

Global biome changes over the last 21,000 years inferred from model-data comparisons

Response to comments of Anonymous Referee #2

1. General comments

Reviewer comment: (1) *The paper of Li et al. uses a global set of pollen data to reconstruct megabiomes since the last ice age. This reconstruction is then compared with biomized outputs from Earth System Models in order to evaluate the fidelity of the model simulations. The biome reconstructions are quite interesting, and I appreciate the large fossil datasets compiled by the authors, this is huge effort to put together.*

Response: We appreciate the positive feedback on our work and the recognition of the effort involved in compiling the global pollen dataset for megabiome reconstructions. While we included a model-data comparison as an example study, the primary aim of our research is to present a new biomization dataset that offers the possibility to evaluate Earth System Models (ESMs). We have clarified this in our revised section “Summary and Conclusions.” (Please see the next response)

2. Specific Comments

Reviewer comment: (1) *However, I have some comments about the methods as well as about the scientific contribution this makes through the interpretation of the data-model comparison. In particular, I find the conclusions to be very general and technical, and I hope that the authors are able to make the impacts of their study clearer.*

Response: Thank you for your comment, we have revised the Conclusions.

Revised text: (in red)

“This study presents a global megabiome reconstruction for 43 timeslices at 500-year intervals over the past 21,000 years, based on the most extensive taxonomically and temporally standardized fossil pollen dataset. The dataset’s reliability is supported by a high agreement (~80%) with modern potential natural vegetation, and its general consistency with the paleosimulation ensemble further underscores its robustness for exploring past biome dynamics. With its high temporal and spatial coverage, it offers an unprecedented resource, not only for exploring long-term vegetation dynamics and their drivers, but also for diverse research contexts, including paleoclimate, biodiversity, and land-use studies. Furthermore, the dataset supports the evaluation of ESM-based paleo-megabiome simulations and offer insights for identifying potential biases in climate models. Its consistent

structure and broad applicability allow us to advance our integrative understanding of past, present, and future Earth system dynamics.”

Reviewer comment: (2) *In my comment above, I say that I find the interpretation of the data-model comparison to be overly general. This is already observed in the abstract. The abstract ends with the statement: To some extent, these mismatches could be attributed to systematic model biases in the simulated climate, as well as to the different plant representations and low taxonomic resolution of pollen in the reconstructions.*

I find this to be so general that it makes it really hard for the reader to glean any nuance the help us understand specific insights about model bias or data issues.

I suggest that the authors place more emphasis on the actual biome reconstruction from the pollen (which takes up more of the discussion, but is not much emphasized in the abstract) and take look deeper into the sources of mismatch to leave the reader with some key takeaways that relate directly to their stated goal (goal in abstract: to evaluate the paleosimulations from ESMs).

Response: We have revised the Abstract based on your comments as follows:

Revised text:

“We present a global megabiome reconstruction for 43 timeslices at 500-year intervals throughout the last 21,000 years based on an updated and thus currently most extensive global taxonomically and temporally standardized fossil pollen dataset of 3,455 records. The evaluation with modern potential natural vegetation distributions yields an agreement of ~80%, suggesting a high reliability of the pollen-based megabiome reconstruction. With its high temporal and spatial resolution, this reconstruction is a robust dataset for various applications, such as the evaluation of paleo-simulations from Earth System Models (ESMs).

We compare the reconstruction with an ensemble of six biomized simulations based on transient vegetation simulations performed by ESMs. The global spatiotemporal patterns of megabiomes estimated by the simulation ensemble and reconstructions are generally consistent. That is, there has been a global shift from open glacial non-forest megabiomes to Holocene forest megabiomes since the Last Glacial Maximum (LGM), in line with the general climate warming trend and continental ice-sheet retreat. The shift to a global megabiome distribution generally similar to today’s took place during the early Holocene. We also found that enhanced anthropogenic disturbances since the Late Holocene have not altered broad-scale megabiome patterns. However, certain data-model deviations are evident in specific regions and periods, which could be attributed to systematic climate biases in ESMs or biases in the pollen-based biomization method. For example, at a global scale over the last 21,000 years, the largest deviations between reconstructions and simulation ensembles are observed during the LGM and early deglaciation periods. These discrepancies are probably attributed to systematic summer cold biases in the ESMs that lead to an overestimation of tundra in periglacial regions. Additionally, steppes are overrepresented on the Tibetan Plateau in the reconstruction, because steppes share dominant characteristic taxa with tundra and are preferential allocated due to fewer plant functional types (PFTs) compared to tundra. Moderate deviations during

the Holocene mainly occur in non-forest megabiomes in the Mediterranean and North Africa, with increasing discrepancies over time. These deviations may result from the underestimation of woody PFT cover in simulations due to systematic biases, such as overly warm summers with dry winters in the Mediterranean, and the overrepresentation of woody taxa in reconstructions, misclassifying deserts as savanna in North Africa. On the whole, our reconstructions are suitable for the evaluation of ESM-based paleo-megabiome simulations, as well as providing clues for improving systematic model biases.”

Reviewer comment: (3) *This continues in the discussion with some very general statements about the sources of uncertainty in the comparison such as: We assume that the simulations used in this study share this rather common problem of a cold bias in boreal latitudes, resulting in the overestimation of tundra in simulations. There is no reference here to support the assumption and no sign that this potential bias was evaluated for the simulations used in the study.*

Response: We do not have pollen-independent climate reconstructions. So we cannot really say when and why the models have a climate that is too different, causing differences in vegetation compared to the reconstructions. There are some other reconstructions available, but it is not always clear which proxy records which climate variable, and deciding this is beyond our expertise, and a fair comparison of the past model climate with the reconstructions would be a huge effort and beyond the scope of this paper. Consequently, we limited the evaluation of the simulated climate to a comparison of the 0ka BP time-slice with modern observed climate data, which we added in the revised text.

New text in Method:

“Modern observational climate data provide a crucial foundation for the assessment of climate simulations. The Climatic Research Unit gridded Time Series (CRU TS hereafter), version 4.08, is a widely used modern observational climate dataset covering all land domains of the world except Antarctica (spatial resolution: $\sim 0.5^\circ \times 0.5^\circ$ on a Gaussian grid; Harris et al., 2020). The CRU TS dataset is interpolated from extensive networks of weather station observations and provides monthly temperature and precipitation data from 1901-2023 C.E. However, the early record of this dataset may have high uncertainty due to the sparse observation networks (Duan et al., 2024), and the late record is strongly influenced by anthropogenic CO₂ increases (Cheng et al., 2022). We, therefore, selected monthly climatological means from 1931-1970 to generate more biologically meaningful bioclimatic variables for evaluating climate simulations at 0 cal. ka BP (O’Donnell and Ignizio, 2012; Supplementary Data 7). These bioclimatic variables represent extreme or limiting environmental factors, namely, mean temperature of warmest quarter (T_{warm}), mean temperature of coldest quarter (T_{cold}), precipitation of warmest quarter (P_{warm}), and precipitation of coldest quarter (P_{cold}). Temperature is given in degrees Celsius (°C), precipitation in millimeters (mm), and a quarter is a period of three consecutive months (1/4 of the year).”

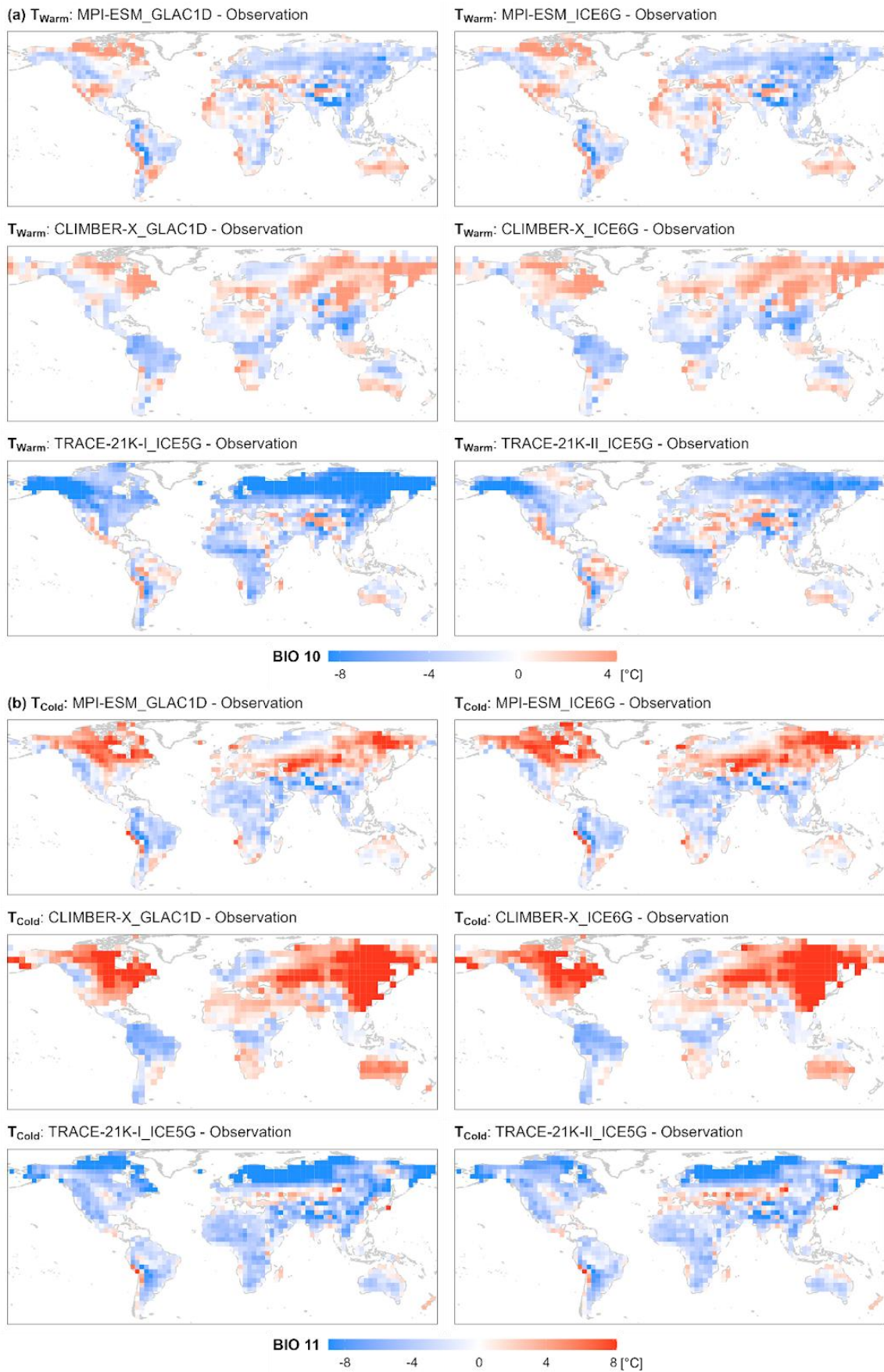
Revised text in Results and Discussion:

“The agreement between modern potential megabiomes and simulated megabiomes at timeslice 0 cal. ka BP is higher for the ESM-representative megabiome (cf. Sect. 2.3) than for individual ESM-based simulation (64.1% vs. 20.0–60.2%; Table 3). As a result, the ESM-representative megabiome depicts more reliable patterns of megabiome dynamics and distribution than individual simulations, with higher agreement especially in Alaska, the Iberian Peninsula, the Alps, the Atlantic Coastal Plain of North America, and the southeastern United States (Fig. 1 and Fig. A2). However, there are still certain regions with low agreement, probably due to climatic biases. These include nearly all highlands (such as the central-southern Rockies, the central Andes, and the Tibetan Plateau) for which an overestimation of the temperature can be expected in the models due to a much lower orography than in reality caused by the smoothing in the coarse spatial resolution ($3.75^\circ \times 3.75^\circ$ and $5^\circ \times 5^\circ$) of the model grids (Fig. A3a–b). All models simulate non-forest megabiomes instead of forest in the Mediterranean region, which can be attributed to the models simulating a climate that is too seasonally dry, with, for example, too-warm summers and too-dry winters (Fig. A3a, d). The TRACE-21K simulation as well as the MPI-ESM simulations fail to reproduce the boreal forest (BOFO) in Alaska, which is then also reflected in the ESM-representative megabiomes. This failure is likely due to the simulated climate being too cold in this region, preventing the establishment of boreal forests under modeled conditions (Fig. A3a, d). Similar to the reconstructions, the transition zones between temperate forest (TEFO) and non-forest megabiomes, such as the East Asian summer monsoon margin, are regions with lower simulated megabiome agreement to the modern potential megabiome distribution. In North Africa, the models also tend to underestimate the northern extension of the grassland and dry shrubland (STEP) and incorrectly assign (warm) savanna and dry woodland (SAVA) records to tropical forest (TRFO). This is related to the biomization procedure for the model results that only relies on simulated vegetation cover fractions and simulated climate, whereas savannas are additionally determined by other ecological processes such as fire intensity and frequency (Dallmeyer et al., 2019) or grazing (van Langevelde et al., 2019).”

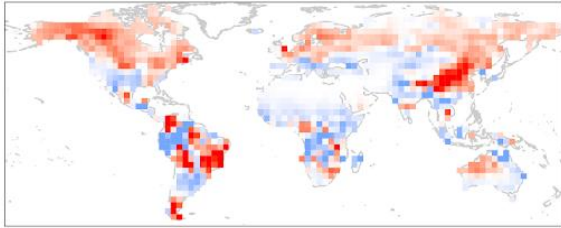
[...]

“Different estimates of tundra in the circum-Arctic areas and the Tibetan Plateau are the primary sources of the strong global data-model deviations during the LGM and early deglaciation periods (Fig. 4d) at 21 and 16 cal. ka BP (Fig. 3). We observe inconsistent estimates of tundra (TUND) and boreal forest (BOFO) from the pollen-based reconstructions and the ESM-based simulations in northern Siberia (AS1), Alaska (NA1), and the East Siberian Highlands (AS2). To some extent, this mismatch could be attributed to systematic model biases in the simulated climate, as climate models tend to underestimate summer temperature in the periglacial areas compared to proxy-based reconstructions, as previously indicated in studies with different models (Deplazes et al., 2013; Alley, 2000) for that period. The simulations used in this study, especially the MPI-ESM and TRACE-21K simulations, also share this rather common problem in modern times, i.e. a summer cold bias in boreal latitudes (Fig. A3a and Table A1), resulting in an overestimation of tundra in the simulations. However, CLIMBER-X simulations perform better in these regions because they overestimate summer temperatures and produce more boreal forests.”

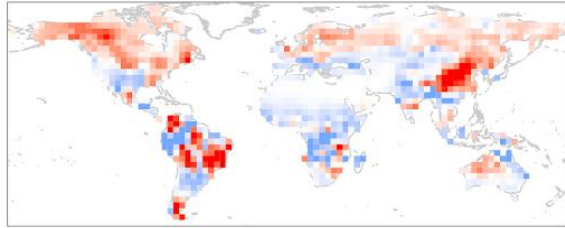
New figure (Appendix A3):



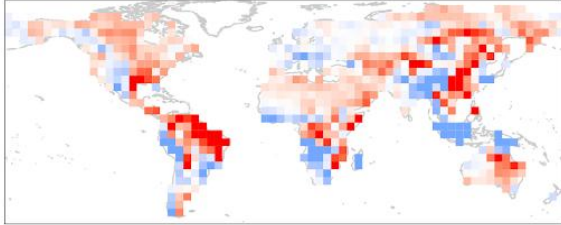
(c) P_{Warm}: MPI-ESM_GLAC1D - Observation



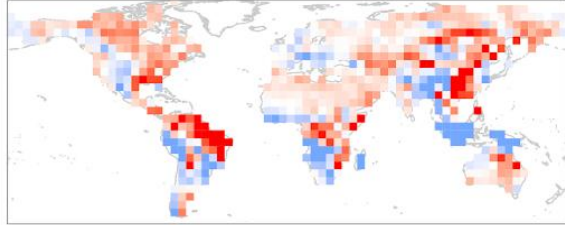
P_{Warm}: MPI-ESM_ICE6G - Observation



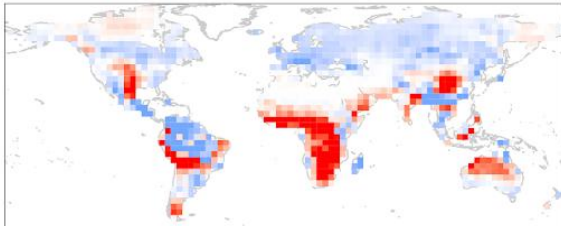
P_{Warm}: CLIMBER-X_GLAC1D - Observation



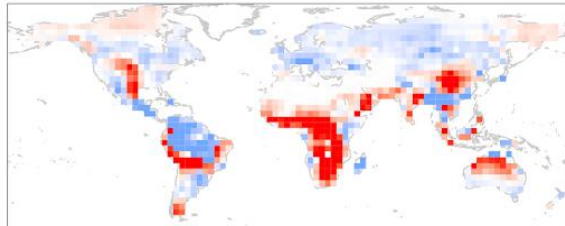
P_{Warm}: CLIMBER-X_ICE6G - Observation



P_{Warm}: TRACE-21K-I_ICE5G - Observation

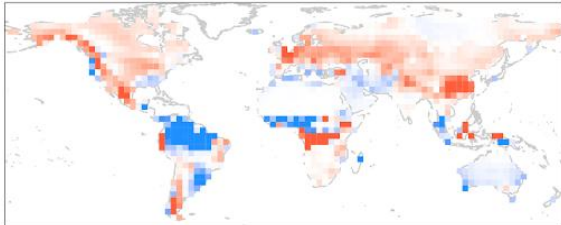


P_{Warm}: TRACE-21K-II_ICE5G - Observation

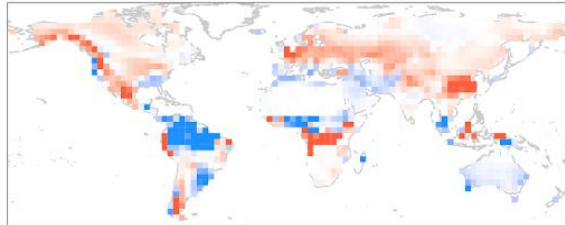


BIO 18  [mm]

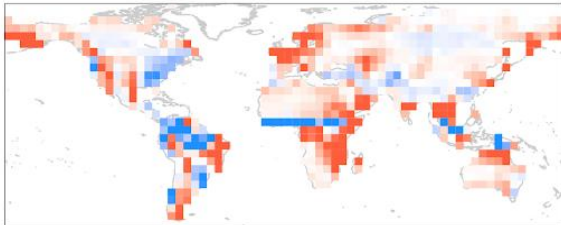
(d) P_{Cold}: MPI-ESM_GLAC1D - Observation



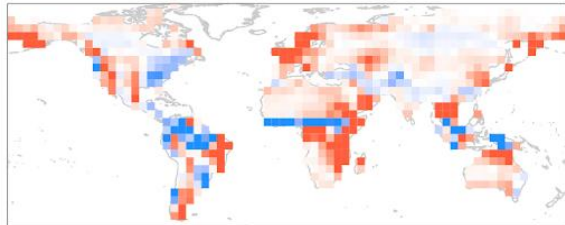
P_{Cold}: MPI-ESM_ICE6G - Observation



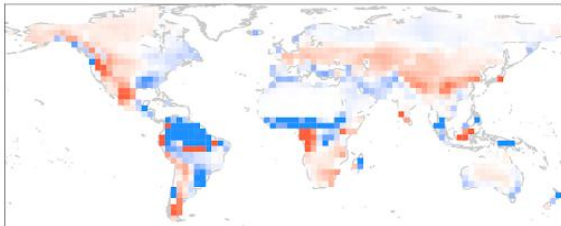
P_{Cold}: CLIMBER-X_GLAC1D - Observation



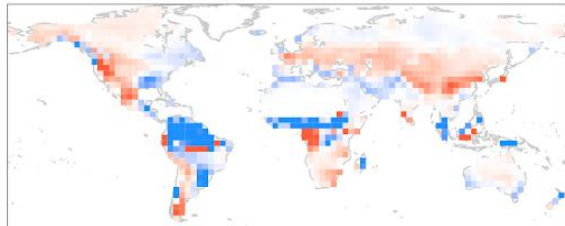
P_{Cold}: CLIMBER-X_ICE6G - Observation



P_{Cold}: TRACE-21K-I_ICE5G - Observation



P_{Cold}: TRACE-21K-II_ICE5G - Observation



BIO 19  [mm]

Figure A3. Differences in bioclimatic variables between ESM-based simulations at 0 cal. ka BP and observations. The bioclimatic variables include (a) mean temperature of warmest quarter (T_{warm}), (b) mean temperature of coldest quarter (T_{cold}), (c) precipitation of warmest quarter (P_{warm}), and (d) precipitation of coldest quarter (P_{cold}). Notable biases include overestimated temperatures (T_{warm} and T_{cold}) in highlands (e.g., Rockies, Andes, Tibetan Plateau), excessively dry Mediterranean summers (P_{warm}), and colder-than-observed conditions in Alaska (T_{warm} and T_{cold}).

Reviewer comment: (4) *Another point I would add here is that the authors acknowledge the limitation of their modern validation exercise in incorporating human land use impacts to ecosystems when comparing with models that don't include such impacts. Please expand on how this might also impact data-model comparisons of paleo-simulations.*

Response: Thank you for your comment. We acknowledge the limitation of our modern validation exercise in not fully accounting for human land-use impacts, as the ESMs used in our comparisons do not include anthropogenic modifications. This has been clarified in the revised text, noting that while localized human activities may influence vegetation patterns, their impact on broad spatial and long-term paleo-simulations appears limited.

Revised text:

“Anthropogenic modification of pollen assemblages has, to some extent, contributed to mismatches in forested areas. For example, incorrectly reconstructed grasslands and dry shrublands (STEP) in North China may reflect intensive land use (e.g., deforestation).

[...]

Mid-Holocene to Late Holocene (represented by the timeslices 6 and 3 cal. ka BP): The spatial patterns of megabiome distributions during this period are only slightly different from those of the early Holocene. TRFO, for example, expanded in Mesoamerican reconstructions and simulations. **It is also worth noting that the forest megabiomes have not obviously shifted since the Late Holocene, as revealed by both reconstructions and simulations. Given that the simulated vegetation was in a quasi-equilibrium with the climate and unaffected by humans, this implies a relatively stable climate in that period. Therefore, we propose that enhanced anthropogenic disturbances over this time period did not promote forest degradation at board spatial scale, and that biomization is robust as regards as this disturbance (Prentice et al., 1996; Gotanda et al., 2008)”**

Reviewer comment: (5) *What about the impact of fire, I assume this is not included in ESMs? Could the lack of these processes in the models result in mismatch?*

Response: Thank you for your comment. All models used in this study include a fire module, which has been clarified in the revised text:

Revised text:

“The dynamic vegetation in all models is represented by different sets of plant functional types (PFTs) that can coexist in the grid-cells. The occurrence of each PFT is constrained by fixed temperature thresholds, and the dynamics of PFT cover fraction are depends for instance on the moisture availability and plant requirements. **The fraction of PFTs is furthermore reduced by disturbances such as fire, windthrow, natural mortality, which are already coupled in the dynamic vegetation module (Dallmeyer et al., 2022). For instance, fire disturbances regularly decrease the tree and shrub PFT cover fractions, while promoting herbaceous PFTs expansion (Reick et al., 2021; Burton et al., 2019).”**

3. Minor comments

Reviewer comment: (1) *Abstract: line 31 I don't understand term: global spatial megabiome. Does this mean the megabiomes of any particular time slice? I think there should be a way to simplify this.*

Response: We have revised the text as follows:

Revised text: (in red)

“The shift to a global megabiome distribution pattern similar to today's occurred during the early Holocene.”

Reviewer comment: (2) *line 79: “8 of our own new records” there are no references for these.*

Response: We have included an overview table in Supplementary Data 1, which provides site metadata and lists the references for all records.

Revised text:

“Also, 52 records from the ACER 1.0 database (<https://doi.org/10.1594/PANGAEA.870867>; Sánchez Goñi et al., 2017), 177 records from the Chinese fossil pollen dataset (Zhou et al., 2023; Cao et al., 2022), and 8 of our own new records (AWI; **for a detailed description see Supplementary Data 1, <https://owncloud.gwdg.de/index.php/s/ijMPmsrahKFeY3Q/download>) were included.”**

Reviewer comment: (3) *line 71: 3691 pollen records are in this compilation, but how many are included in the analysis after data filtration and quality control? This question applies to the numbers of records in Table 1 as well.*

Response: We have revised the text and updated Table 1 as follows:

Revised text:

“We converted pollen data from LegacyPollen 2.0 into megabiomes using the biomization method of Prentice et al. (1996). We only analyzed records over the last 21,000 years, resulting in a final megabiome dataset of 55,868 timeslices at 500-year intervals from 3,455 records (Supplementary Data 1 and Data 4; <https://owncloud.gwdg.de/index.php/s/ijMPmsrahKFeY3Q/download>).”

Revised table:

Table 1: Overview of the number of pollen records, pollen taxa, plant functional types (PFTs), and megabiomes used in the biomization procedures, along with references to biomization schemes by continent. The lists of taxa-PFTs and PFTs-megabiome assignments are available in Supplementary Data 2 and Data 3.

Continent	Pollen records	Taxa	PFTs	Megabiomes	References
Europe	1,359	243	41	7	Ni et al. (2014) Binney et al. (2017) <u>Marinova</u> et al. (2018) Cao et al. (2019)
Asia	636	424	49	8	Chen et al. (2010) Ni et al. (2014) Binney et al. (2017) Tian et al. (2018) Cao et al. (2019)
North America	1,078	393	47	8	Thompson and Anderson (2000) Ortega-Rosas et al. (2008) Bigelow et al. (2003) Ni et al. (2014) Cao et al. (2019)
Africa	145	556	8	6	<u>Vincens</u> et al. (2006) <u>Lézine</u> et al. (2009)
Indo-Pacific	60	429	22	8	Pickett et al. (2004)
South America	177	576	19	8	Marchant et al. (2001 & 2009)
Total	3,455	1,447	98	8	

Reviewer comment: (4) line 82-83: following the previous question, I know this paper which provides recommendations for data best practices, but it doesn't specify specific practices for any study. Could you please tell us specifically how you filtered data? How many dates were required for age models, how were age models generated, how many pollen samples or counts were requires, etc?

Response: We have revised the text according to your suggestion as follows:

Revised text:

“To improve comparability between pollen records as well as data quality, we followed the practices recommended by Flantua et al. (2023) for large-scale paleoecological data synthesis when updating the dataset.

Specifically, the following key steps were involved: first, metadata of pollen records from different data sources were examined to avoid duplicate inclusion; second, age-depth models were re-estimated for each record (≥ 2 radiocarbon dates) using the Bayesian framework implemented in Bacon (Blaauw and Christen, 2011; for a detailed description see Li et al., 2022); third, pollen morphotypes were harmonized to reduce the effect of taxonomic uncertainty and nomenclatural complexity, i.e. woody taxa and major herbaceous taxa have been harmonized to genus level and other herbaceous taxa to family level (for a detailed description see Herzschuh et al., 2022).”

Reviewer comment: (5) *Line 90: great that dois for specific datasets were included! This is great, helps attribute credit to individual record generators!*

Response: We appreciate your recognition of the inclusion of DOIs for specific datasets.

Reviewer comment: (6) *Line 110-111 “Larix and Pinus were multiplied by factors of 15 and 0.5” This is probably sensible for NA and Europe, but what about other overrepresented taxa in other regions?*

Response: We now acknowledge that the lack of calibration for taxa other than Larix and Pinus somewhat limits the accuracy of reconstructions in certain regions. However, we consider our global-scale, pollen-based megabiome reconstructions reliable because record-by-record comparisons of reconstructed megabiomes at timeslice 0 cal. ka BP from 2,232 available records with modern potential megabiomes indicate an 80.2% agreement.

Revised text:

“The different pollen representation (including production, dispersion, and preservation) of plant taxa is the principal reason for inadequate separation of forest and open landscape ecotones. For example, the high pollen productivity of key taxa (such as *Artemisia*; Xu et al., 2014) has resulted in an overestimation of grasslands and dry shrublands (STEP) in the East Asian summer monsoon northern marginal zone and the Great Plains of North America. However, studies on pollen productivity and dispersal ability to date are mostly limited to a few taxa in north-central Europe and China (Wieczorek and Herzschuh, 2020), which limits large-scale calibration of pollen representation.”

Reviewer comment: (7) *Line 121: “Furthermore, the assignment of pollen taxa to megabiomes and biomization routines were performed independently for each continent.” Is there specific information on the differences for each continent in that supplementary material or somewhere else? This is not clear to me. For example, different harmonization schemes have been published for different geographic areas, but I don’t see a reference to this or other geographically specific procedures.*

Response: Yes, we have included the taxa-to-PFT-to-megabiome assignment scheme for each continent in the supplementary materials. We have clarified this point in the revised text:

Revised text:

“Furthermore, the assignment of pollen taxa to megabiomes and biomization routines were performed independently for each continent (Table 1; Supplementary Data 2 and Data 3, <https://owncloud.gwdg.de/index.php/s/ijMPmsrahKFeY3Q/download>).”

Reviewer comment: (8) Line 159: *regarding the tool of Dallmeyer et al., 2021, please provide a few details about how this works.*

Response: We have added details about how the tool of Dallmeyer et al., 2021 works. Please refer to the revised text below:

Revised text:

“The PFTs distributions are converted into the same eight megabiomes used in the reconstructions by applying the tool of Dallmeyer et al. 2019. This tool converts the simulated PFT distributions based on assumptions of the minimum PFT cover fractions that is needed for the assignment of steppe/tundra or forest biomes and bioclimatic constraints derived from 2 m temperature distributions to distinguish different forest biomes (for a detailed description see Dallmeyer et al. 2019). These constraints largely adhere to the limitation rules used in the classical biome models such as BIOME4 (Kaplan et al., 2003). This two-way approach of using temperature constraints and PFT cover fractions is needed to assure the general application of the tool to all standard ESMs, that sometimes only calculate two different PFTs (herbaceous and trees). ”

References:

Alley, R. B.: The Younger Dryas cold interval as viewed from central Greenland, *Quat. Sci. Rev.*, 19, 213–226, [https://doi.org/10.1016/S0277-3791\(99\)00062-1](https://doi.org/10.1016/S0277-3791(99)00062-1), 2000.

Blaauw, M. and Christen, J. A.: Flexible paleoclimate age-depth models using an autoregressive gamma process, *Bayesian Analysis*, 6, 457–474, <https://doi.org/10.1214/11-BA618>, 2011.

Burton, C., Betts, R., Cardoso, M., Feldpausch, T. R., Harper, A., Jones, C. D., Kelley, D. I., Robertson, E., and Wiltshire, A.: Representation of fire, land-use change and vegetation dynamics in the Joint UK Land Environment Simulator vn4.9 (JULES), *Geosci. Model Dev.*, 12, 179–193, <https://doi.org/10.5194/gmd-12-179-2019>, 2019.

Cao, X., Tian, F., Herzsuh, U., Ni, J., Xu, Q., Li, W., Zhang, Y., Luo, M., and Chen, F.: Human activities have reduced plant diversity in eastern China over the last two millennia, *Glob. Change Biol.*, 28, 4962–4976, <https://doi.org/10.1111/gcb.16274>, 2022.

Cheng, W., Dan, L., Deng, X., et al.: Global monthly gridded atmospheric carbon dioxide concentrations under the historical and future scenarios, *Sci. Data*, 9, 83, <https://doi.org/10.1038/s41597-022-01196-7>, 2022.

Dallmeyer, A., Claussen, M., and Brovkin, V.: Harmonising plant functional type distributions for evaluating Earth system models, *Clim. Past*, 15, 335–366, <https://doi.org/10.5194/cp-15-335-2019>, 2019.

Dallmeyer, A., Kleinen, T., Claussen, M., Weitzel, N., Cao, X., and Herzsuh, U.: The deglacial forest conundrum, *Nat. Commun.*, 13, 6035, <https://doi.org/10.1038/s41467-022-33646-6>, 2022.

Deplazes, G., Lückge, A., Peterson, L. C., Timmermann, A., Hamann, Y., Hughen, K. A., Röhl, U., Laj, C., Cane, M. A., Sigman, D. M., and Haug, G. H.: Links between tropical rainfall and North Atlantic climate during the last glacial period, *Nat. Geosci.*, 6, 213–217, <https://doi.org/10.1038/ngeo1712>, 2013.

Duan, R., Huang, G., Wang, F., Tian, C., and Wu, X.: Observations over a century underscore an increasing likelihood of compound dry-hot events in China, *Earth's Future*, 12, e2024EF004546, <https://doi.org/10.1029/2024EF004546>, 2024.

Flantua, S. G. A., Mottl, O., Felde, V. A., Bhatta, K. P., Birks, H. H., Grytnes, J. A., Seddon, A. W. R., and Birks, H. J. B.: A guide to the processing and standardization of global palaeoecological data for large-scale syntheses using fossil pollen, *Global Ecol. Biogeogr.*, 32, 1377–1394, <https://doi.org/10.1111/geb.13693>, 2023.

Gotanda, K., Nakagawa, T., Tarasov, P. E., and Yasuda, Y.: Disturbed vegetation reconstruction using the biomization method from Japanese pollen data: Modern and Late Quaternary samples, *Quat. Int.*, 184, 56–74, <https://doi.org/10.1016/j.quaint.2007.09.030>, 2008.

Harris, I., Osborn, T.J., Jones, P. and Lister, D.: Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset, *Sci. Data* 7, 109. <https://doi.org/10.1038/s41597-020-0453-3>, 2020.

Herzsuh, U., Li, C., Böhmer, T., Postl, A. K., Heim, B., Andreev, A. A., Cao, X., Wieczorek, M., and Ni, J.: LegacyPollen 1.0: a taxonomically harmonized global late Quaternary pollen dataset of 2831 records with standardized chronologies, *Earth Syst. Sci. Data*, 14, 3213–3227, <https://doi.org/10.5194/essd-14-3213-2022>, 2022.

Kaplan, J.O., Bigelow, N.H., Prentice, I.C., Harrison, S.P., Bartlein, P.J., Christensen, T.R., Cramer, W., Matveyeva, N.V., McGuire, A.D., Murray, D.F. and Razzhivin, V.Y.: Climate change and Arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. *J. Geophys. Res. Atmos*, 108, <https://doi.org/10.1029/2002JD002559>, 2003.

Li, C., Postl, A. K., Böhmer, T., Cao, X., Dolman, A. M., and Herzschuh, U.: Harmonized chronologies of a global late Quaternary pollen dataset (LegacyAge 1.0), *Earth Syst. Sci. Data*, 14, 1331–1343, <https://doi.org/10.5194/essd-14-1331-2022>, 2022.

O'Donnell, M. S. and Ignizio, D. A.: Bioclimatic predictors for supporting ecological applications in the conterminous United States, U.S. Geological Survey Data Series, 691, 1–10, 2012.

Prentice, C., Guiot, J., Huntley, B., Jolly, D., and Cheddadi, R.: Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka, *Clim. Dyn.*, 12, 185–194, <https://doi.org/10.1007/BF00211617>, 1996.

Reick, C. H., Gayler, V., Goll, D., Hagemann, S., Heidkamp, M., Nabel, J. E. M. S., Raddatz, T., Roeckner, E., Schnur, R., and Wilkenskield, S.: JSBACH 3 - The land component of the MPI Earth System Model: documentation of version 3.2, *Berichte zur Erdsystemforschung*, Hamburg: MPI für Meteorologie, <https://doi.org/10.17617/2.3279802>, 2021.

Wieczorek, M. and Herzschuh, U.: Compilation of relative pollen productivity (RPP) estimates and taxonomically harmonised RPP datasets for single continents and Northern Hemisphere extratropics, *Earth Syst. Sci. Data*, 12, 3515–3528, <https://doi.org/10.5194/essd-12-3515-2020>, 2020.

Xu, Q., Cao, X., Tian, F., Zhang, S., Li, Y., Li, M., Li, J., Liu, Y., and Liang, J.: Relative pollen productivities of typical steppe species in northern China and their potential in past vegetation reconstruction, *Sci. China Earth Sci.*, 57, 1254–1266, <https://doi.org/10.1007/s11430-013-4738-7>, 2014.