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Spatial climate dynamics in the Iberian Peninsula since 15000 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

- ⁵ 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 15 and 3 ka. A functional principal component analysis was
- ¹⁰ used in order to summarise the spatial evolution of climate. Using a clustering method we have identified areas that share similar climate evolutions 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 between millonia are apparent with the existence of multiple refugial areas in the Iberian Penin
- ¹⁵ millenia are coherent with the existence of multiple refugial areas in the Iberian Peninsula.

1 Introduction

The pattern of present biodiversity is the result of a dynamic process driven at a broad temporal scale by geological events and climatic oscillations (Hewitt, 2000). This rela-

tion between climate and biodiversity is likely to be maintained in the future with alarming consequences for species resulting from current climate warming trend. The largest implications are 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 invaluable knowledge for the current species conservation effort dealing with the global climate change predicted for the following decades (Anderson et al., 2006; Willis

¹⁰ global climate change predicted for the following decades (Anderson et al., 2006; W et al., 2010).

Refugia have been generally defined based on species survival with an evident relationship to climatic components (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; Asheroft, 2010). The

- ¹⁵ 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 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; Ched-
- ²⁰ dadi et al., 2006). 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 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;

- ⁵ 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 Constant).
- 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
- ¹⁵ 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 renders the Iberian Peninsula as a unique area
- ²⁰ 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

25 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 15 000 and 3000 years BP (Table 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

¹⁵ misinterpretations. Despite the anthropogenic influence on the pollen abundances, we assume that modern distributions are in equilibrium with climate at large scales covering the species range. Using taxa distribution data is, thus, reducing the bias resulting from local changes and supports our assumption. The different sensibility of taxa to the various sources of disturbance is balanced by the use of the multiple taxa identified in
 ²⁰ each core.

2.1 Data sources

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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 1 February 2011). 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 km). The global historic climate data (1950–2000) for January minimum temperature (T_{jan}), July maximum temperature (T_{jul}) and monthly precipitation data were obtained from Worldclim

⁵ database (Hijmans et al., 2005, www.worldclim.org) with 5' resolution (10 km) and values were aggregated by the mean value to the resolution of 30'. Precipitation was further processed to obtain the minimum annual precipitation (P_{min}) 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

¹⁰ 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 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 ¹⁵ 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 percent-

ages. A univariate kernel estimator was used to build the single dimension PDF from the modern plant distributions and the T_{jan} , T_{jul} and P_{min} 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 distribu-

tion of species with non-normal distributions.

Fluctuations in pollen abundances are related to several factors including the physiology of the species (Hicks, 2006), but have also a strong climatic component through the influence that climate has on land cover. We used the pollen percentage as a mea-

²⁵ sure of the taxon proportion throughout the time span of the core. Thus, the minimum non-zero pollen percentage 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 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.

- The PDF is filtered using the pollen proportion as a threshold. We assume that higher ⁵ pollen proportions reveal near optimum conditions for the taxon that correspond to 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 10 the PDF around highest densities at maximum pollen detection. A threshold of 0.5, for
- example, would constrain the PDF 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 value found that allowed the intersection of
- all taxa present in a sample (Table 1). 15

The reconstructed climate value 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 20 climate value 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 for each climate value. The union of the PDFs of each taxon present is less sensitive to the climate affinity of the taxa present than
- to the intersection. For example, when more warm dependent taxa are available due 25 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

⁵ 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.

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.

10 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 reso-

- ¹⁵ lution) from the reconstructed one for each time slice and each site. Anomaly values were projected into a 30' resolution grid and interpolated onto a 5' resolution grid using thin-plate smoothing splines. 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.

A surrogate for climate stability was defined as the average difference between millenia for each variable. The differences were calculated for the period reconstructed (15 to 3 ka) between a given age and its previous one.

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).

3 Results

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The reconstruction of three climate variables exhibited high spatial variability over the period between 15 and 3 ka (Figs. 3 and S1). 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) The Iberian Peninsula had extensive areas with extremely low T_{jan} that gradually increased to higher values, and markedly after 10 ka. Conversely, the pattern of T_{jul} over the same time span remained quite 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.

²⁰ Between 15 and 7 ka the areas with increasing values of P_{min} have expanded, with the exception between 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 P_{min} than the early Holocene. The clustering of the first fPCA component of the three reconstructed variables iden-

tified areas with congruent spatial structure (Fig. 4), and allowed summarising the evolution of these three climate variables in the Iberian Peninsula (Figs. 5 and S3). The first two components of each variable explained more than 89% of the variation (T_{ian} :



77.0%, 12.3%; *T*_{iul}: 91.7%, 6.7%; *P*_{min}: 90.3%, 5.5%, for the first and second components, respectively). The cluster C1 (15% of the total area) is located mostly on north and eastern Iberia and includes the Iberian mountain ranges (average altitude is 1082 ± 395 m) but also low altitude areas. It is the coldest area in the late-Quaternary, s with T_{ian} from -11.4 °C to -3.9 °C, T_{iul} ranging between 21.1 °C and 22.1 °C and the wettest with P_{min} between 31.5 mm and 37.4 mm. The cluster C2 (21 % of the total area with average altitude of 470 ± 218 m) occupies most of the southern Iberian Plateau. It holds the warmest values for T_{ian} varying between -5.4 °C and 2.0 °C and T_{iul} between 26.1 °C and 28.9 °C. The temperature dissimilarities between clusters C3 and C4 (29 % and 35 % of the total area and average altitude of, 472 ± 383 and 657 ± 304 , respectively) occur mainly in T_{ian} , having the former higher temperatures (-4.3 to -0.1 °C) than the latter (-6.5 to -0.9 °C). However, P_{min} shows a major difference between these two clusters, which indicates that C3 is generally wetter (26.2-29.4 mm) than C4 (19.4–25.2 mm), which represents the driest areas in the late-Quaternary. Most of the area of the Balearic Islands is within cluster C4, except the mountain range in 15 northern Maiorca (Fig. 4).

The average differences between millenia (Fig. 6) have higher values for T_{jan} and P_{min} , whereas T_{jul} 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 T_{jan} change between millenia and P_{min} exhibits a similar pattern.

4 Discussion

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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 the low number of sequences available according to our quality criteria for spatial climate reconstruction, both in terms of sampling resolution and number of ¹⁴C



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 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 of the peninsula. Given the link between climate and species distributions (Hewitt, 2000), it is likely that these because had an impact on the location, extent and evolution of the refusio and the re-

- ¹⁰ 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) 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
- ¹⁵ 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 coherent areas that shared similar climate evolution during the late-Quaternary (Fig. 4). The coldest and wettest cluster C1 predominantly located at high altitudes and with smooth climate changes, contrasts with the warmest and lowed bits of the start of
- ²⁰ 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.

Our results show that January temperatures exhibited a general warming trend during the studied period which corresponds in average to an increase of 5 °C. The center of the Iberian Peninsula holds most of the change between millenia and the coastal areas offers more resilience to the change. This pattern is less obvious in July temperatures or precipitation, where variations showed a smaller amplitude albeit these variables are markedly different between clusters, and thus contributing to the climate



division of the study area (Figs. 5 and S1). 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 5 non-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. The OD (18 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, especially for cluster C2, with colder conditions between 15 and 14 ka, followed by a warming trend until 13 ka (Fig. 5). Cluster C1, on the other hand, shows
a decreasing temperature trend until 13 ka. This is reflected in a contrasted Iberian Peninsula dominated by extreme January temperatures (Figs. 3 and S1).

The evolution of precipitation during the last 15 ka in the Iberian Peninsula has a constant pattern: northern areas were generally dryer while the south was wetter than today (Fig. S1). Precipitation values are low between 15 and 14 ka except in the moun-

tainous areas comprised mostly in the first cluster, which remain more humid than the other areas (Figs. 3 and 5). Nevertheless, the average trend is a decrease of precipitation until 12 ka.

As described earlier in Europe (Renssen and Isarin, 2001; Heiri et al., 2004), T_{jan} shows wider changes in amplitude than T_{jul} . The cold to warm transitions that occurred

²⁵ at 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 T_{jan} (Figs. 3 and S1). The increasing variability of T_{jan} after 14 ka is related to the expansion of trees from glacial refugia which have modified the albedo (Cheddadi and Bar-Hen, 2009).



4.2 The Holocene

The BA is followed by the cold YD (12.9 to 11.6 ka), marking the beginning of the Holocene. We observe a reduction of the warmer areas at 13 and 11 and an expansion of the aridity (Figs. 3 and 5). However, the area covered by the coldest cluster

⁵ 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 T_{jan} showing a fast increase until 9 ka, and T_{jul} remaining stable in most Iberia, with the exception of cluster C2 where a decrease of 2 °C was observed. Davis et al. (2003), showed a similar Summer and Winter amplitude of changes for South-western Europe.

The Holocene warm period (approximately between 8.2 and 5.6 ka, depending on where 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

- ¹⁵ 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. Concerning the precipitation, there is evidence of a wetter climate between 9 and 6 ka which confirms what was previously known for the southern European lowlands (Cheddadi et al., 1997).
- Between 6 and 5 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 precipitation increase in the north (Fig. S1), contributing to the final pattern of a slight increase in precipitation values.
- ²⁵ The behaviour of the reconstructed variables after 5 ka 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 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) depicting areas with different
¹⁵ 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 charac-
- terised by a stable climate evolution during the late-Quaternary with smaller amplitudes of change (clusters C3 and C4). The cluster C3 coincides at a great extent with areas that offered more resilience to change between millenia (Fig. 6). Within these areas, temperature and precipitations were suitable to support the survival of temperate trees,



likely acting as refugia. On the other hand, the cold areas of the first cluster and the fast changes of the second 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 cluster (Fig. 4) 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 minimum January temperature evolved with a lower amplitude (4 °C) and was less sensitive to extreme fluctuations than the other clusters, with climate gradually evolving to
- ¹⁰ current pattern, which is compatible with the persistence of species in these areas. The southern plateau, mostly comprised in the second cluster (Fig. 4), recorded also mild conditions which are often associated with southern refugia but a rapid feedback to late-Quaternary events may have prevented persistence or recolonisation processes.

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 on the Iberian Peninsula has an increased interest for conservation issues, especially under the expected future climate change.

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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 (T_{jan}), maximum July temperature (T_{jul}) and minimum annual precipitation (P_{min}) for each site are shown.

Name	Source	Latitude	Longitude	T _{jan}	$T_{\rm jul}$	P_{\min}
Albufera Alcudia	EPD	39.793	3.119	0.45	0.27	0.11
Algendar	EPD	39.941	3.959	0.31	0.31	0.14
Antas	EPD	37.208	-1.824	0.5	0.39	0.18
Banyoles	EPD	42.133	2.75	0.31	0.42	0.79
Barbaroxa	Queiroz (1999)	38.071	-8.809	0.42	0.09	0.11
Cala Galdana	EPD	39.937	3.965	0.21	0.13	0.13
Cala n' Porter	EPD	39.871	4.131	0.44	0.26	0.12
CC-17	Dorado Valiño et al. (2002)	39.08	-3.87	0.46	0.37	0.11
Charco da Candieira	EPD	40.342	-7.576	0.56	0.36	0.16
Gádor	Carrión et al. (2003)	36.9	-2.917	0.32	0.23	0.08
Golfo	Queiroz (1999)	38.561	-9.135	0.28	0.15	0.12
Guadiana	Fletcher et al. (2007)	37.267	-7.45	0.46	0.21	0.12
Hoya del Castilho	EPD	41.25	-0.5	0.51	0.26	0.23
Lago de Ajo	EPD	43.05	-6.15	0.71	0.45	0.48
Laguna de la Roya	EPD	42.217	-6.767	0.54	0.38	0.27
Lake Racou	EPD	42.554	2.008	0.36	0.33	0.14
Las Pardillas Lake	Sánchez-Goñi and Hannon (1999)	42.03	3.03	0.57	0.37	0.11
Lourdes	Reille and Andrieu (1995)	43.033	-0.075	0.73	0.45	0.45
Monge	Reille and Andrieu (1995)	43.05	-0.017	0.65	0.41	0.62
Moura	Reille (1993)	43.45	-1.55	0.44	0.28	0.12
Navarrés	EPD	39.1	-0.683	0.66	0.4	0.11
Padul	Pons and Reille (1988)	37	-3.667	0.52	0.36	0.17
Puerto de Belate	EPD	43.033	-2.05	0.55	0.31	0.11
Puerto de Los Tornos	EPD	43.15	-3.433	0.59	0.33	0.13
Quintanar de la Sierra	EPD	42.033	-3.017	0.55	0.31	0.12
Roquetas de Mar	EPD	36.794	-2.589	0.55	0.35	0.12
Saldropo	EPD	43.05	-2.717	0.24	0.31	0.14
San Rafael	EPD	36.773	-2.601	0.59	0.43	0.13
Sanabria Marsh	EPD	42.1	-6.733	0.62	0.43	0.76
Santo André	Santos and Sánchez-Goñi (2003)	38.08	-8.78	0.56	0.33	0.12
Siles	Carrión (2002)	38.4	-2.5	0.49	0.27	0.12



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Figure 2. Example of the influence of pollen abundance on the. The area of the PDF is filtered using the pollen thresholds related to the proximity 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 (b) are originated farther from the core and from optimum conditions. This results in different ranges of the variable that are related to the different densities.







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)** minimum annual precipitation.



Figure 4. Hierarchical cluster analysis of the functional PCA components of T_{jan} , T_{jul} and P_{min} in the last 15 ka 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 the cluster.





Figure 5. Minimum and maximum temperatures of January and July, respectively, and minimum 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.





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.

