

1 **New Palynological data from the Late Pleistocene glacial refugium of South-West**

2 **Iberia: the case of Doñana**

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38

39 **Abstract**

40 The Doñana area in southern Iberia is one of the most renowned protected areas of
41 Europe, mostly due to the diversity and value of its wetland ecosystems. Additionally,
42 the large biogeographical significance of this territory and the outstanding availability
43 of sedimentary archives have made this region a hotspot of palaeobotanical research in
44 the Iberian Peninsula. Specifically, the organic deposits on El Asperillo Cliff have been
45 extensively studied during the past few decades from the geomorphological and
46 palaeobotanical (pollen, macrofossils) points of view. However, large uncertainties
47 remain concerning the chronology of certain sections of the exposed profile and the
48 palaeobotanical potential of this site has not been fully exploited yet. In this study, we
49 revisited El Asperillo with the aims of completing the palaeobotanical record and
50 refining the chronology of this site. The age of the studied deposits ranges from ca.

51 22,000 to 30,900 cal. yr BP according to the radiocarbon dates obtained, thus embracing
52 the particularly cold and dry Heinrich Event 2 and the Last Glacial Maximum. Our
53 palynological results allow inferring the presence of a coastal marshland system with
54 seasonal flooding in El Asperillo at that time. Additionally, the new pollen records from
55 El Asperillo Cliff highlight the relevance and diversity of pines (*Pinus nigra-sylvestris*
56 type, *P. pinaster*, *P. halepensis-pinea* type) in the Late Pleistocene landscape of
57 Doñana. These data are in large agreement with previous research not only in the study
58 area (macrofossil finds of *Pinus nigra* and *P. pinaster*) but also in the Iberian
59 Southwest, reinforcing the native status of pines. Last but not least, the results stress the
60 persistence of a highly diverse woody flora in Doñana during the harshest periods of the
61 last glacial cycle, highlighting the importance of this enclave in postglacial vegetation
62 recolonization of the Iberian Peninsula.

63

64 **Key words:** palaeobotany, historical biogeography, Quaternary, Pleistocene, Doñana,
65 Iberian Peninsula.

66

67 **1. Introduction**

68 The Doñana Protected Area (DPA), which includes the Doñana Natural and
69 National Parks. is an extremely interesting enclave for paleopalynological studies due to
70 its geographical location at the southwestern edge of the European continent very close
71 to Africa and its great physiographic complexity. Doñana itself hosts a notably
72 heterogeneous landscapes whit numerous plant communities, a highly diverse flora rich
73 in endemics, and a complex network of ecological interactions, that justify its large
74 international ecological and biogeographical interest. In fact, DPA is one of the most
75 emblematic protected areas of Europe (Sousa et al., 2009). It was declared a UNESCO

76 Biosphere Reserve in 1980, Wetland of International Importance (RAMSAR
77 Agreement) in 1982, Special Protection Area for Birds (ZEPA) in 2003, and a Site of
78 Community Importance in 2006. In 2015, it joined the IUCN Green List of Protected
79 and Conserved Areas. The geomorphology of the peridunal ponds is particularly
80 noteworthy, gathering one of the highest concentrations of potential
81 palaeoenvironmental archives of the Eurasian continent in the form of ponds and marsh
82 systems and being a Wetland of International Importance (RAMSAR Agreement) in
83 1982. These ponds have been seriously affected by anthropogenic activities in the past
84 few decades (Stevenson and Harrison, 1992; Díaz-Paniagua, 2015; Díaz-Paniagua and
85 Aragonés, 2015; López-Sáez et al., 2018; Manzano et al., 2018), making urgent to
86 recover such sedimentary archives and investigate long-term environmental change or
87 at least establish a repository of material useful for future conservation biology studies.
88 In this scientific framework, we have selected for this study the El Asperillo Cliffs,
89 located in the Doñana Natural Park, mainly because of the Pleistocene age of several
90 strata (Salvany and Custodio, 1995; Salvani et al., 2011) and the palynological potential
91 the peat rich sediments (Carrión and Dupré, 1996; Carrión et al. 2001; Abel-Chad and
92 López-Sáez, 2013; Camuera et al., 2019; López-Sáez et al., 2020a). Our main goal is to
93 shed light on the late Pleistocene vegetation dynamics in the area.

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

96 (a) studies on the Miocene of the Guadalquivir Basin (Valle and Peñalba, 1987; Valle
97 and Rivas Carballo, 1990), Gibraleón (Peñalba, 1985; Barrón et al., 2010) and Survey
98 “Huelva” (Valle and Peñalba, 1987; Rivas Carballo and Valle, 2005);
99 (b) for the Pliocene, La Matilla (Jiménez-Moreno et al., 2019), Lepe (Muñiz et al.,
100 1999; Barrón et al., 2003) and Casa del Pino (Peñalba, 1985; Barrón et al., 2010);

101 (c) for the Quaternary, palynological studies of the Upper Pleistocene of Vanguard and
102 Gorham's Cave at Gibraltar (Finlayson and Carrión, 2007; Carrión et al., 2008, 2018),
103 close to Doñana and
104 (d) for the Holocene, the Algarve, in Portugal (Fletcher et al. 2007; Schneider et al.,
105 2010; Connor et al., 2019), Pocito Chico lagoon (López-Sáez et al., 2002, 2018),
106 Dehesilla cave (García-Rivero et al., 2018, 2019), Laguna de Medina (Schröder et al.,
107 2018, 2020), Las Madres, El Acebrón and other pollen records in the DPA (Stevenson,
108 1985; Stevenson and Harrison, 1992; Stevenson and Moore, 1988; Yll et al., 2003;
109 Yáñez et al., 2007; Jiménez-Moreno et al., 2015; López-Sáez et al., 2018; Manzano et
110 al., 2018, 2019).

111 The first paleobotanical studies at El Asperillo date back to Caratini and
112 Viguier (1973), and Stevenson (1984), which supposed Holocene and Late Glacial ages
113 respectively. In his detailed palynological survey, Stevenson (1984) showed the
114 continuous presence of grassland formations with abundance of pines (a landscape
115 probably similar to a wooded savannah) and minor occurrences of *Quercus*, *Betula*,
116 *Alnus*, *Corylus*, *Salix*, *Phillyrea*, *Ephedra*, *Corema album*, and *Juniperus*. Heliophilous
117 shrubs would have been dominated by *Artemisia*, *Erica lusitanica*, *Erica umbellata*,
118 Chenopodiaceae and a variety of Asteraceae, among others. The high pollen frequencies
119 of Cyperaceae and the occurrence of *Sparganium*, *Myriophyllum* and *Potamogeton*
120 point to a marsh sedimentary context. Grasses and pines could be over-represented in
121 the pollen spectra due to their potential abundance in the basin and marginal vegetation
122 (Suc and Cravatte, 1982; Franco-Múgica et al., 1998; López-Sáez et al., 2008; García-
123 Antón et al., 2011; Morales-Molino et al., 2012). Later palaeoecological studies by Zazo
124 et al. (2005), Postigo-Mijarra et al. (2010a) and Morales-Molino et al. (2011)
125 investigated sediments from the cliff and the intertidal area, dating back to the interval

126 between the Marine Isotopic Stages (MIS) 4 and 2 according to the authors. These
127 studies also included macroremains and emphasized the occurrence of pines around a
128 local wetland environment. Due to age discrepancies between the different studies, a
129 more detailed chronological study on the Pleistocene beds was considered pertinent.

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

133

134 **2. The site**

135 The El Asperillo Cliff extends along ca. 22.5 km of the coast of the Gulf of
136 Cadiz (Atlantic Ocean) between the towns of Mazagón and Matalascañas
137 (municipalities of Palos de la Frontera, Moguer and Almonte) in the SW Iberia
138 (province of Huelva, Spain) (Fig. 1). Erosion has carved the cliff in the fossil dune
139 system of the El Abalario Dome, exposing a complete section of the largest Upper
140 Pleistocene-Holocene eolian sedimentary deposit in the Iberian Peninsula (Zazo et al.,
141 1999, 2005). Within the Doñana Natural Park, El Asperillo Cliff landscape has been
142 declared Natural Monument (BOJA, 2002).

143 The sampling areas are located at various points on the El Asperillo Cliff,
144 between Torre del Oro and Torre de la Higuera from sandy-peaty layers rich in organic.
145 The pollen record from Asperillo zone I (AspI) located between the coordinates 37° 04'
146 55''N and 06° 42' 41''W (Fig. 1), is represented by four points (sites A to D)
147 corresponding to different peaty layers between 20-2 m a.s.l. (Fig. 2). The pollen record
148 from Asperillo zone II (AspII) corresponds to a fragment of peaty compacted sands
149 located 18 m a.s.l. (37° 02' 34.18''N/ 06° 38' 04.16''W) and 8 km east of AspI (Fig. 1
150 and 3).

151

152 *2.1. Geomorphology and sedimentology*

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

161 The sedimentological studies of the Asperillo fossil dunes by Zazo et al. (1999,
162 2005) established 7 aeolian units spanning that cover the last 125,000 years (Fig. 4).
163 These units reflect the complex evolution experienced throughout that time, which are
164 the result of the interaction between coastal dynamics, with associated wind processes,
165 and changes in sea level (Zazo et al., 2005; Rodríguez-Vidal et al., 2014). Tectonics has
166 also played an important role in the distribution of these units, since the Torre del Oro
167 gravitational fault (TLF) configures two blocks in which different formations emerge in
168 their lower sections (Fig. 4).

169 In the NW upthrown block the oldest units outcrop at the base, with a paleosol
170 developed on a Plio-Pleistocene deltaic platform related to the Guadalquivir paleo-
171 mouth (Salvany and Custodio, 1995; Zazo et al., 1999). This paleosol is the result of a
172 hiatus in sedimentation probably prior to the Last Interglacial (MIS 7 or MIS 5) (Zazo et
173 al., 2005). As the interglacial MIS 5 advances, and therefore the increase in
174 temperatures, the sea level rises to cover the complete delta and other subsequent fluvial
175 deposits with marine sediments, reaching a maximum sea level about ca. 125,000

176 years (Polyak et al., 2018). The sedimentary sequence continues with the deposit of the
177 wind unit U0 formed on the marine deposits emerged after the withdrawal of the sea, at
178 the end of MIS 5. Between MIS 5-4 the Torre del Loro fault (TLF) was formed,
179 preserving the previous formations in the upthrown block.;

180 Aeolian units U1 to U3 were developed only in the SE downthrown block
181 against the fault scarp. U1 wind deposits that occur by the interstate, deposited in
182 temperate-humid conditions during MIS 3, U2 during the Last Glacial Maximum
183 (LGM) in colder and humid conditions, and finally U3 developed in the lateglacial MIS
184 1 in increasingly arid conditions (Fig. 4, Table 1). An extensive erosional surface rich
185 in iron oxides, denominated as “Super-surface of Fe-oxides” (SsFe) by previous studies
186 with an age stimated at ~5kyr (Zazo et al., 2011), (Fig. 4), represent the limit between
187 fossil and an active Mid-Late Holocene aolian units (U4 to U7). The rapid rising sea
188 levels during the Holocene has caused the erosion of the coast, giving rise to the
189 powerful El Asperillo Cliff with the outcrop of the different wind units studied (Zazo et
190 al., 1999, 2005; Sancho Royo et al., 2018).

191

192 *2.2. Present-day climate and vegetation*

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

201 Although the presence of human activity in the El Abalario territory has been
202 well documented for a long time, its most relevant impact corresponds to the extensive
203 stone pine (*Pinus pinea*) and eucalyptus (*Eucalyptus globulus*, *E. rostrata*)
204 afforestations. However, this activity is mainly recorded from 1940 to 1970, and since
205 Doñana became a Natural Park in 1989, environmental restoration measures have led to
206 the partial replacement of eucalypts by stone pines and cork oaks (García Murillo and
207 Sousa, 1997, 1999; García Murillo, 2001), which cover the inner area of El Abalario. In
208 2017, a large wildfire swept away the vegetation cover of this place (García Murillo,
209 2018). At present it shows a good state of recovery, due to the resilience of native
210 species and the restoration tasks carried out by the managers of the protected area.

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

214 The sandy cliff of the El Asperillo is subjected to continuously pounding waves
215 and therefore erosive processes that prevent stable vegetation to establish on the beach.
216 However, in the beach areas below the cliff, we find the pioneering vegetation
217 represented by *Cakile maritima* and *Salsola kali*. A little further inland it is possible to
218 observe incipient dunes, which are colonized in the highest places by *Ammophila*
219 *arenaria* subsp. *arundinacea*, *Achillea maritime* (= *Otanthus maritimus*) and *Elymus*
220 *farctus* subp. *boreali-atlanticus*, and in the lower parts by *Artemisia campestris* subsp.
221 *maritima* (= *A. crithmifolia*), *Crucianella maritima*, *Pancratium maritimum*, *Eryngium*
222 *maritimum*. Areas of groundwater discharge in the cliff are easily noticeable because
223 they host a very characteristic vegetation dominated by *Phragmites australis*, *Plantago*
224 *macrorrhiza*, *Ditrichia viscosa* and *Polygonum maritimum*, among others, which are
225 also adapted to continuous sandy collapses (López Albacete, 2009). At the top of the

226 cliff, exposed to the sea winds are more or less incipient dunes, which contain:
227 *Ammophyla arenaria* subsp. *arundinacea*, *Helichrysum serotinum* subsp. *pichardii* and
228 *Corinephorus canescens*. These mobile sands are also home to *Juniperus oxycedrus*
229 subsp. *Macrocarpa*, which grows accompanied by *Corema album*, *Halimium*
230 *calycinum*, *Cytisus grandiflorus* subsp. *cabezudodoi* and mixed with *Pinus pinea* that
231 come from the reforestation of the first half of the 20th century.

232 *Juniperus phoenicea* subsp. *turbinata* dominates the vegetation on table dunes
233 protected from ocean winds and with higher edaphic humidity. On drier soils with very
234 low organic matter grows a scrub community known as “Monte Blanco” (e.g. *Halimium*
235 *halimifolium*, *Stauracanthus genistoides*, *Cistus salvifolius*, *Genista ancystrocarpa*,
236 *Lavandula stoechas*, *Rosmarinus officinalis*, *Thymus mastichina*, etc.). On wetter soils
237 with higher amount of organic matter, a heatland of Atlantic influence locally-called
238 “Monte Negro”, characterized by *Erica scoparia*, *Ulex australis*, *Cistus salvifolius* and
239 *Calluna vulgaris*, gets dominant. The spatial distribution of “Monte Blanco” and
240 “Monte Negro” shrublands in Doñana defines a very characteristic mosaic-like
241 landscape according to soil properties. As mentioned above, *Pinus pinea* stands coming
242 from reforestation carried out in the first half of the 20th century are still a major
243 feature of the Doñana vegetation. The El Abalario area is plenty of temporary ponds
244 that host a typical hydrophilic vegetation dominated by Juncaceae and Cyperaceae
245 (*Juncus effusus*, *Juncus maritimus*, *Juncus heterophyllus*, *Schoenoplectus corymbosus*,
246 *Scirpoides holoschoenus*, *Eleocharis palustris*) with some other hydrophytes such as
247 *Ranunculus peltatus*, *Myriophyllum alterniflorum*, *Isöetes velata*, *Callitrichia brutia*, and
248 several species of *Chara* and *Nitella*. Along streams, the riparian vegetation consists of
249 willow trees (*Salix atrocinerea*) and brambles (*Rubus ulmifolius*, *Rosa*), intimately
250 connected to sclerophyllous cork oak (*Quercus suber*) stands with wild olive trees (*Olea*

251 *europaea*), strawberry trees (*Arbutus unedo*) and other shrubs (*Phyllirea angustifolia*,
252 *Myrtus communis*), as well as a remarkable abundance and diversity of lianas (*Smilax*
253 *aspera*, *Lonicera implexa*, *Tamus communis* (García Murillo, 2001, 2007; Sancho Royo
254 et al., 2018). Peatlands are rare, but some such as Ribatehilos still preserved such as
255 Ribatehilos mire are still preserved which reached its maximum extension during the
256 Little Ice Age (García Murillo, 2005, 2007). The local vegetation there is dominated by
257 ciliated heather (*Erica ciliaris*), gorses (*Ulex minor*, *Genista ancistrocarpa*) and purple
258 moor-grass (*Molinia caerulea* subsp. *arundinacea*), and in some spots it is possible to
259 find peat mosses (*Sphagnum inundatum*).

260

261 **3. Palynological methods**

262 We have studied twenty-eight sediment samples for pollen analysis. The pollen
263 record AspI is represented by 15 samples distributed in four points between the U2 and
264 U4 stratigraphic levels by Zazo et al. (1999, 2005) (Fig. 2 and 4) dated at c. 30,943,
265 27,987; 22,048; and 26,779 cal years BP (Table 2). Two samples come from Site A
266 (AspI-A1 to AspI-A2), a peat layer, located approximately 20 m a.s.l., corresponding to
267 the Holocene (AspI-A2 ca. 7100 cal BP; Table 2). We took four samples from Site B
268 (AspI-B3 to AspI-B6), taken at 12 m a.s.l. on a 23 cm-thick Pleistocene sandy layer rich
269 in organic matter (ca. 22,000—26,800 cal BP; Table 2). The six samples from Site C
270 (AspI-C7 to AspI-C12) come from a level rich in iron oxides at 4 m a.s.l., consisting of
271 clayey sandstones with a thickness of approximately 100 cm of Pleistocene age (ca.
272 28,000 cal BP; Table 2). Finally we collected three samples from Site D (AspI-D13 to
273 AspI-D15), from a 15 cm thick sandy-peaty layer located at 10 m a.s.l. (ca. 30,900 cal
274 BP; Table 2). The pollen record AspII is represented by 13 samples studied (AspII-1 to

275 AspII-13), taken at 2 cm intervals (Fig. 8), dating to the Pleistocene (four radiocarbon
276 dates from ca. 23,000 to 25,400 cal BP; Table 2).

277 Laboratory treatment followed conventional procedures (Delcourt et al., 1959;
278 Dimbleby, 1985), with the modifications proposed by Girard and Renault-Miskovsky
279 (1969) for the concentration of pollen grains by means of the flotation method with
280 heavy liquids. We added tablets of *Lycopodium clavatum* spores to each sample to
281 evaluate the quality of the laboratory processing and to calculate pollen concentrations
282 (Stockmar, 1971). The samples were mounted on slides with the use of glycerogelatin
283 and liquid paraffin. We identified pollen and other palynomorphs using an optical
284 microscope at 40x and 100x magnifications. We assigned damaged pollen grains whose
285 identification was not feasible to the category “indeterminable”. We plotted pollen
286 diagrams using Psimpoll palaeoecological analysis program version 4.27 (Bennett,
287 2008). Eight out of the 15 samples studied in AspI, were non polleniferous, mostly
288 because palynomorphs were at too low concentrations or totally absent (AspI-A1,
289 AspI-A2, AspI-C7, AspI-C9, AspI-C10, AspI-C11, AspI-C12, AspI-D15) (Fig. 2). In
290 the pollen diagram, we have not represented this palynologically sterile samples (Fig.
291 9). In contrast all the samples from AspII were polleniferous (Fig. 10). Along with
292 spores and non-pollen palynomorphs, we excluded the pollen grains of Asteroideae,
293 Cichorioideae, *Centaurea* and Cyperaceae from the total pollen sum assuming these
294 groups are overrepresented in the pollen spectra.

295

296 **4. Results**

297 *4. 1. Pollen stratigraphy El Aperillo zone I (AspI)*

298 Samples from Site A were palynologically sterile (Fig. 2). Pollen spectra from
299 site B (AspI-B3, AspI-B4, AspI-B5 and AspI-B6: Figs. 2, 9) were dominated by

300 arboreal pollen (AP), which reaches percentages close to 70%. The abundance of *Pinus*
301 *halepensis-pinea* is noteworthy (35-41%); Ericaceae abundance ranges between 6 and
302 12%; *Alnus* always >4% and it is also worth noting the amount of deciduous *Quercus*
303 and the presence, although limited, of *Juniperus*, *Corylus* and *Ulmus*. Accompanying
304 AP are evergreen *Quercus*, *Quercus suber*, *Olea*, *Taxus*, *Phillyrea*, *Erica australis* and
305 *Ephedra fragilis*. In non-arboreal elements NAP, Cistaceae, Asteroideae, Poaceae and
306 Cyperaceae are noteworthy. Fabaceae, Apiaceae and *Typha* exceed 2%. Cichorioideae,
307 *Potamogeton* and *Myriophyllum* are below 2%. It is worth highlighting the abundance
308 of fungal spores is worth highlighting, with percentages between 19 and 51% (Fig. 11).
309 The presence of Zygnemataceae spores (15-26%) is significant. Trilete spores attain
310 frequencies of ~11%, and Monolete spores >3%. Similarly, *Pseudoschizaea*, *Debarya*
311 and *Botryococcus* are present.

312 Site C is represented by the sample AspI-C8. The pollen of arboreal type reaches
313 values close to 50%. *Pinus halepensis-pinea* type is about 28%, Cupressaceae about
314 8%; along with other non-arboreal elements such as Ericaceae exceeds 7% and
315 *Artemisia* reaches 11%. Accompanying AP include deciduous *Quercus*, *Alnus*, *Olea*,
316 *Phillyrea*, and *Calluna*. Poaceae (5%), *Myriophyllum* (>10%), and Cistaceae,
317 Cichorioideae and Fabaceae with percentages ~2% are also features of this sample.
318 Asteroideae, Caryophyllaceae, *Plantago*, Cerealia and *Potamogeton* are also
319 represented in this pollen spectrum. Fungal spores are less abundant than in the former
320 samples (Fig. 11). Triletes (2%), Monoletes (1%), *Spyrogyra* (12%) and other
321 Zygnemataceae (11%), together with *Pseudoschizaea*, *Mougeotia* and *Debarya*, are also
322 remarkable.

323 Site D includes samples AspI-D13, AspI-D14 and AspI-D15, with the last being
324 sterile (Fig. 2). AP dominates the assemblage, surpassing 60%. The most noteworthy

325 feature of this site is the abundance of *Pinus*, with percentages around 16-37%. We
326 found high percentages of Cupressaceae (8-14%) and Ericaceae (4-14%). *Alnus* shows
327 an increase of more than 6%. *Taxus*, evergreen *Quercus*, *Olea*, Chenopodiaceae and
328 *Ephedra fragilis* are well represented. With respect to NAP, the presence of Cistaceae,
329 Asteroideae, Poaceae, *Lemna* and *Myriophyllum* (Fig. 9). Non-pollen microfossils are
330 represented by a large number of fungal palynomorphs, reaching out-of-total
331 frequencies close to 50% (Fig. 11). Monolete spores reach a percentage maximum of
332 33% while Trilete spores values range from 10 to 15%. Zyg nemataceae (21-42%) and
333 *Debarya* (24%) are relatively high.

334

335 4.2. Pollen stratigraphy El Asperillo zone II (AspII)

336 This site includes 13 pollen spectra (Fig. 10) with predominant AP, reaching
337 values >84%, except in sample 9, in which the lowest percentage of AP (37%) in the
338 sequence is reached. *Pinus halepensis-pinea* type is highly fluctuating from values close
339 to 34% until falling in samples 3 and 9 to < 9%. *Pinus pinaster* type oscillates between
340 1 and 18%, while *Pinus nigra-sylvestris* type varies between 4 and 24%. *Juniperus*
341 attains percentages between 4 and 14%. *Quercus* evergreen is 2-8%, *Quercus* deciduous
342 reaches 4% and *Quercus* indeterminate exceeds 5%. Remarkably, *Abies* ~7% (AspII-9).
343 The occurrence of *Taxus*, *Alnus*, *Betula*, *Corylus*, *Olea*, *Populus*, *Salix*, *Ephedra*
344 *distachya*, *Erica* and *Cistus* is significant, as well as the limited presence of *Quercus*
345 *suber*, *Ulmus*, *Castanea*, *Juglans*, *Myrtus*, Genistae, Fabaceae, *Ilex*, *Ephedra fragilis*,
346 *Arbutus*, *Daphne* and *Sambucus*. Among NAP Poaceae (7-58%) and Cyperaceae (1-9%)
347 are remarkable (Fig. 10). *Artemisia*, Asteroideae and Cichorioideae (out of the pollen
348 sum), *Chenopodium*, Amaranthaceae, *Plantago coronopus*, *Plantago lanceolata*,
349 Liliaceae and *Typha* are also frequent. Fungal spores, pteridophytes and algae abound

350 (Fig. 11). Monolete spores reach a maximum percentage of 38%, while Trilete spores
351 peak up to 63%. In a similar way, the presence of *Monoporisporites*, Hyphae,
352 *Exesisporites*, *Scleroderma*, Zygemataceae and *Inapertisporites* is significant.

353

354 **5. Discussion**

355 *5.1. Wetland environments*

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

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

374 *Alnus*, Taxodiaceae, Clethraceae, Cyrillaceae, *Myrica*) and riparian vegetation with
375 *Salix*, *Populus*, *Fraxinus* and Ulmaceae (Peñalba, 1985).

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

390 In the present study, the occurrence of aquatic palynomorphs such as
391 Zygnemataceae undiff., *Spirogyra*, *Debarya*, *Mougeotia* and *Botryococcus* in the AspI
392 and AspII sites (particularly abundant in AspI) suggests the presence of lagoon or lake
393 with water temperatures high enough to facilitate algal production and the growth of
394 hygrophytes such as *Myriophyllum* during the Late Pleistocene (Fig. 10 and 11). The
395 presence of *Pseudoschizaea* cysts and especially the high concentration of fungal
396 palynomorphs (*Inapertisporites*, *Monoporisorites*, *Fusiformisporites*, *Scleroderma*,
397 *Exesisporites*, among others), and hyphae, indicators of organic matter decomposition
398 and even erosive phases (*Glomus*), suggest that these environments dried out

399 temporarily (López-Sáez et al., 2000; Carrión, 2002) (Fig. 11). These conditions clearly
400 correspond to a littoral system of marshes with alternating episodes of flooding and
401 desiccation. In addition, tree taxa such as *Alnus* and *Quercus* probably colonized the
402 lakeshores as the basins infilled (Fig. 9 and 10).

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

417

418 5.2. Relevance of pinewoods in the Iberian Southwest

419 Without doubt, the Iberian Peninsula has been a land of pine woodland in the
420 past (Gil et al., 1990; Gil, 1991; García-Antón et al., 1997, 2011; Carrión et al., 2000;
421 Franco-Múgica et al., 2001, 2005; García-Amorena et al., 2007; Rubiales et al., 2009,
422 2010; Carrión, 2010; González-Sampériz et al., 2010, 2020; Postigo-Mijarra et al.,
423 2010b; Morales-Molino et al., 2017, 2018; Camuera et al., 2019; López-Sáez et al.,

424 2020b). The first evidences of *Pinus* in the Iberian Southwest corresponds to the late
425 Miocene pollen record of Gibraleón (Peñalba, 1985; Barrón et al., 2010). Here pines
426 appear accompanied by thermo-Mediterranean elements (Arecaceae, *Cornus*, Oleaceae
427 and *Quercus*) in a predominantly steppic environment with Asteraceae, *Plantago*,
428 Poaceae and *Rumex*, enriched by subtropical taxa such as Clethraceae, Cyrillaceae,
429 *Nyssa*, and Symplocaceae (Barrón et al., 2010).

430 Abundant *Pinus* is also recorded in the area during the Early Pliocene climatic
431 optimum. This is deduced by the palynological study of La Matilla core (Jiménez-
432 Moreno et al., 2019), which records warmest and most humid conditions at ~ 4.35 Ma.;
433 as well as studies of macro-remains in the outcrop of Lepe (Barrón et al., 2003) that
434 shows *Pinus* along with a cohort of subtropical and warm-temperate elements
435 (Lauraceae, Cesalpinoideae, Papilioideae, *Quercus*). The Casa del Pino site
436 (Peñalba, 1985) shows a continuous *Pinus* pollen curve within a mixed formation
437 together with subtropical (*Nyssa*, *Platycarya*, Sapotaceae) and temperate (*Juglans*,
438 *Quercus*, *Fraxinus*, *Populus*, *Salix*, *Fraxinus*, Ulmaceae) elements. These pine forests
439 were progressively replaced with steppes and oak forests with Mediterranean elements
440 such as *Quercus ilex-coccifera*, *Olea*, *Phillyrea* and *Vitis*. The core site G1 (Feddi et al.,
441 2011) located off the coast of Málaga in the south of the Iberian Peninsula and scarcely
442 150 km from Doñana records for the Piacenzian an alternation of mixed coniferous and
443 deciduous oak forests with thermophilous taxa (*Cathaya*, *Olea*, *Quercus* t. *ilex-*
444 *coccifera*) that are progressively replaced as we enter into the Upper Pleistocene by less
445 thermophilous conifers (*Cedrus*, *Tsuga*, *Abies*, *Picea*, *Pinus*) and *Artemisia-Ephedra*
446 steppes.

447 During the Upper Middle Pleistocene, there is also evidence of regional pine
448 forests. The Lucio de Mari López pollen record (Zazo et al., 1999; Yll et al., 2003) at

449 the core of the DPA shows pine forests with *Artemisia* during a MIS 4-3 phase later
450 replaced by evergreen *Quercus* during MIS 3. The marine pollen sequences indicate the
451 presence of pine forests throughout the Middle and Upper Pleistocene with continuous
452 pollen curves and with high percentages, such as in MD01-2443 (Roucoux et al., 2006)
453 for MIS 9-6, MD95-2042 (Sánchez-Goñi et al., 1999) for MIS 6-4, 8057-B
454 (Hooghiemstra et al., 1992) and SU 81-18 (Turón et al., 2003) for MIS 2-1. However, in
455 those marine records an over-representation of pine pollen influenced by the
456 taphonomic processes of marine deposition cannot be ruled out. Not surprisingly, pine
457 is usually excluded from the pollen sum (Turón et al., 2003; Roucoux et al., 2006;
458 Carrión et al., 2015). Nevertheless, the Pleistocene variation of pine in SU81-13 (Parra,
459 1994) shows close similarities with continental records such as the Padul peat bog (Pons
460 and Reille, 1988; Camuera et al., 2019) and Carihuela cave (Carrión, 1992; Carrión et
461 al., 1998, 1999, 2019; Fernández et al., 2007). The pine species involved were probably
462 the same as those of the Lower Guadalquivir Basin (Postigo-Mijarra et al., 2010a).
463 Thus, although *Pinus pinea* spread through the area in prehuman antiquity, historical
464 testimonies indicate that its presence in Doñana dates back to the end of the 18th
465 century, in the Marismillas area, as a crop introduced by the Casa de Medina Sidonia
466 (Granados Corona, 1987; Ojeda Ribera, 1987, 1992). There was also no *P. pinea* in El
467 Asperillo and El Abalario until the middle of the 20th century (see orthophoto of the
468 American flight of 1946, where those territories are covered by practically bare sand).

469 In the El Asperillo Cliffs, Stevenson (1984) showed abundance of pines (Fig. 5)
470 and the macro-remains studied by Postigo-Mijarra et al. (2010a) and Morales-Molino et
471 al. (2011) from the Upper Pleistocene (MIS 4-3, 45 kyr cal. BP) sandy deposits (Fig. 6),
472 allowed the identification of two gymnosperms at species level (*Pinus pinaster* and *P.*
473 *nigra*), which is first evidence of mixed pine forests in the lower Guadalquivir Basin.

474 This association is also found in the palynological record of AspI and AspII (Figs. 9,
475 10) as well as in the pollen records of Gorham's cave for the MIS 3-2 (Carrión et al.,
476 2008). According to Postigo-Mijarra et al. (2010a), mixed *Pinus nigra*-*Pinus pinaster*
477 stands are extremely rare today in the Iberian Peninsula (Sierra de Albarracín, Duero
478 basin, Sierra de Almijara-Sierra Nevada) (Blanco-Castro et al., 2005). The mixed pine
479 forests of the Sierra de Villafuerte (northeastern Baetic Ranges) in the northwest of
480 Murcia province should be added to that list (CARM, 2003) which probably occupied
481 more extensive areas during the Pleistocene. Also for El Asperillo, Morales-Molino et
482 al. (2011) found significant amounts of pine pollen during an early stadial of the last
483 glacial cycle (MIS 5-4) (Fig. 7) in a general context of steppe vegetation with *Artemisia*,
484 Chenopodiaceae and Poaceae.

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

496 The native status of *Pinus pinea* in the southwest of the Iberian Peninsula has
497 long been debated (Rivas Martínez, 1987, 2011; Pérez Latorre et al., 1999; Martínez
498 and Montero, 2004; López Albacete, 2009). The palaeobotanical records of *Pinus*

499 attests to the presence of pine forests, including those of *Pinus pinea*, in Doñana and
500 other southwestern Iberian sites since at least, the Late Pleistocene (Menéndez Amor
501 and Florschültz, 1964; Stevenson, 1984, 1985; Stevenson and Moore, 1988; Stevenson
502 and Harrison, 1992; López-Sáez et al., 2002; Yll et al., 2003; Carrión et al., 2008, 2018;
503 Jiménez-Moreno et al., 2015; Manzano et al., 2018, 2019). The relative abundance of
504 *Pinus pinea* macrofossils such as pinecones, bracts and seeds in fossil records from
505 southwestern Iberia (Martínez and Montero, 2004), brings further support to the pollen-
506 based identification of *Pinus pinea* within the *P. pinea-halepensis* type. Additionally,
507 macrobotanical evidence from Cueva de Nerja (Badal, 2001; Badal et al., 2012)
508 supports the survival of this pine species during the cold stages of the Upper
509 Pleistocene, while similar findings show that *Pinus pinea* grew around Cueva de los
510 Murciélagos (Zapata et al., 2005; Peña-Chocarro, 2007) and in Puerto de Santa María
511 (López Sáez et al., 2001, 2002) during the Holocene. Charcoal (strobili and charred
512 wood) also confirms the local presence of *Pinus pinea* in Gorham's Cave (Carrión et al.,
513 2008). In addition to the above, there is pollen evidence of *P. pinea* in Bajondillo cave
514 (López-Sáez et al., 2007) and Abrigo 3 del Complejo del Humo (Ochando et al., 2020).

515 It seems that the coniferous forests of the Upper Pleistocene at these latitudes
516 featured certain taxonomic diversity. Our new data from El Asperillo Cliff add *Abies* to
517 the list of conifers in the paleoecosystem of Doñana, alongside several pine and juniper
518 species (Fig. 10). The cold and dry conditions of the LGM possibly pushed *Abies*
519 towards these coastal settings seeking warmer temperatures but by mainly higher
520 moisture. Analog situations were previously observed in other refugial areas (Carrión et
521 al., 2015) such as Vanguard Cave in Gibraltar (Carrión et al., 2008), Bajondillo Cave
522 (López-Sáez et al., 2007; Cortés-Sánchez et al., 2008), Abrigo 3 del Complejo del
523 Humo (Ochando et al., 2020), Padul (Camuera et al., 2019), Malladetes in Valencia

524 (Dupré, 1980), and Creixell and Castelló d'Empúries in Catalonia (Burjachs and
525 Schulte, 2003; Burjachs et al., 2005). It is unlikely that *Abies* pollen appearing in
526 Abrigo 3 del Complejo del Humo belonged to *Abies pinsapo* (García López and Allué
527 Camacho, 2005; Alba-Sánchez et al., 2010). *Abies* pollen probably belongs to *Abies*
528 *pinsapo*, since it occurs near the study area at present, restricted to some specific points
529 in the Ronda mountain range (Sierra Bermeja, Sierra de las Nieves and Sierra de
530 Grazalema (Blanco-Castro et al., 1997; Alba-Sánchez and López-Sáez, 2013; Alba-
531 Sánchez et al., 2018).

532 The Holocene pollen sequences of the DPA and surrounding areas, such as El
533 Acebrón (Stevenson and Harrison, 1992), Las Madres (Stevenson, 1981, 1985;
534 Stevenson and Harrison, 1992; Yll et al., 2003), Laguna de Medina (Reed et al., 2001),
535 S11 and S7 core (Jiménez-Moreno et al., 2015), Lucio de la Cancela de la Aulaga
536 (Manzano et al., 2018), Laguna del Sopetón (Manzano et al., 2019) and S1 core (López-
537 Sáez et al., 2018), show continuous presence of pinewoods, whose densities
538 experienced fluctuations due to climatic changes and anthropic activities. A number of
539 postglacial sequences in the Iberian Peninsula record decreases in pine forest cover
540 along with deciduous elements contemporaneous with increases in xerophytes due to
541 climate change from the Mid-Holocene onwards (Yll et al., 1994; Pantaleón-Cano et al.,
542 2003; Carrión et al., 2004; Fletcher et al., 2007; Fuentes et al., 2007; Anderson et al.,
543 2011). Lake records from Sierra Nevada (Spain) also indicate increasing aridification
544 and Saharan dust input from Mid Holocene onwards (Jimenez-Espejo et al., 2014), in
545 agreement with the reactivation of the aeolian deposits at the studied location. During
546 the Late Holocene, different pollen sequences in the region show dramatic vegetation
547 changes caused by anthropogenic disturbances such as fire, agriculture or overgrazing
548 (García-Antón et al., 1997; Carrión et al., 2001, 2002, 2003a, 2007, 2010, 2018; Ruiz-

549 Zapata et al., 2002; Carrión-Marco, 2005; Rubiales et al., 2008; Ejarque et al., 2009;
550 López-Merino et al., 2009; Gil-Romera et al., 2009, 2010; Abel-Schaad et al., 2009;
551 Morales-Molino et al., 2011, 2013; Abel-Schaad, 2012; Abel-Schaad and López-Sáez,
552 2013; Connor et al., 2019), unfortunately the AspI samples for this period are
553 palynologically sterile (Fig. 2).

554

555 5.3. SW glacial refugia

556 Former palaeoecological works in the Iberian Peninsula showed the conventional
557 pattern of vegetation change during the Quaternary consisting in an episodic alternation
558 of forested environments during temperate climatic pulsations and xero-heliophytic
559 steppes during cold and dry phases (González-Sampériz et al., 2010; Carrión et al.,
560 2010, 2013). Gymnosperms, especially pines, occurred not only sparse in steppes but
561 also mixed with oaks and other trees during the forested interglacials and insterstadials.
562 The existence of permanent woody angiosperm refuges, enabled the survival of a large
563 number of thermo- and meso-mediterranean species providing starting points for
564 recolonization in each postglacial phase (González-Sampériz et al., 2010; Carrión et al.,
565 2015; Magri et al., 2017; Fernández et al., 2018). Although concerning only the end of
566 the last glacial phase, the data presented here prove the existence of a glacial refuges in
567 Doñana for temperate and Mediterranean trees and scrub, including several species of
568 conifers. Interestingly, our records registered the Heinrich Events 2 (HE2; 26.5 to 24.3
569 kyr cal BP (Sánchez-Goñi and Harrison, 2010) and the Last Glacial Maximum (23 to 19
570 kyr cal BP from MARGO Project, 2009). HE2 and LGM are among the most extreme
571 events regarding climate conditions that took place in Europe, when massive European
572 Ice Sheet melting promoted dramatic cooling in the European Atlantic facade and the
573 Western Mediterranean (HE2) (e.g., Jiménez-Espejo et al., 2007) and maximum global

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

581 The new site of El Asperillo show the occurrence of the following woody taxa
582 under full-glacial conditions in the Doñana area: *Pinus nigra* and/or *P. sylvestris*, *P.*
583 *pinaster*, *P. pinea*, *P. halepensis*, *Taxus*, *Abies*, *Juniperus*, deciduous and evergreen
584 *Quercus*, *Q. suber*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Castanea*, *Salix*, *Populus*, *Juglans*,
585 *Ilex*, *Arbutus*, *Myrica*, *Olea*, *Phillyrea*, *Erica cf. australis*, *Calluna*, *Myrtus*, *Cistus*,
586 *Daphne*, *Sambucus*, and Genisteae. Finds of walnut and chestnut pollen confirms the
587 native character of *Juglans regia* and *Castanea sativa* to the western Mediterranean
588 (García-Antón et al., 1990; García-Antón and Sainz-Ollero, 1991; Carrión and Sánchez-
589 Gómez, 1992; Carrión, 2002; Postigo-Mijarra et al., 2008, 2010b; Aranbarri et al.,
590 2016). The natural occurrence of *Pinus pinaster* (Carrión et al., 2000) and *Pinus pinea*
591 is also supported, in the last case with the reinforcement of macrofossil findings (Badal,
592 2001; López-Sáez et al., 2001, 2002; Badal et al., 2012; Zapata et al., 2005; Peña-
593 Chocarro, 2007; Carrión et al., 2008).

594 It is also pertinent to highlight the work on modern pollen rain in Doñana by
595 Stevenson (1984), who suggested that taxa such as *Corylus* and *Betula* may have been
596 more abundant in the past millennia and, doubtless, much closer to the current area of
597 Doñana. Anthropogenic forest depletion and loss of tree diversity is certainly not

598 exclusive to the region, but it is observed in many other sequences of southern Spain,
599 sometimes in dramatic detail such as in Sierra de Gádor (Carrión et al., 2003a).

600 The present work reinforces previous hypotheses on glacial refugia. The Doñana
601 Lucio de Mari López sequence (Zazo et al., 1999; Yll et al., 2003), records the
602 dominance of pine woodlands and open formations of *Artemisia*, grasses and several
603 Asteraceae during MIS 4-3, but also, highlighting the continuous presence of *Quercus*
604 and *Olea*. The palynological and archaeological charcoal studies in Gorham's
605 (Finlayson and Carrión, 2007; Carrión et al., 2008) and Vanguard Caves (Carrión et al.,
606 2018), Gibraltar, reveal a huge plant diversity dominated by a tree layer of oaks and
607 pines (*Pinus pinea*, *Juniperus phoenicea*, *Quercus ilex-coccifera*, *Q. suber*, *Erica*
608 *arborea*, *Arbutus unedo*, *Pistacia terebinthus*, *Olea*) in mosaic with riparian forests,
609 savannas, grasslands, shrub-lands and steppes. To this structure we must add coastal
610 xerothermophilous elements such as *Maytenus senegalensis*, *Withania frutescens*,
611 *Calicotome villosa* and *Myrtus communis* together with *Olea europaea*, *Phillyrea*
612 *angustifolia-latifolia*, *Ephedra fragilis*, *Bupleurum gibraltaricum* and *Tamarix africana*,
613 indicators of the most thermal refuge of the late Quaternary (Carrión et al., 2018).

614 The palynological samples of the El Asperillo organic layers in U2-U3 aeolian
615 units (Fig. 4), dated at ca. 21-16 kyr cal. BP (Zazo et al., 2005), as well as the macro-
616 remains from the same stratigraphical unit contain thermophilous elements such as
617 *Alnus*, *Betula* and *Quercus* (Morales-Molino et al., 2011). Finally, marine cores such as
618 SU81-13 (Parra 1994), MD95-2043 (Fletcher and Sánchez Goñi, 2008; Fletcher et al.,
619 2010), MD95-2042 (Paillet and Bard, 2002; Chabaud et al., 2014), ODP site 976
620 (Combourieu-Nebout et al., 2009; Dormoy et al., 2009), SU81-18 (Bard et al., 2000;
621 Turon et al., 2003), U1385 (Oliveira et al., 2018), and D13882 (Naughton et al., 2019)
622 depict the changes in the coastal and mountainous vegetation near the coasts of the

623 Iberian Peninsula and Morocco throughout the last 20,000 years. They show the
624 persistence of pine woodlands mixed with holm oak and cork oak, even during the Last
625 Glacial Maximum and with expanded later during the Holocene. Because of its
626 temperature requirements, it is worth stressing the lateglacial abundance of *Olea*
627 *europaea*.

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

642

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648

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1277

1278 **FIGURE LEGENDS**

1279 **Figure 1.** Location of the Asperillo sites ASPI and ASPII within Doñana in the Iberian
1280 Southwest, and palaeoenvironmental records mentioned in the text: 1. El Asperillo, 2.

1281 Gibraleón, 3. Lepe, 4. Casa del Pino, 5. Lucio de la Cancela de la Aulaga, 6. Laguna del
1282 Sopetón, 7. La Matilla, 8. Gorham's Cave, 9. Vanguard Cave, 10. Beliche (Algarve),
1283 11. Carcavai (Algarve), 12. Quarteira (Algarve), 13. Pocito Chico, 14. Dehesilla cave,
1284 15. Laguna de Medina, 16. Las Madres, 17. Acebrón, 18. Core G1, 19. MD01-2443, 20.
1285 MD95-2042, 21. 8057-B, 22. SU81-18, 23. SU81-13, 24. Padul, 25. Carihuera, 26.
1286 Cueva de Nerja, 27. Cueva de los Murciélagos, 28. Puerto de Santa María, 29.
1287 Bajondillo cave, 30 Cueva del Humo, 31. S1, 32. Gádor, 33. Lucio of Mari López, 34.
1288 ODP site 976, 35. U1385, 36. D13882.

1289 **Figure 2.** AspI showing radiocarbon dating and position of pollen samples at Site A (a),
1290 Site B (b), Site C (c) and Site D (d). Sterile samples in yellow. Photos by Manuel
1291 Munuera

1292 **Figure 3.** Pollen sampling in AspII, El Asperillo Cliff

1293 **Figure 4.** Location of pollen, macrofossil, and radiocarbon samples within the
1294 lithostratigraphy of El Asperillo Cliff according to former studies by Zazo et al. (2005),
1295 Morales-Molino et al. (2011), and Postigo-Mijarra et al. (2010a)

1296 **Figure 5.** Synthetic pollen diagram of selected taxa from El Asperillo. Redrawn from
1297 Stevenson (1984) and Carrión et al. (2013)

1298 **Figure 6.** Synthetic pollen diagram of El Asperillo. Redrawn from Postigo-Mijarra et
1299 al. (2010a)) and Morales-Molino et al. (2011).

1300 **Figure 7.** Plant macro-remains of El Asperillo according Postigo-Mijarra et al. (2010a)
1301 and Morales-Molino et al. (2011)

1302 **Figure 8.** Pollen samples and radiocarbon dating on the peaty sand strata from AspII

1303 **Figure 9.** Pollen diagram of AspI

1304 **Figure 10.** Pollen diagram of AspII

1305 **Figure 11.** Palynological diagram of non-pollen palynomorphs of AspI and AspII

1306

1307

Figure 1

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Figure 2

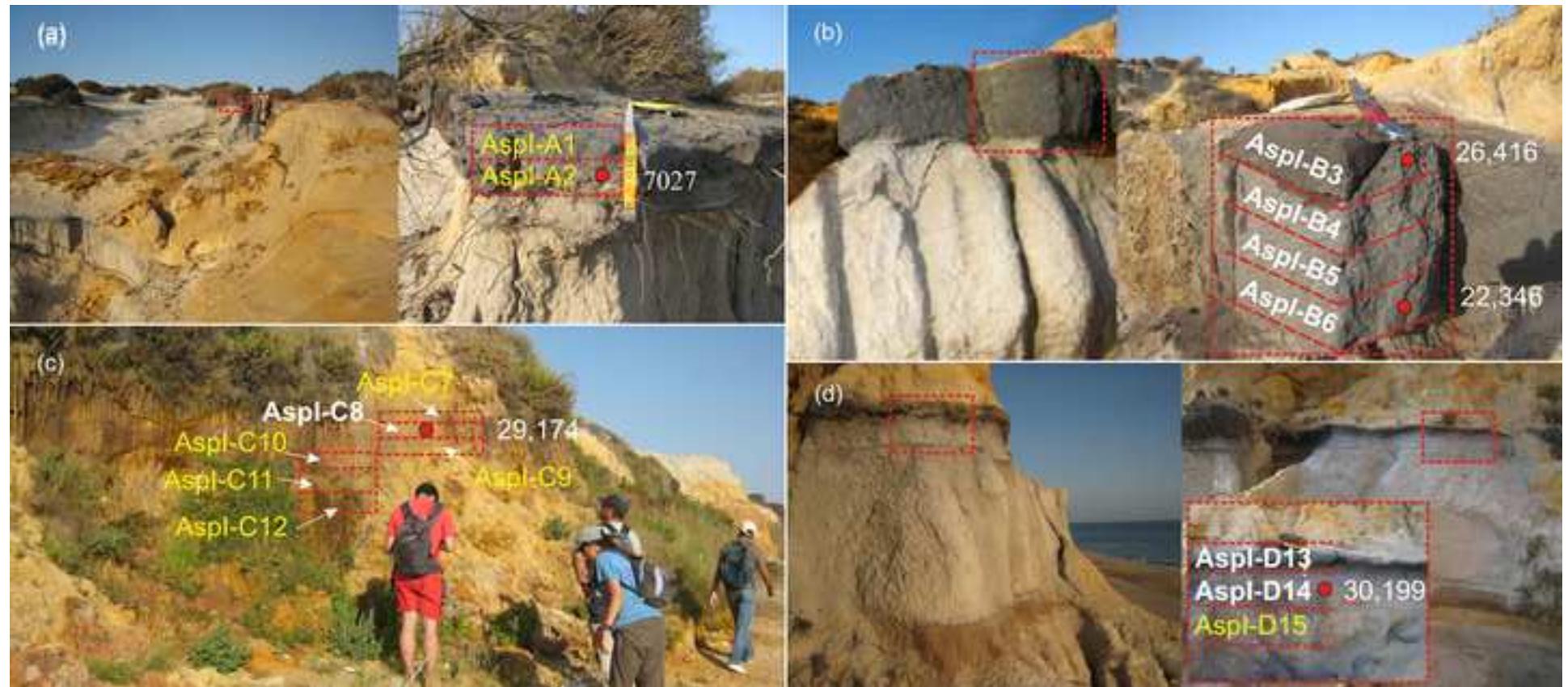
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Figure 3

[Click here to access/download;Figure;Figure 3.jpg](#) ↗

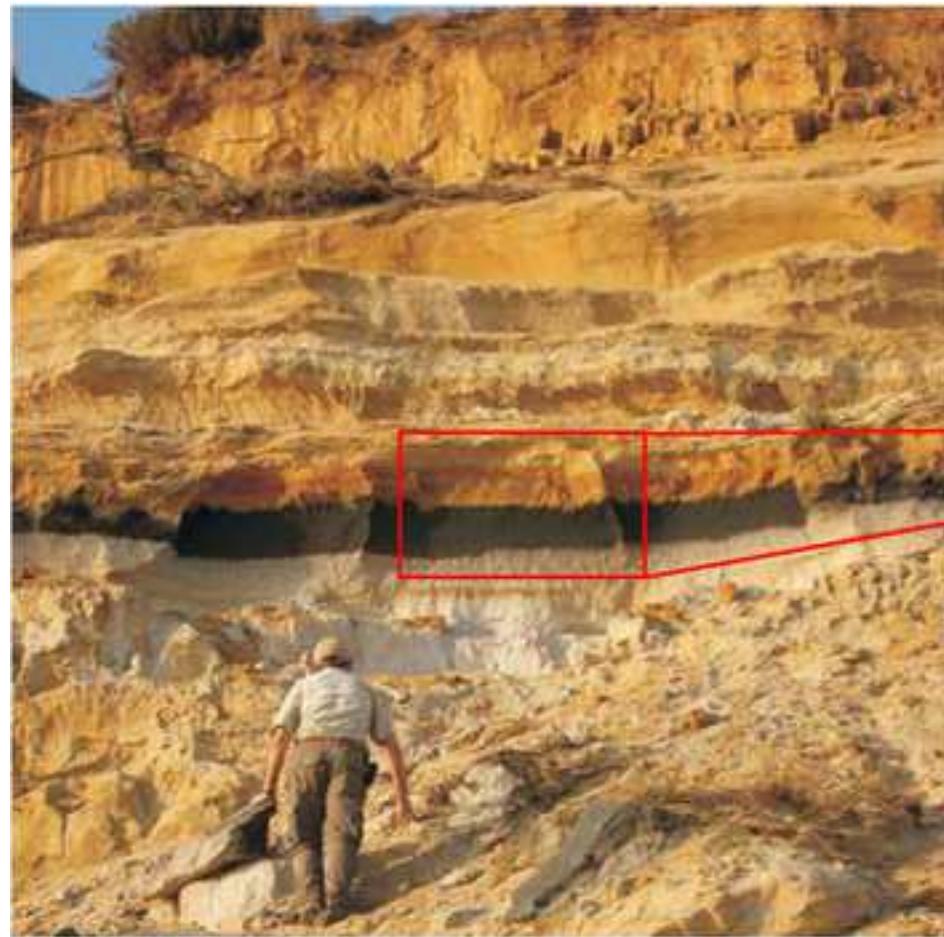


Figure 4

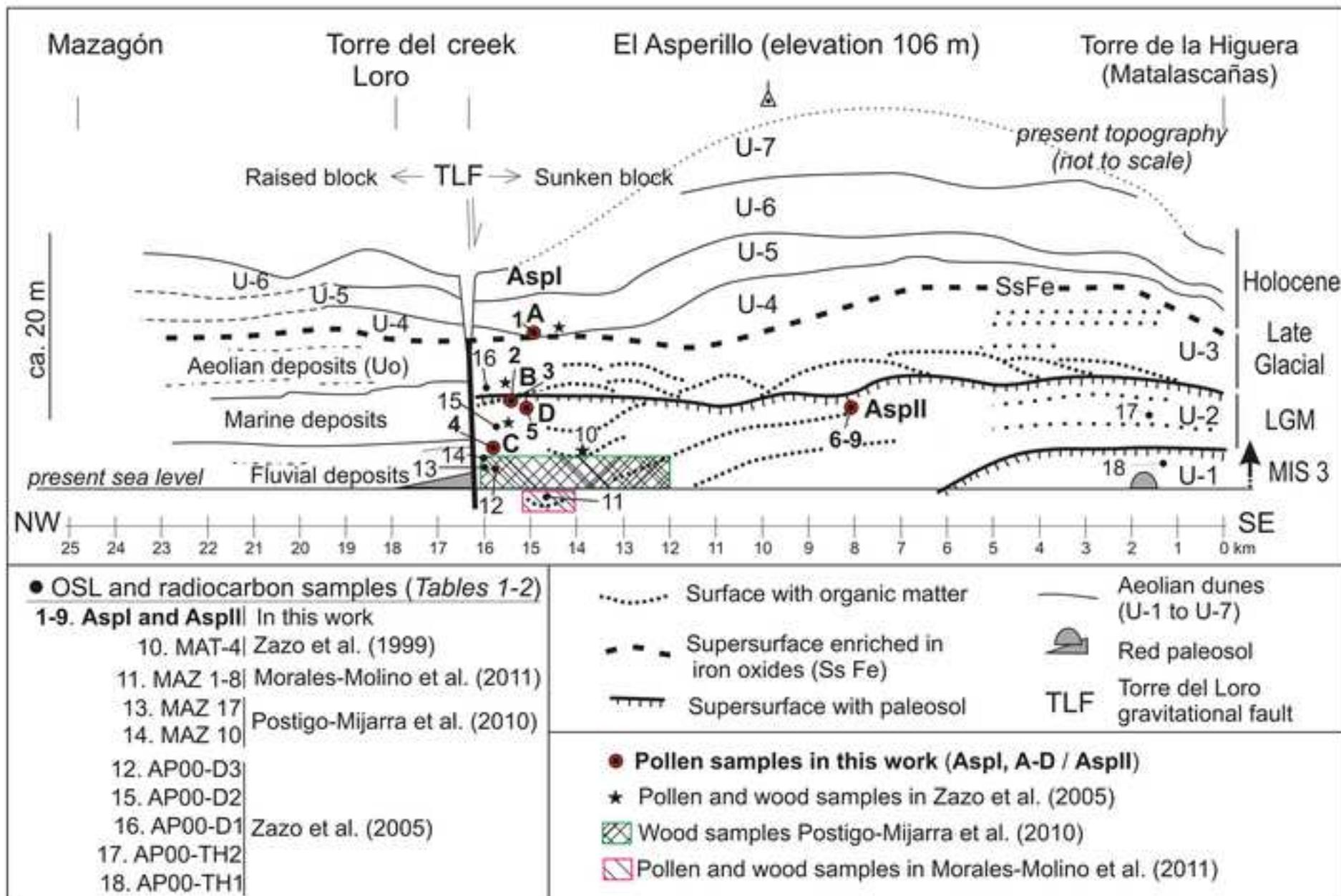
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Figure 5

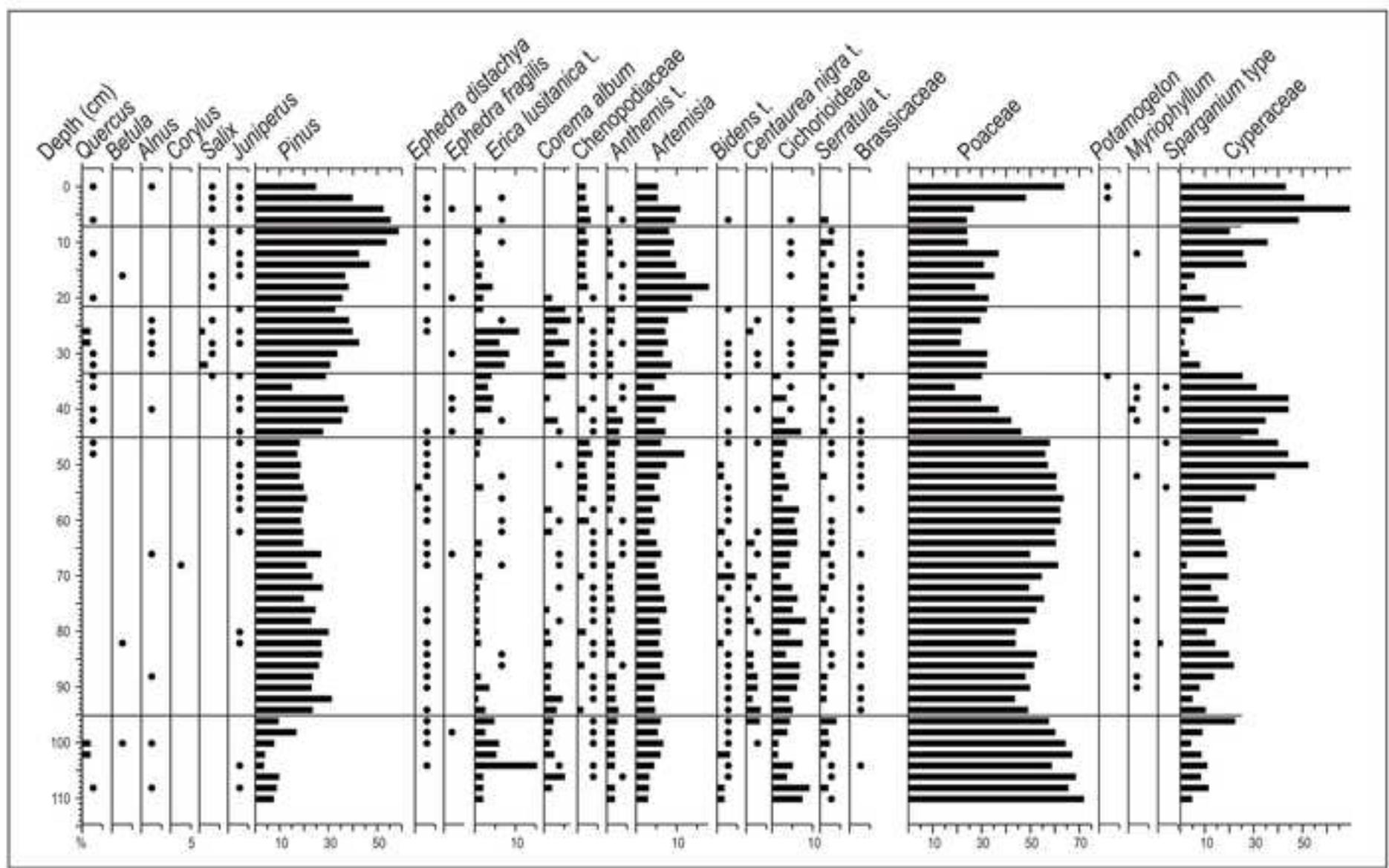
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Figure 6

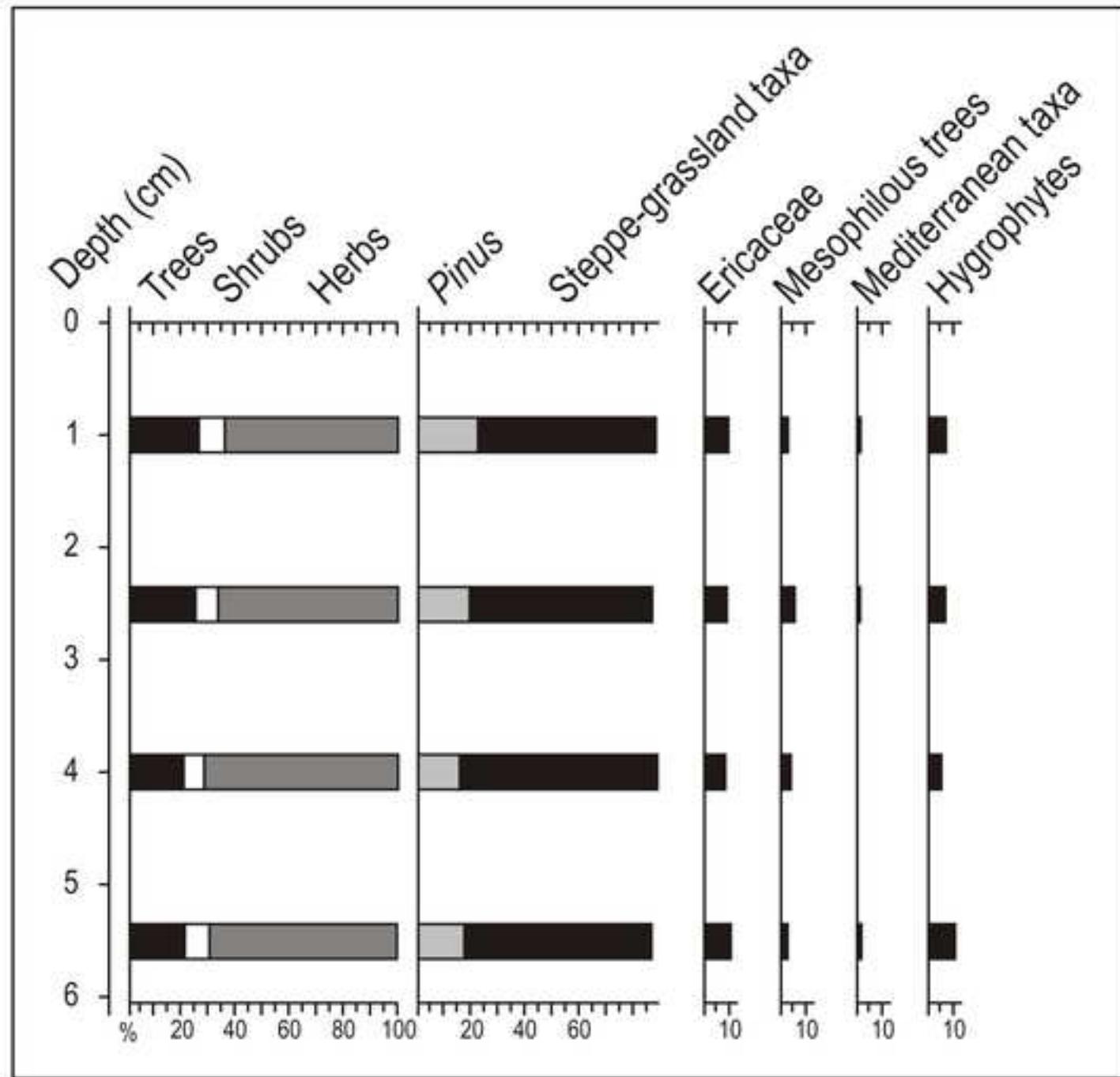
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Figure 7

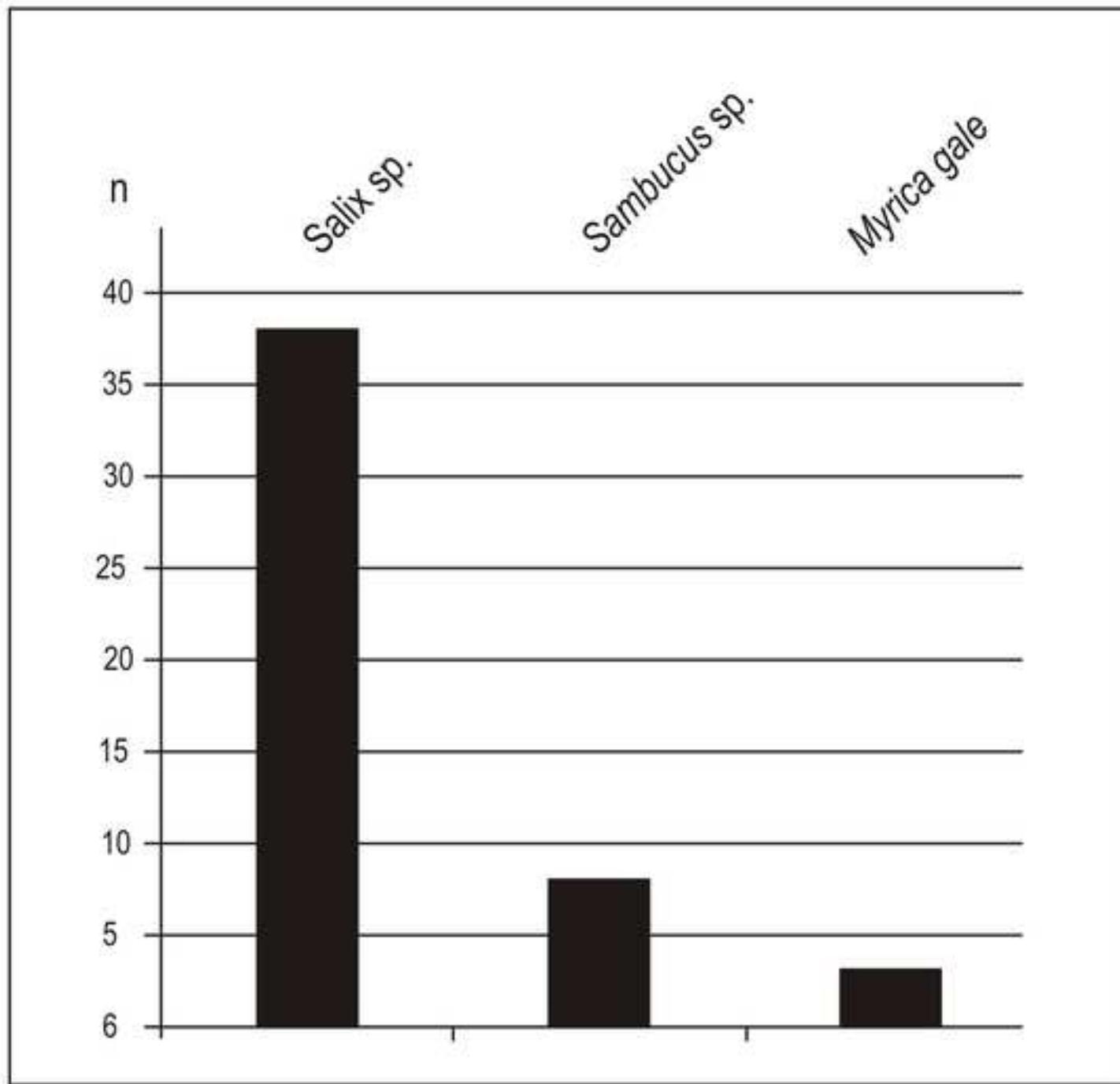
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Figure 8

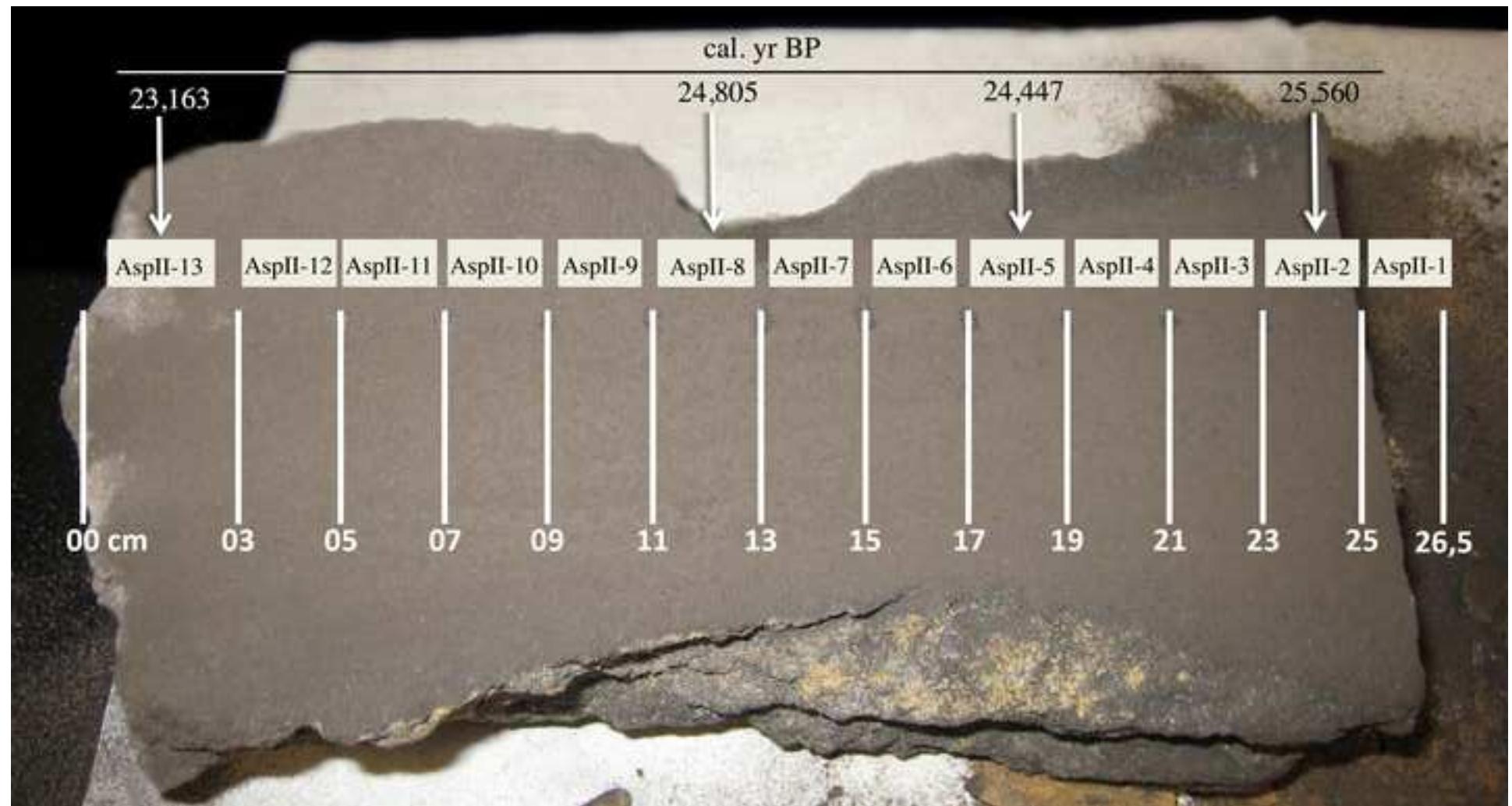
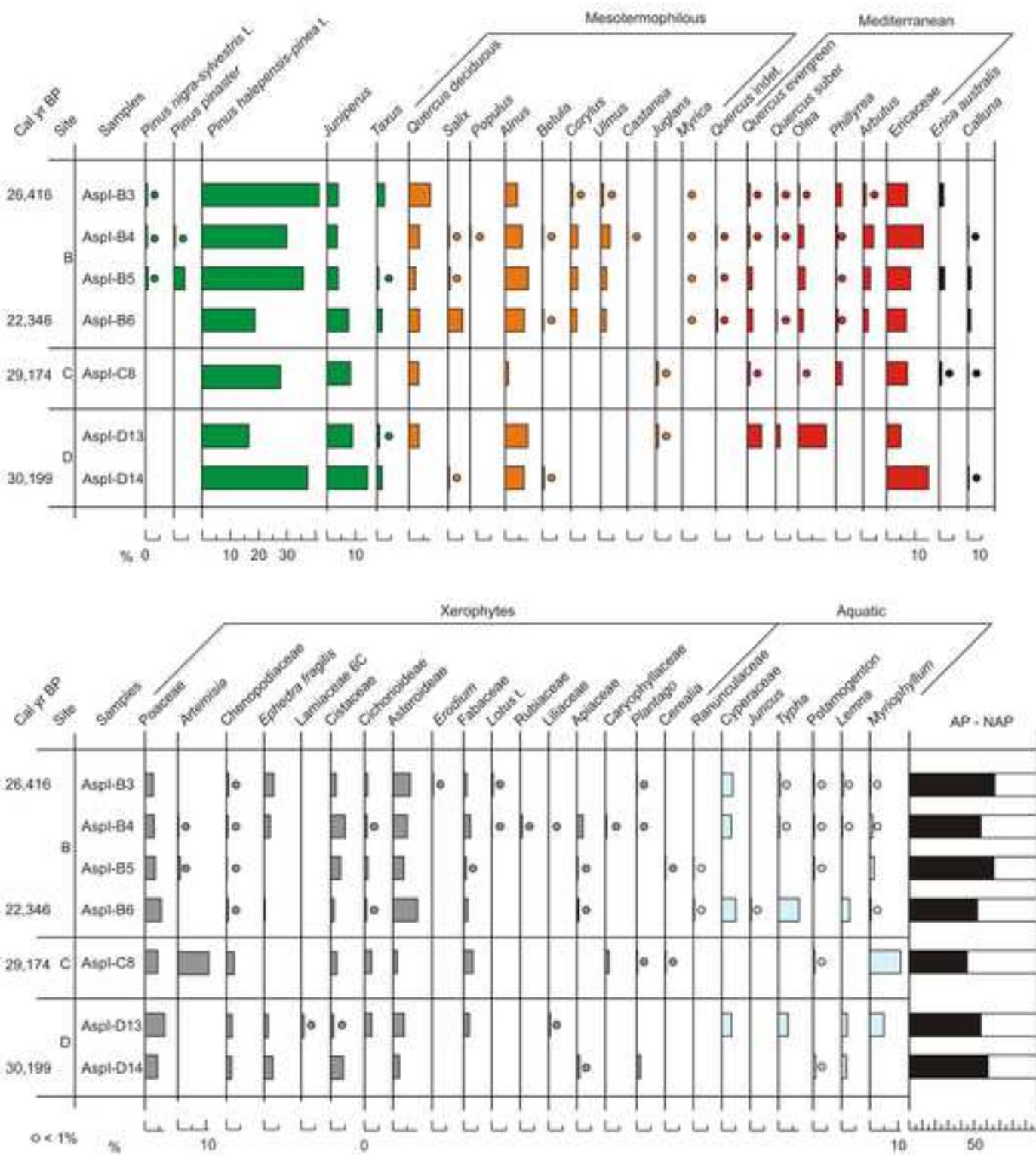
[Click here to access/download;Figure;Figure 8.jpg](#)

Figure 9

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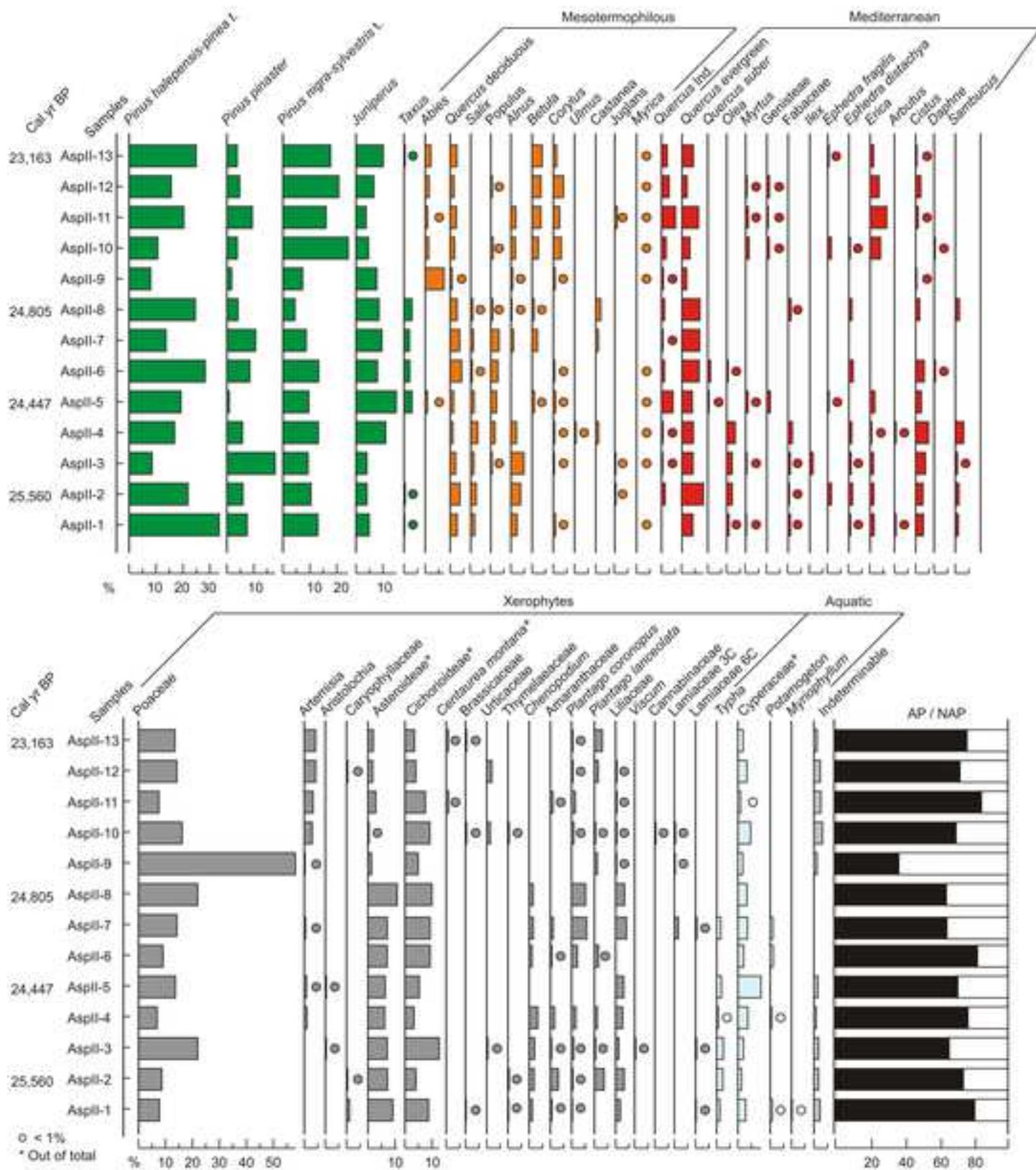


Figure 11

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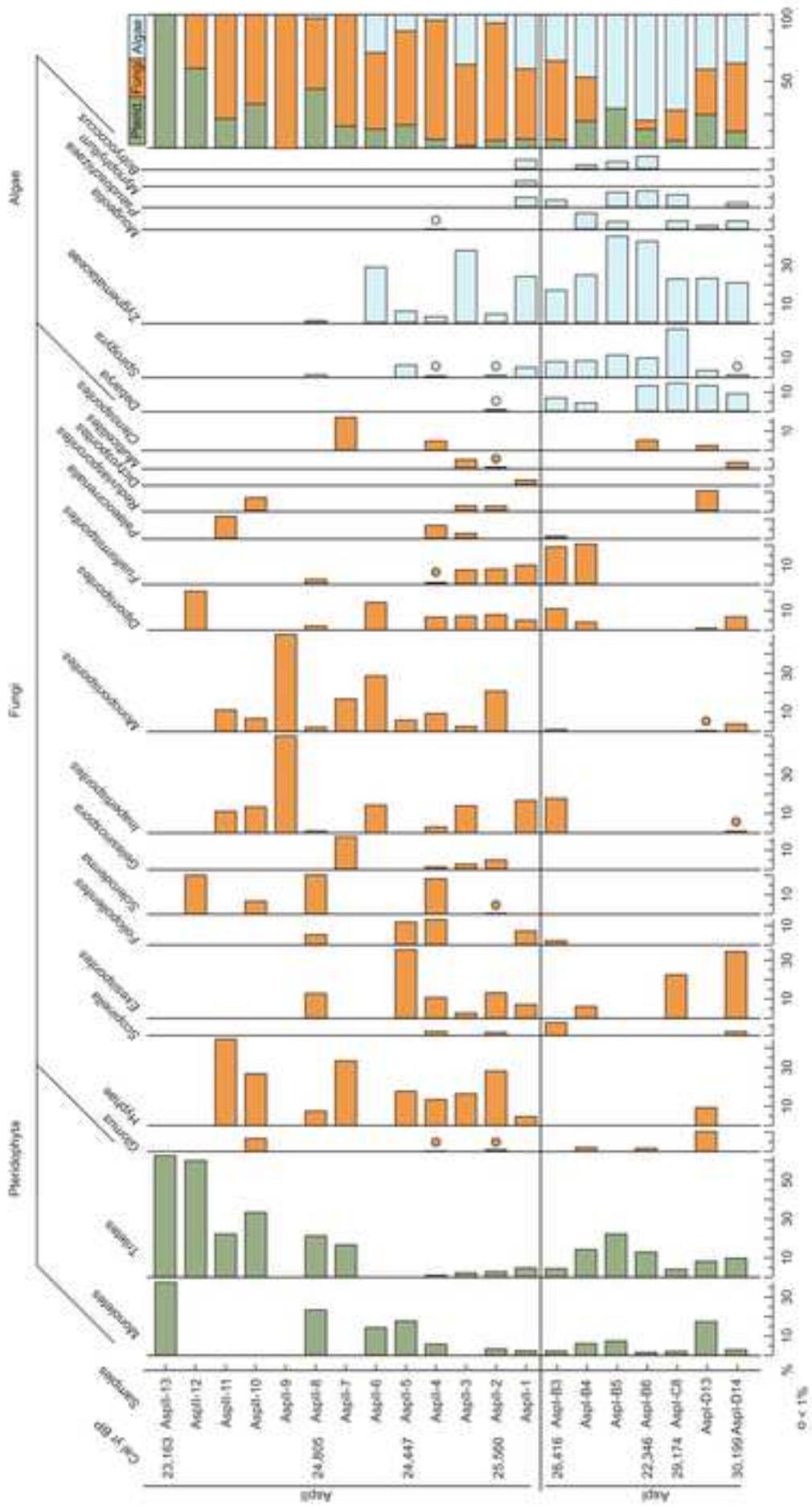


Table 1

OSL and radiocarbon dates of El Asperillo obtained from samples of Zazo et al. (1999, 2005), Postigo-Mijarra et al. (2010) 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	-
			Wood	47,500	
11	MAZ 1-8 ^d	CNA-122		± 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

^aZazo et al. (1999), ^bZazo et al. (2005), ^c Postigo-Mijarra et al. (2010), ^dMorales-Molino et al. (2011). OM=organic sediment. * Age considered unreliable (Morales-Molino et al., 2011)

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 2σ (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	$22,170 \pm 170$	25,990-26,934	26,416
3	AspI-B6	Poz-52098	OM	$18,420 \pm 90$	22,161-22,494	22,346
4	AspI-C8	Poz-52102	OM	$24,960 \pm 150$	28,811-29,701	29,174
	AspI-		OM			
5	D14	Poz-52099		$25,960 \pm 150$	29,962-30,728	30,199
6	AspII-13	Poz-52103	OM	$19,250 \pm 90$	22,961-23,703	23,163
7	AspII-8	Poz-52106	OM	$20,590 \pm 110$	24,368-25,132	24,805
8	AspII-5	Poz-52105	OM	$20,350 \pm 100$	24,160-24,794	24,447
9	AspII-2	Poz-52104	OM	$21,220 \pm 110$	25,259-25,803	25,560

OM=organic sediment

We have a conflict of interest with Saul Manzano Rodríguez (University of Cape Town, South Africa) and Lourdes López-Merino (Complutense University of Madrid), through some recent publications, especially in Doñana.

Thank you very much.

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