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

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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 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 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 climate stability between millenia are coherent with the existence of multiple refugial areas in 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 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 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 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).

Species glacial refugia have been generally defined based on species survival with 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, 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. 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
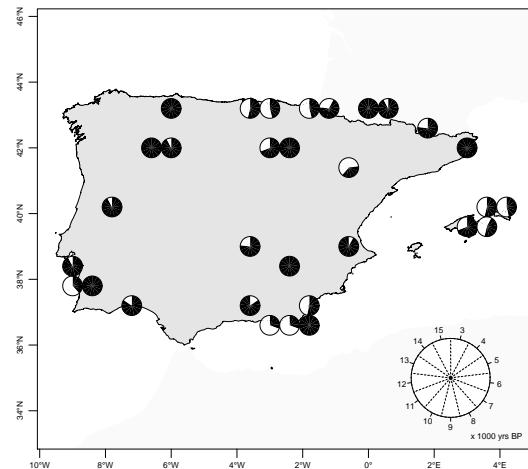

Figure 1. Study area with sample points. The black area inside each circle represents the ages available in each pollen sequence.

pattern (Weiss and Ferrand, 2007). All together it renders the Iberian Peninsula as 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.

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). 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 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; Fig. 1). For the recon-

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 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.

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

struction process we assume that modern distributions are in equilibrium with climate at the distribution scale covering the species range. Using taxa full distribution data is reducing the bias resulting from local changes and 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 botan-

ical 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 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) and values were aggregated by the mean value to the resolution of 30'. Precipitation was further processed to obtain the annual precipitation (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 was successfully used to reconstruct temper-

atures 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). 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 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 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.

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 multiple factors related to the physiology of the species (Hicks, 2006), with a differential pollen production among different species, but it also has a strong climatic component through the influence that climate has on distributions. We have used these data as the proportion of pollen found relative to the maximum pollen found. The minimum non-zero 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 avoids the bias of different pollen production by distinct taxa and thus allows quantifying the presence of a species relative to its maximum detection within each site.

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 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 de-
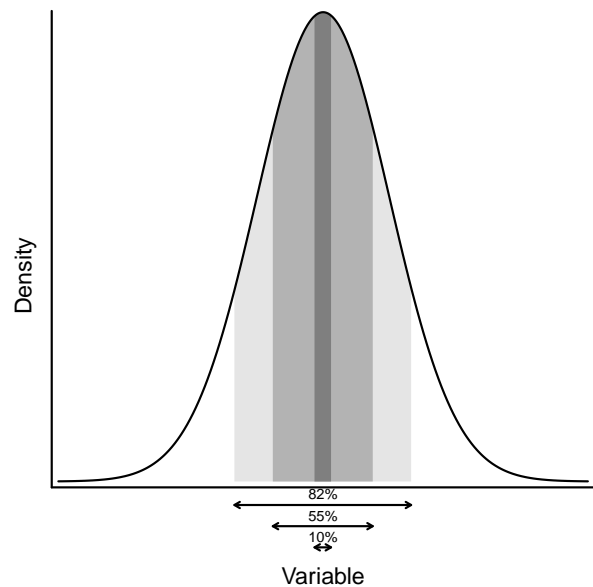

Figure 2. Example of the influence of pollen proportion (pp) on the calculation of the density of taxa presence intersection. The shades of gray indicate the effect of different pp when the pollen adjustment value (pa) is set to 0.9 and arrows indicate the assumed presence range. The first case (dark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

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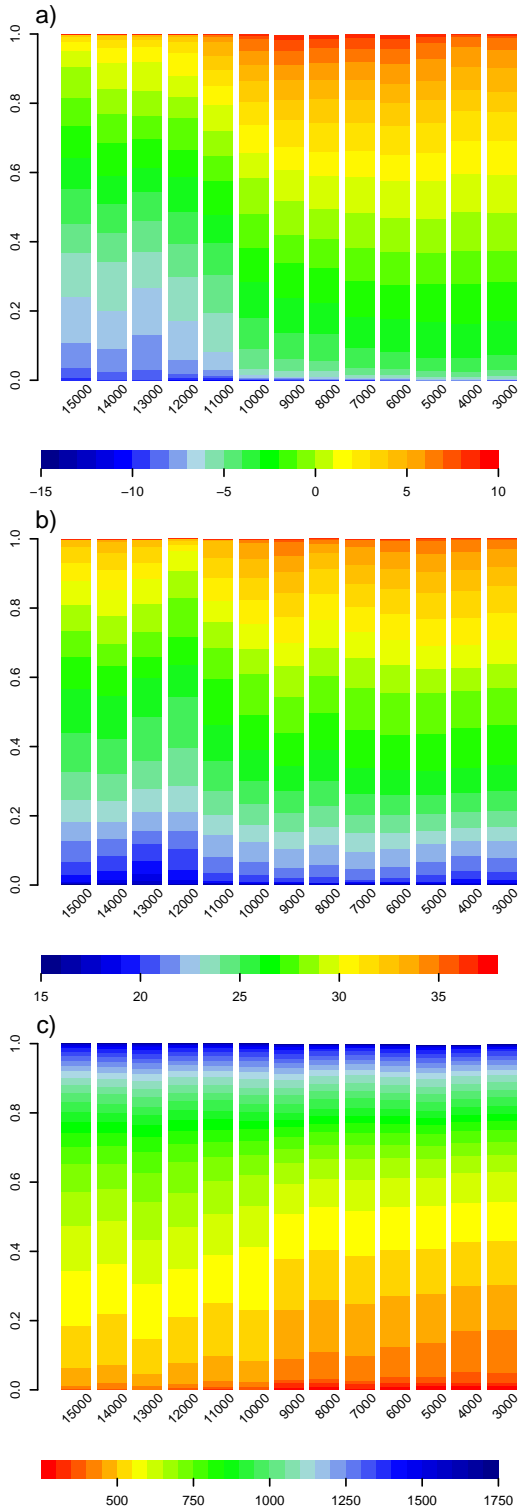
Figure 3. Distribution of the reconstructed climate variables in the Iberian Peninsula and Balearic Islands in the last 15 ka. Colours show the proportion of area covered with each class of a) minimum temperature of January; b) maximum temperature of July and c) annual precipitation.

riod around 100 BP (1850 AD) was used as reference climate to calculate anomalies. This period is often used as baseline in climate 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 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) 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. Climate stability was calculate for each variable 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). 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 ≤ 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, Appendix A, B). The uncertainty associated with the spatial interpolations is usually low, suggesting a good sampling coverage, with the exception of the north-west area (Appendix D). 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 stable, with lower values before 12 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 were spatial structured (Fig. 5), and allowed summarising the evolution of these three climate variables in the Iberian Peninsula (Fig. 4). The first component of each variable explained more than 95% of the variation (Tjan: 95.5%; Tjul: 99.2%; Aprc: 99.5%). The cluster C1 (27% of the total area) is located mostly on north and western Iberia and includes part of the north-Iberian mountain ranges (average altitude is 679±454m) but also low altitude coastal areas. This is the wettest cluster, with Aprc ranging from 1055 to 1115mm, the coldest in July (21.6 < Tjul < 24.1°C) and with very low January minimum temperatures (-5.6 < Tjan < 0.1°C). The cluster C2 encompasses part of the Cantabrian mountain range and the central Iberian system (29% of the total area with average altitude of 856±301m) and occupies most of the northern plateau. It has the lowest January temperature (-5.7 < Tjan < -1.3°C) but has warmer in July than C1 (25.1 < Tjul < 27.7 °C) showing high seasonal amplitude with very low precipitation (536 < Aprc < 621mm), similarly to C3 and C4. The dissimilarities between clusters C3 and C4 (24% and 20% of the total area and average altitude of 610±297 and 278±231, respectively) occur mainly in temperature, with C4 being generally warmer and wetter than the C3 cluster. These are the warmest areas in both January (C3: -1.7 < Tjan < 3.0°C; C4: 1.0 < Tjan < 6.4°C) and July (C3: 29.4 < Tjul < 33.4°C; C4: 27.2 < Tjul < 30.2°C) and with low annual precipitation (C3: 505 < Aprc < 615mm; C4: 555 < Aprc > 683mm). 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 the last 15ka was not spatially uniform (Fig. 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
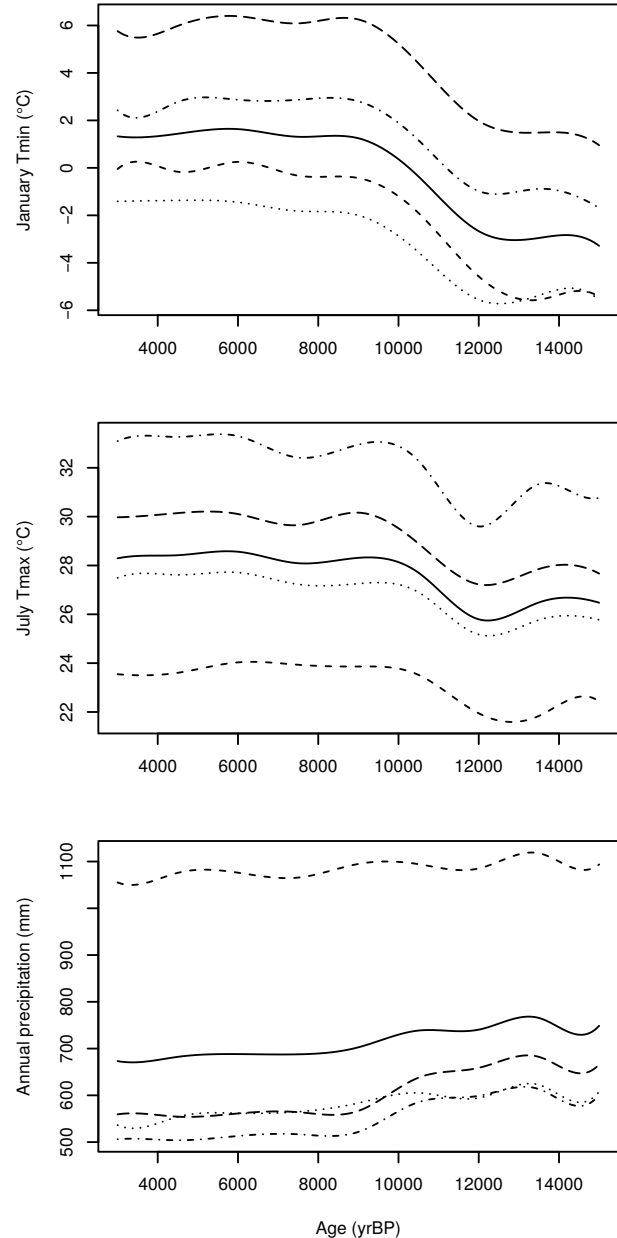

Figure 4. Minimum and maximum temperatures of January and July, respectively, and annual precipitation during the last 15 ka. The solid line represents the average climate in the study area. The remaining lines are the average of each cluster found: C1: short dash line; C2: dotted line; C3: dash-dot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

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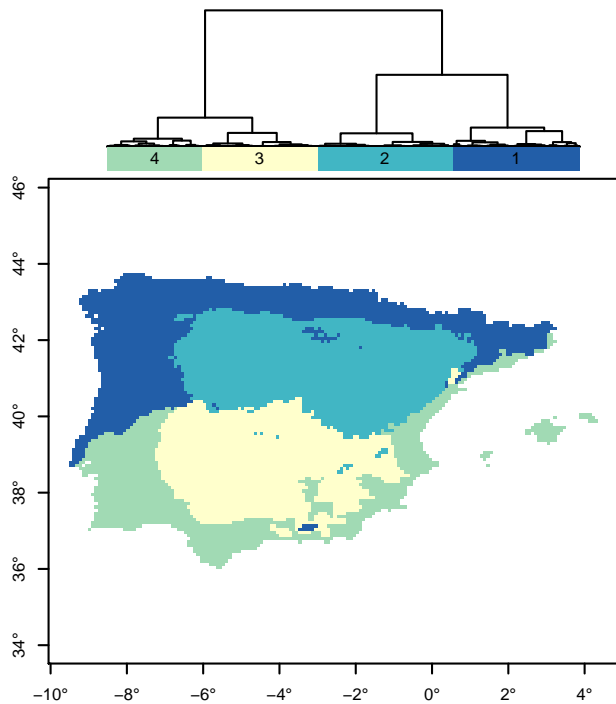
Figure 5. Hierarchical cluster analysis of the functional PCA components of Tjan, Tjul and Aprc in the last 15ka found in the study area. The top dendrogram represents the size of the clusters of similar climate evolution and the relations between them. Numbers correspond to each identified cluster.

scales (Bartlein et al., 2010). The 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. 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 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 recoloni-

sation processes during the post-glacial period. Nonetheless, the reconstructed overall trend is a noticeable warming in winter temperatures after the 15 ka (Fig. 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). An evident pattern that strikes from the results presented here is the division of the peninsula in spatially structured areas that shared similar climate evolution during the late-Quaternary (Fig. 5). The wettest and cold cluster C1 predominantly located at 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 ~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, where variations showed a smaller amplitude albeit this variable is markedly different between clusters, and thus contributing to the climate division of the study area (Fig. 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 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 undetectable. The OD (~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 to 12.9 ka). Our results show a similar pattern with colder conditions between 15 ka and 13 ka, followed by a warming trend after 13 ka (Fig. 4). All clusters show these warming trens, although clusters C1 and C2 are colder. This is reflected in a contrasted Iberian peninsula dominated by extreme January temperatures (Fig. 3, Appendix B,C). The evolution of precipitation during the last 15 ka in the Iberian Peninsula has a very stable pattern: northern areas comprised in C1 had high precipitation values during the whole studied time, but the south was wetter than today (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
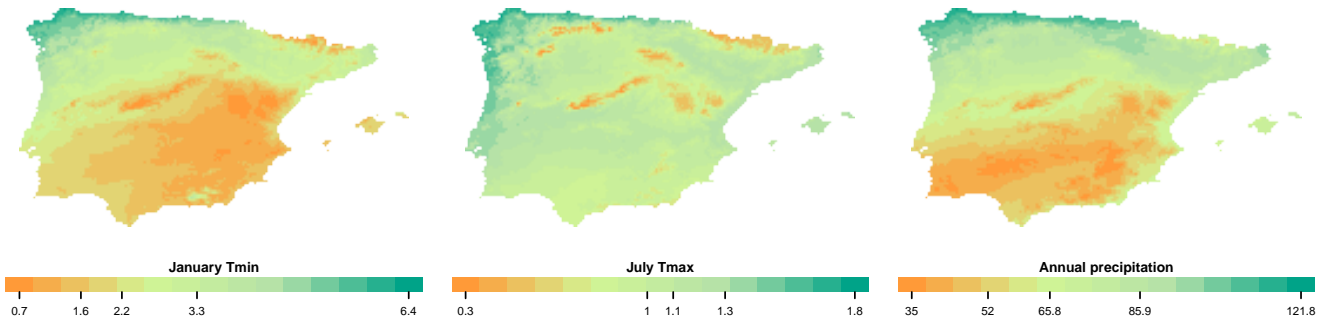
Figure 6. Average differences between millenia for each of the climate variables. Calculation of the differences are computed between a given age and the previous one. Isolines in each map indicate the average value of change.

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).

4.2   The Holocene

The BA is followed by the cold YD (~12.9 to 11.6 ka), marking the beginning of the Holocene. 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 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 in Northern Europe and the Alps and simultaneous with a 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 a slightly wetter climate between at 7 ka (Fig. 3) which confirms what was previously known 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 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 high precipitation values in the north (Fig. 4, Appendix B, C), contributing to the final pattern of a a temperate north and a southern mediterranean climate in Iberia.

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 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. 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 Aprc (Fig. 6). The 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 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 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 rapid T_{jul} oscillations associated with a cold T_{jan} 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 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. Liking past climate and diversity on the Iberian peninsula 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.

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