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

P. Uzquiano [a, *], MaB. Ruiz-Zapata [b], MaJ. Gil-Garcia [b], S. Fernández [c], J.S. Carrión [c]

[a] Dept of Prehistory, Universidad Nacional de Educación a Distancia UNED C/Mediodía Grande, 17, 28005 Madrid, Spain
[b] Dept of Geology, Universidad de Alcalá de Henares, Ed. Ciencias, 28871, Alcalá de Henares, Madrid, Spain
[c] Dept Biologia Vegetal (Botánica), Campus de Espinardo, Universidad de Murcia, 30100, Murcia, Spain

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ABSTRACT

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 relictual 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; Aseguinolaza 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-Goñi et al., 2008). During the Late Glacial and particularly the Holocene, its presence was frequent in pollen deposits from N

* Corresponding author.
E-mail addresses: p_uzquiano@hotmail.com (P. Uzquiano), blanca.ruiz@uah.es (MaB. Ruiz-Zapata), santiago@um.es, carrion@um.es (S. Fernández).

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Spain (Carrión et al., 2012). The Holocene record of Qi in western France was also significant in Boreal deposits at the Bordeaux 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 taxon 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 (Peñalba, 1989, 1992, 1994; Ramil et al., 1998) and anthracology (Uzquiano, 1992, 1995; Zapata and Meaza, 1998; Uzquiano and Zapata, 2000; Zapata, 2002).

This article provides the most complete charcoal evidence of Qi currently available for archaeological sites in the Cantabrian region (Basque Country, Cantabria and Asturias), supported by a set of radiometric data ranging from 45 to 3.7 Kyr cal BP and contemporary pollen samples of the same area. Pollen data was mostly collected from peat and lake sediments, with some contributions from archaeo-palynological records. Pollen and charcoal data are here presented and discussed independently because of their particular analytical and interpretation methodologies. They are nevertheless compared in the discussion to depict a more coherent picture of the spread, distribution and exploitation of *Quercus ilex*-type dominated formations and their connection with Cantabrian prehistoric groups, and the location of refuge areas. Greater emphasis was placed on the relationships between Qi and the deciduous oaks dynamics by using Principal Components Analysis (PCA) which integrated pollen and charcoal information.

The Cantabrian mountain range is an ecotonal environment between the Eurosiberian and the Mediterranean floristic domains. Therefore several archaeobotanical and palaeobotanical studies from southern Cantabrian and NW Iberian Mountain ranges need to be considered to illustrate the distribution patterns for Qi in both regions.

2. The study area and biogeography of *Quercus ilex*-type in N Spain

2.1. Geographical and chronological settings

The Cantabrian region covers a territory of about 20–40 km wide lying between the coastal strip and the northern foothills of the Cordillera (Cendrero et al., 1986). This part of the Eurosiberian region presents oceanic climate conditions but the east-west disposition of the main mountain reliefs gradually attenuates the prevailing westerly wet winds and heavy rainfalls in a north-south gradient (Bertrand, 1974). Similarly, the distribution of mountains and valleys inasmuch as the intense hydrological system and the discontinuity of substrates have conditioned an important diversity of plant communities (Cendrero et al., 1986).

Flora is defined by deciduous oak communities which depend on substrate affinities and slope orientation. Hence, acidophilous oak woods prefer littoral areas with siliceous substrates which get strongly acidified due to the high rainfall regime, whereas mixed deciduous woods of *Corylus* and *Fraxinus* settle in the fresh soils of the valleys, and the pyrenean oak woods are found in the siliceous sunny slopes of inland areas. Strong human impact along time has significantly reduced their former extension, particularly in littoral and pre-littoral areas, and replaced them by heathland species. Evergreen oak woods settled on the calcareous outcrops, distributed discontinuously throughout the territory (Fig. 1). There is a marked contrast between siliceous reliefs with limited arboreal vegetation and abundant heathland species and calcareous massifs, where dense and more closed vegetation develops, crop fields, pastures, hay meadows, several buildings and the various reforestations resulting from human pressure (Aseguinolaza et al., 1989).

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 northernmost 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

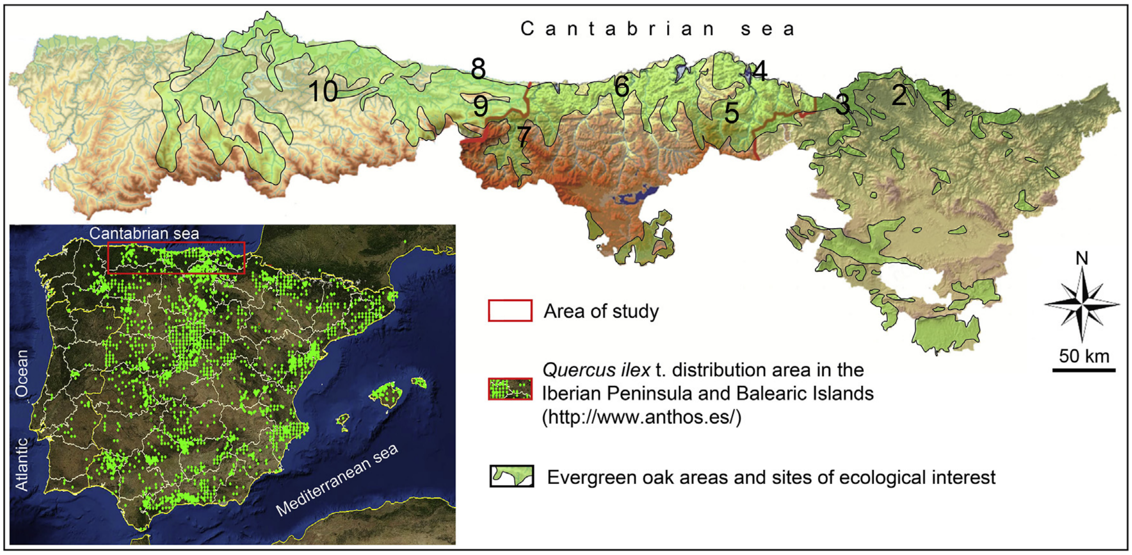

Fig. 1. *Quercus ilex*-type in the Iberian Peninsula and its current distribution throughout the Cantabrian region indicating the most relevant evergreen oak woods localities. From East to West: 1-Lekeitio, 2-Guernica, 3-Nervión estuary; 4-Monte Buciero; 5-Asón Valley; 6-Pas estuary; 7-Hermida Gorge/Liébana region; 8-Eastern Asturias coastal platform; 9-Cares valley; 10-Trubia valley.

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 Collinean 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

Table 1
General table with the list of N Spain palaeobotanical sites where *Quercus ilex*-type were recorded by pollen, charcoal and waterlogged wood including some archaeological sites with pollen and charcoal information. The sites selected for the elaboration of Fig. 6 appear in italics.

Sites (N° as per Fig. 2a)	Altitude (m asl)	Latitude	Longitude	Chronology/(Material)
1-MD99-2331/MD03-2697 (Galicia)	>2100 deep	42°09′N	09°41′W	MIS 9/
		42°09′N	09°42′W	MIS 5, 4, 3, 2, 1
2- MD01-2447 (Galicia)	2080 deep	42°09′N	09°40′W	MIS 7/MIS 11
3-Area Longa (Galicia)	0	43°36′N	07°18′W	MIS 3, 4, 5c
4-Peña da Candela (Galicia)	920	43°29′16″N	07°26′18″W	Middle-Late Holocene
5-Turbera de Penido Vello (Galicia)	700	43°26′N	07°32′W	Late Holocene
6-Pozo do Carballal (Galicia)	1330	42°42′20″N	07°06′40″W	Late Glacial/Holocene
7-A Cespedosa (Galicia)	1425	42°52′44″N	06°51′36″W	Middle-Late Holocene
8-A Golada (Galicia)	1100	42°42′20″N	07°00″00″W	Late Holocene
9-Laguna de Lucenza (Galicia)	1375	42°35′32″N	07°06′47″W	Late Pleniglacial/Holocene
10-Campo Lameiro[c] (Galicia)	310	42°32′48″N	08°31′40″W	Middle-Late Holocene (peatbog charcoal)
11-Pala da Vella[c] (Galicia)	830	42°29′ N	06° 51′W	Late Holocene (Archaeological Charcoal)
12-Las Dueñas (Asturias)	127	43°33′43″N	06°10′18″W	Holocene
13-Alto de la Espina (Asturias)	650	43°22′52″N	06°19′38″W	Late Glacial/Holocene
14-Ría de Villaviciosa (Asturias)	0	43°29′15″N	00°26′00″W	Holocene (Pollen and waterlogged wood)
46-Corteguero (As°turias)	1500	43°07′10″N	05°21′55″W	Middle Holocene
17-Puerto de Tarna (Asturias)	1415	43°07′N	05°15′W	Late Pleniglacial/Holocene
18-Lago Enol (Asturias)	1070	43°16′20″N	04°59′32″W	Late Glacial/Holocene
20-Llano Roñanzas/Borbolla Río Bederna (Asturias)	220/50	43°22′20″N	04°39′56″W	Mid-Late Holocene (Pollen and waterlogged wood)
21-Los Tornos (Cantabria)	920	43°09′02″N	03°26′28″W	Holocene
24-Peña Parda[c] (Basque Country)	975	42°36′04″N	02°37′28″W	Bronze age (Archaeological Pollen and Charcoal)
25-Labeko Koba (Basque Country)	246	43°03′45″N	02°29′21″W	Upper Pleistocene (MIS 3)
26-Urtiaga (Basque Country)	160	43°16′05″N	02°19′05″W	Late Pleniglacial Holocene
27-Belate (Navarra)	847	43°02′51″N	01°36′54″W	Mid-Late Holocene
28-Atxurri (Navarra)	500	43°15′05″N	01°33′01″W	Late Holocene
29-Ibón de las Ranas (Aragón)	2092	42°49′23″N	00°30′17″W	Holocene
30-El Portalet (Aragón)	1802	42°48′00″N	00°23′52″W	Upper Pleistocene/Holocene
31-Tramacastilla (Aragón)	1682	42°43′27″N	00°22′07″W	Late Glacial Holocene
32-°Las Médulas[c] (León)	554	42° 27′N	06° 45′W	I-IIth AD
	760			III-Ith BC
				(Archaeological Charcoal)
33-Puerto de Leitariegos (León)	1700	42°59′44″N	06°24′44″W	Late Glacial Holocene
34-Laguillín (León)	1850	42°52′51″N	06°02′25″W	Late Pleniglacial Holocene
35-La Piedra (Burgos)	950	42°38′00″N	03°52′45″W	Late Glacial Holocene
47-Dolina: (Atapuerca Mts.) (Burgos)	980	42°21′N	03°31′W	Mid-Upper Pleistocene
37-Las Pardillas (Burgos)	1850	42°02′36″N	03°02′45″W	Mid-Late Holocene
39-La Franca[a] (Asturias)	0	43°23′23″N	04°34′51″W	Eemian/Upper Pleistocene
42-Marbella and Le Moura[b] (Atlantic Pyrenees, SW France)	40	43°28′49″N	01°31′35″W	Holsteinian Holocene
43-Xan de Llamas (NW León)	1500	42°18′15″N	06°19′17″W	Late Holocene
44-Brañas de Lamela (NW León)	1280	42°46′05″N	06°51′00″W	Late Holocene
45-Pinar de Lillo (NE León)	1360	43°03′46″N	05°15′31″W	Late Holocene

Pollen sites with occasionally charcoal and/or waterlogged wood deposits (after Carrión et al., 2012).
[a] After Mary et al., 1975.
[b] After Oldfield and Huckerby, 1979; Oldfield, 1968; Reille, 1993.
[c] Other charcoal sites (after Carrión et al., 2012).

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.

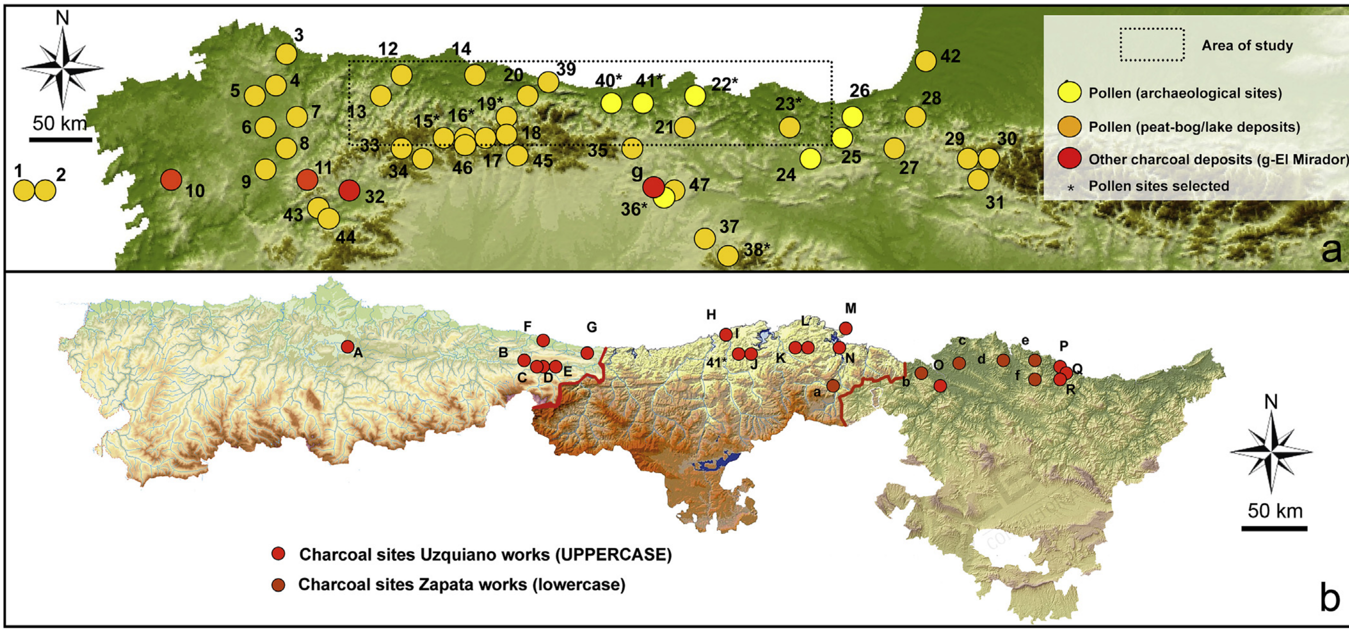

Fig. 2. a: N Spain complete pollen record of *Quercus ilex*-type (after Carrión et al., 2012) together with other palaeobotanical sites. Names, number of sites and setting information are summarized in Tables 1 and 2. The pollen sites under consideration appear with (*). b: Complete charcoal record of *Quercus ilex*-type throughout the Cantabrian Region. Archaeological sites aim of this work appears in capital letters (see names and information in Table 3, except for E-Tiu Llines; K-Cueva del Mar; L-La Garma B and R-Laminak II excluded of the in-deep study). Other charcoal studies with *Quercus ilex*-type data appears in lowercase: a-El Mirón (Cantabria); b-Pico Ramos, c-Hirumugarrieta 1–2, d-Antoliñako koba, e-Kobaedera, f-Kobeaga II (Basque Country) (after Zapata, 2002, 2012).

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 inversed 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 (Coval) 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 (Brñ, 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* (Coval, Cbrt, Brñ) 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, AtP) 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 (AtP) 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

Table 2
List and setting information of selected peatland, lakes and archaeological sites that provided the pollen information considered for the integrated study (Fig. 3).

Sites (N° as per Fig. 2a)	Altitude (m asl)	Latitude	Longitude	^{14}C dates	cal yr BP[a]	References
19-Comella (SC2a) (Asturias)	834	43°16′58″N	04°59′22″W	40,480 ± 820	43,232 –45,003	Ruiz-Zapata et al., 2002b Jiménez-Sánchez et al., 2003
19-Comella (SC2b) (Asturias)	834	43°16′58″N	04°59′22″W	3190 ± 70 3820 ± 70 8350 ± 80	3358–3499 4207–4340 9242–9447	Ruiz-Zapata et al., 2000 Jiménez-Sánchez et al., 2003
15-Brañagallones (Brñ) (Asturias)	1415	43°07′56″ N	05°17′48″	28,990 ± 230	33,123 –33,847	Jiménez-Sánchez et al., 2003
16-Nalona (Nal) (Asturias)	1230	43° 07′56″N	05°15′45″W	20,640 ± 300	24,158 –25,000	Jiménez-Sánchez et al., 2003
41-Covalejos (Coval) (Cantabria)	105	43°23′48″N	03°55′58″W	30,380 ± 250 32,840 ± 280 41,640 ± 650	34,311 –34,736 36,650 –38,017 44,299 –45,976	Ruiz-Zapata and Gil-García, 2005
22-Cobrante (Cbrt) (Cantabria)	80	43°19′28″N	03°31′38″W	30,480 ± 250 33,320 ± 310	34,370 –34,894 37,092 –38,607	Ruiz-Zapata and Gil-García, 2009
40-Cualventi (Cual) (Cantabria)	75	43°23′11″N	04°09′13″W	15,950 ± 70	18,895 –19,331	Ruiz-Zapata and Gil-García, in press
23-Saldropo 1 (Sald) (Basque Country) *Saldropo 2*	625	43°03′33″N	02°43′38″W	920 ± 100 2460 ± 100 4510 ± 150 840 ± 50 3590 ± 90 5630 ± 70	752–928 2405–2681 4961–5383 715–840 3769–4037 6344–6494	García-Antón et al., 1989 Peñalba, 1989, 1994
36-El Portalón (AtP) (Atapuerca Mts Burgos)	980	42°21′N	03°31′W	2050 ± 40 3330 ± 70 3680 ± 40 5230 ± 40 6270 ± 40 16,890 ± 60 30,200 ± 190	1964–2084 3488–3654 3957–4079 5946–6090 7175–7248 19863 –20382 34227 –34553	Martínez-Pillado et al., 2014 López-García et al., 2010
38-Quintanar de la Sierra (QS-2) (Burgos)	1470	42°01′20″N	03°01′25″W	330 ± 110 2760 ± 50 6070 ± 40 7820 ± 70 8010 ± 30 9700 ± 50 10,650 ± 60 12,040 ± 40 16,630 ± 50 17,150 ± 100	199–475 2806–2924 6880–6985 8536–8743 8809–8982 10,927 –11,190 12,575 –12,719 13,818 –14,227 19,610 –20,202 20,234 –20,892	Ruiz-Zapata et al., 2002a

[a] Calibrated dates CalPAL (http://www.calpal-online.de/).

14.1–13.7 Kyr cal BP). Qi reached their maxima during the Late Glacial (12.6–12.2 Kyrs 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 Kyrs 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 littler 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).

Sites (location and coordinates) (Letters as per Fig. 2b)	Altitude (m.a.s.l)	Layers with *Quercus ilex*	Cultures	^{14}C/TL dates	cal yr BP[a]	References
A-El Conde (CON) (Asturias) 43° 17′ 23″ N, 05° 58′ 54″ W	180	20C 20B 20A 10	Aurignacian Aurignacian Mousterian Mousterian	32,530 ± 440 34,730 ± 500 38,250 ± 390	36,226 −37,882 39,004 −40,747 42,205 −43,182	Uzquiano et al., 2008 Carrión et al., 2012
B-Coimbre (CMB) (Asturias) 43° 33′07″N 04° 69′00″W	135	1 2 4 6	Upper Magdalenian Upper Magdalenian Lower Magdalenian Gravetian	12,840 ± 70 Not communicated Not communicated Not communicated	15,112 −15,647 17,160 −15,690 19,970 −18,720 29,660 −28,560	Uzquiano, unpublished data Yravedra et al., 2016
C-Arangas (ARG) (Asturias) 43° 32′61″N 04° 79′91″ W	345	A/H/B/E C D 2B/3/4 5A/B	Bronze age Chalcolithic Neolithic Mesolithic Azilian	3540 ± 29 TL4078 ± 805 4454 ± 56 8280 ± 55 Undated	3759–3872 4982–5241 9171–9384	Uzquiano, unpublished data
D-Los Canes (CAN)(Asturias) 43° 19′ 33″N 04° 48′ 03″ W	335	UE 8/11 UE 7 UE 6III	Bronze age Neolithic Mesolithic	5865 ± 70 6930 ± 95	6588–6767 7689–7873	Uzquiano, 1992 Carrión et al., 2012
F-La Llana (LL) (Asturias) 43°24′24″N 04°43′00″W	45	L-I	Mesolithic	Undated		Uzquiano, 1992
G-Mazaculos (MZ) (Asturias) 43° 23′23″ N 04° 34′51″ W	35	A2/A2fondo A3	Neolithic/Meso- Neo. Mesolithic	51,00 ± 120 7030 ± 120	5718–5988 7740–7962	Uzquiano, 1992, 1995 Carrión et al., 2012
H-Salinas (SAL) (Cantabria) 43° 72′71″ N 03° 97′66″ W	20	L-2	Mesolithic shellmidden	6930 ± 50	7715–7812	Uzquiano, unpublished data Pérez Bartolomé pers comm. (datations)
I-Covalejos (CVL) (Cantabria) 43° 23′48″ N 03° 55′ 58″ W	105	B C D/E H/I/J	Aurignacian Aurignacian Mousterian Mousterian	30,380 ± 250 32840 ± 280 41,640 ± 650 TL38344 ± 3560	34,311 −34,736 36,650 −38,017 44,299 −45,976	Uzquiano, 2005, 2008 Carrión et al., 2012
J-Cubrizas (CUB) (Cantabria) 43°23′17″ N 03° 56′10″W	160	I/II/III IV	Iron Age Bronze Age	Undated		Uzquiano, unpublished data
M-Peña del Perro (PP) (Cantabria) 43°26′39″N 03°25′35″W	60	1 2A/2B	Mesolithic Azilian	9260 ± 110 10,160 ± 110	10,314 −10,590 11,526 −12,052	Uzquiano, 1992, 2014 Carrión et al., 2012
N-El Carabión (CRB) (Cantabria) 43°21′00″W 03°30′00″W	20	1b1 1b2 3	Meso-Neolithic Mesolithic Azilian	5750 ± 40 7800 ± 50 10,310 ± 60	6503–6618 8524–8628 11,990 −12,383	Uzquiano, 2014
O-Arenaza (ARZ) (Country Basque) 43° 15′30″ N 03° 05′57″ W	180	8/9/10	Early-Middle Bronze	3580 ± 70	3776–3978	Uzquiano and Zapata, 2000
P-Santa Catalina (StCAT) (C.Basque) 43° 22′38″ N 02° 30′36″ W	30	I II III	Azilian Late Magdalenian Upper Magdalenian	10,530 ± 110 11,961 ± 61 12,425 ± 90	12,216 −12,635 13,716 −14,115 14,303 −15,018	Uzquiano, 1992, 1995 Berganza et al., 2012 Ruiz-Alonso et al., 2014
Q-Lumentxa(LMX) (C. Basque) 43° 21′ 56″ N 02° 30′ 12″ W	70	5/6/7/8	Bronze age	Undated		Uzquiano, unpublished data
a-El Mirón (Cantabria) 43°14′44″N 03°27′10″W	250	2 3 4 6	Bronze age Chalcolitic Neolithic Mesolithic	3700 ± 40 3740 ± 120 4680 ± 60 5280 ± 40	3990–4104 3947–4294 5347–5533 6002–6156	Zapata, 2012

(continued on next page)

Table 3 (*continued*)

Sites (location and coordinates) (Letters as per Fig. 2b)	Altitude (m.a.s.l)	Layers with *Quercus ilex*	Cultures	^{14}C/TL dates	cal yr BP[a]	References
		7		5570 ± 50	6320–6404	
		8		8700 ± 40	9588–9709	
		9				
		10				
		10.1				
g- El Mirador	1033	MIR-4[b]	Bronze age	3020 ± 40[b]	3168–3308	Carrión et al., 2012
(Atapuerca, Burgos)		MIR-6[b]	Neolithic	4760 ± 40[b]	5437–5568	Euba et al., 2015
42° 20′ 31″ N		MIR-11[b]	Mesolithic	5340 ± 50[b]	6039–6203	
03° 30′25″ W		MIR-16[b]		5700 ± 70[b]	6423–6596	
		MIR-23[b]		6300 ± 50[b]	7184–7277	
		MIR-Base[b]		7030 ± 40[b]	7833–7924	

[a] Calibrated dates CalPAL (http://www.calpal-online.de/).
[b] Selected layers and ^{14}C dates.

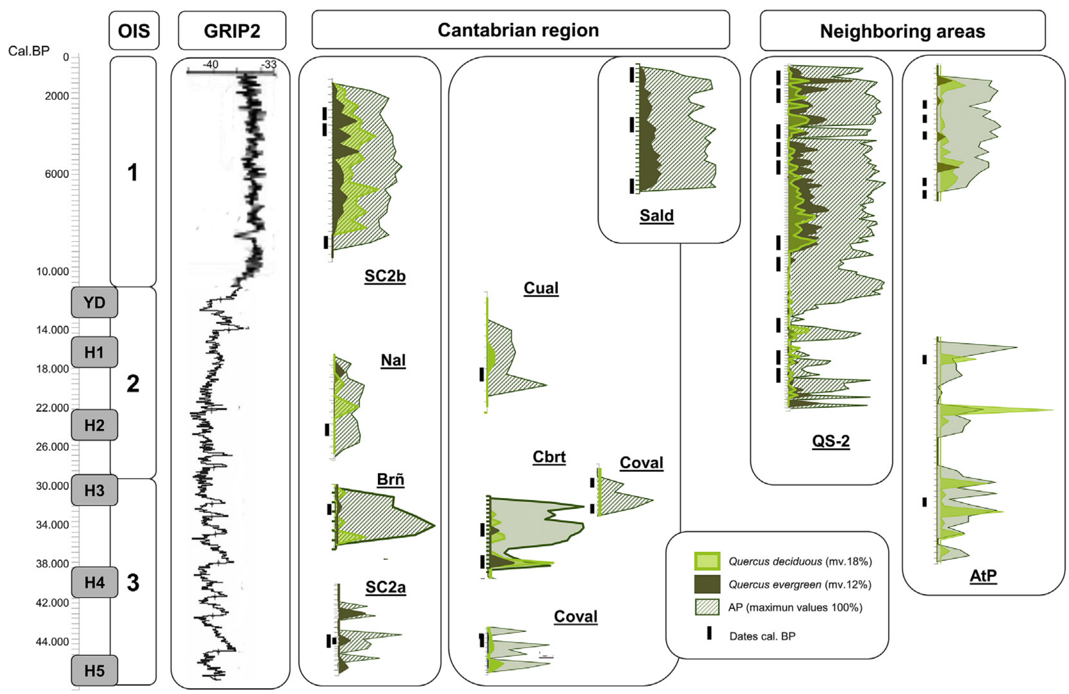

Fig. 3. Synthetic graph of Cantabrian region and neighbouring areas of southern slopes of the Cantabrian and NW Iberian mountain ranges pollen records showing the diachronic evolution of *Quercus ilex*-type and deciduous *Quercus* throughout the Upper Pleistocene and Holocene. See Table 2 for the full name of sites selected for this study and their corresponding abbreviations.

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 45.9–44.2 Kyr cal BP and at 38.6–37 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-Goñi, 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 BP and 34.8–33.8 Kyr BP may be connected with warmer and drier conditions between MIS 3 climatic oscillations (Sc2a, Brñ, 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

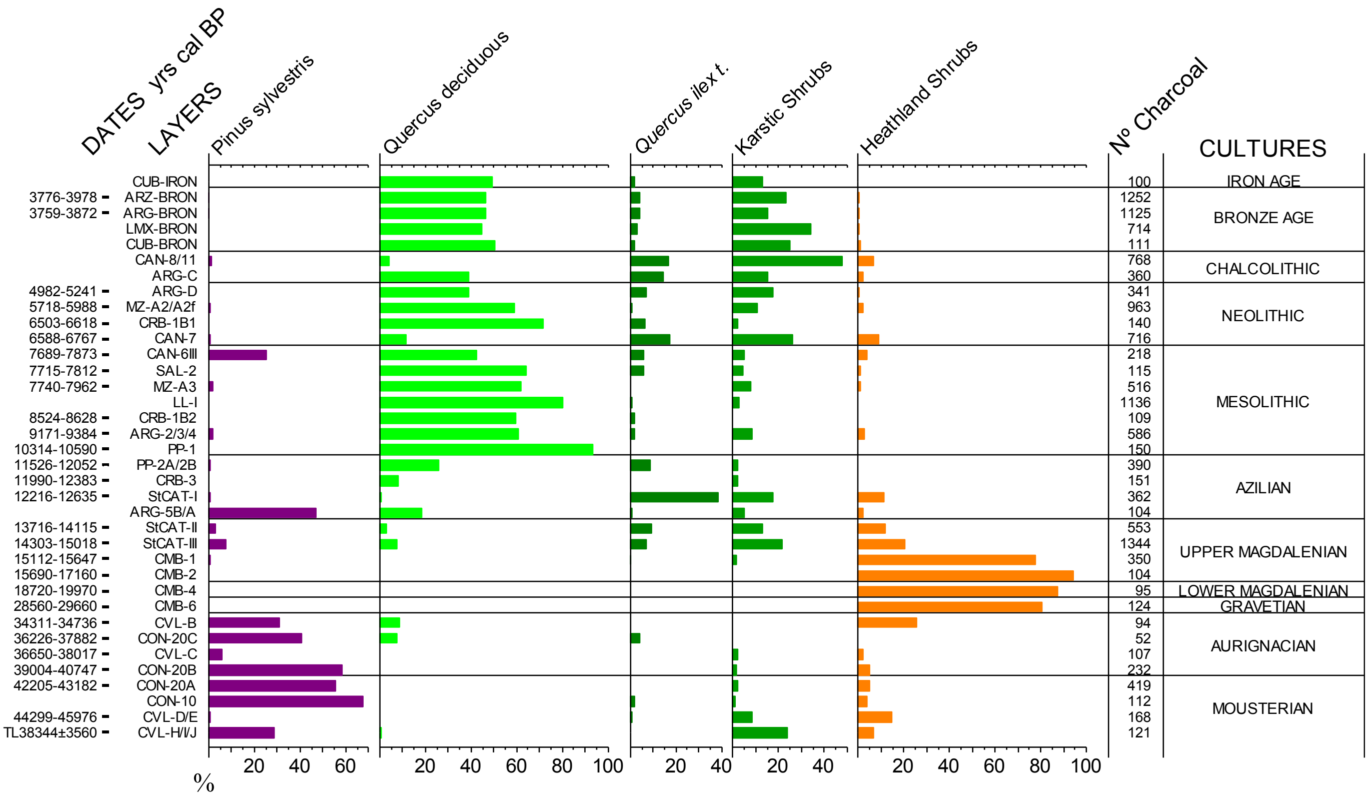

Fig. 4. Synthetic charcoal diagram with the evolution of *Quercus ilex*-type among other selected key taxa: deciduous *Quercus*, *Pinus*, Heathland* and Karstic** shrubs throughout the Upper Pleistocene and Holocene (from Mousterian to Iron Age). See Table 3 for the full name of sites and their corresponding abbreviations. *Heathland shrubs includes Fabaceae family (mainly *Cytisus* and *Ulex*) and *Erica* sp. **Karstic shrubs group mainly integrates the shrub vegetation growing up in the karstic massifs (calcareous substrates) (after Cendrero et al., 1986) located on littoral and pre-littoral areas of the studied region nearby evergreen oak plant communities with which share the same substrate: i.e. *Cornus sanguinea*, *Sambucus nigra*, *Crataegus monogyna*, *Prunus amygdalus*, *P. spinosa*, *P. mahaleb*, *P. avium*, *Arbutus unedo*, *Rhamnus alaternus*, *Laurus nobilis*, *Phillyrea* sp., *Pistacia terebinthus*.

Upper Pleistocene would therefore be located nearby the inland upper mountain valleys in Asturias (Sc2a, Nal), while the lower Cantabria 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

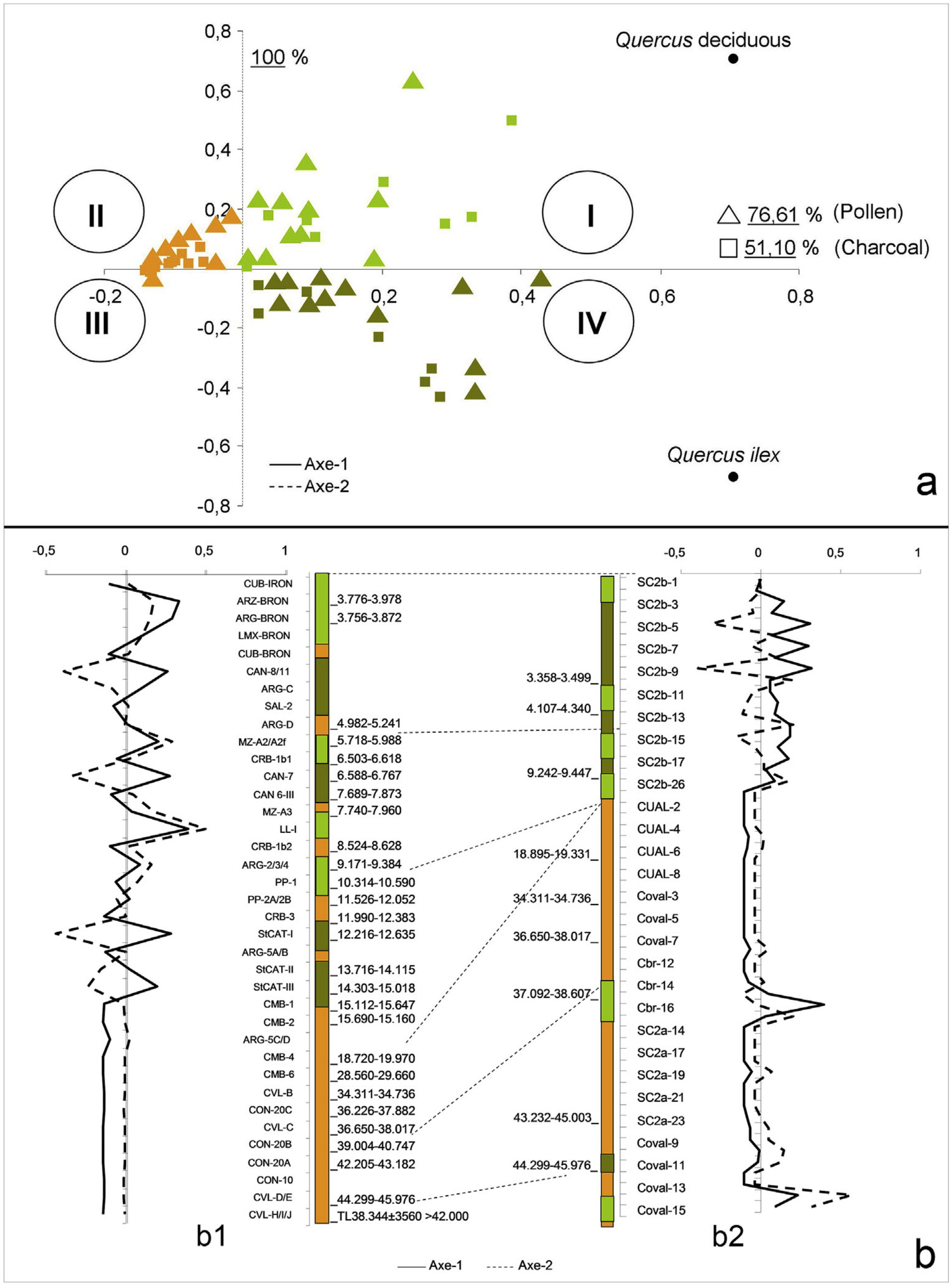

Fig. 5. a: Principal Component Analysis (PCA) showing the integrated pollen and charcoal information about evergreen-deciduous oaks relationships. Pollen and charcoal are represented by triangles and squares respectively. Deciduous *Quercus* appears in Quadrant I and *Quercus ilex*-type appears in Quadrant 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.)

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 provided 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

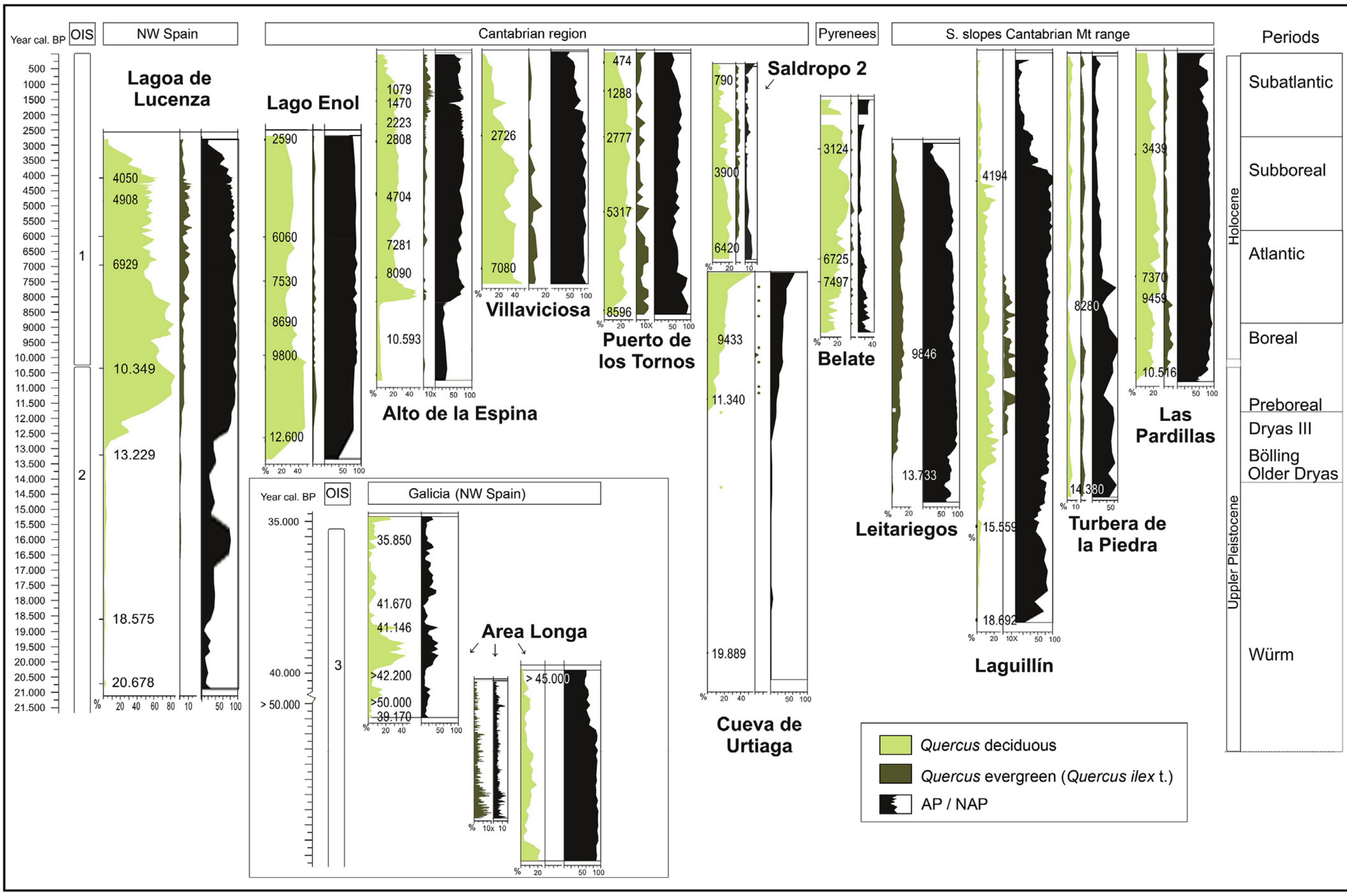

Fig. 6. Additional pollen curves covering all northern Iberian territories both from W to E and from N to S of the Cantabrian mountain range to complement the evolution of both species of *Quercus* in N Spain (redrawn after Carrión et al., 2012). The names and information of sites selected are shown in italics in Table 1 except for *Saldropo 2* included in Table 2.

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

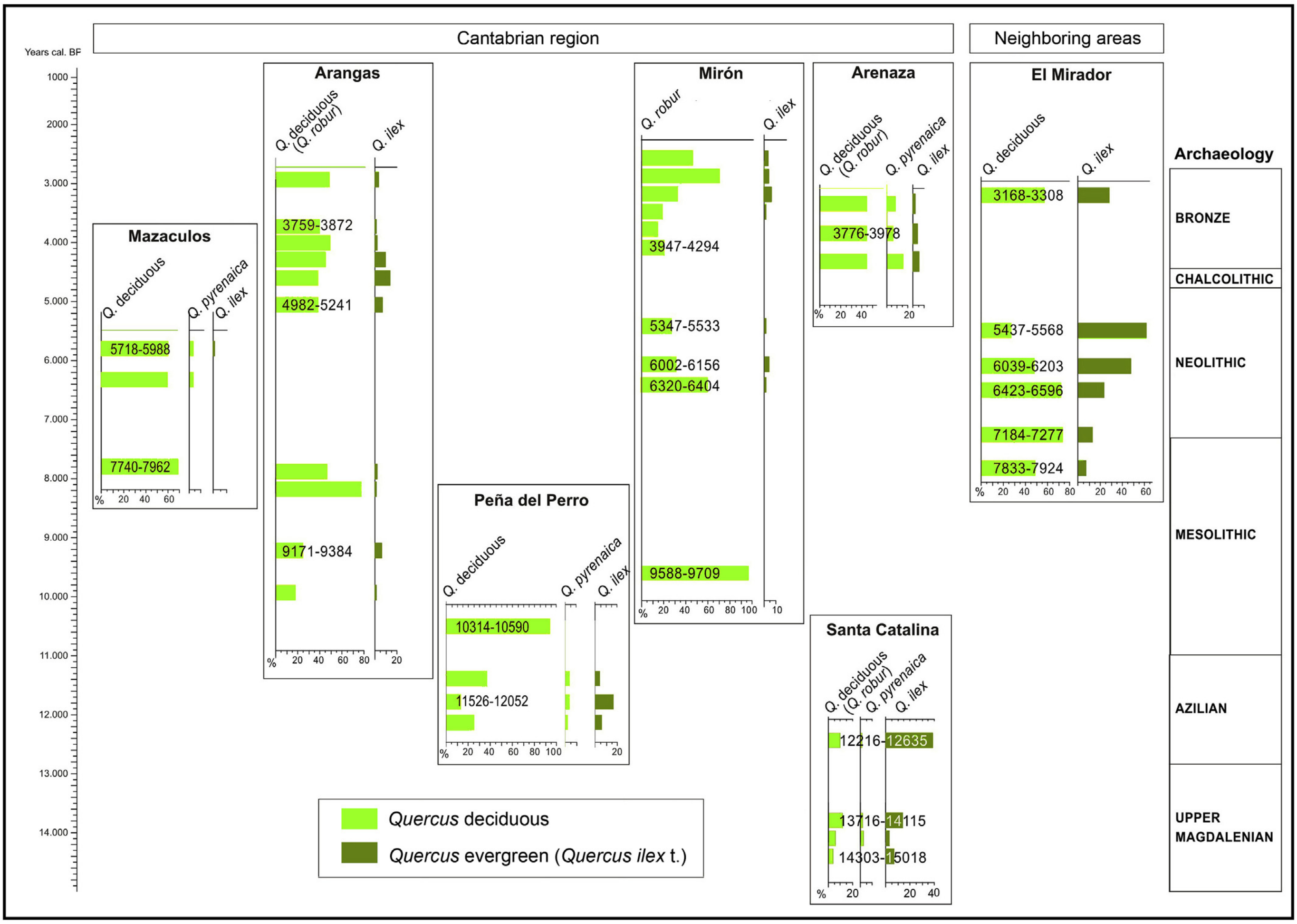

Fig. 7. Evolution experienced by deciduous and evergreen *Quercus* in N Spain from selected charcoal sites located both in a N-S and E-W gradients (redrawn from Carrión et al., 2012: El Mirador; Uzquiano, 1992, 1995 and unpublished data: Mazaculos, Peña del Perro, Santa Catalina, Arangas; Uzquiano and Zapata, 2000: Arenaza; Zapata, 2012: El Mirón).

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 practises 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 practises 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 Chalcolitic (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 (Carrión 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 contemporaneous 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; Carrión 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 palynological 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.

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