Late Quaternary developments of Mediterranean oaks in the Atlantic domain of the Iberian Peninsula: The case of the Cantabrian region (N Spain)

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A R T I C L E  I N F O

Article history:
Received 10 February 2016
Received in revised form 19 October 2016
Accepted 21 October 2016

Keywords:
Evergreen oaks
Palaeoecology
Historical biogeography
Pleistocene
Holocene
SW Europe

A B S T R A C T

A synthesis of the occurrence of the evergreen oak (Quercus ilex-type) in the Cantabrian region (northern Spain) is presented on the basis of integrated charcoal and pollen analyses. Archaeological charcoal comes largely from sites along the littoral and pre-littoral territories of the Basque Country, Cantabria and Asturias dated from 45 to 3.7 Kyr cal BP, and culturally ranging from Mousterian to Iron Age. Pollen information is produced from a few archaeological sites but mainly from peats and lake sediments. Q. ilex-type is observed as early as at 45–30 Kyr cal BP, with sporadic occurrences in vegetation contexts dominated by Pinus sylvestris-type, which was widely exploited by Mousterian and Aurignacian inhabitants. Afterwards, during the Upper Palaeolithic, there is an important decline, and Q. ilex-type is hardly present between 29 and 15 Kyr cal BP, with open environments dominated by heathland shrubs. From Late Magdalenian onwards, Q. ilex-type expanded again, remaining in the landscape of the Cantabrian region throughout the Holocene, although subordinated in deciduous oak forests under the influence of oceanic climate conditions. Q. ilex-type had a more favourable position than deciduous Quercus across the Cantabrian southern slopes and northwest of the adjacent Iberian Cordillera, where oceanic influences have become attenuated by summer drought and continentality.

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1. Introduction

The presence of Quercus ilex-type (Qi) in the Cantabrian region of northern Spain has traditionally been the focus of biogeographical discussion by both botanists and plant ecologists (e.g. Allorge, 1941a, b; Bertrand, 1974; Montserrat and Monserrat, 1987, 1988; Meaza and Cuesta, 2010). For instance it was considered as a reliclacial formation from past climates (Allorge, 1941a, b; Bertrand, 1974) in line with the approach of most botanists (e.g. Rivas-Martínez, 1982, 1987; Cendrero et al., 1986; Asegünolaza et al., 1989; Aedo et al., 1990; Varas et al., 2006). However other authors (e.g. Montserrat and Monserrat, 1987, 1988; Lozano et al., 2002; Meaza, 1988; Meaza and Cuesta, 2010) suggested instead a more recent origin connected to human influence on the vegetal landscape.

According to palaeobotanical evidence from Western Europe (e.g. Pons and Vernet, 1971; Andrés and Llamas, 1988; Denk et al., 2012; Hubert et al., 2014), Qi sprouted up in southern Europe at the Cenozoic where it grew in drier and temperate climates. From the Quaternary, it became increasingly adapted to the colder climates generated by the successive glaciations as observed in several warm and colder periods of the basal Pleistocene in France (Pons and Vernet, 1971). In the Middle Pleistocene, Qi could be traced to the French Basque Country coastal areas, coinciding with the Holsteinian interglacial (Oldfield, 1968; Oldfield and Huckerby, 1979). Going westwards by the Cantabrian shoreline, Qi was associated to both the glacial and interglacial stages of the Upper Pleistocene in eastern Asturias -La Franca (Eemian) (Mary et al., 1975)- and Galicia -Area Longa (MIS 5c, MIS 4, MIS 3) (Gómez-Orellana et al., 2007). According to the marine cores of the NW Iberian margin, this taxon was recorded at different marine isotope stages since the MIS 11 (Desprat et al., 2009; Naughton et al., 2007; Sánchez-Goni et al., 2008). During the Late Glacial and particularly the Holocene, its presence was frequent in pollen deposits from N
Spain (Carrión et al., 2012). The Holocene record of Qi in western France was also significant in Boreal deposits at the Bourdeaux and Normandy regions (Pons and Vernet, 1971).

The hypothesis of a northward migration through corridors with favourable climatic conditions (Xerothermic period) was proposed to explain the delayed entrance of evergreen oak woods in the Basque shoreline (Vizcaya) and Pre-Pyrenees via the Nervión and Ebro valleys respectively (Montserrat and Monserrat, 1987, 1988). However no definite evidence is available to support this hypothesis yet (Meaza and Cuesta, 2010). On one side there are authors who suggested that Qi would have existed in the region before the post-glacial warming (Pons and Vernet, 1971) as a result of successive migrations waves related to glacial-interglacial alternations of the Pleistocene (Allorge, 1941a,b); they are those who even regarded the local evergreen oak as a relict of the laurisylve, a remain of the pre-Quaternary palaeoenvironment (Bertrand, 1974) as the current distribution of the sub-tropical fern Osmunda regalis would support (Mayor and Díaz, 1977; Varas et al., 2006). However no palaeobotanical data have been recovered so far to confirm a Cenozoic date for Qi in N Spain. On the other side are those who postulated a more recent development with human influence as the only cause for its Holocene extension. Thus, the increasing human pressure in areas with well-developed soils favoured evergreen oak woods which gradually replaced deciduous trees (Zapata and Meaza, 1998; Lozano et al., 2002; Meaza and Cuesta, 2010).

Both pollen and charcoal studies, supported by a set of radiometric data, have proved useful to identify vegetation changes – or even the development of an individual taxonomic history-, shedding light on the hypotheses proposed by neontological studies. Accordingly, the origin and presence of Qi and other sclerophyllous plants in N Spain were previously discussed in terms of palynology (~P. Uzquiano et al., 2012) and archaeobotany (Zapata and Meaza, 1998; Uzquiano and Zapata, 1992, 1995; Zapata et al., 2002). The complete pollen record for Qi in N Spain (Table 1; Fig. 2a) covers geographically from the coastal area of the French Basque Country to Galicia, including all the geographical areas in the Cantabrian region: littoral, pre-littoral valleys and the northern most mountain inner basins. To the south, it extends towards the southern slopes of the Cantabrian Mountains, the western-central Pyrenees and the North Iberian Mountain range.

Pollen sites considered for this work (Table 2), are mostly located in the Cantabrian region in dominant oceanic climate conditions (Fig. 2a, sites marked with *, with the exception of the Atapuerca site of El Portalón (AtP) and QS-2 pollen records geographically located in the Mediterranean sector, where oceanic influences were attenuated by continental and sub-Mediterranean types (López-García et al., 2010; Martínez-Pillado et al., 2014; Ruiz-Zapata et al., 2002a). The record considered chronologically extends from MIS 3 to the late Holocene.

The archaeobotanical information (i.e. charcoal analysis) integrated in our thorough study (Table 3) is geographically limited to coastal areas and pre-littoral valleys of the Cantabrian region with prevailing oceanic climatic conditions (Fig. 2b). Similarly to the palynological sample, it chronologically spans from the Upper Pleistocene (MIS 3) to the mid-late Holocene, covering Mousterian, virtually all Upper Palaeolithic, the Mesolithic, Neolithic, Chalcolithic, Bronze and Iron Age cultures.

2.2. Current distribution of evergreen oak woods in N Spain

Qi grows along the Mediterranean Basin as far as properly Mediterranean climate is dominant (Ozenda, 1994). Indeed, it is the most widespread tree in the Iberian Peninsula throughout the Meso-Mediterranean belt (400—800 masl) reaching up to 2000 masl in Sierra Nevada, southern Spain (Blanco et al., 1997; Villar et al., 2012) (Fig. 1).

However in N Spain (Eurosiberian region), Qi populations are mainly restricted to calcareous substrates, edaphically drier than the average for this region characterised by heavy rainfall (Fig. 1). Qi grows in outcrops of the littoral and pre-littoral karstic massifs, parallel to shoreline, with poorly developed soils, low water-holding capacity and steep slopes (Aseguinolaza et al., 1989; Meaza, 1998). The east-west orientation of the Cantabrian mountain range, joining the littoral with transitional areas between both
sides of the Cantabrian watershed, prevents the entrance of both western wet winds and heavy rainfalls (Cendrero et al., 1986; Díaz-González and Fernández Prieto, 1994). A gradual, rainfall decline leads to a more open and clearer atmosphere that facilitates the development of Cantabrian evergreen oak woods in inner valleys and gorges of large limestone hillocks. Here, trees grow up sheltered by the sunny slope areas such as the Pre-littoral Depression in eastern Asturias, La Hermida gorge and Liebana region in western Cantabria or the Asón valley in eastern Cantabria (Fig. 1). Altitude ranges between 0 and 600–800 masl, extending throughout the Collinear and the lower part of the Montane bioclimatic belts in the southernmost areas of Basque Country and Cantabria (Varas et al., 2006).

Cantabrian evergreen oak woods appear throughout the homonymous territory as discontinuous patches (islands) of dense and close dark green vegetation which contrast with the lighter green shade of deciduous plant communities. Qi is integrated in an ensemble of evergreen shrubs together with a nearby large variety of thorny deciduous shrubs (see Aseguinolaza et al., 1989; Aedo et al., 1990).

Evergreen oak woods have been exploited from historical times to provide rural habitat with wood and firewood, and produce charcoal to supply the many forges and ironworks (Zapata and Meaza, 1998). Furthermore, fruit collection for both human and animal consumption, winter grazing, hunting activities and continuous limestone extraction contributed to the progressive degradation and disappearance of many patches of evergreen oak woods, remaining only on the steeper and most inaccessible places (Meaza and Cuesta, 2010). In coastal areas, Qi was replaced by shrubs communities dominated by Arbutus unedo and Laurus nobilis (Bertrand, 1974; Meaza, 1998; Aedo et al., 1990). Finally, the best preserved holm oak formations are located in Biosphere Reserves (Fig. 1).

3. Material and methods

3.1. Pollen and charcoal

The pollen and charcoal information has been obtained from previous works (see references in Tables 2 and 3) in which their respective methods of sampling and analysis were clearly described. However, some issues should be noted. Although it is not possible to discern modern and fossil members of Quercus group ilex from Europe and East Asia, in particular regarding Quercus ilex and Q. coccifera, by means of pollen morphology (Denk and Grimm, 2009; Denk and Tekleva, 2014), pollen and charcoal analyses assigned generally Quercus ilex-type (or Q. evergreen-type) in most of pollen and charcoal studies of Iberia. This group includes both Quercus ilex subsp. ilex—which grows on the coast and in the Atlantic valleys of the Eurosiberian region- and Quercus ilex subsp. ballota (Quercus rotundifolia), with an innermost location in areas with prevailing continental to sub-Mediterranean climatic conditions. However, these two subspecies of evergreen oak can be only identified on the basis of leaves and acorns.

Pollen and charcoal of Q. coccifera cannot be distinguished from Q. ilex at light microscopy, although its presence could be assumed if this taxon ranks among the current vegetation of the area of study considered (e.g. the Mediterranean floristic domain of Iberia). Most of the sites considered in this review are all located in the Eurosiberian region (Fig. 2a and b; Table 2) devoid of any current evidence of this taxon, so that Quercus identifications would rather correspond to Quercus ilex-type. Nevertheless scattered stands of Q. coccifera grow up in some southern areas of Cantabria (Aedo et al., 1990) already located in the transitional area of Continental to Mediterranean climates. In this case the nomenclature Quercus ilex-coccifera has been employed in charcoal assemblages from archaeological sites located in the aforementioned transitional areas such as El Mirón and El Mirador caves (Zapata, 2012; Euba et al., 2015).

Quercus suber is also present in the vegetation of the area of study (Cendrero et al., 1986; Aseguinolaza et al., 1989). Although both pollen (see Carrión et al., 2012) and charcoal records (Uzquiano, 1992 and unpublished data) of this area have provided indication of Q. suber, it has not been taken into account within the framework of this study, because the record is very erratic.

Pollen sites (Fig. 2a) are mostly peatbogs and lake cores, although a few archaeological sites also yielded Qi pollen information. From the whole pollen record (Table 1; Fig. 2a), only 9 of the sites were studied by two of us (Table 2) and selected to draw synthetic pollen curves of Quercus which considered the
relationship between deciduous and evergreen oaks throughout the Cantabrian region. Taking into account the geographical position of the Iberian Peninsula at the limit of two floristic domains, additional pollen data from southern slopes of the Cantabrian mountain range and the NW sector of the Iberian mountains also studied by two of us, have been also included to compare the evolution of Qi both in the Eurosiberian and Mediterranean regions. In turn, both curves were correlated with the evolution of arboreal pollen (AP) in order to assess the representation of both types of Quercus in the tree cover assemblage (Fig. 3).

Most of the charcoal database here presented (Fig. 2b; Table 3) was studied by one of us. It facilitated the elaboration of a synthetic diagram where Qi was diachronically displayed throughout all the Cantabrian Region, together with deciduous Quercus and other selected key taxa (Fig. 4).

Additionally the most representative evergreen oak pollen curves from W to E and from littoral to innermost territories throughout N Spain (see Table 1, sites in italics) were also incorporated to complement the pollen record here presented. Likewise, the most representative deciduous and evergreen charcoal records presented here have been selected due to its E-W position and to its littoral and pre-littoral location throughout Asturias, Cantabrian and Basque Country. Two additional charcoal sites not studied by us have been also incorporated (see Table 2) to complete the N-S gradient from the Cantabrian littoral to southern Cantabrian slopes.

All this has enabled to consider the variations experienced by deciduous and evergreen Quercus depending on its geographical position from E to W and at both sides of the Cantabrian range from the Upper Pleistocene (MIS 3) and Holocene.

### 3.2. Principal Component Analysis (PCA)

Principal Component Analysis (PCA), integrating the information provided by both approaches was only performed for the Eurosiberian sites by using the Biplot application in Microsoft Excel to determine the weight of both Quercus species in each of samples analysed (Fig. 5a) and how they changed along time in both profiles (Fig. 5b). The latter (Fig. 5b) complements the information provided by Fig. 5a where both the name and age of each pollen and charcoal records considered doesn’t appear.
The first two components together added up to 100% of data variability. Component 1 comprised about 76.61% of pollen samples and about 51.10% of charcoal (Fig. 5a). The kind of discrimination of each component is inferred from the distribution of taxa. Thus Component 1 discriminated according to the weight that both Quercus have among the rest of floristic data. Component 2 in turn discriminated according to the weight exerted by one or another type of Quercus (deciduous and/or evergreen).

4. Results

4.1. Pollen

The bulk of Qi pollen data selected chronologically covered from the Middle Pleniglacial (MIS 3) to the late Holocene, but the information was not always continuous (Fig. 3).

By 45.9—44.2 Kyr cal BP two inverted situations were observed: Qi was dominant in Asturias (SC2a), while its presence was reduced to some scattered occurrences beside dominant values of deciduous Quercus in Cantabria (Covar) by the same period. After 44 Kyr cal BP (SC2a) both Quercus species disappeared from the record, coinciding with a sharp decrease in the AP pollen curve (Fig. 3).

By 38.6—37 Kyr cal BP (Brln, Cbrt) the spread of deciduous Quercus and, to a lesser extent, of Qi conditioned the increase in AP (Asturias and Cantabria). Both taxa gradually decreased and by 34.8—33.8 Kyr cal BP, Qi disappeared, and only deciduous Quercus (Covar, Cbrt, Brln) remained (Fig. 3).

Prior to 24.1 Kyr cal BP (Nal, Fig. 3) there is no evidence of Quercus. Between 24.1 and 19 Kyr cal BP, only deciduous Quercus was present and its values were decreasing to be replaced by Qi at the top of the record (Nal, Fig. 3). By 19 Kyr cal BP a slight retrieval of deciduous Quercus is noticed, but both Quercus species disappeared from the Asturias record after 19 Kyr cal BP. There is no pollen data for both types of Quercus until the Holocene (Fig. 3).

Between 20 and 10 Kyr cal BP there is hardly any evidence of both Quercus in the pollen record of Cantabria (Fig. 3). By 19.3—18.8 (Cual) Kyr cal BP only deciduous Quercus occur and, despite its slight increase, it does not seem responsible for AP values (Fig. 3). The best evidence regarding both types of Quercus for this time-interval is found in the NW Iberian Mountain range, already included in the Mediterranean sector (Fig. 3). Qi values are higher than those of deciduous Quercus between 22 and 20 Kyr cal BP. Afterwards, evergreen oak was almost absent, and deciduous oaks remain in low amounts until the onset of the Holocene. However in the southern slopes of the Cantabrian Mountains (El Portalón, AIT) Qi is not present until the Holocene (Fig. 3).

The beginning of the Holocene is characterised by the expansion of both Quercus. Pollen records (QS-2, SC2b) showed two regression phases of both types of oaks, the first one prior to 6000 cal BP and the second one around 2000 cal BP. Deciduous Quercus was always more abundant than evergreen Quercus in the Cantabrian region (SC2b), while in the North Iberian Mountain Range (QS-2) the situation was inverted (Fig. 3). However this scenario favourable to evergreen oak does not take place in the Atapuerca site of El Portalón (AIT) notwithstanding the influence of summer drought in this territory.

As regards the Basque Country (Sald), the record of Quercus was undifferentiated (Fig. 3). The new record available from the same site (Saldropo2), though, also pictured more favourable values for deciduous than evergreen Quercus (Peñalba, 1994).

4.2. Charcoal

A synthetic charcoal diagram (Fig. 4) shows the presence of Qi as early as 45.9—44.2 Kyr cal BP (MIS 3) although it was nevertheless scanty within an environment dominated by Pinus sylvestris (between 45.9—44.2 and 34.7—34.3 Kyr cal BP). During the MIS 2 this taxon, as well as pines, declined at its maximum while Fabaceae became dominant in the landscape (between 29.6—28.5 and
14.1–13.7 Kyr cal BP). Qi reached their maxima during the Late Glacial (12.6–12.2 Kyr cal BP), although in lower amounts than deciduous oaks, which became dominant from the Late Glacial and throughout the Holocene, coinciding with the decrease and disappearance of pines (Fig. 4).

An ensemble of shrubs associated to karstic substrates (Arbutus unedo, Laurus nobilis, Pistacia terebinthus, Rhamnus alaternus, Phillyrea latifolia, Phillyrea sp., Prunus avium, P. spinosa, P. amygdalus, P. mahaleb, Crataegus monogyna, Cornus sanguinea, Sambucus nigra), is also significant since MIS 3 (45.9–44.2 and 34.7–34.3 Kyr cal BP) when it started decreasing in importance to finally disappear in the period of the Fabaceae dominance, and reappear with high and continuous amounts since the Late Glacial. The whole of karstic shrubs reached even higher values than those of evergreen oaks during the Holocene (Fig. 4).

### 4.3. Principal Component Analysis (PCA)

Three groups of samples are distinguished by PCA (Fig. 5a). Quadrant I, represents positive values in both axis, and brings together the weight of deciduous Quercus. Quadrant II (negative values of both axes) is characterised by the scarce weight of both types of Quercus. Finally, quadrant IV (positive values of component 1 and negative values of component 2) includes the weight of evergreen Quercus.

The evolution of the weight of components 1 and 2 (Fig. 5b) in both approaches arranged chronologically throughout the time period herein considered was individually determined for charcoal (Fig. 5b1) and pollen samples (Fig. 5b2) and later correlated.

The period between 45 and 15 Kyr cal BP shows a limited weight for both Quercus (Fig. 5a: Quadrant II) and there is littleter fluctuation. The same trend prevail in the right column (Fig. 5b2 pollen)
Table 3
List and setting information of archaeological sites that have provided the charcoal data considered in the integrated study ([Fig. 4], including El Mirón and El Mirador caves ([Fig. 7]).

<table>
<thead>
<tr>
<th>Sites (location and coordinates) (Letters as per Fig. 2b)</th>
<th>Altitude (m.a.s.l.)</th>
<th>Layers with Quercus ilex</th>
<th>Cultures</th>
<th>^14C/TL dates</th>
<th>cal yr BP*</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-El Conde (CON) (Asturias) 43° 17’ 23” N, 5° 05’ W</td>
<td>180</td>
<td>20C</td>
<td>Aurignacian</td>
<td>32,530 ± 440</td>
<td>36,226</td>
<td>Uzquiano et al., 2008</td>
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<td></td>
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<td>20B</td>
<td>Aurignacian</td>
<td>34,730 ± 500</td>
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<td>Carrión et al., 2012</td>
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<td>-43,182</td>
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<td>135</td>
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<td>29,660</td>
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<td>C-Arangas (ARC) (Asturias) 43° 32’ 61” N, 7° 19’ W</td>
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<td>A/H/B/E</td>
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<td>3540 ± 29</td>
<td>3759 – 3872</td>
<td>Uzquiano, unpublished data</td>
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<td></td>
<td></td>
<td>D</td>
<td>Chalcolithic</td>
<td>TL4078 ± 805</td>
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<td>6588 – 6767</td>
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<td>7689 – 7873</td>
<td>Carrion et al., 2012</td>
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<td>45</td>
<td>L-I</td>
<td>Mesolithic</td>
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<td>Uzquiano, 1992</td>
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<td>Undated</td>
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<td>G-Mazaculos (MZ) (Asturias) 43° 23’ 23” N, 0° 34’ W</td>
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<td>A2/AZfondo</td>
<td>Neolithic/Meso-Neo</td>
<td>51,00 ± 120</td>
<td>5718 – 5988</td>
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<td>7030 ± 120</td>
<td>7740 – 7962</td>
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<td>30,380 ± 250</td>
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<td>Carrion et al., 2012</td>
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<td>D/E/L/J</td>
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<td>I/II/III</td>
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<td></td>
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<td>IV</td>
<td>Bronze Age</td>
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<td>M-Peña del Perro (PP) (Cantabria) 43° 26’ 39” N, 0° 25’ 35” W</td>
<td>60</td>
<td>1</td>
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<td>9260 ± 110</td>
<td>10,314</td>
<td>Uzquiano, 1992, 2014</td>
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<tr>
<td></td>
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<td>2A/2B</td>
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<td>10,160 ± 110</td>
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<tr>
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<td>1b1</td>
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<td>6503 – 6618</td>
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<td>7800 ± 50</td>
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<td>O-Arenaza (ARZ) (Country Basque) 43° 15’ 30” N, 0° 05’ 57” W</td>
<td>180</td>
<td>8/9/10</td>
<td>Early-Middle Bronze</td>
<td>3580 ± 70</td>
<td>3776 – 3978</td>
<td>Uzquiano and Zapata, 2000</td>
</tr>
<tr>
<td>P-Santa Catalina (SICAT) (C.Basque) 43° 22’ 38” N, 0° 30’ 36” W</td>
<td>30</td>
<td>I</td>
<td>Azilian</td>
<td>10,530 ± 110</td>
<td>12,216</td>
<td>Uzquiano, 1992, 1995 Berganza et al., 2012</td>
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<td></td>
<td></td>
<td>II</td>
<td>Late</td>
<td>11,961 ± 61</td>
<td>-12,635</td>
<td>Ruiz-Alonso et al., 2014</td>
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<tr>
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<td>III</td>
<td>Magdalenian</td>
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<td>Magdalenian</td>
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<tr>
<td>Q-Lumentxa (LMX) (C. Basque) 43° 21’ 56” N, 0° 30’ 12” W</td>
<td>70</td>
<td>2</td>
<td>Bronze age</td>
<td>3700 ± 40</td>
<td>3990 – 4104</td>
<td>Zapata, 2012</td>
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<td>3740 ± 120</td>
<td>3947 – 4294</td>
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<td>4</td>
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<td>4680 ± 60</td>
<td>5347 – 5533</td>
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<td></td>
<td>6</td>
<td>Mesolithic</td>
<td>5280 ± 40</td>
<td>6002 – 6156</td>
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</table>
| (continued on next page)
although in this case some scattered evidence throughout the graphic, indicate certain amount of both *Quercus* (Fig. 5a: Quadrants I and IV) prior 45 Kyr cal BP, at 44.2 Kyr cal BP and at 37 Kyr cal BP, similarly manifested in the fluctuations recorded in the curve (Fig. 5b2).

In the time interval between 15.6—15.1 and 12.3—11.9 Kyr cal BP, the alternation of both *Quercus* is representing exclusively by charcoal samples (Fig. 5b1) due to the limited presence of pollen data for this period in the area considered.

From 10.5 to 10.3/9.4—9.2 Kyr cal BP onwards both proxies reflect an alternation of the evergreen and deciduous *Quercus*, implying both pollen and charcoal. The weight of evergreen oak initially seems to dominate to be later replaced by deciduous oak in both columns (Fig. 5b1, b2).

5. Discussion

5.1. Pollen

Pollen information depicts a scattered, discontinuous but recurring presence of Qi since the Upper Pleistocene (MIS 3) (Fig. 3). The highly variable climatic conditions during the MIS 3 (Dansgaard et al., 1993; Sánchez-Goni, 2006) allowed the existence of a limited tree cover. The occurrence of evergreen oaks at 45.9—44.2 Kyr cal BP; 38.6—37 Kyr cal BP and 34.8—33.8 Kyr cal BP may be connected with warmer and drier conditions between MIS 3 climatic oscillations (Sc2a, Brt, Cbrt), as climatic trends mainly favoured deciduous oak (Fig. 3). The high instability of MIS 2 regarding glacial conditions (LGM) and increased aridity periods (H2, H1) were not favourable to Qi in the Eurosiberian region. Indeed, Qi was only occasionally recorded in the Asturias record around 25—24.1 Kyr cal BP (Nal) - probably related to drier conditions derived from the H2 event (Fig. 3) - and disappeared during the rest of MIS 2. However, favourable conditions linked to sheltered situations should also be considered. The discontinuous evidence of Qi, aside from regional climate conditions, would match the existence of scattered enclaves distributed throughout the uppermost mountain basins, and middle and lower Atlantic valleys of the study area, the topographic and edaphic features creating sheltered conditions. The most significant sheltered areas for Qi during the

Table 3 (continued)

<table>
<thead>
<tr>
<th>Sites (location and coordinates) [Letters as per Fig. 2b]</th>
<th>Altitude (m.a.s.l)</th>
<th>Layers with <em>Quercus ilex</em> Cultures</th>
<th>C14/TL dates cal yr BP</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>g- El Mirador (Atapuerca, Burgos)</td>
<td>1033</td>
<td>MIR-4&lt;sup&gt;b&lt;/sup&gt; Bronze age</td>
<td>3020 ± 40&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3168—3308</td>
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<td></td>
<td>MIR-6&lt;sup&gt;b&lt;/sup&gt; Neolithic</td>
<td>4760 ± 40&lt;sup&gt;b&lt;/sup&gt;</td>
<td>5437—5568</td>
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<td></td>
<td>MIR-11&lt;sup&gt;b&lt;/sup&gt; Mesolithic</td>
<td>5340 ± 50&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6039—6203</td>
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<td></td>
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<td>MIR-16&lt;sup&gt;b&lt;/sup&gt;</td>
<td>5700 ± 70&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6423—6596</td>
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<tr>
<td></td>
<td></td>
<td>MIR-23&lt;sup&gt;3&lt;/sup&gt;</td>
<td>6000 ± 50&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7184—7277</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MIR-Base&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7030 ± 40&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7833—7924</td>
</tr>
</tbody>
</table>

<sup>a</sup> Calibrated dates CalPAL (http://www.calpal-online.de/).

<sup>b</sup> Selected layers and 14C dates.

Fig. 3. Synthetic graph of Cantabrian region and neighbouring areas of southern slopes of the Cantabrian and NW Iberian mountain ranges pollen records showing the diachronic evolution of *Quercus ilex*-type and deciduous *Quercus* throughout the Upper Pleistocene and Holocene. See Table 2 for the full name of sites selected for this study and their corresponding abbreviations.
Upper Pleistocene would therefore be located nearby the inland upper mountain valleys in Asturias (Sc2a, Nal), while the lower Cantabrian valleys near the coast, with a major oceanic influence (Coval, Cbrt, Cual) would have made deciduous oaks more relevant in some areas (Cbrt) (MIS 3), and even exclusive (Cual) (MIS 2) (Fig. 3). This situation is pertinent to most Mid-Upper Pleistocene pollen records throughout N Spain from Galicia to western Pyrenees (i.e. Area Longa, Lucenza, Fig. 6) whether there are near the coast or inwards throughout the southern slopes of the Cantabrian and Pyrenean mountain ranges (Ramil et al., 1998; Peñalba, 1989; Carrión et al., 2012).

From the Late Glacial pollen data here discussed have provided quite limited information for this period both in Asturias and Cantabria (Fig. 3), which contrasts with the more significant evidence of Qi obtained in the pollen records of northern Iberia (Carrión et al., 2012), although these findings are geographically irregular (Fig. 6). Thus Qi was practically absent from coastal areas of NW Spain (Ramil et al., 1998) and their inland presence turned more representative, towards the Eurosiberian mountains (i.e. Leitariegos, Fig. 6).

Regarding the Mediterranean sector of northern Iberia no evidence of evergreen oak was recorded in the Upper Pleistocene sediments of El Portalón site (AtP) (Fig. 3). Therefore the north Iberian Mountain range provided the most complete information about the evolution of both Quercus species throughout the MIS 2 (QS2) (Ruiz-Zapata et al., 2002a). Qi was discontinuously present during this period, and its values were low when compared to the more continuous amounts of deciduous oaks. However between 22 and 20 Kyr cal BP they were still higher than the ones for deciduous Quercus, probably as a prelude to its postglacial developments (Fig. 3). A combination of environmental factors and the proximity of refugia would be responsible for such evidence at the time of the H2 event.

Towards the outcome of the Holocene, Qi developed in line with climatic amelioration although being always less abundant than deciduous Quercus (Sc2b). These dynamics match the estimations proposed by Peñalba (1989) for the pollen sites located in the Basque Country and Navarra (i.e. Saldropo2, Belate, Fig. 6). This situation is reverted in the North Iberian mountain range (QS-2), paralleling as well the vegetational dynamics usual in the Mediterranean region (i.e. Quintanar de la Sierra, Peñalba, 1994; Peñalba et al., 1997). Qi taxon is present in the holocene sediments of El Portalón site (AtP), its values are however scarce compared with deciduous oaks in this site (Fig. 3). However in other sites located in the Mediterranean sector of northern Iberia, such as Los Tornos (south-eastern Cantabria) and Las Pardillas (Burgos), Qi a more continuous record although its values are always lower than deciduous Quercus (Fig. 6).

5.2. Charcoal

The charcoal record of Qi for the timescale under discussion presented sparse and discontinuous occurrences during the MIS 3, culturally corresponding to the late Mousterian and early Upper Palaeolithic (Fig. 4). By that time (45–34 Kyr cal BP) human exploitation territories were located in the lower basins of the main rivers like Covalejos (CVL), in the lower Pas valley (Cantabria), and relatively close to the coastal areas, as well as in the valleys of small...
adjacent tributaries located in the middle basins of such rivers, such as Conde (CON), in the Trubia valley (Asturias), where large calcareous outcrops were visible. Management of wood resources was mainly focused on these substrates, which were intensively resorted to as seen in the high amounts of *Pinus* recorded and the low but continuous frequencies of shrubs associated to these soils (Fig. 4). The scanty Qi would be thus related to firewood supply, revealing in both areas the existence of small enclaves where this taxon would be already settled thanks to local environmental conditions triggered by its sheltered position on the calcareous sunny slopes. Charcoal data of this time interval matches the aforementioned MIS 3 pollen evidence (Fig. 3) bearing in mind the location of Conde cave (Asturias), in the same basin downstream where there is SC2a site, and Covalejos correspond to the same site. However, eastwards Cobrante cave did not provide any Qi charcoal evidence in the same layers where Qi pollen evidence appeared. The crossing of pollen and charcoal data demonstrates the complementary character of both disciplines.

The record of Qi practically disappears during most of MIS 2 -between 29.6–28.5 and 15.6–15.1 Kyr cal BP- coinciding with the

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**Fig. 5.** a: Principal Component Analysis (PCA) showing the integrated pollen and charcoal information about evergreen-deciduous oaks relationships. Pollen and charcoal are represented by triangles and squares respectively. Deciduous *Quercus* appears in Quadrant I and *Quercus ilex*-type appears in Quadrant IV. The scarce weight of both taxa appears in Quadrant II. b: Graphs showing the evolution of the weight that both *Quercus* species had on the vegetal landscape over the period of time covered by this work, obtained by both Anthracological (b1) and Palynological (b2) approaches and correlated. Deciduous and evergreen *Quercus* appear in light/dark green colours respectively. The scarce weight of both *Quercus* is represented in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Last Glacial Maximum (LGM). By this time, human settlements (Gravettian, Solutrean and most Magdalenian) were characterised by short and strongly seasonal occupations located close to the coastal platform (lower Atlantic valleys). Human groups were then constantly moving from place to place as a survival strategy carried out in such changing environments. The dominant Fabaceae became the most suitable firewood for these itinerant and short human occupations, given their combustion properties (Uzquiano, 2014). Siliceous substrates, typical of the coastal platform, were then intensively exploited at the expense of calcareous soils, as low amounts of Pinus and the disappearance of the karstic shrubs suggested (Fig. 4). The absence of Qi in the charcoal record of LGM period also matches the trend observed in the MIS 2 pollen record here considered although the latter has provided some scant Qi occurrences (Fig. 3).

Qi as well as associated shrubs reappeared by 15–14.3 Kyr cal BP (StCAT III, II) (Fig. 3). By the Late Glacial climatic amelioration and the onset of the Holocene, the sites of Santa Catalina (StCAT) and Peña del Perro (PP) yielded higher values of Qi than those of deciduous Quercus, coinciding with the Late Magdalenian and Azilian cultures (Fig. 7). These findings suggest exploitation of wood resources focused on the calcareous outcrops where these two coastal sites opened. Such exploitation clearly denotes its installation in the Cantabrian coastal areas prior to the Holocene climatic amelioration. We have previously questioned its Holocene migration across corridors in the Mediterranean area as proposed by Montserrat and Montserrat (1987, 1988) and suggested another scenario based on the spread of Qi in the Cantabrian coastal calcareous massifs from very close shelters (Uzquiano, 1992, 1995). These refugia were probably part of the exploitation territories of Late Glacial and early Holocene human habitats. Bearing in mind the ecological requirements of Qi, it might be possible that its gradual extension was at the expense of Pinus, which was disappearing from karstic coastal areas at the time (Uzquiano, 1992) as charcoal data suggest (Fig. 4). No Qi pollen evidence was recorded for this time interval (Fig. 3) and regarding N Spain pollen record it rarely appears (i.e. Lucenza, La Piedra, Leitariegos, Fig. 6).

Throughout the Holocene, Qi was already continuous, although the amounts recorded were always lower than those of deciduous Quercus, which became the main wood resource to supply domestic hearths during the Mesolithic and successive prehistoric periods (Figs. 4 and 7). Such management of wood resources was perfectly adapted to Holocene vegetation dynamics regarding the spread of both types of Quercus as defined by the palynology in the Eurosiberian sector of northern Iberia (Peñalba, 1989, 1994; Ramil et al., 1998; González-Sampériz et al., 2010; Carrión et al., 2012) (Fig. 6).

Holocene fluctuations of Qi observed in the charcoal record would be also related to the geographical position of each site (in an eastern/western, coastal/interior dichotomy) as well as to the mobility associated to economic practises developed (Fig. 7). Thus the record of Qi during the Mesolithic (10.5–10.3 to 7.8–7.6 Kyr cal BP) would have regressed when considering its higher amounts in the previous Azilian occupations (Fig. 4). Most of the Mesolithic charcoal information came from western Cantabrian coastal sites such as Mazaculos (MZ-A3) and La Llana (LL-I) caves (Eastern Asturias) (Figs. 4 and 7), where dominant deciduous Quercus woods
become more intensively exploited by human communities. However, the best record of Qi is observed in the inland sites of the Asturias Pre-littoral Depression throughout the Neolithic and Chalcolithic with economic practices basically associated to itinerant herding. Here Qi amounts were higher than those of deciduous Quercus, as seen in Los Canes site (CAN 7 and CAN 8/11, Fig. 4). The E-W arrangement of Eastern Asturias reliefs (i.e. Sierra de Cuera), is responsible of such differences between deciduous and evergreen oaks as these mountains act as a barrier that attenuates westerly winds laden with moisture and heavy rainfalls.

Similarly occurs in eastern Cantabria between the Peña del Perro coastal rockshelter and El Mirón Cave (Fig. 7) the latter located upstream near the watershed divide of the Cantabrian mountain range. At the southern slopes of the Cantabrian Mountains charcoal data from El Mirador (Sierra de Atapuerca, Burgos) provided relevant amounts of both Quercus (Fig. 7) (Euba et al., 2015). The representation of Qi in this site contrasts with its scarce occurrences in the pollen record of the nearby site of El Portalón (ATP) (Fig. 3).

Karstic shrubs ran parallel to the Qi record, but their values were always higher, especially between the Neolithic and Chalcolithic (Fig. 4). This high exploitation of shrubs would be mostly related to the seasonal movements of Mesolithic hunters to the inland valleys following paths similar to the ones crossed by red deer herds and, subsequently, of the similarly itinerant herding practices since the Neolithic onwards.

During the Bronze and Iron Ages, the exploitation of both Quercus remained similar. However, the values of Qi were no longer significant compared to those recorded by karstic shrubs, which reached their maximum by this period. These dynamics suggests the gradual disappearance of the taxon from many areas, especially those with better developed soils at the lower and middle slopes as the consequence of the gradual forest clearance resulting from crop fields and pastures for livestock during the Neolithic and Chalcolithic (Uzquiano and Zapata, 2000; Zapata, 2002, 2012). However, as we move inward the representation of evergreen oak are more balanced with regard to deciduous oaks as the Bronze Age charcoal data of El Mirón and El Mirador caves suggest (Fig. 7).

5.3. Integrated Quercus ilex dynamics in relation with PCA graphics

Pollen and charcoal data show similarities and they complement at tracing temporal changes for Qi. PCA reflects the main features derived from both pollen and charcoal data (Fig. 5a and b).

The weight of deciduous Quercus (Quadrant I, Fig. 5a) is a reflection of the dominance of these plant formations throughout the Holocene in the study area (Figs. 3 and 4), embedded in the Eurosiberian vegetation circle. On the contrary, the weight of evergreen oak (Quadrant IV) indicates that, despite Qi expansion and development throughout the Cantabrian region in the Holocene, its values never became dominant. This situation may be due...
to its extension limited to the discontinuous calcareous substrates and the regional climatic conditions in process. Furthermore, Quadrants II and III—which includes the scarce weight of both *Quercus* (Fig. 5a) seem also to indicate the relevance of deciduous *Quercus* over evergreen trees since the Upper Pleistocene (~40 Kyr cal BP), considering that component 2 discriminates the type of both *Quercus* and the samples are mostly concentrated in Quadrant II (Fig. 5a). Upper Pleistocene pollen and charcoal data also reveals a more relevant presence of deciduous oak (Figs. 3 and 4).

The weight of both *Quercus* over time in both approaches (Fig. 5b1, b2) was limited during the Upper Pleistocene in the pollen record and virtually absent in the charcoal sample. However, from the Late Glacial in the case of the charcoal record and throughout the Holocene for both records, the evergreen-deciduous oak alternation starts out in the study area following the ecological needs of both trees and the geographical position of sites: coastline, pre-littoral depression, upper mountain valleys, and the woodland resource management developed. Holocene climate dynamics were eventually favourable to the spread of deciduous oak forests (Fig. 5b—1, 5b2) that became the major area of woodland exploitation in the different cultural stages of recent Prehistory (Fig. 4). The prevailing climatic conditions developed in Eurosiberian and Mediterranean areas determined specific vegetation climax: deciduous oak woods were distinctive in the former and evergreen oak woods were dominant in the latter (Figs. 6 and 7). Thus palaeobotanical and archaeobotanical data here presented do not support that the origin of Cantabrian evergreen oak woods originated exclusively from anthropic activities (Zapata and Meaza, 1998; Meaza and Cuesta, 2010) but rather it was the result of climatic factors which from recent Prehistory and historical times combined with the increasing human pressure, as other works have already argued (Pons and Vernet, 1971; Peñalba, 1989, 1994; Uzquiano, 1992, 1995).

Lastly, in the Mediterranean region, the opposite situation was recorded regarding the Holocene evolution of deciduous and evergreen *Quercus*, according both to pollen and charcoal assemblages (Figs. 3, 6 and 7).

6. Conclusions

The combination of palaeobotanical and archaeobotanical data presented here provides significant information regarding the presence, spread and exploitation of Qi in northern Spain at different environmental and cultural stages of the Upper Pleistocene and Holocene. This taxon was documented at different places of the Basque-Cantabrian shoreline (N Iberia/SW France) since the Middle Pleistocene according to previous palaeobotanical studies, suggesting its survival throughout several interglacial and glacial climatic stages. Pollen and charcoal data bring evidences of Qi in the Cantabrian region from the Upper Pleistocene. Since then in those sites where both species of *Quercus* were present, there was a more favourable position for deciduous than evergreen oaks being the values of the latter very low and/or discontinuous matching the rest of pollen records of N Iberia (Carrion et al., 2012). Pollen and charcoal evidence reveal the same overall trend during several episodes of the Upper Pleistocene, somehow foreshadowing its subsequent Holocene dynamics related to the prevailing climate. Nonetheless, MIS 3 environmental conditions seemed to have been more favourable to evergreen oak than those characterising MIS 2. Qi was undoubtedly present in the catchment area of contemporary prehistoric populations who occasionally exploited it, including last Neanderthals and Modern Human populations at their respective cultural stages of the Middle and Upper Palaeolithic. The presence of Qi in charcoal assemblages was related to woodland exploitation focused on scattered sheltered areas (calcareous sunny slopes) close to human settlements, where the taxon remained, like in Asturias and Cantabria.

Similarly to palaeobotanical records from N Spain (Peñalba, 1989, 1994; Ramil et al., 1998; Carrion et al., 2012), the pollen and charcoal data presented here suggest that Qi spread from nearby refugia as a consequence of the Holocene climatic amelioration. Eurosiberian climatic characteristics favoured the deciduous oak communities which had remained as dominant in the Cantabrian region despite the strong exploitation developed throughout the Holocene prehistoric cultures. Climatic and edaphic features would have limited the spread of Qi to drier calcareous sunny slopes.

Holocene pollen and charcoal assemblages suggest an irregular distribution of Qi from east to west in the Cantabrian region. The western Basque Country and the eastern Cantabria shoreline, which are currently considered areas of ecological interest regarding evergreen oak woods, yield evidence of an important exploitation of this taxon from the end of Late Glacial and the onset of the Holocene. However, to the west, the dominant oceanic influences probably attenuated the spread of Qi in the Asturias coast, with occasional higher representation than those of deciduous oak in the pre-littoral depression of Eastern Asturias, confirming previous palaeobotanical works (Peñalba, 1989; Ramil et al., 1998).

Several southern Cantabrian slopes areas and the northwest Iberian Mountain range, already located in the Mediterranean region, show a distinct trend regarding oak dynamics with Qi always more abundant than deciduous *Quercus* prior the Holocene (22-20 Kyr cal BP) and throughout the Holocene as observed in the QS-2 pollen record. The charcoal assemblage (i.e. El Mirador) shows that the exploitation of both communities was balanced since the early Neolithic while from late Neolithic Qi experienced a sharp increase and became the main firewood supply exploited in a prevailing climate dynamics more favourable to sclerophyllous woods on the southern slopes of the Cantabrian Mountains (Euba et al., 2015).

The presence of Qi in Cantabrian Spain might be taken back to the Pleistocene according to the palaeobotanical record. Although our data do not cover the whole Cenozoic, its presence is proved to be related to climatic factors of a mainly interglacial nature (Holocene) but also to drier environmental events (H1, H2) included in the glacial periods as well (MIS 3, MIS 2). Its scattered presence in the study area prior the Holocene times suggests its endurance in various areas thanks to local natural factors related to substrate type and slope orientation. In addition, these areas were exploited by human groups at different cultural stages of Prehistory according to the archaeobotanical record. Thus, the Holocene spread of Qi neither originated from distant southern migrations (Montserrat and Monserrat, 1987) but rather from nearby Cantabrian refugia, nor was it exclusively due to human pressure (Zapata and Meaza, 1998; Meaza and Cuesta, 2010). It was rather the combination of long term natural and human factors which determined in the Cantabrian region (northern Cantabrian slopes) the prevalence of deciduous oak woods communities.

Acknowledgements

This review includes the palaeobotanical and archaeobotanical works where *Quercus ilex*-type has been recorded and published over the last two decades as well as some recent unpublished archaeobotanical data. The list of people and institutions is too long to include here but we are very grateful to all of them for facilitating at the time the samples selected for this synthesis. However we want to dedicate this synthesis to Dr Lydia Zapata archaeobotanist and professor from the University of the Basque Country who should have participate in it if her sudden death wouldn’t have occurred, farewell Lydia. Moreover the authors would also like to
thank Aixa Vidal for her assistance with the English text throughout the several revisions of the manuscript. JS Carrión thanks the projects Séneca 1943/P/14, and MINECO CGL-BOS-2012-34717, CGL-BOS-2015-68604 for financial support.

References


