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New palynological data from the Late Pleistocene glacial refugium of South-West Iberia: The case of Doñana

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ABSTRACT

The Doñana area in southern Iberia is one of the most renowned protected areas of Europe, mostly due to the diversity and value of its wetland ecosystems. The large biogeographical significance of this territory and the outstanding availability of sedimentary archives have made this region a hotspot of paleobotanical research in the Iberian Peninsula. Specifically, the organic deposits on El Asperillo Cliff have been studied during the past few decades from the geomorphological and paleobotanical (pollen, macrofossils) points of view. However, large uncertainties remain concerning the chronology of certain sections of the exposed profile and the paleobotanical potential of this site has not been fully exploited yet. In this study, we revisited El Asperillo with the aims of completing the paleobotanical record and refining the chronology of this site. The age of the studied deposits ranges from ca. 22,000 to 30,900 cal. yr BP according to the radiocarbon dates obtained, thus embracing the particularly cold and dry Heinrich Event 2 and the Last Glacial Maximum. Our palynological results allow inferring the presence of a coastal marshland system. Additionally, the new pollen records highlight the relevance and diversity of pines (*Pinus nigra*-sylvestris type, *P. pinaster*, *P. halepensis*-pinea type) in the Late Pleistocene landscape of Doñana, reinforcing the native status of pines. Last but not least, the results stress the persistence of a highly diverse woody flora in Doñana during the harshest periods of the last glacial cycle, highlighting the importance of this enclave in postglacial vegetation recolonization of the Iberian Peninsula.

1. Introduction

The Doñana Protected Area (DPA), which includes the Doñana Natural and National Parks, is an extremely interesting enclave for paleopalynological studies due to its geographical location at the south-western edge of the European continent very close to Africa and its great physiographic complexity. Doñana itself hosts a notably heterogeneous landscapes with numerous plant communities, a highly diverse flora rich in endemics, and a complex network of ecological interactions, that justify its large international ecological and biogeographical interest. In fact, DPA is one of the most emblematic protected areas of Europe (Sousa et al., 2009). It was declared a UNESCO Biosphere Reserve in 1980, Wetland of International Importance (RAMSAR Agreement) in 1982, Special Protection Area for Birds (ZEPA) in 2003, and a Site of Community Importance in 2006. In 2015, it joined the IUCN Green List

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of Protected and Conserved Areas. The geomorphology of the peridunal ponds is particularly noteworthy, gathering one of the highest concentrations of potential paleoenvironmental archives of the Eurasian continent in the form of ponds and marsh systems. These ponds have been seriously affected by anthropogenic activities in the past few decades (Stevenson and Harrison, 1992; Díaz-Paniagua, 2015; Díaz-Paniagua and Aragonés, 2015; López-Sáez et al., 2018; Manzano et al., 2018), making urgent to recover such sedimentary archives and investigate long-term environmental change or at least establish a repository of material useful for future conservation biology studies. In this scientific framework, we have selected for this study the El Asperillo Cliffs, located in the Doñana Natural Park, mainly because of the Pleistocene age of several strata (Salvany and Custodio, 1995; Salvany et al., 2011) and the palynological potential the peat rich sediments (Carrión and Dupré, 1996; Carrión et al., 2001; Abel-Schaad and López-Sáez, 2013; Camuera et al., 2019; López-Sáez et al., 2020a). Our main goal is to shed light on the late Pleistocene vegetation dynamics in the area.

To delimitate the geological context and refine the paleoecology of the site, some antecedents are worth mentioning:

(a) studies on the Miocene of the Guadalquivir Basin (Valle and Peñalba, 1987; Valle and Rivas Carballo, 1990), Gibraleón (Peñalba, 1985; Barrón et al., 2010) and Survey "Huelva" (Rivas-Carballo and Valle, 2005; Valle and Peñalba, 1987);

(b) for the Pliocene, La Matilla (Jiménez-Moreno et al., 2019), Lepe (Muñiz et al., 1999; Barrón et al., 2003) and Casa del Pino (Peñalba, 1985; Barrón et al., 2010);

(c) for the Quaternary, palynological studies of the Upper Pleistocene of Vanguard and Gorham's Cave at Gibraltar (Finlayson and Carrión, 2007; Carrión et al., 2008, 2018), close to Doñana and

(d) for the Holocene, the Algarve, in Portugal (Fletcher et al., 2007; Schneider et al., 2010; Connor et al., 2019), Pocito Chico lagoon (López-Sáez et al., 2002, 2018), Dehesilla cave (García-Rivero et al., 2018, 2019), Laguna de Medina (Schröder et al., 2018, 2020), Las Madres, El Acebrón and other pollen records in the DPA (Stevenson, 1985; Stevenson and Harrison, 1992; Stevenson and Moore, 1988; Yll et al., 2003; Yáñez et al., 2007; Jiménez-Moreno et al., 2015; López-Sáez et al., 2018; Manzano et al., 2018, 2019).

The first paleobotanical studies at El Asperillo date back to Caratini and Viguier (1973), and Stevenson (1984), which supposed Holocene and Late Glacial ages respectively. In his detailed palynological survey, Stevenson (1984) showed the continuous presence of grassland formations with abundance of pines (a landscape probably similar to a wooded savannah) and minor occurrences of *Quercus, Betula, Alnus*, *Corylus*, *Salix*, *Phillyrea*, *Ephedra*, *Corema album*, and *Juniperus*. Heliophilous shrubs would have been dominated by *Artemisia, Erica lusitanica, Erica umbellata*, Chenopodiaceae and a variety of Asteraceae, among others. The high pollen frequencies of Cyperaceae and the occurrence of *Sparganium, Myriophyllum* and *Potamogeton* point to a marsh sedimentary context. Grasses and pines could be over-represented in the pollen spectra due to their potential abundance in the basin and marginal vegetation (Suc and Cravatte, 1982; Franco Múgica et al., 1998; López-Sáez et al., 2008; García-Antón et al., 2011; Morales-Molino et al., 2012). Later paleoecological studies by Zazo et al. (2005), Postigo-Mijarra et al. (2010a) and Morales-Molino et al. (2011) investigated sediments from the cliff and the intertidal area, dating back to the interval between the Marine Isotopic Stages (MIS) 4 and 2 according to the authors. These studies also included macroremains and emphasized the occurrence of pines around a local wetland environment. Due to age discrepancies between the different studies, a more detailed chronological study on the Pleistocene beds was considered pertinent.

Further encouragement to carry out a new palynological study in the Asperillo deposit comes from the scarcity of continental Pleistocene pollen records for the southwestern region of the Iberian Peninsula (see Carrión et al., 2013, for compilation).

2. The site

The El Asperillo Cliff extends along ca. 22.5 km of the coast of the Gulf of Cádiz (Atlantic Ocean) between the towns of Mazagón and Matalascañas (municipalities of Palos de la Frontera, Moguer and Almonte) in the SW Iberia (province of Huelva, Spain) (Fig. 1). Erosion has carved the cliff in the fossil dune system of the El Abalario Dome, exposing a complete section of the largest Upper Pleistocene–Holocene eolian sedimentary deposit in the Iberian Peninsula (Zazo et al., 1999, 2005). Within the Doñana Natural Park, El Asperillo Cliff landscape has been declared Natural Monument (BOJA, 2002).

The sampling areas are located at various points on the El Asperillo Cliff, between Torre del Oro and Torre de la Higuera from sandy-peaty layers rich in organic. The pollen record from Asperillo zone I (AspI) located between the coordinates 37° 04′ 55″N and 06° 42′ 41″W (Fig. 1), is represented by four points (sites A to D) corresponding to different peaty layers between 20 and 2 m a.s.l. (Fig. 2). The pollen record from Asperillo zone II (AspII) corresponds to a fragment of peaty compacted sands located 18 m a.s.l. (37° 02′ 34.18″N/ 06° 38′ 04.16″W) and 8 km east of AspI (Figs. 1 and 3).

2.1. Geomorphology and sedimentology

The El Abalario area has a smooth elongated dome morphology in a NW-SE direction (Rodríguez-Vidal et al., 2014). It is mainly constituted by eolian sediments that accumulate in different phases and moments throughout the Quaternary and it constitutes the headland of the Doñana spit bar system. The most recent wind systems in the area are arranged overlapping, like imbricated dunes, up to heights of over 100 m. This whole set is cut by the El Asperillo Cliff, which reaches between 10 and 15 m high. The Cliff has developed throughout the Holocene due to erosion caused by the rise in the sea level, leaving the entire sedimentary complex visible.

The sedimentological studies of the Asperillo fossil dunes by Zazo et al. (1999, 2005) established 7 eolian units spanning that cover the last 125,000 years (Fig. 4). These units reflect the complex evolution experienced throughout that time, which are the result of the interaction between coastal dynamics, with associated wind processes, and changes in sea level (Zazo et al., 2005; Rodríguez-Vidal et al., 2014). Tectonics has also played an important role in the distribution of these units, since the Torre del Loro gravitational fault (TLF) configures two blocks in which different formations emerge in their lower sections (Fig. 4).

In the NW upthrown block the oldest units outcrop at the base, with a paleosol developed on a Plio-Pleistocene deltaic platform related to the Guadalquivir paleo-mouth (Salvany and Custodio, 1995; Zazo et al., 1999). This paleosol is the result of a hiatus in sedimentation probably prior to the Last Interglacial (MIS 7 or MIS 5) (Zazo et al., 2005). As the interglacial MIS 5 advances, and therefore the increase in temperatures, the sea level rises to cover the complete delta and other subsequent fluvial deposits with marine sediments, reaching a maximum sea level about ca. 125,000 years (Polyak et al., 2018). The sedimentary sequence continues with the deposit of the wind unit U0 formed on the marine deposits emerged after the withdrawal of the sea, at the end of MIS 5. Between MIS 5-4 the Torre del Loro fault (TLF) was formed, preserving the previous formations in the upthrown block (Fig. 1).

Eolian units U1 to U3 were developed only in the SE downthrown block against the faut scarp. U1 wind deposits that occur by the interstate, deposited in temperate-humid conditions during MIS 3, U2 during the Last Glacial Maximum (LGM) in colder and humid conditions, and finally U3 developed in the lateglacial MIS 1 in increasingly arid conditions (Fig. 4, Table 1). An extensive erosional surface rich in iron oxides represent the limit between fossil and an active Mid-Late Holocene eolian units (U4–U7). This level has been called "Super-surface of Fe-oxides" (SsFe, Fig. 4) by previous studies with an age stimated at ~5 kyr (Zazo et al., 2011). The rapid rising sea level during the Holocene

Fig. 1. Location of the Asperillo sites ASPI and ASPII within Doñana in the Iberian Southwest, and paleoenvironmental records mentioned in the text: 1. El Asperillo, 2. Gibraleón, 3. Lepe, 4. Casa del Pino, 5. Lucio de la Cancela de la Aulaga, 6. Laguna del Sopetón, 7. La Matilla, 8. Gorham's Cave, 9. Vanguard Cave, 10. Beliche (Algarve), 11. Carcavai (Algarve), 12. Quarteira (Algarve), 13. Pocito Chico, 14. Dehesilla cave, 15. Laguna de Medina, 16. Las Madres, 17. Acebrón, 18. Core G1, 19. MD01-2443, 20. MD95-2042, 21. 8057-B, 22. SU81-18, 23. SU81-13, 24. Padul, 25. Carihuela, 26. Cueva de Nerja, 27. Cueva de los Murciélagos, 28. Puerto de Santa María, 29. Bajondillo cave, 30 Cueva del Humo, 31. S1, 32. Gádor, 33. Lucio of Mari López, 34. ODP site 976, 35. U1385, 36. D13882.

has caused the erosion of the coast, giving rise to the powerful El Asperillo Cliff with the outcrop of the different wind units studied (Zazo et al., 1999, 2005; Sancho Royo et al., 2018).

2.2. Present-day climate and vegetation

The area of the El Asperillo Cliffs show a Mediterranean climate of Atlantic influence: an average annual temperature of 16–17 °C with contrasting values between the summer and winter seasons, and an average annual precipitation of 500–600 mm. Two rainfall maxima occur, in autumn and spring, respectively (Yáñez et al., 2007; Morales-Molino et al., 2011). Soils are predominantly sandy, with very little water holding capacity, which generates locally extreme edaphoclimatic conditions and make groundwater discharge to play a crucial role in defining the composition and structure of plant communities (Sancho Royo et al., 2018).

Although the presence of human activity in the El Abalario territory has been well documented for a long time, its most relevant impact corresponds to the extensive stone pine (*Pinus pinea*) and eucalyptus (*Eucalyptus globulus*, *E. rostrata*) afforestations. However, this activity is mainly recorded from 1940 to 1970, and since Doñana became a Natural Park in 1989, environmental restoration measures have led to the partial replacement of eucalypts by stone pines and cork oaks (García Murillo and Sousa, 1997, 1999; García Murillo, 2001), which cover the inner area of El Abalario. In 2017, a large wildfire swept away the vegetation cover of this place (García Murillo, 2018). At present it shows a good state of recovery, due to the resilience of native species and the restoration tasks carried out by the managers of the protected area.

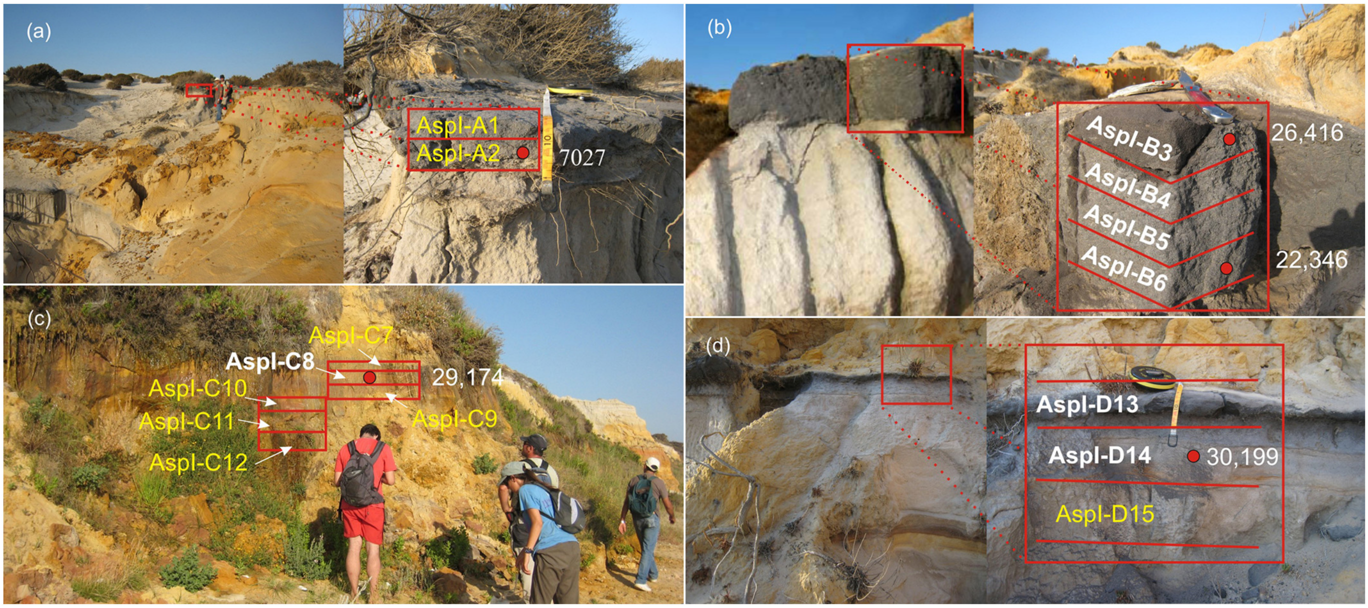

Fig. 2. AspI showing radiocarbon dating and position of pollen samples at Site A (a), Site B (b), Site C (c) and Site D (d). Sterile samples in yellow. Photos by Manuel Munuera.

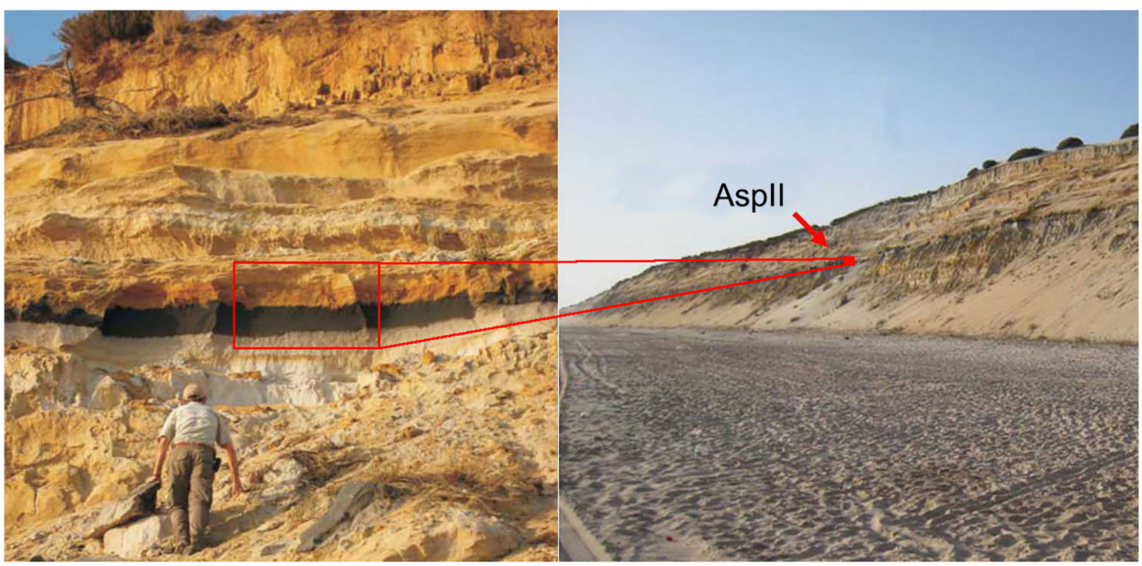

Fig. 3. Pollen sampling in AspII, El Asperillo Cliff.

Overall, the Doñana vegetation is largely determined by the water table and dune dynamics (Finlayson, 2006), revealing a great diversity of plant communities between the El Asperillo Cliffs and the Arroyo de la Rocina.

The sandy cliff of the El Asperillo is subjected to continuously pounding waves and therefore erosive processes that prevent stable vegetation to establish on the beach. However, in the beach areas below the cliff, we find the pioneering vegetation represented by *Cakile maritima* and *Salsola kali.* A little further inland it is possible to observe incipient dunes, which are colonized in the highest places by *Ammophila arenaria* subsp. *arundinacea*, *Achillea maritime* (= *Otanthus maritimus*) and *Elymus farctus* subsp. *boreali-atlanticus*, and in the lower parts by *Artemisia campestris* subsp. *maritima* (= *A. crithmifolia*), *Crucianella maritima*, *Pancratium maritimum*, *Eryngium maritimum*. Areas of groundwater discharge in the cliff are easily noticeable because they host a very characteristic vegetation dominated by *Phragmites australis, Plantago macrorrhiza, Dittrichia viscosa* and *Polygonum maritimun*, among others, which are also adapted to continuous sandy collapses (López Albacete, 2009). At the top of the cliff, exposed to the sea winds are more or less incipient dunes, which contain: *Ammophyla arenaria* subsp. *arundinacea*, *Helichrysum serotinum* subsp. *pichardii* and *Corinephorus canescens.* These mobile sands are also home to *Juniperus oxycedrus* subsp. *macrocarpa*, which grows accompanied by *Corema album*, *Halimium calycinum*, *Cytisus grandiflorus* subsp. *cabezudodoi* and mixed with *Pinus pinea* that come from the reforestations of the first half of the 20th century.

Juniperus phoenicea subsp. *turbinata* dominates the vegetation on table dunes protected from ocean winds and with higher edaphic humidity. On drier soils with very low organic matter grows a scrub community known as "Monte Blanco" (e.g. *Halimium halimifolium*, *Stauracanthus genistoides*, *Cistus salvifolius*, *Genista ancystrocarpa*, *Lavandula stoechas*, *Rosmarinus officinalis*, *Thymus mastichina*, etc.).

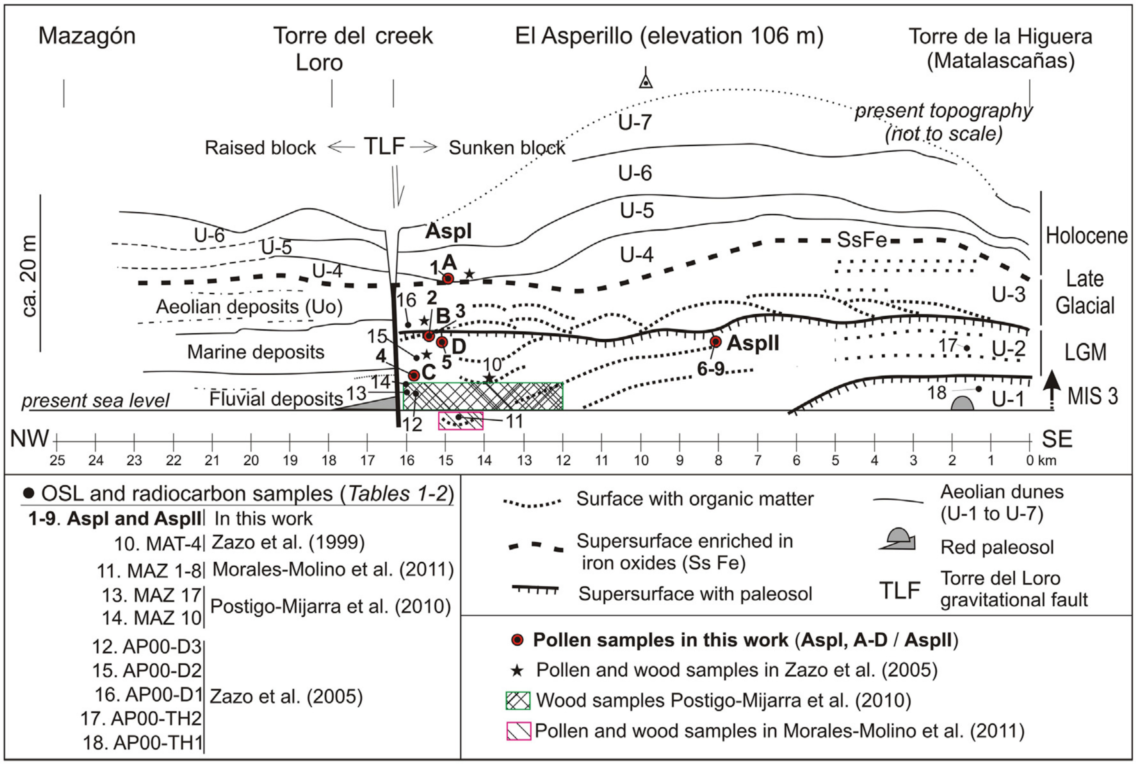

Fig. 4. Location of pollen, macrofossil, and radiocarbon samples within the lithostratigraphy of El Asperillo Cliff according to former studies by Zazo et al. (2005), Morales-Molino et al. (2011), and Postigo-Mijarra et al. (2010a).

On wetter soils with higher amount of organic matter, a heatland of Atlantic influence locally-called "Monte Negro", characterized by *Erica scoparia*, *Ulex australis, Cistus salvifolius* and *Calluna vulgaris*, gets dominant. The spatial distribution of "Monte Blanco" and "Monte Negro" shrublands in Doñana defines a very characteristic mosaic-like landscape according to soil properties. As mentioned above, *Pinus pinea* stands coming from reforestations carried out in the first half of the 20th century are still a major feature of the Doñana vegetation. The El Abalario area consists of numerous temporary ponds that host a typical hydrophilic vegetation dominated by Juncaceae and Cyperaceae (*Juncus efussus, Juncus maritimus, Juncus heterophyllus*, *Schoenoplectus corymbosus*, *Scirpoides holoschoenus*, *Eleocharis palustris*) with some other hydrophytes such as *Ranunculus peltatus*, *Myriophyllum alterniflorum*, *Isöetes velata, Callitriche brutia*, and several species of *Chara* and *Nitella*. Along streams, the riparian vegetation consists of willow trees (*Salix atrocinerea*) and brambles (*Rubus ulmifolius*, *Rosa canina*), intimately connected to sclerophyllous cork oak (*Quercus suber*) stands with wild olive trees (*Olea europaea*), strawberry trees (*Arbutus unedo*) and other shrubs (*Phillyrea angustifolia, Myrtus communis*), as well as a remarkable abundance and diversity of lianas (*Smilax aspera, Lonicera implexa, Tamus communis* (García Murillo, 2001, 2007; Sancho Royo et al., 2018). Peatlands are rare, but there are still some, such as the Ribatehilos peatbog (García Murillo, 2005, 2007). The local vegetation there is dominated by ciliated heather (*Erica ciliaris*), gorses (*Ulex minor, Genista ancistrocarpa*) and purple moor-grass (*Molinia caerulea* subsp. *arundinacea*), and in some spots it is possible to find peat mosses (*Sphagnum inundatum*).

Table 1
OSL and radiocarbon dates of El Asperillo obtained from samples of Zazo et al. (1999, 2005), Postigo-Mijarra et al. (2010a) and Morales-Molino et al. (2011).

No (Fig. 2)	Sample	Lab no	Material	^{14}C yr BP	OSL (kyr)
10	MAT-4[a]	UtC-3938	Wood	>45,000	–
11	MAZ 1-8[d]	CNA-122	Wood	47,500 ± 2500*	–
12	AP00-D3[b]	–	OM	–	48 ± 5
13	MAZ 17[c]	Beta-116168	Wood	>46,410	
14	MAZ 10[c]	Beta-116167	Wood	>42,000	
15	AP00-D2[b]	–	OM	–	32 ± 5
16	AP00-D1[b]	–	OM	–	16 ± 3
17	AP00-TH2[b]	–	OM	–	74 ± 8
18	AP00-TH1[b]	–	OM	–	106 ± 19

OM = organic sediment.
[a] Zazo et al. (1999).
[b] Zazo et al. (2005).
[c] Postigo-Mijarra et al. (2010a).
[d] Morales-Molino et al. (2011).
* Age considered unreliable (Morales-Molino et al., 2011).

3. Palynological methods

We have studied 28 sediment samples for pollen analysis. The pollen record AspI is represented by 15 samples distributed in four points between the U2 and U4 stratigraphic levels by Zazo et al. (1999, 2005) (Figs. 2 and 4) dated at c. 30,943, 27,987; 22,048; and 26,779 cal years BP (Table 2). Two samples come from Site A (AspI-A1 to AspI-A2), a peat layer, located approximately 20 m a.s.l., corresponding to the Holocene (AspI-A2 ca. 7100 cal BP; Table 2). We took four samples from Site B (AspI-B3 to AspI-B6), taken at 12 m a.s.l. on a 23 cm-thick Pleistocene sandy layer rich in organic matter (ca. 22,000–26,800 cal BP; Table 2). The six samples from Site C (AspI-C7 to AspI-C12) come from a level rich in iron oxides at 4 m a.s.l., consisting of clayey sandstones with a thickness of approximately 100 cm of Pleistocene age (ca. 28,000 cal BP; Table 2). Finally we collected three samples from Site D (AspI-D13 to AspI-D15), from a 15 cm thick sandy-peaty layer located at 10 m a.s.l. (ca. 30,900 cal BP; Table 2). The pollen record AspII is represented by 13 samples studied (AspII-1 to AspII-13), taken at 2 cm intervals

Table 2
Radiocarbon dating results of sediment samples from El Asperillo cliff. Radiocarbon ages were calibrated based on the IntCal20 calibration curve and CALIB 8.2, standard error 2 σ (95,4% confidence) (Stuiver et al., 2020).

No (Fig. 4)	Sample	Lab no	Material	^{14}C age ± error (^{14}C yr BP)	2 σ calibrated age range (cal yr BP)	Median age (cal yr BP)
1	AspI-A2	Poz-52101	OM	6135 ± 35	6906–6915	7027
2	AspI-B3	Poz-52097	OM	22,170 ± 170	25,990-26,934	26,416
3	AspI-B6	Poz-52098	OM	18,420 ± 90	22,161–22,494	22,346
4	AspI-C8	Poz-52102	OM	24,960 ± 150	28,811–29,701	29,174
5	AspI-D14	Poz-52099	OM	25,960 ± 150	29,962–30,728	30,199
6	AspII-13	Poz-52103	OM	19,250 ± 90	22,961–23,703	23,163
7	AspII-8	Poz-52106	OM	20,590 ± 110	24,368–25,132	24,805
8	AspII-5	Poz-52105	OM	20,350 ± 100	24,160–24,794	24,447
9	AspII-2	Poz-52104	OM	21,220 ± 110	25,259–25,803	25,560

OM = organic sediment.

(Figs. 3, 8), dating to the Pleistocene (four radiocarbon dates from ca. 23,000 to 25,400 cal BP; Table 2).

Laboratory treatment followed conventional procedures (Delcourt et al., 1959; Dimbleby, 1985), with the modifications proposed by Girard and Renault-Miskovsky (1969) for the concentration of pollen grains by means of the flotation method with heavy liquids. We added tablets of *Lycopodium clavatum* spores to each sample to evaluate the quality of the laboratory processing and to calculate pollen concentrations (Stockmar, 1971). The samples were mounted on slides with the use of glycerogelatin and liquid paraffin. We identified pollen and other palynomorphs using an optical microscope at 40× and 100× magnifications. We assigned damaged pollen grains whose identification was not feasible to the category "indeterminable". We plotted pollen diagrams using Psimpoll paleoecological analysis program version 4.27 (Bennett, 2008). Eight out of the 15 samples studied in AspI, were non polleniferous, mostly because palynomorphs were at too low concentrations or totally absent (AspI-A1, AspI-A2, AspI-C7, AspI-C9, AspI-C10, AspI-C11, AspI-C12, AspI-D15) (Fig. 2). In the pollen diagram, we have not represented this palynologically sterile samples (Fig. 9). In contrast all the samples from AspII were polleniferous (Fig. 10). Along with spores and non-pollen palynomorphs, we excluded the pollen grains of Asteroideae, Cichorioideae, *Centaurea* and Cyperaceae from the total pollen sum assuming these groups are overrepresented in the pollen spectra.

4. Results

4.1. Pollen stratigraphy El Aperillo zone I (AspI)

Samples from Site A were palynologically sterile (Fig. 2). Pollen spectra from site B (AspI-B3, AspI-B4, AspI-B5 and AspI-B6: Figs. 2, 9) were dominated by arboreal pollen (AP), which reaches percentages close to 70%. The abundance of *Pinus halepensis-pinea* is noteworthy (35–41%); Ericaceae abundance ranges between 6 and 12%; *Alnus* always >4% and it is also worth noting the amount of deciduous *Quercus* and the presence, although limited, of *Juniperus*, *Corylus* and *Ulmus*. Accompanying AP are evergreen *Quercus*, *Quercus suber*, *Olea*, *Taxus*, *Phillyrea*, *Erica australis* and *Ephedra fragilis*. In non-arboreal elements NAP, Cistaceae, Asteroideae, Poaceae and Cyperaceae are noteworthy. Fabaceae, Apiaceae and *Typha* exceed 2%. Cichorioideae, *Potamogeton* and *Myriophyllum* are below 2%. It is worth highlighting the abundance of fungal spores, with percentages between 19 and 51% (Fig. 11). The presence of Zygnemataceae spores (15–26%) is significant. Trilete spores attain frequencies of ~11%, while Monolete spores >3%. Similarly, *Pseudoschizaea*, *Debarya* and *Botryococcus* are present.

Site C is represented by the sample AspI-C8. The arboreal pollen reaches values close to 50%. *Pinus halepensis-pinea* type is about 28%, Cupressaceae about 8%. Ericaceae exceeds 7% and *Artemisia* is higher than 11%. Accompanying AP include deciduous *Quercus*, *Alnus*, *Olea*, *Phillyrea*, and *Calluna*. Poaceae (5%), *Myriophyllum* (>10%), and Cistaceae, Cichorioideae and Fabaceae with percentages ~2% are also features of this sample. Asteroideae, Caryophyllaceae, *Plantago*, Cerealia and *Potamogeton* are also represented in this pollen spectrum. Fungal spores are less abundant than in the former samples (Fig. 11). Triletes (2%), Monoletes (1%), *Spyrogira* (12%) and other Zygnemataceae (11%), together with *Pseudoschizaea*, *Mougeotia* and *Debarya*, are also present.

Site D includes samples AspI-D13, AspI-D14 and AspI-D15, with the last being sterile (Fig. 2). AP dominates the assemblage, surpassing 60%. The most noteworthy feature of this site is the abundance of *Pinus*, with percentages around 16–37%. We found high percentages of Cupressaceae (8–14%) and Ericaceae (4–14%). *Alnus* shows an increase of more than 6%. *Taxus*, evergreen *Quercus*, *Olea*, Chenopodiaceae and *Ephedra fragilis* are well represented. With respect to NAP, it is worth mentioning the presence of Cistaceae, Asteroideae, Poaceae, *Lemna* and *Myriophyllum* (Fig. 9). Non-pollen microfossils are represented by a large number of fungal palynomorphs, reaching out-of-total frequencies close to 50% (Fig. 11). Monolete spores reach a percentage maximum of 33% while Trilete spores values range from 10 to 15%. Zygnemataceae (21–42%) and *Debarya* (24%) are relatively high.

4.2. Pollen stratigraphy El Asperillo zone II (AspII)

This site includes 13 pollen spectra (Fig. 10) with predominant AP, reaching values >84%, except in sample 9, in which the lowest percentage of AP (37%) in the sequence is reached. *Pinus halepensis-pinea* type is highly fluctuating from values close to 34% until falling in samples 3 and 9 to <9%. *Pinus pinaster* type oscillates between 1 and 18%, while *Pinus nigra-sylvestris* type varies between 4 and 24%. *Juniperus* attains percentages between 4 and 14%. *Quercus* evergreen is 2–8%, *Quercus* deciduous reaches 4% and *Quercus* indeterminate exceeds 5%. Remarkably, *Abies* ~ 7% (AspII-9). The occurrence of *Taxus*, *Alnus*, *Betula*, *Corylus*, *Olea*, *Populus*, *Salix*, *Ephedra distachya*, *Erica* and *Cistus* is significant, as well as the limited presence of *Quercus suber*, *Ulmus*, *Castanea*, *Juglans*, *Myrtus*, Genisteae, Fabaceae, *Ilex*, *Ephedra fragilis*, *Arbutus*, *Daphne* and *Sambucus*. Among NAP Poaceae (7–58%) and Cyperaceae (1–9%) are remarkable (Fig. 10). *Artemisia*, Asteroideae and Cichorioideae (out of the pollen sum), *Chenopodium*, Amaranthaceae, *Plantago coronopus*, *Plantago lanceolata*, Liliaceae and *Typha* are also frequent. Fungal spores, pteridophytes and algae abound (Fig. 11). Monolete spores reach a maximum percentage of 38%, while Trilete spores peak up to 63%. In a similar way, the presence of *Monoporisporites*, Hyphae, *Exesisporites*, *Scleroderma*, Zygnemataceae and *Inapertisporites* is significant.

5. Discussion

5.1. Wetland environments

One of the main characteristics of the current DPA landscape is its diversity of aquatic environments, like temporary ponds, peatlands, the extensive Guadalquivir marshes, or the network of streams (e.g. the Rocina stream) and side channels of the River Guadalquivir that provide freshwater to the Doñana marshes (Finlayson, 2006) (Fig. 1). The aquatic elements present in the paleobotanical records of the DPA permit local paleolimnological inferences, which help with in the general paleoecological interpretation.

There is evidence of wetlands in this region since the Miocene. The Messinian sequence of Gibraleón (about 50-km distant) recorded the presence of aquatic taxa such as Cyperaceae, *Epilobium*, *Potamogeton*, *Sparganium* and *Typha* (Peñalba, 1985). The Lower Pliocene plant macro-remains sequence of Lepe shows diverse aquatic and phreatophytic communities indicative of the occurrence of different types of wetlands: (i) swampy areas with monocots, *Liquidambar europaea* and Taxodiaceae; (ii) riverbanks with *Salix*, *Populus* and *Platanus*; and (iii) areas with a high water table occupied by Lauraceae and Ulmaceae (Barrón et al., 2003). From these data, the authors inferred a subtropical riparian climate for the Pliocene of Andalucía. The pollen record of Casa del Pino corroborates the macrofossil data of Lepe, with subtropical taxa forming forests associated with swampy wetlands (*Nyssa*, *Platycarya*, Sapotaceae, *Alnus*, Taxodiaceae, Clethraceae, Cyrillaceae, *Myrica*) and riparian vegetation with *Salix, Populus, Fraxinus* and Ulmaceae (Peñalba, 1985).

For the Pliocene–Pleistocene transition, pollen analyses in a stratigraphic section of El Asperillo Cliff, close to the Torre del Loro Faults by Zazo et al. (1999), highlighted the presence of the aquatic taxon *Myriophyllum* in a fluvial unit considered as a coastal plain with tidal influence (Fig. 4). *Myriophyllum* also appears in the pollen record published by Morales-Molino et al. (2011) from the intertidal area of El Asperillo beach assigned to MIS 5-4. This taxon is present in ASPI and ASPII together with other wetland indicators such as *Potamogeton*, *Juncus*, *Typha*, Cyperaceae and Ranunculaceae (Figs. 9 and 10). To this floristic assemblage the occurrence of *Salix* macroremains must be included (Postigo-Mijarra et al., 2010a), suggesting gallery forests in agreement with the palynological data presented here. The joint occurrence of those typically riparian elements together with mesophytes such as deciduous *Quercus*, *Betula*, *Corylus*, *Juglans* and *Castanea* cannot be ruled out, especially during the most arid phases. This pattern has been common during the Holocene in a numerous pollen records from southern Iberian Peninsula (Carrión et al., 2003a, 2003b, 2013).

In the present study, the occurrence of aquatic palynomorphs such as Zygnemataceae undiff., *Spirogyra*, *Debarya*, *Mougeotia* and *Botryococcus* in the AspI and AspII sites (particularly abundant in AspI) suggests the presence of lagoon or lake with water temperatures high enough to facilitate algal production and the growth of hygrophytes such as *Myriophyllum* during the Late Pleistocene (Figs. 10 and 11). The presence of *Pseudoschizaea* cysts and especially the high concentration of fungal palynomorphs (*Inapertisporites, Monoporisporites, Fusiformisporites, Scleroderma, Exesisporites*, among others), and hyphae, indicators of organic matter decomposition and even erosive phases (*Glomus*), suggest that these environments dried out temporarily (López-Sáez et al., 2000; Carrión, 2002) (Fig. 11). These conditions clearly correspond to a littoral system of marshes with alternating episodes of flooding and desiccation. In addition, tree taxa such as *Alnus* and *Quercus* probably colonized the lakeshores as the basins infilled (Figs. 9 and 10).

Paleolimnological features of these environments have been previously described in detail by Manzano et al. (2018) based on the Lucio de la Cancela de la Aulaga record which shows alternating assemblages during the Early to Mid-Holocene. Evaluating the degree of similarity between samples using non-metric multidimensional scaling (NMDS), these authors showed that negative loadings of upland taxa (deciduous *Quercus*, *Quercus suber*, and *Tamarix*, along with Monte Negro scrub) were associated with higher water tables, vernal pools and groundwater discharge areas. In contrast, the taxa with positive loadings, such as evergreen *Quercus*, thrive in phreatic water-restricted sites. In another study Laguna del Sopetón (Manzano et al., 2019), decreases in the algae *Spirogyra scrobiculata* and *Mougeotia latevirens* were associated with variable environments, while the proliferation of macrophytes (*Potamogeton* and Ranunculaceae), suggested the establishment of a persistent water table. In general, the macrophytes and filamentous algae assemblages make up deep, stagnant and seasonally fluctuating environments.

5.2. Relevance of pinewoods in the Iberian Southwest

Without doubt, the Iberian Peninsula has been a "land of pines" in the past (Gil et al., 1990; Gil, 1991; García-Antón et al., 1997, 2011; Carrión et al., 2000; Franco-Múgica et al., 2001, 2005; García-Amorena et al., 2007; Rubiales et al., 2009, 2010; Carrión, 2010; González-Sampériz et al., 2010, 2020; Postigo-Mijarra et al., 2010b; Morales-Molino et al., 2017, 2018; Camuera et al., 2019; López-Sáez et al., 2020b). The first evidences of *Pinus* in the Iberian Southwest corresponds to the late Miocene pollen record of Gibraleón (Peñalba, 1985; Barrón et al., 2010). Here pines appear accompanied by thermo-Mediterranean elements (Arecaceae, *Cornus*, Oleaceae and *Quercus*) in a predominantly steppic environment with Asteraceae, *Plantago*, Poaceae and *Rumex*, enriched by subtropical taxa such as Clethraceae, Cyrillaceae, *Nyssa*, and Symplocaceae (Barrón et al., 2010).

Abundant *Pinus* is also recorded in the area during the Early Pliocene climatic optimum. This is deduced by the palynological study of La Matilla core (Jiménez-Moreno et al., 2019), which records warmest and most humid conditions at ~4.35 Ma.; as well as studies of macro-remains in the outcrop of Lepe (Barrón et al., 2003) that shows *Pinus* along with a cohort of subtropical and warm-temperate elements (Lauraceae, Cesalpinioideae, Papilionoideae, *Quercus*). The Casa del Pino site (Peñalba, 1985) shows a continuous *Pinus* pollen curve within a mixed formation together with subtropical (*Nyssa, Platycarya*, Sapotaceae) and temperate (*Juglans, Quercus, Fraxinus, Populus, Salix, Fraxinus*, Ulmaceae) elements. These pine forests were progressively replaced with steppes and oak forests with Mediterranean elements such as *Quercus ilex-coccifera, Olea, Phillyrea* and *Vitis*. The core site G1 (Feddi et al., 2011) located off the coast of Málaga in the south of the Iberian Peninsula and scarcely 150 km from Doñana records for the Piacenzian an alternation of mixed coniferous and deciduous oak forests with thermophilous taxa (*Cathaya*, *Olea*, *Quercus ilex-coccifera*) that are progressively replaced as we enter into the Upper Pleistocene by less thermophilous conifers (*Cedrus, Tsuga, Abies, Picea, Pinus*) and *Artemisia–Ephedra* steppes.

During the Upper Middle Pleistocene, there is also evidence of regional pine forests. The Lucio of Mari López pollen record (Zazo et al., 1999; Yll et al., 2003) at the core of the DPA shows pine forests with *Artemisia* during a MIS 4-3 phase later replaced by evergreen *Quercus* during MIS 3. The marine pollen sequences indicate the presence of pine forests throughout the Middle and Upper Pleistocene with continuous pollen curves and with high percentages, such as in MD01-2443 (Roucoux et al., 2006) for MIS 9-6, MD95-2042 (Sánchez-Goñi et al., 1999) for MIS 6-4, 8057-B (Hooghiemstra et al., 1992) and SU 81-18 (Turon et al., 2003) for MIS 2-1. However, in those marine records an over-representation of pine pollen influenced by the taphonomic processes of marine deposition cannot be ruled out. Not surprisingly, pine is usually excluded from the pollen sum (Turon et al., 2003; Roucoux et al., 2006; Carrión et al., 2015). Nevertheless, the Pleistocene variation of pine in SU81-13 (Parra, 1994) shows close similarities with continental records such as the Padul peat bog (Pons and Reille, 1988; Camuera et al., 2019) and Carihuela cave (Carrión, 1992; Carrión et al., 1998, 1999, 2019; Fernández et al., 2007). The pine species involved were probably the same as those of the Lower Guadalquivir Basin (Postigo-Mijarra et al., 2010a). Thus, although *Pinus pinea* spread through the area in prehuman antiquity, historical testimonies indicate that its presence in Doñana dates back to the end of the 18th century, in the Marismillas area, as a crop introduced by the Casa de Medina Sidonia (Granados Corona, 1987; Ojeda Ribera, 1987, 1992). There was also no

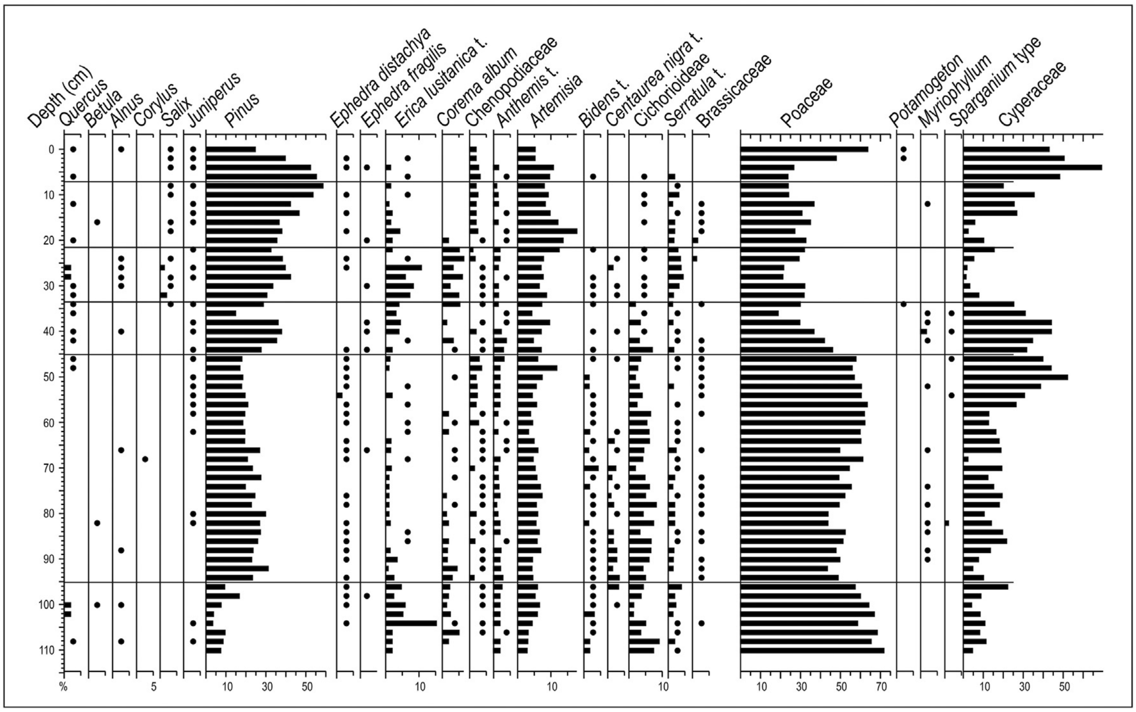

Fig. 5. Synthetic pollen diagram of selected taxa from El Asperillo. Redrawn from Stevenson (1984) and Carrión et al. (2013).

P. pinea in El Asperillo and El Abalario until the middle of the 20th century (see orthophoto of the American flight of 1946, where those territories are covered by practically bare sand).

In the El Asperillo Cliffs, Stevenson (1984) showed abundance of pines (Fig. 5) and the macro-remains studied by Postigo-Mijarra et al. (2010a) and Morales-Molino et al. (2011) from the Upper Pleistocene (MIS 4-3, 45 kyr cal. BP) sandy deposits (Fig. 6), allowed the identification of two gymnosperms at species level (*Pinus pinaster* and *P. nigra*), which is first evidence of mixed pine forests in the lower Guadalquivir Basin. This association is also found in the palynological record of AspI and AspII (Figs. 9, 10) as well as in the pollen records of Gorham's cave for the MIS 3-2 (Carrión et al., 2008). According to Postigo-Mijarra et al. (2010a), mixed *Pinus nigra–Pinus pinaster* stands are extremely rare today in the Iberian Peninsula (Sierra de Albarracín, Duero basin, Sierra de Almijara-Sierra Nevada) (Blanco-Castro et al., 2005). The mixed pine forests of the Sierra de Villafuerte (northeastern Baetic Ranges) in the northwest of Murcia province should be added to that list (CARM, 2003) which probably occupied more extensive areas during the Pleistocene. Also for El Asperillo, Morales-Molino et al. (2011) found significant amounts of pine pollen during an early stadial of the last glacial cycle (MIS 5-4) (Fig. 7) in a general context of steppe vegetation with *Artemisia*, Chenopodiaceae and Poaceae.

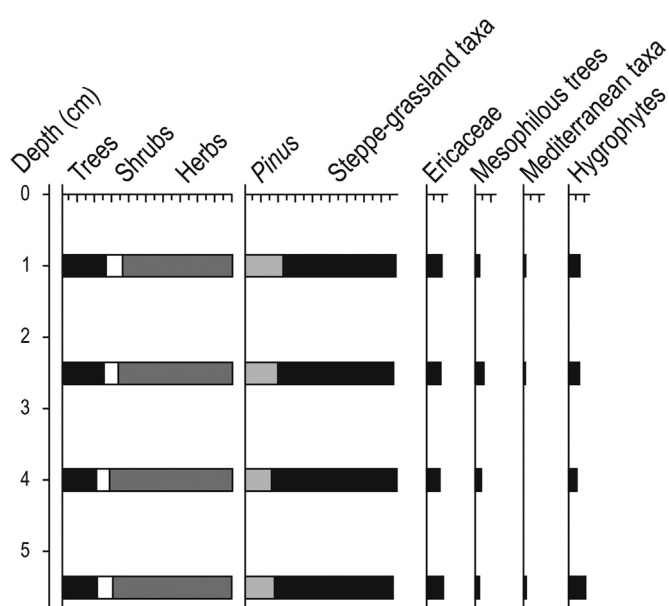

Fig. 6. Synthetic pollen diagram of El Asperillo. Redrawn from Postigo-Mijarra et al. (2010a)) and Morales-Molino et al. (2011).

The data presented here add diversity to the previously described Pleistocene pine woodlands. In addition to the mixed formations of *Pinus pinaster* and *P. nigra*, the AspI and AspII sequences show the continuous presence of Mediterranean pine forests of *Pinus pinea-halepensis* since the late MIS 3 (Figs. 9, 10), in line with the findings of the Pleistocene of Gibraltar (Carrión et al., 2018). In addition, this study shows that the pine forests of *P. nigra–sylvestris* occurred only occasionally during MIS 3 to increase significantly later in the MIS 2 (Figs. 9, 10), probably favored by the low temperatures of the LGM and higher moisture availability related to the proximity to the sea. Nowadays natural stand of these pine species in southern Iberia (e.g. Sierra de Baza and Sierra Nevada) thrive at high elevations (usually above 1500–2000 m asl) on relatively humid soils (López González, 2001).

The native status of *Pinus pinea* in the southwest of the Iberian Peninsula has long been debated (Rivas-Martínez, 1987; Rivas Martínez, 2011; Pérez Latorre et al., 1999; Martínez and Montero, 2004; López Albacete, 2009). The paleobotanical records of *Pinus* attests to the presence of pine forests, including those of *Pinus pinea*, in Doñana and other southwestern Iberian sites since at least, the Late Pleistocene (Menendez Amor and Florschutz, 1964; Stevenson, 1984, 1985; Stevenson and Moore, 1988; Stevenson and Harrison, 1992; López-Sáez et al., 2002; Yll et al., 2003; Carrión et al., 2008, 2018;

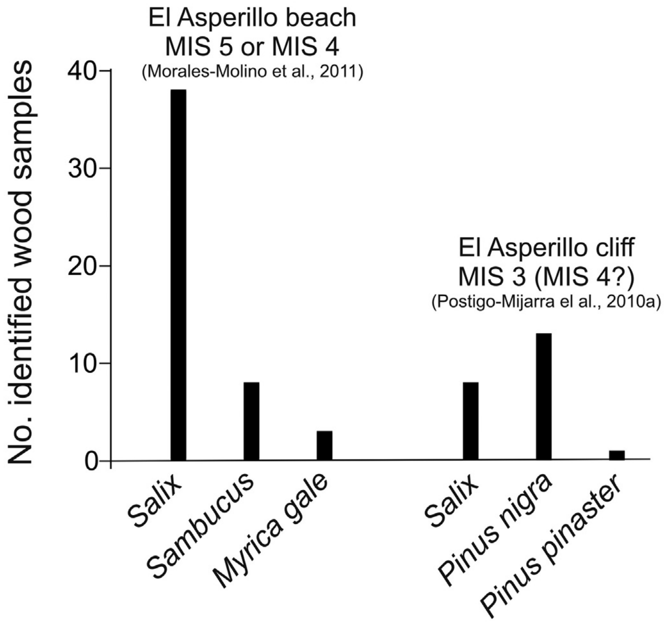

Fig. 7. Plant macro-remains of El Asperillo according Postigo-Mijarra et al. (2010a) and Morales-Molino et al. (2011).

Jiménez-Moreno et al., 2015; Manzano et al., 2018, 2019). The relative abundance of *Pinus pinea* macrofossils such as pinecones, bracts and seeds in fossil records from southwestern Iberia (Martínez and Montero, 2004), brings further support to the pollen-based identification of *Pinus pinea* within the *P. pinea–halepensis* type. Additionally, macrobotanical evidence from Cueva de Nerja (Badal, 2001; Badal et al., 2012) supports the survival of this pine species during the cold stages of the Upper Pleistocene, while similar findings show that *Pinus pinea* grew around Cueva de los Murciélagos (Zapata et al., 2005; Peña-Chocarro, 2007) and in Puerto de Santa María (López-Sáez et al., 2001, 2002) during the Holocene. Charcoal (strobili and charred wood) also confirms the local presence of *Pinus pinea* in Gorham's Cave (Carrión et al., 2008). In addition to the above, there is pollen evidence of *P. pinea* in Bajondillo cave (López-Sáez et al., 2007) and Abrigo 3 del Complejo del Humo (Ochando et al., 2020).

It seems that the coniferous forests of the Upper Pleistocene at these latitudes featured certain taxonomic diversity. Our new data from El Asperillo Cliff add *Abies* to the list of conifers in the paleoecosystem of Doñana, alongside several pine and juniper species (Fig. 10). The cold and dry conditions of the LGM possibly pushed *Abies* towards these coastal settings seeking warmer temperatures but by mainly higher moisture. Analog situations were previously observed in other refugial areas (Carrión et al., 2015) such as Vanguard Cave in Gibraltar (Carrión et al., 2008), Bajondillo Cave (López-Sáez et al., 2007; Cortés-Sánchez et al., 2008), Abrigo 3 del Complejo del Humo (Ochando et al., 2020), Padul (Camuera et al., 2019), Malladetes in Valencia (Dupré, 1980), and Creixell and Castelló d'Empúries in Catalonia (Burjachs and Schulte, 2003; Burjachs et al., 2005). It is unlikely that *Abies* pollen appearing in Abrigo 3 del Complejo del Humo belonged to *Abies pinsapo* (García López and Allué Camacho, 2005; Alba-Sánchez et al., 2010). *Abies* pollen probably belongs to *Abies pinsapo*, since it occurs near the study area at present, restricted to some specific points in the Ronda mountain range (Sierra Bermeja, Sierra de las Nieves and Sierra de Grazalema (Blanco-Castro et al., 1997; Alba-Sánchez and López-Sáez, 2013; Alba-Sánchez et al., 2018).

The Holocene pollen sequences of the DPA and surrounding areas, such as El Acebrón (Stevenson and Harrison, 1992), Las Madres (Stevenson, 1981, 1985; Stevenson and Harrison, 1992; Yll et al., 2003), Laguna de Medina (Reed et al., 2001), S11 and S7 core (Jiménez-Moreno et al., 2015), Lucio de la Cancela de la Aulaga (Manzano et al., 2018), Laguna del Sopetón (Manzano et al., 2019) and S1 core (López-Sáez et al., 2018), show continuous presence of pinewoods, whose densities experienced fluctuations due to climatic changes and anthropic activities. A number of postglacial sequences in the Iberian Peninsula record decreases in pine forest cover along with deciduous elements contemporaneous with increases in xerophytes due to climate change from the Mid-Holocene onwards (Yll et al., 1994; Pantaleón-Cano et al., 2003; Carrión et al., 2004; Fletcher et al., 2007; Fuentes et al., 2007; Anderson et al., 2011). Lake records from Sierra Nevada (Spain) also indicate increasing aridification and Saharan dust input from Mid Holocene onwards (Jiménez Espejo et al., 2014), in agreement with the reactivation of the eolian deposits at the studied location. During the Late Holocene, different pollen sequences in the

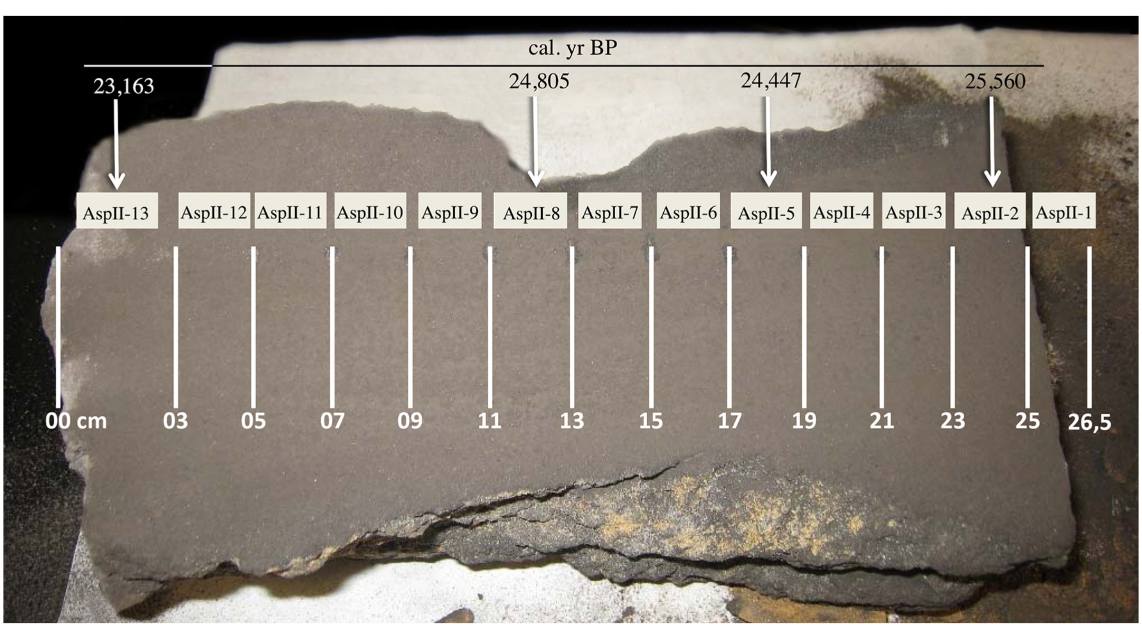

Fig. 8. Pollen samples and radiocarbon dating on the peaty sand strata from AspII.

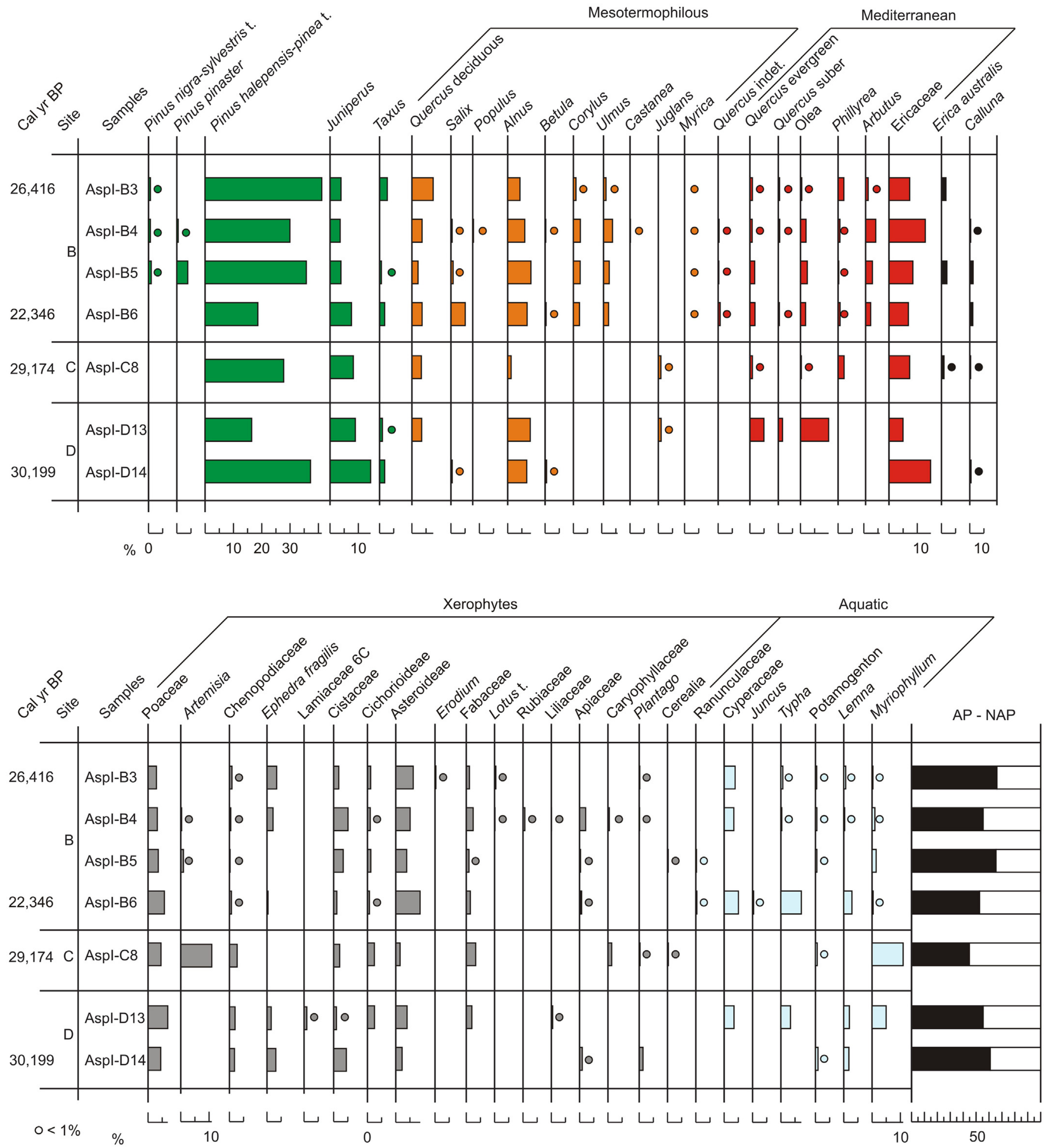

Fig. 9. Pollen diagram of AspI.

region show dramatic vegetation changes caused by anthropogenic disturbances such as fire, agriculture or overgrazing (García-Antón et al., 1997; Carrión et al., 2001, 2002, 2003a, 2007, 2010, 2018; Ruiz-Zapata et al., 2002; Carrión-Marco, 2005; Rubiales et al., 2008; Ejarque et al., 2009; López-Merino et al., 2009; Gil-Romera et al., 2009, 2010; Abel-Schaad et al., 2009; Morales-Molino et al., 2011, 2013; Abel-Schaad, 2012; Abel-Schaad and López-Sáez, 2013; Connor et al., 2019), unfortunately the AspI samples for this period are palynologically sterile (Fig. 2).

5.3. SW glacial refugia

Former paleoecological works in the Iberian Peninsula showed the conventional pattern of vegetation change during the Quaternary consisting in an episodic alternation of forested environments during temperate climatic pulsations and xero-heliophytic steppes during cold and dry phases (González-Sampériz et al., 2010; Carrión et al., 2010, 2013). Gymnosperms, especially pines, occurred not only sparse in steppes but also mixed with oaks and other trees during the forested

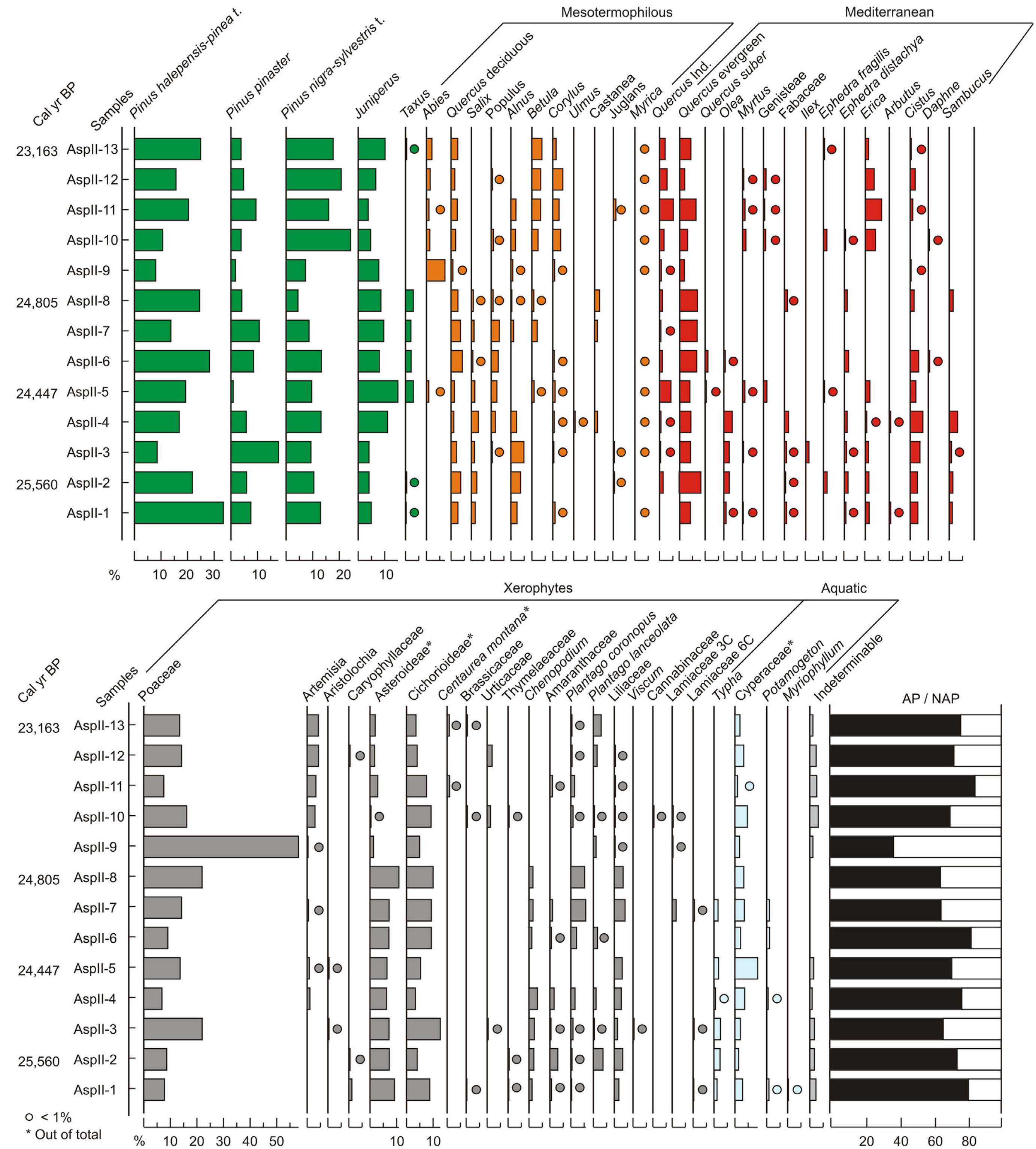

Fig. 10. Pollen diagram of AspII.

interglacials and insterstadials. The existence of permanent woody angiosperm refuges, enabled the survival of a large number of thermo- and meso-mediterranean species providing starting points for recolonization in each postglacial phase (González-Sampériz et al., 2010; Carrión et al., 2015; Magri et al., 2017; Fernández et al., 2018). Although concerning only the end of the last glacial phase, the data presented here prove the existence of a glacial refuge in Doñana for temperate and Mediterranean trees and scrub, including several species of conifers. Interestingly, our records registered the Heinrich Events 2 (HE2; 26.5–24.3 kyr cal BP (Sánchez-Goñi and Harrison, 2010) and the Last Glacial Maximum (23–19 kyr cal BP from MARGO Project, 2009). HE2 and LGM are among the most extreme events regarding climate conditions that took place in Europe, when massive European Ice Sheet melting promoted dramatic cooling in the European Atlantic facade and the

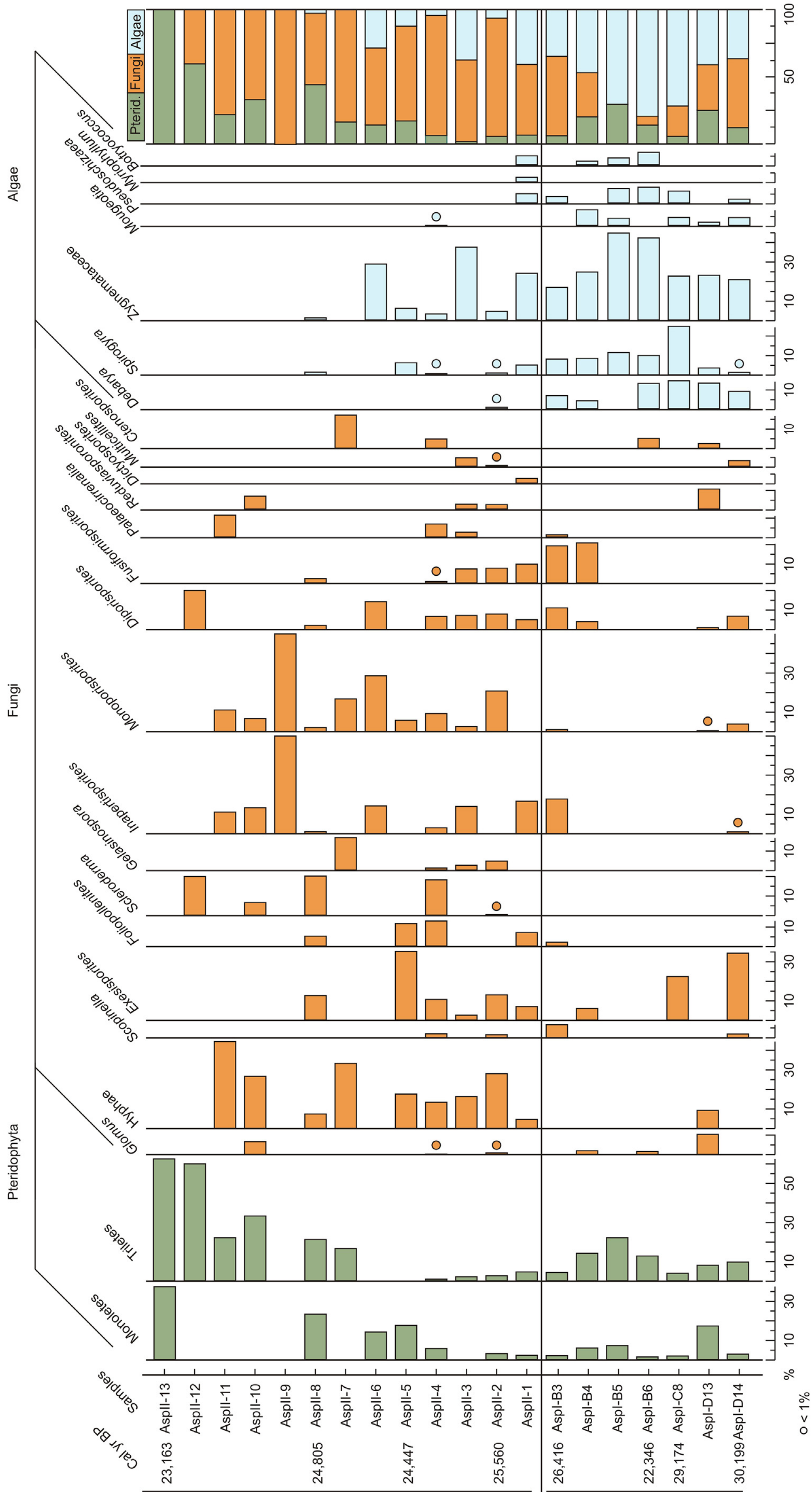

Fig. 11. Palynological diagram of non-pollen palynomorphs of AspI and AspII.

Western Mediterranean (HE2) (e.g., Jiménez Espejo et al., 2007) and maximum global ice-sheet expansion took place (LGM). The diversity of woody taxa observed in the El Asperillo pollen assemblages during these particularly harsh stages reinforces the importance of the Doñana refuge in the western Mediterranean context. This was perhaps relevant for human evolution population history since southermost Iberia is the region of survival for the last Neanderthals (Finlayson et al., 2006; Finlayson and Carrión, 2007; Jennings et al., 2011) clearly linked with optimal climatic conditions (Finlayson, 2020).

The new site of El Asperillo show the occurrence of the following woody taxa under full-glacial conditions in the Doñana area: *Pinus nigra* and/or *P. sylvestris*, *P. pinaster, P. pinea, P. halepensis, Taxus, Abies, Juniperus,* deciduous and evergreen *Quercus, Q. suber, Alnus, Betula, Corylus, Ulmus, Castanea, Salix, Populus, Juglans, Ilex, Arbutus, Myrica, Olea, Phillyrea, Erica* cf. *australis, Calluna, Myrtus, Cistus, Daphne, Sambucus,* and Genisteae. Finds of walnut and chestnut pollen confirms the native character of *Juglans regia* and *Castanea sativa* to the western Mediterranean (García-Antón et al., 1990; García-Antón and Sainz-Ollero, 1991; Carrión and Sánchez-Gómez, 1992; Carrión, 2002; Postigo-Mijarra et al., 2008, 2010b; Aranbarri et al., 2016). The natural occurrence of *Pinus pinaster* (Carrión et al., 2000) and *Pinus pinea* is also supported, in the last case with the reinforcement of macrofossil findings (Badal, 2001; López-Sáez et al., 2001, 2002; Badal et al., 2012; Zapata et al., 2005; Peña-Chocarro, 2007; Carrión et al., 2008).

It is also pertinent to highlight the work on modern pollen rain in Doñana by Stevenson (1984), who suggested that taxa such as *Corylus* and *Betula* may have been more abundant in the past millennia and, doubtless, much closer to the current area of Doñana. Anthropogenic forest depletion and loss of tree diversity is certainly not exclusive to the region, but it is observed in many other sequences of southern Spain, sometimes in dramatic detail such as in Sierra de Gádor (Carrión et al., 2003a).

The present work reinforces previous hypotheses on glacial refugia. The Doñana Lucio of Mari López sequence (Zazo et al., 1999; Yll et al., 2003), records the dominance of pine woodlands and open formations of *Artemisia*, grasses and several Asteraceae during MIS 4-3, but also, highlighting the continuous presence of *Quercus* and *Olea*. The palynological and archeological charcoal studies in Gorham's (Finlayson and Carrión, 2007; Carrión et al., 2008) and Vanguard Caves (Carrión et al., 2018), Gibraltar, reveal a huge plant diversity dominated by a tree layer of oaks and pines (*Pinus pinea, Juniperus phoenicea, Quercus ilex-coccifera, Q. suber, Erica arborea, Arbutus unedo, Pistacia terebinthus, Olea*) in mosaic with riparian forests, savannas, grasslands, shrublands and steppes. To this structure we must add coastal xerothermophilous elements such as *Maytenus senegalensis, Withania frutescens, Calicotome villosa* and *Myrtus communis* together with *Olea europaea, Phillyrea angustifolia–latifolia, Ephedra fragilis, Bupleurum gibraltaricum* and *Tamarix africana*, indicators of the most thermal refuge of the late Quaternary (Carrión et al., 2018).

The palynological samples of the El Asperillo organic layers in U2–U3 eolian units (Fig. 4), dated at ca. 21–16 kyr cal. BP (Zazo et al., 2005), as well as the macro-remains from the same stratigraphical unit contain thermophilous elements such as *Alnus, Betula* and *Quercus* (Morales-Molino et al., 2011). Finally, marine cores such as SU81-13 (Parra, 1994), MD95-2043 (Fletcher and Sánchez-Goñi, 2008; Fletcher et al., 2010), MD95-2042 (Pailler and Bard, 2002; Chabaud et al., 2014), ODP site 976 (Combourieu Nebout et al., 2009; Dormoy et al., 2009), SU81-18 (Bard et al., 2000; Turon et al., 2003), U1385 (Oliveira et al., 2018), and D13882 (Naughton et al., 2019) depict the changes in the coastal and mountainous vegetation near the coasts of the Iberian Peninsula and Morocco throughout the last 20,000 years. They show the persistence of pine woodlands mixed with holm and cork oak. Because of its temperature requirements, it is worth stressing the lateglacial abundance of *Olea europaea*.

To this bulk of paleobotanical data, we must add the floristic evidence of glacial refugia in this area of southern Iberia obtained from the current floristic composition, which includes species of undoubtedly tropical or subtropical origin such as *Rhododendron ponticum, Myrica gale, Prunus lusitanica* and *Culcita macrocarpa*. Eastwards, in the particularly dry Iberian Southeast, the list would also include *Maytenus senegalensis, Periploca angustifolia, Ziziphus lotus, Halogeton sativus* and *Launaea arborescens* (Ojeda Ribera et al., 1996; Costa Tenorio et al., 1997; Arroyo-García et al., 2001; Postigo-Mijarra et al., 2009, 2010a; Verdú et al., 2020). Additional evidence is provided by studies of the genetic structure of the actual plant species populations (Arroyo-García et al., 2001; Verdú et al., 2020). Both data series suggest that the far south-southwestern corner of the Iberian Peninsula has been a refuge for Euro-Siberian, Mediterranean and Ibero-Maghrebian plants during the Quaternary, even during extreme periods as the HE2 and LGM. It is certainly a unique territory worthy of ecological conservation.

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Erratum

Erratum to "New palynological data from the Late Pleistocene glacial refugium of South-West Iberia: The case of Doñana" [Review of Palaeobotany and Palynology (2021) PALBO 104431]

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