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 partial pressure of ~~concentration of~~ carbon dioxide (pCO_2) increased substantially ~~fromsignificantly~~ fro~~r~~m ~180 to ~280 ppm – yet its impact on veget~~g~~ation dynamics ~~through~~across this major climatic transition~~s in Iberia peninsula~~ remains~~. However, the impact of pCO_2 changes on vegetation across the last deglaciation remains poorly~~ insufficiently understood. In ~~P~~particular~~ly~~, ~~the~~ Iberian pollen records reveal an intriguing feature that can be related to ~~These findings focus on the~~an often overlooked role of pCO_2 in shaping vegetation responses during last ~~the~~ deglaciation~~s climatic transitions~~. These records ~~reflect~~reveal ~~, which could explain an intriguing feature observed in Site U1385 and other Iberian margin records, being~~ the ~~almost~~near disappearance of forest during the cold Last Glacial Maximum (LGM) and Heinrich Stadial 1 (HS1) phases ~~to~~and an unexpected~~ly~~ recovery during the Younger Dryas (YD) cold phase, when pCO_2 increased~~s.~~ ~~Under full glacial lowUnder glacial conditions, low pCO_2 likely constrained plant photosynthesis, particularly limiting forest development. 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 rising pCO_2 rise couldmay have (1) gradually relieved the physiological limitations on plants, allowing forests to expand when moisture was sufficient even if temperatures were low; and (2) enhanced forest growth under warmer and wetter conditions.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.~~ 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) ~~records~~conditions from ~~To test this, in~~ the southwestern (SW) Iberian margin ~~site~~ Integrated Ocean Drilling Program Site U1385 ("Shackleton site") for the last 22 cal ka BP~~, we analysed~~ . ~~The~~ in ~~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")~~. This direct land-sea comparison approach~~ed, throughout the Last Glacial Maximum (LGM) and last deglaciation~~ allows~~ed~~ us to ~~track~~investigate how ~~and compare~~ the Iberian Peninsula vegetation responded to major global ~~changes with shifts in global~~ pCO_2 changes of the last deglaciation.~~.~~

Our results show that ~~the Last Glacial maximumThe LGM cool~~cold and moderately humid conditions of the LGM ~~is characterised by a~~supported a grassland-heathland mosaic ~~type~~ ecosystem, ~~triggered by cool and moderately humid conditions~~ but low pCO_2 ~~levels may have exacerbated~~likely caused physiological drought and suppressed forest development. ~~During Heinrich Stadial~~HS1, ~~(HS1)~~the coldest and most arid ~~conditions~~period, combined with sustained low pCO_2 values ~~to precluded~~almost ~~completely~~ suppress~~ed~~ forest ~~development~~growth in ~~and resulted in the dominance of~~favour~~ing~~ of Mediterranean steppe ~~or~~ and semi-desert vegetation. In contrast, the ~~The~~warmer Bølling-Allerød ~~(BA)~~, is characterised by a temperature optimum ~~(warmest SSTs and forest development)~~ and ~~variable~~variable but ~~moisture condition~~generally wetter conditions, along with the rising ~~while increasing~~ of pCO_2 ~~which~~ above 225 ppm at ~15 cal ka BP contributed to ~~the highest levels of significant~~substantial forest development~~, associated with the rise of pCO_2 above 225 ppm. Within the BA, significant SW Iberian forest development occurred at ~15 cal kayr B.P.~~BP

~~associated with an increase in pCO_2 above 225 ppm~~. During the ~~Younger~~ YD ~~Dryas (YD)~~, ~~cooler temperatures combined with~~ sufficient moisture combined with~~and the~~ increasing ~~of~~ pCO_2~~availability~~ allowed the ~~maintenance~~persistance of a mixed grassland-forest mosaic despite cooler temperatures. Our study suggests that during cold and low pCO_2 periods (LGM and HS1), the role of ~~the~~pCO_2 ~~latter~~ on SW Iberian vegetation dynamics wa~~i~~s more pronounced compared to periods of higher pCO2. Temperature and precipitation changes during periods of relatively high pCO2 play the main role in shaping the distribution and composition of the vegetation.

~~These findings focus on the often overlooked role of pCO_2 in shaping vegetation responses during the deglaciation climatic transitions, which could explain an intriguing feature observed in Site U1385 and other Iberian margin records, being the almost disappearance of forest during the LGM and HS1 to recover during the YD, when pCO_2 increases.~~

~~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.~~

~~, 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; Last Glacial Maximum; Direct ~~sea-land~~land-sea comparison; ~~Cclimatic space;~~ Climatic parameters vs pCO_2; Forest development; Pollen analysis

1. Introduction

The last deglaciation, spanning from 20-19 cal ka BP (e.g. Denton et al., 1981; Toucanne et al., 2008; Denton, 2010) to ~7 cal ka BP (e.g. Dyke and Prest, 1987; Carlson et al., 2008) ~~As~~ ~~t~~was punctuated by a series of rapid climate shifts ~~superimposed to~~accompanying the progressive melting of ~~he last ice ended and glaciers melted across the~~ n~~N~~orthern hemisphere glaciers~~, a period known as the last deglaciation~~~~, spanning from 20-19 ka (e.g. Denton et al., 1981; Toucanne et al., 2008; Denton, 2010) to ~7 ka (e.g. Dyke and Prest, 1987; Carlson et al., 2008)~~ ~~is punctuated by a series of rapid climate shifts~~. This interval was marked by a global mean temperature increase of 5-10˚C, depending on latitude (Bard et al., 1987; Alley and Clark, 1999; Clark et al., 2012) interrupted by ~~, however the warming was not uniform. Instead,~~an alternation of cold and warm phases. The warmer Bølling-Allerød (BA, 15-12.5 cal ka BP~~ DATES~~) was bracketed by t~~t~~wo major cold phases~~events~~: the Heinrich Stadial 1 (HS1, 18.5-15 cal ka BP~~DATES~~) and the Younger Dryas (YD, 12.9 - 11.6 cal ka BP~~ DATES~~)~~, interrupted the warmer Bølling-Allerød (BA)~~. ~~Based on a direct comparison between terrestrial and marine climatic indicators These alternation of colder (HS1 and YD) and warmer phases have been widely researched due its global impacts (e.g. 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). from the SW Iberian margin sedimentary sequences, While severalome workrecords have focusedcompared on the mechanisms underlying land and sea indicators the regional atmospheric and oceanic responses to the last deglaciation off the SW Iberian margin (Boessenkool et al., 2001; Turon~~

~~et al., 2003; Chabaud et al., 2014; Oliveira et al., 2018; Naughton et al., 2019). However, , few of these records span the entire deglaciation, and none offer resolution or chronological precision to detect short-term vegetation and climate shifts in detail. The high temporal resolution offrom IODP Site U1385, provides a uniquen opportunity to compare sea and land signals, to detect significant vegetation and climatic shifts in SW Iberia during this transional period.~~ This period was also characterized by an increase in ~~global~~ atmospheric ~~of~~ carbon dioxide (pCO_2) concentrations ~~increasing~~ from ~180 ppmv to 280 ppmv (Monnin et al., 2001; Shakun et al., 2012; Marcott et al., 2014), one of the largest shifts in pCO_2 of the last 800,000 years (Lüthi et al., 2008). High-resolution data from the West Antarctic Ice Sheet Divide ice core reveals that the rise was not gradual, but in 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 (Marcott et al., 2014). Based on a direct comparison between terrestrial and marine climatic indicators from the SW Iberian margin sedimentary sequences, several works~~ have~~ 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~~s~~ a valuable opportunity to evaluate vegetation response to climate and pCO_2 changes in SW Iberia during this transitional period. ~~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, 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 pCO_2 throughout time as a climate driver ~~throughout the ice ages is still~~ remains intensely debated.~~;~~ ~~however, it has been mainly considered as either~~Studies suggest the pCO_2 acted as (1) a primary driver of the climatic changes, ~~in which the CO_2 led the~~ leading to temperature ~~records~~chnages in the Northern Hemisphere (Shakun et al., 2012; Marcott et al., 2014); (2) a climate~~n~~ amplifier, ~~responding as positive feedback to the~~ reinforcing warming that began through other processes (Alley and Clark, 1999; Clark et al., 2012); or (3) as a consequence of climate change~~ing~~, responding to temperature shifts rather ~~rather~~ than ~~a cause of climatic changes~~causing them (Denton et al., 2010).

Beyond its role in shaping global climate, pCO_2 ~~Besides its impact on climate, the~~ directly influences plant physiolo~~gica~~gy ~~l~~and~~influenc~~ how vegetation~~e~~ responds to environmental change. The annual exchange of pCO_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). During photosynthesis, atmospheric pCO_2 plays a critical role in plant physiology;~~,~~ plants absorb pCO_2 through their stomata which are small leaf pores, lo~~o~~sing water. At lower pCO_2 ~~concentrations~~, such as during glacial periods, plants must open these pores wider or increase their number to capture enough pCO_2 (Royer et al., 2001). While this enhances gas exchange, it also leads to greater water loss through transpiration, reducing water-use efficiency (WUE), 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. 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 ~~atmospheric~~ 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 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 ~~shifts in~~ pCO_2 shifts (e.g. Tognetti et al., 2008). Recent coupled vegetation-climate modelling and multiproxy reconstructions have demonstrated that pCO_2 significantly impacts 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~~dynamics in reconstructions of past vegetation, particularly~~ when interpreting pollen data or evaluating biome shifts (Prentice et al., 2017; Cao et al., 2019). While the current pCO_2 fertilization has received~~ing~~ considerable attention (e.g. Piao et al., 2020) studies focusing on the ~~limitations the imposed by~~effects of low pCO_2 on vegetation, or major transitions from low to high pCO_2, ~~during ice ages~~ are equally critical.

~~In this context, the Mediterranean region, and particularly southwest Iberia, offers an ideal setting to investigate the role of pCO_2 limitations due to its pronounced seasonal water stress and glacial vegetation dynamics. 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.~~ Last deglaciation v~~V~~egetation changes have been widely studied across the Iberian Peninsula ~~for the last deglaciation as recorded in~~ from palaeoecological ~~proxies~~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 ~~(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 Casas-Gallego et al., 2025)~~. However, growing evidence shows that ~~most~~many climate reconstructions for glacial periods based on vegetation records ~~are~~may be biased as they~~it~~ neglect~~s~~ the influence of pCO_2 on ~~, which leads to bias in climatic interpretations, being essential to recognise that pCO_2 is correlated with~~ WUE ~~and looking at the balance between carbon assimilation and transpiration (water loss)~~. Neglecting this influence may contribute to the ~~unreliability of moisture 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; 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). ~~Palaeovegetation (pP paleovegetation and paleoclimatic areatand scales ; Elenga et al., 2000; Svenning et al., 2008; 0Wu et al., 20078Within 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.~~

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). ~~but~~However, the inverse modelling approach ~~it~~ has some limitations ~~due~~relating to ~~its~~ low taxonomic resolution, and dependence on~~f~~ the ~~available~~ vegetation model that is not always comparable with pollen assemblages (Chevalier et al., 2020; Prentice et al., 2022). ~~Lately~~Recently, quantitative 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~~reference~~). ~~For example, the Villarquermado record suggests systematic underestimation of precipitation for the last 130 ka when pCO_2 is not considered.~~ By contrast, under interglacial conditions with higher pCO_2 levels, model experiments suggest that forest expansion in SW Iberia is mostly controlled by precipitation than by pCO_2 levels (Oliveira et al., 2018; 2020).

Despite these advances, there is a need for additional regional-based palaeoecological research~~, such as for the SWsouthwest Iberian Peninsula~~. 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 (> 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 evapotranspiration 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 climate change, such as the deglaciation in the southwest Iberian Peninsula, deserves particular attention. Understanding the temporal dynamics of regional forest cover—specifically Temperate and Mediterranean Forests (TMF)—requires considering the combined influence of temperature, precipitation, and pCO_2.~~ Recognising th~~is interaction~~e role of pCO_2 is a key issue not only to ~~reconstructeing~~interpret the drivers of past ecosystems accurately, but also to anticipate~~ing~~ the future responses of semi-arid landscapes to ongoing climate change.

The new multiproxy study of IODP 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 changes in the~~ vegetation changes in SW Iberia along with sea surface temperature (SST) trends ~~-based atmospheric conditions and SSTs over~~in its ~~the SW Iberian~~ margin during the LGM, HS-1, B-A and the YD. This new paleoenvironmental record will serve to ~~, as well as its comparison with available Iberian records. The aims of this study are to:~~

- ~~Document terrestrial and marine responses to past climate changes at the 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;~~

~~E~~explore the main factors driving forest development during the LGM and the last deglaciation, and ~~;~~

e~~E~~valuate the ~~evidence for indications of~~potential pCO$_2$ thresholds for we~~a~~stern Mediterranean forest development.

~~(Cowling and Sykes 1999; Crucifix et al., 2005; Ward et al., 2005; Gerhart and Ward, 2010; Harrison and Sanchez Goñi, 2010).~~~~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-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 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:~~

~~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;~~

~~Explore the main factors driving forest development during the LGM and last deglaciation;~~

~~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 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 ka 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 (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 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) and a.~~ 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~~ A new set of eleven samples for AMS ^{14}C were selected ~~and processed at the Keck Carbon Cycle AMS Facility, (University of California, Irvine),~~ from monospecific ~~monospecific~~ foraminifer samples of *G. bulloides,* and a mixed assemblage of *G. bulloides* and *G. inflata* processed at the Keck Carbon Cycle AMS Facility, University of California, Irvine (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) using the Marine20 calibration curve (Heaton et al., 2020). ~~). 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.~~

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 between 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. Cold HF (hydrofluoric acid). 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 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. 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~~a~~; for example: 100 * *Pinus* / (Main sum + *Pinus*) and 100* *Cedrus* / (main sum + *Cedrus*)~~; the same applies to local taxa~~. ~~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 or Rif ~~M~~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 ~~(CONISS)~~ determined the five statistically significant pollen assemblage zones~~-~~ ~~(CONISS)~~ (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 calculat~~at~~ed the~~a~~ sum of Poaceae and Cyperaceae (Fig. 3g), to check the potential ~~representatitivity~~importance of C4 plants in the Iberian Peninsula. While~~, although~~ most of the present-day Poaceae and Cyperaceae in this region belongs to the C3 plants type ~~despite its potential current low representation in the Iberian Peninsula~~ (Casas-Gallego et al., 2025), it is possible that C4 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~~-~~ ~~IP~~Iberian Peninsula 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~~ 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 – 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 T~~TMF~~ MF (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 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. Villanueva and Grimalt, 1997; 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; Struck et al., 2020). This relation encompasses the adaptation of plants, by increasing leaf wax ~~production~~long chain production, to reduce water loss during the photosynthetic processes and prevent desiccation promoted by harsh winds or more arid conditions (Bush and McInerney, 2013). ~~If the i~~Index values~~is~~ >1~~, it is~~are typically considered to reflect higher quantities of C_{29} *n*-alkanes ~~by~~ produced by trees and shrubs, while values ~~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; Rodrigues et al., 2009; Ortiz et al., 2010; ~~Rodrigues et al., 2009~~). However, the interpretation of this index may vary across biomes and dependent on source vegetation types (Carr et al., 2014; Diefendorf and Freimuth, 2017).~~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 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 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 (21500 – 17990cal 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 - Combourieu 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 (17990 – 15230 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 – Combourieut 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 (15230 – 12780 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 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 (12780 – 11190cal 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 (11190 – 4260 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.~~

4~~5~~. ~~Discussion~~Results and discussion

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

4.1.~~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, precipitation), we hypothesise that ~~past~~ 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 ~~informed~~supported by the present-day environmental and climatic space, considering the temperature and precipitation ~~occupied by~~in which different taxa exist in ~~Portugal~~Iberian Peninsula and characterising the ~~(Temperate Mediterranean~~TMF ~~forest~~ – *Quercus* sp., the Heathland (ERI) – Ericaceae family and the semi-desert (STE)~~ic~~ landscapes~~taxa)~~ (~~S.M.~~SM Fig. 2).

4.1.1. LGM

The pollen-based vegetation record from Site U1385 shows that during the LGM (pollen zone U1385-1: 21.500 – 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~~a grassland-heathland mosaic dominated the landscape (Fig. 3d, e and Fig. 4d), a distinctive non-analogue glacial vegetation cover~~.

The prevalence of heath (*Erica* spp.) ~~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~~ of Heinrich stadials (~~Naughton et al. 2007;~~ Roucoux et al., 2005; Naughton et al., 2007; Fletcher and Sánchez-Goñi, 2008; Combourieu-Nebout et al., 2009; Sánchez-Goñi ~~Sanchez-Goni~~ et al., 2009~~9; Combourieu-Nebout et al. 2009; Fletcher and Sanchez-Goni 2008~~). ~~Nevertheless the juxstaposition of high abundances of semi-desert and heathland taxa remains intriguing~~. Nevertheless there is a somewhat complex picture with respect to the prevailing moisture availability for vegetation during this interval. ~~-~~Semi-desert taxa, ~~are t~~typically found in arid conditions are abundant, while heathland taxa, ~~are~~ associated with more humid environments, reach their maximum in the record (Fig. 3; SM Fig. S2c). ~~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).~~ Forest taxa were represented in low percentages (5-15%) (Fig. 3c), suggesting cold and relatively dry conditions over the continent. The TMF values are consistent across the U1385 record and GAM-fitting to the data compilation (Fig. 3c), 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 - 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~~Iberian Peninsula (MD99-2331 and MD03-2697- Naughton et al., 2007; 2016).

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 (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? ~~The first answer could~~A possible explanation ~~be~~could be associated with ~~cold~~cold atmospheric temperatures (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). ~~As such~~ Hence, in addition to temperature ~~a potential controlling factor could be~~ the low levels of pCO$_2$ during the LGM ranging between 180-190 ppmv, could have been another important controlling factor ~~during the LGM of between 180-190 ppmv,~~ which ~~is amongst~~ 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 ~~corrected~~ for LGM pCO$_2$ (185 ppm), ~~conditions~~ showing qualitative differences in the distribution of vegetation types (Shao et al., 2018). Under low pCO$_2$ grasslands were~~as~~ favoured to the detriment of evergreen broadleaf, evergreen and deciduous needle leaf forest. This~~at~~ 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 note that the LGM corresponds 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~~ favourable for heathland development in the Iberian Peninsula (Fletcher and Sánchez-Goñi ~~Sanchez Goni~~, 2008; Sánchez-Goñi et al.~~Sanchez Goni~~, 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~~Gomes et al., 2020~~; Oliveira et al., 2018; Gomes et al., 2020 ~~Chabaud et al., 2014~~). ~~As such, during the LGM, the precession maximum promoting wetter summers should have been a trigger for heathland development .~~ Furthermore, in addition of requiring less humidity than forests, 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 pCO2 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 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 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 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~~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~~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.). ~~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).~~

Long-term studies considering CO$_2$ limitations on vegetation ~~slightly~~ contrast~~s~~ in their perspectives;~~,~~ Gosling et al., (2022) ~~refers~~argue that during the last 500k, precipitation and fire exert the main controls on woody cover in tropical Africa while~~ere~~ CO$_2$ effects were relatively small. In Asia, Clément et al., (2024) also emphasize~~s~~ 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 ~~trigger~~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 ~~southwest~~SW 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~~ colder 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~~simulations of~~g~~ 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). When we assess the relationship between pCO$_2$, SST and TMF across the LGM and deglaciation events we observe that the LGM ~~occurrence of TMF~~ (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). Therefore, extremely low pCO$_2$ below a critical threshold of ~220-225 ppmv may have been the critical determinant of low forest development in the LGM. 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 MIS13 at ~216 ppmv (Oliveira et al., 2020) and MIS18 at ~215 ppmv under relatively high temperatures and increased winter rainfall (Sánchez-Goñi et al., 2023).Temperatures during the LGM in 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 southwestern Iberia.

4.1.2.

HS1

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) ~~resulted~~ corresponded to ~~from~~ the lowest SSTs~~temperatures~~ of the record (SST~12ºC, Fig. 3j), and highest levels of aridity ~~observed within the studied interval~~ are suggested by the maximum of semi-desert taxa and minimum TMF (Fig. 3 and 5c). Additionally, high $C_{37:4}$ values (~8.2%, Fig. 3i) reflect~~ing~~ major~~xima of~~ meltwater pulses, associated with extreme cold conditions ~~and a clear expression~~ of HS1 in the Atlantic Ocean. The notable decrease ~~observed~~ in ~~more moisture-demanding~~ heaths (ERI, Fig.3e) as well as terrestrial marshes and wetlands (decrease in *Isoetes* undiff.) ~~likely result of~~further support increased moisture stress (SM Table S1 and SM Fig. S1). The dominance of STE during HS1 is consistent across the majority of the ~~IP~~Iberian Peninsula 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), reflected also in the long-term minimum in modelled forest levels (Fig. 3c).

Throughout HS1~~During this event~~, the potential effect of increasing pCO_2 (from ~185 to ~225 ppm) from 18.1 to ~16 cal ka ~~B.P.~~BP (Fig. 3b) was not enough to counteract the limiting effect of extreme ~~the climate conditions (~~cold~~est~~ and dry~~iest~~ atmospheric conditions~~), and indeed should have exacerbated aridity stress at this time.~~. Regional models - Weather and Research Forecast Model ~~–~~- simulat~~reconstruct~~ing the potential vegetation with a pCO_2 correction show a reduction in arboreal vegetation and increase of sparsely vegetated soil for the Iberian~~P~~ region during HS1 compared with the LGM (Ludwig et al., 2018). The simulat~~reconstruct~~ed precipitation values for ~~the~~ SW~~southwestern~~ Iberia~~n Peninsual~~ (Tagus hydrographic basin catchment), show values below 700 mm/yr for HS1, which agrees with the pollen ~~data and again~~ evidence for ~~the~~ widespread semi-desert~~ic~~ taxa development. Interestingly, the differences between HS1 and LGM concerning temperature, precipitation and pCO2~~????~~ are quite relevant. The climatic extremes of HS1, despite rising pCO2, were most likely responsible for the loss of heathland following the LGM~~, which could explain the stronger development of the heathland in the LGM~~. ~~The reconstructed atmospheric temperature showed a longitudinal variation (Do you mean that in the eastern part of Iberia the temperature is higher and HS1 colder??? I do not understand) between the HS1 and LGM varying from -2.5 to -1.5 °C,; which isare in line with the high percentages of semi-desertic taxa of Site U1385, as well as other Iberiannearby 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 SST~~temperatures~~ below 15.5°C and pCO_2 below 225 ppmv (Fig. 5).

4.1.3. BA

The BA (Pollen zone U1385-3: 15230 – 12780 cal yr BP; SM Fig. S1) was~~is~~ 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°ªC, Fig. 3 j) ~~high temperature~~ and a dry to wet trend are likely the primary drivers of progressive forest development during the BA. ~~HoweverAlso~~Additionally, the increase of pCO_2 from ~230 to 245 ppmv ~~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~~should have promoted a "fertilisation effect" ~~of the stepwise increases of pCO_2 by ~15 ppmv around this~~during 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~~ to the detriment of the ericaceous scrubland (Jolly and Haxeltine, 1997).

Within age uncertainties of the archives, ~~The~~ abrupt increases in pCO_2 at 16.3 k~~K~~a and 14.8 k~~K~~a (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 subsequent highest peaks of forest development observed during the BA, respectively ~~(within age uncertainties of both archives)~~ (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. ~~, by minimising moisture limitation (Why limitation of moisture if during the B-A there is a humidity increase in Europe?) 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 in SW Iberia was ~~quasi-optimal~~favourable, increases in pCO_2 levels (>225 ppmv) may have amplified TMF expansion during this period (Fig. 4b and Fig. 5).

4.1.4. YD

The YD (pollen zone U1385-4: 12780 – 11190 cal yr BP, SM Fig. S1) is characterised by an initial ~~first~~ weak forest contraction followed by its progressive expansion (Fig. 3c). At the regional scale, the~~The proposed~~ landscape likely consisted of a forest–grassland mosaic, as suggested by the relatively high presence of forest elements coexisting with semi-desert taxa ~~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), (equivalent to LGM SSTs or even cooler), with a minimum of 13.2 °C in the record, without signiifcant freshwater pulses, may have been associated with cooler land surface temperatures.

However, this impact may have been muted by ~~bothoffset by~~ the positive effect of ~~sufficient~~ 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 described for this interval, especially in the southeast of the ~~IP~~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 record and other Iberian margin and ~~IP~~Iberian Peninsula 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~~Iberian Peninsula (Fig. 3c).

Unfortunately, there is a lack of independent precipitation proxies for ~~this~~ SW Iberia ~~region~~, and Dennison et al. (2018) highlight a lack of reliability in the speleothem proxies for 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~~e~~ notable YD forest development occurred, counterintuitively,~~s~~ in association with similar SSTs to those of the LGM and only slightly higher than those of HS1. Alongside higher summer insolation, higher pCO_2 (>240 ppmv, Fig. 5) may have been a key factor supporting forest development. A climate simulation from transient experiments using LOVECLIM, for the site SHAK06-5K / MD01-2444 located nearby 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).~~To support, Villarquemado (NE Spain) climate reconstruction indicates wetter conditions (accounting for the CO_2 effect) as well as cooler summer and a slight decrease in winter temperature (Wei et al., 2021). In addition, a climate simulation from transient experiments using LOVECLIM, for the site SHAK06-5K and MD01-2444 nearby U1385, obtained a weaker AMOC, as well as colder winter temperature, but a lower precipitation for the YD (But you have sais before that Wei et al. reconstruct wetter conditions) comparing with the LGM, (Cutmore et al., 2021). Meanwhile, pCO_2 was above the 225 ppmv threshold throughout the YD, (reaching maximum values of ~260 ppmv, at ~12 kKa) (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 it certainly was not as restricted as in previous cold periods (Svenning et al., 2011), as ~~pollen data also suggests~~ TMF abundances support (Fig. 3c). ~~Also, s~~Simultations~~imulated 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 and winter precipitation in the Mediterranean region (Meijer and Tuenter, 2007~~, Journal of Marine Systems~~) cannot be neglected as a promotor of forest development, at least where trees w~~h~~ere 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 colder winters and drier summer conditions compared to the B-A~~ temperatures andwith substantial seasonal variation (warmer than the HS1 Am I right?~~, seems to be best explained by the combined interaction between precipitation variability, maximum insolation ~~higher atmospheric temperatures, at least during summer (promoting forest development),~~ and increasing pCO_2 (between ~245 and 265 ppmv) (Fig. 4a). ~~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).~~

4.1.5 Early to Middle Holocene

Pollen zone U1385-5 (11190 – 4260 cal yr BP) corresponds to the Early to Middle Holocene. This zone is marked by the expansion of TMF and warm-loving Mediterranean elements, reflecting a regional increase in temperature and precipitation alongside warm SSTs (>18°C). Despite 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), 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 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 across the Last Deglaciation thus may represent an important factor underlying the forest development in SW Iberia.

4~~5~~.2. C_{29}/C_{31} ratio and C_3/C_4 dynamics: potential~~s~~ and limitations

Insights into the dominance of different plant physiological pathways in response to contrasting levels of pCO_2 and humidity can be potentially gained using C_{29}/C_{31} n-alkanes of Site U1385~~A (Fig. 3h)~~. The C_{29}/C_{31} 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} is positively correlated (Pearson's correlation coefficient, r = 0.52, p-value = 2.473e-08) with the semidesert pollen group and negatively correlated (r = -0.63, p-value = 2.821e-12) with TMF (Fig. 3c, d and h).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, ~~regional~~ differences are observed ~~across the world and~~ between global regions and biomes in terms of what long-chain n-alkanes a species ~~is~~ produces~~ing~~ (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 correlated (Pearson's correlation coefficient, : r = 0.52, p-value < XXXX)% and (negatively correlated (: r = -0.63%, p-value < XXXX) correlated (Pearson's correlation coefficient) with the semi-desertic and TMF groups, respectively (temperate Mediterranean forest) signals within this region over the same interval (Fig. 3c, d and h). Therefore~~Here, we ~~note~~ 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 ~~does not~~ holds for our datasets ~~(indeed the reverse is evident)~~. Instead, we offer two possible interpretations. First~~ tentatively infer that~~, C_{29}/C_{31} ratio in this setting ~~is~~ may reflect ~~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). ~~W~~We could expect ~~that~~ arid, ~~/~~cold and windy conditions to be more disturbing for woody plants; with demanding physiological requirments compared to grasses. Therefore, such harsh environments could exert greater stress on woody plants than on herbaceous taxa.Consequently the increase of the C_{29}/C_{31} during HS1 and YD, could suggest a climatic adaptation of woody plants (TMF and ERI) by increasing the production of leaf wax C_{29} as a protective strategy to survive under these challenging conditions (Fig. 3h). Second, the shifts in chain-lengths may primarily reflect compositional shifts between woody-dominated vegetation that includes diverse ecological tolerances, from semi-desert dwarf shrubs such as *Artemisia* to mesophyll broad-leaved trees. As such, a prevailing "trees vs grasses" interpretative structure may not be adequate for the Iberian Peninsula setting. The~~However, 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 hypothes~~i~~ees to be explored for understanding the role of different forcing on the Mediterranean forest development during deglaciations ~~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 that is favoured by arid conditions (Sage, 2017). Unfortunately, ~~but with~~ pollen analysis cannot discriminate ~~, there is no confidence about the~~ Poaceae and Cyperaceae pollen ~~morphologic types~~morphotypes ~~being~~from 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 to represent C4 plants in Iberia as we know that less than 10% of the grasses in this region belong to C4 plants at present (Casas-Gallego et al., 2025) (Fig. 3g). Across the last deglaciation, t~~T~~his 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. 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. In laboratory studies, C3 grasses outperform 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 C3 and C4 plants perform equally. This crossover depends on both temperature and CO_2 levels. Modeling across 0–45°C and CO_2 levels from 150–700 ppm shows that whether C3 or C4 plants are favored is determined by the interaction between these two factors, unfortunately humidty was not considered ~~(And humidity???)~~(Ehleringer et al., 1997; Edwards et al., 2010). ~~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).~~ 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, most of the ~~a recent studty as demonstrated that~~ C4 plants ~~in Iberia, nowadays comprise less than 10% of the grasses (Casas-Gallego et al., 2025), C_4 plants nowadays are mostly they~~ are confined to the tropical grasslands and savannahs; ~~they are~~being 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 vegetation in SW~~the~~ Iberia after the LGM (Fig. 3 and 5) should be mainly composed of~~by~~ C_3 plants; considering the estimated SSTs indicating relatively cold temperatures (Fig. 5) and the high percentages of *Artemisia* spp (C_3 plant) (~~S.M.~~SM Fig. S1).

However, it is not currently possible to entirely rule out an increased importance of C_4 plants in the glacial vegetation of~~in~~ SW Iberia~~the IP~~, because pollen morphology does not allow the separation of these groups. 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 implement. There is important scope for further study of ~~and~~ biomarker~~s~~ proxies ~~have not been tested or reported~~ to clarify the dynamic between C_3/C_4 plants in the Temperate/Mediterranean (Warm-temperate) 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 implement.~~ This highlights the ~~theoretical possibility of the~~ fact that C_3/C_4 plant dynamic observed in Africa (e.g. Dupont et al., 2019) and other savannahs ecosystems is not ~~being~~ replicable ~~(with the current knowledge)~~ in our study area so far. Biomarker species/groups fingerprinting studies are required in order to ~~eventually~~ distinguish between C_3 and C_4 plants and ~~then go onto exploring~~ test for an increased abundance of ~~the dynamics observed between C_3 and~~ C_4 plants~~,~~ within Iberian~~P~~ Mediterranean ecosystems during the last deglaciation.

5~~6~~. Conclusion

This study presents high-resolution pollen and~~n~~ ~~and~~ SST records from Site U1385 off the SW Iberian Margin, offering valuable data for understanding ~~regional terrestrial-marine interaccations~~past vegetation dynamics ~~in the which can be used in future regional and global reconstructions and models, especially for the Iberian Peninsula~~ 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 negatively with TMF, revealing its potential as a proxy of aridity in the Mediterranean region).

The ~~enhanced~~high temporal resolution analysis and robust radiocarbon chronology allow~~ a~~ consistent and more accurate comparisons with regional datasets, making this study a valuable contribu~~i~~tion for future palaeo~~e~~nvironmental reconstructions and model simulations.~~.~~ ~~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.~~ Rather than simply interpreting our dataset in terms of past temperature and precipitation changes, we examine the U1385 record 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. ~~Our analysis focus on Besides, our study~~We suggest~~s~~ that low pCO_2 acted~~s~~ as a modulator of vegetation response during the LGM. Cold temperatures, low seasonality, and exacerbated drought stress resulting from plant physiological impacts of ~~—partly (mostly?) driven by~~ low pCO_2 likely restricted forest growth ~~-~~while favoring heathlands. Traits of Mediterranean Ericaceae, such as deep roots and thick waxy leaves, may have given these plants a competitive advantage

During ~~Heinrich Stadial 1 (~~HS1~~)~~, woody vegetation was significantly suppressed due to cold and arid conditions, exacerbated by low atmospheric pCO_2 levels. ~~This was followed by a~~The subsequent notable expansion of temperate Mediterranean forests (TMF) during the Bølling-Allerød (BA) was~~,~~ driven by warmer and moister conditions~~, an increase in seasonality (No, there is lower seasonality during the Greenland Interstadials, such as the B-A, than during the colder phases such as the Heinrich Stadials when winter are very cold and summer temperatures remain high.~~ 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 increased moisture availability and sustained higher pCO_2 levels.

~~the dynamics of~~

~~We explore the understanding of TMF dynamics under the influence of climatic change and increasing~~ ~~pCO_2~~ ~~throughout the LGM and deglaciation.Special attention was given to the role of 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 modulatoryet critical in modulation change. The significant findings that emerge form this study arerelated with:~~

~~**Vegetation Dynamics Across Major Climate Transitions**: during Heinrich Stadial 1 (HS1), woody vegetation was significantly suppressed due to cold and arid conditions, exacerbated by low atmospheric~~ ~~pCO_2~~ ~~levels. This was followed by a notable expansion of temperate Mediterranean forests (TMF) during the Bølling-Allerød (BA), driven by warmer and moister conditions, an increase in seasonality, and rising~~ ~~pCO_2~~ ~~concentrations. During the Younger Dryas (YD), despite a return to colder temperatures, forest–grassland mosaics persisted—primarily supported by increased moisture availability and sustained higher~~ ~~pCO_2~~ ~~levels.~~

~~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.~~

Furthermore, our study ~~identifies~~supports a ~~Low pCO_2 as a Modulator of Vegetation During the LGM: Cold temperatures, low seasonality, and exacerbated drought stress—partly driven by atmospheric pCO_2 depression—likely restricted forest growth while favoring heathlands. Traits of Mediterranean Ericaceae, such as deep roots and thick waxy leaves, may have given these plants a competitive advantage.~~

~~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.~~

c~~C~~ritical pCO_2 t~~T~~hreshold for f~~F~~orest e~~E~~xpansion during the deglaciation ~~that is~~at ~~(~~~225 ppmv~~): The study identifies~~ . Below this value, arboreal populations were generally restricted in their development (e.g. LGM) and the impact of climatic aridification and cooling (e.g. HS1) was detrimental. Above this value, arboreal populations developed strongly (e.g. BA) and the impact of climatic deterioration (e.g. YD) was moderated. ~~a pCO_2 concentration of ~225 ppmv as a critical lower threshold for TMF expansion during the deglaciation.~~ This value aligns with several observations from Mediterranean to the tropical African environments (e.g. Dupont et al., 2019; Oliveira et al.,2020; Koutsodendris et al., 2023; Sánchez-Goñi et al., 2023~~)~~). ~~previous cold stages (e.g., MIS13 – Olivbeira et al., 2020) (But MIS 13 is not a cold stage!!!), and other locations and~~The concept should be further tested in regional vegetation models~~s~~ to determine the ~~ecological~~vegetation response~~ range~~ to pCO2 fluctuations ~~$_2$ on regional vegetation, as well as, in~~ during past cold periods.

~~Implications for Present and Future Climate Change:~~ Our f~~F~~indings highlight the importance of pCO_2 as a key driver of vegetation change in ~~arid and semi-arid systems~~the Mediterranean region through its influence on moisture availability in plants (Koutsodendris et al., 2023). The paleo-data offer~~ a~~ valuable ~~analogue~~context for ~~predicting~~elucidating vegetation responses under future climate scenarios involving rising CO_2 and shifting precipitation patterns. They also highlight~~ths~~ the need ~~of~~for ~~paying~~ further ~~attention~~investigation of~~ to~~

t~~T~~he relationship between long-chain *n*-alkanes and present-day vegetation and C_3/C_4 plants ratio as the long-chain alkanes do not yet provide a reliable ~~picture~~basis to disentangle the dynamic between woody plants and grasses~~ 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 periodsin the Mediterranean region., albeit in a regionally-specific way, and noting that this is not in agreement with previous inferences 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. FuFurthermore, 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
*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)

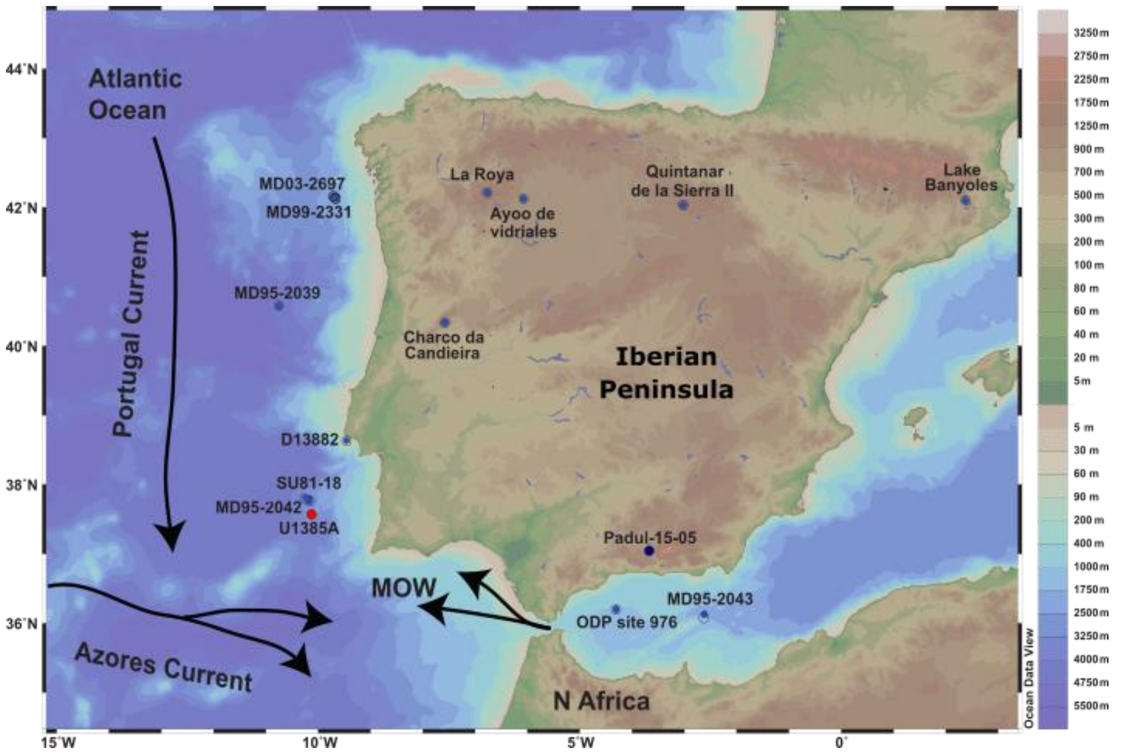
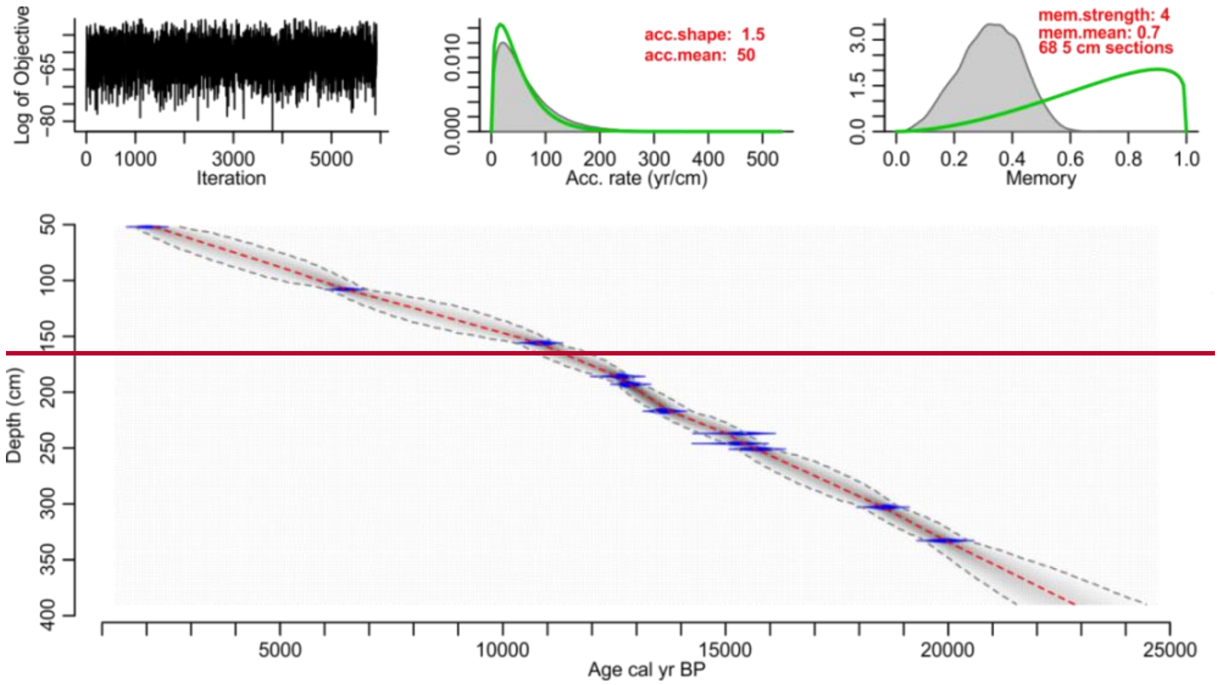


Figure 1 – Location of the IODP Site U1385 and of the marine and terrestrial pollen records discussed in the text. Marine sedimentary records: MD03-2697 (Naughton et al., 2016); MD99-2331 (Naughton et al., 2007); MD95-2039 (Roucoux et al., 2005); D13882 (Gomes et al., 2020); MD95-2043 (Fletcher and Sánchez Goñi, 2008); MD95-2042 (Chabaud et al., 2014); SU81-18 (Turon et al., 2003); ODP Site 976 (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.


Log of Objective
−65
−80
0
1000
3000
5000
Iteration
0.000
0.010
acc.shape: 1.5
acc.mean: 50
0
100
200
300
400
500
Acc. rate (yr/cm)
0.0
1.5
3.0
mem.strength: 4
mem.mean: 0.7
68 5 cm sections
0.0
0.2
0.4
0.6
0.8
1.0
Memory
Depth (cm)
50
100
150
200
250
300
350
400
5000
10000
15000
20000
25000
Age cal yr BP

~~**New fig.**~~

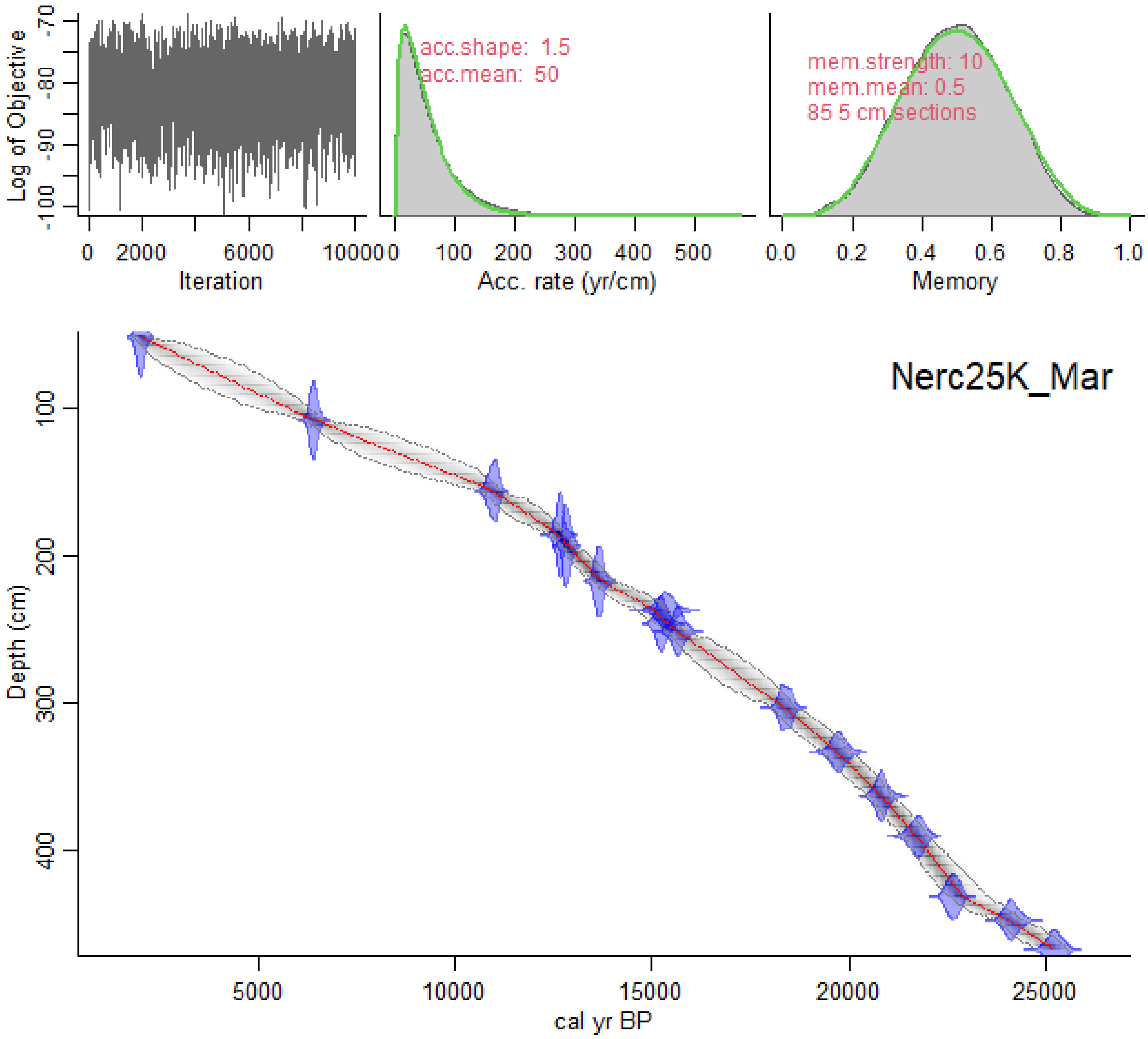
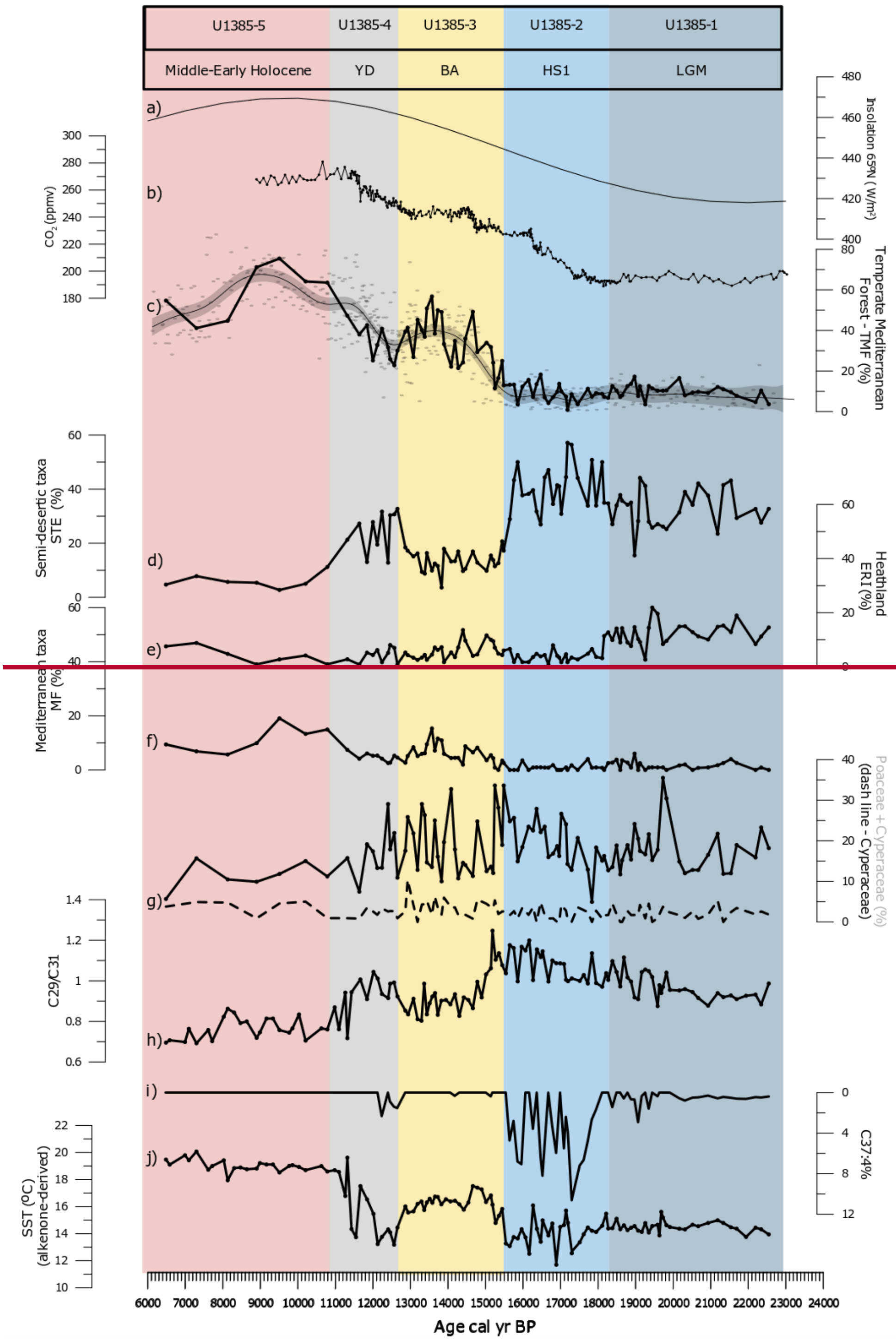


Figure 2 – Age-depth model for IODP Site U1385 using a Bayesian approach with Bacon v.2.3.9.1 (Blaauw and Christen, 2011). The original dates were calibrated using Marine20 (Heaton et al., 2020) grey stippled line show 95% confidence intervals; red curve shows single "best" model based on the mean age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


U1385-5
U1385-4
U1385-3
U1385-2
U1385-1
Middle-Early Holocene
YD
BA
HS1
LGM
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
Insolation 65ºN (W/m²)
480
460
440
420
400
CO₂ (ppmv)
300
280
260
240
220
200
180
Temperate Mediterranean Forest - TMF (%)
80
60
40
20
0
Semi-desertic taxa STE (%)
60
40
20
0
Heathland ERI (%)
60
40
20
0
Mediterranean taxa MF (%)
60
40
20
0
Poaceae + Cyperaceae (%) (dash line - Cyperaceae)
40
30
20
10
0
C29/C31
1.4
1.2
1
0.8
0.6
C37:4%
0
4
8
12
SST (ºC) (alkenone-derived)
22
20
18
16
14
12
10
6000
7000
8000
9000
10000
11000
12000
13000
14000
15000
16000
17000
18000
19000
20000
21000
22000
23000
24000
Age cal yr BP

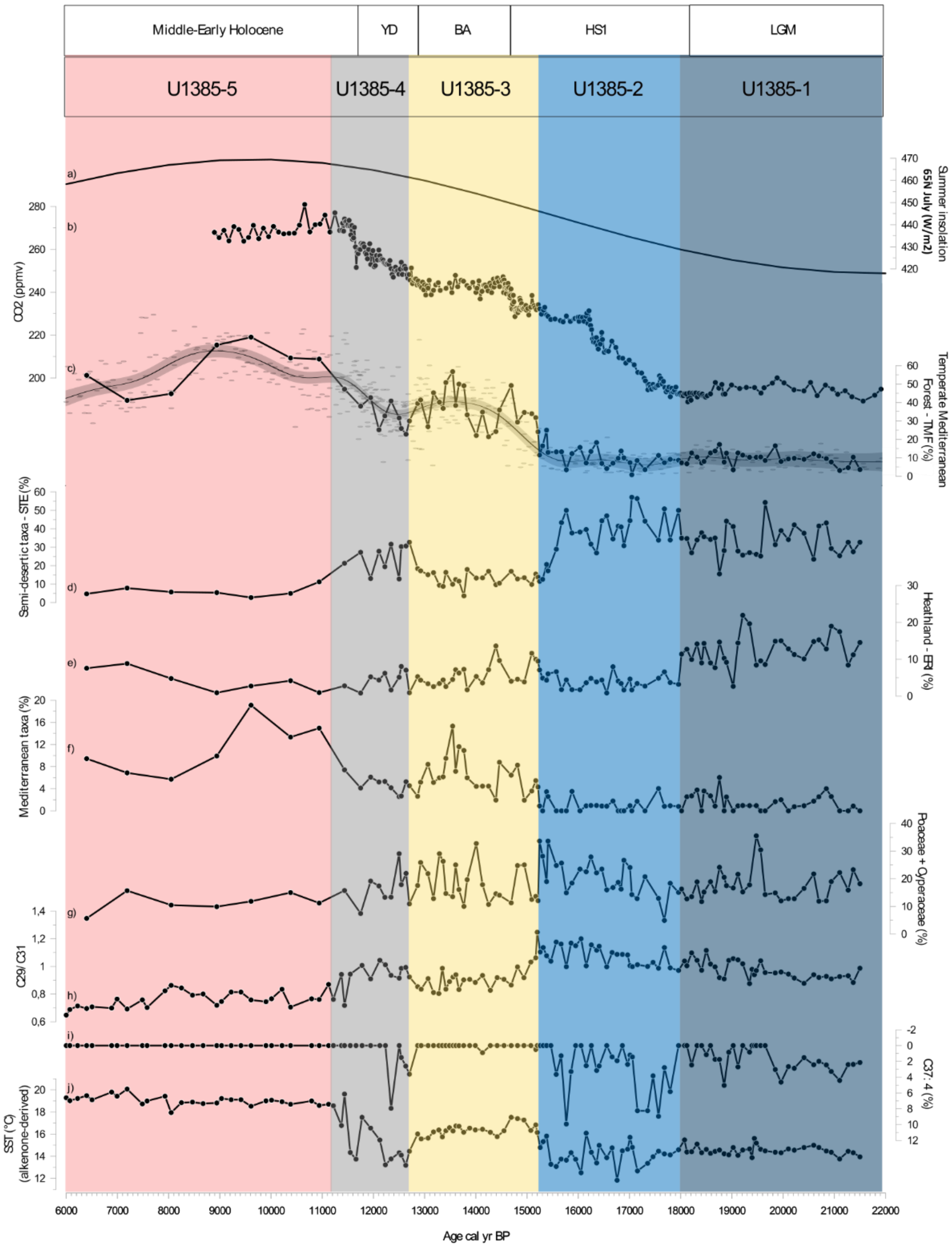


Figure 3 – Comparison of multiproxy records from the Site U1385 with a) 65˚N July (W/m^2) summer insolation (Berger and Loutre, 1991) ~~and~~ b) CO2 (ppmv) composite from WAIS (Marcott et al., 2014) ~~; b) CO$_2$ (ppmv)~~(; Principal pollen-based ecological groups: c) Temperate Mediterranean Forest from Site U1385 (%) (solid black line) and c~~C~~ompilation of Iberian Margin TMF records (D13882, MD03-2697; MD95-2042; MD95-2043; ODP-976; U1385) – GAM (curve with grey (%), d) Semi-desertic taxaincluding *Amaranthaceae* (previously *Chenopodiaceae*), *Artemisia*, and *Ephedra*. (%), e) Heathlandincluding members of the *Ericaceae* family (including various *Erica* spp) and *Calluna* spp (%), 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. S1 and ~~S.M.~~SM Table S1) and were connected with the periods indicated.

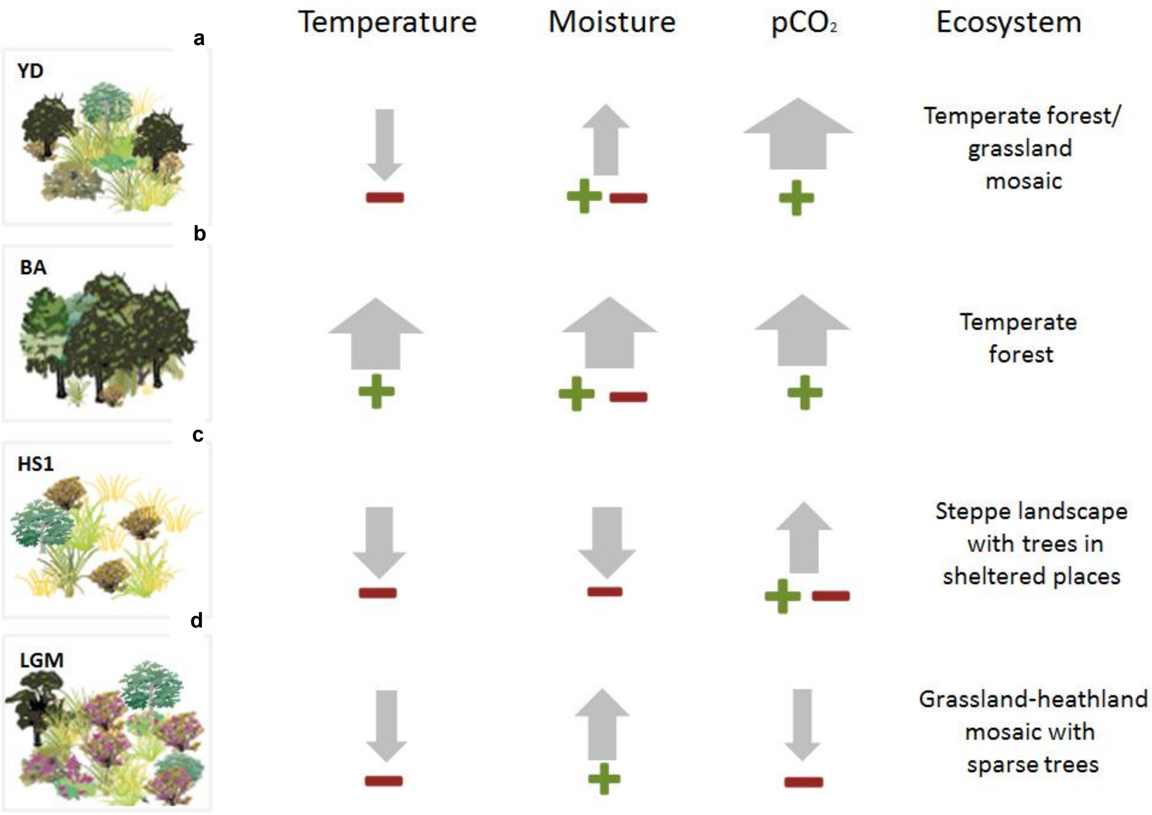


Figure 4 – Schematic representation of the ~~influence~~relative change of climatic inferred parameters (precipitation and temperature) based on pollen-vegegation groups, biomarkers, SST as well as the physiological contribution of CO_2 for each period showing a schematic reconstruction of the potential 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).

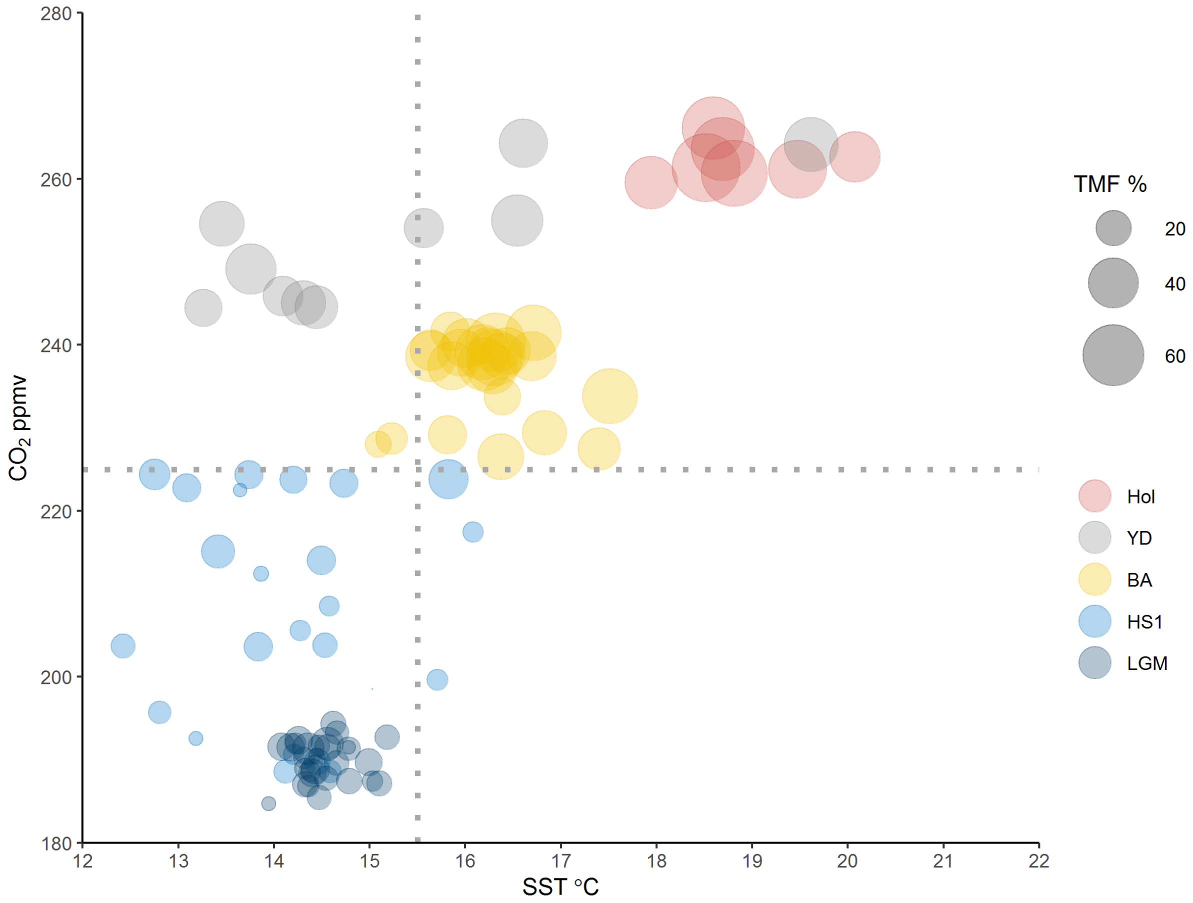


Figure 5 – Dispersion plot showing the relation between CO_2 (Marcott et al., 2014) and SST in relation to TMF % across the different intervals of the deglaciation, following the pollen zones boundaries.