

Davis et al. The climate and vegetation of Europe, North Africa and the Middle East during the Last Glacial Maximum (21,000 years BP) based on pollen data CP-2022-59

We would like to thank the reviewers for the time and effort that they have put into their reviews of our manuscript. Their comments and suggested changes have greatly improved the manuscript.

We respond to the reviewers comments line-by-line below (their comments are highlighted in yellow). We include both our response and details of the relevant action that we have taken. Additions to the original text are also highlighted in the revised manuscript. We start with reviewer 2 who had two major comments:

Reviewer 2

My first point concerns the choice of the method to reconstruct LGM climate changes. You have selected the MAT: why? It's a key point because previous studies have evidenced that it's not easy to find reliable modern analogues for the LGM vegetation, and that assuming past CO₂ equivalent to modern one may induce biases in climate reconstruction (Guiot et al., 2009; Prentice et al., 2017). So why do you use the MAT on your data instead of the IM or the Cleator method which are the only methods to take into account the CO₂ changes? I like the MAT for Holocene but I think that the MAT, as used here for LGM, is not appropriate for several reasons.

1) The first one is that the vegetation of the LGM is mostly steppe, and there is, with the MAT, a possible confusion between warm and cold steppes, which can lead to a bias to the reconstruction of too warm climate conditions for the LGM. There is a method that take into account this bias by distinguishing warm and cold steppes (Tarasov et al 1998, JQS) , but this is not what was used here. Here, the MAT is applied directly to the PFT scores of the undifferentiated steppe biome. I think that the fact of not differentiating the steppes can lead to an important bias in the results obtained in this study. You should add a figure (with the basic statistical tests R², RMSE) plotting the climate parameters estimated/observed for the modern samples of the steppe biome and see if we have no deviation. We should also add a figure (supp mat ?) with the location of the modern analogues chosen for each of the fossil spectra classified in steppe.

Response: The reviewer suggests that our MAT-based reconstruction does not take into account the difference between warm and cold steppe. This is not true. As stated in the methods section we reconstruct climate using the PFT classification of Tarasov et al 1998 and Peyron et al. 1998. This means that our analysis includes both the warm grass steppe (wgs) and cool grass steppe (cgs) PFT's that are used by both authors to distinguish between warm and cold steppe biomes.

The reviewer mentions the Tarasov et al (1998) method to better differentiate between cold and warm steppe pollen biomes using the Prentice et al (1996) pollen biomisation algorithm. The method of Tarasov et al (1998) is designed to overcome a problem at the biome level, and not the PFT level used in our MAT method. It is applied after the calculation of the PFT scores. The method essentially works by using the presence or

absence of thermophilous arboreal taxa to re-assign steppe and desert PFT's into ONLY either warm or cold varieties. As such it artificially exaggerates the difference between the PFT's that make up the warm or cold steppe biomes. This artificial separation acts to increase the biome score of either the warm or cold steppe biome relative to each other, as well as relative to other competing biomes, making it more likely that one of the steppe biomes will become the dominant biome (the dominant biome is the one with the highest cumulative PFT score of all the PFT's within that biome). However, using these re-assigned PFT scores for MAT makes no sense because it undermines the basic assumption that PFT scores (and the underlying vegetation that they represent) vary in a consistent and uniform manner with climate.

At the reviewer's suggestion we have undertaken an analysis of the performance of our MAT transfer function based on a sub-set of modern pollen samples from steppe environments. For this, we selected 1588 samples from the Eurasian Modern Pollen Database (EMPD) (Davis et al 2020) that were classified as belonging to the steppe pollen biome (the pollen biome is included in the metadata for each sample in the database). The results show little difference between the steppe samples and the performance using the complete dataset. They do not indicate any specific weakness as suggested by the reviewer.

	All surface samples		Steppe only	
	RMSE	R2	RMSE	R2
TANN	2.28	0.9	2.51	0.87
TDJF	3.35	0.91	3.26	0.88
TJJA	2.21	0.81	2.49	0.82
PANN	224.94	0.69	185.7	0.71
PDJF	78.51	0.69	66.5	0.66
PJJA	52.49	0.75	43.8	0.79

The reviewer mentions problems with finding modern analogues for LGM pollen samples, especially steppe. This was often mentioned in early studies but this was probably because they used particularly small modern surface sample datasets, as well as both modern and fossil datasets that were often digitized or from secondary sources that did not include the full pollen assemblage. We show in the paper, as others have shown before us (Pini et al 2021, Magyari et al 2014a), that there are in fact many available analogues for LGM pollen samples in the new bigger and more spatially extensive modern surface sample datasets such as the EMPD2. We also use PFT scores rather than individual taxa which increases the potential to find modern analogues. Based on the square-chord distance measurement we did not find any fossil sample where we could not find 6 close modern analogues in the EMPD2 (a 'close' analogue being defined as a chord distance <0.3, as suggested by Huntley 1990).

The reviewer suggests providing maps showing the location of the analogues. This would require generating a lot of maps (the dataset includes 524 samples from 63 sites) which might not be very helpful. We already intended to include the list of 6 analogues for each fossil sample in the supplementary files, which would allow anyone to investigate the location and nature of the analogues in detail. Instead, we have included a table in the appendix (Table A4) which shows the main ecoregion where most of the analogues

originated for each site. This probably represents a more accessible summary of the modern location and vegetation landscape of the analogues being used.

Action: The analysis of steppe samples is now mentioned in the text (lines 550-555) and shown in the appendix table A3. A summary table is provided in the appendix (A4) showing the ecoregion from where most of the modern analogues originated for each site. This is also mentioned in the text (lines 683-685).

2) *The second one is that CO₂ is not really taken into account in this paper. 2.1) You compare the results obtained here with the MAT with the already published results of Wu et al (2007) based on IM developed by Guiot et al. 2000 (Guiot et al., 2009). I consider that it is insufficient because the datasets used (modern and fossil) are different and therefore hardly comparable.*

Response: We justify the use of the MAT method for the LGM by showing that our MAT reconstruction produces results that are essentially indistinguishable from an Inverse Modelling (IM) reconstruction by Wu et al 2007 from the same fossil dataset of 10 sites. We cannot be absolutely sure we used exactly the same fossil samples as Wu et al, since the dataset used by Wu et al is poorly documented, but we can say that it is from the same site, the same pollen record, from the same time period, and has the same reconstructed pollen-biome. We therefore consider the fossil datasets and therefore the results, to be comparable. We are not sure what the reviewer means by suggesting that the MAT and IM modern pollen datasets are not comparable, since the IM method does not require use of a modern pollen dataset.

Action: None

2.2) *It would be necessary to compare your results with the recent results of Cleator et al (2020, values are available in supplementary mat).*

Response: As far as we can see, the results of both Cleator et al. 2020a and 2020b are only available as a gridded dataset in the supplementary material to these papers. Unfortunately, the authors do not provide the site data that would allow us to make a comparison.

Action: None

2.3) *The solution that I recommend is to apply the Inverse modelling developed by Guiot on your new datasets presented here, or the algorithm developed by Cleator et al (2020), cf in Pini et al (2022).*

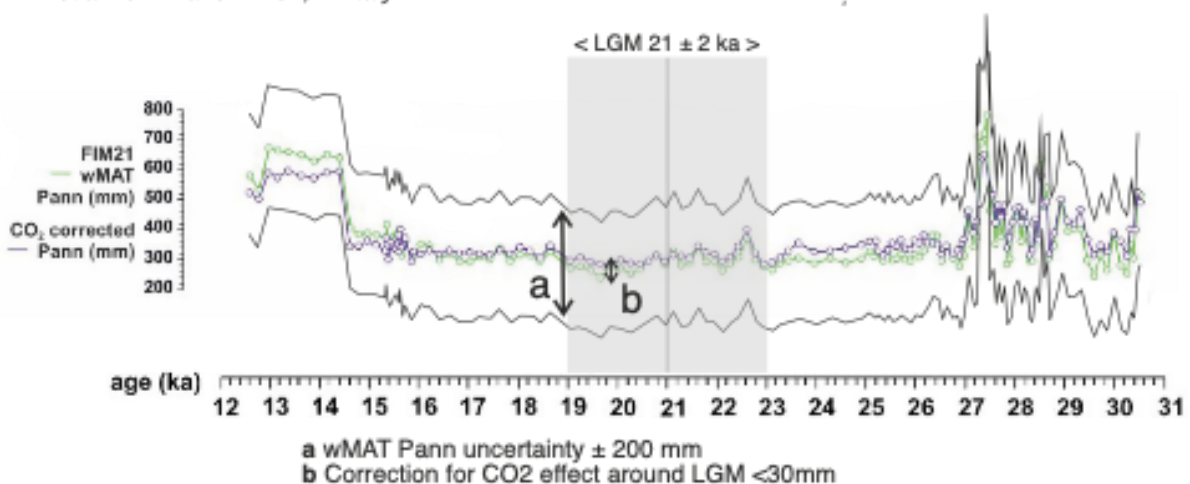
Response: As we mentioned in reply to reviewer Response 2.1, we show in our analysis that our MAT method produces almost exactly the same results as the inverse modelling method for essentially the same samples from the same 10 sites (Fig 7). It is not therefore clear why undertaking an Inverse modelling analysis, as the reviewer proposes, would substantially change these results.

Given the reviewers concerns about the CO2 problem, we think that it is important here to place the problem in perspective. Firstly, it is now generally considered that glacial-level atmospheric CO2 concentrations mainly affects inferred precipitation or moisture balance in pollen-based paleoclimate reconstructions as opposed to temperature. This is evidenced by the fact that in both of the papers by Cleator et al. (2020) and Pini et al. (2022) cited by the reviewer, the CO2 correction algorithm is applied only to precipitation reconstructions, since they do not consider the the effects of low CO2 to be sufficiently important to apply to temperature variables “*Low [CO2] will not impact reconstructions of temperature, but has a large impact on moisture-related variables*” (Pini et al., 2022).

Secondly, it is important to ask “IF there really is a problem with reconstructing precipitation, exactly how big a problem is it?”, especially in relation to other uncertainties.

As a demonstration of this point we show below the effects of the Cleator et al (2020) correction algorithm as applied by Pini et al (2022) on a Modern Analogue Technique (MAT) reconstruction of mean annual precipitation (Pann) at the Lake Fimon site in Northern Italy. Here we include the authors’ uncertainty bounds of their MAT reconstruction because it provides perspective when viewing the CO2 correction (Pini et al 2022, figure 6F and 7G). As can be seen in the figure below, the correction ‘b’ during the LGM (21K +/-2k highlighted) is in fact very minor (roughly ~22mm on average for the 23 samples over this time period). This compares with the uncertainties ‘a’ of the MAT reconstruction itself (+/-200mm) which are approximately an order of magnitude greater. In other words, Pini et al 2022 show pretty much the same result as we do, that any CO2 effect is essentially indistinguishable from the overall uncertainties of the MAT reconstruction.

Pini et al 2022 Lake Fimon, N. Italy



In addition, Pini et al (2022) do not provide uncertainties for the CO2 correction itself, and this does not appear to be discussed in any of the Cleator et al papers or is included in the code (as shown in Wei et al 2021 supplementary). Pini et al 2022 explain that the correction algorithm is based on inputs of growing season temperature, cloud cover and insolation. We must therefore assume that at least the first two of these variables are themselves estimates with their own uncertainties. Pini et al 2022 say that they undertook a sensitivity analysis of the role of these different variables but unfortunately, they do not show the results of this in their paper, and only mention that cloud cover appeared to explain most of

the variance during the glacial period. In any case it seems surprising that the size of the CO₂ correction throughout the record does not appear to be closely related to the actual atmospheric CO₂ concentration, with a correction close to zero for a number of samples around the LGM period when CO₂ was at its lowest compared to the present day.

Action: We have amended the text to include reference to the Pini et al (2022) paper in support of our conclusions about the CO₂ effect (lines 852-869).

2.4) If this is not possible, one of the solutions would be to apply to your data a multi-methods approach - WA-PLS or machine learning methods (Random Forest, Boosted Regression Trees)- as often applied now (Salonen et al.,2014; Brewer et al., 2008; Peyron et al., 2013; Robles et al. 2022 ...) to be sure of your results.

Response: We are not sure why any of these methods would be better at addressing the CO₂ problem, since all of them use a modern calibration dataset and therefore rely on the same assumptions about modern analogues as MAT. Also, we are not sure how a multi-method approach helps one to be 'sure' of the results? This would suggest that some kind of combination of methods is better than one, although none of the publications cited appear to provide a clear scientific justification for this more complex approach. The assumption appears to be that if more methods agree then the reconstruction is somehow more robust, but they may just as well be agreeing on being wrong. In some cases some of these pollen-climate methods may be quite inappropriate. For instance, machine learning methods can suffer from over-tuning and by 'black boxing' provide poor analytical insight, while WA-PLS only really works well when the fossil samples and their modern analogues are regionally well constrained, something that can quickly breakdown during the LGM when the best analogues are to be found on the other side of continents (e.g. Siberia, Mongolia).

Instead we prefer to evaluate our reconstruction in the light of the CO₂ problem in 3 key ways 1) we compare on a site-by-site basis with a pollen-based INV method (ie the results presented by the Wu et al 2008 study) that is designed specifically to account for the CO₂ effect, we 2) compare on a sample-by-sample basis with a chironomid-based method which represents an entirely different proxy (fauna not flora), and 3) we undertake an extensive discussion that compares our reconstruction with a wide variety of records from a wide variety of proxies from across Europe.

Action: We emphasise all of the above points in our revised manuscript text

Minor points :

3) Abstract, line 28 "Previous pollen-based climate reconstructions based on MAT show...": which ones? The MAT has not been often used to reconstruct LGM climate, and the PFTs method of Peyron et al., Tarasov et al and others references IS not a variant of the MAT, so correct it.

Response: The comparison of ANN and MAT is really in reference to their common use of a modern surface sample dataset, and therefore both are dependent on 'modern analogues'.

In this sense ANN is more similar to MAT than Inverse Modelling. However, we agree it is confusing, so have corrected this throughout.

Action: MAT-NN has been changed to ANN throughout. Abstract, line 28 has been changed from “*Previous pollen-based climate reconstructions based on MAT show a much colder and drier climate for the LGM than both Inverse Modelling and climate model simulations*” to “*Previous pollen-based climate reconstructions **using modern pollen calibration datasets** show a much colder and drier climate for the LGM than both Inverse Modelling and climate model simulations*” (line 33).

4) Introduction

-lines 40 to 52 : more references are needed

Response: Ok

Action: The following references have been added- Ehlers et al. 2011, Arslanov et al. 2007, Lehmkuhl et al. 2021, Grichuk 1992 (lines 51-62)

5) -lines 62-34: “*the pollen-based reconstructions that show the greatest disagreement with climate models have themselves been criticized for not considering the possible effect of low atmospheric CO₂ on the physiological relationship between plants and climate (Ramstein et al., 2007)*”. *The significant bias of CO₂ in climate reconstructions for glacial periods must be further explained here, as well as the developed methods that take it into account: inverse modelling by Guiot et al., 2000, 2009; the recent algorithm of Prentice et al., 2017 and Cleator et al., 2020.*

Response: This is similar to a comment shared by reviewer 1

Action: The following section has been added to the introduction: “**Methods that use modern pollen samples for calibration purposes are based on the assumption that the relationship between vegetation and climate remains the same through time, and that this is independent of change in CO₂ concentration. Studies have shown however that plant growth processes and plant resilience are sensitive to CO₂ concentration, and particularly water-use efficiency which would make plants more drought sensitive in low CO₂ environments (Cowling & Sykes 1999). Atmospheric CO₂ during the LGM was around 190 ppm, some 100 ppm lower than the pre-industrial period, and 200 ppm lower than the levels experienced in the last 50 years. Concerns about the effects of lower CO₂ during the LGM has directly led to the development of pollen-climate reconstruction methods that can take account of CO₂ effects, either through use of a process-based vegetation model run in inverse mode (Guiot et al. 2000, Guiot et al. 2009), or through the use of a correction algorithm (Prentice et al. 2017).**” (lines 77-89)

6) -line 65 Inverse modelling, the ref is missing; please add Guiot et al, 2000 (Guiot, J., et al Inverse vegetation modeling by Monte Carlo sampling to reconstruct paleoclimate under changed precipitation seasonality and CO₂ conditions: application to glacial climate in Mediterranean region, Ecol. Model., 1, 119–140, 2000.) and Guiot et al 2009.

Response: OK.

Action: The two references (Guiot et al. 2000, 2009) have been added, see response to previous comment. (lines 87-88)

-line 100-103 the chronology of the LGM needs to be further explained here as the LGM time window is very close to the Heinrich stadial 1 (17.7 ka) and 2 (23.7 ka).

Response: Ok

Action: The text has been changed from “This is particularly important because the 21 ± 2.0 ka time slice commonly used to represent the LGM period in PMIP data-model comparisons and other synthesis studies (MARGO members, 2009; Bartlein et al., 2011) occurs immediately after the glacial maxima in the Alps, which occurs around 26-23 ka (Heiri et al., 2014; Spötl et al., 2021), and is therefore likely to be represented by a different vegetation and climate.” to “This is particularly important because the 21 ± 2.0 ka time slice commonly used to represent the LGM period in PMIP data-model comparisons and other synthesis studies (MARGO members, 2009; Bartlein et al., 2011) occurs immediately after the glacial maxima in the Alps **around 26-23 ka (Heiri et al., 2014; Spötl et al., 2021) and Heinrich stadial HS-2 (24.3-26.5), whilst also being closely followed by Heinrich stadial HS-1 (15.6-18.0 ka) (Sanchez-Goñi & Harrison, 2010. These closely associated time periods can therefore be expected to represent both a different vegetation and climate than the LGM itself.**” (lines 135-138)

-line 126: other proxies: which ones? Speleothems?

Response: It seems unnecessary and distracting to list in the introduction all the proxies that we mention in the discussion. Such a list would include for example chironomids, oxygen isotopes from molluscs shells and soil calcites, macrofossils, mammal bone assemblages, tree leaf lipids, sedimentary lipids, molluscs, glacial modelling, diatoms, alkenones, foraminifera, Mg/Ca etc

Action: None

Methods

*-line 177 “more recent studies”: which ones?,
“although the exact record (EPD site #Entity) “: ???*

Response: The answer is contained in the sentence following the one that the reviewer refers to where we list the studies and estimate the number of sites/entities involved.

Action: The text has been changed from “(EPD site #Entity)” to “(EPD Entity number)” (line 228). The ‘more recent studies’ are cited in lines 229-231

-lines 178-180 “ We estimate that we have excluded 16 of the 17 European sites used by Binney et al. (2017) , 5 of the 6 European sites used by Allen et al. (2010), 28 of the 33 sites used by Cao et al. (2019) and 27 of the 71 sites used by Kaplan et al. (2016)”. So finally, how

large is your dataset? How many marine cores ? How is the spatial coverage of these new sites?

Response: OK.

Action: *So finally, how large is your dataset?* The text has been changed from “The distribution of sites included in our study” to “The distribution of **the 63** sites included in our study” (line 182), *How many marine cores ?* The has been changed from “For completeness, we also include marine records” to “For completeness, we also include **7** marine records” (line 196) *How is the spatial coverage of these new sites?* We have added the following text “**Nevertheless, our dataset includes sites from this region, as well as North Africa and eastern Central Europe through to Iran, although most sites are located in an arc across eastern Spain, the Alps, and Italy.**” (lines 186-188)

-line 194 « The count of *Larix* was amplified by a factor of 10 due to its low pollen representation (Binney et al., 2017)”: why only *Larix*? Other taxa are under or over represented: how do you manage that?

Response: We apply the correction for *Larix* in common with many other authors. It is an important forest forming boreal tree indicative of a particular climate, and it has a particularly low pollen dispersal compared to other trees that occur in the LGM dataset.

Action: As well as Binney et al 2017, we have now added the following authors who have also applied a similar correction for *Larix* pollen: **Edwards et al. 2000, Bigelow et al. 2003, Tarasov et al. 1998, 2000, 2013** (lines 248-249)

-line 213“ we did not apply this additional procedure and present only the merged steppe biome”: I disagree with that (see my major point) because a possible confusion between warm and cold steppes can lead to a bias in the climate reconstruction to too warm climate conditions for the LGM.

Response: Please see the response to the earlier comment 1. The climate reconstruction is based on pft’s, not biomes, therefore it differentiates between warm and cold steppe.

Action: None

-line 220 “to match fossil samples with modern calibration pollen samples”: the MAT is an assemblage approach which require no statistical calibration, so correct it (the modern pollen samples dataset is not a calibration dataset as it’s the case for the WAPLS for example).

Response: The term calibration is widely used with respect to MAT in the literature. See Simpson (2007) “The modern analogue technique, described below, is an inverse multivariate **calibration** approach.” Or Juggins & Birks (2012) for instance figure 14.3, part of which is shown below.

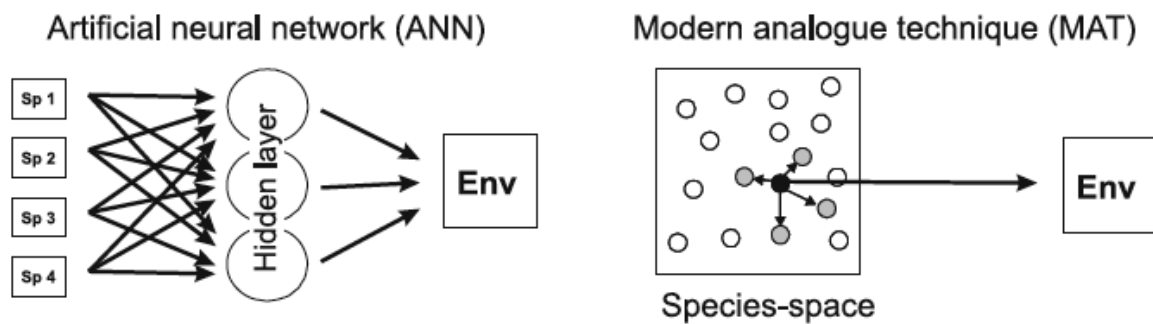


Fig. 14.3 Conceptual diagram illustrating the different approaches to multivariate calibration. Sp are biological taxa in the modern training-set and Env is the environmental variable of interest in the modern data. C are components

Simpson (2007) *Analogue Methods in Palaeoecology: Using the analogue Package* doi: 10.18637/jss.v022.i02
 Juggins & Birks (2012) doi:10.1007/978-94-007-2745-8_14,

Action: None.

-line 221-223 “This is a similar approach to that used by Peyron et al. (1998) and Jost et al. (2005) who also applied pollen PFT scores to reconstruct LGM climate from pollen data, but who used a neural network technique which is a variant of the standard MAT (Chevalier et al., 2020)”. I disagree with that, there is a confusion here in the principle of each method. The Artificial neural networks used by peyron et al and others studies IS NOT a variant of the MAT. It’s a method close to machine-learning methods, with a real calibration dataset and not easy to check because similar to a black box; in contrast the MAT is very simple, based on an dissimilarity calculation. The only common point is that both methods use PFTs scores to overcome problems associated with the lack of modern analogue but that is all.

Response: Already agreed, see answer to earlier comment 3.

Action: See answer to comment 3.

-line 242 “The size and distribution of the modern training set in climate and vegetation space is important”: yes, I strongly agree with that, the role of the modern dataset is a key one see papers of Turner et al., 2021; Salonen et al; Dugerdil et al., 2021 for example. I think that the differences in the different climate reconstructions evidenced here are mainly due to the size of the modern dataset.

Response: Agreed, we make the same point.

Action: The additional references have been added (lines 307-308)

-line 259 "It was therefore decided not to apply this filter", so how do you take into account the autocorrelation in your data?

Response: In common with many studies that use MAT, we do not take account of the effects of autocorrelation. We highlight to the reader the autocorrelation problem, and why we do not apply the h-block method developed to reduce the effects of autocorrelation, mainly because it creates as many problems as it solves.

Action: We explain our reasoning in lines 310-326.

-line 263 A part on the climate parameters reconstructed here is lacking, as statistical tests to be sure that these climate parameters are not autocorrelated; how is calculated the error bars?

Response: We are not quite sure what the reviewer is wanting here. Almost all of the common climate parameters used for reconstructions in the palaeo sciences are correlated to some extent with each other, it's the nature of the climate system. It is almost impossible to distinguish for instance whether a proxy, and especially a biological proxy, is responding to degree days, frost days, absolute minimum or mean monthly temperature etc. This is a problem inherent in climate reconstruction and is beyond the scope of this paper (see e.g. the discussion in section 3.4 of Chevalier et al 2021). We calculate error bars using the standard MAT method, we can add a description of this.

Action: The following text has been added (lines 328-332) to describe the calculation of uncertainties: "***Uncertainties for the pollen-climate reconstructions were calculated using the standard method for MAT (Juggins 2020), that is, as a function of the spread of the climates associated with the best modern pollen analogues used for each fossil sample. The closer the climates of the best modern pollen analogues (6 in the case of this study) then the smaller are the uncertainties assigned to the reconstructed climate of the fossil pollen sample.***"

-lines 267-272: refs are missing;

Response: OK.

Action: The following references have been added: ***Davis 1963, Gaillard et al. 2010, Zanon et al. 2018*** (lines 343-344)

-line 312 "Similarly, quantitative climate methods have been applied to individual marine pollen records (Combourieu Nebout et al., 2009; Fletcher et al., 2010)": some key references are missing, as the MF Sanchez Goni team.

Response: Unfortunately, the reviewer does not provide any details of the key references that are supposed to be missing. While MF Sanchez Goni and her team have published many important papers, we cannot find any that involve quantitative reconstructions of climate based on pollen, which is the subject of the sentence.

Action: None

-line 331 "In this study we have taken the closest point on land as the modern climate for the calculation of anomalies": better to take a regional temperature range

Response: The reviewer suggests taking the climate of a region, but then the problem becomes, what region? There is no easy answer. The region represented by the source area is one of the key problems for interpreting pollen from marine cores, which is why we make specific reference to this problem in the text. Should it be weighted for distance from the core site? What about the land that is now covered by the sea but which would have contributed pollen when sea levels were lower during the LGM? Many studies show that pollen discharged by rivers close to marine core sites can be a significant source of pollen, should this also be taken into account? We agree that the option we have chosen is somewhat unsatisfactory, but then it would appear that every solution seems unsatisfactory. We suggest instead to include the modern climate values in the appendix so that the reader can adjust the anomalies as they see fit.

Action: We have included the modern climate values for all 63 sites in our dataset the appendix, Table A2. The problems (and advantages) associated with marine sites are discussed in lines 400-427.

-lines 337-347 "we did not adjust the pollen assemblage for the over-representation of Pinus in the marine pollen samples" This poses the problem of Pinus transport over very long distances in open environments as the LGM vegetation; this is particularly true for marine cores but it is also true for some terrestrial sites. So the question of excluding or keeping Pinus needs to be more investigated and tested may be on a site-by-site basis.

Response: Agreed, but the problem of over (or under) representation due to differential transport is a problem that is intrinsic to the science of palynology with no straight-forward answer. Fundamental to this is the fact that although the risk of under/over representation can be acknowledged, it is generally very difficult to detect and correct in any detail. One of the closest attempts at this can be seen in the use of MAT methods to reconstruct tree cover, which we apply in our study. This 'black box' approach at least makes some attempt to take into account the potential over-representation of *Pinus* in both terrestrial and marine environments, at least where this problem is also found in the modern analogue samples that are matched with the fossil samples.

From the point of view of the marine pollen records, we find it more appropriate to include rather than exclude *Pinus* because it is a key forest forming tree in the coastal regions close to the marine sites and to remove it completely would create an artificially arid assemblage that would certainly undermine the ability of the transfer function to reconstruct precipitation. Reconstructions of temperature would be less affected because *Pinus* is a generalist found in both hot and cold regions and so carries only a weak temperature signal compared to the rest of the assemblage. We can add this clarification to the text.

Action: The following text has been added to clarify the problem for the reader (lines 435-439) *"Removing Pinus from the assemblage would almost certainly create an artificially*

arid assemblage in these circumstances, undermining the ability of the transfer function to reconstruct precipitation, although temperature would likely be less affected since Pinus is a generalist found in both hot and cold temperature regions.”.

-line 363 “such as [site #3] and [site #58]” ; better to give the name of the sites

Response: OK.

Action: Site names have been added throughout the text.

-lines 377-380 “The main arboreal biomes found at the LGM include Taiga (TAIG), Cool Mixed Forest (COMX), Cool Conifer Forest (COCO) and Xerophytic Scrub (XERO), with just a single occurrence of Cold Mixed Forest (COMX) and Warm Mixed Forest (WAMX). We do not record any Temperate Deciduous Forest (TEDE), Tundra (TUND) or Desert (DESE) biomes at any site at the LGM.” Could you explain more the location of the different biome patterns?

Response: Ok

Action: The text has been changed from: “The main arboreal biomes found at the LGM include Taiga (TAIG), Cool Mixed Forest (COMX), Cool Conifer Forest (COCO) and Xerophytic Scrub (XERO), with just a single occurrence of Cold Mixed Forest (COMX) and Warm Mixed Forest (WAMX). We do not record any Temperate Deciduous Forest (TEDE), Tundra (TUND) or Desert (DESE) biomes at any site at the LGM.” to “**Of the main arboreal biomes, Taiga (TAIG) is the dominant biome at 3 sites at the eastern end of the Alpine ice sheet, as well as at a site just to the north in northern Germany and a site in Slovakia, while Cool Conifer Forest (COCO) is found at 1 site close to the Scandinavian ice sheet in Lithuania. Cool Mixed Forest (COMX) is found much more widely at 8 sites south of the Alps from southwest Iberia to Romania, with Xerophytic Scrub (XERO) occurring at 8 sites with a similar distribution but not as far east or west. Cold Mixed Forest (CLMX) occurs at just two sites in Georgia and the Alboran Sea at the far east and west of the study area, while Warm Mixed Forest (WAMX) is the dominant biome at just 1 site in Southern Spain. We do not record Temperate Deciduous Forest (TEDE), Tundra (TUND) or Desert (DESE) as the dominant biome at any site at the LGM, although they do occur as lesser biomes.**” (lines 477-487)

- in the text, many taxa are not in italic: please correct it

Response: This was also mentioned by Reviewer 1

Action: Taxa names are now italicised (where appropriate) throughout the text.

- lines 441-443 “The first test was to compare our MAT results with previous pollen-climate reconstructions based on the same LGM sites but using different methods. These previous reconstructions include the neural-network methodology of Peyron et al. (1998) and Jost et al. (2005)”. I don't agree, it's not a validation test: not the same method, not the same

surface datasets, so we cannot really compare the results. Moreover, the LGM spectra used in previous studies and here are probably not the same, that too can bias the results. OK for me in the discussion but not in this part as a validation test. Same for Wu et al, 2007. -lines 443-444 “the neural-network methodology of Peyron et al. (1998) and Jost et al. (2005) which we call MAT-NN, as well as the Inverse Modelling approach by Wu et al. (2007) which we call INV.” First, the neural networks methodology of peyron et al. is NOT a MAT method, so you cannot call it MAT-NN, it’s a non-sense. Second, could you use the name of the method given in the reference papers? Please check, I guess it’s the PFT method for Peyron et al and I.M. for Wu et al. which are correct.

Response: The evaluation/comparison section has been moved to the discussion. We intended our method acronyms to be as self-explanatory as possible. ‘PFT’ is not the defining feature of the Peyron et al 1998 method, since the use of PFT scores can, and has, been used in other methods such as MAT. We therefore prefer to use the acronym ‘ANN’ for Artificial Neural Network (as used by Chevalier et al 2019).

Action: The section mentioned by the reviewer has been moved to the discussion as they suggest. MAT-NN has been changed to ANN throughout.

-line 472 “We compare the chironomid record with our MAT reconstruction...”: you don’t compare the chironomid record, you compare the temperature inferred from the chironomid record, please correct it

Response: Ok.

Action: This section of text has been re-written as part of the move to the discussion section. See lines 876-888.

Samartin et al (2016) not Samaratin et al (2016)

Response: Ok

Action: Corrected

-lines 510-512 « The second consequence of lower seas levels is that terrestrial pollen sites were located further from the moderating effect of the ocean than they are today, resulting in a localised modification of the climate experienced by the site irrespective of regional or global changes.”: a ref is lacking

Response: OK.

Action: The following reference has been added: **Geiger, R.: The climate near the ground. Cambridge: Blue Hill Met. Observ. Harvard University, 1960.** (line 602)

-lines 531-538: “In terms of regional climate, the major ice sheets would have provided significant barriers to westerly atmospheric circulation, or even north-south circulation in the case of the Alps and Pyrenees. As well as representing a physical obstruction, the

thermodynamic response of the atmosphere to these high, cold obstructions would have been to encourage the formation of areas of semi-permanent high pressure, similar to those found today for instance over the Greenland ice sheet. In addition, the Laurentide ice sheet located over North America would have generated downstream effects over Europe. These physical and thermodynamic effects would have affected the direction of storm tracks, as well as more local climatic effects commonly associated with ice sheets such as strong katabatic winds.”: refs are lacking

Response: OK.

Action: We have added the following references: COHMAP (1988), Kageyama, et al. 2021, Velasquez et al 2021, Luetscher et al 2015, Lefort et al 2019 (lines 633-634)

-Line 563: “despite arboreal pollen forming 70-80% of the pollen assemblage”: a significant part of the arboreal pollen is due to Pinus which is clearly overestimated in LGM pollen assemblages due to long distance transport in open areas as during the LGM.

Response: The point being made in the sentence is that the biomisation algorithm is indicating that steppe is the dominant biome, even when arboreal pollen forms 70-80% of the pollen assemblage. This problem is not caused by high levels of arboreal pollen from long-distance transport but is simply a quirk of the biomisation algorithm. However, the reviewer is right in that some samples may be affected by long distance transport of Pine in the open environments of the LGM. However there also appear to be plenty of samples with low or even very low (<20%) arboreal percentages, so not all sites in open areas may be affected by long-distance transport of *Pinus* in the same way. Again, this is one of the reasons why we have applied the MAT tree-cover reconstruction rather than rely on % arboreal pollen.

Action: We acknowledge the points above in our revised manuscript (lines 671-674)

-lines 615-616: “expected, areas of forest reconstruct similar or increased precipitation compared to today, and areas of steppe indicate decreased precipitation (see next section).” The CO2 effect on climate reconstruction (see recent papers by Cleator et al. and Prentice et al) is not discussed, please add a part on this point.

Response: Ok

Action: The CO2 problem is revisited in the discussion (lines 852-869)

-line 618 correct “archaeozoological”

Response: Ok

Action: changed to “archaeozoological” (line 735)

-line 669 PMIP = Paleoclimate Modelling Intercomparison Project, not "Palaeo-model Intercomparison Project", correct it; many key refs on PMIP project are missing: Jost et al., 2005; Tarasov et al ...

Response: Ok. We are not sure what the Tarasov et al reference is though.

Action: "Palaeo-model Intercomparison Project" has been corrected to "**Paleoclimate Modelling Intercomparison Project**" Jost et al 2005 and Kageyama et al 2021 have also been added. (line 800, 803)

-line 372: "suffer from the same problems of dating control, unclear provenance and a potentially limited taxa assemblages." I don't agree with that, you kept a lot of them for your study.

Response: We reject 16 out of 26 records used in PMIP studies, which is a lot of sites on which previous conclusions will have been based.

Action: This text has been removed.

- line 677: "and the Neural Networks method which is a version of MAT (MAT-NN) " : the method developed by Peyron et al and Tarasov et al is named the PFT method and IS NOT a version of the MAT. It's a method based on Artificial neural networks close to machine-learning methods, with a real calibration dataset and similar to a black box; both methods use PFTs scores to overcome problems associated with the lack of modern analogue but that is all.

Response: Agreed, this has been corrected

Action: See earlier comments

-lines 678-690: see my major concern; I think that the fact of not differentiating the steppes can lead to the warm temperatures reconstructed here with the MAT; please check.

Response: See earlier comments, there appears to be some confusion between biomes and pft's. Warm and cold steppe is differentiated at the PFT level used in the MAT reconstructions

Action: None

-line 721: diatom not Diatom

Response: Ok

Action: "Diatom" changed to "**diatom**" (line 927)

-line 730 check "Hughes et al (Hughes et al., 2006)"

Response: Agreed

Action: Corrected to *Hughes et al (2006)* (line 937)

-line 755 "19.1 °C" or -19.1 °C ?

Response: Agreed

Action: Corrected to **-19.1** (line 970)

-line 763 "This compares with -7.2 °C for our 63 pollen sites": not sure it makes sense to calculate the mean for 63 sites given the regional climate patterns

Response: We agree with the reviewer, but in this case we are comparing with Allen et al (2008) who undertook a similar calculation.

Action: None

-lines 778-784: Good to add a comparison with the brGDDTs temperature record from Padul (Rodrigo-Gámiz et al., 2022).

Response: We are reluctant to include this study by Rodrigo-Gámiz et al. 2022 because this record looks quite odd. In particular, it appears warmer than the present day for much of the glacial period and has a long-term trend very similar to pH. This is important because the brGDDT proxy has been criticised for being influenced by pH as well as temperature, although this potential bias does not appear to be mentioned in the paper. We do not think that excluding the study would make any significant difference to the conclusions of the paper.

Action: None

-line 806: I think a part on the comparison of these results with LGM model outputs is lacking.

Response: We agree, but including a comprehensive data-model comparison would greatly extend the paper. We have a different paper in preparation which addresses this (Russo et al.), and of course the results will be made available for the whole community as soon as our manuscript is accepted for publication.

Action: None

-lines 856-857 "Nevertheless, one of the most consistent signals in our dataset is for an increase in summer precipitation over many areas of Southern Europe and the Mediterranean". In south Spain, the reconstructed biomes is steppe or xerophytic, with a lot of Artemisia and chenopodiaceae: these taxa are characteristic of dry environments (semi-desert), so how do you explain the wetter than today conditions reconstructed?

Response: It may seem a little counter-intuitive, but it is still possible to have quite a large change in climate without radically changing the vegetation, especially the pollen biome. For instance, a semi-arid climate ranges from 250-500mm rainfall a year, so we could expect a semi-arid vegetation to be dominant even if the rainfall increases 250mm. Even beyond 500mm per year, you can still find *Artemisia* and *Chenopodiaceae* in the landscape where edaphic conditions are favourable, for instance with a saline geology in the Mediterranean, or even somewhere like the heathlands of northern Germany.

Action: The following text has been added (lines 1098-1104):). *“It may seem counter-intuitive to see an increase in reconstructed precipitation in the same regions where we also find a preponderance of steppe or xerophytic biomes and taxa, including *Artemisia* and *Chenopodiaceae*. This is attributable to the fact that climate can change quite markedly with necessarily invoking a major change in vegetation, and especially the pollen biome. For instance, a semi-arid climate ranges from 250-500mm rainfall a year, so we could expect a semi-arid vegetation to be dominant even if the rainfall increases 250mm (100%).”*

-check your reference list : Allen et al., 2008 a and b, two refs for Peyron et al 1998 ..

Response: Ok

Action: These have been corrected, the duplicate Peyron et al 1998 has been removed and the Allen et al 2008 a and 2008b references have been cited in the text at the appropriate point.

Reviewer 1

One of the main places to improve the paper is the graphical representation of the findings. There is a detailed comparison of results from this study with other published records of vegetation, faunistic (zoological remains), and climate. I wonder if it is possible to show some of these values /comparisons on the figures. Otherwise, there are pages of text in the manuscript with no possibility of seeing this visually, which is a pity, as this would significantly improve the paper's impact.

Response: We agree with the reviewer, but we were worried about over-crowding the figures.

Action: We have added this comparison to the figures and show them in appendix figures A4 and A5.

More specific Response:

40 to 52, a nice overview; please add some references to support these statements. Here and in other places in the text, please see a very recent book describing the landforms of the European glacial landscapes:

<https://www.sciencedirect.com/book/9780323918992/european-glacial-landscapes#book-description>

Response: Agreed, see response to the same comment by Reviewer 2. Unfortunately the book is behind a paywall but we have added some other references.

Action: The following references have been added: *Ehlers et al. 2011*, *Arslanov et al. 2007*, *Lehmkuhl et al. 2021*, *Grichuk 1992* (lines 51-62)

64-67 Please extend the relationship between climate CO2 and vegetation slightly.

Response: Agreed, see response to the same comment by Reviewer 2

Action: See earlier comment by reviewer 2, the paragraph has been extended to include this information (lines 77-89)

89 perhaps also add the rates of plant expansion; generally, these are very high assuming the postglacial expansion from southern refugia, and generally, this does not fit modeling results (for example, *Nogués-Bravo et al. 2018*; *TREE*, 33, 765-76; *Feurdean et al., 2013*, *Plos One*, 26, 8 71797, etc).

Response: Agreed, a good addition

Action: The following sentence has been added: “*Modelling have shown difficulty in supporting the very high rates of postglacial expansion that would be necessary for southern refugia (Feurdean et al., 2013, Nogués-Bravo et al. 2018).*” (lines 118-120)

138, so there were 63 records, 27 with raw counts, and 35 digitized? Please re-write this sentence to make these numbers more transparent.

Response: Ok

Action: The following sentence has been changed from “Overall, 35 out of 63 records were digitized, while the rest of the data consisted of raw pollen counts” to “**Overall we have included 63 records in our study, of which 35 were digitized and 28 consisted of the original pollen counts (Table 1).**” (lines 178-180)

L172-180 may consider moving these levels of detail at the SI

Response: We include this information in the main text because we think it is important to place the current study in the context of previous work. The quality control criteria is one of the key innovations of the study, and the exclusion of records that have been included in previous studies shows the impact of applying this quality control criteria.

Action: None

248-251 is too long and a complicated sentence, please rephrase

Response: Ok

Action: The following sentence has been changed from : “*To reduce this problem it is possible to systematically exclude closely located modern samples from the analogue matching process, for instance, by excluding samples that fall within a certain spatial range (h-block filter) (Telford and Birks, 2009).*” To “***To reduce this problem it is possible to exclude closely located samples from the analogue matching process using a filter based on a set distance (h-block filter) (Telford and Birks, 2009)***” (lines 312-314)

l.261 What exactly is meant here by modern climate?

Response: Ok

Action: The following sentence has been changed from: “*These have been calculated with respect to modern climate at each core site location using WorldClim 2*” to “*These have been calculated with respect to modern climate (1970-2000 average) at each core site location using WorldClim 2*” (lines 334-337)

l.267-272, these lines should be supported by a ref

Response: Agreed, this was also a comment from reviewer 2

Action: The following references have been added: ***Davis 1963, Gaillard et al. 2010, Zanon et al. 2018*** (lines 343-344)

The names of taxa (Pinus, pine, birch, to name a few) appear wrongly written everywhere I guess it is due to the software conversion; please amend.

Response: Agreed.

Action: Taxa names have been italicised where appropriate

Results. I think one should avoid comparisons/ references to other studies in the Results and should be placed in the discussion

Response: This is similar to a comment by reviewer 2, this section has been modified and a large part moved to the discussion

Action: See response to earlier comment

418 I am surprised to see the low percentages of Chenopodiaceae, Asteraceae, and Artemisia, over most of Europe

Response: The values are still high at some sites (40%+), but it is true, they are not high at many sites. This is one of our main conclusions, that there was more diversity in the vegetation landscape across Europe at the LGM than has previously been suggested. It wasn't all cold steppe.

Action: This is discussed in section 4.1, lines 638 onwards

502 ff Chapter 4.0 also, please see the new book 2022 *European glacial landscape: the last deglaciation* <https://www.sciencedirect.com/book/9780323918992/european-glacial-landscapes#book-description>

Response: This looks like a nice book but unfortunately it is behind a paywall.

Action: None

626 ff see also Demay et al., 2021 *Quaternary International* 581-582, 258–289.

Response: Agreed, nice paper.

Action: Demay et al 2021 has been added (line 745)

Conclusions: I found them overall too long, too many details. I think they should provide better summaries of the essential findings, for ex. L.889-891, l.903-904 sound like results, and the overall ending phrase is missing.

Response: Ok

Action: The conclusion has been re-written and shortened to better emphasise the main findings

The number of graphs and figures made the number of illustrations very high and somehow redundant. Better keep the maps and send graphs to SI. This way, one can accommodate a comparative figure with published records described extensively in the discussion.

Response: Ok.

Action: The chronology table has been moved to the appendix, table A1. The tree-cover figure and the pollen diagram figure have also been moved to the appendix (figures A1 and A2 respectively). The comparative figures are now included, although we have put these in the appendix and not in the main text because adding the results of the other studies does make them very busy (temperature figure A4, precipitation figure A5).