

Author's response to Editor

Dear Sandra,

Thank you for your thorough responses to reviewers' comments. Based on those, I have decided your manuscript needs a major revision. Please revise your text accordingly based on your responses to the specific comments. Please also focus on the general clarity of the text mentioned by both reviewers.

Dear editor Petr Kuneš,

Thank you for your comments and for the opportunity to revise our manuscript. We greatly appreciate both your feedback and that of the reviewers, which have been invaluable in significantly improving the quality of our work.

We are pleased to submit the revised version of the manuscript, along with a "Track Changes" document that highlights all the modifications made. Below, we provide detailed responses to each reviewer comment, with the original comments presented in bold, followed by our point-by-point replies. Please note that some of our responses have been slightly revised as well, reflecting adjustments made during manuscript editing to improve clarity and to be more direct.

As requested, we have carefully revised the manuscript throughout to improve its readability and clarity. In particular, the **Abstract** and **Introduction** have undergone substantial rewriting to better communicate the research aims and findings. Additionally, to streamline the presentation, we have merged Section 4.2 and incorporated with previous discussion in Section 5.1, now it stands as results and discussion section 4. This restructuring helps deliver a more cohesive, less repetitive and concise narrative.

We have also introduced the majority of the suggested references, along with several new and relevant citations to strengthen the contextual framework of our study. Furthermore, we have upgraded two figures to enhance their readability and ensure clearer visualization of our results.

We believe these revisions have significantly strengthened the manuscript and addressed all concerns raised by the reviewers. We sincerely thank you and the reviewers again for your constructive feedback, which has contributed greatly to improving the overall quality and impact of our work.

We look forward to your further evaluation.

Kind regards,

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

Author's responses to Reviewer#1:

a) General comments:

While the topic of the manuscript is suitable for publication in BG, the paper is rather difficult to read without a strong paleoclimate background due to using a lot of not properly introduced paleoclimate jargon. Since BG is not a paleo-specific journal and the manuscript topic could also gather interest from outside the paleo-community, it would be valuable if you could make it easier to follow for non-paleo scientists.

Response: We sincerely appreciate your feedback and recognize the importance of making this study accessible to a broader interdisciplinary audience. Our research integrates multiple fields, including ecology, palynology, biogeochemistry, quantitative analyses, paleoclimatology, modeling, and functional ecology, all of which contribute to understanding the complex interactions between climate change and various environmental variables over time.

We acknowledge that some paleoclimate-specific terminology may not be familiar to all readers, particularly those outside the paleo-community. Given that *Biogeosciences* is not exclusively a paleo-focused journal, **we have defined key** paleoclimate terms and concepts more clearly to ensure accessibility for a wider readership.

Thank you for your constructive comments. We have improved the manuscript to better serve the diverse scientific community interested in land-ocean ecosystem interactions and their broader implications within the scope of *Biogeosciences*.

In Sect. 4.2, vegetation changes are directly associated with warmer/colder and wetter/drier conditions. Since the main conclusion of the manuscript is a potentially larger role for CO₂ than previously thought, I find this confusing and would recommend a more careful wording when inferring climatic conditions from the vegetation composition. In particular, it should be clarified that the interpretations are just describing changes "felt" by the plants but not necessarily actual climatic changes (unless they are supported by vegetation-independent proxies).

Response: The paleoclimatic conditions inferred in our study are based on pollen-derived vegetation groups, which serve as indicators of variations in temperature, precipitation, and other climate-related factors. Since atmospheric CO₂ strongly influences moisture availability, our interpretations provide a qualitative assessment of relative climate changes rather than absolute quantitative reconstructions. To improve clarity and avoid repetition, we have merged this section with the previous Section 5.2, integrating the results and discussion within the new Section 4.1. Additionally, we have revised the Methods section (Lines 263–266) to explicitly clarify the scope of our climate inferences as follows: *"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)."*

Williams, J.W., Shuman, B.N., Webb, T., Bartlein, P.J., and Leduc, P.L.: Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes, *Ecological*

Monographs, 71, 305–331, [https://doi.org/10.1890/0012-9615\(2001\)071\[0305:LQVDIN\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0305:LQVDIN]2.0.CO;2), 2001.

The role of moisture availability variations remains largely unconstrained in the manuscript which complicates the attribution of the vegetation variability to temperature and/or CO₂ changes. The spatial pattern of SST anomalies in the North Atlantic was likely different between HS1 and YD (e.g., Pedro et al., 2022; Weitzel et al., 2024) which could lead to differing precipitation amounts during HS1 and YD. To what extent can you rule out that the moisture availability conditions during the YD were more favorable for forest development than during HS1/LGM? If you cannot constrain the moisture availability changes better at this point, this should be stated as a limitation.

Response: Moisture availability, alongside temperature, is inferred from our pollen-based vegetation groups. Pollen studies are essential in this context, as they enable reconstruction of past environmental conditions by leveraging the known ecological requirements of modern plant communities. As previously explained, the presence of steppe indicators is interpreted as evidence of drier conditions, whereas the transition toward heathland and forest assemblages suggests a shift to wetter environments.

We acknowledge the absence of independent precipitation proxies, as noted in line 544, and we have addressed this limitation in our discussion (lines 552–557) by considering the complementary information provided by climate simulations from Cutmore et al. (2021). We have updated the references accordingly to reflect these additions.

Cutmore, A., Ausín, B., Maslin, M., Eglinton, T., Hodell, D., Muschitiello, F., ... & Tzedakis, P. C.: Abrupt intrinsic and extrinsic responses of southwestern Iberian vegetation to millennial-scale variability over the past 28 ka. *J. Quat. Sci.*, 37(3), 420–440, <https://doi.org/10.1002/jqs.3392>, 2022.

b) Specific comments:

I. 60: What is meant by "variable moisture condition"?

Response: We change it to "generally wetter conditions" (now Line 59)

I. 91: Do the 5- 10°C refer to local, zonal mean, or global mean temperature changes? Please specify.

Response: The global temperature increases of 5 to 10 °C, depending on latitude, reported by Bard et al. (1987), Alley and Clark (1999), and Clark et al. (2012), are based primarily on sea surface temperature (SST) reconstructions derived from alkenone proxies, generally calibrated using the Müller et al. (1998) approach. These reconstructions represent *global mean SST*. To improve precision in our terminology, we have clarified this in Line 75 by specifying "global mean temperature representing global mean SST."

I. 114- 127: It would be worth mentioning that there are also previous studies inferring the importance of CO₂ changes for the vegetation evolution using multi-proxy approaches (e.g., Gosling et al., 2022; Koutsodendris et al., 2023) and model-data comparison (e.g., Adam et al., 2021). Of particular interest for this study, Koutsodendris et al. (2023) suggests a major role for CO₂ in modulating Mediterranean forest growth in Greece.

Response: We have introduced relevant information from *Gosling et al.* (2022) at Line 419, and from *Koutsodendris et al.* (2023) at Lines 125, 700 and 704 particularly within the Introduction and Discussion sections. Additionally, we have incorporated further references addressing multi-proxy approaches to provide broader context and strengthen our interpretations, and we have updated the reference list accordingly.

Clément, C., Martinez, P., Yin, Q., Clemens, S. C., Thirumalai, K., Prasad, S., Anupama, K., Su, Q., Lyu, A., Grémare, A., & Desprat, S.: Greening of India and revival of the South Asian summer monsoon in a warmer world. *Commun. Earth Environ.*, 5(1), 685, 2024.

Gosling, William D., Charlotte S. Miller, Timothy M. Shanahan, Philip B. Holden, Jonathan T. Overpeck, and Frank van Langevelde: A Stronger Role for Long-Term Moisture Change Than for CO₂ in Determining Tropical Woody Vegetation Change. *Science* 376 (6593): 653–56. <https://doi.org/10.1126/science.abg4618>, 2022.

Izumi, K., and Bartlein, P. J.: North American paleoclimate reconstructions for the Last Glacial Maximum using an inverse modeling through iterative forward modeling approach applied to pollen data. *Geophys. Res. Lett.*, 43(20), 10-965, <https://doi.org/10.1002/2016GL070152>, 2016.

Koutsodendris, A., Dakos, V., Fletcher, W. J., Knipping, M., Kotthoff, U., Milner, A. M., Müller, U. C., Kaboth-Bahr, S., Kern, O. A., Kolb, L., Vakhrameeva, P., Wulf, S., Christanis, K., Schmiedl, G., and Pross, J.: Atmospheric CO₂ forcing on Mediterranean biomes during the past 500 kyrs, *Nat. Commun.* 14, 1664, <https://doi.org/10.1038/s41467-023-37388-x>, 2023.

Wei, D., González-Sampériz, P., Gil-Romera, G., Harrison, S. P., and Prentice, I. C.: Seasonal temperature and moisture changes in interior semi-arid Spain from the last interglacial to the Late Holocene, *Quaternary Res.*, 101, 143–155, <https://doi.org/10.1017/qua.2020.108>, 2021.

I. 152: What simulations are meant here? As far as I know, most simulations of glacial vegetation include the effect of lower CO₂.

Response: Thank you for this valuable observation. You are correct that simulations of glacial vegetation include the effects of reduced atmospheric CO₂. The Introduction has undergone major restructuring to improve clarity and coherence, to avoid confusion, in this context this sentence was deleted.

Section 2: In addition to describing the current regional climate, it would be informative to.

Response: We have added a new paragraph to Section 2, “Materials and Environmental Setting,” addressing the biogeography of the region (Lines 191–201). This addition is supported by relevant and up-to-date references to provide a more comprehensive environmental context.

Asensi, A. and Díez-Garretas, B.: Coastal Vegetation, in *The Vegetation of the Iberian Peninsula*, edited by: Loidi, J., Plant and Vegetation, vol. 13, Springer, Cham, Switzerland, pp. 397–432, https://doi.org/10.1007/978-3-319-54867-8_8, 2017.

Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T.E., and Rivas-Sáenz, S.: Bioclimatology of the Iberian Peninsula and the Balearic Islands, in *The Vegetation of the Iberian Peninsula*, edited by: Loidi, J., Plant and Vegetation, vol. 12, Springer, Cham, Switzerland, pp. 29–80, https://doi.org/10.1007/978-3-319-54784-8_2, 2017.

I. 224: Is there a reason for not using IntCal20 instead of the older Marine13 calibration curve? Do you expect this to make a difference?

Response: We have re-run the model using the Marine20 calibration curve, incorporating additional radiocarbon dates. Please see the updated Section 3.1, Table 1, and Figure 2 for details.

Heaton, T.J., Köhler, P., Butzin, M., Bard, E., Reimer, R.W., Austin, W.E., Ramsey, C.B., Grootes, P.M., Hughen, K.A, Kromer, B., Reimer, P.J., Adkins, J., Burke, A., Cook, M.S., Olsen, J., Skinner, L.C. :Marine20—the marine radiocarbon age calibration curve (0–55,000 cal BP), *Radiocarbon*, 62(4), 779–820, <https://doi.org/10.1017/RDC.2020.68>, 2020.

Section 3.3: Why is the Villarquemado record not included in the regional compilation for which interesting work on the role of CO₂ exists (Wei et al., 2021)?

Response: We appreciate the reviewer’s suggestion to include this reference. Accordingly, we have incorporated relevant information from it at several points in the manuscript: the Introduction (Lines 125, 142, 151) and the Discussion (Line 429). However, we would like to emphasize that this record originates from a significantly different climatic and ecological setting and therefore does not directly represent the ecosystems present in our study region. For example, heathland vegetation is only incipient at the Vilarquemado site. Additionally, the record has some limitations, including lower resolution and hiatuses affecting certain events during the deglaciation period.

Wei, D., González-Sampériz, P., Gil-Romera, G., Harrison, S. P., and Prentice, I. C.: Seasonal temperature and moisture changes in interior semi-arid Spain from the last inter glacial to the Late Holocene, *Quaternary Res.*, 101, 143–155, <https://doi.org/10.1017/qua.2020.108>, 2021.

I. 269: Using the original chronologies of the records will likely lead to some smoothing of the abrupt (centennial-to-millennial scale) variability when computing the regional averages. Could this affect your results?

Response: We appreciate the reviewer’s comment and acknowledge that each record carries its own dating uncertainties, which may cause some misalignment when comparing abrupt climatic events. As noted, this could introduce smoothing in regional averages and potentially affect the depiction of centennial-to-millennial-scale variability.

However, in this study, our primary focus is on the overall trend of TMF throughout the deglaciation rather than the precise timing of individual abrupt events across records.

Therefore, we do not believe this smoothing significantly impacts our findings, as our interpretations are based on broader climatic patterns rather than event-scale variability.

I. 278-280: What kind of response function do you use to fit the GAM? Given that pollen percentages are restricted to the interval 0 to 100, a beta or binomial response function is more suitable than a standard Gaussian response function (e.g., Adam et al., 2021; Wei et al., 2020).

Response: We appreciate the reviewer's suggestion and acknowledge the importance of selecting an appropriate response function for GAMs when working with pollen percentage data. After testing different models, we ultimately employed a Gaussian GAM with an identity link. While this approach may not be ideal for highly skewed data or values near 0% or 100%, we tested for these issues and determined that the model provided a reasonable fit. We also considered that using REML for smoothness selection helps balance avoiding overfitting and maintaining interpretability.

Nonetheless, we recognize that a quasi-binomial approach might be more appropriate in some cases. If the reviewer has concerns, we are open to revisiting the analysis or, alternatively, removing the graph since it does not significantly affect the overall interpretation of the results.

We have retained the graph and analysis because, although not fundamental to the main discussion, it contributes relevant information illustrating the observed trends. Importantly, the original motivation for producing this synthesis was to demonstrate a consistent wider regional pattern, which increases the geographical relevance of our argument and supports the representativeness of our record.

I. 301: Does 0.5°C correspond to a 1 σ standard error?

Response: Yes, usually it is, unless otherwise specified in the study (now Line 309).

Prahl, F.G., Muehlhausen, L.A., & Zahnle, D.L. (1988). Further evaluation of long-chain alkenones as indicators of paleoceanographic conditions. *Geochimica et Cosmochimica Acta*, 52(9), 2303–2310.

I. 336: Does "dry" here refer to the actual climate conditions or the perceived climate conditions of the vegetation (i.e., a combination of moisture availability and CO₂)? As stated above, a more careful wording would improve the clarity of this section.

Response: The term "dry" here refers to the perceived climate conditions as inferred from pollen-based ecological groups, grounded in current ecological knowledge. We acknowledge the importance of clarifying this distinction and will refine the wording accordingly. Importantly, whether or not CO₂ effects are considered, the presence of steppe indicators reliably signals relatively dry conditions. It is common practice in pollen interpretation to use such ecological groupings as proxies for moisture availability, recognizing that they reflect integrated environmental factors rather than direct climate measurements.

As mentioned previously, we have revised the Methods section (Lines 263–266) to explicitly clarify the scope of our climate inferences as follows:

“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).”

Williams, J.W., Shuman, B.N., Webb, T., Bartlein, P.J., and Leduc, P.L.: Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes, *Ecological Monographs*, 71, 305–331, [https://doi.org/10.1890/0012-9615\(2001\)071\[0305:LQVDIN\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0305:LQVDIN]2.0.CO;2), 2001.

I. 378-380: Why would the moisture availability change less abruptly than the temperature? Could there also be a role for CO₂ or internal vegetation dynamics in explaining the delayed response of the vegetation?

Response: Regarding the role of CO₂, we do not expect it to have played a significant role during the Bølling–Allerød period. The discussion of the delayed forest response during the BA was primarily related to climate variability and has been addressed in other studies of the Iberian Peninsula (e.g., Naughton et al., 2016). To improve focus and clarity, we have deleted this results after merging the previous Section 4.2 with Section 5 (now section 4.1), thereby concentrating more directly on the main results and their implications in relation to CO₂ impacts.

I. 441-443: Could the presence of large herbivores also play a role in promoting heathland rather than forests (Zhu et al., 2018)?

Response: Thank you for this interesting question and for providing the reference to Zhu et al. (2018). I agree that large herbivores can influence vegetation dynamics, particularly by helping to maintain heathland landscapes through grazing and browsing. However, I do not think they played a major role in promoting heathlands over forests during the Last Glacial Maximum (LGM), given the combined effects of low atmospheric CO₂ concentrations and moisture deficits at that time. Low CO₂ would have severely constrained tree growth by limiting photosynthesis, thereby restricting forest expansion regardless of herbivore activity.

Furthermore, in the other records we analyzed — and considering their own local ecology, climate, and fauna — we consistently find evidence of incipient forest development, suggesting that the main limiting factors were climatic and atmospheric rather than primarily related to herbivore pressure.

As mentioned in my previous response, while there are some relevant archaeological studies addressing herbivore impacts, they focus on periods several thousand years older than the time frame considered in our article. Therefore, I think a detailed discussion of this issue would introduce a new topic and deviate from our main focus. However, this would certainly be an interesting avenue to explore in future work, by integrating qualitative archaeological and palaeoecological data with models or simulations, in this particular region.

I. 467: Why should the precession maximum specifically trigger heathland rather than forest development?

Response: Thank you for raising this point. I have clarified this aspect in the revised manuscript (see Lines 386–393). Specifically, I explain that the LGM coincided with a precession maximum, which is known to weaken seasonal contrasts (i.e., reduce summer dryness). This climatic configuration has been consistently associated with heathland development in the Iberian Peninsula (Fletcher and Sánchez-Goñi, 2008; Sánchez-Goñi et al., 2008; Margari et al., 2014) across both glacial and interglacial periods (e.g., Oliveira et al., 2017), including the Middle to Late Holocene (Chabaud et al., 2014; Oliveira et al., 2018; Gomes et al., 2020).

Margari, V., Skinner, L.C., Hodell, D.A., Martrat, B., Toucanne, S., Grimalt, J.O., Gibbard, P.L., Lunkka, J.P. and Tzedakis, P.C.: Land-ocean changes on orbital and millennial time scales and the penultimate glaciation. *Geology*, 42(3), pp.183-186, <https://doi.org/10.1130/G35070.1>, 2014.

I. 502: I don't understand why the bias could extend to vegetation reconstructions as these only associate pollen assemblages with vegetation composition. Are you mixing up reconstructions and simulations here? For simulations, it is of course important to account for CO₂ changes (which most of them do).

Response: I agree that pollen-based vegetation reconstructions are based on associating pollen assemblages with vegetation composition, and thus are not directly subject to CO₂ biases in the same way as model simulations. To improve clarity, we will rephrase the paragraph and replace the term “*vegetation reconstructions*” with “*simulations of glacial vegetation*” in line 439. This more accurately conveys our intention to discuss the emulation of potential modern vegetation and glacial vegetation under different CO₂ scenarios.

I. 568-569: What is meant by” in a general assumption”?

Response: The wording “*in a general assumption*” was included as part of a sentence to qualify the statement regarding “*sufficient moisture*,” acknowledging that moisture availability is inherently dependent on specific climatic conditions. However, upon re-reading, I agree that this qualification is unnecessary and potentially confusing. The discussion section, including the part addressing the Bølling-Allerød, has undergone significant revisions, and this statement has been rewritten accordingly to improve clarity.

I. 593-597: My understanding of the methodology of Shao et al. (2018) is that they account for CO₂ changes by deriving transition matrices from the simulation output of Woillez et al. (2011). If this is correct, it is expected that the two studies agree on the influence of CO₂ on the LGM vegetation.

Response: Thank you for your insightful comment. You are correct that Shao et al. (2018) derive transition matrices from the simulation output of Woillez et al. (2011), and thus both studies highlight the significant role of increased atmospheric CO₂ in promoting forest development during the LGM. They are consistent in emphasizing that rising CO₂ levels were a crucial driver of vegetation changes at a global scale during this period.

We have rephrase the relevant section (now section 4.1) in the manuscript to make this consistency more explicit. Additionally, we have clarified this topic in the updated discussion

of the Younger Dryas (Section 4.1.4), which does not contradict the points made regarding CO₂ influence on LGM vegetation (Section 4.1.1).

I. 602: What do you mean by "with some seasonality"?

Response: Thank you for your comment. I agree that the phrase "temperatures with some seasonality" is somewhat vague in a scientific context. To improve clarity and precision, we have rephrased the sentence in the manuscript (lines 573–576) as follows:

"In summary, the persistence of TMF during the YD, despite cold temperatures and seasonal variation (warmer than HS1), seems to be best explained by the combined interaction between sufficient moisture availability, higher atmospheric temperatures—at least during summer (promoting forest development)—and increasing pCO₂ (between ~245 and 265 ppmv) (Fig. 4a)."

I. 644-647: Under which baseline temperature was this experiment conducted? Is the effect dependent on the background temperature?

Response: I appreciate these comments as they highlight a misinterpretation in the original sentence. To better explain the baseline conditions, I have rewritten the passage in the manuscript (Lines 646–653) as follows:

"In laboratory studies, C3 grasses outperform C4 grasses when temperatures rise by 5 to 15°C at a low CO₂ 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 CO₂ levels. Modeling across 0–45°C and CO₂ levels from 150–700 ppm shows that whether C3 or C4 plants are favored is determined by the interaction between these two factors, unfortunately humidity was not considered (Ehleringer et al., 1997; Edwards et al., 2010)."

Fig. 3: Equating the pollen zones and the geologic periods YD, BA, and HS1 can be misleading since the start and end dates of the pollen zones do not coincide with the official definitions of the geologic periods. For example, pollen zone 4 ending later than the actual YD is not in agreement with the SST reconstruction reaching Holocene level temperatures already during the later stages of pollen zone 4. Therefore, I would recommend to display the limits of the pollen zones separately from the limits of YD, BA, and HS1 in Fig. 3

Response: We have updated Figure 3 to display the boundaries of the pollen zones separately from those of the geologic periods (YD, BA, and HS1). This adjustment preserves the integrity of both datasets while making their temporal distinctions clearer and avoiding potential misinterpretation.

Fig. 4: Based on what data are the schematics for moisture during LGM, HS1, BA, and YD assigned? Do the schematics represent absolute values, anomalies, or trends?

Response: The schematics in Figure 4 represent qualitative changes in each parameter based on the interpretation of multiple proxies, including pollen assemblages, sea surface temperatures (SST), and n-alkanes. For moisture, we specifically consider the presence of heathland, tropical montane forest (TMF), and steppe (STE) vegetation groups.

The plus (+) and minus (–) signs indicate fluctuations in moisture conditions throughout each period. Arrows or values are shown relative to the preceding period for the parameter in question. We will add this clarification to the figure caption for improved transparency.

Because temperature and moisture are inferred from percentage-based pollen ecological groups, quantitative values are not directly available; instead, we focus on relative changes. For readers seeking comparative values, Figure 3 presents percentage curves of these groups across each period. To enhance clarity, we have revised the Figure 4 caption as follows:

“Figure 4 – Schematic representation of the relative changes in climate-inferred parameters (precipitation and temperature) based on pollen-vegetation groups, biomarkers, SST, and the physiological contribution of CO₂ for each period, illustrating potential ecosystem scenarios. Temperature inferences are derived from pollen groups (TMF and STE), SST, and n-alkanes; moisture inferences are based on heathland, TMF, and STE groups.”

Table S1: The Top Age for zone 4 should be 11050.

Response: Thank you for highlighting this. However, the age of 11,050 no longer applies, as the new age model provides updated chronological boundaries for zone 4. We have revised Table S1 accordingly to reflect these new age estimates.

Fig. S1 and S2: These two figures are rather blurry. Can you improve their resolution?

Response: We apologize for the quality issues with these figures, which were also noted by Reviewer 2. We have improved the resolution of Figures S1 and S2 to enhance their clarity and readability.

Technical comments:

I kindly ask you to check the manuscript for typos and grammatical errors again. In particular, there are a number of missing spaces between words (e.g., “ofthe” in l. 178, “elements (Fig.”, in l. 366, and “anda” in l. 366).

The spelling and use of age units differs throughout the manuscript (e.g., “ka” in l. 9, “cal yr BP” in l. 200, “Ka” in l. 560). I kindly ask you to define an age unit in the introduction and use it throughout the manuscript.

Response: We kindly appreciate the technical comments, and we have corrected them for consistency. We appreciate your attention to this point and have corrected the manuscript for consistency including in the use of age units. We have adopted *cal ka BP* where calibrated ages are confirmed, and *ka* where calibration is not certain. In the tables and for specifying

age ranges, we prefer to use *cal yr BP*, as it provides the most precise chronological reference without rounding.

Response to anonymous reviewer 2

General comments:

...However, the paper is too descriptive, the interpretation of lower-concentration CO₂ impacts on vegetation is overly general, and some key information is missing.

Response: Thank you for these valuable comments. Following this feedback, we have thoroughly revised the manuscript to improve clarity, especially in the abstract and introduction, and by integrating the previous Chapter 4.2 into Section 5.1 in a more concise manner while reducing overly descriptive elements in the data presentation.

Regarding the interpretation of low atmospheric CO₂ impacts on vegetation, we have expanded on several key points:

a) After Line 99, we further discuss how CO₂ limitations affect photosynthesis and plant growth, including the impacts of reduced water-use efficiency (WUE) under low CO₂ concentrations, which influence stomatal regulation, increase water loss, and heighten drought vulnerability.

b) After Line 113, we expanded the discussion on the role of CO₂ in shaping plant community composition, particularly explaining why heathlands may have dominated LGM landscapes given their resilience to low CO₂ and cooler conditions.

Finally, addressing the comment on missing key information, we have incorporated relevant aspects from recent studies (e.g., Izumi and Bartlein, 2016; Chevalier et al., 2020; Wei et al., 2021; Prentice et al., 2022) into both the Introduction and Discussion to strengthen and update the manuscript.

Chevalier, M., Davis, B. A. S., Heiri, O., Seppä, H., Chase, B. M., Gajewski, K., Lacourse, T., Telford, R. J., Finsinger, W., Guiot, J., Köhl, N., Maezumi, S. Y., Tipton, J. R., Carter, V. A., Brussel, T., Phelps, L. N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., de Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P. S., Chaput, M., and Kupriyanov, D.: Pollen-based climate reconstruction techniques for late Quaternary studies, *Earth Sci. Rev.*, 210, 103384, <https://doi.org/10.1016/j.earscirev.2020.103384>, 2020.

Chevalier, M., Chase, B. M., Quick, L. J., Dupont, L. M., and Johnson, T. C.: Temperature change in subtropical southeastern Africa during the past 790,000 yr, *Geology*, 49, 71–75, <https://doi.org/10.1130/G47841.1>, 2021.

Izumi, K., and Bartlein, P. J.: North American paleoclimate reconstructions for the Last Glacial Maximum using an inverse modeling through iterative forward modeling approach applied to pollen data. *Geophys. Res. Lett.*, 43(20), 10–965, <https://doi.org/10.1002/2016GL070152>, 2016.

Prentice, I. C., Villegas-Diaz, R., and Harrison, S. P.: Accounting for atmospheric carbon dioxide variations in pollen-based reconstruction of past hydroclimates, *Global Planet. Change*, 211, 103790, <https://doi.org/10.1016/j.gloplacha.2022.103790>, 2022.

Wei, D., González-Sampériz, P., Gil-Romera, G., Harrison, S. P., and Prentice, I. C.: Seasonal temperature and moisture changes in interior semi-arid Spain from the last interglacial to the Late Holocene, *Quaternary Res.*, 101, 143–155, <https://doi.org/10.1017/qua.2020.108>, 2021.

Specific comments:

The authors described that “The study of increased plant growth and global vegetation greening under higher concentrations of pCO₂ (CO₂ fertilisation) is very topical within discussions of current global climate change (e.g., Piao et al., 2019), whilst the inverse scenario (low pCO₂) has received less attention.” at line 116-119. However, recent papers about pollen-based climate reconstructions (e.g., Izumi and Bartlein, 2016; Chevalier et al., 2020; Wei et al., 2021; Prentice et al., 2022; and Izumi et al., 2023) have discussed the impacts of lower atmospheric CO₂ on vegetation. The reference papers listed here are pollen-based climate reconstructions using an inverse-modeling approach related to the papers the authors already cited, Guiot et al. (2000), Wu et al. (2007), and Prentice et al. (2017). Pollen-based climate reconstructions using inverse modeling methods have not differed significantly from temperature reconstructions using conventional statistical methods such as regression analysis and modern analogue techniques. On the other hand, large differences are produced in reconstructing hydrological climate from the traditional methods that tend to overestimate dryness during glacial periods. This may influence the authors’ interpretation of climate from vegetation. As a result, the authors potentially need to largely rewrite the “Abstract”, “Introduction”, “Discussion”, and “Conclusion”. Moreover, the paper, Piao et al. (2019) is not in the reference.

Response: As requested, we have carefully revised the manuscript throughout to improve its readability and clarity. In particular, the Abstract and Introduction have undergone substantial rewriting to better communicate the research aims and findings. Additionally, to streamline the presentation, we have merged Section 4.2 and incorporated its discussion into Section 5.1. This restructuring helps deliver a more cohesive, less repetitive, and concise narrative.

To address the reviewers’ concerns, we have integrated the suggested references and included several new ones in the manuscript, ensuring a more comprehensive discussion of the various approaches used in pollen-based climate reconstructions.

Comment L49-54. The purpose of the authors' study should be to investigate vegetation changes and the effects of pCO₂ changes on vegetation on the Iberian Peninsula margin, not to track and compare them with global pCO₂ changes.

Response: We appreciate the reviewer’s observation and have rephrased the statement accordingly to clarify the study’s focus. The revised sentence now reads (Lines 50–51): *“This direct land-sea comparison approach allows us to investigate how vegetation on the Iberian Peninsula margin responded to the major pCO₂ changes during the last deglaciation.”*

Comment L130-132. About stomatal conductance and stomatal density under low pCO₂ concentration: Is this correct? Does stomatal density change with application to climate over short periods? Is this the author’s idea? If not, please put the paper cited.

Response: Indeed, the original sentence lacked a supporting reference, which we now include for completeness. It is correct that changes in atmospheric pCO₂ can significantly influence stomatal development. Several experimental studies have demonstrated that both elevated and sub-ambient CO₂ levels can affect the initiation and density of stomata, even

over relatively short timescales. To support this point, we have added the following reference to the revised manuscript:

Royer, D. L. : Stomatal density and stomatal index as indicators of paleoatmospheric CO₂ concentration. *Rev. Palaeobot. Palynol.*, **114**, 1–28. [https://doi.org/10.1016/S0034-6667\(00\)00074-9](https://doi.org/10.1016/S0034-6667(00)00074-9), 2001.

L152-154. I disagree with this sentence, at least about climate reconstructions. In section 3.3, the authors need to describe ecological groups other than the temperate and Mediterranean forests in Figure 3. Which pollen taxa belong to the “semi-desertic taxa” and “heathland”, respectively?

Response: To avoid overgeneralization, we have rewritten the Introduction and removed the original sentence regarding the “majority” statement. Regarding the reviewer’s disagreement, we note that recent studies (e.g., Prentice et al., 2022; Cruz-Silva et al., 2023) emphasize that some models still do not incorporate the effects of CO₂ in their climate reconstructions.

We appreciate the valuable comment from Reviewer 2. Based on the suggested references, we have updated the manuscript to better reflect the ecological groups highlighted in those studies. In particular, we have introduced a detailed description of these groups in the caption of Figure 3, specifying the pollen taxa they include:

- **Semi-desertic taxa:** *Amaranthaceae* (previously *Chenopodiaceae*), *Artemisia*, and *Ephedra*.
- **Heathland taxa:** members of the *Ericaceae* family (including various *Erica* species) and *Calluna* species.

These changes have been incorporated accordingly in the manuscript, including the updated Figure 3 caption.

Why do the authors apply a Generalised Additive Model (GAM) to TMF alone? Why not use it for the other ecological groups?

Response: We have retained the graph and analysis because, although not fundamental to the main discussion, it contributes relevant information illustrating the observed trends. Importantly, the original motivation for producing this synthesis was to demonstrate a consistent, wider vegetation/ecological communities–based regional pattern, which increases the geographical relevance of our argument and supports the representativeness of our record.

Regarding the application of the Generalized Additive Model (GAM), we chose to apply it exclusively to the temperate Mediterranean forest (TMF) group to help reduce noise stemming from site locations, counting and chronological uncertainties when integrating pollen data from multiple sites into a single curve. The TMF group exhibited greater variability and complexity that justified this smoothing approach. In contrast, the other ecological groups showed more stable and consistent trends. Therefore, the decision to limit the GAM to the TMF group reflects a targeted effort to improve data clarity where it was most needed.

L309-316. Is the high production of C29 n-alkanes by trees and shrubs interpreted as a high distribution of these vegetations? The explanations in this text (L309-312) do not help for interpretation for the result.

Response: We have rephrased this section in Lines 315–326 and provided two hypotheses for interpretation in the Results and Discussion (Section 4.2, Lines 612–623) as follows:

“Instead, we offer two possible interpretations. First, we tentatively infer that the C29/C31 ratio in this setting may reflect an adaptation of plants to aridity and possibly increased wind strength, which together alter the moisture balance. The n-alkanes of leaf waxes are produced to protect plants against water loss during photosynthesis (Post-Beittenmiller, 1996; Jetter et al., 2006). We expect that arid, cold, and windy conditions are more challenging for woody plants, which have more demanding physiological requirements compared to grasses. Therefore, such harsh environments could exert greater stress on woody plants than on herbaceous taxa. Consequently, the increase in the C29/C31 ratio during HS1 and the Younger Dryas could suggest a climatic adaptation of woody plants (TMF and ERI) by increasing the production of C29 leaf waxes as a protective strategy to survive under these challenging conditions (Fig. 3h). Second, the shifts in chain lengths may primarily reflect compositional changes within woody-dominated vegetation, which includes species with diverse ecological tolerances ranging from semi-desert dwarf shrubs such as *Artemisia* to mesophyll broad-leaved trees.”

The content in L313-316 should be put before the description of index < 1 or index > 1. L415.

Response: We agree with the reviewer comment; we have implemented this change.

What are the +/- and up/down arrow values for each period (the YD, BA, HS1, and LGM) in the figure (Fig. 4) compared to? Wouldn't it be better to have a quantitative discussion?

Response: The schematics in Figure 4 represent qualitative changes in each parameter based on the interpretation of multiple proxies, including pollen assemblages, sea surface temperatures (SST), and n-alkanes. For moisture, we specifically consider the presence of heathland, tropical montane forest (TMF), and steppe (STE) vegetation groups.

The plus (+) and minus (–) signs indicate fluctuations in moisture conditions throughout each period. Arrows or values are shown relative to the preceding period for the parameter in question. We will add this clarification to the figure caption for improved transparency.

Because temperature and moisture are inferred from percentage-based pollen ecological groups, quantitative values are not directly available; instead, we focus on relative changes. For readers seeking comparative values, Figure 3 presents percentage curves of these groups across each period. To enhance clarity, we have revised the Figure 4 caption as follows:

“Figure 4 – Schematic representation of the relative changes in climate-inferred parameters (precipitation and temperature) based on pollen-vegetation groups, biomarkers, SST, and the physiological contribution of CO₂ for each period, illustrating potential ecosystem scenarios. Temperature inferences are derived from pollen groups (TMF and STE), SST, and n-alkanes; moisture inferences are based on heathland, TMF, and STE groups.”

L423-426. The authors need to elaborate more, especially on how to read the S.M. Fig.2. Moreover, the figure is difficult to read because of unclear, and its caption is inadequate.

This approach seems to work if the relationship between vegetation and climate is constant regardless of CO₂ concentration. How would we use this figure if the

relationship between vegetation and climate changes with changes in CO₂ concentration?

Response: We have updated Supplementary Material Figure S2 to improve clarity and readability. Additionally, we have revised the figure caption to provide a more detailed explanation on how to interpret the figure, ensuring it effectively guides the reader through the key elements presented. The updated figure and caption are now included in the revised Supplementary Material.

The purpose of Figure S2 is to provide a baseline representation of how vegetation responds under current conditions, serving as a starting point for our hypotheses regarding ecological requirements. We acknowledge that the relationship between vegetation and climate is not constant and can be influenced by changing CO₂ concentrations. To address this, we draw Figure 5, which illustrates the constraints on vegetation dynamics through time in relation to temperate and Mediterranean forest (TMF), incorporating the effects of varying temperature and CO₂ levels.

In Section 5.1, the authors need to discuss the influences of lower concentration CO₂ on vegetation changes, including the more recent papers, especially pollen-based climate reconstruction during the LGM and last glaciation periods.

Response: We have incorporated a series of new references, including the suggested recent studies, to enhance the discussion of how lower CO₂ concentrations influenced vegetation changes during the LGM and last glaciation periods. These additions have been integrated into the introduction and Section 4 to provide a more comprehensive and up-to-date perspective on pollen-based climate reconstructions and their implications.

In Section 6, what are the key messages of this study? The authors could have described them more briefly and effectively. This is also true in the Abstract.

Response: We have addressed this comment by thoroughly revising multiple sections of the manuscript. Major changes include rewriting the Abstract, Introduction, and Conclusion to clearly and effectively highlight the key messages of the study. Additionally, we merged Section 4.2 with 5.1 to streamline the Results and Discussion, improving clarity and focus on the main findings.

The other comments

Due to rewriting several parts, some aspects were removed, while in other cases typos, abbreviations, references, and minor edits were made to improve the text's readability.

L57. “(HS1)the” to “(HS1), the”

L60. “condition” to “conditions”

Response: We have added an “s” as suggested.

L64. “mosaic,” to “mosaic;”

L77. The authors should define the period of “the last deglaciation” here (not L90). Moreover, the authors’ definition, from 21 to 6 ka, is not true. The last deglaciation does not include the mid Holocene period.

Response: We thank the reviewer for this important comment. We acknowledge the initial imprecision regarding the definition of the last deglaciation period. The onset of the last deglaciation is generally considered to occur around 20–19 ka (e.g., Denton et al., 1981; Toucanne et al., 2008; Denton, 2010) and extends until the final retreat of the Laurentide Ice Sheet around 7–6.8 ka (e.g., Dyke, 1987; Carlson et al., 2008). While some studies define the last deglaciation broadly as 20 to 6 ka cal BP (e.g., <https://doi.org/10.5194/cp-6-245-2010>, 2010). We have updated the manuscript accordingly to clarify this timeframe and included the relevant references.

L104. “in Northern Hemisphere” to “in the Northern Hemisphere”

L184. “at centennial-scale resolution” to “at the centennial-scale resolution”

Response: L165 changed to “*at high (centennial-scale) temporal resolution*”

L202. “the the” to “the”

Response: We have deleted the extra “the” as suggested.

L205-207. “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.”

Response: I add a reference to support this information (AEMET, 2011).

Agencia Estatal de Meteorología (AEMET) and Instituto de Meteorología (IM, Portugal): Atlas Climático Ibérico: Temperatura del aire y precipitación (Experiment Normais 1971–2000), AEMET & IM, Gobierno de España, Madrid and Lisbon, ISBN 978-84-7837-079-5, 2011.

L235 and L236. What are “HCl” and “HF”

Response: We understand that not all readers may be familiar with the chemical abbreviations used. Therefore, we have replaced the abbreviations with the full names of the acids for clarity. HCl stands for hydrochloric acid, and HF stands for hydrofluoric acid (an aqueous solution of hydrogen fluoride, which is a liquid at room temperature). These changes have been made at Lines 229 and 230.

L251-252. It is an unclear sentence to me.

Response: We appreciate the comment and agree the original sentence was unclear. The calculation follows a standard procedure, but the explanation could be clearer. When calculating pollen percentages, we use the total count of most terrestrial pollen grains, excluding certain taxa that tend to be overrepresented due to factors like high production, transport, or aquatic origin.

Pollen percentages are calculated as:

- For most taxa: $(\text{Pollen count of taxon}) / (\text{Main pollen sum}) \times 100$
- For overrepresented taxa (e.g., Pinus, Cedrus), percentages are calculated as:
 $100 \times (\text{Taxon count}) / (\text{Main pollen sum} + \text{Taxon count})$

We included these equations in the manuscript for clarity (Lines 245–248).

L258. Remove “(CONISS)”

Response: We removed it.

L258. “(U 1385-1 to 5)” to “(U 1385-1 to 5 in Fig. 3 and Table S1)”

Response: We have edited it (now Line 254).

L265. “eight pollen records” to “eight marine cores” (?)

Response: We re-wrote it to “eight marine pollen records” (now Line 274)

L311. “value” to “values”

Response: We added the “s”.

L392. “inin” to “in”

L636-643. Basic information on Poaceae and Cyperaceae (Fig. 3g) should be described in Section 3.3 first. It is unclear in the result section why the authors treated Poaceae and Cyperaceae with Fig.3. I

Response: We have included a brief explanation in Section 3.2 (Lines 257–261) to clarify the treatment of Poaceae and Cyperaceae in Figure 3. It now reads as follows: “*In addition to the pollen-based ecological groups, we calculated the sum of Poaceae and Cyperaceae (Fig. 3g), to check the potential importance of C4 plants in the Iberian Peninsula. While most of the present-day Poaceae and Cyperaceae in this region belongs to the C3 plants type (Casas-Gallego et al., 2025), it is possible that C4 plants were more important at other moments in recent Earth history.*”

Casas-Gallego, M., Postigo-Mijarra, J. M., Sánchez-de Dios, R., Barrón, E., Bruch, A. A., Hahn, K., & Sainz-Ollero, H. (2025). Changes in distribution of the Iberian vegetation since the Last Glacial Maximum: A model-based approach. *Quaternary Science Reviews*, 351, 109162.

In Table S1, “1105” to “11050” about the U1385-4 period

Response: We will correct it.

Thank you for highlighting this. However, the age of 11,050 no longer applies, as the new age model provides updated chronological boundaries for zone 4. We have revised Table S1 accordingly to reflect these new age estimates.