Taxonomic composition of the Holocene forests of the northern coast of Spain, as determined from their macroremains

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Abstract: Eight sites distributed over a distance of some 400 km of the Cantabrian coast (northern Spain) provided 153 wood, 50 fruit and over 350 leaf remains belonging to the area's Holocene forests. The high taxonomic precision with which these macroremains were identified (in many cases at the species level), plus the accurate information available regarding the original growth locations of these plants, provide new geobotanical insights into the history of northern Spain's Atlantic forests. Radiocarbon dating of the wood samples showed the collected material to have lived between 8550 and 800 cal. BP. Analysis of the macroremains showed the deciduous mixed forests of the Holocene to contain a majority of *Quercus robur* and *Corylus avellana*, accompanied by *Acer pseudoplatanus*, *Ulmus minor*, *Castanea* sp., and hygro-thermophilous taxa (*Arbutus*, *Laurus* and *Vitis vinifera*). The remains of hygrophilous communities, dominated by *Salix atrocinerea*, *Alnus glutinosa* and *Fraxinus* sp., show these to have expanded during the Holocene. The absence of conifer macroremains is interpreted as reflecting the disappearance of Würmian conifer populations at the beginning of the Holocene. The different taxa (eg, *Ilex* spp. and *V. vinifera*) that survived the last glaciation in the refugia offered by Spain's northern coast persisted in the same areas during the Holocene. A leaf sample of *Ulmus minor* dating to 3950 ± 120 cal. BP reveals for the first time the natural occurrence of this species on the northern coast of Spain.

Key words: Macroremains, Iberian Peninsula, coastal forest, vegetation history, taxonomic composition, Holocene, *Quercus robur*, *Ulmus minor*, *Vitis vinifera*.

Introduction

Over the last 20 years, palaeobotanical studies of non-archaeological substrates have considerably increased our knowledge of the Quaternary vegetation over large parts of Europe's Atlantic regions (Peñalba, 1994; Ramil-Rego *et al.*, 1998a; Birks, 2003; Froyd, 2005). The coastal areas themselves, however, have been the exception, since the record of their past vegetation is generally poor (Gómez-Orellana, 2002; García-Amorena *et al.*, 2007). Palaeobotanical studies of prehistoric human settlements have therefore provided the main basis for reconstructing the botanical history of northern Spain's Atlantic coast. Broadleaved deciduous species and thermophilous elements seem to have been a feature of the Iberian Atlantic facade over the last 15 000 years (Isturiz and Sánchez Goñi, 1990; Mary, 1990; Sánchez Goñi, 1990; Uzquiano, 1992; Iriarte, 2003). However, the records suggesting this are biased by stratigraphic problems (animal and human-induced erosion, pollution via percolation, etc.) and representation constraints (eg, plants that are useful to humans may be found more often; extrapolation to the natural landscape may therefore be unreliable) (Sánchez Goñi, 1993).

Only a few palynological studies on non-archaeological sediments have provided precise data regarding the natural palaeovegetation of Spain's northern coast, but all report the important role of deciduous *Quercus*, *Corylus* and *Alnus* during the Holocene (Mary, 1973; van Mourik, 1986; García Antón *et al.*, 2006). Nonetheless, the low taxonomic precision of identifications made using the pollen record hampers the interpretation of vegetation dynamics (Bradshaw, 1991; Birks and Birks, 2000); information is simply lacking on the exact vegetation types that were present and the species that were most characteristic. This has prevented an accurate assessment being made of the role of Spain's northern coast as a provider of refugia for forest vegetation during cold climatic phases. Indeed, some authors questioned whether this area truly provided such refugia (Turner and Hannon, 1988; Huntley, 1990; Bennett *et al.*, 1991).

Fortunately, macroremains found *in situ* on unaltered substrates are an exceptional source of geobotanical data and provide very precise information on the local distribution of plant species (Willis and van Andel, 2004). Such information is particularly

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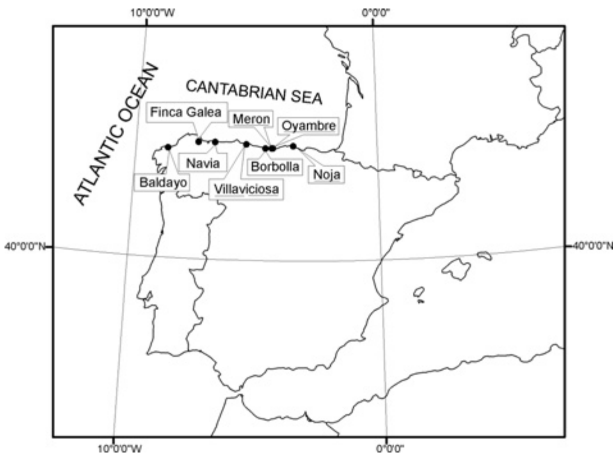


Figure 1 Location of the study sites; the sites underlined have been the subject of other palaeoecological studies (Villaviciosa (Pagés *et al.*, 2003), Merón, Oyambre (Mary, 1990; Garzón *et al.*, 1996) and Noja (Cearreta, 1993; Salas *et al.*, 1996))

important when attempting to identify refugia. Sites with such material have shown the western coast of Iberia to have provided refugia where *Pinus* gr. *sylvestris-nigra-uncinata* managed to escape the conditions of the Würm glaciation (García-Amorena *et al*., 2007). This paper reports the analysis of numerous plant macroremains (wood, branches, leaves, fruits and seeds) collected at Holocene sites along a 400 km strip of Spain's northern coast. Wood-, fruit- and cuticle-based analyses allowed the identification of these fossils with great taxonomic precision; in many cases identifications were possible at the species level. The information provided by these analyses improves our knowledge of the composition of the Holocene forest of Spain's northern coast.

Study area

Macroremains were collected at eight sites along a coastal strip that extended 400 km along Spain's northern coast from the eastern part of Cantabria (Noja) to northern Galicia (Baldayo) (Figure 1).

This area, located between 42º and 44ºN, is bound to the north by the Cantabrian Sea and to the south by the Cantabrian Mountains. Steep rivers flow from these mountains to the sea, eroding a complex geological system to form narrow canyons that widen towards the coast. Metamorphic and sedimentary Palaeozoic to Cenozoic rocks provide a rugged coastal relief, with steep cliffs alternating with bays and estuaries containing Quaternary sediments (Vera, 2004). These sediments sometimes preserve peat bog deposits and ancient forest soils rich in fossil plant material (eg, Garzón *et al*., 1996; Salas *et al*., 1996; García Antón *et al*., 2006).

A number of marine to continental abrasion platforms are found in this coastal area, from 260 m above sea level (a.s.l.) down to 1 m a.s.l. These platforms correlate well with the warmest periods of the Pliocene–Pleistocene and the Flandrian transgression, when the sea level reached 1 m a.s.l. some 6000–7000 years BP (Mary, 1983, 1990; Garzón *et al.*, 1996). However, the Holocene sea level maximum is not evident all along the coast. Two transgressive pulses at 8000 and 3000 BP are recorded at some sites (Cearreta, 1993) while at others there is no evidence of sea levels higher than those of the present (Alonso and Pagés, 2000; Soares de Carvalho *et al.*, 2002; Pagés *et al.*, 2003). Tectonic movements and eustatic processes have sometimes been argued to explain these discrepancies (Mary, 1990; Granja and De Groot, 1996; Zazo *et al.*, 1997; García-Amorena *et al.*, 2007).

The study area belongs to the Atlantic European biogeographic region (Ozenda and Borel, 2001; Rivas-Martínez *et al.*, 2002). As a consequence of the warm Gulf stream, the present climate is characterized by mild conditions, with annual mean temperatures ranging from 12ºC to 15ºC and no days of frost (Font Tullot, 1983). The annual rainfall, distributed equally throughout the year, generally exceeds 1000 mm. A summer drought of less than two months occurs only at the westernmost extreme (Allué, 1990).

The area has been highly modified by intense human activity. The coast is home to cropland, pasture and tree plantations (eg, *Pinus pinaster*, *P. radiate* and *Eucalyptus* spp.), and urbanization has occurred along its entire length. Only remnants of the original vegetation can be found, and the natural landscape is now dominated by secondary shrub formations (*Ulex* spp., *Erica* spp., *Cytisus* spp., and *Pteridium aquilinum)*, the result of the abandonment of agriculture and stock raising (Peinado and Rivas-Martínez, 1987; Costa *et al.*, 1997; Ruiz de la Torre, 2002). Patches of deciduous mixed forests can be found, however, mainly on siliceous soils in the west of the study area. Oak (*Quercus robur*) is the dominant canopy species; ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), birch (*Betula alba*), sweet chestnut (*Castanea sativa*), cherry (*Prunus avium*) and hazel (*Corylus avellana*) commonly appear as companion species. Pyrenean oak (*Quercus pyrenaica*) forests also occur in the most xeric areas. Well preserved Mediterranean holm oak (*Quercus ilex* subsp. *ilex)* woodlands are found on limestone substrates, which predominate in the eastern half of the study area.

Small, Mediterranean, sclerophyllous trees and shrubs (eg, *Laurus nobilis*, *Arbutus unedo*, *Phillyrea* spp., *Olea europea*, *Viburnum tinus* and *Rhamnus alaternus*) locally enrich the forest understorey all along the coast. Hygrophilous taxa (eg, *Alnus glutinosa*, *Populus nigra*, *Salix* spp.) are found along the estuaries and rivers. Elm (*Ulmus glabra*), beech (*Fagus sylvatica*) and large-leaved linden (*Tilia platyphyllos*) increasingly appear towards the interior.

Site descriptions

Eight coastal sites were sampled between 1994 and 2005 (Figure 1). These are home to Quaternary sediments that contain remains of the forests that once existed in the vicinity (Vera, 2004).

Sites subject to tidal flux or wave erosion

Remains of peat bog sediments were found on beach surfaces and cliffs after storm events at the Noja, Oyambre, Merón and Baldayo sites (Figure 1).

The Noja site (43º28′N, 3º29′W; 0 m a.s.l.) is a karst depression infilled with continental sand, silt and clay sediments. In these sediments, several peat bog layers up to 100 cm thick, dated to between ~3230 and ~4590 cal. BP, are found intercalated between 0 and 4 m below sea level (Cearreta, 1993; Salas *et al.*, 1996). Wood and root remains were found in their living positions in these peat bog sediments.

The Merón and Oyambre sites (43º23′N, 4º22′W; 0 m a.s.l. and (43º23′N, 4º20′W; 0 m a.s.l., respectively) consist of Holocene sediments that infilled the course of a river that cut into a sandy beach (dated to >7000 yr BP) that lies over a Cenozoic marl layer. The Holocene deposit is formed of a sequence of 3 m thick sediments (on average) spreading along more than 2000 m of the coast, with a peat bog at the base (6000–7000 yr BP) and aeolic sand at the top (Garzón *et al.*, 1996). *In situ* stumps, logs, leaves, fruits and seeds were found in the peat bog sediment.

At the Baldayo site (43º17′N, 8º39′W; 0 m a.s.l.), Quaternary sand sediment lies on a Precambrian granite basement (Vera, 2004). In the cutting left by marine tidal currents, a peat bog layer some 30 cm thick protrudes from the sand sediment for some 500 m. In this layer, many non-*in situ* ligneous remains were found.

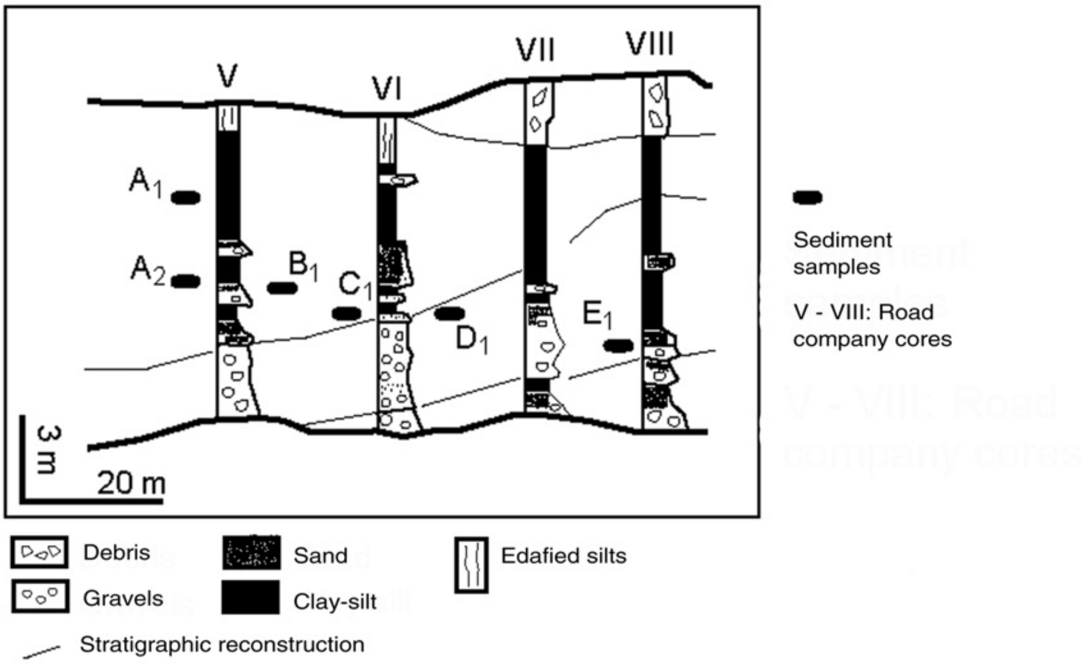


Figure 2 Stratigraphic reconstruction of the Villaviciosa estuary (after Pagés *et al.*, 2003) showing the original location of the A_1, A_2, B_1, C_1, D_1 and E_1 sediment samples. Grey lines: stratigraphic discontinuities. V–VIII: cores performed by the road company

Estuaries

The recent construction of the Cantabrian highway exposed a number of Holocene organic-rich layers in several estuaries (Pagés *et al*., 2003; García Antón *et al*., 2006). Logs, leaves, fruits and seeds were collected from these layers at road cuttings, and bulk material was extracted from pillar base excavations at three estuaries.

The deposits at Villaviciosa (43º29′N, 5º26′W; 12 m a.s.l.) and Navia (43º31′N, 6º43′W; 4 m a.s.l.) consist of Holocene infills of different thickness lying over ancient valleys in Jurassic (Permotrias and Bundsandstein) materials (Vera, 2004). The Villaviciosa sedimentary sequence, revealed by the cores taken by the civil engineering company that built the road, allowed the reconstruction of the estuary's infilling process. The sequence was similar to the Navia sequence (Pagés *et al.*, 2003; García-Amorena, 2007), and the cores showed that an active channelling process occurring on sandy tidal flats predominated during the early Holocene. This system was substituted by marshes and muddy tidal flats caused by the increase in sea level around 7000 BP. A continental facies covered the marshes during the second part of the Holocene owing to the relative stabilization of the sea level (Figure 2). In this estuary, however, the lateral displacement of the channels complicates the interpretation of the infilling process (Pagés *et al.*, 2003).

Inland sites

Two sites were sampled in inland areas where the proximity of the ocean can only be noticed by its effect on the climate. The Finca Galea site (43º31′N, 7º24′W; 65 m a.s.l.) is located 12 km from the coast in a wide valley dominated by 833 m high hills (Sierra Togiza). A number of trunks were extracted from the Holocene sediment covering the granite basement (Vera, 2004) thanks to civil engineering excavations in the area. The La Borbolla site (43º23′N, 4º37′W; 50 m a.s.l.) is located in a narrow valley 2 km from the coast and is surrounded by 220 m high hills (Sierra de la Franca). Here, Holocene sediments cover Jurassic sandstone and Carboniferous limestone basements. Non-*in situ* trunks were extracted from a peat bog sediment at this site.

Methods and materials

At the Finca Galea, La Borbolla and Navia sites, the study material was obtained by excavation employing different methods. At the Finca Galea site, a digger extracted logs at depths of 0.5–2 m during the laying of a pipe. At the La Borbolla site, fossil trunks were dug out with a hoe from a peat bog 50 cm below the ground level. At the Navia estuary, drilling equipment pulled out wood pieces from depths of up to 28 m.

Surface sampling was performed by collecting all wood and fruit remains that protruded from the Baldayo, Oyambre, Merón, Noja and Villaviciosa sites. At the sites subject to tidal flux or wave erosion (Baldayo, Oyambre, Merón and Noja), sampling was performed after storm events when tidal fluctuations were at their maximum. At Villaviciosa, a sediment profile 200 m long × 30 m deep exposed during the construction of the Villaviciosa tunnel was sampled (Figure 3). This surface (located between cores five and eight taken by the construction company; Figure 2) was divided into five strata (A to E) to facilitate surface sampling (Figure 3). All macroremains were labelled according to their stratigraphic position.

Stratified sampling was also performed at the Baldayo, Oyambre, Merón, Noja and Villaviciosa sites. Here, 5 cm × 10 cm × 10 cm sediment samples were taken from all the organic-rich layers to further search for leaves and other small (<5 mm) remains. All sediment samples were sieved with 50 g/l tetrasodium pyrophosphate ($Na_4P_2O_7$ $10H_2O$) to dilute the clay. Plant remains were carefully brushed and, when necessary, immersed in 30% fluoric acid (HF) to remove the remaining silica.

Thin laminas of the main planes (see Figure 4) were prepared from the ligneous samples, and identifications made using keys and descriptions (Greguss, 1945, 1959; Jacquiot *et al.*, 1973; Core

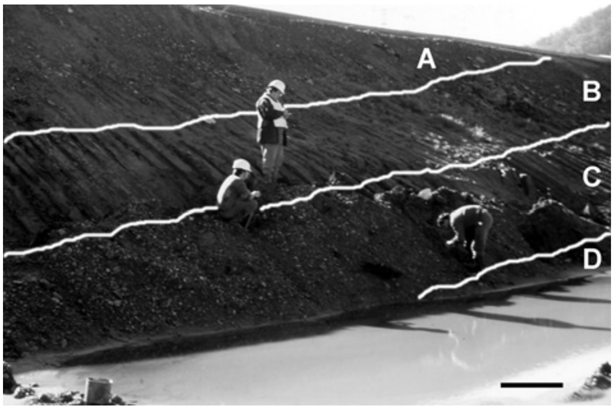


Figure 3 The Villaviciosa site (Asturias); the locations of the sampled A, B, C and D are shown. Scale bar: 1 m

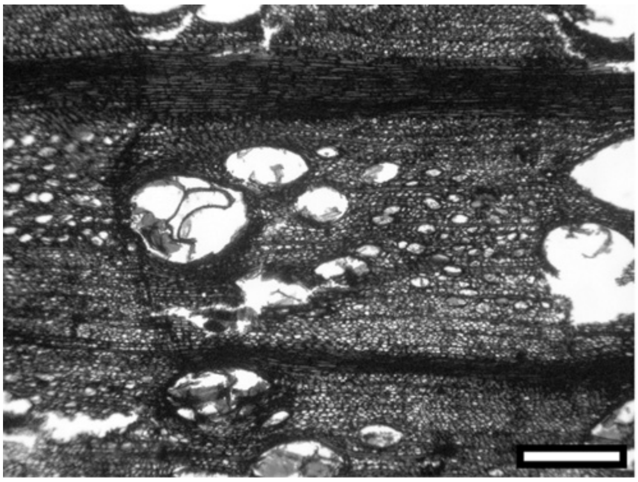


Figure 4 Transverse section of *Quercus* subgen. *quercus*. Scale bar: 200 μm

et al., 1979; Wheeler *et al.*, 1986; Schweingruber, 1990; Dallwitz *et al.*, 1993 onwards; Richter and Dallwitz, 2000 onwards). All identifications were assessed by comparing samples with present-day material belonging to the wood collection of the Escuela Técnica Superior de Ingenieros de Montes [ETSIM], Universidad Politécnica de Madrid.

For the analysis of the leaf samples, 5 mm × 5 mm pieces from the central area – where the epidermal variables are more stable (Poole *et al.*, 1996) – were cut and bleached in 4% sodium hypochlorite ($NaHClO_2$) for 30 s. After rinsing for 5 min in distilled water the cuticles were mounted in glycerine jelly on microscope slides for light microscopic analysis (see Figure 4). Cuticle characteristics were identified using keys and descriptions (Wilkinson, 1979; Peñas *et al.*, 1994; Westerkamp and Demmelmeyer, 1997; Uzunova *et al.*, 1997). The leaf samples were then identified at the species level according to their cuticle and morphological characteristics (Castroviejo *et al.*, 1986–2004), and by comparing them with present-day material.

All the sampled layers from all eight sites were subjected to conventional ^{14}C dating. With the exception of the Villaviciosa-A1, Oyambre and Noja layers, for which radiocarbon dates were already available, all the fossil wood material collected was sent to Beta Analytic Inc. (University Branch, Miami FL, USA) or Quadru, CSIR Environmentek (Brummeria, Pretoria, South Africa) for analysis. Conventional radiocarbon ages were calibrated and are expressed as cal. BP (Stuiver *et al.*, 2005; Reimer *et al.*, 2004).

Results

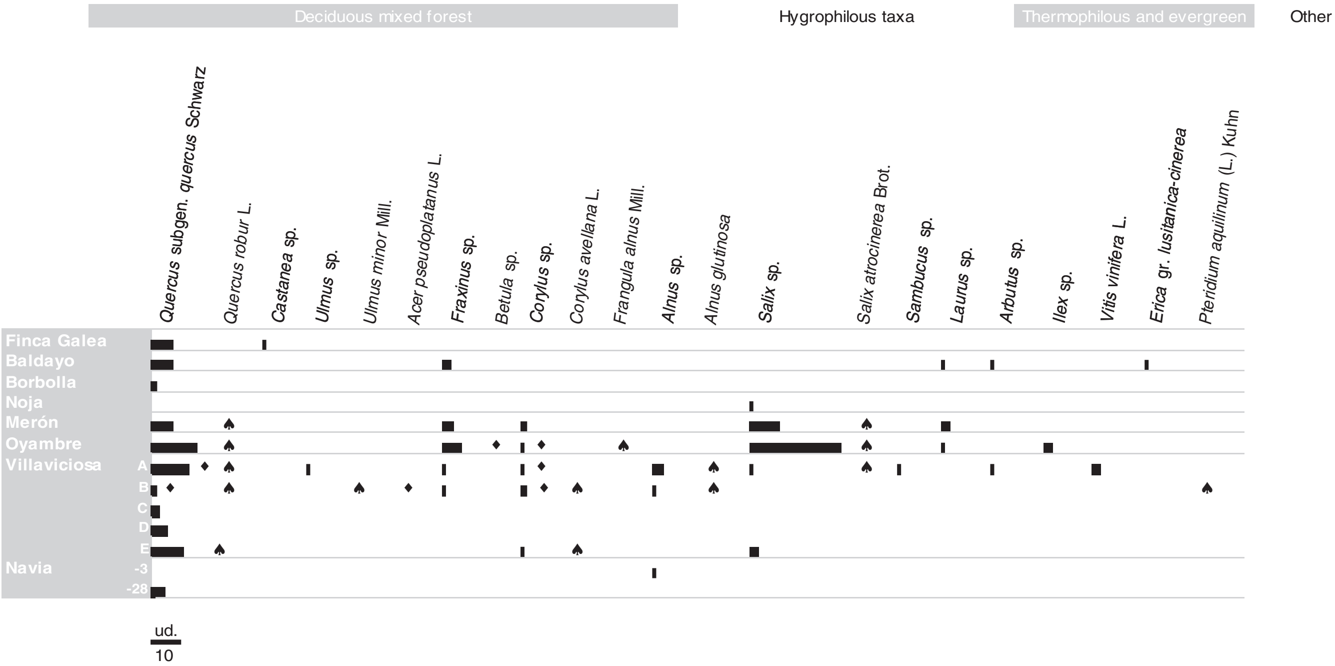
Radiocarbon dating showed that the collected material spanned the time period from 8550 to 800 cal. BP (Table 1). Except for the Villaviciosa site, which covered the period 7260 to 1130 cal. BP, all sites spanned less than 2000 successive years. The most recent sediments (Baldayo and La Borbolla) were younger than 900 cal. BP. The deepest layers at Navia, Merón, Oyambre and Villaviciosa held the remains of vegetation dated to >6000 cal. yr BP.

Table 1 ^{14}C radiocarbon dates (BP; before present) calibrated (2σ cal. BP) using the CALIB 5.0 software with the IntCal04 data set (Reimer *et al.*, 2004; Stuiver *et al.*, 2005)

Site		^{14}C dates (uncal. BP)	^{14}C date (2σ cal. BP)	Reference
Baldayo		980 ± 50	870 ± 90	BAL.02.C[a]
Finca Galea		860 ± 50	800 ± 120	FG.3[a]
		2000 ± 50	1960 ± 100	FG.9[a]
Navia		7810 ± 50	8550 ± 110	E7-P3[a]
Villaviciosa		1230 ± 70	1130 ± 160	Pages *et al.* (2003) (A1)
	A	3750 ± 40	4110 ± 130	VIL.A02.O.26.01.03 (A2)
	B	3620 ± 50	3950 ± 120	VIL.10[a] (B1)
	C	5130 ± 70	5910 ± 250	Ria VIL.C1.01.[b] (C1)
	D	4750 ± 70	5460 ± 140	Ria VIL.D.O.[b] (D1)
	E	5130 ± 60	5860 ± 130	VIL.E1.O[a] (E1)
		6360 ± 70	7260 ± 160	VIL.01.AS.19.6.04[a] (trunk)
La Borbolla		1000 ± 50	880 ± 90	ROD.02[a]
Oyambre		5880 ± 30	6710 ± 70	Mary (1990)
		5250 ± 20	6050 ± 120	Mary (1990)
		5300 ± 120	6030 ± 280	Mary (1990)
		6210 ± 85	7100 ± 210	Garzón *et al.* (1996)
Merón		6180 ± 70	7030 ± 220	M-30[a]
		5920 ± 70	6730 ± 180	M1B[a]
Noja		4070 ± 100	4590 ± 240	Cearreta (1993)
		3080 ± 100	3230 ± 350	Mary (1990)

[a]Beta Analytic Inc. (University Branch, Miami FL, USA); [b]Quadru, CSIR Environmentek (Brummeria, Pretoria, South Africa).

Table 2 Macroremains identified at the eight sites and their ecological groups. The sites appear from younger (800 ± 90 cal. BP) to older (8550 ± 110 cal. BP)



Type of remains: wood (solid rectangles), leaves (leaf symbols) and fruits or seeds (solid diamonds). The scale bar refers to the number of wood samples found.

A total of 50 fruits, 153 wood samples and over 350 leaf remains were recovered and identified from the eight sites (Figure 4). At the Finca Galea site the digger extracted nine logs 38–80 cm in diameter. Two logs, 30 and 40 cm in diameter, were dug out from the La Borbolla peat bog. Four logs up to 60 cm in diameter were drilled out at the Navia estuary from depths of between 3 and 28 m. At the Merón site, 28 wood remains 5 to 30 cm in diameter were found. Five of these were found *in situ*. At the Oyambre site 24 fruit remains and 36 woody remains (nine *in situ*) were collected. Over 200 leaf fragments were recovered from the Oyambre and Merón sediment samples. Several wood samples up to 10 cm in diameter were taken from branches exposed at the Noja peat bog after a storm. At the Baldayo site, 14 ligneous remains less than 15 cm in diameter were collected from the peat bog outcrop. Finally, five sediment samples were taken from the five organic-rich levels found over the Villaviciosa profile (A1 at 3 m depth, A2 at 6 m depth, B1 at 8 m depth, D1 at 10 m depth and E1 at 15 m depth) (Figure 2). Surface and stratified sampling returned 60 wood remains up 60 cm in diameter and 26 fruit remains.

Quercus subgen. *Quercus* Schwartz (Figure 4) (ie, *Q. robur* and *Q. petraea*) accounted for the majority of the remains identified, followed by *Salix* sp., *Corylus* sp. and *Alnus* sp. At the Villaviciosa site, over 150 leaf remains revealed the presence of *Quercus robur* (Figure 5), *Corylus avellana* and *Alnus glutinosa* between 1000 and 6000 cal. BP (Tables 1 and 2). Three *Vitis vinifera* wood remains dated to >4000 cal. yr BP were also found in the Villaviciosa A and B layers. Other taxa enriched the fossil record of the Villaviciosa site (eg, *Fraxinus* sp., *Ulmus minor* (Figure 6), *Acer pseudoplatanus*, *Sambucus* sp., *Arbutus* sp. and *Pteridium aquilinum*).

The oldest sites (Navia, Oyambre and Merón) were rich in *Quercus* wood remains. At the Oyambre and Merón sites the percentage of *Salix* sp. wood was greater than that of *Q.* subgen. *quercus* wood. *Ilex* sp., *Laurus* sp. or *Fraxinus* sp. Ligneous remains of *Corylus* sp. were represented to an even lesser extent. Many *Corylus* sp. fruits and one *Betula* sp. seed were also found (Table 2). Over 250 *Q. robur* and 100 *Corylus avellana* leaf fragments were identified at the Oyambre and Merón sites. Three *Q. robur* type leaves from the Merón site had *Q. petraea* trichomes, indicating hybridization. A complete fossil leaf of *Frangula alnus* revealed the presence of this species at Oyambre some 6000 to 7000 years ago.

At the Noja site, only wood remains of *Salix* sp. (dated to 3000 to 4000 cal. BP) were identified. One *Castanea* sp. (800 cal. BP) and eight *Q.* subgen. *quercus* (one of them dated to 1960 cal. BP) logs were found at the Finca Galea site. The Baldayo site was the richest of the youngest sites (870 cal. BP), and showed small numbers of *Fraxinus* sp., *Laurus* sp., *Arbutus* sp. and *Erica cinerea-vagans* group macroremains, accompanied by others of *Q.* subgen. *quercus*. At the La Borbolla site, two *Q.* subgen. *quercus* trunks dated to 880 cal. BP were identified (Tables 1 and 2).

Discussion

The macroremains found at the eight study sites provided precise information regarding the Holocene vegetation of the northern coast of Spain.

Composition of the coast's deciduous mixed forests during the Holocene

The presence of wood belonging to *Quercus* subgen. *Quercus*, ie, *Q. robur* and *Q. peatraea*, at almost all the study sites shows these species grew on the Cantabrian coast during the Holocene (Table 2). The numerous *Q. robur* leaves found at Oyambre, Merón and Villaviciosa show (for the first time) the presence of this species in these areas from 7030 cal. BP to 1130 cal. BP. The available pollen data for this area concur with these findings, showing that deciduous *Quercus* species expanded at the beginning of the Holocene to occupy the spaces where open woodlands of *Juniperus*, *Pinus* and

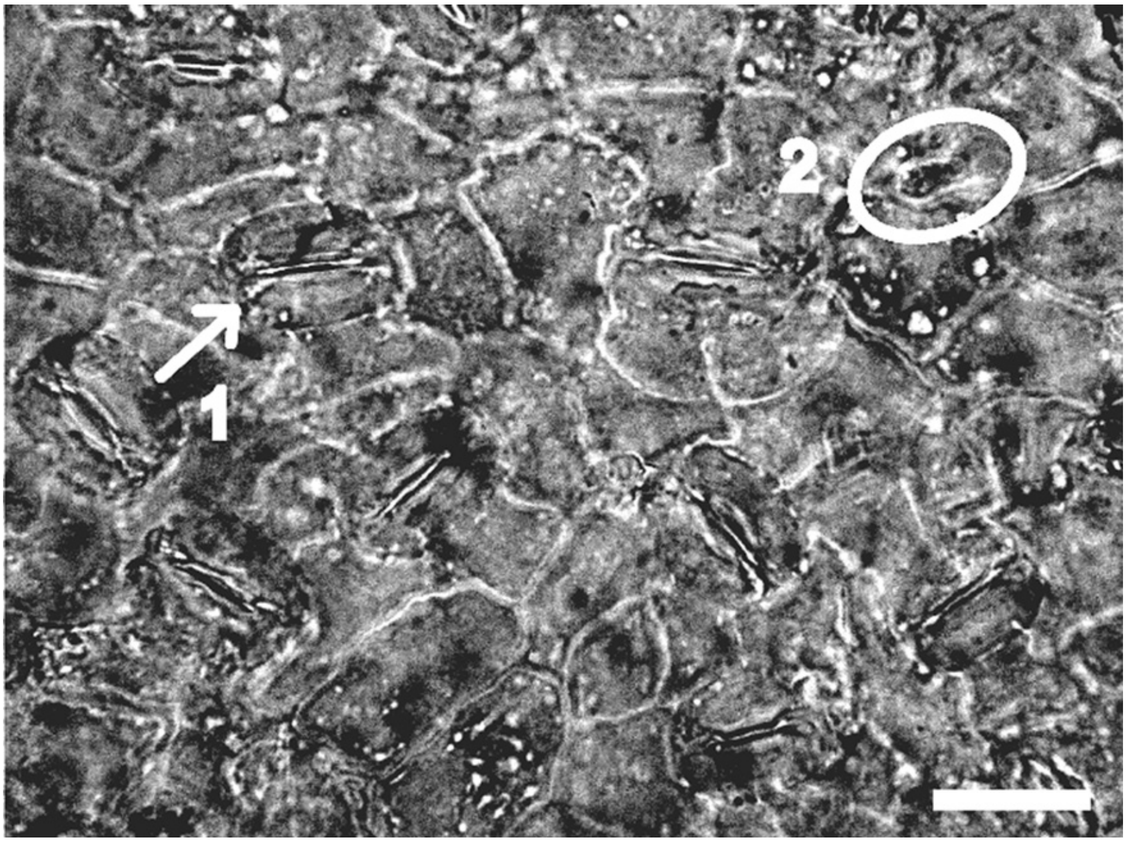


Figure 5 Abaxial leaf cuticle of *Quercus robur* with a stoma (1) and a glandular trichome (2). Scale bar: 20 μm

Figure 6 Fossil leaf of *Ulmus minor* (Villaviciosa B; 3950 ± 120 cal. BP). Scale bar: 1 cm

Betula formerly existed (Oldfield, 1964; Saá and Díaz-Fierros, 1988; Mary, 1990; Iriarte, 2003; García Antón *et al.*, 2006).

No *Q. petraea* leaf was found among the more than 250 *Quercus* leaf fragments from the Oyambre, Merón and Villaviciosa sites from 7000 cal. BP onwards. At present, *Q. petraea* is found at over 500 m a.s.l. in the Cantabrian Mountains. Treeless landscape characterized these mountains during the Lateglacial (10 000–15 000 years ago) (Peñalba, 1994), suggesting that during this period both oak species may have lived close together on the coast, giving rise to the hybrids found for the Holocene. At the onset of the Holocene, however, *Q. petraea* had to migrate to higher altitudes while *Q. robur* remained at the coast. Although isolated *Q. petraea* remnant trees and hybrids may have survived during this period, the separation of the two parent species would have minimized the introgression of *Q. petrea* into *Q. robur*, thus explaining the very few *Q. petraea* trichomes found in fossil *Q. robur* leaves.

The number of *Corylus* sp. remains found at the Oyambre, Merón and Villaviciosa sites show that it was a very common taxon from 7000 cal. BP onwards. Additionally, the few *Corylus* sp. leaves found in the deepest layers of the Villaviciosa site show characteristics exclusive to *C. avellana* (Westerkamp and Demmelmeyer, 1997) (Table 2). Thus, this species must have been present along the Cantabrian coast during the mid Holocene. This agrees with other palaeobotanical data from this region that show the importance of hazel in the mixed forests of Spain's northern coast during the Holocene (Mary, 1973; López *et al.*, 1993; Iriarte, 2001; Iriarte and Arrizabalaga, 2003; García Antón *et al.*, 2006). The more than 40 nuts found at Oyambre and Villaviciosa (dated from ~7000 to ~1000 cal. BP) might have to do with human activity; hazel nuts have a high nutritive value and hazel trees colonize open areas after timber felling (Iriarte, 2003). However, the continuously high pollen percentages for *Corylus* since the onset of the Holocene (Oldfield, 1964; Saá and Díaz-Fierros, 1988; García Antón *et al.*, 2006) show the importance of hazel in the study area during this period, independent of any human activity.

Other deciduous broadleaved taxa were also found at the study sites: *Acer pseudoplatanus* and *Ulmus minor* (3950 cal. BP), *Fraxinus* sp. (7060 to 1130 cal. BP), *Castanea* sp. (800 cal. BP), and some shrub species such as *Frangula alnus* (7060–6030 cal. BP). These finding complement those of earlier palaeobotanical studies that record the presence of the genera to which these belong since the Lateglacial period. These studies also recorded *Fagus* sp., *Juglans* sp., *Tilia* sp., *Carpinus* sp. and *Sorbus* sp. (Oldfield, 1964; Boyer-Klein, 1980, 1984; Dupré Ollivier, 1980; Barandiarán *et al.*, 1985; Mary, 1990; Isturiz and Sánchez Goñi, 1990; Uzquiano, 1992; López *et al.*, 1993; Sánchez Goñi, 1994; Uzquiano, 1994; García Antón *et al.*, 2006). Thus, deciduous, broadleaved forests expanded from their Atlantic coastal refugia to less protected areas at the start of the Holocene – a consequence of the climatic amelioriation that took place during the Lateglacial–Holocene transition. The macroremains identified in this study detail the taxonomic composition of these broadleaved, Holocene, Atlantic forests (*Q. robur*, *C. avellana*, *A. pseudoplatanus*, *U. minor* and *F. alnus*) and the locations where they existed.

The few remains of *Betula* sp. (only one wind-dispersed seed at the Oyambre site, 7060–6030 cal. BP) compared with those of *Corylus* sp. might reflect the differing importance of these species in the Atlantic coastal landscape. Several authors report large numbers of *Corylus* sp. remains on the Cantabrian coast and increasing numbers of *Betula* sp. towards the inland mountain areas (Menéndez Amor and Florschütz, 1961; Mary, 1973; Mariscal, 1993; Peñalba, 1994; Muñoz-Sobrino *et al.*, 2005). The *Betula* sp. seed found might belong either to the mountain stands or to an isolated *Betula* sp. tree; even today isolated trees can be found in deciduous broadleaved forests (Costa *et al*., 1997).

The Finca Galea macroremains from the northwestern coast of Iberia prove that *Quercus* subgen. *Quercus* has been present over the last 2000 years. *Castanea* sp., *Fraxinus* sp. and other thermo-hygrophilous species (*Laurus* sp. and *Arbutus* sp.) were also present for the last 1000 years at this and the Baldayo site (Table 2). Unfortunately, no other palaeobotanical records are available to help in the reconstruction of the Holocene vegetation for this area. However, the pollen information from the closest Holocene sites shows certain similarities, including the presence of deciduous broadleaved forests in the Galician subcoastal mountains and very few thermo and thermo-hygrophilous taxa (eg, *Olea europaea* and *Arbutus* sp., *Ilex* sp.) (van Mourik, 1986; Saá and Díaz-Fierros, 1988; López *et al.*, 1993; Ramil-Rego *et al.*, 1998a; Muñoz-Sobrino *et al.*, 2005). The patchy palaeobotanical record does not allow conclusions to be drawn on whether the thermo and thermo-hygrophilous pollen grains found in the subcoastal mountains represent the coastal vegetation at that time or small populations in refugia.

Ulmus minor

A complete leaf of *Ulmus minor* found in the 3950 cal. BP sediment sample (B1) from Villaviciosa (Figure 6), together with its fossil wood, shows the natural occurrence of this species along the northern coast of Spain. This species is at present widely distributed among the riparian vegetation of the Iberian Peninsula. It was believed that *U. minor* in the Iberian Peninsula was of allochthonous origin (Huntley and Birks, 1983; Richens and Jeffers, 1986). The use of elm as a cattle feed, in the manufacture of agriculture tools and as supporting material for vines adds weight to this idea. However, there is palaeobotanical evidence that suggests the Tertiary origin of the genus *Ulmus* in the Iberian Peninsula (López, 2000) and its presence during the Lateglacial and Holocene (Mary, 1973, 1990; Boyer-Klein, 1980; Mariscal, 1993; Ramil-Rego *et al.*, 1998a; López, 2000). Genetic evidence also supports the existence of authoctonous *U. minor* in the Iberian Penisula (Martín *et al*., 2006).

Hygrophilous taxa

The numerous ligneous and leaf remains of *Salix atrocinerea*, *Alnus glutinosa* (Figure 7), *Fraxinus* sp. and *Sambucus* sp. found at the coastal sites (Noja, Merón, Oyambre, Villaviciosa and Navia) representing the last ~7000 years (Tables 1 and 2) show the importance of hygrophilous communities on the northern Spanish coast during the Holocene. The coastline fluctuations that occurred during this period (Dias *et al.*, 2000) gave rise to an alternation of peaty bogs and freshwater and brackish lagoons along the coast (Garzón *et al.*, 1996; Granja and De Groot, 1996; Soares de Carvalho *et al.*, 2002; García-Amorena *et al.*, 2007). In some places on the northern Iberian coast the sea level reached a maximum of ~1 m a.s.l. 6000–7000 years ago (Mary, 1983, 1990; Garzón *et al.*, 1996). Some of the habitats associated with this level are studied in this work (ie, the Merón and Oyambre sites). Owing to tectonic movements and eustatic processes, other areas record the maximum sea level at different times (Alonso and Pagés, 2000; Pagés *et al.*, 2003). For example, the Noja site records the maximum sea level 3000 to 4000 years ago (Cearreta, 1993). Hygrophilous vegetation had to expand in the variety of habitats that accompanied these sea level fluctuations, in which the macro- and microremains were found (Table 2). Pollen diagrams produced by other authors have often recorded the importance of these taxa (Oldfield, 1964; Saá and Díaz-Fierros, 1988; Isturiz and Sánchez Goñi, 1990; García Antón *et al.*, 2006). However, *Salix* pollen is generally absent, which highlights the importance of macroremains studies when trying to acquire a detailed knowledge of past vegetation.

Thermophilous and evergreen broadleaved taxa

Among the evergreen broadleaved taxa, *Arbutus* sp., *Laurus* sp. and *Ilex* sp. were found at the Merón, Oyambre, Villaviciosa and Baldayo sites from ~7000 BP onwards. Macroremains of *Vitis vinifera* were also found in Villaviciosa for the last ~4000 years (Table 2). These remains show that hygrophilous and thermophilous taxa were present in Cantabrian coastal forests during the Holocene.

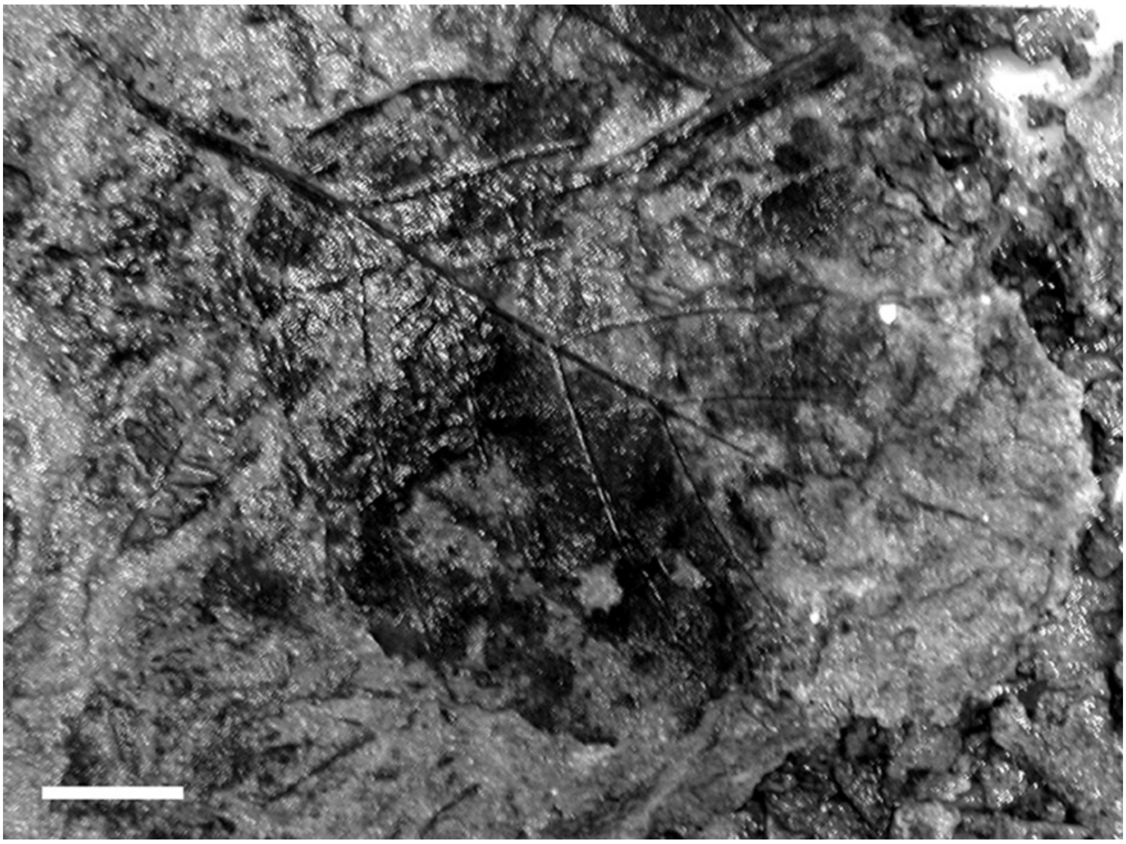


Figure 7 Fossil leaf of *Alnus glutinosa* (Villaviciosa B; 3950 ± 120 cal. BP) in the clay sediment before being sieved. Scale bar: 1 cm

In agreement with the present results, extensive data are available that support the presence of these elements close to the Atlantic coast since the beginning of the Holocene (Oldfield, 1964; Iriarte and Arrizabalaga, 2003; García Antón et al., 2006). For the Würmian period, remains of thermophilous taxa such as Phillyrea sp., Olea europaea, Arbutus sp. and Viburnum sp. have been found along the eastern Cantabrian coastline (Oldfield, 1964; Uzquiano, 1992, 1994; Iriarte and Arrizabalaga, 2003) and in the subcoastal mountains of the western part of this coastline (Ramil-Rego et al., 1998b). The occurrence of Ilex sp. in the Cantabrian region during the Pleistocene and Holocene has long been known from different pollen records for this region (Mary, 1973; Peñalba et al., 1987; Uzquiano, 1995). This evidence supports the idea that the Cantabrian coast was home to hygrophilous and thermophilous species during the late Quaternary, allowing these taxa to survive colder climatic periods. The macroremains found at the present study sites show that these species were indeed present on the Cantabrian coast during the Holocene, and record the very locations where they grew.

The finding of *Vitis vinifera* wood remains dating back to ~4000 BP at the Villaviciosa site (Table 2), together with other pollen remains older than 3000 BP at Le Moura and Villaviciosa (Oldfield, 1964; García Antón *et al.*, 2006), confirm the natural occurrence of this species on the Cantabrian coast.

Conifer taxa

The reduced importance of conifer taxa in the make-up of current lowland Cantabrian natural vegetation agrees with the absence of conifer macroremains at all the study sites. Pollen records from other Iberian Atlantic coastal sites show a similar trend, with up to only 15% *Pinus* sp. pollen recorded throughout the Holocene (Menéndez Amor and Florschütz, 1961; Oldfield, 1964; van Mourik, 1986; Saá and Díaz-Fierros, 1988; Mary, 1990; García Antón *et al.*, 2006). This may correspond to pollen of allochthonous origin or to isolated trees close to the study sites (Huntley and Birks, 1983). However, *Pinus* sp. pollen appears to have been dominant in certain areas during the first half of the Holocene, after which it almost disappeared. This is the case of the Abauntz (eastern Cantabrian coast) (López, 1982) and Los Azules (central Cantabrian coast) (López, 1981) sites, where a 40% *Pinus* sp. pollen peak has been recorded for the beginning of the Holocene. In these studies, a new increase in *Pinus* sp. pollen is recorded for the most recent past, a consequence of the introduction of *Pinus* spp. plantations (Ruiz de la Torre, 2002). In light of these records, it can be inferred that the absence of *Pinus* sp. macroremains at the present study sites is the result of there being no large *Pinus* sp. populations close by during the Holocene.

No macroremains of *Abies* sp. or *Picea* sp. were found at the study sites. This agrees with other palaeobotanical studies undertaken in this region, where *Abies* sp. pollen and *Picea* sp. wood remains appear for the last time during the Lateglacial period (Boyer-Klein, 1985; Uzquiano, 1995). The finding of *Picea* sp. pollen from ~7000 cal. BP in the Bidasoa Estuary (Cearreta *et al.*, 1997) reflects the transition between the eastern extreme of the Cantabrian mountains and the Pyrenees. However, it is likely that *Abies* sp. and *Picea* sp. would have been sparsely distributed. At the onset of the Holocene, these taxa probably disappeared (Mariscal, 1993; Peñalba, 1994; Ramil-Rego *et al.*, 1998a). The low proportion of Holocene *Pinus* sp. pollen found at the Cantabrian coastal sites suggests an extra-regional pollen source from small populations that may have temporally survived in favourable habitats during the first half of this period. These stands would eventually have become extinct – the fate suffered by *Pinus* gr. *sylvestris* populations along the northern coast of Portugal (García-Amorena *et al.*, 2007).

Human activity

The presence of some plant remains has traditionally been related to human activity, including those of *Castanea*, *Vitis vinifera* and *Ulmus minor* (Aura *et al.*, 1998; Gil *et al.*, 2004), of which several were found in this study. However, to know whether these remains are a consequence of human activity, the history of the study area has to be known. The Cantabrian coast has been densely populated by humans at least since the last glacial maximum (Madeyska and Kurenkov, 1992; Aura *et al.*, 1998), but intensive forest clearance has taken place only since the Neolithic expansion of agriculture and stock raising (Isturiz and Sánchez Goñi, 1990). The growing of *Cerealia* and *Leguminosae*, the use of fire, the stone industry, mining and logging progressively led to the demise of the area's forests over the last 6000 years (Aira Rodriguez, 1986; Martínez Cortizas *et al.*, 2005; Peña-Chocarro *et al.*, 2005). The first evidence of forest clearance dates from 2630 BP (Aira and Vázquez, 1985; Isturiz and Sánchez Goñi, 1990). From 2000 BP onwards, the mid mountain landscape became extensively altered by human activity, leading to an increase in heath shrub vegetation (ie, *Calluna* sp., *Erica* sp.) and *Castanea sativa, Ulmus minor* and *Vitis vinifera* cultivation (Torras Troncoso *et al.*, 1980; van Mourik, 1986; Díaz Losada *et al.*, 1990; Ramil-Rego *et al.*, 1998a; Ezquerra and Gil, 2004; Martínez Cortizas *et al.*, 2005; Muñoz-Sobrino *et al.*, 2005; García Antón *et al.*, 2006). The Finca Galea site contained a *Castanea* wood fossil from 800 cal. BP, and the Villaviciosa site provided *V. vinifera* wood and *Ulmus* macroremains ranging from 4110 to 1130 cal. BP (Tables 1 and 2). These records show that *U. minor* and *V. vinifera* were present before human influence on the landscape became extensive. The *Castanea* sp. remains date from a period when humans had already greatly altered their environment. However, the available palaeobotanical information suggests the natural origin of these taxa in the Cantabrian region (van Mourik, 1986; Díaz Losada *et al.*, 1990; Uzquiano, 1994, 1995; Iriarte, 2003).

Conclusions

The macroremains from the eight study sites are consistent with the results of palynological and archaeological studies of the Cantabrian region. The present work shows the added value of macroremains in their provision of precise information on the Holocene vegetation of northern Spain's coastline. The following findings are of particular importance: (a) the results provide precise information regarding the species composition of the area's Holocene forests, and show that it was similar to that of today's natural forest remnants; (b) the numerous leaves and fruits found provide critical data that allowed identification at the species level; and (c) the precise local origin of the studied macroremains shows the persistence during the Holocene of vegetation that survived the Würm period in Cantabrian coastal refugia.

A comparison of the Holocene macroremains data reported in this work with other palaeobotanical records, confirms the predominance of deciduous broadleaved forests (van Mourik, 1986; Costa *et al.*, 1990; Sánchez Goñi, 1994; Iriarte, 2003), the importance of hygrophilous communities (Dupré Ollivier, 1980; Torras Troncoso *et al.*, 1980; López, 1982; García Antón *et al.*, 2006), the remarkable presence of evergreen, broadleaved, thermophilous taxa (Uzquiano, 1994; Ramil-Rego *et al.*, 1998b) and the low abundance of plant species from secondary plant communities and the *Coniferae* group.

The results also show *Quercus robur* and *Corylus avellana* to have been widespread along the coast of northern Spain since at least 7000 cal. BP. A small introgression by *Q. petraea* provides evidence that this species migrated to the nearby mountains early in the Holocene. *Acer pseudoplatanus*, *Ulmus minor*, *Fraxinus* sp., *Castanea* sp., *Betula* sp., *Frangula alnus* and *Betula* sp. (all in small proportions) complete the composition of the region's Holocene deciduous forest. Pollen records indicate that these taxa, together with *Fagus* sp., *Juglans* sp., *Carpinus* sp., *Tilia* sp. and *Sorbus* sp., have been present in northern Spain since the last glacial period.

The numerous macroremains of *Salix atrocinerea*, *Alnus glutinosa* and *Fraxinus* sp. illustrate the importance of hygrophilous communities in the light of the increase in the Holocene sea level. The absence (or very small numbers) of *Salix* in the available pollen records highlights the importance of macroremains analysis.

The macroremains of thermophilous and hygro-thermophilous taxa revealed the presence of *Arbutus* sp. and *V. vinifera* since 4100 cal. BP, and of *Laurus* sp. and *Ilex* sp. since 7060 cal. BP along the Cantabrian coast. This is consistent with other records that report *Olea europea*, *Phillyrea* sp., *Viburnum* sp. and *Ilex* sp. woods, together with the above-mentioned species, as surviving the last glaciation on the north coast of the Iberian Peninsula.

The absence of *Pinus* macroremains, in line with the results of palynological studies, suggests that its populations almost disappeared in the first half of the Holocene.

The presence of *Ulmus minor* and *Vitis vinifera* macroremains preceding the anthropogenic spread of these taxa shows them to be natural to the northern coast of Spain.

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