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 atmospheric partial pressure of carbon dioxide (pCO_2) increased substantially from ~180 to ~280 ppm, yet its impact on vegetation dynamics across this major climatic transition remains insufficiently understood. In particular, Iberian pollen records reveal an intriguing feature that can be related to an often overlooked role of pCO_2 in shaping vegetation responses during the last deglaciation. These records reveal the near disappearance of forests during the cold Last Glacial Maximum (LGM) and Heinrich Stadial 1 (HS1) phases and an unexpected recovery during the Younger Dryas (YD) cold phase when pCO_2 increased. Here, we present high-resolution tracers 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) conditions from the southwestern (SW) Iberian margin Integrated Ocean Drilling Program Site U1385 ("Shackleton site") for the last 22 cal. kyr~~a~~ BP. This direct land-sea comparison approach allows us to investigate how the Iberian Peninsula vegetation responded to major global pCO_2 changes during the last deglaciation.
Our results show that cool and moderately humid conditions of the LGM supported a grassland-heathland mosaic ecosystem, but low pCO_2 likely caused physiological drought and suppressed forest development. HS1, the coldest and most arid period, combined with sustained low pCO_2 values almost suppressed~~s~~ forest growth in favour of Mediterranean steppe. In contrast, the warmer Bølling-Allerød, characterised by a temperature optimum and variable but generally wetter conditions, along with the rising of pCO_2 above 225 ppm at ~15 cal. kyr~~a~~ BP, contributed to substantial forest development. During the YD, sufficient moisture combined with increasing pCO_2 enabled~~allowed~~ the persistence~~persistance~~ of a mixed grassland-forest mosaic despite cooler temperatures. Our study suggests that during cool and humid~~low pCO_2~~ periods (LGM and YD) ~~and HS1), the role of~~ different pCO_2 values lead to contrasting~~onvalues shapon~~ SW Iberian vegetation responses~~dynamics was more pronounced compared to periods of higher pCO2~~. In contrast, during periods of relatively high pCO2, ~~t~~Ttemperature and precipitation ~~changes during periods of relatively high pCO2~~ played the main role in shaping the distribution and composition of the vegetation.

Keywords:
Iberian margin; Deglaciation; Last Glacial Maximum; Direct land-sea comparison; Climatic parameters vs pCO_2; Forest development; Pollen analysis

1. Introduction

The last deglaciation, spanning 20-19 cal. kyr~~a~~ BP (e.g. Denton et al., 1981; Toucanne et al., 2008; Denton, 2010) to ~7 cal. k~~a~~yr BP (e.g. Dyke and Prest, 1987; Carlson et al., 2008) was marked by a global annual mean surface air temperature increase of 5°C ~~a global mean temperature increase of ~5°C~~, ~~depending on latitude~~ (Annan et al., 2022) ~~Bard et al., 1987; Alley and Clark, 1999; Clark et al., 2012~~), driving~~during~~ progressive melting of Northern Hemisphere glaciers. This interval was interrupted by an alternation of cold and warm phases: the warmer Bølling-Allerød (BA, 15-12.5 cal. kyr~~a~~ BP) was bracketed by two major cold phases, ~~the~~ Heinrich Stadial 1 (HS1, 18.5-15 cal. kyr~~a~~ BP) and the Younger Dryas (YD, 12.9 - 11.6 cal. k~~a~~yr BP), particularly in the North Atlantic region. This period was also characterized by an increase in atmospheric carbon dioxide ~~(pCO_2)~~ concentration~~s~~ (pCO_2) from ~180 to ~280 ppmv (Monnin et al., 2001; Shakun et al., 2012; Marcott et al., 2014), one of the largest shifts of the last 800,000 years (Lüthi et al., 2008). This rise was not gradual, rather there were three main rapid (<200 years) pCO_2 rises, of ~10 to 15 ppmv, at the end of HS1, within the BA and at the onset of the YD, as recorded in the West Antarctic Ice Sheet Divide ice core (Marcott et al., 2014). ~~Based on a direct comparison between terrestrial and marine climatic indicators from the SW Iberian margin sedimentary sequences, several works focused on the mechanisms underlying the regional atmospheric and oceanic responses to the last deglaciation (Boessenkool et al., 2001; Turon et al., 2003; Chabaud et al., 2014; Oliveira et al., 2018; Naughton et al., 2019; Cutmore et al., 2021). However, few of these records span the entire deglaciation, or offer resolution or chronological precision to detect short-term vegetation and climate shifts in detail. The high temporal resolution and robust chronology of IODP Site U1385, provide a valuable opportunity to evaluate vegetation response to climate and pCO_2 changes in SW Iberia during this transitional period.~~

~~The role of pCO_2 throughout time as a climate driver remains intensely debated. Studies suggest the pCO_2 acted as (1) a primary driver of the climatic changes, leading to temperature changeschnages in the Northern Hemisphere (Shakun et al., 2012; Marcott et al., 2014); (2) a climate amplifier, reinforcing warming that began through other processes (Alley and Clark, 1999; Clark et al., 2012); or (3) as a consequence of climate change, responding to temperature shifts rather than causing them (Denton et al., 2010).~~

Beyond its role in shaping global climate, pCO_2 directly influences plant physiology and the nature of~~how~~ vegetation respon~~d~~ses to environmental change. The annual atmospheric-biospheric exchange of pCO_2 from ~~between the atmosphere and biosphere due to~~ photosynthetic activity is~~corresponds to~~ more than one-third of the total ~~pCO_2~~ stored in the atmosphere (Farquhar and Lloyd, 1993). A~~During photosynthesis, a~~tmospheric pCO_2 plays a critical role in plant physiology; plants absorb ~~p~~CO_2 through their stomata (~~, which are~~ small leaf pores)~~,~~ and lose~~ing~~ water. At lower pCO_2, such as during glacial periods, plants must open these pores wider or increase their number to capture enough ~~p~~CO_2 (Royer et al., 2001), which ~~. While this~~whilst enhancing~~es~~ gas exchange, ~~it~~ also increases ~~leads to greater~~ water loss through transpiration, reducing water-use efficiency (WUE) and~~,~~ inducing physiological drought stress, even under moderate climatic conditions (Street-Perrot et al., 1997; Körner, 2000). ~~These effects are especially pronounced in semi-arid environments. , where water limitation already constrains plant growth.~~ **P~~This p~~lasticity in stomatal conductance and density~~frequency~~ is considered an adaptive trait that evolved under declining Cenozoic CO_2 levels, enabling plants to sustain carbon uptake as concentrations approached glacial minima (~180–190 ppmv), though at the cost of greater water loss (Wagner et al., 1997).** These effects are especially pronounced in semi-arid environments. Under low pCO_2 conditions, species better adapted to drought and nutrient stress - ~~—~~such as those typical of steppes - ~~—~~are more likely to dominate, and are typically observed in colder periods. Conversely, higher pCO_2 ~~levels~~ promotes forest expansion and higher plant productivity, particularly in trees that benefit from improved WUE (Huang et al., 2007; Randall et al., 2013). However, the response to pCO_2 is not globally uniform, with differences in water and nutrient availability, alongside other environmental constraints, mediating the response (e.g. Tognetti et al., 2008).~~.~~

While many reconstructions of past vegetation focus only on temperature and precipitation, the importance of pCO_2 as a limiting factor in plant productivity, coverage, and WUE is now widely supported by both empirical and model-based studies (e.g. Cowling and Sykes, 1999; Harrison and Prentice, 2003; Claussen et al., 2013; Piao et al., 2020).
~~Variations in pCO_2 not only affect plant physiological function but can also influence the composition and structure of vegetation communities. Under low pCO_2 conditions, species better adapted to drought and nutrient stress—such as those typical of steppes—are more likely to dominate, and typically are observed in colder periods. Conversely, higher pCO_2 levels promote forest expansion and higher plant productivity, particularly in trees that benefit from improved WUE (Huang et al., 2007; Randall et al., 2013). However, the response to CO_2 is not globally uniform. Regional differences in water and nutrient availability, along with other environmental constraints, mediate how vegetation responds to pCO_2 shifts (e.g. Tognetti et al., 2008).~~ The BIOME4 model and a biome-scale reconstruction compiled from pollen records covering the last 40,000 kyr across the Northern Hemisphere (> 30°N) reveal a level of

unexplained variability in vegetation patterns across both space and time (Cao et al., 2019), and provide key insights into other factors than temperature, precipitation and potential evapotranspiration that drive changes in vegetation dynamics and composition, such as pCO_2 (Ludwig et al., 2018; Cao et al., 2019). Similarly, ~~Recent~~ coupled vegetation-climate modelling and multiproxy reconstructions ~~have~~ demonstrate~~d~~ that pCO_2 significantly impacts regional vegetation extent and productivity across glacial-interglacial transitions (Wu et al., 2007; Wei et al., 2021; Koutsodendris et al., 2023; Clément et al., 2024). These findings underscore the need to include pCO_2 changes when interpreting pollen data or evaluating biome shifts (Prentice et al., 2017; Cao et al., 2019). While ~~the~~ current-day pCO_2 fertilization ~~has~~ receive~~d~~s considerable attention (e.g. Piao et al., 2020), studying~~ies focusing on~~ the effects of low pCO_2, and ~~major on vegetation, or~~ major transitions from low to high pCO_2, are equally critical.

~~Last deglaciation vegetation changes have been widely studied across the Iberian Peninsula from palaeoecological records (e.g. Peyron et al., 1998; Carrión et al., 2002; Chabaud et al., 2014; 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) and, alongside ecological niche modeling (Casas-Gallego et al., 2025), are traditionally interpreted as a result of the combined effects of temperature, precipitation and evaporation changes. However, g~~

Growing evidence shows that many climate reconstructions for glacial periods based on vegetation records may be biased as they neglect the influence of low pCO_2 on WUE. Neglecting this influence may contribute to the 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; Izumi and Bartlein, 2016; Chevalier et al., 2021), a concern still highlighted by recent studies (e.g. Wei et al., 2021; Prentice et al., 2022). ~~To address pCO_2-related biases, inverse modelling studies to account for CO_2 correction have been evolving for a while (e.g. Guiot et al., 2000; 2007; Wu et al., 2007; Izumi and Bartlein, 2016) and compared with reconstructions using Modern Analogue Techniques (Davis et al., 2024). However, the inverse modelling approach has some limitations relating to low taxonomic resolution and dependence on the vegetation model that is not always comparable with pollen assemblages (Chevalier et al., 2020; Prentice et al., 2022). Recently, Qquantitative reconstructions using methods like Tolerance Weighted Averaging Partial Least Squares show that pCO_2 constraints on plant growth can make glacial conditions appear drier than they likely were (Wei et al., 2021).~~ By contrast, under interglacial conditions with higher pCO_2 levels, model experiments suggest that forest expansion in SW Iberia is mostly controlled by precipitation rather than by pCO_2 levels (Oliveira et al., 2018; 2020).

~~Despite these advances, there is a need for additional region-based palaeoecological research. This need was highlighted in a recent model-data comparison using the BIOME4 model and a biome-scale reconstruction compiled from pollen records across the Northern Hemisphere (> 30°N), 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 factors other than temperature, precipitation and potential evapotranspiration that drive changes in vegetation dynamics and composition, such as pCO_2 (Ludwig et al., 2018; Cao et al., 2019).~~

Recognising the role of pCO_2 is crucial,~~a key issue~~ not only to interpret the drivers of past ecosystems accurately, but also for anticipating how semi-arid landscapes - particularly in the Iberian Peninsula and Mediterranean region, which are~~is~~ predicted to experience significantly increased aridity - will respond to ongoing climate change. The terrestrial and marine climatic

indicators from the SW Iberian margin sedimentary sequences provide an extremely valuable record of environmental change, and last deglaciation vegetation changes have been widely studied here using palaeoecological records (e.g. Peyron et al., 1998; Carrión et al., 2002; Chabaud et al., 2014; 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) and ecological niche modeling (Casas-Gallego et al., 2025). However, these are traditionally interpreted as a result of the combined effects of temperature, precipitation and evaporation changes, rather than ~~the role of~~ pCO_2. Furthermore, few of the existing records span the entire deglaciation, or offer resolution or chronological precision to detect short-term vegetation and climate shifts in detail.~~, and mainly focus on the mechanisms underlying the regional atmospheric and oceanic responses to the last deglaciation. to anticipate the future responses of semi-arid landscapes to ongoing climate change.~~

~~The~~

Here we present a new multiproxy study of IODP Site U1385 that allows a~~the~~ direct comparison between terrestrial and marine climatic indicators across the LGM and deglaciation at high (centennial-scale) temporal resolution. Hence, this record provides a~~, and therefore, the~~a detailed reconstruction of vegetation changes in SW Iberia along with sea surface temperature (SST) trends in its margin during the LGM, HS1, B-A and the YD. Our~~This~~ new paleoenvironmental record enables~~facenables~~ the ~~ilitates an will serve to~~ exploreation of the main factors driving forest development during the LGM and the last deglaciation, and an evaluation of~~e~~ ~~the~~ potential pCO_2 thresholds for western Mediterranean forest development.

2. Materials and environmental setting

[Figure 1]

IODP Site U1385 is a composite record of five 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 Promontório dos Príncipes 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 ~21.5 and 6.4 cal. kyr~~a~~ BP. The sediment supply, including pollen grains, to Site 1385 is mainly derived via fluvial transport from 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 (average ~22 °C in the warmest month~~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 (AEMET, 2011).

The present-day vegetation of southwestern Iberia reflects a transitional biogeographical zone between temperate and Mediterranean climates (Rivaz-Martinez et al., 2017). Coastal areas, influenced by oceanic humidity and milder winters, support thermophilous evergreen species such as *Quercus suber*, *Olea europaea* var. *sylvestris*, *Myrtus communis*, and *Pistacia lentiscus* (Asensi and Díez-Garretas et al., 2017). Inland, as elevation increases and oceanic

influence diminishes, Mesomediterranean forests dominate, composed of both evergreen (*Q. suber*, *Q. rotundifolia*, *Q. coccifera*) and deciduous oaks (*Q. faginea*, *Q. robur*), often combined with heathlands or aromatic scrublands (e.g. *Cistus* spp.). Distinctive oak–juniper woodlands appear in drier zones, and pine forests (*Pinus pinaster*, *P. pinea*) are common on sandy coastal soils. Riparian zones feature *Alnus glutinosa* and *Salix* spp., while widespread *Cistus* and *Erica* shrublands reflect the area's susceptibility to fire.

3. Methods

3.1. Chronological framework
[Table 1, Figure 2, Figure 3, SM Figure S1]

Sixteen 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 of these were ~~previously~~ published by Oliveira et al.~~,~~ (2018), based on monospecific *Globigerina bulloides* samples and analysed at the Vienna Environmental Research Accelerator (VERA), University of Vienna, Austria. A new set of eleven samples for AMS ^{14}C analysis was selected primarily from monospecific assemblages of *G. bulloides*. When sample size requirements could not be met, a mixed assemblage of *G. bulloides* and *G. inflata* was used. All samples were processed at the Keck Carbon Cycle AMS Facility, University of California, Irvine (Table 1). ~~A new set of eleven samples for AMS 14C was selected primarly from monospecific foraminifer samples of G. bulloides, when not enoughand a mixed assemblage of G. bulloides and G. inflata was processed at the Keck Carbon Cycle AMS Facility, University of California, Irvine (Table 1)~~. The new age model, using solely the available radiocarbon dates for sedimentary record U1385 without any tuning, was calculated using a Bayesian approach through the software Bacon implemented in R (Blaauw and Christen, 2011; R Development Core Team, 2020) using the Marine20 calibration curve (Heaton et al., 2020). The studied interval encompasses the period from ~22 to 6 ka, as shown by the radiocarbon age model (Fig. 2). The average temporal resolution for the pollen and organic biomarkers across the deglaciation is 110 and 104 years, respectively, or slightly lower (174 and 135 years, respectively) when including the Holocene section (Fig. 3 and SM Fig. S1).

3.2. Pollen analysis

A total of 97 samples (including 25 ~~previously~~ published by Oliveira et al., 2018) were analysed from 3.84 to 1.08 crmcd in Hole A, and prepared at the University of Bordeaux, France, using the standard protocol of the UMR EPOC laboratory (Georget et al., 2025). The sediment was firstly separated using coarse sieving at 150 µm, retaining the fine fraction. A sequence of chemical treatments, starting with cold HCl (hydrochloric acid) at increasing concentrations (10%, 25%, 50%), eliminated calcium carbonate particles. Followed by cold HF (hydrofluoric acid) at increasing strength (45% and 70%) to eliminate the 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 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), photographic atlases (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. ~~Aquatic plants were excluded because their abundant and local pollen comes from water bodies and can be transported far from where it grew, while Pinus and spores were excluded because their lightweight pollen wind transported may overrepresent regional vegetation. In pollen analysis, we generally excluded aquatic plants because they produce large amounts of pollen that can be carried far from water bodies, and thus do not reliably reflect local vegetation. Pinus and spores were excluded because their lightweight pollen can travel long distances, overrepresenting regional rather than local plants.~~The pollen percentages are calculated against the main pollen sum; but the percentages of over-represented taxa were calculated on the basis of the main sum plus the counts for that particular individual taxon; for example: 100 * *Pinus* / (Main sum + *Pinus*) and 100* *Cedrus* / (main sum + *Cedrus*). Aquatic plants and spores were excluded because their abundant pollen originates in or near water bodies and can be transported far from their source, potentially overrepresenting regional vegetation. *Pinus* pollen, which is typically overrepresented in marine deposits, is transported by rivers from the Tagus and Sado's watersheds (Naughton et al., 2007). In contrast, the overrepresented *Cedrus* is transported by wind from the Atlas or Rif mountains in Morocco, were also excluded from the main sum.~~Aquatic plants and spores were excluded because their abundant pollen originates close or in water bodies and can be transported far from where they grew, and may overrepresent regional vegetation. Pinus pollen is generally overrepresented in marine deposits and therefore excluded from the main sum (Naughton et al., 2007). Cedrus, being an exotic component transported by wind from the Atlas or Rif mountain chains (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 determined the five statistically significant pollen assemblage zones (U1385-1 to 5 in Fig. 3, SM Fig.1 and Table S1) based on a dissimilarity matrix of Euclidean distances with pollen taxa ≥ 1% (Grimm, 1987; Bennet et al., 2009).

In addition to ~~the~~ pollen-based ecological groups, we calculated the sum of Poaceae and Cyperaceae (Fig. 3g), to check the potential importance of C4 plants in the Iberian Peninsula. While most of the present-day Poaceae and Cyperaceae in this region chiefly belong~~s~~ to the C3 photosynthetic-pathway plant type~~plants type~~ (Casas-Gallego et al., 2025), it is possible that C4 pathway plants were more important at other moments in recent Earth history. Pollen analysis is a core method in palaeoclimatology and palaeoecology, used to assess past climate conditions based on the ecological affinities of specific taxa grouped into pollen-based ecological groups. These groups reflect present-day vegetation–climate relationships, allowing inferences about dry, cold, warm, or moist conditions. As such, our pollen data reflect ecological responses rather than absolute quantitative climate parameters (Williams et al., 2001). A pollen diagram with clustering analysed (SM Fig. S1) was produced revealing four main episodes over the LGM and the Last deglaciation (Fig. 3, further details in SM Table S1).

3.3. Compilation of Iberian margin pollen records

In order to assess vegetation and climate changes more widely in the Iberian Peninsula region across the LGM and last deglaciation, we compiled available marine records along the Iberian margin covering the period from 23 to 6 cal.kyr BP~~ka~~. Pollen count datasets from eight marine 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 – Combourieu ~~Comborieut~~ Nebout et al., 1998; 2002; 2009; SU81-18 Turon et al., 2003; Site U1385 – this study) were used with the original published chronologies, without any additional alignment or synchronization. Pollen percentages were recalculated against the main pollen sum. A uniform calculation of the pollen-based ecological group TMF (Temperate and Mediterranean forest) 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 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 used~~fitted the model using~~ a standard GAM with REML smoothness selection, specifying ~~with~~ 30 basis functions (*k*=30) and a smoothing parameter of 0.0001 (*sp*=0.0001). The relatively high K allowed the model to capture potential nonlinear patterns in the data without overfitting, while the small *sp* ensured sufficient smoothness; these values were chosen after exploratory analysis and diagnostic checks. To assess~~check~~ the validity of the smooth terms and confirm that the~~if the used~~ basis functions adequately captured the data wiggliness, we applied ~~a test using~~ the *gam.check*() function of the *mgcv* package. The resulting *k-index* was greater~~obtained higher~~ than 1, and the *p-value* supported the hypothesis that ~~in both cases,~~ enough basis~~n~~ functions were used. The~~curve shows the~~ fitted GAMs curves for TMF are presented~~,~~ along with ~~an~~ approximate 95% confidence intervals (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 (Villanueva et al.,1997; 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. Villanueva and Grimalt, 1997; Rodrigues et al., 2017). The $U^{k'}_{37}$ index (Prahl and Wakeman, 1987) was converted to temperature~~s~~ values using the global calibration equation defined by Müller et al.~~,~~ (1998) with an analytical uncertainty of 0.5ºC (Grimalt et al., 2001). Nevertheless, uncertainties remain, since $U^{k'}_{37}$ SST reconstructions may be affected by calibration biases, seasonal and ecological effects related to coccolithophorid production, and potential lateral transport or diagenetic alteration of alkenones (e.g. Conte et al., 2006; Ausín et al., 2022). As such, the derived SSTs should be regarded as robust indicators of large-scale SST trends. 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 and~~vs~~ grasses plants of the adjacent continent (Cranwell 1973, Tareq et al., 2005, Bush et al., 2013; Struck et al., 2020). This relation encompasses the adaptation of plants~~,~~ by increasing the production of~~ leaf wax~~ long~~-~~chain leaf wax~~ production~~, which~~to~~ reduces water loss during the photosynthetic processes and prevents~~prevent~~ desiccation promoted by harsh winds or more arid conditions (Bush and McInerney, 2013). Index values >1 are typically considered to reflect higher quantities of C_{29} *n*-alkanes produced by trees and shrubs, ~~-~~while values <1 are generally considered to indicate higher quantities of C_{31} *n*-alkanes by grasses and herbaceous plants (Cranwell, 1973; Rodrigues et al., 2009; Ortiz et al., 2010~~;~~). However, the interpretation of this index may vary across biomes and depend~~ dependent~~ on source vegetation types~~-~~, and depositional processes (Carr et al., 2014; Diefendorf and Freimuth, 2017).

4. Results and discussion

[Figure 4, Figure 5, Table S1, SM Figure S2]

4.1. 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~~ variations in~~of~~ the main climatic parameters (temperature, precipitation), we hypothesise that changes in pCO_2 played an essential role in vegetation change, specifically in the deglacial forest expansion. Here, we evaluate the drivers of vegetation change by explicitly considering the evolution of pCO_2 through the deglaciation. Our discussion is supported by the present-day environmental and climatic space, considering the temperature and precipitation in which different taxa exist in the Iberian Peninsula and characterising the TMF – *Quercus* sp., the Heathland (ERI) - Ericaceae family and the semi-desert (STE) landscapes (SM Fig. S2).

4.1.1. Last Glacial Maximum (LGM, 23-19 cal. kyr BP)

The pollen-based vegetation record from Site U1385 shows that during the LGM (pollen zone U1385-1: 21500 – 17990 cal. yr BP, SM Fig. S1) a grassland–heathland mosaic dominated the landscape, with semi-desert taxa (STE, ~40%) and heathland taxa (ERI, ~10–20%) (Fig. 3d, e; Fig. 4d), forming a distinctive non-analogue glacial vegetation cover.

~~-~~The prevalence of heath (*Erica* spp.) in Iberian pollen records underpins the classic view of the LGM in Iberia as a fairly humid interval, certainly compared with the extreme aridity of Heinrich stadials (Roucoux et al., 2005; Naughton et al., 2007; Fletcher and Sánchez-Goñi, 2008; Combourieu-Nebout et al., 2009; Sánchez-Goñi et al., 2009).

Nevertheless, the signals for moisture availability are somewhat complex~~there is a somewhat complex picture with respect to the prevailing moisture availability for vegetation during this interval~~. Semi-desert taxa, typically found in arid conditions, are abundant, while heathland taxa, associated with more humid environments, reach their maximum in the record (Fig. 3; SM Fig. S2c). Forest taxa ~~we~~are represented in low percentages (5-15%) (Fig. 3c), suggesting

cold and relatively dry conditions over the continent. The TMF values are consistent throughout the~~troughoutacross the~~ U1385 record and GAM-fitting to the data compilation (Fig. 3c). Similiar patterns are observed~~, being consistently observed~~ across the marine records in southerly locations off the Iberian Peninsula (MD95-2043 - Fletcher and Sánchez Goñi, 2008 and ODP Site 976 - Combourieu ~~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 Iberian Peninsula (MD99-2331 and MD03-2697- Naughton et al., 2007; 2016). Interestingly, the modern 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 (SM Fig. S2b). 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? A possible explanation could be associated with cold atmospheric temperatures (SST~~'~~s average~~SST´s average~~ ~14.5ºC, Fig. 3j), 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). Hence, in addition to temperature, the lowest~~est~~ levels of pCO_2 during the LGM (~~ranging between~~ 180-190 ppmv), could have been another important controlling factor, as they rank among ~~which are among~~ 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 conditions and for LGM pCO_2 (185 ppm), showing qualitative differences in the distribution of vegetation types (Shao et al., 2018). Under low pCO_2, grasslands were favoured to the detriment of evergreen broadleaf, evergreen and deciduous needle leaf forest. This study, however, did not include 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.

At the same time, the LGM coincides with a precession maximum, a configuration recognised to reduce seasonal contrasts (i.e., reduced summer dryness) and thus favour heathland development in the Iberian Peninsula, as documented in both glacial and interglacial contexts, including the Middle to Late Holocene (Fletcher and Sánchez Goñi, 2008; Sánchez Goñi et al., 2008; Margari et al., 2014; Oliveira et al., 2017, 2018; Chabaud et al., 2014; Gomes et al., 2020).~~At the same time, the we note that the LGM corresponds to a maximum in the precession cycle, which is recognised to promote a weakening of seasonal contrasts (reduced summer dryness) favourable for heathland development in the Iberian Peninsula (Fletcher and Sánchez-Goñi , 2008; Sánchez-Goñi et al., 2008; Margari et al.,. 2014), in both glacials and interglacials (e.g. Oliveira et al., 2017), including the Middle to Late Holocene (Chabaud et al., 2014; Oliveira et al., 2018; Gomes et al., 2020).~~ Furthermore, heathland ecosystems thrive on acidic, low-nutrient soils, which can develop as a result of altered hydrological cycles during precession maxima. The ecological advantages of *Erica* also include less demanding edaphic requirements (low nutrient demand), more competitive re-sprouting strategy after disturbance, including fires, as well as a higher dispersal capacity compared with *Quercus* sp. for example (Pausas, 2008). However, these observations do not rule out a key impact of low pCO_2~~2~~ on vegetation composition during the LGM.

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; Izumi and Bartlein, 2016; Shao et al., 2018). However, 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 t~~hought 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 model 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 BIOMEE3~~OD~~ 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 replace 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* spp.).

Long-term studies considering CO_2 limitations on vegetation contrast in their perspectives; Gosling et al.~~,~~ (2022) argue that during the last 500 kyr, precipitation and fire exert the main controls on woody cover in tropical Africa while CO_2 effects were relatively small. In Asia, Clément et al.~~,~~ (2024) also emphasize the role of precipitation as the driver of vegetation distribution during interglacials, and that vegetation is not sensitive to CO_2 above 250 ppmv (value characterizing most of the interglacials); however, during glacial CO_2 conditions (<~185 ppmv), CO_2 is an important factor, favouring the increase of C_4 plants. 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). A similar impact is evident in the Last Glacial moisture reconstruction based on the pollen record of El Cañizar de Villarquemado in eastern Iberia;~~,~~ including a correction for the direct physiological effects of low pCO_2, yields a wetter reconstruction of glacial climate (Wei et al., 2021). The implications of these experiments are important for the SW Iberian region and may help to solve the~~solveresolve 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 summers under LGM pCO_2, instead of the colder conditions simulated with present-day levels of CO_2 (Guiot et al., 2000). In Europe, pollen reconstruction with steppe vegetation indicated warmer winter temperatures for LGM pCO_2 compared with the modern pCO_2~~-~~ (Wu et al., 2007). The bias could extend to simulations of glacial vegetation; 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), and to our knowledge no experimental work currently tests forest development under such low values. However, modelling approaches indicate that in C_3 plants,

photosynthetic capacity declines sharply once atmospheric CO_2 falls below ~300 ppmv, making carbon assimilation increasingly limiting for plant growth (Wagner et al., 1997). When we assess the relationship between pCO_2, SST and TMF across the LGM and deglaciation events we observe that the LGM (i) corresponds to SSTs below 15.5°C and pCO_2 below 225 ppmv, and (ii) that TMF values remain below 20% (Fig. 5). In African mountain environments, a pCO_2 threshold of approximately 220 ppmv has been suggested as the minimum above which forests could develop (Dupont et al., 2019). These results suggest that~~Therefore,~~ extremely low pCO_2 below a critical threshold of ~220-225 ppmv, played an important role in limiting~~may have been the critical determinant of low~~ forest development during~~in~~ the LGM. However, we emphasize that such thresholds should not be considered universal, as they may depend on plant taxa, edaphic conditions and microclimate. Nevertheless, these~~These pCO_2 threshold~~ values, despite differences in baseline conditions such as insolation, are broadly consistent with other time intervals where Mediterranean forest expansion occurred, for example during MIS_13 at ~216 ppmv (Oliveira et al., 2020) and MIS_18 at ~215 ppmv under relatively high temperatures and increased winter rainfall (Sánchez-Goñi et al., 2023). Temperatures during the LGM in SW~~southwestern~~ Iberia may have been sufficiently mild for forest development with sea surface temperatures of ~15.5 °C (Fig. 3j) aligned with the broader threshold for forest development (Sánchez-Goñi et al., 2008). For this reason, one could speculate that a hypothetical increase in pCO_2 above the observed critical threshold during the LGM could have permitted forest development in SW~~southwestern~~ Iberia. Thus, while uncertainties remain, the convergence of multiple lines of evidence supports a key role for low pCO_2 in constraining forest development specially during glacial periods.

4.1.2. Heinrich Stadial 1 (HS1, 18.5-15 cal. kyr BP)

During HS1 (Pollen zone U1385-2: 17990 – 15230 cal. yr BP, SM Fig. S1), a Mediterranean steppe landscape (Fig. 3d) with minimum arboreal development (Fig. 3c) corresponded to the lowest SSTs of the record (SST~12ºC, Fig. 3j).

The dominance of semi-desert taxa and minimum TMF (Fig. 3 and 5c) indicate the~~, and~~ highest levels of aridity~~ are suggested by the maximum of semi-desert taxa and minimum TMF (Fig. 3 and 5c)~~. Additionally, high $C_{37:4}$ alkenone values (~8.2%, Fig. 3i) reflect major meltwater pulses, associated with severe cooling in the North Atlantic during ~~extreme cold conditions were recorded of~~ HS1~~ in the Atlantic Ocean~~. Vegetation signals reinforce this picture of moisture stress. A sharp decrease in ~~The notable decrease in~~ heaths (ERI, Fig.3e) and aquatic taxa such as *Isoetes* ~~as well as terrestrial marshes and wetlands (decrease in *Isoetes* undiff.)~~ (SM Table S1 and SM Fig. S1) suggests significant drying of terrestrial marshes and wetlands~~further supports~~s increased moisture stress (SM Table S1 and SM Fig. S1)~~. The dominance of STE during HS1 is consistent with records across the~~ majority of the~~ Iberian Peninsula ~~records~~ (Roucoux et al., 2005; Naughton et al., 2007; 2016; MD95-2043 - Fletcher and Sánchez Goñi, 2008; ODP Site 976 -~~–~~ Combourieu ~~Comborieut~~ Nebout et al., 2002), and is reflected also in a~~the~~ long-term minimum in reconstructed~~modelled~~ forest levels (Fig. 3c).

Throughout HS1, despite the gradual ~~the potential effect of~~ increase~~ing~~ of pCO_2 ~~(~~from ~185 to ~225 ppm between~~) from~~ 18.1 to ~16 cal kyr~~a~~ BP (Fig. 3b), this rise was insufficient~~not enough~~ to counteract the limiting effects of extreme cold and arid~~ity~~~~dry atmospheric conditions~~. Simulations with the~~Regional models -~~ Weather and Research Forecast m~~M~~odel that incorporate~~ simulating~~ ~~the potential vegetation with~~ a pCO_2 correction show a reduction in arboreal vegetation and an expansion~~increase~~ of sparsely vegetated soils across~~for the~~ Iberian region during HS1 compared with the LGM (Ludwig et al., 2018). The simulated

precipitation values for SW Iberia (Tagus hydrographic basin catchment), remain~~show values~~ below 700 mm/yr for HS1, which agrees with the pollen evidence for widespread semi-desert taxa~~ development~~.

Interestingly, the differences between HS1 and LGM concerning temperature, precipitation and pCO_{2}~~2~~ are quite relevant. While pCO_2 levels rose modestly, the climatic extremes of HS1 - marked by severe cooling and aridity - likely drove the observed loss of heathland and constrained forest development across the peninsula. ~~The climatic extremes of HS1, despite rising pCO2, were most likely responsible for the loss of heathland following the LGM.~~ 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 shows scattered values of TMF (below 20%) occurring at SST below 15.5°C and pCO_2 below 225 ppmv (Fig. 5), underscoring the combined climatic and physiological constraints on forest expansion.~~.~~

4.1.3. Bølling-Allerød~~BA~~ (BA, 15-12.5 cal. kyr BP)

The BA (Pollen zone U1385-3: 15230 – 12780 cal. yr BP; SM Fig. S1) had generally more ~~wereas characterised broadly by~~ favourable climatic conditions (higher temperatures, higher moisture availability) for TMF development (Fig. 3c) including a minor increase in thermophilous Mediterranean elements (Fig. 3c and f) and a reduction of STE (Fig. 3d). The combination of warming (SST above 16°C, Fig. 3 j) and a dry to wet trend are likely the primary drivers of progressive forest development during the BA. Additionally, the increase of pCO_2 from ~230 to 245 ppmv should have promoted a ~~–~~"fertilisation effect" during this time interval (Fig. 3b). ~~The simulations produced by~~ BIOME3 simulations 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. When pCO_2 exceeds 250 ppmv with a temperature change of ~-6°C the development of forests expand at expense of ericaceous scrubland (Jolly and Haxeltine, 1997).

Within age uncertainties~~ of the archives~~, 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 the subsequent highest peaks of forest development observed during the BA, respectively (Fig. 3c). Cao et al. (2019), using pollen-based biome reconstruction, suggested that 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. During the BA, considering that temperature and moisture availability in SW Iberia was favourable, increases in pCO_2 levels (>225 ppmv) may have amplified TMF expansion during this period (Fig. 4b and Fig. 5).

4.1.4. Younger Dryas (YD, 12.9 - 11.7 cal. kyr BP)

The YD (pollen zone U1385-4: 12780 – 11190 cal. yr BP, SM Fig. S1) is characterised by an initial weak forest contraction followed by its progressive expansion (Fig. 3c). At the regional scale, the landscape likely consisted of a forest–grassland mosaic, as suggested by the

relatively high presence of forest elements coexisting with semi-desert taxa (Fig. 3c, d and Fig. 4a). Strong SST cooling (Fig. 3j), (equivalent to LGM SSTs or even cooler), with a minimum of 13.2 ºC~~ in the record~~, without significant~~signiifcant~~ freshwater pulses, may have been associated with cooler land surface temperatures. However, this impact may have been muted by the positive effect of higher moisture availability (based on the presence of TMF, Naughton et al., 2019) and/or the increasing trend of pCO_2 (Fig. 3b). The fairly weak reduction in TMF observed in our record and corroborated by the compiled records (Fig. 3c) contrasts with the steppe environment often described for this interval, especially in the southeast of the Iberian Peninsula (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 numerous Iberian 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 -~~–~~ Combourieu-~~Comborieut~~ Nebout et al., 2002) show a relatively high percentage of TMF during the YD compared to HS1 (Fig. 3c).

Unfortunately, there is a lack of independent precipitation proxies for SW Iberia, and Dennison et al. (2018) highlight the limited ~~una lack of~~ reliability of~~in the~~ speleothem proxies as indicators of precipitation~~effor precipitation~~ in this region for this time interval. More widely in the Iberian Peninsula, a double hydrological structure with a drier first phase and wetter second phase was proposed, the latter favouring the expansion of mountain glaciers (García-Ruiz et al., 2016; Baldini et al., 2019). We observe that the notable YD forest development occurred, counterintuitively, in association with similar SSTs to those of the LGM and only slightly higher than those of HS1. Along with~~Alongside woth~~ higher summer insolation, higher pCO_2 (>240 ppmv, Fig. 5) may have been a key factor in supporting forest development. A climate simulation from transient experiments using LOVECLIM, for the site SHAK06-5K / MD01-2444 located near~~by~~ U1385, obtained a weaker AMOC, colder winter temperature, and lower precipitation for the YD compared with the LGM (Cutmore et al., 2021). This supports the scrutiny of additional factors, notably pCO_2 influence on moisture availability for plants, to explain the substantial levels of TMF observed in the Iberian margin records (Fig. 3c). 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 forest~~in the forest~~ development if enough moisture is available.Tree cover may have been confined to suitable moist microhabitats and areas close to refugia; however, it was clearly less restricted than during earlier cold periods (Svenning et al., 2011), as indicated by the TMF abundances ~~It may be that the tree cover was restricted to suitable, moist microhabitats and close to refuge zones, but it certainly was not as restricted as in previous cold periods (Svenning et al., 2011), as TMF abundances support~~ (Fig. 3c). Simul~~t~~ations 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 role~~influence~~ of increasing pCO_2 as a critical factor for global forest~~globalworldwide 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 and winter precipitation in the Mediterranean region (Meijer and Tuenter, 2007), cannot be neglected as a driver~~promoteror~~ of forest development, at least

where trees were not excessively water-stressed. However, disentangling the contribution of insolation vs pCO_2 requires sensitivity experiments, not yet performed. In summary, the persistence of TMF during the YD, despite colder winters and drier summer conditions compared to the B-A, ~~s~~is most plausibly explained by~~eems to be best explained~~ by the combined interaction between precipitation variability, maximum insolation and increasing pCO_2 (between ~245 and 265 ppmv) (Fig. 4a).

4.1.5 Early to Middle Holocene (11.7-4.2 cal. kyr BP)

Pollen zone U1385-5 (11190 – 4260 cal yr BP) corresponds to the Early to Middle Holocene. This interval is~~intervalzone is~~ marked by the expansion of TMF and thermofilous Mediterranean elements, reflecting a regional increase in temperature and precipitation in parallel with ~~alongside~~ warm SSTs (>18°C). Despite coarser~~the low~~ temporal resolution for this interval, the U1385 record is consistent with nearby records showing a maximum forest development at ~~around~~ 9000 cal yr B.P. (Fig. 3c). The ~~, noting that the~~ specific timing of the Holocene forest maximum varied across the Iberian Peninsula along a gradient of regional moisture availability (Gomes et al., 2020). The Early Holocene pCO_2 exceeded 260 ppmv, representing full interglacial conditions. The combination of coupled interglacial ocean-atmosphere conditions (reflected in high SSTs) and high pCO_2 supported maximum forest development (Fig. 5). The impact on plant moisture availability ~~for plants~~ compared to the preceding glacial conditions would have been profound, supporting high productivity and further increases in WUE. The progressive lifting of CO_2 constraints on photosynthesis throughout ~~across~~ the Last Deglaciation ~~thus~~ may thus represent an important factor underlying ~~the~~ forest development in SW Iberia.

4.2. C_{29}/C_{31} ratio and C_3/C_4 dynamics: potential and limitations

Long-chain alkanes with odd-numbers~~ed n-alkane~~, such as C_{29}, C_{31}, C_{33}, are epicuticular waxes produced by terrestrial plants. In lake sediments, higher abundance of~~, with~~ C_{29} occurs in catchments with more trees, while higher abundance of ~~while grassy catchments often representing woody plants and~~ C_{31} is observed in grassy catchments~~es~~ (Meyers, 2003). However, caution is required when interpreting C_{29}/C_{31} in taxonomic terms because both woody plants (trees and shrubs) and grasses can produce C_{29} and C_{31} chain lengths (Ortiz et al., 2010; Bush and McInerney, 2013). Additionally, n-alkane chain-length patterns differ across species and environments, so C_{29}/C_{31} ratios cannot be interpreted as strict woody vs. grass markers (Bush and McInerney, 2013). Insights into the dominance of different plant physiological pathways in response to contrasting levels of pCO_2 and humidity can be potentially gained by analysing ~~using~~ C_{29}/C_{31} n-alkanes from~~of~~ Site U1385. The C_{29}/C_{31} ratio~~curve~~ shows important variability between climatic phases, with increasing values during the LGM, high values during HS1 and the YD, and lower values during the BA and Holocene (Fig. 3h). The C_{29}/C_{31} ratio i~~i~~s positively correlated (Pearson's correlation coefficient, r = 0.52, p-value = 2.473e-08) with the STE~~semidesert~~ pollen group and negatively correlated (r = -0.63, p-value = 2.821e-12) with TMF (Fig. 3c, d and h), indicating a link between pollen-based vegetation changes and n-alkane chain-length distributions. Notably, the expected simple interpretation of C_{29}/C_{31} as "trees vs grasses" does not appear to hold for this dataset across the different phases.~~These observations support a coherent link between pollen-based vegetation changes on the adjacent continent and n-alkane chain-lengths. 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 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, differences are observed between global regions and biomes in terms of what long-chain n-alkanes a species produces (Bush and McInerney, 2013). Here, we do not find that the anticipated general interpretation of the C_{29}/C_{31} ratio as an indicator of the relative abundance of trees vs grasses holds for our datasets.We propose Instead, we offer~~ We propose two possible interpretations, which may explain the observed C29/C31 variability. First:~~,.1) First~~ a physiological stress response hypothesis:~~,~~ the C_{29}/C_{31} ratio in this setting may reflect an adaptation of plants to aridity. ~~The Nn~~Leaf-waxes n-alkanes ~~of leaf waxes are produced to~~ protect plants against the loss of water during the photosynthesis~~tic process~~ (Post-Beittenmiller, 1996; Jetter et al., 2006). We could expect that arid, cold and windy conditions impose greater physiological stress on~~to be more disturbing for~~ woody plants than on grasses~~;~~ ~~with demanding physiological requirementsrequirments compared to grasses~~. ~~Therefore, such harsh environments could exert greater stress on woody plants than on herbaceous taxa.~~Consequently, ~~the~~ increases in~~of~~ the C_{29}/C_{31} values during HS1 and YD, may~~could~~ suggest that~~a climatic adaptation of~~ woody plants (TMF and ERI) responded to climatic stress by enhancing ~~increasing the production of~~ leaf wax C_{29} production as a protective strategy ~~to survive under these challenging conditions~~ (Fig. 3h). Second, a vegetation compositional shift response: alternatively~~,~~ changes in C_{29}/C_{31} may ~~reflect the shifts~~ that~~in chain-lengths may~~ primarily reflect compositional shifts between woody-dominated vegetation with diverse~~withthat includes diverse~~ ecological tolerances, ranging from~~from~~ semi-desert dwarf shrubs such as *Artemisia* to mesophyll broad-leaved trees. In this context~~As such~~, a prevailing "trees vs grasses" interpretative framework~~structure~~ may not ~~be~~ adequately represent the~~represente for the~~ Iberian vegetation patterns~~Peninsula setting~~. We stress that both hypotheses are plausible but require further validation. Nevertheless, the coherent climate signal observed in the U1385 record is encouraging for future studies aimed at linking leaf-wax chemistry of contributing species and vegetation dynamics in this region (Cutmore, 2021). ~~The traditional taxonomic generalisation of C_{29} woody versus C_{31} grasses (Meyers, 2003), still needs some caution and further research to develop a fuller picture of the leaf-wax characteristics of contributing species in the region is required (Cutmore, 2021). However, the coherent climate signature evident in the U1385 is encouraging for this endeavour. Other hypotheses to be explored for understanding the role of different forcings on the Mediterranean forest development during deglaciations include the connection between the long-chain n-alkanes and the dynamic between C_3 and C_4 plants.~~ Beyond taxonomic shifts, the link between n-alkane chain-length distributions and the C_3/C_4 plant dynamic is also relevant.~~Nowadays,~~ African savannahs are dominated by C_4 plants, and~~ biomarkers (including~~ C_{31} n-alkanes~~)~~ have been associated with~~can be used to infer~~ their presence in past landscapes (Dupont et al., 2019). Worldwide, 80% of Poaceae (grasses) and Cyperaceae (sedges) use~~present~~ a C_4 photosynthetic pathway that is favoured by arid conditions (Sage, 2017). However~~Unfortunately~~, pollen analysis cannot discriminate between Poaceae~~discriminate Poaceae~~ and Cyperaceae pollen morphotypes exclusively~~morphotypes from exclusively~~ or in its majority of C_4 plants. We have grouped the Poaceae and the Cyperaceae pollen taxa, noting the inherent limitations of this grouping to represent C_4 ~~C4~~ plants in Iberia as we know that C_3 are the dominant grasses across the region~~less than 10% of the grasses in this region belong to C4 plants at present~~ (Casas-Gallego et al., 2025) (Fig. 3g). Accordingly, the grouping of Poaceae + Cyperaceae pollen must be interpreted with

caution. During ~~Across~~ the last deglaciation, this group (Poaceae + Cyperaceae) shows~~presents~~ relatively high but fluctuating values ~~with considerable oscillations~~ between the LGM and the BA ~~and more stable behaviour onwards~~ stabilising thereafter, without a clear correlation with other proxies (TMF, STE, or C_{29}/C_{31}). ~~. No particular correlation with other indicators (TMF, or STE, or C_{29}/C_{31}) was evident, apart from the apparent instability before the Holocene. Therefore, we do not observe particular evidence to suggest an increased importance of grasses and sedges during arid intervals or low pCO2 intervals of the LGM and deglaciation.~~Thus, we do not find strong evidence for an increased role of grasses/sedges, or of C4 plants specifically, during arid or low pCO_2 intervals. Experimental studies~~In laboratory studies~~, show that C_3~~C3~~ grasses outperform C_4~~C4~~ grasses when temperatures rise by 5 to 15°C at a low CO_2 concentration of 200 ppm. Research on the *quantum yield of photosynthesis* identified a "crossover temperature"—the point at which C_3~~C3~~ and C_4~~C4~~ plants perform equally. This crossover depends on both temperature and CO_2 levels. Modelling across 0-~~–~~45°C and CO_2 levels from 150-~~–~~700 ppm shows that whether C_3 ~~C3~~ or C_4~~C4~~ plants are favoured is determined by the interaction between these two factors, unfortunately humidity~~humidty~~ was not considered (Ehleringer et al., 1997; Edwards et al., 2010).Since ~~Furthermore~~, most ~~of the~~ C_4~~C4~~ plants are confined to ~~the~~ tropical grasslands and savannahs; being better adapted to ~~environments with~~ higher temperatures, arid~~ity~~, ~~poor~~ nutrient poor environments~~soils~~, with intensive~~with and intensive~~ disturbance caused by animals or fire regimes (Bond et al., 2005; Edwards et al., 2010). Likewise, one should expect that vegetation in SW Iberia after the LGM (Fig. 3 and 5) should be dominated~~bedominated~~ by ~~mainly composed of~~ C_3 plants. This interpretation~~interpreation~~ is consistent with the relatively cold SSTs~~; considering the estimated SSTs indicating relatively cold temperatures~~ (Fig. 5) and the high percentages of *Artemisia* spp (C_3 plant) in the pollen record (SM Fig. S1).

However, it is not ~~currently~~ possible to completely~~entirely~~ rule out a~~n~~ role~~irolencreased importance~~ of C_4 plants in the glacial vegetation of SW Iberia, because pollen morphology does not allow the separation of these groups. Stable isotope studies on ancient grass pollen were able to discriminate ~~ofdiscriminateThe discrimination of~~ C_3/C_4 grasses, but single-grain analyses remain technically challenging~~. with challenges at the single grain measurements 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 technically challenging to implement. There is aimportant scope for further study of biomarker proxies to clarify the dynamic between C_3/C_4 plants in the Temperate/Mediterranean (Warm-temperate) biomes. This highlights the fact that C_3/C_4 plant dynamicsdynamic observed in Africa (e.g. Dupont et al., 2019) and other savannahs ecosystems are notis not replicable in our study area so far. Biomarker species/groups fingerprinting studies are required in order to distinguish between C_3 and C_4 plants and test for an increased abundance of C_4 plants within Iberian Mediterranean ecosystems during the last deglaciation~~. Further biomarker research is therefore needed to resolve C_3/C_4 dynamics in temperate–Mediterranean biomes. Current evidence suggests that the C_3/C_4 shifts documented in African savannahs (e.g., Dupont et al., 2019) are not directly applicable to our study area. Species-level biomarker fingerprinting will be essential to test whether C_4 plants played a significant role in Iberian Mediterranean ecosystems during the last deglaciation.

In summary, although future isotopic and biomarker approaches hold great promise for resolving C_3/C_4 dynamics, the current evidence strongly supports C_3 dominance in SW Iberia during the deglaciation. This interpretation is consistent with the modern distribution of plants

in the region, where less than 10% of grasses are C4 (Casas-Gallego et al., 2025), and with the prevailing cool and humid conditions of the LGM and YD, which ~~favor~~favour C_3 over C_4 photosynthesis. Thus, while acknowledging the limitations of pollen-based proxies, the available data indicate that C_3 plants were the dominant contributors to the Iberian vegetation signal.

5. Conclusion

This study presents high-resolution pollen and biomarkers~~SST~~ records from Site U1385 off the SW Iberian Margin, providing new insights into vegetation dynamics during key climate transitions of the last deglaciation and the associated pCO_2 changes.~~offering valuable data for understanding past vegetation dynamics during key climate transitions and $_p$CO2 changes of the LGM and deglaciation~~. *We applied a biomarker proxy* (leaf wax C_{29}/C_{31} ratio), *which is positively correlated with* the semi-desert pollen curve and ~~a~~ negatively correlated~~ion~~ with TMF, ~~we~~ demonstrating~~e~~ its potential as an indicator of aridity in marine cores of the Western Mediterranean region.~~We applied a biomarker proxy (leaf wax C29/C31 ratio), which is positively correlated with the semi-desert pollen curve and negatively with TMF, we demonstraterevealing its potential as a proxy of aridity in the Mediterranean region)~~. The high temporal resolution of the record, combined with a ~~analysis and~~ robust radiocarbon chronology, enables~~allow~~ consistent and more accurate comparisons with regional datasets, strengthening its ~~making this study a valuable~~ contribution for future palaeoenvironmental ~~palaeonvironmental~~ reconstructions and model simulations.

Rather than simply interpreting our dataset in terms of past temperature and precipitation changes, we examine the U1385 record In the context of the body~~an increasing in light of the growing corpus~~ of modern and palaeo observational and modelling studies that support a significant influence of pCO_2 on past vegetation distribution and composition. During the LGM, cold temperatures, low seasonality, and strong physiological drought stress under low pCO_2 restricted forest growth and favoured heathlands.~~We suggest that low pCO_2 acted as a modulator of vegetation response during the LGM. Cold temperatures, low seasonality, and exacerbated drought stress resulting from plant physiological impacts of low pCO_2 likely restricted forest growth while favouring heathlands.~~ Traits of Mediterranean Ericaceae, such as deep roots and thick waxy leaves, may have given these plants a competitive advantage. During HS1, woody vegetation was significantly suppressed due to cold and arid conditions, exacerbated by low ~~atmospheric~~ pCO_2~~ levels~~. The subsequent ~~notable~~ expansion of temperate Mediterranean forests~~ (TMF)~~ during the Bølling-Allerød~~ (BA)~~ was promoted by warmer, wetter conditions and ~~was driven by warmer and moister conditions, and also~~ favoured by rising pCO_2 concentrations. During the Younger Dryas~~ (YD)~~, despite a return to colder temperatures, forest–grassland mosaics persisted ~~primarily~~ supported by adequate~~increased~~ moisture availability and sustained higher pCO_2 levels.

Furthermore, our study suggests a critical pCO_2 threshold for forest expansion at ~225 ppmv.~~study supports a critical pCO_2 threshold for forest expansion during the deglaciation at ~225 ppmv.~~ Below this value (e.g. LGM and HS1), arboreal populations were generally restricted in their development with~~being~~ the~~(e.g. LGM) and the~~ impact of ~~climatic~~ aridification and cooling ~~(e.g. HS1) was~~ being detrimental. Above this value, forests~~forets~~ expanded~~arboreal populations developed strongly~~ (e.g. during the BA) and and the effects of adverse climatic conditions ~~the impact of climatic deterioration~~ (e.g. during the YD) was buffered~~ moderated~~. This threshold~~value~~ is consistent with~~aligns with several~~ observations

from Mediterranean to tropical~~to the tropical~~ African environments (e.g. Dupont et al., 2019; Oliveira et al.,2020; Koutsodendris et al., 2023; Sánchez-Goñi et al., 2023). The concept should be further tested in regional vegetation models to determine the vegetation response to pCO2 fluctuations during past cold periods.

Finally, our~~Our~~ findings highlight the importance of pCO_2 as a key driver of vegetation change in the Mediterranean region through its control on plant moisture-availability and water-use efficiency~~use efficiency~~~~its influence on moisture availability in plants~~ (Koutsodendris et al., 2023). These palaeo-data provide critical context for understanding vegetation responses under future climate scenarios with rising CO_2 and shifting precipitation regimes.~~offer valuable context for elucidating vegetation responses under future climate scenarios involving rising CO_2 and shifting precipitation patterns~~. At the same time, they underscore the need for further research on the relationship between long-chain n-alkanes, vegetation types, and C_3/C_4 plant dynamics, as the long-chain alkanes do not yet provide a reliable basis to disentangle the dynamics between woody plants and grasses in the Mediterranean ecosystems.

~~since long-chain alkanes currently offer only limited capacity to disentangle woody vs. grassy contributions in Mediterranean~~ ~~They also highlight the need for further investigation of the relationship between long-chain *n*-alkanes and present-day vegetation and the C_3/C_4 plants ratio as the long-chain alkanes do not yet provide a reliable basis to disentangle the dynamics between woody plants and grasses in the Mediterranean domain.~~

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 performed~~perfomed~~ assemblage foraminifers picking for radiocarbon dating and drew~~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.

Data accessibility

The data supporting the findings of this study will be made available upon publication. Interested researchers can access the data by contacting the first author directly or through a publicly accessible data repository.

Competing interests

The authors declare that they have no conflict of interest.

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Tables and figures

Table 1 – AMS ~~R~~radiocarbon ages of IODP Site U1385.

Lab code	Core Depth (crmcd)	Material	Conv. AMS ^{14}C (yr B.P.)	Error
*20140801r9_MSGforam01_5ox	52	*G. bulloides*	2525	28
*20140801r5_MSGforam01_1ox	108	*G. bulloides*	6181	35
*20140801r6_MSGforam01_2ox	156	*G. bulloides*	10060	33
UCIAMS-219300	186	*G. bulloides*	11310	60
*20140801r7_MSGforam01_3ox	193	*G. bulloides*	11499	43
UCIAMS-219301	217	*G. bulloides*	12300	40
UCIAMS-219302	237	*G. bulloides*	13430	110
*20140801r8_MSGforam01_4ox	246	*G. bulloides*	13355	45
UCIAMS-219303	251	*G. bulloides*	13670	60
UCIAMS-219304	303	*G. bulloides*	15890	70
UCIAMS-219305	333	*G. bulloides*	17090	90
UCIAMS-235000	363	*G. bulloides* *G. inflata*	18010	60
UCIAMS-235001	390	*G. bulloides* *G. inflata*	18700	70
UCIAMS-235002	431	*G. bulloides* *G. inflata*	19540	70
UCIAMS-235003	447	*G. bulloides* *G. inflata*	20910	90
UCIAMS-235004	467	*G. bulloides* *G. inflata*	21830	100

* ~~AMS from~~ Oliveira et al. (2018)

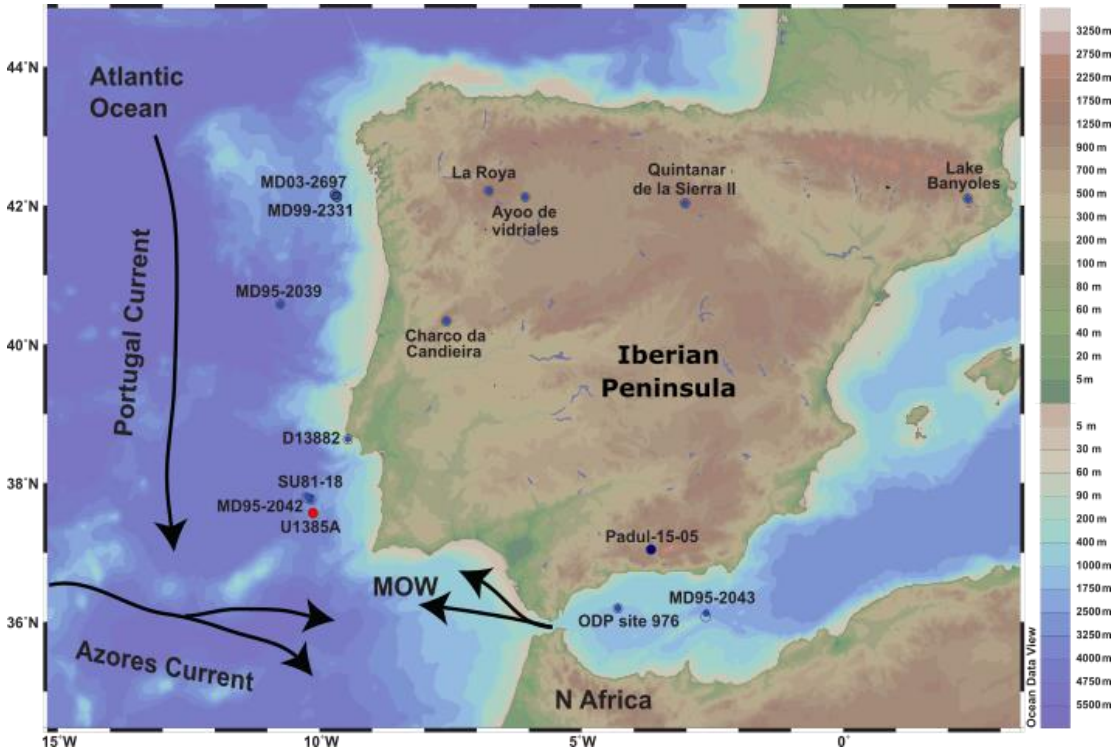

Figure 1 – Location of ~~the~~ IODP Site U1385 and of the marine and terrestrial pollen records discussed in the text. Marine sedimentary records: MD03-2697 (Naughton et al., 2016); MD99-2331 (Naughton et al., 2007); MD95-2039 (Roucoux et al., 2005); D13882 (Gomes et al., 2020); MD95-2043 (Fletcher and Sánchez Goñi, 2008); MD95-2042 (Chabaud et al., 2014); SU81-18 (Turon et al., 2003); ODP Site 976 (Combourieu ~~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 v~~v~~idriales (Morales-Molino and Garcia-Anton, 2014); Charco da Candieira (Van der Knaap and van Leeuwen, 1997); Padul_15-05 (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.

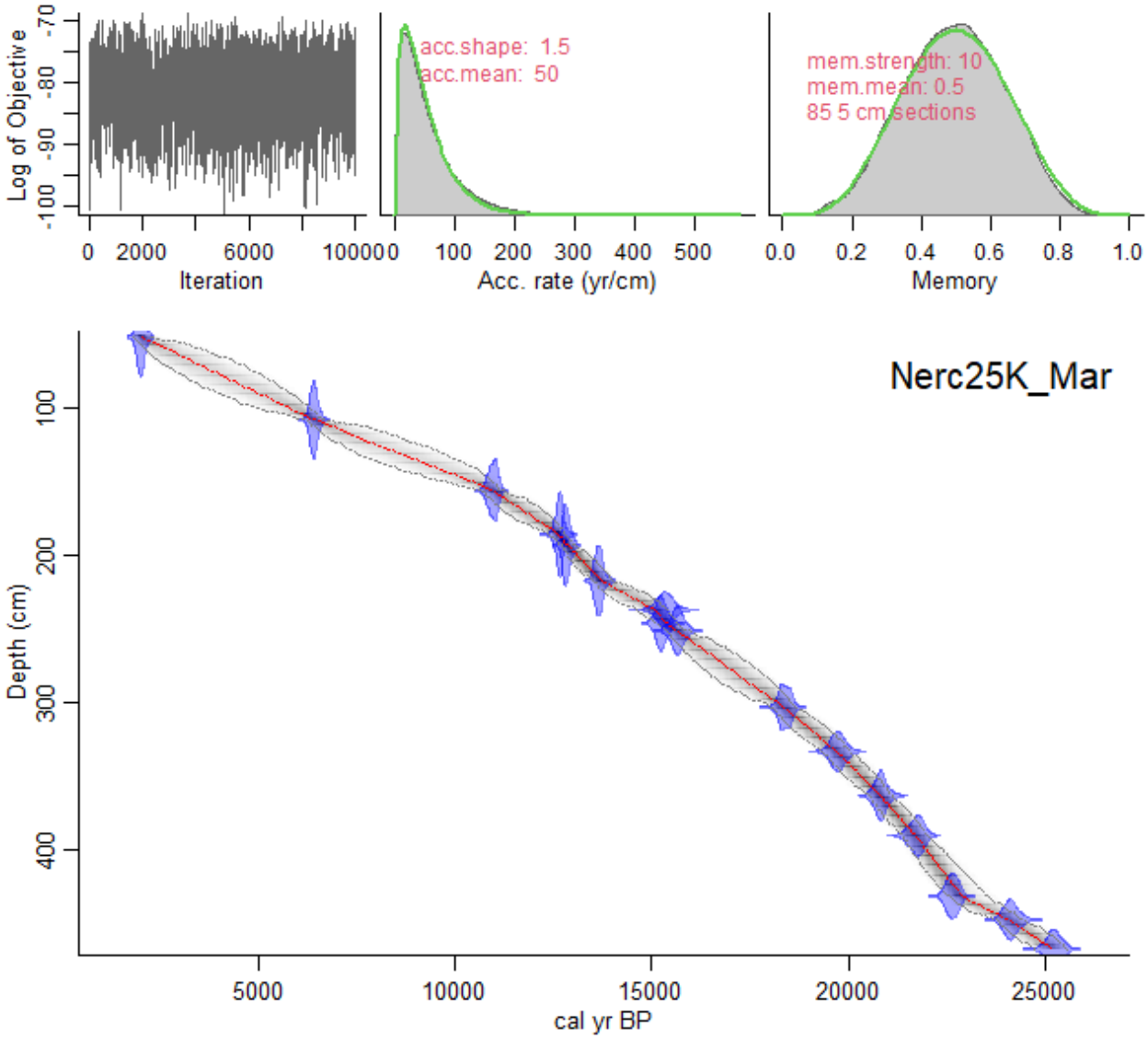

Figure 2 – Age-depth model for IODP Site U1385 using a Bayesian approach with Bacon v.2.3.9.1 (Blaauw and Christen, 2011). The original dates were calibrated using Marine20 (Heaton et al., 2020). ~~g~~Grey stippled lines show 95% confidence intervals; red curve shows~~s~~ single "best" model based on 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).

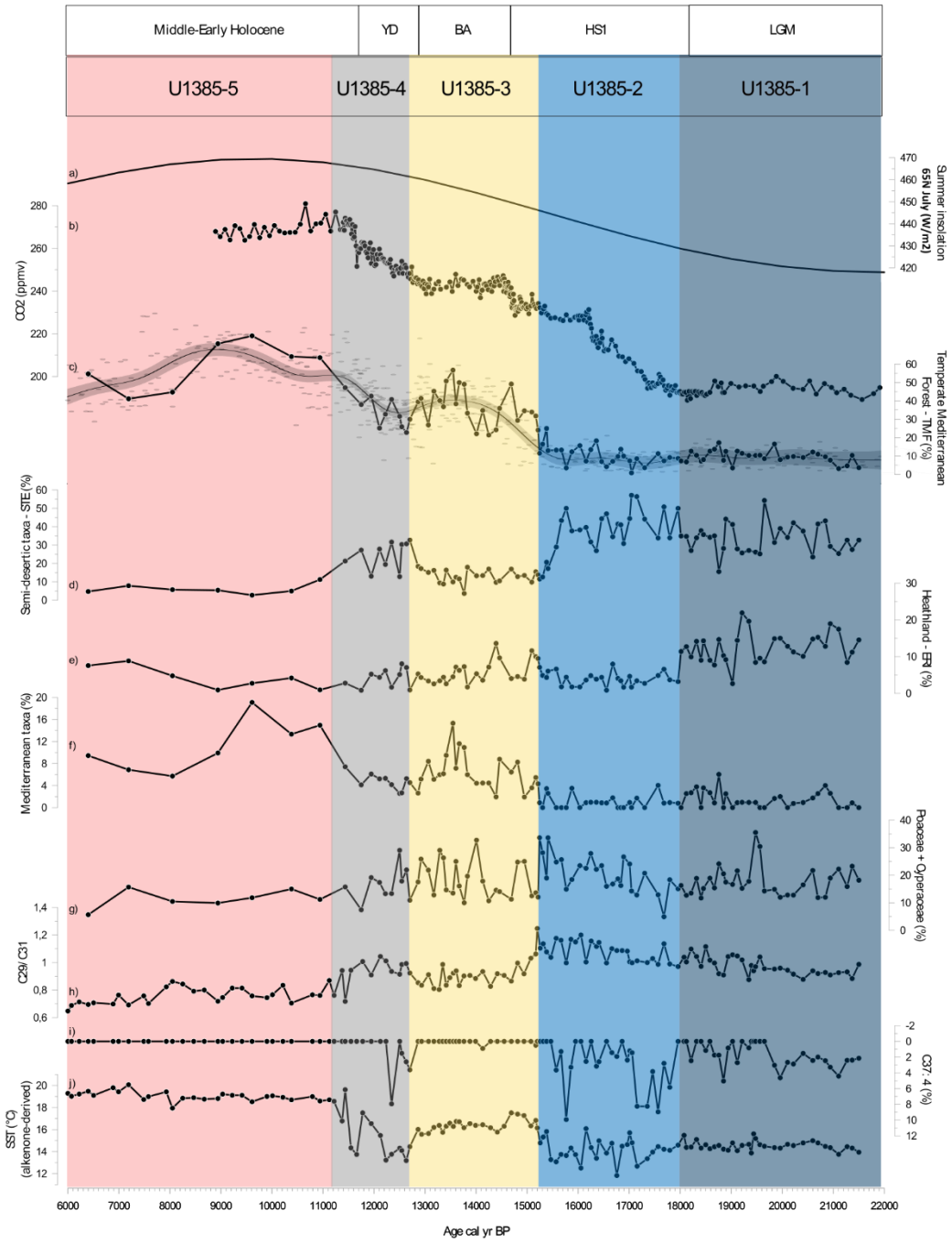

Figure 3 – Comparison of multiproxy records from ~~the~~ Site U1385 with a) 65˚N July (W/m^2) summer insolation (Berger and Loutre, 1991) b) CO2 (ppmv) composite from WAIS (Marcott et al., 2014). ~~(;~~ Percentages of the ~~P~~principal pollen-based ecological groups: c) Temperate Mediterranean Forest from Site U1385 ~~(%)~~ (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-desert~~ic~~ taxa including *Amaranthaceae* (previously *Chenopodiaceae*), *Artemisia*, and *Ephedra*. ~~(%)~~, e) Heathland including members of the *Ericaceae* family (including various *Erica* spp) and *Calluna* spp ~~(%)~~, f) Mediterranean taxa ~~(%)~~ and g) Poaceae + Cyperaceae ~~(%)~~; 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. S1 and SM Table S1) and were connected with the periods indicated.

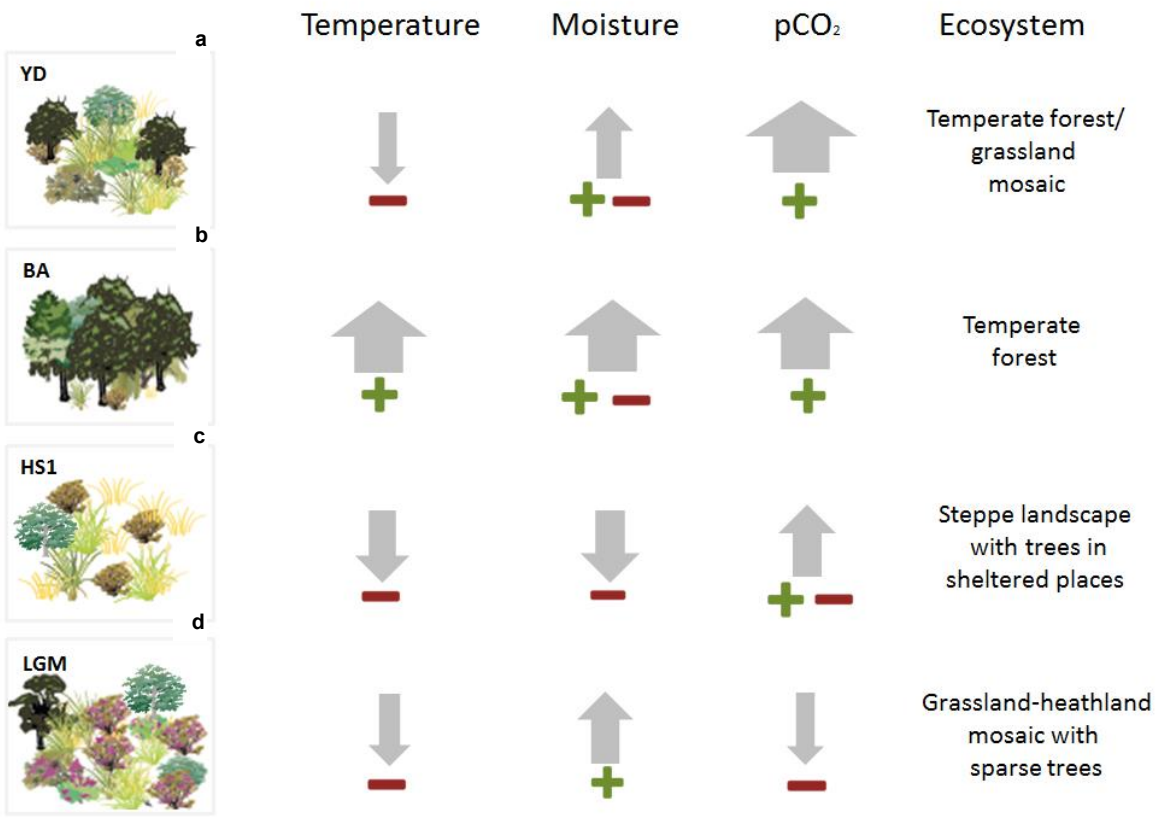

Figure 4 – Schematic representation of the relative change of climatic inferred parameters (precipitation and temperature) based on pollen-vegegation ~~vegegation~~ groups, biomarkers, SST as well as the physiological contribution of CO_2 for each period showing a schematic reconstruction of the potential ecosystem scenarios. The perceived temperature used the interpretation of pollen (TMF and STE groups), SST and n-alkanes; the perceived moisture (ERI, TMF and STE).

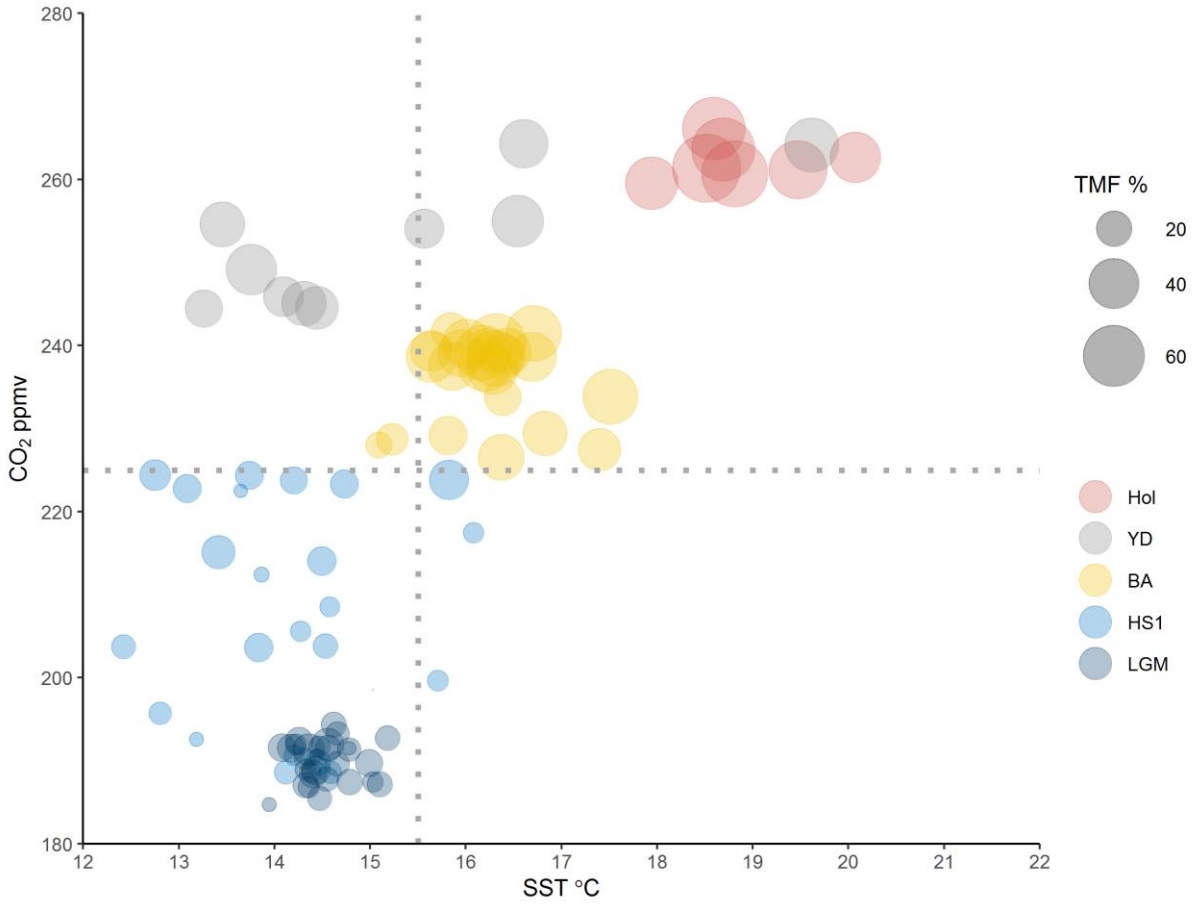

Figure 5 – Dispersion plot showing the relation between CO_2 (Marcott et al., 2014) and SST in relation to TMF % across the different intervals of the Last deglaciation, following the pollen zones boundaries.