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The Late Quaternary coastal forests of western Iberia: A study of their macroremains

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Abstract

Plant remains collected from the Portuguese coast, some of them *in situ*, were examined to provide local information on the vegetation of the Iberian Atlantic area over the last 35,000 years. *Pinus* gr. *sylvestris-nigra* from the Würm period was identified in sandy soils, along with *Quercus* gr. *robur-petraea* and *Fraxinus* sp. The presence of *in situ* remains of this *Pinus* group on the northern Portuguese coast indicates the local temperature and precipitation conditions that must have reigned at this time. Thirty two *in situ Pinus pinaster* remains close to the mouth of the River Tagus show the importance of this taxon in this area during the first half of the Holocene. Other Holocene macroremains indicate the presence of non-riparian taxa (*Quercus* gr. *robur-petraea* and *Castanea* sp.), hygrophilous plants (*Fraxinus* sp., *Populus* sp., *Alnus* sp. and *Sambucus* sp.), and shade intolerant taxa (*Erica cinerea-vagans*).

Keywords: Holocene; Pleistocene; Portugal; *Pinus*; Refugia; Coast

1. Introduction

The many palaeobotanical studies performed in Europe have provided the information necessary to construct a contraction/expansion model for the continent's vegetation over the cold/warm fluctuations of the Quaternary (Turner and Hannon, 1988; Huntley, 1990a,b; Willis and van Andel, 2004). The effects of cold climatic episodes caused a loss of diversity in northern Europe (Taberlet et al., 1998). It has been recognised that during these episodes a large proportion of the biota survived in areas of central and southern Europe (Bennett et al., 1991; Hewitt, 1999; Petit et al., 2002; Cheddadi et al., 2006). Although the refuge role played by the Iberian Peninsula during glacial periods has been questioned by some authors (Huntley, 1990b; Bennett et al., 1991), sweet chestnut (*Castanea sativa* Mill.), black poplar (*Populus nigra* L.), common ash (*Fraxinus excelsior* L.) holm oak (*Quercus ilex* L.) and Scots pine (*Pinus sylvestris* L.), among other taxa, are known to have sheltered in the Iberian Peninsula during the last glacial period (Lumaret et al., 2002; Heuertz et al., 2004; Cottrell et al., 2005; Robledo-Arnuncio et al., 2005).

Despite the importance of the Atlantic Iberian coast in the development of the European flora during the

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Quaternary (Costa Tenorio et al., 1990), few palaeobotanical sites are known in this area. The generalisation to the entire Iberian Peninsula of conclusions drawn from findings at just a few sites (and generally at an altitude of over 1000 m) has, not surprisingly, led to a picture of a uniform vegetation quite unlike that currently seen. However, recent archaeological studies have improved our knowledge of the palaeovegetation of the Peninsula's Atlantic face (Figueiral, 1995; Aura et al., 1998; Carrión, 2005; Figueiral and Carcaillet, 2005). These studies have been very valuable in reconstructing its past vegetation, although the interpretation of the remains found at archaeological sites is hindered due to stratigraphic problems caused by animal and human-induced erosion, contamination via percolation, and problems in representing the landscape given the selection humans make of plants in their environment (Küster, 1991; Sánchez Goñi, 1993). Palaeobotanical studies performed at sites with macroremains found *in situ* – such as that described in the present work – are an additional source of information on past plant life: they provide the most reliable information on local vegetation (Birks and Birks, 2000).

This work examines macroremains collected from nine sites along the northern Portuguese coast (Fig. 1) over a period of two decades. These remains, exposed on beaches or in cuttings caused by sea erosion following storms, help clarify the role of the western littoral zone of the Iberian Peninsula in the vegetation dynamics of Europe during the Late Quaternary. The *in situ* plant remains found provide detailed taxonomic information on the coastal pinewoods of the Late Quaternary. The numerous reforestation campaigns undertaken with species of *Pinus*, especially *P. pinaster* Aiton, hinder the interpretation of the origin of these populations, but the existence of extensive pre-Roman coastal pine forests in Portugal is known from palynological studies on natural sediments (Mateus, 1989; Santos and Goñi, 2003). The similarity of the pollen grains belonging to the different pine species of the Iberian Peninsula renders it impossible to resolve the current debate surrounding the dynamics of these formations (Carrión et al., 2000). Macroremain analysis is an important source of information on past plant life since on many occasions material can be identified at the species level (Lowe and Walker, 1997). Studies on pre-Roman archaeological sites have shown *P. pinea* L. and *P.* gr. *pinea-pinaster* (which includes *P. pinea* and *P. pinaster*) to have grown along or near the coast of Portugal (Ramil-Rego et al., 1994; Figueiral, 1995; Carrión, 2005). Other authors have identified *Pinus* gr. *sylvestris-nigra* (*P. sylvestris*, *P. nigra* Arnold and *P. uncinata* Miller ex Mirbel) as growing during colder periods in the same area (Figueiral, 1995; Figueiral and Carcaillet, 2005). The macroremains analysed in the present study – many of them found *in situ* – provide exceptional taxonomic and chronological information on the area's geobotanical history. Additionally, the finding of *in situ* plant remains belonging to different groups of taxa, like those currently linked to settings with high soil humidity (*e.g. Fraxinus* sp., *Alnus* sp., *Salix* sp., *Populus* sp., *Sambucus* sp.), provide evidence of such environments.

The contemporary ecological requirements of the taxa found *in situ* in the present study supply additional information on the past environmental conditions of the Portuguese coast (Lowe and Walker, 1997). The available climatic reconstructions for the Last Ice Age indicate that summer and winter temperatures were from 1.5 to 20 °C below their current values, and that mean annual precipitation was lower by up to 60% compared that currently recorded for the study area (Duplessy et al., 1993; Peyron et al., 1998; Frenzel et al., 1992; de Vernal et al., 2005). The temperature and rainfall conditions in which the identified plants grew are identified in the present study by a palaeoclimate method based on the use of indicator species (Mosbruger and Utescher, 1997; Pross et al., 2000). This approach contributes towards a quantitative reconstruction of the Quaternary's climatic history.

2. Description of the study area and materials

From the Pleistocene through to the Holocene, the coast where the samples were collected has a complex history in terms of its tectonics and changes in sea-level. Relict Pleistocene aeolian and wet aeolian deposits overlain by a podzol, are themselves overlain by Little Ice Age dunes (Granja, 1999; Granja et al., 2003). Vegetation became established on this substrate, the remains of which are sometimes found.

Currently, the climate of the western coast of the Iberian Peninsula occupies the transition zone between the European Atlantic and Mediterranean climatic areas (Fig. 1) (Ozenda and Borel, 2001). The short period of summer drought experienced by the northwest of the Peninsula becomes longer as one travels south, until eventually lasting some three months (Ninyerola et al., 2005). Similarly, the >1000 mm rainfall received by the northwestern coast is reduced by half in the extreme southwest. In Oporto, the present mean annual temperature, mean January temperature, and mean annual rainfall precipitation, are 15.15±0.35 °C, 9.25±0.05 °C and 1100±10 mm respectively. These climatic conditions

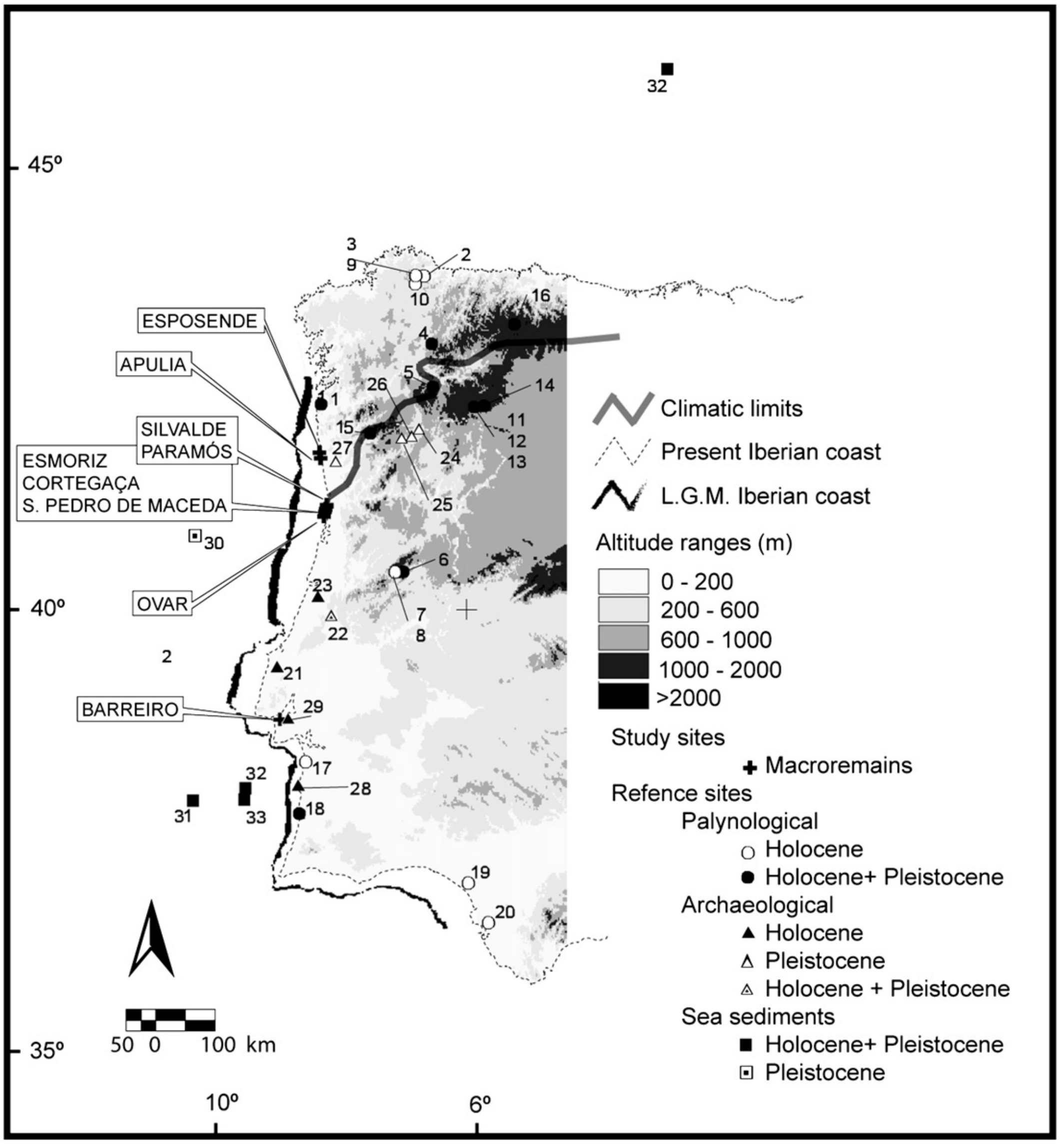

Fig. 1. Location (and altitude) of the studied sites (crosses) and the most important 'consulted' sites (*i.e.*, from which data were already available). Consulted sites: Circles: Palynological sites [1 — Mougás (Saá and Díaz-Fierros, 1988; Ramil-Rego et al., 1998), 2 — Pena Vella (Ramil-Rego et al., 1994, 1998), 3 — Chan do Lamoso (Ramil-Rego et al., 1994, 1998; Muñoz-Sobrino et al., 2005), 4 — Pozo do Carballal (Ramil-Rego et al., 1998), 5 — Lagoa Lucenza (Muñoz-Sobrino et al., 2001) 6 — Charco da Candiera, 7 — Lagoa Comprida and 8 — Covao do Boieiro (van der Knaap and van Leeuwen, 1997), 9 — Penido Vello (Muñoz-Sobrino et al., 2005), 10 — Pena da Candela (Martínez Cortizas et al., 2005), 11 — Lleguna and 12 — Las Sanguijuelas (Muñoz-Sobrino et al., 2004), 13 — La Roya (Allen et al., 1996), 14 — Sanabria (Watts, 1986; Turner and Hannon, 1988), 15 — Lagoa do Marinho (Ramil-Rego et al., 1998), 16 — Lago de Ajo (Watts, 1986; Allen et al., 1996), 17 — Lagoa travessa (Mateus, 1989), 18 — Santo André (Santos and Goñi, 2003), 19 — El Acebrón (Steevenson and Moore, 1988), 20 — Laguna del Gallo (López Sáez et al., 2002)]. Triangles: archaeological sites with anthracological remains [21 — Cabeza de Porto Marinho (Figueiral, 1995), 22 — Gruta do Caldeirao (Figueiral, 1995), 23 — Buraca Grande (Figueiral and Terral, 2002), 24 — Vinha da Soutilha, 25 — San Lourenço and 26 — Alto de Santa Ana (Vernet and Figueiral, 1993; Figueiral, 1995), 27 — Castro de Lenices (Figueiral, 1995), 28 — Vale Pincel I and 29 — Ponta da Passadeira (Carrión, 2005)]. Squares: marine sites [30 — MD95-2039 (Roucoux et al., 2005), 31 — SU 8118 (Duplessy et al., 1993; Turon et al., 2003), 32 — SO75 6KL (Boessenkool et al., 2001), 33 — SO75 26KL (Zahn et al., 1997), 34 — CH 6719 (Duplessy et al., 1981)]. Dark symbols: Holocene and Pleistocene ages. Empty symbols: Holocene age. Symbols with central dot: Pleistocene age. Black line: sea level (between −120 and −130 m) reached during the Last Ice Age. Grey line: Mediterranean/European Atlantic climatic limits (Ozenda and Borel, 2001).

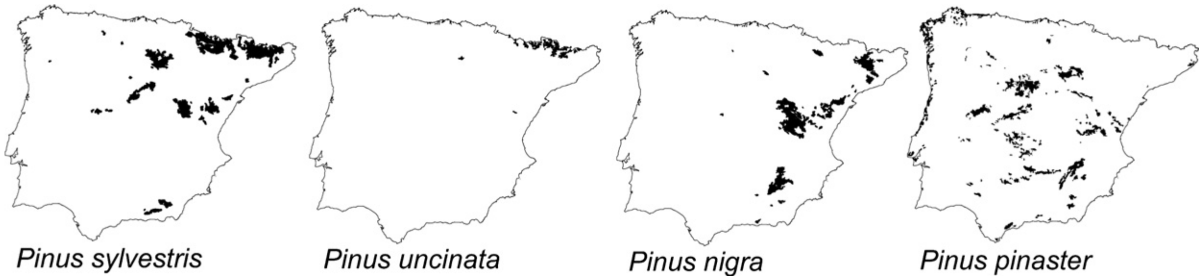

Fig. 2. Iberian distribution of mountain *Pinus* species, after Costa et al. (1997) and Ruiz de la Torre (2002).

allow the development of meso- and thermo-temperate oaks (*Quercus suber* L., *Q. robur* L.) together with scrub plants (*Ulex* sp., *Cytisus* sp.) and heather (*Erica* sp.). In the study area, *Fraxinus excelsior*, *Fraxinus angustifolia* Vahl., *Alnus glutinosa* (L.) Gaertn., *Salix* sp. and *Populus* sp. currently grow in environments with high soil humidity (Costa et al., 1997). *Pinus pinaster* populations grow on the northern Portuguese coast (Fig. 2), while *P. pinea* grows in the south. However, human pressure has profoundly changed the landscape by the felling of forests, the planting of certain native species, and the introduction of allochthonous species (*e.g.*, *Eucalyptus* sp., *Acacia* sp.) (Devy-Vareta, 1985).

Natural *Pinus* gr. *sylvestris-nigra* woods are currently found in the mountain areas of the Iberian Peninsula (Fig. 2) (Costa et al., 1997). The forests of this taxonomic group closest to the study sites grow in the Sierra de Gerês (*P. sylvestris*) and in the Sierra de Gredos (*P. sylvestris* and *P. nigra*). The proximity of the coast to areas with altitudes of 1500–2000 m (the Gerês and Estrela Ranges) offers the plants of the latter areas the possibility to find, within <100 km, ecological conditions suitable for their development during the reign of adverse climatic conditions. The mountainous area of the northern half of Portugal is dissected by rivers that connect the coastal area to the interior of the Peninsula, where *P. uncinata* currently grows (Sierra de Cebollera — Iberian Range).

Of the nine sites studied, eight are situated in the Minho and Douro Litoral regions (Fig. 1, Table 1). This part of the coast is home to dunes and coastal lakes on Plio-Pleistocene and Holocene sediments which are at their widest in the most southerly part of this territory (Aveiro) (Granja, 1999). Both on the beach surface and in the cliffs between the Rivers Minho and Espinho, the remains of peat bog sediments, ancient lagoon bottoms (locally known as *tijucas*) and the soils of ancient forests (podsoils) can be found. Between 1986 and

Table 1
Characteristics of the sites studied: U.T.M. coordinates, stratigraphic units, age as determined by radiocarbon dating (^{14}C in years B.P.) and correspondence to real ages (*Cal. B.P*, 2σ probability) (Reimer et al., 2004; Stuiver et al., 2005)

Site	UTM	Stratigraphic units	^{14}C (years BP)	cal BP ranges (95.4%)
Esposende	29TNF172991	1 — Peat	4571±80	5570–4970
			5590±80	6600–6210
		2 — 300 m NE light house	140±1	270–10
		3 — Settlement (under the dunes)	280±40	470–280
Apúlia	29TNF185922	1 — Capela Velha Peat bog	2570±41	2760–2490
			2830±40	3070–2850
Silvalde	29TNF298377	1 — Roman fishing equipment	1700±30	2360–2210
Esmoriz	29TNF291342	1 — N Cortegaça-1990	19910±260	24,480–22,890
			24,500±260	*
			29,000±510	*
			33,960±800	*
Cortegaça	29TNF288323	1 — Sur espigón-2002	2610±80	2880–2370
		2 — Sur espigón-1998	150±1	270–10
San Pedro de Maceda	29TNF282299	1 — Low tide	28900±240	*
Ovar	29TNF272245	1 — Dune	Holocene**	–
Paramos	29TNF295365	1 — Tijuca	180±25	290–0
Barreiro	29SMC950809	1 — Low tide	6780±135	7930–7430

*Outside the calibration range. ** Stratigraphic dating.

Fig. 3. Fossil tree trunks at the Barreiro site.

2005, 27 tree trunks (seven *in situ*) and 16 other woody remains of lesser size were collected in these areas.

The remaining site at Barreiro, at the mouth of the River Tagus (Fig. 1, Table 1), lies over Quaternary sediments that were deposited in a Cenozoic basin (Vera, 2004). In the alternating sand and clay strata of these Quaternary sediments, 32 fossil tree stumps were found *in situ* (Fig. 3).

3. Methods

3.1. Chronology

^{14}C dating (Table 1) was performed on at least one sample from each stratum at each site. Dating was undertaken by Beta Analytic (Miami, U.S.A.) and Quadru (Pretoria, South Africa). Ages <24,000 years uncal BP were converted into cal BP using Calib 5.0.2 software (Stuiver et al., 2005) and employing a dendrochronological database (Reimer et al., 2004).

3.2. Taxonomy

Thin sections were prepared in each of the main planes to analyse microscopic characteristics with a transmitted light microscope. All samples were identified using keys and descriptions (Greguss, 1955; Jacquiot et al., 1973; Queiroz and Van der Burgh, 1989; Schweingruber, 1990; García et al., 2002; InsideWood, 2004-onwards, among others) and by comparison with present day material belonging to the wood collection of the *Escuela Técnica Superior de Ingenieros de Montes [ETSIM]*, *Universidad Politécnica*, Madrid.

The xylological characteristics of some pine species can be very similar, therefore the following characteristics were used to distinguish the different taxa:

3.2.1. *Pinus gr. sylvestris-nigra*

This group includes the species *P. nigra* Arnold, *P. sylvestris* L., and *P. uncinata* Mill. ex Mirb. Members are identified by their cross-fields with window-like pits (Greguss, 1955) (Fig. 4). Some authors also report the shape of the teeth and ramifications of the radial

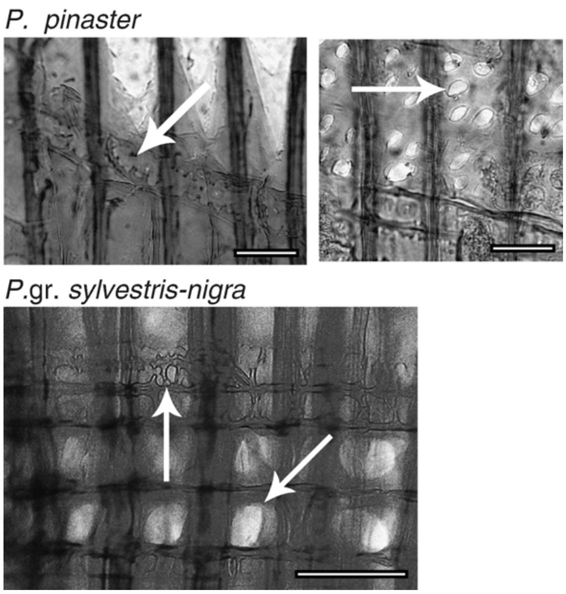

Fig. 4. Details of radial section of *Pinus pinaster* and *P.* gr. *sylvestris-nigra*, showing the teeth of the radial tracheid walls and the cross pits. Scale bar = 30 μm.

tracheids, and the position and morphology of the resin canals as reliable features for distinguishing between *P. nigra* and *P. sylvestris* (Jacquiot, 1955; Vernet, 2001; García et al., 2002). In the present work, however, these features seemed unable to differentiate test samples from different parts of Europe in the ETSIM collection; no such distinctions were therefore drawn between the experimental samples.

3.2.2. Pinus pinaster Aiton

The shape and distribution of the teeth of the radial tracheids (Fig. 4) distinguished between *P. pinaster* and *P. pinea* L. (*e.g.*, Greguss, 1955; Schweingruber, 1990).

3.3. Climate reconstruction

To reconstruct the past climate of the Portuguese coastal area where the macroremains were found, an indicator species approach (involving the presence/absence of taxa) was used (Mosbruger and Utescher, 1997; Pross et al., 2000). This quantitative method is based on the assumption that the ecological requirements of the Late Quaternary taxa are similar to those of their nearest living populations. Therefore, the climate associated with living populations of the plants found *in situ* on the Portuguese coast, is understood to represent the conditions in which their ancestors lived. For this purpose, the mean annual temperature, mean January temperature and mean annual rainfall precipitation of the Iberian populations currently growing at their optimum conditions were taken into account (Ruiz de la Torre and Ceballos, 1979; Gandullo and Sánchez, 1994; Costa et al., 1997; Ninyerola et al., 2005; Rubio and Sánchez, 2005).

4. Results

All the macroremains found dated from the Upper Pleistocene to the Holocene (Table 1), and show complex changes to have occurred along the northern coast of Portugal. The Pleistocene age of the macroremains from Esmoriz and San Pedro de Maceda contrasted with the Holocene age of those from the *tijuca* at Cortegaça. The ^{14}C dating performed on the macroremains from the Esposende, Apúlia, Silvalde, Cortegaça, Ovar, Paramos and Barreiro sites reveal peat bogs and *tijucas* to have developed during the last two thirds of the Holocene.

Five of the 75 samples identified showed different degrees of carbonisation (Table 2): (1) a completely carbonised *P. pinea-pinaster* sample from the Esposende human settlement (280–470 years cal BP), (2) a

Table 2
Number of samples studied anatomically, their taxonomic identification and stratigraphic position

Site	Stratigraphic unit	*Pinus* gr. *sylvestris-nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus pinaster* cf. *pinea*	*Quercus* gr. *robur-petreae*	*Fraxinus* cf. *angustifolia*	*Fraxinus* sp.	*Alnus* sp.	*Castanea* sp.	*Populus* sp.	*Sambucus* sp.	*Juniperus* sp.	*Erica* cinerea-vagans	*Acacia* sp.
Esposende	1								2^{+}*						
	2			1											
	3				1^{c}										
Apúlia	1					2	1	1	1^{c}				1		
Silvalde	1									2				1	
Esmoriz	1	18^{+}*						1^{c}							
Cortegaça	1													1^{c}	
	2				1*										1
San Pedro de Maceda	1	4*				1^{c}									
Ovar	1										1				
Paramos	1								1^{c}			1			
Barreiro	1		32^{+}*												

*Some remains *in situ*. $^{+}$Some trunks with diameter >10 cm. ^{c}Carbonised.

completely carbonised 7 cm diameter piece of *Alnus* sp. wood found in the peat bog at Apulia (2490–3070 years cal BP), (3) a completely carbonised sample of *Erica cinerea-vagans* found in the ancient, charcoal-rich soil at Cortegaça (2370–2880 years cal PB), (4) a partially carbonised 10 cm diameter piece of *Quercus robur-petraea* wood from the San Pedro de Maceda site (28,900±420 years uncal BP), and (5) and a partially carbonised piece of *Alnus* sp. from the Paramos *tijuca* (0–290 years cal BP).

Seven of the 27 tree trunks from the Minho and Douro Litoral regions were found *in situ* (Table 2), indicating the local presence of this taxon in the past. A 15 cm diameter trunk (6210–6600 years cal BP) collected at Esposende was assigned to *Alnus* sp. Four Würmian *P.* gr. *sylvestris-nigra* trunks up to 26 cm in diameter were found at Esmoriz, plus one more, dating from 28,900±240 years uncal BP, at San Pedro de Maceda. Finally, a 10–270 years cal BP *P. pinaster-pinea* trunk was found at Cortegaça. At the mouth of the River Tagus, 32 fossil tree stumps were discovered *in situ*, one of which dated from some 7430–7930 years cal BP (Figs. 1 and 3).

The 75 samples were assigned to 13 different taxonomic groups (Table 2). The second half of the Würm is represented at the San Pedro de Maceda and Esmoriz sites by numerous tree trunks, identified in large measure as belonging to *Pinus* gr. *sylvestris-nigra*. These remains date from between 19,910±260 and 33,960±800 uncal years BP. A trunk of a deciduous *Quercus* (*Q.* gr. *robur-petraea*) was also found, as well as the remains of branches some 6 cm in diameter belonging to *Fraxinus* sp. Holocene macroremains were found ranging from 8000 years cal BP until the present (Table 1).

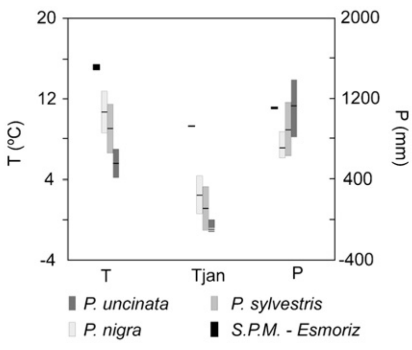

Fig. 5. Shaded squares: climatic range of the current forests of *P. nigra*, *P. sylvestris* and *P. uncinata* currently growing under optimum conditions. Division lines: optimum values of climatic conditions. Black squares: present day climatic conditions at the San Pedro de Maceda (S.P.M.) and Esmoriz sites (Ninyerola et al., 2005). T: mean annual temperature (°C). Tjan: mean January temperature (°C). P: mean annual rainfall (mm) (Ruiz de la Torre and Ceballos, 1979; Gandullo and Sánchez, 1994; Rubio and Sánchez, 2005).

Table 3
Last Ice Age-modern climate differences deducted from the species belonging to *P.* gr. *sylvestris-nigra*

Species	*T* (°C)	TJan (°C)	*P* (%)
Pinus nigra	2–8.9	4.9–8.7	25–45
Pinus sylvestris	3.3–8.9	5.9–10.3	0–43
Pinus uncinata	7.8–11.3	>9.2	0–22

These results were obtained by comparing the optimum climatic interval of *Pinus* gr. *sylvestris-nigra* currently growing in the Iberian Peninsula and the climatic conditions of the sites where its macroremains were found. *T* (°C): mean annual temperature. TJan (°C): mean January temperature. *P* (%): Percentage reduction in mean annual rainfall (Ruiz de la Torre and Ceballos, 1979; Gandullo and Sánchez, 1994; Figueiral and Carcaillet, 2005; Ninyerola et al., 2005; Rubio and Sánchez, 2005).

The Barreiro *P. pinaster* stumps formed the majority of the Holocene remains, although broad leaved taxa also formed an important proportion. *Quercus robur-petraea* and *Fraxinus* sp. were found at Apulia. Two woody remains of *Castanea* sp. were found at Silvalde, one of which was associated with a piece of Roman fishing equipment. The other chestnut sample was a natural remain dating from 2210–2360 years cal BP. *Alnus* sp. was found *in situ* at Esposende, Paramos (carbonised with *Sambucus* sp.), and in the 2490–3070 years cal BP Apulia site (with *Q. robur-petraea*, *Fraxinus* sp. and *Juniperus* sp.). *Erica cinerea-vagans* was found at Silvalde and Cortegaça during the Subboreal and Subatlantic Holocene periods. Recent remains of *P. pinea* were also identified at Esposende, as were those of *Acacia* sp. at Cortegaça, along with a Holocene branch of *Populus* sp. at Ovar.

4.1. Climate reconstruction

The temperature and precipitation intervals associated with the current Iberian populations of *P.* gr. *sylvestris-nigra* help characterise the past climate at Esmoriz and San Pedro de Maceda (Figs. 2 and 5) between 19,910±260 and 33,960±800 years uncal BP (Table 3). This climate differed from that currently reigning in the area. The mean annual temperature during the Last Ice Age was some 2–11.3 °C cooler than it is now. The mean January temperature was also cooler by at least some 4.9 °C. The rainfall of the Last Ice Age could have been 45% less than that presently recorded for the San Pedro de Maceda and Esmoriz sites.

5. Palaeoenvironment reconstruction

5.1. Geomorphological environment

The contrasting ages of the different samples collected at the present sea level can be explained by the existence of faults and related tectonic movements along the northern coast of Portugal (Granja, 1999). The ancient soils, dune fields, peat bogs, and freshwater and brackish lagoons where the fossil material was found to reflect the different environments to which the study area was home during the Late Quaternary. The recession of the coastline (corresponding to a 120–130 m drop in sea level) during the Last Ice Age (Shackleton, 1987; Dias et al., 2000) uncovered large areas of sand, gravel and mud distributed in ancient river valleys and ravines of different orientation (Rodrigues et al., 1991). This would have offered a wide variety of biotopes for the occupying vegetation. The rapid rise in sea level that accompanied the global rise in temperature between 18,000 and 6000 years BP (Shackleton, 1987) led to a reduction in the land available to plants. After 6000 years BP, the sea level began to rise more slowly, although continuously, until reaching its present position (Alonso and Pagés, 2000; Dias et al., 2000). The fluctuations in the water table along the Portuguese coast during the Holocene, a consequence of regional tectonic movements and changes in the climate (Zazo et al., 1997), led to the alternation of different conditions. Throughout the Holocene the coastline was close to the sampling sites, and these remained intermittently protected from wave action by sand bars (Granja et al., 1996). The exposure of the collected samples along the current coastline is the result of sea erosion due to the present increase in relative sea level (Granja, 1999).

5.2. Climate

The reconstructed mean annual temperature, mean January temperature and mean annual precipitation for the Last Ice Age (Table 3) provide climatic information for the local area. Although the confidence intervals provided by the presence of *P.* gr. *sylvestris-nigra* are wider than those afforded by some authors (*e.g.*, Frenzel et al., 1992), they provide valuable additional information for calculations at the regional scale (see for example de Vernal et al., 2005).

Studies of the sea bed and continental records indicate there to have been a much greater temperature drop in the Iberian Peninsula as a whole during the Last Ice Age than that suggested by the remains of *P. sylvestris-nigra* — perhaps up to 15 °C (Duplessy et al., 1993; Peyron et al., 1998). Temperature conditions along the Portuguese coast during the Last Ice Age, therefore, were milder than those experienced in the interior and at higher latitudes (Peñalba et al., 1997; de Vernal et al., 2005).

Similarly, the 45% maximum reduction in precipitation between the Last Ice Age and the present suggested by the study material (Table 3) is less than the up to 60% reduction indicated by other authors for the Iberian Peninsula (Frenzel et al., 1992; Peyron et al., 1998). Accordingly, the insignificant proportion of xerophilic taxa recorded in the pollen diagrams for areas close to the coast during the Last Ice Age (Allen et al., 1996; Peñalba et al., 1997; van der Knaap and van Leeuwen, 1997; Ramil-Rego et al., 1998; Muñoz-Sobrino et al., 2001) indicate that it did not experience the reduction in rainfall suffered by the interior.

6. The coastal forests of the Last Ice Age

6.1. *Pinus gr. sylvestris-nigra forests*

The number of *Pinus* gr. *sylvestris-nigra* trunks found dating from between ~20,000 and ~34,000 years BP – some of them *in situ* – indicate the presence of this taxonomic group along the Portuguese coast during the Last Ice Age. The low temperatures that characterised the Würmian period (Fig. 6) might have favoured the expansion of this pioneering, microthermal taxon (Costa et al., 1997) to the sandy soils that appeared after the ocean retreated some tens of kilometres (Dias et al., 2000).

The only palynological Würmian site known along the study coast (Mougás, no. 1 Fig. 1) (Saá and Díaz-Fierros, 1988) reveals a once large mass of pines during the Heinrich H1 event (Fig. 6) at 42° N, in a landscape co-dominated by Poaceae. Marine core MD95-2039 (no. 30, Fig. 1) also reveals the presence of *Pinus* in a landscape dominated by steppe taxa for the northwest of the Iberian Peninsula during the Last Ice Age (Fig. 6) (Roucoux et al., 2005). The few pollen diagrams available for the Peninsula during this period also suggest scant tree cover and the predominance of dry steppe species in mountain areas and the interior of the Peninsula up until the Bølling–Allerød interstage (Watts, 1986; Allen et al., 1996; Peñalba et al., 1997; van der Knaap and van Leeuwen, 1997; Muñoz-Sobrino et al., 2001, 2004). Therefore, the record of *Pinus* from the ocean bed might reflect the pines established near the coast.

Numerous charcoal remains of *Pinus* gr. *sylvestris-nigra* have also been found (during archaeological studies)

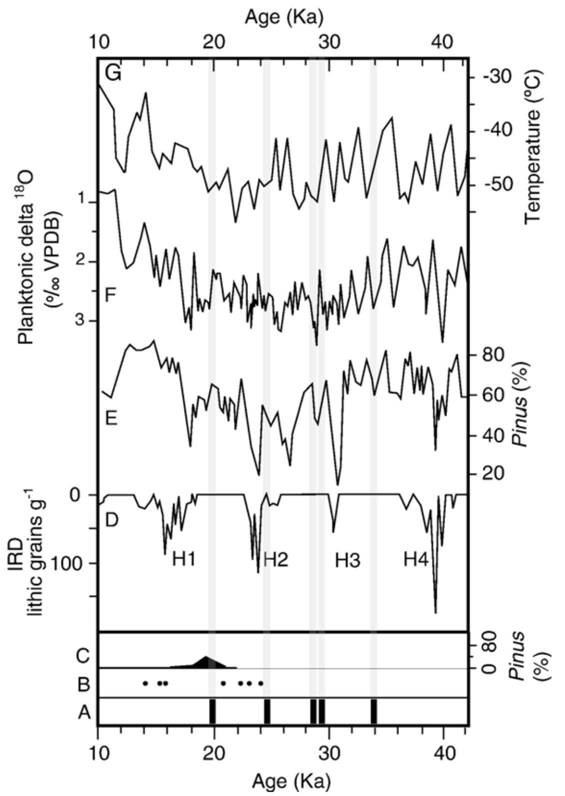

Fig. 6. (A) Age of the *P.* gr. *sylvestris-nigra* macroremains and (B) of charcoal remains of the same group, as reported by Figueiral and Carcaillet (2005). (C) Absolute percentages of *Pinus* in the Mougás pollen diagram (Saá and Díaz-Fierros, 1988). (D) Heinrich events recorded by core MD95-2039 (Roucoux et al., 2005) plus its (E) *Pinus* pollen and plankton δ^{18}O (F) records. (G) δ^{18}O-GRIP (72.58°N 37.64°W) isotopic temperature in modified °C (Johnsen et al., 2001).

near the central and northern Portuguese coasts dating from the times of the H1 and H2 events (Fig. 6) (Figueiral and Terral, 2002; Figueiral and Carcaillet, 2005). This agrees with the expansion of *P.* gr. *sylvestris-nigra* along the northern Atlantic face of Portugal during the Würmian period.

Natural *P. sylvestris* woods are currently found in the Sierra de Gerês, and forests of *P. sylvestris* and *P. nigra* grow in the Sierra de Gredos (Costa et al., 1997), areas that were devoid of trees during the Last Ice Age (Fig. 6) (Watts, 1986; van der Knaap and van Leeuwen, 1997). This suggests that the mountainous areas of the northern half of Portugal acted as an area of expansion for these species during times of warming, as they do now. Pleistocene remains of this group found on the Portuguese coast 60 and 280 km from where its members currently grow, suggest that a migration towards lower altitudes took place in response to temperature decline (Huntley, 1990a; Williams et al., 2002).

6.2. Other formations

Along with the Würmian mountain pines discovered at the San Pedro de Maceda and Esmoriz sites, broad leaved taxa (*Quercus robur-petraea* and *Fraxinus* sp.) were discovered. These taxa, Atlantic and Mediterranean in nature (Costa et al., 1997), would have found an ideal environment for their development in the wet soils of the emerged land after the ocean retreated.

The landscape of the Würmian coast of northern Portugal was also home to human settlements at Buraca Grande (no. 23, Fig. 1) and Cabeço de Porto Marinho (no. 21, Fig. 1) (Figueiral, 1995; Figueiral and Terral, 2002) (Fig. 1), where archaeological remains have been found. These sites contain thermophilous elements of Mediterranean/Submediterranean affinity as well as representatives of the Eurosiberian flora that formed spiny shrubland in the open spaces of Atlantic, broad leaved, deciduous woods (Costa et al., 1997).

No macroremains of Würmian *P. pinaster* were found at the present sampling sites. However, at the Cabeço de Porto Marinho site (no. 21, Fig. 1), charcoal remains of this species dating from 33,000 years BP can be found (they make up 93% of all the remains present) (Figueiral, 1993). The importance of *P. pinaster* on the coastal sands of Würmian Portugal has already been reported (Mateus and Queiroz, 1993).

6.3. Refuge areas

In this work, refuge areas are defined as those where species of boreal distribution survived glacial climatic conditions (Hewitt, 1999). The finding of macroremains of taxa that currently grow in the mountains of the Iberian Peninsula (*P.* gr. *sylvestris-nigra*), along with a small percentage of broad leaved species (*Q.* gr. *robur-petraea* and *Fraxinus* sp.), and at a time when there were no large tree formations in the interior (García Antón et al., 2002), shows that the northern Portuguese coast behaved as a refuge. The variety of the topography and the diversity of the soils that emerged after the marine recession phases offered a great variety of ecological niches where even the most thermophilous species (Figueiral, 1993, 1995) could survive the Last Ice Age. During the climatic variations of the Quaternary, the rugged topography of the Iberian Peninsula facilitated the survival of plants, as different species could have found adequate environments at different altitudes that involved only short migrations.

7. The coastal forests of the Holocene

The Holocene macroremains found along the Portuguese coast show a variety of taxa that reflect the mosaic of woods, shrublands, marshlands and estuaries that became established there at that time indicated by other authors (Saá and Díaz-Fierros, 1988; Steevenson and Moore, 1988; Ramil-Rego et al., 1998).

7.1. *Pinus forests*

The 32 stumps found *in situ* at the Barreiro site (Table 2) correspond to a stand of *P. pinaster* more than 7000 years old. The sandy substrate in which these remains rest, which also contains clay strata, reflect the adaptation of *P. pinaster* to poor, compact and non-compact soils that are difficult for other species to colonise. Anthracological records for *P. pinaster* in human settlements also show that this pine developed near the coast during the Upper Palaeolithic in central Portugal (Figueiral, 1995; Figueiral and Carcaillet, 2005). These results demonstrate that *P. pinaster* was present on the southern coast of Portugal during the first half of the Holocene.

Near Barreiro, archaeological digs at the Vale Pincel I site (no. 28, Fig. 1) and the Ponta da Passadeira site (no. 29, Fig. 1) turned up numerous Epipalaeolithic and Neolithic charcoals and cone remains of *P. pinea* and *P. pinea-pinaster* (Carrión, 2005). This and other *P. pinea* carpological remains found in southern Portugal belonging to the Bronze and Copper Ages (Ramil-Rego et al., 1994), suggest this taxon to have occupied areas of the southwestern coast of the Iberian Peninsula during the Holocene.

Close to Barreiro, the Holocene pollen diagrams for Lagoa Travessa (no. 17, Fig. 1) and Santo André (no. 18, Fig. 1) reflect a vegetation that grew on sandy soils similar to that of the Barreiro site (Mateus, 1989; Mateus and Queiroz, 1993; Santos and Goñi, 2003). These figures show absolute percentages of up to 70% for *Pinus* during the first half of the Holocene. Marine cores that record the pollen production of the Tagus basin (no. 31, 32 and 33, Fig. 1) show a reduction in the area occupied by *Pinus* during this time (Boessenkool et al., 2001; Turon et al., 2003). The findings at the Barreiro site and the information in the above macroremain and pollen diagrams for the coast, contrast with the events of the Peninsular interior.

7.2. *Other formations*

Given the hygrophytic nature of *Alnus* sp., the remains found at Esposende (*in situ*), Apúlia and Paramos dating from 6000–180 years cal BP (Tables 1 and 2), probably represent hygrophilous vegetation that became established at different points along the coast during the Holocene (Costa et al., 1997). Other hygrophytic taxa such as *Sambucus* sp. (at Apúlia) or *Populus* sp. (at Ovar) (Table 2) were also found. Archaeological and palynological remains confirm the great importance of hygrophilous taxa such as *Alnus* sp. and *Salix* sp. during the Mid Holocene at the Atlantic coast of Iberian Peninsula (Oldfield, 1964; Saá and Díaz-Fierros, 1988; Steevenson and Moore, 1988; Mateus, 1989). However, in mountain sites, *Alnus* sp. became progressively less important towards the interior (Ramil-Rego et al., 1994; Allen et al., 1996; van der Knaap and van Leeuwen, 1997; Muñoz-Sobrino et al., 2001, 2005).

The presence of *Populus* sp. at Ovar (Table 2) also reflects the existence of habitats with a high soil humidity. However, no anthracological remains of this genus have been found in Holocene coastal sites, and palynological studies have only rarely recorded this genus (Steevenson and Moore, 1988; Mateus, 1989; Allen et al., 1996; Muñoz-Sobrino et al., 2001; Santos and Goñi, 2003). These records suggest it was therefore of little importance along the Iberian Atlantic coast of the Holocene.

Evidence of hygrophilous mixed woods from 2000–3000 years cal BP was found at the Apúlia site. *Fraxinus* sp. appears associated with *Alnus* sp. and *Quercus* gr. *robur-petraea* (Table 2). The pollen of deciduous *Quercus* is well represented throughout the Holocene at different coastal and marine sites (Oldfield, 1964; Duplessy et al., 1981; Saá and Díaz-Fierros, 1988; Mateus, 1989; Boessenkool et al., 2001). Ash, however, is only poorly represented.

Among the temperate taxa located on or near the studied coast (Table 2, Figueiral and Terral, 2002), a *Castanea* remain dating from 2210–2370 years cal BP was found at the Silvalde site (Table 2). This pre-Roman remain supports the natural origin of this taxon on the Atlantic coast of the Iberian Peninsula, as previously suggested by other authors (López et al., 1996; Uzquiano, 1995; Ramil-Rego et al., 1998; Krebs et al., 2004).

The macroremains of *Juniperus* sp. from the second half of the Holocene at Apúlia (Table 2) might come from formations that became installed on sands poor in nutrients (Costa et al., 1997). However, the palaeopalynological record for the Iberian Atlantic coast only registers this taxon as exceptional during the Holocene (Mateus, 1989; López, 2001; Muñoz-Sobrino et al., 2004, 2005). These data suggest that their formations were not very extensive.

The remains of heather (*Erica cinerea-vagans*) found at the Cortegaça and Silvalde sites, dating from 1700–2600 years cal BP (Table 2), provide taxonomic information that improves the available from pollen diagrams. In addition, the carbonised heather remain found at the Cortegaça site in ancient soil, along with many small charcoal fragments, might be related to forest-clearing by fire. According to palynological/archaeological records, Neolithic Man began to clear forests through the use of fire around 6000–7000 years BP (Mateus, 1989; Zilhão, 1993; Aura et al., 1998; Santos and Goñi, 2003). The information contained in human settlements and in continental and marine sediments shows the importance of heather formations during the wettest times of the Holocene, and during the times when anthropic influence was greatest (Saá and Díaz-Fierros, 1988; Mateus, 1989; Figueiral, 1995; Lezine and Denefle, 1997; Figueiral and Terral, 2002; Martínez Cortizas et al., 2005).

Other species found at the Silvalde, Esmoriz, Cortegaça and Paramos sites reflect anthropic activity. The macroremain of chestnut wood, which formed part of a piece of Roman fishing equipment, and a recent *Acacia* sp. of allochthonous origin, are two clear examples. An increase in cultivated taxa is also seen in the pollen record for the second half of the Holocene; this is consistently observed in the post-Mesolithic palaeobotanical sites of the Iberian Atlantic coast (López, 2001; Martínez Cortizas et al., 2005).

8. Conclusions

The variety of taxa identified at the nine coastal sites is a reflection of the following environments:

- → *Sandy soil environments*; dominated by species of the genera *Pinus* during the Last Ice Age and the Holocene.
- → *Hygrophytic environments*; characterised by the presence of *Fraxinus* sp., *Alnus* sp., and, to a lesser extent, *Populus* sp. and *Sambucus* sp., during the Holocene.
- → *Nemoral environments*; home to broad leaved, deciduous *Quercus* during the Last Ice Age and the Holocene. *Castanea* sp. would have enriched this type of environment during this period.
- → *Environments exposed to high luminosity*; home of heather (*Erica cinerea-vagans*) during the Holocene.

The examined macroremains show that the study area's mean annual temperature during the Last Ice Age was some 2–11.3 °C cooler than it is now. The mean January temperature was also cooler at least by 4.9 °C. Compared to the present, there was probably a maximum reduction in rainfall of some 45%.

During the Würmian period, *Pinus* gr. *sylvestris-nigra* found refuge on the northern Portuguese coast, living alongside more thermophilous species such as ash and oak.

The many remains of *P. pinaster* found *in situ* and with an age of some 7000 years together represent the most important fossil forest of the Iberian coastline. These remains bear witness to the mosaic formed by different formations during the first half of the Holocene along the Portuguese coast.

The remains of the Holocene sites studied agree with the establishment of warmer, damper climatic conditions that facilitated the expansion of mesophilic species such as deciduous *Quercus*, *Castanea* sp. and *Fraxinus* sp. The generalisation of such an environment along the coast during the Holocene also favoured the expansion of hygrophilous species such as *Alnus* sp.

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