

Author's response to Editor

Dear Sandra,

We have now evaluated the manuscript together with two reviewers. Both suggest another moderate revision. I am giving you another chance to incorporate their suggestions and also resolve following issues:

Shorten and focus the introduction (as suggested by rev #2)

Add more detail on constructing the age-depth model (model parameters that are not obvious from methods or results)

Please use the full names of the periods in the subsection titles in the results/discussion section, also use the dating

Add data accessibility statement - where is the primary data, or will it be accessible upon publication?

Dear editor Petr Kuneš,

Thank you for your constructive comments and for giving us the opportunity to further improve our manuscript. We are very grateful for the thoughtful feedback provided by both you and the reviewers, which has guided us in strengthening the clarity and focus of the paper.

As requested, we have made the following additional revisions:

- **Introduction:** The section has been shortened and focused to better frame the study within its key objectives and relevance.
- **Chronological framework (Methods 3.1):** We have added details on the construction of the age–depth model, including model parameters and a clarification of how chronological uncertainties were handled.
- **Results/Discussion structure:** The subsection titles now use the full names of the climatic periods and their corresponding chronological ranges for greater clarity and consistency.
- **Data accessibility:** We have introduced the following statement:

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

We are resubmitting the revised manuscript together with a “Track Changes” version that highlights all modifications made. We believe these updates, in combination with our previous revisions, have addressed all the points raised by you and the reviewers.

We sincerely thank you again for your valuable guidance throughout the review process and look forward to your further evaluation.

Kind regards,

Sandra D. Gomes, on behalf of the co-authors

Author's responses to Reviewer#1:

I greatly value the time and constructive comments you have provided on the paper I submitted.

The revised manuscript distinguishes more clearly between climatological moisture availability and perceived dryness by plants (due to either changes in climatological moisture availability or changes in water use efficiency in response to different atmospheric CO₂ concentrations). However, in my opinion, the term moisture availability should refer only to a climate variable (a function of precipitation, soil moisture, evapotranspiration and/or potential evapotranspiration) and not the perceived dryness by plants. Therefore, I would recommend to not use "moisture availability" when referring to the perceived moisture availability by plants (e.g., in Fig. 4), but either "perceived dryness" or "perceived moisture availability".

Response: We thank the reviewer for this valuable comment and agree that the term "moisture availability" could be reserved for climate-related variables (precipitation, soil moisture, evapotranspiration, and/or potential evapotranspiration). After discussion, we considered the suggested term "*perceived moisture availability*," but we feel that the notion of "*perception*" could imply sensory mechanisms, which may be misleading in the context of plant physiology. As an alternative, we have adopted the term "*plant-available moisture*" throughout the manuscript, which we believe better captures the intended meaning while maintaining scientific clarity and avoiding confusion.

- I. 62-66: The last two sentences of the abstract are rather difficult to understand. Maybe you can reformulate them to convey a clearer message.

Response: The last two phrases were reformulated to better convey the message "*Our study suggests that during cold and humid periods (LGM and YD) different pCO₂ values lead to contrasting SW Iberian vegetation responses. In contrast, temperature and precipitation changes during periods of relatively high pCO₂ play the main role in shaping the distribution and composition of the vegetation.*"

- I. 75-76: A "global mean temperature increase of 5-10°C" is not in line with recent studies by Annan et al. (2022), Osman et al. (2021), and Tierney et al. (2020). Please update the provided range accordingly.

Response: We thank the reviewer for this helpful suggestion. We have updated the statement to align with recent studies. The revised text now reads:

"The last deglaciation, spanning 20–19 cal. kyr BP (e.g., Denton et al., 1981; Toucanne et al., 2008; Denton, 2010) to ~7 cal. kyr BP (e.g., Dyke and Prest, 1987; Carlson et al., 2008), was

marked by a global annual mean surface air temperature increase of ~5°C (Annan et al., 2022), during progressive melting of Northern Hemisphere glaciers. ”

This change removes the outdated 5–10°C range and reflects the more constrained estimates provided by recent studies.

- I. 77-79: It should be noted that the warming/cooling during HS1/BA/YD refers mainly to the North Atlantic region (or the Northern Hemisphere). In the Southern Hemisphere, the changes during these periods are (partly) different.

Response:

We thank the reviewer for this useful clarification. To address this point, we have specified the geographical context by adding “during progressive melting of Northern Hemisphere glaciers” at the end of the referred statement.

- I. 294: ”basis” instead of ”basin”.

Response: We thank the reviewer for noting this typo. The word “*basin*” has been corrected to “*basis*.”

- I. 363: Consider using ”the modern environmental space” instead of ”the environmental space”

Response: We thank the reviewer for this helpful suggestion. We have revised the text to use “*the modern environmental space*” for clarity, and we have also updated the caption of Fig. S2 accordingly.

- I. 473: I suggest to use ”reconstructed” instead of ”modelled”.

Response: We thank the reviewer for this suggestion. The term “*modelled*” has been replaced with “*reconstructed*” as recommended.

- I. 1229: In the brackets, it should be ”perceived moisture availability” or ”perceived dryness” instead of ”precipitation”

Response: As discussed previously we changed it to “*plant-available moisture*”.

Author's responses to Reviewer#2:

We greatly value the time and constructive comments you have provided on the paper I submitted.

General comments:

Modify the introduction because it is long and complex, covering multiple concepts (climate dynamics, CO₂ physiology, modelling uncertainties, regional paleoecology), which overwhelms readers and hides the main message.

Response: The introduction was shortened and organized to better reflect the paper's message.

Strengthen the discussion on why approximately 225 ppmv is a critical threshold (link to plant physiology studies).

Response: We thank the reviewer for this valuable suggestion. In the revised manuscript, we have strengthened the discussion on why ~225 ppmv represents a critical threshold for vegetation development by integrating insights from plant physiology studies. Specifically, we introduced a new sentence in the *Introduction*: *"This plasticity in stomatal frequency is considered an adaptive trait that evolved under declining Cenozoic CO₂ levels, enabling plants to sustain carbon uptake as concentrations approached glacial minima (~180–190 ppmv), though at the cost of greater water loss (Wagner et al., 1997)."* Additionally, in the *Discussion* (section 4.1.1), we now state: *"However, modelling approaches indicate that in C₃ plants, photosynthetic capacity declines sharply once atmospheric CO₂ falls below ~300 ppmv, making carbon assimilation increasingly limiting for plant growth (Wagner et al., 1997)."* These additions explicitly link the proposed ~225 ppmv threshold to well-established physiological mechanisms, while emphasizing that it should be interpreted as a critical range rather than a fixed universal limit.

Address biomarker uncertainties with more explicit caveats.

Response: We thank the reviewer for pointing out the need to more explicitly acknowledge biomarker-related uncertainties. In the revised manuscript, we have expanded section 3.4 (Methods) to state:

"Nevertheless, uncertainties remain, since U^k₃₇ SST reconstructions may be affected by calibration biases, seasonal and ecological effects related to coccolithophorid production, and potential lateral transport or diagenetic alteration of alkenones (e.g., Conte et al., 2006; Ausín et al., 2022). Therefore, while the derived SSTs provide reliable insights into large-scale temperature variability, they should be interpreted with caution regarding the magnitude and seasonality of past changes."

This addition highlights the caveats more explicitly while reinforcing the robustness of the trends we report.

Conte, M. H., Sicre, M.-A., Rühlemann, C., Weber, J. C., Schulte, S., Schulz-Bull, D., and Blanz, T.: Global temperature calibration of the alkenone unsaturation index (UK'37) in surface waters and comparison with surface sediments, *Geochem. Geophys. Geosyst.*, 7, Q02005, <https://doi.org/10.1029/2005GC001054>, 2006.

Ausín, B., Haghipour, N., Bruni, E., and Eglinton, T.: The influence of lateral transport on sedimentary alkenone paleoproxy signals, *Biogeosciences*, 19, 613–627, <https://doi.org/10.5194/bg-19-613-2022>, 2022.

Typographical and stylistic issues, including mixing British and American English, should be corrected for clarity and consistency (see line-by-line comments).

Response: We sincerely appreciate the reviewer's careful attention to typographical and stylistic issues. All spelling, grammar, and punctuation errors have been corrected, and the manuscript has been revised for consistency. We have also standardized the use of English throughout the text to maintain clarity, avoiding mixing British and American conventions.

Specific comments

In Methods (3.1. Chronological framework), the authors need to briefly describe why the combination of monospecific and mixed foraminiferal assemblages was used for dating. Are there implications for age reliability? You also clarify whether the chronological uncertainty from the Bacon model was incorporated into subsequent analyses.

Response: We have modified the Methods section (3.1 Chronological framework) to clarify the rationale for using a combination of monospecific and mixed foraminiferal assemblages:

*"A new set of eleven samples for AMS ¹⁴C analysis was selected primarily from monospecific assemblages of *G. bulloides*. When sample size requirements could not be met, a mixed assemblage of *G. bulloides* and *G. inflata* was used. All samples were processed at the Keck Carbon Cycle AMS Facility, University of California, Irvine (Table 1)."*

As standard practice, monospecific *G. bulloides* assemblages are preferred for radiocarbon dating. Mixed assemblages are used only when sample weight is insufficient. While potential age offsets may exist in mixed assemblages, these are generally modest and context-dependent. Previous studies have addressed similar issues, such as Barker et al. (2007) for the North Atlantic and Ausín et al. (2019) for the Iberian margin (though using *G. ruber*). The ERC project *Passenger* also highlights challenges related to age offsets and reservoir differences across deglaciation events.

Regarding the age model, the *Bacon* software incorporates chronological uncertainty by using Bayesian modelling of accumulation rates and the probability distribution of each radiocarbon date. We included calibration using the Marine20 curve, which accounts for reservoir effects.

While the age model does not aim for ultra-high precision in dating well-known deglacial events, it provides a robust and regionally consistent chronological framework suitable for the goals of this study.

In Methods (3.2. Pollen analysis), the reason for excluding aquatic plants and spores from the total could be briefly explained for non-specialist readers.

Response: We have revised the Methods section (3.2 Pollen analysis) to provide the requested explanation for non-specialist readers. The sentence now reads:

"Aquatic plants and spores were excluded because their abundant pollen originates in or near water bodies and can be transported far from their source, potentially overrepresenting regional vegetation. Pinus pollen, which is typically overrepresented in marine deposits, is transported by rivers from the Tagus and Sado's watersheds (Naughton et al., 2007). In contrast, the overrepresented *Cedrus* is transported by wind from the Atlas or Rif mountains in Morocco. Both overrepresented taxa were also excluded from the main sum."

In Methods (3.3 Compilation of Iberian margin pollen records), the authors can indicate whether chronological alignment or any synchronization across sites was performed, or if all records rely solely on published age models. The GAM model parameters are well-described; however, a brief explanation of why $k = 30$ and $sp = 0.0001$ were chosen would strengthen the statistical justification.

Response:

We have revised the Methods section (3.3 Compilation of Iberian margin pollen records) to clarify the chronological framework and GAM justification.

All Iberian margin pollen records rely on published age models; no additional chronological alignment or synchronization across sites was performed. For clarity we add to that particular sentence this " *without any additional alignment or synchronization*"

The GAM model was fitted using the gam() function of the mgcv package (version 1.8.24; Wood, 2017) in R (version 3.6.3; R Core Team, 2020). We used a standard GAM with REML smoothness selection, specifying 30 basis functions ($k = 30$) and a smoothing parameter of 0.0001 ($sp = 0.0001$). The relatively high k allowed the model to capture potential nonlinear patterns in the data without overfitting, while the small sp ensured sufficient smoothness; these values were selected after exploratory analysis and diagnostic checks. To assess the validity of the smooth terms and confirm that the basis functions adequately captured the data wiggleness, we applied the gam.check() function. The resulting k -index was greater than 1, and the p -values supported the hypothesis that sufficient basis functions were used. The fitted GAM curves for TMF are presented along with approximate 95% confidence intervals (Simpson, 2018).

In the Results and Discussion section, although the content is dense and scientifically rich, some parts, especially 4.1.1, 4.1.2, and 4.2, would benefit from clearer and more concise organization. The authors might consider dividing long paragraphs into thematic subsections (e.g., separating observational results from interpretive

commentary). There is a slight imbalance between the narrative discussion and data presentation. It could be helpful to include more direct references to quantitative changes (such as percentage increases/decreases, Δ SST, pCO₂ rise rates) within the text to more explicitly connect interpretations to measured trends.

Response: Thank you for this constructive feedback. In response, we have reorganized Sections 4.1.1, 4.1.2, and 4.2 to improve clarity and readability. Long paragraphs have been divided into thematic subsections, starting with vegetation and climate-inferred observations, followed by model-based evidence, and concluding with an interpretive synthesis. This structure allows the reader to follow the progression from data presentation to interpretation more clearly.

All quantitative information, including pollen percentages, SST minima and maxima, and pCO₂ changes, was already included in the original manuscript. Our main effort in this revision was therefore focused on simplifying complex sentences, breaking up dense paragraphs, and improving the overall flow of the text. Figure 5 has also been emphasized in the interpretive synthesis to visually integrate TMF, SST, and pCO₂ data, helping to guide the reader through the key trends.

We believe these revisions address the reviewer's concerns regarding organization and readability while maintaining the richness of the scientific content.

The identification of a potential pCO₂ threshold (~225 ppmv) for forest development is compelling and well-supported by cross-referenced records. However, some statements treat this threshold as fixed or universal. Consider emphasizing that thresholds may vary by taxa, edaphic conditions, or microclimate, and explicitly acknowledge uncertainties in this area.

Response: We thank the reviewer for this valuable comment. In the revised manuscript (Section 4.1.2), we have clarified that the ~220–225 ppmv pCO₂ values should not be considered a fixed universal threshold, as they likely vary depending on plant taxa, edaphic conditions, and microclimate. We have also emphasized the uncertainties associated with defining strict thresholds, given the lack of experimental studies testing forest development under very low pCO₂ levels (most existing work focuses on high pCO₂ impacts). To strengthen this point, we now note that modelling approaches indicate photosynthetic capacity in C₃ plants declines sharply once atmospheric CO₂ concentrations fall below ~300 ppmv, making carbon assimilation increasingly limiting for growth (Wagner et al., 1997). The revised paragraph therefore highlights both the potential role of low pCO₂ in constraining forest development during the LGM and the importance of interpreting these values as a critical range rather than a fixed limit.

Wagner F., Below R., de Klerk P., Dilcher D. L., Joosten H., Kürschner W. M. & Visscher H. (1997). *A natural experiment on plant acclimation: lifetime stomatal frequency response of an individual tree to annual atmospheric CO₂ increase*. Proceedings of the National Academy of Sciences of the United States of America, 93(21), 11705–11708. <https://doi.org/10.1073/pnas.93.21.11705>

The discussion on C29/C31 ratios is thoughtful and cautiously presented, but it could be clearer by organizing it to distinguish between established knowledge, such as the

plant physiology of leaf waxes, site-specific observations like correlations in U1385, and interpretive hypotheses, including stress responses versus vegetation shifts. The latter should be explicitly marked as speculative or needing further validation.

Response: We thank the reviewer for the insightful suggestion. In response, we have reorganized section 4.2 on C₂₉/C₃₁ ratios to clearly distinguish between established knowledge, site-specific observations, and interpretive hypotheses, as suggested. We have also revised the wording regarding the variability of n-alkane production across species and regions. This phrasing emphasizes the limitations of using the C₂₉/C₃₁ ratio as a strict taxonomic proxy while maintaining the context for interpreting site-specific patterns at U1385. ***The treatment of C₃/C₄ dynamics is detailed and shows scepticism toward simple explanations. The authors correctly highlight the limitations of pollen resolution and suggest promising future directions, such as isotopic or compound-specific research. However, this section could benefit from a summary that outlines the current data limitations and reinforces why C₃ dominance remains the most supported interpretation for SW Iberia during this period.***

Response: We thank the reviewer for this constructive comment. Following the suggestion, we have added a concluding paragraph to this section that, in our understanding, flows from the current uncertainties and highlights the need for future isotopic and biomarker research, while also emphasizing that the available evidence supports C₃ dominance in SW Iberia during deglaciation. The added text reads:

"In summary, although future isotopic and biomarker approaches hold great promise for resolving C₃/C₄ dynamics, the current evidence strongly supports C₃ dominance in SW Iberia during deglaciation. This interpretation is consistent with the modern distribution of plants in the region, where less than 10% of grasses are C₄ (Casas-Gallego et al., 2025), and with the prevailing cool and humid conditions of the LGM and YD, which favour C₃ over C₄ photosynthesis. Thus, while acknowledging the limitations of pollen-based proxies, the available data indicate that C₃ plants were the dominant contributors to the Iberian vegetation signal."

The hypothesis that pCO₂ played a significant and previously underrecognized role in governing vegetation development during the last glacial cycle is compelling and well-supported. This discussion makes a valuable contribution to debates in paleoclimatology, paleoecology, and vegetation modelling, although future data-model comparisons and experimental validations will be crucial to test some of the more speculative physiological mechanisms proposed.

Response: We fully agree with this assessment. In our effort to explore this further, we contacted some vegetation modellers to attempt simulations for the YD and LGM. However, as we understood, the temporal resolution and computational resources required made such simulations challenging at that time. We remain very open to collaborating on future model-data comparisons, particularly at a regional scale, to further test the proposed physiological mechanisms.

Line-by-line comments

Response: We sincerely appreciate the technical comments regarding spelling, grammar, and punctuation, and have corrected them for consistency in the revised manuscript.