Response to comments

Pedro Tarroso et al.

We have revised the previously submitted manuscript entitled "Spatial climate dynamics in the Iberian Peninsula since 15 000 Yr BP". We have addressed all reviewer comments with modifications in the text and figures. In the few cases where we felt no modification was needed, we try to properly justify it.

Many modifications were made, including changes in methods, figures and text as suggested by the reviewers. The reconstruction method was modified to follow more closely the original PDF method and our changes are described as an addition to the method. The text referring this part was rewritten and we expect that is now better explained. The spatial interpolation method was also modified accordingly to reviewer's comments and figures adapted to the new results we additional changes as suggested. Larges figures of the anomalies are given as supplementary material.

We provide an point-by-point response to the reviewers and a marked-up version oaf the manuscript where all changes are documented.

We appreciated the comments and we feel that this new version of the manuscript as largely improved. We hope that this manuscript fulfills now all your requirements for publication.

Point-by-point response to the reviews

Reviewer 1

Major issues: 1) page 3903, Introduction; page 3906, Methods and other: The authors do not include in their analysis the last 3000 years. This they explain is because of the influence of anthropogenic disturbance on the vegetation, which has disturbed the equilibrium state between vegetation and climate over the last 3000 years. However, the authors also use the modern vegetation distribution to calibrate their transfer function, despite the modern period having had probably the greatest human impact on the vegetation. They then also highlight the role of future climate change as having an important impact on future vegetation distribution rather than being dominated by even greater human impact. The authors seem aware of the contradiction but it nevertheless seems to somewhat undermine the justification for their methodology. While the calibration of the pdf transfer function based on modern vegetation occurs at continental scales where climate is probably dominant, the transfer function will in actuality be more heavily reliant on the vegetation distribution of the study region, since this is where the closest analogue vegetation/climate is to be found. Part of the problem here is that the authors do not assess the robustness of their pdf method (see point 6).

REPLY: The reviewer poses an interesting and common critique to the method. Nevertheless, this contradiction is very illusive. Gathering distribution data at macroecological level allows to decrease the anthropogenic influence on the distribution as well as other microecological factors that might determine plant presence at smaller spatial scales. Removing presence data with anthropogenic origin is also performed to further decrease the human influence on distributions (Kuhl et al 2002). This was performed using information on atlases and the data on the GBIF tables (e.g. remove presences on botanical gardens). These presences are usually very sparse. However, a main point of gathering these data is to build the PDF that best depict the climatic tolerances of the species. The main disturbances result from planting species outside their natural range or removing trees and/or populations from their natural range. It is known that distribution data from invasive ranges can be also used to better depict the niche tolerances (Broennimann and Guisan 2008). Thus, using full distributions at coarser spatial scales (for instance, 0.5) is likely providing a good estimation of the niche. In the second case, removing species from their natural range, might reduce the climate envelope if the disturbance is very important but this does affect the overall climate range under which the assemblage is found. The reconstruction is performed per taxa, meaning that no analogues have to be found. The presence of the taxa in the pollen assemblage will indicate a similar climate. Multiplying this with all the taxa found in the pollen assemblage, we can get a likely value for the climate. We assume that presence of a particular taxa in the pollen assemblage during the last 3000 thousand years might be less related to climate and may be of anthropogenic origin. Due to this fact, we do not provide climate estimations for this period as they would likely be biased. By using the pollen taxa present we also assume that local conditions are reflected in the combination of the taxa present. Therefore, we gathered more data on the Mediterranean species to achieve better reconstructions in the Iberian Peninsula.

2) page 3906, Data Sources: The authors apply the PDF approach by geo-referencing the distribution of 246 taxa from Flora Europaea and the Global Biodiversity Information Facility. It is not clear how these botanical taxa were matched against the pollen taxa used in the reconstruction. They need to include a table providing a list of pollen taxa and their botanical taxa equivalent used in the calibration. Without this information it is impossible to see how this took place, and to be able to potentially reproduce this aspect of their methodology. There are many problems that are likely to be associated with this, particularly since many pollen taxa are only resolved to genus or family level, and this needs to be shown.

REPLY: A table showing all taxa used will be added to the revised version.

3) page 3907: The authors reconstruct 3 climate variables. They need to explain why they chose these three particular variables, since they are not commonly (have ever been?) used in pollen-climate reconstructions. They also need to explain what these variables are; January minimum temperature for example, is this the mean monthly minimum, or the lowest ever recorded in this month?, July maximum temperature , is this the mean monthly maximum, or the highest ever recorded in this month?, Minimum annual precipitation what is this? The lowest mean monthly precipitation recorded in any month? Or the lowest ever? And why is it described as annual? Very confusing and not at all clear why this is preferable to the much more commonly used mean annual precipitation, or moisture balance. Following on from this, it is also confusing to then refer to these variables as Tjul, Tjan since these are usually used to denote mean monthly values, and Pmin is similarly confusing. Try and choose something a bit more self-explanatory. Problems with the chosen climate variables also extend to the discussion, where these are used much too loosely in discussions of warmer/colder and wetter/drier conditions. For instance, 3913, 17-22, the authors talk about precipitation values showing more humid conditions, but is *this appropriate given that the reconstruction is for the driest month only (if this is really what was reconstructed). For instance, what if the mean annual precipitation increased but the driest month got drier? We then have wetter conditions on an annual basis, but drier conditions for the one month. Similar on page 3914, lines 20-25.*

REPLY: The variables were chosen due to their likely influence on plant distributions. The temperature variables follow the same nomenclature as the climate data source (http://www.worldclim.org/; Hijmans et al. 2005). We assume that the precipitation variable name can be misleading. As the reviewer suggests, it was the precipitation of the driest month. However, in this new version we have changed the reconstructed precipitation variable to Annual Precipitation.

4) 3907, 11-12: You need to explain which software was used for the PDF analysis, and state precisely which method. Is this a direct reproduction of a previous method using the same software, or something new or adapted? Following from point 2, you seem to have added additional taxa information, if not additional taxa. Also, why did you choose to use the PDF method and not other more commonly applied methods such as modern analogue? There are certainly known weaknesses in other methods, what are the strengths and weaknesses of the PDF method that led you to choose it over other methods?

REPLY: We have developed the code in R language to apply the method. This code will be distributed soon in its final version (still need to improve the associated manuals) but a beta version is already available (webpages.icav.up.pt/-pessoas/ptarroso/pollenclim/pollenclim.html). The pdf-method uses presence data and does not rely on modern analogues, thus, it is not dependent on the availability of modern analogues, neither it depends on modern co-occurrence of taxa (Kuhl et al 2002). It generates a most likely reconstructed values with its uncertainty (Kuhl et al 2002). We have changed the applied method to follow more closely the published method by Kuhl et al (2002). The taxa list was added.

5) 3907, 16-17: We need to know how the pollen sum was calculated since the percentage values appear important and are strongly influenced by what is included in/excluded from the sum. For instance, a standard sum based on total terrestrial taxa, or just the taxa used in the transfer function? (see point 2).

REPLY: This was further explained in the text. The method relies in pollen proportions to reconstructed the climate but the results are not strongly influenced by them, but rather by the PDF of the available taxa. Discarding this important source of information was seen as an disadvantage of the method (Birks et al. 2010) and thus we have included them in the reconstruction.

6) 3908: A serious failing of the whole analysis appears to be the lack of any evaluation. How reliable is the reconstruction? What have you done to evaluate the method and what evidence is there to support the robustness of your reconstructions? Can you provide some form of evaluation using modern pollen surface samples for instance? Or perhaps provide some direct comparison of other reconstructions for the study area based on other proxies and/or pollen-based studies? Interpolation uncertainties are shown in figure S2, but no reference is made to reconstruction uncertainties. The time series area-averages shown in figure 5 are a combination of reconstruction and interpolation uncertainties, but these are not acknowledged.

REPLY: As said above, we do not expect that the modern surface pollen distribution is purely affected by climate. Human has changed the landscape at this level at it is reflected on the pollen surface samples. Reconstructions using these data would not provide a good evaluation of the method. Nevertheless, we added a new test including the sites with more recent samples (¡ 500 years) to provide a general assessment of the reconstruction quality.

7) page 3909: How were the time windows calculated? For example, by averaging all the samples within a time frame eg 11,000 +/- 500 years BP? Or by choosing the sample closest to the target time eg 11,000 BP? Or by interpolating to the target time.. Please explain. Also, how were the individual age-depth models arrived at and how were 14C calibration issues dealt with?

REPLY: 14C dates were calibrated with Calib 7.0 (Reimer et al. 2013) using the calibration data set intcal13 (http://radiocarbon.pa.qub.ac.uk/calib/). Calibrated 14C dates were then used to build an age/depth model for each pollen series.

The time frame windows were calculated by the thin-plate splines of the reconstructions. We will rephrase the text to make this point more clearly stated in the revised manuscript.

8) pages 3909, 3911, 3912: The interpolation is based on anomalies, but the results in the main figures are presented as absolute values, which are also the basis of the discussion. Why the use of absolute values?, and especially for area-average calcula- tions? I can see how you might like to use these to make the maps look nicer, since it will help pick out the topographic features, but they *are of little value to the average reader who is unfamiliar with (for instance) the area-average maximum July temper- ature of Iberia and simply wants to know the change relative to the present. Was it warmer or cooler or drier or wetter than today? This also allows us to compare with other studies both within and distant from the study region, and is particularly useful in this case because the reconstruction does not include the present day values of the climate variables.*

REPLY: The absolute values of the reconstructed temperatures were preferred due to the direct applicability on a wide range of biogeographical studies. The figures and discussion will be adapted to anomalies in the revised version.

9) 3909: How was the interpolation done?, please describe. It looks like a 2- dimensional spline was fitted, since the interpolated anomaly maps are very smooth. If you had used a 3-dimensional spline you might have found that the interpolation un- certainties were reduced. Using a 2-d method assumes that lapse rates have been constant for the last 15,000 years, something that is extremely unlikely. Climate varies vertically as well as horizontally. Sites at different altitudes will undergo different tem- perature/precipitation changes relative to each other as a result of these lapse rate changes. The difference between your C1 region and the other regions probably reflects this (3912, 18-19), and using a 3-d interpolation would have highlighted this more.

REPLY: We changed the interpolation method to include 3-D splines as suggested. This includes both horizontal dimensions as well as altitude as vertical dimension.

10) page 3910: The maps shown in figure S1 and S2 need to be bigger, and the scaling easier to read with more numbers. Space is not limited in online materials so make the most of it, you have some interesting results here. The scaling of Figure S2 would be easier to read if it was monochromatic. What are the units of the variance shown in figure S2 and how was this calculated? I am presuming this is the standard error of the interpolation generated by the spline (an output of the fields package), please state this. The text says that this is low, although the values in figure S2 actually look very large compared to the changes in the Holocene shown in figure 5, again uncertainties need to be considered.

REPLY: The figures with anomalies are bigger now.

11) pages 3912, 3913: The discussion talks about climate change in terms of val- ues, but not in terms of climate itself. There are some interesting results here, what is causing them? How and why did climate in the past potentially *differ from that of the present? The role of the Atlantic and Mediterranean, the interaction of air masses, the trajectory of the winter storm tracks, the strength of the westerly circulation, continen- tality etc? There is one attempt where the authors state that the increase in summer insolation from 15k BP was the cause of the observed increase in winter temperatures (3912, 11-12); but how could this be so?? And why no change in summer tempera- tures? This the authors appear to explain by some kind of physiological upper limit to the growth response to temperature (3913, 4-5), but how and why? Does this mean that we cannot reconstruct summer temperature from vegetation beyond a certain limit? The authors also appear to explain the increasing variability of minimum January tem- perature after 14k as a result of the expansion of trees, which modified albedo (3913, 27-28); how and why do trees/albedo increase winter temperature variability on this timescale?, and how are alternative explanations discounted? It is not clear from the cited reference. Similar on page 3915, line 1; how and why does human impact cause lower temperatures, and why can other reasons be discounted?*

REPLY: Most of the discussion was rephrase to include many of both reviewers suggestions. Since the methods changed with implication on the results, some discussion suggested was not included.

Minor issues: 1) 3904, 7: at the molecular

REPLY: Done

2) 3904, 10: predicted for future decades

REPLY: Done

3) 3910, 8-10: Please state more clearly what software was used for what analysis

REPLY: Done

4) 3913, 4-5: are likely resulting in non-responsive July temperature what does this mean?

REPLY: Rephrased

5) 3913, 10, 12; 3914, 2 etc: OD, BA, YD etc acronyms need to be defined

REPLY: Done

6) 3915, 28: precipitation was

REPLY: Done

7) Table 1: Please include site altitude, number of 14C dates (or other absolute dates)

REPLY: Done

Reviewer 2

The subject of the paper is quite interesting and is well written. However, the methodology is quite confusing and the results of the climatic variables reconstructed sometimeshas no sense from a physical point view. In addition there is some other important issues that the authors should clarify before publication. I am totally in agreement with all comments posted by referee #1. Following i highlight some of his comments and add some more others.

Major comments.

-Which is the temporal resolution of pollen data? 1000 years? if it is less why to loss this finer time resolution?

REPLY: The 1000 years is a good compromise for such spatial study because it is based on a heterogeneous data-set of times series which have different time resolutions.

-I can not understand the election of the climatic variables employed in this study. The authors should first clarify the variables (see comments ref #1) and later to argument why they choose such variables. From my point of view probably each place and kind of pollen taxa should respond in a different way to different variables depending on the area, mainly due to the large spatial climate heterogeneity in the Iberian Peninsula. This means that in one place proxy data can give valuable information on one climatic variable while in other area this

could be totally different. A previous evaluation of this would be desirable.

REPLY: Mostly answered in reviewer 1 response. The heterogeneity of Iberian Peninsula is noticeable at climate and vegetation level. Different plant compositions will yield different climate reconstructions. Thus, by using most of the taxa found at the pollen assemblage for which we have modern distributions, we can build these reconstructions and get the past spatial patterns reveling the heterogeneity of the climate. Therefore, is because different pollen sites respond differently that we can have climate reconstructions.

-The authors state that the main objective of the paper is to define areas within the Iberian Peninsula that share similar climate evolution. For this task they firstly construct the climatic fields and later apply a clustering method for grouping areas with similar time evolution. I can not find the sense of grouping Tjan, Tjul, Pmin in a unique area. Probably it has much sense to make a classification for each climate variable. In fact i can not find the sense of the regions obtained. For example in the south-east of the Iberian Peninsula there is a strain mix of clusters (probably this is connected with the next point). In addition it has no sense that regions that are together and that at annual time scales vary in a similar way present so strong changes at millenian time scales (for example for Tjan)

REPLY: Maybe we misunderstood the point of this question but Tjan, Tjul, Pmin have not been grouped. What we have done is a clustering of the first component of the fPCA in order to depict regions of matches and mismatches since the last glacial period. The clustering is aimed to define, on a statistical basis, where, how and if there are areas where a reconstructed climate variable may show some coherent patterns. This method depicts areas where similar evolutions of the climate represented by those three variables occur.

-Other aspect of the methodology i can not understand is why the final resolution is so fine. What is the sense of this? nicer maps? The effects of the repeated spatial inter- polations performed could be quite dangerous, specially when there is some periods (the beginning) with just a few data. If the data purely reconstructed are the 31 points why do not perform the clustering exercises just over this data?. Why not working only with anomalies?. More examples of this can be the reconstructed maps of Figure S-1.

REPLY: As said above in the response to reviewer 1 comments, we added the anomalies as suggested. There is no objective reason to choose the spatial resolution of the interpolation in this case. Although maps are in fact nicer, this was not the reason to choose this scale. It was the applicability to biogeographical studies.

- Regarding the maps of the climate variables, do the authors really think that it is any probability that coastal areas of the Mediterranean were much colder (Tjan) than the North Plateau (most than 10 degrees), or. differences of the anomalies of almost 30 degrees? I think that authors should check the physical consistence of this results be- cause they are almost impossible from a climatic point of view. Other aspect probably related to interpolation is that some times the largest anomalies appear in places where data is scarce, like in the center/west of the Iberian Peninsula or around the Ebro River mouth.

REPLY: The changes in the methods influenced these results. The uncertainty is shown as supplementary figure.

In summary, apart from the comments of referee 1, the authors first should argument clearly the selection of the climatic variables to reconstruct.

REPLY: We have changed the reconstructed variables.

Second they should check the physical consistency of the series reconstructed at places where they have proxy data.

REPLY: A new analyses of reconstruction success was done.

And if they desire to present full maps of the IP they should indicate the value reconstructed and the error associated to such statistical prediction. Kriging permits to do this and it is the most commonly used in the construction of climate grid data.

REPLY: Uncertainties of the spatial interpolation are shown as the variance. However, with the modification of the interpolation method also these maps change since the last version. The multivariate thin plate splines, as suggested by reviewer 1, were preferred to kriging.

REFERENCES:

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biology letters, 4, 585589.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 19651978.

Kuhl N, Gebhardt C, Litt T, Hense A (2002) Probability Density Functions as Botanical-Climatological Transfer Functions for Climate Reconstruction. Quaternary Research, 58, 381392.

Reimer P (2013) IntCal13 and Marine13 Radiocarbon Age Calibration Curves 050,000 Years cal BP. Radiocarbon, 55, 18691887.

Birks, H., Heiri, O., Seppa, H., and Bjune, A.: Strengths and weaknesses of quantitative climate reconstructions based on Late-Quaternary biological proxies, The Open Ecology Journal, 3, 68110, 2010.

Marked-up version

Manuscript prepared for Clim. Past
with version 2014/05/30 6.91 Copernicus papers of the LaTeX class copernicus.cls.
Date: 1 June 2015

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

Pedro Tarroso[1,2,3], José Carrión[4], Miriam Dorado-Valiño[5], Paula Queiroz[6], Luisa Santos[7], Ana Valdeolmillos-Rodríguez[8], Paulo Célio Alves[1,2], José Carlos Brito[1], and Rachid Cheddadi[3]

[1]InBio/CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto, Campus Agrário de Vairão, Vairão 4485-661, Portugal
[2]Departamento de Biologia da Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal
[3]Institut des Sciences de l'Evolution, UMR CNRS 5554, 34090 Montpellier, France
[4]Department of Plant Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain
[5]Research Group of Archaeobiology, History Institute, CCHS, CSIC, Albasanz 26-28, 28037 Madrid, Spain.
[6]Terra Scenica, Centro para a criatividade partilhada das Ciências, Artes e Tecnologias, Lisboa
[7]Facultad de Ciencias, Universidade da Coruña, Campus A Zapateira, 15071 A Coruña, Spain
[8]C/ Teniente Ruiz 5, 2B, 28805 Alcalá de Henares, Madrid, Spain

Correspondence to: Pedro Tarroso (ptarroso@cibio.up.pt)

Abstract. The evolution of the climate in the Iberian Peninsula since the last glacial maximum is associated with distributional shifts of multiple species. We rely on this dynamic relationship between past climate and biodiversity patterns to quantify climate change using fossil pollen records widespread throughout the Iberian Peninsula and modern spatial distribution of plant taxa and climate. We have reconstructed spatial layers (1 ka interval) of January minimum temperature, July maximum temperature and ~~minimum~~ annual precipitation using a method based on probability density functions and covering 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 areas that share similar climate ~~evolutions~~ 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 over the studied period. The clustering scheme and ~~patterns of change~~ climate stability between millenia are coherent with the existence of multiple refugial areas in the Iberian Peninsula.

1 Introduction

The ~~pattern of present biodiversity~~ distribution pattern of biodiversity today is the result of a dynamic process driven by geological events and climatic oscillations at a broad temporal scale ~~by geological events and climatic oscillations (Hewitt, 2000) . This~~ (Hewitt, 2000) . The change from the glacial period to the current interglacial was followed by species with distributional shifts and extinctions as studied from the fossil record (Taberlet and Cheddadi, 2002) or the genetic footprint of demographic changes (Hewitt, 2000) . The relation between climate and biodiversity is likely to be maintained in the future, however with alarming consequences ~~for species resulting from current climate warming trend. The largest implications are~~ due to the current trend of climate warming of anthropogenic origin, including major distributional 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). The biodiversity hotspots retain high levels of endemism and are considered as the best candidates for preserving species diversity in the future (Myers et al., 2000). The Mediterranean basin hotspot, in particular, was shown to play 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 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 biodiversity patterns ~~is~~ offers invaluable knowledge for the current species conservation effort dealing with the global climate change predicted for the following decades (Anderson et al., 2006; Willis et al., 2010).

~~Refugia~~ Species glacial refugia have been generally defined based on species survival with ~~an evident relationship to climatic components~~ a strong relationship with climatic (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 have proven useful to locate species diversity and migration routes ~~(Petit et al., 2003; Cheddadi et al., 2006)~~ (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 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 fossil record. ~~Pollen holds invaluable~~ Fossil pollen sequences provide information from past climates and is, thus, 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). Using proxy data to derive a definition of refugia in terms of climate in a spatial context, may provide further insights to the potential location of suitable climate favouring long species persistence and serving as refugia.

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 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 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 during harsh glacial conditions and highlight the importance of this peninsula 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 area favouring species persistence, the 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 to the refugia-within-refugia pattern (Weiss and Ferrand, 2007). All together it renders the Iberian Peninsula as ~~a~~ an unique area to study the climate processes during the late-Quaternary, with a highly dynamic vegetation response to climate (Carrión et al., 2010b) and high importance for biodiversity conservation.

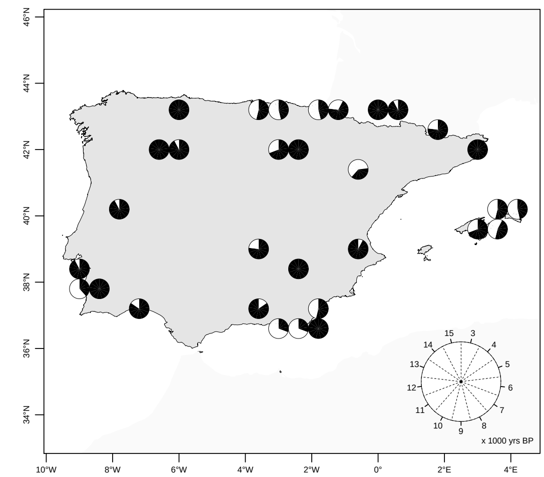

Figure 1. Study area with sample points. The black area inside each circle represents the ages available in each pollen sequence.

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

2 Methods

The area for the spatial reconstruction extends throughout the land area of the Iberian Peninsula and the Balearic islands (Fig.~~1~~ 1). The method used to produce past climate grids is based on probability density functions (PDF) and requires both fossil pollen records and full distribution of modern plant taxa (Kühl et al., 2002). PDFs for each taxon are created using modern distributions in the climate space. 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

Table 1. Origin and description of the data sources of fossil pollen used to reconstruct the climate in the Iberian Peninsula. ~~The optimized threshold values for minimum January temperature (Tjan), maximum July temperature~~ Source is either the European Pollen Database (~~Tjul~~EPD) or author contribution. Longitude and ~~minimum annual precipitation (Pmin)~~ latitudes correspond to the centroid of the nearest cell to the site and altidude as extracted from WorldClim dataset, all at 5' spatial resolution. The ^{14}C are the number of dates available for each site~~are shown~~.

Name	Source	
Albufera Alcudia	~~EPD39.793~~epd	
Algendar	~~EPD39.941~~epd	
Antas	~~EPD37.208-1.8240.50.390.18BanyolesEPD42.133~~epd	
Barbaroxa	Queiroz (1999)	
Cala Galdana	~~EPD39.937~~epd	
Cala n' Porter	~~EPD39.871~~epd	
CC-17	Dorado Valiño et al. (2002)	
Charco da Candieira	~~EPD40.342~~epd	
Gádor	Carrión et al. (2003)	
Golfo	Queiroz (1999)	
Guadiana	Fletcher et al. (2007)	
Hoya del Castilho	~~EPD41.25~~epd	
Lago de Ajo	~~EPD43.05~~epd	
Laguna de la Roya	~~EPD42.217~~epd	
Lake Racou	~~EPD42.554~~epd	
Las Pardillas Lake	Sánchez-Goñi and Hannon (1999)	~~42.033.030.570.370.11LourdesReille and Andrieu (1995) 43.033-0.0~~
Navarres 1	~~0.65~~epd	
Puerto de Belate	~~-1.55~~epd	
Puerto de Los Tornos	~~39.1~~epd	
Quintanar de la Sierra	~~Pons and Reille (1988)~~ epd	
Roquetas de Mar	~~0.17Puerto de Belate~~epd	
Saldropo	~~0.31~~epd	~~0.~~
Sanabria Marsh	~~0.59~~epd	
San Rafael	~~-3.017~~epd	
Santo André	~~36.794~~Santos and Sánchez-Goñi (2003)	
Siles	~~EPD~~Carrión (2002)	
Padul	~~0.14San Rafael~~Pons and Reille (1988)	
Lourdes	~~0.43~~Reille and Andrieu (1995)	
Monge	~~0.62~~Reille and Andrieu (1995)	
Moura	~~-8.78~~Reille (1993)	
Banyoles	~~38.4~~epd	

fit a quality criteria regarding the number of radiometric dates (>3 in each site) and gave preference to those with higher sampling resolution. Using these criteria we selected a total of 31 records which cover different time spans between 15000 and 3000 years BP (Table~~1~~ 1; Fig.~~1). The last 3000 years were discarded from this analysis because human activity is known to have strongly impacted the Iberian Peninsula landscape since then (Carrión et al., 2010a) and therefore the fossil data may be biased and may lead to misinterpretations. Despite the anthropogenic influence on the pollen abundances,~~ 1). For the reconstruction process we assume that modern distributions are in equilibrium with climate at ~~large scales~~ the distribution scale covering the species range. Using taxa full distribution data is ~~, thus,~~ reducing the bias resulting from local changes and ~~supports~~ supporting our assumption. The different sensibility of taxa to the various sources of disturbance is balanced by the use of the multiple taxa identified in each core.

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 from botanical and herbarium collections and observations stored at a lower spatial resolution than 30'. The georeferenced geographical distributions were then rescaled to the resolution of 30' (~~-55~~ ~55 km). The global historic climate data (~~-~~1950-2000) for January minimum temperature (Tjan), July maximum temperature (Tjul) and monthly precipitation data were obtained from Worldclim database (Hijmans et al., 2005, www.worldclim.org) with 5' resolution (~~-10km~~ ~10km) and values were aggregated by the mean value to the resolution of 30'. Precipitation was further processed to obtain the ~~minimum~~ annual precipitation (~~Pmin~~Aprc) from the monthly data by recording for each pixel the minimum value of precipitation in the 12 months.

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. This approach ~~has already proven successful~~ was successfully used to reconstruct temperatures from fossil pollen data (Kühl et al., 2002; Cheddadi and Bar-Hen, 2009). With the superimposition of the PDFs 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). ~~The area of each PDF available for intersection is defined after applying a threshold limit based on the pollen percentages. A univariate kernel estimator was used~~ A univariate normal and log-normal density distributions were fitted to the temperature and precipitation data, respectively, at each species presence in order to build the ~~single dimension~~ PDF from the modern plant distributions~~and the Tjan, Tjul and Pmin data . Kernel estimators and parametric estimators provide similar results when we fit with a normally distributed variable (Kühl et al., 2002) , however, kernel estimators follow closely the real distribution of species with non-normal 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 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 2ºC for temperature variables and 20mm for precipitation. This procedure decrease the weight of the most frequent climate values occurring in the study area and increased those, in the distribution of the species, that occur less frequently in the study area (Kühl et al., 2002) .

The reconstructed climate from 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 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 a taxon as present in the sample, and minimum of five taxa are needed to reconstruct a climate value.

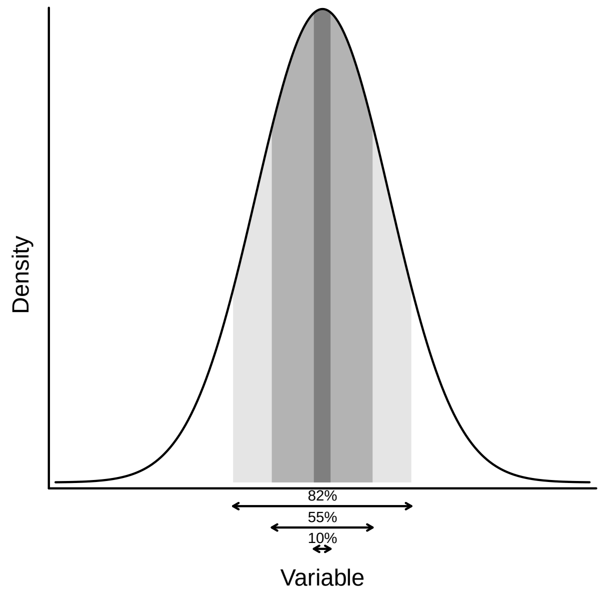

Figure 2. Example of the influence of pollen proportion (pp) on the calculation of the density of taxa presence intersection. The shades of gray indicate the effect of different pp when the pollen adjustment value (pa) is set to 0.9 and arrows indicate the assumed presence range. The first case (dark 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).

Using presence data is both seen as an advantage of the PDF method (Kühl et al., 2002) but also as a weakness due to the exclusion of the quantitative data resulting from the pollen abundances (Birks et al., 2010) . Fluctuations in pollen abundances are related to ~~several factors including~~ multiple factors related to the physiology of the species (Hicks, 2006), ~~but have also~~ with a differential pollen production among different species, but it also has a strong climatic component through the influence that climate has on ~~land cover. We used the pollen percentage as a measure of the taxon proportion throughout the time span of~~ distributions. We have used these data as the ~~core. Thus, the~~ proportion of pollen found relative to the maximum pollen found. The minimum non-zero pollen ~~percentage~~ proportion corresponds to the presence of the taxon while the maximum defines its highest abundance within the fossil record. Using pollen proportions ~~instead of the proportion of pollen of each taxon in a specific~~ per taxa instead of per age avoids the bias of different pollen production by distinct taxa and thus allows quantify-ing the presence of a species relative to its maximum detection within each site.

~~The PDF is filtered~~ 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 ~~a threshold. We assume that higher pollen proportions reveal near optimum conditions for the taxon that correspond to~~ alpha values to reduce the species climate tolerance towards the peak density value (Fig. 2). To avoid the selection of a unique climate value with maximum detection of a species, 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 detection, the ~~area of the PDF where the taxon is found at higher densities.Restricting the PDF probability area based on the relation of density of taxa and pollen percentage results in narrower range of reconstructed values.The threshold influence on the PDF is controlled by a coefficient: “0” results in no effect of the pollen percentage and uses the full profile for taxa intersection; whereas “1” will likely result in a very narrow area of the PDF around highest densities at maximum pollen detection. A threshold of 0.5, for example, would constrain the PDF~~ climate presence will be set to the area ~~where densities are higher than 50% at the maximum detection of the taxon. (Fig. 2). We used an optimised value for this threshold corresponding to the maximum valuefound that allowed the intersection of all taxa present in a sample (Table 1).~~

~~The reconstructed climate value~~ 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 the ~~weighted mean of the intersection of the PDF area of all taxa identified in a sample. A coefficient with the maximum value of 1 was added to control the number of species in the intersection. This value was set to 0.95 for all reconstructed variable which means that the intersection area is defined by, at least, 95% of the number of species intersecting. The reconstructed climatevalue is given by the average of the values present within the intersecting taxa. To generate more accurate values, we used a weighted mean with the density value of the union of the PDFs as weights~~ product of the climate PDF with the taxa intersection.

In order to quantify the success of the reconstruction method in predicting recent climate, we have compared data from the reconstruction with global historic climate data (1950-2000) with linear regressions for each climate ~~value. The union of the PDFs of each taxon present is less sensitive to~~ variable. This procedure was done with all available samples with age inferior to 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 of the reconstruction success, the linear regression is used to estimate a spatial baseline for calculating the anomalies. The preindustrial period around 100 BP (1850 AD) was used as reference climate to calculate anomalies. This period is often used as baseline in climate ~~affinity of the taxa present than to the intersection. For example, when more warm dependent taxa are available due to sampling bias, the intersection would be biased towards higher temperature values whereas the union eliminates the increasing influence of multiple taxa with similar PDFs. This effect is more striking in the case of precipitation. This variable is very challenging to reconstruct because xerophyte taxa are less frequent than taxa supporting average to high precipitation, although their presence is clearly indicative of more arid environments. Moreover, taxa well adapted to dryness in the Mediterranean climate have highest densities with some precipitation, adding a bias towards higher values of precipitation and a misrepresentation of the lowest precipitation values. Increasing the number of available arid taxa in the reconstruction might help retrieving lower values, but this will also be limited by the resolution of taxa identification in the pollen analysis and by the scarce geographical distribution of many Mediterranean taxa~~models, facilitating data-model comparison, 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 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 time slices were extracted.

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 for each site ~~by subtracting the current climate variable (30’ spatial resolution) from the reconstructed one for each time slice and each site~~with the difference between the reconstructed climate and the reference climate calculated as explained above. Anomaly values were projected into a 30’ resolution grid and interpolated onto a 5’ resolution grid using 3D thin-plate smoothing splines with two spatial dimensions plus altitude. This interpolation method was chosen because when used with climate data it generates accurate predictions (Jarvis and Stuart, 2001) and it was used to generate the present data 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 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 summarised in a few components. ~~Cheddadi and Bar-Hen (2009)~~ (Cheddadi and Bar-Hen, 2009) applied a fPCA in 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 over the past 15 ka.

~~A surrogate for climate stability was defined as the average difference between millenia~~ Climate stability was calculate for each variable ~~. The differences were calculated for the period reconstructed (15 to 3 ka) between a given age and its previous one~~as the mean absolute deviance from the current climate as available in WorldClim dataset.

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).

~~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) minimum annual precipitation.~~ 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 500 years have a linear trend with the current climate, thus revealing the reconstruction method predicts well the recent climate ($p \leq 0.016$ for all variables; Appendix A).

The reconstruction of three climate variables exhibited high spatial variability over the period between 15 ka and 3 ka (Fig.~~3, S1~~ 3, Appendix A, B). The uncertainty associated with the spatial interpolations is usually low, suggesting a good sampling coverage, with the exception of the ~~extreme~~ northwest area (~~Fig. S2)~~Appendix D). The Iberian Peninsula had extensive areas with extremely low Tjan that gradually increased to higher values, and markedly after 10 ka. ~~Conversely, the~~ The pattern of Tjul over the same time ~~span remained quite~~ remained stable, with ~~extended areas of lower values at 12, 11 and 5 ka. Areas with the highest reconstructed temperatures were found between 15 and 13 ka at the southern plateau. Between 15 and 7 ka the areas with increasing values of Pmin have expanded, with the exception between~~ lower values before 12 ~~and 11 ka , when extensive areas with very low precipitation values were observed.After 6 ka, a general trend towards aridification of the Iberian Peninsula was observed, with extended areas with lower Pmin than the early Holocene.~~ ka. In the studied period, there is a trend for the decrease of precipitation, especially after 10 ka (Fig. 4). This decrease towards a more arid peninsula happens mostly in the south-eastern portion of its area (Appendix B)

The clustering of the first fPCA component of the three reconstructed variables ~~identified areas with congruent spatial structure~~ were spatial structured (Fig.~~4~~ 5), and allowed summarising the evolution of these three climate variables in the Iberian Peninsula (Fig.~~5, S3~~ 4). The first ~~two components~~ component of each variable explained more than ~~89~~95% of the variation (Tjan: ~~77.0%, 12.3~~95.5%; Tjul: ~~91.7%, 6.7%; Pmin: 90.3%, 5.5%, for the first and second components, respectively~~99.2%; Aprc: 99.5%). The cluster C1 (~~15~~27% of the total area) is located mostly on north and ~~eastern~~ western Iberia and includes ~~the Iberian~~ part of the north-Iberian mountain ranges (average altitude is ~~1082~~679±~~395m~~454m) but also low altitude ~~areas. It is the coldest area in the late-Quaternary, with Tjan from -11.4ºC to -3.9ºC, Tjul ranging between 21.1~~coastal areas. This is the wettest cluster, with Aprc ranging from 1055 to 1115mm, the coldest in July (21.6 < Tjul < 24.1ºC~~and 22.1~~) and with very low January minimum temperatures (-5.6 < Tjan < 0.1ºC~~and the wettest with Pmin between 31.5mm and 37.4mm~~). The cluster C2 ~~(21~~encompasses part of the Cantabrian mountain range and the central Iberian system (29% of the total area with average altitude of ~~470~~856±~~218m)~~ 301m) and occupies most of the ~~southern Iberian Plateau. It holds the warmest values for Tjan varying between -5.4ºC and 2.0~~northern plateau. It has the lowest January temperature (-5.7 < Tjan < -1.3ºC~~and Tjul between 26.1~~) but has warmer in July than C1 (25.1 < Tjul < 27.7 ºC~~and 28.9ºC. The temperature~~) showing high seasonal amplitude with very low precipitation (536 < Aprc < 621mm), similarly to C3 and C4. The dissimilarities between clusters C3 and C4 (~~29% and 35~~24% and 20% of the total area and average altitude of ~~, 472~~610±~~383 and 657~~297 and 278±~~304~~231, respectively) occur mainly in ~~Tjan, having the former higher temperatures (-4.3~~temperature, with C4 being generally warmer and wetter than the C3 cluster. These are the warmest areas in both January (C3: -1.7 < Tjan < 3.0ºC~~–0.1~~; C4: 1.0 < Tjan < 6.4ºC) ~~than the latter (-6.5~~and July (C3: 29.4 < Tjul < 33.4ºC~~–0.9~~; C4: 27.2 < Tjul < 30.2ºC) ~~. However, Pmin shows a major difference between these two clusters, which indicates that~~ and with low annual precipitation (C3~~is generally wetter (26.2 – 29.4mm) than~~ : 505 < Aprc < 615mm; C4~~(19.4 – 25.2mm), which represents the driest areas in the late-Quaternary. Most of the area of the Balearic Islands is within cluster~~ : 555 < Aprc > 683mm).

The Balearic Islands are fully included in the C4 ~~, except the mountain range in northern Maiorca~~ cluster (Fig.~~4~~ 5).

The ~~average differences between millenia~~ mean absolute deviance from the current climate showed that the stability of the climate in the last 15ka was not spatially uniform (Fig.~~6)have higher values for Tjan and Pmin, whereas Tjul shows near zero average change for most Iberian Peninsula. The extreme north and south areas, together with the extreme south-west and north-east of the peninsula had smaller amplitude of Tjan change between millenia and Pmin exhibits a similar pattern~~ 6). The Tjan and Aprc exhibited higher stability in the southern Iberia, although the first has lower values of deviance (higher stability) towards the eastern coast the the second 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.

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 (Bartlein et al., 2010). The ~~major constraint we found in the Iberian Peninsula was~~ method used here provides acceptable climate reconstructions, despite the low number of sequences available according to our quality criteria for spatial climate reconstruction, both in terms of sampling resolution and number of ^{14}C dates. ~~Nevertheless, the resulting climate reconstruction is consistent with other studies (Davis et al., 2003; Cheddadi and Bar-Hen, 2009) providing a general assessment of the reconstruction quality~~The residuals in the linear regressions were high, resulting in a low coefficient of determination. However, this is expected since we were comparing the historical climate with the 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 biasing the results. Nevertheless, a significant linear trend was found between reconstructed climate and historical climate that allow us to produce a reference dataset using this model and the historical climate. The results provided here reinforce the Iberian Peninsula as a particular case in Europe due to its role as a general European glacial refugium and holding enough climate variation since the LGM to support a network of smaller refugial areas (Weiss and Ferrand, 2007).

The climate of the last 15 ka in the Iberian Peninsula was dynamic, with oscillations of temperature and precipitation occurring mostly at the ~~center~~ 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 (Fig.~~5~~ 4) that results from 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 with very low temperatures (Fig.~~3~~ 3). An evident pattern that strikes from the results presented here is the division of the peninsula in spatially ~~coherent~~ structured areas that shared similar climate evolution during the late-Quaternary (Fig.~~4~~ 5). The ~~coldest and wettest~~ wettest and cold cluster C1 predominantly located at ~~high altitudes and with smooth climate changes, contrasts with the warmest and low-altitude cluster C2, swept rapidly with high amplitude changes (Fig. 5). This relationship between topography and velocity of climate change since the last glaciation was demonstrated globally (Sandel et al., 2011) . Our data suggests that at the regional scale and with extensive time-series data, this relation is preserved~~norther and north-western Iberia occupies most of the current Atlantic bioclimatic region. Although very similar with C2, it contrasts in the seasonal amplitude and precipitation.

Our results show that January temperatures exhibited a general warming trend during the studied period which corresponds in average to an increase of ~~5ºC. The center of the Iberian peninsula holds most of the change between millenia and the coastal areas offers more resilience to the change~~~5.5ºC. The southern part of the Peninsula is more resilient to change, particularly for Tjan and Aprc, whereas the northern had major changes. This pattern is less obvious in July temperatures~~or precipitation~~, where variations showed a smaller amplitude albeit ~~these variables are~~ this variable is markedly different between clusters, and thus contributing to the climate division of the study area (Fig.~~5, S1~~ 4, Appendix C). 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 enough energy to plant growth (Sykes et al., 1996), and are likely resulting in ~~non-responsive~~ less responsive July temperature.

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 enough resolution to analyse general patterns of climate evolution resulting from larger stadials and interstadials, but abrupt climate events are generally ~~unnoticeable~~undetectable. The OD (~~18~~ ~8 to 14.7 ka) is characterised in Iberia by a vegetation changes compatible with cold and humid conditions followed by a warming trend (Naughton et al., 2007). The OD is followed by the warmer BA (~~14.7~~ ~14.7 to 12.9 ka). Our results show a similar pattern ~~, especially for cluster C2,~~ with colder conditions between 15 ka and ~~14~~ 13 ka, followed by a warming trend ~~until~~ after 13 ka (Fig.~~5). Cluster~~ 4). All clusters show these warming trens, although clusters C1 ~~, on the other hand, shows a decreasing temperature trend until 13 ka~~and C2 are colder. This is reflected in a contrasted Iberian peninsula dominated by extreme January temperatures (Fig.~~3, S1).~~

3, Appendix B,C). The evolution of precipitation during the last 15 ka in the Iberian Peninsula has a ~~constant~~ very stable pattern: northern areas ~~were generally dryer while~~ comprised in C1 had high precipitation values during the whole studied time, but the south was wetter than today (~~Fig. S1). Precipitation values are low between 15 ka and 14 ka except in the mountainous areas comprised mostly in the first cluster, which remain more humid than the other areas (Fig. 3,5). Nevertheless, the average trend is a decrease of precipitation until 12 ka.~~Appendix B,C). During the OD period, there is a slight increase in precipitation in all clusters (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~~ ~14.7 and 11.5 ka (Renssen and Isarin, 2001; von Grafenstein et al., 2012) in Europe had a spatial impact that is ~~well depicted in Tjan~~ noticeable in the reconstructed temperatures (Fig.~~3, S1). The increasing variability of Tjan after 14 ka is related to the expansion of trees from glacial refugia which have modified the albedo (Cheddadi and Bar-Hen, 2009) .~~ 3, Appendix B, C).

4.2 The Holocene

The BA is followed by the cold YD (~~–12.9~~ ~12.9 to 11.6 ka), marking the beginning of the Holocene. ~~We observe a reduction of the warmer areas at~~ This period is reconstructed here with a warming trend in the Tjan but with a sudden decrease of Tjul temperatures (Fig. 4), with a reduction of the warmer areas at 13 and ~~11 ka and an expansion of the aridity (Fig. 3, 5). However, the area covered by the coldest cluster C1 responds differently with a constant warming in this period. The effect of topography might be offering higher resilience to fast changes in the mountainous cluster C1 (Sandel et al., 2011) . Differences are also observed later between Tjan showing a fast increase until 9 ka, and Tjul remaining stable in most Iberia, with the exception of cluster C2 where a decrease of ~2ºC was observed.Davis et al. (2003) , showed a similar Summer and Winter amplitude of changes for South-western Europe~~12 ka (Fig. 3).

The Holocene warm period (approximately between ~~–8.2~~ ~8.2 and 5.6 ka, depending on ~~where~~ the location in Europe) is characterised by increasing summer temperatures (Seppä and Birks, 2001), being more evident in Northern Europe and the Alps and simultaneous with a cooling at lower latitudes (Davis et al., 2003). Our results ~~show this dichotomy within the Iberian Peninsula where three clusters (C1, C3 and C4) exhibit a stable trend between 9 and 5 ka while the second cluster record a cooling stage~~point to a decrease on Tjul temperature but a stable minimum temperature, indicating mild summers. Concerning the precipitation, there is evidence of a slightly wetter climate between ~~9 ka and 6 ka~~ at 7 ka (Fig. 3) which confirms what was previously known for the southern European lowlands (Cheddadi et al., 1997).

Between 6 and ~~5~~ 3 ka, areas with low precipitation expand in the Iberian peninsula (Fig.~~3~~ 3) corresponding to the expansion of the mediterranean taxa (Naughton et al., 2007; Carrión et al., 2010b, a). The increasing aridity in the south is balanced by the ~~precipitation increase~~ high precipitation values in the north (Fig.~~S1~~ 4, Appendix B, C), contributing to the final pattern of a ~~slight increase in precipitation values~~a temperate north and a southern mediterranean climate in Iberia.

The behaviour of the reconstructed variables ~~after~~ 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 ~~lower temperatures at~~ biased temperatures 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 (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 between climate change and biodiversity patterns, the clustering scheme (Fig.~~4~~ 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 ~~stable~~ climate evolution during the late-Quaternary with smaller ~~amplitudes~~ amplitude of change (clusters C3 and C4). ~~The cluster C3~~ This area largely coincides with area of higher stability for Tjan and Aprc (Fig. 6). The cluster C4 coincides at a great extent with areas that offered more resilience to change between millenia (Fig.~~6~~ 5). Within these areas, temperature and precipitations were suitable to support the survival of temperate trees, likely acting as glacial refugia. On the other hand, the cold areas of the first ~~cluster and the fast changes of the second cluster~~ 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 ~~third~~ fourth cluster (Fig.~~4~~ 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 ~~evolved with a lower amplitude (4ºC) and was less sensitive to extreme fluctuations than the other clusters, with climate gradually evolving to current pattern~~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.~~4~~ 5), recorded also mild conditions which are often associated with southern refugia but a rapid ~~feedback to late-Quaternary events~~ Tjul oscillations associated with a cold Tjan and low precipitation may have prevented ~~persistence or recolonisation processes~~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 altitudes offer more resilience to change, particularly to July temperature and lower areas may be swept rapidly with occurring changes (see Appendix E). 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 cliamte data (Ohlemüller et al., 2012) , but our studied time frame extends to 15 ka, which does not cover the glacial maximum (~21 ka). At this period, an 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 be seen as a macrorefugia, offering conditions for large population effectives at glacial conditions (Mee and Moore, 2014) . Microrefugia is known to occur at 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. ~~Thus, such study~~ Liking past climate and diversity on the Iberian peninsula ~~has~~ and its quantification will have an increased interest for conservation issues, especially under the expected future climate change.

Appendix A: Linear regression of the reconstructed climate and worldclim data.

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

Appendix C: Climate anomalies maps.

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

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

Acknowledgements. PT was funded with ~~a~~ PhD grant (SFRH/BD/42480/2007) and post-doc grant (SFRH/BPD/93473/2013) and JCB has a contract (~~Programme Cincia 2007~~IF/00459/2013), both from Fundação para a Ciência e Tecnologia. JC contribution was funded by the project Paleoflora y Paleovegetación ibérica, Plan Nacional de I+D+i, Ref. CGL-2009-06988/BOS. LS acknowledges the contribution of M. C. Freitas and C. Andrade (University of Lisbon) who provide the cores. The authors would like to acknowledge all contributors of the European Pollen Database and the Global Biodiversity Information Facility for making their datasets publicly available to the scientific community. We are very grateful to Basil Davis, for his kind support and comments. We also thank William Fletcher and Maria Sanchez-Goñi for data contribution and comments, and also Penélope González-Sampériz contributions. Their contributions greatly improved the quality of the manuscript. This is an ISEM-contribution n° xx-xxxx

References

Anderson, N. J., Bugmann, H., Dearing, J. A., and Gaillard, M.-J.: Linking palaeoenvironmental data and models to understand the past and to predict the future., Trends in Ecology & Evolution, 21, 696–704, 2006.

Araújo, M. B., Thuiller, W., and Pearson, R. G.: Climate warming and the decline of amphibians and reptiles in Europe, Journal of Biogeography, 33, 1712–1728, 2006.

Ashcroft, M. B.: Identifying refugia from climate change, Journal of Biogeography, 37, 1407–1413, 2010.

Bartlein, P. J., Harrison, S. P., Brewer, S., Connor, S., Davis, B. a. S., Gajewski, K., Guiot, J., Harrison-Prentice, T. I., Henderson, a., Peyron, O., Prentice, I. C., Scholze, M., Seppä, H., Shuman, B., Sugita, S., Thompson, R. S., Viau, a. E., Williams, J., and Wu, H.: Pollen-based continental climate reconstruction at6 and 21 ka: a global synthesis, Climate Dynamics, 37, 775–802, 2010.

Bennett, K. and Provan, J.: What do we mean by ‘refugia’?, Quaternary Science Reviews, 27, 2449–2455, 2008.

Berger, A.: Long-term variations of caloric insolation resulting from the Earth’s orbital elements, Quaternary Research, 9, 139–167, 1978.

Bickel, P., Diggle, P., Fienberg, S., Gather, U., Olkin, I., Zeger, S., Ramsay, J., and Silverman, B.: Functional data analysis, Springer, New York, 2nd edn., 2005.

Birks, H., Heiri, O., Seppä, H., and Bjune, A.: Strengths and weaknesses of quantitative climate reconstructions based on Late-Quaternary biological proxies, The Open Ecology Journal, 3, 68–110, 2010.

Branco, M., Monnerot, M., Ferrand, N., and Templeton, A. R.: Postglacial dispersal of the European rabbit (Oryctolagus cuniculus) on the Iberian peninsula reconstructed from nested clade and mismatch analyses of mitochondrial DNA genetic variation., Evolution, 56, 792–803, 2002.

Carrión, J., Fernández, S., Jiménez-Moreno, G., Fauquette, S., Gil-Romera, G., González-Sampériz, P., and Finlayson, C.: The historical origins of aridity and vegetation degradation in southeastern Spain, Journal of Arid Environments, 74, 731–736, 2010a.

Carrión, J. S.: Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe, Quaternary Science Reviews, 21, 2047–2066, 2002.

Carrión, J. S., Sánchez-Gómez, P., Mota, J. F., Yll, R., and Chaín, C.: Holocene vegetation dynamics , fire and grazing in the Sierra de Gádor Spain, The Holocene, 13, 839–849, 2003.

Carrión, J. S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J. a., Fierro, E., and Burjachs, F.: Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands, Review of Palaeobotany and Palynology, 162, 458–475, 2010b.

Cheddadi, R. and Bar-Hen, A.: Spatial gradient of temperature and potential vegetation feedback across Europe during the late Quaternary, Climate Dynamics, 32, 371–379, 2009.

Cheddadi, R., Yu, G., Guiot, J., Harrison, S., and Prentice, I. C.: The climate of Europe 6000 years ago, Climate Dynamics, 13, 1–9, 1997.

Cheddadi, R., Vendramin, G. G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J.-M., de Beaulieu, J.-L., Sadori, L., Jost, A., and Lunt, D.: Imprints of glacial refugia in the modern genetic diversity of Pinus sylvestris, Global Ecology and Biogeography, 15, 271–282, 2006.

Cheddadi, R., Birks, H. J. B., Tarroso, P., Liepelt, S., Gömöry, D., Dullinger, S., Meier, E. S., Hülber, K., Maiorano, L., and Laborde, H.: Revisiting tree-migration rates: Abies alba (Mill.), a case study, Vegetation History and Archaeobotany, 23, 113–122, 2014.

Chevalier, M., Cheddadi, R., and Chase, B. M.: CREST (Climate REconstruction SofTware): a probability density function (PDF)-based quantitative climate reconstruction method, Climate of the Past, pp. 2081–2098, 2014.

Cox, N., Chanson, J., and Stuart, S.: The status and distribution of reptiles and amphibians of the Mediterranean Basin, IUCN, Gland, Switzerland and Cambridge, U.K, 2006.

Davis, B. A. S., Brewer, S., Stevenson, A. C., Guiot, J., and Contributors, D.: The temperature of Europe during the Holocene reconstructed from pollen data, Quaternary Science Reviews, 22, 1701–1716, 2003.

Dorado Valiño, M., Rodríguez, A. V., Zapata, M. B. R., García, M. J. G., and Gutiérrez, I. D. B.: Climatic changes since the Lateglacial/Holocene transition in La Mancha Plain (South-central Iberian Peninsula, Spain) and their incidence on Las Tablas de Daimiel marshlands, Quaternary International, 93-94, 73–84, 2002.

Fletcher, W. J., Boski, T., and Moura, D.: Palynological evidence for environmental and climatic change in the lower Guadiana valley, Portugal, during the last 13 000 years, The Holocene, 17, 481–494, 2007.

Fuentes-Utrilla, P., Venturas, M., Hollingsworth, P. M., Squirrell, J., Collada, C., Stone, G. N., and Gil, L.: Extending glacial refugia for a European tree: genetic markers show that Iberian populations of white elm are native relicts and not introductions., Heredity, 112, 105–13, 2014.

Furrer, R., Nychka, D., and Sain, S.: fields: Tools for spatial data, 2012.

Godinho, R., Mendonça, B., Crespo, E. G., and Ferrand, N.: Genealogy of the nuclear beta-fibrinogen locus in a highly structured lizard species: comparison with mtDNA and evidence for intragenic recombination in the hybrid zone., Heredity, 96, 454–63, 2006.

Guiot, J.: Palaeoclimatology: Back at the last interglacial, Nature, 388, 25–27, 1997.

Heiri, O., Tinner, W., and Lotter, A. F.: Evidence for cooler European summers during periods of changing meltwater flux to the North Atlantic., PNAS, 101, 15 285–8, 2004.

Hewitt, G.: The genetic legacy of the Quaternary ice ages., Nature, 405, 907–13, 2000.

Hicks, S.: When no pollen does not mean no trees, Vegetation History and Archaeobotany, 15, 253–261, 2006.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A.: Very high resolution interpolated climate surfaces for global land areas, International Journal of Climatology, 25, 1965–1978, 2005.

Hu, F. S., Hampe, A., and Petit, R. J.: Paleoecology meets genetics: deciphering past vegetational dynamics, Frontiers in Ecology and the Environment, 7, 371–379, 2009.

Jalas, J. and Suominen, J., eds.: Atlas Florae Europaeae. Distribution of vascular plants in Europe. Vols. 1-10., The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki, Finland, 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991, 1994.

Jalas, J., Suominen, J., and Lampinen, R., eds.: Atlas Florae Europaeae. Distribution of vascular plants in Europe. Vol. 11., The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki, Finland, 1996.

Jalas, J., Suominen, J., Lampinen, R., and Kurtto, A., eds.: Atlas Florae Europaeae. Distribution of vascular plants in Europe. Vol. 12., The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki, Finland, 1999.

Jarvis, C. H. and Stuart, N.: A Comparison among Strategies for Interpolating Maximum and Minimum Daily Air Temperatures. Part II: The Interaction between Number of Guiding Variables and the Type of Interpolation Method, Journal of Applied Meteorology, 40, 1075–1084, 2001.

Keitt, T. H., Bivand, R., Pebesma, E., and Rowlingson, B.: rgdal: Bindings for the Geospatial Data Abstraction Library, 2012.

Kühl, N., Gebhardt, C., Litt, T., and Hense, A.: Probability Density Functions as Botanical-Climatological Transfer Functions for Climate Reconstruction, Quaternary Research, 58, 381–392, 2002.

Laurent, J. M., Bar-Hen, A., François, L., Ghislain, M., and Cheddadi, R.: Refining vegetation simulation models: from plant functional types to bioclimatic affinity groups of plants, Journal of Vegetation Science, 15, 739–746, 2004.

MacDonald, G., Bennett, K., Jackson, S., Parducci, L., Smith, F., Smol, J., and Willis, K.: Impacts of climate change on species, populations and communities: palaeobiogeographical insights and frontiers, Progress in Physical Geography, 32, 139–172, 2008.

Mauri, a., Davis, B., Collins, P., and Kaplan, J.: The climate of Europe during the Holocene: a gridded pollen-based reconstruction and its multi-proxy evaluation, Quaternary Science Reviews, 112, 109–127, 2015.

Médail, F. and Diadema, K.: Glacial refugia influence plant diversity patterns in the Mediterranean Basin, Journal of Biogeography, 36, 1333–1345, 2009.

Médail, F. and Quézel, P.: Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities, Conservation biology, 13, 1510–1513, 1999.

Mee, J. a. and Moore, J.-S.: The ecological and evolutionary implications of microrefugia, Journal of Biogeography, 41, 837–841, 2014.

Miraldo, A., Hewitt, G. M., Paulo, O. S., and Emerson, B. C.: Phylogeography and demographic history of Lacerta lepida in the Iberian Peninsula: multiple refugia, range expansions and secondary contact zones., BMC Evolutionary Biology, 11, 170, 2011.

Myers, N., Mittermeier, R., Mittermeier, C., Da Fonseca, G., and Kent, J.: Biodiversity hotspots for conservation priorities, Nature, 403, 853–858, 2000.

Naughton, F., Sanchez-Goñi, M., Desprat, S., Turon, J.-L., Duprat, J., Malaizé, B., Joli, C., Cortijo, E., Drago, T., and Freitas, M.: Present-day and past (last 25000 years) marine pollen signal off western Iberia, Marine Micropaleontology, 62, 91–114, 2007.

Nogués-Bravo, D., Ohlemüller, R., Batra, P., and Araújo, M. B.: Climate predictors of late quaternary extinctions., Evolution, 64, 2442–9, 2010.

Ohlemüller, R., Huntley, B., Normand, S., and Svenning, J.-C.: Potential source and sink locations for climate-driven species range shifts in Europe since the Last Glacial Maximum, Global Ecology and Biogeography, 21, 152–163, 2012.

Parmesan, C. and Yohe, G.: A globally coherent fingerprint of climate change impacts across natural systems, Nature, 421, 37–42, 2003.

Pebesma, E. J.: Multivariable geostatistics in S: the gstat package, Computers & Geosciences, 30, 683–691, 2004.

Perez-Obiol, R., Jalut, G., Julia, R., Pelachs, a., Iriarte, M. J., Otto, T., Hernandez-Beloqui, B., and Pérez-Obiol, R.: Mid-Holocene vegetation and climatic history of the Iberian Peninsula, The Holocene, 21, 75–93, 2011.

Petit, R. J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J. P., Rendell, S., and Vendramin, G. G.: Glacial refugia: hotspots but not melting pots of genetic diversity., Science, 300, 1563–5, 2003.

Pons, A. and Reille, A.: The Holocene and Upper Pleistocene pollen record from Padul (Granada, Spain): a new study, Palaeogeography, Palaeoclimatology, Palaeoecology, 66, 243–263, 1988.

Queiroz, P.: Ecologia Histórica da Paisagem do Noroeste Alentejano, Phd thesis, Lisbon University, 1999.

R Development Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2012.

Ramsay, J. O., Wickham, H., Graves, S., and Hooker, G.: fda: Functional Data Analysis, 2012.

Rebelo, H., Tarroso, P., and Jones, G.: Predicted impact of climate change on European bats in relation to their biogeographic patterns, Global Change Biology, 16, 561–576, 2010.

Reille, M.: L'interface Tardiglaciaire–Holocène dans un site du littoral atlantique sud-européen: le Moura (Pyrénées Atlantiques, France), Comptes rendus de l'Académie des sciences. Série 3, Sciences de la vie, 316, 463–468, 1993.

Reille, M. and Andrieu, V.: The late Pleistocene and Holocene in the Lourdes Basin, western Pyrenees, France: new pollen : analytical and chronological data., Vegetation History and Archaeobotany, 4, 1–21, 1995.

Renssen, H. and Isarin, R. F. B.: The two major warming phases of the last deglaciation at 14.7 and 11.5 ka cal BP in Europe: climate reconstructions and AGCM experiments, Global and Planetary Change, 30, 117–153, 2001.

Roucoux, K., Abreu, L. D., Shackleton, N. J., and Tzedakis, P. C.: The response of NW Iberian vegetation to North Atlantic climate oscillations during the last 65kyr, Quaternary Science Reviews, 24, 1637–1653, 2005.

Sánchez-Goñi, M. F. and Hannon, G. E.: High-altitude vegetational pattern on the Iberian Mountain Chain (north-central Spain) during the Holocene, The Holocene, 9, 39–57, 1999.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J., and Svenning, J.-C.: The influence of Late Quaternary climate-change velocity on species endemism, Science, 334, 660–664, 2011.

Santos, L. and Sánchez-Goñi, M. F.: Lateglacial and Holocene environmental changes in Portuguese coastal lagoons 3: vegetation history of the Santo André coastal area, The Holocene, 13, 459–464, 2003.

Seppä, H. and Birks, H.: July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian treeline area: pollen-based climate reconstructions, The Holocene, 11, 527–539, 2001.

Sinervo, B., Méndez-de-la Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Cruz, M. V.-S., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., la Riva, I. J. D., Sepulveda, P. V., Rocha, C. F. D., Ibargüengoytía, N., Puntriano, C. A., Massot, M., Lepetz, V., Oksanen, T. A., Chapple, D. G., Bauer, A. M., Branch, W. R., Clobert, J., and Jr., J. W. S.: Erosion of lizard diversity by climate change and altered thermal niches., Science, 328, 894–9, 2010.

Sykes, M. T., Prentice, I. C., and Cramer, W.: A Bioclimatic Model for the Potential Distributions of North European Tree Species Under Present and Future Climates Published by : Blackwell Publishing Stable URL : http://www.jstor.org/stable/2845812, Journal of Biogeography, 23, 203–233, 1996.

Taberlet, P. and Cheddadi, R.: Quaternary refugia and persistence of biodiversity., Science, 297, 2009–10, 2002.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainer, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, l. L., and Williams, S. E.: Extinction risk from climate change, Nature, 427, 145–148, 2004.

Tzedakis, P. C., Lawson, I. T., Frogley, M. R., Hewitt, G. M., and Preece, R. C.: Buffered tree population changes in a quaternary refugium: evolutionary implications., Science, 297, 2044–7, 2002.

Van der Wiel, A. M. and Wijmstra, T. A.: Palynology of the lower part (78-120 m) of the core Tenaghi Philippon II, Middle Pleistocene of Macedonia, Greece, Review of Palaeobotany and Palynology, 52, 73–88, 1987a.

Van der Wiel, A. M. and Wijmstra, T. A.: Palynology of the 112.8-197.8 m interval of the core Tenaghi Philippon III, middle Pleistocene of Macedonia, Review of Palaeobotany and Palynology, 52, 89–108, 1987b.

von Grafenstein, U., Erlenkeuser, H., Brauer, A., Jouzel, J., Johnsen, S. J., and von Grafenstein, U.: A Mid-European Decadal Isotope-Climate Record from 15 , 500 to 5000 Years B .P., Science, 1654, 1654–1657, 2012.

Webb, R. S., Anderson, K. H., Webb, T., and Others: Pollen response-surface estimates of late-Quaternary changes in the moisture balance of the northeastern United States, Quaternary Research, 40, 213–227, 1993.

Weiss, S. and Ferrand, N., eds.: Phylogeography of Southern European Refugia, Springer, 2007.

Wijmstra, T.: Palynology of the first 30 m. of a 120m. deep section in northern Greece, Acta Botanica Neerlandica, 18, 511–527, 1969.

Wijmstra, T. A. and Smith, A.: Palynology of the middle part (30–78 metres) of the 120 m deep section in northern Greece (Macedonia), Acta Botanica Neerlandica, 25, 297–312, 1976.

Willis, K. J., Bailey, R. M., Bhagwat, S. a., and Birks, H. J. B.: Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data., Trends in Ecology & Evolution, 25, 583–91, 2010.

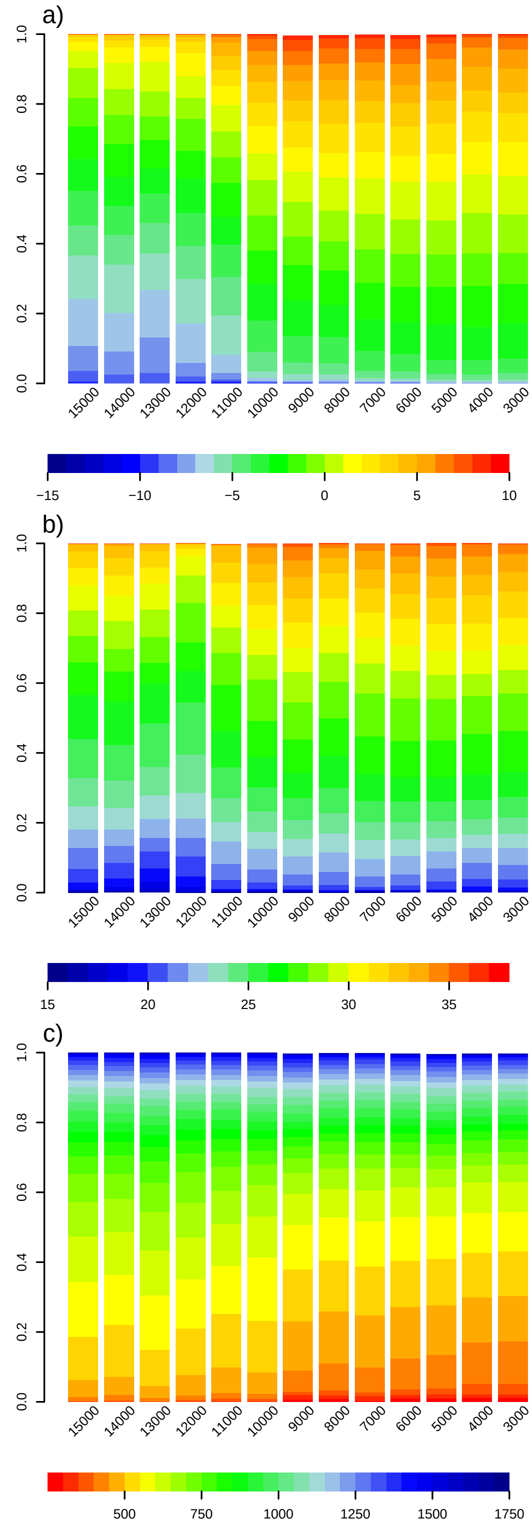

Figure 3. ~~Example of the influence~~ Distribution of ~~pollen abundance on~~ the ~~. The area of~~ reconstructed climate variables in the ~~PDF is filtered using~~ Iberian Peninsula and Balearic Islands in the ~~pollen thresholds related to~~ last 15 ka. Colours show the ~~proximity~~ proportion of area covered with each class of ~~core distribution centres: higher pollen percentages (~~a) ~~are assumed to originate near the distribution core and, thus, have higher densities and lower pollen percentages (~~minimum temperature of January; b) ~~are originated farther from the core and from optimum conditions. This results in different ranges~~ maximum temperature of ~~the variable that are related to the different densities~~July and c) annual precipitation.

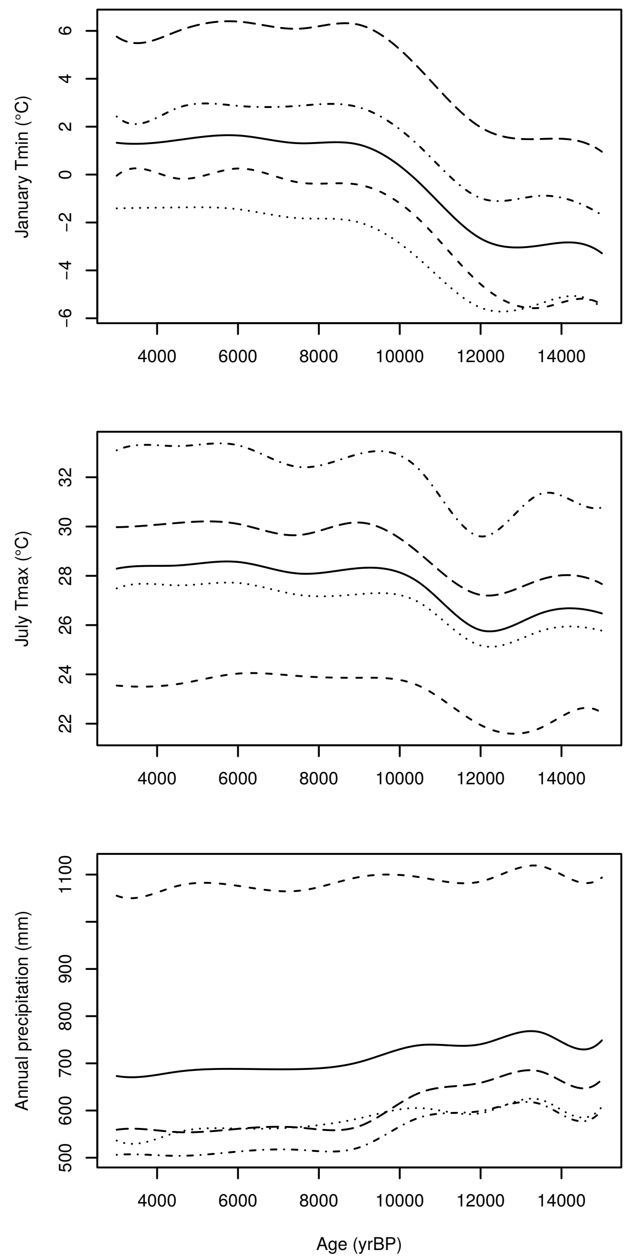

Figure 4. ~~Hierarchical cluster analysis of the functional PCA components~~ Minimum and maximum temperatures of ~~Tjan~~January and July, respectively, ~~Tjul~~ and ~~Pmin in~~ annual precipitation during the last ~~15ka found in the study area~~15 ka. The ~~top dendrogram~~ solid line represents the ~~size of the clusters of similar~~ average climate ~~evolution and~~ in the ~~relations between them~~study area. ~~Numbers correspond to~~ 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.

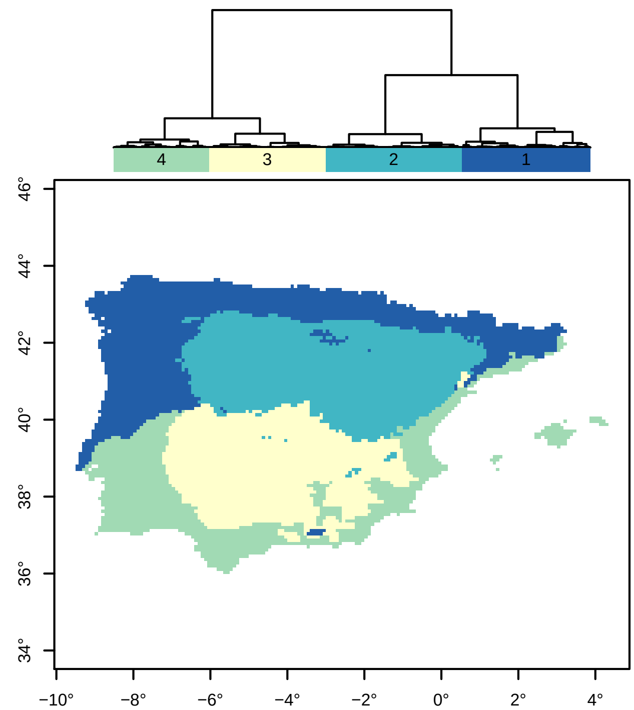

Figure 5. ~~Minimum and maximum temperatures~~ Hierarchical cluster analysis of ~~January and July, respectively~~the functional PCA components of Tjan, Tjul and ~~minimum annual precipitation during~~ Aprc in the last ~~15 ka. The solid line represents the average climate~~ 15ka found in the study area. The ~~remaining lines are~~ top dendrogram represents the ~~average~~ size of the clusters of similar climate evolution and the relations between them. Numbers correspond to each identified cluster~~found: C1: short dash line; C2: dotted line; C3: dash-dot line and C4: long dashed line~~.

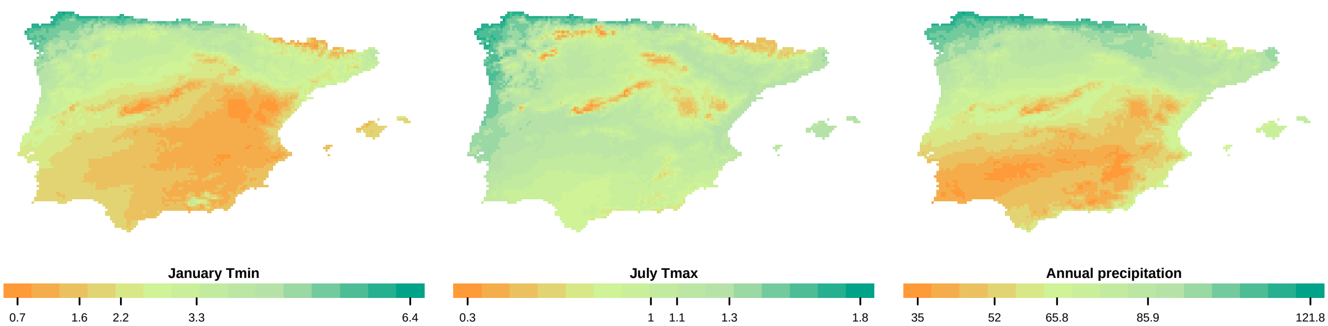

Figure 6. Average differences between millenia for each of the climate variables. Calculation of the differences are computed between a given age and the previous one. Isolines in each map indicate the average value of change.