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Holocene environmental change on the Atlantic coast of NW Iberia as inferred from the Ponzos wetland sequence

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The intertidal environment of the Ponzos beach (NW Iberian Peninsula) hosts a sedimentary sequence (including large wood fragments) deposited during the first half of the Holocene in a hygrophilous continental wetland. Pollen and macrofossil data alongside radiocarbon dating allow reconstruction of the changes that occurred during the Early and Middle Holocene in the landscape of the NW Iberia coastal lowlands, as well as the local wetland plant communities, in response to the climate variations and the eustatic sea-level oscillations. The sequence represents the evolution of a coastal wetland from its initial phases as a hygrophilous wetland towards the subsequent installation of a freshwater lagoon. Pollen data show the dominant role of Atlantic (mainly deciduous) woody taxa, the scarcity of conifers and the lack of Mediterranean elements in the coastal landscapes around the Ponzos site. The presence and abundance of some taxa such as deciduous *Quercus*, *Castanea*, *Fagus*, *Tilia* and *Ulmus* during the Early Holocene provides further support for the occurrence of glacial refuges in the Cantabrian-Atlantic area during the Last Glaciation. The diverse vegetation that characterizes the modern landscapes in this territory established later, spreading from these glacial reservoirs of biodiversity. In this sense, the notable and early presence of *Fagus* at the beginning of the Holocene, a tree also previously recorded during several phases of the Last Glacial Cycle on the NW Iberia coasts, is noteworthy. In addition, during the Early and Middle Holocene are recorded other trees that are currently extirpated as natural taxa in the area, such as *Pinus*, *Tilia* and *Carpinus*.

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The palaeoecological information obtained in Europe over the last 30 years has confirmed that certain areas of the Iberian, Italian and Balkan Peninsulas would have acted as refuge areas for thermophilous and mesophilous flora during the Pleistocene. From these areas, during the Holocene, those taxa spread and expanded towards other nearby territories. The location of shelter areas for thermophilous and mesophilous taxa has been linked to low-altitude territories, located below the mountain altitudes affected by permanent or semi-permanent snow. The refuge areas are identified with systems of narrow valleys and depressions, where different species could accommodate their areas of distribution according to climate fluctuations, and also expand during the periods of more favourable conditions (Ramil-Rego *et al*. 1998a, 2000; Carrión *et al*. 2003; Gómez-Orellana *et al*. 2007, 2012, 2013; González-Sampériz *et al*. 2010; Tzedakis *et al*. 2013; Birks 2019).

In the Iberian Peninsula, the palaeoecological record shows three main patterns of vegetation history that can be identified, with at least three bioregions. Firstly, the Atlantic bioregion, enclosing the littoral, sublittoral and mountainous territories along the northern coast (Cantabrian littoral) and extending along the Atlantic coast. It covers areas that during the majority of the Holocene recorded mild winter temperatures and absence of summer droughts. Secondly, the southern part of the Atlantic littoral and its analogous territory on the Mediterranean coast belonging to the Mediterranean bioregion, with a climate during the Holocene marked by mild winters, and warm and dry summers. Thirdly, the Iberian Peninsula hinterlands, consisting of extensive plateaus and various mountainous ranges, forming the Iberian Continental bioregion that during the Holocene had climate conditions that were warm and dry in summer, and very cold in winter.

The presence of refuge areas for thermophilous and sclerophyllous flora has been argued from various pollen sequences obtained in the Mediterranean bioregion (e.g. Carrión *et al*. 2003), linked to the persistence of taxa such as *Quercus ilex*, *Olea*, *Phillyrea*, *Pistacia*, *Rhamnus* and *Buxus*. Likewise, in studies carried out in the Atlantic bioregion, palynological evidence attests to the occurrence of refuge areas for various mesophilous elements such as deciduous *Quercus*, *Corylus*, *Tilia*, *Ulmus*, *Castanea*, *Fagus*, *Carpinus*, and even evergreen taxa such as *Quercus ilex*, *Ilex aquifolium* and *Laurus nobilis* (Ramil-Rego *et al*. 1998a, 2000; Gómez-Orellana *et al*. 2012, 2013). The knowledge of the Iberian continental

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bioregion is still scarce and fragmented and it does not allow in-depth assessment about the possible presence of refuges, even more so when the available sequences come from mountainous areas located in the transition between the Mediterranean and Atlanticbioregions (e.g. Morales-Molino & García-Antón 2014).

Four main biogeographical units exist within the Atlantic bioregion. These have maintained, through the Lateglacial and the Holocene, common and differentiated characteristics in relation to the species present and the dominant landscapes (Ramil-Rego *et al.* 2006). The first unit comprises the littoral territories, from sea level to 200 m a.s.l. (Fig. 1). The second unit includes the sublittoral territories, far from the coastline and extending towards the main mountainous units. The third unit corresponds to the Atlantic mountains as a whole, with a main system, the Cantabrian Range (700–2650 m a.s.l.), stretching E–W, and other reliefs of lower entity and altitude located east and west of that main range (Fig. 1). The fourth unit corresponds to an area of transition between the Atlantic mountains unit and the Iberian continental bioregion that runs through a set of river basins and valleys defined by the mountain reliefs (Ramil-Rego *et al.* 1998a).

The high-resolution records for the Lateglacial and the beginning of the Holocene in the Atlantic bioregion of the Iberian Peninsula correspond to deposits formed in different types of wetlands (blanket bogs, peatlands, lakes, lagoons, etc.). Most of them are located in the mountain unit, particularly in the Cantabrian Range and in other nearby mountains: the Northern Galician Mountains (Van Mourik 1986; Ramil-Rego *et al.* 1996, 1998a; Muñoz Sobrino *et al.* 2005), the Galician-Minho Mountains (Ramil-Rego *et al.* 1998a) and the Galician-Duero Mountains (Allen *et al.* 1996; Muñoz Sobrino *et al.* 2004, 2007, 2013) (Fig. 1). Most of these deposits are far from the coastal lowlands, where the main refuge areas for the mesophilous taxa during the Pleistocene would have most probably been located. Thus, at present, a great number of mesophilous flora located in other territories of the Atlantic biogeographical region are not present in these inner areas.

The palaeobotanical analyses carried out on the sediments from the different types of littoral and sublittoral wetlands of the Iberian Atlantic bioregion have provided uneven and fragmented information. The cause of this unequal spread of data lies in the geomorphological characteristics (absence of great basins or settings favourable to the establishment of large wetlands, effects of erosion processes, changes in the superficial hydrological configuration and the coastal line, etc.). Besides, human action has been progressively destroying these deposits due to the increase of agricultural, forestry and urban activities.

The end of the glacial period marked a turning point in the littoral ecosystems of the Cantabrian and Atlantic coasts of the Iberian Peninsula. The warmer and moister climate favoured the dissemination and expansion of several taxa, and the sea level rise caused the spatial reconfiguration of the ecosystems. Some littoral sections lost part of their coastal habitats (dunes, wetlands, cliffs), which were destroyed by the inland progression of coastline, while in other stretches the coastal habitats were reconfigured or even established on the old continental territories. In relation to these dynamics, different limnic remains have been identified as ancient organic deposits formed on continental wetlands in the littoral. Nowadays, these remains are located between the eulittoral and infralittoral areas, and record different periods of the last glacial–interglacial cycle. Only the palynological sequence of Area Longa covers the last glacial (Gómez-Orellana *et al.* 2007). A number of pollen sites record different periods of the MIS 3 (Nonn 1966; Mary *et al.* 1977; Granja & De Groot 1996; Gómez-Orellana *et al.* 2007, 2013); and other groups of sites record the second half or the last third of the Holocene (Santos *et al.* 2001; García Anton *et al.* 2006; Bao *et al.* 2007; Costas *et al.* 2009; Granja *et al.* 2010, 2016; Gómez-Orellana *et al.* 2014; Muñoz Sobrino *et al.* 2016; Sáez *et al.* 2018). Finally, pollen sequences recording the Lateglacial or the beginning of the Holocene are limited to the deposits of Mougás (Gómez-Orellana *et al.* 1998) and Urdaibai (Iriarte Chiapusso *et al.* 2006).

The presence of continental ancient wetland deposits that remain permanently or temporarily submerged in the sea also has been found in different Atlantic areas, such as in the case of the Doggerland area (North Sea). This area is a wide continental space that served as a bridge between the British Isles and the European continent, but that has remained below sea level since 8450–8150 BC (Gaffne *et al.* 2007; Coles 2014; Krüger *et al.* 2017).

This paper presents the palaeoecological data obtained from a fossil deposit accumulated in an ancient wetland located at the present-day beach of Ponzos, in the NW of the Iberian Peninsula (Galicia, Spain). The site is located in the northern end of the Atlantic littoral, in the coastal stretch designated as 'Costa Ártabra' (Fig. 1), only 50 km in a straight line from the area with the highest altitude of the northern Galician Mountains (Xistral mountains; Fig. 1). This mountain area provides a wide range of palaeobotanical information obtained from different types of peatlands and organic deposits located between 650 and 1050 m a.s.l. (Ramil-Rego *et al.* 1996, 1998a; Muñoz Sobrino *et al.* 2005; Iriarte Chiapusso *et al.* 2016). Among this mountain range and the littoral, the sublittoral unit includes N–S or W–E oriented small and narrow river valleys, where remains of ancient forests are located. Deciduous species (*Quercus robur*, *Quercus pyrenaica*, *Corylus avellana*, *Betula alba*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Fraxinus angustifolia*, *Ulmus glabra*, *Frangula alnus*) are dominant in these forests, with a scarce representation of evergreen species (*Arbutus unedo*, *Ilex aquifolium*, *Taxus*

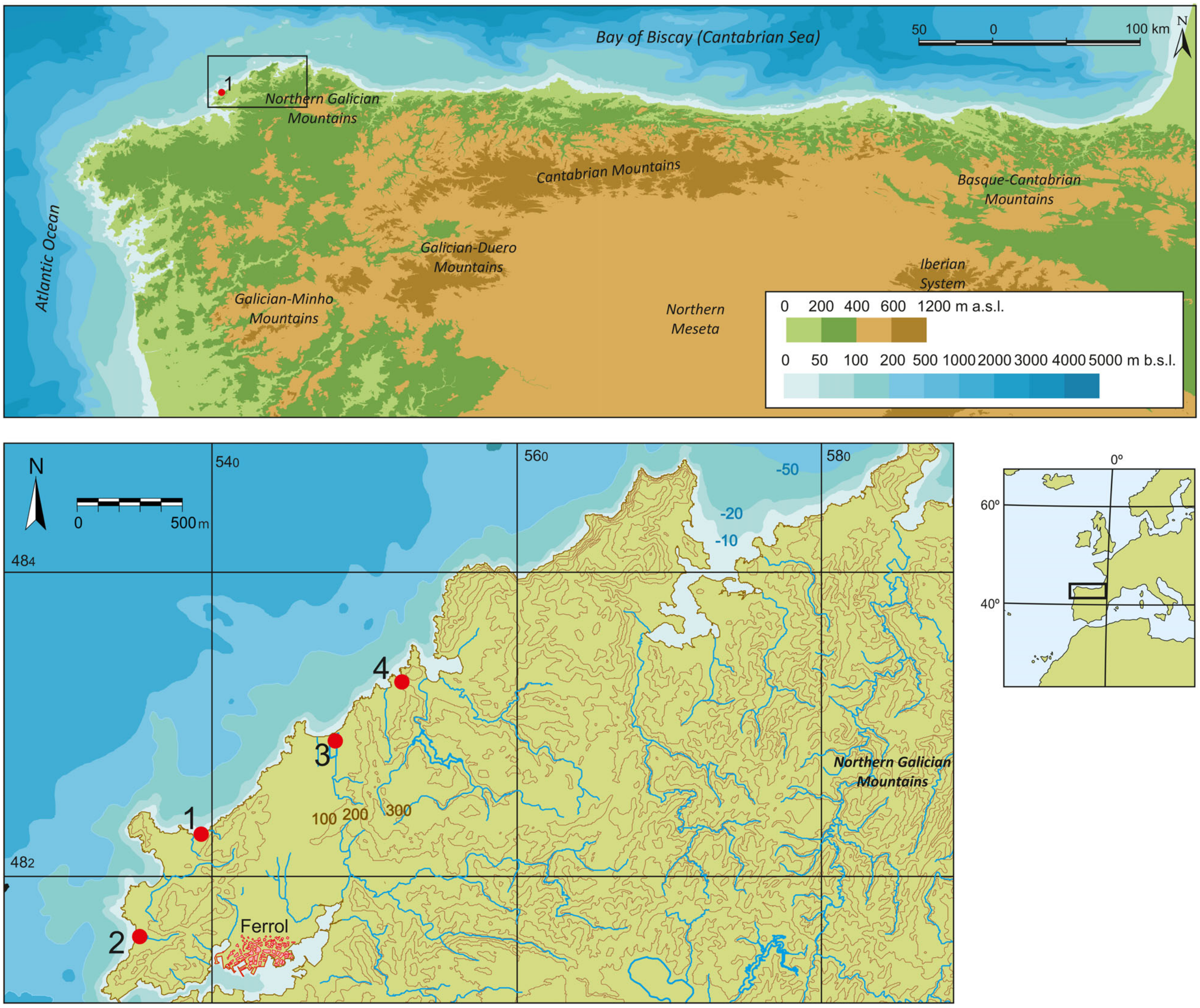

Fig. 1. Location of the Ponzos wetland and other coastal lagoons currently existing in the area (1 = Ponzos deposit; 2 = Lagoon of Doniños; 3 = Lagoon of Frouxeira; 4 = Lagoon of Pantín).

baccata, *Laurus nobilis*). Besides, these ancient forests also host an important nemoral flora, including the presence of fern species considered as palaeo-relicts and that stand out for their high value for biodiversity conservation. The present-day distribution area of these fern species is not included in the Palaearctic ecozone: *Culcita macrocarpa*, *Woodwardia radicans*, *Hymenophyllum tunbrigense*, *H. wilsonii*, *Vandenboschia speciosa* (Jermy 1984; Sermolli *et al.* 1988; Rita 1990; Pausas & Sáez 2000; Amigo *et al.* 2017). Besides, they show a clear stenoecious behaviour regarding the demands of their habitats (absence of frost, continuous high humidity, low direct incidence of sunlight) as well as a low dispersal capacity.

The aim of this study is to reconstruct the landscape of the NW Iberia coastal lowlands during the phases of expansion and arboreal domination in the Holocene, as well as to decipher the dynamics of the coastal wetlands in relation to the Holocene marine transgression.

Material and methods

Sampling

The Costa Ártabra littoral (Fig. 1) is dominated by granitic rocks (two-mica granites and leucogranites) combined with other geological materials. Geomorphological processes have led to the emergence of long sectors of cliffs and pebble beaches, in contrast to small bays that have, in their inner stretches, wide sand beaches, estuaries and different types of coastal wetlands (lagoons, marshlands, and hygrophilous and swamp environments). Ponzos beach (latitude 43°33′N, longitude 8°15′W) is 1.2 km long (Figs 1, 2). Behind the beach there is a wide and complex dune system measuring more than 100 hectares, formed by embryonic dunes, mobile white dunes of *Ammophila arenaria* and fixed grey dunes with herbaceous vegetation and small shrubs (*Daphne*, *Calluna*, *Erica*, *Ulex*, *Helichrysum*, *Othantus*). The grey dune includes small humid depressions with ponding and high humidity between autumn and spring, decreasing or almost disappearing with the arrival of summer. The transition to the continental environment occurs over an area of fossil dunes covered by shrubs dominated by *Erica vagans* and small representations of dry heathlands on the dunes, hygrophilous wetlands with herbaceous and wooded formations, and small representations of rocky environments (Fig. 2).

During spring tide periods, a thick organic sediment package appears at the western edge of the beach, in the intertidal area. This deposit normally remains covered by the sand of the present-day beach. This organic sediment was continuously monitored from 2009 to 2020 to take advantage of the spring tides in order to document and collect different macro-remains. The outcropping surface of the organic sediment package reaches 900 m^2, comprising a great number of wood fragments, among which the appearance of long trunks or branches (>5 m long and >40 cm in diameter) is noteworthy. They are located above the deposit or embedded, and chaotically distributed around different areas of the outcrop. When the sediment surrounding the wood remains was manually removed, it was determined that some of these are in living position and include both the main roots and the initial part of the trunk. During the sampling, some of these macro-remains were collected for botanical identification and dating.

We drilled the surface of the deposit in different sites with Eijkelkamp percussion drilling equipment, using cores of 10 and 3 cm in diameter. All of the probes reached the rocky basement. The drill-cores recovered in the different tests were very similar. The main differences concern the thickness of the organic package and the characteristics of the upper levels (absence or presence of sands and large wood remains). The thickest core (250 cm) obtained was chosen for the palynological and chronological analysis. The lithology of the core was described in the laboratory and then divided into 125 samples of 2 cm thick. All samples remained stored at 5 °C until analysis.

Pollen analysis

The samples were prepared for pollen analysis using standard methods (Fægri *et al.* 1989; Moore *et al.* 1991). The mounted slides were analysed using light

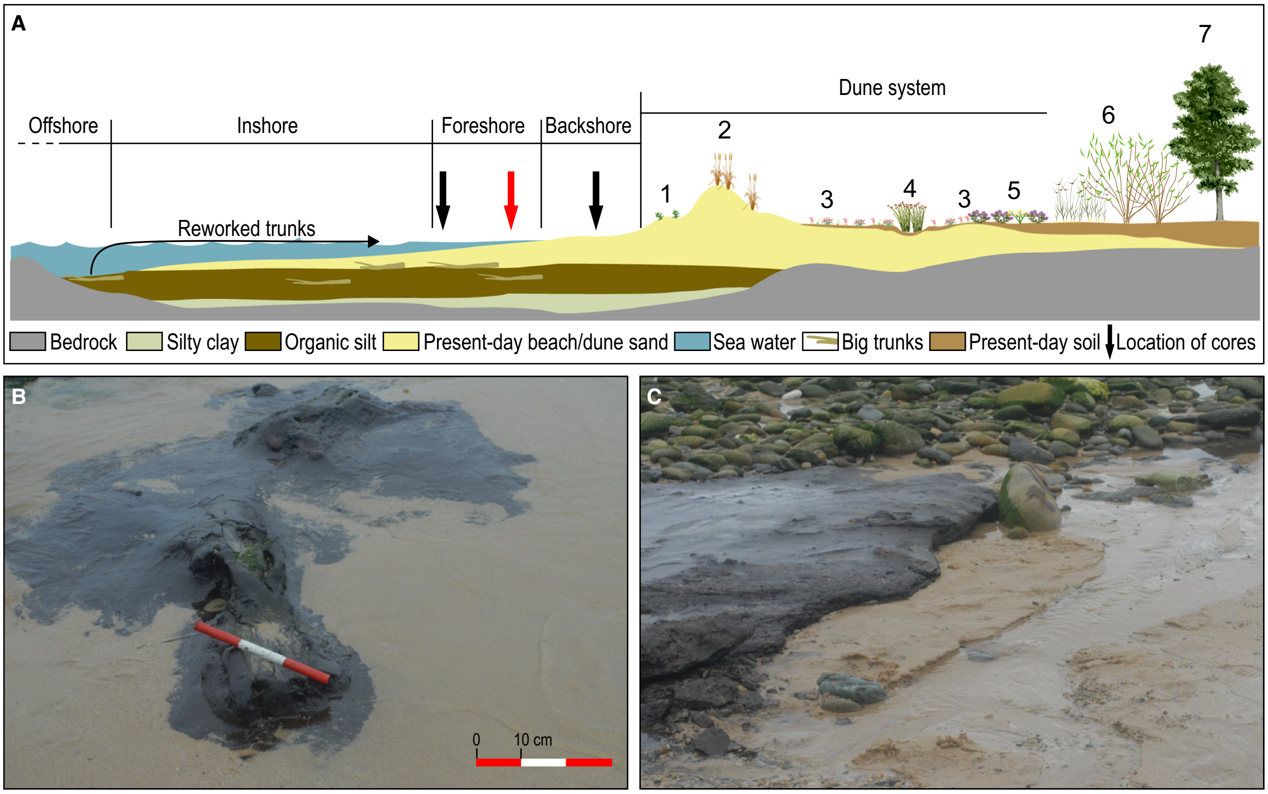

Fig. 2. A. Idealized section of the Ponzos deposit, indicating the different facies present, the sampling points (the red arrow shows the location of the core analysed) and the configuration of the area. 1 = embryonic shifting dunes; 2 = shifting dunes along the shoreline with *Ammophila arenaria* (white dunes); 3 = fixed coastal dunes with herbaceous vegetation (grey dunes); 4 = humid dune slacks; 5 = Atlantic decalcified fixed dunes; 6 = herbaceous and woody wetlands; 7 = forest. B. Photograph of a trunk at Ponzos. C. Outcrop of peaty sediment at Ponzos.

microscopy. The total sum of pollen in all samples ranges between 411 and 789 grains. Terrestrial pollen percentages were calculated using a total terrestrial pollen sum (>300 grains), including trees, shrubs and upland herbs. The total sum of pollen was used to calculate percentages of the aquatics and cryptograms. The software TILIA 1.7.14 (Grimm 1990–2015) was used for calculations and graphic representation of results. Pollen diagrams were zoned using constrained incremental sum of squares (CONISS) cluster analysis (Fig. 3).

Chronology

Five radiocarbon dates were obtained for the core, four using AMS dating methods and one more using the conventional ^{14}C method (Table 1). ^{14}C age determinations were carried out at the Centrum voor Isotopen Onderzoek, Groningen University and at the ICA Lab, Florida. Radiocarbon ages were converted to cal. a BP (2σ) using Calib 8.2 (Stuiver *et al.* 2020; Table 1).

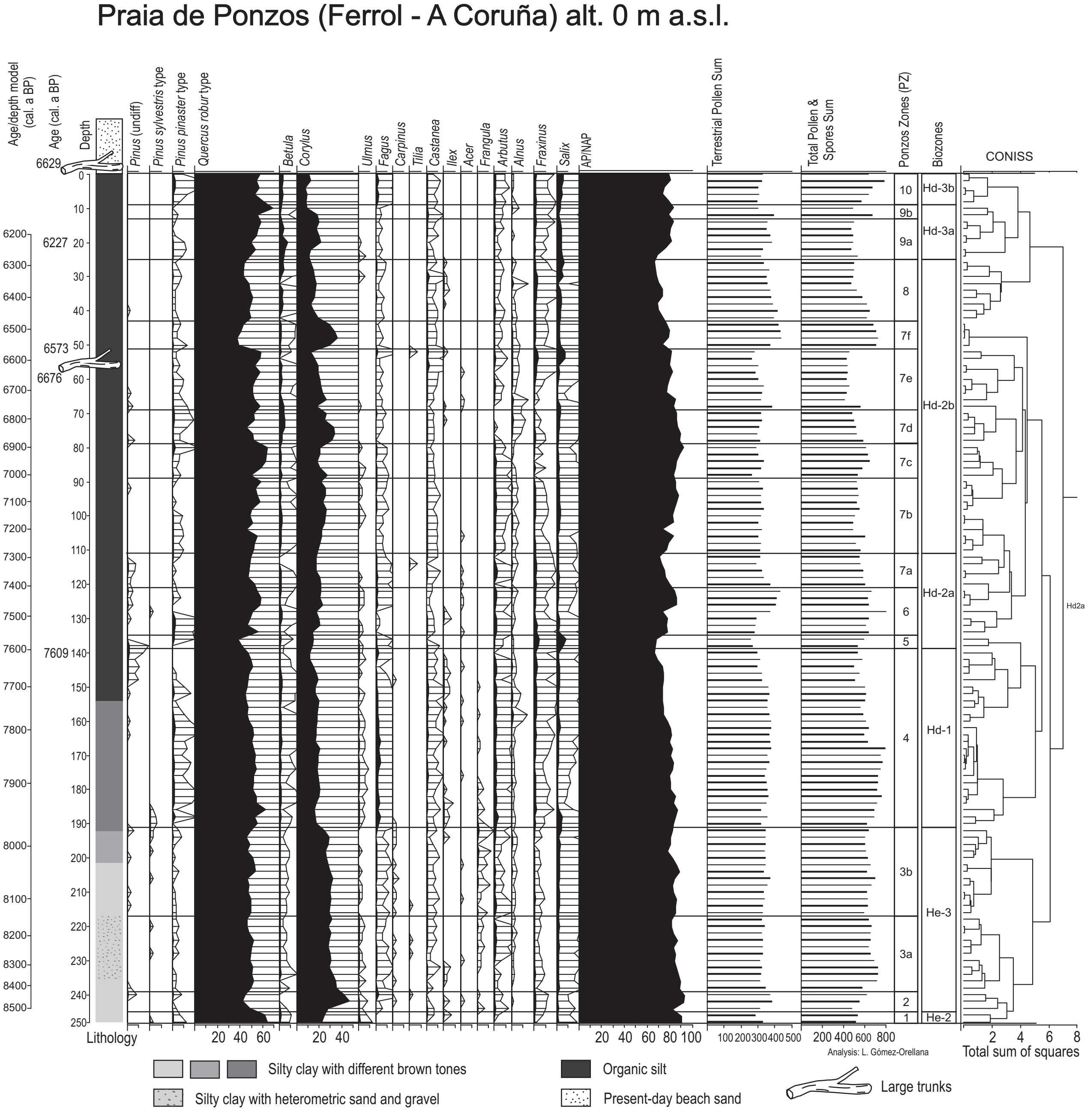

Fig. 3. Pollen percentages diagram of the arboreal taxa recorded in the Ponzos deposit. Biozones: He = Holocene arboreal expansion; Hd = Middle Holocene, from Muñoz Sobrino *et al.* (2005). Depth/age model is given on the left, based on the dating and the well-dated palyno-stratigraphical regional event, related to the expansion of *Corylus* (8500 cal. a BP).

Table 1. Radiocarbon and calibrated ages from Ponzos. All dates were calibrated by using the CALIB Rev 8.2 program and IntCal20 data set (Stuiver *et al.* 2020). 2-sigma (95.4%) confidence intervals and their relative areas were used as well as the median probability.

Laboratory no.	Depth (cm)	Material	Radiocarbon age uncal. a BP	Method	2σ cal. a BP age ranges (relative area)	Cal. a BP median probability
GrN 32293	0	*Salix*	6075±35	Conventional	7149–7126 (0.03) 6841–7017 (0.94) 6838–6833 (0.00) 6818–6798 (0.03)	6929
ICA-20OS/ 0901	20–22	Sediment	5380±40	AMS	6171–6283 (0.65) 6103–6158 (0.18) 6010–6081 (0.16)	6227
GrA-65937	52–54	Sediment	5775±40	AMS	6479–6668 (1)	6573
GrA 66804	56	*Salix*	5860±40	AMS	6778–6763 (0.03) 6596–6756 (0.91) 6594–6562 (0.06)	6676
GrA-65936	140–142	Sediment	6720±40	AMS	7555–7663 (0.85) 7510–7544 (0.15)	7609

Results

Biostratigraphy and radiocarbon dates

The obtained cores include different organic and inorganic facies, their bases being directly placed on bedrock. The deepest core obtained in Ponzos beach achieved a depth of 250 cm and comprises several well-differentiated facies (Fig. 3). The basal part (250–154 cm depth) is formed by grey-brown silty clay, with different brown tones, probably related to changing organic matter content. The brown tone increases from the bottom up and it is possible to distinguish up to three facies (Figs 2, 3). Between 216 and 236 cm depth, there is a high content of quartz heterometric sands. Above, there is a very dark silty layer with high content of organic matter and presence of plant remains. It is 154 cm thick, with large wooden embedded fragments of *Salix* (Figs 2, 3). On top of this layer, there is an important set of large-sized plant macro-remains (Figs 2, 3). The uppermost level is a pack of sand, 75–100 cm thick, corresponding to the current beach.

Five radiocarbon datings were obtained, three from bulk sediment and two from two wood fragments (Table 1). One of the fragments was recovered at 56 cm depth from inside the sampled core, embedded within the sediment. The other was recovered within the macro-remains that appear on the sediment surface.

Palaeobotanical analyses

The inorganic and organic sediments of the active halophilous wetlands (infralittoral and eulittoral environments of marshes and coastal lagoons) located in the Atlantic bioregion are characterized by high salt content, and they form efflorescences when dry. These usually have macro-remains of shells, carapaces, spicules or other carbonated structures belonging to marine invertebrates, as well as characteristic micro-remains of halophytic biocenosis. No efflorescence appears in the dried sediments obtained in Ponzos. Also, the analysis of the residues under 10× and 30× magnification after sieving through 0.5, 0.1 and 0.05 mm found no evidence of marine invertebrate remains, nor was any carbonic reaction after acid attack noted. The entirety of the recovered macro-remains corresponds to vascular plants, fibrous remains, small roots (<2 mm diameter), as well as pieces of leaves and stems of Poaceae and Cyperaceae.

The different facies include abundant plant macro-remains, especially at the most organic level (0–154 cm). Most of them correspond to fibrous tissues of herbaceous vascular plants and woody fragments of different sizes. The largest woody remains correspond to 25 large branches and trunks over 2 m long (up to 5–7 m) and 30–40 cm in diameter. Some of these large fragments correspond to roots and basal fragments of the trunk in living disposition. However, most of them are located on the surface of the deposit, either embedded in it or free. The majority of our woody samples are from willow (according to the present-day regional flora, most probably correspond to *Salix atrocinerea*) and to a lesser extent, from deciduous oaks (according to the present-day regional flora, most probably correspond to *Quercus robur*/*Quercus pyrenaica*).

The content of micro-remains consists of abundant pollen as well as moss and fern spores, in a good conservation status. In addition, several fungus remains (spores, hyphae), as well as diatoms and other non-pollen micro-fossils were found. The content in micro-remains is similar to the pollen signal obtained in different non-halophilous wetlands in the littoral area (peatlands, wet heaths, high marshes, marsh areas surrounding coastal lagoons, etc).

Figures 3, 4 and 5 show the pollen diagrams obtained. The identified pollen zones follow the results of the cluster analysis. Ten local pollen assemblage zones (LPAZ) were recognized, and designated as Ponzos

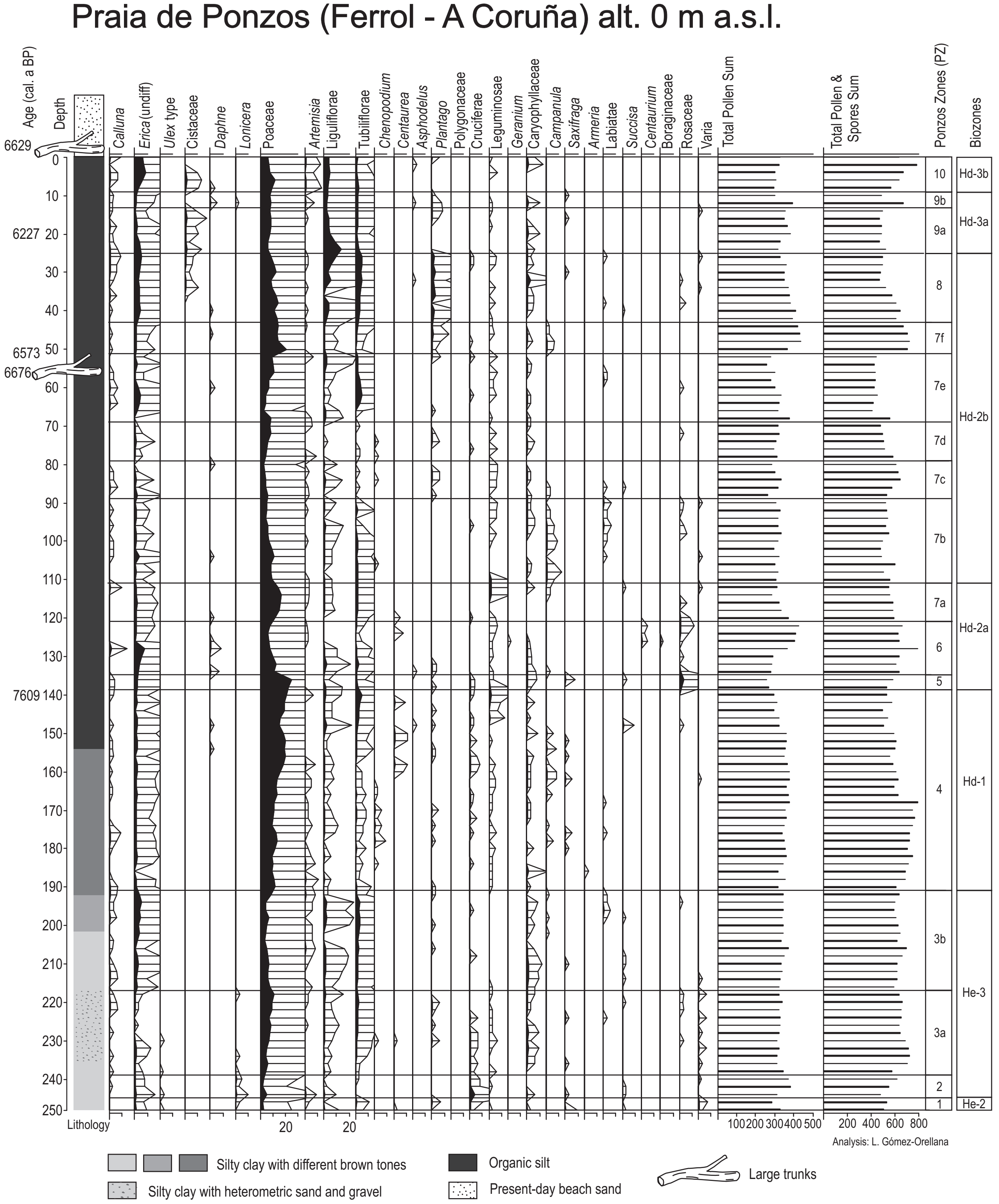

Fig. 4. Pollen percentages diagram of the herbs and shrubs recorded in the Ponzos deposit. Biozones: He = Holocene arboreal expansion; Hd = Middle Holocene, from Muñoz Sobrino *et al.* (2005).

Zones (PZ), but some of them were subdivided in order to highlight some particular facts related to the vegetation dynamics.

PZ-1 (250–248 cm) marking the start of the sequence is characterized by dominance of trees, including a maximum of *Quercus robur-type* and around 20% of

Corylus. Hereafter, PZ-2 (248–238 cm) starts with a slight decrease in total tree pollen, marked by the decline of the *Quercus robur-type* but the subsequent expansion and maximum of *Corylus*.

PZ-3 (238–192 cm) evidences the recovery of the total tree pollen (>85%). The dominant deciduous tree species are *Quercus robur-type* and *Corylus*, with scarce presence of *Pinus*. In subzone 3a there is a slight increase of Poaceae while in subzone 3b *Erica* decreases and Compositae increase. PZ-4 (192–140 cm) reflects a slight total tree pollen detriment due to the decrease of *Corylus*. *Fagus* and *Arbutus* increase and the continuous curve of *Ulmus* starts. The percentages of Poaceae increase and the percentages of *Erica* and *Compositae* decrease. The top of the zone has been dated at 7609 cal. a BP (Table 1, Fig. 3). PZ-5 (140–134 cm) reflects a detriment in total tree pollen and represents the tree minimum of the sequence, together with the maximum of Poaceae (Fig. 4).

In PZ-6 (134–120 cm) there is a rise of the tree pollen percentages that reflects the recovery of the deciduous forests, with the successive expansion of *Quercus robur-type* and *Corylus*, and *Arbutus* and *Fagus* increasing. Besides, a slight increase of *Erica* occurs, while Poaceae decline (Fig. 4).

PZ-7 (120–44 cm) represents an initial decrease in tree pollen (PZ-7a) and its subsequent recovery (PZ-7b). Subzone PZ-7c reflects an increase of *Quercus robur-type,* followed by increases of *Corylus* and *Betula* and the minimum values of *Arbutus* (PZ-7d). Subzone PZ-7e shows a new increase in *Quercus robur-type, Erica* and Poaceae (Figs 3, 4). The top of subzone PZ-7e has been dated at 6573 cal. a BP (Table 1, Fig. 3). Finally, PZ-7f shows the replacement of *Corylus* by *Quercus robur-type* (Fig. 3) and the continuous increase of Poaceae (Fig. 4). PZ-8 (44–26 cm) shows a moment of arboreal detriment, mainly due to decreases in *Corylus* and *Quercus robur-type*. PZ-9 (26–10 cm) reflects a subsequent recovery of the total tree pollen that is initiated with the increase of *Betula* and *Corylus* (PZ-9a) and then *Quercus robur-type* (PZ-9b). Subzone PZ-9a has been dated at 6227 cal. a BP (Table 1, Fig. 3). *Quercus robur-type* and *Corylus* decline in PZ-10 (10–0 cm), while *Betula*, *Fagus*, *Pinus pinaster-type* and *Erica* increase.

The lowermost levels of the sequence could not be dated by radiocarbon techniques due to their scarce organic matter content. Above them, different dates were obtained from bulk sediment and macro-remains (Table 1, Fig. 3).

The interpretation and correlation of these pollen zones with the reference regional sequences for the Atlantic ecoregion (Ramil-Rego 1992; Muñoz Sobrino *et al.* 2005) and the ^{14}C dates obtained allow the attribution of the entire sequence to the beginning of the Holocene. The base of the sequence represents a phase of *Corylus* expansion and *Quercus robur-type* detriment dated before 7069 cal. a BP. This allows the age of the base of the sequence to be estimated at some time between the regional expansions of *Quercus* (10 950 cal. a BP) and *Corylus* (8500 cal. a BP). The date of 6227 cal. a BP (Table 1) obtained at the top of the sequence (20 cm deep) would place the end of the sequence around 6000 cal. a BP (Fig. 3).

Discussion

The local ecosystem

The sedimentological and palynological data (Fig. 5) allow us to consider that the depositional environment in the Ponzos site was a coastal wetland. Initially (250–120 cm depth) it would have been a freshwater wetland without a permanent body of water and formed by different tall herbaceous communities. *Cladium mariscus* and probably *Phragmites australis* would have been present, as they exist today in different wetlands of the area, forming part of estuaries and lagoons. Besides, other secondary herbaceous taxa (*Iris*, Caryophyllaceae, Umbelliferae, *Osmunda regalis*, *Equisetum*, etc.) existed, as well as different small fern communities. These include *Isoetes*, with two species distributed at present in the hygrophilous wetlands of the area (*Isoetes durieui* and *I. histrix*) and *Ophioglossum*, which in the Iberian Atlantic bioregion currently comprises two species, *Ophioglossum lusitanicum* and *O. vulgatum* (López González 1986). Furthermore, different trees (*Salix*, *Alnus*, *Corylus*, *Fraxinus*, *Betula*) were also present in the wetland. In relation to the dominance of the hygrophilous species, some typical elements of swamp and peatland communities (*Sphagnum*) are noticeably absent in the first part of the sequence. Later, *Sphagnum* spores appear in the more organic facies, but noticeably underrepresented in relation to what happens in sequences from nearby peat bogs located at higher elevations (Ramil-Rego 1992).

Between 120–0 cm depth hygrophilous environments persist, but different taxa indicative of fresh open waters also appear, which reveals significant changes in the ecological conditions of the site (Fig. 5). Particularly, the presence of *Ranunculus* and *Potamogeton* may be linked to the occurrence of shallow biotopes (<1–1.5 m depth). In the coastal lagoons of the Iberian Atlantic region, the native species *Potamogeton pectinatus* is characteristic of halophytic environments; but most of the other native species (*Potamogeton natans*, *Potamogeton perfoliatus*, *Potamogeton polygonifolius*, *Potamogeton trichoides*) inhabit subhalophytic environments and fresh waters. The species *Nymphaea alba* may be the only representative of *Nymphaea*, which usually configures dense biocenoses in freshwater wetlands and adjusts its seasonal changes to the flood levels. Finally, *Myriophyllum* is a hydrophyte that lives suspended close to the water surface, always in environments of reduced salinity. In coastal lagoons, as in inland lagoons, *Myriophyllum*

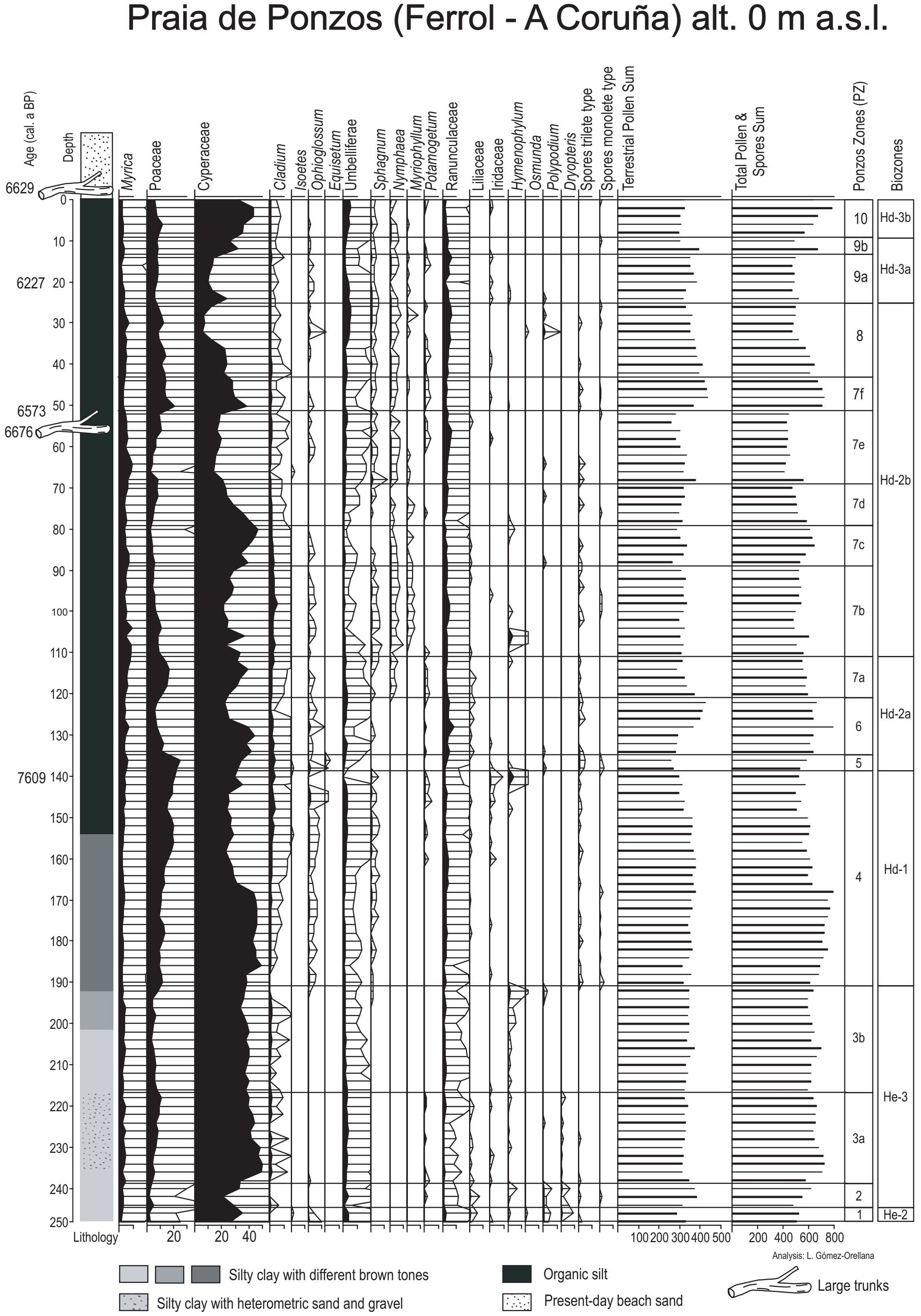

Fig. 5. Pollen percentages diagram of the taxa linked to freshwater environments recorded in the Ponzos deposit. Biozones: He = Holocene arboreal expansion; Hd = Middle Holocene, from Muñoz Sobrino *et al.* (2005).

species (*M. alterniflorum*, *M. verticillatum*) usually form dense formations with *Ceratophyllum demersum*.

In summary, the sedimentological characteristics and the data presented above, as well as the absence of macro-remains and pollen from any halophilous hydrophytes that are typical of coastal lagoons in the Atlantic bioregion (*Ruppia maritima*, *Zostera noltii*, *Najas marina*), allow the typification of the lacustrine environment of Ponzos as characteristic of a coastal lagoon of subhalophytic waters.

Nowadays, these types of wetlands still exist in the Atlantic bioregion of the Iberian Peninsula, three of them in the Costa Ártabra littoral: Doniños, Frouxeira and Pantín (Fig. 1). The ecological configuration of these wetlands is very similar. A sandbar encloses a small bay or inlet, creating a dune system that comprises a lagoon environment, as well as, typically, different hygrophilous wetlands. Depending on the configuration of the sandbar, the lagoon and the hygrophilous wetlands can be temporarily or permanently affected by tides, storms or changes in the sea level. Alternatively, during the most stable periods, they tend to stay closed. In the coastal lagoons of the Iberian Atlantic bioregion, there is a clear spatial gradation of environments and biocenosis. Halophilous habitats develops on the areas close to the sandbar and the beach; but subhalophilous and continental communities prevail in distal environments. The configuration of the ancient lagoon (and the associated hygrophilous habitats) that can be deduced from the pollen diagram of Ponzos is comparable to the currently observed configuration of different coastal lagoons within the Atlantic-Cantabrian area of Iberia.

The Ponzos record also reveals the existence of a process of expansion of hygrophilous forest over the wetland, represented by the presence of large *Salix* macro-remains embedded in the sediment (Figs 2, 3). The date 6676 cal. a BP obtained for one of these fragments is coherent with the date obtained for the sediment (6600 cal. a BP). In addition, the dating of the large pieces of wood on the top of the sediment is coherent with the date of the trunk recovered inside the sediment (Fig. 3, Table 1). These pieces of evidence suggest that the wood remains scattered on the deposit surface were reworked from the inner part of the sediment by the erosive action of the sea (Fig. 2).

Hygrophilous tree species growing over the wetland also occurred at similar times in other deposits in the area (Ramil-Rego 1992; Muñoz Sobrino *et al.* 2005). These changes probably have corresponded to modifications of the hydrological regime of the wetlands and, therefore, were probably linked to the regional and local climate conditions, as well as to the configuration of the wetland opening system. After the stage of tree invasion, the wetlands of Ponzos recovered their previous configuration. This last change is marked by the increases of *Corylus* and Cyperaceae (Figs 3, 5).

Landscape configuration and dynamics

The beginning of the Ponzos pollen record shows the regional expansion of *Quercus robur-type* and *Corylus*, followed by a long period of tree dominance (Fig. 3). This sequence of events can be correlated with other pollen records obtained from peatlands located in the northern Galician Mountains (Menéndez Amor & Florschütz 1961; Van Mourik 1986; Ramil-Rego 1992; Ramil-Rego *et al.* 1996, 1998a, b, 2000) and other sequences from the Atlantic bioregion (Ramil-Rego *et al.* 2000; Muñoz Sobrino *et al.* 2005, 2007; Iriarte Chiapusso *et al.* 2016). In Ponzos, after the maximum of *Quercus* and *Corylus*, there are no decreases in total tree pollen or significant increases in herbs or shrubs. This is a remarkable difference from what happens in a number of diagrams from the nearby Cantabrian-Atlantic Mountains, where several peaks of Poaceae, *Juniperus* or *Erica* correlate with the 9.3 and 8.2 cal. ka BP events (Muñoz Sobrino *et al.* 2005; Iriarte Chiapusso *et al.* 2016). The absence of a relevant pollen signal for those rapid climatic events in Ponzos during the Early Holocene (beyond the local development of a hygrophilous wetland without a free water body during the first part of the sequence) probably derives from its low altitude, its proximity to the ocean, and the lack of nearby sharp ecotones.

The dominance of tree pollen with the codominance of *Quercus robur-type* and *Corylus* reflects the importance of deciduous forests in the landscape. These forests were likely dominated by deciduous broad-leaf trees (oaks, hazel), but the new evidence suggests that other deciduous species (*Acer*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Corylus*, *Frangula*, *Fraxinus*, *Salix*, *Tilia*, *Ulmus*), a small group of evergreen taxa (*Arbutus*, *Ilex*) and some gymnosperms (*Pinus pinaster-type, Pinus sylvestris-type)* were still present.

Except for *Quercus robur-type* and *Corylus*, which record a clear episode of expansion and dominance that denotes their important role in the configuration of the landscape, the rest of the tree taxa recorded only show phases of diffusion, i.e. discontinuous pollen evidence or continuous pollen curves with low percentages (Fig. 3). Deciduous forest dominance extending until the Middle Holocene also has been described from other pollen sites in the western subcoastal mountains of the Atlantic bioregion of Iberia: Buio peatland I & II (Menéndez Amor & Florschütz 1961; Van Mourik 1986), Pena Vella, Chao do Lamoso, Rio das Furnas I & II (Ramil-Rego 1992; Ramil-Rego & Aira Rodríguez 1993a; Ramil-Rego *et al.* 1996, 1998a). The presence of *Pinus* increases towards the east of the Cantabrian littoral and the south of the Atlantic coast (Iriarte Chiapusso *et al.* 2006; Granja *et al.* 2016), and even becomes dominant, further south, during the Middle Holocene (Connor *et al.* 2021).

Several trees recorded in the Ponzos pollen diagram (Fig. 3) lack native populations in the Atlantic bioregion of Iberia at present. The only natural populations of *Carpinus* currently existing are located in the eastern Cantabrian corner (Aizpuru & Catalán 1984; Remón *et al.* 2002; Muñoz Sobrino *et al.* 2018). Nowadays, *Tilia* has been extirpated from the littoral areas, and *Pinus* from the whole of NW Iberia. Nevertheless, *Tilia* maintains wild populations in different zones of the Cantabrian range but is extinct in Galicia and Portugal. Meanwhile, *Pinus* only maintains small wild populations in some mountainous areas, such as the Gerês range (Pavia *et al.* 2014; Fernandes *et al.* 2015) and the Cantabrian range (Ramil-Rego & Aira Rodríguez 1993b; García *et al.* 1997; Franco *et al.* 2001; Muñoz Sobrino *et al.* 2003).

The Ponzos sequence shows continuous presence of *Fagus* pollen since before 7600 cal. a BP (Fig. 3), which indicates the presence of local forests of this taxon in locations situated at low altitude, close to the ocean, and further west than its present-day range. A similar behaviour of beech occurs during different temperate stages of the Last Glacial Cycle in other sequences in the area (Gómez-Orellana *et al.* 2007, 2013). According to new data, *Fagus* persisted in coastal areas of NW Iberia at least until the Middle Holocene, which reinforces the existence of local refuges for this taxon in Iberia (Ramil-Rego *et al.* 2000; Muñoz Sobrino *et al.* 2009).

The presence of gymnosperms in the Atlantic bioregion is documented with pollen data and macro-remains since the Tertiary, showing an important group of taxa: *Abies*, *Cedrus*, *Juniperus*, *Pinus*, *Taxodium*, *Taxus*, *Juniperus* (Alcalde Olivares *et al.* 2004; Tereso *et al.* 2011). During the Pleistocene, the presence of gymnosperms is significantly scarce (*Abies*, *Cedrus*, *Juniperus*, *Pinus*, *Taxus, Juniperus*). At the beginning of the Holocene it is even further reduced, and the only gymnosperms recorded are *Pinus*, *Taxus* and *Juniperus* (Gómez-Orellana *et al.* 2007; Ramil-Rego *et al.* 2011; Tereso *et al.* 2011). The representation of the gymnosperms in the landscape is also different, being dominant in the mountain areas and inner depressions, while their presence in the oceanic areas is scarce, almost marginal. This situation has been exacerbated during the Holocene because human activities have caused a strong retraction of woodlands. This has determined the local or regional extinction of different species, among them, pines (Ramil-Rego 1992; Ramil-Rego & Aira Rodríguez 1993b, 2009, 2019; Figueiral 1999). In the 19th century, pines no longer had wild populations in Galicia, but small formations persist in mountainous areas in north Portugal and Castilla-León. The extant pine formations currently existing in NW Iberia derive from old and recent reforestations that mainly used allochthonous genetic material.

The Ponzos diagram also shows the continuous presence of *Castanea* (Fig. 3). The chestnut tree (*Castanea sativa*) has also been recorded in NW Iberia and, in general, in the Atlantic bioregion, throughout the Tertiary and the Pleistocene (Gómez-Orellana *et al.* 2007, 2013; Tereso *et al.* 2011). Usually, it is an element with scarce representation, and no record suggests its predominance in the landscape or the existence of formations dominated by this taxon. *Castanea* pollen also appears in low percentages at the beginning of the Holocene (Ramil-Rego 1992). The regional expansion of *Castanea* is only recorded during the Middle Ages and linked to local cultivation. In the Touriz diagram (Van Mourik 1986), chestnut expansion is dated from 950 cal. a BP (AD 1000). The beginning of its cultivation and the use of graft-chimaeras mark this phase of expansion, when chestnut plantations occupied large areas frequently modifiing the local landscapes. This favoured, in many cases, its co-occurrence with other native species and the development of shrub and herbaceous strata similar to natural forests. These chestnut plantations using graft-chimaeras had great importance in the landscape from the Middle Ages until the end of the 19th century and the start of the 20th century. Later, the spread of blight disease (Vieitez Cortizo *et al.* 1996) and the emergence of forestry crops, aimed to satisfy industrial demands, significantly reduced its presence, especially in the littoral area and lowlands. In the mountainous areas of the west of the Atlantic bioregion, masses of old-growth chestnut chimaeras have persisted for over 100–200 years.

One of the most singular elements of the native forests of the Atlantic bioregion is the presence of nemoral ferns, considered as relicts. Most of these ferns are located in the last great representations of the ancient forests that persist in the sublittoral valleys of the Eume, Belelle, Mera, Sor, Landro and Ouro rivers. These include species such as *Culcita macrocarpa*, *Woodwardia radicans*, *Vandenboschia speciosa*, *Hymenophyllum tunbrigense* and *Hymenophyllum wilsonii*, all of them with low dispersion and colonization capacities (Dupont 2015).

The presence of *Hymenophyllum* spores is regularly recorded in the pollen analysis of Ponzos (Fig. 5). Currently, two species of this genus inhabit the Atlantic bioregion of Iberia. The most frequent is *H. tunbrigense*, which currently maintains a scattered area of distribution including Macaronesia, Scotland, Italy, Germany and the Iberian Peninsula. In Iberia, its distribution is restricted to the Atlantic bioregion, specifically the littoral and sublittoral territories of A Coruña, Lugo, Asturias, Cantabria and Euskadi. Less frequent is *H. wilsonii*, with presence in Açores, Andalucía, Northern Portugal and Galicia (A Coruña). Currently, both species include populations located in a radius of below 20 km from the Ponzos deposit.

In addition to tree vegetation and wetlands, the pollen record of Ponzos attests to the presence of elements that are characteristic of other coastal environments as cliffs and dune systems (e.g. *Armeria* and *Artemisia*). There are also shrubs dominated by Ericaceae (*Erica*, *Calluna*) and leguminous thorny shrubs (*Ulex*), with *Daphne* (*Daphne* *gnidium*) and Cistaceae (*Cistus salviifolius*) and a number of herbs: *Centaurium*, *Campanula*, *Saxifraga*, *Succisa*, *Chenopodium*, *Asphodelus*, *Lonicera*, *Centaurea* (Fig. 3). Finally, it must be noted the lack of taxa indicating an influence of anthropic activities in the landscape, especially crops (Fig. 4).

The great diversity of trees recorded from the beginning of the Holocene in the sequence of Ponzos reinforces the evidence obtained in other areas of the Iberian Peninsula, especially in the Atlantic bioregion. All of these data support that local refuges for demanding trees existed in this area, from which they spread. Thus, some of them expanded in the region during the Holocene but others become underrepresented (Ramil-Rego *et al.* 1998b, 2000; Gómez-Orellana *et al.* 2007, 2012, 2013; Muñoz Sobrino *et al.* 2007, 2009).

Effects of the sea level rise

The climate oscillations during the Quaternary have caused modifications in the volume of continental ice, determining significant changes in the sea level (Bard *et al.* 1990; Dias *et al.* 2000; Leorri *et al.* 2013). These influence the configuration of coastal habitats, changing their distribution areas and causing fragmentation, redistribution or even the disappearance of certain environments. Along the littoral of the Atlantic bioregion of the Iberian Peninsula, the remains of ancient wetlands developed along different periods of the Pleistocene or the Holocene usually appear.

The available data for NW Iberia (Dias *et al.* 2000; Leorri *et al.* 2013) point to a phase of rapid increase of the marine level at the beginning of the Holocene (11.2–9.4 cal. ka BP) with strong rates of annual increase. For this period, the records obtained in coastal wetlands show remains of beach and marine sediments (Granja *et al.* 2008, 2010; Sáez *et al.* 2018), but organic sedimentation is only recorded in the sequence of Mougás (Gómez-Orellana *et al.* 1998). Between 9.4 and 6.8 cal. ka BP both the rate of eustatic sea level rise and the annual rate of rise were reduced. During this time, the organic sedimentation in Mougás ceased. The Mougás deposit was the most recent site representative of a wide group of wetlands that occupied the emerged areas during the Würm glacial period, and whose remains are currently fossilized (Gómez-Orellana 2002; Gómez-Orellana *et al.* 2007, 2013). Now, the new pollen and chronological data obtained establish the beginning of the Ponzos sequence between 10 950 and 8500 cal. a BP.

Later, between 6.8 and 4.2 cal. ka BP, a stage of stabilization of the sea level occurred, during which NW Iberia littoral freshwater wetlands were reactivated and produced new organic sediments on the coasts (Santos & Vidal 1993; Salas *et al.* 1996; Bao *et al.* 2007; Costas *et al.* 2009; Granja *et al.* 2010, 2016; Ribeiro *et al.* 2011; Sáez *et al.* 2018). Finally, between 4.2–0 cal. ka BP, a new stage of relative sea level rise occurred with a high rate of annual increase. Littoral environments were restructured, with the sedimentation ceasing in some wetlands that become destroyed and, sometimes, new wetlands developing nearby (Gómez-Orellana *et al.* 2001; Santos *et al.* 2001; Granja *et al.* 2016; Sáez *et al.* 2018).

The data obtained in the uppermost part of the new sequence enable us to connect the destruction of the ancient wetland with a stage of eustatic sea level increase. Nevertheless, there is no evidence of an ecological transition process towards desiccation or salinization of the site. In this sense, the sandbar rupture and the entrance of the tides would have generated an erosive process that would probably have affected the upper levels of the sequence and removed any evidence of that transition process.

Conclusions

The results obtained from the high-resolution sequence of the Ponzos wetland shed light on the modifications of the vegetation in the coastal lowlands of the Atlantic bioregion of NW Iberia during the first half of the Holocene. New data increase our knowledge of the bioregion, mainly about the littoral zone, where the information existing was scarce and very fragmented. The sequence starts during the regional expansion of the forests and extends until the final part of the stage of forest dominance. Besides, these data allow the assessment of the dynamics of a coastal wetland in relation to the changes provoked in the littoral ecosystems by the Holocene marine transgression.

The sequence is characterized by high values of tree pollen and the lack of an obvious pollen signal of the climatic relapses (9.3 and 8.2 ka BP isotopic anomalies) previously described in the nearby sublittoral mountains.

From the beginning of the Holocene, the landscape of these coastal lowlands sheltered deciduous forests dominated by the *Quercus–Corylus* pairing. The high diversity of tree species recorded represents more than the entirety of the trees currently existing in the forests of the area, including several species currently extinct in the littoral and Atlantic sublittoral of NW Iberia, such as *Carpinus*, *Tilia*, *Fagus* and *Pinus*.

The high diversity of tree elements recorded at the beginning of the Holocene, and the regular evidence of the relic fern *Hymenophyllum* reinforce the idea of the occurrence of local refuges in the NW of the Atlantic bioregion of Iberia that persisted until the end of the Last Glacial Cycle. Regarding other tree formations, the presence of *Pinus* was rare and evidence of sclerophyllous trees is very scarce.

The instability in littoral areas, linked to the Holocene transgression, determines a strong fragility of the coastal wetlands, that generally only developed during short stages of stabilization. In Ponzos, the wetland formation began around 9000 cal. a BP as a hygrophilous wetland without a permanent body of water. Subsequently, the wetland became permanently covered by a body of fresh water. During this stage, there was an invasion of the hygrophilous forest into the wetland. Finally, after 6000 BP, the sandbar that disconnected the lagoon from the sea was broken and the seawater invaded the wetland.

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