We thank the referees for the extensive reviews that bring much to the manuscript. We addressed all comments, either by correcting the manuscript (most) or by replying here. As expected in the discussion between authors and referees, we do not agree with some of the comments but we try to explain our point of view in those cases. We provide here some indication of the changes, as well as we attach a pdf of the manuscript with the changes highlighted. For guidance, we show here the referee comments in light gray and our reply in black.

Reviewer #1

Revised manuscript

The authors appear to have taken on board many of the comments made in the first round of review. However, there are still substantive problems remaining. Three of the most important are:

1. The methodology still remains opaque. From the methods presented it would still not be possible to independently reproduce the results of the study from reading the paper and accessing the resources it refers to. As a minimum, the paper should include enough information so that the study could be independently reproduced. This is particularly important in this case because the method appears to differ significantly from previous pdf methodologies that are otherwise well documented. Even if we take on trust that the R scripts can be obtained from the author (although it would be better to upload these to a recognized R script archiving site), the authors still do not provide information about the taxa list and how they resolved the not insignificant problem of equating modern distribution data available at species level with pollen taxa which are of variable taxonomic resolution. Until this information is made available, it is not possible to say that this has been done satisfactorily.

The methods section was revised and hopefully now is clear enough.

Concerning the reproducibility issue. The raw data is available either in public databases or published in scientific journals. The scripts for the reconstruction method are available at the link given in the previous round of revision. The assignment of pollen taxa to plant species is an issue that affects all pollen-based climate and vegetation reconstructions as the identification of pollen grains is known to be less accurate than that of the originating plants and our method has also this plant/pollen assignment bias. Finally, we provided in this revised version the pollen taxa list with the assigned plants for the climate reconstruction.

The method does not differ substantially from Kühl et al. (2002).. We improved it by taking into account a suggestion made by Birks et al. (2010). Thus, instead of using only binary data (presence/absence of each taxon), we used the pollen percentages to weight median value of the taxa pdfs. Such weighting allows to refine the PDF by assuming that species are more abundant in their optimal niche.

In our previous submission, we made all scripts available in the public domain. However, we found it disappointing that our effort was most likely disregarded by the reviewer. Scripts often serve a simple task of automating methods that would be otherwise cumbersome to do, either by the nature of the method itself, or by the nature of the data. This automation is often for personal use and thus it results in scripts that are not easily adapted for other needs. In this case, due to the high amount of data from several sources, the scripts dealt with access to a spatial SQLite database, and multiple folders organized in a very specific way to store several temporary and final results. In the last revision we decided to change that issue and converted our scripts to an R package that anyone could easily use. There was a link sent in the revision and we expected that the work would be a major key aspect to guarantee the needed reproducibility of the study. Thus, any users (including the reviewers), may have access to a fully working package to reconstruct climate as provided in our work.

2. Critically, there still remains no proper evaluation of the reliability of the technique, and no evaluation of potential error in the reconstruction through time. This is such a fundamental part of transfer-function development, let alone the scientific method, that I am somewhat shocked to find the authors scrabbling around to put together some kind of evaluation at this stage. It is great to find so much effort has been put into developing a new method, but ultimately you still need to ask the question is it any good? how do we know it is any good? can we quantify how good it is, and can we make that assessment back in time? The evaluation provided by the authors in this revised manuscript is not sufficiently rigorous to provide this information, and would not be acceptable in comparison with previous studies where such evaluations have been provided. The authors have only to look at the literature associated with other pollen-based climate reconstruction techniques to see what is required, and particularly those based on the pdf method.

Response given bellow, on the main comments.

3. The English has deteriorated considerably from the first draft, to the point that almost every other sentence (including figure captions) has some issue or other. These are far too numerous to correct, but absolutely need to be corrected before the paper could be considered for publication. I believe the co-authors should be asked for help here, or a professional proof reader employed. At times the entire meaning of the sentence is not clear, and this has made the task of reviewing the paper more difficult.

The English was reviewed.

Main comments:

p3, Section 2.1: Still needs taxa list, see 1) above

The taxa list was added as supplementary material for the manuscript (Appendix A).

p3, Section 2.1: The acronyms for the temperature parameters Tjan and Tjul are not self descriptive, something like Tjan_min and Tjul_max would be better. However, Aprc should definitely not be used and should be replaced with the standard Pann, which is also consistent with the chosen temperature acronyms.

We opted for maintaining the Tjan and Tjul acronyms for minimum January temperature and maximum July temperature. These are defined in the text and should not cause confusion as we do not use any other January or July temperatures. We follow the reviewers suggestion for annual precipitation and changed the acronym to Pann.

p4: lines 198-232: I still find the description of the method difficult to follow, and as a result quite opaque. Perhaps this may have something to do with the English terminology used, which may mean something different to the average reader than the author. I would suggest that the author asks someone unfamiliar with the technique to read the passage and then recount (without prompting) the method to test the effectiveness of the description.

The method section was fully reviewed.

p4, lines 233 onwards: The authors now include an evaluation of the method. This is described, but the results of the evaluation are not discussed. What is the average error for each climate variable, and what is the standard deviation? Are there any systematic errors? (for instance, reconstructed summer temperatures look systematically cooler than expected). The method used to assess these errors is very poor. For instance, the comparison of samples within the last 500 years against a modern baseline does not take into account changes in climate over the last 500 years that would undermine the comparison even if the transfer function worked perfectly. Critically, no uncertainties are provided for the palaeoclimate reconstruction back in time. It seems to be a serious failing in the development of the method that no consideration was given to assessing transfer function performance.

The uncertainties of the reconstruction are given as appendix. We used the 95% confidence interval that is related to the standard error, similarly to Kühl and Gobet (2010). Additionally the section (lines 235-245) was revised to introduce some of the discussion suggested by the reviewer.

p4, line 238: do you not mean 'all samples younger than 500 years BP' rather than 'inferior'?

Changed.

p5, line 243-251: How was the 100 BP baseline calculated? Is this based on eg historical climate data, the top sample of each core or a gridded reconstruction? This is not described clearly.

This paragraph was rephrased to include better descriptions of the baseline calculation (lines 263-279).

p5, line 252-254: How are the 1000 year timeslices defined? For example, using a time window (+/-500 years), or exactly every 1000 years using the interpolation between samples? Please explain.

The timeslices were extracted from the continuous interpolation. The paragraph was revised to be more clear (lines 242-245)

p6, line 297-300: The authors apply an unusual evaluation of uncertainty. The description (Appendix A) is written in poor English 'A set of 250 replicates were performed by sample randomly one reconstructed age within 500 years for each site (gray lines) and than averaged.' but I presume this means that they iteratively refitted a linear regression line 250 times after randomly removing one of the samples in the training set on each iteration. This is not a normal cross-validation method, which involves the ability of the model to predict an individual missing sample and not some kind of global regression relationship. The evaluation shown by the authors only demonstrates that the sample values are symmetrically distributed about the mean, and that with enough samples in the dataset the removal *of one sample does not unduly disturb the regression line. The ability of the transfer function model is not based on a regression line, but the ability of the individual samples to reproduce the present climate, which should be a one-on-one relationship. It is the deviation from this one-on-one relationship (residuals), which is the measure of uncertainty. If the present day January Tmin climate at the sample site is -2 but the reconstruction gives a value of -8.2, then the reconstruction is in error by -6.2. It is common to report some kind of global average error based on all of the samples in the evaluation training set, but this is not the same as reported by the authors. Looking at the figures, the ability of the reconstructed values to reproduce the modern climate on a sample by sample basis indicates substantial errors. These are probably no worse than other methods that have large uncertainties (eg inverse modeling), but they should be properly evaluated and reported using a commonly used methodology. This evaluation should also be extended to the fossil samples, so that each fossil sample also has an uncertainty. See Norbert Kuhl's work to see how this could be applied to the pdf method.*

We changed this evaluation to a more classic approach. We now have a single regression based on the mean of the last 500 years for each site. With the plot (Appendix B) it is also possible to assess the evaluation that the referee suggests, i.e., the difference between reconstructed and modern climate values, that is also summarized in a root mean squared error. See also lines 246-279.

However, we are more interested in a macro-scale perspective: do the observed current warm sites correspond to the warm ones in the reconstruction? For this we tend to focus on the slope of the regression and, particularly, on the Pearson correlation score. If positive, as it happens for our datasets, then it indicates that the relation between sites is consistent. For assessing the significance level of this correlation we provide a randomization test, were we shuffle one of the sites and retest the correlation 1000 times.

We agree with the reviewer that this provides a different approach for evaluating the error. In fact, the assumptions for the reconstruction method are not valid for the modern times due to the human disturbances. Therefore, even if a site-by-site evaluation of the pdf-method fails to predict modern climate, it does not necessarily signify a poor performance. Such potential discrepancy might only be related to recent ecosystem disturbances which were translated into the pollen composition. This potential biasing effect is very difficult to avoid, and thus we prefer to analyze the trend for the collection of sites we have, showing if the spatial distribution of the climate is affected (warmer sites at particular locations are also reconstructed warmer than colder sites at other locations).

Uncertainties from Nobert Kuhl's work are based on the standard deviation of the normal distribution of the reconstructed climate (Kühl and Gobet, 2010). This method was applied to a single or a few sites. In the present study we have multiple sites and we are seeking to build a spatial reconstruction. This makes it more difficult to provide similar estimates of uncertainty. We provide as supplementary material the 95% confidence interval for the reconstructions that is related to the standard error and deviance of the mean reconstruction for each site and reconstructed time slice (Lines 239-242)

p6 Section 3 Results: There is a long description of the climate reconstruction results based on absolute values. As I mentioned in my first review, and indeed this was also mentioned by the second reviewer, the use of absolute climate values rather than anomalies greatly reduces the relevance of this section to the average reader. I respect the decision of the author to insist on presenting their results in *this form, and can understand the relevance to bioclimatic parameters, but I would again strongly recommend presenting the anomalies first, and absolute values second. Even just showing modern day values for the different regions in figure 4 would help.*

We understand the insistence of the referee on the anomaly maps. We, however, prefer the absolute values as it was our main objective and it was how we designed this research. However, in addition to the absolute values we have added the anomalies in this version of the manuscript.

p7, line 366-374: Comments about the evaluation of the method would be better placed altogether in the methods or results section rather than spread about the text. What is the 'historical' climate referred to on line 368? is this the modern climatology? if so, the word historical is very confusing, if not then its use needs to be explained. What is meant by a 'significant linear trend'? on line 367, as discussed previously the importance is not that the line is linear, or that there is a regression line at all, only the deviation from the expected fit and the spread of the residuals.

The sentence was rephrased. The 'historical climate' is now defined as 'observed climate' in the lines 246-248, as the average climate from the period between 1950-2000. We added a few sentences about this issue in the methods section, however, we still find the need to discuss it here. See also comment above.

p7, line 383-385: As was mentioned in the first round of reviews, why does winter temperature rise in response to a falling trend in summer insolation? the authors need to explain their logic.

Summer insolation tends to decrease in the northern hemisphere after its optimum around 9ka. However, the trend for the winter insolation is rather towards an increase (e.g. Davis et al., 2003 or Mayewski et al., 2004) which is in line with our reconstructed winter temperature (lines 414-423).

p7, line 407-410: Again, this was already mentioned in the first round of reviews, the authors need to explain their logic better here. The comment "Summer temperatures, on the other hand, provide enough energy to plant growth (Sykes et al., 1996), and are likely resulting in less responsive July temperature." does not make sense, neither grammatically or scientifically. You might have a good point, something about plants becoming insensitive to progressively higher temperatures because their energy needs are non-linear with respect to temperature, but you need to explain and justify it better.

The sentence was rephrased (lines 444-451)

p7, section 4.1: 'OD', 'BA' what are these undefined acronyms? I take it that they are probably something like 'Older Dryas' etc but such things need to be defined for the reader. If it is the Older oledeDryas, then the date provide on line 416 is wrong (~8 to 14.7 ka). Also section 4.2 etc 'YD' etc

The acronyms and dates were corrected throughout the discussion.

p7, line 425: 'extreme January temperatures'? 'extreme' depends on your perspective, an anomaly of -5 doesn't look very extreme compared to other parts of Europe.

The sentence was rephrased (lines 464-467).

p8, line 445: I think you mean 'depending on the location in Northern Europe' since as you say later in *the sentence, Southern Europe experienced a cooling at this time.*

The paragraph was rephrased (lines 487-498).

p8, line 449-451: "Our results point to a decrease on Tjul temperature but a stable minimum temperature, indicating mild summers." doesn't make sense, even if you meant 'in' not 'on'. Are you saying that Tjul temperatures were lower than present? and what does a 'mild summer' mean? colder or warmer than today? when talking about minimum temperature, do you mean your Tjan reconstruction? Please be more precise in your use of language.

The sentence was rephrased (lines 492-495).

p8, line 473: Seppa and Birks only refer to Northern Europe, the 'warm period' experienced in Northern Europe is not typical of Europe as a whole and particularly Southern Europe which experienced a cooling.

With the previous modifications, the sentence lost its meaning. We have rephrased it to remove the reference to Seppa and Birks (lines 513-518).

p9, 532-534: Appendix E is not well explained, but I presume this is a plot of the maximum temperature change for each grid point arranged by altitude. This suggests that each grid point represents an independent observation, but in fact this is based on interpolation from just a few sites often distant in both horizontal and vertical space. I think you could make some general inference at an aggregate level, but to make a plot of the grid points like this without any consideration of both the interpolation and reconstruction uncertainties is very misleading.

We agree with the reviewer that only a general pictures could be obtained. We do not intend otherwise also. We added the real value at each site to better depict the general trend.

Data archiving: are the reconstructions and associated uncertainties to be made public through a data repository such as NOAA paleoclimate or PANGAEA? Also it would be very helpful if the pollen data that is included in the study but is not publicly available is made available through the European Pollen Database.

We will send the reconstructions as HDF format upon publication acceptance. The pollen data was published elsewhere by the respective authors and references given. It is the responsibility of the authors of those publications (to whom different constraints for data sharing might apply) to make the data available through any public database.

Finally, the English needs extensive correction, far too numerous to list here since almost every other sentence needs attention. This has deteriorated significantly from the first draft. Perhaps some of the co-authors can help here, since their English is excellent, else the manuscript needs to be professionally proof read. Here are just a few examples on page 2 alone:

The manuscript was reviewed by all co-authors.

p2, line 57: “with a strong relationship with climatic” with a strong relationship with climate
p2, line 71: “understanding this climate dynamics” understand climate dynamics
p2, line 73: “this intimate relation” this intimate relationship
p2, line 75/76: “and is, thus” and are therefore
p2, line 81-83: “the potential location of suitable climate favouring long species persistence and serving as refugia” grammar
p2, line 94: “milder climate than the northern” milder climate than northern
p2, line 127: “taxon are created” taxon were created
p2, line 127: “distributions in the cl

All corrected.

Reviewer #2

I think this is a relevant study raising very important questions on the Lateglacial evolution of the Iberian Peninsula (IP) climate as well as in its role as postglacial refuge. I believe the paper certainly builds on an important debate regarding refugia and I learnt and enjoyed reading on the use of PDFs for proxy-based climate reconstructions.
Authors present a coherent hypothesis based on a long-lasted topic (the IP as a refugial region) and the methods, results and discussion are consistent with the hypothesis.

I have added sticky notes to the -pdf file upload in this platform but I will only detail some issues here in case you can't follow my comments on the file itself (be that the case, please inform the editorial group and I will put those notes in a proper text file).

1- Authors try to prove the IP singularity as a climate refugial region in the European context. However they only show results for the IP and not for any other region in Europe. I know showing the same approach for the whole continent would demand much extra work, however we cannot asses singularity if do not compare the IP with anything else. Thus, authors either rephrase all the sections where IP is presented as singular in the European context (I bet it will be similar in all other Mediterranean peninsulas for instance) or you add some comparisons with other regions in Europe.

Our main idea was to show, in the introduction, that the IP is an important glacial refugial area for biodiversity. European glacial refugia are commonly associated with the southern peninsulas as a whole, including Italy and the Balkan's area. In this work, we intended to show that, despite that notion of general refugia, the refugia-within-refugia pattern (Weiss and Ferrand 2007) does apply, and Iberia has enough variation to support several refugia. That is why studying refugia inside a main refugial area is the aim of our study. Climate reconstructions have already been performed by other authors (Huntlet & Prentice, 1988, Davis et al., 2003, Cheddadi et al., 2006 etc). We have rephrased parts of the text to better convey this message (e.g. lines 82-103).

2- Connected with the previous, one of the reasons the IP might be special, as authors eventually find in their results, is that it is subject to two extremely different climate regimes: Atlantic vs Mediterranean. This is not discussed anywhere and I think some input on the current day IP climate context is really needed as it may serve later in the discussion. I would probably add in the sites table (table 1) whether the site is in the Eurosiberan or Mediterranean climate type.

The Temperate vs Mediterranean discussion is indeed interesting as it currently is a main driver shaping general patterns of biodiversity. We added some related discussion to the text and the information was added to the table 1 (see lines 91-96; 423-434; 502-506)

3- Authors are well aware that their data are fragmentary both spatially and in time scales. This might bias the results as some areas lack any fossil pollen information to infer the PDFs from. In order to validate their climate reconstruction authors correlate their result to current day instrumental series, for the last 500 years. My question here would be whether that correlation does not violate the assumption of climate driven plant dynamics, as in the last 500 years human activity as certainly alter the so-called "climate-plant" equilibrium. Can the authors expand, discuss that?

As we discussed above in the referee #1 comments, it is extremely difficult to do this evaluation without violating some of the assumptions. We agree with the reviewer but we believe that the general pattern is still possible to confirm (warmer areas/sites are reconstructed as warmer and vice-versa). We added some discussion about this subject (lines 256-263; 392-404)

4- Authors discussed very thoroughly in the introduction how the LGM was the main forcing factor for animal and plant taxa to migrate. However they chose (or they are force to chose) to reconstruct climate from 15k...the criteria for the chosen time frame is not very well explained and it need revision. From my understanding having since the LGM would allow to see which areas within the IP presented a larger intermillennial variation as most likely those millennia between the LGM and 15k were probably key for plants to allocate their potential refugia. Is this a question of available data in the EPD or not longer enough time series in IP?

We added more information to the text (lines 130-137). Unfortunately it is a limitation of the available data. As we go farther back in time, the available data decreases. We set up a time threshold so that our spatial data interpolation should be based on a minimum number of 10 sites. This is the reason why we begin our climate reconstruct from 15ka on.

5- Following on time frame covered by each record, the western part of IP presents a more complete time record, as almost all sites record the last 15k. Can you explain which can be the impact of this in your results? It seems as your northern sites are less resilient, more affected by climate variation...can be this an effect of simply longer time series?

We believe that the longer time-series are well spread throughout the study area. Nevertheless the western portion of the IP has more sites that are providing more information to the middle time slices, resulting in better spatial interpolations. We added more details on this issue in the manuscript (lines 381-392).

6- Some small things:
- Despite Fig 1 is informative for some readers might be useful (especially those know he area) to have the time frame covered by each site in table 1.

These were added to the table.

- IN my version of the pdf file I can't read the differences in line styles in Fig 4...to me they all look dashed but for the average.

In our version there is no problem with the different dashed lines.

All minor comments are made in sticky notes on the pdf itself.

All comments were taken into account.

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Spatial climate dynamics in the Iberian Peninsula since 15 000 Yr BP

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Abstract. ~~The evolution of the climate~~ Climate changes in the Iberian Peninsula since the last glacial maximum ~~is~~ are associated with distributional shifts of ~~multiple species. We rely on this~~ major Mediterranean and European temperate species. The dynamic relationship between ~~past climate and biodiversity patterns to quantify climate change using fossil pollen records widespread throughout~~ climate and species in the past may be retrieved from the fossil records available in the Iberian Peninsula~~and modern spatial distribution of plant taxa and climate~~. We have ~~reconstructed~~ used an extensive set of pollen records to reconstruct spatial layers (1 ka interval) of January minimum temperature, July maximum temperature and annual precipitation ~~using a method based on probability density functions and covering~~ over the time period between 15ka and 3ka. A functional principal component analysis was used ~~in order~~ to summarise the spatial evolution of climate ~~. Using a clustering method we have identified~~ in areas that share similar climate ~~evolution during the studied time period. The spatial reconstructions show a highly dynamic pattern in accordance with the main climatic trends. The four cluster areas we found exhibit different climate evolution~~ trends. When compared between them, the identified four areas show different climate trends over the studied period ~~. The clustering scheme and climate stability between millenia~~ and are coherent with the existence of multiple refugial areas ~~in~~ within the Iberian Peninsula.

1 Introduction

The distribution pattern of biodiversity today is the result of a dynamic process driven by geological events and climatic oscillations at a broad temporal scale (Hewitt, 2000). The ~~change from the glacial period to the current interglacial was followed by species with distributional shiftsand extinctions as studied~~ climate change since the last glacial period was tracked by species through major range shifts, migrations and/or extinctions which may be analyse at the genetic level or from the fossil record ~~(Taberlet and Cheddadi, 2002) or the genetic footprint of demographic changes (Hewitt, 2000). The relation~~ (Hewitt, 2000; Taberlet and Cheddadi, 2002; Cheddadi et al., 2014). The relationship between climate and biodiversity ~~is likely to~~ will be maintained in the future ~~, however with alarming~~ with major consequences due to the current trend of climate warming ~~of anthropogenic origin, including major distributional~~ related to anthropogenic activities, including range shifts (Parmesan and Yohe, 2003; Rebelo et al., 2010), diversity depletion (Araújo et al., 2006; Sinervo et al., 2010) and, more dramatically, species extinction ~~(Hewitt, 2000; Thomas et al., 2004)~~(Thomas et al., 2004). The biodiversity hotspots retain high levels of endemism and are considered as the best candidates for preserving species diversity ~~in~~ for the future (Myers et al., 2000). The Mediterranean basin hotspot, in particular ~~, was shown to~~

~~play~~ played the role of refugia to diverse ecosystems over several hundreds of millenia ~~by palaeoenvironmental studies~~ (Wijmstra, 1969; Wijmstra and Smith, 1976; Van der Wiel and Wijmstra, 1987a, b; Tzedakis et al., 2002). Often, those areas where species have persisted during glacial ~~periods~~ times are referred to as glacial refugia (Bennett and Provan, 2008; Carrión et al., 2010b; Hewitt, 2000; Hu et al., 2009; MacDonald et al., 2008; Willis et al., 2010) and the predicted high levels of diversity found at species level in these areas are corroborated at molecular level (Hewitt, 2000; Petit et al., 2003). Understanding how the past processes ~~affected~~ impacted biodiversity patterns offers invaluable knowledge for the current species conservation effort dealing with the ongoing global climate change ~~predicted for the following decades~~ (Anderson et al., 2006; Willis et al., 2010).

Species glacial refugia have been generally defined based on species survival with a strong relationship with ~~climatic~~ climate (Hewitt, 2000; Bennett and Provan, 2008; Cheddadi and Bar-Hen, 2009; Médail and Diadema, 2009). Nevertheless, the term has been used recently with multiple definitions (Bennett and Provan, 2008; Ashcroft, 2010). The classic definition of refugia is related to the physiological limits of species that under an increasingly stressing environment experience distributional shifts to near suitable areas (Bennett and Provan, 2008). Paleoenvironmental ~~data and molecular analysis~~ and molecular data have proven useful to locate species diversity and migration routes (Petit et al., 2003; Cheddadi et al., 2006, 2014). However, the locations and extension range of putative refugia still lack spatial consensus and quantification of its dynamic nature. Reconstructing past environments from proxy data will help ~~understanding this~~ understand climate dynamics and how it may have affected biodiversity patterns. ~~In fact, this intimate relation between changing climate and species distributions left evidence of the past climate change in~~ The past climate changes, species distributions and the interplay between them may be reconstructed from the fossil record. Fossil pollen ~~sequences provide information from past climates and is, thus,~~ records have proven to be an appropriate proxy for ~~the quantitative reconstruction of climate variables (Webb et al., 1993; Cheddadi et al., 1997; Guiot, 1997; Davis et al., 2003; Cheddadi and Bar-Hen, 2009; Bartlein et al., 2010)~~ quantifying past climate variables (Webb et al., 1993; Cheddadi et al., 1997; Guiot, 1997; Davis et al., 2003; Bartlein et al., 2010). Using proxy data to derive a definition of refugia in terms of suitable climate in a spatial context, may provide further insights ~~to the potential location of suitable climate favouring long species persistence and serving as refugia~~on the persistence of species in the past but also on the location of potential areas that may serve as future refugia for the species persistence.

Climate oscillations in Europe during the last 15,000 years exhibited latitudinal and longitudinal variations (Cheddadi et al., 1997; Davis et al., 2003; Roucoux et al., 2005; Cheddadi and Bar-Hen, 2009; Carrión et al., 2010b). During the last glacial maximum (LGM), several species ~~found refugia~~ persisted in refugia located in the southern peninsulas (Hewitt, 2000; Tzedakis et al., 2002; Petit et al., 2003; Weiss and Ferrand, 2007; Bennett and Provan, 2008; Hu et al., 2009; Médail and Diadema, 2009; Ohlemüller et al., 2012). The Iberian Peninsula, with a milder climate than ~~the~~ northern European latitudes (Renssen and Isarin, 2001; Carrión et al., 2010b; Perez-Obiol et al., 2011) served as a general refugium to several species that persisted in this area during the LGM. The current patterns of high biological diversity in the Iberian Peninsula derive partially from this ~~role~~ favourable climate during harsh glacial conditions and highlight the importance of this ~~peninsula~~ area in the broader Mediterranean hotspot (Médail and Quézel, 1999; Cox et al., 2006). ~~Although the concept of Iberian refugia may be confounded with a rather homogenous areafavouring species persistence, the~~ However, the Iberian peninsula is not a geographically homogenous area. Currently Iberian Peninsula is divided in two main climate zones: the temperate at the northern portion of the peninsula and the mediterranean, occupying most of the central and southern part (Olson et al., 2001). This pronounced difference in climate patterns in the Iberian Peninsula also promotes differentiation of the biodiversity patterns (Sillero et al., 2009). Additionally, the past vegetation and climate dynamics ~~in Iberia~~ reveal a quite complex picture (Roucoux et al., 2005; Naughton et al., 2007; Perez-Obiol et al., 2011)~~and multiple areas of smaller refugia were identified leading~~. Thus, multiple areas were identified as small refugia which lead to the refugia-within-refugia ~~pattern~~ "concept" (Weiss and Ferrand, 2007). All together it renders the Iberian Peninsula as an unique area ~~to study the climate processes during the late-Quaternary,~~ for studying the late-Quaternary climate processes with a highly dynamic vegetation response ~~to climate (Carrión et al., 2010b) and~~ (Carrión et al., 2010b) which is of a high importance for biodiversity conservation.

Our main objective in this study is to define areas within the Iberian Peninsula (Balearic Islands included) that share similar climate ~~evolution~~ trends and which may have served as a potential ~~refugia~~refugium. We reconstructed three climate variables and quantified their changes over ~~several thousand years. Using statistical methods, we defined~~ the past 15,000 years and we also summarised the geographical areas that have undergone similar climate changes and analysed their spatial dynamics ~~throughout the Holocene~~between 15,000 and 3,000 years.

2 Methods

The ~~area for the spatial reconstruction~~ study area extends throughout the ~~land area of the~~ Iberian Peninsula and the Balearic islands (Fig. 1). The method used to ~~produce past climate grids~~ reconstruct past climate variables is based on the probability density functions (PDF) ~~and requires both~~ of plant taxa identified in fossil pollen records and ~~full~~ it requires a georeferenced distribution of modern plant

Table 1. Origin and description of the data sources of fossil pollen used to reconstruct the climate in the Iberian Peninsula. Source is either the European Pollen Database (EPD) or author contribution. Longitude and ~~latidues~~ latitudes correspond to the centroid of the nearest cell to the site and ~~altidude~~ altitude as extracted from WorldClim dataset, all at 5’ spatial resolution. ~~The ^{14}C are~~ Each site has information about the number of ^{14}C dates available, the temporal range covered (see also Fig. 1 for ~~each site~~the spatial distribution) and the respective biome following the classification of Olson et al. (2001).

Name	Source	Longitude	Latitude	Altitude	^{14}C	Range	Biome
Albufera Alcudia	epd	3.125	39.792	11	4	3000-11000	Mediterranean
Algendar	epd	3.958	39.958	80	4	3000-9000	Mediterranean
Antas	epd	−1.792	37.208	14	6	3000-9000	Mediterranean
Barbaroxa	Queiroz (1999)	−8.792	38.042	38	4	3000-7000	Mediterranean
Cala Galdana	epd	3.958	39.958	80	5	3000-8000	Mediterranean
Cala n~~’~~” Porter	epd	4.125	39.875	81	4	4000-9000	Mediterranean
CC-17	Dorado Valiño et al. (2002)	−3.875	39.042	617	3	3000-12000	Mediterranean
Charco da Candieira	epd	−7.542	40.375	1221	30	3000-14000	Mediterranean
Gádor	Carrión et al. (2003)	−2.958	36.875	1413	6	3000-6000	Mediterranean
Golfo	Queiroz (1999)	−9.125	38.542	53	5	3000-14000	Mediterranean
Guadiana	Fletcher et al. (2007)	−7.458	37.292	52	8	3000-13000	Mediterranean
Hoya del Castilho	epd	−0.542	41.292	271	3	6000-10000	Mediterranean
Lago de Ajo	epd	−6.125	43.042	1744	6	3000-15000	Temperate
Laguna de la Roya	epd	−6.792	42.208	1780	6	3000-15000	Mediterranean
Lake Racou	epd	2.042	42.542	1906	8	3000-12000	Mediterranean
Las Pardillas Lake	Sánchez-Goñi and Hannon (1999)	−3.042	42.042	23	5	3000-11000	Mediterranean
Navarres 1	epd	−0.708	39.125	278	5	4000-15000	Mediterranean
Puerto de Belate	epd	−2.042	43.042	622	3	3000-8000	Temperate
Puerto de Los Tornos	epd	−3.458	43.125	893	4	3000-9000	Temperate
Quintanar de la Sierra	epd	−3.042	42.042	1546	20	3000-15000	Mediterranean
Roquetas de Mar	epd	−2.625	36.792	94	3	3000-6000	Mediterranean
Saldropo	epd	−2.708	43.042	645	3	3000-8000	Temperate
Sanabria Marsh	epd	−6.708	42.125	1220	8	3000-14000	Mediterranean
San Rafael	epd	−2.625	36.792	94	6	3000-15000	Mediterranean
Santo André	Santos and Sánchez-Goñi (2003)	−8.792	38.042	38	8	3000-15000	Mediterranean
Siles	Carrión (2002)	−2.542	38.375	1246	12	3000-15000	Mediterranean
Padul	Pons and Reille (1988)	−3.708	37.042	1236	17	5000-15000	Mediterranean
Lourdes	Reille and Andrieu (1995)	−0.042	43.042	727	9	3000-15000	Temperate
Monge	Reille and Andrieu (1995)	−0.042	43.042	727	15	3000-14000	Temperate
Moura	Reille (1993)	−1.542	43.458	40	6	4000-12000	Temperate
Banyoles	epd	2.708	42.125	172	2	3000-15000	Mediterranean

taxa ~~(Kühl et al., 2002)~~and a database of modern climate variables. PDFs for each taxon ~~are created using~~ were built relating the modern distributions in the climate space geographically. The raw fossil pollen data were gathered from author’s contributions and from the European Pollen Database (www.europeanpollendatabase.net). ~~We checked each site to fit a~~ Each selected site fits quality criteria regarding the number of radiometric dates (>3 in each site) and ~~gave preference to those with higher sampling resolution~~ a sampling resolution of at least 200 years. Using these criteria we selected a total of 31 records which cover different time spans between 15000 and 3000 years BP (Table 1; Fig. 1). ~~For the reconstruction process~~ Although having the LGM as lower limit would have provided interesting data, the availability of sites for the spatial interpolation is very small before the Holocene. Thus, we focused on the 15000 years when there are still available 10 sites that are necessary for a reliable spatial data interpolation (Table 1; Fig. 1). For the climate reconstruction we assume that modern distributions are in equilibrium with climate ~~at the distribution scale covering~~ over the species range. ~~Using taxa full distribution data is reducing~~ This is a reasonable assumption when considering the spatial resolution of this study. Using georeferenced full plants distributions reduces the bias resulting from local ~~changes and supporting our assumption. The different sensibility of taxa to the various sources of disturbance is~~ or isolated presence of species. These biases are also balanced by the ~~use of the~~ inclusion of multiple taxa identified in each core for the climate reconstruction.

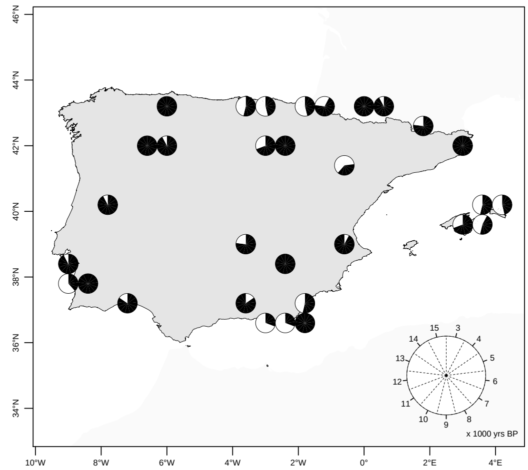

Figure 1. Study area with sample points. The black area inside each circle represents the ages available in each pollen sequence.

2.1 Data sources

The current distribution data for 246 taxa was obtained by georeferencing the Atlas of Flora Europaea (Jalas and Suominen, 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991, 1994; Jalas et al., 1996, 1999; Laurent et al., 2004). We gathered additional occurrence data for the Mediterranean flora from the Global Biodiversity Information Facility data portal (data.gbif.org; last access 2011-02-01). These data ~~was checked for correctness by removing data~~ were checked and corrected by removing species presences from botanical and ~~herbarium collections andobservations stored at a~~ herbaria collections and/or observations with lower spatial resolution than 30’ ~~.~~ (∼55 km). The final taxa list and the assignment of pollen taxa to and modern taxa distributions is given in appendix A.

The georeferenced geographical distributions were ~~then~~ rescaled to the resolution of 30’ (~~∼55 km~~∼55km). The global ~~historic~~ observed climate data (1950-2000) for January minimum temperature (Tjan), July maximum temperature (Tjul) and ~~monthly precipitation~~ annual precipitation (Pann) data were obtained from Worldclim database (Hijmans et al., 2005, www.worldclim.org) with 5’ resolution (∼10km)~~and values were aggregated by~~. The climate data was downscaled to the same spatial resolution of the plant distribution data by aggregating the mean value to the resolution of 30’. ~~Precipitation was further processed to obtain the annual precipitation (Apre) from the monthly data by recording for each pixel the minimum value of precipitation in the 12 months~~All computing was performed using R (R Development Core Team, 2012) with the package rgdal (Keitt et al., 2012).

2.2 Reconstruction of past climate variables

The climate reconstruction method is based on the PDF of each taxon identified in a fossil dated pollen assemblage. Pollen taxa were assigned to georeferenced plant taxa (see appendix A). This approach was successfully used to reconstruct ~~temperatures~~ climate variables from fossil pollen data ~~(Kühl et al., 2002; Cheddadi and Bar-Hen, 2009). With the superimposition of the PDFs~~ (Kühl et al., 2002; Cheddadi and Bar-Hen, 2009; Kühl and Gobet, 2010) Using the PDFs intersection of all taxa ~~present at a particular age and for a specific climate variable, is possible to obtain the intersection defining the likely past climate at that age (Kühl et al., 2002). A univariate~~ identified in a fossil sample we obtain the most likely climate value within which the fossil plant assemblage may occur (Kühl et al., 2002). It has been observed that normal and log-normal ~~density distributions were fitted to the~~ (right skewed) distributions fitted to temperature and precipitation~~data~~, respectively, ~~at each species presence in order to build the PDF from the modern plant distributions. While normal distribution may be used to represent temperature tolerance, log-normal distribution, by being right skewed~~ tend to better represent the ~~precipitation~~ data (Chevalier et al., 2014). To avoid sampling the climate spatial distribution instead of the species tolerance, we corrected for the ~~possible bias using a histogram of the~~ potential bias by using binned climate within the ~~rectangular extent of the~~ species range as a weighting factor for each climate value (Kühl et al., 2002). The chosen bin size ~~of the weighting histogram was~~ is 2ºC for temperature variables and 20mm for precipitation. This procedure ~~decrease~~ decreases the weight of the most frequent climate values ~~occurring in the study area and increased~~ and increases those, in the distribution of the species, that occur less frequently in the study area (Kühl et al., 2002).

The reconstructed climate ~~from~~ using the PDF method results from combining the individual PDFs of the species ~~found in the pollen sequence in a depth sample. This combination is done as the~~ identified in each pollen sample. The product of the PDFs ~~resulting in a representation of the likely climate in the past (Kühl et al., 2002; Chevalier et al., 2014). A threshold of three pollen grains was chosen to classify~~ provides the most likely climate value (Kühl et al., 2002; Chevalier et al., 2014). To identify a taxon as present in the sample, ~~and~~ a threshold of three pollen grains was chosen. A minimum of five taxa ~~are needed~~ present is required to reconstruct a climate value for each fossil sample.

Using presence data is both seen as an advantage of the PDF method (Kühl et al., 2002) but also as a weakness due

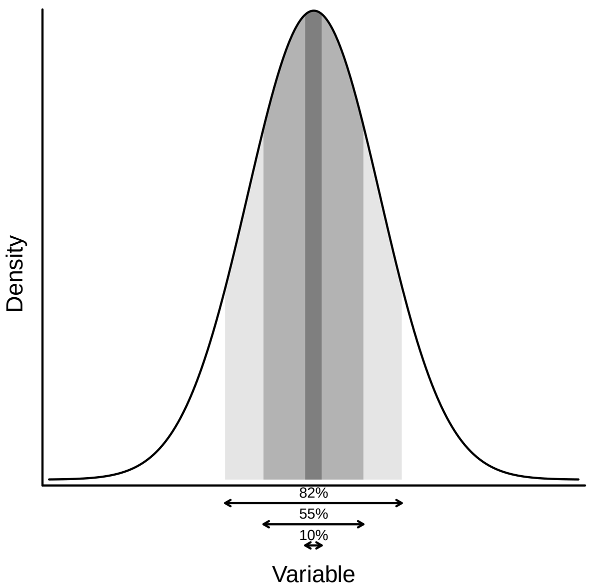

Figure 2. Example of the influence of pollen proportion (pp) on the calculation of the density of taxa presence intersection. The shades of gray indicate the effect of different pp when the pollen adjustment value (pa) is set to 0.9 and arrows indicate the assumed presence range. The first case (dark gray) results from $pp = 1.0$, which represents the highest detectability and is assumed to be found near the core distribution area an, thus, near optimum conditions. The presence is assumed in a narrow range around peak density with $\alpha = \frac{pp*pa}{2}$ (corresponding to 10% of the area). When $pp = 0.5$ (middle gray) the corresponding area is 55% and with $pp = 0.2$ (light gray) is used the widest presence range (82% of the PDF area).

to the exclusion of the quantitative data resulting from the pollen abundances (Birks et al., 2010). Fluctuations in pollen abundances are related to multiple factors ~~related to the physiology of the species (Hicks, 2006), with a~~ such as the species ecophysiology, differential pollen production~~among different species, but it also has a strong climatic component through the influence that climate has on distributions~~, dispersal capacity and other traits (Hicks, 2006). We have used ~~these data as the proportion of pollen found relative to~~ the ~~maximum pollen found~~pollen proportions to weight the PDFs of the respective taxa. The minimum ~~non-zero~~ positive pollen proportion corresponds to the presence of the taxon while the maximum defines its highest abundance within the fossil record. Using pollen proportions ~~per taxa instead of per age~~ of a taxon within a time series instead of within a sample avoids the bias of ~~different pollen production by distinct taxa~~ differential pollen production and thus allows ~~quantifying~~ estimating the presence of a species relative to its maximum ~~detection within each site~~percentages in the whole record.

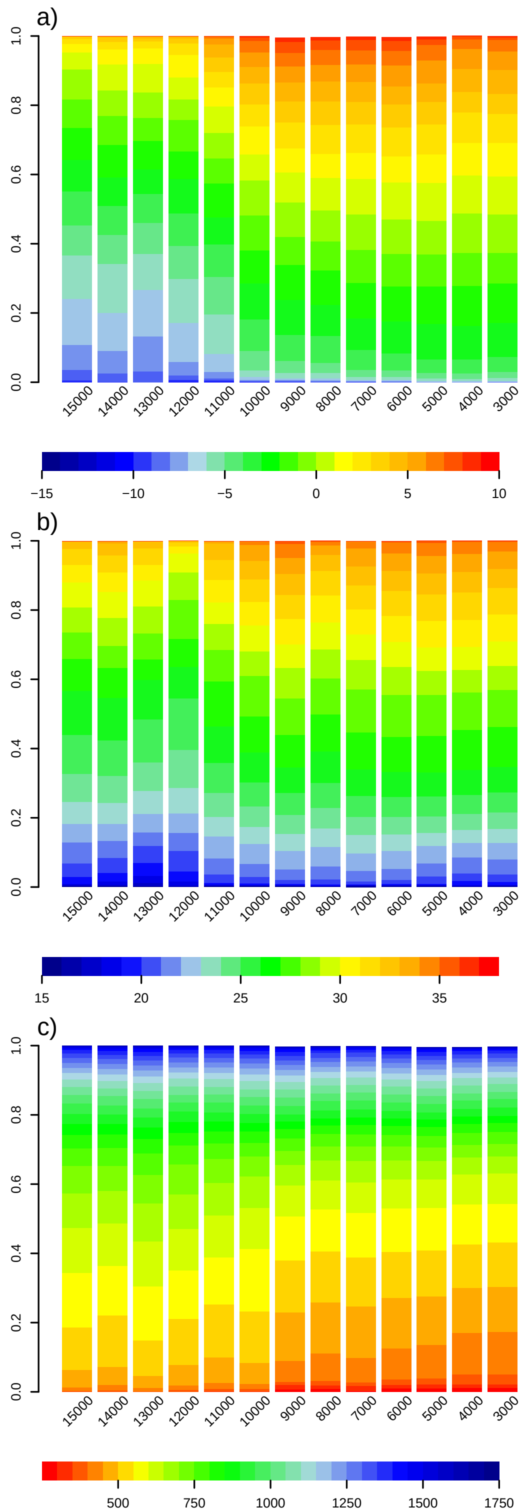

Figure 3. Distribution of the reconstructed climate variables in the Iberian Peninsula and Balearic Islands in the last 15 ka. Colours show the proportion of area covered with each class of a) minimum temperature of January; b) maximum temperature of July and c) annual precipitation.

~~In order to include the pollen proportions in the reconstruction method, we calculate the density of taxa intersections. This is done by using the pollen proportion as alpha valuesto reduce~~ The pollen proportions were converted to alpha values, reducing the species climate tolerance towards the peak density ~~value~~ values (Fig. 2). We assumed that the pollen proportion has an inverse relation to the proximity of near-optimal conditions. To avoid the selection of a unique climate value ~~with~~ from the PDF when the maximum detection of a species occurs, i.e. when its pollen proportion is found to be one, we use a pollen adjustment value set to 0.9. This means that at the maximum taxon detection, the ~~climate presence will be set~~ PDF will be reduced to the area of the density corresponding to 10% of the probability ~~. Since the pollen proportion is calculated through the pollen core, the maximum detection may not indicate optimal conditions, but near optimal . Using this adjustment value allows to take this into account, by referring to a tolerance interval instead of a tolerance value. The intersection of taxa is calculated by adding the tolerance intervals of all species found in a depth sample. The combined reconstruction is obtained by~~ (Fig. 2). The maximum detection of a taxon indicates a near optimal climate niche and the adjustment value set to a value near but not equal to one allows some degree of uncertainty in the reconstruction. On the other hand, setting this value to zero will not allow any influence of the pollen proportion, resulting in a binary presence/absence reconstruction (Kühl et al., 2002). For each sample, the collection of the taxa tolerance intervals built this way are added resulting in a taxon profile, showing where in the climate space the frequency of the taxon is higher, taking into account the proximity to optimal conditions. The final climate reconstruction value is the product of the climate PDF with the taxa ~~intersection~~profile. The reconstructed value and associated uncertainty are usually extracted from the PDF as the mean and standard deviation (Kühl et al., 2002; Kühl and Gobet, 2010). Assuming a normal distribution, we extract the peak density value and the 95% confidence interval from the density profile. The confidence interval range shows the uncertainty around the reconstructed value and is related to the standard deviation. The reconstructed values for each site were fitted with a smoothing spline to produce continuous time-series, from which 1000-years time slices were extracted.

In order to ~~quantify the success~~ evaluate the robustness of the reconstruction method~~in predicting recent climate~~, we have compared ~~data from the reconstruction with global historic~~ modern reconstructed and observed climate data (1950-2000) ~~with linear regressions for each climate variable. This procedure was done with all available samples with age inferior to~~ from WorldClim database. For reconstructing climate from pollen data, we have used all samples available within the last 500 years~~and with the historic climate data extracted with the pollen site coordinate. Since both climate data represent a similar period, a linear relation was expected. Parallel to the quantification~~. Climate values were averaged for all sites with more than one sample. The correlation between the two data-sets was tested using a Pearson's correlation score. To provide the significance of the correlation value, a set of 999 replicates were performed where the observed climate variable was shuffled without repetition. Although this evaluation does not take into account neither the climate oscillations during the last 500 years nor the human disturbances it still provides a broad evaluation of the reconstruction ~~success, the linear regression is~~ method because 1) it depicts per site the relationship between observed climate data with reconstructed values and 2) the slope direction of the regression and the related correlation signal indicate that the reconstruction is spatially coherent. A linear regression was used to estimate a ~~spatial~~ baseline for calculating the anomalies ~~. The preindustrial~~ at each site using the observed climate. The pre-industrial period around 100 BP (1850 AD) ~~was~~ is commonly used as reference ~~climate to calculate~~ climatology to compute anomalies. This period is also often used as a baseline in climate models, facilitating data-model ~~comparison~~comparisons, and it is less biased with recent climate warming allowing to better depict past warming (Davis et al., 2003; Mauri et al., 2015). Although a specific year is selected, the time window often includes +- 500 years (Mauri et al., 2015), which is equivalent to the period we have used ~~here.~~

~~The reconstructed values for each site were fitted with a smoothing spline to produce a continuous time-series, from which 1000-years timeslices were extracted~~in our study. The regression allows to build a climate baseline without artificially adding samples to compensate for differential number of samples available for recent periods in a 4D (spatial plus time) interpolation (Mauri et al., 2015) and the linear equations provide all the information to generate the baseline with the observed climate data.

2.3 Spatial analysis of past climate

Thirteen climate grids, ranging from 15 to 3 thousand calendar years BP (hereafter, “ka”) with a 1000 years interval, were obtained for each reconstructed variable by spatial interpolation of the climate anomalies at each available site. The anomalies were ~~first calculated~~ computed for each site ~~with the difference~~ between the reconstructed climate and the ~~reference climate calculated as explained above. Anomaly values were projected into~~ modern reference climate. Anomalies were projected onto a 30' (~55km) resolution grid and interpolated onto a 5' (~10km) resolution grid using 3D thin-plate smoothing splines with two spatial dimensions ~~plus~~ including altitude. This interpolation method ~~was chosen because when used with climate data it generates accurate~~ generates accurate climate predictions (Jarvis and Stuart, 2001) and it was used ~~to generate the present data~~ for the WorldClim variables (Hijmans et al., 2005).

To further summarise the spatial and temporal variability of the data we applied a functional principal component analysis (fPCA). ~~This method~~ The fPCA extends the exploratory data analysis of the principal components analysis to functional data (Bickel et al., 2005), depicting both spatial and time patterns ~~on the original data~~ that are then summarised in a few components. (Cheddadi and Bar-Hen, 2009) applied a fPCA ~~in~~ to nearly the same timescale as the present study to depict January temperature patterns from European pollen data. Here we have broadened the approach to each climate time-series available in each grid cell to produce gridded spatial components. The functional data was built by combining B-spline basis functions to fit the time-series. We have retained the components that explain more than 90% of the variance and rescaled the range from -1 to 1. We used hierarchical cluster analysis over the produced first components grids of each variable to identify areas in the Iberian Peninsula that ~~shared similar climate evolution~~ share similar climate trends over the past 15 ka. Climate stability was ~~calculate~~ computed for each variable as the mean absolute deviance from the current climate as available in WorldClim ~~dataset~~data-set.

All analysis were performed using the R Project for Statistical Computing (R Development Core Team, 2012) with packages fields (Furrer et al., 2012), rgdal (Keitt et al., 2012), gstat (Pebesma, 2004) and fda (Ramsay et al., 2012). The climate reconstructions were performed with R scripts developed by the authors and available at request.

3 Results

The ~~reconstructions values for the sites within the last~~ modern climate reconstructions (500 years~~have a linear trend with the current climate , thus revealing~~) show a high degree of agreement with the observed climate data ($RMSE_{Tjan} = 5.01$; $RMSE_{Tjul} = 3.85$; $RMSE_{Pann} = 399.85$; Appendix B). These data-sets show a positive linear trend and a significant positive correlation ($p \leq 0.006$ for all variables), revealing that the reconstruction method predicts well the ~~recent climate (p ≤ 0.016 for all variables; Appendix A~~spatial distribution of climate. The standard error associated with the climate reconstruction is in average low but increases with age (Appendix C).

The ~~reconstruction of~~ reconstructed three climate variables ~~exhibited~~ exhibit high spatial variability ~~over the period~~ between 15 ka and 3 ka (Fig. 3, Appendix ~~A, B~~D). The uncertainty associated with the spatial interpolations is usually low, suggesting a good sampling coverage, ~~with the exception of the northwest~~ except in the northwestern area (Appendix ~~D~~E). The Iberian Peninsula had extensive areas with extremely low Tjan that gradually increased ~~to higher values, and~~ markedly after 10 ka. The pattern of Tjul over the same time ~~remained~~ remains stable, with lower values before 12 ka. ~~In the studied period, there is a trend for the decrease~~

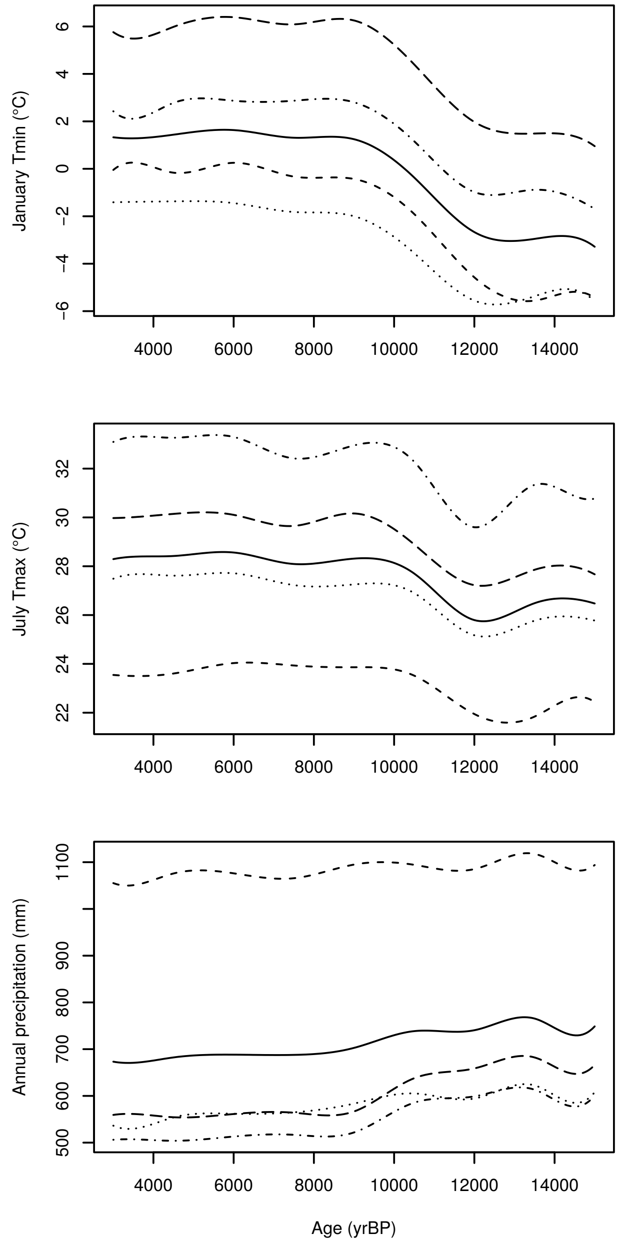

Figure 4. Minimum and maximum temperatures of January and July, respectively, and annual precipitation during the last 15 ka. The solid line represents the average climate in the study area. The remaining lines are the average of each cluster found: C1: short dash line; C2: dotted line; C3: dash-dot line and C4: long dashed line.

There is a decreasing trend of precipitation, especially after 10 ka (Fig. 4) ~~. This decrease towards a more arid peninsula happens~~ which is marked mostly in the south-eastern ~~portion~~ part of its area (Appendix ~~B~~D)

The clustering of the first fPCA component ~~of~~ for the three reconstructed variables ~~were spatial~~ are spatially structured (Fig. 5), and ~~allowed summarising the evolution of these three climate variables in the Iberian Peninsula~~ allow to summarise their overall trends (Fig. 4). The first component of each variable ~~explained~~ explains more than 95% of the variation (Tjan: 95.5%; Tjul: 99.2%; ~~Apre~~Pann: 99.5%). ~~The cluster~~ Cluster C1 (27% of the total area) is located mostly ~~on~~ in the north and western Iberia and includes part of the north-Iberian mountain ranges but also low altitudinal coastal areas (average altitude is 679±454m)~~but also low altitude coastal areas~~. This is the wettest cluster ~~, with Apre ranging from 1055~~ with Pann ranging from 1054 to 1115mm, the coldest in July (~~21.6~~ 21.7 < Tjul < ~~24.1~~24.2ºC) and with very low January minimum temperatures (~~-5.6~~ -5.5 < Tjan < ~~0.1~~0.2ºC). The ~~cluster~~ C2 cluster encompasses part of the Cantabrian mountain range and the central Iberian system (~~29~~28% of the total area with an average altitude of ~~856~~859±~~301m)and~~ 303m). It occupies most of the northern plateau ~~. It~~ where it has the lowest January temperature (-5.7 < Tjan < -1.3ºC) ~~but has warmer in July than C1~~ whereas July (25.1 < Tjul < 27.7 ºC) ~~showing~~ is warmer than within C1. This shows high seasonal amplitude with ~~very~~ low precipitation (~~536~~ 537 < ~~Apre~~ Pann < 621mm), similarly to C3 and C4. The dissimilarities between clusters C3 and C4 (~~24~~25% and 20% of the total area and average altitude of ~~610~~613±~~297~~ 296m and 278±~~231~~232m, respectively) ~~occur mainly in temperature, with~~ concern mainly the temperature. Cluster C4 ~~being generally~~ is warmer and wetter than ~~the~~ C3~~cluster~~. These are the warmest areas ~~in~~ for both January (C3: -1.7 < Tjan < 3.0ºC; C4: 1.0 < Tjan < 6.4ºC) and July (C3: 29.4 < Tjul < 33.4ºC; C4: 27.2 < Tjul < ~~30.2~~30.3ºC) and with low annual precipitation (C3: ~~505~~ 504 < ~~Apre~~ Pann < ~~615mm~~614mm; C4: 555 < ~~Apre~~ Pann > ~~683mm~~682mm). The Balearic Islands are fully included in the C4 cluster (Fig. 5).

The mean absolute deviance from the current climate ~~showed that the stability of the climate in~~ shows that the climate stability during the last 15ka was not spatially uniform (Fig. 6). ~~The Tjan and Apre~~ Tjan and Pann exhibited higher stability in the southern Iberia, although ~~the first~~ Tjan has lower values of deviance (higher stability) towards the eastern coast ~~the the second~~ and Pann towards the western coast. ~~The~~ Tjul exhibited lower deviance at higher altitudes, particularly at the central system, northern mountains and Pyrenees, but also in the southern Sierra Morena.

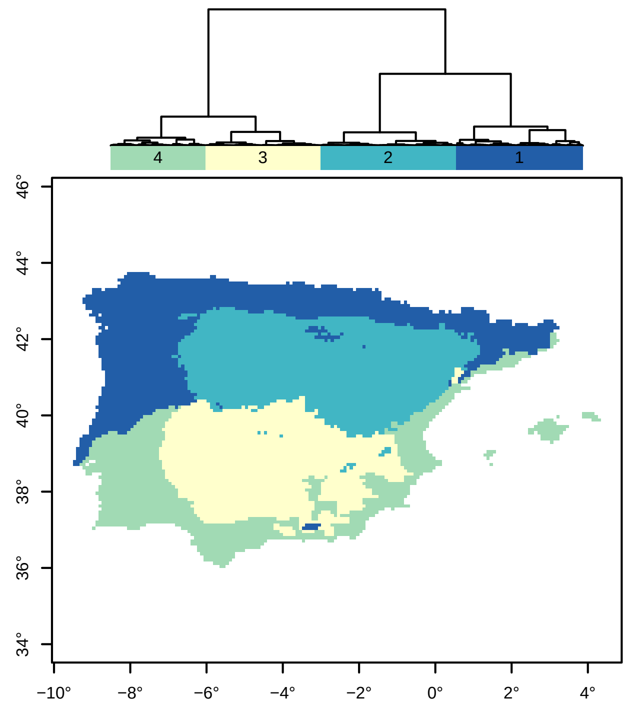

Figure 5. Hierarchical cluster analysis of the functional PCA components of Tjan, Tjul and ~~Apre~~ Pann in the last 15ka found in the study area. The top dendrogram represents the size of the clusters of similar climate evolution and the relations between them. Numbers correspond to each identified cluster.

4 Discussion

Fossil pollen data provide a record of vegetation changes which constitutes a valuable proxy for reconstructing past climate changes, especially using ~~multiple sites at large scales~~ large data-sets (Bartlein et al., 2010). The method used here provides ~~acceptable~~ reliable climate reconstructions, despite the low number of sequences ~~available~~ selected according to our quality criteria for spatial climate reconstruction, both in terms of sampling resolution and number of ^{14}C dates. The ~~residuals in the linear regressions~~ western part of the peninsula has a better data coverage which provides more robust spatial interpolations, particularly for the most recent to middle time periods analysed. Nevertheless, the spatial uncertainty related to the interpolation show a uniform variance for all time periods (Appendix E). The only exception is the north-western part of the study area, where the lack of data promotes higher uncertainty for the spatial interpolation. The residuals between observed climate and reconstructed climate were high, resulting also in a low coefficient of determination for the linear regression (Appendix B). However, this is ~~expected~~ expectable since we were comparing ~~the historical climate with the~~ observed climate data with reconstructed values of the last 500 years ~~, and climate variations within this period are increasing the residuals, plus the anthropogenic influence on land cover in this period that is likely~~ and averaging the climate variation in this period tend to increase the residuals. In addition, the anthropogenic impact on the ecosystems is likely also biasing the results. Nevertheless, a ~~significant linear trend was~~ positive linear trend with a significant positive correlation were found between reconstructed climate and ~~historical~~ observed climate that allow us to produce a reference dataset using this model and the ~~historical~~ observed climate. The results provided here reinforce the role of the Iberian Peninsula as ~~a particular case in Europe due to its role as a general European glacial~~

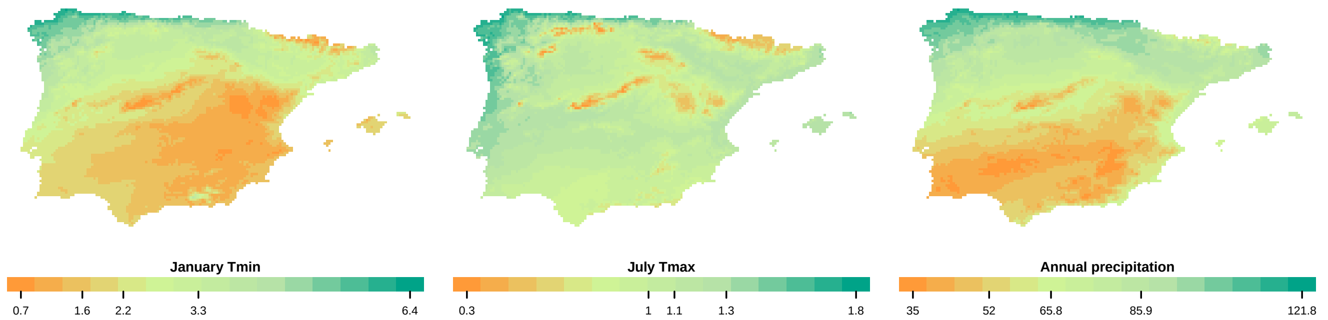

Figure 6. Average differences between millenia for each of the climate variables. Calculation of the differences are computed between a given age and the previous one. Isolines in each map indicate the average value of change.

~~refugium~~ European glacial refugia and holding enough climate variation ~~since the LGM~~ (Fig. 5) to support a network of smaller refugial areas (Weiss and Ferrand, 2007).

~~The climate~~ Climate of the last 15 ka ~~in the Iberian Peninsula~~ was dynamic, with oscillations of temperature and precipitation occurring mostly at the southern part of the peninsula. Given the link between climate and species distributions (Hewitt, 2000), it is likely that these changes had an impact on the location, extent and evolution of the refugia and the recolonisation processes during the post-glacial period. Nonetheless, the reconstructed overall trend is a noticeable warming in winter temperatures after ~~the~~ 15 ka, particularly between 12 and 9 ka (Fig. 4) that ~~results from~~ is likely due to the increase of the summer insolation in the northern hemisphere (Berger, 1978). This warming ~~has a correspondent trend in the spatial occupancy of temperature as shown in the reducing of the area~~ trend tends to reduce the area in the Iberian Peninsula with very low temperatures (Fig. 3). ~~An evident pattern that strikes from the results presented here is the division~~ Although insolation peaks at 9ka and decreases afterwards, it does not translate to a general cooling and in south-western Europe is seen an increase of insolation in both summer and winter (Davis et al., 2003). A striking pattern is the partitioning of the peninsula in spatially structured areas that shared similar climate ~~evolution during~~ trend over the late-Quaternary (Fig. 5). The wettest and cold cluster C1 is predominantly located at ~~norther~~ the northern and north-western Iberia and occupies most of the current ~~Atlantic bioclimatic region~~temperate climate zone. Although very similar with C2, it contrasts in the seasonal amplitude and precipitation amount. Interestingly, the pattern of current bioclimate zones in Iberian Peninsula is retrieved on the clusters scheme, suggesting the persistence of a transition area between very different climate zones, although the magnitude of the differences have changed in the past.

Our results show that January temperatures exhibited a general warming trend ~~during the studied period~~ over the last 15,000 years which corresponds in average to an increase of ~5.5ºC. The southern part of the Peninsula is more resilient to change, particularly for Tjan and ~~Apre~~Pann, whereas the northern ~~had~~ part recorded major changes. This pattern is less obvious ~~in~~ for July temperatures, where variations showed a smaller amplitude albeit this variable is markedly different between clusters, and thus contributing to the climate ~~division~~ split of the study area (Fig. 4, Appendix ~~C~~F). The minimum winter temperatures constrain the physiologic ability of plants to further development and, thus, are a major factor restricting distributions (Sykes et al., 1996). ~~Summer temperatures, on the other hand, provide~~ Higher summer insolation provides enough energy to plant growth ~~(Sykes et al., 1996), and are likely resulting in less responsive July temperature~~ and July temperature in the Mediterranean is a less limiting variable for growth than Tjan which makes more complex the reconstruction of summer months and its interpretation.

4.1 The end of the Pleistocene

~~We have based the climate reconstructions on data with an interval of 1 ka. This provides us with~~ The 1000 years time interval provides enough resolution to analyse general patterns of climate evolution~~resulting from larger stadials and interstadials, but~~ . However, abrupt climate events are ~~generally undetectable. The OD (~8 to 14.7~~ not detectable. The end of the Oldest Dryas (OD; ending around 14.5 ka) is characterised in Iberia by a vegetation ~~changes~~ change compatible with cold and humid conditions ~~followed by a warming trend (Naughton et al., 2007). The OD~~ (Naughton et al., 2007, 2015) and is followed by the ~~warmer BA (~14.7 to 12.9~~ Bölling-Allerød warm period (B-A; ending around 13 ka). Our results show a similar pattern with colder conditions between 15 ka and 13 ka ~~, followed by a warming trend after 13 ka~~ and a higher humidity (Fig. 4)~~. All clusters show these warming trens, although clusters~~ , particularly evident in the central and southern clusters. Although all clusters show a similar trend, the C1 and C2 are colder ~~. This is reflected in a contrasted Iberian peninsula dominated by extreme~~ than average. The general pattern in the Iberian Peninsula is a contrast between a colder north and a warmer south but, nevertheless, and area dominated by low January temperatures (Fig. 3, ~~Appendix B,C~~Appendices D,F). The evolution of precipitation during the last 15 ka in the Iberian Peninsula ~~has~~ shows a very stable pattern: northern areas comprised in C1 had high precipitation values during the ~~whole studied time, but~~ period analysed while the south was wetter than today (~~Appendix B,C). During the OD period, there is a~~ Appendices D,F). The increase of the moisture availability during the B-A (Naughton et al., 2015) is in line with the slight increase in precipitation in all clusters between 14 and 13 ka (Fig. 3).

As described earlier in Europe (Renssen and Isarin, 2001; Heiri et al., 2004), Tjan shows wider changes in amplitude than Tjul. The cold to warm transitions that occurred at ~14.7 and 11.5 ka (Renssen and Isarin, 2001; von Grafenstein et al., 2012) in Europe had a spatial impact that is noticeable in the reconstructed temperatures (Fig. 3, ~~Appendix B,C~~Appendices D,F).

4.2 The Holocene

The ~~BA~~ B-A warm stage is followed by the cold ~~YD (~~Younger Dryas (YD; between ~12.9 ~~to 11.6~~ and ~11.7 ka), marking the beginning of the Holocene. This period ~~is reconstructed here with~~ records a warming trend ~~in the Tjan but with a sudden decrease of Tjul temperatures~~ for Tjan while Tjan decrease abruptly (Fig. 4) ~~,~~ with a reduction of the warmer areas ~~at~~ between 13 and 12 ka (Fig. 3).

The Holocene warm period (approximately between ~8.2 and 5.6 ka, depending on the location in Europe) is characterised by increasing summer temperatures (Seppä and Birks, 2001)~~, being more evident~~. Such trend is more obvious in Northern Europe and the Alps ~~and simultaneous with a~~ while we observe a rather cooling at lower latitudes (Davis et al., 2003). Our results point to a ~~decrease on Tjul temperature but a stable minimum temperature , indicating mild summers. Concerning the precipitation, there is evidence of~~ slight decrease of Tjan and Tjul around 7 ka but the overall temperature pattern is rather stable. This is likely affected by the temporal resolution of this study, failing to clearly detect rapid events. Pann shows a slightly wetter climate ~~between~~ at 7 ka (Fig. 3) which ~~confirms what was previously known~~ is consistent with earlier reconstruction for the southern European lowlands (Cheddadi et al., 1997).

Between 6 and 3 ka, areas with low precipitation expand in the Iberian peninsula (Fig. 3) ~~corresponding to~~ which allows the expansion of the ~~mediterranean~~ Mediterranean taxa (Naughton et al., 2007; Carrión et al., 2010b, a). The increasing aridity trend in the south is balanced by the high precipitation values in the north (Fig. 4, ~~Appendix B,C~~Appendices D,F), contributing to the ~~final pattern of a a temperate north and a southern mediterranean climate in Iberia~~shaping of the current Iberia pattern of two contrasting bioclimatic regions: the North is temperate and wet while the south is a dry and warm.

The behaviour of the reconstructed variables at 5ka is likely to be influenced by non-natural ecosystem changes due to human activities such as the forest degradation that begun in lowlands and later in mountainous areas (Carrión et al., 2010a). These human impacts add confounding effects in the fossil pollen record and may lead to ~~reconstructed biased temperatures~~ slightly biased temperature reconstructions after 5 ka. On the other hand, human impact at larger scales, capable of leaving noticeable imprints on landscape were likely to happen later (Carrión et al., 2010a) and, furthermore, there are evidences of a cooling and drier stage ~~after 5 ka, marking the end of the Holocene warm period in Europe (Seppä and Birks, 2001), and particularly~~ in the Iberian Peninsula after 5 ka (Dorado Valiño et al., 2002).

4.3 Climate role in Iberian refugia

The climate change since the LGM in the Iberian Peninsula had an impact on the persistence of temperate species, migrating pathways and on the overall recolonisation processes during the postglacial period within the peninsula (Hewitt, 2000; Naughton et al., 2007; Carrión et al., 2010b). During this period, climate favoured migrations and expansion processes that culminated in secondary contacts for several lineages previously isolated in patches of suitable habitat (Branco et al., 2002; Godinho et al., 2006; Weiss and Ferrand, 2007; Miraldo et al., 2011). ~~Given the link~~ Particularly the B-A warming phase and the warming stage after the YD, that we show here and which have highly affected the spatial organisation of the climate in the Iberian Peninsula, are likely favouring expansion processes of warm-dependent organisms. Given the relationship between climate change and biodiversity patterns, the clustering scheme (Fig. 5) depicting areas with different climate evolution is consistent with the molecular evidence of a network of putative refugia within Iberia (Weiss and Ferrand, 2007). Refugia have been associated with climate and habitat stability, with both playing complementary roles (Ashcroft, 2010). However, as shown by large scale landscape analysis (Carrión et al., 2010b, a) and climate reconstructions (Davis et al., 2003; Cheddadi and Bar-Hen, 2009), both have a strong dynamic nature in the Iberian Peninsula, and likely promoted the formation of patches of suitable habitat during harsh conditions. The highly structured populations that many species exhibit in the Iberian Peninsula have contributed decisively to the idea of refugia diversity (Hewitt, 2000; Weiss and Ferrand, 2007). Overall, the information included in the multidimensional climate data allowed us to define areas characterised by a climate evolution during the late-Quaternary with smaller amplitude of change (clusters C3 and C4). ~~This area largely coincides with area of higher stability for Tjan and Apre~~ These areas showed higher stability of both Tjan and Pann (Fig. 6). ~~The cluster~~ Cluster C4 coincides at a great extent with areas that offered more resilience to change between millenia (Fig. 5). Within these areas, temperature and ~~precipitations~~ precipitation were suitable to support the survival of temperate trees, likely acting as glacial refugia. On the other hand, the cold areas of the first and second cluster associated also with faster changes cluster likely diminished the suitability for the long term persistence of species. One might infer that the defined clusters are associated with potential isolation or dispersal events of species throughout the studied time span. Particularly, the fourth cluster (Fig. 5) includes areas that have already been described as glacial refugia for several animal and plant species (Weiss and Ferrand, 2007, see chapter 5 for a review of refugia in Iberian Peninsula). In the area represented by this cluster, the reconstructed ~~minimum January temperature~~ Tjan indicate a mild climate with higher precipitation than currently, which is compatible with the persistence of species in these areas. The southern plateau, mostly comprised in the second cluster (Fig. 5), recorded also mild conditions which are often associated with southern refugia but ~~a~~ the rapid Tjul oscillations associated with a cold Tjan and low precipitation may have prevented long term persistence but are likely compatible with a recolonisation process.

The pattern of stability indicates a southern Iberia with less change, particularly ~~with reconstructed January temperature and annual precipitation. The higher~~ Tjan and Pann. High altitudes offer more resilience to change, particularly to July temperature and lower areas may be swept rapidly with occurring changes (see Appendix ~~E~~G). Our data suggests that at the regional scale and with extensive time-series data, this relation is preserved. Areas of lower velocity of change, hence more stable, are associated with high levels of endemicity at global scales (Sandel et al., 2011), and areas of high velocity are often associated with species extinction (Nogués-Bravo et al., 2010). Our results indicate higher stability in the southern part of the Peninsula similarly to other studies based on ~~climte data (Ohlemüller et al., 2012), but~~ climate data (Ohlemüller et al., 2012). However, our studied time frame extends to 15 ka, which does not cover the glacial maximum (~21 ka). At ~~this period, an~~ that time period, a higher degree of fragmentation of the stability is expected due to ~~the~~ colder conditions, and areas compatible with refugia would be also less contiguous. ~~This could also~~ These could be seen as a macrorefugia, offering conditions for large population ~~effectives at glacial conditions~~ during glacial times (Mee and Moore, 2014). Microrefugia ~~is~~ are known to occur ~~at~~ in the northern areas of the Iberian Peninsula (e.g. Fuentes-Utrilla et al., 2014) but the spatial scale used ~~here~~ and the number of pollen sites available renders microrefugia undetectable in this study.

5 Conclusions

The reconstruction of past climates using biological data is an invaluable resource for the study of the dynamics of glacial refugial areas. Although there is a limited number of available sites and time range coverage, the spatial combination of fossil pollen data provides a continuous record with a climate signal that can be translated into spatially explicit analysis of climate dynamics.

The reconstructed climate variables for the post-glacial period show different patterns of evolution but clearly marked by the lasting impact of climatic events. The Iberian Peninsula had areas that shared similar climate evolution during the late-Quaternary. Some areas that we have suggested as potential refugia are consistent with those areas where genetic diversity was found to be high and which are often considered as refugial areas for several animal and plant species.

The analysis of these areas and the related climate provides new insights about the dynamics of refugia through time and space which helps a better understanding of the evolution of biodiversity hotspots both at the species and the intraspecific levels. ~~Liking~~ Linking past climate and diversity ~~on~~ in the Iberian peninsula ~~and its quantification will have an increased interest~~ is a major issue for conservation issues, especially under the expected future climate change.

Appendix A: ~~Linear regression of the reconstructed climate~~ Taxa list and ~~worldclim data~~conversion between pollen taxa and used taxa in the reconstruction.

Appendix B: Linear regression and correlation of the reconstructed climate and observed climate data.

Appendix C: Climate reconstruction values and associated uncertainty.

Appendix D: Reconstructed variables in the Iberian Peninsula and the Balearic Islands.

Appendix E: ~~Climate anomalies maps.~~

Appendix E: Spatial distribution of the variance associated of the Thin-Plate spline interpolation of the reconstructed data.

Appendix F: Climate anomalies maps.

Appendix G: Relation between stability and altitude for each reconstructed variable.

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