Vegetation and environmental conditions in the Doñana Natural Park coastal area (SW Iberia) at the beginning of the last glacial cycle

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ABSTRACT

Detailed reconstructions of the vegetation of Iberia during the last glacial inception are rare due to the limited number of terrestrial sites recording this period. Active retreat of El Asperillo cliff, located on the Atlantic coast of southwestern Iberia, has exposed a fossil organic level dating back to one of the early stades of the last glacial cycle. Pollen and macrofossil analyses from this site show that the Doñana area was covered mainly by steppic vegetation; temperate trees survived the coldest periods, albeit in reduced numbers. Mediterranean taxa are extremely reduced, in contrast with other dry areas of southern Iberia over this time span. This vegetation suggests cold and arid climatic conditions, in accordance with paleoclimatic reconstructions based on several Atlantic marine cores.

Introduction

The Iberian fossil record for Marine Isotopic Stage (MIS) 5d, MIS 5b, and MIS 4 (the early Würm stades) features few continental sites. This situation has prevented spatially precise reconstructions of paleovegetation and paleoclimate in this area of southwestern Europe. Most paleoclimatic and paleobotanical information from the beginning of the last glacial cycle in southern Iberia comes from several Atlantic deep-sea cores taken from the continental margin (e.g., Sánchez Goñi et al., 1999, 2005; Roucoux et al., 2001, 2005). These sequences provide valuable information, although they do not offer fine spatial resolution. Continental sites recording this period are very rare in southern and western Iberia (Fig. 1A). Existing sites, including Padul (Pons and Reille, 1988), Carihuela Cave (Carrión, 1992; Fernández et al., 2007), and Area Longa (Gómez-Orellana et al., 2007), are located in areas environmentally and geographically distant from southwestern Iberia. Moreover, some fossil evidence indicates (e.g., Carrión et al., 2008; Rodríguez-Sánchez et al., 2008) that southern Iberia was a refugium for biodiversity during cold stages, but the spatial extent of the refugial area has not been determined. It is also important to confirm whether the continental fossil record from southwestern Iberia is in accordance with paleoclimatic reconstructions based on marine cores (e.g., Sánchez Goñi et al., 2005). This is especially relevant in an area such as the Gulf of Cádiz, where climatic evolution and associated environmental consequences have been widely discussed (e.g., d'Errico and Sánchez Goñi, 2003, 2004; Finlayson et al., 2004).

In this paper, pollen and plant macrofossils from a fossil organic layer are studied together, providing a complete reconstruction of the local and regional vegetation (Birks and Birks, 2000) covering the Gulf of Cádiz during a stade at the beginning of the last glacial cycle. The data presented here also expand upon previous work on the sedimentary sequences exposed along the coast of the Gulf of Cádiz (Zazo et al., 2005, 2008), providing more detailed information about past climatic conditions than was afforded by sedimentological and geomorphological analyses. Lastly, environmental conditions recorded in El Asperillo are compared to those of other Iberian sites during the early stades of the last glacial cycle to assess similarities and differences in the vegetational response to the climatic oscillations characterizing this period.

Study area

For this study, we analyzed an organic level located in the intertidal area of El Asperillo beach (37°4′N, 6°41′W; Fig. 1B), in Doñana Natural Park (Huelva, Spain). The current climate is Mediterranean with an Atlantic influence. The mean annual temperature is 16–17°C, and the average annual rainfall is 500–600 mm. Today, *Pinus pinea* stands are the most extensive vegetation type on the sandy soils of the Doñana
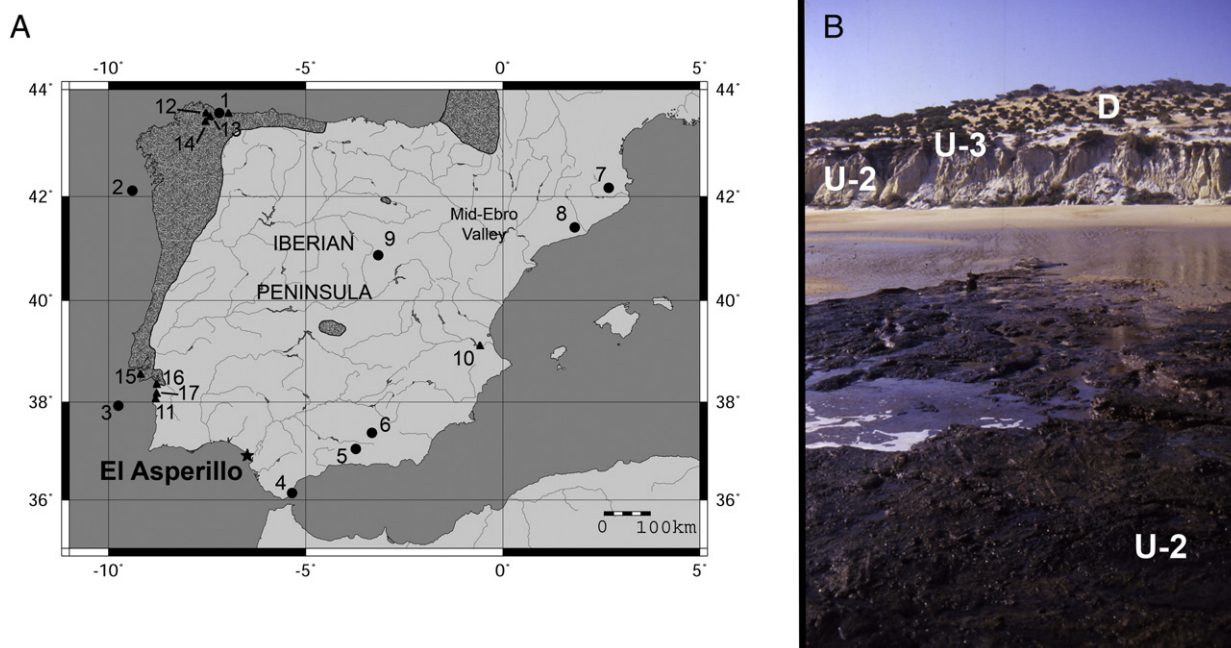
Figure 1. (A) Map showing the location of the El Asperillo intertidal site (black star) and other Iberian sites mentioned in the text, represented by black dots [1, Area Longa (Gómez-Orellana et al., 2007); 2, MD99-2331 (Sánchez Goñi et al., 2005); 3, MD95-2042 (Sánchez Goñi et al., 1999); 4, Gorham's Cave (Carrión et al., 2008); 5, Padul (Pons and Reille, 1988); 6, Carihuela Cave (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007); 7, Pla de l'Estany (Burjachs, 1990); 8, Abric Romani (Burjachs and Julià, 1994); 9, Los Torrejones (Carrion et al., 2007)]. 'Mid-Ebro Valley': several palynological sequences dated from MIS 2 have been obtained in this area [Valmadrid, Salada Mediana and San Juan de Mozarrifar (González-Sampériz et al., 2005)]. Shaded areas show current distribution area of *Myrica gale* in Iberia [modified from Jalas and Suominen (1976) and ANTHOS (2006)]. Quaternary Iberian sites recording *Myrica*-type pollen are represented by black triangles [1, Area Longa (Gómez-Orellana et al., 2007); 10, Navarrés (Carrión and Van Geel, 1999); 11, Lagoa Santo André (Santos and Sánchez Goñi, 2003); 12, Chan do Lamoso (Muñoz Sobrino et al., 2005); 13, Penido Vello (Muñoz Sobrino et al., 2005); 14, Pena Vella (Ramil-Rego et al., 1998); 15, Estacada (Queiroz, 1989) and Apostiça (Queiroz and Mateus, 1994); 16, Lagoa Travessa (Mateus, 1989); 17, Lagoa de Melides (Queiroz and Mateus, 1994)]. (B) View of El Asperillo beach showing the fossil limnetic level and the cliff in the background. U-2 and U-3 are aeolian units described by Zazo et al. (1999, 2005); D are semimobile and mobile Holocene aeolian units.

area, and *Juniperus oxycedrus* and *Juniperus phoenicea*-dominated shrublands cover the deeper sand sheets and dunes.

El Abalario Dome is a morphological dome elongated in a NW-SE direction that separates the Neogene Guadalquivir Basin from the Atlantic Ocean. Its southwestern flank is dissected by the El Asperillo cliff, which forms the present coastline and extends roughly 25 km from Mazagón to Matalascañas, with average heights of 16–20 m. The beach that we studied is located at the base of this coastal cliff. Geomorphic and neotectonic evolution of this sector was studied and presented by Zazo et al. (1999, 2005) on the basis of a chronostratigraphic framework supported by radiocarbon and optically stimulated luminescence (OSL) datings.

The sedimentary sequence consists largely of weakly cemented sandstones with intercalated reddish pedogenic horizons and laterally discontinuous blackish layers rich in organic matter. The Torre del Loro gravitational fault (TLF) separates two different paleogeographical domains exposed along the cliff wall (Zazo et al., 2005). Shallow-marine, coastal, fluvial, and aeolian deposits have been preserved on the northwestern upthrown fault block (from Torre del Loro to Mazagón). In contrast, only aeolian deposits occur on the downthrown block (from Torre del Loro to Matalascañas), and three units, called U-1, U-2, and U-3 in ascending stratigraphic order, separated by laterally continuous deflation surfaces, have been distinguished (Fig. 2A). These units accumulated between MIS 5 and early MIS 1 (Zazo et al., 2005). The top of unit U-1, exposed near Matalascañas at the southeastern extremity of the coastal cliff, is a red paleosol. The thick weathering profile suggests a moist, temperate climate. This unit was most likely deposited during an interglacial or interstadial period of MIS 5, since the OSL age of this deposit is 106 ± 19 ka (Zazo et al., 2005). Unit U-2, which includes the organic layer studied in this paper, accumulated mainly during MIS 4 and MIS 2, since the OSL ages range from 74 ± 7 ka to 32 ± 3 ka and

radiocarbon ages range from > 45,000 to $17,720 \pm 400$ ^{14}C yr BP (Zazo et al., 2005). Sedimentation of unit U-3 took place during late glacial and early Holocene times, and has been dated from around 16,000 cal yr BP to less than 12,000 cal yr BP on the basis of radiocarbon and OSL dates (Zazo et al., 2005).

Materials and methods

Samples were collected from three adjacent areas separated from one another by 200–300 m, belonging to a single organic layer 6–30 cm thick. Forty-nine wood samples (stumps, trunks, and branches) were collected from the organic level, taking advantage of the low tide (mean annual tide range is approximately 2 m). We also collected a peat section 6 cm thick from the organic level where plant macrofossils were embedded, in order to obtain a short pollen sequence associated with macrofossils (Fig. 2B). All samples were kept at 4°C until they were analyzed. The wood showed signs of biodegradation and carbonification. However, in general, the tissues are well conserved, and the absence of mineralization allows the wood to be classified as preserved in an unaltered state (Spicer, 1991).

Wood samples were studied in thin sections, prepared using a sliding microtome and usually observed without staining due to their dark color (Schweingruber et al., 2006). These wood samples were identified using keys of wood anatomy (García Esteban and Guindeo, 1990; Schweingruber, 1990; Schoch et al., 2004) and comparison with the reference collections of U.D. Tecnología de la Madera and U.D. Botánica (E.T.S.I. Montes, U.P.M., Madrid). Pollen analyses were performed on four samples 0.5-cm thick at 1-cm intervals taken from the collected peat section. This low number of analyzed samples is due to the small thickness of the organic layer studied, and the need for selecting the innermost section of the layer to avoid contamination
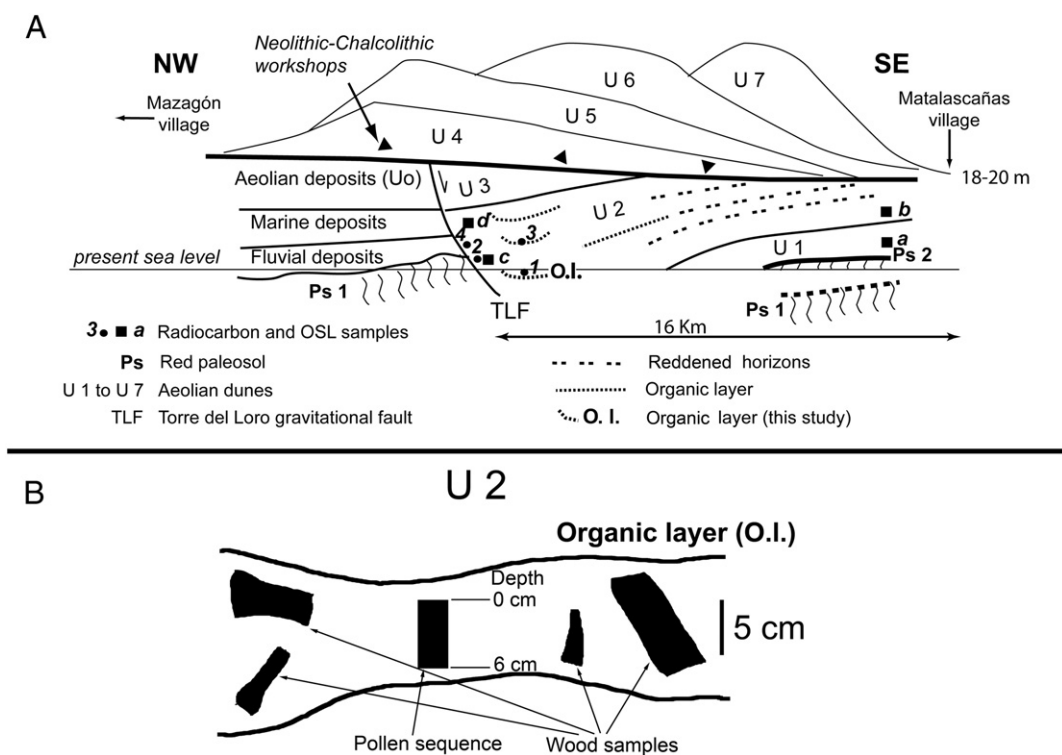
Figure 2. (A) Schematic profile showing the distribution of Pleistocene and Holocene deposits along El Asperillo cliff. OSL samples are as follows: a, AP00-TH1; b, AP00-TH2; c, AP00-D3; d, AP00-D2. Radiocarbon samples are as follows: 1, MAZ 1-8; 2, MAZ 17; 3, MAT 4; 4, MAZ 10. The ages of the OSL and radiocarbon samples are shown in Tables 1 and 2, respectively. (B) Schematic profile of the studied organic layer showing the relative location of the analyzed pollen and wood samples.

by modern pollen. Each sample was treated following Faegri and Iversen (1989). *Lycopodium* tablets were added at the beginning of the treatment to estimate pollen concentrations (Stockmarr, 1971). The pollen sum was always above 300 pollen grains. Spores and pollen of aquatic plants were excluded from this sum. Pollen diagrams were plotted using the programs TILIA 2.0 and TILIAGRAPH 2.0 (Grimm, 1992). To more accurately establish the age of the fossil organic level, a new wood sample from this layer was radiocarbon-dated.

Results and discussion

Chronological framework

The organic layer, from which the pollen and fossil wood samples were collected, is a part of U-2 and crops out of the downthrown fault block just at the lowermost part of the cliff and largely in the intertidal zone, close to the gravitational fault surface. Unit U-2, the thickest and most complex of the three units exposed along the cliff, shows deposition of dune fields moved by western and northwestern winds on a coastal plain. Features indicative of dunes, interdune depressions, paleochannels and pond environments have been recognized.

Zazo et al. (2005) collected three samples for OSL measurements in this unit (Fig. 2A and Table 1). Sample AP00-TH2 (collected 1 m above the red paleosol dating back 106 ± 19 ka that tops U-1) yields

an age of 74 ± 7 ka, sample AP00-D3 has an age of 48 ± 5 ka and sample AP00-D2 has an age of 32 ± 3 ka. The last two samples were taken from the cliff wall, opposite the organic level, 0.7 m and 6.5 m above the maximum high tide water mark, respectively. The sampled organic layer is about 2 m below the maximum high tide level.

Radiocarbon measurements of several wood samples collected from the sedimentary record of the cliff (Fig. 2A and Table 2) have yielded ages of >45,010 ^{14}C yr BP (Zazo et al., 1999), >42,020 ^{14}C yr BP, and >46,410 ^{14}C yr BP (Postigo-Mijarra et al., 2010). A new sample from the organic layer studied in this paper (MAZ 1-8) was dated $47,500 \pm 2500$ ^{14}C yr BP. All of these ages are considered unreliable because they fall beyond the range of the radiocarbon method.

The chronological interpretation of the organic layer requires some consideration. The stratigraphy and sedimentary features of U2, such as paleosols and the boundary surfaces, evidence variation in the

Table 1
OSL ages of aeolian units U-1 and U-2 estimated from the Torre del Loro Fault downthrown block (from Zazo et al., 2005). Elevation expressed in meters above sea level. Datum 0 m refers to mean annual high-tide level.

Sample	GPS location	Elevation (m a.s.l.)	Aeolian unit	Age (ka)
AP00-TH1	37°00′54″N, 06°47′51″W	1.5	U-1	106 ± 19
AP00-TH2	37°00′54″N, 06°47′51″W	5.5	U-2	74 ± 8
AP00-D3	37°04′59″N, 06°42′33″W	0.7	U-2	48 ± 5
AP00-D2	37°04′59″N, 06°42′33″W	6.5	U-2	32 ± 3

Table 2
Radiocarbon dates obtained from samples taken at El Asperillo cliff sedimentary unit U-2, belonging to the downthrown block of Torre del Loro Fault (see Zazo et al., 1999; Postigo-Mijarra et al., 2010). Elevation expressed in meters above sea level. Datum 0 m refers to mean annual high-tide level.

Sample name	Laboratory-sample code	Sampled material	Elevation (m a.s.l.)	Radiocarbon age (^{14}C yr BP)
MAT-4[a]	UtC-3938[b]	Wood	4	>45,000
MAZ 10[c]	Beta-116167	Wood	3.5	>42,020
MAZ 17[c]	Beta-116168	Wood	1.3	>46,410
MAZ 1-8[d]	CNA-122[b]	Wood	−2	$47,500 \pm 2500$[e]

Laboratory codes: UtC: Van der Graaf Laboratory, Utrecht, Netherlands; Beta: Beta Analytic, Miami, USA; CNA: Centro Nacional de Aceleradores, Seville, Spain.
[a] Data from Zazo et al. (1999).
[b] AMS analysis.
[c] Data from Postigo-Mijarra et al. (2010).
[d] This work.
[e] Age considered unreliable. It is at the upper age limit of the technique and may have been contaminated with younger carbon from a carbon-rich environment such as the intertidal area (see Kaiser et al., 2009).

tilting (5° to 10°) of both between Matalascañas and the TLF (Zazo et al., 2005). This variation prevents us from establishing a direct correlation between the organic layer and the deposits for which OSL ages have been obtained. Thus, the studied organic layer could have been deposited during a relatively short interval at the beginning of the last glacial cycle, and the paleobotanical evidence presented below indicates it was likely a stadial period during either MIS 5 or MIS 4.

The vegetation of Doñana at the beginning of the last glacial cycle: biogeographical implications

These pollen and plant macrofossil data allow us to reconstruct the vegetation of the Doñana area during a stade at the beginning of the last glacial cycle (Figs. 3 and 4). The studied organic layer was most likely deposited at the bottom of a depression or a paleochannel.

Previous studies on pollen representation in these environments (Carrión, 2002) have shown that entomophilous taxa are usually underrepresented, while producers of abundant, well-dispersed pollen may be overrepresented. Nevertheless, it is likely that El Asperillo pollen spectra reflect both regional and local vegetation, as entomophilous pollen is relatively abundant in the analyzed samples. Moreover, pollen preservation was good and a relatively high diversity of pollen types was recorded (43 pollen types). In this context, regional landscapes must have been mainly open (low arboreal pollen percentages: 30–35%) and dominated by steppe–grassland communities with *Artemisia*, Chenopodiaceae, and Poaceae. *Pinus* pollen (20–25%) could be produced by scattered individuals near the deposition site or by more extensive pinewoods growing far from the sampled site. *Pinus pinaster* and *Pinus nigra* could be the species dominating these stands, considering that several trunks and branches ascribed to these species have been found along the El Asperillo cliff
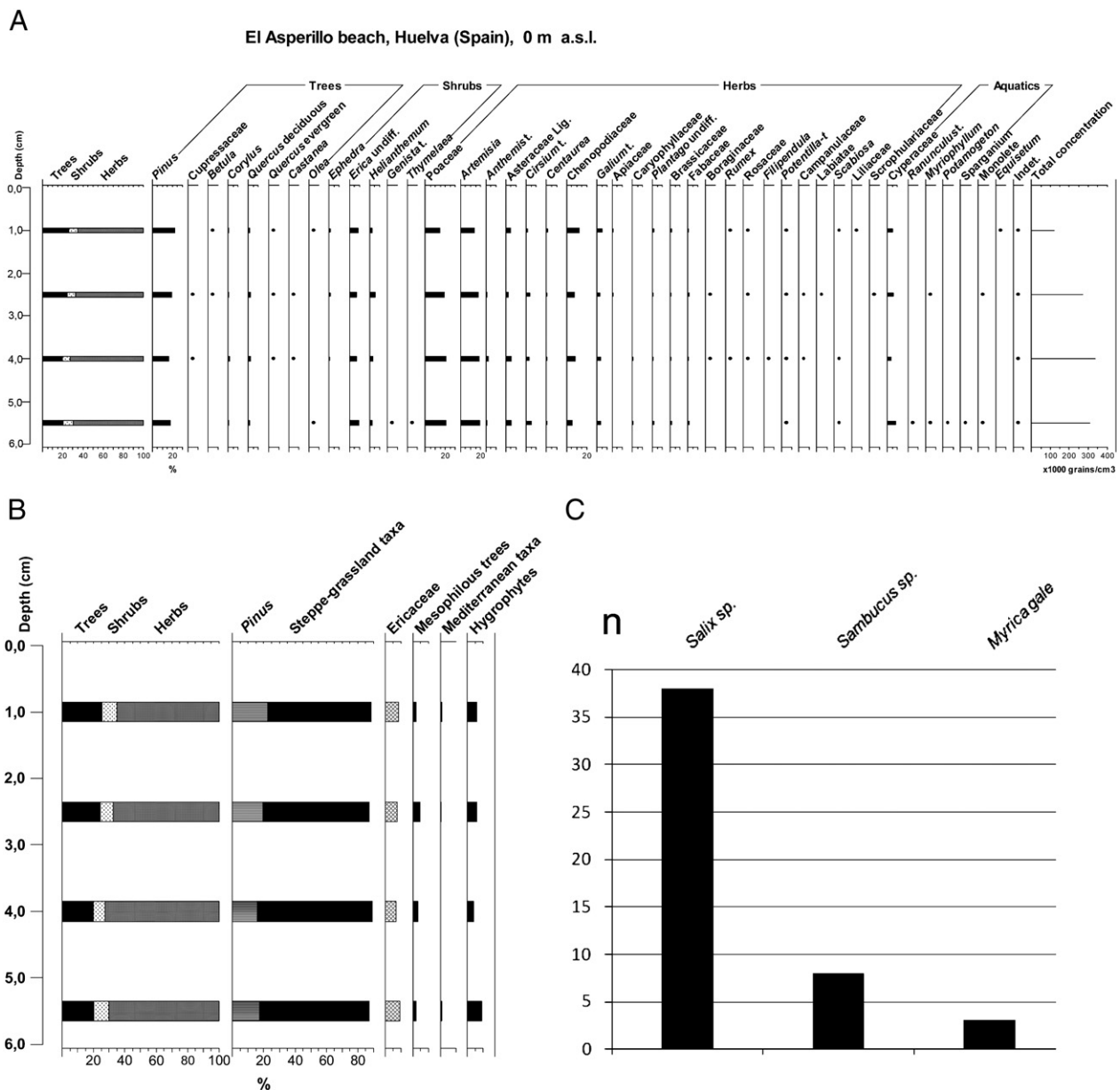
Figure 3. Paleobotanical record from El Asperillo beach. (A) Pollen percentage diagram. Black dots represent values lower than 1%. (B) Summary pollen diagram. Steppe–grassland taxa: herbs, *Ephedra*, Cupressaceae, *Helianthemum*, *Genista*, *Thymelaea*. Mesophilous trees: *Betula*, *Corylus*, deciduous *Quercus*, *Castanea*. Mediterranean taxa: *Olea*, evergreen *Quercus*. Hygrophytes: aquatic plants. (C) Plant macrofossil diagram. Vertical axis shows absolute frequencies.
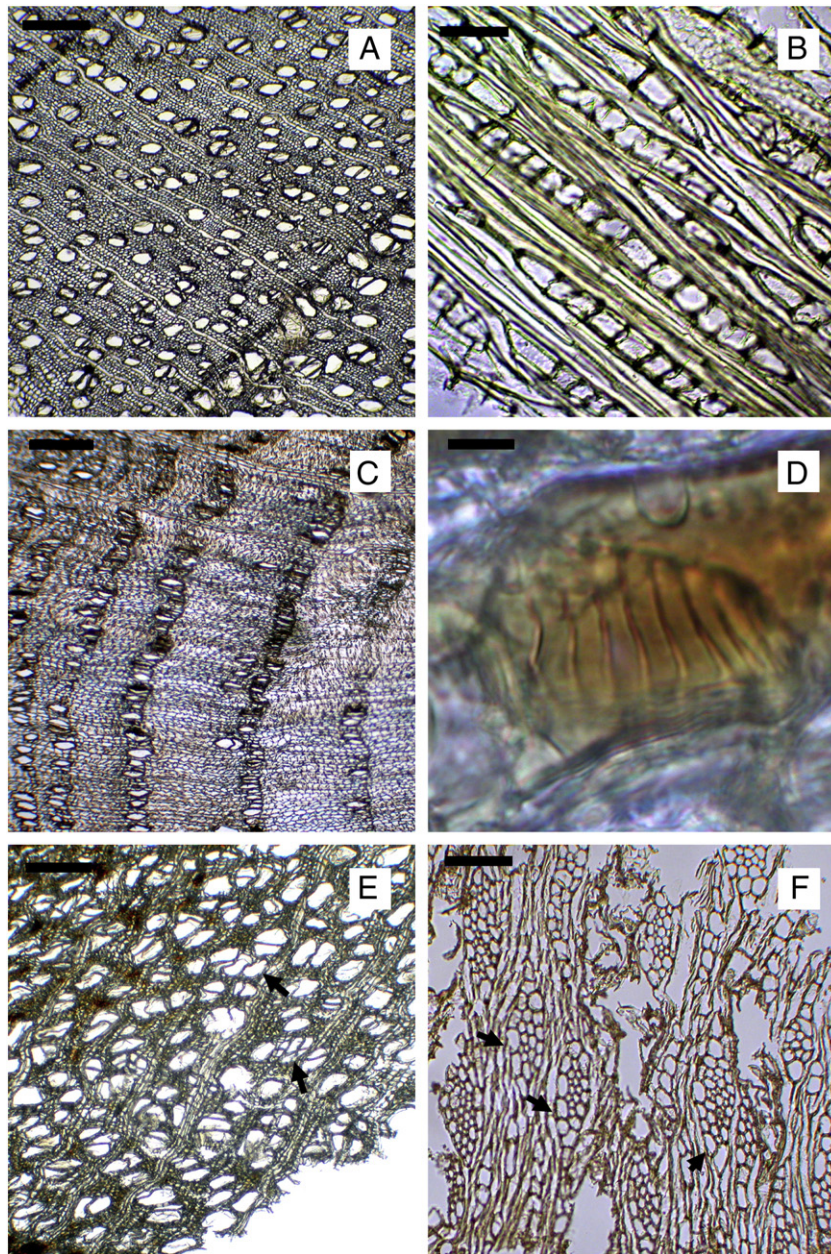
Figure 4. Wood anatomy microphotographs of fossil wood samples from El Asperillo beach. (A) *Salix*. MAZ 2–3 transverse section: diffuse–porous wood. Scale bar = 250 μm. (B) *Salix*. MAZ 3–9 tangential section: uniseriate heterogeneous rays and libriform fibers. Scale bar = 50 μm. (C) *Myrica gale*. MAZ 3–11 transverse section: ring-porous wood with marked ring boundaries. Scale bar = 200 μm. (D) *M. gale*. MAZ 3-11 radial section: scalariform perforation plate with less than 10 bars. Scale bar = 20 μm. (E) *Sambucus*. MAZ 1-1 transverse section: diffuse-porous wood, with pores usually grouped in tangential and oblique clusters (black arrows). Scale bar = 250 μm. (F) *Sambucus*. MAZ 1-1 tangential section: multiseriate and heterogeneous rays, 2–5 cells wide, with sheath cells (black arrows). Scale bar = 100 μm.

dating back to the MIS 3 or the late MIS 4 cold stages (Postigo-Mijarra et al., 2010).

The pollen and macrofossil records suggest the presence of small stands of deciduous trees, including *Corylus*, *Sambucus*, *Betula*, *Castanea*, and deciduous *Quercus*, probably covering areas with wetter soils, such as interdune depressions and valley bottoms linked to paleochannels. These environments were locally present during the deposition of the studied organic level, as has been demonstrated by geomorphic and sedimentological evidence (Zazo et al., 2005). High percentages of Ericaceae pollen are recorded, suggesting that heathlands could be an abundant vegetation community bordering these deciduous stands on relatively humid soils. Currently, Ericaceae species are widespread across western Iberia, usually growing

on acidic and relatively wet soils, including seasonally flooded depressions (Cabezudo, 1987). The presence of trunks and stumps of *Salix*, *Sambucus*, and *Myrica gale* proves the local presence of freshwater environments, since these plant macrofossils are not transported far from the place where they originated. This fossil evidence suggests that *Salix*, *Sambucus*, and *M. gale* could have dominated the riparian forests over the area, while the pollen record of Cyperaceae and *Sparganium* points to a dense wetland vegetation bordering those freshwater environments.

Three wood samples from El Asperillo have been identified as *Myrica gale*. This plant has been commonly identified in the Quaternary fossil record both from its pollen (e.g., Carrión and Van Geel, 1999; Gómez-Orellana et al., 2007) and from its seeds and leaves

(e.g., Birks, 1972), primarily in northern regions with maritime climate. The Quaternary record of *Myrica* in Iberia is restricted to maritime areas (Queiroz, 1989; Queiroz and Mateus, 1994; Ramil-Rego et al., 1998; Muñoz Sobrino et al., 2005; Gómez-Orellana et al., 2007); *Myrica*-type pollen has also been identified in Lagoa Travessa (Mateus, 1989), Lagoa de Melides (Queiroz and Mateus, 1994) and Lagoa Santo André (Santos and Sánchez Goñi, 2003) in southern Portugal and in Navarrés, Valencia (Carrión and Van Geel, 1999) (Fig. 1A). Thus, data presented in this paper represent the first record of *Myrica gale* based on its fossil wood on the Iberian Peninsula. The current European distribution of *Myrica gale* is concentrated mainly near the Atlantic coastline (Jalas and Suominen, 1976). In particular, its Iberian range features areas close to the Cantabrian and Atlantic coastlines, north of the Tagus estuary, together with several small and isolated populations in the Iberian Range and the Toledo Mountains (Jalas and Suominen, 1976; ANTHOS, 2006; Fig. 1A). Therefore, El Asperillo represents the southernmost Quaternary record in Europe for this species, indicating that its distribution during cold periods reached the southernmost extremity of the continent.

It is notable that Mediterranean floristic elements are rare in the El Asperillo fossil record, in marked contrast with other late Pleistocene sites from southern Iberia such as Gorham's Cave, where the paleobotanical record spans MIS 3 and 2 (Carrión et al., 2008). The presence of several Eurosiberian and mesohygrophilous trees such as *Corylus*, *Betula*, deciduous *Quercus*, and *Castanea* (although these taxa do not reach high percentages in the pollen record) suggests that this area could have been a 'classical refugium' (as described by Bennett and Provan, 2008) for temperate trees. Previous geomorphological research has documented the existence of braided paleochannels and interdune depressions developed on a coastal plain during U2 sedimentation over the studied area (Zazo et al., 2005). These topographical features, together with the maritime climate, may have generated areas with wetter soils where these relatively hygrophilous trees could cope with the regionally dry climatic conditions of a stade. In a similar way, the existence of glacial refugia for temperate trees during the LGM in the mid-Ebro Valley lowlands, northeastern Spain, was linked to the presence of lake depressions and paleochannels (González-Sampériz et al., 2005). This complements the classical concept of refuge areas, which suggests that the mountainous areas of southern Europe were the most suitable sites to provide refuge to temperate trees during the Quaternary cold stages (Bennett et al., 1991).

The finding of *Castanea* pollen is especially remarkable since the autochthony of this taxon in Iberia was controversial until recent times, when it was clearly confirmed (e.g., Sánchez Goñi, 1988; García Antón et al., 1990; Krebs et al., 2004). However, the role of southern Iberia as a glacial refugium for this species had not been considered (Krebs et al., 2004). Taken together, data from El Asperillo, Padul (Pons and Reille, 1988) and Gorham's Cave (Carrión et al., 2008) support the persistence of *Castanea* in southern Iberia throughout the late Pleistocene, probably as an element of relict mixed deciduous forest stands located on wet soil sites, gorges or valley bottoms (as suggested in Postigo-Mijarra et al., 2008).

Paleoclimatic considerations from the fossil assemblage

The low presence of tree pollen, the near absence of thermophilous and Mediterranean plants, and the dominance of *Artemisia*, Chenopodiaceae, *Ephedra*, and Poaceae in the pollen spectra reflect steppe–grassland vegetation, suggesting the cold, dry conditions characteristic of a stadial period (Fig. 3). However, the persistence of several Eurosiberian taxa in this area and the importance of heathlands in the landscape suggest that the relative vicinity of the Atlantic Ocean could attenuate dryness.

These considerations are consistent with the advance of the polar front to southern latitudes, even reaching southern Iberia as

evidenced by the multi-proxy study of the MD95-2042 deep-sea core (Sánchez Goñi et al., 1999). This situation was associated with several ice-rafting events identified on the northwestern Iberian coasts (Sánchez Goñi et al., 2005, 2008). As a consequence of these phenomena, aridification and cooling processes (Sánchez Goñi et al., 2005) took place in southwestern Iberia. These cold and dry conditions were widespread all over Europe (e.g., Müller et al., 2003; Brauer et al., 2007; Fletcher et al., 2009), and drops of up to 12°C in the mean temperature of the coldest month have been estimated (Allen et al., 1999).

The stades at the beginning of the last glacial cycle in Iberia

MIS 5 and MIS 4 stades are not well-represented periods in the Iberian fossil record (Fig. 1A). There are only two continental pollen sequences covering these stages in southern Iberia: Padul and Carihuela Cave (Granada province, SE Spain). The Carihuela Cave area (Carrión, 1992; Carrión et al., 1998; Fernández et al., 2007) appears to have been covered with an open and steppe-like vegetation during these cold stages, consisting mainly of *Artemisia*, Poaceae, and Chenopodiaceae with sparse or/and open *Pinus* stands also present. The Padul peat bog (Pons and Reille, 1988) also shows high percentages of steppic pollen taxa, but it is remarkable that both evergreen and deciduous *Quercus* were important in the landscape. Mediterranean taxa (e.g., Oleaceae, *Pistacia*, Cistaceae, *Buxus*) are more diverse and appear in higher percentages in Carihuela and Padul sequences than at El Asperillo. This is a notable floristic difference between western and eastern sites on the Iberian Peninsula (previously reported by Fletcher et al., 2009). The vegetation covering Tajo basin (central Iberia) was dominated by steppic communities (*Artemisia*, Chenopodiaceae, *Ephedra*), but pinewoods and heathlands were also abundant, as revealed by the Atlantic deep-sea core MD95-2042 (Sánchez Goñi et al., 1999). Mediterranean taxa nearly disappeared, while the persistence of Eurosiberian trees in the pollen record suggests the presence of certain suitable areas where mixed deciduous stands survived (Sánchez Goñi et al., 1999).

In the Area Longa site in NW Iberia (Gómez-Orellana et al., 2007), heathlands and mesophytic grasslands were the main types of vegetation, and mesophilous trees were present as well. The pollen signal from the Duero and Galician basins (NW Iberia) has been recorded by the marine core MD99-2331 (Sánchez Goñi et al., 2005). Based on these data, it can be suggested that the regional vegetation was quite similar to that of Area Longa (Poaceae and Ericaceae-dominated and a modest presence of temperate trees), but there was also a significant presence of steppic elements. The landscapes must have been similar in some northeastern Iberian areas, as revealed by the Pla de l'Estany pollen record (Burjachs, 1990). Nevertheless, vegetational reconstruction on the basis of Abric Romaní (NE Iberia) pollen data shows a pine-dominated landscape where thermophilous and steppic taxa were important and Ericaceae were almost absent (Burjachs and Julià, 1994), in marked contrast to Atlantic area sites where acidic soils and a wetter climate were present. The only paleobotanical record from inland Iberia recording this period is the Los Torrejones site (Carrion et al., 2007), where the landscape was composed mainly of steppe–grasslands with sparse pine stands. *Juniperus*, *Quercus*, and small populations of broad-leaved trees were certainly present in the surroundings of the Los Torrejones Cave.

In summary, the vegetation reconstructed from the El Asperillo fossil record is similar to that inferred from the Atlantic cores MD95-2042 and MD99-2331. The abundance of Ericaceae and the near-absence of Mediterranean taxa in these records may indicate the prevalence of maritime climatic conditions. This is in marked contrast to the importance of evergreen *Quercus* to the landscapes surrounding the Carihuela Cave and Padul sites. The El Asperillo record, together with all the previous sequences from Atlantic Iberian areas, reinforces the refugial character of these areas for Eurosiberian and Atlantic taxa

during cold stages, as was previously described by Roucoux et al. (2001). However, the fossil record suggests some important differences, including higher taxonomic diversity of arboreal taxa (e.g., *Carpinus*, *Ilex*) in NW Iberia, and greater abundance of heathlands in NW Iberia than in the Gulf of Cádiz area, where steppic taxa were more dominant (Fletcher et al., 2009). Nevertheless, the discontinuous and scarce Pleistocene record from SW Iberia compared with that from the NW of the Iberian Peninsula makes this comparison provisional and highlights the need of further research on this period over the southern extreme of Iberia.

Conclusions

During one of the initial stades of the last glacial cycle, the vegetation covering the Doñana Natural Park area was mainly composed of steppe–grassland communities. Trees would have been present in the area both as isolated individuals and as scattered stands (mainly pine-dominated ones). The presence of certain temperate trees such as deciduous *Quercus*, *Castanea*, and *Corylus* as well as the importance of heathlands on the landscape are notable. El Asperillo represents the southernmost European site recording the presence of *Myrica gale* (fossil or recent). Its fossil record also suggests the persistence of *Castanea* in southern Iberia during Pleistocene cold stages. The pollen and plant–macrofossil records suggest that the climate in the Gulf of Cádiz area was cold and dry, in spite of its location at the southernmost extreme of the European continent. Nevertheless, some hygrophilous plants (e.g., Ericaceae, *Myrica gale*) persisted over this area, suggesting that the presence of paleochannels and freshwater environments provided habitats where dry conditions were attenuated.

Acknowledgments

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