Review of Palaeobotany and Palynology 290 (2021) 104431

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

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

S. Fernández [a,*], J.S. Carrión [a,b], J. Ochando [a], P. González-Sampériz [c], M. Munuera [d], G. Amorós [a], J.M. Postigo-Mijarra [e], C. Morales-Molino [f], P. García-Murillo [g], G. Jiménez-Moreno [h], J.A. López-Sáez [i], F. Jiménez-Espejo [j], L.M. Cáceres [k], J. Rodríguez-Vidal [k], G. Finlayson [l,m,n], S. Finlayson [l,m], C. Finlayson [l,m,n,o]

[a] Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain
[b] Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa
[c] Pyrenean Institute of Ecology (IPE-CSIC), Av/Montañana 1005, 50059, Zaragoza, Spain
[d] Department of Agricultural Science and Technology, Polytechnic University of Cartagena, 30203 Cartagena, Spain
[e] Dpto. de Silvopascicultura, Unidad de Botánica, Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica, Ciudad Universitaria, Madrid 28040, Spain
[f] Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland
[g] Department of Plant Biology and Ecology, Faculty of Pharmacy, University of Seville, Seville, Spain
[h] Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain
[i] Environmental Archaeology Research Group, Institute of History, CSIC, CCHS, Albasanz 26-28, 28037 Madrid, Spain
[j] Instituto Andaluz de Ciencias de la Tierra (CSIC-UGR), Armilla, Spain
[k] Department of Earth Sciences, Faculty of Experimental Sciences, University of Huelva, Campus del Carmen, Av. Tres de Marzo s/n, 21071 Huelva, Spain
[l] The Gibraltar National Museum, 18-20 Bomb House Lane, P.O. Box 939, Gibraltar
[m] Institute of Life and Earth Sciences, The University of Gibraltar, Gibraltar National Museum Campus, Gibraltar
[n] Department of Life Sciences, Liverpool John Moores University, Liverpool, United Kingdom
[o] Department of Anthropology, University of Toronto, Scarborough campus, Toronto, Canada

ARTICLE INFO

Article history:
Received 24 February 2021
Received in revised form 14 April 2021
Accepted 19 April 2021
Available online 21 April 2021

Keywords:
Paleobotany
Historical biogeography
Quaternary
Pleistocene
Iberian Peninsula

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

---

* Corresponding author.
E-mail addresses: santiago@um.es, santiagofj@gmail.com (S. Fernández).

https://doi.org/10.1016/j.revpalbo.2021.104431

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.

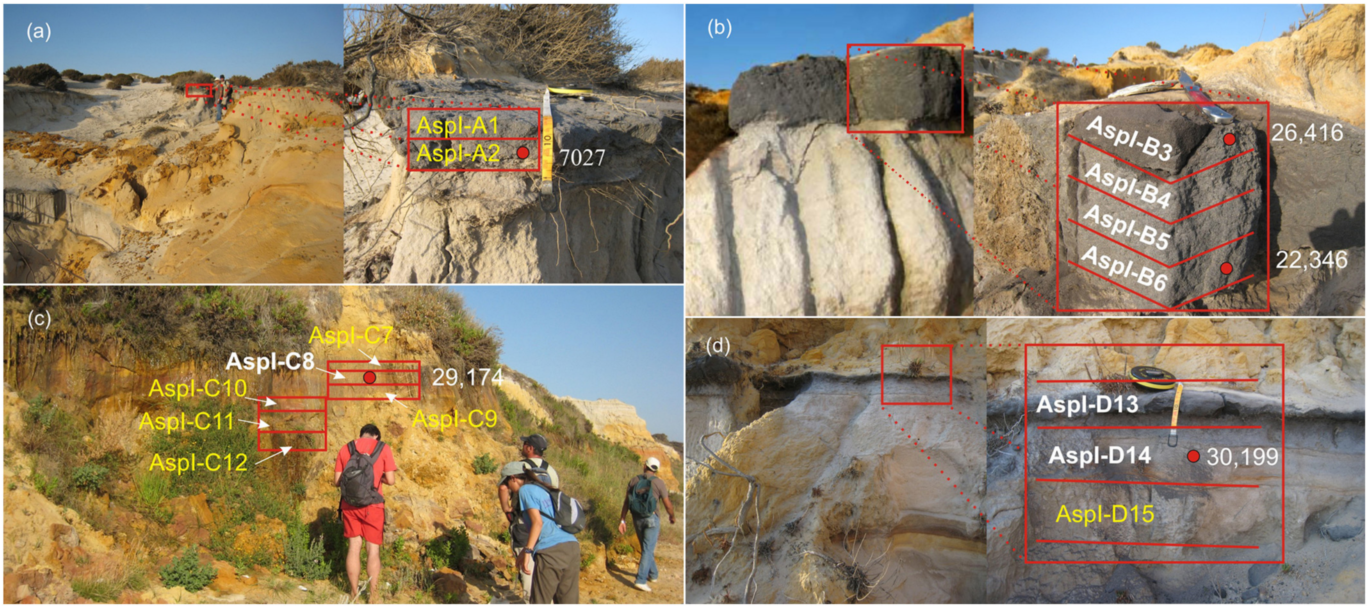

Fig. 2. AspI showing radiocarbon dating and position of pollen samples at Site A (a), Site B (b), Site C (c) and Site D (d). Sterile samples in yellow. Photos by Manuel Munuera.

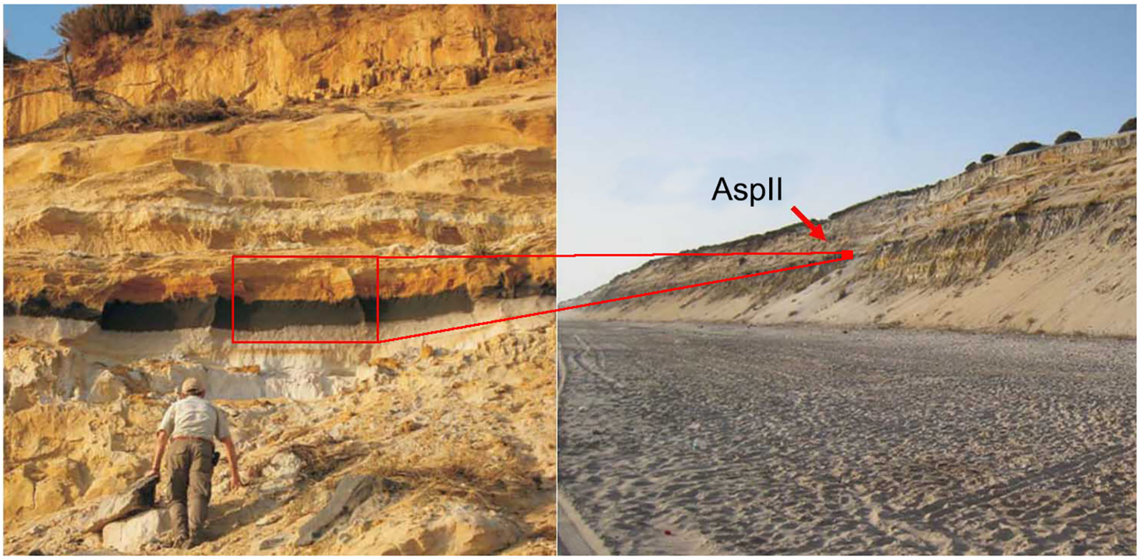

Fig. 3. Pollen sampling in AspII, El Asperillo Cliff.

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.).

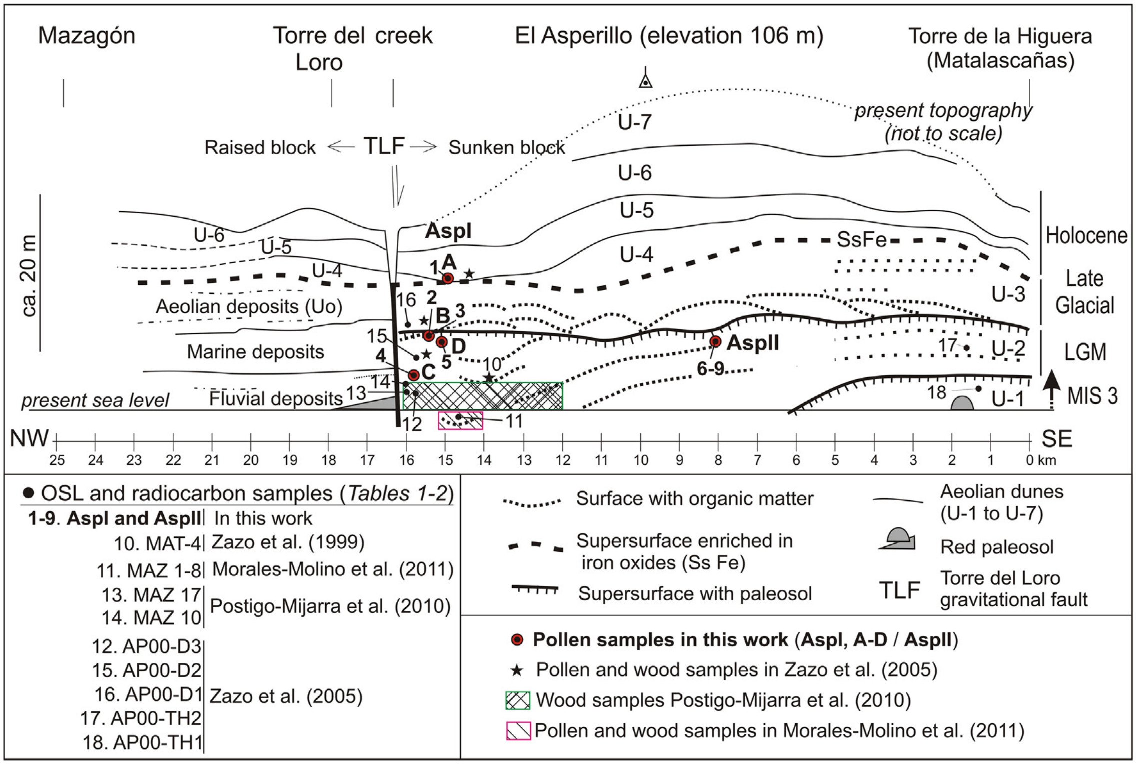

Fig. 4. Location of pollen, macrofossil, and radiocarbon samples within the lithostratigraphy of El Asperillo Cliff according to former studies by Zazo et al. (2005), Morales-Molino et al. (2011), and Postigo-Mijarra et al. (2010a).

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 macroremains 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

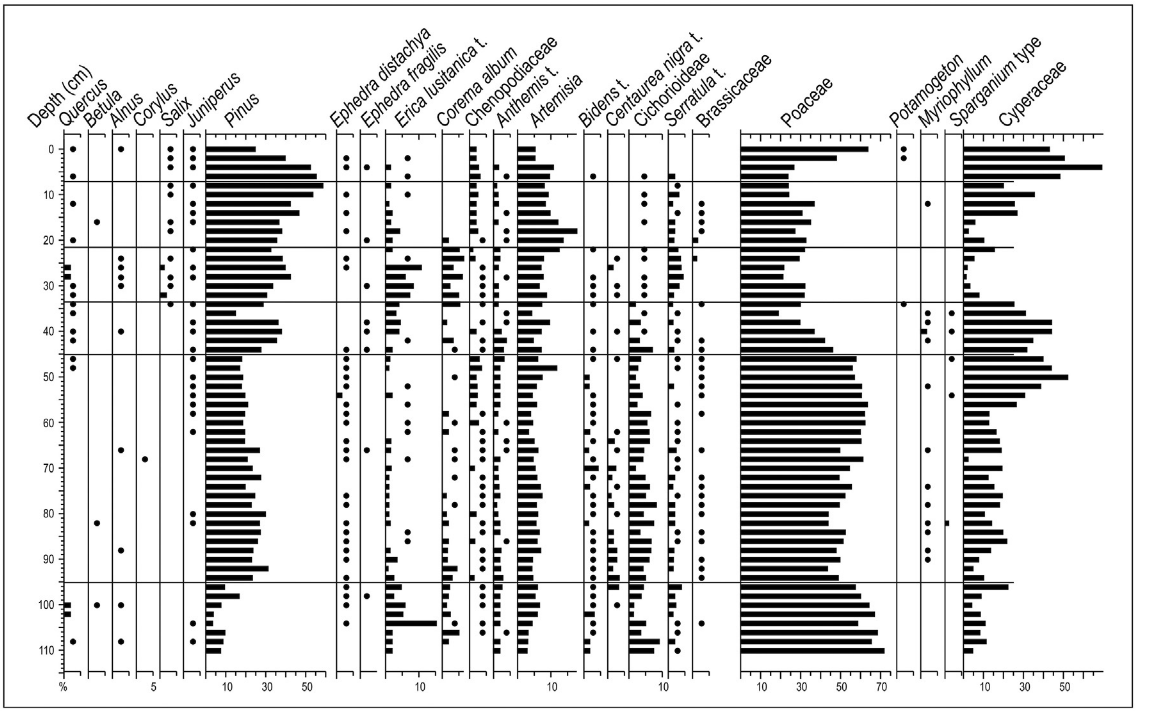

Fig. 5. Synthetic pollen diagram of selected taxa from El Asperillo. Redrawn from Stevenson (1984) and Carrión et al. (2013).

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.

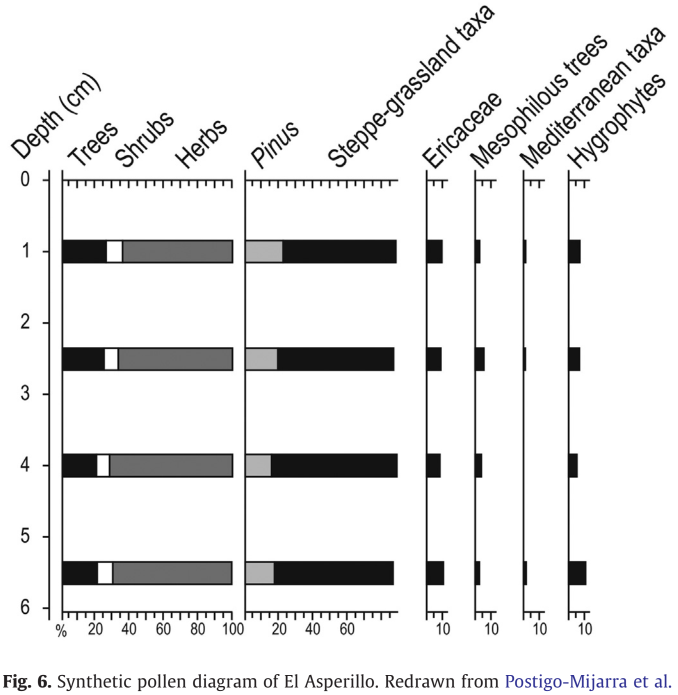

Fig. 6. Synthetic pollen diagram of El Asperillo. Redrawn from Postigo-Mijarra et al. (2010a)) and Morales-Molino et al. (2011).

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;

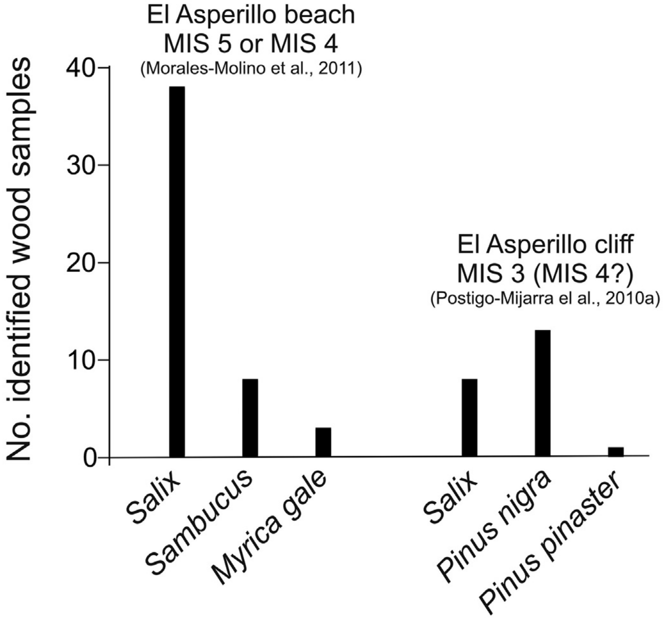

Fig. 7. Plant macro-remains of El Asperillo according Postigo-Mijarra et al. (2010a) and Morales-Molino et al. (2011).

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

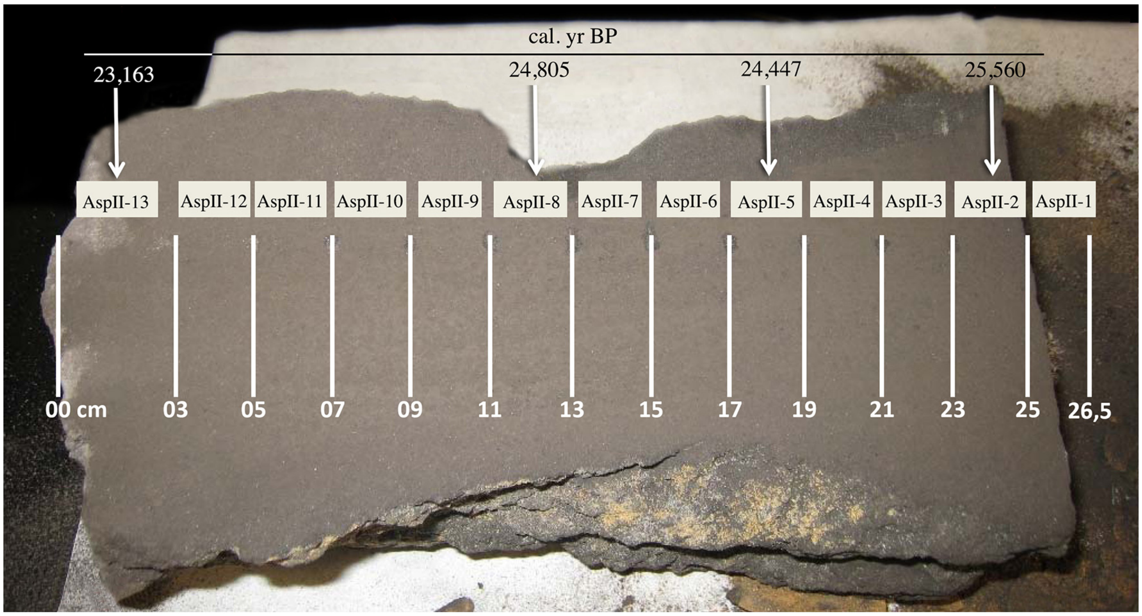

Fig. 8. Pollen samples and radiocarbon dating on the peaty sand strata from AspII.

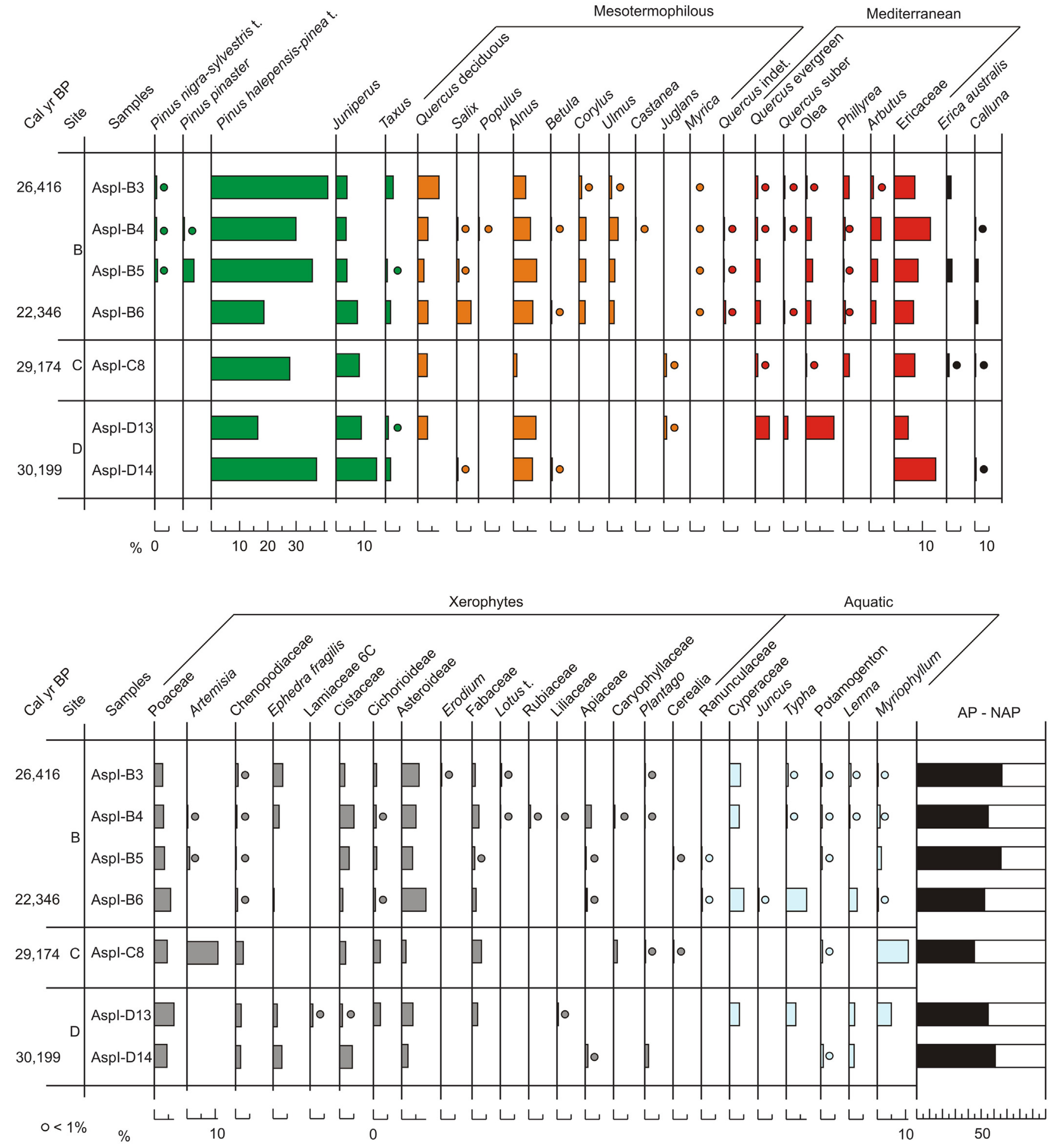

Fig. 9. Pollen diagram of AspI.

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

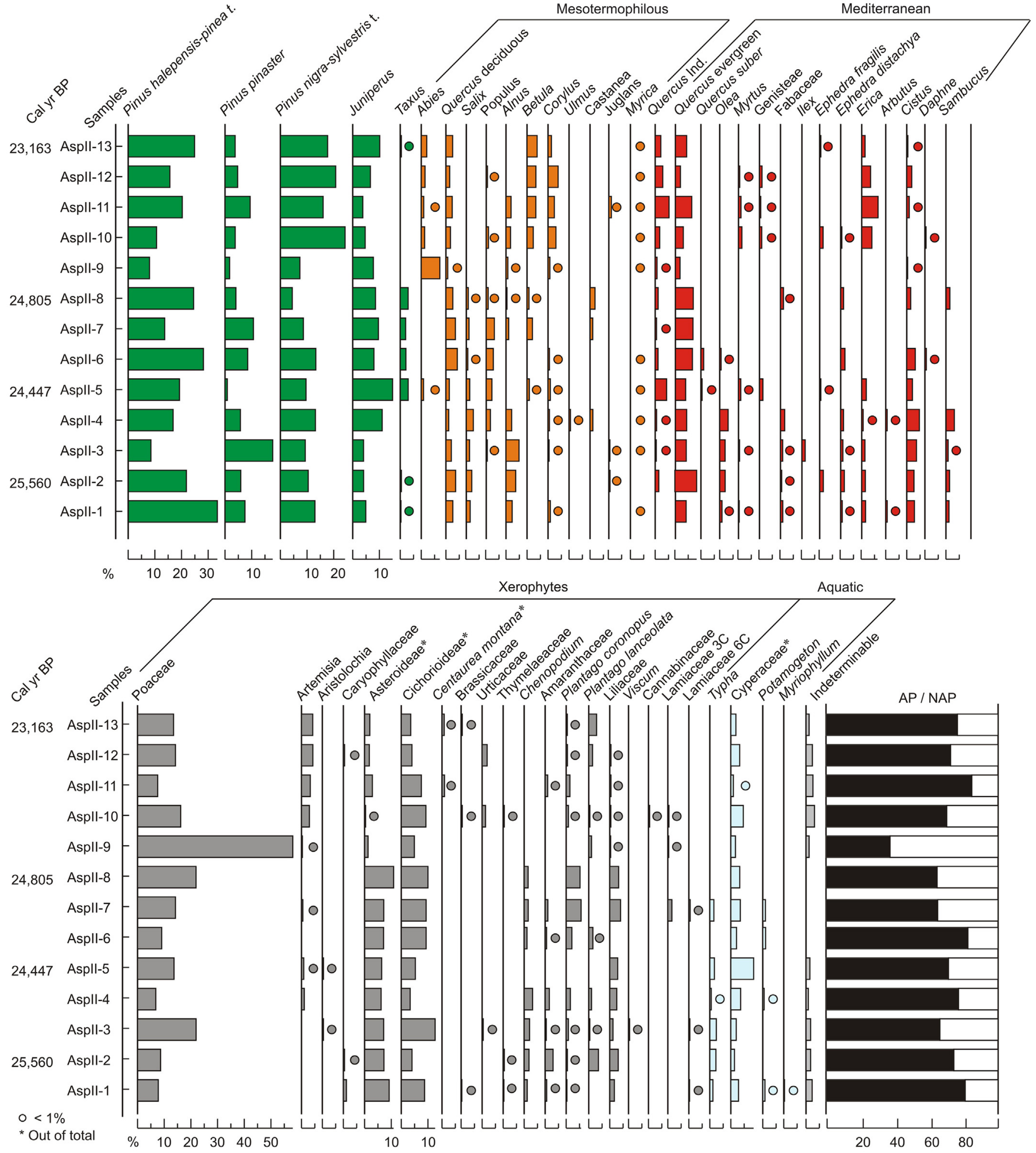

Fig. 10. Pollen diagram of AspII.

interglacials and interstadials. 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

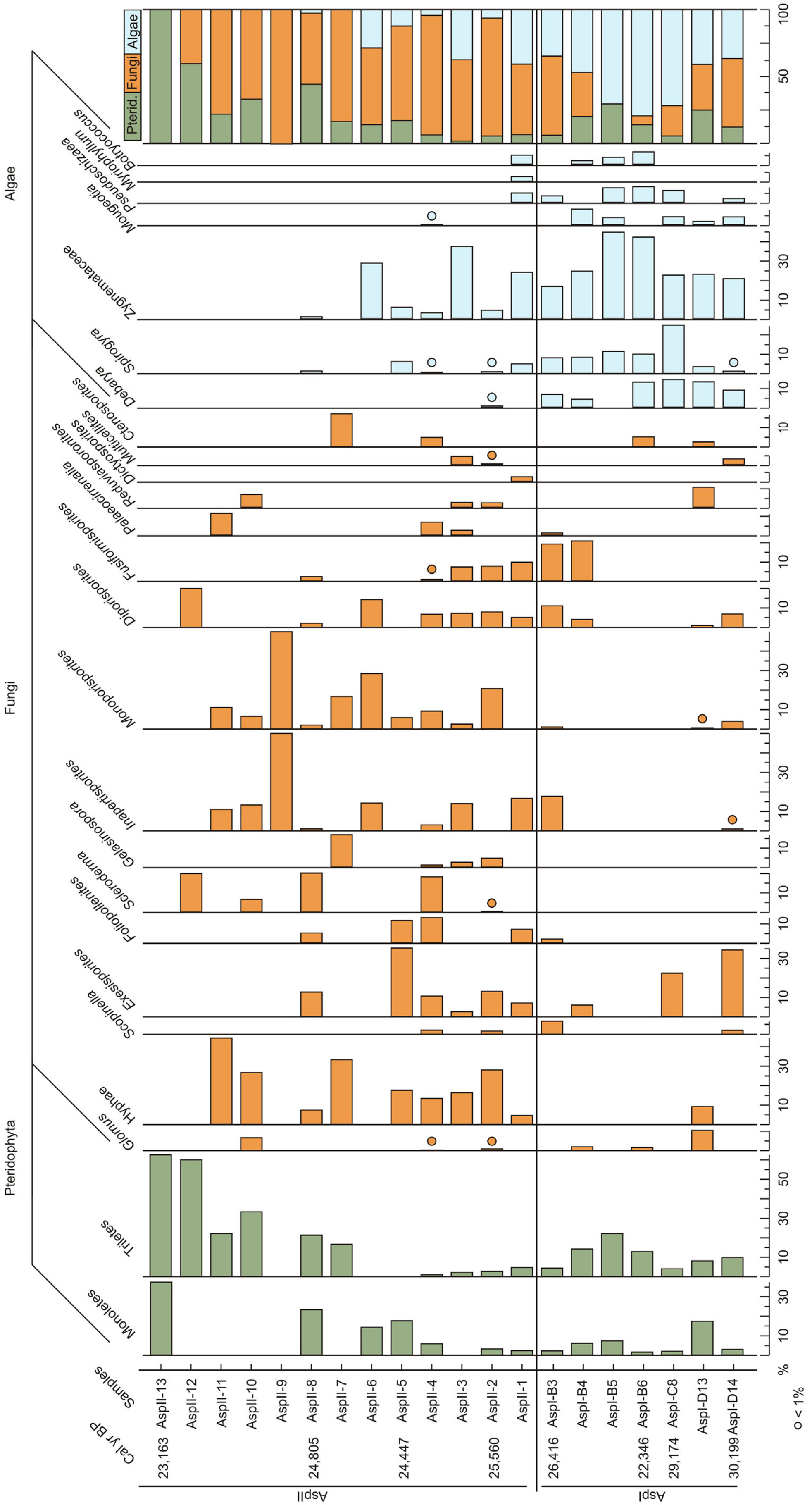

Fig. 11. Palynological diagram of non-pollen palynomorphs of AspI and AspII.

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.

Acknowledgments

The development of this work was supported by Projects FEDER/ Ministry of Science and Innovation, Agencia Estatal de Investigación CGL-BOS2015-68604-P and PID2019-1049449GB-I00), 261-2011 Organismo Autónomo de Parques Nacionales and Fundación Séneca grant 20788/PI/18.

References

Abel-Schaad, D., 2012. Evolución de la vegetación Durante el Holoceno Reciente en la Vertiente extremeña del Sistema Central a Partir del análisis palinológico. Tesis doctoral. Universidad de Extremadura, Plasencia.

Abel-Schaad, D., López-Sáez, J.A., 2013. Vegetation changes in relation to fire history and human activities at the Peña Negra mire (Béjar Range, Iberian Central Mountain System, Spain) during the past 4.000 years. Veg. Hist. Archaeobot. 22, 199–214.

Abel-Schaad, D., Hernández Carretero, A.M., López-Merino, L., Pulido Díaz, F.J., López-Sáez, J.A., 2009. Cabras y quemorros: Tres siglos de cambios en el paisaje de la vertiente extremeña de la Sierra de Gredos. Rev. Est. Extrem. 65, 449–478.

Alba-Sánchez, F., López-Sáez, J.A., 2013. Paleobiogeografía del pinsapo en la Península ibérica durante el Cuaternario. In: López Quintanilla, J. (Ed.), Los pinsapares en Andalucía (*Abies pinsapo* Boiss.), Conservación y sostenibilidad en el siglo XX. Junta de Andalucía. Sevilla, pp. 33–51.

Alba-Sánchez, F., López-Sáez, J.A., De Benito Pando, B., Linares, J.C., Nieto-Lugilde, D., López-Merino, L., 2010. Past and present potential distribution of the Iberian Abies species: a phytogeographic approach using fossil pollen data and species distribution models. Div. Distrib. 16, 214–228.

Alba-Sánchez, F., Abel-Schaad, D., López-Sáez, J.A., Sabariego Ruiz, S., Pérez-Díaz, S., González-Hernández, A., 2018. Paleobiogeografía de Abies spp. y Cedrus atlantica en el Mediterráneo occidental (península ibérica y Marruecos). Ecosistemas 27, 26–37.

Anderson, R.S., Jiménez-Moreno, G., Carrión, J.S., Pérez-Martínez, C., 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Nevada, southern Spain. Quat. Sci. Rev. 30, 1615–1629.

Aranbarri, J., Bartolomé, M., Alcolea, M., Sancho, C., Celant, A., González-Sampériz, P., Arenas, C., Magri, D., Rodríguez-Lázaro, J., 2016. Palaeobotanical insights from early-mid Holocene fluvial tufas in the Moncayo natural park (Iberian range, NE Spain): regional correlations and biogeographic implications. Rev. Palaeobot. Palynol. 234, 31–43.

Arroyo-García, R., Martínez-Zapater, J.M., Fernández Prieto, J.A., Álvarez-Arbesú, R., 2001. AFLP evaluation of genetic similarity among laurel populations (*Laurus* L.). Euphytica 122, 155–164.

Badal, E., 2001. La recolección de piñas durante la prehistoria de la Cueva de Nerja (Málaga). En. In: Villaverde, V. (Ed.), De Neandertales a Cromañones. El inicio del poblamiento humano en tierras valencianas. Universitat de València, Valencia, pp. 21–40.

Badal, E., Villaverde, V., Zilhão, J., 2012. Middle Palaeolithie wood charcoal from thee sites in south and west Iberia: Biogeographi implications. (coord.). In: Badal, E., et al. (Eds.), Wood and charcoal. Evidence for human and natural history. Sagvntvm Extra-13. Valencia, pp. 13–24.

Bard, E., Rostek, F., Turon, J.L., Gendreau, S., 2000. Hydrological impact of Heinrich events in the subtropical Northeast Atlantic. Science 289, 1321–1324.

Barrón, E., Muñiz, F., Mayoral, E., 2003. Aspectos macroflorísticos del Plioceno de Lepe (Cuenca del Guadalquivir, Huelva, España). Consideraciones paleoecológicas. Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.) 98, 91–109.

Barrón, E., Rivas-Carballo, R., Postigo-Mijarra, J.M., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., Valle-Hernández, M., 2010. The Cenozoic vegetation of the Iberian Peninsula: a synthesis. Rev. Palaeobot. Palynol. 162, 382–402.

Bennett, K.D., 2008. Documentation for psimpoll 4.26 and pscomb 1.03: C programs for plotting pollen diagrams and analysing pollen data. Available at:. http://chrono.qub.ac.uk/psimpoll/psimpoll.html/.

Blanco-Castro, E., Casado González, M.A., Costa Tenorio, M., Escribano Bombín, R., García Antón, M., Génova Fuster, M., Gómez Manzaneque, A., Gómez Manzaneque, F., Moreno Saiz, J.C., Morla Juaristi, C., Regato Pajares, P., Sainz Ollero, H., 1997. Los Bosques ibéricos. 1st ed. Editorial Planeta, Barcelona.

Blanco-Castro, E., Casado Gonzalez, M.A., Costa, T.M., 2005. Los Bosques ibéricos. Una interpretación geobotánica. Planeta, Barcelona ISBN 8408058207.

BOJA, 2002. Boletín Official de la Junta de Andalucía (BOJA no 3/2002, de 8 de Enero). Monumento Natural Acantilado del Asperillo. Junta de Andalucía, Spain.

Burjachs, F., Schulte, L., 2003. El paisatge vegetal del Penedès entre la Prehistòria i el Món Antic. In: Guitart, J., Palet, J.M., Prevosti, M. (Eds.), Territoris Antics a la Mediterrània I a la Cossetània Oriental. Departament de Cultura, Generalitat de Catalunya, Barcelona, pp. 249–254.

Burjachs, F., Bach, J., Buxó, R., Llàcer, P., McGlade, J., Picazo, M., Piqué, R., Ros, M.T., 2005. El territori d'Emporion i les seves dades paleoambientals. Empúries 54, 21–28.

Camuera, J., Jiménez-Moreno, G., Ramos-Román, M.J., García-Alix, A., Toney, J.L., Scott-Anderson, R., Jiménez-Espejo, F., Bright, J., Webster, C., Yanes, Y., Carrión, J.S., 2019. Vegetation and climate changes during the last two glacial-interglacial cycles in the western Mediterranean: a new long pollen record from Padul (southern Iberian Peninsula). Quat. Sci. Rev. 205, 86–105.

Caratini, C., Viguier, C.I., 1973. Estud. Geol. 29, 325–328.

CARM, 2003. Plan de manejo de especies forestales catalogadas "de interés especial" según el Catálogo Regional de Flora silvestre protegida de la Región de Murcia: *Pinus pinaster* Aiton. Dirección General del Medio Natural. Comunidad Autónoma de la Región de Murcia, Murcia.

Carrión, J.S., 1992. Late Quaternary pollen sequence from Carihuela Cave, Southern Spain. Rev. Palaeobot. Palynol. 71, 37–77.

Carrión, J.S., 2002. Patterns and processes of Late Quaternary environmental change in a montane region of Southwestern Europe. Quat. Sci. Rev. 21, 2047–2066.

Carrión, J.S., 2010. The concepts of potential natural vegetation and other abstractions (trying to pick up fish with wet hands). J. Biogeogr. 37, 2209–2215.

Carrión, J.S., Dupré, M., 1996. Late Quaternary vegetational history at Navarrés, eastern Spain. A two core approach. New Phytol. 134, 177–191.

Carrión, J.S., Sánchez-Gómez, P., 1992. Palynological data in support of the survival of walnut (*Juglans regia* L.) in the western Mediterranean area during last glacial times. J. Biogeogr. 19, 623–630.

Carrión, J.S., Munuera, M., Navarro, C., 1998. The palaeoenvironment of Carihuela Cave (Granada, Spain): a reconstruction on the basis of palynological investigations of cave sediments. Rev. Palaeobot. Palynol. 99, 117–144.

Carrión, J.S., Munuera, M., Navarro, C., Burjachs, F., Dupré, M., Walker, M., 1999. Palaeoecological potential of pollen records in caves: the case of Mediterranean Spain. Quat. Sci. Rev. 18, 67–78.

Carrión, J.S., Navarro, C., Navarro, J., Munuera, M., 2000. The interpretation of cluster pine (*Pinus pinaster*) in floristic-phytosociological classifications from a palaeoecological perspectiva. The Holocene 10, 243–252.

Carrión, J.S., Andrade, A., Bennett, K.D., Munuera, M., Navarro, C., 2001. Crossing forest thresholds: inertia and collapse in a Holocene pollen sequence from south-central Spain. The Holocene 11, 635–653.

Carrión, J.S., Riquelme, J.A., Navarro, C., Munuera, M., 2002. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 176, 193–205.

Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, El, Chaín, C., 2003a. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, Southern Spain. The Holocene 13, 839–849.

Carrión, J.S., Yll, E., Walker, M., Legaz, A., Chaíns, C., López, A., 2003b. Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neandertal man sites. Glob. Ecol. Biogeogr. 12, 119–129.

Carrión, J.S., Yll, E.I., Willis, K.J., Sánchez-Gómez, P., 2004. Holocene forest history of the eastern plateaux in the Segura Mountains (Murcia, southeastern Spain). Rev. Palaeobot. Palynol. 132, 219–236.

Carrión, J.S., Fuentes, N., González-Sampériz, P., Sánchez-Quirante, L.S., Finlayson, J.C., Fernández, S., Andrade, A., 2007. Holocene environmental change in a montane region of southern Europe with a long history of human settlement. Quat. Sci. Rev. 26, 1455–1475.

Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. Quat. Sci. Rev. 27, 2118–2135.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J.A., Fierro, E., Burjachs, F., 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Rev. Palaeobot. Palynol. 162, 458–475 Special issue: Carrión, J.S., Leroy, S. (Eds.), Iberian Floras through Time: Land of Diversity and Survival.

Carrión, J.S., Fernández, S., González-Sampériz, P., López-Merino, L., Peña, L., Burjachs, F., López-Sáez, J.A., García-Antón, M., Carrión-Marco, Y., Uzquiano, P., Postigo, J.M., Barrón, E., Allué, E., Badal, E., Dupré, M., Fierro, E., Munuera, M., Rubiales, J.M., García-Amorena, I., Jiménez-Moreno, G., Gil-Romera, G., Leroy, S., García-Martínez, M.S., Montoya, E., Fletcher, W., Yll, E., Vieira, M., Rodríguez-Ariza, M.O., Anderson, S., Peñalba, C., Gil-García, M.J., Pérez-Sanz, A., Albert, R.M., Díez, M.J., Morales, C., Gómez-Manzaneque, F., Parra, I., Ruiz-Zapata, B., Riera, S., Zapata, L., Ejarque, A., Vegas, T., Rull, V., Scott, L., Andrade, A., Pérez-Díaz, S., Abel-Schaad, D., Moreno, E., Hernández-Mateo, L., Ochando, J., Pérez Navarro, M.A., Sánchez Baena, J.J., Riquelme, J.A., Iglesias, R., Franco, F., Chaín, C., Figueiral, I., Grau, E., Matos, M., Jiménez-Espejo, F., Arribas, A., Garrido, G., Finlayson, G., Finlayson, C., Ruiz, M., Pérez-Jordá, G., Miras, Y., 2013. Paleoflora Ibérica: Plioceno-Cuaternario, 2 vols. Ministerio de Economía y Competitividad, Madrid. Universidad de Murcia y Fundación Séneca ISBN 84-616-6797-2.

Carrión, J.S., Fernández, S., González-Sampériz, P., López-Merino, L., Peña, L., Burjachs, F., López-Sáez, J.A., García-Antón, M., Carrión-Marco, Y., Uzquiano, P., Postigo, J.M., Barrón, E., Allué, E., Badal, E., Dupré, M., Fierro, E., Munuera, M., Rubiales, J.M., García-Amorena, I., Jiménez-Moreno, G., Gil-Romera, G., Leroy, S., García-Martínez, M.S., Montoya, E., Fletcher, W., Yll, E., Vieira, M., Rodríguez-Ariza, M.O., Anderson, S., Peñalba, C., Gil-García, M.J., Pérez-Sanz, A., Albert, R.M., Díez, M.J., Morales, C., Gómez-Manzaneque, F., Parra, I., Ruiz-Zapata, B., Riera, S., Zapata, L., Ejarque, A., Vegas, T., Rull, V., Scott, L., Andrade, A., Pérez-Díaz, S., Abel-Schaad, D., Moreno, E., Hernández-Mateo, L., Ochando, J., Pérez Navarro, M.A., Sánchez-Baena, J.J., Riquelme, J.A., Iglesias, R., Franco, F., Chaín, C., Figueiral, I., Grau, E., Matos, M., Jiménez-Espejo, F., Arribas, A., Garrido, G., Finlayson, G., Finlayson, C., Ruiz, M., Pérez-Jordá, G., Miras, Y., 2015. Cinco Millones de años de Cambio florístico Y Vegetal en la Península Ibérica e Islas Baleares. Ministerio de Economía y Competitividad, Madrid https://play.google.com/store/books/details/JOS%C3%89_CARRI%C3%93N_coordinador_CINCO_MILLONES_DE_A%C3%91OS_DE?id=JEh1CQAAQBAJ.

Carrión, J.S., Ochando, J., Fernández, S., Munuera, M., Amorós, G., Blasco, R., Rosell, J., Finlayson, S., Giles, F., Jennings, R., Finlayson, G., Giles-Pacheco, F., Rodríguez-Vidal, J., Finlayson, C., 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard Cave. Rev. Palaeobot. Palynol. Special Issue (Carrión, J. S., deMenocal, P., Scott, L., eds.): Human evolution and palaeofloras: the contribution and potential of palaeobotany in the environmental reconstruction of hominin-bearing sites. Rev. Palaeobot. Palynol. 259, 63–80.

Carrión, J.S., Fernández, S., Jiménez, J., Munuera Giner, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, Ch., Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. Quat. Sci. Rev. 217, 194–216.

Carrión-Marco, Y., 2005. La vegetación mediterránea y atlántica de la península Ibérica. Nuevas secuencias antracológicas. Trabajos Varios de S.I.P. (Servicio de Investigación Prehistórica) 104, 314.

Chabaud, L., Sánchez Goñi, M.F., Stéphanie Desprat, S., Rossignol, L., 2014. Land–sea climatic variability in the eastern North Atlantic subtropical region over the last 14,200 years: atmospheric and oceanic processes at different timescales. The Holocene 24, 787–797.

Combourieu Nebout, N., Peyron, O., Dormoy, I., Desprat, S., Beaudouin, C., Kotthoff, U., Marret, F., 2009. Rapid climatic variability in the west Mediterranean during the last 25 000 years from high resolution pollen data. Clim. Past 5, 503–552.

Connor, S.E., Vannière, B., Colombaroli, D., Anderson, R.S., Carrión, J.S., Ejarque, A., Gil Romera, G., González-Sampériz, P., Hoefer, D., Morales-Molino, C., Revelles, J., Schneider, H., van der Knaap, W.O., Van Leeuwen, J.F., Woodbridge, J., 2019. Humans take control of fire-driven diversity changes in Mediterranean Iberia's vegetation during the mid–late Holocene. The Holocene 29, 886–901.

Cortés-Sánchez, M., Morales Muñiz, A., Simón Vallejo, M.D., Bergadà Zapata, M.M., Delgado Huertas, A., López García, P., López-Sáez, J.A., Lozano Francisco, M.C., Riquelme Cantal, J.A., Roselló Izquierdo, E., Sánchez Marco, A., Vera-Peláez, J.L., 2008. Paleoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. Quat. Sci. Rev. 27, 2176–2193.

Costa Tenorio, M., Morla Juaristi, C., Sainz Ollero, H., Blanco, E., Casado, M.A., Escribano, R., García, M., Génova, M., Gómez, A., Gómez, F., Moreno, J.C., Regato, P., 1997. Los Bosques ibéricos. Una interpretación geobotánica, Planeta, Barcelona ISBN 9788408058205.

Delcourt, A., Mullenders, W., Piérard, P., 1959. La préparation des spores et des grains de pollen actuels et fossiles. Les naturalistes belges 40, 91–120.

Díaz-Paniagua, C. (Coord.), 2015. El Sistema de Lagunas Temporales de Doñana, una red de hábitats acuáticos singulares. Organismo Autónomo de Parques Nacionales. Miniterio de Agricultura, Alimentación y Medio Ambiente, p. 289 ISBN: 978-84-8014-880-1.

Díaz-Paniagua, C., Aragonés, D., 2015. Permanent and temporary ponds in Doñana National Park (SW Spain) are threatened by desiccation. Limnetica 34, 407–424.

Dimbleby, G.W., 1985. The Palynology of Archaeological Sites. Academic Press, London.

Dormoy, I., Peyron, O., Nebout, N.C., Goring, S., Kotthoff, U., Magny, M., Pross, J., 2009. Terrestrial climate variability and seasonality changes in the Mediterranean region between 15 000 and 4000 years BP deduced from marine pollen records. Clim. Past 5, 615–632.

Dupré, M., 1980. Análisis polínico de sedimentos arqueológicos de la cueva de Les Malladetes (Barx, Valencia). Cuadernos de Geografía 26, 1–22.

Ejarque, A., Julià, R., Riera, S., Palet, J.M., Orengo, H.A., Miras, Y., Gascón, C., 2009. Tracing the history of highland human management in the eastern Pre-Pyrenees: an interdisciplinary palaeoenvironmental study at the Pradell fen, Spain. The Holocene 19, 1241–1255.

Feddi, N., Fauquette, S., Suc, J.-P., 2011. Histoire plio-pléistocène des écosystèmes végétaux de Méditerranéesud-occidentale: apport de l'analyse pollinique de deux sondagesen mer d'Alboran. Geobios 44, 57–69.

Fernández, S., Carrión, J.S., Fuentes, N., González-Sampériz, P., Montoya, E., Gil-Romera, G., Vega-Toscano, L.G., Riquelme, J.A., 2007. Palynology of Carihuela Cave, southern Spain: completing the record. Geobios 40, 75–90.

Fernández, S., Ochando, J., Munuera, M., Amorós, G., Carrión, J.S., 2018. Forests in movement. Cauistry during the late Quaternary in the Iberian Peninsula. Ameghiniana. Gondw. Paleontol. J. 18, 171–197.

Finlayson, G., 2006. Climate, Vegetation and Biodiversity. A multi-scale study of the south of the Iberian Peninsula. Ph. D. Thesis. Anglia Ruskin University, Cambridge.

Finlayson, S., 2020. Birds in the Neanderthal Ecological Niche – Using Birds from Pleistocene Cave Archives to Characterise the Relationship between Neanderthals and Birds. Ph. D. Thesis. Anglia Ruskin University, Cambridge.

Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends Ecol. Evol. 22, 213–222.

Finlayson, C., Giles Pacheco, F., Rodríguez-Vidal, J., Fa, D., Gutiérrez, J.M., Santiago, A., Finlayson, G., Allué, E., Baena, J., Cáceres, I., Carrión, J.S., Fernández-Jalvo, Y., Gleed-Owen, P., Jiménez Espejo, F.J., López, P., López Sáez, J.A., Riquelme, J.A., Sánchez Marco, A., Giles Guzmán, F., Brown, K., Fuentes, N., Valarino, C., Villalpando, A., Stringer, C.B., Martínez Ruíz, F., Sakamoto, T., 2006. Late survival of Neanderthals at the southernmost extreme of Europe. Nature 443, 850–853.

Fletcher, W.J., Sánchez-Goñi, M.F., 2008. Orbital- and sub-orbital-scale climate impacts on vegetation of the western Mediterranean basin over the last 48,000 yr. Quat. Res. 70, 451–464.

Fletcher, W.J., Boski, T., Moura, D., 2007. Palynological evidence for environmental and climatic change in the lower Guadiana valley, Portugal, during the last 13 000 years. The Holocene 17, 481–494.

Fletcher, W.J., Sánchez-Goñi, M.F., Peyron, O., Dormoy, I., 2010. Abrupt climate changes of the last deglaciation detected in a Western Mediterranean forest record. Climate of the Past, European Geosciences Union (EGU), 2010. 6, pp. 245–264.

Franco Múgica, F., García Anton, M., Sainz Ollero, H., 1998. Vegetation dynamics and human impact in the Sierra de Guadarrama, central system, Spain. Holocene 8, 69–82.

Franco-Múgica, F., García-Antón, M., Maldonado Ruiz, J., Morla, C., Sainz-Ollero, H., 2001. The Holocene history of Pinus forests in the Spanish Northern Meseta. The Holocene 11, 343–358.

Franco-Múgica, F., García-Antón, M., Maldonado Ruiz, J., Morla, C., Sainz-Ollero, H., 2005. Ancient pine forest on inland dunes in the Spanish northern meseta. Quat. Res. 63, 1–14.

Fuentes, N., Carrión, J.S., Fernández, S., Nocete, F., Lizcano, R., Pérez Bareas, C., 2007. Análisis polínico de los yacimientos arqueológicos Cerro del Alcázar de Baeza y Eras del Alcázar de Úbeda (Jaén). An. Biol. 29, 85–93.

García López, J.M., Allué Camacho, C., 2005. Caracterización y potencialidades fitoclimáticas de abetales (*Abies alba* Mill.) en la península ibérica. Ecología 19, 11–28.

García Murillo, P., 2001. Restauración del Complejo Palustre del Abalario: la reconstrucción del paisaje. In: Ministerio de Medio Ambiente (Ed.), En: 1ª Reunión Internacional de Expertos sobre la Regeneración Hídrica de Doñana. Ponencias y Conclusiones. Ministerio de Medio Ambiente, Madrid, pp. 117–130.

García Murillo, P., 2005. Reconstrucción del paisaje del Abalario: un referente para la restauración ambiental en Doñana. En. In: Agua y Biosfera, Doñana, Martín, C., García Novo, F. (Eds.), Conferederación Hidrográfica del Guadalquivir, Ministerio de Medio Ambiente. Madrid, pp. 271–275.

García Murillo, P., 2007. Flora, vegetation and climatic changes. (Coords.). In: Sousa, A., García-Barrón, L., Jurado, V. (Eds.), El cambio climático en Andalucía: evolución y consecuencias medioambientales. Consejería de Medio Ambiente (Junta de Andalucía), pp. 155–166.

García Murillo, P., 2018. El incendio de Las Peñuelas de 2017. In: Novo, Garcia, Casal, Pausas (Eds.), Ecología de la regeneración de zonas incendiadas. Academia de Ciencias Sociales y del Medio Ambiente de Andalucía. Sevilla, pp. 175–195 ISBN 978-84-09-05946-1.

García Murillo, P., Sousa, A., 1997. Vegetation changes in Abalario (Natural Park Entorno de Doñana, SW of Spain). Lagascalia 19, 737–744.

García Murillo, P., Sousa, A., 1999. El Paisaje vegetal de la zona oeste del Parque Natural de Doñana (Huelva). Lagascalia 21, 111–132.

García-Amorena, I., Gómez-Manzaneque, F., Rubiales, J.M., Granja, H.M., Soares, G., Morla, C., 2007. The Late Quaternary coastal forests of western Iberia: a study of their macroremains. Palaeogeogr. Palaeoclimatol. Palaeoecol. 254, 448–461.

García-Antón, M., Sainz-Ollero, H., 1991. Pollen recordsnfrom the Middle Pleistocene Atapuerca site (Burgos, Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 85, 199–206.

García-Antón, M., Morla, C., Sainz-Ollero, H., 1990. Consideraciones sobre la presencia de algunos táxones relictos terciarios durante el Cuaternario en la Península Ibérica. Bol. Real Soc. Esp. Hist. Nat. (Sección Biol.) 86, 95–105.

García-Antón, M., Franco-Múgica, F., Maldonado Ruiz, J., Morla, C., Sainz-Ollero, H., 1997. New data concerning the evolution of the vegetation in Lillo Pinewood (León, Spain). J. Biogeogr. 24, 929–934.

García-Antón, M., Franco-Múgica, F., Morla, C., Maldonado Ruiz, J., 2011. The biogeographical role of Pinus forest on the Central Spanish Meseta: a new Holocene sequence. Quat. Sci. Rev. 30, 757–768.

García-Rivero, D., Taylor, R., Pérez-Aguilar, L.G., Pérez-Jordá, G., García-Viñas, E., López-Sáez, J.A., Zurro, D., Peña Chocarro, L., Bernáldez Sánchez, E., 2018. Andalusi populations at La Dehesilla Cave (Sierra de Cádiz, Southern Iberia): an interdisciplinary approach to their rural economic systems. J. Islam. Archaeol. 5, 119–151.

García-Rivero, D., Pérez Jordá, G., García Viñas, E., López-Sáez, J.A., Taylor, R., Peña Chocarro, L., Bernáldez, E., Pérez Díaz, S., 2019. Ecological patterns and use of natural resources during the Neolithic of the south of the Iberian Peninsula: an update from the 6th to 4th millennia cal BC sequence of Dehesilla Cave. Quat. Sci. Rev. 219, 218–235.

Gil, L., 1991. Consideraciones históricas sobre *Pinus pinaster* Aiton en el paisaje vegetal de la Península Ibérica. Estud. Geogr. 202, 5–27.

Gil, L., Gordo, J., Alía, R., Catalán, G., Pardos, J.A., 1990. *Pinus pinaster* Aiton en el paisaje vegetal de la Península Ibérica. Ecol. fuera de serie 1, 469–495.

Gil-Romera, G., Carrión, J.S., McClure, S., Schmich, S., Finlayson, C., 2009. Holocene vegetation dynamics in Mediterranean Iberia: historical contingency and climatehuman interactions. J. Anthropol. Res. 65, 271–285.

Gil-Romera, G., Carrión, J.S., Pausas, J.G., Sevilla-Callejo, M., Lamb, H.F., Fernández, S., Burjachs, F., 2010. Holocene fire activity and vegetation response in South Eastern Iberia. Quat. Sci. Rev. 29, 1082–1092.

Girard, M., Renault-Miskovsky, J., 1969. Nouvelles techniques de preparation en palynologie appliques a trois sediments du Quaternaire final de l'Abri Corneille (lstres-Bouches-du-Rhone). Bull. Assoc. Fr. Et. Quat. 4 (275), 284.

González-Sampériz, P., Leroy, S., Carrión, J.S., García-Antón, M., Gil-García, M.J., Figueiral, I., 2010. Steppes, savannahs and botanic gardens during the Pleistocene. Rev. Palaeobot. Palynol. Spec. 162, 427–457.

González-Sampériz, P., Gil-Romera, G., García-Prieto, E., Aranbarri, J., Moreno, A., Morellón, M., Sevilla-Callejo, M., Leunda, M., Santos, L., Franco-Múgica, F., Andrade, A., Carrión, J.S., Valero-Garcés, B.L., 2020. Strong continentality and effective moisture drove unforeseen vegetation dynamics since the last interglacial at inland Mediterranean areas: the Villarquemado sequence in NE Iberia. Quat. Sci. Rev. 242, 106425.

Granados Corona, M., 1987. Transformaciones Historicas de los Ecosistemas del Parque Nacional de Doñana. Tesis Doctoral. Universidad de Sevilla.

Hooghiemstra, H., Stalling, H., Agwu, C.O.C., Dupont, L.M., 1992. Vegetational and climaticchanges at the northern fringe of the Sahara 250,000–5000 years BP: evidence from 4 marine pollen records located between Portugal and the Canary Islands. Rev. Palaeobot. Palynol. 74, 1–53.

Jennings, R., Finlayson, C., Fa, D., Finlayson, G., 2011. Southern Iberia as a refuge for the last Neanderthal populations. J. Biogeogr. https://doi.org/10.1111/j.1365-2699.2011.02536.x. http://wileyonlinelibrary.com/journal/jbi.

Jiménez Espejo, F., Martínez Ruiz, F., Finlayson, C., Paytan, A., Sakamoto, T., Ortega Huertas, M., Finlayson, G., Iijima, K., Gallego Torres, D., Fa, D., 2007. Climate forcing and Neanderthal extinction in Southern Iberia: insights from a multiproxy marine record. Quat. Sci. Rev. 26, 836–852.

Jiménez Espejo, F.J., García Alix, A., Jiménez Moreno, G., Rodrigo Gámiz, M., Anderson, R.S., Rodríguez Tovar, F.J., Martínez Ruiz, F., Giralt, S., Delgado Huertas, A., Pardo Igúzquiza, E., 2014. Saharan aeolian input and effective humidity variationsover western europe during the holocene from high altitude record. Chem. Geol. 374-375, 1–12.

Jiménez-Moreno, G., Rodríguez-Ramírez, A., Pérez-Asensio, J.N., Carrión, J.S., López-Sáez, J.A., Villarías-Robles, J.J.R., Celestino-Pérez, S., Cerrillo-Cuenca, E., León, A., Contreras, C., 2015. Impact of late-Holocene aridification trend, climate variability and geodynamic control on the environment from a coastal area in SW Spain. The Holocene 25, 607–617.

Jiménez-Moreno, G., Pérez-Asensio, J.N., Larrasoaña, J.C., Sierro, F.J., Garcia-Castellanos, D., Salazar, A., Salvany, J., Ledesma, S., Mata, M.P., Mediavilla, C., 2019. Early Pliocene climatic optimum, cooling and early glaciation deduced by terrestrial and marine environmental changes in SW Spain. Glob. Planet. Change. 180, 89–99.

López Albacete, I., 2009. Vegetación del manto eólico de Doñana. Ph. D. Thesis. Universidad de Huelva.

López González, G., 2001. Los árboles y arbustos de la Península Ibérica e Islas Baleares. Mundi Prensa Libros ISBN: 84-7114-953-2.

López-Merino, L., López-Sáez, J.A., Alba Sánchez, F., Pérez Díaz, S., Carrión, J.S., 2009. 2,000 yr of pastoralism and fire shaping high-altitude vegetation of Sierra de Gredos in central Spain. Rev. Palaeobot. Palynol. 158, 42–51.

López-Sáez, J.A., van Geel, B., Martín Sánchez, M., 2000. Aplicación de los microfósiles no polínicos en Palinología Arqueológica. (Coord. Ed.). In: Oliveira Jorge, V. (Ed.), Contributos das Ciências e das Technologias para a Arqueologia da Península Ibérica. Actas 3° Congresso de Arqueologia Peninsular. vol. 9. Vila-Real, Portugal. Adecap, Porto, pp. 11–20.

López-Sáez, J.A., López-García, P., Martín-Sánchez, M., 2001. Análisis palinológico del yacimiento arqueológico de Pocito Chico (El Puerto de Santa María): el paisaje prehistórico y protohistórico durante el Holoceno reciente en las Marismas de Cádiz. Cuat. Geomor. 15, 45–59.

López-Sáez, J.A., López-García, P., Martín-Sánchez, M., 2002. Palaeoecology and Holocene environmental change from a saline lake in south-West Spain: the Protohistorical and prehistorical vegetation in Cádiz Bay. Quat. Int. 93–94, 197–206.

López-Sáez, J.A., López-García, P., Cortés Sánchez, M., 2007. Paleovegetación del Cuaternario reciente: Estudio arqueopalinológico. In: Cortés Sánchez, M. (Ed.), Cueva Bajondillo (Torremolinos). Secuencia cronocultural y paleoambiental del Cuaternario reciente en la Bahía de Málaga. Centro de Ediciones de la Diputación de Málaga, Junta de Andalucía. Universidad de Málaga, Fundación Cueva de Nerja y Fundación Obra Social de Unicaja, Málaga, pp. 139–156.

López-Sáez, J.A., López-Merino, L., Pérez-Díaz, S., 2008. History of the vegetation: an archeopalynological approach. ANTIQVITAS 20, 41–47.

López-Sáez, J.A., Pérez-Díaz, S., Rodríguez-Ramírez, A., Blanco-González, A., Villarías-Robles, J.J.R., Luelmo-Lautenschlaeger, R., Jiménez-Moreno, G., Celestino-Pérez, S., Cerrillo-Cuenca, E., Pérez-Asensio, J.N., León, A., 2018. Mid-late Holocene environmental and cultural dynamics at the south-west tip of Europe (Doñana National Park, SW Iberia, Spain). J. Archaeol. Sci. Rep. 22, 58–78.

López-Sáez, J.A., Carrasco, R.M., Turu, V., Ruíz-Zapata, B., Gil-García, M.J., Luelmo-Lautenschlaeger, R., Pérez-Díaz, S., Alba-Sánchez, F., Abel-Schaad, D., Ros, X., Pedraza, J., 2020a. Late Glacial-early holocene vegetation and environmental changes in the western Iberian Central System inferred from a key site: the Navamuño record, Béjar range (Spain). Quat. Sci. Rev. 230, 106167.

López-Sáez, J.A., Camarero, J.J., Abel-Schaad, D., Luelmo-Lautenschlaeger, R., Pérez-Díaz, S., Alba-Sánchez, F., Carrión, J.S., 2020b. Don't lose sight of the forest for the trees! Discerning Iberian pine communities by means of pollen-vegetation relationships. Rev. Palaeobot. Palynol. 281, 104285.

Magri, D., Di Rita, F., Arambarri, J., Fletcher, W., González-Sampériz, P., 2017. Quaternary disappearance of tree taxa from Southern Europe: timing and trends. Quat. Sci. Rev. 163, 23–55.

Manzano, S., Carrión, J.S., López-Merino, L., Ochando, J., Munuera, M., Fernández, S., González-Sampériz, P., 2018. Early to Mid-Holocene spatiotemporal vegetation changes and tsunami impact in a paradigmatic coastal transitional system (Doñana National Park, southwestern Europe). Glob. Planet. Change. 161, 66–81.

Manzano, S., Carrión, J.S., García-Murillo, P., López-Merino, L., 2019. When dynamism is the baseline: long-term ecology of a Mediterranean seasonal wetland in the Doñana National Park (Southwestern Europe). Biodivers. Conserv. 28, 501–522.

MARGO Project Members, 2009. Constraints on the magnitude and patterns of ocean cooling at the Last Glacial Maximum. Nat. Geosci. 2, 127–132.

Martínez, F., Montero, G., 2004. The *Pinus pinea* L. woodlands along the coast of South-western Spain: data for a new geobotanical interpretation. Plant Ecol. 175, 1–18.

Menendez Amor, J., Florschutz, F., 1964. Resultados del análisis paleobotánico de una capa de turba en las cercanías de Huelva (Andalucía). Estud. Geol. 20, 183–186.

Morales-Molino, C., Postigo-Mijarra, J.M., García-Antón, M., Zazo, C., 2011. Vegetation and environmental conditions in the Doñana Natural Park coastal area (SW Iberia) at the beginning of the last glacial cycle. Quat. Res. 75, 205–212.

Morales-Molino, C., Postigo-Mijarra, J.M., Morla, C., García-Antón, M., 2012. Longterm persistence of mediterranean pine forest in the duero basin (central Spain) during the Holocene: the case of *Pinus pinaster* aiton. Holocene 22, 561–570.

Morales-Molino, C., García-Antón, M., Postigo-Mijarra, J., Morla, C., 2013. Holocene vegetation, fire and climate interactions on the westernmost fringe of the Mediterranean Basin. Quat. Sci. Rev. 59, 5–17.

Morales-Molino, C., Tinner, W., Garcia-Anton, M., Colombaroli, D., 2017. The historical demise of *Pinus nigra* forest in the Northern Iberian Plateau (south-western Europe). J. Ecol. 105, 634–646.

Morales-Molino, C., Colombaroli, D., Tinner, W., Perea, R., Valbuena-Carabaña, M., Carrión, J.S., Gil, L., 2018. Vegetation and fire dynamics during the last 4000 years in the Cabañeros National Park (central Spain). Rev. Palaeobot. Palynol. 253, 110–122.

Muñiz, F., Mayoral, E., Barrón, E., Cachão, M., 1999. Nuevos datos sobre macroflora del Plioceno en el Suroeste de la Península Ibérica (Lepe, Huelva, España). Geogaceta 25, 143–146.

Naughton, F., Costas, S., Gomes, S.D., Desprat, S., Rodrigues, T., Sanchez Goñi, M.F., Renssen, H., Trigo, R., Bronk-Ramsey, C., Oliveira, D., Salgueiro, E., Voelker, A.H.L., Abrantes, F., 2019. Coupled ocean and atmospheric changes during Greenland stadial 1 in southwestern Europe. Quat. Sci. Rev. 212, 108–120.

Ochando, J., López-Sáez, J.A., Pérez-Díaz, S., Ramos-Fernández, J., Munuera, M., Fernández, S., Galacho-Jiménez, F.B., Luelmo-Lautenschlaeger, R., Carrión, J.S., 2020. A new pollen sequence from southern Iberia suggesting coastal Pleistocene phytodiversity hotspot. Rev. Palaeobot. Palynol. 281, 104281.

Ojeda Ribera, F., 1987. Organización del territorio en Doñana y su entorno próximo (Almonte): Siglos XVII-XX. Madrid. Pesca y Alimentación, Ministerio de Agricultura.

Ojeda Ribera, F., 1992. Políticas forestales y medio ambiente en Doñana y su entorno. Agric. Soc. 11, 303–357.

Ojeda Ribera, F., Marañón, T., Arroyo, J., 1996. Patterns of ecological, chorological and taxonomic diversity at both sides of the Strait of Gibraltar. J. Veg. Sci. 7, 63–72.

Oliveira, D., Desprat, S., Yin, Q., Naughton, F., Trigo, R., Rodrigues, T., Abrantes, F., Sánchez Goñi, M.F., 2018. Unraveling the forcings controlling the vegetation and climate of the best orbital analogues for the present interglacial in SW Europe. Clim. Dyn. 51, 667–686.

Pailler, D., Bard, E., 2002. High frequency palaeoceanographic changes during the past 140,000 yr recorded by the organic matter in sediments of the Iberian margin. Palaeogeogr. Palaeoclimatol. Palaeoecol. 181, 431–452.

Pantaleón-Cano, J., Yll, E.I., Pérez-Obiol, R., Roure, J.M., 2003. Palynological evidence for vegetational history in semi-arid areas of the western Mediterranean (Almería, Spain). The Holocene 13, 109–119.

Parra, I., 1994. Quantification des precipitations à partir des espectres polliniques actuels et fossils: du Tardiglaciaire à l'Holocène supérieur de la côte méditerranéenne espagnole. Tesis doctoral. Université Montpellier II, France, p. 217.

Peña-Chocarro, L., 2007. Early agriculture in southern and central Spain. In: Colledge, S., Conolly, J. (Eds.), The Origins and Spread of Domestic Plants in Southwest Asia and Europe. Left Coast Press & UCL, California, pp. 173–187.

Peñalba, C., 1985. Estudio esporopolínico del Neógeno Occidental de la Cuenca del Guadalquivir. M.Sc. Thesis. Univ, Salamanca, Spain.

Pérez Latorre, A.V., Galán de Mera, A., Cabezudo, B., 1999. Propuesta de aproximación a la sintaxonomía de las formaciones de gimnospermas de la provincia Bética (España). Acta Bot. Malac. 24, 257–262.

Polyak, V.J., Onac, B.P., Fornós, J.J., Hay, C., Asmeron, Y., Dorale, J.A., Ginés, J., Tuccimei, P., Ginés, A., 2018. A highly resolved record of relative sea level in the western Mediterranean Sea during the last interglacial period. Nat. Geosci. 11, 860–864.

Pons, A., Reille, M., 1988. The Holocene and Upper Pleistocene pollen record from Padul (Granada, Spain): a new study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 66, 243–263.

Postigo-Mijarra, J.M., Gómez-Manzaneque, F., Morla, C., 2008. Survival and long-term maintenance of tertiary trees in the Iberian Peninsula during the Pleistocene. First record of *Aesculus* L. (Hippocastanaceae) in Spain. Veg. Hist. Archaeobot. 17, 351–364.

Postigo-Mijarra, J.M., Barrón, E., Gómez-Manzaneque, F., Morla, C., 2009. Floristic changes in the Iberian Peninsula and the Balearic Islands during the Cenozoic. J. Biogeogr. 36, 2025–2043.

Postigo-Mijarra, J.M., Gómez Manzaneque, F., Morla Juaristi, C., Zazo, C., 2010a. Palaeoecological significance of late Pleistocene pine macrofossils in the lower Guadalquivir Basin (Doñana natural park, southwestern Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 295, 332–343.

Postigo-Mijarra, J.M., Morla, C., Barrón, E., Morales-Molino, S., García, S., 2010b. Patterns of extinction and persistence of Arctotertiary flora in Iberia during the Quaternary. Rev. Palaeobot. Palynol. 162, 416–426.

Reed, J.M., Stevenson, A.C., Juggins, S., 2001. A multi-proxy record of Holocene climatic change in southwestern Spain: the Laguna de Medina, Cadiz. Holocene 11, 707–719.

Rivas Martínez, S., 2011. Mapa de series, geoseries y geopermaseries de vegetación de España (Memoria del mapa de vegetación potencial de España). Itinera Geobot. 18, 1–2.

Rivas-Carballo, M.R., Valle, M.F., 2005. Polen y dinoflagelados del límite Tortoniense/ Messiniense del sondeo de testigo continuo «Huelva» (Cuenca del Guadalquivir, España). Interpretación paleoambiental Revista de la Sociedad Geológica de España 18, 233–239.

Rivas-Martínez, S., 1987. Nociones sobre Fitosociología, Biogeografía y Bioclimatología. In: Peinado, M., Rivas-Martínez, S. (Eds.), La vegetación de España, pp. 19–45.

Rodríguez-Vidal, J., Bardají, T., Zazo, C., Goy, J.L., Borja, F., Dabrio, C.J., Lario, J., Cáceres, L.M., Ruiz, F., Abad, M., 2014. Coastal dunes and marshes in Doñana National Park. In: Gutiérrez, F., Gutiérrez, M. (Eds.), Landscape and landforms of Spain. Serie: World Geomorphological Landscapes. Springer Science + Business Media, Dordrecht, pp. 229–238.

Roucoux, K.H., Tzedakis, P.C., de Abreu, L., Shackleton, N.J., 2006. Climate and vegetation changes 180,000 to 345,000 years ago recorded in a deep-sea core off Portugal. Earth Planet. Sci. Lett. 249, 307–325.

Rubiales, J.M., García-Amorena, I., García-Álvarez, S., Gómez-Manzaneque, F., 2008. The Late Holocene extinction of *Pinus sylvestris* in the western Cantabrian Range (Spain). J. Biogeogr. 35, 1840–1850.

Rubiales, J.M., García-Amorena, I., García-Álvarez, S., Morla, C., 2009. Anthracological evidence suggests naturalness of *Pinus pinaster* in inland southwestern Iberia. Plant Ecol. 200, 155–160.

Rubiales, J.M., García-Amorena, I., Hernández, L., Génova, M., Martínez, F., Gómez-Manzaneque, F., Morla, C., 2010. Late Quaternary dynamics of pinewoods in the Iberian Mountains. Rev. Palaeobot. Palynol. 162, 476–491.

Ruiz-Zapata, M.B., Gil-García, M.J., Dorado-Valiño, M., Valdeolmillos, A., Pérez-González, A., 2002. Clima y vegetación durante el Tardiglaciar y Holoceno en la Sierra de Neila (Sistema Ibérico Noroccidental). Rev. Cuat. Geo. 16, 9–20.

Salvany, J.M., Custodio, E., 1995. Características litoestratigráficas de los depósitos pliocuaternarios del bajo Guadalquivir en el área de Doñana: implicaciones hidrogeológicas. Rev. Soc. Geol. Esp. 8, 21–31.

Salvany, J.M., Larrasoaña, J.C., Mediavilla, C., Rebollo, A., 2011. Chronology and tectono-sedimentary evolution of the Upper Pliocene to Quaternary deposits of the lower Guadalquivir foreland basin, SW Spain. Sediment. Geol. 241, 22–39.

Sánchez-Goñi, M.F., Harrison, S., 2010. Millennial-scale climate variability and vegetation changes during the Last Glacial: concepts and terminology. Quat. Sci. Rev. 29, 2823–2827.

Sánchez-Goñi, M.F., Eynaud, F., Turon, J.L., Shackleton, N.J., 1999. High resolution palynological record off the Iberian margin: direct land-sea correlation for the Last Interglacial complex. Earth Planet. Sci. Lett. 171, 123–137.

Sancho Royo, F., Fernández-Palacios, J.M., García Murillo, P., Espina Argüello, J., Olmedo Granados, F., Estévez Herranz, A., 2018. El Abalario, un paisaje en construcción. Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía ISBN: 978-84-16591-06-0.

Schneider, H., Höfer, D., Trog, C., Busch, S., Schneider, M., Baade, J., Daut, G., Maüsbacher, R., 2010. Holocene estuary development in the Algarve Region (Southern Portugal)– a reconstruction of sedimentological and ecological evolution. Quat. Int. 221, 141–158.

Schröder, T., van't Hoff, J., López-Sáez, J.A., Viehberg, F., Melles, M., Reicherter, K., 2018. Holocene climatic and environmental evolution on the southwestern Iberian Peninsula: a high-resolution multi-proxy study from Lake Medina (Cádiz, SW Spain). Quat. Sci. Rev. 198, 208–225.

Schröder, T., López-Sáez, J.A., van't Hoff, J., Reicherter, K., 2020. Unravelling the Holocene environmental history of south-western Iberia through a palynological study of Lake Medina sediments. The Holocene 30, 13–22.

Sousa, A., García-Murillo, P., Morales, J., García-Barrón, L., 2009. Anthropogenic and natural effects on the coastal lagoons in the southwest of Spain (Don˜ana National Park). ICES J. Mar. Sci. 66, 1508–1514.

Stevenson, A.C., 1981. Pollen studies in semi-arid environments: N.E. Irán and S.W. Spain. Tesis doctoral. University of London.

Stevenson, A.C., 1984. Studies on the vegetational history of S.W. Spain. III. Palynological investigations at El Asperillo, Huelva. J. Biogeogr. 11, 527–551.

Stevenson, A.C., 1985. Studies in the vegetational history of S.W. Spain. II. Palynological investigations at Laguna de las Madres. J. Biogeogr. 12, 293–314.

Stevenson, A.C., Harrison, R.J., 1992. Ancient forests in spain: a model for land-use and dry forest management in south-west Spain from 4000 BC to 1900 AD. Proc. Prehist. Soc. 58, 227–247.

Stevenson, A.C., Moore, P.D., 1988. Studies in the vegetational history of S.W. Spain. IV: palynological investigations at El Acebrón, Huelva. J. Biogeogr. 15, 339–361.

Stockmar, J., 1971. Tablets spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Stuiver, M., Reimer, P.J., Reimer, R.W., 2020. CALIB 8.2 (WWW program) at. http://calib.org accessed 2021-02-04.

Suc, J.P., Cravatte, J., 1982. Étude palynologique du Pliocène de Catalogne (Nord-Est de l'Espagne). Apports à la connaissance de l'histoire climatique de la Méditerranée occidentale et implications chronostratigraphiques. Paléobiol. continentale 13, 1–31.

Turon, J.L., Lézine, A.M., Denèfle, M., 2003. Land-sea correlations for the last glaciation inferred from a pollen and dinocyst record from the Portuguese margin. Quat. Res. 59, 88–96.

Valle, M.F., Peñalba, C., 1987. Aspectos palinológicos en el Neógeno del Suroeste de España. Paleontología del neógeno de Huelva (W. Cuenca del Guadalquivir). Ed. Dpto. de Pleontología. Universidad de Salamanca, pp. 153–158.

Valle, M.F., Rivas Carballo, M.R., 1990. Palinología del Triásico Tortoniense-Messiniense en las facies neógenas del borde norte de la Cuenca del Guadalquivir (E. de Sevilla). In: Blanca, G., et al. (Eds.), Polen, Esporas y sus aplicaciones, pp. 453–457.

Verdú, M., Pausas, J.G., Postigo-Mijarra, J.M., Barrón, E., Casas-Gallego, M., Arroyo, J., Carrión, J.S., 2020. Phylogenetic diversity in the Iberian flora through the Cenozoic. Environ. Exp. Bot. 170, 103888.

Yáñez, C., Rodríguez, A., Carrión, J.S., 2007. Cambios en la vegetación de la franja litoral de las marismas de Doñana durante el Holoceno reciente. An. Biol. 28, 85–94.

Yll, E.I., Roure, J.M., Pantaleón-Cano, J., Pérez-Obiol, R., 1994. Análisis polínico de una secuencia holocénica en Roquetas de Mar (Almería). In: Mateu, I., Dupré, M., Güemes, J., Burgaz, M.E. (Eds.), Trabajos de palinología básica y aplicada. Editiones de la Universitat de València, València, pp. 189–198.

Yll, E.I., Zazo, C., Goy, J.L., Pérez-Obiol, R., Pantaleón-Cano, J., Civis, J., Dabrio, C., González, A., Borja, F., Soler, V., Lario, J., Luque, L., Sierro, F., González-Hernández, F.M., Lezine, A.M., Denèfle, M., Roure, J.M., 2003. Quaternary palaeoenvironmental changes in South Spain. In: Ruiz-Zapata, M.B., Dorado, M., Valdeolmillos, A., Gil-García, M.J., Bardají, T., de Bustamante, I., Martínez, I. (Eds.), Quaternary climatic changes and environmental crises in the Mediterranean Region. International Union for Quaternary Research (INQUA), Madrid, pp. 1–13.

Zapata, L., Peña-Chocarro, L., Pérez-Jordà, G., Stika, H.P., 2005. Difusión de la agricultura en la Península Ibérica. In: Arias, P., Ontañón, R., García-Moncó, C. (Eds.), Actas del III Congreso del Neolítico en la Península Ibérica. Santander.

Zazo, C., Dabrio, C.J., Borja, F., Goy, J.L., Lezine, A.M., Lario, J., Polo, D.M., Hoyos, M., Boersma, J.R., 1999. Pleistocene and Holocene aeolian facies along the Huelva coast (southern Spain): climatic and neotectonic implications. Geol. Mijnb. 77, 209–224.

Zazo, C., Mercier, N., Silva, P.G., Dabrio, C.J., Goy, J.L., Roquero, E., Soler, V., Borja, F., Lario, J., Polo, D., de Luque, L., 2005. Landscape evolution and geodynamic controls in the Gulf of Cadiz (Huelva coast, SW Spain) during the Late Quaternary. Geomorphology 68, 269–290.

Zazo, C., Dabrio, C.J., Goy, J.L., Borja, F., Silva, P.G., Lario, J., Roquero, E., Bardají, T., Cabero, A., Polo, D., Borja, C., 2011. El complejo eólico de El Abalario (Huelva). En. In: Sanjaume, E., Gracia, F.J. (Eds.), Las Dunas en España. Sociedad Española de Geomorfología, Fundación Empresa. Universidad Gallega ISBN 978-84-615-3780-8.

Update

Review of Palaeobotany and Palynology

Volume 296, Issue , January 2022, Page

DOI: https://doi.org/10.1016/j.revpalbo.2021.104566

Review of Palaeobotany and Palynology 296 (2022) 104566

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

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]

S. Fernández [a,*], J.S. Carrión [a,b], J. Ochando [a], P. González-Sampériz [c], M. Munuera [d], G. Amorós [a], J.M. Postigo-Mijarra [e], C. Morales-Molino [f], P. García-Murillo [g], G. Jiménez-Moreno [h], J.A. López-Sáez [i], F. Jiménez-Espejo [j], L.M. Cáceres [k], J. Rodríguez-Vidal [k], G. Finlayson [l,m,n], S. Finlayson [l,m], C. Finlayson [l,m,n,o]

[a] *Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain*
[b] *Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa*
[c] *Pyrenean Institute of Ecology (IPE-CSIC), Av/Montañana 1005, 50059 Zaragoza, Spain*
[d] *Department of Agricultural Science and Technology, Polytechnic University of Cartagena, 30203 Cartagena, Spain*
[e] *Dpto. de Silvopascicultura, Unidad de Botánica, Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica, Ciudad Universitaria, Madrid 28040, Spain*
[f] *Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland*
[g] *Department of Plant Biology and Ecology, Faculty of Pharmacy, University of Seville, Seville, Spain*
[h] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain*
[i] *Environmental Archaeology Research Group, Institute of History, CSIC, CCHS, Albasanz 26–28, 28037 Madrid, Spain*
[j] *Instituto Andaluz de Ciencias de la Tierra (CSIC-UGR), Armilla, Spain*
[k] *Department of Earth Sciences, Faculty of Experimental Sciences, University of Huelva, Campus del Carmen, Av. Tres de Marzo s/n, 21071 Huelva, Spain*
[l] *The Gibraltar National Museum, 18–20 Bomb House Lane, P.O. Box 939, Gibraltar*
[m] *Institute of Life and Earth Sciences, The University of Gibraltar, Gibraltar National Museum Campus, Gibraltar*
[n] *Department of Life Sciences, Liverpool John Moores University, Liverpool, United Kingdom*
[o] *Department of Anthropology, University of Toronto, Scarborough campus, Toronto, Canada*

The publisher regrets that an erroneous Declaration of Competing interests was accidentally included in the original version and has been removed in article.

The publisher would like to apologise for any inconvenience caused.

DOI of original article: https://doi.org/10.1016/j.revpalbo.2021.104431.

* Corresponding author.
E-mail address: santiago@um.es (S. Fernández).

https://doi.org/10.1016/j.revpalbo.2021.104566
0034-6667/