maximum (LGM) and last deglaciation allowed us to track and compare the changes with shifts in global pCO_2. The LGM is characterised by a grassland-heathland mosaic type ecosystem, triggered by cool and moderately humid conditions but low pCO_2 levels may have exacerbated physiological drought and suppressed forest development. During Heinrich Stadial 1 (HS1)the coldest and most arid conditions combined with sustained low pCO_2 values precluded forest development and resulted in the dominance of Mediterranean steppe or semi-desert vegetation. The Bølling-Allerød (BA) is characterised by a temperature optimum (warmest SSTs and forest development) and variable moisture condition, while increasing pCO_2 which contributed to the highest levels of forest development. Within the BA, significant SW Iberian forest development occurred at ~15 cal kyr B.P. associated with an increase in pCO_2 above 225 ppm. During the Younger Dryas (YD), cool temperatures combined with sufficient moisture availability allowed the maintenance of a grassland-forest mosaic, the increasing values of pCO_2 in this period should have offset the low temperature as well as the moisture levels and allow the forest to persist. The overlooked role of pCO_2 could explain an intriguing feature observed in Site U1385 and other Iberian margin records, namely the near absence of forest during the LGM and HS1 but relatively high forest cover during the YD. Our study aims to shed light on the influence of climatic factors (temperature and moisture availability) together with pCO_2 as thresholds on forest response to deglacial climate changes across the Iberian Peninsula.

Keywords:
Iberian margin; Deglaciation; LGM; Direct sea-land comparison; climatic space; Climatic parameters vs pCO_2; Forest development; Pollen analysis

1. Introduction

The last deglaciation is characterised by a series of "classic" abrupt climate events, being one of the periods widely studied for its particular succession of cold and warm events (Alley and Clark, 1999; Lynch-Stieglitz, 2007; Fletcher et al., 2010a; 2010b; Salgueiro et al., 2014; Marcott et al., 2014; Martrat et al., 2014; Naughton et al., 2016; Ausín et al., 2020). While some records based on direct sea-land comparison are available for SW Iberian margin (Boessenkool et al., 2001; Turon et al., 2003; Chabaud et al., 2014; Oliveira et al., 2018; Naughton et al., 2019), few exist that cover the entire deglaciation, and none have the required resolution or chronological precision to detect abrupt vegetation and climate shifts in detail**.** The high temporal resolution, direct sea-land comparison provided by Site U1385 enables,

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therefore, the detection of significant vegetation and climatic shifts in SW Iberia across the last deglaciation.

The interactions between the lithosphere, hydrosphere (oceanic and terrestrial), cryosphere and atmosphere during extreme climate events are crucial to understanding the climate system behaviour. The last deglaciation, from 21 to 6 ka, was accompanied by a global temperature increase of 5 to 10˚C, depending upon the latitude (Bard et al., 1987; Alley and Clark, 1999; Clark et al., 2012), although the warming was not continuous. Two major abrupt climatic cooling episodes, associated with ocean-atmospheric perturbations were superimposed on the warming trend, the Heinrich Stadial 1 (HS1) and the Younger Dryas (YD), bracketing the intervening Bølling-Allerød (BA) interstadial. During the last deglaciation, global atmospheric concentrations of carbon dioxide (pCO_2) increased from ~180 ppmv to 280 ppmv (Monnin et al., 2001; Shakun et al., 2012; Marcott et al., 2014), being among the highest amplitude shifts in pCO_2 of the last 800,000 years (Lüthi et al., 2008). The high-temporal resolution West Antarctic Ice Sheet Divide ice core furthermore shows three main rapid (< 200 years) pCO_2 rises, each of ~10 to 15 ppmv, which took place at the end of HS1; within the BA and at the onset of the YD (Marcott et al., 2014).

The role of CO_2 as a climate driver throughout the ice ages is still intensely debated; however, it has been mainly considered as either (1) a primary driver of the climatic changes, in which the CO_2 led the temperature records in Northern Hemisphere (Shakun et al., 2012; Marcott et al., 2014); (2) an amplifier responding as positive feedback to the warming (Alley and Clark, 1999; Clark et al., 2012); or (3) as a consequence rather than a cause of climatic changes (Denton et al., 2010). Besides its impact on climate, the physiological influence of pCO_2 as a limiting factor over plant development on Quaternary timescales has also been discussed (Cowling and Sykes 1999; Crucifix et al., 2005; Ward et al., 2005; Gerhart and Ward, 2010; Harrison and Sanchez Goñi, 2010). However, its role is often neglected, for example in vegetation-based climate reconstructions which do not account for pCO_2 effects (e.g. Elenga et al.; 2000; Sánchez Goñi et al., 2002; Peyron et al., 1998; Fletcher et al., 2010a; Bartlein et al., 2011; Tarroso et al., 2016).

The annual exchange of CO_2 between the atmosphere and biosphere due to photosynthetic activity corresponds to more than one-third of the total pCO_2 stored in the atmosphere (Farquhar and Lloyd, 1993). The study of increased plant growth and global vegetation greening under higher concentrations of pCO_2 (CO_2 fertilisation) is very topical within discussions of current global climate change (e.g. Piao et al., 2019) whilst the inverse scenario (low pCO_2) has received less attention. The influence of lowering pCO_2 on vegetation has been examined in coupled climate-vegetation models (e.g. Harrison and Prentice, 2003; Sitch et al., 2003; Crucifix et al., 2005; Ramstein et al., 2007; Wu et al., 2007; Prentice and Harrison 2009; Bartlein et al., 2011; Woillez et al., 2011; Svenning et al., 2008; 2011; Claussen et al., 2013; Prentice et al., 2017; Shao et al., 2018; Cao et al., 2019). It has been suggested that pCO_2 changes play an essential role on the development of vegetation (Wu et al., 2007), its coverage (e.g. Harrison and Prentice 2003; Woillez et al., 2011; Harrison et al., 2016; Cao et al., 2019), vegetation productivity (Claussen et al., 2013) and water use efficiency (WUE) (Polley et al., 1995; Cramer et al., 2001).

The role of pCO_2 in plant physiology is well known, in particular during photosynthesis, but the magnitude of its influence on the composition and distribution of past vegetation remains poorly understood. Under low pCO_2 concentrations, stomatal conductance and stomatal density must increase to maintain an adequate CO_2 gradient between the atmosphere and the leaf during photosynthesis. The evaporative demand increases and higher amounts of water are lost through transpiration, reducing WUE and imposing a physiological drought (Street-

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Perrot et al., 1997; Körner, 2000). One should expect that the CO_2 limitations on plant development are, and were, not globally or temporally uniform, depending mainly on the regional level of water-stress. The particular influence of CO_2 limitations in arid and semi-arid areas is highlighted by evidence for global greening of arid areas due to CO_2 fertilisation (Randall et al., 2013). Global evidence supports an atmospheric CO_2 fertilisation effect, especially trees growing in drought-stressed conditions which benefit from increased WUE to enhance growth (Huang et al., 2007). Nevertheless, at local scales, nutrient limitations may limit the response of vegetation to rising CO_2 (e.g. Tognetti et al., 2008). The Mediterranean region, with its characteristic annual hydrological deficit and seasonal water stress, is a key place for exploring the potential role of pCO_2 limitation on vegetation growth. Therefore, past vegetation dynamics in this region may be considered as a significant (inverse) analogue to understand the current impact of increasing temperature and pCO_2 within semi-arid and arid ecosystems.

Vegetation changes across the Iberian Peninsula for the last deglaciation as recorded in palaeoecological proxies are traditionally interpreted as a result of the combined effects of temperature, precipitation and evaporation changes (e.g. Peyron et al., 1998; Carrión et al. 2002; Sánchez Goñi et al., 2002; Combourieu Nebout et al., 2009; Dormoy et al., 2009; Fletcher et al., 2010a; Arranbari et al., 2014; Bartlein et al., 2011; Naughton et al., 2011; 2019; Tarroso et al., 2016). The majority of climate reconstructions and simulations for glacial periods based on vegetation records do not consider the influence of CO_2 and may, therefore, be biased when the effect of pCO_2 is not included. Palaeovegetation (pollen-based) data is vital for testing climate model simulations, both as temporal trends and reconstructions of spatial distributions (Prentice et al., 1992; 2001; Jolly and Haxeltine, 1997; Harrison and Prentice, 2003; Bartlein et al., 2011; Prentice et al., 2011; Harrison et al., 2016; Cao et al., 2019). Within this, reconstructions of vegetation assemblage (Elenga et al., 2000; Svenning et al., 2008) and quantitative estimates of climatic variables (Wu et al., 2007; Svenning et al., 2008; Prentice et al., 2017) are both critical. It is essential to recognise that pCO_2 is correlated with WUE or the balance between carbon assimilation and transpiration (water loss). Neglecting this influence may contribute to the unreliability of precipitation reconstructions, specifically underestimation of past precipitation under full glacial conditions (Jolly and Haxeltine, 1997; Cowling and Skyes, 1999; Gerhart and Ward, 2010; Prentice et al., 2017; Cleator et al., 2020). In contrast, the influence of CO_2 on forest development in the southwest Iberian Peninsula under interglacial conditions may be neglible compared with precipitation changes, as recently revealed by transient model experiments (Oliveira et al., 2018).

The need for additional regional-based palaeoecological studies, such as for the southwest Iberian Peninsula, is highlighted in a recent model-data comparison using the BIOME4 model and a biome-scale reconstruction compiled from pollen records across the Northern Hemisphere (> 30ºN), which reveals a level of unexplained variability in patterns across both space and time (Cao et al., 2019). Detailed pollen assemblage datasets may provide key insights into other factors than temperature, precipitation and potential evaporation that drive changes in vegetation dynamics and composition, such as pCO_2 (Ludwig et al., 2018; Cao et al., 2019). The importance of pCO_2 during periods of abrupt change, such as the ones that occurred in the SW IP during the deglaciation, deserves particular attention. Understanding the temporal dynamics of the regional forest cover, hereafter TMF (Temperate and Mediterranean Forest), requires exploration ofthe role of different parameters (temperature, precipitation and CO_2). The new multiproxy study of Site U1385 allows the direct comparison between terrestrial and marine climatic indicators across the LGM and deglaciation at high (centennial-scale) temporal resolution, and therefore, the detailed reconstruction of abrupt

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changes in the vegetation-based atmospheric conditions and SSTs over the SW Iberian margin, as well as its comparison with available Iberian records. The aims of this study are to:

a) Document terrestrial and marine responses to past climate changes at centennial-scale resolution for the LGM and last deglaciation, including the main abrupt events of the last deglaciation (HS1; B-A and YD) at Site U1385A;
b) Explore the main factors driving forest development during the LGM and last deglaciation;
c) Evaluate the evidence for indications of pCO_2 thresholds for forest development.

2. Materials and environmental setting
[Figure 1]

IODP Site U1385 is a composite record of four drillings in the SW Iberian margin (37°34.285′N; 10°7.562′W, 2587 m below sea level - mbsl) located on a spur at the continental slope of the Promontorio dos Principes de Avis, which is elevated above the abyssal plain and free from turbidite influence (Hodell et al., 2015) (Fig. 1). This work focuses on Hole A, a continuous record of 10 corrected revised meter composite depth (crmcd) mainly composed of hemipelagic silt alternating with clay (Hodell et al., 2015). For this study, Hole A was sampled from 3.84 to 1.08 crmcd, which corresponds to the period between 22550 and 6480 cal yr BP. The sediment supply, including pollen grains, to Site 1385 is mainly derived via fluvial transport from the the Tagus and Sado hydrographic basins, providing a reliable signature of the vegetation of the adjacent continent (Naughton et al., 2007; Morales-Molino et al., 2020). The present-day climate of southwestern Iberia is characterised by a Mediterranean climate strongly influenced by the Atlantic Ocean, Köppen classification CSa with warm summers (around 22°C as the average temperature of the warmest month) mean annual temperatures between 12.5°C and 17.5°C, and mean annual precipitation from 400 to 1000 mm/yr. The rainy season peaks in the winter between November and January and drought occurs in the summer generally from June to September.

3. Methods
3.1. Chronological framework
[Table 1, Figure 2, Figure 3, S.M. Fig. 1]

Eleven AMS ^{14}C dates were used to generate a new age-model for the last deglaciation at Site U1385 (Table 1 and Fig. 2). Five previously published AMS ^{14}C dates from Oliveira et al. (2018) (analysed at the Vienna Environmental Research Accelerator (VERA), Isotope Physics Research Group, University of Vienna, Austria, from monospecific foraminifer samples of *Globigerina bulloides*) were also used (Table 1). A new set of six samples for AMS ^{14}C were selected and processed at the Keck Carbon Cycle AMS Facility, (University of California, Irvine), from monospecific foraminifer samples of *Globigerina bulloides* (Table 1). The new age-model was calculated using a Bayesian approach, through the software Bacon implemented in R (Blaauw and Christen, 2011; R Development Core Team, 2020). We used the Marine13.14d calibration curve (Reimer et al., 2013) which integrates a marine reservoir correction (R) of 500 ± 200 years (Bard et al., 2004a; 2004b; 2013). We calculate a weighted mean DeltaR, based on the ten neighbouring sites (around Site U1385) of 143 ± 139 years, at 1 s.d using CALIB 7.1 (Stuiver et al., 2020) to account for regional effects.

3.2. Pollen analysis

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A total of 97 samples (including 25 previously published by Oliveira et al., 2018) were analysed between 3.84 to 1.08 crmcd in Hole A, and prepared at the University of Bordeaux using the standard protocol of the the UMR EPOC laboratory The sediment was firstly separated using coarse-sieving at 150 µm, retaining the fine fraction. A sequence of chemical treatments, starting with cold HCl at increasing concentrations (10%, 25%, 50%) eliminated calcium carbonate particles. Cold HF. at increasing strength (45% and 70%) eliminated silicates. The remaining residue was micro-sieved (10 µm mesh), retaining the coarse fraction. Exotic *Lycopodium* spore tablets of known concentration were added to each sample to calculate pollen concentrations (Stockmarr, 1971). The obtained residue was mounted in a mobile medium composed of phenol and glycerol 1% (w/v), to allow the pollen/spore rotation and accurate identification. Samples were counted using a transmitted light microscope at 400X and 1000X (oil immersion) magnifications. To perform pollen identification, we used identification keys (Faegri and Iversen, 1989; Moore et al., 1991), a photographic atlas (Reille, 1992; 1995) and the SW Mediterranean modern reference collection.

The total count ranged from 198 to 1545 pollen and spores per sample, with a minimum of 100 terrestrial pollen grains and 20 pollen morphotypes to provide statistical reliability of the pollen spectra (McAndrews and King, 1976; Heusser and Balsam, 1977). The main pollen sum was calculated following previous palynological studies of Site U1385 (e.g. Oliveira et al., 2016) that excluded *Pinus*, *Cedrus*, aquatic plants, Pteridophyte and other spores, and indeterminable pollen. The pollen percentages are calculated against the main pollen sum; *Pinus* and *Cedrus* percentages as well local taxa are calculated against the main pollen sum plus the taxon. *Pinus* pollen, being an anemophilous taxon, is generally overrepresented in marine deposits and therefore excluded from the main sum (Naughton et al., 2007). *Cedrus* being an exotic component possibly transported by wind from the Atlas Mountain (Morocco), is also excluded. PSIMPOLL 4.27 (Bennett, 2009) was used to plot percentages for selected taxa, grouped by ecological affinities (Gomes et al., 2020). Stratigraphically constrained cluster analysis by Sum of Squares (CONISS) determined the five statistically significant pollen assemblage zones (CONISS) (U1385-1 to 5) based on a dissimilarity matrix of Euclidean distances with pollen taxa ≥ 1% (Grimm, 1987; Bennet et al., 2009).

3.3. Compilation of Iberian margin pollen records

In order to assess vegetation and climate changes in the IP region across the LGM and the last deglaciation, we compiled available marine records along the Iberian margin covering the period from 23 to 6 ka. Pollen count datasets from eight pollen records (D13882 - Gomes et al. 2020; MD03-2697 - Naughton et al., 2016; MD95-2039 – Roucoux et al., 2005; MD95-2043 Fletcher and Sánchez Goñi, 2008; MD95-2042 – Chabaud et al., 2014; ODP Site 976 – Comborieut Nebout et al., 1998; 2002; 2009; SU81-18 Turon et al., 2003; Site U1385 – this study) were used with the original published chronologies. Pollen percentages were recalculated against the main pollen sum. A uniform calculation of the pollen-based ecological group TMF was made for each record, integrating the following taxa of 1)Temperate trees and shrubs: deciduous *Quercus, Acer, Betula, Cannabis/Humulus, Carpinus, Castanea, Fraxinus excelsior-type, Hedera helix, Hippophae, Ilex, Juglans, Myrica and Vitis;* and 2) Mediterranean taxa: evergreen *Quercus, Quercus suber, Arbutus type, Buxus, Daphne, Jasminum, Ligustrum, Myrtus, Olea, Phillyrea, Pistacia, Rhamnus, Rhus.*

To assess the general trend of vegetation patterns throughout the deglaciation, we applied a Generalised Additive Model (GAM), considered as a more robust statistical approach than

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loess curves (Wood, 2017; Simpson, 2018). The GAM model was fitted using the *gam*() function of the *mgcv* package (version 1.8.24; Wood, 2017) for R (version 3.6.3; R Core Team, 2020). We fitted the model using a standard GAM with REML smoothness selection, with 30 basis functions (*k*=30) and a smoothing parameter of 0.0001 (*sp*=0.0001). To check the validity of the smooth terms and if the used basis functions captured the wiggliness, we applied a test using the *gam.check*( ) function of the *mgcv* package. The *k-index* obtained higher than 1, and the *p-value* supported the hypothesis that in both cases, enough basin functions were used. The curve shows the fitted GAMs for TMF with an approximate 95% confidence interval (Simpson, 2018).

3.4. Molecular biomarkers

Marine biomarker analyses were carried out in 123 levels, including 30 already published by Oliveira et al. (2018). All analyses were performed following the extraction and analytical methods described in Villanueva et al. (1997) and Rodrigues et al. (2017).
Marine coccolithophorid algae synthesise organic compounds including alkenones (Volkman et al., 1980) (Fig. 3i and j). Seawater temperature changes influence the amounts of di-, tri- and tetra-unsaturated alkenones produced by algae (Brassell et al., 1986). The use of organic solvents to separate the total lipid fraction from sediments allows the sea surface temperature alkenone-based reconstruction ($U^{k'}_{37}$ - SST) (e.g. Rodrigues et al., 2017, Villanueva and Grimalt, 1997), The $U^{k'}_{37}$ index (Prahl and Wakeman, 1987) was converted to temperatures values using the global calibration equation defined by Müller et al. (1998) with an uncertainty of 0.5ºC (Grimalt et al., 2001). Additionally, tetra-unsaturated alkenone ($C_{37:4}$) percentages were calculated due to their potential to identify the occurrence of cold freshwater pulses associated with iceberg discharges (Bard et al., 2000; Martrat et al., 2007; Rodrigues et al., 2011, 2017) and therefore, changes in the reorganisation of surface water masses in the North Atlantic (Rodrigues et al., 2017).
The ratio between C_{29} and C_{31} n-alkanes was also calculated to understand how epicuticular wax production in terrestrial plants varied through the time (Eglinton and Hamiltom 1967). This index is generally considered to encompass the dynamic between woody plants vs grasses plants of the adjacent continent (Cranwell 1973, Tareq et al., 2005, Bush et al., 2013). If the index is >1, it is typically considered to reflect higher quantities of C_{29} *n*-alkanes by trees and shrubs, while value of the index <1 are generally considered to indicate the production of higher quantities of C_{31} *n*-alkanes by grasses and herbaceous plants (Cranwell, 1973; Ortiz et al., 2010; Rodrigues et al., 2009). This relation encompasses the adaptation of plants, by increasing leaf wax production, to reduce water loss during the photosynthetic processes and prevent desiccation promoted by harsh winds or more arid conditions (Bush and McInerney, 2013).

4. Results and interpretation

4.1. Age model

The studied interval encompasses the period from ~23 to 6 ka, as shown by the radiocarbon age model (Fig. 2). The average temporal resolution for the pollen and marine biomarkers

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across the deglaciation is 127 and 116 years, respectively, or slightly lower (171 and 131 years, respectively) when including the Holocene section (Fig. 3 and S.M. Fig. 1).

4.2. Major vegetation and climatic shifts in SW Iberia during the last deglaciation

The U1385 pollen diagram with clustering analysis (SM Fig.1) and SST profile reveals four main episodes over the LGM and the last deglaciation (Fig. 3, further details in S.M. Table 1). We emphasise the findings of the new U1385 record but also showcase the excellent correspondence between the record and the Iberian margin compilation (Fig. 3c), highlighting generally strong parallels in forest development across the compilation of eight records:

Pollen zone U1385-1 (22550 – 18130 cal yr B.P.) corresponds to the LGM, and shows the dominance of semi-desertic taxa (STE, ~40%), reflecting dry conditions over the continent (Fig. 3d). The high values of C_{29}/C_{31} between 0.8 and 1 detected during this interval, might suggest an increase in epicuticular wax production by woody plants in response to dry conditions (Fig. 3h). Although STE were the dominant taxa, the moderate presence of heathland (ERI, ~10-20%) suggests some moisture availability (Fig. 3e) as at present-day they develop preferentially under oceanic (temperate and moist) climate (e.g. Polunin and Walters, 1985). The low percentages of TMF (5-15%) (Fig. 3c), suggesting cold and dry conditions over the continent, are consistently observed across the marine records in southerly locations off the Iberian Peninsula (MD95-2043 - Fletcher and Sánchez Goñi, 2008 and ODP Site 976 - Comborieut Nebout et al., 1998; 2002; 2009 in the Mediterranean Sea, and SU81-18- Turon et al., 2003 in the Atlantic Ocean) as well as further North off the IP (MD99-2331 and MD03-2697- Naughton et al., 2007; 2016). This zone is also characterised by moderately cool SSTs (average ~14.5ºC, Fig. 3j), and minor influence of meltwater pulses as revealed by the low (not significant, < 2%) $C_{37:4}$ values (Fig. 3i).

Pollen zone U1385-2 (18130 – 15400 cal yr B.P.) corresponds to HS1, and reveals the maximum expansion of STE (Fig. 3d) suggesting extreme dry conditions over the southwestern Iberian Peninsula. The decrease observed in more moisture-demanding heaths (ERI) as well as terrestrial marshes and wetlands (decrease in *Isoetes* undiff.) could be likely the result of increased moisture stress (Fig. 3e, S.M. Table 1 and S.M. Fig. 1). The high C_{29}/C_{31} values (mostly above 1) observed consistently in this zone suggest a further increase in epicuticular wax production by the vegetation cover as compared with the preceding LGM (Fig. 3h). At the same time, the TMF, and especially the thermophilous components, almost disappeared, confirming dry but also extreme conditions (Fig. 3c and f, S.M. Fig. 1 and S.M. Table 1). The dominance of STE during HS1 is consistent across the majority of the IP records (Roucoux et al., 2005; Naughton et al., 2007; 2016; MD95-2043 - Fletcher and Sánchez Goñi, 2008; ODP Site 976 – Comborieut Nebout et al., 2002). In conjunction, SSTs drop to minimum values (~12ºC, Fig. 3j), reflecting the coldest sea surface conditions of the deglaciation in SW Iberian margin. The high $C_{37:4}$ values (~8.2%, Fig. 3i) reflect maxima of meltwater pulses, associated with extreme cold conditions and a clear expression of HS1 in the Atlantic Ocean.

Pollen zone U1385-3 (15400 – 12760 cal yr B.P.) shows a strong development of TMF including a minor increase in Mediterranean elements(Fig. 3c and f) anda reduction of STE (Fig. 3d) reflecting a trend of increasing warmth and humidity marking the Bølling-Allerød episode in the southwestern Iberian Peninsula. Although STE decreases at the onset of this episode, grasses expand, suggesting still relatively dry conditions during the beginning of this episode (Fig. 3g and d). The increase of SSTs parallels the terrestrial/atmospheric warming trend (Fig. 3j and c, although the maximum SST (17.5ºC) was attained before maximum TMF expansion. The asynchrony, observed at the onset of this zone, between TMF (gradual

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increase, Fig. 3c) and SST (maximum values, Fig. 3j) could indicate some moisture deficit at the start of this zone, and this assumption can be supported not only by the high abundance of grasses but also by the continued high C_{29}/C_{31} ratio at the onset of this interval (Fig. 3g and h). Indeed, several other pollen records across IP show a similar pattern of dryness during the initial phase of the BA (Van der Knaap and van Leeuwen, 1997; Roucoux et al., 2005; Naughton et al., 2007; 2016; ODP Site 976 – Comborieut Nebout et al., 2002). The most likely explanation for the delayed response of the TMF is the existence of a moisture deficit at the start of the BA (Naughton et al., 2016). The rise in Mediterranean elements towards the end of the zone suggests an increasing expression of warm but dry summers. The high C_{29}/C_{31} ratio at the onset of this zone shifts towards low values by the end of this episode, possibly reflecting an overall decrease of wax production by plants in response to reduced aridity (Fig. 3h).

Pollen zone U1385-4 (12760 – 11050 cal yr B.P.) corresponds to the YD and initial Holocene. This zone is marked by a TMF contraction and expansion of STE (Fig. 3c and d), reflecting regional cooling and drying over the southwestern Iberian Peninsula. There is a slight increase registered by the C_{29}/C_{31} ratio, consistent with the patterns observed in preceding zones which could again be associated with an increase in the leaf wax production under more arid conditions (Fig. 3h). A significant SST reduction is observed with a minimum of 13.2 ºC in the record (Fig. 3j). However, in contrast to HS1, freshwater pulses are insignificant during this phase (Fig. 3i). The fairly weak reduction in TMF observed inin our record and corroborated by the compiled records (Fig 3c) contrasts with the steppe environment described for this interval, especially in the southeast of the IP (Carrión et al., 2002; Camuera et al., 2019). A more pronounced forest contraction is observed in the high altitude terrestrial/lacustrine cores (Quintanar de la Sierra II – Peñalba et al., 1997; and La Roya - Allen et al., 1996) in which the near-disappearance of the forest might reflect the altitudinal adjustments in vegetation belts (Aranbarri et al., 2014). However, the U1385 record and other Iberian margin and IP records (e.g. Lake de Banyoles – Perez-Obiol and Julià, 1994; MD03-2697 – Naughton et al., 2007; MD95-2039 – Roucoux et al., 2005; Charco da Candieira – van der Knaap and van Leeuwen, 1997; MD95-2042 – Chabaud et al., 2014; D13882 - Naughton et al., 2019; MD95-2043- Fletcher and Sánchez Goñi, 2008; ODP Site 976 – Comborieut Nebout et al., 2002) show a relatively high percentage of TMF during the YD when compared with the previous HS1 in the SW IP (Fig. 3c).

Pollen zone U1385-5 (11050 – 4500 cal yr B.P.) corresponds to the early to Middle Holocene. This zone is marked by the expansion of TMF as well as the Mediterranean forest, reflecting a regional increase in temperature and precipitation. Despite the low temporal resolution it is consistent with nearby records with a maximum forest development at around 9000 cal yr B. P. (Gomes et al., 2020). Minimum values of C_{29}/C_{31} ratio suggested a decrease in epicuticular wax production by vegetation possibly do to the most favourable conditions for vegetation development compared with the preceding zones.During this zone is noethworthy the warmer SST around 18-20 ºC.

5. Discussion

[Figure 4], [Figure 5]

5.1. The effect of pCO_2 on biome changes during the LGM and deglaciation

Whilst a classic interpretation of ecosystem dynamics as described for Site U1385 can be proposed solely considering the variation of the main climatic parameters (temperature,

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precipitation), we hypothesise that past changes in pCO_2 played an essential role in vegetation change, specifically in the deglacial forest expansion. Here we re-evaluate the drivers of vegetation change, explicitly considering the evolution of pCO_2 through the deglaciation. Our discussion is informed by the present-day environmental and climatic space occupied by different taxa in Portugal (Temperate Mediterranean forest – *Quercus* sp., Heathland - Ericaceae family and semi-desertic taxa) (S.M. Fig. 2).

LGM

The pollen-based vegetation record from Site U1385 shows that during the LGM a grassland-heathland mosaic dominated the landscape (Fig. 3d, e and Fig. 4d), a distinctive non-analogue glacial vegetation cover. The prevalence of heath pollen in Iberian pollen records underpins the classic view of the LGM in Iberia as a fairly humid interval, certainly compared with the extreme aridity evident during Heinrich stadials (Naughton et al. 2007; Roucoux et al. 2005; Sanchez-Goni et al. 2009; Combourieu-Nebout et al. 2009; Fletcher and Sanchez-Goni 2008). Nevertheless the justaposition of high abundances of semi-desert and heathland taxa remains intriguing. In terms of their present-day climatic space distribution, the STE and ERI taxa differ in that the latter can occupy niches with high humidity, which contrasts with the arid-loving conditions of the former (S.M. Fig. 2c). Interestingly, the environmental space for the Ericaceae group (namely *Erica arborea*, *E. australis*, *Calluna vulgaris*) coincides with that occupied by the *Quercus* genus, the main constituent of the TMF group (S.M. Fig. 2b). This begs the question, if the environmental conditions that support heathland overlap with those for *Quercus* sp., then why were forests not thriving during the LGM? The first answer could be cold atmospheric temperatures, even if during the LGM the temperatures were not as extreme as the ones observed during the HS1 (Bond et al., 1993; Rasmussen et al., 1996). As such a potential controlling factor could be the low levels of pCO_2 during the LGM of between 180-190 ppmv, which is amongst the lowest concentrations recorded during the history of land plants (Pearson and Palmer, 2000; Tripati et al., 2009). The global distribution of different vegetation types as a function of temperature and precipitation was modelled under modern and corrected for LGM CO_2 (185 ppm) showing qualitative differences in the distribution of vegetation types (Shao et al., 2018). Under low pCO_2 grassland was favoured to the detriment of evergreen broadleaf, evergreen and deciduous needle leaf forest. That study, however, did not include ericaceous heathlands specifically, and it is not known whether this group has adaptations permitting better functioning under low pCO_2 levels. We speculate that drought-adapted traits in Mediterranean Ericaceae especially *E. arborea* including thick cuticles, small leaf size, large photosynthetic thermal window and deep root system with large diameter and a massive underground lignotuber (Gratani and Varone, 2004) may have been beneficial in coping with the challenging trade-off between photosynthesis and water loss under very low pCO_2. As such, the Ericaceae of the LGM may represent part of vegetation that coped well with physiological constraints of the low pCO_2 world.

At the same time, we notethatthe LGM correpsonds to a maximum in of the precession cycle, which is recognised to promote a weakening of seasonal contrasts(reduced summer dryness) and consistently associated with heathland development in the Iberian Peninsula (Fletcher and Sanchez Goni, 2008; Sanchez Goni, 2008), in both glacials and interglacials (e.g. Oliveira et al., 2017), including the Middle to Late Holocene (Gomes et al., 2020; Oliveira et al., 2018; Chabaud et al., 2014). As such, during the LGM, the precession maximum promoting wetter summers should have been a trigger for heathland development .

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Diverse vegetation models have been used to understand the influence of climatic parameters and pCO_2 during the LGM (e.g. Harrison and Prentice, 2003; Woillez et al., 2011; Shao et al., 2018). There is a disagreement about the magnitude of the pCO_2 influence, from being considered to have an equal influence (Izumi and Lezine, 2016) to being thought to be less critical than climatic parameters (Woillez et al., 2011; Shao et al., 2018; Chen et al., 2019). Harrison and Prentice (2003) also highlight models differences and the variable regional expression of the influence of pCO_2 (with higher impact in tropical areas). However, these studies agree that low pCO_2 had a negative physiological impact on forest development during the LGM in different continents (Jolly and Haxeltine, 1997; Cowling, 1999; Harrison and Prentice, 2003; Woillez et al., 2011; Shao et al., 2018; Chen et al., 2019). Jolly and Haxeltine (1997) used BIOMOD to simulate LGM vs pre-industrial CO_2 levels under different climatic conditions scenarios (temperature and precipitation) in tropical Africa; CO_2 was considered the primary driver of biome change from tropical montane forests to shrubby heathland ecosystems. This model included a photosynthetic scheme able to simulate plant response to different levels of CO_2 and its impact on stomatal conductance and water stress. This study showed that increasing pCO_2 (above ~190 ppmv), offsets the lower temperatures (changes of -4 to -6 °C), allowing the forest to thrive and substitute heathland. However, plants with higher climatic demands (temperature and precipitation), which is the case of most temperate trees, are less competitive under low pCO_2 conditions, compared with evergreen microphyllous species (e.g. *Erica* sp.). The ecological advantages of *Erica* sp. also include less demanding edaphic requirements (low nutrient demand), more competitive re-sprouting strategy after disturbance, especially fires, as well as a higher dispersal capacity compared with *Quercus* sp. for example (Pausas, 2008).

The inclusion of pCO_2 in climatic reconstructions for LGM for Africa and Europe yields a wetter LGM compared with reconstructions assuming pCO_2 present-day concentrations (Wu et al., 2007). The implications of these experiments are important for the southwest Iberian region and may help to resolve the apparent contradiction between vegetation (abundance of semi-desertic plants and presence of heathland) and climate simulations which indicate enhanced winter precipitation over southern Iberian and Northwest Africa due to southward shifting of the wintertime westerlies (Beghin et al., 2016). In the absence of pCO_2 correction, temperature could also be misinterpreted; the LGM vegetation for Mediterranean sites was simulated and associated with warmer summer under LGM pCO_2, instead of the more cold conditions simulated with present-day levels of CO_2 (Guiot et al., 2000). In Europe, pollen reconstruction with steppe vegetation indicated warmer winter temperature for LGM pCO_2 compared with the modern pCO_2 (Wu et al., 2007). The bias could extend to vegetation reconstructions; without the pCO_2 effect, the cover of boreal and temperate forests is reduced, and evergreen forests are overestimated for the LGM (Woillez et al., 2011).

Experiments determining plant thresholds in response to low pCO_2 have not received as much attention as research on the impact of high pCO_2 levels (Gerhart and Ward, 2010; Dusenge et al., 2019). When we assess the relationship between pCO_2, SST and TMF across the LGM and deglaciation events we observe that LGM occurrence of TMF (i) corresponds to SSTs below 15.5°C and pCO_2 below 225 ppmv and (ii) that values remain below 20% (Fig. 5). Within African mountain environments, a value of 220 ppmv of pCO_2 has been suggested as a threshold above which the forest could develop (Dupont e al, 2019). Therefore, we can infer that the forest development In SW of Iberian during LGM may have been constrained by the interaction of relatively low temperatures (with seasonal oscillations)and low levels of pCO_2 (~185 ppmv). One could speculate that a hypothetical increase of pCO_2, above 225 ppmv values during the LGM would have permitted forest development in the southwest Iberian

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Peninsula, although independent proxies for terrestrial temperatures and precipitation amount are highly desirable.

HS1

During HS1, a Mediterranean steppe landscape with minimum arboreal development resulted from the lowest temperatures and highest levels of aridity observed within the studied interval (Fig. 3 and 5c). During this event, the potential effect of increasing pCO_2 (from ~185 to ~225 ppm) from 18.1 to ~16 cal ka B.P. (Fig. 3b) was not enough to counteract the limiting effect of the climate conditions (coldest and driest atmospheric conditions), and indeed should have exacerbated aridity stress at this time.. Regional models (Weather and Research Forecast Model – WRF) reconstructing the potential vegetation with a pCO_2 correction show a reduction in arboreal vegetation and increase of sparsely vegetated soil for the IP region during HS1 compared with the LGM (Ludwig et al., 2018). The reconstructed precipitation values for the southwestern Iberian Peninsual (Tagus hydrographic basin catchment), show values below 700 mm/yr for HS1, which agrees with the pollen data and again the widespread semi-desertic taxa development. Interestingly, the differences between HS1 and LGM are quite relevant, which could explain the stronger development of the heathland in the LGM. The reconstructed atmospheric temperature showed a longitudinal variation between the HS1 and LGM varying from -2.5 to -1.5 °C; which are in line with the high percentages of semi-desertic taxa of Site U1385, as well as other nearby IP records (Peñalba et al., 1997; Perez-Obiol and Julia, 1984; Comborieu Nebout et al., 2002; Roucoux et al., 2005; Naughton et al., 2007; Fletcher and Sánchez Goñi, 2008). Besides, the forest development was constrained across the territory, and based on pollen data from marine and terrestrial records we do not observe any significant (<5% TMF) latitudinal difference when comparing northern (e.g. Peñalba et al., 1997; Perez-Obiol and Julia, 1984; Roucoux et al., 2005; Naughton et al., 2007) with southern (e.g. this study; Comborieu Nebout et al., 2002; Fletcher and Sánchez Goñi, 2008) pollen records. Furthermore, the relationship between pCO_2, SST and TMF across the HS1 show scattered values of TMF (below 20%) occurring at temperatures below 15.5°C and pCO_2 below 225 ppmv (Fig. 5).

BA

The BA is characterised by favourable climatic conditions (higher temperatures, higher moisture availability) for TMF development (Fig. 3c). The high temperature and a dry to wet trend are likely the primary drivers of progressive forest development during the BA. However, it is important also to consider a possible role of increasing of soil maturation (higher organic matter content, pH, plant nutrients, during succession/development of this biome), as well as a possible "fertilisation effect" of the stepwise increases of pCO_2 by ~15 ppmv around this time interval (Fig. 3b). The simulations produced by BIOME3 for African Biomes (Tropical forest/Ericaceous scrub) with a present climate showed that above 190 ppmv, the increase of pCO_2 at intervals <20 ppmv, gradually offsets the negative effect of temperature changes; above 250 ppmv with a maximum temperature change of ~-6°C the development of forest will be promoted in detriment of the ericaceous scrubland (Jolly and Haxeltine, 1997).
The abrupt increases in pCO_2 at 16.3 Ka and 14.8 Ka (Marcott et al., 2014) (Fig. 3b), could tentatively be associated with the slight increase of forest at the onset of the BA and with the highest peaks of forest development observed during the BA (within age uncertainties of both archives) (Fig. 3c). Cao et al. (2019), using pollen-based biome reconstruction, suggested that

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worldwide expansion of forests was a consequence of the increasing pCO_2 superimposed over the temperature increase between 21 ka and 14 ka. Cao et al. (2019) further emphasise the role of CO_2 after the LGM driving a general northward expansion of forests and replacement of grassland by temperate forests in Europe, by minimising moisture limitation and enhancing WUE. Afterwards, from 14 ka to 9 ka, sufficient moisture (in a general assumption) might also have played a significant role(Cao et al., 2019), whilst the higher levels of pCO_2 may have been able to offset, at least at the end of the BA, the effect of any potential reductions in moisture availability. During the BA, considering that temperature and moisture availability was quasi-optimal, increases in pCO_2 levels (>225 ppmv) may have amplified TMF expansion during this period (Fig. 4b and Fig. 5).

YD

The YD is characterised by a forest-grassland mosaic, as indicated by relatively high levels of forest coexisting with semi-desertic taxa (Fig. 3c, d and Fig. 4a). Strong SST cooling (Fig. 3j) may have been associated with cooler land surface temperatures. However, this impact may have been offsetby the positive effect of sufficient moisture availability (based on the presence of TMF, Naughton et al. 2019) and the increasing trend of pCO_2 (Fig. 3b). Unfortunately, there is a lack of independent precipitation proxies for this region, and Dennison et al. (2018) highlight a lack of reliability in the speleothem proxies for precipitation in this region for this time interval. We observe that the YD forest development occurs in association with similar SSTs to those of the LGM and slightly higher than those of HS1. Meanwhile, pCO_2 was above the 225 ppmv thresholdthroughout the YD, (reaching maximum values of ~260 ppmv, at ~12 Ka) (Fig. 5). The increase in pCO_2 may have enhanced plant productivity and WUE (Cowling and Sykes, 1999; Ward et al., 2005) during the YD, partially compensating for the impact of atmospheric cooling and drying. Schenk et al. (2018) suggest pCO_2 may play an essential role in the forest development if enough moisture is available. It may be that the tree cover was restricted to suitable, moist microhabitats and close to refuge zones, but was not as restricted as in previous cold periods (Svenning et al., 2011), as pollen data also suggests (Fig. 3c). Also, simulated data from vegetation-climate models based on pollen records for biome reconstruction (Shao et al., 2018) and in a dynamic vegetation model (ORCHIDEE) driven by outputs from an AOGCM (Woillez et al., 2011) emphasise the influence of increasing pCO_2 as a critical factor for worldwide forest development during the period including the YD (Shao et al., 2018). Underlying these changes the increase in summer insolation (Fig. 3a), which contributed to the increase of summer temperatures cannot be neglected as a promotor of forest development, at least where trees where not excessively water-stressed. However disentangling the isolated contribution of insolation vs pCO_2 requires sensitivity experiments, not yet performed. In summary, the persistence of TMF during the YD, despite cold temperatures with some seasonality, (warmer than the HS1), seems to be best explained by the combined interaction between sufficient moisture availability, higher atmospheric temperature, at least during summer (promoting forest development) and increasing pCO_2 (between ~245 and 265 ppmv) (Fig. 4a).

5.2. C_{29}/C_{31} ratio and C_3/C_4 dynamics: potentials and limitations

Insights into the dominance of different plant physiological pathways can be potentially gained using C_{29}/C_{31} n-alkanes of Site U1385A (Fig. 3h). In general, C_{29} and C_{31}, as well as other long-chain alkanes with odd carbon numbers (e.g. C_{29}, C_{31}, C_{33}), are epicuticular waxes produced

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by terrestrial plants, from which C_{29} could represent woody plants and C_{31} grasses (Meyers, 2003). However, caution in interpreting the C_{29}/C_{31} ratio in terms of taxonomic groups is required since woody plants and grasses are both capable of producing C_{29} and C_{31} chain lengths (Ortiz et al., 2010; Bush and McInerney, 2013). Furthermore, regional differences are observed across the world and between biomes in terms of what long-chain n-alkanes a species is producing (Bush and McInerney, 2013). Noting this limitation, the analysis of C_{29}/C_{31} curve shows increasing values during the LGM to yield high values during the HS1, followed by the YD underlying a decreasing trend towards the Holocene (Fig. 3h). The C_{29}/C_{31} is positively: r = 52% (negatively: r = -63%) correlated (Pearson's correlation coefficient) with the semi-desertic (temperate Mediterranean forest) signals within this region over the same interval (Fig. 3c, d and h). Therefore, we note that the anticipated general interpretation of the C_{29}/C_{31} ratio as an indicator of the relative abundance of trees vs grasses does not hold for our datasets (indeed the reverse is evident). Instead, we tentatively infer that C_{29}/C_{31} ratio in this setting is expressing an adaptation of plants to aridity, and perhaps an increase in wind strength conditions, which alter the moisture balance. The n-alkanes of leaf waxes are produced to protect plants against the loss of water during the photosynthetic process (Post-Beittenmiller, 1996; Jetter et al., 2006). We could expect that arid/cold conditions to be more disturbing for woody plants than for grasses, as such the increase of the C_{29}/C_{31} during HS1 and YD, could suggest a climatic adaptation of woody plants by increasing the production of leaf wax C_{29}. However, the traditional taxonomic generalisation of C_{29} woody versus C_{31} grasses (Meyers, 2003), still needs some caution.

Other hypotheses to be explored and understood include the connection between the long-chain n-alkanes and the dynamic between C_3 and C_4 plants. Nowadays, African savannahs are dominated by C_4 plants, and biomarkers (including C_{31} n-alkanes) can be used to infer their presence in past landscapes (Dupont et al., 2019). Worldwide, 80% of Poaceae (grasses) and Cyperaceae (sedges) present a C_4 photosynthetic pathway (Sage, 2017) but with pollen analysis, there is no confidence about the Poaceae and Cyperaceae pollen morphologic types being exclusively or in its majority C_4 plants. We have grouped the Poaceae and the Cyperaceae pollen taxa, noting the inherent limitations of this grouping (Fig. 3g). This group (Poaceae + Cyperaceae) presents relatively high values with considerable oscillations (potentially related to differences in time resolution) between the LGM and the BA and more stable behaviour onwards. No particular correlation with other indicators (TMF or STE or C_{29}/C_{31}) was evident, apart from the apparent instability before the Holocene. Interestingly, within a laboratory setting, C_3 grasses are favoured in comparison with C_4 grasses, when temperatures increase by 5 to 15˚C with a pCO_2 of 200 ppm (Ehleringer et al., 1997; Edwards et al., 2010). Furthermore, C_4 plants nowadays are mostly confined to the tropical grasslands and savannahs; they are better adapted to environments with higher temperatures, aridity, poor nutrient soils, and intensive disturbance caused by animals or fire regimes (Bond et al., 2005; Edwards et al., 2010). Likewise, one should expect that in the Iberia after the LGM (Fig. 3 and 5) should be mainly composed by C_3 plants; considering the estimated SSTs indicating relatively cold temperatures (Fig. 5) and the high percentages of *Artemisia* (C_3 plant) (S.M. Fig. 1).

However, it is not currently possible to entirely rule out an increased importance of C_4 plants in the glacial vegetation in the IP, because pollen morphology does not allow the separation of these groups and biomarkers proxies have not been tested or reported to clarify the dynamic between C_3/C_4 plants in the Temperate/Mediterranean biomes. The discrimination of C_3/C_4 grasses has been made on the basis of stable isotopes of ancient grass pollen (Nelson et al., 2016) although the single grain isotopic measurements employed remain challenging to

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implement. This highlights the theoretical possibility of the C_3/C_4 plant dynamic observed in Africa (e.g. Dupont et al., 2019) and other savannahs ecosystems not being replicable (with the current knowledge) in our study area. Biomarker species/groups fingerprinting studies are required in order to eventually distinguish between C_3 and C_4 plants and then go onto exploring the dynamics observed between C_3 and C_4, within IP-Mediterranean ecosystems during the last deglaciation.

6. Conclusion

This study presents high-resolution pollen and SST records from Site U1385 which can be used in future regional and global reconstructions and models, especially for the Iberian Peninsula. A long-term analysis of climatic changes was comparable and consistent across the Iberian records analysed, with the advantage of the new record having an average higher resolution and a more robust radiocarbon chronology.

We explore the understanding of TMF dynamics under the influence of climatic change and increasing pCO_2 throughout the LGM and deglaciation. Our analysis suggests that forest development during the LGM may have been also constrained at least in part due to the low pCO_2, acting as a modulator. The baseline climatic conditions to support heathland development at present in the region are relatively similar to the ones required by some *Quercus* sp, however, trees development benefits from more warmth months (Polunin and Walters, 1984). During the LGM, the associated cold conditions and low seasonality together with the exacerbation of drought stress resulting from the low concentration of pCO_2 might have limited forest expansion. We speculate that certain traits of the Mediterranean Ericaceae, including small leaf size, thick cuticular waxes and deep rooting which contribute to drought tolerance at present may have promoted the development of heathlands during the LGM, as previously observed in African uplands. During HS1, woody plant development was further restricted by the impact of low temperatures as well aridity, under low pCO_2 and associated with wider climatic perturbation evidenced in freshwater pulses. The BA characterises the most suitable conditions for TMF development – warm, rising temperatures, moisture availability, amplification of seasonality, and the increase of pCO_2. The TMF persistence, and the forest–grassland mosaic, during the YD, can be best explained by the joint imprint of moisture availability and higher pCO_2. The role of pCO_2 was, in our opinion, fundamental for the significant TMF development during the late glacial in southwestern Iberia, by comparison with precedent cold intervals (LGM and HS1). Although other co-hypotheses must be better assessed, ideally against future development of independent (non-vegetation) proxies for precipitation and temperature during this time-slice, so far there are no regional reconstructions that consider the co-effect of moisture and pCO_2.

Considering the response of TMF and xerophytic taxa in our pollen record, we consider the pCO_2 value of ~225 ppmas a critical limit for forest expansion in the IP during the last deglaciation. This hypothesis should be explored through model simulations to establish the amplitude and critical thresholds of pCO_2 impacts on regional vegetation, as well as, in past cold periods.

The relation of C_3 and C_4 plants in the Mediterranean domain needs further attention since the long-chain *n*-alkanes do not yet provide a reliable picture to disentangle the dynamic between woody plants and grasses. We applied a biomarker proxy C_{29}/C_{31} which is positively correlated with the semi-desertic pollen curve and negatively with TMF. This points to its potential as a proxy of aridity, testifying the increase of leaf-wax C_{29} production during the dry periods, albeit in a regionally-specific way, and noting that this is not in agreement with previous inferences

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regarding the discrimination of herbaceous and arboreal taxa. Another suggestion is to test the C_{29}/C_{31} ratio for other periods in the past, throughout glacial periods.

Many global-scale LGM and deglacial reconstructions have been undertakenwith a preferential focus on the LGM and YD. An enhanced effort by the modelling community in developing transient regional simulations covering the last deglaciation may be valuable, to allow a more precise comparison/testing with proxy data. Our new data and regional pollen synthesis provide a good target for modelling. Furthermore, this study can provide a baseline understanding and essential context (potential analogue) for present-day world changes in arid and semi-arid ecosystems in terms of their potential future evolution under rapidly changing pCO_2.

Author contribution

SDG, WF, FN and AS contributed to the conception and design of the study, data analysis and interpretation. Also they were responsible for the grant application to NERC. SDG performed pollen analysis. TR performed biomarkers analysis. AR perfomed assemblage foraminifers picking for radiocarbon dating and draw figure 1. SDG prepared the original draft and wrote the manuscript including figures with the critical input (edition and revision) from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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Tables and figures

Table 1 – Radiocarbon ages of IODP Site U1385.

Lab code	Core Depth (crmcd)	Material	Conv. AMS ^{14}C (yr B.P.)	Error	Weighted mean deltaR
*20140801r9_MSGforam01_5ox	52	*G. bulloides*	2525	28	143
*20140801r5_MSGforam01_1ox	108	*G. bulloides*	6181	35	143
*20140801r6_MSGforam01_2ox	156	*G. bulloides*	10060	33	143
UCIAMS-219300	186	*G. bulloides*	11310	60	143
*20140801r7_MSGforam01_3ox	193	*G. bulloides*	11499	43	143
UCIAMS-219301	217	*G. bulloides*	12300	40	143
UCIAMS-219302	237	*G. bulloides*	13430	110	143
*20140801r8_MSGforam01_4ox	246	*G. bulloides*	13355	45	143
UCIAMS-219303	251	*G. bulloides*	13670	60	143
UCIAMS-219304	303	*G. bulloides*	15890	70	143
UCIAMS-219305	333	*G. bulloides*	17090	90	143

* AMS from Oliveira et al. (2018)

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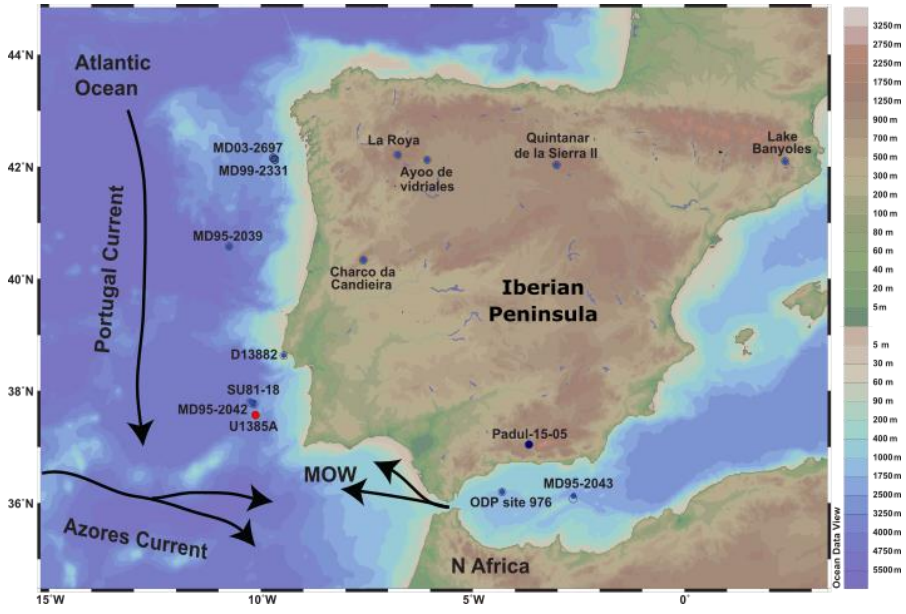

Figure 1 – Location of the IODP Site U1385 and of the marine and terrestrial pollen records discussed in the text. Marine sedimentary records: MD03-2697 (Naughton et al., 2016); MD99-2331 (Naughton et al., 2007); MD95-2039 (Roucoux et al., 2005); D13882 (Gomes et al., 2020); MD95-2043 (Fletcher and Sánchez Goñi, 2008); MD95-2042 (Chabaud et al., 2014); SU81-18 (Turon et al., 2003); ODP Site 976 (Comborieut Nebout et al., 1998; 2002; 2009); Continental sedimentary records: Lake de Banyoles (Pèrez-Obiol and Julià,1994); Quintanar de la Sierra II (Peñalba et al., 1997); La Roya (Allen et al., 1996); Ayoo de vidriales (Morales-Molino and Garcia-Anton, 2014); Charco da Candieira (Van der Knaap and van Leeuwen, 1997); Padul15-05 (Camuera et al., 2019). Black arrows represent the surface water circulation (MOW, Portugal and Azores Current). Note that coastline boundaries are for the present day.

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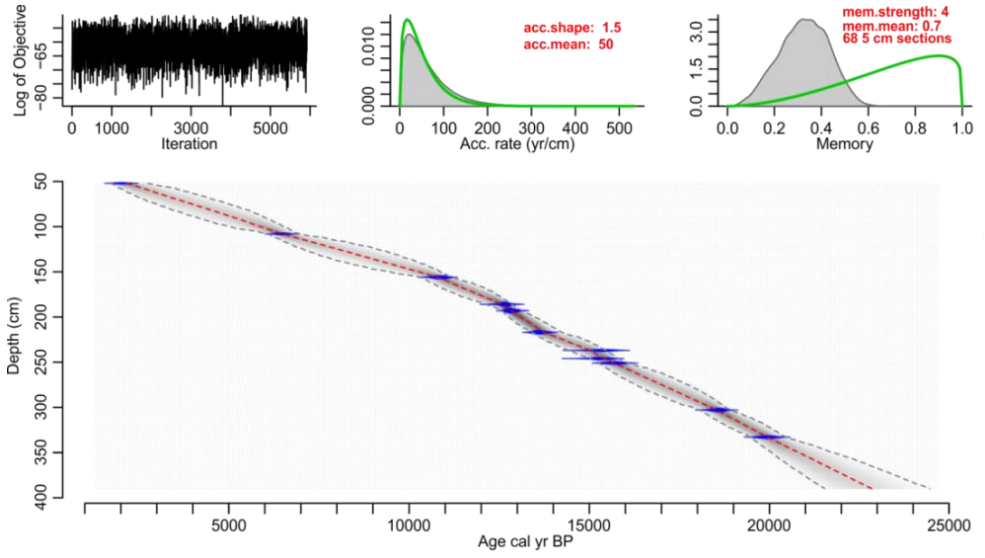

Figure 2 – Age-depth model for IODP Site U1385 using a Bayesian approach with Bacon v.2.3.5 (Blaauw and Christen, 2011). The original dates were calibrated using Marine 13.14c (Reimer et al., 2013) grey stippled line show 95% confidence intervals; red curve shows single "best" model based on the mean age for each depth. Upper graphs show from left to right: Markov Chain Monte Carlo (MCMC) iterations and priors (green line) and posteriors (dark grey line with a grey fill) for the accumulation rate and variability/memory. Note: the depth (Y axis) was converted to cm from the corrected revised meter composite depth (crmcd).

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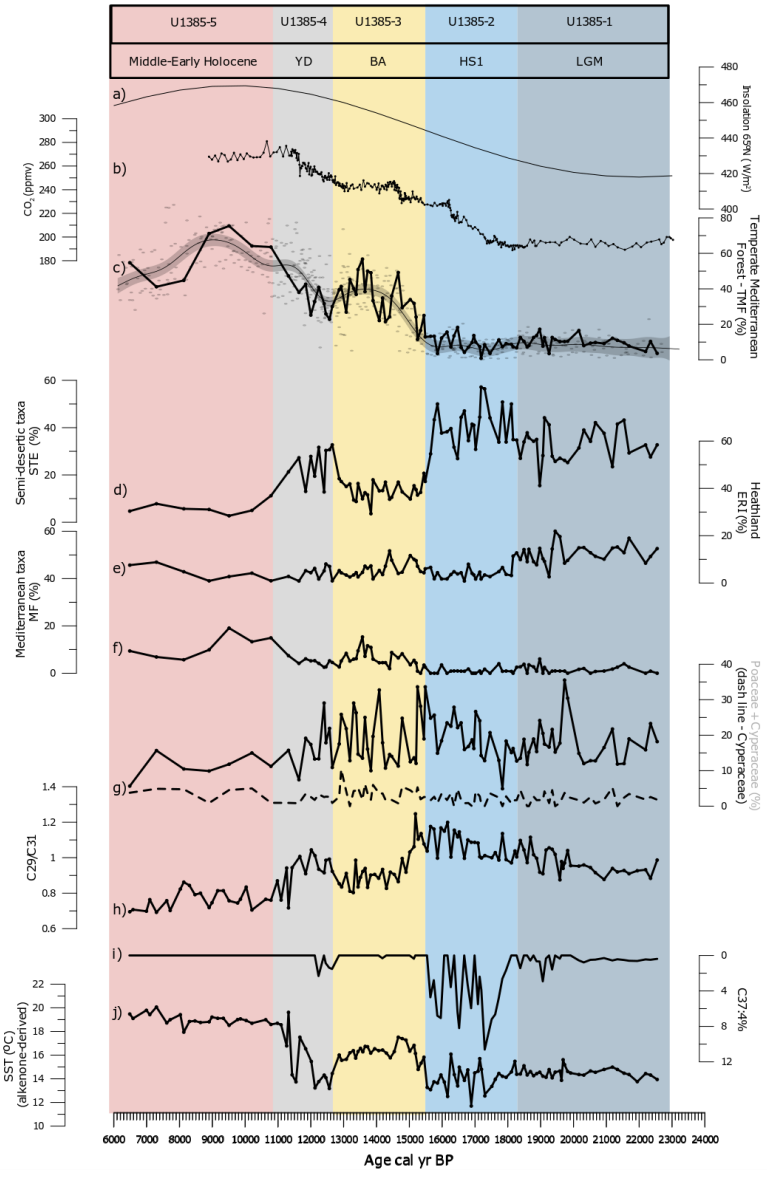

Figure 3 – Comparison of multiproxy records from the Site U1385 with 65˚N July (W/m^2) summer insolation (Berger and Loutre, 1991) and CO2 composite from WAIS (Marcott et al., 2014) ; b) CO_2 (ppmv); Principal pollen-based ecological groups: c) Temperate Mediterranean Forest (%) (solid black line) and Compilation of Iberian Margin TMF records (D13882, MD03-2697; MD95-2042; MD95-2043; ODP-976; U1385) – GAM (curve with grey (%), d) Semi-desertic taxa (%), e) Heathland (%), f) Mediterranean taxa (%) and g) Poaceae + Cyperaceae (%, dash line); h) C_{29}/C_{31} ratio, i) $C_{37:4}$ (%) and j) SST (°C). The different coloured shading corresponds to the pollen zones (SM Fig.1 and S.M. Table 1) and were connected with the periods indicated.

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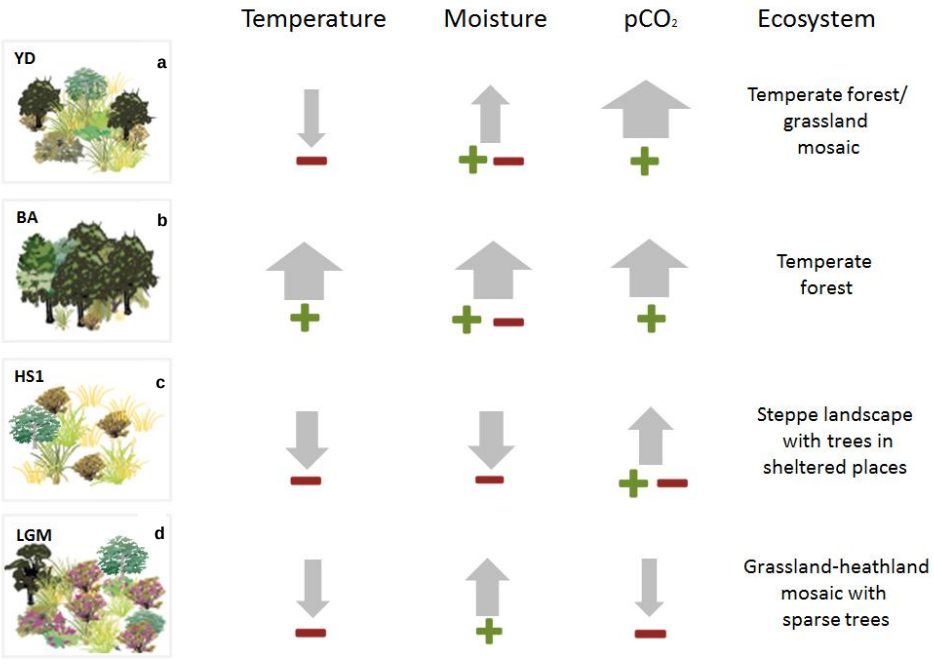

Figure 4 – Schematic representation of the influence of climatic parameters (precipitation and temperature) as well as the physiological contribution of CO2 for each period showing a schematic reconstruction of the ecosystem scenarios.

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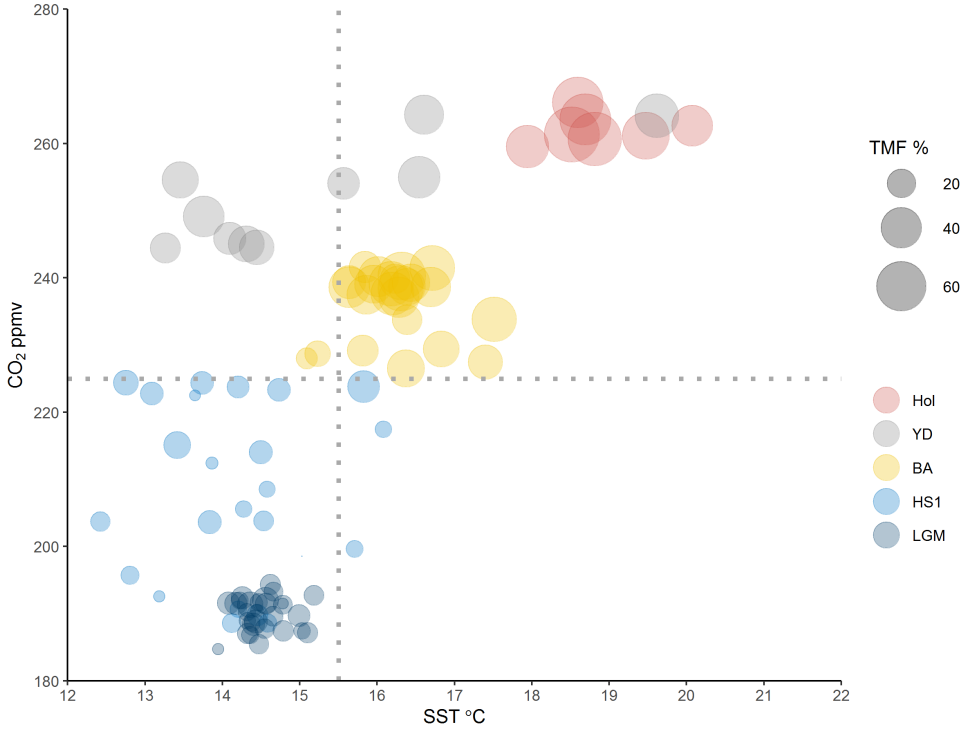

Figure 5 – Dispersion plot showing the relation between CO_2 (Marcott et al., 2014) and SST in relation to TMF % across the different intervals of the deglaciation, following the pollen zones boundaries.